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DNA BARCODING AS A TOOL FOR SPECIES DISCOVERY AND DOCUMENTATION IN THE SUPERFAMILY ICHNEUMONOIDEA

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THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science
in the College of Agriculture, Food and Environment
at the University of Kentucky

By

Sarah Meierotto

Director: Dr. Michael Sharkey, Professor of Entomology

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ABSTRACT OF THESIS

DNA BARCODING AS A TOOL FOR SPECIES DISCOVERY AND DOCUMENTATION IN THE SUPERFAMILY ICHNEUMONOIDEA

Changes to traditional taxonomic methods to incorporate new technologies and techniques have already improved the quality of species hypotheses, but more work can be done to improve the speed of new species documentation. The mitochondrial COI DNA barcode has been successfully used to identify species with high accuracy since the early 2000s, and has been used in conjunction with morphological examinations and other DNA markers to discover and delimit new species. This thesis explores the application of DNA barcodes as the primary data for delimitation and diagnosis of new species of ichneumonoids.

The genera *Zelomorpha* and *Hemichoma* are revised and 18 new species from the Área de Conservación Guanacaste in Costa Rica are diagnosed based on COI barcodes. Two additional species are described based on morphology. An illustrated morphological key and morphological diagnoses for each species are also included.

KEYWORDS: Braconidae, DNA barcode, species delimitation, taxonomy, revision, new species

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24 July 2018

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TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1: Introduction

Rapid biodiversity loss and inadequate knowledge of biodiversity form some of the most serious challenges facing the natural sciences. Biodiversity is critical for ecosystems to provide services that humans rely on, including productivity and nutrient dynamics [1, 2]. Biodiversity is also a large contributing factor to an ecosystem's stability and resilience [3]. For example, temperate forests have fewer species than tropical forests and are more prone to population crashes and outbreaks of pests and diseases. It is hypothesized that the redundancy among species' functional traits enables diverse ecosystems to better withstand perturbations and resist invasions, but in such highly complex systems, there remains much to be discovered [4, 5]. Opportunities to understand and protect biodiversity are shrinking as species are lost to extinction. Anthropogenic influences are now causing biodiversity loss at a rate high enough to classify as the 6th major extinction event of the planet [6]. Invasive species, habitat destruction, climate change, and over-exploitation have led to a conservative estimate of 477 vertebrate species extinctions in the last 100 years [6]. However, as most animals on the planet are arthropods, most global extinctions are likely occurring among this group [7]. Insect populations are generally so poorly known that only 70 insect extinctions have been documented in the last 600 years [8]. Assuming the same proportion of arthropod species have gone extinct as vertebrate species, the number of extinctions may have exceeded 50 thousand in the last century. Some insect species, such as those with specialized feeding habits and/or short dispersal abilities may be even more prone to extinctions than vertebrates, while the short generation time and smaller resource requirements of individuals could make others more resilient [8]. Most insect extinctions likely occur among species which have never been documented by science. Each species lost is a tragedy in itself, but also decreases our ability to understand large scale patterns in evolution and ecology. To facilitate the study and conservation of insect biodiversity, two capabilities of the scientific community must be improved: 1, the ability to identify large numbers of insects, and 2, the ability to recognize and document new species.

The objective of this thesis is to improve documentation of new species using methods often applied to insect identification. Here I will demonstrate a future direction for the field of taxonomy using DNA barcode based species diagnoses, with a multi-step revision of *Zelomorpha* and *Hemichoma,* two closely related genera in the huge superfamily Ichneumonoidea. An overview of superfamily, challenges in the taxonomic field, DNA barcoding and its current applications, and my plan to apply DNA barcodes to alpha-taxonomy are outlined in Chapter 1. In Chapter 2, species of *Zelomorpha* and *Hemichoma* are revised to comply with the most recently published concepts of the genera. This creates the necessary foundation on which to apply DNA barcoding methods to document new species *Zelomorpha* and *Hemichoma* in Chapter 3. In Chapter 4, I apply simple morphological diagnoses to the newly described species and provide a morphological key to the *Zelomorpha* and *Hemichoma* of the Área de Conservación Guanacaste, Costa Rica.

Importance of Ichneumonoidea

Ichneumonoidea contains the families Ichneumonidae and Braconidae and is the largest superfamily within the order Hymenoptera. With few exceptions, immature ichneumonoids are parasitoids of arthropods. Ichneumonoids are widely acknowledged a play vital role in all terrestrial ecosystems by providing top-down control of their hosts, the majority of which are herbivorous insects [8]. Most orders of insects and some non-insect arthropods are hosts to ichneumonoids. Ichneumonoids are generally specialists, attacking only one or a few species of hosts. Little is known of the specific biology of the majority of described species: the hosts and habits of countless species (and some entire subfamilies, i.e. Masoninae, Apozyginae, Betylobraconinae, Khoikhoinae, Oxytoryinae, Tatogastrinae) are yet to be discovered [9, 10]. Much of the work conducted on the better known species occurred over 80 years ago and with outdated nomenclature [11]. Despite gaps in life history information, many species have been used in biological pest control programs [12, 13]. Additionally, Ichneumonoidea has the potential to serve as a useful indicator group. As they attack a wide range of arthropods and are host specific, a survey of ichneumonoids could provide great insight into the overall arthropod diversity at a site.

The taxonomic impediment

Research is slowed by the taxonomic impediment [14], i.e., there are simply not enough qualified taxonomists to identify and describe the millions of arthropod specimens needed to answer an endless number of biological questions. In 1982, Terry Erwin estimated 30 million arthropod species globally [15]. Most recent estimates fall between 3 and 10 million arthropod species, which is still an incredible number. Since Linnaeus's time in the 1700s, fewer than one million insect species have been described [16].

Over 43,000 of those described species are ichneumonoids (braconids ≈ 19,500 and ichneumonids ≈ 24,300) [9]. Even the number of described species is difficult to determine, as descriptions and synonymies are scattered through the literature [17]. Estimates of total species richness for this group are quite variable. Dolphin and Quicke estimated there are between 30 and 50 thousand braconid species in the world, using species description rates and comparisons to mammalian diversity patterns [18]. Based on decades of experience working on the morphologically based taxonomy of the family, Cornelis van Achterberg estimated a rough minimum of 120,000 braconid species in the world, and a roughly equal number or ichneumonids [19]. Rodriguez et al. used the ratio of described wasp species to lepidopteran hosts from relatively well studied sites to estimate the total number of species in the subfamily Microgastrinae, which currently has about 2,000 described species [20]. They estimated there are between 17,000 and 46,000+ species of Microgastrinae in the world, but noted this is likely an underestimate due to the many undescribed species of Microgastrinae from the well-studied sites used to make the extrapolations. Five out of every one hundred described ichneumonoid species are microgastrines [9]; assuming that this ratio holds true for undescribed species and that the estimates made by Rodriguez et al. are sound, there could be between 300,000 to 900,000 species of Ichneumonoidea. Quicke has even suggested that parasitoid wasps are too under-described to make useful estimates of patterns of richness

[21]. The amount of work needed to describe a new species increases with the number of described species in a group as the characteristics of the new putative species must be compared to all previously described. From 2000 to 2011, an average of 468 species of ichneumonoids were described per year (Figure 1). At the current rate, all ichneumonoids could be described somewhere between the years 2560 and 3842. Many will no longer exist by that time.

The number of unknown species is but one part of the taxonomic impediment. Even if all species were described, specimens must be identified; a job which requires an expert to reach species level among the Ichneumonoidea and many other arthropod groups. A single week-long Malaise trap sample can contain thousands of specimens. Many samples over months or years are needed to collect the data needed to tackle important questions. Studies focusing on diversity, food webs, invasive species monitoring, conservation, etc., all rely on a foundation of taxonomic information. Basset et al. identified 130 thousand arthropod specimens from Panama, but took over a million dollars and 10 years to do so [22]. The huge amount of taxonomic work needed and the lack of funding and workforce to do it slows research in other fields. New methods are required if we are to enter a new era of taxonomy which can meet the challenges ahead.

In addition to improving our capacity to identify and describe species, we must improve the objectivity and reliability with which we carry out those tasks. Human activity is encroaching on biodiversity hotspots, especially in the tropics, and choices are being made as to which natural areas will be protected and which will not. A greater knowledge of arthropod diversity could help inform policy makers on these hard decisions. As previously discussed, accurate arthropod biodiversity assessment is hampered by the high species-richness and lack of expertise in the scientific community [22]. In addition, when resources are on the line, the species concept used by a taxonomist to guide their decisions moves from an academic matter to a political one. Twenty two different species concepts were recognized by Mayden in 1997, and individual taxonomists or para-taxonomists often interpret concepts or species defining traits differently [23]. Current methods for biodiversity comparisons may weigh taxa differently based on their abundances or phylogenetic distances, but all assume individuals are accurately identified [24-27]. An objective method for biodiversity inventory is essential for making the best conservation decisions.

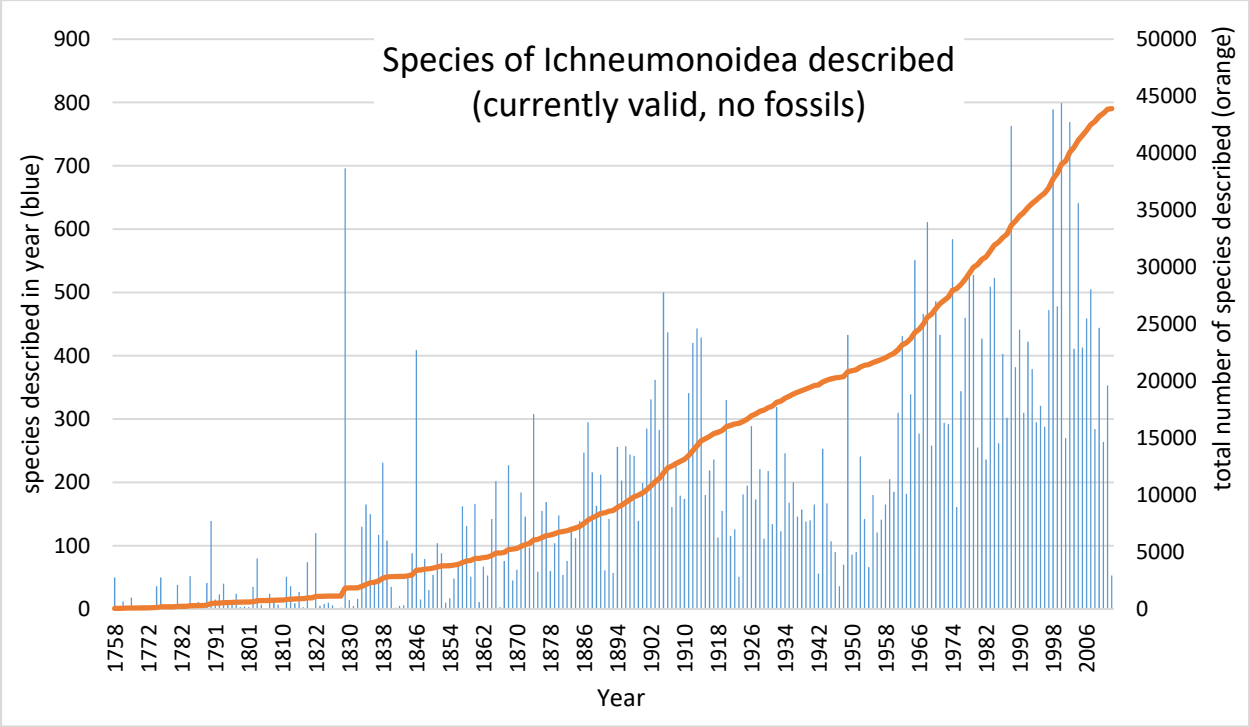


Figure 1.1. Description rate of Ichneumonoidea species. Data from Taxapad (Yu, 2012).

DNA Barcoding

Molecular identification methods like DNA barcoding provide an alternative to morphological identification. Barcoding has the potential to produce cheaper, faster, and more accurate identifications. DNA barcoding uses a short sequence of DNA agreed upon by the scientific community to identify organisms. The Folmer region of the mitochondrial cytochrome oxidase subunit 1 (COI) gene has been accepted as the "barcode" region for animal life [28, 29]. Other markers are used for plants, fungi, and microbes. Because COI is a mitochondrial sequence, many more copies are present than nuclear DNA sequences. COI is highly variable among animal species, providing good identification power, and it is flanked by conserved regions that make good primer sites. It is also short, only 658 bp, making it easy to sequence. Even shorter regions, called mini-barcodes have been found effective for identification [30, 31]. The shorter amplicons have the advantage of being compatible with current next-generation-sequencing technology. Identifications are made using DNA barcodes by comparing a query sequence to a library of pre-identified sequences. Current barcode libraries are far from comprehensive, but they are growing. Other genes, such as ribosomal 16S and 28S do not have large databases for identification purposes and are not considered barcode genes, but are valuable for providing greater taxonomic resolution and commonly used in the construction of phylogenies [32, 33]. There are drawbacks to using COI as a barcode, including potential confusion with nuclear mitochondrial paralogs, *Wolbachia* mediated introgression, hybridization, and incomplete lineage sorting [34-37]. However, the huge and growing libraries of COI sequences and other benefits mentioned currently make

COI the best candidate for DNA barcoding despite its drawbacks. Surveys and studies of many taxa have been conducted using DNA barcodes [38-43].

GenBank and BOLD are the most widely used libraries for DNA barcoding purposes. GenBank contains many sequences, but provides less associated data, and there is no vetting process to insure accurate species identifications. The Barcode of Life Data Systems (BOLD) database was built specifically to support DNA barcoding. A complete BOLD library record includes a photograph of the habitus of the specimen and all collection information (locality, date, collector, etc.), raw sequencing data (Sanger sequencing trace files), and the consensus sequence. This information is linked to the DNA library along with information on matches to the sequence [28]. Highly similar sequences are clustered into BINs, which act as putative species just as rough morphological groupings can be used as morpho-species [44]. Costs to generate a barcode this way vary, but can be as low as $3. Alternative sequencing methods can lower the price [45]. There are currently over 4.5 million barcode sequences in BOLD, representing about 440 thousand putative species. Most species with barcodes not currently in the BOLD database can still be identified to genus, family, or higher levels [46, 47]. The identification power of the DNA libraries will increase as more species are added to them, but the collecting location will become an important factor to consider in making an identification [48].

COI for species description

No taxonomist would argue that an identification made solely based on a COI barcode is as solid as one made considering morphology, biology, and multiple genes. But the fact that identifications can be made without specialist training or biological context and have been shown to be accurate for more than 90% of the species tested make barcoding a very powerful tool [39, 49-51]. In many cases, differences between DNA barcode species assessments and morphological ones illuminate errors in the morphological taxonomic hypotheses, rather than a failure of the barcodes to properly separate species [52, 53]. Why can this same concept not be extended to new species descriptions? There is no stipulation in the International Code of Zoological Nomenclature that prevents or discourages DNA based descriptions. Requirements for the publication of new species include either a description or diagnosis which can separate the new species from any species with which they are likely to be confused [54]. The lack of molecular diagnoses thus far is likely due to cultural resistance among taxonomic community. Current best practices for description of new species involve integration of many sources of information, including but not limited to detailed morphological examinations and images, multi-locus DNA analyses, and ecological information. These studies produce well supported species hypotheses, but are time intensive, requiring years in some cases to publish species names. Molecular descriptions have been proposed before, but have yet to be embraced and used by taxonomists [55-59]. When paired with decreasing manpower and financial support for taxonomic work, DNA barcode based descriptions may be the best option to meet the demand for new species documentation produced by current ecological crises.

The Ichneumonoidea are particularly good candidates for DNA based descriptions. This groups is extremely species rich, includes high numbers of rare

species, frequent cases of cryptic species, and specimens are usually collected with little to no ecological information. Additionally, DNA barcodes have already been used to discover many cryptic species of braconids and ichneumonids [53, 60-62].

Chapter 2: Review of the genera *Zelomorpha* Ashmead and *Hemichoma* Enderlein (Hymenoptera, Braconidae, Agathidinae) with assignment of new combinations based on literature.

Like other members of the subfamily Agathidinae, species of *Zelomorpha* and *Hemichoma* are koinobiont endoparasitoids of lepidopteran larvae. As members of the tribe Disophrini, they attack free living, late instar caterpillars [13]. Most species are solitary with a single individual developing per host, but *Zelomorpha gregaria* (as *Coccygidium gregaria*) is an exception [63].

William H. Ashmead described the genera *Zelomorpha* in 1900, including only the type species *Zelomorpha arizonensis* [64]. In 1927, Muesebeck synonymized the genera *Caenophylax* Schulz*, Neophylax* Ashmead*,* and *Zelomorphidea* Viereck with *Zelomorpha*. Muesebeck also provided a full description of *Zelomorpha arizonensis*, which was lacking from Ashmead's original publication [65]. *Lisitheria* Cameron*, Spilomicrodus* Cameron, and *Xanthomicrodus* Cameron were synonymized with *Zelomorpha* by Muesebeck and Walkley in 1951 [66]. Throughout the 1970s, 80s, and 90s, various authors debated the limits of *Zelomorpha* and *Coccygidium* de Saussure 1982; some argued for the synonymization of *Zelomorpha* under *Coccygidium* [67, 68], while others argued they should remain separate [69]. The key difference between these two genera was the length of the foretibial spurs: long in *Coccygidium* and relatively short in *Zelomorpha*. Short spurs are a plesiomorphic trait, leaving *Zelomorpha* with no autapomorphies to distinguish the genus. *Dichelosus* Szépligeti was synonymized with the concept of *Coccygidium* defined to include *Zelomorpha* in 2005 [70]. *Zelomorpha* was supported as a monophyletic group in a combined morphological and molecular phylogeny by Sharkey et al. in 2006 [71]. This work implied that all New World species of *Coccygidium* and *Biroia* belonged in *Zelomorpha* but made no formal taxonomic changes. *Dichelosus* was synonymized with *Zelomorpha* in 2017, but no new combinations were published [72].

Hemichoma was described by Günther Enderlein in 1920, with *Hemichoma fenestratum* as the type species and *Hemichoma pulchrum* as the only other member [73]. Sharkey et al. in 2006 postulated *Hemichoma* may be a junior synonym of *Zelomorpha* [71], but *Hemichoma* was found to be sister to *Zelomorpha* by Sharkey and Chapman in 2017 [72].

Zelomorpha can be distinguished from all other Agathidinae genera by the following combination of morphological characters: fore tarsal claws cleft and not pectinate; foretibial spur shorter than first tarsomere; ovipositor shorter than half the length of the metasoma; frons bordered by carinae; hind trochantellus with one or two longitudinal ridges; notauli variable, usually distinct; gena not produced.

Hemichoma shares diagnostic morphological characters with *Zelomorpha* except: notauli absent, mesoscutum lacking distinct lobes; occiput sharply indented and gena greatly produced posteroventrally.

Here, the species of *Zelomorpha* and *Hemichoma* suggested by previous works are consolidated and new combinations applied. Some additional species from various genera are moved into *Zelomorpha* or *Hemichoma* based on notes and photographs of the type specimens (Sharkey, M., Sarmiento C., unpublished data).

Museum acronyms follow The insect and spider collections of the world website [74].

ANSP: Academy of Natural Sciences. Philadelphia, USA
HNHM: Hungarian Natural History Museum. Budapest, Hungary
INBIO: Instituto Nacional de Biodiversidad. Santo Domingo de Heredia, Costa Rica
MNHN: Muséum National d'Histoire Naturelle. Paris, France
MZPW: Museum and Institute of Zoology. Warsaw, Poland
MRSN: Museo Regionale di Scienze Naturali. Italy, Torino
NHMUK: The Natural History Museum. London, United Kingdom
NHRS: Naturhistoriska riksmuseet. Stockholm, Sweden
USNM: National Museum of Natural History. Washington D.C., USA
ZMUC: University of Copenhagen Zoological Museum. Copenhagen, Denmark

The following list is formatted as follows:

- *Current name* (original author, year of publication) **status if changed**
    - *Original name* author, year, abbreviated journal name. volume: page. Country of type specimen (museum, sex, type identifier if assigned).
        - *Other combination*: Author of combination, year: page.
    - *Synonym name* original author, year, abbreviated journal name. volume: page. Country of type specimen (museum, sex, type identifier if assigned). Synonymized with *Species name* by author, year: page.

- *Hemichoma atrata* (Enderlein, 1920) **new combination**
    - *Biroia atrata* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 195. Ecuador (MZPW, ♀).

- *Hemichoma bicolor* (Szépligeti, 1902), **new combination**
    - *Biroia bicolor* Szépligeti, 1902, Természetr. Füz. 25: 73. Brasil (HNHM, "♀" = ♂, 675).
        - *Dichelosus bicolor*: Papp, 2004: 159.

- *Hemichoma intermedia* (Szépligeti, 1908) **new combination**
    - *Biroia intermedia* Szépligeti, 1908, Annls. Hist.nat. Mus. Natn. Hung. 6: 417. Bolivia (HNHM, ♀, 682).
        - *Dichelosus intermedius*: Papp, 2004: 159.

- *Hemichoma fenestratum* Enderlein, 1920
    - *Hemichoma fenestratum* Enderlein, 1920, Arch. Naturgesh. 84(A)11: 184. Peru (MZPW, ♀).

- *Hemichoma pulchrum* (Szépligeti, 1904) **combination renewed**

- *Euagathis pulcher* Szépligeti, 1904, Annls. Hist. nat. Mus. Natn. Hung. 2: 195. Peru (HNHM, ♀, 856).
    - *Biroia pulcher*: Szépligeti, 1908: 416.
    - *Hemichoma pulchrum*: Enderlein, 1920: 184.
    - *Euagathis pulcher*: Papp, 2004:164.

- *Zelomorpha amoena* (Brullé, 1846) **new combination**
    - *Agathis amoena* Brullé, 1846, Hist. Nat. Insectes, Hym. 4: 498. Guyana (MNHN, ♂).
        - *Agathis amsena*: Szépligeti, 1904: 127. [misspelling]

- *Zelomorpha anator* (Fabricius, 1804) **new combination**
    - *Bracon anator* Fabricius, 1804, Systema Piezatorum: 110. South America (ZMUC, ♀).
        - *Coccygidium anator*: Sarmiento & Sharkey, 2005: 65.

- *Zelomorpha annulifovea* (Enderlein, 1920) **new combination**
    - *Disophrys annulifovea* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 192. Mexico (MZPW, ♀).

- *Zelomorpha areolaris* (Szépligeti, 1908) **new combination**
    - *Biroia areolaris* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 417. Suriname (HNHM, Lectotype ♀, "683". Designation by Papp in Shenefelt 1970: 368).
        - *Dichelosus areolaris*: Papp, 2004: 159.

- *Zelomorpha arizonensis* Ashmead, 1900
    - *Zelomorpha arizonensis* Ashmead, 1900, Proc. U.S. natn. Mus. 23: 129. United States (USNM, ♀, 16221).
        - *Coccygidium arizonensis,* Chou & Sharkey, 1989: 178.

- *Zelomorpha brasiliensis* (Szépligeti, 1902) **new combination**
    - *Dichelosus brasiliensis* Szépligeti, 1902, Természetr. Füz. 25: 72. Brasil (HNHM, ♂, 688).
        - *Coccygidium brasiliensis*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha championi* (Cameron, 1887) **new combination**
    - *Microdus championi* Cameron, 1887, Biologia Cent.-am. Hym. 1: 402. Guatemala (NHMUK, "♂" = ♀, 3.c.965).
        - *Agathis championi*: Shenefelt, 1970: 324.

- *Zelomorpha conjugens* (Enderlein, 1918) **new combination**
    - *Disophrys conjungens* Enderlein, 1918 (1920), Arch. Naturgesch. 84(A)11: 191. Suriname (MZPW, ♂).

- *Zelomorpha concinna* (Brullé, 1846) **new combination**

- *Agathis concinna* Brullé, 1846 Hist. nat. Insectes Hym. 4: 499. Brasil (MNHN, ♀).

- *Zelomorpha coxata* (Holmgren, 1868) **new combination**
  - *Agathis coxatus* Holmgren, 1868, Eugenies Resa, Insecta: 428. Ecuador (NHRS, ♀).
    - *Disophrys coxata*: Roman, 1910: 121. **unjustified emendation**

- *Zelomorpha coxalicus* (Cameron, 1887) **new combination**
  - *Microdus coxalis* Cameron, 1887 Biologia cent.-am. Hym. 1: 403. Panama (NHMUK, ♀, 3.c.967)
    - *Agathis coxalis* (not Spinola, 1840): Shenefelt, 1970: 328. Preoccupied by Spinola, 1840.
  - *Agathis coxalicus* Shenefelt, 1970: 328. Replacement name for *A. coxalis* (Cameron, 1887).

- *Zelomorpha cramptoni* (Brues & Richardson, 1913) **new combination**
  - *Disophrys cramptoni* Brues & Richardson, 1913, Bull. Am. Mus. Nat. Hist. 32: 501. Guyana (AMNH, ♀, 21104).

- *Zelomorpha cucullifera* (Enderlein, 1920) **new combination**
  - *Disophrys cucullifera* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 191. Mexico (MZPW, ♀♂).

- *Zelomorpha demerarus* (Enderlein, 1920) **new combination**
  - *Dichelosus demerarus* Enderlein, 1920, Arch. Naturgesch. 84(A)11:197, Guyana, Panama (MZPW, ♀).
    - *Coccygidium demerarus*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha dubiosus* (Szépligeti, 1908) **new combination**
  - *Dichelosus dubiosus* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 418. Suriname (HNHM, ♀, 686).
    - *Coccygidium dubiosus*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha elegans* (Brullé, 1846) **new combination**
  - *Agathis elegans* Brullé, 1846, Hist. Nat. Insectes Hym. 4: 500. French Guiana (MNHN, ♀).

- *Zelomorpha fascipennis* (Cresson, 1865) **combination renewed**
  - *Microdus fascipennis* Cresson, 1865, Proc. ent. Soc. Philad. 4:64-65. Cuba (ANSP, ♀, 208).
    - *Zelomorphidea fasciipennis*: Bradley, 1916: 140.
    - *Zelomorpha fascipennis*: Shenefelt, 1970: 426.
    - *Coccygidium fascipennis*: Sharkey, 2004:134.

- *Zelomorpha flavifemur* (Enderlein, 1918) **new combination**

- *Disophrys flavifemur* Enderlein, 1918 (1920), Arch Naturgesch. 84(A)11: 190. Suriname (MZPW, ♀).

- *Zelomorpha flavipennis* (Enderlein, 1918) **new combination**
  - *Biroia flavipennis* Enderlein, 1918 (1920), Arch. Naturgesch. 84(A)11: 197. (not Enderlein, 1905: 451). Peru (MZPW, ♀).

- *Zelomorpha fuscipennis* (Brullé, 1846) **new combination**
  - *Bracon fuscipennis* Brullé, 1846, Hist. Nat. Insectes Hym. 4: 396. Mexico (MNHN, ♀).
    - *Euagathis fuscipennis*: Shenefelt, 1970: 411.

- *Zelomorpha gregaria* (Sarmiento & Sharkey, 2004) **new combination**
  - *Coccygidium gregarium* Sarmiento & Sharkey, 2004; in Sarmiento, Sharkey & Janzen, 2004, J- Hym. Res. 13 (2): 295. Costa Rica (INBIO, ♀).

- *Zelomorpha hospitator* (Fabricius, 1775) **new combination**
  - *Ichneumon hospitator* Fabricius, 1775, Syst. Ent. 335. Brazil (ZMUC, ♀).
    - *Bracon hospitor* Fabricius, 1804: 106. **unjustified emendation**
    - *Coccygidium hospitator*: Sarmiento & Sharkey, 2005: 61.
  - *Ichneumon ornator* Fabricius, 1787, Mant. Insect. 1: 264. French Guiana (ZMUC, ♀). Synonymized with *C. hospitator* by Sarmiento & Sharkey, 2005: 66.
    - *Bracon ornator*: Fabricius, 1804: 106.
  - *Dichelosus fuscipennis* Szépligeti, 1902 Természetr. Füz. 25: 71. Brasil (HNHM, ♀). Synonymized with *C. hospitator* by Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha imitatrix* (Enderlein, 1920) **new combination**
  - *Biroia imitatrix* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 196. Suriname (MZPW, ♀).

- *Zelomorpha imperfecta* (Szépligeti, 1908) **new combination**
  - *Disophrys imperfecta* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 414. Bolivia (MZPW, HNHM, ♂, 749).

- *Zelomorpha melanostoma* (Cameron, 1887) **new combination**
  - *Microdus melanostoma* Cameron, 1887, Biol. cent. Am., Hymenoptera 1: 401. Panama (NHMUK, "♂" = ♀, 3.c.963).
    - *Agathis melanostoma*: Shenefelt, 1970: 343.

- *Zelomorpha melanota* (Viereck, 1912) **combination renewed**
  - *Zelomorpha (Zelomorphidea) melanota* Viereck, 1912, Proc. U.S. natn. Mus. 42: 630, Paraguay (USNM, ♀)
    - *Zelomorpha melanota*: Muesebeck, 1927: 7.

        - *Coccygidium melanota*: Chou & Sharkey, 1989:178.

- *Zelomorpha nigriceps* (Cameron, 1911) **combination renewed**
    - *Spilomicrodus nigriceps* Cameron, 1911, Timehri, 1: 324. Guyana. (NHMUK, ♀, 3.c.938).
        - *Zelomorpha nigriceps*: Muesebeck & Walkley, 1951:116.
        - *Coccygidium nigriceps*: Chou & Sharkey, 1989: 178.

- *Zelomorpha nigricepsibol* (Shenefelt, 1970) **new combination**
    - *Disophrys nigriceps* Szépligeti, 1908: 415 Annls. Hist. nat. Mus. Natn. Hung 6: 414. Bolivia, (MZPW, HNHM, "♂" = ♀, 749) Preoccupied by *D. nigriceps* Saussure, 1892.
    - *Disophrys nigricepsibol*: Shenefelt, 1970: 400. Replacement name of *D. nigriceps* Szépligeti, 1908.

- *Zelomorpha nigricoxa* (Enderlein, 1920) **new combination**
    - *Disophrys nigricoxa* Enderlein, (1918) 1920, Arch Naturgesch. 84(A)11: 192. Mexico (MZPW, ♀).

- *Zelomorpha nigrobalteata* (Cameron, 1911) **new combination**
    - *Cremnops nigrobalteata* Cameron, 1911, Timehri 1: 323. Guyana (NHMUK, ♀, 3.c.654).
        - *Microdus nigrobalteatus*: Turner 1918: 82.
        - *Agathis nigrobalreata*: Shenefelt, 1970: 346. [misspelling]

- *Zelomorpha ophthalmatica* (Szépligeti, 1908) **new combination**
    - *Disophrys ophthalmica* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung 6: 414. Brasil. (MZPW, HNHM, ♀, 749 Lectotype designated by Papp in Shenefelt 1970: 401)

- *Zelomorpha pennator* (Fabricius, 1804), **new combination**
    - *Ophion pennator* Fabricius, 1804, Systema Piezatorum: 135. South America (ZMUC, ♀).
        - *Ichenumon pellator* Thunberg 1824, Mem. Acad. St. Petesburg 9: 314. **Emendation.**
        - *Coccygidium pennator*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha peronata* (Cameron, 1887) **new combination**
    - *Microdus peronatus* Cameron, 1887, Biologia Cent.-am. Hym. 1: 403. Panama (NHMUK, ♂ ♀, 3.c.966).
        - *Agathis peronata*: Shenefelt, 1970:348.

- *Zelomorpha peruensis* (Szépligeti, 1902) **new combination**
    - *Dichelosus peruensis* Szépligeti, 1902, Természetr. 184. Füz. 25: 72. Peru (HNHM, ♀, 689).
        - *Coccygidium peruensis*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha pilipes* (Cameron, 1911) **new combination**
    - *Disophrys pilipes* Cameron, 1911, Timehri, 1: 324. Guyana. (NHMUK, ♀).

- *Zelomorpha pulchricornis* (Szépligeti, 1908) **new combination**
    - *Disophrys pulchricornis* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 415. Suriname and Bolivia (HNHM, ♀).

- *Zelomorpha pulchripennis* (Cameron, 1887) **new combination**
    - *Microdus pulchripennis* Cameron, 1887, Biologia cent. Am., Hym. 1: 402. Panama (NHMUK, ♀, 3.c.964).
        - *Agathis pulchripennis*: Shenefelt, 1970: 350.

- *Zelomorpha ruficollis* (Cameron, 1911) **new combination**
    - *Biroia ruficollis* Cameron, 1911, Timehri 1:321. Guyana (NHMUK, ♀, 3.c.393).

- *Zelomorpha rufimana* (Brullé, 1846) **new combination**
    - *Agathis rufimana* Brullé, 1846, His. Nat. Insectes, Hym. 4: 494. Brasil (MNHN, ♂).
        - *Biroia rufimana*: Szépligeti, 1908: 416.

- *Zelomorpha sarothriceps* (Enderlein, 1920) **new combination**
    - *Biroia sarothriceps* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 195. Ecuador (MZPW, ♀).

- *Zelomorpha scita* (Enderlein, 1920) **new combination**
    - *Disophrys scita* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 191. Suriname (MZPW, ♀).

- *Zelomorpha similis* (Szépligeti, 1908) **new combination**
    - *Dichelosus similis* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 418. Suriname (HNHM, ♀, 690).
        - *Coccygidium similis*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha surinamensis* (Szépligeti, 1908) **new combination**
    - *Biroia surinamensis* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 416. Suriname (HNHM, Lectotype ♀, 676. Designation by Papp in Shenefelt 1970: 369).
        - *Dichelosus surinamensis*: Papp, 2004: 159.

- *Zelomorpha szepligetii* (Meierotto, 2018) **new combination and replacement name**
    - *Disophrys variegata* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 415. Bolivia (MZPW, HNHM, ♂, 749).

        - *Zelomorpha variegata*: Preoccupied by *Dichelosus variegata* Szépligeti, 1908.

- *Zelomorpha taeniolata* (Enderlein, 1920) **new combination**
    - *Biroia taeniolata* Enderlein, 1920 Arch. Naturgesch. 84(A)11: 196. Suriname. (MZPW, ♀).

- *Zelomorpha tarsalis* (Szépligeti, 1902) **new combination**
    - *Biroia tarsalis* Szépligeti, 1902, Természter. Füz. 25: 73. Peru (HNHM, ♀, 674).
        - *Dichelosus tarsalis:* Papp, 2004:159.

- *Zelomorpha trailii* (Cameron, 1905) **new combination**
    - *Agathis trailii* Cameron, 1905 Trans. Am. Ent. Soc. 31: 386. Brazil or Peru (NHMUK, ♀, 3.c.937).

- *Zelomorpha tropicola* (Szépligeti, 1908) **new combination**
    - *Biroia tropicola* Szépligeti, 1908, Annls hist. nat. Mus. Natn. Hung. 6: 416. Suriname (HNHM, ♀).
        - *Dichelosus tropicola*: Papp, 2004: 159.

- *Zelomorpha variegata* (Szépligeti, 1908) **new combination**
    - *Dichelosus variegatus* Szépligeti, 1908, Annls. Hist. nat. Mus. Natn. Hung. 6: 418. Bolivia (HNHM, ♀).
        - *Coccygidium variegatus*: Sarmiento & Sharkey, 2005: 66.

- *Zelomorpha varigatenda* (Shenefelt, 1970) **new combination**
    - *Disophrys variegata* Enderlein, 1920, Arch. Naturgesch. 84(A)11: 189. Guyana (MZPW, ♂ ♀). Preoccupied by Szépligeti 1908.
    - *Disophrys variegatenda*: Shenefelt, 1970: 403. Replacement name of *D. variegata* Enderlein, 1920.

- *Zelomorpha vesmaeli* (Spinola, 1840) **new combination**
    - *Agathis vesmaeli* Spinola, 1840. Annls. Soc. Ent. Fr. 9: 193. French Guiana (MRSN, ♂)
        - *Agathis wesmaeli*: Spinola 1851: 37 **unjustified emendation**

- *Zelomorpha xanthostigma* (Szépligeti, 1902) **new combination**
    - *Biroia xanthostigma* Szépligeti, 1902, Természetr. Füz. 25: 72. Brasil (HNHM, ♀, 673).
        - *Bassus xanthostigma*: Papp, 2004: 160.

Chapter 3: Barcode-based taxonomic revision of *Zelomorpha* Ashmead and *Hemichoma* Enderlein (Hymenoptera, Braconidae, Agathidinae) from the Área de Conservación Guanacaste, Costa Rica with diagnoses of 19 new species

Note: this chapter is formatted separately from chapter 4 (which contains morphological characters to many of the species described here) to reflect my plan to publish molecular diagnoses independent of morphological characters.

Abstract

Here I elucidate and justify the diagnostic barcode approach that can be applied over the coming years to name thousands of species of ichneumonoids. Each description consists of a short COI diagnostic, a lateral habitus image of the specimen, and type specimen information required by the International Code of Zoological Nomenclature. This approach is likely useful for many other understudied hyperdiverse taxa, but the arguments presented are restricted to this one superfamily. Due to Ichneumonoidea's extreme diversity, very low percentage of described species, and lack of detailed information for most described species, the integrated taxonomic approach is inefficient. A barcode-based approach will provide a solid foundation of species hypotheses from which comprehensive descriptions can be developed. In the following text, I will elucidate these arguments, detail methodology, and provide exemplary descriptions of new species in the genera *Hemichoma* and *Zelomorpha* from the Área de Conservación Guanacaste in Costa Rica. *Zelomorpha arizonensis* is given a barcode diagnosis and the following new species are described: *Zelomorpha angelsolisi*, *Zelomorpha bobandersoni*, *Zelomorpha danjohnsoni*, *Zelomorpha donwindsori*, *Zelomorpha effugia*, *Zelomorpha johnchemsaki*, *Zelomorpha kellyanneae*, *Zelomorpha larrykirkendalli*, *Zelomorpha mariyavladmirovnae*, *Zelomorpha mikeiviei*, *Zelomorpha myricagaleae*, *Zelomorpha noahjaneae*, *Zelomorpha paulgoldsteini*, *Zelomorpha terryerwini*, *Zelomorpha willsflowersi*, *Hemichoma donwhiteheadi*, *Hemichoma frankhovorei*, and *Hemichoma johnkingsolveri*.

Introduction

Systematists today have many powerful tools at their disposal for delimiting and describing new species, and an integrated taxonomic approach combining morphological characters, multiple molecular markers, ecological data, and multiple methods of data analysis is currently the gold standard for new species descriptions [59, 75, 76]. Such rigorous investigation will produce high quality species hypotheses and should be considered an ultimate goal in the study of most organisms. However, such an approach is highly labor and resource intensive, as admitted by the authors who champion it [59, 75, 76]. When this reality is paired with decreasing manpower and financial support for taxonomic work [77], integrated taxonomic workflows cannot meet the demand for new species documentation produced by current ecological crises. I propose the publication of new species based primarily on the DNA barcode molecular marker as a first step in the systematic study of terminal groups in the highly diverse superfamily Ichneumonoidea. These descriptions will encourage and accelerate 1) the accumulation of additional

information on the described species, 2) scientific discussion of the groups treated, and 3) opportunities for the refinement of presented species hypotheses.

The superfamily Ichneumonoidea contains the two largest families of Hymenoptera (Braconidae and Ichneumonidae). As parasitoids, ichneumonoids provide critical top-down control of their hosts and contribute to ecosystem stability and diversity [78, 79]. Many species have economic importance as biological control agents [13]. Ichneumonoidea included over 44,000 valid, described species as of 2012 [9]; the true number of species is difficult to estimate. As discussed in Chapter 1 of this thesis, there may be as many as 900,000 species of ichneumonoids in the world.

Recent revisions of ichneumonoids in the subfamilies Agathidinae and Microgastrinae have investigated the utility of the DNA barcoding region of the gene cytochrome *c* oxidase for species delimitation paired with morphological and ecological host-use characters. Kang et al. created initial molecular operational taxonomic units (MOTUs) for the genus *Lytopylus* using a neighbor joining and a maximum likelihood trees, clustering species with boundaries at a genetic distance of 2% [80]. The MOTUs matched the final species concepts for *Lytopylus* at 96.6%. Similarly, revisionary studies of the agathidinae genera *Alabagrus* [81], *Aerophilus* [82], *Euagathis* [83], *Aphelagathis* [84], and *Cremnops* [85] used COI data for formation of preliminary MOTUs for species delimitation and found high concordance between MOTUs and final species delimitations. An investigation of the Microgastrinae of the Área de Conservación Guanacoste in Costa Rica (again using morphology, COI DNA barcodes, and ecological host data) found all morphological species concepts were perfectly delimited by barcodes [53]. Additionally, barcodes could accurately distinguish morphologically cryptic but ecologically distinct species.

While there have been some calls to use molecular species descriptions [55, 56], few studies have been published which describe arthropod species based on molecules [59]. There is no stipulation in the International Code of Zoological Nomenclature that prevents or discourages DNA based descriptions and diagnoses [54]. Requirements for the publication of new species include that they are properly named, properly published, have a designated type, and accompanied by either a description or diagnosis which can separate them from any species with which they are likely to be confused. Barcode based descriptions will allow species to be documented and data accumulated using clear and reproducible methods. By naming these species, we give them a permanent and traceable record in the literature. Unlike provisional names, the official names allow the species concepts to be discussed and revised by the scientific community without ambiguity.

Methods

Specimen collection

All specimens were collected via rearing of host caterpillars from the Área de Conservación Guanacoste in Costa Rica. Caterpillar hosts were collected by a team of parataxonomists as part of the ongoing project to document all non-leaf-mining Lepidoptera, their host plants, and their parasitoids [86]. These caterpillars were databased with collection information, host plant information, and often a photograph, and they were reared to adulthood. When an adult moth, butterfly, or parasitoid emerged, the specimen was preserved and a leg was outsourced for DNA barcoding. Genus was

confirmed for all specimens of *Hemichoma* and *Zelomorpha* using morphological characters. Focus-stacked images of specimens were taken using a JVC digital camera mounted on a Leica microscope and compiled with the program Automontage. Image post processing was done in Adobe Photoshop.

DNA extraction and sequencing

All molecular work was carried out at the Canadian Centre for Biodiversity Genomics using their standard protocols. A leg of each specimen destructively sampled for DNA extraction, carried out using a glass fiber protocol [87]. Extracted DNA was amplified for a 658-bp region near the 5' terminus of the CO1 gene using standard insect primers LepF1 (5'-ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'-TAAACTTCTGGATGTCCAAAAAATCA-3') [88]. If initial amplification failed, additional amplifications were conducted following the established protocols using internal primer pairs, LepF1-C113R (130 bp) or LepF1-C_ANTMR1D (300 bp) and MLepF1-LepR1 (400 bp) to generate shorter overlapping sequences. Amplified products were sequenced using Sanger technology.

Sequence analysis and species determination

Sequences at least 500 base pairs long were assigned to operational taxonomic units called barcode index numbers (BINs) using refined single linkage analysis [44]. BIN assignments and Sanger sequencing trace files were downloaded from the Barcode of Life Data Systems database: http://www.boldsystems.org/. Bi-directional sequences were assembled and edited using Geneious Pro software. Sequences were aligned using MAFFT version 7 [89] and visually inspected using Bioedit Sequence Alignment Software [90]. Barcode sequences from two specimens of *Zelomorpha arizonensis* collected in Arizona in the United States were included in the dataset. A 100-replicate maximum likelihood (ML) analysis was conducted using Garli [91] under the default settings, partitioned by codon position and using the GTR+I+G model. Nodal support was assessed by conducting a 200 replicate bootstrap analysis under default settings. *Cremnops cameronii* and *Euagathis forticarinata* were chosen as outgroups. *Euagathis* is a member of the tribe Disophrini, as are *Zelomorpha* and *Hemichoma. Cremnops* is a member of the closely related tribe, Cremnoptini [72]. P-distances were calculated for sequences over 500 base pairs in MEGA5 [92].

Morphology and host information were compared to BIN assignments and placement in the ML tree. Specimen groupings suggested by all data sources were considered species. Type specimens of all previously described *Zelomorpha* and *Hemichoma* species were examined by MJS and his notes were used to verify the novelty of species described here.

Consensus barcodes were created for each species using BioEdit [90] and aligned to the *Drosophila melanogaster* complete mitochondrial genome from the NCBI Reference Sequence Database, accession number NC_024511. Consensus barcodes for all species in each genus were compared to all other species in the genus. Nucleotides and amino acids that were shared by all specimens of a species and no specimens of any other species were recorded as diagnostic characters. Diagnostic characters are called by their position in the alignment with the *D. melanogaster* reference sequence.

For *Zelomorpha arizonensis,* the only previously described species found in the dataset, two sequences from specimens collected from Arizona were included in the ML tree in addition to the sequences of specimens from ACG. Additional publicly available sequences of *Z. arizonensis* were downloaded from BOLD and edited as above. These were included in the consensus barcode used to determine molecular diagnostic characters.

Specimen Information

Holotypes are deposited in the insect collection (EMUS) in the Biology Department of Utah State University in Logan, Utah. Paratypes are split between the EMUS and the Hymenoptera Institute Collection (HIC), currently at the University of Kentucky. Specimens of *Zelomorpha arizonensis* collected in the United States are housed at the Centre for Biodiversity Genomics at the University of Guelph, Ontario (BIOUG). Detailed specimen records are available on Janzen's database (http://janzen.sas.upenn.edu/caterpillars/database.lasso) by searching for specimen voucher codes (DHJPARxxxxxxx). Additional specimen information on host caterpillars can be found by searching for their xx-SRNP-xxxx voucher codes. Some host species are still awaiting full identification and are given interim names. For example, *Hemiceras* plusiataDHJ01 is identified to genus *Hemiceras* and is the first recorded in a species complex which resembles *H. plusiata.* When these species are assigned an official epithet in the future, the interim name will remain searchable in Janzen's database. Complete DNA sequence and specimen information is available at www.boldsystems.org under the project (to be determined) and by searching for specimen voucher codes.

Results

Species delimitation

227 specimens with COI barcodes were determined as 20 species in two genera. BIN assignments corresponded to final species hypotheses in all cases (Appendix 1. Full NJ tree with annotations). *Zelomorpha arizonensis* is the only previously described species found in this dataset. All other species are described as new. The ML analysis found all species monophyletic with the exception of *Z. johnchemsaki* and *Z bobandersoni* (Figure 3.1, node A). Although these two species have a small minimum interspecific p-distance of 2.29% (Appendix, Table 1), there is a clear gap between them due to the low variation within species: maximum intraspecific p-distances are 0.30% and 0.16% for *Z. johnchemsaki* and *Z bobandersoni*, respectively. The separation of *Z. johnchemsaki* and *Z bobandersoni* is also supported by host plant and host caterpillar differences and consistent morphological differences (Appendix 1). *Hemichoma frankhovorei* (Figure 3.1, node B) contains the greatest interspecific p-distance with a maximum of 0.93%, but with no clear subgroupings by morphology, barcode, or ecology.

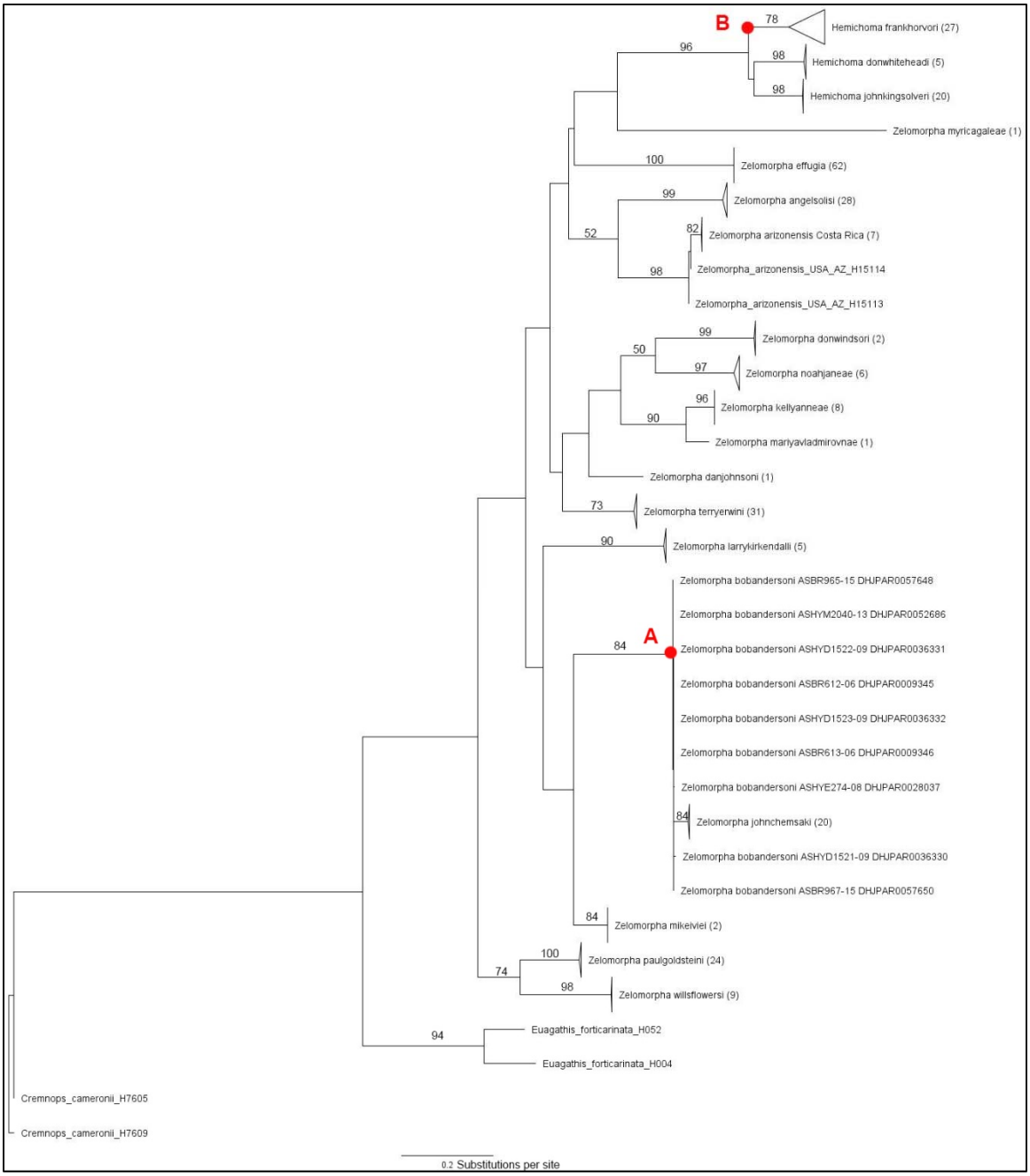


Figure 3.1. Tree of highest log-likelihood from 100 ML search reps of a dataset including all type specimens. ML bootstrap values appear above the branches. Full majority rule tree from bootstrap analysis is provided in Appendix 2. Branches with bootstrap values less than 50 were not labeled. Triangles at branch tips represent collapsed clades. The width of the triangles represent the distances from the node to the tip of the longest contained branch. Red labeled node are discussed in the text Node A: *Z. bobandersoni* was not found monophyletic. Node B: *H. frankhovorei* contains the greatest intraspecific barcode variation.

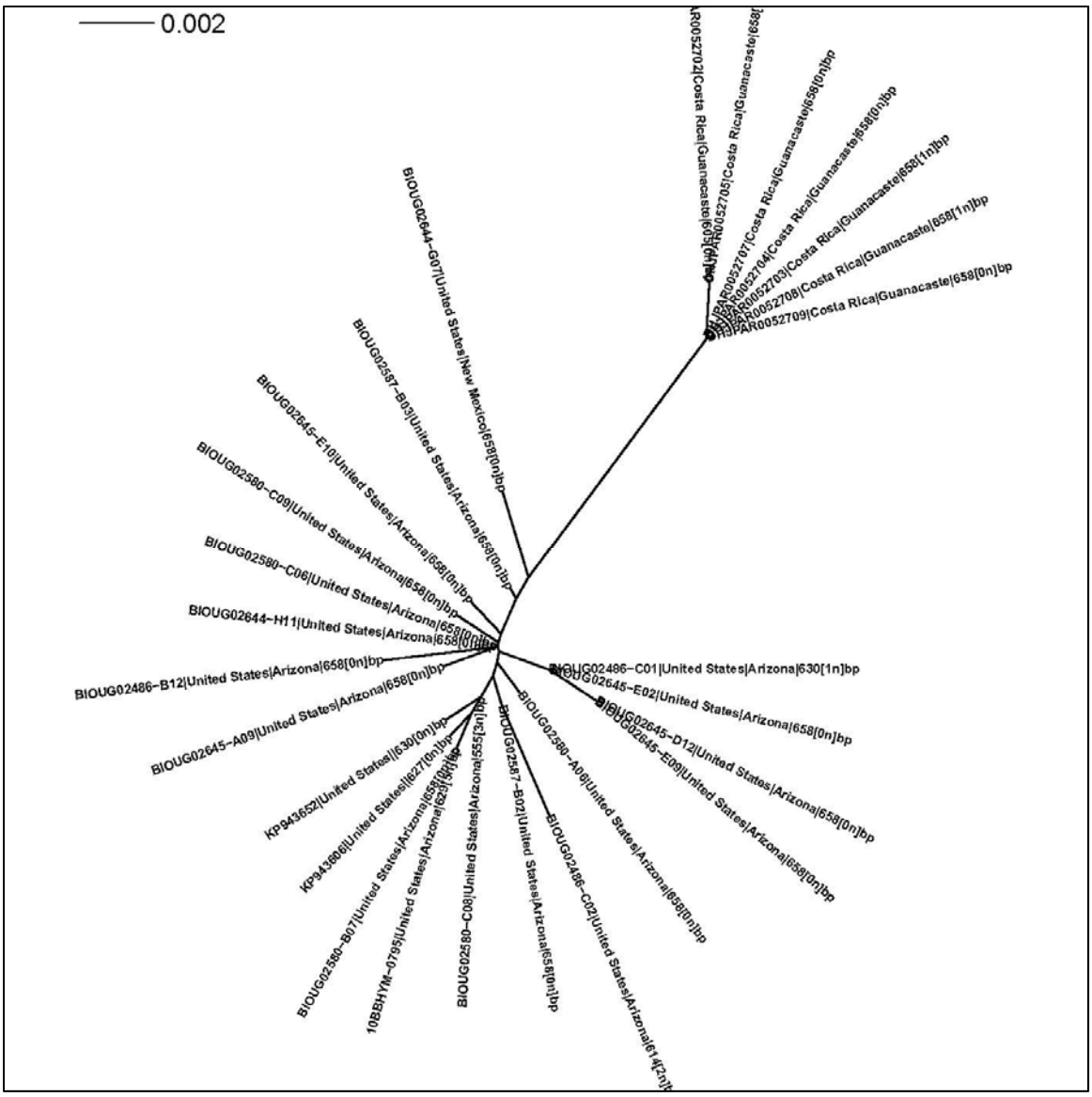


Figure 3.2. Unrooted neighbor joining tree containing all members of the BIN BOLD:AAG7943 which includes Costa Rican and North American members of *Zelomorpha arizonensis*. Tree was generated in BOLD using a P-distance model and pairwise deletion between taxa for missing data. Sequences were aligned in the BOLD aligner.

Systematics

Zelomorpha Ashmead 1900
Type species. *Zelomorpha arizonensis*, (by monotypy) [64].
Diagnosis. *Zelomorpha* can be distinguished from all other Agathidinae genera by the following combination of morphological characters: fore tarsal claws cleft and not pectinate; foretibial spur shorter than first tarsomere; ovipositor shorter than half the length of the metasoma; frons bordered by carinae; hind trochantellus with one or two longitudinal ridges; notauli variable, usually distinct; gena not produced.
Biology. *Zelomorpha* are koinobiont endoparasitoids of free living, late instar lepidopteran larvae [13]. Pupation usually occurs within the host's cocoon.
Distribution. Restricted to the New World, from the southwestern USA to Argentina, primarily Neotropical [71, 72].
Species diversity. Including the fifteen species described here, there are 67 described species of *Zelomorpha*.

Zelomorpha angelsolisi Meierotto, sp. n. Figure 3.3.
Molecular diagnosis: Nucleotides 43-45 TTA, 54-57 CTTT, 75 G, 136-138 GTG, 165 T, 321 G, 417 G, 462 G, 477 C, 561 G, 684 G
Amino Acids 15 L, 19 F, 46 V, 55 I
Biology: This species has characteristics associated with nocturnal habits: pale coloration, large compound eyes and ocelli. Specimens were reared from caterpillars in the family Erebidae feeding on Fabaceae: *Azeta ceramina* on *Acosmium panamense*, *Chabora* repugnalisDHJ01 on *Indigofera costaricensis*, and *Coenipeta bibitrix* on *Enterolobium cyclocarpum*. Host caterpillars were collected in April, May, and November.
Notes: Many specimens of this species were previously identified as *Zelomorpha arizonensis* based on morphology. P-distances between *Z. arizonensis* collected from the type locality of Arizona, USA and *Z. angelsolisi* were greater than 8%.
Type material: Holotype ♀: DHJPAR0009310, Costa Rica, Área de Conservación Guanacaste, Sector Mundo Nuevo, 10.7416 N, 85.42734 W, 420m elevation, Mariano Pereira coll., reared from *Azeta ceramina* 05-SRNP-56517, host collected 30 May 2005, wasp eclosed 17 June 2005, (EMUS). Paratypes: DHJPAR0009321, DHJPAR0009322, DHJPAR0009314, DHJPAR0009315, DHJPAR0009316, DHJPAR0009313, DHJPAR0009318, DHJPAR0009317, DHJPAR0009311, DHJPAR0009312, DHJPAR0009319, DHJPAR0009320, DHJPAR0009323, DHJPAR0021152, DHJPAR0028276, DHJPAR0028275, DHJPAR0015578, DHJPAR0015593, DHJPAR0015584, DHJPAR0015592, DHJPAR0015579, DHJPAR0015577, DHJPAR0015556, DHJPAR0029184, DHJPAR0015590, DHJPAR0015588.
Etymology: *Zelomorpha angelsolisi* is named in honor of Angel Solis of INBio and the Museo Nacional de Costa Rica, a master Coleoptera taxonomist and curator who has massively contributed to the inventory of Costa Rican Coleoptera.

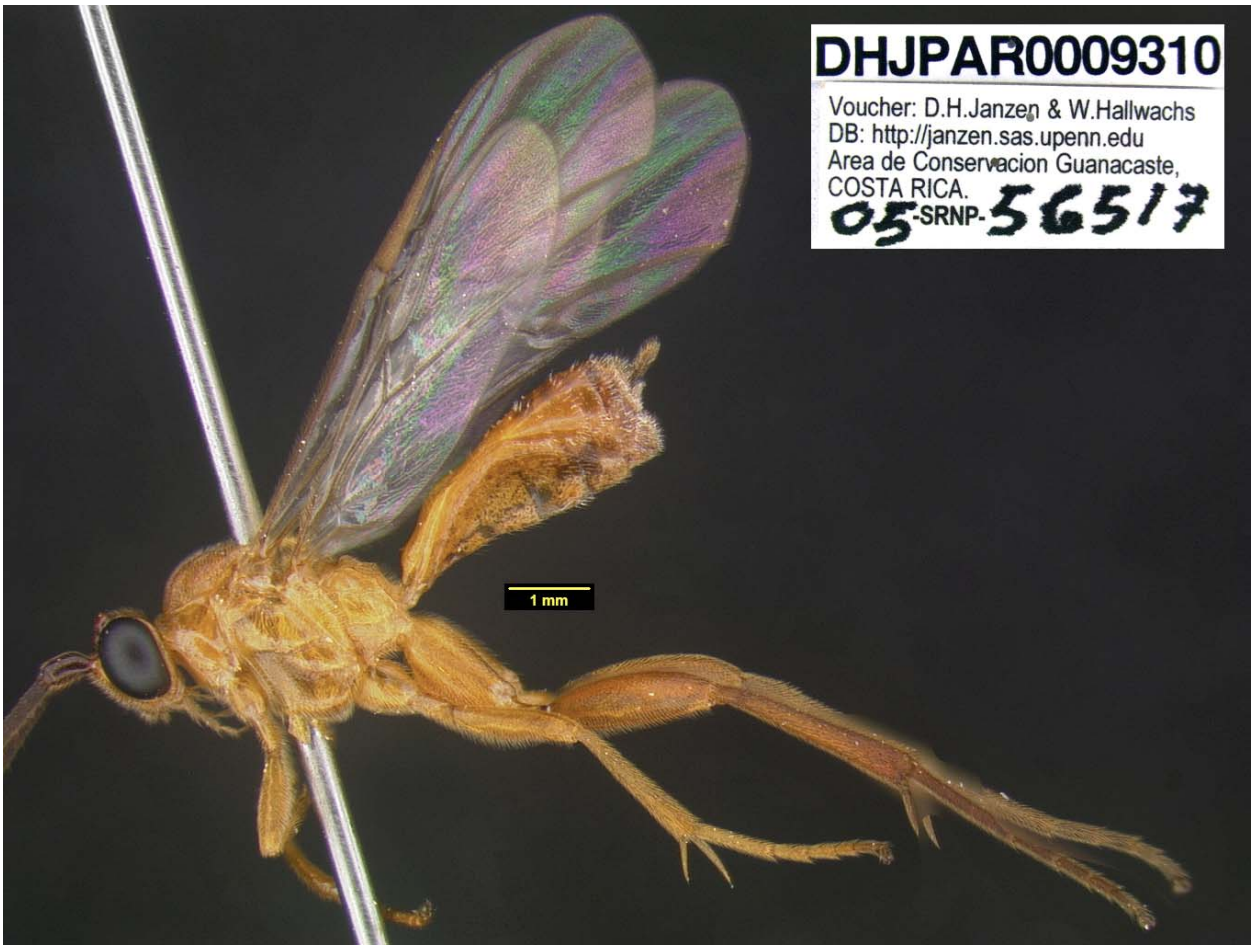


Figure 3.3. Lateral habitus of *Z. angelsolisae* holotype female.

***Zelomorpha arizonensis* Ashmead 1900**. Figure 3.4
Molecular diagnosis: Nucleotides 515 C, 648 T
Amino Acids 172 T
Biology: Adults of this species have characteristics associated with nocturnal habits: pale coloration, large compound eyes and ocelli. All individuals from the ACG were reared from *Bulia mexicana* (Erebidae) caterpillars feeding on *Prosopis juliflora* (Fabaceae) at the edge of mangrove swamps in the month of July.
Notes: The host of *Z. arizonensis* from the type locality in the southwestern United States is unknown. However, the range of *Prosopis juliflora* extends northwards through Mexico and into the United States, where it is fed upon by several species of *Bulia.* P-distances between specimens from Costa Rica and the US are close to 1.5% (Figure 3.2), which is more than separates many morphologically and ecologically distinctive species from the ACG [52, 93, 94], including *Z. johnchemsaki* and *Z. bobandersoni*. It is possible that two cryptic species will eventually be confirmed with larger samples of both populations. Two additional diagnostic characters were found when non-Costa Rican specimens were excluded from the dataset: 114 G, 402 C.
Material examined: Pictured specimen ♀: DHJPAR0052709, Costa Rica, Área de Conservación Guanacaste, Sector Santa Rosa, 10.78004 N, 85.66405 W, 5m elevation, Guillermo Pereira coll., reared from *Bulia mexicana* 13-SRNP-17758, host collected 13 July 2013, wasp eclosed 29 July 2013, (EMUS). Other specimens: Costa Rica: DHJPAR0052704, DHJPAR0052702, DHJPAR0052703, DHJPAR0052708 (EMUS), DHJPAR0052705, DHJPAR0052707 (HIC). Arizona: HICH015113, HICH015114 (HIC), BIOUG02486-B12, BIOUG02486-C01, BIOUG02486-C02, BIOUG02580-A06, BIOUG02580-B07, BIOUG02580-C06, BIOUG02580-C08, BIOUG02580-C09, BIOUG02587-B02, BIOUG02587-B03, BIOUG02644-H11, BIOUG02645-A09, BIOUG02645-D12, BIOUG02645-E02, BIOUG02645-E09, BIOUG02645-E10, 10BBHYM-0795, 09BBHYM-158, 09BBHYM-159, 09BBHYM-1106, 09BBHYM-1107, 09BBHYM-1108, 09BBHYM-1109, 09BBHYM-1110, 09BBHYM-1111 (BIOUG). New Mexico: BIOUG02644-G07 (BIOUG). Texas: 09BBHYM-1112 (BIOUG).
Etymology: *Zelomorpha arizonensis* was named for the type locality.

Figure 3.4. Lateral habitus of *Z. arizonensis* female.

Zelomorpha bobandersoni Meierotto, sp. n. Figure 3.5.
Molecular diagnosis: Nucleotides: 72-75 GGGT, 163 G, 222-225 GGGG, 264 G
Amino acid: 55 V
Biology: All known individuals were reared from *Hemiceras* plusiataDHJ01 (Notodontidae) feeding on *Tachigali costaricense* (Fabaceae). Host caterpillars were collected in January, February, April, and June through October.
Notes: Both COI and morphology of *Z. bobandersoni* are similar to *Z. johnchemsaki*, but show consistent differences in color pattern and host preference.
Type material: Holotype ♀: DHJPAR0028037, Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, 10.99697 N, 85.39666 W, 470m elevation, Mauricio Siezar coll., reared from *Hemiceras* plusiataDHJ01 08-SRNP-71265, host collected 10 July 2008, wasp eclosed 11 August 2008, (EMUS). Paratypes: DHJPAR0009346, DHJPAR0009345, DHJPAR0036332, DHJPAR0036330, DHJPAR0036331, DHJPAR0052686.
Etymology: *Zelomorpha bobandersoni* is named in honor of Bob Anderson of the Canadian Museum of Nature, Ottawa, in recognition of his taxonomic and curatorial support for understanding the Curculionidae of Costa Rica.

Figure 3.5. Lateral habitus of *Z. bobandersoni* holotype female.

Zelomorpha danjohnsoni Meierotto, sp. n. Figure 3.6
Molecular diagnosis: Nucleotides: 98 G, 111 G, 264 C, 310 G, 375 A, 452 T, 495 A, 507 G, 513 G, 648 G
Amino acids: 33 S, 151
Biology: The host of the holotype and one additional specimen lacking COI data were collected in June. Both were reared from *Diastema morata* (Noctuidae) on *Lantana camara* (Verbenaceae).
Type material: Holotype ♀: DHJPAR0009409, Costa Rica, Área de Conservación Guanacaste, Sector Cacao, 10.88996 N, 85.47966 W, 550m elevation, Dunia Garcia coll., reared from *Diastema morata* 05-SRNP-45510, host collected 7 June 2005, wasp eclosed 14 July 2005, (EMUS).
Etymology: *Zelomorpha danjohnsoni* is named in honor of C. Dan Johnson (RIP) of Arizona State University, in recognition of his taxonomic support for understanding the Bruchidae of Costa Rica.

Figure 3.6. Lateral habitus of *Z. danjohnsoni* holotype female.

Zelomorpha donwindsori Meierotto, sp. n. Figure 3.7.
Molecular diagnosis: Nucleotides: 78 A, 213 C, 243 A, 390 G, 429 G, 456 G, 506-507 CT, 513 T, 585 G, 588 G, 603 C, 636 C, 660 G, 678-679 TG
Amino acids: 171 I, 173 D
Biology: The two identified specimens of this species were both reared from caterpillars in the family Euteliidae, genus *Paectes*: *Paectes lunodes* on *Ocotea veraguensis* (Lauraceae) and *Paectes fuscescens* on the introduced species *Anacardium occidentale* (Anacardiaceae). Host caterpillars were collected in November and July.
Type material: Holotype ♀: DHJPAR0048721, Costa Rica, Área de Conservación Guanacaste, Sector El Hacha, 11.03226 N, 85.52776 W, 290m elevation, Elieth Cantillano coll., reared from *Paectes fuscescens* 11-SRNP-23258, host collected 15 November 2011, wasp eclosed 9 January 2012, (EMUS). Paratype: DHJPAR0052679.
Etymology: *Zelomorpha donwindsori* is named in honor of Don Windsor of the Smithsonian Tropical Research Institute in Panama, a master Chrysomelidae taxonomist who also contributed to the early development of ACG.

Figure 3.7. Lateral habitus of *Z. donwindsori* holotype female.

Zelomorpha effugia Meierotto, sp. n. Figure 3.8.
Molecular diagnosis: Nucleotides: 46 A, 96-97 TG, 102 T, 124-127 TTAA, 130 G, 285 G, 352-353 TC
Amino acids: 16 M, 33 V, 34 F, 42 L, 44 D, 118 S
Biology: This species has been reared only from *Cosmosoma hercyna* (Erebidae) caterpillars. Host plants include *Lacistema aggregatum* (Lacistemataceae), *Lozania pittieri* (Lacistemataceae), and *Gymnanthes riparia* (Euphorbiaceae). Hosts were collected in September, November, January, and February.
Type material: Holotype ♀: DHJPAR0015541, Costa Rica, Área de Conservación Guanacaste, Sector Rincon Rain Forest, 10.86666 N, 85.24528 W, 320m elevation, Minor Carmona coll., reared from *Cosmosoma hercyna* 05-SRNP-43568, host collected 30 November 2005, wasp eclosed 27 December 2005, (EMUS). Paratypes: DHJPAR0015535, DHJPAR0009432, DHJPAR0009431, DHJPAR0015538, DHJPAR0009381, DHJPAR0009336, DHJPAR0015546, DHJPAR0015552, DHJPAR0009328, DHJPAR0015553, DHJPAR0015547, DHJPAR0009329, DHJPAR0009330, DHJPAR0009331, DHJPAR0009332, DHJPAR0015551, DHJPAR0015550, DHJPAR0009333, DHJPAR0015548, DHJPAR0009334, DHJPAR0015544, DHJPAR0009335, DHJPAR0015545, DHJPAR0015549, DHJPAR0009337, DHJPAR0009338, DHJPAR0009339, DHJPAR0009340, DHJPAR0009341, DHJPAR0009342, DHJPAR0009343, DHJPAR0009379, DHJPAR0009380, DHJPAR0017282, DHJPAR0017281, DHJPAR0017283, DHJPAR0017275, DHJPAR0017278, DHJPAR0017280, DHJPAR0017279, DHJPAR0054489, DHJPAR0054516, DHJPAR0054472, DHJPAR0054473, DHJPAR0054481, DHJPAR0054479, DHJPAR0054484, DHJPAR0054483, DHJPAR0054477, DHJPAR0054475, DHJPAR0054482, DHJPAR0054476, DHJPAR0054478, DHJPAR0054474, DHJPAR0056359, DHJPAR0057453, DHJPAR0057454, DHJPAR0057455, DHJPAR0057456, DHJPAR0057452, DHJPAR0056979.
Etymology: *Zelomorpha effugia* is named in honor of the podcast Escape Pod, whose short science fiction stories provided the first author with inspiration and motivation during the work of this manuscript.

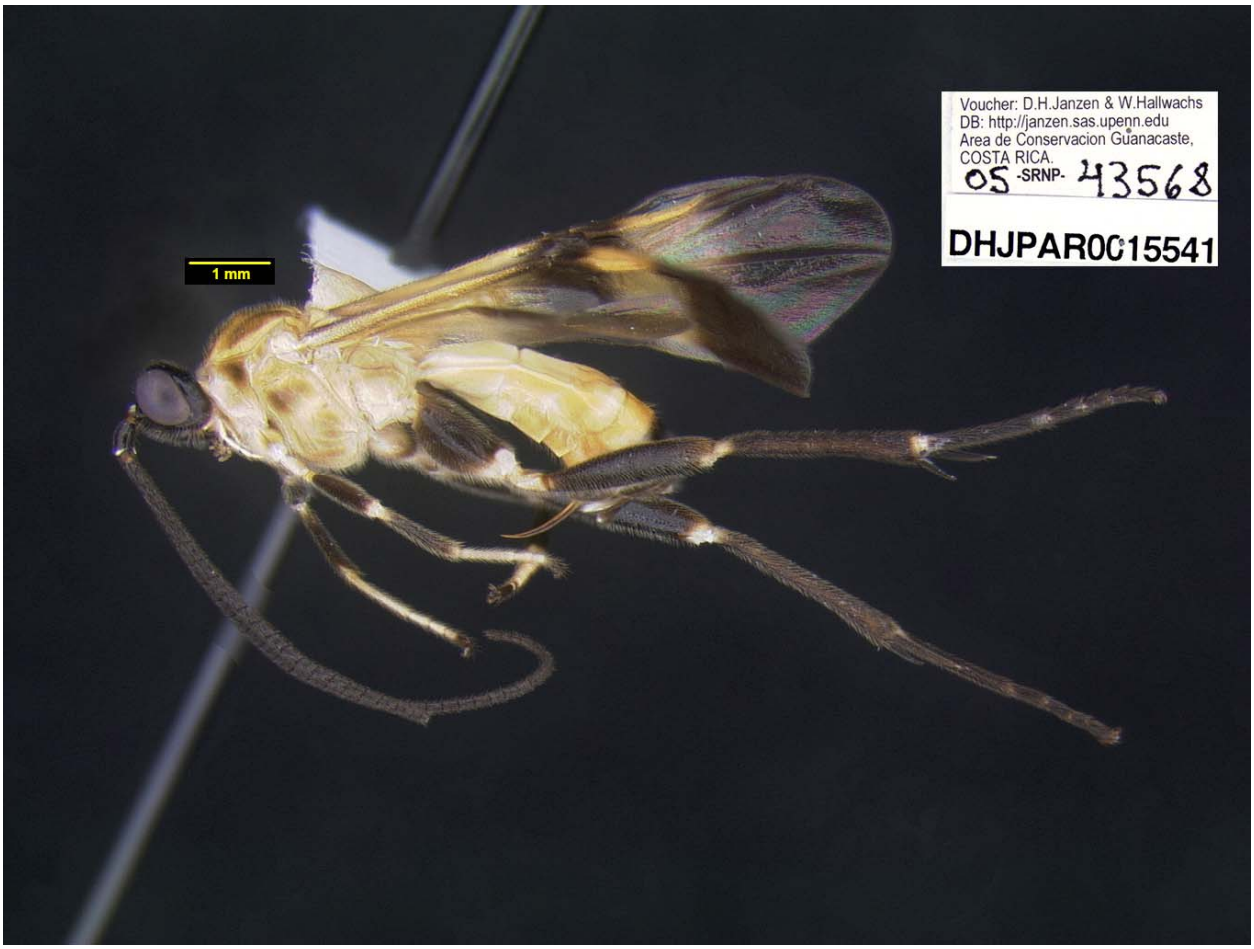


Figure 3.8. Lateral habitus of *Z. effugia* holotype female.

Zelomorpha johnchemsaki Meierotto, sp. n. Figure 3.9.
Molecular diagnosis: Nucleotides: 261 G, 279 C, 537-538 GC, 571 G
Amino acids: 119 V
Biology: Hosts for this species include *Hemiceras pallidula* (Notodontidae) on *Inga vera* and *Inga oerstediana* (Fabaceae), and *Hemiceras clarkii* on *Inga vera.* Most of the hosts were collected in August, one was collected in October.
Notes: Both COI and morphology of *Z. johnchemsaki* are similar to *Z. bobandersoni*, but the two species show consistent differences in color pattern and host preference.
Type material: Holotype ♀: DHJPAR0040547, Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, 10.9867 N, 85.38503 W, 440m elevation, Ricardo Calero coll., reared from *Hemiceras pallidula* 09-SRNP-71580, host collected 14 July 2009, wasp eclosed 10 August 2009, (EMUS). Paratypes: DHJPAR0023296, DHJPAR0036326, DHJPAR0040539, DHJPAR0040536, DHJPAR0040540, DHJPAR0040546, DHJPAR0040537, DHJPAR0040543, DHJPAR0040541, DHJPAR0036325, DHJPAR0040535, DHJPAR0036369, DHJPAR0040538, DHJPAR0040542, DHJPAR0040545, DHJPAR0040544, DHJPAR0036327, DHJPAR0036328, DHJPAR0036368.
Etymology: *Zelomorpha johnchemsaki* is named in honor of John Chemsak (RIP) of the University of California, Berkeley, in recognition of his taxonomic support for understanding the ACG Cerambycidae.

Figure 3.9 Lateral habitus of *Z. johnchemsaki* holotype female.

Zelomorpha kellyanneae Meierotto, sp. n. Figure 3.10.
Molecular diagnosis: Nucleotides: 348 C, 421 A
Amino acids: 43 T, 141 I
Biology: This species has been reared from *Nephodia* Janzen01(Geometridae) on *Heteropterys macrostachya* and *Heteropterys laurifolia* (Malpighiaceae). Host caterpillars were collected in November, February, and May.
Type material: Holotype ♀: DHJPAR0015536, Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, 11.02865 N, 85.48669 W, 280m elevation, Lucia Ríos coll., reared from *Nephodia* Janzen01 05-SRNP-25234, host collected 21 November 2005, wasp eclosed 10 December 2005, (EMUS). Paratypes: DHJPAR0029301, DHJPAR0009395, DHJPAR0009394, DHJPAR0015543, DHJPAR0015542, DHJPAR0042809, DHJPAR0042806.
Etymology: *Zelomorpha kellyanneae* is named in honor of Kelly Meierotto, sister of SM and up and coming archaeologist.

Figure 3.10. Lateral habitus of *Z. kellyanneae* holotype female.

Zelomorpha larrykirkendalli Meierotto, sp. n. Figure 3.11.
Molecular diagnosis: Nucleotides: 81 G, 273 G, 324 T, 369 A, 432 G, 522 A, 662 G
Amino acids: 33 M, 108 I, 174 M
Biology: This species has been reared from four species of *Opisthoxia* (Geometridae) on three species of Primulaceae: *Opisthoxia* sp. and *O. molpadia* on *Parathesis glabra*, *O. bella* on *Ardisia compressa*, and *O. uncinata* on *Ardisia auriculata*. Caterpillars were collected in February, March, June, July, and September.
Type material: Holotype ♀: DHJPAR0015540, Costa Rica, Área de Conservación Guanacaste, Sector San Cristobal, 10.90037 N, 85.37254 W, 500m elevation, Yessenia Mendoza coll., reared from *Opisthoxia bella* 04-SRNP-4505, host collected 6 September 2004, wasp eclosed 26 September 2004, (EMUS). Paratypes: DHJPAR0055988, DHJPAR0055084, DHJPAR0052087, DHJPAR0055981.
Etymology: *Zelomorpha larrykirkendalli* is named in honor of Larry Kirkendall of the University of Bergen, Norway, in recognition of his intense taxonomic interest in Neotropical Scolytidae and now, those of ACG.

Figure 3.11. Lateral habitus of *Z. larrykirkendalli* holotype female.

Zelomorpha mariyavladmirovnae Meierotto, sp. n. Figure 3.12.
Molecular diagnosis: Nucleotides: 250 A, 354 G, 462 C, 543 G
Amino acids: 84 M
Biology: The single specimen of this species was reared from *Ormetica sicilia* (Erebidae) on *Inga vera* (Fabaceae).
Type material: Holotype ♀: DHJPAR0023528, Costa Rica, Área de Conservación Guanacaste, Sector Mundo Nuevo, 10.77175 N, 85.434 W, 305m elevation, Jose Cortez coll., reared from *Ormetica sicilia* 07-SRNP-61364, host collected 28 December 2007, wasp eclosed 14 January 2008, (EMUS).
Etymology: *Zelomorpha mariyavladmirovnae* is named in honor of Mariya Frahm, for her guidance and support given to SM.

Figure 3.12. Lateral habitus of *Z. mariavladmirovnae* holotype female

Zelomorpha mikeiviei Meierotto, sp. n. Figure 3.13.
Molecular diagnosis: Nucleotides: 111 C, 411 G, 549 G, 567 G, 661 T
Amino acids: none
Biology: This species has been reared from two unidentified, different species of host feeding on two different host plants: a species of Geometridae feeding on *Ruellia inundata* (Acanthaceae) and a species of Noctuidae feeding on *Colubrina spinosa* (Rhamnaceae). Host caterpillars were collected in January and June.
Type material: Holotype ♀: DHJPAR0029297, Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, 11.01926 N, 85.40997 W, 440m elevation, Calixto Moraga coll., reared from Noctuidae 04-SRNP-30170, host collected 12 January 2004, wasp eclosed 6 February 2004, (EMUS). Paratype: DHJPAR0040325.
Etymology: *Zelomorpha mikeiviei* is named in honor of Mike Ivie of Montana State University, a master Coleoptera taxonomist who has massively contributed to the inventory of Caribbean Coleoptera and ACG inventory.

Figure 3.13. Lateral habitus of *Z. mikeiviei* holotype female.

Zelomorpha myricagaleae Meierotto, sp. n. Figure 3.14.
Molecular diagnosis: Nucleotides: 44 C, 55 A, 64 G, 98 C, 126 C, 135 G, 163 T, 168 G, 183-186 GGTA, 246 C, 258 G, 357-358 GG, 369 G, 381 C, 400-401 AA, 505 T, 519-520 CG, 525 G, 570 A, 603 G, 606 G
Amino acids: 15 T, 19 M, 22 V, 55 L, 120 A, 134 N, 169 C, 174 V, 176 L, 221 M
Biology: The single specimen of this species was reared from an unidentified species of Noctuidae feeding on *Smilax spinosa* (Smilacaceae).
Notes: Known from a single specimen. Holotype is somewhat damaged, missing antennae.
Type material: Holotype ♀: DHJPAR0028033, Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, 11.02681 N, 85.49547 W, 290m elevation, Lucia Ríos coll., reared from Erebidae 08-SRNP-21458, host collected 11 June 2008, wasp eclosed 8 July 2008, (EMUS).
Etymology: *Zelomorpha myricagaleae* is named in honor of Myrica Gale Meierotto, cousin of SM and fierce competitor.

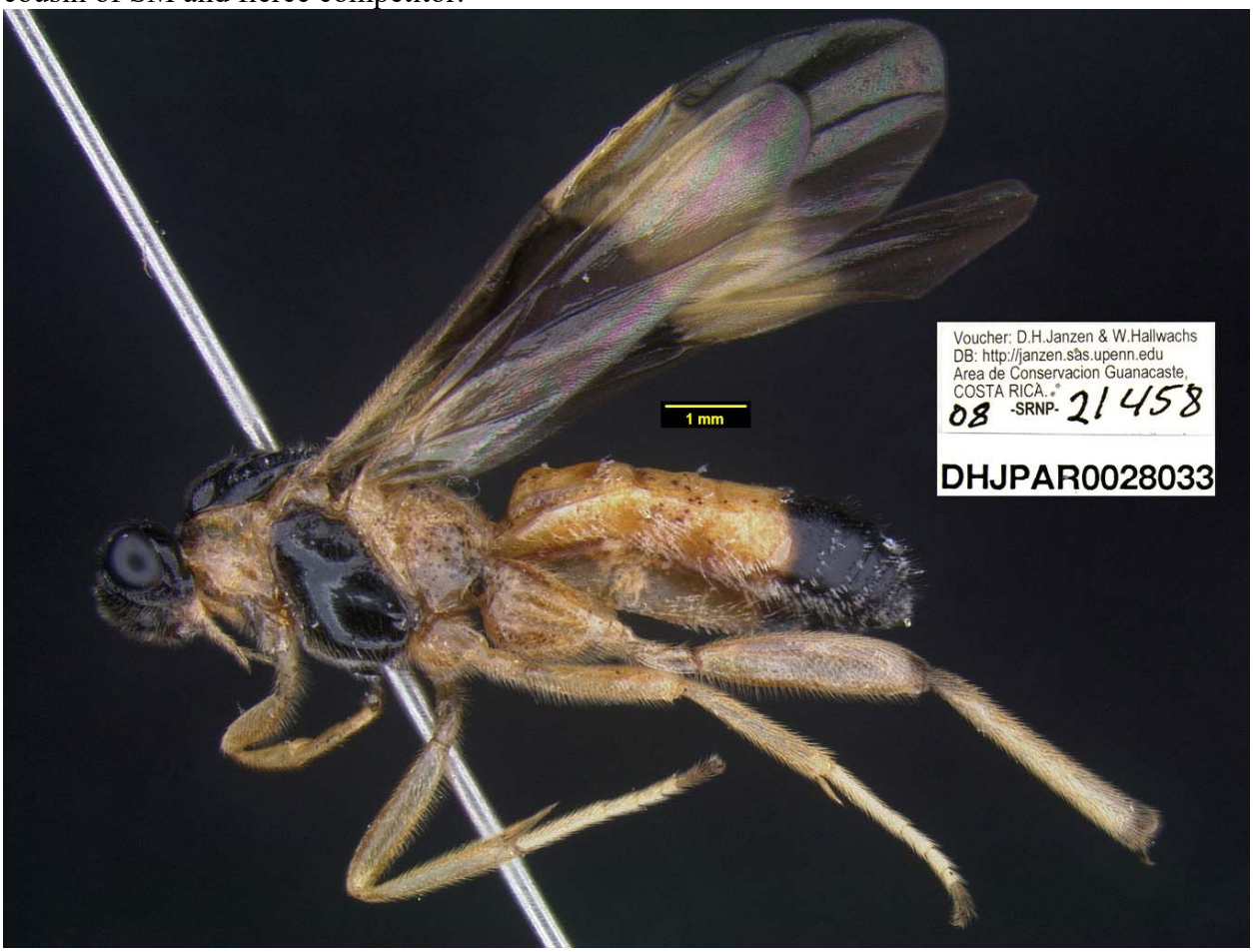


Figure 1.14.. Lateral habitus of Z. *myricagaleae* holotype female.

Zelomorpha noahjaneae Meierotto, sp. n. Figure 3.15.
Molecular diagnosis: Nucleotides: 108 G, 123 G, 333 G, 519 A, 693 CG
Amino acids: none
Biology: Specimens of this species were reared from three species of Euteliidae on Anacardiaceae host plants: *Paectes fuscescens* on the introduced *Anacardium occidentale*, *Eutelia chrysotermina* on *Anacardium excelsum*, and *Paectes* Poole10 on *Mosquitoxylum jamaicense.* Caterpillars were collected in July and November.
Type material: Holotype ♀: DHJPAR0048720, Costa Rica, Área de Conservación Guanacaste, Sector El Hacha, 11.03226 N, 85.52776 W, 290m elevation, Elieth Cantillano coll., reared from *Paectes fuscescens* 11-SRNP-23262, host collected 15 November 2011, wasp eclosed 30 December 2011, (EMUS). Paratypes: DHJPAR0048723, DHJPAR0048719, DHJPAR0052678, DHJPAR0028023, DHJPAR0028024.
Etymology: *Zelomorpha noahjaneae* is named in honor of Noah Meierotto, cousin of SM and an aspiring scientist / possible future entomologist.

Figure 3.15.. Lateral habitus of *Z. noahjaneae* holotype female.

Zelomorpha paulgoldsteini Meierotto, sp. n. Figure 3.16.
Molecular diagnosis: Nucleotides: 216 G, 327 G, 345-346 AA, 352-354 ACA, 517 C
Amino acids: 118 T, 173 H
Biology: This species has been reared from a relatively wide range of hosts in the families Erebidae and Noctuidae, but all hosts are fern feeders. Caterpillars of type specimens were collected in every month except March and April.

Table 3.1. Host caterpillars and host plants of *Z. paulgoldsteini.*

Host family	Host species	Host plant family	Host plant species
Erebidae	*Nicetas* antonalisDHJ02	Cyatheaceae	*Cyathea multiflora*
Erebidae	*Nicetas* Janzen02	Woodsiaceae	*Diplazium myriomerum*
Erebidae	*Nicetas* Poole22	Dryopteridaceae	*Elaphoglossum doanense*
Erebidae	*Rejectaria* Janzen02	Cyatheaceae	*Cyathea multiflora*
Erebidae	*Rejectaria* Janzen02	Lomariopsidaceae	*Lomariopsis vestita*
Erebidae	*Rejectaria* Janzen06	Cyatheaceae	*Alsophila firma*
Erebidae	*Rejectaria* sp.	Cyclanthaceae	*Cyclanthus bipartitus*
Erebidae	*Rejectaria splendida*	Cyclanthaceae	*Asplundia utilis*
Erebidae	*Rejectaria splendida*	Cyclanthaceae	*Carludovica costaricensis*
Erebidae	*Rejectaria* splendidaDHJ01	Cyclanthaceae	*Asplundia utilis*
Erebidae		Dryopteridaceae	*Didymochlaena truncatula*
Noctuidae	*Callopistria floridensis*	Blechnaceae	*Blechnum occidentale*
Noctuidae	*Callopistria floridensis*	Davalliaceae	*Nephrolepis biserrata*
Noctuidae	*Callopistria mexicana*	Dryopteridaceae	*Bolbitis portoricensis*
Noctuidae		Dennstaedtiaceae	*Hypolepis repens*

Type material: Holotype ♀: DHJPAR0040222, Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, 11.00025 N, 85.45614 W, 585m elevation, Roster Moraga coll., reared from *Callopistria mexicana* 10-SRNP-21839, host collected 5 August 2010, wasp eclosed 29 August 2010, (EMUS). Paratypes: DHJPAR0044986, DHJPAR0057443, DHJPAR0057447, DHJPAR0057458, DHJPAR0057460, DHJPAR0015539, DHJPAR0009404, DHJPAR0057649, DHJPAR0030382, DHJPAR0054469, DHJPAR0054470, DHJPAR0054485, DHJPAR0036684, DHJPAR0028032, DHJPAR0041152, DHJPAR0041153, DHJPAR0041159, DHJPAR0042357, DHJPAR0042808, DHJPAR0042810, DHJPAR0052697, DHJPAR0016425, DHJPAR0016426.
Etymology: *Zelomorpha paulgoldsteini* is named in honor of Paul Goldstein of the USDA Systematic Entomology Laboratory at the Smithsonian Institution, in honor of his inordinate fondness for the fern-eating caterpillars parasitized by this wasp.

Figure 3.16. Lateral habitus of *Z. paulgoldsteini* holotype female.

Zelomorpha terryerwini Meierotto, sp. n. Figure 3.17.
Molecular diagnosis: Nucleotides: 66 G, 359 G, 492 C, 621 G
Amino acids: 120 C
Biology: Hosts of type specimens were collected in January and May through November.
Table 3.2. Host caterpillars and host plants of *Z. terryerwini.*

Host family	Host species	Host plant family	Host plant species
Noctuidae	*Cropia cedica*	Cordiaceae	*Cordia alliodora*
Noctuidae	*Cropia cedica*	Cordiaceae	*Cordia panamensis*
Noctuidae	*Cropia connecta*	Cordiaceae	*Cordia alliodora*
Noctuidae	*Cropia europs*	Cordiaceae	*Cordia alliodora*
Noctuidae	*Cropia phila*	Cordiaceae	*Cordia panamensis*
Noctuidae	*Cropia rivulosa*	Cordiaceae	*Cordia alliodora*
Noctuidae	*Cropia rivulosa*	Cordiaceae	*Cordia panamensis*
Noctuidae	*Cropia rivulosa*	Cordiaceae	*Cordia bicolor*
Noctuidae	*Heterodelta nea*	Hypericaceae	*Vismia baccifera*
Noctuidae	*Nephelistis* Poole01	Asteraceae	*Lepidaploa tortuosa*
Noctuidae	*Perigea agnonia*	Asteraceae	*Lepidaploa patens*
Nolidae	*Iscadia* Poole02DHJ03	Hypericaceae	*Vismia baccifera*

Type material: Holotype ♀: DHJPAR0054486, Costa Rica, Área de Conservación Guanacaste, Sector Rincon Rain Forest, 10.94076 N, 85.3177 W, 461m elevation, Edwin Apu coll., reared from *Iscadia* Poole02DHJ03 13-SRNP-80618, host collected 13 November 2013, (EMUS). Paratypes: DHJPAR0009349, DHJPAR0015554, DHJPAR0022188, DHJPAR0023284, DHJPAR0009420, DHJPAR0009419, DHJPAR0009422, DHJPAR0009421, DHJPAR0015555, DHJPAR0021145, DHJPAR0028156, DHJPAR0057947, DHJPAR0009382, DHJPAR0009383, DHJPAR0009384, DHJPAR0021203, DHJPAR0053595, DHJPAR0054480, DHJPAR0009423, DHJPAR0041605, DHJPAR0040343, DHJPAR0041606, DHJPAR0041183, DHJPAR0049658.
Etymology: *Zelomorpha terryerwini* is named in honor of Terry Erwin of the Smithsonian Institution, a master Coleoptera taxonomist who has massively contributed to the inventory of Latin American Coleoptera.

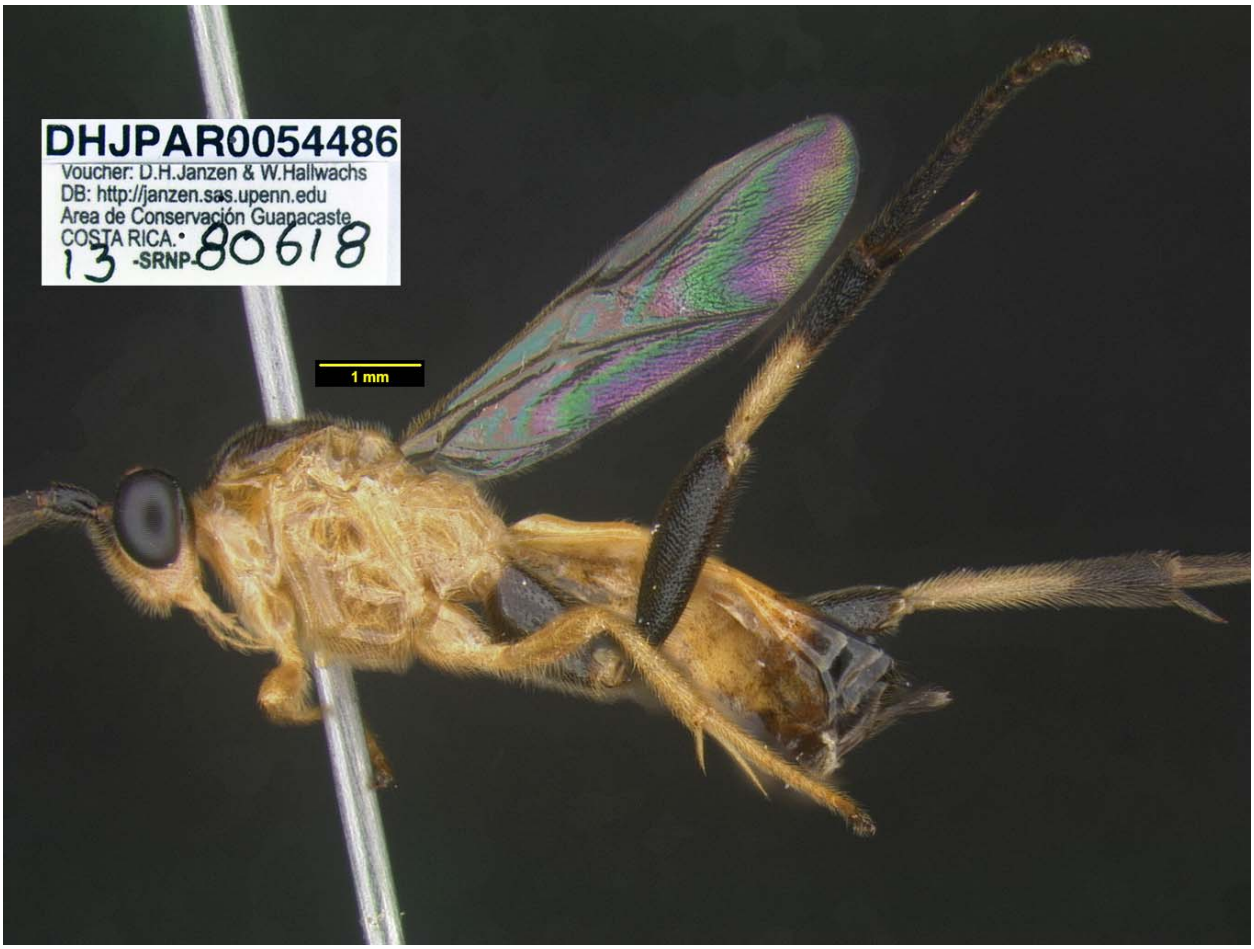


Figure 3.17. Lateral habitus of *Z. terryerwini* holotype female.

Zelomorpha willsflowersi Meierotto, sp. n. Figure 3.18.
Molecular diagnosis: Nucleotides: 207 G, 303 G, 345 G, 360 G, 398 G, 579 G, 661-663 GTG, 678 G
Amino acids: 133 S
Biology: This species was reared from three species of Erebidae feeding on Fabaceae: *Coenipeta bibitrix* on *Enterolobium cyclocarpum* and *Samanea saman*, *Goniohelia* Poole02 on *Senegalia tenuifolia*, and *Tyrissa acygonia* on *Senegalia tenuifolia*. Host caterpillars were collected in May, June, and July.
Type material: Holotype ♀: DHJPAR0009415, Costa Rica, Área de Conservación Guanacaste, Sector Santa Elena, 10.9257 N, 85.608 W, 270m elevation, Elieth Cantillano coll., reared from *Coenipeta bibitrix* 05-SRNP-21918, host collected 5 June 2005, wasp eclosed 22 June 2005, (EMUS). Paratypes: DHJPAR0021205, DHJPAR0010194, DHJPAR0021146, DHJPAR0009412, DHJPAR0009413, DHJPAR0009414, DHJPAR0009418, DHJPAR0057944.
Etymology: *Zelomorpha willsflowersi* is named in honor of Wills Flowers of Florida State University, a master Coleoptera taxonomist who has massively contributed to the inventory of Costa Rican Chrysomelidae.

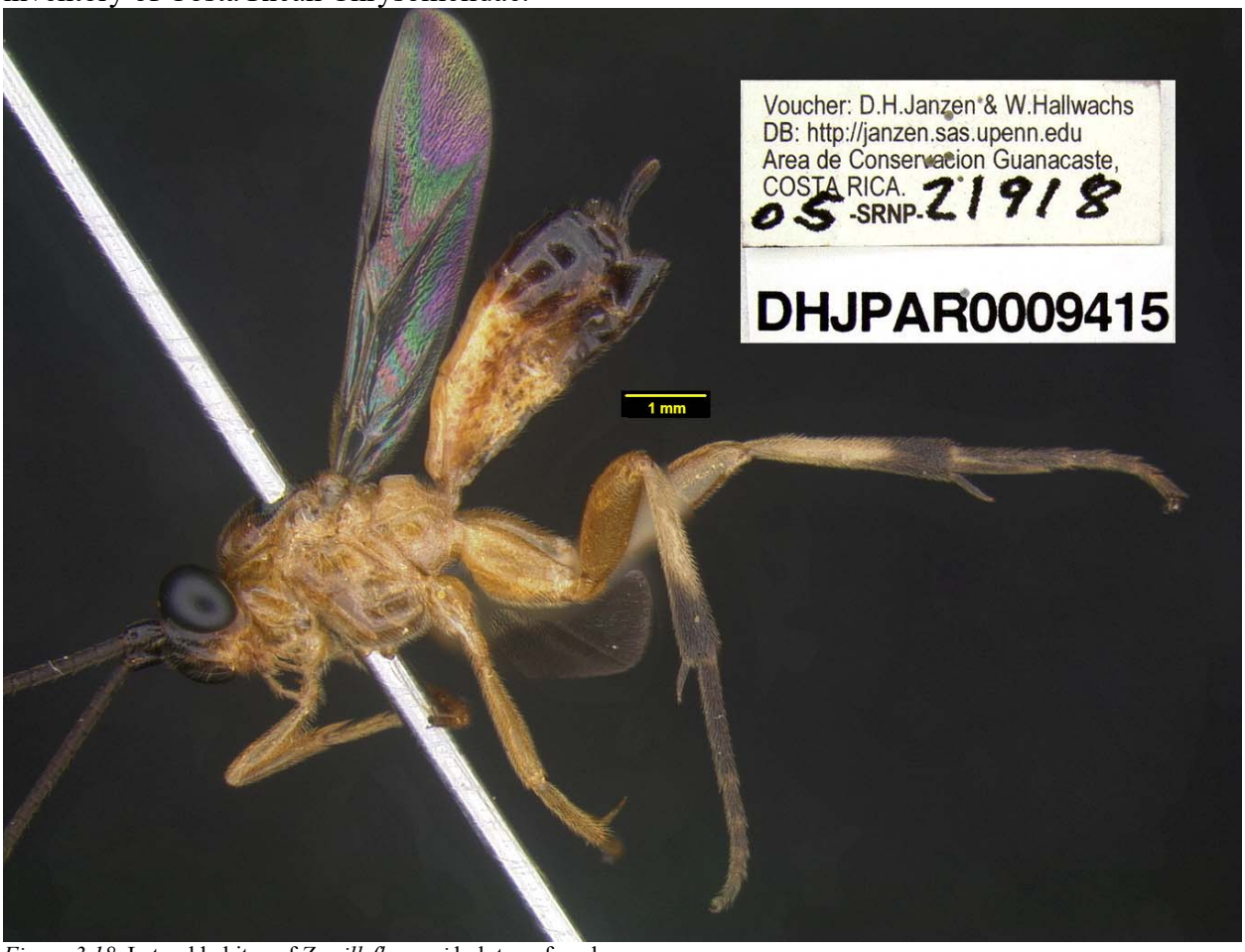


Figure 3.18. Lateral habitus of *Z. willsflowersi* holotype female.

Hemichoma Enderlein, 1920
Type species. *Hemichoma fenestratum* Enderlein, 1920

Diagnosis. *Hemichoma* shares diagnostic morphological characters with *Zelomorpha* except: notauli absent, mesoscutum lacking distinct lobes; gena greatly produced posteroventrally.
Biology. Members of *Hemichoma* are, like *Zelomorpha*, koinobiont endoparasitoids of late instar lepidopteran larvae.
Distribution. Restricted to the New World, known from the Mexico to Argentina.
Species diversity. Including the three species described here, there are eight described species of *Hemichoma*.

Hemichoma donwhiteheadi Meierotto, sp. n. Figure 3.19.
Molecular diagnosis: Nucleotides: 72 G, 78 G, 90 G, 114 G, 162 T, 168 A, 204 C, 207 G, 216 G, 225 G, 306 G, 318 T, 322 T, 346 G, 357 T, 409-410 GC, 414 G, 492 A, 516 G, 564 A, 585 GC
Amino acids: 81 I, 108 L, 116 V137 A
Biology: All specimens of this species were reared from *Pelochyta misera* (Erebidae). Host plants include *Heliocarpus appendiculatus* (Malvaceae), the introduced species *Psidium guajava* (Myrtaceae), *Inga oerstediana* and *Erythrina costaricensis* (Fabaceae). Host caterpillars were collected in June, August, November, and October.
Notes: This species shows sexual dimorphism in color pattern: females possess bicolored wings and a mostly orange mesosoma, while males have infuscate wings and a black mesosoma.
Type material: Holotype ♀: DHJPAR0016918, Costa Rica, Área de Conservación Guanacaste, Sector San Cristobal, 10.9305 N, 85.37223 W, 527m elevation, Elda Araya coll., reared from *Pelochyta misera* 06-SRNP-9643, host collected 27 November 2006, (EMUS). Paratypes: DHJPAR0021147, DHJPAR0016917, DHJPAR0029296, DHJPAR0022191.
Etymology: *Hemichoma donwhiteheadi* is named in honor of Don Whitehead (RIP) of the Smithsonian Institution, a master weevil taxonomist who helped greatly with the taxonomy of ACG Curculionidae.

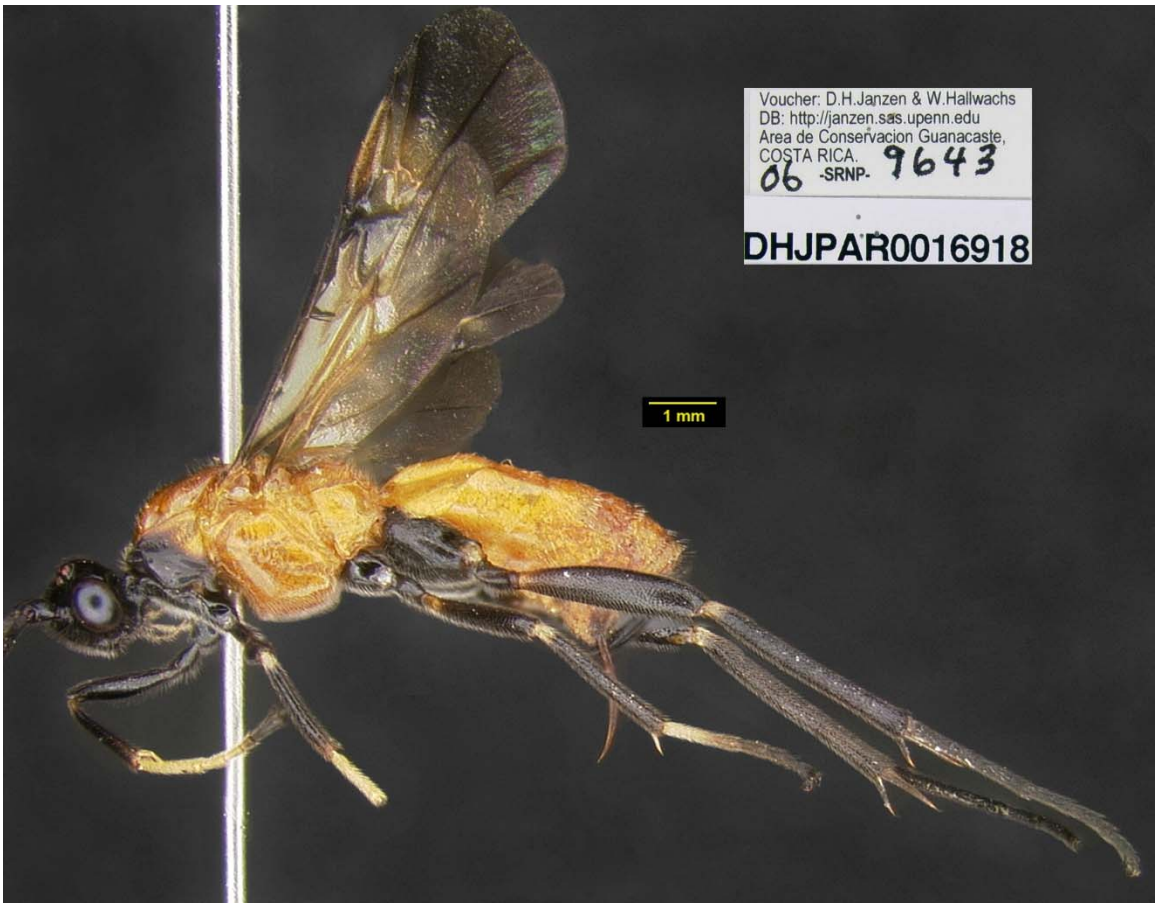


Figure 3.19. Lateral habitus of *H. donwhiteheadi* holotype female.

Hemichoma frankhovorei Meierotto, sp. n. Figure 3.20.
Molecular diagnosis: Nucleotides: 117 G, 228 c, 243 A, 357 A, 414 A, 477 T, 513 T, 570 A, 615 G, 645 T, 60 A, 663 T
Amino acids: 171 I, 172 M
Biology: Multiple species of *Halysidota* (Erebidae) are used as hosts for this species: *H. orientalis, H. pectenella, H. schausi,* and *H. underwoodi* on *Trema micrantha* (Cannabaceae), *Bernardia nicaraguensis* (Euphorbiaceae), and *Acalypha macrostachya* (Euphorbiaceae). Host caterpillars of type specimens were collected between the months of September and December.
Type material: Holotype ♀: DHJPAR0054503, Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, 11.01602 N, 85.38053 W, 380m elevation, Ricardo Calero coll., reared from *Halysidota schausi* 13-SRNP-71924, host collected 2 December 2013, wasp eclosed 12 January 2014, (EMUS). Paratypes: DHJPAR0015563, DHJPAR0030385, DHJPAR0030386, DHJPAR0037925, DHJPAR0037926, DHJPAR0054501, DHJPAR0054502, DHJPAR0036689, DHJPAR0036708, DHJPAR0036713, DHJPAR0028242, DHJPAR0028243, DHJPAR0028244, DHJPAR0028247, DHJPAR0028248, DHJPAR0028249, DHJPAR0028252, DHJPAR0028254, DHJPAR0028258, DHJPAR0028260, DHJPAR0028263, DHJPAR0028264, DHJPAR0041156, DHJPAR0041160, DHJPAR0041161, DHJPAR0029304.
Etymology: *Hemichoma frankhovorei* is named in honor of Frank Hovore (RIP) of California, a master cerambycid taxonomist who helped greatly with the taxonomic inventory of Costa Rican Cerambycidae.

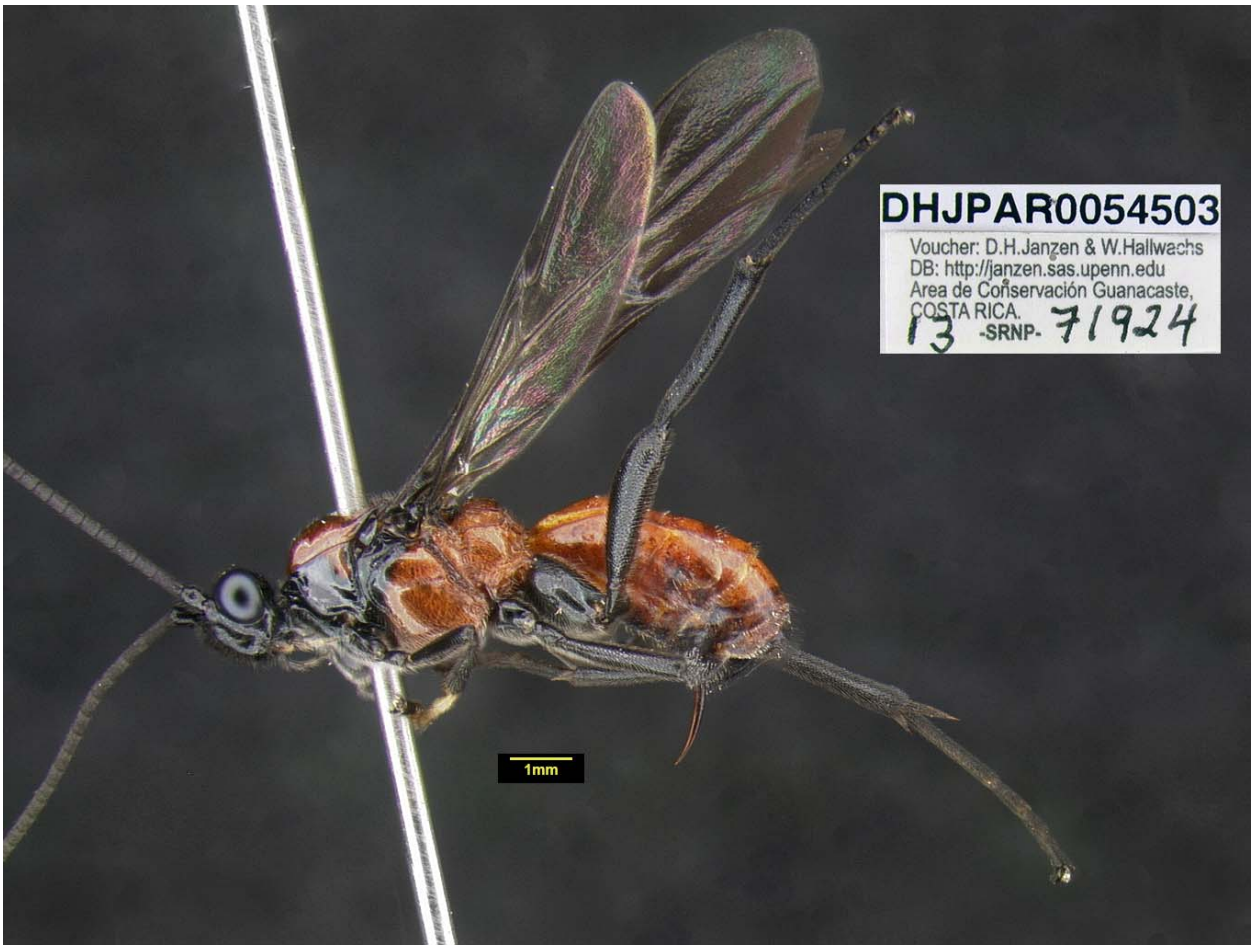


Figure 3.20. Lateral habitus of *H. frankhovorei* holotype female.

Hemichoma johnkingsolveri Meierotto, sp. n. Figure 3.21.
Molecular diagnosis: Nucleotides: 77 C, 84 G, 108 T, 111 A, 122 C, 141 T, 297 T, 327 G, 357 G, 414 T, 465 A, 579 G, 582 G, 591 G, 648 G, 678 GC
Amino acids: 26 A, 41 T, 173 N, 204 M
Biology: This species has been reared from *Carathis septentrionalis* (Erebidae) on *Ocotea cernua* (Lauraceae) and *Pachydota saduca* (Erebidae) on several species of *Ocotea* and *Netendra* (Lauraceae). Host caterpillars of type specimens were collected throughout the year, except between March and May.
Type material: Holotype ♀: DHJPAR0036333, Costa Rica, Área de Conservación Guanacaste, Sector Rincon Rain Forest, 10.93332 N, 85.25331 W, 135m elevation, Keiner Aragon coll., reared from *Pachydota saduca* 09-SRNP-44900, host collected 4 July 2009, wasp eclosed 8 September 2009, (EMUS). Paratypes: DHJPAR0022195, DHJPAR0057457, DHJPAR0046730, DHJPAR0046731, DHJPAR0046732, DHJPAR0015558, DHJPAR0015559, DHJPAR0015560, DHJPAR0057646, DHJPAR0038613, DHJPAR0041168, DHJPAR0042358, DHJPAR0042359, DHJPAR0057945, DHJPAR0058547, DHJPAR0058548, DHJPAR0060427, DHJPAR0060428, DHJPAR0060429.
Etymology: *Hemichoma johnkingsolveri* is named in honor of John Kingsolver (RIP) of the USDA Systematic Entomology Laboratory at the Smithsonian Institution, a master Bruchidae taxonomist and supporter of ACG.

Figure 3.21. Lateral habitus of *H. johnkingsolveri* holotype female.

Discussion

Ichneumonoid taxonomists have been stuck in a paradigm created for well-known fauna and flora. There is great utility in a morphological key to the 30 species of butterflies that occur in a suburban backyard in eastern North America since all of these are described, are associated with plentiful data, and are relatively easy to distinguish. A key to the 50 species of *Dinotrema* (Braconidae: Alysiinae) that occur in the same area is much less useful because, a) they mostly look the same, b) 90% are undescribed, c) knowing the species name would not give you much additional information, i.e., life history, geographic range, phenology. Now that there is an alternative to morphological keys and descriptions, the effort to create them can be reserved for situations where there is demand for them or until a fairly complete dataset has been accumulated.

Unlike the revision of charismatic and well known fauna, the probability of influencing legislation by making taxonomic judgements is negligible in this case. Too little is known or will be known for many years to determine if these species are eligible for protection under conservation laws. Biodiversity counts (number of species present in a location) could impact legislation, but because very closely related species (which would likely be difficult to delimit) are usually not found in sympatry [48], there should be few cases where an error in my decisions could change species richness estimates significantly.

In addition, the need for revision of species diagnosed by molecular characters in the future can be easily identified. With online, public databases, DNA sequences from type specimens can be instantly accessed and compared. If new specimens are collected with COI barcodes highly similar to a described species, but not matching some diagnostic characters, taxonomists can rapidly identify inadequate species concepts. In combination with high quality images and other digitized specimen attributes, online molecular data can enable revisionary work to occur without the need for physically visiting museums or shipping specimen loans. In other words, the consequences of making a mistake in species delimitation are not severe and relatively easy to catch. It should be noted that physical collections remain essential as repositories for types and voucher specimens. Although a large portion of the information considered taxonomically valuable today can be digitally accessed, no one can predict which data will be valuable in the future with new technologies and perspectives.

I recognize that DNA barcodes may fail to accurately delimit species. Just as there are no morphological characters capable of unfailingly separating species, there is currently no universal standard for separating species using molecular characters. As more specimens are captured and barcoded, additional interspecific variation will doubtlessly be discovered, perhaps making some diagnostic characters invalid. Again, the same is true of morphological diagnoses.

Chapter 4. Morphological identification key to the species of *Zelomorpha* Ashmead and *Hemichoma* Enderlein (Hymenoptera, Braconidae, Agathidinae) from the Área de Conservación Guanacaste, Costa Rica and diagnosis of two new species.

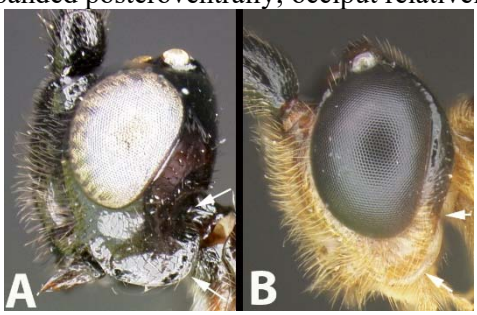
Four species of *Zelomorpha* reared from the ACG have yet to be successfully DNA barcoded. These include *Zelomorpha gregaria* (Sarmiento & Sharkey, 2004), *Zelomorpha jeffersoni* n.sp. *Zelomorpha guanacastensis* n.sp. and *Zelomorpha* Sharkey10. An illustrated key to the twenty known species of *Zelomorpha* and three species of *Hemichoma* from the ACG with morphological diagnoses and an image plate for each species are included.

Methods

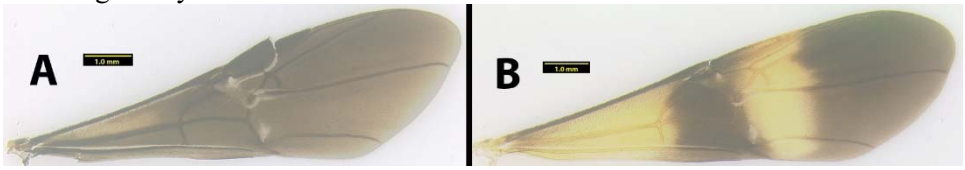
Specimens were reared from wild collected caterpillars by a team of parataxonomists under Drs. Dan Janzen and Winnie Hallwachs in the ACG using methods described in Chapter 3. Morphological characters were recorded and organized in DELTA editor version 1.02 [95]. Specimens examined include those designated as types in Chapter 3 and additional specimens listed under each diagnosis. Full specimen information for reared wasps that were not sampled for barcoding at the Canadian Centre for DNA Barcoding can be found by searching for the specimen voucher code of the host caterpillar (xx-SRNP-xxxx). Type specimens of all previously described *Zelomorpha* and *Hemichoma* species were examined by MJS and his notes were used to verify the novelty of species described here. Specimens are deposited in EMUS and HIC unless otherwise noted.

Key to the species of *Zelomorpha* and *Hemichoma* from the Área de Conservación Guanacaste, Costa Rica

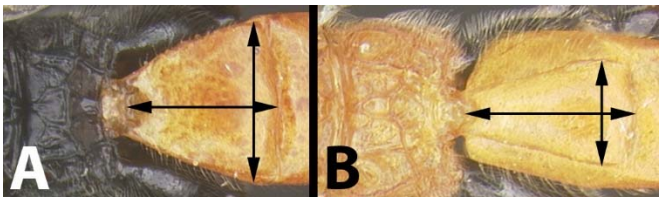
1. Gena expanded posteroventrally; occiput excavated;.....genus *Hemichoma* 2
   Gena normal, not expanded posteroventrally; occiput relatively flat... genus *Zelomorpha* 5



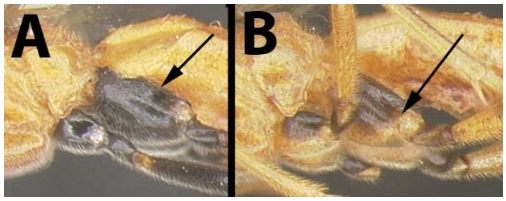
2(1). Forewing entirely infuscate or infuscate with clear areas, lacking yellow color..... 3
   Forewing with yellow and melanic color 4



3(2). Median tergite 1 wider.....***Hemichoma frankhovorei***
   Median tergite 1 narrower ..... ***Hemichoma donwhiteheadi* (males)**



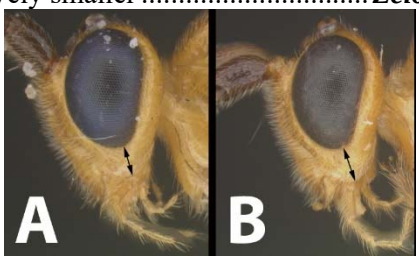
4(2). Hind coxa in lateral view entirely black or brown .. ***Hemichoma donwhiteheadi*** **(females)**
Hind coxa in lateral view bicolored..... ***Hemichoma johnkingsolveri***



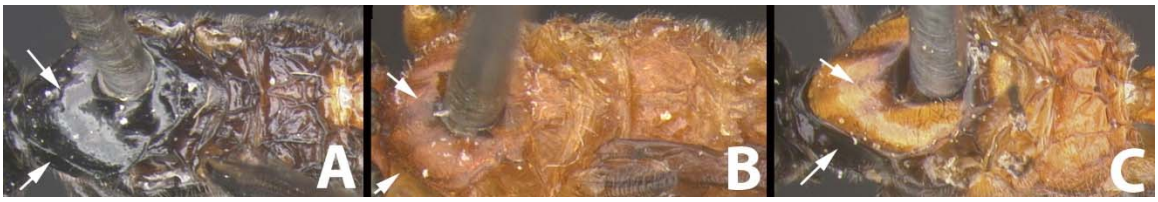
5(1). Forewing completely hyaline 6
Forewing completely infuscate, or infuscate with clear areas 8
Forewing with combined hyaline and infuscate, pattern; and/or colored areas..... 10

6(5). Hind tibia melanic apically, contrasting with yellow in basal 4/5ths ..... ***Zelomorpha arizonensis***
Hind tibia not significantly darker apically, if somewhat darker then it is a gradual transition from a paler base. 7

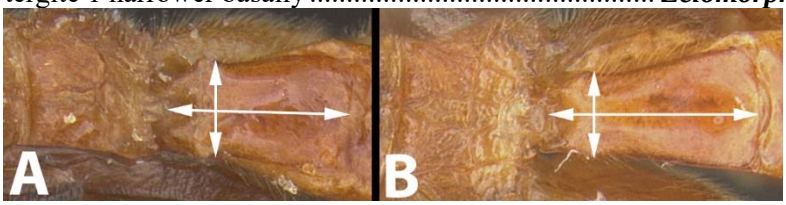
7(6). Gena shorter, eye relatively larger..... ***Zelomorpha angelsolisi***
Gena longer, eye relatively smaller ..... ***Zelomorpha guanacastensis*** **sp. n.**



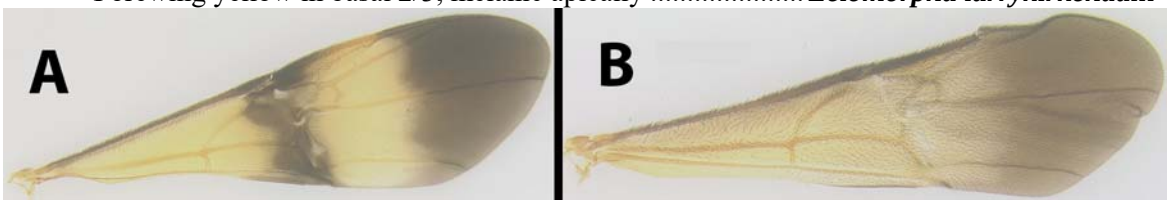
8(5). Mesoscutum and pronotum melanic..... ***Zelomorpha gregaria***
Mesoscutum and pronotum pale (yellow-orange) 9
Mesoscutum pale (yellow-orange), pronotum melanic ..... ***Zelomorpha*** **Sharkey10**



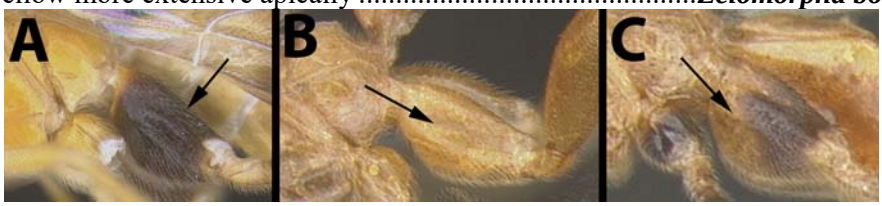
9(8). Median tergite 1 wider basally ..... ***Zelomorpha jeffersoni* sp. n.**
Median tergite 1 narrower basally ..... ***Zelomorpha danjohnsoni***



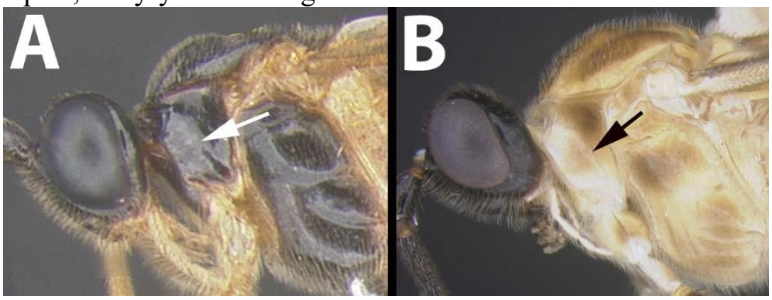
10(5). Forewing banded; yellow, melanic, yellow, melanic 11
Forewing yellow in basal 2/3, melanic apically ..... ***Zelomorpha larrykirkendalli***



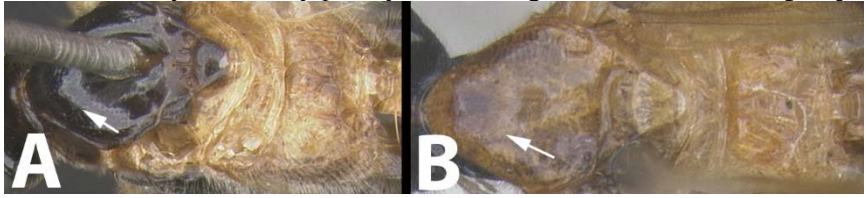
11(10). Hind coxa in lateral view almost entirely melanic or entirely melanic 12
Hind coxa in lateral view entirely or almost entirely yellow to orange..... 19
Hind coxa in lateral view bicolored with an almost even mix of yellow and melanic color, yellow more extensive apically .....***Zelomorpha bobandersoni***



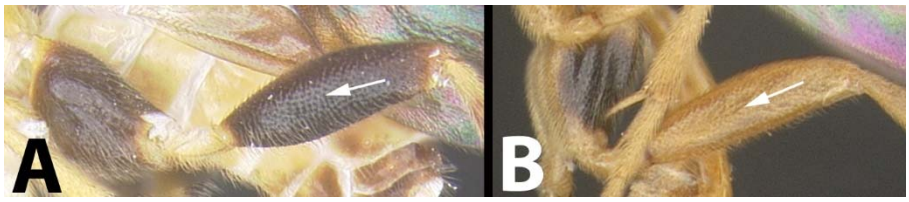
12(11). Pronotum mostly or entirely melanic 13
Pronotum pale, ivory-yellow-orange..... 14



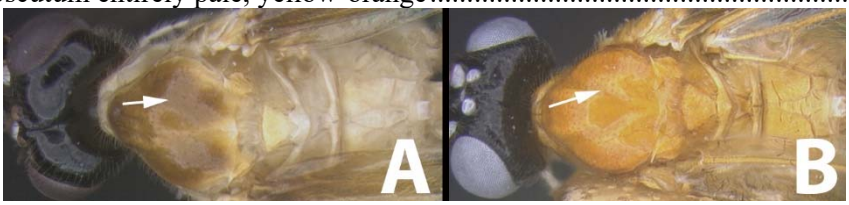
13(12). Mesoscutum mostly or entirely melanic.....***Zelomorpha donwindsori***
Mesoscutum mostly or entirely pale, yellow-orange.....***Zelomorpha johnchemsaki***



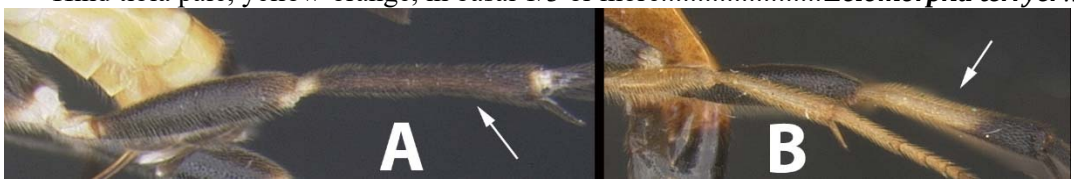
14(12). Hind femur mostly or entirely melanic in lateral view..... 15
Hind femur mostly or entirely pale, yellow-orange, in lateral view..... 18



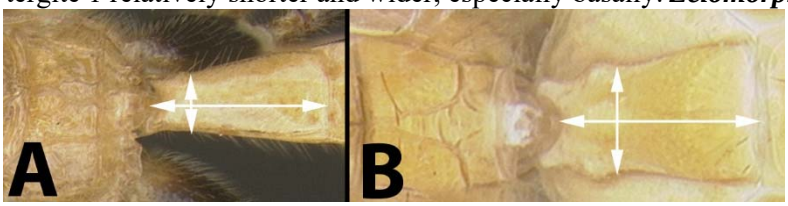
15(14). Mesoscutum partly or entirely melanic 16
Mesoscutum entirely pale, yellow-orange 17



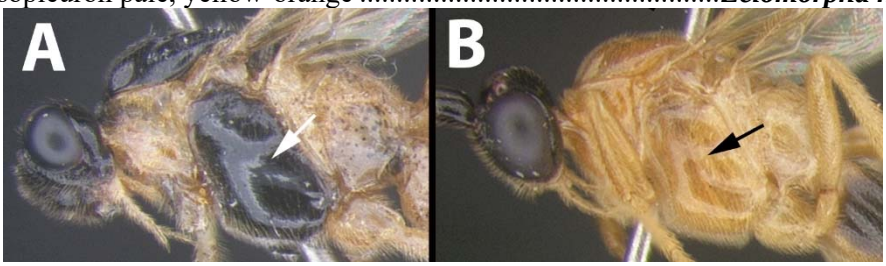
16(15). Hind tibia almost entirely melanic..... ***Zelomorpha effugia***
Hind tibia pale, yellow-orange, in basal 1/3 or more..... ***Zelomorpha terryerwini***



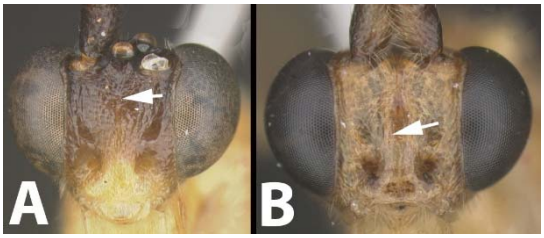
17(15). Median tergite 1 relatively longer and narrower, especially basally ..... ***Zelomorpha paulgoldsteini***
Median tergite 1 relatively shorter and wider, especially basally. ***Zelomorpha kellyanneae***



18(14). Mesopleuron mostly or entirely melanic ..... ***Zelomorpha myricagaleae***
Mesopleuron pale, yellow-orange ..... ***Zelomorpha noahjaneae***



19(11). Face mostly melanic, distinctly darker dorsally ..... ***Zelomorpha mikeiviei***
Face mostly or entirely pale, yellow-orange, not darker dorsally ..... ***Zelomorpha mariyavladmirovnae***



Morphological diagnoses

Zelomorpha Ashmead 1900
Type species. *Zelomorpha arizonensis*, (by monotypy).
Diagnosis. *Zelomorpha* can be distinguished from all other Agathidinae genera by the following combination of morphological characters: fore tarsal claws cleft and not pectinate; foretibial spur shorter than first tarsomere; ovipositor shorter than half the length of the metasoma; frons bordered by carinae; hind trochantellus with one or two longitudinal ridges; notauli variable, usually distinct; gena not produced.
Species diversity. Including the two species described here, there are 69 described species of *Zelomorpha*.

Zelomorpha angelsolisi Meierotto, 2018
Diagnosis: Forewing completely hyaline. Head yellow. Hind coxa in lateral view yellow or orange. Mesosoma pale. Precoxal groove slightly indented, sculptured. Gena shorter, eye relatively larger. Hind tibia pale, less than 10% of length melanic at distal tip. Medial areola of propodeum pentagonal or triangular and complete, i.e., closed.
Material examined In addition to the types listed in Chapter 3: DHJPAR0029181, 93-SRNP-542, 93-SRNP-559, 93-SRNP-603, 99-SRNP-17896, 99-SRNP-17902, DHJPAR0015585, 99-SRNP-18082, DHJPAR0015583, 99-SRNP-18307, 99-SRNP-18315, 05-SRNP-56447, 08-SRNP-12418.

Figure 4.20. Lateral habitus, dorsal view and wings of *Z. angelsolisi* holotype female.

Zelomorpha arizonensis Ashmead, 1900

Diagnosis: Forewing completely hyaline. Head yellow. Hind coxa in lateral view yellow. Mesosoma pale. Hind tibia bicolored, proximally pale and distally melanic with more than 10% of either color. Gena shorter, eye relatively larger. Medial areola of propodeum variable but closed.

Material examined In addition to the specimens listed in Chapter 3: 05-SRNP-56447, 08-SRNP-12418.

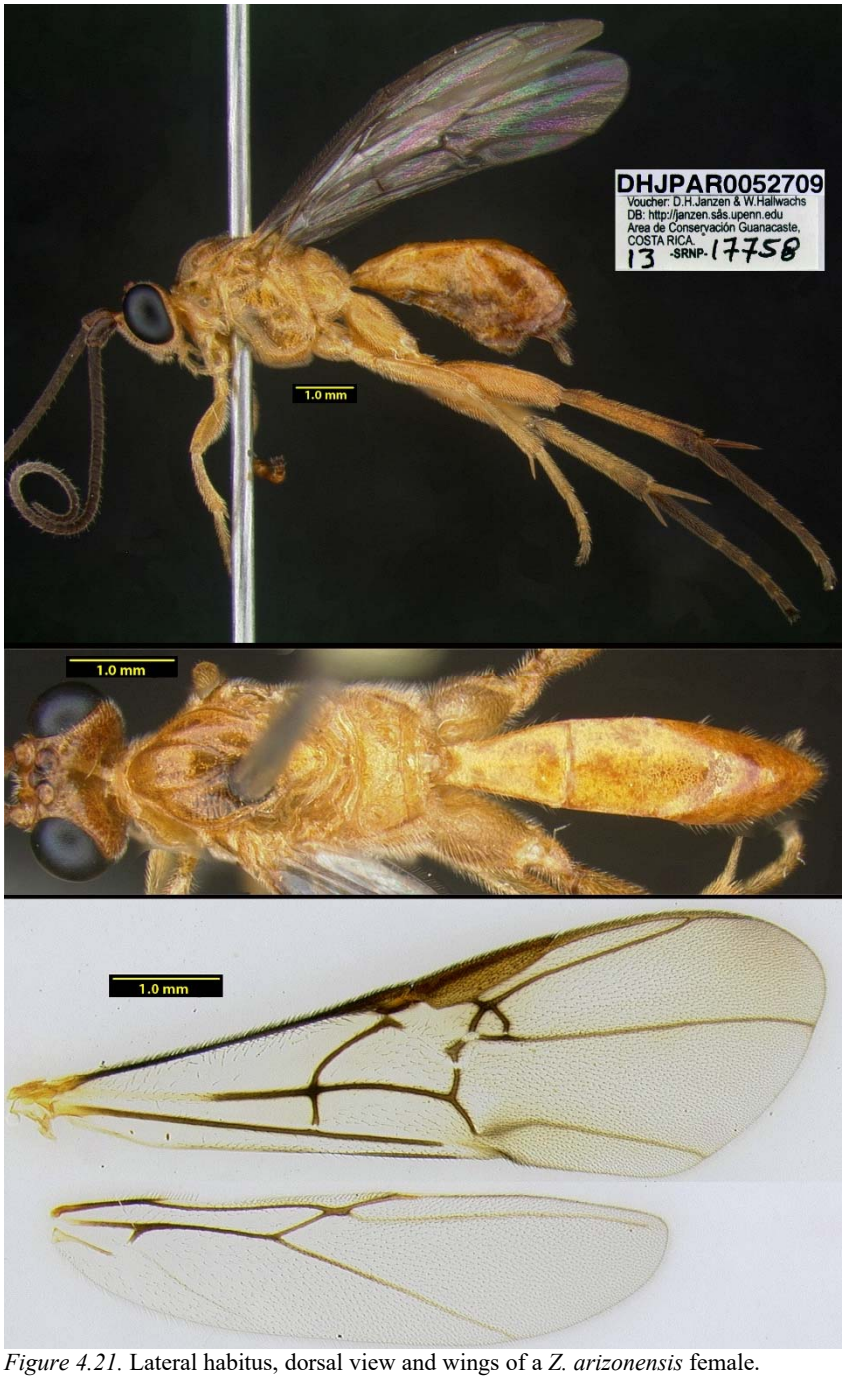


Figure 4.21. Lateral habitus, dorsal view and wings of a *Z. arizonensis* female.

Zelomorpha bobandersoni Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head black. Hind coxa in lateral view bicolored; lighter proximally. Mesosoma multicolored; mostly pale with partially black pronotum. Precoxal groove slightly indented, sculptured. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum triangular and complete.
Material examined In addition to the specimens listed in Chapter 3: DHJPAR0057647, 02-SRNP-6841, 02-SRNP-6946, 02-SRNP-15210, 02-SRNP-7995, 02-SRNP-7998, 03-SRNP-29007.

Figure 4.22. Lateral habitus, dorsal view and wings of *Z. bobandersoni* holotype female.

Zelomorpha danjohnsoni Meierotto, 2018
Diagnosis: Forewing completely infuscate. Head mostly or completely yellow-orange. Hind coxa in lateral view yellow or orange. Hind tibia bicolored, proximally pale and distally melanic with more than 10% of either color. Mesosoma pale. Median tergite 1 relatively narrow. Precoxal groove slightly indented, sculptured. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum variable.
Material examined In addition to the types listed in Chapter 3: DHJPAR0009411.

Figure 4.23. Lateral habitus, dorsal view and wings of *Z. danjohnsoni* holotype female.

Zelomorpha donwindsori Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly or completely black. Hind coxa in lateral view black. Hind tibia bicolored, pale proximally and melanic distally with more than 10% of either color. Mesosoma multicolored; pale with black pronotum, mesonotum, and mesopleuron. Precoxal groove slightly indented, smooth or sculptured. Medial areola of propodeum triangular and complete.
Material examined In addition to the types listed in Chapter 3: none.

Figure 4.24. Lateral habitus, dorsal view and wings of *Z. donwindsori* holotype female.

Zelomorpha effugia Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly or completely black. Hind coxa in lateral view black or brown. Hind tibia mostly or completely melanic, 90% or more. Mesosoma pale, or mostly pale with brown patches. Precoxal groove slightly indented, smooth. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle indented medially, M-shaped. Medial areola of propodeum variable; jagged and irregular or triangular, complete and closed or incomplete.
Material examined In addition to the types listed in Chapter 3: 01-SRNP-24028, 01-SRNP-24028.01, 01-SRNP-24028.02, 01-SRNP-24028.04, 01-SRNP-24028.05, 03-SRNP-8106, 03-SRNP-8671.

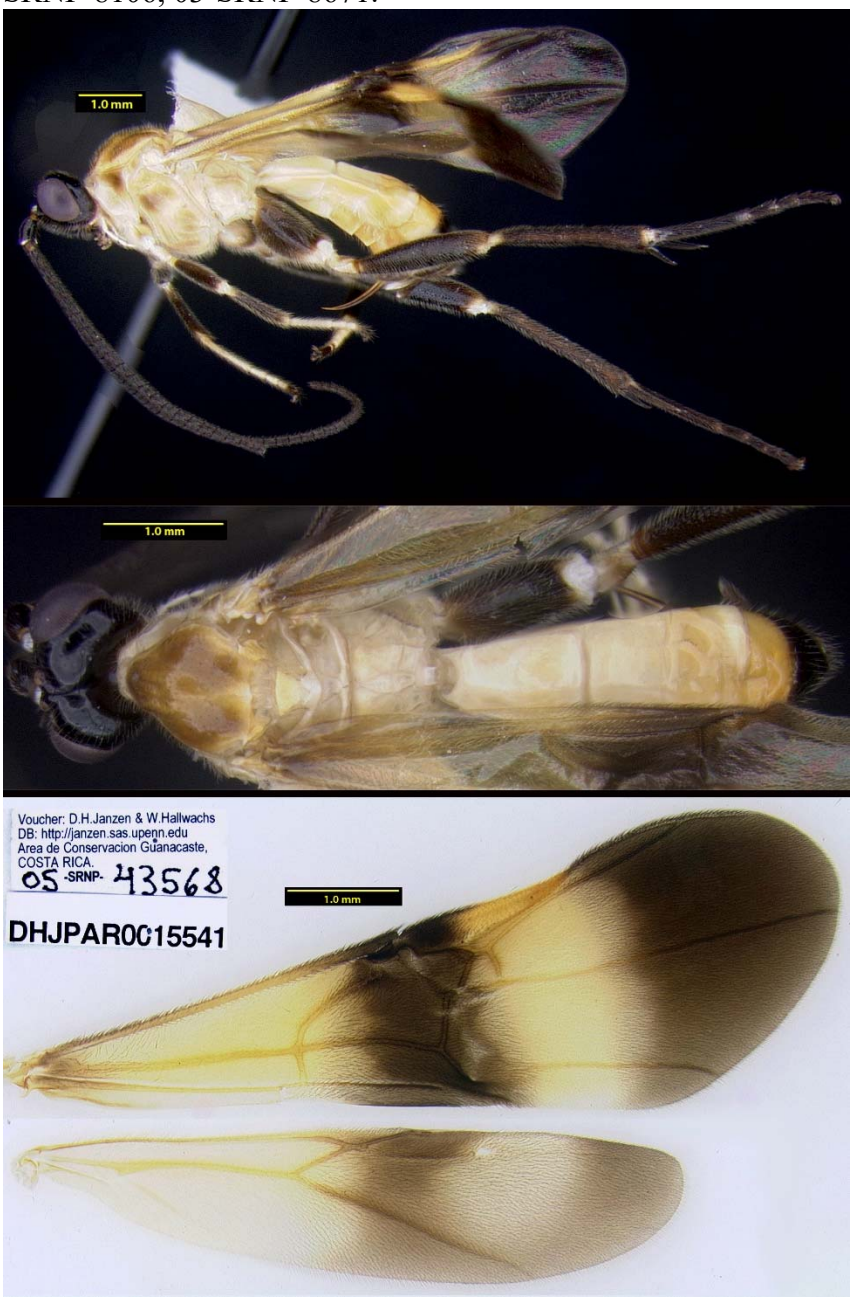


Figure 4.25. Lateral habitus, dorsal view and wings of *Z. effugia* holotype female.

Zelomorpha gregaria (Sarmiento & Sharkey, 2004)
Diagnosis: Forewing completely infuscate. Head black. Hind coxa in lateral view black. Mesosoma melanic, somewhat lighter propodeum. Precoxal groove absent. Posterior surface of scutellar triangle sculptured. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum triangular, complete.
Biology: This is the only known gregarious species of Agathidinae, meaning multiple conspecific individuals develop within the same host caterpillar. It has been reared from two unidentified species of *Euglyphis* (Lasiocampidae) and *Euglyphis deusta*, all feeding on Lauraceae: *Beilschmiedia costaricensis*, *Ocotea mollifolia*, and *Nectandra hihua*.
Material examined: Holotype ♀: 99-SRNP-1161, Costa Rica, Área de Conservación Guanacaste, Sector Cacao, 10.92691 N, 85.46822 W, 1150m elevation, Mariano Pereira coll., reared from *Euglyphis* sp., host collected 15 July 1999, wasp eclosed 22 August 1999, (INBIO). 14 additional specimens reared from 99-SRNP-1161. 04-SRNP-3526, 04-SRNP-3528, 04-SRNP-3597, 99-SRNP-4860.
Etymology: This species was named for its unusual gregarious development.

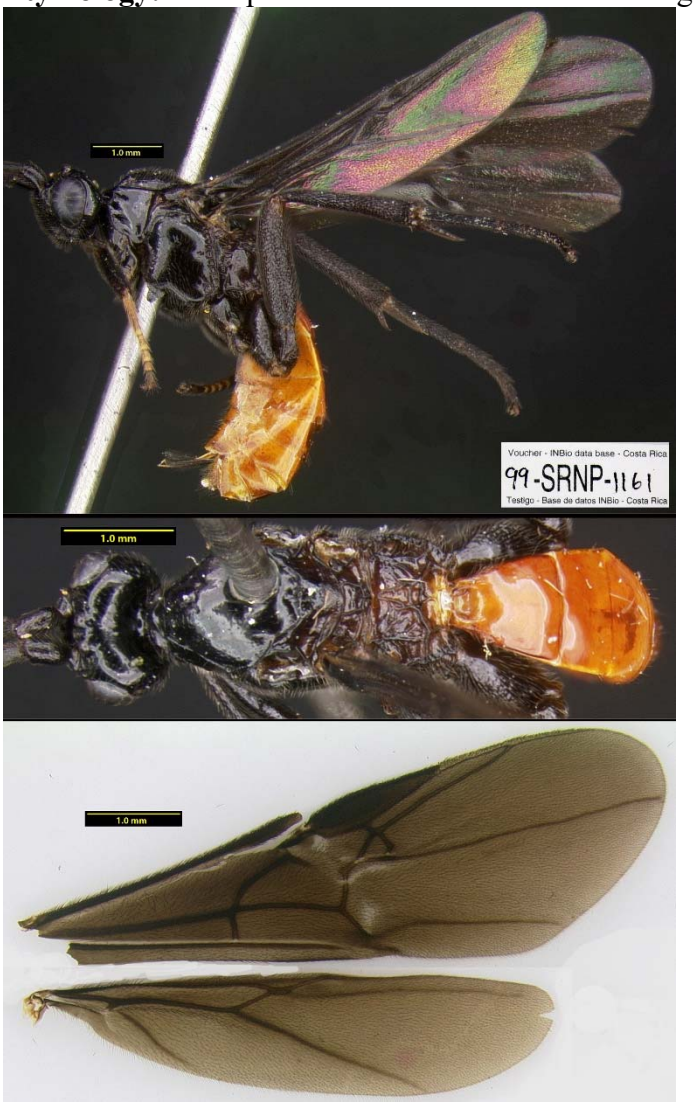


Figure 4.26. Lateral habitus, dorsal view and wings of a *Z. gregaria* female.

Zelomorpha guanacastensis Meierotto, sp. n.
Diagnosis: Forewing completely hyaline. Head yellow. Hind coxa in lateral view yellow. Mesosoma pale. Precoxal groove slightly indented, sculptured. Hind tibia pale, less than 10% of length melanic at distal tip. Gena longer, eye relatively smaller. Medial areola of propodeum pentagonal or triangular, and complete.
Biology: This species has been reared from unidentified species of Noctuidae feeding on *Baltimora recta* (Asteraceae).
Material examined: Holotype ♀: 94-SRNP-9228, Costa Rica, Área de Conservación Guanacaste, Sector Marino, 10.85928 N, 85.91422 W, 50m elevation, gusaneros coll., host collected 17 October 1994, wasp ecolsed 10 November 1994 (EMUS).
Etymology: *Zelomorpha guanacastensis* is named in honor of the type locality.

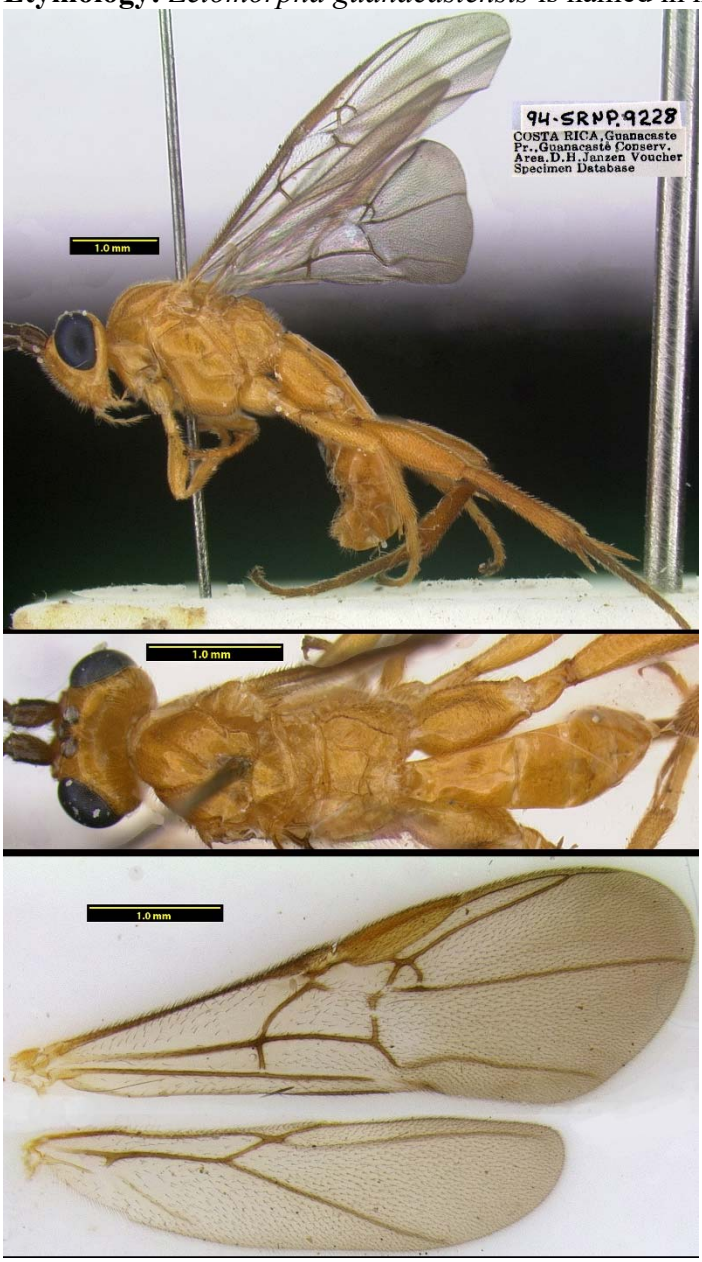


Figure 4.27. Lateral habitus, dorsal view and wings of *Z. guanacastensis* holotype female.

Zelomorpha jeffersoni Meierotto, sp. n.
Diagnosis: Forewing completely infuscate. Head yellow. Hind coxa in lateral view yellow or orange. Hind tibia bicolored, proximally pale and distally melanic with more than 10% of either color. Mesosoma pale. Median tergite 1 relatively wide. Precoxal groove slightly indented, sculptured. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum triangular and complete.
Biology. Reared from *Ogdoconta* Poole02 (Noctuidae) on *Verbesina gigantean* (Asteraceae).
Material examined: Holotype ♀: 98-SRNP-10228, Costa Rica, Área de Conservación Guanacaste, Sector Santa Rosa, 10.85827 N, 85.61089 W, 280m elevation, Guillermo Pereira coll., reared from *Ogdoconta* Poole02, host collected 21 July 1998, wasp eclosed 9 August 1998, (EMUS).
Notes. Known from 1 specimen, damaged: missing antennae, middle legs, and protibia.
Etymology. *Zelomorpha jeffersoni* is named in honor of Jefferson Giraldo (RIP), dear friend of SLM.

Figure 4.28. Lateral habitus, dorsal view and wings of *Z. jeffersoni* holotype female.

Zelomorpha johnchemsaki Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head black. Hind coxa in lateral view mostly black. Hind tibia mostly or completely melanic, 90% or more. Mesosoma multicolored; mostly pale with black pronotum. Precoxal groove slightly indented, smooth. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum triangular and complete.
Material examined In addition to the types listed in Chapter 3: 09-SRNP-71556, 09-SRNP-71559, 09-SRNP-71561, DHJPAR0022194, DHJPAR0023295, DHJPAR0036324.

Figure 4.29. Lateral habitus, dorsal view and wings of *Z. johnchemsaki* holotype female.

Zelomorpha kellyanneae Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly or completely black. Hind coxa in lateral view black or brown. Hind tibia mostly melanic, or bicolored, lighter. Mesosoma pale. Propodeal carina reduced, posterior medial and lateral areolae largely fused. Precoxal groove slightly indented, smooth. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum triangular and complete.
Material examined In addition to the types listed in Chapter 3: DHJPAR0015534.

Figure 4.30. Lateral habitus, dorsal view and wings of *Z. kellyanneae* holotype female.

Zelomorpha larrykirkendalli Meierotto, 2018
Diagnosis: Forewing hyaline with infuscate apical band; hyaline areas with yellow color. Antennae, hind tarsi, and distal tip of hind tibia dark brown; remainder of body yellow. Medial areola of propodeum pentagonal and complete, i.e., closed.
Material examined In addition to the types listed in Chapter 3: DHJPAR0053605.

Figure 4.31. Lateral habitus, dorsal view and wings of *Z. larrykirkendalli* holotype female.

Zelomorpha mariyavladmirovnae Meierotto, 2018

Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly yellow. Hind coxa in lateral view yellow. Hind tibia bicolored, proximally pale and distally melanic. Mesosoma pale. Medial areola of propodeum triangular and complete.

Material examined In addition to the types listed in Chapter 3: none.

Figure 4.32. Lateral habitus, dorsal view and wings of *Z. mariyavladmirovnae* holotype female.

Zelomorpha mikeiviei Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly black or bicolored, melanic dorsally, pale ventrally. Hind coxa in lateral view yellow. Hind tibia bicolored, pale and melanic with more than 10% of either color. Mesosoma pale. Lacking concave groove present between antennae extending to dorsal 1/3 of face. Medial areola of propodeum jagged and irregular or pentagonal, complete.
Material examined In addition to the types listed in Chapter 3: DHJPAR0058546.

Figure 4.33. Lateral habitus, dorsal view and wings of *Z. mikeiviei* holotype female.

Zelomorpha myricagaleae Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head black. Hind coxa in lateral view yellow or orange. Mesosoma multicolored; mostly pale, with black mesopleuron and mesonotum. Medial areola of propodeum triangular and complete.
Material examined In addition to the types listed in Chapter 3: none.

Figure 4.34. Lateral habitus, dorsal view and wings of *Z. myricagaleae* holotype female.

Zelomorpha noahjaneae Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head mostly or completely black. Hind coxa in lateral view mostly black. Hind tibia bicolored, pale apically and melanic distally with more than 10% of either color. Mesosoma pale. Propodeal carina strong, posterior medial and lateral areolae clearly separated. Precoxal groove slightly indented, smooth or sculptured. Medial areola of propodeum triangular and complete.
Material examined In addition to the types listed in Chapter 3: DHJPAR0028239, DHJPAR0028240.

Figure 4.35. Lateral habitus, dorsal view and wings of *Z. noahjaneae* holotype female.

Zelomorpha paulgoldsteini Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head black. Hind coxa in lateral view black or brown. Hind tibia bicolored, pale proximally and melanic distally with more than 10% of either color. Mesosoma pale. Precoxal groove slightly indented, sculptured. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum jagged and irregular or pentagonal, complete.
Material examined In addition to the types listed in Chapter 3: DHJPAR0028300, DHJPAR0052696, 04-SRNP-3921, 02-SRNP-6055.

Figure 4.36. Lateral habitus, dorsal view and wings of *Z. paulgoldsteini* holotype female.

Zelomorpha terryerwini Meierotto, 2018

Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head bicolored, melanic dorsally, pale ventrally. Hind coxa in lateral view black or brown. Mesosoma multicolored; mostly pale with black mesonotum. Medial areola of propodeum pentagonal and complete.

Material examined In addition to the types listed in Chapter 3: DHJPAR0036329, DHJPAR0016427, DHJPAR0009410, 94-SRNP-3517, 94-SRNP-3518, 92-SRNP-3888, 04-SRNP-42305, 10-SRNP-12945, 10-SRNP-12946, 10-SRNP-12947, 94-SRNP-9332, 81-SRNP-750, 03-SRNP-15598.

Figure 4.37. Lateral habitus, dorsal view and wings of *Z. terryerwini* holotype female.

Zelomorpha willsflowersi Meierotto

Diagnosis: Forewing banded; yellow, melanic, yellow, melanic. Head bicolored, melanic dorsally, pale ventrally. Hind coxa in lateral view yellow. Hind tibia bicolored, pale apically and melanic distally with more than 10% of either color. Mesosoma pale. Concave groove present between antennae extending to dorsal 1/3 of face. Medial areola of propodeum pentagonal or triangular, and complete.

Material examined In addition to the types listed in Chapter 3: DHJPAR0010195, DHJPAR0010192, DHJPAR0010193, 00-SRNP-8403, 91-SRNP-670, 00-SRNP-8334, 00-SRNP-8392, 00-SRNP-8396, 00-SRNP-8400, 05-SRNP-21919, 91-SRNP-185.13, 94-SRNP-1394, 96-SRNP-1322, 96-SRNP-1323, 96-SRNP-1729, 96-SRNP-1731, 96-SRNP-1734, 96-SRNP-1736, 96-SRNP-1741, 96-SRNP-1743, 96-SRNP-1744, 96-SRNP-1745, 96-SRNP-1746, 96-SRNP-1747, 96-SRNP-1783, 96-SRNP-1784, 96-SRNP-1787, 96-SRNP-1791, 96-SRNP-1793, 96-SRNP-1794, 96-SRNP-1797, 96-SRNP-1798, 96-SRNP-1799, 96-SRNP-1800, 96-SRNP-1805, 96-SRNP-1806, 96-SRNP-1828, 96-SRNP-1831, 96-SRNP-1832, 96-SRNP-1833, 96-SRNP-2023, 96-SRNP-2024, 96-SRNP-2025, 96-SRNP-2027, 94-SRNP-9681, 99-SRNP-17756, 01-SRNP-11575, 01-SRNP-11585, 01-SRNP-11890.

Figure 4.38. Lateral habitus, dorsal view and wings of *Z. willsflowersi* holotype female.

***Zelomorpha* Sharkey10**

Diagnosis: Forewing completely infuscate. Head black. Hind coxa in lateral view black or brown. Mesosoma multicolored: mostly orange with black pronotum and some brown carinae. Precoxal groove slightly indented, sculptured. Posterior surface of scutellar triangle sculptured. Posterior transverse ridge of scutellar triangle not indented medially, not M-shaped. Medial areola of propodeum pentagonal and complete.

Material examined: ♀: 00-SRNP-15467, Costa Rica, Área de Conservación Guanacaste.

Notes. Known from one specimen. Rearing record is questionable: specimen is identified to Microgastrinae in BOLD and Janzen databases.

Figure 4.39. Lateral habitus, dorsal view and wings of a *Z.* Sharkey10 female.

Hemichoma Enderlein, 1920
Type species. *Hemichoma fenestratum* Enderlein, 1920
Diagnosis. *Hemichoma* shares diagnostic morphological characters with *Zelomorpha* except: notauli absent, mesoscutum lacking distinct lobes; gena greatly produced posteroventrally.
Species diversity. There are eight described species of *Hemichoma*.

Hemichoma donwhiteheadi Meierotto, 2018
Diagnosis: Forewing banded yellow and melanic. Median tergite 1 relatively narrow. Head black. Hind coxa in lateral view black or dark brown. Mesosoma multicolored: mostly yellow with pronotum melanic. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle indented medially, M-shaped. Medial areola of propodeum pentagonal or triangular and complete, i.e., closed. Males differ as follows: Forewing entirely infuscate or infuscate with clear areas, lacking yellow color. Mesosoma melanic.
Material examined In addition to the types listed in Chapter 3: 04-SRNP-3791.

Figure 4.40. Lateral habitus of *H. donwhiteheadi* male.

Figure 4.41. Lateral habitus, dorsal view and wings of *H. donwhiteheadi* holotype female.

Hemichoma frankhovorei Meierotto, 2018

Diagnosis: Forewing entirely infuscate, infuscate with hyaline patches, or hyaline with infuscate apical band. Forewing hyaline areas lacking yellow color. Median tergite 1 relatively wide. Head black. Hind coxa in lateral view black. Mesosoma melanic, yellow-orange, or multicolored. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle indented medially, M-shaped. Medial areola of propodeum pentagonal and complete.

Material examined In addition to the types listed in Chapter 3: DHJPAR0006774, DHJPAR0015562, DHJPAR0028245, DHJPAR0028241, DHJPAR0028251, DHJPAR0015561, DHJPAR0028265, DHJPAR0028253, DHJPAR0029303, DHJPAR0028250, DHJPAR0028266, DHJPAR0028262, DHJPAR0028261, DHJPAR0028259, DHJPAR0028246, DHJPAR0041157, DHJPAR0041154, DHJPAR0041158, DHJPAR0041155, 81-SRNP-140, 81-SRNP-142, 81-SRNP-143, 03-SRNP-27233, 88-SRNP-526, 89-SRNP-419.

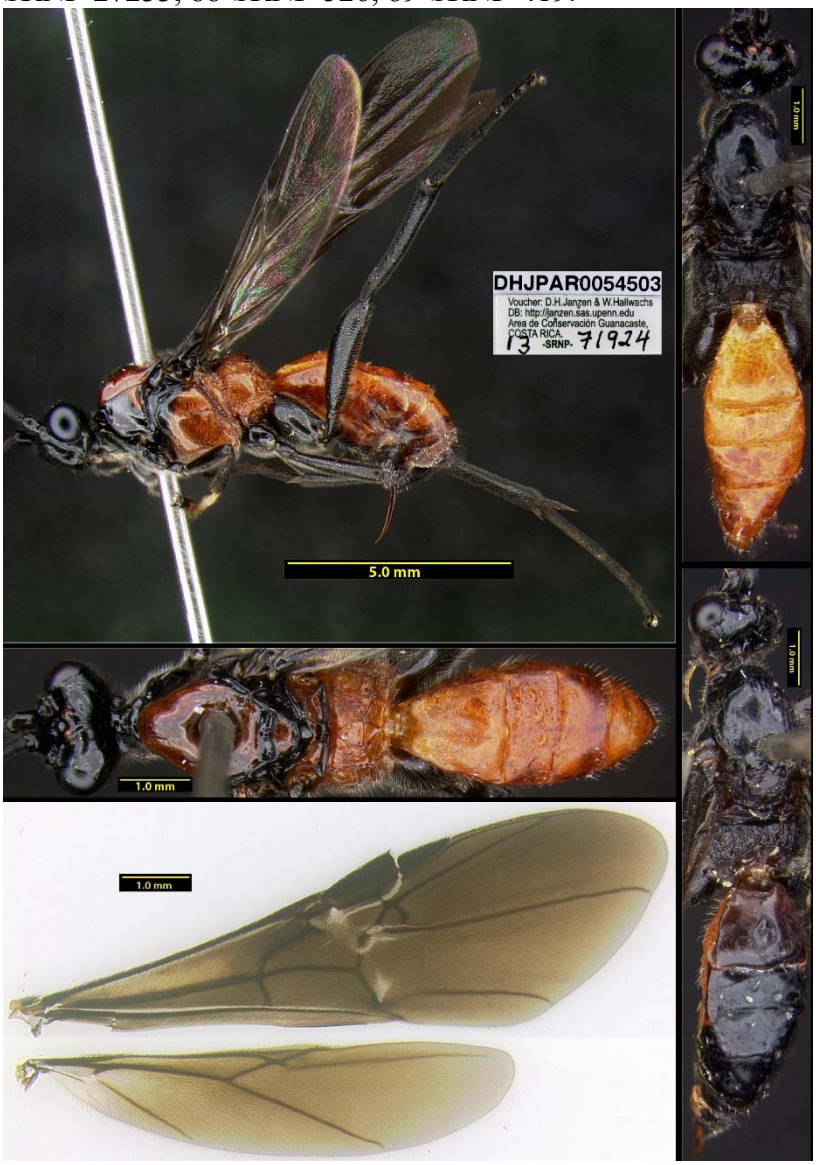


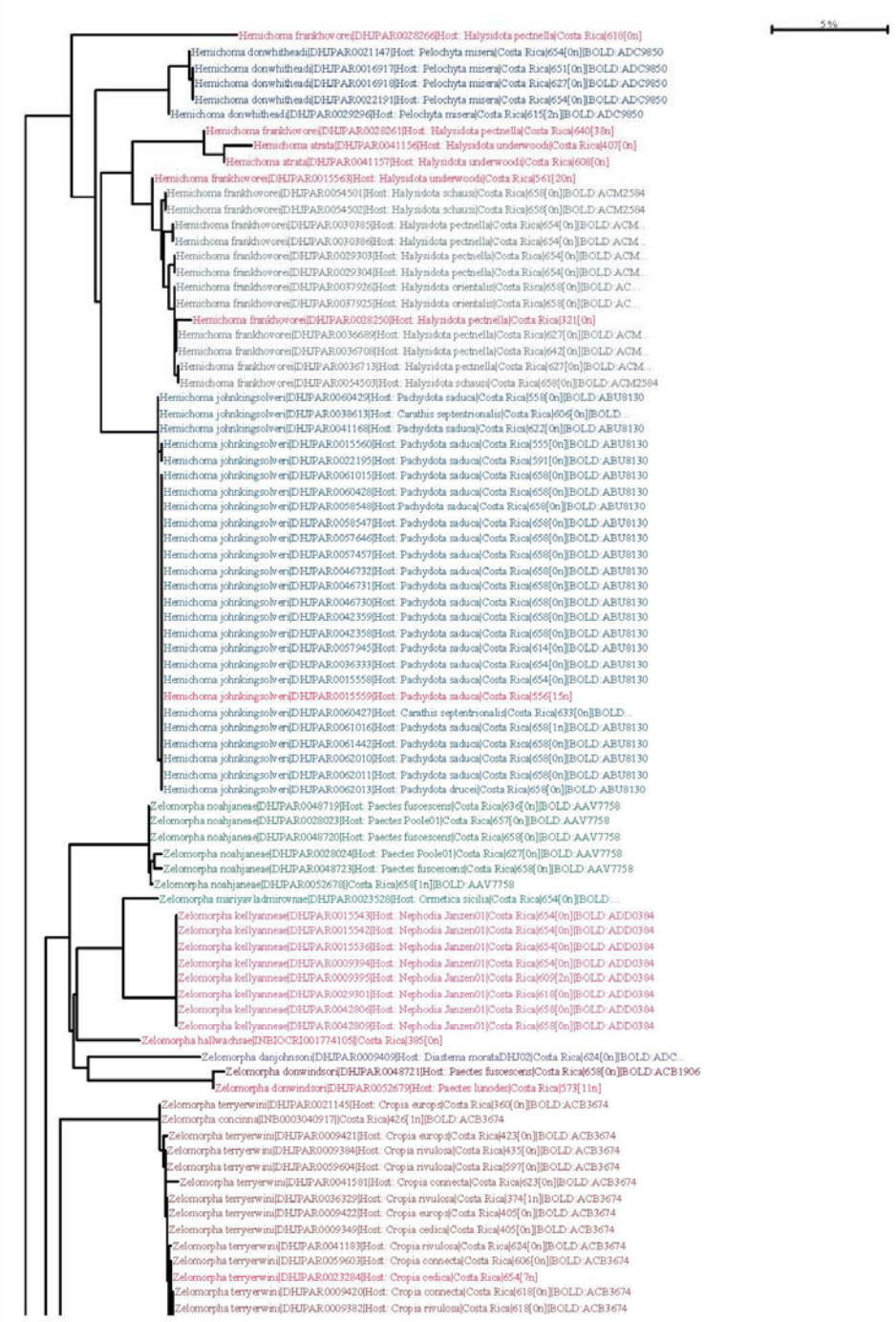
Figure 4.42. Lateral habitus, dorsal view and wings of *H. frankhovorei* holotype female. Dorsal views on right side show variation.

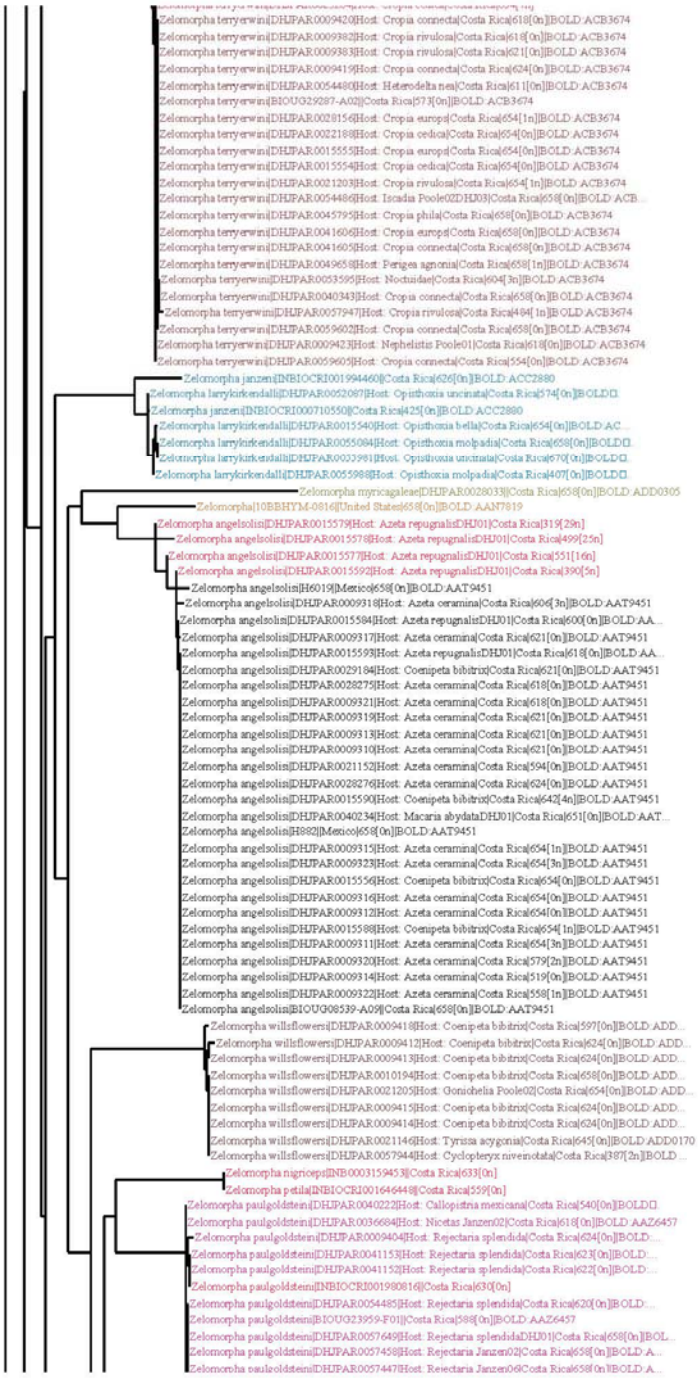
Hemichoma johnkingsolveri Meierotto, 2018
Diagnosis: Forewing banded; yellow, melanic. Head black. Hind coxa in lateral view bicolored. Mesosoma multicolored, mostly yellow with pronotum melanic, a few with mesosoma completely melanic. Posterior surface of scutellar triangle smooth. Posterior transverse ridge of scutellar triangle indented medially, M-shaped. Medial areola of propodeum pentagonal or triangular and complete.
Material examined In addition to the types listed in Chapter 3: 02-SRNP-34065, 04-SRNP-41599, DHJPAR0015566, DHJPAR0015565, DHJPAR0015564, DHJPAR0015557, 04-SRNP-4025, DHJPAR0058549, 03-SRNP-31087.

Figure 4.43. Lateral habitus, dorsal view and wings of *H. johnkingsolveri* holotype female.

Appendix 1. Neighbor joining tree with host and BIN information.

Tree generated in BOLD by searching for all specimens identified as *Zelomorpha* and *Hemichoma* on June 9th 2018, 474 specimen records found, 326 with sequence data. The Kimura 2 Parameter distance model was selected, and tree is colored by BIN assignment. Nodes are labeled by species, specimen number, associated taxa (host), country, sequence length, and BIN number.

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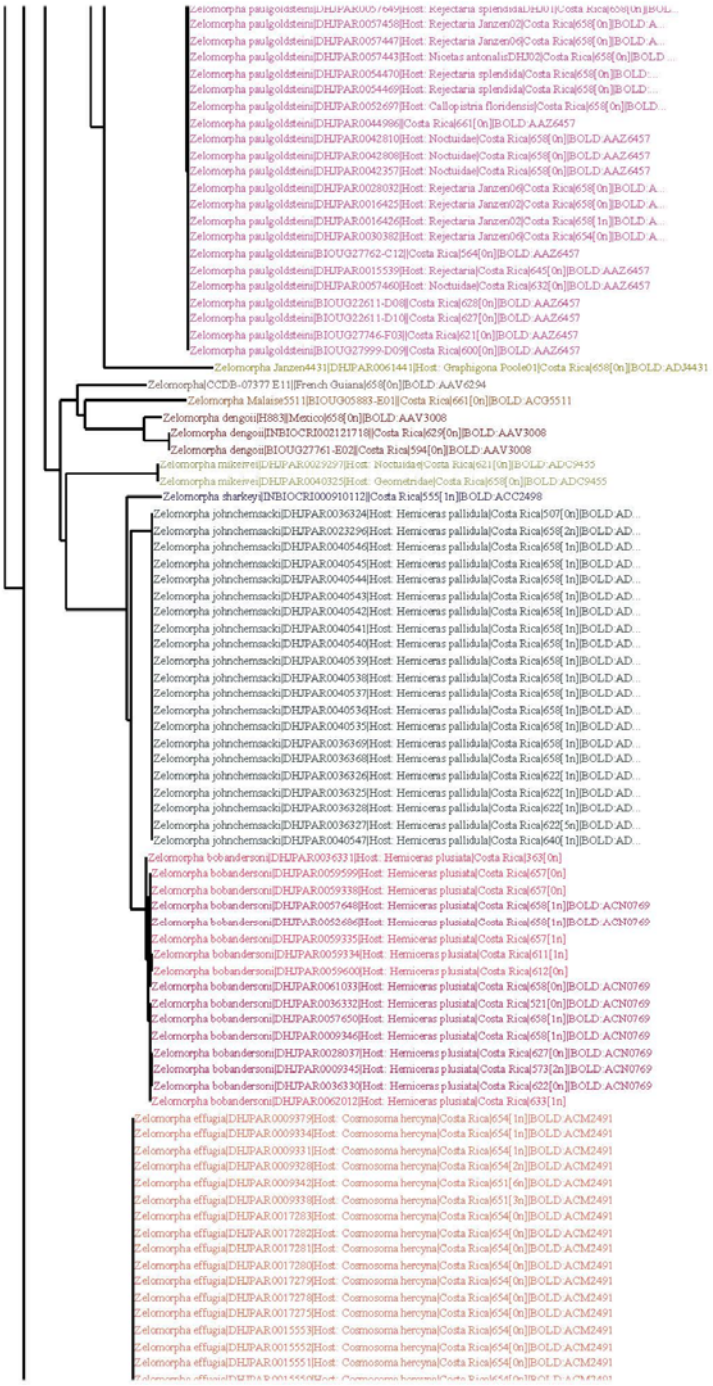
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Zelomorpha paulgoldsteini[BIOUG22611-D08]|Costa Rica[628[0n]]BOLD:AAZ6457
Zelomorpha paulgoldsteini[BIOUG22611-D10]|Costa Rica[627[0n]]BOLD:AAZ6457
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Zelomorpha paulgoldsteini[BIOUG27999-D09]|Costa Rica[600[0n]]BOLD:AAZ6457
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Zelomorpha dengoii|H883|Mexico|658[0n]|BOLD:AAV3008
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Zelomorpha dengoii|BIOUG27761-E02|Costa Rica[594[0n]]BOLD:AAV3008
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Zelomorpha bobandersoni[DHJPAR0059338]Host: Hemiceras plusiata]Costa Rica[657[0n]
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Zelomorpha bobandersoni[DHJPAR0059600]Host: Hemiceras plusiata]Costa Rica[612[0n]
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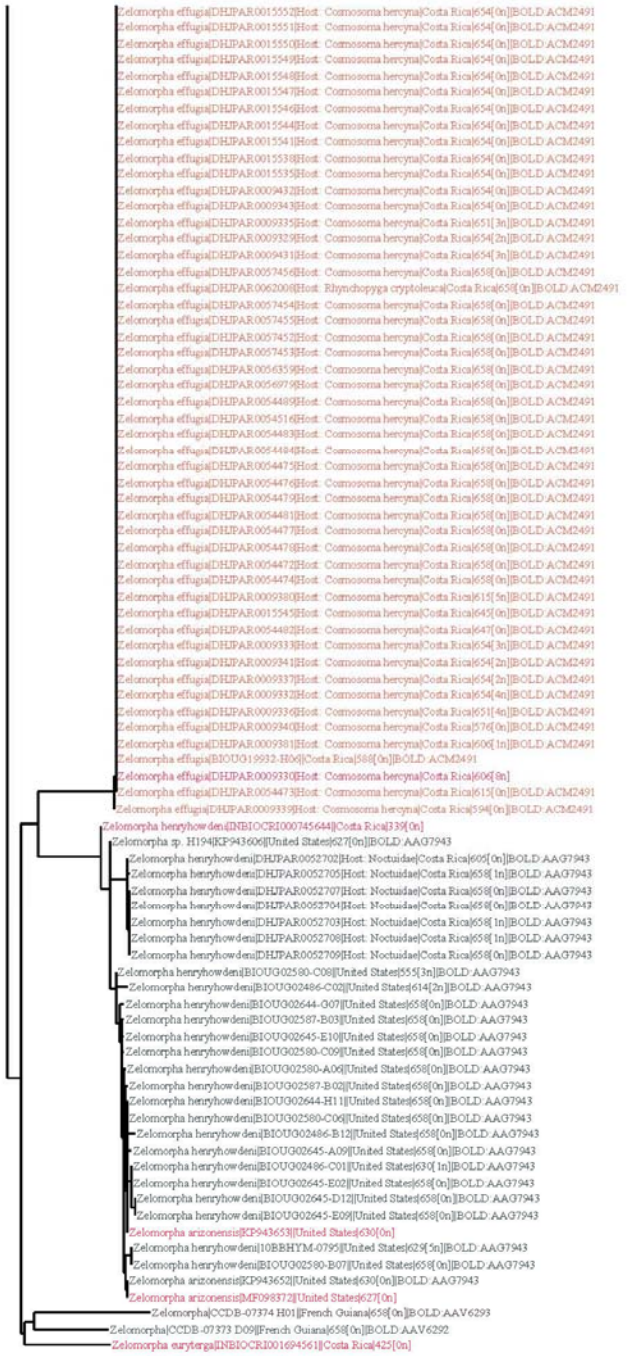
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Zelomorpha henryhowdeni[DHJPAR0052703|Host: Noctuidae|Costa Rica|658[1n]|BOLD:AAG7943
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Zelomorpha henryhowdeni[DHJPAR0052709|Host: Noctuidae|Costa Rica|658[0n]|BOLD:AAG7943
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Zelomorpha arizonensis|MF098372|United States|627[0n]
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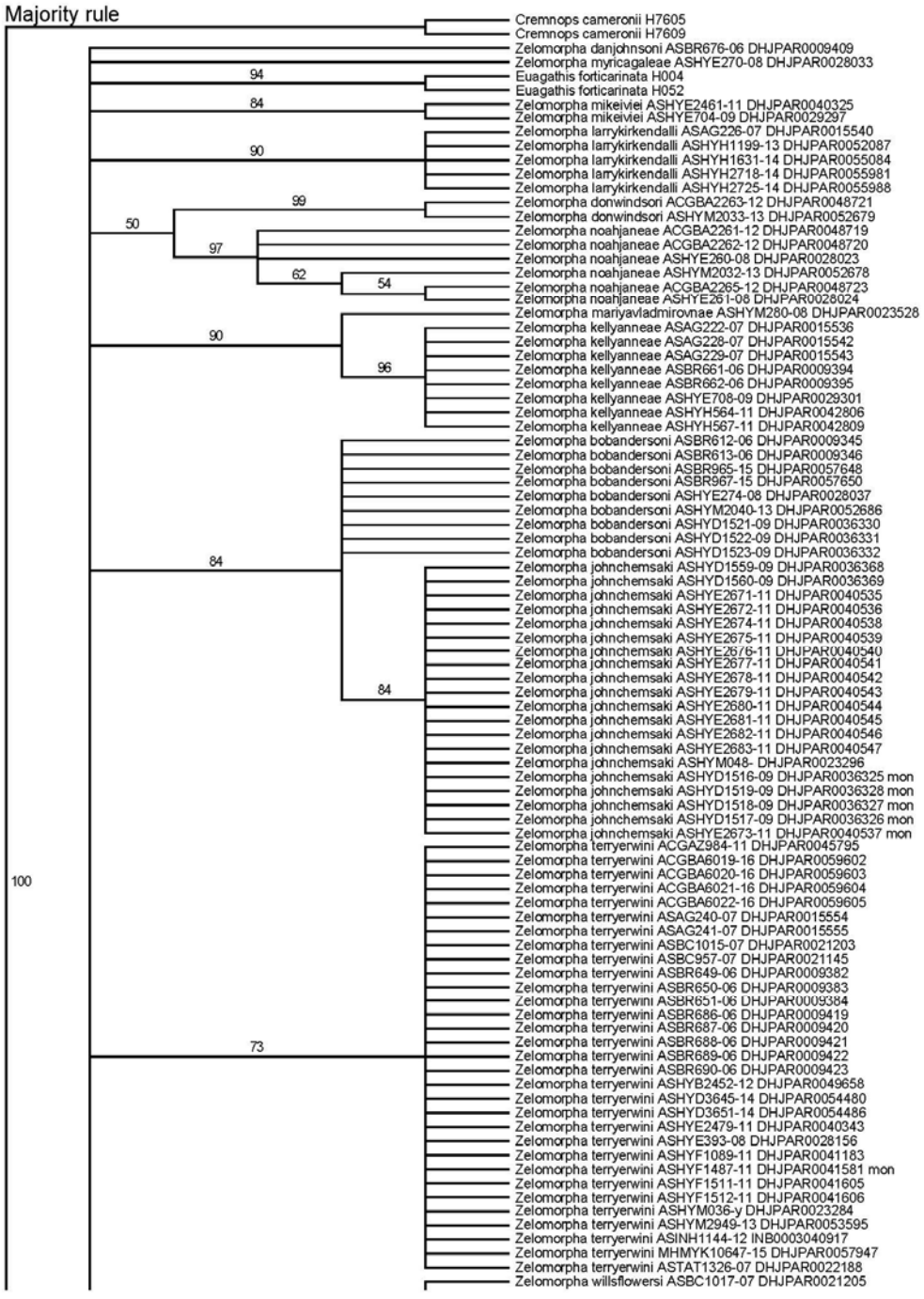
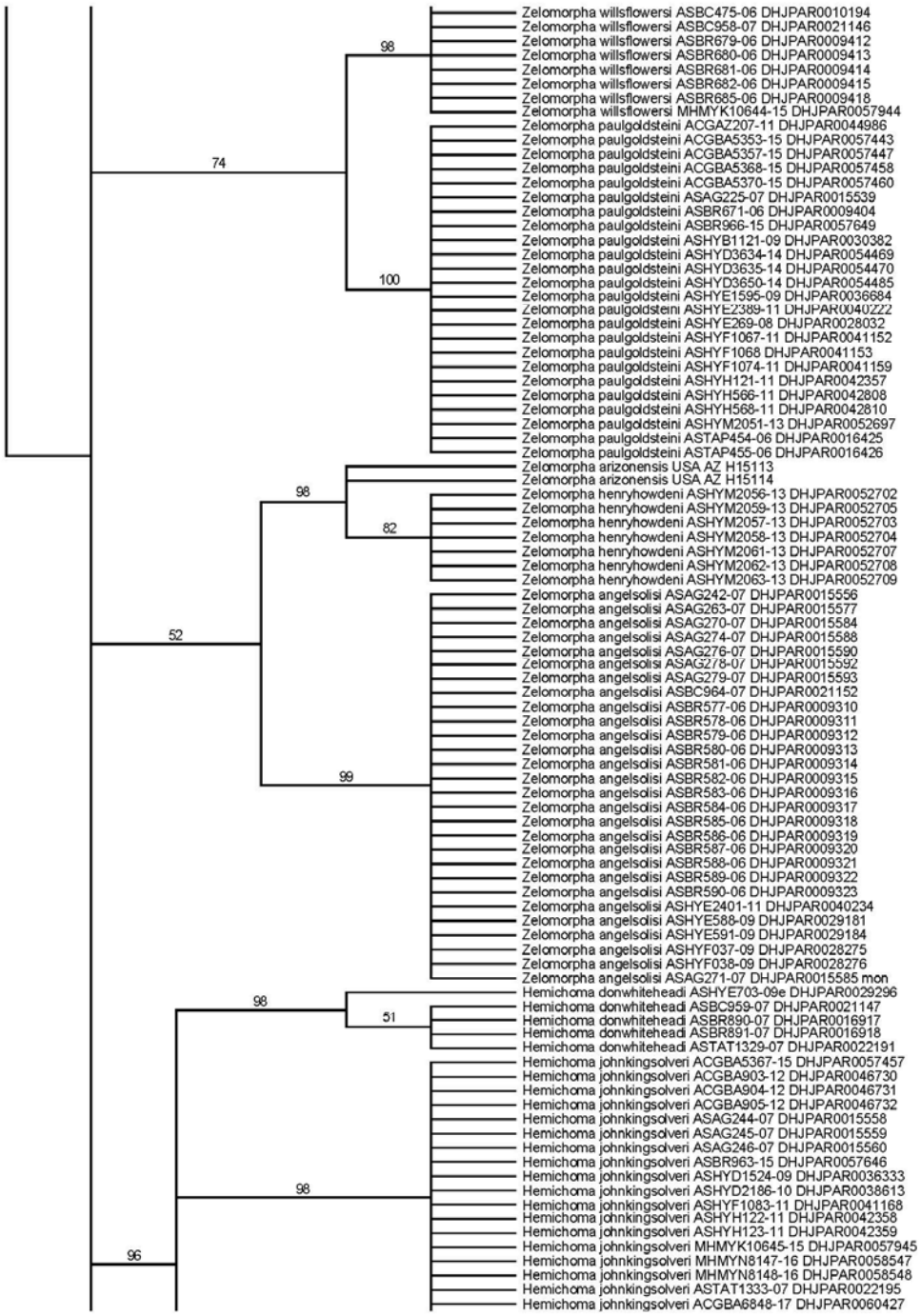
Appendix 2. 200 rep ML bootstrap majority rule tree**.**

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Zelomorpha willsflowersi MHMYK10644-15 DHJPAR0057944
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Zelomorpha arizonensis USA AZ H15114
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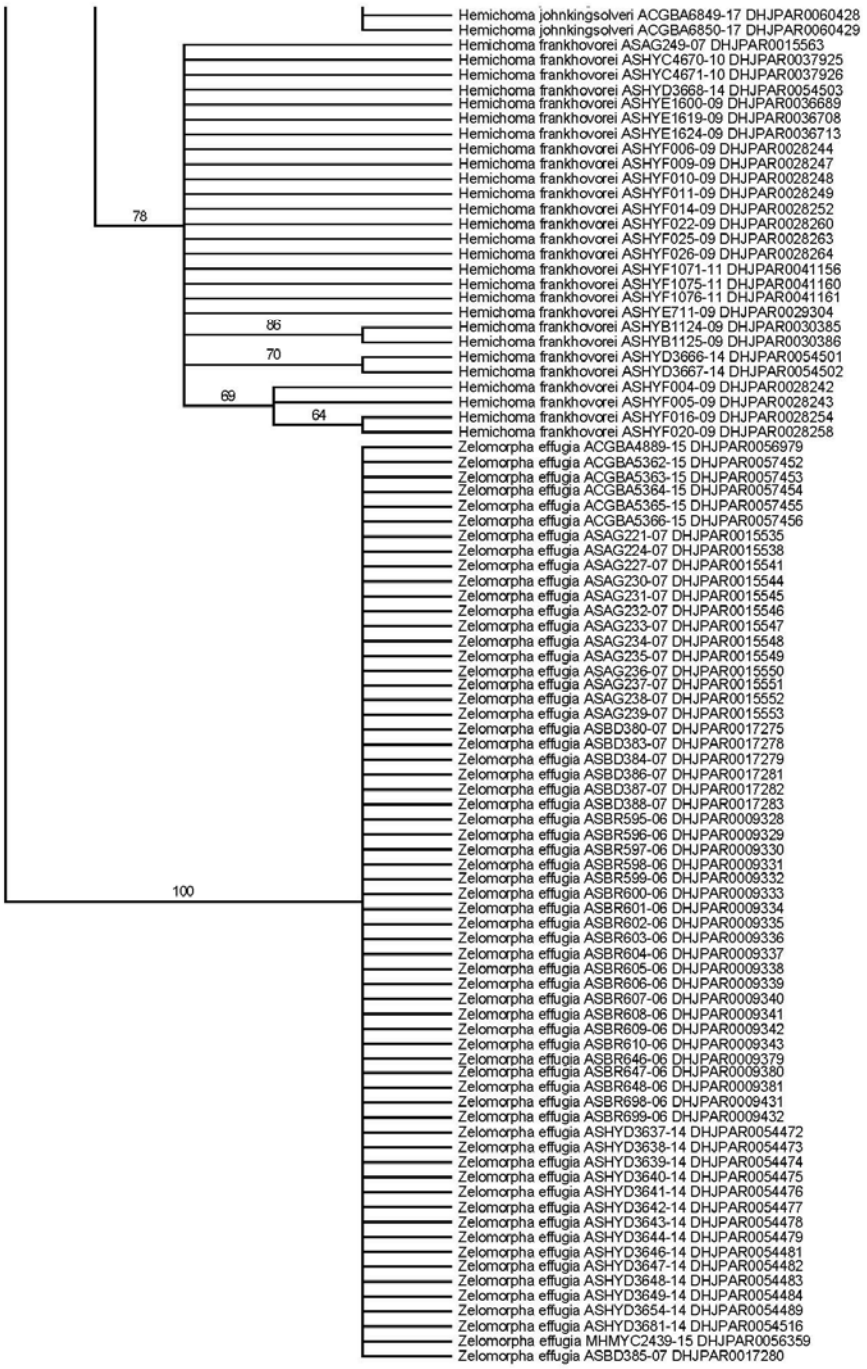
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Toolik Field Station, Alaska

Entomology Field Technician April - August 2012
Coffman Cove, Prince of Wales Island, Alaska

Entomology Lab Technician April - August 2011
University of Alaska Museum Insect Collection, Fairbanks, Alaska

Scholastic and Professional Honors

2nd place, Linnaean Games, North Central Branch meeting of the ESA. 2018.

1st place, Triplehorn Challenge, North Central Branch meeting of the ESA. 2018.

1st place, Master's student poster competition, North Central Branch meeting of the ESA. 2017.

National Science Foundation: East Asia and Pacific Summer Institute for US graduate students (EAPSI). 2016.

University of Alaska, Fairbanks, Entomology Book Award. 2011.

University of Alaska Scholars Award. 2009.

Chancellor's Award from University of Alaska, Fairbanks. 2009.

University of Alaska Athletic scholarship. 2009-2013.

John Kelly Scholarship for Alaskan students. 2009.

Professional publications

Meierotto S, Sharkey MJ, Janzen DJ, Hallwachs W, Smith MA. (in press). Barcode based descriptions of Zelomorpha Ashmead and Hemichoma Enderlein (Hymenoptera, Braconidae, Agathidinae) species from the Area de Conservación Guanacaste, Costa Rica.

Sharkey MJ, Meierotto S, Chapman EG, Janzen DJ, Hallwachs W, Dapkey T, Alma Solis M. 2018. Alabagrus Enderlein (Hymenoptera, Braconidae, Agathidinae) species of Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. *Contributions in Science*. 526: 31-180.

Sikes, D. S., Bowser, M., Daly, K., Høye, T., Meierotto, S., Mullen, L., Slowik, J., Stockbridge, J. 2017. The value of museums in the production, sharing, and use of entomological data to document hyperdiversity of the changing North. *Arctic Science.* 3(3): 498-514.

Sikes, D. S., Bowser, M., Morton, J. M., Bickford, C., Meierotto, S., Hildebrandt, K. 2016. Building a DNA barcode library of Alaska's non-marine arthropods. *Genome*. 60.3: 248-259. doi:10.1139/gen-2015-0203