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The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution

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Abstract. Here we present a phylogeny of beetles (Insecta: Coleoptera) based on DNA sequence data from eight nuclear genes, including six single-copy nuclear protein-coding genes, for 367 species representing 172 of 183 extant families. Our results refine existing knowledge of relationships among major groups of beetles. Strepsiptera was confirmed as sister to Coleoptera and each of the suborders of Coleoptera was recovered as monophyletic. Interrelationships among the suborders, namely Polyphaga (Adephaga (Archostemata, Myxophaga)), in our study differ from previous studies. Adephaga comprised two clades corresponding to Hydradephaga and Geadephaga. The series and superfamilies of Polyphaga were mostly monophyletic. The traditional Cucujoidea were recovered in three distantly related clades. Lymexyloidea was recovered within Tenebrionoidea. Several of the series and superfamilies of Polyphaga received moderate to maximal clade support in most analyses, for example Buprestoidea, Chrysomeloidea, Coccinelloidea, Cucujiformia, Curculionoidea, Dascilloidea, Elateroidea, Histeroidea and Hydrophiloidea. However,

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many of the relationships within Polyphaga lacked compatible resolution under maximum-likelihood and Bayesian inference, and/or lacked consistently strong nodal support. Overall, we recovered slightly younger estimated divergence times than previous studies for most groups of beetles. The ordinal split between Coleoptera and Strepsiptera was estimated to have occurred in the Early Permian. Crown Coleoptera appeared in the Late Permian, and only one or two lineages survived the end-Permian mass extinction, with stem group representatives of all four suborders appearing by the end of the Triassic. The basal split in Polyphaga was estimated to have occurred in the Triassic, with the stem groups of most series and superfamilies originating during the Triassic or Jurassic. Most extant families of beetles were estimated to have Cretaceous origins. Overall, Coleoptera experienced an increase in diversification rate compared to the rest of Neuropteroidea. Furthermore, 10 family-level clades, all in suborder Polyphaga, were identified as having experienced significant increases in diversification rate. These include most beetle species with phytophagous habits, but also several groups not typically or primarily associated with plants. Most of these groups originated in the Cretaceous, which is also when a majority of the most species-rich beetle families first appeared. An additional 12 clades showed evidence for significant decreases in diversification rate. These clades are species-poor in the Modern fauna, but collectively exhibit diverse trophic habits. The apparent success of beetles, as measured by species numbers, may result from their associations with widespread and diverse substrates – especially plants, but also including fungi, wood and leaf litter – but what facilitated these associations in the first place or has allowed these associations to flourish likely varies within and between lineages. Our results provide a uniquely well-resolved temporal and phylogenetic framework for studying patterns of innovation and diversification in Coleoptera, and a foundation for further sampling and resolution of the beetle tree of life.

Introduction

Beetles (Insecta: Coleoptera; Fig. 1), with >380 000 named living species, account for ∼25% of known species on Earth and ∼40% of insects (Ślipiński *et al.*, 2011). The number of extant species is, however, much higher (e.g. Oberprieler *et al.*, 2007). Beetles exhibit an astonishing diversity of body sizes, shapes and structures, reflecting an equally diverse range of habits. They include some of the smallest and lightest insects (e.g. Ptiliidae: *Nanosella* Motschulsky, at ∼0.25 mm and ∼0.0005 g) and some of the largest and heaviest (e.g. Cerambycidae: *Macrodontia* Lepeletier & Audinet-Serville, at max. ∼175 mm, and Scarabaeidae: *Goliathus* Linnaeus, larvae max. ∼100 g). Beetles occur in almost all terrestrial ecosystems and have invaded aquatic habitats at least ten times as larvae, adults or both (e.g. Beutel, 1996; McKenna *et al.*, 2014). Specialized coevolved habits are the norm, including endo- and ecto-parasitism, granivory, inquilinism, mycophagy, parasitoidism, phytophagy, pollenivory, saprophagy, sporophagy, xylophagy and zoophagy (Crowson, 1981; Lawrence & Newton, 1982; Beutel & Leschen, 2005a; Leschen *et al.*, 2010; Lawrence & Ślipiński, 2013b; Leschen & Beutel, 2014). Beetles are among the most serious pests of agriculture and forestry and at the same time ecosystem architects, for example, through wood boring, soil burrowing and interactions with other invertebrates and plants.

The earliest known ancestors of modern beetles are fossil stem group Coleoptera from the Early Permian (Artinskian-Kungurian Stages, ∼280 to 270 Ma) belonging to the extinct suborder Protocoleoptera Crowson (Beckemeyer & Engel, 2008; Kukalová-Peck & Beutel, 2012; Kirejtshuk *et al.*, 2013). Proposed crown group representatives of all four extant suborders of beetles – Adephaga (∼45 500 species; ground beetles, tiger beetles, predaceous diving beetles, wrinkled bark beetles, etc.), Archostemata (∼40 species; reticulated beetles, telephone-pole beetles, etc.), Myxophaga (∼102 species; minute bog beetles, skiff beetles, etc.) and Polyphaga (∼335 000 species; checkered beetles, click beetles, fireflies, ladybird beetles, leaf beetles, long horned beetles, metallic wood-boring beetles, rove beetles, scarab beetles, soldier beetles, weevils, etc.) (Ślipiński *et al.*, 2011) – first appear in the Triassic fossil record, during and subsequent to the Sardinian Stage, ∼240 Ma (Ponomarenko, 2002; Papier *et al.*, 2005). However, it is worth noting that Kirejtshuk *et al.* (2013) assign the Permian fossil Tshekardocoleidae to Archostemata (others place it in Protocoleoptera). Most extant beetle families are proposed to have Jurassic or Cretaceous origins (Grimaldi & Engel, 2005; Hunt *et al.*, 2007; McKenna & Farrell, 2009).

Fig. 1. An adult weevil – *Cholus cinctus* Schoenherr in the family Curculionidae – taking flight in lowland tropical rain forest (Heredia Province, Costa Rica). Note the forewings hardened to form elytra, a feature characteristic of the order Coleoptera (beetles). Curculionidae is the second most diverse family of metazoans (surpassed only by the rove beetle family Staphylinidae, which is older) with more than 51 000 named extant species in more than 4600 genera. Conservatively, it is estimated that there are more than 200 000 additional undescribed species of Curculionidae alone (Oberprieler *et al.*, 2007). Photo ©Piotr Naskrecki, used with permission.

Factors responsible for the apparent success of beetles are widely debated. The most trivial factor is the age of beetles; they have had more time to diversify than younger clades. Other factors that could explain the diversity of beetles are high speciation rates and/or low extinction rates, perhaps through mechanisms such as ecological opportunity (Crowson, 1981; Farrell, 1998; Grimaldi & Engel, 2005; Hunt *et al.*, 2007; McKenna *et al.*, 2009). Ecological opportunity is proposed to operate by way of entry into new 'adaptive zones', whether through the evolution of 'key innovations' – for example, hardened forewings forming elytra that confer the ability to occupy concealed tight spaces by protecting the folded hindwings (Crowson, 1981; Lawrence & Newton, 1982; Beutel, 1997; Grimaldi & Engel, 2005) or facilitate the invasion of arid or aquatic habitats through elytral covering of the spiracles (Lawrence & Newton, 1982; Beutel, 1996) – or via existing 'pre-adaptations' such as feeding strategies that facilitate exploitation of newly available niches (Leschen, 1993; McKenna & Farrell, 2006; Leschen & Buckley, 2007). Examples include the diversification and rise to dominance of angiosperms (flowering plants) facilitating diversification of angiosperm-associated beetles (e.g. Farrell, 1998; Bernhardt, 2000; McKenna *et al.*, 2009). High diversification rates, whether arising from high origination rates, low extinction rates or both, are expected to produce more species over a given period than lineages with lower diversification rates.

Two broadly taxon-sampled molecular timetrees have been produced for beetles: Hunt *et al.* (2007) is based on data from three genes for 340 species, and McKenna & Farrell (2009) is based on *18S* rDNA sequences for 955 species. Both studies recovered relatively little resolution and nodal support at deep nodes; however, their estimates for the timing of the subordinal splits in beetles are very similar, falling in the middle to Late Permian Period. That their age estimates are similar is not surprising because they are based on largely overlapping *18S* rRNA datasets. Molecular timetrees focused on individual series or superfamilies of beetles have now been estimated for the superfamilies Chrysomeloidea (Farrell, 1998; Gómez-Zurita *et al.*, 2007), Curculionoidea (Farrell, 1998; McKenna *et al.*, 2009), Hydrophiloidea (Bloom *et al.*, 2014), Scarabaeoidea (Ahrens *et al.*, 2014) and Tenebrionoidea (Kergoat *et al.*, 2014a).

Existing large-scale molecular phylogenetic studies of beetles are based on DNA sequence data from nuclear ribosomal genes (*28S*, *18S*) and/or mitochondrial genes (*COI*, *COII*, *16S*, mitochondrial genomes) (Shull *et al.*, 2001; Caterino *et al.*, 2002; Vogler, 2005; Hunt *et al.*, 2007; Hunt & Vogler, 2008; Sheffield *et al.*, 2008, 2009; McKenna & Farrell, 2009; Song *et al.*, 2010; Bocak *et al.*, 2014). These studies are based on data from four or fewer genes (except for those based on mitochondrial genomes, which are based upon only one linkage group) and typically contain much missing data, resulting in matrices where some combinations of taxa lack overlapping data and phylogenetic signal. Nodal support in the resulting phylogenies is characteristically weak, molecular data sampling in some subgroups of beetles, such as the suborder Archostemata, is typically very limited, and rooting and outgroups are often problematic or little-explored. Nonetheless, these datasets collectively sample a large fraction of extant beetle subfamilies, and some of these studies, perhaps most notably Hunt *et al.* (2007), McKenna & Farrell (2009) and Bocak *et al.* (2014), report some of the most densely taxon-sampled phylogenies available for any ordinal-level group of insects (e.g. Bocak *et al.*, 2014, sampled >8000 beetle terminals).

Mitochondrial genomes have been widely used to reconstruct the phylogeny of beetles or suprafamilial groups of beetles (Sheffield *et al.*, 2008, 2009; Cameron *et al.*, 2009; Kim *et al.*, 2009; Pons *et al.*, 2010; Song *et al.*, 2010; Timmermans & Vogler, 2012; Haran *et al.*, 2013; Gillett *et al.*, 2014). Although such data have contributed to resolving the internal phylogeny of some subfamilies, families and (to a lesser degree) superfamilies, they usually do not provide definitive results and can be problematic at higher taxonomic levels, for example between suborders, series and superfamilies, due to base-compositional heterogeneity and among-site rate variation (e.g. Song *et al.*, 2010).

To date, no near-comprehensive molecular phylogenetic studies of beetles have included data from nuclear protein-coding (NPC) genes, even though they have been shown to help resolve many problematic relationships in beetles (e.g. Wild & Maddison, 2008; McKenna *et al.*, 2009; McKenna, 2011a,2011b). A lack of primers and protocols for amplifying and sequencing these genes across beetles contributed to their relatively infrequent use at higher taxonomic levels prior to the publications of Wild & Maddison (2008) and McKenna *et al.* (2009) which made public many of the primers and protocols established for NPC and other genes as part of the Beetle Tree

of Life (BToL) Project. Even so, many NPC genes remain difficult to amplify and/or sequence in certain groups of beetles because of the deep evolutionary divergences in beetles and widely varying evolutionary rates among taxa.

Morphological data have been widely used to reconstruct the phylogeny of beetles (reviewed in the *Handbook of Zoology* volumes on beetles: e.g. Beutel & Leschen, 2005a; Leschen *et al.*, 2010; Leschen & Beutel, 2014), including the most comprehensive family-group study to date, by Lawrence *et al.* (2011), which sampled 516 adult and larval characters for 359 beetle taxa plus seven outgroups (OG), including most of the same beetle families and genera as in the present study. Topologies recovered to date from phylogenetic analyses of morphological data differ, often substantially, from those recovered through analyses of molecular data. As for molecular phylogenetic trees of beetles to date, phylogenetic trees of beetles based on morphological data generally lack resolution and nodal support at higher taxonomic levels.

Most higher-level relationships in beetles therefore remain contentious, unresolved or inadequately tested (reviewed in McKenna, 2014). Here we present a study of beetle molecular phylogeny and evolution based on analyses of nuclear DNA sequence data (eight genes, six of which are NPC) with nearly comprehensive family-level sampling. We incorporate exemplars of most (172 of 183) extant families of beetles, including 20 families not included in other such studies to date, and Strepsiptera (twisted-wing parasites), the recently confirmed sister group of beetles (Niehuis *et al.*, 2012; McKenna, 2014; Misof *et al.*, 2014; Peters *et al*., 2014). Through analyses of these data, we establish working hypotheses for the composition and relationships of the major taxonomic groups of beetles (including comprehensive family-level samples of most supra-ordinal groups of beetles), and present a reconstruction of timing and patterns of beetle macroevolution. Our results provide a foundation for further sampling of beetle taxa and molecular phylogenetic data towards a comprehensive and maximally resolved reconstruction of beetle phylogeny and evolution, and provide much-needed evolutionary context for interpreting observations emerging from comparative studies involving beetles.

Materials and methods

Taxon sampling

We sampled 367 beetle species (Table S1), including representatives of all extant suborders, series, superfamilies and 172/183 families of beetles. We use the classification of Bouchard *et al.* (2011), with the exception of Curculionoidea, which follows the weevil chapters of Volume 3 of the *Handbook of Zoology* (Leschen & Beutel, 2014), Hydrophiloidea s.s., according to Short & Fikáček (2013), Buprestoidea, which follows Bellamy (2003), and select additional taxa that have recently been elevated to family-rank (see below). Our taxon sample includes all families of Adephaga, Bostrichoidea, Buprestoidea, Byrrhoidea, Chrysomeloidea, Curculionoidea, Derodontoidea, Histeroidea, Hydrophiloidea s.s., Lymexyloidea, Myxophaga, Scirtoidea, Staphylinoidea and Tenebrionoidea, and a broad cross-section of subfamilies. Missing from our taxon sample were the archostematan families Crowsoniellidae (monotypic: only the type series is known) and Jurodidae (monotypic: only the holotype is known), and the polyphagan families Belohinidae (Scarabaeoidea: monotypic), Plastoceridae (Elateroidea: two species), Rhinorhipidae (Elateroidea: monotypic), Mauroniscidae (Cleroidea: 26 species), Lamingtoniidae (Cucujoidea s.s.: three species), Phloiophilidae (Cucujoidea s.s.: monotypic) and Tasmosalpingidae (Cucujoidea s.s.: two species). We also did not include members of the family Rhadalidae (Cleroidea: 294 species; Peacock, 1987; Bocakova *et al.*, 2012) or the family Cybocephalidae (Cucujoidea s.s.: ~150 species; Cline *et al.*, 2014), both of which were elevated to family-rank after data collection was completed for this study (they were previously treated as subfamilies). Our taxon sample was therefore missing two families of Archostemata, one family of Scarabaeoidea, two families of Elateroidea, two families of Cleroidea and four families of Cucujoidea (in the former broad concept of the superfamily). These missing families together contain just 482 (~0.001%) of the ~385 000 described extant species of beetles. Our family-level taxon sample is therefore broadly representative of extant beetles as a whole.

Our OG taxon sample included one species from each of the three neuropterid orders [Megaloptera (*Sialis* Latreille), Neuroptera (*Plega* Navás) and Raphidioptera (*Agulla* Handlirsch)], and one species of Strepsiptera (*Mengenilla* Hofeneder) (Table S1). Neuropterida and Strepsiptera are known near OGs of beetles based on analyses of genomic and transcriptomic data (Niehuis *et al.*, 2012; McKenna, 2014; Misof *et al.*, 2014; Peters *et al*., 2014). Two relatively more distant OGs were sampled from the order Hymenoptera [*Apis* Linnaeus (Apidae) and *Cephus* Latreille (Cephidae)] for a total sample of 373 species. Voucher specimens from which DNA was extracted are deposited at the Harvard University Museum of Comparative Zoology (MCZ) in Cambridge, MA, U.S.A. (most species; subset of OGs and most Polyphaga), or at the Oregon State University Arthropod Collection (OSAC) in Corvallis, OR, U.S.A.

DNA extraction, amplification and sequencing

Specimens for DNA were mostly collected as adults and preserved in 90–100% EtOH. Total genomic DNA was extracted from the thorax, one or more legs, or the entire specimen, by soaking or grinding, using the QIAquick DNeasy Tissue Kit (Qiagen Inc., Alameda, CA, U.S.A.), and otherwise following the kit manufacturer's protocol. Amplification via PCR was typically carried out using one of two protocols. Some samples were amplified in 25-μL reactions containing 11.6 μL HPLC water, 5 μL 5× buffer, 0.2 μL 10 mM dNTPs, 1.5 μL $MgCl_2$, 0.2 μL Taq DNA Polymerase (all from Qiagen) and 1 μL of each primer (10 mM); additionally, 5 μL of Q solution (Qiagen) was added to each reaction for *18S* and *28S*. The remainder were amplified in 25–30-μL reactions using TaKaRa Ex Taq (Clontech) and the basic protocols recommended by the manufacturer. We targeted approximately 9000 bp of double-stranded DNA sequence

data for each specimen, exclusive of introns. These data included ~1350 bp of *28S* rDNA, ~1850 bp of *18S* rDNA and parts of six NPC genes: ~1000 bp of elongation factor-1α (*EF1-α*), ~475 bp of *wingless* (*WG*), ~2000 bp of carbamoyl-phosphate synthase domain (*CAD*), ~725 bp of arginine kinase (*AK*), ~900 bp of alpha-spectrin (*AS*) and ~650 bp of phosphoenolpyruvate carboxykinase (*PEPCK*).

28S was amplified using the paired primers ZX1 (Van der Auwera *et al.*, 1994) and OP2 (Mallat & Sullivan, 1998), yielding a *c.* 2900-bp product. The first *c.* 1300 bp comprising the 5′ end of this amplification product was sequenced with the primers ZX1 and rd5b (Whiting, 2002). We used the primers ZX1 and rd5b for amplification when the initial primers (ZX1 and OP2) failed. The primers ZR1 (Mallat & Sullivan, 1998), rd4.2b (Whiting, 2002) and rd7b1 (Whiting, 2002) were used for amplification and/or sequencing when the aforementioned primers failed. Typical amplification conditions for *28S* included a single incubation at 94°C for 1 h 30 min, followed by six cycles (each starting with 30 s at 94°C) at each of the following six annealing temperatures and times (a touchdown profile): 65°C/63.5°C/62°C/60.5°C/59°C/57.5°C for 1 min, 72°C for 2 h 30 min, with a single extension step of 7 min at 72°C. *18S* and *EF1-α* were amplified using the primers and protocols in McKenna *et al.* (2009). We gel-extracted *28S*, *18S* and *EF1-α* amplification products using the QIAquick Gel Purification Kit (Qiagen). The nuclear protein-coding genes *WG*, *CAD*, *AK*, *AS* and *PEPCK* were amplified using the primers and protocols in Wild & Maddison (2008).

Amplification products were purified using shrimp alkaline phosphatase and exonuclease I (GE Healthcare), were gel purified using the QIAquick Gel Purification Kit, or were purified using EdgeBioSystems ExcelaPure PCR purification blocks (by University of Arizona's UAGC facility). We used the ABI PRISM BigDye Terminator Cycle Sequencing Kit, v3.1 (Life Technologies Corp.), and cycle sequencing reactions were sequenced on an ABI PRISM 3730 automated sequencer (Life Technologies) at Harvard University, the University of Arizona UAGC facility, or the University of Tennessee Health Science Center. Nucleotide sequences were assembled and edited using Sequencher v4.7 (Gene Codes), Geneious v5.5 (Biomatters) (Drummond *et al.*, 2012b) or Phred (Green & Ewing, 2002) and Phrap (Green, 1999) as orchestrated by Mesquite's Chromaseq package (Maddison & Maddison, 2009) with subsequent modifications by manual inspection. Sequences newly produced for this study are deposited in GenBank (see Table S1).

Nucleotide sequence alignment and masking

18S and *28S* were separately aligned using the E-INS-i algorithm in MAFFT v6.8 (default parameters; keeping existing gaps) (Katoh *et al.*, 2002; Katoh & Toh, 2008). The resulting alignments were then manually refined in Mesquite v2.75+ (Maddison & Maddison, 2011) in cases where the alignment algorithm clearly did not find the optimal solution. The program Gblocks v0.91b (Castresana, 2000; Talavera & Castresana, 2007) was used to separately mask the aligned *18S* and *28S* DNA sequence matrices, thereby reducing the amount of white space in the matrix and improving the signal-to-noise ratio in the *28S* and *18S* alignments. Analyses were executed separately on *18S* and *28S* in the command line version of Gblocks using the 'less stringent parameters' (implemented by the Gblocks webserver; minimum number of sequences for a conserved position = 1/2 the number of sequences, minimum number of sequences for a flank position = 1/2 the number of sequences, maximum number of contiguous nonconserved positions = 8, min. length of a block = 5, allowed gap positions = 'with half'). The *18S* and *28S* characters identified by Gblocks for exclusion were then removed from the matrices.

Nucleotide sequences for the NPC genes *AK*, *AS*, *CAD*, *EF1-α*, *PEPCK* and *WG* were first viewed and manually aligned as nucleotides. The alignment of exons was then refined manually by viewing as translated amino acids (AA) in Mesquite. After alignment, incomplete codons were trimmed from the ends of the sequences. In the case of incomplete codons within the sequence, 'N's were added to those containing at least one actual base, leaving only complete codons in the sequence. In the case of incomplete codons composed entirely of 'N's and adjacent to a gap containing 'N's, we converted the 'N's that did not complete a codon to gaps because the number of 'N's that belonged there was sometimes unclear. All missing data was then converted to gaps. The DNA sequence matrices for each of the NPC genes were then translated into AAs in Mesquite and each matrix was aligned using the program Opal v2.0.1 (Wheeler & Kececioglu, 2007) implemented via Mesquite, with the default alignment parameters (gap costs: 60/16/38/36, Blosum62 matrix, fast alignment, with polish). Obviously suboptimal alignment regions were manually refined using the matrix editor in Mesquite. The nucleotide sequence matrix was then aligned to the Opal-aligned AAs using Mesquite. Gblocks was used to improve the signal-to-noise ratio and reduce the amount of white space in the matrix (using the same 'less stringent parameters' as were applied to *18S* and *28S*; see above). The regions identified by Gblocks for exclusion (masking) were removed, leaving only the aligned, final nucleotides. The regions identified for exclusion (masking) by Gblocks in the AA alignments were also removed, leaving only the aligned, final AAs. Uncertainties and polymorphisms in the AA matrices were converted to missing. The files output by Gblocks after processing each matrix are available as supporting information (File S1).

Data partitions and model selection

The masked nucleotide sequence alignments for the eight nuclear genes were concatenated in Mesquite to produce a supermatrix containing 8377 aligned nucleotide positions for 373 species (File S2). The greedy algorithm in the program PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) was used for selection of both a data-partitioning scheme and best-fitting models of nucleotide substitution for each partition. The supermatrix was analysed with 20 partitions (*18S*, *28S* and each NPC gene partitioned by codon position) and the best-fit substitution model for each partition was selected using the Bayesian

Information Criterion (Sullivan & Joyce, 2005). A scheme with three unlinked partitions: (i) *28S* and *18S*, (ii) NPC gene first and second positions, and (iii) NPC gene third positions, employing the GTR+I+G model of nucleotide substitution for all partitions, was identified as optimal.

The protein sequence alignments for all six NPC genes were concatenated in Mesquite to produce a supermatrix containing 1973 aligned AA positions for 373 species. All taxa that were missing data from more than 50% of the aligned AA positions (see Table S1) were removed from the supermatrix. The resulting matrix contained 1747 aligned AA positions for 319 species (File S3). The greedy algorithm in PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) was used for selection of both a data-partitioning scheme and best-fitting substitution models for each partition. The supermatrix was analysed with six partitions, one for each gene, and the best-fit substitution model for each partition was selected using the Bayesian Information Criterion (Sullivan & Joyce, 2005). A scheme with one partition employing the LG+I+G model was identified as optimal for this AA matrix. A scheme with one partition employing the GTR+I+G model of nucleotide substitution for all partitions, was identified as optimal for the corresponding matrix of nucleotide sequences (see below).

Phylogenetic analyses

Unconstrained partitioned searches under maximum-likelihood inference (ML; 500 replicates) were executed in the program Garli v2.0 (Zwickl, 2006) on the concatenated DNA sequence matrix (all genes) using fast ML stepwise addition starting trees, the abovementioned partitioning scheme and the GTR+I+G substitution model. Additional ML analyses were executed using starting trees with suprafamilial relationships constrained to be consistent with Beutel & Haas (2000; morphological data), Hunt *et al.* (2007; molecular data), McKenna & Farrell (2009; molecular data) and Lawrence *et al.* (2011; morphological data), and using the 25 best ML trees obtained from all analyses as starting trees for additional ML searches. A separate starting tree was used for each study. Partitioned ML rapid bootstrapping (MLB; 1000 replicates) was executed on the concatenated DNA sequence matrix in the program RAxML GUI v1.2 (RAxML v7.3.2) (Stamatakis, 2006; Stamatakis *et al.*, 2008; Silvestro & Michalak, 2011). In unconstrained analyses, Strepsiptera was sometimes drawn to various nonpolyphagan ingroup taxa (see Results). However, recent phylogenomic studies, such as Niehuis *et al.* (2012), McKenna (2014), Misof *et al.* (2014) and Peters *et al.* (2014), show that Strepsiptera is the sister group of beetles. Strepsiptera was also recovered as the sister group of beetles in the morphological cladogram of Lawrence *et al.* (2011). With this in mind, we performed an additional partitioned MLB analysis (1000 replicates) on the DNA sequence matrix with Strepsiptera constrained to the OG, to explore how such an analytical constraint affected the results. We also executed unconstrained MLB analyses on matrices containing: (i) the AA sequences alone (one partition; LG+I+G substitution model), (ii) the concatenated nucleotide sequences from the six NPC genes alone (same partitioning scheme for these genes as in the above ML analysis of all eight genes; GTR+I+G), and (iii) on a matrix containing the nuclear rDNA sequences (*18S* and *28S*) plus the aforementioned AA sequences (two partitions; GTR+I+G for rDNA; LG+I+G for AAs). We used the greedy algorithm in PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) for selection of data partitioning schemes and best-fitting models of nucleotide substitution for each partition. MLB support for all analyses (DNA nucleotides, AA and rDNA nucleotides plus AA) was interpreted as follows in the Results and Discussion: 100% MLB = maximal clade support, ≥ 95% and <100% = strong clade support, ≥75 and <95% = moderate clade support, ≥50 and <75% = weak clade support, and <50% = negligible clade support.

Divergence time estimates

Bayesian analyses were implemented in the program BEAST v1.8.0 (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) on an .xml file produced in the program BEAUTi v1.7.5 (Drummond *et al.*, 2006, 2012a) from the concatenated DNA sequence data, fossil priors and monophyly constraints (see Tables 1 and S2). The BEAST analyses (uncorrelated lognormal relaxed clock, Yule prior) employed temporal information from 15 fossils as priors and used a starting tree randomly selected from among the top 25 trees obtained from the unconstrained ML search in GARLI. The ML tree was prepared for use as a starting tree in BEAST by transforming the branch lengths to ultrametric using NPRS (Sanderson, 1997, 2003) in the program TreeEdit X version 0.5 (Page, 1996). The branches were then scaled to be compatible with the fossil constraints by using the minimum age of the earliest known unequivocal fossil crown group archostematan (Table 1) to scale the tree. The resulting chronogram was then imported into BEAUTi as a user-specified starting tree for inclusion in the .xml file that was later executed in BEAST.

Monophyly constraints were placed on nodes in the phylogeny corresponding to fossil constraints on node age and on select suprafamilial nodes with indication of monophyly based on the ML tree and/or previous studies (Table S2). We conservatively selected fossils and applied age constraints as priors based on a review of the literature and our collective knowledge of the fossil record of Coleoptera (Table 1). The boundaries of geological stages and associated terminology used are consistent with the International Commission on Stratigraphy (Cohen *et al.*, 2012). Except for the root, prior estimates of divergence dates were specified using lognormal distributions, with a mean of 30 and log (stdev) of 0.75. All age-specific priors were applied to stem groups, except for constraints on the age of the root. We applied a normal prior distribution to the age of the root, with initial and mean values of 302 Ma and a standard deviation of 30 Ma based on the age of fossilized galls on the fronds of tree ferns that are proposed to have been caused by holometabolous insects (Carboniferous, Gzhelian Stage; Labandeira & Phillips, 1996). We established an upper boundary on the prior distribution of the age of the root (truncated to 396 Ma) based on the age of the

Table 1. Fossils and corresponding references used in the node dating analyses implemented in BEAST, along with the minimum and mean age for the offset-lognormal priors on node ages. Character evidence in support of the placement of these fossils can be found in the references cited.

Node assigned (see Fig. 2)	Fossil taxon (stratum and provenance, when relevant)	Label in Fig. 2	Prior on node age (Ma)	References
Adephaga (stem)	Triaplidae and Colymbothetidae (e.g. Madygen Formation, Kyrgyzstan, and Tologoy Formation, Kazakhstan)	E	225 (offset)	Ponomarenko (1977b) and Grimaldi & Engel (2005)
Archostemata (stem)	Cupedidae (e.g. Denmark Hill, Queensland, Australia)	D	199.6 (offset)	Ponomarenko (1963, 2002) and Grimaldi & Engel (2005)
Buprestoidea (stem)	Buprestidae (Karatau, Kazakhstan)	J	152 (offset)	Alexeev (1993), Lawrence & Ślipiński (2013b) and Grimaldi & Engel (2005)
Chrysomeloidea (stem)	*Cerambyomima* (Karatau, Kazakhstan)	N	152 (offset)	Prado *et al.* (2012) and Grimaldi & Engel (2005)
Coleoptera (stem)	Protocoleoptera: Tshekardocoleidae (Obora, Czech Republic and Tshekarda, Russia)	F	270 (offset)	Ponomarenko (1963), Grimaldi & Engel (2005) and Beckemeyer & Engel (2008)
Cucujoidea (stem)	Cucujidae (Burmese amber)	M	100 (offset)	Rasnitsyn & Ross (2000), Grimaldi *et al.* (2002) and Grimaldi & Engel (2005)
Curculionoidea (stem)	Nemonychidae (Karatau, Kazakhstan)	O	152 (offset)	Arnoldi (1977), Kuschel (1983), Gratshev & Zherikhin (1995) and Oberprieler *et al.* (2007)
Elateroidea (stem)	Elateridae (e.g. Karatau, Kazakhstan)	K	152 (offset)	Dolin (1975, 1980) and Grimaldi & Engel (2005)
Hydrophiloidea s.s. (stem)	Hydrophilidae: Helophorinae: *Helophorus* (*Mesosperchus*) (Trans-Baikal, Mongolia and Siberia, Russia)	H	145 (offset)	Fikáček *et al.* (2012a,2012b)
Hymenoptera (stem)	*Triassoxyela* and *Asioxyela* (Madygen Formation, Kyrgyzstan)	A	235 (offset)	Ronquist *et al.* (2012)
Neuropterida (stem)	Megaloptera: Parasialidae: *Parasialis,* and *Sonjanasialis* (northern Russia) and Megaloptera: Tychtodelopteridae: *Tychtodelopterum* (Kuzneksk Basin, south-central Russia)	B	252.2 (offset)	Engel (2004); Ponomarenko (1977a, 2000), New & Theischinger (1993) and Grimaldi & Engel (2005)
Scarabaeoidea (stem)	*Antemnacrassa* (Karatau, Kazakhstan)	I	152 (offset)	Lawrence & Ślipiński (2013b) and Grimaldi & Engel (2005)
Staphylinoidea (stem)[a, b]	Staphylinidae: Glypholomatinae: *Juroglypholoma antiquum* (Daohugou Formation, China)	G	163.5 (offset)	Cai *et al.* (2012)
Tenebrionoidea (stem)[c]	Aderidae (Lebanese amber)	L	125 (offset)	Grimaldi & Engel (2005)
Root	holometabolous insect galls	C	302 (initial and mean)	Labandeira & Phillips (1996)
Root	*Rhyniognatha* Tillyard, 1928	C	396 (upper bound)	Engel & Grimaldi (2004)
Root	Protocoleoptera: Tshekardocoleidae (Obora, Czech Republic and Tshekarda, Russia)	C	270 (lower bound)	Ponomarenko (1963), Grimaldi & Engel (2005) and Beckemeyer & Engel (2008)

[a] Plus Jacobsoniidae as in the ML tree (Figure S1) and in Lawrence *et al.* (2011).
[b] The oldest reported fossil Staphyliniformia (family Staphylinidae) are from North American Upper Triassic Period deposits (Carnian stage: 225–230 Ma) (Fraser *et al.*, 1996; Chatzimanolis *et al.*, 2012). However, attribution of these fossils to Staphylinidae has been questioned (Grebennikov & Newton, 2012).
[c] Plus Lymexyloidea as in the ML tree (Figure S2), Hunt *et al.* (2007) and McKenna & Farrell (2009).

earliest known fossil insect, *Rhyniognatha* Tillyard (Engel & Grimaldi, 2004). The lower boundary on the prior distribution was conservatively truncated to 270 Ma based on the earliest known unambiguous fossil stem group Coleoptera [Tshekardocoleidae from the Lower Permian of Obora, Czech Republic, and Tshekarda, Russia (Ponomarenko, 1963; Kukalová, 1969; Grimaldi & Engel, 2005; Beckemeyer & Engel, 2008; Kukalová-Peck & Beutel, 2012)]. These boundaries readily accommodate the ages of several additional relevant fossils that were not specifically used as constraints, including: *Stephanastus polinae* Kirejtshuk & Nel (Gzhelian Stage 298.9–303.7 Ma), a proposed stem group representative of Coleopterida (Coleoptera + Strepsiptera) (Nel *et al.*, 2013); *Avioxyela gallica* Nel (Moscovian Stage 307.0–315.2 Ma; Nel *et al.*, 2013); a proposed stem group hymenopteran; and *Westphalomerope maryvonneae* Nel *et al.* (Bashkirian Stage 315.2–323.2 Ma; Nel *et al.*, 2007), a proposed Carboniferous Mecopteran**.**

We conducted three separate analyses of the combined DNA sequence data in BEAST with partitions as determined by PartitionFinder (see Data Partition and Model Selection), estimated base frequencies and four gamma categories – the same partitioning scheme and analytical conditions used in the ML analyses. Posterior distributions were estimated via MCMC sampling, with tree and parameter values sampled every 1000 generations for 100 million generations per run. To diagnose convergence, determine an appropriate burn-in, and otherwise check performance and accuracy of the BEAST analyses, we performed graphical and statistical analyses on the resulting log files in the program Tracer v1.5 (Rambaut *et al.*, 2011). This included an examination of: (i) the frequency distribution, mean, standard deviation, confidence intervals and other statistics for each logged analysis parameter, (ii) the Bayesian posterior density plot for each analysis parameter, (iii) a trace of each parameter against generation number (to check mixing, choose a suitable burn-in and to look for trends that might suggest problems with convergence), and (iv) estimated sample sizes of combined traces (to show cases where individual traces are sampling different distributions) (Rambaut, 2009).

These analyses indicated that each of the BEAST runs had converged by 5×10^7 generations. We retained all trees sampled after 5×10^7 generations from each of the three analyses (50 000 trees per analysis), for a combined total of 150 000 trees. To reduce the number of trees requiring downstream analysis, we subsampled these trees at a frequency of 1/10 000 generations using the program Logcombiner v1.8.0 (part of the BEAST package). We used Mesquite (Maddison & Maddison, 2011) to obtain a 50% majority-rule consensus tree from the resulting 15 000 post burn-in trees. Bayesian posterior probabilities (BPPs) were interpreted as follows in the Results and Discussion sections: 1.0 = maximal clade support, ≥0.95 and <1.0 = strong clade support, ≥0.75 and <0.95 = moderate clade support, ≥0.50 and <0.75 = weak clade support, and <0.50 = negligible clade support. We used the program Treeannotator v1.8.0 (Drummond & Rambaut, 2007) to obtain the maximum clade credibility (MCC) timetree (Fig. 2) for viewing in the program Figtree v1.4.0 (Rambaut, 2009). The MCC tree has the highest product of clade posterior probabilities. The MCC tree was rooted with the two hymenopteran OGs following Wiegmann *et al.* (2009a,2009b), McKenna & Farrell (2010), Niehuis *et al.* (2012), Misof *et al.* (2014) and McKenna (2014).

Diversification rates

MEDUSA (Alfaro *et al.*, 2009; Harmon *et al.*, 2011) was used to integrate information about the timing of splits along the backbone of the beetle phylogeny with taxonomic richness data (described species), in order to estimate diversification rates in Neuropteroidea and Coleoptera. Analyses were executed using the MCC timetree modified so that terminals reflected monophyletic family-level (or nearest possible equivalent) groupings of taxa within Coleoptera (Figure S1; Table S3). In some cases this required forming terminals from groupings of taxa that have not previously been treated as families or monophyla. We used R (R Development Core Team, 2011) to perform these analyses using the packages Ape (Paradis *et al.*, 2004), Geiger (Harmon *et al.*, 2008, 2011) and Laser (Rabosky, 2007), following the methods of Alfaro *et al.* (2009).

We established the background tempo of diversification for Neuropteroidea as a whole and for its constituent group Coleoptera using estimates for described extant family-level species diversity within Coleoptera from Ślipiński *et al.* (2011). We used estimates for ordinal-level species diversity for Neuropterida and Strepsiptera (Grimaldi & Engel, 2005) because these groups were not sampled at the family-level in our study. Other sources were consulted when sub-familial taxon numbers were needed to provide taxonomic richness estimates for families of Coleoptera that were split apart or lumped together in the MCC tree along infrafamilial lines (see Table S3). However, when a family was split into two groups (none were split into more than two), the extent of the resulting groups was typically uncertain (establishing this would require sampling additional taxa), so, to avoid introducing unnecessary bias, the total number of described species in the family was split evenly between the two separately-recovered lineages for the analysis of diversification rates. MEDUSA was then used to determine which family-level clades within Coleoptera are too species-rich (increase in rate) or species-poor (decrease in rate) to result from the estimated background diversification rate for the order.

Results

Phylogenetic trees and clade support

The phylogenetic hypothesis for Coleoptera in Fig. 2 shows relationships resulting from a Bayesian analysis (with monophyly constraints; see also Table S2 and Figure S9. Relationships and clade support (BPPs) estimated under Bayesian inference should therefore be interpreted cautiously) of concatenated nucleotides from all eight nuclear genes. The ML tree shown in Figure S2 resulted from an unconstrained partitioned likelihood analysis of the same dataset. Clade support values resulting from ML bootstrap (MLB) analyses of nucleotides alone

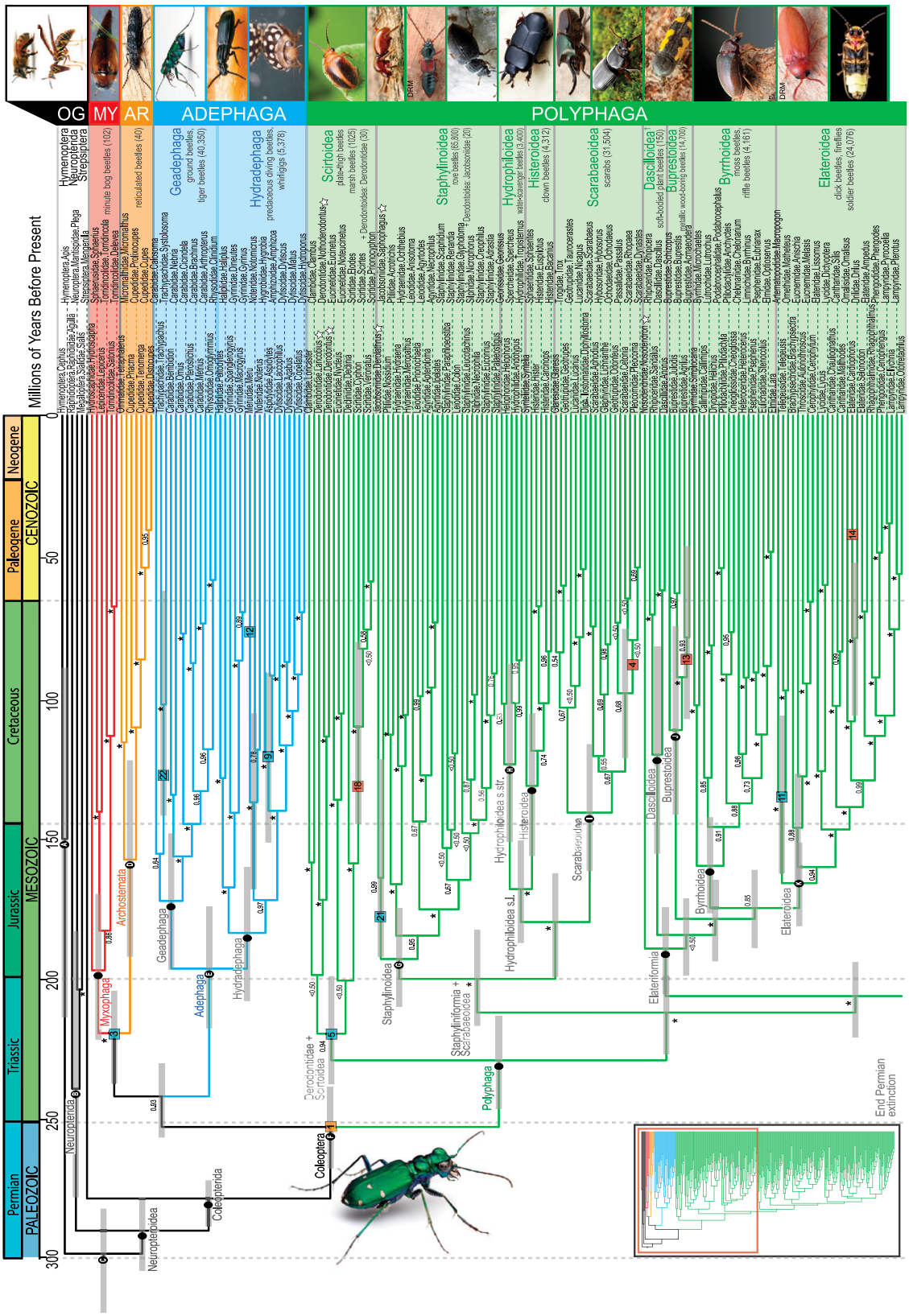

Fig. 2. Legend follows figure.

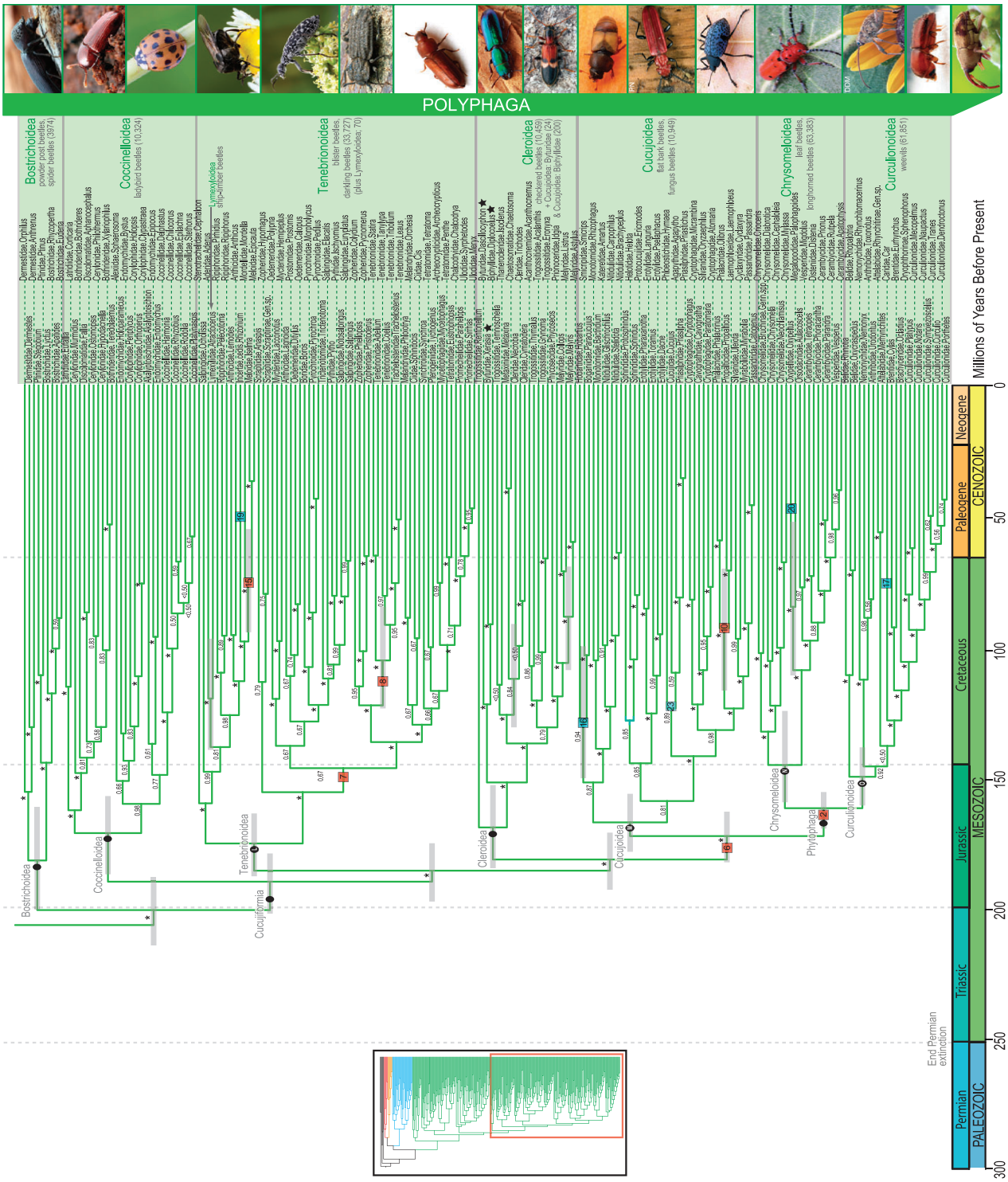

Fig. 2. Continued. Legend on Next page.

[unconstrained (Figure S3) and with Strepsiptera constrained to the OG (Figure S7)] and rDNA nucleotides + AAs from the six NPC genes (Figure S4) are summarized on the ML tree. The topologies obtained from Bayesian (Fig. 2) and ML analyses (Figure S2) are summarized and compared in detail in Figs 3–15. MLB values from analysis of the AAs alone (Figure S5) are not shown in Figure S2 because taxa with data for less than 50% of the AA positions were excluded from the analysis, resulting in a smaller taxon sample (see Materials and methods). The same applies to the MLB analysis of nucleotides from the six NPC genes alone, for which the same taxa were excluded from analysis on account of missing data (Figure S6). The MLB analysis of AAs alone (Figure S5) and the MLB analysis of NPC nucleotides alone (Figure S6) therefore cannot be directly compared to the results from the other MLB analyses because they contain different numbers of species. We only compare and contrast these results with the results of the other analyses (below) when specifically noted.

Higher-level relationships and near relatives of beetles

Coleoptera was monophyletic in the ML tree ($-\ln L = 871077.08$) resulting from analysis of the concatenated nucleotide sequences alone (Figure S2), and Strepsiptera (*Mengenilla*) was its sister group. These orders together formed the clade Coleopterida (Strepsiptera + Coleoptera; Kukalová-Peck & Lawrence, 2004). Likelihood trees with Strepsiptera recovered within the beetle suborder Myxophaga (63% MLB nucleotides alone, Figure S3; 57% MLB rDNA nucleotides + AAs, Figure S4), or with Strepsiptera sister to the beetle suborder Archostemata, had likelihood scores only slightly worse than the ML tree (<25 units higher). Clade support for Coleopterida was moderate in the MLB analyses of nucleotides alone (Figure S3), rDNA nucleotides plus AAs (Figure S4), and AAs alone (Figure S5), weak in the MLB analysis of nucleotides alone with Strepsiptera constrained to the OG (Figure S7), and lacking in the analysis of NPC nucleotides alone (Figure S6). MLB support increased for many relationships when Strepsiptera was constrained to the OG (Figures S2 and S7). For example, in the analysis of nucleotides alone, MLB support for the sister-group relationship between Archostemata and Myxophaga increased from 51% (Figure S3) to 90% (Figure S7). Coleopterida was sister to Neuropterida [comprising Megaloptera (*Sialis*), Raphidioptera (*Agulla*) and Neuroptera (*Plega*)], forming the clade Neuropteroidea (containing Coleoptera + Strepsiptera + Neuropterida) in all analyses (Figs 2, 3; Figure S2). MLB support for Neuropterida was moderate in the analysis of nucleotides alone (Figure S3), the analysis of rDNA nucleotides plus AAs (Figure S4) and the analysis of AAs alone (Figure S5), strong (99%) in the analysis of nucleotides alone with Strepsiptera constrained to the OG (Figure S7), and lacking in the analysis of NPC nucleotides alone (Figure S6). Within Neuropterida, Neuroptera and Megaloptera were sister taxa, and these together were sister to Raphidioptera in all analyses (Figs 2, 3; Figure S2). Neuropteroidea was sister to Hymenoptera (*Apis* and *Cephus*), the most distant OG in our analyses. These relationships are the same as in the BI tree (Fig. 2).

Interrelationships of the suborders of beetles

The subordinal relationships recovered in the ML and BI trees were the same – Polyphaga (Adephaga (Myxophaga, Archostemata)) (Figs 2, 3; Figure S2) – and each of the suborders of Coleoptera was monophyletic. MLB support for the suborders varied among analyses. Archostemata received strong to maximal MLB support in all analyses (Figure S2). MLB support for Myxophaga was weak in the analyses of nucleotides alone (Figure S3) and rDNA nucleotides plus AAs (Figure S4), negligible in the analysis of AAs alone (Figure S5), and lacking in the analysis of NPC nucleotides alone (Figure S6) (in all of these Strepsiptera was included). However, MLB support for Myxophaga increased substantially (from 63 to 93%) in the analysis of nucleotides with Strepsiptera (*Mengenilla*) constrained to the OG (Figures S3 and S7). MLB support for Adephaga was moderate in the analysis of nucleotides alone (Figure S3), strong in the analyses of rDNA nucleotides plus AAs (Figure S4) and AAs alone (Figure S5), maximal in the analysis of nucleotides with Strepsiptera constrained to the OG (Figure S7), and weak in the analysis of NPC nucleotides alone (Figure S6). MLB support for Polyphaga was weak in the analyses of rDNA nucleotides plus AAs (Figure S4) and AAs alone (Figure S5),

Fig. 2. Maximum clade credibility timetree for beetles (367 species representing 171/183 families) and OGs (six species representing five orders), resulting from partitioned Bayesian analyses of DNA sequences from eight nuclear genes in the program BEAST. Note that the top/right row/column entries are interdigitated between the bottom/left ones, as connected by the broken lines. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches (an asterisk indicates nodes with maximal BPP support of 1.0) and 95% confidence intervals around node age estimates (series, superfamilies, and select other higher-level groups mentioned in the text) are shown as grey bars. Background colours: black/white = OGs; red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga. Monophyly constraints from the BEAST analysis are shown as black ovals, with node ages constrained by fossil priors indicated by letters within the ovals (A–O; see Table S3). White stars mark species of Derodontoidea. Black stars mark species of Cucujoidea s.l. (Biphyllidae and Byturidae) recovered in positions separate from other members of the superfamily. Numbers of extant species for superfamilies (in parentheses) are from Ślipiński *et al.* (2011). The timing and taxonomic location of increases or decreases in diversification rate in beetles are marked in the phylogeny with boxes numbered 1–23, with individual net diversification rates ($r = b - d$) and relative extinction rates ($\varepsilon = d/b$) summarized by number in Table 3. Clades showing an inferred significant increase in diversification rate are marked with red boxes, whereas clades showing a significant decreases in rate are marked with blue boxes. Photo credits: ©David R. Maddison (DRM), ©Duane D. McKenna (DDM), ©Piotr Naskrecki (PN), and ©Alex Wild (unlabelled). A high-resolution version of this figure is available in Figure S8. 95% confidence intervals for all nodes are shown in Figure S9. † = Plus Derodontoidea: Nosodendridae.

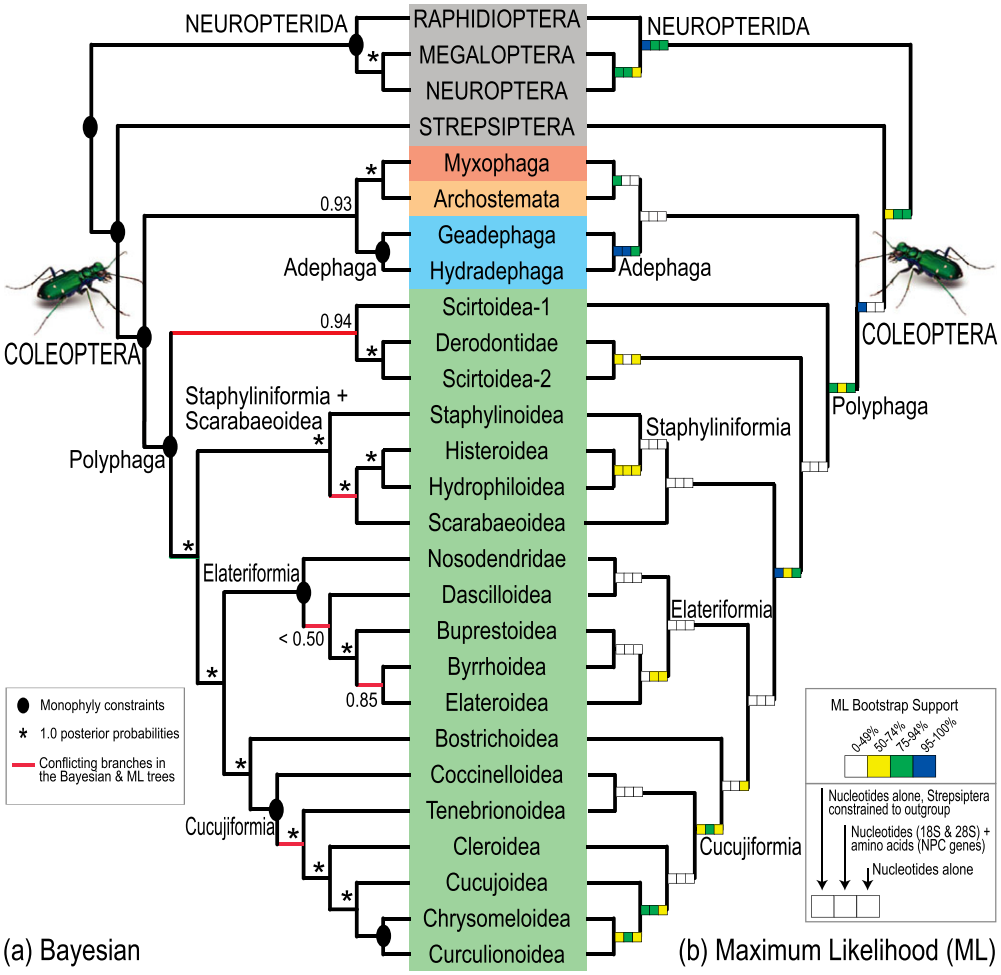

Fig. 3. (a) Bayesian and (b) maximum-likelihood (ML) summary trees showing higher-level groups of beetles and OGs, resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legend). Background colours: gray = OGs; red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga. Monophyly constraints from the BEAST analysis are shown as black ovals [Note, monophyly constraints on taxa shown as terminals are not marked (see Table S2)]. Photo credit for *Cicindela* Linnaeus: Alex Wild.

lacking in the analysis of NPC nucleotides alone (Figure S6), and moderate in the analyses of nucleotides alone with and without Strepsiptera constrained to the OG (Figures S3 and S7).

Relationships within Archostemata and Myxophaga

Within Archostemata, internal relationships were recovered with variable (moderate to maximal, but mostly strong to maximal) MLB and BPP support, except for the sister-group relationship between *Cupes* Fabricius and *Distocupes* Neboiss (Cupedidae), which had weak to negligible support in MLB analyses but strong support under BI (Fig. 4). *Micromalthus* Leconte (Micromalthidae) formed a clade with *Tetraphalerus* Waterhouse (Ommatidae) with strong to maximal MLB and BPP support, sister to Cupedidae. Myxophagan relationships were the same in the ML and BI trees (Fig. 4; Figure S2). The monophyly of Torridincolidae (three exemplars) received strong to maximal support in all analyses (Fig. 2; Figures S2–S7). The clade [Sphaeriusidae (*Sphaerius* Waltl) + Lepiceridae (*Lepicerus* Motschulsky)] was sister to Torridincolidae. Hydroscaphidae (*Hydroscapha* Leconte) was sister to all other Myxophaga sampled.

Relationships within Adephaga

Adephaga comprised two large clades in the ML and BI trees, corresponding to the traditional Hydradephaga and Geadephaga (Figs 2, 5; Figure S2). MLB support for Hydradephaga was mostly weak in unconstrained analyses (Figures S2–S4); however, in the analysis of nucleotides alone with Strepsiptera

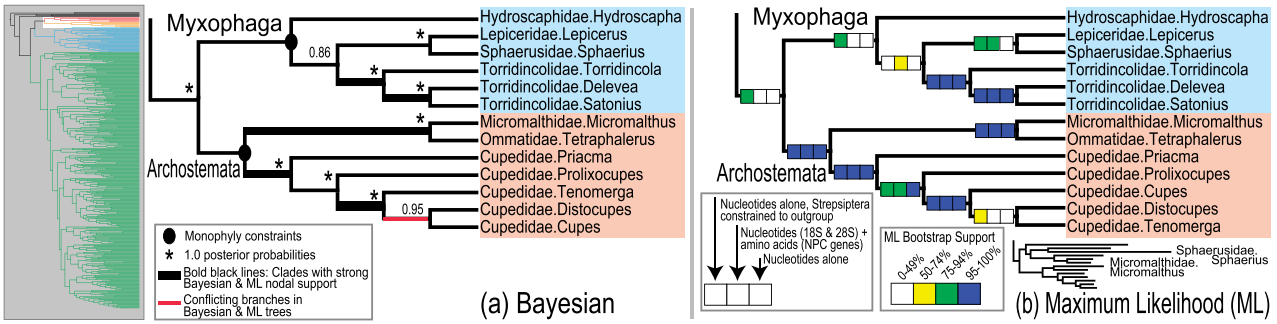

Fig. 4. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Archostemata and Myxophaga, resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from three of the five extant families of Archostemata, and all living families and subfamilies of Myxophaga. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

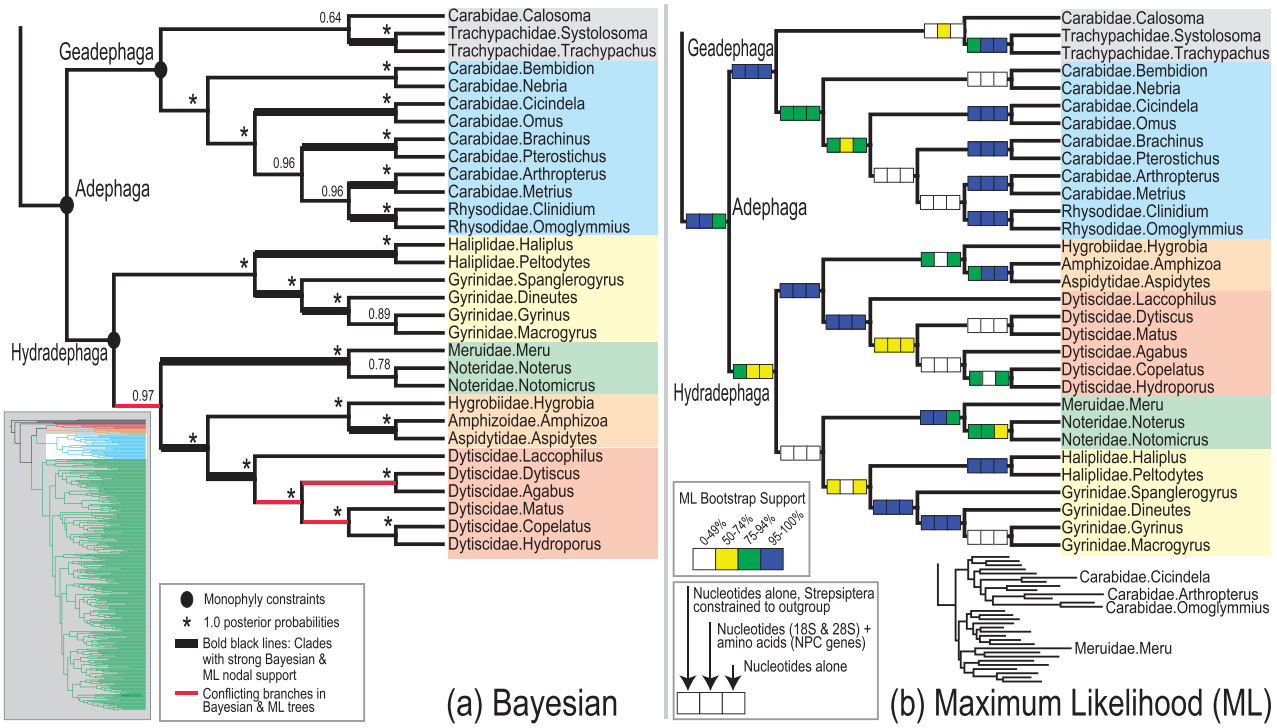

Fig. 5. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Adephaga resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all 11 extant families of Adephaga. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

(*Mengenilla*) constrained to the OG (Figure S7), MLB support for Hydradephaga increased substantially – from 61 to 85%. Geadephaga received strong to maximal support in all ML analyses, and had the same internal relationships under ML (nucleotides alone) and BI. Support for the internal relationships of Hydradephaga and Geadephaga was variable, but mostly moderate to maximal; relatively few clades within Adephaga had weak or negligible support. At the family level within Hydradephaga, Dytiscidae and Gyrinidae were strongly to maximally supported as monophyletic. *Aspidytes* Ribera, Beutel, Balke & Vogler (Aspidytidae) was sister to *Amphizoa* Leconte (Amphizoidae) in all analyses, and had moderate to strong MLB support and maximal BPP support. *Meru* Spangler & Steiner (Meruidae) was recovered sister to Noteridae (*Noterus* Schellenberg and *Notomicrus* Sharp) with moderate to maximal MLB support and maximal BPP support. Within Geadephaga,

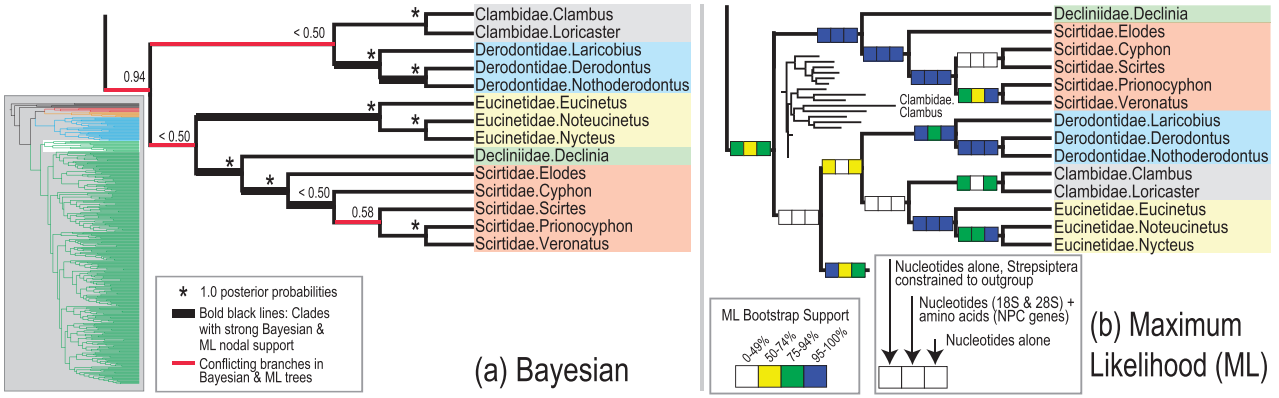

Fig. 6. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Scirtoidea + Derodontidae resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all four extant families of Scirtoidea, and all three extant families of Derodontoidea; however, Derodontoidea is polyphyletic, and only Derodontidae is recovered here. The other two families of Derodontoidea, Nosodendridae and Jacobsoniidae, are recovered in association with Elateriformia and Staphylinoidea, respectively. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees.

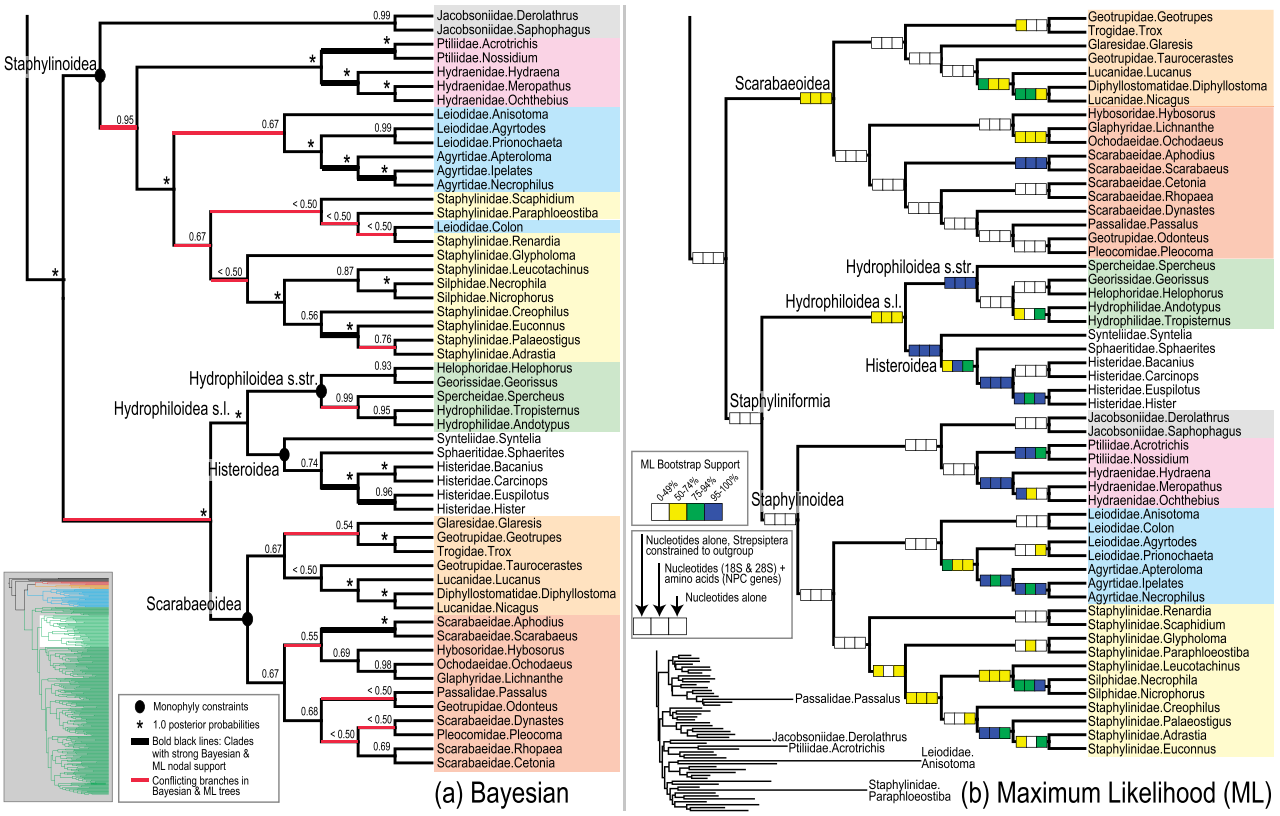

Fig. 7. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Staphyliniformia and Scarabaeiformia (plus Jacobsoniidae) resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families except Belohinidae (Scarabaeoidea). Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

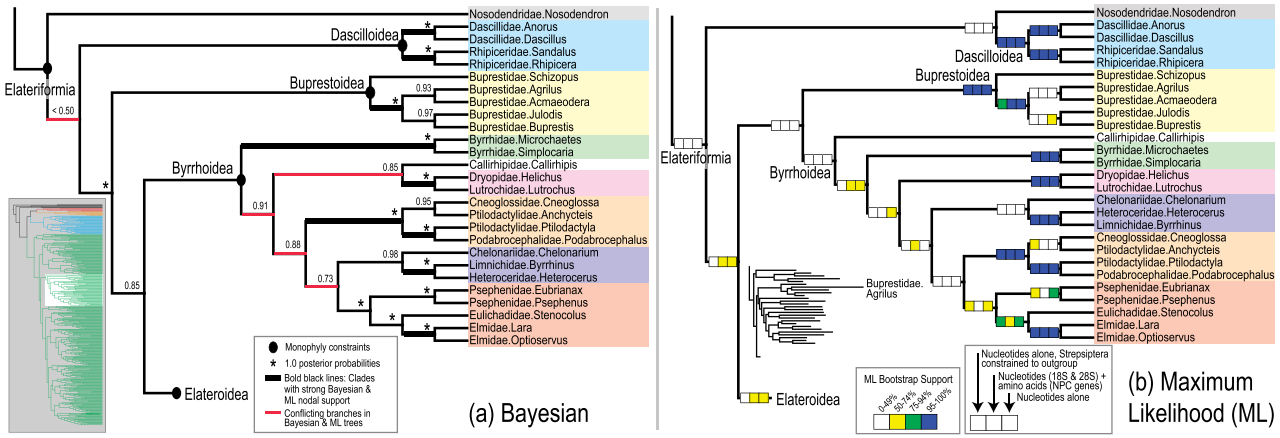

Fig. 8. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Elateriformia minus Elateroidea resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Byrrhoidea, Buprestoidea and Dascilloidea. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

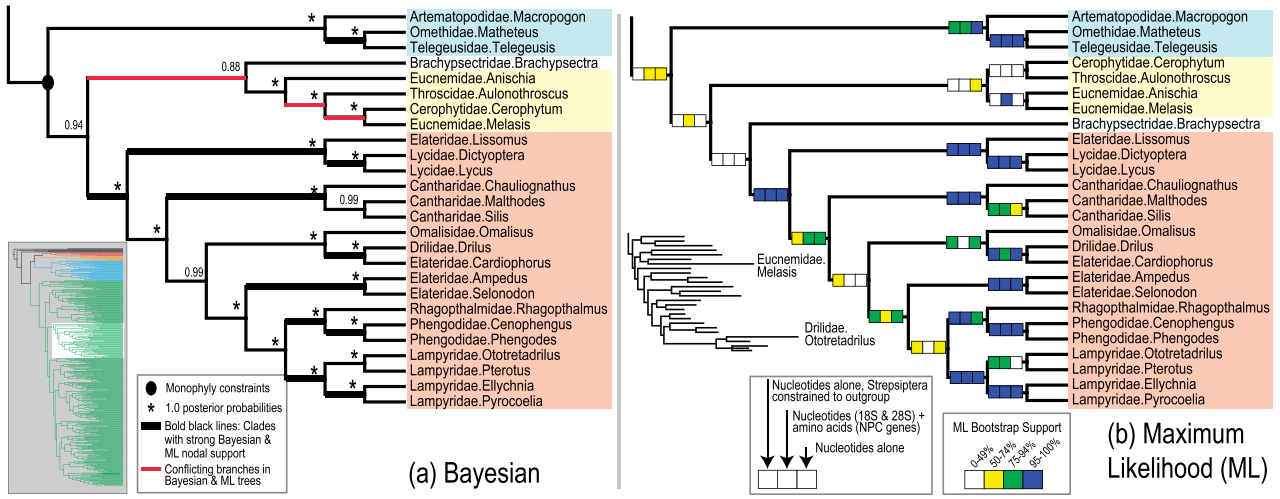

Fig. 9. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Elateroidea, resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Elateroidea except Rhinorhipidae and Plastoceridae. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

Calosoma Weber (Carabidae) was sister to Trachypachidae (*Systolosoma* Solier in Gay and *Trachypachus* Motschulsky), and these together were sister to the remaining Carabidae plus Rhysodidae (*Clinidium* Kirby and *Omoglymmius* Ganglbauer), thereby rendering Carabidae paraphyletic. However, the sister relationship between Trachypachidae and *Calosoma* had negligible to weak MLB and BPP support, except in the analysis of AAs (Figure S5; 83% MLB, moderate support). *Calosoma* was sister to all other Carabidae plus Rhysodidae in some likelihood tree searches, but these trees had slightly worse likelihood scores (<25 units higher) than the ML tree. Carabidae plus Rhysodidae minus *Calosoma* received moderate nodal support in most MLB analyses, and maximal BPP support. Rhysodidae was recovered well within Carabidae, in a position sister to Paussinae (*Arthropterus* MacLeay in Smith and *Metrius* Eschscholtz) under both ML and BI. Cicindelinae was recovered within Carabidae under both ML and BI.

Series and superfamily-level relationships within Polyphaga

Scirtoidea was rendered paraphyletic under ML both by the inclusion of Derodontidae (Derodontoidea; three exemplars),

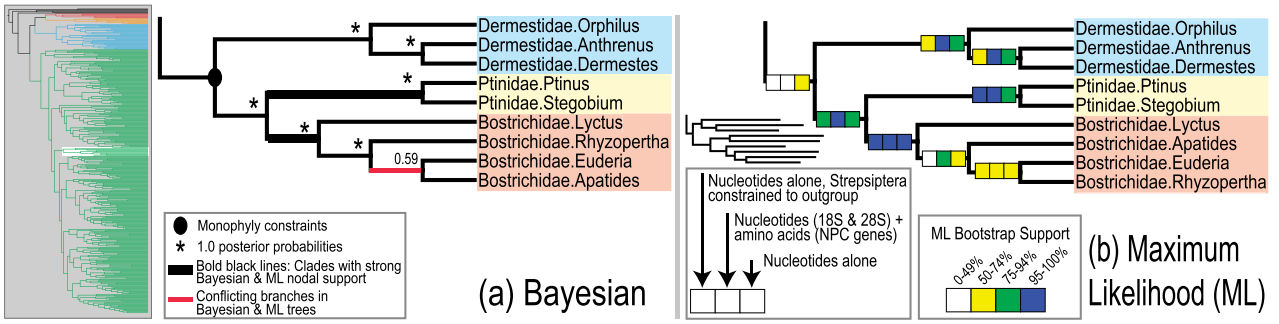

Fig. 10. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Bostrichoidea resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Bostrichoidea except Endecatomidae. However, we did include *Endecatomus* (Endecatomidae) in preliminary analyses (not shown here; see Discussion). Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

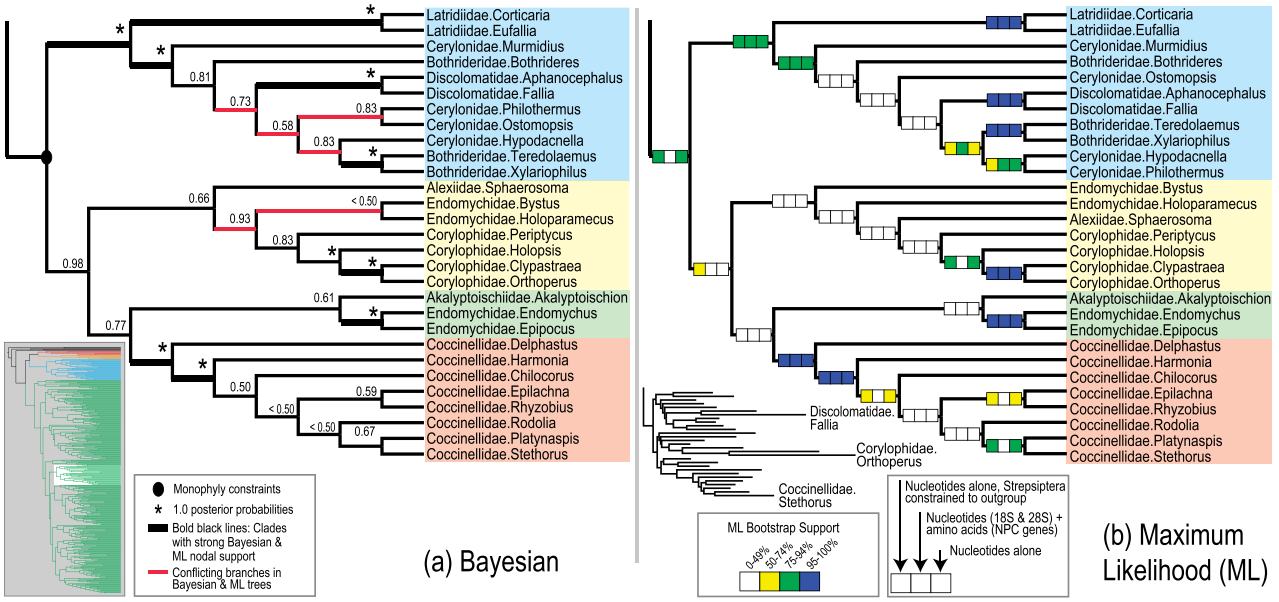

Fig. 11. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Coccinelloidea resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). We included data from all extant families of Coccinelloidea. Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

and by its separation into two clades that were successive sister taxa to all other Polyphaga. However, the basal splits forming these clades had negligible to weak MLB support in most analyses (Figs 3, 6; Figure S2). Under BI, Scirtoidea plus Derodontidae formed a clade with moderate BPP support (Figs 2, 3, 6), sister to the remaining Polyphaga. Derodontoidea *sensu* Lawrence *et al.* (2010a) was therefore polyphyletic in all analyses (Fig. 2; Figure S2), and the remaining two families of Derodontoidea – Jacobsoniidae (*Derolathrus* Sharp and *Saphophagus* Sharp) and Nosodendridae (*Nosodendron* Latreille) – formed two additional clades under both ML and BI, which were recovered in separate positions elsewhere within Polyphaga. Jacobsoniidae was recovered within Staphyliniformia in close relation to Staphylinoidea, and Nosodendridae was recovered sister to Dascilloidea (ML) or sister to Elateriformia (BI). Polyphaga minus Scirtoidea and Derodontidae received variable MLB support and maximal BPP support (Figs 2, 3; Figure S2). Many of the series and superfamilies of Polyphaga, and several other major clades, received MLB and BPP support in most analyses (not counting the BI analysis in cases where a clade was constrained to be monophyletic) (Figs 3; Figure S2). These included Buprestoidea (Fig. 7), Buprestoidea + Byrrhoidea + Elateroidea (Fig. 8), Chrysomeloidea (Fig. 15), Coccinelloidea (Fig. 11),

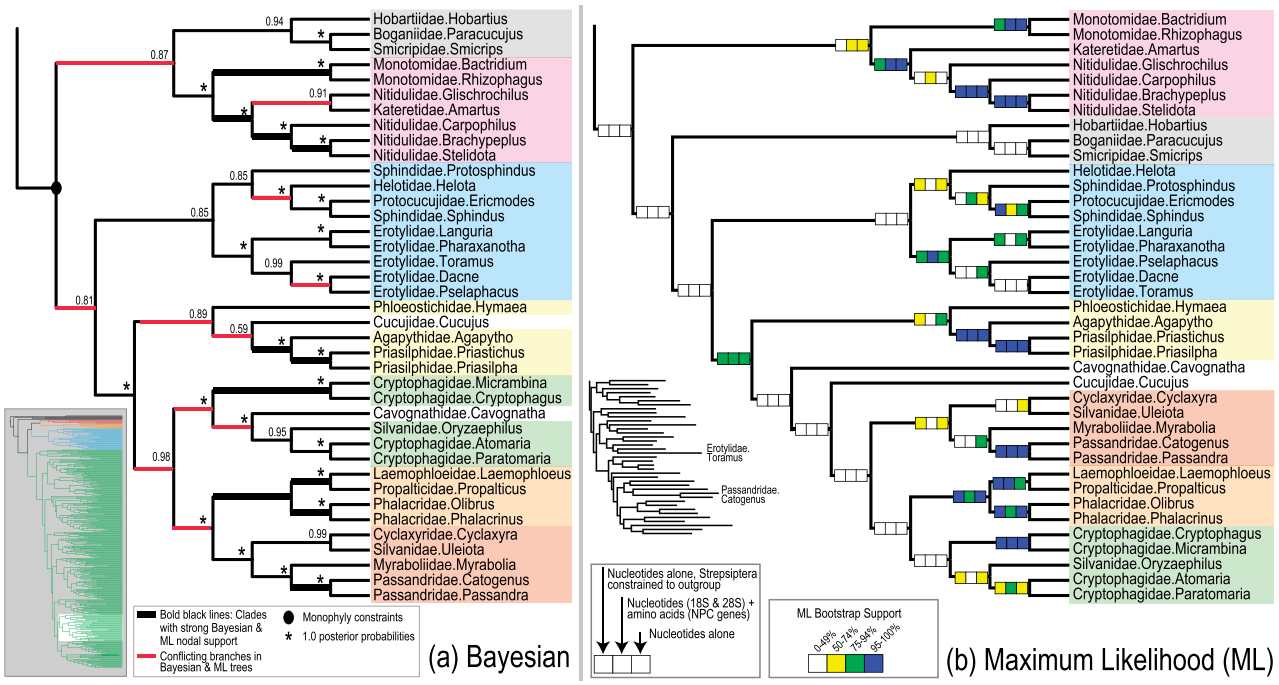

Fig. 12. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Cucujoidea s.s. resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Cucujoidea s.s., except Cybocephalidae, Lamingtoniidae, Phloiophilidae and Tasmosalpingidae. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

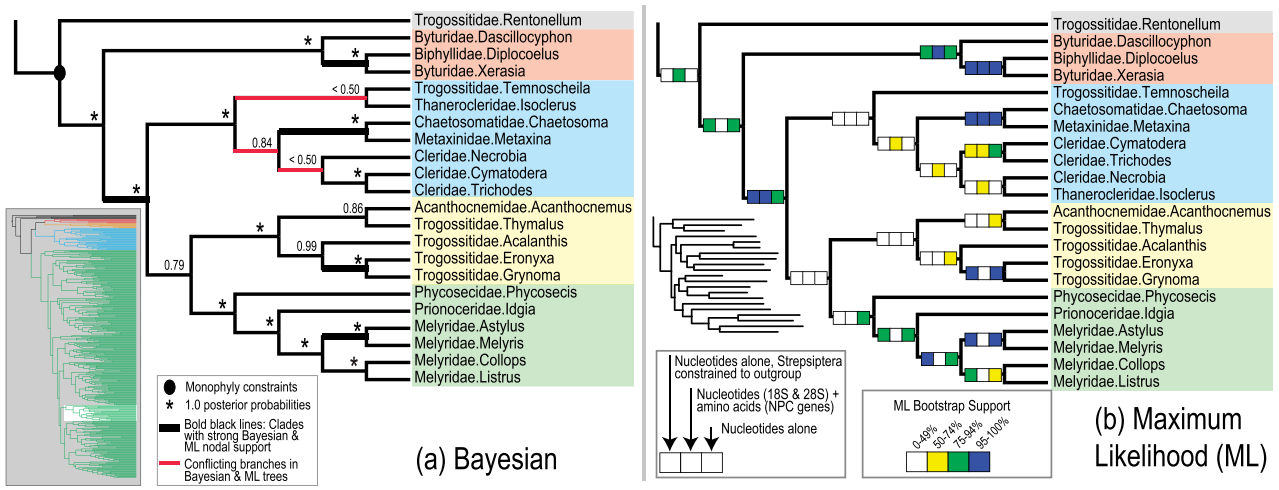

Fig. 13. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Cleroidea (including Biphyllidae and Byturidae) resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Cleroidea except Mauroniscidae, Phloiophilidae, and Rhadalidae. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

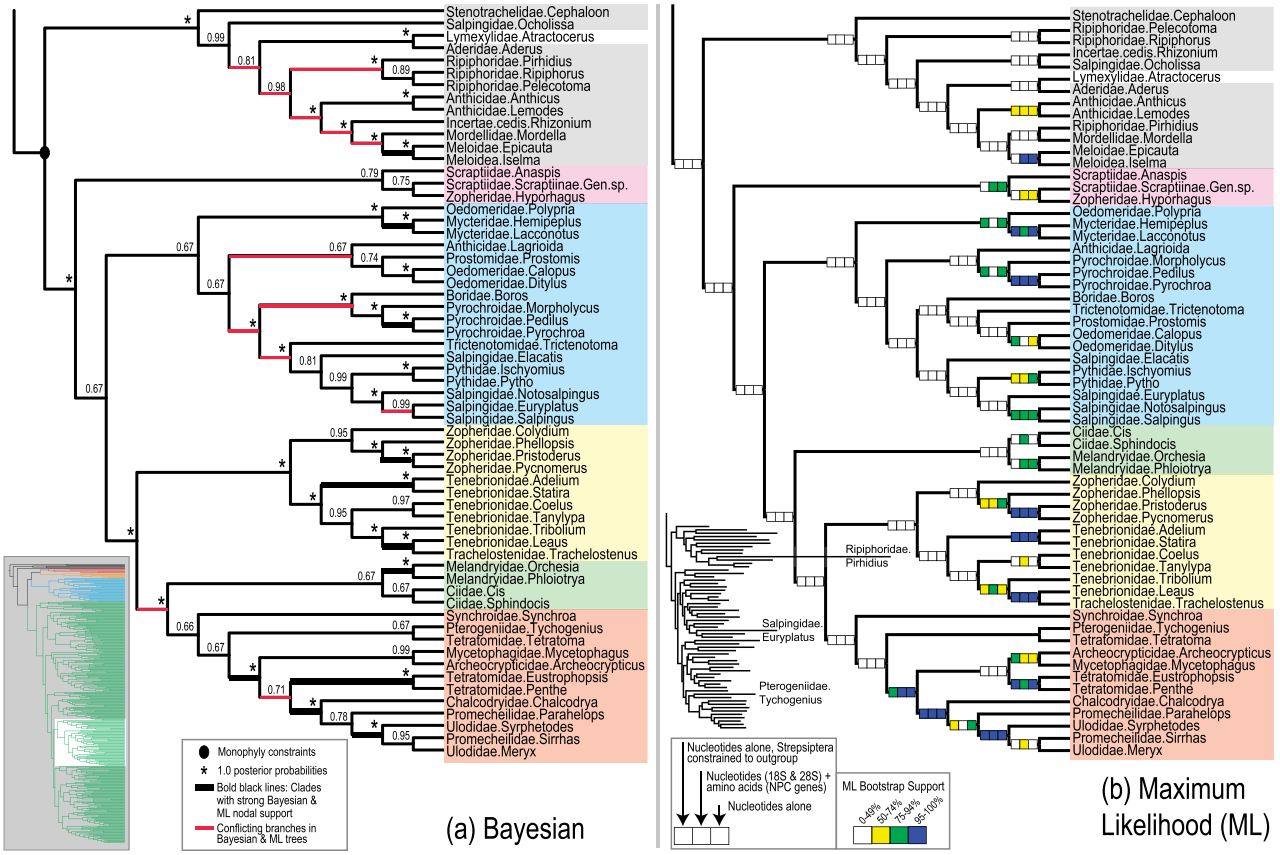

Fig. 14. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Tenebrionoidea resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Tenebrionoidea. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

Cucujiformia (Fig. 3; Figure S2), Curculionoidea (Fig. 15), Dascilloidea (Fig. 8), Elateroidea (Fig. 9), Histeroidea (Fig. 7), Hydrophiloidea (s.l. and s.s.) (Fig. 7), and Phytophaga + Cucujoidea s.s. (Figs 2, 3; Figure S2).

Scarabaeoidea was sister to Hydrophiloidea s.l. in the BI tree (with maximal BPP support), and these together were sister to Staphylinoidea (including Jacobsoniidae), rendering series Staphyliniformia paraphyletic. This large clade (Staphyliniformia + Scarabaeoidea + Jacobsoniidae) received maximal BPP support (Figs 2, 7). However, in the ML tree, Staphyliniformia (including Jacobsoniidae, which was sister to Staphylinoidea) was sister to Scarabaeoidea. This large clade had negligible support in all MLB analyses. Within this clade, superfamilies Histeroidea and Hydrophiloidea s.s. were sister groups under ML and BI, (Fig. 7; Figure S2). Staphyliniformia and Staphylinoidea, though both present in the ML tree (Staphylinoidea, but not Staphyliniformia, was present in the BI tree as a monophyly constraint) received negligible MLB support in all analyses. MLB support for Scarabaeoidea was weak in all analyses.

Series Elateriformia (Figs 2, 8, 9; Figure S2), containing the superfamilies Buprestoidea, Byrrhoidea, Dascilloidea and Elateroidea, was monophyletic including *Nosodendron* (Nosodendridae), but had negligible MLB support in all analyses. Under ML, Nosodendridae was sister to a strongly to maximally supported superfamily Dascilloidea, and these together were sister to the remaining Elateriformia. Under BI, *Nosodendron* was sister to the traditional Elateriformia, and Dascilloidea was sister to a clade containing the other superfamilies of series Elateriformia, the latter with negligible MLB support. Superfamily Buprestoidea was monophyletic and received strong to maximal MLB support in all analyses (Fig. 8). Buprestoidea was recovered as the sister group of Byrrhoidea under ML (with negligible MLB support), or as the sister group of Byrrhoidea + Elateroidea under BI, with maximal BPP support. Byrrhoidea [plus the elateroid *Podabrocephalus* Pic (Podabrocephalidae)] was monophyletic, but with negligible MLB support. The monophyly of superfamily Bostrichoidea received negligible to weak MLB support in all analyses. Its placement sister to series Cucujiformia in both the ML and Bayesian trees (Figs 2, 10; Figure

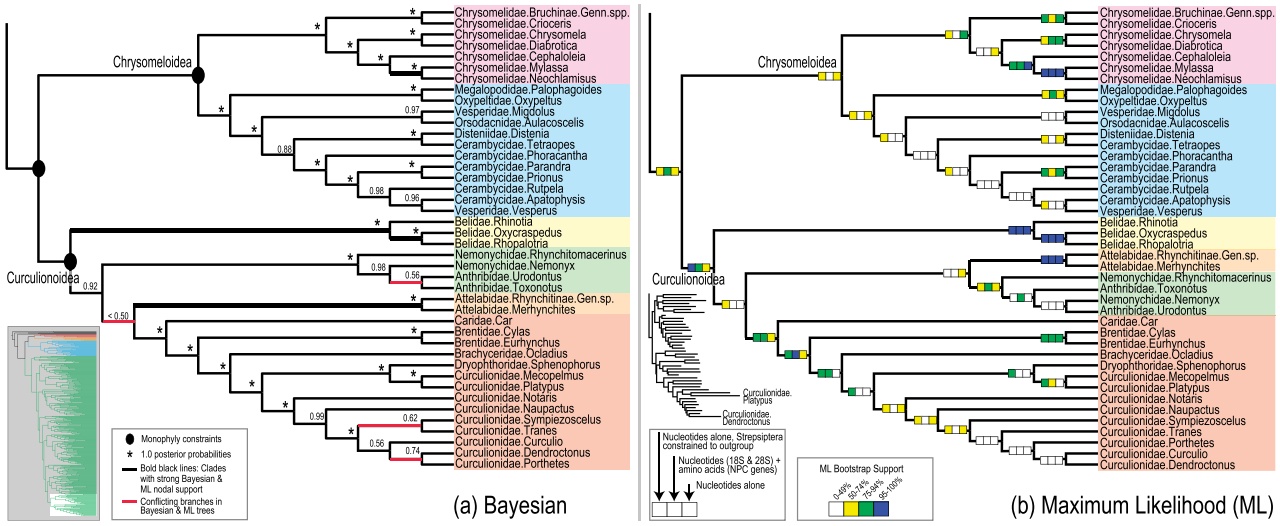

Fig. 15. (a) Bayesian and (b) maximum-likelihood (ML) summary trees for Phytophaga (Chrysomeloidea and Curculionoidea) resulting from partitioned phylogenetic analyses of DNA sequences from eight nuclear genes (see Materials and methods). We included data from all extant families of Phytophaga. Statistical measures of Bayesian posterior probability (BPP) support are shown along branches in the Bayesian tree (an asterisk indicates nodes with maximal BPP support of 1.0). Partitioned ML bootstrap support under various analytical schemes is noted by coloured boxes along branches in the ML tree (see embedded legends). Background colours indicate major clades present in both trees. Monophyly constraints from the BEAST analysis are shown as black ovals (see Table S3).

S2) received maximal BPP support and negligible to weak MLB support (Fig. 3; Figure S2).

Series Cucujiformia was recovered in the ML tree with mostly weak to moderate MLB support (Figs 2, 3; Figure S2). Most Cucujoidea (in the traditional broad sense of the superfamily) were recovered in one of two large clades. One clade contained the Cerylonid Series of families (Akalyptoischiidae, Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae and Latridiidae) (Figs 2, 11; Figure S2), here called Coccinelloidea, following Robertson *et al.* (2015) and the other clade contained the remaining Cucujoidea (Figs 2, 12; Figure S2; here called Cucujoidea s.s.), except Biphyllidae and Byturidae, which were recovered within Cleroidea (Figs 2, 13; Figure S2) (see below for more information). Coccinelloidea was monophyletic in both the ML and BI trees, with mostly moderate MLB support. Coccinelloidea was sister to Tenebrionoidea under ML, and these together were sister to the remaining Cucujiformia, but with negligible MLB support. Under BI, Coccinelloidea was sister to the remaining Cucujiformia, and Tenebrionoidea was sister to the clade Cleroidea + Cucujoidea s.s. + Curculionoidea + Chrysomeloidea, with maximal BPP support. Tenebrionoidea (including Lymexyloidea) was monophyletic in the ML and BI trees. However, MLB support for Tenebrionoidea was negligible in all analyses (Figs 2, 14; Figure S2). The monophyly of Cleroidea plus the traditional cucujoid families Biphyllidae and Byturidae received negligible to moderate MLB support (Figs 2, 13; Figure S2). The main cluster of Cucujoidea (Cucujoidea s.s.) contained those taxa that do not belong to Coccinelloidea or Cleroidea. Its monophyly was recovered in the ML and Bayesian trees, but MLB support for Cucujoidea s.s. was negligible in all analyses (Figs 2, 12; Figure S2). A subset of Cucujoidea s.s. [Nitidulidae, Kateretidae (*Amartus* Leconte), Monotomidae (*Bactridium* Kunze and *Rhizophagus* Herbst), Boganiidae (*Paracucujus* Sen Gupta & Crowson) and Hobartiidae (*Hobartius* Sen Gupta & Crowson), or *Paracucujus* and *Smicrips* Leconte, or *Paracucujus* alone] was recovered sister to Phytophaga (forming a paraphyletic grade of Cucujoidea s.s.) in some likelihood trees. These trees had only slightly worse likelihood scores than the ML tree (<25 units higher), in which Cucujoidea s.s. was monophyletic.

The clade Phytophaga (the sister superfamilies Chrysomeloidea and Curculionoidea) was sister to Cucujoidea s.s. in both the ML and Bayesian trees, with mostly moderate MLB support and maximal BPP support (Figs 2, 15; Figure S2). Phytophaga was monophyletic and received weak to moderate MLB support. Chrysomeloidea and Curculionoidea were each monophyletic. MLB support for Chrysomeloidea was mostly weak. MLB support for Curculionoidea was strong in the analysis of nucleotides alone, and varied from weak to moderate in the other MLB analyses.

Internal relationships of the series and superfamilies of Polyphaga

The scirtoid families Clambidae, Eucinetidae and Scirtidae were each monophyletic and moderately to maximally supported in all analyses. *Declinia* Nikitsky, Lawrence, Kirejtshuk & Gratshev (Decliniidae) was strongly to maximally supported as sister to Scirtidae. The relationships of Clambidae and Eucinetidae to Derodontidae (Derodontoidea) differed between the ML and BI trees, but had negligible to weak nodal support in

all analyses. Jacobsoniidae, previously assigned to superfamily Derodontoidea, was recovered within Staphylinoidea, sister to a clade formed by Hydraenidae (three exemplars) + Ptiliidae (*Acrotrichis* Motschulsky and *Nossidium* Erichson) under ML (Fig. 7; Figure S2), but with negligible MLB support for both its inclusion in Staphylinoidea and its position as sister to Hydraenidae + Ptiliidae. Jacobsoniidae was sister to Staphylinoidea under BI (Figs 2, 7). Among staphylinoid subgroups, the Ptiliid group and its constituent families (Ptiliidae and Hydraenidae) were recovered with strong BPP (Figs 2, 7) and variable MLB support (except Ptiliidae in the unconstrained analysis of nucleotides alone; Figures S2 and S3).

The internal relationships of Hydrophiloidea s.s. differed under ML and BI and had mostly negligible MLB support and moderate to strong BPP support (Figs 2, 7; Figure S2). Under ML, Spercheidae (*Spercheus* Kugelann) was sister to the remaining Hydrophiloidea s.s.; in contrast, under BI, Helophoridae (*Helophorus* Fabricius) and Georissidae (*Georissus* Latreille) were together sister to a clade comprising Spercheidae plus Hydrophilidae (*Andotypus* Spangler and *Tropisternus* Solier). The sister relationships between Georissidae and Helophoridae and between the two Hydrophilidae were supported in all analyses. *Syntelia* Westwood (Synteliidae) was the sister taxon to all other Histeroidea in the ML and BI analyses, and *Sphaerites* Duftschmid (Sphaeritidae) was consistently recovered sister to Histeridae (four exemplars). The internal relationships of Histeroidea (Fig. 7) were the same under ML and BI and had mostly strong to maximal BPP and MLB support.

Neither the Leiodid group (Leiodidae + Agyrtidae) nor Leiodidae (four exemplars) was recovered under BI because of the odd separation of *Colon* Herbst (Leiodidae: Coloninae) from the remainder, although the group was recovered in the ML tree, where it received negligible nodal support (Fig. 7; Figure S2). Agyrtidae (three exemplars), in contrast, was moderately to maximally supported in all analyses. The Staphylinid group (Silphidae + Staphylinidae including Scydmaeninae) was recovered in the ML tree, but received negligible MLB support. Silphidae (*Necrophila* Kirby & Spence and *Nicrophorus* Fabricius) (ML and BI) and *Colon* (BI only) rendered Staphylinidae paraphyletic (Fig. 7). Silphidae was moderately to maximally supported in all MLB analyses. Within Staphylinidae (nine exemplars), sparse taxon sampling limits testing of the four subfamily groupings of Lawrence & Newton (1982, 1995), but Scydmaeninae (three exemplars) was consistently recovered sister to *Creophilus* Samouelle (Staphylininae) (Fig. 7), as expected for those sole representatives of the Staphylinine group. The omaliine (*Paraphloeostiba* Steel and *Glypholoma* Jeannel) and osoriine (*Renardia* Motschulsky and *Scaphidium* Olivier) groups were each recovered under ML, but not under BI (Fig. 7). The single included member of the Tachyporine group (*Leucotachinus* Coiffait & Sáiz) was sister to Silphidae in both the ML tree (negligible to weak MLB support) and BI tree (moderate BPP support).

The deep nodes within Scarabaeoidea were all recovered with negligible MLB support and negligible to weak BPP support (Fig. 7). The three species of Geotrupidae sampled were recovered in the same three separate clades in the ML and Bayesian trees. *Geotrupes* Latreille (Geotrupinae) was recovered sister to *Trox* Fabricius (Trogidae) with negligible to weak MLB support and maximal BPP support, *Taurocerastes* Philippi (Taurocerastinae) was sister to Lucanidae + *Diphyllostoma* Fall (Diphyllostomatidae) with negligible MLB and BPP support, and *Odonteus* Samouelle (Bolboceratinae) was recovered along with *Pleocoma* Leconte (Pleocomidae) and *Passalus* Fabricius (Passalidae) in a clade with negligible MLB and BPP support that was otherwise composed of Scarabaeidae. Therefore, the topologies are different, but in both trees Scarabaeidae is not monophyletic. The sister-group relationship between the dung beetle subfamilies Scarabaeinae (*Scarabaeus* Linnaeus) and Aphodiinae (*Aphodius* Illiger) was maximally supported in all analyses. A clade comprising *Lucanus* Scopoli (Lucanidae: Lucaninae), *Nicagus* Leconte (Lucanidae: Nicaginae) and *Diphyllostoma* (Diphyllostomatidae) was recovered in the ML and BI trees, with weak to moderate MLB support and maximal BPP support. Overall, relatively few internal relationships in Scarabaeoidea had >50% MLB support or >0.75 BPP support.

Within Elateriformia (also see above section Series and Superfamily-level Relationships within Polyphaga), Schizopodidae (*Schizopus* Leconte) was moderately to maximally supported as sister to Buprestidae (four exemplars). We recovered strong to maximal MLB and BPP support for inclusion of the elateroid *Podabrocephalus* (Podabrocephalidae; Fig. 8) in the byrrhoid family Ptilodactylidae (*Anchycteis* Horn and *Ptilodactyla* Illiger), which also included *Cneoglossa* Guérin-Méneville (Cneoglossidae). *Callirhipis* Latreille in Cuvier (Callirhipidae) was sister to all other Byrrhoidea under ML, with weak MLB support. *Callirhipis* was nested within early-divergent Byrrhoidea under BI, sister to a clade comprising Dryopidae (*Helichus* Erichson) and Lutrochidae (*Lutrochus* Erichson), with moderate BPP support. Within Elateroidea, most relationships were recovered with moderate to strong MLB and BPP support (Fig. 9). *Lissomus* Dalman (Lissominae) was unexpectedly recovered with strong to maximal support in a position sister to Lycidae (*Dictyoptera* Latreille and *Lycus* Fabricius) – and not in Elateridae – in both the ML and BI trees (Fig. 9).

The family-level relationships of Bostrichoidea were mostly moderately to strongly supported under ML and BI. Dermestidae (three exemplars) was recovered in both the ML and BI trees as sister to the remaining Bostrichoidea (Bostrichidae and Ptinidae). The superfamily as a whole was sister to Cucujiformia in both the ML and BI trees (Fig. 2; Figure S2). MLB support for this placement was maximal under BI, and negligible to weak under ML.

Nodal support was negligible for most (especially deep) nodes in Tenebrionoidea. Tetratomidae (three exemplars) was polyphyletic, with *Eustrophopsis* Champion (Eustrophinae) and *Penthe* Newman (Penthinae) sister to a clade containing *Sirrhas* Champion (Promecheilidae) + Ulodidae (*Meryx* Latreille and *Syrphetodes* Pascoe) + *Chalcodrya* Redtenbacher (Chalcodryidae) (Figs 2, 14; Figure S2). *Tetratoma* Buetschli (Tetratomidae: Tetratominae) was recovered elsewhere, sister to *Tychogenius* Burckhardt & Löbl (Pterogeniidae). *Trachelostenus* Solier in Gay (Trachelostenidae) and *Leaus* Matthews & Lawrence

(Tenebrioninae) were sister taxa with strong to maximal MLB and BPP support, well within Tenebrionidae. Salpingidae (five exemplars) was polyphyletic, with its major part (*Salpingus* Illiger, *Notosalpingus* Blackburn, *Euryplatus* Motschulsky and *Elacatis* Pascoe) in a clade with *Pytho* Latreille (Pythidae), but *Ocholissa* Pascoe (subfamily Prostominiinae) with the *incertae sedis* genus *Rhizonium* Sharp in a separate clade with Ripiphoridae (three exemplars), Meloidae (*Epicauta* Mannerheim and *Iselma* Haag-Rutenburg), Lymexyloidea: Lymexylidae (*Atractocerus* Palisot de Beauvois), Anthicidae (*Anthicus* Paykull and *Lemodes* Boheman), Mordellidae (*Mordella* Linnaeus) and Aderidae (*Aderus* Stephens). *Polypria* Chevrolat (Oedemeridae: Polypriinae) was sister to Mycteridae (*Hemipeplus* Latreille and *Lacconotus* Leconte) with mostly moderate MLB support and maximal BPP support. *Hyporhagus* Thomson (Zopheridae: Monommatini) was recovered within Scraptiidae with mostly weak MLB support and moderate BPP support, and the combination was well removed from other Zopheridae, which were sister to Tenebrionidae in both analyses. Lymexyloidea (*Atractocerus*) was sister to *Aderus* (Aderidae) in a large clade with overall negligible MLB backbone support and moderate to mostly strong/maximal BPP support (see above). This clade was sister to the rest of the Tenebrionoidea, and overall its internal relationships had negligible BPP and MLB support, and differed markedly between the ML and BI trees (Fig. 14).

Superfamily Cucujoidea (in the former broad sense of the superfamily) was polyphyletic, forming three clades (i) the newly recognized grouping Coccinelloidea (Robertson *et al.*, 2015) (Fig. 11), (ii) Biphyllidae (*Diplocoelus* Guérin-Méneville) and Byturidae (*Dascillocyphon* Everts and *Xerasia* Lewis) within Cleroidea (Fig. 13), and (iii) the remaining Cucujoidea s.s. (see above section Series and Superfamily-level Relationships within Polyphaga; Fig. 12). Within Coccinelloidea (Fig. 11), two major clades were recovered: (i) a strongly supported clade with Latridiidae (*Corticaria* Marsham and *Eufallia* Muttkowski), Cerylonidae (four exemplars, not monophyletic), Bothrideridae (three exemplars, not monophyletic), and Discolomatidae (*Aphanocephalus* Wollaston and *Fallia* Sharp), and (ii) a weakly supported clade comprising the rest of the Cerylonid Series. Bothrideridae and Cerylonidae were intermingled, and these together were rendered paraphyletic by Discolomatidae in both the BI and ML trees (Fig. 11). The two exemplars of Latridiidae, representing the two described subfamilies, were recovered together with strong nodal support. Endomychidae (four exemplars) was polyphyletic. In the BI tree, *Bystus* Guérin-Méneville (Anamorphinae) and *Holoparamecus* Curtis (Merophysiinae) form a monophyletic group within a larger clade including Corylophidae and Alexiidae. In the ML tree, *Bystus* and *Holoparamecus* are rendered paraphyletic by the other two families. The remaining endomychid exemplars, *Endomychus* Panzer (Endomychinae) and *Epipocus* Germar (Epipocinae), form a monophyletic group that, with Akalyptoischiidae, form the sister taxon to Coccinellidae (eight exemplars). MLB and BPP support for these relationships is mostly negligible to weak. Corylophidae (four exemplars) was monophyletic in both the ML and BI trees, but with negligible MLB support and moderate BPP support. Coccinellidae was monophyletic and received strong to maximal MLB and BPP support in all analyses. The lone representative of Microweiseinae (*Delphastus* Casey) was sister to the seven other coccinellid exemplars (whose internal relationships were the same in the ML and BI trees but had mostly negligible to weak MLB and BPP support), all representing subfamily Coccinellinae. This arrangement received strong to maximal MLB and BPP support.

Nearly all of the backbone relationships in Cucujoidea s.s. had negligible MLB support (Fig. 12). Erotylidae (five exemplars) was monophyletic in the ML and BI trees and had moderate to strong MLB support and maximal BPP support. Sphindidae (*Protosphindus* Sen Gupta & Crowson and *Sphindus* Chevrolat) was rendered paraphyletic by Protocucujidae under ML and by Helotidae and Protocucujidae under BI. Nodal support for these relationships was moderate, at best. Phalacridae (*Olibrus* Erichson and *Phalacrinus* Blackburn) was sister to a clade containing *Laemophloeus* Dejean (Laemophloeidae) + *Propalticus* Sharp (Propalticidae). Monotomidae (*Bactridium* and *Rhizophagus*) was sister to the clade Kateretidae (*Amartus*) + Nitidulidae (four exemplars) in the ML tree. In the BI tree, Kateretidae rendered Nitidulidae paraphyletic. Cryptophagidae (four exemplars) and Silvanidae (*Uleiota* Latreille, *Oryzaephilus* Ganglbauer) were polyphyletic.

Cleroidea plus the cucujoid families Biphyllidae and Byturidae was monophyletic in the ML and BI trees (see above section Series and Superfamily-level Relationships within Polyphaga; Figs 2, 13; Figure S2). We recovered maximal BPP support and mostly moderate MLB support for Cleroidea minus the trogossitid *Rentonellum* Crowson, which was sister to all other Cleroidea (plus Biphyllidae and Byturidae). The cleroid family Trogossitidae (six exemplars) was polyphyletic. *Temnoscheila* Westwood (Trogossitinae) was sister to *Isoclerus* Lewis (Thanerocleridae). *Rentonellum* Crowson (Rentoniinae) was, as noted above, sister to all other Cleroidea plus Biphyllidae and Byturidae. The trogossitids *Acalanthis* Erichson in Germar (Trogossitinae) and *Thymalus* Latreille, *Grynoma* Sharp, and *Eronyxa* Reitter (all Peltinae) were recovered in a clade along with *Acanthocnemus* Perris (Acanthocnemidae). *Phycosecis* Pascoe (Phycosecidae) was sister to a clade containing *Idgia* Laporte (Prionoceridae) and Melyridae (four species sampled) as sister taxa.

Chrysomeloidea and Curculionoidea formed the clade Phytophaga, with weak to moderate MLB support (Figs 2, 15; Figure S2). Within Chrysomeloidea, we recovered two major clades. One clade corresponded to the family Chrysomelidae (seven exemplars), which had negligible to moderate MLB support and maximal BPP support. Chrysomelidae contained three clades: (i) Bruchinae Genn. spp. + *Crioceris* Geoffroy (Criocerinae), (ii) *Chrysomela* Linnaeus (Chrysomelinae) + *Diabrotica* Chevrolat (Galerucinae) and (iii) *Cephaloleia* Chevrolat in Dejean (Cassidinae) + *Neochlamisus* Karren and *Mylassa* Stål (both Cryptocephalinae). The other chrysomeloid clade included representatives of the remaining chrysomeloid families (Cerambycidae, Disteniidae, Megalopodidae, Orsodacnidae, Oxypeltidae, and Vesperidae), and had negligible to weak MLB support and mostly strong to maximal BPP support. *Palophagoides* Kuschel in Kuschel & May (Megalopodidae)

and *Oxypeltus* Blanchard in Gay (Oxypeltidae) formed a clade sister to all of the other families in this clade. *Aulacoscelis* Duponchel and Chevrolat in d'Orbigny (Orsodacnidae) and *Palophagoides* (Megalopodidae) rendered the traditional Cerambycidae s.l. (containing Cerambycidae s.s., Disteniidae, Oxypeltidae, and Vesperidae) paraphyletic. Cerambycidae s.s. (Cerambycinae, Dorcasominae, Lamiinae, Lepturinae, Necydalinae, Parandrinae, Prioninae, and Spondylidinae) was rendered paraphyletic by the inclusion of *Vesperus* Dejean (Vesperidae: Vesperinae). Vesperidae [*Migdolus* Westwood (Anoplodermatinae) and *Vesperus*] was polyphyletic. The interrelationships of the subfamilies of Cerambycidae s.s. had mostly negligible to weak MLB support, except for the sister relationship between *Parandra* Latreille (Parandrinae) and *Prionus* Geoffroy (Prioninae) which had maximal BPP support and mostly moderate MLB support. The internal branches separating these taxa were mostly very short.

Within Curculionoidea, Nemonychidae (represented by Nemonychinae: *Nemonyx* Redtenbacher and Rhynorhynchinae: *Rhynchitomacerinus* Kuschel) and Anthribidae (represented by Urodontinae: *Urodontus* Louw and Anthribinae: *Toxonotus* Lacordaire) together formed a clade (Fig. 15) with negligible to moderate MLB support and maximal BPP support. However, Nemonychidae was rendered paraphyletic by the placement of *Nemonyx* sister to Anthribidae (with strong BPP support). Under ML, *Nemonyx* was recovered within Anthribidae with negligible to moderate MLB support, still rendering Anthribidae paraphyletic. The split in Curculionoidea between Belidae (three exemplars) and the remaining families had negligible to weak MLB support and moderate BPP support (Figs 2, 15; Figure S2), but a basal dichotomy between a clade comprising Nemonychidae + Anthribidae and a clade containing the remaining weevil families was recovered in the analysis of *18S* and *28S* nucleotides plus amino acids (Figure S4). Attelabidae (Rhynchitinae Gen. sp. and *Merhynchites* Sharp) was sister to the clade (Caridae (Brentidae, Curculionidae)) under BI (Figs 2, 15) though with negligible BPP support, and sister (with mostly negligible MLB support) to the clade formed by Nemonychidae + Anthribidae under ML. The sister-group relationships of *Car* Blackburn (Caridae) to the clade Brentidae (*Cylas* Latreille and *Eurhynchus* Kirby) + Curculionidae (ten exemplars), and between the latter two families, were recovered with moderate to maximal support in most analyses (Figs 2, 15; Figure S2). The terminals of the subfamilies of Curculionidae sampled were related as follows: *Ocladius* Schönherr (Brachycerinae) sister to all other Curculionidae, *Sphenophorus* Schönherr (Dryophthorinae) sister to a clade comprising *Mecopelmus* and *Platypus* Herbst (both Platypodinae), and *Notaris* Germar (Brachycerinae) sister to the 'Higher Curculionidae,' here represented by six terminals currently classified in the subfamilies Cossoninae, Curculioninae, Entiminae, Molytinae and Scolytinae. Brachycerinae was therefore polyphyletic. Within Higher Curculionidae, the clade containing Cossoninae, Curculioninae, Molytinae and Scolytinae had overall mostly negligible to weak MLB and BPP support and very short internal branches.

Timing the diversification of beetles

The split between Neuropteroidea (Coleoptera + Neuropterida + Strepsiptera) and Hymenoptera was reconstructed via BI to have occurred ~298 Ma (319 to 282 Ma) (Fig. 2, Table 2) – in the late Carboniferous or start-Early Permian. The split between Neuropterida and Coleopterida (Coleoptera + Strepsiptera) was estimated to have occurred in the Early Permian ~290 Ma (304 to 278 Ma), followed by the split between Coleoptera and Strepsiptera ~278 Ma (288 to 272 Ma), also in the Permian. Crown group Coleoptera are estimated to have appeared in the Late Permian ~253 Ma (268 to 239 Ma), with the concomitant basal split producing a clade comprising Archostemata, Adephaga and Myxophaga (~242 Ma; 257 to 230 Ma) and the clade Polyphaga (~229 Ma; 247 to 213 Ma). The split between Archostemata and Myxophaga occurred ~220 Ma (237 to 205 Ma), with crown Myxophaga appearing in the Triassic (~197 Ma; 222 to 170 Ma), and crown Archostemata appearing in the Jurassic (~158 Ma; 192 to 123 Ma). Crown Adephaga were estimated to have appeared in the Late Triassic or earliest Jurassic (~197 Ma; 218 to 175 Ma), forming (basal split) the terrestrial Geadephaga (~173 Ma; 197 to 149 Ma) and the aquatic Hydradephaga (~184 Ma; 208 to 161 Ma).

The basal split in Polyphaga between Scirtoidea + Derodontidae and the remaining Polyphaga (under BI) was estimated to have occurred in the Triassic ~229 Ma (247 to 213 Ma) (Table 2). Crown group Scirtoidea + Derodontidae were estimated to have appeared ~220 Ma (238 to 199 Ma) and the crown group of the remaining Polyphaga ~212 Ma (227 to 199 Ma). Most of the polyphagan series and all of their constituent superfamilies were estimated to have first appeared during the end-Late Triassic or the Jurassic. Crown group Staphyliniformia (including Scarabaeoidea) are estimated to have appeared ~200 Ma (217 to 183 Ma), crown group Staphylinoidea (including Jacobsoniidae) ~193 Ma (210 to 175 Ma), crown group Scarabaeoidea ~141 Ma (161 to 117 Ma) and crown group Hydrophiloidea s.l. ~168 Ma (188 to 151 Ma). Crown group Elateriformia (including Nosodendridae: *Nosodendron*) are estimated to have appeared ~189 Ma (206 to 175 Ma), with crown group Elateroidea (~166 Ma; 182 to 152 Ma) and Byrrhoidea (~160 Ma; 177 to 143 Ma) appearing in rapid succession during the middle Jurassic, followed by the Cretaceous appearance of crown Dascilloidea (~120 Ma; 156 to 82 Ma) and Buprestoidea (~112 Ma; 142 to 75 Ma). Crown group Bostrichoidea (Bostrichiformia) first appeared in the Jurassic (~182 Ma; 201 to 161 Ma). Crown group Cucujiformia appeared ~190 Ma (202 to 179 Ma), with its constituent superfamilies estimated to have appeared in rapid succession during the middle Jurassic, for example Coccinelloidea (~171 Ma; 187 to 157 Ma), Tenebrionoidea (including Lymexyloidea), Cleroidea (including Biphyllidae and Byturidae; ~169 Ma; 185 to 153 Ma) and Cucujoidea s.s. (~167 Ma; 178 to 156 Ma). Crown group Phytophaga also appeared in the Jurassic (~162 Ma; 170 to 156 Ma), with crown group Chrysomeloidea (~145 Ma; 159 to 125 Ma) and Curculionoidea (~150 Ma; 161 to 138 Ma) appearing shortly thereafter. Most modern families of beetles, including the crown groups of a

Table 2. Point estimates of molecular divergence dates and confidence intervals (95% height posterior density; HPD) for suprafamilial groups of beetles, based on the results of BEAST (Bayesian) analyses (see Materials and methods).

Crown group taxon	Node age (crown group; Ma) median and 95% HPD	Corresponding node age in Hunt *et al.* (2007); median and 95% CI
Holometabola (Neuropteroidea + Hymenoptera)	297.97 (318.95 to 281.96)	N/A
Neuropteroidea (Coleoptera + Neuropterida + Strepsiptera)	289.77 (304.06 to 278.31)	N/A; also Strepsiptera not sampled
Coleopterida (Coleoptera + Strepsiptera)	278.33 (288.28 to 271.89)	N/A; Strepsiptera not sampled
Coleoptera	252.89 (267.68 to 238.78)	285 (fixed *a priori*)
Archostemata + Adephaga + Myxophaga	242.01 (256.67 to 230.37)	N/A
Archostemata + Myxophaga	219.55 (237.45 to 204.51)	227.0 (229–225)
Archostemata	157.82 (192.43 to 122.62)	N/A; one exemplar sampled
Myxophaga	197.18 (221.87 to 170.13)	Paraphyletic; 227 (229 to 225) incl. Archostemata
Adephaga	196.58 (217.84 to 174.74)	237.2 (240 to 234)
Geadephaga	172.50 (196.99 to 148.61)	215.7*
Hydradephaga	183.89 (208.15 to 160.58)	219.8 (224 to 216)
Polyphaga	229.2 (246.57 to 213.49)	270.5 (273 to 268)
Scirtoidea + Derodontoidea s.s.	219.72 (237.74 to 199.33)	N/A; paraphyletic grade
Other Polyphaga (= 'Core Polyphaga')	212.21 (227.13 to 199.0)	249.4*
Derodontoidea s.s.	172.13 (200.19 to 139.36)	N/A
Staphyliniformia (+ Scarabaeiformia/Scarabaeoidea)	200.23 (216.96 to 182.84)	N/A; paraphyletic grade
Staphylinoidea (+ Jacobsoniidae)	193.16 (210.26 to 175.26)	N/A; polyphyletic
Scarabaeoidea	141.11 (161.0 to 116.87)	191.4*
Hydrophiloidea s.l.	168.31 (187.52 to 151.09)	N/A; polyphyletic
Hydrophiloidea s.s.	123.93 (151.66 to 88.34)	175.4 (198–152)
Histeroidea	131.60 (156.60 to 106.09)	190.8 (200 to 181)
Elateriformia (+ *Nosodendron*)	189.45 (205.74 to 175.0)	217.0 (228–206)
Elateroidea	166.18 (181.57 to 151.83)	188.1 (210 to 166)
Dascilloidea	120.47 (155.79 to 82.36)	73.1*
Buprestoidea	111.76 (141.94 to 74.96)	N/A
Byrrhoidea	160.03 (176.96 to 142.85)	Polyphyletic; 175.9* excl. Byrrhidae
Bostrichoidea (here = Bostrichiformia)	181.65 (200.53 to 161.39)	219.4 (230 to 208)
Cucujiformia	189.76 (202.06 to 179.03)	236.2 (244 to 229)
Coccinelloidea	171.18 (187.0 to 157.09)	202.9 (214 to 191)
Tenebrionoidea + Lymexyloidea	175.15 (187.75 to 163.74)	206.5*
Lymexyloidea	N/A; one exemplar	N/A; polyphyletic
Cleroidea (+ Biphyllidae and Byturidae)	169.02 (184.68 to 152.9)	190.4*
Cucujoidea s.s. (– Biphyllidae and Byturidae)	167.08 (178.4 to 156.24)	N/A; polyphyletic
Phytophaga (Chrysomeloidea + Curculionoidea)	161.66 (169.54 to 155.56)	N/A; paraphyletic
Chrysomeloidea	145.14 (159.47 to 124.55)	N/A; polyphyletic
Curculionoidea	149.64 (160.70 to 138.46)	171.5 (199 to 144)

A comparison is made with corresponding estimates (when available) from Hunt *et al.* (2007) – the only other study to date to report such dates across all suborders of beetles. Ages with an asterisk were not reported in Hunt *et al.* (2007) but were estimated by McKenna & Farrell (2009) from data provided by the authors. The age of crown Coleoptera is estimated at 266.8 Ma (269 to 265 Ma) by McKenna & Farrell (2009) – the only other study published to date to build a molecular chronogram for Coleoptera. McKenna & Farrell (2009) did not estimate node ages below the subordinal-level due to the lack of well-supported resolution at lower taxonomic levels in their tree.

majority of the most species-rich families, were estimated to have originated during the Cretaceous (Figs 2, 16).

Diversification rates

The background family-level diversification rate in beetles and the timing and taxonomic location of increases or decreases in diversification rate resulting from the MEDUSA analyses are summarized in Fig. 2. The background diversification rate for Neuropteroidea as a whole was estimated at 0.025 lineages per Ma, with a significant increase in diversification rate at the node representing crown group Coleoptera (0.037 lineages/Ma; Table 3). Within Coleoptera, 10 clades were identified as too species-rich to result from the background diversification rate (Fig. 2; Figure S1; Table 3), and are therefore proposed to have experienced significant increases in diversification rate. These were: the Phytophaga (Chrysomeloidea + Curculionoidea), Scarabaeidae + Pleocomidae, Cucujoidea s.s. + Phytophaga, a subset of Tenebrionoidea (Polypriinae to Ulodidae), Tenebrionidae (including *Trachelostenus*: Trachelostenidae), Laemophloeidae + Phalacridae and Propalticidae, Buprestidae in part (Acmaeoderinae + Agrilinae), Elateridae in part (= Elateridae 2 in Figure S1 and Table S3), Meloidae + Mordellidae, and Scirtidae. Another 12 clades, widely distributed across the phylogeny of Coleoptera, were identified as too species-poor to result from the background diversification rate in beetles, and are therefore proposed to have experienced significant decreases in diversification rate or significantly higher extinction rates

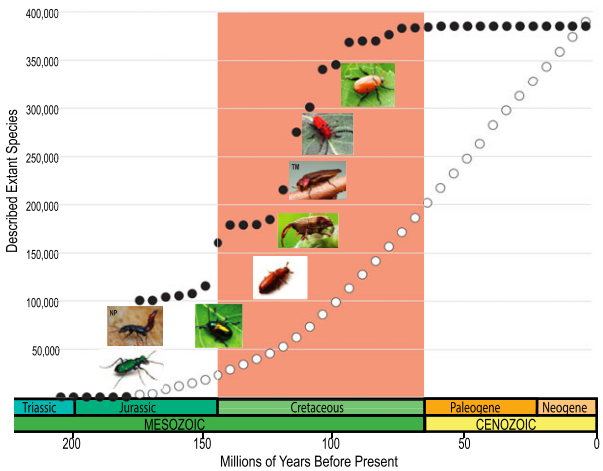

Fig. 16. Superimposed plots of crown group divergence times for beetle families[1] and cumulative totals of described extant species diversity showing that most Modern beetle diversity has its origins in the Cretaceous. White circles: species diversity modelled as accruing at a constant rate over time, w/out extinction, from time of family origin to present (5 Ma intervals; actual time-specific rates unknown). Black circles: species diversity modelled as accruing immediately (without extinction) at the time of origin (5 Ma intervals; actual time-specific rates unknown). The irregular pattern of diversification shown in this plot (black circles) is therefore due in part to a lack of information about diversification rates within families. Note that the small difference in total species between the plots is due to rounding effects. Photo credits (used by permission): ©Alex Wild (unlabelled), ©Ted C. MacRae (TM), and ©Nick Porch (NP).

than other clades (Fig. 2; Figure S1; Table 3). These were: Archostemata + Myxophaga, Derodontidae + Scirtoidea, Amphizoidae + Aspidytidae and Hygrobiidae, Meruidae, Artematopodidae + Omethidae and Telegeusidae, Boganiidae + Hobartiidae and Smicripidae, Caridae, *Rhizonium*, Oxypeltidae, Jacobsoniidae, Trachypachidae, and Phloeostichidae and allied families. Six to seven of the 10 total increases in diversification rate we identified in beetles occurred in the Cretaceous, three to four in the Jurassic, and one in the Cenozoic (Fig. 2; Figure S1; Table 3). The overall rate increase identified for Coleoptera occurred at or near the Permian/Triassic Boundary. Seven of the twelve decreases in diversification rate that we identified occurred in the Cretaceous, two in the Jurassic, one in the Triassic and two in the Cenozoic (Fig. 2; Table 3).

Discussion

Higher-level relationships and near relatives of beetles

The interrelationships and internal relationships of our OGs are consistent with other recent studies (e.g. Wiegmann *et al.,* 2009a,b; McKenna & Farrell, 2010; Beutel *et al.,* 2011; Ishiwata *et al.,* 2011; Niehuis *et al.,* 2012; McKenna, 2014; Peters *et al.*, 2014). For example, Neuropteroidea was sister to Hymenoptera, as expected, because Mecopterida (caddisflies, butterflies, scorpionflies, fleas, true flies), which would otherwise be sister to Neuropteroidea, were not included in our OG taxon sample. Mecopterida is the established sister group of Neuropteroidea, and Hymenoptera is the sister group of all other endopterygote insect orders. Within Coleoptera, our results broadly confirm existing knowledge of relationships, with departures from the expected relationships either poorly supported in our study, or falling mostly among clades without an existing consensus (poorly supported or with varying resolutions in other studies to date).

Strepsiptera have long been difficult to place in the insect tree of life due to their extreme sexual dimorphism, bizarre life histories, unusual morphological and developmental characteristics, and high rates of molecular evolution (e.g. Carmean & Crespi, 1995; Niehuis *et al.,* 2012). Several recent molecular phylogenetic studies containing small samples of beetles have shown that Strepsiptera are part of Neuropteroidea (Wiegmann *et al.,* 2009a,b; Longhorn *et al.,* 2010; McKenna & Farrell, 2010; Ishiwata *et al.,* 2011). The largest morphological cladistic analysis of Coleoptera performed so far (Lawrence *et al.*, 2011) included one exemplar from Strepsiptera (Mengenillidae: *Eoxenos* Peyerimhoff), which was recovered sister to Coleoptera. The extensive morphological study of Holometabola by Beutel *et al.* (2011) also recovered Strepsiptera sister to Coleoptera. Recent studies using very large molecular (phylogenomic) datasets (Niehuis *et al.*, 2012; McKenna, 2014; Peters *et al.*, 2014) confirm the higher-level phylogeny of Neuropteroidea, including the sister-group relationship between Strepsiptera and Coleoptera. Results from the present study are compatible with this view, recovering Strepsiptera (here represented by *Mengenilla*) as the sister group of a monophyletic order Coleoptera (only in some analyses, in others Strepsiptera falls within non-polyphagan Coleoptera). However, this placement had negligible MLB support, and other placements had similar (though not better) likelihood scores and weak nodal support (see Results). Therefore, although analyses of morphological data (Beutel *et al.*, 2011; Lawrence *et al.*, 2011) and (separately) phylogenomic data (Niehuis *et al.*, 2012; McKenna, 2014; Peters *et al.*, 2014) containing relatively few exemplars recover a sister-group relationship between beetles and Strepsiptera, nodal support for this placement is still lacking in studies (like the present one) containing a broad and representative sample of beetle families and subfamilies, and Strepsiptera. The long terminal branches that characterize Strepsiptera, and to a lesser degree certain early-divergent Coleoptera, contribute to the difficulty of resolving these relationships. A sister-group relationship between Strepsiptera and beetles nonetheless seems highly likely. Beetles and Strepsiptera thus share features including posteromotorism, an enlarged metathorax and a pupa with immobile mandibles due to common ancestry. Certain tenebrionoid beetles, particularly certain Ripiphoridae, have additional features in common with Strepsiptera, including active host-seeking first instar larvae, flabellate antennae and hypermetamorphosis; however, these features are the result of evolutionary convergence (Beutel *et al.*, 2011; Niehuis *et al.*, 2012; McKenna, 2014).

[1]Monophyletic family-level groupings of taxa used to estimate diversification rates (see Materials and methods; Figure S1 and Table S3).

Table 3. The background diversification rate in Coleoptera, and individual net diversification rates (r = b − d) and relative extinction rates (ε = d/b) summarized by number. Asterisks indicate subclades where values cannot be estimated without additional data.

	Clade	Cut at	Rate (r)	ε	ΔA/C
	Background rate Neuropteroidea	Node	0.025	*	*
	1. Background rate Coleoptera	Node	0.037	0.930	*
Rate increases	2. Phytophaga	Stem	0.043	0.990	70.2
	4. Scarabaeidae + Pleocomidae	Stem	0.100	*	44.3
	6. Cucujoidea + Phytophaga	Stem	0.052	*	22.0
	7. Subset Tenebrionoidea: Polypriinae to Ulodidae	Stem	0.052	*	23.2
	8. Tenebrionidae + Trachelostenidae	Stem	0.081	*	25.7
	10. Laemophloeidae + Phalacridae + Propalticidae	Node	0.074	*	13.9
	13. Buprestidae in part (Acmaeoderinae + Agrilinae)	Stem	0.086	*	11.2
	14. Elateridae in part (= Elateridae 2 in Figure S1)	Stem	0.106	*	11.9
	15. Meloidae + Mordellidae	Node	0.103	*	16.9
	18. Scirtidae	Stem	0.042	*	8.7
Rate decreases	3. Archostemata + Myxophaga	Node	0.019	*	61.2
	5. Derodontidae + Scirtoidea	Node	0.022	*	22.2
	9. Amphizoidae + Aspidytidae + Hygrobiidae	Node	0.014	*	22.6
	11. Artematopodidae + Omethidae + Telegeusidae	Node	0.030	*	12.5
	12. Meruidae	Stem	0.000	*	11.5
	16. Boganiidae + Hobartiidae + Smicripidae	Node	0.019	*	10.1
	17. Caridae	Stem	0.014	*	9.5
	19. Rhizonium	Stem	0.000	*	7.5
	20. Oxypeltidae	Stem	0.013	*	7.0
	21. Jacobsoniidae	Stem	0.016	*	6.6
	22. Trachypachidae	Stem	0.012	*	6.3
	23. Phloeostichidae and Allied Families	Node	0.028	*	6.1

Clades showing an inferred significant increase in diversification rate are marked in red, whereas clades showing a significant decreases in rate are marked in blue. The timing and taxonomic location of increases or decreases in diversification rate in beetles are shown in Fig. 2.

Misof *et al.* (2014) sampled eight terminals representing the four suborders of Coleoptera, two genera of Strepsiptera and 134 other taxa from groups outside Coleopterida. Phylogenetic analyses of data from their preferred matrix (AA sequences from 1478 orthologous genes), recovered Polyphaga sister to a clade containing the other three suborders. Adephaga was sister to Archostemata (*Priacma* Leconte), and these together were sister to Myxophaga (*Lepicerus*). These relationships are compatible with the results of Peters *et al.* (2014), who sampled transcriptomic data from five Coleoptera and one Strepsiptera (among many other non-Coleopterida), but did not include any Myxophaga. The subordinal relationships in Misof *et al.* (2014) differ from the relationships recovered herein, only in the placement of Myxophaga, and the results of Peters *et al.* (2014; although lacking Myxophaga) are fully compatible with the present study. Notably, these studies recover a basal split between Polyphaga and the other suborders. These subordinal relationships have not otherwise been recovered in a phylogenetic analysis of molecular or morphological data.

Monophyly and interrelationships of the suborders of beetles

All of the suborders of Coleoptera were monophyletic in our study, in contrast to previous molecular phylogenetic studies containing hundreds to thousands of taxa, where Archostemata was recovered in Myxophaga or was otherwise not consistently recovered as a clade (e.g. Hunt *et al.*, 2007; McKenna & Farrell, 2009; Bocak *et al.*, 2014). The subordinal relationships we recovered were the same under both BI and ML (Fig. 3), but differ from other arrangements proposed to date. However, none of the subordinal relationships that have been proposed in molecular or morphological studies to date has consistently strong nodal support or has otherwise emerged as the consensus topology (e.g. Shull *et al.*, 2001; Caterino *et al.*, 2002; Hughes *et al.*, 2006; Hunt *et al.*, 2007; Maddison *et al.*, 2009; McKenna & Farrell, 2010).

Lawrence *et al.* (2011) in a large companion study of morphological data containing most of the same higher taxa as the present study (both were part of the BToL Project), recovered Archostemata and Adephaga as sister groups, and Myxophaga and Polyphaga as sister groups, but the subordinal relationships lacked strong statistical support (as here). The morphological studies of Beutel & Haas (2000), Beutel *et al.* (2008) and Friedrich *et al.* (2009) suggest a sister-group relationship between Archostemata and the remaining three suborders (Adephaga and a clade comprising Polyphaga and Myxophaga). An aspect in common between the recent analysis of morphological data by Lawrence *et al.* (2011) and the present molecular study is that Adephaga share a more recent common ancestor with Archostemata than with Polyphaga (Fig. 2). The molecular study of Bocak *et al.* (2014) was rooted with Archostemata. In contrast with Bocak *et al.* (2014) and recent morphological studies, there was no evidence in our analyses for a sister-group relationship between Archostemata and the other three suborders.

Some differences between our results and the results of previous studies, particularly at higher taxonomic levels, are clearly due to differences in rooting and outgroups (or lack thereof) (e.g. Caterino *et al.*, 2002; Yang & Rannala, 2012). However, differences in the numbers and kinds of genes analysed are likely also important (e.g. McKenna, 2014). Although it would be interesting to investigate extensively the relative contributions of different subsets of genes (for example, only NPC genes), the limited data available within any subset makes this problematic. For example, in our matrices, 54 taxa (~15% of the total, including OGs) contain less than half of the NPC AA sequences, making the results from analyses of these data alone difficult to compare to the results from combined analyses. For this reason, the analyses herein are focused on the combined 8-gene dataset. Comparative analyses of the results from different groups of genes will be more fruitfully done once genomic methods yield more extensive data.

A sister-group relationship between Polyphaga and the other suborders of Coleoptera, as recovered herein, implies that extensive simplifications of the thoracic skeleto-muscular system took place independently in the non-archostematan suborders, especially in Myxophaga and Polyphaga (Beutel & Haas, 2000; Friedrich *et al.*, 2009). The archostematan families Ommatidae and Cupedidae have preserved the most ancestral condition of this character system (Friedrich *et al.*, 2009) and also exhibit elytral window punctures and a tuberculate surface structure, which likely belong to the groundplan of Coleoptera in the widest sense (e.g. Beutel, 1997). A sister-group relationship between Archostemata and Myxophaga, as recovered herein, is not currently supported by any morphological characters, except perhaps certain features of wing folding in repose (e.g. Crowson, 1981; Grimaldi & Engel, 2005), and these small relict groups differ strikingly in their life habits, the former being associated with wood (larvae, to the extent known, are xylophagous) and the latter with hygropetric or riparian habitats. Nonetheless, the separation of Polyphaga from the other beetles in our study is supported by data from wing venation (Kukalová-Peck & Lawrence, 1993, 2004), and is compatible with Peters *et al.* (2014) who analysed transcriptomic data from exemplars of Holometabola and outgroups (1343 genes; their small sample of beetles did not include Myxophaga). The congruent subordinal-level topologies recovered in the present study under BI and ML, and the reciprocal monophyly of the suborders in our study – also monophyletic in the morphological study of Lawrence *et al.* (2011) – are similarly encouraging. Nonetheless, except for the sister-group relationship between Archostemata and Myxophaga [also recovered in several other recent molecular phylogenetic studies, e.g. Maddison *et al.* (2009), and McKenna & Farrell (2010)], the interrelationships of the suborders lack consistently strong nodal support in the present study and should therefore be viewed as tentative. The relationships we recovered among series, superfamilies and families, are similar in many respects to those reported in other recent molecular and morphological phylogenetic studies, but show improvements in resolution and nodal support. However, the interrelationships of series and superfamilies in the present study varied somewhat between the ML and BI trees. Clade support was similarly variable, and often negligible or weak in the ML tree, which lacked monophyly constraints.

The low MLB and BPP values recovered for many deep nodes, for example between suborders, series and superfamilies, in this and other higher-level molecular phylogenetic studies of beetles to date are likely a result of some combination of insufficient/weak phylogenetic signal, conflicting phylogenetic signal, rogue taxa (due to the other factors noted here), missing data, short internal branches and/or extreme variation in evolutionary rates among taxa. Strepsiptera clearly contributed to reduced nodal support at multiple depths within our trees, perhaps most notably at deep nodes, as evidenced by comparing the results of unconstrained analyses with results from analyses where Strepsiptera was constrained to the OG (see Results; Fig. 2; Figures S2 and S3). Subordinal relationships in Coleoptera have not yet been comprehensively assessed by analysing a phylogenomic dataset, such as one containing Strepsiptera and at least one exemplar from each of the suborders, series and superfamilies of Coleoptera, and a large number of nucleotide and AA characters from NPC genes. Myxophaga and most series and superfamilies of Polyphaga are lacking from all such studies to date (Niehuis *et al.*, 2012; McKenna, 2014; Peters *et al.,* 2014). However, preliminary analyses of such a dataset (D.D. McKenna, unpublished data) suggest that unambiguously resolving subordinal relationships will be a persistent challenge.

Relationships within Archostemata

Limited representation of Archostemata (by taxa and/or data) has been the norm in all otherwise broadly taxon-sampled studies to date. Hunt *et al.* (2007) sampled a single archostematan, *Distocupes varians* Lea, for one gene (*18S*). McKenna & Farrell (2009) included two genera/species of Archostemata and one gene (18S). Bocak *et al.* (2014) sampled six species of Archostemata for up to four genes, but data were missing in their study for more than half of the taxon-by-gene combinations for Archostemata. In the present study, seven species of Archostemata were sampled for up to eight genes, with relatively few (16%) missing data. Eight percent (half) of the missing data for Archostemata in the present study was from the difficult NPC gene alpha-spectrin. Our study thus provides the most robust insights to date into: (i) the internal phylogeny of Archostemata and (ii) the phylogenetic placement of Archostemata relative to the other three suborders of beetles, based on molecular phylogenetic analyses. Nonetheless, two extant archostematan families – Crowsoniellidae and Jurodidae – both monospecific in the living fauna and known only as type specimens, were not available for our analysis. The placement of *Priacma* sister to the remaining Cupedidae is consistent with the morphological study of Beutel & Hörnschemeyer (2002). An ommatid–micromalthid clade (containing *Tetraphalerus* and *Micromalthus* in the present study) is in contrast to a strongly supported cupedid–micromalthid clade found in morphology-based studies (Beutel & Hörnschemeyer, 2002; Beutel *et al*., 2008; Friedrich *et al*., 2009; but not Lawrence *et al.*, 2011). However, neither Ommatidae

nor Cupedidae were monophyletic in the results of Lawrence *et al.* (2011), and reconstructing the phylogeny of Archostemata using morphological data is impeded by the miniaturization and highly aberrant adult morphology of Micromalthidae and by the possibly secondary soil-dwelling habits of larvae of Ommatidae (Lawrence, 1999, 2001), which may have resulted in convergent structural modifications. Thus, the present phylogenetic hypothesis should be viewed as a suitable starting point for additional investigations, whether morphological or molecular.

Relationships within Myxophaga

Considering morphological data and the similar habits/habitats of Myxophaga (hygropetric or riparian habitats, algophagy) a monophyletic origin of the suborder is highly likely (Beutel *et al.*, 1998; Beutel, 1999). Notably, the branching patterns within Myxophaga resulting from BI and ML analyses of the nucleotide sequence data alone are identical (Hydroscaphidae (Torridincolidae (Sphaeriusidae, Lepiceridae))). Nonetheless, this topology contrasts with the results of morphology-based analyses, which suggest the relationships (Lepiceridae (Torridincolidae (Sphaeriusidae, Hydroscaphidae))) (Beutel *et al.*, 1998; Beutel, 1999). A basal position of Lepiceridae is also suggested by plesiomorphies retained in a putative larva of *Lepicerus*, such as the presence of six stemmata (five or less in the other families), the absence of spiracular gills (present in the other families) and an abdomen distinctly longer than the thorax (equally long or shorter in the other families) (Lawrence *et al*., 2013). Previous analyses of molecular data have mostly recovered Torridincolidae and Hydroscaphidae as sister groups (e.g. Hunt *et al.,* 2007), with varying placements for the other families. The presence of an unique type of tracheal gill in Myxophaga strongly suggests a clade of all Myxophaga except Lepiceridae, and semi-entognathous mouthparts and rows of lancet-shaped tergal setae suggest a sister-group relationship of Sphaeriusidae and Hydroscaphidae (Beutel *et al.,* 1998; Beutel, 1999; Lawrence *et al.,* 2013).

Relationships within Adephaga

Our analyses support the reciprocal monophyly of the aquatic Hydradephaga (containing the families Amphizoidae, Aspidytidae, Dytiscidae, Gyrinidae, Haliplidae, Hygrobiidae, Meruidae and Noteridae) and terrestrial Geadephaga (containing the families Carabidae, Rhysodidae and Trachypachidae). The monophyly of Hydradephaga is in contrast with the recent morphological study of Beutel *et al.* (2013) (and many other earlier studies, e.g. Kavanaugh, 1986), which suggests a sister-group relationship between Gyrinidae (here placed in a clade with Haliplidae) and the remaining adephagan families, but is consistent with several other molecular phylogenetic studies (e.g. Shull *et al.*, 2001; Ribera *et al.*, 2002; Vogler, 2005; Hunt *et al.*, 2007; Wild & Maddison, 2008; McKenna & Farrell, 2009). The widely accepted Dytiscoidea (e.g. Beutel *et al.*, 2013) were confirmed in the present study, but only under BI . The miniaturized monospecific Meruidae were recovered sister to Noteridae, corroborating some earlier studies based on morphological or molecular data (Beutel *et al.*, 2006; Balke *et al.*, 2008; Dressler *et al.*, 2011; Bocak *et al.*, 2014), but conflicting with others based only on morphology (Dressler & Beutel, 2010; Alarie *et al.*, 2011; Short *et al.*, 2012) which placed Meruidae in a position sister to the remaining Dytiscoidea. The monogeneric Aspidytidae were sister to Amphizoidae, consistent with Balke *et al*. (2008). The monophyly of Geadephaga is strongly supported in our analyses and its internal relationships are consistent with recent studies using *18S* (Shull *et al.*, 2001) or *18S + 28S + WG* (Maddison *et al.*, 2009). The placement of Trachypachidae is unclear in our study. Its appearance as sister to *Calosoma* in some analyses (with weak BPP support and mostly negligible MLB support) is similar to that seen in some other analyses (e.g. Maddison *et al.*, 2009). Trachypachidae is nonetheless the sister group of the remaining Geadephaga in our analyses, either alone, or in combination with *Calosoma* and perhaps other Carabini. The phylogenetic placement of Rhysodidae has long been uncertain. It has been placed well outside Carabidae (e.g. Regenfuss, 1975; Deuve, 1988) or as a relative of the scaritine or clivinine carabids (Bell, 1967; Baehr, 1979; Beutel, 1990). We recovered Rhysodidae well within Carabidae, consistent with other molecular phylogenetic studies (e.g. Maddison *et al.*, 2009). The sister-group relationship between Haliplidae and Gyrinidae was unexpected. We recovered Cicindelinae within Carabidae, in contrast to the results of Bocak *et al.* (2014) who recovered this group outside of Carabidae.

Interrelationships and internal relationships of the series and superfamilies of Polyphaga

Most of the traditionally recognized series and superfamilies of Polyphaga were monophyletic or were recovered in arrangements consistent with recent studies (Fig. 3). However, the interrelationships and internal relationships of the series and superfamilies of Polyphaga generally lack consistently strong nodal support in this study in the absence of monophyly constraints, consistent with previous studies. Nonetheless, even in the absence of strong nodal support and fully compatible resolution in the Bayesian MCC tree and ML tree (from analysis of nucleotides), some relationships are consistent with most other recent studies. For example, superfamily Scirtoidea and the family Derodontidae are either together sister to the remaining Polyphaga (present study, BI), or form a paraphyletic grade subtending the remaining Polyphaga (present study, ML; Hunt *et al.*, 2007; McKenna & Farrell, 2009; Bocak *et al.*, 2014). Series Staphyliniformia (including Jacobsoniidae, a family previously considered to be related to Derodontidae), series Elateriformia, and superfamily Scarabaeoidea form the earliest-diverging branches in Polyphaga other than Scirtoidea and Derodontidae. The interrelationships of Staphyliniformia (including Jacobsoniidae), Elateriformia, and Scarabaeoidea remain uncertain, although Elateriformia (including Nosodendridae, a family previously considered to be related to Derodontidae) is most likely outside of the other two groups. The placement of superfamily Bostrichoidea, although not among early-divergent or highly

derived Polyphaga, is uncertain in the present study on account of negligible to weak nodal support. Although it is probably the sister group of the species-rich series/clade Cucujiformia (as found herein), other molecular phylogenetic studies have recovered Bostrichoidea in different, rather distant positions. Relationships among the superfamilies of Cucujiformia also remain uncertain. However, Cucujoidea in the traditional broad sense is clearly polyphyletic, consistently forming three clades: (i) Coccinelloidea, (ii) Biphyllidae + Byturidae (an early-divergent clade within Cleroidea) and (iii) Cucujoidea s.s., which may be monophyletic or paraphyletic, likely forming the sister group of the Phytophaga (Chrysomeloidea and Curculionoidea) or a paraphyletic grade subtending the Phytophaga. In the present study, Coccinelloidea is either sister to all other Cucujiformia (under BI) or sister to Tenebrionoidea (under ML). Other molecular phylogenetic studies also recover the polyphyly of Cucujoidea, for example Hunt *et al.* (2007), Marvaldi *et al.* (2009), Robertson (2010) and Robertson *et al.* (2015). Although the extensively taxon-sampled studies of Hunt *et al.* (2007) and Bocak *et al.* (2014) recover a polyphyletic or paraphyletic Phytophaga, it appears highly likely that this informal grouping is monophyletic (as in the present study), and its constituent superfamilies (Chrysomeloidea and Curculionoidea) are monophyletic sister groups.

Polyphaga: Derodontoidea and Scirtoidea

The same or similar placements for Scirtoidea and Derodontidae relative to the remaining Polyphaga have been recovered in other recent studies (e.g. Hunt *et al.*, 2007; McKenna & Farrell, 2009; Bocak *et al.*, 2014). However, the derodontoid family Jacobsoniidae has not been included in any other molecular phylogenetic studies to date. It is worth noting that McKenna *et al.* (2014) included the same species of Jacobsoniidae examined in the present study in their preliminary phylogenetic analyses of Staphyliniformia and Scarabaeiformia based on DNA sequence data from *28S* rDNA and the NPC gene *CAD*, recovering Jacobsoniidae as a clade within Staphyliniformia in close relation to Staphylinoidea (as in the present study) in most analyses. Jacobsoniidae were ultimately excluded from the analyses in McKenna *et al.* (2014) because the lack of sampling of beetle taxa outside of Staphyliniformia and Scarabaeiformia made justifying inclusion of Jacobsoniidae difficult, particularly because the two species we sampled are on long terminal branches and their placement within Staphyliniformia thus could have resulted from long-branch attraction or some other artefact. However, the present study includes many other non-staphyliniform beetles, including many other long-branched taxa, and Jacobsoniidae are still recovered within Staphyliniformia (see below for more discussion of this placement). Nosodendridae was ambiguously placed in Bocak *et al.* (2014), although always part of a clade containing Scarabaeiformia, Bostrichiformia and Elateriformia. The placement of *Nosodendron* (Nosodendridae) in the present study as either the sister group of Elateriformia, or within Elateriformia in a position sister to Dascilloidea, is therefore compatible with Bocak *et al.* (2014), but more localized (though lacking nodal support). Nonetheless, placement far from other Derodontoidea further suggests that Derodontoidea as classified in Bouchard *et al.* (2011) is polyphyletic, as also found by Lawrence *et al.* (2010a, 2011). Notably, Böving & Craighead (1931) associated Nosodendridae with Dascilloidea.

Polyphaga: series Staphyliniformia

With respect to higher-level relationships of and within Staphyliniformia (excluding Scarabaeiformia, discussed below), the ML and BI trees are largely compatible with each other and with several other recent studies (e.g. Caterino *et al*., 2005; Beutel & Leschen, 2005b Hunt *et al*., 2007; Lawrence *et al*., 2011; Bocak *et al.*, 2014; McKenna *et al*., 2014), although the deepest divergences remain ambiguous. A monophyletic Staphyliniformia (containing Hydrophiloidea s.l. and Staphylinoidea) is sometimes recovered (e.g. McKenna *et al.*, 2014; BI only; present study, ML only). However, Bocak *et al.* (2014) recovered Staphyliniformia as a paraphyletic grade and recovered a polyphyletic Staphylinoidea. Scarabaeiformia, Hydrophiloidea s.s. and Histeroidea are each nearly always supported as monophyletic, and a clade uniting them is strongly supported by the present Bayesian analyses (in which there were some monophyly constraints on the constituent superfamilies; Table S2). Such an arrangement has been previously proposed on the basis of morphological characters (Beutel & Leschen, 2005b). The reciprocal monophyly of Histeroidea and Hydrophiloidea s.s., together forming the clade Hydrophiloidea s.l. in both analyses, was unsurprising. A clade comprising Histeroidea + Hydrophiloidea (s.s.) was found in McKenna *et al*. (2014), in addition to all of the analyses reported herein. In contrast, Lawrence *et al.* (2011) and Bernhard *et al.* (2009; except for their Bayesian analysis) failed to recover a monophyletic Hydrophiloidea s.s., instead recovering Histeroidea as sister to part of Hydrophiloidea s.s.; Short & Fikáček (2013) assumed but did not test the monophyly of Hydrophiloidea s.s.

Within Hydrophiloidea s.s., the clades Georissidae + Helophoridae and Hydrophilidae s.s. (*Andotypus* + *Tropisternus*) were each also well-supported in other recent studies, such as Bernhard *et al.* (2006, 2009), Lawrence *et al.* (2011), Short & Fikáček (2013) and McKenna *et al.* (2014). In contrast, the position of Spercheidae (*Spercheus*) in relation to these two clades varies widely: as sister to Hydrophilidae s.s. in the present BI analyses (Spercheidae + Hydrophilidae within Hydrophiloidea s.s.), Bernhard *et al.* (2009, Bayesian analysis), Lawrence *et al.* (2011) and McKenna *et al.* (2014); part of a trichotomy with the other two clades in Short & Fikáček (2013); sister to all other Hydrophiloidea s.s. in the present ML tree and in Bernhard *et al.* (2006); sister to Histeroidea in Bernhard *et al.* (2009, parsimony analysis), or even sister to all other Hydrophiloidea s.l. in Bernhard *et al.* (2009, bootstrap consensus). Lawrence *et al.* (2011) recovered the clade Georissidae + Helophoridae as the sister group to Histeroidea, with Spercheidae + Hydrophilidae s.s. as sister to this larger clade. The clade Spercheidae + Hydrophilidae, which we recovered

within Hydrophiloidea s.s., and Hydrophiloidea s.s. sister to Histeroidea, is in agreement with earlier studies based on morphology [e.g. Hansen, 1991 (preferred cladogram); Beutel & Komarek, 2004], and the clade Georissidae + Helophoridae [part of the helophorid lineage of Hansen (1991)] is in agreement with results from a recent molecular study of Hydrophiloidea s.s. (Short & Fikáček, 2013). Within Histeroidea, we recovered Synteliidae (Sphaeritidae + Histeridae) – although Caterino & Vogler (2002) found Sphaeritidae sister to the other two and Lawrence *et al.* (2011) found weak support for Histeridae sister to a clade comprising the others. Staphylinoidea found support only in McKenna *et al*. (2014) and the current study, although in the current study with Jacobsoniidae (Derodontoidea) included within it under ML, and as sister to it under BI.

Within Staphylinoidea, the leiodid genus *Colon* oddly fell outside the Leiodid group in McKenna *et al*. (2014; ML only) and the current study (BI only). The Staphylinid group (Staphylinidae, including Silphidae and Scydmaeninae) is monophyletic in most studies [but not in Hunt *et al*., 2007, where Scydmaeninae (as Scydmaenidae) strangely fell outside as sister to Histeroidea], but with only weak nodal support in Lawrence *et al*. (2011) and with *Colon* misplaced within it in the Bayesian analysis (herein). Silphidae and Staphylinidae: Scydmaeninae (following Grebennikov & Newton. 2009; formerly treated as a separate family] were each monophyletic, and in most studies fell within some part of Staphylinidae, which (because of Silphidae) was not monophyletic. Staphylinidae was consistently paraphyletic with respect to Silphidae, which was sister to the staphylinid *Leucotachinus* (Tachyporinae: Tachyporini). Within Staphylinidae, sparse taxon sampling limits the testing of the four-subfamily groupings of Lawrence & Newton (1982, 1995), but Scydmaeninae were consistently recovered as sister to *Creophilus* (Staphylininae), as expected for those sole representatives of the Staphylinine group. The representatives of the Omaliine (*Paraphloeostiba* and *Glypholoma*) and Osoriine (*Renardia* and *Scaphidium*) groups were each recovered as monophyla under ML but not BI. The single included member of the Tachyporine group (*Leucotachinus*) was unexpectedly recovered with strong support as sister to Silphidae, consistent with the unexpected results of McKenna *et al.* (2014). Silphidae was recovered or otherwise considered to belong within Staphylinidae in other recent studies [e.g. Lawrence & Newton, 1982; Newton & Thayer, 1995; Hansen, 1997; Ballard *et al.*, 1998; Grebennikov & Newton, 2009 (molecular data only); Bocak *et al.*, 2014], but without clear placement.

The inconsistent position of the leiodid *Colon*, and the placement of Jacobsoniidae are among the most unexpected results within Staphyliniformia, and require further investigation. The position of Jacobsoniidae as sister of Ptiliidae + Hydraenidae under ML, or as sister of all Staphylinoidea under BI, echoes its surprising association with Staphylinoidea in Lawrence *et al.* (2011); based on analyses of morphological data, the two genera of Jacobsoniidae came out as successive sister groups to (((Ptiliidae)(Hydraenidae)) (Leiodidae + Agyrtidae)). Crowson (1959) commented on a larval feature (fimbriate galea) occurring in Jacobsoniidae and in some Staphylinoidea. He also noted (Crowson, 1960) that *Saphophagus* (Jacobsoniidae) wing venation is 'completely staphylinoid'. However, the inconsistency of placement and low levels of nodal support recovered herein and in Lawrence *et al.* (2011) leave it uncertain whether and how Jacobsoniidae is related to Staphylinoidea.

Polyphaga: superfamily Scarabaeoidea

Scarabaeoidea is a well-established monophyletic group (Scholtz, 1990; Browne & Scholtz, 1999; Grebennikov & Scholtz, 2004; Hunt *et al.*, 2007). However, its sister group has long been uncertain. Proposed sister taxa include the Dascilloidea, Hydrophiloidea + Staphylinoidea + Histeroidea (= Haplogastra; Kolbe, 1908) or Hydrophiloidea s.l. Our results support a sister relationship with either Hydrophiloidea s.l. (under ML; Figure S2) or Hydrophiloidea + Staphylinoidea (= Staphyliniformia) (under BI; Fig. 2), and are consistent with other molecular and morphological studies (e.g. Caterino *et al.*, 2005; Beutel & Leschen, 2005b; Smith *et al.*, 2006; Hunt *et al.*, 2007) in refuting Dascilloidea as a possible sister group of Scarabaeoidea (e.g. Lawrence *et al.*, 2011). Taxa included in major clades within the superfamily are largely consistent based on the ML and BI trees, but the interrelationships of these taxa within clades differ (Fig. 7). Within Scarabaeoidea, notable differences between our results and other recent studies include the relationship of Passalidae to derived scarabs rather than early-divergent scarabs and inclusion of the Pleocomidae within the derived clade of phytophagous scarabs (Pleurosticti). However, these and other results for Scarabaeoidea should be considered cautiously because of missing DNA sequence data in our matrices (more than for any other superfamily) due to the use of poorly-preserved tissue for DNA extraction of many species of Scarabaeoidea studied.

There is little consensus regarding early diverging scarabaeoid lineages. Previous analyses suggest that Passalidae (Grebennikov & Scholtz, 2004), Trogidae (Lawrence *et al.*, 2011), Glaresidae (Scholtz *et al.*, 1994), Pleocomidae + Passalidae + Geotrupidae (Smith *et al.*, 2006), Glaresidae + Lucanidae (Ahrens *et al.*, 2014) or Glaresidae + Lucanidae + Trogidae (McKenna *et al*., 2014) are among the earliest-divergent extant Scarabaeoidea. However, in our results these groups are among the most derived of scarabs. Glaresids, in particular, have been considered by some to be the earliest-divergent extant group of Scarabaeoidea (Browne & Scholtz, 1995) or to belong to the family Trogidae (Smith *et al.*, 2006). The strongly supported sister relationship of Trogidae + Geotrupinae (Geotrupidae) (BPP = 1.0) in the present study is unexpected, whereas some studies (e.g. Ahrens *et al.*, 2014; Bocak *et al.*, 2014) have supported a relationship of Trogidae + Bolboceratinae [the latter as Bolboceratidae in Bocak *et al.* (2014) and Ahrens *et al.* (2014)]. The strongly supported clade Lucanidae + Nicaginae + Diphyllostomatidae (BPP = 1.0) was also found by Smith *et al.* (2006), whereas Lucanidae + Glaresidae were sister groups in Ahrens *et al.* (2014). We recovered three distant clades (= subfamilies) of Geotrupidae. Relationships of the subfamilies of Geotrupidae sampled here are consistent with the proposed polyphyly of the

family, and the general findings of other authors (e.g. Scholtz, 1990; Scholtz & Chown, 1995; Scholtz & Browne, 1996; Scholtz & Grebennikov, 2005a,2005b; Ahrens *et al*., 2014). However, this contradicts the results of Lawrence *et al.* (2011) and Smith *et al.* (2006) wherein Geotrupidae was considered monophyletic.

The sister-group relationship recovered in the present study between the dung-associated Scarabaeinae and Aphodiinae is well established (e.g. Howden, 1982; Browne & Scholtz, 1998; Smith, 2006; Smith *et al.*, 2006; Lawrence *et al.*, 2011; Ahrens *et al.*, 2014). This clade is proposed to have codiversified with mammals in the Cenozoic (e.g. Scholtz & Chown, 1995; Ahrens *et al.*, 2014), a scenario temporally consistent with our results, which suggest a Late Cretaceous to early Cenozoic origin for the clade (Fig. 2). The clade comprising Hybosoridae + Glaphyridae + Ochodaeidae recovered herein was previously proposed by Lawrence & Newton (1982) based on morphological characters, and later also supported by Scholtz *et al.* (1988), Browne (1993), and Browne & Scholtz (1995, 1999). This clade was also recovered by Smith *et al.* (2006) in a phylogenetic analysis of *18S* and *28S* rDNA sequence data from a large sample of species of Scarabaeoidea.

The largely phytophagous Pleurostict Clade (= the 'Phytophagous Clade', containing the species-rich scarabaeoid subfamilies Cetoniinae, Melolonthinae, Rutelinae, and Dynastinae) is widely accepted as monophyletic (e.g. Erichson, 1847; Browne & Scholtz, 1998; Smith *et al.*, 2006; Hunt *et al.*, 2007). However, in the present study this large clade contains a few unexpected groups that are typically recovered elsewhere in Scarabaeoidea: Pleocomidae, Passalidae, and Bolboceratinae. Most previous studies have treated Passalidae and Pleocomidae as early-divergent scarabaeoids (e.g. Grebennikov & Scholtz, 2004). The tendency for groups that are usually considered early divergent to belong to the most derived subclades was noted by Lawrence *et al.* (2011) who also recovered Geotrupidae and Pleocomidae with groups that are usually considered derived scarabs. Bocak *et al.* (2014) recovered Pleocomidae nested in a derived group of Geotrupidae. Inclusion of these groups renders Scarabaeidae nonmonophyletic, consistent with Ahrens *et al.* (2014) and Bocak *et al.* (2014), but contrary to McKenna *et al.* (2014), Lawrence *et al.* (2011), Hunt *et al.* (2007) and Smith *et al.* (2006).

Polyphaga: series Elateriformia

The phylogenetic position of Nosodendridae (also discussed above), although almost certainly within or sister to Elateriformia, remains unclear because of negligible nodal support and variable placement in the analyses reported herein. It is nonetheless recovered near the base of Elateriformia, contradicting the concept of Derodontoidea as delimited in Lawrence *et al.* (2010a). The monophyly and composition of superfamily Dascilloidea were unsurprising. Within Buprestoidea, Schizopodidae was recovered sister to the remaining Buprestidae, consistent with its recognition as a family distinct from Buprestidae as originally proposed by LeConte (1859) and advocated by Nelson & Bellamy (1991) and Bellamy (2008). These results are also consistent with Evans *et al.* (2014), except that in the present study *Agrilus* Heyden & Heyden (Agrilinae) and *Acmaeodera* Eschscholz (Polycestinae) are sister groups and Julodinae and Buprestinae are sister groups, whereas in Evans *et al.* (2014) Agrilinae and Buprestinae are sister groups and Julodinae and Polycestinae are sister groups. Outside the placement of Schizopodidae, however, these relationships lack strong nodal support under ML (but not BI) in the present study. *Podabrocephalus* (Elateroidea) was nested within the byrrhoid family Ptilodactylidae, a position consistent with Wittmer (1969) and Lawrence *et al.* (2010b, 2011). The position of *Eulichas* Jacobson (Eulichadidae) sister to Elmidae is notable, because phylogenetic placement of the former has long been controversial. The sister-group relationship of Elateroidea and Byrrhoidea in the BI tree is consistent with the results of Kundrata *et al.* (2014), but under ML we recovered Byrrhoidea and Burprestoidea as sister taxa, and these together sister to Elateroidea. Within Elateroidea, the recovery of Lissominae sister to Lycidae (and not in Elateridae) was unexpected, but is not unprecedented; the recognition of Lissomidae as a family separate from Elateridae or Throscidae was suggested by Burakowski (1973, 1975). Other relationships within Elateriformia and Elateroidea were in general agreement with previous studies (e.g. Bocakova *et al.*, 2007; Kundrata *et al.* 2014).

Polyphaga: superfamily Bostrichoidea

The monophyly and family-level relationships of Bostrichoidea were compatible with some analyses in the recent molecular phylogenetic study of Ptinidae by Bell & Philips (2012), which also included exemplars from the families Dermestidae and Bostrichidae. It is worth noting that in the present study insufficient data were available from *Endecatomus* Mellie (Endecatomidae) to include it in our final analyses. However, exploratory molecular phylogenetic analyses that included this taxon placed it sister to all other sampled Bostrichoidea. Placement of Bostrichoidea sister to Cucujiformia (with cryptonephric Malpighian tubules as a synapomorphy) in both the ML and BI analyses is inconsistent with Lawrence *et al.* (2011) and recent molecular phylogenetic studies (e.g. Hunt *et al.*, 2007; Bocak *et al.*, 2014), which place Bostrichoidea near or among early-divergent Polyphaga (Staphyliniformia, Scarabaeiformia, Elateriformia). However, none of these studies recovers consistently strong support for the placement of Bostrichoidea within Polyphaga.

Polyphaga: series Cucujiformia

Crowson (1960) proposed that Cucujiformia originated from a 'dermestoid type'. This view is compatible with the results of our phylogenetic analyses, in which Bostrichoidea is recovered sister to series Cucujiformia. Superfamily Cucujoidea was polyphyletic, consistent with other recent studies (e.g. Vogler, 2005; Hunt *et al.*, 2007; Robertson *et al.*, 2008; Hunt & Vogler,

2008; Marvaldi *et al.*, 2009; Bocak *et al.*, 2014). The superfamily therefore appears to be a convenience group for beetles that share certain features (e.g. clubbed antennae, non-heteromerous tarsi, ring-shaped aedeagus) but do not fit elsewhere. Indeed, no synapomorphies are known to support its monophyly (Leschen *et al.*, 2005). Morphological studies first suggested Cucujoidea was not monophyletic. For example, Leschen *et al.*'s (2005) cladistic analysis of 'basal Cucujoidea' (i.e. Cucujoidea not including the Cerylonid Series) demonstrated that from a morphological perspective, basal cucujoids could not be separated from Cleroidea. Wanat (2007) studied the male genitalia of Curculionoidea and other beetle groups and noted that not only was the tegmen or parameres of Coccinellidae not homologous to those of the remaining Cucujoidea, but that Cucujoidea may further be paraphyletic with respect to Phytophaga given the inferred homology of tegminal plates between these groups.

The cucujoid families Biphyllidae and Byturidae were recovered as an early-divergent clade within Cleroidea as in other recent molecular phylogenetic studies (e.g. Hunt *et al.*, 2007; Bocak *et al.*, 2014). They were also suggested by Lawrence & Newton (1995) to belong in Cleroidea based on morphology. Ample support now exists to justify the reclassification of these families to Cleroidea. We consistently recovered a cucujoid clade comprising the Cerylonid Series, a group that was originally proposed by Crowson (1955), recognizable by several larval and adult characters (Robertson *et al.*, 2008). Although the constitution of the Cerylonid Series has been refined since 1955, the currently recognized families have consistently been recovered as a clade in molecular phylogenetic studies (e.g. Hunt *et al.*, 2007; Robertson *et al.*, 2008; Marvaldi *et al.*, 2009; Robertson, 2010; Bocak *et al.*, 2014). However, the morphological study of Lawrence *et al.* (2011) did not recover a monophyletic Cerylonid Series. Nonetheless, given its relative diversity and the strong, consistent support that it receives in all other phylogenetic studies to date, this clade warrants superfamilial status as 'Coccinelloidea', following Robertson *et al*. (2015). We recovered the remaining Cucujoidea (not including Byturidae and Biphyllidae) as a clade, again consistent with Robertson *et al.* (2015). However, other recent molecular phylogenetic studies with dense cucujoid taxon sampling have not recovered this group as a clade (e.g. Hunt *et al.*, 2007; Hunt & Vogler, 2008; Bocak *et al*., 2014), and the results of some of our analyses were suggestive of its potential paraphyly with respect to Phytophaga (see above and Results). Hunt *et al.* (2007) supported Silvanidae and Phloeostichidae imbedded within Phytophaga. Nitidulidae, Kateretidae and Passandridae were recovered together forming the sister group to Curculionoidea in Bocak *et al.*'s (2014) analysis, and Sphindidae + Cybocephalidae were supported as more closely allied to Phytophaga than the remaining Cucujoidea s.s.

Within Coccinelloidea, the division into two major clades is a recurring pattern found in other molecular phylogenetic studies (e.g. Hunt *et al.*, 2007; Robertson *et al.*, 2008; Bocak *et al*., 2014), with one exception: Latridiidae is often recovered in the clade containing Coccinellidae and allies (Hunt *et al.*, 2007; Robertson, 2010; Bocak *et al*., 2014), not in the clade with Cerylonidae, Bothrideridae and Discolomatidae (present study; Robertson *et al.*, 2008). Cerylonidae, Bothrideridae and Discolomatidae were also close relatives in Hunt *et al.* (2007), Robertson *et al.* (2008) and Bocak *et al.* (2014). Bothrideridae and Cerylonidae were paraphyletic with respect to each other and to Discolomatidae in the present study. Most previous studies lacked the exemplar diversity needed to rigorously test the monophyly of these families. However, Hunt *et al.* (2007) and Robertson *et al.* (2015) reach the same conclusions, and the polyphyly of these families has been suspected based on morphological evidence (Ślipiński, 1990; Lawrence, 1991a; Ślipiński & Pakaluk, 1991). The current definitions of these three families are formally revised in light of these findings in Robertson *et al.* (2015). The two exemplars of Latridiidae, representing the two recognized subfamilies, were recovered together with strong nodal support. The placement of Latridiidae, be it with Cerylonidae, Bothrideridae and Discolomatidae, or within the clade comprising Coccinellidae, Endomychidae and allies, is not consistent among recent molecular phylogenetic studies. Both Hunt *et al.* (2007) and Bocak *et al.* (2014) support the latter placement, whereas the present study strongly supports Latridiidae as forming the sister group to the former clade. The enigmatic genus *Akalyptoischion* Andrews was not recovered near Latridiidae, supporting the decision by Lord *et al.* (2010) to remove it from that family and recognize the monogeneric family Akalyptoischiidae.

Endomychidae was polyphyletic; another result that has been suspected based on morphology (Ślipiński & Pakaluk, 1991) and demonstrated with molecular data (Hunt *et al.*, 2007). A subset of endomychid exemplars appears in a clade where they are rendered paraphyletic with respect to Corylophidae and Alexiidae. The placement of *Bystus* (Endomychidae: Anamorphinae) closely allied with Corylophidae is not surprising and consistent with previous studies (Robertson *et al.*, 2008, 2012). The other endomychid exemplars (*Endomychus, Epipocus*) appear in a second clade where, with Akalyptoischiidae, they form the sister group to Coccinellidae. These findings are consistent with those of Robertson *et al.* (2008). Even though the taxonomic representation in the two studies is quite different [e.g. neither Alexiidae nor Akalyptoischiidae were sampled in Robertson *et al.* (2008)], both studies recover one endomychid clade with Anamorphinae (Endomychidae) and Corylophidae, and a second endomychid clade comprising the 'Higher Endomychidae' of Tomaszewska (2005) with Coccinellidae. Endomychidae was also polyphyletic in Lawrence *et al.* (2011). Surprisingly, we found only modest support for the monophyly of Corylophidae. The internal relationships are, however, entirely consistent with Robertson *et al.* (2012), and consistent with Ślipiński *et al.* (2009) in the recovery of *Periptyctus* Blackburn sister to all other taxa sampled. Coccinellidae is a well-supported clade in our analyses, as might be expected given the support found for the group in other studies to date (e.g. Robertson *et al.*, 2008; Seago *et al.*, 2011). In addition, the internal relationships of Coccinellidae are consistent with the two-subfamily classification proposed by Seago *et al.* (2011) [see also Ślipiński (2007)]; the lone representative of Microweiseinae (*Delphastus*) separates from the seven other coccinellid exemplars, all representing

Coccinellinae, at the basal split in the family, as expected. All higher relationships between the coccinellids are poorly supported, a recurring pattern for phylogenetic studies of the family (e.g. Giorgi *et al.*, 2009; Magro *et al.*, 2010; Seago *et al.*, 2011).

Within Cucujoidea s.s. [the basal Cucujoidea of Leschen *et al.* (2005) minus Biphyllidae and Byturidae], all analyses recovered Erotylidae with strong nodal support. These findings confirm previous studies (e.g. Węgrzynowicz, 2002; Leschen, 2003b; Robertson *et al.*, 2004; Leschen & Buckley, 2007) that support subsuming Languriidae within Erotylidae. Sphindidae was rendered paraphyletic by Protocucujidae, a family generally considered to be very closely related (Sen Gupta & Crowson, 1979; McHugh, 1993; Ślipiński, 1998; Chiao & McHugh, 2000; Leschen *et al.*, 2005), and also Helotidae under BI. Sphindidae lacks an unambiguous morphological synapomorphy, and adult *Ericmodes* Reitter and *Protosphindus* are strikingly similar anatomically. Myxomycophagy was proposed as a potential synapomorphy for Sphindidae, but the biology of Protocucujidae is poorly known. The relationship of these two families should nonetheless be re-examined. The location of the clade Sphindidae + Protocucujidae in the current study is intuitively pleasing because Sphindidae is generally considered to have features of a basal cucujoid. In other recent, deeply taxon-sampled molecular phylogenetic analyses, the placement of Sphindidae has been inconsistent, often puzzling. For example, Hunt *et al.* (2007) recovered Sphindidae sister to the large clade Lymexyloidea + Tenebrionoidea. In Bocak *et al*. (2014), and Cline *et al.* (2014) Sphindidae was recovered in a small clade as the sister group of Cybocephalinae (Nitidulidae). The cause for this instability is not clear. However, these and many of the other branches deep within Cucujoidea s.s. and deep within Cucujiformia as a whole, are among the shortest in the whole beetle tree (Figure S2).

Laemophloeidae and Propalticidae were recovered as sister taxa, consistent with previous morphological (e.g. Leschen *et al*., 2005) and molecular studies (Hunt *et al.*, 2007; Bocak *et al.*, 2014). McElrath *et al.* (2015) found Propalticidae to be deeply nested within Laemophloeidae and formally subsumed the family there. Phalacridae was sister to a clade comprising Laemophloeidae + Propalticidae, consistent with the results of Hunt *et al.* (2007), Bocak *et al*. (2014), and McElrath *et al.* (2015). There is strong support for the monophyly of Nitidulidae + Kateretidae, as in Lawrence *et al.* (2011). These families have historically been considered confamilial. Although there is strong support for some clades within Nitidulidae, there is relatively weak support for the family as a whole. Monotomidae has been considered by other authors to be part of a 'nitiduloid assemblage' (Leschen *et al.*, 2005), and its placement sister to Nitidulidae + Kateretidae is consistent with this thinking. It is noteworthy that *Smicrips* (Smicripidae), which also has been proposed to be part of the 'nitiduloid assemblage', is not recovered in this clade, instead appearing (but with negligible ML support) in a clade with Boganiidae and Hobartiidae. Crowson thought Boganiidae was a potential sister taxon of Chrysomeloidea (Crowson, 1990). However, here Boganiidae (represented by *Paracucujus*) is embedded in Cucujoidea s.s., suggesting that its peculiar characters (e.g. articulated larval mala, distinct area of microsculpture on the hindwing, etc.) are derived. Nonetheless, the phylogenetic positions of *Hobartius, Paracucujus* and *Smicrips* – and to a lesser degree, Nitidulidae, Kateretidae and Monotomidae – were unstable in our analyses, and nodal support for the placement of these taxa, and for the deep splits in Cucujoidea s.s. in general, were mostly negligible, further highlighting the uncertainty surrounding the monophyly and deep splits in Cucujoidea s.s. The ML tree contains a clade of small austral families, including Priasilphidae + Agapythidae, sister to *Hymaea* (Phloeostichidae). This grouping is not surprising given that all of these families were considered to be members of one family, Phloeostichidae, until recently (Leschen *et al*., 2005). The polyphyly of both Cryptophagidae (four exemplars) and Silvanidae (two exemplars) was unexpected and is inconsistent with previous analyses of morphological (e.g. Lawrence *et al.*, 2011) and molecular data (e.g. McElrath *et al.*, 2015), which suggest these families, at least to the extent sampled, are monophyletic.

Tenebrionoidea, with the inclusion of Lymexyloidea: Lymexylidae was monophyletic, but its monophyly and early splits lacked strong nodal support, as in other recent molecular phylogenetic studies (e.g. Gunter *et al.*, 2014). The phylogenetic placement of Lymexyloidea relative to other Tenebrionoidea was unclear in our study because of the lack of nodal support across the backbone of Tenebrionoidea. Nonetheless, Lymexyloidea was recovered within early-divergent Tenebrionoidea in the ML and BI trees. Other molecular phylogenetic studies recover Lymexyloidea within Tenebrionoidea (Hunt *et al.*, 2007) or sister to Tenebrionoidea (Bocak *et al.*, 2014; Gunter *et al.*, 2014), but they, too, lack nodal support for these relationships. We sampled only one species of Lymexyloidea (Lymexylidae: *Atractocerus*); therefore, we were unable to assess the monophyly of the superfamily.

Within Tenebrionoidea, Lymexylidae, Aderidae, Anthicidae, Meloidae, Mordellidae, Ripiphoridae and Stenotrachelidae formed a well-supported clade sister to the rest of the superfamily. Similar relationships were recovered in the morphological study of Lawrence *et al*. (2011) and several other molecular phylogenetic studies (Hunt *et al.*, 2007; Bocak *et al.*, 2014; Gunter *et al.*, 2014; (Kergoat *et al.*, 2014a,b). However, this contrasts with the traditional view that Tetratomidae, Mycetophagidae, Archeocrypticidae, Pterogeniidae and Ciidae represent ancestral forms within the superfamily (Crowson, 1966; Lawrence, 1977). Tetratomidae, Salpingidae, Ulodidae and Promecheilidae were polyphyletic, consistent with the morphological study of Lawrence *et al.* (2011). *Trachelostenus* (Trachelostenidae) and *Leaus* (*incertae sedis*) were recovered as sister taxa well within Tenebrionidae, as suggested by Matthews & Lawrence (1992). The Bayesian tree strongly supports the monophyly of the Salpingid group (Watt, 1987), which includes Boridae, Pyrochroidae [added by Pollock (1994)], Pythidae, Salpingidae and Trictenotomidae. The three Southern Hemisphere families Chalcodryidae, Promelcheilidae and Ulodidae formed a strongly supported clade under both ML and BI. *Polypria* (Oedemeridae: Polypriinae) was unexpectedly sister to Mycteridae (*Hemipeplus* and *Lacconotus*), contradicting its placement by Lawrence (2005) in the family

Oedemeridae. *Hyporhagus* (Zopheridae: Monommatini) was sister to Scraptiidae, well removed from the other Zopheridae sampled, and in contradiction to the results of morphological studies by Ślipiński & Lawrence (1997, 1999). However, many apomorphies in the Zopheridae are larval characters that may be convergent. Placement of the Incertae sedis taxon *Rhizonium* was not strongly supported, but it was recovered in the above-mentioned early-divergent clade in both the Bayesian and ML analyses. This is in contrast with its placement in the Zopheridae: Colydiinae (Lawrence, 1980; Ivie & Ślipiński, 1990), or Zopheridae incertae sedis (Leschen, 2003a). The family-level placement of the enigmatic genus *Lagroida* Fairmaire & Germain (currently placed in Anthicidae; Lawrence & Britton, 1991; Costa *et al.*, 1995; Lawrence *et al.*, 2010c) was uncertain in our analyses, although none of our molecular phylogenetic analyses recover it within Anthicidae.

Within Cleroidea, the trogossitids *Acalanthus*, *Eronyxa, Grynoma* and *Thymalus* were recovered as a clade, sister to Acanthocnemidae, contradicting Majer (1994) who considered Acanthocnemidae to be part of the melyrid lineage. Lawrence & Leschen (2010) suggested a more basal position of Acanthocnemidae within Cleroidea based on the newly discovered larva. The morphological analysis of Lawrence *et al*. (2011) also supported a relationship of Acanthocnemidae to Trogossitidae and not the melyrid group. The placement of *Temnoscheila* (Trogossitidae: Trogossitinae) sister to *Isoclerus* (Thanerocleridae) is inconsistent with the results of the molecular analysis of Gunter *et al.* (2013), which included only cleroid taxa and resulted in a cladogram in which Thanerocleridae was within the main clerid clade (excluding only Tillinae). Whether these results indicate a further splitting of Trogossitidae into more than two groups [the aforementioned plus *Rentonellum* (Rentoniinae), which was sister to all other Cleroidea and has not been included in any molecular phylogenetic studies of Cleroidea to date], is not clear. Trogossitidae is nonetheless clearly not monophyletic, as has been observed in other studies (Hunt *et al.*, 2007; Gunter *et al.*, 2013; Bocak *et al.*, 2014). Phycosecidae is placed within the remaining melyrid lineage as suggested by Majer (1987), and the sister relationship between *Idgia* (Prionoceridae) and Melyridae corroborates results from the recent molecular phylogenetic studies of Bocakova *et al.* (2012), Gunter *et al.* (2013) and Bocak *et al.* (2014). The placement of Rentoniinae (Trogossitidae) sister to the remaining cleroids is similar to the results of Lawrence *et al*. (2011). Potential long-branch issues aside, doubts have been expressed about the placement of Rentoniinae in Trogossitidae (Lawrence & Ślipiński, 2013a; Gimmel & Leschen, 2014). Although the placement of Biphyllidae + Byturidae sister to the cleroid clade excluding Rentoniinae contradicts the results of most morphological analyses [in particular, Leschen *et al.* (2005), which places both families within Cucujoidea s.s.], the presence of a cleroid-like aedeagus in both families was noted by Lawrence & Newton (1995) and Lawrence *et al.* (2014), and this result is consistent with other molecular phylogenetic studies (discussed above).

The informal grouping Phytophaga – superfamily Chrysomeloidea plus its sister taxon, superfamily Curculionoidea – was recovered as a clade in all analyses, corroborating previous studies with fewer genes and (generally) less clade support (e.g. Farrell, 1998; Marvaldi *et al.*, 2009; McKenna *et al.*, 2009). This is, however, the first broadly sampled molecular phylogenetic study of Coleoptera to report a monophyletic Phytophaga. In Bocak *et al.* (2014), Phytophaga was rendered paraphyletic by Nitidulidae (Cucujoidea s.s.), which was sister to Curculionoidea. In Hunt *et al.* (2007), Phytophaga was rendered paraphyletic by Silvanidae and Phloeostichidae (Cucujoidea s.s.), which were sister to Curculionoidea in their 320-taxon dataset, and Chrysomeloidea was polyphyletic. Within Phytophaga, superfamily Chrysomeloidea contained two major clades: the family Chrysomelidae, and the family Cerambycidae s.l. (plus Megalopodidae and Orsodacnidae), and with internal relationships mostly in agreement with results from other recent molecular or morphological studies (e.g. Reid, 1995, 2000; Farrell, 1998; Farrell & Sequeira, 2004; Gomez-Zurita *et al*., 2007; Švácha & Lawrence 2014a–d). The polyphyly of Vesperidae was unexpected and is not supported by morphology (e.g. Švácha & Lawrence, 2014a). No molecular phylogenetic studies have sampled more than one species of Vesperidae. Nonetheless, these relationships are not well supported, and the internal branches uniting these taxa are all very short, whereas the terminals are relatively long.

Within Curculionoidea, the unstable placement of *Nemonyx*, rendering Nemonychidae paraphyletic under BI, and rendering Anthribidae paraphyletic under ML suggests a closer affiliation of *Nemonyx* (Nemonychinae) with Anthribidae (including Urodontinae) than with other taxa currently placed in Nemonychidae. This (or similar) has been noted in other studies (e.g. Oberprieler *et al.*, 2007; McKenna *et al.*, 2009). Certain other family-level relationships, such as the placement of Belidae and Attelabidae, were inconsistent across analyses and with relationships reported in other previously published studies, but lacked strong nodal support. There is nonetheless agreement between the present results and previous studies about the earliest divergence of Curculionoidea leading to nemonychid-like and belid-like weevils. Moreover, our results from analysis of *18S* and *28S* nucleotides plus AAs (Figure S4) are concordant with the morphological hypothesis on weevil interfamilial relationships (e.g. Marvaldi *et al*., 2002; Oberprieler *et al.*, 2007), showing a basal split between the Nemonychidae–Anthribidae clade and the remaining curculionoid families. The sister-group relationship of Caridae to the clade Brentidae + Curculionidae, and the internal higher level relationships of the family Curculionidae are in general agreement with current views on weevil phylogeny based on morphological and/or molecular data (e.g. Marvaldi *et al.*, 2002, 2009; Oberprieler *et al.*, 2007; McKenna *et al.*, 2009; Haran *et al.*, 2013; Gillett *et al.*, 2014). Within Curculionidae, two members of the Brachycerinae appear in separate, though relatively basal, positions, suggesting that this subfamily is not monophyletic, again consistent with other studies (e.g. McKenna *et al.*, 2009; Gillett *et al.*, 2014). Notably, the platypodines form a clade with the Dryophthorinae, a relationship contentious with traditional views that link platypodines with the Scolytinae (e.g. Kuschel *et al.*, 2000). A close relationship of Platypodinae to Dryophthorinae was, however, originally suggested by Marvaldi (1997) based on morphological evidence

from immatures and is now supported by evidence from several molecular phylogenetic studies (e.g. McKenna *et al.*, 2009; Haran *et al.*, 2013; Bocak *et al.*, 2014; Gillett *et al.*, 2014).

Timing and patterns of diversification in beetles

We report the first timetree for beetles reconstructed using Bayesian methods that co-estimate node ages along with phylogeny (see Materials and methods). The reconstructed timing of the split between Neuropteroidea (comprising Coleoptera + Neuropterida + Strepsiptera) and Hymenoptera at ∼298 Ma (95% HPD: 319 to 282 Ma) is compatible with the fossil record and the developing view (e.g. Nel *et al.*, 2013; Misof *et al.*, 2014) that Holometabola originated in the Carboniferous. The split between Coleoptera and Strepsiptera is estimated to have occurred in the latest Carboniferous or Early Permian at which time all of Earth's major landmasses were united as the supercontinent Pangaea. The largest mass extinction in the Phanerozoic occurred near the end of the Permian, peaking ∼253 Ma (uppermost Permian), approximately the same time as the estimated appearance of crown group Coleoptera. The basal split in Coleoptera produced the clade Archostemata + Adephaga + Myxophaga and the clade Polyphaga in the Early to Middle Triassic, with the split between Archostemata and Myxophaga and the split between Adephaga and Archostemata + Myxophaga occurring shortly thereafter (also in the Triassic). Crown Myxophaga, Adephaga and Archostemata appeared in the latest Triassic or earliest Jurassic. The supercontinent of Pangaea existed until the mid-Triassic, after which it began to gradually rift into Laurasia to the north and Gondwana to the south, with the continental climate eventually shifting from mostly dry (Triassic) to mostly humid (Jurassic and Cretaceous). The implications of such changes for beetles remain unclear, but many of the series and superfamilies that dominate the modern beetle fauna originated during this time, perhaps facilitated by the increase in landscape-level heterogeneity and complexity, latitudinal expansion of characteristically tropical habitats and biotas, and the further development of intimate and coevolved interactions with plants (especially involving flowering plants during the Cretaceous) and animals, not to mention the invasion of beetles into novel arid or aquatic habitats, to which they may have been preadapted by way of elytral covering of the spiracles and other features (Lawrence & Newton, 1982; Beutel, 1997).

We generally recovered slightly younger mean estimated divergence times for most subordinal-, series- and superfamily-level relationships in beetles than previous ordinal-level molecular studies (Table 2; Hunt *et al.,* 2007[2]; McKenna & Farrell, 2009). This may result at least in part from the use of well-established, and therefore typically more conservative fossils for calibration, and/or the misidentification of early fossil Coleoptera used in other studies as belonging to crown groups when they instead belong to stem groups. For example, proposed crown group Archostemata are known from the Late Triassic (201–235 Ma) (e.g. Ommatidae in Ponomarenko, 1963), suggesting that the estimated age for crown group Archostemata reported herein (median ∼158 Ma, 95% HPD: 192 to 123 Ma) may be too young, and that the real age lies beyond the estimated 95% HPD in our study. However, it is of course also possible that Late Triassic fossil Archostemata actually belong to the archostematan stem group, which is estimated to have split from Myxophaga in the Triassic ∼220 Ma (95% HPD: 237 to 205 Ma), and that the first crown group Archostemata indeed do not appear until the Jurassic.

The two previous estimates of the age of the suborders of beetles based on near-comprehensive molecular phylogenies calibrated with fossil data have been fairly consistent. Hunt *et al.* (2007) used seven fossil age constraints to calibrate their Bayesian consensus tree, and dated internal nodes via penalized likelihood (Sanderson, 2002). The age of the split between the suborders Myxophaga + Archostemata and the suborders Adephaga + Polyphaga was fixed in their analyses at 285 Ma. McKenna & Farrell (2009), using nonparametric rate smoothing (Sanderson, 1997), estimated that the split between Adephaga and Polyphaga occurred ∼269 to 265 Ma (mean 266.4 Ma), just slightly later than Hunt *et al.* (2007) (Table 2), who estimated this split to have occurred ∼277 Ma. However, the subordinal-level topologies of Hunt *et al.* (2007) and McKenna & Farrell (2009) were the same, and differ substantially from the subordinal-level topology reported herein. Further, Hunt *et al.* (2007) and McKenna & Farrell (2009) were both deeply taxon-sampled, but used data from just 1–3 genes. In the case of the three-gene study (Hunt *et al.,* 2007), the matrix also had considerable missing data, and both studies incorporated fewer fossils into their analyses than were included in the analyses reported herein. McKenna & Farrell (2009) reported only subordinal divergence times on account of the lack of resolution and nodal support at lower taxonomic levels in their trees. Nonetheless, some comparisons can be made to the present study. For example, in the present study Archostemata and Myxophaga split from their sister group (Adephaga) at ∼242 Ma, whereas in McKenna & Farrell (2009) Archostemata + Myxophaga split from their sister group (Adephaga + Polyphaga) at ∼267 Ma. In the present study, unlike the aforementioned previous studies, only one or two lineages of crown group Coleoptera are proposed to have survived the end Permian extinction, with stem group representatives of all four extant suborders appearing by the end of the Triassic.

Misof *et al.* (2014), which was focused on Hexapoda, but included eight exemplar Coleoptera, estimated the timing of origin of crown Coleopterida (Coleoptera + Strepsiptera) at ∼286 Ma (Permian) and the origin of crown Coleoptera at ∼270 Ma (also Permian). These dates are similar to the estimates reported herein. For example, the timing of origin of Coleopterida was estimated at 278 Ma, 8 Ma younger than the mean estimate of Misof *et al.* (2014) which falls within its 95% HPD, and the timing of the origin of crown group Coleoptera was estimated at 253 Ma, 17 Ma less than the mean estimate of Misof *et al.* (2014).

[2]Hunt *et al.* (2007) is the only previous ordinal-level study to report estimated divergence times within Polyphaga.

Our results within Polyphaga are generally compatible with the fossil record as characterized by Grimaldi & Engel (2005). One of several notable differences involves the superfamily Staphylinoidea. In the present study, crown group Staphylinoidea are estimated to have originated ~193 Ma (95% HPD: 210 to 175 Ma). However, a proposed crown group staphylinid, *Leehermania prorova*, is known from the Carnian (235 to 228 Ma) of southern Virginia, and an undescribed possible staphylinid is known from the Anisian (247 to 242 Ma) of Grès à Voltzia, France (Papier *et al.,* 2005; Chatzimanolis *et al.,* 2012). These fossils are substantially older than the estimated 95% HPD for even stem group Staphyliniformia (+ Scarabaeiformia: Scarabaeoidea) in our study (median 200 Ma, 95% HPD: 217 to 183 Ma). Although attribution of these fossils to Staphylinidae has been questioned[3] [Chatzimanolis *et al.* (2012) and Grebennikov & Newton (2012), respectively], they highlight the possibility that some of the divergence times in the BEAST chronogram (Fig. 2) may be underestimated because we used relatively unambiguous, and therefore often conservative, fossil-based ages as priors on node ages in our analyses. Unequivocal crown group staphylinids occur by the Middle Jurassic Period (e.g. Chatzimanolis *et al.,* 2012), consistent with our results.

Convergence between our nodal age estimates and those of most lower-level studies further suggests that our estimates are reasonable. For example, crown group Chrysomeloidea and Curculionoidea are estimated herein to have appeared near the end of the Jurassic (~145 and ~150 Ma, respectively), near the first appearance of flowering plants (Bell *et al.,* 2010), and consistent with estimated divergences within Phytophaga and its descendant superfamilies Curculionoidea and Chrysomeloidea, as reported by McKenna *et al.* (2009). A recently described fossil derodontid from the middle Jurassic (~165 Ma; Cai *et al.*, 2014), is not only the first known for the early-divergent polyphagan family Derodontidae, but also fully consistent with our results, which indicate that crown group Derodontidae first appeared ~175 Ma. Some estimated ages in our study are much older than select other estimates. For example, Gomez-Zurita *et al.* (2007) propose a relatively young age for crown Chrysomelidae (~75 Ma). This is much younger than in the present study (~130 Ma) and younger than in other molecular timetrees to date (e.g. Hunt *et al.*, 2007; Wang *et al.*, 2013). Most modern families and subfamilies of Coleoptera, including the crown groups of a majority of the most species-rich families, are estimated herein to have Cretaceous origins (Figs 2, 16), in contrast to the results of Hunt *et al.* (2007), which indicate a Jurassic origin for many such lineages.

Diversification rates

Crown group Coleoptera experienced an increase in diversification rate over Neuropteroidea as a whole (Table 3; Fig. 2). However, these rates, which are 0.025 lineages per million years (Ma) for Neuropteroidea and 0.037 lineages/Ma for Coleoptera, are not unusually high when compared to other animals. For example, Neoaves has an estimated rate of 0.089 lineages/Ma (Alfaro *et al.*, 2009), but that clade is much younger than Coleoptera, highlighting the role of clade age in extant beetle diversity. Hunt *et al.* (2007) estimated a rate of 0.05–0.07 lineages/Ma for Coleoptera, approximately twice the rate calculated herein. Nonetheless, in the present study 10 clades within Coleoptera were identified as too species-rich to result from the background diversification rate, all belonging to the suborder Polyphaga (Table 3; Fig. 2) and including most major groups of beetles proposed by other authors to have undergone rapid diversification. These include most phytophagous beetles that feed on living or dead plant material (including wood and often also involving fungi), for example the Phytophaga, Buprestidae, Meloidae + Mordellidae and Scarabaeidae, but notably also including groups not typically associated with plants, such as Elateridae and Tenebrionidae + Trachelostenidae. Five of these eleven clades have diversification rates approaching or exceeding the above-mentioned rate for Neoaves. Interestingly, six to seven of the 10 significant increases in diversification rate were in beetle clades that originated in the Cretaceous, which is also when most modern beetle families, including the crown groups of a majority of the most species-rich families, first appeared (Table 3; Figs 2, 16; Figure S1). The Cretaceous Period is well known for the diversification of angiosperms and their rise to ecological dominance (Lidgard & Crane, 1988, 1990). Many other groups of organisms also diversified at this time – a phenomenon that has been referred to as the 'Cretaceous Terrestrial Revolution' (Lloyd *et al.*, 2008). However, neither phytophagy, nor specialized associations with angiospermous plants uniquely characterize the groups of beetles that have undergone statistically significant increases in diversification rate – at least to the extent that this can be estimated with extant species numbers. The 12 clades of beetles identified as exhibiting decreases in diversification rate are species-poor in the modern fauna, but collectively exhibit diverse trophic habits, notably including phytophagy – though sometimes the associations are with gymnosperms [e.g. Caridae (Cupressaceae)] rather than with angiosperms. These and most others have relictual, often Gondwanan distributions, suggesting that floral and faunal turnover itself may have played an important role in their present low diversities and limited distributions.

Conclusions

Our results provide a uniquely well-resolved temporal and phylogenetic framework for studying patterns of innovation and diversification in beetles, and a foundation for further sampling and resolution of the Coleoptera tree of life. They also provide much-needed evolutionary context for interpreting observations emerging from the study of beetle life histories, behaviour, morphology, microbiomes, genetics and genomics. However, our results are not definitive, particularly with regard to resolution of the deepest splits in the beetle tree. Furthermore, some of our estimated divergence times are younger than expected based on the Mesozoic beetle fossil record.

[3]Which is why these fossils were not included in the BEAST analysis as priors on node ages.

Many have proposed explanations for the apparent success of beetles (e.g. Crowson, 1981; Farrell, 1998; Barraclough *et al.*, 1998; Grimaldi & Engel, 2005; Hunt *et al.,* 2007). Some hypotheses, including the evolution of hardened forewings (elytra) which protect the hindwings, thereby facilitating a cryptic lifestyle (Crowson, 1981; Grimaldi & Engel, 2005) and the invasion of arid or aquatic habitats through elytral covering of the spiracles (Lawrence & Newton, 1982), apply to nearly the entire lineage Coleoptera. Other hypotheses only apply to a subset of major lineages. For example, the Phytophaga were proposed by Farrell (1998) to have diversified because of their intimate associations with flowering plants (angiosperms). The large series Staphyliniformia (rove beetles and allies) and Scarabaeiformia (scarab beetles and allies) are proposed to have radiated at least in part as a consequence of (pre)adaptations gained through ecological and evolutionary opportunities and challenges faced as part of life in the ancestral litter environment (McKenna *et al.*, 2014). Based on the timing discussed above, the increasing humidity of the climate in the early stages of their evolution may also have contributed to their rapid and dramatic diversification. There are numerous additional lineage-specific hypotheses that warrant mention.

Hunt *et al.* (2007) concluded that the success of beetles is not readily explained by 'exceptional net diversification rates nor by a predominant role of herbivory and the Cretaceous rise of angiosperms'. Instead, they proposed that the success of beetles is due to low extinction rates and 'sustained diversification in a variety of niches', observations consistent to some degree with the results of the present study. Beetles as a whole have, however, experienced a statistically significant increase in diversification rate over their near relatives (Fig. 2). Furthermore, descendant lineages of polyphagan beetles that are associated with plants, especially angiosperms, are frequently (but not always) species rich (Farrell, 1998; Evans *et al.*, 2014; McKenna *et al.*, 2014)[4] and were identified as among those clades in the phylogeny exhibiting statistically significant increases in diversification rate, for example Phytophaga, Meloidae + Mordellidae, Acmaeoderinae + Agrilinae. In fact, some of these clades exhibit diversification rates (Table 3) that can reasonably be characterized as 'exceptional' in the context of other groups of animals (see Alfaro *et al.*, 2009).

Flowering plants and beetles both apparently underwent extensive taxonomic diversification during the Cretaceous, a phenomenon seen in other groups of organisms. Six to seven of the 11 significant increases in diversification rate that we identified in beetles occurred during the Cretaceous (Table 3; Fig. 2), although not all are among plant-associated beetle groups. Most modern beetle families, including the crown groups of a majority of the most species-rich families, also originated in the Cretaceous (Figs 2, 15). Thus, the apparent success of beetles, as measured by species numbers, may ultimately result from their associations with widespread and 'diverse' substrates – including plants, of which, flowering plants are most diverse, (Farrell, 1998; McKenna *et al.*, 2009; Ahrens *et al.*, 2014), fungi (Robertson, 2010; Robertson *et al.*, 2015) and leaf litter (McKenna *et al.*, 2014) – but what facilitated these associations in the first place or has allowed these associations to flourish likely varies within and between lineages. Proximate explanations for the apparent success of beetles therefore might most profitably be sought on a lineage-specific basis, for example by identifying and characterizing features of beetle morphology, genomes, microbiomes, etc. that facilitate ecological and taxonomic diversification and likely also promote temporal persistence via increased diet breadth, range size and/or dispersal ability. These are, of course, not new ideas (e.g. Harnik *et al.*, 2012; Jablonski *et al.*, 2013). The lineage-specific 'features' that facilitate diversification are unlikely to be the same in disparate clades of beetles, although certain general patterns of innovation may emerge, such as specialized interactions with endosymbionts (e.g. Scully *et al.*, 2014), and lateral gene transfer from plants and/or microbes to beetles (e.g. Kirsch *et al.*, 2014), both facilitating access to 'new' ecological adaptive zones. The extraordinary collective ecological breadth, apparent evolutionary plasticity, and morphological, taxonomic and ecological diversity of the lineage Coleoptera not surprisingly appears to result from multiple factors, each with relevance to different numbers of beetle clades at or over different geographic and temporal scales.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12132

Figure S1. Maximum clade credibility timetree from BEAST with OGs removed and terminals collapsed to reflect monophyletic family-level (or nearest possible equivalent[5]) groupings of taxa for use in estimating diversification rates in the program MEDUSA (see Materials and methods and Table S3).

Figure S2. Maximum-likelihood (ML) phylogenetic tree for 367 species of beetles representing 171/183 extant families, plus OGs (six species representing five orders), resulting from an unconstrained partitioned analysis of concatenated DNA sequence data from eight nuclear genes, implemented in Garli (see Materials and methods). Note that the top/right row/column entries are interdigitated between the bottom/left ones, as connected by the broken lines. ML bootstrap support ≥50% from partitioned analyses in RAxML (see Materials and methods) is indicated along branches using coloured squares, as shown in the graphical key. The embedded phylogram shows branch lengths proportional to the number of nucleotide substitutions. ML bootstrap support from the analysis of AA sequences alone is not shown because of differences in taxon sampling (see Figure S5). AR, Archostemata; MY, Myxophaga; OG, outgroups.

[4]More than half of all beetle species are associates of plants, even if not all are strictly or clearly plant-feeding.

[5]This required forming some terminals from groupings of taxa that have not previously been treated as families.

White stars mark species of Derodontoidea. Black stars mark species of Cucujoidea s.l. (Biphyllidae and Byturidae) recovered in positions separate from other members of the superfamily.

Figure S3. (In three parts) 50% majority-rule consensus tree for 367 species of beetles plus OGs (six species in five orders), resulting from a partitioned maximum-likelihood bootstrap (MLB) analysis of aligned nucleotide sequences from eight nuclear genes, implemented in the program RAxML (see Materials and methods). MLB support is shown along branches. Background colours indicate suborders and OGs (red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga; white = OGs). These data are summarized on the ML tree in Figure S2.

Figure S4. (In three parts) 50% majority-rule consensus tree for 367 species of beetles plus OGs (six species in five orders), resulting from a partitioned maximum-likelihood bootstrap (MLB) analysis of nucleotide sequences from *18S* and *28S* rDNA, plus AA sequences from six nuclear protein-coding genes. Analyses were implemented in the program RAxML (see Materials and methods). MLB support is shown along branches. Background colours indicate suborders and OGs (red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga; white = OGs). These data are summarized on the ML tree in Figure S2.

Figure S5. Fifty percent majority-rule consensus tree for 313 species of beetles plus OGs (six species representing five orders), resulting from a partitioned maximum-likelihood bootstrap (MLB) analysis of AA sequences from six nuclear protein-coding genes, implemented in RAxML (see Materials and methods). MLB support is shown along branches. Beetles for which ≥50% of AA positions had data were excluded from the analysis; therefore, these results are not summarized in Figure S2 (which contains data from all 373 taxa). Background colours indicate suborders and OGs (red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga; white = OGs).

Figure S6. Fifty percent majority-rule consensus tree for 313 species of beetles and OGs (six species representing five orders), resulting from a maximum-likelihood bootstrap (MLB) analysis of nucleotide sequences from six NPC genes. Analyses were implemented in RAxML (see Materials and methods). MLB support is shown along branches. Background colours indicate suborders and OGs (red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga; white = OGs).

Figure S7. Fifty percent majority-rule consensus tree for 367 species of beetles and OGs (six species representing five orders), resulting from a partitioned maximum-likelihood bootstrap (MLB) analysis of nucleotide sequences from eight nuclear genes, with Strepsiptera (*Mengenilla moldryzki*) constrained to the OG, i.e. constrained to fall outside Coleoptera, but not constrained in its placement outside of Coleoptera. Analyses were implemented in RAxML (see Materials and methods). MLB support is shown along branches. Background colours indicate suborders and OGs (red = Myxophaga; orange = Archostemata; blue = Adephaga; green = Polyphaga; white = OGs). These data are summarized on the ML tree in Figure S2.

Figure S8. Large format version of Fig. 2, see bottom of figure for legend.

Figure S9. Maximum clade credibility timetree for beetles and OGs from Fig. 2 showing 95% confidence intervals around node age estimates as red bars, and estimated node ages (see Fig. 2 for more information).

Table S1. Taxonomic placement, DNA code(s), and collection and GenBank DNA sequence accession numbers for all taxa included in this study. Species marked with an asterisk (*) were excluded from analyses of AA sequences alone (these contained <50% of the targeted AA positions). Families marked with a pound sign (#) have not previously been included in higher-level studies of beetle phylogeny. Italicized GenBank accession numbers indicate previously published DNA sequences obtained from GenBank.

Table S2. Monophyly constraints applied in the BEAST analysis.

Table S3. Estimated total numbers of described extant species for monophyletic family-level (or nearest possible equivalent [6]) groupings of taxa (see Materials and methods, Figure S1). Species numbers were obtained from Ślipiński *et al.* (2011) except when sub-familial taxon numbers were needed to provide estimates for groups that were split apart or lumped together along sub-familial lines (cited individually in the table). However, typically when a family was split into two or more groups, the extent of the resulting groups was unclear, so the total number of described species in the family was split evenly between the two separately recovered lineages. Estimated species numbers for Neuropteroidea other than Coleoptera were obtained from Grimaldi & Engel (2005).

File S1. Files output by Gblocks v0.91b (Castresana, 2000; Talavera & Castresana, 2007) for each nucleotide and AA sequence matrix for *18S*, *28S*, *AK*, *AS*, *CAD*, *EF1-α*, *PEPCK* and *WG*.

File S2. Supermatrix containing the concatenated masked nucleotide sequence alignments for the eight nuclear genes included in this study. The supermatrix contains 8377 aligned nucleotide positions for 373 species.

[6]In some cases this required forming terminals from groupings of taxa that have not previously been treated as families or monophyla.

File S3. Supermatrix containing the concatenated masked AA sequence alignments for the six NPC genes included in this study. All taxa that were missing data from more than 50% of the aligned AA positions (marked with * in Table S1) were removed from the supermatrix. The resulting supermatrix contains 1747 aligned AA positions for 319 species.

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