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Received: 1 September 2026 | Accepted: 28 October 2026

DOI: 10.1111/syen.70083

ORIGINAL ARTICLE

Systematic Entomology

Royal Entomological Society

UCE-based phylogenomics traces evolution of ant-mimicry in phyline plant bugs (Hemiptera: Miridae: Phylinae)

Sarah Schroeder[1] | Veronica Tyts[1] | Rochelle Hoey-Chamberlain[1] | M. C. Fox[1] | Randall T. Schuh[2] | Michael Forthman[3] | Fedor V. Konstantinov[4] | Anna A. Namyatova[5,6] | Michael D. Schwartz[7] | H. M. Yeshwanth[8] | Katrina Menard[9] | Catherine Nance[10] | Wei Song Hwang[11] | Christiane Weirauch[1]

[1]Department of Entomology, University of California, Riverside, Riverside, California, USA

[2]Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA

[3]California Department of Food and Agriculture, California State Collection of Arthropods, Plant Pest Diagnostics Branch, Sacramento, California, USA

[4]National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria

[5]Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia

[6]All-Russian Institute of Plant Protection, St Petersburg, Russia

[7]Agriculture & Agri-Food Canada, Canadian National Collection of Insects, Ottawa, Ontario, Canada

[8]Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, India

[9]Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA

[10]Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, Florida, USA

[11]Lee Kong Chian Natural History Museum, National University of Singapore, Singapore, Singapore

Correspondence
Sarah Schroeder, Department of Entomology, University of California, Riverside,
165 Entomology Bldg, Citrus Drive, Riverside, CA 92521, USA.
Email: sarah.schroeder@ucr.edu

Funding information
National Science Foundation, Grant/Award Number: DEB-2317209; Ministry of Science and Higher Education of the Russian Federation, Grant/Award Numbers: 125012901042-9, FGEU-2025-0001

Abstract

Miridae are the most taxonomically diverse family of true bugs and are economically important, but phylogenetic hypotheses have remained relatively data- and taxon-poor. Phylinae, the second-largest subfamily (>2700 spp.), include the highest proportion of myrmecomorphic taxa among all subfamilies of Miridae. Ant mimicry in Phylinae occurs in several lineages and ranges from inaccurate mimicry with simple illusory coloration to accurate mimicry involving striking changes in morphology. This variation makes them a good model to test the 'perfecting hypothesis', which predicts that inaccurate mimics represent an unstable state and that mimetic accuracy evolved in a stepwise manner. We here present the first UCE-based phylogenomic hypothesis for Phylinae, combining 247 newly sequenced taxa with legacy Sanger data for 90 additional taxa to boost sampling across geographic regions and ant-mimetic diversity. Our phylogeny shows that the existing heavily Sanger-based classification will need to be further adjusted to better align with the evolutionary history of the group. Ancestral trait reconstruction of myrmecomorphic traits combined into a composite accuracy score indicates that ant mimicry

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originated six times independently in Phylinae. Our analyses document that—consistent with the perfecting hypothesis—accurate mimics always evolved from an inaccurate ancestor, but also that non-mimetic or inaccurately mimetic morphology constitutes the optimal trait value, a result that is not compatible with the perfecting hypothesis. More densely sampled phylogenies and ecological and behavioural data are critical to advance our understanding of the evolution of myrmecomorphy in Phylinae.

KEYWORDS
Heteroptera, Miridae, myrmecomorphy, Phylinae, phylogenomics, trait evolution, ultraconserved elements

INTRODUCTION

Heteroptera, the true bugs, comprise >45,000 species and are known for their diversity of natural history strategies (Henry, 2017; Schuh & Weirauch, 2020). Miridae Hahn are the most speciose heteropteran family, with >11,000 described species in seven subfamilies, and belong to the superfamily Miroidea, one of the two predominantly plant-feeding lineages of Heteroptera (Cassis & Schuh, 2012; Schuh & Weirauch, 2020). Having originated in the Jurassic, Miridae now occur in all biogeographic regions (Oh et al., 2023; Schuh & Weirauch, 2020). With >2,700 described species, Phylinae Douglas & Scott are the second-largest subfamily of Miridae (Cassis & Schuh, 2012; Schuh & Menard, 2013). This cosmopolitan group has the highest diversity in Mediterranean-type and temperate regions, with relatively few species described from the Neotropics (Cassis & Schuh, 2012). Phylinae have a long taxonomic history, and numerous major works have provided the foundation for the current classification and sound evidence for a sister relationship with Orthotylinae (Schuh, 1984, 1995). The early history of phyline taxonomy was heavily influenced by the classification and catalogue of Miridae published by Carvalho (1952, 1958a, 1958b) recognizing three tribes (Phylini, Hallodapini and Dicyphini), as well as the work of Wagner (1955) in which Dicyphini were moved to the Bryocorinae. Subsequently, morphological characteristics including pretarsal structures and male and female genitalia were used to justify several updates to the phyline classification, including the transfer of Pilophorini from Orthotylinae to Phylinae and recognition of two since dissolved tribes, Pronotocrepini (now within Cremnorrhinini) and Auricillocorini Schuh (now within Hallodapini) (Eyles & Schuh, 2003; Menard & Schuh, 2011; Schuh, 1974, 1976, 1984, 1989, 1991; Schuh & Schwartz, 1988). These efforts culminated in the current classification of Phylinae put forth by Schuh and Menard (2013) based on a combined morphological and molecular phylogeny and examination of specimens (Menard et al., 2014). Subsequent works have continued to revise tribal diagnoses as substantial numbers of new species have been described (Schuh & Schwartz, 2016; Schwartz et al., 2018; Wyniger et al., 2023).

The current classification of Phylinae comprises nine tribes and nine subtribes (Schuh & Menard, 2013) (Figure 1a). The largest and nominal tribe, Phylini Douglas & Scott (>150 genera), is cosmopolitan with greatest diversity in the Northern Hemisphere and comprises three subtribes: Phylina Douglas & Schott, Oncotylina Douglas &

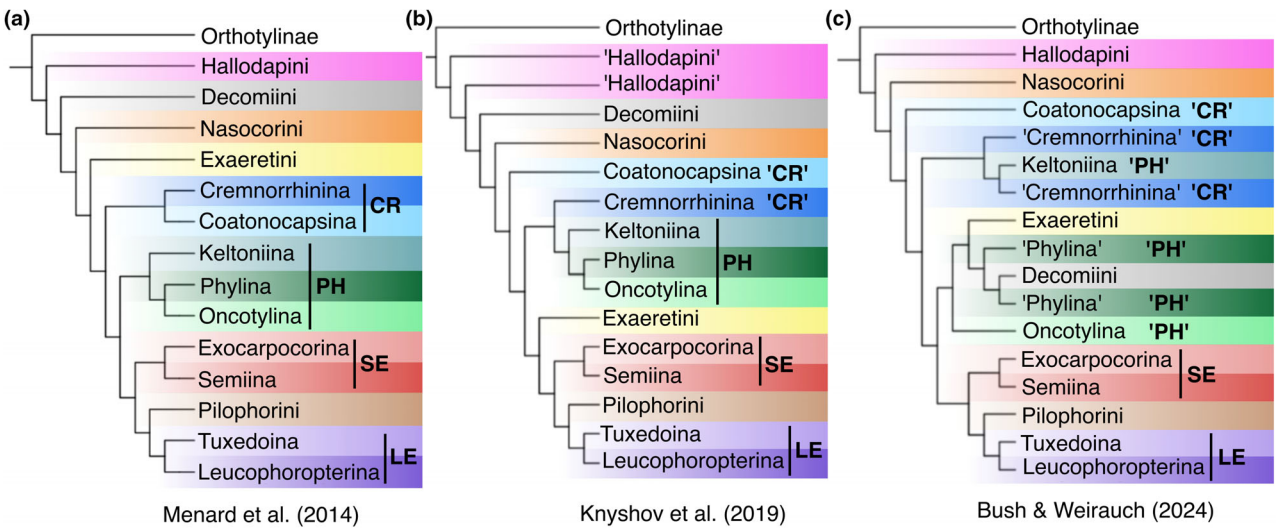


FIGURE 1 Summary cladograms of previous molecular phylogenetic hypotheses for Phylinae. (a) Analysis of Menard et al. (2014); (b) Analysis of Knyshov et al. (2019); (c) Analysis of Bush and Weirauch (2024). Colour coding of tribes and subtribes as in subsequent figures.

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Scott and Keltoniina Schuh & Menard (Schuh & Menard, 2013). This tribe has a complex history as a home for genera lacking attributes placing them in other tribes (Carvalho, 1952, 1958a, 1958b; Schuh, 1974, 1984, 1995; Wagner, 1974, 1975). It has long been noted to be polyphyletic (Schuh, 1974, 1984) and Schuh and Menard (2013) recognized continued issues with the classification of this group. Pilophorini Douglas & Scott (>20 genera), Hallodapini Van Duzee (>50 genera) and Leucophoropterini Schuh (containing Tuxedoina Schuh & Menard and Leucophoropterina Schuh and >25 genera) largely comprise ant-mimicking taxa, with greatest diversity in the Palearctic, Australian, and Indo-Malayan realms (Menard & Schuh, 2011; Schuh & Schwartz, 1988; Wyniger et al., 2023; Yasunaga et al., 2019). Cremnorrhinini Reuter comprise two subtribes and >50 genera, the Holarctic and Australian Cremnorrhinina Reuter, with lesser diversity in the Nearctic, and largely South African Coatonocapsina Schuh & Menard. Cremnorrhinini now contain several genera with a complex classification history most recently unified in Pronotocrepini Knight by Wyniger (2010). In the absence of consistent unifying morphological characters, Cremnorrhinini were united by Menard et al. (2014) largely on the basis of molecular data. Similarly, the analysis of Menard et al. (2014) found no morphological synapomorphies for Nasocorini Reuter; however, Schuh and Menard (2013) expanded the tribal concept to include many additional mostly Holarctic genera for a total of >60 genera. Substantial generic treatments have revised large nasocorine genera, for example: *Atractotomus* Fieber (Stonedahl, 1990), *Campylomma* Reuter (Malipatil, 1992; Schuh, 1984; Yasunaga et al., 2015), *Megalopsallus* Knight (Schuh, 2000a) and *Rhinacloa* Reuter (Schuh & Schwartz, 1985), among others. Exaeretini Puton, with greatest diversity in the Palearctic, now include >25 genera with similar pretarsal and endosomal structures (Schuh & Menard, 2013). Decomiini Schuh & Menard contain 6 genera largely Indomalayan in distribution, with the exception of a single Nearctic genus, *Aurantiocoris* Schuh & Schwartz. Finally, Semiini Knight comprise two subtribes and >40 genera, Exocarpocorina Schuh & Menard and Semiina Knight (Schuh & Menard, 2013). Exocarpocorina are the only grouping within Phylinae with a documented transantarctic distribution, with the majority of diversity within Australia and New Zealand and three genera restricted to Chile and Argentina (Eyles & Schuh, 2003; Schuh & Menard, 2013; Schwartz et al., 2018; Weirauch & Schuh, 2011). Semiina have a wider geographic distribution including the Nearctic, Palearctic, African and Australian regions and are united by a simple endosoma with a weakly developed secondary gonopore. Semiini have received significant generic treatments including *Pseudosthenarus* Poppius and *Parapseudosthenarus* Schuh (Schuh & Salas, 2011), Myrtaceae feeding genera (Schwartz et al., 2018), *Semium* Reuter (Henry, 2018; Schuh, 2017) and *Tytthus* Fieber (Henry, 2012) among others.

Despite numerous descriptions of new taxa over the last 50 years (e.g., Schuh, 1974, 1984, 2000a, 2000b, 2001, 2004, 2006; Schuh & Schwartz, 1988; Yasunaga et al., 2019; Yasunaga & Duwal, 2015, 2021), and publication of a revised tribal- and subtribal-level classification (Schuh & Menard, 2013), published phylogenetic hypotheses for Phylinae are not particularly data- and taxon-rich and lack robust support for many critical nodes. Menard et al. (2014) combined 122 morphological characters and four Sanger loci for 164 taxa, and the resulting phylogeny provided the basis for the current phyline classification (Schuh & Menard, 2013) (Figure 1a). While the analysis of Menard et al. (2014) was a milestone in advancing our understanding of the systematics of Phylinae, support for many of the deeper nodes was poor and taxon sampling was biased towards the Nearctic and Australian regions. Two subsequent studies slightly expanded the molecular dataset of Menard et al. (2014) by including 18 species of Tuxedoina and Oncotylina (Knyshov et al., 2019) (Figure 1b) and 27 additional species of Western Nearctic Phylinae (Bush & Weirauch, 2024) (Figure 1c), resulting in a dataset of 193 ingroup taxa in the latter analysis; neither study analysed combined morphological and molecular datasets.

Several tribes and subtribes were recovered as non-monophyletic in the phylogeny by Bush and Weirauch (2024) (Figure 1c), including Cremnorrhinini, Cremnorrhinina, Phylini, Phylina, Keltoniina and Oncotylina. Across published analyses, Hallodapini have consistently been recovered as the sister clade to the remaining Phylinae, followed by Decomiini as the next diverging lineage in all analyses except Bush and Weirauch (2024) (Figure 1). Nasocorini were monophyletic and sister to the remaining Phylinae excluding Hallodapini and Decomiini (Knyshov et al., 2019; Schuh & Menard, 2011) or just Hallodapini (Bush & Weirauch, 2024). Leucophoropterini and Pilophorini were also monophyletic and sister taxa in all analyses, with the monophyletic Semiini as sister taxon to that clade. In contrast, Exaeretini were recovered in different phylogenetic positions across analyses. The subtribes of Cremnorrhinini were monophyletic in Knyshov et al. (2019), but with the inclusion of additional taxa, Cremnorrhinina were rendered paraphyletic by Keltoniina in Bush and Weirauch (2024). All published analyses had fairly poor representation of Palearctic taxa and failed to include substantial diversity from Australia. It is evident that a more taxon- and data-rich phylogeny of Phylinae with more balanced geographic sampling is crucial to resolve tribal relationships and to serve as the basis for evolutionary hypothesis testing, including divergence dating, biogeographic analyses and ancestral state reconstructions of morphological and biological traits.

Phylinae could be perceived as the least morphologically diverse among the three largest plant bug subfamilies, with relatively small sizes, fairly uniform body shapes and muted colour palettes (Schuh, 2000a, 2000b, 2001, 2006; Weirauch, 2006; Wyniger et al., 2023). Some species, however, feature specific colours and shapes that may aid in avoiding predation, including coloration that blends with leaves, stems or inflorescences of the host plant, aposematic coloration and myrmecomorphy (Figure 2) (McIver, 1987; McIver & Stonedahl, 1987a; Schuh, 1974, 1984, 2001, 2006; Wheeler, 2001; Yasunaga & Duwal, 2019). Myrmecomorphy occurs in at least some taxa in five of the nine tribes of Phylinae (Cremnorrhinini, Hallodapini, Leucophoropterini, Pilophorini and Semiini) (Menard & Schuh, 2011; Schuh & Menard, 2013), suggesting that it evolved several times independently in this subfamily. Little is known about ant-mimetic behaviour, chemical ecology or the function of mimicry in Phylinae. In the plant-feeding species *Coquillettia insignis*

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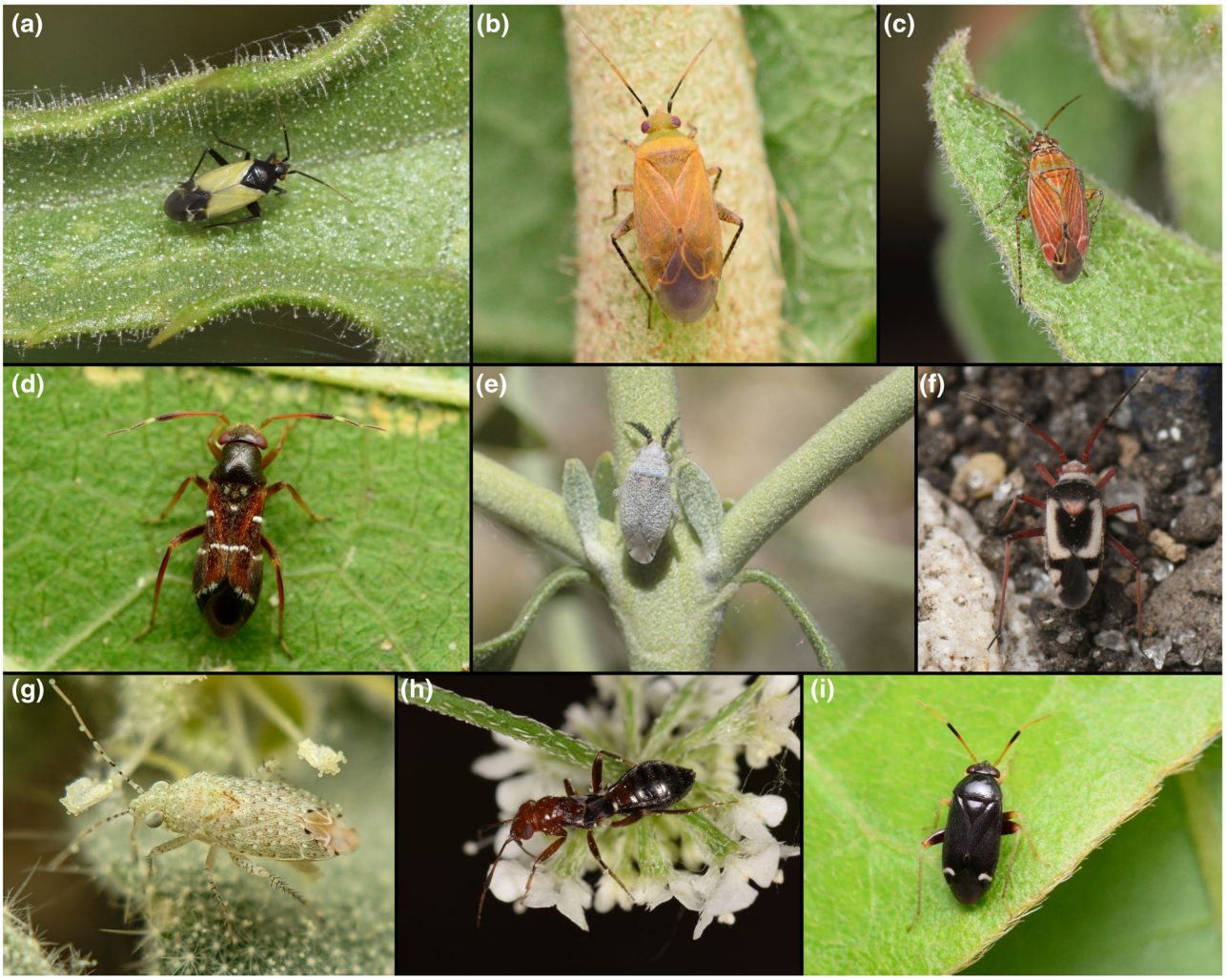


FIGURE 2 Morphological diversity of Phylinae. Photos retrieved from iNaturalist (a) *Macrotylus bicolor* Fieber (Cremnorrhinini: Cremnorrhinina), © Francisco Rodriguez Luque; (b) *Parapsallus vitellinus* Scholtz (Phylini: Oncotylina), © WonGun Kim; (c) *Pachyxyphus lineellus* Mulsant & Rey (Cremnorrhinini: Cremnorrhinina), © Barış ÇerÇi; (d) *Pilophorus koreanus* Josifov (Pilophorini), © WonGun Kim; (e) *Larinocerus balius* Froeschner (Nasocorini), © SaraC; (f) *Semium hirtum* Reuter (Semiini: Semiina), © Joe Mdo; (g) *Pseudatomoscelis seriatus* Reuter (Phylini: Keltoniina), © Carol Blaney; (h) *Mimocoris rugicollis* Costa (Hallodapini), © Barış ÇerÇi; (i) *Sejanus yasunagai* Oh, Duwal, & Lee (Leucophoropterini: Leucophoropterina) © WonGum Kim.

Uhler and *Orcetoderus obliquus* Uhler, ant mimicry is likely a strategy of Batesian mimicry for decreasing predation by visual predators, and this strategy could be widespread among plant-feeding phyline myrmecomorphs (Henry, 1994; McIver & Stonedahl, 1987a, 1987b; Yeshwanth, 2013). The predatory myrmecomorphic phyline *Sohenus uvarovi* Ballard is associated with the ant *Camponotus compressus* Fabricius attending scale insects and membracid nymphs (Yeshwanth, 2013). Thus, predatory species may use myrmecomorphy not to evade predators, but rather as a means of living alongside ants and obtaining prey while avoiding aggression, as seen in other myrmecomorphic arthropods (Allan et al., 2002; Allan & Elgar, 2001; Elgar & Allan, 2004; Ikeshita et al., 2017).

Ant mimicry is seen widely among arthropods, including 16 families of Araneae Clerck and many Staphylinidae Latreille (Cushing, 2012; Ikeshita et al., 2017; Luo et al., 2025; McIver & Stonedahl, 1993; Oliveira, 1985; Rasekh et al., 2009). In both groups, chemical and behavioural mimicry are extensively documented (e.g., behavioural mimicry in myrmecomorphic spiders (Ceccarelli, 2008; Cushing, 1997, 2012; Jackson, 1986; Reiskind, 1977) and staphylinid acquisition of cuticular hydrocarbons for chemical mimicry (Avşar & Turan, 2024)). In contrast, the behaviour of ant-mimicking Miridae is poorly documented, chemical mimicry has not been investigated, and ant models remain unknown for most species (Henry, 1994; McIver, 1987; McIver & Stonedahl, 1987a; Yeshwanth, 2013). Ant-like morphology in Miridae has largely been documented as part of taxonomic descriptions rather than in studies focused on myrmecomorphy. Ant-mimetic features listed in these taxonomic papers include: a large and globular head giving the impression of large mandibles and prognathous mouth parts (McIver & Stonedahl, 1993), variably coloured and sized antennal segments giving the

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illusion of clubbed or elbowed antennae (McIver & Stonedahl, 1993), pronotal projections giving the appearance of petiole spines (Wyniger, 2010), reduction of wings (Wyniger, 2010, 2011), restriction of the posterior portion of the thorax mimicking a petiole and an enlarged abdomen (Jackson & Drummond, 1974; Menard & Schuh, 2011; Schaffner & Carvalho, 1985; Schuh, 1974, 1984; Schuh & Lattin, 1980; Schuh & Schwartz, 1988; Wyniger, 2011; Xu & Liu, 2007; Yasunaga, 2012; Yasunaga et al., 2019). In species where wings are not reduced, hemelytra may be convex and are often dark with contrasting white transverse or oblique lines giving the illusion of a meso- and metasoma (McIver & Stonedahl, 1993; McMah & Cassis, 2024). Ant mimics within Phylinae may display any combination of these characters, resulting in species that resemble ants to various degrees (Carvalho & Gross, 1982; McIver & Stonedahl, 1993; Yasunaga & Schuh, 2013).

Carvalho and Gross (1982) identified this variation in accuracy of mirid myrmecomorphy and referred to less mimetic forms as "simply ant mimics" and highly mimetic forms as "myrmecomorphic species". Here, we adopt the terms "inaccurate" and "accurate" mimics commonly used to describe variation in myrmecomorphy in other arthropods (Mappes & Alatalo, 1997; Pekár & Jarab, 2011). In some species, mimetic characters may vary from male to female, for example *Orectoderus* Uhler spp. females are micropterous and males are macropterous with illusive banding (McIver & Stonedahl, 1987a; Wyniger, 2010, 2011; Wyniger et al., 2023). Additionally, accuracy of mimicry may vary with life stage, and immatures may be the most strikingly mimetic life stage with less accurately mimetic adults (e.g., *Coquillettia mimetica*) or immatures may be less accurately mimetic than adults (e.g., *Orectoderus obliquus* Uhler) (Akingbohungbe et al., 1973; McIver & Stonedahl, 1987a; Wyniger, 2010, 2011; Wyniger et al., 2023). Variation in mimetic accuracy across life stages may be widespread throughout myrmecomorphic Phylinae, but immature morphology is rarely documented (Cobben, 1986; Menard & Schuh, 2011; Schuh, 1974, 1984; Wyniger et al., 2023). Based on a preliminary survey of available images across myrmecomorphic groups, it is clear that mimetic accuracy of adults can vary within a tribe (e.g., within Leucophoropterini, the inaccurately mimetic *Ausejanus* Menard & Schuh spp. and the accurately mimetic *Waterhouseana* Carvalho spp.) and even within a genus (e.g., the inaccurate mimic *Pilophorus brunneus* Poppius and the accurate mimic *Pilophorus giraffoides* Yasunaga & Schuh). However, the specific evolutionary processes behind mimetic accuracy and the maintenance of inaccurate mimicry remain unknown.

Ruxton et al. (2018) suggested that mimics should experience selection driving them to resemble their models as closely as possible to gain protection from predators (i.e., positive selection for accurate mimicry). Yet this assumption is challenged by the abundance of mimics that inaccurately resemble their models (Dittrich et al., 1993; Edmunds, 2000; Kikuchi & Pfennig, 2013). Hypotheses for the maintenance and stability of inaccurate mimicry have been extensively reviewed by McLean et al. (2019) and broken down into adaptive and nonadaptive hypotheses that have been tested and reviewed (Kikuchi & Pfennig, 2013; McLean et al., 2019; Ruxton et al., 2018; Sherratt & Peet-Paré, 2017). Adaptive hypotheses suggest that mimics only need to resemble a model to the extent that the receiver, for example, a predator, is unable to detect the difference between the mimic and the model (Ford, 1953; McLean et al., 2019). This set of hypotheses also include selection trade-offs with other life-history functions or traits that are affected by mimicry, including thermoregulation, ability to camouflage and sexual selection (Edmunds, 2000; Haugsten Holen & Johnstone, 2004; Kikuchi & Pfennig, 2013; Pekár et al., 2011; Reiskind, 1977; Sherratt, 2002; Taylor et al., 2016). Nonadaptive hypotheses suggest that species are constrained to imperfect mimicry or in the process of evolving out of that state (McLean et al., 2019). The 'perfecting hypothesis', a nonadaptive hypothesis, posits that accurate mimicry evolves in a stepwise manner and that inaccurate mimics are in the process of evolving increased accuracy (i.e., inaccurate mimicry is an unstable evolutionary state) (McLean et al., 2019; Nesse, 2005; Nur, 1970; Pekár, 2014).

Unlike other hypotheses explaining the persistence of imperfect mimicry, the perfecting hypothesis can be tested with morphological data in the absence of biological data, the latter being unavailable for many taxa, including many Miridae. This hypothesis has been tested using phylogenetic hypotheses and ancestral character state reconstructions in ant-mimicking spiders (Kelly et al., 2025; Pekár, 2014), showing that mimetic accuracy evolved from less accurate mimics in a step-by-step manner. However, further investigation of model parameters (i.e., optimum trait value (θ) estimated by the Ornstein-Uhlenbeck (OU) model of trait evolution) indicated that inaccurate mimicry represented an adaptive optimum while highly accurate mimics were evolutionarily labile, frequently reversing to less mimetic states (Kelly et al., 2025). Thus, only partial support was found for the perfecting hypothesis. Aligning with the perfecting hypothesis, mimetic accuracy in Phylinae has been thought to increase in more derived lineages within the phylogeny, with inaccurate mimics being recovered as early diverging lineages of a given clade (McIver & Stonedahl, 1993; Schuh, 1984). The perfecting hypothesis has yet to be investigated in myrmecomorphic insects. Phylinae, with a large number of mimetic species and a wide range of mimetic accuracy, provides a good system to do so. In order to rigorously test this hypothesis, a well-resolved and highly supported phylogeny is necessary.

To create the most data- and taxon-rich phylogeny of Phylinae, we utilized ultraconserved elements (UCEs) from 247 newly sequenced species combined with 90 species from legacy Sanger datasets for a total of 337 taxa (309 ingroup and 28 outgroup). UCEs are highly conserved across divergent taxa, with increasing sequence variability as distance increases from the UCE core (Bejerano et al., 2004; Faircloth et al., 2012). This makes them ideal for simultaneous analysis at different phylogenetic scales, from deep divergences (Derkarabetian et al., 2025; Faircloth et al., 2013) to species or population levels (Harvey et al., 2016; Manthey et al., 2016), allowing for better resolution and support than Sanger markers (COI, 16S, 18S, 28S). However, there is value in combining phylogenomic datasets including UCE data with legacy Sanger data under certain circumstances. The Sanger dataset of Menard et al. (2014) includes key genera that we were unable to sequence for the present UCE dataset,

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including a number of rarely collected ant-mimetic taxa crucial for our analysis. The current combined dataset includes all phyline tribes and subtribes with representatives of 167 genera [~40% of described genera, increased from ~22% in Bush and Weirauch (2024)] and all major biogeographic regions. Geographic sampling biases of previous datasets are mitigated in the present dataset with the inclusion of additional species from the Palearctic (64 taxa), Afrotropical (24 taxa), Australian (27 taxa) and Neotropical (12 taxa) regions.

We used the resulting phylogeny to investigate the evolution of mimetic accuracy in Phylinae. Ant mimicry encompasses a complicated suite of characters that can co-occur and, in summation, contribute to the overall effect of accuracy. We recognize that morphological, behavioural and chemical characters may contribute to mimetic accuracy, but only morphological data can be scaled feasibly to a project that includes hundreds of species of Miridae. Morphological trait-based approaches for assessing mimicry have been compared to other quantification methods (e.g., geometric morphometrics) and were found to be highly correlated (Kelly et al., 2021). We here followed the approach of Kelly et al. (2025) in defining 11 morphological characters that appear to be central to ant mimicry in Phylinae. The evolution of these characters was reconstructed, and a composite score was calculated and optimized on the phylogeny to determine patterns of mimetic accuracy across Phylinae and test if they are congruent with the perfecting hypothesis.

MATERIALS AND METHODS

Taxon sampling

In total, 337 terminals were included in this analysis (309 ingroup and 28 outgroup terminals). Outgroup sampling included one representative of Pentatomomorpha, two non-Miroidea cimicomorphans, two species of Tingidae, one species of Thaumastocoridae and 22 non-phyline Miridae representing all other subfamilies of Miridae, with dense sampling of the putative phyline sister taxon Orthotylinae. NCBI accession numbers for newly sequenced material can be found in Table S1. This study builds upon the dataset assembled by Bush and Weirauch (2024). The 90 taxa represented by Sanger loci (16S, 18S and 28S rDNA) from that dataset complement the taxonomic sampling of our newly sequenced material represented by UCEs, and NCBI accession numbers can be found in Table S2. For newly sequenced material, specimens of 247 taxa were obtained from field collections and museum loans. Collections and collaborators that contributed material can be found in the acknowledgements. Freshly collected material was obtained by members of the Weirauch lab at UCR and collaborators on the plant bug phylogenomics project (NSF# DEB-2317209), preserved in 95%–100% ethanol (EtOH) and stored at −18°C until DNA extraction. Museum material was preserved dry on point mounts until DNA extraction. Of the newly sequenced material, 56 specimens were dry preserved with collection years ranging from 1968 to 2010, and 191 specimens were preserved in ethanol. Preservation method, collection year and specimen origin for newly sequenced material are available in Table S1, as are unique specimen identifier information for voucher specimens. Voucher specimens are deposited in the Entomology Research Museum at UCR, unless otherwise indicated in Table S1. Specimens were identified by experts based on dorsal habitus, male genitalia, host plant records, and collection locality using relevant literature and reference collections. All specimens were collected ethically with proper permits where necessary.

DNA extraction and sequencing

DNA extraction was performed on whole specimens, with thorax and abdomen separated from both dry and ethanol-preserved specimens. The Qiagen DNeasy Blood & Tissue Kit was used following manufacturer protocols, with the exception of using water for elution instead of AE buffer. Samples were prepared for sequencing using the NEBNext Ultra II FS NDA Library Prep Kit. Manufacturer protocols were followed at a third of the original volume. The enzymatic fragmentation thermocycler protocol was altered as follows: to obtain an ideal DNA fragment length of ~150–200 bp: 15 min at 37°C, 30 min at 65°C and held at 4°C. Depending on the concentration of each sample, the number of PCR cycles for final PCR enrichment was altered following recommendations in the manufacturer's protocols. Libraries were sequenced at approximately 20× coverage by Admera Health LLC on an Illumina NovaSeq X Plus 25B 2 × 150 sequencing platform.

UCE probe design for Miroidea

A custom UCE probe set targeting Miroidea was developed following the general workflow for UCE probe development described by Faircloth (2017) using PHYLUCE v1.6.8 (Faircloth, 2016). Because relatively few high-quality miroid genomes were available when the probe set was developed, we used a two-stage design strategy to identify taxa and loci that would provide broad and consistent recovery across Miroidea. In an initial screening workflow, 20 genomes and 5 transcriptomes representing Miroidea, other Cimicomorpha and Pentatomomorpha were evaluated against a *Halyomorpha halys* (Stål) base genome to identify conserved loci and assess locus recovery across taxa. Results from this screening were then used to select a phylogenetically representative subset of miroids for a second, Miroidea-focused probe-design workflow.

For the final design, *Thaumastocoris peregrinus* Carpintero & Dellapé was used as the base genome together with the following mirid exemplars spanning major lineages within Miridae: *Coridromius* sp., *Deraeocoris* sp., *Larinocerus balius* Froeschner, *Pachypeltis micranthus* Mu & Liu and *Peritropis setosicornis* Bergroth. This targeted design prioritized recovery of conserved loci within Miroidea, particularly Miridae, while retaining loci with broader utility across the superfamily. Following screening of candidate probes and reduction to the desired probe-set size, the final Miroidea probe kit comprised 41,276 probes

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targeting 5172 UCE loci. Full details of taxon sampling, probe-design procedures, filtering criteria and in silico validation are provided in Data S2. The miroid probe set is available in Data S1.

UCE identification, extraction and trimming

Sequence demultiplexing was conducted by Admera Health LLC using bcl2fastq. Fastp 0.23.2 (Chen, 2023) was used for sequence quality assessment, filtering and adapter trimming. Paired reads were merged with BBMerge within BBMap 39.08 (Bushnell et al., 2017). Genome assembly was performed on merged and unmerged reads with SPAdes 4.2.0 (Prjibelski et al., 2020) using the single-cell parameter. The PHYLUCE pipeline (Faircloth, 2016) was used to extract target loci from assembled genomes. Final reads were aligned with MAFFT 7.505 (Katoh & Standley, 2013) including the adjustdirectionaccurately parameter. The alignment was trimmed with GBlocks 0.91b (Talavera et al., 2007) using the following parameters: b2 = 0.5, b3 = 12, b4 = 7. Further trimming was then conducted with spruceup 2024.7.20 (Borowiec, 2019) with a cutoff of 0.97. To create a manageable data set size and mitigate missing data, we chose to limit our analyses to ~500 loci. The Phyluce command, "phyluce align get only loci with min taxa", was used to filter the alignment to retain only loci present in a minimum percentage of taxa. As such, an 87% completion matrix, including 517 UCE loci with at least 87% of the total taxa retained, was created for use in phylogenetic analyses.

Inclusion of Sanger loci

For each taxon sequenced in this analysis, Sanger loci were extracted from unassembled, trimmed genome reads using the targeted assembler aTRAM 2.4.4 (Allen et al., 2018). Resulting assembled Sanger loci were inspected in AliView (Larsson, 2014) to ensure accuracy and aligned with select taxa from the Sanger loci dataset of Bush and Weirauch (2024) using MAFFT 7.505 (Katoh & Standley, 2013). The Sanger dataset was then concatenated with the UCE dataset with FASconCAT-G 1.0 (Kück & Longo, 2014).

Phylogenetic inference

Maximum likelihood phylogenetic inference of the concatenated Sanger + UCE dataset was performed with IQ-TREE 2.2.2.6 (Minh et al., 2020) with 10,000 ultrafast bootstrap replicates ('-B') and 1,000 Shimodaira–Hasegawa-like approximate likelihood ratio test replicates ('-aLRT'). ModelFinder ('MF') was used within IQ-TREE for model selection with separate partitions for each locus. Ten independent maximum likelihood analyses were performed. A coalescent-based approach was applied to the Sanger + UCE dataset to account for gene tree discordance due to incomplete lineage sorting or introgression. Individual gene trees were inferred for each UCE and Sanger locus using IQ-TREE 3.0.1 (Wong et al., 2026) and MF. Species trees were estimated in ASTRAL 5.15.5 (Zhang et al., 2018). The tree with the best likelihood score derived from the IQ-TREE analysis was used for downstream analyses.

Ancestral character state reconstruction

To assess mimetic accuracy and test the perfecting hypothesis, we selected 11 morphological traits thought to contribute to ant-mimicry in Miridae (McIver & Stonedahl, 1993; McMah & Cassis, 2024) (Figure 3). While it is known that immatures in certain species may exhibit differing mimetic accuracy from adults (Akingbohungbe et al., 1973; Wyniger, 2011), it is not feasible to compile a dataset based on immatures due to lack of documentation in the literature, and our analysis is therefore restricted to adults. Taxa were scored for the 11 selected traits, with state 1 representing the condition hypothesized to contribute to ant mimicry and state 0 representing the alternative condition. An accuracy score was then calculated by summing the number of characters scored in the mimetic state for each species. The perfecting hypothesis was accepted if accurate species were nested within clades of inaccurate species, and rejected if accurate species were nested within clades of non-mimetic species. Character coding can be found in Table S3.

Characters:

1. Pedicel: (0) same width throughout, (1) swollen distally, giving the impression of elbowed or clubbed antennae (McIver & Stonedahl, 1993).
2. Apex of pedicel: (0) same colour as remaining antennal segments, (1) darker, giving the impression of elbowed or clubbed antennae (McIver & Stonedahl, 1993).
3. Flagellomeres: (0) filiform, (1) expanded and similar in diameter to pedicel, giving the impression of ant-like antennae. This character has not previously been characterized; however, increased diameter of flagellomeres is seen among many mimetic species, giving the illusion of thickened or clubbed flagellomeres seen in ants.
4. Base of flagellomere: (0) same colour as remaining antennal segments, (1) lighter, giving impression of elbowed or clubbed antennae (McIver & Stonedahl, 1993).
5. Corium: (0) solid colour, (1) dark with one or more light cream to white bands, giving the illusion of restriction between the head and the mesosoma (McMah & Cassis, 2024).
6. Cuneus: (0) solid colour, (1) dark with light-cream to white band, giving the illusion of a restriction between the mesosoma and the gaster (McMah & Cassis, 2024).
7. Lateral margin of hemelytra: (0) straight to slightly convex, (1) concave, giving the illusion of a petiole (McIver & Stonedahl, 1993; McMah & Cassis, 2024).
8. Wings: (0) macropterous, (1) micropterous or apterous in at least one sex (McIver & Stonedahl, 1993).
9. Head shape: (0) triangular, (1) rounded in dorsal view, giving the illusion of a prognathous head and enlarged mandibles (McIver & Stonedahl, 1993).

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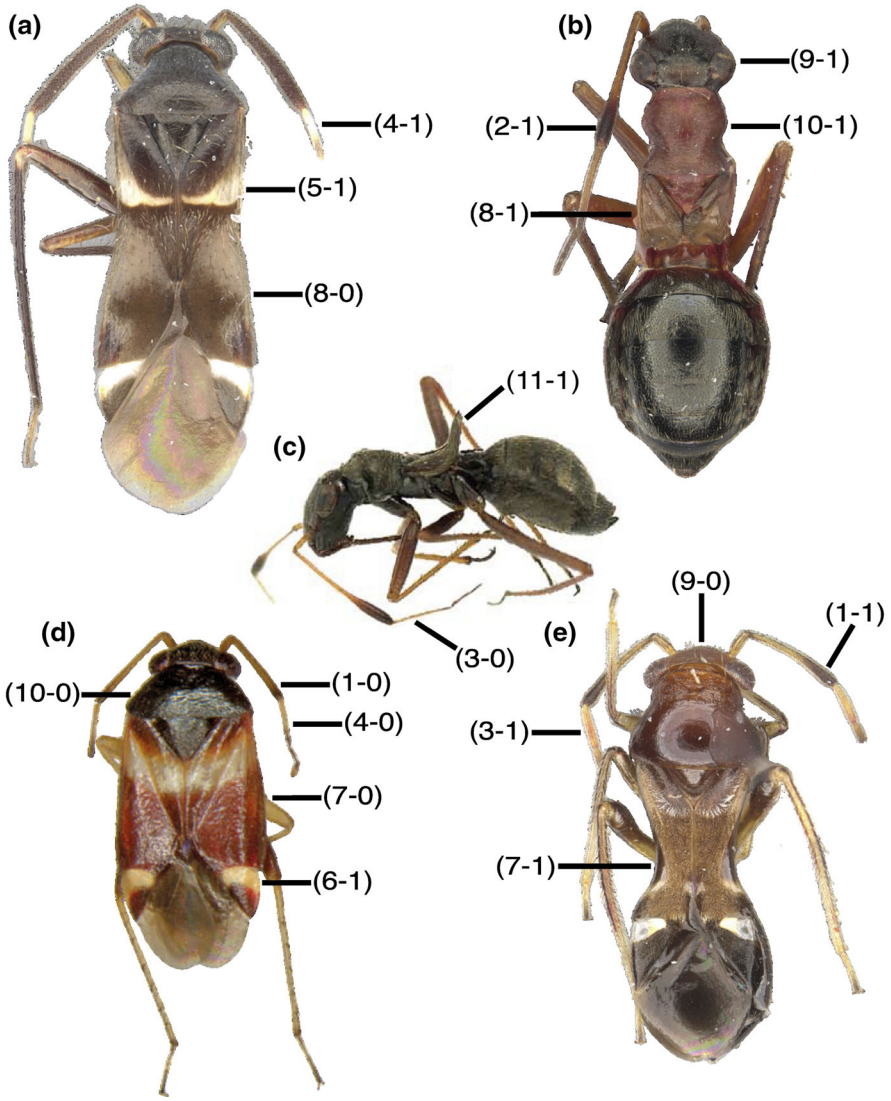


FIGURE 3 Myrmecomorphic character states used in the current study. (a) Male *Blesingia gularis* Carvalho & Gross (Leucophoropterini: Leucophoropterina); (b) Female *Orectoderus montanus* Knight (Cremnorrhinini: Cremnorrhinina); (c) Lateral view of female *O. montanus*. Photo modified from Wyniger (2010); (d) Female *Ausejanus meridionalis* (Carvalho & Gross) (Leucophoropterini: Leucophoropterina). Photo modified from Menard and Schuh (2011); (e) *Arafuramiris queenslandensis* Menard & Schuh (Leucophoropterini: Leucophoropterina). Characters and states are explained in the material and methods, with state 1 representing the ant-mimetic state and 0 alternative condition.

10. Pronotum: (0) trapezoidal without constriction between anterior pronotal lobe and posterior pronotal lobe, (1) with constriction, mimicking the distinct prothorax of an ant. This character is an expansion of one characterized in McMah and Cassis (2024) to emphasize not only the shape of the pronotum but also constrictions between the pronotal lobes.
11. Dorsum: (0) without spine or apical projections, (1) with spine or apical projection giving the illusion of a petiole spine (McIver & Stonedahl, 1993).

Evolution of each of the 11 discrete characters was reconstructed individually using the function *ace* in the package *ape* 5.8–1 (Paradis & Schliep, 2019). SYM (symmetrical; assumes that the transition rate between state A and state B is equal to the reverse rate from state B to state A) and ARD (all-rates-different; transitions between different states are independently estimated parameter values) models were tested for each character, and the best-fitting model was selected using the corrected Akaike information criterion (AICc). Because all characters were binary, ER (equal rates) and SYM models were equivalent; therefore, the ER model was not evaluated. Results were visualized with *ggtree* 3.13.1 (Xu et al., 2022). The mimetic accuracy score was treated as a continuous character, and its evolution was reconstructed using the *fitContinuous* function within *geiger* 2.0.11 (Pennell et al., 2014). Both Brownian motion (traits change in random directions) and Ornstein-Uhlenbeck (OU; traits pulled towards optimal value) models were tested, and the best-fitting model was selected using AICc. The *contMap* function within *phytools* 2.3-0 (Revell, 2024) was used to plot estimated ancestral trait states. As this function by default estimates node states based on Brownian motion, to visualize the results of the OU model, the tree was transformed according to

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the estimated alpha value using the rescale function in *phytools*. The rescaled tree was then used for visualization with *contMap*. To assess optimal trait value (θ) within mimetic clades, OU analyses were also performed separately on pruned subtrees of mimetic clades containing both inaccurate and accurate mimics for Hallodapini, Leucophoropterina and *Pilophorus*.

RESULTS

UCE extraction

The total number of UCEs recovered after filtering ranged from 187 (3% recovery) to 4,255 (82% recovery), with an average of 3,276 loci (62% recovery). UCE recovery for all taxa can be found in Table S1. To create a manageable dataset size for analyses and mitigate missing data, we chose to limit the dataset to ~500 loci present in a minimum percentage of taxa. The final alignment of the 87% completion matrix + Sanger loci dataset contained 521 loci and had a total alignment length of 255,383 bp.

Phylogenetic analyses

The likelihood scores of the 10 IQ-TREE runs ranged from −11,128,274.252 to −11,128,124.089. The majority-rule consensus tree of all ML trees is shown in Figure 4. Overall, all likelihood trees showed high topological congruence, with the exception of relationships at the species level within *Pilophorus* Hahn, *Europiella* Reuter and *Plagiognathus* Fieber. The placement of taxa represented by UCEs was

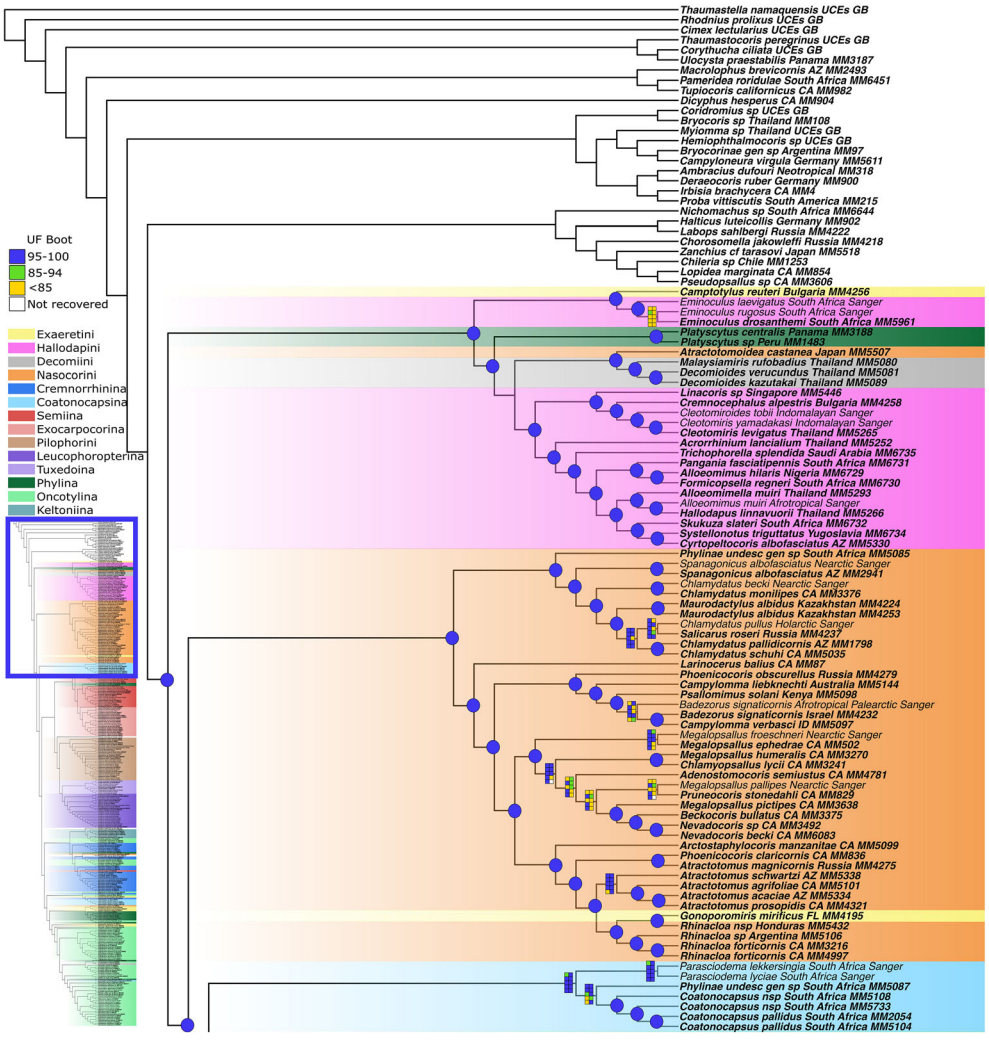


FIGURE 4 Majority consensus tree of 10 maximum likelihood runs. Ultrafast bootstrap support is displayed as a circle if the same across the 10 runs and as a rug if it varies. The country of origin for each specimen is listed in the taxon label. A two-letter code is used for US states (AZ: Arizona; CA: California; CO: Colorado; CT: Connecticut; FL: Florida; ID: Idaho; MT: Montana; OR: Oregon; TX: Texas; WY: Wyoming). Taxa represented only by Sanger loci are denoted in taxon labels. Taxon labels are bolded for newly sequenced species represented by ultraconserved elements.

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largely the same between the ASTRAL and IQ-TREE phylogenies, with the exception of Coatonocapsina [in part] being sister to all of Phylinae except for Hallodapini, Decomiini and Nasocorini in the likelihood tree (Figure 4, part 1) and sister to Cremnorrhinina + Phylini in the ASTRAL tree (Figure S1), and a non-monophyletic Pilophorini and Leucophoropterini in the ASTRAL tree. The ASTRAL analysis was unable to resolve the placement of some Sanger-only taxa as they were represented by only three gene trees (e.g., species of *Pilophorus* and *Ausejanus* Menard & Schuh). This outcome is expected given the amount of missing data in the combined UCE and legacy Sanger loci alignment (Portik et al., 2023). Therefore, we chose not to use the ASTRAL phylogeny for downstream analyses.

In our analyses, all tribes except Pilophorini are recovered as non-monophyletic in the strict sense (Figure 4). However, in many tribes and subtribes a core assemblage of genera forms a monophyletic group, while individual genera are recovered outside these clades. The following paragraph outlines the phylogenetic positions of these rogue taxa. We refrain from indicating paraphyletic taxa by quotes because paraphyly is prevalent and in many cases can be resolved by moving specific taxa to different tribes and subtribes (but is not an objective of the current study). Hallodapini are rendered paraphyletic by including *Camptotylus reuteri* Jakovlev (Exaeretini), two species of *Platyscytus* Reuter (Phylina), *Atractotomoidea* Yasunaga (Nasocorini) and all Decomiini included in this

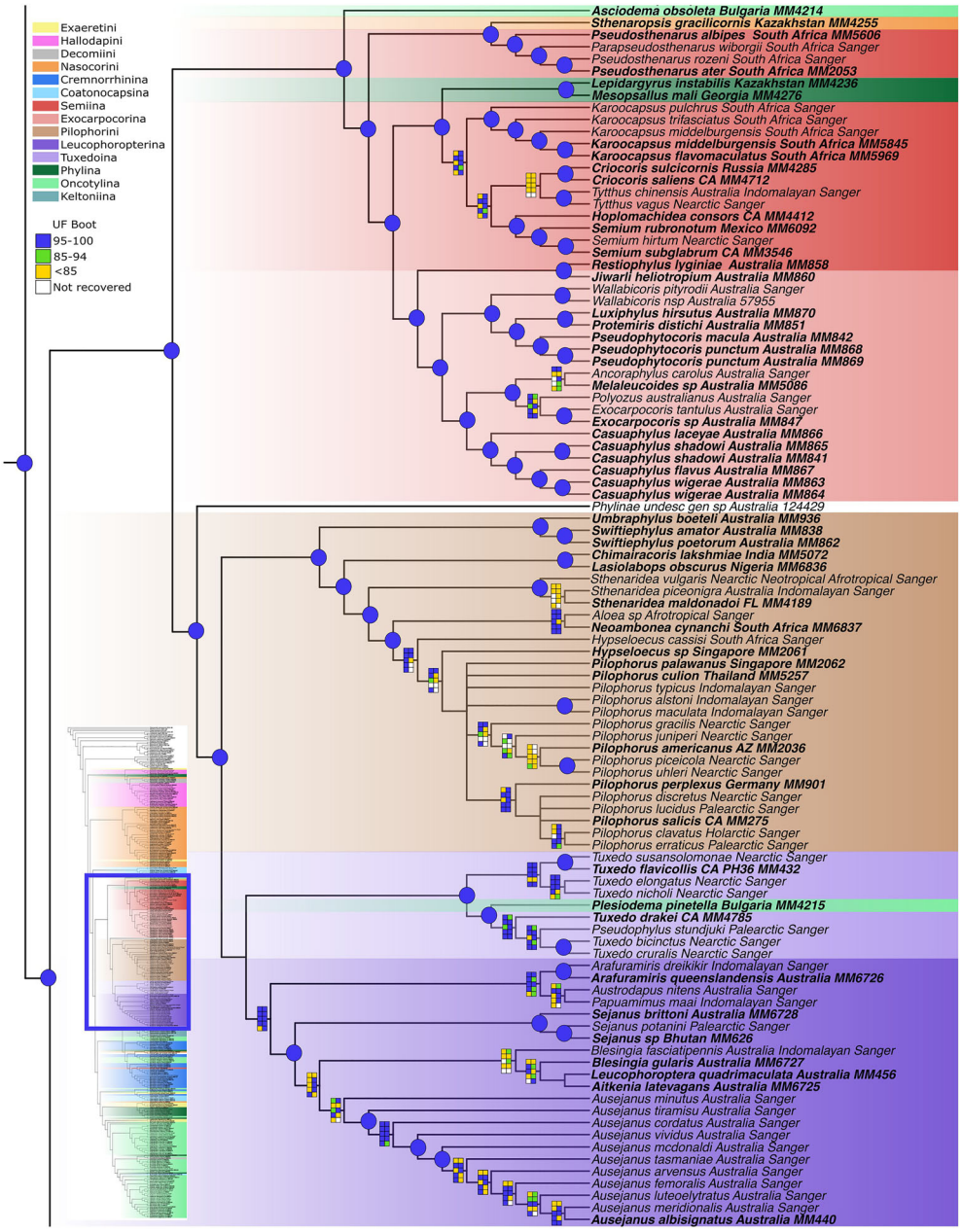


FIGURE 4 (Continued)

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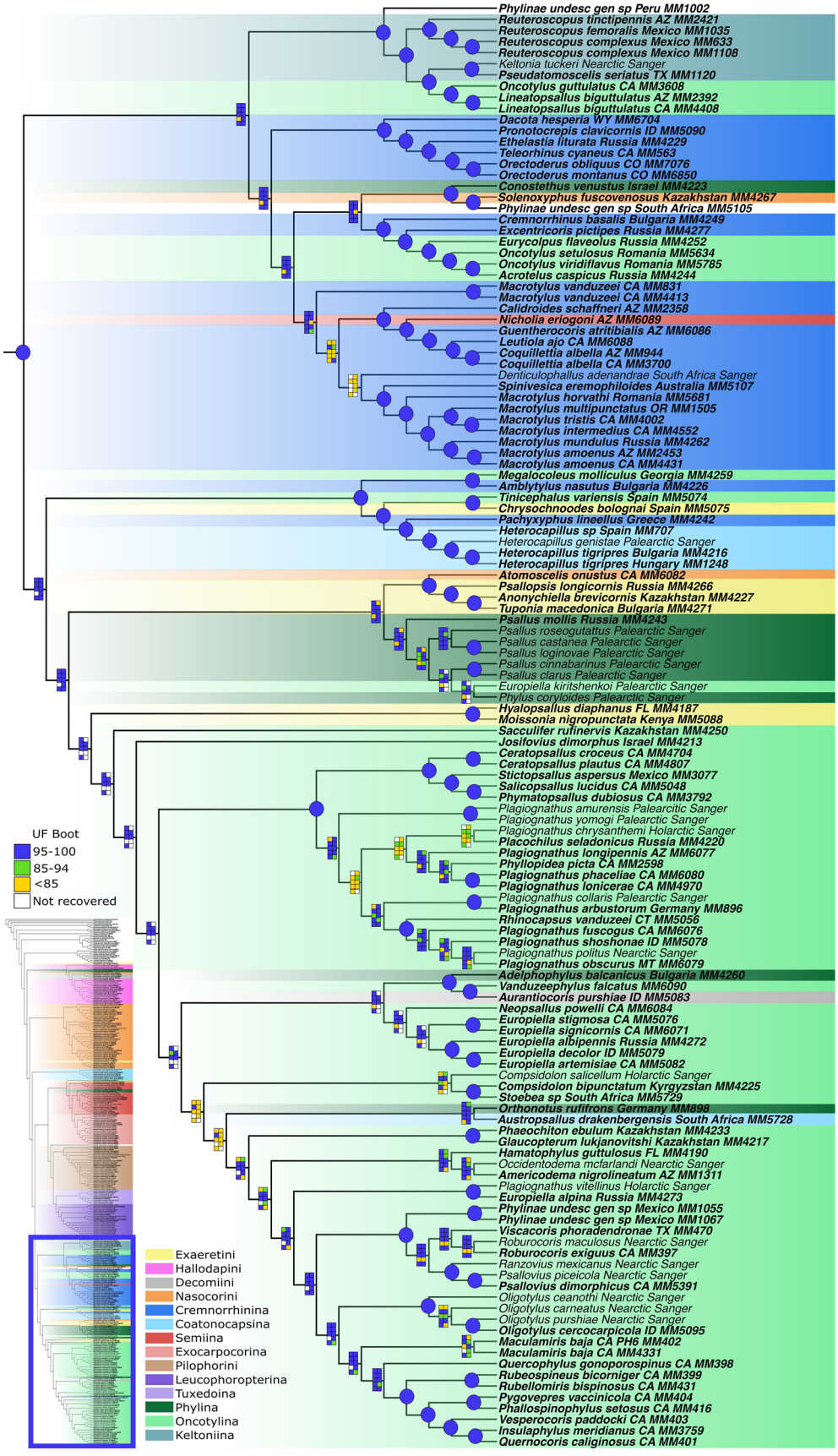


FIGURE 4 (Continued)

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analysis (Figure 4, part 1). The hallodapine *Eminoculus* Schuh, together with its sister taxon *Camptotylus reuteri*, forms the earliest diverging lineage of this composite clade. The bulk of taxa included in Nasocorini form a monophyletic group and are the next diverging lineage of Phylinae. However, *Gonoporomiris* Schuh (Exaeretini) is nested within Nasocorini, and several nasocorine genera are nested within other tribes (*Atractotomoidea* Yasunaga: sister to Decomiini within Hallodapini; *Sthenaropsis* Poppius: within Semiini; *Solenoxyphus* Reuter: within Cremnorrhinina; *Atomoscelis* Reuter: sister to Exaeretini [in part]). Semiini (Figure 4, part 2) are the sister taxon to (Pilophorini + Leucophoropterini). The bulk of taxa currently classified as Semiini form a monophyletic group, except for *Nicholia* Knight, which is recovered within Cremnorrhinina. This genus was mistakenly classified within Semiina by Schuh and Menard (2013), despite being correctly allied with genera belonging to Cremnorrhinina by Schwartz (2005). Semiina are non-monophyletic as *Pseudosthenarus* Poppius is sister to all remaining Semiini. In addition, *Lepidargyrus instabilis* Reuter (Phylina) and *Mesopsallus mali* (Meyer-Dur) (Phylina) are nested within Semiina. Exocarpocorina are monophyletic, but *Restiophylus* Leon & Weirauch (Semiina) forms the sister lineage to *Jiwarli heliotropium* Soto & Weirauch, and they together are the earliest diverging lineage of the subtribe. Leucophoropterini are monophyletic except for *Plesiodema* Reuter (Oncotylina) that is nested within Tuxedoina. Leucophoropterina are monophyletic. Cremnorrhinini (Figure 4, parts 1 and 3) are polyphyletic with Coatonocapsina forming two distinct clades in different phylogenetic positions in the tree: *Heterocapillus* Wagner with Oncotylina, Exaeretini and Cremnorrhinina [in part] (*Amblytylus* Fieber and *Pachyxyphus* Fieber) together are sister to Phylini [in part] (Figure 4, part 3), and a clade of South African genera (*Coatonocapsus* Schuh, *Parasciodema* Poppius; Figure 4, part 1) is the sister lineage to all of Phylinae except for Hallodapini, Decomiini and Nasocorini (Figure 4, part 1). Cremnorrhinina are polyphyletic, intermingled with many genera currently classified as Phylina (*Conostethus* Fieber), Oncotylina (*Acrotelus* Reuter, *Oncotylus* Fieber, *Eurycolpus* Reuter), Nasocorini (*Solenoxyphus*) and Semiini (*Nicholia*) (Figure 4, part 3). Phylini are also polyphyletic and recovered in nine lineages throughout the tree (Figure 4, parts 1, 2 and 3). Oncotylina form a large clade deeply nested in the tree (Figure 4, part 3), but several genera are scattered throughout other tribes as previously mentioned (Figure 4, parts 2 and 3). Part of the type genus, *Oncotylus*, represented by the Nearctic species *Oncotylus guttulatus* Uhler, is nested within Keltoniina, while Palearctic species of *Oncotylus* were recovered within Cremnorrhinina. Phylina are polyphyletic (Figure 4, parts 1, 2 and 3). The type genus, *Phylus* Hahn, is recovered in a clade also containing Exaeretini [in part] and *Atomoscelis* (Nasocorini) that is sister to Oncotylina. Exaeretini are polyphyletic and recovered in five lineages throughout the tree, including those previously mentioned, as well as *Moissonia* Reuter and *Hyalopsallus* Carvalho & Schaffner, sister to Oncotylina (Figure 4, parts 1 and 3). Several large genera were recovered as non-monophyletic, including *Megalopsallus*, *Atractotomus* and *Plagiognathus*.

Ancestral character state reconstruction of mimetic accuracy

Ancestral character state reconstructions for the 11 discrete characters can be found in Figures S2–S12. The best-fitting model for each character can be found in Table S4. For ancestral character state reconstruction of the mimetic accuracy score, the OU model was the best fit (OU AICc = 1094.961; BM AICc = 1102.701; ΔAICc = 7.74). The resulting reconstruction is shown in Figure 5.

The following paragraph indicates results for investigation of the perfecting hypothesis. The average mimetic accuracy score across the dataset was low (average = 1; min–max: 0–9; SD = 1.9). Within the dataset, 274 taxa were scored as non-mimetic (0–2), 42 were scored as inaccurate mimics (3–5) and 19 were scored as accurate mimics (6–9). No taxon had a perfect mimicry score of 11. The reconstruction of the evolution of mimetic accuracy supports the theory of mimetic accuracy evolving through the gradual accumulation of myrmecomorphic characters. However, the optimum trait value (θ) calculated by the OU model was 0.36, indicating that evolution is being drawn towards a non-mimetic state. When the OU model was run on pruned trees for clades that included accurately mimetic species, the optimal trait values were as follows: Hallodapini, θ = 3.9; Leucophoropterina, θ = 4.2; *Pilophorus*, θ = 5.2. Therefore, in clades with both accurate and inaccurate mimics, the optimal character state is to be inaccurately mimetic.

We recovered six independent origins of ant mimicry within Phylinae, with accurate mimics in four of the six clades (Figure 5). Within ant-mimetic clades, accurate mimicry evolved 14 independent times, always from an inaccurately mimicking ancestor. There are 12 reversals from inaccurate mimicry to non-mimicry and no reversals from accurate mimicry. Notably, the ancestor of Leucophoropterini was recovered as inaccurately mimetic, and an immediate reversal to the non-mimetic state occurred in the ancestor of Tuxedoina (Figure 5), while accurate mimicry evolved in Leucophoropterina (Figure 5). Further, within Leucophoropterina, inaccurate mimicry reversed to non-mimicry four times within the genus *Ausejanus* (Figure 6). Within Pilophorini, the ancestor of *Pilophorus* was recovered to be an inaccurate mimic, with three independent origins of accurate mimicry within the clade (Figure 7). Though the ancestor of Hallodapini was recovered as non-mimetic, the majority of extant species are mimetic and six independent origins of accurate mimicry were recovered (Figure 8).

DISCUSSION

Relationships within Phylinae

The current classification of Phylinae (Schuh & Menard, 2013) is based on the combined morphology and molecular POY parsimony analysis of Menard et al. (2014), though a combined parsimony analysis using TNT and a molecular-only maximum likelihood analysis were also conducted. Topologies varied among the three analyses, with

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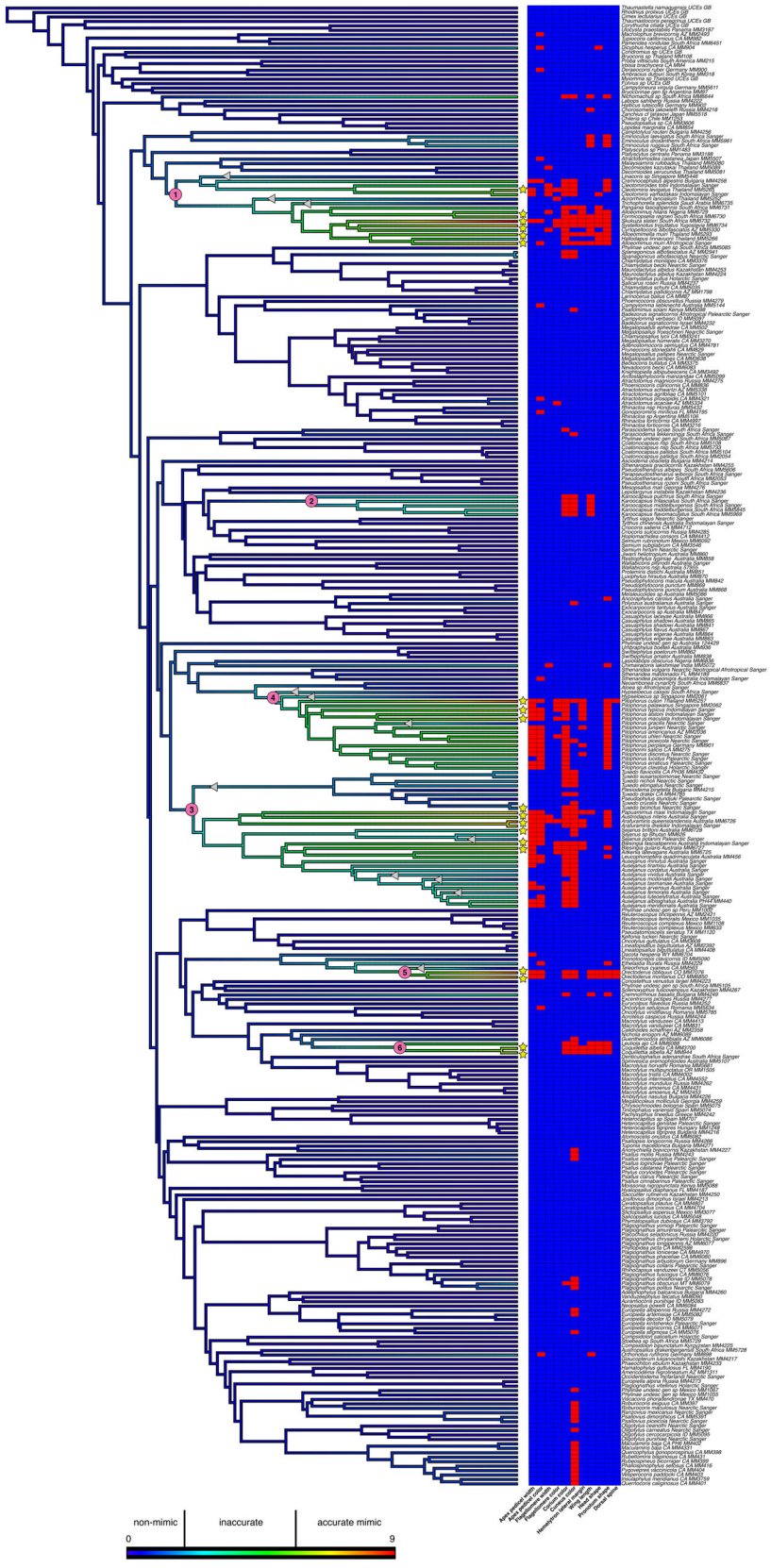


FIGURE 5 Ancestral character state reconstruction of mimetic accuracy score estimated with the OU model. Coloured squares at branch tips represent the presence (red) or absence (blue) of the 11 ant-mimetic morphological characters. Numbered circles on nodes represent origins of mimicry, and stars at branch tips represent accurate mimics. Reversals from inaccurate mimicry to non-mimicry are denoted by triangles.

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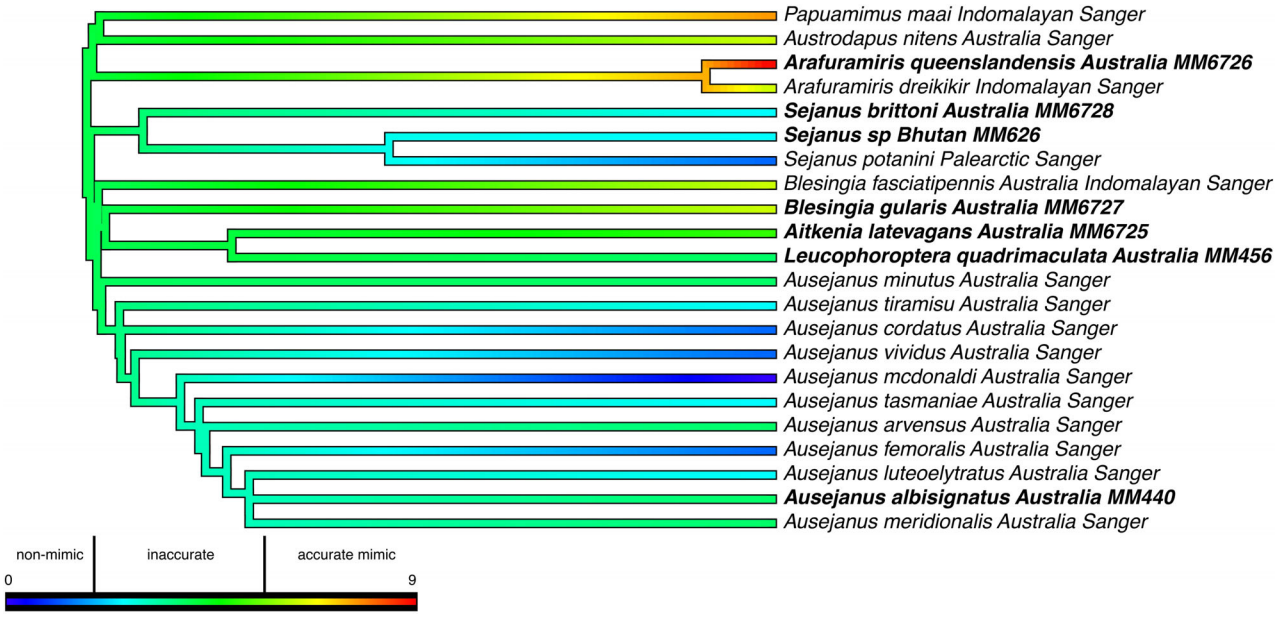


FIGURE 6 Ancestral character state reconstruction of mimetic accuracy score estimated with OU model for Leucophoropterina.

consistently low support along the backbone and for many clades. These analyses highlight the instability of the dataset on which the current classification is built, with Cremnorrhinini recovered as non-monophyletic in both the RAxML and TNT trees and non-monophyletic Phylini and Leucophoropterini in the TNT tree. That dataset included 164 species of Phylinae (~17% of described species of Phylinae), so for those genera not included, educated assessments based on morphology were used for classification. As no non-homoplastic morphological synapomorphies were recovered from the combined morphological and molecular analysis to diagnose tribal and subtribal groupings, the diagnoses are often complex sets of non-exclusive characters. It is therefore believable that many genera were incorrectly classified and that the present analysis recovers more monophyletic (or nearly monophyletic) tribes and subtribes. Our phylogeny shows that the existing classification will need to be further adjusted to better align with the evolutionary history of the group.

Tribal level relationships in our phylogeny show some congruence with relationships recovered in previous phyline phylogenies (Figures 1 and 4). Hallodapini are recovered as sister to remaining Phylinae in all analyses and are also recovered as paraphyletic with respect to *Eminoculus* in the analysis of Knyshov et al. (2019). Our analysis supports the relationship of Nasocorini as sister to remaining Phylinae following Hallodapini and Decomiini as seen in previous phyline phylogenies (Figures 1 and 4, part 1). Congruent with Knyshov et al. (2019) and Bush and Weirauch (2024), we recovered Phylini and Cremnorrhinini as polyphyletic. The sister relationship of Semiini + (Leucophoropterini + Pilophorini) remains well supported in the present analysis as in all previous analyses (Figures 1 and 4, part 2). A summary and further comparison of tribal level relationships recovered in previous and this analysis can be found in Table S5. Discussion of the tribal level relationships, including placement of rogue taxa, recovered in the present analysis is presented below.

Hallodapini and Exaeretini

Hallodapini have long been diagnosed by the presence of a flattened pronotal collar (Carvalho, 1952, 1958a; Schuh, 1974, 1984; Schuh & Menard, 2013; Wagner, 1974). Most species of *Eminoculus* have a flattened pronotal collar, but the structure of male genitalia and pretarsus (Schuh & Wu, 2009) are distinct from the remaining Hallodapini. Future analyses should redefine Hallodapini to accommodate *Eminoculus* and other genera recovered within the tribe or establish additional tribes. *Camptotylus* Fieber (Exaeretini) has not previously been included in a phylogenetic analysis, and the relationship of this genus with *Eminoculus* has not been previously hypothesized based on morphology. *Camptotylus* was placed in Exaeretini based on similarity of male genitalia; however, it is clear from the present analysis that the characters identified as uniting Exaeretini are likely the result of convergent evolution. It is possible that additional genera noted as resembling *Camptotylus* (e.g., *Yotvata* Linnavuori, *Eurycranella* Reuter, *Compsonannus* Reuter, *Camptozorus* Kerzhner) might form a clade with *Eminoculus* + *Camptotylus* if included in a phylogenetic analysis. The only character uniting Exaeretini in Menard et al. (2014) is a relatively long labium extending past the hind coxae. This character occurs in several non-exaeretine genera (*Casuaphylus* Schroeder & Weirauch; *Grandivesica* Schuh & Schwartz; *Leptospermia* Schwartz, Weirauch, & Schuh; *Melaleucacoris* Schwartz, Weirauch, & Schuh; *Omnivoriphylus* Schuh & Schwartz; *Pulvillophylus* Schuh & Schwartz; *Swiftiephylus* Schroeder & Weirauch; and *Xiphoides* Schwartz, Weirauch, & Schuh, among others) and is homoplastic.

Decomiini

Decomiini represent a monophyletic grouping with the exception of *Aurantiocoris*. *Aurantiocoris* was placed in Decomiini based on

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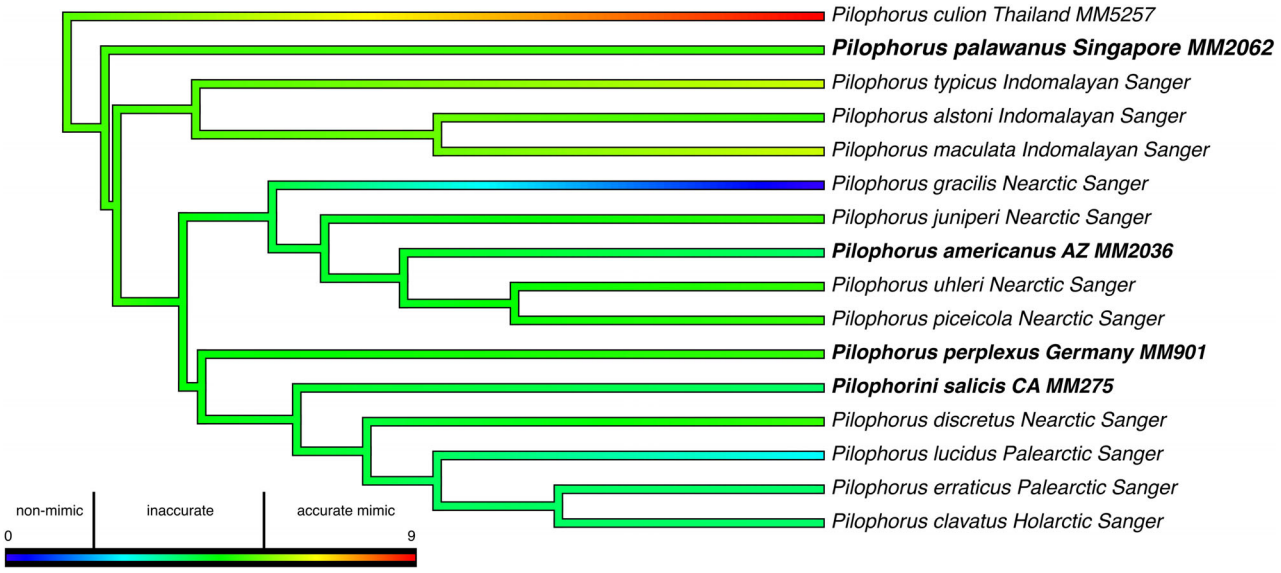


FIGURE 7 Ancestral character state reconstruction of mimetic accuracy score estimated with OU model for *Pilophorus*.

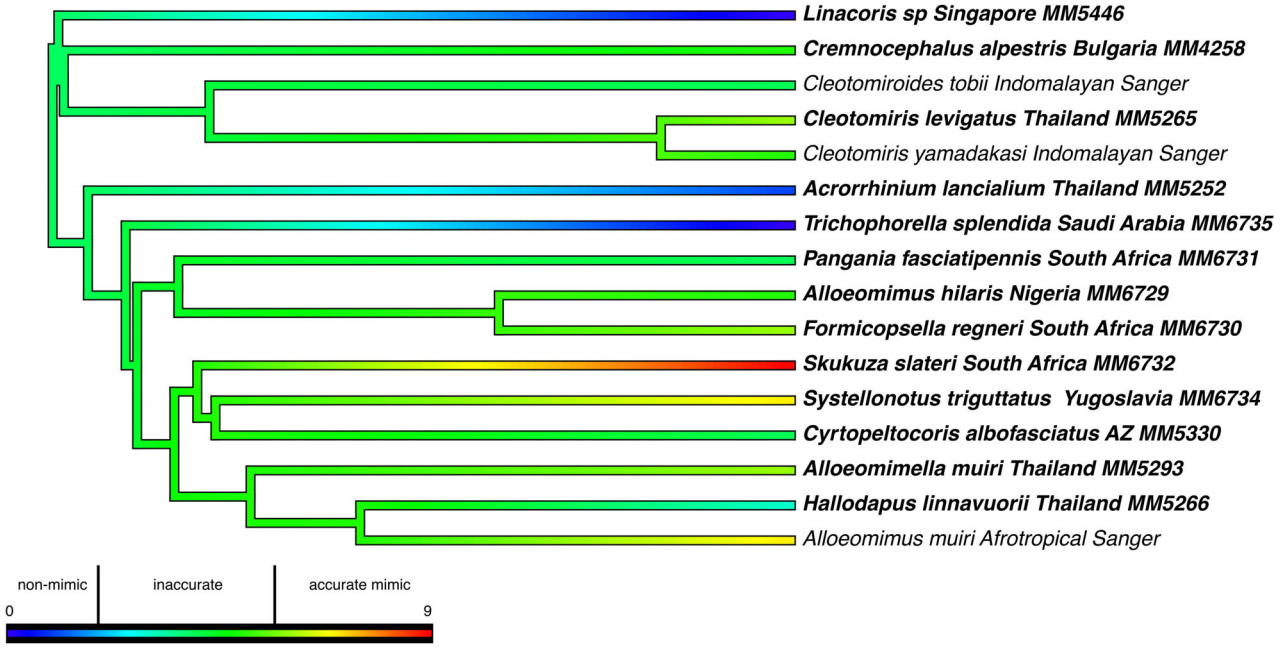


FIGURE 8 Ancestral character state reconstruction of mimetic accuracy score estimated with OU model for Hallodapini.

the molecular analysis of Menard et al. (2014), but no morphological characters support this placement. The morphology of the male genitalia as well as the geographic distribution of the two species of *Aurantiocoris* (North America) differ from those in the remaining Decomiini (Paleotropical and Oriental distributions) but are similar to closely related genera of Oncotylina in the present analysis. *Atractotomoidea castanea* Yasunaga (Nasocorini) is recovered within Decomiini. This genus has not previously been included in a phylogenetic analysis, and further comment on the classification is made below.

Nasocorini

Nasocorini are largely a monophyletic group despite the analysis of Menard et al. (2014) not recovering any morphological synapomorphies for the group. The few genera classified as Nasocorini recovered within other tribes had not previously been included in phylogenetic analyses. As examples, *Solenoxyphus*, *Atomoscelis*, *Atractotomoidea* and *Sthenaropsis* were classified in Nasocorini based on similarity in shape of the endosoma, but these similarities are likely convergences. Based on current molecular phylogenetic and morphological data for

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genitalic structures across Phylinae, similar endosomal shapes may have evolved repeatedly in different clades within the subfamily.

Semiini

With the exception of *Nicholia* recovered within Cremnorrhinina, Semiini are monophyletic. The placements of *Lepidargyrus* and *Mesopsallus* within Semiina are consistent with the simplified, tubular morphology of the endosoma and this is likely the correct classification of these genera (Drapolyuk, 1993; Konstantinov, 2023; Schuh & Menard, 2013). The South African genera *Pseudosthenarus* and *Parapseudosthenarus* Schuh were recovered as sister to all Semiini, rendering Semiina paraphyletic, while *Karoocapsus* Schuh, the remaining South African semiine included in this analysis, is nested within Semiina. It is possible that the inclusion of additional South African genera, described and undescribed, will give better insight into subtribal groupings within Semiini. The Australian genus *Restiophylus* was placed in the Semiina by Leon and Weirauch (2015) based on the results of a small morphology-based parsimony analysis that recovered problematic phyline relationships unsupported by all molecular phylogenies (e.g., polyphyletic Leucophoropterini sister to remaining Phylinae, Semiini polyphyletic with respect to Cremnorrhinini and polyphyletic Nasocorini and Phylini). All other Australian genera of Semiini belong to the tribe Exocarpocorina, and it is clear from the present analysis that *Restiophylus* should be classified in Exocarpocorina as well. Exocarpocorina are an almost entirely Australian and New Zealand subtribe, with the exception of three southern Neotropical genera not included in the present analysis: *Ampimpacoris* Weirauch & Schuh, *Araucanophylus* Carvalho and *Chiloephylus* Carvalho. These genera were placed within Exocarpocorina due to assumed relatedness to other exocarpocorine genera based on morphological character data (Schuh & Menard, 2013; Weirauch & Schuh, 2011). If they were included in a molecular phylogenetic analysis, they may be recovered elsewhere, resulting in an entirely Australian and New Zealand Exocarpocorina.

Leucophoropterini and Pilophorini

Leucophoropterini and Pilophorini are strongly supported tribes in all phylogenetic analyses. They both remain monophyletic in the present analysis, with the exception of *Plesiodema* within Leucophoropterini (Figure 4, part 2). Schuh and Menard (2013) noted the resemblance of *Tuxedo* Schuh and *Plesiodema* male genitalia, so the recovery of this oncotyline genus within Tuxedoina is not surprising. Our analyses further corroborate the non-monophyly of *Tuxedo* with respect to *Pseudophylus*, as seen in previous phylogenies (Bush & Weirauch, 2024; Knyshov et al., 2019; Menard et al., 2014). The placement of a currently undescribed Australian genus as sister to Leucophoropterini + Pilophorini underscores that currently unknown genera, particularly from Australia, may provide the link to unite this clade into a single tribe or result in the description of a new tribe.

Cremnorrhinini

The subtribes of Cremnorrhinini do not seem to represent natural groupings, consistent with the lack of morphological characters supporting the tribe in Menard et al. (2014). Cremnorrhinina are defined by the presence of an elongate postocular region (Menard et al., 2014; Schuh & Menard, 2013); however, this character appears to be unreliable for diagnosing the group, as several genera classified as Cremnorrhinina appear within other tribes, and several genera without this character are recovered within Cremnorrhinina (e.g., *Oncotylus*, *Acrotelus*, *Eurycolpus*, *Solenoxyphus*, *Conostethus*, *Nicholia*). Coatonocapsina form two clades in the present analysis, distinct in their geographic distribution. The first contains South African genera, and the second the Palearctic *Heterocapillus* and several Palearctic genera classified in other tribes. Coatonocapsina are entirely South African in distribution except for *Heterocapillus*, so it is not surprising that this genus may belong to a different clade. As in the cases described above, the inclusion of additional South African genera, both described and undescribed, may resolve the classification of Coatonocapsina.

Phylini

Phylini have a complex history as the dumping grounds of phyline genera not easily unified or classified by morphological characters (e.g., Carvalho, 1952, 1958b; Schuh, 1974, 1984, 1995; Schuh & Menard, 2013), though some attempts were made to recognize subgroupings within the tribe (Wagner, 1974, 1975). The analysis of Menard et al. (2014) led to the implementation of justified subtribal groupings, in which taxa were placed largely on the basis of morphology, or incertae sedis where data was insufficient to classify them elsewhere. Oncotylina and Keltoniina largely remain monophyletic groupings in the present analysis. Notably, all but one genus of Keltoniina are included in the present analysis, and the subtribe is monophyletic except for the inclusion of *Oncotylus guttulatus*, the single Nearctic species of the type genus of Oncotylina. Schuh and Menard (2013) proposed examining whether *O. guttulatus* is congeneric with the type species of *Oncotylus*, and our analysis suggests that *O. guttulatus* should in fact be accommodated elsewhere. Palearctic species of *Oncotylus* are recovered within Cremnorrhinina. The diagnosis for Oncotylina notes that there are no morphological synapomorphies uniting this diverse lineage. It is remarkable that despite this, the subtribe largely represents a natural grouping, with the exception of several rogue genera. Phylina are defined by two non-exclusive morphological characters and are unsurprisingly polyphyletic throughout the tree.

Evolution of ant mimicry

Our analysis of ant mimicry in Phylinae focused on the perfecting hypothesis given the lack of biological, behavioural and/or ecological

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data necessary for testing alternative hypotheses. We pursued two lines of investigation (McLean et al., 2019; Nesse, 2005; Nur, 1970; Pekár, 2014). First, we evaluated if the phylogenetic pattern of non-mimics, inaccurate mimics and accurate mimics is consistent with the perfecting hypothesis. Second, we estimated the optimal trait values using the OU model to determine if inaccurate mimicry is an unstable state, one of the predictions of the perfecting hypothesis. For the first line of investigation, our ancestral trait reconstruction provides evidence that accurate mimics almost always evolve from an inaccurate ancestor in Phylinae (Figure 5), a phylogenetic pattern consistent with the perfecting hypothesis. The only exceptions are *Orectoderus obliquus* and *Orectoderus montanus* Knight, two accurate mimics that are nested within a non-mimetic clade. *Orectoderus* belongs to a small clade that is sister to the remaining Cremnorrhinina. That clade may be under-sampled in our study, precluding the generation of a clearer picture of the evolution of mimetic accuracy in this lineage.

In contrast, our investigation of the optimal trait value of mimetic accuracy estimated by the OU model contradicts the perfecting hypothesis. Across the subfamily, the optimal trait value was estimated to be non-mimetic (mimetic accuracy score of <1). Within subtree analyses of ant-mimetic clades (Hallodapini, Leucophoropterina, *Pilophorus*), the optimal trait values were modelled to be inaccurately mimetic, suggesting that inaccurate mimicry in these groups represents a stable evolutionary state. Interestingly, our results mirror those of Kelly et al. (2025). Both studies found evidence that accurate mimics are always nested within clades of inaccurate mimics, but the most stable evolutionary state is estimated to be inaccurate mimicry. Our results also recovered 12 instances of reversals from inaccurately mimetic ancestors to non-mimetic descendants. These are not necessarily instances of mimetic breakdown, as this term is associated with non-mimetic descendants of accurately mimetic ancestors (Brower, 1960; Harper & Pfennig, 2007). Many of these reversals were recovered within *Pilophorus* and *Ausejanus*; however, species-level relationships and support varied among ML runs for these genera, as many species were represented only by Sanger data. A more data-rich examination of species relationships in these genera may alter the inferred pattern of mimicry loss. Mimicry may have been lost in these cases due to a loss of selection pressure to remain mimetic after the loss of a mimetic receiver (e.g., a predator the mimic is gaining protection from) or due to fitness trade-offs associated with maintaining myrmecomorphic morphological characters. Similarly, inaccurate mimicry may represent a stable evolutionary state due to fitness trade-offs linked to evolving additional ant-like morphological characters. The least common myrmecomorphic character states seen among taxa in the present data set are those associated with changes in shape and length of the hemelytra, shape of the head, width of the flagellomeres and presence of dorsal spines. Though these characters contribute heavily to the illusion of being an ant and are largely seen only in accurately mimetic taxa, they may also pose greater biological consequences than benefits gained from increased myrmecomorphy. Reduction or constriction of wings may result in decreased dispersal ability; however, flightlessness may also be associated with reproductive benefits that mitigate these negative impacts (Guerra, 2011). Fitness trade-offs associated with accurate morphological characters in myrmecomorphic spiders have been recorded, including decreased jumping ability and decreased prey capture (Hashimoto et al., 2020), though this may not be true for all species (Yu et al., 2024). Additionally, morphological adaptations of accurate mimicry are associated with decreased central nervous system volume in myrmecomorphic spiders, providing support for a fitness trade-off between accurate mimicry and internal anatomy (Kelly et al., 2024). Some biological consequences may be mitigated in myrmecomorphic Miridae by a combination of other characters giving a similar illusion of ant-like body form, of which there is no evidence for decreased fitness. For example, concave hemelytra with black and white banding may give an impression of ant-like body form good enough to deceive potential predators (Cobben, 1986). Inaccurate morphological mimicry may be combined with ant-like behaviour to enhance mimetic signal, as seen in *Coquillettia insignis* and other myrmecomorphic heteropterans (Cobben, 1986; McIver & Stonedahl, 1987a, 1993). Some of these trade-offs may also be circumvented by immature ant mimics who have not yet developed wings. Further, it is possible that species that are inaccurately mimetic as adults were quite accurate immature mimics (Akingbohungbe et al., 1973; Wyniger, 2011), allowing their survival and driving selection for inaccurately mimetic adult species. A similar phenomenon has been suggested in *Hyalymenus* Amyot & Serville (Alydidae), in which each instar undergoes colour and size changes hypothesized to mimic various castes of an ant model (Oliveira, 1985). Documentation of immature Miridae biology and morphology, as done for several Asian myrmecomorphic species by Duwal et al. (2017), Fukuda et al. (2020) and Yasunaga and Schuh (2013), among other publications, would allow investigations of these hypotheses. Finally, in the case of predatory myrmecomorphic species, accurate visual mimicry may not be necessary for invading ant colonies and accessing prey, as seen in some myrmecomorphic staphylinid beetles (Hölldobler, 1971; Staniec et al., 2017; Zagaja et al., 2017), as ants rely not only on visual cues but also chemical signals to recognize nestmates (Sturgis & Gordon, 2012). Further investigation into the biology and chemical mimicry of myrmecomorphic Miridae could help determine whether chemical and behavioural cues contribute to the maintenance of inaccurate visual mimicry.

While it is clear from our study that phyline mirids present an intriguing system to study the evolution of myrmecomorphy in groups other than arachnids, several gaps will need to be filled to further advance this system. First, ecological and behavioural studies for plant bug species, associated ants and potential plant bug predators are critical to better understand which factors may drive myrmecomorphy in Phylinae. Second, ideally these ecological datasets would be comparative, meaning they are available for several species across a gradient from non-mimetic to accurately mimetic. And third, while our phylogeny provides solid taxon sampling and high resolution of ant-mimetic tribes, additional taxa of Hallodapini, Leucophoropterina and Pilophorini should be included in future analyses to further disentangle the evolution of mimetic accuracy. Our results support previous hypotheses regarding the evolution of phyline ant mimicry, stating that mimetic accuracy increases within a given lineage, with the

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earliest-evolving species being least mimetic (e.g., as seen in Hallodapini) (McIver & Stonedahl, 1993; Schuh, 1984). While we are unable to find full support for the perfecting hypothesis, advances in our knowledge of plant bug ecology and behaviour, including that of immatures, will allow the investigation of additional hypotheses (e.g., adaptive hypotheses and additional nonadaptive hypotheses) regarding the maintenance of inaccurate myrmecomorphy.

AUTHOR CONTRIBUTIONS

Sarah Schroeder: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation; project administration. **Veronica Tyts:** Methodology; writing – review and editing. **Rochelle Hoey-Chamberlain:** Methodology. **M. C. Fox:** Conceptualization. **Randall T. Schuh:** Writing – review and editing; resources. **Michael Forthman:** Conceptualization; writing – review and editing; supervision; funding acquisition. **Fedor V. Konstantinov:** Resources. **Anna A. Namyatova:** Writing – review and editing; resources. **Michael D. Schwartz:** Resources. **H. M. Yeshwanth:** Resources. **Katrina Menard:** Resources; writing – review and editing. **Catherine Nance:** Resources. **Wei Song Hwang:** Resources. **Christiane Weirauch:** Conceptualization; investigation; writing – review and editing; supervision; funding acquisition; project administration.

ACKNOWLEDGEMENTS

We sincerely thank all curators, collection managers and collaborators for collection efforts, access to specimens and preparation and mailing of the material provided for this study: American Museum of Natural History (Ruth Salas, Jessica Ware), Texas A&M University Insect Collection (John Oswald), California Academy of Sciences (Brian Fisher, Christopher Grinter), Zoological Institute of the Russian Academy of Sciences (Anna Namyatova and Fedor Konstantinov), Florida Department of Agriculture and Consumer Services, Division of Plant Industry (Catherine Nance), National University of Singapore, Lee Kong Chian Natural History Museum (Wei Song Hwang) and the University of Kentucky, Hymenoptera Institute Collection (Michael Sharkey). The collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia, is supported by the Ministry of Science and Higher Education of the Russian Federation grant 125012901042-9, and field trips within Russia were partially sponsored by the Ministry of Science and Higher Education of the Russian Federation grant FGEU-2025-0001. Many thanks to Greety Wuysang, David Canseco Vielma, Aleja Anderson and Caitlyn Campbell for dedicated work on specimen processing and sorting. We are grateful to Jason E. Bond for his guidance during method formulation and John Heraty for manuscript review. Finally, we acknowledge the National Science Foundation for the funding that made this work possible (NSF# DEB-2317209).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data from this study are available at NCBI BioProject (https://www.ncbi.nlm.nih.gov/) PRJNA1415893. Additional data and resources by searching the following DOI in figshare: https://doi.org/10.6084/m9.figshare.c.8676075 (Schroeder et al., 2026).

ORCID

Sarah Schroeder https://orcid.org/0009-0009-1785-8509
Veronica Tyts https://orcid.org/0000-0001-5574-5024
Rochelle Hoey-Chamberlain https://orcid.org/0000-0002-1950-6613
M. C. Fox https://orcid.org/0009-0002-9933-204X
Michael Forthman https://orcid.org/0000-0002-6987-8503
Fedor V. Konstantinov https://orcid.org/0000-0002-7013-5686
Anna A. Namyatova https://orcid.org/0000-0001-9678-3430
Wei Song Hwang https://orcid.org/0000-0003-3462-2142
Christiane Weirauch https://orcid.org/0000-0003-4492-4515

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. ASTRAL tree with local posterior probabilities.

Figure S2. Ancestral character state reconstruction of character 1 (apex pedicel width).

Figure S3. Ancestral character state reconstruction of character 2 (apex pedicel colour).

Figure S4. Ancestral character state reconstruction of character 3 (flagellomere width).

Figure S5. Ancestral character state reconstruction of character 4 (flagellomere base colour).

Figure S6. Ancestral character state reconstruction of character 5 (corium colour).

Figure S7. Ancestral character state reconstruction of character 6 (cuneus colour).

Figure S8. Ancestral character state reconstruction of character 7 (hemelytra lateral margin).

Figure S9. Ancestral character state reconstruction of character 8 (wing length).

Figure S10. Ancestral character state reconstruction of character 9 (head shape).

Figure S11. Ancestral character state reconstruction of character 10 (pronotum shape).

Figure S12. Ancestral character state reconstruction of character 11 (dorsal spine).

Data S1. Supporting information.

Data S2. Table A. Genomic and transcriptomic resources used for probe design.

Table B. The number of recovered, validated conserved loci per exemplar that are shared between four or more taxa based on the initial probe-design workflow using the Halyomorpha halys base genome. Triple and single asterisks indicate the miroid taxa selected as the base and exemplars, respectively, for the second, taxon-restricted probe-design workflow.

Table C. The number of probes per taxon in the 61,887-master probe list. Asterisks indicate the taxa selected for subsetting the master probe list for final bait set design.

Figure A. Maximum likelihood best tree from in silico extracted UCE loci. Four taxa with four asterisks were included in the Miroidea-v1-40K probe set. The numbers in parentheses correspond to the total number of UCEs (out of 5172 targeted) extracted from contigs prior to alignment (left) and those that made it into the final alignment (right). Nodes without support values had 100% ultrafast bootstrap support.

Table S1. Voucher information and NCBI BioSample accession numbers for newly sequenced material.

Table S2. NCBI accession numbers for legacy Sanger data.

Table S3. Ancestral character states coding.

Table S4. Model testing for ancestral character state reconstruction.

Table S5. Comparison of tribal relationships among phyline phylogenetic analyses.

How to cite this article: Schroeder, S., Tyts, V., Hoey-Chamberlain, R., Fox, M.C., Schuh, R.T., Forthman, M. et al. (2026) UCE-based phylogenomics traces evolution of ant-mimicry in phyline plant bugs (Hemiptera: Miridae: Phylinae). *Systematic Entomology*, 51(4), e70083. Available from: https://doi.org/10.1111/syen.70083

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