Developmental and Phylogenetic Patterns of Antennal Expansion in Leaf-Footed Bugs (Hemiptera: Coreidae)

Mariana Polli[1,a], Ummat Somjee[2,3,b], Alexandre V. Palaoro[1,c]

Correspondence:
Mariana Polli: Sala 545, Departamento de Zoologia, Setor de Ciências Biológicas, Centro Politécnico, Av. Cel. Francisco H. dos Santos, 100 - Jardim das Américas, Curitiba - PR, ZIP: 81531-980
E-mail: marianapolli12@gmail.com

[1] Universidade Federal do Paraná, Paraná State, Brazil
[2] Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama
[3] Nomis Foundation, Claridenstrasse 26, CH-8002 Zürich, Switzerland
[a] 0009-0005-0018-4561
[b] 0000-0002-5130-3605
[c] 0000-0002-8629-0728

Acknowledgements
MP thanks CNPq (process no: 164884/2025-4) for the undergraduate scholarship. AVP thanks CNPq for the research grant (process no: 407090/2025-8). The authors thanks Virginia Corral, Timothy Allen Cota, Renato Ignacio Guzman, Dennis Mayo, @miguel1958, Matias Bucat, @vsvogelaar, Joseph Richards , Marco Kunz, Lærke Haffgaard, David Kohl, Juan Sangiovanni, Pierre Lamothe, @iwo2022 and Esteban Diego Koch, by the photos posted in iNaturalist used in the paper.

Funding Statement:
MP was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) - process no: 164884/2025-4
US was supported by the NOMIS Fellowship Program at STRI.
AVP was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) - process no: 407090/2025-8
This study was supported by the NOMIS Foundation.

Conflict of interest disclosure
We declare none.

Developmental and Phylogenetic Patterns of Antennal Expansion in Leaf-Footed Bugs (Hemiptera: Coreidae)

ABSTRACT

1) Insect antennae morphology is highly conserved in many insect families, yet in some clades elaborations of antennae form are more common. Leaf-footed bugs (Hemiptera: Coreidae) are one case where there is considerable variation in antennal morphology. Antennae can be rectilinear, with cylindrical antennomeres, or have laterally flattened antennomeres, that differ in which antennomeres they occur. Strikingly, such variation is also found across development, where nymphs and adults can also display different antennal shapes. Thus, Coreidae presents an unique opportunity to study how much shared ancestry and how much development influences antennal variation.
2) We characterized the antennal expansion across a recent Coreidae phylogeny using research-grade iNaturalist photos and primary taxonomic descriptions of adults (species) and nymphs (genus). We then performed ancestral reconstructions to estimate how many transitions between antennal states occurred across the phylogeny, and compared it between adults and nymphs.
3) We found that adult antennal expansions are rare and restricted to Coreinae. The reconstructed history is consistent with repeated transitions to expanded adult antennae across Coreinae, with expansion most commonly confined to the third antennomere and concentrated in a few genera.
4) In contrast, nymphal data reveal that antennal expansions are more widespread and often occur in genera whose adults lack expansions, suggesting that conspicuous antennal morphologies can be developmentally transient and frequently lost before adulthood.
5) Together, our results indicate that adult antennal expansion is associated with nymphal expansion in the sampled genera and may reflect repeated retention or prolongation of a morphology expressed during development. Additionally, we provide a comparative framework for future work on the functional and developmental bases of exaggerated antennal forms.

Keywords: Ancestral state; Comparative methods; Morphological diversity; Nymph;

INTRODUCTION

For many insects, the antennae function as interfaces to the world which gather chemical, mechanical, and other environmental information (Elgar et al. 2018). These functions may be facilitated by the morphology of the antennae in addition to sensory structures (Donley et al. 2022; Wang et al. 2018). Thus, antennae morphology may be linked to behaviours such as host-plant searching, foraging, mate finding, communication, predator detection and navigation (Schneider, 1964; Gill et al. 2013; Elgar et al., 2018). Nymphs in many insect species may use increased surface area of modified cuticle in gliding or directed aerial descent (Zhao et al. 2024; Zeng et al. 2024). Given these diverse roles, antennae vary substantially among insects in their length, proportions, segmentation, surface structure and arrangement of sensory equipment (Dirks & Dürr, 2011; French et al. 2025; Puchalski et al. 2024). Such variation provides an opportunity to investigate how morphological traits are distributed through evolutionary history and how recurring forms may arise, persist or disappear among related lineages.

Insect antennae are composed of distinct segments (antennomeres), which act as discrete phenotypic modules. In many insect groups antennomere elaboration is not an evolutionary labile trait (Nunes et al. 2020; Pacheco et al. 2022). While multiple studies have examined the distribution of antennal sensory structures in a phylogenetic context within a group (Nihei et al. 2022; Faucheux et al. 2006; Pacheco et al. 2022; Xie et al. 2025), fewer studies examine the patterns of morphological elaboration of discrete antennal modules across species (French et al. 2025; Johnson et al. 2022). Closely related species may retain similar antennal forms because of shared ancestry (Chazot et al. 2016; Ancajima et al. 2025), whereas similar morphologies may also evolve independently when lineages experience comparable selective conditions (Trontelj et al. 2012). Conversely, conspicuous morphological modifications may be lost if their benefits change across life stages or ecological contexts (Ebenman 1992). Thus, mapping antennal morphology onto a phylogeny can reveal where shared ancestry is likely to explain the patterns observed, and where selective pressures may have modified the antenna. Such phylogenetic patterns do not, by themselves, identify the function of the antennae; however, they provide an essential first step for generating and prioritizing hypotheses about the ecological, developmental and functional processes that may underlie morphological diversity.

Leaf-footed bugs (Hemiptera: Coreidae) provide an opportunity to study the evolution of antennal variation. Coreidae are a diverse group of phytophagous heteropterans that display considerable morphological antennal variation; variation

that is sometimes used as a diagnostic character in species identification (Costa and Campos 2022; Ruckes 1955). The typical antennae have approximately cylindrical or rectilinear antennomeres (i.e., antennal segments), whereas some species have antennomeres that are laterally flattened or widened, here termed antennal expansions (Fig. 1). These expansions also differ in antennomeres in which they occur (Fig. 1). Consequently, analyzing the patterns of each antennomere type, rectilinear vs expanded, might provide additional robustness to inferences about how the underlying selective pressures or shared ancestry shaping the evolution of the trait.

Antennal expansion in Coreidae also appears to change depending on the developmental stage the individual is in. Available observations and published descriptions indicate that some nymphs bear expanded antennomeres that are absent in the corresponding adults, whereas other taxa retain conspicuous expansions after the final moult (e.g. Chacón-López et al., 2012; Brailovsky et al. 1998) and others bear rectilinear antennomeres in all development stages (e.g. Brailovsky et al 1995). For instance, in *Anisoscelis foliacea marginella*, the nymphs bear expanded antennomeres that are lost gradually at each molt, whereas in *Holhymenia clavigera*, the expansions decrease in size during growth to adulthood, but are never lost completely (Rodrigues and Moreira 2005). This developmental variation raises the possibility that adult antennal expansion may represent retention of a morphology expressed more broadly during nymphal development. Further, it also raised important questions about the evolution of these traits, since antennal expansions are recorded in multiple Coreidae nymph species in fossil record (Cumming and Tirant 2021; Cumming et al. 2024). However, we are still uncertain about how nymphal morphology influences the patterns of antennal expansions in adults. Nymphs are difficult to identify reliably to species, especially when most descriptions and identifications key only describe adults (Brailovsky 2014; Serna-Muñoz 2026), and antennal morphology may change among instars (Rodrigues and Moreira 2005), thus generating a gap in knowledge that prevents stronger inferences about antennal evolution in Coreidae. A comparative approach that considers both adults and nymphs can therefore provide a more complete view of antennal evolution in Coreidae, and explain the relationship between adults and nymphs antenna morphology.

Here, we characterized the distribution of antennal expansion across the Coreidae phylogeny using Research Grade photographs from *iNaturalist* and information from taxonomic descriptions. We first examined adult antennal morphology at the species level, scoring both the presence of expansion and the antennomeres in which expansion occurs. We then compile nymphal information at the genus level and compare the occurrence of expanded antennae between nymphs and

adults on a matched phylogenetic framework. Specifically, we asked: (1) how is antennal expansion distributed among the sampled Coreidae lineages?; (2) Has antennal expansion likely arisen repeatedly across the phylogeny?; (3) Are particular antennomeres more frequently expanded than others?; And (4) is antennal expansion more widespread during nymphal development than in adults?

If expanded adult antennae commonly represent retention of a nymphal morphology, we predicted a pattern with three outcomes: (i) lineages with expanded adults will also show expansion during nymphal development, (ii) some lineages will show expansion only in nymphs, (iii) there will be no lineages that show expansions only in the adults. By documenting these phylogenetic and developmental patterns, our study provides a broad comparative basis for future work on the developmental mechanisms and functional consequences of antennal expansion in leaf-footed bugs. In particular, the patterns identified here can guide targeted studies testing whether expanded antennomeres differ in sensillar composition, sensory performance, mechanical properties, visual signalling or other ecological functions.

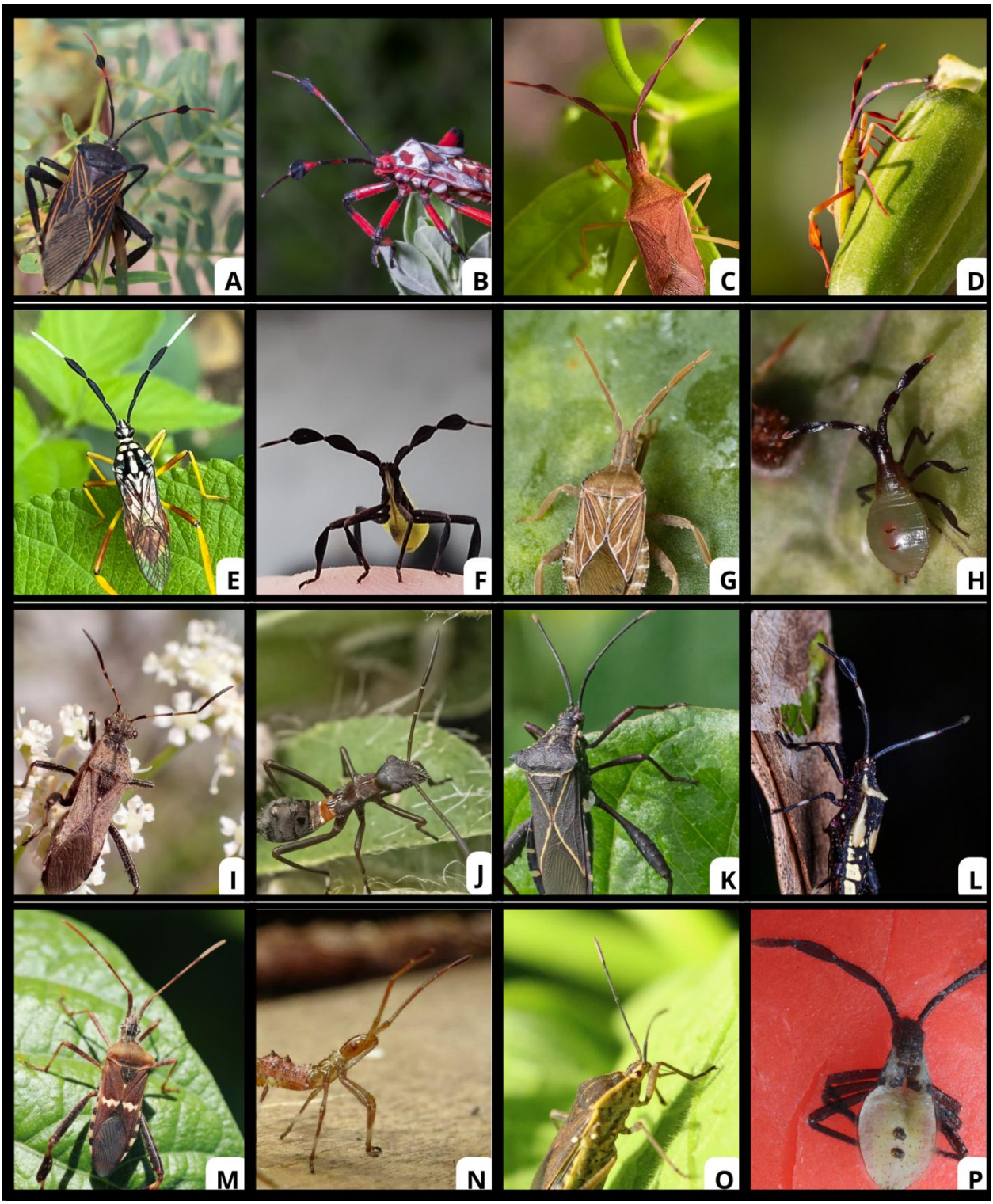

Figure 1: Antennae variation among species. A) *Pachylis neocalifornicus* by Virginia Corral (@letebile) in *iNaturalist*. B) Nymph of *Pachylis sp.* by Timothy Allen Cota (@timothycota). C) *Chondrocera laticornis* by Renato Ignacio Guzman (@renatoguzman). D) Nymph of *Chondrocera sp.* by Dennis Mayo (@dmayo77). E) *Holhymenia histrio* by @miguel1958. F) Nymph of *Holhymenia sp.* by Matias Bucat (@matias_bucat). G) *Chelinidea tabulata* by @vsvogelaar. H) Nymph of

Chelinidea sp. by Joseph Richards (@jrich_tx). I) *Alydus calcaratus* by Marco Kunz (@lausannois). J) Nymph of *Alydus sp.* by Lærke Haffgaard (@alauda_crispus). K) *Acanthocerus cruciger* provided by David Kohl (@djhiker). L) Nymph of *Acanthocerus sp.* by Juan Sangiovanni (@jsangiovanni). M) *Leptoglossus clypealis* by Pierre Lamothe (@pierlamothe). N) Nymph of *Leptoglossus sp.* by @iwo2022 O) *Anasa trilineata* by Esteban Diego Koch (@esteban_koch). All by *iNaturalist* (CC-NC BY 4.0) P) Nymph of *Anasa trilineata*.

METHODS

Phylogeny and Antennae Categorization

To search for antennal morphology, we searched data of nymphs and adults of all the species present in the phylogeny (Forthman et al. 2024), using two approaches. First, we searched each species by Genus and species in *iNaturalist*. When matches were found, we examined how many records showed similar individuals, and if antennae morphology was consistent across the records. For each species, we selected one photograph meeting *iNaturalist*'s 'research grade' standard with completely visible antennae. When we encountered: (i) inconsistencies in antennal morphology within species; (ii) images lacking entirely visible antennae; (iii) absence of *iNaturalist* observations; or (iv) taxonomic uncertainty in image identifications, we searched for the species taxonomical description using the Coreoidea Species File (Coreoidea Species File Online, 2025), and used information therein to categorize antennal morphology. This classification procedure was conducted independently for adults and nymphs. All data, classifications, images, and reference links were archived on GitHub (see Data Accessibility section).

We classified antennae as either 'rectilinear' or 'expanded', as this was a reliable categorization that could be made with high confidence, and is also present in taxonomic descriptions (e.g., Costa & Campos 2022; Ruckes 1955; Schuh & Slater 1995). If the antenna had a constant radial shape across all antennomeres, we classified it as rectilinear (Fig. 1I, J, K, M, O). Species that had one or more antennomere with any other shape were classified as expanded (Fig. 1A, B, C, D,E, F, G, H, L, P). For the species we did not find reference images nor descriptions reporting the antennomere shape, and tips identified at genus level (e.g., "*Cloresmus* sp."), we classified them as "*no data*" and removed them from the final reconstruction. We also annotated in which antennomere the expansion was present.

Since identifying nymphs to the species level is not reliable, especially when using photographs, we only identified nymphs to the genus level. However, there were a few species in which we were certain about the identification, either because we raised the species ourselves (*Anasa trilineata*, *Zicca annulata*), or because of taxonomic descriptions of development (e.g. Alarcón & Cazorla 2020). Because of this, we could confirm the presence and absence of antennal expansions in some genera. With this

information in addition to *iNaturalist* data, we could find some variation in the presence of antennal expansions and in which antennomere the expansion was present. In these cases, we kept the species terminals in the phylogeny to ensure we encompassed known variation to our dataset. Further, antennal expansion can change throughout the nymphal stages. Thus, we used the lowest instar recorded for the genus and annotated that information in the spreadsheet. To compare the nymphal evolutionary tree with the species-level evolutionary tree of the adults, we also collapsed the adult tree at the genus level, with the same species terminals of the nymphs tree.

Antennal shape evolution

To assess the evolutionary history of antennal expansions, we divided our analyses in two parts. First, we assessed the evolutionary history of antennal expansion in the species-level tree for adults. Our goal with this analysis was to answer if antennal expansions present repeated evolution across the phylogeny or are present only in a few taxa, and which antennomere is more likely to be expanded in adults. Second, we assessed the evolutionary history of antennal expansion in the genus-level tree for nymphs and adults. With these analyses, our goal was to test if evolutionary history differed between nymphs and adults, in which developmental stage expansions were more frequent, and the correspondence between nymphs and adults, i.e., if lineages only presented expansion if it was present in nymphs.

To implement these analyses, we coded each antennomere as either rectilinear (1) or expanded (2). We did not categorize the fourth antennomere because it did not vary among species. We then summed the three antennomeres to have an index of expansion: 3 if there were no antennomeres expanded, 4 if only one antennomere was expanded, 5 if two antennomeres were expanded, and 6 if all were expanded. Because expansion followed a nested pattern in our dataset—antennomere III was expanded whenever any expansion was present, antennomere II was added when two segments were expanded, and antennomere I only when all three were expanded—the number of expanded antennomeres uniquely represented the observed combinations of expanded segments. Thus, we had four character states that could transition among themselves. Using Mk models, we estimated two types of transition matrices, one in which all transition rates were equal (*equal rates,* ER), and another in which all transition rates were different (*all rates differ*, ARD). We also used the *hidden states* model to test if there was more than one evolutionary rate along the phylogeny. The models were the same as before, ER and ARD. Both were implemented using the *phytools* package (Revell 2024). To test which one of the models best described antennal evolution, we compared them using Akaike's Information Criterion (AIC). We chose the model with the smallest AIC as the best and,

when the differences were less than two AIC units, we picked the one with the lowest degrees of freedom. Lastly, we also used two types of root ancestral state: 'equal', where all states are considered as equally likely; and 'fitzjohn' where the ancestral state is estimated as a nuisance parameter along with the data. In case both root states were equally likely, we opted for the 'fitzjohn' root estimation. After the best model was chosen, we used the function "*make.simmap()*" in *phytools* with 1,000 simulations to calculate the number of transitions and the total time the tree spent in each state.

RESULTS

Species-level tree - Adults

We found reliable information for 174 Coreidae species. We found that 161 (92.53%) have rectilinear antennae and 13 (7.47%) have at least one antennomere expanded antennae (Figure 2). The most common case was only one antennomere expanded (8 species), always the third antennomere; two and three antennomeres expanded were more rarely recorded (3 and 2 species, respectively). All species exhibiting antennal expansions belonged to subfamily Coreinae, and antennae expansions appeared at least four times independently across Coreinae. Intriguingly, there are no higher-level lineages where all species present the antennal expansion. Instead, it seems that the presence of expansion is tied to specific genera, where it is concentrated among sampled species. For example, *Pachylis* shows antennomere expansions in all of the 17 described species, also being used as a species diagnostic trait (Costa and Campos 2022). *Chelinidea* and *Chariesterus* follow a similar pattern, where expansions are present in all species of the genus (Hamlin 1924; Ruckes 1955). Therefore, it seems that shared ancestry plays a role in the presence of antennal expansion, but only at the genus level.

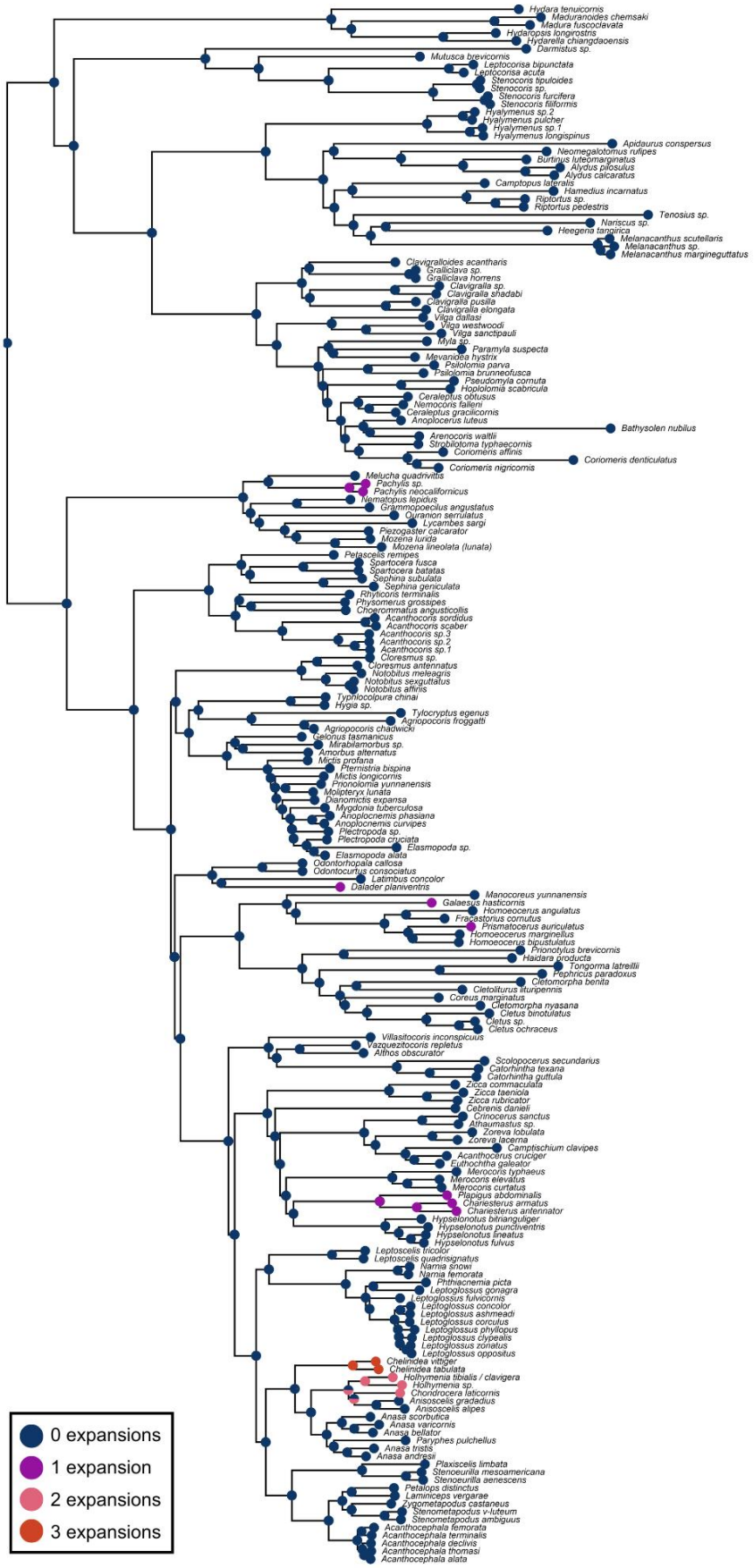
Hydara tenuicornis
Maduranoides chemsaki
Madura fuscoclavata
Hydaropsis longirostris
Hydarella changdaoensis
Darmistus sp.
Mutusca brevicornis
Leptocorisa bipunctata
Leptocorisa acuta
Stenocoris tpuloides
Stenocoris sp.
Stenocoris furcifera
Stenocoris filiformis
Hyalymenus sp.2
Hyalymenus pulcher
Hyalymenus sp.1
Hyalymenus longispinus
Apidaurus conspersus
Neomegalotomus rufipes
Burtinus luteomarginatus
Alydus pilosulus
Alydus calcaratus
Camptopus lateralis
Hamedius incarnatus
Riptortus sp.
Riptortus pedestris
Tenosius sp.
Neriscus sp.
Heegena tangirica
Melanacanthus scutellaris
Melanacanthus sp.
Melanacanthus margineguttatus
Clavigralloides acantharis
Gralliclava sp.
Gralliclava horrens
Clavigralla sp.
Clavigralla shadabi
Clavigralla pusilla
Clavigralla elongata
Vilga dallasi
Vilga westwoodi
Vilga sanctipauli
Myla sp.
Paramyla suspecta
Mevaniosa hystrix
Psilolomia parva
Psilolomia brunneofusca
Pseudomyla cornuta
Hoplolomia scabricula
Ceraleptus obtusus
Nemocoris fallenii
Ceraleptus gracilicornis
Anoplocerus luteus
Bathysolen nubilus
Arenocoris waltlii
Strobilotoma typhaecornis
Coriomeris affinis
Coriomeris denticulatus
Coriomeris nigricornis
Melucha quadrivittis
Pachylis sp.
Pachylis neocalifornicus
Nematopus lepidus
Grammopoecilus angustatus
Quranion serrulatus
Lycambes sargi
Piezogaster calcarator
Mozena lurida
Mozena lineolata (lunata)
Petascelis remipes
Spartocera fusca
Spartocera batatas
Sephina subulata
Sephina geniculata
Rhytiocoris terminalis
Physomerus grossipes
Choerommatus angusticollis
Acanthocoris sordidus
Acanthocoris scaber
Acanthocoris sp.3
Acanthocoris sp.2
Acanthocoris sp.1
Cloresmus sp.
Cloresmus atternatus
Notobitus meleagris
Notobitus sexguttatus
Notobitus affinis
Typhlocolpura chinai
Hygia sp.
Tylocryptus egenus
Agriopocoris froggatti
Agriopocoris chadwicki
Gelonus tasmanicus
Mirabiamorbus sp.
Amorbus alternatus
Mictis profana
Pternistria bispina
Mictis longicornis
Prionolomia yunnanensis
Moliterya lunata
Diaromictis expansa
Mygdonia tuberculosa
Anoplocnemis phasiana
Anoplocnemis curvipes
Plectropoda sp.
Plectropoda cruciata
Elasmopoda sp.
Elasmopoda alata
Odontorhopala callosa
Odontocuritus consociatus
Latimbus concolor
Dalader planiventris
Manocoreus yunnanensis
Galaesus hasticornis
Homoeocerus angulatus
Fracastorius cornutus
Prismatocerus auriculatus
Homoeocerus marginellus
Homoeocerus bipustulatus
Prionotylus brevicornis
Haidara producta
Tongorma latreillii
Pephricus paradoxus
Cletomorpha benita
Cletoliturus lituripennis
Coreus marginatus
Cletomorpha nyasana
Cletus binotulatus
Cletus sp.
Cletus ochraceus
Villasitocoris inconspicuus
Vazquezitocoris repletus
Althos obscurator
Scolopocerus secundarius
Catorhintha texana
Catorhintha guttula
Zicca commaculata
Zicca taeniola
Zicca rubricator
Cebrenis danieli
Crinocerus sanctus
Athaumastus sp.
Zoreva lobulata
Zoreva lacerna
Camptschium clavipes
Acanthocerus cruciger
Euthochtha galeator
Merocoris typhaeus
Merocoris elevatus
Merocoris curtatus
Plagiops abdominalis
Chariesterus armatus
Chariesterus antennator
Hyselonotus bitriangulger
Hyselonotus punctiventris
Hyselonotus lineatus
Hyselonotus fulvus
Leptoscelis tricolor
Leptoscelis quadrisignatus
Narnia showi
Narnia femorata
Phthiacnemia picta
Leptoglossus gonagra
Leptoglossus fulvicornis
Leptoglossus concolor
Leptoglossus ashmeadi
Leptoglossus corculus
Leptoglossus phyllopus
Leptoglossus clypealis
Leptoglossus zonatus
Leptoglossus oppositus
Chelinidea vittiger
Chelinidea tabulata
Holhymenia tibialis / clavigera
Holhymenia sp.
Chondrocera laticornis
Anisoscelis gradadius
Anisoscelis alipes
Anasa scorbutica
Anasa varicornis
Anasa bellator
Paryphes pulchellus
Anasa tristis
Anasa andresii
Plaxiscelis limbata
Stenoeurilla mesoamericana
Stenoeurilla senescens
Petalops distinctus
Laminiceps vergarae
Zygometapodus castaneus
Stenometapodus v-luteum
Stenometapodus ambiguus
Acanthocephala femorata
Acanthocephala terminalis
Acanthocephala declivis
Acanthocephala thomasi
Acanthocephala alata
0 expansions
1 expansion
2 expansions
3 expansions

Figure 2: Coreidae phylogeny (based on Forthmann et al. 2024) of adults at species level showing the number of antennomere expanded across the evolutionary history of the group. Blue denotes a "rectilinear" antenna, purple denotes an antenna with 1 antennomere expanded, pink with 2 antennomere expanded, and orange with three antennomere expanded. Pie charts in the nodes denote the ancestral state reconstruction.

The most likely ancestral state of Coreidae is a rectilinear antennae in adults. Our analyses show that the evolutionary transition model with the greatest support was the equal rates model (ER; Table S1;). There were approximately 8 transitions among the number of expansions, in which transitions from no expansions to one expansion were far more common than the others (4.96 transitions versus 1.5 transitions from zero to two, and 1.05 transitions from zero to three expansions). Rectilinear antennae also encompassed most of the total phylogenetic branch length (96.45%).

Genera-level tree - Nymphs and Adults

We found that the nymphal stages of most genera have some degree of expansion in their antennomere (Figure 3). Out of 87 genus analyzed (with a few exceptions, see Methods), 59 (67.82%) have a rectilinear antenna and 28 (32.18%) have at least one antennomere expanded. The most common case was only one antennomere expanded (12 genus), always the third antennomere; followed by two antennomeres expanded (10 genus) and the less common case was three antennomeres expanded (6 genus). Differently from what we found for the species-level tree for adults, we found one genus out of Coreinae with an expanded antenna (*Clavigralla* sp.) belonging to Pseudophloeinae, where the nymphal stage shows antennal expansion but the adult does not. However, all other genera that had expansions were within Coreinae. We also found multiple tribes where all genera had nymphal stages with antennal expansion (e.g., Acanthocerini, Merocorini), while other tribes showed variation. For adults, the pattern was maintained, with only a few genera showing expanded antennae. Both in nymphs and adults the antennomeres showed the same pattern of expansions. When it was present, the expansions were always present in the third antennomere. When more than one antennomere was expanded, only the second antennomere was expanded. The first antennomere was only expanded if all three antennomeres were expanded. Our results also showed that 19 genera in the matched dataset had recorded antennal expansion during at least one nymphal stage but rectilinear as adults (Figure 3). Therefore, nymphal stages do show more variation than adults in Coreidae and the only lineages where adults show expansions are lineages where nymphs also show them.

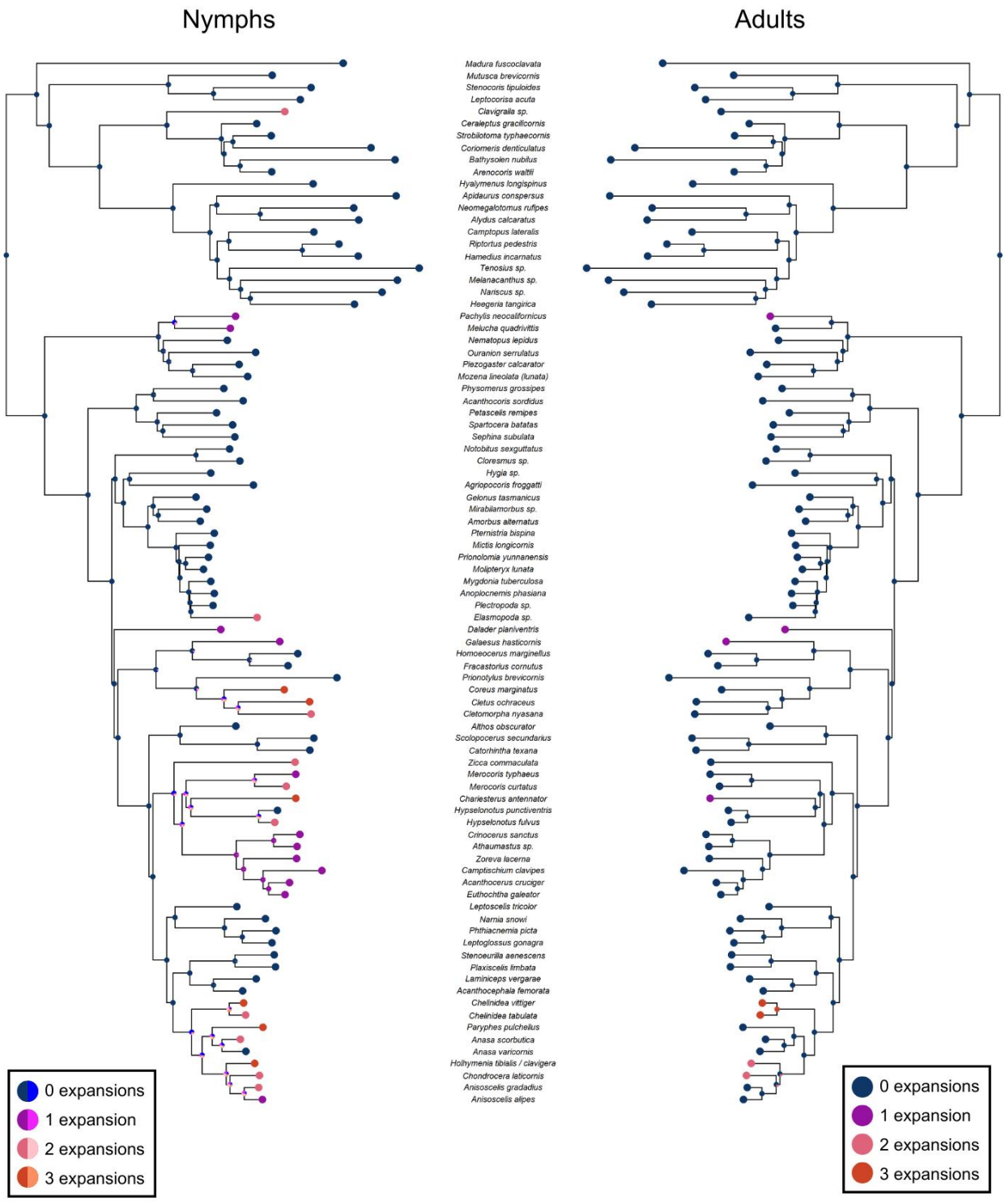

Figure 3: Comparison between Coreidae phylogenies (based on Forthmann et al. 2024) of Nymphs (on the left) and Adults (on the right) at the genus level. In both phylogenies blue denotes rectilinear antenna (i.e. 0 antennomeres expanded), purple denotes 1 antennomere expanded, pink denotes 2 antennomeres expanded, and orange denotes 3 antennomeres expanded. On Nymphal reconstruction lighter colors means a different evolutionary rates in the

trait based on the hidden rates model. Pie charts in the nodes denote the ancestral state reconstruction.

The equal rates model with hidden rates showed the strongest support for nymphs (HRM-ER; Table S2) and equal rates without hidden rates for adults (ER; Table S3). Nymphs showed 23 transitions between the number of antennomeres expanded (against only 8 in adults), while spending 79.52% of total phylogenetic branch length as rectilinear, 7.90% with one expansion, 8.26% with two expansions and 4.32% with three expansions. The most common transition occurred between zero expansions to two antennomeres expanded (5.09 transitions), while zero expansions to one antennomere expanded was similarly common (4.21 transitions), and two antennomeres expanded to three antennomeres expanded (3.06 transitions) and no expansions to three antennomeres expanded (2.36 transitions) were the rarest.

DISCUSSION

We investigated how antennal expansion is distributed across the Coreidae phylogeny, whether expanded antennae have arisen repeatedly, whether expansion is concentrated in particular antennomeres, and whether its occurrence differs between nymphs and adults. Our results show that expanded antennae are uncommon among adults and, in the sampled phylogeny, are restricted to Coreinae; nevertheless, their distribution is consistent with multiple independent occurrences rather than a single origin within the subfamily. By incorporating antennomere-specific information and a genus-level comparison of nymphs and adults, we further found that expansion is more widespread and morphologically variable during nymphal development. Most importantly, all genera with expanded antenna in adults in the matched dataset also showed antennal expansion during at least one observed nymphal stage, whereas several genera showed expansion only during the nymphal stages. These patterns indicate that adult antennal diversity should be interpreted in a developmental context and motivate future tests of the ecological conditions associated with retention of expansion into adulthood.

Our results suggest that the adult pattern of antennal expansion may be linked to developmental variation during the nymphal stages. The occurrence of expanded antennae in all genera with expanded adults, together with the presence of nymphal expansions in several genera whose adults have rectilinear antennae, is consistent with the interpretation that adult expansion may represent retention of a morphology expressed earlier in ontogeny. Available ontogenetic series in Coreidae further indicate that antennal expansions can decrease in relative size during development, either disappearing before adulthood or persisting as comparatively smaller expansions in

adults (Rodrigues and Moreira 2005). Thus, differences in the timing or extent of antennal expansion reduction across moults can contribute to the diversity of antennal expansions in adults. Under this hypothesis, the repeated transitions to expanded antennae inferred for adults may reflect repeated evolutionary retention or prolongation of a morphology expressed during nymphal development, rather than repeated *de novo* evolution of the developmental capacity to produce antennal expansion. If at least some developmental processes that produce antennal expansion early in ontogeny are shared across Coreidae, evolutionary changes that reduce, maintain, or prolong this condition could generate the observed combination of phylogenetic clustering within some genera and independent occurrences among more distant lineages. Such a mechanism would make adult expansion evolutionarily labile because relatively small changes in the developmental trajectory of an existing structure could produce conspicuous morphological differences among species. This interpretation remains speculative because little is known about the developmental basis of antennal growth and remodelling in true bugs (but see Deng et al. 2026 for other insects). Yet, recent studies in moths have revealed a distinct role of patterning genes such as *aristaless* in the evolution of diverse antennal morphologies (Ando et al. 2018). Nevertheless, it provides a testable hypothesis for the developmental origin of adult antennal expansion in Coreidae.

Adult antennal expansions were recorded only in Coreinae in our sampled phylogeny, although we identified an expanded nymphal antenna outside this subfamily in *Clavigralla* (Pseudophloeinae). This adult pattern raises the question of whether features of Coreinae ecology or development have favoured the retention of expansions after the final moult. Schaefer and Mitchell (1983), in their seminal review, found no single, clear pattern of food-plant association across Coreinae, in contrast to the more characteristic associations reported for other coreid subfamilies. However, host use within Coreinae is highly variable, ranging from restricted to broad diets . Thus, rather than implying that all Coreinae occupy more variable environments, the ecological diversity of the subfamily may provide a useful context in which to investigate whether adult antennal expansion is associated with host breadth, host-plant structure, microhabitat, or other ecological variables.

One possible explanation is that expanded antennomeres alter sensory performance. Expansion may increase the external surface available for sensory structures, potentially affecting the number, distribution, or types of sensilla; however, external enlargement alone does not demonstrate greater sensory sensitivity. This hypothesis is especially relevant because the broader occurrence of expansion in nymphs may indicate that antennal morphology is important before adulthood, when

individuals must locate suitable feeding sites and respond to local environmental cues with less mobility than adults. Adult retention could then be favoured in lineages in which a modified antenna continues to provide an advantage during dispersal, host finding, mate location, or other adult behaviours. Testing this explanation will require comparative analyses of sensillum density, sensillum types, antennal surface area, and behavioural or electrophysiological responses in species with expanded and rectilinear antennae.

A second, non-exclusive hypothesis is that expanded antennae influence interactions with predators. For example, a conspicuous or laterally expanded appendage could potentially alter the apparent outline of the insect, divert an attack away from the body, or contribute to crypsis or warning display. This is especially relevant for nymphs, which stay close to the host-plant and might be able to regenerate missing antennae (Maginnis 2008; Emberts et al. 2016). However, there is currently no evidence that expanded antennae function as sacrificial targets in Coreidae. Experiments using predator attacks on nymphs and adults, together with observations of antennal damage, survival, and regeneration across moults, would be required to evaluate whether antennae provide a defensive benefit. More broadly, comparing expanded and rectilinear antennae across ecological settings will be necessary to determine whether similar external morphologies serve a common function or represent distinct evolutionary solutions in different Coreinae lineages. Alternatively, recent studies suggest an important role of cuticular expansions, especially those of the limbs but also including those of the antennae, in directed aerial descent, or gliding in hemipteran nymphs (Zeng et al. 2024; Zhao et al. 2024). This function in gliding in nymphs, which is not necessary for flighted adults, may explain the higher occurrence of this morphology in nymphs relative to adults. However, whether antennal expansions have a comparable role in Coreidae remains unknown, but provide an alternative functional hypothesis for the greater occurrence of expansion in nymphs.

We emphasize the only one record of antennal expansions in nymphs out of Coreinae as a possible lack of records of younger nymphs (i.e. younger than fifth instar). The disappearance of the trait in later nymphal stages can be a tricky problem, mainly because nymphs of fifth instar are more often identified at genus or species level, which hinders taxonomical identifications of younger nymphs on *iNaturalist*. Our results suggest increased attention to understanding the role that these antennal expansions play at nymphal stages in this group, and raises the question of why antennal expansion was retained in adults only in some species of Coreinae.

In conclusion, antennal expansion in Coreidae appears to be a developmentally dynamic trait whose adult expression may result, at least in part, from the retention of a

morphology that is more broadly expressed during nymphal development. The repeated occurrence of expanded adults within Coreinae, together with phylogenetic clustering within some genera, is consistent with evolutionary changes in developmental trajectories rather than with repeated origin of entirely novel adult structures. At present, the function of these expansions remains unresolved: they may influence sensory performance, predator interactions, communication, or multiple functions that differ among lineages and life stages. By documenting the phylogenetic, antennomere-level and ontogenetic distribution of expansion, our study provides a comparative framework for future work integrating developmental series, antennal ultrastructure, sensory physiology, behaviour and ecology to determine why some lineages retain expanded antennae as adults whereas others do not.

REFERENCES

ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R." _Bioinformatics_, *35*, 526-528. doi:10.1093/bioinformatics/bty633

Alarcón, Maritza, and Dalmiro Cazorla. 2020. DESCRIPCIÓN DE LOS ESTADIOS INMADUROS Y CICLO DE VIDA DE ANISOSCELIS (BITTA) HYMENIPHERUS WESTWOOD, 1840 (HETEROPTERA: COREIDAE: COREINAE: ANISOSCELINI).

Ancajima, Georgette Paola, Igor Eloi, and Marcelo Duarte. 2025. "Sexual Dimorphism and Allometric Patterns in Hawkmoth Epiphyses (Lepidoptera: Sphingidae)." Scientific Reports 15 (1): 11405. https://doi.org/10.1038/s41598-025-86837-8.

Ando, Toshiya, Haruhiko Fujiwara, and Tetsuya Kojima. 2018. "The Pivotal Role of Aristaless in Development and Evolution of Diverse Antennal Morphologies in Moths and Butterflies." *BMC Evolutionary Biology* 18 (1): 8. https://doi.org/10.1186/s12862-018-1124-2.

Brailovsky, Harry. 2014. "Illustrated Key for Identification of the Species Included in the Genus Leptoglossus (Hemiptera: Heteroptera: Coreidae: Coreinae: Anisoscelini), and Descriptions of Five New Species and New Synonyms." Zootaxa 3794 (1). https://doi.org/10.11646/zootaxa.3794.1.7.

Brailovsky Harry, Guillermina Ortega León, Cristina Mayorga and Ernesto Barrera. 1998. “Estadios ninfales de los coreidos del Valle de Tehuacán, Puebla, México (Hemiptera-Heteroptera). III. Anasa ruficornis y Scolopocerus uhleri”. Anales del Instituto de Biología, UNAM (Serie Zoología).69 (1): 53-64. https://anales.ib.unam.mx/index.php/SerZool/article/view/2568

Brailovsky, Harry, Cristina Mayorga, Guillermina Ortega León and Ernesto Barrera. 1995. “Estadios ninfales de los coreidos del Valle de Tehuacán, Puebla, México (Hemiptera-Heteroptera) 11. especies asociadas a huizacheras (Acacia spp.) y mezquiteras (Prosopis spp.): Mozena lunata, Pachylis hector, Savius jurgiosus jurgiosus y Thasus gigas". Anales del Instituto de Biología, UNAM (Serie Zoología). 66(1): 57-80. https://anales.ib.unam.mx/index.php/SerZool/article/view/2426

Chacón-López, Adriana, Marcela Briceño-Baez, and Luis Cervantes-Peredo. 2012. “Ciclo de vida de Anasa litigiosa (Hemiptera: Heteroptera: Coreidae).” *Revista Mexicana de Biodiversidad* 83 (2). https://doi.org/10.22201/ib.20078706e.2012.2.935.

Chazot, Nicolas, Stephen Panara, Nicolas Zilbermann, et al. 2016. “Morpho Morphometrics: Shared Ancestry and Selection Drive the Evolution of Wing Size and Shape in Morpho Butterflies: MORPHO MORPHOMETRICS.” Evolution 70 (1): 181–94. https://doi.org/10.1111/evo.12842.

Coreoidea Species File Online. Version 5.0/5.0. 2025. “CoreoideaSF Team.” http://Coreoidea.SpeciesFile.org.

Cumming, Royce T., Stéphane Le Tirant, and Huarong Chen. 2024. *An Additional Cretaceous Ferriantenna Cumming & Le Tirant, 2021 Species with Wildly Exaggerated Antennae (Hemiptera, Coreidae)*. 1–6. 1-6. https://doi.org/10.57800/FAUNITAXYS-12(5).

Cumming, Royce T., and Stephane Le Tirant. 2021. “Drawing the Excalibur Bug from the Stone: Adding Credibility to the Double-Edged Sword Hypothesis of

Coreid Evolution (Hemiptera, Coreidae)." *ZooKeys* 1043 (June): 117–31. https://doi.org/10.3897/zookeys.1043.67730.

Costa, Wanessa S., and Luiz A. Campos. 2022. "Phylogeny of Pachylis Lepeletier & Serville, 1825 (Hemiptera, Coreidae, Coreinae) with Thasus Stål, 1865 as a New Synonym, and the Redescription of Pachylis Laticornis (Fabricius, 1798)." *Zoosystema* 44 (21). https://doi.org/10.5252/zoosystema2022v44a21.

Deng, Yuping, Zhiping Xing, Tao Lu, Hui Dong, Zhipeng Li, and Bo Hu. 2026. "BmAHR Regulates Antennal Development and Olfactory Gene Expression to Control Mating Behavior in Bombyx Mori." Insect Biochemistry and Molecular Biology 192 (July): 104584. https://doi.org/10.1016/j.ibmb.2026.104584.

Dirks, Jan-Henning, and Volker Dürr. 2011. "Biomechanics of the Stick Insect Antenna: Damping Properties and Structural Correlates of the Cuticle." *Journal of the Mechanical Behavior of Biomedical Materials* 4 (8): 2031–42. https://doi.org/10.1016/j.jmbbm.2011.07.002.

Donley, Griffin, Yueming Sun, Günther Pass, et al. 2022. "Insect Antennae: Coupling Blood Pressure with Cuticle Deformation to Control Movement." Acta Biomaterialia 147 (July): 102–19. https://doi.org/10.1016/j.actbio.2022.05.044.

Ebenman, Bo. 1992. "Evolution in Organisms That Change Their Niches during the Life Cycle." The American Naturalist 139 (5): 990–1021. https://doi.org/10.1086/285370.

Elgar, Mark A, Dong Zhang, Qike Wang, et al. 2018. *Insect Antennal Morphology: The Evolution of Diverse Solutions to Odorant Perception*.

Emberts, Zachary, Colette M. St. Mary, and Christine W. Miller. 2016. "Coreidae (Insecta: Hemiptera) Limb Loss and Autotomy." Annals of the Entomological Society of America 109 (5): 678–83. https://doi.org/10.1093/aesa/saw037.

Faucheux, Michel J., Niels P. Kristensen, and Shen-Horn Yen. 2006. "The Antennae of Neopseustid Moths: Morphology and Phylogenetic Implications, with

Special Reference to the Sensilla (Insecta, Lepidoptera, Neopseustidae)." *Zoologischer Anzeiger - A Journal of Comparative Zoology* 245 (2): 131–42. https://doi.org/10.1016/j.jcz.2006.05.004.

French, Rowan L. K., Magdalena Kowalewska Groszkowska, Locke Rowe, D. Luke Mahler, and Lech Karpiński. 2025. "Why the Long 'Horns'? Fine-Scale Morphology Suggests Tactile Demands Contributed to the Exaggeration of Male Longhorned Beetle Antennae (Coleoptera: Cerambycidae)." Ecology and Evolution 15 (5): e71380. https://doi.org/10.1002/ece3.71380.

Forthman, Michael, Hannah Phan, Christine W Miller, and Rebecca T Kimball. 2024. "Phylogenetic Placement of the Leaf-Footed Bug Tribes Agriopocorini, Amorbini, and Manocoreini (Heteroptera: Coreidae) Using Ultraconserved Elements." *Zoological Journal of the Linnean Society* 202 (3): zlae024. https://doi.org/10.1093/zoolinnean/zlae024.

Gill, Katherine P., Ellen Van Wilgenburg, David L. Macmillan, and Mark A. Elgar. 2013. "Density of Antennal Sensilla Influences Efficacy of Communication in a Social Insect." *The American Naturalist* 182 (6): 834–40. https://doi.org/10.1086/673712.

Hamlin, John C. 1924. "A Review of the Genus Chelinidea (Hemiptera-Heteroptera) with Biological Data.*." Annals of the Entomological Society of America 17 (2): 193–208. https://doi.org/10.1093/aesa/17.2.193.

Johnson, Tamara L., Mark A. Elgar, and Matthew R. E. Symonds. 2022. "Movement and Olfactory Signals: Sexually Dimorphic Antennae and Female Flightlessness in Moths." *Frontiers in Ecology and Evolution* 10 (August): 919093. https://doi.org/10.3389/fevo.2022.919093.

Maginnis, Tara Lynne. 2008. "Autotomy in a Stick Insect (Insecta: Phasmida): Predation Versus Molting." Florida Entomologist 91 (1): 126–27. https://doi.org/10.1653/0015-4040(2008)091%255B0126:AIASII%255D2.0.CO;2.

548 Nihei, Silvio S., Genting Liu, Qike Wang, et al. 2022. "Comparative Morphology of
549 Antennal Ultrastructure in Tachinidae Parasitoid Flies (Diptera): The
550 Phylogenetic Importance of Antennal Sensilla." *Arthropod Structure &*
551 *Development* 71 (November): 101202. https://doi.org/10.1016/j.asd.2022.101202.

552 Nunes, V. C. S., P. M. Souto, A. Minelli, K. F. Stanger-Hall, and L. F. L. Silveira. 2020.
553 "Antennomere Numbers in Fireflies (Coleoptera: Lampyridae): Unique
554 Patterns and Tentative Explanations." *Zoologischer Anzeiger* 286 (May): 1–10.
555 https://doi.org/10.1016/j.jcz.2020.02.006.

556 Pacheco, Thaynara L., Claudia Bohacz, Alberto Ballerio, Paul Schoolmeesters, and
557 Dirk Ahrens. 2022. "Revisiting Trends in Morphology of Antennal Sensilla in
558 Scarabaeoid Beetles." *Zoomorphology* 141 (3–4): 315–26.
559 https://doi.org/10.1007/s00435-022-00565-5.

560 phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and
561 other things). PeerJ, 12, e16505.

562 Puchalski, Adam, Zoë McCarthy, Alexandre Varaschin Palaoro, et al. 2024.
563 "Flexural Rigidity of Hawkmoth Antennae Depends on the Bending Direction."
564 Acta Biomaterialia 184 (August): 273–85.
565 https://doi.org/10.1016/j.actbio.2024.06.036.

566 R: A Language and Environment for Statistical Computing_. R Foundation for
567 Statistical Computing, Vienna, Austria. https://www.R-project.org/

568 Revell, Liam J. 2024. "Phytools 2.0: An Updated R Ecosystem for Phylogenetic
569 Comparative Methods (and Other Things)." PeerJ 12: e16505.
570 https://doi.org/10.7717/peerj.16505.

571 Rodrigues, Daniela, and Gilson R. P. Moreira. 2005. "Comparative Description of
572 the Immature Stages of Two Very Similar Leaf Footed Bugs, Holymenia
573 Clavigera (Herbst) and Anisoscelis Foliacea Marginella (Dallas) (Hemiptera,
574 Coreidae, Anisoscelini)." Revista Brasileira de Entomologia 49 (1): 7–14.
575 https://doi.org/10.1590/S0085-56262005000100003.

Ruckes, Herbert. 1955. “The Genus Chlzriesterus de Laporte (Heteroptera, Coreidae).” AMERICAN MUSEUM NOVITATES.

Schaefer, Carl W., and Paula Levin Mitchell. 1983. “Food Plants of the Coreoidea (Hemiptera: Heteroptera).” Annals of the Entomological Society of America 76 (4): 591–615. https://doi.org/10.1093/aesa/76.4.591.

Schuh, Randall T., and James A. Slater. 1995. CLASSIFICATION AND NATURAL HISTORY.

Serna-Muñoz, Sebastian. 2026. “Neotropical Leaf-Footed Bugs (Hemiptera, Coreidae): New Taxa, Synonym and Distributional Notes.” Papéis Avulsos de Zoologia 66 (April): e202666016. https://doi.org/10.11606/1807-0205/2026.66.016.

Schneider, Dietrich. 1964. “Insect Antennae.” *Annual Review of Entomology* 9 (Volume 9, 1964): 103–22. https://doi.org/10.1146/annurev.en.09.010164.000535.

Trontelj, Peter, Andrej Blejec, and Cene Fišer. 2012. “ECOMORPHOLOGICAL CONVERGENCE OF CAVE COMMUNITIES: CONVERGENCE OF CAVE COMMUNITIES.” Evolution 66 (12): 3852–65. https://doi.org/10.1111/j.1558-5646.2012.01734.x.

Wang, Qike, Yidan Shang, Douglas S. Hilton, Kiao Inthavong, Dong Zhang, and Mark A. Elgar. 2018. “Antennal Scales Improve Signal Detection Efficiency in Moths.” Proceedings of the Royal Society B: Biological Sciences 285 (1874): 20172832. https://doi.org/10.1098/rspb.2017.2832.

Xie, Jinting, Yi Liu, Junjue Li, Leming Zhou, Xiu Xu, and Zhende Yang. 2025. “Comparison of Morphological Characteristics of Antennae and Antennal Sensilla Among Three Species of Gall Wasps (Hymenoptera: Eulophidae).” *Insects* 16 (9): 976. https://doi.org/10.3390/insects16090976.

Zeng, Yu, Grisanu Naing, Vivian Lu, Yuexiang Chen, and Robert Dudley. 2024. “Biomechanics and Ontogeny of Gliding in Wingless Stick Insect Nymphs

(*Extatosoma Tiaratum*)." *Journal of Experimental Biology* 227 (24): jeb247805. https://doi.org/10.1242/jeb.247805.

Zhao, Xin, Jing-Xin Liu, Tristan Charles-Dominique, et al. 2024. "Petal-Shaped Femoral Lobes Facilitate Gliding in Orchid Mantises." *Current Biology* 34 (1): 183-189.e4. https://doi.org/10.1016/j.cub.2023.11.003.