

Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia)

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Abstract. A large-scale phylogenetic study is presented for Cucujoidea (Coleoptera), a diverse superfamily of beetles that historically has been taxonomically difficult. This study is the most comprehensive analysis of cucujoid taxa to date, with DNA sequence data sampled from eight genes (four nuclear, four mitochondrial) for 384 coleopteran taxa, including exemplars of 35 (of 37) families and 289 genera of Cucujoidea. Maximum-likelihood analyses of these data present many significant relationships, some proposed previously and some novel. Tenebrionoidea and Lymexyloidea are recovered together and Cleroidea forms the sister group to this clade. Chrysomeloidea and Curculionoidea are recovered as sister taxa and this clade (Phytophaga) forms the sister group to the core Cucujoidea (Cucujoidea *s.n.*). The nitidulid series is recovered as the earliest-diverging core cucujoid lineage, although the earliest divergences among core Cucujoidea are only weakly supported. The cerylonid series (CS) is recovered as monophyletic and is supported as a major Cucujiform clade, sister group to the remaining superfamilies of Cucujiformia. Currently recognized taxa that were not recovered as monophyletic include Cucujoidea, Endomychidae, Cerylonidae and Bothrideridae. Biphyllidae and Byturidae were recovered in Cleroidea. The remaining Cucujoidea were recovered in two disparate major clades: one comprising the nitidulid series + erotylid series + Boganiidae and Hobartiidae + cucujid series, and the other comprising the cerylonid series. Propalticidae are recovered within Laemophloeidae. The cerylonid series includes two major clades, the bothriderid group and the coccinellid group. Akalyptoischiidae are recovered as a separate clade from Latridiidae. Eupsilobiinae are recovered as the sister taxon to Coccinellidae. In light of these findings, many formal changes to cucujiform beetle classification are proposed. Biphyllidae and Byturidae are transferred to Cleroidea. The cerylonid series is formally recognized as a new superfamily,

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Coccinelloidea **stat.n.** Current subfamilies elevated (or re-elevated) to family status include: Murmidiidae **stat.n.**, Teredidae **stat.n.**, Euxestidae **stat.n.**, Anamorphidae **stat.rev.**, Eupsilobiidae **stat.n.**, and Mycetaeidae **stat.n.** The following taxa are redefined and characterized: Cleroidea **s.n.**, Cucujoidea **s.n.**, Cerylonidae **s.n.**, Bothridiidae **s.n.**, Endomychidae **s.n.** A new subfamily, Cyclotominae **stat.n.**, is described. Stenotarsinae **syn.n.** is formally subsumed within a new concept of Endomychinae **s.n.**

Introduction

Cucujoidea

The beetle series Cucujiformia is a uniquely diverse lineage of life on Earth, containing >173 000 species. The group is currently divided into six superfamilies: Lymexyloidea (ship-timber beetles; *c.* 50 species), Tenebrionoidea (darkling beetles, blister beetles, tumbling flower beetles, etc.; >34 000 species), Cleroidea (checkered beetles, soft-winged flower beetles, etc.; >10 200 species), Cucujoidea (flat bark beetles, pleasing fungus beetles, lady beetles, etc.; >19 000 species), Chrysomeloidea (leaf beetles, longhorn beetles, etc.; >50 000 species) and Curculionoidea (weevils; >60 000 species) (Young, 2002; Hunt *et al.*, 2007; Oberprieler *et al.*, 2007; Gunter *et al.*, 2013, 2014). Of the six cucujiform superfamilies, Cucujoidea is the most problematic with regard to classification and no synapomorphies supporting its monophyly have been identified (Leschen *et al.*, 2005; Leschen & Ślipiński, 2010). Cucujoidea is a heterogeneous group of beetles which have a similar appearance (e.g. small, drab colouration, clubbed antennae) (Fig. 1) that could not be placed satisfactorily elsewhere. The group was established for convenience and represents the largest taxonomic dumping ground among the superfamilies of Coleoptera. Cleroidea in particular shares many characters with certain groups of Cucujoidea such that these two superfamilies are difficult to separate (Crowson, 1955; Lawrence & Newton, 1982). As such, characterizing Cucujoidea is problematic. The current classification recognizes 37 families of Cucujoidea (Leschen *et al.*, 2005; Leschen & Ślipiński, 2010; Lord *et al.*, 2010; Cline *et al.*, 2014). Cucujoids exhibit a broad range of host utilization and typically have cryptic life histories in leaf litter, dead wood or fungi (Fig. 2).

Cucujoidea is an extremely diverse and taxonomically difficult superfamily. In Crowson's (1955) classification of the families of Coleoptera, he states 'In the number of families included, the Cucujoidea greatly exceed any other superfamily of Coleoptera, and the diversity of structure and habit among them is correspondingly great; the establishment of a rational order or natural key to these families is a task beset with the most formidable difficulties' (p. 87). The verity of Crowson's assessment is reflected in the fact that more than half a century later, the current family concepts and hypothesized relationships of higher cucujoid taxa remain unstable.

In their review of the classification of Coleoptera, Lawrence & Newton (1982) outlined three major advances in the taxonomy

and classification of Cucujoidea. The first was the recognition of several presumed 'primitive', primarily south temperate groups such as Protocucujidae (Crowson, 1955), Boganiidae, Hobartiidae, Phloeostichidae and Cavognathidae (Sen Gupta & Crowson, 1966, 1969a; Crowson, 1973). Members of these families were either misplaced among existing taxa or previously unknown. The second contribution was the transfer of several taxa from Cryptophagidae to other families, primarily Languriidae (now Erotylidae) (Sen Gupta & Crowson, 1969b, 1971). The third major advancement in cucujoid systematics was the recognition of a group of beetles related to Cerylonidae, termed the cerylonid group, or cerylonid series (CS) (Crowson, 1955).

More recently, Leschen *et al.* (2005) performed a formal cladistic study of the 'basal Cucujoidea,' an informal group comprising all non-CS cucujoid families. The objective of their study was primarily to determine the relationships of taxa allied to the family Phloeostichidae using adult and larval morphology. Leschen *et al.* (2005) recognized five new families of Cucujoidea that were previously treated as subfamilies within Phloeostichidae. Their study did not include any taxa belonging to the CS.

Hunt *et al.* (2007) performed the first large-scale molecular study focused on reconstructing the higher-level relationships within the entire order Coleoptera using *18S*, *16S* and *COI* and broad taxon sampling across all major beetle groups. The study included 54 exemplars representing 24 families of Cucujoidea in their 320 taxa dataset and their results recovered Cucujoidea as grossly polyphyletic. Silvanidae and Phloeostichidae were recovered sister to Curculionoidea; Byturidae and Biphylidae were placed within Cleroidea; the CS was recovered as the sister group to Cleroidea; the family Sphindidae was supported as the sister group to Tenebrionoidea (including Lymexyloidea); the remaining cucujoid exemplars formed a large clade sister to Chrysomeloidea.

Bocak *et al.* (2014) constructed and analysed a supermatrix of all Coleoptera sequences available in GenBank combined with a substantial number of sequences new to that study for four markers: nuclear ribosomal *18S* and *28S* and mitochondrial *rrnL* and *COI*. Their supermatrix comprised over 8000 terminals (not all were different species). Cucujoidea were recovered as polyphyletic with Byturidae + Biphylidae recovered sister to Cleroidea; Sphindidae + Cybocephalidae [= Cybocephalinae (Nitidulidae) (Cline *et al.*, 2014)] were supported as an isolated cucujiform lineage; most of the core cucujoids formed a clade sister to Phytophaga; Nitidulidae (most, including Passandridae) + Kateretidae formed the sister group

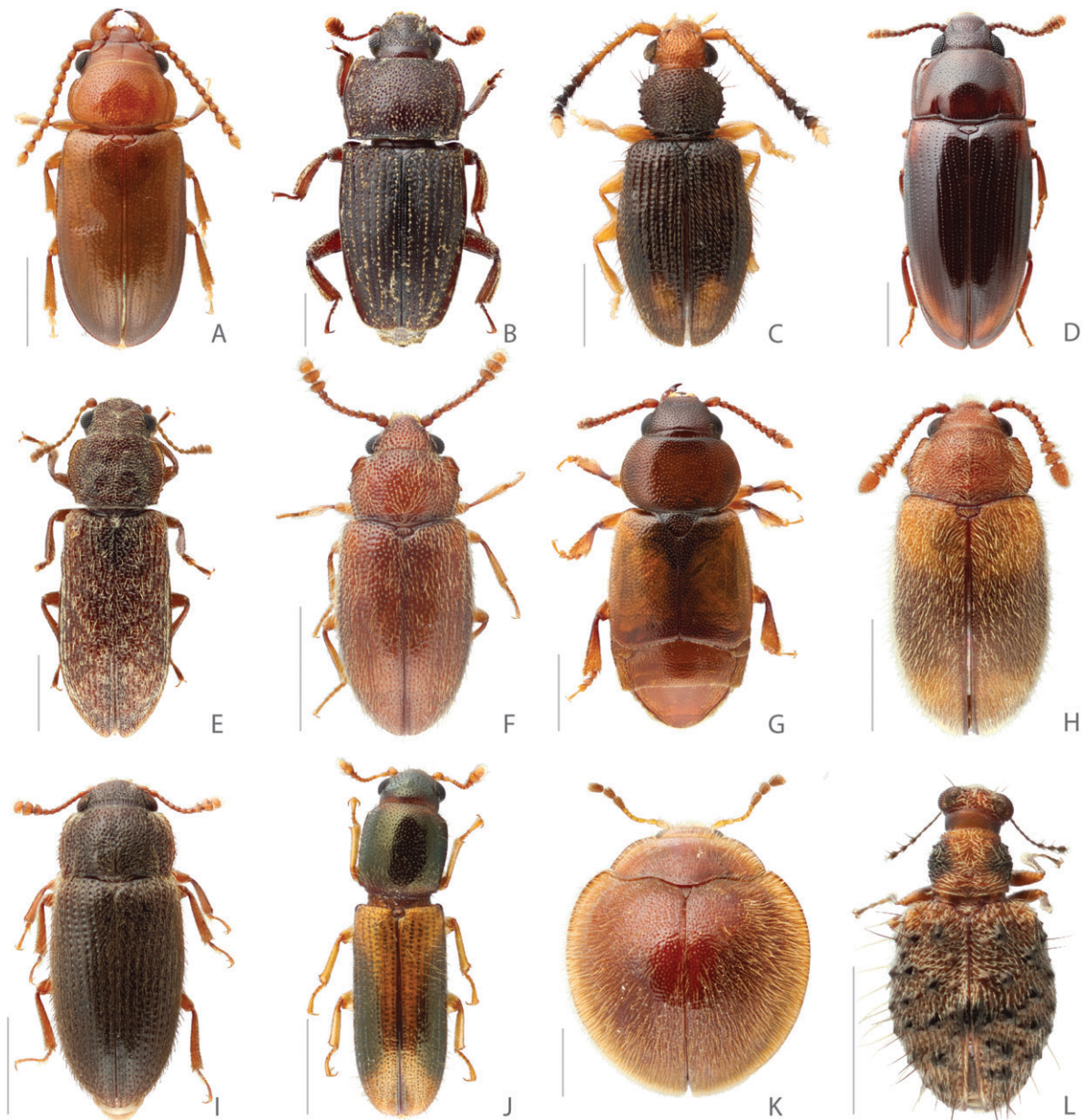


Fig. 1. Habitus photographs of cucujoid (A–H), cleroid (I) and coccinelloid (J–L) taxa. Taxonomy follows proposed classification introduced in the text. (A) *Paracucujus rostratus* (Boganiidae). (B) *Megauchenia* sp. (Nitidulidae). (C) *Psammoecus* sp. (Silvanidae). (D) *Pharaxonotha* sp. (Erotylidae). (E) *Ericmodes sylvaticus* (Protocucujidae). (F) *Cryptophagus* sp. (Cryptophagidae). (G) *Anthonaeus agavensis* (Kateretidae). (H) *Hobartius* sp. (Hobartiidae). (I) *Diplocoelus* sp. (Biphylidae). (J) *Teredolaemus* sp. (Teredidae **stat.n.**). (K) *Bystus* sp. (Anamorphidae **stat.n.**). (L) *Bicava* sp. (Latridiidae). Scale bars = 1 mm. Photos by JAR.

to the weevils (Curculionoidea); and the CS were supported as the sister group to the remaining cucujiform lineages.

Lawrence *et al.* (2011) conducted a monumental phylogenetic study of Coleoptera based on 516 adult and larval morphological characters, and 359 taxa representing 165 beetle families and 314 subfamilies. Their analysis recovered a grossly polyphyletic Cucujoidea with taxa classified as Cucujoidea recovered in five different clades within Cucujiformia. Surprisingly, the CS was also not recovered as monophyletic.

Cerylonid series

The cerylonid series is a cluster of presumably highly derived families within Cucujoidea (Crowson, 1955) comprising Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, Latridiidae and most recently Akalyptoischiidae (Lord *et al.*, 2010). Together, the CS families comprise 32 subfamilies, 54 tribes (Bouchard *et al.*, 2011; Robertson *et al.*, 2013), 660 genera and nearly



Fig. 2. Photos of cucujoid taxa in their corresponding microhabitats. (A) *Cucujus cinnaberinus* (Cucujidae) (photograph by Siga, Wikimedia Commons). (B) *Stephostethus lardarius* (Latridiidae) (photograph by Pavel Krásenský, used by permission). (C) *Aethina tumida* (Nitidulidae) (photograph by Alex Wild, used by permission). (D) *Philothermus* sp. (Cerylonidae) (photograph by Alex Wild, used by permission). (E) *Bothrideres bipunctatus* (Bothrideridae) (photograph by Walter Pfliegler, used by permission). (F) *Cholovocera* sp. (Endomychidae) (photograph by Luigi Lenzini, used by permission).

10 000 species. It is one of the few hypothesized groupings of Cucujoidea (Sen Gupta & Crowson, 1973; Ślipiński, 1990; Ślipiński & Pakaluk, 1991) that has been consistently shown to form a clade (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Bocak *et al.*, 2014).

Recently, several molecular phylogenetic studies covering higher-level relationships of CS taxa have emerged: Hunt *et al.* (2007), Robertson *et al.* (2008) and Bocak *et al.* (2014). Hunt *et al.* (2007) included 21 CS exemplars in their sampling of 320 beetle taxa and recovered the CS as monophyletic. Whereas Hunt *et al.*'s (2007) study indicates that the CS families Endomychidae and Cerylonidae are not monophyletic, most of the inter-familial and subfamilial clades of the series were not resolved (see fig. S2 therein). Noteworthy CS internal relationships that were recovered in their study include a

sister grouping of Corylophidae and the endomychid subfamily Merophysiniinae (as Holoparamecinae). Hunt *et al.* (2007) also recovered a well-supported clade comprising Bothrideridae, Cerylonidae and Discolomatidae (although Bothrideridae and Cerylonidae were not recovered as monophyletic) that forms the sister group to the remaining CS taxa.

The monophyly of the CS was also supported by Robertson *et al.* (2008), the first molecular phylogenetic analysis to focus solely on CS relationships. Robertson *et al.* (2008) sampled two nuclear genes, *18S* and *28S* for 61 CS taxa, representing seven of the nine families and roughly half of the CS subfamilies. This study also supported the monophyly of many CS families and subfamilies, while revealing the paraphyletic nature of some higher-level taxa, including Endomychidae, potentially Latridiidae, and multiple subfamilies recognized at that time

(e.g. Corylophinae s.s., Chilocorinae, Scymninae). Nonetheless, it should be noted that the analysis of Robertson *et al.* (2008) lacked many key taxa, thus the monophyly and the internal relationships of multiple CS taxa remain equivocal. Although recovered as monophyletic, the tests of monophyly for the families Cerylonidae, Bothrideridae and Corylophidae were weak due to the small and unrepresentative taxon sampling included for these taxa. Notable internal relationships recovered by Robertson *et al.* (2008) include a sister grouping of the endomychid subfamily Anamorphinae with Corylophidae, and this clade forms a trichotomy with Coccinellidae and the clade comprising the remaining Endomychidae. The results of Robertson *et al.* (2008) also indicate a close affiliation of Bothrideridae, Cerylonidae and Discolomatidae.

Bocak *et al.* (2014) were the first to sample all of the CS families (with *Akalyptoischion* Andrews treated as Latridiidae). Key results of Bocak *et al.* (2014) include several novel hypotheses of relationships and monophyly for groups within the CS. For example, Bocak *et al.* (2014) recovered all CS families as monophyletic except for Bothrideridae, which were paraphyletic with respect to Discolomatidae and Cerylonidae. Endomychidae were supported as the sister group to Corylophidae, and Alexiidae formed the sister group to Coccinellidae.

Taken together, the studies of Hunt *et al.* (2007), Robertson *et al.* (2008) and Bocak *et al.* (2014) suggest a basal dichotomy of two superfamilial CS clades: one clade comprising Bothrideridae, Cerylonidae and Discolomatidae; a second clade including Corylophidae, Coccinellidae Endomychidae and usually Latridiidae. The analysis of Bocak *et al.* (2014) further indicates that Alexiidae and Akalyptoischiidae are also included in the second clade. Nonetheless, with roughly only half of the CS subfamilies represented in the above molecular studies (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Bocak *et al.*, 2014), these hypotheses of CS phylogeny should be taken as preliminary. Indeed, the inclusion of all CS families, subfamilies, and major or enigmatic tribes and genera is needed to clarify the historically problematic relationships among this diverse lineage.

The morphological analysis of Lawrence *et al.* (2011) is the only phylogenetic study to date to not recover a monophyletic CS. Members of the CS family Bothrideridae were recovered in two disparate regions of the topology: *Xylariophilus* Pal and Lawrence (*Xylariophilinae*) and *Teredolaeus* Sharp (Teredinidae) were placed among the main cluster of non-CS cucujoids sister to Monotomidae; *Bothrideres* Dejean (Bothriderinae) was recovered sister to Passandridae, forming a clade that subtends Phytophaga. *Hypodacnella* Ślipiński (Cerylonidae) + *Bystus* Guérin-Méneville (Endomychidae) was recovered as a sister grouping within a small, isolated cucujiform clade including the cucujoid families Phalacridae, Cavognathidae and Myraboliidae. The above placements of CS taxa are unexpected, not consistent with traditional views and warrant further investigation.

Here we present a large-scale molecular phylogeny of Cucujoidea with an emphasis on the CS based on the most comprehensive dataset of Cucujoidea to date. We test the monophyly of the superfamily Cucujoidea with respect to the remaining cucujiform lineages. We also test the monophyly of the CS,

CS families, subfamilies and higher taxa. We investigate the placement of the CS within Cucujoidea and attempt to clarify family relationships within Cucujoidea. Using a denser taxonomic sampling, we investigate the higher-level relationships within the CS and each of the CS families. Finally, we use our results to present a revised higher-level classification within Cucujiformia.

Materials and methods

Taxon sampling

The terminal taxa used in this study are listed in Table S1. This sampling includes 384 taxa representing all six superfamilies of Cucujiformia, 35 of the 37 families of Cucujoidea (including all nine CS families), 26 of the 32 CS subfamilies and nearly 300 genera. The two missing cucujoid families are Tasmosalpinae (two species) and Lamingtoniidae (three species), both of which are monotypic, rarely collected taxa restricted to Tasmania and other select regions of Australia. Given the likelihood of Cucujoidea not being monophyletic (Leschen *et al.*, 2005; Hunt *et al.*, 2007; Robertson *et al.*, 2008; Lawrence *et al.*, 2011; Bocak *et al.*, 2014), we attempted to include sufficient representation of the remaining superfamilies of Cucujiformia in order to provide a rigorous test of monophyly for this superfamily. We sampled within Tenebrionoidea (15 exemplars representing 12 families), Cleroidea (13 exemplars representing 6 families), Chrysomeloidea (8 exemplars representing 4 families), Curculionoidea (10 exemplars representing 7 families) and Lymexyloidea (1 exemplar). Seven beetle taxa outside Cucujiformia – representing Buprestoidea, Dascilloidea, Derodontoidea, Elateroidea and two Caraboidea (Adephaga), *Calosoma* Weber (Carabidae) and *Macrogyrus* Régimbart (Gyrinidae) – were included as distant outgroups. Our sampling throughout the CS is particularly extensive, with 271 exemplars including 27% of the known generic diversity (181 of 660 genera represented). To the extent possible, sampling within each CS family is commensurate with lineage and species diversity, and is as follows. Akalyptoischiidae: three exemplars (monogeneric, 100% generic representation); Alexiidae: two species (monogeneric, 100% generic representation); Bothrideridae: 21 species, 12 of 38 genera included (32% generic representation); Cerylonidae: 28 species, 14 of 52 genera included (27% generic representation); Coccinellidae: 87 species, 70 of 360 genera included (19% generic representation); Corylophidae: 39 species, 16 of 27 genera included (59% generic representation); Discolomatidae: seven exemplars, 4 of 16 genera included (25% generic representation); Endomychidae: 63 species, 41 of 135 genera included (30% generic representation); and Latridiidae: 23 species, 16 of 29 genera included (55% generic representation). Five CS subfamilies are not represented in the current analysis: Notiophyginae, Pondonatinae and Cephalophaninae (Discolomatidae), and Danascelinae and Xenomycetinae (Endomychidae). Although these represent enigmatic taxa, particularly the endomychids, we were unable to obtain molecular-grade specimens due to their rarity.

Authorship and publication dates for most family group names follow Bouchard *et al.* (2011) and Lawrence & Newton (1995).

Molecular sampling and techniques

Specimens used in this study were collected into 100% EtOH and stored at -80°C . Techniques and protocols associated with specimen dissection and vouchering, follow that outlined in Robertson *et al.* (2004, 2013). For each specimen the abdomen was carefully disarticulated from the metathorax and the remainder of the specimen (head and thorax intact) was used for the clearing process during the genomic DNA extraction procedure. Once cleared, the specimen was retained with the intact abdomen in 100% EtOH. Genomic DNA was extracted using the Qiagen DNeasy tissue kit (Valencia, CA). Voucher specimens are deposited in: the University of Georgia Coleoptera Tissue Collection (UGCA), Athens, GA, U.S.A. (most); the Brigham Young University Insect Genomics Collection (BYU IGC), Provo, UT, U.S.A.; the Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, CA, U.S.A. [CO477 *Reveliera californica* Fall, CO488 *Dienerella intermedia* Belon, CO902 *Oxylaemus californicus* Crotch, CO905 *Deretaphrus oregonensis* Horn, CO931 *Mychocerus discretus* (Casey), CO934 *Aenigmaticum californicus* Casey]; and the Australian National Insect Collection (ANIC), CSIRO, Canberra, Australia (ccoc_234 *Boganiium* Sen Gupta and Crowson).

We sampled eight genes in this study: nuclear 18S rRNA (*18S*), 28S rRNA (*28S*), histone subunit 3 (*H3*) and carbamoyl-phosphate synthetase (CPS locus of *CAD*), and mitochondrial 12S rRNA (*12S*), 16S rRNA (*16S*), cytochrome-c oxidase subunit I (*COI*) and cytochrome-c oxidase subunit II (*COII*). The nuclear gene Arginine kinase (*ArgK*) was also initially sampled but was found to have paralogous copies and was thus not included in the present analysis. Primers and protocols for the amplification and sequencing of target genes are outlined in Robertson *et al.* (2013). Product yield, specificity, and potential contamination were monitored by agarose gel electrophoresis. PCR products were purified using MANU 96-well filtration plates, sequenced using BigDye Terminator v3.1 (Applied Biosystems, Foster City, CA) on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA). DNA fragments were sequenced in both directions with sufficient overlap to ensure the accuracy of sequence data. Assembly of sequence fragments and editing of contig sequences was performed in Sequencher 4.2.2 (Gene Codes Corp., Ann Arbor, MI). All resulting nucleotide and AA (protein encoding genes) sequences were BLASTed prior to use in this study. Sequences generated in this study are deposited on GenBank under the accession numbers KP828836-KP829929 and KR351312-KR351323. Gene coverage for the 384 terminal taxa included herein is presented in Table S1 but summarized as follows [gene: # of terminals for which gene is sampled]: *18S*: 380; *28S*: 380; *H3*: 247; *CAD*: 184; *12S*: 338; *16S*: 312; *COI*: 356; *COII*: 313. In general, terminal taxa were included in the analysis if three or more markers were available with one of those being either *18S* or *28S*. The two exceptions to

this criterion are *Periptyctus* Blackburn (*28S* only) and *Carinodulinka* Ślipiński & Tomaszewska (*COI* and *COII* only); both represent important genera with phylogenetic placement previously well established (Ślipiński *et al.*, 2009; Seago *et al.*, 2011; Robertson *et al.*, 2013).

Sequence alignment

The protein encoding genes *H3* and *COI* were length-invariant; thus alignment of these genes was trivial, based on conservation of amino acid (AA) reading frame. Both *COII* and *CAD*, however, contained a length-variable region in the coding sequence. Using Mesquite 2.75 (Maddison & Maddison, 2011), *CAD* and *COII* were translated into AA sequence and aligned using MUSCLE (Edgar, 2004) as implemented in Mesquite. The *CAD* and *COII* nucleotide sequences were then aligned via Mesquite to match the aligned AA sequences. Alignment of ribosomal genes was achieved using the MAFFT 6.5 webserver (Katoh & Toh, 2008) (<http://align.bmr.kyushu-u.ac.jp/mafft/online/server>) using the G-INS-i search strategy. Owing to their longer length, *18S* and *28S* were each spliced into three regions prior to alignment in an effort to facilitate more efficient alignment, minimize computational constraints and to accommodate gapped or otherwise incomplete sequences. Resulting alignments were visually inspected to check for ambiguously aligned regions and alignment artifacts. Four length-variable regions in *28S* were found to contain obvious alignment artifacts (most often caused by one to several sequences containing a large expansion region) and were each realigned using MAFFT as described above. In both the *18S* and *28S* alignments multiple length-variable regions remained ambiguously aligned and were removed from the alignment and excluded from further analysis. In total, 308 and 1079 characters were removed from the *18S* and *28S* alignments, respectively.

Phylogenetic inference

We used PartitionFinder 1.0.1 (Lanfear *et al.*, 2012) to simultaneously select the best-fit partitioning scheme and the corresponding nucleotide substitution models for our data. The data were initially partitioned with ribosomal markers partitioned by gene- and protein-encoding genes partitioned by codon position. The analysis was run using a greedy search scheme (search = greedy), with all models considered (models = all) using the Akaike information criteria (AIC). Alignments of the individual markers were concatenated using Sequence Matrix 1.7.8 (Vaidya *et al.*, 2011) and subsequent analyses were performed using this combined dataset using maximum-likelihood inference (ML). Heuristic ML searches were performed using the program RAXML (Stamatakis *et al.*, 2005) hosted on the Cipres Science Gateway (Miller *et al.*, 2010) (www.phylo.org/). Initial RAXML analyses were executed for each gene to monitor potential contamination and assess gene performance. We performed RAXML rapid bootstrapping with a subsequent ML search (Stamatakis *et al.*, 2006, 2008) executing 500

bootstrap inferences using a GTR + Γ model [as recommended in Stamatakis *et al.* (2008; the RAxML 7.0.3 manual)]; we additionally implemented these analyses using a GTR + Γ + I model (the best fit model for the data). We performed the RAxML analyses on the concatenated data both as unpartitioned (a single subset and model) and as partitioned (using the data subsets and models suggested by PartitionFinder). Four independent analyses for each partition/model regime were performed on the combined molecular dataset to ensure convergence.

Results

Sequence partitioning and models

PartitionFinder subdivided the data into four subsets as follows: (1) 18S and 28S combined; (2) 12S and 16S combined; (3) CAD codon positions 1–3, H3 codon positions 1–3, COI codon positions 1–2, COII codon positions 1–2; (4) COI codon position 3, COII codon position 3. Each of the four subsets of data best fitted the GTR + Γ + I model of evolution. Running the analyses without the highly variable third codon position of mitochondrial markers COI and COII (i.e. subset 4) resulted in a very similar but overall better-supported topology (indicating that the third codon position of COI and COII was mostly contributing noise), thus this subset was excluded from further analysis. Concatenation of the three remaining subsets yielded a matrix of 8260 nucleotides, 4714 of which were informative.

Phylogenetic results

The ML analyses implementing the varying model (GTR + Γ vs GTR + Γ + I) and partitioning strategies (undivided vs. divided into subsets/partitions) resulted in very similar topologies differing only in the resolution of a few clades (e.g. Hobartiidae + Boganiidae relative to the Nitidulidae group and/or the clade comprising Helotidae, Erotylidae and allies) and placement of select taxa (e.g. Phloiophilidae placed sister to Biphylidae + Byturidae). The ML analyses using a partitioned dataset and GTR + Γ scheme produced a tree that although very similar to the topologies resulting from the remaining schemes, contained two aberrant placements of taxa: the nitidulid series was recovered as the sister group of Phytophaga, and Boganiidae and Hobartiidae were not recovered as sister taxa.

In general, much of the tree is characterized by moderately long terminal branches with relatively short internal branches comprising the backbone of the tree. This general pattern is consistent with other broad-scale, molecular phylogenetic studies of Coleoptera (McKenna & Farrell, 2009; McKenna, 2014; McKenna *et al.*, 2014). Not surprisingly, low branch support often corresponds to several major divergences comprising short branches along the backbone of the topology, whereas major clades are in general strongly supported. When discussing support for clades of interest below, the relevant ML bootstrap value is listed in parentheses.

Of the six superfamilies of Cucujiformia, only Curculionoidea and Chrysomeloidea were recovered as monophyletic in the present study. The monophyly of Lymexyloidea was not tested in the present analysis because only one exemplar was included. Tenebrionoidea were paraphyletic with respect to Lymexyloidea; although the grouping of these two superfamilies was well supported, the nesting of Lymexyloidea within Tenebrionoidea was only weakly supported. Byturidae and Biphylidae were strongly supported as the sister group of Cleroidea. The superfamily Cucujoidea was polyphyletic. Chrysomeloidea and Curculionoidea were recovered as sister taxa and this clade (Phytophaga) formed the sister group to the non-CS cucujoids (core Cucujoidea). The nitidulid series was recovered as the earliest-diverging core cucujoid lineage, although the earliest divergences among core Cucujoidea were only weakly supported.

The CS was recovered as monophyletic and was supported as a major Cucujiform clade, sister group to the remaining superfamilies of Cucujiformia. The CS families Discolomatidae, Corylophidae, Coccinellidae and Latridiidae were recovered as monophyletic. Bothrideridae were paraphyletic with respect to Cerylonidae and Discolomatidae; Cerylonidae were paraphyletic with respect to Bothrideridae (Anommatae, Teredinae, Xylariophilinae) and Discolomatidae; the latter was recovered as the sister group to *Murmidius* Leach. Endomychidae were not recovered as monophyletic due to the placement of Mycetinae and Eupsilobiinae closely allied to Coccinellidae, and the recovery of Anamorphinae as sister to Corylophidae. Akalyptoischiidae (*Akalyptoischion*) were not allied with Latridiidae and were supported as a distinct family within the CS. CS subfamilies not supported as monophyletic include Teredinae (Bothrideridae), Endomychinae (Endomychidae) and Stenotarsinae (Endomychidae).

Discussion

Major cucujiform lineages

Phylogenetic studies that specifically address the major cucujiform relationships are lacking (Leschen & Ślipiński, 2010). However, molecular studies treating the phylogenetic relationships of specific subgroups of Cucujiformia (Robertson *et al.*, 2008; Marvaldi *et al.*, 2009; McKenna *et al.*, 2009; Kergoat *et al.*, 2014) or Coleoptera as a whole (Hunt *et al.*, 2007; Bocak *et al.*, 2014) provide myriad hypotheses and arrangements of cucujiform taxa. In fact, there is little consensus regarding the major divergences within Cucujiformia between these studies. Given the anatomical heterogeneity, varied taxonomic history and recent phylogenetic analyses of Cucujoidea (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Marvaldi *et al.*, 2009; McKenna *et al.*, 2009; Bocak *et al.*, 2014; Kergoat *et al.*, 2014), the failure to recover this superfamily as monophyletic in the present study is not surprising. Taxa currently classified as Cucujoidea were recovered in three isolated, well-supported clades (Fig. 3): (i) the CS was strongly supported as the sister group to the remaining Cucujiformia, (ii) Byturidae and Biphylidae were strongly

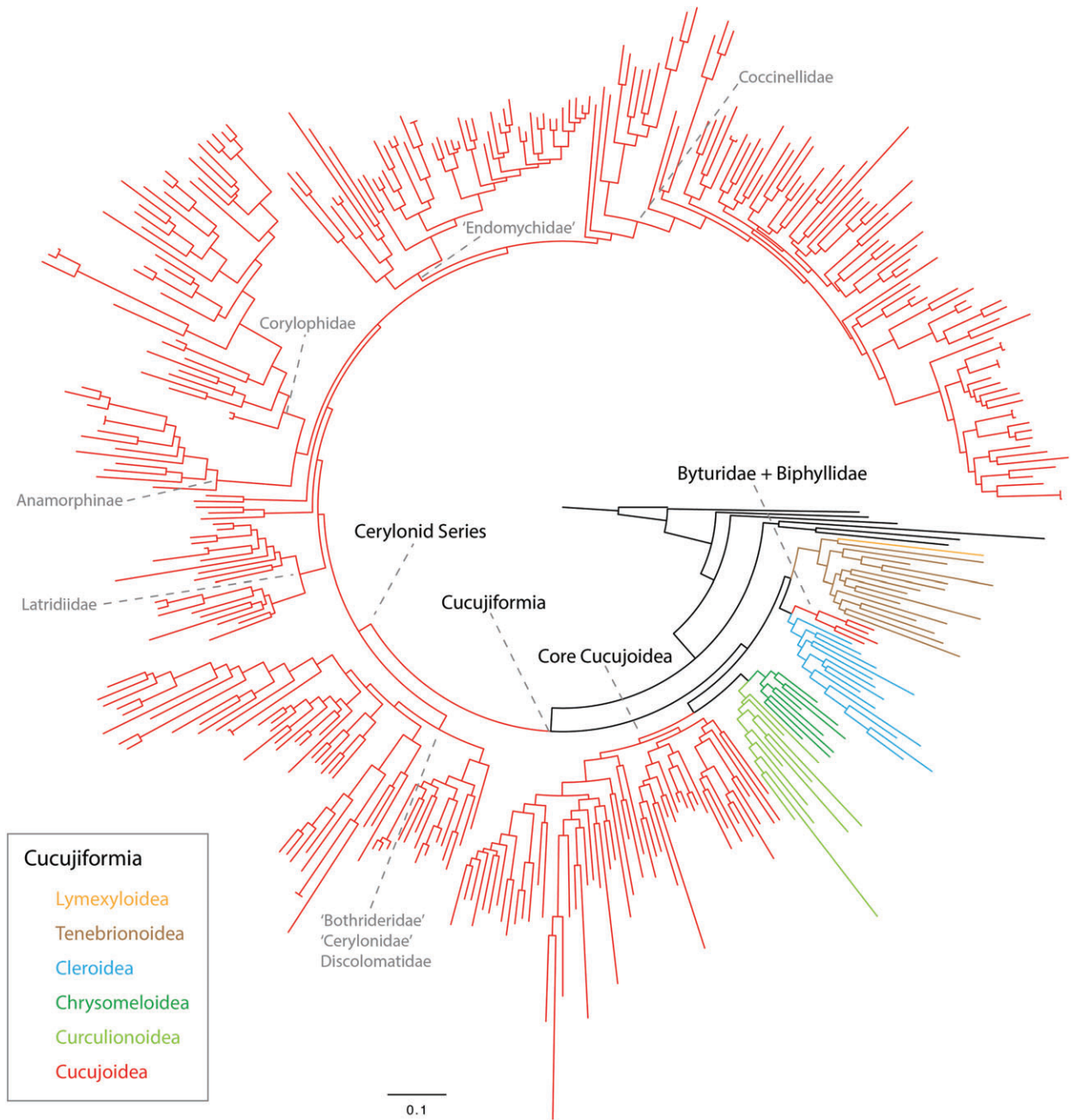


Fig. 3. Maximum-likelihood tree illustrating the polyphyly of Cucujoidea. Cucujiform superfamilies are coloured following the inset. Byturidae and Biphyllidae are recovered sister to Cleroidea, the core Cucujoidea forms the sister group to Phytophaga and the Cerylonid Series forms the sister group to the remaining cucujiform lineages. Major Cerylonid Series lineages are labelled in grey.

supported as the sister group of Cleroidea, (iii) the remaining ‘basal cucujoid’ families, or core Cucujoidea, formed a clade sister to Phytophaga (Chrysomeloidea + Curculionoidea). Leschen *et al.*’s (2005) designation of ‘basal Cucujoidea’ was not meant as a hypothesis of monophyly but was more of an informal grouping of convenience, thus it is interesting that most of these families did in fact form a monophyletic group in the present study.

The megadiverse Phytophaga were strongly supported as the sister group to the core Cucujoidea (90). Among previous large-scale molecular studies, this sister grouping was supported only in the study of Marvaldi *et al.* (2009), even though Crowson (1960) implied a close relationship of these major groups when he suggested that the chrysomeloid–curculionoid stock might be an offshoot of the cucujoid stock. In all our analyses, Tenebrionoidea (including Lymexyloidea) and

Cleroidea (including Byturidae and Biphyllidae) were recovered as sister taxa; however, bootstrap support for this sister grouping was consistently low (<50). A sister grouping of Tenebrionoidea + Cleroidea represents a novel hypothesis for cucujiform superfamilial relationships. The strongly supported position of the CS forming the sister group to the remaining Cucujiformia and therefore being distantly related to the remaining core cucujoid taxa explains why Crowson (1955) considered this clade 'highly derived' compared to the other cucujoid families. Interestingly, within Cucujoidea the CS is the only subgroup that has been repeatedly hypothesized to form a clade, when in fact the CS is not even part of Cucujoidea (see below).

Tenebrionoidea and Lymexyloidea

Our sampling within the diverse superfamily Tenebrionoidea is not extensive, with only 11 of 28 families (Bouchard *et al.*, 2011) represented. Furthermore, topological support among tenebrionoid lineages was generally low, as in other studies to date (Haran *et al.*, 2013; Gunter *et al.*, 2014; Kergoat *et al.*, 2014). However a few noteworthy results recovered herein bear upon tenebrionoid relationships and should be noted. Lymexyloidea were recovered as the sister group to Mordellidae, albeit with weak support (<50) (Fig. 4). Although the placement of Lymexyloidea nested within Tenebrionoidea was somewhat unexpected, Hunt *et al.* (2007) also recovered this placement for Lymexyloidea in their study. The clade comprising Lymexyloidea and Tenebrionoidea was well supported (93); thus, despite the unconvincing nodal support for the nesting of Lymexyloidea within Tenebrionoidea, our results suggest that these two superfamilies at least form a clade together, possibly as sister taxa as suggested by Bocak *et al.* (2014) and Gunter *et al.* (2014).

Cleroidea

The placement of Biphyllidae and Byturidae has challenged coleopterists historically. These taxa have been considered allied with Cucujoidea (Crowson, 1955; Ślipiński & Pakaluk, 1991; Leschen *et al.*, 2005), Tenebrionoidea (Crowson, 1960; Lawrence, 1977) and Cleroidea (Lawrence & Newton, 1995; Hunt *et al.*, 2007; Bocak *et al.*, 2014). Despite their current classification within Cucujoidea, the placement of Biphyllidae and Byturidae within Cleroidea has been repeatedly demonstrated in recent molecular phylogenetic studies (Hunt *et al.*, 2007; Bocak *et al.*, 2014) and in the present one (Fig. 4). Furthermore, this placement is supported by a number of morphological features, the most characteristic being the nature of the aedeagus, which in a number of cleroids – as well as Biphyllidae and Byturidae – includes a tegmen of the 'double' type (Crowson, 1964a) with paired tegminal struts in addition to the common anterior strut. Given the overwhelmingly strong evidence for Biphyllidae and Byturidae belonging to Cleroidea, we formally transfer both families to Cleroidea **s.n.**

Our taxonomic sampling within Cleroidea was moderately strong, with 6 of the 11 families represented. Phloiophilidae

were supported as an early diverging cleroid lineage (Fig. 4), consistent with previous views (Crowson, 1960). Phloiophilidae were alternatively recovered as the sister group to Biphyllidae + Byturidae in the partitioned GTR + Γ + I analysis. Crowson (1955) outlined the similarities of Biphyllidae and *Phloiophilus* Stephens including the nature of the metendosternite and a fungivorous life history, and suggested that Phloiophilidae may in fact represent Cucujoidea rather than Cleroidea. Interestingly, *Xerasia* Lewis (Byturidae) was included in the family Phloiophilidae by Pic (1926) (see also Crowson, 1955). Several larval features are unique to Biphyllidae, Byturidae and Phloiophilidae including frontal arms lyriform (V- or U-shaped in most remaining Cleroidea), maxillary articulating area present (absent in most remaining Cleroidea), and having the inner apical angle of mandible with one or more teeth (character states from Lawrence & Leschen, 2010; Lawrence *et al.*, 2011). Trogossitidae is an enigmatic and morphologically heterogeneous family with a convoluted taxonomic history rich with rank changes depending on the author (see Kolibáč & Leschen, 2010). Crowson (1964a) considered the family to have diverged relatively early from the remaining cleroid lineages and further (1964a, 1966, 1970) elevated the rank of several subfamilies, leading to the recognition of three separate families: Trogossitidae, Peltidae, Lophocateridae. Recent molecular analyses also indicate that the family Trogossitidae as currently circumscribed is not monophyletic (Hunt *et al.*, 2007; Gunter *et al.*, 2013; Bocak *et al.*, 2014). The results of the present study corroborate the above hypotheses with *Ostoma* Laicharting, *Temnoscheila* Westwood, *Grynocharis* Thomson and *Larinius* Carter and Zeck scattered among the remaining sampled cleroids (Fig. 4), indicating that this family is not monophyletic and is in critical need of a thorough phylogenetic revision. Other internal cleroid relationships recovered in the present study, including Prionoceridae recovered as the sister group to Melyridae (including *Dasytes* Paykull) and the melyrid lineage closely allied to Cleridae, are consistent with the results of Gunter *et al.* (2013).

Phytophaga

Consistent with previous studies (e.g. Farrell, 1998; Marvaldi *et al.*, 2009; McKenna *et al.*, 2009) the phytophagan superfamilies Chrysomeloidea (60) and Curculionoidea (60) were recovered with only weak to moderate support in the present study (Fig. 4). Our analysis also provided weak support for the monophyly of Phytophaga (Chrysomeloidea + Curculionoidea) (<50). Although the monophyly of Phytophaga is not questioned from a morphological and ecological standpoint, several recent large-scale molecular analyses (e.g. Hunt *et al.*, 2007; Bocak *et al.*, 2014) have surprisingly failed to recover Phytophaga as monophyletic. The weak support for Phytophaga, Chrysomeloidea and Curculionoidea in the present study, may be attributed to the inadequacy of the suite of molecular loci used herein for recovering these divergences, terminals jumping around (potential rogue taxa), the relatively sparse taxon sampling within these megadiverse taxa, and/or short internal

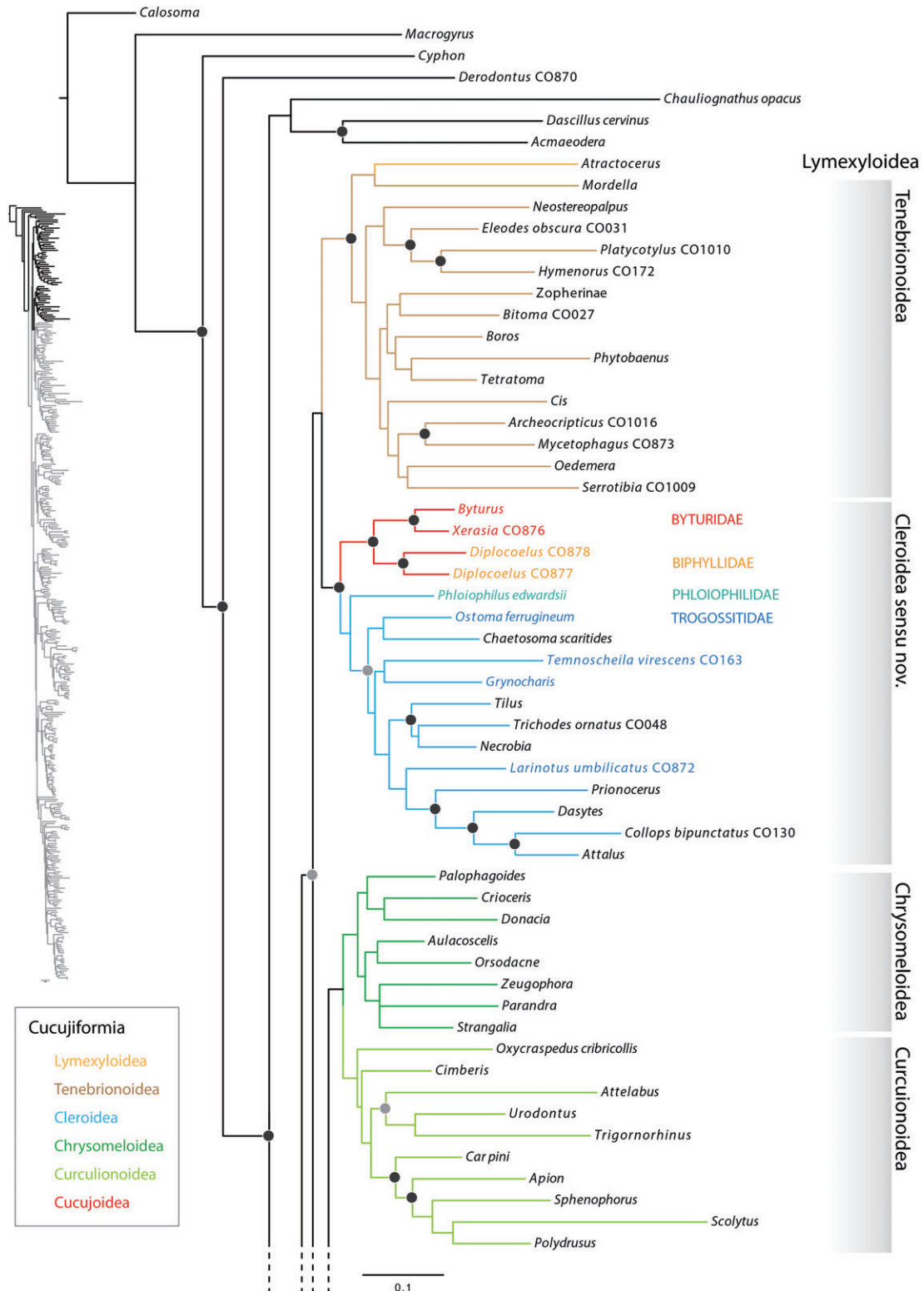


Fig. 4. Maximum-likelihood tree (part 1 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured by superfamilial classification prior to this study following the legend. Select families are coloured as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

branches spanning the divergences of these major radiations comprising relatively long terminals.

Early diverging core Cucujoidea

The early diverging lineages of core Cucujoidea recovered in the present study include three major clades: (i) Monotomidae + nitidulid series, (ii) erotyloid series (Helotidae-Protocucujidae-*Protosphindus* Sen Gupta & Crowson-Erotylidae), (iii) Boganiidae + Hobartiidae (see Fig. 5); all three lineages comprise taxa that have been considered as early diverging cucujoids and plesiomorphic from a morphological perspective (Crowson, 1955, 1960, 1990). For example, Crowson (1955) postulated that Nitidulidae, Smicripidae and Monotomidae were closely related to Protocucujidae and Sphindidae based on anatomical characters of the adult form. He considered Protocucujidae to represent the most plesiomorphic form of extant cucujoids. Crowson (1990) also suggested a potential relationship between Boganiidae and Chrysomeloidea. This hypothesis was based on both having distinctive microsculpture on the hindwing of the adult and an articulated mala in the larval form; the fossil *Parandrexia* Martynov representing a putative intermediate form between boganiids and chrysomeloids bolstered his suspicion. Whereas the previous major clades comprise the early diverging core cucujoid lineages in the present study, their relative position at the base of core Cucujoidea was unstable across analyses as reflected in the weak nodal support spanning these three clades. Based on the present analysis and patterns of support, any one of the above three lineages (Monotomidae + nitidulid series, erotyloid series, Boganiidae + Hobartiidae) represents a viable candidate for the earliest diverging lineage of core Cucujoidea. At present, additional data are needed to identify the earliest diverging core cucujoid lineage.

Nitidulid series and Monotomidae

Members of the Nitidulidae group (Leschen *et al.*, 2005) – or nitidulid series – including Kateretidae, Smicripidae and Nitidulidae, formed a monophyletic group, albeit with only weak support (<50) (Fig. 5). Whereas morphology strongly supports this grouping (Leschen *et al.*, 2005; Jelínek *et al.*, 2010; Cline, 2010; but see also Lawrence *et al.*, 2011 for an exception), the present study is the first phylogenetic analysis based on molecular data to recover a monophyletic nitidulid series; previous studies did not include sufficient representation of the series, or did not recover it as monophyletic (Hunt *et al.*, 2007; Bocak *et al.*, 2014). Hunt *et al.* (2007) only sampled Nitidulidae in their three-gene analysis. Their taxon-heavy analysis of 18S data alone also included several exemplars of Kateretidae, but these were not recovered as a monophylum with Nitidulidae; rather, Kateretidae was placed within Phytophaga, allied with Cerambycidae and Silvanidae (Hunt *et al.*, 2007). Bocak *et al.*'s (2014) analysis recovered a sister grouping of Kateretidae and Nitidulidae, but the family Passandridae was

nested within the latter, rendering Nitidulidae paraphyletic. The study of Cline *et al.* (2014) focused on the higher-level relationships within Nitidulidae and recovered a well-supported clade comprising Kateretidae + Nitidulidae. The enigmatic and monotypic family Smicripidae was not represented in Hunt *et al.* (2007), Bocak *et al.* (2014) nor Cline *et al.* (2014). Lawrence *et al.* (2011), based on morphological data, did recover a sister grouping of Kateretidae + Nitidulidae, but *Smicrips* LeConte was far removed, recovered as the sister group to *Rentonellum* Crowson (Cleroidea: Trogossitidae) which, in turn, was sister to Laemophloeidae + Propalticidae. Although *Smicrips* is an enigmatic taxon, this poorly supported grouping with *Rentonellum* and others is not consistent with traditional views (Cline, 2010).

Nitidulidae is among the more ecologically diverse and species-rich families of Cucujoidea with *c.* 4500 species classified in *c.* 351 genera (Jelínek *et al.*, 2010). In contrast, Kateretidae and Smicripidae exhibit meagre to poor species diversity with *c.* 95 and six species, respectively (Cline, 2010; Jelínek & Cline, 2010). Historically there has been much debate regarding the internal relationships both among, and within, the families of the nitidulid series, with considerable taxonomic instability among taxa variously classified within these families. As reviewed by Cline (2010), major suites of characters support all three possible sister-group relationships between Nitidulidae, Smicripidae and Kateretidae. Our results support a sister grouping of Nitidulidae and Kateretidae (78) with *Smicrips* subtending this clade.

Monotomidae was weakly supported (<50) as the sister taxon to the nitidulid series (Fig. 5), another relationship formally recovered for the first time in the present study yet consistent with previous views (e.g. Crowson, 1955). Monotomidae are an enigmatic group with dubious phylogenetic affinity within Cucujoidea. Crowson (1955) noted the similarity of Monotomidae and the nitidulid group based on shared adult anatomical features including aedeagus uninverted and of the cucujoid type, elytra truncate, and procoxae transverse with the trochantin exposed. The phylogenetic position of Monotomidae remained dubious in the analysis of Leschen *et al.* (2005) based on adult and larval characters. In both Hunt *et al.* (2007) and Bocak *et al.* (2014) Monotomidae are allied with Protocucujidae and Helotidae, the former representing another family cited by Crowson (1955) as potentially allied with Monotomidae based on the form of the metendosternite and male tarsi (5-5-4). The well-supported yet aberrant placement of Monotomidae in Lawrence *et al.* (2011) as the sister group to teredine and xylariophiline Bothriideridae is likely a result of convergent general similarity in body shape and form (JAR, NPL, personal observation). It should be noted that only two exemplars of Monotomidae, *Lenax* Sharp and *Bactridium* Kunze (Monotominae), were sampled in the present study. A sister grouping of Monotomidae + the nitidulid series is supported by multiple character states including abdominal tergite VII exposed in dorsal view and tergite VIII in the male with sides curved ventrally forming a genital capsule (Leschen *et al.*, 2005; Jelínek *et al.*, 2010). Given the lack of support and consensus with the current suite of morphological and molecular data, it is clear

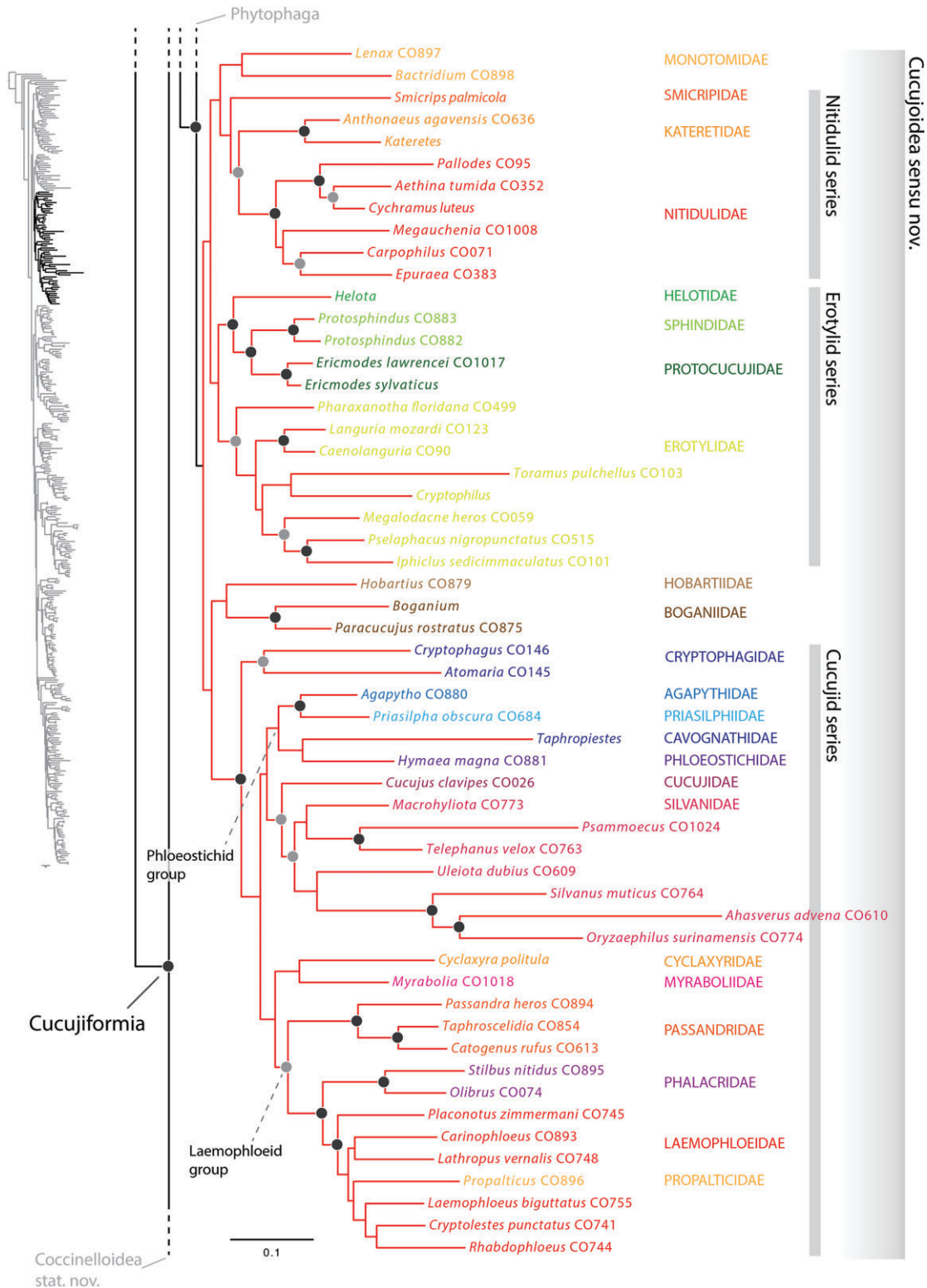


Fig. 5. Maximum-likelihood tree (part 2 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured red for Cucujoidea following the legend in the previous figures. Families are coloured as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

that more work is needed to clarify the phylogenetic position of Monotomidae.

Erotylid series: Helotidae, Protocucujidae, Sphindidae and Erotylidae

The sister grouping of *Ericmodes* Reitter (Protocucujidae) and *Protosphindus* (Sphindidae) is strongly supported in the present study (97) (Fig. 5). A close relationship of these taxa has long been recognized (Crowson, 1955; Thomas, 1984b) and is well supported by morphological data (McHugh, 1993; Leschen *et al.*, 2005). Along with *Ericmodes* and *Protosphindus*, *Helota* Maclay has been considered to be a relatively early diverging cucujoid. Helotidae in particular is an enigmatic taxon. The family exhibits several anatomical features that are considered to be plesiomorphic for Cucujiformia. They are the only cucujoids with a complete discrimen and transverse suture (katepisternal suture) on the metaventricle. The family also possess excavate metacoxae that extend laterally to the elytral epipleura in adults and a divided mala in the larval form. Previous authors suspected a close relationship with Nitidulidae, owing to similarities of the aedeagus (Sharp & Muir, 1912) and labrum-epipharynx (Kirejtshuk, 2000). However, to date no formal phylogenetic analysis has supported a sister grouping or close relationship of Helotidae and Nitidulidae; rather, most have recovered Helotidae sister to Protocucujidae and relatively close to Monotomidae and Erotylidae (Leschen *et al.*, 2005; Hunt *et al.*, 2007; Bocak *et al.*, 2014). In the present study, we consistently recovered *Helota* sister to the clade *Ericmodes* + *Protosphindus* with low to moderate support (67), with Erotylidae forming the sister group to this clade. A significant portion of what is now considered Erotylidae was until recently scattered in other families, primarily Languriidae and Cryptophagidae. Accordingly, most of the historical hypotheses for the sister group of Erotylidae included one of these two families. With Languriidae now subsumed within Erotylidae in its entirety (Węgrzynowicz, 2002; Leschen, 2003; Robertson *et al.*, 2004) including the former cryptophagids that linked Erotylidae to Cryptophagidae, few sister-group hypotheses for Erotylidae have been proposed recently. Previous molecular data point to Erotylidae being closely related to Protocucujidae, Helotidae and Monotomidae (Hunt *et al.*, 2007; Bocak *et al.*, 2014); surprisingly, Bocak *et al.* (2014) recovered Boganiidae well nested within Erotylidae, a hypothesis neither consistent with traditional views nor the present study.

Boganiidae + Hobartiidae

Boganiidae and Hobartiidae were originally classified together in a broader family concept of Boganiidae (Sen Gupta & Crowson, 1966, 1969a). Lawrence (1991) formally recognized the family Hobartiidae presumably based on the larval form described therein. As reviewed by Tomaszewska & Ślipiński (2010), Hobartiidae and Boganiidae share very few anatomical features and those that are in common are widespread in other

cucujoids and presumed to be plesiomorphic. In Leschen *et al.* (2005) *Paracucujus* Sen Gupta & Crowson and *Hobartiis* Sen Gupta & Crowson were far removed from each other. The present study is the first molecular phylogenetic analysis to include members of both Boganiidae and Hobartiidae. The recovery of these taxa forming a sister group (Fig. 5) is therefore intriguing, yet this relationship is only weakly supported (<50) and warrants further investigation.

Cucujid series

We recovered a strongly supported clade (95) comprising Cryptophagidae and the remaining core cucujoid families (Fig. 5). In terms of the families included, this clade is nearly consistent with the cucujid series of Hunt *et al.* (2007) and Bocak *et al.* (2014), although the series is not consistent between those two studies: Hunt *et al.* (2007) does not include Silvanidae in the cucujid series, whereas Bocak *et al.* (2014) does not include Passandridae. Our results strongly supported both Silvanidae and Passandridae included within the cucujid series clade as well as a south temperate clade (see below) comprising Phloeostichidae and allies; these results are consistent with the findings of McElrath *et al.* (2015). The internal relationships within the cucujid series clade recovered in the present study and that published previously (Hunt *et al.*, 2007; Bocak *et al.*, 2014; McElrath *et al.*, 2015) are only partially concordant. In all four analyses Laemophloeidae and Propalticidae form a clade and Phalacridae subsumes this group. The placement and monophyly of the families Cryptophagidae, Cucujidae, Silvanidae, Passandridae and Phloeostichidae and allies vary between studies (see below).

Phloeostichid group

Until recently, the family Phloeostichidae comprised a heterogeneous assortment of Notogean taxa that had been placed previously in a wide variety of families and superfamilies (see Lawrence & Ślipiński, 2010). Leschen *et al.* (2005) demonstrated that this family circumscription did not reflect a monophyletic group and recognized several new, mostly monogeneric, families accordingly, including Agapythidae, Priasilphidae, Tasmosalpingidae and Myraboliidae, leaving four genera in a redefined Phloeostichidae. This study represents the first molecular analysis to include exemplars of these enigmatic, species-poor families. We recovered a weakly supported clade comprising south temperate taxa including *Agapytho* Broun (Agapythidae), *Priasilpha* Broun (Priasilphidae), *Taphropiestes* Reitter (= *Cavognatha* Crowson) (Cavognathidae) and *Hymaea* Pascoe (Phloeostichidae) (Fig. 5). Within this clade *Agapytho* formed the sister group to *Priasilpha obscura* Broun (97); the remaining nodes were only weakly supported. The position of *Taphropiestes* in the present study was unstable. Although *Taphropiestes* was recovered as the sister group of *Hymaea* (<50), it often placed within the clade comprising *Myrabolia* Reitter and *Cyclaxyra* Broun in preliminary analyses. The alternative support for this placement is evident in the poor

branch support along the backbone divergences spanning these alternate placements. Multiple larval features of *Taphropiastes* point to an affiliation with *Myrabolia* and *Cyclaxyra* (see below). The phylogenetic position of Cavognathidae within Cucujoidea has been elusive. When *Cavognatha* was originally described it was attributed to Cucujoidea but was not classified at the family level (Crowson, 1964b), owing to it belonging to an undescribed family. Sen Gupta & Crowson (1966) later described the family Boganiidae and treated Cavognathidae as a subfamily within the newly erected family. Sen Gupta & Crowson (1969a) elevated Cavognathidae to family level and pointed out features suggesting an affiliation with the family Cryptophagidae. Whereas our results do not support an affiliation with Cryptophagidae, this study does support the recognition of Cavognathidae at the family level.

Cucujidae + Silvanidae

Our analyses consistently recovered a sister grouping of Cucujidae + Silvanidae (Fig. 5) with moderate support (78). Both families were at one time classified together with Laemphloeidae and Passandridae in a broadly defined Cucujidae (Cucujidae s.l.). Crowson (1955) recognized at the familial level both Passandridae (with reservation) and Silvanidae, thereby removing them from Cucujidae s.l. The laemphloeids were retained in Cucujidae s.l. for some time later until Thomas (1984a,b, 1993) demonstrated that they were more closely related to passandrids and phalacrids than Cucujidae (Thomas, 1993). To date, no phylogenetic study has supported the monophyly of Cucujidae s.l. (see McElrath *et al.*, 2015). However, multiple studies have shown that Cucujidae and Silvanidae are likely sister taxa (Leschen *et al.*, 2005; McElrath *et al.*, 2015) or otherwise treated them as such (Thomas & Nearn, 2008). Several anatomical features support Cucujidae and Silvanidae as sister taxa (see Leschen *et al.*, 2005). Surprisingly, few molecular studies have supported this sister grouping.

Cucujidae is a relatively small family with 48 species (Thomas & Leschen, 2010a) classified in four genera: *Cucujus* Fabricius, *Pediacus* Shuckard, *Palaestes* Perty and *Platusus* Erichson. An unanticipated result in Bocak *et al.* (2014) was the paraphyly of Cucujidae: *Cucujus* was recovered sister to Silvanidae but *Pediacus* was supported as the sister group to *Cyclaxyra* in that study. It should be noted that only one of four molecular markers was available for the exemplars of *Pediacus* in that analysis, thus it is possible that the significant amount of missing data may have contributed to this surprising result. Even so, the monophyly of Cucujidae has never been the subject of rigorous phylogenetic investigation.

In contrast to Cucujidae, Silvanidae is more species-rich with nearly 500 species placed among 58 genera (Thomas & Leschen, 2010b). The internal classification of Silvanidae currently includes two subfamilies, Silvaninae and Brontinae, with two brontine tribes – Brontini and Telephanini (Thomas, 2003; Thomas & Nearn, 2008). Our results strongly supported the monophyly of Silvaninae (100). This clade was characterized by some of the longest branches in our phylogeny. We did not

recover Brontinae or the tribe Brontini as monophyletic either due to the placement of *Uleiota* Latreille (Brontini) sister to Silvaninae. Branch support for this relationship as well as that for *Macrohyliota* Thomas (Brontini) sister to Telephanini was weak (57, 53, respectively), thus these relationships are only tentative. In a study that focused entirely on the relationships among and within the families formerly included in Cucujidae s.l. (McElrath *et al.*, 2015), support for the monophyly of Brontinae and Brontini between analyses was inconsistent; the ML results of McElrath *et al.* (2015) did not support either Brontinae or Brontini whereas the Bayesian results did recover these higher taxa as monophyletic, albeit with weak support. Thomas & Nearn (2008) conducted a cladistic analysis of the family Silvanidae based on 15 characters of the adult and larval form. Most of their resulting clades were consistent with the existing classification; the monophyly of Brontini, however, was in question. Clearly, additional work is needed to clarify the relationships and limits of higher taxa within Brontinae and refine the classification if necessary.

Cyclaxyra and Myrabolia

The monogeneric family Cyclaxyridae, comprising two species restricted to New Zealand, was until recently (Lawrence *et al.*, 1999) classified within the family Phalacridae, with earlier ties to the families Sphindidae (Crowson, 1955) and Nitidulidae (see Leschen *et al.*, 2010). *Cyclaxyra* was placed sister to Tasmosalpingidae (not sampled here) in Leschen *et al.* (2005), a monotypic family with two Tasmanian species. Despite its previous classification in the family Phalacridae, beyond superficial resemblance including a convex body form, there have been no convincing synapomorphies uniting *Cyclaxyra* and Phalacridae. In the recent cladistic analysis of Phalacridae by Gimmel (2013), *Cyclaxyra* was recovered as the sister group to phalacrids based on several anatomical characters; however, it should be noted that the outgroup sampling in Gimmel (2013) was not extensive because the scope of that study was to infer the internal relationships of Phalacridae. In Lawrence *et al.* (2011) *Cyclaxyra* was recovered as the sister group to Lamingtoniidae (not sampled here), whereas Phalacridae was surprisingly found as the sister to *Hypodacnella* (Cerylonidae) + *Bystus* (Endomychidae). The spurious affiliation of Phalacridae, *Hypodacnella* and *Bystus* in Lawrence *et al.* (2011) is not consistent with previous views (Leschen *et al.*, 2005; Hunt *et al.*, 2007), nor is it consistent with the present study. In our analyses *Cyclaxyra* was consistently recovered as the sister group to *Myrabolia* Reitter (Myraboliidae) (Fig. 5) with weak support (50), a grouping that has never been suggested previously; this study is the first molecular analysis to include exemplars of either family. Myraboliidae represents another species-poor, monogeneric family with 13 species restricted to Australia. The inclusion of *Myrabolia* in multiple cucujoid families historically (e.g. Cucujidae, Silvanidae and Phloeostichidae; see Ślipiński *et al.*, 2010a) reflects the unclear phylogenetic position of this enigmatic genus. In Leschen *et al.* (2005) *Myrabolia* formed the sister group to a large clade comprising several cucujoid

families, whereas in Lawrence *et al.* (2011) it was recovered sister to *Taphropiestes* (= *Cavognatha*). The clade comprising *Myrabolia* and *Cyclaxyra* represents a second Notogean cucujoid lineage supported by the present study (see phloeostichid group above). Interestingly, the clade *Myrabolia* + *Cyclaxyra* forms the sister group to the laemophloeid group. Several larval features corroborate this clade and suggest that *Taphropiestes* may also be affiliated with this superfamilial grouping. The larval form of *Myrabolia*, *Cyclaxyra*, *Taphropiestes* and the laemophloeid group have the mesal surface of the mandible without a mola, the maxillary articulating area absent, and the hypopharyngeal sclerome absent (from Lawrence *et al.*, 2011). Although these larval states represent losses of features, our phylogenetic results suggest that they are likely homologous.

Laemophloeid group

Thomas (1984a) suggested that Laemophloeidae, Propalticidae, Phalacridae and Passandridae form a natural lineage based on a number of morphological features including unequal protibial spurs, structural similarities of the male genitalia, and the presence of pronotal lines and elytral cells. Our results support this grouping (hereafter referred to as the laemophloeid group) (Fig. 5) as the above four families form a clade with moderately high branch support (89). Interestingly, previous molecular (Hunt *et al.*, 2007; Bocak *et al.*, 2014; McElrath *et al.*, 2015) and morphological phylogenetic studies (Leschen *et al.*, 2005; Lawrence *et al.*, 2011) have not recovered the laemophloeid group as monophyletic; the present study represents the first instance in which this clade has been supported in a formal phylogenetic analysis. In most cases, the failure to recover the laemophloeid group in the above studies is due to the placement of the enigmatic family Passandridae elsewhere [e.g. sister to Cucujidae (Hunt *et al.*, 2007), sister to Bothriderinae (Lawrence *et al.*, 2011), nested within Nitidulidae (Bocak *et al.*, 2014)]. The study of McElrath *et al.* (2015), which focuses on the relationships of Laemophloeidae and allied families, recovered a clade nearly concordant with the laemophloeid group, with Passandridae supported as more closely related to Cyclaxyridae and Myraboliidae than to the remaining laemophloeid group taxa. Laemophloeidae and Propalticidae have been considered to be sister taxa (e.g. Lawrence & Newton, 1995; Leschen *et al.*, 2005; Hunt *et al.*, 2007; Lawrence *et al.*, 2011). Interestingly, our results recovered *Propalticus* Sharp nested within Laemophloeidae (Fig. 5). These results concur with recent findings by Bocak *et al.* (2014) and McElrath *et al.* (2015), and support the proposal by McElrath *et al.* (2015) to subsume Propalticidae within Laemophloeidae.

Cerylonid series

The strongly supported position of the CS forming the sister group to the remaining Cucujiformia and therefore not allied with any of the existing superfamilies of Cucujiformia, including the remaining Cucujoidea, was one of the most significant

results of the present study. The support for the CS clade was high (97), as was the support for Cucujiformia (98) and the clade comprising the remaining cucujiform lineages (83) (Fig. 5). Although the exact placement of the CS in Hunt *et al.* (2007) and Bocak *et al.* (2014) is not concordant with our results, both studies independently demonstrated the isolated position of the CS clade relative to the remaining cucujiform lineages. Given our resulting topology and previously published results (Hunt *et al.*, 2007; Bocak *et al.*, 2014), there seems no reasonable way to treat the CS except to recognize it as a new superfamily of Cucujiformia. Of the CS family group taxa, Coccinellidae Latreille has priority (Latreille, 1807). Thus we formally recognize the cucujiform superfamily Coccinelloidea **stat.n.**, which in terms of taxonomic constitution is synonymous with the current concept of the cerylonid series.

Internal relationships of Coccinelloidea

Our results corroborated previous molecular results (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Bocak *et al.*, 2014) in recovering a basal dichotomy of two well-supported superfamilial coccinelloid clades: one clade comprising Bothrideridae, Cerylonidae and Discolomatidae (hereafter referred to as the bothriderid group) (100); the second clade including Alexiidae, Akalyptoischiidae, Corylophidae, Coccinellidae, Latridiidae and multiple endomychid lineages (hereafter referred to as the coccinellid group) (87).

Bothriderid group (Bothrideridae, Cerylonidae, Discolomatidae)

The grouping of the families Bothrideridae, Cerylonidae and Discolomatidae (Fig. 6) has been suspected by previous authors (Ślipiński, 1990; Lawrence, 1991; Ślipiński & Pakaluk, 1991) and is consistent with recent molecular phylogenetic studies (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Bocak *et al.*, 2014). The bothriderid group exhibits a broad range of phenotypic variation and comprises *c.* 1250 species. Members of the bothriderid group are typically subcortical with either a mycophagous, myxophagous, predaceous or parasitoid life history. Some of these beetles are also known to inhabit leaf litter, fungi and similar microhabitats. Despite the varied biology, members of all three families are known to produce silken cocoons to house the pupal stage (Ślipiński, 1990; Lord & McHugh, 2013; JAR, personal observation e.g. *Bothrideres*, *Cassidoloma* Kolbe), a characteristic rare among beetles and not known in any of the other coccinelloid or cucujoid families. Even so, not all taxa within the bothriderid group have been observed to produce silken cocoons [e.g. *Teredolaemus leai* (Grouvelle)] (Ślipiński *et al.*, 2010b). To date, no anatomical synapomorphies have been identified uniting members of all three families. With a single exception [*Sosylopsis* Grouvelle (Bothrideridae)] adult bothriderids, cerylonids and discolomatids have the procoxal cavities internally open (Robertson, 2010). Little is known about the internal phylogenetic relationships within the bothriderid group.

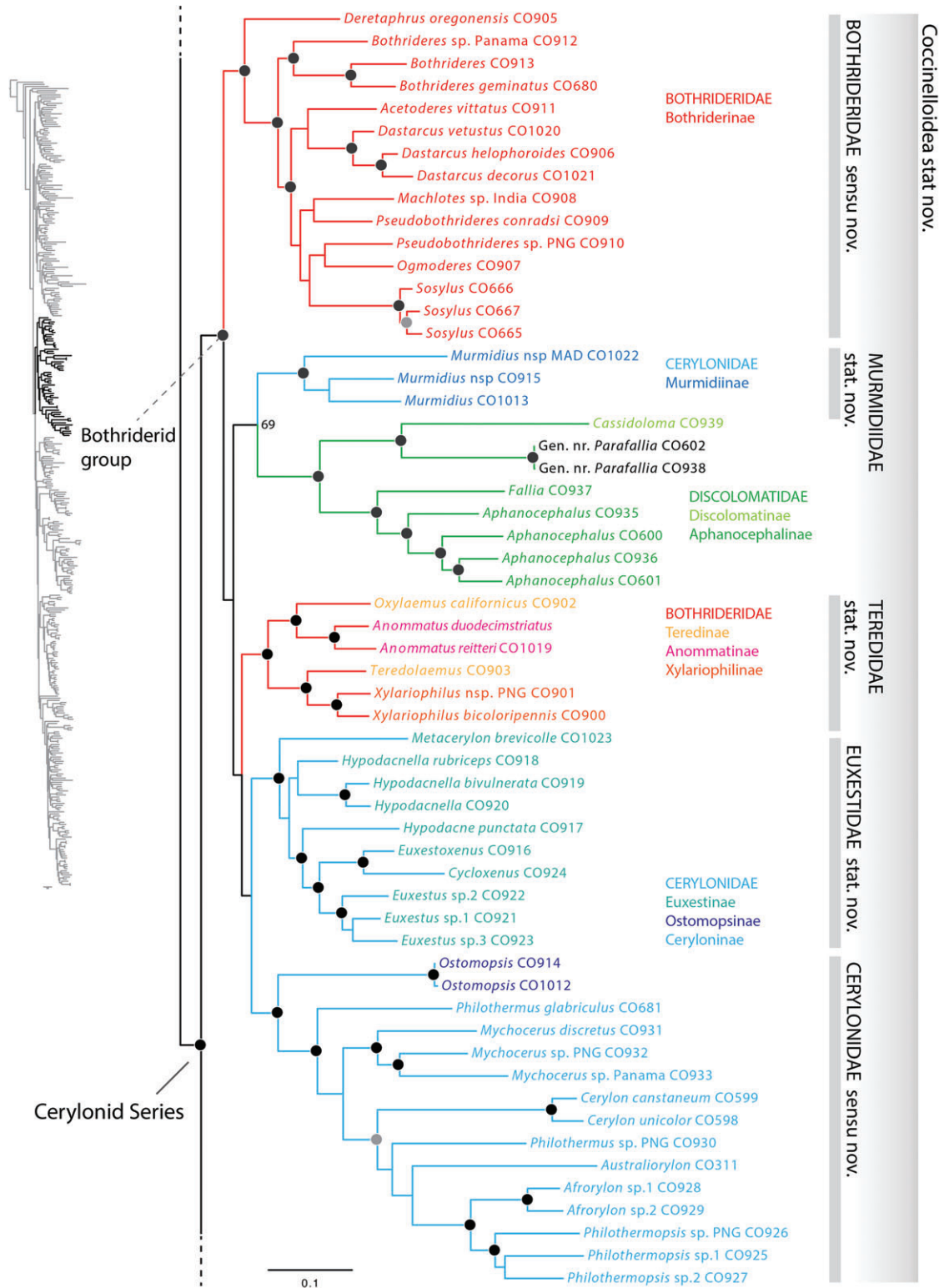


Fig. 6. Maximum-likelihood tree (part 3 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured by family and terminals by subfamily as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

The monophyly of the families Bothrideridae and Cerylonidae has been questioned by several authors (Pal & Lawrence, 1986; Ślipiński, 1990; Ślipiński & Pakaluk, 1991; Ślipiński & Lawrence, 2010). Most of these assertions concern the difficulty of distinguishing Euxestinae (Cerylonidae) from free-living Bothrideridae (i.e. Teredinae, Xylariophilinae, Anommatainae) based on morphology. The enigmatic Metacerylonini (Euxestinae) in particular bear many anatomical and life history similarities to the above bothriderid taxa and were considered by Dajoz (1980) to be subordinate to Bothrideridae. This study represents the first analysis with adequate taxon sampling to formally address the phylogenetic relationships of the bothriderid group.

Our results indicate that within the bothriderid group the ectoparasitoid subfamily Bothriderinae (Bothrideridae) is sister to the remaining taxa (Fig. 6). The monophyly of Bothriderinae was well supported (99). The enigmatic genus *Deretaphrus* Newman, comprising 25 species (Lord & McHugh, 2013), formed the sister group to the remaining bothriderines. *Deretaphrus* is unique among the entire Coccinelloidea for having the hindwing with a closed radial cell and four anal veins in the medial field. Lord & McHugh (2013) list additional anatomical features of the adult form that potentially set *Deretaphrus* apart from the remaining bothriderines including the unique form of the submentum and the male genitalia. The current tribal classification of Bothriderinae places *Deretaphrus* and *Sosylus* Erichson in Deretaphrini, a group based on having the anterior coxae contiguous or nearly so (widely separated in Bothriderini), a broadly rounded intercoxal process of abdominal ventrite 1 (truncated apically in Bothriderini) and having the first tarsal segment distinctly longer than the second one (typically subequal in length in Bothriderini) (Ślipiński & Pal, 1985). Members of Deretaphrini are typically elongate and subcylindrical, typical of beetles inhabiting wood galleries. Surprisingly, the present analysis did not support the bothriderine tribal classification, due to the placement of *Sosylus* deeply nested within Bothriderini. Interestingly, species of *Sosylus* employ a slightly different parasitic strategy than nearly all other bothriderines, which have a broader host range (Ślipiński *et al.*, 2010b). By contrast, the species-rich *Sosylus* specializes on ambrosia beetles (Curculionidae: Platypodinae) (Roberts, 1980). Based on our phylogenetic findings, the anatomical similarity of *Deretaphrus* and *Sosylus* (e.g. elongate subcylindrical body form, closely situated fore coxae, rounded and relatively narrowed intercoxal process of abdominal ventrite 1, tarsomere I distinctly longer than tarsomere II) is likely to be the result of morphological convergence associated with occupying the galleries of their wood-boring hosts.

The genus *Bothrideres* was strongly supported (100, 97) as the second earliest diverging bothriderine lineage of those sampled in the present study. Beyond these well-supported early divergences, the internal relationships within this subfamily were only weakly supported. One moderately well supported result that warrants further investigation was the polyphyly of *Pseudobothrideres* Grouvelle; the two *Pseudobothrideres* exemplars sampled from Zambia and Papua New Guinea did not form a clade. Much taxonomic and phylogenetic work remains to be done within this fascinating lineage (Lord & McHugh, 2013).

Within the remaining bothriderid group we recovered four well-supported, major lineages: (i) Murmidiinae (Cerylonidae) + Discolomatidae, (ii) a clade comprising all free-living bothriderids (Teredinae, Xylariophilinae, Anommatainae), (iii) Euxestinae (Cerylonidae), and (iv) Ostomopsinae (Cerylonidae) + Ceryloninae. The relationships between these four clades, however, were only weakly supported (Fig. 6). Murmidiinae comprised three genera – *Murmidius* Leach, *Mychocerinus* Ślipiński and *Botrodus* Casey. The subfamily is unique among Coccinelloidea for having a median endocarina in the larval form (Ślipiński, 1990). However, it should be noted that the larval stage is only known for the genus *Murmidius*. The placement of *Murmidius* as the sister group to Discolomatidae was moderately supported in the present study (69). The family Discolomatidae has a convoluted taxonomic history with previous ties to the families Coccinellidae, Endomychidae, Corylophidae, Latridiidae, Colydiidae, Nitidulidae, Cerylonidae and Trogossitidae (see Cline & Ślipiński, 2010). van Emden (1932, 1938) was the first to suggest a relationship between *Murmidius* and Discolomatidae and this hypothesis has been echoed by subsequent authors (Ślipiński, 1990; Lawrence, 1991; Ślipiński & Pakaluk, 1991). In fact, Ślipiński (1990) suspected that discolomatids should be subsumed within Cerylonidae due to the many anatomical features uniting them with Murmidiinae, including adults with the spiculum gastrale absent and ovipositor reduced, without styli, and larvae onisciform (Ślipiński, 1990; Ślipiński & Pakaluk, 1991). Many of the above features were considered putative synapomorphies for Murmidiinae relative to the remaining cerylonid subfamilies, but our results indicated that they are synapomorphies for Murmidiinae + Discolomatidae. It is interesting to note that in the study of Lawrence *et al.* (2011) *Murmidius* formed the sister group to the clade *Ostomopsis* Scott + Discolomatidae. The larval form of *Murmidius* and Discolomatidae in particular share many apomorphic character states, yet the larval stage is not yet known for *Ostomopsis*. Thus the absence of this informative suite of data for *Ostomopsis* likely influenced the separation of *Murmidius* and Discolomatidae by *Ostomopsis*. In terms of coccinelloid subfamilial diversity, the family Discolomatidae was poorly represented in the present analysis, with only two of the five discolomatid subfamilies sampled. The monophyly of the family Discolomatidae is not in question, being supported by several unique apomorphies including adults with glandular openings lining the lateral pronotal and elytral margins and the meso- and metacoxae long and transverse but nearly concealed by meso- and metaventral plates. By contrast, the internal relationships and validation of the currently recognized higher taxa are entirely untested. Despite the relatively weak subfamilial representation, our analysis indicated that the subfamily Aphanocephalinae is monophyletic. Interestingly, an undescribed genus resembling *Parafallia* Arrow (Aphanocephalinae) was strongly supported as more closely related to *Cassidoloma* (Discolomatinae). Much more work is needed to clarify the internal relationships of Discolomatidae.

The 'free-living' bothriderids (Anommatainae, Teredinae and Xylariophilinae) (Ślipiński *et al.*, 2010b) formed a well-supported clade (96) subtending the remaining cerylonid

taxa (Fig. 6). The internal relationships recovered within this clade were consistently strongly supported. Anommatinae were strongly supported as sister to *Oxylaemus* Erichson (Teredinae) (96). *Teredolaemus* (Teredinae) formed the sister group to *Xylariophilus* (Xylariophilinae) (100), thereby rendering Teredinae paraphyletic. These internal relationships, although inconsistent with the current classification, are consistent from an anatomical perspective (Robertson, 2010). Several enigmatic genera currently classified as Teredinae were not included in the present study, including *Rustleria* Stephan, known from only a single specimen from SW Arizona, and the anatomically odd genera *Sosylopsis* (endemic to Madagascar) and *Syolus* Grouvelle (Indo-Malaysia and Central America). Much work is needed to clarify the internal relationships of this lineage, but based on our results, it is clear that the free-living taxa do not form a monophyletic group with the parasitoidal bothriderids and should be treated as their own family.

The monophyly of the cerylonid subfamily Euxestinae was strongly supported (100) in our analyses (Fig. 6). Among cerylonids, this subfamily has been the most difficult to place among the remaining subfamilies, mostly due to shared anatomical features with free-living bothriderids. Unlike the remaining cerylonid groups, Euxestinae have seven pairs of functional abdominal spiracles, subantennal grooves well developed, lacinia with apical uncus and hindwing with anal lobe present (Ślipiński, 1990). Ślipiński (1990) suggested that Euxestinae should be recognized as its own family or be transferred to Bothrideridae, but felt formal action prior to a comprehensive phylogenetic study of the entire CS would be imprudent. Indeed, our results support the recognition of Euxestinae at the family level. Note that whereas the subfamily Euxestinae is recovered sister to other cerylonid groups (e.g. Ostomopsinae + Ceryloninae), the support for this sister grouping is negligible (40) and in preliminary analyses Euxestinae were often recovered sister to the free-living bothriderids.

The generic diversity of Euxestinae was fairly well represented in our analyses, with over half (6 of 11) of the genera sampled. The enigmatic *Metacerylon*, which especially bears many anatomical and life history traits common with free-living bothriderids, was supported as the earliest diverging euxestine lineage. *Euxestoxenus* Arrow and *Cycloxenus* Arrow were strongly supported (100) as sister taxa; the former is a known myrmecophile and both are known termitophiles. *Hypodacne punctata* LeConte is also suspected to be myrmecophilous given previous natural history observations (Stephan, 1968), but very little is known regarding the nature of this association (Ślipiński, 1990).

The monogeneric Ostomopsinae comprising only a few species was originally classified as a tribe in Murmidiinae by Sen Gupta & Crowson (1973) and elevated to subfamily level by Lawrence & Stephan (1975). The genus *Ostomopsis* is unique among cerylonids for having a peculiar antennal club that is emarginated laterally and bears specialized sensilla, the peculiar form of maxillary palps exclusive for the genus, the pronotal edges serrulate and the apical flange of elytra widened apically with the elytra longitudinally striate (Ślipiński, 1990). The phylogenetic position of *Ostomopsis* among the remaining cerylonid lineages has been unclear (Ślipiński, 1990). Ślipiński

(1990) postulated a close relationship between Ostomopsinae and either Murmidiinae or Ceryloninae based on different sets of features. In Lawrence *et al.* (2011) *Ostomopsis* was recovered as the sister group to Discolomatidae (see above). In the present study *Ostomopsis* was strongly supported (95) as forming the sister group to the species-diverse Ceryloninae (Fig. 6). This was the first molecular phylogenetic analysis to sample the enigmatic Ostomopsinae. Anatomical features common to both *Ostomopsis* and Ceryloninae include adults with hindwing lacking medial fleck, procoxal cavities internally widely open with the intercoxal process narrow and parallel-sided, spiculum gastrale present, ovipositor with well-developed styli and dorsum setose (Ślipiński, 1990). The larval form of *Ostomopsis* is unknown. The discovery of the larval form of *Ostomopsis* may illuminate larval features uniting Ostomopsinae and Ceryloninae.

Ceryloninae is the largest and best-defined cerylonid subfamily. The group was well supported in our analyses (100) as well as by morphology (Ślipiński, 1990). Ślipiński (1990) postulated a sister relationship between Ceryloninae and the monotypic Loeblioryloninae (not sampled here) based on both possessing aciculate palps and lacking the frontoclypeal suture. Cerylonines are further characterized by having the last abdominal ventrite crenulate in adults and the mandibles stylet-like and either endognathous (e.g. *Cerylon* Latreille) or enclosed within a tubular beak (e.g. *Philothermus* Aubé, *Mychocerus* Erichson) in larvae. Note that whereas both Murmidiinae and Ostomopsinae also have a crenulate last abdominal ventrite, the homology of the elytral locking mechanisms exhibited in these three subfamilies (Ceryloninae, Murmidiinae, Ostomopsinae) is dubious because different structures are involved (Ślipiński, 1990).

Given the strong support for the polyphyly of Bothrideridae and Cerylonidae here and in previous studies (Hunt *et al.*, 2007; Bocak *et al.*, 2014), we formally recognize a new familial classification for members of the bothriderid group. We recognize a new concept of Bothrideridae **s.n.** to include only the parasitoidal subfamily Bothriderinae.

We further recognize the family Teredidae **stat.n.**, to accommodate the free-living bothriderids: Anommatinae, Teredinae and Xylariophilinae. Murmidiinae is elevated to family status as Murmidiidae **stat.n.** Euxestine cerylonids are elevated to family status as Euxestidae **stat.n.** Finally, we retain Ostomopsinae, Ceryloninae and Loeblioryloninae in a new concept of the family Cerylonidae **s.n.**

Coccinellid group

Latridiidae and Akalyptoischiidae

Latridiidae comprise a cosmopolitan family with over 1000 described species classified in 28 genera (Hartley & McHugh, 2010). Latridiids are the quintessential LBJs ('little brown jobs') and until recently have received little higher-level systematic attention. Historically, many taxa were classified in this family on account of being minute, having 3-3-3 tarsi and a similar habitus [e.g. *Anommatus* (Bothrideridae), *Dasycerus* Brongniart (Staphylinidae), *Merophysiinae* (Endomychidae)]. Using molecular data, Lord *et al.* (2010) conducted the first

phylogenetic investigation of the family and found the enigmatic *Akalyptoischion* to be more closely related to other CS taxa than the remaining Latridiidae. *Akalyptoischion* includes 24 described species restricted to western North America (Hartley *et al.*, 2008). Based on their results and accompanying morphological justification, Lord *et al.* (2010) recognized a new family, Akalyptoischiidae, to accommodate *Akalyptoischion*. Latridiidae are recovered here with strong support (100) as the earliest diverging lineage in the coccinellid group (Fig. 7). This placement is in agreement with the results of Bocak *et al.* (2014), but differs from other molecular studies which place Latridiidae as sister group to all remaining coccinelloid families including the bothriderid group (Lord *et al.*, 2010), or weakly supported as the sister group to a clade comprising a grade of leistine and merophysine endomychids + Corylophidae (Hunt *et al.*, 2007). The internal relationships of Latridiidae recovered herein only partially overlap with those of Lord *et al.* (2010). In both studies, the two subfamilies, Latridiinae and Corticariinae are strongly supported as monophyletic, but the internal relationships within these groups, particularly Corticariinae, are not concordant.

We recovered *Akalyptoischion* as the second earliest diverging lineage within the coccinellid group, corroborating the recognition of this lineage at the family level (Akalyptoischiidae). It should be noted however that the topological support separating Akalyptoischiidae and Latridiidae (i.e. the clade comprising Akalyptoischiidae and the remaining coccinellid group taxa) was rather weak (60). Akalyptoischiidae are far removed from Latridiidae in the Bocak *et al.* (2014) study, but recovered sister to the main cluster of Endomychidae.

Alexiidae

The monotypic Alexiidae comprise *c.* 50 species distributed in the Mediterranean region (Ślipiński & Tomaszewska, 2010). The family was traditionally included as a subfamily (Sphaerosomatinae) within Endomychidae, but Sen Gupta & Crowson (1973) recognized the distinctiveness of *Sphaerosoma* Samouelle and elevated the subfamily to family status, as Sphaerosomatidae. Recent molecular phylogenetic analyses support the distinctiveness of Alexiidae. In Hunt *et al.* (2007) Alexiidae are weakly supported as the sister group to anamorphine endomychids, whereas in Bocak *et al.* (2014) the family forms the sister group to Coccinellidae. In the present study, Alexiidae was recovered as sister to the clade comprising Corylophidae, Coccinellidae and multiple endomychid lineages (Fig. 7). This large clade is generally characterized by somewhat convex beetles with elytral puncturation irregularly aligned, not forming rows, and pseudotrimerous tarsi (Robertson, 2010). Support for this sister grouping (60) and that of the clade comprising Corylophidae, Coccinellidae and the endomychid taxa (71) is moderate.

Anamorphinae

Corroborating the results of Robertson *et al.* (2008, 2013), our study supports a moderately strong sister grouping of Anamorphinae (Endomychidae) and Corylophidae (86) (Fig. 7), indicating that Anamorphinae should be elevated to family status.

In fact, all molecular analyses including anamorphines have failed to recover them with the core Endomychidae. Hunt *et al.* (2007) recovered Anamorphinae sister to Alexiidae, whereas in Bocak *et al.* (2014) Anamorphinae is nested within Corylophidae. Morphological character states uniting Corylophidae and Anamorphinae include adults with the penis being broad and stout with endophallic sclerites, and larvae with the antennal socket located far from the mandibular articulation (Robertson *et al.*, 2013). The relationship of anamorphines to the remaining endomychid taxa has been questioned historically. Sasaji (1978) established the subfamily Anamorphinae (= Mychotheninae) for several genera (e.g. *Mychothenus* Strohecker, *Bystodes* Strohecker, *Bystus*, *Dialexia* Gorham, etc.) that were previously included in a broadly defined Mycetaeinae by Strohecker (1953) and did so based on anatomical features unique for Endomychidae including adults with the anterior arms of the tentorium separate throughout their length and mesocoxal cavities closed by ventrites. Sasaji (1987, 1990) later elevated the subfamily to family status, but this action did not receive much attention or subsequent following. The cladistic analyses of Tomaszewska (2000, 2005) did recover Anamorphinae within Endomychidae, but because the scope of these studies focused on the internal relationships of the family neither analysis implemented a broad sampling of outgroup taxa thus the test of monophyly for the family was relatively weak. From an ecological perspective anamorphines differ from most of the remaining endomychids by their apparent obligate sporophagy (spore specialists) as both adults and larvae (Pakaluk, 1986). This niche is reflected in the highly specialized mandibles in both active life stages of anamorphines, with a well-developed mandibular mola that works like a spore mill, a brush-like prosthema and a bifid apical incisor; the larvae have the incisor lobe highly reduced or absent (Tomaszewska, 2000, 2005, 2010). Morphological features that separate Anamorphinae from core Endomychidae include adults with anterior arms of tentorium separate (fused in core Endomychidae, except one species of Merophysinae), mesocoxal cavities widely closed by the meso- and metaventrite (open to mesepimeron in core endomychids, except Merophysinae and Pleganophorinae, which are narrowly closed), pretarsal claws modified, penis broad, stout, weakly curved with endophallic sclerites (penis variable in core Endomychidae). Given the strong evidence for the phylogenetic distinction of Anamorphinae from the core Endomychidae, we formally recognize a new family, Anamorphidae **stat rev.**, for all taxa previously assigned to Anamorphinae. Within the clade comprising anamorphids (Fig. 7), we recovered the Holarctic genus *Symbiotes* Redtenbacher as the earliest diverging taxon. A primarily Old World clade comprising the genera *Papuella* Strohecker, *Clemmus* [*C. minor* (Crotch) is the only Nearctic sp.] and *Mychothenus*, was also strongly supported as an early diverging lineage. This study did not include the enigmatic genus *Erotendomychus* Lea, another viable candidate for the earliest diverging anamorphid. *Erotendomychus* includes 15 species restricted to eastern Australia and is anatomically odd with respect to the remaining anamorphids in having the anterior arms of the tentorium broadly fused medially, intercoxal process of mesoventrite rounded and prominent anteriorly (truncate, not produced

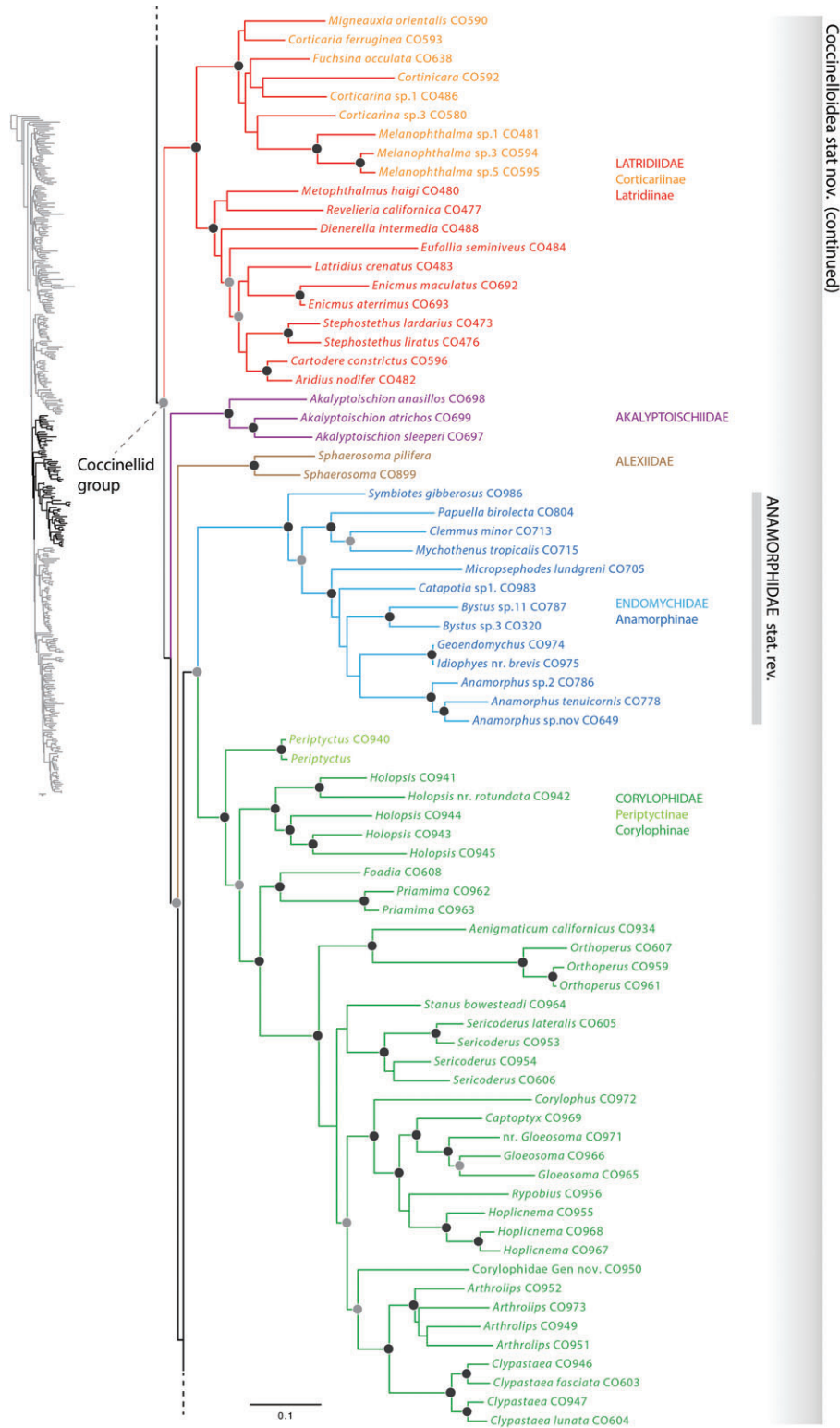


Fig. 7. Maximum-likelihood tree (part 4 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured by family and terminals by subfamily as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

anteriorly in remaining anamorphids), the metacoxae widely separated, more than 1.5× the coxal width (between $\frac{1}{3}$ and 1× the coxal width in remaining anamorphines) and the trochanterofemoral attachment strongly heteromeroid (Tomaszewska, 2004; Robertson, 2010; J.A. Robertson, personal observation). Interestingly, several of the above character states are consistent with early diverging lineages of Corylophidae (Robertson *et al.*, 2013), such as widely separated metacoxae and the strongly heteromeroid trochanterofemoral attachment. Indeed, *Erotendomychus* is in some regards an anatomical intermediate between anamorphids and corylophids, but the form of the antennae of *Erotendomychus* is not characteristic of either group. It may also be noteworthy that the earliest diverging corylophid lineage, Periptyctinae (comprising three species-poor genera), is also endemic to Australia (Ślipiński *et al.*, 2009). Furthermore, *Periptyctus* Blackburn (Periptyctinae), was classified within Endomychidae and only recently transferred to Corylophidae (Ślipiński *et al.*, 2001). The larval form of *Erotendomychus* is not known. Including this enigmatic taxon represents an important and exciting potential element for future studies.

Corylophidae

The internal relationships and patterns of support within Corylophidae (Fig. 7) are entirely concordant with those in Robertson *et al.* (2013). This is not surprising because the corylophid taxa and molecular data sampled in the present study overlaps entirely with that of Robertson *et al.* (2013). *Periptyctus* is recovered as the earliest diverging corylophid lineage. *Holopsis* Broun & Foadiini are also supported as early diverging lineages and the remaining corylophid lineages form a strongly supported clade (100).

Endomychidae

The family Endomychidae is a heterogeneous group comprising c. 1800 species classified in 135 genera (Shockley *et al.*, 2009a). Endomychidae have a convoluted taxonomic history, rich with rank changes and movement of higher taxa among endomychid subfamilies and coccinelloid families. Tomaszewska (2000) conducted the first cladistic analysis of the family using adult morphology and refined the subfamilial classification. Adding larval data and an expanded taxon sampling within the diverse Lycoperdininae, Tomaszewska (2005) provided resolution between the endomychid subfamilies and lycoperdinine species groups. Most taxa currently classified as Endomychidae formed a well-supported clade (100) in the present analyses (Fig. 8). The subfamilies Anamorphinae, Mycetinae and Eupsilobinae, however, were not recovered with the core Endomychidae. In general, branch support within the core Endomychidae was consistently high. Within the clustering of core endomychids, there were two strongly supported, major lineages. The first clade (hereafter referred to as the merophysiine complex) (100) comprised the subfamilies Pleganophorinae (100), Leiestinae (100) and Merophysiinae (100). The merophysiine complex is not consistent with the cladistic analyses of Tomaszewska (2000, 2005), nor has it been suggested previously. However, there are several anatomical and ecological features that bolster

these relationships. Members of the merophysiine complex have the mesotrochantin concealed (exposed in remaining core Endomychidae), have tarsi simple (pseudotrimerous in remaining core Endomychidae) and exhibit modified and sexually dimorphic antennae in adults whereas their larvae have the frontal arms lyriform (Tomaszewska, 2005). Species of Merophysiinae and Pleganophorinae are known to be inquiline, living in direct association with termites and ants (Shockley *et al.*, 2009b). Given what is known of feeding habits of the family, in these cases it seems likely that the beetles are feeding on some type of fungus that occurs with the associated organism. In addition, both Merophysiinae and Pleganophorinae have the mesocoxal cavities closed (Tomaszewska, 2010), whereas in the remaining core endomychids these cavities are open. The subfamily Leiestinae was strongly supported as the sister group to Merophysiinae (100). Both Leiestinae and Merophysiinae have the metendosternite with two vertical admedian processes from which the tendons arise (Robertson, 2010; J.A. Robertson, A. Ślipiński, J.V. McHugh, personal observation) and their larvae are relatively cylindrical in form without processes or tubercles, with simple vestiture and mandibles without prosthema (Burakowski & Ślipiński, 2000).

The second major clade of core Endomychidae (hereafter referred to as the endomychine complex) (100) corresponds to Tomaszewska's (2005) 'higher Endomychidae' and includes taxa classified as Endomychinae, Stenotarsinae, Epipocinae and Lycoperdininae (Fig. 8). These taxa were supported as a clade in Tomaszewska's (2005) cladistic analysis by having adults with pseudotrimerous tarsi and larvae with well developed V- or U- shaped frontal arms and four pairs of stigmata. Our analyses indicated that neither Endomychinae nor Stenotarsinae are monophyletic. Endomychinae currently includes five genera: *Endomychus* Panzer, *Cyclotoma* Mulsant, *Meilichius* Gerstaecker, *Bolbomorphus* Gorham and *Eucteanus* Gerstaecker (Shockley *et al.*, 2009a); only the first three were sampled here. *Cyclotoma* and *Meilichius* (Endomychinae) formed a well-supported clade (100) that subtends the remaining endomychine complex. *Endomychus*, however, was nested within Stenotarsinae, sister group to the clade comprising *Saula* and the paraphyletic genus *Danae* Reiche. Whereas the placement of *Cyclotoma* + *Meilichius* relative to the remaining endomychines and stenotarsines was equivocal, it is clear that this clade does not form a monophyletic group with *Endomychus*. Relative to the nominate genus, *Endomychus*, the remaining taxa currently assigned to Endomychinae are unique. For example, all Endomychinae except *Endomychus* have the labial prementum in the adult form entirely sclerotized without a distinct ligula (the ligula is distinct and partially membranous in all other Endomychidae including *Endomychus*) and the penis in the adult male is curled along the proximal $\frac{1}{3}$ of its length (smooth in remaining Endomychidae including *Endomychus*) (Tomaszewska, 2005). Given the strong support for the polyphyly of Endomychinae and paraphyly of Stenotarsinae, we formally recognize the subfamily, Cyclotominae **stat.n.**, to accommodate the genera *Cyclotoma*, *Meilichius*, *Bolbomorphus* and *Eucteanus*. Although the genera *Bolbomorphus* and *Eucteanus* were not sampled here, we tentatively include them in Cyclotominae

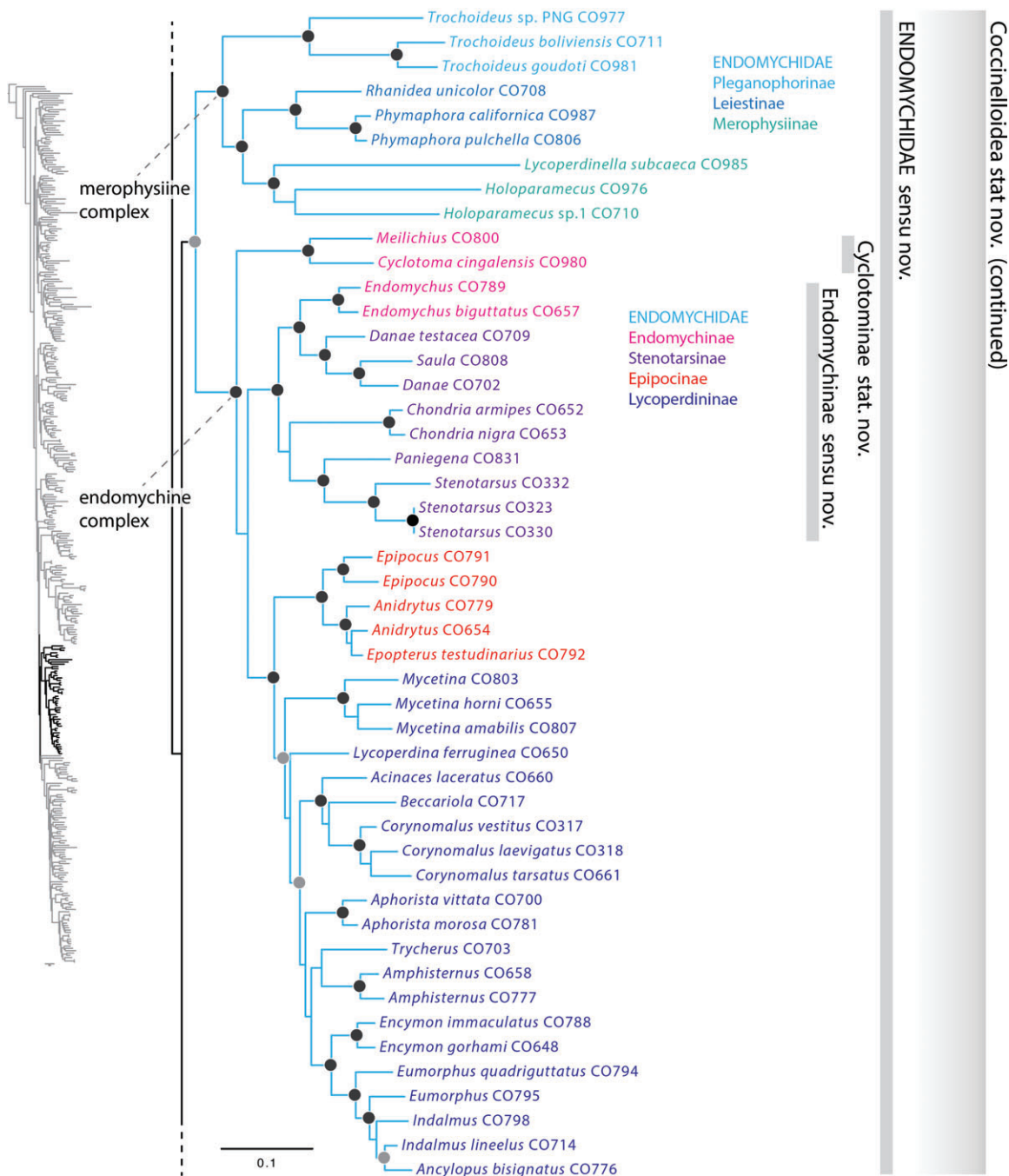


Fig. 8. Maximum-likelihood tree (part 5 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured by family and terminals by subfamily as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

stat.n. because these genera share the anatomical features outlined above. We further formally subsume Stenotarsinae within a new concept of Endomychinae **s.n.**, which includes *Endomychus* and all taxa previously classified as Stenotarsinae.

The subfamilies Epipocinae and Lycoperdininae were strongly recovered as sister taxa (100); both are well defined from an

anatomical standpoint (Tomaszewska, 2000, 2005). Lycoperdininae is not only the largest endomychid subfamily, with 43 genera and over 700 species (Tomaszewska, 2012), but also includes some of the most striking species with aposematic colouration and ornamentation (Tomaszewska, 2005). Tomaszewska (2005) investigated the internal relationships of

Lycoperdininae and recognized five species groups based on cladistic analysis of adult and larval data. In the present study, the major divergences within Lycoperdininae were generally not strongly supported. However, several clusters of genera recovered in our analyses overlap in part with Tomaszewska's (2005) lycoperdinine species groups. For example, the clade (100) comprising *Encymon* Gerstaecker, *Eumorphus* Weber, *Indalmus* Gerstaecker and *Ancylopus* Costa is part of Tomaszewska's (2005) *Eumorphus* group; *Acinaces* Gerstaecker, *Beccariola* Arrow and *Corynomalus* Chevrolat (= *Amphix* Laporte) belong to the *Corynomalus* group. However, our results were not entirely consistent with any of the proposed lycoperdinine groups.

The present analysis placed the subfamilies Mycetaeinae and Eupsilobiinae as more closely allied to the family Coccinellidae than the main cluster of endomychid taxa (Fig. 9). Although Mycetaeinae and Eupsilobiinae were not supported as sister taxa, both exhibit a unique rigid tooth-like prosthema in the larval form (Tomaszewska, 2005). Mycetaeinae includes two genera, *Agaricophilus* Motschulsky and *Mycetaea* Stephens, with two and five species, respectively (Shockley *et al.*, 2009a). The monophyly of Mycetaeinae may be in question as the two constituent genera are quite different anatomically in both the adult and larval forms. Nothing is known about the natural history of *Agaricophilus*. Only *Mycetaea* was sampled in the present study, thus the monophyly of this small enigmatic taxon remains uncertain. Eupsilobiinae includes seven genera and 16 species, with most distributed in small endemic areas of Central and South America, and South Africa; *Eidoreus* Sharp is widely distributed. The group is generally accepted as monophyletic (Pakaluk & Ślipiński, 1990; Tomaszewska, 2005). Eupsilobiinae are unique among endomychids in having short subantennal grooves [long or absent (most) in remaining endomychids], anterior arms of tentorium widely divergent, narrowly fused medially [only slightly divergent and broadly fused forming a laminatentorium in remaining endomychids, or entirely separate (Anamorphidae)] and the form of the mesoventrite, abdominal ventrite 1 and male genitalia (see below).

Eupsilobiinae + Coccinellidae

The sister group to the species-rich and economically important Coccinellidae has been of great interest yet elusive. Historically, Endomychidae has been considered the sister group to Coccinellidae, primarily based on both having members with pseudotrimerous tarsi.

Formal phylogenetic studies have recovered myriad hypotheses for the sister group of Coccinellidae including Alexiidae + Anamorphinae (Hunt *et al.*, 2007), Endomychidae (Robertson *et al.*, 2008; Giorgi *et al.*, 2009; Seago *et al.*, 2011), Corylophidae (Robertson *et al.*, 2008, 2013; Lawrence *et al.*, 2011) and Alexiidae (Bocak *et al.*, 2014). Recent molecular phylogenetic studies focusing on Coccinellidae (Giorgi *et al.*, 2009; Seago *et al.*, 2011) relied on exemplars of Endomychidae and Corylophidae as outgroup taxa, assuming a sister group with one of these families. Our analyses consistently recovered Eupsilobiinae (Endomychidae) as the sister group to Coccinellidae (Fig. 9). Eupsilobiinae have previously never been sampled

in a molecular phylogenetic analysis. Interestingly, Crowson (1981) postulated a close relationship between *Eidoreus* (Eupsilobiinae) and Coccinellidae; others also have noted anatomical similarities between the two (e.g. Pakaluk & Ślipiński, 1990; Tomaszewska, 2010). In the cladistic analysis of Tomaszewska, Eupsilobiinae was deeply nested among the remaining monophyletic endomychid taxa. Tomaszewska (2010) later reviewed the distinctiveness of Eupsilobiinae with respect to the remaining endomychids but conceded that its phylogenetic position was unclear. Even so, eupsilobiines share several compelling anatomical character states with Coccinellidae. Both groups have the anterior edge of the mesoventrite on a different plane than the metaventrite [independently occurs in *Holopsis* and *Orthoperus* Stephens (Corylophidae)] (J.A. Robertson, A. Ślipiński, J.V. McHugh, personal observation). Eupsilobiines and coccinellids have abdominal ventrite 1 with postcoxal lines; all other taxa currently classified as Endomychidae lack abdominal postcoxal lines (with two exceptions: *Xenomycetes* Horn, but these are different in form, and *Cholovocera* Belon). In addition, most eupsilobiines and Coccinellidae have postcoxal lines on the metaventrite. One of the strongest defining character states for the family Coccinellidae is the unique form of the aedeagus, comprising a well-developed, ring-like tegminal phallobase that projects forward forming a penis guide, an articulated anterior tegminal strut (trabes), a pair of parameres, and an elongate, slender and curved penis (siphon) with a proximal T-shaped capsule. It is significant that Eupsilobiinae have essentially the same aedeagal components in similar form as coccinellids, including the characteristic penis, being elongate, slender and curved with the base sclerotized and T-shaped. The recovery of Eupsilobiinae + Coccinellidae is one of the more significant results of the present study. Given the support here for the separation of both Mycetaeinae and Eupsilobiinae from the core Endomychidae, we formally recognize both at the family level – Mycetaeidae **stat.n.** and Eupsilobiidae **stat.n.**

Coccinellidae

The monophyly of Coccinellidae is strongly supported in the present analyses (100) (Fig. 9) and is well supported from a morphological standpoint (see Ślipiński, 2007; Seago *et al.*, 2011). With over 6000 species, Coccinellidae is by far the largest of the coccinelloid families. Despite the economic importance of Coccinellidae, little is known regarding the higher-level relationships of the family. The first attempt to address the phylogenetic relationships of Coccinellidae was Sasaji (1968), who, using narrative justification based on adult and larval characters, proposed six subfamilies and several constituent tribes. Treating a broader diversity for the family, Kovář (1996) proposed a similar arrangement of taxa but recognized a seventh subfamily, Orthalinae, and 38 tribes. Later authors (Vandenberg, 2002; Ślipiński, 2007; Vandenberg & Perez-Gelabert, 2007) recognized the artificial nature of several subfamilies and higher taxa. Accordingly, Ślipiński (2007) proposed a classification that placed several anatomically distinct sticholotidine taxa together in the subfamily Microweiseinae and all other coccinellid species into an expanded concept of Coccinellinae. Only recently have rigorous,

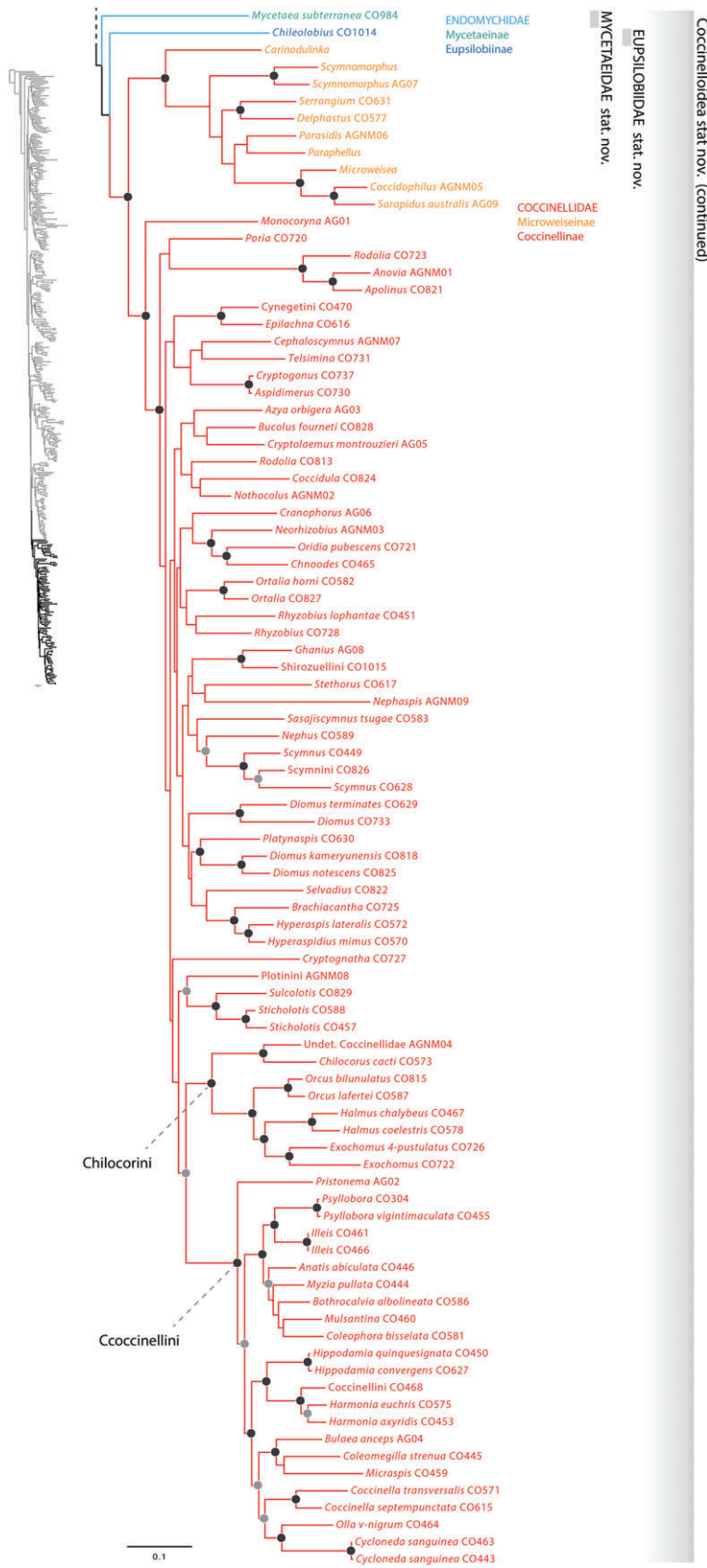


Fig. 9. Maximum-likelihood tree (part 6 of 6). The full topology is shown to the left of the figure with the emboldened region enlarged and coloured for discussion. Branches are coloured by family and terminals by subfamily as indicated to the right of the corresponding terminals. Nomenclatural changes proposed in this study are denoted to the far right of the tree with grey bars. Nodes supported by bootstrap support ≥ 90 are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

molecular phylogenetic hypotheses emerged for Coccinellidae (e.g. Giorgi *et al.*, 2009; Magro *et al.*, 2010; Seago *et al.*, 2011), all of which have demonstrated the nonmonophyly of the traditional subfamilies of Sasaji (1968) and Kovář (1996). One aspect of coccinellid evolutionary history that is borne out in previous molecular studies (e.g. Giorgi *et al.*, 2009; Seago *et al.*, 2011) and corroborated here is the tempo and pattern of coccinellid diversification. The coccinellid topology is characterized by moderately long terminal branches with very short internal branches spanning the backbone and major divergences of the tree (Fig. 9): the hallmark of a rapid radiation. Indeed, based on this characteristic branching pattern produced by three independent sets of molecular data, it is clear that inferring the evolutionary history of Coccinellidae, particularly recovering the major divergences of the coccinelline tribes, presents a significant challenge. Even so, in the present study we recovered a well-resolved topology with several strongly supported groups. Corroborating Giorgi *et al.* (2009) and Seago *et al.* (2011), we recover a basal split comprising Microweiseinae and the species-rich Coccinellinae (Fig. 9). The subfamily Microweiseinae currently includes three tribes: Carinodulini, Microweiseini (including Sukunahikonini) and Serangiini (Escalona & Ślipiński, 2012). Within Microweiseinae the anatomically bizarre *Carinodulinka* (Carinodulini) was recovered as the earliest diverging lineage, corroborating the results of Seago *et al.* (2011). Our results strongly support the monophyly of the microweiseine tribe Serangiini (99), whereas Microweiseini was rendered paraphyletic by Serangiini. We recovered a well-supported clade comprising *Microweisea* Cockerell, *Coccidophilus* Brèthes and *Parasidis* (= *Sarapidus*) *australis* (Gordon). González (2008) recently synonymized *Sarapidus* Gordon under *Parasidis* Brèthes, but this action is not supported here because *P. australis* (formerly *Sarapidus australis*) is far removed from the remaining *Parasidis* sampled herein. Also consistent with previous molecular studies (Giorgi *et al.*, 2009; Seago *et al.*, 2011) was the placement of the Oriental genus *Monocoryna* Gorham as sister to the remaining Coccinellinae. This relationship was here well supported (97, 99). *Monocoryna* was only recently moved to Coccinellidae from Endomychidae (Miyatake, 1988) and is unique in having the antennal club comprising a single large antennomere, and the male genitalia with the penis guide reduced and phallobase complex (Seago *et al.*, 2011).

The tribes Coccinellini (100) and Chilacorini (including *Chilocorellus* Miyatake) (100) were each strongly supported as monophyletic and were recovered as sister taxa with moderately high support (77). Both Magro *et al.* (2010) and Seago *et al.* (2011) recovered Coccinellini + Chilacorini as well. Branch support for the internal relationships within Coccinellini and Chilacorini was generally high in the present study. Within Coccinellini, *Pristonema* Erichson was recovered as the earliest diverging taxon with moderately high support (85), consistent with the analysis of Giorgi *et al.* (2009). *Pristonema* and related taxa from South America, sometimes recognized as tribe Discotomini, are unique with respect to the remaining Coccinellini in having antennae with pectinate antennal club. The internal relationships of Chilacorini were strongly supported and entirely concordant with those in Giorgi *et al.* (2009); the results

of Seago *et al.* (2011) differ only in the resolution of *Halmus* Mulsant, *Exochomus* Redtenbacher and *Orcus* Mulsant. The clade comprising *Chilocorus* Leach + *Chilocorellus* was supported as the earliest diverging chilacorine lineage in the present study and Seago *et al.* (2011). Beyond the placement of *Monocoryna*, sister grouping of Coccinellini + Chilacorini, and the internal relationships within Coccinellini and Chilacorini, there is little agreement between the recovered major relationships within Coccinellinae between the present study and previous ones (Giorgi *et al.*, 2009; Magro *et al.*, 2010; Seago *et al.*, 2011). Although several small super-generic or tribal clades were recovered with high support in the present analyses [e.g. Shirozuellini; *Hyperaspidius* Crotch + *Brachiacantha* Chevrolat; *Neorhizobius* Crotch (*Oridia* Gorham + *Chnodes* Chevrolat); *Sulcolotis* Miyatake + *Sticholotis* Crotch], most higher-level coccinelline relationships subtend very short branches that were only weakly supported, such that little confidence can be placed on many of these internal coccinelline relationships.

Revised classification

Crowson (1981: 685) stated ‘The very heterogeneous Cucujoidea may well merit division into two or more superfamilies, not necessarily on present Clavicornia [Cucujoidea]-Heteromera [Tenebrionoidea] lines.’ The results of the present study strongly support such an action as implemented in the following.

Cleroidea Latreille, 1802 s.n.

Clerii Latreille, 1802: 110

Type genus. *Clerus* Geoffroy, 1762: 303

Diagnosis. Cleroidea s.n. are characterized by the following combination of features: adults with hindwing with basal portion of RP very short (Lawrence *et al.*, 2011), empodium well developed and visible between tarsal claws (Lawrence *et al.*, 2011; Robertson *et al.*, unpublished), tergite VIII not concealed by tergite VII in both male and female (Lawrence *et al.*, 2011). Larvae with one pretarsal seta and usually without mola (Ślipiński, 1992; Lawrence *et al.*, 2011). In addition, most cleroids are characterized by adults with mandibular mola absent (present in Byturidae and Biphylidae and some Trogossitidae), metacoxae extending laterally to meet elytral epipleura (most; exceptions: Byturidae and Biphylidae), aedeagus with paired tegminal struts in addition to the common anterior strut (Crowson, 1964a) (part, e.g., Byturidae, Biphylidae, most Trogossitidae, Acanthocnemidae); larvae with mandibular mola absent (most; exceptions: Byturidae and Biphylidae).

Included taxa. The superfamily Cleroidea s.n. includes Byturidae and Biphylidae and all families formerly classified as Cleroidea including Phloiophilidae, Trogossitidae, Chaetosomatidae, Metaxinidae, Thanerocleridae, Cleridae,

Acanthocnemidae, Phycosecidae, Prionoceridae, Mauroniscidae and Melyridae (Leschen, 2010).

Comments. There is no combination of character states that unites all the families of Cleroidea, and the addition of Byturidae and Biphyllidae only exacerbates the problem. Despite the phenotypic heterogeneity within this superfamily, Cleroidea **s.n.** are a strongly supported group based on molecular data (present study; Hunt *et al.*, 2007; Bocak *et al.*, 2014). Cleroidea is characterized by adults with mandibular mola absent, metacoxae extending laterally to meet elytral epipleura (most); larvae with mandibular mola absent, hypopharyngeal sclerome absent. However, these character states are not found in Byturidae and Biphyllidae. Early diverging cucujoids (e.g. Boganiidae, Hobartiidae) exhibit several features in common with Byturidae and Biphyllidae, hence their long classification within Cucujoidea. Anatomical features separating Byturidae and Biphyllidae from Cucujoidea **s.n.** are few, but include larvae with a single pretarsal seta (two in most Cucujoidea).

Cucujoidea Latreille, 1802 s.n.

Cucujipes Latreille, 1802: 210

Type genus. *Cucujus* Fabricius, 1775: 204

Diagnosis. Cucujoidea **s.n.** are characterized by the following combination of features: adults with procoxal cavities internally open (most), tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male (rarely 4-4-4), tergite VIII in female dorsally concealed by tergite VII (Lawrence *et al.*, 2011), tergite X (proctiger) in male completely membranous (Lawrence *et al.*, 2011). Larvae with frontal arms lyriform (most; exceptions: *Dacne*, *Hymaea*, *Propalticus*, Laemophloeidae, some Nitidulidae), mesal surface of mandible with well-developed mola (most; exceptions: *Myrabolia*, *Taphropiestes*, *Cyclaxyra*, laemophloeid group), maxillary articulating area present (most; exceptions: some Nitidulidae, *Smicrips*, *Lamingtonium* Sen Gupta & Crowson, *Taphrosclidia* Crotch, *Cyclaxyra*, laemophloeid group), hypopharyngeal sclerome present (most; exceptions: *Myrabolia*, *Cyclaxyra*, *Taphropiestes*, *Lamingtonium*, laemophloeid group), two pretarsal setae.

Included taxa. The superfamily Cucujoidea **s.n.** includes 25 families: Boganiidae, Hobartiidae, Helotidae, Protocucujidae, Sphindidae, Erotylidae, Monotomidae, Smicripidae, Kateretidae, Nitidulidae, Cryptophagidae, Agapythidae, Priasilphidae, Phloeostichidae, Silvanidae, Cucujidae, Myraboliidae, Cyclaxyridae, Cavognathidae, Passandridae, Phalacridae, Laemophloeidae (including Propalticidae; see McElrath *et al.*, 2015), Cybocephalidae, Tasmosalpingidae and Lamingtoniidae.

Comments. Even in the new, condensed concept of Cucujoidea, this superfamily remains difficult to characterize owing to the phenotypic heterogeneity exhibited in this group. Like

Cleroidea, there are no character states that unite all the families of Cucujoidea. Several subgroups of Cucujoidea are well defined anatomically such as the nitidulid series, cucujid series, laemophloeid group + *Cyclaxyra* and *Myrabolia*. More anatomical investigations are needed for Cucujoidea to identify shared morphological character states and provide more practical diagnostic features for this complicated group.

Coccinelloidea Latreille, 1807 stat.n.

Coccinellidae Latreille, 1807: 70

Type genus. *Coccinella* Linnaeus, 1758: 364

Diagnosis. Coccinelloidea are characterized by the following combination of anatomical features: adults with tarsal formula reduced (4-4-4 or 3-3-3), hindwings lacking a closed radial cell, hindwings with anal veins reduced, hind coxae separated by more than $\frac{1}{3}$ coxal width, intercoxal process of abdominal ventrite 1 broadly rounded or truncate (most), aedeagus resting on side when retracted, and phallobase (tegmen) reduced (exception: Coccinellidae). Larvae with pretarsal claw unisetae, spiracles usually annular, and sensory appendage of second antennomere usually as long as the third antennomere.

Included taxa. The superfamily Coccinelloidea comprises those taxa formerly considered the Cerylonid Series of Cucujoidea and includes the following 15 families: Bothrideridae **s.n.**, Teredidae **stat.n.**, Euxestidae **stat.n.**, Murrinidae **stat.n.**, Discolomatidae, Cerylonidae **s.n.**, Latridiidae, Akalyptoischidae, Alexiidae, Corylophidae, Anamorphidae **stat.rev.**, Endomychidae **s.n.**, Mycetaeidae **stat.n.**, Eupsilobiidae **stat.n.** and Coccinellidae.

Comments. Coccinelloidea **stat.n.** have been repeatedly shown to be only distantly related to the remaining cucujoid families (Hunt *et al.*, 2007; Robertson *et al.*, 2008; Marvaldi *et al.*, 2009; Bocak *et al.*, 2014) and are strongly supported here as a distinct cucujiform lineage.

Bothrideridae Erichson, 1845 s.n.

Bothriderini Erichson, 1845: 287

Type genus. *Bothrideres* Dejean, 1835: 312

Diagnosis. Bothrideridae **s.n.** are characterized by the following combination of anatomical features: adults with antennal insertions exposed from above, frontoclypeal suture distinct, gular sutures strongly convergent or confluent anteriorly, subantennal grooves well-developed, tentorium absent (part), pronotal disc variously modified with deep grooves or raised costae (most), mesocoxal cavities closed, metepisternum long and narrow, metepimeron strongly reduced, fused to metepisternum and concealed from below by elytra and metepisternum, metacoxae subcircular to circular, trochanters highly reduced

and concealed within excavation of femur, unequal protibial spurs, tarsi 4-4-4 in both sexes, elytral intervals costate or variously raised, apical abdominal ventrite with expanded margins fitting into interlocking devices of elytra, functional spiracles on abdominal segments I–VII, aedeagus symmetrical, phallobase long with articulated parameres (most) and long anterior tegminal strut, penis long and narrow with paired anterior struts, sternite VIII in female with long spiculum ventrale, and styli of ovipositor long and subapical. First instar larvae (triungulin) with labrum and clypeus fused to head capsule, single or two stemmata on each side, antenna two-segmented with very long antennomere 2 bearing long terminal seta, antennal sensorium on segment 1 elongate but shorter than antennomere 2, mandible narrow, sickle-shaped without mola or prosthema, ventral mouth parts protracted, maxillary palps two- or three-segmented, labial palps long, two-segmented, legs long, five-segmented, pretarsal seta single, segment IX with pair of long setae, spiracles annular. Latter instar larvae (ectoparasitic, grub like) with head capsule distinctly narrower than prothorax, stemmata absent, antennae very short one- or two-segmented, mandible short without mola or prosthema but with acute process at base, ventral mouthparts retracted with large maxillary articulating area, frons and clypeus fused, labrum free, legs variable, abdominal segment IX sometimes with short urogomphi, and spiracles annular.

Included taxa. This family includes all taxa formerly assigned to Bothriderinae including *Antibothrus* Sharp, *Acetoderes* Pope, *Asosylus* Grouvelle, *Bothrideres* Dejean, *Chinikus* Pope, *Cosmothroax* Kraatz, *Craspedophilus* Heinze, *Cylindromicrus* Sharp, *Dastarcus* Walker, *Deretaphrus* Newman, *Emmaglaeus* Fairmaire, *Erotylathris* Motschulsky, *Leptoglyphus* Sharp, *Lithophorus* Sharp, *Mabomus* Pope, *Ogmoderes* Ganglbauer, *Patroderes* Ślipiński, *Petalophora* Westwood, *Prolyctus* Zimmermann, *Machlotes* Horn, *Pseudantibothrus* Pope, *Pseudobothrideres* Grouvelle, *Pseudososylus* Grouvelle, *Roplyctus* Pope, *Shekarus* Pope, *Sosylus* Erichson, *Triboderus* Grouvelle.

Comments. In addition to the anatomical character states defining this strongly supported group, Bothrideridae are unique from an ecological standpoint for their parasitoid life history on wood-inhabiting larvae and pupae of Coleoptera and Hymenoptera.

Teredidae Seidlitz, 1888 stat.n.

Teredini Seidlitz, 1888 [Gatt.]: 57

Type genus. *Teredus* Dejean, 1835: 313

Diagnosis. Teredidae **stat.n.** are characterized by the following: adults with elongate body form, antennal insertions exposed from above, frontoclypeal suture distinct, gular sutures well-separated, subantennal grooves well-developed and extending posteriorly to midpoint of eye or beyond, tentorium

well-developed, corpotentorium with median process (most), labral rods club-like (absent in *Sysolus*), lacinia with apical uncus, mesocoxal cavities closed (narrowly open in *Sysolus*), hindwing with medial fleck divided (wings absent in *Anommatus*) and anal lobe present, trochanterofemoral attachment heteromeroid, apex of protibia spinose with fixed teeth, subequal protibial spurs, tarsi 4-4-4 or 3-3-3 (*Anommatus*) in both sexes, intercoxal process of abdominal ventrite 1 narrow with acute apex (broadly rounded in *Anommatus*), functional spiracles on abdominal segments I–VII, abdominal pleurites heavily sclerotized on all segments represented by a ventrite, *Xylariophilus*, *Teredolaemus* and *Sysolus* have the inner (anterior) edge of the last abdominal ventrite crenulate, anterior edge of sternite VIII in male with median strut, aedeagus symmetrical, phallobase long with articulated parameres and long anterior tegminal strut, penis long and narrow with paired anterior struts, sternite VIII in female with long spiculum ventrale, and styli of ovipositor long and subapical. Larvae with prognathous head bearing short epicranial stem (absent in *Anommatus*) and lyriform frontal arms, labrum free, frontoclypeal suture weak or absent, stemmata 0 or 5, antenna three-segmented with sensorium longer than apical antennomere, mandible with well developed mola but reduced or absent prosthema, ventral mouth parts retracted with large articulating area, hypostomal rods long and diverging posteriorly, thoracic and abdominal terga often granulose but without sclerotized plates, legs long, tergum IX complex but with upturned urogomphi, and spiracles annular (*Anommatus*) or annular-biforous.

Included taxa. The family Teredidae **stat.n.** comprises those taxa formerly classified as Anommatinae, Teredinae and Xylariophilinae, including *Abromus* Reitter, *Anommatus* Wesmael, *Kocherius* Coiffait, *Oxylaemus* Erichson, *Rustleria* Stephan, *Sosylopsis* Grouvelle, *Sysolus* Grouvelle, *Teredolaemus* Sharp, *Teredomorphus* Heinze, *Teredus* Dejean and *Xylariophilus* Pal & Lawrence.

Comments. Teredidae **stat.n.** share many character states with Euxestidae **stat.n.** but can usually be distinguished by their elongate body form [although *Metacerylon* (Euxestidae) is also relatively elongate], apex of protibiae spinose (setose in Euxestidae except *Metacerylon neotropicalis* Ślipiński), abdominal ventrite 1 narrow with apex acute or broadly rounded (*Anommatus*) (truncate in Euxestidae), aedeagus symmetrical (asymmetrical in Euxestidae), phallobase long with articulated parameres (parameres indistinct in Euxestidae) and long anterior tegminal strut (strut absent in Euxestidae).

Euxestidae Grouvelle, 1908 stat.n.

Euxestinae Grouvelle, 1908: 397

Type genus. *Euxestus* Wollaston, 1858: 411

Diagnosis. Euxestidae **stat.n.** are characterized by the following combination of anatomical features: adults with oval

to oblong body form (elongate in *Metacerylon*), subantennal grooves well-developed and extending posteriorly to midpoint of eye or beyond, frontoclypeal suture distinct, corpotentorium with median process, labral rods club-like, lacinia with apical uncus, mesocoxal cavities closed externally, hindwing with medial fleck divided (absent in *Metacerylon* Grouvelle) and anal lobe present, trochanterofemoral attachment usually heteromeroid, apex of protibiae setose (spinose in *Metacerylon neotropicalis* Ślipiński), subequal protibial spurs, tarsi 4-4-4 in both sexes, intercoxal process of abdominal ventrite 1 broad with angulate or truncate apex (Robertson *et al.*, unpublished), functional spiracles on abdominal segments I–VII, aedeagus with phallobase asymmetrical, median tegminal strut absent, parameres indistinct (distinct in *Pseudodacne*), and penis long and sclerotized (Ślipiński, 1990). Larvae with prognathous head without epicranial stem or frontal arms, labrum free, frontoclypeal suture absent, stemmata 0 or 2, antenna relatively long three-segmented with sensorium longer than apical antennomere, mandible with well developed mola and ventral accessory process, prostheca absent, ventral mouth parts retracted with articulating area, hypostomal rods sometimes visible and diverging posteriorly, thoracic and abdominal terga often granulate but without sclerotized plates sometimes with simple or branched processes, legs long, tergum IX with straight urogomphi, and spiracles annular-biforous, sometimes on short processes.

Included taxa. The family Euxestidae **stat.n.** comprises those taxa formerly classified as Euxestinae and includes the following genera: *Bradycycloxenus* Arrow, *Cycloxenus* Arrow, *Euxestoxenus* Arrow, *Euxestus* Wollaston, *Globoeuxestus* Ślipiński, *Hypodacne* LeConte, *Hypodacnella* Ślipiński, *Metacerylon* Grouvelle, *Metaxestus* Ślipiński, *Protoxestus* Sen Gupta & Crowson, *Pseudodacne* Crotch.

Comments. Euxestidae **stat.n.** and Teredidae **stat.n.** are anatomically similar and share many character states. However, Euxestidae can be distinguished from Teredidae by euxestid adults having the body form oval to oblong (elongate in *Metacerylon*, Teredidae), apex of protibia setose (spinose in *Metacerylon neotropicalis*, Teredidae), intercoxal process of abdominal ventrite 1 broad with angulate or truncate apex [acute (most) or broadly rounded in Teredidae], phallobase asymmetrical (symmetrical in Teredidae), median tegminal strut absent (present and long in Teredidae), parameres indistinct (distinct in *Pseudodacne*; Teredidae), and penis long and sclerotized (Ślipiński, 1990).

Murmidiidae Jacquelin Du Val, 1858 stat.n.

Murmidiides Jacquelin Du Val, 1858: 227

Type genus. *Murmidius* Leach, 1822: 41

Diagnosis. Murmidiidae **stat.n.** are characterized by the following combination of features: adults with broadly oval to

oblong body form with head deeply retracted into prothorax, frontoclypeal suture and transverse occipital carina distinct, corpotentorium with median process, antenna ten-segmented with one-segmented club, labral rods club-like, lacinia with apical spine, prothorax with antennal cavities at anterior angles, mesocoxal cavities closed externally, hindwing with medial fleck divided but without anal lobe, trochanterofemoral attachment heteromeroid, tarsi 4-4-4, intercoxal process of abdominal ventrite 1 broad with truncate apex, postcoxal lines present on metaventrite and abdominal ventrite 1, functional spiracles on abdominal segments I–V, ventrite 5 with hind margin crenulate, aedeagus with phallobase asymmetrical, median tegminal strut present, parameres distinct, and penis moderately long and sclerotized. Larvae broadly oval, disc-like with head completely hidden under pronotum, head prognathous without epicranial stem or frontal arms but with median endocarina, labrum free, frontoclypeal suture absent, stemmata absent, antenna long three-segmented with sensorium longer than apical antennomere, mandible with well developed mola and ventral accessory process, prostheca hyaline, ventral mouth parts retracted with large articulating area, hypostomal rods absent, thoracic and abdominal terga often granulate and asperate without sclerotized plates, abdominal terga I–VIII with lateral gland openings, tergum IX without urogomphi, and spiracles annular.

Included taxa. *Botrodus* Casey, *Murmidius* Leach and *Myhocerinus* Ślipiński.

Cerylonidae Billberg, 1820 s.n.

Cerylonides Billberg, 1820: 47

Type genus. *Cerylon* Latreille, 1802: 205

Diagnosis. Cerylonidae **s.n.** are characterized by the following combination of features: adults with frontoclypeal suture absent, corpotentorium with median process, labral rods long and narrow, maxillary and labial palps aciculate, hindwing without medial fleck or anal lobe, trochanterofemoral attachment elongate, functional spiracles on abdominal segments I–V, ventrite 5 with hind margin crenulate, aedeagus with tegmen reduced or absent, parameres very rarely distinct, and penis moderately long, heavily sclerotized and usually with complex internal sac. Larvae oval to onisciform with thoracic and abdominal terga variously lobed or expanded, head opisthognathous hidden under prothorax, epicranial stem and frontal arms absent, stemmata absent, labrum and clypeus fused, frontoclypeal suture absent, mouthparts modified with mandibles stylet-like united in tubular beak or endognathous (*Cerylon* Latreille); articulating area absent, spiracles annular, and tergite IX without urogomphi.

Included taxa. The family Cerylonidae **s.n.** includes *Ostomopsis* Scott, *Loebliorylon* Ślipiński and all taxa recognized in Ceryloninae by Ślipiński (1990).

Anamorphidae Strohecker, 1953 stat.n.

Anamorphini Strohecker, 1953: 15

Type genus. *Anamorphus* LeConte, 1878: 445

Diagnosis. This family is characterized by the following combination of anatomical features: adults with anterior arms of tentorium separate, corpotentorium present, mesocoxal cavities closed by the meso- and metaventrite, mesotrochantin concealed, pretarsal claws often modified, tarsi 4-4-4 or 3-3-3 (rarely 3-3-4 or 3-4-4), abdomen with five pairs of functional spiracles (functional spiracles absent on segments VI and VII), and penis broad and stout with endophallic sclerites. Larvae with body lacking tergal plates or sclerotization, covered with simple setae, mandibular apex reduced or absent, protheca absent, stemmata absent but may be present as a single pair in some *Bystus* spp., frontal arms absent or very poorly developed, and maxillary mala falciform.

Included taxa. Anamorphidae **stat.n.** include all taxa previously recognized as Anamorphinae (see Shockley *et al.*, 2009a).

Endomychidae Leach, 1815 s.n.

Endomychides Leach, 1815: 116

Type genus. *Endomychus* Panzer, 1795: 175

Diagnosis. Endomychidae **s.n.** are characterized by the following combination of features: adults with frontoclypeal suture distinct, straight (arcuate in some Merophysiinae) anterior arms of tentorium fused medially, corpotentorium present (most), subantennal groove absent (present in some Merophysiinae), pronotum often with basal and paired lateral sulci, visible portion of procoxae subglobular, tarsi 4-4-4 or 3-3-3 (Merophysiinae) usually pseudotrimerous (simple in Pleganophorinae, Merophysiinae, Leiestinae) (Tomaszewska, 2000), mesocoxal cavities open (closed in Merophysiinae and Pleganophorinae) mesotrochantin exposed (concealed in Pleganophorinae, Merophysiinae, Leiestinae), mesoventral postcoxal openings present, metaventral paired postcoxal openings present (Robertson, 2010), abdomen with five pairs of functional spiracles (functional spiracles absent on segments VI and VII), abdominal ventrite 1 without postcoxal lines, aedeagus variable, and tegmen with tegminal plate very short and fused parameres (long tegminal plate present in Leiestinae, whereas articulated parameres are present in *Phymaphora*, Leiestinae). Larvae with frontal arms well developed and long, typically U- or V-shaped (most), lyriform in Leiestinae, Pleganophorinae and Merophysiinae (poorly developed in Xenomycetinae), stemmata hemispherical in shape, four pairs (most), three pairs in Leiestinae and Xenomycetinae, two pairs in Pleganophorinae, absent in Merophysiinae.

Included taxa. Includes the genus *Endomychus* and all taxa previously classified as Danascelinae, Endomychinae,

Epipocinae, Leiestinae, Lycoperdininae, Merophysiinae, Pleganophorinae and Xenomycetinae (see Shockley *et al.*, 2009a).

Comments. The present study does not include exemplars of the subfamilies Danascelinae and Xenomycetinae. Although the family in its redefined constitution is well supported in the present study, the group remains anatomically heretogeneous.

Endomychinae Leach, 1815: 116 s.n.

Endomychides Leach, 1815: 116

Type genus. *Endomychus* Panzer, 1795: 175

Diagnosis. Endomychinae **s.n.** are characterized by the following combination of features: adults with body densely pubescent (glabrous in most species of *Endomychus*), pronotum with broad lateral, raised margins (most) (except for *Saula* and *Endomychus*), tegmen strongly reduced to simple, short ring encircling penis in half length, with long membranous flat strut (Tomaszewska, 2005), and basal parts of the coxites deeply excised (Tomaszewska, 2000, 2005) (entire in *Endomychus*). Larvae anatomically diverse, with abdominal terga provided with lateral parascoli (absent in *Endomychus* and *Ectomychus*) (Tomaszewska & Zaitsev, 2012), thoracic and abdominal terga with median ecdysial line present, frontal arms U-shaped (V-shaped in *Ectomychus*), hypostomal rods absent (present in *Ectomychus* and *Endomychus*), and mola well developed or replaced by membranous lobe in *Endomychus*.

Included taxa. *Endomychus* and all taxa previously classified as Stenotarsinae are included in this new concept of Endomychinae (see Shockley *et al.*, 2009a).

Comments. Although well supported by the present study, the newly defined subfamily Endomychinae is anatomically heterogenous in adult and even more so in larval stages. However, the combination of characters listed above separates Endomychinae **s.n.** from Cyclotominae **stat.n.** (including most former Endomychinae).

Cyclotominae Imhoff, 1856 stat.n.

Cyclotomidae Imhoff, 1856: [2] 151

Type genus. *Cyclotoma* Mulsant, 1851: 71

Diagnosis. Cyclotominae **stat.n.** are characterized by the following combination of anatomical features: adults with body highly convex, brightly coloured and ornamented, labial prementum entirely sclerotized without a distinct ligula (Tomaszewska, 2005), pronotal sulci absent or weakly developed, prosternal process broadly separates front coxae and extends posteriorly beyond them, penis curled along the proximal 1/3 of its length, sperm duct connected to broad attachment

between spermatheca and accessory gland (Tomaszewska, 2005).

Included taxa. *Cyclotoma*, *Meilichius*, *Bolbomorphus* and *Eucteanus*.

Comments. Cyclotominae **stat.n.** as circumscribed above are a distinctive and clearly defined group of Endomychidae. The larval form is not known for this subfamily.

Mycetaeidae Jacquelin Du Val, 1857 stat.n.

Mycetéides Jacquelin Du Val, 1857: 102

Type genus. *Mycetaea* Stephens, 1829: 87

Diagnosis. Mycetaeidae **stat.n.** are characterized by the following combination of anatomical features: adults with body vestiture consisting of long and suberect setae, anterior arms of tentorium fused medially, corpotentorium present, mentum with small triangular setose tubercle medially (Tomaszewska, 2005), mesoventral and metaventral postcoxal openings absent (Robertson, 2010), mesocoxae laterally open, mesotrochantin concealed, and abdomen with five pairs of functional spiracles (functional spiracles absent on segments VI and VII).

Larvae of *Mycetaea* and *Agaricophilus* are notably different anatomically, but both genera share two pairs of stemmata, a rigid tooth-like prosthema and frontal arms absent or at most poorly developed (Tomaszewska, 2005).

Included taxa. *Mycetaea* and *Agaricophilus*.

Comments. This family is anatomically heterogeneous. *Agaricophilus* was not sampled in the present study so the monophyly of Mycetaeidae remains in question. As reviewed by Tomaszewska (2005), *Mycetaea* and *Agaricophilus* are quite different anatomically in both the adult and larval forms, being united by only a single adult character state: mentum with small triangular setose tubercle medially.

Eupsilobiidae Casey, 1895 stat.n.

Eupsilobiini Casey, 1895: 452

Type genus. *Eupsilobius* Casey, 1895: 454 [= *Eidoreus* Sharp, 1885: 146]

Diagnosis. Eupsilobiidae **stat.n.** are characterized by the following combination of features: adults with frontoclypeal suture present (absent in *Chileolobius*), subantennal grooves short, anterior arms of tentorium widely divergent and narrowly fused medially, antennal club comprising one or two antennomeres, procoxae internally closed and externally widely open, anterior edge of the mesoventrite on a different plane as the metaventrite, mesocoxae laterally open, mesoventral and metaventral

postcoxal openings absent, metacoxae transverse, metaventral postcoxal lines moderately to well developed (absent in *Natalinus* and *Ibicarella*), tarsal formula 4-4-4, abdomen with five pairs of functional spiracles (functional spiracles absent on segments VI and VII), abdominal ventrite 1 with postcoxal lines, penis elongate, slender and curved with the base sclerotized and T-shaped, tegmen complex but with parameres fused, and sperm duct modified, partly sclerotized and inflated or twisted (Tomaszewska, 2011). Larvae with body covered with frayed setae, a rigid tooth-like prosthema, two pairs of stemmata, and frontal arms absent (Tomaszewska, 2005).

Included taxa. *Cerasommatidia* Brèthes, *Chileolobius* Pakaluk & Ślipiński, *Eidoreus* Sharp, *Evolocera* Sharp, *Ibicarella* Pakaluk & Ślipiński, *Microxenus* Wollaston and *Natalinus* Tomaszewska.

Comments. Eupsilobiidae shares many anatomical features with Coccinellidae and Endomychidae; the combination of characters listed above distinguishes Eupsilobiidae from both families.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12138

Table S1. Terminal taxa and genes used in this study. Taxonomy follows classification prior to changes introduced in the text. The subfamily or tribe is given when relevant.

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