PHYLOGENETIC SYSTEMATICS OF THE CERYLONID SERIES OF CUCUJOIDEA (COLEOPTERA)

by

JAMES A. ROBERTSON

(Under the Direction of Joseph V. McHugh)

ABSTRACT

We conduct a large-scale phylogenetic investigation of the Cerylonid Series (C.S.) of Cucujoidea, a diverse group of cucujoid beetles comprising 9,600 species classified in eight families, using morphological data (76 taxa × 147 adult and larval characters), molecular data (341 taxa × 9 genes: 18S, 28S, H3, 12S, 16S, COI, COII, CAD and ArgK) and a combination of the two datasets.

In total, our analyses suggest the following: the C.S. is a monophyletic group based on both morphological and molecular evidence; the superfamily Cucujoidea is paraphyletic with respect to the remaining superfamilies in the series Cucujiformia; the C.S. represents a unique clade within Cucujiformia and should be recognized as its own supferfamily, Coccinelloidea, within the series; Byturidae and Biphyllidae should be transferred to Cleroidea; the C.S. families Corylophidae, Coccinellidae, Latridiidae, and Discolomatidae, are monophyletic; Cerylonidae, Endomychidae, and Bothrideridae are paraphyletic. Bothrideridae is split into two distinct families comprising the former Bothriderinae (as Bothrideridae) and the other including the remaining subfamilies (as Teredidae); the cerylonid subfamily Euxestinae is included within Teredidae; the new concept of Cerylonidae includes the following subfamilies: Ceryloninae, Ostomopsinae, Murmidiinae, Discolomatinae and Loebliorylonininae (inserte sedis); the status of the putative new C.S. family, Akalyptoischiidae, is uncertain; the endomychid subfamily Anamorphinae is elevated to familial status, as Anamorphidae.

INDEX WORDS: Cucujoidea, Coleoptera, Alexiidae, Bothrideridae, Cerylonidae, Corylophidae, Coccinellidae, Latridiidae, Endomychidae

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DEDICATION

This work is dedicated to my dear wife, Emily Robertson, who has believed in me from day one. Without her continued support, love, sacrifice, and taking care of things in the home, I simply could not have accomplished this work. Indeed, the completion of this dissertation is just as much of an accomplishment for her as it is for me.

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CHAPTER 1

INTRODUCTION

The dissertation research presented herein comprises a four-tiered approach to investigating the phylogenetic relationships and evolution of the Cerylonid Series (C.S.) of Cucujoidea, a diverse group of beetles comprising 9,600 species classified in eight families. The dissertation is written in article style and attempts to produce the following: 1) a preliminary phylogenetic analysis of the C.S. using 18S and 28S rDNA sequences, 2) an extensive morphological study and cladistic analysis of the C.S., 3) an investigation of the phylogeny of Cucujoidea with insight regarding the evolution of host utilization, and 4) a revision of the classification of the C.S. based on a phylogenetic analysis of morphological and molecular data.

The first major component of my dissertation research includes an initial investigation of the monophyly and internal relationships of the C.S. using molecular data (18S and 28S rDNA). At the onset of this research, multiple phylogenetic studies of individual C.S. families (e.g., Latridiidae, Coccinellidae, Endomychidae) in conjunction with an NSF funded PEET grant were being conducted in PI J. V. McHugh's lab. At the time very little was known regarding the higher-level relationships within the C.S., making it difficult to select appropriate outgroup taxa for phylogenetic studies of individual C.S. families. This analysis is meant to serve as an initial pass where we identify problematic areas of the current classification and specific questions to address using an expanded data set in subsequent studies. We attempt to identify natural lineages within this diverse beetle clade. This study serves as a baseline for subsequent systematic studies of the C.S. in its entirety or for any of the C.S. families. This component of my dissertation is published in the journal *Molecular Phylogenetics and Evolution* and was reprinted here with permission as Chapter 3.

The second research component includes an extensive morphological study of the C.S. We construct an extensive morphological character matrix (147 characters) for an exemplar taxon sampling (76 taxa) covering C.S. familial and subfamilial diversity. We investigate the validity of the historical characters used to define the C.S. We attempt to discover new and refine existing synapomorphies for higher-level clades within the C.S. in an effort to provide resolution among some of the historically more problematic lineages. This research is presented in Chapter 4.

Chapter 5 includes a large-scale phylogenetic analysis of the superfamily Cucujoidea with emphasis on the C.S. We present a phylogeny of Cucujoidea with an emphasis on the C.S. based on possibly the largest dataset of Coleoptera to date. We use the above dataset to test the monophyly of Cucujoidea with respect to the remaining superfamilies of Cucujiformia and test the monophyly of the C.S., C.S. families, subfamilies, and higher taxa. We also explore the relationships among non-C.S. cucujoids and the placement of the C.S. within Cucujoidea and investigate the internal relationships of the C.S. Finally, we investigate the evolution of host utilization and attempt to reconstruct the evolutionary history of cucujoid associations with diverse host types.

In Chapter 6 we apply a total evidence approach to inferring relationships among C.S. taxa. Using a subset of data from Chapters 4 and 5, we reconstruct the phylogeny for an exemplar sampling of C.S. taxa. With the resulting robust phylogenetic framework in hand, we revise the classification and constitution of the constituent C.S. families as warranted in light of our results.

In the final chapter, I attempt to summarize the above research.

CHAPTER 2

REVIEW OF THE CERYLONID SERIES OF CUCUJOIDEA

Of the six superfamilies in the mega-diverse infraorder Cucujiformia, Cucujoidea is the most problematic; no synapomorphies supporting its monophyly have been identified (Leschen and Ślipiński, 2010). Cucujoidea is a heterogeneous group of beetles that have a similar habitus (e.g. small, drably colored, clubbed antennae) with non-heteromerous tarsi that could not be placed satisfactorily elsewhere. It was established for convenience and represents the largest taxonomic dumping ground among the superfamilies of Coleoptera. Cleroidea in particular shares many characters with certain groups of Cucujoidea such that these two superfamilies are difficult to separate (Crowson, 1955; Lawrence and Newton, 1982). As such, Cucujoidea is difficult to characterize. The current classification recognizes 36 families of Cucujoidea (Leschen, et al., 2005).

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

Notwithstanding, a number of important advances in cucujoid relationships and corresponding improvements to the classification have been made in the past 50 years. In their review of the classification of Coleoptera, Lawrence and Newton (1982) outlined three major advances in the taxonomy and classification of Cucujoidea. The first was the recognition of several presumed "primitive," primarily south temperate groups such as Protocucujidae (Crowson, 1955), Boganiidae, Hobartiidae, Phloeostichidae, and Cavognathidae (Sen Gupta and Crowson, 1966; 1969; Crowson, 1973). Members of the above families were either misplaced among existing taxa or previously unknown. The second contribution was the removal of several taxa from Cryptophagidae and placed in other families, primarily Languriidae (now Erotylidae) (Sen Gupta and 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 (C.S.) (Crowson, 1955).

The Cerylonid Series is a cluster of presumably highly derived families within Cucujoidea comprising Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae.

Crowson's (1955) original concept of the Cerylonid Series included Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, Merophysiidae and Latridiidae. Since then the constitution of the group has been modified via family-level refinement that was accomplished primarily by the work of Lawrence (1980, 1982, 1985, 1991). Lawrence (1982, 1991) elevated the endomychid subfamily Sphaerosomatinae to familial status (= Alexiidae), although the distinctness of Sphaerosomatinae and the need for its elevation to family status had been recognized previously (e.g., Sen Gupta and Crowson, 1973). Merophysiidae was subordinated within Endomychidae (Lawrence, 1982, 1991). The subfamily Bothrideridae was removed from the tenebrionoid family Colydiidae (= Zopheridae) and recognized as a distinct family (Lawrence, 1980; in accord with earlier suggestions by Craighead, 1920) within the C.S. of Cucujoidea (Lawrence 1980, 1985, 1991; Pal and Lawrence 1986).

Although only eight families make up the C.S., the group is incredibly diverse including 39 subfamilies and more than half the genera (646 of 1,237) and species (9,600 of 19,090) of the entire superfamily Cucujoidea (Lawrence, 1991; Lawrence and Newton, 1995). It is one of the few large groupings of Cucujoidea that has been hypothesized to form a clade (Hunt et al. 2007; Robertson et al., 2008; Sen Gupta and Crowson, 1973; Ślipiński, 1990; Ślipiński and Pakaluk, 1991).

Cerylonid Series beetles have exploited a wide variety of natural resources. Host utilization within the C.S. ranges from diverse forms of mycophagy (e.g., utilizing Basidiomycetes, Ascomycetes, & Zygomycetes), to phytophagy, myxomycophagy, predation, cleptoparasitism and parasitoidism. Cerylonid Series beetles are often associated with fungi or decaying plant matter. They are commonly collected in leaf litter, on vegetation, and on or under the bark of dead and dying trees. Many C.S. taxa are attracted to lights. The predaceous forms are often swept from vegetation where their prey occur.

Crowson (1955) characterized the C.S. with a combination of morphological characters as follows: adults with tarsal formula reduced (4-4-4 or 3-3-3), hind wings lacking a closed radial cell, hind wings with anal veins reduced, aedeagus resting on side when retracted, and tegmen reduced; larvae with pretarsal claw unisetose, spiracles usually annular, and sensory appendage of 2nd antennomere usually as long as the 3rd antennomere.

As reviewed by Ślipiński and Pakaluk (1991), the above suite of defining characters for the C.S. is somewhat problematic. For instance, many of the characters used to recognize the

C.S. are reductions. Other proposed synapomorphies are widespread in unrelated groups (e.g., aedeagus resting on side when retracted occurs in other cucujoid families) or are lacking in some C.S. taxa (e.g., a well-developed phallobase occurs in Coccinellidae; a closed radial cell occurs in the bothriderid genus *Deretaphrus*). Furthermore, the use of larval characters is problematic because so few C.S. taxa are known in their larval stage.

Several studies of the classification of the Cerylonid Series have been provided (e.g., Pal and Lawrence, 1986; Paulian, 1988; Sasaji, 1987; Sen Gupta and Crowson, 1973; Ślipiński and Pakaluk, 1991); none was based on a formal phylogenetic analysis. Ślipiński and Pakaluk (1991) reviewed the classification of the C.S. and pointed out many serious problems and expressed concerns about the present family limits and the lack of resolution within the C.S.

Most higher-level systematic treatments within the C.S. comprise studies restricted to individual subgroups, families, or subfamilies within the series [e.g., Bothrideridae and Cerylonidae (Pal and Lawrence, 1986), Eupsilobiinae (Endomychidae) (Pakaluk and Ślipiński, 1990), Cerylonidae (Ślipiński, 1990), Endomychidae (Tomaszewska, 2000, 2005), Corylophidae (Ślipiński et al., 2009), Coccinellidae (Sasji, 1968)]. Prior to the commencement of the research outlined in the present work, rigorous systematic studies of the entire C.S. were nil.

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CHAPTER 3

SEARCHING FOR NATURAL LINEAGES WITHIN THE CERYLONID SERIES (COLEOPTERA: CUCUJOIDEA)[1]

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[1] Robertson, J.A., M.F. Whiting, and J.V. McHugh. 2008. *Molecular Phylogenetics and Evolution.* 46:193-205. Reprinted here with permission of publisher.

Abstract

Phylogenetic relationships within the diverse beetle superfamily Cucujoidea are poorly known. The Cerylonid Series (C.S.) is the largest of all proposed superfamilial cucujoid groups, comprising eight families and representing most of the known cucujoid species diversity. The monophyly of the C.S., however, has never been formally tested and the higher-level relationships among and within the constituent families remain equivocal. Here we present a phylogenetic study based on 18S and 28S rDNA for 16 outgroup taxa and 61 C.S. ingroup taxa, representing seven of the eight C.S. families and 20 of 39 subfamilies. We test the monophyly of the C.S., investigate the relationships among the C.S. families, and test the monophyly of the constituent families and subfamilies. Phylogenetic reconstruction of the combined data was achieved via standard static alignment parsimony analyses, Direct Optimization using parsimony, and partitioned Bayesian analysis. All three analyses support the paraphyly of Cucujoidea with respect to Tenebrionoidea and confirm the monophyly of the C.S. The C.S. families Bothrideridae, Cerylonidae, Discolomatidae, Coccinellidae and Corylophidae are supported as monophyletic in all analyses. Only the Bayesian analysis recovers a monophyletic Latridiidae. Endomychidae is recovered as polyphyletic in all analyses. Of the 14 subfamilies with multiple terminals in this study, 11 were supported as monophyletic. The corylophid subfamily Corylophinae and the coccinellid subfamilies Chilocorinae and Scymninae are recovered as paraphyletic. A sister grouping of Anamorphinae + Corylophidae is supported in all analyses. Other taxonomic implications are discussed in light of our results.

Key words: Classification; evolution; systematics; taxonomy; phylogeny; Cerylonid Series; Cucujoidea; Bothrideridae; Cerylonidae; Coccinellidae; Corylophidae; Discolomatidae; Endomychidae; Latridiidae.

Introduction

The superfamily Cucujoidea (Coleoptera) is large and difficult to characterize. While some are conspicuous and brightly colored (e.g., some Erotylidae, Endomychidae, and Coccinellidae), most cucujoids fall into the category of "Little Brown Jobs" (LBJs). Cucujoidea is a presumed artificial assemblage of typically small, difficult to identify, drably colored, nondescript beetles that live cryptic lifestyles in leaf litter, dead wood, or fungi. It was long recognized for those beetles with non-heteromerous tarsi and clubbed antennae that could not be placed satisfactorily elsewhere, and thus has served as a taxonomic dumping ground for any LBJ with the above features (Ślipiński and Pakaluk, 1991).

Current classifications place members of Cucujoidea among 34 families (Lawrence and Newton, 1995; Leschen et al., 2005). Crowson (1955) was the first to recognize the "Cerylonid Series" (C.S.), a cluster of presumably highly derived families within Cucujoidea characterized by the following features: adults with tarsal formula reduced (4-4-4 or 3-3-3 in both sexes), wings lacking a closed radial cell, anal veins reduced, aedeagus resting on side when retracted, tegmen reduced, larvae with tarsungulus unisetose, larval spiracles usually annular, and larval sensory appendage of 2nd antennomere usually as long as the 3rd antennomere.

The Cerylonid Series comprises the families Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae. Although only eight families make up the C.S., the group includes 39 subfamilies and more than half the genera (646 of 1,237) and species (9,600 of 19,090) of the entire superfamily Cucujoidea (Lawrence, 1991; Lawrence and Newton, 1995). It is one of the few large groupings of Cucujoidea that has been hypothesized to form a clade (Sen Gupta and Crowson, 1973; Ślipiński, 1990; Ślipiński and Pakaluk, 1991), though its monophyly has never been formally tested.

Several studies of the classification of the C.S. have been provided (e.g., Pal and Lawrence, 1986; Paulian, 1988; Sasaji, 1987b; Sen Gupta and Crowson, 1973); however, none was based on a formal phylogenetic analysis. Ślipiński and Pakaluk (1991) reviewed the classification of the C.S. and pointed out many serious problems outlined below. Within the C.S. there is a lack of clear family definitions. Many of the characters used to recognize the C.S. are reductions. Other proposed synapomorphic characters are widespread in unrelated groups (e.g., aedeagus resting on its side) or are lacking in some C.S. taxa (e.g., coccinellids have a well-developed tegmen and some bothriderids have an R-cell in wing). The use of larval characters is problematic because so few C.S. taxa are known in their immature stages. Ślipiński and Pakaluk (1991) expressed concern about the present family limits and the lack of resolution within the series before concluding that a "phylogenetic study, in its modern sense, of the higher-level relationships of the cerylonid series is desperately needed" (pg. 82) and that "a complete reevaluation of characters is essential for reordering the cerylonid series into a maximally informative and predictive classification." (pg. 79).

Furthermore, the internal relationships within the series remain dubious as reflected in the historically unstable internal classification among C.S. taxa. Indeed, C.S. families, subfamilies, and genera have been moved among multiple families within the series. For example, the bothriderid subfamily Anommatinae has been treated within three other C.S. families [Cerylonidae (Sen Gupta and Crowson, 1973), Endomychidae (Merophysiinae) (Crowson, 1955), Latridiidae (see Crowson, 1955)] in addition to being recognized as its own family, Anommatidae (Dajoz, 1977). Prior to the addition of Anommatinae and Xylariophilinae, Bothrideridae in its entirety (then comprising Bothriderinae and Teredinae) was long treated within the tenebrionoid family Zopheridae (= Colydiidae), a placement it held until only recently

(Lawrence, 1980, 1985, 1991; Pal and Lawrence, 1986). Such shifting in the classification at the superfamilial level underscores the historically poor understanding of relationships among these beetles. Likewise, constituents of Endomychidae have been treated as their own distinct families [e.g., Mychothenidae (Sasaji, 1987a, 1987b), Merophysiidae (Crowson, 1955)], and multiple currently recognized subfamilies have been treated within different C.S. families [e.g., Merophysiinae within Latridiidae (Hetschko, 1926) (see also Crowson, 1955), Eupsilobiinae within Cerylonidae (Hetschko, 1930) (see also Sen Gupta and Crowson, 1973)]. Other C.S. families have had equally unstable taxonomic histories (see Crowson, 1955).

Recently, Leschen et al. (2005) provided a morphological phylogenetic analysis of the 'basal Cucujoidea,' a group comprising all cucujoids except the C.S., (Leschen et al., 2005). The primary purpose of their analysis was to delimit the family Phloeostichidae and its allies. However, no representatives of the C.S. were included in their analysis and thus the group's phylogenetic position and monophyly remain unclear.

This study is the first attempt to formally test the monophyly of the C.S. and its constituent families and subfamilies, and investigate the phylogenetic relationships among its major lineages via a rigorous phylogenetic analysis based on molecular sequence data.

Materials and Methods

Taxonomic exemplars for this analysis (Table 1) were obtained for seven of the eight C.S. families including Bothrideridae (1 of 4 subfamilies represented), Cerylonidae (1 of 5 subfamilies represented), Coccinellidae (6 of 6 subfamilies represented), Corylophidae (2 of 5 subfamilies represented), Discolomatidae (2 of 5 subfamilies represented), Endomychidae (6 of 12 subfamilies represented), and Latridiidae (2 of 2 subfamilies represented). The one missing C.S. family, Alexiidae, is monotypic and restricted to the Mediterranean region. Most of the missing subfamilies are rare, species-poor taxa that are difficult to collect. The outgroup taxa comprised representatives of ten non-C.S. families within Cucujoidea (Kateretidae, Nitidulidae, Passandridae, Cucujidae, Silvanidae, Laemophloeidae, Phalacridae, Monotomidae, Cryptophagidae, Erotylidae), three families of Tenebrionoidea (Zopheridae, Ciidae, Tenebrionidae), and two families of Cleroidea (Cleridae, Trogossitidae) (Table 1). This provided a total of 77 taxa in this study.

For these taxa, the abdomen was carefully disarticulated from the metathorax and retained untouched, thus reducing the possibility of introducing contaminant from the gut as well as preserving the integrity of the taxonomically-significant genitalia. The remainder of the specimen (head and thorax intact) was subjected to 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) and voucher specimens were deposited at the BYU Insect Genomics Collection and the University of Georgia Coleoptera Tissue Collection. Target genes 18S rDNA and 28S rDNA were amplified via polymerase chain reaction (PCR). PCR primers and protocols are published elsewhere (Jarvis et al., 2004; Whiting, 2002). Primer combinations utilized for 18S include 1F + B3.9, a0.7 + bi and a2.0 + 9R (Jarvis et al., 2004; Whiting, 2002). Primer combinations used for 28S include 1a + 28Sb, 28Sa + 5b and 4.8a +7b1 (Whiting, 2002). PCR product yield, specificity, and potential contamination were monitored by agarose gel electrophoresis. PCR products were purified using MANU 96-well filtration plates, sequenced using d-Rhodamine chemistry, and fractionated on an ABI 3730 DNA analyzer. Assembly of contig sequences and editing of nucleotide fragments was performed using Sequencher 3.1.1 (Genecodes, 1999). Each gene was partitioned into variable and conserved domains (corresponding roughly to stem and loop regions) resulting in 7 and 12 partitions for 18S and 28S respectively. A highly variable region of 28S, ranging from 38 to 629 bp in length, occurring at nucleotide position 2045 in the 28S alignment was removed and excluded from further analysis based on the premise that it is too length variable to be reasonably aligned. There is no apparent correspondence of the length variability of this region with relatedness of the taxa in this analysis.

Alignment of these data was performed in MUSCLE (Edgar, 2004) using default parameters. Phylogenetic reconstruction of the concatenated 18S and 28S data under parsimony criteria was performed in TNT (Goloboff et al., 2003) implementing 5000 replicates with sectorial searches, tree drifting, tree fusing, and ratcheting. Heuristic searches were unrooted, gaps were treated as missing data and all characters were weighted equally. Resulting trees from all analyses were subsequently rooted to *Trichodes ornatus* (Cleroidea).

Partitioned Bayesian analysis (Nylander et al., 2004) of the 18S and 28S data was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) using the MUSCLE alignments. Modeltest (Posada and Crandall, 1998) was used to select an appropriate model of sequence evolution for each gene under the AIC (Akaike Information Criterion) and these models were implemented in the Bayesian analysis. The partitioned Bayesian analysis comprised four separate runs each utilizing 20 million generations, flat priors, unlinked partitions, four chains (one cold and three hot), and trees sampled every 1000 generations. Log-likelihood scores were plotted to determine stationarity and convergence of runs. Trees sampled after the "burn-in" from the four runs were combined and used to construct a 50% majority rule consensus tree.

In addition to the analyses of the static alignment above, these data were analyzed in POY 3.0.11 via Direct Optimization (DO) (Wheeler, 1996; Wheeler, 2003) under parsimony criterion. Direct Optimization allows for simultaneous alignment and phylogenetic analysis, permitting a given set of analytical parameters to be applied uniformly throughout the alignment and tree reconstruction process. Thus tree searching and character homology can be assessed simultaneously in order to find the globally optimal solution. Partitioned gene regions were analyzed simultaneously via Direct Optimization (DO) in POY 3.0.11 (Wheeler et al., 2003) as implemented in parallel on an IBM SP-2 supercomputer (http://marylou.byu.edu/resources.htm) containing 316 power3 processors (375 MHz). POY search parameters are as follows for equivalent cost ratios (indels/tv/ts): "-sprmaxtrees 1 -impliedalignment -tbrmaxtrees 1 -maxtrees 5 -holdmaxtrees 25 -slop 5 -checkslop 10 -buildspr -buildmaxtrees 2 -replicates 256 -stopat 25 -multirandom -treefuse -fuselimit 10 -fusemingroup 5 -fusemaxtrees 50 -ratchetspr 2 -ratchettbr 2 -checkslop 10 -repintermediate -time -indices –stats."

Topological support for TNT trees was assessed via partitioned Bremer support (Baker and DeSalle, 1997) and nonparametric bootstrap values. TreeRot (Sorenson, 1999) as implemented in PAUP* 4.0 (Swofford, 2002) was used to calculate partitioned Bremer support values (Baker and DeSalle, 1997) for each gene and nonparametric bootstrap values were calculated in TNT using 1000 replicates with 10 random additions per replicate. For DO trees, jackknife values were calculated in POY using 100 replicates employing the same search strategy listed above for each pseudoreplicate. Branch support for the Bayesian trees was assessed with posterior probabilities determined via the 50% majority rule consensus percentages.

Results

Alignment of the molecular data in MUSCLE (Edgar, 2004) yielded a matrix of 2024 characters for 18S and 2355 characters for 28S. These matrices comprise 408 and 797 parsimony informative characters for 18S and 28S respectively.

Two most parsimonious trees of length 8,175 were recovered from the static alignment analyses in TNT, the strict consensus of which is shown in Figure 3.1. Nodes in Figure 3.1 are numbered for reference in the discussion below. Bootstrap and partitioned Bremer support values for the TNT tree are given in Table 2. Direct Optimization of the combined data in POY resulted in 14 most parsimonious trees of length 8,572. The strict consensus of the POY trees (Figure 3.3) is very similar to the TNT tree (above) differing most notably in recovering Cerylonidae + Bothrideridae sister to the remaining C.S. The POY tree also is distinct in the placement of a few outgroup taxa and the internal relationships of Latridiinae (Latridiidae), Corticariinae (Latridiidae), Lycoperdininae (Endomychidae) and Coccinellidae (see Figs. 3.1, 3.3).

The hierarchical AIC as implemented in Modeltest yielded the General Time Reversible + Invariable Site + Gamma Distribution (GTR+I+G) model of sequence evolution as most appropriate for both the 18S and 28S partitions. All Bayesian runs reached stationarity by 100,000 generations. The sampled trees from these first 100,000 generations (100 trees per run, 400 trees total) were discarded as "burn in" and the remaining 79,600 sampled trees from the four runs were combined and used to construct the 50% majority rule consensus tree (Fig. 3.2). The 50% majority rule consensus tree that was obtained from the Bayesian analysis (Fig. 3.2) is similar to both the parsimony TNT and DO trees, however it is unique in multiple key aspects as shown in Figure 3.2 and discussed below.

Overall the topological support for the TNT, DO, and Bayesian trees recover a similar pattern of support: high bootstrap values, Bremer support values, jackknife values and posterior probabilities generally correspond to familial, subfamilial and generic clades. However, many of the deeper nodes representing relationships between families have relatively poor nodal support.

In a few families (e.g., within Coccinellidae) support is also poor. Partitioned Bremer support values indicate that the relative contribution of 18S and 28S to the topology is extremely close: 18S provides 49.5% and 28S provides 50.5% of the total Bremer support (Table 2). 18S provides moderate support throughout most of the ingroup and supplies all of the positive support for all coccinellid clades except one, namely Coccinellinae (clade # 60, see Figure 3.1). 28S affords moderate support throughout most of the topology, contributing most of the positive support along the deep nodes comprising outgroup taxa.

All three analyses support the paraphyly of Cucujoidea with respect to Tenebrionoidea and confirm the monophyly of the C.S. These data further recovered each of the following C.S. families as monophyletic: Bothrideridae, Cerylonidae, Discolomatidae, Coccinellidae and Corylophidae. Endomychidae is recovered as polyphyletic. Of the 14 subfamilies with multiple terminals in this study, 11 were supported as monophyletic. The corylophid subfamily Corylophinae and the coccinellid subfamilies Chilocorinae and Scymninae are recovered as paraphyletic. Only the Bayesian analysis recovered Latridiidae as monophyletic.

Discussion

Cucujoidea has long been regarded as an artificial group (Crowson, 1955; Leschen et al., 2005; Pakaluk et al., 1994), thus its paraphyly as recovered in this study is not surprising and is consistent with other higher-level molecular studies of beetle phylogeny (Robertson et al., 2004; Vogler, 2005; Vogler and Caterino, 2003). This analysis does not include a comprehensive sampling of all cucujoid families and thus the exact position of the C.S. remains uncertain. Nonetheless, our sampling of cucujoid families permits an initial investigation of relationships among “basal cucujoids” and insight regarding the general position of the C.S. Cryptophagidae and Erotylidae are supported as sister taxa in all analyses, though nodal support is not high across analyses. The "Nitidulidae group" of Leschen et al. (2005) (Nitidulidae, Kateretidae, Smicripidae—the latter not represented in current study) is not supported in both the TNT and DO analyses and is unresolved in the Bayesian analysis. Cucujidae *sensu lato* (Cucujidae, Passandridae, Silvanidae, and Laemophloeidae) is paraphyletic due to the placement of Phalacridae as the sister taxon to Laemophloeidae. All three analyses implemented in the current study recover a monophyletic C.S. with moderate nodal support. These data support the C.S. as a relatively derived "cucujoid" lineage forming the sister clade to Tenebrionoidea. As exemplars of the remaining cucujoid families are incorporated into future studies, particularly Byturidae and Biphyllidae—taxa which have been suggested as possible sister taxa of the C.S. (Crowson, 1955; Pal and Lawrence, 1986; Ślipiński and Pakaluk, 1991)—it is possible that this proposed sister group relationship may not be substantiated.

Ślipiński and Pakaluk (1991) discuss two potentially important morphological characters with respect to C.S. phylogeny: 1) number of abdominal spiracles in adults (five vs. seven), and 2) degree of closure of mesocoxal cavities (open vs. closed laterally by meso- and metasternum). When they mapped these two binary characters on their intuitive phylogeny for the C.S., both characters were rendered homoplasious. Interestingly, when these two characters are mapped on our tree a posteriori, the spiracular character is homoplasious but the mesocoxal cavity character is not. All taxa comprising clade 42 (Fig. 3.1) have the mesocoxal cavities open while those taxa belonging to clade 16 (Fig. 3.1) have the mesocoxal cavities closed. Our topology supports seven abdominal spiracles as the plesiomorphic condition for the C.S., with five abdominal spiracles originating at least three independent times throughout C.S. evolution. Taxa comprising clades 18, 33, 36, and 42 (Fig. 3.1) have five abdominal spiracles. While this may not be a rigorous test of homology, it suggests that of these two characters which historically have been considered phylogenetically important, the closure of mesocoxal cavities is the more informative one for superfamilial groupings of C.S. taxa. We are currently generating a morphological matrix for these taxa, an analysis of which will more clearly elucidate the evolution and taxonomic utility of these and other characters.

Bothrideridae and Cerylonidae

Bothrideridae, Cerylonidae and Discolomatidae were at one time included in the tenebrionoid family Colydiidae (presently Colydiinae, Zopheridae). Horn (1878) revised the North American Colydiidae and erected Discolomatidae (as Discolomidae). More recently, Cerylonidae (Crowson, 1955) and Bothrideridae (Lawrence, 1980, 1985, 1991; Pal and Lawrence, 1986) were removed from Colydiidae and placed into the C.S. of Cucujoidea. Each of these reclassifications is supported by the present phylogenetic study.

While this analysis strongly supports the monophyly of the families Bothrideridae and Cerylonidae, only a single subfamily is represented for each (Bothriderinae and Ceryloninae respectively) and both subfamilies have strong support for monophyly based on morphology (Ślipiński et al., 1989; Ślipiński, 1990). Thus the test for monophyly for Cerylonidae and Bothrideridae in this study is rather weak. Though most of the remaining subfamilies for both families are relatively species-poor, they comprise some of the more enigmatic taxa which have been taxonomically difficult in the past [e.g., Anommatinae (Bothrideridae), Ostomopsinae (Cerylonidae)]. The monophyly of both Bothrideridae and Cerylonidae as presently constituted has been questioned (Pal and Lawrence, 1986; Ślipiński et al., 1989; Ślipiński, 1990) and based on morphology it is likely that they are paraphyletic with respect to each other. Our current taxon sampling confirms the suspected close relationship of Cerylonidae and Bothrideridae (Pal and Lawrence, 1986; Ślipiński, 1990; Ślipiński et al., 1989) as these families are closely related in the Bayesian analysis and are recovered as sister taxa in both of the present parsimony analyses. Nonetheless, it is quite possible that future studies that include additional cerylonid and bothriderid lineages will fail to recover these families as monophyletic groups. Thus the inclusion of the remaining bothriderid and cerylonid subfamilies is essential for delimiting these families and clarifying one important aspect of C.S. relationships.

Discolomatidae

Discolomatidae is exceptional among the remaining C.S. families in that its constitution and internal classification historically have been stable and its constituents have not experienced the shifting between families that is characteristic of other C.S. taxa. Indeed, from a morphological standpoint, Discolomatidae is perhaps *a priori* the most strongly supported monophyletic C.S. family. Discolomatids possess unique coxae: all three pairs are transverse but are mostly enclosed by the sterna making them appear small, globular and widely separated. They have a distinct one-segmented antennal club, glandular pores along the lateral margins of the pronotum and elytra, and ventrite 1 is much longer than 2 (Lawrence and Britton, 1994). Thus the effect of reduced taxon sampling may not be as significant for Discolomatidae as for other C.S. families. Given its well recognized homogeneity, a test of monophyly for Discolomatidae is perhaps of lesser concern. Of greater interest are the internal relationships within Discolomatidae and the placement of the family among the remaining C.S. taxa. At present our discolomatid sampling does not permit a rigorous evaluation of the former issue, though it is certainly adequate for beginning to address the latter. Parsimony analyses place Discolomatidae sister to Anamorphinae + Corylophidae. This placement for Discolomatidae has never been proposed before, and although it is only weakly supported in this analysis [Bremer support (BS) = 5, bootstrap (BT) = < 50, jackknife (JK) = < 50], preliminary morphological data corroborate a close affinity between these taxa (Ślipiński, pers. com.).

In contrast, the Bayesian analysis (Fig. 3.2) of the present study strongly supports [posterior probability (PP) = 100] a clade comprising Discolomatidae, Cerylonidae, and Bothrideridae, with an internal sister grouping of Discolomatidae and Cerylonidae. Despite the poor support for this internal sister grouping (PP = 65), this hypothesis for the sister taxon of Discolomatidae is intriguing, as some cucujoid specialists consider the cerylonid subfamily Murmidiinae to be the sister group of Discolomatidae (e.g., Lawrence, 1991; Ślipiński, 1990). Potential synapomorphies uniting Murmidiinae and Discolomatidae include spiculum gastrale absent and ovipositor reduced (Ślipiński, 1990). Our current taxonomic sampling does not include any murmidiine exemplars, and at present, these data are insufficient to confidently identify the sister taxon of Discolomatidae. The inclusion of additional cerylonid taxa, particularly Murmidiinae, may help to elucidate the placement of this family among the C.S.

Latridiidae

Our taxonomic sampling for Latridiidae is relatively strong, with both currently recognized subfamilies and eight of the 29 known genera represented. Of the three phylogenetic analyses employed in the current study, only the Bayesian analysis recovered Latridiidae as monophyletic (Fig. 3.2). While it is generally considered to comprise a monophyletic group, there are no strong synapomorphies that have been proposed to support the family Latridiidae as presently constituted (Ślipiński and Pakaluk, 1991). Currently the family Latridiidae is characterized primarily by the small, elongate oval body and reduced tarsal formula (3-3-3). The two latridiid subfamilies, however, are distinct from a morphological standpoint and both are supported by the current analyses as monophyletic groups. Latridiinae have the procoxal cavities well separated and broadly closed behind. They are glabrous, often covered with a waxy exudate and usually possess pores, grooves and carinae on different regions of the body, particularly on the pronotum. Corticariinae are pubescent and are generally devoid of pores and carinal ornamentation. The procoxal cavities of corticariines are very close together and are not broadly closed behind. Corticariinae was recovered as a monophyletic group in an unpublished phylogenetic study of Latridiidae (Lord, pers. com.).

If the relationships found in the parsimony analyses (Figs. 3.1, 3.3) are supported by additional data, either Latridiinae and Corticariinae would each need to be elevated to familial status, or several C.S. family groups (e.g., Discolomatidae, Corylophidae and Anamorphinae (Endomychidae)) would have to be subsumed within Latridiidae Certainly, the former action is preferable as it maximizes taxonomic stability and recognizes families (Anamorphinae = Anamorphidae; see discussion of Endomychidae) comprising natural lineages each delimited by a unique suite of morphological character states. The monophyly of Latridiidae needs to be investigated further via subsequent phylogenetic studies utilizing additional data.

Corylophidae

Corylophidae is generally considered to be a monophyletic group (Bowestead, 1999; Ślipiński and Pakaluk, 1991) though many of the defining characters for the family are considered plesiomorphic (Ślipiński and Pakaluk, 1991). Bowestead (1999) provides the only phylogenetic hypothesis of corylophid relationships. However, it was not generated using modern phylogenetic methodology and was regionally restricted in its taxon sampling. The present study supports the monophyly of the family Corylophidae with strong nodal support (BS = 23, BT = 99, JK = 95, PP = 100). Our current taxon sampling, however, does not include exemplars of three phylogenetically enigmatic corylophid taxa: Aenigmaticini (Corylophinae), Peltinodinae and Periptyctinae. Periptyctinae comprises two Australian genera, *Periptyctus* and *Pakalukodes*, which were treated within Endomychidae until recently (Ślipiński et al., 2001). The monotypic Peltinodinae (*Holopsis*) is atypically large in size and is distinct among corylophids in having the procoxal cavities externally open. Aenigmaticini are unique in that they have an exposed head, are elongate and flattened, and are generally latridiid-like in appearance. The inclusion of these taxa in future analyses will provide a more rigorous test of monophyly for Corylophidae and a more lucid understanding of the internal relationships within this C.S. family.

Our results support the paraphyly of the subfamily Corylophinae with respect to the monotypic subfamily Orthoperinae (Figs. 3.1, 3.2). Although current classification (Bowestead, 1999; Bowestead et al., 2001; Ślipiński et al., 2001) does not indicate a close relationship of these taxa, an unpublished phylogenetic analysis of the family based on morphological data corroborates this finding (Ślipiński and Tomaszewska, unpublished data).

Corylophidae is considered the sister taxon of Latridiidae (Ślipiński and Pakaluk, 1991; Bowestead, 1999), though this hypothesis has never been formally tested. The parsimony analyses in the present study support a relatively close relationship between these families, but the results are unusual in including Anamorphinae (Endomychidae) and Discolomatidae nested within that clade. The Bayesian analysis, however, does not support a close affiliation of Latridiidae and Corylophidae, but places the former taxon as the sister to a clade comprising Cerylonidae, Discolomatidae, and Bothrideridae. The sister group relationship of Corylophidae and Anamorphinae as supported in the current study is discussed below.

Coccinellidae

Coccinellidae is by far the largest of the C.S. families with over 360 genera and 6,000 species (Vandenberg, 2002). It is a well-supported monophyletic group based on morphological features. Adult coccinellids have postcoxal lines on the first abdominal ventrite and have a unique aedeagus with a long curved sipho (= penis) and a well-developed tegmen that comprises a forward-extending basal lobe, a pair of parameres, the basal piece, and the median strut (Vandenberg, 2002). Despite the family's economical importance and general charisma, the higher-level phylogenetic relationships of constituent coccinellid taxa remain poorly known. Of the existing phylogenetic hypotheses for the family (Kovar, 1996; Sasaji, 1968; Yu, 1994), most are intuitive trees (e.g., Kovar, 1996; Sasaji, 1968) not generated via a formal phylogenetic analysis. In contrast, Yu (1994) performed a cladistic analysis for 21 coccinellid exemplars based on morphological data. However, Yu's (1994) analysis is problematic as some of the character codings are incorrect (Vandenberg, pers. com.). Our taxonomic sampling of Coccinellidae includes exemplars from all six subfamilies, permitting a strong test of monophyly for the family and a preliminary investigation of higher-level internal relationships. The current analysis strongly supports the monophyly of Coccinellidae with high topological support (BS = 18, BT = 100, JK = 100, PP = 100).

These data strongly support the monophyly of the coccinellid subfamilies Coccinellinae (BS = 40, BT = 100, JK = 100, PP = 100) and Epilachninae (BS = 25, BT = 100, JK = 100, PP = 100). Both of these subfamilies are fairly distinctive based on behavioral and morphological features. Coccinellinae comprise the typical "ladybugs" of the family and are large beetles characterized by having relatively long antennae and the terminal maxillary palpomere securiform (Vandenberg, 2002). Epilachninae comprises all of the phytophagous members of the family and is distinctive among coccinellids in possessing multidenticulate mandibles and antennae that are inserted on the frons (Vandenberg, 2002). Yu's (1994) analysis also supports the monophyly of Coccinellinae; however, it did not include multiple exemplars of Epilachninae and was thus unable to test the monophyly for this subfamily. The paraphyly of Chilocorinae and Scymninae is not surprising as neither, as currently delimited, are characterized by strong morphological or behavioral synapomorphies.

Sticholotidinae has been suggested as the basal-most coccinellid subfamily (Kovar, 1996; Sasaji, 1968; Yu, 1994). In contrast, Sticholotidinae, here represented by *Sticholotis*, is nested deeply within the coccinellid clade. The current parsimony analyses support a clade of chilocorine taxa (*Chilocorus* + *Halmus*) as sister to the remaining Coccinellidae, while Bayesian analysis places all coccinellid exemplars in one of two large sister clades (Figs. 3.1, 3.2).

These data alone are insufficient to robustly resolve the internal relationships of Coccinellidae. The coccinellid relationships recovered in the Bayesian analysis greatly differ from those resulting from the parsimony analyses (Figs. 3.1, 3.2). There is even a significant amount of discordance between both the TNT and DO parsimony trees (Figs. 3.1, 3.3). Consistent with the topological incongruence between methods is the extremely low branch support for all three topologies for most coccinellid clades. Some aspects of our coccinellid phylogeny, however, are consistent with an unpublished phylogenetic analysis of Coccinellidae (Giorgi, pers. com.), such as the apical placement of Sticholotidinae and the paraphyletic nature of Chilocorinae and Scymninae.

Coccinellidae usually is considered to be most closely related to Alexiidae (not represented) and Endomychidae (see Ślipiński and Pakaluk, 1991; Vandenberg, 2002). Although the current study does not recover a consistent, well-supported sister group for Coccinellidae, these data do suggest that the sister to Coccinellidae is, at least in part, a member of the current Endomychidae. The Bayesian analysis places Coccinellidae unresolved with a clade comprising most of Endomychidae and the Anamorphinae + Corylophidae clade. The sister group relationship between Leiestinae (Endomychidae) and Coccinellidae recovered in the parsimony analyses was unexpected and is discussed below.

Endomychidae

Endomychidae is unique among C.S. families in that multiple higher-level phylogenetic hypotheses based on cladistic methodology exist for the family (Tomaszewska, 2000, 2005). Tomaszewska's original analysis (2000) delineated the currently recognized 12 endomychid subfamilies and recovered Coccinellidae as the family's sister group. The follow-up study (Tomaszewska, 2005) provided resolution among the subfamilies and recovered Coccinellidae + Corylophidae as the sister group to Endomychidae. Coccinellidae has always been closely allied with Endomychidae and is generally considered its sister group (Ślipiński and Pakaluk, 1991; Vandenberg, 2002). In both of the above analyses, Tomaszewska (2000, 2005) recovered a monophyletic Endomychidae. Despite these results, the outgroup sampling in both of Tomaszewska's analyses was inadequate to rigorously test the monophyly of Endomychidae or identify its sister group, as it lacked critical C.S. taxa that have been allied with endomychids.

In contrast, the taxon sampling of the present study permits a more rigorous test of the monophyly and sister taxon of Endomychidae. Contrary to previous hypotheses (Tomaszewska, 2000, 2005), our results indicate that Endomychidae, as currently defined, is polyphyletic. Given the family's unstable taxonomic history and lack of unambiguous defining characters, this finding is not surprising and is consistent with an unpublished phylogenetic study of Endomychidae based on morphological and molecular data (Shockley, pers. com.). Our results place Anamorphinae as sister to Corylophidae, and the parsimony analyses recover Leiestinae as the sister taxon to Coccinellidae (Fig. 3.1). Our sampling, however, lacks exemplars of six endomychid subfamilies; most of these are species-poor taxa, however they represent a few of the more enigmatic lineages that historically have been difficult to place among the C.S. families (e.g., Merophysiinae, Eupsilobiinae). Thus their inclusion will most likely only increase the degree of polyphyly for this family, though this needs to be formally investigated. Most of Endomychidae (Stenotarsinae, Endomychinae, Epipocinae and Lycoperdininae) form a clade in the present study. This lineage is consistent with the "Higher Endomychidae" recovered in Tomaszewska's (2005) analysis, comprising Stenotarsinae, Endomychinae, Epipocinae and Lycoperdininae. Synapomorphies for this group include adults with pseudotrimerous tarsi and larvae with well developed V- or U-shaped frontal arms, and 4 pairs of stemmata (Tomaszewska, 2005).

The endomychid subfamily Anamorphinae, however, is nested in a separate clade as the sister taxon to Corylophidae. Ślipiński and Pakaluk (1991) suggest that Anamorphinae is not subordinate to the remaining Endomychidae, based on the closure of the mesocoxal cavities by the meso- and metathoracic sterna. (Sasaji, 1987a, 1987b, 1990) also advocated the recognition of Anamorphinae as distinct from other Endomychidae and treated it as its own family, "Mychothenidae." The results of the present study corroborate the above authors' views regarding Anamorphinae, namely that it should be recognized as its own family, Anamorphidae. Although a close relationship between Anamorphinae and Corylophidae has never been suggested before, all our analyses recover this sister grouping. Nonetheless, nodal support for this sister relationship is relatively weak (BS = 5, BT = < 50, JK = < 50, PP = 61). If these results are confirmed by additional studies based on larger samplings of taxa and characters, Anamorphinae would have to be recognized as a separate family, or would have to be transferred into Corylophidae. Certainly the former action is preferable, but such action should await analyses that include the remaining endomychid subfamilies in the event they would group with Anamorphinae. The parsimony analyses place the Anamorphinae + Corylophidae clade close to Discolomatidae and Latridiidae, while the Bayesian analysis places it in an unresolved trichotomy with the clade comprising the remaining endomychid taxa and the Coccinellidae clade.

Bayesian analysis places Leiestinae, here represented by *Phymaphora pulchella*, as the sister to the remaining Endomychidae. Given our current endomychid taxon sampling, this basal placement is consistent with Tomaszewska's (2005) results. In contrast, the parsimony analyses both recover Leiestinae outside of Endomychidae as sister to Coccinellidae. This placement is unexpected and represents a novel hypothesis for the sister taxon of Coccinellidae. Leiestinae is a relatively small subfamily, comprising 6 genera. Based on morphological data it appears to be monophyletic (Tomaszewska, 2000, 2005). If this sister group relationship is corroborated by additional phylogenetic studies, Leiestinae would either need to be transferred to Coccinellidae or be elevated to familial status.

Conclusions

This study represents the first formal phylogenetic analysis of the Cerylonid Series. We confirm the monophyly of the C.S. and provide a tentative placement for this clade among cucujoid and tenebrionoid lineages. The tests of monophyly for the families Cerylonidae, Discolomatidae, Bothrideridae and Corylophidae were relatively weak due to the small and unrepresentative taxon sampling that was available. The tests of Latridiidae, Endomychidae and Coccinellidae were stronger. Of these, only Coccinellidae was recovered as monophyletic in all of the analyses. Notable internal relationships recovered in this analysis include the sister grouping of Anamorphinae + Corylophidae and a close affiliation of Cerylonidae and Bothrideridae. This analysis supports the elevation of the endomychid subfamily Anamorphinae to familial status. Latridiinae, Corticariinae, and Leiestinae may also need to be elevated in rank if the relationships recovered in the parsimony analyses are substantiated in subsequent studies.

The lack of strong support for interfamilial relationships indicates that these data alone are insufficient to clearly resolve relationships among C.S. families and some subfamilies. Future work which builds on this study should provide additional insight regarding the relationships among these enigmatic lineages, and establish a basis for a more natural and stable classification for this group of little brown beetles.

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The following taxonomic works were used to identify specimens used in this study: Bothrideridae: (Ślipiński et al., 1989; Stephan, 1989); Cerylonidae: (Lawrence and Stephan, 1975; Ślipiński, 1990); Coccinellidae: (Gordon, 1985; Vandenberg, 2002) Ślipiński, unpublished data); Corylophidae: (Bowestead and Leschen, 2002); Discolomatidae: (John, 1959); Endomychidae: (Roubik and Skelley, 2001; Strohecker, 1953); Latridiidae: (Andrews, 1976a, 1976b, 1989; Fall, 1899; Walkley, 1952). In addition, specimen identifications were provided by

Adam Ślipiński (Coccinellidae), Chris Hartley (Latridiidae), Adriano Giorgi (Coccinellidae), Natalia Vandenberg (Coccinellidae), and Floyd Shockley (Endomychidae).

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Figure Captions

Table 3.1: Terminal taxa used in this analysis with GenBank Accession numbers

Table 3.2: Nodal support for the combined 18S and 28S standard MP topology (Fig. 3.1).

Figure 3.1: Strict consensus of two most parsimonious trees found in the TNT analysis using the concatenated static alignments of the 18S and 28S data (Length = 8,175; CI = 0.329; RI = 0.545). Taxonomic names in quotation represent paraphyletic taxa. The series of shaded or unshaded boxes beneath each node reflect the general amount of branch support (1st and 2nd boxes), partition congruence (3rd box), and concordance with both the POY (4th box) and Bayesian (5th box) topologies. Full shading indicates a bootstrap value ≥ 75, a Bremer support ≥ 10, overall character congruence among the 18S and 28S partitions (Yes), the presence of that node in the POY tree, and the presence of that node in the Bayesian tree (Present) for boxes 1-5, respectively. An unshaded box indicates either a bootstrap value < 75, a Bremer support < 10, overall character conflict among the 18S and 28S partitions (No), or the absence of that node in the POY tree and Bayesian tree (Not Present). When the third to fifth boxes are half shaded, it indicates a missing data partition (NA), an unresolved node in the POY tree, or an unresolved node in the Bayesian tree (Unresolved), respectively. Nodes are numbered and exact bootstrap, Bremer, and partitioned Bremer support values are given in Table 2.

Figure 3.2: Bayesian analysis tree. This topology was derived by taking a 50% majority rule consensus of 79,600 trees sampled following the burn in of the partitioned Bayesian analysis. Branch length and posterior probability are indicated for each node.

Figure 3.3: Strict consensus of 14 most parsimonious trees recovered via Direct Optimization of the combined data in POY (L = 8,572). Jackknife values computed in POY are indicated for each node.

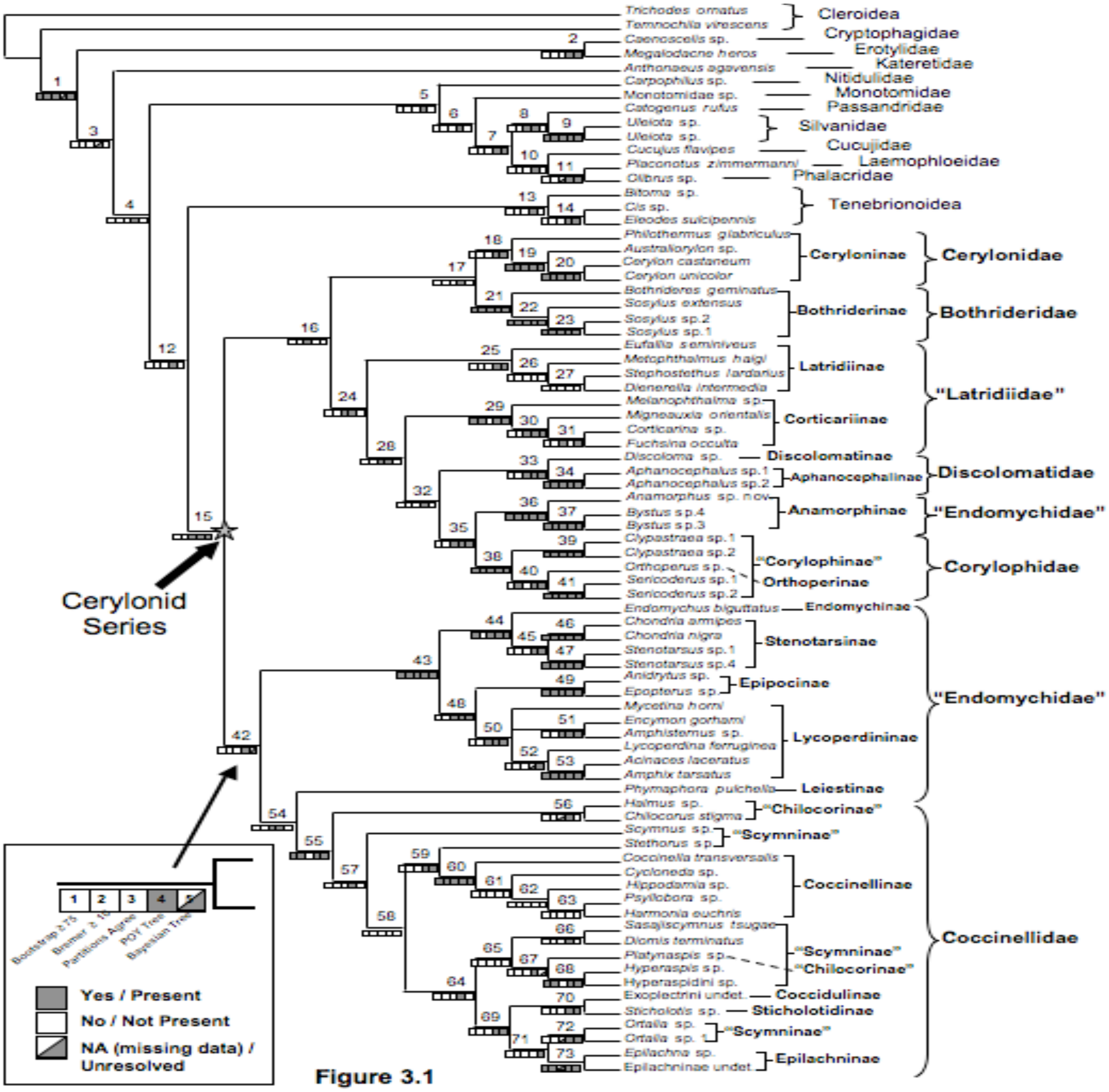
Table 3.1: Terminal taxa used in this analysis with GenBank accession numbers.

Family	Subfamily	Taxon	18S	28S
Cleridae		*Trichodes ornatus* Say	AF423775	EU145663, EU145713
Trogossitidae		*Temnochila virescens* Fabricius	EU145654	EU145711, EU145720
Zopheridae		*Bitoma* sp.	AF423768	AY310661
Ciidae		*Cis* sp.	AY310605	AY310666
Tenebrionidae		*Eleodes obscura* Say	AY310606	AY310667
Cucujidae		*Cucujus clavipes* Fabricius	AF423767	AY310660
Passandridae		*Catogenus rufus* (Fabricius)	EU145651	EU145709
Laemophloeidae		*Placonotus zimmermanni* (LeConte)	EU145649	EU145707, EU145718
Silvanidae		*Uleiota* sp.	EU145653	EU145710
Silvanidae		*Uleiota* sp.	AY310604	AY310665
Nitidulidae		*Carpophilus* sp.	AY310603	AY310664
Kateretidae		*Anthonaeus agavensis* (Crotch)	EU145648	EU145706, EU145717
Monotomidae		Monotomidae sp.	EU145650	EU145708, EU145719
Phalacridae		*Olibrus* sp.	EU145652	
Cryptophagidae		*Caenoscelis* sp.	EU145627	EU145686
Erotylidae		*Megalodacne heros* (Say)	AY310636	AY310697
Bothrideridae	Bothriderinae	*Sosylus* sp. 1	EU145596	EU145657
Bothrideridae	Bothriderinae	*Sosylus* nr. *extensus* (Say)	EU145595	EU145656
Bothrideridae	Bothriderinae	*Sosylus* sp. 2	EU145594	EU145655
Bothrideridae	Bothriderinae	*Bothrideres geminatus* Casey	EU145597	EU145658
Cerylonidae	Ceryloninae	*Philothermus glabriculus* LeConte	EU145601	EU145662
Cerylonidae	Ceryloninae	*Australiorylon* sp.	EU145598	EU145659, EU145712
Cerylonidae	Ceryloninae	*Cerylon castaneum* Say	EU145599	EU145660
Cerylonidae	Ceryloninae	*Cerylon unicolor* (Ziegler)	EU145600	EU145661
Coccinellidae	Chilocorinae	*Halmus* sp.	EU145607	EU145669
Coccinellidae	Chilocorinae	*Chilocorus stigma* (Say)	EU145610	
Coccinellidae	Chilocorinae	*Platynaspis* sp.	EU145619	EU145678
Coccinellidae	Coccidulinae	*Exoplectrini* sp.	EU145606	EU145668
Coccinellidae	Coccinellinae	*Cycloneda* sp.	EU145602	EU145664
Coccinellidae	Coccinellinae	*Psyllobora* sp.	EU145604	EU145666
Coccinellidae	Coccinellinae	*Harmonia euchris* (Mulsant)	EU145612	EU145672
Coccinellidae	Coccinellinae	*Hippodamia* sp.	EU145605	EU145667
Coccinellidae	Coccinellinae	*Coccinella transversalis* Fabricius	EU145609	EU145670
Coccinellidae	Epilachninae	*Epilachna* sp.	EU145616	EU145675
Coccinellidae	Epilachninae	Epilachninae sp.	EU145608	
Coccinellidae	Scymninae	Hyperaspidini sp.	EU145620	EU145679
Coccinellidae	Scymninae	*Hyperaspis* sp.	EU145611	EU145671, EU145714
Coccinellidae	Scymninae	*Scymnus* sp.	EU145603	EU145665
Coccinellidae	Scymninae	*Diomis terminatus* Say	EU145618	EU145677
Coccinellidae	Scymninae	*Sasajiscymnus tsugae* (Sasaji and McClure)	EU145615	EU145674
Coccinellidae	Scymninae	*Stethorus* sp.	EU145617	EU145676
Coccinellidae	Scymninae	*Ortalia* sp.	EU145614	
Coccinellidae	Scymninae	*Ortalia* sp.	EU145621	EU145680

Coccinellidae	Sticholotidinae	*Sticholotis* sp.	EU145613	EU145673
Corylophidae	Corylophinae	*Clypastraea* sp. 1	EU145622	EU145681
Corylophidae	Corylophinae	*Clypastraea* sp. 2	EU145623	EU145682
Corylophidae	Corylophinae	*Sericoderus* sp. 1	EU145624	EU145683, EU145715
Corylophidae	Corylophinae	*Sericoderus* sp. 2	EU145625	EU145684
Corylophidae	Orthoperinae	*Orthoperus* sp.	EU145626	EU145685
Discolomatidae	Aphanocephalinae	*Aphanocephalus* sp. 1	EU145628	EU145687
Discolomatidae	Aphanocephalinae	*Aphanocephalus* sp. 2	EU145629	EU145688
Discolomatidae	Discolomatinae	*Discoloma* sp.	EU145630	
Endomychidae	Anamorphinae	*Anamorphus* sp. nov. FWS	EU145636	EU145694
Endomychidae	Anamorphinae	*Bystus* sp. 4	EU145631	EU145689
Endomychidae	Anamorphinae	*Bystus* sp. 3	EU145632	EU145690
Endomychidae	Endomychinae	*Endomychus biguttatus* Say	EU145643	EU145701
Endomychidae	Epipocinae	*Anidrytus* sp.	EU145640	EU145698
Endomychidae	Epipocinae	*Epopterus* sp.	EU145642	EU145700
Endomychidae	Leiestinae	*Phymaphora pulchella* Newman	EU145645	EU145703
Endomychidae	Lycoperdininae	*Acinaces laceratus* Gerstaecker	EU145646	EU145704
Endomychidae	Lycoperdininae	*Amphisternus* sp.	EU145644	EU145702
Endomychidae	Lycoperdininae	*Amphix tarsatus* Erichson	EU145647	EU145705
Endomychidae	Lycoperdininae	*Encymon gorhami* Csiki	EU145635	EU145693
Endomychidae	Lycoperdininae	*Lycoperdina ferruginea* LeConte	EU145637	EU145695
Endomychidae	Lycoperdininae	*Mycetina horni* Crotch	EU145641	EU145699
Endomychidae	Stenotarsinae	*Chondria armipes* Strohecker	EU145638	EU145696
Endomychidae	Stenotarsinae	*Chondria nigra* Strohecker	EU145639	EU145697
Endomychidae	Stenotarsinae	*Stenotarsus* sp. 1	EU145633	EU145691, EU145716
Endomychidae	Stenotarsinae	*Stenotarsus* sp. 4	EU145634	EU145692
Latridiidae	Corticariinae	*Corticarina* sp.	EU164622	EU164664
Latridiidae	Corticariinae	*Fuchsina occulta* Fall	EU164630	EU164667
Latridiidae	Corticariinae	*Melanophthalma* sp.	EU164632	EU164670
Latridiidae	Corticariinae	*Migneauxia orientalis* Reitter	EU164636	EU164665
Latridiidae	Latridiinae	*Dienerella intermedia* (Belon)	EU164638	EU164647
Latridiidae	Latridiinae	*Eufallia seminiveus* Motschulsky	EU164614	EU164645
Latridiidae	Latridiinae	*Metophthalmus haigi* Andrews	EU164643	EU164649
Latridiidae	Latridiinae	*Stephostethus lardarius* (Degeer)	EU164625	EU164651

Table 3.2: Nodal support for the combined 18S and 28S standard MP topology (Fig. 3.1).

Node	Bootstrap support	Bremer support	Partitioned Bremer		Node	Bootstrap support	Bremer support	Partitioned Bremer	
			18S	28S				18S	28S
1	100	16	7	9	38	99	23	16.5	6.5
2	53	2	4	-2	39	100	81	31	50
3	< 50	2	-4	6	40	84	12	-1	13
4	< 50	2	-6.5	8.5	41	99	24	4	20
5	< 50	2	-6.5	8.5	42	84	7	7.5	-0.5
6	< 50	2	-5	7	43	99	16	1.5	14.5
7	< 50	3	-1	4	44	95	9	2.8	6.2
8	< 50	3	2.5	0.5	45	< 50	1	-0.5	1.5
9	100	31	31	0	46	100	36	4.5	31.5
10	< 50	1	-3	4	47	100	33	5.5	27.5
11	67	6	6	0	48	62	3	2.5	0.5
12	< 50	2	-5	7	49	100	33	8.5	24.5
13	77	2	-5	7	50	< 50	1	0.5	0.5
14	53	2	-2.5	4.5	51	89	8	3.5	4.5
15	60	8	2	6	52	< 50	1	2.5	-1.5
16	< 50	2	0	2	53	95	10	2	8
17	52	4	6	-2	54	57	6	4.5	1.5
18	83	7	6.8	0.2	55	100	18	18.5	-0.5
19	98	16	7.5	8.5	56	86	8	8	0
20	100	66	63	3	57	< 50	3	4	-1
21	98	13	12	1	58	< 50	1	2	-1
22	100	41	7.5	33.5	59	73	7	8	-1
23	72	2	1	1	60	100	40	26.5	13.5
24	< 50	7	6.8	0.2	61	< 50	2	4	-2
25	< 50	5	-1	6	62	< 50	2	4	-2
26	61	5	-1	6	63	< 50	2	4	-2
27	< 50	5	-1	6	64	< 50	2	4	-2
28	< 50	4	1.7	2.3	65	< 50	2	4	-2
29	94	18	-2	20	66	< 50	2	4.5	-2..5
30	76	6	1.2	4.8	67	< 50	1	2	-1
31	87	8	4	4	68	100	15	15.3	-0.3
32	< 50	5	-5.5	10.5	69	< 50	2	6	-4
33	84	7	6.8	0.2	70	< 50	2	6	-4
34	100	25	24.8	0.2	71	< 50	2	6	-4
35	< 50	5	3.5	1.5	72	< 50	2	2	0
36	100	40	16.3	23.7	73	100	25	25	0
37	100	61	19	42					
							Total partitioned Bremer support	**435**	**444.5**
							Percent of total Bremer support	**49.5%**	**50.5%**


Trichodes ornatus
Temnochila virescens
Cleroidea
Caenoscelis sp.
Cryptophagidae
Megalodacne heros
Erotylidae
Anthonaeus agavensis
Kateretidae
Carpophilus sp.
Nitidulidae
Monotomidae sp.
Monotomidae
Catogenus rufus
Passandridae
Uleiota sp.
Uleiota sp.
Silvanidae
Cucujus flavipes
Cucujidae
Placonotus zimmermanni
Laemophloeidae
Olibrus sp.
Phalacridae
Bitoma sp.
Cis sp.
Eleodes sulcipennis
Tenebrionoidea
Philothermus glabriculus
Australiorylon sp.
Cerylon castaneum
Cerylon unicolor
Ceryloninae
Cerylonidae
Bothrideres geminatus
Sosylus extensus
Sosylus sp.2
Sosylus sp.1
Bothriderinae
Bothrideridae
Eufallia seminiveus
Metophthalmus haigi
Stephostethus lardarius
Dienerella intermedia
Latridiinae
"Latridiidae"
Melanophthalma sp.
Migneauxia orientalis
Corticarina sp.
Fuchsina occulta
Corticariinae
Discoloma sp.
Discolomatinae
Aphanocephalus sp.1
Aphanocephalus sp.2
Aphanocephalinae
Discolomatidae
Anamorphus sp. nov.
Bystus sp.4
Bystus sp.3
Anamorphinae
"Endomychidae"
Clypastraea sp.1
Clypastraea sp.2
Orthoperus sp.
Sericoderus sp.1
Sericoderus sp.2
"Corylophinae"
Orthoperinae
Corylophidae
Endomychus biguttatus
Endomychinae
Chondria armipes
Chondria nigra
Stenotarsus sp.1
Stenotarsus sp.4
Stenotarsinae
Anidrytus sp.
Epopterus sp.
Epipocinae
Mycetina horni
Encymon gorhami
Amphisternus sp.
Lycoperdina ferruginea
Acinaces laceratus
Amphix tarsatus
Lycoperdininae
Phymaphora pulchella
Leiestinae
"Endomychidae"
Halmus sp.
Chilocorus stigma
"Chilocorinae"
Scymnus sp.
Stethorus sp.
"Scymninae"
Coccinella transversalis
Cycloneda sp.
Hippodamia sp.
Psyllobora sp.
Harmonia euchris
Coccinellinae
Sasajiscymnus tsugae
Diomis terminatus
Platynaspis sp.
Hyperaspis sp.
Hyperaspidini sp.
"Scymninae"
"Chilocorinae"
Exoplectrini undet.
Coccidulinae
Sticholotis sp.
Sticholotidinae
Ortalia sp.
Ortalia sp. 1
"Scymninae"
Epilachna sp.
Epilachninae undet.
Epilachninae
Coccinellidae
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68
69
70
71
72
73
Cerylonid Series
1
2
3
4
5
Bootstrap ≥ 75
Bremer ≥ 10
Partitions Agree
POY Tree
Bayesian Tree
Yes / Present
No / Not Present
NA (missing data) / Unresolved

Figure 3.1

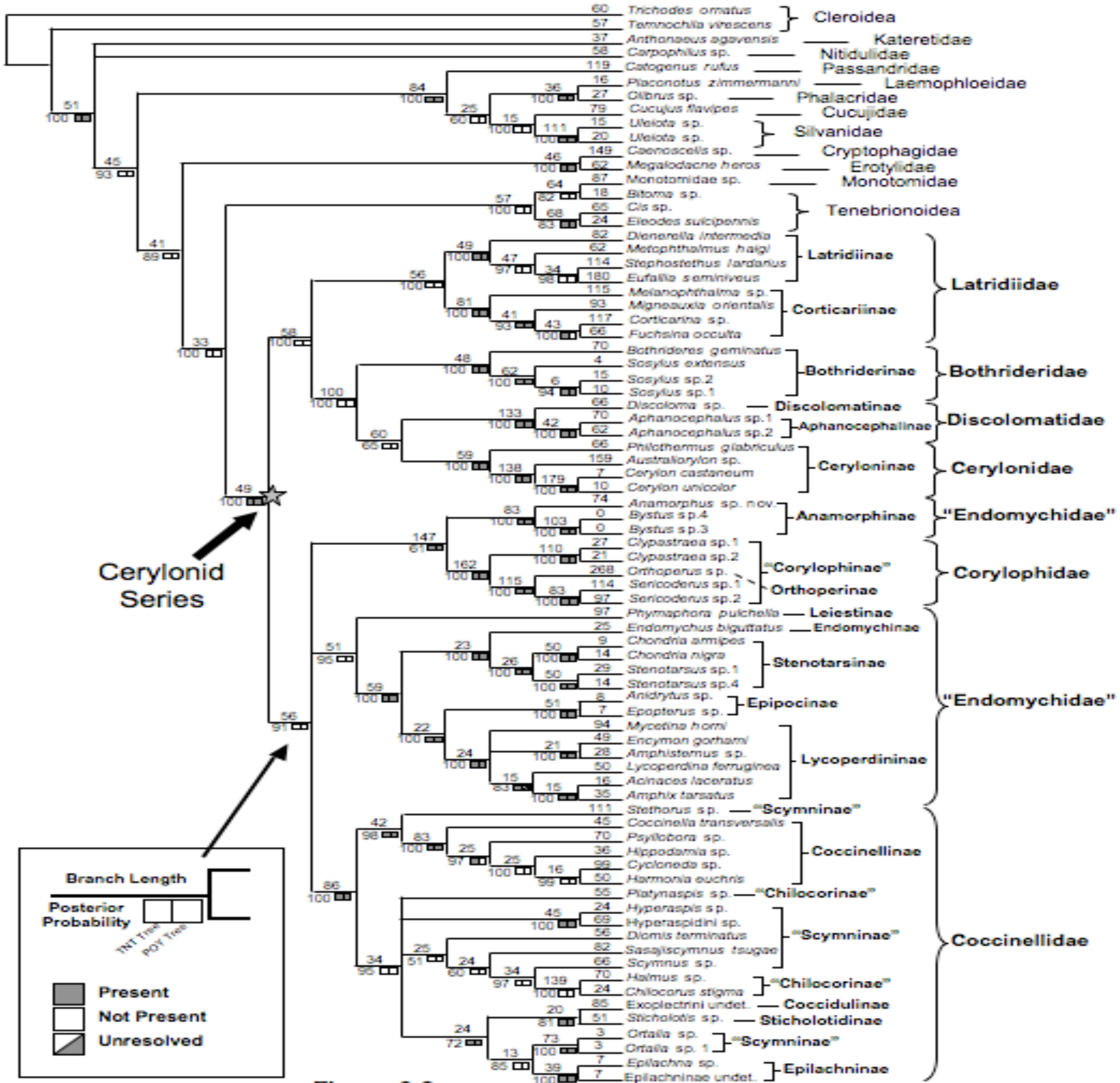
60 Trichodes ornatus
57 Temnochila virescens
Cleroidea
37 Anthonaeus agavensis
Kateretidae
58 Carpophilus sp.
Nitidulidae
119 Catogenus rufus
Passandridae
16 Placonotus zimmermanni
Laemophloeidae
27 Olibrus sp.
Phalacridae
79 Cucujus flavipes
Cucujidae
15 Uleiota sp.
20 Uleiota sp.
Silvanidae
149 Caenoscelis sp.
Cryptophagidae
62 Megalodacne heros
Erotylidae
87 Monotomidae sp.
Monotomidae
18 Bitoma sp.
65 Cis sp.
24 Eleodes sulcipennis
Tenebrionoidea
82 Dienerella intermedia
62 Metophthalmus haigi
114 Stephostethus lardarius
180 Eufallia seminiveus
Latridiinae
115 Melanophthalma sp.
93 Migneauxia orientalis
117 Corticarina sp.
66 Fuchsina occulta
Corticariinae
Latridiidae
70 Bothrideres geminatus
4 Sosylus extensus
15 Sosylus sp.2
10 Sosylus sp.1
Bothriderinae
Bothrideridae
66 Discoloma sp.
Discolomatinae
70 Aphanocephalus sp.1
62 Aphanocephalus sp.2
Aphanocephalinae
Discolomatidae
66 Philothermus glabriculus
159 Australiorylon sp.
7 Cerylon castaneum
10 Cerylon unicolor
Ceryloninae
Cerylonidae
74 Anamorphus sp. nov.
0 Bystus sp.4
0 Bystus sp.3
Anamorphinae
"Endomychidae"
27 Clypastraea sp.1
21 Clypastraea sp.2
268 Orthoperus sp.
114 Sericoderus sp.1
97 Sericoderus sp.2
"Corylophinae"
Orthoperinae
Corylophidae
97 Phymaphora pulchella
Leiestinae
25 Endomychus biguttatus
Endomychinae
9 Chondria armipes
14 Chondria nigra
29 Stenotarsus sp.1
14 Stenotarsus sp.4
Stenotarsinae
8 Anidrytus sp.
7 Epopterus sp.
Epipocinae
94 Mycetina horni
49 Encymon gorhami
28 Amphisternus sp.
50 Lycoperdina ferruginea
16 Acinaces laceratus
35 Amphix tarsatus
Lycoperdininae
"Endomychidae"
111 Stethorus sp.
"Scymninae"
45 Coccinella transversalis
70 Psyllobora sp.
36 Hippodamia sp.
99 Cycloneda sp.
50 Harmonia euchris
Coccinellinae
55 Platynaspis sp.
"Chilocorinae"
24 Hyperaspis sp.
69 Hyperaspidini sp.
56 Diomis terminatus
82 Sasajiscymnus tsugae
66 Scymnus sp.
"Scymninae"
70 Halmus sp.
24 Chilocorus stigma
"Chilocorinae"
85 Exoplectrini undet.
Coccidulinae
51 Sticholotis sp.
Sticholotidinae
3 Ortalia sp.
3 Ortalia sp. 1
"Scymninae"
7 Epilachna sp.
7 Epilachninae undet.
Epilachninae
Coccinellidae
Cerylonid Series
Branch Length
Posterior Probability
TNT Tree
POY Tree
Present
Not Present
Unresolved

Figure 3.2

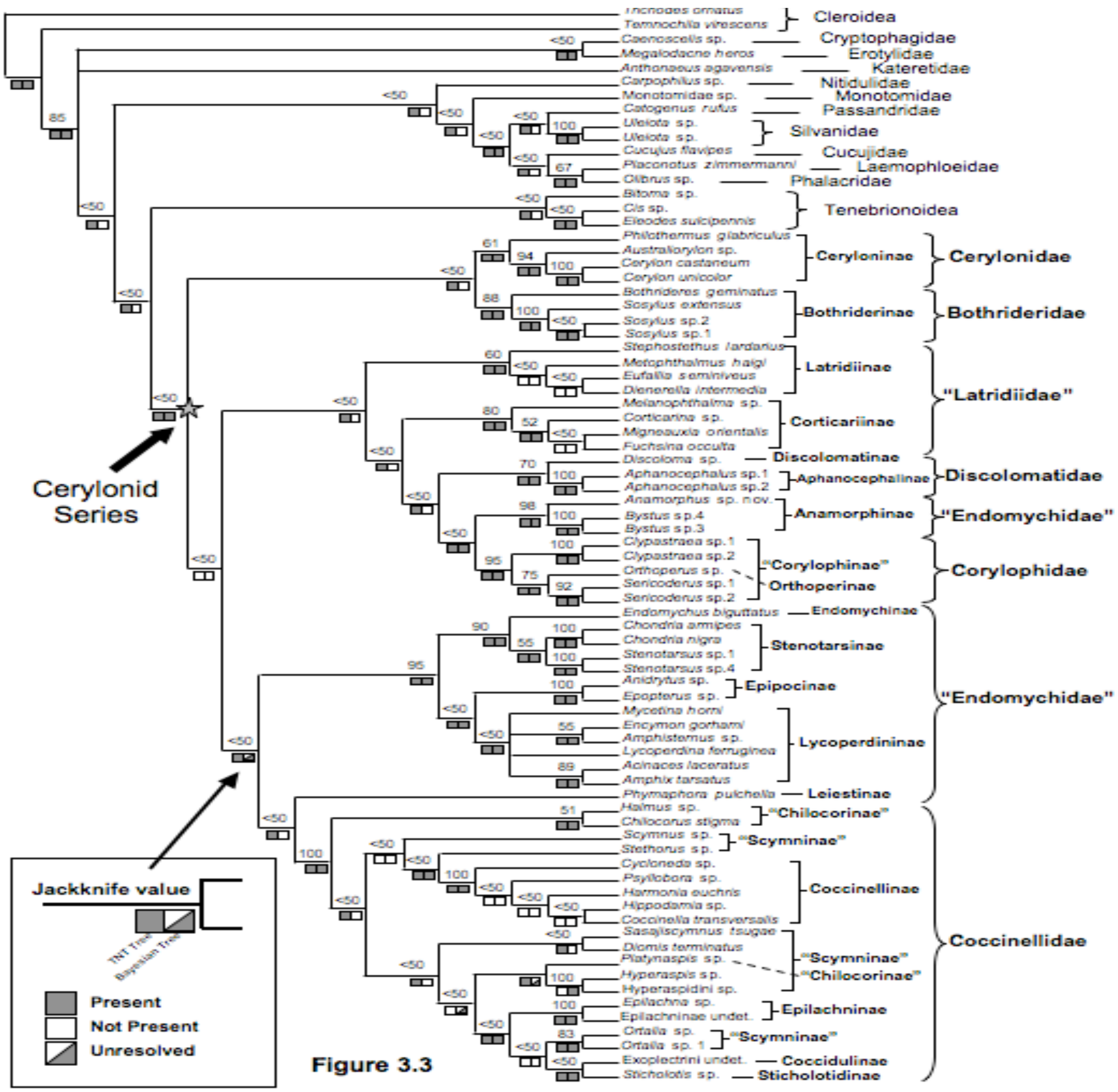
Trichodes ornatus
Temnochila virescens
Cleroidea
Caenoscelis sp.
Cryptophagidae
Megalodacne heros
Erotylidae
Anthonaeus agavensis
Kateretidae
Carpophilus sp.
Nitidulidae
Monotomidae sp.
Monotomidae
Catogenus rufus
Passandridae
Uleiota sp.
Uleiota sp.
Silvanidae
Cucujus flavipes
Cucujidae
Placonotus zimmermanni
Laemophloeidae
Olibrus sp.
Phalacridae
Bitoma sp.
Cis sp.
Eleodes sulcipennis
Tenebrionoidea
Philothermus glabriculus
Australiorylon sp.
Cerylon castaneum
Cerylon unicolor
Ceryloninae
Cerylonidae
Bothrideres geminatus
Sosylus extensus
Sosylus sp.2
Sosylus sp.1
Bothriderinae
Bothrideridae
Stephostethus lardarius
Metophthalmus haigi
Eufallia seminiveus
Dienerella intermedia
Latridiinae
"Latridiidae"
Melanophthalma sp.
Corticarina sp.
Migneauxia orientalis
Fuchsina occulta
Corticariinae
Discoloma sp.
Discolomatinae
Aphanocephalus sp.1
Aphanocephalus sp.2
Aphanocephalinae
Discolomatidae
Anamorphus sp. nov.
Bystus sp.4
Bystus sp.3
Anamorphinae
"Endomychidae"
Clypastraea sp.1
Clypastraea sp.2
Orthoperus sp.
Sericoderus sp.1
Sericoderus sp.2
"Corylophinae"
Orthoperinae
Corylophidae
Endomychus biguttatus
Endomychinae
Chondria armipes
Chondria nigra
Stenotarsus sp.1
Stenotarsus sp.4
Stenotarsinae
Anidrytus sp.
Epopterus sp.
Epipocinae
Mycetina horni
Encymon gorhami
Amphisternus sp.
Lycoperdina ferruginea
Acinaces laceratus
Amphix tarsatus
Lycoperdininae
Phymaphora pulchella
Leiestinae
"Endomychidae"
Halmus sp.
Chilocorus stigma
"Chilocorinae"
Scymnus sp.
Stethorus sp.
"Scymninae"
Cycloneda sp.
Psyllobora sp.
Harmonia euchris
Hippodamia sp.
Coccinella transversalis
Coccinellinae
Sasajiscymnus tsugae
Diomis terminatus
Platynaspis sp.
Hyperaspis sp.
Hyperaspidini sp.
"Scymninae"
"Chilocorinae"
Epilachna sp.
Epilachninae undet.
Epilachninae
Ortalia sp.
Ortalia sp. 1
"Scymninae"
Exoplectrini undet.
Coccidulinae
Sticholotis sp.
Sticholotidinae
Coccinellidae
Cerylonid Series
Jackknife value
TNT Tree
Bayesian Tree
Present
Not Present
Unresolved

Figure 3.3

CHAPTER 4

A MORPHOLOGICAL STUDY AND CLADISTIC ANALYSIS OF THE CERYLONID SERIES (COLEOPTERA: CUCUJOIDEA)[1]

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[1] Robertson, J.A., S.A. Ślipiński, K.B. Miller, and J.V. McHugh. To be submitted to *Systematic Entomology*.

Abstract

Phylogenetic relationships within the diverse Cerylonid Series (C.S.) remain poorly known. Here we present the first formal phylogenetic study of the C.S. based on morphological data of the adult and larval forms. Cladistic analysis of 147 (108 adult; 39 larval) characters for 76 taxa (including 69 C.S. exemplars) yields a well-resolved topology. Our results support the monophyly of Corylophidae, Coccinellidae, Discolomatidae and Bothrideridae. Cerylonidae, Endomychidae and Latridiidae were not recovered as monophyletic. Notable internal relationships recovered include Alexiidae as sister to the remaining C.S., Corylophidae as sister to Coccinellidae and a clade comprising Bothrideridae, "Cerylonidae" and Discolomatidae. Discolomatidae is nested within Cerylonidae, sister to *Murmidius*. Euxestinae is more closely related to Bothrideridae than to the remaining Cerylonidae. Eupsilobiinae and Mycetaeinae both represent distinct C.S. lineages. Many new synapomorphies and characters of interest for higher-level clades within the C.S. are discussed.

Key words: morphology, adult characters, larval characters, Cerylonid Series, Cucujoidea, Coleoptera, Corylophidae, Coccinellidae, Discolomatidae, Bothrideridae, Cerylonidae, Endomychidae, Latridiidae, Alexiidae

Introduction

Cucujoidea is a difficult group. It was long recognized for those beetles with non-heteromerous tarsi and clubbed antennae that could not be placed satisfactorily elsewhere, and thus has served as a taxonomic dumping ground for any “LBJ” (little brown job) with the above features. Consequently, the historical classification, family concepts and relationships of higher taxa have been dubious at best. Very few higher-groupings within Cucujoidea have been proposed [e.g., the Cerylonid Series (Crowson, 1955), and the Nitidulidae group (Crowson, 1955; Leschen, et al., 2005)]; of these the Cerylonid Series (C.S.) is the best-supported (Hunt et al., 2007; Robertson et al., 2008). As defined by Crowson (1955) the C.S. includes the families Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae and Latridiidae and is characterized by a number of adult and larval characters as follows: Adults with reduced tarsal formula (4-4-4 or 3-3-3) (Figure 4.1), hind wing lacking closed radial cell (Figure 4.2), hind wing with reduced anal veins (Figure 4.2), aedeagus resting on side when retracted (Figure 4.3), and aedeagus with tegmen reduced (Figure 4.4); larvae with pretarsal claw with one seta, antennal segment with sensorium as long or longer than segment 3, and spiracles usually annular. Despite the recognition of this putative natural lineage, the internal relationships among C.S. taxa remain equivocal and there has been a great deal of taxonomic instability among the families, subfamilies and genera of this group (see Ślipiński and Pakaluk, 1991; Robertson et al. 2008).

In their review of the classification of the C.S., Ślipiński and Pakaluk (1991) call for a comprehensive, morphological, phylogenetic treatment of the major C.S. taxa to be undertaken. They highlight the need to abandon previous concepts about the limits of certain C.S. taxonomic groups and reevaluate general views of morphological character evolution in this problematic beetle group (Ślipiński and Pakaluk, 1991). Such a study, comprising a complete reappraisal of the limits of C.S. families, subfamilies and higher taxa with an examination of the evolution of morphological characters supporting these groups, has yet to be undertaken.

It is interesting to note that since Ślipiński and Pakaluk's (1991) critical review, a few molecular phylogenetic studies including C.S. taxa have emerged (Hunt et al., 2007; Robertson et al., 2008; Giorgi et al., 2009; Magro et al., 2010; Lord et al., in press). Hunt et al.'s (2007) paper focused on reconstructing the higher-level relationships within the order Coleoptera using 18S, 16S and COI sequence data for a broad taxon sampling across all major beetle groups; included were 21 C.S. exemplars. The study by Robertson et al. (2008) focused entirely on C.S. relationships using 18S and 28S data for 61 C.S. taxa. Both Giorgi et al. (2009) and Magro et al. (2010) investigated higher-level relationships of the C.S. family Coccinellidae, using 18S and 28S × 56 ingroup taxa and 18S, 28S, 12S, 16S and COI × 61 ingroup taxa respectively. Most recently, Lord et al. (in press) focused on the internal relationships of the C.S. family Latridiidae and utilized seven genes × 27 latridiid exemplars. It is not the intent of the authors to discuss the above studies in detail here; rather we wish to illustrate that a large suite of molecular data for C.S. taxa and related cucujoid beetles has recently become available. Given the present state of systematics amid the age of comparative genomics and DNA barcoding this is hardly surprising and this trend is likely to continue.

In sharp contrast, morphology continues to be overlooked for this incredibly diverse group of beetles and has yet to be utilized in a cladistic framework for the C.S.. Morphological data not only represent an untapped wealth of information from which to infer phylogeny for the C.S., but it is immensely important in providing a morphological framework upon which taxonomic groupings may be defined (e.g., via synapomorphy), and anatomical evolution can be inferred. Thus the use of morphology is critical to establish a robust phylogeny and practical, character-based classification system for the C.S.

Here we perform an extensive morphological study of the C.S. covering the external and internal anatomy of both adult and larval forms. Using our resulting morphological matrix, we test the monophyly of the C.S. families and higher taxa in a phylogenetic framework. Refinement of the current classification of higher-level C.S. taxa is discussed based upon our phylogenetic results.

Materials and Methods

Taxonomic sampling

The terminal taxa used in this study include exemplars of all major C.S. groups, including representatives of all eight C.S. families, 35 of the 39 traditional C.S. subfamilies, and other notable or otherwise enigmatic taxa [e.g., *Sysolus* (Bothrideridae); *Akalyptoischion* (Latridiidae)]. The four missing C.S. subfamilies [Pondonatinae, Cephalophaninae (Discolomatidae); Danascelinae (Endomychidae); Rhypobiinae (Corylophidae)] are extremely rare, difficult to obtain, monotypic taxa (except Rhypobiinae) and their absence (particularly the discolomatid taxa) is not likely to influence major phylogenetic conclusions resulting from this study.

We included four exemplars of non-C.S. Cucujoidea [*Biphyllus* (Biphyllidae), *Paracucujus* (Boganiidae), *Ericmodes* (Protocucujidae), and *Pharaxonotha* (Erotylidae)], and one exemplar each from the superfamilies Tenebrionoidea (*Mycetophagus*), Cleroidea (*Temnoschila*), and Derodontoidea (*Derodontus*). *Derodontus* was used as the root. This provided a total of 76 taxa in this analysis (Table 1). Our rationale for choosing this taxon sampling was primarily to represent C.S. lineage and species diversity, and secondarily survey those families and subfamilies that historically have been taxonomically problematic (e.g., Endomychidae, Cerylonidae, Bothrideridae).

At present, the larval stage is unknown for a significant number of C.S. taxa. In addition, the larval descriptions of *Euxestoxenus* (Jeannel and Paulian, 1945) and *Oxylaemus* (Klausnitzer, 1975) are dubius and are not in accordance with other known larvae in these groups. Thus the larval dataset includes missing data for 11 of the terminals in this study (see Table 1).

Morphological characters

We performed an extensive literature review of morphology-based studies of C.S. taxa and related cucujoid groups. Despite the lack of an extensive morphological treatment of the entire C.S., there have been a number of morphological studies of groups within the series (e.g., Bothrideridae and Cerylonidae (Pal and Lawrence, 1986), Eupsilobiinae (Endomychidae) (Pakaluk and Ślipiński, 1990), Cerylonidae (Ślipiński, 1990), Endomychidae (Tomaszewska, 2000, 2005), Corylophidae (Ślipiński et al., 2009)) and some important studies of broader groups of Coleoptera (e.g., basal Cucujoidea (Leschen, et al., 2005), and Coleoptera (Lawrence et al., 1999)).

Select characters and corresponding states were extracted from these sources, consolidated and modified as necessary. We additionally added a number of novel characters based on our observations during the course of the present study. The resulting morphological dataset includes 147 characters covering external and internal morphology of the adult (108 characters) and larval (39 characters) forms. Mesquite 2.72 (Maddison and Maddison, 2009) was used to host these data.

Morphological terminology largely follows Lawrence (1991) for larvae and Lawrence and Britton (1994) for adults with modifications for pterothorax and hind wing terminology by

Lawrence et al. (1999) and Kukalova-Peck and Lawrence (2004) respectively. The term phallobase is used synonymously with tegmen.

Adult characters

0. Postocular constriction

    0 absent

    1 present

Many beetles possess a slight to distinct constriction posterior to the eyes. This constriction of the head may be located immediately behind the eyes or well behind them, such that distinct temples are formed.

1. Vertexal line

    0 absent

    1 present

The vertexal line (Leschen et al., 2005), or transverse occipital carina (Lawrence et al., 1999), is a sharp transverse carina that extends along the dorsal surface of the head behind the eyes.

2. Median occipital stridulatory file

    0 absent

    1 single

    2 double

Some cucujoids possess a broad, median file located just anterior to the occipital foramen. The file may be a single, or it may be divided medially such that two separate files are formed.

3. Paired occipital incisions

    0 absent

    1 present

The paired occipital incisions refer to two invaginations along the dorsal, posterior edge of the head capsule (dorsal edge of occipital foramen), forming a somewhat rounded lobe between them.

4. Frontoclypeal suture

   0 present

   1 absent

5. Apical maxillary palpomere shape

   0 cylindrical to fusiform

   1 aciculate

   2 expanded to securiform

In most cucujoids the maxillary palpomere is cylindrical to fusiform. Aciculate maxillary palpi occur in cerylonine and loebliorylonine cerylonids, while expanded to securiform palpi occur in most Coccinellidae included in the broadly defined Coccinellinae of Ślipiński (2007).

6. Antennal insertions

   0 exposed from above

   1 concealed by frontal ridge

7. Antennal club

   0 1-segmented

   1 2-segmented

   2 3-segmented

   3 indistinct

   4 4-segmented

Most C.S. taxa have an antennal club comprising three articles; in a number of C.S. taxa the number of club articles has been reduced to 2 (e.g., Eupsilobiinae, some cerylonids and most bothriderids) or 1 (e.g., Serangini, *Holoparamaecus*, most cerylonids).

8. Subantennal groove

0 absent

1 not extending below or behind eye

2 extending below or behind eye

This groove originates directly below the insertion of the antenna; in many cases it is short and houses the scape only, but sometimes it extends as a narrow groove below and behind the eye and houses several antennomeres.

9. Gular sutures

0 fused at least at base

1 separated

2 absent

In most beetles the gular sutures are separated for their entire length. In some taxa, the gular sutures may be partly or completely fused together. The majority of Corylophidae lack distinct gular sutures; exceptions include Periptyctinae, *Holopsis*, *Foadia* and *Priamima* (not included in present sampling).

10. Anterior tentorial arms

0 complete

1 strongly reduced, visible at base only or absent

Most Corylophidae have strongly reduced tentorial arms; those corylophid taxa with traces of gular sutures (Periptyctinae, *Holopsis*, *Foadia*, *Priamima*) have complete tentorial arms.

11. Anterior tentorial arms

0 entirely separate

1 at least partially fused

The anterior tentorial arms may be entirely separate for their entire length or curved inwardly such that they meet and are fused together. Most Endomychidae (except Anamorphinae) have partially fused tentorial arms

12. Corpotentorial bridge

0 present

1 absent

13. Median process of corpotentorial bridge

0 long and well developed

1 produced only as a short knob

2 absent

All Cerylonidae, select anommatine, xylariophiline and teredine Bothrideridae, and *Biphyllus* possess a well-developed, median process on the corpotentorial bridge that extends anteriorly. In *Corticaria* (Latridiidae), a median process is present but produced as only a small knob.

14. Membranous vesicles on club segments

0 absent

1 present

All Corylophidae posses membranous sensory vesicles on the club articles of the antennae. Following Ślipiński et al. (2009), we treat the variously shaped sensilla in this family as homologous.

15. Anterior cervical sclerites

0 neither contiguous with head capsule nor placed within paired emarginations

1 contiguous with head capsule and usually placed within paired emarginations on ventral edge of occipital foramen

2 apparently absent

16. Clypeus

0 apically as broad as, or narrower than basal margin at frontoclypeal suture

1 broadened apically, distinctly wider than basal margin at frontoclypleal suture

In Discolomatidae and most Cerylonidae (Ostomopsinae, Murmidiinae, Ceryloninae), the clypeus is distinctly broadened apically. Among the taxa examined here, *Periptyctus*, *Enicmus* and *Stephostethus* also possess state 1.

17. Labrum externally

0 visible

1 not visible

18. Labrum

0 as broad or narrower than anterior margin of clypeus

1 distinctly wider than clypeus

In Latridiidae, the labrum is distinctly wider than the anterior margin of the clypeus.

19. Epipharyngeal impression

0 present

1 absent

This is a medial impression on the inner surface of the labrum (Pal and Lawrence, 1986) and occurs in some Bothriderinae.

20. Labral rods

0 present

1 absent

21. Labral rods (shape)

0 club-like

1 rod-like

Labral rods may be long and narrow (rod-like) or wide and robust basally (club-like). Club-like labral rods occur in loebliorylonine and euxestine cerylonids and most bothriderids (except bothriderines).

22. Tormae

0 present, well developed

1 present, greatly reduced to small knobs

2 absent

In Coccinellidae, the tormae are greatly reduced to small knobs.

23. Mesal arms of tormae

0 perpendicular

1 oblique

2 acute

The mesal arms may extend from the tormae in a perpendicular manner, such that a right angle is formed between the two (e.g., *Cerylon*), or they may come off at either an oblique (directed posteriorly) or acute (directed anteriorly) angle. Acute, or "recurved" mesal arms are considered relatively rare by Pakaluk & Slipinski (1990); however they appear to be more widespread than previously considered.

24. Apex of mandible

0 unidentate

1 multidentate

Here we do not follow the convention of Leschen et al. (2005); rather here a tooth/lobe is a tooth/lobe and if there are three distinct teeth/lobes it is coded as multidentate. Leschen et al. (2005) apply a more strict definition to what constitutes multiple teeth along the edge of the mandible. If two adjacent teeth are more or les coplanar and of similar size, whereas a third tooth is smaller and subapical, then this is considered bidentate by Leschen et al. (2005). In the instance there are three lobes/teeth, if the middle tooth is the longest of these then it is coded as multidentate.

25. Dorsal surface of mandible

0 without tubercle fitting into lateral clypeal emargination

1 with tubercle fitting into lateral clypeal emargination

26. Dorsal surface of mandible

0 without cavity

1 with glabrous cavity

2 with setose cavity

27. Mandibular mola

0 present

1 absent

Here a taxon is coded as state 0 (mola present) only if the molar region of the mandible is raised, sclerotized with a rough surface for grinding.

28. Mandibular prostheca

0 brush like

1 membranous lobe

2 sclerotised tubercle or process

3 absent

4 sclerotised comb at apex of elongate membranous process

29. Galea

0 at least 2.5 X as wide as lacinia

1 between 1 and 2.5 X as wide as lacinia

2 distinctly narrower than lacinia

3 absent

30. Lacinial uncus

0 absent

1 present

This structure is an extension of the lacina, not to be confused with socketed spines or stout setae.

31. Mentum medially

0 with median setose tubercle

1 flat

32. Lateral pronotal carinae

0 complete

1 incomplete

2 absent

33. Gland openings along lateral pronotal and elytral margins

0 present

1 absent

34. Anterior portion of prosternum at midline

0 longer than prosternal process

1 as long as prosternal process

2 shorter than prosternal process

35. Apex of prosternal process

0 without lateral projections

1 with lateral projections

36. Shortest distance between procoxal cavities

0 less than half as great as mid length of cavity

1 more than half as great but less than mid length of cavity

2 more than mid length of cavity

37. Notosternal suture

0 complete

1 incomplete or absent

38. Procoxa

0 without concealed lateral extension

1 with short, concealed lateral extension (less than 0.75 × the length of exposed portion of the coxa)

2 with long, concealed lateral extension (at least 0.75 × the length of the exposed portion of the coxa)

39. Protrochantin

0 exposed

1 concealed

An exposed protrochantin is rare among C.S. taxa, occurring only in *Sphaerosoma* (Alexiidae) and *Holopsis* (Corylophidae) among those taxa examined here.

40. Procoxal cavity

0 transverse

2 about as long as wide

41. Procoxal cavities externally

0 open

1 closed

42. Procoxal cavity

0 without narrow lateral notch (slit)

1 with narrow lateral notch (less than 0.25 × mid length of cavity)

43. Procoxal cavity internally

0 open

1 closed

44. Protibial spurs

0 2 unequal

1 2 subequal

2 1

3 absent

45. Trochanterofemoral attachment

0 normal to elongate

1 heteromeroid

A taxon is considered to have heteromeroid trochanterofemoral attachment if the trochanter is strongly oblique such that the base of the femur is in contact or nearly so with the coxa. Both of the above states are common among C.S. taxa.

46. Trochanter (concealment)

    0 not reduced or concealed, clearly visible externally

    1 highly reduced and concealed within excavation of femur

In Bothriderinae, the trochanter is reduced significantly such that it is concealed within and excavation of the femur.

47. Elytral punctation

    0 not seriate or striate

    1 seriate or striate

48. Scutellary striole

    0 absent

    1 present

All C.S. taxa lack a scutellary striole.

49. Elytral sutural flange

    0 not widened apically

    1 widened apically

50. Epipleuron

    0 complete to apex of elytron

    1 incomplete apically

    2 absent

51. Mesoventrite anterior surface

0 with cavity or fossa receiving prosternal process

1 without median cavity

52. Shortest distance between mesocoxal cavities

0 less than half as great as shortest diameter of cavity

1 more than half as great as shortest diameter of cavity

53. Meso-metaventral junction

0 dicondylic

1 monocondylic

2 simple

3 not in contact--coxae continuous

Among C.S. taxa examined here, only *Anommatus* and *Oxylaemus* (Bothrideridae) possess state 3. The dicondylic condition does not seem to occur in the C.S.

54. Mesocoxae (shape)

0 circular

1 transverse

55. Mesocoxal cavities laterally

0 open (partly closed by mesepimeron)

1 closed (by meeting of mesoventrite and metaventrite)

This is considered a significant character for C.S. higher-level relationships (Ślipiński and Pakaluk, 1991). Ślipiński and Pakaluk (1991) discuss this character at length with respect to various scenarios of C.S. family relationships. Among C.S. taxa, Cerylonidae, Latridiidae, Discolomatidae, Bothrideridae (except *Sysolus*), Anamorphinae and Merophysiinae

(Endomychidae), and most Corylophidae have the mesocoxal cavities closed by the meso- and metaventrites.

56. Mesotrochantin

0 exposed

1 hidden

Relatively few C.S. taxa have an exposed mesotrochantin; in the present study, *Sysolus*, *Sphaerosoma* (Alexiidae) and many of the "higher Endomychidae" of Tomaszewska (2005) have state 0.

57. Mesoventral postcoxal pits

0 present

1 absent

These occur only in the family Endomychidae and are located on the lateral margins of the procoxal rests on the anterior half of the mesoventrite.

58. Metaventral postcoxal pits

0 present

1 absent

Metaventral postcoxal pits also occur only in some Endomychidae and are located along the anterior margin of the metaventrite, posterior the mesocoxae. The occurrence of mesoventral and metaventral postcoxal pits overlap considerably; however they do not covary as there are a number of Endomychidae that have only the metaventral pits [e.g., *Beccariola* (Lycoperdininae)].

59. Metaventral femoral lines

0 present

1 absent

60. Metaventral discrimen

0 complete

1 incomplete or absent

The metaventral discrimen is a median, longitudinal suture that represents the invagination of the metendosternite.

61. Metaventral transverse suture (katepisternal suture)

0 present

1 absent

This is a transverse suture located near the posterior margin of the metaventrite. The metaventral transverse suture does not occur in any C.S. taxa; rather it is considered a plesiomorphic condition for Cucujoidea and only occurs in *Paracucujus* and *Derodontus* in the taxon sampling of the present study.

62. Metacoxal proximity

0 contiguous or narrowly separated (at most by 1/3 of coxal width)

1 moderately separated (more than 1/3 of coxal width)

2 widely separated (more than coxal width)

3 extremely separated (more than 1.5 × coxal width)

In general, the metacoxae of C.S. taxa are distinctly separated compared to most other cucujoids. In the present study, all non-C.S. taxa exhibit narrow separation of the metacoxae; teredine and xylariophiline Bothrideridae also have a narrowly separated metacoxae. Among C.S. taxa most have a moderate separation of the metacoxae (state 1). Eupsilobiinae (Endomychidae), Murmidiinae (Cerylonidae) and most Euxestinae (Cerylonidae) exhibit a wide separation (state 2) while Corylophidae and Bothriderini exhibit extreme separation of the metacoxae (state 3).

63. Metacoxae

0 extending laterally to meet elytral epipleura, ventrite 1 not in contact with metepimeron

1 not extending laterally to meet elytral epipleura, ventrite 1 in contact with metepimeron

When the metacoxae do not extend laterally to meet the elytral epipleura (state 1), there is typically a raised portion of ventrite 1 that fills the space between the lateral margin of the coxa and the elytral epipleura. In those taxa with state 0, this space does not exist as the coxae abuts the elytral epipleura.

64. Metacoxal carina

0 present

1 absent

65. Metacoxal extensions

0 externally visible

1 concealed

In Discolomatidae, the transverse metacoxae are mostly concealed by the metaventrite such that the visible portion of the coxae is small and round.

66. Metendosternal anterior tendon attachments (remnants of divided anterior process)

0 well developed, distinctly longer than broad

1 knob-like, no longer than broad

2 absent

67. Anterior tendons of metendosternite

0 narrowly separated

1 widely separated

68. Radial cell of hind wing

0 complete (closed basally)

1 incomplete or absent

The lack of a closed radial cell is one of Crowson's (1955) original synapomorphies used to define the C.S. This putative synapomorphy for the C.S. is not without exception however, due to *Deretaphrus* (Bothriderinae) possessing a closed radial cell in the hind wing; all other C.S. taxa have the radial cell incomplete or absent.

69. Free veins in medial area of hind wing

0 five

1 four

2 three

3 two

4 one

5 none

Having the number of anal veins in the hind wing reduced to three or fewer is another character used by Crowson (1955) to define the C.S.. For a vein to be considered "free," it must be a single vein (not including MP1+2) extending toward the wing margin. For example, the hind wing of *Dastarcus* (Figure 4.2) has three free anal veins in the medial field. Although we do not treat all reductions of anal veins as single state here, all C.S. taxa do have three or fewer veins and thus are coded as one of states 2-5. Coding in this manner is favorable as the homology statement is more objective; however it results in this character not being an uncontroverted synapomorphy for the C.S..

70. Medial fleck of hind wing

0 present

2 absent

71. Medial fleck of hind wing, divided

0 divided

1 undivided

72. Anal lobe of hind wing

0 present

1 absent

73. Tarsal formula in male

0 5-5-5

1 5-5-4

2 4-4-4

3 3-3-3

A reduced tarsal formula (4-4-4 or 3-3-3) is one of Crowson's (1955) synapomorphies for the C.S.. Again, we consider the diversity of tarsomere reduction in our coding and do not code 4-4-4 or 3-3-3 as a combined single state. However, all C.S. taxa do have the number of tarsomeres reduced and are thus coded as having either state 2 or 3 accordingly.

74. Tarsal formula in female

0 5-5-5

1 5-5-4

2 4-4-4

3 3-3-3

There is sexual dimorphism in tarsal formula for a number of cucujoids, thus the number of tarsi is coded for both genders.

75. Penultimate mesotarsomere

    0 not or slightly reduced and not enclosed within lobe on previous tarsomere

    1 highly reduced and partly or entirely enclosed within ventral lobe of previous tarsomere

76. Tarsomere II

    0 lobed below

    1 simple

77. Metacoxae shape

    0 circular

    1 transverse

78. Number of visible abdominal ventrites

    0 6

    1 5

79. Number of basal ventrites connate

    0 none

    1 two

    2 three

All Coccinellidae have the first two abdominal ventrites connate.

80. Abdominal postcoxal lines

    0 absent

    1 present

81. Intercoxal process of abdominal ventrite I

0 narrow with acute apex

1 broad with rounded apex

2 broad with angulate or truncate apex

Many cucujoids have a narrow intercoxal process of abdominal ventrite I with an acute apex. In most C.S. taxa, the intercoxal process of abdominal ventrite I is broad with an angulate or truncate apex; the few exceptions belong to Bothrideridae, where all three states occur.

82. Ventrites with internal apodemes

0 absent

1 present

Most C.S. taxa possess ventrites with internal apodemes. These apodemes may be long and well developed extending well into the preceding abdominal segment (e.g., Cerylonidae, Bothrideridae) or not as prevalent, represented by a short, broad shelf-like extension (e.g., *Holopsis*). Some Coccinellidae and a few Endomychidae (*Endomychus*, *Amphix*) and Corylophidae (*Sericoderus*) lack internal apodemes of the abdominal ventrites.

83. Abdominal tergite 7

0 concealed from above by elytra

1 exposed from above

84. Pygidium

0 with median groove

1 smooth

Discolomatidae possess a median grove on the pygidium (tergite VIII) that receives the elytra and serves as part of the elytral interlocking mechanism.

85. Posterior edge of last abdominal ventrite

0 smooth

1 crenulate

This character is unique to cerylonine, murmidiine and ostomopsine Cerylonidae and forms the interlocking mechanism with the corresponding crenulations beneath the elytral apices.

86. Functional spiracle on abdominal segment VII

0 present

1 absent

This is another character that has historically been considered to be significant for higher-level C.S. relationships (Ślipiński and Pakaluk, 1991). Bothrideridae, Euxestinae, Latridiidae and all Corylophidae (except *Orthoperus*) have seven abdominal spiracles; all other C.S. taxa have only five and thus lack the spiracle on abdominal segment VII.

87. Tergite 8 in male

0 completely dorsal

1 with sides curved ventrally

2 with sides and apex curved ventrally to form genital capsule

88. Anterior edge of sternite 8 in male

0 without median strut

1 with median strut

89. Tergite 9 in male

0 distinct

1 divided into hemisternites

2 strongly reduced or absent

90. Apex of sternite 9 in male

0 with mesal lobe

1 without mesal lobe

91. Anterior edge of sternite 9 in male

0 without spiculum gastrale

1 with spiculum gastrale

2 with two large rods

3 with single rod

92. Aedeagus orientation at rest

0 rotated 90 degrees

1 not rotated

Having the aedeagus resting on its side when retracted is one of the characters Crowson (1955) used to characterize the C.S.. A rotated aedeagus is known to occur in a number of non-C.S. families however, including Sphindidae (Sen Gupta and Crowson, 1977; McHugh, 1993), Boganiidae (Sen Gupta and Crowson, 1979; Lawrence, 1982), Protocucujidae (Ślipiński and Beutel, 2010) and Erotylidae (Crowson, 1955; Lawrence, 1982).

93. Tegmen (type)

0 encircling penis

1 ventral to penis

2 dorsal to penis

3 absent

94. Paired dorsal and ventral tegminal struts

0 present

1 absent

The phallobase in Cleroidea, Byturidae and Biphyllidae is unique among Cucujiformia in that in addition to the anterior ventral tegminal strut the anterior part of the tegmen bears a pair of lateral struts that extend ventrally and partly enclose the penis. In the current sampling *Temnoscheila* and *Biphyllus* are coded as state 1.

95. Anterior ventral tegminal strut

    0 fixed

    1 articulated

    2 absent

96. Base of tegmen

    0 broadly rounded or truncate

    1 narrowly rounded to acute

    2 produced anteriorly forming strut

97. Parameres

    0 free from one another

    1 fused into single piece

    2 absent

98. Parameres

    0 articulated to phallobase

    1 fused to phallobase

99. Apical portion of tegmen including parameres (does not include anterior strut)

    0 asymmetrical

    1 symmetrical

100. Penis

0 not divided into distinct basal and apical sections

1 divided into distinct basal and apical sections

A divided penis occurs in some non-C.S. Cucujoidea including Priasilphidae, *Agapytho* (Agapythidae) and *Cucujus* (Cucujidae) (Leschen et al., 2005). In the present study, this condition occurs only in *Saula* (Endomychidae) and *Dastarcus* (Bothrideridae).

101\. Basal portion of penis

0 distinctly wider than apical portion

1 as wide as or narrower than apical portion

2 sclerotized T-shaped

102\. Base of penis

0 without median carina

1 with median carina

103\. Anterior edge of penis

0 without struts

1 with paired struts

2 with single strut

104\. Penis

0 with complex endophallic sclerities

1 without endophallic sclerites

Complex endophallic sclerites are considered to be an uncontroverted synapomorphy uniting all of Corylophidae (Ślipiński et al., 2009). In the course of the present study however, we discovered that Anamorphinae (Endomychidae) also possess them.

105\. Styli of ovipositor

0 present

1 absent

106. Anterior edge of sternite VIII in female with fixed median strut (spiculum ventrale) with articulated median strut (spiculum ventrale)

0 without median strut

1 with median strut (spiculum ventrale)

107. Spermatheca

0 absent

1 present

Larval characters

108. LARVA: Stemmata number

0 six

1 five

2 four

3 three

4 two

5 one

6 none

109. LARVA: Antennal socket separation from mandibular articulation

0 by very narrow strip of cuticle

1 by broad strip of cuticle

110. LARVA: Antennal length

0 less than .15 times head width

1 .15 to .5 times head width

2 more than .5 times head width

111. LARVA: Number of antennomeres

0 1

1 2

2 3

112. LARVA: Antennomere II

0 less than 2 times as long as wide

1 more than twice as long as wide

113. LARVA: Sensorium

0 shorter or equal to apical antennomere

1 longer than apical antennomere

The presence of a long sensorium is another character state often used to characterize the C.S. (Crowson, 1955). Among taxa examined here exceptions are widespread throughout the C.S..

114. LARVA: Labrum

0 separated from head capsule by complete suture

1 partly or completely fused to head capsule (suture incomplete or absent)

115. LARVA: Apex of mandible

0 unidentate

1 bidentate

2 tridentate or multidentate

3 reduced to absent

4 hyaline and reduced

5 endomethous

116. LARVA: Accessory ventral process of mandible

0 absent

1 present

117. LARVA: Mesal surface of mandibular base

0 with asperate or tuberculate mola

1 with 1 to 3 hyaline processes

2 simple

118. LARVA: Mandibular prostheca

0 present

1 absent

119. LARVA: Ventral mouthparts

0 strongly retracted (distance between mandibular and maxillary articulations greater than width of stipes)

1 protracted or slightly retracted (distance between mandibular and maxillary articulations less than width of stipes)

120. LARVA: maxillary articulating area

0 well-developed

1 highly reduced or absent

121. LARVA: Inner apex of mala or lacinia

0 rounded or truncate

1 falciform

122. LARVA: Maxillary cardo and stipes

0 distinct

1 fused together

123. LARVA: Number of labial palpomeres

0 two

1 one

124. LARVA: Labial palpi

0 contiguous or separated by less than width of first palpomeres

1 separated by more than width of first palpomere

125. LARVA: Ligula

0 absent

1 present

126. LARVA: Hypopharyngeal sclerome form

0 absent

1 a transverse bar

2 an irregularly concave molar-like tooth

127. LARVA: Hypostomal rods

0 subparallel

1 diverging

2 absent

128. LARVA: Ventral epicranial ridges

0 absent

1 present

129. LARVA: Gula

0 wider than long

1 longer than wide

2 absent

130. LARVA: Thoracic and most abdominal terga

0 without long lateral processes

1 with long lateral processes

131. LARVA: Mesocoxae separation

0 less than two coxal diameters

1 more than two coxal diameters

132. LARVA: Apex of tibiotarsus

0 with simple setae

1 with modified setae

2 with two spatulate setae

133. LARVA: Number of pretarsal setae

0 two

1 one

2 none

134. LARVA: Pretarsal claw shape

0 simple

1 with basal tooth

135. LARVA: Pretarsal seta

0 normal, pointed apically

1 modified, spatulate

136. LARVA: Thoracic terga

0 with parascoli

1 without parascoli

137. LARVA: Abdominal gland openings

0 absent

1 on segments 1-4

2 on segments 1-7(8)

3 on segments 1 and 7 (8) only

138. LARVA: Abdominal tergites

0 without rows of asperities

1 with curved rows of asperities

139. LARVA: Abdominal tergum

0 not forming articulated plate

1 forming articulated plate

140. LARVA: Abdominal tergum

0 simple

1 with paired urogomphi

141. LARVA: Urogomphi curvature

0 straight

1 curved upwards

142. LARVA: Urogomphi orientation

0 subparallel

1 strongly diverging

143. LARVA: Sternum 9 exposure

0 partly or entirely exposed

1 completely concealed or apparently absent

144. LARVA: Segment 10 and anal opening

0 posterior or terminal

1 posteroventral

2 ventral

145. LARVA: Spiracles

0 annular

1 annular-biforous or uniforous

Annular larval spiracles are another character used by Crowson (1955) to characterize the C.S..

146. LARVA: Abdominal spiracles

0 not at ends of spiracular tubes

1 at ends of short spiracular tubes on segments 1 to 8

2 at ends of long spiracular tubes on segments 1 to 8

3 at end of spiracular tubes on segments 8 only

Specimens and sources of material

One major difficulty when performing a morphological study spanning this breadth of beetle diversity is specimen availability. In molecular systematic studies specimen acquisition is often the limiting factor due to the necessity of obtaining fresh molecular-grade material. In contrast, specimen acquisition is generally not an issue in most morphological studies; dry specimens are typically readily obtainable via loans from research collections of major institutions. However, many C.S. and cucujoid taxa are extremely rare, and it is often the case that these obscure taxa represent major C.S. lineages [e.g., Anommatinae (Bothrideridae); Loebliorylоninae, Ostomopsinae (Cerylonidae); Pondonatinae, Cephalophaninae (Discolomatidae); Mycetaeinae, Eupsilobiinae, Xenomycetinae, Danascelinae (Endomychidae); Aenigmaticini (Corylophidae)] and are thus important for inclusion in any comprehensive phylogenetic study. Indeed, representative reference collections of adult Cucujoidea at even the subfamilial level are extremely rare in the world. The relative rarity of credibly identified larval cucujoids compounds this problem significantly.

In general, scoring of the adult characters was performed by JAR while the larval coding was largely performed by SAS. Observations were made using a Leica MZ8 stereomicroscope or a Leica Leitz DMRB compound microscope. Characters were photographed using either a Microptics™ Lab XLT Workstation (Microptics, Inc., Ashland, VA, USA) or a Sony DKC-5000 camera attached to a Leica WILD M10. In the case that multiple images were taken at sequential focal planes, the individual photos in the series were montaged using either CombineZ v 5.3 (Alan Hadley, U.K.) or Automontage Pro v. 5.01 (Synoptics, Ltd., Frederick, MD, USA). The scored matrix is found in Table 2.

One of the goals of this study was to compile a representative collection of Cucujoidea to augment the current holdings of the UGCA. Through our collecting efforts and that of collaborators, as well as through generous loans from collections, we have successfully put together an extensive reference collection of disarticulated Cucujoidea as part of the UGCA.

Specimens used in this study were cleared using one of two methods as outlined below. Most specimens were subjected to a mild KOH solution at room temperature for four to seven days. Throughout the clearing process specimens were checked at minimum each day. When cleared to the desired extent, specimens were rinsed with distilled water and any remaining tissue was removed manually with forceps or a syringe via a blast of distilled water. Wings were either removed prior to treatment in the KOH solution or after a day or two of clearing. Alternatively, specimens were cleared using proteinase-K and ATL buffer at 55° C for 3 hours during the Qiagen DNeasy (Valencia, CA) extraction protocol for DNA extraction of animal tissues (Qiagen DNeasy Blood & Tissue Kit).

Cleared specimens were stored on open glycerol slides, with a fine bead of silicon around the depression for larger specimens. Adult specimens were fully disarticulated and wings were removed and mounted on the slide next to the glycerol-filled depression (Figure 4.5). In some cases, specimens were stained using Chlorazol Black to facilitate the visualization of internal structures. Morphological vouchers are retained at either the ANIC or UGCA.

This study would not have been possible without assistance and specimen loans from the following individuals and institutions.

SASC	S. Adam Ślipiński personal collection, CSIRO, Entomology, Canberra, Australia
ANIC	Australian National Insect Collection, CSIRO, Entomology, Canberra, Australia (Adam Ślipiński)
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, CA, USA (Michael Caterino)
UGCA	The University of Georgia Collection of Arthropods, Athens, GA, USA
FSRC	Floyd Shockley Research Collection, UGA, Athens, GA, USA
JARC	James A. Robertson personal collection, UGA, Athens, GA, USA

Phylogenetic analysis

Phylogenetic analysis of the combined adult and larval dataset was performed in NONA Goloboff (1995) as implemented in WinClada (Nixon, 2000), utilizing 200 ratchet replications. All characters were treated as unordered and weighted equally and trees were rooted to *Derodontus*. Branch support was assessed by calculating bootstrap values in NONA via WinClada. Character states were optimized on the topology using unambiguous optimization using WinClada and Mesquite (Maddison and Maddison, 2009).

Results

Of the 147 characters in the combined adult and larval matrix, 136 are parsimony informative. The remaining 11 uninformative characters (4 constant, 7 variable uninformative) would be informative with an expanded representation of non-C.S. cucujoid outgroup taxa. Nona produced 46 most parsimonious trees of length 968 (CI = 20; RI = 65), the strict consensus of which is shown in Figure 4.6. Although the consensus topology is overall well-resolved, there is a high amount of homoplasy as indicated by the low CI and the low number of uncontroverted synapomorphies. Given the morphological diversity in the C.S., this result is not surprising. Similarly, the resulting topology is weakly supported along the base of the tree, with moderate to high bootstrap values corresponding to familial and subfamilial clades.

Although testing the monophyly of the C.S. was not an explicit goal of this study nor is the current outgroup sampling among Cucujoidea sufficiently broad to provide a rigorous test of monophyly for the C.S., our results support the C.S. as monophyletic. These results support the following C.S. families as monophyletic: Corylophidae, Coccinellidae, Discolomatidae and Bothrideridae. Cerylonidae, Endomychidae and Latridiidae however, were not recovered as monophyletic. Notable internal relationships include Alexiidae as the sister taxon to the remaining C.S., Corylophidae as the sister taxon to Coccinellidae, and a clade comprising Bothrideridae, "Cerylonidae" and Discolomatidae. Discolomatidae is nested within Cerylonidae, sister to *Murmidius*. Euxestinae is more closely related to Bothrideridae than to the remaining Cerylonidae.

A convention we will follow while discussing character states that support specific nodes in our resulting topology is to list the number of the character, followed by a dash then the relevant state. For example, character 20 (labral rods) state 1 (present) would be listed as 20-1. If the character is an uncontroverted synapomorphy, an asterisks will follow the listed character-state (e.g. 20-1*). In the discussion we often refer to a character state as being a strong or robust synapomorphy for a given clade. In these cases the character state is not an uncontroverted synapomorphy, yet is shared by only a few other distantly related taxa.

Discussion

Cerylonid Series

Although the present study focused on the internal relationships of the C.S. and the taxon sampling of other Cucujoidea was inadequate to provide a rigorous test of the monophyly of the group, we did recover a monophyletic C.S. in our analysis. The C.S. is a relatively well-supported clade in the topology (bootstrap = 77) and is supported by the following 14 characters/states: antennal insertions exposed from above (6-1), procoxal cavity without narrow lateral slit (42-0), metaventral femoral lines present (59-0), metacoxae moderately separated, by more than 1/3 coxal width (62-1*), metacoxal carina absent (64-2*), radial cell of hind wing incomplete or absent (68-1), no free veins in hind wing (69-5), anal lobe of hind wing absent (72-1*), abdominal postcoxal lines present (80-1), intercoxal process of abdominal ventrite I broad with angulate or truncate apex (81-2), ventrites with internal apodemes present (82-1), anterior edge of penis without struts (103-0), larval antennomere II less than 2 times as long as wide (112-0) and larval hypostomal rods absent (127-2). One uncontroverted synapomorphy for the C.S. clade, metacoxal carina absent (64-2*), cannot be considered truly an uncontroverted apomorphy for this group, as this state occurs in many non-C.S. cucujoids (Leschen, et al., 2005) which are not included in the present study. Likewise, anal lobe of hind wing absent (72-1*), although this state is uncontroverted, there are a number of reversions within the C.S. to having an anal lobe present [e.g., Coccinellidae (part), Endomychidae (part), Euxestinae, Bothrideridae].

Some of the above synapomorphies for the C.S. are here considered rather weak (e.g., 59, 80) with a high number of C.S. taxa not sharing the state lending support to this clade. These character states are only considered synapomorphies for the C.S. due to their optimization on this specific topology resulting from the first few basal nodes within the C.S. clade sharing the same state. Given the weak support among the basal branches of this topology, we consider the above states as only tentative or weak synapomorphies for the C.S. until the relationships herein are corroborated.

Perhaps some of the more robust homoplasious synapomorphies for the C.S. in this analysis include 6-1, 42-0, 68-1, 81-1, 82-2, as in all of these cases there are only a few taxa or minor, deeply-nested clades that possess an alternative state from the remaining C.S. taxa thus rendering the character state controverted/homoplasious. Because most of the C.S. share the same character state for these characters, the optimization of the character state is not sensitive to minor topological rearrangements within the C.S. clade, particularly among the basal splits of the C.S.. It follows that in future analyses these characters will likely continue to provide support for the C.S. clade irrespective of differences in character state optimization resulting from minor changes in the topology.

Of the adult characters that Crowson (1955) used to define the C.S. only a few appear to provide support for the C.S. clade. This is due in part to the fact that we expanded the states of two of Crowson's characters [wings with reduced anal veins—here treated as: free veins in medial area of hind wing (character 69); reduced tarsal formula—here treated as: tarsi in male (character 73); tarsi in female (character 74)] for the sake of making sound homology statements and to reflect the observed diversity. Crowson (1955) was correct that all C.S. taxa have a reduced tarsal formula (4-4-4 or 3-3-3) and if treated as its own state, this character state would indeed be an uncontroverted synapomorphy for the C.S.. Likewise, all C.S. taxa have hind wings with reduced anal venation (three or fewer anal veins) and if treated as a single state would also be a strong character supporting the C.S.. Nonetheless, it should be noted that the reduced anal venation character (character 69) still comprises a synapomorphy for the C.S. in this analysis (as discussed above). Despite not serving as uncontroverted synapomorphies for the C.S. in the present analysis, both the above characters as defined by Crowson are certainly appropriate and useful for characterizing the C.S..

The hind wing lacking a closed radial cell (68-1) is a synapomorphy for the C.S. in the present study (see above) in accord with Crowson's (1955) diagnosis for the C.S.. *Deretaphrus* (Bothriderinae) is the only C.S. taxon that has a closed radial cell; thus this character state would constitute an uncontroverted synapomorphy if not for this one exception.

Crowson (1955) also used two male genitalic characters to distinguish the C.S. from other Cucujoidea. The aedeagus resting on its side when retracted (92-0) is not considered a synapomorphy for the C.S. in the present study. This is due in part to the ambiguous coding of this character for *Sphaerosoma*. In our specimen of *Sphaerosoma* the aedeagus was not distinctly rotated, yet the genital segments of the abdomen appeared to be somewhat extended, thus it was difficult to determine whether or not the aedeagus was not rotated simply because it was about to be protracted. As *Sphaerosoma* is the sister group to the remaining C.S. taxa, this ambiguous coding bears important ramifications for this character state, rendering it a non-synapomorphic state for the C.S.. In addition, two outgroup taxa (*Paracucujus*, *Ericmodes*) have the aedeagus rotated when retracted, thus as noted above, this character state is not exclusive to C.S. taxa.

We did not include the final adult character used by Crowson (1955) (viz., aedeagus with reduced tegmen) in the present study because it proved too difficult to objectively determine at what point a tegmen should be considered reduced.

Of Crowson's three larval characters defining the C.S., none are supported as synapomorphies for the series in the present study. The elongate condition of the antennal sensorium (character 113-1) is quite variable in the C.S.. While our data support Crowson's (1955) proposal that all C.S. taxa have only a single seta on the pretarsal claw (133-1), this character cannot be considered a synapomorphy for the C.S. since *Temnoscheila* also shares this state, rendering the optimization of this character ambiguous at the base of the C.S.. It is likely that with an expanded outgroup taxon sampling (e.g., including intermediate taxa between *Temnoscheila* and the C.S.) this character will become optimized such that it is synapomorphic for the C.S.. Crowson's (1955) larval spiracular character (i.e., usually being annular) for the C.S. represents another feature that characterizes most of the C.S. (character 145-0). Only a few C.S. taxa have larvae lacking annular spiracles, including *Hypodacnella*, *Anommatus*, *Xylariophilus*, *Teredolaemus* and *Sphaerosoma*. The distribution of the alternative state (145-1) in the first four taxa for this character represent two independent reversions back to the ancestral condition for the C.S.. However, once again given the placement of *Sphaerosoma* as sister to the remaining C.S., the optimization of this spiracular character fails to recover it as a synapomorphy for the C.S. node.

Characters of interest

Ślipiński and Pakaluk (1991) propose two other characters that are potentially significant for C.S. higher-level relationships: degree of closure of the mesocoxal cavity (character 55), and number of abdominal spiracles (character 86; here treated as: functional spiracle on abdominal segment VII, present/absent). Ślipiński and Pakaluk (1991) discuss both of these features at length with respect to various scenarios of C.S. family relationships, but fail to reconcile the apparent homoplasious nature of these characters when mapped on an intuitive phylogeny representing the consensus of relationships of higher-level C.S. taxa. Given that non-C.S. cucujoids have 7 abdominal spiracles, they suggest that the 5 abdominal spiracles seen in the C.S. represent a derived condition and propose that a new system placing all C.S. taxa with 5 abdominal spiracles together should be considered (Ślipiński and Pakaluk, 1991). Five abdominal spiracles are present in Endomychidae, Coccinellidae, *Orthoperus* (Corylophidae) Cerylonidae (except Euxestinae) and Discolomatidae. Our results however, indicate that this character is homoplasious, requiring 6 steps on our topology with 3 independent transitions from 7 to 5 abdominal spiracles within the C.S. and 3 subsequent independent reversions back to 7 spiracles. The mesocoxal cavity closure character requires 5 steps on the topology, with 4 independent origins of closed mesocoxal cavities with a single subsequent reversion to open cavities (*Sysolus*). Among C.S. taxa, Cerylonidae, Latridiidae, Discolomatidae, Bothrideridae (except *Sysolus*), Anamorphinae and Merophysiinae (Endomychidae) and most Corylophidae have the mesocoxal cavities closed by the meso- and metaventrites. Thus, while both of the above characters are important in that they support multiple higher-level clades within the C.S., neither represents an uncontroverted synapomorphy for C.S. taxa nor justifies any classification changes.

Alexiidae

Alexiidae is a monotypic family thus testing the monophyly of this taxon is of little interest. Of more concern is whether or not Alexiidae represents a distinct C.S. lineage or is subordinate to another C.S. family. Until recently, Alexiidae was treated as a subfamily (Sphaerosomatinae) within Endomychidae. Sen Gupta and Crowson (1973) and Lawrence (1982, 1991) recognized the distinctiveness of *Sphaerosoma* and elevated it to family status (Lawrence, 1982, 1991). The specific placement of Alexiidae among the remaining C.S. families remained uncertain. In the current study, the placement of Alexiidae as sister to the remaining C.S. is interesting and certainly supports its recognition as a distinct family. This placement is supported by the characters at the node uniting all the remaining C.S. taxa (39, 56, 86). Alexiidae has the protrochantin exposed (39-0); all other C.S. taxa (except *Holopsis*) have the protrochantin concealed (39-1). Similarly, alexiids have the mesotrochantin exposed (56-0) while in the majority of C.S. taxa the mesotrochantin is hidden (56-1). Finally, Alexiidae possess 7 abdominal spiracles (86-0) along with all of the outgroup taxa and several other C.S. taxa (see above).

Corylophidae

The family Corylophidae is a strongly supported monophyletic group based on the present study with high bootstrap support (97) and 11 synapomorphies lending support to this clade (14-1*, 29-3*, 41-1, 59-1, 62-3, 78-0, 86-0, 97-2, 104-0, 119-1, 129-1). The presence of membranous vesicles on club segments of the antennae (14-1*) and galea absent (29-3*) are uncontroverted synapomorphies for Corylophidae. Prior to this study it was held that an additional uncontroverted synapomorphy for Corylophidae was the presence of complex endophallic sclerites (Ślipiński et al., 2009). However, in the course of this study we discovered these specialized sclerites in a few other cucujoids, most notably among anamorphine Endomychidae. This discovery is of particular interest as Corylophidae and Anamorphinae were strongly supported as sister taxa in the molecular analysis of Robertson et al. (2008).

The degree of separation of the metacoxae found in Corylophidae is extreme [metacoxae separated by more than 1.5 × coxal width (62-3)] and rare among Cucujoidea. Only members of Bothriderini have comparably separated metacoxae and thus share this state. This degree of separation is found exclusively in these two groups among the C.S. and likely among the entire Cucujoidea as well. Two larval characters, the ventral mouthparts protracted or slightly retracted (119-1) and gula longer than wide (129-1), are robust synapomorphies for Corylophidae.

The internal relationships of Corylophidae recovered here are overall fairly concordant with that of Ślipiński et al. (2009). For instance, *Periptyctus* (Periptyctinae) is sister to the remaining Corylophidae (Corylophinae *sensu* Ślipiński et al., 2009) and the basal most taxon of Corylophinae is *Foadia* (Foadiini).

Coccinellidae

It is not surprising that Coccinellidae was recovered as monophyletic in this analysis. The monophyly for the coccinellid node is well supported (bootstrap = 77) by five synapomorphies (22-1*, 45-0, 79-1*, 89-0, 108-3). All Coccinellidae have the tormae greatly reduced to small knobs (22-1*) and this character state is unique among the taxa investigated in this study. Another uncontroverted synapomorphy for Coccinellidae is having the two basal ventrites of the abdomen connate (79-1*). Tergite IX in the male is distinct (89-0) in almost all Coccinellidae examined here (except *Rhyzobius* and *Rodolia*), and this condition is relatively rare among the taxa in this study. Coccinellidae also have a normal to elongate trochanterofemoral attachment (45-0) and larvae with 3 stemmata (108-3).

Within Coccinellidae our results support a basal dichotomy of clades, corresponding to Ślipiński's (2007) Microweisiinae and broadly defined Coccinellinae. The Microweisiinae are a well-supported group (bootstrap = 97) with six synapomorphies lending support to this clade. The remaining coccinellids, Coccinellinae *sensu* Ślipiński (2007), is supported by two synapomorphies, one of which appears to be a fairly robust synapomorphy for this group (anal lobe of hind wing present (72-0)).

Discolomatidae

Discolomatidae is perhaps the most strongly supported monophyletic family of the C.S. (bootstrap 100). Members of Discolomatidae share 16 apomorphies (12-1, 33-0*, 35-1, 37-1, 41-1, 47-0, 65-1*, 73-3, 74-2, 84-0, 85-0, 87-2, 89-2, 108-3, 111-1, 115-2) in the present study. The two uncontroverted synapomorphies for Discolomatidae are the presence of glandular openings along the lateral pronotal and elytral margins (33-0*) and concealed metacoxal extensions (65-1*).

Although not considered an uncontroverted synapomorphy here, the character state pygidium with a median groove (84-0) is only found in one other distantly related taxon in this study (*Serangium*) (although this condition also occurs in Sphindidae, a basal cucujoid family) and is thus considered a robust synapomorphy for discolomatids as well. Other robust adult synapomorphies for Discolomatidae include the following: corpotentorial bridge absent (12-1), notosternal sutures incomplete or absent (37-1), elytral punctation not seriate or striate (47-0), and tergite IX in the male strongly reduced or absent (89-2). Larval characters supporting the monophyly of Discolomatidae include larvae with three stemmata (108-3), two antennomeres (111-1) and apex of mandible tridentate or multidentate (115-2).

Bothrideridae

Of the families recovered as monophyletic in the present study, Bothrideridae is perhaps the most poorly supported, with bootstrap support less than 50 and only 2 synapomorphies (7-1, 93-1) uniting members of this family. An antennal club comprising two articles (7-1) occurs in all Bothrideridae except for three genera (*Deretaphrus*, *Sysolus*, and *Sosylopsis*—not included in the present study). Bothrideridae is additionally supported in this analysis by having the aedeagus not rotated when retracted (93-1). The alternative state to this character—aedeagus rotated 90 degrees in the resting position—is one Crowson used to characterize the C.S.; this character is not consistent within the C.S. due in part to the observed condition in Bothrideridae (see above). Although support for the family was weak, this analysis does find strong support for the monophyly of the subfamily Bothriderinae (bootstrap = 96). Synapomorphies uniting the bothriderines include (13, 20, 23, 44, 46*, 77*, 87, 111, 126, 131)

Latridiidae

The paraphyly of Latridiidae as supported here is somewhat surprising and is caused by the placement of the enigmatic cerylonid *Loebliorylon*, sister to the equally interesting *Akalyptoischion* (Latridiidae). *Loebliorylon* is monotypic, representing a unique subfamily of Cerylonidae (Loebliorylonidae). *Akalyptoischion* is morphologically distinct with respect to the remaining Latridiidae is thought to represent a unique family in the C.S. (Lord et al., in press). While this sister grouping is supported by 4 synapomorphies (41-0, 43-0, 91-3, 103-1), this result is quite unexpected. The aberrant placement of *Loebliorylon* within Latridiidae may be the result of convergent reductions between these taxa. For instance, all Latridiidae have 3-3-3 tarsi in both sexes (73-3, 74-2). Aside from Discolomatidae, no other C.S. family is entirely or even mostly composed of taxa with 3-3-3 tarsi, yet isolated reductions from 4-4-4 to 3-3-3 tarsi have occurred independently in four C.S. families [Bothrideridae (*Anommatus*), Cerylonidae (*Loebliorylon, Ostomopsis*), Endomychidae (Anamorphinae, Merophysiinae) and Coccinellidae (*Coccidophilus*, *Micoweisea*). Both *Akalyptoischion* and *Loebliorylon* lack hind wings, which represents another common reduction that has occurred independently in multiple C.S. lineages [e.g., Endomychidae (*Chilieolobius*), Corylophidae (*Aenigmaticum*), Coccinellidae (*Sukunahikona*), Discolomatidae (*Notiophygus*), and Bothrideridae (*Anommatus*)].

The synapomorphies supporting *Akalyptoischion* and *Loebliorylon* as sister taxa, are interesting when consider the distribution of these states among related C.S. taxa. Having the anterior edge of penis with paired struts (103-1) also occurs in *Ostomopsis.* Having the anterior edge of sternite IX in males rod-like (91-3) also occurs in *Philothermus*. Internally open procoxal cavities (43-0) occur in all Cerylonidae, Discolomatidae, and Bothrideridae, but they do not occur in any other Latridiidae; externally open procoxal cavities (41-0) occur in all Cerylonidae included (except *Cerylon*), and again, this condition does not occur in any other Latridiidae.

The larval forms for both *Akalyptoischion* and *Loebliorylon* remain unknown. Perhaps the placement of these enigmatic taxa will be clarified by the future discovery of the immature stages for these taxa and the growing pool of molecular data that are available for phylogenetic analyses.

Endomychidae

Endomychidae is an extremely heterogenous group (Ślipiński and Pakaluk, 1991; Tomaszewska, 2000, 2005, 2010), the monophyly of which has been questioned in the past

(Ślipiński and Pakaluk, 1991). Confirming these suspicions, our results recovered members of Endomychidae scattered throughout the topology.

The largest clustering of Endomychidae, comprising exemplars of the subfamilies Anamorphinae, Pleganophorinae, Endomychinae, Stenotarsinae, Epipocinae, and Lycoperdinae, is supported by six synapomorphies (29-0, 45-0, 78-0, 97-2, 99-0, 112-1) and placed sister to a large C.S. clade composed of other Endomychidae, Latridiidae, Cerylonidae, Discolomatidae and Bothrideridae. Included in this main group of Endomychidae is the "Higher Endomychidae" of Tomaszewska (2005). Perhaps the strongest apomorphy uniting this group is parameres absent (97-2), a state inconsistent with all but one (*Rhanidea*) of the remaining Endomychidae in this study.

In contrast to the results of Tomaszewska (2000, 2005), the exemplars of Xenomycetinae, Leiestinae, and Merophysiinae are here not included with the main group of Endomychidae, but instead form a basal grade leading to the family Latridiidae. This eclectic clade is supported by two synapomorphies (108, 144-0), one of which, segment 10 and anal opening of the larva posterior or terminal (144-0) is a fairly robust apomorphy for this group. *Holoparamecus* (Merophysiinae) is supported as sister group to Latridiidae. Merophysiinae has in the past been treated within Latridiidae (Hetschko, 1926; see also Crowson, 1955), a placement consistent with the present study.

Eupsilobiinae (*Chileolobius* + *Eidorius*) is placed as one of the early diverging lineages of the C.S.. If this placement is confirmed in subsequent studies, Eupsilobiinae should be recognized as an independent family within the C.S.. The monophyly of Eupsilobiinae is strongly supported (bootstrap = 94) by seven adult characters/states (7-1, 8-2, 62-2, 73-3, 74-2, 97-2, 101-2). A subantennal groove that extends below or behind the eye (8-2), widely separated metacoxae (62-2), and a sclerotized T-shaped basal protion of the penis (101-2) are rare character states among other Endomychidae. In addition, 3-3-3 tarsi (73-3, 74-2) is relatively rare in the rest of the family. Immatures for Eupsilobiinae are unknown and the discovery of the larval stage for this group might provide additional insight into its placement within the C.S., however, the current study strongly suggests that this group represents a distinct lineage within the C.S..

The endomychid subfamily Mycetaeinae (represented by *Agaricophilus*) is also far removed from the main cluster of Endomychidae. The present study supports the placement of *Agaricophilus* as sister to the clade comprising Corylophidae + Coccinellidae and is supported by characters of the mesoventrite and tarsi (51-0, 75-1, 76-0). If subsequent studies confirm the placement of Mycetaeinae outside of the remaining Endomychidae, Mycetaeinae would have to be elevated to family status.

Cerylonidae

Another heterogenous group (Ślipiński, 1990; Ślipiński and Pakaluk, 1991; Ślipiński and Lawrence, 2010), Cerylonidae is not supported as monophyletic in the current analysis. Our results support Discolomatidae being nested within Cerylonidae, as sister to *Murmidius*; Euxestinae is more closely related to Bothrideridae and is itself a grade rather than a monophyletic group; *Loebliorylon* is nested within Latridiidae (discussed above). Despite this gross paraphyly, with the exception of the aberrant placement of *Loebliorylon*, the above relationships are not surprising and have been suggested previously (Ślipiński, 1990; Ślipiński and Lawrence, 2010) (see Clades of interest below).

The main body of taxa currently assigned to Cerylonidae, including Ostomopsinae, Ceryloninae and Murmidiinae and the family Discolomatidae form a clade supported by four synapomorphies (16-1, 45-0, 70-1, 85-1*). All members of this group have the clypeus broadened apically, distinctly wider than the basal margin at the frontoclypeal suture (16-1). Among the taxa examined here, only a few unrelated taxa (*Periptyctus*, *Enicmus* and *Stephostethus*) share this state and thus we consider this a fairly robust synapomorphy for this group. Additional characters, including trochanterofemoral attachment normal to elongate (45-0), medial fleck of hind wing absent (70-1), posterior edge of last abdominal ventrite crenulate (85-1*) (with subsequent reversion in Discolomatidae) also support this group. If this clade is recovered in subsequent analyses, particularly those employing molecular data, then Ostomopsinae, Ceryloninae, Murmidiinae and Discolomatidae should be formally recognized as the family Cerylonidae, suppressing the family name Discolomatidae.

Clades of interest

Perhaps one of the strengths of the resulting topology lies in the well-supported higher-level clades within the C.S..

Corylophidae + Coccinellidae

Historically, Endomychidae has been considered to be the sister group to Coccinellidae, both families sharing the pseudotrimerous condition of the tarsi (Latreille, 1804). However, the present study supports a sister grouping of Corylophidae + Coccinellidae (bootstrap = 67). This sister grouping is supported by the following character states: frontoclypeal suture absent (4-1), corpotentorial bridge absent (12-1), medial fleck of hind wing absent (70-1), maxillary cardo and stipes fused together (122-1), and hypopharyngeal sclerome absent (126-0). One additional character that supports this grouping but is not optimized as such due to the missing larval data of *Agaricophilus* is maxillary articulating area highly reduced or absent (120-1).

While the support for this sister grouping is relatively high, it should be noted that of the synapomorphies uniting Corylophidae and Coccinellidae, all but one (22-1) are reductions. Given the above, the Corylophidae + Coccinellidae sister grouping should be investigated further (e.g., using molecular data) in the event that their grouping together in this analysis is simply due to independent, convergent reductions.

Murmidinae + Discolomatidae

Multiple authors have suggested a potential sister group pairing of Murmidiinae and the family Discolomatidae (van Emden, 1928; Crowson, 1955; Ślipiński, 1990; Lawrence, 1991; Ślipiński & Pakaluk, 1991). Murmidiine cerylonids and discolomatids share a number of adult and larval morphological features including ovipositor (styli) of the female absent (105-1), antennomere II of larva more than twice as long as wide (112-1), larval mandibular prostheca present (118-0), and mesocoxae of larva separated by more than two coxal diameters (131-1). In addition to the above characters, the larvae of *Murmidius* and Discolomatidae are both onisciform (disk-like). All of the above synapomorphies uniting these taxa are robust and we are fairly confident that this sister grouping is not simply an aberration.

Euxestinae & Bothrideridae

Both Pal and Lawrence (1986) and Ślipiński (1990) demonstrated that from a morphological standpoint Euxestinae could not be separated from free-living Bothrideridae (Anommatinae, Teredinae, Xylariophilinae). The enigmatic Metacerylonini (Euxestinae) in particular bears many morphological similarities to the above bothriderid taxa and was considered by Dajoz (1980) to be subordinate to Bothrideridae.

Our study confirms the observations of Pal and Lawrence (1986) and Ślipiński (1990) and places the Euxestinae, here forming a grade, into a clade with Bothrideridae. The Euxestinae and Bothrideridae clade is supported the following synapomorphies: labral rods club-like (21-0), apex of prosternal process with lateral projections (35-1), procoxal cavities externally closed (41-1), (69-4), (72-0), and functional spiracle on abdominal segment VII present (86-0). Of the above character states uniting Euxestinae and Bothrideridae, 21-0, 72-0 and 86-0 are robust synapomorphies for this group.

Taxonomic implications

Several significant classification changes are warranted based on these results. The current constitution of Endomychidae must be reevaluated. Our results strongly suggest that both Eupsilobiinae and Mycetaeinae are unique from other Endomychidae and represent distinct C.S. lineages. Thus should these results be corroborated by other evidence (e.g., molecular data) then these two endomychid subfamilies should be elevated to familial status, Eupsilobiidae and Mycetaeidae.

The family Cerylonidae also requires higher-level revision. The results of the present study strongly support the need to transfer Euxestinae to Bothrideridae. Furthermore, Discolomatidae should be subsumed within Cerylonidae. Based on the present study, the revised constitution of Cerylonidae should include Ostomopsinae, Ceryloninae, Murmidiinae, Discolomatinae (including all discolomatids), and perhaps Loebliorylonimae.

We choose to refrain from formally making classification changes here as we are currently preparing an extensive molecular dataset for these taxa. The results of this study combined with our molecular analysis will provide the necessary justification for making any warranted classification changes, including those suggest here.

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Figure Captions

Table 4.1: Terminal taxa used in the present study.

Table 4.2: Character matrix used in the present study.

Figure 4.1: Leg of *Sphaerosoma* sp. illustrating one of several adult characters used by Crowson (1955) to define the Cerylonid Series: adults with reduced tarsal formula 4-4-4 or 3-3-3.

Figure 4.2: Hind wing of *Dastarcus helophoroides* illustrating two of several adult characters used by Crowson (1955) to define the Cerylonid Series: hind wing lacking closed radial cell, hind wing with reduced anal veins.

Figure 4.3: Abdomen of *Rhyzobius* sp. illustrating one of several adult characters used by Crowson (1955) to define the Cerylonid Series: aedeagus resting on its side when retracted.

Figure 4.4: Tegmen of *Loebliorylon* sp. illustrating one of several adult characters used by Crowson (1955) to define the Cerylonid Series: aedeagus with tegmen reduced.

Figure 4.5: Cleared specimens used in this study were stored on open glycerol slides, with a fine bead of silicon around the depression for larger specimens. Specimens were fully disarticulated and wings were removed and mounted on the slide next to the glycerol-filled depression.

Figure 4.6: Strict consensus topology of 46 most parsimonious trees of length 968 (CI = 20; RI = 65) (first section of tree shown only; see following figure for remaining portion). Circles at each node represent synapomorphies supporting that clade. Corresponding character and state numbers are indicated above and below each circle respectively. Filled circles represent uncontroverted synapomorphies. Open circles represent homoplasious synapomorphies. Nodes with bootstrap support ≥ 70 are marked with a red box.

Figure 4.7: Same as in previous figure (second section of tree shown only; see previous figure for remaining portion).

Table 4.1 Terminal taxa used in this study.

Superfamily	**Family**	**Subfamily** (Traditional Classification)	**Subfamily** (Alt. Classification)	**Taxon**
Derodontoidea	Derodontidae			*Derodontus*
Cleroidea	Trogossitidae			*Temnoscheila*
Tenebrionoidea	Mycetophagidae			*Mycetophagus*
Cucujoidea	Boganiidae			*Paracucujus*
Cucujoidea	Protocucujidae			*Ericmodes*
Cucujoidea	Biphyllidae			*Biphyllus*
Cucujoidea	Erotylidae			*Pharaxonotha*
Cucujoidea *Cerylonid Series*				
	Alexiidae	Alexiinae		*Sphaerosoma*
	Bothrideridae	Teredinae		*Oxylaemus**
	Bothrideridae	Teredinae		*Sysolus**
	Bothrideridae	Teredinae		*Teredolaemus*
	Bothrideridae	Xylariophilinae		*Xylariophilus*
	Bothrideridae	Anommatinae		*Anommatus*
	Bothrideridae	Bothriderinae		*Bothrideres*
	Bothrideridae	Bothriderinae		*Dastarcus*
	Bothrideridae	Bothriderinae		*Deretaphrus*
	Bothrideridae	Bothriderinae		*Sosylus*
	Cerylonidae	Euxestinae		*Euxestoxenus**
	Cerylonidae	Euxestinae		*Hypodacne*
	Cerylonidae	Euxestinae		*Hypodacnella*
	Cerylonidae	Euxestinae		*Metacerylon**
	Cerylonidae	Loebliorylоninae		*Loebliorylon**
	Cerylonidae	Ostomopsinae		*Ostomopsis**
	Cerylonidae	Murmidiinae		*Murmidius*
	Cerylonidae	Ceryloninae		*Mychocerus*
	Cerylonidae	Ceryloninae		*Philothermus*
	Cerylonidae	Ceryloninae		*Cerylon*
	Discolomatidae	Notiophyginae		*Notiophygus*
	Discolomatidae	Discolomatinae		*Cassidoloma*
	Discolomatidae	Discolomatinae		*Discoloma*
	Discolomatidae	Aphanocephalinae		*Aphanocephalus*
	Endomychidae	Merophysiinae		*Holoparamecus*
	Endomychidae	Pleganophorinae		*Trochoideus*
	Endomychidae	Anamorphinae		*Austroclemnus*
	Endomychidae	Anamorphinae		*Bystus*
	Endomychidae	Anamorphinae		*Mychothenus*
	Endomychidae	Leiestinae		*Phymaphora*
	Endomychidae	Leiestinae		*Rhanidea*
	Endomychidae	Mycetaeinae		*Agaricophilus*
	Endomychidae	Eupsilobiinae		*Chileolobius**
	Endomychidae	Eupsilobiinae		*Eidoreus**
	Endomychidae	Xenomycetinae		*Xenomycetes*
	Endomychidae	Endomychinae		*Endomychus*
	Endomychidae	Epipocinae		*Epipocus*
	Endomychidae	Stenotarsinae		*Saula*
	Endomychidae	Stenotarsinae		*Stenotarsus*
	Endomychidae	Lycoperdininae		*Amphix*
	Endomychidae	Lycoperdininae		*Lycoperdina*
	Coccinellidae	Coccidulinae	Coccinellinae ‡	*Rhyzobius*
	Coccinellidae	Coccidulinae	Coccinellinae ‡	*Rodolia*

Coccinellidae	Scymninae	Coccinellinae ‡	*Diomus*
Coccinellidae	Chilocorinae	Coccinellinae ‡	*Chilocorus*
Coccinellidae	Chilocorinae	Coccinellinae ‡	*Halmus*
Coccinellidae	Chilocorinae	Coccinellinae ‡	*Platynaspis*
Coccinellidae	Epilachninae	Coccinellinae ‡	*Epilachna*
Coccinellidae	Coccinellinae	Coccinellinae ‡	*Coccinella*
Coccinellidae	Coccinellinae	Coccinellinae ‡	*Illeis*
Coccinellidae	Sticholotidinae	Coccinellinae ‡	*Sticholotis*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Coccidophilus*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Delphastus*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Microweisea*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Serangium**
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Sukunahikona*
Corylophidae	Periptyctinae	Periptyctinae +	*Periptyctus*
Corylophidae	Peltinodinae	Corylophinae +	*Holopsis*
Corylophidae	Orthoperinae	Corylophinae +	*Orthoperus*
Corylophidae	Corylophinae	Corylophinae +	*Aenigmaticum**
Corylophidae	Corylophinae	Corylophinae +	*Foadia*
Corylophidae	Corylophinae	Corylophinae +	*Stanus*
Corylophidae	Corylophinae	Corylophinae +	*Clypastraea*
Corylophidae	Corylophinae	Corylophinae +	*Sericoderus*
Latridiidae	Latridiinae		*Akalyptoischion**
Latridiidae	Latridiinae		*Enicmus*
Latridiidae	Latridiinae		*Stephostethus*
Latridiidae	Corticariinae		*Corticaria*
Latridiidae	Corticariinae		*Melanopthalma*

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* Larval stage not known (although see text regarding *Oxylaemus* and *Euxestoxenus*).

‡ After Ślipiński, 2007

+ After Ślipiński et al., 2009

Table 4.2 Morphological character matrix.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Derodontus	1	0	0	0	1	0	0	2	0	1	0	1	1	-	0	0	0	0	0	1	1	-	0	0	1	0	0	0	1	1	1	1	0	1	2	1	0
Temnoscheila	0	0	0	0	1	0	1	2	0	0	?	?	?	?	0	0	0	0	0	1	1	-	0	?	1	0	0	1	0	2	0	1	0	1	0	1	1
Mycetophagus	0	0	0	0	0	0	1	3	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	2	1	0	0	0	1	1	0	1	0	1	1	0	0
Paracucujus	0	0	0	0	0	0	1	3	0	1	0	0	0	2	0	0	0	1	0	1	1	-	0	0	1	1	2	1	0	1	1	1	0	1	1	0	0
Ericmodes	0	0	0	0	1	0	1	2	1	1	0	0	0	2	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0
Biphyllus	0	1	0	1	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	1	1	-	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0
Pharaxonotha	0	1	2	0	1	0	1	2	0	1	0	0	0	2	0	0	0	1	0	1	1	-	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
Sphaerosoma	0	0	0	0	0	2	0	2	0	1	0	0	0	2	0	0	0	0	0	1	1	?	0	2	1	0	0	0	1	0	0	1	?	1	2	0	0
Oxylaemus	1	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0
Sysolus	1	0	0	0	0	0	0	2	1	1	0	0	0	2	0	0	0	0	0	1	1	-	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0
Teredolaemus	1	0	0	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0
Xylariophilus	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0
Anommatus	0	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0
Bothrideres	0	0	0	0	0	0	0	1	1	1	0	0	0	2	0	2	0	0	0	1	1	-	0	0	1	0	0	0	1	1	1	1	2	1	0	1	2
Dastarcus	1	0	0	0	0	0	0	1	2	1	0	0	0	2	0	0	0	0	0	1	1	-	0	2	1	0	0	1	2	1	1	1	0	1	0	1	2
Deretaphrus	1	0	0	0	0	0	0	2	2	1	0	0	0	2	0	0	0	0	0	1	1	-	0	0	1	0	0	1	3	1	1	1	0	1	0	0	0
Sosylus	0	0	0	0	0	0	0	1	2	1	0	0	0	2	0	0	0	0	0	0	1	-	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
Euxestoxenus	1	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	1	2
Hypodacne	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	1	1	1
Hypodacnella	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	1	2
Metacerylon	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	?	1	0	1	0
Loebliorylon	1	0	0	0	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	1	1	0	1	2	1	0	0	0
Ostomopsis	1	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	1	0	1	0	0	1
Murmidius	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	2	1	1	?	1	0	?	0	1	1	0	0	0	1	1	0	1	?	1	0	0	2
Mychocerus	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	2	1	0	0	0	1	1	?	1	0	1	0	1	2
Philothermus	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	2	1	0	0	0	1	1	0	1	0	1	0	0	0
Cerylon	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	?	0	0	0	1	1	0	1	0	1	0	0	0
Notiophygus	1	0	0	0	0	0	0	0	?	1	0	0	1	-	0	0	1	0	0	1	1	-	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0
Cassidoloma	0	0	0	0	0	0	0	0	1	1	0	0	1	-	0	0	1	1	0	1	0	1	0	1	1	0	0	0	2	1	?	1	0	0	0	1	1
Discoloma	0	0	0	0	0	0	0	0	2	1	0	0	1	-	0	0	1	1	0	1	0	1	0	1	1	0	0	0	4	1	0	1	0	0	0	1	2
Aphanocephalus	1	0	0	0	0	0	0	0	2	1	0	0	1	-	0	0	1	0	0	1	0	1	0	1	1	0	0	0	4	1	0	1	0	0	1	1	1
Holoparamecus	1	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	0	0	0	1	1	?	0	2	1	0	0	0	1	1	0	1	0	1	0	0	0
Trochoideus	1	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
Austroclemnus	0	0	0	0	0	0	0	2	2	1	0	0	0	2	0	0	0	0	0	1	1	-	0	1	1	0	0	0	1	0	0	1	0	1	2	0	0
Bystus	1	0	0	0	0	0	0	2	1	1	0	0	0	2	0	0	0	0	0	1	1	-	0	1	1	0	0	0	1	0	0	1	0	1	2	0	0
Mychothenus	1	0	0	0	0	0	0	2	1	1	0	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	?	1	?	1	2	0	1
Phymaphora	1	0	0	0	0	0	0	4	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	0	1	0	0	0	1	1	1	1	0	1	1	0	0
Rhanidea	1	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	2	1	0	0	0	1	1	?	1	0	1	0	0	0

Table 4.2 (continued) Morphological character matrix.

											1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Agaricophilus	0	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	?	1	0	0	0	1	1	?	1	0	1	1	0	0
Chileolobius	0	0	0	0	1	0	0	1	2	1	0	1	0	2	0	0	0	0	0	1	1	-	0	2	1	0	0	0	1	1	0	1	0	1	0	0	0
Eidoreus	0	0	0	0	0	0	0	1	2	1	0	1	0	2	0	0	0	0	0	1	0	1	0	2	1	0	0	0	1	1	0	1	?	1	0	0	0
Xenomycetes	1	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	1	1	0	0	0	1	1	1	1	?	1	0	0	0
Endomychus	0	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	?	?	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0
Epipocus	0	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	1	-	0	1	1	0	0	0	1	0	0	1	0	1	2	0	0
Saula	0	0	0	0	0	0	0	2	0	1	0	1	1	-	0	0	0	0	0	1	1	-	0	0	0	0	0	0	1	0	1	1	0	1	2	0	0
Stenotarsus	0	0	0	0	0	0	0	2	0	1	0	1	1	-	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	1	1	0	1	1	0	0
Amphix	0	0	1	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	?	2	0	0
Lycoperdina	0	0	1	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0
Rhyzobius	0	0	0	0	1	2	0	2	2	1	0	0	1	-	0	0	0	0	0	1	1	-	1	?	1	0	0	1	1	1	0	1	0	1	1	0	?
Diomus	0	0	0	0	1	2	0	2	1	1	0	0	1	-	0	0	0	0	0	1	1	?	1	2	1	0	0	1	1	1	0	1	0	1	1	0	0
Chilocorus	0	0	0	0	1	2	1	2	1	1	0	0	1	-	0	0	?	0	0	1	?	?	1	2	0	0	0	1	2	1	0	1	0	1	1	0	0
Halmus	0	0	0	0	1	2	1	2	1	1	0	0	1	-	0	0	?	0	0	1	?	?	1	0	0	0	0	1	2	1	0	1	0	1	1	0	0
Platynaspis	0	0	0	0	1	2	1	2	1	?	0	0	1	-	0	0	?	0	0	1	?	?	1	?	1	0	0	1	1	?	?	1	?	1	0	0	0
Rodolia	0	0	0	0	1	2	0	2	1	1	0	0	1	-	0	0	0	0	0	1	1	?	1	2	1	0	0	1	1	1	0	1	?	1	2	0	0
Epilachna	0	0	0	0	1	2	0	2	0	1	0	0	1	-	0	0	0	0	0	1	1	?	1	2	1	0	0	1	1	1	0	1	0	1	1	0	0
Coccinella	0	0	0	0	1	2	0	2	1	1	0	0	1	-	0	0	0	0	0	1	1	-	1	?	1	0	0	1	1	1	0	1	0	1	0	0	0
Illeis	0	0	0	0	1	2	0	2	1	1	0	0	1	-	0	0	0	0	0	1	?	?	1	?	1	0	0	1	1	1	0	1	0	1	0	0	0
Coccidophilus	0	0	0	0	1	0	0	1	1	1	0	0	1	-	0	?	0	0	0	1	1	?	1	?	0	0	0	1	3	1	0	1	0	1	1	0	0
Delphastus	0	0	0	0	1	0	0	0	1	1	0	0	1	-	0	0	0	0	0	1	1	?	1	1	0	0	0	1	1	1	0	1	0	1	0	0	0
Microweisea	0	0	0	0	1	0	0	2	1	1	0	0	1	-	0	0	0	0	0	1	1	-	1	1	0	0	0	1	3	1	0	1	0	1	2	0	0
Serangium	0	0	0	0	1	0	0	0	2	1	0	0	1	-	0	0	0	0	0	1	1	?	1	1	0	0	0	1	3	0	0	1	?	1	0	0	0
Sticholotis	0	0	0	0	1	0	0	2	0	1	0	0	1	-	0	0	0	0	0	1	1	?	1	1	1	0	0	1	1	1	?	1	?	1	1	0	1
Sukunahikona	0	0	0	0	1	0	0	2	1	1	0	0	1	-	0	0	0	0	0	1	1	?	1	1	0	0	0	1	3	1	0	1	0	1	2	0	0
Periptyctus	0	0	0	0	1	0	0	2	1	1	0	0	1	-	1	2	1	0	0	1	1	-	0	1	0	0	0	1	1	3	?	1	0	1	0	0	0
Holopsis	0	0	0	0	1	0	0	2	1	1	0	1	1	-	1	0	0	0	0	1	?	?	0	?	0	0	0	0	3	3	?	1	0	1	2	0	0
Aenigmaticum	0	0	0	0	1	0	0	2	0	2	1	-	1	-	1	0	0	0	0	1	1	-	0	2	?	0	0	?	?	3	?	1	0	1	1	0	0
Foadia	0	0	0	0	1	0	0	2	0	1	0	1	1	-	1	0	0	0	0	1	1	?	0	?	0	0	0	0	1	3	?	1	0	1	0	1	0
Stanus	0	0	0	0	1	0	0	2	0	1	1	-	1	-	1	?	0	0	0	1	?	?	0	?	1	0	0	0	2	3	?	1	0	1	1	0	0
Orthoperus	0	0	0	0	1	0	0	2	0	2	1	-	1	-	1	2	0	0	0	1	?	?	0	?	?	0	0	0	?	3	?	1	0	1	1	0	0
Clypastraea	0	0	0	0	1	0	0	2	0	1	1	-	1	-	1	0	0	0	0	1	1	?	0	?	1	0	0	0	1	3	?	1	0	1	2	1	0
Sericoderus	0	0	0	0	1	0	0	2	0	2	1	-	1	-	1	0	0	0	0	1	1	-	0	1	1	0	0	1	1	3	?	1	0	1	2	0	0
Enicmus	1	0	0	0	0	0	0	2	2	1	0	0	0	2	0	0	1	0	1	1	1	-	0	?	0	0	0	0	1	-	-	1	0	1	1	0	0
Stephostethus	1	0	0	0	0	0	0	2	2	1	0	0	0	2	0	0	1	0	1	1	1	-	0	?	0	0	0	0	1	-	-	1	0	1	1	0	0
Corticaria	1	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	1	1	?	?	0	2	0	0	0	0	1	-	-	1	0	1	1	0	0
Melanopthalma	1	0	0	0	0	0	0	2	0	1	0	1	0	2	0	0	0	0	1	1	0	1	0	2	1	0	0	0	1	-	-	1	0	1	2	0	0
Akalyptoischion	1	0	0	0	0	0	0	2	0	1	0	0	0	2	0	2	0	0	1	1	1	-	0	2	1	0	0	0	1	0	0	1	0	1	0	0	0

Table 4.2 (continued) Morphological character matrix.

	37	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**
Derodontus	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	3	0	0	0	1	1	1	0	0	0	0	0	0	2	0	1	2	2	-	0	0
Temnoscheila	1	1	?	0	1	1	0	0	0	0	0	0	1	1	1	1	2	0	0	0	1	1	1	1	1	0	0	0	0	?	0	0	0	2	-	0	2
Mycetophagus	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	2	0	0	0	1	1	1	1	1	0	1	0	0	2	1	0	2	0	0	0	2
Paracucujus	0	1	0	0	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	2	2	-	0	1
Ericmodes	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Biphyllus	0	0	1	0	1	1	1	1	1	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	2	-	0	0
Pharaxonotha	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	0	1	-	0	1	1	1	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0
Sphaerosoma	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	2	0	0	0	1	1	0	1	1	1	1	1	0	2	1	1	5	0	0	1	2
Oxylaemus	0	2	1	2	0	0	0	1	1	0	1	0	0	0	1	0	3	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	2	0	0	0	2
Sysolus	0	2	1	2	0	0	0	1	1	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	1	0	1	1	0	0	0	1	2	0	1	0	2
Teredolaemus	0	2	1	2	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	0	0	0	1	2	0	1	0	2
Xylariophilus	0	2	1	2	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	0	2	0	1	4	0	1	0	2
Anommatus	0	2	1	2	0	0	0	1	1	0	1	0	0	0	1	0	3	0	1	1	1	1	1	1	1	1	1	1	0	2	1	-	-	-	-	-	3
Bothrideres	0	2	1	2	1	0	0	0	1	1	1	0	0	0	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	4	2	-	0	2
Dastarcus	0	2	1	2	1	0	0	2	1	1	1	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	2	2	-	0	2
Deretaphrus	0	2	1	2	1	0	0	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	2	2	-	0	2
Sosylus	0	2	1	2	1	0	0	0	1	1	1	0	0	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	4	2	-	0	2
Euxestoxenus	0	2	1	2	1	0	0	3	1	0	1	0	0	0	1	1	2	0	1	1	1	1	1	1	1	2	1	1	0	2	1	1	4	0	1	0	2
Hypodacne	0	2	1	0	1	0	0	1	1	0	1	0	0	0	1	1	2	0	1	1	1	1	0	1	1	2	1	1	0	0	0	1	4	0	1	0	2
Hypodacnella	0	1	1	2	1	0	0	3	1	0	1	0	0	0	1	1	2	0	1	1	1	1	0	1	1	2	1	1	0	0	0	1	3	0	1	0	2
Metacerylon	0	2	1	2	1	0	0	1	1	0	1	0	0	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	4	2	-	0	2
Loebliorylon	1	2	1	2	0	0	0	3	1	0	1	0	0	2	1	0	1	0	1	1	1	1	1	1	1	?	1	1	0	2	0	-	-	-	-	-	3
Ostomopsis	0	2	1	2	0	0	0	3	0	0	1	0	0	0	1	1	2	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	5	2	-	1	3
Murmidius	0	2	1	2	0	0	0	3	0	0	1	0	0	0	1	1	2	?	1	1	1	1	0	0	1	2	1	1	0	2	1	1	5	0	1	1	2
Mychocerus	0	2	1	2	0	0	0	?	0	0	1	0	0	0	0	1	2	0	1	1	1	1	0	1	1	1	1	1	0	2	1	1	4	2	-	1	2
Philothermus	0	2	1	2	0	0	0	1	0	0	1	0	0	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	4	2	-	1	2
Cerylon	0	2	1	2	1	0	0	?	0	0	1	0	0	0	1	1	2	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	5	2	-	1	2
Notiophygus	1	2	1	2	1	0	0	3	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	?	-	-	-	-	-	3
Cassidoloma	1	2	1	2	1	0	0	?	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	5	2	-	0	3
Discoloma	1	2	1	2	1	0	0	3	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	?	1	5	2	-	1	3
Aphanocephalus	1	2	1	2	1	0	0	3	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	5	2	-	0	3
Holoparamecus	0	2	1	2	0	1	1	3	0	0	0	0	0	1	0	1	2	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	5	0	0	1	3
Trochoideus	0	1	1	0	0	0	1	3	0	0	0	0	0	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	2	1	1	4	2	-	0	2
Austroclemnus	0	1	1	0	0	0	1	3	0	0	0	0	0	1	?	1	2	0	1	1	0	0	1	1	1	1	1	1	0	2	1	1	5	0	0	1	3
Bystus	0	1	1	0	0	0	1	3	0	0	0	0	0	0	0	1	2	0	1	1	0	0	1	1	1	1	1	1	0	2	1	1	4	0	0	1	2
Mychothenus	0	2	1	0	0	0	1	?	0	0	0	0	0	1	0	1	2	0	1	1	0	0	1	1	1	1	1	1	0	2	1	1	5	0	1	1	3
Phymaphora	0	1	1	0	0	1	1	3	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	4	0	0	1	2
Rhanidea	0	1	1	0	0	1	1	3	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	4	0	0	1	2

Table 4.2 (continued) Morphological character matrix.

	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Agaricophilus	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	0	0	1	5	0	0	1	2
Chileolobius	0	0	1	0	0	0	1	3	1	0	0	0	0	1	1	1	2	0	0	1	1	1	0	1	1	2	1	1	0	2	1	-	-	-	-	-	3
Eidoreus	0	1	1	0	0	0	1	3	1	0	0	0	0	1	1	1	2	0	0	1	1	1	0	1	1	2	1	1	0	2	1	1	5	0	0	1	3
Xenomycetes	0	2	1	2	0	0	1	3	1	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	5	0	0	1	2
Endomychus	0	2	1	0	0	0	1	3	0	0	0	0	0	1	1	1	2	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	4	0	0	0	2
Epipocus	0	1	1	0	0	0	1	3	0	0	0	0	0	1	1	1	2	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	4	0	0	0	2
Saula	0	2	1	0	0	0	1	3	0	0	0	0	0	0	0	1	2	0	0	1	1	1	1	1	1	1	1	1	0	2	0	1	4	0	0	0	2
Stenotarsus	0	2	1	0	0	0	1	3	0	0	0	0	0	1	0	1	2	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	4	0	1	0	2
Amphix	0	2	1	0	0	0	1	3	1	0	0	0	0	1	1	1	2	0	0	0	0	0	1	1	1	1	1	1	0	2	0	1	3	0	0	0	2
Lycoperdina	0	2	1	2	0	0	1	3	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	4	0	0	0	2
Rhyzobius	0	2	1	0	0	0	1	?	0	0	0	0	0	1	1	1	2	0	0	1	1	1	0	0	1	1	1	1	0	0	0	1	4	0	0	0	2
Diomus	0	2	1	?	0	0	1	?	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	2	0	1	5	2	-	0	3
Chilocorus	0	1	1	0	0	0	1	?	0	0	0	0	0	0	0	1	2	1	0	1	1	1	0	0	1	1	1	1	0	0	0	1	4	2	-	0	2
Halmus	0	1	1	0	0	0	1	?	0	0	0	0	0	0	0	1	2	1	0	1	1	1	0	0	1	1	1	1	0	2	0	1	3	0	0	0	2
Platynaspis	0	1	1	0	0	?	1	?	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	1	0	1	4	2	-	0	2
Rodolia	1	0	1	0	0	0	1	2	0	0	0	0	0	1	1	1	2	1	0	?	1	1	0	1	1	1	1	?	0	1	0	1	4	2	-	0	3
Epilachna	0	1	1	0	0	0	1	2	0	0	0	0	0	0	0	1	2	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1	4	2	-	0	2
Coccinella	0	1	1	0	0	0	1	?	0	0	0	0	0	0	1	0	2	0	0	1	1	1	0	1	1	1	1	1	0	1	0	1	4	0	0	0	2
Illeis	0	1	1	0	0	0	1	3	0	0	0	0	0	0	0	1	2	0	0	?	1	1	0	1	1	1	1	1	0	1	0	1	3	2	-	0	2
Coccidophilus	0	2	1	0	0	?	1	?	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	2	?	1	5	2	-	1	3
Delphastus	0	1	1	0	0	0	1	?	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	2	1	1	5	2	-	1	2
Microweisea	0	2	1	0	0	0	1	3	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	2	1	1	5	2	-	1	3
Serangium	0	1	1	0	0	0	1	3	0	0	0	0	0	1	0	1	2	0	0	?	1	1	0	1	1	1	1	1	0	2	1	1	5	2	-	1	2
Sticholotis	0	2	1	0	0	0	1	?	0	0	0	0	0	0	0	1	2	0	0	1	1	1	0	0	1	1	1	1	0	2	1	1	5	2	-	0	2
Sukunahikona	0	2	1	0	0	1	1	?	0	0	0	0	0	1	0	1	2	0	0	1	1	1	0	1	1	1	1	1	0	2	?	-	-	-	-	-	2
Periptyctus	0	1	1	0	1	1	1	?	1	0	0	0	0	1	0	1	2	0	0	1	1	1	1	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Holopsis	1	0	0	0	0	0	1	2	1	0	0	0	0	1	1	1	2	1	1	1	1	1	0	1	1	3	1	1	0	2	1	1	5	0	0	1	2
Aenigmaticum	1	2	1	0	1	0	1	2	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	?	?	?	?	?	2
Foadia	0	2	1	2	1	0	1	?	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Stanus	1	1	1	0	1	0	1	2	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Orthoperus	1	1	1	0	0	0	1	?	1	0	0	0	0	1	0	1	2	1	1	1	1	1	0	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Clypastraea	1	2	1	0	1	0	1	?	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Sericoderus	1	2	1	0	1	0	1	?	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	1	1	3	1	1	0	2	1	1	5	2	-	1	2
Enicmus	1	1	1	2	1	0	1	3	0	0	1	0	0	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	0	2	1	1	4	0	1	1	3
Stephostethus	1	1	1	2	1	0	1	3	0	0	1	0	0	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	0	2	1	1	4	0	1	1	3
Corticaria	1	2	1	2	1	0	1	?	1	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1	?	1	1	?	0	2	1	1	4	0	1	1	3
Melanopthalma	1	2	1	2	1	0	1	?	0	0	1	0	0	1	0	1	2	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	4	0	1	1	3
Akalyptoischion	1	?	1	2	0	0	0	?	1	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	2	1	-	-	-	-	-	3

Table 4.2 (continued) Morphological character matrix.

	74	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**
Derodontus	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	1	-	0	0	0	0	0	1	0	1	1	0	0	?	0	0	1
Temnoscheila	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	2	0	1	1	0	1	0	1	1	0	1	1	2	0	0
Mycetophagus	2	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	-	0	0	1	1	0	1	0	1	1	0	1	0	2	0	1
Paracucujus	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	2	1	-	2	0	0	1	0	1	0	1	0	0	1	1	0	0	2
Ericmodes	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	2	1	-	2	2	-	1	0	1	0	1	0	0	1	1	1	0	1
Biphyllus	0	0	1	1	1	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	0	0	2	2	-	1	0	1	0	1	1	0	1	0	0	0	0
Pharaxonotha	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	?	1	1	1	1	-	0	0	0	1	0	1	1	2	1	0	1	1	2	0	1
Sphaerosoma	2	0	1	1	1	0	1	2	1	0	1	0	0	0	0	1	1	3	?	2	1	0	2	0	1	1	0	1	0	0	1	0	1	1	1	0	1
Oxylaemus	2	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	2	1	2	1	1	2	0	0	1	0	1	0	1	1	0	1	?	?	?	?
Sysolus	2	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	?	?	0	1	1	2	0	0	1	0	1	0	1	1	0	1	?	?	?	?
Teredolaemus	2	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	2	1	0	1	1	2	0	0	1	0	1	0	1	1	0	1	?	?	0	1
Xylariophilus	2	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	2	1	0	1	1	2	0	0	1	0	1	0	1	1	0	1	1	0	0	1
Anommatus	3	0	1	1	1	0	0	1	1	0	1	0	0	0	0	?	1	0	?	2	1	1	2	0	1	?	0	1	0	1	1	0	1	?	6	0	0
Bothrideres	2	0	1	0	1	0	0	2	1	0	1	0	0	2	0	1	1	0	1	0	1	-	0	0	1	1	0	1	0	0	1	0	1	?	6	1	0
Dastarcus	2	0	1	0	1	0	1	2	1	0	1	0	0	1	0	0	1	1	1	0	1	1	2	1	1	1	1	1	0	1	1	0	1	?	6	1	0
Deretaphrus	2	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	1	1	2	0	1	1	0	1	0	1	1	0	1	?	6	1	0
Sosylus	2	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	1	0	1	1	2	1	1	1	1	1	0	1	1	0	1	?	6	1	0
Euxestoxenus	2	0	1	1	1	0	0	2	1	0	1	0	0	0	0	1	1	0	0	0	1	1	2	0	1	1	0	1	0	1	1	0	?	1	?	?	?
Hypodacne	2	0	1	1	1	0	0	2	1	0	1	0	0	0	1	1	1	1	0	0	1	1	2	0	1	1	0	1	0	0	1	0	0	?	6	?	1
Hypodacnella	2	0	1	1	1	0	1	2	1	0	1	0	0	0	1	1	1	1	0	0	1	1	2	0	1	1	0	1	0	0	1	0	0	?	4	1	?
Metacerylon	2	0	1	1	1	0	1	2	1	0	1	0	0	0	1	?	1	1	0	0	1	1	2	0	1	1	0	1	0	1	1	?	?	?	?	?	?
Loebliorylon	3	0	1	1	1	0	0	2	1	0	1	0	1	1	1	1	1	3	0	0	1	1	2	1	1	0	0	1	0	1	1	0	?	1	?	?	?
Ostomopsis	3	0	1	1	1	0	0	2	1	0	1	1	1	0	0	1	1	1	1	0	1	1	2	0	-	1	0	1	0	1	1	0	1	?	?	?	?
Murmidius	2	0	1	1	1	0	1	2	1	0	1	1	1	0	0	1	1	0	0	0	1	0	2	1	1	1	0	1	0	0	1	1	0	?	6	0	1
Mychocerus	2	0	1	1	1	0	1	2	1	0	1	1	1	0	?	?	?	?	0	?	1	-	?	2	?	1	0	1	0	0	1	0	1	1	6	0	2
Philothermus	2	0	1	1	1	0	0	2	1	0	1	1	1	1	0	1	1	3	0	0	1	0	2	2	-	1	0	1	0	0	1	0	1	1	6	0	2
Cerylon	2	0	1	1	1	0	0	2	1	0	1	1	1	1	0	2	1	0	0	3	-	-	-	-	-	-	0	1	0	0	1	0	1	1	6	0	1
Notiophygus	3	0	1	1	1	0	0	2	1	0	0	0	1	2	0	2	1	0	0	0	1	?	2	2	-	1	0	1	0	0	1	1	0	1	3	0	2
Cassidoloma	3	0	1	1	1	0	0	2	1	0	0	0	1	2	0	2	1	0	0	0	1	0	2	2	-	1	0	1	0	0	1	1	0	1	3	0	2
Discoloma	3	0	1	1	1	0	0	2	1	0	0	0	1	2	0	2	1	0	0	0	1	1	2	2	-	1	0	1	0	0	1	1	0	1	3	0	2
Aphanocephalus	3	0	1	1	1	0	0	2	1	0	0	0	1	2	0	2	1	0	0	0	1	0	2	2	-	1	0	1	0	0	1	1	0	1	3	0	2
Holoparamecus	3	0	1	1	0	0	0	2	1	0	1	0	1	0	0	1	1	3	0	0	1	-	0	0	1	1	0	1	0	0	1	0	0	?	6	0	0
Trochoideus	2	0	1	1	0	0	0	2	1	0	1	0	1	0	0	1	1	3	0	0	1	1	2	2	?	0	0	1	0	2	1	0	0	?	6	1	1
Austroclemnus	3	0	1	1	0	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	2	2	-	0	0	1	0	0	0	?	?	?	6	0	1
Bystus	2	0	1	1	0	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	2	2	-	0	0	1	0	0	0	0	0	?	6	1	1
Mychothenus	3	0	1	?	0	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	2	2	-	0	0	1	0	0	1	?	0	?	6	1	1
Phymaphora	2	0	1	1	0	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	?	3	1	1
Rhanidea	2	0	1	1	0	0	0	2	1	0	1	0	1	0	0	1	1	1	0	0	1	-	0	2	-	1	0	1	0	0	1	0	0	?	3	1	1

Table 4.2 (continued) Morphological character matrix.

	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
Agaricophilus	2	1	0	1	1	0	1	2	1	0	1	0	1	0	0	1	1	1	0	0	1	-	2	0	1	1	0	1	0	0	1	0	0	1	4	?	1
Chileolobius	3	0	1	1	1	0	1	2	1	0	?	0	1	0	0	1	1	1	0	0	1	1	2	2	-	0	0	2	0	0	1	?	?	?	?	?	?
Eidoreus	3	0	1	1	1	0	1	2	1	0	1	0	1	0	0	1	1	1	0	0	1	1	2	2	-	1	0	2	0	0	1	?	?	?	?	?	?
Xenomycetes	2	0	0	1	1	0	0	2	1	0	1	0	1	2	0	0	1	1	0	0	1	?	?	0	1	?	0	1	0	0	1	0	0	1	3	0	1
Endomychus	2	1	0	1	0	0	0	2	0	0	1	0	1	0	0	1	1	1	0	0	1	0	2	2	-	0	0	1	0	0	1	0	0	?	2	1	1
Epipocus	2	1	0	1	0	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	2	2	-	0	0	1	0	0	1	1	0	1	2	1	1
Saula	2	1	0	1	0	0	0	2	1	0	1	0	1	0	0	1	1	1	0	0	1	1	2	2	-	0	1	0	0	0	1	1	0	?	2	1	1
Stenotarsus	2	1	0	1	0	0	0	2	1	0	1	0	1	0	0	1	1	1	0	0	1	0	2	2	-	0	0	1	0	0	1	1	0	?	2	1	1
Amphix	2	1	0	1	1	0	0	2	0	0	1	0	1	0	0	1	1	1	0	0	1	0	2	2	-	0	0	0	0	0	1	1	0	?	2	1	1
Lycoperdina	2	1	0	1	1	0	0	2	1	0	1	0	1	0	0	0	1	1	0	0	1	0	2	2	-	0	0	1	0	0	1	1	?	?	2	1	1
Rhyzobius	2	1	0	1	1	1	1	2	1	0	1	0	1	0	0	1	1	1	0	0	1	1	2	0	0	1	0	2	0	0	1	1	0	?	3	0	1
Diomus	3	0	0	1	0	1	1	2	0	0	1	0	1	0	0	0	1	3	0	0	1	1	2	0	0	1	0	2	0	0	1	1	0	1	3	1	1
Chilocorus	2	1	0	1	0	1	1	2	1	0	1	0	1	0	0	0	1	3	0	0	1	1	2	0	0	1	0	2	0	0	1	0	0	?	3	1	0
Halmus	2	1	0	1	0	1	1	2	1	0	1	0	1	0	0	0	1	3	0	0	1	1	2	0	0	1	0	2	0	0	1	0	0	1	3	1	0
Platynaspis	2	1	0	1	0	1	1	2	0	0	1	0	1	0	0	0	?	3	0	0	1	1	2	0	0	1	0	2	0	0	1	?	?	?	3	1	0
Rodolia	3	0	0	1	0	1	1	2	0	0	1	0	1	0	0	1	1	0	0	0	1	1	2	0	0	1	0	2	0	0	1	1	0	?	3	0	0
Epilachna	2	1	0	1	0	1	1	2	0	0	1	0	1	0	0	0	1	3	0	0	1	1	2	0	0	1	0	2	0	0	1	0	0	1	3	1	1
Coccinella	2	1	0	1	0	1	1	2	0	0	1	0	1	0	0	0	1	?	0	0	1	1	2	0	0	1	0	2	0	0	1	0	0	?	3	0	0
Illeis	2	1	0	1	0	1	1	2	0	0	1	0	1	0	0	0	1	?	0	0	1	1	2	0	0	1	0	2	0	0	1	0	?	?	3	1	0
Coccidophilus	3	0	0	1	0	1	1	2	1	0	1	0	1	0	0	0	1	1	0	0	1	1	2	0	1	0	0	0	0	0	1	0	0	1	3	0	0
Delphastus	2	1	0	1	1	1	1	2	1	0	?	0	1	0	0	0	1	1	0	0	1	1	2	0	1	0	0	0	0	0	1	0	0	1	3	1	1
Microweisea	3	0	0	1	0	1	1	2	1	0	1	0	1	0	0	0	1	1	0	0	1	1	2	0	1	0	0	0	0	0	1	0	0	1	3	0	0
Serangium	2	1	0	1	1	1	1	2	1	0	0	0	1	0	0	0	1	1	0	0	1	1	2	0	1	0	0	0	0	0	1	0	0	1	?	?	?
Sticholotis	2	1	0	1	1	1	1	2	1	0	1	0	1	0	0	0	1	0	0	0	1	1	2	0	0	1	0	2	0	0	1	0	0	1	3	1	0
Sukunahikona	2	1	0	1	0	1	1	2	1	0	1	0	1	0	0	0	1	1	0	0	1	1	2	0	1	0	0	2	0	0	1	0	0	1	3	?	0
Periptyctus	2	1	0	1	0	0	0	2	1	0	1	0	0	0	0	1	1	?	0	0	1	0	2	2	-	1	0	1	0	0	0	?	0	?	4	1	2
Holopsis	2	1	0	1	0	0	1	2	1	0	1	0	0	0	0	2	1	0	0	0	1	0	2	2	0	1	0	1	0	0	0	?	0	?	4	1	2
Aenigmaticum	2	1	0	1	0	0	0	2	1	1	1	0	0	0	0	2	1	0	0	0	1	0	2	2	?	1	0	0	0	0	0	?	0	?	?	?	?
Foadia	2	1	0	1	0	0	1	2	1	1	1	0	0	0	0	2	1	0	0	0	1	?	?	?	?	1	0	1	0	0	0	?	0	?	4	1	1
Stanus	2	1	0	1	0	0	0	2	1	1	1	0	0	0	0	2	1	0	0	0	1	0	2	2	-	1	0	1	0	0	0	0	0	?	4	1	1
Orthoperus	2	1	0	1	0	0	1	2	1	0	1	0	1	0	0	2	1	0	0	0	1	0	2	2	-	1	0	1	0	0	0	?	0	?	4	1	1
Clypastraea	2	1	0	1	0	0	0	2	1	1	0	0	0	0	0	2	1	0	0	0	1	0	2	2	?	1	0	1	0	0	0	0	0	?	4	1	1
Sericoderus	2	1	0	1	0	0	0	2	0	0	1	0	0	0	0	1	1	0	0	0	1	0	2	2	-	1	0	1	0	0	0	?	0	?	4	1	1
Enicmus	3	0	1	1	1	0	0	2	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	2	-	1	0	1	0	0	1	1	0	?	1	1	2
Stephostethus	3	0	1	1	1	0	0	2	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	2	-	1	0	1	0	0	1	1	0	?	3	1	2
Corticaria	3	0	1	1	1	0	0	2	1	0	1	0	0	0	0	1	1	0	1	0	1	1	2	2	-	1	0	1	0	0	1	0	0	?	3	0	1
Melanopthalma	3	0	1	1	0	0	1	2	1	0	?	0	0	0	0	1	1	0	1	2	1	-	0	2	-	1	0	1	0	2	1	0	0	0	1	0	1
Akalyptoischion	3	0	1	1	1	0	0	2	1	0	?	0	0	0	0	2	1	3	0	0	1	1	2	2	?	1	0	1	0	1	1	0	0	1	?	?	?

Table 4.2 (continued) Morphological character matrix.

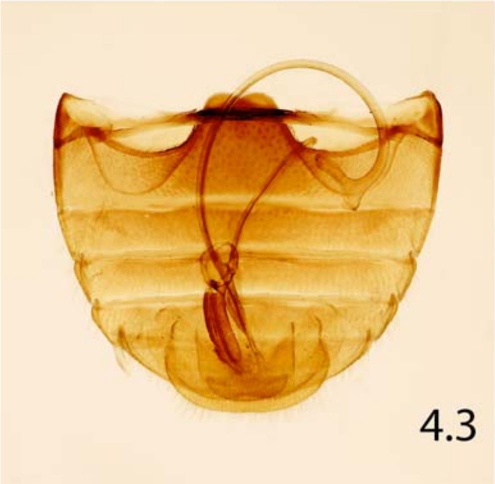
	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146
Derodontus	2	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1	2	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	1	1
Temnoscheila	2	1	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0
Mycetophagus	2	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	0
Paracucujus	2	1	0	0	0	1	0	0	0	0	1	0	0	1	1	2	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Ericmodes	2	1	0	0	2	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	2
Biphyllus	2	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0
Pharaxonotha	2	1	0	0	1	1	0	0	0	0	1	0	0	1	1	2	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	1	0
Sphaerosoma	2	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	2	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	0
Oxylaemus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sysolus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Teredolaemus	2	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0	1	1	0
Xylariophilus	2	0	1	0	2	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	1	1
Anommatus	2	0	?	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0
Bothrideres	1	0	0	1	1	0	2	1	0	1	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Dastarcus	1	0	0	1	0	0	2	1	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Deretaphrus	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0
Sosylus	1	0	0	1	0	0	2	1	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Euxestoxenus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hypodacne	2	0	1	0	2	0	0	1	0	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0
Hypodacnella	2	0	0	0	2	0	0	1	0	0	1	0	0	1	1	1	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1
Metacerylon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Loebliorylon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ostomopsis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Murmidius	2	1	1	0	1	1	0	0	0	0	0	0	0	1	1	2	2	0	1	0	1	0	1	0	0	1	0	0	0	0	-	-	0	2	0	0
Mychocerus	2	0	1	1	0	0	2	1	0	1	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Philothermus	2	0	1	1	0	0	2	1	0	1	1	0	0	0	1	0	2	0	2	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Cerylon	2	0	1	1	0	0	2	1	0	1	1	1	1	0	0	0	2	0	2	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Notiophygus	1	1	-	0	2	0	0	0	0	0	0	0	0	1	1	?	2	0	0	0	1	0	1	0	0	1	1	0	0	0	-	-	0	1	0	0
Cassidoloma	1	1	-	0	2	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Discoloma	1	1	-	0	2	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Aphanocephalus	1	1	-	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Holoparamecus	2	0	0	0	2	0	0	1	0	0	0	0	0	0	1	2	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Trochoideus	2	1	1	0	1	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Austroclemnus	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	2	2	0	0	0	0	1	1	0	0	1	0	0	0	0	-	-	0	1	0	3
Bystus	2	1	0	0	3	0	0	1	0	0	1	0	0	1	1	2	2	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Mychothenus	2	1	1	0	3	0	0	1	0	0	1	0	0	1	1	1	2	0	0	0	0	1	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Phymaphora	2	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Rhanidea	2	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0

Table 4.2 (continued) Morphological character matrix.

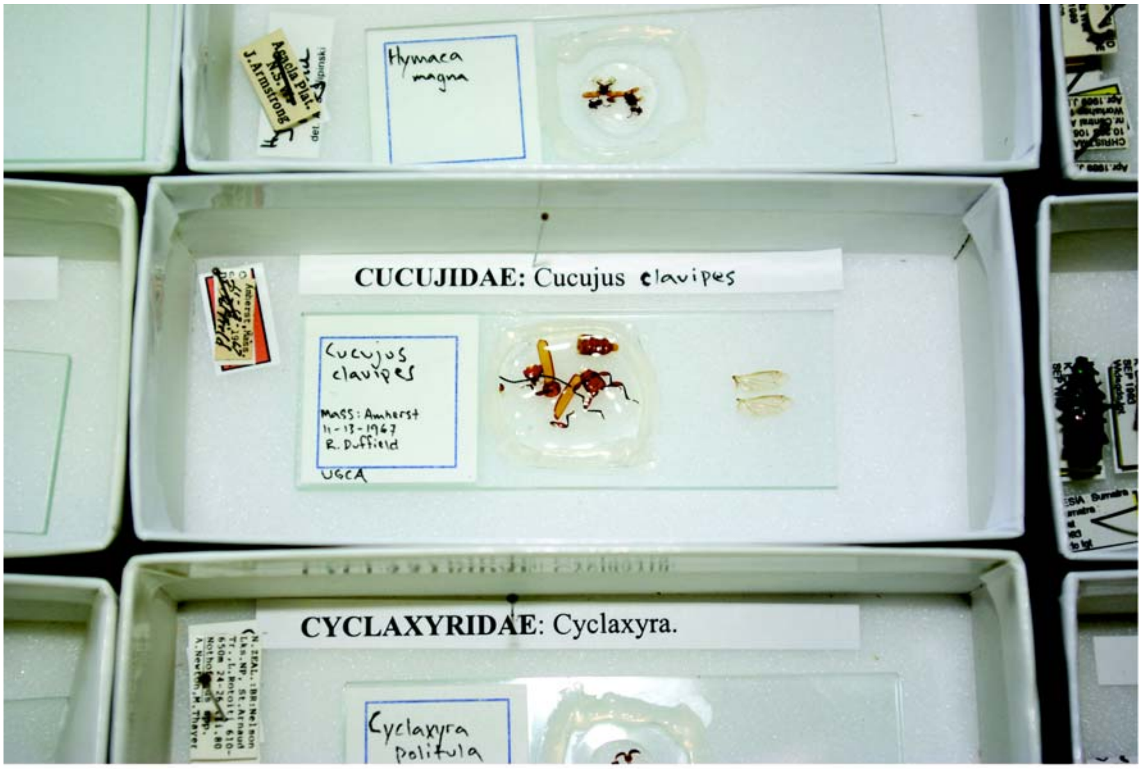
	111	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**
Agaricophilus	2	0	1	?	1	0	0	0	0	?	0	0	0	?	?	1	?	?	?	0	?	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Chileolobius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eidoreus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xenomycetes	2	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Endomychus	?	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Epipocus	2	1	0	0	2	1	0	0	0	0	0	0	0	1	1	?	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Saula	2	1	1	0	2	0	0	0	0	1	1	0	0	1	1	0	?	0	0	0	?	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Stenotarsus	2	1	1	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Amphix	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Lycoperdina	2	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0
Rhyzobius	2	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	-	-	0	1	0	0
Diomus	2	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	2	0	2	1	0	1	1	0	0	1	2	0	0	0	-	-	0	1	0	0
Chilocorus	0	0	-	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	2	0	0	1	0	1	0	1	0	0
Halmus	0	0	-	0	1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	2	0	0	1	0	0	0	1	0	0
Platynaspis	2	0	1	0	0	0	2	1	0	1	0	1	0	1	1	0	2	0	2	0	0	1	1	1	0	1	2	0	0	0	-	-	1	2	0	0
Rodolia	1	0	1	0	0	0	1	1	0	1	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Epilachna	2	1	0	0	2	0	2	1	0	1	0	1	0	1	1	0	2	0	0	1	0	1	1	1	0	0	0	0	0	?	0	0	0	1	0	0
Coccinella	2	0	1	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	-	-	0	0	0	0
Illeis	2	0	1	0	2	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	-	-	0	0	0	0
Coccidophilus	2	0	1	0	0	0	2	1	0	1	1	1	0	1	0	0	2	0	2	0	1	1	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Delphastus	2	0	0	0	0	0	2	1	0	1	1	1	0	1	0	0	2	0	2	0	1	2	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Microweisea	2	0	1	0	0	0	2	1	0	1	1	1	0	1	0	0	2	0	2	0	1	2	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Serangium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sticholotis	2	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	2	0	0	0	0	1	1	0	0	1	2	0	0	0	-	-	0	1	0	0
Sukunahikona	2	0	1	0	0	0	2	1	0	1	1	1	0	1	0	0	2	0	2	0	?	2	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Periptyctus	2	1	0	1	1	0	0	0	1	1	0	1	0	1	1	0	2	0	1	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Holopsis	2	1	0	1	5	0	0	1	1	1	0	1	1	0	0	0	2	0	1	0	0	0	1	0	0	1	3	0	0	0	-	-	0	1	0	0
Aenigmaticum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Foadia	2	0	1	0	2	0	0	1	1	1	0	1	0	1	1	0	?	0	1	0	0	0	1	0	0	1	0	0	0	0	-	-	0	1	0	0
Stanus	2	0	0	0	2	0	0	1	1	1	0	1	0	1	1	0	2	0	1	0	0	0	1	0	0	1	2	0	0	0	-	-	0	1	0	0
Orthoperus	2	0	1	0	2	0	0	1	1	1	0	1	1	0	0	0	2	0	1	0	0	0	1	0	1	1	2	0	0	0	-	-	0	1	0	0
Clypastraea	2	0	0	0	2	0	0	1	1	1	0	1	0	0	0	0	2	0	1	0	0	0	1	0	1	1	2	0	0	0	-	-	0	1	0	1
Sericoderus	2	1	1	0	2	0	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0	1	1	3	0	0	0	-	-	0	1	0	0
Enicmus	2	1	0	0	4	0	0	0	1	1	0	1	0	1	0	1	1	0	1	0	1	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Stephostethus	2	1	0	0	4	0	0	0	1	1	0	1	1	1	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Corticaria	2	1	0	0	4	0	0	0	0	0	0	0	1	1	0	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Melanopthalma	2	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	0	0	0	0
Akalyptoischion	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?


4.1

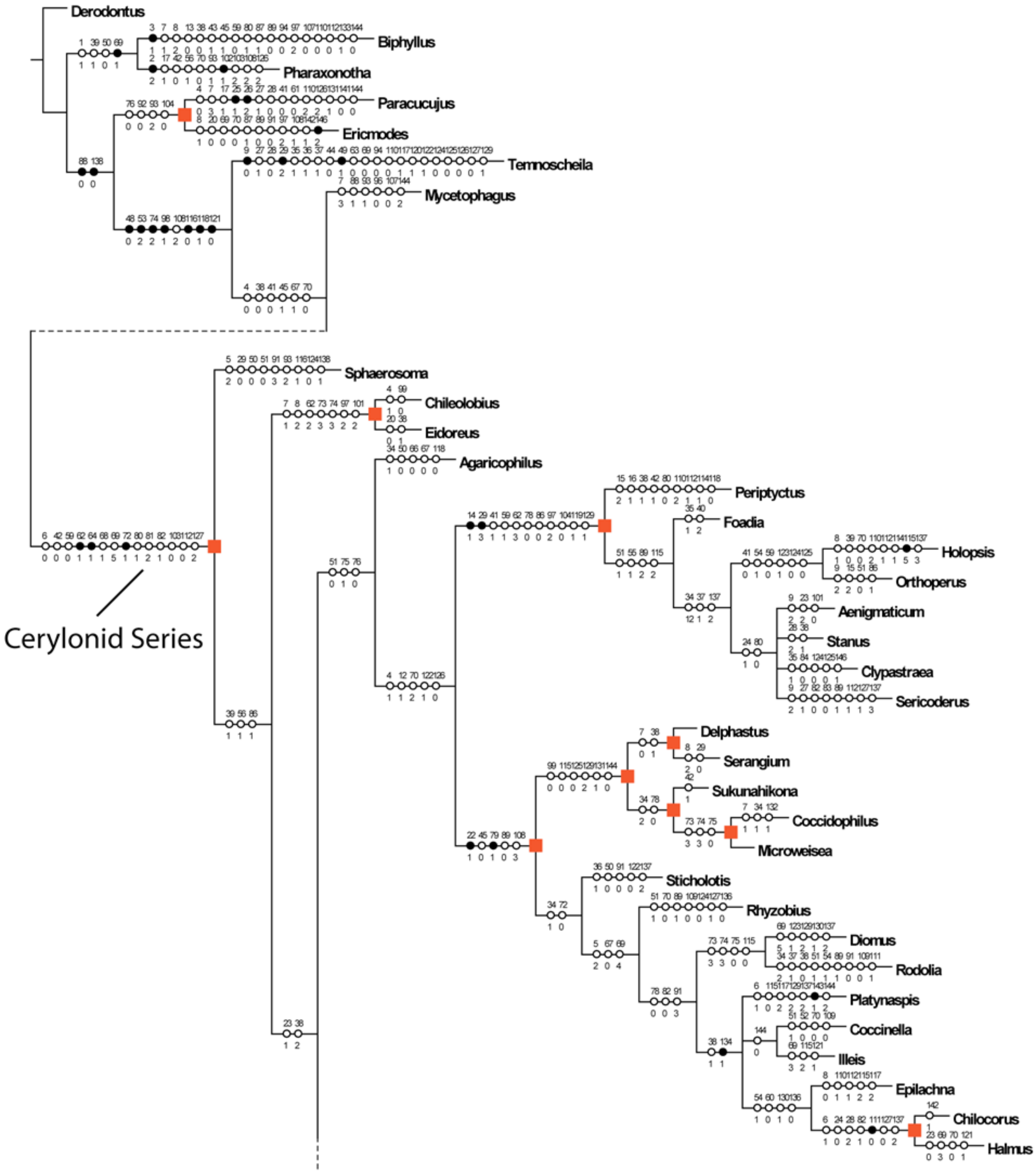

4.2


4.3


4.4


Hymaca magna
CUCUJIDAE: Cucujus clavipes
Cucujus clavipes
MASS: Amherst
11-13-1967
R. Duffield
UGCA
CYCLAXYRIDAE: Cyclaxyra.
Cyclaxyra politula

4.5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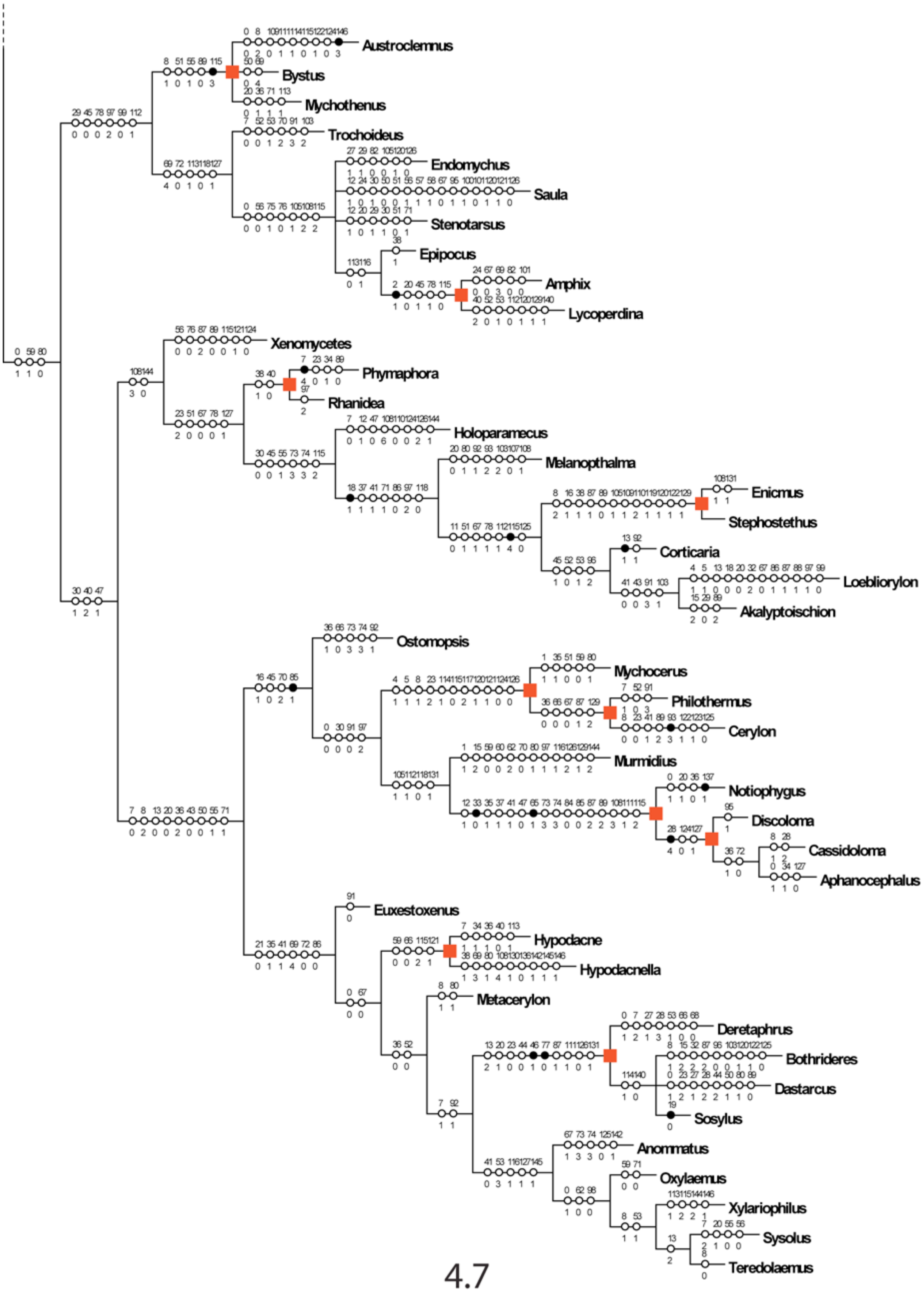
Biphyllus
Pharaxonotha
Paracucujus
Ericmodes
Temnoscheila
Mycetophagus
Sphaerosoma
Chileolobius
Eidoreus
Agaricophilus
Periptyctus
Foadia
Holopsis
Orthoperus
Aenigmaticum
Stanus
Clypastraea
Sericoderus
Delphastus
Serangium
Sukunahikona
Coccidophilus
Microweisea
Sticholotis
Rhyzobius
Diomus
Rodolia
Platynaspis
Coccinella
Illeis
Epilachna
Chilocorus
Halmus
Cerylonid Series

4.6


Austroclemnus
Bystus
Mychothenus
Trochoideus
Endomychus
Saula
Stenotarsus
Epipocus
Amphix
Lycoperdina
Xenomycetes
Phymaphora
Rhanidea
Holoparamecus
Melanopthalma
Enicmus
Stephostethus
Corticaria
Loebliorylon
Akalyptoischion
Ostomopsis
Mychocerus
Philothermus
Cerylon
Murmidius
Notiophygus
Discoloma
Cassidoloma
Aphanocephalus
Euxestoxenus
Hypodacne
Hypodacnella
Metacerylon
Deretaphrus
Bothrideres
Dastarcus
Sosylus
Anommatus
Oxylaemus
Xylariophilus
Sysolus
Teredolaemus

4.7

CHAPTER 5

HOST PREFERENCE AND PHYLOGENY OF CUCUJOIDEA (COLEOPTERA)[1]

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[1] Robertson, J. A., S. A. Ślipiński, K. B. Miller, M. F. Whiting, and J. V. McHugh. To be submitted to *Proceedings of the National Academy of Sciences.*

Abstract

A phylogeny of Cucujoidea with an emphasis on the Cerylonid Series (C.S.) is presented based on arguably the largest dataset of Coleoptera to date (341 taxa × 9 genes: nuclear 18S, 28S, H3, CAD and ArgK, and mitochondrial 12S, 16S, COI and COII). Maximum likelihood and Bayesian inference methods of phylogenetic inference were used for the above dataset to 1) test the monophyly of Cucujoidea with respect to the remaining superfamilies of Cucujiformia; 2) test the monophyly of the C.S., C.S. families, subfamilies and other higher-level taxa; 3) investigate the relationships among non-C.S. cucujoids and the placement of the C.S. within Cucujoidea; 4) investigate the higher-level relationships within the C.S. and each of the C.S. families; and 5) investigate the evolution of host utilization, examine the change in diversification rates as a response to host shifts, and reconstruct the evolutionary history of cucujoid associations with diverse host types.

Cucujoidea is not recovered as monophyletic. The C.S. is recovered as monophyletic and is supported as a major Cucujiform clade, sister group to the remaining superfamilies of Cucujiformia. The following C.S. families are recovered as monophyletic: Discolomatidae, Corylophidae, and Coccinellidae. Bothrideridae is paraphyletic with respect to Cerylonidae. Cerylonidae is paraphyletic with respect to Discolomatidae, the later recovered as sister group to *Murmidius*. Endomychidae is not recovered as monophyletic due to the placement of the Eupsilobiinae + Mycetaeinae clade as sister to Coccinellidae, and the placement of Anamorphinae as sister to Corylophidae. *Akalyptoischion* is supported as a distinct family with the C.S. We investigate the evolution of host utilization among beetles and attempt to reconstruct the evolutionary history of cucujoid associations with diverse host types. Inferences regarding trends and the impact of host utilization in Cucujoidea are made in light of the phylogenetic results.

Key words: Classification; evolution; systematics; taxonomy; phylogeny; Cerylonid Series; Cucujoidea; Bothrideridae; Cerylonidae; Coccinellidae; Corylophidae; Discolomatidae; Endomychidae; Latridiidae; argine; kinase (ArgK); carbamoyl-phosphate synthetase (CAD).

Introduction

Cucujoidea

Of the six superfamilies in the mega-diverse infraorder Cucujiformia, Cucujoidea is the most problematic; no synapomorphies supporting its monophyly have been identified (Leschen and Ślipiński, 2010). Cucujoidea is a heterogeneous group of beetles that have a similar habitus (e.g., small, drab coloration, clubbed antennae) with non-heteromerous tarsi that could not be placed satisfactorily elsewhere. It was established for convenience and represents the largest taxonomic dumping ground among the superfamilies of Coleoptera. Cleroidea in particular shares many characters with certain groups of Cucujoidea such that these two superfamilies are difficult to separate (Crowson, 1955; Lawrence and Newton, 1982). As such, Cucujoidea is difficult to characterize. The current classification recognizes 36 families of Cucujoidea (Leschen, et al., 2005).

Cucujoidea is an extremely diverse and taxonomically difficult group. In Crowson's (1955) monumental work on the natural classification of the families of Coleoptera, he states "In the number of families included, the Cucujoidea greatly exceed any other superfamily of Coleoptera, and the diversity of structure and habit among them is correspondingly great; the establishment of a rational order or natural key to these families is a task beset with the most formidable difficulties" (pg. 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 dubious at best.

Notwithstanding, a number of important advances in cucujoid relationships and corresponding improvements to the classification have been made in the past 50 years. In their review of the classification of Coleoptera, Lawrence and Newton (1982) outlined three major advances in the taxonomy and classification of Cucujoidea. The first was the recognition of several presumed "primitive," primarily south temperate groups such as Protocucujidae (Crowson, 1955), Boganiidae, Hobartiidae, Phloeostichidae, and Cavognathidae (Sen Gupta and Crowson, 1966; 1969; Crowson, 1973). Members of the above 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 and 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 (C.S.) (Crowson, 1955).

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

Cerylonid Series

The Cerylonid Series (C.S.) is a cluster of presumably highly derived families within Cucujoidea comprising Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae. Together, the C.S. families comprise 39 subfamilies and more than half the genera (646 of 1,237) and species (9,600 of 19,090) of the entire superfamily Cucujoidea (Lawrence, 1991; Lawrence and Newton, 1995). It is one of the few large groupings of Cucujoidea that has been hypothesized to form a clade (Hunt et al. 2007;

Robertson et al., 2008; Sen Gupta and Crowson, 1973; Ślipiński, 1990; Ślipiński and Pakaluk, 1991).

The Cerylonid Series is characterized by the following morphological features (Crowson, 1955): adults with tarsal formula reduced (4-4-4 or 3-3-3), hind wings lacking a closed radial cell, hind wings with anal veins reduced, aedeagus resting on side when retracted, and phallobase (tegmen) reduced; larvae with pretarsal claw unisetose, spiracles usually annular, and sensory appendage of 2nd antennomere usually as long as the 3rd antennomere.

As reviewed by Ślipiński and Pakaluk (1991), the above suite of defining characters for the C.S. is somewhat problematic. For instance, many of the characters used to recognize the C.S. are reductions. Other proposed synapomorphies are widespread in unrelated groups or are lacking in some C.S. taxa. Furthermore, the use of larval characters is problematic because so few C.S. taxa are known in their larval stage. Ślipiński and Pakaluk (1991) reviewed the classification of the C.S. and pointed out many serious problems and expressed concerns about the present family limits and the lack of resolution within the C.S. They conclude by calling for a comprehensive, phylogenetic treatment of the major C.S. taxa to be undertaken.

Recently, two molecular phylogenetic studies covering higher-level relationships of C.S. taxa have emerged: Hunt et al. (2007) and Robertson et al. (2008). Hunt et al.'s (2007) paper focused on reconstructing the higher-level relationships within the order Coleoptera using 18S, 16S and COI and a broad taxon sampling across all major beetle groups. While investigating the relationships among C.S. taxa was not the primary goal of their study, Hunt et al. (2007) included 21 C.S. exemplars in their sampling of 320 beetle taxa and recovered the C.S. as monophyletic. While Hunt et al.'s (2007) study indicates that the C.S. families Endomychidae and Cerylonidae are paraphyletic, most of the inter-familial and subfamilial clades of the series were not resolved (Figure 5.1). Noteworthy C.S. internal relationships that were recovered in this study include a sister group of Corylophidae and the endomychid subfamily Merophysiinae (as "Holoparamecinae"). Hunt et al. (2007) also recovered a well-supported clade comprising Bothrideridae, Cerylonidae and Discolomatidae (though Bothrideridae and Cerylonidae were not recovered as monophyletic) that forms the sister group to the remaining C.S. taxa.

The monophyly of the C.S. was also supported by the first formal phylogenetic analysis to focus on C.S. relationships, Robertson et al. (2008), a molecular analysis that included 61 C.S. taxa, representing 7 of the 8 families and 20 of 39 C.S. subfamilies. This study also supported the monophyly of many C.S. families and subfamilies, while revealing the paraphyletic nature of some higher-level taxa, including Endomychidae, potentially Latridiidae, and multiple subfamilies (e.g., Corylophinae, Chilocorinae, Scymninae). Nonetheless, it should be noted that the analysis of Robertson et al. (2008) lacked many key taxa; therefore, the monophyly and the internal relationships of multiple C.S. taxa remain equivocal. Thus although recovered as monophyletic, the tests of monophyly for the families Cerylonidae, Bothrideridae and Corylophidae were weak due to the small and unrepresentative taxon sampling included for these taxa.

Notable internal relationships recovered in Robertson et al.'s (2008) study (Figure 5.2) include a sister grouping of the endomychid subfamily Anamorphinae with Corylophidae, and this clade is unresolved with the Coccinellidae clade and the clade comprising the remaining Endomychidae. This analysis also suggests a close affiliation of Bothrideridae, Cerylonidae, and Discolomatidae.

The studies of Hunt et al. (2007) and Robertson et al. (2008) both suggest a basal dichotomy of two superfamilial clades: one clade comprising Bothrideridae, Cerylonidae, and

Discolomatidae; the second clade includes Corylophidae, Coccinellidae and Endomychidae. Latridiidae is placed sister to the clade of Bothrideridae, Cerylonidae, and Discolomatidae in Robertson et al.'s (2008) tree, while in the Hunt et al. (2007) analysis Latridiidae is included in the Corylophidae, Coccinellidae and Endomychidae clade.

Nonetheless, with roughly only half of the C.S. subfamilies represented in the Hunt et al. (2007) and Robertson et al. (2008) studies, the above hypotheses of C.S. phylogeny should be taken as preliminary. Indeed, the inclusion of all C.S. families, subfamilies, and major or enigmatic tribes and genera in future studies will certainly further clarify the historically problematic relationships among this diverse cucujoid lineage.

Trends and Impact of Host Utilization in Coleoptera

With approximately 375,000 described species and estimates of total extant beetle species exceeding ten million, the insect order Coleoptera (beetles) is arguably the most successful lineage of life on Earth. The evolution of this lineage represents a huge portion of the planet's natural and evolutionary history, and while many factors are responsible for this diversification, host utilization (food preference) is among the foremost. Notwithstanding, little effort has been made to understand the impact of diverse host types on the evolution of beetles (although see Hunt et al., 2007 for an initial significant contribution).

While studies exist suggesting the major role of angiosperm utilization on beetle diversification (Farrell, 1998), until recently little to no attention has been given to the impact of other host resources on beetle evolution on a comparably broad scale. Hunt et al. (2007) however, investigate host utilization across Coleoptera and suggest diverse niches other than angiosperm utilization played important roles in the evolution of beetles. While their study represents a significant initial contribution to understanding the evolution of host utilization in beetles, their study has some serious shortcomings. Although the sampling of taxa in their two datasets is quite broad (340 taxa × 3 genes, and 1880 taxa × 1 gene (18S)) with all major groups of Coleoptera represented, it is arguable that given the breadth of diversity they attempted to cover (all of Coleoptera, >350,000 species) their sampling is simply inadequate to confidently reconstruct transformations given the huge percentage of unrepresented taxa. Additionally, Hunt et al.'s (2007) topology is generally poorly resolved (see their SFig. 2) with rampant spurious placements of taxa (e.g., Silvanidae + Curculionidae). The dubious relationships recovered in their 1880 taxa dataset are such that little to no confidence can be placed thereon, demonstrating the inability of 18S to accurately recover divergences spanning such a large range of taxonomic levels.

We attempt to explore the role of host utilization and host shifting in beetle diversification using the C.S. as a diverse model taxon. Cucujoid beetles have exploited a huge diversity of natural resources. Within the C.S. alone, host utilization ranges from diverse forms of mycophagy (e.g., utilizing Basidiomycetes, Ascomycetes, & Zygomycetes), to phytophagy, myxomycophagy, predation, cleptoparasitism and parasitoidism. Given an adequately extensive taxon sampling and a phylogenetic framework, this broad spectrum of host preferences permits an investigation of trends in host shifting and an assessment of the impact of these shifts on beetle lineage radiation. Specifically, we will address the following questions: 1) Do certain ancestral host conditions give rise to certain apomorphic host conditions more often than others? (i.e., Are there any trends regarding shifts from one food source to another?); 2) Do shifts to or from certain food types result in evolutionary radiation or stagnation? (i.e., Are there any feeding transitions that are repeatedly associated with disproportionately diverse clades?) Our proposed phylogeny for the C.S. and cucujoid outgroup taxa will provide a diverse phylogenetic framework to investigate the evolution of host utilization, examine the change in diversification rates as a response to host shifts and allow us to address the above questions.

Parasitoidism in beetles is relatively rare, occurring in only 11 families (Crowson, 1981; Eggleton and Belshaw, 1992), two of which belong to Cucujoidea (Bothrideridae & Passandridae). Various transitions to the parasitoid lifestyle in beetle groups have been proposed (e.g., see Eggleton and Belshaw, 1992). Of these, the most common ancestral (precursor) state is thought to be mycophagy, though predation is also considered significant. Once the transition to a parasitoid lifestyle has occurred, shifting away from this state is extremely rare (Eggleton and Belshaw, 1992). However, most of these inferences about host utilization transitions were framed outside of empirical phylogenetic evidence. Therefore, the adjacency of these character states in a transformation series and the directionality of transitions between them could not be determined.

For example, host utilization within the C.S. family Bothrideridae is as diverse as it is intriguing. Members of the subfamily Bothriderinae are ectoparasitoids on wood boring insects (e.g., ambrosia beetles, longhorn beetles, jewel beetles, etc.). Species of Anommatinae are parthenogenic and feed on Zygomycetes and Myxomycetes associated with soil, leaf litter, and subterranean wood while xylariophiline bothriderids feed on ascomycete (Xylariaceae) fungi. Interestingly, members of Teredinae (e.g., *Teredolaemus*) feed on Ascomycetes exclusively within the tunnels of ambrosia beetles. As teredine bothriderids usurp the fungus farmed by the ambrosia beetles in their tunnels, this may be considered a type of cleptoparasitism. Crowson (1981) suggested that this transition series follows from microfungi to Ascomycetes to Ascomycetes farmed by ambrosia beetles to ectoparasitoidism on wood boring beetles.

For the family Passandridae however, ectoparasitoidism is thought to have originated from a predaceous ancestral state in a Cucujidae-like ancestor. Using a phylogenetic context, we will specifically test whether the transition to ectoparasitoidism within Bothrideridae and Passandridae follow the pathways previously proposed for each family (Crowson, 1981) and for ectoparasitoid beetles in general (Eggleton and Belshaw, 1992) (i.e., derived from mycophagy). We will additionally test to see if there are any instances of shifting away from a parasitoid condition within these families.

Objectives

Here we present a phylogeny of Cucujoidea with an emphasis on the C.S. based on arguably the largest dataset of Coleoptera to date in terms of number of taxa, breadth of diversity covered, lineage representation, and number of genes. We use the above dataset to attempt the following: 1) test the monophyly of Cucujoidea with respect to the remaining superfamilies of Cucujiformia; 2) test the monophyly of the C.S., C.S. families, subfamilies and higher taxa; 3) investigate the relationships among non-C.S. cucujoids and the placement of the C.S. within Cucujoidea; 4) investigate the higher-level relationships within the C.S. and each of the C.S. families; and 5) investigate the evolution of host utilization, examine the change in diversification rates as a response to host shifts and reconstruct the evolutionary history of cucujoid associations with diverse host types.

Materials and Methods

Taxon sampling

The terminal taxa used in this study are listed in Table 5.1. This sampling includes 341 taxa representing all 6 superfamilies of Cucujiformia, 29 families of Cucujoidea (including all 8

C.S. families), 35 of the 39 C.S. subfamilies and a total of 242 genera. Included is one exemplar outside Cucujiformia, *Derodontus*, which is included as a distant outgroup.

Our sampling throughout the C.S. is particularly extensive, with 268 exemplars including 27% of the known generic diversity (175 of 640 genera represented). To the extent possible sampling within each C.S. family is commensurate with lineage and species diversity. Sampling within each C.S. family is a follows: Alexiidae: 1 exemplar (monotypic, 100% generic representation); Bothrideridae: 21 taxa, 12 of 38 genera included (32% generic representation); Cerylonidae: 28 taxa, 14 of 52 genera included (27% generic representation); Coccinellidae: 85 taxa, 72 of 360 genera included (20% generic representation); Corylophidae: 39 taxa, 16 of 27 genera included (59% generic representation); Discolomatidae: 7 taxa, 3 of 16 genera included (19% generic representation); Endomychidae: 63 taxa, 41 of 120 genera included (34% generic representation); Latridiidae: 23 taxa, 16 of 29 genera included (55% generic representation).

With such extensive taxon sampling, we feel confident that the potential for inferring artifactual host transitions will be minimal, especially given the taxonomic level at which we will treat the host (see below). The four missing C.S. subfamilies [Pondonatinae, Cephalophaninae (Discolomatidae); Danascelinae, Xenomycetinae (Endomychidae)] are extremely rare, difficult to obtain, monotypic taxa and their absence is not likely to influence major phylogenetic conclusions resulting from this study.

Molecular data

We sampled nine genes in this study: nuclear 18S rRNA (18S), 28S rRNA (28S), histone subunit 3 (H3), arginine kinase (ArgK) and carbamoyl-phosphate synthetase (CAD), and mitochondrial 12S rRNA (12S), 16S rRNA (16S), cytochrome oxidase subunit 1 (COI) and cytochrome oxidase subunit 2 (COII). The loci 18S, 28S, H3, 12S, 16S, COI and COII have been used extensively in higher-level phylogenetic studies of Coleoptera (e.g., Robertson et al., 2004, 2008; Jordal et al., 2006; Hunt et al., 2007; Marvaldi et al., 2009; Giorgi et al., 2009; McKenna et al., 2009; Magro et al., 2010; Lord et al., in press); thus their molecular characteristics and phylogenetic utility is well-documented.

More recently, CAD and ArgK have been used, showing great promise for recovering beetle divergences at various taxonomic levels (Jordal et al., 2007; Wild and Maddison, 2008; McKenna et al., 2009). Indeed, in their study investigating the utility of nuclear protein-coding markers in beetles, Wild and Maddison (2008) found CAD to be the highest performing gene fragment (in terms of recovering the known test clades with the greatest amount of support) of the eight loci studied. CAD provides strong support at deep and shallow divergences, has only a few short introns in some taxa and has no known paralogs. Likewise, ArgK is another marker surveyed by Wild and Maddison (2008) that performed exceptionally well, particularly with recovering deeper divergences. There is no evidence of paralogs for ArgK and most beetles lack the intron present in other insect groups [e.g., Diptera (Moulton and Wiegmann, 2004), Hymenoptera (Danforth et al., 2006)] (Wild and Maddison, 2008). Notwithstanding, the use of CAD and ArgK in beetle phylogenetics is relatively scant and much remains unknown regarding the performance, characteristics and utility of these two markers in Coleoptera. In the present study, we attempt to add CAD and ArgK to the suite of molecular artillery for cucujoid beetles.

The sequences for Lymexyloidea, Chrysomeloidea, Curculionoidea, *Ericmodes sylvaticus*, and *Anommatus duodecimstriatus* used in this study (7 taxa in total) were taken from GenBank (see Table 5.1 for corresponding GenBank accession numbers). Likewise, we used sequences from Robertson et al. (2008), Giorgi, et al. (2009), Lord et al., (in press) and Shockley et al. (unpublished data).

Molecular 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, largely follow that outlined in Robertson et al. (2004; 2008). For each specimen the abdomen was carefully disarticulated from the metathorax and the remainder of the specimen (head and thorax intact) was used for the clearing process during the genomic DNA extraction procedure. Once cleared, the specimen was retained with the intact abdomen in 100% EtOH. Genomic DNA was extracted using the Qiagen DNeasy tissue kit (Valencia, CA). Voucher specimens are deposited in the University of Georgia Coleoptera Tissue Collection, Athens, GA, USA (most), the Brigham Young University Insect Genomics Collection (BYU IGC), Provo, UT, USA, the Santa Barbara Museum of Natural History, Santa Barbara, CA, USA (CO477 *Reveliera californica*, CO488 *Dienerella intermedia*, CO902 *Oxylaemus californicus*, CO905 *Deretaphrus oregonensis*, CO931 *Mychocerus discretus*, CO934 *Aenigmaticum californicus*) and the ANIC, CSIRO Entomology, Canberra, ACT, Australia (ccoc_234 *Boganium*).

Target genes were amplified via polymerase chain reaction (PCR) using 25 μl reactions with the following reagent volumes: 16 μl water; 2.5 μl 10X buffer; 2.5 μl MgCl (25 mM), 2.5 μl dNTP (10 mM), 0.25 μl forward primer, 0.25 μl reverse primer, 1 μl DMSO (nuclear genes only), 0.06 μl Taq, 1.5 μl template. PCR cycling conditions were 94° C for 2 min, followed by 35-40 cycles of 94° C for 1 min, 50-56° C for 1 min, 72° C for 1:15 min with a final extension of 72° C for 7 min. Primers and specific annealing temperatures for each gene are given in Table 5.2. Primer combinations for 18S and 28S were as follows: 18S: 1F + b3.0, a0.7 + bi, a2.0 + 9R; 28S: Rd1a + 28SC, 28SA + Rd 5b, Rd 4.8a + Rd 7b1. For COII, we often used both reverse primers in a single reaction with the forward primer, with subsequent sequencing using the internal primer (9b). For both CAD and ArgK, we used a hemi-nested approach (D. McKenna, pers. com.). We performed an initial PCR reaction using CD338F + CD688R and ArgKforB2 + ArgKrevB1 for CAD and ArgK respectively. One μl of product from the previous reaction is used as template for the hemi-nested reaction using primers CD338F + CD668R and ArgK4B4 + ArgKrevB1. We found that using DMSO with CAD drastically improved amplification results; for ArgK the difference was negligible.

Product yield, specificity, and potential contamination were monitored by agarose gel electrophoresis. PCR products were purified using MANU 96-well filtration plates, sequenced using d-Rhodamine chemistry, and separated on an ABI 3730 DNA Analyzer (ABI, Foster City, CA). DNA fragments were sequenced in both directions with sufficient overlap to ensure accuracy of sequence data. Assembly of sequence fragments and editing of contig sequences was performed in Sequencher 4.2.2 (Genecodes, 1999). All resulting nucleotide and AA (protein coding genes) sequences were blasted prior to use in this study.

Sequence Alignment

A number of corylophids contained an intron in CAD ranging from 53-134 bp in length roughly 550 bp downstream from the beginning of our fragment. Likewise, ArgK had a number of introns for several taxa at varying locations in our resulting fragment: one species of *Holopsis* (Corylophidae) contained an 86 bp intron starting at 165 downstream of our fragment; several coccinellids contained an intron beginning at bp 204 of the exon fragment ranging from 52-707 bp in length; one species of *Melanopthalma* (Latridiidae) contained and intron starting at bp 241 of our fragment of 779 bp in length; lastly, a few bothriderids contained an intron 66 bp from the end of our fragment approximately 60 bp in length. All introns were removed from both CAD and ArgK sequences prior to further analysis.

The protein coding genes, H3, ArgK, and COI exon fragments were length invariable; thus alignment of these genes were trivial, based on conservation of amino acid (AA) reading frame. Both COII and CAD contained a length variable region in the exon fragment. The length variable region in CAD is A-rich, ranges from 84 to 120 bp in length and begins at bp 238 in our resulting fragment. Similarly, the length variable region in COII is approximately 312 bp in length and begins 625 bp downstream from the start of the ORF. Using Mesquite 2.72 (Maddison and Maddison, 2009) the variable region in both CAD and COII were excised, translated into AA sequence, aligned using muscle (Edgar, 2004) (as implemented in Mesquite), translated back to nucleotide sequence, and replaced back into the respective CAD and COII alignment.

Alignment of ribosomal genes was achieved using an online implementation of MAFFT 6.5 (Katoh and Toh, 2008) (http://align.bmr.kyushu-u.ac.jp/mafft/online/server) using the G-INS-i search strategy. Due to their longer length, 18S and 28S were each spliced into three regions prior to alignment in an effort to facilitate more efficient alignment and minimize computational constraints.

Phylogenetic Inference

Initial phylogenetic analyses of the individual markers were performed to monitor potential contamination of sequences and gene performance (see below). Alignments of the individual markers were concatenated in MacClade 4.08 (Maddison and Maddison, 2003) and subsequent analyses were performed using this combined data set using maximum likelihood (ML) and Bayesian inference (BI) as outlined below.

We used the Akaike information criteria (AIC) as implemented in Modeltest 3.7 (Posada and Crandall, 1998) and PAUP* 4.0b10 (Swofford, 2000) to select an appropriate model of sequence evolution for each gene and for the combined molecular data. Heuristic ML analyses were performed using the program RAxML (Stamatakis et al., 2005) hosted on the Cipres portal (www.phylo.org/). We performed RAxML rapid bootstrapping with a subsequent ML search (Stamatakis et al., 2008) executing 500 bootstrap inferences using GTR + G + I model (as suggested by Modeltest). Single RAxML analyses were executed for each gene; 4 independent analyses were performed on the combined molecular dataset and the topology with the best likelihood score is discussed below.

A mixed-model Bayesian analysis (Nylander, et al., 2004) was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) using the models generated in Modeltest for the separate data partitions (by gene). The partitioned Bayesian analysis comprised four separate runs each utilizing 20 million generations, flat priors, unlinked partitions, four chains (one cold and three hot) and trees sampled every 1000 generations. BI analyses were performed on the Cipres portal (www.phylo.org/). We used the program Tracer 1.5 (Rambaut and Drummond, 2009) to graphically determine stationarity, a suitable burn-in, mixing and convergence of runs. Trees sampled after the burn-in from the four runs were combined and used to construct a 50% majority rule consensus tree. Nodal support was assessed with the resulting posterior probabilities (Huelsenbeck and Ronquist, 2001).

Host Preference Data

One potential danger when making inferences of character evolution is inferring artifactual transitions as a result of inadequate taxon sampling. The precision achievable when making inferences of character evolution is dependent upon two factors: The first is the thoroughness of the sampling of terminal taxa used. Phylogenetic studies are almost never complete and there will always be intermediate taxa that cannot be considered and thus potential transitions that are not inferred. Given our extensive taxon representation (ca. 27% of the known C.S. generic diversity) we feel confident that the potential for inferring artifactual host transitions will be minimal.

The second factor is the level upon which one investigates the character, in this case the host shift (i.e., the taxonomic level at which hosts are coded for the terminal taxa). We initially scored host information using the following broadly defined feeding habits: phytophagous; predaceous; mycophagous; saprophagous; myxomycophagous; ectoparasitoidic; lichenophagous; euryphagous (omnivorous). We attempted to refine these broad feeding categories in an effort to better characterize specific life histories within the above broad categories (e.g., multiple types of mycophagy: basidiomycete, ascomycete, zygomycete, deuteromycete, or phycomycete feeding). Doing so was problematic however, as many of the host records for these taxa likely represent incidental occurrences, or the precise data was not known beyond the generalization (e.g., mycophagy). Thus for the present study we resorted to using the original broad categories above. Given our treatment of hosts on a relatively broad scale and our extensive taxon sampling, we are confident that we will miss few, if any, major transitions (except in cases of missing data).

Information regarding the specific habits and habitats of many cucujoid beetles is relatively scarce. Host information for the terminal taxa in this analysis was complied from a number of sources, but we relied heavily on Handbuch der Zoologie (Beutel and Leschen, eds., 2010). For a number of taxa we were not able to score the feeding preference due to the lack of either known host information for that taxon or an adequately specific identification for the terminal. Our summary of host information for the terminal taxa in this study is compiled in

Table 5.4. Mesquite 2.72 (Maddison and Maddison, 2009) was used to optimize host preference data on our resulting topology using unambiguous parsimony optimization.

Results

Sequences generated in this study are deposited on GenBank under the accession numbers #####-##### [accession numbers provided upon acceptance]. Alignment and sequence statistics for individual markers, partitions and the concatenated matrix are given in Table 5.3. Concatenation of the individual aligned markers yielded a matrix of 11022 characters, 5453 of which are parsimony informative. The AIC as implemented in Modeltest yielded the General Time Reversible model with a proportion of invariant sites and an estimation of the alpha-parameter of rate heterogeneity (GTR + I + G) as being the most suitable model of sequence evolution for each of the individual markers and the combined data set. As such, we applied this model in the ML analyses in RAxML. ML analyses of the individual markers indicate that our datasets were sound and free of contamination (as indicated by a lack of isolated radical placements of taxa). The topologies resulting from the 4 separate RAxML runs of the combined dataset are overall very similar, differing primarily in a few minor placements of certain taxa (e.g., members of Chrysomeloidea). The best scoring topology from the 4 runs had a likelihood score of -618130.751804 and is used for further discussion below.

Given the size of our dataset (341 taxa × 11022 characters) it is not surprising that the mixed model BI analysis ran extremely slowly, despite utilizing one of the fastest supercomputers available for implementing MrBayes (CIPRES). We launched the analysis as described above 8 times, with successively increasing overall run times. None of our BI analyses ran to completion through all 20 million generations; the longest run successfully produced 5.2 million generations. Nonetheless, graphical inspection of the MCMC parameter files from this BI analysis in Tracer indicated that 2 of the 4 runs reached stationarity by 3.8 million generations. All trees sampled prior to 3.8 million generations were discarded as burn-in. The remaining trees sampled from the posterior distribution from the combined runs were used to calculate the 50% majority rule consensus BI tree.

Results from the ML and BI analyses are highly concordant in tree topology and patterns of branch support. The BI tree differs from the ML tree most notably in a few relationships among non-C.S. taxa including Chrysomeloidea + Curculionoidea not being recovered as monophyletic, rather these taxa scattered throughout the basal cucujoids (e.g., *Cimberis* as sister to Protocucujidae + *Protosphindus*; *Orsodacne* as sister to Boganiidae); Both Cryptophagidae and Monotomidae are paraphyletic; Myraboliidae is sister to Passandridae. Instances of inconcordance within the C.S. clade are minor and relatively few. Within Coccinellidae a few of the higher clades are placed differently. Among the remaining C.S. families, there are less than 8 topological differences, all of which are very minor differences in the resolution among congeners. Given the high level of concordance between the ML and BI topologies, only the ML topology is shown below (Figures 5.3-5.7) and is used as the reference topology while discussing relationships and hypotheses of host transitions.

The results of the present study support the monophyly of the superfamiles Cleroidea and Chrysomeloidea. The monophyly of Curculionoidea and Lymexyloidea in the present analysis is uncertain because only one exemplar was included for each of these groups. Tenebrionoidea is paraphyletic with respect to Lymexyloidea. These results fail to recover a monophyletic Cucujoidea. Biphyllidae and Byturidae are placed as sister to Cleroidea. Most members of Sphindidae comprise a clade outside the main body of non-C.S. cucujoid taxa. Chrysomeloidea and Curculionoidea are recovered as sister taxa and this clade (Phytophaga) forms the sister group to the non-C.S. cucujoids (basal Cucujoidea). The failure to recover Chrysomeloidea and Phytophaga in the BI analysis is certainly due to the high amount of missing data for these terminals; the monophyly of both Chrysomeloidea and Phytophaga is well-supported (McKenna et al., 2009).

The C.S. is recovered as monophyletic and is supported as a major Cucujiform clade, sister group to the remaining superfamilies of Cucujiformia. The C.S. families Discolomatidae, Corylophidae, and Coccinellidae are recovered as monophyletic. Bothrideridae is paraphyletic with respect to Cerylonidae. Cerylonidae is paraphyletic with respect to Discolomatidae, the later is recovered as the sister group to *Murmidius*. Endomychidae is not recovered as monophyletic due to the placement of the Eupsilobiinae + Mycetaeinae clade as sister to Coccinellidae, and the placement of Anamorphinae as sister to Corylophidae. *Akalyptoischion* is not allied with any other C.S. family and is supported as a distinct lineage within the C.S.

Optimizing host utilization data on our topology indicates that mycophagy represents the ancestral condition for Cucujiformia. There have been at least five shifts to a predatory life history and five independent origins of myxomycophagy. Host shifting has played a major role in cucujiform diversification. In general, most major host shifts correspond to diverse clades representing beetle families and subfamilies and other diverse lineages.

Discussion

CAD and ArgK

The resulting CAD exon fragment for the present taxon sampling contained a length variable region ranging from 84 to 120 bp in length (see above for details). In addition introns were found in the CAD sequences of several members of the C.S. family Corylophidae. According to the initial survey of Wild and Maddison (2008) introns in ArgK in Coleoptera are known to occur in two locations. With the taxonomic diversity and number of ArgK sequences generated here we have discovered introns occurring in four unique regions of our resulting ArgK fragment for distinct taxon groups (Corylophidae, Coccinellidae, Latridiidae, Bothrideridae). Furthermore, the length range of the ArgK introns discovered in the present study range from 52-779 bp in length, vastly expanding the known intron length range for ArgK in Coleoptera (90-300 bp) (Wild and Maddison, 2008). This greatly adds to the current knowledge of the diversity and characteristics of these loci for beetles.

Currently, there are 148 CAD and 256 ArgK sequences for Coleoptera available on GenBank. In the present study, we successfully generated 171 CAD and 157 ArgK sequences, thereby increasing the number of available beetle CAD and ArgK sequences by 116% and 61% respectively. We consider this a significant contribution to the current pool of sequences available for further study for these promising, yet relatively new, loci for beetle phylogenetics.

Taxonomic Implications

Cucujiformia and basal Cucujoidea

The monophyly of Cleroidea, Chrysomeloidea and Phytophaga (Chrysomeloidea + Curculionoidea) is well supported in the present study (Figure 5.3) and consistent with previous morphological and molecular evidence (Hunt et al. 2007). Although the placement of Lymexyloidea nested within Tenebrionoidea is somewhat unexpected, Hunt et al. (2007) also recovered this placement for Lymexyloidea in their study.

Given the heterogeneity and the checkered taxonomic history of Cucujoidea, the failure to recover this superfamily as monophyletic is not surprising. What is perhaps more interesting however, is that the majority of basal cucujoid families do in fact form a clade (Figure 5.3).

Leschen's designation of basal Cucujoidea was not meant as a hypothesis of monophyly but was more of an informal grouping of convenience (Leschen et al., 2005).

The placement of Biphyllidae and Byturidae has challenged coleopterists historically. These taxa have been considered allied with Cucujoidea (Crowson, 1955; Ślipiński and Pakaluk, 1991; Leschen et al., 2005), Tenebrionoidea (Crowson, 1960; Lawrence, 1977) and Cleroidea (Lawrence and Newton, 1995; Hunt et al., 2007). Nonetheless, the placement of Biphyllidae and Byturidae as sister to Cleroidea is well supported by a number of morphological features, foremost is the nature of the aedeagus which in a number of cleroids and Biphyllidae and Byturidae the tegmen is of the "double" type (Crowson 1964) with paired tegminal struts in addition to the common anterior strut.

Most of the members of Sphindidae (all except *Protosphindus*) form a clade outside the main body of non-C.S. cucujoid taxa (Figure 5.3). Once again this placement is consistent with that of Hunt et al. (2007). The paraphyletic nature of the family however has never been suggested previously due to the number of strong morphological apomorphies uniting this family [(e.g., dorsal surface of mandible with a large central tubercle and setose cavity) (McHugh, 1993)]. The placement of *Protosphindus* sister to Protocucujidae is well supported (BS = 100; PP = 100). Indeed, from a morphological perspective *Protosphindus* is clearly distinct from the remaining sphindid taxa (McHugh, 1993) and was considered the sister group to the remaining family, which in turn was thought to be sister group to Protocucujidae (McHugh, 1993). Our results suggest that *Protosphindus* and Protocucujidae should be treated as a single family. Likewise, the remaining sphindid taxa hold an isolated position among the cucujiform superfamilies. If this placement is corroborated in subsequent studies, the main sphindid clade should be treated as a superfamily of Cucujiformia.

The Phytophaga, including Chrysomeloidea and the megadiverse Curculionoidea is supported as the sister group to the basal Cucujoidea (Figure 5.3). The basal most clade within the basal Cucujoidea is Boganiidae + Hobartiidae. This result is consistent with previous views; both Hobartiidae and Boganiidae have been considered as relatively basal groups within Cucujoidea (Leschen, 2005; Lawrence and Ślipiński, 2010). Crowson (1990) suggested a possible relationship between Boganiidae and Chrysomeloidea. Interestingly, in some of our combined ML analyses this sister group was recovered. In light of the host preference of boganiids and presumed basal members of Chysomeloidea (Megalopodidae), a potential sister grouping of these lineages is certainly intriguing; both feed on the pollen of cycads (see below).

Members of the Nitidulidae group, including Kateretidae and Nitidulidae (Leschen, 2005) form a well-supported clade (BS = 98; PP = 100) (Figure 5.3). The remaining family included in this group, Smicripidae, was not included in the present study. Monotomidae is weakly supported (BS < 50) as the sister group to the Nitidulidae group, a placement consistent with previous views (Crowson, 1955).

Thomas (1984) suggested that Laemophloeidae, Propalticidae, Phalacridae and Passandridae form a natural lineage based on a number of morphological features including unequal protibial spurs, structural affinities of the male genitalia, and the presence of pronotal lines and elytral cells. Our results support this grouping as the above four families form a clade with moderate to high branch support (BS = 69; PP = 100) (Figure 5.3). Interestingly, *Propalticus* is nested within Laemophloeidae. These taxa have been considered to be sister taxa (Lawrence and Newton, 1995; Leschen, et al., 2005); our results suggest that *Propalticus* should be subsumed within Laemophloeidae.

Cerylonid Series

The C.S. is not allied with any one of the existing superfamilies of Cucujiformia (including the remaining "Cucujoidea") (Figure 5.3), rather it is sister group to the remaining cucujiform lineages. Indeed, given our resulting topology, there is no other way to treat the C.S. except to recognize it as a new superfamily of Cucujiformia. Of the C.S. higher taxa, Coccinellidae, Latreille, 1802 has priority. Thus the new superfamily would be Coccinelloidea and would be synonymous with the current concept of the Cerylonid Series. The support for the C.S. clade is moderately high (BS = 83; PP = 100).

Our results corroborate the studies of Hunt et al. (2007) and Robertson et al. (2008) in recovering a basal dichotomy of two superfamilial C.S. clades: one clade comprising Bothrideridae, Cerylonidae, and Discolomatidae (hereafter "BCD" clade); the second clade including Alexiidae, Corylophidae, Coccinellidae and multiple endomychid and latridiid lineages (Hunt et al., 2007) (hereafter "ACCEL" clade).

Bothrideridae, Cerylonidae, Discolomatidae (BCD)

Within the BDC clade (Figure 5.4), the ectoparasitic subfamily Bothriderinae is sister to the remaining taxa. Bothriderinae is well supported (BS = 100; PP = 100). The enigmatic genus *Deretaphrus* forms the sister group to the remaining bothriderines. *Deretaphrus* is unique among the entire C.S. for having the hind wing with a closed radial cell and 4 anal veins in the medial field (see Chapter 4). The current tribal classification of Bothriderinae places *Deretaphrus* and *Sosylus* in Deretaphrini, a group based on possessing a broadly rounded intercoxal process of abdominal ventrite I (in contrast to being truncated apically: Bothriderini) and having the first tarsal segment distinctly longer than the second one (Ślipiński and Pal, 1985). The present analysis does not support the bothriderine tribal classification, due to the placement of *Sosylus* deeply nested within Bothriderini.

The remaining bothriderid subfamilies, or “free-living” bothriderids (Anommatinae, Teredinae, and Xylariophilinae) (Ślipiński et al., 2010), form a clade subtending “Cerylonidae” (Figure 5.4). Anommatinae is strongly supported as sister to *Oxylaemus* (Teredinae), a placement supported as well by morphological evidence (see Chapter 4). *Teredolaemus* is sister to *Xylariophilus*, thereby rendering Teredinae paraphyletic.

The paraphyly of both Bothrideridae and Cerylonidae has been suggested previously by many authors (Pal and Lawrence, 1986; Ślipiński, 1990; Ślipiński and Pakaluk, 1991; Ślipiński and Lawrence, 2010). Most of these assertions concerned the lack of diagnostic characters to separate members of the subfamilies Teredinae (Bothrideridae) and Euxestinae (Cerylonidae). Thus it is somewhat surprising that these two subfamilies are not allied more closely.

The placement of *Murmidius* as sister to Discolomatidae, rendering Cerylonidae paraphyletic, is well-supported in the present study (BS = 66; PP = 100) (Figure 5.4). Multiple authors have suggested a potential sister group pairing of Murmidiinae and the family Discolomatidae (Ślipiński, 1990; Lawrence, 1991; Ślipiński & Pakaluk, 1991). Murmidiine cerylonids and discolomatids share a number of adult and larval morphological features including adults with the spiculum gastrale absent and ovipositor reduced, without styli, and larvae onisciform (Ślipiński, 1990; Ślipiński & Pakaluk, 1991).

The monotypic Ostomopsinae is supported as forming the sister group to the speciose Ceryloninae with high support (BS = 90; PP = 100). Both taxa share a specialized elytral interlocking mechanism comprising crenulations on the apex of the last abdominal ventrite;

murmidiines, however, also share this feature. Ceryloninae well-supported in this analysis (BS = 100; PP = 100) as well as by morphology (Ślipiński, 1990).

Latridiidae

In agreement with Hunt et al. (2007) Latridiidae is not placed within the BDC clade, rather its constituents are included with the remaining C.S families (BS = 69; PP = 100) (Figure 5.5). The monophyly of Latridiidae in the traditional, broad sense to include the enigmatic genus *Akalyptoischion* (Latridiidae s.l.)*,* is not supported in the present study. Rather Latridiidae in the strict sense (excluding *Akalyptoischion*; Latridiidae s.s.), is recovered as sister to *Akalyptoischion* + the remaining ACCEL (BS = 64; PP = 81). The uniqueness of *Akalyptoischion* compared to other Latridiidae and the remaining C.S. lineages was recently suggested and considered a putative new family (Lord et al., in press); these results corroborate such an action. The internal relationships of Latridiidae s.s. are strongly supported including the subfamilies Corticariinae (BS = 100; PP = 100) and Latridiinae (BS = 99; PP = 100).

Alexiidae

Alexiidae is recovered as sister to the clade comprising Corylophidae, Coccinellidae, and "Endomychidae" (Figure 5.5). Support for this sister grouping (BS = 64; PP = 100) and that of the clade comprising Corylophidae, Coccinellidae, and "Endomychidae" (BS = 64; PP = 100) is fairly strong.

Anamorphinae

Corroborating Robertson's (2008) results, our study supports a strong sister grouping of Anamorphinae (Endomychidae) and Corylophidae (Figure 5.5), indicating that Anamorphinae should be elevated to family status. Morphological evidence supporting this sister grouping includes both taxa having complex endophallic sclerites in the median lobe of the aedeagus (see Chapter 4).

Corylophidae

The internal relationships within Corylophidae are largely concordant with those proposed by Ślipiński et al. (2009), recovering a monophyletic Periptyctinae and Corylophinae sensu Ślipiński et al. (2009) (e.g., *Periptyctus* sister to the remaining taxa) (Figure 5.5). *Holopsis* comprises the basal most lineage within Corylophinae, a position not in accordance with the findings of Ślipiński et al. (2009). The tribe Foadiini, including *Foadia* and *Priamima*, is recovered and given a relatively basal placement in the tree. In contrast, the Aenigmaticini, including *Aenigmaticum* and *Stanus*, are not monophyletic.

In many corylophids the pronotum is enlarged anteriorly into a broad shelf-like projection that conceals the head from dorsal view. Members of Foadiini and Aenigmaticini are often referred to as "latridiid-like" corylophids, because they have more elongate bodies with the head not concealed underneath an expanded pronotum; instead it is fully exposed. Ślipiński et al. (2009) demonstrate that the "latridiid-like" corylophids are not monophyletic; however our results suggest there have been even more independent appearances of an elongate form.

Endomychidae

Most taxa classified as Endomychidae form a well-supported clade (BS = 100; PP = 100) (Figure 5.6). Within this main clustering of endomychids, there are two major lineages. The first comprises the subfamilies Pleganophorinae (BS = 100; PP = 100), Leiestinae (BS = 100; PP = 100;) and Merophysiinae (BS = 100; PP = 100;). The second major clade corresponds to Tomaszewska's (2005) "higher Endomychidae" and includes the subfamilies Endomychinae, Stenotarsinae, Epipocinae and Lycoperdininae. Endomychinae and Stenotarsinae are paraphyletic with respect to each other. The above results and internal endomychid relationships recovered herein are consistent with that of a different, unpublished, molecular dataset (Shockley, pers. com.).

Mycetaeinae + Eupsilobiinae

The present analysis places Mycetaeinae and Eupsilobiinae as sister taxa, representing a distinct lineage in the C.S. (Figure 5.6). Both are considered somewhat enigmatic members of Endomychidae (Tomaszewska, 2005). In the present study, this lineage represents the sister grouping to the mega-diverse Coccinellidae, representing a novel evolutionary hypothesis for this economically important C.S. family.

Coccinellidae

The monophyly of Coccinellidae is strongly supported in the present analysis (BS = 100; PP = 100). Corroborating Giorgi et al. (2009), we recover a basal split comprising a number of presumably basal Sticholotidinae representing one lineage and the remaining coccinellid taxa forming the second, more speciose lineage (Figure 5.7). This basal split is consistent with the recent classification proposed by Ślipiński (2007) which formally recognizes the basal sticholotidine assemblage as the subfamily Microweisiinae and places all other coccinellid taxa into an expanded concept of Coccinellinae.

Also consistent with Giorgi et al. (2009) is the placement of *Monocoryna*, as sister to the remaining Coccinellinae sensu Ślipiński (2007). This relationship is here well supported (BS = 100; PP = 100).

In contrast to the remaining C.S. lineages, in the present study the internal relationships within Coccinellidae are in general not well-supported, with most strongly-supported clades representing terminal sister groupings; a few notable exceptions are Microweisiinae sensu

Ślipiński (2007) (BS = 100; PP = 100), Chilochorinae (most) (BS = 100; PP = 100), Coccinellinae sensu stricto (BS = 100; PP = 100) and the internal relationships of these 3 groups. In addition, the present study corroborates previous hypotheses of rampant paraphyly of the historical coccinellid subfamilies (Giorgi et al., 2009; Magro et al., 2010). Only the subfamilies Epilachninae and Coccinellinae are supported as monophyletic. The weak support for most internal branches is such that little confidence can be placed on many of the internal relationships recovered here.

Host preference

Mycophagy

Our results support mycophagy as the ancestral condition within Cucujiformia. Although our outgroup, *Derodontus*, also feeds on fungi, this taxon represents a basal lineage within Polyphaga (Hunt et al., 2007) and the inferred shared mycophagous state given our taxon sampling and topology is surely an artifact of not having the diverse basal and intermediate polyphagan superfamilies represented in the current analysis. The basal and non-cucujiform polyphagan lineages comprise mostly saprophagous, predaceous, and phytophagous taxa (Hunt et al., 2007) with only a few isolated instances of fungivory arising in deeply nested, minor taxa [e.g., Eucnemidae, Scaphidiinae (Staphylinidae), Lycidae]. Indeed, Hunt et al. (2007) found strong evidence supporting a shift to mycophagy at the root of Cucujiformia. Thus a transition to mycophagy probably occurred at the base of Cucujiformia, although this transition is not apparent in the present study due to our outgroup selection. Cucujiformia includes over half of all beetle species and 90 families (Lawrence and Newton, 1995). This transition to mycophagy produced one of the largest radiations in the planet's history.

Given our broad treatment of mycophagy types, it is difficult to infer the impact of transitions to specific types of mycophagy (e.g., basidiomycete, ascomycete, deuteromycete, zygomycete, and phycomycete feeding) on specific lineages. Nonetheless, a few interesting observations and generalizations can be made. Members of the family Latridiidae utilize a variety of fungal types including Ascomycetes, Deuteromycetes, and Phycomycetes. Corylophids also exhibit a diverse range of mycophagy: Most feed on Ascomycetes and Deuteromycetes, though *Holopsis* feeds on Ascomycetes and Basidiomycetes while *Sericoderus* consumes zygomycete and ascomycete fungi. Constituents of the family Endomychidae are primarily mycophagous, with most feeding on Basidiomycetes. It is possible that the basidiomycete feeding seen in Endomychidae represents an independent origin at this region of the tree, given the host preferences of several clades subtending Endomychidae (e.g., Corylophidae, Latridiidae, *Akalyptoischion*). In either case, Endomychidae have diversified into the second largest family of the C.S. with ca. 1300 species (Tomaszewska, 2010).

Phytophagy

We applied a broad definition of phytophagy to include xylophagy (wood feeding), pollenophagy (pollen feeding), antherophagy (flower feeding), and consumption of stored plant products. We infer at least 12 independent origins of phytophagy, in one of its various forms, within Cucujiformia. The two origins of phytophagy within the tenebrionoid/lymexyloid clade (*Platycotylus*, *Atractocerus*) represent instances of xylophagy. The remaining 10 origins of phytophagy occur in the following lineages/taxa: *Anthoneus agavensis* (Kateretidae) is antherophagous on yucca; *Oryzaephilus surinamensis* (Silvanidae) feeds on stored plant products; Epilachninae (Coccinellidae) feed on leaves of plants; *Bulaea* (Coccinellidae) feeds on leaves and pollen while the feeding habits of *Coleomegilla* are quite broad including predation and phytophagy; *Olibrus* (Phalacridae) feeds on pollen; *Pharaxonotha* feeds on the pollen of cycads; *Aethina tumida* steals pollen and other plant products from bee nests; boganiids are pollenophagous, with *Paracucujus* feeding on cycads; *Xerasia* (Byturidae) is pollenophagous; there is a single origin of phytophagy within Phytophaga, with *Cimberis*, *Orsodacne* and *Palophagoides* all feeding on pollen, with the later feeding on cycads (Clark and Riley, 2002).

A number of interesting trends may be drawn from the above information. First, all but one shift to phytophagy was from a mycophagous ancestral state; the optimization for the ancestral condition of the remaining phytophagous origin in *Atractocerus* is equivocal. This suggests that mycophagy is an important precursor for shifting to phytophagy.

Another significant trend is the widespread occurrence of pollenophagy. Indeed, of the 12 shifts to a phytophagous life history, more than half represent a shift to pollen feeding. In a recent study on the feeding preferences of Coccinellidae (Giorgi et al., 2009), it was suggested that pollen feeding played an important role in transitioning to a new feeding life history. Based on the observed relative frequency of the different types of phytophagy, our data suggests that it is significantly easier to shift to pollenophagy compared with other phytophagous host types.

In some cases, the host shift to pollen feeding yielded major evolutionary consequences. Our current sampling of Chrysomeloidea and Curculionoidea comprise exemplars of the basal lineages of the megadiverse Phytophaga [Nemonychidae (*Cimberis*), Orsodacnidae (*Orsodacne*), Megalopodidae (Palophagoides)] (McKenna, 2009), a group including ca. 135,000 species (Farrell, 1998). Megalopodidae and Orsodacnidae are considered as the basal lineages within Chrysomeloidea. Nemonychidae is supported as the basal weevil group (McKenna et al., 2009) and feeds on the pollen of conifers. Indeed, the first several basal nodes of the weevil groups are conifer feeders, with subsequent shifts to monocot and angiosperm hosts resulting in the evolution of the most diverse group of animals, with ca. 62,000 species. Although Farrell (1998) suggested the tie between phytophagan diversity and the role of angiosperms, it is important to note that the relationship between the precursor state, namely mycophagy and the relatively common shifts to pollenophagy, likely facilitated the evolution of this uniquely diverse lineage.

Predation

Our results suggest predation in Cucujiformia has arisen independently least 5 times, occurring in the following lineages: Trogossitidae, Cleridae, Monotomidae (polymorphic), Cucujidae, *Cryptolestes punctatus* (polymorphic) (Laemophloeidae) and in Coccinellidae. The predaceous condition found in Trogossitidae and Cleridae may be the result of a single evolutionary event. Trogossitids and cucujids occur under bark and are predaceous on subcortical insects. The predatory monotomid, *Rhizophagus*, lives in the galleries of scolytine bark beetles where it feeds on the eggs of these beetles (Bousquet, 2010). The larvae of *Trichodes ornatus* prey on bees; adults deposit eggs directly into the hive or more commonly on the bees that frequent the flowers where these beetles often occur (Opitz, 2002). Each of the above predatory niches is fairly specialized. These predatory cleroid and basal cucujoid taxa are relatively species-poor [Cucujidae (< 40 spp.) (Thomas and Leschen, 2010), Trogossitidae (< 100 spp.), *Rhyzophagus* (ca. 50 spp.) (Bousquet, 2010), *Cryptolestes* (only 2 spp. are predaceous) (Thomas and Leschen, 2010)], thus the above transitions from a mycophagous state did not result in a major radiation in these lineages.

In contrast, the transition from mycophagy to predation in Coccinellidae gave rise to the evolution of a lineage comprising over 6000 species (Vandenberg, 2002). Predation in Coccinellidae, in and of itself, may not be the key to diversification of this lineage per se, as this same transition to a predatory life history also occurred in the above cleroid and cucujoid taxa, none of which have resulted in lineage radiation at any comparable scale with that seen in Coccinellidae. Perhaps the key factor of the success of the shift to predation in Coccinellidae (in comparison with remaining predatory groups) lies in the specific predatory niche assumed by coccinellids. Most Coccinellidae prey on Sternorrhyncha (aphids, mealybugs, scale insects, etc.; Hemiptera) (see Giorgi, et al., 2009). Sternorrhynchans are diverse, feed on a huge range of plant hosts and are thus widely distributed, abundant and readily accessible. This host shift resulted in an enormously rapid radiation of coccinellid taxa, particularly within the Coccinellinae sensu Ślipiński (2007) as evidenced by the short internal nodes among major internal groupings (Figure 5.7).

Interestingly, each of the above observed independent shifts to a predatory life history resulted from a mycophagus ancestral state. A mycophagous ancestral state is likely an important precursor for the evolution of predation, and given the constancy of this pattern among the observed shifts herein, this transition series likely represents an important trend in the evolution of cucujiform lineages and Coleoptera in general.

Ectoparsitoidism

Ectoparsitoidism occurs in the family Passandridae and the bothriderid subfamily Bothriderinae. Many hypotheses regarding the transitions to the parasitoid lifestyle in beetle groups have been proposed (e.g., see Eggleton and Belshaw, 1992). The most common ancestral (precursor) state of parasitoidism is thought to be mycophagy; predation is also important.

Our results support the placement of both Passandridae and Bothrideridae within mycophagous clades. This result is more or less consistent with hypotheses for the origin of ecotparasitism in Bothrideridae, however for the family Passandridae ectoparasitoidism is thought to have originated from a predaceous ancestral state in a Cucujidae-like ancestor. Our result refute this hypothesis.

Given the internal relationships among bothriderid and cerylonid taxa (e.g., Bothriderinae sister to the remaining BCD taxa), it is difficult to make any additional concrete inferences regarding the evolution of parasitoidism in Bothrideridae, other than it arose from a mycophagous ancestor. Crowson's (1981) hypothesis including a simple progression from feeding on "microfungi" (*Anommatus*), to Ascomycete feeding (*Xylariophilus*) to feeding upon the Ascomycetes farmed by ambrosia beetles (*Teredolaemus*) to parasitoidism (all bothriderines) is not supported in the present study. This does not preclude the possibility that parasitoidism followed a similar transition series and that stem group bothriderines were indeed commensals in the tunnels of wood boring beetles; rather it is not evident by the present analysis and set of taxa.

Myxomycophagy

We infer 5 independent origins of myxomycophagy among cucujiform lineages. Among Coleoptera, the family Sphindidae is unique in that all its members are strictly myxomycophagous as larvae and adults (Forrester and McHugh, 2010). Myxomycete feeding is not exclusive within the remaining families in which this life history is known to occur. Nonetheless, as our phylogenetic results place members of Sphindidae in two separate lineages, we have to infer two separate origins of myxomycete feeding, in *Protosphindus* and the remaining sphindid taxa. The host data for the sister group to *Protosphindus,* namely Protocucujidae, is unknown. The remaining inferred 3 origins of this feeding type occur within the family Latridiidae. Feeding strategies of latridiids are extremely diverse; most utilize Ascomycetes, Deteromycetes, and Phycomycetes. However, a few genera, *Enicmus*, *Eufallia*, and *Revelieria*, also have a preference for feeding on Myxomycetes, the later genus feeding exclusively on slime molds.

Additionally, there is strong evidence that at least some cerylonine Cerylonidae are myxomycophagous (Ślipiński, 1990). Newton and Stephenson (1990) provided the first concrete observation of myxomycete feeding in Cerylonidae by examining the gut contents of *Spinocerylon mirabilis,* which were packed with spores of its host slime mould. We took a conservative approach and did not code any cerylonids as myxomycophagous (*Spinocerylon* is not represented in the present study). It should be noted that within Cerylonidae there is at least one origin of myxomycete feeding; it remains unknown how widespread this state is throughout the family.

Lichenophagy

Lichenophagy is rather rare among cucujiforms, with only two independent origins of this feeding strategy supported by the current results. One origin of lichenophagy occurs within the family Tenebrionidae; perhaps a better sampling within this family and corresponding superfamily would reveal more instances of lichenophagy. The second occurrence of lichen feeding oringinates in the family Propalticidae. Propalticus is polyphagous, feeding on both lichens and fungi.

Saprophagy

The occurrence of saprophagy is also relatively rare among cucujiform, or at least cucujoid lineages. Here we infer at least two independent origins of this feeding strategy. At least one (maybe more) origins of saprophagy occurred among the Tenebrionoidea, in Salpingidae and Archeocrypticidae. Discolomatidae are also thought to be saprophagous in combination with mycophagous on basidiomycetes. This represents a unique condition in the

C.S. and may have contributed to the diversification of this moderately diverse family comprising 400 species (Cline and Ślipiński, 2010) compared to its sister group Murmidiinae which comprises only 14 species (Ślipiński, 1990).

In summary, we find evidence that Cucujoidea, in its present constitution, is grossly paraphyletic. Our results suggest that Byturidae and Biphyllidae should be transferred to Cleroidea. Lymexylidoidea should be subsumed within Tenebrionoidea. Our results further support the paraphyly of Sphindidae, with most members of this family forming a clade outside the remaining basal Cucujoidea. The family Proplaticidae is supported as a highly derived member of the family Laemophloeidae. We find support that the Cerylonid Series comprises a lineage on a comparable scale to the remaining cucujiform superfamilies; it is not allied with any one of the existing superfamilies of Cucujiformia. In the present analysis the C.S. forms the sister group to the remaining Cucujiformia suggesting it should be recognized as its own superfamily within Cucujiformia, namely Coccinelloidea. The C.S. families Bothrideridae, Cerylonidae, Latridiidae, and Endomychidae are not supported as monophyletic groups and the higher-level classification of these families is in need of revision.

Host shifting has played an important role in the evolution of cucujiform lineages. Many changes in host utilization have led to diverse raditions (e.g. Coccinellidae). In particular, mycophagy appears to represent an important precursor state for facilitating changes in feeding life histories, particularly to a phytophagous or predaceous feeding habit. In host shifts from a mycophagous to Phytophagous life history, Pollenophagy is supported as playing an important role.

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Figure Captions

Table 5.1: Terminal taxa used in the present study.

Table 5.2: Primers and corresponding information for genes used in this study.

Table 5.3: Alignment and sequence statistics for genes and partitions used in this study.

Table 5.4: Host information for the taxa used in this study.

Figure 5.1: Hypothesis of phylogenetic relationships of C.S. taxa after Hunt et al. (2007), Fig. S1, redrawn with condensed terminals.

Figure 5.2: Hypothesis of phylogenetic relationships of C.S. taxa after Robertson et al. (2008), Fig. 2, redrawn with condensed terminals.

Figure 5.3: Maximum likelihood tree of the combined molecular data (part 1 of 5). The full tree is shown at the top of the figure, with the bracketed region enlarged below for discussion. Nodes with a bootstrap value ≥ 70 are indicated by a red box. Parentheses indicate paraphyletic taxa.

Figure 5.4: Maximum likelihood tree of the combined molecular data (part 2 of 5). The full tree is shown at the top of the figure, with the bracketed region enlarged below for discussion. Nodes with a bootstrap value ≥ 70 are indicated by a red box. Parentheses indicate paraphyletic taxa.

Figure 5.5: Maximum likelihood tree of the combined molecular data (part 3 of 5). The full tree is shown at the top of the figure, with the bracketed region enlarged below for discussion. Nodes with a bootstrap value ≥ 70 are indicated by a red box. Parentheses indicate paraphyletic taxa.

Figure 5.6: Maximum likelihood tree of the combined molecular data (part 4 of 5). The full tree is shown at the top of the figure, with the bracketed region enlarged below for discussion. Nodes with a bootstrap value ≥ 70 are indicated by a red box. Parentheses indicate paraphyletic taxa.

Figure 5.7: Maximum likelihood tree of the combined molecular data (part 5 of 5). The full tree is shown at the top of the figure, with the bracketed region enlarged below for discussion. Nodes with a bootstrap value ≥ 70 are indicated by a red box. Parentheses indicate paraphyletic taxa.

Figure 5.8: Maximum likelihood tree of the combined molecular data with host preference data optimized for the terminal taxa using unambiguous optimization. Taxa with unknown host information are shaded gray. Black shading represents equivocal ancestral state reconstruction. An independent host shift to a given food type is indicated by a star. An asterisk represents pollenophagy. Cerylonid Series families and other major taxa are marked.

Table 5.1 Terminal taxa and genes used in this study.

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Derodontoidea	Derodontidae		*Derodontus maculatus*	CO870	X	X	X	X	X	X	X	X	X
Tenebrionoidea	Archeocrypticidae		*Archeocripticus*	CO1016	X	X	X				X		X
Tenebrionoidea	Salpingidae		*Serrotibia*	CO1009	X	X	X	X	X	X	X		
Tenebrionoidea	Mycetophagidae		*Litargus*	CO873	X	X	X	X	X	X	X	X	X
Tenebrionoidea	Tenebrionidae		*Eleodes sulcipennis*	CO031	AY310606	AY310667	X	X	X	X	X	X	
Tenebrionoidea	Tenebrionidae		*Platycotylus?*	CO1010	X	X	X	X	X		X		
Tenebrionoidea	Tenebrionidae		*Hymenorus*	CO172	X	X	X	X	X	X	X	X	X
Tenebrionoidea	Zopheridae		*Bitoma*	CO027	AF423768	AY310661	X		X	X	X	X	X
Lymexyloidea	Lymexylidae		*Atractocerus*		AY748185	DQ202671		DQ202605		DQ222011			
Curculionoidea	Nemonychidae		*Cimberis*		FJ867746	FJ867673		AJ495446		FJ867848			FJ859932
Chrysomeloidea	Cerambycidae		*Parandra*		AJ841538	AJ841667							FJ859979
Chrysomeloidea	Megalopodidae		*Palophagoides*		AF267418	FJ867700				FJ867810			
Chrysomeloidea	Orsodacnidae		*Orsodacne*		AJ781623	FJ867697		AJ781560		AM283241			
Cleroidea	Cleridae		*Trichodes ornatus*	CO048	AF423775	EU145663, EU145713	X	X	X	X	X	X	X
Cleroidea	Melyridae		Melyridae undet.	CO130		X	X	X	X	X			
Cleroidea	Trogossitidae		*Larinotus umblicutus*	CO872	X	X	X	X	X			X	
Cleroidea	Trogossitidae		*Temnoschila virescens*	CO163	EU145654	EU145711, EU145720			X	X	X	X	X
Cucujoidea	Agapythidae		*Agapytho*	CO880	X	X	X	X	X	X	X	X	X
Cucujoidea	Biphyllidae		*Biphyllus?*	CO877	X	X	X	X	X	X	X	X	X
Cucujoidea	Biphyllidae		*Diplocoelus*	CO878	X	X	X	X	X	X		X	X
Cucujoidea	Boganiidae		*Boganium*	ccoc_234		X			X	X	X	X	
Cucujoidea	Boganiidae		*Paracucujus rostratus*	CO875	X	X	X	X	X		X	X	X
Cucujoidea	Byturidae		*Xerasia*	CO876	X	X	X	X	X	X	X	X	X
Cucujoidea	Cryptophagidae		*Atomaria*	CO145	X	X	X	X	X	X	X	X	X
Cucujoidea	Cryptophagidae		*Cryptophagus*	CO146	X	X	X	X	X	X	X	X	X
Cucujoidea	Cucujidae		*Cucujus clavipes*	CO026	AF423767	AY310660	X	X	X	X	X	X	X
Cucujoidea	Erotylidae		*Megalodacne*	CO059	AY310636	AY310697	X			X	X	X	X
Cucujoidea	Erotylidae		*Iphiclus sedicimmaculatus*	CO101	X	X	X	X	X	X	X		
Cucujoidea	Erotylidae		*Pharaxanotha floridana*	CO499	X	X	X	X	X	X	X	X	X
Cucujoidea	Erotylidae		*Pselaphacus nigropunctatus*	CO515	EU164627	EU164657	EU164568	EU164590, X	EU164744	EU164678	EU164712		
Cucujoidea	Hobartiidae		*Hobartius*	CO879	X	X	X		X	X	X	X	X
Cucujoidea	Kateretidae		*Anthonaeus agavensis*	CO636	EU145648	EU145706, EU145717	X	X	X	X	X	X	X
Cucujoidea	Laemophloeidae		*Cryptolestes punctatus*	CO741	X	X	X	X	X	X	X		
Cucujoidea	Laemophloeidae		*Rhabdophloeus*	CO744	X	X	X	X	X	X	X		
Cucujoidea	Laemophloeidae		*Placonotus zimmermani*	CO745	X	X	X	X	X	X	X		
Cucujoidea	Laemophloeidae		*Lathropus vernalis*	CO748	X	X	X	X		X	X		
Cucujoidea	Laemophloeidae		*Laemophloeus biguttatus*	CO755	X	X	X	X	X	X	X		X
Cucujoidea	Laemophloeidae		*Carinophloeus*	CO893	X	X	X	X		X	X	X	X
Cucujoidea	Monotomidae		*Lenax*	CO897	X	X	X		X	X	X	X	X
Cucujoidea	Monotomidae		*Rhizophagus*	CO898	X	X	X	X	X	X	X	X	X
Cucujoidea	Myraboliidae		*Myrabolia*	CO1018	X	X	X			X	X	X	X
Cucujoidea	Nitidulidae		*Carpophilus*	CO071	AY310603	AY310664	X	X	X	X		X	X
Cucujoidea	Nitidulidae		*Epuraea*	CO383	X	X	X	X	X	X	X		

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Cucujoidea	Nitidulidae		*Aethina tumida*	CO352	X	X	X	X	X	X	X		
Cucujoidea	Nitidulidae		Nitidulidae undet.	CO1008	X	X	X	X	X		X		
Cucujoidea	Passandridae		*Catogenus rufus*	CO613	EU145651	EU145709	X	X	X	X	X	X	X
Cucujoidea	Passandridae		*Taphroscelidia*	CO854	X	X	X	X		X			
Cucujoidea	Passandridae		*Passandra heros*	CO894	X	X	X	X		X	X	X	X
Cucujoidea	Phalacridae		*Olibrus*	CO074	EU145652	X	X	X	X	X	X	X	X
Cucujoidea	Phalacridae		*Stilbus nitidus*	CO895	X	X	X	X	X	X	X		X
Cucujoidea	Phloeostichidae		*Hymaea magna*	CO881	X	X			X			X	X
Cucujoidea	Priasilphidae		*Priasilpha obscura*	CO684	AY748179		X	X		X	X	X	X
Cucujoidea	Propalticidae		*Propalticus*	CO896	X	X	X	X	X	X	X	X	X
Cucujoidea	Protocucujidae		*Ericmodes lawrencei*	CO1017	X	X	X			X	X	X	X
Cucujoidea	Protocucujidae		*Ericmodes sylvaticus*		AJ850051	FJ867681		DQ202617		FJ867850			FJ859939
Cucujoidea	Silvanidae		*Psamoecus*	CO1024	X	X	X			X	X		X
Cucujoidea	Silvanidae		*Uleiota dubius*	CO609	EU145653	EU145710	X	X	X	X	X	X	
Cucujoidea	Silvanidae		*Ahasverus advena*	CO610	X	X	X	X	X	X	X	X	X
Cucujoidea	Silvanidae		*Telephanus velox*	CO763	X	X	X	X	X	X	X		
Cucujoidea	Silvanidae		*Silvanus muticus*	CO764	X	X	X	X		X	X		
Cucujoidea	Silvanidae		*Macrohyliota*	CO773	X	X	X	X	X	X	X		
Cucujoidea	Silvanidae		*Oryzaephilus surinamensis*	CO774	X	X	X	X		X	X		
Cucujoidea	Sphindidae		*Aspidiphorus*	CO887	X	X	X	X		X	X		
Cucujoidea	Sphindidae		*Aspidiphorus*	CO888	X	X	X	X	X	X	X		
Cucujoidea	Sphindidae		*Protosphindus bellus*	CO882	X	X	X	X		X	X		
Cucujoidea	Sphindidae		*Protosphindus chilensis*	CO883	X	X	X	X	X	X		X	X
Cucujoidea	Sphindidae		*Sphindus americanus*	CO611	X	X	X	X		X	X		
Cucujoidea	Sphindidae		*Sphindus*	CO884	X	X	X	X		X	X	X	
Cucujoidea	Sphindidae		*Sphindus*	CO885			X	X		X	X		
Cucujoidea	Sphindidae		*Odontosphindus clavicornis*	CO886	X	X	X	X	X	X	X		
Cucujoidea	Sphindidae		*Genisphindus*	CO890			X	X			X		
Cucujoidea	Sphindidae		*Eurysphindus hirtus*	CO891	X	X	X	X	X	X	X		
Cucujoidea	Sphindidae		*Eurysphindus*	CO892	X	X	X	X	X	X	X		
Cucujoidea CS	Alexiidae		*Sphaerosoma*	CO899	X	X	X	X	X	X	X		X
Cucujoidea CS	Bothrideridae	Anommatinae	*Anommatus reitteri*	CO1019	X	X	X				X	X	X
Cucujoidea CS	Bothrideridae	Anommatinae	*Anommatus duodecimstriatus*		AY748140	DQ202627		DQ202527		EF517588			
Cucujoidea CS	Bothrideridae	Bothriderinae	*Acetoderes vittatus*	CO911	X	X	X	X	X	X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Bothrideres*	CO912	X	X	X	X	X	X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Bothrideres*	CO913	X	X	X	X	X	X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Bothrideres geminatus*	CO680	EU145597	EU145658	X	EU164600	EU164735	X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Dastarcus decorus*	CO1021	X	X	X	X		X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Dastarcus helophoroides*	CO906	X	X	X	X	X	X	X		X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Dastarcus vetustus*	CO1020	X	X	X						
Cucujoidea CS	Bothrideridae	Bothriderinae	*Deretaphrus oregonensis*	CO905	X	X	X	X	X		X		
Cucujoidea CS	Bothrideridae	Bothriderinae	*Machlotes*	CO908	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Ogmoderes*	CO907	X	X	X	X	X	X		X	
Cucujoidea CS	Bothrideridae	Bothriderinae	*Pseudobothrideres*	CO910	X	X	X		X	X	X	X	X

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Cucujoidea CS	Bothrideridae	Bothriderinae	*Pseudobothrideres conradsi*	CO909	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus nr. extensus*	CO666	EU145595	EU145656	X	X	X	X		X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus sp. 1*	CO667	EU145596	EU145657		X	X	X	X	X	X
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus sp. 2*	CO665	EU145594	EU145655	X	X					
Cucujoidea CS	Bothrideridae	Teredinae	*Oxylaemus californicus*	CO902	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Bothrideridae	Teredinae	*Teredolaemus leae*	CO903	X	X	X		X	X	X	X	X
Cucujoidea CS	Bothrideridae	Xylariophilinae	*Xylariophilus bicolorpennis*	CO900	X	X	X		X	X	X	X	
Cucujoidea CS	Bothrideridae	Xylariophilinae	*Xylariophilus sp. nov*	CO901	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Ceryloninae	*Afrorylon sp. 1*	CO928	X	X	X	X	X	X	X	X	
Cucujoidea CS	Cerylonidae	Ceryloninae	*Afrorylon sp. 2*	CO929	X	X	X	X	X	X	X		
Cucujoidea CS	Cerylonidae	Ceryloninae	*Australiorylon*	CO311	EU145598	EU145659, EU145712	EU164555	EU164589	EU164737	EU164677	EU164710		
Cucujoidea CS	Cerylonidae	Ceryloninae	*Cerylon canstaneum*	CO598	EU145599	EU145660	X	X		X			X
Cucujoidea CS	Cerylonidae	Ceryloninae	*Cerylon unicolor*	CO599	EU145600	EU145661	X	X		X	X		X
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus*	CO932	X		X	X	X	X	X	X	
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus*	CO933	X	X	X		X	X	X	X	
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus discretus*	CO931	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 1*	CO925	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 2*	CO927	X	X	X	X	X	X	X		
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 3*	CO926	X	X	X	X		X	X	X	
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermus*	CO930			X	X	X		X	X	
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermus glabriculus*	CO681	EU145601	EU145662	EU164556	EU164586	EU164733	EU164676	X	X	
Cucujoidea CS	Cerylonidae	Euxestinae	*Metacerylon brevicolle*	CO1023	X	X				X	X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestoxenus*	CO916	X	X	X	X	X	X	X		X
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacne punctata*	CO917	X	X	X		X	X	X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella rubriceps*	CO918	X	X	X		X	X	X		
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella bivulnerata*	CO919	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella*	CO920	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO921	X	X	X	X	X	X	X		
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO922	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO923	X	X	X	X	X		X	X	X
Cucujoidea CS	Cerylonidae	Euxestinae	*Cycloxenus*	CO924	X	X	X	X	X		X	X	X
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO1013	X	X	X				X		
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO1022	X		X	X		X			
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO915	X	X	X	X	X	X	X		X
Cucujoidea CS	Cerylonidae	Ostomopsinae	*Ostomopsis*	CO1012	X	X	X	X	X	X	X	X	
Cucujoidea CS	Cerylonidae	Ostomopsinae	*Ostomopsis*	CO914	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Chilocorinae	*Chilocorus cacti*	CO573	EU145610	X	X	X		X	X		
Cucujoidea CS	Coccinellidae	Chilocorinae	*Exochomus*	CO722	X	X	X	X	X			X	
Cucujoidea CS	Coccinellidae	Chilocorinae	*Halmus chalybeus*	CO467	EU145607	EU145669	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Chilocorinae	*Halmus coelestris*	CO578	X	X	X		X	X	X	X	
Cucujoidea CS	Coccinellidae	Chilocorinae	*Orcus bilunulatus*	CO815	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Chilocorinae	*Orcus lafertei*	CO587	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Chilocorinae	*Platynaspis*	CO630	EU145619	EU145678	X	X		X	X		X
Cucujoidea CS	Coccinellidae	Chilocorinae	*Telsimia*	CO731	X	X	X	X	X	X	X	X	

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	**Family**	**Subfamily/Tribe**	**Species**	**Voucher**	**18S**	**28S**	**12S**	**16S**	**H3**	**COI**	**COII**	**CAD**	**ArgK**
Cucujoidea CS	Coccinellidae	Coccidulinae	*Monocoryna*	AG01	X	X	X		X	X	X		X
Cucujoidea CS	Coccinellidae	Coccidulinae	*Azya orbigera*	AG03	X	X	X	X					
Cucujoidea CS	Coccinellidae	Coccidulinae	*Anovia*	AGNM01	X	X	X			X	X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Nothocolus*	AGNM02	X	X		X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccidulinae	*Neorhizobius*	AGNM03		X	X	X		X	X		
Cucujoidea CS	Coccinellidae	Coccidulinae	*Chnoodes*	CO465	EU145606	EU145668	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Cryptolaemus*	AG05	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Coccidulinae	*Oridia pubescens*	CO721	X	X	X	X		X	X	X	X
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rodolia*	CO723	X	X	X	X		X	X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rhyzobius*	CO728	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rhyzobius lophantae*	CO451	X	X	X		X		X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rodolia*	CO813	X	X	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Coccidulinae	*Coccidula*	CO824	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccidulinae	*Bucolus*	CO828	X	X	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Coccidulinae	*Cranophorus*	AG02?	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Anatis abiculata*	CO446	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccinellinae	*Bothrocalvia albolineata*	CO586	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Bulaea anceps*	AG04	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinella septempunctata*	CO615	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinella transversalis*	CO571	EU145609	EU145670	X	X		X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinellini*	CO468	X	X	X	X		X	X		X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coleomegilla strenua*	CO445	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coleophora bisselata*	CO581	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccinellinae	*Cycloneda sanguinea*	CO443	EU145602	EU145664	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Cycloneda sanguinea*	CO463	X	X	X	X		X	X		X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Harmonia axyridis*	CO453	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccinellinae	*Harmonia euchris*	CO575	EU145612	EU145672	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Hippodamia convergens*	CO627	EU164617	EU164644	EU164553	EU164588	EU164743	EU164681	EU164707	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Hippodamia quinquesignata*	CO450	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Illeis*	CO461	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Illeis*	CO466	X	X	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Micraspis*	CO459	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Mulsantina*	CO460	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Myzia pullata*	CO444	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Coccinellinae	*Olla v-nigrum*	CO464	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Coccinellinae	*Pristonema*	AG06	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Psyllobora*	CO304	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Coccinellinae	*Psyllobora vigintimaculata*	CO455	EU145604	EU145666	X	X	X	X		X	
Cucujoidea CS	Coccinellidae	Epilachninae	*Cynegetini*	CO470	EU145608	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Epilachninae	*Epilachna*	CO616	EU145616	EU145675	X		X	X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Apolinus*	CO821	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Scymninae	*Cryptogonus*	CO737	X	X	X	X		X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Aspidimerus*	CO730	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Brachiacantha*	CO725	X	X	X	X		X	X		X
Cucujoidea CS	Coccinellidae	Scymninae	*Cryptognatha*	CO727	X	X	X	X		X	X	X	X

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Cucujoidea CS	Coccinellidae	Scymninae	*Decadiomis*	CO733	X		X			X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis kameryunensis*	CO818	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis notescens*	CO825	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis terminatus*	CO629	EU145618	EU145677	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Hyperaspidius mimus*	CO570	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Hyperaspis lateralis*	CO572	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Scymninae	*Nephaspis*	AGNM09	X	X	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Scymninae	*Nephus*	CO589	X	X	X		X	X	X	X	
Cucujoidea CS	Coccinellidae	Scymninae	*Ortalia*	CO827	EU145621	EU145680	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Ortalia horni*	CO582	EU145614	X	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Scymninae	*Poria*	CO720	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Scymninae	*Sasajiscymnus tsugae*	CO583	EU145615	EU145674	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnini*	CO826	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnus*	CO449	EU145603	EU145665	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnus*	CO628	X	/	X	X	X	X	X		X
Cucujoidea CS	Coccinellidae	Scymninae	*Selvadius*	CO822	X	X	X		X	X	X	X	X
Cucujoidea CS	Coccinellidae	Scymninae	*Stethorus*	CO617	EU145617	EU145676	X	X		X	X	X	X
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Serrangium*	CO631	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Cephaloscymnus*	AGMN07		X	X						
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Chilocorellus*	AGNM04	X	X	X		X	X	X	X	X
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Coccidophilus*	AGMN05	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Delphastus*	CO577	X	X	X	X	X	X	X	X	
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Exochomus 4-pustulatus*	CO726	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Ghanius*	AG08	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Parasitis*	AGNM06	X	X			X		X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	Plotinini	AGNM08	X	X	X		X	X	X	X	
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sarapidus australis*	AG09	X	X	X	X		X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Shirozuellini*	CO1015	X	X	X		X	X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sticholotis*	CO457	X	X	X	X	X	X	X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sticholotis*	CO588	X	X	X		X	X	X	X	
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sukuhanikona*	AG07		X	X	X	X		X		
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sulcolotis*	CO829	X	X	X	X		X	X	X	
Cucujoidea CS	Corylophidae	Periptyctinae	*Periptyctus*	CO940	X	X	X	X	X	X	X		X
Cucujoidea CS	Corylophidae	Aenigmaticini	*Aenigmaticum californicus*	CO934	X	X	X	X		X	X		
Cucujoidea CS	Corylophidae	Aenigmaticini	*Stanus bowsteadi*	CO964	X	X	X	X		X	X	X	X
Cucujoidea CS	Corylophidae	Corylophini	*Corylophus?*	CO972	X	X		X		X	X		X
Cucujoidea CS	Corylophidae	Foadiini	*Foadia*	CO608	X		X	X			X		
Cucujoidea CS	Corylophidae	Foadiini	*Priamima*	CO962	X	X	X		X	X	X	X	X
Cucujoidea CS	Corylophidae	Foadiini	*Priamima??*	CO963	X	X	X	X	X	X	X		X
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO607	EU145626	EU145685	X			X	X		
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO959	X	X	X	X	X	X	X		
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO961	X	X	X	X		X	X	X	
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea fasciata*	CO603	EU145622	EU145681	X	X	X	X	X	X	X
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea lunata*	CO604	EU145623	EU145682	X	X	X	X	X		
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea*	CO946	X	X	X	X		X	X	X	X
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea*	CO947	X	X	X		X	X	X		

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	**Family**	**Subfamily/Tribe**	**Species**	**Voucher**	**18S**	**28S**	**12S**	**16S**	**H3**	**COI**	**COII**	**CAD**	**ArgK**
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO949	X	X	X	X	X	X	X		X
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO950	X	X	X	X		X	X	X	
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO951	X	X	X	X		X	X		
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO952	X	X	X	X	X	X	X		
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO941	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis* nr. *rotundata*	CO942	X	X	X		X		X		
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO943	X	X	X	X	X	X	X		
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis?*	CO944	X	X	X	X	X	X	X	X	
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO945	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO956	X	X	X			X	X	X	X
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO965	X	X	X	X		X	X	X	X
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO966	X	X	X				X	X	X
Cucujoidea CS	Corylophidae	Rypobiini	*Hoplicnema*	CO967	X	X	X	X	X	X	X	X	
Cucujoidea CS	Corylophidae	Rypobiini	*Hoplicnema*	CO968	X	X	X	X	X	X	X	X	
Cucujoidea CS	Corylophidae	Rypobiini	*Catoptyx*	CO969	X	X	X	X		X	X	X	
Cucujoidea CS	Corylophidae	Rypobiini	*Gloeosoma*	CO970	X	X	X					X	X
Cucujoidea CS	Corylophidae	Rypobiini	*Gloeosoma?*	CO971	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus lateralis*	CO605	EU145624	EU145683, EU145715	X	X	X	X	X	X	X
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO606	EU145625	EU145684	X	X		X	X		X
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO953	X	X	X	X	X	X	X		
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO954	X	X	X	X		X	X		
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO955	X	X	X		X	X	X	X	
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus (Anisomeristes)*	CO957	X	X	X	X		X	X		
Cucujoidea CS	Corylophidae	Sericoderini	*Aposericoderus?*	CO958	X	X	X	X		X	X	X	X
Cucujoidea CS	Corylophidae	Corylophidae undet.	Corylophidae undet.	CO973	X	X	X	X	X	X	X		X
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO600	EU145628	EU145687	EU164554	EU164591	EU164734	EU164675	EU164711	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO601	EU145629	EU145688	X	X	X	X	X	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO935	X	X	X	X		X	X	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO936	X	X	X	X	X	X	X	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO937	X	X	X			X	X	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO938	X	X	X	X	X	X	X	X	
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO602	EU145630	X	X			X	X	X	
Cucujoidea CS	Discolomatidae	Discolomatinae	*Cassidoloma*	CO939	X	X	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus sp. 2*	CO786	X	X	X	X	X				
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus sp.1*	CO649	EU145636	EU145694	X		X			X	X
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus tenuicornis*	CO778	X	X	X	X		X	X	X	X
Cucujoidea CS	Endomychidae	Anamorphinae	*Bystus piceus*	CO320	EU145632	EU145690	X	X		X	X	X	
Cucujoidea CS	Endomychidae	Anamorphinae	*Bystus sp. nov*	CO787	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Endomychidae	Anamorphinae	*Catapotia sp. 1*	CO983	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Anamorphinae	*Clemmus minor*	CO713	X					X			
Cucujoidea CS	Endomychidae	Anamorphinae	*Geoendomychus*	CO974	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Anamorphinae	*Idiophyes nr. Brevis*	CO975	X	X	X	X			X		X
Cucujoidea CS	Endomychidae	Anamorphinae	*Micropsephodes lundgreni*	CO705	X	X	X	X	X	X			
Cucujoidea CS	Endomychidae	Anamorphinae	*Mychothenus tropicalis*	CO715	X	X	X	X		X	X	X	X
Cucujoidea CS	Endomychidae	Anamorphinae	*Papuella birolecta*	CO804	X	X	X	X	X	X	X		X

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Cucujoidea CS	Endomychidae	Anamorphinae	*Symbiotes gibberosus*	CO986	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Endomychinae	*Endomychus biguttatus*	CO657	EU145643	EU145701	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Endomychinae	*Endomychus*	CO789	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Endomychinae	*Meilichius*	CO800	X	X	X	X	X	X			
Cucujoidea CS	Endomychidae	Endomychinae	*Cyclotoma cingalensis*	CO980	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Endomychidae	Epipocinae	*Anidrytus*	CO654	EU145640	EU145698	X	X	X	X			
Cucujoidea CS	Endomychidae	Epipocinae	*Anidrytus*	CO779	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Epipocinae	*Epipocus*	CO790	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Epipocinae	*Epipocus*	CO791	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Epipocinae	*Epopterus testudinarius*	CO792	X	X	X	X		X	X		
Cucujoidea CS	Endomychidae	Eupsilobiinae	*Chileolobius*	CO1014	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Leiestinae	*Rhanidea unicolor*	CO708	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Leiestinae	*Phymaphora pulchella*	CO806	X	X	X		X	X	X		X
Cucujoidea CS	Endomychidae	Leiestinae	*Phymaphora californica*	CO987	X	X	X		X	X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Acinaces laceratus*	CO660	EU145646	EU145704	X		X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphisternus*	CO658	EU145644	EU145702	X	X	X	X			X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphisternus*	CO777	X	X	X	X		X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix laevigatus*	CO318	EU164639	EU164646	EU164558	X	EU164731	EU164679	EU164709	X	X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix tarsatus*	CO661	EU145647	EU145705	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix vestitus cinctus*	CO317	X	X	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Lycoperdininae	*Ancylopus melanocephalus*	CO776	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Aphorista morosa*	CO781	X	X	X	X		X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Aphorista vittata*	CO700	X	X	X			X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Beccariola*	CO717	X	X	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Lycoperdininae	*Encymon gorhami*	CO648	EU145635	EU145693	X			X			X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Encymon immaculatus*	CO788	X	X	X	X		X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Eumorphus*	CO795	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Eumorphus quadriguttatus*	CO794	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Hylaia*	CO831	X	X	X	X	X	X			X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Indalmus*	CO798	X	X	X		X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Indalmus lineelus*	CO714	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Lycoperdininae	*Lycoperdina ferruginea*	CO650	EU145637	EU145695	X			X			X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Mycetina*	CO803	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Mycetina horni*	CO655	EU145641	EU145699	X		X	X			X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Pseudindalmus*	CO807	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Lycoperdininae	*Trycherus*	CO703	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Merophysiinae	*Holoparamecus*	CO710	X	X	X	X		X	X	X	X
Cucujoidea CS	Endomychidae	Merophysiinae	*Holoparamecus*	CO976	X	X	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Merophysiinae	*Lycoperdinella subcaeca*	CO985	X	X	X				X	X	
Cucujoidea CS	Endomychidae	Mycetaeinae	*Mycetaea subterranea*	CO984	X	X	X	X	X	X	X	X	X
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus boliviensis*	CO711	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus*	CO977	X	X	X	X		X	X	X	
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus goudoti*	CO981	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO323	EU145634	EU145692	X	X	X	X	X		X

Table 5.1 Terminal taxa and genes used in this study (continued).

Superfamily	Family	Subfamily/Tribe	Species	Voucher	18S	28S	12S	16S	H3	COI	COII	CAD	ArgK
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO330	X	X	X	X	X	X	X		
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO332	X	X	X	X	X	X	X	X	
Cucujoidea CS	Endomychidae	Stenotarsinae	*Chondria armipes*	CO652	EU145638	EU145696	X	X		X		X	X
Cucujoidea CS	Endomychidae	Stenotarsinae	*Chondria nigra*	CO653	EU145639	EU145697	X	X	X	X		X	X
Cucujoidea CS	Endomychidae	Stenotarsinae	*Danae*	CO702	X	X	X		X	X	X	X	X
Cucujoidea CS	Endomychidae	Stenotarsinae	*Danae testacea*	CO709	X	X	X	X	X	X	X		X
Cucujoidea CS	Endomychidae	Stenotarsinae	*Saula*	CO808	X	X	X		X		X		X
Cucujoidea CS	Latridiidae	Corticariinae	*Corticaria ferruginea*	CO593	EU164637	EU164668	EU164582	EU164612	EU164757	EU164703	EU164728		
Cucujoidea CS	Latridiidae	Corticariinae	*Corticarina*	CO486	EU164622	EU164664	EU164577	EU164613	EU164752	EU164702	EU164727	X	X
Cucujoidea CS	Latridiidae	Corticariinae	*Corticarina*	CO580	EU164626	EU164666	EU164578	EU164602	EU164755	EU164697	EU164725	X	
Cucujoidea CS	Latridiidae	Corticariinae	*Cortinicara*	CO592	EU164615	EU164662	EU164583	EU164611	EU164754	EU164706		X	
Cucujoidea CS	Latridiidae	Corticariinae	*Fuchsina occulta*	CO638	EU164630	EU164667	EU164576		EU164756	EU164701	EU164724		
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO481	EU164632	EU164670	EU164564	EU164599	EU164738	EU164696	EU164719		
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO594	EU164633	EU164672	EU164566	EU164593	EU164739	EU164698	EU164721		X
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO595	EU164635	EU164671	EU164565	EU164594	EU164740	EU164700	EU164723		X
Cucujoidea CS	Latridiidae	Corticariinae	*Migneauxia orientalis*	CO590	EU164636	EU164665	EU164579	EU164601	EU164753	EU164704	EU164726		
Cucujoidea CS	Latridiidae	Latridiinae	*Aridius nodifer*	CO482	EU164641	EU164656	EU164581	EU164605	EU164751	EU164689	EU164718		X
Cucujoidea CS	Latridiidae	Latridiinae	*Cartodere constrictus*	CO596	EU164640	EU164655	EU164580	EU164606	EU164750	EU164690	EU164714		X
Cucujoidea CS	Latridiidae	Latridiinae	*Dienerella intermedia*	CO488	EU164638	EU164647	EU164557	EU164603	EU164747	EU164691		X	X
Cucujoidea CS	Latridiidae	Latridiinae	*Enicmus aterrimus*	CO693	EU164629	EU164652	EU164570	EU164609		EU164687	EU164716		
Cucujoidea CS	Latridiidae	Latridiinae	*Enicmus maculatus*	CO692	EU164628	EU164653	EU164571	EU164585		EU164688	EU164715		X
Cucujoidea CS	Latridiidae	Latridiinae	*Eufallia seminiveus*	CO484	EU164614	EU164645	EU164551	EU164596	EU164746	EU164674		X	X
Cucujoidea CS	Latridiidae	Latridiinae	*Latridius crenatus*	CO483	EU164623	EU164654	EU164574	EU164607	EU164749	EU164685	EU164717		X
Cucujoidea CS	Latridiidae	Latridiinae	*Metopthalmus haigi*	CO480	EU164643	EU164649	EU164569	EU164595	EU164745	EU164694			X
Cucujoidea CS	Latridiidae	Latridiinae	*Revelieria californica*	CO477	EU164642	EU164648	EU164563	EU164598	EU164736	EU164686	EU164713		
Cucujoidea CS	Latridiidae	Latridiinae	*Stephostethus lardarius*	CO473	EU164625	EU164651	EU164573	EU164608	EU164748	EU164693	EU164729		
Cucujoidea CS	Latridiidae	Latridiinae	*Stephostethus liratus*	CO476	EU164624	EU164650	EU164559	EU164604		EU164692	EU164730		X
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion sleeperi*	CO697	EU164619	EU164659	EU164561	EU164587	EU164742		X	X	X
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion anasillos*	CO698	EU164618	EU164658	EU164575			EU164682	X	X	X
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion atrichos*	CO699	EU164620	EU164660	EU164560		EU164741	EU164684			X

Taxa lacking a primary voucher number represent taxa and corresponding sequences that were not generated by our research group but were obtained from GenBank.
Genbank accession numbers will be provided upon acceptance.

Table 5.2 Primers and corresponding information for genes used in this study.

Gene	Primer	Direction	Sequence (5'- 3')	Length	Annealing temp	DMSO
12S	12S ai	Forward	AAACTACGATTAGATACCCTATTAT	25	50° C	No
	12S bi	Reverse	AAGAGCGACGGGCGATGTGT	20		
16S	16S A	Forward	CGCCTGTTTATCAAAAACAT	20	50° C	No
	16S B	Reverse	CTCCGGTTTGAACTCAGATCA	21		
COI	Mtd6	Forward	GGAGGATTTGGAAATTGATTAGTTCC	26	50° C	No
	Pat	Reverse	TCCAATGCACTAATCTGCCATATTA	25		
COII	F-leu	Forward	TCTAATATGGCAGATTAGTGC	21	50° C	No
	9b	Reverse	GTACTTGCTTTCAGTCATCTWATG	24		
	R-lys	Reverse	GAGACCAGTACTTGCTTTCAGTCATC	26		
18S	18S 1F	Forward	TACCTGGTTGATCCTGCCAGTAG	23	54-56° C	Yes
	18S b3.0	Reverse	GACGGTCCAACAATTTCACC	20		
	18S a0.7	Forward	ATTAAAGTTGTTGCGGTT	18		
	18S bi	Reverse	GAGTCTCGTTCGTTATCGGA	20		
	18S a2.0	Forward	ATGGTTGCAAAGCTGAAAC	19		
	18S 9R	Reverse	GATCCTTCCGCAGGTTCACCTAC	23		
28S	28S Rd 1a	Forward	CCCSCGTAAYTTAGGCATAT	20	54° C	Yes
	28S C	Reverse	ATAGTTCACCATCTYTCGGG	20		
	28S A	Forward	GACCCGTCTTGAAGCACG	18		
	28S Rd 5b	Reverse	CCACAGCGCCAGTTCTGCTTAC	22		
	28S Rd 4.8a	Forward	ACCTATTCTCAAACTTTAAATGG	23		
	28S Rd 7b1	Reverse	GACTTCCCTTACCTACAT	18		
H3	H3 AF	Forward	ATGGCTCGTACCAAGCAGACVGC	23	50° C	Yes
	H3 AR	Reverse	ATATCCTTRGGCATRATRGTGAC	23		
CAD	CD338F	Forward	ATGAARTAYGGYAATCGTGGHCAYAA	26	50° C	Yes
	CD668R	Reverse	ACGACTTCATAYTCNACYTCYTTCCA	26		
	CS688R	Reverse	TGTATACCTAGAGGATCDACRTTYTCCATRTTRCA	35		
ArgK	ArgK forB2	Forward	GAYTCCGGWATYGGWATCTAYGCTCC	26	50° C	Yes
	ArgK forB4	Forward	GAYCCCATCATCGARGACTACC	22		
	ArgK revB1	Reverse	TCNGTRAGRCCCATWCGTCTC	21		

Table 5.3 Alignment and sequence statistics for genes and partitions used in this study.

	18S	28S	12S	16S	H3	COI	COII	CAD	AK	Combined
Prealigned length range*	1856-1982	1706-2801	334-360	492-516	NA	NA	603-624	930-966	NA	NA
Aligned length	2305	3814	411	553	327	1239	639	1005	729	11022
Variable sites	978	2263	329	383	162	799	478	723	393	6508
Informative sites	758	1708	296	342	142	742	456	654	355	5453
Frequency A	0.246603	0.238418	0.390392	0.364864	0.270197	0.308664	0.347612	0.320538	0.285267	0.281426
Frequency C	0.234671	0.241939	0.061550	0.087920	0.272734	0.158471	0.147509	0.193064	0.235975	0.201518
Frequency G	0.274589	0.303577	0.132763	0.153697	0.249923	0.140898	0.110232	0.216521	0.233299	0.231669
Frequency T	0.244137	0.216065	0.415296	0.393519	0.207145	0.391967	0.394647	0.269877	0.245459	0.285387
AIC	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G
# taxa	333	333	326	276	244	309	293	171	157	341

* For length-variable protein coding genes this only includes the exon fragment.

Table 5.4 Host information for the taxa used in this study.

Superfamily	Family	Subfamily/Tribe	Species	Voucher	Trophic group/Host info
Derodontoidea	Derodontidae		*Derodontus maculatus*	CO870	Mycophagous: Basidiomycetes
Tenebrionoidea	Archeocrypticidae		*Archeocrypticus*	CO1016	Saprophagous: Leaf litter; Mycophagous?
Tenebrionoidea	Salpingidae		*Serrotibia*	CO1009	Saprophagous: Decaying vegetation; Mycophagous?
Tenebrionoidea	Mycetophagidae		*Litargus*	CO873	Mycophagous: Ascomycetes (usually for Litargus); Basidiomycetes (for many Mycetophagids)
Tenebrionoidea	Tenebrionidae		*Eleodes sulcipennis*	CO031	"Euryphagous" (i.e., omnivorous on organic material)
Tenebrionoidea	Tenebrionidae		*Platycotylus?*	CO1010	Xylo-mycetophagous (i.e., fungus permeated rotten wood)
Tenebrionoidea	Tenebrionidae		*Hymenorus*	CO172	Lichenophagous
Tenebrionoidea	Zopheridae		*Bitoma*	CO027	Mycophagous: Ascomycetes
Lymexyloidea	Lymexylidae		*Atractocerus*		Xylophagous
Curculionoidea	Nemonychidae		*Cimberis*		Phytophagous: Pollenivorous @
Chrysomeloidea	Cerambycidae		*Parandra*		Phytophagous @
Chrysomeloidea	Megalopodidae		*Palophagoides*		Phytophagous @
Chrysomeloidea	Orsodacnidae		*Orsodacne*		Phytophagous: Pollenivorous @
Cleroidea	Cleridae		*Trichodes ornatus*	CO048	Predacious
Cleroidea	Melyridae		Melyridae undet.	CO130	[can't score without better ID]
Cleroidea	Trogossitidae		*Larinotus umblicutus*	CO872	Mycophagous? (in decaying leaf litter) @
Cleroidea	Trogossitidae		*Temnoschila virescens*	CO163	Predacious (on bark beetles)
Cucujoidea	Agapythidae		*Agapytho*	CO880	Mycophagous: Ascomycetes (on sooty mold on Margarodidae exudates)
Cucujoidea	Biphyllidae		*Biphyllus?*	CO877	Mycophagous
Cucujoidea	Biphyllidae		*Diplocoelus*	CO878	Mycophagous
Cucujoidea	Boganiidae		*Boganium*	ccoc_234	Phytophagous: Pollenivorous
Cucujoidea	Boganiidae		*Paracucujus rostratus*	CO875	Phytophagous: Pollenivorous (on cycads)
Cucujoidea	Byturidae		*Xerasia*	CO876	Phytophagous: Pollenivorous (at least as larvae), adults reported from oak galls
Cucujoidea	Cryptophagidae		*Atomaria*	CO145	Mycophagous
Cucujoidea	Cryptophagidae		*Cryptophagus*	CO146	Mycophagous
Cucujoidea	Cucujidae		*Cucujus clavipes*	CO026	Predacious
Cucujoidea	Erotylidae		*Megalodacne*	CO059	Mycophagous: Basidiomycetes !
Cucujoidea	Erotylidae		*Iphiclus sedicimmaculatus*	CO101	Mycophagous: Basidiomycetes !
Cucujoidea	Erotylidae		*Pharaxanotha floridana*	CO499	Phytophagous: Pollenivorous (on cycads) !
Cucujoidea	Erotylidae		*Pselaphacus nigropunctatus*	CO515	Mycophagous: Basidiomycetes !
Cucujoidea	Hobartiidae		*Hobartius*	CO879	Mycophagous
Cucujoidea	Kateretidae		*Anthonaeus agavensis*	CO636	Phytophagous: Antherophagous ("flower feeding"), (on yucca)
Cucujoidea	Laemophloeidae		*Cryptolestes punctatus*	CO741	Mycophagous? Predacious?
Cucujoidea	Laemophloeidae		*Rhabdophloeus*	CO744	Mycophagous?
Cucujoidea	Laemophloeidae		*Placonotus zimmermani*	CO745	Mycophagous?
Cucujoidea	Laemophloeidae		*Lathropus vernalis*	CO748	Mycophagous?
Cucujoidea	Laemophloeidae		*Laemophloeus biguttatus*	CO755	Mycophagous?
Cucujoidea	Laemophloeidae		*Carinophloeus*	CO893	Mycophagous?
Cucujoidea	Monotomidae		*Lenax*	CO897	Mycophagous?
Cucujoidea	Monotomidae		*Rhizophagus*	CO898	Mycophagous? Predacious?
Cucujoidea	Myraboliidae		*Myrabolia*	CO1018	???
Cucujoidea	Nitidulidae		*Carpophilus*	CO071	Mycophagous??? need better ID
Cucujoidea	Nitidulidae		*Epuraea*	CO383	Mycophagous??? need better ID
Cucujoidea	Nitidulidae		*Aethina tumida*	CO352	Phytophagous (stealing pollen and other plant material in bee nests)
Cucujoidea	Nitidulidae		Nitidulidae undet.	CO1008	??? need better ID
Cucujoidea	Passandridae		*Catogenus rufus*	CO613	Predacious (ectoparasites)
Cucujoidea	Passandridae		*Taphroscelidia*	CO854	Predacious (ectoparasites)???
Cucujoidea	Passandridae		*Passandra heros*	CO894	Predacious (ectoparasites)
Cucujoidea	Phalacridae		*Olibrus*	CO074	Phytophagous: Pollenivorous@

Table 5.4 (continued) Host information for the taxa used in this study.

Superfamily	Family	Subfamily/Tribe	Species	Voucher	Trophic group/Host info
Cucujoidea	Phalacridae		*Stilbus nitidus*	CO895	Mycophagous
Cucujoidea	Phloeostichidae		*Hymaea magna*	CO881	???
Cucujoidea	Priasilphidae		*Priasilpha obscura*	CO684	Mycophagous
Cucujoidea	Propalticidae		*Propalticus*	CO896	Mycophagous? Lichenophagous
Cucujoidea	Protocucujidae		*Ericmodes lawrencei*	CO1017	???
Cucujoidea	Protocucujidae		*Ericmodes sylvaticus*		???
Cucujoidea	Silvanidae		*Psamoecus*	CO1024	Mycophagous
Cucujoidea	Silvanidae		*Uleiota dubius*	CO609	Mycophagous
Cucujoidea	Silvanidae		*Ahasverus advena*	CO610	Phytophagous (stored products)
Cucujoidea	Silvanidae		*Telephanus velox*	CO763	Mycophagous
Cucujoidea	Silvanidae		*Silvanus muticus*	CO764	Mycophagous
Cucujoidea	Silvanidae		*Macrohyliota*	CO773	Mycophagous
Cucujoidea	Silvanidae		*Oryzaephilus surinamensis*	CO774	Phytophagous (stored products)
Cucujoidea	Sphindidae		*Aspidiphorus*	CO887	Myxomycophagous
Cucujoidea	Sphindidae		*Aspidiphorus*	CO888	Myxomycophagous
Cucujoidea	Sphindidae		*Protosphindus bellus*	CO882	Myxomycophagous
Cucujoidea	Sphindidae		*Protosphindus chilensis*	CO883	Myxomycophagous
Cucujoidea	Sphindidae		*Sphindus americanus*	CO611	Myxomycophagous
Cucujoidea	Sphindidae		*Sphindus*	CO884	Myxomycophagous
Cucujoidea	Sphindidae		*Sphindus*	CO885	Myxomycophagous
Cucujoidea	Sphindidae		*Odontosphindus clavicornis*	CO886	Myxomycophagous
Cucujoidea	Sphindidae		*Genisphindus*	CO890	Myxomycophagous
Cucujoidea	Sphindidae		*Eurysphindus hirtus*	CO891	Myxomycophagous
Cucujoidea	Sphindidae		*Eurysphindus*	CO892	Myxomycophagous
Cucujoidea CS	Alexiidae		*Sphaerosoma*	CO899	Mycophagous (Basidiomycetes: Agaricales)
Cucujoidea CS	Bothrideridae		*Anommatus reitteri*	CO1019	???
Cucujoidea CS	Bothrideridae		*Anommatus duodecimstriatus*		???
Cucujoidea CS	Bothrideridae		*Acetoderes vittatus*	CO911	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Bothrideres*	CO912	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Bothrideres*	CO913	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Bothrideres geminatus*	CO680	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Dastarcus decorus*	CO1021	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Dastarcus helophoroides*	CO906	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Dastarcus vetustus*	CO1020	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Deretaphrus oregonensis*	CO905	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Machlotes*	CO908	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Ogmoderes*	CO907	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae		*Pseudobothrideres*	CO910	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae	Bothriderinae	*Pseudobothrideres conradsi*	CO909	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus nr. extensus*	CO666	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus sp. 1*	CO667	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae	Bothriderinae	*Sosylus sp. 2*	CO665	Predacious (ectoparasite) #
Cucujoidea CS	Bothrideridae	Teredinae	*Oxylaemus californicus*	CO902	Mycophagous #
Cucujoidea CS	Bothrideridae	Teredinae	*Teredolaemus leae*	CO903	Mycophagous #
Cucujoidea CS	Bothrideridae	Xylariophilinae	*Xylariophilus bicolorpennis*	CO900	Mycophagous #
Cucujoidea CS	Bothrideridae	Xylariophilinae	*Xylariophilus sp. nov*	CO901	Mycophagous #
Cucujoidea CS	Cerylonidae	Ceryloninae	*Afrorylon sp. 1*	CO928	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Afrorylon sp. 2*	CO929	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Australiorylon*	CO311	Mycophagous

Table 5.4 (continued) Host information for the taxa used in this study.

Superfamily	**Family**	**Subfamily/Tribe**	**Species**	**Voucher**	**Trophic group/Host info**
Cucujoidea CS	Cerylonidae	Ceryloninae	*Cerylon canstaneum*	CO598	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Cerylon unicolor*	CO599	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus*	CO932	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus*	CO933	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Mychocerus discretus*	CO931	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 1*	CO925	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 2*	CO927	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermopsis sp. 3*	CO926	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermus*	CO930	Mycophagous
Cucujoidea CS	Cerylonidae	Ceryloninae	*Philothermus glabriculus*	CO681	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Metacerylon brevicolle*	CO1023	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestoxenus*	CO916	Mycophagous (termite inquiline?)
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacne punctata*	CO917	Mycophagous (ant inquiline)
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella rubriceps*	CO918	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella bivulnerata*	CO919	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Hypodacnella*	CO920	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO921	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO922	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Euxestus*	CO923	Mycophagous
Cucujoidea CS	Cerylonidae	Euxestinae	*Cycloxenus*	CO924	Mycophagous (termite inquiline?)
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO1013	Mycophagous
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO1022	Mycophagous
Cucujoidea CS	Cerylonidae	Murmidiinae	*Murmidius*	CO915	Mycophagous
Cucujoidea CS	Cerylonidae	Ostomopsinae	*Ostomopsis*	CO1012	Mycophagous
Cucujoidea CS	Cerylonidae	Ostomopsinae	*Ostomopsis*	CO914	Mycophagous
Cucujoidea CS	Coccinellidae	Chilocorinae	*Chilocorus cacti*	CO573	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Exochomus*	CO722	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Halmus chalybeus*	CO467	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Halmus coelestris*	CO578	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Orcus bilunulatus*	CO815	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Orcus lafertei*	CO587	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Platynaspis*	CO630	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Chilocorinae	*Telsimia*	CO731	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Monocoryna*	AG01	???
Cucujoidea CS	Coccinellidae	Coccidulinae	*Azya orbigera*	AG03	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Anovia*	AGNM01	Predacious (on Sternorrhyncha) !
Cucujoidea CS	Coccinellidae	Coccidulinae	*Nothocolus*	AGNM02	???
Cucujoidea CS	Coccinellidae	Coccidulinae	*Neorhizobius*	AGNM03	???
Cucujoidea CS	Coccinellidae	Coccidulinae	*Chnoodes*	CO465	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Cryptolaemus montrouzieri*	AG05	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Oridia pubescens*	CO721	???
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rodolia*	CO723	Predacious (on Sternorrhyncha) !
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rhyzobius*	CO728	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rhyzobius lophantae*	CO451	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Rodolia*	CO813	Predacious (on Sternorrhyncha) !
Cucujoidea CS	Coccinellidae	Coccidulinae	*Coccidula*	CO824	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Bucolus*	CO828	Predacious (on Formicidae) ^
Cucujoidea CS	Coccinellidae	Coccidulinae	*Cranophorus*	AG02?	???
Cucujoidea CS	Coccinellidae	Coccinellinae	*Anatis abiculata*	CO446	Predacious (on Sternorrhyncha) ^

Table 5.4 (continued) Host information for the taxa used in this study.

Superfamily	**Family**	**Subfamily/Tribe**	**Species**	**Voucher**	**Trophic group/Host info**
Cucujoidea CS	Coccinellidae	Coccinellinae	*Bothrocalvia albolineata*	CO586	???
Cucujoidea CS	Coccinellidae	Coccinellinae	*Bulaea anceps*	AG04	Phytophagous (leaves & pollen) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinella septempunctata*	CO615	Predacious (on Sternorrhyncha) !
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinella transversalis*	CO571	Predacious (on Sternorrhyncha) !
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coccinellini*	CO468	??? need better ID
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coleomegilla strenua*	CO445	??? genus has broad feeding habits (diverse forms of predation and herbivory) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Coleophora bisselata*	CO581	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Cycloneda sanguinea*	CO443	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Cycloneda sanguinea*	CO463	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Harmonia axyridis*	CO453	Predacious (on Sternorrhyncha and other insects) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Harmonia euchris*	CO575	Predacious (on Sternorrhyncha and other insects) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Hippodamia convergens*	CO627	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Hippodamia quinquesignata*	CO450	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Illeis*	CO461	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Illeis*	CO466	Mycophagous (on Erysiphaceae) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Micraspis*	CO459	Mycophagous (on Erysiphaceae) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Mulsantina*	CO460	Predacious (on Sternorrhyncha)
Cucujoidea CS	Coccinellidae	Coccinellinae	*Myzia pullata*	CO444	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Olla v-nigrum*	CO464	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Pristonema*	AG06	???
Cucujoidea CS	Coccinellidae	Coccinellinae	*Psyllobora*	CO304	Mycophagous (on Erysiphaceae) ^
Cucujoidea CS	Coccinellidae	Coccinellinae	*Psyllobora vigintimaculata*	CO455	Mycophagous (on Erysiphaceae) ^
Cucujoidea CS	Coccinellidae	Epilachninae	*Cynegetini*	CO470	Phytophagous ^
Cucujoidea CS	Coccinellidae	Epilachninae	*Epilachna*	CO616	Phytophagous ^
Cucujoidea CS	Coccinellidae	Scymninae	*Apolinus*	CO821	Predacious (on Sternorrhyncha) WWW
Cucujoidea CS	Coccinellidae	Scymninae	*Cryptogonus*	CO737	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Aspidimerus*	CO730	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Brachiacantha*	CO725	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Cryptognatha*	CO727	Predacious (on Sternorrhyncha) WWW
Cucujoidea CS	Coccinellidae	Scymninae	*Decadiomis*	CO733	???
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis kameryunensis*	CO818	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis notescens*	CO825	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Diomis terminates*	CO629	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Hyperaspidius mimus*	CO570	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Hyperaspis lateralis*	CO572	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Nephaspis*	AGNM09	Predacious (on Sternorrhyncha) WWW
Cucujoidea CS	Coccinellidae	Scymninae	*Nephus*	CO589	Predacious (on Sternorrhyncha) WWW
Cucujoidea CS	Coccinellidae	Scymninae	*Ortalia*	CO827	Predacious (on Auchenorrhyncha and Formicidae) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Ortalia horni*	CO582	Predacious (on Auchenorrhyncha and Formicidae) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Poria*	CO720	???
Cucujoidea CS	Coccinellidae	Scymninae	*Sasajiscymnus tsugae*	CO583	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnini*	CO826	??? need better ID
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnus*	CO449	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Scymnus*	CO628	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Scymninae	*Selvadius*	CO822	Predacious (on Sternorrhyncha)??? (Gordon, 1985)
Cucujoidea CS	Coccinellidae	Scymninae	*Stethorus*	CO617	Predacious (on Acari) ^
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Catana*	CO631	Predacious (on Sternorrhyncha) (Gordon, 1985)
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Cephaloscymnus*	AGMN07	Predacious (on Sternorrhyncha)??? (Gordon, 1985)
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Chilocorellus*	AGNM04	???

Table 5.4 (continued) Host information for the taxa used in this study.

Superfamily	**Family**	**Subfamily/Tribe**	**Species**	**Voucher**	**Trophic group/Host info**
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Coccidophilus*	AGMN05	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Delphastus*	CO577	Predacious (on Sternorrhyncha) (Gordon, 1985)
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Exochomus 4-pustulatus*	CO726	Predacious (on Sternorrhyncha) (Gordon, 1985)
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Ghanius*	AG08	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Parasitis*	AGNM06	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	Plotinini	AGNM08	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sarapidus australis*	AG09	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Shirozuellini*	CO1015	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sticholotis*	CO457	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sticholotis*	CO588	Predacious (on Sternorrhyncha) ^
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sukuhanikona*	AG07	???
Cucujoidea CS	Coccinellidae	Sticholotidinae	*Sulcolotis*	CO829	???
Cucujoidea CS	Corylophidae	Periptyctinae	*Periptyctus*	CO940	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Aenigmaticini	*Aenigmaticum californicus*	CO934	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Aenigmaticini	*Stanus bowsteadi*	CO964	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Corylophini	*Corylophus?*	CO972	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Foadiini	*Foadia*	CO608	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Foadiini	*Priamima*	CO962	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Foadiini	*Priamima??*	CO963	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO607	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO959	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Orthoperini	*Orthoperus*	CO961	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea fasciata*	CO603	Mycophagous (Ascomycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea lunata*	CO604	Mycophagous (Ascomycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea*	CO946	Mycophagous (Ascomycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Clypastraea*	CO947	Mycophagous (Ascomycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO949	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO950	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO951	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Parmulini	*Arthrolips*	CO952	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO941	Mycophagous (Ascomycetes and Basidiomycetes)
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis* nr. *rotundata*	CO942	Mycophagous (Ascomycetes and Basidiomycetes)
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO943	Mycophagous (Ascomycetes and Basidiomycetes)
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis?*	CO944	Mycophagous (Ascomycetes and Basidiomycetes)
Cucujoidea CS	Corylophidae	Peltinodini	*Holopsis*	CO945	Mycophagous (Ascomycetes and Basidiomycetes)
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO956	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO965	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Rypobiini	*Rypobius*	CO966	Mycophagous (Ascomycetes and Deuteromycetes)
Cucujoidea CS	Corylophidae	Rypobiini	*Hoplicnema*	CO967	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Rypobiini	*Hoplicnema*	CO968	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Rypobiini	*Catoptyx*	CO969	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Rypobiini	*Gloeosoma*	CO970	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Rypobiini	*Gloeosoma?*	CO971	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus lateralis*	CO605	Mycophagous (Zygomycetes and Ascomycetes)
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO606	Mycophagous (Zygomycetes and Ascomycetes)
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO953	Mycophagous (Zygomycetes and Ascomycetes)
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO954	Mycophagous (Zygomycetes and Ascomycetes)
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus*	CO955	Mycophagous (Zygomycetes and Ascomycetes)
Cucujoidea CS	Corylophidae	Sericoderini	*Sericoderus (Anisomeristes)*	CO957	Mycophagous (Zygomycetes and Ascomycetes)

Table 5.4 (continued) Host information for the taxa used in this study.

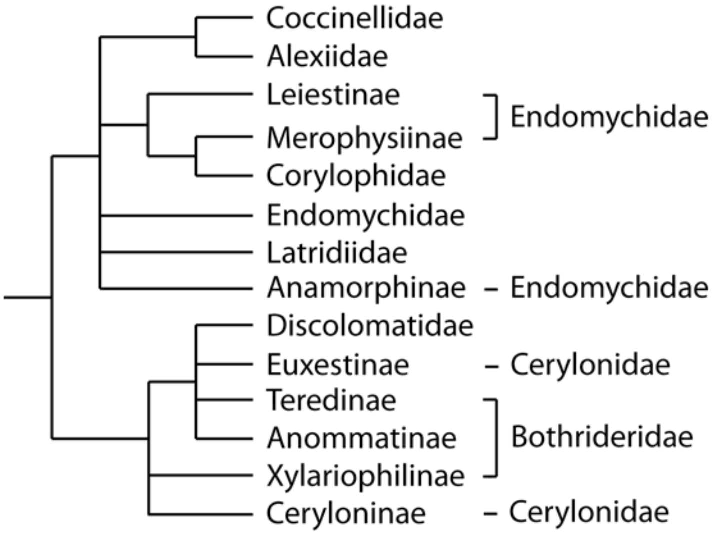
Superfamily	Family	Subfamily/Tribe	Species	Voucher	Trophic group/Host info
Cucujoidea CS	Corylophidae	Sericoderini	*Aposericoderus?*	CO958	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Corylophidae	undet.	Corylophidae undet.	CO973	Mycophagous (Ascomycetes and Deuteromycetes)???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO600	Detritivorous/Mycophagous (Basidiomycetes)???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO601	Detritivorous/Mycophagous (Basidiomycetes)???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO935	Detritivorous/Mycophagous (Basidiomycetes)???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Aphanocephalus*	CO936	Detritivorous/Mycophagous (Basidiomycetes)???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO937	Detritivorous/Mycophagous???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO938	Detritivorous/Mycophagous???
Cucujoidea CS	Discolomatidae	Aphanocephalinae	*Fallia*	CO602	Detritivorous/Mycophagous???
Cucujoidea CS	Discolomatidae	Discolomatinae	*Cassidoloma*	CO939	Detritivorous/Mycophagous???
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus sp. 2*	CO786	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus sp.1*	CO649	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Anamorphus tenuicornis*	CO778	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Bystus piceus*	CO320	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Bystus sp. nov*	CO787	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Catapotia sp. 1*	CO983	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Clemmus minor*	CO713	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Geoendomychus*	CO974	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Idiophyes nr. Brevis*	CO975	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Micropsephodes lundgreni*	CO705	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Mychothenus tropicalis*	CO715	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Papuella birolecta*	CO804	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Anamorphinae	*Symbiotes gibberosus*	CO986	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Endomychinae	*Endomychus biguttatus*	CO657	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Endomychinae	*Endomychus*	CO789	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Endomychinae	*Meilichius*	CO800	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Endomychinae	*Cyclotoma cingalensis*	CO980	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Epipocinae	*Anidrytus*	CO654	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Epipocinae	*Anidrytus*	CO779	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Epipocinae	*Epipocus*	CO790	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Epipocinae	*Epipocus*	CO791	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Epipocinae	*Epopterus testudinarius*	CO792	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Eupsilobiinae	*Chileolobius*	CO1014	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Leiestinae	*Rhanidea unicolor*	CO708	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Leiestinae	*Phymaphora pulchella*	CO806	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Leiestinae	*Phymaphora californica*	CO987	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Acinaces laceratus*	CO660	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphisternus*	CO658	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphisternus*	CO777	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix laevigatus*	CO318	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix tarsatus*	CO661	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Amphix vestitus cinctus*	CO317	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Ancylopus melanocephalus*	CO776	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Aphorista morosa*	CO781	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Aphorista vittata*	CO700	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Beccariola*	CO717	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Encymon gorhami*	CO648	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Encymon immaculatus*	CO788	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Eumorphus*	CO795	Mychophagous (Basidiomycetes) $

Table 5.4 (continued) Host information for the taxa used in this study.

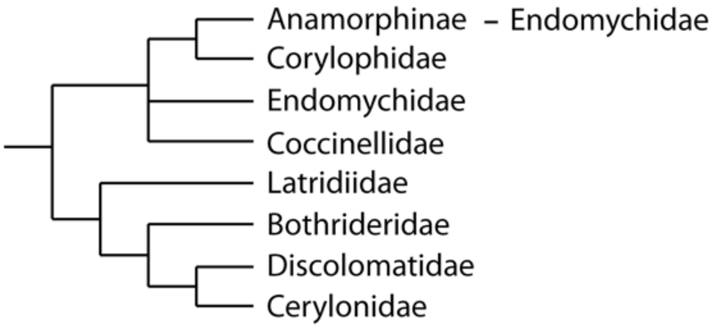
Superfamily	Family	Subfamily/Tribe	Species	Voucher	Trophic group/Host info
Cucujoidea CS	Endomychidae	Lycoperdininae	*Eumorphus quadriguttatus*	CO794	Mychophagous (Basidiomycetes) and Herbivorous? $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Hylaia*	CO831	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Indalmus*	CO798	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Indalmus lineelus*	CO714	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Lycoperdina ferruginea*	CO650	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Mycetina*	CO803	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Mycetina horni*	CO655	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Pseudindalmus*	CO807	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Lycoperdininae	*Trycherus*	CO703	Mychophagous (Basidiomycetes) and Lichenivorous $
Cucujoidea CS	Endomychidae	Merophysiinae	*Holoparamecus*	CO710	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Merophysiinae	*Holoparamecus*	CO976	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Merophysiinae	*Lycoperdinella subcaeca*	CO985	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Mycetaeinae	*Mycetaea subterranea*	CO984	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus boliviensis*	CO711	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus*	CO977	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Pleganophorinae	*Trochoideus goudoti*	CO981	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO323	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO330	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Stenotarsus*	CO332	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Chondria armipes*	CO652	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Chondria nigra*	CO653	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Danae*	CO702	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Danae testacea*	CO709	Mychophagous (Basidiomycetes) $
Cucujoidea CS	Endomychidae	Stenotarsinae	*Saula*	CO808	Predacious (on Sternorrhyncha) $
Cucujoidea CS	Latridiidae	Corticariinae	*Corticaria ferruginea*	CO593	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Corticarina*	CO486	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Corticarina*	CO580	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Cortinicara*	CO592	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Fuchsina occulta*	CO638	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO481	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO594	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Melanopthalma*	CO595	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Corticariinae	*Migneauxia orientalis*	CO590	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Aridius nodifer*	CO482	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Cartodere constrictus*	CO596	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Dienerella intermedia*	CO488	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Enicmus aterrimus*	CO693	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes) and Myxomycophagous
Cucujoidea CS	Latridiidae	Latridiinae	*Enicmus maculatus*	CO692	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes) and Myxomycophagous
Cucujoidea CS	Latridiidae	Latridiinae	*Eufallia seminiveus*	CO484	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Latridius crenatus*	CO483	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Metopthalmus haigi*	CO480	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Revelieria californica*	CO477	Myxomycophagous
Cucujoidea CS	Latridiidae	Latridiinae	*Stephostethus lardarius*	CO473	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Stephostethus liratus*	CO476	Mycophagous (on Phycomycetes, Deuteromycetes and Ascomycetes)
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion sleeperi*	CO697	Mycophagous?
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion anasillos*	CO698	Mycophagous?
Cucujoidea CS	Latridiidae	Latridiinae	*Akalyptoischion atrichos*	CO699	Mycophagous?

References:
@ = American Beetles; $ = Shockley et al.; ^ = Giorgi et al.; # = Tree of Life webpage www.tolweb.org; ! = personal reference/observation; All others taken from Handbuch der Zoologie, 2010 (Beutel and Leschen, eds.)

Hunt et al. (2007)

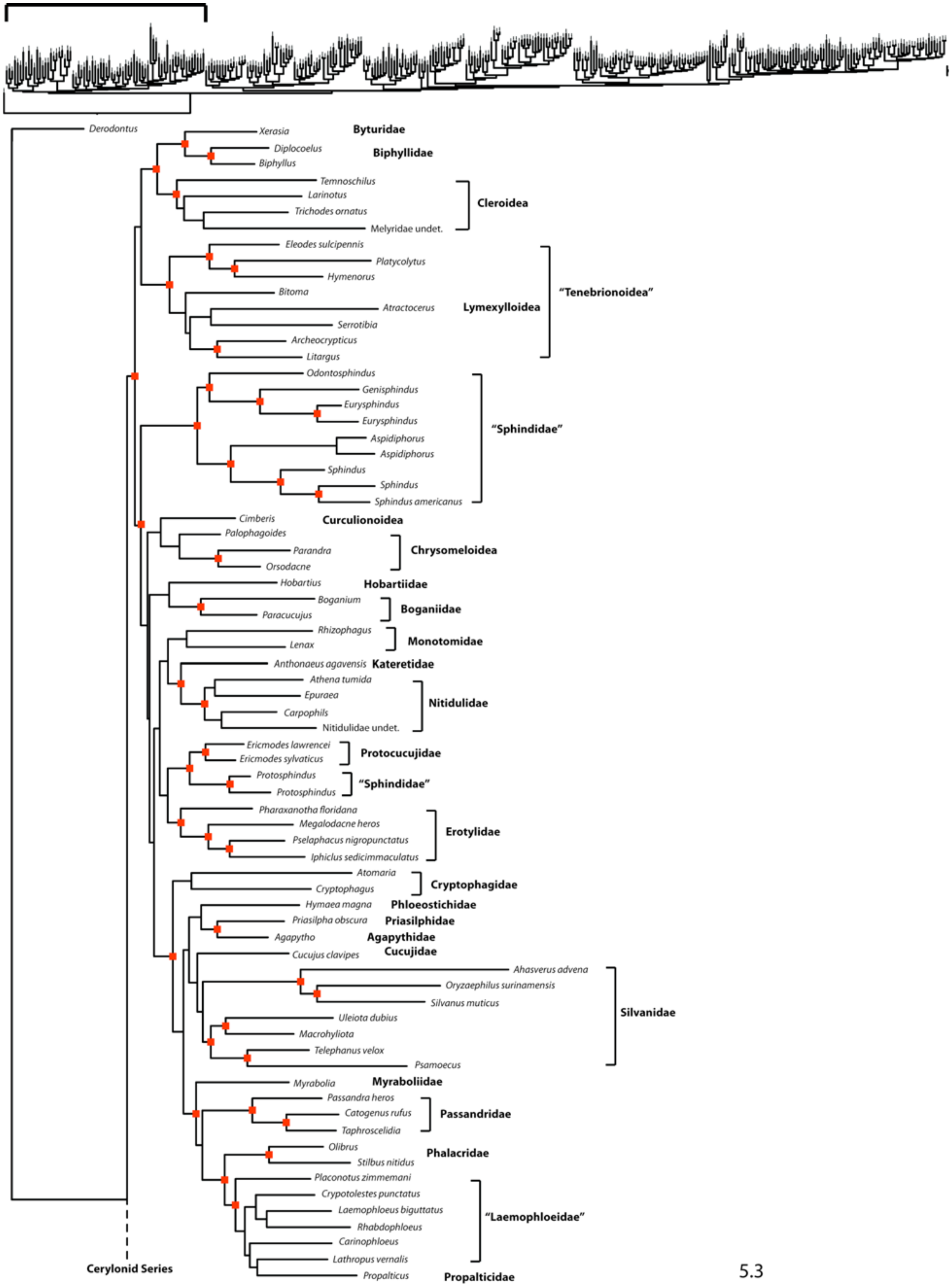


5.1

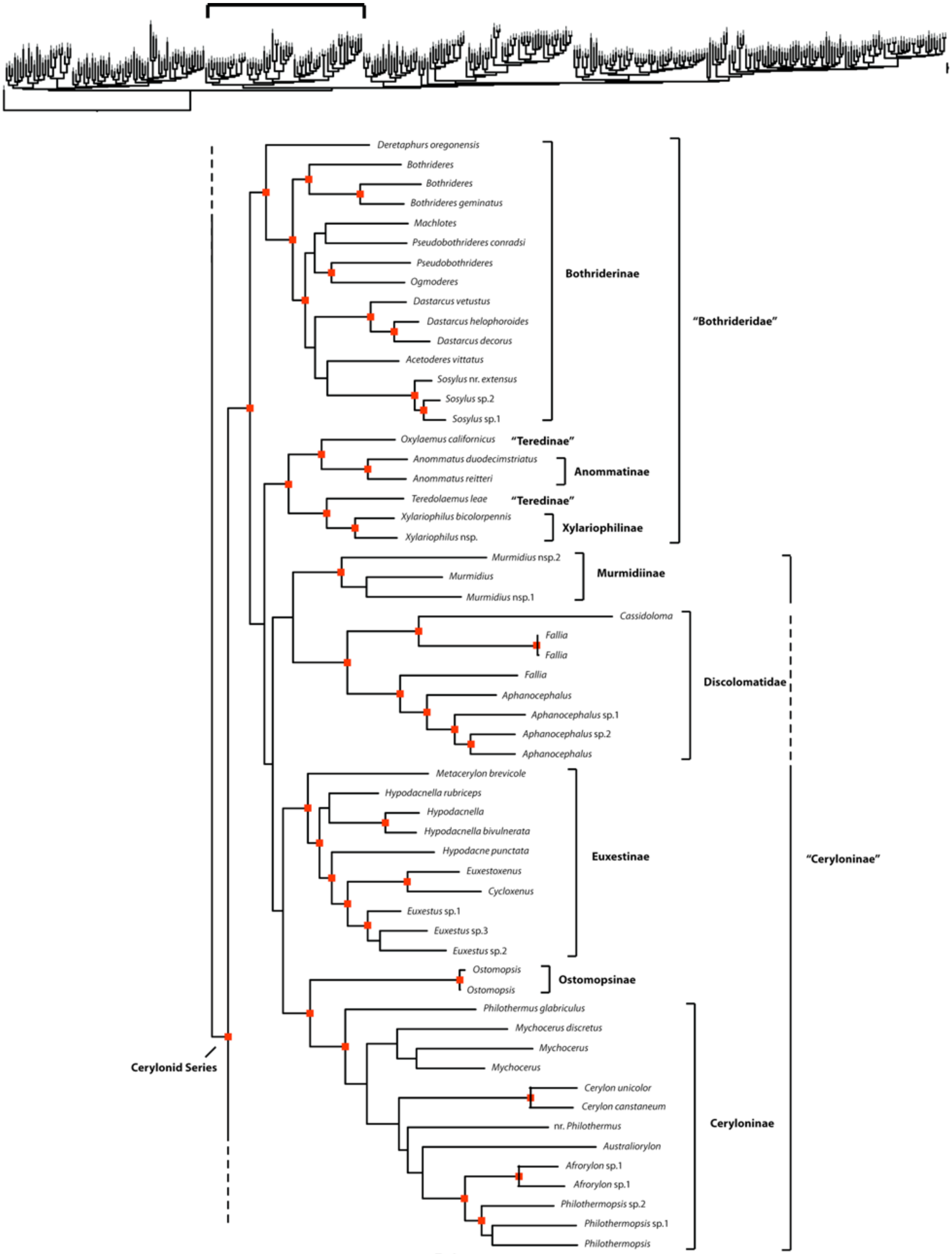


Robertson et al. (2008)

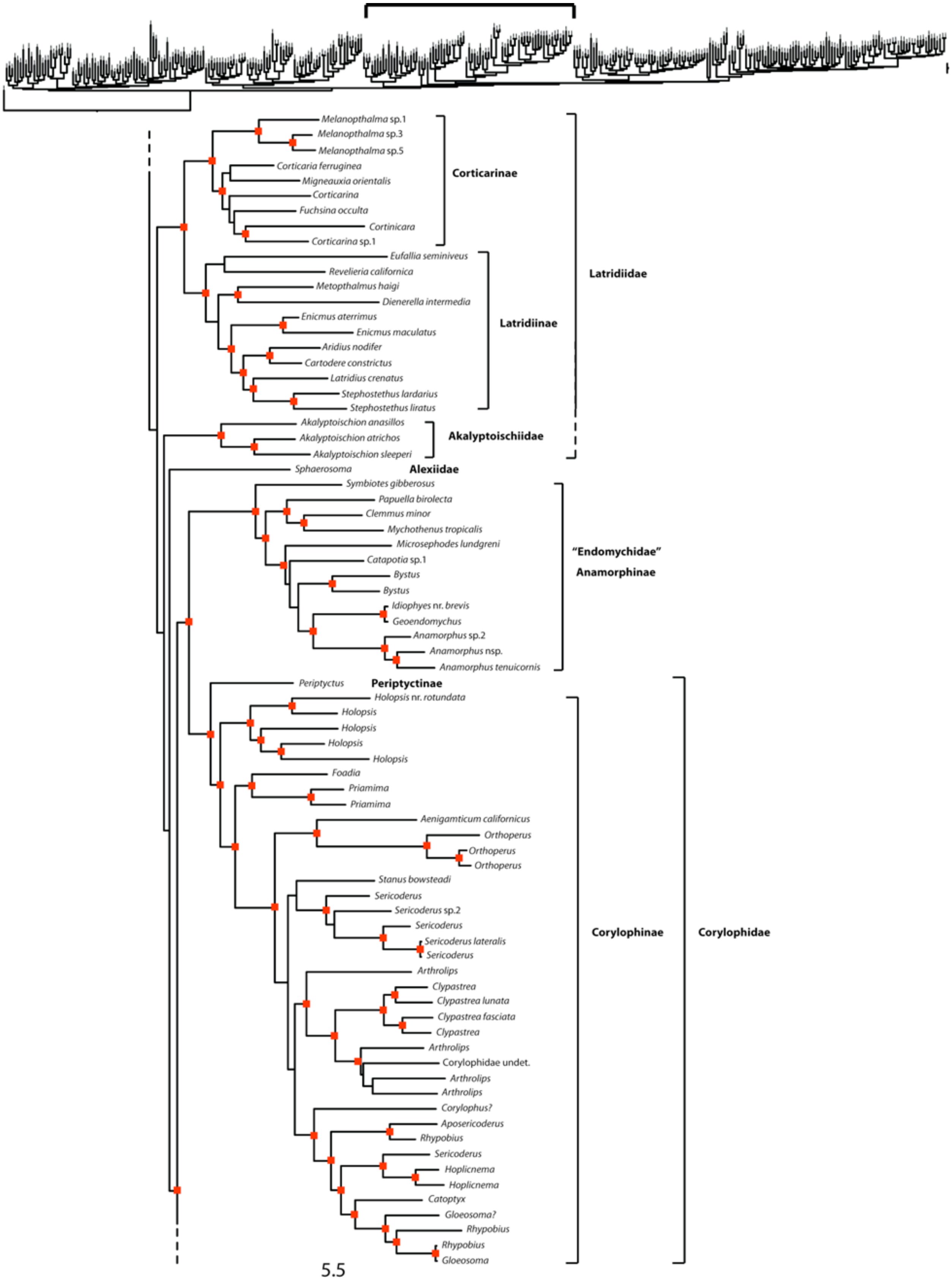
5.2


Derodontus
Xerasia
Byturidae
Diplocoelus
Biphyllus
Biphyllidae
Temnoschilus
Larinotus
Trichodes ornatus
Melyridae undet.
Cleroidea
Eleodes sulcipennis
Platycolytus
Hymenorus
Bitoma
Atractocerus
Lymexylloidea
Serrotibia
Archeocrypticus
Litargus
"Tenebrionoidea"
Odontosphindus
Genisphindus
Eurysphindus
Eurysphindus
Aspidiphorus
Aspidiphorus
Sphindus
Sphindus
Sphindus americanus
"Sphindidae"
Cimberis
Curculionoidea
Palophagoides
Parandra
Orsodacne
Chrysomeloidea
Hobartius
Hobartiidae
Boganium
Paracucujus
Boganiidae
Rhizophagus
Lenax
Monotomidae
Anthonaeus agavensis
Kateretidae
Athena tumida
Epuraea
Carpophils
Nitidulidae undet.
Nitidulidae
Ericmodes lawrencei
Ericmodes sylvaticus
Protocucujidae
Protosphindus
Protosphindus
"Sphindidae"
Pharaxanotha floridana
Megalodacne heros
Pselaphacus nigropunctatus
Iphiclus sedicimmaculatus
Erotylidae
Atomaria
Cryptophagus
Cryptophagidae
Hymaea magna
Phloeostichidae
Priasilpha obscura
Priasilphidae
Agapytho
Agapythidae
Cucujus clavipes
Cucujidae
Ahasverus advena
Oryzaephilus surinamensis
Silvanus muticus
Uleiota dubius
Macrohyliota
Telephanus velox
Psamoecus
Silvanidae
Myrabolia
Myraboliidae
Passandra heros
Catogenus rufus
Taphroscelidia
Passandridae
Olibrus
Stilbus nitidus
Phalacridae
Placonotus zimmemani
Crypotolestes punctatus
Laemophloeus biguttatus
Rhabdophloeus
Carinophloeus
Lathropus vernalis
"Laemophloeidae"
Propalticus
Propalticidae
Cerylonid Series

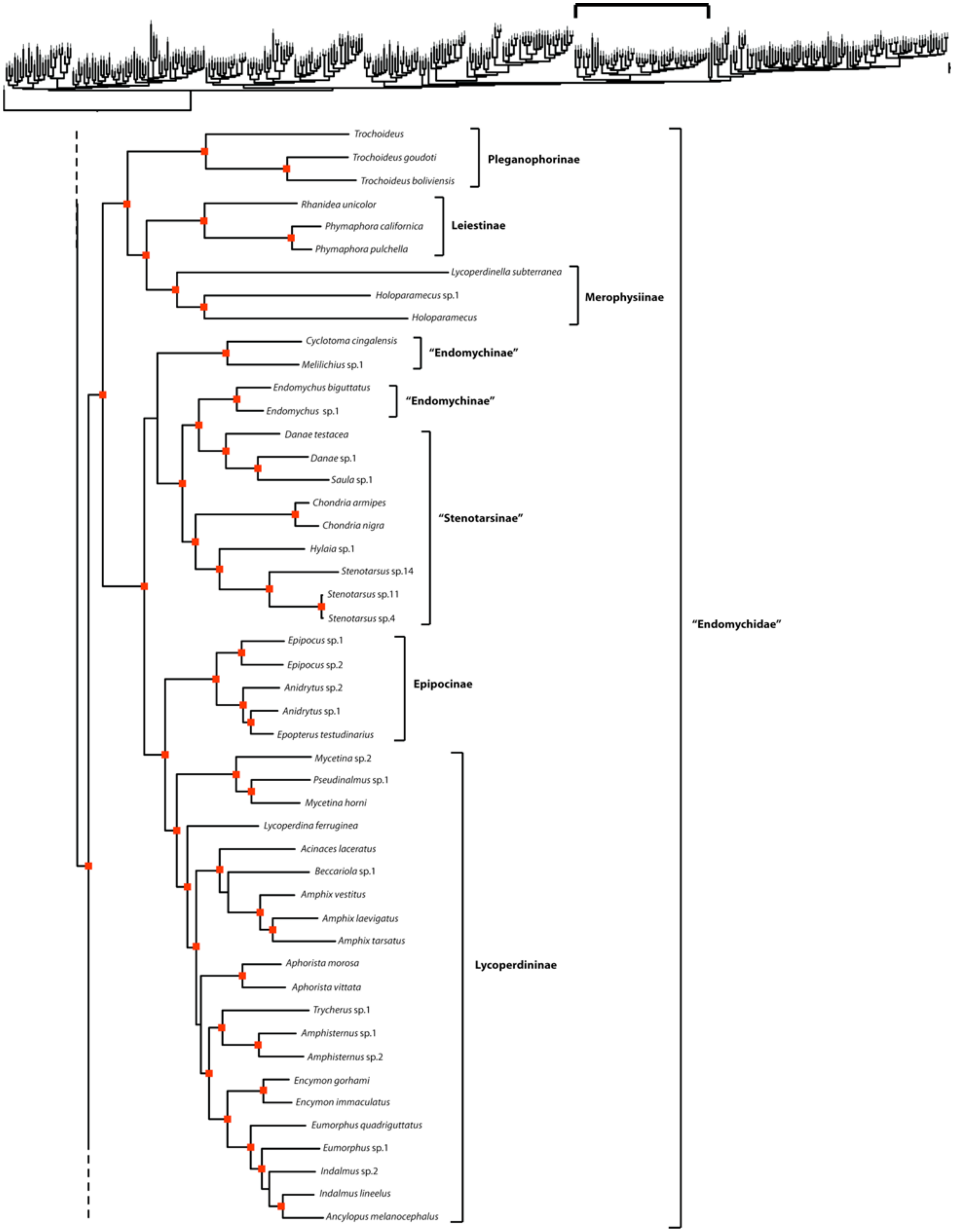
5.3


Deretaphurs oregonensis
Bothrideres
Bothrideres
Bothrideres geminatus
Machlotes
Pseudobothrideres conradsi
Pseudobothrideres
Ogmoderes
Dastarcus vetustus
Dastarcus helophoroides
Dastarcus decorus
Acetoderes vittatus
Sosylus nr. extensus
Sosylus sp.2
Sosylus sp.1
Bothriderinae
"Bothrideridae"
Oxylaemus californicus
"Teredinae"
Anommatus duodecimstriatus
Anommatus reitteri
Anommatinae
Teredolaemus leae
"Teredinae"
Xylariophilus bicolorpennis
Xylariophilus nsp.
Xylariophilinae
Murmidius nsp.2
Murmidius
Murmidius nsp.1
Murmidiinae
Cassidoloma
Fallia
Fallia
Fallia
Aphanocephalus
Aphanocephalus sp.1
Aphanocephalus sp.2
Aphanocephalus
Discolomatidae
Metacerylon brevicole
Hypodacnella rubriceps
Hypodacnella
Hypodacnella bivulnerata
Hypodacne punctata
Euxestoxenus
Cycloxenus
Euxestus sp.1
Euxestus sp.3
Euxestus sp.2
Euxestinae
"Ceryloninae"
Ostomopsis
Ostomopsis
Ostomopsinae
Philothermus glabriculus
Mychocerus discretus
Mychocerus
Mychocerus
Cerylon unicolor
Cerylon canstaneum
nr. Philothermus
Australiorylon
Afrorylon sp.1
Afrorylon sp.1
Philothermopsis sp.2
Philothermopsis sp.1
Philothermopsis
Cerylonid Series
Cerylonidae

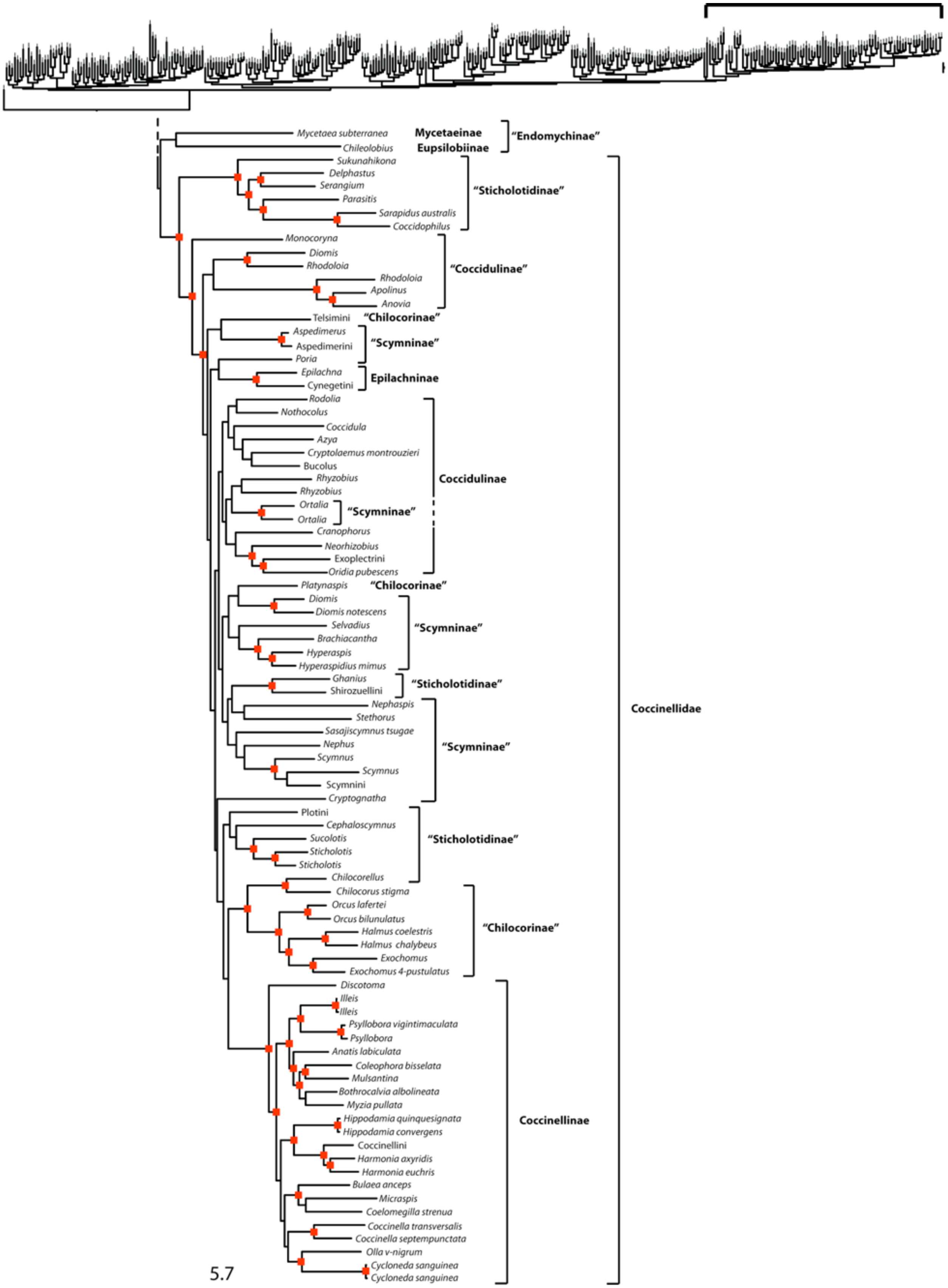
5.4


Melanopthalma sp.1
Melanopthalma sp.3
Melanopthalma sp.5
Corticaria ferruginea
Migneauxia orientalis
Corticarina
Fuchsina occulta
Cortinicara
Corticarina sp.1
Corticarinae
Eufallia seminiveus
Revelieria californica
Metopthalmus haigi
Dienerella intermedia
Enicmus aterrimus
Enicmus maculatus
Aridius nodifer
Cartodere constrictus
Latridius crenatus
Stephostethus lardarius
Stephostethus liratus
Latridiinae
Latridiidae
Akalyptoischion anasillos
Akalyptoischion atrichos
Akalyptoischion sleeperi
Akalyptoischiidae
Sphaerosoma
Alexiidae
Symbiotes gibberosus
Papuella birolecta
Clemmus minor
Mychothenus tropicalis
Microsephodes lundgreni
Catapotia sp.1
Bystus
Bystus
Idiophyes nr. brevis
Geoendomychus
Anamorphus sp.2
Anamorphus nsp.
Anamorphus tenuicornis
"Endomychidae"
Anamorphinae
Periptyctus
Periptyctinae
Holopsis nr. rotundata
Holopsis
Holopsis
Holopsis
Holopsis
Foadia
Priamima
Priamima
Aenigamticum californicus
Orthoperus
Orthoperus
Orthoperus
Stanus bowsteadi
Sericoderus
Sericoderus sp.2
Sericoderus
Sericoderus lateralis
Sericoderus
Arthrolips
Clypastrea
Clypastrea lunata
Clypastrea fasciata
Clypastrea
Arthrolips
Corylophidae undet.
Arthrolips
Arthrolips
Corylophus?
Aposericoderus
Rhypobius
Sericoderus
Hoplicnema
Hoplicnema
Catoptyx
Gloeosoma?
Rhypobius
Rhypobius
Gloeosoma
Corylophinae
Corylophidae

5.5


Trochoideus
Trochoideus goudoti
Trochoideus boliviensis
Pleganophorinae
Rhanidea unicolor
Phymaphora californica
Phymaphora pulchella
Leiestinae
Lycoperdinella subterranea
Holoparamecus sp.1
Holoparamecus
Merophysiinae
Cyclotoma cingalensis
Melilichius sp.1
"Endomychinae"
Endomychus biguttatus
Endomychus sp.1
"Endomychinae"
Danae testacea
Danae sp.1
Saula sp.1
Chondria armipes
Chondria nigra
Hylaia sp.1
Stenotarsus sp.14
Stenotarsus sp.11
Stenotarsus sp.4
"Stenotarsinae"
Epipocus sp.1
Epipocus sp.2
Anidrytus sp.2
Anidrytus sp.1
Epopterus testudinarius
Epipocinae
Mycetina sp.2
Pseudinalmus sp.1
Mycetina horni
Lycoperdina ferruginea
Acinaces laceratus
Beccariola sp.1
Amphix vestitus
Amphix laevigatus
Amphix tarsatus
Aphorista morosa
Aphorista vittata
Trycherus sp.1
Amphisternus sp.1
Amphisternus sp.2
Encymon gorhami
Encymon immaculatus
Eumorphus quadriguttatus
Eumorphus sp.1
Indalmus sp.2
Indalmus lineelus
Ancylopus melanocephalus
Lycoperdininae
"Endomychidae"

5.6


Mycetaea subterranea
Chileolobius
Mycetaeinae
Eupsilobiinae
"Endomychinae"
Sukunahikona
Delphastus
Serangium
Parasitis
Sarapidus australis
Coccidophilus
"Sticholotidinae"
Monocoryna
Diomis
Rhodoloia
Rhodoloia
Apolinus
Anovia
"Coccidulinae"
Telsimini
"Chilocorinae"
Aspedimerus
Aspedimerini
Poria
"Scymninae"
Epilachna
Cynegetini
Epilachninae
Rodolia
Nothocolus
Coccidula
Azya
Cryptolaemus montrouzieri
Bucolus
Rhyzobius
Rhyzobius
Ortalia
Ortalia
"Scymninae"
Cranophorus
Neorhizobius
Exoplectrini
Oridia pubescens
Coccidulinae
Platynaspis
"Chilocorinae"
Diomis
Diomis notescens
Selvadius
Brachiacantha
Hyperaspis
Hyperaspidius mimus
"Scymninae"
Ghanius
Shirozuellini
"Sticholotidinae"
Nephaspis
Stethorus
Sasajiscymnus tsugae
Nephus
Scymnus
Scymnus
Scymnini
Cryptognatha
"Scymninae"
Plotini
Cephaloscymnus
Sucolotis
Sticholotis
Sticholotis
Chilocorellus
"Sticholotidinae"
Chilocorus stigma
Orcus lafertei
Orcus bilunulatus
Halmus coelestris
Halmus chalybeus
Exochomus
Exochomus 4-pustulatus
"Chilocorinae"
Discotoma
Illeis
Illeis
Psyllobora vigintimaculata
Psyllobora
Anatis labiculata
Coleophora bisselata
Mulsantina
Bothrocalvia albolineata
Myzia pullata
Hippodamia quinquesignata
Hippodamia convergens
Coccinellini
Harmonia axyridis
Harmonia euchris
Bulaea anceps
Micraspis
Coelomegilla strenua
Coccinella transversalis
Coccinella septempunctata
Olla v-nigrum
Cycloneda sanguinea
Cycloneda sanguinea
Coccinellinae
Coccinellidae

5.7


Byturidae, Biphyllidae
Cleroideaa
Tenebrionoidea
Lymexyloidea
"Sphindidae"
Phytophaga
"Basal Cucujoidea"
"Bothrideridae"
"Cerylonidae"
Discolomatidae
"Cerylonidae"
"Latridiidae"
Alexiidae
Anamorphinae
Corylophidae
"Endomychidae"
Coccinellidae
Mycophagous
Phytophagous
Predaceous
Saprophagous
Myxomycophagous
Lichenophagous
Parasitoid
Euryphagous
Equivocal
Unkown
Independent host shift
Pollenophagy

5.8

CHAPTER 6

PHYLOGENY AND CLASSIFICATION OF THE CERYLONID SERIES OF CUCUJOIDEA (COLEOPTERA)[1]

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[1] Robertson, J.A., S.A. Slipinski, M.F. Whiting, K.B. Miller, and J.V. McHugh. To be submitted to *Molecular Phylogenetics and Evolution.*

Abstract

A total evidence phylogenetic analysis for the Cerylonid Series (C.S.) of Cucujoidea using the morphology of the adult and larval forms with an extensive molecular dataset is presented. Maximum parsimony (MP) and mixed model Bayesian inference (BI) methods are used to reconstructed the phylogeny for the major groups within the C.S. Using the resulting phylogenetic framework, the higher classification of the C.S. is revised. Synapomorphies supporting C.S. families and subfamilies are discussed. Discolomatidae is recognized as a subfamily within Cerylonidae, as Discolomatinae **stat. nov.**; Bothrideridae is split into two distinct families: 1) Bothrideridae **sensu nov.**, comprising the former Bothriderinae, and 2) Terediidae **stat. nov.**, including the remaining former subfamilies Teredinae, Anommatinae, Xylariophilinae and Euxestinae. The status of the putative new C.S. family, Akalyptoischiidae, is uncertain. The endomychid subfamily Anamorphinae is elevated to familial status, Anamorphidae **stat. nov**.

Key Words: Coleoptera, Cucujoidea, Cerylonid Series, Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, Latridiidae, Akalyptoischiidae, Terediidae, Anamorphidae.

Introduction

The “Cerylonid Series” (C.S.) is an incredibly diverse cluster of presumably highly derived families within Cucujoidea comprising Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae.

Until recently, no systematics studies in the modern sense had been conducted for the C.S. However, in a series of studies presented previously (see Chapters 4 and 5) we examine the higher-level phylogenetic relationships of this group based on morphology (Chapter 4) and molecular data (Chapter 5). In the above studies we identified a number of problems with the current family concepts and corresponding classification of the C.S. (e.g., paraphyletic Cerylonidae, Endomychidae, and potentially Bothrideridae). Likewise, we have set forth a number of putative synapomorphies for the C.S. clade and its major constituent lineages.

The robustness of the above phylogenetic hypotheses and the taxonomic and evolutionary interpretations that they suggest, however, rest entirely on the phylogenetic analysis upon which they are based. As such, it is critical when inferring phylogenetic relationships to utilize as much data as possible so long as they are appropriate to the questions investigated (Kluge, 1998). Therefore despite repeatedly recovering many of the above results, we have refrained from making any formal changes in the classification and constitution of the constituent C.S. families until an extensive analysis based on the combination of morphological and molecular data was available to guide such actions. When all appropriate character data is synthesized in a single analysis, the resulting hypothesis explains more data; therefore it is arguable that one should have more confidence in the resulting relationships. Such analyses ultimately yield a phylogenetic framework that is more stable than hypotheses of relationships based on only a single data source (Kluge, 1998). In addition a total evidence approach allows the utilization of a vast amount of character data for phylogenetic inference via sequence data while also including the critical morphological information which produces a practical, character-based framework for use in defining and characterizing resulting lineages.

In the present study, we perform a total evidence phylogenetic analysis for the C.S. using the morphology of the adult and larval forms in combination with an extensive molecular dataset comprising 9 loci. Using the resulting phylogenetic framework, we revise the higher classification of the C.S.

Materials & Methods

Data for phylogenetic inference

The morphological data used herein is that of Robertson et al. (in prep; see Chapter 4). The morphological dataset includes 147 characters covering external and internal morphology of the adult (108 characters) and larval (39 characters) forms. Mesquite 2.72 (Maddison and Maddison, 2009) was used to host these data. Specific information regarding the morphological characters, states, and coding practices are outlined the above study (see Chapter 4).

Similarly, we use the 9 gene fragments of Robertson et al. (in prep; see Chapter 5) including 18S (ca. 1850 bp), 28S (ca. 2300 bp), H3 (327 bp), 12S (ca. 350 bp), 16S (ca. 500 bp), COI (1239 bp), COII (ca. 639 bp), CAD (1005 bp) and ArgK (ca. 729 bp). The combined aligned fragments yield a molecular matrix of 11022 characters. Molecular protocols are outlined in that study (see Chapter 5). The combined morphological and molecular matrix includes 11169 characters.

Taxonomic sampling

In the present study we use 70 exemplar taxa representing all 8 C.S. families and 32 of the 39 C.S. subfamilies. Of necessity, we combined a number of terminals used in this analysis, forming chimeric taxa. Chimeras used in this study are of two types: 1) molecular/molecular and 2) morphological/molecular. In an effort to maximize gene coverage in the molecular dataset, for a few taxa (e.g., *Akalyptoschion*) with missing data for some of the more powerful genes (e.g., CAD), a gene sequence of a congener was used, thus forming a molecular/molecular chimera. In most cases, chimeras were formed by including a single sequence for a closely related congeneric taxon for a single locus (e.g., CAD). Chimeras were only made for genera where monophyly is strongly supported (e.g., *Dastarcus*, *Sosylus, Akalyptoschion*). There were 8 instances of molecular/molecular chimeras.

In addition to the above, we created 3 morphological/molecular chimeras, due to the lack of overlap among the taxa present in the morphological and molecular datasets. In a few cases, however, there was no close overlap (e.g., congeners) between the two datasets and we had to select the mostly closely related non-congeneric taxa. In such cases, the taxa combined are still closely related and the monophyly of the higher group to which the combined taxa belong is certain. We created 3 morphological/molecular chimeras as follows: for *Mycetophagus* we used the sequence data of the closely related genus *Litargus*; the morphological data of *Agaricophilus* was used in combination with *Mycetaea* sequences to form the *Agaricophilus* terminal; likewise, the morphological data of *Discoloma* was combined with the molecular data of *Cassidoloma* for the *Discoloma* terminal.

Phylogenetic analysis

Phylogenetic analysis of the combined morphological and molecular dataset was performed in NONA Goloboff (1995) as implemented in WinClada (Nixon, 2000), utilizing 500 ratchet replications. All characters were treated as unordered and weighted equally and trees were rooted to *Derodontus*. Branch support was assessed by calculating bootstrap values in

NONA via WinClada. Character states were optimized on the topology using unambiguous optimization using WinClada and Mesquite (Maddison and Maddison, 2009).

Alignment of molecular loci followed that outlined in Robertson et al. (in press; see Chapter 5). We used the Akaike Information Criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall, 1998) and PAUP* 4.0b10 (Swofford, 2000) to select an appropriate model of sequence evolution for each gene.

A mixed-model Bayesian analysis (Nylander, et al., 2004) was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) using the models generated in Modeltest for the separate genes. The morphology partition was analyzed using a single rate category (Mk1 model). The partitioned Bayesian analysis comprised four separate runs each utilizing 20 million generations, flat priors, unlinked partitions, four chains (one cold and three hot) and trees sampled every 1000 generations. We used the program Tracer 1.5 (Rambaut and Drummond, 2009) to graphically determine stationarity, a suitable burn-in, mixing and convergence of runs. Trees sampled after the burn-in from the four runs were combined and used to construct a 50% majority rule consensus tree. Nodal support was assessed with the resulting posterior probabilities (Huelsenbeck and Ronquist, 2001).

A convention we will follow while discussing character states that support specific nodes in our resulting topology is to list the number of the character, followed by a dash then the relevant state. For example, character 20 (labral rods) state 1 (present) would be listed as 20-1. If the character is an uncontroverted synapomorphy, an asterisk will follow the listed character-state (e.g., 20-1*). Here we used the option of recognizing uncontroverted synapomorphies by character state as opposed to by character. In the discussion we often refer to a character state as being a strong or robust synapomorphy for a given clade. In these cases the character state is not an uncontroverted synapomorphy, yet is shared by only a few distantly related taxa.

Results

Of the 11169 characters in the combined adult and larval matrix, 5589 are parsimony informative. NONA produced 4 most parsimonious trees of length 44252. Graphical inspection of the MCMC parameter files from the BI analysis in Tracer indicated that all runs reached stationarity by 5 million generations and proper mixing (large-scale fluctuations in the traces) and convergence of runs (comparable means, variances and high EES values) was achieved. All trees sampled prior to 5 million generations were discarded as burn-in. The remaining trees sampled from the posterior distribution from the combined runs were used to calculate the 50% majority rule consensus BI tree.

Results from the MP and BI analyses are fairly similar in tree topology and patterns of branch support, though there are some notable differences. The MP topology differs from the BI tree (Figures 6.1-6.2) in recovering Latridiidae sensu stricto (i.e., excluding *Akalyptoischion*) as the sister group to the remaining C.S. taxa. *Akalyptoischion* is recovered as the sister group of Alexiidae and together these taxa form a relatively basal clade within the C.S. Other differences in the MP topology are as follows: the bothriderid subfamily Bothriderinae is sister to *Murmidius* + Discolomatidae; Euxestinae is paraphyletic with respect to Ostomopsinae and Ceryloninae; the clade comprising *Chileolobius* + *Agaricophilus* is recovered as the sister group to the endomychid clade including Merophysiinae, Pleganophorinae and Leiestinae; within Corylophidae, *Foadia* and *Holopsis* form a clade; *Epilachna* (Coccinellidae) is placed sister to the clade including *Diomus* and *Platynaspis*.

The BI topology is shown in Figures 6.1-6.2 and is used as the reference topology while discussing relationships and proposed classification changes. These results support the following C.S. families as monophyletic: Corylophidae, Coccinellidae, Discolomatidae and Latridiidae sensu stricto (BI only). Bothrideridae is paraphyletic with respect to Cerylonidae. Cerylonidae is paraphyletic with respect to Teredinae (Bothrideridae) and Discolomatidae, the later is recovered as the sister group to *Murmidius*. Endomychidae is not recovered as monophyletic due to the placement of Anamorphinae as the sister group of Corylophidae.

Our results corroborate those of Hunt et al. (2007) and Robertson et al. (2008) in recovering a basal dichotomy of two superfamilial C.S. clades: one clade comprising the families Bothrideridae, Cerylonidae, and Discolomatidae (hereafter "BCD" clade); the second clade including Alexiidae, Corylophidae, Coccinellidae and two endomychid lineages (Hunt et al., 2007) (hereafter "ACCEL" clade).

Discussion

Cerylonid Series

The C.S. is a well-supported clade in the present study [posterior probability (PP) = 100] and is supported by the following 7 characters/states: procoxal cavity without narrow lateral slit (42-0), mesotrochantin hidden (56-1), metacoxae moderately separated, by more than 1/3 coxal width (62-1), metacoxal carina absent (64-2*), radial cell of hind wing incomplete or absent (68-1), no free veins in hind wing (69-5), intercoxal process of abdominal ventrite I broad with angulate or truncate apex (81-2*), ventrites with internal apodemes present (82-1), and larval spiracles annular (145-0). One apparently uncontroverted synapomorphy for the C.S. clade, metacoxal carina absent (64-2*), cannot be considered truly uncontroverted, as this state occurs in many non-C.S. cucujoids (Leschen, et al., 2005) which are not included in the present study.

Latridiidae

The present study strongly supports the monophyly of the family Latridiidae in its historical sense (sensu lato), including *Akalyptoischion* (PP = 99). Synapomorphies uniting *Akalyptoischion* and the remaining latridiids (i.e., synapomorphies for Latridiidae sensu lato) include the following characters/states (Figure 6.1): postocular constriction present (0-1), labrum distinctly wider than clypeus (18-1*), notosternal suture incomplete or absent (37-1), tarsi in male 3-3-3 (73-3), and tarsi in female 3-3-3 (74-3).

The status of Akalyptoischiidae (Lord, et al., in press) is not clear given the findings of our present and previous studies taken together. Molecular data support *Akalyptoischion* as a distinct lineage in the C.S. that is not allied with the remaining latridiid taxa (Lord, et al., in press; see also Chapter 5). However, the present analysis based on morphology and 9 genes places this enigmatic taxon sister to the remaining Latridiidae. Only one morphological apomorphy unites the remaining latridiid taxa (i.e., separates Latridiidae sensu stricto) thereby distinguishing *Akalyptoischion* from the remaining latridiids: procoxal cavities closed internally (43-1). It is clear from the current study and that of Lord et al. (in press) that *Akalyptoischion,* if included within Latridiidae, forms the sister group to the remaining taxa. If *Akalyptoischion* is indeed sister to the remaining taxa, then it would be hard to justify not subordinating the new family Akalyptoischiidae from a morphological standpoint, since all the synapomorphic states for Latridiidae sensu lato (e.g., labrum distinctly wider than clypeus, etc.) would be considered plesiomorphic character states for Latridiidae sensu stricto, leaving few if any solid morphological synapomorphies to unite Latridiidae sensu stricto.

Alexiidae

The present analysis supports the monotypic family Alexiidae as a distinct C.S. lineage placed as the sister group to the clade comprising Coccinellidae, Corylophidae and "Endomychidae" (Figure 6.2). This higher C.S. clade is interesting as it includes primarily those taxa with elytral punctation not seriate or striate (47-1); this node is also supported by the presence of a cavity or fossa for receiving the prosternal process located on the anterior surface of the mesoventrite (51-0). Apomorphies distinguishing Alexiidae from other C.S. taxa include the following: apical maxillary palpomere expanded to securiform (5-20), procoxae without concealed lateral extension (38-0), protrochantin exposed (39-0), mesotrochantin exposed (56-0), tegmen situated dorsal to penis (93-2), larval accessory ventral process of mandible present (116-1), larval labial palpi contiguous or separated by less than width of first palpomere (124-0), larval abdominal tergites with curved rows of asperities (138-1), and larval spiracles annular-biforous or uniforous (145-1). Most of these are robust apomorphies for this family [e.g., all other C.S. taxa (except *Holopsis*) have the protrochantin concealed (39-1); in the majority of C.S. taxa the mesotrochantin is hidden (56-1); most C.S. taxa have annular larval spiracles (145-0)].

Corylophidae

The family Corylophidae is a strongly supported monophyletic group based on the present study (Figure 6.2) with high branch support (PP = 100) and 7 synapomorphies (14-1*, 24-0, 29-3*, 62-3, 86-0, 119-1, 129-1). The presence of membranous vesicles on club segments of the antennae (14-1*) and galea absent (29-3*) are uncontroverted synapomorphies for Corylophidae. Other apomorphies include the following: apex of mandible unidentate (24-0) and functional spiracle present on abdominal segment VII (86-0) (except *Orthoperus*, which has 5 abdominal spiracles).

The degree of separation of the metacoxae found in Corylophidae is extreme [metacoxae separated by more than 1.5 × coxal width (62-3)] and rare among Cucujoidea. Only members of Bothriderini have comparably separated metacoxae and thus share this state. Two larval characters are robust synapomorphies for Corylophidae: the ventral mouthparts protracted or slightly retracted (119-1) and gula longer than wide (129-1).

The present study supports *Periptyctus* (Periptyctinae) as sister to the remaining Corylophidae (Corylophinae *sensu* Ślipiński et al., 2009), in agreement with the recent classification proposed by Ślipiński et al. (2009).

Coccinellidae

It is not surprising that Coccinellidae was recovered as monophyletic in this analysis. The monophyly for the coccinellid clade is well supported (PP = 100) by seven synapomorphies (Figure 6.2) (22-1*, 27-1, 29-1, 79-1*, 101-2, 108-3, 117-2). All Coccinellidae have the tormae greatly reduced to small knobs (22-1*) and this character state is unique among the taxa investigated in this study. Another uncontroverted synapomorphy for Coccinellidae is having the two basal ventrites of the abdomen connate (79-1*). Coccinellids also have the following synapomorphies: well developed mandibular mola lacking (27-1), galea between 1 and 2.5 X as wide as lacinia (29-1), penis with T-shaped sclerotized basal portion (101-2), larvae with 3 stemmata (108-3), and larvae with the mesal surface of the mandibular base simple (117-2).

Within Coccinellidae our results support a basal dichotomy of clades, corresponding to Ślipiński's (2007) Microweisiinae and broadly defined Coccinellinae. The Microweisiinae are a well-supported group (BI = 100) with six synapomorphies lending support to this clade (24-0, 28-3, 121-1, 125-0, 129-2, 144-0). The remaining coccinellids, Coccinellinae *sensu* Ślipiński (2007), is supported by five synapomorphies: apical maxillary palpomere expanded to securiform (5-2), anterior tendons of metendosternite widely separated (67-0), one free medial vein in the hind wing (69-4), anal lobe of hind wing present (72-0), anterior edge of sternite IX in male with a single rod (91-3). Of these features, 5-2, 72-0, and 91-3 appear to be a fairly robust synapomorphies for this group.

Bothrideridae, Cerylonidae, Discolomatidae

Little is known about the internal phylogenetic relationships of Cerylonidae and Bothrideridae. Pal and Lawrence (1986) discussed the position of Cerylonidae, Bothrideridae and related taxa and highlighted many problems with the constitution of these two families with respect to each other (see also Ślipiński, 1990). They transferred Anommatinae from Cerylonidae to Bothrideridae based on the form of the aedeagus, the spinose tibial apices and larvae with fixed upturned urogomphi and well-developed hypostomal rods (Pal & Lawrence, 1986). Both Pal and Lawrence (1986) and Ślipiński (1990) demonstrated that from a morphological standpoint Euxestinae could not be separated from free-living Bothrideridae (Anommatinae, Teredinae, Xylariophilinae). The enigmatic Metacerylonini (Euxestinae) in particular bears many morphological similarities to the above bothriderid taxa and was considered by Dajoz (1980) to be subordinate to Bothrideridae.

The results of the present study confirm a close relationship between teredine bothriderids and euxestine cerylonids, the two here recovered as sister taxa (Figure 6.1). This sister grouping however, is only weakly supported (PP = 63). Synapomorphies uniting these taxa include: labral rods club-like (21-0*) and anterior edge of sternite VIII in male with a median strut (88-1). The monotypic cerylonid, *Loebliorylon* (not included in the present analysis), also possess club-like labral rods. Although possessing a median strut on the anterior edge of sternite VIII in the male is not common in the C.S. outside teredines and euxestines, it is neither all inclusive (e.g., *Anommatus* and *Euxestoxenus* lack one) nor is it exclusive (e.g., *Derodontus*, *Pharaxonotha*, *Mycetophagus*, and *Biphyllus* also have this state).

One finding that has been repeatedly demonstrated is the paraphyly of Teredinae as currently constituted (Figure 6.1). All of our analyses place *Oxylaemus* as the sister group to *Anommatus*, while *Teredolaemus* is consistently recovered as the sister group to *Xylariophilus*, thus rendering Teredinae paraphyletic.

The monophyly of the subfamily Bothriderinae is well supported (PP = 100) and is supported by a number of synapomorphies (Figure 6.1) including having 2 unequal protibial spurs (44-0), trochanter highly reduced and concealed within the excavation of the femur (46-1*), circular metacoxae (77-0*), tergite VIII with sides curved ventrally (87-1), anterior edge of sternite VIII in female with median strut (spiculum ventrale) (109-1), antennal length of larva is less than 0.15 times the head width (110-0), larva with 2 antennomeres (111-1), larva lacking hypopharyngeal sclerome (126-0), and separation of mesocoxae in larva less than two coxal diameters (131-1). Another strong apomorphic character state that unites this group is their parasitoid life history.

The main body of taxa currently assigned to Cerylonidae, including Ostomopsinae, Ceryloninae and Murmidiinae and the family Discolomatidae form a clade supported by four synapomorphies (16-1, 45-0, 69-5, 86-1) (Figure 6.1). All members of this group have the clypeus broadened apically, distinctly wider than the basal margin at the frontoclypeal suture (16-1). Among the taxa examined here, only a few unrelated taxa (*Periptyctus*, *Enicmus* and *Stephostethus*) share this state and thus we consider it to be a fairly robust synapomorphy for this group. Additional supporting characters include: trochanterofemoral attachment normal to elongate (45-0), hind wing without anal veins (69-5), and functional spiracle on abdominal segment VII absent (86-1). In addition, the posterior edge of last abdominal ventrite is crenulate (85-1*) (with subsequent reversion in Discolomatidae).

Multiple authors have suggested a potential sister group pairing of Murmidiinae and the family Discolomatidae (van Emden, 1928; Crowson, 1955; Ślipiński, 1990; Lawrence, 1991; Ślipiński & Pakaluk, 1991; see also Chapters 4 and 5). Murmidiine cerylonids and discolomatids share a number of adult and larval morphological features (Figure 6.1), including: ovipositor (styli) of the female absent (105-1), anterior edge of sternite VIII in female without a median strut (106-0), larval antennomere II more than twice as long as wide (112-1), larval mandibular prostheca present (118-0), and larval mesocoxae separated by more than two coxal diameters (131-1). In addition to the above characters, the larvae of *Murmidius* and Discolomatidae are both onisciform (disk-like).

Discolomatidae

Discolomatidae is perhaps the most strongly supported monophyletic family of the C.S. (bootstrap 100). Members of Discolomatidae share 16 apomorphies (12-1, 28-4*, 33-0*, 35-1, 37-1, 47-0, 65-1*, 73-3, 74-2, 84-0, 87-2, 89-2, 108-3, 110-2, 111-1, 115-2) in the present study (Figure 6.1). The three uncontroverted synapomorphies for Discolomatidae are the presence of mandibular prostheca comprising a sclerotised comb at apex of elongate membranous process (28-4), glandular openings along the lateral pronotal and elytral margins (33-0*) and concealed metacoxal extensions (65-1*). The first of these is not present in some discolomatids that are not represented in the current analysis (e.g., *Notiophygus*).

Although not considered an uncontroverted synapomorphy here, the character state pygidium with a median groove (84-0) is only found in one other distantly related taxon in this study (*Serangium*) (although this condition also occurs in Sphindidae, a basal cucujoid family) and is thus considered a robust synapomorphy for discolomatids as well. Other robust adult synapomorphies for Discolomatidae include the following: corpotentorial bridge absent (12-1), notosternal sutures incomplete or absent (37-1), elytral punctation not seriate or striate (47-0), and tergite IX in the male strongly reduced or absent (89-2). Larval characters supporting the monophyly of Discolomatidae include three stemmata (108-3), two antennomeres (111-1) and tridentate or multidentate mandibular apex (115-2).

Endomychidae

Most of the taxa currently classified as Endomychidae form a clade, albeit with only moderate topological support (PP = 82) and only 2 morphological synapomorphies. This clade is supported by having the anterior tentorial arms separated for their entire length (11-0) and the mandibular prostheca present in the larval form (118-0).

Corroborating Robertson's (2008) results, our study supports a strong sister grouping of Anamorphinae (Endomychidae) and Corylophidae (Figure 5.5), indicating that Anamorphinae should be elevated to family status. Morphological evidence supporting this sister grouping however is sparse, with only one synapomorphy supporting this group: both taxa have complex endophallic sclerites in the median lobe of the aedeagus (104-0) (not optimized on the topology due to us applying unambiguous optimization).

Nonetheless, the monophyly of Anamorphine is strongly supported (PP = 100) in the analysis and is additionally supported by the following apomorphic character states: mesoventral postcoxal pits present (57-0), metaventral postcoxal pits present (58-0), and apex of the mandible in the larva reduced to absent (115-3*); the first two characters are shared by a number of endomychids.

One of the perplexing results of the present study is the position of the Eupsilobiinae + Mycetaeinae clade as sister to the remaining Endomychidae (except Anamorphinae). In both the morphology alone and molecular alone analyses (see Chapters 4 and 5 respectively), these taxa were not allied with the remaining endomychid taxa, but instead were far removed from them. Given the above, we treat Eupsilobiinae and Mycetaeinae within Endomychidae (without Anamorphinae).

Revised Classification of the Cerylonid Series

A number of changes in the current classification are warranted based on the results of the present study.

Biphyllidae and Byturidae

Biphyllidae and Byturidae have been repeatedly recovered within the superfamily Cleroidea (Hunt et al., 2007; see also Chapter 5) and this placement is again well supported in the present analysis. We thus formally transfer Biphyllidae and Byturidae to Cleroidea.

Cerylonid Series

We formally recognize 10 families in the Cerylonid Series including Akalyptoichiidae, Alexiidae, Anamorphidae **stat. nov.**, Bothrideridae **sensu. nov.**, Cerylonidae **sensu. nov.**, Corylophidae, Coccinellidae, Endomychidae **sensu nov.**, Latridiidae, and Teredidae **sensu. nov.** as justified above.

Bothrideridae Erichson, 1845 **sensu. nov.**

Bothriderinae is elevated to family status.

Constitution:

Bothrideridae **sensu. nov.** includes all members formally classified within the subfamily Bothriderinae.

Diagnosis:

Bothrideridae **sensu. nov.** is characterized by the following combination of features: 2 unequal protibial spurs (44-0), trochanter highly reduced and concealed within the excavation of the femur (46-1*), circular metacoxae (77-0*), tergite VIII with sides curved ventrally (87-1), anterior edge of sternite VIII in female with median strut (spiculum ventrale) (109-1), antennal length of larva is less than 0.15 times the head width (110-0), larva with 2 antennomeres (111-1), larva lacking hypopharyngeal sclerome (126-0), and separation of mesocoxae in larva less than two coxal diameters (131-1). Another strong apomorphic character state that unites this group is their parasitoid life history.

Within Bothrideridae **sensu. nov.** we recognize two subfamilies: Deretaphrinae, including only the genus *Deretaphrus*, and Bothriderinae. The position of *Deretaphrus* as sister to the remaining bothriderines has been demonstrated repeatedly (see Chapters 4 and 5). All remaining Bothrideridae are classified in the subfamily Bothriderinae. The placement of enigmatic genera not included in the present study, such as *Sosylopsis,* remains uncertain.

Teredidae Seidlitz, 1888 **stat. nov.**

Constitution:

The family Teredidae includes the former Euxestinae of Cerylonidae and the free-living bothriderids, including Anommatinae, Teredinae and Xylariophilinae. We recognize the two subfamilies Euxestinae and Teredinae for the family Teredidae.

Diagnosis:

The family Teredinae is characterized by the following features: labral rods club-like (21-0*), anterior edge of sternite VIII in male with a median strut (88-1), pleural regions of abdominal segments hardened and sclerotized, and subantennal grooves distinct.

Cerylonidae Billberg, 1820 **sensu. nov.**

Constitution:

Discolomatidae is subordinated as a subfamily within Cerylonidae and the former Euxestinae is transferred to Tereididae. The new concept of the family Cerylonidae **sensu. nov.** includes the following taxa: Murmidiinae, Discolomatinae **stat. nov.**, Ostomopsinae, Ceryloninae and Loebliorylominae (insertae sedis).

Diagnosis:

Members of the family Cerylonidae **sensu. nov.** are characterized by the following combination of features: clypeus broadened apically, distinctly wider than the basal margin at the frontoclypeal suture (16-1), antennae with 6 to 11 articles and a compact antennal club that is typically 1 or 2-segmented, 3-3-3 or 4-4-4 tarsi, trochanterofemoral attachment normal to elongate (45-0), hind wing without anal veins (69-5), and functional spiracle on abdominal segment VII absent (86-1), and posterior edge of last abdominal ventrite is crenulate (85-1*) (with a subsequent reversion in Discolomatidae).

The subfamilial classification is as follows: Murmidiinae, Discolomatinae **stat. nov.**, Ostomopsinae, Ceryloninae and Loebliorylominae.

Anamorphidae Strohecker, 1953 **stat. nov.**

Constitution:

Anamorphinae is elevated to family status, as the family Anamorphidae.

Diagnosis:

The family Anamorphidae can be characterized as follows: corpotentorial bridge present, anterior tentorial arms separate for their entire length, tarsi usually 3-3-3 or 4-4-4, mesocoxal cavities externally closed, mesotrochantin concealed, median lobe simple, apex of the mandible in the larva reduced to absent (115-3*).

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Figure Captions

Table 6.1: Terminal taxa used in the present study.

Figure 6.1: Bayesian topology, first section of tree (see following figure for second section). Circles at each node represent synapomorphies supporting that clade. Corresponding character and state numbers are indicated above and below each circle respectively. Filled circles represent uncontroverted synapomorphies, by state. Open circles represent homoplasious synapomorphies. Red squares at nodes indicate posterior probabilities ≥ 90.

Figure 6.2: Bayesian topology, second section of tree (see previous figure for first section). Circles at each node represent synapomorphies supporting that clade. Corresponding character and state numbers are indicated above and below each circle respectively. Filled circles represent uncontroverted synapomorphies, by state. Open circles represent homoplasious synapomorphies. Red squares at nodes indicate posterior probabilities ≥ 90.

Table 6.1 Terminal taxa used in this study.

Superfamily	**Family**	**Subfamily** (Traditional Classification)	**Subfamily** (Alt. Classification)	**Taxon**
Derodontoidea	Derodontidae			*Derodontus*
Cleroidea	Trogossitidae			*Temnoscheila*
Tenebrionoidea	Mycetophagidae			*Mycetophagus*
Cucujoidea	Boganiidae			*Paracucujus*
Cucujoidea	Protocucujidae			*Ericmodes*
Cucujoidea	Biphyllidae			*Biphyllus*
Cucujoidea	Erotylidae			*Pharaxonotha*
Cucujoidea *Cerylonid Series*				
	Alexiidae	Alexiinae		*Sphaerosoma*
	Bothrideridae	Teredinae		*Oxylaemus*
	Bothrideridae	Teredinae		*Teredolaemus*
	Bothrideridae	Xylariophilinae		*Xylariophilus*
	Bothrideridae	Anommatinae		*Anommatus**
	Bothrideridae	Bothriderinae		*Bothrideres*
	Bothrideridae	Bothriderinae		*Dastarcus**
	Bothrideridae	Bothriderinae		*Deretaphrus*
	Bothrideridae	Bothriderinae		*Sosylus**
	Cerylonidae	Euxestinae		*Euxestoxenus*
	Cerylonidae	Euxestinae		*Hypodacne*
	Cerylonidae	Euxestinae		*Hypodacnella*
	Cerylonidae	Euxestinae		*Metacerylon*
	Cerylonidae	Ostomopsinae		*Ostomopsis*
	Cerylonidae	Murmidiinae		*Murmidius*
	Cerylonidae	Ceryloninae		*Mychocerus*
	Cerylonidae	Ceryloninae		*Philothermus*
	Cerylonidae	Ceryloninae		*Cerylon*
	Discolomatidae	Discolomatinae		*Cassidoloma*
	Discolomatidae	Discolomatinae		*Discoloma*
	Discolomatidae	Aphanocephalinae		*Aphanocephalus*
	Endomychidae	Merophysiinae		*Holoparamecus*
	Endomychidae	Pleganophorinae		*Trochoideus*
	Endomychidae	Anamorphinae		*Austroclemnus**
	Endomychidae	Anamorphinae		*Bystus*
	Endomychidae	Anamorphinae		*Mychothenus*
	Endomychidae	Leiestinae		*Phymaphora*
	Endomychidae	Leiestinae		*Rhanidea*
	Endomychidae	Mycetaeinae		*Agaricophilus*
	Endomychidae	Eupsilobiinae		*Chileolobius*
	Endomychidae	Endomychinae		*Endomychus*
	Endomychidae	Epipocinae		*Epipocus*
	Endomychidae	Stenotarsinae		*Saula*
	Endomychidae	Stenotarsinae		*Stenotarsus*
	Endomychidae	Lycoperdininae		*Amphix*
	Endomychidae	Lycoperdininae		*Lycoperdina*
	Coccinellidae	Coccidulinae	Coccinellinae ‡	*Rhyzobius*
	Coccinellidae	Coccidulinae	Coccinellinae ‡	*Rodolia**
	Coccinellidae	Scymninae	Coccinellinae ‡	*Diomus*
	Coccinellidae	Chilocorinae	Coccinellinae ‡	*Chilocorus**
	Coccinellidae	Chilocorinae	Coccinellinae ‡	*Halmus**
	Coccinellidae	Chilocorinae	Coccinellinae ‡	*Platynaspis*
	Coccinellidae	Epilachninae	Coccinellinae ‡	*Epilachna*

Coccinellidae	Coccinellinae	Coccinellinae ‡	*Coccinella*
Coccinellidae	Coccinellinae	Coccinellinae ‡	*Illeis*
Coccinellidae	Sticholotidinae	Coccinellinae ‡	*Sticholotis*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Coccidophilus*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Delphastus*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Serangium*
Coccinellidae	Sticholotidinae	Microweisiinae ‡	*Sukunahikona*
Corylophidae	Periptyctinae	Periptyctinae +	*Periptyctus*
Corylophidae	Peltinodinae	Corylophinae +	*Holopsis*
Corylophidae	Orthoperinae	Corylophinae +	*Orthoperus*
Corylophidae	Corylophinae	Corylophinae +	*Aenigmaticum*
Corylophidae	Corylophinae	Corylophinae +	*Foadia*
Corylophidae	Corylophinae	Corylophinae +	*Stanus*
Corylophidae	Corylophinae	Corylophinae +	*Clypastraea*
Corylophidae	Corylophinae	Corylophinae +	*Sericoderus*
Latridiidae	Latridiinae		*Akalyptoischion**
Latridiidae	Latridiinae		*Enicmus*
Latridiidae	Latridiinae		*Stephostethus*
Latridiidae	Corticariinae		*Corticaria*
Latridiidae	Corticariinae		*Melanopthalma*

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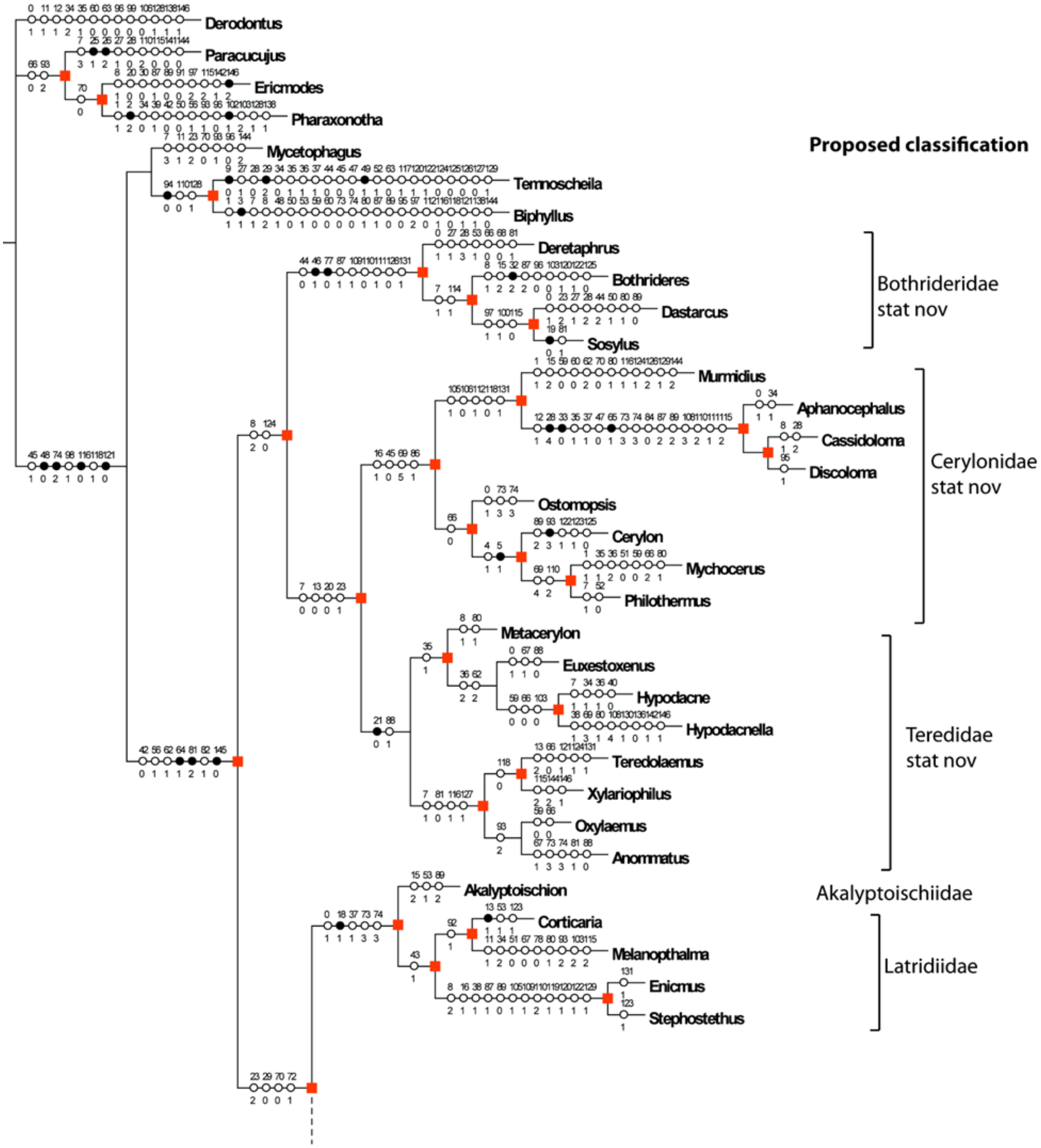
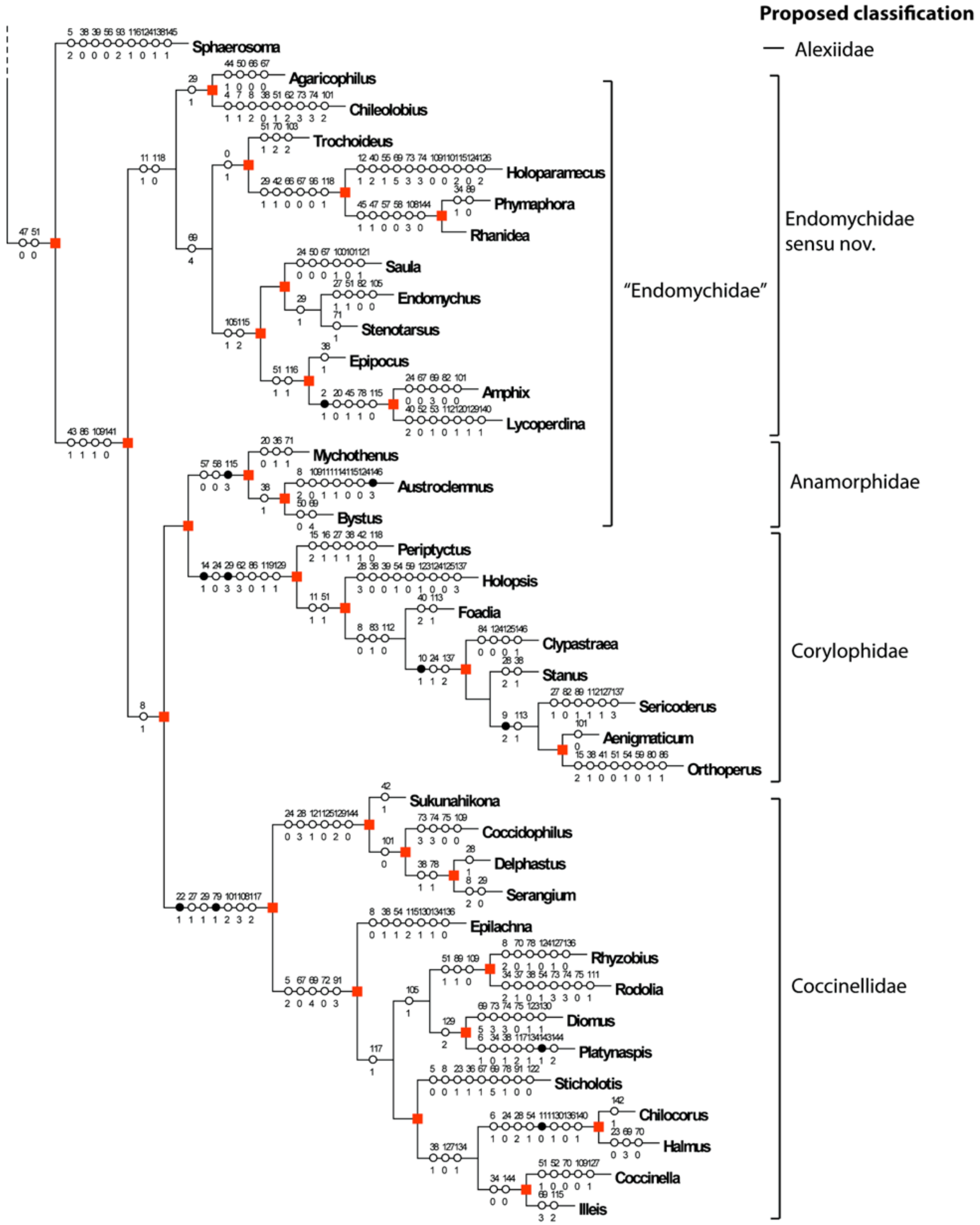
* Indicates taxa comprising molecular/molecular chimeras (see text for morphological/molecular chimeras).
‡ After Ślipiński, 2007
+ After Ślipiński et al., 2009


Derodontus
Paracucujus
Ericmodes
Pharaxonotha
Proposed classification
Mycetophagus
Termoscheila
Biphyllus
Deretaphrus
Bothrideres
Dastarcus
Sosylus
Bothrideridae stat nov
Murmidius
Aphanocephalus
Cassidoloma
Discoloma
Cerylonidae stat nov
Ostomopsis
Cerylon
Mychocerus
Philothermus
Metacerylon
Euxestoxenus
Hypodacne
Hypodacnella
Teredidae stat nov
Teredolaemus
Xylariophilus
Oxylaemus
Anommatus
Akalyptoischion
Akalyptoischiidae
Corticaria
Melanopthalma
Latridiidae
Enicmus
Stephostethus

6.1


Proposed classification
Alexiidae
Endomychidae sensu nov.
"Endomychidae"
Anamorphidae
Corylophidae
Coccinellidae
Sphaerosoma
Agaricophilus
Chileolobius
Trochoideus
Holoparamecus
Phymaphora
Rhanidea
Saula
Endomychus
Stenotarsus
Epipocus
Amphix
Lycoperdina
Mychothenus
Austroclemnus
Bystus
Periptyctus
Holopsis
Foadia
Clypastraea
Stanus
Sericoderus
Aenigmaticum
Orthoperus
Sukunahikona
Coccidophilus
Delphastus
Serangium
Epilachna
Rhyzobius
Rodolia
Diomus
Platynaspis
Sticholotis
Chilocorus
Halmus
Coccinella
Illeis

6.2

CHAPTER 7

CONCLUSIONS

We conduct a large-scale phylogenetic investigation of the Cerylonid Series (C.S.) of Cucujoidea, a diverse group of cucujoid beetles comprising 9,600 species classified in eight families, using morphological data (76 taxa × 147 adult and larval characters), molecular data (341 taxa × 9 genes) and a combination of the two datasets.

The breadth of morphological diversity in the C.S. presents major challenges to the discovery of meaningful characters that can be used for phylogenetic inference across all taxa. Primary assessment of homology for all character states across taxa is a particularly complex yet fundamental task. Despite the above challenges, we have successfully compiled an extensive morphological character matrix for the C.S. that yields support and resolution throughout the topology. During this study we discovered and refined a number of apparent synapomorphies for many higher-level clades within the C.S., providing resolution among some of the more historically problematic lineages (e.g., Bothrideridae, Cerylonidae, Endomychidae). Our results provide a solid character-based phylogenetic framework from which natural lineages may be recognized and thus contribute significantly to improving the classification for one of the most challenging superfamilies in the megadiverse order Coleoptera.

Our molecular dataset for Cucujoidea, with an emphasis on Cerylonid Series lineage diversity, is possibly the largest dataset for Coleoptera to date (341 taxa × 9 genes: 18S, 28S, H3, 12S, 16S, COI, COII, CAD and ArgK). Phylogenetic inference of the above molecular data permitted the first rigorous investigation of the placement of the C.S. within Cucujoidea, allowed us to test the monophyly of Cucujoidea with respect to the remaining superfamilies of Cucujiformia, and investigate the higher-level relationships within the C.S. and each of the C.S. families with a level of precision. This dataset also allowed us to investigate the evolution of host utilization in the above beetle groups and reconstruct the evolutionary history of cucujoid associations with diverse host types.

In the present study, we successfully generated 171 CAD and 157 ArgK sequences, thereby increasing the number of available beetle CAD and ArgK sequences by 116% and 61% respectively, a significant contribution to the current pool of sequences available for these promising, yet relatively new, loci for beetle phylogenetics.

In total, our analyses suggest the following: the C.S. is a monophyletic group based on both morphological and molecular evidence; the superfamily Cucujoidea is paraphyletic with respect to the remaining superfamilies in the series Cucujiformia; the C.S. represents a unique clade within Cucujiformia and should be recognized as its own superfamily, Coccinelloidea, within the series; Byturidae and Biphyllidae should be transferred to Cleroidea; the C.S. families Corylophidae, Coccinellidae, Latridiidae, and Discolomatidae, are monophyletic; Cerylonidae, Endomychidae, and Bothrideridae are paraphyletic. Discolomatidae is recognized as a subfamily within Cerylonidae; Bothrideridae is split into two distinct families comprising the former Bothriderinae (as Bothrideridae) and the other including the remaining subfamilies (as Teredidae); the cerylonid subfamily Euxestinae is included within Teredidae; the new concept of Cerylonidae includes the following subfamilies: Ceryloninae, Ostomopsinae, Murmidiinae, Discolomatinae and Loebliorylоninae (inserte sedis); the status of the putative new C.S. family, Akalyptoischiidae, is uncertain; the endomychid subfamily Anamorphinae is elevated to familial status, as Anamorphidae.