Phylogenetic analysis of the minute brown scavenger beetles (Coleoptera: Latridiidae), and recognition of a new beetle family, Akalyptoischiidae fam.n. (Coleoptera: Cucujoidea)

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Abstract. We infer the first phylogenetic hypothesis for Latridiidae Erichson (Coleoptera: Cucujoidea). Portions of seven genes (18S ribosomal DNA, 28S ribosomal DNA, 12S ribosomal DNA, 16S ribosomal DNA, cytochrome *c* oxidase I and II and histone III) were analysed. Twenty-seven latridiid species were included, representing both subfamilies and more than half of the currently recognized genera. Eight outgroup taxa from other families of Cucujoidea were included. Parsimony and partitioned Bayesian analyses were performed on the combined dataset. In both phylogenetic analyses, the enigmatic *Akalyptoischion* Andrews (Latridiinae) was recovered outside of Latridiidae. The subfamilies Corticariinae and Latridiinae (without *Akalyptoischion*) were each recovered as monophyletic in both analyses. A new family, Akalyptoischiidae **fam.n.** is erected based on the results of the phylogenetic study and further support from adult morphology, key features of which are illustrated.

Introduction

The family Latridiidae Erichson, commonly known as minute brown scavenger beetles, is an obscure, but cosmopolitan, group of 29 genera and more than 1050 species placed in two subfamilies, Latridiinae Erichson and Corticariinae Curtis (Andrews, 2002). Latridiids are small (1–3 mm), cryptically coloured (brown to black) beetles. The main diagnostic characters traditionally used to separate this family from the remaining cucujoid families are their small size,

3-3-3 tarsal formula and elongate-oval shape. The subfamilial classification of Latridiidae is unstable due to the lack of discrete family-level synapomorphies, with few higher-level characters that adequately encompass the heterogeneity of the group. The placement of certain genera in the family, notably *Akalyptoischion* Andrews and *Eufallia* Muttkowski, is questionable due to morphological incongruence with the rest of the family (Fall, 1899; Crowson, 1955; Andrews, 1976c). The circumscription of several other genera remains ambiguous because of problematic or overlapping character combinations. Although Ślipiński & Pakaluk (1991) state that the family appears monophyletic based on their study of morphological characters within the Cerylonid Series of the Cucujoidea, a comprehensive phylogenetic analysis of Latridiidae has never been carried out.

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Classification

Considerable confusion surrounds the valid name for this family. The oldest available family-group name is Corticariidae (Curtis, 1829). However, Erichson (1842) proposed a family-group name based on the genus *Latridius* Herbst, and it has been used almost exclusively since then (Hartley & McHugh, 2010). Although it is clear that the name Corticariidae (Curtis, 1829) has priority over Latridiidae (Erichson, 1842), we use the latter (commonly used) name in this paper. We feel that use of Corticariidae Curtis would threaten the stability of the group, particularly as an appeal to the International Commission on Zoological Nomenclature for the suppression of Corticariidae Curtis is currently underway (Bousquet *et al.*, in preparation).

Latridiidae originally included four tribes: Dasycerini Reitter, Merophysiini Seidlitz, Latridiini Erichson and Corticariini Curtis. Belon (1898) included the Dasycerini in the Latridiini (as Lathridiini). Reitter (1887) later circumscribed a fifth tribe, Holoparamecini, which included some taxa previously placed in the Merophysiini (*Holoparamecus* Curtis and *Hyplathrinus* Reitter). Crowson (1955) included Latridiidae (as Lathridiidae) in the Cerylonid Series of the superfamily Cucujoidea, elevated the tribe Dasycerini to family status (Dasyceridae) within the Staphylinoidea and elevated Latridiini (as Lathridiini) and Corticariini to subfamilial status (Latridiinae and Corticariinae) within the Latridiidae. He also transferred Merophysiini and Holoparamecini from Latridiidae to a new family, Merophysiidae (Crowson, 1955), which was subsequently placed in Endomychidae (Lawrence & Newton, 1995). Several other genera (e.g. *Ostomopsis* Scott, *Anommatus* Wesmael) have been variously included or excluded from Latridiidae.

Each of the two currently recognized subfamilies, Latridiinae and Corticariinae, are characterized by several morphological characters (see Fall, 1899; Watt, 1969; Andrews, 1976c, 2002). Members of the subfamily Latridiinae have widely separated procoxal cavities that are broadly closed behind. The clypeus is on a lower plane than the frons and is sharply delimited by a deep transverse suture. Latridiines are generally glabrous and are frequently covered with a waxy secretion. The pronota of latridiines often have conspicuous grooves and carinal ornamentation. Members of the subfamily Corticariinae have narrowly separated procoxal cavities that are broadly closed behind. The clypeus and frons are on the same plane and are either separated by a fine transverse suture or fused. Corticariines are generally pubescent and lack the grooves, carinae and waxy exudate common in latridiines.

Belon (1898, 1900, 1902) conducted a series of works treating the family and reviewed generic definitions within the Latridiidae. Following these works, several new genera were described within Latridiidae (e.g. *Akalyptoischion* Andrews) and other genera were reclassified or synonymized. Walkley (1948, 1952) outlined the persistent nomenclatural instability within Latridiidae.

Biology

Latridiids occur in nearly all major biogeographical regions and terrestrial habitats. Adults and larvae are frequently found in decaying vegetation where they feed predominantly on the spores and conidia of Ascomycetes (Eurotiales, Erysiphales, Pyrenomycetes), Deuteromycetes and Zygomycetes (Mucorales) (Lawrence, 1977, 1991; Lawrence & Newton, 1980). Two genera, *Enicmus* Thompson and *Revelieria* Perris, feed on the spores of Myxomycetes (Stephenson *et al.*, 1994). One species of *Lithostygnus* Broun has been observed feeding on puffballs (Lycoperdonales) in New Zealand (R.A.B. Leschen, personal observation). Thirty species, representing several genera, have been associated with stored food products (Hinton, 1941a), but the food preference of most latridiids is unknown or unconfirmed. *Eufallia seminiveus* Motschulsky is of minor medical significance as it was reported once to bite humans (Parsons, 1969). *Dienerella filum* Aubé has been found to be a potential pest of air conditioning systems in Arkansas, U.S.A. (Carlton, 1988), presumably feeding on mould.

Morphological variation

Although a small family, Latridiidae exhibits much anatomical diversity. Because most latridiids are small, leaf-litter-dwelling fungivores, apterous and brachypterous species are common. Within the subfamily Latridiinae, the genera *Dienerella* Reitter, *Metophthalmus* Wollaston, *Revelieria* and *Eufallia* all have fused elytra (Fall, 1899; Watt, 1969). Of those, all are apterous except *Revelieria*, which is brachypterous (Fig. 1). Within the Corticariinae, several species of *Adistemia* Fall, *Corticaria* Marsham and *Fuchsina* Fall are apterous or brachypterous (Hinton, 1941a; Johnson, 1974a, 1977, 1985). Many *Corticarina* Reitter are brachypterous (Johnson, 1974b, 1979, 1990, 1997), and one species of *Herfordia* Halstead is apterous (Johnson, 1971).

Eye reduction (Fig. 2) to a small number of facets and eye loss (Fig. 3) also occurs in several members of the family. Within the Latridiinae, all *Adistemia* and *Metophthalmus* species have reduced eyes (Fall, 1899; Hinton, 1941a, b; Andrews, 1976a). The only North American species of *Eufallia* (*E. seminiveus*) has reduced eyes. Although *Dienerella intermedia* Belon exhibits eye reduction, the character is variable across the genus. Several members of *Cartodere* Thomson exhibit eye reduction (Fall, 1899; Walkley, 1948). Within the Corticariinae, the only genus without large, fully developed eyes is *Fuchsina*. Of the two known *Fuchsina* species, one has only one eye facet (*F. arida* Andrews, not included in the analysis, see below), and the other (*F. occulta* Fall, included in the analysis, see below) lacks eyes entirely (Fig. 3) (Fall, 1899; Andrews, 1976b).

Species of *Eufallia* exhibit long, exposed, cylindrical trochanters (Fig. 4), a characteristic shared with several other genera within the family (e.g. *Mumfordia* van Dyke, *Eufalloides* Hinton, *Herfordia* Halstead, *Metophthalmus*) (Fall, 1899; Van Dyke, 1932; Hinton, 1941b; Crowson, 1955;
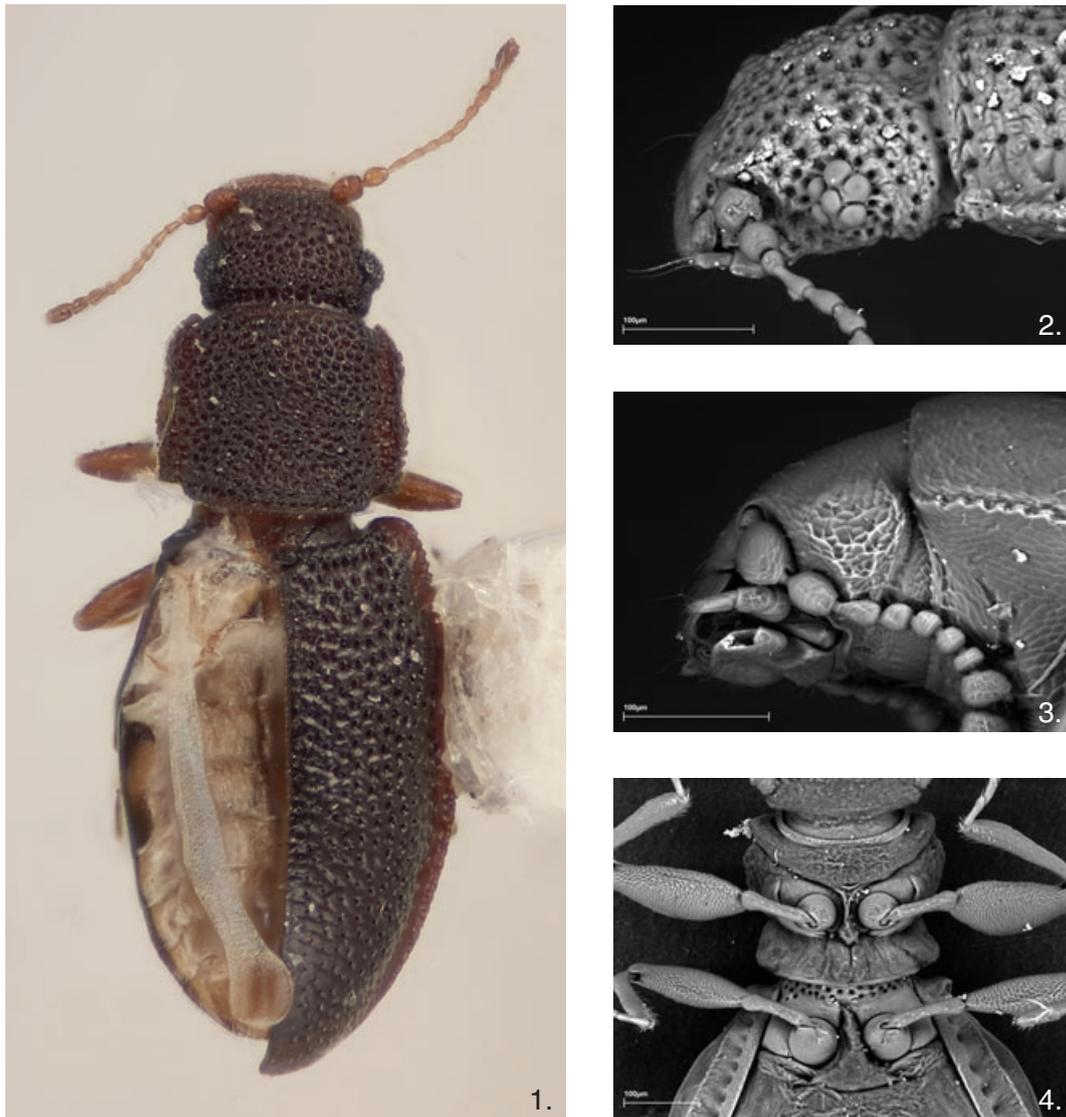
Figs 1–4. Unusual anatomical features within Latridiidae: 1, brachyptery, *Revelieria californica*; 2, microphthalmy, *Dienerella* sp.; 3, anophthalmy, *Fuchsina occulta*; 4, elongate, cylindrical trochanters on meso- and metalegs, *Eufallia seminiveus*.

Halstead, 1967; Andrews, 1976a). The functional significance of this elongation is unknown.

The placement of certain genera, most notably *Akalyptois-chion* and *Eufallia*, is questionable in part due to major departures from the typical latridiid anatomy (Fall, 1899; Crowson, 1955; Andrews, 1976c).

Objectives

Previous classifications were based on morphology and used relatively few characters. These classifications remain untested by a modern phylogenetic analysis. This work reports on the first rigorous phylogenetic analysis for this group of beetles in order to achieve the following goals: (i) to test the monophyly of the family and subfamilies and (ii) to evaluate the placement of enigmatic genera.

Materials and methods

Taxon sampling

This analysis included 27 ingroup species, representing more than half of the known genera (16/29) and both subfamilies of Latridiidae (Table S1). Of these, 15 are from Latridiinae and 12 are Corticariinae. Also included in the analysis were eight outgroup taxa representing six other cucujoid families (Table S1). The topologies were rooted to *Pselaphacus nigropunctatus* Percheron (Erotylidae), the only taxon included from outside

the Cerylonid Series. The family Corylophidae (Cucujoidea: Cerylonid Series) was not included in the analysis. Corylophidae has been hypothesized to be the sister taxon to Latridiidae (Ślipiński & Pakaluk, 1991), but this conclusion was based on few morphological characters. In recent papers by Robertson *et al.* (2008), Hunt *et al.* (2007) and Shockley (in preparation), Corylophidae was recovered nested within the Endomychidae, sister group to the Anamorphinae in Robertson *et al.* (2008) and sister to Merophysiinae in Hunt *et al.* (2007), rather than sister to the previously hypothesized Latridiidae. Several ingroup taxa were not identified below the generic level due to the poor state of taxonomy in those groups and the high probability of encountering undescribed species. Primary voucher specimens are deposited in the University of Georgia Coleoptera Tissue Collection in Athens, GA, U.S.A. (majority) and in the Santa Barbara Museum of Natural History Collection in Santa Barbara, CA, U.S.A. (CO 477, CO 488; see Table S1). DNA extraction vouchers were deposited in the BYU Insect Genomics Collection. Sequences are submitted to GenBank (Table S1).

Data sampling

DNA was extracted using the Qiagen (Valencia, CA, U.S.A.) DNEasy kit for animal tissues. The abdomen was removed prior to extraction, and the whole specimen was placed in buffer. After incubation, the specimen was removed from the buffer, rinsed, and retained as primary voucher specimens deposited in the Coleoptera frozen tissue collection at the University of Georgia. Seven genes were amplified and sequenced: 18S ribosomal DNA, 28S ribosomal DNA, 12S ribosomal DNA, 16S ribosomal DNA, cytochrome *c* oxidase I (COI), cytochrome *c* oxidase II (COII) and histone III. Polymerase chain reaction (PCR) amplification was run on a DNA Engine DYAD™ Peltier thermal cycler (Bio-Rad Laboratories, Hercules, CA). Amplification conditions used in PCR reactions are given in Table S2a. PCR product yield, specificity and contamination were monitored using gel electrophoresis. PCR products were purified using the Montage PCR$_{96}$ Cleanup Kit (Millipore®, Billerica, MA). The primer sequences and the protocol used in amplifying and sequencing are given in Table S2b (Simon *et al.*, 1994; Colgan *et al.*, 1998; Whiting, 2002; Jarvis *et al.*, 2004; Svenson & Whiting, 2004, 2009; Miller *et al.*, 2009a). Sequencing reactions were carried out using ABI Prism Big Dye® (Version 3), and reaction products were purified using Sephadex™ G-50 medium. Sequencing was carried out using an ABI 3730xl DNA analyser (BYU DNA Sequencing Center, Provo, UT). Data editing and contig assembly was carried out using SEQUENCHER® 4.0 (Genecodes, 1999).

Analytical methods

Alignment of COI, COII and histone 3 was carried out in SEQUENCHER based on conservation of the codon reading frame. Alignment of 12S, 16S, 18S and 28S ribosomal DNA was carried out using MUSCLE (Edgar, 2004) under the default settings. Gaps were treated as missing data.

A combined parsimony analysis was performed in NONA (Goloboff, 1995) as implemented by WINCLADA (Nixon, 1999–2002), with the 'heuristics' option and the commands set to hold 5000 trees in total ('h 5000'), 50 replications ('mu*50'), 40 trees held per replication ('h/40') and multiple TBR + TBR ('max*'). Bootstrap values were calculated in NONA as implemented by WINCLADA using 1000 replications, ten search replications (mults), one starting tree per rep, 'don't do max*(TBR)' and saving the consensus of each replication. Partitioned Bremer support values (Baker & DeSalle, 1997) were calculated in PAUP* (Swofford, 2000) using a batch file generated by TREEROT (Sorenson, 1999).

Partitioned Bayesian analyses were conducted using MRBAYES version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Six different partitioning strategies were implemented to further test tree topology and placement of *Akalyptoischion* (Table S5). The data were partitioned as follows: P0 – unpartitioned (0 partitions); P1 – by gene (seven partitions); P2 – by gene with COI and COII combined (six partitions); P3 – by gene, by separate codon position (13 partitions); P4 – by gene with COI and COII combined and by separate codon position (ten partitions); and P5 – by gene with COI and COII combined and by separate codon position, with positions 1 and 2 combined [eight partitions; see Miller *et al.* (2009a) for justification of this strategy]. It should be noted that it was not our goal to test various partitioning strategies, rather to investigate the sensitivity of the resulting topologies due to various partitioning strategies. Optimal models of evolution for each data partition were identified using the Akaike Information Criterion [Akaike, 1973; see Posada & Buckley (2004) for justification], as implemented in MRMODELTEST 2.3 (http://www.abc.se/~nylander/). Bayesian analyses were run through use of the CIPRES portal version 2.1 (Miller *et al.*, 2009b) for two runs of four chains for 11×10^6 generations, sampling every 1000 generations. Stationarity in all Bayesian analyses was achieved near 30 000 generations (examined graphically from Bayesian analysis outputs); therefore, the first 60 000 generations were discarded as burn-in to assure conservative estimation. In order to compare the performance of alternative partitioning strategies [see Brandley *et al.* (2005) and McGuire *et al.* (2007) for justification], the marginal likelihoods for each Bayesian analysis (including Monte Carlo error) and Bayes factors (Table S3) were calculated with TRACER 1.4 (http://tree.bio.ed.ac.uk/software/tracer/), following the procedure and test statistics of Dixon *et al.* (2009).

Preliminary results suggested the polyphyly of Latridiidae with *Akalyptoischion* resolved among the outgroup taxa. Because of this, constrained parsimony and Bayesian analyses were conducted to further test the placement of *Akalyptoischion* by confining the genus within Latridiidae sensu lato. The constrained parsimony and Bayesian analyses were performed with the same settings as above, respectively. Tree lengths, consistency index, retention index and topologies were compared for
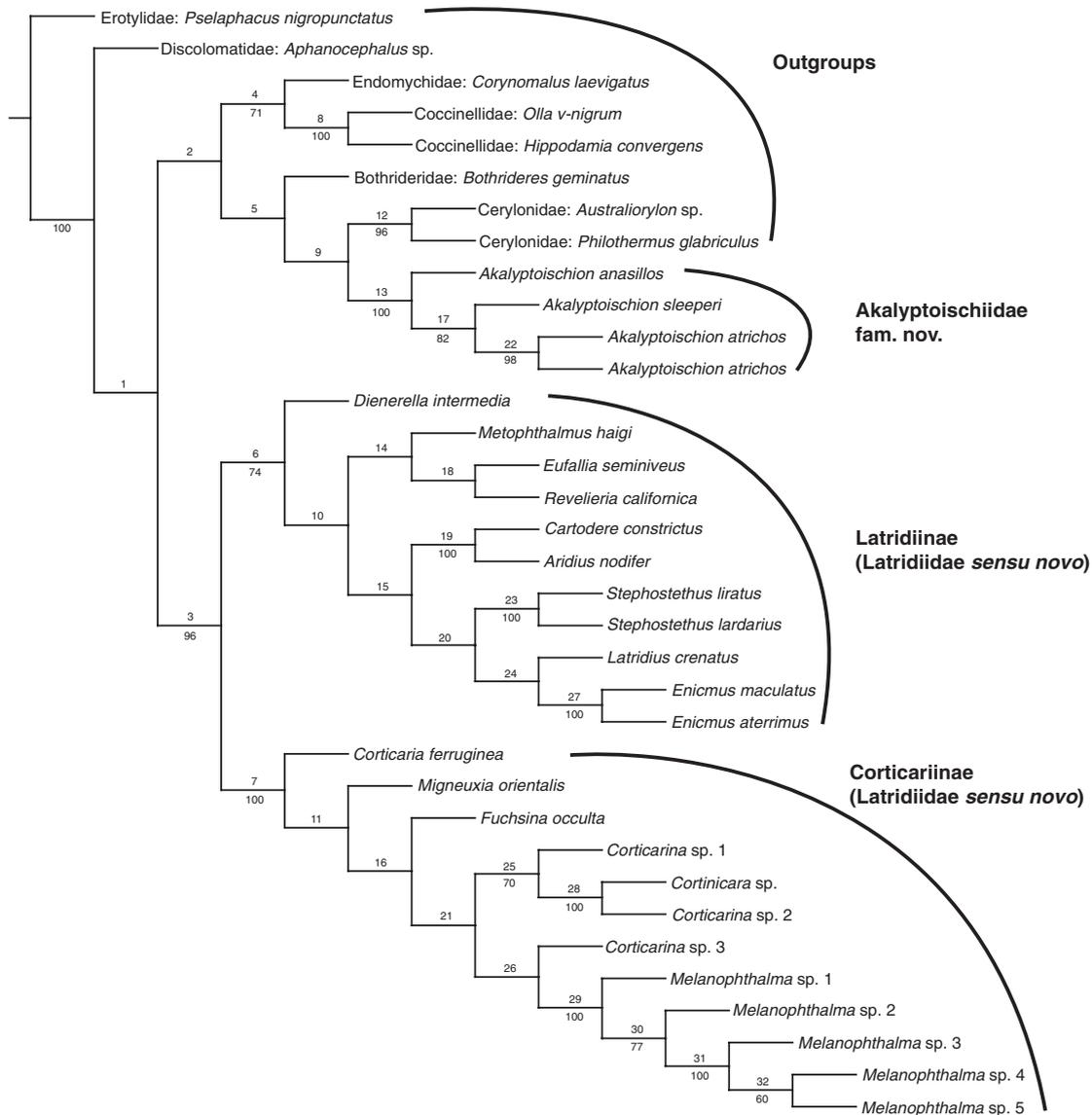
Fig. 5. Single most-parsimonious cladogram (length = 12 580; consistency index = 38; retention index = 40) for the combined, unconstrained dataset. The values below branches indicate bootstrap values (only values >50 are shown). The values above branches indicate clade number (see partitioned Bremer values, Table S4).

both constrained and unconstrained parsimony analyses, and the posterior probabilities, topologies, marginal likelihoods and Bayes factors were compared for both constrained and unconstrained Bayesian analyses.

Results

The combined dataset produced an alignment with 9465 bases. Of these 2171 were parsimony informative (Table S5). The parsimony analysis resulted in a single most-parsimonious tree (Fig. 5) (length = 12 580, consistency index = 38, retention

index = 40). Bootstrap values greater than 50 are displayed in Fig. 5. Partitioned Bremer support values (Table S4) indicate that 28S ribosomal DNA was the most influential partition in determining the most-parsimonious topology, providing 50.3% of total support (21.2% of normalized support, see Table S4).

The six Bayesian analyses yielded very similar topologies and posterior probabilities. The five partitioned Bayesian analyses (partitioning strategies 1–5) yielded nearly identical topologies. Only the placement of *Eufallia seminiveus* varied among the resultant topologies of partitioning strategies 1–5. Under partitioning strategies 1–2, *Eufallia seminiveus* grouped with *Enicmus aterrimus* + *Enicmus maculatus*, forming a
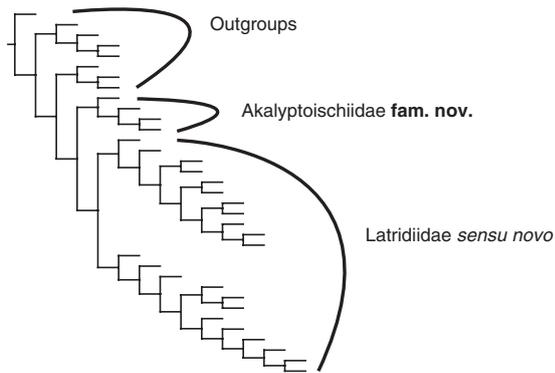
Fig. 6. Fifty percent consensus topology of trees sampled from the posterior distribution (at stationarity) from the preferred unconstrained Bayesian analysis of seven genes (ten partitions, P4, see Table S3). The values below branches indicate posterior probabilities.

clade within the remaining Latridiinae. Under partitioning strategies 3–5, *Eufallia seminiveus* did not group with the *Enicmus aterrimus* + *Enicmus maculatus* clade, but was recovered within the remaining Latridiinae. The posterior probabilities of partitioning strategies 1–2 and 3–5 varied by, at most, 0.01 and 0.15, respectively. The marginal likelihoods and 2×ln Bayes factor values (Table S3) indicated that partitioning by gene with COI and COII combined and by separate codon position (P4) was the ideal partitioning strategy in a Bayesian analysis due to highest marginal likelihood. Following Kass & Raftery (1995), $2 \times \ln BF_{P \text{ vs. } P*} > 10$ is considered strong support for P, whereas $2 \times \ln BF_{P \text{ vs. } P*} < -10$ is considered

strong support for $P*$. By comparison with P4, all other partitioning strategies were weakly supported except for P3, which was found to be only slightly less ideal ($2 \times \ln BF = 1.734$, Table S3) than P4. The unpartitioned Bayesian analysis (partitioning strategy 0) had similar posterior probabilities at most nodes and only differed from the partitioned analysis in the placement of one taxon (*Dienerella intermedia*). Therefore, only the tree with the highest marginal likelihood (partitioning strategy P4, see Table S3) is provided (Fig. 6).

The results of the parsimony and Bayesian analyses differed in topology, although the results were congruent in many important aspects (Figs 5, 6). In both analyses, Latridiidae

Fig. 7. Single most-parsimonious cladogram (length = 12 593; consistency index = 38; retention index = 40) for the combined, constrained dataset (*Akalyptoischion* clade + Latridiidae, sensu lato).

Fig. 8. Topology from the constrained Bayesian analysis under the preferred partitioning strategy (ten partitions, P4C, see Table S3).

sensu lato was recovered as polyphyletic. *Akalyptoischion*, historically classified within the subfamily Latridiinae, was not recovered within Latridiidae in either analysis. The subfamilies Corticariinae and Latridiinae (without *Akalyptoischion*) were recovered as monophyletic in both topologies. The position of *Eufallia* varied between the Bayesian and parsimony topologies, but both analyses recovered it within the subfamily Latridiinae. The internal nodes within the subfamily Corticarinae exhibit considerable incongruence between the two trees.

In all parsimony and Bayesian analyses with Latridiidae constrained to be monophyletic (i.e. with *Akalyptoischion* forced to resolve with other members of Latridiidae), *Akalyptoischion* was recovered as sister to the rest of Latridiidae (Figs 7, 8, respectively). The constrained parsimony analysis resulted in a single tree (Fig. 7) (length = 12 593, consistency index = 38, retention index = 40), and the cost of constraining Latridiidae to be monophyletic (i.e. cost of forcing *Akalyptoischion* into the latridiid clade) is 13 additional steps. The unconstrained Bayesian analyses yielded high posterior probabilities and the marginal likelihoods and Bayes factors for all constrained Bayesian analyses resulted in $2 \times \ln\text{BF}_{PC*} > -10$ (compared with corresponding unconstrained analyses), providing strong support against the constrained topologies (see Table S3). The comparison of both the Bayesian and parsimony constrained and unconstrained analyses support the exclusion of *Akalyptoischion* from Latridiidae. If future studies should happen to return *Akalyptoischion* to Latridiidae, the genus would probably form a new subfamily within the group, sister to the rest of Latridiidae sensu novo.

Discussion

Taxonomic implications

The resulting topologies (Figs 5, 6) indicate a polyphyletic Latridiidae sensu lato. Corticariinae was recovered as monophyletic, and Latridiinae sensu lato is polyphyletic with respect to *Akalyptoischion*, which was recovered nested among the
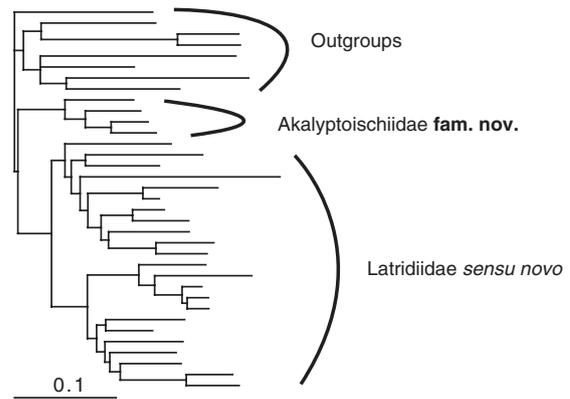
outgroup taxa. When *Akalyptoischion* was constrained to be monophyletic with the rest of Latridiidae, the genus was recovered as sister to the remaining latridiid taxa in both analyses under all partitioning strategies (Figs 7, 8). With support from morphological characters (see Table S6), evidently *Akalyptoischion* should not remain within Latridiidae.

Although there is strong evidence supporting the placement of *Akalyptoischion* outside the latridiid clade, the relationships between this genus and the outgroup taxa are not well established. The taxon sampling was inadequate to establish with confidence the sister group to *Akalyptoischion* among the outgroup taxa included in this analysis.

Within the Latridiinae sensu novo (without *Akalyptoischion*), the genera *Stephostethus* and *Enicmus* were recovered as monophyletic (Figs 5, 6) (the monophyly of each of the other genera was not tested due to limited taxon sampling). *Eufallia*, the other morphologically divergent taxon within the subfamily, showed incongruent placements in the parsimony and Bayesian analyses, but was consistently resolved within the Latridiinae in both analyses with strong support (Figs 5, 6).

The subfamily Corticariinae was recovered as monophyletic, but several genera were recovered as paraphyletic. Bootstrap values and Bayesian posterior probabilities, however, showed weak support for many of the internal nodes. *Melanophthalma* Motschulsky was recovered as monophyletic in both topologies with significant support. In the parsimony topology, *Corticarina* was paraphyletic in relation to *Cortinicara* Johnson and *Melanophthalma*. In the Bayesian topology, *Corticarina* was paraphyletic in relation to *Cortinicara* and *Fuchsina occulta*. The placement of *Migneauxia*, *Fuchsina*, *Cortinicara* and *Corticaria* was incongruent between the most-parsimonious and Bayesian analyses. Inclusion of additional exemplars of this subfamily will probably be required to resolve these relationships.

Both the Bayesian and parsimony analyses recovered a monophyletic *Akalyptoischion* that was resolved outside of Latridiidae with strong support; however, they are incongruent regarding the precise placement of the genus among the other Cerylonid Series families. The placement of *Akalyptoischion*
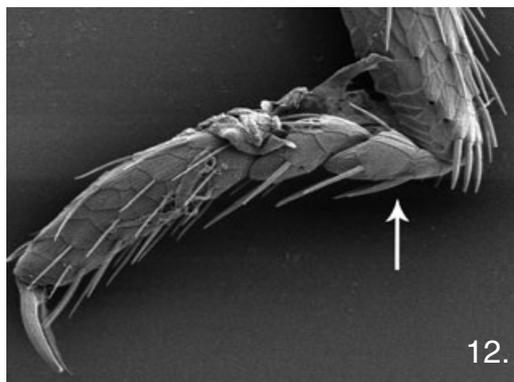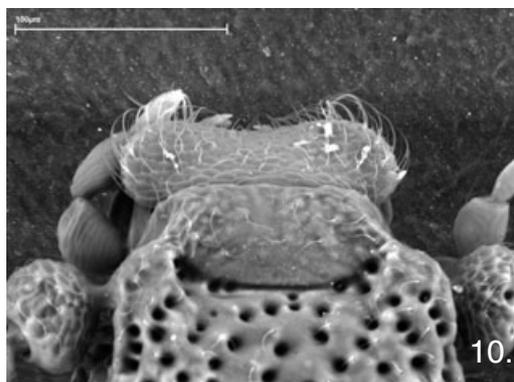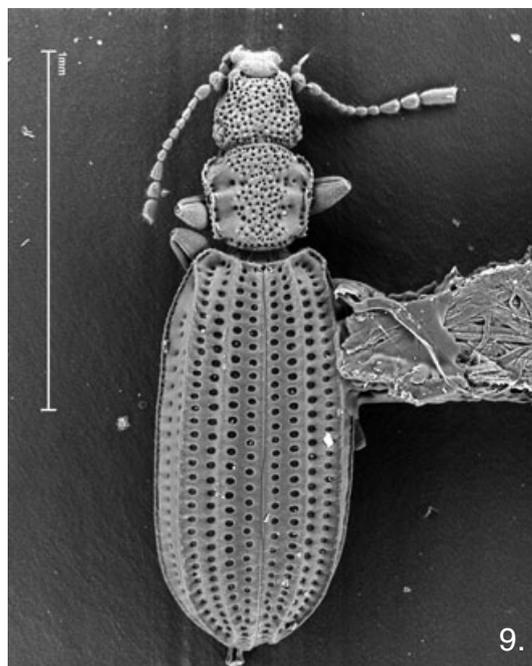
Figs 9–13. *Akalyptoischion atrichos* adult illustrating diagnostic features of Akalyptoischiidae: 9, dorsal habitus; 10, laterally expanded labrum; 11, reduced eyes positioned on posterior angles of head; 12, pseudosegmented tarsomere I.

outside Latridiidae is further supported based on adult morphology.

Putative morphological synapomorphies distinguishing this genus from the rest of Latridiidae include: posteriorly open procoxal cavities, a large, laterally expanded labrum, small eyes (two to six facets) located at the posterior angles of the head, and large, heavily sclerotized mandibles. All *Akalyptoischion* species are apterous. On all legs in all species, tarsomere I is pseudosegmented, which seems to be intermediate between 3-3-3 (as in Latridiidae) and 4-4-4 (as in several other families of Cucujoidea) (Hartley *et al.*, 2007). This pseudosegmentation, presumed to represent an incomplete fusion of these tarsomeres, is externally represented by a clear annulation and by the setation pattern. The antennae are 11-segmented, are inserted behind the base of the mouthparts, and end in a weak, two- or three-segmented club. The metaventrite bears a round fovea between the mesocoxal cavities and a transverse fovea between the metacoxal cavities. The generic revision by Hartley *et al.* (2007) included descriptions and a key to the species. Although *Akalyptoischion* species superficially resemble members of the latridiid genera *Adistemia, Dienerella* and *Metophthalmus*, the combination of the open procoxal cavities, pseudosegmented basal tarsomeres, large serrate mandibles and a large, laterally rounded labrum distinguishes this genus from the remaining members of Latridiidae.

Both phylogenetic analyses recovered *Akalyptoischion* as monophyletic and provided strong support for its placement outside the rest of Latridiidae. These findings, coupled with the compelling morphological evidence presented above, call for the recognition of a new family to accommodate *Akalyptoischion*.

Akalyptoischiidae Lord, Hartley, Lawrence, McHugh, Whiting and Miller fam.n.

Type genus: *Akalyptoischion* Andrews, 1976 by monotypy, here designated.

Diagnosis (Figs 9–13). Akalyptoischiidae is characterized by the following combination of adult characters: (i) antenna with 11 antennomeres ending in a loose, two- to three-segmented club; (ii) eyes reduced, composed of two to six facets; (iii) labrum large, laterally expanded; (iv) frontoclypeal suture distinctly impressed; (v) basal tarsomere pseudo-segmented; (vi) procoxal cavities open posteriorly; (vii) metathoracic wings absent; (viii) mesocoxal cavities narrowly separated; and (ix) with seven abdominal spiracles.

Included taxa. This family includes the genus *Akalyptoischion* Andrews with 24 species (see Hartley *et al.*, 2007).

Distribution. The genus is known primarily from the western U.S.A. Specimens have been collected from California, Arizona, Nevada, Utah, Oregon, Idaho, Texas and Mexico (see Hartley *et al.,* 2007).

Relationships. Our analyses of 9465 bp of nucleotide sequence data found significant support for the placement of the genus *Akalyptoischion* within the Cerylonid Series of Cucujoidea, but outside of the clade that includes the rest of Latridiidae. These results and the combination of morphological features found in *Akalyptoischion* effectively exclude it from all other established families in the Cerylonid Series (see Appendix).

Comments. The recent revision by Hartley *et al.* (2007) provides an identification key and descriptions for all *Akalyptoischion* species as well as a comprehensive review of the biology, morphology, distribution and taxonomy of the group. Fall (1899) described *Cartodere quadrifoveolata* as being unlike other members of the family in having highly reduced eyes, elytra with six rows of punctures and a narrowed clypeus. Walkley (1948) transferred several *Cartodere* (including *C. quadrifoveolata*) into a new genus, *Microgramme* Walkley. *Akalyptoischion* was erected by Andrews (1976c) to accommodate *C. quadrifoveolata* along with seven new species. No further work was carried out on the group until the generic revision by Hartley *et al.* (2007), which included descriptions of 16 new species. *Akalyptoischion* occurs in western North America, where it is associated most often with oak leaf litter (*Quercus* spp.). Many specimens have also been collected from the litter found in the nests of wood rats (*Neotoma* spp.). Adults are flightless and are generally collected through Berlese extraction of leaf litter (Andrews, 1976c; Hartley *et al.*, 2007). The immature stages are unknown.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-3113.2010.00532.x

Table S1. Taxa included in the analyses with corresponding GenBank accession numbers.

Table S2a. Amplification conditions used in polymerase chain reactions.

Table S2b. Primers used for amplification and sequencing.

Table S3. Marginal likelihoods, their Monte Carlo error, and the test statistic 2 × lnBF for the tested partitioning strategies of the unconstrained (P0–P5) and constrained (P0C–P5C) Bayesian analyses.

Table S4. Results of the partitioned Bremer analysis.

Table S5. Base pair distribution.

Table S6. Diagnostic features of *Akalyptoischion* species that exclude them from each currently recognized Cerylonid Series family.

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Acknowledgements

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