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Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea)

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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.

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1. 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-heteronomous 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.

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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 1237) and species (9600 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” (p. 82) and that “a complete reevaluation of characters is essential for reordering the Cerylonid Series into a maximally informative and predictive classification.” (p. 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,b), 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.

2. Materials and methods

Taxonomic exemplars for this analysis (Table 1) were obtained for seven of the eight C.S. families including Bothrideridae (one of four subfamilies represented), Cerylonidae (one of five subfamilies represented), Coccinellidae (six of six subfamilies represented), Corylophidae (two of five subfamilies represented), Discolomatidae (two of five subfamilies represented), Endomychidae (six of 12 subfamilies represented), and Latridiidae (two of two 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, and Erotylidae), three families of Tenebrionoidea (Zopheridae, Ciidae, and Tenebrionidae), and two families of Cleroidea (Cleridae and 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

Table 1

Terminal taxa used in this analysis with GenBank accession numbers

Family	Subfamily	Taxon	18S	28S
Cleridae		<i>Trichodes ornatus</i> Say	AF423775	EU145663, EU145713
Trogossitidae		<i>Temnochila virescens</i> Fabricius	EU145654	EU145711, EU145720
Zopheridae		<i>Bitoma</i> sp.	AF423768	AY310661
Ciidae		<i>Cis</i> sp.	AY310605	AY310666
Tenebrionidae		<i>Eleodes obscura</i> Say	AY310606	AY310667
Cucujidae		<i>Cucujus clavipes</i> Fabricius	AF423767	AY310660
Passandridae		<i>Catogenus rufus</i> (Fabricius)	EU145651	EU145709
Laemophloeidae		<i>Placonotus zimmermanni</i> (LeConte)	EU145649	EU145707, EU145718
Silvanidae		<i>Uleiota</i> sp.	EU145653	EU145710
Silvanidae		<i>Uleiota</i> sp.	AY310604	AY310665
Nitidulidae		<i>Carpophilus</i> sp.	AY310603	AY310664
Kateretidae		<i>Anthonaeus agavensis</i> (Crotch)	EU145648	EU145706, EU145717
Monotomidae		Monotomidae sp.	EU145650	EU145708, EU145719
Phalacridae		<i>Olibrus</i> sp.	EU145652	
Cryptophagidae		<i>Caenoscelis</i> sp.	EU145627	EU145686
Erotylidae		<i>Megalodacne heros</i> (Say)	AY310636	AY310697
Bothrideridae	Bothriderinae	<i>Sosylus</i> sp. 1	EU145596	EU145657
Bothrideridae	Bothriderinae	<i>Sosylus</i> nr. <i>extensus</i> (Say)	EU145595	EU145656
Bothrideridae	Bothriderinae	<i>Sosylus</i> sp. 2	EU145594	EU145655
Bothrideridae	Bothriderinae	<i>Bothrideres geminatus</i> Casey	EU145597	EU145658
Cerylonidae	Ceryloninae	<i>Philothermus glabriculus</i> LeConte	EU145601	EU145662
Cerylonidae	Ceryloninae	<i>Australiorylon</i> sp.	EU145598	EU145659, EU145712
Cerylonidae	Ceryloninae	<i>Cerylon castaneum</i> Say	EU145599	EU145660
Cerylonidae	Ceryloninae	<i>Cerylon unicolor</i> (Ziegler)	EU145600	EU145661
Coccinellidae	Chilocorinae	<i>Halmus</i> sp.	EU145607	EU145669
Coccinellidae	Chilocorinae	<i>Chilocorus stigma</i> (Say)	EU145610	
Coccinellidae	Chilocorinae	<i>Platynaspis</i> sp.	EU145619	EU145678
Coccinellidae	Coccidulinae	<i>Exoplectrini</i> sp.	EU145606	EU145668
Coccinellidae	Coccinellinae	<i>Cycloneda</i> sp.	EU145602	EU145664
Coccinellidae	Coccinellinae	<i>Psyllobora</i> sp.	EU145604	EU145666
Coccinellidae	Coccinellinae	<i>Harmonia euchris</i> (Mulsant)	EU145612	EU145672
Coccinellidae	Coccinellinae	<i>Hippodamia</i> sp.	EU145605	EU145667
Coccinellidae	Coccinellinae	<i>Coccinella transversalis</i> Fabricius	EU145609	EU145670
Coccinellidae	Epilachninae	<i>Epilachna</i> sp.	EU145616	EU145675
Coccinellidae	Epilachninae	Epilachninae sp.	EU145608	
Coccinellidae	Scymninae	Hyperaspidiini sp.	EU145620	EU145679
Coccinellidae	Scymninae	<i>Hyperaspis</i> sp.	EU145611	EU145671, EU145714
Coccinellidae	Scymninae	<i>Scymnus</i> sp.	EU145603	EU145665
Coccinellidae	Scymninae	<i>Diomis terminatus</i> Say	EU145618	EU145677
Coccinellidae	Scymninae	<i>Sasajiscymnus tsugae</i> (Sasaji and McClure)	EU145615	EU145674
Coccinellidae	Scymninae	<i>Stethorus</i> sp.	EU145617	EU145676
Coccinellidae	Scymninae	<i>Ortalia</i> sp.	EU145614	
Coccinellidae	Scymninae	<i>Ortalia</i> sp.	EU145621	EU145680
Coccinellidae	Sticholotidinae	<i>Sticholotis</i> sp.	EU145613	EU145673
Corylophidae	Corylophinae	<i>Clypastraea</i> sp. 1	EU145622	EU145681
Corylophidae	Corylophinae	<i>Clypastraea</i> sp. 2	EU145623	EU145682
Corylophidae	Corylophinae	<i>Sericoderus</i> sp. 1	EU145624	EU145683, EU145715
Corylophidae	Corylophinae	<i>Sericoderus</i> sp. 2	EU145625	EU145684
Corylophidae	Orthoperinae	<i>Orthoperus</i> sp.	EU145626	EU145685
Discolomatidae	Aphanocephalinae	<i>Aphanocephalus</i> sp. 1	EU145628	EU145687
Discolomatidae	Aphanocephalinae	<i>Aphanocephalus</i> sp. 2	EU145629	EU145688
Discolomatidae	Discolomatinae	<i>Discoloma</i> sp.	EU145630	
Endomychidae	Anamorphinae	<i>Anamorphus</i> sp. nov. FWS	EU145636	EU145694
Endomychidae	Anamorphinae	<i>Bystus</i> sp. 4	EU145631	EU145689
Endomychidae	Anamorphinae	<i>Bystus</i> sp. 3	EU145632	EU145690
Endomychidae	Endomychinae	<i>Endomychus biguttatus</i> Say	EU145643	EU145701
Endomychidae	Epipocinae	<i>Anidrytus</i> sp.	EU145640	EU145698
Endomychidae	Epipocinae	<i>Epopteris</i> sp.	EU145642	EU145700
Endomychidae	Leiestinae	<i>Phymaphora pulchella</i> Newman	EU145645	EU145703
Endomychidae	Lycoperdininae	<i>Acinaces laceratus</i> Gerstaecker	EU145646	EU145704
Endomychidae	Lycoperdininae	<i>Amphisternus</i> sp.	EU145644	EU145702
Endomychidae	Lycoperdininae	<i>Amphix tarsatus</i> Erichson	EU145647	EU145705
Endomychidae	Lycoperdininae	<i>Encymon gorhami</i> Csiki	EU145635	EU145693

(continued on next page)

Table 1 (continued)

Family	Subfamily	Taxon	18S	28S
Endomychidae	Lycoperdininae	<i>Lycoperdina ferruginea</i> LeConte	EU145637	EU145695
Endomychidae	Lycoperdininae	<i>Mycetina horni</i> Crotch	EU145641	EU145699
Endomychidae	Stenotarsinae	<i>Chondria armipes</i> Strohecker	EU145638	EU145696
Endomychidae	Stenotarsinae	<i>Chondria nigra</i> Strohecker	EU145639	EU145697
Endomychidae	Stenotarsinae	<i>Stenotarsus</i> sp. 1	EU145633	EU145691, EU145716
Endomychidae	Stenotarsinae	<i>Stenotarsus</i> sp. 4	EU145634	EU145692
Latridiidae	Corticariinae	<i>Corticarina</i> sp.	EU164622	EU164664
Latridiidae	Corticariinae	<i>Fuchsina occulta</i> Fall	EU164630	EU164667
Latridiidae	Corticariinae	<i>Melanophthalma</i> sp.	EU164632	EU164670
Latridiidae	Corticariinae	<i>Migneauxia orientalis</i> Reitter	EU164636	EU164665
Latridiidae	Latridiinae	<i>Dienerella intermedia</i> (Belon)	EU164638	EU164647
Latridiidae	Latridiinae	<i>Eufallia seminiveus</i> Motschulsky	EU164614	EU164645
Latridiidae	Latridiinae	<i>Metophthalmus haigi</i> Andrews	EU164643	EU164649
Latridiidae	Latridiinae	<i>Stephostethus lardarius</i> (Degeer)	EU164625	EU164651

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 seven 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, 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–check-slop 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.

3. 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 8175 were recovered from the static alignment analyses in TNT, the strict consensus of which is shown in Fig. 1. Nodes in Fig. 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 8572. The strict consensus of the POY trees (Supplemental Fig. S1) is very similar to the TNT tree (above) differing most notably in recovering Cerylonidae + Bothri-deridae 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), Corticari-inae (Latridiidae), Lycoperdininae (Endomychidae), and Coccinellidae (see Fig. 1 and Supplemental Fig. S1).

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. 2). The 50% majority rule consensus tree that was obtained from the Bayesian analysis (Fig. 2) is similar to both the parsimony TNT and DO trees, however it is unique in multiple key aspects as shown in Fig. 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 Fig. 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: Bothri-deridae, Cerylonidae, Discolomatidae, Coccinellidae, and Corylo-phidae. Endomychidae is recovered as polyphyletic. Of the 14 subfamilies with multiple terminals in this study, 11 were supported as monophyletic. The corylophid sub-family Corylophinae and the coccinellid subfamilies Chilo-corinae and Scymninae are recovered as paraphyletic. Only the Bayesian analysis recovered Latridiidae as monophyletic.

4. 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, Passandri-idae, 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. 1) have the mesocoxal cavities open while those taxa belonging to clade 16 (Fig. 1) have the mesocoxal cavities closed. Our topology supports seven abdominal spiracles as the

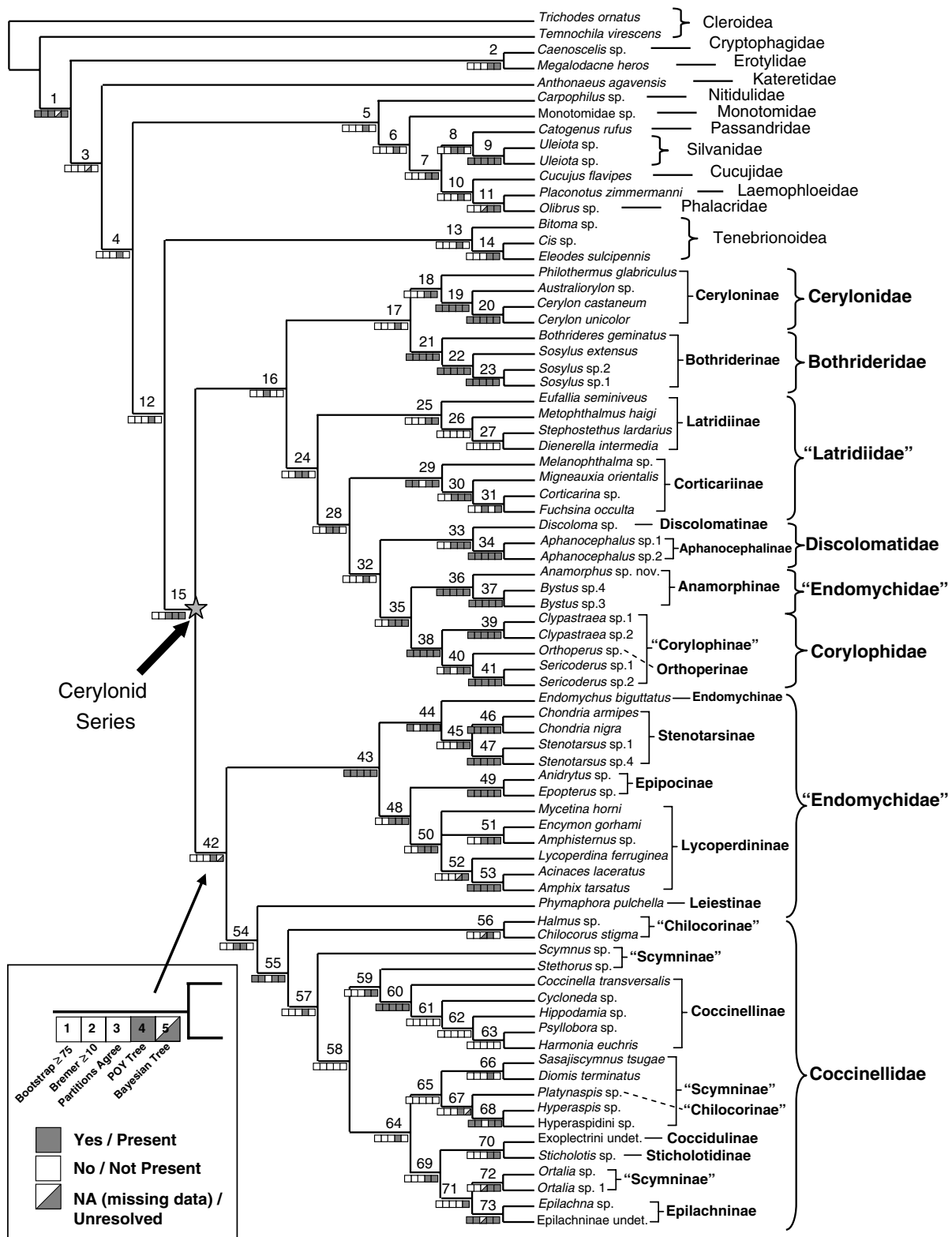


Fig. 1. Strict consensus of two most parsimonious trees found in the TNT analysis using the concatenated static alignments of the 18S and 28S data (length = 8175; CI = 0.329; and RI = 0.545). Taxonomic names in quotation represent paraphyletic taxa. The series of shaded or unshaded boxes beneath each 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.

Table 2
Nodal support for the combined 18S and 28S standard MP topology (Fig. 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%

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. 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.

4.1. Bothrideridae and Cerylonidae

Bothrideridae, Cerylonidae, and Discolomatidae were at one time included in the tenebrionoid family Colydiidae (presently Colydiinae and 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., Anommatainae (Bothrideridae),

Ostomopsinae (Cerylonidae)]. The monophyly of both Bothriideridae 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 Bothriideridae (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 bothriiderid lineages will fail to recover these families as monophyletic groups. Thus the inclusion of the remaining bothriiderid and cerylonid subfamilies is essential for delimiting these families and clarifying one important aspect of C.S. relationships.

4.2. *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, and jackknife (JK) = <50], preliminary morphological data corroborate a close affinity between these taxa (Ślipiński, personal communication).

In contrast, the Bayesian analysis (Fig. 2) of the present study strongly supports [posterior probability (PP) = 100] a clade comprising Discolomatidae, Cerylonidae, and Bothriideridae, 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 cucuj-

oid 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.

4.3. *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. 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, personal communication).

If the relationships found in the parsimony analyses (Fig. 1, Supplemental Fig. S1) 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.

4.4. *Corylophidae*

Corylophidae is generally considered to be a monophyletic group (Bowstead, 1999; Ślipiński and Pakaluk, 1991)

though many of the defining characters for the family are considered plesiomorphic (Ślipiński and Pakaluk, 1991). Bowstead (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, and 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. 1 and 2). Although current classification (Bowstead, 1999; Bowstead 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; Bowstead, 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.

4.5. Coccinellidae

Coccinellidae is by far the largest of the C.S. families with over 360 genera and 6000 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 siphon (=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, personal communication). 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, and PP = 100).

These data strongly support the monophyly of the coccinellid subfamilies Coccinellinae (BS = 40, BT = 100, JK = 100, and PP = 100) and Epilachninae (BS = 25, BT = 100, JK = 100, and 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. 1 and 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. 1 and 2). There is even a significant amount of discordance between both the TNT and DO parsimony trees (Fig. 1 and Supplemental Fig. S1). 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, personal communication), 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.

4.6. 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, personal communication). Our results place Anamorphinae as sister to Corylophidae, and the parsimony analyses recover Leiestinae as the sister taxon to Coccinellidae (Fig. 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., Merophysinae and 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,b, 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, and 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.

5. 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, Bothrioderidae, 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 Leistinae 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: (Bowstead and Leschen, 2002); Discolomatidae: (John, 1959); Endomychidae: (Roubik and Skelley, 2001; Strohecker, 1953); Latridiidae: (Andrews, 1976a,b, 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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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ympev.2007.09.017](https://doi.org/10.1016/j.ympev.2007.09.017).

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