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Integrated phylogenomics and fossil data illuminate the evolution of beetles

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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.*, Nosodendriformia *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-× 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 (x^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’, ‘rgene_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

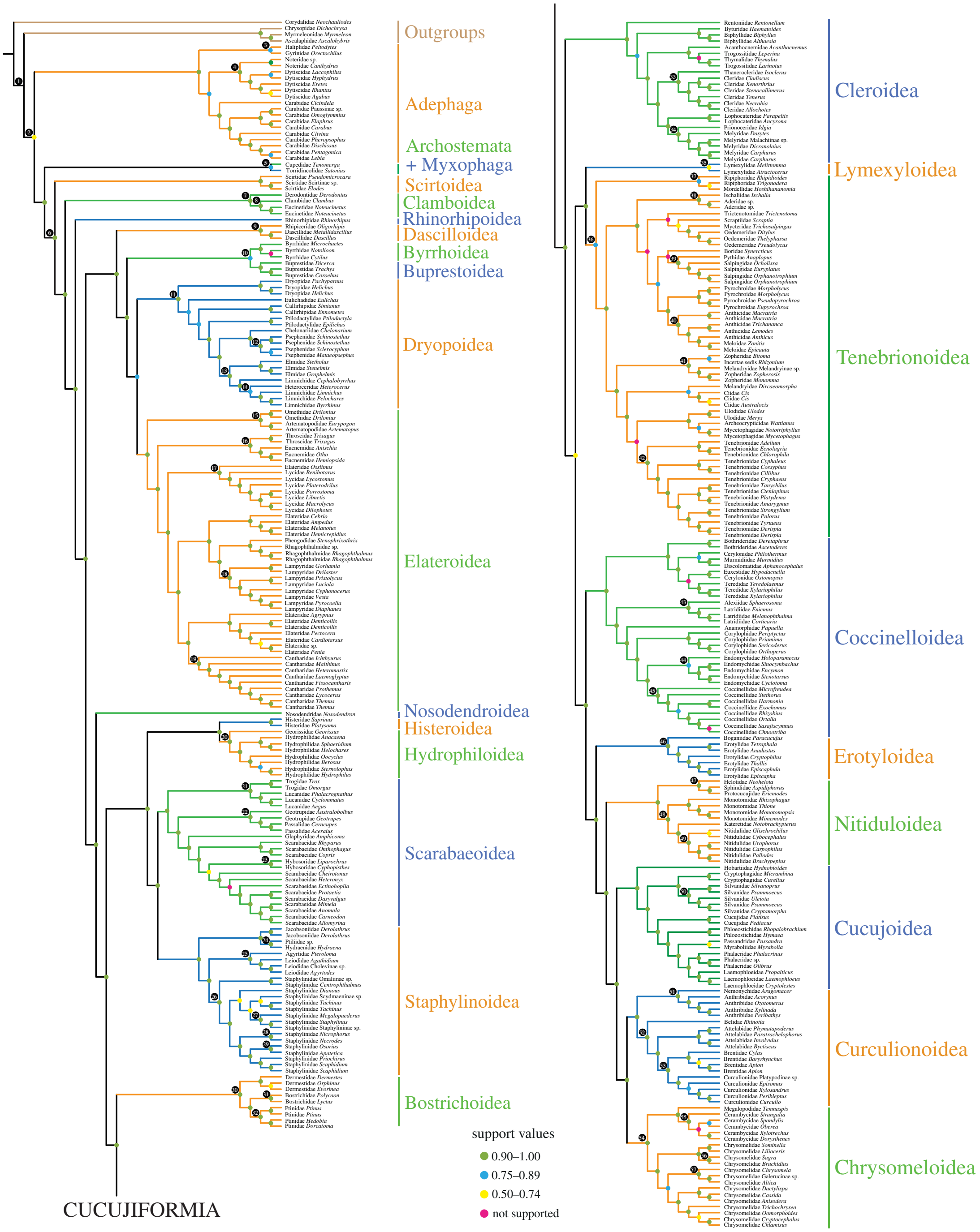

Figure 1. A full phylogeny of beetles displaying the systematic position of all sampled taxa analysed under the site-heterogeneous CAT-GTR + G4 model. Branch lengths have been omitted for clarity. Newly proposed taxonomic changes are followed. Support values are shown as BPP. Black numbered nodes indicate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

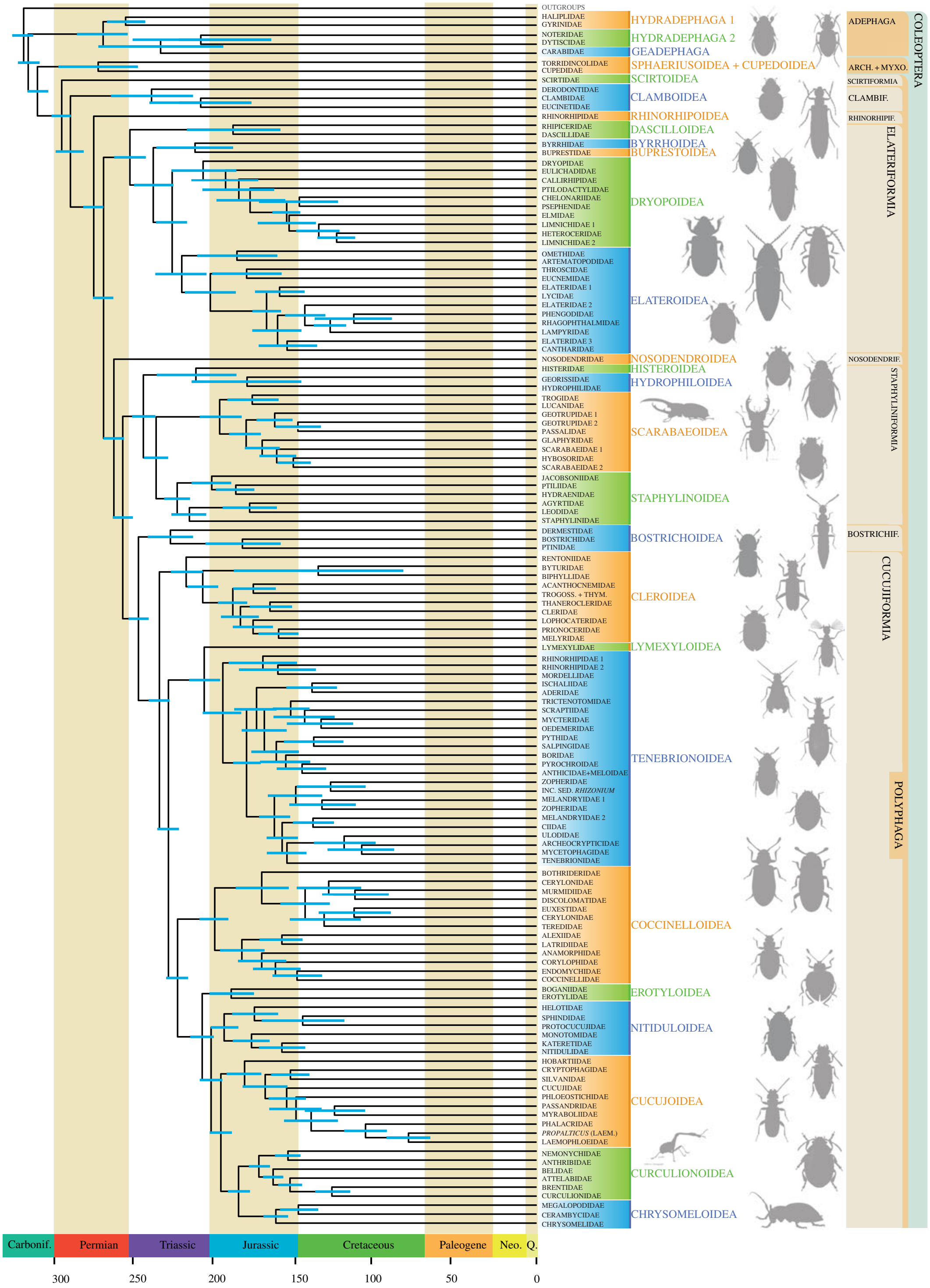

Figure 2. Timescale of beetle evolution displayed as a family-level tree adapted from figure 1. Ages were estimated based on 57 calibrated nodes, integrating the results of analyses using IR and AC molecular clock models in MCMCtree. Newly proposed taxonomic changes are followed. Abbreviations: Arch.,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

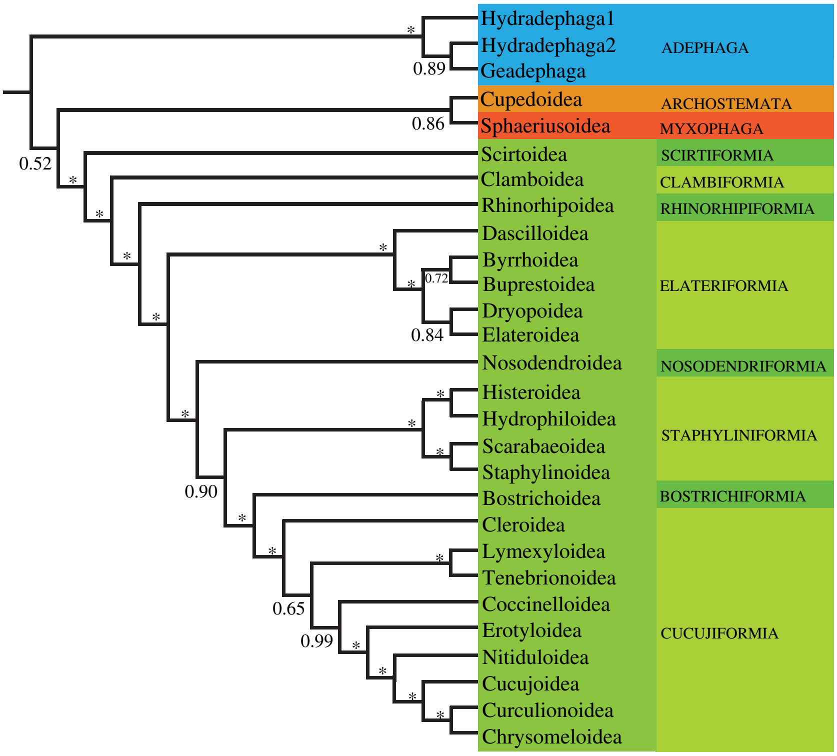

Figure 3. Proposed classification of Coleoptera showing the relationships of the suborders, series and superfamilies of beetles. Asterisks denote well-supported nodes with BPP ≥ 0.95.

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* Kundrata *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 Biphyllidae 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 ± 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 Commentry 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 Staphylinoidea 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

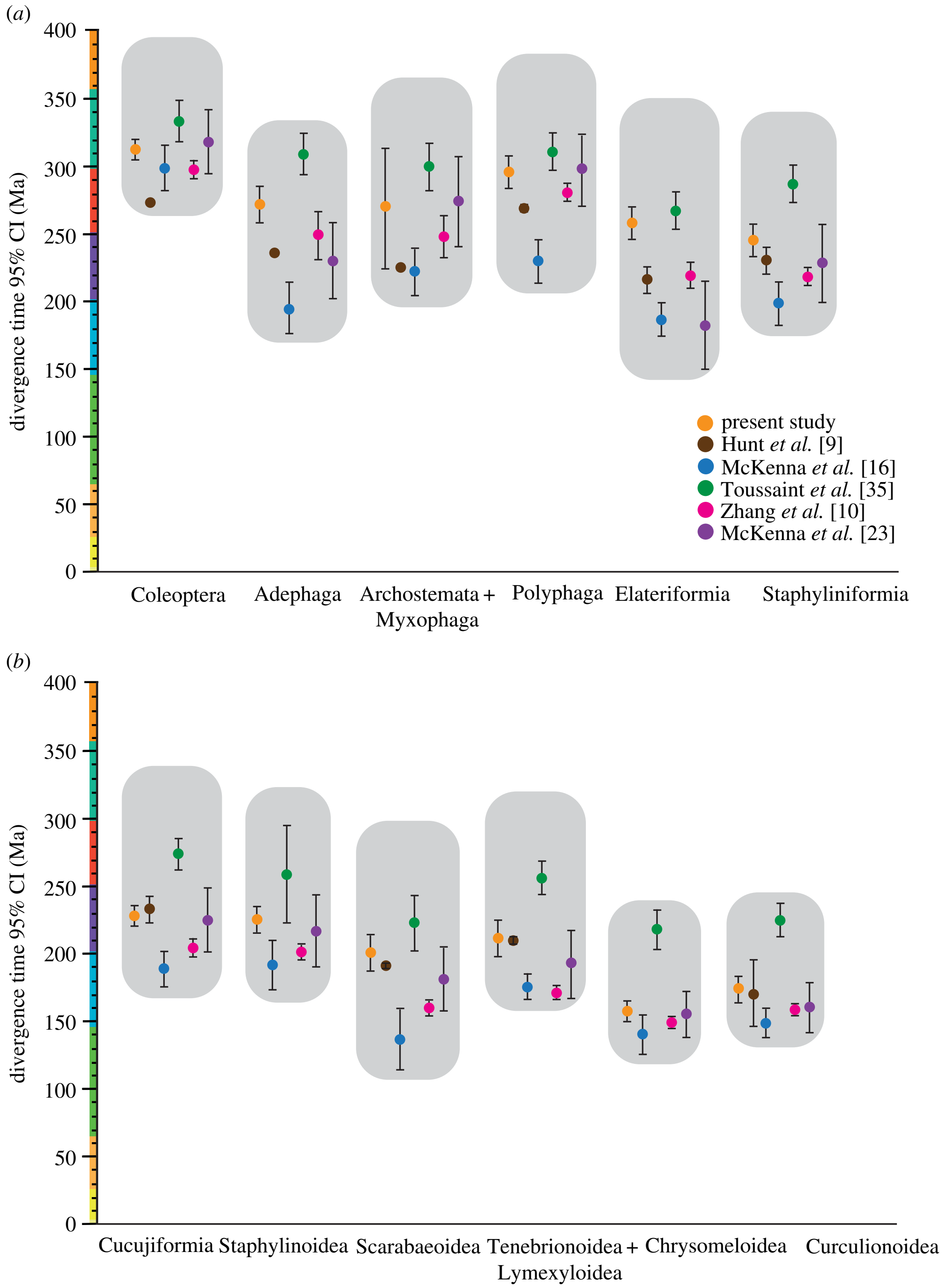

Figure 4. 95% CIs for the divergence of selected major beetle clades in the present and previous studies.

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 Staphylinoidea, 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 Staphylinoidea, 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.Ś.: 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.

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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 Zacoleoptera 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 Staphylinoidea 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

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Supplementary Information

Integrated phylogenomics and fossil data illuminate the evolution of beetles

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Contents

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Taxonomic treatment

SCIRTIFORMIA Lawrence, Ślipiński, Seago, Thayer, Newton and Marvaldi, 2011 / Superfamily SCIRTOIDEA Fleming, 1821 **sensu nov.**

Type genus: *Scirtes* Illiger, 1807.

Diagnosis: Adult head distinctly declined. Accessory ventral process of mandible present (partim). Ventral side of head with subgenal ridges. Prosternum very short in front of procoxae. Pterothoracic ventrites connected by membranes. Muscles *M. episterno-trochanteralis 2 (M. 70)*, *M. episterno-coxalis 3 (M. 103)*, and *M. furca-coxalis posterior 3 (M. 109)* absent. Functional spiracles on abdominal segment VIII absent. Hind wing AA4 joining anal fold posteriorly. Mesothoracic trochantins externally exposed. Metacoxal plates weakly to moderately enlarged. Larva with mandibular mola. Larval galea non-articulated.

Included taxa: †Boleopsidae Kirejtshuk and Nel, 2013; Decliniidae Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994; †Elodophthalmidae Kirejtshuk and Azar, 2008; Scirtidae Fleming, 1821.

Discussion: The series Scirtiformia and the superfamily Scirtoidea are herein restricted to only the extant families Scirtidae and Decliniidae, as well as the poorly-known extinct families †Elodophthalmidae from Lower Cretaceous Lebanese amber and †Boleopsidae from lower Eocene French (Oise) amber, whose placement however remains preliminary (Kirejtshuk and Azar 2008; Kirejtshuk and Nel 2013; Lawrence 2019a). The remaining families formerly affiliated with Scirtoidea are removed and placed into a redefined Clambiformia *ser. nov*. (which includes the single superfamily Clamboidea *sensu nov*.).

The basal position of the families Clambidae, Decliniidae, Derodontidae, Eucinetidae, and Scirtidae within Polyphaga was long recognised (Crowson 1955, 1960; Lawrence and Newton 1982; Lawrence et al. 1995b). However, disentangling the relationships among these families has proved challenging. Given that phylogenomic studies (Zhang et al. 2018; McKenna et al. 2019) have now firmly established Scirtidae as the earliest diverging polyphagan lineage, this renders the traditional series Scirtiformia and the superfamily Scirtoidea *sensu* Lawrence et al. (1995b) polyphyletic with the traditional Derodontoidea nested within it, thus mandating a taxonomic change to establish the two as natural groups reflecting evolutionary relationships. Adult Scirtidae are distinguished from Clambiformia *ser. nov*. by an enlarged metacoxal meron and a rounded radial cell of the hind wing, both of which may represent apomorphies of the family. Scirtids further have cone-shaped, distinctly elongated mesocoxae, an elongated metafurcal stalk, and have separated *M. noto-epimeralis (L 34)* and *M*. *epimero-subalaris (M. 52)* (Friedrich and Beutel 2006). The larval mandible of Scirtidae bears three putative apomorphies: flattening, suppression of mandibular teeth, and presence of a strong ventral hook at base (Zwick and Zwick 2008).

It should be noted that the position of the rare and monogeneric Decliniidae endemic to eastern Russia and Japan, not sampled in the present analysis, is not fully settled. It was consistently recovered as sister to Scirtidae in morphological (Lawrence et al. 2011) and molecular analyses of six genes (McKenna et al. 2015b). Their sister relationship is supported by the hind wing AA_4 joining anal fold posteriorly, a character otherwise found only in Adephaga. Adults of both families also lack functional spiracles on the eighth abdominal segment (Lawrence et al. 2011). Contrary to this arrangement, Anton et al. (2016) pointed out two potential synapomorphies of Clambidae and Decliniidae: a distinct ventral antennal furrow and a longitudinal carina on the laterodorsal surface of the mandibles. It is clear that the assessment of the systematic position of Decliniidae will require the sequencing of more genes and further morphological studies, especially of adult musculature. For now, the position of the family should be considered as tentative.

CLAMBIFORMIA Cai and Tihelka **ser. nov**. / Superfamily CLAMBOIDEA Fischer, 1821 **sensu nov.**

Type genus: *Clambus* Fischer, 1821.

Diagnosis: Adult head distinctly declined (prognathous in Derodontidae). Accessory ventral process of mandible present (partim). Ventral side of head with subgenal ridges (lost in Derodontidae). Prosternum very short in front of procoxae. Pterothoracic ventrites connected by membranes. Muscles *M. episterno-*

trochanteralis 2 (M. 70), *M. episterno-coxalis 3 (M. 103)*, and *M. furca-coxalis posterior 3 (M. 109)* absent. Functional spiracles on abdominal segment VIII present. Hind wing AA4 not joining anal fold posteriorly. Incision between anal field and medial field very deep (in Derodontidae) to moderately deep (in remaining families). Mesothoracic trochantins exposed (except in *Eucinetus*). Metacoxal plates weakly to greatly enlarged. Larva with mandibular mola. Larval galea non-articulated.

Included taxa: Clambidae Fischer, 1821; Derodontidae LeConte, 1861; Eucinetidae Lacordaire, 1857; †Mesocinetidae Kirejtshuk and Ponomarenko, 2010.

Discussion: The series Clambiformia *ser. nov*. and the superfamily Clamboidea *sensu nov*. as defined herein include Clambidae, Derodontidae, and Eucinetidae, previously placed into the non-monophyletic Scirtiformia / Scirtoidea and Derodontiformia / Derodontoidea *sensu* Lawrence and Newton (1982), Lawrence (1991), Beutel (1996) and Lawrence et al. (2010). When Derodontoidea was defined by Lawrence and Newton (1982), it was understood primarily as a taxon of convenience for Derodontidae and the two other problematic families, Nosodendridae and Jacobsoniidae, and was noted to be "almost certainly paraphyletic". The taxonomic position of the two above-mentioned families was indeed phylogenetically exceptionally problematic and they were historically placed in a range of positions within Polyphaga, sometimes as *incertae sedis* (reviewed in Lawrence et al. 1995a, 2010). Recent phylogenomic studies have strongly favored the placement of Jacobsoniidae within Staphyliniformia (Zhang et al. 2018; McKenna et al. 2019), which is also supported by morphological characters such as similar hind wing structures and the maxillary galea of adults and larvae (Crowson 1959; 1960). The problematic Nosodendridae represent an isolated lineage sister to Staphyliniformia, Bostrichiformia, and Cucujiformia (Zhang et al. 2018; McKenna et al. 2019).

Because Derodontidae is consistently recovered with high support as sister to Clambidae and Eucinetidae (McKenna et al. 2015b, 2019; Zhang et al. 2018), we herein define the series Clambiformia *ser. nov*. and the superfamily Clamboidea *sensu nov*. to only include the families Clambidae, Derodontidae, and Eucinetidae. This new series is similar in composition to Crowson's (1981) Eucinetiformia, which included Scirtidae, Eucinetidae, and Clambidae. Morphological similarity between Derodontidae and the abovementioned families, mainly in terms of adult musculature, has been discussed by Kukalová-Peck and Lawrence (2004). Among the important characters uniting Derodontidae with Clambidae and Eucinetidae is the membranous connection of the pterothoracic ventrite. This character is only visible when the mesocoxae are removed from their cavities. It is present in Archostemata (Baehr 1975), but absent in Myxophaga while in Adephaga the two segments are secondarily joined by the interlocking of the meso- and metaventrites. Following Friedrich and Beutel (2006), we consider it to represent a putative shared plesiomorphy of Scirtiformia / Scirtoidea *sensu nov.* and Clambiformia *ser. nov*. / Clamboidea *sensu nov*. It was subsequently gained independently in some polyphagan groups, such as Leiodidae (Friedrich and Beutel 2006; Ge et al. 2007). The absence of *M. episterno-trochanteralis 2 (M. 70)* is a feature shared by Scirtoidea and Clamboidea *sensu nov*., in the sense presented here, although it has also been secondarily lost in some groups of polyphagan beetles such as Nosodendridae, and some groups in Scarabaeoidea, Pyrochroidae, and Dermestidae, while the absence of *M. episterno-coxalis 3 (M. 103)* can be considered a derived feature of the two groups (Friedrich and Beutel 2006; Ge et al. 2007). Following Ge et al. (2007), the shared loss of these three muscles, which are otherwise widespread in the remaining Polyphaga, can be considered another potential apomorphy of Scirtiformia / Scirtoidea *sensu nov.* and Clambiformia *ser. nov*. / Clamboidea *sensu nov.*

The remaining diagnostic features of Clambiformia *ser. nov*. are mainly plesiomorphic characters found also in Scirtiformia / Scirtoidea that exclude these taxa from the remaining polyphagan series. Nonetheless, it should be noted that even Scirtiformia / Scirtoidea *sensu* Lawrence et al. (1995b) was difficult to define and its diagnosis was likewise based in a large part on plesiomorphies (Lawrence and Newton 1995; Lawrence 2001). An externally exposed mesothoracic trochantin is also present in some Staphylinidae, Myxophaga, some Adephaga, and most Archostemata (Baehr 1975; Hansen 1997; Larsén 1966; Friedrich and Beutel 2006). Coxal plates are also present in Adephaga, Myxophaga, and some polyphagan groups such as Dascillidae and Ptiliidae (Hansen 1997; Beutel and Leschen 2005; Friedrich and

Beutel 2006). An accessory ventral process of the adult mandible is also present Dascillidae and Scarabaeoidea (Beutel et al. 2018).

The extinct family Mesocinetidae from the Upper Jurassic of Mongolia (Kirejtshuk and Ponomarenko 2010) shares similarities with eucinetids and may be their sister group (Lawrence 2019b). The family is therefore treated as a member of Clambiformia *ser. nov*., although this placement should be considered as only tentative.

RHINORHIPIFORMIA Cai, Tihelka and Engel **ser. nov.**

Type genus: *Rhinorhipus* Lawrence, 1988.

Diagnosis: As for family Rhinorhipidae (Lawrence 1988, Kusy et al. 2018a): adult head hypognathous, with long temporal regions, lacking transverse occipital ridge or epicranial suture. Cranium with a short, median occipital endocarina and raised antennal insertions. Frontoclypeal region strongly declined and lacking a frontoclypeal suture. Clypeus long and narrow. Corpotentorium very broad. Oral cavity surrounded by setae. Labrum highly reduced, membranous. Mandibles long and with a setose dorsal cavity at base. Maxillae highly reduced, membranous, and setose. Pronotum without lateral carinae, anteriorly constricted and with a pair of elongate, vertical cavities. Procoxae slender and conical, trochantins completely visible, promesothoracic interlocking mechanism weakly developed. Mesothorax with a moderately developed mesoventral cavity reaching to the middle of the ventrite and a pair of well-developed procoxal housings on the mesanepisterna. Mesocoxae greatly projecting, mesotrochantin setose. Metaventrite with a moderately short discrimen. Metendosternite with long, curved lateral arms, anterior process with foramen at its base and a pair of expanded, ear-like, ventrolateral processes. Each elytron with 12 rather complete rows of deep punctures; epipleuron virtually absent, represented by slight thickening without lateral internal locking groove. Hind wing with r-m meeting stub of Rs; CuA3+4 meeting AA3, closing off anal (wedge) cell, cell acute; jugal lobe absent. Legs with enlarged and mesally produced metatrochanters, apically expanded metatibiae; tarsi simple, without pads, brushes, or membranous lobes; pretarsi with a well-developed empodium with two or three setae, and pectinate pretarsal claws (ungues). Abdominal tergite VIII of female dorsally concealed by tergite VII. Six Malphigian tubes. Larvae unknown.

Included taxa: Rhinorhipidae Lawrence, 1988.

Discussion: The enigmatic family Rhinorhipidae, represented in the modern fauna by a single species known only from northern New South Wales and southern Queensland (Lawrence 1988) is without a doubt one of the most mysterious beetle families. It possesses a suite of unusual characters that make resolving its systematic position difficult. Morphological analyses suggest an affinity to Elateriformia (Lawrence 1988; Lawrence et al. 1995b). As such, it has been included in Elateroidea (Bouchard et al. 2011; Lawrence et al. 2011) or placed as Elateriformia *incertae sedis* (Lawrence and Newton 1995). In a comprehensive morphological analysis, Lawrence (1988) recovered *Rhinorhipus* as sister to Elateroidea, while Lawrence et al. (1995b) recovered it as a sister to Byrrhoidea (all characters) or as sister to Buprestidae + Dascillidae (adult characters). A more recent extensive analysis of adult and larval morphological characters has recovered the family as sister to the elateriform family Rhipiceridae (Lawrence et al. 2011). Kusy et al. (2018a) recovered the family as the earliest diverging group within Elateroidea or as sister to Elateriformia and the rest of the derived Polyphaga. Consequently, the authors erected the superfamily Rhinorhipoidea to accommodate the group. In the more extensive analyses of McKenna et al. (2019) and our own analyses which account for long-branch artifacts, Rhinorhipidae are sister to Elateriformia and the remaining Polyphaga. Because it falls outside of Elateriformia, and would render the group paraphyletic, we erect the new series Rhinorhipiformia Cai, Engel and Tihelka *ser. nov*. for this unique family.

BYRRHOIDEA Latreille, 1804 **sensu. nov.**

Type genus: *Byrrhus* Linnaeus, 1767.

Diagnosis: Adult body strongly sclerotized, highly convex and compact, often possessing mechanisms for compaction such as cavities for the reception of legs and fitting of hypognathous head against the anterior edge of the prosternum. Head strongly deflexed at base and deeply inserted into prosternum. Mandibles short and broad. Clypeus reduced. Base of labrum on lower plane than apex and usually forming a deep transverse impression between labrum and an abrupt frontal ridge. Eyes small and finely faceted, without interfacetal setae. Pro-mesothoracic interlocking device absent. Prosternum anteriorly not forming a produced chin-piece, but a head rest sometimes present. Procoxal and mesocoxal cavities widely separated. Transverse metaventral suture asbent. Epipleuron abruptly narrowed. Basal three (less often two) abdominal ventrites connate.

Included taxa: Byrrhidae Latreille, 1804.

Discussion: Byrrhids have been traditionally regarded as isolated groups within Elateriformia and treated as the sole members of Byrrhoidea (Crowson 1955, 1982; Beutel 2016). Lawrence (1988) subjected Elateriformia to the first cladistic analysis and expanded Byrrhoidea to include buprestids, byrrhids, and dryopoids. Lawrence and Britton (1991) subsequently resurrected Buprestoidea, which is supported by our results and retained in our classification system. The monophyly of Byrrhoidea as defined by Lawrence and Newton (1995) proved challenging to confirm based on adult, larval, and combined morphological datasets (Beutel, 1995; Lawrence et al., 1995, 2011; Costa et al., 1999). Early molecular studies based on a handful of genes have likewise yielded mixed results (Hunt et al., 2007; Bocak et al., 2014; McKenna et al., 2015). Analyses based on 89 (McKenna et al., 2019) and 68 genes (herein) have supported a clade unifying the former Buprestoidea and Byrrhoidea, together forming a sister group to a clade largely consistent with Dryopoidea of Crowson (1960, 1973, 1978, 1982) and Kasap and Crowson (1975). Hence, we herein resurrect the old concept of Byrrhoidea of Crowson (1955).

While different topologies supporting Buprestidae inside the old Byrrhoidea have been recovered by other recent morphological and molecular studies (e.g., Lawrence 1988; Lawrence et al. 2011; Bocakova et al. 2007; Bocak et al., 2014, Kundrata et al. 2014, 2017), it should be noted that the relationships of the ‘byrrhoid-buprestoid complex’ represent a lasting controversy in coleopteran systematics that should be addressed with more complete molecular and taxon sampling in future works.

DRYOPOIDEA Billberg, 1820 (1817) **stat. res.**

Type genus: *Dryops* A. G. Olivier, 1791.

Diagnosis: Adult with frontoclypeal suture mostly distinct. Hind margin of pronotum crenulate or not. Procoxae projecting. Tarsomere 5 often as long as the basal 4 tarsomeres. Functional spiracles on 8th abdominal segment absent. Wing folding of “dryopoid” type. Most larvae with a well-developed and usually setose prostheca, short and wide prepharyngeal tube, broad and sclerotised gula, maxilla and labium closely connected, mandibular mola absent, labrum present, and a characteristic abdominal apex formed by tergite IX.

Included taxa: Callirhipidae Emden, 1924; Chelonariidae Blanchard, 1845; Cneoglossidae Champion, 1897; Dryopidae Billberg, 1820 (1817); Elmidae Curtis, 1830; Eulichadidae Crowson, 1973; Heteroceridae MacLeay, 1825; Limnichidae Erichson, 1846; Lutrochidae Kasap and Crowson, 1975; Protelmidae Jeannel, 1950; Psephenidae Lacordaire, 1854; Ptilodactylidae Laporte, 1838.

Discussion: Dryopoidea was defined by Crowson (1955, 1960, 1973, 1978, 1982) and Kasap and Crowson (1975) as a heterogeneous elateriform group that included beetles whose larvae are often aquatic and adults predominantly terrestrial. This early concept of the superfamily contained the families Chelonariidae, Dryopidae, Elmidae, Eulichadidae, Heteroceridae, Limnichidae, Lutrochidae, Psephenidae, and Ptilodactylidae. Lawrence and Newton (1982) added Callirhipidae which were earlier part of Artematopoidea or Rhipiceroidea, and Lawrence (1988) transferred here Cneoglossidae from Cantharoidea. Lawrence (1988) placed dryopoid beetles in a redefined broader concept of Byrrhoidea, which was adopted by subsequent authors (Lawrence and Newton 1995, Beutel 2016). Characters shared by most dryopoid larvae were discussed by Beutel (1995). On the molecular level, the superfamily is characterised by a unique rearrangement of tRNA gene order (Timmermans and Vogler 2012). Dryopoidea was monophyletic in Hunt et al. (2007), McKenna et al. (2015b; 2019), in the mitogenome analyses of Timmermans and Vogler (2012), and Timmermans et al. (2016), Zhang et al. (2018), and the present study.

NOSODENDRIFORMIA Cai and Tihelka **ser. nov.**

Type genus: *Nosodendron* Latreille, 1804.

Diagnosis: As for the family Nosodendridae (Beutel 1996; Ge et al. 2007; Leschen and Beutel 2010; Lawrence and Ślipiński 2013): Body oval and black, strongly convex dorsally, flattened ventrally. Head prognathous, inserted into the prothorax, with an enlarged mentum concealing the mouthparts. Frontoclypeal suture absent. Eyes large, almost meeting dorsally. Antennal insertions concealed from above by frontal projections. Antennae with a compact three-segmented apical club. All three segments of the thorax shorter than the maximum width of the metaventrite. Prothorax in front of procoxae short. Prosternal process long and wide, extending to mesoventrite. Cavities between hypomeron and prolegs present, further cavities for housing legs present on pterothorax and ventrites. Mesothoracic discriminal line absent. Mesocoxal cavities separated by a broad intercoxal process. Protrochantins concealed. *M. noto-trochantinalis* absent. Procoxae and procoxal cavities transverse. Metacoxal plates well-developed and complete. Metaventrite with more or less complete transverse suture. Radial cross-vein 3 absent, anal field strongly enlarged. Tarsal formula 5-5-5. Larva with labrum and clypeus fused, abdominal apex formed by posterior edge of segment VIII, and anal pads present.

Included taxa: Nosodendridae Erichson, 1846.

Discussion: The systematic placement of the problematic family Nosodendridae, the wounded-tree beetles, has always represented a persistent problem in systematic coleopterology. Earlier authors placed Nosodendridae into Byrrhoidea and Dascilloidea (Hayes and Chu 1946; Endrödy-Younga 1989), mainly due their gross similarity to byrrhids which also have an adult with a compact and convex body form. Crowson (1959) placed the family into the superfamily Dermestoidea. Lawrence and Newton (1995) considered the family to belong to Bostrichoidea, while Lawrence et al. (2010) placed the family into their Derodontiformia.

Ge et al. (2007) proposed several autapomorphies of Nosodendridae: the three segments of the thorax collectively shorter than the width of the metaventrite; accessory ridge laterally produced into a short, blunt tooth; presence of a hypomeral antennal groove; apical plate of the trochantinopleura distinctly enlarged; strongly shortened precoxal portion of the prosternum; wide prosternal process between procoxae; protrochantins concealed; transverse procoxae and procoxal cavities; mesothoracic discriminal line absent; broad intercoxal process separating mesocoxal cavities; anterior pronotal extension; dentiform process of the pronotal accessory ridge; the extensive apical plate of the trochantinopleura; radial cross-vein 3 absent; anal field strongly enlarged; *M. noto-trochantinalis* absent; and the beetle’s strongly reduced flight musculature. The larvae of *Nosodendron* possess the following autapomorphies: labrum and clypeus fused; abdominal apex formed by posterior edge of segment VIII; and anal pads present (Beutel 1996).

STAPHYLINIFORMIA Lameere, 1900 **sensu nov.**

Type genus: *Staphylinus* Linnaeus, 1758.

Diagnosis: Antennae filiform or capitate, rarely serrate or pectinate. Mandibles more-or-less exposed, not concealed under labrum when abducted. Maxillary muscle *M. craniobasimaxillaris* present. Sternite II visible only as a lateral rudiment in nearly all representatives. Aedeagus never of cucujoid type. Metendosternite never of hylecoetoid type. Mesothoracic spiracles concealed under the hypomeron (most representatives). Radial cell primitively eyelet-like but weakened proximally by the obliteration of the base of RA 3+4. Radial bar with a single apical hinge, reinforced by the pinching together of RA 3+4 with the anterior wing margin. RA4 and RP 1 approaching one another and remaining parallel or fused together to form a Y-shaped support for the anterior apical wing margin and large apical field. Posterior coxae with oblique, non-excavate posterior face (absent in some staphylinoids). Protibia often strongly spinose or toothed outwardly. Tarsal formula usually 5-5-5 and simple. Malpighian tubules free, usually four present (Kukalová-Peck and Lawrence 1993; Hansen 1997; Lawrence and Ślipiński 2013).

Included taxa: Histeroidea Gyllenhaal, 1808; Hydrophiloidea Latreille, 1802; Scarabaeoidea Latreille, 1802; Staphylinoidea Latreille, 1802.

Discussion: Staphyliniformia, as presented here in its revised form, roughly corresponds to Kolbe's (1908) concept of Haplogastra, which included superfamilies united by having sternite II visible only as a lateral rudiment and pleural sclerite – Hydrophiloidea, Staphylinoidea, Histeroidea and Scarabaeoidea (Grebennikov and Scholtz 2004). The remaining Polyphaga (Kolbe's Heterogastra) has sternite II completely membranous. The Haplogastra concept was subsequently followed, with various modifications, by Peyerimhoff (1933), Jeannel and Paulian (1944), and Crowson (1955, 1960). The concept was later revived in analyses of wing characters (Kukalová-Peck and Lawrence 1993; referred to as the 'hydrophiloid lineage') and combined analysis of adult and larval morphological characters (Hansen 1997) and also appears to be well-supported by molecular data (Caterino et al. 2005; Song et al. 2010; McKenna et al. 2015b, 2019; Zhang et al. 2018).

The constriction of the hypopharynx between the maxillary bases is hourglass-shaped in cross sections in most staphyliniforms, as defined here, although exceptions are known in Silphidae (as Silphinae herein), some Leiodidae, and some Staphylinidae (Beutel and Leschen 2005). The early-diverging scarabaeoid genus *Glaresis* shares its paired ligular lobes, strongly sclerotised and setose anteriorly, with Hydrophiloidea (Anton and Beutel 2004; Beutel and Leschen 2005). In pupae, the presence of a maximum of only four functional abdominal spiracles has been suggested as a possible apomorphy of Staphyliniformia including Scarabaeoidea, or at least a large part of this group since some members such as some Scarabaeoidea, Hydrophilidae, Synteliidae, and Tachyporini have more (Lawrence and Newton 1982, Newton 2020). Anton and Beutel (2012) cited some potential apomorphies supporting Staphyliniformia *sensu nov*. They noted that scarabaeoids share with Hydrophiloidea antenna with asymmetrically widened club segments and discussed the possibility of a shared origin of the deep sensory pouch on the third club segment in Staphylinoidea and Scarabaeoidea. Staphyliniformia *sensu nov*. is also characterised by the shared presence of *M. craniobasimaxillaris*, an unusual maxillary muscle apparently found only in members of this group. Scarabaeoidea and some other members of the series also share the sclerotised labrum at least 2.5 times as broad as long, combined length of the scapus and pedicellus exceeding one third of the entire antennal length, and a cupuliform antennal segment VIII preceding three-segmented club. The same condition was suggested as an autapomorphy of Hydrophiloidea. Further characters typical of Staphyliniformia *sensu nov.* were listed by Lawrence and Ślipiński (2013).

EROTYLOIDEA Latreille, 1802 **stat. nov.**

Type genus: *Erotylus* Fabricius, 1775.

Diagnosis: Adults with procoxal cavities internally open or closed by a slender bar. Glandular openings on the body, especially at the fore- and hind angles of the pronotum and prosternum. Tergite VIII in female dorsally concealed by tergite VII. Tarsal formula 5-5-5 in both sexes. Penis not divided into basipenis and distipenis, usually curved in lateral view, anterior edge usally with two penile struts. Adults phytophagous (Boganiidae, many Erotylidae), some pollinivorous, and mycophagous. Larvae with frontal arms lyriform (V-shaped in some Erotylidae), mesal surface of mandible with well-developed mola (some), maxillary articulating area present, hypopharyngeal sclerome present (missing in some Erotylidae). Some characters modified from Robertson et al. (2015).

Included taxa: Boganiidae Sen Gupta and Crowson, 1966; Erotylidae Latreille, 1802.

Discussion: The large and diverse Erotylidae was confirmed as monophyletic (Robertson et al. 2004; Wegrzynowicz 2002; Leschen 2003), as was the less diverse Gondwanan Boganiidae (Escalona et al. 2015). A close relationship between Erotylidae and Boganiidae was not generally suspected until these groups were recovered as sister taxa by Marvaldi et al. (2009) in an analysis of two rDNA fragments, albeit with considerably limited taxon sampling. In a four-gene analysis, Bocak et al. (2014) recovered Boganiidae as nested within Erotylidae. Genomic analyses have, however, unequivocally recovered Boganiidae and Erotylidae as a clade sister to the remaining Cucujoidea *sensu lato* (Zhang et al. 2018; McKenna et al. 2019; present study).

Boganiidae was not been sampled in many past analyses of Cucujoidea and so the set of characters supporting the superfamily is not extensive. Some Boganiidae (Escalona et al. 2015) and Erotylidae have glandular ducts (Crowson 1990, 1991; McHugh et al. 1997; Leschen 2003), some of which penetrate deep within the body. Similar ducts are present in several other families that are now placed in Coccinelloidea (Discolomatidae) and Cucujoidea (Cryptophagidae), and they also bear resemblance to ducts present in Chrysomeloidea and elsewhere (e.g, Drilling et al. 2013). Tightly bundled glandular ducts, referred to as a microtubulate condition by Leschen (2003), are present in Boganiinae (Boganiidae) and Pharaxonothinae (Crowson 1990, 1991; Leschen 2003). The penis, which is not divided into two parts that characterise several members of the Cucujoidea (e.g., Leschen et al. 2005; Lawrence et al. 2011) is of a single piece and often curved in lateral view, resting in the abdomen on its side. The anterior edge usually bears two elongate struts, which are short in Boganiinae, but elongate in most remaining taxa and fused into a single process. The extent to which aedeagal characters could be considered potential synapomorphies requires additional study.

Both Boganiidae and some phytophagous Erotylidae also share some ecological similarities, even though the ancestral state, at least of Erotylidae, may be fungus feeding. Both contain species that visit cycads in high numbers and probably contribute to their pollination (Crowson 1991; Leschen and Buckley 2007; Suinyuy et al. 2009; Prado et al. 2011). Given the discovery of Cretaceous boganiids preserved alongside cycad pollen, it is likely that the association between Erotyloidea *stat. nov*. and cycads is over 100 Ma old (Cai et al. 2018b).

Some of the families traditionally included in the 'basal Cucujoidea' that lack genetic data may eventually be placed into Erotyloidea; but at present there is no compelling morphological evidence to place them here.

Similarities between the monogeneric *Lamingtonium* and Boganiidae + Erotylidae were discussed by Sen Gupta and Crowson et al. (1969), and the external habitus and fungal feeding behaviour of the group are suggestive. However, the true affinities of the family are difficult to demonstrate conclusively (Lawrence et al. 2011), they lack the glandular ducts present in the families above, and the genitalia differ (Lawrence and Leschen 2003). Lawrence and Leschen (2003) discussed the possible relationship between Erotylidae, Lamingtoniidae, and Cyclaxyridae based on larval characters, and the sister relationship of Tasomosalpingidae and Cyclaxyridae was shown by Leschen et al. (2005). Cyclaxyridae lack glandular ducts and the Tasmosalpingidae have trichome-like structure at the posterior margin of the prothorax that interrupts the pronotal carina but doesn't appear to have the glandular ducts similar to Erotylidae or Boganiinae. Among the aforementioned families, the bipartite penis may not be present, and similar penile struts present in most erotylids also occur in Cyclaxyridae and Tasmosalpingidae, but the former has been placed among Cucujoidea by McKenna et al. (2015b) and Robertson et al. (2015) that placed it as sister taxon to Myraboliidae.

NITIDULOIDEA Latreille, 1802 **stat. nov.**

Type genus: *Nitidula* Fabricius, 1775.

Diagnosis: Adults rarely with elongate rostrum. Dorsal part of mandible without setose cavity (except Sphindidae). Subantennal grooves well-developed (except Nitidulidae: Calonecrinae, Smicripidae). Antennae never fully filiform or moniliform, and a club is always present. Gular sutures never confluent (except some Nitidulidae, some Monotomidae). Ventral or lateral portion of prothorax on each side never with incomplete notosternal suture or without sutures (except some Nitidulidae, some Sphindidae, some Monotomidae). Cuticular glands, where present, consist of single ducts. Procoxal cavities internally open (most). Tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male (rarely 4-4-4). Ventrite 1 never much longer than ventrite 2 (except some Nitidulidae and Monotomidae). Abdominal tergite VII exposed in dorsal view and tergite VIII in male with sides curved ventrally forming a genital capsule (in Kateretidae, Monotomidae, Nitidulidae, and Smicripidae). Tergite VIII in female dorsally concealed by tergite VII, tergite X in male completely membranous. Spiculum gastrale present (absent in Sphindidae and some Monotomidae). Larvae with frontal arms lyriform (most), mesal surface of mandible with well-developed mola (most), maxillary articulating area present (most), hypopharyngeal sclerome present (most).

Included taxa: Helotidae Chapuis, 1876; Kateretidae Kirby, 1837; Monotomidae Laporte, 1840; Nitidulidae Latreille, 1802; Protocucujidae Crowson, 1954; Smicripidae Horn, 1880; Sphindidae Jacquelin du Val, 1860.

Discussion: The former superfamily Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982), more or less corresponding to the old Clavicornia, is a very heterogeneous group containing mostly minute to moderately sized brown to dark beetles that are difficult to place elsewhere (Leschen et al. 2005). As such, the old Cucujoidea has been considered to represent a taxonomically complicated 'wastebasket group' that may or may not be monophyletic (Leschen and Ślipiński 2010). There have historically been ample proposals to divide the group, which were reviewed in detail by Lawrence et al. (1995a). Robertson et al. (2015) provided the first step to splitting the traditional Cucujoidea with the use of molecular data, erecting the superfamily Coccinelloidea for ladybird beetles, handsome fungus beetles, and their relatives, and removing the Biphyllidae and Byturidae to Cleroidea. No other divisions of Cucujoidea have been formalised since then. It is notable that in the latter part of his career, Crowson considered the establishment of a separate superfamily for sap beetles and their allies, Nitiduloidea (Audiso 1993; Crowson 1995), although this was never proposed formally. Nonetheless, the group of families surrounding Nitidulidae has been consistently recovered in morphology-based phylogenies and has often been referred to as the 'nitidulid lineage', 'nitidulid series' or 'nitidulid assemblage' (Ślipiński 1998; Leschen et al. 2005; Cline et al. 2014; McKenna et al. 2015b). Genome-scale analyses have unambiguously established the existence of a clade containing the 'nitidulid lineage' and the more basal families Helotidae, Sphindidae, Protocucujidae, and Monotomidae (McKenna et al. 2019).

The monophylum consisting of Monotomidae, Nitidulidae, Kateretidae, and Smicripidae is supported by abdominal tergite VII exposed in dorsal view and tergite VIII in males with sides curved ventrally forming a genital capsule (Leschen et al. 2005). LeConte (1861) treated this group as a unified Nitidulidae. Crowson (1955) also considered Monotomidae to belong to the nitidulid group, although he later revised this idea (unpublished, cited in Leschen et al. 2005). The clade containing only Nitidulidae, Kateretidae, and Smicripidae is strongly supported by the frontoclypeal suture present (most), anterior cervical sclerite not contiguous with head capsule or placed in paired emarginations, galea absent (most), anterior pronotal angles absent or not produced forwards, anterior tendons of metendosternite narrowly separated, abdominal tergite VII exposed in dorsal view, tergite VIII in males with sides curved ventrally forming a genital capsule, paired endocarinae absent in the ventral head capsule of larvae, four or fewer stemmata, apex of larval mandible bidentate (most), mesal surface of larval mandible with asperate or tuberculate mola, labial palpi 1-segmented in larva, and larval hypopharyngeal sclerome an irregular molar-like tooth (most) (Leschen et al. 2005). Of these, the absence of a galea is apparently autapomorphic for the group. The basal clade Protocucujidae + Sphindidae has traditionally been well-accepted (Sen Gupta and Crowson 1979; McHugh 1993; Ślipiński 1998) and is supported by the following shared morphological characters: frontoclypeal suture present, apex of mandible tridentate, anterior portion of prosternum at midline as long as prosternal process, procoxal cavity internally open, metendosternal laminae well developed, 5 free veins present in medial area of the hind wing, 5-5-4 male tarsal formula, aedeagus with U-shaped sclerite near apex, loss of articulated parameres, internal sac with basal complex sclerite, labrum of larvae vertical, apex of larval mandible tridentate, and ventral epicranial ridges of larval head capsule absent (Thomas 1984a; Ślipiński 1998; Beutel and Ślipiński 2001; Leschen et al. 2005). Similarities between the two taxa are especially evident in the South American genus *Protosphindus* Sen Gupta and Crowson (1979).

Characters shared by nitidulid families are listed above in the diagnosis section. Identifying characters that support the whole of the eco-morphologically remarkably diverse Nitiduloidea, as defined here, is more difficult. This is not surprising, however, because the same was the case for the old Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) which likewise lacked a set of unique and widespread apomorphies (Kirejtshuk 2000; Leschen and Ślipiński 2010). Nonetheless, commonalities of the whole Nitiduloidea *stat. nov*. have been noted by coleopterists for over a century. Sharp and Muir (1912) noted similarities of the aedeagus of Helotidae, Monotomidae, and Nitidulidae, although they noted that their taxon sampling was not wide enough to draw definitive conclusions.

Because of the inherent difficulties associated with studying the phylogeny of cucujoid beetles, the division of Cucujoidea *sensu* Robertson et al. (2015) proposed by us into three separate superfamilies leaves several enigmatic families of uncertain placement that were not included in our analyses because of the unavailability of sequences and lack of consensus in morphology-based phylogenies. In the morphological phylogenetic analysis of Leschen et al. (2005), Tasmosalpingidae formed a monophyletic group with Cyclaxyridae but was simultaneously also close to Nitiduloidea based on all characters or adult characters only. When larval characters were analysed alone, it was recovered as sister to Phalacridae. The placement of the fossil families †Parandrexidae and †Wabbelidae has not been formally tested (Kirejtshuk 1994; Escalona et al. 2015; Alekseev, 2017). These fossil taxa are treated as Cucujiformia incertae sedis, as they cannot be placed for sure in either Erotyloidea stat. nov., Nitiduloidea stat. nov., or Cucujoidea sensu nov. with certainty.

CUCUJOIDEA Latreille, 1802 **sensu nov.**

Type genus: *Cucujus* Fabricius, 1775.

Diagnosis: Adults typically with dorsoventrally flattened bodies (except Cyclaxyridae, some Passandridae, Phalacridae). Head sometimes with elongate rostrum, longer than wide (some Silvanidae, some Laemophloeidae). Dorsal part of mandible without a setose cavity (present in some Silvanidae, some Phloeostichidae). Subantennal grooves weakly developed or absent (except some Passandridae, some Laemophloeidae, Myraboliidae). Antennae filiform or moniliform (some Silvanidae, Cucujidae, some Passandridae, some Laemophloeidae). Tentorium with a medial process (except Myraboliidae, Phalacridae, and Laemophloeidae). Gular sutures at least partly confluent (only in Passandridae). Ventral or lateral portion of prothorax on each side with incomplete notosternal suture or without sutures (some Cryptophagidae, some Silvanidae, some Phloeostichidae, Laemophloeidae). Cuticular glands, where present, consist of single ducts. Procoxal cavities internally open (except some Passandridae, Phalacridae). Ventrite 1 sometimes much longer than ventrite 2 (some Cryptophagidae, some Silvanidae, Myraboliidae). Tergite VIII in female dorsally concealed by tergite VII, tergite X in male completely membranous. Unequal anterior tibial spurs (some, in Passandridae, Phalacridae and Laemophloeidae). Tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male (rarely 4-4-4 or 4-5-4). Penis may be clearly divided into basipenis and distipenis (Leschen, pers. obs.) or undivided with a single, often broad penile strut. Larvae with frontal arms lyriform (most), mesal surface of mandible with well-developed mola (most), maxillary articulating area present (most), hypopharyngeal sclerome present (most).

Included taxa: Agapythidae Sen Gupta and Crowson, 1969; Cavognathidae Sen Gupta and Crowson, 1966; Cryptophagidae Kirby, 1826; Cucujidae Latreille, 1802; Cyclaxyridae Gimmel, Leschen and Ślipiński, 2009; Hobartiidae Sen Gupta and Crowson, 1966; Laemophloeidae Ganglbauer, 1899; Lamingtoniidae Sen Gupta and Crowson, 1969; Myraboliidae Lawrence and Britton, 1991; Passandridae Blanchard, 1845; Phalacridae Leach, 1815; Phloeostichidae Reitter, 1911; Priasilphidae Crowson, 1973; Silvanidae Kirby, 1837; Tasmosalpingidae Lawrence and Britton, 1991.

Discussion: Cucujoidea, in the strict sense as conceived here, corresponds to the most derived clade of the old Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) and the 'basal Cucujoidea' of Leschen et al. (2005) recovered in our and previous genome-scale molecular studies (Zhang et al. 2018; McKenna et al. 2019). As with the former Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) or Cucujoidea *sensu* Robertson et al. (2015), finding definitive apomorphies of the group is difficult. The definitions of many of the cucujoid families discussed here have been considerably fluid in the past, often lacking definitive apomorphies, but most concern groups broadly defined in recent decades as Cucujidae and Phleoeostichidae. Nonetheless, Cucujoidea *sensu nov.* contains several clades that were strongly suspected to be monophyletic based on morphological studies, in some cases long before the advent of molecular systematics. These include Laemophloeidae, Phalacridae, and Passandridae (Thomas 1984b); Leschen's (1996) 'cucujid line' consisting of Cucujidae, Hobartiidae, Phloeostichidae, Cryptophagidae, Cavognathidae, and Silvanidae, following Thomas (1984a); and the 'basal Cucujoidea' of Leschen et al. (2005). Cucujoidea *sensu nov*. is also mostly congruent with the 'cucujid series' as recovered in molecular studies by Hunt et al. (2007), Bocak et al. (2014), McElrath et al.

(2015), and Robertson et al. (2015).

The relationships among the family groups and potential synapomorphies for Cucujoidea have been discussed in several papers, but none of the characters are conclusive synapomorphies, as discussed in Leschen (1996), relevant chapters in Leschen et al. (2010), and the study by McElrath et al. (2015) where some salient features of the adults were reconstructed over the Cucujoidea tree. Some characters like the presence or absence of the tentorial spine in the adult or the number of tarsungular setae in the larva (Leschen 1996) are too variable within the group to be identified as a synapomorphy (Leschen 1996). One feature relevant for defining Cucujoidea may be the presence of a bipartite or subdivided penis (Leschen, unpubl.). The penis in Cucujiformia is highly diverse (Lawrence and Slipinski 2013) and many groups have a single or double penile strut. Several members of the Cucujoidea as defined here have a bipartite penis (Cavognathidae, Priasilphidae, Cucujidae, Agapythidae, and Silvanidae; Leschen et al. 2005; Lawrence et al. 2011) and the anterior part could be homologous to the penile strut. Examination of dissections of Hobartiidae and Passandridae and images of Myraboliidae indicate that these may also have a subdivided penis, whereas the remaining families clearly have an undivided penis (Cyclaxyridae, Lamingtoniidae, Phloeostichidae, Phalacridae and Tasmosalpingidae). If we examine this variation in light of our tree and those of Zhang et al. (2018) and McKenna et al. (2019), a bipartite aedeagus is optimised as a synapomorphy, the undivided type (in different forms) as derived. These aedeagal types are similarly optimised on the trees in McElrath et al. (2015) and Robertson et al. (2015).

†ALPHACOLEOPTERA Engel, Cai, and Tihelka **subord. nov.**

Type family: †Tshekardocoleidae Rohdendorf, 1944.

Diagnosis: Procoxal cavities closed posteriorly; mesothorax shortened and metathorax enlarged; forewings complete, flat over abdomen at reset, with wide epipleura, meeting along and putatively locking along sutural margin except apices acute and typically not meeting along sutural margin (thus, largely but not completely covering metasoma), venation complete, reticulate, longitudinal sectors typically forking (sometimes zigzagged), with multiple cells between veins, small field proximally between Sc and RA (except Permosynoidea), anal vein following sutural margin (posterior trailing margin opposite leading edge), with shoulder placed proximally on A1+2; mesoventrite longer than prosternum; tarsal formula 5-5-5; telescopic ovipositor scarcely sclerotized.

Included taxa: Superfamily †Permocupedoidea Martynov, 1932, Superfamily †Permosynoidea Tillyard, 1924, and Superfamily †Coleopsoidea Kirejtshuk and Nel, 2016.

Etymology: The name of this suborder is a combination of Greek *álpha* (*ἄλφα*), first letter of the Ancient Greek alphabet and an allusion to “first”, and Coleoptera, itself a combination of Greek *koleós* (*κολεός*), meaning, “sword-sheath”, and *pterá* (*πτερά*, plural of pterón, *πτερόν*), meaning, “wings”.

Discussion: This group has often been referred to as †Protocoleoptera Tillyard, 1924. Unfortunately, Protocoleoptera was established explicitly for the extinct family †Protocoleidae Tillyard, 1924, a group today known to be a lineage of polyneopteran insects allied to the earwigs (Dermaptera). Another extinct famly, †Permophilidae Tillyard, 1924, from the same fossil beds was later established as †Paracoleoptera Laurentiaux, 1953, and also considered a lineage allied to the beetles. †Permophilidae, like †Protocoleidae, are polyneopterans (*e.g.*, Forbes, 1928; Kukalová, 1966). Accordingly, †Protocoleoptera and †Paracoleoptera are objective synonyms of †Protelytroptera, are unrelated to Coleoptera, and, in fact, do not belong to the Eumetabola. Neither †Protocoleoptera nor †Paracoleoptera can be used as suborders of Coleoptera. Similarly, Crowson (1981) established an extinct suborder, †Archecoleoptera, which he considered to exclude the most primitive of beetles but be confined to the Permian. Crowson still considered †Protocoleoptera to be a lineage of early beetles including the †Tshekardocoleidae and others, and therefore excluded them from his ill-defined †Archecoleoptera. †Archecoleoptera were not established on the basis of an specific taxon or characters, but was meant to exclude at the least †Tshekardocoleidae and other early extinct beetles. Thus, the basalmost and extinct suborder of beetles remains without an appropriate name and one is therefore established here.

ZACOLEOPTERA Engel, Cai, and Tihelka **capaxord. nov.**

Diagnosis: Procoxal cavities distinct and open; narrow prosternal process present.

Included taxa: Suborder Metaxycoleoptera nov. and Hyporder Eucoleoptera nov.

Etymology: The name of this capaxorder is a combination of Aeolian Greek *zá* (*ζά*), meaning, “very”, and Coleoptera.

†METAXYCOLEOPTERA Engel, Cai, and Tihelka **subord. nov.**

Type family: †Ponomarenkiumidae Lawrence and Bouchard nom. nov.

Diagnosis: Fossil beetles with: antenna moniliform; elytra without window punctures; propleuron exposed; absence of coxal plates; absence of broad contact between meso- and metaventrites; procoxal cavities distinct and open; narrow prosternal process present; internalized metatrochantin; metanepisternum only marginally part of closure of mesocoxal cavity; transverse ridge of mesoventrite; short metacoxae not reaching hind margin of abdominal sternite III. They share with Eucoleoptera open procoxal cavities and a narrow prosternal process.

Included taxa: Family †Ponomarenkiumidae Lawrence and Bouchard nom. nov.

Etymology: The name of this suborder is a combination of Greek *metaxú* (*μετᾰξῠ*), meaning, “between”, and Coleoptera.

Discussion: This extinct group is likely sister to the Eucoleoptera, *i.e.*, the clade comprising all extant beetle suborders.

EUCOLEOPTERA Engel, Cai, and Tihelka **hypord. nov.**

Type family: Carabidae Latreille, 1802.

Diagnosis: Preëpisternal cervical sclerites lacking; procoxal cavities present and distinctly countersunk (secondarily modified in several clades); broad prothoracic postcoxal bridge lacking; narrow prosternal process; mesothoracic discrimen absent (secondarily reversed in various clades); mesothoracic meron absent; mesoscutellar-elytron locking device present; hind wing triangular (pivitol) fold proximal to RA3+4 (*i.e.*, not dividing vein), with vein typically incompletely proximally; mesocoxal cavities deep and completely demarcated mesally and posteriorly by distinct ridge (secondarily reduced numerous times); metascutal fissure present; alacristae present; metapostnotum undivided; metathoracic meron absent; metacoxae transverse, with metacoxal cavities distinct, completely demarcated posteriorly by carina; reduced costal crossvenation; sternite I reduced; female tergite IX divided into paraprocts on either side of tergite X.

Included taxa: Adephaga Clairville, 1806, Archostemata Kolbe, 1908, Myxophaga Crowson, 1955, and Polyphaga Emery, 1886.

Etymology: The name of this hyporder is a combination of Greek *eû* (*εὖ*), meaning, “good” or “true”, and Coleoptera.

Discussion: This group comprises all extant suborders of Coleoptera, distinct from the exclusively Permian alphacoleopterans.

Notes on the classification of beetles

†MAGNOCOLEIDAE Hong, 1998 *syn. nov*. – The monotypic fossil family †Magnocoleidae was described by the preeminent Chinese palaeoentomologist Professor Youchong Hong (1998) based on isolated elytra from the Lower Cretaceous Qingshila Formation of China, which were named as *Magnocoleus huangjiapuensis*. No further species belonging to the family have been described since, probably owing to the poorly accessible original description published in Chinese with only a brief English summary in a regional geological bulletin. Hong compared the new family with Permian, Triassic, and Jurassic protocoleopterans and archostematans, and differentiated it based on elytral venation characters. However, it should be noted that the elytral wing venation pattern of *Magnocoleus* falls well within the range of morphological variation observed in Mesozoic Cupedidae and Ommatidae. Using Ponomarenko's (1969) key to Archostemata *sensu lato*, the presence of five principal elytral veins, together with the shortened ones, and the complete reduction of CuP places *Magnocoleus* into Cupedidae or Ommatidae. Indeed, in a phylogenetic analyses of elytral characters *Magnocoleus* was recovered as sister to Ommatidae and Cupedidae (Lubkin 2007). We thus consider †Magnocoleidae as a junior synonym of Cupedoidea and *Magnocoleus* as *incertae sedis* within that superfamily. The lack of complete body fossils makes it difficult to determine whether the beetles belonged to Ommatidae or Cupedidae, as the two families cannot be reliably distinguished on the basis of elytral venation alone (Lawrence 1999).

†PONOMARENKIUMIDAE Lawrence and Bouchard *nom. nov.* – The family-group name Ponomarenkiidae Yan, Lawrence, Beattie & Beutel, 2017 is permanently invalid (see ICZN 1999, Article 39) since its type genus *Ponomarenkia* Yan, Lawrence, Beattie & Beutel, 2017 is a junior homonym of *Ponomarenki* Perkovsky, 2001 in Agyrtidae. While *Ponomarenkium* Yan, Lawrence, Beattie & Beutel, 2018 was proposed as a replacement name for *Ponomarenkia* Yan, Lawrence, Beattie & Beutel, 2017, the family-group name Ponomarenkiidae also needs a replacement name because it lacks an available synonym. Ponomarenkiumidae Lawrence and Bouchard *nomen novum* is proposed here, with its stem based on the entire name of the type genus *Ponomarenkium* Yan, Lawrence, Beattie & Beutel, 2018 to avoid homonymy with Ponomarenkiidae (see ICZN 1999, Article 29.6).

HETEROCERIDAE MacLeay, 1825. – The variegated mud-loving beetles were recovered as nested within Limnichidae with moderate support. Heterocerids are characterised by a set of morphological characters that represent extreme adaptations for life in near-water environments, such as fossorial legs and body covered with dense water-repellent setae (Vanin et al. 2016). Historically, the monophyly of Limnichidae, the minute marsh-loving beetles, has been doubted on the basis of both morphological and molecular data (Hinton 1939; Crowson 1978; Beutel 1995; Costa et al. 1999; Bocak et al. 2014). Crowson (1978) regarded Heteroceridae as a sister group to Limnichidae. In a morphological phylogenetic analysis, Beutel (1995) recovered Limnichidae as the sister group to Heteroceridae based on larval morphological characters, while Costa et al. (1999) placed Heteroceridae in a clade with Dryopidae + paraphyletic Limnichidae. Heteroceridae was placed within a paraphyletic Limnichidae in Kundrata et al.'s (2017) analysis of four DNA fragments and the phylogenomic studies of Zhang et al. (2018) and an 89 gene dataset in McKenna et al. (2019). In our analyses, *Heterocerus* was recovered as sister to Limnichinae with full support, although the subfamilies Hyphalinae and Thaumastodinae were not sampled. In the analysis of McKenna et al. (2019), *Heterocerus* was sister to Cephalobyrrhinae.

Regardless of the precise sister group of Heteroceridae it shares with apparently all Limnichidae the presence of a frontoclypeal suture on the adult head, absence of the radial cell in the hindwing, asymmetrical base of the basal piece of the aedeagus, as well as the following larval synapomorphies: head with dense vestiture of long and short setae, presence of accessory anterior tentorial bridge, and a short antenna with a large hyaline sensorium (Crowson 1978; Beutel 1995; Costa et al. 1999). Crowson (1978) furthermore pointed out that the larvae in both families share mandibles with a plumose prostheca and retractable anal tracheal gills in at least some taxa.

We treat Heteroceridae as a separate family, although its incorporation within Limnichidae should be considered if future studies arrive at identical conclusions with increased gene sampling and higher statistical support.

JACOBSONIIDAE Heller, 1926. – The family Jacobsoniidae is herein treated as a member of the superfamily Staphylinoidea. Jacobsoniidae have been placed in a variety of basal polyphagan superfamilies in the past, namely in Bostrichiformia (Lawrence and Newton 1995), Cucujiformia (Sen Gupta 1979) and Derodontiformia (Lawrence and Leschen 2010). Recently, Lawrence (2016) removed Jacobsoniidae from Derodontiformia and treated it as series and superfamily *incertae sedis*.

The placement of some or all of members of Jacobsoniidae within Staphylinoidea is supported by morphological and molecular studies (Lawrence et al. 2011; McKenna et al. 2015b, 2019; Toussaint et al. 2017; Zhang et al. 2018). The three very different-looking genera have not been included together in any recent analyses, and only two (*Derolathrus* and *Saphophagus*) have genetic data available. Ptiliidae, which together with Hydraenidae formed the sister group to Jacobsoniidae in our analyses, shares with the family reduced hindwing venation and very long fringe hairs forming a "feather-wing", with a complex folding pattern aided by spicules on the abdominal tergites (Crowson 1960; Yamamoto et al. 2017). The jacobsoniid larval galea also suggests a relationship with Staphylinoidea (Crowson 1960). It should nonetheless be noted that our analyses are only based on the jacobsoniid genus *Derolathrus*; however, *Saphophagus* was placed in the same position in McKenna et al. (2019). Due to the considerable morphological differences between the three genera, it is not certain whether Jacobsoniidae as presently defined is in fact monophyletic (Löbl and Burckhardt 1988), and genetic data for *Sarothrias* (senior synonym of the type genus of the family) would test this hypothesis and settle the superfamily placement of the family.

COLONIDAE Horn, 1880 (1859) *stat. nov*. – The leiodid subfamily Coloninae is herein treated as a separate family of Staphylinoidea, in agreement with some historical treatments of Leiodidae and related families (e.g., Jeannel 1936; Perkovsky 1997). In addition to having a brick-wall pattern of abdominal intersegmental membranes, unique outside of Staphylinidae sensu nov. as noted below under Silphinae, colonines lack the conspicuous leiodid character of an "interrupted club" with smaller antennomere 8 (e.g., Perkovsky 1997), and have many other characters that are unique or unusual within Leiodidae, including cervical sclerites absent, procoxal cavities closed by fusion of the pronotal and prosternal processes, abdominal spiracles 7-8 absent, and others noted by Newton (1998). Recent molecular phylogenetic studies have also placed Coloninae as an isolated staphylinoid group well outside of an otherwise monophyletic Leiodidae, either as a sister to Hydraenidae+Ptiliidae (McKenna et al. 2015a), or sister to Agyrtidae+Leiodidae (minus Coloninae) (Lü et al. 2020). Recent discovery of mid-Cretaceous fossils (Cai and Huang 2017; Yamamoto and Takahashi 2018) further supports this separation by showing that an unreduced antennomere 8 was already present then and not likely a later secondary development within Leiodidae as previously proposed (e.g., Hansen 1997).

SILPHINAE Latreille, 1806 *stat. nov.* – The family Silphidae *sensu* Sikes (2016) is herein treated as a subfamily of Staphylinidae *sensu nov*. Difficulties in clearly distinguishing the two groups were pointed out by coleopterists for almost a hundred years; Hatch (1927) treated the burying beetles as a subfamily of Staphylinidae, but his proposal was not widely accepted. A number of morphological and molecular studies conducted since have firmly established Silphinae *stat. nov.* as either nested within Staphylinidae or at most a sister group to that family, together forming a monophyletic clade (Hansen 1997, Beutel and Molenda 1997; Beutel and Leschen 2005; Caterino et al. 2005; Hunt et al. 2007; Grebennikov and Newton 2009, 2012; Lawrence et al. 2011; McKenna et al. 2015a, 2015b, 2019; Zhang et al. 2018; Lü et al. 2020; Song, et al. 2021). The sister group of Silphinae *stat. nov*. is not resolved, as past studies have suggested a range of topologies often placing the subfamily as sister to the remaining staphylinids (e.g., Grebennikov and Newton 2012) or associated with the subfamily Phloeocharinae (Caterino et al. 2005) or Tachyporinae (McKenna et al. 2015a, 2015b; Lü et al. 2020; Song et al. 2021; Yamamoto 2021). In our analyses, the burying beetles were recovered as sister to a clade containing Osoriinae, Apateticinae, and Scaphidiinae. This rather derived placement within Staphylinidae is consistent with the hypothesis of Lawrence and Newton (1982).

The inclusion of Silphinae *stat. nov*. within Staphylinidae *sensu nov.* is supported by a typical brick-wall pattern of minute sclerites in the abdominal intersegmental membranes, which may represent a synapomorphy of the two groups, although it also occurs in the enigmatic leiodid genus *Colon* Herbst (Hansen 1997) and is not present in many groups (Thayer 2016). The two taxa share a number of morphological characters, most likely correlated with reduced elytra that are abbreviated apically and associated with a more flexible abdomen: a unique wing hinge and asymmetrical folding pattern, aedeagus usually everted asymmetrically and with a large basal bulb and internal muscles for evaginating the internal sac, larvae without labral tormae and mandibular molae but with a modified tentorium whose posterior arms attach directly to the ventral surface of the head and whose bridge is directed posteriorly (Lawrence and Newton 1982; Newton 1997; Sikes et al. 2016). We consider this evidence, together with the results of molecular phylogenetic studies, as sufficient for formally treating the carrion beetles as members of Staphylinidae *sensu nov*.

The former subfamilies of Silphinae *stat. nov*. are downgraded to tribal level: Silphini Latreille, 1806 and Nicrophorini Kirby, 1837 (both *stat. nov*.).

CLEROIDEA Latreille, 1802. – Gimmel et al. (2019) recently conducted the first in-depth molecular analysis of the relationships within the superfamily Cleroidea, sampling four genes across a wide range of taxa. While the taxon sampling in our study was insufficient to test all their newly proposed classification changes in the superfamily, we did recover their newly proposed Thymalidae, represented by *Thymalus*, nested within Trogossitidae *sensu stricto* of Gimmel et al. (2019). While *Thymalus* was historically placed within the trogossitid subfamily Peltinae (now Peltidae), it does not fit the diagnosis of Trogossitidae in the new, restricted sense, which includes only taxa with broadly closed procoxal cavities (Gimmel et al. 2019). We defer this issue to a subsequent study that includes more taxa of the Trogossitidae (*sensu stricto*) and the other subfamily of Thymalidae, the Decamerinae.

CYBOCEPHALINAE Jacquelin du Val, 1858 *stat. nov*. – The family Cybocephalidae is herein treated as subfamily Cybocephalinae stat. nov. within Nitidulidae. The rank and systematic position of this peculiar group was recently discussed by Kirejtshuk and Mantič (2015) and Lawrence (2019c).

MELOIDAE Gyllenhal, 1810. – The family Meloidae *sensu* Bologna et al. (2010) was recovered nested within Anthicidae. Due to their unusual life habits and a similarly unusual morphology, the systematic position of blister beetles has long been considered unresolved. A relationship with the family Anthicidae has been hypothesised by a number of coleopterists in the past (Crowson 1955; Abdullah 1965a, b, 1969; Selander 1966, 1991; Bologna and Pinto 2001). The subtribe Protomeloina has been regarded by Abdullah (1965a, b) as a link between the family and the remaining Anthicidae. The same author also proposed that blister beetles are in fact derived anthicids (Abdullah 1969). Meloidae have been recovered as nested within Anthicidae in the phylogenomic analyses of Zhang et al. (2018) and McKenna et al. (2019) as well as in some analyses of fewer genes (Gunter et al. 2014). Both families share a strongly deflexed head, a somewhat inflated vertex, a narrow neck, and a pronotum lacking lateral carinae (Bologna et al. 2010). Indeed, some meloids and anthicids can be easily confused and unsurprisingly there is a long history of taxa transferred between the two groups. It is interesting to note that some anthicid beetles are attracted to blister beetles and feed on the cantharidin they secrete, which is possibly used for predator defense and/or as a mating attractant, leading Abdullah (1964) to postulate that the production of this substance may have been ancestral to the two groups. This hypothesis seems supported by the fact that some male anthicids have been recorded to secrete cantharidin (Schütz and Dettner 1992). At present, we regard Meloidae as a separate family, but note that the accumulation of further molecular evidence may result into the group being joined within Anthicidae. An alternative treatment may be to divide Anthicidae, which currently contains several sufamilies with apparently disparate morphology, depending on future morphological and molecular evidence.

Classification of beetles (families and subfamilies)

Order COLEOPTERA Linnaeus, 1758

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

- †Superfamily **Coleopsoidea** Kirejtshuk and Nel, 2016
  - †Family Coleopsidae Kirejtshuk and Nel, 2016

- †Superfamily **Permocupedoidea** Martynov, 1932
  - †Family Tshekardocoleidae Rohdendorf, 1944
  - †Family Labradorocoleidae Ponomarenko, 1969
  - †Family Oborocoleidae Kukalová, 1969
  - †Family Permocupedidae Martynov, 1932
    - †Subfamily Permocupedinae Martynov, 1932
    - †Subfamily Taldycupedinae Rohdendorf, 1961

- †Superfamily **Permosynoidea** Tillyard, 1924
  - †Family Ademosynidae Ponomarenko, 1968
  - †Family Permosynidae Tillyard, 1924

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

Suborder **METAXYCOLEOPTERA** Engel, Cai, and Tihelka, nov.

- †Family Ponomarenkiumidae Lawrence and Bouchard *nov.*

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

Suborder **ADEPHAGA** Claireville, 1806

- †Family Tritarsusidae Hong, 2002
- †Family Triaplidae Ponomarenko, 1977
- Family Haliplidae Aubé, 1836
- Family Gyrinidae Latreille, 1810
  - Subfamily Spanglerogyrinae Folkerts, 1979
  - Subfamily Gyrininae Latreille, 1810
  - Subfamily Heterogyrinae Brinck, 1955
- †Family Coptoclavidae Ponomarenko, 1961
  - †Subfamily Timarchopsinae Wang, Ponomarenko and Zhang, 2010
  - †Subfamily Charonoscaphinae Ponomarenko, 1977
  - †Subfamily Coptoclavinae Ponomarenko, 1961
  - †Subfamily Coptoclaviscinae Soriano, Ponomarenko and Delclòs, 2007
  - †Subfamily Hispanoclavinae Soriano, Ponomarenko and Delclòs, 2007
- Family Noteridae Thomson, 1860
  - Subfamily Notomicrinae Branden, 1884
  - Subfamily Noterinae Thomson, 1860
- Family Meruidae Spangler and Steiner, 2005
- Family Aspidytidae Ribera, Beutel, Balke and Vogler, 2002
- Family Amphizoidae LeConte, 1853
- Family Hygrobiidae Régimbart, 1879 (1837)
- Family Dytiscidae Leach, 1815
  - Subfamily Matinae Branden, 1885
  - Subfamily Lancetinae Branden, 1885
  - Subfamily Agabinae Thomson, 1867

Subfamily Colymbetinae Erichson, 1837
Subfamily Copelatinae Branden, 1885
Subfamily Laccophilinae Gistel, 1848
Subfamily Cybisterinae Sharp, 1880
Subfamily Dytiscinae Leach, 1815
Subfamily Coptotominae Branden, 1885
Subfamily Hydrodytinae Miller, 2001
Subfamily Hydroporinae Aubé, 1836
†Subfamily Palaeogyrininae Schlechtendal, 1894
†Subfamily Liadytiscinae Prokin and Ren, 2010
†Family Colymbotethidae Ponomarenko, 1994
†Family Parahygrobiidae Ponomarenko, 1977
†Family Liadytidae Ponomarenko, 1977
Family Trachypachidae Thomson, 1857
†Subfamily Eodromeinae Ponomarenko, 1977
Subfamily Trachypachinae Thomson, 1857
Family Cicindelidae Latreille 1802
Family Carabidae Latreille, 1802
†Subfamily Protorabinae Ponomarenko, 1977
†Subfamily Conjunctiinae Ponomarenko, 1977
Subfamily Rhysodinae Laporte, 1840
Subfamily Nebriinae Laporte, 1834
Subfamily Carabinae Latreille, 1802
Subfamily Loricerinae Bonelli, 1810
Subfamily Omophroninae Bonelli, 1810
Subfamily Elaphrinae Latreille, 1802
Subfamily Migadopinae Chaudoir, 1861
Subfamily Hiletinae Schiødte, 1848
Subfamily Scaritinae Bonelli, 1810
Subfamily Broscinae Hope, 1838
Subfamily Apotominae LeConte, 1853
Subfamily Siagoninae Bonelli, 1813
Subfamily Melaeninae Csiki, 1933
Subfamily Gehringiinae Darlington, 1933
Subfamily Trechinae Bonelli, 1810
Subfamily Patrobinae Kirby, 1837
Subfamily Psydrinae LeConte, 1853
Subfamily Nototylinae Bänninger, 1927
Subfamily Paussinae Latreille, 1806
Subfamily Cicindinae Csiki, 1927
Subfamily Brachininae Bonelli, 1810
Subfamily Harpalinae Bonelli, 1810

Suborder **ARCHOSTEMATA** Kolbe, 1908

Superfamily **Cupedoidea** Laporte, 1838
= †Family Magnocoleidae Hong, 1998 **syn. nov.**
Family Crowsoniellidae Iablokoff-Khnzorian, 1983
Family Cupedidae Laporte, 1838
Subfamily Priacminae Crowson, 1962
†Subfamily Mesocupedinae Ponomarenko, 1969
Subfamily Cupedinae Laporte, 1838

Family Micromalthidae Barber, 1913
Family Ommatidae Sharp and Muir, 1912
†Subfamily Brochocoleinae Hong, 1982
Subfamily Ommatinae Sharp and Muir, 1912
Subfamily Tetraphalerinae Crowson, 1962
†Family Triadocupedidae Ponomarenko, 1966

†Superfamily **Asiocoleoidea** Rohdendorf, 1961
†Family Asiocoleidae Rohdendorf, 1961
†Family Tricoleidae Ponomarenko, 1969

†Superfamily **Rhombocoleoidea** Rohdendorf, 1961
†Family Rhombocoleidae Rohdendorf, 1961

†Superfamily **Schizocoleoidea** Rohdendorf, 1961
†Family Schizocoleidae Rohdendorf, 1961
†Family Phoroschizidae Bouchard and Bousquet, 2020
†Family Catiniidae Ponomarenko, 1968

Suborder **MYXOPHAGA** Crowson, 1955

Superfamily **Lepiceroidea** Hinton, 1936 (1882)
Family Lepiceridae Hinton, 1936 (1882)

Superfamily **Sphaeriusoidea** Erichson, 1845
Family Torridincolidae Steffan, 1964
Subfamily Torridincolinae Steffan, 1964
Subfamily Deleveinae Endrödy-Younga, 1997
†Family Triamyxidae Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg, and Niedźwiedzki, 2021
Family Hydroscaphidae LeConte, 1874
Family Sphaeriusidae Erichson, 1845

Suborder **POLYPHAGA** Emery, 1886

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

Superfamily **Scirtoidea** Fleming, 1821 **sensu nov.**
Family Decliniidae Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994
Family Scirtidae Fleming, 1821
†Subfamily Mesernobiinae Engel, 2010
Subfamily Nipponocyphoninae Lawrence and Yoshitomi, 2007
Subfamily Stenocyphoninae Lawrence and Yoshitomi, 2007
Subfamily Scirtinae Fleming, 1821
†Family Elodophthalmidae Kirejtshuk and Azar, 2008
†Family Boleopsidae Kirejtshuk and Nel, 2013

Series CLAMBIFORMIA Cai and Tihelka **ser. nov.**

Superfamily **Clamboidea** Fischer, 1821 **sensu nov.**
Family Derodontidae LeConte, 1861
Subfamily Peltasticinae LeConte, 1861
Subfamily Derodontinae LeConte, 1861

Subfamily Laricobiinae Mulsant and Rey, 1864
Family Clambidae Fischer, 1821
Subfamily Calyptomerinae Crowson, 1955
Subfamily Acalyptomerinae Crowson, 1979
Subfamily Clambinae Fischer, 1821
Family Eucinetidae Lacordaire, 1857
†Family Mesocinetidae Kirejtshuk and Ponomarenko, 2010

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

Superfamily **Rhinorhipoidea** Lawrence, 1988
Family Rhinorhipidae Lawrence, 1988

Series ELATERIFORMIA Crowson, 1960

Superfamily **Dascilloidea** Guérin-Méneville, 1843 (1834)
Family Dascillidae Guérin-Méneville, 1843 (1834)
Subfamily Dascillinae Guérin-Méneville, 1843 (1834)
Subfamily Karumiinae Escalera, 1913
Family Rhipiceridae Latreille, 1834
Subfamily Rhipicerinae Latreille, 1834
Subfamily Sandalinae Jakobson, 1913

Superfamily **Byrrhoidea** Latreille, 1804 **sensu nov.**
Family Byrrhidae Latreille, 1804
Subfamily Byrrhinae Latreille, 1804
Subfamily Syncalyptinae Mulsant and Rey, 1869
Subfamily Amphicyrtinae LeConte, 1861
†Subfamily Lidryopinae Kirejtshuk and Nel, 2016

Superfamily **Buprestoidea** Leach, 1815
Family Schizopodidae LeConte, 1859
Family Buprestidae Leach, 1815
Subfamily Julodinae Lacordaire, 1857
Subfamily Polycestinae Lacordaire, 1857
Subfamily Galbellinae Reitter, 1911
Subfamily Chrysochroinae Laporte, 1835
Subfamily Buprestinae Leach, 1815
Subfamily Agrilinae Laporte, 1835
†Subfamily Parathyreinae Alexeev, 1994

Superfamily **Dryopoidea** Billberg, 1820 (1817) **stat. res.**
Family Lutrochidae Kasap and Crowson, 1975
Family Dryopidae Billberg, 1820 (1817)
Family Eulichadidae Crowson, 1973
Family Callirhipidae Emden, 1924
Family Ptilodactylidae Laporte, 1838
Subfamily Cladotominae Pic, 1914
Subfamily Anchytarsinae Champion, 1897
Subfamily Aploglossinae Champion, 1897
Subfamily Araeopidiinae Lawrence, 1991

    - Subfamily Ptilodactylinae Laporte, 1838
- Family Cneoglossidae Champion, 1897
- Family Chelonariidae Blanchard, 1845
- Family Psephenidae Lacordaire, 1854
    - Subfamily Afroeubriinae Lee, Satô, Shepard and Jäch, 2007
    - Subfamily Eubriinae Lacordaire, 1857
    - Subfamily Psephenoidinae Bollow, 1938
    - Subfamily Eubrianacinae Jakobson, 1913 (1880)
    - Subfamily Psepheninae Lacordaire, 1854
- Family Protelmidae Jeannel, 1950
- Family Elmidae Curtis, 1830
    - Subfamily Larainae LeConte, 1861
    - Subfamily Elminae Curtis, 1830
- Family Limnichidae Erichson, 1846
    - Subfamily Hyphalinae Britton, 1971
    - Subfamily Limnichinae Erichson, 1846
    - Subfamily Cephalobyrrhinae Champion, 1925
    - Subfamily Thaumastodinae Champion, 1924
- Family Heteroceridae MacLeay, 1825
    - Subfamily Elythomerinae Pacheco, 1964
    - Subfamily Heterocerinae MacLeay, 1825

Superfamily **Elateroidea** Leach, 1815
- Family Artematopodidae Lacordaire, 1857
    - Subfamily Electribiinae Crowson, 1975
    - Subfamily Allopogoniinae Crowson, 1973
    - Subfamily Artematopodinae Lacordaire, 1857
- Family Omethidae LeConte, 1861
    - Subfamily Driloniinae Crowson, 1972
    - Subfamily Matheteinae LeConte, 1881
    - Subfamily Omethinae LeConte, 1861
    - Subfamily Telegeusinae Leng, 1920
- Family Brachypsectridae Horn, 1881
- Family Throscidae Laporte, 1840
- Family Eucnemidae Eschscholtz, 1829
    - Subfamily Perothopinae Lacordaire, 1857
    - Subfamily Phyllocerinae Reitter, 1905
    - Subfamily Pseudomeninae Muona, 1993
    - Subfamily Schizophilinae Muona, 1993
    - Subfamily Palaeoxeninae Muona, 1993
    - Subfamily Phlegoninae Muona, 1993
    - Subfamily Anischiinae Fleutiaux, 1936
    - Subfamily Melasinae Fleming, 1821
    - Subfamily Eucneminae Eschscholtz, 1829
    - Subfamily Macraulacinae Fleutiaux, 1923
- Family Cerophytidae Latreille, 1834
- Family Jurasaidae Rosa, Costa, Kramp and Kundrata, 2020
- Family Elateridae Leach, 1815
    - Subfamily Elaterinae Leach, 1815
    - Subfamily Tetralobinae Laporte, 1840
    - Subfamily Omalisinae Lacordaire, 1857
    - Subfamily Agrypninae Candèze, 1857

  - Subfamily Hapatesinae Kusy, Motyka and Bocak, 2021
  - Subfamily Pityobiinae Hyslop, 1917
  - Subfamily Lissominae Laporte, 1835
  - Subfamily Thylacosterninae Fleutiaux, 1920
  - Subfamily Campyloxeninae Costa, 1975
  - Subfamily Hypnoidinae Schwarz, 1906 (1860)
  - Subfamily Dendrometrinae Gistel, 1848
  - Subfamily Negastriinae Nakane and Kishii, 1956
  - Subfamily Cardiophorinae Candèze, 1859
  - Subfamily Oestodinae Hyslop, 1917
  - Subfamily Hemiopinae Fleutiaux, 1941
  - Subfamily Physodactylinae Lacordaire, 1857
  - Subfamily Subprotelaterinae Fleutiaux, 1920
  - Subfamily Morostominae Dolin, 2000
  - Subfamily Parablacinae Kundrata, Gunter, Douglas and Bocak, 2016
  - †Subfamily Protagrypninae Dolin, 1973
- Family Sinopyrophoridae Bi and Li, 2019
- Family Lycidae Laporte, 1838
  - Subfamily Dexorinae Bocak and Bocakova, 1989
  - Subfamily Calochrominae Lacordaire, 1857
  - Subfamily Erotinae Leconte, 1881
  - Subfamily Ateliinae Kleine, 1928
  - Subfamily Lycinae Laporte, 1838
  - Subfamily Lyropaeinae Bocak and Bocakova, 1989
  - Subfamily Metriorrhynchinae Kleine, 1926
- Family Iberobaeniidae Bocak, Kundrata, Andújar and Vogler, 2016
- †Family Berendtimiridae Winkler, 1987
- †Family Cretophengodidae Li, Kundrata, Tihelka and Cai, 2021
- Family Phengodidae LeConte, 1861
  - Subfamily Cydistinae Paulus, 1972
  - Subfamily Phengodinae LeConte, 1861
  - Subfamily Mastinocerinae LeConte, 1881
  - Subfamily Penicillophorinae Paulus, 1975
- Family Rhagophthalmidae Olivier, 1907
- Family Lampyridae Rafinesque, 1815
  - Subfamily Luciolinae Lacordaire, 1857
  - Subfamily Pterotinae LeConte, 1861
  - Subfamily Ototretinae McDermott, 1964
  - Subfamily Lamprohizinae Kazantsev, 2010
  - Subfamily Chespiritoinae Ferreira, Keller and Branham, 2020
  - Subfamily Cyphonocerinae Crowson, 1972
  - Subfamily Psilocladinae McDermott, 1964
  - Subfamily Amydetinae Olivier in Wytsman, 1907
  - Subfamily Cheguevariinae Kazantsev, 2007
  - Subfamily Photurinae Lacordaire, 1857
  - Subfamily Cladodinae Bocakova, Campello-Gonçalves and Silveira, 2022
  - Subfamily Lampyrinae Rafinesque, 1815
- †Family Mysteriomorphidae Alekseev and Ellenberger, 2019
- Family Cantharidae Imhoff, 1856 (1815)
  - Subfamily Cantharinae Imhoff, 1856 (1815)
  - Subfamily Silinae Mulsant, 1862

        Subfamily Dysmorphocerinae Brancucci, 1980
        Subfamily Malthininae Kiesenwetter, 1852
        Subfamily Chauliognathinae LeConte, 1861

Series NOSODENDRIFORMIA Cai and Tihelka **ser. nov.**

  Superfamily **Nosodendroidea** Erichson, 1846
    Family Nosodendridae Erichson, 1846

Series STAPHYLINIFORMIA Lameere, 1900 **sensu nov.**

Superfamily **Histeroidea** Gyllenhaal, 1808
    Family Synteliidae Lewis, 1882
    Family Sphaeritidae Shuckard, 1839
    †Family Cretohisteridae Zhou, Caterino, Ślipiński and Cai, 2018
    Family Histeridae Gyllenhal, 1808
        Subfamily †Antigracilinae Zhou, Caterino, Ren and Ślipiński, 2020
        Subfamily Niponiinae Fowler, 1912
        Subfamily Abraeinae MacLeay, 1819
        Subfamily Saprininae Blanchard, 1845
        Subfamily Dendrophilinae Reitter, 1909
        Subfamily Onthophilinae MacLeay, 1819
        Subfamily Tribalinae Bickhardt, 1914
        Subfamily Histerinae Gyllenhal, 1808
        Subfamily Haeteriinae Marseul, 1857
        Subfamily Chlamydopsinae Bickhardt, 1914

Superfamily **Hydrophiloidea** Latreille, 1802
    Family Hydrophilidae Latreille, 1802
        Subfamily Hydrophilinae Latreille, 1802
        Subfamily Chaetarthriinae Bedel, 1881
        Subfamily Enochrinae Short and Fikáček, 2013
        Subfamily Acidocerinae Zaitzev, 1908
        Subfamily Cylominae Zaitzev, 1908
        Subfamily Sphaeridiinae Latreille, 1802
    Family Helophoridae Leach, 1815
    Family Epimetopidae Zaitzev, 1908
    Family Georissidae Laporte, 1840
    Family Hydrochidae Thomson, 1859
    Family Spercheidae Erichson, 1837

Superfamily **Scarabaeoidea** Latreille, 1802
    †Family Alloioscarabaeidae Bai, Ren and Yang, 2012
    †Family Septiventeridae Bai, Ren, Shih and Yang, 2013
    Family Lucanidae Latreille, 1804
        †Subfamily Protolucaninae Nikolajev, 2007
        Subfamily Aesalinae MacLeay, 1819
        †Subfamily Ceruchitinae Nikolajev, 2006
        Subfamily Syndesinae MacLeay, 1819
        Subfamily Lampriminae MacLeay, 1819
        Subfamily Lucaninae Latreille, 1804
        †Subfamily Paralucaninae Nikolajev, 2000
        †Subfamily Litholampriminae Nikolajev, 2015
    Family Trogidae MacLeay, 1819

- †Subfamily Kresnikinae Tihelka, Huang and Cai, 2019
- Subfamily Troginae MacLeay, 1819
- Subfamily Omorginae Nikolajev, 2005

Family Glaresidae Prudhomme de Borre, 1886
Family Pleocomidae LeConte-, 1861
- †Subfamily Cretocominae Nikolajev, 2002
- †Subfamily Archescarabaeinae Nikolajev, 2010
- Subfamily Pleocominae LeConte, 1861

Family Bolboceratidae Mulsant, 1842
- Subfamily Athyreinae Lynch Arribálzaga, 1878
- Subfamily Bolboceratinae Mulsant, 1842

Family Diphyllostomatidae Holloway, 1972
Family Geotrupidae Latreille, 1802
- Subfamily Taurocerastinae Germain, 1897
- Subfamily Geotrupinae Latreille, 1802

†Family Passalopalpidae Boucher and Bai, 2016
Family Passalidae Leach, 1815
- Subfamily Aulacocyclinae Kaup, 1868
- Subfamily Passalinae Leach, 1815

Family Belohinidae Paulian, 1959
Family Ochodaeidae Streubel, 1846
- †Subfamily Cretochodaeinae Nikolajev, 1995
- Subfamily Ochodaeinae Streubel, 1846
- Subfamily Chaetocanthinae Scholtz, 1988

Family Glaphyridae MacLeay, 1819
- †Subfamily Cretoglaphyrinae Nikolajev, 2005
- Subfamily Glaphyrinae MacLeay, 1819
- Subfamily Amphicominae Blanchard, 1845

Family Hybosoridae Erichson, 1847
- †Subfamily Mimaphodiinae Nikolajev, 2007
- Subfamily Anaidinae Nikolajev, 1996
- Subfamily Ceratocanthinae Martínez, 1968
- Subfamily Hybosorinae Erichson, 1847
- Subfamily Liparochrinae Ocampo, 2006
- Subfamily Pachyplectrinae Ocampo, 2006

Family Scarabaeidae Latreille, 1802
- †Subfamily Lithoscarabaeinae Nikolajev, 1992
- Subfamily Chironinae Blanchard, 1845
- Subfamily Aegialiinae Laporte, 1840
- Subfamily Eremazinae Stebnicka, 1977
- Subfamily Aphodiinae Leach, 1815
- Subfamily Aulonocneminae Janssens, 1946
- Subfamily Termitotroginae Wasmann, 1918
- Subfamily Scarabaeinae Latreille, 1802
- †Subfamily Prototroginae Nikolajev, 2000
- †Subfamily Cretoscarabaeinae Nikolajev, 1995
- Subfamily Dynamopodinae Arrow, 1911
- †Subfamily Electrorubesopsinae Bai and Wang, 2019
- Subfamily Phaenomeridinae Erichson, 1847
- Subfamily Orphninae Erichson, 1847
- Subfamily Allidiostomatinae Arrow, 1940

        - Subfamily Aclopinae Blanchard, 1850
        - Subfamily Melolonthinae Leach, 1819
        - Subfamily Oncerinae LeConte, 1861
        - Subfamily Podolasiinae Howden, 1997
        - Subfamily Rutelinae MacLeay, 1819
        - Subfamily Dynastinae MacLeay, 1819
        - Subfamily Cetoniinae Leach, 1815

- Superfamily **Staphylinoidea** Latreille, 1802
    - Family Jacobsoniidae Heller, 1926
    - Family Ptiliidae Erichson, 1845
        - Subfamily Nossidiinae Sörensson and Delgado, 2019
        - Subfamily Ptiliinae Erichson, 1845
    - Family Hydraenidae Mulsant, 1844
        - Subfamily Orchymontiinae Perkins, 1997
        - Subfamily Prosthetopinae Perkins, 1994
        - Subfamily Hydraeninae Mulsant, 1844
        - Subfamily Ochthebiinae Thomson, 1859
    - Family Colonidae Horn, 1880 (1859) **stat. nov.**
    - Family Agyrtidae Thomson, 1859
        - Subfamily Agyrtinae Thomson, 1859
        - Subfamily Necrophilinae Newton, 1997
        - Subfamily Pterolomatinae Thomson, 1862
    - Family Leiodidae Fleming, 1821 **sensu nov.**
        - Subfamily Camiarinae Jeannel, 1911
        - Subfamily Catopocerinae Hatch, 1927 (1880)
        - Subfamily Leiodinae Fleming, 1821
        - Subfamily Cholevinae Kirby, 1837
        - Subfamily Platypsyllinae Ritsema, 1869
    - Family Staphylinidae Latreille, 1802 **sensu nov.**
        - Subfamily Silphinae Latreille, 1806 **stat. nov., sensu nov.**
        - Subfamily Apateticinae Fauvel, 1895
        - Subfamily Trigonurinae Reiche, 1866
        - Subfamily Scaphidiinae Latreille, 1806
        - Subfamily Piestinae Erichson, 1839
        - Subfamily Osoriinae Erichson, 1839
        - Subfamily Oxytelinae Fleming, 1821
        - †Subfamily Protactinae Heer, 1847
        - Subfamily Omaliinae MacLeay, 1825
        - Subfamily Microsilphinae Crowson, 1950
        - Subfamily Glypholomatinae Jeannel, 1962
        - Subfamily Empelinae Newton and Thayer, 1992
        - Subfamily Proteininae Erichson, 1839
        - Subfamily Micropeplinae Leach, 1815
        - Subfamily Neophoninae Fauvel, 1905
        - Subfamily Dasycerinae Reitter, 1887
        - Subfamily Protopselaphinae Newton and Thayer, 1995
        - Subfamily Pselaphinae Latreille, 1802
        - Subfamily Mycetoporinae Thomson, 1859
        - Subfamily Tachyporinae MacLeay, 1825
        - Subfamily Phloeocharinae Erichson, 1839
        - Subfamily Trichophyinae Thomson, 1858

    - Subfamily Habrocerinae Mulsant and Rey, 1876
    - Subfamily Aleocharinae Fleming, 1821
    - Subfamily Leptotyphlinae Fauvel, 1874
    - Subfamily Oxyporinae Fleming, 1821
    - Subfamily Megalopsidiinae Leng, 1920
    - Subfamily Steninae MacLeay, 1825
    - Subfamily Euaesthetinae Thomson, 1859
    - Subfamily Solieriinae Newton and Thayer, 1992
    - Subfamily Scydmaeninae Leach, 1815
    - Subfamily Pseudopsinae Ganglbauer, 1895
    - Subfamily Olisthaerinae Thomson, 1858
    - Subfamily Paederinae Fleming, 1821
    - Subfamily Staphylininae Latreille, 1802

Series BOSTRICHIFORMIA Forbes, 1926

- Superfamily **Bostrichoidea** Latreille, 1802
  - Family Dermestidae Latreille, 1804
    - Subfamily Dermestinae Latreille, 1804
    - Subfamily Thorictinae Agassiz, 1846
    - Subfamily Orphilinae LeConte, 1861
    - Subfamily Trinodinae Casey, 1900
    - Subfamily Attageninae Laporte, 1840
    - Subfamily Megatominae Leach, 1815
  - Family Bostrichidae Latreille, 1802
    - Subfamily Endecatominae LeConte, 1861
    - Subfamily Dysidinae Lesne, 1894
    - Subfamily Polycaoninae Lesne, 1896
    - Subfamily Bostrichinae Latreille, 1802
    - Subfamily Psoinae Blanchard, 1851
    - Subfamily Dinoderinae Thomson, 1863
    - Subfamily Lyctinae Billberg, 1820
    - Subfamily Euderiinae Lesne, 1934
  - Family Ptinidae Latreille, 1802
    - Subfamily Eucradinae LeConte, 1861
    - Subfamily Ptininae Latreille, 1802
    - Subfamily Dryophilinae Gistel, 1848
    - Subfamily Ernobiinae Pic, 1912
    - Subfamily Anobiinae Fleming, 1821
    - Subfamily Ptilininae Shuckard, 1839
    - Subfamily Alvarenganiellinae Viana and Martínez, 1971
    - Subfamily Xyletininae Gistel, 1848
    - Subfamily Dorcatominae Thomson, 1859
    - Subfamily Mesocoelopodinae Mulsant and Rey, 1864

Series CUCUJIFORMIA Lameere, 1938

- Superfamily **Cleroidea** Latreille, 1802
  - Family Rentoniidae Crowson, 1966
  - Family Byturidae Gistel, 1848
    - Subfamily Byturinae Gistel, 1848
    - Subfamily Platydascillinae Pic, 1914
  - Family Biphyllidae LeConte, 1861

- Family Acanthocnemidae Crowson, 1964
- Family Protopeltidae Crowson, 1966
- Family Peltidae Kirby, 1837
- Family Lophocateridae Crowson, 1964
- Family Trogossitidae Latreille, 1802
  - Subfamily Calityinae Houlbert, 1922
  - Subfamily Egoliinae Lacordaire, 1854
  - Subfamily Larinotinae Slipinski, 1992
  - Subfamily Trogossitinae Latreille, 1802
- Family Thymalidae Léveillé, 1888
  - Subfamily Thymalinae Léveillé, 1888
  - Subfamily Decamerinae Crowson, 1964
- Family Phycosecidae Crowson, 1952
- Family Prionoceridae Lacordaire, 1857
- Family Mauroniscidae Majer, 1995
- Family Rhadalidae LeConte, 1861
  - Subfamily Gietellinae Constantin and Menier, 1987
  - Subfamily Rhadalinae LeConte, 1861
- Family Melyridae Leach, 1815
  - Subfamily Malachiinae Fleming, 1821
  - Subfamily Melyrinae Leach, 1815
  - Subfamily Dasytinae Laporte, 1840
- Family Phloiophilidae Kiesenwetter, 1863
- Family Chaetosomatidae Crowson, 1952
- Family Thanerocleridae Chapin, 1924
  - Subfamily Zenodosinae Kolibáč, 1992
  - Subfamily Thaneroclerinae Chapin, 1924
- Family Cleridae Latreille, 1802
  - Subfamily Tillinae Fischer, 1813
  - Subfamily Korynetinae Laporte, 1838
  - Subfamily Epiclininae Gunter, Leavengood and Bartlett, 2013
  - Subfamily Clerinae Latreille, 1802

Superfamily **Lymexyloidea** Fleming, 1821

- Family Lymexylidae Fleming, 1821
  - Subfamily Hylecoetinae Germar, 1818
  - Subfamily Lymexylinae Fleming, 1821
  - Subfamily Atractocerinae Laporte, 1840
  - Subfamily Melittommatinae Wheeler, 1986

Superfamily **Tenebrionoidea** Latreille, 1802

- Family Ripiphoridae Laporte, 1840
  - Subfamily Pelecotominae Guérin-Méneville, 1857
  - Subfamily Ptilophorinae Gerstaecker, 1855
  - Subfamily Hemirhipidiinae Heller, 1921
  - Subfamily Ripidiinae Gerstaecker, 1855
  - Subfamily Ripiphorinae Laporte, 1840
- Family Mordellidae Latreille, 1802
  - †Praemordellinae Ščegoleva-Barovskaya, 1929
  - Subfamily Ctenidiinae Franciscolo, 1951
  - Subfamily Mordellinae Latreille, 1802
- †Family Apotomouridae Bao, Walczynska, Moody, Wang and Rust, 2018
- Family Aderidae Csiki, 1909

Family Ischaliidae Blair, 1920
Family Trictenotomidae Blanchard, 1845
Family Scraptiidae Gistel, 1848
    Subfamily Scraptiinae Gistel, 1848
    Subfamily Anaspidinae Mulsant, 1856
Family Mycteridae Perty, 1840
    Subfamily Mycterinae Perty, 1840
    Subfamily Eurypinae Thomson, 1860
    Subfamily Hemipeplinae Lacordaire, 1854
Family Oedemeridae Latreille, 1810
    Subfamily Polypriinae Lawrence, 2005
    Subfamily Calopodinae Costa, 1852
    Subfamily Oedemerinae Latreille, 1810
Family Boridae Thomson, 1859
    Subfamily Borinae Thomson, 1859
    Subfamily Synercticinae Lawrence and Pollock, 1994
Family Pythidae Solier, 1834
Family Salpingidae Leach, 1815
    Subfamily Othniinae LeConte, 1861
    Subfamily Prostominiinae Grouvelle, 1914
    Subfamily Agleninae Horn, 1878
    Subfamily Inopeplinae Grouvelle, 1908
    Subfamily Dacoderinae LeConte, 1862
    Subfamily Aegialitinae LeConte, 1862
    Subfamily Salpinginae Leach, 1815
Family Pyrochroidae Latreille, 1806
    Subfamily Tydessinae Nikitsky, 1986
    Subfamily Pilipalpinae Abdullah, 1964
    †Subfamily Waidelotinae Bukejs, Alekseev and Pollock, 2019
    Subfamily Pedilinae Lacordaire, 1859
    Subfamily Pyrochroinae Latreille, 1806
    Subfamily Pogonocerinae Iablokov-Khnzorian, 1985
    Subfamily Agnathinae Lacordaire, 1859
Family Anthicidae Latreille, 1819
    Subfamily Eurygeniinae LeConte, 1862
    Subfamily Macratriinae LeConte, 1862
    Subfamily Steropinae Jacquelin du Val, 1863
    Subfamily Copobaeninae Abdullah, 1969
    Subfamily Lemodinae Matthews, 1987
    Subfamily Tomoderinae Bonadona, 1961
    Subfamily Anthicinae Latreille, 1819
    Subfamily Notoxinae Stephens, 1829
Family Meloidae Gyllenhal, 1810
    Subfamily Eleticinae Wellman, 1910
    Subfamily Meloinae Gyllenhal, 1810
    Subfamily Tetraonycinae Böving and Craighead, 1931
    Subfamily Nemognathinae Laporte, 1840
Family Stenotrachelidae Thomson, 1859
    Subfamily Stenotrachelinae Thomson, 1859
    Subfamily Cephaloinae LeConte, 1862
    Subfamily Nematoplinae LeConte, 1862

        - Subfamily Stoliinae Nikitsky, 1985
    - Family Tetratomidae Billberg, 1820
        - Subfamily Tetratominae Billberg, 1820
        - Subfamily Piseninae Miyatake, 1960
        - Subfamily Penthinae Lacordaire, 1859
        - Subfamily Hallomeninae Gistel, 1848
        - Subfamily Eustrophinae Gistel, 1848
    - Family Melandryidae Leach, 1815
        - Subfamily Melandryinae Leach, 1815
        - Subfamily Osphyinae Mulsant, 1856 (1839)
    - Family Synchroidae Lacordaire, 1859
    - Family Prostomidae Thomson, 1859
    - Family Ciidae Leach, 1819
        - Subfamily Sphindociinae Lawrence, 1974
        - Subfamily Ciinae Leach, 1819
    - Family Ulodidae Pascoe, 1869
    - Family Archeocrypticidae Kaszab, 1964
    - Family Pterogeniidae Crowson, 1953
    - Family Mycetophagidae Leach, 1815
        - Subfamily Esarcinae Reitter, 1882
        - Subfamily Mycetophaginae Leach, 1815
        - Subfamily Bergininae Leng, 1920
    - Family Tenebrionidae Latreille, 1802
        - Subfamily Lagriinae Latreille, 1825 (1820)
        - Subfamily Nilioninae Oken, 1843
        - Subfamily Phrenapatinae Solier, 1834
        - Subfamily Zolodininae Watt, 1975
        - Subfamily Pimeliinae Latreille, 1802
        - Subfamily Kuhitangiinae Medvedev, 1962
        - Subfamily Blaptinae Leach, 1815
        - Subfamily Tenebrioninae Latreille, 1802
        - Subfamily Alleculinae Laporte, 1840
        - Subfamily Diaperinae Latreille, 1802
        - Subfamily Stenochiinae Kirby, 1837
    - Family Zopheridae Solier, 1834
        - Subfamily Colydiinae Billberg, 1820
        - Subfamily Zopherinae Solier, 1834
    - Family Promecheilidae Lacordaire, 1859
    - Family Chalcodryidae Watt, 1974
    - Family *incertae sedis*
        - Subfamily Afreminae Levey, 1985
        - Subfamily Lagrioidinae Abdullah and Abdullah, 1968

- Superfamily **Coccinelloidea** Latreille, 1807
    - Family Bothrideridae Erichson, 1845
    - Family Cerylonidae Billberg, 1820
        - Subfamily Ostomopsinae Sen Gupta and Crowson, 1973
        - Subfamily Loeblioryloninae Ślipiński, 1990
        - Subfamily Ceryloninae Billberg, 1820
    - Family Murmidiidae Jacquelin du Val, 1858
    - Family Discolomatidae Horn, 1878
        - Subfamily Notiophyginae Jakobson, 1915

    - Subfamily Discolomatinae Horn, 1878
    - Subfamily Aphanocephalinae Jakobson, 1904
    - Subfamily Cephalophaninae John, 1954
    - Subfamily Pondonatinae John, 1954
- Family Euxestidae Grouvelle, 1908
- Family Tereditidae Seidlitz, 1888
    - Subfamily Teredinae Seidlitz, 1888
    - Subfamily Anommatinae Ganglbauer, 1899
    - Subfamily Xylariophilinae Pal and Lawrence, 1986
- Family Alexiidae Imhoff, 1856
- Family Akalyptoischiidae Lord, Hartley, Lawrence, McHugh, Whiting and Miller, 2010
- Family Latridiidae Erichson, 1842
    - Subfamily Latridiinae Erichson, 1842
    - Subfamily Corticariinae Curtis, 1829
- Family Anamorphidae Strohecker, 1953
- Family Corylophidae LeConte, 1852
    - Subfamily Periptyctinae Ślipiński, Lawrence and Tomaszewska, 2001
    - Subfamily Corylophinae LeConte, 1852
- Family Endomychidae Leach, 1815
    - Subfamily Merophysiinae Seidlitz, 1872
    - Subfamily Pleganophorinae Jacquelin du Val, 1858
    - Subfamily Leiestinae Thomson, 1863
    - Subfamily Xenomycetinae Strohecker, 1962
    - Subfamily Danascelinae Tomaszewska, 2000
    - Subfamily Cyclotominae Imhoff, 1856
    - Subfamily Endomychinae Leach, 1815
    - Subfamily Epipocinae Gorham, 1873
    - Subfamily Lycoperdininae Bromhead, 1838
- †Family Tetrameropsidae Kirejtshuk and Azar, 2008
- Family Mycetaeidae Jacquelin du Val, 1857
- Family Eupsilobiidae Casey, 1895
- Family Coccinellidae Latreille, 1807
    - Subfamily Microweiseinae Leng, 1920
    - Subfamily Monocoryninae Miyatake, 1988
    - Subfamily Coccinellinae Latreille, 1807

Superfamily **Erotyloidea** Latreille, 1802 **stat. nov.**

- Family Boganiidae Sen Gupta and Crowson, 1966
    - Subfamily Paracucujinae Endrödy-Younga and Crowson, 1986
    - Subfamily Boganiinae Sen Gupta and Crowson, 1966
- Family Erotylidae Latreille, 1802
    - Subfamily Cryptophilinae Casey, 1900
    - Subfamily Languriinae Hope, 1840
    - Subfamily Xenoscelinae Ganglbauer, 1899
    - Subfamily Pharaxonothinae Crowson, 1952
    - Subfamily Loberinae Bruce, 1951
    - Subfamily Erotylinae Latreille, 1802

Superfamily **Nitiduloidea** Latreille, 1802 **stat. nov.**

- Family Helotidae Chapuis, 1876
- Family Sphindidae Jacquelin du Val, 1860
    - †Subfamily Libanopsinae Kirejtshuk, 2015

    - Subfamily Protosphindinae Sen Gupta and Crowson, 1979
    - Subfamily Odontosphindinae Sen Gupta and Crowson, 1979
    - Subfamily Sphindiphorinae Sen Gupta and Crowson, 1979
    - Subfamily Sphindinae Jacquelin du Val, 1860
  - Family Protocucujidae Crowson, 1954
  - Family Monotomidae Laporte, 1840
    - Subfamily Rhizophaginae Redtenbacher, 1845
    - Subfamily Monotominae Laporte, 1840
  - Family Kateretidae Kirby, 1837
  - Family Nitidulidae Latreille, 1802
    - Subfamily Cryptarchinae Thomson, 1859
    - Subfamily Prometopiinae Böving and Craighead, 1931
    - Subfamily Amphicrossinae Kirejtshuk, 1986
    - Subfamily Carpophilinae Erichson, 1842
    - Subfamily Cybocephalinae Jacquelin du Val, 1858 **stat. nov.**
    - Subfamily Calonecrinae Kirejtshuk, 1982
    - Subfamily Epuraeinae Kirejtshuk, 1986
    - Subfamily Meligethinae Thomson, 1859
    - Subfamily Nitidulinae Latreille, 1802
    - Subfamily Maynipeplinae Kirejtshuk, 1998
    - Subfamily Cillaeinae Kirejtshuk and Audisio, 1986
  - Family Smicripidae Horn, 1880

- Superfamily **Cucujoidea** Latreille, 1802 **sensu nov.**
  - Family Hobartiidae Sen Gupta and Crowson, 1966
  - Family Cryptophagidae Kirby, 1826
    - Subfamily Cryptophaginae Kirby, 1826
    - Subfamily Atomariinae LeConte, 1861
  - Family Silvanidae Kirby, 1837
    - Subfamily Brontinae Blanchard, 1845
    - Subfamily Silvaninae Kirby, 1837
  - Family Cucujidae Latreille, 1802
    - Subfamily Cucujinae Latreille, 1802
    - Subfamily Pediacinae Jin, Zwick, Ślipiński, Marris, Thomas and Pang, 2020
    - Subfamily Platisinae Jin, Zwick, Slipiński, Marris, Thomas and Pang, 2020
  - Family Phloeostichidae Reitter, 1911
  - Family Agapythidae Sen Gupta and Crowson, 1969
  - Family Priasilphidae Crowson, 1973
  - Family Cavognathidae Sen Gupta and Crowson, 1966
  - Family Lamingtoniidae Sen Gupta and Crowson, 1969
  - Family Tasmosalpingidae Lawrence and Britton, 1991
  - Family Cyclaxyridae Gimmel, Leschen and Ślipiński, 2009
  - Family Passandridae Blanchard, 1845
    - †Subfamily Mesopassandrinae Jin, Ślipiński, Zhou and Pang, 2019
    - Subfamily Passandrinae Blanchard, 1845
  - Family Myraboliidae Lawrence and Britton, 1991
  - Family Phalacridae Leach, 1815
    - Subfamily Phaenocephalinae Matthews, 1899
    - Subfamily Phalacrinae Leach, 1815
  - Family Laemophloeidae Ganglbauer, 1899

Series **Cucujiformia** Lameere, 1938 ***incertae sedis***

- †Family Parandrexidae Kirejtshuk, 1994
- †Family Wabbelidae Alekseev, 2017

Superfamily **Curculionoidea** Latreille, 1802
- Family Cimberididae Gozis, 1882
- Family Nemonychidae Bedel, 1882
  - Subfamily Rhinorhynchinae Voss, 1922
  - †Subfamily Brenthorrhininae Arnoldi, 1977
  - †Subfamily Distenorrhininae Arnoldi, 1977
  - †Subfamily Eobelinae Arnoldi, 1977
  - †Subfamily Paleocartinae Legalov, 2003
  - †Subfamily Metrioxenoidinae Legalov, 2009
  - †Subfamily Cretonemonychinae Gratshev and Legalov, 2009
  - †Subfamily Selengarhynchinae Gratshev and Legalov, 2009
  - †Subfamily Slonikinae Zherikhin, 1977
  - †Subfamily Eccoptarthrinae Arnoldi, 1977
  - Subfamily Nemonychinae Bedel, 1882
- Family Anthribidae Billberg, 1820
  - Subfamily Urodontinae Thomson, 1859
  - Subfamily Choraginae Kirby, 1819
  - Subfamily Anthribinae Billberg, 1820
- Family Belidae Schönherr, 1826
  - †Subfamily Montsecbelinae Legalov, 2015
  - Subfamily Oxycoryninae Schönherr, 1840
  - Subfamily Belinae Schönherr, 1826
- †Family Mesophyletidae Poinar, 2006
  - †Subfamily Aepyceratinae Poinar, Brown and Legalov, 2017
  - †Subfamily Mesophyletinae Poinar, 2006
- Family Attelabidae Billberg, 1820
  - Subfamily Attelabinae Billberg, 1820
  - Subfamily Apoderinae Jekel, 1860
  - Subfamily Rhynchitinae Gistel, 1848
  - Subfamily Pterocolinae Lacordaire, 1865
- Family Caridae Thompson, 1992
  - †Subfamily Baissorhynchinae Zherikhin, 1993
  - Subfamily Chilecarinae Legalov, 2009
  - Subfamily Carinae Thompson, 1992
- Family Brentidae Billberg, 1820
  - Subfamily Ithycerinae Schoenherr, 1823
  - Subfamily Brentinae Billberg, 1820
  - Subfamily Microcerinae Lacordaire, 1863
  - Subfamily Eurhynchinae Lacordaire, 1863
  - Subfamily Apioninae Schönherr, 1823
  - Subfamily Nanophyinae Gistel, 1848
- Family Curculionidae Latreille, 1802
  - Subfamily Brachycerinae Billberg, 1820
  - Subfamily Dryophthorinae Schönherr, 1825
  - Subfamily Platypodinae Shuckard, 1839
  - Subfamily Bagoinae Thomson, 1859
  - Subfamily Hyperinae Marseul, 1863 (1848)
  - Subfamily Entiminae Schönherr, 1823
  - Subfamily Cyclominae Schönherr, 1826

    - Subfamily Curculioninae Latreille, 1802
    - Subfamily Baridinae Schönherr, 1836
    - Subfamily Ceutorhynchinae Gistel, 1848
    - Subfamily Conoderinae Schönherr, 1833
    - Subfamily Cossoninae Schönherr, 1825
    - Subfamily Molytinae Schönherr, 1823
    - Subfamily Cryptorhynchinae Schönherr, 1825
    - Subfamily Lixinae Schönherr, 1823
    - Subfamily Mesoptiliinae Lacordaire, 1863
    - Subfamily Scolytinae Latreille, 1804
    - Subfamily Orobitidinae Thomson, 1859
    - Subfamily Xiphaspidinae Marshall, 1920
- †Family Ulyanidae Zherikhin, 1993
- †Family Obrieniidae Zherikhin and Gratshev, 1994
    - †Subfamily Kararhynchinae Zherikhin and Gratshev, 1994
    - †Subfamily Obrieniinae Zherikhin and Gratshev, 1994
    - †Subfamily Pseudobrieniinae Legalov, 2012

Superfamily **Chrysomeloidea** Latreille, 1802

- Family Oxypeltidae Lacordaire, 1868
- Family Vesperidae Mulsant, 1839
    - Subfamily Philinae Thomson, 1861
    - Subfamily Vesperinae Mulsant, 1839
    - Subfamily Anoplodermatinae Guérin-Méneville, 1840
- Family Disteniidae Thomson, 1861
- Family Cerambycidae Latreille, 1802
    - Subfamily Dorcasominae Lacordaire, 1868
    - Subfamily Prioninae Latreille, 1802
    - Subfamily Cerambycinae Latreille, 1802
    - Subfamily Lepturinae Latreille, 1802
    - Subfamily Spondylidinae Audinet-Serville, 1832
    - Subfamily Lamiinae Latreille, 1825
- Family Megalopodidae Latreille, 1802
    - Subfamily Megalopodinae Latreille, 1802
    - Subfamily Palophaginae Kuschel and May, 1990
    - Subfamily Zeugophorinae Böving and Craighead, 1931
- Family Orsodacnidae Thomson, 1859
    - Subfamily Orsodacninae Thomson, 1859
    - Subfamily Aulacoscelidinae Chapuis, 1874
- Family Chrysomelidae Latreille, 1802
    - Subfamily Chrysomelinae Latreille, 1802
    - Subfamily Galerucinae Latreille, 1802
    - Subfamily Synetinae LeConte and Horn, 1883
    - Subfamily Sagrinae Leach, 1815
    - Subfamily Bruchinae Latreille, 1802
    - Subfamily Donaciinae Kirby, 1837
    - Subfamily Criocerinae Latreille, 1804
    - Subfamily Cassidinae Gyllenhal, 1813
    - Subfamily Eumolpinae Hope, 1840
    - Subfamily Lamprosomatinae Lacordaire, 1848
    - Subfamily Cryptocephalinae Gyllenhal, 1813
    - Subfamily Spilopyrinae Chapuis, 1874

- †Subfamily Protoscelidinae Medvedev, 1968

INCERATE SEDIS

Crown **COLEOPTERA** ***incerate sedis***

- †Subfamily Avitortorinae Nikolaev 2007

Suborder **POLYPHAGA** Emery, 1886 ***incertae sedis***

- †Family Lasiosynidae Kirejtshuk, Chang, Ren and Kun, 2010
- †Family Peltosynidae Yan, Beutel and Ponomarenko, 2018
- Family Jurodidae Ponomarenko, 1985

Phylogenetic and age justifications for fossil calibrations

Node 1: (Megaloptera + Neuroptera) **–** Coleoptera: **298.75 Ma – 324 Ma.**

Fossil taxon and specimen**:** *Stephanastus polinae* Kirejtshuk and Nel, 2013 [holotype, MNHN.A.49011 (exoskeleton with legs and elytra): Palaeoentomological Laboratory, Muséum national d'Histoire naturelle, Paris, France] from the Commentry Shales Formation in Allier, France (Nel et al. 2013).
Phylogenetic justification**:** Megaloptera and Neuroptera, along with Raphidioptera, form the clade Neuropterida, which is strongly supported by both molecular and morphology-based phylogenies. As discussed in Nel et al. (2013), the extinct *Stephanastus* (family Stephanastidae) is sister to the stem coleopterids, which include the extant Coleoptera. Since the Neuropterida is a sister group to Stephanastidae + coleopterids, the fossil species *Stephanastus polinae* is a crown group of the clade ((Megaloptera, Neuroptera), Coleoptera).
Minimum age**:** 298.75 Ma.
Soft maximum age**:** 324 Ma.
Age justification**:** *Stephanastus polinae* occurs in the Commentry Shales Formation in Allier, France. Although no geochemical dating of the fossil deposit has been carried out, the formation has been regarded as Gzhelian (late Carboniferous) based on stratigraphic evidence. The top of Gzhelian has been dated to 298.9 ± 0.15, which provides a conservative minimum constraint (298.75 Ma). The soft maximum constraint is based on the earliest occurrence of Archaeorthoptera from the early Carboniferous, which also represents the earliest known Pterygota (including almost all insects (Ectognatha), but not the Archaeognatha or the Zygentoma, two primitively wingless insect orders). This earliest pterygote fossil was described from the Upper Silesian Basin in the Czech Republic (Prokop et al. 2005). The deposit has been dated as the early Carboniferous (Namurian A/E1, ca. 324 Ma) (Jirásek et al. 2013). Regardless the alternative interpretations of the Czech specimen (Dvořák et al. 2019), the other oldest uncontested candidate for the earliest pterygote, is the practically contemporaneous palaeopteran *Delitzschala bitterfeldensis* from near Bitterfeld, Germany (Brauckmann et al. 1994; Brauckmann and Schneider 1996).

Node 2: Crown Coleoptera: **251.878 Ma – 307.1 Ma.**

Fossil taxon and specimen**:** *Ponomarenkium belmonthensis* Yan, Lawrence, Beattie and Beutel, 2018 [holotype, 40278; paratype, 41618 (exoskeletons without legs): Australian Museum, Sydney] from the Tatarian insect beds, Newcastle Coal Measures at Belmont, north of Sydney, Australia (Yan et al. 2018a, b).
Phylogenetic justification**:** This clade comprises four extant beetle suborders Adephaga, Archostemata, Myxophaga, and Polyphaga, their last common ancestor and all of its descendants, but excludes putative stem coleopterans known collectively as Protocoleoptera (Crowson 1975). Yan et al. (2018a) did not provide a formal phylogenetic analysis of *Ponomarenkium* but compared it with related fossil taxa and representatives of four modern suborders. *Ponomarenkium* lacks the ancestral broad and apically truncated prosternal process and a broad prothoracic postcoxal bridge, which suggest it as a crown group Coleoptera (Yan et al. 2018a). Specifically, *Ponomarenkium* may belong to the stem group of either Polyphaga or Myxophaga, or more likely the stem group of a clade comprising more than one of the extant suborders (Yan et al. 2018a).
Minimum age**:** 251.878 Ma.
Soft maximum age**:** 307.1 Ma.
Age justification**:** *Ponomarenkium belmonthensis* was recovered from the late Permian Tatarian insect beds located within the Upper Newcastle Coal Measures of New South Wales, Australia (Yan et al. 2018d). The Belmont insect bed was considered to be Tatarian-aged (late Permian), but no precise dating of the fossil bed has been published. The minimum age for the fossil can be taken from the top of the Changhsingian (dated at 251.902 ± 0.024 Ma), providing a conservative minimum age for *Ponomarenkium*. The earliest definitive beetle, *Coleopsis archaica* is from the early Permian of Germany (Kirejtshuk et al. 2014; Kirejtshuk and Nel 2016). Like most Permian beetles, *C. archaica* belongs to the stem group of Coleoptera. Béthoux (2009) regarded *Adiphlebia lacoana* from the Pennsylvanian (Carboniferous) of Mazon Creek as the oldest beetle, but this hypothesis was rejected based on a critical re-analysis of the anatomy and taphonomy of the fossil.

The original interpretation of *Adiphlebia* as Coleoptera by Béthoux (2009) was based on clay artefacts attached to the wing membrane (Kukalová-Peck and Beutel, 2012). The Mazon Creek Lagerstätte is one of the best records of late Palaeozoic ecosystems, which has yielded diverse insects (11 orders and more than 210 species) preserved within siderite concretions (Clements et al. 2019). Despite the high palaeodiversity of the entomofauna, no beetles, one of most diverse animal group in today's terrestrial ecosystems, have been documented. Palynological and palaeobotanical evidence indicates that the age of the Mazon Creek Lagerstätte equates to the upper part of the Moscovian stage (Clements et al. 2019), the top of which has been dated at 307.0 ± 0.1. The age 307.1 Ma thus provides a conservative soft maximum constraint.

Node 3: Gyrinidae – Haliplidae: **251.878 Ma – 293.69 Ma.**

Fossil taxon and specimen: *Tunguskagyrus planus* Yan, Beutel and Lawrence, 2018 [holotype, PIN 5381/32 (exoskeleton without legs): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Lebedevskian Horizon at the Anakit locality, which has been correlated with the Kedrovskian layers of the Maltsevo Formation, Krasnoyarsk region, Russia (Yan et al. 2018c).

Phylogenetic justification: The placement of *Tunguskagyrus planus* in the extant family Gyrinidae is supported by numerous derived features of the head, but it bears many ancestral characters, indicating it as a stem group gyrinid (Yan et al. 2018c). *Tunguskagyrus* demonstrates that the specialised lifestyle of whirligig beetles probably changed little over the past 250 million. As such, *T. planus* is the oldest record of crown group of the Gyrinidae + Haliplidae clade.

Minimum age: 251.878 Ma.

Soft maximum age: 293.69 Ma.

Age justification: *Tunguskagyrus planus* occurs in the Lebedevskian Horizon. The age of this layer was identified as either Permian or Triassic. In a recent biostratigraphical study by Sadovnikov (2016), it was attributed to the Changhsingian of the uppermost Permian. The minimum age for the fossil can be taken at the top of the Changhsingian, which is currently dated at 251.902 ± 0.024 (International Chronostratigraphic Chart, v. 2018/08). Therefore, the minimum age constraint for this node is 251.878 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

The earliest known beetle, *Coleopsis archaica* (family Coleopsidae), has been reported from the early Permian of Germany (Kirejtshuk et al. 2014). As in many Permian species and some Mesozoic early beetle species, *C. archaica* has well sclerotised elytra with remains of primary venation, which is not developed in crown group beetles. Although *C. archaica* was placed in the extant suborder Archostemata by Kirejtshuk et al. (2014), Beutel et al. (2008) conducted a morphological phylogenetic analysis that supported Tshekardocoleidae as a stem Coleoptera, sister to the other remaining extinct and extant beetles sampled in the study. Permian beetles are largely represented by extinct stem group beetle families, such as Permocupedidae and Tshekardocoleidae (Kirejtshuk et al. 2014). Recently, an intriguing well-preserved fossil beetle, *Ponomarenkia belmonthensis* Yan et al. 2018 (family Ponomarenkiumidae), was described from the mid-Permian of Australia that can be excluded from the earliest stem group coleopterans and the four extant suborders. As such, *P. belmonthensis* likely belongs to the stem group of one of the extant suborders or in the stem group of a clade comprising more than one of them (Yan et al. 2018a). Given the discussion above, the age of the oldest beetle, *Coleopsis archaica*, provides a maximum age constraint on the node. *Coleopsis archaica* was recovered from the top of the Meisenheim Formation at Grügelborn, Germany. Schneider and Werneburg (2006, 2012) proposed a Sakmarian age for this horizon based on the occurrence of the biostratigraphically important cockroach *Spiloblattina odernheimensis* Schneider. Therefore, we consider the bottom of the Sakmarian, 293.69 Ma (293.52 ± 0.17 Ma), as the soft maximum constraint.

Node 4: Dytiscidae – Noteridae: **155 Ma** – **251.878 Ma.**

Fossil taxon and specimen: *Palaeodytes gutta* Ponomarenko, 1987 [holotype, PIN2066/2654 (exoskeleton): Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chimkent Region, Chayan District, southern Kazakhstan (Ponomarenko 1987).

Phylogenetic justification: The extinct genus *Palaeodytes*, currently classified as subfamily *incertae sedis* within Dytiscidae, includes three Mesozoic species: *P. baissensis*, *P. gutta*, and *P. sibiricus* (Prokin et al. 2013). Among them, the Jurassic *P. gutta* represents the oldest unequivocal record for the genus. The phylogenetic position of *Palaeodytes* within Dytiscidae remains untested, but *P. gutta* represents a crown group of Dytiscidae + Noteridae. Ponomarenko (1963) described a dytiscid species, *Angaragabus jurassicus*, from the Lower Jurassic of Irkutsk Oblast (Russia) based on a fossil larva. A re-examination of the fossil confirmed its placement in the superfamily Dytiscoidea, but not necessarily within the extant family Dytiscidae. Instead, *A. jurassicus* probably belongs to the extinct group Liadytidae (Prokin et al. 2013).
Minimum age: 155 Ma.
Soft maximum age: 251.878 Ma.
Age justification: *Palaeodytes gutta* is from the Karabastau Formation in Karatau, Kazakhstan. The precise age of the Karabastau Formation is uncertain within the Late Jurassic, but floras (Doludenko and Orlovskaya, 1976), insects (Rohdendorf, 1968) and stratigraphy (Kirichkova and Doludenko, 1996) suggest a mid–Late Jurassic date, around 155 Ma. Zheng et al. (2018) reported an unnamed beetle belonging to the superfamily Dytiscoidea from the mid-Triassic Tongchuan entomofauna (Shaanxi, central China), which was dated as approximately 237–238 Ma. This dytiscoid fossil, characterised by a streamlined body, smooth elytra, and second abdominal sternite divided by metacoxae, closely resembles some representatives of Noteridae. The soft maximum constraint (251.878 Ma) is based on the oldest occurrence of the suborder Adephaga (a stem group of Gyrinidae) from Late Permian deposits of the Anakit area in Middle Siberia as discussed in node 3.

Node 5: Cupedidae – Torridincolidae: **235 Ma – 293.69 Ma.**

Fossil taxon and specimen: *Kirghizocupes cellulosus* Ponomarenko, 1966 [holotype, PIN 2069/107 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Madygen Formation at the Dzhailyau-Cho locality, Lyailyakskii District, Batken Region, southwest Kyrgyzstan (Ponomarenko 1966).
Phylogenetic justification: *Kirghizocupes cellulosus* was originally placed in the extinct family Triadocupedidae (Ponomarenko 1966), which is currently regarded as stem group Coleoptera sister to all four extant suborders or as a member of Archostemata (Yan et al. 2018d). Kirejtshuk et al. (2016) attributed *Kirghizocupes* to the subfamily Cupedinae (= Cupedidae *s.s.*, here adopted, *viz* Classification of beetles) based on an extensive comparative study of fossil cupedids, representing the earliest known record of the group. Although the systematic position of *K. cellulosus* among Cupedidae *s.s.* remains untested, it represents a crown group of the Cupedidae + Torridincolidae clade.
Minimum age: 235 Ma.
Soft maximum age: 293.69 Ma.
Age justification: The earliest records of *Kirghizocupes* occur in the Madygen Formation at Dzhailyau-Cho in Kyrgyzstan. The Madygen Formation was dated as Ladinian–Carnian based on the evidence of megaflora (Dobruskina 1995), but the insect assemblage, namely the orders Blattodea, Orthoptera, and Hemiptera, were suggested to be more primitive than the Carnian-aged entomofaunas from South Africa and Australia, which suggests that a Ladinian age is more probable for the Madygen Formation (Shcherbakov 2008). Recent biostratigraphic and radioisotopic data indicated a mid-Triassic age (237 ± 2 Ma, late Ladinian to early Carnian) of the Madygen Formation (Voigt et al. 2017). Thus, the minimum age constraint on the node is 235 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

Node 6: Crown Polyphaga: **237 Ma – 293.69 Ma.**

Fossil taxon and specimen: undescribed taxon of the series Elateriformia [NIGP162053 (exoskeleton without legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Ladinian Tongchuan entomofauna at Hejiafang, Shaanxi, central China (Zheng et al. 2018).
Phylogenetic justification: Although the fossil was not formally named, it is well preserved and displays many features of Elateriformia (e.g., Dascilloidea and Elateroidea), including a robust body with a distinct prosternal intercoxal process and produced hind pronotal angles. The fossil clearly represents a crown group

polyphagan.
Minimum age: 237 Ma.
Soft maximum age: 293.69 Ma.
Age justification: The elateriform beetle originates from the Tongchuan Formation in central China**.** The insect-bearing layer of this formation was dated to 237 to 238 Ma, providing a minimum age of 237 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

Node 7: Derodontidae – (Clambidae + Eucinetidae): **165 Ma – 251.878 Ma.**

Fossil taxon and specimen: *Juropeltastica sinica* Cai, Lawrence and Huang, 2014 [holotype, NIGP157738 (exoskeleton without legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2014a).
Phylogenetic justification: *Juropeltastica sinica* from the Middle Jurassic represents the only Mesozoic fossil of the family Derodontidae. Derodontidae currently comprises three subfamilies: Peltasticinae (*Peltastica*), Derodontinae (*Derodontus*), and Laricobiinae (*Laricobius* and *Nothoderodontus*). *Juropeltastica* is placed in the extant subfamily Peltasticinae based on derived characters such as its explanate pronotum and carinate elytra. Additionally, it shares with *Derodontus* the relatively narrow pronotum and densely punctate postgena, prosternum, and meso- and metaventrite. Molecular-based phylogenetic analyses of three genera of Derodontidae by McKenna et al. (2015) indicated *Laricobius* as sister to *Derodontus + Nothoderodontus*. As such, *J. sinica* with toothed, explanate pronotum and carinate elytra is a crown derodontid.
Minimum age: 165 Ma.
Soft maximum age: 251.878 Ma.
Age justification: *Juropeltastica sinica* was recovered from the Daohugou beds of the Haifanggou Formation, Inner Mongolia, from northeastern China (Huang 2016). The precise age of the Daohugou beds has been controversial (He et al. 2004; Gao and Ren, 2006; Wang et al. 2005; Zhang 2015). Ar/Ar and SHRIMP U-Pb dating indicated that the age of the intermediate-acid volcanic rock overlaying the Daohugou fossiliferous beds is approximately 164–165 Ma, and so the age of the fossil deposit is older than or equal to 165 Ma, corresponding to the Callovian of the Middle Jurassic (Chen et al. 2004), an age widely adopted by palaeoentomologists (Gao and Ren, 2006). Indeed, the fossil insects from the Daohugou beds may be correlated to those from the slightly younger deposit in Karatau (Kazakhstan) (Zhang 2015), but there is strong evidence indicating that the age of the Daohugou beds may be older (Huang 2016). As such, the most conservative age of the deposit is 165 Ma, providing a minimum age for *Juropeltastica*. The soft maximum constraint, 251.878 Ma, is based on the oldest occurrence of the suborder Adephaga from Late Permian deposits of the Anakit area in Middle Siberia as discussed in node 4.

Node 8: Clambidae – Eucinetidae: **145 Ma – 235 Ma.**

Fossil taxon and specimen: *Mesocinetus aequalis* Kirejtshuk and Ponomarenko, 2010 [holotype, PIN 4270–48, with part and counterpart; paratypes, PIN 4270–1079; PIN 4270–1071, PIN 4270–1078: Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Upper Jurassic of Shar-Teg, southwestern Mongolia (Kirejtshuk and Ponomarenko 2010).
Phylogenetic justification: The extinct genus *Mesocinetus*, along with four other extinct genera, was placed in the extinct family Mesocinetidae, which apparently has close affinity to the extant families Scirtidae and Eucinetidae (Kirejtshuk and Ponomarenko 2010). In particular, *Mesocinetus* strongly resembles extant genera of Eucinetidae, namely *Eucinetus*, in having a characteristic body form with a strongly declined head, and 5-segmented tarsi. The close morphological resemblance indicates that *Mesocinetus* is probably a member of the extant Eucinetidae, rather than Mesocinetidae. Although the phylogenetic position of *Mesocinetus* has not been formally tested, their apomorphies (e.g., declined head and long hind legs) indicate that the genus is a crown group of the Clambidae + Eucinetidae clade.
Minimum age: 145 Ma.
Soft maximum age: 235 Ma.

Age justification: *Mesocinetus aequalis* was discovered in the Shar Teg Lagerstätte in southwestern Mongolia. The deposit has not been dated geochemically but its age has been inferred from comparisons of insect assemblages among Middle-Late Jurassic entomofaunas, such as those from Karatau (Late Jurassic) and Daohugou (late Middle Jurassic) (Ponomarenko et al. 2014). The minimum age constraint on the node is thus given by the boundary between the Jurassic and the Cretaceous, *ca*. 145 Ma. The soft maximum age (*ca*. 235 Ma) is derived from the age of the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. The entomofauna of the Triassic Madygen fossil locality is dominated by beetles, which constitute one quarter of total insects collected from the Madygen Formation. Among beetles, about 90% of specimens belong to Archostemata, and polyphagans are rare, including the well-known stem group polyphagan beetles belonging to the genus *Peltosyne* Ponomarenko (Ponomarenko 1977; Yan et al. 2018d). *Peltosyne triassica* and *P. varyvrosa* are is the earliest-occurring beetles placed in the polyphagan stem group based on specific apomorphies and plesiomorphic features compared to extant lineages.

Node 9: Rhipiceridae – Dascillidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Parelateriformius communis* Yan and Wang, 2010 [holotype, NIGP, nos. 151537a, 151537b (part and counterpart of almost completely preserved beetle; legs missing, antennae partly missing): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Yan and Wang 2010).

Phylogenetic justification: The genus *Parelateriformius* has been assigned to the extinct polyphagan family Lasiosynidae, a group that apparently shares similarities with Dascillidae. While the most obvious apomorphies of Dascillidae, namely the strongly reduced lacinia and male flabellate antennae (Jin et al. 2013a), are not preserved in the fossil, it shows other important similarities with *Dascillus* (Jin et al. 2013b): presence of a distinct frontoclypeal suture, head lacking a posterior constriction, eyes large and somewhat protuberant, exposed antennal insertions; antenna 11-segmented and serrate, pronotum with a complete lateral carina, prosternum in front of procoxae long, prosternal process complete between coxae, procoxal cavities transverse and with lateral notches exposing protrochantins, mesocoxal cavities narrowly separated, metaventrite with discrimen and katepisternal sutures almost complete; hind coxae transverse with large coxal plates, 5-segmented tarsi, simple claws lacking an empodium, and abdomen with 5 ventrites. This would place it within crown Dascilloidea.

Minimum age: 165 Ma.

Soft maximum age: 235 Ma.

Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 10: Buprestidae – Byrrhidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Sinoparathyrea bimaculata* Pan, Chang and Ren, 2011 [holotype, CNU-COL-NN2010408 (exoskeleton with legs, elytra, and wings): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Pan et al. 2011).

Phylogenetic justification: *Sinoparathyrea bimaculata* was described as a member of Buprestidae and placed into the extinct subfamily Parathyreinae (Pan et al. 2011). Cai et al. (2015a), however, pointed out that the characters used to define Parathyreinae (Alekseev 1993), namely the straight katepisternal suture, may be a plesiomorphy. In fact, *Sinoparathyrea* shares a number of characters with members of Schizopodidae, a group that was included as a subfamily within Buprestidae by some authors. These include the relatively short prosternum in front of the procoxae, short and broad prosternal process, and a relatively large radial cell of the hind wing (Cai et al. 2015a). This indicates that *S. bimaculate* belongs to the crown group of Buprestidae – Byrrhidae.

Minimum age: 165 Ma.

Soft maximum age: 235 Ma.
Age justification: See node 7 for the minimum age justification of the Daohugou locality. The soft maximum is from the Madygen Formation at the Dzhailyau-Cho locality, Lyailyakskii District, Batken Region, southwest Kyrgyzstan, Central Asia, as justified in node 7.

Node 11: Dryopoidea: **112.6 Ma – 165 Ma.**

Fossil taxon and specimen: undescribed taxon of the series family Dryopidae [AMNH SA43296: American Museum of Natural History, New York, USA] from the Lower Cretaceous (Aptian) Crato Formation, northeastern Brazil (Grimaldi and Engel 2005).
Phylogenetic justification: The specimen (Fig. 10.35 in Grimaldi and Engel 2005), together with other undescribed material from the deposit, can be placed into the family Dryopidae based on its characteristic habitus, 5-segmented tarsi without lobes, and peculiar antennae with the basal segments expanded.
Minimum age: 112.6 Ma.
Soft maximum age: 165 Ma.
Age justification: The oldest fossil dryopid was recovered from the Crato Formation in the Araripe Basin, northeastern Brazil. This unit is generally agreed to date back to around the Aptian/Albian border (Martill et al. 2007). The Crato Formation has been dated using palynomorphs (Pons et al. 1990) to the Aptian. The upper boundary of the Aptian, at 113.0 Ma ± 0.4 Ma, gives a minimum date of 112.6 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 12: Crown Psephenidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Vetujinbrianax cretaceus* Cai and Huang, 2018 [holotype, NIGP168215 (amber inclusion, male): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai and Huang 2018).
Phylogenetic justification: *Vetujinbrianax cretaceus* is known from a well-preserved adult from mid-Cretaceous Burmese amber. It can be placed into the family on the basis of the following characters: body apparently soft, antennae pectinate in the males, protrochantins exposed, maxillary palps relatively long, and tarsi simple and 5-segmented. *Vetujinbrianax* can be placed in the extant subfamily Eubrianacinae based on the presence of plesiomorphic characters such as short prosternal process and paired tibial apical spurs, similar to the extant Oriental genus *Jinbrianax* (Lee et al. 2007; Cai and Huang 2018). *V. cretaceus* represents the oldest fossil record of Eubrianacinae, as well as the first definitive adult fossil of Psephenidae from the Mesozoic. Further specimens of psephenid larvae, also belonging to the subfamily Eubrianacinae from Burmese amber were reported by Bao et al. (2018) and described as *Succinumanax birmaniasis*. They represent the oldest fossil record of Psephenidae, and show a high similarity in morphology with fossils from the Eocene Messel pit, Germany. A phylogenetic analysis demonstrated that *S. birmaniasis* and the Messel specimen can be placed in Psephenidae.
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: The specimen is preserved in Burmese amber (burmite) mined in the Hukawng Valley, Kachin State, northern Myanmar. Volcanoclastic matrix from the amber-bearing horizon was dated radiometrically at 98.79 ± 0.62 Ma (Shi et al. 2012), although this estimate should be taken as a minimum age (Mao et al. 2018). A mid-Cretaceous age is consistent with paleontological evidence (Grimaldi et al. 2002). The discovery of an ammonite in the amber indicates that it is at most Albian in age (Yu et al., 2019). Here we use 98.17 Ma as the conservative minimum age of Burmese amber from northern Myanmar. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 13: Elmidae – (Limnichidae + Heteroceridae): **105 Ma – 165 Ma.**

Fossil taxon and specimen: *Elmadulescens rugosus* Peris, Maier and Sánchez-García, 2015 [holotype, CES–

567 (amber inclusion): Institut de Recerca de la Biodiversitat (IRBio), Facultat de Geologia, Universitat de Barcelona, Martí i Franquès s/n, 08028 Barcelona, Spain] El Soplao amber outcrop located of the El Soplao Cave, Celis, Cantabria, Spain (Peris et al. 2015a).
Phylogenetic justification: *Elmadulescens rugosus* can be placed into Elmidae on the basis of its long, slender and widely inserted antennae, large and protuberant eyes, a pentagonal scutellum abruptly elevated anteriorly, long legs with elongate and simple 5-segmented tarsi, metacoxae with a posterior face, pronotum with complete lateral carinae, the last tarsomere longer than the other four combined, large pretarsal claws, and five abdominal ventrites (Peris et al. 2015a). The holotype is preserved in a transparent amber piece, but is dorsal-ventrally compressed and deformed, making the observation of some characters difficult.
Minimum age: 105 Ma
Soft maximum age: 165 Ma
Age justification: The amber piece was found in Early Albian strata of the Las Peñosas Formation, as determined by biostratigraphy (Najarro et al. 2009). The minimum age is derived from the upper Albian. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 14: Crown Heteroceridae: **122.2 Ma – 165 Ma.**

Fossil taxon and specimen: *Heterocerites magnus* Prokin and Ren, 2011 [holotype, CNU-COL-LB-2010023 (impression of adult beetle with party preserved legs and mandibles): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Prokin and Ren 2011).
Phylogenetic justification: The fossil species from the Yixian Formation was placed in the formal genus *Heterocerites* erected by Ponomarenko (1986) for compression fossils of putative heterocerids. While the genus is probably not monophyletic (Li et al. 2020a), *H. magnus* can be placed into Heteroceridae on the basis of having a densely pubescent body, large head with remnants of prominent mandibles and labrum, characteristically modified antennae with the distal half forming a loosely serrated club, a series of spine at the outer edges of the tibiae, short mesosternum, and stridulate ridges on ventrite 1 (Clarke 1973; Vanin et al. 2016). The dark elytra moreover possess tree pairs of light spots, a pattern similar to those found in extant members of the family (Vanin et al. 2016).
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: Diverse and abundant fossils of the terrestrial Jehol Biota have been discovered from the Yixian Formation and the overlying Jiufotang Formation in Inner Mongolia, Hebei Province and Liaoning Province, northeastern China. The Yixian Formation is Early Cretaceous in age. ^{40}Ar/^{39}Ar dating produced a mean age of 124.6 ± 0.1 Ma for sanidine from one tuff interbedded in the fossiliferous horizons of the lower Yixian Formation near Jianshangou village, and 40Ar/39Ar single- grain total fusion analyses provided an age of 124.6 ± 0.25 Ma for the same tuff from Sihetun village (Swisher et al. 1999). Chang et al. (2009) provided a high precision ^{40}Ar/^{39}Ar dating of the Yixian Formation: the lowest part of the main fossil bed was dated as 124.1± 0.3 Ma, while the uppermost part of the bed was dated as 122.9 ± 0.7 Ma. The latter age provides a conservative minimum constraint on the node, 122.2 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 15: Artematopodidae – Omethidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Sinobrevipogon jurassicus* Cai, Lawrence, Ślipiński and Huang, 2015 [holotype, NIGP160704; paratypes, NIGP160705, NIGP160706 (holotype nearly completely preserved adult beetle, with both dorsal and ventral characters visible, including hindwings); paratype NIGP160705 (displays mainly ventral and some dorsal characters); paratype NIGP160706 (shows mainly dorsal and a few ventral characters such as abdominal ventrites): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2015b).
Phylogenetic justification: *Sinobrevipogon jurassicus* exhibits a number of defining features of

Artematopodidae, including the presence of paired carinae on the prosternum and an internal apical interlocking tongue on the ventral side of each elytron. However, it differs from modern members of Artematopodidae by having the mesocoxal cavities closed by the mesepimeron and the anterolateral edge of metanepisternum. A morphological phylogenetic analysis nonetheless recovered *Sinobrevipogon* within crown Artematopodidae (Cai et al. 2015b; 2020).
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: See node 7 for minimum age justification. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 16: Throscidae – Eucnemidae: **125 Ma – 235 Ma.**

Fossil taxon and specimen: *Potergosoma gratiosum* Kovalev and Kirejtshuk, 2013 [holotype, "750" (amber inclusion, probably male): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kovalev et al. 2013; Li et al. 2020b).
Phylogenetic justification: *Potergosoma gratiosum* possesses clear diagnostic characters of the Throscidae, some regarded as apomorphies of the family. These are the developed metacoxal plates, exposed and heavily sclerotised labrum, antennae with distinctly enlarged apical antennomeres forming an elongate antennal club, characteristic grooves on the underside for receiving antennae and legs, wide prosternal process, and rather widely separated mesocoxae. The genus also possesses several plesiomorphies: complete lateral pronotal carinae, absence of tarsal grooves, simple tarsomere 4, simple tibiae, poorly developed pro-mesothoracic leg impressions, antennal fossae and distinct serial elytral punctures (Muona 2019). Morphological phylogenetic analyses recovered *Potergosoma* as a member of stem Throscidae (Muona 2019; Li et al. 2020b), making it suitable for calibrating the split between Throscidae and Eucnemidae.
Minimum age: 125 Ma.
Soft maximum age: 235 Ma.
Age justification: Krzemiski et al. (2014) indicated a Barremian age for the amber-bearing outcrop at Hammana – Mdeirij in central Lebanon. A recent biostratigraphic study of Lebanese amber by Maksoud et al. (2017) indicated that the pieces of amber with bioinclusions from the middle and upper intervals may have been reworked from the lower interval, so the age of the amber from "Grès du Liban" could be early Barremian or even older in age. As such, the minimum age for *E*. *rugidorsum* can be taken from the top of the Barremian, which is currently estimated at 125.0 Ma (International Chronostratigraphic Chart, v. 2018/08), representing the minimum age constraint for this node. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 17: *Osslimus* (Elateridae) **–** Lycidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Burmolycus compactus* Bocak, Li and Ellenberger, 2019 [holotype, MB.I 7319 (amber inclusion, female): Museum für Naturkunde, Berlin, Germany] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Bocak et al. 2019).
Phylogenetic justification: *Burmolycus compactus* can be placed into the family Lycidae on the basis of having 11-segmented antennae, a ridged pronotum, a very short and transverse prosternum, 5-segmented tarsi, and tarsomeres 2–4 lobed (Bocak and Bocakova 2008, 2010). It can further be assigned to the extant subfamily Dexorinae based on the presence of a prolonged cranium, frontally inserted antennae, antennomere 2 relatively long compared to the antennomere 3, hypognathous head, rounded mouthpart cavity, reduced labium with 1 or 2-segmented labial palpi, and femora obliquely attached to trochanters (Bocak et al. 2019). Other lycids belonging to extant and extinct taxa are known from Burmese amber, making them likewise suitable candidates for calibration of the node (Tihelka et al. 2019; Kazantsev 2019).
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: See node 12 for minimum age justification. The maximum age constraint is based on the

Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 18: Lampyridae – Phengodidae + Rhagophthalmidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Protoluciola albertalleni* Kazantsev, 2015 [holotype, ICM-BU-1687–1 (amber inclusion, male): Insect Centre, Moscow, Russia] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Kazantsev 2015).
Phylogenetic justification: *Protoluciola albertalleni* can be placed into the extant lampyrid subfamily Luciolinae based on the presence of six ventrites, genital segment apparently absent, the presence of a photic organ on the abdomen, 11-segmented antennae inserted anteriorly to the eyes, and five-segmented tarsi with simple claws (McDermott 1964).
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: See node 12 for minimum age justification. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 19: Crown Cantharidae: **105 Ma – 165 Ma.**

Fossil taxon and specimen: *Molliberus albae* Peris and Fanti, 2018 [holotype, CES-522 (amber inclusion): laboratory of the El Soplao Cave, Celis-Rábago, Cantabria, Spain) from Early Cretaceous Spanish amber originating from the El Soplao deposit, Celis municipality, Cantabria, Spain (Peris and Fanti 2018).
Phylogenetic justification: *Molliberus albae* can be placed into the extant subfamily Cantharinae based on the maxillary palpomeres different in length to the last securiform segment, long elytra, symmetrical last abdominal segments, prothorax without lateral processes, the presence of tibial spurs, and the fourth tarsomere undivided (Peris and Fanti 2018). As such, it represents the earliest member of crown Cantharidae.
Minimum age: 105 Ma.
Soft maximum age: 165 Ma.
Age justification: See node 13 for minimum age justification. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 20: Georissidae – Hydrophilidae: **147.28 Ma – 235 Ma.**

Fossil taxon and specimen: *Protochares brevipalpis* Fikáček, Prokin, Yan, Yue, Wang, Ren and Beattie, 2014 [holotype, AMF109568 (exoskeleton preserved in dorsal aspect, with fragments of legs): Department of Earth Sciences, Australian Museum, Sydney, Australia] from Talbragar fossil fish bed, *ca*. 14 km NNW of Ulan, New South Wales, Australia (Fikáček et al. 2014).
Phylogenetic justification: *Protochares brevipalpis* can be assigned to Hydrophilidae based on the unique combination of the following characters: labrum well-sclerotised and largely exposed, clypeus large and with distinct frontoclypeal sutures reaching the lateral margin of the head closely before eyes, scutellum triangular, and head not strongly constricted behind the eyes (Fikáček et al. 2012, 2014).
Minimum age: 147.28 Ma.
Soft maximum age: 235 Ma.
Age justification: Dating the Jurassic Talbragar Lagerstätten fish beds has traditionally been contentious because no palynofloras have been recovered from the beds themselves as the rocks are highly oxidised. SHRIMP dating indicated an age of 151.55 ± 4.27 Ma (Bean 2006). This provides a conservative minimum age constraint on the node. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 21: Trogidae – Lucanidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Juraesalus atavus* Nikolajev, Wang, Liu and Zhang, 2011 [holotype, NIGP 152456 (exoskeleton with legs, preserved in ventral aspect): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Nikolajev et al. 2011).

Phylogenetic justification: *Juraesalus atavus* can be placed into Lucanidae based on the presence of well-developed and somewhat projecting antennae, a complete prosternal process, concealed trochantins, procoxal cavities strongly transverse, closed externally, open internally, mesocoxal cavities narrowly separated and laterally open, 5-segmented tarsi, and a rather elongate and subglabrous body (Holloway 1960, 1969). Nikolajev et al. (2011) considered the fossil to represent a stem group to the extant subfamily Aesalinae based on the presence of a 3-segmented non-lamellate club, mandibles produced beyond apex of clypeus, eyes not divided by canthus, and abdomen with 5 ventrites. However, Kim and Farrell (2015) pointed out that these characters are not unique to Aesalinae and instead considered *J. atavus* to be the oldest member of Lucanidae *s.s.* In either way, the fossil would be suitable for calibrating the split between Trogidae and Lucanidae.
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 22: Passalidae – Geotrupidae: **122.2 Ma – 165 Ma.**

Fossil taxon and specimen: *Parageotrupes incanus* Nikolajev and Ren, 2010 [holotype, CNU-COL-LB2009751 (exoskeleton with partly preserved legs and antennae): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Nikolajev and Ren 2010).
Phylogenetic justification: *Parageotrupes incanus* can be placed into Geotrupidae on the basis of the size and the oval shape of the body, mandibles not hidden by a clypeus, eyes divided by canthus, pygidium hidden by elytra. The clypeus bears a tubercle and is clearly delimited from the vertex, suggesting that the species belongs to the extant subfamily Geotrupinae (Nikolajev and Ren 2010).
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 23: Hybosoridae – Scarabaeidae: **155 Ma – 235 Ma.**

Fossil taxon and specimen: *Protohybosorus grandissimus* Nikolajev, 2010 [holotype, PIN no. 2335/25 (exoskeleton with fragments of legs and antennae): from Karatau–Mikhailovka, Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chayan District, Chimkent Region, southern Kazakhstan (Nikolajev 2010)
Phylogenetic justification: The genus *Protohybosorus*, containing three species, can be assigned to Hybosoridae based on the small size of the species, their developed eyes, labrum and mandibles produced beyond the apex of the clypeus, trapezoidal and convex pronotum with base wider than the elytral base, elytra convex and with well-defined striae, protibia with three teeth, mesotibia and metatibia somewhat dilated at the apex, mesotibia with 2 subequal spurs, mesotibia and metatibia without a transverse carina, and abdomen with five visible sternites (Jameson 2012; Ocampo 2006; Yan et al. 2012).
Minimum age: 155 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of Karatau, see node 5. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 24: Ptiliidae – Hydraenidae: **182 Ma – 235 Ma.**

Fossil taxon and specimen: *Ochtebiites minor* Ponomarenko, 1985 [holotype, PIN 2245/278 (exoskeleton in dorsal and ventral aspect, with fragments of legs): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from trench 82an, Lyagush'ye locality, Kemerovo, Abasheva Formation, Kemerovo

Oblast, Russia (Ponomarenko 1985).
Phylogenetic justification**:** The oldest known representative of the family Hydraenidae is *Ochtebiites minor*. It can be placed in the family based on its small size, elongate body, elongate maxillary palpi, and the presence of an intercoxal sternite between the metacoxae (Jäch et al. 2016).
Minimum age**:** 182 Ma.
Soft maximum age**:** 235 Ma.
Age justification**:** The Abasheva Formation appears to be Pliensbachian in age, based on the fossil flora and fauna (Kovalev 1981; Mogutcheva 2009). The top of the Pliensbachian is 182.7 ± 0.7 (International Chronostratigraphic Chart, v. 2018/08), giving a minimum constraint of 182 Ma. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 25: Agyrtidae – Leiodidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen**:** *Mesecanus communis* Ponomarenko, 1977 [holotype, PIN 3000/926 (exoskeleton with preserved appendages in dorsal and ventral aspects); paratypes, PIN 3000/915, 3000/913, 3000/909, 2744/12: Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia], from Novospasskoye village, Ichetuy Formation, Buryat, Russia (Ponomarenko, 1977; Perkovsky 1999).
Phylogenetic justification**:** The systematic placement of *Mesecanus communis* has been historically quite unstable. Ponomarenko (1977) placed the species into Agyrtidae, while Perkovsky (1999) assigned the fossil to Leiodidae. It was treated as an agyrtid again by Newton (1997). It nonetheless meets all the diagnostic features of Agyrtidae, and we consider it as a member of this group. It has been compared to the extant genus *Ecanus* by Newton (1997)
Minimum age**:** 165 Ma.
Soft maximum age**:** 235 Ma.
Age justification**:** The Novospasskoye locality is usually considered Upper to Middle Jurassic based on biostratigraphy (Ponomarenko 1993). We thus use 166.1 ±1.2 as a conservative constraint on the node, representing the upper boundary of the Callovian, the last stage of the Middle Jurassic (International Chronostratigraphic Chart, v. 2018/08). The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 26: Crown Staphylinidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen**:** undescribed member of Silphidae [NIGP 156145a/b (exoskeleton with preserved appendages): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2014b).
Phylogenetic justification**:** The undescribed specimens can be placed into the former family Silphidae, treated here as a subfamily of Staphylinidae *sensu nov.*, based on their general habitus, clubbed antennae, large mesoscutellum, truncate elytra, and well-separated mesocoxae (Cai et al. 2014b). Given that it has been recently demonstrated that the enigmatic *Leehermania prorova* from the Late Triassic Cow Branch Formation on the Virginia-North Carolina border, USA is in fact not a staphylinid as assumed previously, these burying beetles are the oldest candidates for calibrating the node representing crown Staphylinidae (Chatzimanolis et al. 2012; Fikáček et al. 2020).
Minimum age**:** 165 Ma.
Soft maximum age**:** 235 Ma.
Age justification**:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 27: *Megalopaederus* (Paederinae) – Staphylininae: **122.2 Ma – 165 Ma.**

Fossil taxon and specimen**:** *Megolisthaerus minor* Cai and Huang, 2013 [holotype, NIGP 153697 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Cai and Huang

2013).
Phylogenetic justification: *Megolisthaerus minor* can be placed into Staphylininae on the basis of its relatively large and elongate body, antennae inserted along the anterior margin of the head, pronotal hypomeron lacking postcoxal processes; pro- and mesotarsi 5-segmented, elytron without epipleural keel, and two pairs of paratergites on abdominal segment III–VI (Cai and Huang 2013).
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 28: Silphinae – Staphylinidae *partim*: **165 Ma – 235 Ma.**

Fossil taxon and specimen: As for node 25.
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: As for node 25.

Node 29: Staphylinidae: Apateticinae – Osoriinae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Mesallotrochus longiantennatus* Cai and Huang, 2015 [holotype, NIGP157737 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai and Huang 2015)
Phylogenetic justification: *Mesallotrochus* is placed in the extant osoriine tribe Thoracophorini based on its general habitus, the protibia with the inner edge straight, missing ctenidium, exposed protrochantins, open procoxal cavities, and a more or less flattened body (Cai and Huang 2015). As such, *M. longiantennatus* represents the oldest member of Osoriinae and is suitable for calibrating the split between Apateticinae and Osoriinae.
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 30: Crown Bostrichoidea: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Paradermestes jurassicus* Deng, Ślipiński, Ren and Pang, 2017 [CNU-COL-NN2017001 (exoskeleton) with legs and antennae: Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Deng et al. 2017a).
Phylogenetic justification: *Paradermestes* can be placed into Dermestidae on the basis of having a small deflexed head inserted into the prothorax, a developed antennal club, posterior angles of pronotum projecting posteriorly, excavate metacoxae, and simple tarsomeres. Given its age, it is a suitable calibration point for setting the minimum age of Bostrichoidea (Kirejshuk and Azar 2009).
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 31: Crown Bostrichidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Poinarinius burmaensis* Legalov, 2018 [holotype ISEA no. MA2018/3 (amber inclusion): Institute of Systematics and Ecology of Animals, Novosibirsk, Russia] lowermost Cenomanian, from

an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Legalov 2018)
Phylogenetic justification: *Poinarinius* can be placed into Bostrichidae based on its non- pseudotetramerous tarsi, head lacking paired ocelli, mesocoxal cavities closed laterally, short and triangular metatrochanter, and the femur partially separated from the coxa. Based on the protibia with one apical spine and subequal tarsomeres 1 and 2, the fossil was assigned into the extant subfamily Dinoderinae (Legalov 2018).
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 32: Crown Ptinidae: **105 Ma – 165 Ma.**

Fossil taxon and specimen: *Actenobius magneoculus* Peris, Philips, and Delclòs, 2015 [holotype, SJ-10-18, SJ (amber inclusion): San Just amber collection, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain] from the San Just outcrop, Utrillas, Regachuelo Member, Escucha Formation, Teruel Province, Spain (Peris et al. 2015b).
Phylogenetic justification: *Actenobius magneoculus* is placed in the family Ptinidae by its cylindrical body, deflexed head inserted into the prothorax and covered dorsally by the pronotum; antennae with 11 antennomeres and with the last three segments asymmetrically elongated, large compound eyes, reduced prosternum lengthwise and pronotum convex dorsally, ovoid pro- and mesocoxae, transverse and excavated hind coxae for reception of metafemora, slender femora and tibiae, tarsal formula 5-5-5, and tarsomere 1 longer than tarsomere 5 (Lawrence and Britton 1991; Philips and Bell 2010). It can be assigned to Anobiinae based on the metaventrite and first abdominal segment without grooves for the reception of hind legs, complete lateral border of pronotum, and hypognathous head with mandibles not near the metaventrite with the head retracted (Español 1992)
Minimum age: 105 Ma.
Soft maximum age: 165 Ma.
Age justification: The amber from San Just is early to middle Albian in age based on palynomorph correlation of the Escucha Formation (Peñalver and Delclòs 2010). We thus use 105 Ma as a conservative minimum on the age of the amber deposit. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 33: Thanerocleridae **–** Cleridae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Wangweiella calloviana* Kolibáč and Huang, 2016 [holotype, NIGP162533 (exoskeleton with fragments of legs and antennae): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Kolibáč and Huang 2016).
Phylogenetic justification: *Wangweiella calloviana* can be placed into the clerid subfamily Epiclininae based on its elongate pedicel, absence of paracoxal sutures, basitarsus shortened but not covered from above with the base of tarsomere 2, and tegmen composed of two parts. A morphological phylogenetic analysis recovered the species as sister to the rest of Epiclininae (Kolibáč and Huang 2016), making it suitable for calibrating the split between Thanerocleridae and Cleridae.
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 34: Prionoceridae **–** Melyridae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Idgiaites jurassicus* Liu, Ślipiński, Leschen, Ren and Pang, 2015 [holotype: CNU-

COL-NN2010238 (nearly complete exoskeleton in lateral position): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Liu et al. 2015).
Phylogenetic justification: *Idgiaites jurassicus* belongs to Prionoceridae based on the general body shape and the 11-segmented antenna with three apical segments flattened and the apical segment enlarged (Liu et al. 2015).
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 35: Lymexylidae: **112.6 Ma – 235 Ma.**

Fossil taxon and specimen: *Cratoatractocerus grimaldii* Wolf, 2011 [holotype SMNS-66534 (exoskeleton with fragments of appendages): Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany] from the vicinity of Nova Olinda, southern Ceará, Nova Olinda Member of the Crato Formation, north-east Brazil (Wolf 2011).
Phylogenetic justification: *Cratoatractocerus grimaldii* can be placed into Lymexylidae and the subfamily Atractocerinae based on its long and slender body form, large eyes that occupy almost the entire frons and are narrowly separated, absence of the first radial crossvein, and heavily sclerotised female genitalia (Kurosawa 1985; Wheeler 1986; Wolf 2011).
Minimum age: 112.6 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Crato Formation, see node 11. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 36: Crown Tenebrionoidea: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Archaeoripiphorus nuwa* Hsiao, Yu and Deng, 2017 [holotype: CNU-C-NN-2006841 (exoskeleton with fragments of appendages): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Hsiao et al. 2017).
Phylogenetic justification: *Archaeoripiphorus* was considered to represent a member of Rhipiphoridae by Hsiao et al. (2017) based mainly on overall morphological similarity. Batelka et al. (2018) reviewed the evidence for the classification of the genus and concluded that it cannot be placed into Rhipiphoridae with certainty. It however clearly is a member of Tenebrionoidea, as indicated by its wedge-shaped body and tarsal formula 5-5-4, and is herein used to calibrate the node representing crown Tenebrionoidea.
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 37: Rhipiphoridae – Mordellidae: **98.17 Ma – 235 Ma.**

Fossil taxon and specimen: *Protoripidius burmiticus* Cai, Yin and Huang, 2018 [holotype, NIGP166155 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai et al. 2018a)
Phylogenetic justification: *Protoripidius burmiticus* can be assigned to the rhipiphorid subfamily Ripidiinae based on the combination of the following characters: abdominal sternite II visible externally and similar to

sternite III, eyes coarsely facetted, elytra shortened in the male and widely separated, hind wings not folded transversely, tibial spurs completely absent, claws simple, and body densely clothed with short setae (Falin and Engel 2010; Cai et al. 2018a).
Minimum age: 98.17 Ma.
Soft maximum age: 235 Ma.
Age justification: For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 38: Ischaliidae – Aderidae: **125 Ma – 165 Ma.**

Fossil taxon and specimen: nine undescribed fossils [“JG 204/15”, “96”, “1282”, “AD4A”, “1521”, “1239”, “853-F”, “NBS-2F”, “822” (amber inclusions of various degrees of preservation): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Nabaa Es-Sukkar – Brissa, Hammana – Mdeirij, Ain Dara, Rihane, and Jouar Es-Souss (Bkassine) outcrops, Lebanon (Kirejtshuk and Azar 2013).
Phylogenetic justification: Kirejtshuk and Azar (2013) cite nine members of the family Aderidae from Cretaceous Lebanese amber. The presence of aderids in Lebanese amber was also noted by Grimaldi and Engel (2005).
Minimum age: 125 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 39: Salpingidae – Pythidae: **53 Ma – 165 Ma.**

Fossil taxon and specimen: *Eopeplus stetzenkoi* Kirejtshuk and Nel, 2009 [holotype, PA 891/3 (amber inclusion): Laboratoire de Paléontologie, Muséum National d’Histoire Naturelle, Paris, France] from Eocene French amber obtained from the Farm Le Quesnoy locality, Chevrière, region of Creil, Oise department, northern France (Kirejtshuk and Nel 2009).
Phylogenetic justification: *Eopeplus stetzenkoi* can be placed into the salpingid subfamily Inopeplinae based on its flattened body, pronotum distinctly narrowing posteriorly, and shortened elytra. It moreover shares with recent representatives of the group the shape of the head, structure of antennae, and others (Kirejtshuk and Nel 2009).
Minimum age: 53 Ma.
Soft maximum age: 165 Ma.
Age justification: The age of Oise amber, approximately 53 Ma is indicated by the presence of mammalian fossils corresponding to the MP7 horizon (Kirejtshuk and Nel 2009). The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 40: Anthicidae – Meloidae: **125 Ma – 165 Ma.**

Fossil taxon and specimen: *Camelomorpha longicervix* Kirejtshuk, Azar and Telnov, 2008 [holotype, “846” (amber inclusion, sex undefinable): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk and Azar 2008).
Phylogenetic justification: *Camelomorpha longicervix* can be placed into the anthicid subfamily Macratriinae based on its elongate body, absence of a frontoclypeal suture, elytra with distinct longitudinal sulcus along the lateral margins and parallel to epipleura, mesosternum and mesepisterna fused, without an apparent carina at fusion line (Chandler 2010). It is thus suitable for calibrating the split between Anthicidae and Meloidae.
Minimum age: 125 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Lebanese amber, see node 16. The maximum age

constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 41: Crown Zopheridae: **98.17 Ma – 165 Ma.**
Fossil taxon and specimen: *Paleoendeitoma antennata* Deng, Ślipiński, Ren and Pang, 2017 [holotype, CNU-COL-MA-0312; paratype, CNU-COL-MA-0313 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Deng et al. 2017b).
Phylogenetic justification: *Paleoendeitoma* can be placed in Zopheridae, subfamily Colydiinae, based on the antennal insertions concealed by frontal ridges, antennae distinctly clubbed with antennomere 3 as broad as the pedicel, procoxal cavities lacking lateral extensions, procoxae rounded with concealed trochantins, mesocoxae rounded with their cavities externally closed by sterna and the mesotrochantins concealed, abdomen with five ventrites, legs with visible trochanters and 4-segmented tarsi (Deng et al. 2017b).
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 42: Crown Tenebrionidae: **122.2 Ma – 165 Ma.**
Fossil taxon and specimen: *Alphitopsis initialis* Kirejtshuk, Nabozhenko and Nel, 2011 [holotype, "A 31966" (exoskeleton with legs and fragments of antennae): Henan Geological Museum, Zhengzhou, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Kirejtshuk et al. 2011).
Phylogenetic justification: The species has been assigned to the subfamily Alleculinae and tribe Gonoderini based on its five visible abdominal ventrites, simple tarsomeres without membranous ventral lobes, serrate antennae, and shape of pronotum and the body (Kirejtshuk et al. 2011). It is thus suitable for calibrating the node representing Crown Tenebrionidae.
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 43: Alexiidae – Latridiidae: **125 Ma – 165 Ma.**
Fossil taxon and specimen: *Tetrameropsis mesozoica* Kirejtshuk and Azar, 2008 [holotype, "474A" (amber inclusion, sex indeterminate) Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk and Azar 2008).
Phylogenetic justification: The habitus of the species corresponds to corticariine Latridiidae (Shockley and Alekseev 2014). It was initially placed into its own subfamily, which was later raised to family level by Shockley and Alekseev (2014) where it has been hypothesised to be related to Latridiidae or Latridiidae + Akalyptoischiidae. In either case, the fossil is suitable for calibrating the split between Alexiidae and Latridiidae.
Minimum age: 125 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 44: Crown Endomychidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen: *Palaeomycetes foveolatus* Tomaszewska, Ślipiński and Ren, 2018 [holotype, CNU008072 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Tomaszewska et al. 2018).
Phylogenetic justification: *Palaeomycetes* can be placed into crown Endomychidae based on having a frontoclypeal suture, lacking antennal grooves, antenna 11-segmented with a club, pronotum with transverse basal and longitudinal paired lateral sulci, visible portion of procoxae globular, procoxae separated by prosternal process, mesocoxal cavities externally open, metaventral paired postcoxal openings usually present, elytral epipleura well-developed, tarsi 4-segmented, abdominal ventrite 1 at least as long as ventrites 2 and 3 combined, and abdominal postcoxal lines absent (Tomaszewska 2000; Robertson et al. 2015)
Minimum age: 98.17 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 45: Crown Coccinellidae: **53 Ma – 125 Ma.**

Fossil taxon and specimen: *Rhyzobius antiquus* Kirejtshuk and Nel, 2012 [holotype, MNHN PA 11862 (amber inclusion): Muséum National d'Histoire Naturelle, Paris, France] from Eocene French amber obtained from the Farm Le Quesnoy locality, Chevrière, region of Creil, Oise department, northern France (Kirejtshuk and Nel 2012).
Phylogenetic justification: Affinity to Coccinellidae is indicated a broadly rounded body with a convex dorsum and flattened ventral side, clubbed antennae, the presence of a postcoxal line on the first abdominal ventrite, and pseudotrimerous tarsi (Kirejtshuk and Nel 2012).
Minimum age: 53 Ma.
Soft maximum age: 98.17 Ma.
Age justification: For the minimum age justification of Eocene Oise amber, see node 38. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 46: Boganiidae – Erotylidae: **165 Ma – 235 Ma.**

Fossil taxon and specimen: *Palaeoboganium jurassicum* Liu, Ślipiński, Lawrence, Ren and Pang, 2018 [holotype, CNU-COL-NN201601PC (exoskeleton with appendages): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Liu et al. 2018).
Phylogenetic justification: *Palaeoboganium jurassicum* is the earliest fossil representative of the family Boganiidae, as indicated by the head with an arcuate frontoclypeal suture, labrum not visible externally, mandible with a dorsal tubercle fitting into a depression on lateral edge of clypeus, subantennal grooves absent, antennae short and weakly capitate, pro- and mesocoxae with exposed trochantins, metacoxae narrowly separated and, not extending laterally to meet elytra, and abdomen with five freely articulated ventrites. A phylogenetic analysis of adult external characters recovered *Palaeoboganium* as the sister group of *Paracucujus* and *Metacucujus* (Liu et al. 2018), making it suitable for calibrating the split between Boganiidae and Erotylidae.
Minimum age: 165 Ma.
Soft maximum age: 235 Ma.
Age justification: See node 7 for the minimum age justification of the Daohugou locality. The soft maximum is from the Madygen Formation at the Dzhailyau-Cho locality, Lyailyakskii District, Batken Region, southwest Kyrgyzstan, Central Asia, as justified in node 7.

Node 47: Helotidae – (Protocucujidae + Sphindidae): **125 Ma – 235 Ma.**

Fossil taxon and specimen**:** *Libanopsis poinari* Kirejtshuk, 2015 [holotype, “841 BC” (amber inclusion): Lebanese University, Faculty of Sciences II, Department of Natural Sciences, Beirut, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk et al. 2015a).

Phylogenetic justification**:** *Libanopsis poinari* can be placed within Sphindidae based on the sparse sculpture of dorsal integument, large coarsely faceted eyes, antennal morphology, undulate lateral pronotal carinas, and small serration in pretarsal claws (Kirejtshuk et al. 2015a).

Minimum age**:** 125 Ma.

Soft maximum age**:** 235 Ma.

Age justification**:** For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 48: Monotomidae – (Kateretidae + Nitidulidae): **165 Ma – 235 Ma.**

Fossil taxon and specimen**:** *Jurorhizophagus alienus* Cai, Ślipiński and Huang, 2015 [holotype, NIGP 161706 (exoskeleton with antennae and partly preserved legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2015c).

Phylogenetic justification**:** *Jurorhizophagus alienus* can be placed among monotomids based on its narrowly elongate body, prognathous head with lateral finely faceted eyes, procoxal cavities closed externally, elytra truncate apically and exposing two tergites, and 5-segmented abdomen with relatively long ventrites 1 and 5 (Sen Gupta 1988; Cai et al. 2015c).

Minimum age**:** 165 Ma.

Soft maximum age**:** 235 Ma.

Age justification**:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 49: Crown Nitidulidae: **119 Ma – 165 Ma.**

Fossil taxon and specimen**:** *Crepuraea archaica* Kirejtshuk, 1990 [holotype, PIN 3064/7189 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] Baissa locality situated on the left bank of the Vitim River, 8 km below the mouth of the Baissa River, Buryat Republic, west Transbaikalia, Russia.

Phylogenetic justification**:** As discussed in Kirejtshuk and Ponomarenko (1990) the genus *Crepuraea* has a close affinity to the extant *Epuraea*, which is placed in the subfamily Epuraeinae and tribe Epuraeini (Kirejtshuk 2008). Based on molecular phylogenies of Nitidulidae (Cline et al. 2014), this would place *Crepuraea* well within crown Nitidulidae, making it a suitable candidate for calibrating this node.

Minimum age**:** 119 Ma.

Soft maximum age**:** 165 Ma.

Age justification**:** The exact age of the lacustrine sediments of the Zaza Formation at Baissa is disputable. While early estimates suggested an Early Cretaceous (Neocomian–Aptian) age, most palaeoentomologists date them as Valanginian–Hauterivian (Zherikhin et al. 1999). The co-occurrence of *Coptoclava longipoda, Ephemeropsis trisetalis* and *Lycoptera* in the Zaza Formation as well as the Jiufotang Formation in western Liaoning, China suggests that the two may be contemporaneous. Given that the latter has been dated to 120 ± 1.0 Ma (unpubl. data; Kirejtshuk and Ponomarenko 1990), we use 119 Ma as the minimum constraint on the clade representing crown Nitidulidae. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 50: Crown Silvanidae: **98.17 Ma – 165 Ma.**

Fossil taxon and specimen**:** *Protoliota antennatus* Liu, Ślipiński, Wang and Pang, 2019 [holotype, No. CNU008072 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal

University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Liu et al. 2019).
Phylogenetic justification**:** The placement of *Protoliota* within Silvanidae is supported by its overall body form, long filiform antennae with long scape and without club, 5-5-5 tarsi, and narrowly open procoxal cavities (Liu et al. 2019). The distinctly lobed tarsomeres and prominent sexual dimorphism manifesting in the presence of male mandibular horns and antennal length (Thomas 2004; Cai and Huang 2019) suggest a placement in Brontinae.
Minimum age**:** 98.17 Ma.
Soft maximum age**:** 165 Ma.
Age justification**:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 51: Nemonychidae – Anthribidae: **155 Ma – 235 Ma.**

Fossil taxon and specimen**:** *Protoscelis longicornis* (Medvedev, 1968) [holotype, PIN, no. 2066/3241 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chimkent Region, Chayan District, southern Kazakhstan (Medvedev 1968; Legalov 2013).
Phylogenetic justification**:** The presence of a reduced rostrum, a three-segmented and rather compact antennal club, developed subbasal line on pronotum, and sexually dimorphic antennae place the fossil into Anthribidae (Legalov 2013).
Minimum age**:** 155 Ma.
Soft maximum age**:** 235 Ma.
Age justification**:** For the minimum age justification of the Karatau Range, see node 5. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 52: Belidae – (Attelabidae, (Brentidae, Curculionidae)): **165 Ma – 235 Ma.**

Fossil taxon and specimen**:** *Sinoeuglypheus daohugouensis* Yu, Davis and Shih, 2019 [holotype, CNU-COL-NN2011122 (exoskeleton with appendages preserved in lateral aspect, sex unknown): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Yu et al. 2019).
Phylogenetic justification**:** The species can be assigned to Belidae on the basis of the irregularly arranged punctures on the elytra, elongated first flagellomere of the antennae, outer longitudinal carina and an apical setal brush on the fore tibiae, wide prothoracic cavity for reception of the procoxa, form of the meso- and metathoracic episterna and epimera, small flange along the elytral basal margin, and lateral carinae on the abdominal ventrites (Yu et al. 2019).
Minimum age**:** 165 Ma.
Soft maximum age**:** 235 Ma.
Age justification**:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca*. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

Node 53: Brentidae **–** Curculionidae: **112.6 Ma – 165 Ma.**

Fossil taxon and specimen**:** *Axelrodiellus ruptus* Zherikhin and Gratshev, 2004 [holotype, AMNH 43312 (exoskeleton lacking legs, with fragments of antennae): American Museum of Natural History, New York City, USA] from the Lower Cretaceous (Aptian) Crato Formation, northeastern Brazil (Zherikhin and Gratshev 2004).
Phylogenetic justification: The species is placed in Brentidae on the basis of having an unpaired gular suture, narrow and loose antennal club, enlarged trochanters, and fused and strongly enlarged first two abdominal sternites. Assignment to Eurhynchinae is supported by the sloping trochanters and the bases of the femora

reaching the coxae, complete and deep suture between the first two ventrites, gular suture running from the base of the rostrum to the eyes, and striated gular region (Zherikhin and Gratshev 2004).
Minimum age: 112.6 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Crato Formation, see node 11. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 54: Crown Chrysomelidae: **122.2 Ma – 165 Ma.**

Fossil taxon and specimen: *Mesolpinus antennatus* Kirejtshuk, Moseyko and Ren, 2015 [holotype, CNU-COL-LB-2009840 (exoskeleton with fragments of appendages preserved in ventral aspect): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Kirejtshuk et al. 2015b).
Phylogenetic justification: The genus can be referred to the subfamily Chrysomelinae based on the hypognathous head not narrowed at the base, antennal cavities located in front of eyes and widely separated, frontoclypeus subquadrangular, behind the mandibles and separated from the posterior part of the frons by a wide V-shaped suture, the pronotum laterally margined, all coxae moderately separated, the prosternal process apparently lacking lateral structures for the reception of the procoxae, procoxae distinctly transverse, mesoventrite lacking projections for reception of the mesocoxae, metepisterna simple and lacking projections, the abdomen with ventrite 1 longest and other ventrites subequal in length, not fused, and tarsomere 3 bilobed (Kirejtshuk et al. 2015b).
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 55: Crown Cerambycidae: **122.2 Ma – 165 Ma.**

Fossil taxon and specimen: *Cretoprionus liutiaogouensis* Wang, Ma, McKenna, Yan, Zhang and Jarzembowski, 2014 [holotype, NIGP154953a, b (exoskeleton with appendages): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Wang et al. 2014).
Phylogenetic justification: *Cretoprionus liutiaogouensis* can be assigned to Cerambycidae based on its large and robust body, simple mandibular apex, pseudotetramerous tarsi, raised antennal insertions, and long antennae. It can furthermore be placed in Prioninae due to the very large and robust body, absence of a stridulatory plate on the mesonotum, pseudotetramerous tarsi, mouthparts projecting anteriorly, and lateral carinae on the prothorax (Turnbow and Thomas 2002; Wang et al. 2014; Vitali, 2019).
Minimum age: 122.2 Ma.
Soft maximum age: 165 Ma.
Age justification: For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Node 56: Sagrinae – Bruchinae: **78 Ma – 155 Ma.**

Fossil taxon and specimen: *Mesopachymerus antiqua* Poinar, 2005 [holotype, TMP 91.148.771 (amber inclusion): Royal Tyrrell Museum in Drumheller, Albert Canada] from Cretaceous Canadian amber, obtained from the Grassy Lake amber deposit, Foremost Formation, Alberta, Canada (Poinar 2005).
Phylogenetic justification: The widened protarsus 1 reliably places *Mesopachymerus antiqua* among bruchines, making it a suitable candidate for calibrating the split between Sagrinae and Bruchinae (Poinar 2005).

Minimum age: 78 Ma.
Soft maximum age: 155 Ma.
Age justification: The age of Canadian amber has been estimated as approximately 78 – 79 Ma based on biostratigraphic correlation (McKellar et al. 2013). We conservatively use 78 Ma as the minimum age constraint. The soft maximum age is derived from the Karabastau Formation of the Karatau Range, see node 5 for justification.

Node 57: Galerucinae – Chrysomelinae: **83.4 Ma – 165 Ma.**

Fossil taxon and specimen: *Taimyraltica calcarata* Nadein, 2018 [holotype, PIN 3311/1203 (amber inclusion): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from Cretaceous Taimyr amber collected from the right bank of the Maimecha River, Taimyr Peninsula, Kheta Formation, Krasnoyarskiy Krai, Russia (Nadein and Perkovsky 2018).
Phylogenetic justification: *Taimyraltica* can be attributed to Galerucinae based on its elongate body, hypognathous head without a constriction behind the eyes, antennal insertions situated between eyes at a distance from anterior margin of frons, eyes without emarginations, pronotum with a lateral margin and not constricted, pronotal base with a transverse furrow, procoxae transverse, elytra regularly punctured, and pygidium not vertical (Nadein and Bežđek 2014; Nadein and Perkovsky 2018).
Minimum age: 83.4 Ma.
Soft maximum age: 165 Ma.
Age justification: *Taimyraltica calcarata* occurs in the Late Cretaceous Taimyr amber from the Kheta Formation at the Yantardakh locality, Taimyr Peninsula, Russia. The age of the Kheta Formation is Coniacian-Santonian according to Saks et al. (1959). All amber from the Yantardakh locality has been found in the upper horizons of the formation, and is therefore thought to be Santonian (Zherikhin, 1978) or even upper Santonian based on the presence of marine bivalves of the genus *Inoceramus* in the overlying Mutino Formation (Perkovsky and Makarkin, 2015). As such, the age of Taimyr amber from Yantardakh is late Santonian, the upper boundary of which is dated to 83.6 ± 0.2 Ma (International Chronostratigraphic Chart, v. 2018/08). The minimum age constraint for this node is 83.4 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

Beetle phylogeny and evolutionary timescale

Figure S1. Test of model-depenmdent phylogenetic signal on a reduced 138 taxon dataset analysed with the LG model in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
100
Chrysopidae Dichochrysa IN54
100
Myrmeleontidae Myrmeleon IN53
100
Ascalaphidae Ascalohybris IN56
Torridincolidae Satonius INB116
95
Cupedidae Tenomerga INB118
85
Haliplidae Peltodytes INB121
82
Noteridae Canthydrus INB115
80
Gyrinidae Orectochilus INB037
100
Carabidae Cicindela INB101
100
Carabidae Carabus INB100
87
Dytiscidae Hyphydrus INB114
100
Dytiscidae Agabus INB109
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
98
Eucinetidae Noteucinetus CSR021
100
Clambidae Clambus CSR082
100
Rhinorhipus
Rhipiceridae Oligorhipis CSR049
100
Dascillidae Dascillus INB028
Buprestidae Trachys INB084
100
Buprestidae Coroebus INB018
89
99
Byrrhidae Notolioon CSR008
100
100
Byrrhidae Cytilus INB053
Eulichadidae Eulichas INB025
92
Callirhipidae Ennometes CSR009
53
Ptilodactylidae Ptilodactyla INB015
61
100
Dryopidae Helichus CSR019
100
Psephenidae Mataeopsephus INB081
99
Chelonariidae Chelonarium CSR012
93
Elmidae Stenelmis INB038
94
Limnichidae Limnichus TH1
100
Heteroceridae Heterocerus INB092
95
Omethidae Drilonius INB129
100
Artematopodidae Artematopus CSR004
100
Throscidae Trixagus INB125
100
Eucnemidae Anischia CSR022
100
Cantharidae Fissocantharis INB156
99
Lycidae Lycostomus YL0616
99
100
Elateridae Agrypnus INB160
100
Lampyridae Luciola INB061
95
Rhagophthalmidae Rhagophthalmus CSR132
100
Phengodidae Stenophrixothrix CSR041
Nosodendridae Nosodendron CSR038
Hydrophilidae Anacaena INB105
99
Histeridae Platysoma CSR023
Leiodidae Agathidium CSR032
100
Agyrtidae Pteroloma INB201
99
Staphylinidae Staphylinus INB008
100
100
Silphidae Necrodes INB078
93
Jacobsoniidae Derolathrus CSR026
99
Ptiliidae sp CSR044
99
Hydraenidae Hydraena INB108
100
98
Lucanidae Aegus INB148
92
Trogidae Trox INB036
100
Trogidae Omorgus CSR057
100
Geotrupidae Geotrupes INB097
83
Glaphyridae Amphicoma INB011
100
Scarabaeidae Copris INB146
98
Hybosoridae Cyphopisthes CSR138
98
Dermestidae Dermestes CSR089
100
Ptinidae Ptinus CSR045
100
Bostrichidae Lyctus CSR070
Latridiidae Corticaria CSR029
90
Alexiidae Sphaerosoma CSR002
100
Endomychidae Encymon CSR097
90
Coccinellidae Harmonia C10
98
Anamorphidae Papuella CSR095
100
Bothrideridae Ascetoderes CSR074
100
Murmidiidae Murmidius CSR078
100
Discolomatidae Aphanocephalus CSR018
100
Teredidae Teredolaemus CSR073
88
Euxestidae Hypodacnella CSR010
78
Cerylonidae Ostomopsis CSR079
100
Megalopodidae Temnaspis INB031
56
Cerambycidae Dorysthenes INB150
100
Chrysomelidae Galerucinae sp INB140
100
Chrysomelidae Altica INB141
100
Nemonychidae Aragomacer CSR120
100
Anthribidae Acorynus INB007
100
Belidae Rhinotia CSR067
100
Attelabidae Byctiscus INB076
99
Curculionidae Curculio INB184
100
Brentidae Apion CSR075
100
100
Monotomidae Rhizophagus CSR119
79
Hobartiidae Hydnobioides CSR106
65
Nitidulidae Brachypeplus CSR121
100
Kateretidae Notobrachypterus CSR027
79
Cybocephalidae Cybocephalus CSR088
98
Erotylidae Anadastus CSR100
90
Boganiidae Paracucujus CSR006
86
Protocucujidae Ericmodes CSR129
87
Helotidae Neohelota INB004
61
Silvanidae Uleiota CSR052
87
Cryptophagidae Curelius INB192
88
Phloeostichidae Hymaea CSR127
100
Myraboliidae Myrabolia CSR037
97
Passandridae Passandra CSR125
86
Phalacridae Phalacrinus CSR126
100
Propalticidae Propalticus CSR042
100
Laemophloeidae Laemophloeus CSR110
83
Trogossitidae Rentonellum CSR059
91
Byturidae Haematoides INB039
100
Biphyllidae Biphyllus CSR068
100
Acanthocnemidae Acanthocnemus CSR062
82
Trogossitidae Leperina CSR160
75
Trogossitidae Thymalus INB024
100
Trogossitidae Larinotus CSR058
100
Thanerocleridae Isoclerus CSR055
100
Cleridae Necrobia CSR084
69
Prionoceridae Idgia INB040
100
Melyridae Carphurus CSR117
96
Trogossitidae Parapeltis CSR159
100
Trogossitidae Ancyrona CSR158
96
Lymexylidae Melittomma CSR033
Melandryidae Melandryinae sp INB203
46
Incertae sedis Rhizonium CSR105
81
Ciidae Cis CSR013
92
Zopheridae Zopherosis CSR163
100
Zopheridae Bitoma CSR061
53
Tenebrionidae Adelium CSR149
36
Mycetophagidae Mycetophagus INB047
63
Archeocrypticidae Wattianus CSR066
100
Ulodidae Ulodes CSR161
67
Ulodidae Meryx CSR162
100
100
Oedemeridae Ditylus INB033
76
Mycteridae Trichosalpingus CSR036
74
Scraptiidae Scraptia INB205
71
Aderidae sp INB206
92
Ripiphoridae Rhipidioides CSR133
92
Ischaliidae Ischalia INB049
80
Salpingidae Ocholissa CSR136
93
Pythidae Anaplopus CSR131
92
Trictenotomidae Trictenotoma INB208
99
Boridae Synercticus CSR069
98
Pyrochroidae Morpholycus CSR047
99
Meloidae Epicauta INB093
100
Anthicidae Anthicus CSR063

Figure S2. Test of model-depenmdent phylogenetic signal on a reduced 138 taxon dataset analysed with the WAG model in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
Myrmeleontidae Myrmeleon IN53
Ascalaphidae Ascalohybris IN56
Torridincolidae Satonius INB116
Cupedidae Tenomerga INB118
Haliplidae Peltodytes INB121
Noteridae Canthydrus INB115
Gyrinidae Orectochilus INB037
Carabidae Cicindela INB101
Carabidae Carabus INB100
Dytiscidae Hyphydrus INB114
Dytiscidae Agabus INB109
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
Eucinetidae Noteucinetus CSR021
Clambidae Clambus CSR082
Rhinorhipus
Rhipiceridae Oligorhipis CSR049
Dascillidae Dascillus INB028
Buprestidae Trachys INB084
Buprestidae Coroebus INB018
Byrrhidae Notolioon CSR008
Byrrhidae Cytilus INB053
Eulichadidae Eulichas INB025
Callirhipidae Ennometes CSR009
Ptilodactylidae Ptilodactyla INB015
Dryopidae Helichus CSR019
Psephenidae Mataeopsephus INB081
Chelonariidae Chelonarium CSR012
Elmidae Stenelmis INB038
Limnichidae Limnichus TH1
Heteroceridae Heterocerus INB092
Omethidae Drilonius INB129
Artematopodidae Artematopus CSR004
Throscidae Trixagus INB125
Eucnemidae Anischia CSR022
Cantharidae Fissocantharis INB156
Lycidae Lycostomus YL0616
Elateridae Agrypnus INB160
Lampyridae Luciola INB061
Rhagophthalmidae Rhagophthalmus CSR132
Phengodidae Stenophrixothrix CSR041
Nosodendridae Nosodendron CSR038
Hydrophilidae Anacaena INB105
Histeridae Platysoma CSR023
Leiodidae Agathidium CSR032
Agyrtidae Pteroloma INB201
Staphylinidae Staphylinus INB008
Silphidae Necrodes INB078
Jacobsoniidae Derolathrus CSR026
Ptiliidae sp CSR044
Hydraenidae Hydraena INB108
Lucanidae Aegus INB148
Trogidae Trox INB036
Trogidae Omorgus CSR057
Geotrupidae Geotrupes INB097
Glaphyridae Amphicoma INB011
Scarabaeidae Copris INB146
Hybosoridae Cyphopisthes CSR138
Dermestidae Dermestes CSR089
Ptinidae Ptinus CSR045
Bostrichidae Lyctus CSR070
Latridiidae Corticaria CSR029
Alexiidae Sphaerosoma CSR002
Endomychidae Encymon CSR097
Coccinellidae Harmonia C10
Anamorphidae Papuella CSR095
Bothrideridae Ascetoderes CSR074
Murmidiidae Murmidius CSR078
Discolomatidae Aphanocephalus CSR018
Teredidae Teredolaemus CSR073
Euxestidae Hypodacnella CSR010
Cerylonidae Ostomopsis CSR079
Megalopodidae Temnaspis INB031
Cerambycidae Dorysthenes INB150
Chrysomelidae Galerucinae sp INB140
Chrysomelidae Altica INB141
Nemonychidae Aragomacer CSR120
Anthribidae Acorynus INB007
Belidae Rhinotia CSR067
Attelabidae Byctiscus INB076
Curculionidae Curculio INB184
Brentidae Apion CSR075
Monotomidae Rhizophagus CSR119
Nitidulidae Brachypeplus CSR121
Kateretidae Notobrachypterus CSR027
Cybocephalidae Cybocephalus CSR088
Hobartiidae Hydnobioides CSR106
Boganiidae Paracucujus CSR006
Erotylidae Anadastus CSR100
Protocucujidae Ericmodes CSR129
Helotidae Neohelota INB004
Silvanidae Uleiota CSR052
Cryptophagidae Curelius INB192
Phloeostichidae Hymaea CSR127
Myraboliidae Myrabolia CSR037
Passandridae Passandra CSR125
Phalacridae Phalacrinus CSR126
Propalticidae Propalticus CSR042
Laemophloeidae Laemophloeus CSR110
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
Biphyllidae Biphyllus CSR068
Acanthocnemidae Acanthocnemus CSR062
Trogossitidae Leperina CSR160
Trogossitidae Thymalus INB024
Trogossitidae Larinotus CSR058
Thanerocleridae Isoclerus CSR055
Cleridae Necrobia CSR084
Prionoceridae Idgia INB040
Melyridae Carphurus CSR117
Trogossitidae Parapeltis CSR159
Trogossitidae Ancyrona CSR158
Lymexylidae Melittomma CSR033
Melandryidae Melandryinae sp INB203
Incertae sedis Rhizonium CSR105
Ciidae Cis CSR013
Zopheridae Zopherosis CSR163
Zopheridae Bitoma CSR061
Tenebrionidae Adelium CSR149
Mycetophagidae Mycetophagus INB047
Archeocrypticidae Wattianus CSR066
Ulodidae Ulodes CSR161
Ulodidae Meryx CSR162
Scraptiidae Scraptia INB205
Oedemeridae Ditylus INB033
Mycteridae Trichosalpingus CSR036
Aderidae sp INB206
Ripiphoridae Rhipidioides CSR133
Ischaliidae Ischalia INB049
Salpingidae Ocholissa CSR136
Pythidae Anaplopus CSR131
Trictenotomidae Trictenotoma INB208
Boridae Synercticus CSR069
Pyrochroidae Morpholycus CSR047
Meloidae Epicauta INB093
Anthicidae Anthicus CSR063

Figure S3. Test of model-depenmdent phylogenetic signal on a reduced 138 taxon dataset analysed with the JTT model in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
100
Myrmeleontidae Myrmeleon IN53
100
100
Ascalaphidae Ascalohybris IN56
Torridincolidae Satonius INB116
95
Cupedidae Tenomerga INB118
Haliplidae Peltodytes INB121
86
Noteridae Canthydrus INB115
76
75
Gyrinidae Orectochilus INB037
100
Carabidae Cicindela INB101
100
Carabidae Carabus INB100
85
Dytiscidae Hyphydrus INB114
100
Dytiscidae Agabus INB109
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
100
Eucinetidae Noteucinetus CSR021
100
Clambidae Clambus CSR082
Rhinorhipus
100
Rhipiceridae Oligorhipis CSR049
100
Dascillidae Dascillus INB028
Buprestidae Trachys INB084
100
Buprestidae Coroebus INB018
62
100
Byrrhidae Notolioon CSR008
100
100
Byrrhidae Cytilus INB053
Eulichadidae Eulichas INB025
98
Callirhipidae Ennometes CSR009
67
Ptilodactylidae Ptilodactyla INB015
100
82
Dryopidae Helichus CSR019
100
100
Psephenidae Mataeopsephus INB081
98
Chelonariidae Chelonarium CSR012
89
Elmidae Stenelmis INB038
91
Limnichidae Limnichus TH1
89
100
Heteroceridae Heterocerus INB092
Omethidae Drilonius INB129
100
Artematopodidae Artematopus CSR004
Throscidae Trixagus INB125
100
100
Eucnemidae Anischia CSR022
Cantharidae Fissocantharis INB156
100
100
100
Lycidae Lycostomus YL0616
100
Elateridae Agrypnus INB160
Lampyridae Luciola INB061
100
Rhagophthalmidae Rhagophthalmus CSR132
100
100
Phengodidae Stenophrixothrix CSR041
Nosodendridae Nosodendron CSR038
Hydrophilidae Anacaena INB105
100
Histeridae Platysoma CSR023
Leiodidae Agathidium CSR032
100
Agyrtidae Pteroloma INB201
Staphylinidae Staphylinus INB008
98
98
100
Silphidae Necrodes INB078
79
Jacobsoniidae Derolathrus CSR026
Ptiliidae sp CSR044
98
100
98
94
Hydraenidae Hydraena INB108
Lucanidae Aegus INB148
96
Trogidae Trox INB036
100
Trogidae Omorgus CSR057
100
Geotrupidae Geotrupes INB097
82
Glaphyridae Amphicoma INB011
100
Scarabaeidae Copris INB146
96
Hybosoridae Cyphopisthes CSR138
96
Dermestidae Dermestes CSR089
Ptinidae Ptinus CSR045
100
100
Bostrichidae Lyctus CSR070
Latridiidae Corticaria CSR029
96
Alexiidae Sphaerosoma CSR002
99
Endomychidae Encymon CSR097
96
Coccinellidae Harmonia C10
97
Anamorphidae Papuella CSR095
100
Bothrideridae Ascetoderes CSR074
Murmidiidae Murmidius CSR078
100
100
Discolomatidae Aphanocephalus CSR018
100
Teredidae Teredolaemus CSR073
100
Euxestidae Hypodacnella CSR010
88
85
Cerylonidae Ostomopsis CSR079
Cerambycidae Dorysthenes INB150
Megalopodidae Temnaspis INB031
100
Chrysomelidae Galerucinae sp INB140
75
100
Chrysomelidae Altica INB141
100
Nemonychidae Aragomacer CSR120
100
Anthribidae Acorynus INB007
100
Belidae Rhinotia CSR067
Attelabidae Byctiscus INB076
100
Curculionidae Curculio INB184
98
100
100
Brentidae Apion CSR075
100
Monotomidae Rhizophagus CSR119
79
Hobartiidae Hydnobioides CSR106
70
Cybocephalidae Cybocephalus CSR088
100
Nitidulidae Brachypeplus CSR121
55
Kateretidae Notobrachypterus CSR027
Erotylidae Anadastus CSR100
99
83
Boganiidae Paracucujus CSR006
81
Protocucujidae Ericmodes CSR129
91
Helotidae Neohelota INB004
Silvanidae Uleiota CSR052
63
91
Cryptophagidae Curelius INB192
Phloeostichidae Hymaea CSR127
95
98
Myraboliidae Myrabolia CSR037
Passandridae Passandra CSR125
95
80
Phalacridae Phalacrinus CSR126
90
Propalticidae Propalticus CSR042
100
100
Laemophloeidae Laemophloeus CSR110
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
90
100
Biphyllidae Biphyllus CSR068
Acanthocnemidae Acanthocnemus CSR062
100
Trogossitidae Leperina CSR160
87
Trogossitidae Thymalus INB024
82
100
Trogossitidae Larinotus CSR058
100
Thanerocleridae Isoclerus CSR055
100
Cleridae Necrobia CSR084
Prionoceridae Idgia INB040
76
100
Melyridae Carphurus CSR117
91
Trogossitidae Parapeltis CSR159
98
100
Trogossitidae Ancyrona CSR158
Lymexylidae Melittomma CSR033
Melandryidae Melandryinae sp INB203
Incertae sedis Rhizonium CSR105
84
70
Ciidae Cis CSR013
83
Zopheridae Zopherosis CSR163
Zopheridae Bitoma CSR061
99
47
Tenebrionidae Adelium CSR149
41
Mycetophagidae Mycetophagus INB047
54
Archeocrypticidae Wattianus CSR066
100
Ulodidae Ulodes CSR161
58
100
99
Ulodidae Meryx CSR162
Oedemeridae Ditylus INB033
68
Mycteridae Trichosalpingus CSR036
Scraptiidae Scraptia INB205
68
Aderidae sp INB206
68
Ripiphoridae Rhipidioides CSR133
82
82
Ischaliidae Ischalia INB049
71
Salpingidae Ocholissa CSR136
96
Pythidae Anaplopus CSR131
Trictenotomidae Trictenotoma INB208
87
99
Boridae Synercticus CSR069
Pyrochroidae Morpholycus CSR047
93
Meloidae Epicauta INB093
94
100
Anthicidae Anthicus CSR063

Figure S4. Test of model-depenmdent phylogenetic signal on a reduced 138 taxon dataset analysed with the GTR20 model in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
100
Chrysopidae Dichochrysa IN54
Myrmeleontidae Myrmeleon IN53
100
Ascalaphidae Ascalohybris IN56
100
Torridincolidae Satonius INB116
94
Cupedidae Tenomerga INB118
Haliplidae Peltodytes INB121
85
Noteridae Canthydrus INB115
77
77
Gyrinidae Orectochilus INB037
100
Carabidae Cicindela INB101
100
Carabidae Carabus INB100
84
Dytiscidae Hyphydrus INB114
100
Dytiscidae Agabus INB109
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
97
Eucinetidae Noteucinetus CSR021
100
Clambidae Clambus CSR082
Rhinorhipus
100
Rhipiceridae Oligorhipis CSR049
100
Dascillidae Dascillus INB028
Buprestidae Trachys INB084
100
Buprestidae Coroebus INB018
90
99
Byrrhidae Notolioon CSR008
100
100
Byrrhidae Cytilus INB053
Eulichadidae Eulichas INB025
91
Callirhipidae Ennometes CSR009
57
Ptilodactylidae Ptilodactyla INB015
100
73
Dryopidae Helichus CSR019
100
100
Psephenidae Mataeopsephus INB081
98
Chelonariidae Chelonarium CSR012
90
Elmidae Stenelmis INB038
93
Limnichidae Limnichus TH1
100
89
Heteroceridae Heterocerus INB092
Omethidae Drilonius INB129
100
Artematopodidae Artematopus CSR004
Throscidae Trixagus INB125
100
100
Eucnemidae Anischia CSR022
Cantharidae Fissocantharis INB156
99
100
100
Lycidae Lycostomus YL0616
Elateridae Agrypnus INB160
100
100
98
Rhagophthalmidae Rhagophthalmus CSR132
100
Phengodidae Stenophrixothrix CSR041
Nosodendridae Nosodendron CSR038
Hydrophilidae Anacaena INB105
100
Histeridae Platysoma CSR023
Leiodidae Agathidium CSR032
100
Agyrtidae Pteroloma INB201
100
100
Staphylinidae Staphylinus INB008
100
Silphidae Necrodes INB078
85
Jacobsoniidae Derolathrus CSR026
99
Ptiliidae sp CSR044
99
99
Hydraenidae Hydraena INB108
98
Lucanidae Aegus INB148
94
Trogidae Trox INB036
100
Trogidae Omorgus CSR057
100
Geotrupidae Geotrupes INB097
81
Glaphyridae Amphicoma INB011
100
Scarabaeidae Copris INB146
98
Hybosoridae Cyphopisthes CSR138
95
Dermestidae Dermestes CSR089
100
Ptinidae Ptinus CSR045
100
Bostrichidae Lyctus CSR070
Latridiidae Corticaria CSR029
93
Alexiidae Sphaerosoma CSR002
100
Endomychidae Encymon CSR097
93
Coccinellidae Harmonia C10
96
Anamorphidae Papuella CSR095
100
Bothrideridae Ascetoderes CSR074
Murmidiidae Murmidius CSR078
100
100
Discolomatidae Aphanocephalus CSR018
100
Teredidae Teredolaemus CSR073
90
Euxestidae Hypodacnella CSR010
86
Cerylonidae Ostomopsis CSR079
100
Megalopodidae Temnaspis INB031
52
Cerambycidae Dorysthenes INB150
100
Chrysomelidae Galerucinae sp INB140
100
Chrysomelidae Altica INB141
Nemonychidae Aragomacer CSR120
100
100
Anthribidae Acorynus INB007
100
Belidae Rhinotia CSR067
100
Attelabidae Byctiscus INB076
100
Curculionidae Curculio INB184
100
Brentidae Apion CSR075
100
100
Monotomidae Rhizophagus CSR119
66
Hobartiidae Hydnobioides CSR106
59
Nitidulidae Brachypeplus CSR121
100
Kateretidae Notobrachypterus CSR027
67
Cybocephalidae Cybocephalus CSR088
Erotylidae Anadastus CSR100
68
98
Boganiidae Paracucujus CSR006
70
Protocucujidae Ericmodes CSR129
85
Helotidae Neohelota INB004
55
Silvanidae Uleiota CSR052
93
Cryptophagidae Curelius INB192
97
Phloeostichidae Hymaea CSR127
99
Myraboliidae Myrabolia CSR037
96
Passandridae Passandra CSR125
88
Phalacridae Phalacrinus CSR126
100
Propalticidae Propalticus CSR042
90
100
Laemophloeidae Laemophloeus CSR110
Trogossitidae Rentonellum CSR059
92
Byturidae Haematoides INB039
100
Biphyllidae Biphyllus CSR068
Acanthocnemidae Acanthocnemus CSR062
100
79
Trogossitidae Leperina CSR160
70
Trogossitidae Thymalus INB024
99
Trogossitidae Larinotus CSR058
100
Thanerocleridae Isoclerus CSR055
100
Cleridae Necrobia CSR084
68
Prionoceridae Idgia INB040
100
Melyridae Carphurus CSR117
95
98
Trogossitidae Parapeltis CSR159
100
Trogossitidae Ancyrona CSR158
Lymexylidae Melittomma CSR033
Melandryidae Melandryinae sp INB203
42
Incertae sedis Rhizonium CSR105
80
Ciidae Cis CSR013
92
Zopheridae Zopherosis CSR163
100
48
Zopheridae Bitoma CSR061
40
Tenebrionidae Adelium CSR149
74
Mycetophagidae Mycetophagus INB047
100
Archeocrypticidae Wattianus CSR066
75
Ulodidae Ulodes CSR161
100
Ulodidae Meryx CSR162
90
Oedemeridae Ditylus INB033
72
Mycteridae Trichosalpingus CSR036
58
Scraptiidae Scraptia INB205
58
Aderidae sp INB206
82
Ripiphoridae Rhipidioides CSR133
82
Ischaliidae Ischalia INB049
74
Salpingidae Ocholissa CSR136
86
Pythidae Anaplopus CSR131
Trictenotomidae Trictenotoma INB208
82
99
Boridae Synercticus CSR069
95
Pyrochroidae Morpholycus CSR047
97
Meloidae Epicauta INB093
100
Anthicidae Anthicus CSR063

Figure S5. Test of model-depenmdent phylogenetic signal on a reduced 138 taxon dataset analysed with the C10 model in IQ-TREE.


Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
100
Myrmeleontidae Myrmeleon IN53
100
100
Ascalaphidae Ascalohybris IN56
Torridincolidae Satonius INB116
95
Cupedidae Tenomerga INB118
Gyrinidae Orectochilus INB037
95
Noteridae Canthydrus INB115
100
62
Haliplidae Peltodytes INB121
Carabidae Cicindela INB101
63
100
Carabidae Carabus INB100
96
Dytiscidae Hyphydrus INB114
100
Dytiscidae Agabus INB109
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
95
Eucinetidae Noteucinetus CSR021
98
Clambidae Clambus CSR082
Rhinorhipus
100
Rhipiceridae Oligorhipis CSR049
100
Dascillidae Dascillus INB028
Buprestidae Trachys INB084
100
Buprestidae Coroebus INB018
92
93
Byrrhidae Notolioon CSR008
100
100
Byrrhidae Cytilus INB053
Dryopidae Helichus CSR019
Ptilodactylidae Ptilodactyla INB015
Eulichadidae Eulichas INB025
85
100
100
94
Callirhipidae Ennometes CSR009
100
Psephenidae Mataeopsephus INB081
86
98
Chelonariidae Chelonarium CSR012
97
Elmidae Stenelmis INB038
89
93
Limnichidae Limnichus TH1
100
Heteroceridae Heterocerus INB092
Omethidae Drilonius INB129
100
Artematopodidae Artematopus CSR004
Throscidae Trixagus INB125
99
99
Eucnemidae Anischia CSR022
Lycidae Lycostomus YL0616
100
100
63
Cantharidae Fissocantharis INB156
100
Elateridae Agrypnus INB160
100
Lampyridae Luciola INB061
99
Rhagophthalmidae Rhagophthalmus CSR132
100
Phengodidae Stenophrixothrix CSR041
Nosodendridae Nosodendron CSR038
Hydrophilidae Anacaena INB105
100
Histeridae Platysoma CSR023
Jacobsoniidae Derolathrus CSR026
89
Ptiliidae sp CSR044
94
Hydraenidae Hydraena INB108
98
98
Leiodidae Agathidium CSR032
100
Agyrtidae Pteroloma INB201
57
Staphylinidae Staphylinus INB008
100
Silphidae Necrodes INB078
97
100
Lucanidae Aegus INB148
100
Trogidae Trox INB036
100
Trogidae Omorgus CSR057
100
Geotrupidae Geotrupes INB097
92
Scarabaeidae Copris INB146
100
Hybosoridae Cyphopisthes CSR138
99
Glaphyridae Amphicoma INB011
Dermestidae Dermestes CSR089
99
Ptinidae Ptinus CSR045
100
Bostrichidae Lyctus CSR070
95
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
100
100
Biphyllidae Biphyllus CSR068
Trogossitidae Leperina CSR160
100
98
Acanthocnemidae Acanthocnemus CSR062
76
Trogossitidae Thymalus INB024
100
100
Trogossitidae Larinotus CSR058
Thaneroceridae Isoclerus CSR055
100
Cleridae Necrobia CSR084
94
Prionoceridae Idgia INB040
91
100
Melyridae Carphurus CSR117
98
Trogossitidae Parapeltis CSR159
100
Trogossitidae Ancyrona CSR158
Lymexylidae Melittomma CSR033
100
Ripiphoridae Rhipidioides CSR133
Ciidae Cis CSR013
Melandryidae Melandryinae sp INB203
99
72
Incertae sedis Rhizonium CSR105
Zopheridae Zopherosis CSR163
72
69
87
Zopheridae Bitoma CSR061
94
Tenebrionidae Adelium CSR149
Mycetophagidae Mycetophagus INB047
90
Archeocrypticidae Wattianus CSR066
100
90
Ulodidae Ulodes CSR161
89
100
Ulodidae Meryx CSR162
Oedemeridae Ditylus INB033
76
Mycteridae Trichosalpingus CSR036
72
Scraptiidae Scraptia INB205
71
Ischaliidae Ischalia INB049
99
Aderidae sp INB206
100
87
Salpingidae Ocholissa CSR136
100
Pythidae Anaplopus CSR131
93
Trictenotomidae Trictenotoma INB208
100
Boridae Synercticus CSR069
93
Pyrochroidae Morpholycus CSR047
Tree scale: 0.1
97
Meloidae Epicauta INB093
100
Anthicidae Anthicus CSR063
Latridiidae Corticaria CSR029
100
Alexiidae Sphaerosoma CSR002
100
Anamorphidae Papuella CSR095
100
Endomychidae Encymon CSR097
99
Coccinellidae Harmonia C10
100
Bothrideridae Ascetoderes CSR074
Murmidiidae Murmidius CSR078
100
100
Discolomatidae Aphanocephalus CSR018
100
Teredidae Teredolaemus CSR073
Euxestidae Hypodacnella CSR010
81
80
Cerylonidae Ostomopsis CSR079
Megalopodidae Temnaspis INB031
100
Cerambycidae Dorysthenes INB150
100
Chrysomelidae Galerucinae sp INB140
100
Chrysomelidae Altica INB141
100
Nemonychidae Aragomacer CSR120
100
Anthribidae Acorynus INB007
81
100
Belidae Rhinotia CSR067
100
Attelabidae Byctiscus INB076
99
Curculionidae Curculio INB184
100
Brentidae Apion CSR075
Silvanidae Uleiota CSR052
100
92
Cryptophagidae Curelius INB192
Phloeostichidae Hymaea CSR127
95
95
Myraboliidae Myrabolia CSR037
97
Passandridae Passandra CSR125
Phalacridae Phalacrinus CSR126
95
100
Propalticidae Propalticus CSR042
100
Laemophloeidae Laemophloeus CSR110
91
Erotylidae Anadastus CSR100
69
Boganiidae Paracucujus CSR006
72
Protocucujidae Ericmodes CSR129
75
Helotidae Neohelota INB004
79
Monotomidae Rhizophagus CSR119
85
Hobartiidae Hydnobioides CSR106
62
Kateretidae Notobrachypterus CSR027
100
Nitidulidae Brachypeplus CSR121
80
Cybocephalidae Cybocephalus CSR088

Figure S6. Phylogeny of Coleoptera inferred with the site-heterogeneous Bayesian model CAT-GTR+G4 implemented in PhyloBayes.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
Ascalaphidae Ascalohybris IN56
Myrmeleontidae Myrmeleon IN53
Gyrinidae Orectochilus INB037
Haliplidae Peltodytes INB121
Noteridae Canthydrus INB115
Noteridae sp CSR039
Dytiscidae Hyphydrus INB114
Dytiscidae Laccophilus INB111
Dytiscidae Eretes INB112
Dytiscidae Agabus INB109
Dytiscidae Rhantus INB113
Carabidae Cicindela INB101
Carabidae Omoglymmius INB120
Carabidae Paussinae sp TH2
Carabidae Carabus INB100
Carabidae Elaphrus INB212
Carabidae Clivina INB167
Carabidae Pheropsophus INB168
Carabidae Dischissus INB013
Carabidae Lebia INB170
Carabidae Pentagonica INB171
Cupedidae Tenomerga INB118
Torridincolidae Satonius INB116
Scirtidae Pseudomicrocara CSR143
Scirtidae Elodes INB133
Scirtidae Scirtinae sp INB041
Derodontidae Derodontus CSR091
Clambidae Clambus CSR082
Eucinetidae Noteucinetus CSR021
Eucinetidae Noteucinetus CSR103
Rhinorhipus
Rhipiceridae Oligorhipis CSR049
Dascillidae Dascillus INB028
Dascillidae Metallidascillus INB200
Byrrhidae Microchaetes CSR076
Byrrhidae Cytilus INB053
Byrrhidae Notolioon CSR008
Buprestidae Dicerca INB083
Buprestidae Coroebus INB018
Buprestidae Trachys INB084
Dryopidae Pachyparnus INB166
Dryopidae Helichus CSR019
Dryopidae Helichus INB194
Eulichadidae Eulichas INB025
Callirhipidae Ennometes CSR009
Callirhipidae Simianus INB119
Ptilodactylidae Epilichas INB079
Ptilodactylidae Ptilodactyla INB015
Chelonariidae Chelonarium CSR012
Psephenidae Schinostethus INB052
Psephenidae Schinostethus INB080
Psephenidae Mataeopsephus INB081
Psephenidae Sclerocyphon CSR043
Elmidae Stetholus CSR094
Elmidae Graphelmis CSR093
Elmidae Stenelmis INB038
Limnichidae Cephalobyrrhus INB082
Heteroceridae Heterocerus INB092
Limnichidae Limnichus TH1
Limnichidae Byrrhinus CSR112
Limnichidae Pelochares INB042
Omethidae Drilonius INB127
Omethidae Drilonius INB129
Artematopodidae Artematopus CSR004
Artematopodidae Eurypogon INB202
Throscidae Trixagus CSR056
Throscidae Trixagus INB125
Eucnemidae Anischia CSR022
Eucnemidae Hemiopsida CSR104
Eucnemidae Otho INB035
Elateridae Osslimus CSR092
Lycidae Benibotarus YL0447
Lycidae Lycostomus YL0616
Lycidae Platerodrilus YL0458
Lycidae Libnetis YL0478
Lycidae Porrostoma CSR113
Lycidae Dilophotes YL0454
Lycidae Macrolycus YL0509
Elateridae Cebrio TH4
Elateridae Ampedus INB161
Elateridae Hemicrepidius INB016
Elateridae Melanotus INB211
Phengodidae Stenophrixothrix CSR041
Rhagophthalmidae sp INB128
Rhagophthalmidae Rhagophthalmus CSR048
Rhagophthalmidae Rhagophthalmus CSR132
Lampyridae Drilaster INB157
Lampyridae Gorhamia TH3
Lampyridae Luciola INB061
Lampyridae Pristolycus INB060
Lampyridae Cyphonocerus INB062
Lampyridae Vesta INB059
Lampyridae Diaphanes INB158
Lampyridae Pyrocoelia INB017
Elateridae Agrypnus INB160
Elateridae Denticollis INB162
Elateridae Denticollis INB165
Elateridae Pectocera INB159
Elateridae Cardiotarsus INB210
Elateridae Penia INB163
Elateridae sp INB164
Cantharidae Ichthyurus INB065
Cantharidae Malthinus INB154
Cantharidae Heteromastix CSR077
Cantharidae Laemoglyptus INB153
Cantharidae Fissocantharis INB156
Cantharidae Prothemus INB064
Cantharidae Lycocerus INB155
Cantharidae Themus INB001
Cantharidae Themus INB063
Nosodendridae Nosodendron CSR038
Histeridae Platysoma CSR023
Histeridae Saprinus CSR024
Hydrophilidae Georissus INB106
Hydrophilidae Anacaena INB105
Hydrophilidae Helochares CSR108
Hydrophilidae Sphaeridium INB107
Hydrophilidae Oocyclus INB014
Hydrophilidae Berosus INB152
Hydrophilidae Hydrophilus INB103
Hydrophilidae Sternolophus CSR107
Trogidae Omorgus CSR057
Trogidae Trox INB036
Lucanidae Phalacrognathus INB098
Lucanidae Aegus INB148
Lucanidae Cyclommatus INB099
Geotrupidae Australobolbus CSR137
Geotrupidae Geotrupes INB097
Passalidae Aceraius INB096
Passalidae Ceracupes INB057
Glaphyridae Amphicoma INB011
Scarabaeidae Rhyparus INB002
Scarabaeidae Copris INB146
Scarabaeidae Onthophagus CSR142
Hybosoridae Cyphopisthes CSR138
Hybosoridae Liparochrus CSR025
Scarabaeidae Cheirotonus INB151
Scarabaeidae Heteronyx CSR140
Scarabaeidae Ectinohoplia INB147
Scarabaeidae Dasyvalgus INB149
Scarabaeidae Protaetia INB104
Scarabaeidae Anomala CSR141
Scarabaeidae Mimela INB145
Scarabaeidae Allomyrina INB169
Scarabaeidae Carneodon CSR139
Jacobsoniidae Derolathrus CSR026
Jacobsoniidae Derolathrus CSR109
Hydraenidae Hydraena INB108
Ptiliidae sp CSR044
Agyrtidae Pteroloma INB201
Leiodidae Agathidium CSR032
Leiodidae Agyrtodes CSR030
Leiodidae Cholevinae sp CSR031
Staphylinidae Centrophthalmus INB091
Staphylinidae Omaliinae sp INB176
Staphylinidae Dianous INB175
Staphylinidae Scydmaeninae sp CSR146
Staphylinidae Tachinus INB088
Staphylinidae Tachinus INB090
Staphylinidae Megalopaederus INB030
Staphylinidae Staphylininae sp INB174
Staphylinidae Staphylinus INB008
Silphidae Necrodes INB078
Silphidae Nicrophorus INB022
Staphylinidae Apatetica INB085
Staphylinidae Osorius INB087
Staphylinidae Priochirus INB086
Staphylinidae Scaphidium CSR054
Staphylinidae Scaphidium INB089
Dermestidae Dermestes CSR089
Dermestidae Evorinea CSR090
Dermestidae Orphinus INB130
Bostrichidae Lyctus CSR070
Bostrichidae Polycaon INB032
Ptinidae Ptinus CSR045
Ptinidae Ptinus INB132
Ptinidae Dorcatoma CSR046
Ptinidae Hedobia INB204
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
Biphyllidae Althaesia CSR005
Biphyllidae Biphyllus CSR068
Acanthocnemidae Acanthocnemus CSR062
Trogossitidae Leperina CSR160
Trogossitidae Larinotus CSR058
Trogossitidae Thymalus INB024
Thanerocleridae Isoclerus CSR055
Cleridae Cladiscus INB189
Cleridae Stenocallimerus INB190
Cleridae Xenorthrius INB012
Cleridae Tenerus CSR083
Cleridae Allochotes INB191
Cleridae Necrobia CSR084
Trogossitidae Ancyrona CSR158
Trogossitidae Parapeltis CSR159
Prionoceridae Idgia INB040
Melyridae Dasytes CSR115
Melyridae Dicranolaius CSR116
Melyridae Malachiinae sp INB003
Melyridae Carphurus CSR117
Melyridae Carphurus INB131
Lymexylidae Atractocerus INB094
Lymexylidae Melittomma CSR033
Ripiphoridae Rhipidioides CSR133
Mordellidae Hoshihananomia INB034
Ripiphoridae Trigonodera CSR050
Ischaliidae Ischalia INB049
Aderidae sp CSR001
Aderidae sp INB206
Trictenotomidae Trictenotoma INB208
Scraptiidae Scraptia INB205
Mycteridae Trichosalpingus CSR036
Oedemeridae Ditylus INB033
Oedemeridae Pseudolycus CSR124
Oedemeridae Thelyphassa CSR123
Boridae Synercticus CSR069
Pythidae Anaplopus CSR131
Salpingidae Ocholissa CSR136
Salpingidae Euryplatus CSR134
Salpingidae Orphanotrophium CSR051
Salpingidae Orphanotrophium CSR135
Pyrochroidae Morpholycus CSR047
Pyrochroidae Morpholycus CSR130
Pyrochroidae Eupyrochroa INB027
Pyrochroidae Pseudopyrochroa INB020
Anthicidae Macratria CSR065
Anthicidae Macratria INB050
Anthicidae Lemodes CSR003
Anthicidae Trichananca CSR064
Anthicidae Anthicus CSR063
Meloidae Epicauta INB093
Meloidae Zonitis CSR114
Incertae sedis Rhizonium CSR105
Zopheridae Bitoma CSR061
Melandryidae Melandryinae sp INB203
Zopheridae Monomma CSR060
Zopheridae Zopherosis CSR163
Melandryidae Dircaeomorpha INB055
Ciidae Cis CSR013
Ciidae Australocis CSR081
Ciidae Cis CSR080
Ulodidae Meryx CSR162
Ulodidae Ulodes CSR161
Archeocrypticidae Wattianus CSR066
Mycetophagidae Mycetophagus INB047
Mycetophagidae Nototriphyllus CSR035
Tenebrionidae Adelium CSR149
Tenebrionidae Chlorophila INB046
Tenebrionidae Ecnolagria CSR157
Tenebrionidae Cyphaleus CSR148
Tenebrionidae Cillibus CSR150
Tenebrionidae Cossyphus CSR153
Tenebrionidae Cryphaeus INB181
Tenebrionidae Cteniopinus INB073
Tenebrionidae Tanychilus CSR154
Tenebrionidae Amarygmus CSR147
Tenebrionidae Platydema CSR155
Tenebrionidae Palorus CSR151
Tenebrionidae Strongylium INB180
Tenebrionidae Tyrtaeus CSR156
Tenebrionidae Derispia CSR152
Tenebrionidae Derispia INB072
Bothrideridae Ascetoderes CSR074
Bothrideridae Deretaphrus CSR072
Cerylonidae Philothermus CSR011
Discolomatidae Aphanocephalus CSR018
Murmidiidae Murmidius CSR078
Cerylonidae Ostomopsis CSR079
Euxestidae Hypodacnella CSR010
Teredidae Teredolaemus CSR073
Teredidae Xylariophilus CSR007
Teredidae Xylariophilus CSR071
Alexiidae Sphaerosoma CSR002
Latridiidae Enicmus CSR028
Latridiidae Corticaria CSR029
Latridiidae Melanophthalma CSR111
Anamorphidae Papuella CSR095
Corylophidae Periptyctus CSR086
Corylophidae Priamima CSR085
Corylophidae Orthoperus INB209
Corylophidae Sericoderus CSR014
Endomychidae Holoparamecus CSR096
Endomychidae Encymon CSR097
Endomychidae Sinocymbachus INB005
Endomychidae Cyclotoma CSR020
Endomychidae Stenotarsus CSR098
Coccinellidae Microfreudea C33
Coccinellidae Stethorus C54
Coccinellidae Exochomus C25
Coccinellidae Harmonia C10
Coccinellidae Rhizobius C28
Coccinellidae Ortalia C31
Coccinellidae Chnootriba C04
Coccinellidae Sasajiscymnus C44
Boganiidae Paracucujus CSR006
Erotylidae Anadastus CSR100
Erotylidae Tetraphala INB029
Erotylidae Cryptophilus CSR102
Erotylidae Thallis CSR099
Erotylidae Episcapha INB023
Erotylidae Episcaphula CSR101
Helotidae Neohelota INB004
Protocucujidae Ericmodes CSR129
Sphindidae Aspidiphorus CSR053
Monotomidae Rhizophagus CSR119
Monotomidae Thione INB207
Monotomidae Mimemodes CSR034
Monotomidae Monotomopsis CSR118
Kateretidae Notobrachypterus CSR027
Cybocephalidae Cybocephalus CSR088
Nitidulidae Glischrochilus INB197
Nitidulidae Carpophilus INB196
Nitidulidae Urophorus INB056
Nitidulidae Brachypeplus CSR121
Nitidulidae Pallodes CSR122
Hobartiidae Hydnobioides CSR106
Cryptophagidae Curelius INB192
Cryptophagidae Micrambina CSR015
Silvanidae Psammoecus INB095
Silvanidae Silvanoprus CSR145
Silvanidae Uleiota CSR052
Silvanidae Cryptamorpha CSR144
Silvanidae Psammoecus INB124
Cucujidae Pediacus CSR087
Cucujidae Platisus CSR016
Phloeostichidae Hymaea CSR127
Phloeostichidae Rhopalobrachium CSR128
Myraboliidae Myrabolia CSR037
Passandridae Passandra CSR125
Phalacridae Phalacrinus CSR126
Phalacridae Olibrus INB122
Phalacridae sp CSR040
Propalticidae Propalticus CSR042
Laemophloeidae Cryptolestes INB193
Laemophloeidae Laemophloeus CSR110
Nemonychidae Aragomacer CSR120
Anthribidae Acorynus INB007
Anthribidae Ozotomerus INB043
Anthribidae Peribathys INB102
Anthribidae Xylinada INB054
Belidae Rhinotia CSR067
Attelabidae Paratrachelophorus INB188
Attelabidae Phymatapoderus INB051
Attelabidae Byctiscus INB076
Attelabidae Involvulus INB074
Brentidae Cylas INB199
Brentidae Baryrhynchus INB044
Brentidae Apion CSR075
Brentidae Apion INB075
Curculionidae Platypodinae sp INB045
Curculionidae Episomus INB010
Curculionidae Xylosandrus INB048
Curculionidae Curculio INB184
Curculionidae Peribleptus INB185
Megalopodidae Temnaspis INB031
Cerambycidae Strangalia INB066
Cerambycidae Oberea INB067
Cerambycidae Spondylis INB068
Cerambycidae Dorysthenes INB150
Cerambycidae Xylotrechus INB069
Chrysomelidae Lilioceris INB135
Chrysomelidae Sominella INB138
Chrysomelidae Bruchidius INB144
Chrysomelidae Sagra INB134
Chrysomelidae Chrysomela INB019
Chrysomelidae Altica INB141
Chrysomelidae Galerucinae sp INB140
Chrysomelidae Dactylispa INB136
Chrysomelidae Anisodera INB137
Chrysomelidae Cassida INB006
Chrysomelidae Trichochrysea INB139
Chrysomelidae Oomorphoides INB142
Chrysomelidae Chlamisus INB077
Chrysomelidae Cryptocephalus INB143

Figure S7. Phylogeny of Coleoptera inferred with the site-homogeneous ML model GTR20 implemented in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
Myrmeleontidae Myrmeleon IN53
Ascalaphidae Ascalohybris IN56
Torridincolidae Satonius INB116
Cupedidae Tenomerga INB118
Haliplidae Peltodytes INB121
Gyrinidae Orectochilus INB037
Noteridae sp CSR039
Noteridae Canthydrus INB115
Dytiscidae Laccophilus INB111
Dytiscidae Hyphydrus INB114
Dytiscidae Eretes INB112
Dytiscidae Rhantus INB113
Dytiscidae Agabus INB109
Carabidae Cicindela INB101
Carabidae Paussinae sp TH2
Carabidae Omoglymmius INB120
Carabidae Elaphrus INB212
Carabidae Carabus INB100
Carabidae Clivina INB167
Carabidae Pheropsophus INB168
Carabidae Dischissus INB013
Carabidae Pentagonica INB171
Carabidae Lebia INB170
Scirtidae Pseudomicrocara CSR143
Scirtidae Scirtinae sp INB041
Scirtidae Elodes INB133
Derodontidae Derodontus CSR091
Clambidae Clambus CSR082
Eucinetidae Noteucinetus CSR103
Eucinetidae Noteucinetus CSR021
Rhinorhipus
Rhipiceridae Oligorhipis CSR049
Dascillidae Metallidascillus INB200
Dascillidae Dascillus INB028
Buprestidae Dicerca INB083
Buprestidae Trachys INB084
Buprestidae Coroebus INB018
Byrrhidae Microchaetes CSR076
Byrrhidae Notolioon CSR008
Byrrhidae Cytilus INB053
Dryopidae Pachyparnus INB166
Dryopidae Helichus INB194
Dryopidae Helichus CSR019
Eulichadidae Eulichas INB025
Callirhipidae Simianus INB119
Callirhipidae Ennometes CSR009
Ptilodactylidae Ptilodactyla INB015
Ptilodactylidae Epilichas INB079
Chelonariidae Chelonarium CSR012
Psephenidae Sclerocyphon CSR043
Psephenidae Mataeopsephus INB081
Psephenidae Schinostethus INB080
Psephenidae Schinostethus INB052
Elmidae Stetholus CSR094
Elmidae Stenelmis INB038
Elmidae Graphelmis CSR093
Limnichidae Cephalobyrrhus INB082
Heteroceridae Heterocerus INB092
Limnichidae Limnichus TH1
Limnichidae Pelochares INB042
Limnichidae Byrrhinus CSR112
Artematopodidae Eurypogon INB202
Artematopodidae Artematopus CSR004
Omethidae Drilonius INB129
Omethidae Drilonius INB127
Throscidae Trixagus INB125
Throscidae Trixagus CSR056
Eucnemidae Anischia CSR022
Eucnemidae Otho INB035
Eucnemidae Hemiopsida CSR104
Cantharidae Ichthyurus INB065
Cantharidae Malthinus INB154
Cantharidae Heteromastix CSR077
Cantharidae Laemoglyptus INB153
Cantharidae Lycocerus INB155
Cantharidae Prothemus INB064
Cantharidae Fissocantharis INB156
Cantharidae Themus INB063
Cantharidae Themus INB001
Elateridae Osslimus CSR092
Lycidae Benibotarus YL0447
Lycidae Lycostomus YL0616
Lycidae Platerodrilus YL0458
Lycidae Macrolycus YL0509
Lycidae Dilophotes YL0454
Lycidae Porrostoma CSR113
Lycidae Libnetis YL0478
Elateridae Agrypnus INB160
Elateridae Denticollis INB165
Elateridae Denticollis INB162
Elateridae Pectocera INB159
Elateridae Cardiotarsus INB210
Elateridae sp INB164
Elateridae Penia INB163
Elateridae Cebrio TH4
Elateridae Ampedus INB161
Elateridae Melanotus INB211
Elateridae Hemicrepidius INB016
Phengodidae Stenophrixothrix CSR041
Rhagophthalmidae sp INB128
Rhagophthalmidae Rhagophthalmus CSR132
Rhagophthalmidae Rhagophthalmus CSR048
Lampyridae Gorhamia TH3
Lampyridae Drilaster INB157
Lampyridae Pristolycus INB060
Lampyridae Luciola INB061
Lampyridae Cyphonocerus INB062
Lampyridae Vesta INB059
Lampyridae Pyrocoelia INB017
Lampyridae Diaphanes INB158
Nosodendridae Nosodendron CSR038
Histeridae Saprinus CSR024
Histeridae Platysoma CSR023
Hydrophilidae Georissus INB106
Hydrophilidae Sphaeridium INB107
Hydrophilidae Helochares CSR108
Hydrophilidae Anacaena INB105
Hydrophilidae Berosus INB152
Hydrophilidae Oocyclus INB014
Hydrophilidae Sternolophus CSR107
Hydrophilidae Hydrophilus INB103
Ptiliidae sp CSR044
Hydraenidae Hydraena INB108
Jacobsoniidae Derolathrus CSR109
Jacobsoniidae Derolathrus CSR026
Agyrtidae Pteroloma INB201
Leiodidae Agathidium CSR032
Leiodidae Cholevinae sp CSR031
Leiodidae Agyrtodes CSR030
Staphylinidae Omaliinae sp INB176
Staphylinidae Centrophthalmus INB091
Silphidae Nicrophorus INB022
Silphidae Necrodes INB078
Staphylinidae Apatetica INB085
Staphylinidae Priochirus INB086
Staphylinidae Osorius INB087
Staphylinidae Scaphidium INB089
Staphylinidae Scaphidium CSR054
Staphylinidae Scydmaeninae sp CSR146
Staphylinidae Tachinus INB090
Staphylinidae Tachinus INB088
Staphylinidae Dianous INB175
Staphylinidae Megalopaederus INB030
Staphylinidae Staphylinus INB008
Staphylinidae Staphylininae sp INB174
Trogidae Trox INB036
Trogidae Omorgus CSR057
Lucanidae Phalacrognathus INB098
Lucanidae Cyclommatus INB099
Lucanidae Aegus INB148
Geotrupidae Australobolbus CSR137
Geotrupidae Geotrupes INB097
Passalidae Ceracupes INB057
Passalidae Aceraius INB096
Glaphyridae Amphicoma INB011
Scarabaeidae Rhyparus INB002
Scarabaeidae Onthophagus CSR142
Scarabaeidae Copris INB146
Hybosoridae Liparochrus CSR025
Hybosoridae Cyphopisthes CSR138
Scarabaeidae Cheirotonus INB151
Scarabaeidae Heteronyx CSR140
Scarabaeidae Ectinohoplia INB147
Scarabaeidae Protaetia INB104
Scarabaeidae Dasyvalgus INB149
Scarabaeidae Carneodon CSR139
Scarabaeidae Allomyrina INB169
Scarabaeidae Mimela INB145
Scarabaeidae Anomala CSR141
Dermestidae Dermestes CSR089
Dermestidae Orphinus INB130
Dermestidae Evorinea CSR090
Bostrichidae Polycaon INB032
Bostrichidae Lyctus CSR070
Ptinidae Hedobia INB204
Ptinidae Dorcatoma CSR046
Ptinidae Ptinus INB132
Ptinidae Ptinus CSR045
Bothrideridae Deretaphrus CSR072
Bothrideridae Ascetoderes CSR074
Cerylonidae Philothermus CSR011
Murmidiidae Murmidius CSR078
Discolomatidae Aphanocephalus CSR018
Euxestidae Hypodacnella CSR010
Cerylonidae Ostomopsis CSR079
Teredidae Teredolaemus CSR073
Teredidae Xylariophilus CSR071
Teredidae Xylariophilus CSR007
Alexiidae Sphaerosoma CSR002
Latridiidae Enicmus CSR028
Latridiidae Melanophthalma CSR111
Latridiidae Corticaria CSR029
Anamorphidae Papuella CSR095
Endomychidae Holoparamecus CSR096
Corylophidae Periptyctus CSR086
Corylophidae Priamima CSR085
Corylophidae Sericoderus CSR014
Corylophidae Orthoperus INB209
Endomychidae Stenotarsus CSR098
Endomychidae Cyclotoma CSR020
Endomychidae Sinocymbachus INB005
Endomychidae Encymon CSR097
Coccinellidae Microfreudea C33
Coccinellidae Stethorus C54
Coccinellidae Harmonia C10
Coccinellidae Exochomus C25
Coccinellidae Rhizobius C28
Coccinellidae Chnootriba C04
Coccinellidae Sasajiscymnus C44
Coccinellidae Ortalia C31
Erotylidae Tetraphala INB029
Erotylidae Anadastus CSR100
Erotylidae Thallis CSR099
Erotylidae Cryptophilus CSR102
Erotylidae Episcaphula CSR101
Erotylidae Episcapha INB023
Protocucujidae Ericmodes CSR129
Helotidae Neohelota INB004
Boganiidae Paracucujus CSR006
Sphindidae Aspidiphorus CSR053
Hobartiidae Hydnobioides CSR106
Cryptophagidae Micrambina CSR015
Cryptophagidae Curelius INB192
Silvanidae Silvanoprus CSR145
Silvanidae Psammoecus INB095
Silvanidae Uleiota CSR052
Silvanidae Psammoecus INB124
Silvanidae Cryptamorpha CSR144
Cucujidae Platisus CSR016
Cucujidae Pediacus CSR087
Myraboliidae Myrabolia CSR037
Phloeostichidae Rhopalobrachium CSR128
Phloeostichidae Hymaea CSR127
Passandridae Passandra CSR125
Propalticidae Propalticus CSR042
Laemophloeidae Laemophloeus CSR110
Laemophloeidae Cryptolestes INB193
Phalacridae Phalacrinus CSR126
Phalacridae sp CSR040
Phalacridae Olibrus INB122
Monotomidae Rhizophagus CSR119
Monotomidae Thione INB207
Monotomidae Monotomopsis CSR118
Monotomidae Mimemodes CSR034
Kateretidae Notobrachypterus CSR027
Cybocephalidae Cybocephalus CSR088
Nitidulidae Glischrochilus INB197
Nitidulidae Pallodes CSR122
Nitidulidae Brachypeplus CSR121
Nitidulidae Urophorus INB056
Nitidulidae Carpophilus INB196
Nemonychidae Aragomacer CSR120
Anthribidae Acorynus INB007
Anthribidae Ozotomerus INB043
Anthribidae Xylinada INB054
Anthribidae Peribathys INB102
Belidae Rhinotia CSR067
Attelabidae Involvulus INB074
Attelabidae Byctiscus INB076
Attelabidae Phymatapoderus INB051
Attelabidae Paratrachelophorus INB188
Brentidae Cylas INB199
Brentidae Baryrhynchus INB044
Brentidae Apion INB075
Brentidae Apion CSR075
Curculionidae Platypodinae sp INB045
Curculionidae Episomus INB010
Curculionidae Xylosandrus INB048
Curculionidae Peribleptus INB185
Curculionidae Curculio INB184
Cerambycidae Strangalia INB066
Cerambycidae Spondylis INB068
Cerambycidae Oberea INB067
Cerambycidae Xylotrechus INB069
Cerambycidae Dorysthenes INB150
Megalopodidae Temnaspis INB031
Chrysomelidae Sagra INB134
Chrysomelidae Bruchidius INB144
Chrysomelidae Sominella INB138
Chrysomelidae Lilioceris INB135
Chrysomelidae Chrysomela INB019
Chrysomelidae Galerucinae sp INB140
Chrysomelidae Altica INB141
Chrysomelidae Dactylispa INB136
Chrysomelidae Cassida INB006
Chrysomelidae Anisodera INB137
Chrysomelidae Cryptocephalus INB143
Chrysomelidae Chlamisus INB077
Chrysomelidae Trichochrysea INB139
Chrysomelidae Oomorphoides INB142
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
Biphyllidae Biphyllus CSR068
Biphyllidae Althaesia CSR005
Thanerocleridae Isoclerus CSR055
Cleridae Allochotes INB191
Cleridae Tenerus CSR083
Cleridae Necrobia CSR084
Cleridae Cladiscus INB189
Cleridae Xenorthrius INB012
Cleridae Stenocallimerus INB190
Acanthocnemidae Acanthocnemus CSR062
Trogossitidae Thymalus INB024
Trogossitidae Larinotus CSR058
Trogossitidae Leperina CSR160
Trogossitidae Parapeltis CSR159
Trogossitidae Ancyrona CSR158
Prionoceridae Idgia INB040
Melyridae Dasytes CSR115
Melyridae Carphurus INB131
Melyridae Carphurus CSR117
Melyridae Malachiinae sp INB003
Melyridae Dicranolaius CSR116
Lymexylidae Melittomma CSR033
Lymexylidae Atractocerus INB094
Ripiphoridae Trigonodera CSR050
Ripiphoridae Rhipidioides CSR133
Mordellidae Hoshihananomia INB034
Scraptiidae Scraptia INB205
Ischaliidae Ischalia INB049
Aderidae sp INB206
Aderidae sp CSR001
Mycteridae Trichosalpingus CSR036
Oedemeridae Ditylus INB033
Oedemeridae Thelyphassa CSR123
Oedemeridae Pseudolycus CSR124
Pythidae Anaplopus CSR131
Salpingidae Ocholissa CSR136
Salpingidae Euryplatus CSR134
Salpingidae Orphanotrophium CSR135
Salpingidae Orphanotrophium CSR051
Trictenotomidae Trictenotoma INB208
Boridae Synercticus CSR069
Pyrochroidae Pseudopyrochroa INB020
Pyrochroidae Eupyrochroa INB027
Pyrochroidae Morpholycus CSR130
Pyrochroidae Morpholycus CSR047
Anthicidae Macratria INB050
Anthicidae Macratria CSR065
Anthicidae Trichananca CSR064
Anthicidae Lemodes CSR003
Anthicidae Anthicus CSR063
Meloidae Zonitis CSR114
Meloidae Epicauta INB093
Melandryidae Dircaeomorpha INB055
Incertae sedis Rhizonium CSR105
Melandryidae Melandryinae sp INB203
Zopheridae Zopherosis CSR163
Zopheridae Monomma CSR060
Zopheridae Bitoma CSR061
Ciidae Cis CSR013
Ciidae Cis CSR080
Ciidae Australocis CSR081
Mycetophagidae Nototriphyllus CSR035
Mycetophagidae Mycetophagus INB047
Archeocrypticidae Wattianus CSR066
Ulodidae Ulodes CSR161
Ulodidae Meryx CSR162
Tenebrionidae Adelium CSR149
Tenebrionidae Ecnolagria CSR157
Tenebrionidae Chlorophila INB046
Tenebrionidae Cryphaeus INB181
Tenebrionidae Cyphaleus CSR148
Tenebrionidae Cossyphus CSR153
Tenebrionidae Cillibus CSR150
Tenebrionidae Platydema CSR155
Tenebrionidae Amarygmus CSR147
Tenebrionidae Tanychilus CSR154
Tenebrionidae Cteniopinus INB073
Tenebrionidae Strongylium INB180
Tenebrionidae Palorus CSR151
Tenebrionidae Tyrtaeus CSR156
Tenebrionidae Derispia INB072
Tenebrionidae Derispia CSR152

Figure S8. Phylogeny of Coleoptera inferred with the site-homogeneous ML model LG+C20 implemented in IQ-TREE.


Tree scale: 0.1
Corydalidae Neochauliodes IN61
Chrysopidae Dichochrysa IN54
Ascalaphidae Ascalohybris IN56
Myrmeleontidae Myrmeleon IN53
Cupedidae Tenomerga INB118
Torridincolidae Satonius INB116
Gyrinidae Orectochilus INB037
Haliplidae Peltodytes INB121
Noteridae Canthydrus INB115
Noteridae sp CSR039
Dytiscidae Hyphydrus INB114
Dytiscidae Laccophilus INB111
Dytiscidae Eretes INB112
Dytiscidae Agabus INB109
Dytiscidae Rhantus INB113
Carabidae Cicindela INB101
Carabidae Omoglymmius INB120
Carabidae Paussinae sp TH2
Carabidae Carabus INB100
Carabidae Elaphrus INB212
Carabidae Clivina INB167
Carabidae Pheropsophus INB168
Carabidae Dischissus INB013
Carabidae Lebia INB170
Carabidae Pentagonica INB171
Scirtidae Pseudomicrocara CSR143
Scirtidae Elodes INB133
Scirtidae Scirtinae sp INB041
Derodontidae Derodontus CSR091
Clambidae Clambus CSR082
Eucinetidae Noteucinetus CSR021
Eucinetidae Noteucinetus CSR103
Rhinorhipus
Rhipiceridae Oligorhipis CSR049
Dascillidae Dascillus INB028
Dascillidae Metallidascillus INB200
Buprestidae Dicerca INB083
Buprestidae Coroebus INB018
Buprestidae Trachys INB084
Byrrhidae Microchaetes CSR076
Byrrhidae Cytilus INB053
Byrrhidae Notolioon CSR008
Dryopidae Pachyparnus INB166
Dryopidae Helichus CSR019
Dryopidae Helichus INB194
Eulichadidae Eulichas INB025
Callirhipidae Ennometes CSR009
Callirhipidae Simianus INB119
Ptilodactylidae Epilichas INB079
Ptilodactylidae Ptilodactyla INB015
Chelonariidae Chelonarium CSR012
Psephenidae Mataeopsephus INB081
Psephenidae Sclerocyphon CSR043
Psephenidae Schinostethus INB052
Psephenidae Schinostethus INB080
Elmidae Stetholus CSR094
Elmidae Graphelmis CSR093
Elmidae Stenelmis INB038
Heteroceridae Heterocerus INB092
Limnichidae Cephalobyrrhus INB082
Limnichidae Limnichus TH1
Limnichidae Byrrhinus CSR112
Limnichidae Pelochares INB042
Artematopodidae Artematopus CSR004
Artematopodidae Eurypogon INB202
Omethidae Drilonius INB127
Omethidae Drilonius INB129
Throscidae Trixagus CSR056
Throscidae Trixagus INB125
Eucnemidae Anischia CSR022
Eucnemidae Hemiopsida CSR104
Eucnemidae Otho INB035
Elateridae Osslimus CSR092
Lycidae Benibotarus YL0447
Lycidae Lycostomus YL0616
Lycidae Dilophotes YL0454
Lycidae Macrolycus YL0509
Lycidae Platerodrilus YL0458
Lycidae Libnetis YL0478
Lycidae Porrostoma CSR113
Elateridae Agrypnus INB160
Elateridae Denticollis INB162
Elateridae Denticollis INB165
Elateridae Pectocera INB159
Elateridae Cardiotarsus INB210
Elateridae Penia INB163
Elateridae sp INB164
Cantharidae Ichthyurus INB065
Cantharidae Malthinus INB154
Cantharidae Heteromastix CSR077
Cantharidae Laemoglyptus INB153
Cantharidae Lycocerus INB155
Cantharidae Fissocantharis INB156
Cantharidae Prothemus INB064
Cantharidae Themus INB001
Cantharidae Themus INB063
Elateridae Cebrio TH4
Elateridae Ampedus INB161
Elateridae Hemicrepidius INB016
Elateridae Melanotus INB211
Phengodidae Stenophrixothrix CSR041
Rhagophthalmidae sp INB128
Rhagophthalmidae Rhagophthalmus CSR048
Rhagophthalmidae Rhagophthalmus CSR132
Lampyridae Drilaster INB157
Lampyridae Gorhamia TH3
Lampyridae Luciola INB061
Lampyridae Pristolycus INB060
Lampyridae Cyphonocerus INB062
Lampyridae Vesta INB059
Lampyridae Diaphanes INB158
Lampyridae Pyrocoelia INB017
Nosodendridae Nosodendron CSR038
Histeridae Platysoma CSR023
Histeridae Saprinus CSR024
Hydrophilidae Georissus INB106
Hydrophilidae Anacaena INB105
Hydrophilidae Helochares CSR108
Hydrophilidae Sphaeridium INB107
Hydrophilidae Oocyclus INB014
Hydrophilidae Berosus INB152
Hydrophilidae Hydrophilus INB103
Hydrophilidae Sternolophus CSR107
Hydraenidae Hydraena INB108
Ptiliidae sp CSR044
Jacobsoniidae Derolathrus CSR026
Jacobsoniidae Derolathrus CSR109
Agyrtidae Pteroloma INB201
Leiodidae Agathidium CSR032
Leiodidae Agyrtodes CSR030
Leiodidae Cholevinae sp CSR031
Staphylinidae Centrophthalmus INB091
Staphylinidae Omaliinae sp INB176
Staphylinidae Scydmaeninae sp CSR146
Staphylinidae Megalopaederus INB030
Staphylinidae Staphylininae sp INB174
Staphylinidae Staphylinus INB008
Staphylinidae Dianous INB175
Staphylinidae Tachinus INB088
Staphylinidae Tachinus INB090
Silphidae Necrodes INB078
Silphidae Nicrophorus INB022
Staphylinidae Apatetica INB085
Staphylinidae Osorius INB087
Staphylinidae Priochirus INB086
Staphylinidae Scaphidium CSR054
Staphylinidae Scaphidium INB089
Trogidae Omorgus CSR057
Trogidae Trox INB036
Lucanidae Phalacrognathus INB098
Lucanidae Aegus INB148
Lucanidae Cyclommatus INB099
Geotrupidae Australobolbus CSR137
Geotrupidae Geotrupes INB097
Passalidae Aceraius INB096
Passalidae Ceracupes INB057
Glaphyridae Amphicoma INB011
Scarabaeidae Rhyparus INB002
Scarabaeidae Copris INB146
Scarabaeidae Onthophagus CSR142
Hybosoridae Cyphopisthes CSR138
Hybosoridae Liparochrus CSR025
Scarabaeidae Cheirotonus INB151
Scarabaeidae Heteronyx CSR140
Scarabaeidae Ectinohoplia INB147
Scarabaeidae Dasyvalgus INB149
Scarabaeidae Protaetia INB104
Scarabaeidae Allomyrina INB169
Scarabaeidae Carneodon CSR139
Scarabaeidae Anomala CSR141
Scarabaeidae Mimela INB145
Dermestidae Evorinea CSR090
Dermestidae Dermestes CSR089
Dermestidae Orphinus INB130
Bostrichidae Lyctus CSR070
Bostrichidae Polycaon INB032
Ptinidae Dorcatoma CSR046
Ptinidae Hedobia INB204
Ptinidae Ptinus CSR045
Ptinidae Ptinus INB132
Bothrideridae Ascetoderes CSR074
Bothrideridae Deretaphrus CSR072
Discolomatidae Aphanocephalus CSR018
Murmidiidae Murmidius CSR078
Cerylonidae Philothermus CSR011
Cerylonidae Ostomopsis CSR079
Euxestidae Hypodacnella CSR010
Teredidae Teredolaemus CSR073
Teredidae Xylariophilus CSR007
Teredidae Xylariophilus CSR071
Alexiidae Sphaerosoma CSR002
Latridiidae Enicmus CSR028
Latridiidae Corticaria CSR029
Latridiidae Melanophthalma CSR111
Anamorphidae Papuella CSR095
Corylophidae Periptyctus CSR086
Corylophidae Priamima CSR085
Corylophidae Orthoperus INB209
Corylophidae Sericoderus CSR014
Endomychidae Cyclotoma CSR020
Endomychidae Stenotarsus CSR098
Endomychidae Encymon CSR097
Endomychidae Sinocymbachus INB005
Endomychidae Holoparamecus CSR096
Coccinellidae Microfreudea C33
Coccinellidae Stethorus C54
Coccinellidae Exochomus C25
Coccinellidae Harmonia C10
Coccinellidae Rhizobius C28
Coccinellidae Ortalia C31
Coccinellidae Chnootriba C04
Coccinellidae Sasajiscymnus C44
Nemonychidae Aragomacer CSR120
Anthribidae Acorynus INB007
Anthribidae Ozotomerus INB043
Anthribidae Peribathys INB102
Anthribidae Xylinada INB054
Belidae Rhinotia CSR067
Attelabidae Byctiscus INB076
Attelabidae Involvulus INB074
Attelabidae Paratrachelophorus INB188
Attelabidae Phymatapoderus INB051
Brentidae Cylas INB199
Brentidae Baryrhynchus INB044
Brentidae Apion CSR075
Brentidae Apion INB075
Curculionidae Platypodinae sp INB045
Curculionidae Episomus INB010
Curculionidae Xylosandrus INB048
Curculionidae Curculio INB184
Curculionidae Peribleptus INB185
Megalopodidae Temnaspis INB031
Cerambycidae Spondylis INB068
Cerambycidae Strangalia INB066
Cerambycidae Oberea INB067
Cerambycidae Dorysthenes INB150
Cerambycidae Xylotrechus INB069
Chrysomelidae Bruchidius INB144
Chrysomelidae Sagra INB134
Chrysomelidae Lilioceris INB135
Chrysomelidae Sominella INB138
Chrysomelidae Chrysomela INB019
Chrysomelidae Altica INB141
Chrysomelidae Galerucinae sp INB140
Chrysomelidae Dactylispa INB136
Chrysomelidae Anisodera INB137
Chrysomelidae Cassida INB006
Chrysomelidae Chlamisus INB077
Chrysomelidae Cryptocephalus INB143
Chrysomelidae Oomorphoides INB142
Chrysomelidae Trichochrysea INB139
Boganiidae Paracucujus CSR006
Helotidae Neohelota INB004
Protocucujidae Ericmodes CSR129
Sphindidae Aspidiphorus CSR053
Monotomidae Rhizophagus CSR119
Monotomidae Thione INB207
Monotomidae Mimemodes CSR034
Monotomidae Monotomopsis CSR118
Kateretidae Notobrachypterus CSR027
Cybocephalidae Cybocephalus CSR088
Nitidulidae Glischrochilus INB197
Nitidulidae Brachypeplus CSR121
Nitidulidae Pallodes CSR122
Nitidulidae Carpophilus INB196
Nitidulidae Urophorus INB056
Erotylidae Anadastus CSR100
Erotylidae Tetraphala INB029
Erotylidae Cryptophilus CSR102
Erotylidae Thallis CSR099
Erotylidae Episcapha INB023
Erotylidae Episcaphula CSR101
Hobartiidae Hydnobioides CSR106
Cryptophagidae Curelius INB192
Cryptophagidae Micrambina CSR015
Silvanidae Psammoecus INB095
Silvanidae Silvanoprus CSR145
Silvanidae Uleiota CSR052
Silvanidae Cryptamorpha CSR144
Silvanidae Psammoecus INB124
Cucujidae Pediacus CSR087
Cucujidae Platisus CSR016
Myraboliidae Myrabolia CSR037
Phloeostichidae Hymaea CSR127
Phloeostichidae Rhopalobrachium CSR128
Passandridae Passandra CSR125
Propalticidae Propalticus CSR042
Laemophloeidae Cryptolestes INB193
Laemophloeidae Laemophloeus CSR110
Phalacridae Phalacrinus CSR126
Phalacridae Olibrus INB122
Phalacridae sp CSR040
Trogossitidae Rentonellum CSR059
Byturidae Haematoides INB039
Biphyllidae Althaesia CSR005
Biphyllidae Biphyllus CSR068
Thanerocleridae Isoclerus CSR055
Cleridae Tenerus CSR083
Cleridae Allochotes INB191
Cleridae Necrobia CSR084
Cleridae Cladiscus INB189
Cleridae Stenocallimerus INB190
Cleridae Xenorthrius INB012
Acanthocnemidae Acanthocnemus CSR062
Trogossitidae Larinotus CSR058
Trogossitidae Thymalus INB024
Trogossitidae Leperina CSR160
Trogossitidae Ancyrona CSR158
Trogossitidae Parapeltis CSR159
Prionoceridae Idgia INB040
Melyridae Dasytes CSR115
Melyridae Carphurus CSR117
Melyridae Carphurus INB131
Melyridae Dicranolaius CSR116
Melyridae Malachiinae sp INB003
Lymexylidae Atractocerus INB094
Lymexylidae Melittomma CSR033
Ripiphoridae Trigonodera CSR050
Mordellidae Hoshihananomia INB034
Ripiphoridae Rhipidioides CSR133
Ischaliidae Ischalia INB049
Aderidae sp CSR001
Aderidae sp INB206
Scraptiidae Scraptia INB205
Mycteridae Trichosalpingus CSR036
Oedemeridae Ditylus INB033
Oedemeridae Pseudolycus CSR124
Oedemeridae Thelyphassa CSR123
Boridae Synercticus CSR069
Trictenotomidae Trictenotoma INB208
Pythidae Anaplopus CSR131
Salpingidae Ocholissa CSR136
Salpingidae Euryplatus CSR134
Salpingidae Orphanotrophium CSR051
Salpingidae Orphanotrophium CSR135
Pyrochroidae Eupyrochroa INB027
Pyrochroidae Pseudopyrochroa INB020
Pyrochroidae Morpholycus CSR047
Pyrochroidae Morpholycus CSR130
Anthicidae Macratria CSR065
Anthicidae Macratria INB050
Anthicidae Lemodes CSR003
Anthicidae Trichananca CSR064
Anthicidae Anthicus CSR063
Meloidae Epicauta INB093
Meloidae Zonitis CSR114
Incertae sedis Rhizonium CSR105
Zopheridae Monomma CSR060
Melandryidae Melandryinae sp INB203
Zopheridae Zopherosis CSR163
Melandryidae Dircaeomorpha INB055
Zopheridae Bitoma CSR061
Ciidae Cis CSR013
Ciidae Australocis CSR081
Ciidae Cis CSR080
Mycetophagidae Mycetophagus INB047
Mycetophagidae Nototriphyllus CSR035
Archeocrypticidae Wattianus CSR066
Ulodidae Meryx CSR162
Ulodidae Ulodes CSR161
Tenebrionidae Adelium CSR149
Tenebrionidae Chlorophila INB046
Tenebrionidae Ecnolagria CSR157
Tenebrionidae Cryphaeus INB181
Tenebrionidae Cyphaleus CSR148
Tenebrionidae Cillibus CSR150
Tenebrionidae Cossyphus CSR153
Tenebrionidae Amarygmus CSR147
Tenebrionidae Platydema CSR155
Tenebrionidae Cteniopinus INB073
Tenebrionidae Tanychilus CSR154
Tenebrionidae Palorus CSR151
Tenebrionidae Strongylium INB180
Tenebrionidae Tyrtaeus CSR156
Tenebrionidae Derispia CSR152
Tenebrionidae Derispia INB072

Figure S9. Dated phylogenetic tree of Coleoptera; autocorrelated rate clock.


Corydalidae_Neochauliodes
Chrysopidae_Dichochrysa
Myrmeleontidae_Myrmeleon
Ascalaphidae_Ascalohybris
Haliplidae_Peltodytes
Gyrinidae_Orectochilus
Noteridae_sp
Noteridae_Canthydrus
Dytiscidae_Laccophilus
Dytiscidae_Hyphydrus
Dytiscidae_Eretes
Dytiscidae_Rhantus
Dytiscidae_Agabus
Carabidae_Cicindela
Carabidae_Paussinae_sp
Carabidae_Omoglymmius
Carabidae_Elaphrus
Carabidae_Carabus
Carabidae_Clivina
Carabidae_Pheropsophus
Carabidae_Dischissus
Carabidae_Pentagonica
Carabidae_Lebia
Torridincolidae_Satonius
Cupedidae_Tenomerga
Scirtidae_Pseudomicrocara
Scirtidae_Scirtinae_sp
Scirtidae_Elodes
Derodontidae_Derodontus
Clambidae_Clambus
Eucinetidae_Noteucinetus_1
Eucinetidae_Noteucinetus_2
Rhinorhipidae_Rhinorhipus
Rhipiceridae_Oligorhipis
Dascillidae_Metallidascillus
Dascillidae_Dascillus
Byrrhidae_Cytilus
Byrrhidae_Notolioon
Byrrhidae_Microchaetes
Buprestidae_Dicerca
Buprestidae_Trachys
Buprestidae_Coroebus
Dryopidae_Pachyparnus
Dryopidae_Helichus_1
Dryopidae_Helichus_2
Eulichadidae_Eulichas
Callirhipidae_Simianus
Callirhipidae_Ennometes
Ptilodactylidae_Ptilodactyla
Ptilodactylidae_Epilichas
Chelonariidae_Chelonarium
Psephenidae_Schinostethus_1
Psephenidae_Schinostethus_2
Psephenidae_Sclerocyphon
Psephenidae_Mataeopsephus
Elmidae_Stetholus
Elmidae_Stenelmis
Elmidae_Graphelmis
Limnichidae_Cephalobyrrhus
Heteroceridae_Heterocerus
Limnichidae_Limnichus
Limnichidae_Pelochares
Limnichidae_Byrrhinus
Omethidae_Drilonius_1
Omethidae_Drilonius_2
Artematopodidae_Eurypogon
Artematopodidae_Artematopus
Throscidae_Trixagus_1
Throscidae_Trixagus_2
Eucnemidae_Anischia
Eucnemidae_Otho
Eucnemidae_Hemiopsida
Elateridae_Osslimus
Lycidae_Benibotarus
Lycidae_Lycostomus
Lycidae_Platerodrilus
Lycidae_Porrostoma
Lycidae_Libnetis
Lycidae_Macrolycus
Lycidae_Dilophotes
Elateridae_Cebrio
Elateridae_Ampedus
Elateridae_Melanotus
Elateridae_Hemicrepidius
Phengodidae_Stenophrixothrix
Rhagophthalmidae_sp
Rhagophthalmidae_Rhagophthalmus_1
Rhagophthalmidae_Rhagophthalmus_2
Lampyridae_Gorhamia
Lampyridae_Drilaster
Lampyridae_Pristolycus
Lampyridae_Luciola
Lampyridae_Cyphonocerus
Lampyridae_Vesta
Lampyridae_Pyrocoelia
Lampyridae_Diaphanes
Elateridae_Agrypnus
Elateridae_Denticollis_1
Elateridae_Denticollis_2
Elateridae_Pectocera
Elateridae_Cardiotarsus
Elateridae_sp
Elateridae_Penia
Cantharidae_Ichthyurus
Cantharidae_Malthinus
Cantharidae_Heteromastix
Cantharidae_Laemoglyptus
Cantharidae_Fissocantharis
Cantharidae_Prothemus
Cantharidae_Lycocerus
Cantharidae_Themus_1
Cantharidae_Themus_2
Nosodendridae_Nosodendron
Histeridae_Saprinus
Histeridae_Platysoma
Georissidae_Georissus
Hydrophilidae_Anacaena
Hydrophilidae_Sphaeridium
Hydrophilidae_Helochares
Hydrophilidae_Oocyclus
Hydrophilidae_Berosus
Hydrophilidae_Sternolophus
Hydrophilidae_Hydrophilus
Trogidae_Trox
Trogidae_Omorgus
Lucanidae_Phalacrognathus
Lucanidae_Cyclommatus
Lucanidae_Aegus
Geotrupidae_Australobolbus
Geotrupidae_Geotrupes
Passalidae_Ceracupes
Passalidae_Aceraius
Glaphyridae_Amphicoma
Scarabaeidae_Rhyparus
Scarabaeidae_Onthophagus
Scarabaeidae_Copris
Hybosoridae_Liparochrus
Hybosoridae_Cyphopisthes
Scarabaeidae_Cheirotonus
Scarabaeidae_Heteronyx
Scarabaeidae_Ectinohoplia
Scarabaeidae_Protaetia
Scarabaeidae_Dasyvalgus
Scarabaeidae_Mimela
Scarabaeidae_Anomala
Scarabaeidae_Carneodon
Scarabaeidae_Allomyrina
Jacobsoniidae_Derolathrus_1
Jacobsoniidae_Derolathrus_2
Ptiliidae_sp
Hydraenidae_Hydraena
Agyrtidae_Pteroloma
Leiodidae_Agathidium
Leiodidae_Cholevinae_sp
Leiodidae_Agyrtodes
Staphylinidae_Omaliinae_sp
Staphylinidae_Centrophthalmus
Staphylinidae_Dianous
Staphylinidae_Scydmaeninae_sp
Staphylinidae_Tachinus_1
Staphylinidae_Tachinus_2
Staphylinidae_Megalopaederus
Staphylinidae_Staphylinus
Staphylinidae_Staphylininae_sp
Silphidae_Nicrophorus
Silphidae_Necrodes
Staphylinidae_Osorius
Staphylinidae_Apatetica
Staphylinidae_Priochirus
Staphylinidae_Scaphidium_1
Staphylinidae_Scaphidium_2
Dermestidae_Dermestes
Dermestidae_Orphinus
Dermestidae_Evorinea
Bostrichidae_Polycaon
Bostrichidae_Lyctus
Ptinidae_Ptinus_1
Ptinidae_Ptinus_2
Ptinidae_Hedobia
Ptinidae_Dorcatoma
Trogossitidae_Rentonellum
Byturidae_Haematoides
Biphyllidae_Biphyllus
Biphyllidae_Althaesia
Trogossitidae_Leperina
Acanthocnemidae_Acanthocnemus
Trogossitidae_Thymalus
Trogossitidae_Larinotus
Thanerocleridae_Isoclerus
Cleridae_Cladiscus
Cleridae_Xenorthrius
Cleridae_Stenocallimerus
Cleridae_Tenerus
Cleridae_Necrobia
Cleridae_Allochotes
Trogossitidae_Parapeltis
Trogossitidae_Ancyrona
Prionoceridae_Idgia
Melyridae_Dasytes
Melyridae_Malachiinae_sp
Melyridae_Dicranolaius
Melyridae_Carphurus_1
Melyridae_Carphurus_2
Lymexylidae_Melittomma
Lymexylidae_Atractocerus
Ripiphoridae_Rhipidioides
Ripiphoridae_Trigonodera
Mordellidae_Hoshihananomia
Ischaliidae_Ischalia
Aderidae_sp_1
Aderidae_sp_2
Trictenotomidae_Trictenotoma
Scraptiidae_Scraptia
Mycteridae_Trichosalpingus
Oedemeridae_Ditylus
Oedemeridae_Thelyphassa
Oedemeridae_Pseudolycus
Pythidae_Anaplopus
Salpingidae_Ocholissa
Salpingidae_Euryplatus
Salpingidae_Orphanotrophium_1
Salpingidae_Orphanotrophium_2
Boridae_Synercticus
Pyrochroidae_Morpholycus_1
Pyrochroidae_Morpholycus_2
Pyrochroidae_Pseudopyrochroa
Pyrochroidae_Eupyrochroa
Anthicidae_Macratria_1
Anthicidae_Macratria_2
Anthicidae_Trichananca
Anthicidae_Lemodes
Anthicidae_Anthicus
Meloidae_Zonitis
Meloidae_Epicauta
Zopheridae_Bitoma
Incertae_sedis_Rhizonium
Melandryidae_Melandryinae_sp
Zopheridae_Zopherosis
Zopheridae_Monomma
Melandryidae_Dircaeomorpha
Ciidae_Cis_1
Ciidae_Cis_2
Ciidae_Australocis
Ulodidae_Ulodes
Ulodidae_Meryx
Archeocrypticidae_Wattianus
Mycetophagidae_Nototriphyllus
Mycetophagidae_Mycetophagus
Tenebrionidae_Adelium
Tenebrionidae_Ecnolagria
Tenebrionidae_Chlorophila
Tenebrionidae_Cyphaleus
Tenebrionidae_Cossyphus
Tenebrionidae_Cillibus
Tenebrionidae_Cryphaeus
Tenebrionidae_Tanychilus
Tenebrionidae_Cteniopinus
Tenebrionidae_Platydema
Tenebrionidae_Amarygmus
Tenebrionidae_Strongylium
Tenebrionidae_Palorus
Tenebrionidae_Tyrtaeus
Tenebrionidae_Derispia_1
Tenebrionidae_Derispia_2
Bothrideridae_Deretaphrus
Bothrideridae_Ascetoderes
Cerylonidae_Philothermus
Murmidiidae_Murmidius
Discolomatidae_Aphanocephalus
Euxestidae_Hypodacnella
Cerylonidae_Ostomopsis
Teredidae_Teredolaemus
Teredidae_Xylariophilus_1
Teredidae_Xylariophilus_2
Alexiidae_Sphaerosoma
Latridiidae_Enicmus
Latridiidae_Melanophthalma
Latridiidae_Corticaria
Anamorphidae_Papuella
Corylophidae_Periptyctus
Corylophidae_Priamima
Corylophidae_Sericoderus
Corylophidae_Orthoperus
Endomychidae_Holoparamecus
Endomychidae_Sinocymbachus
Endomychidae_Encymon
Endomychidae_Stenotarsus
Endomychidae_Cyclotoma
Coccinellidae_Microfreudea
Coccinellidae_Stethorus
Coccinellidae_Harmonia
Coccinellidae_Exochomus
Coccinellidae_Rhizobius
Coccinellidae_Ortalia
Coccinellidae_Sasajiscymnus
Coccinellidae_Chnootriba
Boganiidae_Paracucujus
Erotylidae_Tetraphala
Erotylidae_Anadastus
Erotylidae_Cryptophilus
Erotylidae_Thallis
Erotylidae_Episcaphula
Erotylidae_Episcapha
Helotidae_Neohelota
Sphindidae_Aspidiphorus
Protocucujidae_Ericmodes
Monotomidae_Rhizophagus
Monotomidae_Thione
Monotomidae_Monotomopsis
Monotomidae_Mimemodes
Kateretidae_Notobrachypterus
Nitidulidae_Glischrochilus
Cybocephalidae_Cybocephalus
Nitidulidae_Urophorus
Nitidulidae_Carpophilus
Nitidulidae_Pallodes
Nitidulidae_Brachypeplus
Hobartiidae_Hydnobioides
Cryptophagidae_Micrambina
Cryptophagidae_Curelius
Silvanidae_Silvanoprus
Silvanidae_Psammoecus_2
Silvanidae_Uleiota
Silvanidae_Psammoecus_1
Silvanidae_Cryptamorpha
Cucujidae_Platisus
Cucujidae_Pediacus
Phloeostichidae_Rhopalobrachium
Phloeostichidae_Hymaea
Passandridae_Passandra
Myraboliidae_Myrabolia
Phalacridae_Phalacrinus
Phalacridae_sp
Phalacridae_Olibrus
Propalticidae_Propalticus
Laemophloeidae_Laemophloeus
Laemophloeidae_Cryptolestes
Nemonychidae_Aragomacer
Anthribidae_Acorynus
Anthribidae_Ozotomerus
Anthribidae_Xylinada
Anthribidae_Peribathys
Belidae_Rhinotia
Attelabidae_Phymatapoderus
Attelabidae_Paratrachelophorus
Attelabidae_Involvulus
Attelabidae_Byctiscus
Brentidae_Cylas
Brentidae_Baryrhynchus
Brentidae_Apion_1
Brentidae_Apion_2
Curculionidae_Platypodinae_sp
Curculionidae_Episomus
Curculionidae_Xylosandrus
Curculionidae_Peribleptus
Curculionidae_Curculio
Megalopodidae_Temnaspis
Cerambycidae_Strangalia
Cerambycidae_Spondylis
Cerambycidae_Oberea
Cerambycidae_Xylotrechus
Cerambycidae_Dorysthenes
Chrysomelidae_Sominella
Chrysomelidae_Lilioceris
Chrysomelidae_Sagra
Chrysomelidae_Bruchidius
Chrysomelidae_Chrysomela
Chrysomelidae_Galerucinae_sp
Chrysomelidae_Altica
Chrysomelidae_Dactylispa
Chrysomelidae_Cassida
Chrysomelidae_Anisodera
Chrysomelidae_Trichochrysea
Chrysomelidae_Oomorphoides
Chrysomelidae_Cryptocephalus
Chrysomelidae_Chlamisus
-3
-2,5
-2
-1,5
-1
-0,5
0

Figure S10. Dated phylogenetic tree of Coleoptera; independent rate clock.

Corydalidae_Neochauliodes
Chrysopidae_Dichochrysa
Myrmeleontidae_Myrmeleon
Ascalaphidae_Ascalohybris
Haliplidae_Peltodytes
Gyrinidae_Orectochilus
Noteridae_sp
Noteridae_Canthydrus
Dytiscidae_Laccophilus
Dytiscidae_Hyphydrus
Dytiscidae_Eretes
Dytiscidae_Rhantus
Dytiscidae_Agabus
Carabidae_Cicindela
Carabidae_Paussinae_sp
Carabidae_Omoglymmius
Carabidae_Elaphrus
Carabidae_Carabus
Carabidae_Clivina
Carabidae_Pheropsophus
Carabidae_Dischissus
Carabidae_Pentagonica
Carabidae_Lebia
Torridincolidae_Satonius
Cupedidae_Tenomerga
Scirtidae_Pseudomicrocara
Scirtidae_Scirtinae_sp
Scirtidae_Elodes
Derodontidae_Derodontus
Clambidae_Clambus
Eucinetidae_Noteucinetus_1
Eucinetidae_Noteucinetus_2
Rhinorhipidae_Rhinorhipus
Rhipiceridae_Oligorhipis
Dascillidae_Metallidascillus
Dascillidae_Dascillus
Byrrhidae_Cytilus
Byrrhidae_Nosodendron
Byrrhidae_Microchaetes
Buprestidae_Dicerca
Buprestidae_Trachys
Buprestidae_Coroebus
Dryopidae_Pachyparnus
Dryopidae_Helichus_1
Dryopidae_Helichus_2
Eulichadidae_Eulichas
Callirhipidae_Simianus
Callirhipidae_Ennometes
Ptilodactylidae_Ptilodactyla
Ptilodactylidae_Epilichas
Chelonariidae_Chelonarium
Psephenidae_Schinostethus_1
Psephenidae_Schinostethus_2
Psephenidae_Sclerocyphon
Psephenidae_Mataeopsephus
Elmidae_Stetholus
Elmidae_Stenelmis
Elmidae_Graphelmis
Limnichidae_Cephalobyrrhus
Heteroceridae_Heterocerus
Limnichidae_Limnichus
Lutrochidae_Lutrochus
Ptilodactylidae_Byrrhius
Drilonidae_Pelochares
Omethidae_Drilonius_1
Omethidae_Drilonius_2
Artematopodidae_Eurypogon
Artematopodidae_Artematopus
Throscidae_Trixagus_1
Throscidae_Trixagus_2
Eucnemidae_Anischia
Eucnemidae_Otho
Eucnemidae_Hemiopsida
Elateridae_Ossilinus
Lycidae_Benibotarus
Lycidae_Lycostomus
Lycidae_Platerodrilus
Lycidae_Porrostoma
Lycidae_Libnetis
Lycidae_Macrolycus
Lycidae_Dilophotes
Elateridae_Cebrio
Elateridae_Ampedus
Elateridae_Melanotus
Elateridae_Hemicrepidius
Phengodidae_Stenophrixothrix
Rhagophthalmidae_sp
Rhagophthalmidae_Rhagophthalmus_1
Rhagophthalmidae_Rhagophthalmus_2
Lampyridae_Gorhamia
Lampyridae_Drilaster
Lampyridae_Pristolycus
Lampyridae_Luciola
Lampyridae_Cyphonocerus
Lampyridae_Vesta
Lampyridae_Pyrocoelia
Lampyridae_Diaphanes
Elateridae_Agrypnus
Elateridae_Denticollis_1
Elateridae_Denticollis_2
Elateridae_Pectocera
Elateridae_Cardiotarsus
Elateridae_sp
Elateridae_Penia
Cantharidae_Ichthyurus
Cantharidae_Malthinus
Cantharidae_Heteromastix
Cantharidae_Laemoglyptus
Cantharidae_Fissocantharis
Cantharidae_Prothemus
Cantharidae_Lycocerus
Cantharidae_Themus_1
Cantharidae_Themus_2
Nosodendridae_Nosodendron
Histeridae_Saprinus
Histeridae_Platysoma
Georissidae_Georissus
Hydrophilidae_Anacaena
Hydrophilidae_Sphaeridium
Hydrophilidae_Helochares
Hydrophilidae_Cercyon
Hydrophilidae_Berosus
Hydrophilidae_Sternolophus
Hydrophilidae_Hydrophilus
Trogidae_Trox
Lucanidae_Phalacrognathus
Lucanidae_Cyclommatus
Lucanidae_Aegus
Geotrupidae_Australobolbus
Geotrupidae_Geotrupes
Passalidae_Ceracupes
Passalidae_Aceraius
Glaphyridae_Amphicoma
Scarabaeidae_Rhyparus
Scarabaeidae_Onthophagus
Scarabaeidae_Copris
Hybosoridae_Liparochrus
Hybosoridae_Cyphopisthes
Scarabaeidae_Cheirotonus
Scarabaeidae_Heteronyx
Scarabaeidae_Ectinohoplia
Scarabaeidae_Protaetia
Scarabaeidae_Dasyvalgus
Scarabaeidae_Mimela
Scarabaeidae_Anomala
Scarabaeidae_Carneodon
Scarabaeidae_Allomyrina
Jacobsoniidae_Derolathrus_1
Jacobsoniidae_Derolathrus_2
Ptiliidae_sp
Hydraenidae_Hydraena
Agyrtidae_Pteroloma
Leiodidae_Agathidium
Leiodidae_Cholevinae_sp
Leiodidae_Agyrtodes
Staphylinidae_Omaliinae_sp
Staphylinidae_Centrophthalmus
Staphylinidae_Dianous
Staphylinidae_Scydmaeninae_sp
Staphylinidae_Tachinus_1
Staphylinidae_Tachinus_2
Staphylinidae_Megalopaederus
Staphylinidae_Staphylinus
Staphylinidae_Staphylininae_sp
Silphidae_Nicrophorus
Silphidae_Necrodes
Staphylinidae_Osorius
Staphylinidae_Apatetica
Staphylinidae_Priochirus
Staphylinidae_Scaphidium_1
Staphylinidae_Scaphidium_2
Dermestidae_Dermestes
Dermestidae_Orphinus
Dermestidae_Evorinea
Bostrichidae_Polycaon
Bostrichidae_Lyctus
Ptinidae_Ptinus_1
Ptinidae_Ptinus_2
Ptinidae_Hedobia
Ptinidae_Dorcatoma
Trogossitidae_Rentonellum
Biphyllidae_Biphyllus
Biphyllidae_Althaesia
Trogossitidae_Leperina
Acanthocnemidae_Acanthocnemus
Trogossitidae_Thymalus
Trogossitidae_Tenebroides
Thanerocleridae_Isoclerus
Cleridae_Cladiscus
Cleridae_Stenocylidrus
Cleridae_Tenerus
Cleridae_Necrobia
Cleridae_Allochotes
Trogossitidae_Parapeltis
Trogossitidae_Ancyrona
Prionoceridae_Idgia
Melyridae_Malachiinae_sp
Melyridae_Dicranolaius
Melyridae_Laius
Lymexylidae_Melittomma
Lymexylidae_Atractocerus
Ripiphoridae_Ripidiodes
Ripiphoridae_Hoshihananomia
Mordellidae_Hoshihananomia
Ischaliidae_Ischalia
Aderidae_sp_1
Aderidae_sp_2
Trictenotomidae_Trictenotoma
Scraptiidae_Scraptia
Mycteridae_Trichodoma
Oedemeridae_Ditylus
Oedemeridae_Thelyphassa
Oedemeridae_Pseudolycus
Pythidae_Anoplodus
Salpingidae_Ocholissa
Salpingidae_Eurypalus
Boridae_Synercticus
Pyrochroidae_Morpholycus_1
Pyrochroidae_Morpholycus_2
Pyrochroidae_Pseudopyrochroa
Pyrochroidae_Eupyrochroa
Anthicidae_Macratria_1
Anthicidae_Macratria_2
Anthicidae_Trichananca
Anthicidae_Lemodes
Anthicidae_Anthicus
Meloidae_Zonitis
Meloidae_Epicauta
Zopheridae_Bitoma
Incertae_sedis_Rhizonium
Melandryidae_Melandryinae_sp
Zopheridae_Zopherosis
Zopheridae_Monomma
Melandryidae_Dircaeomorpha
Ciidae_Cis_1
Ciidae_Cis_2
Ciidae_Australocis
Ulodidae_Ulodes
Ulodidae_Meryx
Archeocrypticidae_Wattianus
Mycetophagidae_Nototriphyllus
Mycetophagidae_Mycetophagus
Tenebrionidae_Adelium
Tenebrionidae_Ecnolagria
Tenebrionidae_Chlorophila
Tenebrionidae_Cossyphus
Tenebrionidae_Cilibus
Tenebrionidae_Cryphaeus
Tenebrionidae_Tanychilus
Tenebrionidae_Cteniopinus
Tenebrionidae_Platydema
Tenebrionidae_Amarygmus
Tenebrionidae_Strongylium
Tenebrionidae_Palorus
Tenebrionidae_Tyrtaeus
Tenebrionidae_Derispia_1
Tenebrionidae_Derispia_2
Bothrideridae_Deretaphrus
Bothrideridae_Ascetoderes
Cerylonidae_Philothermus
Murmidiidae_Murmidius
Discolomatidae_Aphanocephalus
Euxestidae_Hypodacnella
Cerylonidae_Ostomopsis
Teredidae_Teredolaemus
Coryplophidae_Xylariophilus_1
Coryplophidae_Xylariophilus_2
Alexiidae_Sphaerosoma
Latridiidae_Enicmus
Latridiidae_Melanophthalma
Latridiidae_Corticaria
Anamorphidae_Papuella
Corylophidae_Periptyctus
Corylophidae_Priamma
Corylophidae_Sericoderus
Corylophidae_Orthoperus
Endomychidae_Holoparamecus
Endomychidae_Sinocymbachus
Endomychidae_Encymon
Endomychidae_Stenotarsus
Endomychidae_Cyclotoma
Coccinellidae_Microfreudea
Coccinellidae_Stethorus
Coccinellidae_Harmonia
Coccinellidae_Exochomus
Coccinellidae_Rhizobius
Coccinellidae_Ortalia
Coccinellidae_Sasajiscymnus
Coccinellidae_Chnootriba
Boganiidae_Paracucujus
Erotylidae_Tetraphala
Erotylidae_Anadastus
Erotylidae_Cryptophilus
Erotylidae_Thallis
Erotylidae_Episcapha
Helotidae_Neohelota
Sphindidae_Aspidiphorus
Protocucujidae_Ericmodes
Monotomidae_Rhizophagus
Monotomidae_Thione
Monotomidae_Monotomopsis
Monotomidae_Mimemodes
Kateretidae_Notobrachypterus
Nitidulidae_Gloschrochilus
Cybocephalidae_Cybocephalus
Nitidulidae_Urophorus
Nitidulidae_Carpophilus
Nitidulidae_Pallodes
Nitidulidae_Brachypeplus
Hobartiidae_Hydnobioides
Cryptophagidae_Micrambe
Cryptophagidae_Curelius
Silvanidae_Uleiota
Silvanidae_Silvanoprus
Silvanidae_Psammoecus_2
Silvanidae_Psammoecus_1
Silvanidae_Cryptamorpha
Cucujidae_Platisus
Cucujidae_Pediacus
Phloeostichidae_Rhopalobrachium
Phloeostichidae_Hymaea
Passandridae_Passandra
Myraboliidae_Myrabolia
Phalacridae_Phalacrinus
Phalacridae_sp
Phalacridae_Olibrus
Propalticidae_Propalticus
Laemophloeidae_Laemophloeus
Laemophloeidae_Cryptolestes
Nemonychidae_Aragomacer
Anthribidae_Acorynus
Anthribidae_Ozotomerus
Anthribidae_Xylinada
Anthribidae_Penthabrys
Belidae_Rhinotia
Attelabidae_Phymatapoderus
Attelabidae_Paratrachelophorus
Attelabidae_Involvulus
Attelabidae_Byctiscus
Brentidae_Cylas
Brentidae_Baryrhynchus
Brentidae_Apion_1
Brentidae_Apion_2
Curculionidae_Platypodinae_sp
Curculionidae_Episomus
Curculionidae_Xylosandrus
Curculionidae_Peribleptus
Curculionidae_Curculio
Megalopodidae_Temnaspis
Cerambycidae_Strangalia
Cerambycidae_Spondylis
Cerambycidae_Oberea
Cerambycidae_Xylotrechus
Cerambycidae_Leptura
Chrysomelidae_Sominella
Chrysomelidae_Lilioceris
Chrysomelidae_Sagra
Chrysomelidae_Bruchidius
Chrysomelidae_Chrysomela
Chrysomelidae_Galerucinae_sp
Chrysomelidae_Altica
Chrysomelidae_Dactylispa
Chrysomelidae_Aspidimorpha
Chrysomelidae_Trichochrysea
Chrysomelidae_Colasposoma
Chrysomelidae_Cryptocephalus
Chrysomelidae_Chlamisus
-3
-2.5
-2
-1.5
-1
-0.5
0

Fig. S11. 95% credibility intervals (CIs) for (a) the divergence of selected major beetle clades in the present and previous studies.


Corydalidae_Neochauliodes
Chrysopidae_Dichochrysa
Myrmeleontidae_Myrmeleon
Ascalaphidae_Ascalohybris
Haliplidae_Peltodytes
Gyrinidae_Orectochilus
Noteridae_sp
Noteridae_Canthydrus
Dytiscidae_Laccophilus
Dytiscidae_Hyphydrus
Dytiscidae_Eretes
Dytiscidae_Rhantus
Dytiscidae_Agabus
Carabidae_Cicindela
Carabidae_Paussinae_sp
Carabidae_Omoglymmius
Carabidae_Elaphrus
Carabidae_Carabus
Carabidae_Clivina
Carabidae_Pheropsophus
Carabidae_Dischissus
Carabidae_Pentagonica
Carabidae_Lebia
Torridincolidae_Satonius
Cupedidae_Tenomerga
Scirtidae_Pseudomicrocara
Scirtidae_Scirtinae_sp
Scirtidae_Elodes
Derodontidae_Derodontus
Clambidae_Clambus
Eucinetidae_Noteucinetus_1
Eucinetidae_Noteucinetus_2
Rhinorhipidae_Rhinorhipus
Rhipiceridae_Oligorhipis
Dascillidae_Metallidascillus
Dascillidae_Dascillus
Byrrhidae_Cytilus
Byrrhidae_Notolioon
Byrrhidae_Microchaetes
Buprestidae_Dicerca
Buprestidae_Trachys
Buprestidae_Coroebus
Dryopidae_Pachyparnus
Dryopidae_Helichus_1
Dryopidae_Helichus_2
Eulichadidae_Eulichas
Callirhipidae_Simianus
Callirhipidae_Ennometes
Ptilodactylidae_Ptilodactyla
Ptilodactylidae_Epilichas
Chelonariidae_Chelonarium
Psephenidae_Schinostethus_1
Psephenidae_Schinostethus_2
Psephenidae_Sclerocyphon
Psephenidae_Mataeopsephus
Elmidae_Stetholus
Elmidae_Stenelmis
Elmidae_Graphelmis
Limnichidae_Cephalobyrrhus
Heteroceridae_Heterocerus
Limnichidae_Limnichus
Limnichidae_Pelochares
Limnichidae_Byrrhinus
Omethidae_Drilonius_1
Omethidae_Drilonius_2
Artematopodidae_Eurypogon
Artematopodidae_Artematopus
Throscidae_Trixagus_1
Throscidae_Trixagus_2
Eucnemidae_Anischia
Eucnemidae_Otho
Eucnemidae_Hemiopsida
Elateridae_Osslimus
Lycidae_Benibotarus
Lycidae_Lycostomus
Lycidae_Platerodrilus
Lycidae_Porrostoma
Lycidae_Libnetis
Lycidae_Macrolycus
Lycidae_Dilophotes
Elateridae_Cebrio
Elateridae_Ampedus
Elateridae_Melanotus
Elateridae_Hemicrepidius
Phengodidae_Stenophrixothrix
Rhagophthalmidae_sp
Rhagophthalmidae_Rhagophthalmus_1
Rhagophthalmidae_Rhagophthalmus_2
Lampyridae_Gorhamia
Lampyridae_Drilaster
Lampyridae_Pristolycus
Lampyridae_Luciola
Lampyridae_Cyphonocerus
Lampyridae_Vesta
Lampyridae_Pyrocoelia
Lampyridae_Diaphanes
Elateridae_Agrypnus
Elateridae_Denticollis_1
Elateridae_Denticollis_2
Elateridae_Pectocera
Elateridae_Cardiotarsus
Elateridae_sp
Elateridae_Penia
Cantharidae_Ichthyurus
Cantharidae_Malthinus
Cantharidae_Heteromastix
Cantharidae_Laemoglyptus
Cantharidae_Fissocantharis
Cantharidae_Prothemus
Cantharidae_Lycocerus
Cantharidae_Themus_1
Cantharidae_Themus_2
Nosodendridae_Nosodendron
Histeridae_Saprinus
Histeridae_Platysoma
Georissidae_Georissus
Hydrophilidae_Anacaena
Hydrophilidae_Sphaeridium
Hydrophilidae_Helochares
Hydrophilidae_Oocyclus
Hydrophilidae_Berosus
Hydrophilidae_Sternolophus
Hydrophilidae_Hydrophilus
Trogidae_Trox
Trogidae_Omorgus
Lucanidae_Phalacrognathus
Lucanidae_Cyclommatus
Lucanidae_Aegus
Geotrupidae_Australobolbus
Geotrupidae_Geotrupes
Passalidae_Ceracupes
Passalidae_Aceraius
Glaphyridae_Amphicoma
Scarabaeidae_Rhyparus
Scarabaeidae_Onthophagus
Scarabaeidae_Copris
Hybosoridae_Liparochrus
Hybosoridae_Cyphopisthes
Scarabaeidae_Cheirotonus
Scarabaeidae_Heteronyx
Scarabaeidae_Ectinohoplia
Scarabaeidae_Protaetia
Scarabaeidae_Dasyvalgus
Scarabaeidae_Mimela
Scarabaeidae_Anomala
Scarabaeidae_Carneodon
Scarabaeidae_Allomyrina
Jacobsoniidae_Derolathrus_1
Jacobsoniidae_Derolathrus_2
Ptiliidae_sp
Hydraenidae_Hydraena
Agyrtidae_Pteroloma
Leiodidae_Agathidium
Leiodidae_Cholevinae_sp
Leiodidae_Agyrtodes
Staphylinidae_Omaliinae_sp
Staphylinidae_Centrophthalmus
Staphylinidae_Dianous
Staphylinidae_Scydmaeninae_sp
Staphylinidae_Tachinus_1
Staphylinidae_Tachinus_2
Staphylinidae_Megalopaederus
Staphylinidae_Staphylinus
Staphylinidae_Staphylininae_sp
Silphidae_Nicrophorus
Silphidae_Necrodes
Staphylinidae_Osorius
Staphylinidae_Apatetica
Staphylinidae_Priochirus
Staphylinidae_Scaphidium_1
Staphylinidae_Scaphidium_2
Dermestidae_Dermestes
Dermestidae_Orphinus
Dermestidae_Evorinea
Bostrichidae_Polycaon
Bostrichidae_Lyctus
Ptinidae_Ptinus_1
Ptinidae_Ptinus_2
Ptinidae_Hedobia
Ptinidae_Dorcatoma
Trogossitidae_Rentonellum
Byturidae_Haematoides
Biphyllidae_Biphyllus
Biphyllidae_Althaesia
Trogossitidae_Leperina
Acanthocnemidae_Acanthocnemus
Trogossitidae_Thymalus
Trogossitidae_Larinotus
Thanerocleridae_Isoclerus
Cleridae_Cladiscus
Cleridae_Xenorthrius
Cleridae_Stenocallimerus
Cleridae_Tenerus
Cleridae_Necrobia
Cleridae_Allochotes
Trogossitidae_Parapeltis
Trogossitidae_Ancyrona
Prionoceridae_Idgia
Melyridae_Dasytes
Melyridae_Malachiinae_sp
Melyridae_Dicranolaius
Melyridae_Carphurus_1
Melyridae_Carphurus_2
Lymexylidae_Melittomma
Lymexylidae_Atractocerus
Ripiphoridae_Rhipidioides
Ripiphoridae_Trigonodera
Mordellidae_Hoshihananomia
Ischaliidae_Ischalia
Aderidae_sp_1
Aderidae_sp_2
Trictenotomidae_Trictenotoma
Scraptiidae_Scraptia
Mycteridae_Trichosalpingus
Oedemeridae_Ditylus
Oedemeridae_Thelyphassa
Oedemeridae_Pseudolycus
Pythidae_Anaplopus
Salpingidae_Ocholissa
Salpingidae_Euryplatus
Salpingidae_Orphanotrophium_1
Salpingidae_Orphanotrophium_2
Boridae_Synercticus
Pyrochroidae_Morpholycus_1
Pyrochroidae_Morpholycus_2
Pyrochroidae_Pseudopyrochroa
Pyrochroidae_Eupyrochroa
Anthicidae_Macratria_1
Anthicidae_Macratria_2
Anthicidae_Trichananca
Anthicidae_Lemodes
Anthicidae_Anthicus
Meloidae_Zonitis
Meloidae_Epicauta
Zopheridae_Bitoma
Incertae_sedis_Rhizonium
Melandryidae_Melandryinae_sp
Zopheridae_Zopherosis
Zopheridae_Monomma
Melandryidae_Dircaeomorpha
Ciidae_Cis_1
Ciidae_Cis_2
Ciidae_Australocis
Ulodidae_Ulodes
Ulodidae_Meryx
Archeocrypticidae_Wattianus
Mycetophagidae_Nototriphyllus
Mycetophagidae_Mycetophagus
Tenebrionidae_Adelium
Tenebrionidae_Ecnolagria
Tenebrionidae_Chlorophila
Tenebrionidae_Cyphaleus
Tenebrionidae_Cossyphus
Tenebrionidae_Cillibus
Tenebrionidae_Cryphaeus
Tenebrionidae_Tanychilus
Tenebrionidae_Cteniopinus
Tenebrionidae_Platydema
Tenebrionidae_Amarygmus
Tenebrionidae_Strongylium
Tenebrionidae_Palorus
Tenebrionidae_Tyrtaeus
Tenebrionidae_Derispia_1
Tenebrionidae_Derispia_2
Bothrideridae_Deretaphrus
Bothrideridae_Ascetoderes
Cerylonidae_Philothermus
Murmidiidae_Murmidius
Discolomatidae_Aphanocephalus
Euxestidae_Hypodacnella
Cerylonidae_Ostomopsis
Teredidae_Teredolaemus
Teredidae_Xylariophilus_1
Teredidae_Xylariophilus_2
Alexiidae_Sphaerosoma
Latridiidae_Enicmus
Latridiidae_Melanophthalma
Latridiidae_Corticaria
Anamorphidae_Papuella
Corylophidae_Periptyctus
Corylophidae_Priamima
Corylophidae_Sericoderus
Corylophidae_Orthoperus
Endomychidae_Holoparamecus
Endomychidae_Sinocymbachus
Endomychidae_Encymon
Endomychidae_Stenotarsus
Endomychidae_Cyclotoma
Coccinellidae_Microfreudea
Coccinellidae_Stethorus
Coccinellidae_Harmonia
Coccinellidae_Exochomus
Coccinellidae_Rhizobius
Coccinellidae_Ortalia
Coccinellidae_Sasajiscymnus
Coccinellidae_Chnootriba
Boganiidae_Paracucujus
Erotylidae_Tetraphala
Erotylidae_Anadastus
Erotylidae_Cryptophilus
Erotylidae_Thallis
Erotylidae_Episcaphula
Erotylidae_Episcapha
Helotidae_Neohelota
Sphindidae_Aspidiphorus
Protocucujidae_Ericmodes
Monotomidae_Rhizophagus
Monotomidae_Thione
Monotomidae_Monotomopsis
Monotomidae_Mimemodes
Kateretidae_Notobrachypterus
Nitidulidae_Glischrochilus
Cybocephalidae_Cybocephalus
Nitidulidae_Urophorus
Nitidulidae_Carpophilus
Nitidulidae_Pallodes
Nitidulidae_Brachypeplus
Hobartiidae_Hydnobioides
Cryptophagidae_Micrambina
Cryptophagidae_Curelius
Silvanidae_Silvanoprus
Silvanidae_Psammoecus_2
Silvanidae_Uleiota
Silvanidae_Psammoecus_1
Silvanidae_Cryptamorpha
Cucujidae_Platisus
Cucujidae_Pediacus
Phloeostichidae_Rhopalobrachium
Phloeostichidae_Hymaea
Passandridae_Passandra
Myraboliidae_Myrabolia
Phalacridae_Phalacrinus
Phalacridae_sp
Phalacridae_Olibrus
Propalticidae_Propalticus
Laemophloeidae_Laemophloeus
Laemophloeidae_Cryptolestes
Nemonychidae_Aragomacer
Anthribidae_Acorynus
Anthribidae_Ozotomerus
Anthribidae_Xylinada
Anthribidae_Peribathys
Belidae_Rhinotia
Attelabidae_Phymatapoderus
Attelabidae_Paratrachelophorus
Attelabidae_Involvulus
Attelabidae_Byctiscus
Brentidae_Cylas
Brentidae_Baryrhynchus
Brentidae_Apion_1
Brentidae_Apion_2
Curculionidae_Platypodinae_sp
Curculionidae_Episomus
Curculionidae_Xylosandrus
Curculionidae_Peribleptus
Curculionidae_Curculio
Megalopodidae_Temnaspis
Cerambycidae_Strangalia
Cerambycidae_Spondylis
Cerambycidae_Oberea
Cerambycidae_Xylotrechus
Cerambycidae_Dorysthenes
Chrysomelidae_Sominella
Chrysomelidae_Lilioceris
Chrysomelidae_Sagra
Chrysomelidae_Bruchidius
Chrysomelidae_Chrysomela
Chrysomelidae_Galerucinae_sp
Chrysomelidae_Altica
Chrysomelidae_Dactylispa
Chrysomelidae_Cassida
Chrysomelidae_Anisodera
Chrysomelidae_Trichochrysea
Chrysomelidae_Oomorphoides
Chrysomelidae_Cryptocephalus
Chrysomelidae_Chlamisus
-3
-2,5
-2
-1,5
-1
-0,5
0

Table S1. Fit of maximum likelihood (ML) models to the reduced coleopteran dataset for model sensitivity testing, analysed in ModelFinder. Abbreviations: AIC, Akaike information criterion scores.

Model	AIC
C10	1035697.227
GTR20	1210678.781
LG	1211046.717
JTT	1215087.892
WAG	1220238.554

Table S2. Overview of fossil calibrations for molecular clock analyses.

Node	Clade	Fossil constraint	Minimum age (Ma)	Maximum age (Ma)
1	(Megaloptera + Neuroptera) – Coleoptera	*Stephanastus polinae* Kirejtshuk and Nel, 2013	298.75	324
2	Crown Coleoptera	*Ponomarenkium belmonthensis* Yan, Lawrence, Beattie and Beutel, 2018	251.878	307.1
3	Gyrinidae – Haliplidae	*Tunguskagyrus planus* Yan, Beutel and Lawrence, 2018	251.878	293.69
4	Dytiscidae – Noteridae	*Palaeodytes gutta* Ponomarenko, 1987	155	251.878
5	Cupedidae – Torridincolidae	*Kirghizocupes cellulosus* Ponomarenko, 1966	235	293.69
6	Crown Polyphaga	undescribed Elateriformia, Ladinian of Tongchuan, China	237	293.69
7	Derodontidae – (Clambidae + Eucinetidae)	*Juropeltastica sinica* Cai, Lawrence and Huang, 2014	165	251.878
8	Clambidae – Eucinetidae	*Mesocinetus aequalis* Kirejtshuk and Ponomarenko, 2010	145	235
9	Rhipiceridae – Dascillidae	*Parelateriformius communis Yan and Wang, 2010*	165	235
10	Buprestidae – Byrrhidae	*Sinoparathyrea bimaculata* Pan, Chang and Ren, 2011	165	235
11	Dryopoidea – Byrrhoidea + Buprestoidea	undescribed Dryopidae, Aptian Crato Formation, Brazil	112.6	165
12	Crown Psephenidae	*Vetujinbrianax cretaceus* Cai and Huang, 2018	98.17	165

13	Elmidae – (Limnichidae + Heteroceridae)	*Elmadulescens rugosus* Peris, Maier and Sánchez-García, 2015	105	165
14	Crown Heteroceridae	Heterocerites magnus Prokin and Ren, 2011	122.2	165
15	Artematopodidae – Omethidae	*Sinobrevipogon jurassicus* Cai, Lawrence, Ślipiński and Huang, 2015	165	235
16	Throscidae – Eucnemidae	*Potergosoma gratiosum* Kovalev and Kirejtshuk, 2013	125	235
17	*Osslimus* (Elateridae) – Lycidae	*Burmolycus compactus* Bocak, Li and Ellenberger, 2019	98.17	165
18	Lampyridae – Phengodidae + Rhagophthalmidae	*Protoluciola albertalleni* Kazantsev, 2015	98.17	165
19	Crown Cantharidae	*Molliberus albae* Peris and Fanti, 2018	105	165
20	Georissidae – Hydrophilidae	*Protochares brevipalpis* Fikáček, Prokin, Yan, Yue, Wang, Ren and Beattie, 2014	147.28	235
21	Trogidae – Lucanidae	*Juraesalus atavus* Nikolajev, Wang, Liu and Zhang, 2011	165	235
22	Passalidae – Geotrupidae	*Parageotrupes incanus* Nikolajev and Ren, 2010	122.2	165
23	Hybosoridae – Scarabaeidae	*Protohybosorus grandissimus* Nikolajev, 2010	155	235
24	Ptiliidae – Hydraenidae	*Ochtebiites minor* Ponomarenko, 1985	182	235
25	Agyrtidae – Leiodidae	*Mesecanus communis* Ponomarenko, 1977	165	235

26	Crown Staphylinidae	undescribed Silphidae, Haifanggou Formation, China	165	235
27	*Megalopaederus* (Paederinae) – Staphylininae	*Megolisthaerus minor* Cai and Huang, 2013	122.2	165
28	Silphinae – Staphylinidae *partim*	*Mesecanus communis* Ponomarenko, 1977	165	235
29	Staphylinidae: Apateticinae – Osoriinae	*Mesallotrochus longiantennatus* Cai and Huang, 2015	98.17	165
30	Crown Bostrichoidea	*Paradermestes jurassicus* Deng, Ślipiński, Ren and Pang, 2017	165	235
31	Crown Bostrichidae	*Poinarinius burmaensis* Legalov, 2018	98.17	165
32	Crown Ptinidae	*Actenobius magneoculus* Peris, Philips, and Delclòs, 2015	105	165
33	Thanerocleridae – Cleridae	*Wangweiella calloviana* Kolibáč and Huang, 2016	165	235
34	Prionoceridae – Melyridae	*Idgiaites jurassicus* Liu, Ślipiński, Leschen, Ren and Pang, 2015	165	235
35	Lymexylidae	*Cratoatractocerus grimaldii* Wolf, 2011	112.6	235
36	Crown Tenebrionoidea	*Archaeoripiphorus nuwa* Hsiao, Yu and Deng, 2017	165	235
37	Rhipiphoridae – Mordellidae	*Protoripidius burmiticus* Cai, Yin and Huang, 2018	98.17	235
38	Ischaliidae – Aderidae	undescribed Aderidae from Cretaceous Lebanese amber	125	165

39	Salpingidae – Pythidae	*Eopeplus stetzenkoi* Kirejtshuk and Nel, 2009	53	165
40	Anthicidae – Meloidae	*Camelomorpha longicervix* Kirejtshuk, Azar and Telnov, 2008	125	165
41	Crown Zopheridae	*Paleoendeitoma antennata* Deng, Ślipiński, Ren and Pang, 2017	98.17	165
42	Crown Tenebrionidae	*Alphitopsis initialis* Kirejtshuk, Nabozhenko and Nel, 2011	122.2	165
43	Alexiidae – Latridiidae	*Tetrameropsis mesozoica* Kirejtshuk and Azar, 2008	125	165
44	Crown Endomychidae	*Palaeomycetes foveolatus* Tomaszewska, Ślipiński and Ren, 2018	98.17	165
45	Crown Coccinellidae	*Rhyzobius antiquus* Kirejtshuk and Nel, 2012	53	125
46	Boganiidae – Erotylidae	*Palaeoboganium jurassicum* Liu, Ślipiński, Lawrence, Ren and Pang, 2018	165	235
47	Helotidae – (Protocucujidae + Sphindidae)	*Libanopsis poinari* Kirejtshuk, 2015	125	235
48	Monotomidae – (Kateretidae + Nitidulidae)	*Jurorhizophagus alienus* Cai, Ślipiński and Huang, 2015	165	235
49	Crown Nitidulidae	*Crepuraea archaica* Kirejtshuk, 1990	119	165
50	Crown Silvanidae	*Protoliota antennatus* Liu, Ślipiński, Wang and Pang, 2019	98.17	165
51	Nemonychidae – Anthribidae	*Protoscelis longicornis* (Medvedev, 1968)	155	235

52	Belidae – (Attelabidae, (Brentidae, Curculionidae))	*Sinoeuglypheus daohugouensis* Yu, Davis and Shih, 2019	165	235
53	Brentidae – Curculionidae	*Axelrodiellus ruptus* Zherikhin and Gratshev, 2004	112.6	165
54	Crown Chrysomelidae	*Mesolpinus antennatus* Kirejtshuk, Moseyko and Ren, 2015	122.2	165
55	Crown Cerambycidae	*Cretoprionus liutiaogouensis* Wang, Ma, McKenna, Yan, Zhang and Jarzembowski, 2014	122.2	165
56	Sagrinae – Bruchinae	*Mesopachymerus antiqua* Poinar, 2005	78	155
57	Galerucinae – Chrysomelinae	*Taimyraltica calcarata* Nadein, 2018	83.4	165

Table S3. Divergence dates (95% CI of the posterior distribution of age estimates, in Ma) of the crown groups of beetle suborders and series from independent rates (IR) and autocorrelated (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

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