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. Akalyptochiidae 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.
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.,** Eusilobiidae **stat.n.,** and Mycetaeidae **stat.n.** The following taxa are redefined and characterized: Cleroidea **s.n.,** Cucuoidea **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**

**Cucuoidea**

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), Cucuoidea (flat bark beetles, pleasing fungus beetles, lady beetles, etc.; >19 000 species), Chrysolaelioidea (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, Cucuoidea is the most problematic with regard to classification and no synapomorphies supporting its monophyly have been identified (Leschen et al., 2005; Leschen & Sliźniński, 2010). Cucuoidea is the most problematic with regard to classification and no synapomorphies supporting its monophyly have been identified (Leschen et al., 2005; Leschen & Sliźniński, 2010). Cucuoidea 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 Cucuoidea such that these two superfamilies are difficult to separate (Crowson, 1955; Lawrence & Newton, 1982). As such, characterizing Cucuoidea is problematic. The current classification recognizes 37 families of Cucuoidea (Leschen et al., 2005; Leschen & Sliźniński, 2010; Lord et al., 2010; Cline et al., 2014). Cucuoidea exhibit a broad range of host utilization and typically have cryptic life histories in leaf litter, dead wood or fungi (Fig. 2).

Cucuoidea 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 Cucuoidea 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 Cucuoidea. 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 Cucuoidea,’ 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 Cucuoidea 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 Cucuoidea in their 320 taxa dataset and their results recovered Cucuoidea as grossly polyphyletic. Silvanidae and Phloeostichidae were recovered sister to Curculionoidea; Byturidae and Biphyllidae were placed within Cleroidea; the CS was recovered as the sister group to Cleroidea; the family Spinidae was supported as the sister group to Tenebrionoidea (including Lymexyloidea); the remaining cucujoid exemplars formed a large clade sister to Chrysomelidae.

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 rrmL and COI. Their supermatrix comprised over 8000 terminals (not all were different species). Cucuoidea were recovered as polyphyletic with Byturidae + Biphyllidae recovered sister to Cleroidea: Spinidae + Cybocoephalidae (= Cybocoephalinae (Niditulidae)) (Cline et al., 2014]) were supported as an isolated cucujiform lineage; most of the core cucujoids formed a clade sister to Phytophaga; Niditulidae (most, including Passandridae) + Kateretidae formed the sister group...
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 Akalyptoschiidae (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 Krášenský, 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 Coryphidae and the endomychid subfamily Merophysinae (as Holoparamecineae). 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., Chilicorinae, 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 Cerylophidae 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 Cerylophidae, 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 superfamily CS clades: one clade comprising Bothrideridae, Cerylonidae and Discolomatidae; a second clade including Cerylophidae, Coccinellidae Endomychidae and usually Latridiidae. The analysis of Bocak et al. (2014) further indicates that Alexiidae and Akalyptoischidae 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: Xylariophonius Pal and Lawrence (Xylariophilinae) and Teredolaemus Sharp (Teredininae) were placed among the main cluster of non-CS cucujoids sister to Monotomidae; Bothridides Dejean (Bothriderinnae) was recovered sister to Passandridae, forming a clade that subends Phytophaga. Hypodacnella Slipiński (Cerylonidae) + Bystus Guérin-Méneville (Endomychidae) was recovered as a sister grouping within a small, isolated cucujiform clade including the cucujoid families Phalaridiae, Cavognathiidae and Myrabilidiidae. 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 superfamly 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 Tasmosalpingidae (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 superfamly. We sampled within Tenebrionoidea (15 exemplars representing 12 families), Cleridae (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. Akalyptoischidae: three exemplars (monogenic, 100% generic representation); Alexiidae: two species (monogenic, 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); Cerylophidae: 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 Caphalophaninae (Discolomatidae), and Danascelinae and Xenomyctetinae (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 metastarohax 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 Rev- eleviera californica Fall, CO488 Dieranella intermedia Belon, CO902 Oxylaemus californicus Crotch, CO905 Deretaphrus oregonensis Horn, CO931 Mychocerus discretus (Casey), CO934 Aenigmaticus californicus Casey]; and the Australian National Insect Collection (ANIC), CSIRO, Canberra, Australia (ccoc_234 Boganium 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 Periptycus Blackburn (28S only) and Carinodorulinka 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 COII 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 (Madison & 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 + Boganidae relative to the Nitidulidae group and/or the clade comprising Helotiidae, Erotylidae and allies) and placement of select taxa (e.g. Philoophilidae placed sister to Biphyllidae + 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 to Phytophaga, and Boganidae 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 Biphyllidae were strongly supported as the sister group of Cleroidea. The superfamilies 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 (Anonmatinae, Teredininae, 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 Mycetaeinae and Eupsilobiinae closely allied to Coccinellidae, and the recovery of Anamorphinae as sister to Corylophidae. Akalyptoischionidae (Akalyptoischion) were not allied with Latridiidae and were supported as a distinct family within the CS. CS subfamilies not supported as monophyletic include Teredininae (Bothrideridae), Endomychidae (Endomychidae) and Stenotarsinae (Endomychidae).

Discussion

Major cucujiform lineages

Phylogenetic studies that specifically address the major cucujiform relationships are lacking (Leschen & Šlipiński, 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 Biphyllidae 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 familial 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 Cucuoidea 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 Cucuoidea (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 tenebrionid 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 Cucuoidea (Crowson, 1955; Ślipiński & Pakulak, 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 Cucuoidea, 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 tegmental 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.l.

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 Cucuoidea rather than Cleroidea. Interestingly, Xeriasia 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, Tennescheila Westwood, Gyrocharis Thomson and Larinatus 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 Dasystes 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 Cucuoidea

The early diverging lineages of core Cucuoidea recovered in the present study include three major clades: (i) Monotomidae + nitidulid series, (ii) erotylid series (Helotidae-Protocucujidae-Protospinhidus Sen Gupta & Crowson-Erotylidae), (iii) Boganidae + Hobartidae (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 Boganidae 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 Parandrexis Martynov representing a putative intermediate form between boganids 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 Cucuoidea 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, erotylid series, Boganidae + Hobartidae) represents a viable candidate for the earliest diverging lineage of core Cucuoidea. 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 Cucuoidea 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 subverting 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 Cucuoidea. Crowson (1955) noted the similarity of Monotomidae and the nitidulid group based on shared adult anatomical features including aedeagus uninvetered 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 tereidine and xylariophile Bothrideridae 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 Cucujoida 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 $\geq 90$ 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 metaventrite. 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 Tomaszewski & Sliźniś (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 Hobartius 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 Philocestichidae 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 Philocestichidae and allies vary between studies (see below).

Phleocestichid group

Until recently, the family Phleocestichidae comprised a heterogeneous assortment of Notogean taxa that had been placed previously in a wide variety of families and superfamilies (see Lawrence & Sliźniś, 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 Agapthyidae, Priasilphidae, Tasmosalpingidae and Myraboliidae, leaving four genera in a redefined Phleocestichidae. 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 Agapthyo Broun (Agapthyidae), Priasilpha Broun (Priasilphidae), Taphropiestes Reitter (= Cavognatha Crowson) (Cavognathidae) and Hymaea Pascoe (Phleocestichidae) (Fig. 5). Within this clade Agapthyo 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 Cyclaxyla 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 Laemophloeidae 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 laemophloeids 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 & Nears, 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 *Platissus* 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 & Nears, 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 & Nears (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 Nitetulidae (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 Phalacridae 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* (Endomychiidae). 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 (Myrabolidae) (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. Myrabolidae represents another species-poor, monogenic family with 13 species restricted to Australia. The inclusion of *Myrabolia* in multiple cucujoid families historically (e.g. Cucujidae, Silvanidae and Phloeostichidae; see Śipiński *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 Taphromyrmex (= Cavognatha). The clade comprising *Myrabolia* and *Cyclyxura* represents a second Neotropical cucujoid lineage supported by the present study (see phloeostichid group above). Interestingly, the clade *Myrabolia* + *Cyclyxura* forms the sister group to the laemophloeid group. Several larval features corroborate this clade and suggest that *Taphromyrmex* may also be affiliated with this superfamily group. The larval form of *Myrabolia*, *Cyclyxura*, *Taphromyrmex* 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 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 Cyclyxuridae and Myrabolidae 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 \( \geq 90 \) 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, Anommatinae) 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 ectoparasitoidal 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) Murmidinae (Cerylonidae) + Discolomatidae, (ii) a clade comprising all free-living bothriderids (Teredinae, Xylariophilinae, Anommatinae), (iii) Euxestinae (Cerylonidae), and (iv) Ostomopsinae (Cerylonidae) + Ceryloninae. The relationships between these four clades, however, were only weakly supported (Fig. 6). Murmidinae comprised three genera – Murmidius Leach, Mychocerus 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 Murmidinae, 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 Murmidinae relative to the remaining cerylonid subfamilies, but our results indicated that they are synapomorphies for Murmidinae + 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 Aphanonecephalinae is monophyletic. Interestingly, an undescribed genus resembling Parafaellia Arrow (Aphanonecephalinae) 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 (Anommatinae, 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 Oxyleanus 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 Rusiteria Stephan, known from only a single specimen from SW Arizona, and the anatomically odd genera Saxiylopsis (endemic to Madagascar) and Sylosolus 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 cerylons, 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, subantenal 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. Ostomopinae + 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 eustesine lineage. Eustestoxenus Arrow and Cycloxenus Arrow were strongly supported (100) as sister taxa; the former is a known myrmecophile and both are known termotrophs. 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 monogenic Ostomopinae 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 Ostomopinae 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 Ostomopinae. 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 Ostomopinae 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 Loebioryloninae (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. Cylrotion Latreille) or enclosed within a tubular beak (e.g. Philothermus Aubé, Mychocerus Erichson) in larvae. Note that whereas both Murmidiinae and Ostomopinae also have a crenulate last abdominal ventrite, the homology of the eulynid locking mechanisms exhibited in these three subfamilies (Ceryloninae, Murmidiinae, Ostomopinae) 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 Murmididae stat.n. Euxestinae cerylonides are elevated to family status as Euxestidae stat.n. Finally, we retain Ostomopinae, Ceryloninae and Loebioryloninae in a new concept of the family Cerylonidae stat.n.

Coccinellid group

Latridiidae and Akalyptoischidae

Latridiiade 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), Merophasmatinae (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, Akalyptoischidiidae, 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 coccinellid families including the bothridierid group (Lord et al., 2010), or weakly supported as the sister group to a clade comprising a grade of leiestine and merophyline 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 Corticarinae are strongly supported as monophyletic, but the internal relationships within these groups, particularly Corticarinae, 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 (Akalyptoischidiidae). It should be noted however that the topological support separating Akalyptoischidiidae and Latridiidae (i.e. the clade comprising Akalyptoischidiidae and the remaining coccinellid group taxa) was rather weak (60). Akalyptoischidiidae 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 (Slipiński & Tomaszewska, 2010). The family was traditionally included as a subfamily (Sphaerosomatinae) within Endomychidae, but Sen Gupta & Crowson (1973) recognized the distinctiveness of Sphaerospoma 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 anamphine 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 punctuation 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 prostheca and a bifid apical incisor; the larvae have the incisor lobe highly reduced or absent (Tomaszew ska, 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 Merophysoinae), mesocoxal cavities widely closed by the meso- and metaventrite (open to mesepimeron in core endomychids, except Merophysoinae 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 Papsuenta Strohecker, Clemmas [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 $\geq 90$ are indicated by black circles, and nodes with support between 70 and 89 are indicated by grey circles.

anterio rly in remaining anamorphids), the metacoxae widely separated, more than 1.5× the coxal width (between 1/4 and 1× the coxal width in remaining anamorphines) and the trochantero-femoral 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 trochantero-femoral attachment. Indeed, Ero tendomychus 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 (´Slipi´nski et al., 2009). Furthermore, Periptycus Blackburn (Periptyctinae), was classified within Endomychidae and only recently transferred to Corylophidae (´Slipi´nski 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). Periptycus 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 lycoperdine species groups. Most taxa currently classified as Endomychidae formed a well-supported clade (100) in the present analyses (Fig. 8). The subfamilies Anamorphinae, Mycetaeinae and Eupsilobiinae, 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 merophysine 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 merophysine complex have the mesotrochantin concealed (exposed in remaining core Endomychidae), have tarsi simple (pseudotrimorous 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 Merophysinae and Pleganophorinae are known to be inquilines, 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 Merophysinae 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 Merophysinae (100). Both Leiestinae and Merophysiinae have the metendosternite with two vertical admedian processes from which the tendons arise (Robertson, 2010; J.A. Robertson, A. ´Slipi´nski, J.V. McHugh, personal observation) and their larvae are relatively cylindrical in form without processes or tubercles, with simple vestiture and mandibles without prostheca (Burakowski & ´Slipi´nski, 2000).

The second major clade of core Endomychidae (hereafter referred to as the endomychine complex) (100) corresponds to Tomaszew ska’s (2005) ‘higher Endomychidae’ and includes taxa classified as Endomychinae, Stenotarsinae, Epipocinae and Lycoperdineinae (Fig. 8). These taxa were supported as a clade in Tomaszew ska’s (2005) cladistic analysis by having adults with pseudotrimorous tarsi and larvae with well developed V- or U-shaped frontal arms and four pairs of stemmata. Our analyses indicated that neither Endomychinae nor Stenotarsinae are monophyletic. Endomychinae currently includes five genera: Endomychus Panzer, Cyclotoma Mulsant, Melilichus Gerstaecker, Bolbomorphus Gorham and Eucteanus Gerstaecker (Shockley et al., 2009a); only the first three were sampled here. Cyclotoma and Melilichus (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 + Melilichus 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 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, Melilichus, 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 $\geq 90$ 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 Endomychini 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) lycoperdine species groups. For example, the clade (100) comprising Encymon Gerstaecker, Eumorphus Weber, Indalrus Gerstaecker and Ancylopus Costa is part of Tomaszewska’s (2005) Eumorphus group; Acinaces Gerstaecker, Beccariola Arrow and Corynomalus Chevrolat (= Amphis Laporte) belong to the Corynomalus group. However, our results were not entirely consistent with any of the proposed lycoperdine 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 prostheca 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 pseudotramerous 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). Eupsilobiines have previously never been sampled in a molecular phylogenetic analysis. Interestingly, Crowson (1981) postulated a close relationship between Eidoreus (Eupsilobiinae) and Coccinellidae; others have also 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: Xenomyces Horn, but these are different in form, and Cholovocerida 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 terminal phallobase that projects forward forming a penis guide, an articulated anterior terminal strut (trabes), a pair of parameres, and an elongate, slender and curved penis (sipho) 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 coccinellid 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 $\geq 90$ 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 Sasají (1968) and Kowâ (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 Seranginini (Escalona & Slipiński, 2012). Within Microseiseinae the anatomically bizarre Carinodalinka (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 Seranginini (99), whereas Microweiseini was rendered paraphyletic by Seranginini. We recovered a well-supported clade comprising Microseisea 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 Chilocorini (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 + Chilocorini as well. Branch support for the internal relationships within Coccinellini and Chilocorini 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 Chilocorini 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 chilocorine lineage in the present study and Seago et al. (2011). Beyond the placement of *Monocoryna*, sister grouping of Coccinellini + Chilocorini, and the internal relationships within Coccinellini and Chilocorini, 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: *Hyperaspis* Crotch + *Brachiacantha* Chevrolat; *Neorhizobius* Crotch (Oridia Gorham + *Chnodes* Chevrolat); *Salcolotis* Miyatake + *Sticholotis* Crotch], most higher-level coccinelline relationships subdivide 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 Cucujoida may well merit division into two or more superfamilies, not necessarily on present Clavicornia [Cucujoida] - Heteromera [Tenebrionoidea] lines.’ The results of the present study strongly support such an action as implemented in the following.

*Cleroidea Latreille, 1802 s.n.*

Cleri Latreille, 1802: 110

*Type genus. Clerus Geoffroy,* 1762: 303

*Diagnosis.* Cucujoida 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 (Slipiński, 1992; Lawrence et al., 2011). In addition, most cleroids are characterized by adults with mandibular mola absent (present in Byturidae and Biphyllidae and some Trogossitidae), metasternae extending laterally to meet elytral epipleura (most; exceptions: Byturidae and Biphyllidae), aedeagus with paired tegmental struts in addition to the common anterior strut (Crowson, 1964a) (part, e.g., Byturidae, Biphyllidae, most Trogossitidae, Acanthocnemidae); larvae with mandibular mola absent (most; exceptions: Byturidae and Biphyllidae).

*Included taxa.* The superfAMILY Cleroidea s.n. includes Byturidae and Biphyllidae and all families formerly classified as Cleroidea including Philoophilidae, Trogossitidae, Chaetosomatidae, Metoxinidae, Thanerocleridae, Cleridae,
Acanthocoenidae, 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, Hymaena, 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, Taphroscelidia 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, Cystophasidae, Agapthyidae, Priasilphidae, Phloeostichidae, Silvanidae, Cucujidae, Myrabloidae, 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 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 unisette, 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 Cerylionid Series of Cucujoidea and includes the following 15 families: Bothrideridae s.n., Tereididae stat.n., Euxestidae stat.n., Mermisidae stat.n., Discolomatidae, Cerylonidae s.n., Latridiidae, Akalyptoischiidae, 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 antenial 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 metepistemum and concealed from below by elytra and metepistemum, 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 tegmental struts, 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 sternites on each side, antenna two-segmented with very long antennomere 2 bearing long terminal setae, antennal sensorium on segment 1 elongate but shorter than antennomere 2, mandible narrow, sickle-shaped without mola or prostheca, ventral mouth parts protracted, maxillary palps two- or three-segmented, labial palps long, two-segmented, legs long, five-segmented, preoral seta single, segment IX with pair of long setae, spiracles annular. Latter instar larvae (ectoparasitic, grub like) with head capsule distinctly narrower than prothorax, sternum absent, antennae very short one- or two-segmented, mandible short without mola or prostheca 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.


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 from an ecological standpoint for their parasitoid life history on wood-inhabiting larvae and pupae of Coleoptera and their functional spiracles on abdominal segments I– VII, abdominal pleurites heavily sclerotized on all segments represented by a ventrite, Xylarophilus, 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 tegmental struts, 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, sternum absent or 5, antenna three-segmented with sensorium longer than apical antennomere, mandible with well developed mola but reduced or absent prostheca, 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.

Teredinae Seidlitz, 1888 stat.n.

Teredini Seidlitz, 1888 [Gatt.]: 57

Type genus. Teredus Dejean, 1835: 313

Diagnosis. Teredinae 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, mesoscoxal cavities closed (narrowly open in Sysolus), hindwing with medial fleck divided (wings absent in Anommatus) and anal lobe present, trochantero-femoral attachment heteromeroïd, 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, Xylarophilus, 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 tegmental struts, 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, sternum 0 or 5, antenna three-segmented with sensorium longer than apical antennomere, mandible with well developed mola but reduced or absent prostheca, 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.

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*), subanten- 
nal grooves well-developed and extending posteriorly to mid-
point of eye or beyond, frontoclypeal suture distinct, corpoten-
torium with median process, labral rods club-like, labicinia 
with apical uncus, mesoxocaval cavities closed externally, 
hindwing with medial fleck divided (absent in *Metacerylon* Grouvelle) 
and anal lobe present, trochanterofemoral attachment usually 
heteromeroideal, 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), 
fuctional 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, sternmata 0 or 2, antenna rela-
tively long three-segmented with sensorium longer than apical 
antennomere, mandible with well developed mola and ven-
tral accessory process, prostheca absent, ventral mouth parts 
retracted with articulating area, hypostomal rods sometimes 
visible and diverging posteriorly, thoracic and abdominal terga 
often granulose and asperate (´Slipi´nski, 1990). Larvae with prognathous 
head without epicranial stem or frontal arms, labrum free, 
frontoclypeal suture absent, sternmata 0 or 2, antenna rela-
tively long three-segmented with sensorium longer than apical 
antennomere, mandible with well developed mola and ven-
tral accessory process, prostheca absent, ventral mouth parts 
retracted with articulating area, hypostomal rods sometimes 
visible and diverging posteriorly, thoracic and abdominal terga 
often granulose 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: *Bradyxestes* Casey, *Cycloxenus* Arrow, *Cycloxenus arrow*, *Euxestoxenus* Arrow, *Euxestus* Wollaston, *Globoeux-
estus* Ślipiński, *Hypodacne* LeConte, *Hypodacnella* Ślipiński, 
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 protibiae setose (spinose in *Metacerylon neotropicalis* Ślipiński), intercoxal process of 
abdominal ventrite 1 broad with angulate or truncate apex [acute 
(most) or broadly rounded in Teredidae], phallobase asymme-
trical (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 Jacqellen Du Val, 1858 stat.n. 
Murmidiides Jacqellen Du Val, 1858: 227 

* Type genus. *Murmidius* Leach, 1822: 41 

* Diagnosis. Murmidiidae stat.n. are characterized by the follow-
ing combination of features: adults with broadly oval to 
oblong body form with head deeply retracted into prothorax, 
frontoclypeal suture and transverse occipital carina distinct, 
corapotentorium with median process, antenna ten-segmented with 
one-segmented club, labral rods club-like, labicinia with api-
cal spine, prothorax with antennal cavities at anterior angles, 
mesoxocaval cavities closed externally, hindwing with medial 
fleck divided but without anal lobe, trochanterofemoral attach-
ment heteromeroideal, tarsi 4-4-4, intercoxal process of abdomi-
nal ventrite 1 broad with truncate apex, postcoxal lines present 
on metaventrite and abdominal ventrite 1, functional spiri-
cles on abdominal segments I–V, ventrite 5 with hind mar-
gin 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 with-
out epicranial stem or frontal arms but with median endoca-
rina, labrum free, frontoclypeal suture absent, sternmata absent, 
antaenna long three-segmented with sensorium longer than api-
cal antennomere, mandible with well developed mola and ven-
tral accessory process, prostheca hyaline, ventral mouth parts 
retracted with large articulating area, hypostomal rods absent, 
thoracic and abdominal terga often granulose and asperate 
without sclerotized plates, abdominal terga I–VII with lateral 
gland openings, tergum IX without urogomphi, and spiracles 
annular.

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

* Cerylonidae Billberg, 1820 s.n. 
Cerylonides Billberg, 1820: 47 

* Type genus. *Cerylon* Latreille, 1802: 205 

* Diagnosis. Cerylonidae s.n. are characterized by the follow-
ing combination of features: adults with frontoclypeal suture 
absent, corapotentorium with median process, labral rods long 
and narrow, maxillary and labial palps aciculate, hindwing 
without medial fleck or anal lobe, trochanterofemoral attach-
ment 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 abdo-
nominal 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); articu-
latating area absent, spiracles annular, and tergite IX without 
urogomphi.

* Included taxa. The family Cerylonidae s.n. includes *Osto-
mopsis* 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, mesosacral cavities closed by the meso- and metaventrite, mesotrochantin concealed, preterial 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, prostheca 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), subantenal 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, 2005) (entire in Endomychidae), thoracic and abdominal terga with median ecdysial line present, metaventral paired 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 hemisphaerical 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 heterogeneous 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 ½ of its length, sperm duct connected to broad attachment.
between spermatheca and accessory gland (Tomaszewska, 2005).

**Included taxa.** Cyclotoma, Meilichius, Bolboromorphus 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 Mycetae and Agaricophilus are notably different anatomically, but both genera share two pairs of stemmata, a rigid tooth-like prostheca and frontal arms absent or at most poorly developed (Tomaszewska, 2005).

**Included taxa.** Mycetae 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 prostheca, 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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