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Systematics and Evolution of True Bugs (Heteroptera) and Thread-Legged Assassin Bugs (Emesinae: Reduviidae)

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

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by

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ABSTRACT OF THE DISSERTATION

Systematics and Evolution of True Bugs (Heteroptera) and Thread-Legged Assassin Bugs (Emesinae: Reduviidae)

by

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Doctor of Philosophy, Graduate Program in Entomology
University of California, Riverside, June 2023
Dr. Christiane Weirauch, Chairperson

True bugs (Hemiptera: Heteroptera) are one of the most speciose suborders with incomplete metamorphosis, with behaviors including predation on arthropods, hematophagy, mycetophagy and phytophagy, and include species that are important disease vectors, plant pests and biological control agents. However, while relationships between infraorders are largely resolved, relationships between and within superfamilies are still contested, especially within the two largest infraorders, Cimicomorpha and Pentatomomorpha. Using a combined transcriptome and genome dataset covering 74 of the 88 families we resolved relationships between superfamilies and families of Cimicomorpha and Pentatomomorpha. Species within the Emesine Complex (Heteroptera: Reduviidae: Emesinae, Visayanocorinae, Saicinae) are unique among reduviids in having a cosmopolitan distribution, lacking ocelli and fossula spongiosa, and having a close association with spiderwebs. We used a combined high-throughput and Sanger sequencing dataset (384 loci, 15 taxa; 3 loci, 207 taxa) to resolve

relationships between subfamilies and tribes, and discovered rampant paraphyly among subfamilies and tribes, necessitating revisions to the classification. We used ancestral character state reconstructions for 40 morphological characters to identify diagnostic features for a revised classification. Our new classification treats Saicinae and Visayanocorinae as junior synonyms of Emesinae, synonymizes the emesine tribes Ploiariolini Van Duzee and Metapterini Stål with Emesini Amyot and Serville, and recognizes six tribes within Emesinae (Collartidini Wygodzinsky, Emesini, Leistarchini Stål, Oncerotrachelini **trib. nov.**, Saicini Stål **stat. nov.**, and Visayanocorini Miller **stat. nov.**). We then used our phylogenetic hypothesis to test whether the four cosmopolitan genera share similar dispersal patterns and found they each dispersed during the Eocene, but from and to different continents. Based on their dispersal patterns and timing, and the observation that thread-legged bugs are found in flotsam, we further hypothesize that they may have dispersed primarily via rafting. Rarely collected, Collartidini (4 genera, 14 species) are a tribe of Emesinae that have retained a number of plesiomorphic features within Emesinae. The discovery of two undescribed species from Thailand and Malaysia (Borneo) has created the need for a reassessment of genera within Collartidini. We here synonymize the fossil genus *Collarhamphus* and extant genera *Mangabea* and *Stenorhamphus*, provide a revised diagnosis and description of *Stenorhamphus*, and describe *Stenorhamphus segerak*, new species and *S. phuphan*, new species, from Malaysia (Sarawak) and Thailand, respectively.

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INTRODUCTION

Heteroptera, or the true bugs, have more than 45,000 described species and seven infraorders, making them one of the most speciose suborders with incomplete metamorphosis (Henry, 2017; Schuh & Weirauch, 2020). They are also extremely diverse ecologically and behaviorally, occupying terrestrial, aquatic, and even some marine habitats, and with feeding behaviors including predation on other arthropods, hematophagy on vertebrates, mycetophagy, and phytophagy (Panizzi & Grazia, 2015; Schuh & Weirauch, 2020). Heteroptera also include several important disease vectors, nuisance pests, plant pests and beneficial biological control agents (Henry, 2017; Schaefer & Panizzi, 2000). Despite their ecological importance and diversity, many relationships between heteropteran superfamilies (Reduvioidea, Miroidea, Cimicoidea) and families (within Lygaeoidea, Coreoidea, Leptopodomorpha) are still contested or unknown (Johnson et al., 2018; Li et al., 2017; Wang et al., 2017; Weirauch et al., 2019; Weirauch & Schuh, 2011). Phylogenetic analyses have had neither the breadth nor the depth to fully uncover their relationships.

Reduviidae are an almost entirely predatory family within Heteroptera with ~6,800 species, extensive morphological diversity and numerous different life strategies (e.g., prey specialization on termites, bees and millipedes [Maldonado, 1990; Zhang & Weirauch, 2014]). Emesinae stand out within Reduviidae as a subfamily with cosmopolitan distribution, unique morphology, and a range of spiderweb associated behaviors (i.e., free-living, kleptoparasitism, arachnophagy, and a combination of

kleptoparasitism and arachnophagy [Wygodzinsky, 1966; Wignall & Taylor, 2010]). Despite their fascinating behavior and wide distribution range, relationships within Emesinae and between closely related subfamilies Saicinae and Visayanocorinae have never been tested with molecular data.

While transoceanic dispersal appears to be rare in Reduviidae, in some lineages it seems to have resulted in rapid diversification after colonization. Emesinae are unique among assassin bugs in including four genera with cosmopolitan distributions. Their relatively high diversity on islands compared to other reduviids and a potentially young age (~87 MYA) suggest that dispersal rather than vicariance led to their current distribution ranges. However, timing and direction of dispersal within Emesinae has never been tested and would first require a phylogenetic hypothesis of relationships within the Emesine Complex.

Rarely collected, Collartidini make up one of the smallest tribes of Emesinae, with only four genera. A closer look at species within these genera suggests that three of the four genera should be combined into one genus, and the group is in need of revision.

Given my broad interests in insect evolution and systematics, and the above gaps in our knowledge of Heteroptera and Emesinae, my dissertation is focused on the following four chapters:

I. Synonymy of *Mangabea* and *Stenorhamphus*, with the description of two new species (Hemiptera: Reduviidae: Emesinae: Collartidini)

II. Untangling the assassin's web: phylogeny and classification of the spider-associated Emesine Complex (Hemiptera: Reduviidae)

III. Evolution and biogeographic history of thread-legged assassin bugs (Emesinae: Reduviidae)

IV. Phylogenomics of True Bugs sheds light on relationships within Cimicomorpha and Pentatomomorpha

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CHAPTER 1:

Synonymy of Mangabea and Stenorhamphus, with the description of two new species (Hemiptera: Reduviidae: Emesinae: Collartidini)

ABSTRACT: Rarely collected, Collartidini (4 genera, 14 species) are a tribe of Emesinae (Hemiptera: Heteroptera: Reduviidae), the thread legged assassin bugs, that have retained a number of plesiomorphic features within Emesinae. The group has long been believed to be restricted to equatorial Africa, Madagascar, and Sri Lanka, with more recent additions from the Canary Islands, Sudan, Israel, and Taiwan, and a fossil species from Baltic amber. The discovery of two undescribed species from Thailand and Malaysia (Borneo) has created the need for a reassessment of genera within Collartidini. We analysed a morphological matrix of 25 characters and 11 ingroup species that represents the four collartidine genera, finding that while *Collartida* Villiers, 1949 is recovered as monophyletic, *Collarhamphus* Putshkov & Popov, 1995 and *Stenorhamphus* Elkins, 1962 render *Mangabea* Villiers, 1970 paraphyletic. We here synonymise the fossil genus *Collarhamphus* and extant genera *Mangabea* and *Stenorhamphus*, provide a revised diagnosis and description of *Stenorhamphus*, and describe *Stenorhamphus segerak*, new species and *S. phuphan*, new species, from Malaysia (Sarawak) and Thailand, respectively. Lateral and dorsal habitus images as well as images of diagnostic characters are provided. A map showing the known distribution

of *Stenorhamphus* spp. is provided, in addition to images highlighting diagnostic genus and species level characters.

INTRODUCTION

Emesinae, the thread legged assassin bugs, are a species rich subfamily within Reduviidae, including over 950 species in 95 genera (Maldonado, 1990). Emesinae are widely distributed, and one of the few subfamilies of Reduviidae with numerous endemic island species (Wygodzinsky, 1966). Spider-associated behaviors occur in various groups of Emesinae (Soley et al., 2011; Wignall & Taylor, 2011; Mercado & Santiago-Blay, 2015) and may have contributed to their diversification. Collartidini, with only four described genera, two of which are monotypic, is the smallest of the six tribes within Emesinae (Putshkov & Popov, 1995; Villiers, 1970; Wygodzinsky, 1966). Wygodzinsky (1966) hypothesised Collartidini to form the sister group to the rest of Emesinae in his scheme of relationships of Emesinae and closely related subfamilies Saicinae and Visayanocorinae, based on characters such as the relatively unmodified (compared to other Reduviidae) wing venation, simple foreclaws, and setae on the labium. Recent phylogenetic analyses (Smith et al., in prep.) support the notion that Collartidini are a relatively early diverging lineage of Emesinae and place them as sister taxon to Leistarchini within a paraphyletic Emesinae. This effectively supports the original classification by Villiers (1949), who treated *Collartida* as part of the Leistarchini.

The three extant genera included within Collartidini are *Collartida* Villiers, 1949, *Stenorhamphus* Elkins, 1962 and *Mangabea* Villiers, 1970. *Collartida* was originally

described based on one species from the Democratic Republic of Congo, with eight additional species documented from Chad, Sudan, Israel, and Spain (Canary Islands) (Maldonado, 1990), and one more recently from Taiwan (Rédei & Tsai, 2010), resulting in a substantial range extension. *Stenorhamphus* was erected by Elkins (1962) to accommodate a species originally described by Distant (1906) in the genus *Guithera* Distant, 1906, subfamily Leistarchini, from Sri Lanka. When Villiers (1970) discovered collartidine specimens from Madagascar that distinctly differed from the mostly African *Collartida*, he placed this species in his new genus *Mangabea*. The two subsequently described collartidine species from Madagascar were also placed in this genus (Chłond et al., 2018; Weirauch, 2008). The fourth genus of Collartidini is *Collarhamphus* Putshkov & Popov, 1995 that comprises one species from Baltic amber, suggesting that Collartidini are relatively old and have conserved a fairly uniform and distinctive habitus for more than 36 million years (Wolfe et al., 2009). Diagnostic features appear to clearly separate *Collartida* from the three other genera. In contrast, the distinction between *Stenorhamphus* and *Mangabea*, and to a lesser extent *Collarhamphus,* is less clear cut, and is further blurred by the combination of diagnostic features observed in two undescribed species discovered by us from Malaysia (Borneo: Sarawak) and Thailand. While documenting and describing these two species, we realised that a reassessment of generic boundaries across Collartidini based on a cladistic analysis has been overdue.

We here document and describe the two newly discovered species of Collartidini that were collected in a yellow pan trap trail in Sarawak and a Malaise trap in Thailand.

To determine their placement in either *Stenorhamphus* or *Mangabea*, we include the two species in a matrix of morphological characters, with representatives of all extant and fossil collartidine genera, and outgroup taxa.

MATERIAL AND METHODS

Material. The male specimen from Sarawak was collected by two of us in a yellow pan trap, while surveying Heteroptera at the Nanga Segerak Ranger Station in Lanjak Entimau Wildlife Sanctuary. The male specimen from Thailand was collected in a Malaise trap as part of the TIGER (Thailand Inventory Group for Entomologists) initiative. The *Stenorhamphus nubiferus* (deposited at the British Museum of Natural History) and *Mangabea barbiger* (deposited at the California Academy of Sciences) holotypes were examined and imaged by the authors. Images of the *Mangabea orientalis* (deposited at the Muséum National d'Histoire Naturelle, Paris, France) holotype were studied by the authors. *Collarhamphus mixtus* and *Mangabea troglodytes* were documented with such detail that it was not necessary to examine the type specimen.

Imaging, dissections, and measurements. Specimens were imaged using a Leica DFC 450 C110 Microsystems system (Leica, Wetzlar, Germany) with a Planapo 1.0× and 2.0× objective. Leica113 Application Suite V4.3 software was used to stack images, with an average of 30 images per stack. Dissections of male genitalia followed standard protocols for the dissection of Reduviidae (e.g., Forero & Weirauch, 2012).

Measurements were made in Photoshop V19.1.5; head and pronotum lengths were measured dorsally along the midline.

Map. The map was built using the online version of SimpleMappr (Shorthouse, 2010), using localities from holotype collection sites when available, for fossil species locality from center of collection site was used.

Abbreviations. The abbreviations used in figures and text are as follows: bp, basal plate of aedeagus; bpext, basal plate extension of aedeagus; cly, clypeus; cp, capitate process; dps, dorsal phallothecal sclerite; ell, endosomal lateral lobe; escl, endosoma sclerites; est, endosomal struts of aedeagus; evl, endosomal ventral lobe; fsc, fascicle; lr, labrum; ph, phallosoma; prs, posterior pronotal spine; mns, metanotal spine; rm, cross vein between media and radius; st, setae.

Phylogenetic analysis. Building on characters that have previously been used to diagnose collartidine genera (e.g., Wygodzinsky, 1966; Putshkov & Popov, 1995; Weirauch, 2008), we coded a morphology matrix of 25 characters and 11 species of Collartidini and five outgroup taxa representing leistarchine Emesinae (*Bagauda similis* Wygodzinsky, 1966; *Ploiaria stysi* Ishikawa & Okajima, 2008 *in* Ishikawa, Susila & Okajima, 2008), Visayanocorinae (*Carayonia camerunensis* Villiers, 1951), and Saicinae (*Kiskeyana palassaina* Weirauch & Forero, 2007; *Oncerotrachelus amazonensis* Gil-Santana, 2013). Eleven taxa of Collartidini were included, comprising four species of *Collartida,* all three species of *Mangabea*, the single described species of *Stenorhamphus* and *Collarhamphus*, and the two undescribed collartidine species. The

five outgroup taxa consisted of two species of leistarchine Emesinae, two Saicinae, and one Visayanocorinae. Characters were coded using published species descriptions (Villiers, 1949, 1961, 1969, 1979; Elkins 1962; Wygodzinsky, 1966; Linnavuori, 1974; Putshkov & Popov, 1995; Weirauch & Forero, 2007; Ishikawa et al., 2008; Weirauch, 2008; Rédei & Tsai, 2010; Gil-Santana, 2013; Chłond et al., 2018); type images (*Stenorhamphus nubiferus* [Distant, 1906]), as well as specimens examined and/or documented in this paper (*Mangabea orientalis* Villiers, 1970: Muséum National d'Histoire Naturelle, Paris, France; *Mangabea barbiger* Weirauch, 2008: California Academy of Sciences; *Stenorhamphus phuphan,* new species: Queen Sirikit Botanic Garden, Chang Mai (Thailand); *Stenorhamphus segerak,* new species: National University of Singapore, Zoological Reference Collection). A parsimony analysis in TNT V1.5 (Goloboff & Catalano, 2016) using New Technology search with ratchet, sectorial search, drift and tree fusing resulted in three most parsimonious trees. The strict consensus tree was generated in WinClada V1.00.08 (Nixon, 1999–2002).

Morphological characters used in analysis, coded from specimens and the following literature.

1. Total size: less than 5.5 mm (0), greater than 5.5 mm (1). Total size was measured from the apex of the head to the posterior tip of the abdomen, in dorsal view. If membrane surpassed tip of abdomen, measured from apex of head to posterior tip of membrane. When size was not given in a species description we estimated it from figures if a scale bar was provided.

Head (Figs. 1.3B, G, 1.4B, H; Rédei & Tsai, 2010, Fig. 3; Weirauch, 2008, Fig. 1E; Weirauch & Forero, 2007, Fig. 1B; Putshkov & Popov, 1995, Fig. 2; Elkins, 1962, Fig. 19).

2. Head to total length ratio: ratio less than 0.1 (0), ratio between 0.1 and 0.2 (1), ratio greater than 0.2 (2). This ratio was determined using species descriptions and images (approximations). The distance from the apex of the head to the anterior portion of the neck was divided by the total body length.

3. Head, dorsal view: distance from posterior head margin to anterior margin of eye more than 1/3 length of head (0), about 1/3 of head (1), less than 1/3 (2).

4. Eye shape: drop-shaped (Figs. 1.3G, 1.4H) (0), subhemispheric (Weirauch, 2008, Fig. 1E) (1). Putshkov & Popov (1995) used eye shape to distinguish between *Mangabea*, *Stenorhamphus*, *Collartida* and *Collarhamphus.* The shape of the eye in dorsal view is coded as drop-shaped when the anterior and posterior eye margins are straight (or almost so) while the lateral margin (in dorsal view) is curved; all margins are curved in the subhemispheric eye shape.

5. Pair of ventral setae in position 1 (anterior): absent (0), present (Fig. 1.3B) (1). Collartidini may have up to five pairs of setae ventrally on the head (in addition to the fascicle or setae anteriorly on the gena), in the area where the gula merges into the gena in (see Figs. 1.3B, 1.4B). They appear to be species specific and have been used as diagnostic features for several species. The pair of setae we refer to as position 1 is the anteriormost pair.

6. Pair of ventral setae in position 2 (anterior): absent (0), present (Fig. 1.3B) (1). This is the second pair of setae; it is located anterior to the eye.

7. Pair of ventral setae in position 3 (posterior): absent (0), present (Fig. 1.3B) (1). This is the first pair of setae located posterior to the eye.

8. Pair of ventral setae in position 4 (posterior): absent (Fig. 1.3B) (0), present (Fig. 1.4B) (1). This is the second pair of setae posterior to the eye.

9. Pair of ventral setae in position 5 (lateral to eye): absent (Fig. 1.3B) (0), present (Fig. 1.4B) (1). This is the only pair of setae on the lateral surface of the head, directly posterior to the eye.

10. Ventrolateral vestiture anteriorly on gena: absent (Weirauch & Forero, 2007, Fig. 1B) (0), one pair of setae (Rédei & Tsai, 2010, Fig. 3) (1), two pairs of setae (Putshkov & Popov, 1995, Fig. 2) (2), fascicle of multiple setae (Fig. 1.4B) (3). At the anterior-most end of the head, ventrally on the gena, species of Collartidini show a range of types of vestiture, or the vestiture is absent.

11. Second labial (first visible) segment longest: absent (Fig. 1.4B) (0), present (Rédei & Tsai, 2010, Fig. 2) (1). In the original diagnosis of *Collartida* the second labial segment is longer than segments three and four, and it reaches the anterior margin of the eye; the proportion of anterior head region and labial segments is different in other taxa. The second labial segment in Visayanocorinae (*Carayonia camerunensis*) is relative to both the anterior region of the head and other labial segments, longer than that seen in *Collartida*.

12. Third labial (second visible) segment longest: absent (0), present (Fig. 1.3B) (1). The length of the third (second visible) labial segment appears to be more variable, it is not consistently longer when the second labial segment is not the longest. The second and third labial segments can be of equal length, or the fourth labial segment can be the longest.

13. Ventral surface of second labial segment: without setae (Elkins, 1962, Fig. 19) (0), with one or two pairs of setae (Rédei & Tsai, 2010, Fig. 3) (1), at least apical half with dense vestiture (Fig. 1.4B) (2). Vestiture is common on the labium of Collartidini, Saicinae and Visayanocorinae, but the distribution and shape of setae vary.

14. Ventral surface of third labial segment: without setae (Elkins, 1962, Fig. 19) (0), with one or two setae (Rédei & Tsai, 2010, Fig. 3) (1), with row of stiff setae (Fig. 1.3B) (2). The third labial segment does not show the high degree of setal variation found on the second labial segment.

Thorax (Figs. 1.3G, 1.4F, H; Weirauch & Forero, 2007, Fig. 1E).

15. Length of posterior lobe of pronotum (dorsal view): shorter than anterior lobe (0), approximately equal to anterior lobe (Fig. 1.3G) (1), distinctly longer than anterior lobe (Fig. 1.4H) (2).

16. Spine on mesonotum: absent (0), present (Weirauch & Forero, 2007, Fig. 1E) (1).

17. Spine on pronotum: absent (0), present (Fig. 1.4F) (1).

Foreleg (Figs. 1.3A, C, 4A, F; Rédei & Tsai, 2010, Fig. 4; Ishikawa et al., 2008, Fig. 21; Weirauch & Forero, 2007, 1E).

18. Acetabula: forward opening (Fig. 1.3A) (0), not forward opening (Weirauch & Forero, 2007, 1E) (1). Forward opening acetabula in the forelegs have historically been used to diagnose Emesinae and separate them from Saicinae and Visayanocorinae.

19. Number of ventral spine-like setae on forecoxa: none (Ishikawa et al., 2008, Fig. 21) (0), one (1), two (Rédei & Tsai, 2010, Fig. 4) (2), three (3), four (Fig. 1.4F) (4).

20. Large spine-like setae of forefemur: not extending to apex (Rédei & Tsai, 2010, Fig. 4) (0), extending to apex (Fig. 1.4A) (1), absent (2).

21. Foretarsal length: first tarsal segment shortest (Fig. 1.3C) (0), first tarsal segment not shortest (Ishikawa et al., 2008, Fig. 21) (1).

Forewing (Figs. 1.5A, B; Ishikawa et al., 2008, Fig. 23; Weirauch, 2008, Fig. 4B; Rédei & Tsai, 2010, Fig. 5).

22. Shape of basal cell of forewing: roughly rhomboid (Fig. 1.5A, B) (0), roughly pentagonal (Weirauch, 2008, Fig. 4B) (1), roughly triangular (Rédei & Tsai, 2010, Fig. 5) (2), basal cell absent (Ishikawa et al., 2008, Fig. 23) (3). The basal cell is located proximad of the discal cell (as seen in Fig. 1.5). The cell is here coded to be rhomboid when at least two opposing veins are not roughly parallel, pentagonal when there are four veins or cross veins with opposite sides roughly parallel, and roughly triangular when there appear to be only three bordering veins and cross veins.

23. Length of discal cell of forewing: short, less than 3/4 of the length between rm and the tip of wing (Rédei & Tsai, 2010, Fig. 1.5) (0), long, more than 3/4 of length between

rm and tip of wing (Figs. 1.5A, B) (1). The length of the discal cell varies mostly between short (in *Collartida*) and long (in all other ingroup taxa).

24. Cross vein proximal to rm vein: absent (Figs. 1.5A, B) (0), present (Weirauch, 2008, Fig. 4B) (1). This cross vein was first noticed in *Mangabea orientalis* and is also present in *M. barbiger.* The cross vein creates an extra cell in the wing.

25. Distal tip of corium reaching to: about 3/5 between rm cross vein and apex of wing (Fig. 1.5A) (0), 4/5 between rm cross vein and apex of wing (Fig. 1.5B) (1), apex or nearly apex of wing (Ishikawa et al., 2008, Fig. 23) (2), less than 3/5 (3). The distal tip of corium varies in its extension towards the apex of the wing. The coded ratios were obtained by dividing the distance between the rm cross vein and the apex of the distal tip of the corium and the apex of the wing.

PHYLOGENETIC ANALYSIS

The analysis resulted in three most parsimonious trees (see Fig. 1.1). The three trees differ in the relationships between species of *Collartida*; since investigating relationships within this genus are not the focus of this study, we do not discuss these differences. As relationships between *Stenorhamphus* species did not differ between fundamental trees, the first was arbitrarily chosen as an example (Fig. 1.1). Collartidini is supported as a monophyletic group (unambiguous optimisations only) by the distal tip of the corium reaching about 4/5 between rm cross vein and apex of wing (25:1). The small size (total size less than 5.5 mm; char 1:0) is a synapomorphy of *Collartida*, as are the pair of setae anteriorly on the gena (10:1) and the two ventral spine-like setae on the forecoxa (19:2).

The clade comprising *Collarhamphus* + *Stenorhamphus* + *Mangabea* is supported by two synapomorphies, the dense vestiture apically on the ventral surface of the second labial segment (13:2) and a row of stiff setae on the ventral surface of the third labial segment (14:2). *Stenorhamphus nubiferus* and *Collarhamphus mixtus* Putshkov & Popov, 1995, render *Mangabea* paraphyletic; *Stenorhamphus segerak*, new species was recovered as sister to *Stenorhamphus phuphan*, new species + *Stenorhamphus*. *nubiferus.* Though uncommon, several fossils from Baltic amber have been placed within extant genera, e.g., within Coleoptera (Alekseev, 2013). As *Collarhamphus* is nested within the *Mangabea* + *Stenorhamphus* clade and is not the first Baltic fossil placed within an extant genus we feel confident in including it within *Stenorhamphus*. Clearly, for the past 30 or so million years *Stenorhamphus* has maintained a uniform and distinctive morphology. Based on the outcomes of this analysis, we are synonymising *Collarhamphus, Mangabea* and *Stenorhamphus.*

TAXONOMY

***Stenorhamphus* Elkins, 1962**

(Tables 1.1, S1.1, Figs. 1.1–8)

Stenoramphus Elkins, 1962: 422. Type species: *Stenorhamphus nubiferus* (Distant, 1906).

Stenorhamphus Wygodzinsky, 1966: 86.

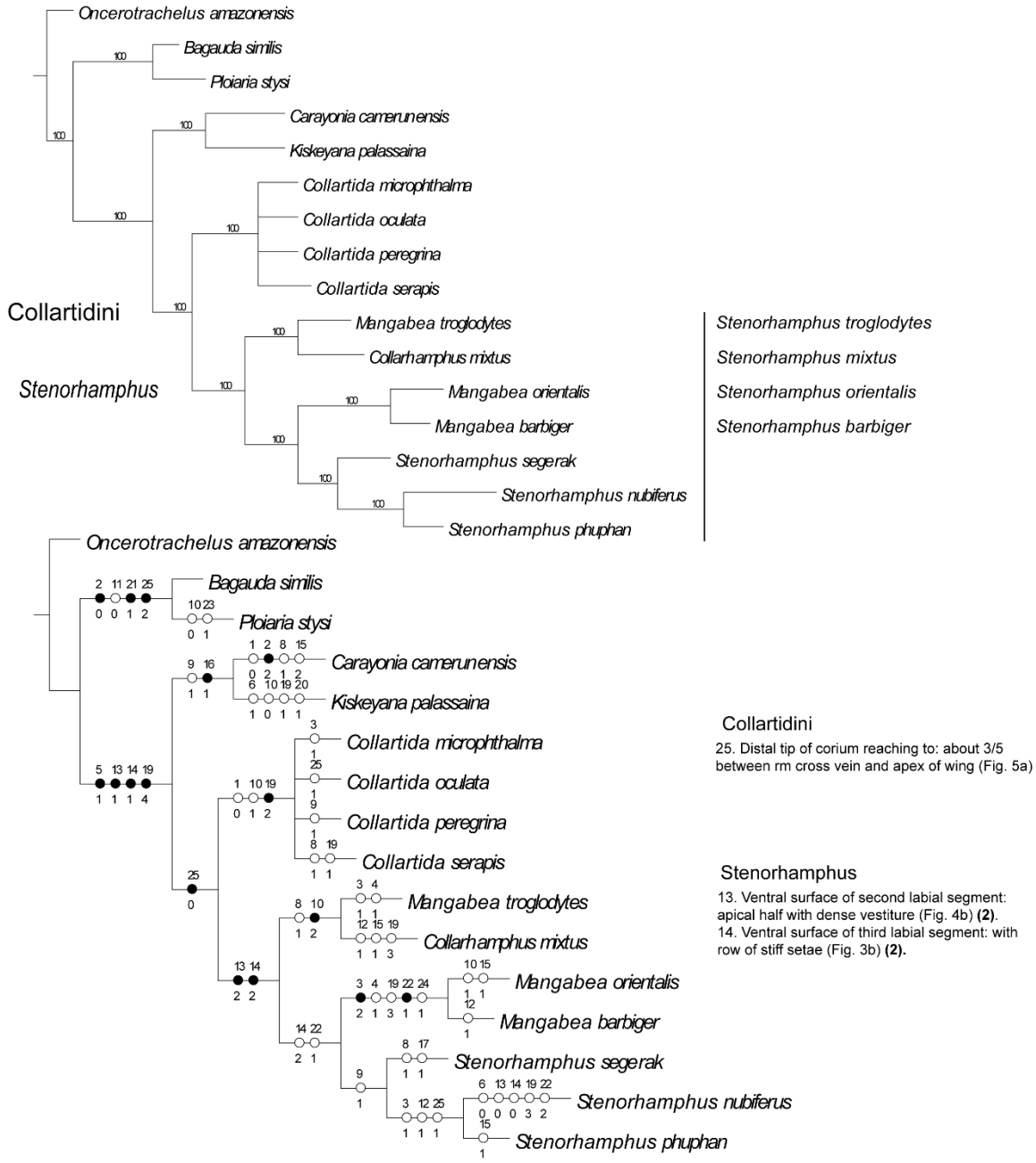

Fig. 1.1. Phylogenetic hypothesis of Collartidini, based on morphological characters. Upper phylogeny: Fundamental parsimony tree, built using 25-character morphology matrix. Percentages above branches are jackknife support values (100 replications). As each fundamental tree differs only in relationships among *Collartida*, the first tree was arbitrarily chosen for jackknife analysis. Lower phylogeny: Strict consensus tree out of three equally parsimonious trees, with 11 Collartidini and 5 outgroup species. Numbers above branches refer to characters from morphology matrix, numbers below branches refer to character states. Synapomorphies for Collartidini and *Stenorhamphus* are listed.

Mangabea Villiers, 1970: 809, **new synonym**. Type species: *Mangabea orientalis* Villiers, 1970.

Type species. *Guithera nubifera* Distant, 1906, by original designation.

Diagnosis. Recognised within Collartidini by long discal cell on the forewing, second labial segment not reaching anterior margin of the eye with either a row of stiff setae along the entire segment or apically, and third labial segment with row of stiff setae.

Redescription. Total length 5.7–11.8 mm. COLOURATION: fairly uniform brown or yellow, coxa and abdomen ventrally often lighter. VESTITURE: Body and appendages covered with evenly spaced, short setae (Figs. 1.3A, B, G, 1.4F); Head: ventral surface of head with three to five pairs of long, stout setae located posterior to antennifer, at anterior and posterior margins of eye (Figs. 1.3B, 1.4B), with either fascicle or two pairs of stout setae on gena ventrad of apex of maxillary plate (Figs. 1.3B, 1.4B); second labial segment (first visible) with fascicle of medium-length stout setae on ventral surface in apical half of segment or with row of stiff setae along entire segment (Figs. 1.3B, 1.4B), third labial segment (second visible) with short setae on entire ventral surface (Figs. 1.3B, 1.4B); scapus of antenna with short setae (Figs. 1.3B, 1.4B) Legs: forecoxa, in addition to short vestiture, with posterodorsal series and three or four stout, long setae (Figs. 1.3A, 1.4A), foretibia and foretarsus with relatively dense vestiture (Figs. 1.3C, 1.4C). STRUCTURE: Head: (Figs. 1.2A, B, C, D, 1.3B, G, 1.4B, H) elongate, anteocular portion long (Figs. 1.3B, 1.4B), postocular large and sometimes semiglobular (Figs. 1.3B, 1.4B), apex of stout antennifer approximately equidistant from apex of clypeus and

anterior margin of eyes (Figs. 1.3B, 1.4B), head anterior to antennifer narrow in dorsal view (Figs. 1.3B, 1.4B), maxillary plate very small, triangular (Fig. 1.3B, 1.4B), mandibular plate very small (Figs. 1.3B, 1.4B); gena with pronounced, elongate anterior portion (Figs. 1.3B, 1.4B), clypeus slender, not produced, labrum small, elongate (Figs. 1.3B, 1.4B). Eyes: either globulose and subsemispheric in dorsal perspective or drop–shaped (Figs. 1.3G, 1.4H); consisting of relatively few, large ommatidia (Figs. 1.3B, 1.4B). Antenna: extremely long, slender (Figs. 1.2A, B, C, D). Labium (Figs. 1.3B, 1.4B): second (first visible) labial segment slender, elongate, not reaching anterior margin of eye, third (second visible) labial segment slender and elongate, fourth (third visible) segment slender, tapering towards apex, second, third or fourth labial segment longest. Thorax (Figs. 1.3B, G, 1.4F, H): pronotum longer than wide, anterior and posterior lobes separated by distinct furrow (Figs. 1.3B, 1.4F); posterior lobe slightly wider than long, distinctly wider than anterior lobe, except in *Stenorhamphus troglodytes*, new combination, where anterior lobe is wider than posterior lobe, slightly depressed medially, posterior margin concave, with *Stenorhamphus segerak*, new species (Fig. 1.4F) or without spine laterally on posterior lobe; scutellum subrectangular (Fig. 1.4G). Legs (Figs. 1.2A, C, 1.3A, C, D, E, 1.4A, C, D, F): slender, foreleg distinctly stouter and shorter than mid and hind leg, hind leg longer than middle leg (Figs. 1.2A, C), tarsi with three, slender tarsomeres, first tarsomere very short, second and third tarsomeres of equal length (Figs. 1.3C, 1.4C); foreleg with coxa very long and slender (Figs. 1.3A, 1.4A), trochanter spined, femur straight, relatively slender (Figs. 1.3E, 1.4A), tibia straight,

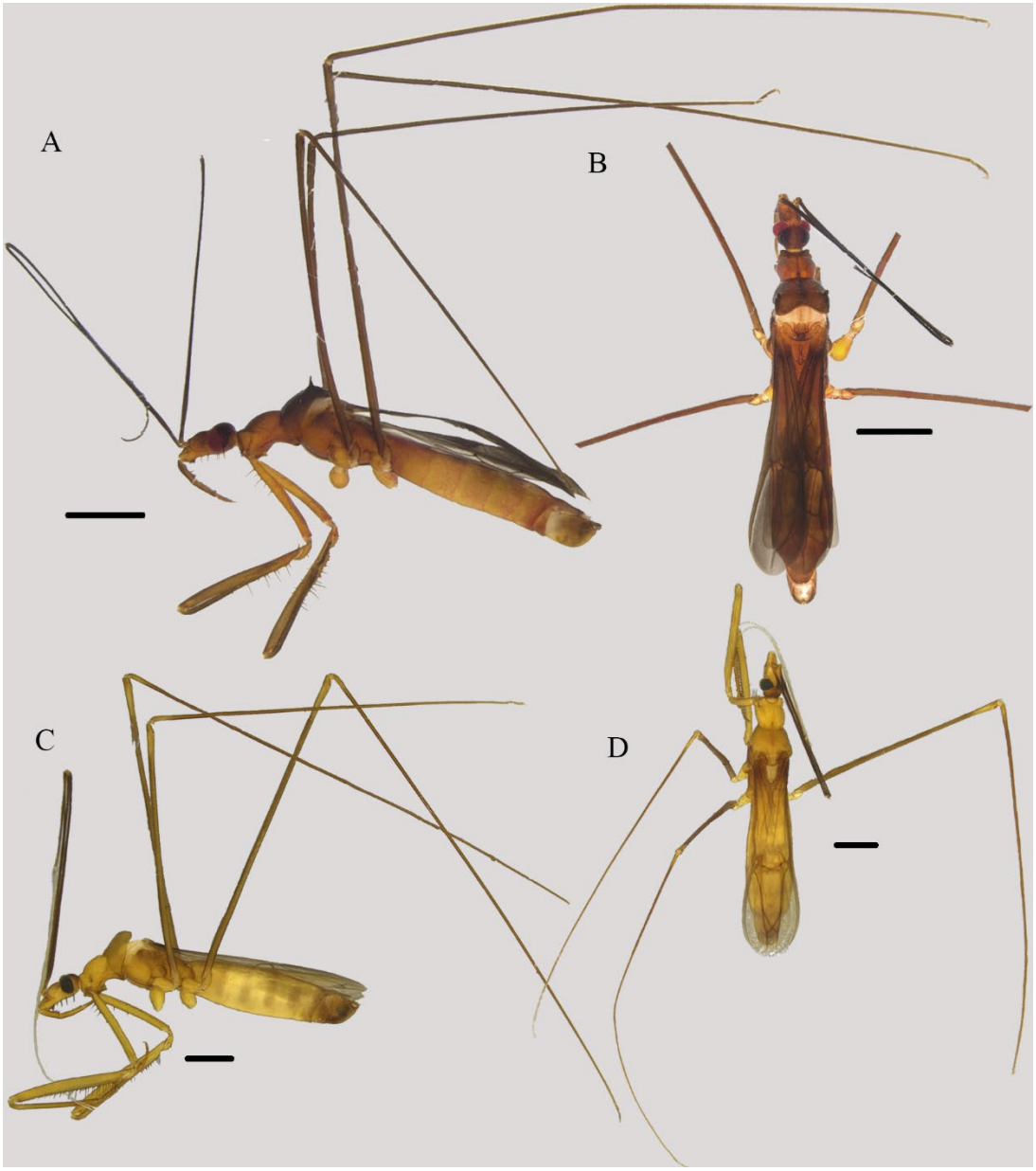

Fig. 1.2. Dorsal and lateral habitus of the holotypes of *Stenorhamphus segerak*, new species and *S. phuphan*, new species. A, *S. segerak*, male, lateral (note four spines on head, spines along labium, spine on posterior lobe of pronotum, long coxa and antenna); B, *S. segerak*, male, dorsal (note spines on posterior lobe of pronotum, length of hemelytra, size of postocular region, length of posterior lobe of pronotum); C, *S. phuphan*, male, lateral (note ventral spines on head, length of mid and hind legs, general colouration); D, *S. phuphan*, male, dorsal (note long legs, postocular segment present).

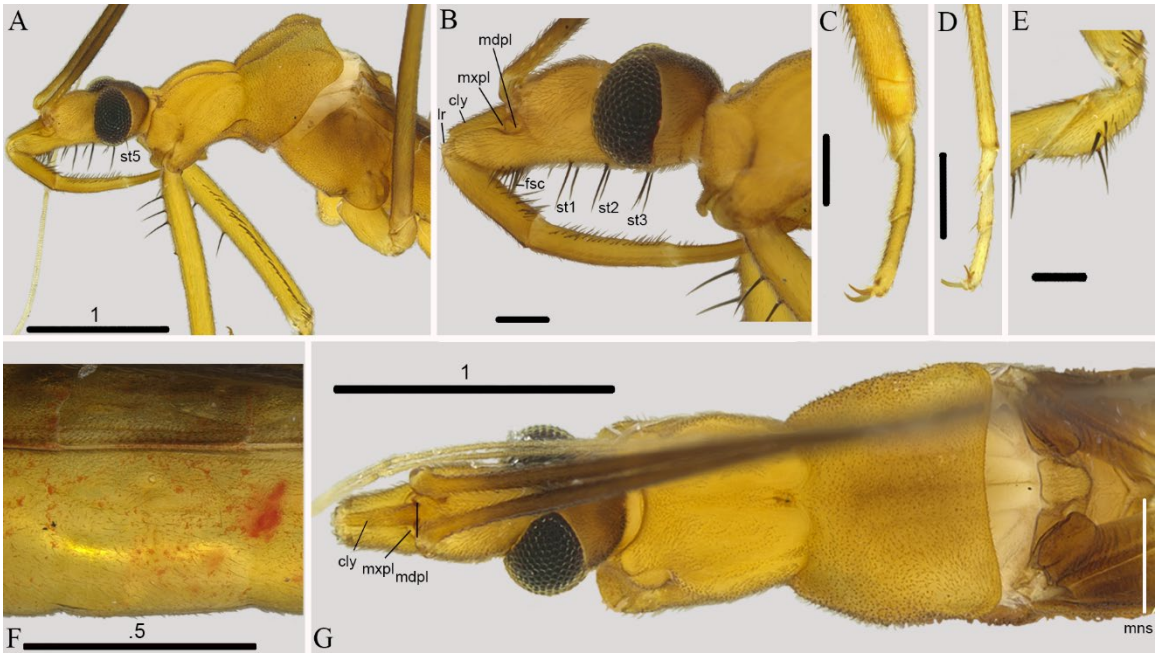

Fig. 1.3. *Stenorhamphus phuphan* details of head, legs and metanotum. Scale set to 0.2 mm unless otherwise specified. A, Head and thorax, lateral view (two pairs of ventral setae anterior to eye, one pair of ventral setae posterior to eye, one pair of lateral setae posterior to eye); B, Head, lateral view (fascicle, setae 1, 2, 3, labrum (lr), clypeus (cly), maxillary plate (mxpl), mandibular plate (mdpl)); C, Foretarsus (simple); D, Midtarsus (simple); E, Foretrochanter (four spines); F, Spiracle on 7th abdominal segment; G, Head, dorsal view, pronotum, metanotum (clypeus, eyes drop-shaped, metanotal spine).

slightly wider toward the apex (Fig. 1.4A); mid and hind legs with coxae ovoid, femora and tibiae very long and slender. Forewing (Figs. 1.5A, B): if macropterous, forewing elongate, R vein with setae along basal portion, basal area between R, M+Cu, Pcu, and posterior margin of wing slightly more sclerotised than actual membrane, M and Cu fused, basal cell rhomboid or pentagonal, discal cell very long and slender, rmcu cross vein absent or present (Figs. 1.5A, B). Abdomen (Figs. 1.2A, B, C, D, 1.3F, 1.4E): elongate ovoid, lateral margin smooth, second to seventh spiracle

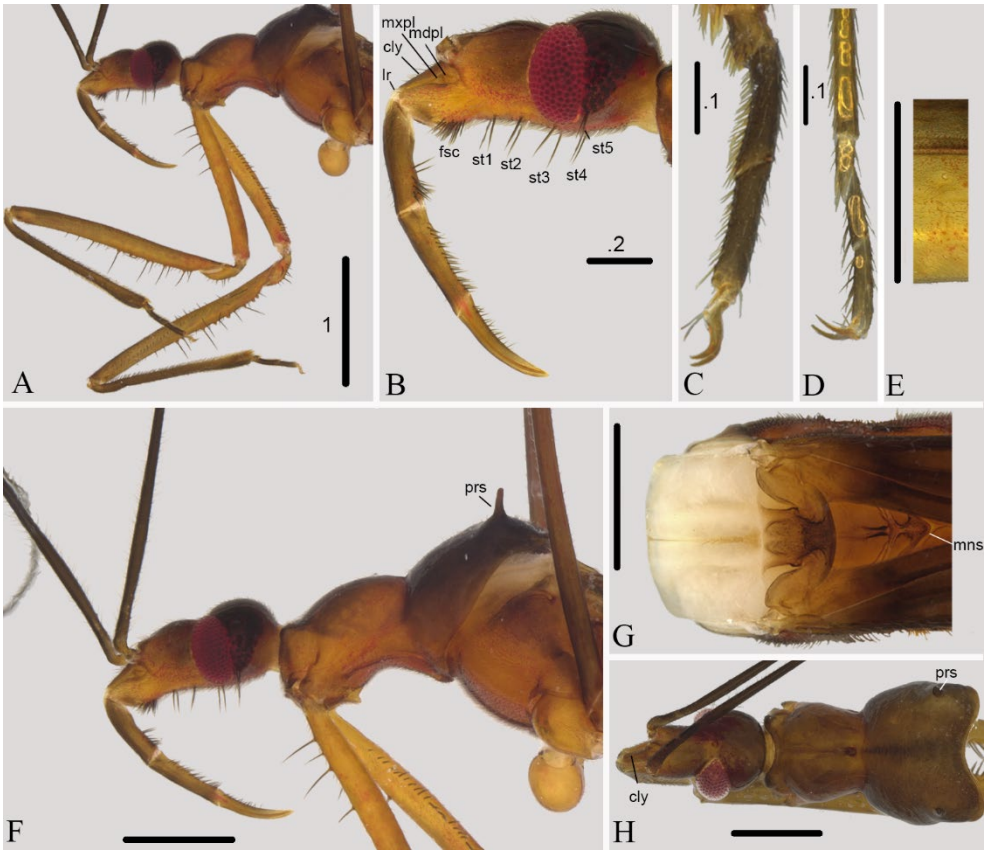

Fig. 1.4. *Stenorhamphus segerak* details of head, legs and metanotum. Scale set to 0.5 mm unless otherwise specified. A, Head and thorax, lateral view (4 spines on forecoxa, spines along femur, trochanter spined); B, Head, lateral view (Four pairs of spines dorsally on head, two pairs laterally postocular, fascicle on apical portion of head, spines along labium, clypeus [cly], maxillary plate [mxpl], mandibular plate [mdpl], gena [ge], labrum [lr]); C, Foretarsus (simple); D, Midtarsus (simple); E, Spiracle on 6th abdominal segment; F, Head and pronotum, lateral view (Spine on posterior lobe of pronotum, evenly spaced hairs along antenna); G, Mesoscutellum (lateral edge rounded ridge, anterior portion sub-rectangular); H, Head, pronotum and metanotum dorsal view (pronotal spine [prs], clypeus, drop-shaped eyes).

small, circular, on mediosternites (Figs. 1.3F, 1.4E), eighth spiracle on dorsolateral surface of segment 8. Genitalia (Figs. 1.6, 1.7): segment 8 well developed, membranous on dorsal surface; pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Fig. 1.6); parameres slender, curved, apex rounded (Fig. 1.6); aedeagus (Fig. 1.7) with basal plates stout and strongly curved and capitulate process relatively

large, ponticulus basilaris slender or nonexistent, basal plate extension relatively short (Figs. 1.7A, D), basal plate struts short (Figs. 1.7G, I), dorsal phallothecal sclerite curved, more heavily sclerotised anteriorly and posteriorly (Fig. 1.7A), endosoma with sclerotised ventral and lateral lobes with small spicules (Fig. 1.7E).

Discussion. Prior to the discovery of the two new Collartidini species from the Oriental Region described below, though morphological differences were small, geographic boundaries kept *Stenorhamphus* (Sri Lanka) and *Mangabea* (Madagascar) separate. However, with the additions of *Stenorhamphus segerak*, new species and *Stenorhamphus phuphan*, new species, it became clear that the characters defining *Collarhamphus, Stenorhamphus* and *Mangabea* overlap, making the assignment of the two new species to genus difficult. The discovery of the species from Borneo also considerably extends the known species range distributions of Collartidini further south in the Oriental Region. As Collartidini are extremely rarely collected, most species descriptions are based solely on the holotype. This makes it impossible to evaluate the variability of morphological features within species, and negatively impacts our ability to identify species-diagnostic characters. Previous authors have also sometimes relied on geographic distribution to assign species to existing or new genera (e.g., Villiers [1970] in describing *Mangabea*). Our phylogenetic analysis is an effort to better understand character distributions across genera, and to identify genus-diagnostic characters that show low homoplasy. We refrain from a full revision of *Stenorhamphus*, and key to species, for two reasons: the recently described taxa from Madagascar (Weirauch, 2008;

Chłond et al., 2018) are well documented and revised diagnoses and descriptions are unnecessary. In contrast, the redescription of *Stenorhamphus nubiferus* by Elkins (1962) does not comprehensively document this species, but since both the holotype and paratype appear to be in poor shape, we believe that fresh material from Sri Lanka will be critical to better document this species. Since the non-Madagascan species of *Stenorhamphus* are currently clearly separated by their geographic distribution, and the three Madagascan species are morphologically very distinct (see Weirauch, 2008; Chłond et al., 2018), we are not providing a key to species.

Elkins (1962) original spelling of *Stenorhamphus nubiferus* was *Stenoramphus nubifera.* Wygodzinsky (1966) used the spelling *Stenorhamphus nubiferus,* which has subsequently been used by all later authors (Maldonado, 1990; Putshkov & Popov, 1995; Rédei, 2004; Rédei & Tsai, 2010) except Weirauch (2008) who included a "[sic]". *Stenorhamphus nubiferus* is therefore in prevailing usage, "that usage of the name which is adopted by at least a substantial majority of the most recent authors concerned with the relevant taxon, irrespective of how long ago their work was published." (International Code of Zoological Nomenclature, fourth edition) and we are adopting the spelling used by Wygodzinsky (1966).

This revision not only greatly enlarges the range of *Stenorhamphus,* but also places the age of the genus at approximately 36 to 54 million years old (Wolfe et al., 2009) greatly increasing our understanding of the evolution of the group. It is now clear that

Stenorhamphus species*,* despite being rarely collected, are widespread, and have maintained relatively similar morphological characters for around 30 million years.

***Stenorhamphus barbiger* (Weirauch, 2008), new combination**

Mangabea barbiger Weirauch, 2008: 394.

Distribution. Currently only known from the holotype collected at Parc National Ranomafana in Fianarantsoa, Madagascar, via Malaise trap at a forest edge at fairly high elevation (1,130 m, 21.2261°S, 47.3698°E), and from one male specimen collected from Province Fianarantsoa, Manombo Special Reserve camp site 32 km SSE of Farafangana via Malaise trap in lowland rainforest (36 m, 23.0218°S, 47.720°E). Deposited at the California Academy of Sciences, UCR_ENT 00005202 and UCR_ENT 00127634.

Discussion. In our analysis, *Stenorhamphus orientalis* and *S. barbiger*, new combination, are identified as sister taxa by several synapomorphies, including wing venation and head shape. *Stenorhamphus barbiger* differs from *S. orientalis* by the fascicle of stout setae on the anterior area of the gena (two pairs of setae in *S. orientalis*) and the posterior pronotal lobe being slightly longer than the anterior. *Stenorhamphus orientalis* is found in NE Madagascar (Villiers, 1970), while *S. barbiger* is found in SE Madagascar (Weirauch, 2008). Though *S. troglodytes* is also found in Madagascar, it was collected along the eastern side of the country in a cave and appears to have diverged significantly from *S. barbiger* and *S. orientalis.*

***Stenorhamphus mixtus* (Putshkov & Popov, 1995), new combination**

Collarhamphus mixtus Putshkov & Popov, 1995.

Holotype. Male, from Baltic amber, Coll. Geological- Paleontological Institute and Museum, University of Hamburg; Typ.Kat.Nr.3602. Locality used in Fig. 8 based on approximation of Baltic amber collection sites.

Discussion. *Stenorhamphus mixtus* was described as a fossil in the genus *Collarhamphus* due to apparently sharing similarities with all three extant Collartidini genera. As the three genera of Collartidini share many similarities, distinguishing between them can be extremely difficult. However, our morphological analyses placed *Collarhamphus* within the *Mangabea + Stenorhamphus* clade. Though not within Emesinae, previously described coleopteran Baltic amber fossils have been placed within extant genera (Alekseev, 2013). We feel confident in synonymising *Collarhamphus* with *Stenorhamphus*. This further emphasises the age of this group to be between 36 to 54 million years old (Wolfe et al., 2009) and that little morphological change appears to have occurred during this period.

***Stenorhamphus nubiferus* (Distant, 1906)**

Guithera nubifera Distant, 1906: 365.

Stenoramphus nubifera: Elkins, 1962: 423.

Stenorhamphus nubiferus: Wygodzinsky, 1966: 86.

Distribution. This species is only known from Peradeniya in Sri Lanka, (approximately 7.26°N, 80.59°E). Both the holotype and the paratype are deposited at British Museum of Natural History. No data is given on how it was collected.

Discussion. *Guithera nubifera* was described by Distant (1906), based on the holotype and one paratype. Elkins (1962) recognised that it did not belong in *Guithera* and erected the new genus *Stenorhamphus* based on examination of the female paratype. We have examined the holotype that is in poor condition.

***Stenorhamphus orientalis* (Villiers, 1970), new combination**

Mangabea orientalis Villiers, 1970: 811.

Distribution. Currently known from Maroantsetra district, Fampanambo in Madagascar (–15.3735° S, 49.6216° E). Holotype and allotype deposited at the Muséum National d'Histoire Naturelle, Paris, France, paratype deposited at the Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

Discussion. See discussion of *S. orientalis*.

***Stenorhamphus phuphan*, new species**

(Figs. 1.1–3, 5B, 1.6E–H, 1.7C, D, H, I, 1.8)

Diagnosis. Recognised within *Stenorhamphus* by the total length approximately 6.9 mm, one pair of setae posterior to each eye, setae along apex of second labial segment, along entire third segment, and basally along the fourth segment, four spines on the trochanter, fascicle of stout setae on the anterior area of the gena, postocular region long, not globulose, posterior lobe of pronotum approximately equal to anterior lobe, legs long, mid and hind coxae longer than length of abdomen, without spines on posterior lobe of pronotum.

Description. *Male*: small (total length, holotype: 6.89 mm) COLOURATION: general colouration yellow, with base of wings and posterior portion of head brown (Figs. 1.2C, D). Head: postocular region brown, anterior anteocular region lighter (Fig. 1.3B). Antenna: brown, flagellomeres light brown. Labium: light brown to yellow. Thorax: anterior pronotum yellow, posterior dark yellow to brown. Legs: coxae light brown to yellow, trochanters, femora, tibiae, and tarsi pale brown. Wings: basally brown, rest hyaline. Abdomen: tergites yellow; mediosternites pale brown, laterosternites somewhat darker; pygophore brown. VESTITURE: as in genus description with the following additions: Head: ventral surface with three to four pairs of long, stout setae located posterior to

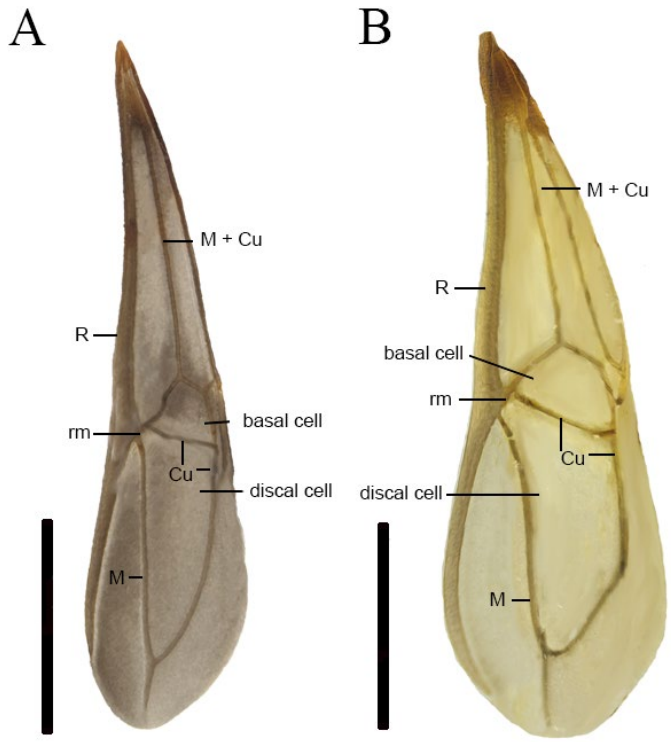

Fig. 1.5. *Stenorhamphus segerak* and *S. phuphan* forewing. Anterior wing margin on the left. A, *S. segerak* forewing, Pcu vein present but not visible in image; B, *S. phuphan* forewing.

antennifer, at anterior and posterior margins of eye, lateral surface of head with one long, stout setae posterior to eye (four ventral and one lateral setae visible on right side, three setae on left) (Figs. 1.3A, B) fascicle of eight stout setae on gena ventrad of apex of maxillary plate (Figs. 1.3A, B); second labial

segment (first visible) with medium-length stout setae on ventral surface in apical half of segment (Figs. 1.3A, B). Legs: forecoxa, in addition to short vestiture, with posterodorsal series and four stout, long setae anteroventral (Figs. 1.3A), foretrochanter with four stout setae on anterior surface (Fig. 1.3E), ventral surface of forefemur with about 16 medium stout setae in basal 2/3, interspersed with short setae (Fig. 1.2C). STRUCTURE: Head (Figs. 1.2C, D, 1.3A, B, G): postocular region long and slender, anteocular region less globulose than in *S. segerak*, new species. Thorax (Figs. 1.2C, D, 1.3A, G): posterior lobe wider than long, distinctly wider than anterior lobe, slightly depressed medially and with distinct, raised, lateral areas in posterior half of lobe, posterior margin slightly concave (Figs. 1.2C, D, 1.3A, G). Raised portion of mesoscutellum tongue shaped (Fig. 1.3G). Legs (Figs. 1.2C, D, 1.3A, C, D, E). Wings (Figs. 1.2D, 1.5B): elongate, surpassing apex of abdomen, rmcu cross vein not present (Fig. 1.5B). Abdomen (Figs. 1.2C, D, 1.3F). Genitalia (Figs. 1.6E, F, G, H, 1.7C, D, H, I): segment 8 well developed; pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Figs. 1.6E, F, G, H); parameres slender, curved, apex pointed (Figs. 1.6E, F, 1.7C); aedeagus (Figs. 1.7D, H, I) with basal plates stout and strongly curved, ponticulus basilaris very slender to nonexistent, basal plate extension relatively short, stout (Fig. 1.7D), dorsal phallothecal sclerite heavily sclerotised posteriorly (Fig. 1.7A), endosoma with ventral and lateral, heavily sclerotised lobes, lateral lobes as tall as wide (Figs. 1.7D, H, I).

Measurements. See Table 1.1.

Female. Unknown.

Etymology. Named after the locality of the holotype, Phu Phan National Park in Thailand; a noun in apposition.

Distribution. Only known from the type locality in Thailand.

Biology. Collected in lowland dry dipterocarp forest with deciduous trees and high canopy cover.

Type material. Holotype: male, THAILAND: Sakon Nakhon: Phu Phan National Park, behind forest protection unit at Huay Wien Prai, 17.1143°N, 104.0054°E, 387m, 25 Feb – 3 March 2007 Malaise trap, Sailom Tongboonchai (RCW4869), type deposited in the Queen Sirikit Botanic Garden, Chang Mai (Thailand) (QSBG).

Table 1.1: *Stenorhamphus phuphan* new species and *S. segerak* new species measurements.

in mm	**Length**						
	total	head	anteocular	ant. pron. lobe	post. pron. lobe	visible scutellum	wing
Stenorhamphus segerak	5.70	0.81	0.20	0.59	0.66	0.12	3.32
Stenorhamphus phuphan	6.89	1.06	0.15	0.65	0.70	0.17	4.43
	Labium			**Width**			
	lab. 2	lab. 3	lab. 4	head	ant. pron. lobe	post. pron. lobe	abdomen
Stenorhamphus segerak	0.31	0.32	0.34	0.52	0.52	0.73	0.86
Stenorhamphus phuphan	0.38	0.50	0.48	0.60	0.63	0.90	1.03

Discussion. Most similar to *S. nubiferus* due to the following shared characters: the distance from the posterior margin of the head to the anterior margin of the eye is approximately 1/3 the total length of the head (3:1), the third labial segment is the longest (12:1), and the pterostigma reaches 4/5 between rm cross vein and apex of wing (25:1). However, it is separated from *S. nubiferus* by the length of the posterior lobe of the pronotum in dorsal view being approximately equal to the anterior lobe (15:1), the pair of ventral setae in position 2 present (6:1), and four ventral spine-like setae on forecoxa (19:4).

***Stenorhamphus segerak*, new species**

(Figs. 1.1, 1.2, 1.4, 1.5A, 1.6A–D, 1.7A, B, E–G)

Diagnosis. Recognised within *Stenorhamphus* by the relatively small total length (5.7 mm), two pairs of stout setae posterior to the eye, spines on the trochanter, fascicle of stout setae on the anterior area of the gena postocular region developed, posterior lobe of pronotum longer than anterior, almost covering metanotum, legs long, mid and hind coxae longer than length of abdomen, forecoxa extending past pronotum, two spines on posterior lobe of pronotum.

Description. *Male:* small (total length, holotype: 5.7 mm) COLOURATION: general colouration brown, with posterior pronotal lobe, pygophore, postocular region and wings darker brown, abdomen, forecoxa and anterior region of head yellowish (Figs. 1.2A, B). Head: postocular region dark brown with spots, anterior anteocular region yellow (Figs. 1.4A, B). Antenna: brown, flagellomeres light brown. Labium: light brown.

Thorax: brown, posterior pronotum darker. Legs: Coxae light brown to yellow, trochanters, femora, tibiae, and tarsi pale brown. Wings: uniformly dark brown. Abdomen: tergites pale brown; mediosternites pale brown, laterosternites somewhat darker; pygophore dark brown. VESTITURE: as in genus description with the following differences: Head: ventral surface with four pairs of long, stout setae located posterior to antennifer, at anterior and posterior margins of eye (Figs. 1.4A, B), fascicle of more than twelve stout setae on gena ventrad of apex of maxillary plate (Fig. 1.4B), two pairs of stout setae dorsolaterally posterior to eye (Fig. 1.4B); second labial segment (first visible) with fascicle of medium-length stout setae on ventral surface in apical half of segment (Fig. 1.4B); Legs: posterodorsal series and four stout, long setae anteroventral, one stout, long seta posteroventral (Figs. 1.4A, F), foretrochanter with five stout setae on anterior surface (Fig. 1.4A), ventral surface of forefemur with about 13 medium and long, stout setae in basal 3/4, interspersed with short setae (Fig. 1.4A). STRUCTURE: as in genus description with the following differences: Head: (Figs. 1.4A, B, H): Eyes: globulose and subhemispheric in dorsal perspective (Fig. 1.4A, H), oval in lateral view, reaching dorsal surface of head, almost reaching ventral surface of head (Figs. 1.4A, B). Antenna: extremely long, slender; scapus (directed posteriad) surpassing hind coxa (Figs. 1.2A, B). Labium (Figs. 1.4A, B). Thorax (Figs. 1.4F, G, H): collar of pronotum pronounced, posterior lobe of pronotum slightly wider than long, distinctly wider than anterior lobe, slightly depressed medially and with raised, spined, lateral areas in posterior half of lobe, posterior margin concave (Figs. 1.4F, H). Mesoscutellum

subrectangular, lateral edge a rounded ridge (Fig. 1.4G). Legs (Figs. 1.4A, C, D). Wings (Fig. 1.5A): basal cell trapezoidal, rmcu cross vein absent (Fig. 1.5A). Abdomen (Figs. 1.2A, B, 1.4E): Genitalia (Figs. 1.6A, B, C, D, 1.7A, B, E, F, G): pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Figs 1.6A, B, C, D); parameres slender, curved, apex rounded (Figs. 1.6A, B, C, D, 1.7B); aedeagus (Figs. 1.7A, F, G) with basal plates stout and strongly curved, a relatively large capitulate process, ponticulus basilaris slender or nonexistent, basal plate extension relatively short (Figs. 1.7A, F, G), basal plate struts short (Figs. 1.7A, G), phallothecal sclerite curved, more heavily sclerotised anteriorly and posteriorly (Fig. 1.7A), endosoma with sclerotised ventral and lateral lobes with small spicules (Fig. 1.7A), lateral lobes long, phallosoma laterally with heavily sclerotised lobe, with short, stout spicules (Fig. 1.7E).

Measurements. See Table 1.1.

Female. Unknown.

Etymology. Named after the collecting locality of the holotype at Nanga Segerak in Sarawak; a noun in apposition.

Distribution. Only known from the type locality.

Biology. Found in lowland dipterocarp forests at mid elevation.

Type material. Holotype: male, Malaysia, Sarawak, Lubok Antu District, Lanjak Entimau Wildlife Sanctuary, Nanga Segerak, 1.4200°N, 112.0044°E, 506 m, yellow pan trap, Hwang et al., 16–17 Oct 2017 [SW17 L46] (RCW5465), type currently deposited in

National University of Singapore, Lee Kong Chian Natural History Museum, Zoological Reference Collection (ZRC).

Discussion. Most closely related to *Stenorhamphus nubiferus* and *S. phuphan,* with which this species shares the presence of a pair of ventral setae in position 5, lateral to the eye (9:1). Distinguished from these two species by the presence of a pair of ventral setae in position 4 (8:1) and a pair of spines on the posterior pronotal lobe (17:1).

***Stenorhamphus troglodytes* (Chłond, Guilbert, Baňař & Davranoglou, 2018), new combination**

Mangabea troglodytes Chłond, Guilbert, Baňař & Davranoglou, 2018: 2.

Distribution. Only known from the type locality at Namoroka Canyon, Tsingy de Namoroka National Park, Grotte Canyon (16.4693°S, 45.3380°E), where it was collected in the deepest part of the cave. Deposited in the Muséum National d'Histoire Naturelle, Paris, France.

Discussion. It is likely that many of the unique characters, such as small eyes and brachyptery, of *Stenorhamphus troglodytes*, new combination, are adaptations for dwelling in caves. Because of these autapomorphies that may obscure morphological synapomorphies with other species, the placement of *Stenorhamphus troglodytes* in our phylogenetic analysis as sister to a clade containing the two remaining Madagascan species and the species from Sri Lanka and Thailand should be considered as tentative.

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CHAPTER 2:

Untangling the assassin's web: phylogeny and classification of the spider-associated Emesine Complex (Hemiptera: Reduviidae)

ABSTRACT: Web-building spiders are formidable predators, yet assassin bugs in the Emesine Complex (Hemiptera: Reduviidae: Emesinae, Saicinae, and Visayanocorinae) prey on spiders. The Emesine Complex comprises >1,000 species and these web-associated predatory strategies may have driven their diversification. However, lack of natural history data and a robust phylogenetic framework currently preclude tests of this hypothesis. We combine Sanger (207 taxa, 3,865 bp) and high-throughput sequencing data (15 taxa, 381 loci) to generate the first taxon- and data-rich phylogeny for this group. We discover rampant paraphyly among subfamilies and tribes, necessitating revisions to the classification. We use ancestral character state reconstructions for 40 morphological characters to identify diagnostic features for a revised classification. Our new classification treats Saicinae Stål and Visayanocorinae Miller as junior synonyms of Emesinae Amyot and Serville, synonymizes the emesine tribes Ploiariolini Van Duzee and Metapterini Stål with Emesini Amyot and Serville, and recognizes six tribes within Emesinae (Collartidini Wygodzinsky, Emesini, Leistarchini Stål, Oncerotrachelini **trib. nov.**, Saicini Stål **stat. nov.**, and Visayanocorini Miller **stat. nov.**). We show that a pretarsal structure putatively involved in web-associated behaviors evolved in the last common ancestor of Emesini, the most species-rich clade within Emesinae, suggesting that web-associations could be widespread in Emesinae.

INTRODUCTION

Web-building spiders are among the most formidable predators in the animal kingdom, using their webs to sense and ensnare prey. Remarkably, a small number of insect species have evolved strategies to exploit the resources provided by spiderwebs. These include kleptoparasites such as Panorpidae which land directly on spiderwebs, stealing prey caught in the web, and predators such as helicopter damselflies which feed exclusively on web building spiders, using their exceptional vision and flight maneuverability to pluck spiders from their webs (van Helsdingen, 2011). Heteroptera, the true bugs within Hemiptera, are unique among insects in including four distantly related lineages adapted to life in spiderwebs (Schuh and Weirauch, 2020). Among these, the thread-legged assassin bugs of the Emesine Complex (Heteroptera: Reduviidae: Emesinae Amyot and Serville, Saicinae Stål, and Visayanocorinae Miller; Fig. 2.1) are by far the most species rich lineage having diversified into ~1,100 described species (Maldonado, 1990). Similar to other web-associated true bugs, Emesinae show specialized behaviors and morphology that may facilitate living on and around spiderwebs (Wignall and Taylor, 2010, 2011; van Helsdingen, 2011; Soley and Taylor, 2012). However, because of the lack of phylogenetic hypotheses and natural history data for many species, it remains unknown if diversification within Emesinae was driven by adaptations to the web environment.

Predatory strategies in Emesinae range from feeding on insects caught in spiderwebs (Howes, 1919) or capturing small insects not associated with webs (Roubaud

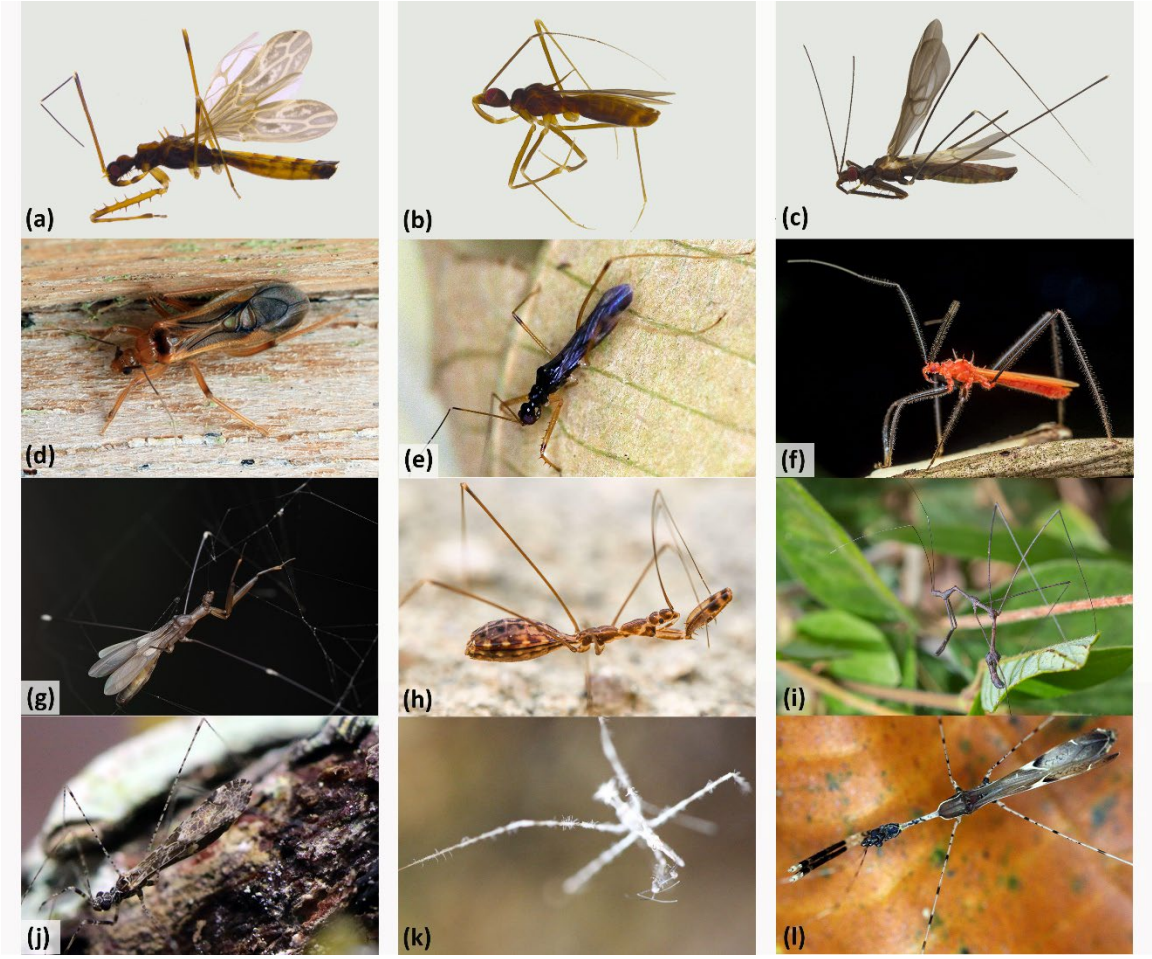

Figure 2.1: Diversity of emesine assassin bugs. Tribes based on new classification. **(a)** Saicini: *Choreutocoris* sp.; **(b)** Visayanocorini: *Carayonia* sp.; **(c)** Collartidini: *Collartida oculata*; **(d)** Oncerotrachelini: *Oncerotrachelus* sp., © Graham Montgomery; **(e)** Saicini: *Tagalis dichroa*; **(f)** Saicini: *Saica* sp., © Nicky Bay; **(g)** Leistarchini: *Bagauda* sp., © Abhi Jith; **(h)** Leistarchini: *Ploiaria chilensis*, © Zhenhao Feng; **(i)** Emesini: *Ghilianella* sp., © Felix Fleck; **(j)** Emesini: *Empicoris morstatti*; **(k)** Emesini: *Polauchenia* sp. **(l)** Emesini: *Emesa annulatus.*

and Weiss, 1927) to preying on spider eggs (Wygodzinsky, 1966) or adult spiders (Usinger, 1941; Wignall and Taylor, 2010; Soley, Jackson and Taylor, 2011; Wignall *et al.*, 2011). Wygodzinsky (1966) speculated that diet is determined by opportunity rather than preference. However, prey repertoire has only been recorded for a small number of emesines and predatory behaviors and diet of Saicinae and Visayanocorinae remain

undocumented. One of the few species of Emesinae with well-documented biology, *Stenolemus bituberus* Stål, uses two alternative behaviors to catch spiders: luring and stalking (Wignall and Taylor, 2010). When stalking spiders, *S. bituberus* approaches the spider by severing and then stretching threads with their forelegs, thus reducing web vibrations. To lure a resident spider, *S. bituberus* strums the spiderweb with its foreleg pretarsi, mimicking vibrations made by prey caught in the web. Foreleg pretarsal claws across Emesinae range from fairly symmetrical, as in other assassin bugs including Saicinae (Fig. 2.2a) and Visayanocorinae, to extremely asymmetrical with one claw being much smaller than the other (Wygodzinsky, 1966; Fig. 2.2b). In *S. bituberus*, manipulation of the web during stalking and luring behaviors is likely facilitated by a notch and a comb-like structure on the foreleg pretarsal claw (Fig. 2.2c, d). These structures occur in some, but not all Emesinae. The presence of the pretarsal notch and comb-like structures in a given species may indicate web-associated behaviors and could therefore allow us to predict lifestyle in taxa where behaviors are undocumented. However, the lack of robust phylogenetic hypotheses for the Emesine Complex currently precludes evolutionary insights into these fascinating predatory strategies.

Emesine, Saicinae, and Visayanocorinae have long been recognized as closely related taxa (Wygodzinsky, 1966; Weirauch, 2008; Weirauch and Munro, 2009; Hwang and Weirauch, 2012). Members of the Emesine Complex are recognized by the absence of several features, namely the ocelli, a well-developed corium on the forewing, dorsal abdominal scent-glands, and a fossula spongiosa on both the fore- and mid legs

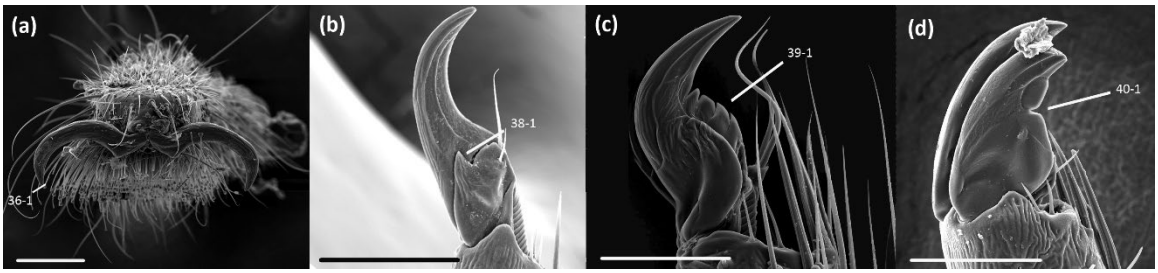

Figure 2.2: Tarsal and pretarsal structures of select Emesinae. Numbers refer to characters and states in the morphology matrix. **(a)** Saicini: *Saica* sp., 36-1: Distal tarsomere, ventral surface with flattened and widened tenant hairs, scale bar 100µm; **(b)** Leistarchini: *Millotina* sp., 38-1: foretarsal claws asymmetrical, scale bar 50µm; **(c)** Emesini: *Stenolemus* sp., 39-1: foretarsal claws, comb-like structure present, scale bar 50µm; **(d)** Emesini: *Emesaya* sp., 40-1: foretarsal claw with a ventral lamella, medially incised, here referred to as notch, scale bar 50µm.

(Wygodzinsky, 1966). All of these characters are present in most other Reduviidae. Emesinae, the thread-legged bugs, differ from Saicinae (Fig. 2.1a,e,f) and Visayanocorinae (Fig. 2.1b) in having extremely elongate and delicate 'thread-like' legs, with the forecoxa usually at least four times as long as wide and the acetabulum of the foreleg opening anteriad. With over 950 species in 95 genera (Maldonado, 1990), Emesinae are species rich, and are the third largest subfamily within Reduviidae (Putshkov and Putshkov, 1985). Emesinae are currently subdivided into five tribes (Wygodzinsky, 1966; Castro-Huertas *et al.,* 2021), the smallest being Collartidini Wygodzinsky (two genera, Fig. 2.1c). Collartidini are found in the Afrotropical and Indomalayan regions. Both Collartidini and Leistarchini Stål (~40 genera, Fig. 2.1g-h), lack the comb-like structure and notch on the foreleg pretarsus, though foreclaws in Leistarchini range from almost symmetrical to strongly asymmetrical. In contrast, many species of Emesini Amyot and Serville (~38 genera, Figs 2.1k-l), have the above-mentioned comb-like and notch structures on the foreleg pretarsus, and comprise the

bulk of genera, including *Stenolemus,* for which spiderweb associations have been documented. Metapterini Stål (~35 genera, Fig. 2.1i) are a large cosmopolitan tribe, with highest diversity in the Neotropics. They are often large, and many genera are apterous. Deliastini Villiers (3 genera) were treated as a separate tribe until recently but are now a junior synonym of Metapterini (Castro-Huertas *et al.*, 2021). Ploiariolini Van Duzee (~40 genera, Fig. 2.1j), are often smaller than most other Emesinae, and have the highest diversity in the Australasian region.

Saicinae (Fig. 2.1a,e,f, 25 genera, ~155 species [Putshkov and Putshkov, 1985; Maldonado, 1990; Melo and Coscarón, 2005; Gil-Santana, Marques and Costa, 2006; Weirauch and Forero, 2007; Gil-Santana *et al.,* 2020; Castro-Huertas *et al.,* 2022]) were traditionally diagnosed from Emesinae by the shorter forecoxa that is at most three times as long as wide, and the second visible labial segment often expanded and basally bulbous. Similar to Emesinae, Saicinae also occur in all biogeographic regions, with diversity highest in the Neotropics. Though Saicinae are not classified into tribes, genera fall into two distinct morphological groups: a smaller group (7 genera) with rows of stout setae or “bristles” on the forefemora and foretibiae (Fig. 2.1f), here referred to as the “bristly clade”, and a larger group (15 genera) where leg armature consists of tuberculate setae or “spines” (Fig. 2.1a,e), that we here refer to as the “spiny clade”. Similar to saicines, the delicate Visayanocorinae (Fig. 2.1b, 2 genera, 11 species [Putshkov and Putshkov, 1985; Ishikawa, Susila and Okajima, 2008]) have a shorter forecoxa that is at most three times as long as wide but are instead characterized by

their long second (visible) labial segment and a foretibial spur that projects beyond the tarsal insertion (Villiers, 1951). They are found in the Afrotropical and Indomalayan regions.

The only published assessment of phylogenetic relationships among Saicinae, Visayanocorinae, and tribes of Emesinae predates algorithm-driven phylogenetics (Wygodzinsky, 1966). According to Wygodzinsky's hypothesis, the forward-opening anterior acetabula and the corium carried beyond the level of the apex of the MCU cell (Fig. 2.3e-j) are synapomorphies of Emesinae. Wygodzinsky (1966) hypothesized Collartidini to be the sister group to all remaining Emesinae, with the remaining tribes forming a clade based on the increase in relative length of the first segment of the foretarsus. Wygodzinsky (1966) further proposed Leistarchini as sister taxon of (Emesini + Metapterini [including Deliastini] + Ploiariolini), with the latter clade recognized by comb-like and notch structures on the ventral surface of the pretarsal forelegs and placement of the M insertion on the R vein. In Wygodzinsky's scheme, relationships between Emesini, Ploiariolini, and Metapterini (including Deliastini) are unresolved. He considered the complete loss of mesonotal and metanotal spines and the large basal process of the posteroventral series of the forefemur as synapomorphies of Metapterini (including Deliastini) and the phallus with conjunctiva and a bifid vesica as synapomorphies for Ploiariolini. Castro-Huertas et al. (2021) published the first morphology-based phylogenetic analysis focused on Emesinae, aiming on testing the monophyly of and relationships within Metapterini. Their analyses found Deliastini to be

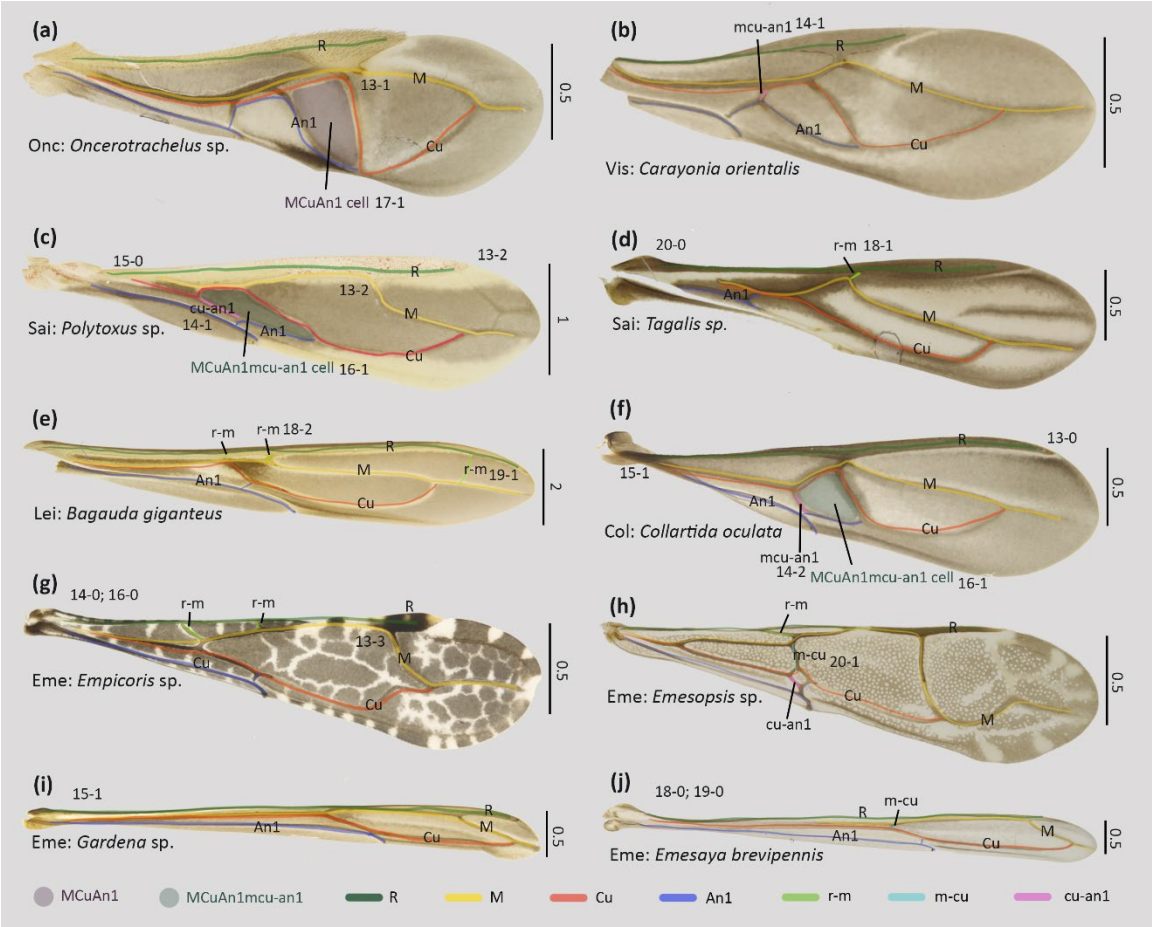

Figure 2.3: Forewing of selected Emesinae showing proposed interpretation of wing venation. Numbers refer to characters and states in the morphology matrix. **(a)** Oncerotrachelini: *Oncerotrachelus* sp.; **(b)** Visayanocorini: *Carayonia orientalis*; **(c)** Saicini: *Polytoxus* sp.; **(d)** Saicini:*Tagalis* sp.; **(e)** Leistarchini: *Bagauda giganteus*; **(f)** Collartidini: *Collartida oculata*; **(g)** Emesini *Empicoris* sp.; **(h)** Emesini: *Emesopsis* sp.; **(i)** Emesini: *Gardena* sp.; **(j)** Emesini: *Emesaya brevipennis*. Tribes follow proposed classification. Onc, Oncerotrachelini; Vis, Visayanocorini; Sai, Saicini; Lei, Leistarchini; Col, Collartidini; Eme, Emesini. Scale shown in mm.

nested within Metapterini and the two tribes were accordingly synonymized under Metapterini. Synapomorphies for Deliastini and Metapterini together include the foretrochanter with sparse short setae, the basal spiniform process of the posteroventral series of the forefemur conspicuously longer than the remaining processes, and the hind wing lacking a M-Cu cross vein. Clearly, a phylogenetic

hypothesis for the Emesine Complex is necessary to test relationships between subfamilies and tribes, and to reconstruct where within this clade unique morphological characters and behaviors may have evolved.

Current best practices suggest high numbers of loci (>200) and taxa increase the power of phylogenetic analyses (Philippe and Telford, 2006; Kapli, Yang and Telford, 2020). The shift towards high-throughput sequencing has left many labs confronted with the challenge of increased costs associated with targeting high numbers of loci and broad taxon sampling for diverse lineages. In addition, many labs have legacy Sanger data, but few studies have tested whether combining Sanger sequencing datasets for many taxa and genomic/transcriptomic datasets for few taxa are a viable option, or if the high amount of missing data skews results. However, when taxa are strategically chosen across a clade for high-throughput sequencing and combined analyses, the effect of missing data can be minimized, allowing for greatly increased taxon sampling when Sanger sequencing data are already available (Fonseca and Lohmann, 2018; Kieran *et al.*, 2021; Azevedo *et al.*, 2022).

We here combine a high-throughput sequencing dataset (15 taxa) with Sanger data (207 taxa) to estimate the first comprehensive phylogenetic hypothesis for the Emesine Complex. Our study aims on testing the monophyly of subfamilies and tribes as well as the phylogenetic hypotheses of tribal-level relationships proposed by Wygodzinsky (1966) and Castro-Huertas et al. (2021). We use this molecular phylogenetic hypothesis to reconstruct ancestral character states in an effort to

objectively identify diagnostic features for the subfamily and tribes recognized in our new classification. To propose a testable hypothesis on the evolution of web-associated behaviors in Emesinae, we reconstruct character state transitions for the two pretarsal structures (comb and notch) that are likely involved in these behaviors.

MATERIALS AND METHODS

Taxon sampling and specimen vouchering

The dataset consists of 174 ingroup taxa representing the Emesine Complex and 48 outgroup taxa (46 other Reduviidae, and two non-reduviid heteropterans), for a dataset of 222 terminals. We sampled four representatives of the small subfamily Visayanocorinae and included three genera (14 terminals) from the “bristly” Saicinae group, and nine genera (14 terminals) from the “spiny” Saicinae group. To test its phylogenetic position, we also included an undescribed genus of Saicinae from Madagascar (see Fig. S1) that shows an unusual combination of characters found in the spiny clade of Saicinae (tuberculate setae on forefemora) and Emesinae (very long forecoxae). All tribes of Emesinae are represented by multiple taxa including the now synonymized Deliastini (Collartidini: five taxa; Leistarchini: 37 taxa; Ploiariolini: 23 taxa; Emesini: 35 taxa; Metapterini: 30 taxa; Deliastini: one taxon). Table S1 provides the current classification for in- and outgroups, unique specimen identifier numbers, voucher depositories, and locality information. Vouchering procedures followed the guidelines laid out in Weirauch and Munro (2009). Specifically, voucher specimens were associated with unique specimen identifiers (USI labels) and databased using the

Arthropod Easy Capture Specimen (AESC) database (https://research.amnh.org/pbi/locality/). Images for voucher specimens were uploaded to the AESC database as well. These specimen records are publicly available through the Heteroptera Species Pages (https://research.amnh.org/pbi/heteropteraspeciespage/) where records are served directly from the AESC database. Vouchers were point-mounted and are deposited in publicly accessible natural history collections (see Table S1 for details).

Sequencing

Sanger sequencing:

Sanger sequencing targeted three gene regions, 28SD2 rDNA, 28SD3-5 rDNA, and 18S rDNA (207 in- and outgroup taxa, 3,865 bp). These three gene regions were also extracted from the high-throughput sequencing datasets (12 ingroup taxa, 3 outgroup taxa). Protocols for extraction, amplification, PCR cleaning, and sequencing followed those described in Weirauch and Munro (2009), with the exception that occasionally abdomens were used for extraction when genomic DNA yield from a leg was too low. PCR products were cleaned using the Bio 101 Geneclean Kit® or SureClean from Bioline. Forward and reverse strands were assembled, edited, and aligned in Geneious 11.1.5 (https://www.geneious.com). Assembled sequences were verified using NCBI BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi).

High-throughput sequencing:

To improve backbone support, we combined Sanger-derived data with 15 high-throughput sequencing datasets (381 loci; 231,153 bp) generated as part of a phylogenomic study across Reduvioidea (Knyshov *et al.,* 2023). In brief, low-coverage genomic, Anchored Hybrid Enrichment (AHE) and transcriptomic data were combined, and 381 protein-coding loci were mined across all taxa using the software package ALiBaSeq (Knyshov, Gordon and Weirauch, 2021). Reads were deposited on SRA, see Table S1 for accession numbers. Although these sequences are derived from different types of sequencing, we here refer to this dataset as the AHE dataset. The AHE dataset includes representatives of the three ingroup subfamilies and all tribes of Emesinae, as well as three outgroup taxa. Taxa represented by AHE datasets are indicated by a triangle on the phylogenetic tree (Fig. 2.4).

Phylogenetic analysis

Phylogenetic relationships were reconstructed using maximum likelihood partitioned analyses in IQ-TREE v2.2.0.5 (Minh *et al.*, 2020). Best fit partitioning schemes were estimated using ModelFinder (Kalyaanamoorthy *et al.*, 2017) in IQ-TREE2, allowing partitions with similar models to be merged to reduce over-parameterization and increase model fit. Tree estimation was sped up using the relaxed clustering algorithm (Lanfear *et al.*, 2014). One thousand replicates of ultrafast bootstrap (UFBoot2) (Hoang *et al.*, 2018) and SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.*, 2010) were performed to estimate node support. To assess differences between the

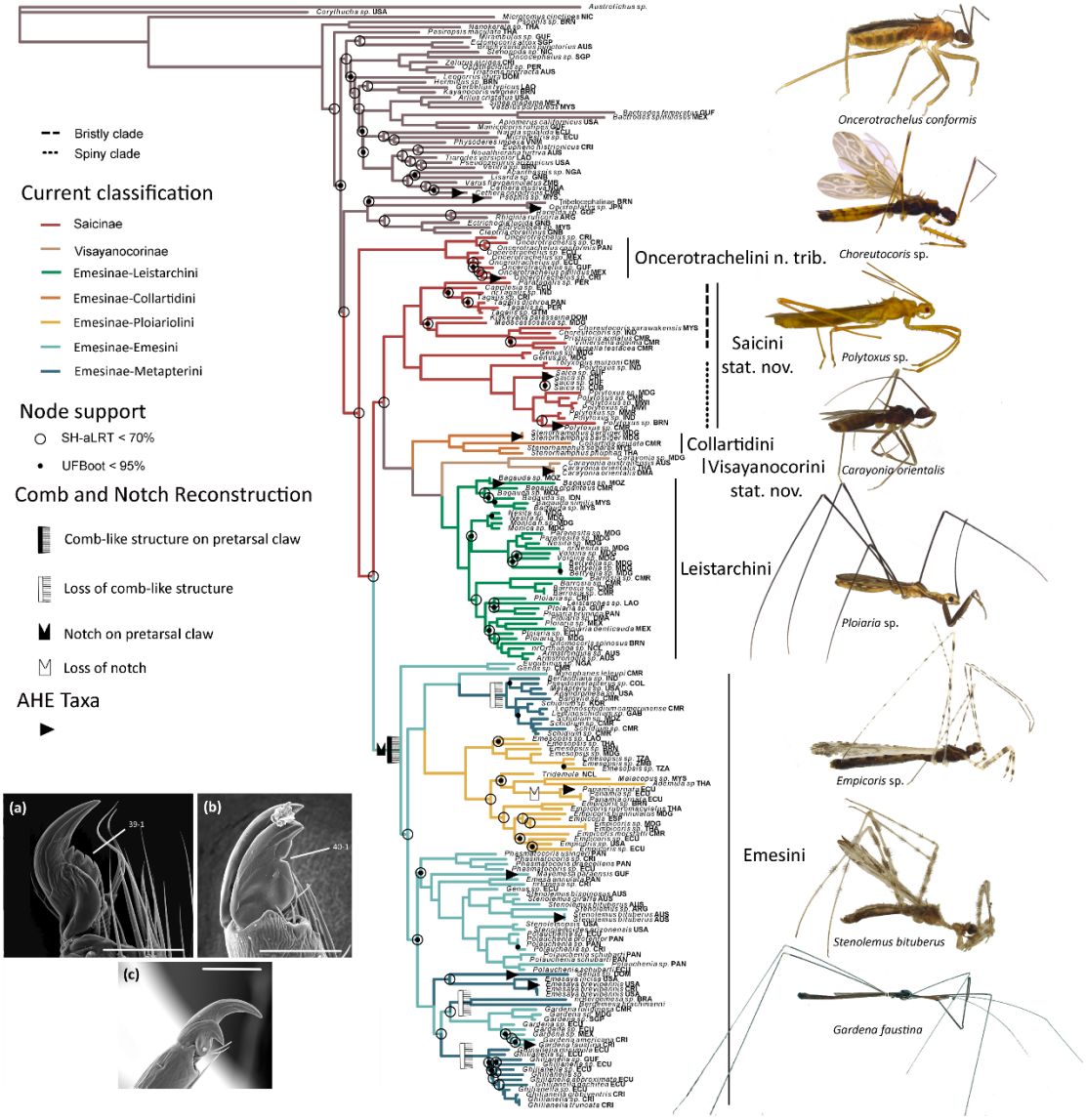

Figure 2.4: Phylogenetic reconstruction produced by a maximum-likelihood analysis of the combined dataset in IQ-TREE2. Small solid black circle at node indicates SH-aLRT support values less than 70%, large empty black circle at node indicates UFbootstrap support less than 95%. Colored branches show the current tribal-level classification of the three subfamilies in the Emesine Complex, with our proposed classification recognizing the subfamily Emesinae with 6 tribes shown on the right. (a) Emesini: Stenolemus sp., 39-1: foretarsal claws, comb-like structure present, scale bar 50µm; (b) Emesini: Emesaya sp., 40-1: foretarsal claw with a ventral lamella, medially incised, here referred to as notch, scale bar 50µm; (c) Emesini: Ghilianella sp., loss of comb and notch, scale bar 50µm. Ancestral character state reconstruction of comb and notch structure shown on tree. Notch and comb gained once at base of Emesini, comb lost three times, notch lost once within Emesini. Taxa represented by AHE datasets are indicated by a triangle on the phylogenetic tree.

Sanger and AHE datasets, two additional IQ-TREE2 analyses were run, one including only the 15 AHE taxa, and one including only Sanger loci.

Morphological dataset

A 40-character morphological matrix was generated (Table S2), with terminology largely following Weirauch (2008) and Wygodzinsky (1966). Primary homology hypotheses were based on Wygodzinsky (1966) and personal assessment following examination of specimens. In the final matrix, 35% of the characters were derived from Wygodzinsky (1966), and 65% are new characters based on personal assessment of specimens. Fore- and hindwing venation of Emesinae differs significantly from other Reduviidae and has not always been consistently named. We therefore selected 11 species representing major groups in the Emesine Complex, imaged fore- and hindwings, and compared venation patterns. Figures 3 and 4 outline our interpretation of wing vein homology that we believe is consistent with those in other Reduviidae. In brief, we hypothesize that the PCU and PCU + 1A veins referred to in Wygodzinsky's Fig. 5 (1966) are the An1 vein (Fig. 2.3) and the cu-pcu crossvein in *Collartida* (Wygodzinsky, 1966 Fig. 5; Fig. 2.3f) is the mcu-an1 crossvein. We also hypothesize the RS vein to be the r-s crossvein, and the cu-pcu crossvein to be the cu-an1 crossvein. Placement of the R, M and CU veins are consistent across both Wygdozinsky's and our hypothesis. See Figs 2.2-3 and 2.5-6 for highlighted characters. We refer to a multicellular external process of the integument as a "spine" (Fig. 2.5h,j). A seta with extended and/or raised socket is referred to as "tuberculate seta" (Fig. 2.5c,d,f), and thick and long setae and thin and hair-like setae

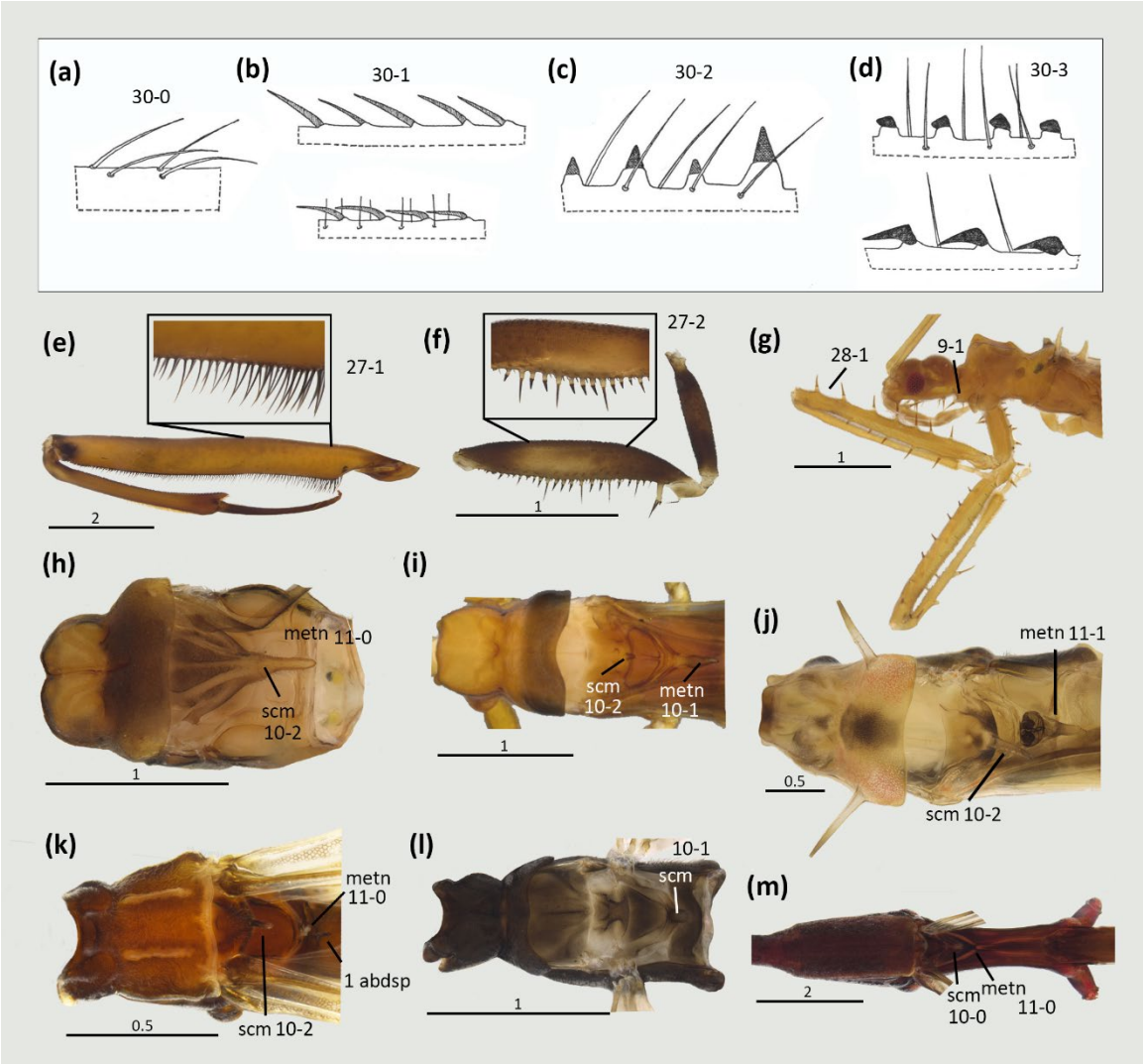

Figure 2.5: Selected thoracic and leg characters of Emesinae. Numbers refer to characters and states in the morphology matrix. (a)-(d) modified from Wygodzinsky (1966). **(a)** Microsetae, 30-0; **(b)** Macrosetae, 30-1; **(c)** Tuberculate setae, 30-2; **(d)** Adpressed tuberculate setae, 30-3; **(e)** Leistarchini: *Bagauda* sp., 27-1: Macrosetae, ventral surface of foretibia; **(f)** Leistarchini: *Monica* sp., 27-2: Tuberculate setae, ventral surface of foretibia; **(g)** Saicini: *Pristicoris* sp., 28-1: Tuberculate setae, posterodorsal surface; **(h)** Oncerotrachelini: *Oncerotrachelus* sp., 9-2: Apex of scutellum with spine, 10-0: metanotum without spine; **(i)** Saicini: *Villiersella* sp., 9-2: Apex of scutellum with spine, 10-1: metanotum with spine; **(j)** Saicini: *Polytoxus* sp., 9-2: Apex of scutellum with spine, 10-1: metanotum with spine ; **(k)** Emesini: *Empicoris* sp., 9-2: Apex of scutellum with spine, 10-0: metanotum without spine, first abdominal segment spined, metanotum with small spine; **(l)** Collartidini: *Collartida* sp., 9-1: Apex of scutellum semicircular with slightly pointed tip, 10-0: metanotum without spine; **(m)** Emesini: *Emesaya brevipennis,* 9-0: Apex of scutellum with no spine or tip present, 10-0: metanotum without spine. 1 abdsp, first abdominal segment spined; metn, metanotum; scm, spine of (meso)scutellum. Scale shown in mm.

are referred to as “macrosetae” (Fig. 2.5b,e) and “microsetae”, (Fig. 2.5a) respectively. The following abbreviations are used in figures: 1 abdsp, first abdominal segment spined; metn, metanotum; scm, scutellum.

Ancestral character state reconstruction:

To determine diagnostic characters for tribes and subfamilies of the Emesine Complex we traced the 40 characters across our combined Sanger/AHE phylogenetic hypothesis using Ancestral Character State Reconstruction (ACSR). Voucher specimens were examined to code character states for each taxon. Maximum likelihood ACSR was run using the function ace in the package Ape v5.7 (Paradis and Schliep, 2019). Model testing with the phytools v1.5 (Revell, 2012) function fitMk supported equal rates as the best fit model. Characters and their optimizations are outlined in the Results. As part of this dataset, we also reconstructed transitions for the comb-like structure and the notch on the pretarsus, two structures that could serve as proxies for spiderweb-associated behaviors.

RESULTS

Phylogenetic results

ModelFinder merged the original 384 (381 protein-coding AHE loci and three ribosomal genes) partitions into 23 partitions. Note that we use the current classification in reporting phylogenetic results but switch to the proposed classification for outlining and discussing results of the ACSR. The topology of the combined AHE and Sanger sequencing dataset (Fig. 2.4) was largely identical to those derived from the Sanger data

only (Fig. 2.S2) and AHE only (Fig. 2.7) datasets, with increased support across the backbone in the combined dataset (Fig. 2.S3) compared to the Sanger sequencing only. The only exception is the placement of *Oncerotrachelus* Stål, a genus traditionally included in "Saicinae". In both the AHE only and combined analyses, *Oncerotrachelus* was recovered as sister taxon to the remaining Emesine Complex, but this genus was supported as sister taxon to Ploiariolini + "Metapterini" + "Emesini" in the Sanger only analysis. All three analyses therefore recover "Saicinae" as paraphyletic (see below). While the exact position of *Oncerotrachelus* will benefit from additional testing, we use the relationships from the AHE and combined analyses for our proposed classification and ACSR of spiderweb-associated morphology.

The remaining "Emesinae", "Saicinae", and Visayanocorinae are split into two well-supported clades: "Saicinae" (excl. *Oncerotrachelus*) together with Collartidini, Leistarchini, and Visayanocorinae were recovered as sister group to the remaining emesine tribes "Emesini", Ploiariolini, and "Metapterini" that also form a well-supported clade, rendering "Emesinae" paraphyletic with respect to "Saicinae" and Visayanocorinae.

All analyses supported "Saicinae" (excl. *Oncerotrachelus*) as the sister group to a clade formed by (Collartidini + (Leistarchini + Visayanocorinae)). "Saicinae" (excl. *Oncerotrachelus*) are split into two well-supported monophyletic groups, the bristly clade including the Neotropical *Saica* Amyot & Serville and Afrotropical and Oriental *Polytoxus* Spinola*,* and the spiny clade. The enigmatic, apterous, undescribed genus of

Saicinae from Madagascar is recovered as sister taxon to the bristly clade. This result suggests that the tuberculate setae (27-2) on the forefemur in the Madagascan saicine are plesiomorphic and retained in this taxon and the spiny clade, and that the long forecoxa (23-1) in the undescribed genus is independently derived from those in other "Emesinae".

Within Collartidini, *Stenorhamphus* Elkins is paraphyletic, with *Collartida* recovered as sister taxon to *S. segarak* and *S. phuphan.* Collartidini are highly supported (100% UFBoot2, 99% SH-aLRT) as sister group to (Leistarchini + Visayanocorinae). Visayanocorinae are highly supported (100% UFBoot2, 90% SH-aLRT) as sister group of the emesine tribe Leistarchini. While the majority of genera within Leistarchini are monophyletic, *Ploiaria* Scopoli is polyphyletic.

The "Emesini" + "Metapterini" + Ploiariolini clade is characterized by rampant paraphyly: while Ploiariolini were monophyletic (100% UFBoot2, 100% SH-aLRT), they formed the sister lineage to a clade containing taxa currently classified as Emesini and Metapterini (e.g., *Myiophanes* Reuter and metapterine genera incl. *Metapterus* Costa and *Schidium* Bergroth). In addition, the "Emesini" genus *Eugubinus* Distant was recovered as the earliest diverging lineage in the entire clade. While the majority of "Emesini" genera included in our analyses were recovered as monophyletic (e.g., *Stenolemus* Signoret, *Polauchenia* McAtee and Malloch, *Emesa* Fabricius, and *Phasmatocoris* Breddin), the species-rich genus *Gardena* Dohrn was nested within a clade otherwise comprised of metapterine genera (e.g., *Emesaya* McAtee and Malloch

and *Ghilianella* Spinola). Our proposed new classification (see below) synonymizes these three tribes under Emesini. Future work should focus on increased sampling within Emesini and test the hypothesis that Ploiariolini remain as a subtribe of Emesini.

Ancestral Character State Reconstruction

Although our morphological matrix provided diagnostic features for our revised classification of the Emesine Complex, many of the 40 characters were homoplastic. Characters found exclusively in one clade, or strict synapomorphies, are defined as synapomorphies below, and those found across several clades, or contradicted synapomorphies, that can still be diagnostic are referred to as plesiomorphic. Reconstructions of all characters are provided in the "Supplementary results ACSR" file and are briefly discussed below. The Supplementary results ACSR file also includes photographs illustrating all characters; character states also illustrated in the body of the manuscript are referenced in the list below. Diagnostic features for each of the six existing and proposed tribes and the new concept of the subfamily Emesinae are shown in Fig. 2.7. In our character discussions below, we use the proposed classification that recognizes Emesinae (with Saicinae and Visayanocorinae as junior synonyms) and six tribes within Emesinae.

Head

1. Postocular portion of head, lateral view: less than twice as tall as wide, not raised well above anteocular portion (0), twice as tall as wide, swollen, almost rounded, raised above anteocular portion (1). The postocular portion of the head

not raised is plesiomorphic for Emesinae, and is retained in most lineages, with the raised and swollen condition being a synapomorphy for Oncerotrachelini.

2. Ventral surface of head, setae: absent (0), macrosetae present (1), tuberculate setae present (Fig. 2.5g) (2). The ventral surface of the head lacking setae is plesiomorphic for Emesinae, with macrosetae independently derived in Oncerotrachelini, Visayanocorini and Collartidini.
3. Ventral surface of labium, first visible segment, setae: absent (0), macrosetae present (1), tuberculate setae present (Fig. 2.5g) (2). Absence of setae on the ventral surface of the labium is plesiomorphic for Emesinae, with macrosetae present independently derived in Oncerotrachelini, Visayanocorini and Collartidini.
4. Ventral surface of labium, second visible segment, setae: absent (0), macrosetae present (1), tuberculate setae present (Fig. 2.5g) (2). Absence of setae on the second visible labial segment is plesiomorphic for Emesinae, with macrosetae present independently derived in Oncerotrachelini, Visayanocorini and Collartidini.
5. Posterior lobe of head, ocelli: absent (0), present (1). A lack of ocelli is plesiomorphic for Emesinae, with only two known emesine species possessing ocelli.
6. Labial segments, relative length: first visible longer than 2nd and 3rd, extends past posterior border of eyes (0), first visible does not extend past posterior

border of eyes (1). The first visible labial segment longer than 2nd or 3rd is independently derived in Oncerotrachelini and Visayanocorini.

7. First visible labial segment, height: similar height to other segments (0), swollen, larger height than other segments (1). The first visible labial segment with similar height to other segments is plesiomorphic for Emesinae. Within the spiny Saicini, a swollen first visible labial segment evolved once.
8. Second visible labial segment, height: similar height to other segments (0), swollen, larger height than other segments (Fig. 2.5g) (1). The second visible labial segment swollen is synapomorphic for Saicini.

Thorax

9. Anteroventral angle of pronotum, spines and setae: absent (0), tuberculate setae present (1), spine present (Fig. 2.5g) (2). The anteroventral angle of pronotum without spines and setae is plesiomorphic for Emesinae.
10. Apex of scutellum: no spine or tip present (Fig. 2.5m) (0), semicircular with slightly pointed tip (Fig. 2.5i,l) (1), spine present (Fig. 2.5h,j,k) (2). The apex of the scutellum without a spine is synapomorphic for Emesini. The apex spined is independently derived in Oncerotrachelini, Saicini and Visayanocorini. Character optimization of MRCA of Emesinae and Leistarchini is unresolved and shared between all three states.
11. Metascutum: bare (Fig. 2.5m) (0), with protuberance (Fig. 2.5i,j) (1). The metascutum with protuberance is synapomorphic for Saicini.

12. Forewing, corium: absent or extremely reduced (Fig. 2.3a-j) (0), well developed (1). The corium absent or extremely reduced is plesiomorphic for Emesinae.
13. Forewing, R and M: separate along MCU cell (Fig. 2.3f) (0), fused along proximal portion of MCU cell (Fig. 2.3a) (1), fused along medial portion of MCU cell (Fig. 2.3c) (2), fused along entire MCU cell via r-m crossveins (Fig. 2.3g) (3). The forewing R and M veins separate along the MCU cell is plesiomorphic for Emesinae. R and M veins fused along the proximal portion of the MCU cell is synapomorphic for Oncerotrachelini. The character optimization of Emesini is unresolved and shared between states (1) and (3).
14. Forewing, mcu-an1 (or cu-an1) crossvein: absent (Fig. 2.3g) (0), proximal-distal orientation (Fig. 2.3c) (1), anterior-posterior wing margin orientation, usually shorter than half the length of portion of An1 forming MCUAn1cu-an1 cell (Fig. 2.3f) (2). The forewing mcu-an1 crossvein in a proximal-distal orientation is synapomorphic for Saicini, with anterior-posterior orientation independently derived in Collartidini and Visayanocorini.
15. Forewing, M and CU, fused along proximal portion of wing: absent (Fig. 2.3c) (0), present (Fig. 2.3f) (1). The forewing M and CU veins not fused along the proximal portion of the wing is synapomorphic for Saicini.
16. Forewing, MCUAn1mcu-an1 (or MCUAn1cu-an1) cell: absent (Fig. 2.3g) (0), present (Fig. 2.3c,f) (1). Absence of forewing MCUAn1mcu-an1 cell is

plesiomorphic for Emesinae, with presence of cell independently derived in Saicini, Collartidini and Visayanocorini.

17. Forewing, MCUAn1 cell: absent (Fig. 2.3f) (0), present (Fig. 2.3a) (1). Absence of MCUAn1 cell is optimized as being found in MRCA of Emesinae, with presence a synapomorphy for Oncerotrachelini.
18. Forewing, r-m crossvein, proximal half of wing: absent (Fig. 2.3a) (0), one crossvein present (Fig. 2.3d) (1) two r-m crossveins present (Fig. 2.3e) (2). Two r-m crossveins in the proximal half of the wing is synapomorphic for Leistarchini.
19. Forewing, r-m crossvein, distal half of wing: absent (Fig. 2.3a) (0), present (Fig. 2.3e) (1). The presence of one r-m crossvein in the distal half of the wing is synapomorphic for Leistarchini.
20. Forewing, m-cu crossvein: absent (Fig. 2.3d) (0), present (Fig. 2.3h) (1). Absence of the m-cu crossvein is optimized as being found in MRCA of Emesinae.
21. Hindwing, m-cu crossvein: absent (Fig. 2.6a) (0), present (Fig. 2.6d) (1). Absence of the m-cu crossvein was hypothesized to be found in MRCA of Metapterini, however our analysis did not support this hypothesis. The presence of the m-cu crossvein in the hindwing is plesiomorphic for Emesinae.

Legs

22. Foreacetabulum, orientation: ventrad (0), anteriad (1). Anteriad orientation of acetabulum was previously used to classify Emesinae, but our analysis did not

support this hypothesis. The ventrad orientation is instead optimized as being found in MRCA of Emesinae.

23. Forecoxa, relative length: less than four times as long as wide (Fig. 2.1a,b,f) (0), four times as long as wide (Fig. 2.1c,g,h,i) (1). The forecoxa less than four times as long as wide is plesiomorphic for Emesinae. The forecoxa four times as long as wide is independently derived within Leistarchini, Collartidini and Emesini.
24. Forecoxa, macrosetae: absent (0), present (1). Macrosetae on the forecoxa is synapomorphic for Collartidini.
25. Foretrochanter setae: no setae, or different combination of characters (0), setae present (1), tuberculate setae present (2). Setae on the foretrochanter is synapomorphic for Leistarchini, Visayanocorini and Collartidini. Tuberculate setae on the foretrochanter is synapomorphic for Saicini.
26. Forefemur, large ventral basal spine: absent (0), present (1). The large ventral basal spine on the forefemur was previously used to classify Metapterini, but our analysis did not support this hypothesis.
27. Forefemur, ventral surface, setae: absent of macro or tuberculate setae (0), composed primarily of macrosetae (Fig. 2.5e) (1), composed primarily of tuberculate setae (Fig. 2.5f) (2). The character optimization of Emesinae is ambiguous and shared between all three states. The ventral surface of the forefemur composed primarily of macrosetae is independently derived in Oncerotrachelini and Leistarchini + Visayanocorini + Collartidini. The ventral

surface of the forefemur composed of tuberculate setae is synapomorphic for Saicini and Emesini.

28. Forefemur, posterodorsal surface, tuberculate setae: absent (0), present (Fig. 2.5g) (1). The posterodorsal surface of forefemur is optimized as being found in MRCA of spiny clade of Saicini.
29. Fore and middle tibia, fossula spongiosa: absent (0), present (1). The absence of fossula spongiosa is plesiomorphic for Emesinae.
30. Foretibia, ventral surface, setae: microsetae present or different combination of characters present (Fig. 2.5a) (0), macrosetae present (Fig. 2.5b) (1), tuberculate setae (Fig. 2.5c) (2), adpressed tuberculate setae (Fig. 2.5d) (3). Macrosetae on the ventral surface of the foretibia is synapomorphic for Leistarchini, with tuberculate setae synapomorphic for Emesini.
31. Foretibia, posterodorsal surface, tuberculate setae: absent (0), present (1). The posterodorsal surface of foretibial with tuberculate setae is optimized as being found in MRCA of spiny clade of Saicini.
32. Foretibial spur projecting beyond tarsal insertion: absent (0), present (1). The foretibial spur projecting beyond the tarsal insertion is synapomorphic for Visayanocorini.
33. Foretarsus, relative length: approximately equal to mid and hind tarsi (0), longer than mid and hind tarsi (1). The foretarsi longer than the mid and hind tarsi is independently derived once within Leistarchini, and three times within Emesini.

34. Foretarsomeres, number: three tarsomeres (0), two tarsomeres (1), not segmented (2). Two tarsomeres evolved twice within Emesini. The foretarsomeres not segmented is independently derived twice within Emesini and once within Leistarchini.
35. Foretarsomeres, relative length: tarsomere 1 longer than other segments combined (0), tarsomere 1 short, 2 and 3 approx. equal in length (1), tarsomeres approximately equal in length (2). The first tarsomere longer than the other segments combined is independently derived within Saicini, Leistarchini and Emesini. The first tarsomere being short is optimized as being found in MRCA of Emesinae.
36. Distal tarsomeres, ventral surface with flattened and widened tenant hairs: absent (0), present (1). The distal tarsomeres ventral surface with flattened and widened tenant hairs is synapomorphic for Saicini.
37. Foretarsal claws, orientation, to each other: subparallel (Fig. 2.2b) (0), 30-120 degree (Fig. 2.2a) (1). Foretarsal claws with subparallel orientation is synapomorphic for Leistarchini.

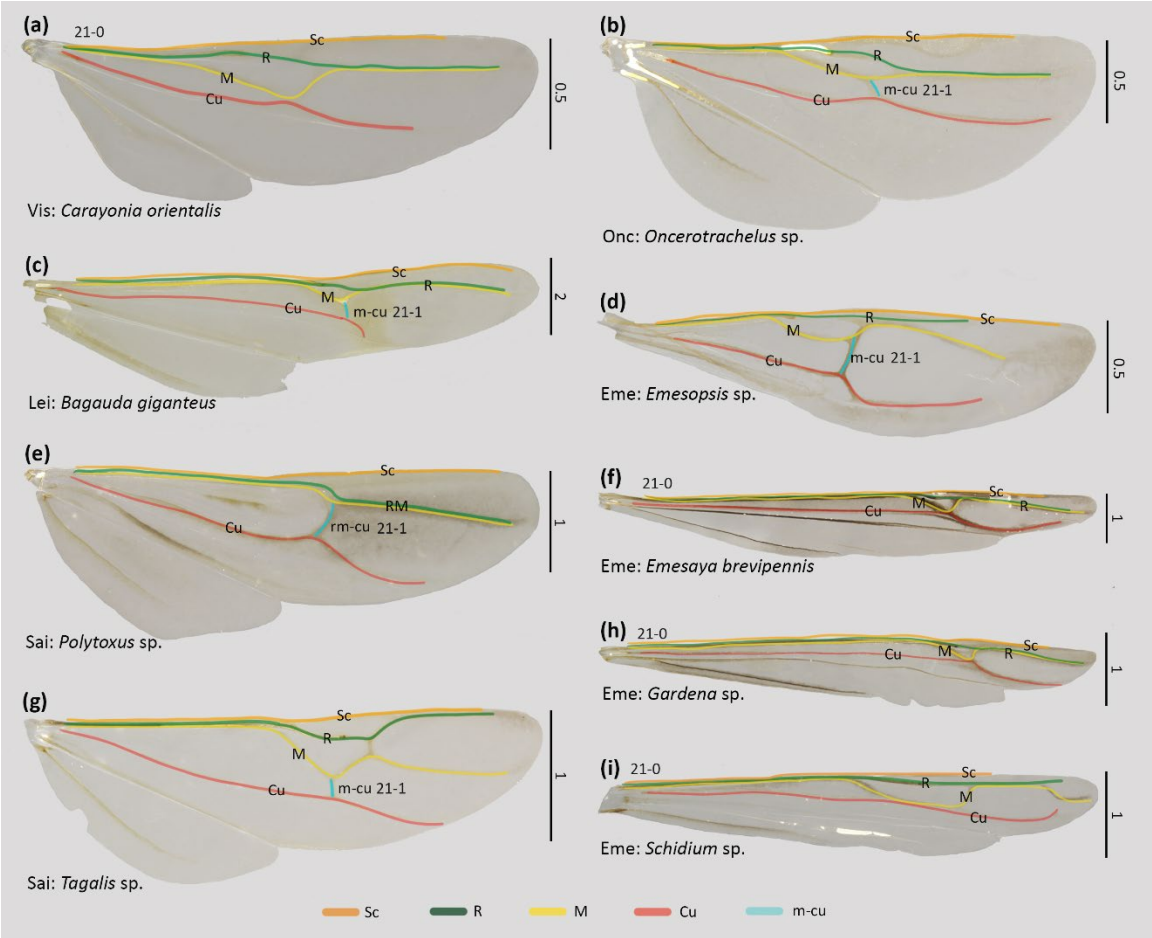

Figure 2.6: Hindwing of selected Emesinae showing proposed interpretation of wing venation. Character 20. **(a)** Visayanocorini: *Carayonia orientalis*; **(b)** Oncerotrachelini: *Oncerotrachelus* sp.; **(c)** Saicini: *Polytoxus* sp.; **(d)** Saicini: *Tagalis* sp.; **(e)** Leistarchini: *Bagauda giganteus*; **(f)** Leistarchini: *Bettyella* sp.; **(g)** Emesini: *Gardena* sp.; **(h)** Emesini: *Emesaya brevipenis*; **(i)** Emesini: *Emesopsis* sp.; **(j)** Emesini: *Schidium* sp. Tribes follow proposed classification. Onc, Oncerotrachelini; Vis, Visayanocorini; Sai, Saicini; Lei, Leistarchini; Col, Collartidini; Eme, Emesini. Scale shown in mm.

38. Foretarsal claws, symmetry: symmetrical (Fig. 2.2d) (0), asymmetrical (Fig. 2.2b) (1). Asymmetry evolved once within Leistarchini and three times within Emesini. However, increased sampling of *Bagauda* within Leistarchini may have skewed ACSR results.

39. Foretarsal claws, comb-like structure: absent (Fig. 2.2a,b,d) (0), present (Fig. 2.2c) (1). The comb-like structure on the foretarsal claws is synapomorphic for Emesini and lost three times within the tribe.
40. Foretarsal claws, ventral lamella, medially incised: absent (0), present (Fig. 2.2d) (1). The ventral lamella is synapomorphic for Emesini and lost once within the tribe.

DISCUSSION

Few insects have adapted to life on the web to the extent found in Emesinae. While much is unknown regarding functional morphology and even diet preferences in Emesinae, the lack of a robust phylogenetic hypothesis has prevented any evolutionary insight into this fascinating behavior. No previous analyses have had the breadth or the depth necessary to resolve relationships in this large and diverse group (Weirauch, 2008; Weirauch and Munro, 2009; Hwang and Weirauch, 2012; Castro-Huertas, Forero and Grazia, 2021). By using a combined AHE and Sanger sequencing dataset, we generated a robust phylogenetic hypothesis and reclassified the Emesine Complex into the subfamily Emesinae with six tribes, opening the door for downstream evolutionary analyses. While this is clearly a major step towards better understanding phylogenetic relationships of Emesinae, increased sampling and study of this rarely collected group is needed to fully understand generic level relationships.

Emesini are now the largest tribe of Emesinae, with a wide variety in behavior, ranging from entirely free living to living their entire life, from egg to adult, on spiderwebs. We found that the notch and comb structures (Figs 2.2c, d, 2.6) were present in the most recent common ancestor of Emesini which likely facilitated stalking and luring behaviors similar to those documented for *S. bituberus*. Based on this result, we hypothesize that the most recent common ancestor of Emesini was associated with spider webs, a lifestyle retained in the majority of species in this tribe. Subsequent losses of the notch (one loss) and comb (three losses) structure within Emesini point to four potential losses of spiderweb association within the clade. While we know very little regarding spiderweb-associated behaviors in Leistarchini, and the comb and notch are not found in this group, it is noteworthy that some species have been found associated with spiderwebs (Wygodzinsky, 1966). While the comb and notch structures may be central to the stalking and luring behaviors in Emesini, we suspect that spider-predatory strategies in Leistarchini employ a different set of morphological and behavioral features. Future research should focus on establishing diet repertoires across the different lineages of Emesinae, investigate spider web-associated behaviors, but also perform functional morphological studies of legs including pretarsal structures to untangle these fascinating predatory strategies.

This is a landmark study in assassin bug phylogenetics and classification, as it is one of the first phylogenetic studies at the subfamily level that is used to propose a revised classification. While the non-monophyly of many subfamily-level assassin bug

taxa has long been recognized (Weirauch, 2008; Hwang and Weirauch, 2012), only a phylogenetic study focused on millipede assassin bugs was translated into a new classification that recognized Tribelocephalinae as a junior synonym of Ectrichodiinae (Forthman and Weirauch, 2017). Large-scale phylogenomic analyses across Reduvioidea (Knyshov et al., in prep.) are now being used to propose a dramatically revised subfamily and tribal classification of assassin bugs (Masonick et al., in prep). Finally, Emesinae are unique among Reduviidae in having a worldwide distribution and containing more fossils than any other subfamily (15 out of the 44 reduviid fossils [Popov and Chłond, 2015]). Together, this makes Emesinae ideal for future biogeographic studies. As gaps in our understanding of the morphology and behavior of Emesinae are filled, we are now able to perform downstream evolutionary analyses, gaining greater understanding into the evolution of this fascinating subfamily.

TAXONOMY

The proposed classification of Emesinae is below. Tribes are organized phylogenetically (Fig. 2.7).

Emesinae Amyot and Serville, 1843

Emesinae Amyot and Serville, 1843: 393.

Saicinae Stål 1859, 3:328. **New synonymy.**

Visayanocorinae Miller 1952, 28:89. **New synonymy.**

Type genus: *Emesa* Fabricius, 1803

Diagnosis: Emesinae are recognized by the absence of ocelli, absence or extreme reduction of the corium (Fig. 2.3), and lack of the fossula spongiosa on the fore and middle tibia.

Oncerotrachelini Standring, Forero and Weirauch trib. nov.

Type genus: *Oncerotrachelus* Stål, 1868

Diagnosis: Recognized among Emesinae by having the postocular portion of the head twice as tall as it is wide, swollen and raised above anteocular portion, the first visible labial segment being the longest and extending past the posterior border of the eyes and on the forewing, and by the presence of the MCUAn1 cell (Fig. 2.3a).

Discussion: Oncerotrachelini (Fig. 2.1d) are comprised of a single genus, *Oncerotrachelus.* They are morphologically distinct from other Emesinae by the postocular portion of the head being twice as tall as it is wide, swollen and raised above anteocular portion. In addition, macrosetae are present on the first and second visible segments of the ventral surface of the labium, and the first visible labial segment is the longest and extends past the posterior border of the eyes. Oncerotrachelini also have a long spine present on the apex of the scutellum. On the forewing, R and M are fused along the proximal portion of the MCU cell. There is also an MCUAn1 cell present (Fig. 2.3a).

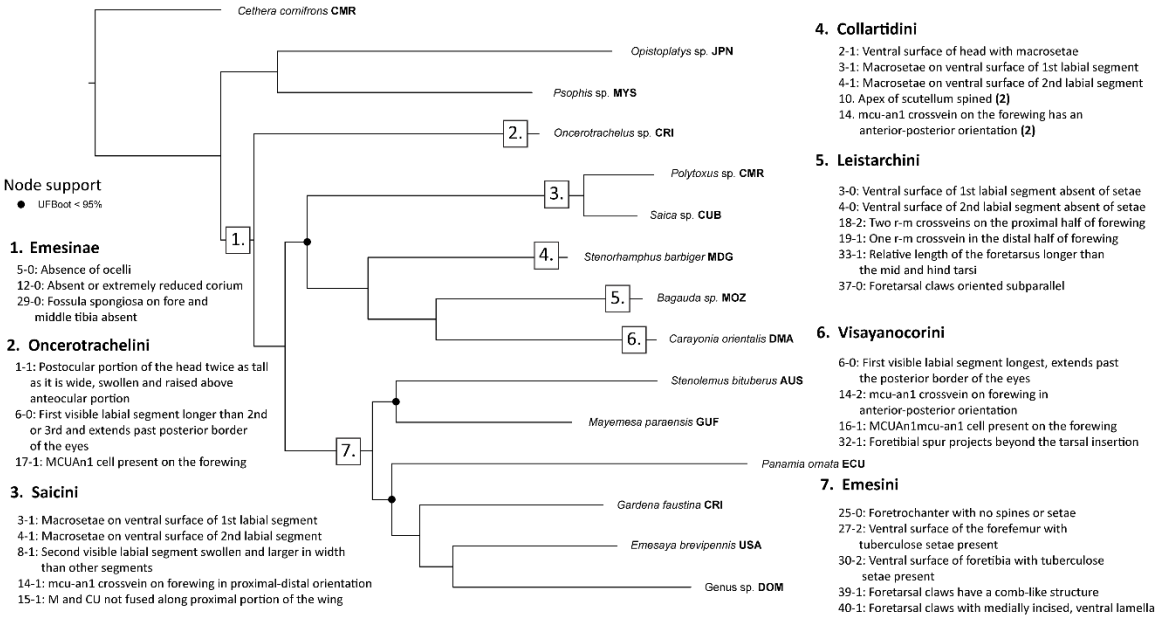

Figure 2.7: Phylogenetic reconstruction produced by a maximum-likelihood analysis of the AHE dataset in IQ-TREE2. Solid black circle at node indicates UFbootstrap support less than 95%. SH-aLRT support values above 75% on all nodes. Character optimizations derived from Ancestral Character State Reconstruction on Figure 6, shown here for ease of visualization.

Saicini Stål stat. nov.

Type genus: *Saica* Amyot and Serville, 1843

Diagnosis: Recognized among Emesinae by the presence of macrosetae or tuberculate setae on the ventral surface of the first and second visible segments of the labium (Fig. 2.5g), the second visible labial segment swollen and larger in width than the other segments, the mcu-an1 crossvein on the forewing is in the proximal-distal orientation and M and CU are not fused along the proximal portion of the wing (Fig. 2.3c,d).

Discussion: The ventral surface of the head carries either macrosetae or tuberculate setae (Fig. 2.5g). The ventral surface of the first segment of the labium has either macrosetae or tuberculate setae (Fig. 2.5g). The ventral surface of the second segment of the labium has macrosetae and rarely tuberculate setae present. The second visible

labial segment is swollen and larger in width than the other segments. The apex of the scutellum carries a long spine (Fig. 2.5j). The metascutum is spined (Fig. 2.5j). The mcu-an1 crossvein on the forewing is in the proximal-distal orientation (Fig. 2.3c, d). M and CU are not fused along the proximal portion of the wing. The foretrochanter, forefemur (ventral and posterodorsal surface) and foretibia (posterodorsal surface) have tuberculose setae. Foretarsomere 1 is longer than the other segments combined. The ventral surface of the distal tarsomeres have flattened and widened tenant hairs (scopula) (Fig. 2a).

There are two primary groups of Saicini, spiny and bristly. An apterous, spiny undescribed genus from Madagascar is sister to the bristly clade. We here refrain from subdividing Saicinae into subtribes, because additional taxa representing the spiny and bristly clades should be included in phylogenetic analyses before this step is taken. However, we predict that *Bagriella* McAtee & Malloch*, Buninotus* Maldonado*, Cuernolestes* Elkins*, Exaeretosoma* Elkins*, Gallobelgicus* Distant*, Panagrocoris* Miller and *Vadonocoris* Villiers will likely be recovered as part of the spiny clade. Similarly, *Banarocoris* Miller*, Micropolytoxus* Elkins and *Spairapeltis* Miller are hypothesized to belong to the bristly clade. These two clades could be treated as subtribes, with the undescribed genus from Madagascar being accommodated in a subtribe on its own.

Collartidini Wygodzinsky, 1966

Type genus: *Collartida* Villiers, 1949

Diagnosis: Recognized among Emesinae by macrosetae present on the ventral surface of the head, the first and second segments of the ventral surface of the labium with macrosetae, the apex of the scutellum spined, and the mcu-an1 crossvein on the forewing oriented anterior-posteriorly to the wing margin (Fig. 2.3f).

Leistarchini Stål, 1862

Type genus: *Leistarches* Dohrn, 1860

Diagnosis: Recognized among Emesinae by the ventral surface of the first and second visible segments of the labium without setae, two r-m crossveins on the proximal half and one r-m crossvein in the distal half of the forewing (Fig. 2.3e), the relative length of the foretarsus longer than the mid and hind tarsi and the foretarsal claws oriented subparallel to each other.

Visayanocorini Miller stat. nov.

Type genus: *Carayonia* Miller, 1952

Diagnosis: Recognized among Emesinae by the first visible labial segment longer than the second or third, extending past the posterior border of the eyes, the mcu-an1 crossvein oriented anterior-posteriorly to the wing margin, the MCUAn1mcu-an1 cell present on the forewing, the m-cu vein absent from the hindwing and the foretibial spur projecting beyond the tarsal insertion.

Emesini Amyot and Serville, 1843

Emesini Amyot & Serville, 1843

Metapterini Stål, 1874. **New synonymy.**

Ploiariolini Van Duzee, 1916. **New synonymy.**

Type genus: *Emesa* Fabricius, 1803

Diagnosis: Recognized among Emesinae by the foretrochanter without spines or setae, the ventral surface of the forefemur and foretibia with tuberculate setae (Fig. 2.5f) and the foreleg pretarsi with a comb-like structure (Fig. 2.2c), and a medially incised, ventral lamella, or notch (Fig. 2.2d).

Discussion: Based on our phylogenetic hypothesis, Ploiariolini and "Metapterini" are synonymized with Emesini. However, while Ploiariolini are nested within the polyphyletic "Emesini" and "Metapterini", they remain monophyletic.

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CHAPTER 3:

Evolution and biogeographic history of thread-legged assassin bugs (Emesinae: Reduviidae)

ABSTRACT: Distribution patterns are the result of vicariance or dispersal, the latter of which occurs actively via flying, walking, or swimming, or through passive dispersal (floating, storms). Transoceanic dispersal appears to be rare in Reduviidae, the assassin bugs, but in some lineages seems to have resulted in rapid diversification after colonization. Emesinae are unique among assassin bugs in including four genera with cosmopolitan distributions. Their relatively high diversity on islands compared to other reduviids and a potentially young age (~87 MYA) suggest that dispersal rather than vicariance led to their current distribution ranges. Estimating a divergence dated phylogeny and biogeographic reconstruction, we here test if dispersal and not vicariance is responsible for extant ranges of the four cosmopolitan genera and examine if dispersal occurred during the same periods and in the same directions, suggesting that they may have been driven by a common mechanism. We found that three of the cosmopolitan genera diverged during the Eocene, and one during the Oligocene, leading us to reject vicariance. Despite the similar timing of divergence, all genera dispersed across different oceans, and mostly originated from different regions. Due to the age and estimated direction of dispersal, dispersal via land bridges is unlikely. Instead, we hypothesize that transoceanic dispersal in Emesinae occurred primarily via flotsam, and that events such as the Chesapeake Bay impact led to increased dispersal during the

Eocene. More densely sampled phylogenies of the cosmopolitan genera and biological data are critical to better understand the historical biogeography of this group of predatory true bugs.

INTRODUCTION

Migration occurs across the animal kingdom through a variety of active and passive methods of locomotion such as flying, swimming, walking, or drifting (Dingle and Alistair Drake, 2007). Birds and whales are common examples of animals with extensive ranges; however, many insects are also capable of migrating across vast distances (Troast *et al.*, 2016). One remarkable example is found within dragonflies, *Pantala flavescens* (Troast *et al.*, 2016). Though primarily circumtropical, *P. flavescens* is also observed in many temperate areas. Studies finding gene flow between all geographic regions suggest *P. flavescens* should be considered a global panmictic population (Troast *et al.*, 2016). In contrast, other insect species have such low rates of dispersal and small endemic ranges that traveling only a short distance may lead to speciation. Between these two extremes there is another option: some insects are capable of long distance dispersal, but only on rare occasions. Predicting the success of speciation for taxa undergoing long distance dispersal is challenging due to the variable nature of colonization and survival and the unknown effects of selection (Gillespie *et al.*, 2012). However, we can develop hypotheses of dispersal mechanisms by analyzing present-day ranges, habitat

preference and morphology, and combining these observations with estimations of ancestral ranges and timing of dispersal.

Assassin bugs (Heteroptera: Reduviidae) are one of the most diverse families of Heteroptera with a wide range of fascinating prey capture strategies, including resin covered legs to trap prey, luring and stalking behavior, and attracting ants with 'feathery legs' and scent glands. Though Reduviidae have a worldwide distribution, only 8 out of the 19 subfamilies are cosmopolitan (Masonick et al., in prep). Of the eight subfamilies, thread-legged assassin bugs, or Emesinae, are unique in including four cosmopolitan genera or generic groups, suggesting that Emesinae are either ancient and their distribution shaped by vicariance or that long distance dispersal has been involved in generating extant distribution ranges. Species richness of Emesinae compared to other Reduviidae is high on some oceanic islands. An example for this is seen in Hawaii, where 18 out of the 28 known Reduviidae species are Emesinae (Hawaiian Terrestrial Arthropod Checklist, 2002). Emesinae are the fourth most diverse subfamily of Reduviidae on the continental island of Madagascar and genus-level endemism is low, suggesting that species in this group may have significant dispersal capabilities (Weirauch, 2022). This is surprising, given that most Emesinae are delicate and while some species can be seen flying around light traps at night, they do not give the appearance of being strong fliers. However, biological data to support this observation are unavailable.

Despite this seeming success in dispersal, little is known about when or how Emesinae dispersed. Two previous dating analyses of Reduviidae suggest that Emesinae diverged from their sister lineage within Reduviidae ~87 MYA (Hwang and Weirauch, 2012) or ~108 MYA (Masonick et al., in prep.), making vicariance an unlikely explanation for the wide ranges of several emesine genera. However, emesine sampling was limited to ten species, and only two emesine fossils were included. Increased taxon sampling and inclusion of additional emesine fossils is critical to test the timing of divergences across Emesinae.

For insect species that have low aerial motility such as Emesinae, land bridges are frequently cited as potential avenues of transoceanic dispersal, but to test this hypothesis an estimation of the timing and direction of their dispersal routes is needed. Aerial dispersal is especially unlikely for two of the emesine genera, *Gardena* Dohrn (~46 spp.) and *Ploiaria* Scopoli (~122 spp.) as they are both poor flyers and include apterous and brachypterous species (Wygodzinsky, 1966). However, both *Stenolemus* Signoret (~80 spp.) and *Empicoris* Wolff (~79 spp.) have a high surface area to volume ratio and all known species are fully winged (Wygodzinsky, 1966). While still relatively poor flyers, it is possible that they traveled via atmospheric pathways (Pretorius *et al.*, 2023). Another possible mode of transoceanic dispersal is floating on flotsam as has been recorded in insects such as termites (Chiu et al., 2021). Before predictions can be made on their mode of dispersal, however, estimations must be made regarding the divergence time of each of the cosmopolitan genera, as well as their ancestral ranges.

Facilitating divergence dating analyses, Emesinae contain more fossils than any other reduviid subfamily (i.e., 14 out of the 43 currently described reduviid fossils [Popov and Chłond, 2015]). However, 12 out of the 14 fossils are found within a single tribe, Emesini, making them largely redundant for fossil calibration purposes given current phylogenies are incompletely sampled (Standring et al., 2023). In addition, nine of the Emesini fossils date to the Middle Miocene and are thus relatively young to be of use as node calibrations. Clearly, careful placement of the fossils is necessary due to the high number of young fossils within one tribe. The aims of this paper are threefold. First, we will use the morphological matrix from Standring et al. (2023) to determine placement of fossils and increase the number of emesine fossils used in dating analyses. Second, using the comprehensive phylogenetic hypothesis for Emesinae by Standring et al. (2023), we will estimate divergence dates across Emesinae and test the hypothesis that Emesinae diverged from their sister lineage in the Mid to Late Cretaceous. Third, we will test if the four cosmopolitan genera originated in the same biogeographic region(s) and around the same time period and if estimated dispersal routes suggest common mechanisms of dispersal.

MATERIAL AND METHODS

Taxon sampling and sequencing

Sequence data were derived from Standring et al. (2023). For detailed taxon sampling and specimen vouchering see Standring et al. (2023). Briefly, the dataset consists of 174

ingroup Emesinae taxa and 48 outgroup taxa (46 other Reduviidae, and two non-reduviid heteropterans), for a dataset of 222 terminals. All six tribes of Emesinae are represented by multiple taxa (Oncerotrachelini: nine taxa; Saicini: 30 taxa, Visayanocorini: four taxa; Collartidini: five taxa; Leistarchini: 37 taxa; Emesini: 89 taxa). Voucher specimens were databased using the Arthropod Easy Capture Specimen (AESC) database (https://research.amnh.org/pbi/locality/), publicly available through the Heteroptera Species Pages (https://research.amnh.org/pbi/heteropteraspeciespage/) where records are served directly from the AESC database.

Protocols for extraction, amplification, PCR cleaning, and sequencing followed those described in Weirauch and Munro (2009), with the exception that occasionally abdomens were used for extraction when genomic DNA yield from a leg was too low. PCR products were cleaned using the Bio 101 Geneclean Kit® or SureClean from Bioline. Forward and reverse strands were assembled, edited, and aligned in Geneious 11.1.5 (https://www.geneious.com). Assembled sequences were verified using NCBI BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi).

Divergence dating analysis

Sanger sequencing data from Standring et al. (2023) was used to estimate divergence dates, targeting three gene regions: 28SD2 rDNA, 28SD3-5 rDNA, and 18S rDNA (207 in- and outgroup taxa, 3,865 bp). These three gene regions were also extracted from the high-throughput sequencing datasets (12 ingroup taxa, 3 outgroup taxa).

To speed up the analysis and increase ESS values we used the phylogenetic hypothesis from Standring et al. (2023) as a fixed tree in our divergence dating analysis. The fixed tree was generated in IQ-TREE2 using a combined Sanger sequencing and AHE dataset and made ultrametric in R using chronos in ape (Paradis & Schliep, 2019).

The Bayesian time-calibrated tree was estimated in BEAST2 v.2.6.6 using the birth-death tree model and the relaxed log-normal clock model. Five fossils were included in the analysis, covering two emesine tribes (Table 3.1). Justification for placement of fossils is based on synapomorphies from the morphology matrix provided in Standring et al. (2023). The default BEAST2 uniform clock prior is set to zero to infinity. This is unspecific and improper (does not integrate to one). To remedy this situation, we used a lognormal prior for ucldMean and increased the speed of convergence by providing a mean value of 0.000001. Rejection of the strict clock model was confirmed with the observation that the 95% credible interval of ucld.stdev excluded zero. Three separate analyses were run to confirm proper mixing of chains.

Chosen amber fossils, their type specimen numbers, publication date, node numbers fossils are placed at and justification for node calibrations are shown below (Table 3.1). For fossil priors, we chose the oldest fossil crown member of a clade when multiple taxa were available; all fossils were chosen with Parham et al. (2012) best practices in mind. A log normal distribution was used for all fossil priors, setting the minimum age possible in the fossil's range as the zero offset and choosing parameters such that the median was the maximum age range for the fossil.

Table 3.1: Age of fossils included in analysis.

Fossil	**Type specimen**	**Publication**	**Fossil placement**	**Age and justification**	**Prior**	**Shape**	**Placement justification**
Emesopsis similis	Hoffeins 1612-4	Popov and Chlond 2015	364	34-48 MYA; Aleksandrova and Zaporozhets, 2008	Log normal	M - 1.5 S - 1.0 Offset - 34	10:1 - Ploiariolini 13:3 - Ploiariolini 14:2 - *Emesopsis* 18:1 - Ploiariolini 20:1 - Ploiariolini
Malacopus wygodzinskyi	SMNS Do-3390-M	Popov, 1987	370	15-20 MYA; Kinzelbach, 1979	Log normal	M - 1.0 S - 1.0 Offset - 15	10:2 - *Malacopus, Empicoris* 13:3 - *Malacopus* 20:0 - *Malacopus*
Emesinae sp.	AMNH C88720	Grimaldi et al., 1989	233	90-92 MYA; Grimaldi, 1999	Log normal	M - 1.5 S - 1 Offset - 90	Forecoxa 4x as long as wide, head shape/thorax typical for Emesinae but can't place within
Stenorhamphus mixtus	GPIG 3602	Putschkov & Popov 1995	307	34-48 MYA; Aleksandrova and Zaporozhets, 2008	Log normal	M - 2.1 S - 1.0 Offset - 34	Based on placement in Smith et al.

Biogeography analysis

We tested the fit of three different dispersal models in BioGeoBEARS v1.1.2; likelihood-based Dispersal-Extinction Cladogenesis (DEC), likelihood version of the Dispersal-Vicariance Analysis (DIVALIKE), and a likelihood range evolution model BAYAREALIKE ((Matzke, 2013). For all models tested, species were restricted to only occupy two states at any given time to decrease run time and because the maximum range of any species in our analysis was one. Recent work has shown that +J models can be included in AICc comparisons (Matzke, 2021). Accordingly, all three models were tested with and without founder-event speciation (+J). We selected the best fitting biogeographical model within the six scenarios using the lowest AICc value. The best selected reconstructed areas model was mapped over the best time-calibrated phylogeny.

RESULTS

Divergence dating analysis

Analysis of log files in Tracer showed ESS values above 700 and mixing across three independent analyses. We found that Emesinae diverged from its sister lineage within Reduviidae (i.e., all remaining Reduviidae except the Phymatine Complex) during the Late Cretaceous 99 MYA (95% HPD 91-107 MYA). Oncerotrachelini diverged from the rest of Emesinae ~95 MYA (95% HPD 90-100 MYA), but diversification within the strictly New World *Oncerotrachelus* did not start until ~31.5 MYA (95% HPD 17-46 MYA). Saicini diverged from ((Leistarchini + Visayanocorini) + Collartidini) ~85 MYA (95% HPD 76-94

MYA), with subsequent diversification within the tribe starting ~71 MYA (95% HPD 58-84 MYA). Collartidini diverged from (Leistarchini + Visayanocorini) ~69 MYA (95% HPD 57-82 MYA), with Visayanocorini and Leistarchini splitting ~66 MYA (95% HPD 53-79 MYA). Leistarchini diversified further during the Eocene 48.5 MYA (95% HPD 38-59). The cosmopolitan leistarchine genus *Ploiaria* diverged from its sister lineage, the Afrotropical genus *Paraluteva* Villiers also during the Eocene, ~37.5 MYA (95% HPD 29-46 MYA). It is important to point out that we refer to the genus *Ploiaria* as the lineage that includes all sampled *Ploiaria* species and also several species currently accommodated in other genera, including *Gnomocoris* McAtee and Malloch (1sp.; Borneo), *Orthunga* Dohrn (~20 spp.; Afrotropical) and *Armstrongula* Wygodzinsky (1 sp.; Australia) that should be synonymized with *Ploiaria* in the future.

Emesini diverged from their sister group ~87.5 MYA (95% HPD 79-96 MYA), with diversification within this lineage starting ~77 MYA (95% HPD 67-87 MYA). Two of the three cosmopolitan genera within Emesini diverged during the Eocene, similar to, but slightly older than the the leistarchine *Ploiaria*; *Gardena* diverged from the Neotropical *Bergemesa* Wygodzinsky ~41 MYA (95% HPD 31-51 MYA) and *Empicoris* from the clade including *Tridemula* Horvath (~9 spp.; Australasian and Indomalayan), *Ademula* McAtee and Malloch (~13 spp.; Indomalayan and Afrotropical), *Malacopus* Stal (~7 spp,; Neotropical), and *Panamia* Kirkaldy (1 sp.; Neotropical) ~34.5 MYA (95% HPD 26-43 MYA). *Stenolemus* was the only cosmopolitan genus to diverge during the Oligocene 23 MYA (95% HPD 15-31 MYA).

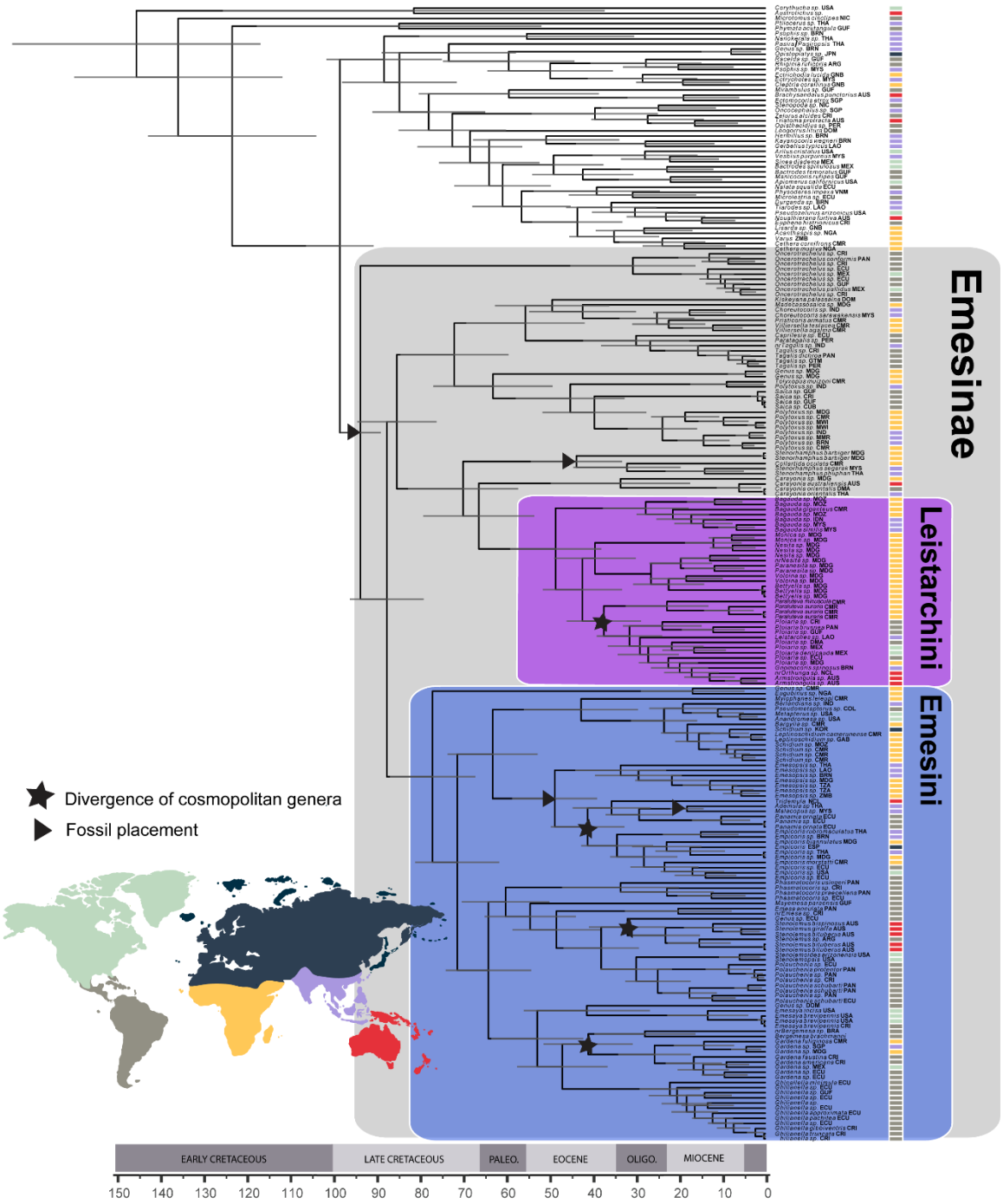

Figure 3.1: Bayesian divergence dated phylogeny, estimated in BEAST2 using the birth-death model. Stars represent cosmopolitan genera. Arrows indicate fossils.

Biogeography analysis

The DIVALIKE +J model had the best fitting AICc values (Table 3.2). This reconstruction estimates that the most recent common ancestor (MRCA) of *Ploiaria* occurred in the Neotropics, with subsequent dispersal, mostly within the Miocene, to the Indomalaysian, Nearctic and Australasian regions (Fig. 3.2). Derived from an ancestor with Neotropical distribution (*Bergemesa* + *Gardena*), the ancestral range for *Gardena* was estimated to be in the Neotropical and Afrotropical regions, with further diversification occurring within the Neotropics and Afrotropics, and subsequent dispersal to the Nearctic and Indomalaysia during the Miocene and Pliocene (Fig. 3.3). *Empicoris* originated in the Afrotropics and Indomalaysia, with subsequent dispersal to the Neotropics, Palearctic and Nearctic regions, mostly during the Oligocene and Miocene (Fig. 3.4). We excluded *Stenolemus* from our biogeography analysis as we were unable to include species from regions other than the Australiasian and Neotropical.

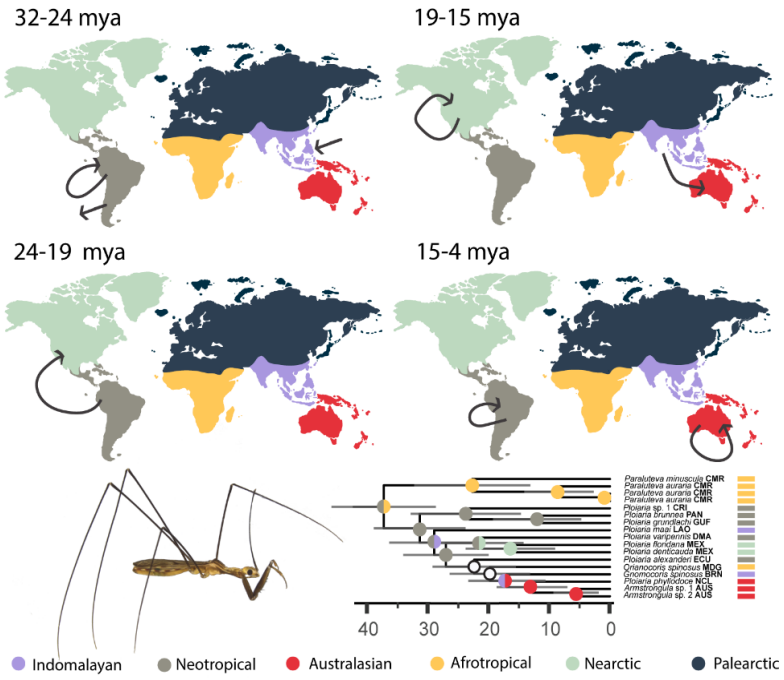

Figure 3.2: "*Ploiaria*" BioGeoBEARS results. Circles represent ancestral areas, not probabilities. When ancestral areas were found less than 90% of the time they were marked as ambiguous.

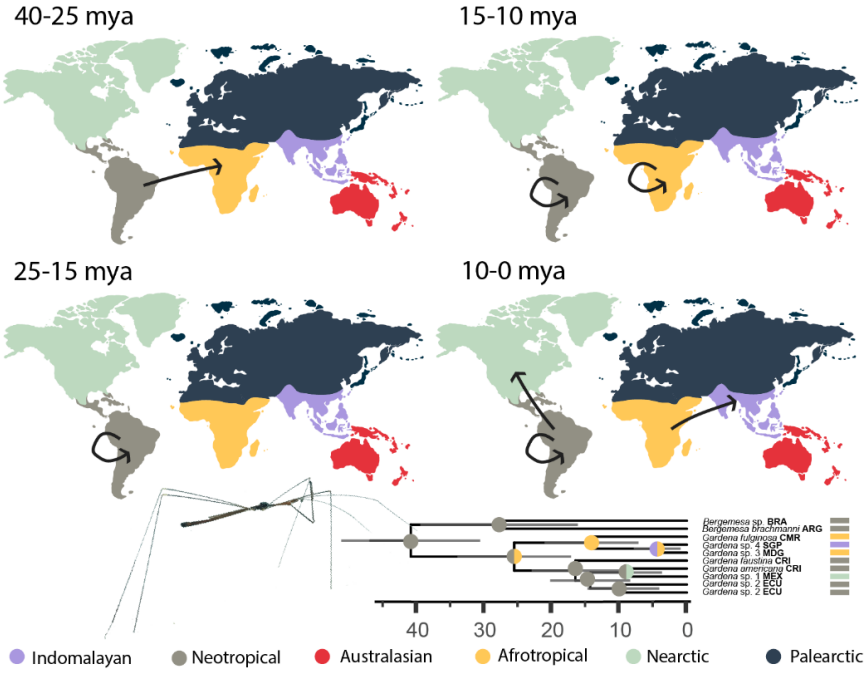

Figure 3.3: *Gardena* BioGeoBEARS results. Circles represent ancestral areas, not probabilities. When ancestral areas were found less than 90% of the time they were marked as ambiguous.

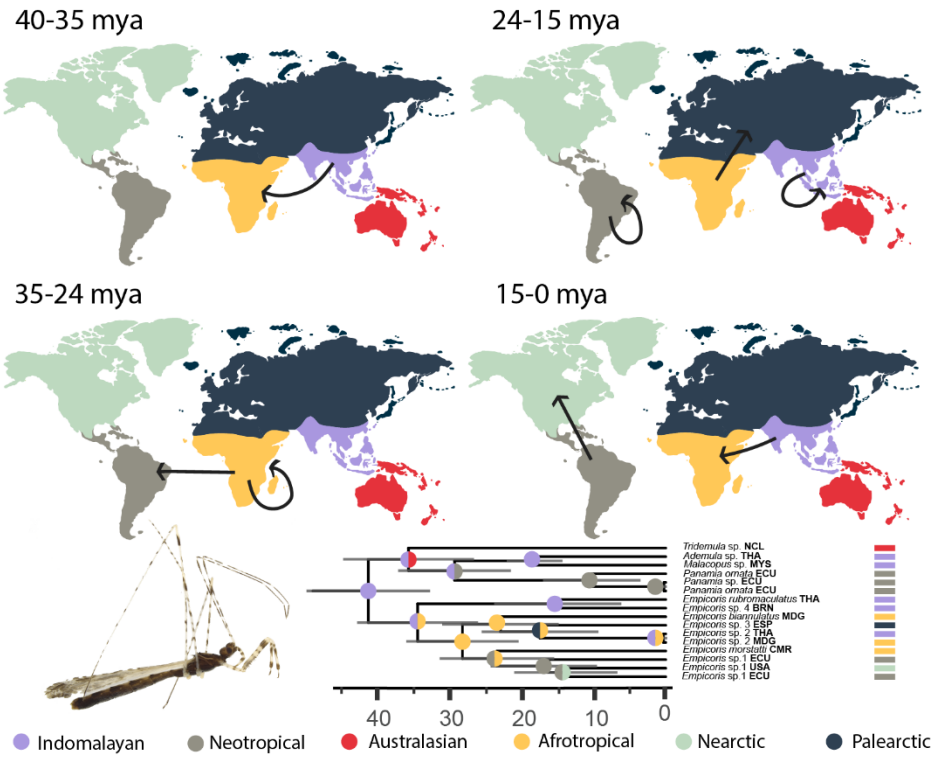

Figure 3.4: *Empicoris* BioGeoBEARS results. Circles represent ancestral areas, not probabilities. When ancestral areas were found less than 90% of the time they were marked as ambiguous.

Table 3.2: Likelihood parameters of ancestral area models tested.

Model	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-383.6	2	0.0021	0.0017	0	771.3	2.70E-47
DEC+J	-276.7	3	1.00E-12	1.00E-12	0.048	559.5	0.27
DIVALIKE	-366.7	2	0.0024	1.00E-12	0	737.5	6.10E-40
DIVALIKE+J	-275.8	3	1.00E-12	1.00E-12	0.047	557.7	0.66
BAYAREALIKE	-551.5	2	0.01	0.01	0	1107	3.50E-120
BAYAREALIKE+J	-278.1	3	1.00E-07	1.00E-07	0.047	562.2	0.069

DISCUSSION

With 14 out of the total 43 reduviid fossils, Emesinae contain more fossils than any other reduviid subfamily (Popov & Chłond, 2015). However, the relatively young age and close relationships of the majority of the fossils made inclusion challenging. We included four of the 14 fossils. Increased sampling of Emesini would allow us to include additional fossils, although overlapping ages with daughter nodes will still prevent inclusion of all 14 fossils. It is interesting to note that the majority of described emesine fossils belong to the clade containing *Empicoris,* one of the four cosmopolitan genera. It is possible that their habitat preference of tree trunks both led to increased dispersal capacity (see below) and to the increased likelihood of fossilization as amber inclusions.

Our estimate for the divergence of Emesinae from their sister group to ~100 MYA (Fig. 3.1) is in line with previous analyses that estimated this divergence to either 87 MYA (Hwang and Weirauch, 2012) or ~108 MYA (Masonick et al., in prep.). The three hypotheses were generated with different taxon samples and only partially overlapping fossil calibrations, but all corroborated the importance of dispersal over vicariance in shaping current emesine distribution ranges. This includes the four species-rich cosmopolitan genera, three of which diverged during the Eocene (56-33 MYA) and one during the Oligocene (33.7 -23.8 MYA). This younger age for *Stenolemus* may in part be due to the small number of species and incomplete sampling of biogeographic regions included in our analysis.

The transition from the Eocene to the Oligocene is marked by significant global cooling, with the first Antarctic ice sheets appearing and several impact events occurring (Prothero, 1994). Some of these impact events may have led to super tsunamis similar to the Chesapeake Bay bolide impact (Poag, 1997). Following the 9.0 magnitude earthquake in Japan, nearly 300 marine species were documented along the western shores of North America, having traveled on flotsam carried by that tsunami (Lindo, 2020). It is likely that super tsunamis generated by impacts during the Eocene would also have led to increased transoceanic dispersal. Based on our analyses, dispersal events during the Eocene occurred across the Atlantic Ocean (*Gardena*; Fig. 3.3) and Indian Ocean (*Empicoris*; Fig. 3.4). As species in the three genera are found predominantly on tree trunks, pieces of wood, dead branches of trees and dead hanging fronds, and therefore microhabitats that have the potential to turn into flotsam, we hypothesize that tsunamis including the Chesapeake Bay bolide impact may have led to the dispersal of *Gardena* across the Atlantic Ocean. Similarly, ocean currents and tsunamis may have played a role in the transoceanic dispersals of the other cosmopolitan genera via flotsam. Supporting our hypothesis is the observation that species of several genera of Emesinae have been found in flood debris in Texas, including species of G*ardena, Ploiaria* and *Empicoris* (Elkins, 1951).

Rafting is a known behavioral tactic in invertebrates, such as the Magellanic sub-Antarctic chironomid *Telmatogeton magellanicus* (Simões et al., 2020), and Antarctic and Arctic Collembola (Coulson *et al.*, 2002; Hawes *et al.*, 2008). This is potentially an

important dispersal pathway for flightless species (Coulson *et al.*, 2002; Hawes *et al.*, 2008) such as many *Gardena* and *Ploiaria*. However, there are many stressors on insects using rafting. Salinity tolerance is required, and there must be enough food available on the raft for insects to survive months at sea. While these make successful transoceanic rafting dispersals less likely to occur frequently, it does not rule out the possibility, as the probability of a single longer dispersal event is greater than the combined probability of two events (Gillespie *et al.*, 2012). Even though transoceanic dispersal might happen rarely in Emesinae, it is highly likely this is their primary mode of long distance dispersal. Subsequent dispersals across the Atlantic Ocean during the Oligocene (*Empicoris*) and the Indian ocean (*Gardena* and *Empicoris*) suggest that while impact events may have led to increased dispersal for Emesinae, rafting still occurred without such major events.

Atmospheric pathways have been found to be a method for long distance migration in certain insect and plant species (Pretorius *et al.*, 2023). Flying and/or floating in an atmospheric pathway is more likely within *Stenolemus* than the other three genera, as it has a higher surface area to volume ratio, and "hair" tufts on their legs would likely add to aerial dispersal. In addition, there are only winged species known from *Stenolemus*. However, without greater sampling from different geographic ranges we cannot estimate their paths of dispersal, and whether aerial or rafting dispersal is more likely. There are only winged species of *Empicoris* known as well, however, as they lack the tufts found on *Stenolemus,* and as there were *Empicoris* found

on flood debris in Texas, we hypothesize that rafting was their primary mode of dispersal.

In conclusion, *Ploiaria, Empicoris* and *Gardena* all diverged during the Eocene, however they dispersed across different oceans, at different times, and at least partially originating from different ancestral ranges. A large number of dispersal events occurred during the Eocene, coinciding with a high number of meteorite impacts such as the Chesapeake Bay Impact that created a super tsunami we hypothesize may have led to the dispersal of *Gardena* across the Atlantic Ocean. Current habitat preference, and collection of several Emesinae species in flood debris, support the hypothesis that Emesinae primarily use flotsam for long distance dispersal, which is highly unusual for Reduviidae.

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CHAPTER 4:

Phylogenomics of True Bugs sheds light on relationships within Cimicomorpha and Pentatomomorpha

ABSTRACT: The true bugs (Heteroptera: Hemiptera) are ecologically and behaviorally diverse and comprise many species of economic importance including agricultural pests, disease vectors and beneficial biological control agents. While recent analyses have largely resolved relationships between infraorders, relationships between superfamilies and families remain uncertain for many groups, and in some cases have yet to be tested. Using the new alignment-based sequence extraction software ALiBaSeq, we extracted loci from a combined transcriptomic and genomic dataset, covering 74 out of the 88 heteropteran families. We used the 2395 orthologous loci from Johnson et al. (2018) as baits and performed reciprocal blast to test for paralogy, resulting in a final dataset of 1447 loci. We then generated a phylogenetic hypothesis in IQTREE2 and tested relationships between infraorders, superfamilies and families. Our results support the monophyly of Leptopodoidea, Naboidea and Microphysoidea, however, we found Termitaphididae rendered Aradidae paraphyletic, Lygaeoidea was paraphyletic and Cydnidae was paraphyletic. Future work should focus on increased sampling of Cimicoidea and Lygaeoidea to resolve relationships between families.

INTRODUCTION

With ~45,000 species, the true bugs (Heteroptera: Hemiptera) are ecologically and behaviorally diverse, including diurnal and nocturnal species as well as herbivores and predators (Henry, 2017). Additionally, many heteropterans are of economic importance, as several are agricultural pests, disease vectors and beneficial biological control agents (Schaefer & Panizzi, 2000). The monophyly of Heteroptera was first suggested by Latreille in 1810, and a few years later the major groups within Heteroptera were recognized by Dufour (Dufour, 1833; Latreille, 1810). It was not until 1975, however, that the seven infraorders (Cimicomorpha, Dipsocoromorpha, Enicocephalomorpha, Gerromorpha, Leptopodomorpha, Nepomorpha and Pentatomomorpha) recognized within Heteroptera today were proposed (Dufour, 1833; Forero, 2008; Latreille, 1810; Ŝtys & Kerzhner, 1975).

Likely in part due to their economic importance, and because of recent advances in sequencing techniques, several published studies have explored relationships among, and to some extent within, the seven infraorders in recent years. Though many relationships are consistently supported (i.e., Terheteroptera [Cimicomorpha + Pentatomomorpha] and Geoheteroptera [Terheteroptera + Leptopodomorpha]), some are still contested (i.e. placement of Nepomorpha and whether Dipsocoromorpha, Enicocephalomorpha or Dipsocoromorpha + Enicocephalomorpha is sister to Gerromorpha) (Li et al., 2017; Li et al., 2012; Mahner, 1993; Shcherbakov & Popov,

2002; Wang et al., 2019; Wang et al., 2016; Weirauch et al., 2019; Wheeler, Schuh, & Bang, 1993; Xie et al., 2008).

While relationships between infraorders are largely resolved, relationships between superfamilies and families remain uncertain for many groups, and in some cases have yet to be tested (Grazia et al., 2008; Wang et al., 2016; Weirauch et al., 2019). Previous phylogenetic studies have been limited in their scope primarily by low taxonomic sampling, insufficient molecular data to resolve relationships, or even complete reliance on morphological characters as in the case of interfamilial relationships in Leptopodomorpha (Forthman et al., 2019; Grazia et al., 2008; Schuh & Polhemus, 1980; Schuh et al., 2009).

The shore bugs (Leptopodomorpha) are composed of the superfamilies Saldoidea (Aepophilidae and Saldidae; Fig. 4.1b) and Leptopodoidea (Omaniidae and Leptopodidae; Fig. 4.1a,c) (Schuh & Polhemus, 1980; Fig. 4.2b). While this classification is consistent with the morphology-based phylogenetic hypothesis by Schuh & Polhemus, (1980), it has not been tested using molecular data.

Figure 4.1: Selected Heteroptera habitus photos. **(a)** Leptopodidae: *Valleriola javanica,* © Fan Gao; **(b)** Saldidae: *Saldula* sp., © creek_chen; **(c)** Omaniidae: *Corallocoris* sp., © Colin Chiu; **(d)** Nabidae: *Gorpis* sp., © Fan Gao; **(e)** Velocipedidae: *Scotomedes* sp., © Marcus F.C. Ng; **(f)** Anthocoridae: *Anthocoris nemorum*, © Mika Ensio Laine; **(g)** Aradidae: *Mezira subsetosa*., © Zachary Dankowicz; **(h)** Plataspidae: *Megacopta*, © A. Restu Dwikelana; **(i)** Cydnidae: *Tritomegas sexmaculatus*, © Fabrice Jullien; **(j)** Megarididae: *Megaris trinotata* © gernotkunz.

With over 20,000 species in seventeen families and five superfamilies, Cimicomorpha have the greatest species diversity among Heteroptera, and a range of feeding behaviors (phytophagy, predation, hematophagy, scavenging and mixed feeding strategies) (Schuh, Weirauch, & Wheeler, 2009; Weirauch et al., 2019). Relationships between superfamilies within Cimicomorpha are tentative, with Reduvioidea typically recovered as sister to all remaining taxa (Ŝtys & Kerzhner, 1975; Wheeler et al., 1993), though not consistently, (i.e., Weirauch et al., 2019). Historically the superfamily Naboidea has been composed of the morphologically similar Medocostidae, Nabidae and Velocipedidae (Carayon, 1970; Kerzhner, 1971; Fig. 4.1d,e). However, these three families were not recovered as monophyletic in phylogenetic analyses using morphological data (Schuh & Ŝtys, 1991). Instead, Medocostidae and Nabidae were recovered as sister taxa with Velocipedidae sister to all non-reduvioid Cimicomorpha. Schuh et al. (2009) were unable to generate molecular data for either Velocipedidade

and Medocostidae and found Naboidea to be paraphyletic in their morphology-only analyses and polyphyletic (with Velocipedidae falling outside the Cimicomorpha) in their combined morphological and molecular dataset.

Traumatic insemination, or insemination through the body wall rather than the female genital tract, is a unique behavior found in at least five of the seven families of Cimicoidea, as well as the mirid genus *Coridromius,* and the nabid subfamily Prostemmatinae (Jung et al., 2023; Carayon, 1966; Tatarnic et al., 2006). However, despite Cimicoidea also including the economically important bed bugs, relationships between families of Cimicoidea remain uncertain, leaving the evolution of this behavior unknown. Previous studies using a combined morphological and molecular dataset found Curaliidae and Lasiochilidae to be sister to the rest of Cimicoidea, however the paraphyletic Anthocoridae (Fig. 4.1f) was undersampled, and molecular data was missing for Polyctenidae (Weirauch et al., 2019). Recent work with much increased sampling of Anthocoridae found Plokiophilidae to be sister to the rest of Cimicoidea, and Anthocoridae to be highly paraphyletic, however Polyctenidae has still not been included (Jung et al., 2023; Fig. 4.2a).

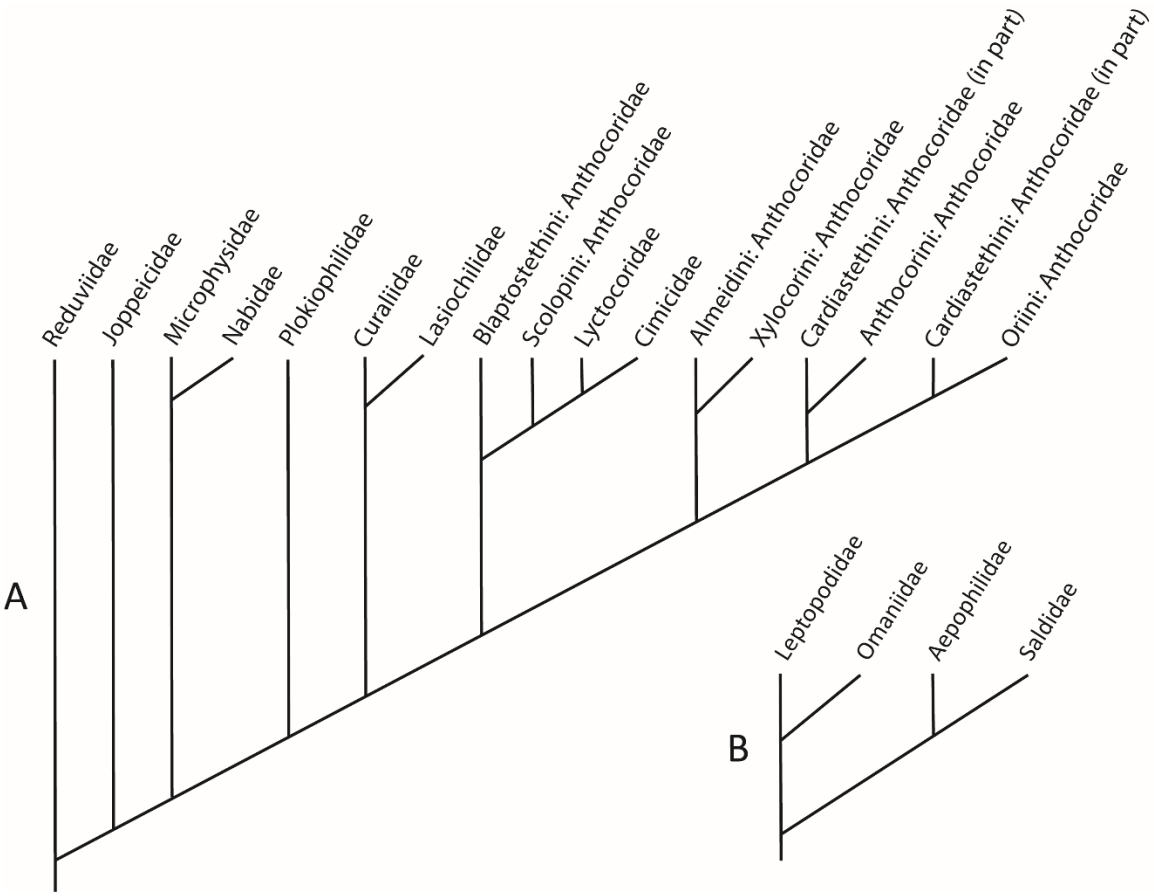

Figure 4.2: Phylogenetic relationships within Cimicomorpha and Leptopodomorpha. **(a)** Maximum Likelihood tree generated using 18S rRNA, 28S rRNA-D3 region, 16S rRNA and COI, testing relationships of Cimicoidea (from Jung et al., 2023); **(b)** Family level phylogenetic relationships of Leptopodomorpha (from Schuch and Polhemus, 1980).

Aradoidea have long been placed as the sister taxon to the remaining Pentatomomorpha (stink bugs and allies) (Henry, 1997; Fig. 4.3c). However, recent work suggests that either Termitaphididae render Aradidae paraphyletic (Cassis and Schuh, 2010; Figs 1g, 3a) or conversely that Aradoidea are not monophyletic, with Termitaphididae sister to Pentatomidae (Marchal and Guilbert, 2015; Fig. 4.3b).

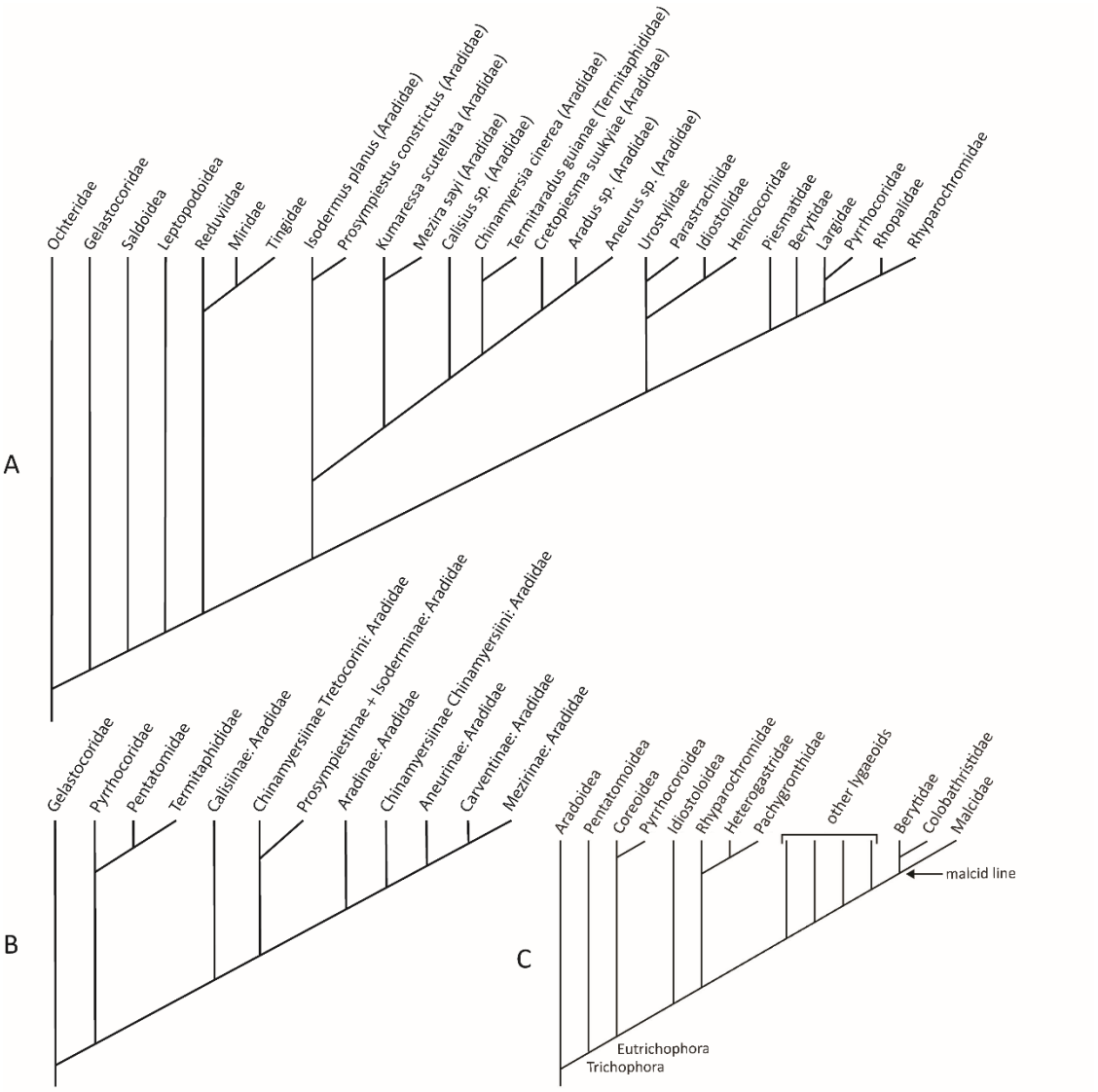

Figure 4.3: Phylogenetic relationships within Pentatomomorpha. **(a)** Single fittest tree produced by PIWE using 78 characters, testing phylogenetic relationships of Aradoidea (from Cassis and Schuh, 2010); **(b)** Parsimonious tree from combined molecular (1650 bp) and morphological (72 characters) analysis, testing relationships of Aradoidea (from Marchal and Guilbert, 2015); **(c)** Strict consensus tree from 57 morphological characters, testing relationships of Pentatomomorpha (from Henry, 1997).

Coreoidea are composed of the five families Alydidae, Coreidae, Hyocephalidae, Rhopalidae and Stenocephalidae. Disagreeing with previous analyses (Henry, 1997; Weirauch et al., 2019) recent analyses found Rhopalidae highly supported as sister to

Alydidae + Coreidae (Forthman et al., 2019). However, Stenocephalidae and Hyocephalidae were not represented in that analysis.

Nine subfamilies are currently recognized within Cydnidae (Amnestinae, Amaurocorinae, Cephalocteinae, Cydninae, Garsauriinae, Parastrachiinae, Sehirinae, Thaumastellinae and Thyreocorinae [Pentatomomorpha; Fig. 4.1i; Schuh & Weirauch, 2020; Dolling, 1981; Grazia et al., 2008; J. A. Lis, 2010]). However, composition within Cydnidae has often been disputed, with Grazia et al. (2008) disagreeing with Dolling (1981) and finding support for raising the subfamily Thyreocorinae (Cydnidae: Pentatomomorpha) to family level under the name Corimelaenidae. Grazia et al. (2008) also found support for including Parastrachiinae within Corimelaenidae, in contrast to Sweet and Schaefer (2002) which gave Parastrachiinae family status.

Megarididae (Fig. 4.1j) and Plataspidae (Fig. 4.1h) are small (5 mm or less) ovoid, strongly convex beetle-like pentatomomorphans. However, their incredibly similar morphology is assumed superficial (McDonald, 1979). Due to the difficulty in collecting these insects, molecular data have never been used to test their relationship, though a combined morphology and molecular analysis placed Megarididae (morphology only) and Plataspidae (morphology and molecular data) as sister taxa (Grazia et al., 2008).

Clearly, a comprehensive phylogenomic analysis including representatives from the superfamilies and families mentioned above is needed to address these issues. We use a combined genomic and transcriptomic dataset covering 74 of the 89 heteropteran

families to test relationships between superfamilies and families of Leptopodomorpha, Cimicomorpha and Pentatomomorpha.

MATERIAL AND METHODS

Taxon sampling

The dataset is composed of 148 specimens, 110 ingroup Heteroptera and 37 outgroup hemipterans. We sampled nine families of Nepomorpha, three families of Dipsocoromorpha, two families of Enicocephalomorpha, six families of Gerromorpha, three families of Leptopodomorpha, 15 families of Cimicomorpha and 36 families of Pentatomorpha. Together, 74 out of the 88 heteropteran families were included in our analysis. Table 4.S1 provides unique specimen identifier numbers, accession numbers, data type and locality information. Vouchering of newly sequenced specimens followed the guidelines laid out in Weirauch and Munro (2009). Voucher specimens were associated with unique identifiers (USI labels) and databased using the Arthropod Easy Capture Specimen (AESC) database (https://research.amnh.org/pbi/locality/). Images for voucher specimens were uploaded to the AESC database as well. These specimen records are publicly available through the Heteroptera Species Pages (https://research.amnh.org/pbi/heteropteraspeciespage/) where records are served directly from the AESC database.

Transcriptome sampling

We included 99 transcriptomes from Johnson et al. (2018) and de Moya et al. (2019) in our analysis, 62 of which were ingroup heteropterans (42 species) and 37 outgroups (62 ingroup). See Johnson et al. (2018) for detailed cleaning and assembly methods. In brief, transcriptomes were sequenced with 100 bp paired-end reads using Illumina HiSeq2000 or HiSeq2500. Paired-end reads were assembled with SOAP-denovo-Trans. Raw reads and filtered assemblies were submitted to NCBI SRA and TSA archives, accession numbers are provided in Table 4.S1.

Genome sampling

To increase sampling of families across Heteroptera, 48 ingroup genomes were sequenced for this analysis. Both the Weirauch lab and the Johnson lab contributed to collecting and extracting specimens. Weirauch lab samples were sent to the Johnson lab for sequencing. They were sequenced using HiSeq 4000. To speed up assembly, deduplification was performed on genomes using clumpify in bbmap (Bushnell et al., 2017). Genomes were trimmed using Trimmomatic, and paired reads were subsequently merged in BBMap v38.95 (Bushnell et al., 2017). Genomes were assembled with SPAdes v3.15.4 (Prjibelski et al., 2020), and assembly quality was assessed using QUAST (Gurevich et al., 2013).

Combining orthologous loci across transcriptomes and genomes

Orthologous loci were selected simultaneously across assembled genomes and transcriptomes using ALiBaSeq (Knyshov et al., 2021). ALiBaSeq uses BLAST results to search fasta files for homologous regions. We used the orthologous bait set developed in Johnson et al. (2018) for our forward search. For the reciprocal blast search, we downloaded *Rhodnius prolixus* from VectorBase. Following selection of orthologous loci, loci not included in 90% of species were removed to reduce missing data, resulting in the final dataset of 1447 loci.

Phylogenetic analysis

Phylogenetic relationships were reconstructed using maximum likelihood partitioned analyses in IQ-TREE v2.2.0.5 (Minh *et al.*, 2020). Best fit partitioning schemes were estimated using ModelFinder (Kalyaanamoorthy *et al.*, 2017) in IQ-TREE2, allowing partitions with similar models to be merged to reduce over-parameterization and increase model fit. Tree estimation was sped up using the relaxed clustering algorithm (Lanfear *et al.*, 2014). One thousand replicates of ultrafast bootstrap (UFBoot2) (Hoang *et al.*, 2018) and SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.*, 2010) were performed to estimate node support.

RESULTS

ModelFinder merged the original 1447 partitions into 275 partitions. Our partitioned dataset produced a well-resolved and highly supported phylogeny (Fig. 4.4). The monophyly of all seven infraorders was supported by 100% UFBoot and SH-aLRT (Fig. S4.1). Nepomorpha were recovered as sister group to the remaining Heteroptera, and Gerromorpha as sister taxon to Enicocephalomorpha + Dipsocoromorpha. Geoheteroptera (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha)) were fully supported (100% UFBoot, 100% SH-aLRT).

Within Leptopodomorpha, Leptopodidae are the sister lineage to Omaniidae, which together are the sister taxon to the Saldidae. However, the sister group relationship of Saldidae and Leptopodidae + Omaniidae is not well supported (92% UFBoot, 76.8% SH-aLRT).

The monophyly of Microphysoidea was confirmed and well supported (100% UFBootstrap, 100% SH-aLRT), with *Joppeicus paradoxus* (Joppeicidae) recovered as sister lineage to *Loricula pselaphiformis* (Microphysidae) and an unusual, coleopteroid undescribed microphysid from South Africa. Naboidea, represented by two species of Nabidae (both subfamilies included) and one species each of Medocostidae and Velocipedidae, were monophyletic and fully supported (100% UFBoot; 100% SH-aLRT), with Velocipedidae recovered as sister taxon to the Medocostidae + Nabidae. Naboidea were well supported as sister lineage to the Cimicoidea (100% UFBoot; 100% SH-aLRT). Within Cimicoidea, we found Plokiophilidae to be sister to the rest of Cimicoidea and

recovered Lasiochilidae as the sister taxon to Anthocoridae. Miroidea were fully supported, with Tingidae + Thaumastocoridae recovered as sister lineage to the Miridae. The monophyly of Miridae was strongly supported (100% UFBoot; 100% SH-aLRT). We also found the Deraeocorinae + Mirinae to form a clade, as did the "core" Orthotylinae (e.g., Orthotylinae except *Coridromius*) + Phylinae, as well as these four lineages together. In contrast, Bryocorinae were polyphyletic, with Dicyphini forming the sister taxon of all remaining Miridae.

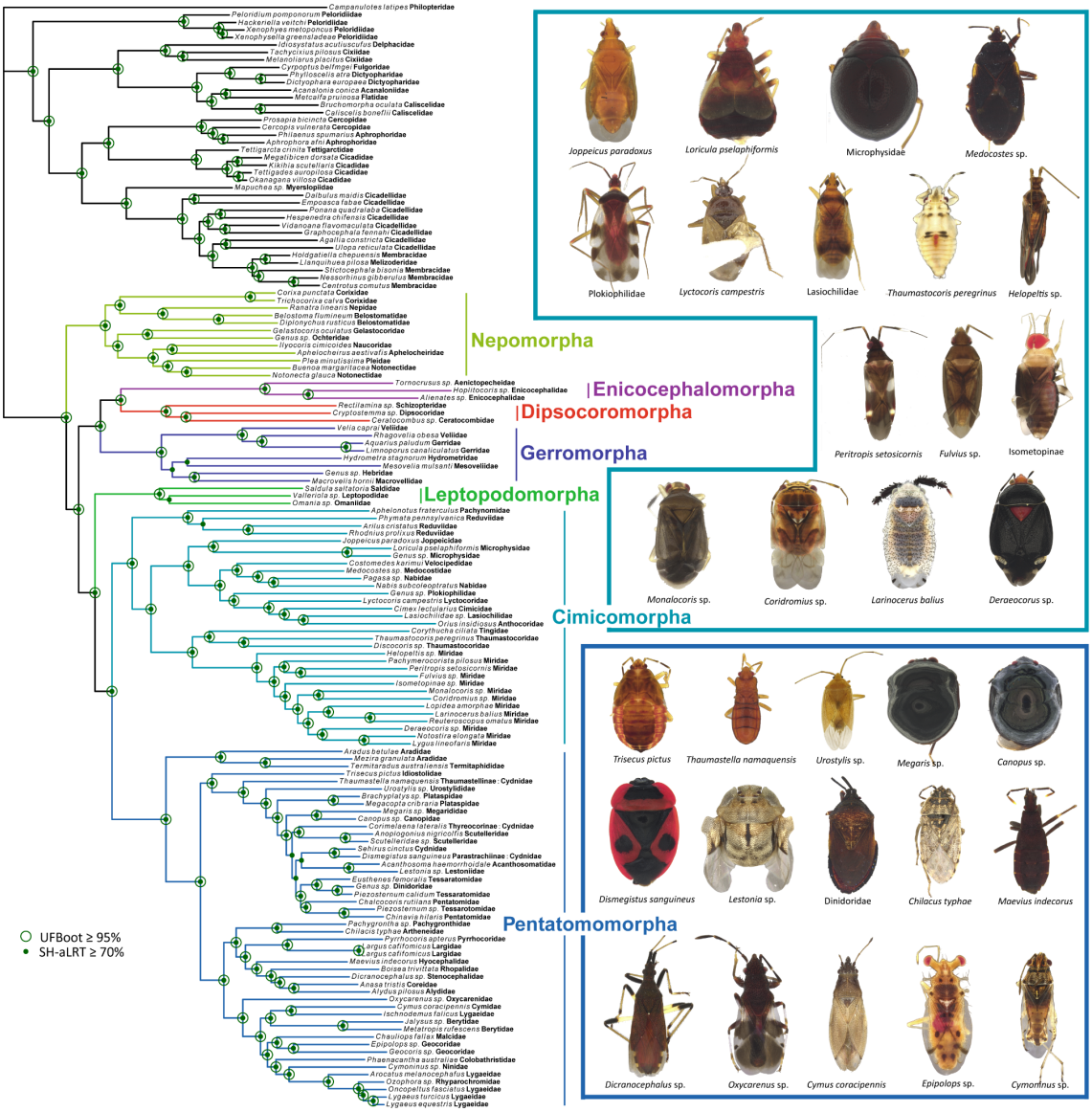

Figure 4.4: Phylogenetic reconstruction of Heteroptera produced by maximum-likelihood analysis of combined transcriptomic and genomic dataset in IQTREE2. Small solid green circles represent SH-aLRT support values greater than or equal to 70%, large empty green circles represent UFBoot support values greater than or equal to 95%. Colored branches differentiate the seven infraorders. Voucher specimens from Cimicomorpha (light blue) and Pentatomomorpha (dark blue) shown on the right.

While the monophyly of Aradoidea was highly supported (100% UFBoot; 100% SH-aLRT), Termitaphididae rendered Aradidae paraphyletic. We found Idiostoloidea to be the sister taxon to the Pentatomoidea with high support (100% UFBoot; 100% SH-aLRT). Cydnidae were polyphyletic, with Thyreocorinae recovered as the sister group to Scutelleridae and Thaumestellinae as sister to the rest of Pentatomomorpha, but Parastrachiinae and Sehirinae together were monophyletic (Cydninae not included). Canopidae were highly supported as sister taxon to the Megarididae (100% UFBootstrap; 100% SH-aLRT). We found Lygaeoidea to be paraphyletic, with Pachygronthidae + Artheneidae recovered as sister taxon to the Pyrrhocoroidea. We found Geocoridae to be monophyletic and to represent the sister lineage to the Malcidae. Rhyparochromidae were nested within a polyphyletic Lygaeidae. Within the Coreoidea, we found Coreidae to be the sister lineage to Alydidae, with Hyocephalidae as the earliest diverging lineage within the superfamily.

DISCUSSION

We used the most extensive phylogenetic analysis to date in terms of family coverage (74 out of 88) and number of loci sampled (1447) to test proposed relationships within the highly diverse Heteroptera. Our approach combines phylogenomic datasets derived from transcriptomes and genomes sequenced from archival as well as freshly collected specimens, allowing for unprecedented taxon sampling at the family level. For a number of species-poor and rarely collected taxa (e.g., Termitaphididae, Medocostidae,

Velocipedidae) our research generated the first sequence data to be included in any phylogenetic or phylogenomic study, allowing for the first tests of hypotheses generated based on morphology-only datasets. The infraorder relationships recovered in our study corroborated hypotheses put forward by de Moya et al. (2019) and Weirauch et al. (2019): Nepomorpha are the sister lineage to all remaining Heteroptera, Gerromorpha are the sister group to Enicocephalomorpha + Dipsocoromorpha, and Geoheteroptera are monophyletic with Leptopodomorpha as the sister lineage to the Terheteroptera.

While combined molecular and morphological analyses generally support the monophyly of Leptopodomorpha, and their relationship as sister lineage to the Cimicomorpha + Pentatomomorpha, or Terheteroptera (Grazia et al., 2008; Schuh et al., 2009; Y. Wang et al., 2016; Weirauch et al., 2019; de Moya et al., 2019), the monophyly of the two superfamilies, Leptopodoidea and Saldoidea, has never been tested using molecular data. We generated the first sequence dataset for Omaniidae and found support for the Schuh and Polhemus (1980; Fig. 4.2b) hypothesis that posits Leptopodidae as the sister lineage to the Omaniidae, forming Leptopodoidea.

We also tested relationships between superfamilies and families within the diverse Cimicomorpha. While recovered in some analyses (Weirauch et al., 2019), the monophyly of Microphysoidea (Joppeicidae and Microphysidae) was not recovered in others (Schuh and Štys, 1991; Jung et al., 2023). Our results confirm the phylogenetic hypothesis presented in Weirauch et al. (2019) in supporting the monophyly of Microphysidae and include an additional undescribed microphysid with highly divergent

morphology (Fig. 4.4). We tested and recovered the monophyly of Naboidea for the first time with molecular data and found Velocipedidae to be the sister group to Medocostidae + Nabidae. Relationships within Cimicoidea differed substantially from Weirauch et al. (2019) and Jung et al. (2023). We found Plokiophilidae to be the sister taxon to the rest of Cimicoidea, corroborating Jung et al. (2023) and rebutting Weirauch et al. (2019). However, while we found Lasiochilidae to be the sister group to Anthocoridae, Lasiochilidae and Curaliidae formed a clade in Jung et al. (2023). Anthocoridae is clearly paraphyletic (Jung et al., 2023), and it is likely that undersampling of Anthocoridae in our study (only *Orius* included) led to this unusual relationship. We recovered Tingidae + Thaumastocoridae as sister lineage to the Miridae, in contrast to previous studies that found Thaumastocoridae as sister group to Miridae + Tingidae (Schuh and Ŝtys, 1991; Weirauch et al., 2019); Thaumastocoridae were not included in previous phylogenomic studies. The monophyly of Miridae was strongly supported. Relationships within Miridae are partially consistent with a published morphology-based phylogenetic hypothesis (Schuh, 1976) and a molecular study based on six gene regions (Oh et al., 2023) in recovering a clade comprised of the three large subfamilies Mirinae, Orthotylinae (minus *Coridromius*), and Phylinae together with Deraeocorinae. However, relationships among the early diverging lineages remain controversial, with Bryocorinae showing rampant polyphyly, similar to the topology recovered by Oh et al. (2023).

We also resolved relationships within the primarily phytophagous Pentatomomorpha. Aradoidea have long been regarded as the sister lineage to the rest of Pentatomomorpha, the Trichophora (Henry, 1997). However, previous analyses have differed in the placement of the rarely collected and morphologically highly specialized Termitaphididae, with Marchal and Guilbert (2015; Fig. 4.3b) recovering Termitaphididae as sister group to the Pentatomidae, rendering Aradoidea polyphyletic, and Cassis and Schuh (2010; Fig. 4.3a) finding Termitaphididae to be nested within Aradidae using morphological data. Our results corroborate Cassis and Schuh (2010), with the monophyly of Aradoidea being highly supported (100% UFBoot; 100% SH-aLRT), but Termitaphididae rendering Aradidae paraphyletic (Fig. 4.4). The placement of the enigmatic Idiostoloidea, a group comprising two families with Gondwanan distribution and lygaeoid overall habitus, has differed in recent analyses, with Henry (1997) recovering them as sister lineage to the Lygaeoidea, while Weirauch et al. (2019) found Idiostoloidea as the sister group to Pentatomoidea. Our results support Weirauch et al. (2019) in recovering Idiostoloidea + Pentatomoidea as a clade with high support (100% UFBoot; 100% SH-aLRT), disagreeing with Henry (1997; Fig. 4.3c). While family status for Cydnidae has long been recognized (Billberg, 1820; Dolling, 1981; Jacobs, 1989; Ŝtys, 1964), the composition of this family has been under debate. Our results disagree with Dolling (1981), and find Cydnidae to be polyphyletic, with Scutelleridae being treated as sister group to the cydnid subfamily Thyreocorinae, and Thaumestellinae as sister group to all remaining Pentatomomorpha. Canopidae were

highly supported as the sister lineage to Megarididae (100% UFBoot; 100% SH-aLRT), disagreeing with McDonald's (1979) morphology based assessment that Megarididae and Canopidae are not closely related. While recent analyses suggest that Coreoidea are monophyletic (Henry, 1997; M. Li et al., 2016; Weirauch et al., 2019), others suggest the group may be in need of revision (H. Li et al., 2005; H. Li et al., 2006; Q. Xie et al., 2005). We included all five families of Coreoidea for the first time with molecular data and found support for the monophyly of Coreoidea. We found Coreidae treated as the sister lineage to Alydidae, agreeing with de Moya et al. (2019) and Liu et al. (2017), while the placement of Stenocephalidae and Rhopalidae differs from de Moya et al. and Liu et al. Though placement of Hyocephalidae differs from Henry, 1997, they are nested within Coreoidea. We recovered Lygaeoidea as paraphyletic, disagreeing with Henry (1997), with Pachygronthidae + Artheneidae recovered as sister to Pyrrhocoroidea. Our analysis included molecular data for Oxycarenidae and Ninidae for the first time, and we found Oxycarenidae to be the sister lineage to the rest of Lygaeoidea, and Ninidae to be sister to the polyphyletic Lygaeidae; these results will need to be corroborated using a more comprehensive sample of lygeaoid taxa.

With our increased sampling size and large molecular dataset, we were able to test previously proposed hypotheses on relationships between superfamilies and families of Leptopodomorpha, Cimicomorpha and Pentatomorpha. This is a step forward in resolving relationships within Heteroptera. Future work should focus on increased

sampling of Cimicoidea and Lygaeoidea to further examine currently proposed relationships within these superfamilies.

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APPENDIX

Table S1.1: Collartidini morphology matrix. Includes 25 characters based on diagnostic characters used in previous analyses. Outgroup taxa listed first, then *Collartida* spp., then *Stenorhamphus* spp.

										1										**2**					
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Bagauda similis	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	2	1	3	0	0	2
Ploiaria stysi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1	0	2
Carayonia camerunensis	0	2	0	0	1	0	1	1	1	3	1	0	1	1	2	1	0	1	4	0	0	2	0	0	3
Kiskeyana palassaina	1	1	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	1	0	?	?	?	?
Oncerotrachelus amazonensis	1	1	0	0	0	0	0	0	0	3	1	0	0	0	2	0	1	1	0	2	0	0	0	1	3
Collartida microphthalma	0	1	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	?
Collartida oculata	0	?	0	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	1
Collartida peregrina	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	0	0	2	0	0	2	0	0	0
Collartida serapis	0	1	0	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	1	?	0	2	0	0	0
Collarhamphus mixtus	1	1	0	0	1	0	1	1	0	2	0	1	2	2	1	0	0	0	3	0	0	0	0	0	0
Mangabea orientalis	1	?	2	1	1	1	1	0	0	1	0	0	3	2	1	0	0	0	3	0	0	1	1	1	0
Mangabea barbiger	1	1	2	1	1	1	1	0	0	3	0	1	2	2	2	0	0	0	3	1	0	1	1	1	0
Mangabea troglodytes	1	1	1	1	1	1	1	1	0	2	1	0	3	2	0	0	0	0	4	0	0	?	?	?	?
Stenorhamphus nubiferus	1	1	1	0	1	0	1	0	1	3	0	1	0	0	2	0	0	0	3	1	0	2	1	0	1
Stenorhamphus phuphan	1	1	1	0	1	1	1	0	1	3	0	1	3	2	1	0	0	0	4	1	0	0	1	0	1
Stenorhamphusa segerak	1	1	0	0	1	1	1	1	1	3	0	0	2	2	2	0	1	0	4	1	0	0	1	0	0

Table S2.1: Current classification for in- and outgroups, unique specimen identifier numbers, voucher depositories, and locality information.

Sequence name				R_CW	USI	Previously published	Voucher depository	Accession #			Data type	Country collected in
								18S (1f-5r)	28SD2 (28S-CW-D2F - 28S-CW-D2R)	28SD3-5		
Bactrodes_spinulosus_956	Bactrodinae	Bactrodes	spinulosus	956	UCR_ENT00003243	Zhang et al. 2015	UCR	KP692827	KP692853	KP692881		MEX
Bactrodes_femoratus_3882	Bactrodinae	Bactrodes	femoratus	3882	UCR_ENT00100012	Zhang et al. 2015	UCR	KP692825	KP692851	KP692880		GUF
R_CW_5255_assembly.fasta	Cetherinae	Cethera	cornifrons	5255	UCR_ENT00127821	Knyshov et al., 2023	UCR	SRR13844059	SRR13844059	SRR13844059	WGS	CMR
Cethera_musiva_779	Cetherinae	Cethera	musiva	779	UCR_ENT00052176	Hwang and Weirauch, 2012	UCR	JQ897552	JQ897630	JQ897707		NGA
Eupheno_histrionicus_1568	Cetherinae	Eupheno	histrionicus	1568	UCR_ENT00014326	Hwang and Weirauch, 2012	INBIO	JQ897556	JQ897636	JQ897712		CRI
Cleptria_corallina_014	Ectrichodiinae	Cleptria	corallinus	14	AMNH_PBI00218770	Weirauch and Munro, 2009	UCR	FJ230462	FJ230543	FJ230621		GNB

Ectrychotes_sp_188	Ectrichodiinae	Ectrychotes	sp.	188	AMNH_PBI 00218932	Weirauch and Munro, 2009	UCR	FJ230503	FJ230584	FJ230661		MYS
Ectrichodia_lucida_013	Ectrichodiinae	Ectrichodia	lucida	13	AMNH_PBI 00218769	Weirauch and Munro, 2009	UCR	FJ230461	FJ230542	FJ230620		GNB
Rhiginia_ruficoria_3947	Ectrichodiinae	Rhiginia	ruficoria	3947	no USI	Knyshov et al., 2023	UCR	PRJNA374220	PRJNA374220	PRJNA374220	RNA-Seq	ARG
Racelda_sp_041	Ectrichodiinae	Racelda	sp.	41	AMNH_PBI 00218801	Weirauch and Munro, 2009	UCR	FJ230472	FJ230553	FJ230631		GUF
Microtomus_cinctipes_141	Hammacerinae	Microtomus	cinctipes	141	AMNH_PBI 00218893	Weirauch and Munro, 2009	UCR	FJ230491	NA	FJ230649		NIC
Arilus_cristatus_071	Harpactorinae	Arilus	cristatus	71	AMNH_PBI 00218826	Weirauch and Munro, 2009	UCR	FJ230477	FJ230558	FJ230636		USA
Vesbius_purpureus_184	Harpactorinae	Vesbius	purpureus	184	UCR_ENT 00001523	Weirauch and Munr	UCR	FJ230501	FJ230582	FJ230659		MYS

						o, 2009						
Sinea_diadema_108	Harpactorinae	Sinea	diadema	108	AMNH_PBI 00218861	Weirauch and Munro, 2009	UCR	FJ230485	FJ230566	FJ230644		MEX
Manicocoris_rufipes_023	Harpactorinae	Manicocoris	rufipes	23	AMNH_PBI 00218778	Zhang et al., 2015	UCR	KP692810	KP692828	*JQ942167		GUF
Apiomerus_californicus_818	Harpactorinae	Apiomerus	californicus	818	UCR_ENT 00004374	Zhang et al., 2016	UCR	KP692826	*JQ942195	*JQ942151		USA
Ptilocerus_sp_587	Holoptilinae	Ptilocerus	sp.	587	UCR_ENT 00001974	Hwang and Weirauch, 2012	UCR	JQ897599	GU188467	GU188448		THA
Triatoma_protracta_294	Triatominae	Triatoma	protracta	294	UCR_ENT 00218742	Weirauch and Munro, 2009	UCR	FJ230520	FJ230603	FJ230675		USA
Peirates_punctorius_216	Peiratinae	Brachysandalus	punctorius	216	AMNH_PBI 00218960	Weirauch and Munro, 2009	UCR	FJ230508	FJ230590	FJ230666		AUS
Ectomocoris_atrox_363	Peiratinae	Ectomocoris	atrox	363	AMNH_PBI 00000088	Weirauch and Munro, 2009	UCR	FJ230527	FJ230595	FJ230682		SGP

Phymata_acutangula_029	Phymatinae	Phymata	acutangula	29	AMNH_PBI00218783	Hwang and Weirauch, 2012	UCR	FJ230468	FJ230550	FJ230627		GUF
Physoderes_impexa_1572	Physoderinae	Physoderes	impexa	1572	UCR_ENT00052181	Hwang and Weirauch, 2012	UCR	JQ897591	JQ897662	JQ897748		VNM
Pasiropsis_maculata_810	Reduviinae	Pasiropsis	maculata	810	UCR_ENT00052227	Hwang and Weirauch, 2012	TIGER	JQ897586	JQ897658	JQ897743		THA
Varus_flavoannulatus_2764	Reduviinae	Varus	flavoannulatus	2764	UCR_ENT00004574	Hwang and Weirauch, 2012	UCR	JQ897613	JQ897683	JQ897768		ZMB
Acanthaspis_sulcipes_737	Reduviinae	Acanthaspis	sulcipes	737	UCR_ENT00052174	Hwang and Weirauch, 2012	UCR	JQ897545	KP692852	JQ897698		NGA
Tiarodes_versicolor_702	Reduviinae	Tiarodes	versicolor	702	UCR_ENT00052171	Hwang and Weirauch, 2012	UCR	JQ897608	JQ897678	JQ897763		LAO
Velitra_sp_1576	Reduviinae	Velitra		1576	UCR_ENT00052201	Hwang and Weirauch, 2012	UCR	JQ897614	JQ897685	JQ897770		BRN
Pseudozelurus_arizonicus_2765	Reduviinae	Pseudozelurus	arizonicus	2765	UCR_ENT00004573	Hwang and Weira	UCR	JQ897595	JQ897666	JQ897751		USA

						uch, 2012						
Noualhierana_furtiva_224	Reduviinae	Noualhierana	furtiva	224	AMNH_PBI 00218966	Weirauch and Munro, 2009	UCR	FJ230510	FJ230592	FJ230668		AUS
Nalata_squalida_1424	Reduviinae	Nalata	squalida	1424	UCR_ENT00002748	Hwang and Weirauch, 2012	UCR	JQ897575	JQ897648	JQ897733		ECU
Microlestria_nr_fuscicollis_1393	Reduviinae	Microlestria	fuscicollis	1393	UCR_ENT00002717	Hwang and Weirauch, 2012	UCR	JQ897568	JQ897643	JQ897726		ECU
Alloeocranum_arboricolum_1579	Reduviinae	Hermillus-like	sp.	1579	UCR_ENT 00052180	Hwang and Weirauch, 2012	UCR	JQ897547	JQ897623	JQ897700		BRN
Kayanocoris_wegneri_1590	Reduviinae	Kayanocoris	wegneri	1590	UCR_ENT 00052216	Hwang and Weirauch, 2012	UCR	JQ897563	JQ897642	JQ897721		BRN
Gerbelius_sp_704	Reduviinae	Gerbelius	cf. typicus	704	UCR_ENT 00052219	Hwang and Weirauch, 2012	UCR	NA	JQ897639	JQ897717		LAO
Leogorrus_litura_009	Reduviinae	Leogorrus	litura	9	UCR_ENT 00000068	Hwang and Weirauch, 2012	UCR	FJ230459	FJ230540	FJ230618		DOM

Opisthacidius_chinai_1285	Reduviinae	Ophistacidius	chinai	1285	UCR_ENT00012957	Hwang and Weirauch, 2012	MUSM	JQ897580	JQ897652	JQ897737		PER
Zelurus_alcides_1571	Reduviinae	Zelurus	alcides	1571	UCR_ENT00014324	Hwang and Weirauch, 2012	INBIO	JQ897615	JQ897686	JQ897771		CRI
Nanokerala_nr_browni_1232	Reduviinae	Nanokerala	sp.	1232	UCR_ENT00052228	Hwang and Weirauch, 2012	TIGER	JQ897577	JQ897650	JQ897735		THA
Psophis_sp_1581	Reduviinae	Psophis	sp.	1581	UCR_ENT00052230	Hwang and Weirauch, 2012	UCR	JQ897597	JQ897668	JQ897753		BRN
R_CW_5123_assembly.fasta	Reduviinae	Psophis	sp.	5123	NA	Knyshov et al., 2023	UCR	SRR13844064	SRR13844064	SRR13844064	WGS	MYS
Lisarda_nr_vandenplasi_177	Salyavatinae	Lisarda	sp.	177	AMNH_PBI00218921	Hwang and Weirauch, 2012	UCR	FJ230498	FJ230579	FJ230656		GNB
Austrotichus rugosus		*Austrotichus*	rugosus	NA	NA	Hwang and Weirauch, 2012	NA	AY252171	NA	AY252517		AUS
Oncocephalus_sp_079	Stenopodainae	Oncocephalus	sp.	79	UCR_ENT00000182	Weirauch and Munr	UCR	FJ230481	FJ230562	FJ230640		SGP

						o, 2009						
Stenopoda_sp_154	Stenopodainae	Stenopoda	sp.	154	AMNH_PBI 00218904	Hwang and Weirauch, 2012	UCR	FJ230493	FJ230574	FJ230651		NIC
R_CW_0355_assembly.fasta	Tribelocephalinae	Opistoplatys	sp.	355	NA	Knyshov et al., 2023	UCR	SRR13844079	SRR13844079	SRR13844079	WGS	JPN
Tribelocephalinae_sp_1592	Tribelocephalinae			1592	UCR_ENT 00052187	Hwang and Weirauch, 2012	UCR	JQ897612	JQ897682	JQ897767		BRN
Mirambulus_niger_1817	Vesciinae	Mirambulus	niger	1817	UCR_ENT 00052182	Hwang and Weirauch, 2012	UCR	JQ897571	JQ897645	JQ897729		GUF
Corythuca_sp_383		Corythuca	sp.	383	UCR_ENT 00000083	Weirauch and Munro, 2009	UCR	FJ230455	FJ230536	FJ230614		USA
RCW2007_Assembly_consensus_sequence	Saicini	Oncerotrachelus	sp.	2007	UCR_ENT 00127829	NA	UCR	OQ947975	OQ969030	OQ973406		CRI
RCW5964	Saicini	Oncerotrachelus	conformis	5964	UCR_ENT 00127970	NA	UCR	OQ948012	OQ969065	OQ973405		PAN
RCW0493	Saicini	Oncerotrachelus	sp.	493	no USI	NA	UCR	NA	NA	OQ973404		CRI
Oncerotrachelus_Mex2_849	Saicini	Oncerotrachelus	sp.	849	UCR_ENT 00129699	NA	UCR	OQ947955	NA	OQ973464		MEX
Oncerotrachelus_Ecu_1415	Saicini	Oncerotrachelus	sp.	1415	UCR_ENT 00002739	NA	UCR	OQ947954	OQ969005	NA		ECU

RCW1456_Assembly_consensus_sequence	Saicini	Oncerotrachelus	sp.	1456	UCR_ENT00002779	NA	UCR	OQ947971	OQ969022	OQ973401		ECU
RCW1637_Assembly_consensus_sequence	Saicini	Oncerotrachelus	sp.	1637	UCR_ENT00003797	NA	UCR	NA	OQ969024	OQ973403		GUF
RCW0050	Saicini	Oncerotrachelus	pallidus	50	AMNH_PBI00218805	NA	UCR	NA	NA	OQ973402		MEX
Oncerotrachelus_3825	Saicini	Oncerotrachelus	sp.	3825	no USI	Knyshov et al., 2023	UCR	PRJNA374322	PRJNA374322	PRJNA374322	RNA-Seq	CRI
I19317_RCW_3759_Saicinae_seq1	Saicini	Polytoxus	sp.	3759	UCR_ENT00129700	Knyshov et al., 2023	UCR	SRR13844015	SRR13844015	SRR13844015	AHE	CMR
Polytoxus_Bru_1549	Saicini	Polytoxus	sp.	1549	UCR_ENT00003640	NA	UCR	OQ947967	OQ969020	OQ973389		BRN
RCW5891	Saicini	Polytoxus	sp.	5891	UCR_ENT00128750	NA	UCR	OQ948007	OQ969059	OQ973330		IND
Polytoxus_Mya_830	Saicini	Polytoxus	sp.	830	UCR_ENT00129701	NA	UCR	OQ947968	OQ969021	OQ973331		MMR
RCW1515_Assembly_consensus_sequence	Saicini	Polytoxus	sp.	1515	UCR_ENT00003606	NA	UCR	NA	OQ969023	NA		MDG
RCW2750_Assembly_consensus_sequence	Saicini	Polytoxus	sp.	2750	UCR_ENT00004534	NA	UCR	OQ947977	OQ969031	OQ973334		MWI
RCW5711	Saicini	Polytoxus	sp.	5711	UCR_ENT00127751	NA	UCR	OQ947997	OQ969054	OQ973333		MWI
RCW3749_Assembly_consensus_sequence	Saicini	Polytoxus	sp.	3749	UCR_ENT00127830	NA	UCR	OQ947980	OQ969035	OQ973332		CMR
RCW5877	Saicini	Polytoxus	sp.	5877	UCR_ENT00128748	NA	UCR	OQ948006	NA	NA		IND
RCW6176	Saicini	Tolyxopus	muizoni	6176	UCR_ENT00127962	NA	UCR	OQ948028	OQ969083	OQ973376		CMR
I19318_RCW_4665_Saicinae_seq1	Saicini	Saica	sp.	4665	UCR_ENT00129705	Knyshov et al., 2023	UCR	SRR13844014	SRR13844014	SRR13844014	AHE	CUB
Saica_sp_042	Saicini	Saica	sp.	42	AMNH_PBI00218796	Hwang and	UCR	FJ230473	FJ230554	FJ230632, FJ230711		GUF

						Weirauch, 2012						
RCW1991_Assembly_consensus_sequence	Saicini	Saica	sp.	1991	UCR_ENT 00004095	NA	UCR	OQ947974	OQ969029	OQ973414		GUF
Saica_CR_534	Saicini	Saica	sp.	534	UCR_ENT 00127859	NA	UCR	OQ948035	OQ969092	OQ973415		CRI
Kiskeyana_palassaina_010	Saicini	Kiskeyana	palassaina Weirauch & Forero	10	AMNH_PBI 00218766/AMNH_PBI 00190561 in database	Hwang and Weirauch, 2012	USNM	FJ230460	FJ230541	FJ230619		DOM
Caprilesia_Ecu_1358	Saicini	Caprilesia	napurunа	1358	UCR_ENT 00002682	Castro-Huertas et al., 2022	QCAZ	OQ947922	OQ968962	OQ973398		ECU
RCW5525	Saicini	Tagalis	sp.	5525	UCR_ENT 00127839	NA	UCR	OQ947995	OQ969050	OQ973394		GTM
RCW3787	Saicini	Tagalis	sp.	3787	UCR_ENT 00127852	NA	UCR	OQ947982	OQ969037	OQ973393		PER
RCW5953	Saicini	Tagalis	dichroa	5953	UCR_ENT 00129702	NA	UCR	OQ948009	OQ969062	OQ973395		PAN
Tagalis_CR_697	Saicini	Tagalis	sp.	697	UCR_ENT 00129703	NA	UCR	NA	OQ969097	NA		CRI
RCW6215	Saicini	nrTagalis	sp.	6215	UCR_ENT 00129704	NA	UCR	OQ948032	OQ969087	OQ973392		IND
RCW5147	Saicini	Paratagalis	new sp	5147	UCR_ENT 00127853	NA	UCR	OQ947987	OQ969042	OQ973397		PER
RCW6218	Saicini	Madecassosaica	sp.	6218	UCR_ENT 00127966	NA	UCR	OQ948033	OQ969088	OQ973420		MDG
RCW5726	Saicini	Choreutocoris	sp.	5726	UCR_ENT 00128751	NA	UCR	OQ947999	OQ969056	OQ973391		IND
RCW5466_Assembly_consensus_sequence	Saicini	Choreutocoris	sarawakensis	5466	UCR_ENT 00127836	NA	UCR	OQ947989	OQ969045	OQ973396		MYS
RCW6167	Saicini	Villiersella	testacea	6167	UCR_ENT 00127977	NA	UCR	OQ948023	OQ969078	OQ973367		CMR

RCW6166	Saicini	Villiersella	agalma	6166	UCR_ENT00127976	NA	UCR	OQ948022	OQ969077	OQ973368		CMR
RCW6170	Saicini	Pristicoris	armatus	6170	UCR_ENT00127958	NA	UCR	OQ948025	OQ969080	OQ973399		CMR
RCW1801_Assembly_consensus_sequence	Saicini	new genus	sp.	1801	UCR_ENT00003957	NA	UCR	OQ947973	OQ969027	OQ973349		MDG
RCW1802	Saicini	new genus	sp.	1802	UCR_ENT00003958	NA	UCR	NA	OQ969028	OQ973350		MDG
I19319_RCW_1501_Mangabea_barbiger	Collartidini	Mangabea	barbiger	1501	UCR_ENT00002828	Knyshov et al., 2023	CAS	SRR13844013	SRR13844013	SRR13844013	AHE	MDG
Mangabea_barbiger_288	Collartidini	Mangabea	barbiger	288	UCR_ENT00005201	Hwang and Weirauch, 2012	CAS	NA	FJ230602	FJ230674		MDG
RCW4869_Assembly_consensus_sequence	Collartidini	Stenorhamphus	phuphan	4869	UCR_ENT00129706	Smith et al., 2019	QSBG	OQ947986	OQ969041	OQ973432		THA
RCW5465	Collartidini	Stenorhamphus	segarak	5465	UCR_ENT00127837	Smith et al., 2019	ZRC	NA	OQ969044	NA		MYS
RCW6171	Collartidini	Collartida	oculata	6171	UCR_ENT00127959	NA	UCR	OQ948026	OQ969081	OQ973421		CMR
I19321_RCW_1472_Carayonia_orientalis	Visayanocorini	Carayonia	orientalis	1473	UCR_ENT00002795	Knyshov et al., 2023	UCR	SRR13844012	SRR13844012	SRR13844012	AHE	DMA
Carayonia_Thai_1473	Visayanocorini	Carayonia	orientalis	1473	UCR_ENT00052232	Hwang and Weirauch, 2012	TIGER	JQ897549	JQ897626	JQ897703		THA
Carayonia_Au_230	Visayanocorini	Carayonia	australiensis	230	AMNH_PBI00218971	Weirauch and Munr	AM	NA	OQ968963	NA		AUS

						o, 2009						
Carayonia_Mad_1536	Visayanocorini	Carayonia	n.sp.	1536	UCR_ENT00003627	Hwang and Weirauch, 2012	CAS	JQ897548	JQ897625	JQ897702		MDG
RCW5486_assembly.fasta	Leistarchini	Bagauda	sp.	5486	UCR_ENT00129708	Knyshov et al., 2023	UCR	SRR13844087	SRR13844087	SRR13844087	WGS	MOZ
RCW5485_Assembly_consensus_sequence	Leistarchini	Bagauda	sp.	5485	UCR_ENT00129707	NA	UCR	OQ947991	OQ969047	OQ973409		MOZ
RCW5488	Leistarchini	Bagauda	sp.	5488	UCR_ENT00127750	NA	UCR	OQ947992	NA	NA		MOZ
RCW5502_Assembly_consensus_sequence	Leistarchini	Bagauda	sp.	5502	UCR_ENT00129683	NA	UCR	OQ947993	OQ969048	OQ973412		MYS
Bagauda_nr_similis_1554	Leistarchini	Bagauda	nr. similis	1554	UCR_ENT00003645	NA	UCR	OQ947921	OQ968960	OQ973411		MYS
Bagauda_sp1_682	Leistarchini	Bagauda	sp.	682	no USI	NA	UCR	NA	OQ968961	OQ973410		IDN
RCW6130	Leistarchini	Bagauda	giganteus	6130	UCR_ENT00129684	NA	UCR	NA	OQ969070	OQ973418		CMR
Voloina_Mad_1528	Leistarchini	Voloina	n.sp.	1528	UCR_ENT00003619	NA	UCR	OQ948040	OQ969098	OQ973453		MDG
cfVolonia_sp_1538	Leistarchini	Voloina	sp.	1538	UCR_ENT00003629	NA	UCR	NA	OQ968964	OQ973422		MDG
RCW6183	Leistarchini	Ambrinemesa	blancae	6183	UCR_ENT00006980	NA	UCR	OQ948029	OQ969084	OQ973457		MDG
Millotina_sp2_1520	Leistarchini	Millotina	sp. 2	1520	UCR_ENT00003611	NA	UCR	NA	OQ969001	OQ973458		MDG
RCW6198	Leistarchini	Bettyella	sp.	6198	CAS UCR_ENT00045416	NA	UCR	OQ948031	OQ969086	OQ973456		MDG
RCW5626	Leistarchini	Lhostella	pauliani	5626	UCR_ENT00127851	NA	UCR	NA	OQ969052	OQ973430		MDG
nrNesita_sp_1524	Leistarchini	Nesita	sp.	1524	UCR_ENT00003615	NA	UCR	NA	OQ969004	OQ973439		MDG

Paranesita_sp_1519	Leistarchini	Paranesita	sp.	1519	UCR_ENT00003610	NA	UCR	NA	OQ969009	OQ973440		MDG
Paranesita_sp2_1540	Leistarchini	Paranesita	sp. 2	1540	UCR_ENT00003631	NA	UCR	NA	OQ969010	OQ973441		MDG
Millotina_sp1_1163	Leistarchini	Ploiaria	phyllodoce	1163	UCR_ENT00003269	NA	UCR	OQ947952	OQ969000	OQ973436		NCL
Ploiaria_sp_698	Leistarchini	Ploiaria	maai	698	UCR_ENT00129685	NA	UCR	NA	NA	OQ973443		LAO
RCW1664	Leistarchini	Armstrongula	n.sp.2	1664	UCR_ENT00003824	NA	UCR	NA	OQ969025	OQ973437		AUS
RCW1672	Leistarchini	Armstrongula	n.sp.1	1672	UCR_ENT00003832	NA	UCR	NA	OQ969026	OQ973438		AUS
Gnomocoris_spinosus_1546	Leistarchini	Gnomocoris	spinosus	1546	UCR_ENT00003637	NA	UCR	OQ947951	OQ968999	OQ973451		BRN
Ploiaria_sp3_1602	Leistarchini	Ploiaria	sp. 1	1602	UCR_ENT00003660	NA	UCR	OQ947962	OQ969015	NA		CRI
RCW6000	Leistarchini	Ploiaria	brunnea	6000	UCR_ENT00127971	NA	UCR	OQ948014	OQ969067	OQ973426		PAN
Ploiaria_sp4_1606	Leistarchini	Ploiaria	gundlachi	1606	UCR_ENT00003664	NA	UCR	OQ947963	OQ969016	OQ973425		GUF
Ploiaria_sp1_1324	Leistarchini	Ploiaria	alexanderi	1324	UCR_ENT00002648	NA	UCR	OQ947961	OQ969014	OQ973448		ECU
Ploiaraia_sp_1557	Leistarchini	Ploiaria	varipennis	1557	UCR_ENT00003648	NA	UCR	OQ947960	OQ969013	OQ973444		DMA
RCW6222	Leistarchini	Orianocoris	spinosus	6222	UCR_ENT00127965	NA	UCR	NA	OQ969091	OQ973455		MDG
Ploiaria_hirticornis_054	Leistarchini	Ploiaria	denticauda	54	AMNH_PBI00218808	Weirauch and Munro, 2009	UCR	FJ230475	FJ230556	FJ230634		MEX
Ploiaria_sp_850	Leistarchini	Ploiaria	floridana	850	UCR_ENT00129686	NA	UCR	OQ947964	OQ969017	OQ973452		MEX
RCW3720_Assembly_consensus_sequence	Leistarchini	Barrosia	auraria	3720	UCR_ENT00129687	NA	UCR	OQ947978	OQ969032	OQ973353		CMR
RCW5709	Leistarchini	Barrosia	auraria	5709	UCR_ENT00127754	NA	UCR	NA	OQ969053	OQ973352		CMR

RCW6168	Leistarchini	Barrosia	auraria	6168	UCR_ENT 00127957	NA	UCR	OQ948024	OQ969079	OQ973351		CMR
RCW6160	Leistarchini	Barrosia	minuscula	6160	UCR_ENT 00127975	NA	UCR	OQ948021	OQ969076	OQ973400		CMR
RCW6189	Leistarchini	Tinnunga	macneilli	6189	CAS UCR_ENT 00045638	NA	UCR	OQ948030	OQ969085	OQ973454		MDG
Orthunga_sp1_1492	Leistarchini	Orthunga	sp. 1	1492	UCR_ENT 00002815	NA	UCR	NA	OQ969006	OQ973460		MDG
RCW6219	Leistarchini	Orthunga	pantherina	6219	UCR_ENT 00127967	NA	UCR	OQ948034	OQ969089	OQ973449		MDG
Nesita_sp2_1502	Leistarchini	Nesita	sp. 2	1502	UCR_ENT 00002829	NA	UCR	NA	OQ969002	OQ973450		MDG
I19322_RCW_1371_Panamia	Emesini	Panamia	cf. ornata	1371	UCR_ENT 00002695	Knyshov et al., 2023	UCR	SRR13844010	SRR13844010	SRR13844010	AHE	ECU
Panamia_sp1_1377	Emesini	Panamia	n.sp.	1377	UCR_ENT 00002701	NA	UCR	OQ947957	OQ969008	OQ973347		ECU
Panamia_ornata_1395	Emesini	Panamia	cf. ornata	1395	UCR_ENT 00002719	NA	UCR	OQ947956	OQ969007	OQ973348		ECU
nrAdemula_1474	Emesini	Ademula	sp	1474	UCR_ENT 00002797	NA	UCR	OQ947953	OQ969003	OQ973459		THA
RCW5853	Emesini	Malacopus ?	n. species?	5853	UCR_ENT 00128754	NA	UCR	OQ948002	OQ969058	NA		MYS
Empicoris_nr_sp1_1334	Emesini	Empicoris	cf. n.sp. 1	1334	UCR_ENT 00002658	NA	UCR	OQ947932	OQ968975	OQ973345		ECU
Empicoris_Ecu_1331	Emesini	Empicoris	n.sp. 1	1331	UCR_ENT 00002655	NA	UCR	OQ947931	OQ968974	OQ973344		ECU
Empicoris_USA_1558	Emesini	Empicoris	sp. 1	1558	UCR_ENT 00003649	NA	UCR	OQ947935	OQ968979	OQ973346		USA
Empicoris_Thai2_1477	Emesini	Empicoris	sp. 2	1477	UCR_ENT 00002800	NA	UCR	OQ947934	OQ968978	OQ973339		THA
Empicoris_RCW1497	Emesini	Empicoris	n.sp. 2	1497	UCR_ENT 00002820	NA	UCR	NA	OQ968976	OQ973340		MDG
RCW6174	Emesini	Empicoris	morstatti	6174	UCR_ENT 00127961	NA	UCR	OQ948027	OQ969082	OQ973342		CMR
RCW6220	Emesini	Empicoris	biannulatus	6220	UCR_ENT 00127968	NA	UCR	NA	OQ969090	OQ973343		MDG

RCW5712	Emesini	Empicoris	sp. 3	5712	UCR_ENT00127752	NA	UCR	OQ947998	OQ969055	OQ973341		ESP
Empicoris_rubromaculatus_1480	Emesini	Empicoris	rubromaculatus	1480	UCR_ENT00002803	NA	UCR	OQ947933	OQ968977	OQ973338		THA
Empicoris_Brun_1516	Emesini	Empicoris	sp. 4	1516	UCR_ENT00003607	NA	UCR	OQ947930	OQ968973	OQ973337		BRN
RCW4284_Assembly_consensus_sequence	Emesini	Tridemula	sp.	4284	UCR_ENT00127832	NA	UCR	NA	OQ969038	NA		NCL
Emesopsis_Thai_1475	Emesini	Emesopsis	sp.	1475	UCR_ENT00002798	NA	UCR	OQ947929	OQ968972	OQ973428		THA
Emesopsis_Laos_700	Emesini	Emesopsis	sp.	700	UCR_ENT00129688	NA	UCR	OQ947928	OQ968970	OQ973442		LAO
RCW_5530	Emesini	Emesopsis	sp.	5530	UCR_ENT00128689	NA	UCR	OQ947969	NA	NA		TZA
RCW_5531	Emesini	Emesopsis	sp.	5531	no USI	NA	UCR	OQ947970	NA	NA		TZA
RCW5625	Emesini	Emesopsis	sp.	5625	UCR_ENT00127848	NA	UCR	OQ947996	OQ969051	OQ973423		ZMB
Emesopsis_Mad1_1500	Emesini	Emesopsis	sp.	1500	UCR_ENT00002827	NA	UCR	NA	OQ968971	OQ973424		MDG
Emesopsis_Brun_1517	Emesini	Emesopsis	sp.	1517	UCR_ENT00003608	NA	UCR	OQ947927	OQ968969	OQ973463		SGP
RCW6158	Emesini	Myiophanes	leleupi	6158	UCR_ENT00127974	NA	UCR	OQ948020	OQ969075	NA		CMR
I19324_RCW_1654_Stenolemus_bituberus	Emesini	Stenolemus	bituberus	1654	UCR_ENT00003814	Knyshov et al., 2023	UCR	SRR13844008	SRR13844008	SRR13844008	AHE	AUS
Stenolemus_Au_1167	Emesini	Stenolemus	bituberus	1167	UCR_ENT00003270	NA	UCR	OQ948037	OQ969094	OQ973407		AUS
Stenolemus_Arg_1553	Emesini	Stenolemus	sp.	1553	UCR_ENT00003644	NA	UCR	OQ948036	OQ969093	OQ973429		ARG
Stenolemus_bispinosus_1644	Emesini	Stenolemus	bispinosus	1644	UCR_ENT00003804	NA	UCR	OQ948038	OQ969095	NA		AUS
RCW1660	Emesini	Stenolemus	bituberus	1660	UCR_ENT00003820	NA	UCR	OQ947972	NA	OQ973427		AUS
Stenolemus_giraffa_1640	Emesini	Stenolemus	giraffa	1640	UCR_ENT00003800	NA	UCR	OQ948039	OQ969096	NA		AUS

Genus_sp_1370	Emesini	n.gen.	n.sp.	1370	UCR_ENT00002694	NA	UCR	OQ947942	OQ968987	OQ973417		ECU
Stenolemoides_arizonensis_304	Emesini	Stenolemoides	arizonensis	304	UCR_218753/AMNH_PBI00218753	Weirauch and Munro, 2009	UCR	FJ230522	FJ230605	FJ230677		USA
RCW5232	Emesini	Stenolemopsis	sp.	5232	UCR_ENT00128749	NA	UCR	OQ947988	OQ969043	OQ973408		USA
Dohrnemesa_Ecu_1389	Emesini	Dohrnemesa	n.sp.	1389	UCR_ENT00002713	NA	UCR	OQ947924	OQ968966	OQ973435		ECU
RCW5976	Emesini	Polauchenia	schubarti	5976	UCR_ENT00129689	NA	UCR	OQ948013	OQ969066	OQ973433		PAN
RCW5957	Emesini	Polauchenia	schubarti	5957	UCR_ENT00129690	NA	UCR	OQ948010	OQ969063	OQ973434		PAN
RCW5947	Emesini	nr Polauchenia	sp.	5947	UCR_ENT00129691	NA	UCR	NA	NA	OQ973462		PAN
RCW5963	Emesini	Polauchenia	protentor	5963	UCR_ENT00127969	NA	UCR	OQ948011	OQ969064	OQ973446		PAN
Polauchenia_CR_1603	Emesini	Polauchenia	n.sp.	1603	UCR_ENT00003661	NA	UCR	OQ947965	OQ969018	OQ973447		CRI
RCW5946	Emesini	Polauchenia		5946	UCR_ENT00129692	NA	UCR	NA	OQ969060	NA		PAN
Polauchenia_Ecu_1391	Emesini	Polauchenia	sp.	1391	UCR_ENT00002715	NA	UCR	OQ947966	OQ969019	OQ973445		ECU
Dohrnemesa_CR_1598	Emesini	Dohrnemesa	sp.	1598	UCR_ENT00003656	NA	UCR	OQ947923	OQ968965	OQ973461		CRI
RCW5948	Emesini	Emesa	annulata	5948	UCR_ENT00129693	NA	UCR	OQ948008	OQ969061	OQ973431		PAN
I19323_RCW_1605_Mayemesa_paraensis	Emesini	Mayemesa	paraensis	1605	UCR_ENT00003663	Knyshov et al., 2023	UCR	SRR13844009	SRR13844009	SRR13844009	AHE	GUF
Phasmatocoris_sp_1601	Emesini	Phasmatocoris	sp.	1601	UCR_ENT00003659	NA	UCR	OQ947959	OQ969012	OQ973416		CRI

Phasmatocoris_sp1_1345	Emesini	Phasmatocoris	n.sp.	1345	UCR_ENT00002669	NA	UCR	OQ947958	OQ969011	OQ973465		ECU
RCW6122	Emesini	Phasmatocoris	praecellens	6122	UCR_ENT00129694	NA	UCR	OQ948016	OQ969069	OQ973466		PAN
RCW6034	Emesini	Phasmatocoris	usingeri	6034	UCR_ENT00127972	NA	UCR	OQ948015	OQ969068	OQ973419		PAN
RCW6156	Emesini	Eugubinus	sp.	6156	UCR_ENT00129695	NA	UCR	OQ948018	OQ969073	OQ973335		CMR
Eugubinus_sp_786	Emesini	Eugubinus	sp.	786	UCR_ENT00001550	NA	UCR	OQ947936	OQ968980	OQ973336		NGA
I19325_RCW_1593_Gardena_faustina	Emesini	Gardena	faustina	1593	UCR_ENT00003760	Knyshov et al., 2023	UCR	SRR13844007	SRR13844007	SRR13844007	AHE	CRI
Gardena_Mex2_1105	Emesini	Gardena	sp. 1	1105	UCR_ENT00002501	NA	UCR	OQ947940	OQ968985	OQ973369		MEX
Gardena_americana_1600	Emesini	Gardena	americana	1600	UCR_ENT00003658	NA	UCR	OQ947937	OQ968981	OQ973372		CRI
Gardena_Ecu2_1350	Emesini	Gardena	sp. 2	1350	UCR_ENT00002674	NA	UCR	OQ947939	OQ968983	OQ973371		ECU
Gardena_Ecu1_1304	Emesini	Gardena	sp. 2	1304	UCR_ENT00003353	NA	UCR	OQ947938	OQ968982	OQ973370		ECU
Gardena_Sing_660	Emesini	Gardena	sp. 4	660	no USI	NA	UCR	OQ947941	OQ968986	OQ973374		SGP
Gardena_Mad_1521	Emesini	Gardena	sp. 3	1521	UCR_ENT00003612	NA	UCR	NA	OQ968984	OQ973375		MDG
RCW6133	Emesini	Gardena	fuliginosa	6133	ENT_UCR00129670	NA	UCR	OQ948017	OQ969071	OQ973373		CMR
RCW5730	Emesini	nrBergemesa	sp.	5730	UCR_ENT00128752	NA	UCR	OQ948000	OQ969057	OQ973390		BRA
RCW2256	Emesini	Pseudometapterus	sp.	2256	UCR_ENT00005098	NA	UCR	OQ947976	NA	OQ973378		COL
RCW5865	Emesini	Anandromesa	sp.	5865	UCR_ENT00127979	NA	UCR	OQ948004	NA	OQ973379		USA
RCW5866	Emesini	Metapterus	sp.	5866	UCR_ENT00127978	NA	UCR	OQ948005	NA	OQ973380		USA
RCW5860	Emesini	Berlandiana	sp.	5860	UCR_ENT00127981	NA	UCR	OQ948003	NA	OQ973387		IND

RCW3742	Emesini	Jamesa	sp.	3742	ENT_UCR00128753	NA	UCR	OQ947979	OQ969034	OQ973382		CMR
RCW4286_Assembly_consensus_sequence	Emesini	Onychomesa	sp.	4286	ENT_UCR00127832	NA	UCR	OQ947983	OQ969033	OQ973384		CMR
RCW6157	Emesini	Schidium	sp.	6157	UCR_ENT00127973	NA	UCR	OQ948019	OQ969074	OQ973383		CMR
RCW5480_Assembly_consensus_sequence	Emesini	Barce	sp.	5480	ENT_UCR00127838	NA	UCR	OQ947990	OQ969046	OQ973381		MOZ
RCW4434_Assembly_consensus_sequence	Emesini	Schidium	sp.	4434	ENT_UCR00127834	NA	UCR	OQ947984	OQ969039	OQ973388		KOR
RCW5783	Emesini	Leptinoschidium	sp.	5783	UCR_ENT00127982	NA	UCR	OQ948001	NA	OQ973386		GAB
RCW6137	Emesini	Leptinoschidium	camerunense	6137	ENT_UCR00129671	NA	UCR	NA	OQ969072	OQ973377		CMR
RCW3752_Assembly_consensus_sequence	Emesini	Bargylia	sp.	3752	ENT_UCR00127831	NA	UCR	OQ947981	OQ969036	OQ973385		CMR
RCW4617	Emesini	Bergemesa	brachmanni	4617	ENT_UCR00127833	NA	UCR	OQ947985	OQ969040	OQ973413		ARG
I19326_RCW_1548_Emesaya_brevipennis	Emesini	Emesaya	brevipennis	1548	UCR_ENT00003639	Knyshov et al., 2023	UCR	SRR13844006	SRR13844006	SRR13844006	AHE	USA
Emesaya_brevipennis_CR_695	Emesini	Emesaya	brevipennis	695	ENT_UCR00129672	NA	UCR	OQ947926	OQ968968	OQ973354		CRI
Emesaya_brevipennis2_1463	Emesini	Emesaya	brevipennis	1463	UCR_ENT00002786	NA	UCR	OQ947925	OQ968967	OQ973355		USA
Emesaya_incisa_282	Emesini	Emesaya	incisa	282	AMNH_PBI00219017	Hwang and Weirauch, 2012	UCR	FJ230515	FJ230598	FJ230672		USA
PispR.Trinity.fasta	Emesini	unknown		3916	no USI	Knyshov et al., 2023	UCR	PRJNA374317	PRJNA374317	PRJNA374317	Transcriptome	DOM
Ghilianella_sp3_1380	Emesini	Ghilianella	sp. 3	1380	UCR_ENT00002704	NA	UCR	OQ947947	OQ968993	NA		ECU

Ghilianella_sp1_1312	Emesini	Ghilianella	sp. 1	1312	UCR_ENT 00003361	NA	UCR	NA	OQ968992	OQ973359		ECU
Ghilianella_sp8_1630	Emesini	Ghilianella	sp. 8	1630	UCR_ENT 00003790	NA	UCR	OQ947950	OQ968997	OQ973360		GUF
Ghilianella_nr_gibbiventris2_536	Emesini	Ghilianella	nr. gibbiventris	536	ENT_UCR 00129673	NA	UCR	OQ947944	OQ968989	OQ973364		CRI
Ghilianella_sp6_1441	Emesini	Ghilianella	sp. 6	1441	UCR_ENT 00002765	NA	UCR	OQ947949	OQ968995	OQ973362		ECU
Ghilianella_nr_pachitea_1311	Emesini	Ghilianella	nr. pachitea	1311	UCR_ENT 00003357	NA	UCR	OQ947946	OQ968991	OQ973358		ECU
Ghilianella_nr_approximata_1382	Emesini	Ghilianella	nr. approximata	1382	UCR_ENT 00002706	NA	UCR	OQ947943	OQ968988	OQ973356		ECU
RCW5507	Emesini	Ghilianella	sp.	5507	UCR_ENT 00127753	NA	UCR	OQ947994	OQ969049	OQ973361		CRI
Ghilianella_sp4_1421	Emesini	Ghilianella	sp. 4	1421	UCR_ENT 00002745	NA	UCR	OQ947948	OQ968994	OQ973363		ECU
Ghilianella_nr_minimula_1310	Emesini	Ghinallelia	nr. minimula	1310	UCR_ENT 00003358	NA	UCR	OQ947945	OQ968990	OQ973357		ECU
Ghilianella_truncata_537	Emesini	Ghilianella	truncata	537	ENT_UCR 00129674	NA	UCR	NA	OQ968998	OQ973365		CRI
Ghilianella_sp7_1623	Emesini	Ghilianella	sp. 7	1623	UCR_ENT 00003781	NA	UCR	NA	OQ968996	OQ973366		CRI

Table S2.2: 40-character morphological matrix, terminology largely following Weirauch (2008) and Wygodzinsky (1966). Primary homology hypotheses were based on Wygodzinsky (1966) and personal assessment following examination of specimens. Source of character coding provided for each specimen coded.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
RCW956	0	0	0	0	1	1	0	0	0	1	0	0	1	2	1	1	0	0	0	0	1	0	0	0	2	0	1	0	0	2	0	0	0	0	1	0	1	1	0	0
RCW3882	0	0	0	0	1	1	0	0	0	1	0	0	1	2	1	1	0	0	0	0	1	0	0	0	2	0	1	0	0	2	0	0	0	0	1	0	1	1	0	0
RCW5255	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW779	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1568	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW014	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW188	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW013	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW3947	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW041	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW141	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
RCW071	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW184	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
RCW108	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW023	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW818	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW587	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW294	0	0	0	0	1	1	0	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0

RCW216	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW363	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW029	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
RCW1572	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW810	0	0	0	0	1	1	0	0	0	2	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW2764	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW737	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW702	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1576	0	0	0	0	1	1	0	0	0	1	0	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW2765	0	0	0	0	1	1	0	0	0	2	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW224	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1424	0	2	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1393	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1579	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1590	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW704	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW009	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0
RCW1285	0	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1571	0	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1232	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW1581	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW5123	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0

RCW177	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Austroti	0	0	0	0	1	-	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW079	0	0	0	0	1	1	0	0	0	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW154	0	0	0	0	1	1	0	0	0	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
RCW0355	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1592	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1817	0	0	0	0	1	1	0	0	0	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW383	0	0	0	0	1	-	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW2007	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW5964	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW0493	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW849	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1415	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1456	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1637	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW0050	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW3825	1	1	1	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW3759	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW1549	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW5891	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW830	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW1515	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0

RCW2750	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW5711	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW3749	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW5877	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW6176	0	1	1	1	0	0	0	1	2	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW4665	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW042	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW1991	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW534	0	1	1	1	0	0	0	1	2	2	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
RCW010	0	2	2	2	0	1	0	1	1	2	1	-	-	-	-	-	-	-	-	-	-	0	0	1	2	0	2	1	0	2	1	0	0	0	0	1	1	0	0	0
RCW1358	0	1	2	2	0	0	1	1	1	2	1	0	0	1	0	1	0	0	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW5525	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW3787	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW5953	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW697	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW6215	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW5147	0	2	2	2	0	1	0	1	1	2	1	0	0	1	0	1	0	0	0	0	1	0	0	1	2	0	2	1	0	1	1	0	0	0	0	1	1	0	0	0
RCW6218	0	2	2	0	0	1	0	1	1	1	1	-	-	-	-	-	-	-	-	-	-	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW5726	0	2	2	0	0	0	1	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW5466	0	2	2	0	0	0	1	1	1	2	1	0	0	1	0	1	0	1	0	0	1	0	0	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW6167	0	2	2	2	0	1	1	1	1	2	1	0	0	1	0	1	0	1	0	0	?	0	0	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW6166	0	2	2	0	0	1	1	1	1	2	1	0	0	1	0	1	0	1	0	0	?	0	0	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0

RCW6170	0	2	2	0	0	0	1	1	1	2	1	-	-	-	-	-	-	-	-	-	-	0	0	1	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW1801	0	0	0	0	0	1	0	0	0	2	1	-	-	-	-	-	-	-	-	-	-	0	1	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW1802	0	0	0	0	0	1	0	0	0	2	1	-	-	-	-	-	-	-	-	-	-	0	1	0	2	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0
RCW1501	0	1	1	1	0	1	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW288	0	1	1	1	0	1	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW4869	0	1	1	1	0	1	0	0	0	1	0	0	1	2	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW5465	0	1	1	1	0	1	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW6171	0	1	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
RCW1472	0	1	1	1	0	0	0	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0
RCW1473	0	1	1	1	0	0	0	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0
RCW230	0	1	1	1	0	0	0	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0
RCW1536	0	1	1	1	0	0	0	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0
RCW5486	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW5485	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW5488	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW5502	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW1554	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW682	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW6130	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
RCW1528	0	2	1	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	1	1	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW1538	0	2	1	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	1	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW6183	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0

RCW1520	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW6198	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW5626	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	2	-	0	0	0	0	0
RCW1524	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	2	0	1	0	0	1	0	0	1	2	-	0	-	1	0	0
RCW1519	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	2	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW1540	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	2	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW1163	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW698	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW1664	0	1	0	0	0	1	0	0	2	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	2	0	2	0	0	1	0	0	1	0	1	0	0	0	0	0
RCW1672	0	1	0	0	0	1	0	0	2	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	2	0	2	0	0	1	0	0	1	0	1	0	0	0	0	0
RCW1546	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	2	1	0	0	1	1	0	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW1602	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW6000	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW1606	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW1324	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW1557	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW6222	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW054	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW850	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	1	1	0	2	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0
RCW3720	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW5709	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW6168	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0

RCW6160	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
RCW6189	0	2	0	0	0	1	0	0	2	1	0	0	0	0	1	0	0	1	1	0	?	1	1	0	1	0	2	0	0	1	0	0	1	2	-	0	-	1	0	0
RCW1492	0	2	0	0	0	1	0	0	2	1	0	-	-	-	-	-	-	-	-	-	-	1	1	0	1	0	2	0	0	1	0	0	1	2	-	0	-	1	0	0
RCW6219	0	0	0	0	0	1	0	0	2	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	1	0	1	0	0	1	0	0	1	2	-	0	-	1	0	0
RCW1502	0	0	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	2	-	0	-	1	0	0
RCW1371	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
RCW1377	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
RCW1395	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
RCW1474	0	0	0	0	0	1	0	0	0	1	0	0	3	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1	1
RCW5853	0	0	0	0	0	1	0	0	0	2	0	0	3	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1
RCW1334	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1331	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1558	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1477	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1497	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW6174	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW6220	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW5712	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1480	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1516	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW4284	0	0	0	0	0	1	0	0	0	1	0	0	3	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1475	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1

RCW700	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW_5530	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW_5531	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW5625	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1500	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW1517	0	0	0	0	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	-	0	1	0	1	1
RCW6158	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	1	1	0	1	1	0	0	0	2	0	0	2	0	0	0	0	1	0	1	0	1	1
RCW1639	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	1	1	0	1	1	0	0	0	2	0	0	2	0	0	0	0	1	0	1	0	1	1
RCW1654	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1167	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1553	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1644	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1660	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1640	0	0	0	0	0	1	0	1	0	2	0	0	3	1	1	1	0	1	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1370	0	0	0	0	0	1	0	0	0	2	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW304	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	1	0	1	1	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW5232	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	1	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	1	-	0	1	0	1	1
RCW1389	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW5976	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW5957	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW5947	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW5963	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1

RCW1603	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW5946	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW1391	0	0	0	0	0	1	0	0	0	2	0	0	3	1	1	0	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	1	1
RCW1598	0	0	0	0	0	1	0	0	0	0	0	0	3	1	1	1	0	0	0	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	1	0	1	0	1	1
RCW5948	0	0	0	0	0	1	0	0	0	0	0	0	3	2	1	0	0	1	1	0	1	1	1	0	0	0	2	0	0	2	0	0	0	0	1	0	1	0	1	1
RCW1605	0	0	0	0	0	1	0	0	0	0	0	0	3	1	1	0	0	0	0	1	1	1	1	0	0	0	2	0	0	2	0	0	0	0	1	0	1	0	1	1
RCW1601	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	2	0	0	1	0	2	0	1	1	1	1
RCW1345	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	2	0	0	1	0	2	0	1	1	1	1
RCW6122	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	2	0	0	1	0	2	0	1	1	1	1
RCW6034	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	2	0	0	1	0	2	0	1	1	1	1
RCW6156	0	0	0	0	0	1	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	1	1	0	2	0	2	0	0	2	0	0	0	0	2	0	1	1	1	1
RCW786	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	1	1	0	0	0	2	0	0	2	0	0	0	0	2	0	?	0	1	1
RCW1593	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW1105	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW1600	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW1350	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW1304	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW660	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW1521	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW6133	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	3	0	0	0	0	2	0	1	0	1	1
RCW5730	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	1	2	0	0	3	0	0	1	1	-	0	1	1	0	1
RCW2256	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	1	1	0	1

RCW5865	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	1	1	1	1
RCW5866	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	1	1
RCW5860	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW3742	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW4286	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW6157	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW5480	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW4434	0	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW5783	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW6137	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW3752	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	2	0	0	1	2	-	0	0	1	0	1
RCW4617	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	1	2	0	0	3	0	0	1	1	-	0	0	1	0	1
RCW1548	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	2	0	0	3	0	0	1	0	0	0	0	0	1	1
RCW695	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	2	0	0	3	0	0	1	0	0	0	0	0	1	1
RCW1463	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	2	0	0	3	0	0	1	0	0	0	0	0	1	1
RCW282	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	2	0	0	3	0	0	1	0	0	0	0	0	1	1
PispR	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
RCW1380	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1312	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1630	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW536	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1441	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1

RCW1311	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1382	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW5507	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1421	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1310	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW537	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1
RCW1623	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	3	0	0	1	2	-	0	0	1	0	1

Table S4.1: Taxa included in analysis, accession number and data type for Chapter 4.

Suborder	Infraorder	Family	Genus	Species	Sequence name	Bioproject No.	Data type
Auchenorrhyncha	Cicadomorpha	Aphrophoridae	*Aphrophora*	*afni*	Aphrophora_alni.fasta	PRJNA272162	transcriptome
Auchenorrhyncha	Cicadomorpha	Aphrophoridae	*Philaenus*	*spumarius*	Philaenus_spumarius.fasta	PRJNA272277	transcriptome
Auchenorrhyncha	Cicadomorpha	Cercopidae	*Cercopis*	*vulnerata*	Cercopis_vulnerata.fasta	PRJNA219537	transcriptome
Auchenorrhyncha	Cicadomorpha	Cercopidae	*Prosapia*	*bicincta*	Prosapia_bicincta.fasta	PRJNA272284	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Agallia*	*constricta*	Agallia_constricta.fasta	PRJNA272213	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Dalbulus*	*maidis*	Dalbulus_maidis.fasta	PRJNA272239	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Empoasca*	*fabae*	Empoasca_fabae.fasta	PRJNA272241	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Graphocephala*	*fennahi*	Graphocephala_fennahi.fasta	PRJNA272183	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Hespenedra*	*chifensis*	Hespenedra_chilensis.fasta	PRJNA272247	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Ponana*	*quadralaba*	Ponana_quadralaba.fasta	PRJNA272282	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Ulopa*	*reticulata*	Ulopa_reticulata.fasta	PRJNA272207	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadellidae	*Vidanoana*	*flavomaculata*	Vidanoana_flavomaculata.fasta	PRJNA272302	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadidae	*Kikihia*	*scutellaris*	Kikihia_scutellaris.fasta	PRJNA295715	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadidae	*Megatibicen*	*dorsata*	Megatibicen_dorsata.fasta	PRJNA272295	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadidae	*Okanagana*	*villosa*	Okanagana_villosa.fasta	PRJNA219585	transcriptome
Auchenorrhyncha	Cicadomorpha	Cicadidae	*Tettigades*	*auropilosa*	Tettigades_auropilosa.fasta	PRJNA295726	transcriptome
Auchenorrhyncha	Cicadomorpha	Melizoderidae	*Llanquihuea*	*pilosa*	Llanquihuea_pilosa.fasta	PRJNA272258	transcriptome
Auchenorrhyncha	Cicadomorpha	Membracidae	*Centrotus*	*comutus*	Centrotus_cornutus.fasta	PRJNA272169	transcriptome

Auchenorrhyncha	Cicadomorpha	Membracidae	*Holdgatiella*	*chepuensis*	Holdgatiella_chepuensis.fasta	PRJNA272249	transcriptome
Auchenorrhyncha	Cicadomorpha	Membracidae	*Nessorhinus*	*gibberulus*	Nessorhinus_gibberulus.fasta	PRJNA272268	transcriptome
Auchenorrhyncha	Cicadomorpha	Membracidae	*Stictocephala*	*bisonia*	Stictocephala_bisonia.fasta	PRJNA272293	transcriptome
Auchenorrhyncha	Cicadomorpha	Myerslopiidae	*Mapuchea*	sp.	Mapuchea_sp.fasta	PRJNA272263	transcriptome
Auchenorrhyncha	Cicadomorpha	Tettigarctidae	*Tettigarcta*	*crinita*	Tettigarcta_crinita.fasta	PRJNA295711	transcriptome
Auchenorrhyncha	Fulgoromorpha	Acanaloniidae	*Acanalonia*	*conica*	Acanalonia_conica.fasta	PRJNA272210	transcriptome
Auchenorrhyncha	Fulgoromorpha	Caliscelidae	*Bruchomorpha*	*oculata*	Bruchomorpha_oculata.fasta	PRJNA272222	transcriptome
Auchenorrhyncha	Fulgoromorpha	Caliscelidae	*Caliscelis*	*boneflii*	Caliscelis_bonelli.fasta	PRJNA272168	transcriptome
Auchenorrhyncha	Fulgoromorpha	Cixiidae	*Melanoliarus*	*placitus*	Melanoliarus_placitus.fasta	PRJNA272269	transcriptome
Auchenorrhyncha	Fulgoromorpha	Cixiidae	*Tachycixius*	*pilosus*	Tachycixius_pilosus.fasta	PRJNA272206	transcriptome
Auchenorrhyncha	Fulgoromorpha	Delphacidae	*Idiosystatus*	*acutiuscufus*	Idiosystatus_acutiusculus.fasta	PRJNA272251	transcriptome
Auchenorrhyncha	Fulgoromorpha	Dictyopharidae	*Dictyophara*	*europaea*	Dictyophara_europaea.fasta	PRJNA272176	transcriptome
Auchenorrhyncha	Fulgoromorpha	Dictyopharidae	*Phylloscelis*	*atra*	Phylloscelis_atra.fasta	PRJNA272279	transcriptome
Auchenorrhyncha	Fulgoromorpha	Flatidae	*Metcalfa*	*pruinosa*	Metcalfa_pruinosa.fasta	PRJNA272198	transcriptome
Auchenorrhyncha	Fulgoromorpha	Fulgoridae	*Cyrpoptus*	*belfmgei*	Cyrpoptus_belfragei.fasta	PrlJNA272237	transcriptome
Coleorrhyncha		Peloridiidae	*Hackeriella*	*veitchi*	Hackeriella_veitchi.fasta	PRJNA357411	transcriptome
Coleorrhyncha		Peloridiidae	*Peloridium*	*pomponorum*	Peloridium_pomponorum.fasta	PRJNA272276	transcriptome
Coleorrhyncha		Peloridiidae	*Xenophyes*	*metoponcus*	Xenophyes_metoponcus.fasta	PRJNA272209	transcriptome
Coleorrhyncha		Peloridiidae	*Xenophysella*	*greensladeae*	Xenophysella_greensladeae.fasta	PRJNA219618	transcriptome
Heteroptera	Cimicomorpha	Anthocoridae	*Orius*	*insidiosus*	Orius_insidiosus.fasta	PRJNA272271	transcriptome
Heteroptera	Cimicomorpha	Cimicidae	*Cimex*	*lectularius*	Cimex_lectularius.fasta	PRJNA272171	transcriptome
Heteroptera	Cimicomorpha	Joppeicidae	*Joppeicus*	*paradoxus*	Joppeicus_paradoxus.fasta		genome
Heteroptera	Cimicomorpha	Lasiochilidae	*Lasiochilidae*	sp.	Lasiochilidae_sp.fasta		genome

Heteroptera	Cimicomorpha	Lyctocoridae	*Lyctocoris*	*campestris*	Lyctocoris_campestris.fasta		genome
Heteroptera	Cimicomorpha	Medocostidae	*Medocostes*	sp.	Medocostes_sp.fasta		genome
Heteroptera	Cimicomorpha	Microphysidae	*Genus*	sp.	Microphysidae_sp.fasta		genome
Heteroptera	Cimicomorpha	Microphysidae	*Loricula*	*pselaphiformis*	Loricula_pselaphiformis.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Coridromius*	sp.	Coridromius_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Deraeocoris*	sp.	Deraeocoris_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Fulvius*	sp.	Fulvius_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Helopeltis*	sp.	Helopeltis_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Isometopinae*	sp.	Isometopinae_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Larinocerus*	*balius*	Larinocerus_balius.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Lopidea*	*amorphae*	Lopidea_amorphae.fasta	PRJNA272259	transcriptome
Heteroptera	Cimicomorpha	Miridae	*Lygus*	*lineofaris*	Lygus_lineolaris.fasta	PRJNA272261	transcriptome
Heteroptera	Cimicomorpha	Miridae	*Monalocoris*	sp.	Monalocoris_sp.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Notostira*	*elongata*	Notostira_elongata.fasta	PRJNA219583	transcriptome
Heteroptera	Cimicomorpha	Miridae	*Pachymerocorista*	*pilosus*	Pachymerocorista_pilosus.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Peritropis*	*setosicornis*	Peritropis_setosicornis.fasta		genome
Heteroptera	Cimicomorpha	Miridae	*Reuteroscopus*	*omatus*	Reuteroscopus_ornatus.fasta	PRJNA272288	transcriptome
Heteroptera	Cimicomorpha	Nabidae	*Nabis*	*subcoleoptratus*	Nabis_subcoleoptratus.fasta	PRJNA272267	transcriptome
Heteroptera	Cimicomorpha	Nabidae	*Pagasa*	sp.	Pagasa_sp.fasta	PRJNA272275	transcriptome
Heteroptera	Cimicomorpha	Pachynomidae	*Aphelonotus*	*fraterculus*	Aphelonotus_fraterculus.fasta	PRJNA272218	transcriptome
Heteroptera	Cimicomorpha	Plokiophilidae	Genus	sp.	Plokiophilidae_sp.fasta		genome
Heteroptera	Cimicomorpha	Reduviidae	*Arilus*	*cristatus*	Arilus_cristatus.fasta	PRJNA272219	transcriptome
Heteroptera	Cimicomorpha	Reduviidae	*Phymata*	*pennsylvanica*	Phymata_pennsylvanica.fasta	PRJNA272280	transcriptome
Heteroptera	Cimicomorpha	Reduviidae	*Rhodnius*	*prolixus*	rhodnius_prolixus.fasta	ACPB03022661	genome-reference
Heteroptera	Cimicomorpha	Thaumastocoridae	*Discocoris*	sp.	Discocoris_sp.fasta		genome
Heteroptera	Cimicomorpha	Thaumastocoridae	*Thaumastocoris*	*peregrinus*	Thaumastocoris_peregrinus.fasta		genome
Heteroptera	Cimicomorpha	Tingidae	*Corythucha*	*ciliata*	Corythucha_ciliata.fasta	PRJNA272173	transcriptome

Heteroptera	Cimicomorpha	Velocipedidae	*Costomedes*	*karimui*	Costomedes_karimui.fasta		genome
Heteroptera	Dipsocoromorpha	Ceratocombidae	*Ceratocombus*	sp.	Ceratocombus_sp.fasta	PRJNA272227	transcriptome
Heteroptera	Dipsocoromorpha	Dipsocoridae	*Cryptostemma*	sp.	Cryptostemma_sp.fasta		genome
Heteroptera	Dipsocoromorpha	Schizopteridae	*Rectilamina*	sp.	Rectilamina_sp.fasta		genome
Heteroptera	Enicocephalomorpha	Aenictopecheidae	*Tornocrusus*	sp.	Tornocrusus_sp.fasta		genome
Heteroptera	Enicocephalomorpha	Enicocephalidae	*Alienates*	sp.	Alienates_sp.fasta		genome
Heteroptera	Enicocephalomorpha	Enicocephalidae	*Hoplitocoris*	sp.	Hoplitocoris_sp.fasta	PRJNA272250	transcriptome
Heteroptera	Gerromorpha	Gerridae	*Aquarius*	*paludum*	Aquarius_paludum.fasta	PRJNA272163	transcriptome
Heteroptera	Gerromorpha	Gerridae	*Limnoporus*	*canaliculatus*	Limnoporus_canaliculatus.fasta	PRJNA272257	transcriptome
Heteroptera	Gerromorpha	Hebridae	Genus	sp.	Hebridae_sp.fasta		genome
Heteroptera	Gerromorpha	Hydrometridae	*Hydrometra*	*stagnorum*	Hydrometra_stagnorum.fasta	PRJNA272188	transcriptome
Heteroptera	Gerromorpha	Macrovellidae	*Macrovelis*	*hornii*	Macrovelis_hornii.fasta		genome
Heteroptera	Gerromorpha	Mesoveliidae	*Mesovelia*	*mulsanti*	Mesovelia_mulsanti.fasta	PRJNA272265	transcriptome
Heteroptera	Gerromorpha	Veliidae	*Rhagovelia*	*obesa*	Rhagovelia_obesa.fasta	PRJNA272289	transcriptome
Heteroptera	Gerromorpha	Veliidae	*Velia*	*caprai*	Velia_caprai.fasta	PRJNA219616	transcriptome
Heteroptera	Leptopodomorpha	Leptopodidae	*Valleriola*	sp.	Valleriola_sp.fasta		genome
Heteroptera	Leptopodomorpha	Omaniidae	*Omania*	sp.	Omaniidae_sp.fasta		genome
Heteroptera	Leptopodomorpha	Saldidae	*Saldula*	*saltatoria*	Saldula_saltatoria.fasta	PRJNA272204	transcriptome
Heteroptera	Nepomorpha	Aphelocheiridae	*Aphelocheirus*	*aestivafis*	Aphelocheirus_aestivalis.fasta	PRJNA272161	transcriptome
Heteroptera	Nepomorpha	Belostomatidae	*Belostoma*	*flumineum*	Belostoma_flumineum.fasta	PRJNA272220	transcriptome
Heteroptera	Nepomorpha	Belostomatidae	*Diplonychus*	*rusticus*	Diplonychus_rusticus.fasta	PRJNA272177	transcriptome
Heteroptera	Nepomorpha	Corixidae	*Corixa*	*punctata*	Corixa_punctata.fasta	PRJNA272172	transcriptome
Heteroptera	Nepomorpha	Corixidae	*Trichocorixa*	*calva*	Trichocorixa_calva.fasta	PRJNA272296	transcriptome
Heteroptera	Nepomorpha	Gelastocoridae	*Gelastocoris*	*oculatus*	Gelastocoris_oculatus.fasta	PRJNA272243	transcriptome
Heteroptera	Nepomorpha	Naucoridae	*Ilyocoris*	*cimicoides*	Ilyocoris_cimicoides.fasta	PRJNA272189	transcriptome
Heteroptera	Nepomorpha	Nepidae	*Ranatra*	*linearis*	Ranatra_linearis.fasta	PRJNA219599	transcriptome
Heteroptera	Nepomorpha	Notonectidae	*Buenoa*	*margaritacea*	Buenoa_margaritacea.fasta	PRJNA272223	transcriptome
Heteroptera	Nepomorpha	Notonectidae	*Notonecta*	*glauca*	Notonecta_glauca.fasta	PRJNA272200	transcriptome

Heteroptera	Nepomorpha	Ochteridae	Genus	sp.	Ochteridae_sp.fasta		genome
Heteroptera	Nepomorpha	Pleidae	*Plea*	*minutissima*	Plea_minutissima.fasta	PRJNA272202	transcriptome
Heteroptera	Pentatomomorpha	Acanthosomatidae	*Acanthosoma*	*haemorrhoidale*	Acanthosoma_haemorrhoidale.fasta	PRJNA219520	transcriptome
Heteroptera	Pentatomomorpha	Alydidae	*Alydus*	*pilosus*	Alydus_pilosus.fasta	PRJNA272214	transcriptome
Heteroptera	Pentatomomorpha	Aradidae	*Aradus*	*betulae*	Aradus_betulae.fasta	PRJNA272164	transcriptome
Heteroptera	Pentatomomorpha	Aradidae	*Mezira*	*granulata*	Mezira_granulata.fasta	PRJNA272266	transcriptome
Heteroptera	Pentatomomorpha	Artheneidae	*Chilacis*	*typhae*	Chilacis_typhae.fasta		genome
Heteroptera	Pentatomomorpha	Berytidae	*Jalysus*	sp.	Jalysus_sp.fasta	PRJNA272253	transcriptome
Heteroptera	Pentatomomorpha	Berytidae	*Metatropis*	*rufescens*	Metatropis_rufescens.fasta	PRJNA272197	transcriptome
Heteroptera	Pentatomomorpha	Canopidae	*Canopus*	sp.	Canopidae_sp.fasta		genome
Heteroptera	Pentatomomorpha	Colobathristidae	*Phaenacantha*	*australiae*	Phaenacantha_australiae.fasta	PRJNA295735	transcriptome
Heteroptera	Pentatomomorpha	Coreidae	*Anasa*	*tristis*	Anasa_tristis.fasta	PRJNA272215	transcriptome
Heteroptera	Pentatomomorpha	Cydnidae	*Sehirus*	*cinctus*	Sehirus_cincutus.fasta	PRJNA272292	transcriptome
Heteroptera	Pentatomomorpha	Cymidae	*Cymus*	*coracipennis*	Cymus_coracipennis.fasta		genome
Heteroptera	Pentatomomorpha	Dinidoridae	*Genus*	sp.	Dinidoridae_sp.fasta		genome
Heteroptera	Pentatomomorpha	Geocoridae	*Epipolops*	sp.	Epipolops_sp.fasta		genome
Heteroptera	Pentatomomorpha	Geocoridae	*Geocoris*	sp.	Geocoris_sp.fasta	PRJNA272244	transcriptome
Heteroptera	Pentatomomorpha	Hyocephalidae	*Maevius*	*indecorus*	Maevius_indecorus.fasta		genome
Heteroptera	Pentatomomorpha	Idiostolidae	*Trisecus*	*pictus*	Trisecus_pictus.fasta		genome
Heteroptera	Pentatomomorpha	Largidae	*Largus*	*cafifomicus*	Largus_californicus_1.fasta	PRJNA272803	transcriptome
Heteroptera	Pentatomomorpha	Largidae	*Largus*	*cafifomicus*	Largus_californicus_2.fasta	PRJNA272256	transcriptome
Heteroptera	Pentatomomorpha	Lestoniidae	*Lestonia*	sp.	Lestoniidae_sp.fasta		genome
Heteroptera	Pentatomomorpha	Lygaeidae	*Arocatus*	*melanocephafus*	Arocatus_melanocephalus.fasta	PRJNA272165	transcriptome
Heteroptera	Pentatomomorpha	Lygaeidae	*Ischnodemus*	*falicus*	Ischnodemus_falicus.fasta	PRJNA272252	transcriptome
Heteroptera	Pentatomomorpha	Lygaeidae	*Lygaeus*	*equestris*	Lygaeus_equestris.fasta	PRJNA272193	transcriptome
Heteroptera	Pentatomomorpha	Lygaeidae	*Lygaeus*	*turcicus*	Lygaeus_turcicus.fasta	PRJNA272260	transcriptome
Heteroptera	Pentatomomorpha	Lygaeidae	*Oncopeltus*	*fasciatus*	Oncopeltus_fasciatus.fasta	PRJNA272270	transcriptome

Heteroptera	Pentatomomorpha	Malcidae	*Chauliops*	*fallax*	Chauliops_fallax.fasta	PRJNA272229	transcriptome
Heteroptera	Pentatomomorpha	Megarididae	*Megaris*	sp.	Megarididae_sp.fasta		genome
Heteroptera	Pentatomomorpha	Ninidae	*Cymoninus*	sp.	Cymoninus_sp.fasta		genome
Heteroptera	Pentatomomorpha	Oxycarenidae	*Oxycarenus*	sp.	Oxycarenidae_sp.fasta		genome
Heteroptera	Pentatomomorpha	Pachygronthidae	*Pachygrontha*	sp.	Pachygrontha_sp.fasta	PRJNA295733	transcriptome
Heteroptera	Pentatomomorpha	Parastrachiidae	*Dismegistus*	*sanguineus*	Dismegistus_sanguineus.fasta		genome
Heteroptera	Pentatomomorpha	Pentatomidae	*Chalcocoris*	*rutilans*	Chalcocoris_rutilans.fasta	PRJNA272224	transcriptome
Heteroptera	Pentatomomorpha	Pentatomidae	*Chinavia*	*hilaris*	Chinavia_hilaris.fasta	PRJNA272230	transcriptome
Heteroptera	Pentatomomorpha	Plataspidae	*Brachyplatys*	sp.	Brachyplatys_sp.fasta	PRJNA295746	transcriptome
Heteroptera	Pentatomomorpha	Plataspidae	*Megacopta*	*cribraria*	Megacopta_cribaria.fasta	PRJNA272264	transcriptome
Heteroptera	Pentatomomorpha	Pyrrhocoridae	*Pyrrhocoris*	*apterus*	Pyrrhocoris_apterus.fasta	PRJNA272203	transcriptome
Heteroptera	Pentatomomorpha	Rhopalidae	*Boisea*	*trivittata*	Boisea_trivittata.fasta	PRJNA272221	transcriptome
Heteroptera	Pentatomomorpha	Rhyparochromidae	*Ozophora*	sp.	Ozophora_sp.fasta	PRJNA295747	transcriptome
Heteroptera	Pentatomomorpha	Scutelleridae	*Anoplogonius*	*nigricolfis*	Anoplogonius_nigricollis.fasta	PRJNA272216	transcriptome
Heteroptera	Pentatomomorpha	Scutelleridae	*Genus*	sp.	Scutelleridae_sp.fasta	PRJNA272291	transcriptome
Heteroptera	Pentatomomorpha	Stenocephalidae	*Dicranocephalus*	sp.	Dicranocephalus_sp.fasta		genome
Heteroptera	Pentatomomorpha	Termataphididae	*Termitaradus*	*australiensis*	Termitaradus_australiensis.fasta		genome
Heteroptera	Pentatomomorpha	Tessaratomidae	*Eusthenes*	*femoralis*	Eusthenes_femoralis.fasta		genome
Heteroptera	Pentatomomorpha	Tessaratomidae	*Piezosternum*	*calidum*	Piezosternum_callidum.fasta	PRJNA272281	transcriptome
Heteroptera	Pentatomomorpha	Tessarotomidae	*Piezosternum*	sp.	Piezosternum_sp.fasta		genome
Heteroptera	Pentatomomorpha	Thaumastellidae	*Thaumastella*	*namaquensis*	Thaumastella_namaquensis.fasta		genome
Heteroptera	Pentatomomorpha	Thyreocoridae	*Corimelaena*	*lateralis*	Corimelaena_lateralis.fasta	PRJNA272234	transcriptome
Heteroptera	Pentatomomorpha	Urostylididae	*Urostylis*	sp.	Urostylis_sp.fasta		genome