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Phylogenomic analysis suggests Coreidae and Alydidae (Hemiptera: Heteroptera) are not monophyletic

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Abstract

Next-generation sequencing technologies (NGS) allow systematists to amass a wealth of genomic data from non-model species for phylogenetic resolution at various temporal scales. However, phylogenetic inference for many lineages dominated by non-model species has not yet benefited from NGS, which can complement Sanger sequencing studies. One such lineage, whose phylogenetic relationships remain uncertain, is the diverse, agriculturally important and charismatic Coreoidea (Hemiptera: Heteroptera). Given the lack of consensus on higher-level relationships and the importance of a robust phylogeny for evolutionary hypothesis testing, we use a large data set comprised of hundreds of ultraconserved element (UCE) loci to infer the phylogeny of Coreoidea (excluding Stenocephalidae and Hyocephalidae), with emphasis on the families Coreidae and Alydidae. We generated three data sets by including alignments that contained loci sampled for at least 50%, 60%, or 70% of the total taxa, and inferred phylogeny using maximum likelihood and summary coalescent methods. Twenty-six external morphological features used in relatively comprehensive phylogenetic analyses of coreoids were also re-evaluated within our molecular phylogenetic framework. We recovered 439–970 loci per species (16%–36% of loci targeted) and combined this with previously generated UCE data for 12 taxa. All data sets, regardless of analytical approach, yielded topologically similar and strongly supported trees, with the exception of outgroup relationships and the position of Hydarinae. We recovered a monophyletic Coreoidea, with Rhopalidae highly supported as the sister group to Alydidae + Coreidae. Neither Alydidae nor Coreidae were monophyletic; the coreid subfamilies Hydarinae and Pseudophloeinae were recovered as more closely related to Alydidae than to other coreid subfamilies. Coreinae were paraphyletic with respect to Meropachyinae. Most morphological traits were homoplastic with several clades defined by few, if any, synapomorphies. Our results demonstrate the utility of phylogenomic approaches in generating robust hypotheses for taxa with long-standing phylogenetic problems and highlight that novel insights may come from such approaches.

KEYWORDS

Alydidae, Coreidae, Coreoidea, phylogeny, ultraconserved elements

1 | INTRODUCTION

The field of phylogenetics has made great strides in its endeavour to infer the Tree of Life, which provides the foundation for all disciplines to investigate evolutionary hypotheses beyond inferring species relationships. The earliest phylogenetic studies relied on morphology and/or traditional Sanger sequencing data (i.e., one to few genes) to infer evolutionary histories within and among non-model species for which genomic resources were not available. While such data and early advances in phylogenetics progressed the field towards its goals, challenges still exist with such traditional data, such as limited sequence data that are unable to resolve challenging nodes (particularly deep divergences), gene tree discordance with species trees and difficulty in filling taxon sampling gaps due to a lack of suitable material. As a means to address these challenges, newer phylogenetic approaches coupled with the development and advances of next-generation sequencing (NGS) technology have since revolutionized molecular systematics. First, the application of NGS allows a cost-effective approach to sequencing hundreds to thousands of loci from non-model species in relatively short time. This allows researchers to complement traditional Sanger approaches by sampling loci throughout all regions of the genome (e.g., exons, introns, other non-coding regions and mitochondrial DNA), which can provide data that allow for phylogenetic resolution at different temporal scales (Faircloth et al., 2012; Lemmon, Emme, & Lemmon, 2012; Li, Hofreiter, Straube, Corrigan, & Naylor, 2013). The ability to sample throughout genomes has also given investigators the ability to increase gene tree sampling and reduce species tree estimation error in summary coalescent analyses (Zhang, Rabiee, Sayyari, & Mirarab, 2018). Furthermore, for some taxonomic groups, phylogenomic approaches have been developed and improved for application to material that has historically been difficult to use with Sanger sequencing approaches (e.g., historical museum samples with highly degraded DNA) (Blaimer, Lloyd, Guillory, & Brady, 2016; McCormack, Tsai, & Faircloth, 2016; Staats et al., 2013), allowing researchers to include critical taxa in phylogenetic analyses. Lastly, more recent studies have shown the integration of existing Sanger data sets with phylogenomic data sets (Hosner, Braun, & Kimball, 2016; Leaché et al., 2014; Persons, Hosner, Meiklejohn, Braun, & Kimball, 2016; Richart, Hayashi, & Hedin, 2016; Zhang et al., 2016), demonstrating the complementarity of these two approaches. Thus, the benefits of NGS technologies have had a profound impact on our ability to resolve some of the most challenging nodes in the Tree of Life, although phylogenetic inference for many lineages dominated by non-model organisms has yet to benefit from NGS approaches.

One such group, whose phylogenetic relationships have remained far from settled, is the diverse, agriculturally important and charismatic Coreoidea (Hemiptera: Heteroptera; Figure 1). Based on the most recent catalog of Coreoidea (Coreoidea Species File, 2018), these phytophagous insects include two species in extinct families (Trisegmentatidae and Yruipopovinidae) and 3,106 extant species in five recognized families: Alydidae (282 species), Coreidae (2,571 species), Hyocephalidae (three species), Rhopalidae (224 species) and Stenocephalidae (30 species). Coreoids are well studied for a number of reasons. Several species are considered to be major agricultural pests (Mitchell, 2000), for example the bean bug, *Riptortus pedestris*, which is also a model organism for symbiont research (Mitchell, 2000; Takeshita & Kikuchi, 2017). Members of this superfamily also include some of the largest, robust, terrestrial heteropterans and several brightly coloured species (Fernandes, Mitchell, Livermore, & Nikunlassi, 2015; Schuh & Slater, 1995). Within this group, there is also diversity of body forms, varying from slender and elongate to large, foliaceous or winglike expansions on the body and/or legs (Schuh & Slater, 1995). Some coreoid families, specifically, the Coreidae, are well known for their odious defensive or alarm pheromones (Aldrich & Blum, 1978; Leal, Panizzi, & Niva, 1994) and a range of intriguing behaviours, such as paternal care (García-González, Nüñez, Ponz, Roldán, & Gomendio, 2003), male–male competition with sexually selected hind leg weapons (Eberhard, 1998; Okada, Suzaki, Okada, & Miyatake, 2011; Procter, Moore, & Miller, 2012) and gregariousness during development and/or mating (Aldrich & Blum, 1978; Flanagan, 1994; Miyatake, 1995). Furthermore, ant mimicry (myrmecomorphy) occurs in many species of Alydidae (Mclver & Stonedahl, 1993; Panizzi & Schaefer, 2015; Schuh & Slater, 1995).

Few cladistic analyses have directly investigated the phylogeny of the Coreoidea, though many more tangential studies included a few representatives but are not very comprehensive. Collectively, no consensus has emerged regarding familial-level relationships. Only limited morphological and traditional Sanger data have, so far, been utilized to understand the evolutionary history of this group. In Table 1 and the following paragraphs, we summarize the current state of knowledge on coreoid classification and phylogenetic hypotheses.

A close relationship between Alydidae and Coreidae has been supported in many past morphological and molecular studies (see Table 1). However, most of these studies have only included one representative of each family. Of those with multiple representatives of at least one family, it is not clear if the families are monophyletic. Within the large family Coreidae, there are currently four recognized subfamilies: Coreinae, Hydarinae, Meropachyinae and Pseudophloeinae (Coreoidea Species Files, 2018). Additional subfamilies have

FIGURE 1 Images of representative Coreoidea. (a) *Dicranocephalus* sp. (© 2014 Serhey Ruban). (b) *Leptocorisa acuta* (© 2018 Jen Feng Yeh). (c) *Hyalymenus tarsatus* (© 2017 Lee Hoy). (d) *Jadera haematoloma* (© 2014 Erinn Shirley). (e) *Golema histrio* (© 2018 Bruno Garcia Alvares). (f) *Gonocerus* sp. (© 2016 Mia Moreau). (g) Phyllomorphini sp. (© 2017 Jesus Tizon). (h) *Anisoscelis* sp. (© 2010 Carlos Mancilla) [Colour figure can be viewed at wileyonlinelibrary.com]

been proposed (e.g., Colpurinae [Štys, 1964; Kumar, 1965], Agriopocorinae [Miller, 1954], Phyllomorphinae [Ahmad, 1970]), but these are given tribal rank by the Coreoidea Species File (2018), which is generally used by current workers and adopted here for testing in our study. Comprehensive analyses investigating the higher-level relationships within the Coreidae or Alydidae have been few and have solely used morphological characters. Among those studies that have looked more comprehensively, Li (1996) found Pseudophloeinae to be sister to all sampled ingroup coreoids, with Hydarinae sister to Rhopalidae + (Alydidae + (Coreinae + Meropachyinae)). A separate morphological analysis on the Coreidae (Li, 1997) corroborated the paraphyly of Coreinae and also found Pseudophloeinae to be sister to Hydarinae + (Coreinae + Meropachyinae). With respect to the Alydidae, Li and Zheng's (1993) analysis recovered the monophyly of the two currently recognized subfamilies, which was supported by Li (1996).

Other less comprehensive and/or non-cladistic studies have also suggested the Pseudophloeinae to be an early diverging lineage within the Coreidae (Ahmad, 1979; Ahmad & Shadab, 1975; Schaefer, 1965). However, these same workers and others have observed many similarities between this subfamily and Alydidae (Štys, 1962; Cobben, 1968; Ahmad, 1970; Dolling, 1978; Shadab, 1972), with Kumar (1965) actually proposing the transfer of Pseudophloeinae to Alydidae. Although not as extensively studied as Pseudophloeinae, the coreid subfamily Hydarinae also possesses similarities in egg traits with Alydidae (Cobben, 1968). Although considered precladistic, Ahmad's (1970) morphological study led him to propose that Pseudophloeinae and Hydarinae have greater affinities to each other than to other coreid taxa. A recent mitochondrial genome analysis by Zhao et al. (2018) found either Pseudophloeinae or Hydarinae as sister to the alydid subfamily Alydinae, depending on the analytical method used; however, taxon sampling was limited to a single species for each of these lineages and remains to be tested with a larger sample.

Given the lack of rigorous analytical tests on higher-level relationships with more modern approaches and the importance of a robust phylogeny for evolutionary hypothesis testing, we constructed the phylogeny of the Coreidae and Alydidae using a large multilocus data set comprised of hundreds of ultraconserved element (UCE) loci. This class

TABLE 1 References of phylogenetic studies supporting clades of interest

Reference	Coreoidea	Rhopalidae + (Alydidae + Coreidae)	Alydidae + Coreidae	Alydidae	Coreidae	Pse + Hyd + Alydidae	Hyd + Alydidae	Pse + (Hyd + Cor + Mer)	Hyd + (Cor + Mer)	Hyd + Cor	"Cor" + Mer
This study	UCE	UCE	UCE	—	—	UCE	—	—	—	—	UCE
Henry (1997)*	Morph	—	Morph	NA	NA	NA	NA	NA	NA	—	NA
Li (1996)	Assumed	—	NA	Morph	NA	NA	NA	NA	NA	NA	Morph
Li (1997)	NA	NA	NA	NA	Assumed	NA	NA	Morph	Morph	—	Morph
Li et al. (2005)	—	—	—	NA	—	NA	NA	NA	NA	NA	NA
Xie et al. (2005)	—	—	Nu	NA	NA	NA	NA	NA	NA	—	NA
Li et al. (2006)	—	—	—	Nu (ML)	—	NA	NA	NA	NA	NA	NA
Hua et al. (2008)	mtGen	mtGen	mtGen	NA	NA	NA	mtGen	NA	NA	NA	NA
Pan et al. (2008)	mtDNA	mtDNA	mtDNA	—	—	NA	NA	NA	NA	NA	NA
Tian et al. (2011)	Nu	Nu	Nu	NA	NA	NA	NA	NA	NA	NA	NA
Song, Liang, and Bu (2012)	mtGen (excluding parismony and ML with long branch taxa)	mtGen (excluding analyses with long branch taxa)	mtGen (excluding parsimony with long branch taxa)	NA	NA	NA	mtGen (excluding parsimony with long branch taxa)	NA	NA	NA	NA
Yao et al. (2012)*	Morph	—	Morph	NA	NA	NA	NA	NA	NA	—	NA
Yuan, Zhang, Guo, Wang, and Shen (2015)	mtGen	mtGen	mtGen	NA	NA	NA	mtGen	NA	NA	—	NA
Gordon, McFrederick, and Weirauch (2016)*	X	X	X	NA	X	NA	NA	NA	NA	NA	NA
Li et al. (2016)	X	X (ML analysis)	X	X	NA	NA	NA	NA	NA	NA	NA
Wang et al. (2016)	X	X	X	X	X	NA	—	NA	NA	X	NA
Valero et al. (2017)	mtGen	mtGen	mtGen	NA	mtGen	NA	—	NA	NA	mtGen	NA
Weirauch et al. (2018)	Y (excluding dynamic homology)	—	—	NA	—	NA	NA	NA	NA	—	NA
Zhao et al. (2018)	mtGen	—	mtGen (only with Alydinae)	—	—	mtGen (only with Alydinae in Bayesian)	mtGen (with Alydinae in ML)	NA	NA	—	NA

Note. Most published analyses were primarily focused on other higher-level relationships within Heteroptera, and often include one representative for one to four coreoid families. Those references that have included all five families are indicated in "*".

Abbreviations: —: tested but not recovered in study or unresolved; Cor: Coreinae; Hyd: Hydarinae; Mer: Meropachyiane; Morph: recovered with morphological data; mtDNA: recovered with mitochondrial data; mtGen: recovered with partial mitochondrial genome data; NA: not tested in study; Nu: recovered with nuclear data; Pse: Pseudophloeinae; UCE: recovered with ultraconserved element loci; X: recovered with nuclear and mitochondrial data; Y: recovered with combined morphology: nuclear: and mitochondrial data.

of genomic loci are highly conserved among divergent taxa (Faircloth, Branstetter, White, & Brady, 2015; Faircloth et al., 2012), and sequence capture based on baits that target the conserved regions also captures more variable flanking nucleotides. Recently, UCE probes for the Order Hemiptera were designed (Faircloth, 2017) and empirically shown (Kieran et al., 2019) to resolve deep and relatively shallower relationships with high support. The study by Kieran et al. (2019) included nine species of Coreidae from two subfamilies, which recovered a paraphyletic Coreinae with respect to Meropachyinae. Given the utility of UCEs in hemipteran phylogenetics, we use these markers to infer the higher-level evolutionary history of Coreidae and Alydidae with greater taxon sampling.

2 | MATERIAL AND METHODS

2.1 | Taxon sampling

Twenty-five taxa were included in this study, including 12 species of Coreidae (representing all four subfamilies), five Alydidae (including both subfamilies) and two species of Rhopalidae as the ingroup. Specimen material for the smallest two families of Coreoidea was lacking, and thus, not included. Because there is a lack of consensus on the sister group of Coreoidea (Henry, 1997; Hua et al., 2008; Valero et al., 2017; Weirauch, Schuh, Cassis, & Wheeler, 2018), we included several representatives of the superfamilies Lygaeoidea and Pyrrhocoroidea and a species of Pentatomidae as an outgroup. Data for nine coreid taxa, as well as the Pentatomidae and Lygaeoidea, were taken from Kieran et al. (2019).

2.2 | DNA extraction, target enrichment and sequencing

We extracted genomic DNA from the hindleg, midleg and/or abdomen—or for small specimens, the whole body—of ethanol-preserved specimens using Qiagen DNeasy Blood and Tissue Kit, following manufacturer's protocol, with the following exceptions: tissue was incubated in 190 µl Buffer ATL and 10 µl proteinase K for 12–48 hr, with DNA eluted twice with 50 µl Buffer AE. We visualized DNA extract quality with 1% agarose gel electrophoresis, quantified DNA concentrations using a Qubit 2.0 fluorometer, and normalized each sample to 10–20 ng/µl. Samples characterized by high molecular weight were fragmented on a Biorupter UCD-300 sonication device for 4–10 cycles of 30 s on and 30 s off to produce fragments that ranged 200–1,000 bp.

We constructed libraries using a KAPA Hyper Prep Kit following manufacturer's protocol with modifications. We used half volume reactions at all steps with iTru universal adapter stubs and iTru 8 bp dual-indexes (Glenn et al., 2016). Library amplification was performed using the following thermocyler protocol: initial 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 for 30 s, with a final extension at 72°C for 5 min. Prior to postamplification cleanup, amplified libraries were inspected by gel electrophoresis. Hydrophobic Sera-Mag SpeedBeads Carboxyl Magnetic Beads were used for all cleanup steps. Cleaned, amplified libraries were quantified with Qubit, subsequently combined in equimolar amounts into 1,000 ng pools, dried at 60°C, and resuspended in 14 µl IDTE.

A custom MYbaits kit containing the subset of Hemiptera UCE probes designed from pentatomomorphan species (2,673 loci, 9,411 probes; Faircloth, 2017) was used for target enrichment; the probe set also included some additional non-UCE probes (M. Forthman, R. T. Kimball, & C. W. Miller, in prep) that were not used in this study. We followed manufacturer's protocol with some modifications. For each library pool, the hybridization mixture used half volume of baits (2.75 µl) and 2.75 µl molecular-grade water. Probes were hybridized with library pools at 65°C for 16–24 hr. Bait–target hybrids were bound to Dynabeads M-280 Streptavidin beads, washed four times, and resuspended in 30 µl IDTE. We used 2.5 µl each of 5 µM iTru P5/P7 primers (Glenn et al., 2016) for the postcapture PCR amplification mix. For postcapture amplification, 14–17 cycles were performed, with an annealing temperature of 65°C and an extension period of 45 s; all other settings followed the manufacturer's protocol. Postamplification cleanup involved Hydrophobic Sera-Mag SpeedBeads Carboxyl Magnetic Beads, followed by two washes in freshly prepared 70% ethanol and resuspension in 22 µl IDTE. Enriched library pools were quantified with Qubit, pooled in equimolar amounts, and sequenced using a single Illumina HiSeq3000 lane with 2x100 run at the University of Florida's Interdisciplinary Center for Biotechnology Research (ICBR).

2.3 | Sequence data processing and alignment

Sequence reads were demultiplexed at ICBR. Duplicate reads were removed using PRINSEQ-lite v0.20.4 (Schmieder & Edwards, 2011). Reads were error-corrected with QuorUM v1.1.0 (Marçais, Yorke, & Zimin, 2015) and *de novo* assembled in Trinity (Grabherr et al., 2011). PHYLUCE v1.5.0 (Faircloth, 2016) was used to identify UCE loci from assembled contigs, and align individual loci using its implementation of MAFFT v7.130 (Katoh, Misawa, Kuma, & Miyata, 2002; Katoh & Standley, 2013). Alignments were internally trimmed using trimAl (Capella-Gutiérrez, Silla-Martínez, & Gabaldón, 2009). We generated three data sets by selecting aligned loci that

contained at least 50%, 60%, and 70% of the total taxa for phylogenetic inference.

2.4 | Phylogenetic estimation

For each data set, single locus alignments were concatenated in PHYLUCE. PartitionFinder v2.1.1 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) was used to select the best-fit partitioning scheme and models of sequence evolution, with the following search settings: individual loci treated as a data block, branch lengths unlinked, all models under the "raxml" option examined (Stamatakis, 2006), model selection based on the corrected Akaike information criterion (AICc) (Hurvich & Tsai, 1989), and partition search using the "rcluster" algorithm (Lanfear, Calcott, Kainer, Mayer, & Stamatakis, 2014).

Twenty partitioned maximum likelihood (ML) optimal searches were conducted using random starting trees, followed by 500 bootstrap (BS) iterations, in RAxML v8.2.10 (Stamatakis, 2014). Bootstrap support was summarized on the best ML tree with SumTrees v4.0.0 (Sukumaran & Holder, 2010).

Concatenation approaches assume that all loci share a similar evolutionary history, yet heterogeneity among gene trees due to incomplete lineage sorting can lead to the most common gene trees conflicting with the true species tree at short branches (Degnan & Rosenberg, 2006, 2009; Kubatko & Degnan, 2007; Roch & Steel, 2015). As a result, concatenation methods can result in misleading support for the incorrect species tree when gene tree discordance is due to high levels of incomplete lineage sorting (Degnan & Rosenberg, 2006, 2009; Kubatko & Degnan, 2007; Roch & Steel, 2015). Thus, for each data set, we also inferred phylogenetic relationships from individual gene trees using a method statistically consistent under the multispecies coalescent model. To do this, we generated optimal trees for each locus in GARLI v2.01 (Zwickl, 2006) by performing 20 ML searches using one of 56 models of sequence evolution selected by MrAIC v1.4.6 (Nylander, 2004) using AICc in PhyML v3.1 (Guindon et al., 2010). We generated 200 BS gene trees for each locus, with the termination condition parameter reduced by half the default value (i.e., genthreshfortopoterm = 10,000) (Zwickl, 2008). Gene trees were permitted to contain polytomies (collapsebranches = 1), which has been shown to improve species tree topology (Zhang et al., 2018). We inferred species trees from these optimal gene trees using the summary coalescent program ASTRAL-III v5.6.1 (Mirarab et al., 2014; Sayyari & Mirarab, 2016; Zhang et al., 2018), with nodal support measured by the 200 multilocus BS replicates (Seo, 2008).

In cases where the summary coalescent species tree was incongruent with that recovered from our supermatrices, we evaluated if the incongruence could be due to incomplete lineage sorting. An expectation of the multispecies coalescent model is that a majority of rooted three-taxon gene trees will yield a resolution identical to the species tree while the two minor alternative resolutions are equiprobable to one another (Degnan & Rosenberg, 2009; Pamilo & Nei, 1988; Richart et al., 2016; Wang, Hosner, Liang, Braun, & Kimball, 2017; Zwickl, Stein, Wing, Ware, & Sanderson, 2014). We tested our minority data sets for asymmetry using an exact two-sided binomial test. We applied this test using our 50% taxon-complete data set and pruned trees to rooted triplets that included three taxa around an incongruent node and an outgroup.

2.5 | Re-evaluation of external morphological support

Few morphological matrices for coreoid families have been analysed with phylogenetic methods, with only one matrix constructed to comprehensively investigate the evolutionary history across higher-level coreoid groups, though several other studies have included a few representatives of this superfamily. We examined these different morphological matrices to identify characters that were likely variable and could be coded for our ingroup taxa. Since both sexes of a given species were often unavailable for examination in our study, we restricted our evaluation to external morphological traits that were not sex-specific. Below, we briefly discuss characters that were included in this analysis, but details on the full assessment of features can be found in Appendix S1.

We first evaluated morphological characters from Li's (1996) matrix for the superfamily, which excluded Stenocephalidae and Hyocephalidae. There was little overlap between Li's taxon sampling and ours, and thus, we coded characters for our species using Li's coding approach. Li's characters and states were generally not modified so as to permit an objective evaluation of the data given a molecular phylogeny. One exception to this included the reorganization of two characters and their states cenetring on the ostiolar peritreme and metathoracic scent gland opening. Li coded the branching pattern of the ostiolar peritreme as one character, and the presence of this character, in conjunction with the presence of the metathoracic scent gland opening, as another. Upon inspection of Li's matrix and our specimens, it was deduced Li coded Rhopalidae as having a simple ostiolar peritreme (the plesiomorphic state for the branching pattern), as was done for taxa with visibly simple peritremes. However, such a structure is not visible in Rhopalidae, and thus, we did not feel it appropriate to code it as the same state. As a result, we coded the ostiolar peritreme branching pattern as (0) peritreme absent, (1) present and simple, and (2) present and branching laterally, with anterior and lateral projections. We, then, coded the presence of the metathoracic scent gland opening as (0) present and (1) absent. We also modified Li's coding with respect to the hamus in the hind wings. Li's original

coding approach was difficult to interpret given our taxon sampling. Since Li's lengths of the vein were given without relation to some other feature, we disregarded length in the new coding scheme. Furthermore, the hamus joins the proximal Cu vein in all ingroup taxa sampled, but it was apparent to us that the junction was more acute than perpendicular in some taxa (Figure S1). Thus, we coded the hamus as (0) present, acutely branching off proximal Cu vein, and (1) present, branching off proximal Cu vein semi-perpendicularly. Our matrix eventually included Li's characters 2, 4–16, and 19–24. Given that Li generally coded for higher-level taxa (tribes or higher ranks) whereas we coded for species exemplars, our character state coding differed from Li's in some cases. We acknowledge some subjectivity in character state interpretations, especially given Li's lack of detailed character state descriptions and list of plesiomorphic conditions, but we were consistent within our own set of species.

We also examined the external characters from Henry's (1997) analysis that did not overlap with Li's characters, had the potential to be phylogenetically informative for our ingroup taxa, and were not ambiguous in character and character state interpretation. This ultimately left Henry's buccula character in our final matrix. As with Li's matrix, our character state coding sometimes differed for the same higher-level taxa for similar reasons as stated above.

Yao, Ren, Rider, and Cai (2012) included four coreoid taxa (two Rhopalidae and one each of Alydidae and Coreidae) in their morphological phylogenetic analysis of Pentatomomorpha. We examined their matrix and identified two external morphological characters. The first character we considered was the antennal segment I character. However, we modified it to reflect overall length of the segment relative to the head and disregarded shape, given the latter could not always be scored objectively with our taxa. We also included the character on the development of the pronotal posterior and humeral angles, but we, too, modified this character. Yao et al. (2012) only coded coreids as having these structures. However, based on personal observations and taxonomic literature, we believed that some ingroup Alydidae and Rhopalidae share similar shapes near the posterior end of the pronotum that are often considered as having developed posterior and humeral angles in coreids. As such, we coded these taxa the same as coreids.

Lastly, a feature that has been proposed in non-cladistic morphological studies was also included: the presence of a pseudoperculum in eggs. This structure is known to occur variably among coreoids and coreid subfamilies (Cobben, 1968; Southwood, 1956). Although data on egg structure for many of our taxa are lacking, previous morphological studies have sampled taxa relatively close to ours or several taxa within a higher-level group. Thus, we coded this character for higher taxonomic levels (i.e., families and subfamilies), where possible.

All morphological features were examined under a Leica M165 C stereo microscope. Character states were coded in Mesquite v3.5 (Maddison & Maddison, 2018). Our final matrix (Appendix S2) included 26 characters, which were optimized with accelerated transformation (ACCTRAN) on the 50% taxon-complete ML best tree and ASTRAL species tree (both topologically similar to other ML best trees and ASTRAL species trees; see Results) in PAUP* v4.0a.16 (Swofford, 2003). Given the lack of material for two coreoid families, doubt about the sister group of Coreoidea, and the limited taxon sampling among our outgroups that may bias optimizations, we excluded outgroups from character optimizations.

3 | RESULTS

3.1 | Target capture sequence data

A total of 76,073,880 pair-end reads were produced (1,820,144–13,121,288; average of 5,851,837 per sample) for our newly generated sequence data, with 31%–62% passing PRINSEQ-lite and QuorUM filtering (mean = 2,992,881 reads). We recovered 3,364–24,904 contigs across samples (mean = 11,333), with an average length of 431 bp. Of the 2,673 UCE loci targeted, we recovered 16%–36% (439–970 loci; mean = 763), with a mean length of 701 bp. A summary of the read, contig, and UCE data generated by our study are given in Table 2. Our 50%, 60%, and 70% taxon-complete matrices included 855, 504, and 284 UCE loci, respectively.

3.2 | Phylogenetic inference of Coreoidea

All data sets, regardless of analytical approach, were topologically similar (Figure 2, Figure S2–S4) and had strong support at most nodes, with the exception of some outgroup relationships and the position of Hydarinae. We always recovered a monophyletic Coreoidea with high support. Within the superfamily, Rhopalidae were highly supported as the sister group to Alydidae + Coreidae, though neither of the latter two families were recovered as monophyletic. The two coreid subfamilies, Hydarinae and Pseudophloeinae, were consistently recovered as more closely related to Alydidae than to the other coreid subfamilies. Hydarinae were either weakly supported as the sister group of the alydid subfamily Micrelytrinae (supermatrix analyses; Figure 2, Figure S2 and S3) or sister to Alydidae + Pseudophloeinae (summary coalescent analyses; Figure S4). Pseudophloeinae were always sister to the Alydinae with high support. The Coreinae were paraphyletic with respect to Meropachyinae, with all relationships within this clade highly supported and congruent with Kieran et al. (2019); Nematopodini were paraphyletic with respect to Meropachyinae, while Mictini and Acanthocephalini were both monophyletic. Thus, even with

TABLE 2 Summary data for sequence reads, contigs, and ultraconserved element loci generated in this study

Family	Subfamily	Genus	Species	Paired reads	Reads passed QC	Contigs	Total bp	Mean contig length	Min contig length	Max contig length	UCE loci	% UCE recovered	Mean UCE length	Min UCE length	Max UCE length
Largidae	Larginae	*Largus*	sp.	2,219,122	1,055,495	5,911	2,403,901	407	201	2,663	608	22.75	620	202	2,547
Pyrrhocoridae		*Dysdercus*	*mimus*	1,820,144	821,870	6,191	2,713,803	438	201	2,723	632	23.64	648	202	2,247
Pyrrhocoridae		*Dysdercus*	*suturellus*	4,146,928	1,793,313	10,869	4,930,290	454	201	3,068	781	29.22	781	201	3,068
Alydidae	Micrelytrinae	*Mutusca*	*brevicornis*	6,714,546	4,130,488	17,668	6,770,894	383	201	3,658	779	29.14	713	203	2,691
Alydidae	Micrelytrinae	*Stenocoris*	*tipuloides*	6,241,202	3,301,830	12,438	6,199,571	498	201	4,337	970	36.29	861	201	4,005
Alydidae	Alydinae	*Hyalymenus*	*longispinus*	5,027,042	2,352,355	14,348	5,854,252	408	201	3,579	824	30.83	702	202	3,045
Alydidae	Alydinae	*Neomegalotomus*	*rufipes*	13,121,288	7,571,212	14,788	6,503,419	440	201	3,951	893	33.41	769	204	3,237
Alydidae	Alydinae	*Haemedius*	*incarnatus*	9,928,228	5,454,199	9,822	4,811,644	490	201	4,450	800	29.93	791	201	3,515
Coreidae	Hydarinae	*Hydara*	*tenuicornis*	8,778,542	4,938,576	24,904	9,768,940	392	201	3,254	845	31.61	713	201	2,920
Coreidae	Pseudophloeinae	*Myla*	sp.	6,619,040	2,858,354	11,339	5,201,847	459	201	4,085	868	32.47	771	201	3,105
Coreidae	Pseudophloeinae	*Clavigralla*	sp.	5,249,954	2,288,859	8,107	3,640,355	449	201	3,237	805	30.12	655	201	2,692
Rhopalidae	Serinethinae	*Jadera*	*haematoloma*	3,070,988	1,369,634	7,576	3,128,797	413	201	3,477	675	25.25	655	201	2,861
Rhopalidae	Rhopalinae	*Harmostes*	*serratus*	3,136,856	971,274	3,364	1,260,743	375	201	2,744	439	16.42	434	202	1,808

our limited taxon sampling, two families, one subfamily, and one tribe within Coreoidea were not monophyletic.

Given that the position of Hydarinae differed between our supermatrix and summary coalescence methods, we tested whether estimated gene trees were consistent with the multispecies coalescent model using the following rooted triplet from our 50% taxon-complete data set: *Stenocoris tipuloides*, *Hydara tenuicornis*, and *Myla* sp., with *Acanthocephala thomasi* as the outgroup. We recovered two minority resolutions with equal frequency (exact two-sided binomial test, $p = 0.3099$), but the majority resolution of gene trees that matched the species tree was not significantly different from one of our minority resolutions ($p = 0.2753$). This indicates that the estimated gene trees are not consistent with the multispecies coalescent and that processes other than incomplete lineage sorting are likely responsible for discordance.

3.3 | External morphological character optimization

Here, we report the accelerated optimization of the 26 morphological characters onto the molecular supermatrix topology, excluding outgroup taxa, which resulted in 54 steps. We recovered a Consistency Index (CI) and Retention Index (RI) of 0.5556 and 0.7333, respectively. Forty unambiguously optimized apomorphies (Figure 3, black markers) were recovered, with 14 additional apomorphies only supported in ACCTRAN but not in decelerated transformation optimization (Figure 3, red markers). Eleven characters had a CI = 1 (Figure 3, solid circles; Table S1), while the remaining 15 characters had CI's ranging from 0.250 to 0.667 (Figure 3, open circles). Thus, the majority of characters exhibited homoplasy, but there was no obvious pattern with respect to specific groups of traits (e.g., head, thoracic, or abdominal characters). When using the summary coalescent species tree topology (Figure S4), tree length, CI, RI, and ci values did not change, though there were several changes in our optimizations, primarily around the Hydarinae + Alydidae + Pseudophloeinae clade (Figure S5). Traits that appeared to be good synapomorphies for higher-level taxa included: strongly developed preclypeus (5-1) in Rhopalidae, sulcate tibiae (14-1) in Coreinae + Meropachyinae, forewing venation (15-1) and abdominal constriction (19-1) in Alydinae, and non-pseudoperculate eggs (22-1) in Alydidae + Hydarinae + Pseudophloeinae.

4 | DISCUSSION

Previous phylogenetic hypotheses, based on cladistic and non-cladistic approaches, have offered little clarity into the familial and subfamilial relationships within Coreoidea. Our

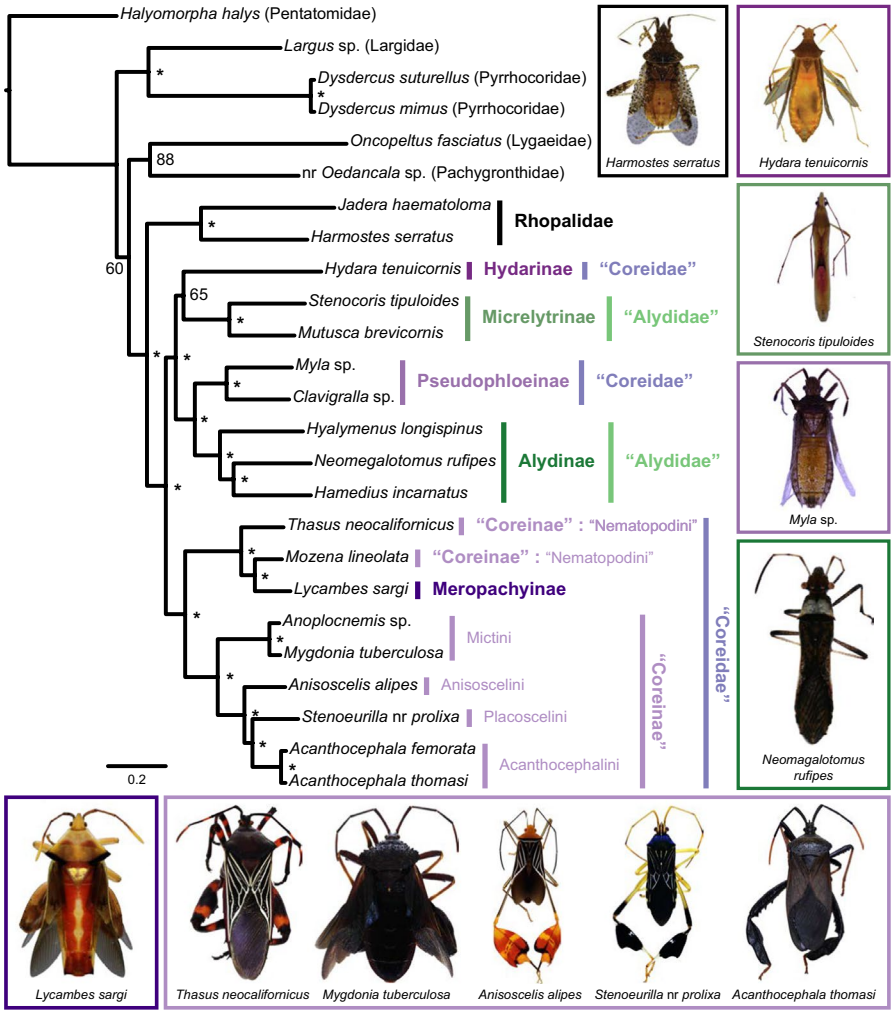

FIGURE 2 Maximum likelihood (ML) best tree for Coreoidea based on ultraconserved element loci from the 50% taxon-complete data set (other data sets yielded similar relationships in ML and ASTRAL analyses, except for the position of Hydarinae among the Pseudophloeinae + Alydidae). Support from 500 bootstrap replicates are given next to nodes, with 100% support denoted by asterisks [Colour figure can be viewed at wileyonlinelibrary.com]

results demonstrate the utility of phylogenomic approaches for resolving long-standing problems in phylogenetics—here, for example, among the coreoid families Coreidae and Alydidae—and highlight that novel insights may come from such approaches. Regardless of analytical approach, we supported a monophyletic Coreoidea, which is congruent with a majority of phylogenetic studies (Table 1). We also found evidence for a close relationship between Alydidae and Coreidae, though neither of these families were monophyletic with respect to the other. Thus, the taxonomic status of each family should be evaluated in further systematic detail to properly revise their classifications.

One complication to coreid and alydid taxonomy has been the reliance on morphological traits considered to be diagnostic for these families but that exhibit widespread variation in expression among species within them. As our results show, most of the external morphological traits we examined were homoplastic, with several clades defined by few or no synapomorphies. This highlights a critical need for more rigorous external character exploration studies for coreoids to better diagnosis higher-level groups. The remainder of our discussion focuses on specific clades of interest.

4.1 | Phylogeny of the Coreoidea

The monophyly of the Coreoidea has largely been supported by previous phylogenetic studies (Table 1), although, as in our case, most have not included Stenocephalidae and Hyocephalidae. That we strongly recovered monophyly of Coreoidea suggests that in those cases where monophyly has not been supported, it may be due to limited power (too few characters), loci selected (e.g., leading to gene trees that may not have matched the species tree or with little power to resolve short internodes), sequence quality, or analytical approaches employed (Li et al., 2005; Xie, Bu, & Zheng, 2005; Weirauch et al., 2018; see Tian et al. (2011) for explanation of issues in some previous analyses). As putative sister group sampling increases, previous hypotheses on morphological apomorphies for Coreoidea, such as those proposed by Li (1996; excluding Stenocephalidae and Hyocephalidae) and Henry (1997), can be better evaluated. Such an evaluation will also require available material that is adequate for dissections to examine sex-specific and internal apomorphies within the group, which we did not possess. In addition, some workers have suggested the potential of ecological data, e.g.,

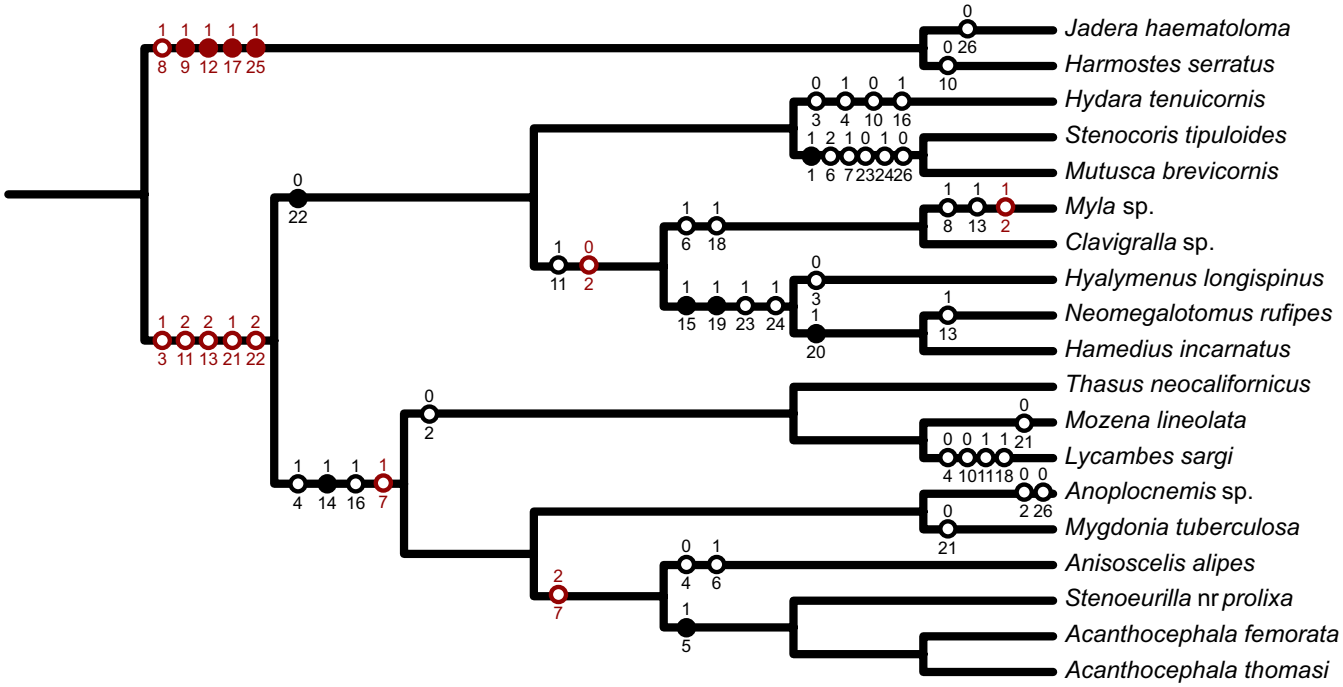

FIGURE 3 PAUP* optimization of 26 external morphological characters onto ML trees for Coreoidea. Outgroups were not included in the analysis. Character numbers for apomorphies are reported below the circles, and the corresponding character states are given above the circles. Black optimizations are unambiguous, whereas those in red were only recovered with accelerated transformation. Homoplastic and non-homoplastic characters are indicated by open and closed circles, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

host plant use (Schaefer, 1980; Schaefer & Mitchell, 1983), to provide phylogenetic information for the superfamily. We also recommend evaluation of such data with a greater sampling of taxa to capture the diversity of host plants and range of specificity across the many coreoid lineages.

4.2 | Rhopalidae

All of our analyses supported Rhopalidae as the sister group of Alydidae + Coreidae, which is congruent with most relevant studies (Table 1). We caution our current hypothesis for this relationship given the exclusion of Stenocephalidae and Hyocephalidae, which have been found to be more closely related to Alydidae + Coreidae in other phylogenetic studies (Table 1). Several putative synapomorphies have been proposed for Rhopalidae by Li (1996) (e.g., presence of the maxillary plates and the anterior curvature of the median suture between abdominal tergites V and VI) and Yao et al. (2012) (e.g., the long bucculae and short antennal segment I). We found support for all of these as synapomorphies though the long bucculae may be plesiomorphic. We also found the absence of the metathoracic scent gland (12-1) to be a synapomorphy for the two rhopalid species we included. However, given conflicting hypotheses on intrafamilial relationships (Li, 1996; Li & Zheng, 1994; Schaefer & Chopra, 1982), these putative synapomorphies should be examined with a larger sample of taxa.

4.3 | Alydidae + Coreidae as a monophyletic group

Our result that Coreidae and Alydidae are closely related is congruent with nearly all of the previously mentioned phylogenetic studies (Table 1). We recovered several putative (i.e., ambiguously optimized) apomorphies for the branches regardless of topology, all of which were homoplastic. However, additional synapomorphies proposed by Henry (1997) (e.g., the dorsal abdominal scent gland openings in nymphs) and Yao et al. (2012) (e.g., antenniferous tubercles arising below the level of the eye and ovipositor platelike) should be re-evaluated with a taxon sampling that exhibits variation in character states for these traits and that are suitable for internal morphological examination.

4.4 | Hydarinae + Alydidae + Pseudophloeinae as a monophyletic group

Our proposed relationship among the Alydidae and the coreid subfamilies Hydarinae and Pseudophloeinae has not been recovered in previous analysis with modern cladistic approaches (i.e., Li, 1996), though a recent mitochondrial DNA Bayesian analysis of Pentatomomorpha supported a clade comprising Hydarinae + Pseudophloeinae + Alydinae (i.e., Alydidae was not monophyletic) (Zhao et al., 2018). In our study, Alydidae was not monophyletic with respect

to Pseudophloeinae and also, in the case of our supermatrix analyses, Hydarinae. The non-monophyly of Alydidae has been supported in few studies (Table 1), though most of these did not include Hydarinae and Pseudophloeinae. Our result is only supported by one non-molecular synapomorphy that has yet to be included in phylogenetic analyses of Coreoidea: non-pseudoperculate eggs (24-0). Cobben (1968) examined coreoid eggs and noted the absence of this trait between all taxa comprising this clade, but present among all other coreids and rhopalids. Others have examined additional features, primarily the genitalia, and shown similarity (e.g., in the male vesica and parameres and female spermatheca) between some or all of the higher-level taxa in this clade (Ahmad & Shadab, 1975; Kumar, 1965; Schaefer, 1965; Shadab, 1972). However, these workers have often considered such traits to be plesiomorphic for these taxa, but this remains to be investigated within a molecular phylogenetic framework. While we have not explored host plant use in our analysis, taxa within this clade primarily feed on legumes (Fabaceae) (see Schaefer, 1980; Schaefer & Mitchell, 1983), but the use of legumes within Coreoidea has been hypothesized to be plesiomorphic (Schaefer & Mitchell, 1983).

4.5 | Phylogenetic placement of Hydarinae

Dependent on the analytical approach, we found Hydarinae to be the sister group to the Micrelytrinae (supermatrix analysis) or to Alydidae + Pseudophloeinae (summary coalescent analysis). Hydarinae have been proposed as one of the early diverging lineages among coreoids (Li, 1996) and coreids (Li, 1997) in morphological phylogenetic analyses. Specifically, the subfamily has been proposed as the sister group of Rhopalidae + Alydidae + the remaining Coreidae excluding Pseudophloeinae (Li, 1996) or Coreinae + Meropachyinae (Li, 1997). Only Li (1996) offered a brief discussion on characters pertaining to the corresponding hypothesis: "More or less laciniate ovipositor and simple aedeagus illustrate their primitiveness of…Hydarinae in the superfamily…are markedly different from the remaining groups of Coreidae, especially in the structure of the genitalia." However, phylogenetic analyses with mitochondrial DNA have supported several positions for the subfamily: (a) as the sister group to the Coreinae with weak support (Valero et al., 2017); (b) Alydinae + Pseudophloeinae (Zhao et al., 2018; Bayesian analysis with moderate to high support); or (c) Alydinae (Zhao et al., 2018; ML analysis, poorly supported). Our two hypotheses regarding the phylogenetic placement of Hydarinae are incongruent with these previous analyses, but demonstrate the non-monophyly of the Coreidae.

Character optimizations on our supermatrix topology did not produce any apomorphies for Hydarinae + Micrelytrinae, whereas non-pseudoperculate eggs were the only synapomorphy for the summary coalescent species tree hypothesis. Because of the competing phylogenetic hypotheses, it is clear that evaluation of genitalic structures and other characters not yet explored are needed within the Hydarinae + Alydidae + Pseudophloeinae clade to clarify the phylogenetic position of the subfamily and identify more apomorphies.

4.6 | Pseudophloeinae sister to Alydinae

To our knowledge, the sister group relationship between the coreid subfamily Pseudophloeinae and the alydid subfamily Alydinae has not been proposed in previous phylogenetic studies, except in the mitochondrial Bayesian analysis of Zhao et al. (2018). Li (1996) found Pseudophloeinae to be the sister to all sampled ingroup taxa (i.e., Rhopalidae + Alydidae + remaining Coreidae). In a more focused analysis of Coreidae (Li, 1997), Pseudophloeinae were sister to all coreids. Contrary to Li (1996, 1997), the potential for a close relationship between Pseudophloeinae and Alydidae, more broadly, has been implicitly or explicitly suggested by others in non-cladistic studies, primarily based on genitalic features, as highlighted above in Section 4.5. Kumar (1965) went so far as to transfer Pseudophloeinae to the Alydidae, although this was not subsequently accepted by others. From our analyses, we found two apomorphies for this clade: presence of a simple ostiolar peritreme (11-1; unambiguous optimization) and a mid-cephalic sulcus (2-0; ACCTRAN optimization).

4.7 | Pseudophloeinae monophyly

The monophyly of Pseudophloeinae has been uncontroversial in previous morphological discussions and phylogenetic studies. Based on phylogenetic analysis, Li (1996) stated that the "primitive" genitalia—along with other unspecified features—greatly distinguish Pseudophloeinae from other coreids. Li (1997) further identified the following apomorphies for the subfamily: eighth abdominal spiracle absent in females, body surface with spines (trait not coded in Li [1997]), posterior margin of the male pygophore depressed (also not coded by Li), and short and thick parameres. From external morphology, we identified two or three apomorphies when optimized on our supermatrix and summary coalescent trees, respectively: well-developed mandibular plates and a narrow preclypeus (6-1), pitted abdominal tergites (20-1), and ocelli closer to eyes than to each other (26-0; summary coalescent topology only, ACCTRAN only).

4.8 | Alydinae monophyly

In addition to our study, support for the monophyly of this second subfamily of Alydidae, as currently recognized by Coreoidea Species Files (2018), comes from the relatively comprehensive analyses of the Alydidae (Li & Zheng, 1993) and Coreoidea (Li, 1996). In their analysis of Pentatomomorpha, Li, Deng, and Wang (2006) also

provide support for a monophyletic Alydinae. Contrary to these studies, only one analysis using cytochrome b and a limited sample of Alydinae did not recover this subfamily as a clade (Pan, Su, & Song, 2008). Li (1996) did not list any apomorphies shared among the Alydinae, but from our analysis of Li's matrix we found the fusion of the Sc and the R + M veins at the base of the fore wing (16-1), constriction of the abdomen (21-1), trilateral head shape (25-1; homoplastic), and closer proximity of ocelli to each other than to eyes (26-1; ML tree; homoplastic) as apomorphies for the clade. Several morphological studies have also provided many genitalic features for the subfamily that remain to be evaluated (Ahmad & Southwood, 1964; Kumar, 1965; Schaefer, 1965; Štys, 1962).

4.9 | Coreinae + Meropachyinae relationship

Relatively few morphological cladistic and non-cladistic analyses have included the coreid subfamily Meropachyinae. This subfamily has traditionally been recognized by the sulcate tibiae (shared with Coreinae), a much smaller head relative to the pronotum, and the hind tibia with an apical spine. To our knowledge, all studies that have examined Meropachyinae have proposed a close relationship with the Coreinae (Li, 1996, 1997; Schaefer, 1965; Štys, 1962), with Li (1996, 1997) and Kieran et al. (2019) providing evidence for a paraphyletic Coreinae, as we corroborated here. The following apomorphies were optimized for the Coreinae + Meropachyinae clade: preclypeus and mandibular plates strongly declivent from the base of the antennae (4-1; supermatrix tree), ocelli present but not on a small tubercle (7-1; ACCTRAN), tibiae dorsally sulcate (14-1), and hamus branching off proximal Cu vein semi-perpendicularly (18-1; supermatrix tree).

5 | CONCLUSION

Phylogenomics has provided great insights on the evolutionary histories of non-model species, such as the Coreoidea. Here, we have shown how UCE loci resolve most phylogenetic nodes with high support, including the monophyly of the superfamily Coreoidea that corroborates previous studies. While a number of studies have failed to support the monophyly of the family Coreidae, few have suggested non-monophyly of Alydidae. Here, our analysis supported the non-monophyly of both Coreidae and Alydidae. The reliance on apparently homoplastic morphological traits—as we have demonstrated here—may explain contradictory results from past studies as most of our clades had few or no synapomorphies. Our results highlight that applying such approaches to other groups could be equally insightful, and further suggest that additional taxon sampling within Coreoidea may be fruitful.

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DATA AVAILABILITY

Sequence read files are available on NCBI's Sequence Read Archive under BioProject PRJNA531965.

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SUPPORTING INFORMATION

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