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Phylogenetic relationships of tribes within Harpalinae (Coleoptera: Carabidae) as inferred from 28S ribosomal DNA and the *wingless* gene

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Abstract

Harpalinae is a large, monophyletic subfamily of carabid ground beetles containing more than 19,000 species in approximately 40 tribes. The higher level phylogenetic relationships within harpalines were investigated based on nucleotide data from two nuclear genes, *wingless* and 28S rDNA. Phylogenetic analyses of combined data indicate that many harpaline tribes are monophyletic, however the reconstructed trees showed little support for deeper nodes. In addition, our results suggest that the Lebiomorph Assemblage (tribes Lebiini, Cyclosomini, Graphipterini, Perigonini, Odacanthini, Lachnophorini, Pentagonicini, Catapiesini and Calophaenini), which is united by a morphological synapomorphy, is not monophyletic, and the tribe Lebiini is paraphyletic with respect to members of Cyclosomini. Two unexpected clades of tribes were supported: the Zuphiitae, comprised of Anthiini, Zuphiini, Helluonini, Dryptini, Galeritini, and Physocrotaphini; and a clade comprised of Orthogoniini, Pseudomorphini, and Graphipterini. The data presented in this study represent a dense sample of taxa to examine the molecular phylogeny of Harpalinae and provide a useful framework to examine the origin and evolution of morphological and ecological diversity in this group.

Keywords: beetle systematics, ground beetles, large subunit ribosomal DNA, lebiomorph, nuclear genes, wingless
Abbreviations: ML - maximum likelihood, **MP** - maximum parsimony, **MPT** - most parsimonius tree, **TBR** - tree bisection reconnection
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Introduction

The carabid beetles are one of the largest groups of terrestrial predators on earth with nearly 35,000 species worldwide (Lorenz 2005). Most of the carabid species are found within the subfamily Harpalinae, a large, well-defined clade that has diversified into over 19,000 species (Lorenz 2005) since the Cretaceous period (Lindroth 1974; Ponomareko 1989; 1992). The monophyly of Harpalinae is well established from 18S rDNA, 28S rDNA, and the *wingless* (*wg*) gene (Maddison et al. 1999; Ober 2002), as well as morphological characteristics such as loss of the seta in the scrobe of the mandible, loss of setae from the male parameres, and marked asymmetry of the parameres (Jeannel 1941). In addition, weaker evidence is provided by the fact that most harpalines use formic acid and hydrocarbons in their defensive secretions (Kanehisa and Kawazu 1985; Kanehisa and Murase 1977; Moore 1979; Moore and Wallbank 1968), and most have a chromosome number in males of 2N = 36 + X (Serrano 1992; Serrano and Yadav 1984).

Harpalines live in a diversity of habitats including deep inside caves (Liebherr and Samuelson 1992; Moore 1995; Ortuno and Salgado 2000) and at the top of tropical rainforest canopies (Erwin 1979a). Some harpalines exhibit unusual morphological forms such as an elongated body in the genus *Agra*, an ant-like form in *Calybe*, snail-shell cracking mandibles in *Licinus* (Brandmayr and Brandmayr 1986), and an extremely dorso-ventrally flattened body as in *Mormolyce*. Not only are members of Harpalinae diverse in morphological form, but they display a variety of unusual lifestyles including granivory and herbivory (Forsythe 1982; Lindroth 1968), myrmecophily and termitophily (Brandmayr et al. 1994; Erwin 1981), ovoviparity (Liebherr and Kavanaugh 1985), ectoparasitism of other insects (Jolivet 1967; Lindroth 1954), specialized host mimicry by ectoparasites and sequestering toxins from their hosts for their own defense (Balsbaugh 1967; Lindroth 1971), and predation of vertebrates such as frogs (Elron et al. 2007).

Exploration of evolution of behaviors including specialized prey feeding and ovoviparity, close association with other organisms such as ants and termites, and specialized habitat preferences such as arboreality and cave-dwelling, and morphological characters associated with these habitats, as well as biogeographical patterns has been hindered by the lack of a well-supported phylogenetic hypothesis of the relationships within Harpalinae. A phylogeny is also critical in understanding the evolution and diversity of tribes, genera, and species within harpalines.

The history of carabid systematics has involved the progressive integration of various morphological (Beutel and Haas 1996; Liebherr and Will 1998; among others) and molecular characters (Maddison et al. 1999), however, the relationships of harpaline tribes have been unstable. Previous studies (Arndt 1993; Ball 1979; Erwin 1985; 1991a; 1991b; Jeannel 1941; Kryzhanovsky 1976) suggested monophyletic groups and sister group relationships based on similarities in one or a few morphological character systems, but phylogenetic analyses was not used to test these relationships. Maddison et al. (1999) were the first to apply molecular tools to study the phylogenetic relationships within Carabidae using 18S rDNA sequences. Ober (2002) used 28S rDNA and *wingless* (*wg*) to investigate the monophyly and sister group relationships of the carabid subfamily Harpalinae. Maddison et al. (1999) and Ober (2002) have demonstrated strong support for a close relationship of brachinine bombardier beetles and austral psydrines to a monophyletic Harpalinae. Previous studies, however, did not sample enough taxa within Harpalinae to examine specific tribal relationships, focused on examining intergeneric relationships, or have selected taxa on a regional basis (Cryan et al. 2001; Marinez-Navarro *et al.* 2005; Ribera et al. 2005; Ribera et al. 2006; Sasakawa and Kubota 2007). Within Harpalinae, no large-scale modern phylogenetic analysis has been undertaken of the tribes of this diverse subfamily. Such an investigation of phylogenetic relationships is important for understanding the evolution of diversification, chemical and morphological evolution, and evolution of ecological interactions of this large subfamily of beetles.

In this study, molecular data were used to examine the phylogenetic relationships within harpalines. Partial sequences of the nuclear genes 28S rDNA and *wg* were analyzed in broadly sampled taxa of harpaline tribes. Previous work (Ober 2002) was extended by adding new 28S sequences from 134 harpaline beetles and 108 new *wg* sequences. Phylogenetic hypotheses are developed for tribal level relationships among harpalines. The present study has two objectives: first, to examine the phylogenetic relationships within the Harpalinae and to determine the evolutionary relationships and monophyly of many of the tribes; and second, to assess the monophyly of the lebiomorph assemblage (Erwin 1991b; Jeannel 1941) and compare the suggested relationships of tribes with those inferred from molecular sequence data.

Methods

DNA extraction, amplification, and sequencing

Genomic DNA samples were prepared from fresh or frozen beetles, beetles preserved in 95–100% EtOH or silica gel following the protocol in Maddison et al. (1999). Voucher specimens have been deposited in the D. Maddison Voucher Collection at the University of Arizona or in the K. Ober Voucher Collection at the College of the Holy Cross. Approximately 1050 base pairs of the D1 - D3 region of 28S rDNA and 500 base pairs of the *wg*

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gene were amplified and purified for each species with the protocols and primers described in Ober (2002) or with the alternative 5′ *wg* primer 5′WGB 5′-ACBTGYTGGATGCGNCTKCC-3′. 28S PCR products from *Diploharpus*, *Oxycrepis*, *Teukrus*, *Endyomena*, *Harpalus*, and *Adrimus* and *wingless* PCR products from *Antimerina*, *Atranus*, *Badister reflexus*, *Brachyctis*, and *Incagonum*, were gel-purified and cloned with a TA-Cloning kit from Invitrogen in the pUC18 plasmid in *Escherichia coli* INVα using standard protocols and sequenced with the M13R and T7 primers. Sequencing of both strands of the PCR product with the PCR primers for *wingless*, and the PCR primers or modified primers (D1ALT 5′-AAAGAAACTAACWAGGTT-3′ and D33′ALT 5′-TTCACCATCTTTCGGGTCC-3′) for sequencing 28S was performed by the DNA Sequencing Service, Laboratory of Molecular Systematics and Evolution, at the University of Arizona, using an ABI automated DNA sequencer. Individual sequences were assembled and ambiguous and conflicting bases were corrected using Sequencher 3.0 (Gene Codes Corp.). The sequences generated for this study have been deposited in GenBank, and their accession numbers are listed in Appendix 1.

Taxon Sampling

Included in this study were members of 34 tribes of Harpalinae (Appendix 1 (#app1-8-52)), representing about 85% of the harpaline tribes (Lorenz 2005). 28S sequences were collected from 213 taxa, 193 harpalines, and 20 outgroup taxa. The outgroup taxa represent carabid lineages considered to be closely related to Harpalinae, including brachinine bombardier beetles and austral psydrines, and other more distantly related taxa to connect harpalines to the rest of Carabidae. The *wg* gene fragment could not be amplified or sequenced from some taxa in this study. Therefore the *wg* data set contained 173 taxa, 157 of which are harpaline taxa, and 16 outgroup taxa.

Alignment

The *wg* gene fragment in this study included the 3′ coding region. *wg* sequences were aligned by eye in MacClade 4.0 (Maddison and Maddison 2000) using the translated amino acid alignment as a guide for the nucleotide alignment. The initial protein alignment was produced by ClustalW 1.7 (Thompson et al. 1997) and adjusted by eye in MacClade with taxon names hidden.

28S rDNA sequences were aligned initially with Clustal W using default settings and subsequently aligned by eye with reference to secondary structure folding models of Gutell et al. (1994) and Gillespie et al. (2004). Taxon names were hidden and sequences were ordered according to the Clustal W guide tree. Regions that could not be aligned unambiguously were excluded from phylogenetic analyses.

ClustalW was used to produce ten different alignments based on the following arbitrary gap opening:gap extension costs: 20:5, 15:3, 12:7,10:5, 10:2, 8:3, 7:2, 5:1, 3:2, and 3:0.05, randomly reordering the taxa for each Clustal alignment (Maddison et al. 1999; Ober 2002). Each of the ten alignments was judged by their obvious misalignments of nucleotides and the number of artificial columns of single or a few nucleotides surrounded by gaps created by Clustal and the number of hyper-variable regions with taxon names hidden and taxon ordering unfamiliar. The Clustal alignments were ranked, and the best one (28SH1, 15:3) was chosen to be the matrix used in phylogenetic inference.

The aligned *wg* data and 28S by eye (28Sbe) alignment were combined into a single a single data matrix, as were the 28S H1 alignment and the *wg* alignment. All 213 taxa were included even though 40 taxa were missing *wg* data. The same regions excluded in the separate 28S data sets were excluded in the combined data sets. Nexus files for all data sets are available from K. Ober.

Phylogenetic Analyses

Maximum parsimony (MP), maximum likelihood (ML) using PAUP* 4.0vb10 (Swofford 2003), and Bayesian Inference using MrBayes v3.1 (Ronquist and Huelsenbeck 2003) were carried out on the *wg* dataset, the 28Sbe data set, and the combined 28Sbe+*wg* data set. Strong molecular evidence from 18S rDNA (Maddison et al., 1999; Ober 2002), 28S rDNA, and *wg* (Ober 2002) indicates that the subfamily Harpalinae (*sensu*Erwin 1985) is monophyletic, therefore all results of analyses presented in this study have Harpalinae constrained to be monophyletic. If Harpalinae is not constrained to be monophyletic, brachinines move within the subfamily in some analyses.

Phylogenetic trees were reconstructed using MP heuristic searches for all data sets (*wg*, 28Sbe, 28SH1, combined 28Sbe+*wg*, and combined 28SH1+*wg*) using the parsimony ratchet (Nixon 1999), as implemented in PAUPRat (Sikes and Lewis 2001) and PAUP*. The ratchet search was run for 200 iterations for each data set followed by TBR branch swapping. The trees resulting from the ratchet search were submitted to an addition TBR heuristic search in PAUP*. All characters were treated as unordered, and gaps were treated as missing data. Internal support was evaluated by nonparametric bootstrap based on 1000 bootstrap replicates saving only 10 trees per replicate using TBR branch swapping and simple stepwise addition. Robustness for clades of particular interest was evaluated using decay scores (Bremer 1988, 1994) using PAUP* and a command file from MacClade 4.0.

Phylogenetic trees for *wg*, 28Sbe, and 28Sbe+*wg* data sets were estimated using ML methods as implemented in PAUP*. Analyses were performed according to the General Time Reversible substitution model with among-site rate variation (i.e., GTR+I+Γ). For all data sets model

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selection was determined by likelihood ratio tests with starting trees obtained from a simple likelihood search as described in Ober (2002). Searches for highest likelihood trees, with fixed parameter values, consisted of SPR branch swapping and two random addition sequence replicates. (See Appendix 2 for ML search parameter values.)

Finally, trees were inferred for the *wg*, 28Sbe, and the 28Sbe+*wg* data sets using MrBayes. Four independent Bayesian runs were performed for each data set using Metropolis-coupled Markov chain Monte Carlo (MCMCMC) simulations run for two million generations for the 28Sbe+*wg* data, three million generations for the *wg* data, and ten million generations for the 28Sbe data, using four simultaneous MCMCMC chains. Trees were sampled every 100 generations from the approximated posterior distribution. The GTR+I+Γ parameters of each process partition (28S partition and *wg* codon positions) were set to be independent and were estimated using Bayesian analysis. Prior distributions for all parameters were set to MrBayes defaults. Bayesian topology and branch posterior probabilities were computed by majority rule consensus after removing all "pre-burnin" trees (Mau et al. 1999). Burnin was determined by plotting likelihood scores against generation number discarding samples before the likelihood score has reached stationarity, approximately the first 30% of all samples.

Hypothesis testing

Additional MP analyses were performed to specifically address several tribal relationships within Harpalinae. MPTs were examined for each data set using the parsimony ratchet as above. In each search, one of the following was constrained to be monophyletic within Harpalinae: lebiomorph assemblage [Lebiini (including *Celeanephes* and excluding *Plagiotelum*), Cyclosomini, Graphipterini, Catapiesini, Odacanthini, Lachnophorini, Pentagonicini, Calophaenini, and Perigonini]; Lebiini (*sensu stricto*); Odacanthitae (Odacanthini, Lachnophorini, Calophaenini, and Pentagonicini); and Graphipterini + Cyclosomini.

Results

The aligned sequence data consisted of 1233 bases (after excluding 537 ambiguous sites of the alignment) for 28Sbe, 831 bases for 28SH1, 544 bases for *wg*, 1777 bases for 28Sbe+*wg*, and 1375 bases for 28SH1+*wg*. Table 1 shows the summary of phylogenetic analysis results for each data set.

Combined 28Sbe+*wg*

MP analyses resulted in four most parsimonious trees (MPTs). A strict consensus of these trees is shown in Figure 1. Bootstrap support for deeper branches and larger clades was low. The results of the ML analyses differed in the deeper relationships among the clades (Figure 2) with low Bayesian posterior probabilities on most deep branches, but the MP and ML trees shared some well-supported similarities (high bootstrap and posterior probabilities) including a monophyletic Zuphiitae (comprised of tribes Anthiini, Dryptini, Galeritini, Helluonini, Physocrotaphini, and Zuphiini) plus Ctenodactylini and Hexagoniini, monophyletic Platynini, monophyletic Harpalini, a clade including pterostichines (plus *Calathus* and *Synuchus*), metiines, abacetines, and loxandrines, and a clade comprised of Graphipterini, Pseudomorphini, and Orthogoniini. Morionines (plus *Badister* in the MP

Table 1. Summary of analyses and results for each molecular data set and analysis method.

Analysis	Data Set	# of Best Trees	Tree Score
MP	28Sbe + wg	4	17924
ML	28Sbe + wg	1	-lnL 76294.233
BI	28Sbe + wg	108,792	
MP	28SH1 Clust+ wg	360	12834
ML	28SH1 Clust + wg	1	-lnL 76298.125
MP	wg	74	7030
ML	wg	3	-lnL 27591.035
BI	wg	5,002	
MP	28Sbe	392	10478
ML	28Sbe	1	-lnL 46349.648
BI	28Sbe	29,004	
MP	28SH1 Clust	2,304	5436
ML	28SH1 Clust	2	-lnL 46362.416

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trees) and the Zuphiitae + Ctenodactylini + Hexagoniini occupied positions sister to the rest of harpalines. The large, diverse tribe of Lebiini was largely monophyletic in both the MP and ML trees (Cyclosomini and *Plagiotelum* were included). A common, but not well-supported relationship was seen among the tribes Oodini, Chlaenini, and Panagaeini. This clade included Perigonini in the MP consensus tree.

The results of ML phylogenetic analyses of combined 28SH1+*wg* Clustal alignment were similar to the 28Sbe+*wg* ML tree in overall topology. The results of the *wg*+28SH1 MP analyses (not shown) had few overall deep relationships similar to the 28Sbe+*wg* MP tree. In the MP and ML trees, the tribes Platynini, Lachnophorini, and Harpalini were monophyletic. Abacetines and loxandrines formed a clade, as did Graphipterini + Pseudomorphini + Orthogoniini. The ML tree had a Zuphiitae clade together with ctenodactylines + hexagoniines, however in the MP tree, some galeritines were not included in the clade.

wingless

Figure 3 shows the strict consensus of 74 MPTs. The deeper branches of the *wg* harpaline tree and most clades have little bootstrap support. Most of the bootstrap support was for clades at the tips of the tree. Lachnophorines, and a clade containing oodines, chlaeniines, and panagaeines were sister to the rest of Harpalinae. The majority of the Zuphitae clade was paraphyletic with respect to Morionini and *Catapiesis*. *Galerita* plus ctenodactylines were found in a group with lebiines. Orthogoniines, pseudomorphines, and graphipterines formed a clade. Platynini and Harpalini were each monophyletic, but many other tribes were not monophyletic. Lebiines were not monophyletic and pieces of this tribe were grouped with Harpalini, Licinini (in part), *Eripus*, *Caelostomus*, and Perigonini. Cyclosomines were not associated with the lebiine clade in this tree.

ML analyses found 3 trees of high likelihood (Figure 4). Like the MPTs, many tribes were polyphyletic. Platynines and harpalines were each monophyletic, and orthogoniines, pseudomorphines, and graphipterines formed a clade. Zuphiitae was not monophyletic and some tribes were associated with other taxa including *Celeanephes*, *Catapiesis*, and morionines among others. Cyclosomines were not associated with the lebiine clade.

28S rDNA

MP analyses of the 28Sbe data set resulted in 392 MPTs in two islands (island 1 of 384 MPTs and island 2 of 8 MPTs). A strict consensus of all 392 MPTs (not shown) suggested little resolution at deeper, tribal level relationships although most tribes were monophyletic but without strong bootstrap support. Pseudomorphines + orthogoniines + graphipterines formed a clade with low bootstrap support. In all MPTs, *Synuchus* and *Calathus* were grouped with pterostichines, and metiines were the sister group to the rest of Harpalinae. Zuphiitae was monophyletic, with moderate bootstrap support, and sister to the ctenodactylines. Lebiines were polyphyletic. One island of MPTs had Licinini (in part) branching after Metiini at the base of Harpalinae. *Celeanephes* + *Amara* were in a clade with odacanthines + pentagonicines and the ctenodactylines + Zuphiitae. The second island of MPTs had *Amara* branching after Metiini at the base of harpalines then a clade of odacanthines + pentagonicines, *Celeanephes*, and pseudomorphines + graphipterines + orthogoniines.

The ML analyses of the 28Sbe data set resulted in a single tree (Figure 5). The Bayesian Inference yielded little support for most clades especially deeper braches at the base of Harpalinae (Figure 5). However, most tribes were monophyletic and many tribal relationships were similar to results of other analyses. A clade of *Amara*, *Celeanephes*, metiines, and licinines formed the sister group to the rest of Harpalinae. Zuphiite tribes formed a clade near Licinini (in part). Pseudomorphines + graphipterines + orthogoniines formed a clade closely related to Lachnophorini and *Calophaena*. Oodines, chlaeniines, and panagaeines are grouped together. Lebiini (plus Cyclosomini and *Plagiotelum*) was one large paraphyletic group that included ctenodactylines and *Catapiesis*.

Results of the ML and MP analyses of the 28SH1 Clustal alignment (not shown) did not share many similarities with other analyses. Most tribes were not monophyletic in the MPTs. The 2304 MPTs showed a Zuphiitae clade, a monophyletic Platynini, a clade with pseudomorphines + orthogoniines, and *Celeanephes* with Lachnophorini. The two best ML trees had most tribes monophyletic and shared many clades in common with the 28Sbe analyses and other data sets, including a monophyletic Zuphitae, monophyletic Pseudomorphini + Graphipterini + Orthogoniini, and Odacanthini + Pentagonicini.

Summary of phylogenetic results

In general, there was very little consensus for the deeper relationships within Harpalinae from 28S rDNA and *wg* data. Results of most analyses conflicted on the intertribal relationships, and there was little or no support for these deep clades. Phylogenetic relationships conflicted among trees from different analyses. Thus, these data sets are sensitive to the optimality criterion and alignment method. However from these analyses a few general similarities can be observed. The lebiomorph assemblage was polyphyletic and the tribes comprising this group were scattered throughout the tree in four to nine groups depending on dataset and analysis. The tribe Lebiini was largely monophyletic or split into a few clades, and included the tribe Cyclosomini and the genus *Plagiotelum*. *Celeanephes* was not grouped with other members of Lebiini, but its position was variable. Odacanthines and lachnophorines do not form a clade, instead pentagonicines

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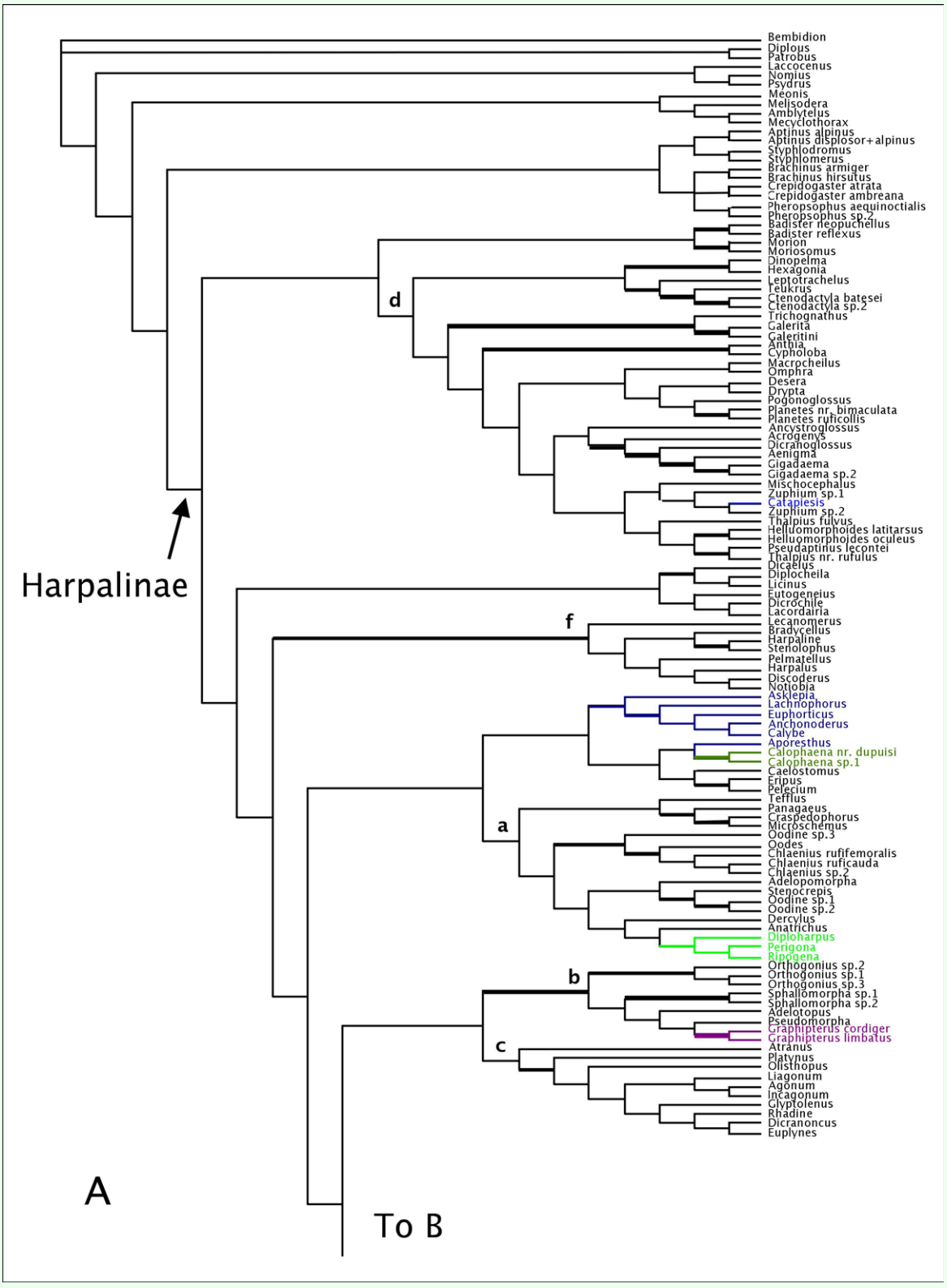


Figure 1. Strict consensus tree of four most parsimonious reconstructions of combined 28Sbe+*wg* dataset. Thick branches show clades supported by greater than 70% bootstrap. Colored branches are members of the lebiomorph assemblage color coded by tribe. Clade (a) represents Chlaenini + Panagaeini + Oodini group, (b) Orthogoniini + Graphipterini + Pseudomorphini clade, (c) Platynini, (d) Zuphiitae clade, (e) Lebiini, (f) Harpalini, (g) Pentagonicini +Odacanthini clade, (i) clade comprised of pterostichines and relatives.

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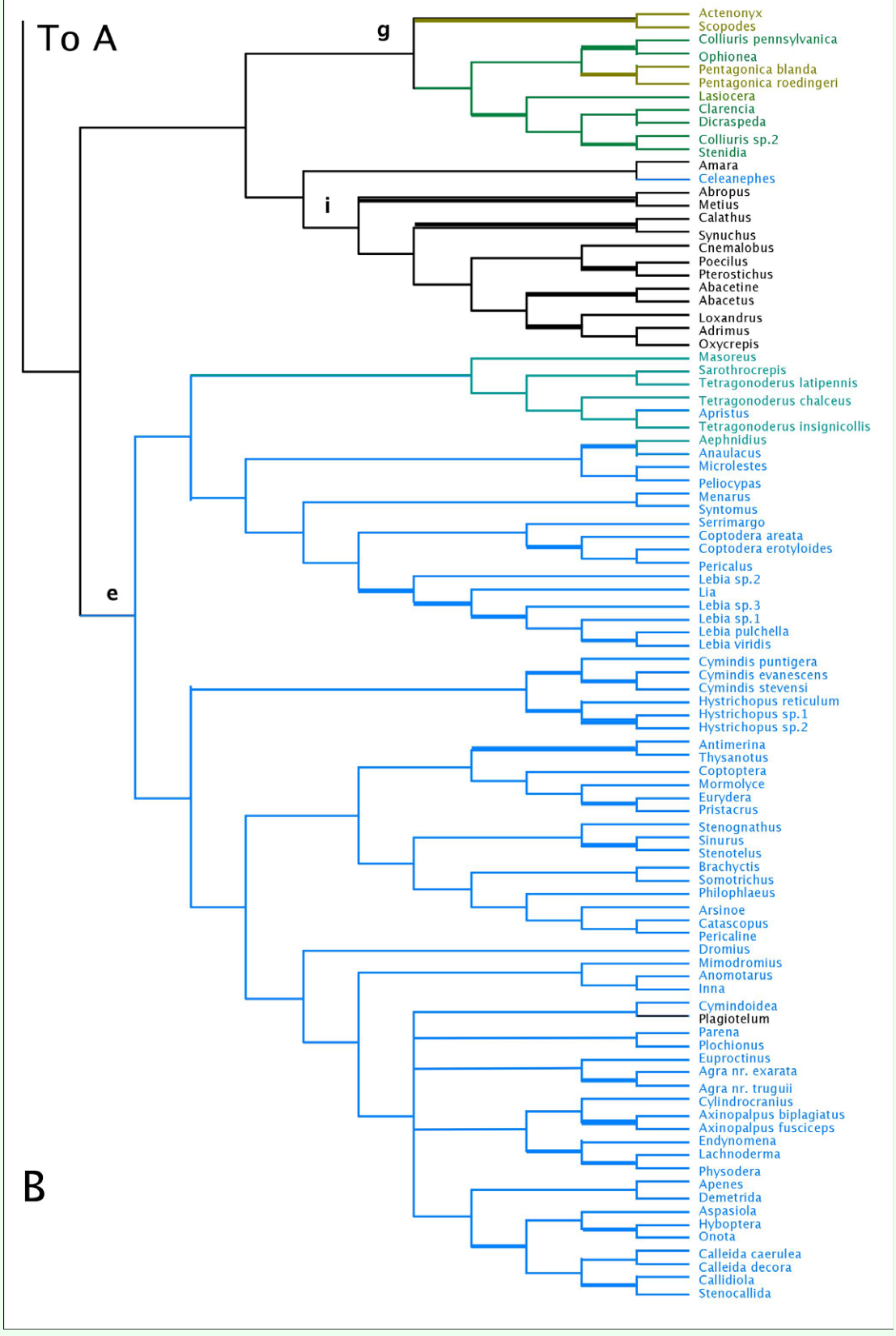


Figure 1 (con't).

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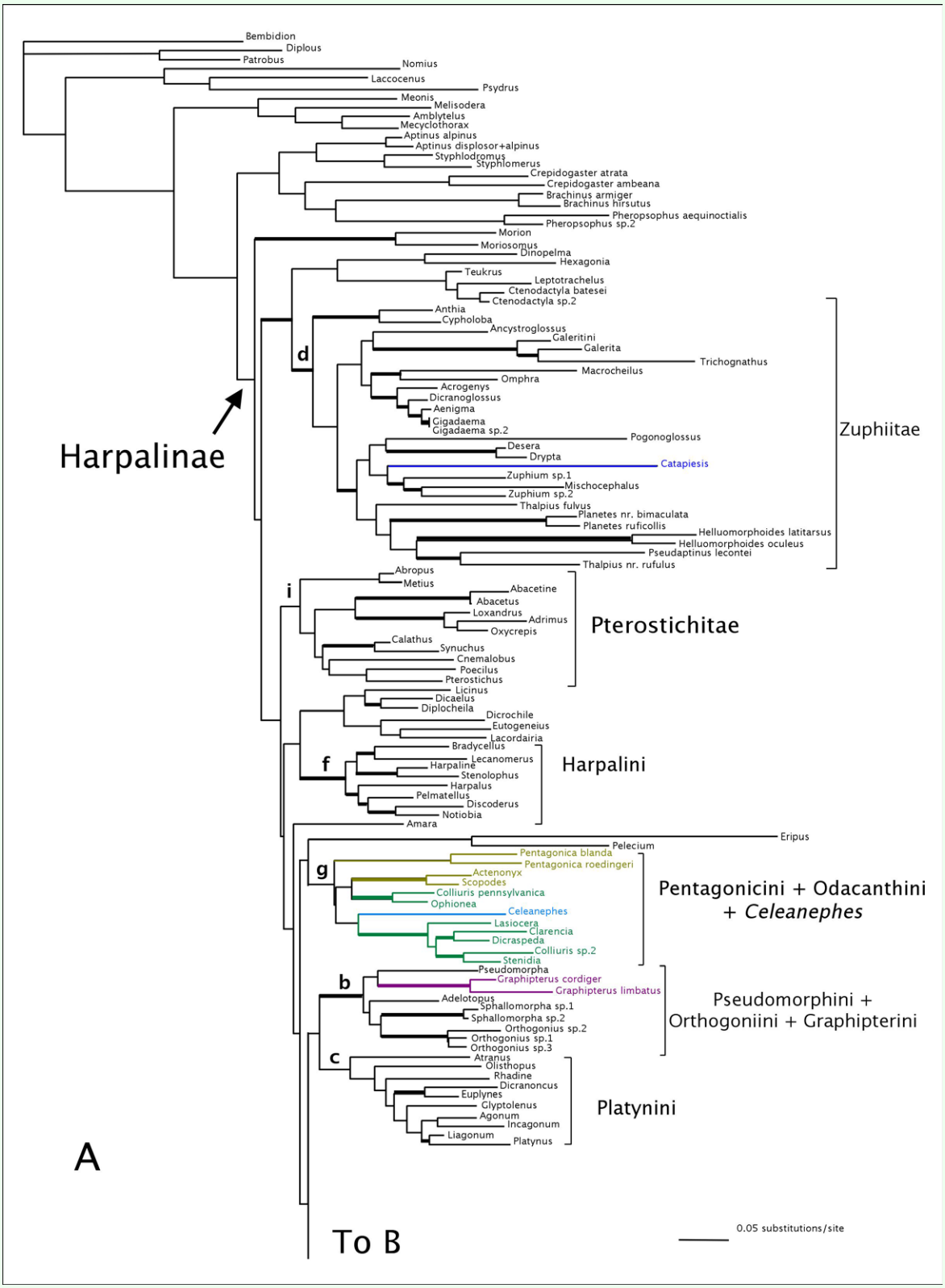


Figure 2. Tree of highest likelihood from the 28Sbe+*wg* dataset. This tree represents the preferred phylogenetic hypothesis of Harpalinae. Thick branches show clades supported by greater than 95% posterior probability from Bayesian inference. Colored branches are members of the lebiomorph assemblage color coded by tribe. Clade (a) represents Chlaenini + Panagaeini + Oodini group, (b) Orthogoniini + Graphipterini + Pseudomorphini clade, (c) Platynini, (d) Zuphiitae clade, (e) Lebiini, (f) Harpalini, (g) Pentagonicini +Odacanthini clade, (h) Lachnophorini + *Calophaena*, (i) clade comprised of pterostichines and relatives.

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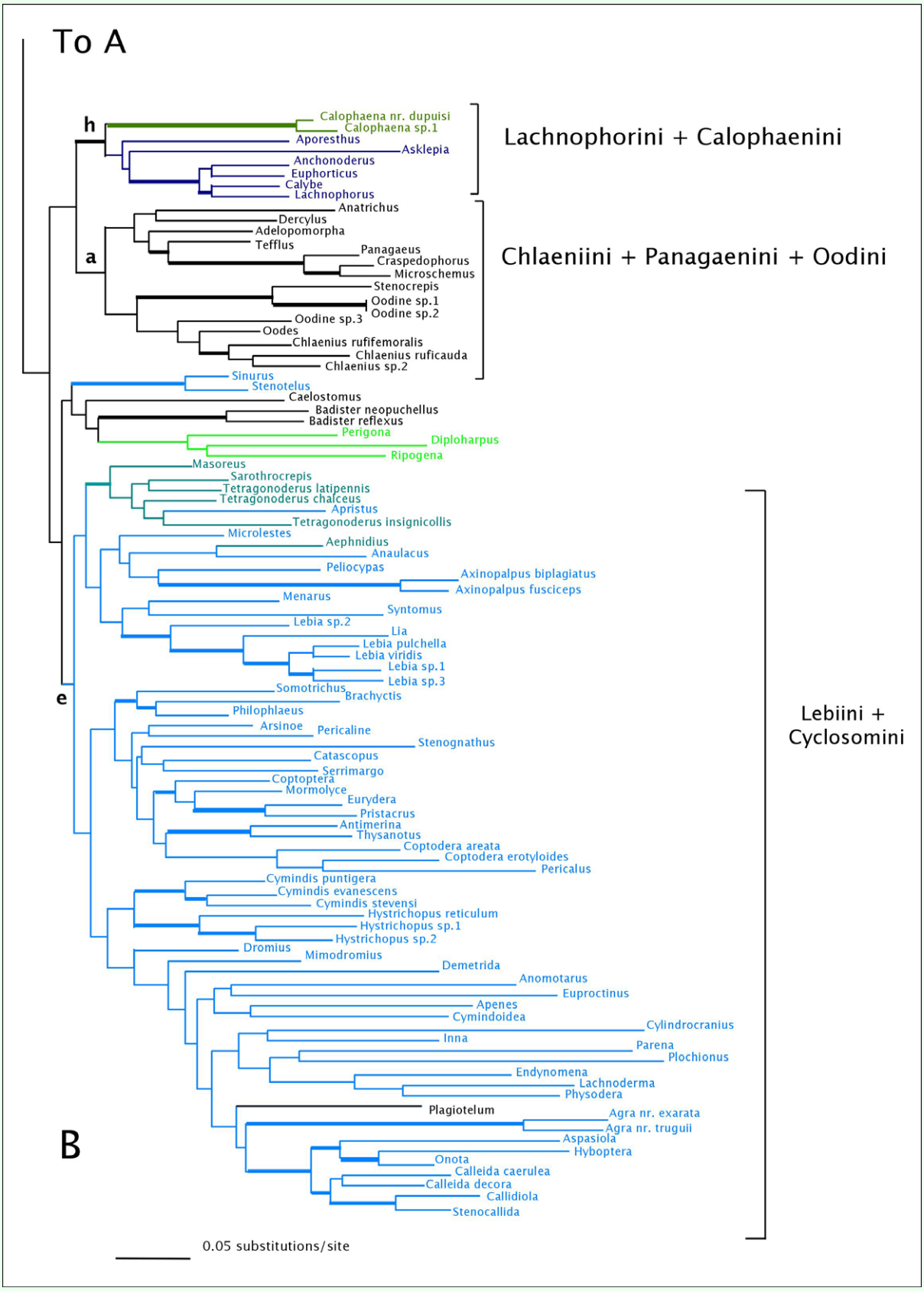


Figure 2 (con't).

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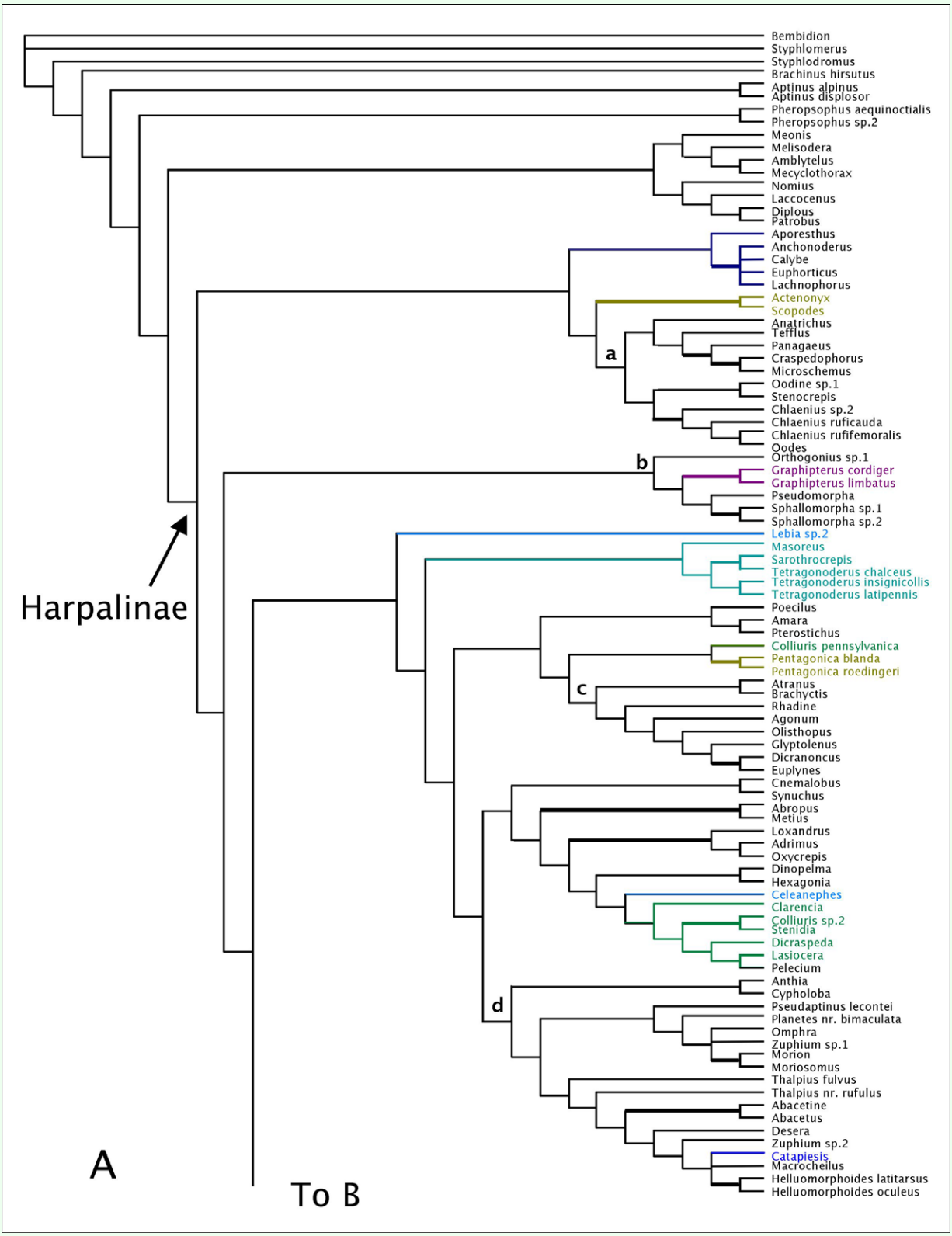


Figure 3. Strict consensus tree of 74 most parsimonious reconstructions of *wg* dataset. Thick branches show clades supported by greater than 70% bootstrap. Colored branches are members of the lebiomorph assembledge color coded by tribe. Clade (a) represents Chlaenini + Panagaeini + Oodini group, (b) Orthogoniini + Graphipterini + Pseudomorphini clade, (c) Platynini, (d) Zuphiitae clade, (e) Lebiini, (f) Harpalini.

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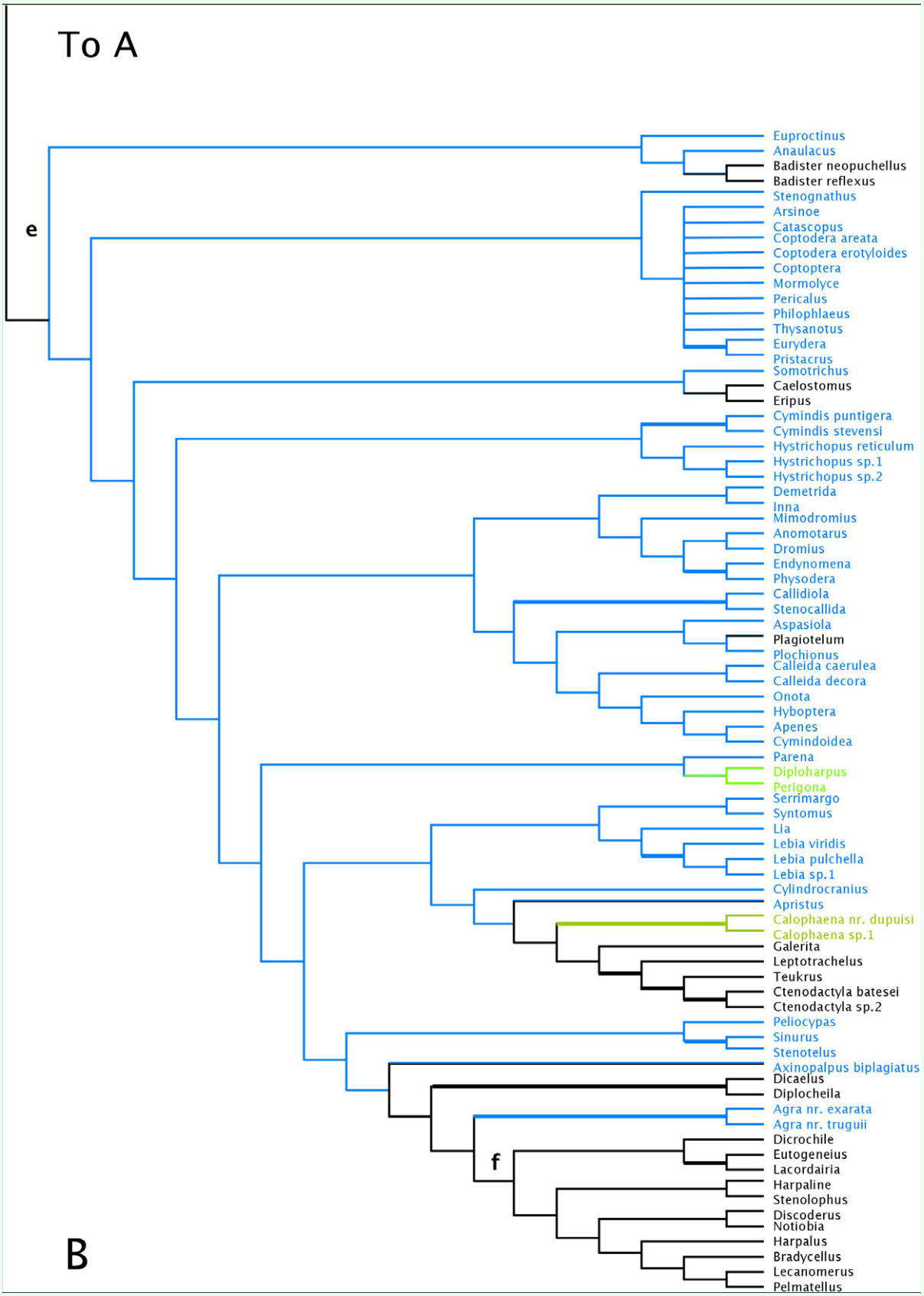


Figure 3 (con't).

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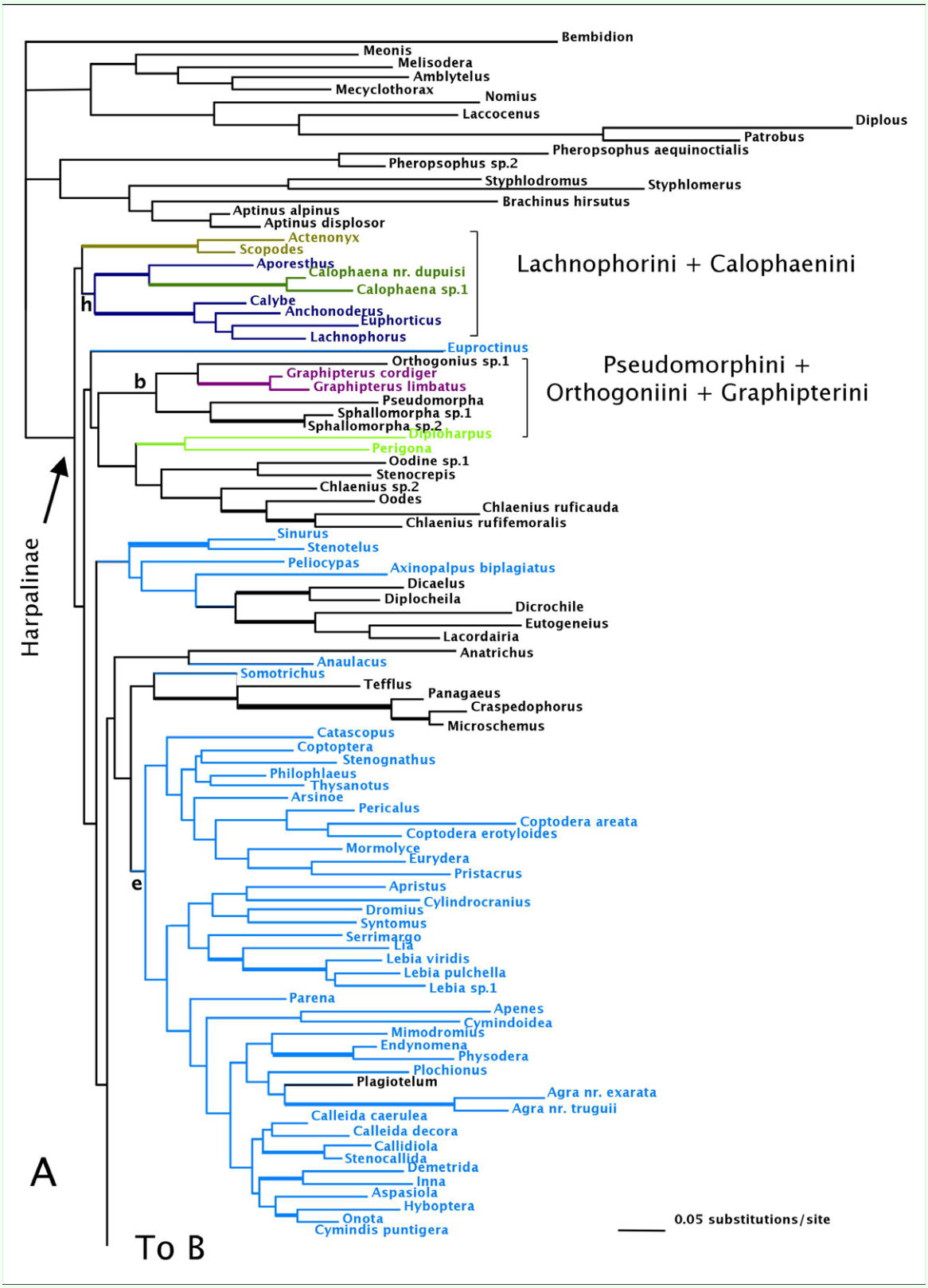


Figure 4. One of three trees of highest likelihood from the *wg* dataset. Thick branches show clades supported by greater than 95% posterior probability from Bayesian inference. Trees differ un the relationships of immediate descendants of the node marked by *. Colored branches are members of the lebiomorph assemblage color coded by tribe. (b) represents Orthogoniini + Graphipterini + Pseudomorphini clade, (c) Platynini, (e) Lebiini, (f) Harpalini, (h) Lachnophorini + *Calophaena*.

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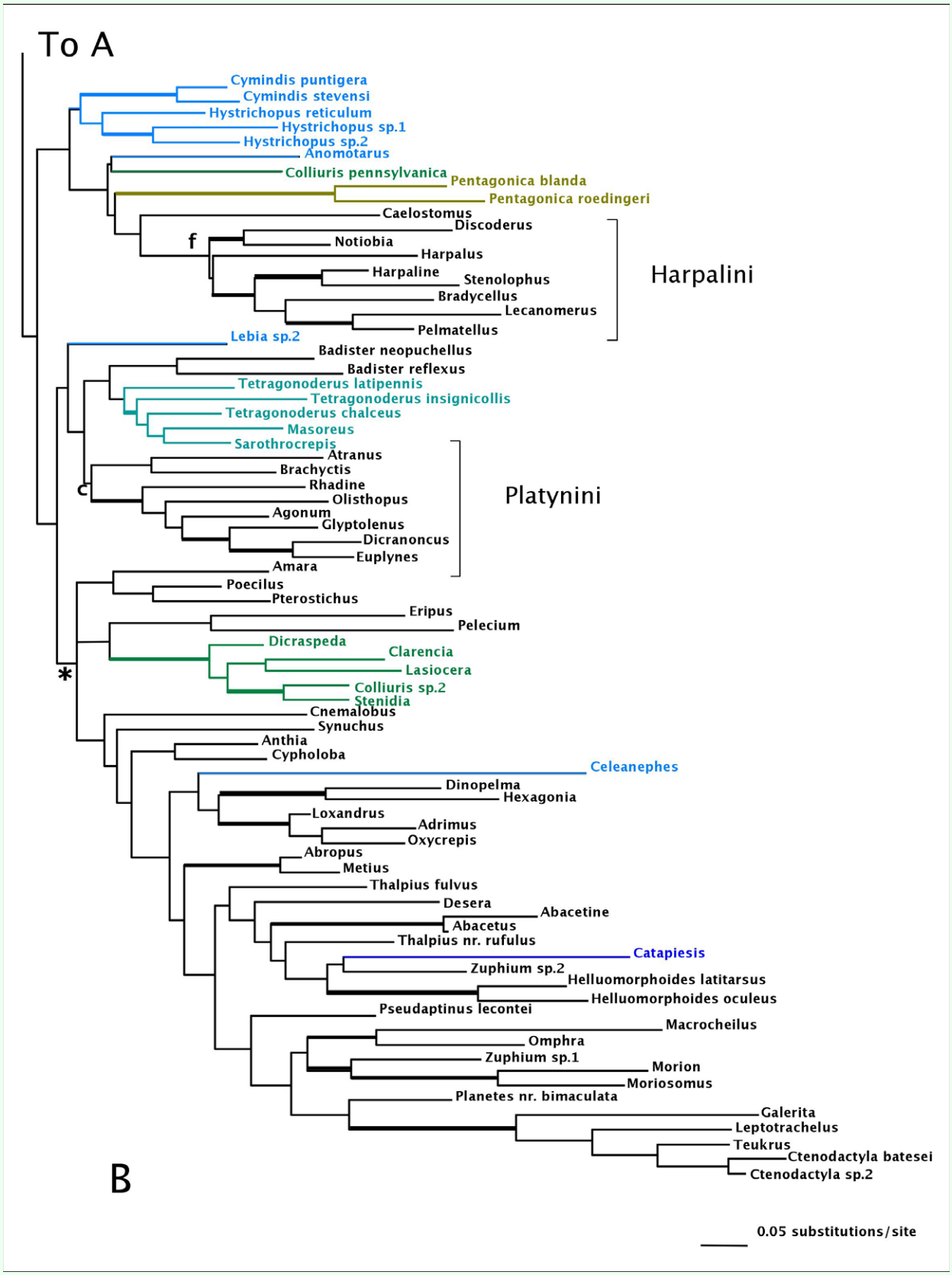


Figure 4 (con't).

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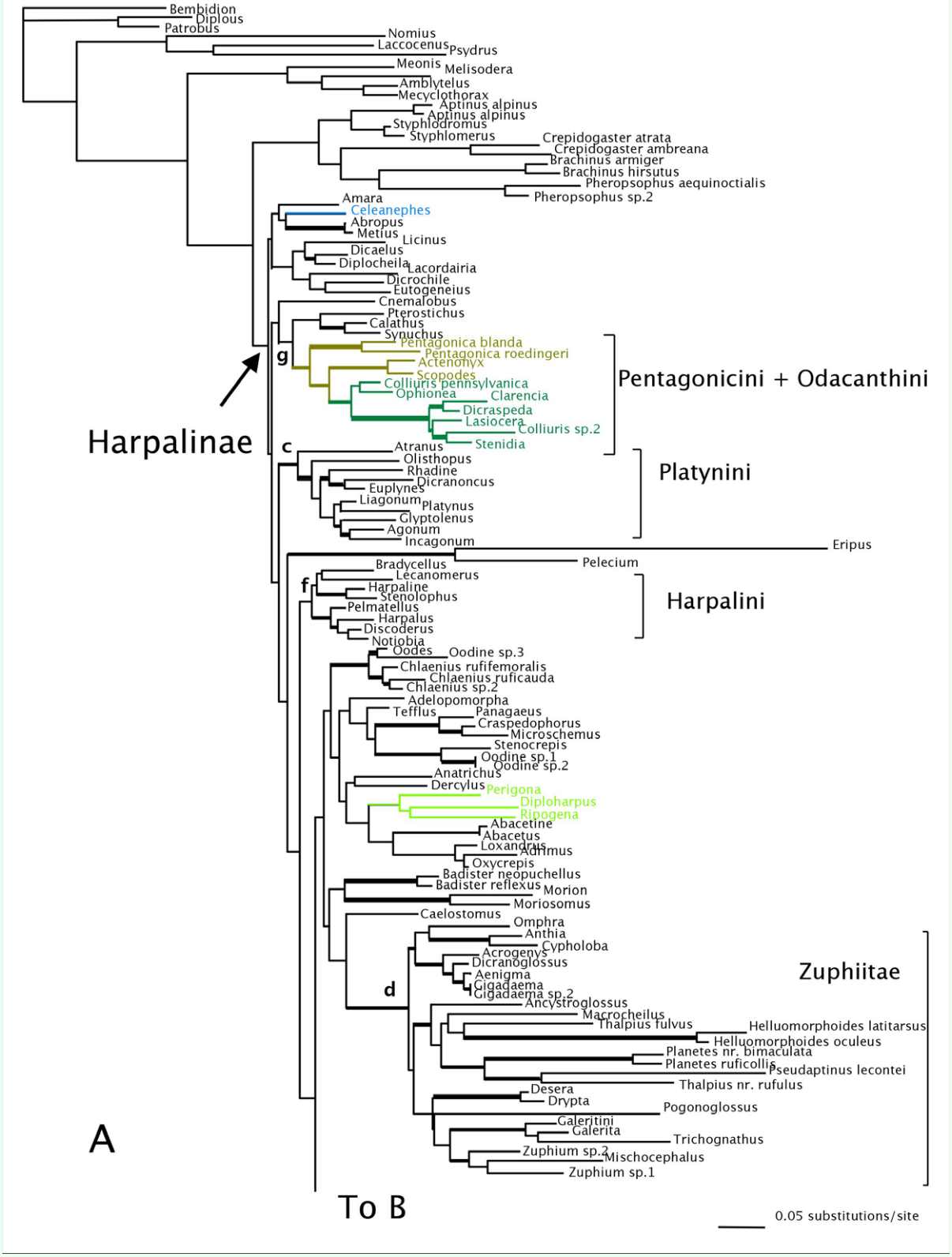


Figure 5. Tree of highest likelihood from the 28Sbe dataset. Thick branches show clades supported by greater than 95% posterior probability from Bayesian inference. Colored branches are members of the lebiomorph assemblage color coded by tribe. (b) represents Orthogoniini + Graphipterini + Pseudomorphini clade, (c) Platynini, (d) Zuphiitae clade, (e) Lebiini, (f) Harpalini, (g) Pentagonicini +Odacanthini clade, (h) Lachnophorini + *Calophaena*.

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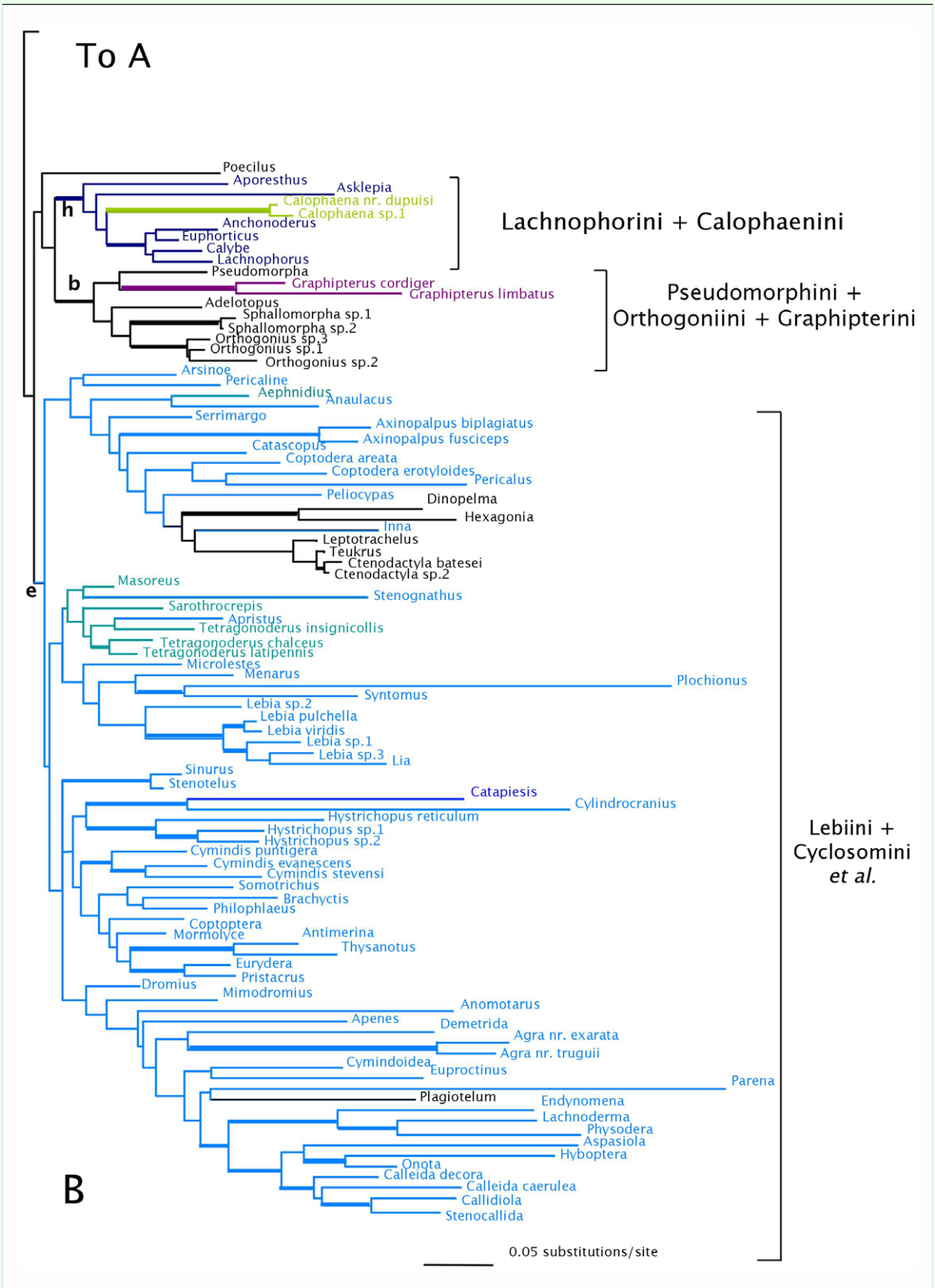


Figure 5 (con't).

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were the sister group to odacanthines and *Calophaena* was the sister group to lachnophorines.

There were some clades that were found in most or all trees, and many include relationships congruent with current classification and morphological studies. Besides the well-supported monophyly of the tribes Platynini and Harpalini, few other clades were well supported. *Calathus* and *Synuchus* were more closely related to pterostichines than platynines. An unexpected clade containing Pseudomorphini + Graphipterini + Orthogoniini was strongly supported (high bootstrap values and posterior probabilities) in nearly all trees. A large Zuphiitae clade containing the tribes Anthiini, Dryptini, Galeritini, Helluonini, Physocrotaphini, and Zuphiini was also well supported in most analyses although some of the tribes within this large clade were not monophyletic. Figure 2 shows the preferred phylogenetic tree of Harpalinae based on the combined 28Sbe+*wg* data set. The results of the phylogenetic analyses in this study are summarized in Tables 1 and 2.

Hypothesis testing

Table 2 summarizes the results of tests for phylogenetic hypotheses of several tribal relationships. The analyses reflected several relationships that have been previously suggest from morphological studies. In all cases, there was no evidence for a monophyletic lebiomorph assemblage containing Lebiini (including *Celeanephes* and excluding *Plagiotelum*), Cyclosomini, Graphipterini, Catapiesini, Odacanthini, Lachnophorini, Pentagonicini, Calophaenini, and Perigonini in a single clade. Likewise there seems to be no evidence to support alternative hypotheses including a strictly monophyletic Lebiini (including *Celeanephes* and excluding Cyclosomini and *Plagiotelum*), a sister group relationship between Graphipterini and Cyclosomini, and a clade consisting of Odacanthini + Lachnophorini + Calophaenini + Pentagonicini.

Discussion

Despite little support for the deeper phylogenetic relationships of Harpalinae, a problem encountered in previous studies (Ober 2002), many of the smaller clades of harpalines were resolved and well supported from 28S and *wg* data (Figure 2). Some conclusions about harpaline relationships can be reached (see below). Tribal affiliations of genera were largely concordant with previously proposed groupings based on morphological traits and were generally well supported. The relationships of a number of tribes and genera are still enigmatic, and may only be resolved by the inclusion of additional data and denser taxon sampling.

Relationships of particular harpaline taxa

Phylogenetic relationships of many lineages within Harpalinae remain unresolved. It is beyond the scope of these analyses to address all of the phylogenetic issues. It appears that 28S and *wg* data alone are not sufficient to clearly resolve the relationships among many of these controversial groups, so we have chosen to highlight a few groups whose relationships are particularly interesting in light of the morphological and molecular data.

Lebiomorph Assemblage

The lebiomorph assemblage is a group of harpaline tribes whose members possess an unusual defensive chemical delivery system: the opening of the ducts that secrete defensive chemicals are located at the eighth abdominal tergite and are shaped like turrets (Deuve 1993; Erwin 1985; Erwin in litt.; Forsyth 1972), and most possess truncate elytra (probably to accommodate the defensive chemical delivery). The lebiomorph assemblage is more or less Lebiitae (tribes Lebiini, Cyclosomini, Graphipterini, Perigonini, Odacanthini, Lachnophorini, and Pentagonicini) of Erwin (1991b), however we have also included in this group Catapiesini and Calophaenini. Catapiesini, previously included in Lebiitae by Erwin (1984), has truncate elytra and specialized eighth abdominal tergite turrets, although the turret size is smaller than in other lebiomorphs. Calophaenini has recently been included within Lachnophorini (part of the lebiomorph assemblage) by Liebherr (1988) based on a notable synapomorphy from the female reproductive tract. Calophaenines have shortened elytra, but no obvious turreted chemical delivery system, and thus were previously considered to have lost this feature.

A monophyletic lebiomorph assemblage was never recovered in any of our analyses. Even when *Plagiotelum*, *Celeanephes* , and *Catapiesis* were excluded from the lebiomorph assemblage, it is still highly polyphyletic. A polyphyletic lebiomorph assemblage has important implications for the evolution of carabid defensive chemical delivery system. Within harpalines, it appears the eighth abdominal tergite turrets have evolved independently at least four times. This character, previously considered to be the synapomorphy for lebiomorphs, is apparently homoplasious and similarities may be due to convergent evolution. It is clear that future work must include a detailed morphological study of these turrets in lebiomorph and other harpaline taxa to determine their structure, function, and evolutionary history.

Odacanthitae

Within the lebiomorph assemblage, Liebherr (1988) described the Odacanthitae, a supertribe united based on a synapomorphy from the female reproductive tract; members of the tribes Lachnophorini, Calophaenini, Odacanthini, and Pentagonicini share a bipartite spermatheca (Leibherr 1988). Results of the molecular analyses did not support the monophyly of Odacanthitae

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Table 2. Status of selected taxa in results of phylogenetic analyses.

Analysis	Lebiom	Zuphiitae	Pseud+Orth+ Graph	Ood+Chlae+ Panag	Hex+Cten	Odacant	Graph+Cyc	Lebiini	Odac+Pent
28Sbe + wg MP	x	M	M	x	M [a]	x	x	x	M
	65			na		36	84	85	
28Sbe + wg ML	x	M	M	M	M [a]	x	x	x	M
28Sbe + wg BI	0%	M	M	M	M [a]	0.20%	0%	0%	M
28S H1 + wg MP	x	x	M	x	x	x	x	x	x
	58	na		na	na	na	na	90	na
28SH1 + wg ML	x	M	M	x	M [a]	x	x	x	x
wg MP	x	x	M	M	x	x	x	x	x
	77	33			na	21	34	74	na
wg ML	x	x	x	x	x	x	x	x	x
wg BI	0%	0%	43%	0%	na	0%	0%	0%	na
28Sbe MP	x	M	M	x	x	x	x	x	M
	37			20	na	32	61	66	
28Sbe ML	x	M	M	M	M	x	x	x	M
28Sbe BI	0%	M	M	M	M	0%	0%	0%	M
28SH1 MP	x	M	x	x	x	x	x	x	x
	44		na	na	na	na	na	39	na
28SH1 ML	x	M	M	M	M [a]	x		x	M

[a] *Plagiotelum* (Ctenodactylini) is not included
Numbers below x indicate number of additional steps in MP to make group monophyletic.
Also indicated is % of post-burnin BI trees observed with clade.
na indicates hypothesis not specifically tested.
Abbreviations for taxon names: Lebiom = Lebiomorph assemblage, Pseud = Pseudomorphini, Orth = Orthogoniini, Graph = Graphipterini, Ood = Oodini, Chlae = Chlaenini, Panag = Panagaeniini, Hex = Hexagoniini, Cten = Ctenodactylini, Odacant = Odacanthitae, Cyc = Cyclosomini, Odac = Odacanthini, Pent = Pentagonicini.

(0.2% of Bayesian trees had a monophyletic Odacanthitae). However, most analyses showed a close relationship between Pentagonicini and Odacanthini (except in trees from the *wg* dataset). Liebherr (1988) combined the pentagonicines *Scopodes*, *Actenonyx*, and *Pentagonica* within Odacanthini, and this combination was supported, for the most part, by the molecular data. *Actenonyx* has sometimes been placed in the Lebiini based on mouthparts and suborbital setae (Ball, Kavanaugh & Moore, 1995s). Britton (1940) also originally placed *Actenonyx* with lebiines, but later Britton (1941) suggested that the genus was more closely allied with the odacanthines. No analysis placed *Actenonyx* with a lebiine taxon, instead it was sister to *Scopodes* usually within the Pentagonicini + Odacanthini clade. The results from most of the analyses place *Calophaena* (Calophaenini) near or within Lachnophorini (except in the *wg* parsimony tree). This is in agreement with morphological analyses by Leibherr (1988). Despite the affinity of *Calophaena* with Lachnophorini and Pentagonicini with Odacanthini, these two clades are not sister groups and the bipartite spermatheca may have evolved multiple times as suggested by its presence in other unrelated taxa such as *Glyptolenus* (Liebherr 1988).

Cyclosomini + Graphipterini

Some morphological classifications have placed two lebiomorph tribes, graphipterines and cyclosomines, in close association. Chaudoir (1876) recorded that adults of Graphipterides (Graphipterini) exhibited modified tibial spurs common to members of the cyclosomines. Jedlicka (1963) also recognized a relationship between graphipterines and cyclosomines (or groups included in or near cyclosomines). Jeannel (1949) included cyclosomines and graphipterines within his "family Masoreidae." Kryzhanovsky (1976) treated Masoreomorphi as a supertribe that included Masoreini (Cyclosomini) and Graphipterini. In most trees from the analyses (except *wg* trees), cyclosomines tended to be associated with members of dromiine and/or cymindine lebiines and never form the sister group of graphipterines. Along with the tibial spur character, cyclosomines and graphipterines also exhibit various sorts of reductions of stylomere two of the female ovipositor. While graphipterines and cyclosomines share reductions in stylomere two, Dromiina lebiines also exhibit the same sort of stylomere reductions (Ball 1982; Habu 1967).

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The inclusion of cyclosomines within lebiines was unexpected but not surprising. Cyclosomines, almost all xeric, ground-dwelling beetles except for the arboreal *Sarothrocrepis*, often appeared in the phylogenies near xeric, ground-dwelling lebiines (dromiines and cymindines). Shaum (1860) recognized that *Masoreus* and *Tetragonoderus* were related to Lebiini, and Csiki (1932) placed members of Lebiini and Cyclosomini next to each other, implying a close relationship among these taxa. Cyclosomines were not always monophyletic in the results of separate and combined analyses. *Anaulacus* was not associated with other cyclosomines and may represent an independent lineage not closely related to the rest of the tribe (Ball and Shpeley 2002).

Lebiini

Lebiini has more than 4200 species (Lorenz 2005) and is represented in all major zoogeographical regions of the world, but is especially diverse in the tropics. Lebiines are strikingly divergent in form, color, and in natural history, making it difficult to provide a clear synapomorphy for the tribe. No overall phylogeny of Lebiini exists, and most efforts of systematists have focused within subtribes. Ball (1975) suggested that subtribes Pericalina and Apenina are primitive, based on the ovipositor, forming the basal stock of lebiines that evolved from a platynine-like ancestor. Cymindines are more evolutionarily intermediate with respect to Calleidina and Lebiina. Phylogenetic analysis of lebiine subtribes based on morphological characters by Ball et al (1995) agreed with these previous ideas of lebiine subtribal relationships. Ball (1975) also suggested that lebiines may be paraphyletic due to the great diversity of form and habitats within the tribe and lack of many clear synapomorphies. Based on female ovipositor characters and characters from the mentum, Basilewsky (1984) seemed to imply a polyphyletic Lebiini from his schematic of the phylogeny of Lebiinae which has many lineages of lebiines placed as paraphyletic with respect to other unidentified harpaline lineages and other tribes such as zuphiines and cyclosomines sharing a close relationship with some lebiines.

Results of analyses in this study indicate that Lebiini (*sensu stricto*) is not monophyletic. Cyclosomines were included within the group, as was *Plagiotelum*, a genus previously classified as a ctenodactyline because of its elongated prothorax and complete elytra. Additionally, *Celeanephes*, an enigmatic genus that has been placed in Lebiini (Ball 1995) was not clearly associated with any lebiine taxa, however its placement varied between analyses. Beyond these nontraditional lebiine taxa the remaining lebiines fell into one or two large lineages, which were sometimes paraphyletic. Our results support a small number of clades containing most lebiines, however support for any single phylogenetic arrangement is low and so the relationship of lebiines to other harpaline tribes remains unclear.

Lebiine clades found in the analyses do not correspond to subtribes, and subtribes were never recovered as monophyletic. However, the classification of lebiine subtribes has been unstable (Ball 1975; Ball and Hilchie 1983; Ball and Shpeley 1983; Ball et al. 1995; Casale 1998; 430 Jeannel 1949; Shpeley 1986), and subtribal boundaries and composition are difficult to determine, but there is no clear correspondence with these previous hypotheses. A group of lebiines, including some traditionally classified in the subtribe Calleidina, appears in most phylogenies and is largely concordant with the calleidine phylogeny of Casale (1998) (e.g. *Physodera* , *Agra* , *Anomotarus* , *Onota* , *Plochoinus* , *Demetrida* , *Mimodromius* , Metallicina, and the "Callides" of Chaudoir (1872)) based mainly on reproductive tract characters from males and females. At present, lebiine phylogenetic relationships remain unresolved and problematic.

Zuphiitae

The well-supported zuphiite clade (comprised of tribes Anthiini, Dryptini, Galeritini, Helluonini, Physocrotaphini, and Zuphiini) was found in most trees (paraphyletic in *wg* trees). However, the tribes Galeritini, Helluonini, and Zuphiini within Zuphiitae were not monophyletic and more taxon sampling needs to be done to explore the tribal boundaries within Zuphiitae. The longest branches within the harpaline clade were found in Zuphiitae. Long branch attraction (Felsenstein 1978) may be one reason for the zuphiite grade seen at the base of the *wingless* parsimony tree or a paraphyletic Zuphiitae seen in the 28S parsimony tree, the *wingless* distance and ML trees, and the 28S+*wingless* combined distance tree, where other long branches such as *Eripus* and *Catapiesis* are sometimes found with zuphiite taxa. In most trees, the Zuphiitae can be found in a basal clade in harpalines.

The six tribes in Zuphiitae were proposed to form a single clade by Basilewsky (1984) based on antennal characters and spination on the first stylomere of the female ovipositor. Jeannel (1949) placed together zuphiines, dryptines, and galeritines in Dryptidae and followed them immediately by Anthiidae (anthiines and helluonines). Erwin (1985) described a similar arrangement. From this, one can infer that these authors regarded the dryptite and anthiite lineages each as monophyletic and the supertribes themselves fairly closely related, but not forming a monophyletic group.

Pseudomorphines + Orthogoniines + Graphipterines

There was an unexpected but strongly supported clade of orthogoniines, graphipterines, and a paraphyletic Pseudomorphini. No obvious morphological synapomorphies link these three tribes. Pseudomorphines have a very unusual ovoid adult body form along with other highly autapomorphic structures and larval habits, due in part to their association with ants (Erwin 1981; Moore 1974). While they are clearly harpalines (Maddison et al.

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1999; Ober 2002), they have been considered a distinct lineage, in some classifications receiving the rank of subfamily (Lindroth 1969) or family (Notman 1925). Evidence from paramere vestiture and basal bulb of the male median lobe on the aedeagus, male tarsal setae (Erwin 1981) suggests that pseudomorphines are related to pterostichines in Harpalinae, and adult chemical defense of formic acid and hydrocarbons (Moore 1979; Moore and Wallbank 1968) places pseudomorphines among the members of Harpalinae. Orthogoniines have never been suggested to be related to either pseudomorphines or graphipterines. They were associated with licinines by Jeannel (1948), to several tribes of the Zuphiitae and lebiines by Kryzhanovsky (1976), and to idiomorphines, catapiesines, and amorphomerines by Erwin (1985; 1991a). Graphipterines were thought to be closely related to cyclosomines as both tribes share a modified hind tibial spur (see above).

While morphology does not support a close relationship among these three tribes, all or some of their members have obligate relationships with social insects. Orthogoniine larvae are obligate symbionts of termite nests (Bousquet and Larochelle 1993; Erwin 1979; Kistner 1982; Wasmann 1902) and prey on termites, and some orthogoniine adults also live in termite nests (Kistner 1982). Pseudomorphines are myrmecophilous and have highly modified morphological structures in adults and larvae for life with ants (Erwin 1981; Moore 1974). Pseudomorphine larvae eat adult and larval ants (Lenko 1972; Moore 1974). Larvae of some species of *Graphipterus* are obligate symbionts in ant nests and prey on ant eggs and larvae as a specialized predator or parasitoid (Brandymayr *et al.* 1994; Paarman 1985). The larvae of all three tribes are physogastric in the last two instars (Erwin 1981; Kistner 1982; Paarman 1985), a condition common to parasitic carabids or inquilines of social insects. It seems likely that relationship with social insects evolved early in the shared evolutionary history of pseudomorphines, orthogoniines, and graphipterines. Future work is required to identify morphological synapomorphies, if they exist, for this surprising clade and investigate its evolutionary history.

Oodini + Chlaenini + Panagaeini + Licinini

Several authors suggest a close relationship of chlaeniines, licinines, panagaeines, and oodines (Jeannel 1942; 1949; Lindroth 1969; Thompson 1979). These tribes have been combined into the Panagaeitae (Castelnau and Brullé 1840; Kirby 1817), a super-tribe in the subfamily Harpalinae containing panagaeines, chlaeniines, oodines, licinines and peleciines, on the basis of the constricted neck and triangular, compressed terminal palpomeres. Erwin (1985), Kryzhanovsky (1976), and Moore et al. (1987) also accepted this grouping. Chaudoir (1878) first suggested that oodines are closely related to panagaeines and chlaeniines. Members of these tribes have a metepisternum coadunate with the elytral epipleuron. Panagaeines and chlaeniines were thought to form a clade based on phenol in secretions from pygidial glands, whereas oodines secrete methacrylic acid (Bousquet 1987b). Some authors (Ball 1960; van Emden 1942; Jakobson 1906; LeConte 1861) combined chlaeniines and oodines into one tribe. Our results indicate there may be a close relationship between chlaeniines and oodines, although neither tribe was always monophyletic. In most trees, oodines, chlaenines, panagaeines, and *Dercylus* were found together in the same clade (in some cases paraphyletic with respect to Perigonini). Licinines and peleciines were not closely related to chlaeniines, oodines, and panagaeines.

Conclusions and future work

Our investigation is the largest molecular study on the phylogenetic relationships of the speciose carabid subfamily Harpalinae, and is another step in the progress toward understanding the evolution of this diverse group. This study revealed new monophyletic groups that were robust to different phylogenetic analysis method implemented here. For example, galeritines, anthiines, dryptines, helluonines, and zuphiines were confidently placed together in a single clade, and cyclosomine taxa were placed within Lebiini. Also, the monophyly of Pseudomorphini + Orthogoniini + Graphipterini was established for the first time. Nonetheless several taxa included in this study remain difficult to place (*Celeanephes*, *Caelostomus*, *Calophaena*, *Catapiesis*, *Badister*, Peleciini, *etc.*) with any confidence. These enigmatic taxa were not consistently associated with any clade across data sets and analysis methods. It is imperative that future studies include denser taxon sampling, more sequence data, and additional analyses in order to determine the relationships of these taxa.

Most basal tribal relationships of Harpalinae were not sufficiently clarified in any of the analyses, suggesting that the molecular data in this study do not provide enough information to detect relationships at this level. Such problems may be alleviated by increasing the number of characters, under the assumption that the nucleotides follow the same evolutionary patterns (Berbee et al. 2000). Data from additional genes are needed to increase the support for deeper nodes. Alternatively, if the observed lack of phylogenetic resolution reflects a rapid harpaline radiation, additional data may not improve statistical support at deeper nodes. Short internal branches in the harpaline molecular phylogenies presented in this study and others (Maddison et al. 1999; Ober 2002) indicate that harpalines underwent a rapid radiation at the splitting of the ancestors of what is now roughly the tribal level. The rapid radiation suggested by these molecular data would also explain the paucity of morphological synapomorphies for higher-level tribal relationships in harpalines. The first fossil of a member of the subfamily Harpalinae and its close relatives is from the late Cretaceous, about 90 Myr ago (Ponomarenko 1992). By the

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Oligocene (approximately 35 Myr ago), species from present day harpaline tribes, even modern genera, are known from Baltic amber (Lindroth 1974). This suggests that the rise of the diversity of present day harpaline tribes was very rapid, and lineage splitting was much faster than accumulation of history-marking changes.

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Appendix 1. Taxa Sampled

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
OUTGROUP				
Nebriini	*Nebria (Boreonebria) hudsonica* LeConte	AF398676[a]	AF398608[a]	Canada: Alberta: Edmonton
Elaphrini	*Elaphrus californicus* Mannerheim	AF398639[a]	AF398563[a]	Canada: Alberta: Bow River near Vauxhall
Gehringiini	*Gehringia olympica* Darlington	AF398702[a]	AF398591[a]	Canada: British Columbia: Alexander Creek, just W of Crowsnest Pass
Promecognathini	*Promecognathus crassus* LeConte	AF398685[a]	AF398621[a]	USA: California: Marin Co.: Lagunitas Creek, 0.1 miles below spillway of Nicasio Dam
Patrobini	*Diplous californicus* Motschulsky	AF398699[a]	AF398587[a]	USA: Idaho: Idaho Co.: Lowell
	Patrobus longicornis Say	AF398700[a]	AF398613[a]	Canada: Alberta: Edmonton
Bembidiini	*Bembidion levettei carrianum* Casey	AF389647[a]	AF398571[a]	Canada: Saskatchewan: North Saskatchewan River at Paynton Ferry
	Tachyta sp.	AF438141	AF438002	USA: Mississippi: Noxubee Co.: Noxubee National Wildlife Refuge, Oktoc Creek
Pogonini	*Diplochaetus planatus* Horn	AF438060	AF437938	USA: Arizona: Cochise Co.:Willcox Playa
	Pachydesus sp.	AF438112	AF437978	Republic of South Africa: Kwazulu-Natal: Ngome Forest Reserve 27.50S 31.24E
Psydrini	*Psydrus piceus* LeConte	AF398684[a]		USA: California: Tuolumne Co., 3.7 mi NE Strawberry
	Laccocenus ambiguus Sloane	AF398675[a]	AF398596[a]	Australia: Queensland: Springbrook
	Nomius pygmaeus Dejean	AF438100	AF437971	USA: Arizona: Pima Co.: Rincon Peak
Austral psydrines	*Amblytelus curtus* Fabricius	AF398683[a]	AF398566[a]	Australia: New South Wales: Kosciusko N.P., Wilsons Valley
	Melisodera picipennis Westwood	AF398640[a]	AF398602[a]	Australia: Victoria: Errinundra Plateau
	Meonis sp.	AF398692[a]	AF398603[a]	Australia: DJ Cook
	Mecyclothorax vulcans Blackburn	AF398648[a]	AF398601[a]	USA: Hawaii: Island of Hawaii: Pu'u Makahala Natural Area
Crepidigastrini	*Crepidogaster atrata* Peringeuy	AF438046		Republic of South Africa: Natal Prov.: Ntendeka Wilderness: Ngome Camp 27°49'03"S 31°24'21"E
	Crepidogaster (Tyronia) ambreana Deuve & Mateu	AF438047		Madagascar: Antsiranana Province: Mtn. D'Ambre National Park vic. Roussettes Research Station
Brachinini	*Brachinus (Neobrachinus) hirsutus* Bates	AF398693[a]	AF398572[a]	USA: Arizona: Pima Co.: Arivaca Creek near Arivaca
	Brachinus (Metabrachinus) armiger Dejean	AF398682[a]		Republic of South Africa: East Cape: Graaff Reinet, 32°13' 24°30'
	Pheropsophus aequinoctialis Linné	AF398678[a]	AF398619[a]	Bolivia: near Santa Cruz de la Sierra
	Pheropsophus sp.	AF398658[a]	AF398618[a]	India: Arsikene

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Appendix 1 (con't).

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Aptinus displosor Dufour		AF398569[a]	Spain: Cadix: Cortijo Salomon
	Aptinus alpinus Dejean & Boisduval	AF398638[a] and AF398710[a]	AF398568[a]	Italy: Alpimarittimei, 1300m, Sambou, M. Vaccia
	Styphlodromus sp.	AF398641[a]	AF398628[a]	Republic of South Africa: Northern Prov.: ca. 8km S Pienaarsrivier
	*Styphlomerus vittaticollis*Péringuey	AF438139	AF438001	Madagascar: Fianarantsoa Province: Ranomafana National Park: Vohiparara village 21.23906S 47.38487E
HARPALINAE				
Metiini	*Metius sp.*	AF398654[a]	AF398604[a]	Chile: Reg. Metropolitana: road to Farellones curve 18
	Abropus carnifex Fabricius	AF438008	AF437897	Chile: Osorno Pr.: P.N. Puyehue, Repucura Trail, 1.0 im E Anticura
Loxandrini	*Loxandrus n. sp. nr.amplithorax* Straneo	AF398661[a]	AF398600[a]	Ecuador: Sucumbios: Cuyabeno Faunal Reserve
	Oxycrepis (Stolonis) n. sp.	AF438111	AF437977	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Adrimus n. sp.	AF438011	AF437899	Ecuador: Sucumbios: Cuyabeno Faunal Reserve: Laguna Grande, Neotropic cabins, camp area and trail to Sendero La Hormiga
Pterostichini	*Pterostichus melanarius* Illiger	AF398707[a]	AF398623[a]	Canada: Alberta: Edmonton
	Poecilus scitulus LeConte	AF398677[a]	AF398620[a]	USA: Arizona: Pima Co.: Santa Catalina Mts.: Mt. Lemmon
Zabrini	*Amara apricaria* Paykull		AF398565[a]	Canada: Alberta: Edmonton
	Amara (Curtonotus) sp.	AF398694[a]		Canada: Alberta: Kenilworth Lake
Morionini	*Morion aridus* Allen	AF398698[a]	AF398606[a]	USA: Arizona: Pima Co.: Tucson Mountains
	Moriosomus seticollis MacLeay	AF398701[a]	AF398607[a]	Ecuador: Cotopaxi Prov.: Otonga Cloud Forest 00°25'28"S 79°00'41"W
Abacetini	*Abacetus sp.*	AF398681[a]	AF398635[a]	India: Arsikere
	Abacetine	AF438007	AF437896	India: Arsikere
Caelostomini	*Caelostomus (Catalainus) n. sp.*	AF398704[a]	AF398573[a]	Madagascar: SE side of Masoala Peninsula, 1°47'S 50°13'E
Cnemalobini	*Cnemalobus sulciferus* Philippi	AF398706[a]	AF398580[a]	Chile: Talca Pr. Area de Protection Vilches
Peleciini	*Pelecium n. sp. nr.sulcipenne* Chaudoir	AF398672[a]	AF398614[a]	Ecuador: Napo Prov.: Yasuni Station
	Eripus nitidus Chaudoir	AF398642[a]	AF398589[a]	Mexico: Vera Cruz: Cofre de Perote
Catapieseini	*Catapiesis brasiliensis* Gray	AF398645[a]	AF398577[a]	Ecuador: Napo Res. Ethnica Waorani: Okane Gare Station, 220 m 00°10'S 76°26'W
Platynini	*Glyptolenus sulcipennis* Chaudoir	AF398671[a]	AF398592[a]	Ecuador: Sucumbios: Reserva Faunistica Cuyabeno: Nuevo Mundo cabins along Rio cuyabeno at jcn with Lago Agrio-Tipishca HWY
	Agonum extensicolle Say	AF398643[a]	AF398564[a]	USA: Arizona:Pima Co.: Arivaca
	Synuchus dubius LeConte	AF398674[a]	AF398629[a]	USA: Arizona: Pima Co.: Santa Catalina Mts.: Mt. Lemmon
	Calathus ruficollis Dejean	AF438033		USA: Arizona: Santa Cruz Co.: Tumacocori

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Appendix 1 (con't).

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Rhadine sp.	AF438128	AF437990	USA: Arizona: Pima Co.: Santa Catalina Mts.: Mount Lemmon
	Liagonum sp.	AF438090		Madagascar: Fianarantsoa Province: Ranomafana National Park, Vohiparara village 21.23906°S 47.38487°E
	Olisthopus micans LeConte	AF438102	AF437973	USA: Michigan: Wayne County: Van Buren Twp.
	Platynus hypolithos Say	AF438123		USA: New York: Tompkins Co.: Ithaca
	Incagonum sp.	AF438079		Argentina: Tierra del Fuego: Ushuaia
	Atranus pubescens Dejean	AF438026	AF437911	USA: New York: Tompkins Co.: Ithaca
	Euplynes limbipennis Bates	AF438067	AF437945	Malaysia: Sabah: Poring Hot Springs, 6° 02.919'N 116° 41.984'E
	Dicranoncus quadridens Motschulsky	AF438056	AF37934	Malaysia: Sabah: Poring Hot Springs, 6° 02.919'N 116° 41.984'E
Pseudomorphini	*Pseudomorpha nr.angustata* Horn	AF398714[a]	AF398622[a]	USA: Arizona: Cochise Co.: Willcox
	Sphallomorpha sp.1	AF398679[a]	AF398636[a]	Australia: Queensland: Mt. Lewis Rd., 16°31'S 146°16'E
	Sphallomorpha sp.2	AF438133	AF437995	Australia: Queensland: Mt. Spurgeon 2 km, 16°27'S 145°12'E
	Adelotopus bolitus Castelnau	AF438010		Australia: Queensland: Enoggera Reservior
Harpalini	Harpaline	AF438072	AF437950	Ecuador: Napo Prov.: Yasuni Station
Pelmatellina	*Pelmatellus sp.*	AF398690[a]	AF398615[a]	Costa Rica: Cerro de la Muerte: Pan American Highway marker 89.3km, 5.7 km from La Jorgina
	Lecanomerus niger Darlington	AF438088	AF437963	Australia: Queensland: Millaa Millaa Falls, 17°30'S 145°36'E
Anisodactylina	*Notiobia sp.*	AF438101	AF437972	Mexico: about 2 mi N Portezuelo
Stenolophina	*Stenolophus (Egadroma) quinquepustulata* Wiedmann	AF438137	AF437999	Malaysia: Pahang: Kuala Tahan
	Bradycellus sp.	AF438032	AF437916	USA: Arizona: Pima Co.: Tucson
Harpalina	*Discoderus cordicollis* Horn	AF398652[a]	AF398588[a]	USA: Arizona: Pima Co.: Tucson
	Harpalus caliginosus Fabricius	AF438073	AF437951	USA: Arizona: Pima Co.: Arivaca
Dercylini	*Dercylus sp.*	AF438054		Ecuador: Napo Prov.: Yasuni Station
Chlaeniini	*Chlaenius ruficauda* Chaudoir	AF398680[a]	AF398578[a]	USA: Arizona: Santa Cruz Co.: Tumacocori
	Chlaenius (Lissauchenius) rufifemoralis bimaculatus Dejean	AF438038	AF437921	Malaysia: Sabah: Kinabatangan River: Uncle Tan's Camp N5°24.688' E118°02.236
	Chlaenius (Callistomimus) sp.2	AF438039	AF437922	Nepal: Prov. Bheri: Nepalganj: Rapti River near airport
Panagaeini		AF298703[a]	AF398630[a]	Kenya: Namunyak, Mathews Range, Sarara Safari Camp
Tefflina	*Tefflus sp.*			
Panagaeina	*Panagaeus sallei* Chaudoir	AF398691[a]	AF398612[a]	USA: Arizona: Graham Co.: Rincon Mts., Ash Creek: Mescal Rd. 10.3 mi from I-10, 32°30'N 110°10'W 4400ft
	Microschemus sp.	AF438096	AF437968	Republic of South Africa: Mpumalanga, Kruger Nat. Park,

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Appendix 1 (con't).

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Craspedophorus rufipalpis LaFerte	AF438045	AF437928	Malaysia: Sabah: Kinabalu Park, Poring Hot Springs, 6°03.096'N 116°42.081'E 540m
Oodini	*Anatrichis sp.*	AF438015	AF437903	Costa Rica: Cerro de la Muerte: Cuerici Biological Station
	Adelopomorpha glabra	EU239505		New Caledonia
	Stenocrepis elegans LeConte	AF398668[a]	AF398627[a]	USA: Arizona: Gila Co.: Winkleman
	Oodine sp.2	AF438106		Ecuador: Sucumbios Prov.: 175 km ESE Coca, La Selva Station 250m
	Oodine sp.1	AF438105	AF437976	Ecuador: Sucumbios Prov.: 175 km ESE Coca, La Selva Station 250m
	Oodine sp.3	AF438107		Republic of South Africa: Mpumalanga, Kruger Nat. Park, vicinity Skuksa
	Oodes amaroides Dejean	AF438104	AF437975	USA: Alabama: Baldwin Co.: 9 miles W Gulf Shores Bon Secour NWR
Licinini		AF398655[a]	AF398586[a]	USA: Mississippi: Oktibbeha Co.: Starkville
Dicaelina	*Dicaelus ambiguus* LaFerte-Senectere			
	Diplocheila striatopunctata LeConte	AF438061	AF437939	Canada: Alberta: Nevis
Licinina	*Badister neopulchellus* Lindroth	AF438029	AF437913	Canada: Alberta: near Nevis
	Badister reflexus LeConte	AF438030	AF437914	USA: South Carolina: Younges Island
	Eutogeneius fuscus Solier	AF438070	AF437948	Chile: Chiloe Pr.: road to Miraflores 0.6 km W Hwy 5
	Licinus cassideus Fabricius	AF438090		Russia: Rostov Dist.: Tagonrog
Dicrochilina	*Dicrochile sp.*	AF438058	AF437936	Australia: Western Australia: Shire of Carnavon: Carnavon rest stop off Hwy 1
Lestignathina	*Lacordairia sp.*	AF438082	AF437992	Australia: Victoria: Keppel Falls Scenic Res., Marysville, Myrtle Loop Tr.
Anthiini		AF398695[a]	AF398584[a]	Republic of South Africa: Northern Province, ca. 8 km S. Pienaars Rivier
Cypholobina	*Cypholoba sp.*			
Anthiina	*Anthia sp.*	AF398696[a]	AF437906	Republic of South Africa: Northern Prov.: Geelhoutbosch farm 24.22S 27.34E
Physocrotaphini	*Pogonoglossus sumatrensis* Gestro	AF438125		Malaysia: Sabah: Kinabatangan River: Uncle Tan's Wildlife Camp, 5°24.898'N 118°02.157'E
Helluonini		AF398662[a]		Australia: Western Australia: Shire of Exmouth: Milerying Information Center
Helluonina	*Gigadaema sp.*			
	Aenigma iridis Newman	AF438012		Australia: Queensland: 5 km S of Moranbah
	Dicranoglossus resplendens Castelnau	AF438055		Australia: Queensland: 5 km S of Moranbah
Omphrina	*Helluomorphoides latitarsis* Casey	AF398689[a]	AF398594[a]	USA: Arizona: Graham Co.: Rincon Mts., Ash Creek: Mescal Rd. 10.3 mi from I-10, 32°30'N 110°10'W 4400ft
	Helluomorphoides oculeus Bates	AF438074	AF37952	Ecuador: Sucumbios Prov.: 175 km ESE of Coca, La Selva Station, 250m
	Omphra sp.	AF398657[a]	AF398610[a]	India: Arsikere

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Appendix 1 (con't).

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Macrocheilus sp.	AF438092	AF437965	China: Yunnan Province: Nujiang Prefecture: Lushui County: Liuku Township: Liuku 25.86010°N 98.85155°E
Orthogoniini	*Orthogonius sp.1*	AF398709[a]	AF398611[a]	Republic of South Africa: Mpumalanga, Kruger Nat. Park, vicinity Skuksa
	Orthogonius sp.2	AF438109		Gabon: Prov. Ogoone - Maritime Res. Monts Doudou
	Orthogonius sp.3	AF438110		Republic of South Africa: Northern Prov., Kruger Nat. Park
Galeritini		AF438122		Malaysia: Sabah: Kinabatangan River: Uncle Tan's Camp N5°24.688' E118°02.236'
Planetina	*Planetes ruficollis* Nietner			
	Planetes sp.	AF438121	AF437986	India: Arsikere
Galeritina	*Galerita lecontei lecontei* Dejean	AF398686[a]	AF398590[a]	USA: New Mexico: Grant Co.: Gila River at Gila
	Galeritine	EU239508		Ecuador: Napo: Misahualli
	Trichognathus sp.	EU239509		Ecuador: Napo: Misahualli
	Ancystroglossus n. sp.	AF438018		Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
Dryptini	*Drypta sp.*	AF438064		India: 15–60 km W Belgaum
	Desera australis Péringeuy	AF398659[a]	AF398585[a]	Kenya: Namunyak, Mathews Range, Sarara Safari Camp
Zuphiini		AF438098		Ecuador: Sucumbios: Reserva Faunistica Cuyabeno: Nueva Mundo cabins along Rio Cuyabeno at jcn with Lago Agrio-Tipishca HWY
Mischocephalina	*Mischocephalus sp.*			
Patriziina	*Thalpius nr. rufulus* LeConte	AF398697[a]	AF398632[a]	USA: Arizona: Santa Cruz Co.: Tumacocori
	Thalpius sp.1	AF438145	AF438004	Australia: Queensland: 5km S of Moranbah
	Pseudaptinus (Pseudaptinus) lecontei Dejean	AF438127	AF37989	USA: Mississippi: Oktibbeha Co.: Starkville
Zuphiina	*Zuphium sp.1*	AF398667[a]	AF398634[a]	Kenya: Namunyak, Mathews Range, Sarara Safari Camp
	Acrogenys sp.	EU239504		Australia:Northeast Queensland: Emerald Hill, Mareeba, 16°58'S 15°26'E
	Zuphium sp.2	AF438147	AF438006	Malaysia: Sabah: Kinabatangan River: Uncle Tan's Camp N5°24.688' E118°02.236'
Hexagoniini	*Hexagonia sp.*	AF438075	AF437953	Republic of South Africa: Kwazulu Natal Umgeni Valley National Res. nr. Howick tributary to Umgeni River along Dwarfs Dwadle tr., 29°28.667S 30°15.701E 3498ft
	Dinopelma nr. immaculatum Andrews	AF438059	AF437937	Malaysia: Sabah: Mt. Kinabalu: Liwagu Trail N6°00.602' E116°32.720'
Ctenodactylini	*Ctenodactyla batesii* Chaudoir	AF398688[a]	AF398582[a]	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m
	Leptotrachelus dorsalis Fabricius	AF398646[a]	AF398599[a]	Mississippi: Grenada Co.: LeFlore, Malmaison Wildlife Management Area
	Plagiotelum irinum Solier	AF438120	AF437985	Chile: Caitom Pr.: P.N. Cnguillio: 1.5km E. Laguna Captren guard sta. 1365m, 38°38.67'S, 71°41.37'W
	Ctenodactyla sp.2	AF438048	AF437929	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m
	Teukrus nr. cruciatus Bates	AF438144	AF438003	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m
Lachnophorini	*Calybe laetula* LeConte	AF398705[a]	AF398576[a]	USA: Arizona: Gila Co. Winkleman

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Appendix 1 (con't).

Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Aporesthus nr. anomalus Bates	AF438021	AF437907	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m
	Lachnophorus elegantulus Mannerheim	AF398650[a]	AF398597[a]	USA: Arizona: Gila Co. Winkleman
	Anchonoderus sp.	AF438017	AF437904	CostaRica: Heredia: La Selva Station, 10°26'N 84°01'W 50m
	Asklepia n. sp.	AF438024		Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Euphorticus pubescens Dejean	AF438066	AF437944	USA: Arizona: Pima Co. Tucson
Odocanthini	*Colliuris pensylvanica* Linné	AF398712[a]	AF398581[a]	USA: Arizona: Graham Co.: Rincon Mts., Ash Creek: Mescal Rd. 10.3 mi from I-10, 32°30'N 110°10'W 4400ft
	Colliuris (Eucolliuris) sp.2	AF438041	AF437924	Republic of South Africa: Northern Prov., Kruger Nat. Park
	Pentagonica roedingeri Liebke	AF398637[a]	AF398616[a]	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Pentagonica nr. blanda Andrewes	AF438115	AF437981	Malaysia: Sabah: Kinabalu Park, Poring Hot Springs: Tropical Garden Trail N06°03.096' E116°42.81'
	Scopodes sp.	AF398656[a]	AF398626[a]	Australia: Lady Talbot Dr. near Marysville
	Actenonyx bembidiodes White	AF438009	AF437898	New Zealand: South Island, Otago, Arrow River at Arrowtown
	Lasiocera sp.	AF438083	AF437958	Republic of South Africa: Northern Prov., Kruger Nat. Park
	Dicraspeda brunnea Chaudoir	AF438057	AF437935	Australia: Queensland: Cow Bay: Crocodylus Village 16.226°S 145.437°E
	Clarencia sp.	AF438040	AF437923	Australia: Queensland: 5 km S of Moranbah
	Stenidia rugucollis Fairmaire	AF438134	AF437996	Madagascar: Fianarantsoa Province: Ranomafana National Park: Vohiparara village 21.23906S 47.38487E
	Ophionea ishii Habu	AF438108		Malaysia: Pahang: Kuala Tahan
Calophaenini	*Calophaena n. sp.*	AF398666[a]	AF398575[a]	Ecuador: Sucumbios: Reserva Faunistica Cuyabeno: Nuevo Mundo cabins along Rio Cuyabeno at jcn with Lago Agrio-Tipishca HWY
	Calophaena nr. dupuisi Liebke	AF438036	AF437919	Ecuador: Sucumbios: Reserva Faunistica Cuyabeno: Laguna Grande, Neotropic cabins camp area and trail to Sendero La Hormiga
Perigonini	*Perigona nigriceps* Dejean	AF398665[a]	AF398617[a]	USA: Massachusetts: Jamaica Plain and Pepperell/Mississippi: Natchez
	Perigona (Ripogena) bembidoides Alluaud	AF438129		Madagascar: Antsiranana Province: Mtn. D'Ambre National Park vic. Roussettes Research Station
	Diploharpus laevissimus Chaudoir	AF438062	AF437940	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
Lebiini	*Demetrida dieffenbachia* White	AF438053	AF437933	New Zealand: Porter's Pass: Canterbury
	Brachyctis rugulosa Chaudoir	AF438031	AF437915	Malaysia: Sabah: Poring Hot Springs, 6°02.919'N 116° 41.984'E
	Celeanephes parallelus	EU239507	EU239503	Australia: Queensland: E. Marlborough, 10.7Km NNE, 22 44'S 49° 51'E
	Sinurus opacus Chaudoir	AF438131	AF437993	Malaysia: Sabah: Poring Hot Springs, 6° 02.919'N 116° 41.984'E
Pericalina	*Stenognathus (Pristolomus) dentifer* Chaudoir	AF438136	AF437998	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m

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Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Coptodera aerata Dejean	AF438042	AF437925	USA: Mississippi: Grenada Co.: LeFlore. Malmaison W MA.
	Pericalus quadrimaculata MacLeay	AF438117	AF437982	Malaysia: Sabah: Kinabalu Park: Poring Hot Springs
	Inna breviformis Chaudoir	AF438080	AF437957	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Catascopus sp.	AF438037	AF437920	Malaysia: Sabah: Kinabalu Park: Poring Hot Springs
	Somotrichus elevatus Fabricius	AF438132	AF437994	USA: Santa Cruz Co.: Santa Cruz River at Tumacocori
	Coptodera erotyloides Bates	AF438043	AF437926	Malaysia: Pahang: Taman Negara: trail to Lubuk Simpon
	Philophlaeus sp.	AF438118	AF437983	Australia: New South Wales: Kosciusko N.P., Wilsons Valley, Maintenance Depot Area 36°21'S 148°21'E 1490m
	Serrimargo verrucifer Chaudoir	AF438130	AF437991	Malaysia: Sabah: Kinabalu Park: Poring Hot Springs: Tropical Garden trail N06°03.096' E116°42.081'
	Pericaline	AF438116		Malaysia: Sabah: Kinabalu Park: Poring Hot Springs
	Menarus testaceus Jedlicka	AF438094		Malaysia: Sabah: Kinabatangan River: Uncle Tan's Camp N05°24.688' E118°02.236
	Mormolyce hagenbachii Westwood	AF438099	AF437970	Malaysia: Pahang: Taman Negara: trail near Bumbun Kumbang N04°26.956' E102°26.290'
	Pristacrus laticollis Gory&Castelnau	AF438126	AF437988	Madagascar: Fianarantsoa Prov.: Ranomafana National Park: Talatakely area 21.25041°S 47.41945°E
	Thysanotus apicalis Alluaud	AF438146	AF438005	Madagascar: Fianarantsoa Province: Ranomafana National Park, Vohiparara 21.24032°S 47.39399°E
	Coptoptera apicalis Péringuey	AF438044	AF437927	Republic of South Africa: Natal Prov.: Ntendeka Wilderness, Ngome Camp 27° 49'03"S 031° 24'21"E
	Stenotelus opacus Bouchard	AF438138	AF438000	Malaysia: Sabah: Kinabalu Park: Poring Hot Springs: at Sungai Kipungit N6°03.096' E116°42.081
	Eurydera unicolor Klug	AF438069	AF437947	Madagascar: Fianarantsoa Prov.: Ranomafana National Park: Talatakely area 21.25041°S 47.41945°E
	Antimerina elegans Alluaud	AF438020		Madagascar: Fianarantsoa Prov.: Ranomafana National Park: Talatakely area 21.25041°S 47.41945°E
Agrina	*Agra exarata group*	AF438013	AF437901	Ecuador: Sucumbios: Reserva Faunistica Cuyabeno, Rio Cuyabeno between Laguna Grande and L. Canagueno
	Agra n. sp. truquii group	AF438014	AF437902	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
Apenina	*Apenes hilariola* Bates	AF398713[a]	AF398567[a]	USA: Santa Cruz Co.: Santa Cruz River at Tumacocori
	Cymindoidea sp.	AF438052	AF437932	Republic of South Africa: Mpumalanga, Kruger Nat. Park, vicinity Skuksa
Calleidina	*Calleida decora* Fabricius	AF398663[a]	AF398574[a]	Costa Rica: Tempisque Valley Conservation Area: Palo Verde National Park
	Mimodromius nigrotestaceus Solier	AF438097	AF437969	Argentina: Santa Cruz District: Dept of Lago Argentina and Peninsular Magllanes 50°25'S 72°45'W 430m
	Onota angulicollis Reiche	AF438103	AF437974	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Plochionus timidus Haldeman	AF438124	AF437987	USA: Arizona: Pima Co.: Tucson

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Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Callidiola (Goniocallida) olsoufieffi Jeannel	AF438035	AF437918	Madagascar: Fianarantsoa Prov.: Ranomafana National Park: Talatakely area 21.25041°S 47.41945°E
	Stenocallida augusticollis Boheman	AF438135	AF437997	Republic of South Africa: Natal Prov.: Ntendeka Wilderness: Ngome Camp 27°49'03"S 31°24'21"E
	Anomotarus (Nototarus) chaudoiri Sloane	AF438019	AF437905	Autralia: Northampton: Hutt River
	Calleida (Philophuga) caerulea Casey	AF438034	AF437917	USA: Arizona: Huachuca Mts.
Cymindina	*Cymindis (Pinacodera) puntigera* LeConte	AF398651[a]	AF398583[a]	USA: Arizona: Pima Co.: Tucson
	Cymindis (Cymindis) evanescens Casey	AF438050		USA: Utah: Kane County: 10.1 miles W of junction of highways 14 & 89 along highway 14
	Cymindis (Taridius) stevensi Andrewes	AF438051	AF437931	Malaysia: Sabah: Kinabatangan River: Uncle Tan's Camp N5°24.688' E118°02.236'
	Hystrichopus (Pseudomasoreus) reticulatus Ball&Hilchie	AF438076	AF437954	Republic of South Africa: Western Cape, Hottentots, Holland Nat. Res., Jonkershoek Mtns, Langrivier
	Hystrichopus (Hystrichopus) sp.1	AF438077	AF437955	Republic of South Africa: North-west Prov.: Rustenburg Nature Preserve 25°43'03"S 27°11'36"E
	Hystrichopus sp.2	AF438078	AF437956	Republic of South Africa: North-west Prov.: Rustenburg Nature Preserve 25°43'03"S 27°11'36"E
Dromiina	*Apristus sp.*	AF438022	AF437908	USA: Arizona: Pima Co.: Tucson
	Microlestes lucidious LeConte	AF438095		USA: California: Hayfield Lake
	Dromius piceus Dejean	AF438063	AF437942	USA: Michigan: Wayne County: Van Buren Twp.
	Axinopalpus fusciceps LeConte	AF438028		USA: Arizona: Pima County: Tucson
	Axinopalpus biplagiatus Dejean	AF438027	AF437912	USA: Santa Cruz Co.: Santa Cruz River at Tumacocori
	Syntomus sp.	AF438140	AF437962	Thailand: Prachinburi Province: Nadee: Watershed management station
Lebiina	*Arsinoe nr. egregia* Péringuey	AF438023	AF437909	Republic of South Africa: Northern Province, Geelhoutbosh Farm
	Lebia viridis Dejean	AF398649[a]	AF398598[a]	USA: Arizona: Santa Cruz Co.: Santa Cruz River nr. Tubac
	Lebia pulchella Dejean	AF438084	AF437959	USA: Arizona: Santa Cruz Co.: Santa Cruz River near Tumacocori
	Lebia sp.1	AF438085	AF437960	Ecuador: Napo Prov.: Yasuni Nat. Park: Tiputini Biodiversity Station
	Lebia sp.2	AF438086	AF437961	Malaysia: Sabah: Poring Hot Springs, 06° 02.919'N 116° 41.984'E
	Lebia sp.3	AF438087		Republic of South Africa; Mpumalanga: Kruger Nat. Park: vic. Skukusa
	Lachnoderma hirsutum Bates	AF438081		Malaysia: Sabah: Kinabalu Park, Poring Hot Springs: Tropical Garden Trail N06°03.096' E116°081'
	Physodera n. sp. nr. bifenestrata Heller	AF438119	AF437984	Malaysia: Sabah: Poring Hot Springs, 6° 02.919'N 116° 41.984'E
	Endynomena sp.	AF438065	AF437943	India: Kallar Bridge
	Aspasiola n.sp.	AF438025	AF437910	Ecuador: Sucumbios Prov.: 175Km ESE Coca, La Selva Station 250m
	Lia quadrinotata Chevrolat	AF438089	AF437964	Mexico: Sonora: ~3mi N of rte 167 on La Luna Miroondas Rd ca. 5mi W of Alamos

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Tribe Subtribe	Species	28S GenBank Number	*wingless* GenBank Number	Locality of specimen
	Hyboptera angulicollis Chaudoir	AF398664[a]	AF398595[a]	Ecuador: Sucumbios: Reserva Faunistica Cuyabeno: Rio Cuyabeno between Laguna Grande and L. Canagueno
Metallicina	*Euproctinus pallidus* Shpeley	AF438068	AF437946	Mexico: Sonora: End of Road, La Lunas Microondas Tower. Off road from Navojoa to Alamos, 2400 ft.
	Parena picea MacLeay	AF438113	AF437979	Australia: Queensland: Moranbah
Demetriina	*Cylindrocranius sp.*	AF438049	AF437930	Republic of South Africa: Northern Province, Geelhoutbosh Farm
	Peliocypas sp.	AF438114	AF437980	Malaysia: Sabah: Poring Hot Springs, 6° 02.919'N 116° 41.984'E
Graphipterini	*Graphipterus cordiger* Dejean	AF398711[a]	AF398598[a]	Republic of South Africa: Northern Prov.: ca. 8km S Pienaarsrivier
	Graphipterus limbatus Castelnau	AF438071	AF437949	Republic of South Africa: N. Cape Prov.: Farm Groot Toren 31.20S 19.44E
Cyclosomini	*Masoreus wetterhalli axillaris* Gyllenhal	AF438093	AF437967	Morocco: Beach 6 Km South Rabat
	Tetragonoderus insignicollis Chaudoir	AF438143	AF437966	Republic of South Africa: Kwazulu natal Iphiva Nat. Res., 1.5km fr. St. Lucia
	Tetragonoderus chalceus Chaudoir	AF438142	AF437941	Argentina: Santa Cruz District: Dept of Lago Argentino Calafate town Laguna Nimes 50°20'S 72°16'W
	Tetragonoderus latipennis LeConte	AF398653[a]	AF398631[a]	USA: Arizona: Pima Co.: Tucson
	Aephnidius sp.	EU239506		Panama: Barro Colorado Island
	Anaulacus (Macrancanthus) n. sp.	AF438016	AF439790	Mexico: Sonora: Alamos
	Sarothrocrepis sp.	AF398670[a]	AF398624[a]	Australia: New South Wales: Kosciusko N.P., Wilsons Valley, Maintenance Depot Area 36°21'S 148°21'E 1490m

[a]Sequences from Ober 2002

Appendix 2. Maximum likelihood analyses rate matrix parameters.

Rate Matrix R	28Sbe	wg	28Sbe+wg	28SH1	28SH1+wg
AC	0.70783	1.37354	0.97869	0.71648	1.00762
AG	6.34909	3.31031	4.86971	6.2926	5.17506
AT	5.14693	1.17333	3.42486	5.13244	3.54092
CG	0.29786	0.87088	0.5459	0.28491	0.54029
CT	5.27214	8.3204	6.11917	5.38266	6.28965
GT	1	1	1	1	1
% I	0.202198	0.293313	0.236383	0.201294	0.238422

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