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**A NEW SPECIES OF ANT-MIMICKING SAC SPIDER CASTIANEIRA REISKINDI (ARANEAE: CORINNIDAE: CASTIANEIRINAE) FROM NICARAGUA AND A PHYLOGENETIC ANALYSIS OF THE AUSTRALIAN CASTIANEIRINAE.**

Matthew P. Leister

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Matthew Leister

*Candidate*

Biology

*Department*

This thesis is approved, and it is acceptable in quality and form for publication:

*Approved by the Thesis Committee:*

Kelly Miller, Chairperson

Sandra Brantley

Robert Raven

Christopher Witt

**A NEW SPECIES OF ANT-MIMICKING SAC SPIDER  
*CASTIANEIRA REISKINDI* (ARANEAE: CORINNIDAE:  
CASTIANEIRINAE) FROM NICARAGUA AND A  
PHYLOGENETIC ANALYSIS OF THE AUSTRALIAN  
CASTIANEIRINAE.**

**by**

**MATTHEW LEISTER**

**BACHELORS OR SCIENCE IN BIOLOGY, UNIVERSITY OF  
NEW MEXICO 2015, MAGNA CUM LAUDE**

**THESIS**

Submitted in Partial Fulfillment of the  
Requirements for the Degree of

**Master of Science in  
Biology**

The University of New Mexico  
Albuquerque, New Mexico

**May, 2021**

## **DEDICATION**

I dedicate this work to my ever patient and supportive wife Michelle, and to my daughter Jasmine for keeping me young at heart.

## ACKNOWLEDGMENTS

I would like to express my deepest appreciation to my committee Kelly Miller, Sandra Brantley and Robert Raven for the hours, days and months of dedication they provided me on this academic journey. I am extremely grateful for Christopher Witt for his willingness to join my committee at the end of my journey to help see me through to the finish.

As an undergraduate Kelly supported my passion for arthropods by allowing me to engage in undergraduate research and giving me the opportunity to join on collecting trips. He then opened the opportunity for me to continue this passion by accepting me as a graduate student. His expertise in arthropod systematic and taxonomy helped mold me into the scientist I am and to form this thesis into what it is, for this I am deeply indebted.

Sandra Brantley took the time to help me understand spider morphology and identification. In our time together she has enlightened me to various collecting techniques, shown me proper museum curation given me a deep appreciation for the time work and dedication needed to maintain museum collections. Her excellent insight has greatly improved my writing so to her I am grateful.

Robert Raven, an expert in many spider groups and a scientist whose work I have looked up to for years. It is an honor to have him on my committee. His help has undoubtable made me a better scientist. By welcoming me into his and home, and allowing me to join him in on a field expedition in remote stretches of Queensland

Australia he increased my appreciation of all forms of wildlife and the importance of colleagues and collaborations.

Finally to Christopher Witt for joining my committee and helping to see me through to the end thank you.

**A new species of ant-mimicking sac spider *Castianeira reiskindi* (Araneae: Corinnidae: Castianeirinae) from Nicaragua and a phylogenetic analysis of the Australian Castianeirinae.**

**by**

**Matthew Leister**

**Bachelors or Science in Biology, University of New Mexico, 2015, Magna Cum Laude**

**Master of Science in Biology, University of New Mexico, 2021**

**ABSTRACT**

Ant-mimicking spiders in the subfamily Castianeirinae have had a number of taxonomic revisions and species descriptions. Despite these advancements, more species exist await formal scientific description and little scientific progress has been made in terms of reconstructing their evolutionary histories. This study 1) describes a new species *Castianeira reiskind* **sp. n.** from cloud forests in Nicaragua; and 2) presents a first look of the Australian Castianeirinae taxa in a phylogenetic framework. This analysis is used to explore the origins of Hymenoptera mimicry in this group, test the monophyly of this subfamily compared to the Corinninae and to test the current genera hypotheses in this group. This study shows a single origin of mimicry with model choice arising multiple times independently. The Castianeirinae was supported as monophyletic with respect to the Corinninae and current genera hypotheses were supported.

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## Chapter 1

### **A new species of ant-mimicking spider, *Castianeira reiskindi* sp. n. (Araneae: Corinnidae: Castianeirinae), from cloud forests in Nicaragua.**

#### **Introduction**

*Castianeira* is a speciose genus of corinnid spider, with *Castianeira reiskindi* **sp. n.** representing the 123rd species described from around the world. Although the American representatives of this genus appear to be monophyletic (Reiskind 1969), there is evidence that globally this genus is paraphyletic and may be a taxonomic dumping ground for many generalized Castianeirinae (Haddad 2013; Rubio et al. 2015). This genus is known for its morphological and behavioral mimicry of ants and other Hymenoptera (Cushing, 1997, 2012; Reiskind, 1969, 1970). *Castianeira reiskindi* **sp. n.** is a convincing morphological ant mimic achieved through various adaptations including an elongate abdomen and carapace, long slender legs and the presence of an abdominal constriction. *Castianeira reiskindi* **sp. n.** is described from two males and one female collected from cloud forests in Nicaragua. This manuscript aids in the understanding of these spiders and helps to better understand the biodiversity of Central American cloud forests.



## **Materials and Methods:**

All material was examined, illustrated and measured using a Zeiss Stereo Discovery V8 stereo microscope equipped with an ocular micrometer with the specimen submerged in 70% ethanol.

Species description and terminology mostly follows Reiskind (1969). The female epigynum was dissected using a #11 blade scalpel and cleared with lactic acid at room temperature until internal structures were visible. Several ratios are used to provide an index of shape including the following: carapace index (CI) = carapace width / carapace length  $\times 100$ ; abdominal index (AI) = abdominal width / abdominal length  $\times 100$ ; male genital index (GI) = embolus length/bulb length. All leg and pedipalp measurements were taken from left appendages and measured with the leg in lateral aspect. Leg length is reported as the total length including coxa, trochanter, femur, patella, tibia, metatarsus, and tarsus. Pedipalp length is reported as the total length including trochanter, femur, patella, tibia, and tarsus. Tibia I ventral spination is denoted by two numbers, the first the number of prolateral ventral spines and the second the number of retrolateral ventral spines. All measurements are reported in millimeters. The holotype male and paratype female are deposited in the Museum of Southwestern Biology, University of New Mexico (MSBA, K.B. Miller, curator).

The following abbreviations are used throughout the text

**AI**, abdominal index; **AL**, abdominal length; **AW**, abdominal width; **AER**, anterior eye row; **ALE**, anterior lateral eye; **AME**, anterior median eye; **BL**, bulb length; **CI**, carapace

index; **CL**, carapace length; **CW**, carapace width; **DS**, dorsal sclerite; **EL**, embolus length; **Em**, embolus; **GI**, male genital index; **GS**, genital sclerite; **PER**, posterior eye row; **PAS**, posterior abdominal setae; **PLE**, posterior lateral eye; **PME**, posterior median eye; **RTA**, retro-lateral tibial apophysis; **SL**, sternum length; **SW**, sternum width; **TL**, total length; **TS**, tracheal sclerite; **VS**, ventral sclerite.

## Taxonomy

**Family: Corinnidae Karsch, 1880**

**Subfamily: Castianeirinae Reiskind, 1969**

**Diagnosis.** Castianeirinae corinnids can be distinguished from other Corinnidae by (a) presence of a tear-shaped palpal bulb, (b) absence of a true retro-lateral tibial apophysis (with the exception of *Nyssus paradoxus* Raven (2015)) (c) presence of a looped sperm duct, (a coiled sperm duct is present in Corinninae) (Figs. 2a–c; 3a–c).

### **Genus *Castianeira***

*Castianeira* Keyserling; type species by original designation: *Castianeira rubicunda* Keyserling, 1879.

**Diagnosis.** Taken globally, the genus *Castianeira* seems to lack specific diagnostic characters despite the claim of monophyly in the North and Central American fauna by Reiskind 1969, and appears to accommodate many less derived Castianeirinae spiders (Haddad 2013; Rubio et al. 2015). A more comprehensive examination of these spiders including the poorly-known South American fauna as well as Asian and African species, are needed to determine if splitting *Castianeira* into separate genera is warranted, though this is beyond the scope of this work. American spiders in the genus *Castianeira* can be distinguished from other American Castianeirinae genera as follows: (a) from *Mazax* by having the AMEs equal to larger than ALE (Fig. 4) and by lacking a distinct and rugose abdominal petiole collar; (b) from *Myrmecotypus* and *Sphecotypus* by the presence of a

thoracic groove and a carapace index greater than 60 (a thoracic groove is absent in *C. trimac* Reiskind 1969 but this species has a carapace index greater than 60)(Figs. 1; 5; 6; 7a, d).

***Castianeira reiskindi* sp. n.**

Figs. 1–10

**Type Material.** Holotype male (MSBA 49613) and paratype female (MSBA 49612)

Nicaragua: Matagalpa: Selva Negra (13.000261, -85.910801), 1300m 21–25 May 2014  
(Colr. Brantley and Mallis)

**Other Material examined.** Male Nicaragua: Granada: Volcan Mombancho 15May 1998  
(Colr. JM Maes).

**Etymology.** *Castianeira reiskindi* **sp. n.** is named in honor of Jonathan Reiskind, whose work has greatly increased the scientific knowledge of the Castianeirinae.

**Diagnosis.** *Castianeira reiskindi* **sp. n.** is placed in the *C. dubia* species group based on the following combination of characters: (a) carapace moderately large (male CL = 2.38, female CL = 3.80) (Figs. 1; 5; 6; 7a, d); (b) abdomen elongate (AI: 31 in the male) (Figs. 5; 7a); (c) spermathecae globose anteriorly with narrower posterior necks (Fig 7e; 8); and (d) AMEs larger than ALEs (Fig. 1e). Males of *C. reiskindi* **sp. n.** differ from other members of this species group by; (a) the longer embolus (GI: 18) (Figs. 2; 3); and (b) by the presence of a medial fold in the sperm duct proximal the embolus not seen in other members of the *C. dubia* species group (Figs. 2a, b; 3a, b). A similar genital index is found in *Castianeira alba* Reiskind 1969 (*C. alba* species group), which also has a medial fold of the sperm duct (Reiskind 1969; fig. 143). *Castianeira reiskindi* **sp. n.** can

be easily separated from *C. alba* by; (a) carapace length, *C. reiskindi* **sp. n.** CI: 58; *C. alba* CI: 69–72; (b) abdominal constriction (*C. alba* has a shorter oval abdomen lacking a medial constriction (Reiskind 1969; fig. 157)) (Figs. 5; 7a; 9); and (c) abdomen shape (*C. reiskindi* **sp. n.** AI: 31; *C. alba* AI: 52–58) (Figs. 5; 7a; 9).

## MALE

**Measurements:** (Based on holotype male MSB 49613). TL: 5.94. CL 2.38; CW1.37; CI 58; SL 1.72; SW 1.04; SI: 60. AME 0.12; ALE 0.08; PME 0.08; PLE 0.08; AME–AME 0.06; AME–ALE 0.03; ALE–ALE 0.49; PME–PME 0.12; PME–PLE 0.12; PLE–PLE 0.56.; AL 3.56; AW 1.09; AI 31; EL 0.19; BL 1.07; GI 18.

### **Description:**

*Carapace* dark brown, granulose, oval, slightly constricted at cephalic region thin white setae on cephalic region longer anteriorly, light and dark feathery setae on carapace mostly apparently removed in holotype but creating a pattern of white lines radiating from the thoracic groove. Slight constriction at thin thoracic groove, carapace highest just behind thoracic groove (Fig. 7c).

*Chilum* entire (Fig. 4).

*Chelicerae* brown, increasingly pale distally, curved setae on antromedial edge on chelicer al fangs.

*Chelicer al teeth* two retro-marginal teeth, two promarginal teeth.

*Sternum* light brown, shield-shaped, intercoxal and precoxal sclerites present.

*Labium*. Brown, pale distally, width greater than length, distal edge with slight convex curve.

*Endites.* Brown proximally, increasingly pale distally, medial edge terminating in scopula.

*Legs.* Ventrally light yellow brown, dorsally darker, lateral faces dark brown, all legs slender and long. All legs armed with socketed spines, light and dark feathery setae throughout. Femur IV with distal constriction on ventral surface.

Leg formula: IV, I, III, II.

*Abdomen.* Dark brown, granulose, long, slender, widest posteriorly, with median constriction. Dorsal sclerite complete. Light and dark feathery setae mostly worn off but creating two transverse stripes, anterior to the constriction and at the constriction, and a white spot at the posterior abdomen (Figs. 5; 7a). Ventral abdomen dark brown, lighter brown spots on lateral side of ventral sclerite at level of abdominal constriction, spots reinforced by white feathery setae. Epigastric sclerite continues anteriorly and connects forming a slightly rugose collar contiguous with dorsal sclerite, genital pore single, with white feathery setae distal and lateral to book lungs. Ventral sclerite complete, contiguous with tracheal sclerite (Figs. 7b; 9). Ventral abdomen adorned with dark feathery setae except were mentioned above.

*Pedipalps.* Palp tibia with pointed distal retrolateral ridge continuing at an angle along the ventral surface to proximal prolateral side (Figs. 2b, c; 3b, c). Tarsus with a globose genital bulb drawn out into a long neck terminating in a moderately long, straight embolus with a terminal twist (Figs. 2a–c; 3a–c). Sperm duct with both medial and lateral loop, distal medial fold present resting above medial loop (Figs. 2a–c; 3a–c).

## **FEMALE:**

**Measurements:** (Based on paratype female MSB 49612). Total length 7.72. CL 3.80; CW 2.19; CI 58; SL 1.60; SW 1.03; SI 64; AME 0.18; ALE 0.12; PME 0.12; PLE 0.12; AME–AME 0.08; AME–ALE 0.03; ALE–ALE 0.75; PME–PME 0.20; PME–PLE 0.13; PLE–PLE 0.89; AL 3.92; AW 1.98; AI 51.

*Carapace, chelicerae, chilum, cheliceral teeth, sternum, labium, endites and legs* as in male.

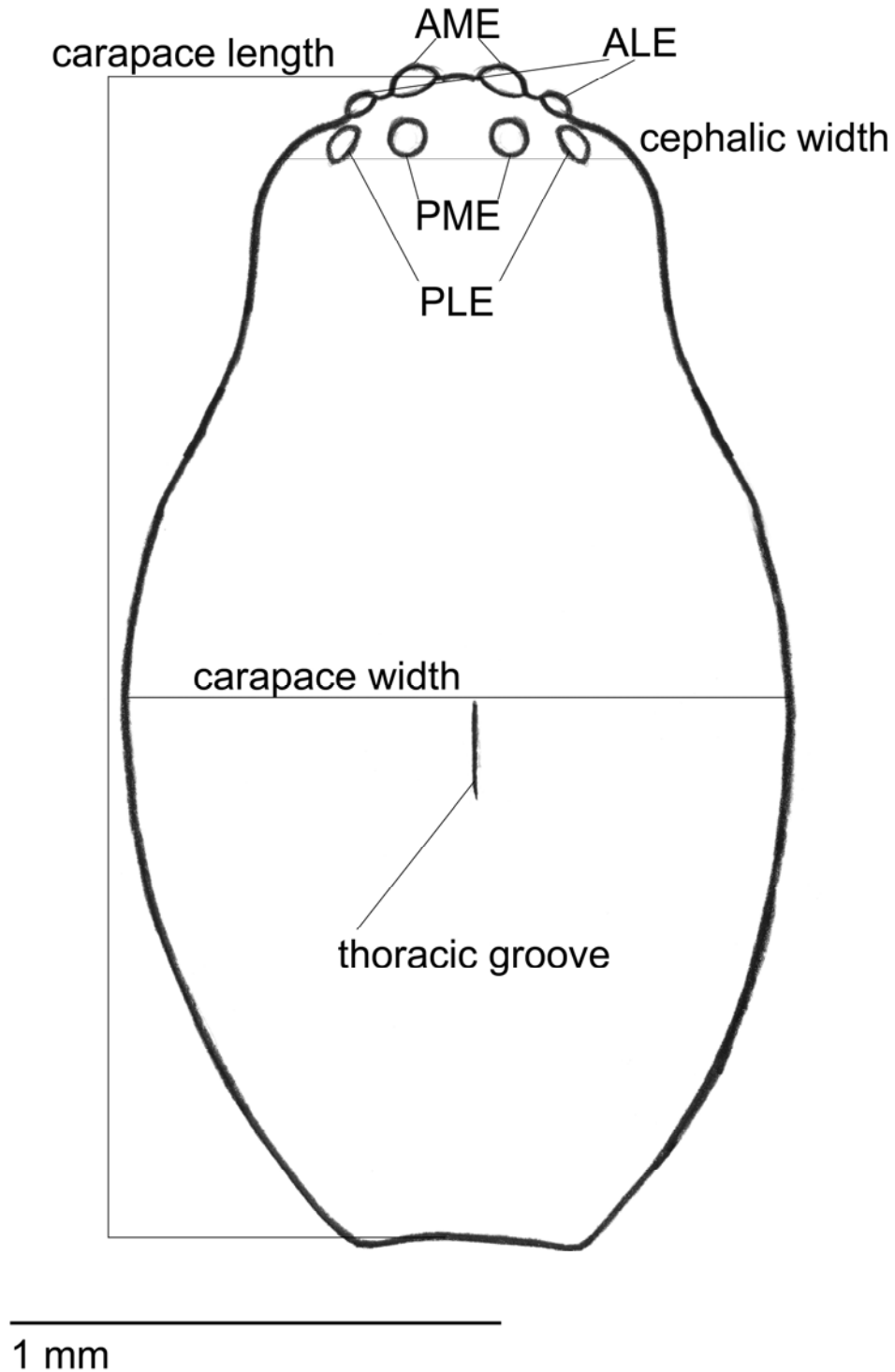
Differences: Anterodistal mound (fang shield mound) present on chelicera bearing thick curved setae (Fig. 14).

Leg formula: IV, I, III, II.

*Abdomen.* Dorsal sclerite less than half abdominal length, abdomen shriveled and many setae worn off, however, white spot of feathery setae on posterior abdomen and two transverse stripes present (Fig. 7d). Ventral abdomen dark with light yellow-brown spots on lateral sides midway down abdomen, spots reinforced by white feathery setae (Fig. 10). Epigastric sclerite continues anteriorly and connects forming a slightly rugose collar contiguous with dorsal sclerite, white feathery setae distal and lateral to book lungs (Fig. 10). Ventral sclerite absent. Tracheal sclerite small, triangular.

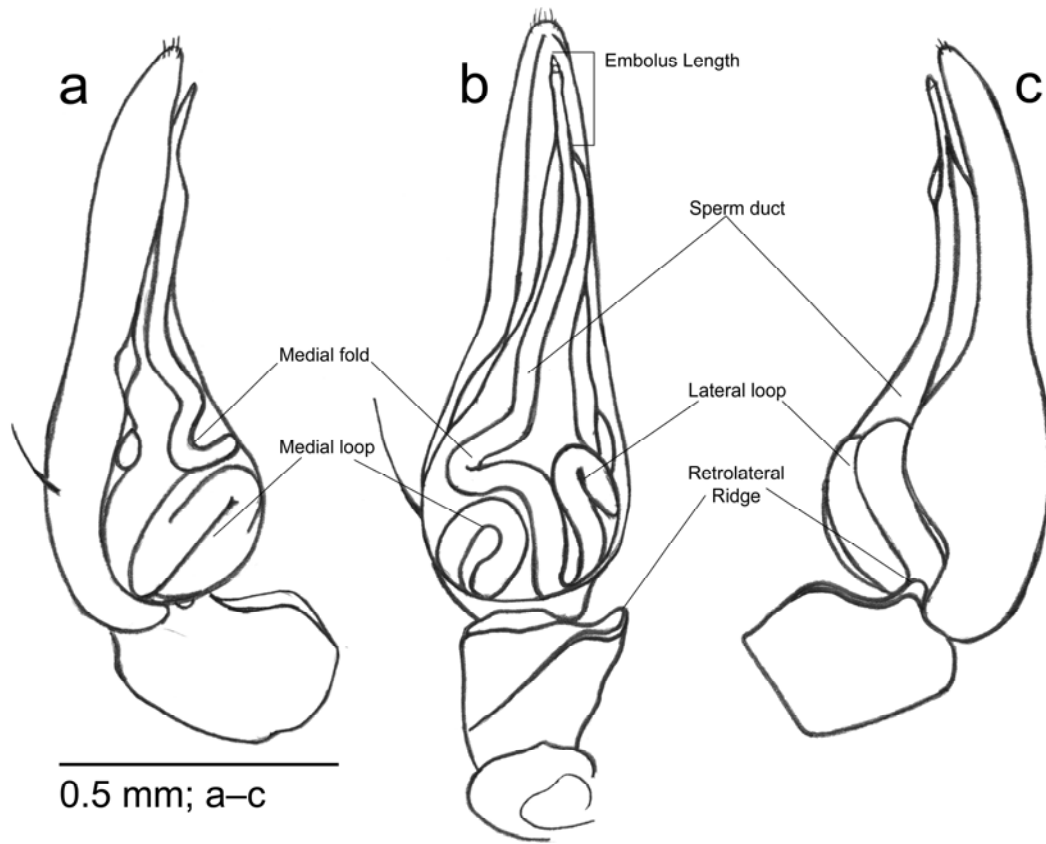
*Epigyne.* Ventral: epigyne with two small circular copulatory openings placed laterally. Dorsal: copulatory ducts short, sub-symmetrical globose spermathecae with thick posterior necks (Fig. 7e).

**Distribution.** *Castianeira reiskindi* **sp. n.** is currently only known from Nicaragua. Specimens have been collected from the cloud forests of Volcan Mombacho and Selva Negra.

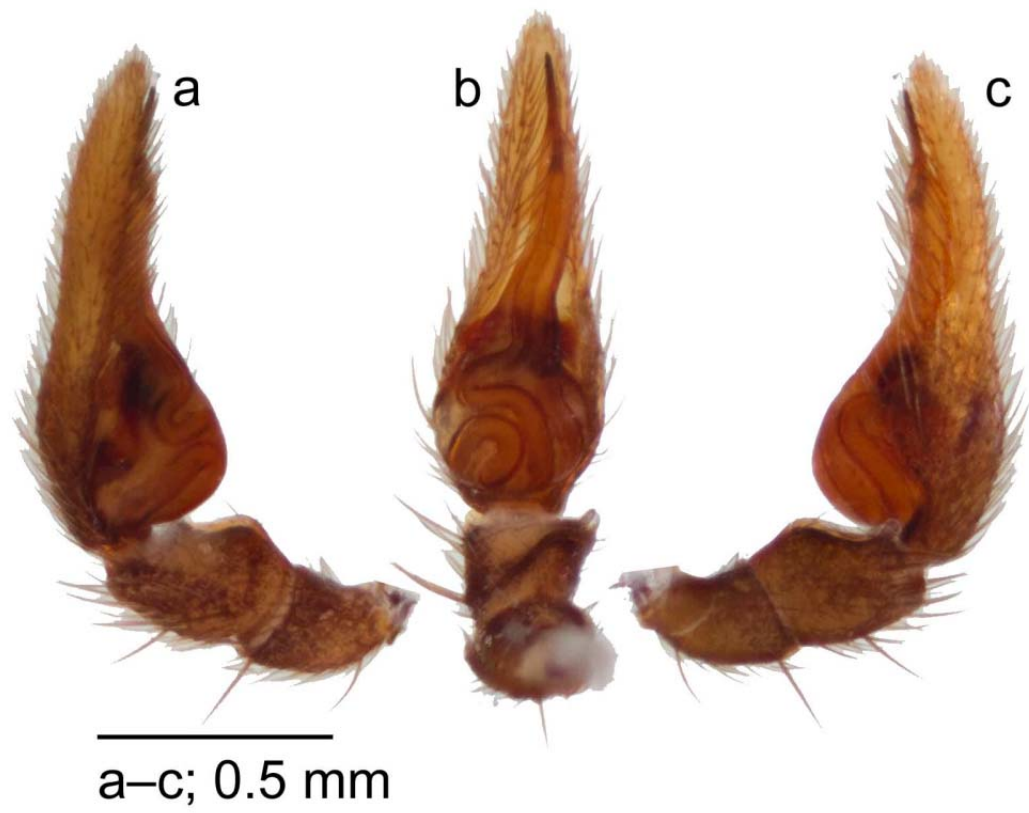


**Figure 1.** *Castianeira reiskindi* sp. n., male carapace; dorsal view. Abbreviations: ALE—anterior lateral eyes; AME—anterior median eyes; PLE—posterior lateral eyes; PME—posterior median eyes.

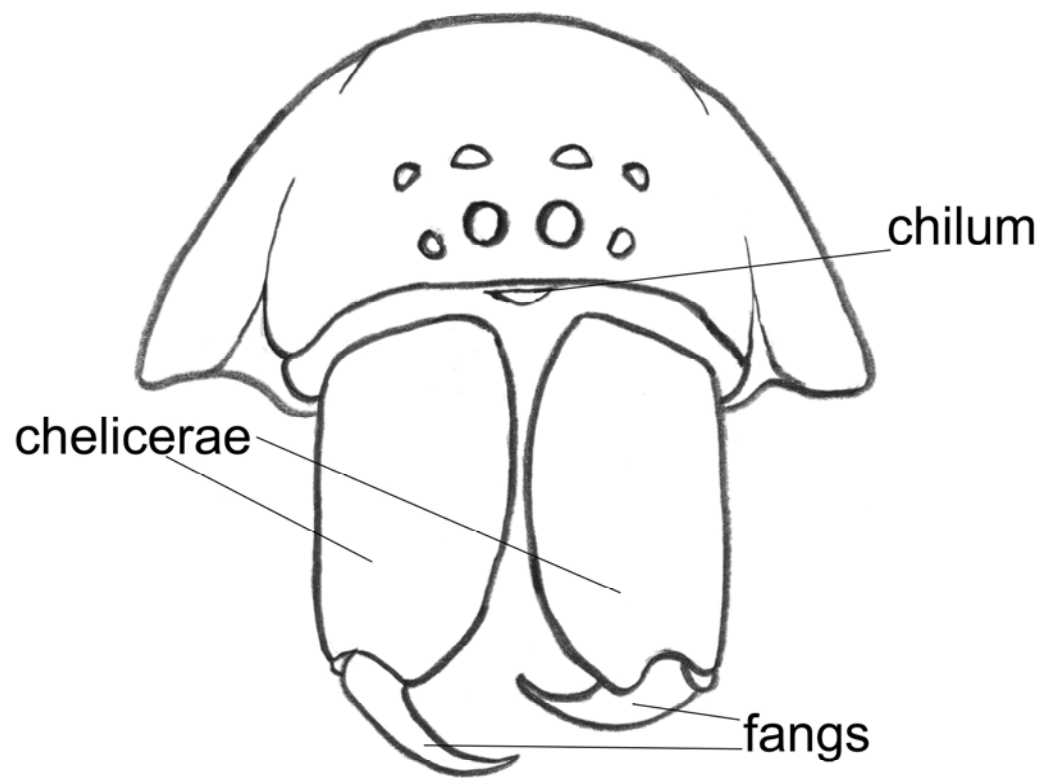




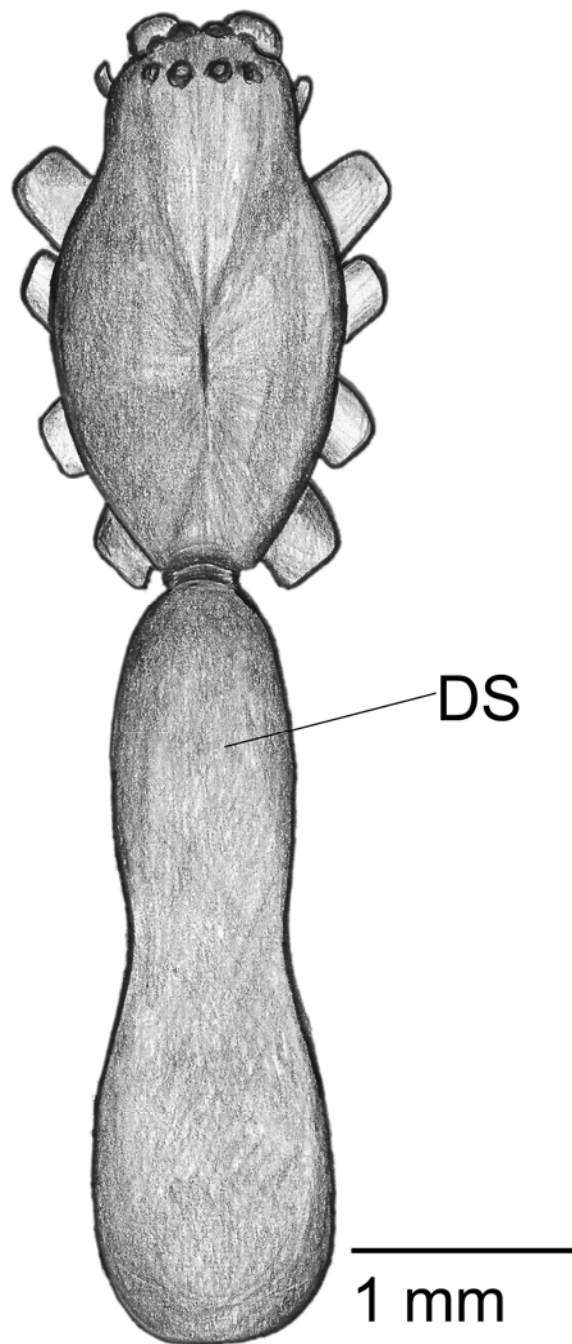
**Figures 2a–c.** *Castianeira reiskindi* sp. n., left male pedipalp: **a.** Prolateral view; **b.** Ventral view; **c.** Retrolateral view.



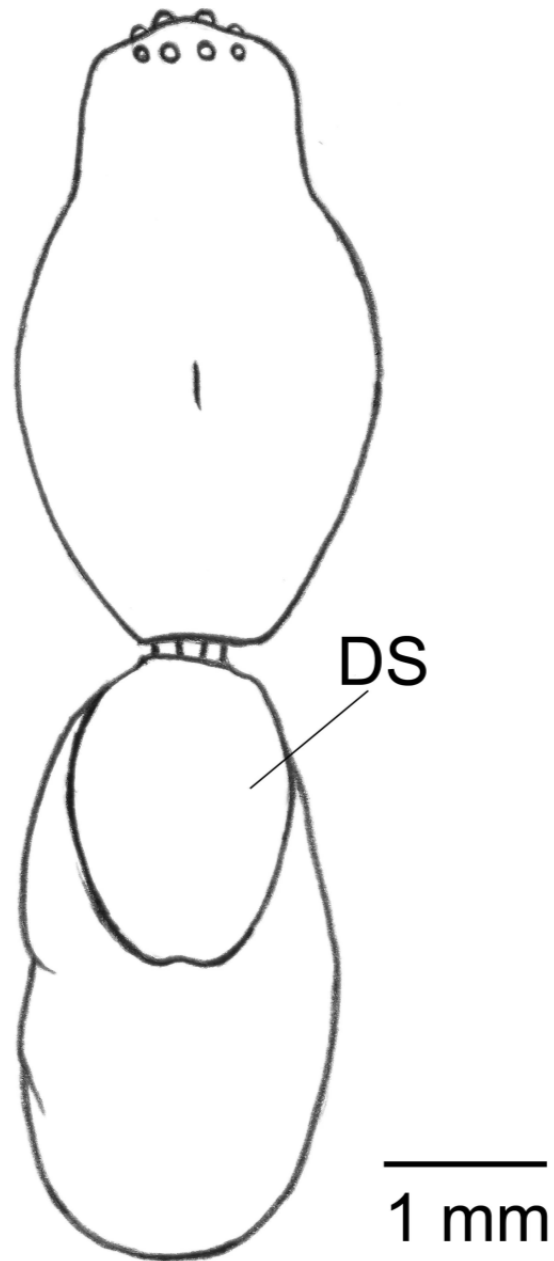
**Figures 3a–c.** *Castianeira reiskindi* sp. n., left male pedipalp: **a.** Prolateral view; **b.** Ventral view; **c.** Retrolateral view.



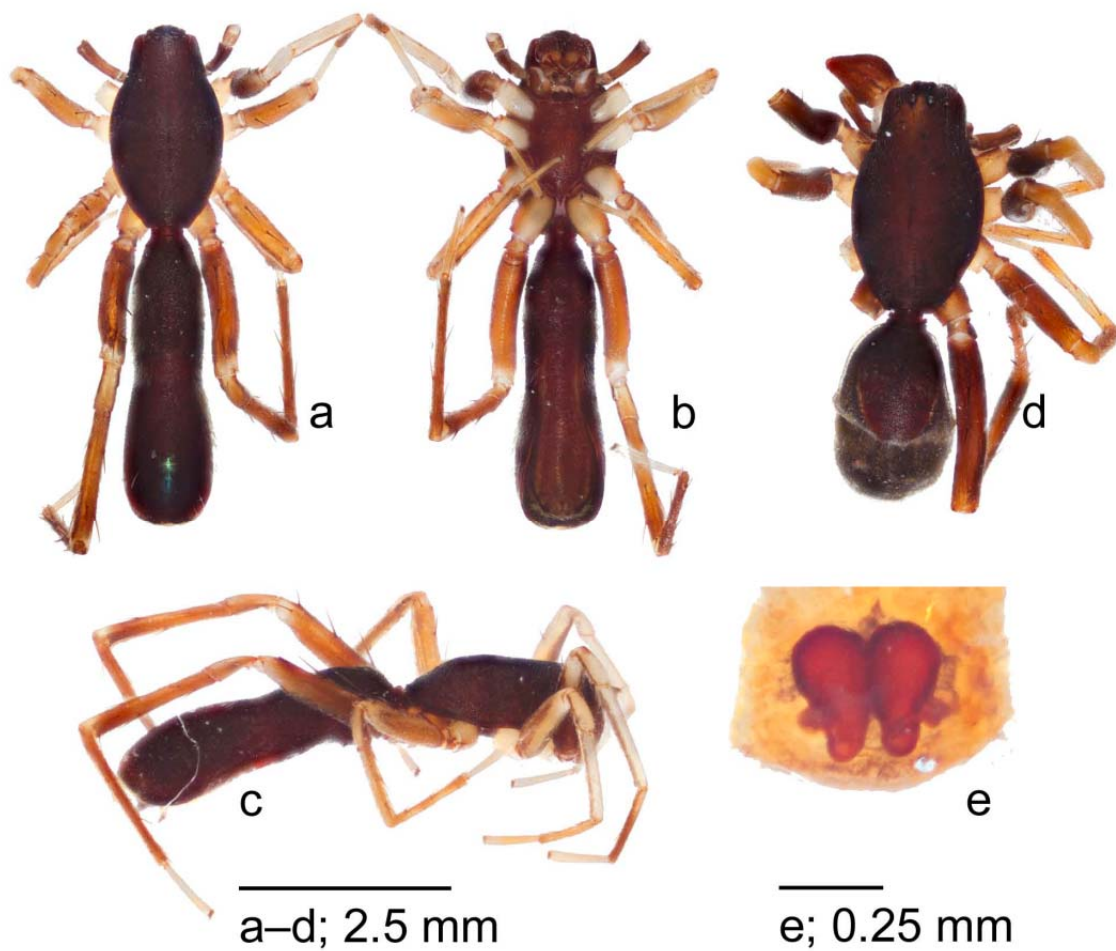
**Figure 4.** *Castianeira reiskindi* **sp. n.**, male carapace; anterior view.



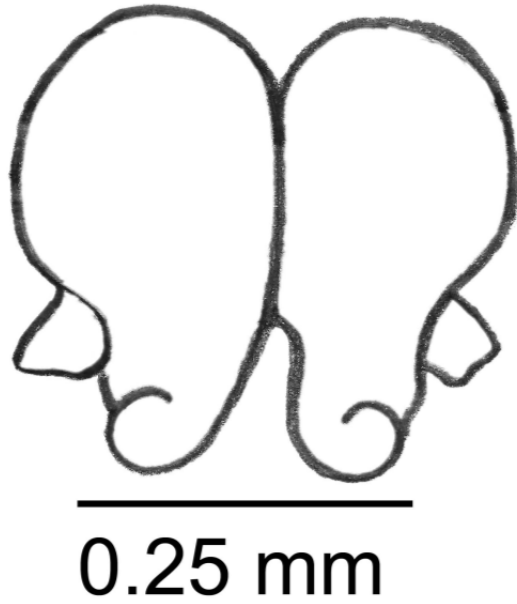
**Figure 5.** *Castianeira reiskindi* sp. n., male habitus; dorsal view. Abbreviations: DS—Dorsal sclerite.



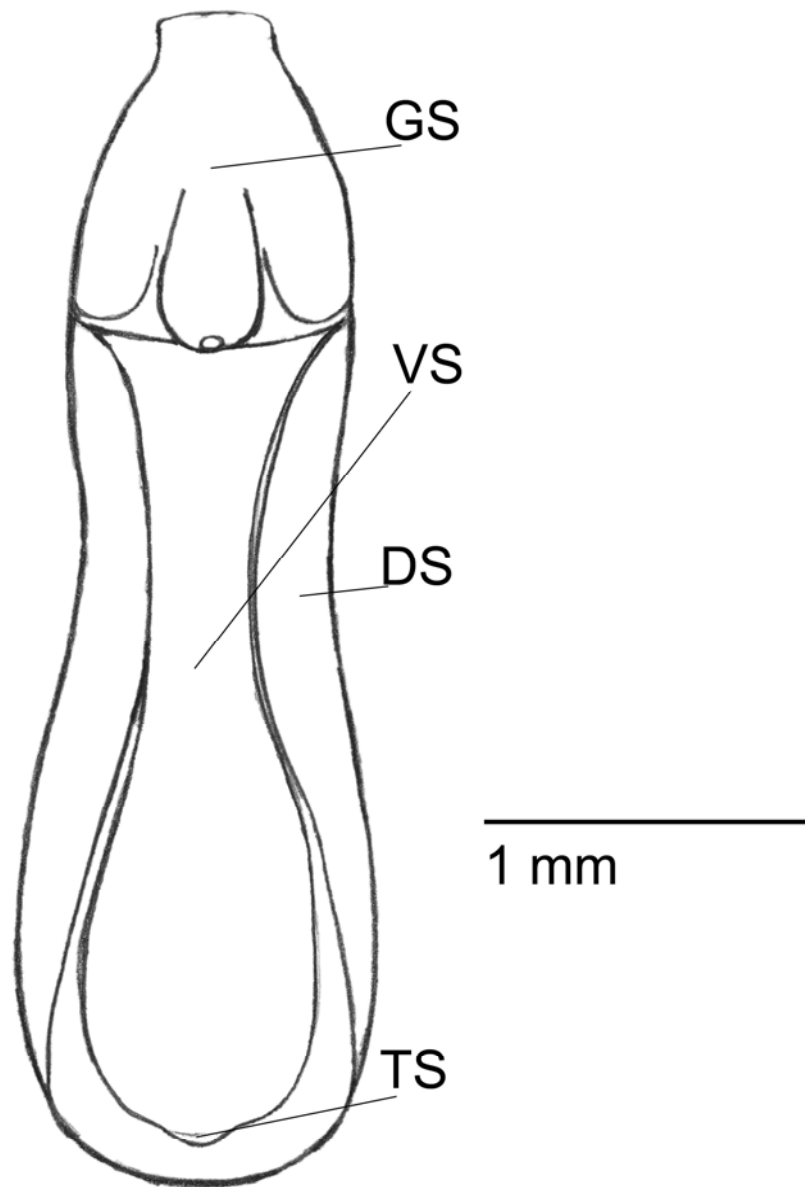
**Figure 6.** *Castianeira reiskindi* **sp. n.**, female habitus; dorsal view. Abbreviations: DS—Dorsal sclerite.



**Figures 7a–e.** *Castianeira reiskindi* sp. n., **a.** male habitus, dorsal view; **b.** male habitus, ventral view; **c.** male habitus, lateral view; **d.** female habitus; dorsal view; **e.** female epigynum, dorsal view.

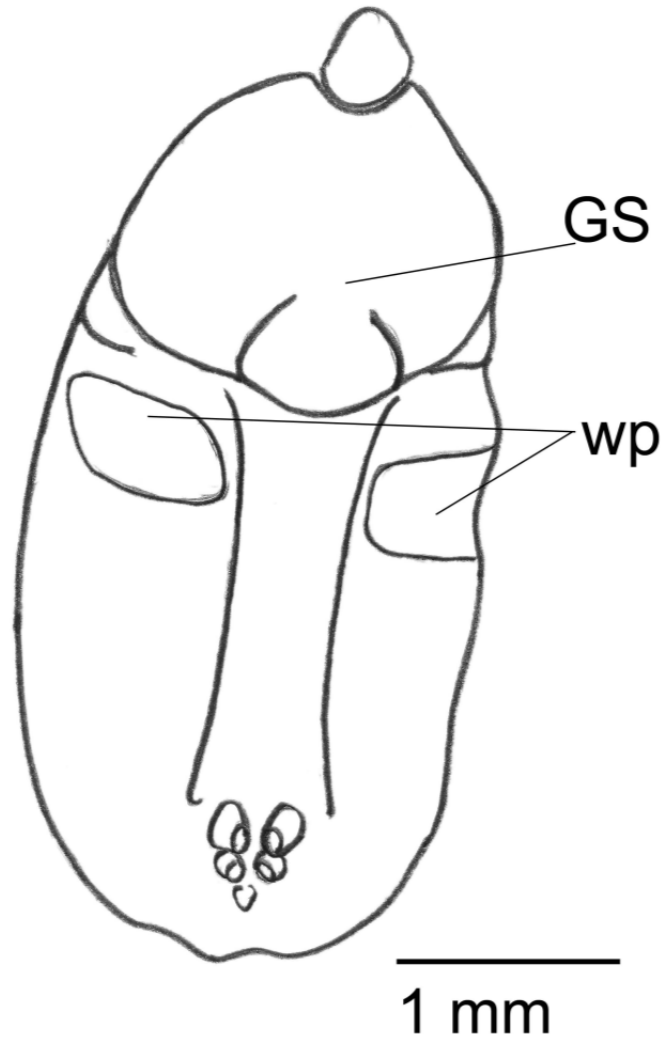


**Figure 8.** *Castianeira reiskindi* sp. n., female epigynum; dorsal view.



**Figure 9.** *Castianeira reiskindi* **sp. n.**, male abdomen; ventral view. Abbreviations: DS—Dorsal sclerite; GS—Genital sclerite; TS—Tracheal sclerite; VS—Ventral sclerite.





**Figure 10.** *Castianeira reiskindi* sp. n., female abdomen; ventral view. Abbreviations: DS—GS—Genital sclerite; wp—white/yellow patterning of feathery setae.

## Chapter 2

### A phylogenetic analysis of the Australian ant-mimicking sac-spiders (Araneae: Corinnidae: Castianeirinae)

#### Introduction

The Corinnidae Karsch, 1880, commonly known as corinnid sac-spiders, are a family of araneomorph spiders currently recognized as having two subfamilies; the Corinninae and the Castianeirinae Reiskind 1969. The monophyly of the subfamily Corinninae is supported by: a) the presence of a coiled sperm duct in the male palpal bulb (Fig. 11a); and b) a highly branched retro-lateral tibial apophysis (RTA) in males (Platnick & Baptista 1995). The monophyly of the subfamily Castianeirinae is supported by: a) having a pear-shaped palpal bulb with a looped sperm duct (Fig. 11b, f, h); b) having a sclerotized embolus but lacking additional sclerites on the male palpal bulb such as a median apophysis or a conductor (Fig. 11b–f); and, a commonly cited character, c) the lack of a true RTA on the male palpal tibia (Reiskind, 1969; Deeleman-Reinhold, 2001; Bosselaers & Jocqué, 2002; Haddad 2013b; Candiani & Bonaldo, 2017). However, the presence of an RTA has been noted for a single Castianeirinae species from Australia, *Nyssus paradoxus* Raven 2015, (Fig. 11f). To further confuse matters a folding of the retro-lateral tibial surface of palps of males creates retro-lateral tibial protuberances common in many Castianeirinae from the Americas and which have been referred to as an RTA by many authors (Reiskind 1969; Haddad 2013b; Leister & Miller 2014a, b; Raven 2015; Candiani & Bonaldo 2017). This folding of the tibial surface however, is not considered homologous with the tibial apophysis seen in the Corinninae (Haddad 2013b).

The Castianeirinae, the focus of this study, have a worldwide distribution with many taxa highly effective mimics of ants and other Hymenoptera both morphologically and behaviorally (Cushing 1997; Rubio et al. 2013; McIver & Stonedahl 2013; Raven 2015). A mimicry system “involves an organism (the mimic) which simulates signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the operator), such that the mimic gains in fitness as a result of the operator identifying it as an example of the model” (Vane-Wright 1980). In the Castianeirinae this mimicry can range from a generalized mimic of seemingly several hymenopterans to highly derived mimics using a single species as a model (Cushing 1997; Haddad 2013a; McIver & Stonedahl 2013). Non-hymenopteran arthropods visually and/or behaviorally mimicking Hymenoptera has been reported numerous times with over 2000 species in 54 families described as mimics (McIver & Stonedahl 1993). The evolution of ant-like morphology and behavior can be attributed to three distinct systems of mimicry: Wasmannian, aggressive, and Batesian (McIver & Stonedahl 1993). In both Wasmannian and aggressive mimicry, the mimic aims to deceive the model typically exploiting resources from the model (Rettenmeyer 1970). In Wasmannian mimicry, this deception is used to facilitate the mimic’s ability to live with its model while in aggressive mimics use the deception to approach the model for parasitic or predaceous purposes (Rettenmeyer 1970). Batesian mimics, however aim to deceive a predaceous operator by resembling models that are unpalatable to the operator. So by advertising these morphological and behavioral similarities to the unpalatable models the mimic is able to deter would-be predators (Rettenmeyer 1970).

The mimicry seen in the Castianeirinae genera is present in other spider groups as well including the family Salticidae, which is known to contain many species that are visually similar to Hymenoptera. This mimicry is believed to be an example of Batesian mimicry (Reiskind 1969; McIver & Stonedahl 1993; Cushing 1997; Nelson & Jackson 2006, 2009; Haddad 2013a; McIver & Stonedahl 2013; Rubio et al. 2013; Leister & Miller 2014a, b; Raven 2015; Candiani & Bonaldo 2017). These spiders stay in close proximity to the model organisms while emulating the model, both morphologically and behaviorally in an attempt to avoid detection by would-be predators (Cutler 1991; Cushing 1997, 2012; Huang et al. 2011; Durkee et al. 2011; Nelson 2012; McIver & Stonedahl 2013). The accuracy of this morphological mimicry in the Castianeirinae are most evident in a) carapace shape; b) leg morphology; c) abdominal shape; and d) body color and pattern. More accurate ant mimics tend to have a long narrow carapace and abdomen occasionally with constrictions (Reiskind 1969; figs 282–290; Leister & Miller 2014; fig 1a–c; Raven 2015; figs 15a, 48a, 98a–e, 99a–c; Candiani & Bonaldo 2017; figs 2–13), long thin legs (Raven 2015; figs 51c, 99a–c; Candiani & Bonaldo 2017; figs 2–13), and pattern that reinforce or give the perception of constrictions on the carapace and/or abdomen (Reiskind 1969; figs 113–122, 148–159; Raven 2015; figs 79 a–d). In the case of mutillid mimics a bold and colorful pattern typically incorporating yellow, red or orange spots is present (Reiskind 1969; figs 113–122, 148–159; Raven 2015; figs 79 a–d).

These spiders can be seen by the human observer as specific or general mimics of hymenoptera. A specific mimic is determined as being visual similarity and closely associated with a specific species or genus of model to the human observer. Whereas a

more general mimic may only be superficially similar to a group of models to the human observer and might not be seen to associate with a particular species of model in nature (Edmund 2000, 2006). Co-evolution between a mimic and its perceived model along with selective pressures from predation may drive a mimic towards specificity (Edmund 2000, 2006; Sherratt 2002; Ceccarelli & Crozier 2007). Several genera of Castianeirinae include species with varying degrees of morphological mimetic specificity, which, depending on the phylogeny, suggests the mimicry may have evolved multiple times in the lineage but that the lineage itself may be prone to evolving mimicry.

Mimicry in spiders has been explored in depth in the salticids (Cushing 1997). Members of the salticid genus *Myrmarachne* MacLeay, 1839 possess similar features, including carapace and abdominal constrictions that are attributed as being visually similar to Hymenoptera (Nelson & Jackson 2006; figs 1a–b). Nelson & Jackson (2006) showed experimentally that visually motivated araneophagic predators preferred lures made of preserved salticids that were not visually similar to Hymenoptera over *Myrmarachne* and ant lures. The predator never chose the ant or the *Myrmarachne* lure (Nelson and Jackson, 2006). When a myrmecophagic predator was used, male *Myrmarachne* lures were chosen at similar rates as encumbered ant lures and a higher rate than female *Myrmarachne* and unencumbered ants (Nelson and Jackson, 2006). Male *Myrmarachne* have enlarged chelicera projecting further forward when compared to conspecific females, making males visually similar to encumbered ants, (Nelson & Jackson 2006; figs 1a–b). The mouthparts of ants and spiders can be used defensively and the selection of an encumbered prey can be perceived as a safer choice when compared to

an unencumbered alternative. This preference towards encumbered prey was shown for araneophagic predators by Jackson et al. 2002.

Nelson & Jackson (2009) tested the palatability and preference for *Myrmarachne* compared to other prey items including ants through the use of both living prey and preserved lures, as individuals and groups, using ants, *Myrmarachne* (mimics), and prey items not visually similar to ants (non-mimics). The non-mimics were attacked more often than ants and mimics both individually and in groups, and individuals of ants and mimics were attacked more often than in groups (Nelson and Jackson, 2009). No preference was shown towards mimics mixed in a group of ants, and predators showed no aversion to groups constructed from non-mimicking lures yet avoided groups of lures constructed from ant, mimics and combination of the two (Nelson and Jackson, 2009). In the palatability test, living prey including ants, ant-like salticids, nonant-like salticids and Diptera were rendered motionless by reducing their temperature, and these prey items were placed in front of predators and the amount of time the predator spent feeding (holding/eating) on the prey after the initial attack was used to determine palatability (Nelson and Jackson, 2009). Ants were dropped almost immediately while other prey items, including the mimic were held significantly longer (Nelson & Jackson 2009; fig 5).

These studies offer support to the hypothesis that these spiders are in fact Batesian mimics of ants and that this mimicry is at least in part driven by the visual similarity between these two organisms. It can be assumed the visual similarity seen between hymenopteran and the Castianeirinae would deter visual predators in a similar fashion. Therefore the visual similarity seen between hymenopteran and the Castianeirinae most

likely also functions as a form of Batesian mimicry, although a comprehensive study of predator choice using the Castianeirinae has yet to support this.

Most published work on the Castianeirinae has been revisionary and descriptive. Major advancements were made by Reiskind (1969), who performed the first large scale revision of the Castianeirinae for the North and Central American members and erected the subfamily. Although this study was primarily a revisionary work of the four recognized genera from these areas and also contained a small phylogenetic section. This section briefly touched on the proposed relationships and monophyly of the four genera of North and Central American Castianeirinae; *Castianeira* Keyserling, *Mazax* O. Pickard-Cambridge, *Myrmecotypus* O. Pickard-Cambridge and *Sphecotypus* O. Pickard-Cambridge. These genera were examined for genitalic characters, eye arrangement and size, cheliceral teeth and mimetic characters. He concluded the North and Central American *Castianeira* and *Mazax* examined were monophyletic but admitted a larger study was required to clarify some questions arising out the potential polyphyletic origin of *Myrmecotypus* citing the variation seen in the genitalia (Reiskind, 1969). *Sphecotypus*, with a single species described from Central America, was thought to possibly represent a “highly derived” form of *Myrmecotypus*. Reiskind (1969) concluded that an additional look at South American fauna was needed to determine these relationships. In other studies, Deeleman-Reinhold (2001) revised the Castianeirinae from Southeast Asia; no attempt at that time was made to determine their evolutionary relationships. Haddad (2013a, b, c) revised several Afrotropical genera and constructed the first cladogram of Castianeirinae spiders using Afrotropical specimens and a single South American specimen (Haddad 2013b). This study showed the Castianeirinae and the Corinninae as

monophyletic groups; however, many of the Castianeirinae genera examined resulted in paraphyletic and polyphyletic groupings within the subfamily (Haddad 2013b). Raven (2015) revised the Australian Castianeirinae and in this work proposed a number of characters that appear to have phylogenetic significance; a cladistics analysis was not performed. Most recently, Candiani & Bonaldo (2017) revised the South American castianeirine genus *Myrmecium* Latreille, but no attempt was made to reconstruct the evolutionary history of the *Myrmecium*.

Despite those taxonomic works, little progress has been made in unraveling the evolutionary history of the Castianeirinae. Most cladistic work that includes the Castianeirinae has been higher level studies to test the hypothesis of the Corinnidae family and the Castianeirinae and Corinninae subfamilies, notably Bosselaers & Jocqué (2002) and Ramírez (2014), with each project adding evidence for the monophyly of the Castianeirinae.

Fourteen genera and 98 species of Corinnidae are known to inhabit Australia (Raven 2015). This group was revised by Raven (2015) who synonymized eight corinnid species, erected and described eight new corinnid genera, and increased the total described number of species from Australia to 98 although Raven (2015; page 7) states “The total number of Australian corinnid species is clearly over 100.” Of the twelve genera of Castianeirinae described in Australia, many are morphological mimics of Hymenoptera with varying degrees of specificity (Raven, 2015). The most specific ant mimics observed in Australia belong to the genera *Iridonyssus* Raven, *Kolora* Raven, and *Poecilipta* Simon, to a lesser extent (general ant mimics) *Disnyssus* Raven, *Leptopicia* Raven and *Nucastia* Raven. Wasp mimics are also represented with the most specific



mimics belonging to the genus *Nyssus* Walckenaer and *Leichhardtus* Raven & Baehr, which including mimics of pompilid and mutillid wasps (Raven 2015). The recent revision of this group as well as the range of mimics represented makes the Australian Castianeirinae an ideal candidate for a cladistic study.

A cladistics analysis of twenty-one species of Australian Castianeirinae; representing all 12 Australian genera, three corinninae species, and a single species of Gnaphosidae as the outgroup was performed to test three hypotheses. First, the monophyly of the Australian Castianeirinae was tested compared to the Corinninae. Second, monophyly of the 12 Australian genera is examined. Of particular interest is the genus *Nyssus*. Raven (2015) questioned the validity of this genus and considered dividing the species groups into separate genera but asserted that such a decision would require evidence from future cladistic studies. Finally, the number of independent evolutionary origins of mimicry was investigated in the Australian Castianeirinae. Since it is known that the morphological adaptation of hymenoptera mimicry has evolved in multiple spider families, the coding of characters subject to that mimicry could be highly biased by adaptive correlation. However that does not mean these characters are not phylogenetically informative. When these characters are combined with multiple characters not likely to be selected as a part of this mimicry syndrome the evolutionary history of mimicry can be unraveled while avoiding the creation of groups based solely on adaptively convergent characters. Mimetic characters most likely represent synapomorphies for groups within the Castianeirinae, yet do not imply relatedness to other groups expressing similar morphology.

Although this study is limited to the Australian genera, characters presented in this study are useful for future analyses of worldwide Castianeirinae genera.

## **Materials and Methods**

### **Specimen Preparation and Examination**

All specimens were examined, illustrated and measured using a Zeiss Stereo Discovery V8 stereo microscope equipped with an ocular micrometer with the specimen submerged in 70% ethanol.

For examination of branched scales; specimens were initially washed with 70% ethanol then placed in a clean petri-dish of fresh 70% ethanol. Slides of the setae were prepared by first removing the specimen from the ethanol and allowing most of the ethanol to evaporate. The opisthosoma of each specimen was then rubbed with a clean dissecting pin at all locations where different types or patterns of setae were observed. The rubbed opisthosoma was pressed slightly against a clean microscope slide to transfer setae to the slide. Remaining ethanol was allowed to evaporate from the slide. A semi-permanent mount was made by applying a drop of PVA mounting medium and a coverslip. Setae were observed using a Ziess compound microscope using transmitted light at 40 – 100 $\times$ .

## Character Analysis

The character matrix (Table 1) was constructed and edited using WinClada version 1.00.08 (Nixon 2002). Data were analyzed using the computer program NONA version 2.0 (Goloboff 1993) as implemented by WinClada heuristics. The commands ‘hold 10000’, ‘hold/100’, ‘mult\*100’ and ‘max\*’ were used to estimate the most parsimonious tree (Fig. 19). Bremer support values (Bremer 1994) were calculated using NONA by reading in the single most parsimonious tree and implementing the commands “hold 10000,” “hold/100,” “suboptimal 10,” and “bsupport 10”.

*Material:* Specimens were borrowed from the following collection (curators in parentheses):

MSB: Museum of Southwestern biology, Albuquerque, New Mexico, USA (K. Miller)

QLDM: Queensland Museum, Brisbane, Queensland, Australia (R. Raven)

### **Taxon Choice:**

A total of 25 taxa consisting of 21 Australian Castianeirinae, representing the 12 genera known from Australia. Nineteen species of Castianeirinae were physically examined, however two species from the genera *Leptopicia* Raven 2015 and *Nucastia* Raven, 2015 were scored from descriptions in literature and from correspondences with Robert Raven of the Queensland Museum as the material was unavailable to be shipped for examination. The correspondence used to score these characters included microphotography of specimens from the Queensland Museum by Robert Raven. Of these Australian Castianeirinae scored, only the genera *Copa*, *Nyssus* and *Poecilipita*, are not endemic to Australia. Other species of the genus *Copa* not examined for this study are known to occur in Africa, Madagascar and Sri Lanka. Other species of the genus *Nyssus* not used in this study are known to occur in Fiji, New Zealand and the Solomon Islands. One species of *Poecilipita* not examined in this study is found in New Caledonia (World Spider Catalog, 2020).

In addition to the Castianeirinae, three representatives of the Corinninae subfamily were included to test the relationship with the Castianeirinae. *Abapeba grassima*, known only from Central and South America; *Creugas gulosus*, from South America, introduced to many regions across the globe; and *Septentrinna bicalcarata*, known from North America. A single species of the distantly related Gnaphosidae was used to root the tree.

This is the most comprehensive cladistic study of the Australian Corinnidae, only recently described/redescribed taxa known from both sexes were coded in this study and limited by specimen availability but spanned the apparent range of taxonomic variation across the group. A list of taxa used in this analysis is seen in Table 1.

Family	Subfamily	Genus	Species	Collection data
Gnaphosidae	Zelotinae	<i>Urozelotes</i>	<i>rusticus</i>	USA; New Mexico, Albuquerque “Bio Park BEMP site”; June 10 – 12, 2013, coll. BEMP staff
Corinnidae	Corinninae	<i>Abapeba</i>	<i>grassima</i>	NICARAGUA; Rio San Juan Dpto., Bartola; May 18 – 23, 2012, coll. K.B. Miller & Arthropod class
Corinnidae	Corinninae	<i>Creugas</i>	<i>gulosus</i>	AUSTRALIA: Queensland, Brisbane; December 1998, coll. Michael Rix]; [Pitcairn Island; August 8, 2001, coll. J.A. Covacevich
Corinnidae	Corinninae	<i>Septentrinna</i>	<i>bicalcarata</i>	USA; New Mexico, Sevilleta National Wildlife Refuge; 1991 – 1995, coll. SL Brantley
Corinnidae	Castianeirinae	<i>Battalus</i>	<i>adamparsoni</i>	AUSTRALIA: Queensland, Lake Broadwater; February 25 – April 22, 1986, coll. QLD MUSEUM & M. Bennie
Corinnidae	Castianeirinae	<i>B.</i>	<i>wallum</i>	AUSTRALIA: Queensland, Fraser Island, Orchid Beach; August 20 – September 17, 1997, coll. QLD MUSEUM]; [AUSTRALIA: Queensland, Mt. Glorious; May 29 – June 5, 1986, coll. Y. Beasset
Corinnidae	Castianeirinae	<i>Copa</i>	<i>kabana</i>	AUSTRALIA: Queensland, Nichol’s Scrub; January 1 – 4 March, 1992, coll. D. J. Cook
Corinnidae	Castianeirinae	<i>Disnyssus</i>	<i>helenmirrenae</i>	AUSTRALIA: Queensland, Boggomoss; November 12, 1996 – January, 1997, coll. D. Cook & G.B. Monteith
Corinnidae	Castianeirinae	<i>D.</i>	<i>judidenchae</i>	AUSTRALIA: Queensland, Mt Deongwar; December 30, 1998 – March 26, 1999, coll. G.B. Monteith; AUSTRALIA: Queensland, Buhot creek, Burbank; October 31 – December 1, 2003, coll. QM party
Corinnidae	Castianeirinae	<i>Iridonyssus</i>	<i>formicans</i>	AUSTRALIA: Queensland, Wetheron; October 10 – December 19, 1998, coll. Monteith & Gough
Corinnidae	Castianeirinae	<i>I.</i>	<i>kohouti</i>	AUSTRALIA: Queensland, Isla Gorge NP; September 22 – December 15, 1997, coll. Monteith & Cook
Corinnidae	Castianeirinae	<i>Kolora</i>	<i>sauverubens</i>	AUSTRALIA: Queensland, Footprint Scrub; December 8, 2006 – February 10, 2007, coll. Monteith & Cook
Corinnidae	Castianeirinae	<i>Leichhardtus</i>	<i>conopalpis</i>	AUSTRALIA: Queensland, Lake Broadwater; November 24, 1985 – January 3, 1986, coll. QLD MUSEUM & M. Benn

**Table 1.** Taxa used in cladistic analysis including locality information.

Family	Subfamily	Genus	Species	Collection data
Corinnidae	Castianeirinae	<i>L.</i>	<i>kroombit</i>	AUSTRALIA: Queensland, Kroombit Tops, lower dry creek; December 11 – 18, 1983, coll. Monteith, Davies, Gallon & Thompson; AUSTRALIA: Queensland, Kroombit Tops, northern escarpment; December 9 – 19, 1983, coll. V.E. Davies & J Gallon
Corinnidae	Castianeirinae	<i>Leptopicia</i>	<i>bimaculata</i>	
Corinnidae	Castianeirinae	<i>Nucastia</i>	<i>virewoods</i>	
Corinnidae	Castianeirinae	<i>Nyssus</i>	<i>albopunctatus</i>	AUSTRALIA: Queensland, N. Stradbroke Is, Dunwich, Bayside Mine; December 8, 1997 – January 19, 1998, coll. Norman Scott, pitfall; AUSTRALIA: Queensland, Carnarvon Station, nr. Peibald Spring; December 13, 2010 – June 15, 2011, coll. C. Zwick & C. Wilson
Corinnidae	Castianeirinae	<i>N.</i>	<i>coloripes</i>	AUSTRALIA: Queensland, Carnarvon Station; October 9 – 16, 2014, coll. B. Baehr; AUSTRALIA: Queensland, Carnarvon Station, nr. Peibald Spring November 24, – December 13, 2010, coll. C. Zwick & C. Wilson
Corinnidae	Castianeirinae	<i>N.</i>	<i>paradoxus</i>	AUSTRALIA: Queensland, Cudmore NP; October 27, 2010 – August 2, 2011, coll. Lambkin, Starick & Bailey
Corinnidae	Castianeirinae	<i>N.</i>	<i>semifuscus</i>	AUSTRALIA: Queensland, Chelsea Rd Bushlands Res; 27°29.0'S, 153°11.3'E, 15m; April 16 – May 27, 2003
Corinnidae	Castianeirinae	<i>N.</i>	<i>yuggera</i>	AUSTRALIA: Queensland, Amamoor creek; January 15 – May 27, 2002, coll. G.B. Monteith
Corinnidae	Castianeirinae	<i>Ozcopa</i>	<i>colloffii</i>	AUSTRALIA: Queensland, Mossman Bluff Track; December 20, 1989 – January 15, 1990, coll. Monteith, Thompson & ANZSES; AUSTRALIA: Queensland, Bellenden-Ker Range; 500m; October 17 – 24, 1981, coll. EARTHWATCH/QLD, MUSEUM
Corinnidae	Castianeirinae	<i>Poecilopta</i>	<i>gloverae</i>	AUSTRALIA: Queensland, Brisbane; February 4 – 24, 2009, coll. T.B Churchill; AUSTRALIA: Queensland, Redlands, Hilliards Ck, nr Weippin Rd; November 21, – December 19, 2008, coll. QM/BAAM party
Corinnidae	Castianeirinae	<i>P.</i>	<i>kgari</i>	AUSTRALIA: Queensland, Karawatha forest; January 2 – 30, 2004, coll. QM party
Corinnidae	Castianeirinae	<i>Ticopa</i>	<i>australis</i>	AUSTRALIA: South Australia, Calperum station; March 1995, coll. K.R. Pullen; AUSTRALIA: Queensland “Windermere”, Glen Morgan; December 1990 – September 1991, coll. R.R., B.J. Symth

**Table 1. continued.**



### **Character coding and description:**

In this study 55, characters (44 binary, 11 multistate) were coded for the selected taxa (Table 1). Since few specimens were available, and are sometimes fragile, more destructive techniques, including dissection of internal genitalia were not used for this study. Many specimens are in a suboptimal condition with legs broken or missing and could not be confidently attributable to an individual specimen or sex. For this reason, many leg characters including spine characters were also not included in this study. Although many phylogenetically informative characters are found in these areas, the potential of missing or erroneous data as well as the destruction of scientifically fragile specimens was deemed too risky to pursue in this study. Autapomorphic characters were excluded from this study. These characters might serve as potential synapomorphies in future analysis of larger number of taxa. Several autapomorphies noted are as follows:

PMEs without convex lenses: (*Urozelotes rusticus*)

Posterior bulge on the ventral surface of the male palpal tibia (*Nyssus yuggera*)

Leg formula 1243: (*Kolora sauverubens*)

Exceptionally long and slender legs: (*Kolora sauverubens*)

Five spigots on the female PMS in linear position: (*Urozelotes rusticus*)

PLS cylindrical in shape: (*Urozelotes rusticus*)

The following characters were coded for this analysis, additive characters are indicated with an \*:

## Eyes

Spiders have a basic eye arrangement of eight eyes forming two transverse rows, an anterior row (AER) and a posterior row (PER). Individual eyes are named based on their location relative to this arrangement: anterior median eyes (AME), anterior lateral eyes (ALE), posterior median eyes (PME) and posterior lateral eyes (PLE). The relative eye size, distance from each other, as well as the curvature of eye rows were scored.

- 1) ***Posterior eye row curvature, in dorsal view; both genders:*** (0) procurved (Figs. 12f–h; Ramírez, 2014; figs. 10G, I; Haddad, 2013; figs. 14, 15); (1) straight to slightly recurved (Fig. 12e. Ramírez, 2014; figs. 4A, G, H; 10G, I, Haddad, 2013b; fig. 16).
- 2) ***Anterior eye row curvature, anterior view:*** (0) sexually dimorphic, straight in males, procurved in females; (1) not sexually dimorphic.
- 3) ***Anterior eye row curvature, non-dimorphic, anterior view; both genders:*** (0) procurved (Fig. 12b, d; Ramírez, 2014; figs. 13A, C; 14F, G; Haddad, 2013; figs. 14, 15); (1) straight (Fig. 12c; Ramírez, 2014; figs. 14F, G).

- 4) ***\*PME relative size; both genders:*** (0) noticeably smaller than PLE; (1) equal to PLE; (2) larger than PLE.
- 5) ***\*AME relative size; both genders:*** (0) noticeably smaller than ALE; (1) equal to ALE; (2) larger than ALE.
- 6) ***\*Distance between PMEs; both genders:*** (0) noticeably smaller than 0.5 the diameter of PME; (1) between 0.5 and the diameter of PME; (2) greater than diameter of PME.
- 7) ***\*Distance between PME and PLE; both genders:*** (0) noticeably smaller than 0.5 the diameter of PME; (1) between 0.5 and the diameter of PME; (2) greater than the diameter of PME.
- 8) ***Distance between AMEs; both genders:*** (0) noticeably smaller than 0.5 the diameter of AME; (1) greater than 0.5 and the diameter of AME.

### **Carapace**

The carapace is the dorsal sclerotized shield of the cephalothorax known as the prosoma; the cephalic region bears eyes anteriorly. The thoracic region is located posteriorly and is delimited anteriorly by the thoracic furrow. The area between the

anterior eyes and the anterior margin of the carapace is known as the clypeus. The area between the clypeus and the base of the chelicera may contain a small sclerite known as the chilum, which, when present, may be a single whole sclerite or divided into two separate sclerites.

- 9) **\*Relative clypeal height; both genders:** (0) about the diameter of AME; (1) clearly greater than the diameter of AME less than 3x the diameter of AME but less than 3x the diameter of the AME; (2) greater than 3x the diameter of AME.

(Haddad 2013; figs. 14–16).

- 10) **Chilum; both genders:** (0) whole (Fig. 12d; Ramírez, 2014; figs. 3A 13D, F 14C); (1) split. Fig. 12a; Ramírez, 2014; figs. 14A). In taxa examined for this study, the chilum can either be a single whole sclerite or two individual sclerites.

In some material examined the chilum presented with a deep cleft, this is considered a whole chilum in this study.

- 11) **Carapace margin; female:** (0) toothed (Fig. 12f; Raven 2015; fig 63); (1) smooth.

- 12) **\*Posterior carapace steepness; both genders:** (0) shallow (less than 30 degrees; Fig. 13a); (1) slight (between 30 and 50 degrees; Fig. 13b); (2) moderate (between 50 and 70 degrees; Fig. 13c); (3) steep (greater than 70 degrees; Fig. 13d). In

lateral view, an angle is measured from a horizontal line made by the ventral carapace and the posterior slope of carapace.

13) *Carapace widest anterior the fovea; both genders:* (0) present (Raven 2015; figs 51d, 63, 108a); (1) absent

14) *Carapace highly circular in dorsal view:* (0) present (Raven 2015; fig 16f); (1) absent

15) *Carapace length to width ratio; both genders:* (0) greater than 1.60; (1) less than or equal to 1.60. This metric is a measurement of how slender a carapace is. A more slender carapace may correlate to a spider's s ability to accurately mimic ants.

### Chelicerae

The chelicerae are the anterior appendages of a spider consisting of a basal paturon and an apical fang. Disto-medially, the paturon contains a groove in which the fangs rest when closed. This cheliceral groove is bordered promarginally and retromarginally by dentations known as cheliceral teeth. The anterior promarginal base of the paturon has an ovoid shield in many specimens examined, known as the fang shield mound (Raven, 2015) or cheliceral promargin pronounced mound (Ramírez, 2014). This mound bears a line of setae that are strongly modified or ornamented in many females examined (see Raven, 2015 figs 4d-f, 20f, 22c, 24e, 47b, c, 48c, 128e, f, 129c, 131b, c,

133b). Dentations seen on the retro- and promargin of the chelicera and are here referred to as retromarginal and promarginal cheliceral teeth. This character is as referred to as “furrow dentation” (Raven, 2015). Ramírez (2014) used a presence/absence of cheliceral teeth (Ramírez, 2014 characters 47 and 48) whereas Haddad, (2013) used tooth counts (Haddad, 2013 characters 26—28). In this study, the use of tooth counts was most informative and therefore used.

16) ***Fang shield mound present; female:*** (0) present Figs. 14d, e; Ramírez, 2014; figs. 18E, 23C, F, 24C—E; (1) absent.

17) ***\*Setae on fang shield mound; female:*** (0) unmodified setae; (1) thick dentate setae (Figs. 14b, e); (2) stout dentate spines. (Figs. 14a, d; Ramírez, 2014; figs. 20D). In many females examined the setae on the fang shield are thickened and modified; this character is common in the Australian fauna examined, yet only noted in a few New World species by Reiskind (1969).

*U. rusticus*, *A. grassima*, *C. gulosus* and *S. bicalcarata* scores as (-) due to the lack of a fang shield mound in these taxa.

18) ***Fang groove; both genders:*** (0) transverse; (1) diagonal. (Raven 2015; fig. 25d).

19) ***Cheliceral promarginal teeth; both genders:*** (0) 3 (Figs. 14b, c); (1) 2.

20) ***Cheliceral retromarginal teeth; both genders:*** (0) more than 3 teeth (Fig. 14c); (1) 3 teeth; (2) 2 or fewer teeth (Fig. 14b).

## Male Pedipalp

The most anterior pair of leg-like appendages are known as the pedipalps. The pedipalps of mature male spiders bear the secondary genitalia. A copulatory bulb is attached to the modified tarsus known as the cymbium. The copulatory bulb consists of one or more sclerites and an internal sperm duct terminating at the tip of the embolus where the sperm is discharged. In many castianeirine spiders, the cymbium is canoe-shaped, and the copulatory bulb is a simple, pyriform structure. Complexity of the bulb, embolus shape, as well as looping of the sperm duct, is taken into consideration. Ornamentation on the cymbium and modifications of the pedipalp femur and tibia are also considered.

21) ***Paracymbial spine (PCS)***: (0) present; (Figs. 11b, f); (1) absent. A socketed spine on the retrolateral surface of the male cymbium is seen in many of the Australian species (Raven 2015 figs. 15b, d, 20e, 23e, 33a, 113c, 130a, c, f, 134c, d) but absent in most New World Castianeirinae. However, *Myrmecotypus olympus* Reiskind 1969 is noted as having “A group of thick, heavy spines near the base of the cymbium, near the lateral edge” (Reiskind 1969, fig. 261). Likewise, in *Castianeria trilineata* (Hentz), Reiskind describes the basal portion of the lateral side of the cymbium as bearing a heavy spine. This character is noted for

Southeast Asian species of *Corinnomma* (Deeleman-Reinhold 2001, fig. 469) and found in many Madagascan species (Raven 2015).

22) ***Retrolateral cymbial process***: (0) present (Bonaldo 2000; figs. 267, 268, 271, 271); (1) absent. The retrolateral cymbial process is an unsocketed process or bulge seen in Corinninae spiders.

23) ***Prolateral cymbial process***: (0) present (Bonaldo 2000; figs. 267); (1) absent. The prolateral cymbial process is an unsocketed process or bulge seen in Corinninae spiders.

24) ***Copulatory bulb complexity***: (0) complex (Figs. 11a, g); (1) simple (limited to bulb and embolus). Most Castianeirinae spiders possess a simple bulb consisting of a tear-shaped bulb with a sclerotized embolus; in Corinninae and in few Castianeirinae, the bulb possesses accessory structures (Raven 2015 figs. 10a, b; 93a—f; 94a—e; 95a, b).

25) ***Conductor***: (0) present (Figs. 11a, g; Ramírez, 2014, figs. 148A; 154C; 159G; 162A; C; Raven 2015, fig. 10b); (1) absent (Ramírez, 2014, figs. 163E; 166E). When present the conductor can be hyaline or sclerotized. This structure is associated with the male embolus and putatively help directs the embolus into the female epigynum. Absent in Castianeirinae but present in Corinninae. The



complexity of the palpal bulb of *Ozocopa colloffi* is reminiscent of a conductor, but is clearly a secondary lobe and therefore is not homologous.

26) ***Pre-embolic ridge***: (0) present (Figs. 11b, c); (1) absent. (Raven 2015, fig. 113a).

A plateau-like ridge at the base of the embolus seen in many males examined.

This character was unable to be determined due to the complexity of the palp bulb in *Ozocopa colloffi* and was scored as a “?”.

27) ***Embolus with micro-sculpturing***: (0) present (Fig. 11c; Raven, 2015, fig. 134b); (1) absent.

28) ***Terminal embolic shape***: (0) curve, no twist (Figs. 1a, c, g; Raven 2015, figs. 10a; 36b, c; 93f; 127b); (1) open spiraled twist (corkscrew-shaped) (Figs. 11b, d, f; Raven 2015; figs. 26d, e; 38a—d; 41a, b; 74a, b, e, f; 80a,b; 112a, b); (2) tight, closed twist (screw shape) (Fig. 11e Raven 2015; figs. 50a, b, f).

29) ***Spiraled sperm duct***: (0) present (Fig. 11a; Ramírez, 2014, fig. 158E); (1) absent.

30) ***Sperm duct with simple looping***: (0) present (Fig. 11b, f; Ramírez, 2014, fig. 158D); (1) absent.

31) ***Retrolateral tibial apophysis (RTA)***: (0) present (Figs. 11a, f, g; Ramírez, 2014; figs. 161F, 166F, Raven 2015; figs. 88a—c); (1) absent. A true RTA is absent

from all Castianeirinae examined except *Nyssus paradoxus* (Fig. 11f). The RTA described by Reiskind (1969) for Castianeirinae is a protuberance formed from a fold in the tibia and a ventral tibial concavity, so is not considered a true RTA.

32) ***Comb of setae on the retrolateral tibia:*** (0) present; (1) absent. A line of typically modified setae seen on the retrolateral tibia. A line of similarly modified setae is seen emerging from the distal edge of the RTA in *N. paradoxus* and is scored as (0).

33) ***Prolateral tibial apophysis:*** (0) present; (1) absent.

34) ***Ventral prodistal modification of the male palp tibia:*** (0) present; (1) absent. A ledge or lip produced on the distal edge of the proventral surface of the tibia.

35) ***Ventral palp femur modification, male:*** (0) present (Fig. 11h; Raven 2015; fig. 53c); (1) absent. The ventral surface of the male pedipalp femur is typically ovoid-cylindrical; however, members of the genus *Leichhardtus* examined show a subtle lump to a large conical projection.

## Leg Characters

Spiders have eight legs in four pairs. Each leg consists of seven articles, proximal to distal: coxa, trochanter, femur, patella, tibia, metatarsus and tarsus.

36) ***Retrocoxal hymen (RCH); both genders:*** (0) present (Fig. 15a; Ramírez, 2014; figs. 3A, 49A-D, Bosselaer & Jocque 2002; fig. 1A); (1) absent. The RCH is a weakly sclerotized portion of the first coxae forming a ‘window’.

37) ***Coxae III with dorsal extension; both genders:*** (0) present; (1) absent. The dorsum of the third coxae is typically unmodified and smooth; however, a small bump is seen on some examined specimens.

38) ***Notched trochanters; both genders:*** (0) present; (1) absent.

39) ***Ventral femur constriction; both genders:*** (0) present (Fig. 15c); (1) absent (Fig. 15b). The basal portion of the third and fourth femur is interrupted by a sudden and steeply angulated constriction on the ventral surface.

40) ***Scopula; both genders:*** (0) present; (1) absent. Scopula is seen as a dense brush of setae along the ventroapical surface of the legs

41) ***Leg IV much longer than legs I – III; both genders:*** (0) present (Raven 2015; fig 99a–c); (1) absent.

## **Abdomen**

The abdomen or opisthosoma is the posterior division of a spider's body. It articulates the prosoma anteriorly via the pedicel. The pedicel is a narrowed connection sometimes referred to as the spiders "waist". The abdomen terminates distally with silk producing structures known as spinnerets. The abdomen may be armored dorsally and ventrally by sclerotized plates. The abdomen may be patterned with setae, or have physical constrictions. These constrictions are seen as a mimetic character, emulating the multiple body regions seen in Hymenoptera.

42) ***Abdominal constriction; both genders:*** (0) present; (1) absent. A mimetic character. In some species that mimic ants, the abdomen possesses a transverse constriction presumably helping to emulate an ant's petiole, postpetiole and gaster.

### **Abdominal sclerites**

Many Castianeirinae have sclerotized plates dorsally and ventrally on the abdomen. These plates are typically larger in males and specific sclerites may occasionally be absent in females. Presence and size of these sclerites are considered informative.

43) ***Dorsal sclerite relative length; male:*** (0) greater than 0.5 abdominal length; (1) less than or equal to 0.5 abdominal length

- 44) **Dorsal sclerite relative length; female:** (0) greater than 0.5 abdominal length (Fig. 16a; Ramírez, 2014; fig. 101I); (1) less than or equal to 0.5 abdominal length (Fig. 16c–d; Ramírez, 2014; fig. 101A); (2) absent (Ramírez, 2014; fig. 101G).
- 45) **Ventral sclerite; male:** (0) present (Figs. 17b–d; Ramírez, 2014 figs. 101D, H); (1) absent (Figs. 17a, e). The ventral sclerite is the ventral, or post epigastric sclerite and is not seen in any females examined in this study.
- 46) **Tracheal sclerite; both genders:** (0) present (Figs. 17); (1) absent.
- 47) **Ventral sclerite fused to tracheal sclerite; male:** (0) fused Figs. 17d; (1) unfused (Figs. 17a–c, e). *U. rusticus*, *A. grassima*, *Creugas gulosus*, *S. bicalcarata*, *Copa kabana*, *Leichhardteus* spp., *N. coloripes*, *N. semifuscus* and *T. australis* lacked a ventral and/or a tracheal sclerite so scored a “-”.

## Scales

Many forms of setae adorn the body of spiders many of which are sensory in nature and aid in the spider’s ability to interact with the natural world. However, several forms of setae lack innervation, and lay appressed to the body surface. These are collectively referred to as scales. In many Castianeirinae these scales appear to assist in coloration and patterning. Many scales examined are branched to varying degrees. The presence of these scales as well as their morphology is considered.

- 48) ***Branched scales; both genders:*** (0) present (Figs. 18a–f; Ramírez, 2014 figs. 92D, F); (1) absent. Scales with at least one pair of obvious lateral appendages scored a (0) different from feathery scales, seen character 50.
- 49) ***Branched scales proximally constricted; both genders:*** (0) present (Figs. 18a–c); (1) absent.
- 50) ***Spine-like scale, shaft textured and edge serrate; both genders:*** (0) present (Fig. 18h); (1) absent.
- 51) ***Scales with single lateral appendage; both genders:*** (0) present (Fig. 18g); (1) absent.
- 52) ***Feathery scale; both genders:*** (0) present (Fig. 18f); (1) absent. In this study, a feathery scale is defined as a relatively long and slender scale with numerous short closely spaced lateral appendages. These scales when present are typically seen forming light colored patterns.

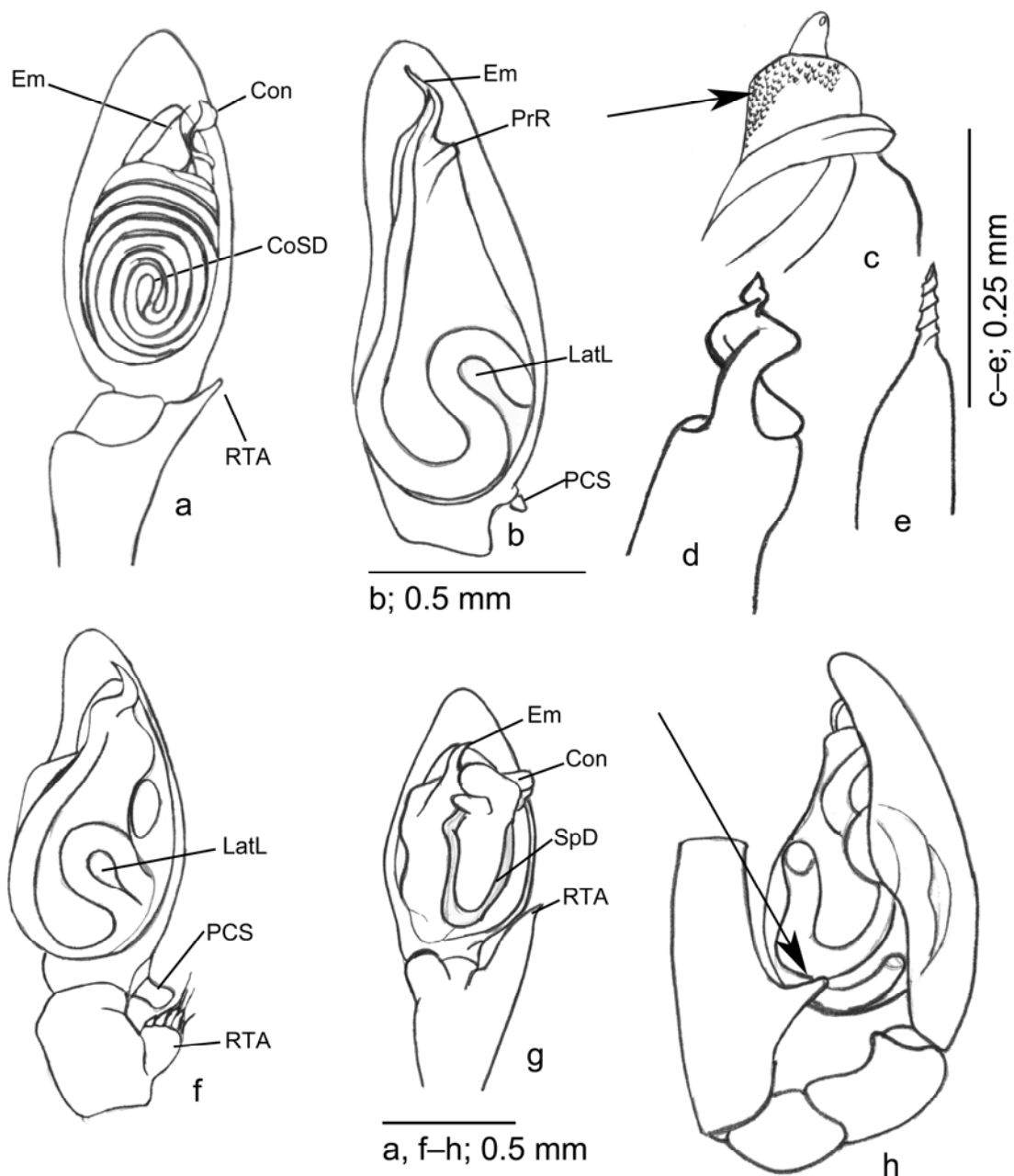
### **Pattern**

Pattern on the carapace, abdomen and legs are considered.

- 53) ***Carapace, abdomen and legs densely covered in setae; both genders:*** 0) present; (1) absent.

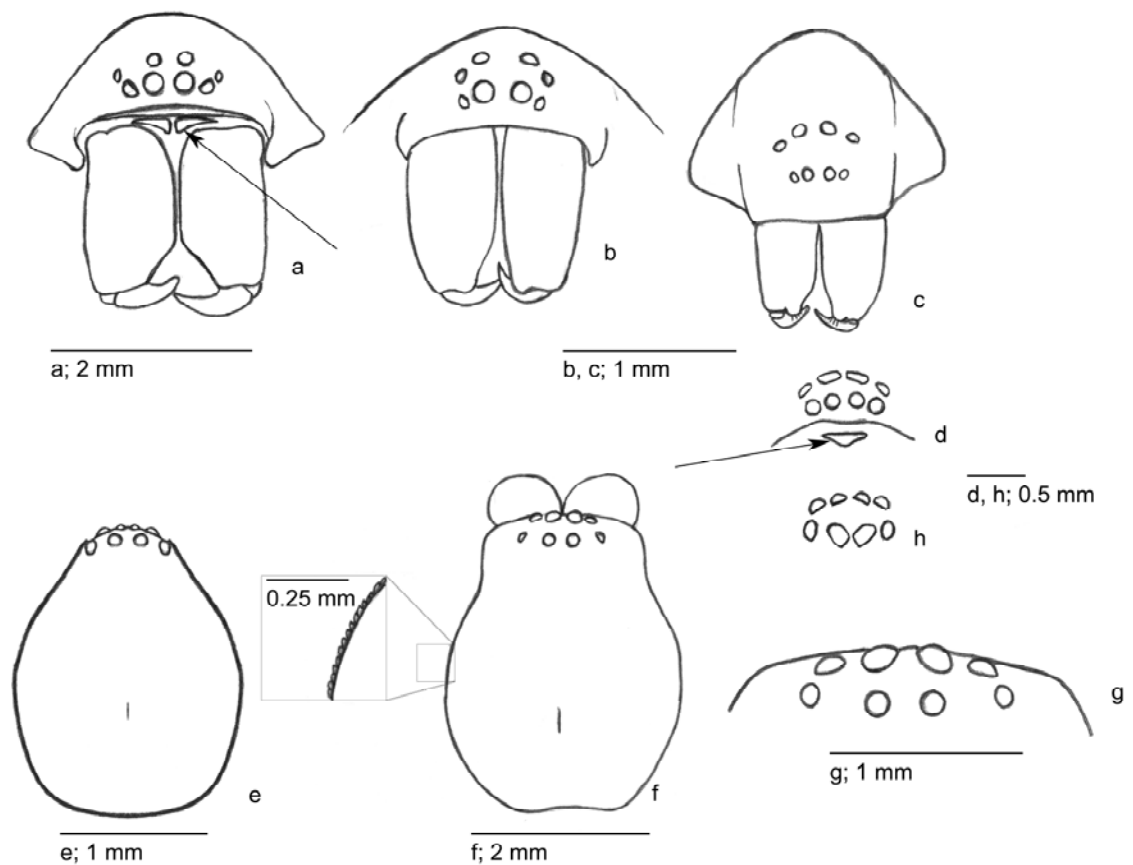
54) *Carapace and body with spots and radiating lines of white, yellow or orange setae; both genders:* 0) present (Raven 2015; figs. 73, 79, 80, 84); (1) absent.

55) *Paramedial pattern on cuticle of carapace; both genders:* 0) present (Raven 2015; fig. 126f); (1) absent.

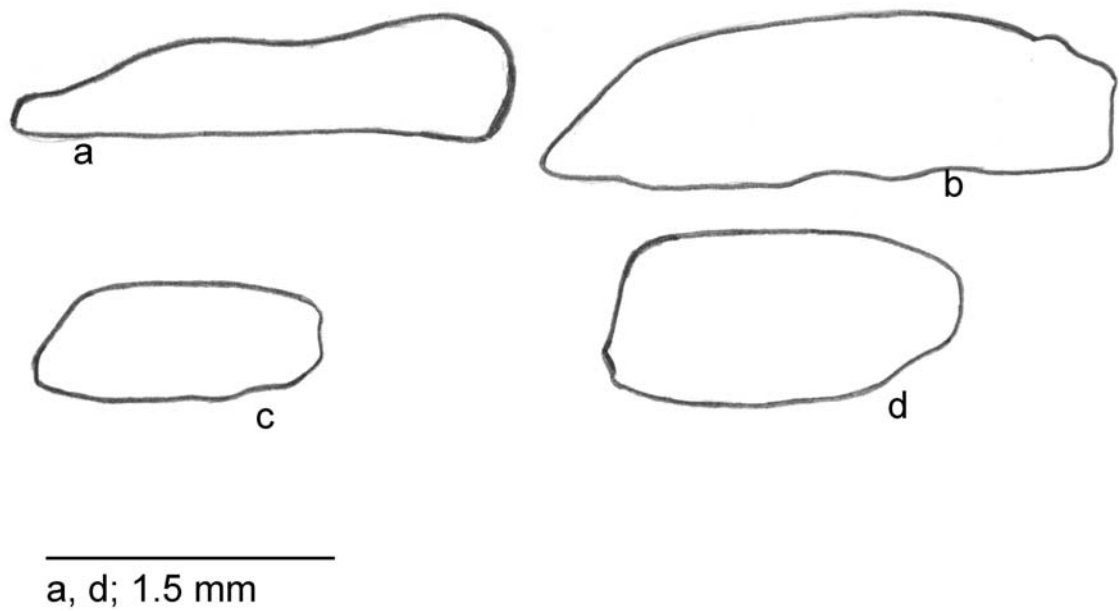


**Figure 11.** Corinnidae and Gnaphosidae, left male pedipalp: a, *Abapeba grassima*, ventral view; b, *Battalus wallum*, ventral view; c, *Ticopa australis*, distal portion of palp bulb arrow indicating micro-sculpturing on embolus; d, *Nyssus yuggera*, embolus; e, *Kolora sauerubens* embolus; f, *Nyssus paradoxus*, ventral view; g, *Urozelotes rusticus*, ventral view; h, *Leichhardteus conopalpis*, left lateral view arrow indicating ventral palp femur modification. Abbreviations: Con—conductor; CoSD—spiraled sperm duct; Em—embolus; LatL—lateral loop of the sperm duct; PCS—paracymbial spine; PrR—pre-embolic ridge; RTA—retrolateral tibial apophysis; SpD—sperm duct.

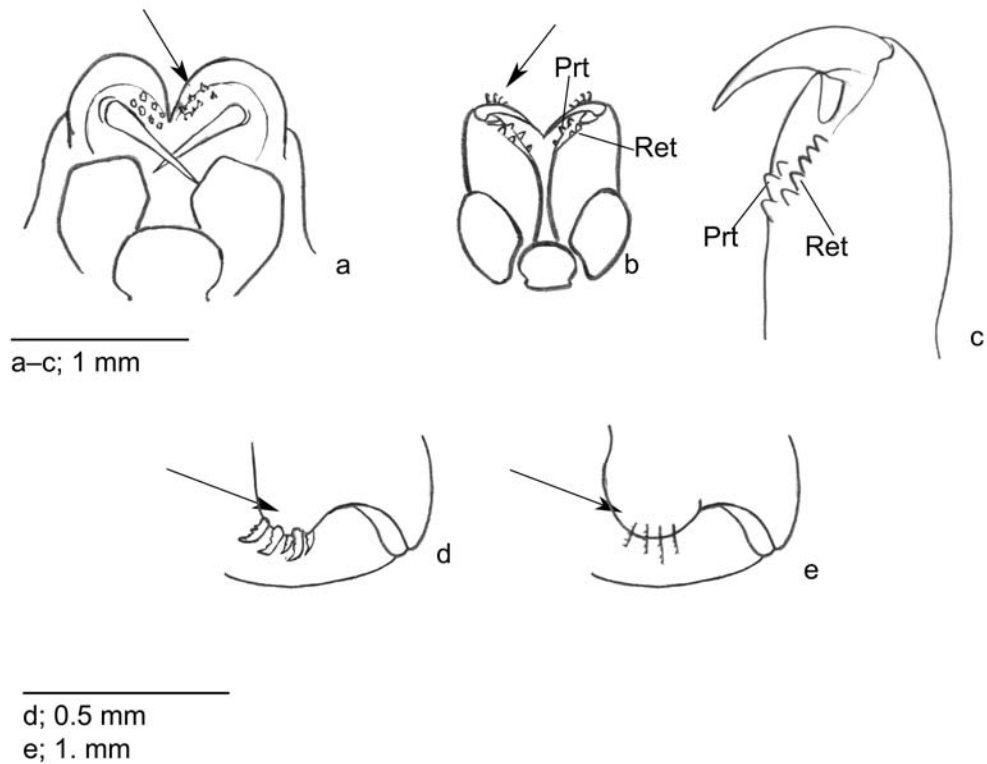




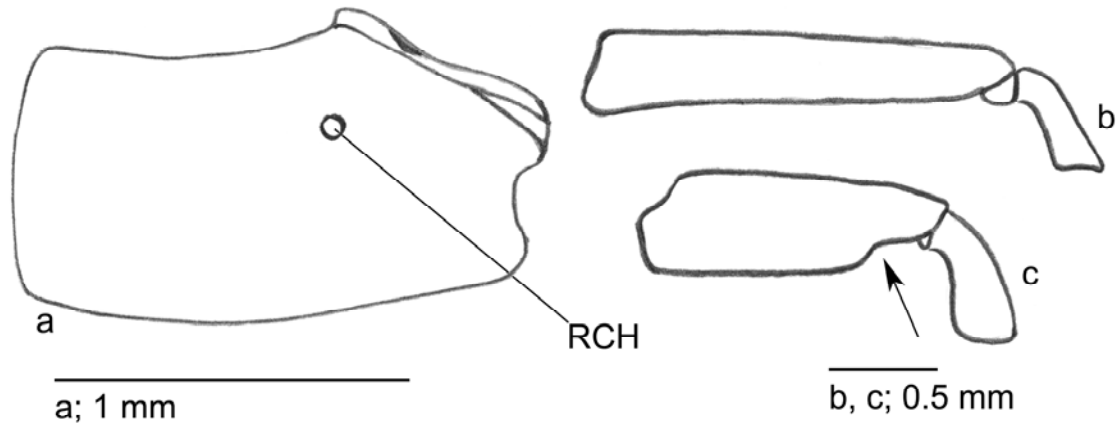
**Figure 12.** Corinnidae and Gnaphosidae, carapace and eyes: a, *Creugas gulosus*, anterior view, arrow pointing to chilum; b, *Copa kabana*, anterior view; c, *Poecilipta gloverae*, anterior view; d, *Urozelotes ruscitus*, eye arrangement, anterior view, arrow pointing to chilum; e, *Disnyssus helenmirrenae*, dorsal view; f & g, *Creugas gulosus*, female; f, dorsal view, box highlighting toothed carapace margin; g, eye arrangement in dorsal view; h, *Urozelotes rusticus* dorsal view anterior eye row above.



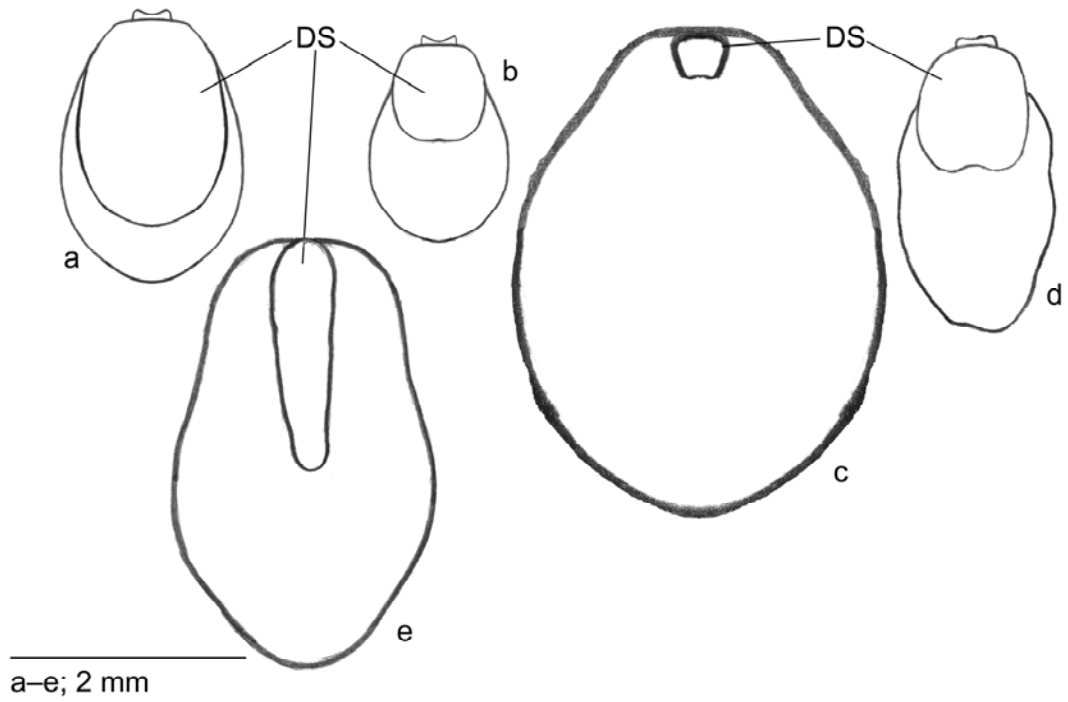
**Figure 13.** Corinnidae, comparative right lateral view of carapace steepness: a, *Kolora sauerubens*; b, *Leichhardteus conopalpis*; c, *Nyssus albopunctatus*; d, *Iridonyssus formicans*.



**Figure 14.** Corinnidae, female chelicera: a, *Battalus adamparsoni*, ventral view, arrow pointing modified spine-like setae on fang shield; b, *Poecilipta gloverae*, ventral view, arrow pointing modified dentate setae on fang shield; c, *Abapeba grassima*, left chelicera ventral view; d *Battalus adamparsoni*, distal portion of left chelicera, arrow pointing to fang shield mound; e, *Poecilipta gloverae*, distal portion of left chelicera, arrow pointing to fang shield mound. Abbreviations: Prt—promarginal cheliceral teeth; Ret—retromarginal cheliceral teeth.



**Figure 15.** Corinnidae, coxa, femur and patella: a, *Septentrinna bicalcarata*, left coxa I left lateral view; b, *Poecilopta gloverae*, left femur and patella III right lateral view; c, *Disneyssus judidenchae*, left femur and patella III right lateral view, arrow pointing to ventral femur constriction. Abbreviations: RCH—retrocoxal hymen.



**Figure 16.** Corinnidae, dorsal abdomen comparing dorsal sclerite: a, *Iridonyssus kohouti* female, dorsal view; b, *Iridonyssus formicans*, female, dorsal view; c, *Battalus wallum*, female, dorsal view; d, *Poecilopta kgari*, female, dorsal view; e, *Creugas gulosus*, male, dorsal view. Abbreviations: DS—dorsal sclerite.

**Figure 17.** Corinnidae, ventral male abdomen comparative: a, *Nyssus semifuscus* male, ventral view; b, *Nyssus yuggera* male, ventral view; c, *Nyssus paradoxus* male, ventral view; d, *Iridonyssus formicans* male, ventral view; e, *Creugas gulosus* male, ventral view. Abbreviations: GS—genital sclerite; VS—ventral sclerite; TS—tracheal sclerite.

**Figure 18.** Corinnidae, scales: a, *Septentrinna bicalcarata*, branched scale; b, *Battalus adamparsoni*, branched scale; c, *Creugas gulosus*, branched scale; d, *Nyssus paradoxus*, branched scale; e, *Iridonyssus formicans*, branched scale; f, *Poecilopta gloverae*, highly branched feathery scale; g, *Kolora sauverubens*, single branched scale; h, *Abapeba grassima*, scale.

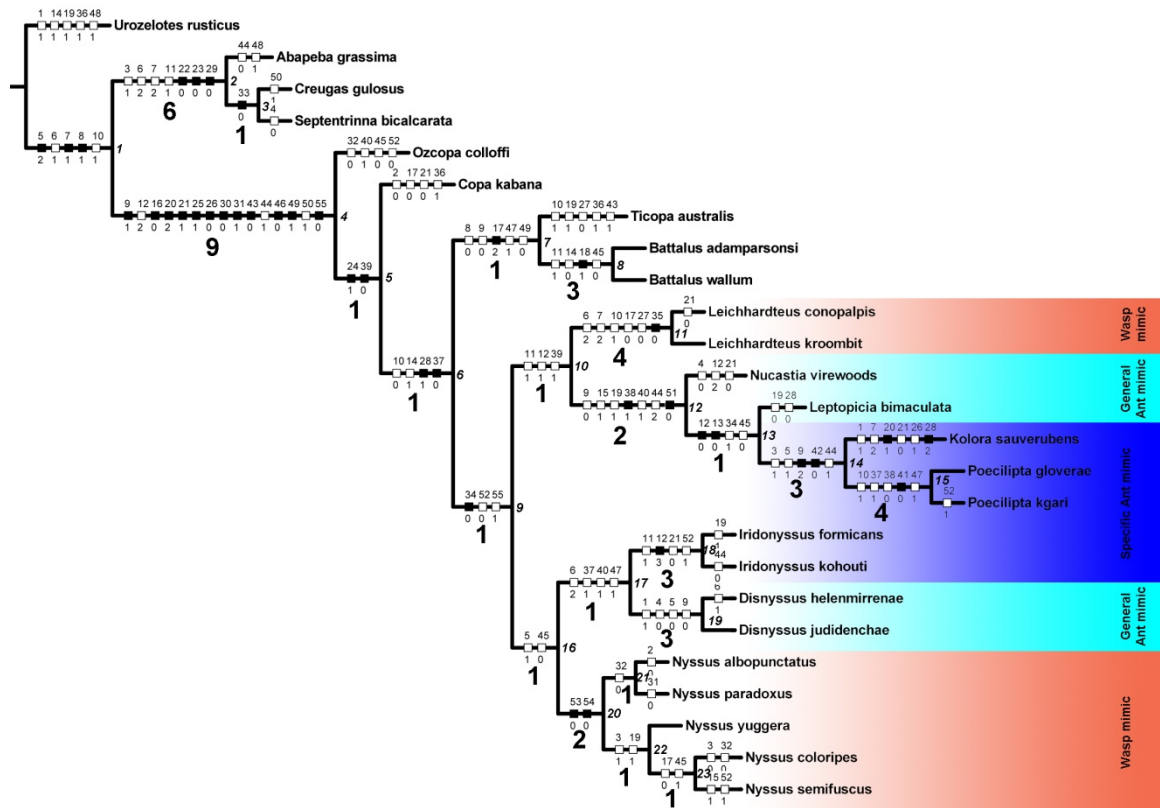
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3				
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	
				+	+		+	+		+							+														
<i>Urozelotes rusticus</i>	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	-	0	1	0	0	1	1	0	0	1	1	0	1	1	
<i>Abapeba grassima</i>	0	1	1	1	2	2	2	1	0	1	1	1	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	1
<i>Creugas gulosus</i>	0	1	1	1	2	2	2	1	0	1	1	1	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	1
<i>Septentrinna bicalcarata</i>	0	1	1	0	2	2	2	1	0	1	1	1	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	1
<i>Battalus adamparsonsi</i>	0	1	0	1	2	1	1	0	0	0	1	2	1	0	0	0	2	1	0	2	1	1	1	1	1	0	1	1	1	1	0
<i>B. wallum</i>	0	1	0	1	2	1	1	0	0	0	1	2	1	0	0	0	2	1	0	2	1	1	1	1	1	0	1	1	1	1	0
<i>Copa kabana</i>	0	0	?	1	2	1	1	1	1	1	0	2	1	0	0	0	0	0	0	2	0	1	1	1	1	1	0	1	0	1	0
<i>Disnyssus helenmirrenae</i>	1	1	0	0	0	1	1	1	0	0	0	2	1	1	0	0	1	0	0	2	1	1	1	1	1	1	0	1	1	1	0
<i>D. judidenchae</i>	1	1	0	0	0	2	1	1	0	0	0	2	1	1	0	0	1	0	0	2	1	1	1	1	1	1	0	1	1	1	0
<i>Iridonyssus formicans</i>	0	1	0	1	1	2	1	1	1	0	1	3	1	1	0	0	1	0	1	2	0	1	1	1	1	1	0	1	1	1	0
<i>I. kohouti</i>	0	1	0	1	1	2	1	1	1	0	1	3	1	1	0	0	1	0	0	2	0	1	1	1	1	1	0	1	1	1	0
<i>Kolora saurverubens</i>	1	1	1	1	1	1	2	1	2	0	1	0	0	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	2	1	0
<i>Leichhardteus conopalpis</i>	0	1	0	1	2	2	2	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	1	1	1	1	0	0	1	1	0
<i>L. kroombit</i>	0	1	0	1	2	2	2	1	1	1	1	1	1	1	0	0	0	0	0	2	1	1	1	1	1	1	0	0	1	1	0
<i>N. albopunctatus</i>	0	0	?	1	1	1	1	1	1	0	0	2	1	1	0	0	1	0	0	2	1	1	1	1	1	1	0	1	1	1	0
<i>N. coloripes</i>	0	1	0	1	1	1	1	1	1	0	0	2	1	1	0	0	0	0	1	2	1	1	1	1	1	1	0	1	1	1	0
<i>N. paradoxus</i>	0	1	0	1	1	1	1	1	1	0	0	2	1	1	0	0	1	0	0	2	1	1	1	1	1	1	0	1	1	1	0
<i>N. semifuscus</i>	0	1	1	1	1	1	1	1	1	0	0	2	1	1	1	0	0	0	1	2	1	1	1	1	1	1	0	1	1	1	0
<i>N. yuggera</i>	0	1	1	1	1	1	1	1	1	0	0	2	1	1	0	0	1	0	1	2	1	1	1	1	1	1	0	1	1	1	0
<i>Ozcopa colloffi</i>	0	1	0	1	2	1	1	1	1	1	0	2	1	0	0	0	1	0	0	2	1	1	1	0	1	?	1	0	1	0	
<i>Poecilipta gloverae</i>	0	1	1	1	1	1	1	1	2	1	1	0	0	1	1	0	1	0	1	2	1	1	1	1	1	1	0	1	1	1	0
<i>P. kgari</i>	0	1	1	1	1	1	1	1	2	1	1	0	0	1	1	0	1	0	1	2	1	1	1	1	1	1	0	1	1	1	0
<i>Ticopa australis</i>	0	1	0	1	2	1	1	0	0	1	0	2	1	1	0	0	2	0	1	2	1	1	1	1	1	1	0	0	1	1	0
<i>Leptopicia bimaculata</i>	0	1	0	1	2	1	1	1	0	0	1	0	0	1	1	0	1	0	0	2	1	1	1	1	1	1	0	1	0	1	0
<i>Nucastia virewoods</i>	0	?	?	0	2	1	1	1	0	0	?	2	1	1	1	0	1	0	1	2	0	1	1	1	1	1	0	1	1	1	0

**Table 2.** Data matrix for twenty-five taxa and fifty-five morphological characters used in the cladistic analysis of Australian Castianeirinae. Additive characters are marked with a “+”, missing or unobserved data with “?” and inapplicable characters with “-”.



	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	
<i>Continued</i>	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
<i>Urozelotes rusticus</i>	0	1	1	1	1	1	1	0	1	0	1	1	1	2	1	1	-	1	-	0	1	1	1	1	1
<i>Abapeba grassima</i>	0	1	1	1	1	0	1	0	1	0	1	1	1	0	1	1	-	1	-	0	1	1	1	1	1
<i>Creugas gulosis</i>	0	1	0	1	1	0	1	0	1	0	1	1	1	2	1	1	-	0	0	1	1	1	1	1	1
<i>Septentrinna bicalcarata</i>	0	1	0	1	1	0	1	0	1	0	1	1	1	2	1	1	-	0	0	0	1	1	1	1	1
<i>Battalus adamparsonsi</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	0
<i>B. wallum</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	0
<i>Copa kabana</i>	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	0	-	0	1	1	1	1	1	0	0
<i>Disnyssus helenmirrenae</i>	1	1	1	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	1	1	1
<i>D. judidenchae</i>	1	1	1	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	1	1	1
<i>Iridonyssus formicans</i>	1	1	1	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	1	1	1	1
<i>I. kohouti</i>	1	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1
<i>Kolora sauerubens</i>	1	1	1	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	1	1	1
<i>Leichhardteus conopalpis</i>	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0	-	0	1	1	1	0	1	1	1
<i>L. kroombit</i>	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0	-	0	1	1	1	0	1	1	1
<i>N. albopunctatus</i>	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1
<i>N. coloripes</i>	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	-	0	1	1	1	0	0	0	1
<i>N. paradoxus</i>	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1
<i>N. semifuscus</i>	1	1	1	0	1	0	0	0	0	0	1	1	0	1	1	0	-	0	1	1	1	1	0	0	1
<i>N. yuggera</i>	1	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1
<i>Ozcopa colloffi</i>	1	0	1	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	1	1	1	0	1	1	0
<i>Poecilipta gloverae</i>	1	1	1	1	1	0	1	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	1	1	1
<i>P. kgari</i>	1	1	1	1	1	0	1	0	1	1	0	0	0	1	0	0	1	0	1	1	1	0	1	1	1
<i>Ticopa australis</i>	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	-	0	0	1	1	1	1	0	0
<i>Leptopicia bimaculata</i>	1	1	1	?	1	0	?	1	1	1	1	1	0	2	0	0	0	0	?	?	?	?	1	1	1
<i>Nucastia virewoods</i>	1	1	1	0	1	0	?	1	1	1	1	1	0	2	1	0	-	0	1	?	?	?	1	1	1

**Table 2.** *Continued.*



**Figure 9.** Single most parsimonious cladogram for Australian Castianeirinae (143 steps, CI 45, RI 71) characters mapped using ACCTRAN (fast) optimization. Numbers above hatchmarks refer to character. Numbers below hatchmarks indicate character state transformations to the state indicated. Homoplasious character state transformations indicated by open hatchmarks. Bold numbers below branches indicate Bremer support values. Italic numbers represent nodes referred to in text. Gradient colors highlight terminal taxa exhibiting various mimetic adaptations; orange, wasp mimics; light blue, general ant mimics; dark blue, specific ant mimics.

## Results and conclusions

The analysis of the 25 terminal taxa resulted in a single most parsimonious tree (Length = 143, CI = 45, RI = 71) (Fig 19).

Monophyly of the Corinninae and Castianeirinae subfamilies are highly supported with branch support of six for the Corinninae and nine for the Castianeirinae. Characters supporting the monophyly of the Corinninae, united at node 2, include: (1) presence of a non-socketed retrolateral cymbial process, (character 22); (2) a prolateral cymbial process, (character 23); (3) and a spiraled sperm duct (character 29, Fig. 11a).

The subfamily Castianeirinae is united at node 4 with very strong branch support, nine, and by a number of characters in this study including: (1) The presence of a fang shield mound on the female (character 16, Fig. 14d, e); (2) the presence of 3 or fewer retromarginal cheliceral teeth (character 20, Figs. 14a–c); (3) The copulatory bulb lacking secondary sclerites such as a conductor (character 25, Fig. 11b, f); (4) A sperm duct with simple looping (character 30, Figs. 11b, f, h); and (5) The presence of a tracheal sclerite in male spiders (character 46, Fig. 17).

Having a relatively simple, tear-shaped palpal bulb, a commonly accepted synapomorphy of the Castianeirinae (character 24; state 1) (Reiskind 1969; Deeleman-Reinhold 2001; Bosselaers & Jocqué 2002; Haddad 2013b; Candiani & Bonaldo 2017) unites all but *Ozcopa*, the most basal genus of Casitineirinae examined, and is found in all the Castianeirinae united at node 5. A second commonly accepted synapomorphy of Castianeirinae is the lack of a true RTA (character 31; state 1). In this study, this

character unites all the Castianeirinae with the exception of an independent evolution of this character in *Nyssus paradoxus* (character 31, Fig. 11f).

The presence of a paracymbial spine (character 21) unites all the Castianeirinae at node 4 with several reversals occurring on the tree. A pre-embolic ridge (character 26) is seen in all Castianeirinae except this trait is ambiguous in *Ozcopa colloffi* due to the complex palpal bulb present, and is lost in *Kolora sauerubens*. A large dorsal sclerite (character 43), also unites the Castianeirinae in this study with a single loss in *Ticopa australis*.

The clade formed at node 7 contains *Ticopa* and *Battalus*. This clade has a low branch support of one but are united by each of these species having the AMEs separated by less than half their diameter (character 8), possessing branched scales that are proximally constricted (character 49 Figs. 18a, b, h) and dentate setal spines on the fang shield mound of the female chelicera (character 17, Fig. 14a). The two species of *Battalus* examined form a monophyletic clade, branch support of three. They are sister to *Ticopa* and supported by a diagonally positioned fang and groove, (character 18).

All taxa united at node 9 represent those species identified visually as hymenoptera mimics. This clade has low branch support of one and is divided into two separate clades at node 10 and node 16. The large group united at node 10, branch support of one, contains the wasp mimicking genus *Leichhardteus*, the general ant mimicking genera *Nucastia* and *Leptopicia* and the specific ant mimics *Kolora* and *Poecilopta*. Members of the genus *Leichhardteus* are contained in node 11 have relatively high branch support of four and are supported by having ventral palp femur

modifications, a synapomorphy of this genus (character 35), PME's separated by more than their diameter (character 6), by having the PME and PLE separated by more than the diameter of the PME's (character 7), and having unmodified setae in the fang shield mound of the female chelicera (character 17). Many of these characters are homoplastic, however and are seen occurring throughout the tree. Node 12 contains the ant mimicking genera *Nucastia*, *Leptopicia*, *Kolora* and *Poecilipta*. This node has a branch support of two and these species all possess a long narrow carapace, a character also seen in *Nyssus semifuscus* (character 15). Although ambiguous in *Nucastia* and *Leptopicia*, the evolution of scales with a single lateral appendage (character 51) also unites this node, as well as un-notched trochanters (character 38), with a return of notched trochanters in the genus *Poecilipta*. The genera *Leptopicia*, *Kolora* and *Poecilipta* are united at node 13 and all possess a shallow slope at the posterior carapace (character 12; Fig. 13a) and have the carapace widest anterior to the fovea (character 19). The clade including the genera *Kolora* and *Poecilipta* are united at node 14 are well supported with a branch support of three and are characterized by containing specific ant-mimics, and each species having abdominal constrictions (character 42), and having a very tall clypeus of more than twice the diameter of the AME's (character 9). The genus *Poecilipta* is well supported with a branch support of four and forms a monophyletic clade at node 15. This clade is united by having leg IV noticeably much longer than legs I–III (character 41) a synapomorphy for this genus.

A second large clade formed at node 16 contains the specific ant mimicking genus *Iridonyssus* as well as the general ant mimicking genus, *Disnyssus* and the wasp mimicking genus *Nyssus*. Species contained in this node have low support value of one,

and all have AMEs equal to or smaller than ALE (character 5). The AMEs are equal in size to the ALEs in *Iridonyssus* and *Nyssus* but have reduced to a size smaller than the ALEs in *Disnyssus*. Having AMEs equal in size to the ALE also occurs in the genus *Poecilopta*. Members of the genus *Iridonyssus* are united at node 18 with good branch support of three, these spiders possess a very steep slope at the posterior carapace (character 12; Fig. 13d) a synapomorphy for this genus. Members of the genus *Disnyssus* are united at node 19 with good branch support of three. These spiders have PER straight to recurved from above (character 1) a synapomorphy for this genus. Members of the genus *Nyssus* are united at node 22 with branch support value of two and is notable for containing wasp mimics, they are distinguished by having the cuticle densely setose, and both the carapace and abdomen are highly patterned with colorful spots, and radiating lines formed by branched scales, (characters 53 and 54).

## Discussion

Although this study confirms the monophyly of the Australian Castianeirinae compared to the Corinninae to infer the relationships within the Corinninae more taxon sampling from multiple genera are needed from that subfamily, these relationships are not the focus of this study and are not discussed here any further.

Of the twelve Castianeirinae genera examined including six that are represented by more than one species and all formed monophyletic groups evidence supporting the current genera hypothesis for these spiders are accurate. Of particular interest was the genus *Nyssus*, this genus is here represented by five species. These species formed a monophyletic clade supporting the current understanding of the *Nyssus* genus hypothesis. At this time, there is no reason to consider splitting this genus into multiple genera.

Specific ant mimics identified by Raven (2015) are seen in the genera *Poecilopta*, *Kolora* and *Iridonyssus*, while more generalized ant mimics are seen in the genera *Nucastia*, *Leptopicia* and *Disnyssus*. Ant mimics tend to have a long narrowed carapace, long legs and abdominal constrictions, and pattern seen on these spiders tend to be limited to transverse abdominal bands that reinforce the appearance of abdominal constriction, when present, or give the appearance of such a constriction when absent (Reiskind 1969; McIver & Stonedahl 1993; Cushing 1997; Raven 2015). These

characters, while present in more generalized ant mimics, tend to become more exaggerated in more specific ant mimics (Raven 2015 fig 48, 99).

General hymenopteran mimics identified by Raven (2015) are seen in the genera *Leichhardtus* and *Nyssus*. The traits that contribute to a spider's ability to mimic wasps differ in distinct ways as that of ant mimicry. In these wasp mimics, notably those seeming to mimic mutillid wasps, the body structure is less narrowed, legs not as long or slender, abdominal constrictions absent, the body is typically patterned with bold colors of red, orange, yellow and white reflecting the aposematic coloration of the models they mimic (Reiskind 1969, McIver & Stonedahl 1993, Cushing 1997, Raven 2015) (Raven 2015, fig.73, 79).

Evidence that these two very different mimetic adaptations evolved independently is seen in the clades united at nodes 10 and 16 both containing a mix of general and specific mimics and may represent a co-evolution with specific models driving these spiders towards a more accurate visual mimicry. Specific ant mimics in clade 14 are united in this study by having a relatively long and narrowed carapace (character 15), a mimetic character, (Reiskind 1969, Leister & Miller 2013 Candiani & Bonaldo 2017). This group is also supported by the following characters; (1) a tall clypeus, greater than 2 times the diameter of the AMEs (character 9); (2) having a shallowly sloped carapace of less than 30 degrees; (3) the carapace thickest anterior to the fovea (not seen in *Nucastia*), (character 13) and; (4) the presence of scales with a single lateral appendage (this character could not be determined in *Nucastia* or *Leptopicia*). These traits are not seen as contributing to the mimicry of these spiders. The inclusion of these non-mimetic



characters within this group help support this as a natural group not being supported strictly on mimetic characters which may be potentially convergent in nature.

This mimicry is not limited to the Australian fauna and can be found globally in the Castianeirinae. Like the Australian fauna these spiders can be general mimics of Hymenoptera as well as mimic specific families, genera or even specific species. For example, the speciose and globally distributed genus *Castianeira*, is notable for having a diversity of mimicry models (Reiskind 1969). Specific ant mimics such as *Castianeira similis* (Banks 1929) that are morphologically similar and found in close association with ponerine ants, specific mutilid mimics including *Castianeira dorsata* (Banks 1898) to generalized mimics and even dimorphic mimicry as seen in *Castianeira rica* Reiskind 1969 are found within this single genus (Reiskind 1969 & 1970). Many other genera mimic various models to varying degrees of specificity. Many of the mimetic characters seen throughout the Castianeirinae subfamily are most likely the result of evolutionary convergence.

Morphological mimicry is only a single phenotypic strategy these spiders have to resemble Hymenoptera, a second mimetic trait seen is behavioral mimicry. Raven (2015) noted that not only behavior while moving is reminiscent of the models they mimic, “The sudden movements with trembling front legs, stopping and restarting in erratic directions across the ground” but also resting behavior as well with leg movements and abdominal bobbing. This behavioral mimicry is also noted in other studies of mimicking spiders as well (Reiskind 1969; McIver & Stonedahl 1993; Cushing 1997; Ceccarelli 2008; Rubio et. al, 2013).

To explore the evolution of mimicry within the Castianeirinae and possibility of mimicry evolving multiple times within this subfamily a more robust analysis incorporating as many Castianeirinae genera as possible from around the globe needs to be conducted. Such an analysis should utilize other, non-morphological characters, including; field observations, natural histories and behavioral data and molecular data would be needed.

Historically authors have described the presence of an RTA on many Castianeirinae (Fig. 2, 3), (Reiskind 1969; Haddad 2013b; Leister & Miller 2013a, b; Candiani & Bonaldo 2017). However, the character noted by these authors is a protuberance on the retrolateral edge of the palp tibia and is the result of a distal folding of this portion of the tibia on these spiders. Therefore, this structure is not homologous with a true RTA seen on the Corinninae (Raven 2015). The re-emergence of a true RTA in the Castianeirinae is restricted to *Nyssus paradoxus*, and represents an independent evolution of this structure.

The paracymbial spine (PCS) noted for a majority of the Australian fauna examined in this study is absent in a majority of worldwide Castianeirinae genera and species. Of the 59 North and Central American species examined by Reiskind only one species, *Castianeira trilineata* (Hentz, 1847), was noted as having a similar structure. This character is not evident in any of the species of *Myrmecium* included in Candiani & Bonaldo's (2017) revision of this South American genus. This character has been noted and illustrated in some Southeast Asian species of the genus *Corinnomma* Karsch, 1880 but not on any of the 12 other genera described and illustrated in Deeleman-Reinhold (2001). This character is said to be present on a large number of madagascan species but

notably missing from afrotropical taxa (Haddad per. comm. to Raven, 2015). This character may be useful in determining the relationships of Castianeirinae spiders in a larger study incorporating genera from around the globe and aid in the understanding of the bio-geographic origins of these groups.

The Australian Castianeirinae examined are united by a simple looped sperm duct and can be used as a synapomorphy for the Australian Castianeirinae examined. In most material from North and Central America examined by Reiskind (1969), the palpal bulb contained not only the lateral loop seen in all Australian fauna examined here but also a median loop not seen in the Australian fauna (Fig. 2, 3; Reiskind 1969; fig. 2). This loop is also evident in many of the illustrations of *Myrmecium*, a South American genus (Candiani & Bonaldo, 2017). This character is absent from almost all Southeast Asian genera in Deeleman-Reinhold (2001) with a notable exception in the genus *Serendib* Deeleman-Reinhold, 2001. This median loop is absent in *Apochinomma* (see Haddad 2013a, figs. 10a, 12a, 13a, 14a, 15a ), *Copuetta* Haddad, 2013, and *Wasaka* Haddad 2013 (see Haddad, 2013c figs. 114 and 170). This character may prove vital in uncovering relationships within the Castianeirinae in a larger study.

Anterior abdominal setae, a character not found useful in this study, may prove to be a useful character in more robust studies. In Reiskind (1969), two pair of modified setae located on the anterior abdomen was noted for many North and Central Castianeirinae examined and in some cases modifications to these setae are diagnostic for genera such as in *Mazax*. In many Australian fauna three distinct pairs could be seen forming a triad. Modified setae were mentioned for the genus *Serendib* by Deeleman-

Reinhold (2001), but an examination of numerous genera are needed to determine if this character is useful across the Castianerinae or if it is an autapomorphy.

Branched scales are a form of seta found in many spiders groups and has been characterized by lacking innervation, laying appressed to body surface and having lateral appendages giving the setae a somewhat feathery appearance (Hill 1979; Griswold et al. 2005; Ramírez 2014).

The use of branched scales and other scales for establishing evolutionary classifications have been demonstrated a number of times for numerous groups and has been used as characters to reconstruct the evolutionary relationships of araneomorph spiders (Griswold et al. 2005; Ramírez 2014). Hill (1979) used scales including branched scales to establish relationships among some Salticidae and Townsend et al. (2001) for Oxyopidae. This character has even been used in a limited capacity on Corinnidae spiders (Bosselaers, J. & Jocqué, R., 2002; Haddad 2013; Ramírez 2014) although its use has been limited to presence/absence. Branched and other scales have been examined in depth on the Gnaphosidae by Zakharov and Ovtcharenko (2015) and concluded that variations seen in these scales are genus specific in the Gnaphosidae and contain stable characters of value for the reconstruction of the evolution of these spiders.

In this study an initial examination performed of branched scales taken from the abdomen of the spiders were examined here. These setae were examined using light microscopy to look for phylogenetically informative characters. Several important characters were identified using this method including; the thickest point of the main shaft; the shape of the terminal end of the shaft; the presence of scales with highly

reduced branching and the presence of extreme branching. These four characters based on branched scales were used and limited by the observational power of light microscopy; however, an examination of these scales under SEM will undoubtedly unveil additional phylogenetic characters useful for more robust studies.

This initial analysis of the Australian Castianeirinae provides a foundation by identifying and formally codes characters in this difficult group and examining the classification and evolution of mimicry in a phylogenetic framework for the first time for Australian taxa. This is a challenging group for taxon sampling as specimens are not common in museum collections and are not commonly encountered in nature. Future studies should emphasize acquiring greater taxonomic representation and be expanded to incorporate global representation of this subfamily. Many characters used in this study can be expanded to include more global representation. Major questions surrounding the evolutionary relationships of the remaining global genera, the monophyly of various groups including the *Castianeria* exist (Haddad 2013b; Rubio et al. 2015). A more robust study can address these questions and look further into the evolution of mimicry within this subfamily.

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