

1 Running head: Phylogenomic analysis of the Coreinae

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3 Title: Phylogenomics of the leaf-footed bug subfamily Coreinae (Hemiptera: Coreidae):  
4 applicability of ultraconserved elements at shallower depths

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24 Abstract

25 Baits targeting invertebrate ultraconserved elements (UCEs) are becoming more common  
26 for phylogenetic studies. Recent studies have shown that invertebrate UCEs typically encode  
27 proteins — and thus, are functionally different from more conserved vertebrate UCEs —can  
28 resolve deep divergences (e.g., superorder to family ranks). However, the ability of the  
29 invertebrate UCE baits to robustly resolve relationships at shallower phylogenetic scales (i.e.,  
30 tribes and congeners) has been generally limited to Coleoptera and Hymenoptera. Here, we  
31 assessed the ability of a recently designed Hemiptera UCE bait set to reconstruct more recent  
32 phylogenetic relationships in the largest leaf-footed bug subfamily, the Coreinae (Hemiptera:  
33 Coreidae), using a taxon-rich sample representing 21 of the 32 coreine tribes. Many well-  
34 supported, novel relationships were congruent in maximum likelihood and summary coalescent  
35 analyses. We also found evidence for the para- and polyphyly of several tribes and genera of  
36 Coreinae, as well as the subfamilies Coreinae and Meropachyinae. Our study, along with other  
37 recent UCE studies, provides evidence that UCEs can produce robust and novel phylogenetic  
38 hypotheses at various scales in invertebrates. Additionally, we used different DNA extraction  
39 and target enrichment protocols and recovered more UCE data using a touch-down hybridization  
40 approach.

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42 Keywords: Phylogenomics, ultraconserved elements, Coreidae, Coreinae, target capture

43

44 Introduction

45 Next-generation sequencing (NGS) technology has made the generation of thousands of  
46 orthologous loci throughout the genome achievable for many non-model organisms. For

47 molecular phylogenetics, one of the advantages of such data is the potential to resolve  
48 challenging nodes in the Tree of Life across various temporal scales (e.g., Faircloth et al. 2012,  
49 Lemmon et al. 2012, Li et al. 2013). Ultraconserved elements (UCEs) are one such class of loci  
50 that can be obtained by using target capture approaches and NGS (see Faircloth et al. 2012).  
51 These loci have been widely used in phylogenetic estimation since Faircloth et al. (2012)  
52 introduced their utility in anchoring loci for phylogenomic analysis in vertebrates. In vertebrates,  
53 UCEs are highly conserved regions of the genome that are believed to be primarily non-coding  
54 regulators of gene expression (Bejerano et al. 2004, Sandelin et al. 2004, Woolfe et al. 2004,  
55 Pennacchio et al. 2006). The high conservation of UCEs across divergent taxa (e.g., >90%  
56 conserved across amniotes) (Bejerano et al. 2004, Faircloth et al. 2012) has allowed capture of  
57 sequences that can resolve deep divergences using a single set of baits (e.g., Crawford et al.  
58 2012, McCormack et al. 2012, Faircloth et al. 2013, Gilbert et al. 2015). Additionally, as  
59 sequence variability increases away from the conserved core region (i.e., flanking regions), more  
60 recent divergences between species and populations can also be achieved (e.g., Smith et al. 2014,  
61 Manthey et al. 2016).

62 Although the use of UCEs in invertebrates is conceptually similar as it is applied in  
63 vertebrates, baits have been designed to target genomic regions with more liberal thresholds of  
64 conservation across taxa (Faircloth 2017), often requiring multiple baits for the same region to  
65 maximize capture of divergent taxa. Furthermore, recent empirical tests of UCE baits have  
66 shown that these loci are primarily protein-coding in invertebrates (Bossert and Danforth 2018,  
67 Kieran et al. 2019) making invertebrate UCEs fundamentally different from those found in  
68 vertebrates. Regardless, invertebrate UCE bait sets have been shown to resolve deep divergences  
69 (e.g., superorder to family ranks) in several taxonomic groups (e.g., Baca et al. 2017, Starrett et

70 al. 2017, Van Dam et al. 2017, Kieran et al. 2019). However, there have been few studies  
71 demonstrating the utility of these primarily protein-coding UCEs at more shallow evolutionary  
72 timescales (i.e., subfamily to congeners) for taxa in which bait sets are available (e.g., Van Dam  
73 et al. 2017, Hedin et al. 2018, Bossert et al. 2019). Recently, Kieran et al. (2019) empirically  
74 tested a UCE bait set for the insect order Hemiptera (Faircloth 2017), showing its utility in  
75 resolving phylogenetic relationships among the suborders down to intrafamilial relationships in  
76 Reduviidae and Coreidae with a small sample of taxa. The utility of UCEs in hemipteran  
77 phylogenetics has also been shown at a relatively shallower scale as seen in Forthman et al.  
78 (2019), who focused on interfamilial and intersubfamilial relationships in the superfamily  
79 Coreoidea. However, the ability of the invertebrate UCE bait sets to robustly resolve  
80 phylogenetic relationships among tribes and congeners has not been widely demonstrated  
81 beyond a few studies primarily focused on Coleoptera and Hymenoptera (e.g., Van Dam et al.  
82 2017, Ješovník et al. 2017, Bossert et al. 2019, Branstetter and Longino 2019).

83 Leaf-footed bugs, or Coreidae (Hemiptera: Heteroptera), are a charismatic group of  
84 phytophagous insects (Fig. 1) that also includes several pests of agricultural systems (see Gentry  
85 1965, Nonveiller 1984, Mitchell 2000). With 2,571 extant species described in four subfamilies  
86 and 37 tribes, this is the largest family of the Coreoidea (CoreoideaSF Team 2019). The  
87 worldwide Coreinae is by far the largest coreid subfamily with 2,320 (90%) species (372 genera,  
88 32 tribes). Some of the largest, stoutest terrestrial heteropterans are members of this subfamily  
89 (e.g., species of *Pachylis*, *Thasus*, and *Petascelis*; Schuh and Slater 1995, Fernandes et al. 2015),  
90 but body forms also vary from sticklike (e.g., *Tylocryptus*, *Prionotylus*) to extravagant foliaceous  
91 or spined expansions (e.g., species of the tribe Phyllomorphini). While many species are dull in  
92 appearance, some are brightly colored and iridescent (e.g., *Petalops*, *Diactor*, *Phthiadema*). The

93 hind legs of males in many species are known to be sexually selected weapons that exhibit  
94 variation in size, shape, and armature (Eberhard 1998, Emlen 2008, Okada et al. 2011, Procter et  
95 al. 2012). Fighting behaviors are also variable in species that exhibit male-male competition;  
96 e.g., some species grapple end-to-end (e.g., *Narnia femorata*; Nolen et al. 2017), while others  
97 kick, flip, and squeeze one another face-to-face (e.g., *Mictis profana*; (Tatarnic and Spence  
98 2013). Aside from their diverse morphology, Coreinae are well known for their odious alarm  
99 pheromones (Aldrich and Blum 1978, Leal and Kadosawa 1992), paternal care in *Phyllomorphidae*  
100 (e.g., García-González et al. 2003), and gregariousness in nymphs (e.g., Aldrich and Blum 1978,  
101 Flanagan 1994, Miyatake 1995). Furthermore, species of the genus *Holhymenia* superficially  
102 appear to be wasp mimics (Pereira et al. 2013). Given these captivating morphological and  
103 behavioral features, the subfamily Coreinae offers an excellent opportunity to investigate the  
104 evolution of various traits and their possible correlates. However, a well-resolved, taxon-rich  
105 phylogeny of Coreinae is lacking. Thus, a comprehensive, robust phylogeny of the group is first  
106 needed before evolutionary questions can be investigated.

107 Although a few molecular phylogenetic analyses of the Coreidae have been performed  
108 (Fang and Nie 2007, Pan et al. 2007, Pan et al. 2008), the most comprehensive (with respect to  
109 taxon sampling) investigation of coreine phylogeny comes from Li's (1997) morphological  
110 phylogenetic analysis of the family Coreidae. Li (1997) recovered a paraphyletic Coreinae with  
111 respect to Meropachyinae, which has also been supported by Li (1996), Kieran et al. (2019), and  
112 Forthman et al. (2019). Li's (1997) analysis further suggested the tribe Colpurini to be the  
113 earliest diverging lineage within the Coreinae, which was also supported by Li (1996). Although  
114 Li (1997) found evidence that at some coreine tribes are not monophyletic, many of the 21  
115 sampled coreine tribes were represented by a single species. Furthermore, many morphological

116 traits analyzed by Li (1997) were recently shown to exhibit homoplasy (Forthman et al. 2019).

117 Since Li's (1997) analysis, hypotheses about inter- and intratribal relationships within the

118 Coreinae remain to be investigated more comprehensively.

119 Here, we use UCEs to develop a more comprehensive understanding of the phylogeny of

120 Coreinae and assess its utility in reconstructing relationships at shallow evolutionary timescales

121 in this subfamily. Our taxon sampling includes representatives of 21 morphologically diverse

122 tribes of Coreinae (out of 32), which is the most extensive sampling of tribes since Li's (1997)

123 analysis. This included several of the most and least speciose tribes (e.g., Hypselonotini and

124 Phyllomorphini, respectively) from all major biogeographic regions. With our taxon sampling,

125 we first examine the circumscription of currently recognized tribes, such as the Anisoscelini and

126 Coreini whose circumscription has varied among studies. Secondly, we test previous hypotheses

127 regarding phylogenetic relationships within Coreinae, such as the early divergence of Colpurini

128 from other tribes (Schaefer 1965, Ahmad 1970), the paraphyly of Nematopodini (Kieran et al.

129 2019, Forthman et al. 2019), and the non-monophyly of the subfamily with respect to the

130 Meropachyinae (Li 1996, 1997, Kieran et al. 2019, Forthman et al. 2019). Third, we explore the

131 suitability of UCEs at shallower scales by including multiple species within several genera

132 whose limits have been generally uncontroversial. Lastly, previous studies have reported

133 improvements in locus recovery by implementing alternative approaches to molecular protocols,

134 such as target enrichment (e.g., Li et al. 2013, Paijmans et al. 2016) or DNA extraction protocols

135 (e.g., Chen et al. 2010) that can impact that quality and quantity of samples — including dried

136 museum samples — for downstream processing. Thus, we examine the use of different DNA

137 extraction and target enrichment approaches and compare overall locus recovery among them.

138

139 Material and methods

140 *Taxon sampling*

141 A total of 124 taxa were sampled for this study, including 104 species of Coreinae from 21  
142 tribes. For 25 of our taxa, we obtained contigs from (Kieran et al. 2019) (NCBI Sequence Read  
143 Archive SRP161492) and (Forthman et al. 2019) (NCBI BioProject PRJNA531965). We  
144 generated new UCE data for the remaining taxa (Table S1) following the protocols discussed  
145 below.

146

147 *DNA extraction*

148 For all new data, genomic DNA was extracted using a 1) Gentra Puregene Tissue, 2) Qiagen  
149 DNeasy Blood and Tissue kit (hereafter DNeasy), or 3) Qiagen DNeasy Blood and Tissue kit  
150 coupled with Qiagen QIAquick PCR purification kit (hereafter DNQIA; see Knyshov et al.  
151 2019). Depending on the size of specimens, we used any part of the body (legs, abdomen, thorax,  
152 head) or the entire body from ethanol-preserved, silica-bead preserved, frozen, or dried  
153 specimens. For the Puregene Tissue Kit, we followed the manufacturer's protocol for 5–10 mg  
154 tissue with several modifications: 10 µL of proteinase K was added to samples and incubated for  
155 24–48 hours; samples were incubated at 37°C for 60 mins after adding 1.5 µL of RNase A  
156 solution, after which samples were placed on ice for 3 mins; two centrifugations, with ice  
157 incubation for 5 mins in between, were performed to ensure precipitated proteins formed a tight  
158 pellet; 600 µL of 100% ethanol was used for the first wash and centrifuged for 10 mins; and 50–  
159 100 µL of molecular grade water or Puregene DNA Hydration Solution was used to resuspend  
160 isolated DNA. We also followed the manufacturer's protocol for the DNeasy kit, but with fewer  
161 modifications: tissue was incubated in 180–190 µL Buffer ATL and 10–20 µL proteinase K for

162 24–48 hours (200 µL total solution volume), and DNA eluted once or twice with 50 µL Buffer  
163 AE depending on the size of the specimens we extracted from.

164 To assess which extraction protocol may perform better with dried museum material that is  
165 likely dominated by degraded DNA, we either used the DNeasy protocol described above or a  
166 modified version of it that follows Knyshov et al. (2019) (i.e., DNQIA). The latter protocol is  
167 specifically designed to extract degraded DNA >100 bp in length. Briefly, the DNQIA protocol  
168 follows the DNeasy kit up to the first centrifugation, using a QIAquick spin column. The  
169 samples are then subjected to the Qiagen QIAquick PCR purification kit, replacing AW1 and  
170 AW2 washes with PE buffer. Under the DNQIA protocol, samples are eluted in 30 µL EB  
171 buffer. We initially attempted to extract genomic DNA from six specimens using the DNeasy  
172 protocol (collected 1946–2016) and ten others using the DNQIA protocol (collected 1935–2015).  
173 Two museum samples (collected 1980 and 1987) initially subjected to the DNeasy protocol did  
174 not yield extracts of sufficient concentration nor produce visual bands after gel electrophoresis  
175 (see below for details on methods); these samples were re-extracted using the DNQIA protocol.

176 DNA quality was assessed with 1% agarose gel electrophoresis and quantified with a Qubit  
177 2.0 fluorometer. Samples were then normalized to 10–20 ng/µL, and high molecular weight  
178 samples were fragmented into 200–1000 bp using a Biorupter UCD-300 sonication device (4–10  
179 cycles of 30 s on/30 s) or a Covaris M220 Focused-ultrasonicator (20–60 s).

180

181 *Library construction, target enrichment, and sequencing*

182 We constructed libraries using the modified KAPA Hyper Prep Kit protocol of Forthman et  
183 al. (2019). Briefly, half volume reactions were used for all steps, as well as iTru universal  
184 adapter stubs and 8 bp dual-indexes (Glenn et al. 2016). Library amplification involved initial

185 denaturation at 98°C for 3 min, followed by 14 cycles of 98°C for 30 s, 60°C for 30 s, and 72°C  
186 for 30 s, with a final extension at 72°C for 5 min. Amplified libraries were inspected by gel  
187 electrophoresis, quantified with Qubit, combined into 1000 ng pools using equimolar amounts,  
188 dried at 60°C, and resuspended in 14 µL IDTE.

189 For target enrichment, we used a custom myBaits kit, based on Faircloth's (2017) probe set  
190 that was subsampled by Forthman et al. (2019). For some samples, we followed Forthman et  
191 al.'s (2019) enrichment protocol while others were subjected to a modified version of the  
192 protocol. We refer to the protocols as TE and TE-touchdown, respectively. For our TE protocol,  
193 a hybridization mixture with half volume of baits (2.75 µL) and 2.75 µL molecular-grade water  
194 was hybridized with each library pool at 65°C for 16–24 hours. In the TE-touchdown protocol,  
195 baits were to hybridize with library pools at 65°C for 18 hours followed by 18 hours at 62°C.  
196 However, samples were prematurely removed during the TE-touchdown protocol before  
197 hybridization was complete. At the recommendation of Arbor Biosciences, we added an  
198 additional 2.75 µL baits to these samples and re-ran the hybridization protocol to completion;  
199 additional baits were added given that the initial beads were subjected to the 95°C denaturation  
200 step, which may limit their effectiveness during hybridization per Arbor Biosciences.

201 Dynabeads M-280 Streptavidin beads were then bound to bait-target hybrids, washed four  
202 times at 65°C (TE) or 62°C (TE-touchdown) and resuspended in 30 µL IDTE. For the post-  
203 capture PCR amplification mix, 2.5 µL each of 5 µM iTru P5/P7 primers (Glenn et al. 2016)  
204 were added. We performed 14–17 cycles of post-capture amplification following manufacturer's  
205 protocol, except we used an annealing temperature of 65°C (TE) or 62°C (TE-touchdown) and  
206 an extension period of 45 s. Hydrophobic Sera-Mag SpeedBeads Carboxyl Magnetic Beads were  
207 used for post-amplification cleanup, followed by two washes in freshly prepared 70% ethanol

208 and resuspension in 22 µL IDTE. We quantified enriched library pools with Qubit, pooled all  
209 library pools in equimolar amounts, and sequenced on a single Illumina HiSeq3000 lane (2x100)  
210 at the University of Florida's Interdisciplinary Center for Biotechnology Research (ICBR).

211

212 *Sequence data processing and alignment*

213 Sequence data were processed following Forthman et al. (2019). Briefly, sequence reads  
214 were demultiplexed at the sequencing facility, and adapters were trimmed with illumiprocessor  
215 (Faircloth 2013, Bolger et al. 2014). Duplicate reads were filtered using PRINSEQ-lite v0.20.4  
216 (Schmieder and Edwards 2011), and the remaining reads error-corrected with QuorUM v1.1.0  
217 (Marçais et al. 2015) and *de novo* assembled in Trinity (Grabherr et al. 2011). We identified and  
218 aligned UCE loci from our assembled contigs using PHYLUCE v1.5.0 (Faircloth 2016). Internal  
219 trimming of alignments was done with trimAl (Capella-Gutiérrez et al. 2009). Locus alignments  
220 with at least 50% and 70% of taxa (hereafter 50p and 70p, respectively) were retained for  
221 phylogenetic inferences. We also subsampled each dataset by just including the 25% most  
222 parsimony informative loci — based on raw counts — to explore the effects of this filtering  
223 strategy on phylogenetic inferences; the use of the 25% most parsimony informative loci have  
224 been shown to improve or recover similar topological support compared to estimates based on  
225 more uninformative or informative gene trees, respectively (Hosner et al. 2016, Meiklejohn et al.  
226 2016).

227

228 *Phylogenetic estimation*

229 For each of the four datasets, we concatenated single locus alignments in PHYLUCE and  
230 then selected the best-fit partition scheme and models of sequence evolution using

231 PartitionFinder v2.1.1 (Lanfear et al. 2017). We used the rcluster algorithm with unlinked branch  
232 lengths and treated individual loci as separate data blocks. All models under the “raxml” option  
233 were examined (Stamatakis 2006), and the best-fit models were selected using the corrected  
234 Akaike Information Criterion (AICc) (Hurvich and Tsai 1989). Twenty partitioned maximum  
235 likelihood (ML) optimal searches were conducted in RAxML v8.2.10 (Stamatakis 2014) using  
236 random starting trees. Bootstrap (BS) support from 500 iterations were summarized on the best  
237 ML tree with SumTrees v4.0.0 (Sukumaran and Holder 2010).

238 We also estimated species trees from individual gene trees using an approach statistically  
239 consistent with the multispecies coalescent model (Degnan and Rosenberg 2006, 2009). We used  
240 MrAIC v1.4.6 (Nylander 2004) to select one out of the 56 models of sequence evolution for each  
241 locus alignment based on the AICc score in PhyML v3.1 (Guindon et al. 2010). We generated  
242 optimal gene trees by performing 20 ML searches in GARLI using results from MrAIC. The use  
243 of polytomous gene trees has been shown to improve species tree estimation (Zhang et al. 2017);  
244 as such, we allowed our input gene trees to have polytomies (collapsebranches = 1). One  
245 hundred bootstrap replicates were also generated by reducing the termination condition  
246 parameter by half the default value (i.e., genthreshfortopoterm = 10000) (see Zwickl 2008).  
247 Species trees were inferred from optimal gene trees in ASTRAL-III v5.6.1 (Mirarab et al. 2014,  
248 Sayyari and Mirarab 2016, Zhang et al. 2018), with clade support measured using 100 multi-  
249 locus bootstrap replicates (Seo 2008).

250 Majority-rule consensus trees were generated in PAUP\* v4.0a.16 (Swofford 2003) for the  
251 following: 1) all resolved optimal trees estimated from every analysis and 2) all optimal trees  
252 with branches having <50% bootstrap support collapsed. We then computed symmetric  
253 differences (2x Robinson-Foulds [RF]) between optimal trees (excluding outgroups) within each

254 of these two groups to assess topological variation across our analyses and to identify if  
255 conflicting nodes still existed after poorly supported branches were collapsed.

256 Because our results produced a polytomy among relatively deeper branches in our majority  
257 rule consensus trees, we evaluated if the incongruence among analyses could be due to  
258 incomplete lineage sorting. Under the multispecies coalescent model, rooted three-taxon gene  
259 trees will yield a majority resolution identical to the species tree (Pamilo and Nei 1988,  
260 Rosenberg 2002, Degnan and Rosenberg 2009). The other two alternative gene tree resolutions  
261 will be equiprobable to one another and proportionally less than the majority resolution (Pamilo  
262 and Nei 1988, Rosenberg 2002, Degnan and Rosenberg 2009). To evaluate whether  
263 incongruence among our analyses was due to incomplete lineage sorting, we tested our 50p total  
264 evidence optimal gene trees for asymmetry among minority gene trees using an exact two-sided  
265 binomial test (Zwickl et al. 2014, Richart et al. 2016, Wang et al. 2017, Forthman et al. 2019).  
266 Gene trees were pruned to include a representative of three clades at the polytomy with the  
267 highest UCE recovery (*Galaesus hasticornis*, *Odontorhopala callosa*, *Anasa tristis*), as well as  
268 an outgroup (*Halyomorpha halys*).

269

270 Results

271 *Data summary*

272 For this study, we recovered 3,750–61,308 contigs across samples (mean = 13,284), with a  
273 mean length of 451 bp (Table S2). We recovered 9–55% of the targeted UCE loci (range across  
274 samples: 242–1,470 loci; mean = 1,040), with a mean length of 668 bp. We found that the TE-  
275 touchdown protocol recovered more contigs and loci on average (per sample: 4,922–61,308  
276 contigs [mean = 18,017]; per sample: 242–1,470 loci [mean = 1,215]) than the TE protocol (per

277 sample: 3,750–18,575 contigs [mean = 8,522]; per sample: 556–1,272 loci [mean = 858]) (Fig.  
278 2). One sample produced an exceptional number of contigs compared to all others, while another  
279 produced very few UCE loci. Removal of these samples still produced qualitatively similar  
280 results (data not shown).

281 Of the 16 dried museum samples in which genomic DNA was extracted, subjected to the  
282 TE-touchdown protocol, and sequenced, only five yielded >200 UCE loci. The remaining  
283 samples yielded too few or no UCE loci. Four of the successful samples were recently collected  
284 (2015–2016), while the fifth sample was much older (collected in 1946). For the more recent  
285 samples, contig recovery did not appear to be dependent on DNA extraction method, but UCE  
286 recovery did differ with the DNQIA extraction protocol yielding substantially more UCEs (Table  
287 S3). Similarly, contig length was not affected by the extraction protocol used, but extraction  
288 method had a noticeable effect on UCE locus length (Table S3). The older sample did not  
289 produce the lowest number of contigs (4,922; 9<sup>th</sup> lowest), but it yielded the lowest number of  
290 UCE loci (242) in this study. Furthermore, this historical sample had smaller contig and UCE  
291 locus lengths on average (Table S3).

292 A summary of parsimony-informative sites and number of loci in each dataset are provided  
293 in Table S4. The most parsimony-informative UCE locus contained 1,079 informative sites, with  
294 the least informative locus having 16 informative sites. As expected, when datasets were  
295 constructed with higher locus informativeness thresholds, there was an increase in the proportion  
296 of parsimony-informative sites. There was also a decrease in the proportion of invariant sites,  
297 while the proportion of parsimony-uninformative sites were similar across all datasets.

298 After pruning outgroup taxa from our trees, symmetric distances were 0–8 among optimal  
299 summary coalescent trees, 0–8 among ML trees, and 2–12 when distances were calculated

300 between coalescent and ML trees (Table S5). We recovered similar values when using trees with  
301 poorly supported branches (BS < 50%) collapsed (Table S6).

302

303 *Higher-level relationships of the Coreinae + Meropachyinae*

304 Most reconstructed relationships within the Coreinae (including Meropachyinae) were  
305 congruent across all analyses (Figs. 3, S1–S8) and highly supported (Fig. 4). Some relationships  
306 were also consistently recovered across our estimates despite lower support (e.g., *Coreus* +  
307 *Cletus*; Cloresmini + Colpurini + Mictini) (Fig. 4). Across all analyses, Coreinae and  
308 Meropachyinae were not supported as monophyletic subfamilies. The meropachyine tribes  
309 Spathophorini and Merocorini were consistently recovered within coreine clades comprised of  
310 Nematopodini + Discogastrini and Acanthocerini + Chariesterini + Hypselonotini (part),  
311 respectively (Figs. 3, S1–S8), with moderate to high support (Fig. 4).

312 The majority rule consensus tree of all estimated trees resulted in a single polytomy near the  
313 base of Coreinae + Meropachyinae (Fig. 3), which was driven by uncertainty in the phylogenetic  
314 placement of Clade A. This clade was either recovered as the sister to all members of Clade B in  
315 summary coalescent analyses (BS 97–100%) (Figs. S1–S4), sister to Clade B + Clade C in most  
316 ML analyses (BS 54–83%) (Figs. S5, S6, S8), or sister to Clade C in one ML analysis (BS =  
317 83%) (Fig. S7). Given this incongruence among analyses, we tested if our estimated gene trees  
318 were consistent with the multispecies coalescent model. While a majority of our gene trees  
319 matched the species tree (46.64%), we detected asymmetry among our minority gene trees  
320 (33.40% and 18.26%; p < 0.05), suggesting incongruence was not driven by incomplete lineage  
321 sorting.

322 When poorly supported branches (BS < 50%) were collapsed in our estimated trees, we  
323 recovered an additional polytomy in our majority rule consensus tree among the Discogastrini +  
324 Nematopodini + Spathophorini (Fig. 3). The only sampled species of Discogastrini was more  
325 often recovered as the sister to the nematopodine genera *Nematopus* + *Grammopoecilius* with  
326 weak to moderate support (BS 55–76%) (Figs. S2–S4, S6, S8), but three analyses recovered this  
327 tribe as sister to all Nematopodini + Spathophorini with high support (BS = 100%) (Figs. S1, S5,  
328 S7). Furthermore, the position of the nematopodine genera *Melucha* + *Thasus* also varied across  
329 analyses, either recovered as the sister group of all other Nematopodini + Discogastrini +  
330 Spathophorini (BS = 100%) (Figs. S2–S4, S8), all remaining Nematopodini + Spathophorini (BS  
331 97–100%) (Figs. S1, S6), or *Ouranion* + *Piezogaster* + *Mozena* + Spathophorini (BS 94–100%)  
332 (Figs. S5, S7).

333 The position of the meropachyne tribe Merocorini was typically found to be sister to  
334 *Hypselonotus* + Chariesterini with weak to high support (Figs. S2, S4–S8). In summary  
335 coalescent analyses that used all loci, Merocorini was recovered as the sister to *Hypselonotus*  
336 (Figs. S1, S3). However, support for this relationship exhibited drastically different values:  
337 support was 82% for our 50p total evidence dataset whereas it was 27% for the 70p total  
338 evidence dataset.

339

340 *Non-monophyly of coreine tribes*

341 At the tribal level, we found support for the non-monophyly of several Coreinae tribes (Figs.  
342 3, 4, S1–S8). Nematopodini was consistently not monophyletic with respect to Spathophorini or  
343 Spathophorini + Discogastrini. The Coreini were polyphyletic, with *Haidara* highly supported as  
344 the sister to Phyllomorphini + Gonocerini + *Coreus* and *Coreus* sister to *Cletus* with poor to high

345 support. *Coreus* rendered Gonocerini paraphyletic with strong support. Weak to high support for  
346 a paraphyletic Daladerini with respect to Latimbini was observed across all analyses. Our results  
347 also recovered a polyphyletic Hypselonotini with five distinct lineages throughout Clade C, as  
348 well as a polyphyletic Anisoscelini with two lineages.

349

350 *Genus-level phylogenetic results*

351 At shallower depths, our results supported most sampled genera as clades comprised of their  
352 respective conspecifics with strong support (Figs. 3, 4, S1–S8). Only a few genera were not  
353 monophyletic. *Leptoglossus* was paraphyletic with respect to *Phthiacnemia*, and *Paryphes*  
354 rendered *Anasa* as paraphyletic, both at high support. We also found evidence for a paraphyletic  
355 *Plectropoda* with respect to *Elasmopoda* with weak to high support.

356

357 Discussion

358 We robustly reconstructed many shallow-level hemipteran relationships in the speciose  
359 coreid subfamily Coreinae. Our study recovered many highly support clades among and within  
360 coreine tribes and genera that were generally congruent across our maximum likelihood and  
361 summary coalescent analyses, although uncertainty still exists among the clades at deeper  
362 branches (i.e., clades A, B, and C in Fig. 3). The majority of our recovered relationships were  
363 novel, though a few were congruent with previous studies (e.g., Schaefer 1965, 1968, O’Shea  
364 1980a, 1980b, Li 1996, 1997, Kieran et al. 2019, Forthman et al. 2019). Additionally, several  
365 tribes and genera — as well as the subfamilies Coreinae and Meropachyinae — were recovered  
366 as para- or polyphyletic, often with robust support; the taxonomic status of these groups should  
367 be evaluated further to revise classification.

368

369 *Evaluation of DNA extraction and target enrichment protocols*

370 We observed a ~1.5– 2x increase in contig and UCE recovery when implementing our TE-  
371 touchdown approach. Such an increase may be due to the moderate reduction in hybridization  
372 temperature (i.e., from 65°C to 62°C). However, our TE-touchdown approach may have been  
373 confounded by early termination of our initial hybridization, although baits from the first  
374 hybridization should have been ineffective during the second attempt. Regardless, our  
375 improvement in locus recovery is consistent with other studies that have implemented a  
376 touchdown approach (e.g., Li et al. 2013, Paijmans et al. 2016), though not as high as has been  
377 reported in some studies (up to 8x increase; Li et al. 2013). This is likely due to our protocols  
378 conservatively reducing hybridization and washing temperatures (i.e., 62°C rather than 50°C).  
379 Further reductions in hybridization temperature during target capture may result in greater locus  
380 recovery with this and other invertebrate bait sets.

381 Our study suggests that recently collected, dried specimen material generally performs better  
382 than older samples in UCE target capture, consistent with other invertebrate UCE studies (e.g.,  
383 Blaimer et al. 2016). However, based on our results, the choice of DNA extraction protocol may  
384 be important for locus recovery in dried material, including those that are more recently collected  
385 (>5 years old). While neither extraction protocol resulted in large differences in contig recovery  
386 or length, we found ~2x increase in the number of UCE loci recovered, as well as generally  
387 longer UCEs, when using the DNQIA protocol (Knyshov et al. 2019). Thus, for these types of  
388 samples, a protocol tailored for the extraction of smaller DNA fragments may improve overall  
389 yield in UCE studies, although the success of any extraction approaches with historical  
390 invertebrate samples may be variable (e.g., Blaimer et al. 2016). Although there is a general

391 negative effect of sample age on target capture yields (Blaimer et al. 2016, McCormack et al.  
392 2016), it is unclear what factors may have contributed to our limited success with our older  
393 samples; all dried samples were subjected to the same molecular protocols and conditions as the  
394 successfully sequenced sample, and equal amounts of starting tissue were used for genomic  
395 DNA extraction. It is possible that factors such as the rate of desiccation and/or preservation  
396 methods prior to curation may affect target capture results (Blaimer et al. 2016).

397

398 *Coreinae paraphyly and Meropachyinae polyphyly*

399 Although Meropachyinae have rarely been included in phylogenetic analyses that sample  
400 Coreidae, there has been morphological and molecular evidence for the paraphyly of Coreinae  
401 with respect to this subfamily (Li 1996, 1997, Kieran et al. 2019, Forthman et al. 2019), which  
402 we corroborate. We found paraphyly of Nematopodini with respect to the meropachyine tribe  
403 Spathophorini, as in previous UCE studies (Kieran et al. 2019, Forthman et al. 2019).  
404 Additionally, the close relationship between Merocorini (Meropachyinae), Chariesterini, and  
405 *Hypselonotus* we recovered is largely consistent with previous cladistic (Li 1996, 1997) and non-  
406 cladistic (Schaefer 1965, Hepburn and Yonke 1971) studies. Both subfamilies have historically  
407 been delimited from the other coreid subfamilies by the presence of a dorsally sulcate tibia (see  
408 Forthman et al. 2019). In the taxonomic literature, the two subfamilies have been diagnosed from  
409 each other primarily by the presence (Meropachyinae) or absence (Coreinae) of an apical spine  
410 or tooth on the hind tibiae, as well as the shape of the hind femora and location of the  
411 metathoracic scent gland orifices. Our results indicate that these traits are likely homoplastic.

412

413 *Uncertain phylogenetic placement of clades A, B, and C*

414 Our study finds robust support for a clade comprised of Dasynini, Homoeocerini, Coreini,  
415 Phyllomorphini, and Gonocerini (Clade A). The phylogenetic position of Clade A, however,  
416 remains uncertain. In our summary coalescent analyses, this clade was sister to Clade B  
417 (Daladerini, Latimbini, Cloresmini, Colpurini, and Mictini; see Fig. 3) with high support, while  
418 the ML analyses recovered two alternative topologies involving the large Clade C  
419 (Hypselonotini, Acanthocerini, Merocorini, Chariesterini, Anisoscelini, Placoscelini,  
420 Acanthocephalini, Chelinideini) with weaker support.

421 The internal branches around the polytomy we recovered are very short relative to other  
422 branches at deep nodes (Figs. S5–S8). The short, successive branches suggest that this region of  
423 the tree might be in an anomaly zone, i.e., a region of the species tree where discordant gene  
424 trees are more common than gene trees that are concordant with the species tree due to  
425 incomplete lineage sorting (Degnan and Rosenberg 2006, Liu and Edwards 2009). However, our  
426 test of minority gene tree asymmetry suggests that our estimated gene trees are inconsistent with  
427 the multispecies coalescent model. Thus, discordance around these branches is likely due to  
428 other processes.

429

430 *Non-monophyly of Nematopodini*

431 A paraphyletic Nematopodini with respect to Spathophorini has also been supported by  
432 Kieran et al. (2019) and Forthman et al. (2019). However, in some of our analyses, Discogastrini  
433 was recovered within Nematopodini rather than as the sister group of Nematopodini +  
434 Spathophorini. This was not dependent on the analytical method or type of dataset used. Thus,  
435 Discogastrini may render Nematopodini (including Spathophorini) not monophyletic. To our  
436 knowledge, there are no previous hypotheses for a relationship between these three taxa.

437 Amyot and Serville (1843) included some members of Discogastrini within the  
438 Nematopodini based on the presence of enlarged, armed hind femora in males (although, in type  
439 images of several genera, the legs of Discogastrini appear slender and unarmed). Discogastrini  
440 was subsequently treated as a distinct group from the Nematopodini by Stål (1867), primarily  
441 due to the position of the abdominal spiracles. In his comparative morphological study, Schaefer  
442 (1965) included the Discogastrini, Homoeocerini, and Latimbini in his *Homoeocerus*-group  
443 (each tribe treated as a separate subgroup) based on the structure of the conjunctiva, metathoracic  
444 scent gland opening, laterotergites, and external genitalia (Nematopodini not examined). Our  
445 results are more in line with Amyot and Serville's (1843) classification, although the shape and  
446 armature of the hind femora may not be synapomorphies for Discogastrini + Nematopodini  
447 (including Spathophorini).

448

#### 449 *Clade A and the non-monophyly of Coreini and Gonocerini*

450 The taxonomic history of the Coreini has undergone drastic changes over the last decade.  
451 Many of the genera once classified in Coreini are now treated as members of Hypselonotini and  
452 other tribes, which we followed here (see CoreoideaSF Team 2019). Our results provide robust  
453 support for the exclusion of these genera from the Coreini, but we do not find evidence for a  
454 monophyletic Coreini. The relatively close relationship of Coreini and Gonocerini — which is  
455 paraphyletic in our study — is congruent with Pan et al. (2007) and Pan et al.'s (2008) Cytb  
456 phylogenies but contradicts Li's (1997) morphological and Fang and Nie's (2007) COII  
457 phylogenies. Schaefer (1965) placed the Coreini (which included genera now in other tribes)  
458 with several others (including Gonocerini and Dasynini) in his large *Coreus*-group. Our  
459 phylogenetic result provides limited support to Schaefer's (1965) study but does not recognize

460 the placement of many other tribes within his *Coreus*-group. Thus, the characters Schaefer  
461 (1965) used to diagnose and describe his *Coreus*-group and subgroups are likely plesiomorphic  
462 or homoplastic synapomorphies based on our molecular phylogenetic hypothesis.

463 The tribe Phyllomorphini has not been included in phylogenetic analyses. Past pre-cladistic  
464 morphological studies led some authors to propose Phyllomorphini as a distinct subfamily due to  
465 the absence of a dorsal tibial sulcus, as well as several genitalic and abdominal traits (Schaefer  
466 1965, Ahmad 1970, 1979). However, we find support for the inclusion of this tribe within the  
467 Coreidae.

468 Lastly, the sister group relationship between Dasynini and Homoeocerini recovered from  
469 our analysis is novel. Schaefer (1965) did not consider these tribes to belong to the same group in  
470 his morphological study. Li (1997) included several species of Dasynini and found this tribe to  
471 be paraphyletic, but none of the sampled species were found to be closely related to  
472 Homoeocerini.

473

474 *Novel relationships of Clade B, the paraphyly of Daladerini, and phylogenetic position of*  
475 *Colpurini*

476 The relationships recovered within our well-supported Clade B do not strictly agree with  
477 previous studies (Schaefer 1965, Li 1997, Fang and Nie 2007). Daladerini and Latimbini were  
478 recovered as the sister of all other tribes within Clade B. We found support for a clade comprised  
479 of Cloresmini, as well as its sister group relationship with Colpurini + Mictini that has not been  
480 previously proposed. Schaefer (1965) included Cloresmini within his *Coreus*-subgroup C with  
481 other tribes not recovered in this clade (although Mictini was included in a separate *Coreus*-  
482 subgroup within a larger *Coreus*-group).

483 Amyot and Serville (1843) classified *Dalader* in the same family-group as genera from  
484 Mictini, but it was subsequently treated as a distinct group by Stål (1873). Li's (1997)  
485 morphological phylogenetic hypothesis suggests that the Daladerini are sister to Acanthocerini  
486 and Acanthocephalini, in support of Stål's (1873) treatment of the tribe as separate from the  
487 Mictini. Our results also support the exclusion of the sampled daladerine genera from Mictini but  
488 find new evidence for the paraphyly of this tribe with respect to Latimbini. Schaefer (1965)  
489 assigned Daladerini to his *Coreus*-subgroup B; he assigned the Latimbini to the *Homoeocerus*-  
490 group but recognized that the position of Latimbini was uncertain.

491 Our results for the phylogenetic placement of Colpurini and treatment as a tribe within  
492 Coreinae is contradictory with all other studies (Štys 1964, Kumar 1965, Schaefer 1965, Li 1997,  
493 Ahmad 1970). Past studies have characterized the Colpurini as “primitive” but with many  
494 characters (primarily genitalia) suggesting an “intermediate” phylogenetic position between  
495 Pseudophloeinae, Hydarinae, and other Coreinae (see Štys 1964, Kumar 1965, Schaefer 1965, Li  
496 1996, 1997, Ahmad 1970). Thus, our results are novel and suggest that genitalic features, as well  
497 as external features, should be re-evaluated in light of our molecular hypothesis.

498

499 *Polyphyly of Hypselonotini*

500 With 356 species, the Hypselonotini is the most speciose tribe within the family Coreidae.  
501 This tribe has not been formally described or diagnosed even when it was first recognized by  
502 Bergroth (1913). Over the last three decades, a number of genera currently recognized within the  
503 Hypselonotini (CoreoideaSF Team 2019) have been previously treated as members of the  
504 Coreini (e.g., Brailovsky 1988, 1990, 1995, 2016, Packauskas 1994). Members of this tribe have  
505 not been included in published phylogenetic analyses and, to our knowledge, appear to have only

506 been examined by Schaefer (1965) in his comparative morphological study (treated as part of  
507 Coreini). Our study supports the exclusion of the sampled hypselonotine genera from the Coreini  
508 but not the monophyly of this large tribe; five independent lineages were robustly supported in  
509 our analyses. Of these, only the taxonomic position of *Hypselonotus* within the *Hypselonotus* +  
510 Chariesterini + Merocorini was not congruent across analyses. It is evident from our results that  
511 the taxonomic status of Hypselonotini is in further need of evaluation. Including additional  
512 genera of this tribe will provide further insights into the extent of hypselonotine polyphyly.

513

514 *Polyphyly of Anisoscelini*

515 The tribe Anisoscelini is a moderately-sized group, with 183 species that exhibit a diversity  
516 of color patterns and morphology, particularly with the shape and size of the foliaceous  
517 expansions on the hind tibiae. Members of Anisoscelini were once divided among two tribes  
518 (Anisosceledini [or Anisoscelini] and Leptoscelidini), primarily based on the presence or absence  
519 of hind tibial expansions (e.g., Stål 1867, Schaefer 1965, Packauskas 1994). Schaefer (1965,  
520 1968) classified both of these former tribes as members of the *Acanthocephala*-group with  
521 Acanthocephalini and Placoscelini. We find some support for Schaefer's (1965, 1968) scheme,  
522 but we do not support his exclusion of Chelinideini and Hypselonotini from the *Acanthocephala*-  
523 group. The two distinct anisosceline lineages we recovered do not appear to correspond to  
524 previously proposed tribal classifications and phylogenetic hypotheses nor appear to be separated  
525 based on the presence of tibial expansions. Like Hypselonotini, careful evaluation of this tribe is  
526 needed to understand the extent of anisosceline polyphyly.

527

528 *Phylogenetic position of Chelinideini*

529 We support a sister group relationship between Chelinideini and our Hypselonotini Lineage  
530 5 + Anisoscelini Lineage 2 clade (Fig. 3), contrary to previous studies. Li's (1997) phylogenetic  
531 hypothesis found a close relationship between Chelinideini and Homoeocerini. Based on a  
532 survey of genitalic morphology, Schaefer (1965) placed this tribe in a *Coreus* subgroup  
533 (subgroup C) that included Gonocerini, Acanthocorini (part), Cloresmini, and Coreini. In fact,  
534 Chelinideini was once classified within the Coreini, but was elevated to tribal rank by Blatchley  
535 (1926). Thus, our results on the phylogenetic position of Chelinideini are novel and require  
536 further comparative work to identify and test potential synapomorphies.

537

538 *Paraphyletic genera*

539 The genera *Plectropoda* and *Elasmopoda* are two of several genera comprising the  
540 *Elasmopoda* complex (Linnauori 1978, O'Shea 1980c) and share many morphological  
541 similarities. Both genera have been treated as separate groups since Stål (1873), but some species  
542 have historically experienced changes in generic assignment between these two groups.  
543 Linnauori (1978) revised the *Elasmopoda* complex but noted that some features used to  
544 diagnosis *Elasmopoda* are also observed in some *Plectropoda* species. This may suggest that one  
545 or both genera are not monophyletic, and our study supports the paraphyly of *Plectropoda* with  
546 respect to *Elasmopoda*. This indicate that the taxonomic limits of these genera should be  
547 evaluated further.

548 The genus *Leptoglossus* is an agriculturally important group (Schaefer and Mitchell 1983,  
549 Jankevicius et al. 1993, Fernandes et al. 2015), with many of the 62 species distributed  
550 throughout the New World, while two species, *L. gonagra* and *L. occidentalis*, occur worldwide  
551 (CoreoideaSF Team 2019). Our study recovered a paraphyletic *Leptoglossus*, with *L. gonagra*

552 recovered as sister to *Phthiacnemia picta*, both of which were sampled from the New World.  
553 Based on our survey of the taxonomic literature and the Coreoidea Species File (CoreoideaSF  
554 Team 2019), these two genera have never been treated as or hypothesized to be the same. Allen  
555 (1969) created two divisions within *Leptoglossus* — Divisions A and B. While we do not support  
556 the monophyly of this genus, we do find limited support for Allen's (1969) separate treatment of  
557 his Division A (i.e., *L. gonagra*) from those of Division B (i.e., *L. phyllopus*, *L. clypealis*, *L.*  
558 *concolor*).

559 The hypselonotine genus *Anasa* is a large genus comprised of 77 New World species  
560 (CoreoideaSF Team 2019), with several of economic importance (Schaefer and Mitchell 1983,  
561 Fernandes et al. 2015). We also found evidence for the paraphyly of *Anasa* with respect to the  
562 hypselonotine genus *Paryphes*. The close relationship between these two genera have not been  
563 previously tested. Stål (1867) provided a framework to separate the two genera based on the  
564 curvature of the head and the structure of the antennal segments. In this same publication, Stål  
565 (1867) transferred a single species from *Paryphes* to *Anasa*. Since then, the taxonomic literature  
566 has recognized these two genera as distinct without suggestion that they are potentially the same.

567

568 Conclusion

569 The results of our phylogenomic analysis suggest para- and polyphyly of several genera,  
570 tribes, and subfamilies of Coreidae, indicating that the taxonomic classification of this diverse  
571 family and its largest subfamily, the Coreinae, is in critical need of evaluation and future  
572 revision. We were able to robustly reconstruct relationships at shallow phylogenetic scales  
573 within the coreid subfamily Coreinae, demonstrating that invertebrate UCEs are suitable at a  
574 variety of scales. Additionally, our results suggest that DNA extraction protocols designed to

575 capture shorter, degraded DNA fragments in dried museum material and lower target capture  
576 hybridization temperatures may increase the number and length of UCE loci in this and  
577 potentially other invertebrate bait sets.

578

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609

610 Data accessibility

611 Sequence read files are available on NCBI's Sequence Read Archive under BioProject  
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613

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897

898 Figures

899 Figure 1. Images of representative Coreinae. (a) *Acanthocephala femorata* (Acanthocephalini)  
900 (© 2015 Kala King). (b) *Chelinidea vittiger* (Chelinideini) (© 2017 Mary Keim). (c) *Holymenia*  
901 sp. nymph (Anisoscelini) (© 2011 Arthur Anker). (d) *Leptoglossus* sp. (Anisoscelini) (© 2006  
902 Sean McCann). (e) *Physomerus grossipes* (Acanthocorini) (© 2014 Anthony Kei C Wong). (f)  
903 *Savius jurgiosus* (Discogastrini) (© 2016 Jeff Gruber). (g) *Mictis profana* (Mictini) (© 2011 Jon  
904 Clark). (h) *Hypselonotus* sp. (Hypselonotini) (© 2015 Jeff Gruber). (i) *Diactor* sp. (Anisoscelini)  
905 (© 2015 Jorge Restrepo). (j) *Phyllocephala laciniata* (Phyllocephalini) (© 2015 Simon Oliver).

906

907 Figure 2. Contig (a) and UCE locus (b) recovery between different DNA extraction and target  
908 enrichment protocols. Abbreviations: DNeasy, Qiagen DNeasy Blood and Tissue kit (including  
909 QIAquick PCR Purification kit); GPT, Gentra Puregene Tissue kit; TE, (Forthman et al. n.d.)  
910 target enrichment protocol; TE-TD, TE-touchdown protocol.

911

912 Figure 3. Majority rule consensus tree of all optimal trees (left) and all trees when branches with  
913 bootstrap support <50% are collapsed (right) across maximum likelihood and summary  
914 coalescent analyses (outgroups pruned for visualization) and datasets (i.e., taxon-sampling and  
915 parsimony informativeness). Species names are provided on the left tree, while the names of the

916 corresponding tribes are provided on the right tree. Select tribes (including the subfamily  
917 Meropachyinae) that are non-monophyletic are color-coded. Red circles at nodes indicate the  
918 location of polytomies in the majority rule consensus trees. Numbers below branches indicate the  
919 proportion of all eight trees that recovered the corresponding clade; branches without numbers  
920 were recovered in 100% of trees.

921

922 Figure 4. Bootstrap support for select Coreinae + Meropachyinae branches from Fig. 3 that  
923 exhibit conflict and/or low support across all analyses. Abbreviations: Bootstrap support, BS;  
924 Hypselonotini Lineage (HL).







