SACRED SYSTEMATICS: THE NOVIINI OF THE WORLD (COLEOPTERA: COCCINELLIDAE)

by

JUANITA A. FORRESTER

(Under the Direction of Joseph V. McHugh)

ABSTRACT

The first description of the egg, larval, and pupal stages of *Anovia circumclusa* (Gorham) are presented, along with notes on intraspecific color variation among adult *Anovia*. All literature pertaining to immature noviines is reviewed, and illustrations for all life stages are provided.

The tribe Noviini is taxonomically treated on a global scale. A literature review is presented encompassing etymology, taxonomic history, biology, feeding preferences, biological control, and chemical defenses for Noviini. A cladistic analysis testing the monophyly of the tribe and included genera supports a monophyletic, mongeneric Noviini. The tribe was formerly comprised of three genera: *Anovia* Casey, *Novius* (Mulsant), and *Rodolia* (Mulsant). A new classification is proposed based on the cladistic analysis: *Anovia* and *Novius* are synonyms, the tribe is now comprised of the single genus, *Rodolia* (Mulsant). The monophyly of the tribe is supported by 8 synapomorphies. 111 nominal species of Noviini are treated: 46 names are valid, 20 names are doubtful, 16 new synonymies and 10 new combinations are proposed, 1 unnecessary replacement name is reported, 1 junior homonym is reported, and a new replacement name is proposed for it. A key to species along with descriptions, illustrations and distributional information is provided.

A novel chemical defense for Noviini is hypothesized based on studies of related taxa and observations of *Rodolia cardinalis* (Mulsant). Hemolymph from *R. cardinalis* (Mulsant) and *Rodolia circumclusa* (Gorham) was tested, and the first records of carminic acid (a known deterrent to predators) being emitted by an adult coccinellid are presented.

INDEX WORDS: Coleoptera, Cucujoidea, Cerylonid Series, Coccinellidae, Noviini, *Anovia*, *Novius*, *Rodolia*, cladistic analysis, taxonomic revision, morphology, egg, larva, pupa, chemical defense

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DEDICATION

Along with a compilation of the world's knowledge of Noviini, this dissertation represents many sacrifices made by those most important to me. It is with a thankful and a very humble heart that I dedicate this work to my family.

The support offered to me by my husband, Barry, is incomparable. He has tolerated many solitary nights, missed phone calls, and "working" holidays and weekends. He has provided caring patience and support during the most stressful times, often forfeiting his own needs for my benefit. For many months, he has operated as a single parent, and he has shouldered the household responsibilities alone.

To my eldest daughter, Annabelle, these pages might represent missed ballgames, missed band booster meetings, and homework help via email or phone. But like her father, she is patient and understanding. I am very proud of the young lady she has become. Although my youngest daughter has enjoyed many nights and mornings spent at her grandparents' houses, she has also had to endure numerous evenings with only one parent present. She is a lesson in adaptability! Both of my daughters have been a tremendous source of support, even when they did not realize it.

I could not have even considered attending graduate school, much less finishing an advanced degree, without the help of my parents, Darrel and Teresa Scroggs. They have been responsible for my children in my absence, and for that I am extremely grateful. The moral support they have provided is incalculable. Regardless of whether my needs were for compassion or toughness, they fulfilled those needs completely. Without the help of my father, especially, I know that this work could not have even begun. For it was he who taught me early on that to quit is to fail, and that if the endeavor is worth pursuing, it is worth pursuing with every ounce of one's being. He lives by that example, and I have tried mightily to follow it.

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My most loyal and unwavering support has come from my grandparents. There has never been a time in my life that they were not completely behind me, offering loving encouragement and unconditional acceptance. There has never been a time in my life that I have not been grateful for them, and I know that whatever success I may enjoy is a direct result of their influence. I have always known that they wanted very much to see me succeed, and it was this knowledge that often kept me going for another hour, even when I was certain I could not go another. My grandmother, Leona Scroggs, taught me very important lessons about perseverance, tolerance, and generosity in the face of adversity, and I hold fast to those teachings. My late grandfather, Paul Scroggs, taught me much about the value of work, and about taking pride in one's work. He carried me for many years when I was a small child, and his memory carries me now.

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CHAPTER 1

INTRODUCTION

“She came in fast, the ladybird,
Lowered her gear and made a spot landing.
She was almost a brand-new model
Three hundred million years ago.”

-Geoffrey Mostyn Lewis: “Advanced Technology”

When early Catholic farmers prayed for deliverance from aphids and other injurious pests, they were convinced that the colorful, dappled insects that saved their crops were sent directly from the heavens. The farmers referred to the insects as “beetles of Our Lady,” believing that the red was symbolic of the Virgin Mary’s red cloak and that the black spots were representative of her sorrows. Coccinellid systematics has advanced significantly since those times, but classification of lady beetles is still problematic.

I. Classification of Coccinellidae

Classification of Coccinellidae, or lady beetles, began with Linnaeus’ landmark *Systema Naturae* in 1758. He recognized 36 species in the genus *Coccinella*, many of which are still considered valid species. The first meaningful internal classification of the family was performed when Redtenbacher (1843) subdivided the family based on feeding habits. His aphidophagous group proved to be a very artificial grouping, but the phytophagous group corresponds to today’s Epilachninae. A major development in the realm of coccinellid taxonomy occurred with Mulsant's (1846) work. He focused only on classifying the Coccinellidae of France, but in 1850 Mulsant attempted to encompass the world fauna. He proposed a new system of classification for lady beetles that separated setose species from glabrous ones. Many of his other groupings involved seemingly obvious characteristics such as color patterns and overall body shape. Unfortunately, this system proved to be quite unstable because of subjectivity. As a result, many of his species were synonomized by later taxonomists. Since Mulsant, many new classifications have been proposed; however, no new methods of deriving a classification scheme were employed. As a result, most of the new classifications were still based on the same types of imprecise characters: size, shape, color, and convexity. The state of the family remained the same until Verhoeff (1895) and Dobzhansky (1926) performed detailed studies on the male internal genitalia. They proposed homologies, developed terminology, and based his species groupings on these characters. Today, the structure of the male genitalia is the most common way to differentiate lady beetle species.

The family currently is placed within the Cerylonid Series, a monophyletic group of highly derived beetle families included in the superfamily Cucujoidea (Crowson 1955; Hunt *et al.* 2007; Robertson *et al.* 2007). The closest relatives of Coccinellidae are hypothesized to be Corylophidae and at least part of Endomychidae (Crowson 1955; Sasaji 1971). Morphological and molecular data supports a relationship between Coccinellidae and Anamorphinae + Corylophidae or with Leisestinae (Robertson *et al.* 2007). At least one study recovered a sister-group relationship between Coccinellidae and Alexiidae + Anamorphinae (Hunt *et al.* 2007). There are six recognized subfamilies of Coccinellidae: Sticholotidinae, Scymninae, Coccidulinae, Chilocorinae, Coccinellinae, and Epilachninae (Booth *et al.* 1990; Pakaluk *et al.*

1994; Lawrence & Newton 1995). The current system of subfamilies and tribes is based on Sasaji's 1968 study.

II. Taxonomic Problems in Coccinellidae

There is no current agreement on the relationships of coccinellid subfamilies. If the subfamilial relationships and definitions are unstable, then the tribal ones are even more so. This is because most tribal and generic level revisions have been conducted regionally, even though the subfamilies are cosmopolitan. The major consequence of these types of studies was that many proposed groups fell outside the revisionist's geographical area and were not considered at all for the taxonomic treatment (Vandenberg 2002). To further complicate matters, generic and higher level taxa are not rigorously defined, and new species descriptions are still mainly based on labile characters, just as they were over a century ago. As a result, countless synonomies have been created. That, combined with the sheer number of species (about 6000 worldwide), as well as the number of species imported to various places worldwide for biological control makes taxonomic endeavors within the family daunting to even the most seasoned coleopterist.

III. The Tribe Noviini

In 1850 Mulsant recognized a group of coccinellids he called *Noviaires.* They were covered with dense, short setae and had pubescent, entire eyes (ocular canthus absent), 8 antennomeres, trimerous tarsi, and 6 visible abdominal sterna. Ganglebauer (1899) referred to this same group as Noviini. Currently placed within the Coccidulinae, the tribe consists of approximately 100 species divided among three genera: *Anovia* Casey, *Novius* Mulsant, and *Rodolia* Mulsant (Gordon 1972). The noviines are of particular interest because many of them are known to be biological control agents, most notably *Rodolia cardinalis* (Mulsant). This beetle is especially well known for its ability to control the cottony cushion scale and is an introduced species on several continents, including North America.

IV. Proposed Dissertation Project (Proposed March 2006)

There are many taxonomic problems within Noviini, most notably the ambiguous generic definitions. In order to gain both taxonomic and nomenclatural stability, a phylogeny should be employed in order to test both the monophyly of Noviini and the monophyly of included genera. The classification for Noviini should be derived from the phylogenetic analysis. Generic definitions based on synapomorphy are more precise and unambiguous. Based on an extensive literature search as well as examination of specimens, at least one genus, maybe more, may be invalid. However, without a phylogeny, that determination cannot be made objectively.

The relationship between *Anovia* and *Rodolia* is of particular interest because the adults are very difficult to separate based on morphological characters. In fact, the only reason the two genera are not united now is because of a single larval study in which Rees (1947) described the larva of *Rodolia* as having two antennal segments and the larva of *Anovia* as having only one. Further study is clearly warranted. It is also apparent that some species currently included in *Novius* will have to be transferred to *Rodolia*. Past efforts (primarily regional treatments) aimed at classifying noviine genera have been grossly insufficient; therefore, for my dissertation research I planned to pursue a worldwide revision of Noviini that was intended to produce the following:

- Monograph of the world Noviini, including a key to all species
- Electronic key to all noviine species
- Phylogenetic analysis of noviine genera based on morphological data
- Natural classification of noviine genera based on a phylogeny

V. Dissertation Research

This dissertation, written in manuscript style, represents a half decade of study devoted to lady beetles. The tribe Noviini was treated on a global scale, and the results take the form of the following three chapters. In order to address the taxonomic questions surrounding the larval morphology of *Anovia* and *Rodolia*, a first larval description for *Anovia circumclusa* (Gorham) is presented. Included in that study are the first descriptions for the egg, larva, and pupa, a redescription of the adult, notes on intraspecific color variation in *A. circumclusa* adults, photographs and illustrations of all life stages, and a summary of the literature pertaining to the immature stages of Noviini.

The largest section of this work is Chapter 4: "A Revision of the World Noviini (Coleoptera: Coccinellidae)". In a nutshell, this chapter represents virtually everything that is known about Noviini, dating all the way back to the tribe's inception 1846. The monophyly of the tribe was supported, and a mongeneric Noviini (including only *Rodolia*) was proposed based on that analysis. 111 species were taxonomically treated, and the paper includes a key to species, descriptions, new synonymies, new combinations, photographs, and illustrations.

The final section of this dissertation, Chapter 5, is fondly titled "Ladybugs Stink! A Novel Chemical Defense for Noviini (Coleoptera: Coccinellidae)," and its focus is exactly that. Noviines employ a method of chemical defense that is unique among all coccinellids, and perhaps among all Coleoptera. An analysis of noviine hemolymph, along with a summary of literature pertaining to the chemical defenses of all coccinellids, is presented.

CHAPTER 2

LITERATURE REVIEW

“*My dear, have you heard of that nice Lady Bird*

Who yet is no lady, and yet is no bird?”

-Jannett Humphreys: “Insect Ways on Summer Days”

Coccinellidae is one of the largest beetle families in the superfamily Cucujoidea, with over 6,000 nominal species. Along with Alexiidae, Bothrideridae, Cerylonidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae, Coccinellidae is included in the Cerylonid Series of Cucujoidea. The closest relatives of Coccinellidae are hypothesized to be Corylophidae and at least part of Endomychidae (Crowson 1955; Sasaji 1971). Morphological and molecular data supports a relationship between Coccinellidae and Anamorphinae + Corylophidae or with Leisestinae (Robertson *et al.* 2007). At least one study recovered a sister-group relationship between Coccinellidae and Alexiidae + Anamorphinae (Hunt *et al.* 2007).

Lady beetle classification began with Linnaeus’ *Systema Naturae* in 1758. He included 36 species in the genus *Coccinella*, many of which are still considered valid. Latreille (1804) recognized a group of beetles that all seemed to have trimerous tarsi; he referred to them as “Tridigités.” Later, Latreille (1807) renamed the family Coccinellidae, and provided the first available family group name for lady beetles. Redtenbacher (1843) attempted one of the first meaningful internal classifications of Coccinellidae, and divided the family into two groups: aphidophagous and phytophagous.

Although the aphidophagous grouping proved to be artificial, the phytophagous group corresponds to the subfamily Epilachninae.

Mulsant's (1846, 1850) works are considered landmark classification events in the history of Coccinellidae. He focused only on the Coccinellidae of France, but in his later work Mulsant (1850) attempted to encompass the world fauna. His treatment was noteworthy because he proposed a new system of classification for lady beetles: he separated setose species from glabrous ones, and also attempted to include overall body shape (hemispherical vs. elliptical, dorsoventrally flattened vs. convex) and color patterns in his groupings (Mulsant 1850). This system was quite unstable due to the subjectivity of the characters chosen for species diagnoses. As a result, many of his species were synonymized by subsequent authors.

Verhoeff (1895) and Dobzhansky (1926) were responsible for a major breakthrough in lady beetle classification. They performed extensive studies of male genitalia, proposed homologies, discussed functionality, and presented new classifications based on these findings. Today, the structure of the male genitalia is the most common way to differentiate lady beetle species.

In 1968, a new method for classifying lady beetles was devised. In *Phylogeny of the Family Coccinellidae*, Sasaji (1968a) presented a phylogenetic hypothesis based on both larval and adult characters. He also provided a comprehensive review of lady beetle classification, with references to both authors and the structures they used to delineate subgroups within the family (Sasaji 1968a, 1971). He recognized six subfamilies of Coccinellidae: Sticholotidinae, Scymninae, Coccidulinae, Chilocorinae, Coccinellinae, and Epilachninae; this system is still followed by most contemporary authors (Gordon

1985; Booth *et al.* 1990; Pakaluk *et al.* 1994; Lawrence & Newton 1995; Kovár 1996; Vandenberg 2002). Alternative classifications were attempted by Chazeau *et al.* (1989) and Fürsch (1996); both researchers built upon Sasaji's classification by adding one or more subfamilies to the family group. Fürsch (1996) even solicited the help of coccinellid experts worldwide, but still no agreement was reached. As a result, current classifications are based on imprecise, subjective characters such as size, shape, color, and convexity, just as they were over a century ago. Although no agreement was ever reached, attempts to provide a sound classification scheme yielded several quality papers regarding the comparative morphology of coccinellid larvae (Gage 1920; Kamiya 1965; Sasaji 1968b; Savoiskaya 1973), pupae (Phuoc & Stehr 1974; Nakamura 1980), and adults (Gordon 1985; Kovár 1996; Vandenberg 2002).

There is still no consensus among lady beetle workers regarding the internal relationships of Coccinellidae. Subfamilial, tribal, and generic boundaries in the family are very ambiguous and poorly defined. Although the relationships within the family are contentious, experts agree that the family is monophyletic. The family currently is placed within the Cerylonid Series, a monophyletic group of highly derived beetle families included in the superfamily Cucujoidea (Crowson 1955; Hunt *et al.* 2007; Robertson *et al.* 2007). The closest relatives of Coccinellidae are hypothesized to be Corylophidae and at least part of Endomychidae (Crowson 1955; Sasaji 1971). Morphological and molecular data supports a relationship between Coccinellidae and Anamorphinae + Corylophidae or with Leisestinae (Robertson *et al.* 2007). At least one study recovered a sister-group relationship between Coccinellidae and Alexiidae + Anamorphinae (Hunt *et al.* 2007).

In 1850 Mulsant recognized a group of coccinellids he called *Noviaires.* They were covered with dense, short setae and had pubescent, entire eyes (no ocular canthus), of 8 antennomeres antennae, trimerous tarsi, and 6 abdominal ventrites. Ganglebauer (1899) referred to this group as “Noviini.” Currently included in the subfamily Coccidulinae, the tribe consists of approximately 80 nominal species divided among three genera: *Anovia* Casey, *Novius* Mulsant, and *Rodolia* (Mulsant) (Gordon 1972). The noviines are of particular interest because of their extensive use as biological control agents. The most famous example is undoubtedly *Rodolia cardinalis* (Mulsant). This beetle is especially well known for its ability to control the cottony cushion scale, *Icerya purchasi* Maskell, and is an introduced species on several continents, including North America.

The taxonomic problems in the tribe Noviini mirror those found within the family, especially the ambiguous generic definitions. Gordon (1972, 1985) noted that *Rodolia* and *Anovia* were virtually indistinguishable in the adult stage, and reported that only a difference in the number of larval antennomeres (Rees 1947) warranted the continued separation of the genera. Unfortunately, Rees’s (1947) study only included one exemplar of *Anovia*. Forrester *et al.* (in prep) provides a new description of *Anovia* larvae and pupae, along with a review of the literature pertaining to immature stages of Noviini.

The extreme morphological similarity in Noviini does not end with the controversial *Rodolia/Anovia* matter. For over a century now, authors have used the generic names *Novius* and *Rodolia* almost interchangeably. Gordon (1972) remarked that “some species presently placed in *Novius* will have to be transferred to *Rodolia,*” and

Ślipiński (2007) transferred all the Australian species of *Novius* to *Rodolia* in one sentence. Both authors were quite thorough in their studies of comparative morphology within the tribe, buy neither Gordon (1972, 1985) nor Ślipiński (2007) attempted to redefine noviine genera in light of their findings. Until now, no cladistic or revisionary treatment of this biologically important group was ever undertaken.

Although Coccinellidae is an extremely large beetle family (over 6000 species divided among 360 genera), several works encompassed biological and ecological aspects for the entire group. Reviews of coccinellid biology and ecology are provided by Clausen (1940); Hagen (1962); Hodek (1973); Majerus (1994); Hodek & Honěk (1996); and Kuznetsov (1997). Iperti (1999), Majerus (1994), and Hodek (1973) summarized general life history patterns for the family, and DeBach & Rosen (1991), Dixon (2000), Hagen *et al.* (1976), and Quezada & DeBach (1973) provided information regarding the use of noviines as biological control agents.

CHAPTER 3

FIRST DESCRIPTION OF THE EGG, LARVA, AND PUPA OF *ANOVIA CIRCUMCLUSA* (GORHAM) (COLEOPTERA: COCCINELLIDAE: NOVIINI), WITH NOTES ON INTRASPECIFIC COLOR VARIATION[1]

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[1] Forrester, J. A., Vandenberg, N. J., and J. V. McHugh. To be submitted to *Zootaxa*.

Abstract

Anovia circumclusa (Gorham), a neotropical lady beetle, recently was recorded in North America for the first time. Only the adult form of this beneficial predator has been described. This paper provides a redescription of the adult and the first descriptions of the egg, pupa, and larva. Diagnostic characters for the genus and species are given. Intraspecific color variation in *Anovia* adults is discussed.

Key words: ladybird, lady beetle, coccinellid, larva, morphology, taxonomy, scale predator, color variation

Introduction

Members of the charismatic beetle family Coccinellidae are well known for their appealing coloration. In agricultural circles, though, they are equally famous for their efficacy as biological control agents. One of the earliest examples of successful biological control involved a lady beetle from the tribe Noviini: *Rodolia cardinalis* (Mulsant) (Koebele 1892; Olliff 1895). This beetle was imported into the U.S. from Australia in the late 19th century and was instrumental in the protection of California's citrus crops from the cottony cushion scale, *Icerya purchasi* Maskell (Caltagirone and Doutt 1989).

Interest in noviines as biocontrol agents has been renewed by the recent discovery of an introduced scale pest in Florida, *Crypticerya genistae* (Hempel) (Hodges 2006). Subsequently, a newly introduced noviine, *Anovia circumclusa* (Gorham) was found feeding on the adventive scale insect (Forrester and Vandenberg 2008). Both predator and prey are apparently native to the neotropics (Gordon 1972; Gordon 1985; Hodges 2006).

The tribe Noviini consists of approximately 80 described species and 3 genera: *Anovia* Casey, *Novius* Mulsant, and *Rodolia* (Mulsant). Despite the large number of species in the tribe, very little taxonomic work has focused on the immature stages. Of those 80 nominal species, only 7 have had the immature stages described: *Anovia virginalis* (Wickham), *Novius cruentatus* Mulsant, *Rodolia koebelei* Olliff, *Rodolia cardinalis* (Mulsant), *Rodolia concolor* Lewis, *Rodolia fausti* (Weise) and *Rodolia limbata* Motschulsky. A review of literature pertaining to the larvae of Noviini is provided in Table 3.1. It is unfortunate that so little work has addressed noviine immatures. Noviine species are effective biocontrol agents as both larvae and adults, so larval descriptions for the tribe are desirable (Rees *et al.* 1994).

Materials and Methods

Examination of specimens for all life stages was accomplished using a Meiji Techno RZ stereoscopic microscope. The egg was photographed using a Zeiss ESEM. Photographs of the pupal and adult habitus were taken with a Microptics digital imaging system (Photografix, Inc., Richmond, Virginia) used in conjunction with Combine Z software (http://www.hadleyweb.pwp.blueyonder.co.uk/CZ4/Docs/combinez4.htm). All photographs were edited with Adobe Photoshop (Adobe Systems, Inc., 2003, San Jose, California). Dissections of freshly killed larvae and adults were performed in warm water and 75% ethanol, respectively. All dissections were slide mounted in glycerol. The illustrations were rendered using a camera lucida attached to a Leitz DMRB compound microscope (Leica Microsystems, Inc., Bannockburn, Illinois). Line drawings were rendered using Adobe Illustrator CS2 (Adobe Systems, Inc., 2003, San Jose, California). Label data is provided verbatim, with all line breaks, capitalization, and punctuation recorded exactly. Integumental armature is described following the terminology of Gage (1920). All specimens of immature stages were obtained from laboratory-reared cultures maintained by USDA, APHIS, Plant Protection and Quarantine, Miami, Florida.

Anovia Casey 1908 (Figs. 3.1 - 3.41)

Anovia Casey, 1908, p. 408. Type species: *Scymnus virginalis* Wickham, by monotypy.

-Leng, 1920, p. 214.

-Korschefsky, 1931, p. 96.

-Gordon, 1972, p. 26.

The type species for the genus was originally described as *Scymnus virginalis* Wickham, but subsequent authors questioned the placement in *Scymnus* (Casey 1908). Noting several morphological similarities to both *Rodolia* Mulsant and *Novius* Mulsant, Casey (1908) erected the genus *Anovia* to accommodate this species and included all three genera in the tribe Exoplectrini. In The Catalog of the Coleoptera of America North of Mexico, Leng (1920) included *Anovia, Novius,* and *Rodolia* in the tribe Noviini for the first time.

Diagnosis. Adults of *Anovia* are diagnosed by the following combination of characters: body convex, subhemispherical dorsum that is widest just posterior to the humeral angles (Figs. 3.17-3.22); all surfaces including eye facets covered with pale, posteriorly-directed vestiture; eye margin entire, not interrupted by an ocular canthus (Fig. 3.23); clypeal apex horizontal (Fig. 3.23); antenna with 8 articles, weakly clubbed (Fig. 3.25); and tarsi trimerous (Figs. 3.32 - 3.34).

Anovia circumclusa (Gorham) (Figs. 3.1 - 3.41)

Zenoria circumclusa Gorham, 1889, p. 262.

-Korschefsky, 1931, p. 108.

-Blackwelder, 1945, p. 443.

Anovia circumclusa: Gordon, 1971, p.1; 1972, p. 27-29 (lectotype designated). Type depository, BMNH.

Egg. Length 0.5 mm, width 0.25 mm. Elongate-oval, color bright magenta. Surface granular, often covered with waxy exudate (Fig. 3.1). Eggs typically oriented horizontally, not placed on end; laid singly or in small clusters on exposed leaf surfaces; often, they are laid on or under prey (Majerus 1994; pers. obs.).

Mature larva. Length 5-7 mm, (Figs. 3.2 - 3.4). Body ovoid, convex, widest at midpoint, laterally arcuate (Figs. 3.2 -3.4). Color bright magenta with waxy, white exudate. Dorsal surface moderately setose, finely granulate, covered with waxy exudate (Figs. 3.2 -3.4). Setae pale, erect, simple, length variable (Figs. 3.2 - 3.4).

Head prognathous, darkly pigmented, subquadrate, about as wide as long; dorsal and lateral surfaces with several chalazae; seta-like asperities lateral to frontal arms (Fig. 3.5). Frontal arms u-shaped; epicranial stem short; median endocarina absent (Fig. 3.5). Stemmata arranged in triangular pattern, three on each side (Figs. 3.5 - 3.7). Antenna inserted frontally, anteromesad to stemmata, 2-segmented (Figs. 3.5 - 3.7). Antennomere I robust, with length ~ 1/3 width; II very small, length subequal to width, sensorium longer than antennomere I (Fig. 3.9). Labrum distinct, subrectangular, weakly bilobed apically (Figs. 3.5, 3.7). Mandible triangular, enlarged basally, falcate apically (Figs. 3.7, 3.8). Maxillolabial complex retracted (Figs. 3.6, 3.7). Maxilla with cardo and stipes fused to form a solid, sclerotized structure with slender, arm-like extensions passing anteriorly and laterally around the labial palpi; maxillary palpomere 2-segmented; I much broader than long; II about as broad as long (Figs. 3.6, 3.7). Mala membranous, broad (Figs. 3.6, 3.7). Hypopharyngeal bracon present, well-developed.

Thoracic segments each with a pair of sclerotized plates; meso-and metathorax each with a pair lateral strumae; struma bearing many chalazae (Figs. 3.2 - 3.4). Legs long, robust, strongly sclerotized dorsally, semi-membranous, unpigmented ventrally (Figs. 3.10 - 3.12). Coxa transverse (Figs. 3.3, 3.10 - 3.12). Femur robust, almost as broad as long (Figs. 3.3, 3.10 - 3.12). Tibia elongate, with ventral surface setose distally; distal setae flat, clavate (Figs. 3.10 - 3.13). Tarsungulus strongly curved, with well-developed basal tooth (Figs. 3.10 - 3.13). Abdomen 10-segmented; segments I-IX with 2 pairs of sclerotized tubercles, 1 pair of chalazate strumae, and 1 pair of annular spiracles; X bearing pygopod (Fig. 3.3).

Diagnosis: The larva of this species resembles all other known noviine larvae, but is distinguishable by the presence of many chalazae on the lateral strumae of the abdominal segments (*R. cardinalis* has 2, and *R. koebelei* has 4).

Pupa. Length 4.5-5.5 mm, width 2.5 - 3.5 mm, exarate (Figs. 3.14 - 3.16). Dorsal habitus elliptical, convex, partially covered in last larval exuvium, attached by cauda to substrate. Color (without exuvium) magenta with pale setae (Figs. 3.15, 3.16). Dark, stout, bristle-like setae present on dorsal surface of head, pronotum, and humeral angles (Fig. 3.16).

Head length subequal to width. Antenna short, not extending beyond outer margin of eye, club indistinguishable from flagellum. Apical maxillary palpomere strongly securiform (Fig. 3.16).

Abdomen with 9 ventrites, I and II reduced and hidden beneath hind coxae; dorsal surface of abdomen with paired transverse tubercles on segments I - VIII; anterolateral angles with annular spiracles; IX with bipartite urogomphi.

Adult. Length 4-4.5 mm. Dorsal habitus hemispherical, laterally arcuate, convex; head strongly deflexed, not visible from above; color variable (Figs. 3.17 - 3.22). Vestiture pale, short, moderately dense, posteriorly-directed (Figs. 3.17 - 3.22).

Head width about twice head length; dorsal surface with evenly spaced, small, shallow punctules; ventral surface narrower; postoccipital rim sinuate (Figs. 3.23, 3.24). Eyes large, covered entirely by pale, suberect setae. Antennal insertion anteromesad to inner eye margin, exposed (Figs. 3.23, 3.24). Antenna with 8 articles; antennomere I asymmetrical, laterally expanded; II subglobose; III-V subequal in length and width; VI- VIII forming loose club, VI-VII asymmetrical, expanded medially; VI about as long as IV + V, VII shorter, VIII broadly tapered apically (Fig. 3.25). Clypeus small, fused to frons (Figs. 3.23, 3.24). Frontoclypeal suture absent. Labrum (Fig. 3.26) emarginate medially, expanded beyond clypeus laterally. Mandible bidentate, apex not flattened, teeth sickle-shaped, not in same plane; prosthecal fringe well-developed (Fig. 3.27). Lacinia slender, elongate, setose apically (Fig. 3.28). Galea broad, elongate, truncate and setose apically (Fig. 3.28). Maxillary palpus 3-segmented, with well-developed palpifer; palpomere I elongate, about three times as long as basal width, broadest apically, with membranous surface exposed; II securiform, mesal edge very short, membranous surface exposed; III strongly securiform, lateral edge twice length of mesal one (Fig. 3.28). Labium narrow, palpus 2-segmented; palpomeres I and II subequal in size; palpomere II gradually narrowed distally to sensory area at apex (Fig. 3.29).

Pronotum with dorsal surface punctulate, moderately setose; anterior angles extending forward just beyond lower margin of eye (Figs. 3.18, 3.20, 3.22); anterior edge just behind head capsule horizontal; posterior edge markedly sinuate, slightly notched opposite scutellum (Fig. 3.30). Prosternum narrow; prosternal process abruptly raised, rectangular with entire margins; procoxal cavities slightly transverse, closed behind (Fig. 3.31).

Scutellum triangular. Meso- and metathorax ventrally flattened, pubescent (Fig. 3.35). Mesoventrite short, narrowest posteriorly (Fig. 3.35). Metaventrite wider than long, finely punctuate. Legs flattened, broad and stout (Figs. 3.32 - 3.34). Femur deeply grooved ventrally for reception of tibia; groove bicarinate, sharply defined, extending almost entire length of femur (Figs. 3.32 - 3.34). Profemur with posterior edge of groove expanded preapically (Figs. 3.32 - 3.34). Tibia slightly widened at mid-length, ventral surface broader than dorsal, deeply grooved for reception of tarsus; groove bicarinate (Figs. 3.32 - 3.34). Tarsal formula 3-3-3; tarsomeres I and II elongate, lobed ventrally with spongy pubescence; III elongate, cylindrical, claws simple (Figs. 3.32 - 3.34, 3.38).

Elytron convex, laterally arcuate, finely punctate, non-striate; epipleuron complete to posterior margin, ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present. Abdomen with broad, slightly cleft intercoxal process; postcoxal line incomplete, not reaching lateral margin; 6 ventrites; I-V rectangular, progressively narrower in width posteriorly; VI narrower, tapering slightly to rounded, emarginated apex (Fig. 3.37). Pygidium subrectangular, setose, broadly rounded apically (Fig. 3.36)

Male genitalia with phallobase widest anteriorly; basal lobe slender, not extended laterally beyond the internal margin of the parameres (Figs. 3.39 - 3.41). Sipho as in Figure 3.41.

Diagnosis: Anovia circumclusa adults are best recognized by the structure of the male genitalia. In *A. circumclusa*, the basal lobe is slender and does not extend laterally beyond the internal margin of the parameres, while in all other *Anovia* species the basal lobe is quite broad distally, overlapping the medial margins of the parameres. Also, in *A. circumclusa* the basal piece is widest basally, not distally as in *A. virginalis*.

Material examined: please see Table 3.2.

Discussion

One of the most significant taxonomic questions about the tribe Noviini is whether or not the included genera are valid. Gordon (1972; 1985) hints that *Rodolia* and *Anovia* should be synonymized because they are virtually impossible to separate on the basis of adult morphological characters, and he cites the larval study by Rees (1947) as the only evidence supporting the recognition of two separate genera. Rees's (1947) study was the first and only attempt to define noviine genera based on larval morphology, but unfortunately, only one species of *Anovia* was examined. The brief description of *A. virginalis* in that study was used to characterize the larvae for the entire genus. As a result, subsequent authors continued to recognize *Rodolia* and *Anovia* as distinct genera based entirely on the presence (*Rodolia*) or absence (*Anovia*) of larval antennomere II (Gordon 1972; Gordon 1985; Rees *et al.* 1994). Examination of the larva, pupa, and adult of *A. circumclusa* supports its inclusion in Noviini. The larva has the cardo and stipes fused and the abdominal terga each bear two pairs of sclerotized tubercles (Rees 1949, Rees *et al.* 1994). The pupa has dense, fine, pale setae on the apex of the hind wing and bipartite urogomphi on abdominal tergum IX (Phuoc & Stehr 1974). The species is native to South America and the adult has an incomplete postcoxal line: both are taxonomic features that Gordon (1972, 1985) used to differentiate *Anovia* from *Rodolia*. Examination of over 1500 specimens of Noviini by the senior author shows that this character is not sufficient to separate the genera. Furthermore, the larva of *A. circumclusa* lacks the critical feature that Rees (1949) proposed to diagnose *Anovia*. Given the extreme morphological similarity of both genera, the validity of *Anovia* is more questionable than ever. A phylogenetic analysis, ideally one including both adult and larval characters, is needed to resolve this issue.

Noviine larvae are very difficult to identify in the field. Besides their overall similarity, all noviine larvae are covered with powdery, granular wax that obscures most aspects of their anatomy (Figs. 2-4). The waxy threads apparently are secreted from the bases of hollow, pointed spicules on the dorsal surface of the larva; the spicules are used for support as the waxy thread grows upward (Pope 1979).

Another taxonomic problem encountered with adult noviines, and coccinellids in general, is intraspecific color variation. Gordon (1972) notes extensive elytral color variation within *Anovia* species, but identification keys for the genus still rely heavily on color patterns. Examination of the world holdings of Noviini by the senior author confirmed that coloration is not a reliable feature for diagnosing any species in the tribe, including *Anovia* species. When representatives of *A. circumclusa* are viewed dorsally side-by-side, a smooth coloration gradient becomes apparent. The elytral color ranges from carmine red with a discrete black ring (Figs. 3.17, 3.18) to almost entirely black (Figs. 3.21, 3.22). Intermediate forms have orange elytra with a broad, vaguely defined dark area laterally and posteriorly (Figs. 3.19, 3.20). A similar gradation in color patterns occurs in *A. punica.*

A number of factors contribute to the wide array of color patterns associated with Coccinellidae. Much of the variation (number of spots, spot position, spot size and shape) is genetic; however, there are other factors that are known to affect coloration (Majerus 1994; Honěk 1996). Honěk (1996) provides a review of temporal and geographic variability in lady beetles, noting that light colored populations tend to occur in arid regions while darker pigmentation is more common in humid areas. Gordon (1972) notes that in rare instances, some lady beetle color patterns can be linked to specimen maturity, although neither habitat nor age seems correlated with the coloration observed in Noviini.

The familiar aposematic colors of many coccinellids often advertise chemical defenses (Bezzerides *et al*. 2007; King & Meinwald 1996). It is unknown whether this is true for Noviini.

Acknowledgments

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Literature cited

Balduf, W. V. (1935) *The Bionomics of Entomophagous Coleoptera*. E. W. Classey, Middlesex. 222 pp.

Blackwelder, R. E. (1945) *Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America. Part 3.* United States National Museum Bulletin 185. 188pp.

Bezzerides, A. L., McGraw, K. J., Parker, R. S., and J. Husseini (2007). Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis*. *Behavioral Ecology and Sociobiology*, 61, 1401 - 1408.

Britton, G., Goodwin, T. W., Harriman, G. E., and Lockley, W. J. S. (1977) Carotenoids of the ladybird beetle, *Coccinella septempunctata*. *Insect Biochemistry*, 7, 337-345.

Caltagirone, L. E. and Doutt, R. L. (1989) The history of the Vedalia Beetle importation into California and its impact on the development of biological control. *Annual Review of Entomology,* 34, 1-16.

Casey, T. L. (1908) Notes on the Coccinellidae. *The Canadian Entomologist,* 40, 393-421.

Dixon, A. F. G. (2000) *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, New York, 257pp.

Emden, van F.1. (1949) Larvae of British beetles. VII. (Coccinellidae). *Entomologist's Monthly Magazine*, 85, 265-283.

Forrester, J. A. and Vandenberg, N. J. (2008) First Florida records for *Anovia circumclusa* (Gorham) (Coleoptera: Coccinellidae: Noviini): A natural enemy of *Icerya genistae* Hempel (Hemiptera: Margarodidae). *Zootaxa,* 1720, 66-68.

Gordon, R. D. (1971) A revision of the genus *Zenoria* Mulsant (Coleoptera: Coccinellidae). *Smithsonian Contributions to Zoology*, 86, 1-22.

Gordon, R. D. (1972) The tribe Noviini in the New World (Coleoptera: Coccinellidae). *Journal of the Washington Academy of Sciences*, 62(1), 23-31.

Gordon, R. D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society*, 93(1), 654-678.

Gorham, H. S. (1899) *Insecta. Coleoptera. Supplement to Endomychidae and Coccinellidae. Biologia Centrali-Americana*. R. H. Porter, London, 276 pp, 13 pl.

Grafton-Cardwell, B. (2002) Stages of the Cottony Cushion Scale (*Icerya purchasi*) and its Natural Enemy, the Vedalia Beetle (*Rodolia cardinalis*). *University of California Division of Agriculture and Natural Resources* 1 - 3.

Honěk, A. (1996). Variability and Genetic Studies. *In:* I. Hodek and I. Honěk (Eds.) *Ecology of Coccinellidae.* Kluwer Academic Publishers, Dordrecht, 464 pp.

Hodges, G. (2006) Pest Alert: *Icerya genistae* (Hemiptera: Margarodidae), a new exotic scale insect for Florida. *Pest Alert* 1-3.

Kamiya, H. (1964) Comparative morphology of larvae of the Japanese Coccinellidae, with special reference to the tribal phylogeny of the family (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science*, 14, 83-100.

Kamiya, H. (1966) On the Coccinellidae attacking the scale insects and mites in Japan and the Ryukus. *Mushi*, 39, 65-93.

Kawaguchi, T. (1935) On *Rodolia concolor* Lewis. *The Insect World,* 34(6), 208.

King, G. A. and Meinwald, J. (1996). Review of the defensive chemistry of coccinellids. *Chemical Reviews*, 96(3), 1105 - 1122.

Klausnitzer, B. and Schulze, J. (1975) The larva of *Novius cruentatus* (Coleoptera: Coccinellidae). *Deutsche Entomologische Zeitschrift*, 4-5, 359-361.

Koebele, A. (1892) Report on Condition of Newly Introduced Species in California. *Report on the Importation of Parasites and Predaceous Insects by the California State Board of Horticulture* 13-15.

Korschefsky, R. (1931) Pars 118, Coccinellidae. *Coleopterorum Catalogus*, W. Junk, Berlin, 224 pp.

Leng, C. W. (1920) Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York, 470 pp.

LeSage, L. (1991) Coccinellidae (Cucujoidea), the lady beetles, ladybirds. *In*: F. W. Stehr, (Ed.) *Immature Insects. Volume II*. Kendall/Hunt. Dubuque, Iowa, pp. 485-494.

Majerus, M. E. N. (1994) *Ladybirds*. Harper Collins, London, 367 pp.

Olliff, M. S. (1895) Entomological notes-A friendly new ladybird. *Agricultural Gazette of New South Wales*, 6, 30-31.

Phuoc, D. T. and. F. W. Stehr. (1974) Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions of the American Entomological Institute*, 10(6), 31-123.

Pope, R. D. 1979) Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology*, 4, 171-196.

Priore, R. (1963) Studio morfo-bollogico sulla *Rodolia cardinalis* Muls. *Bolletino del Laboratorio de Entomologia Argraria Filippo Silvestri di Portici*, 31, 63-193.

Rees, B. E. (1947) Taxonomy of the larvae of some North American Noviini (Coleoptera, Coccinellidae). *The Pan-Pacific Entomologist*, 23, 113-119.

Rees, B. E., Anderson, D. M., Bouk, D., and Gordon, R. D. (1994) Larval key to genera and selected species of North American Coccinellidae (Coleoptera). *Proceedings of the Entomological Society of Washington*, 96, 387-413.

Savoïskaya, G. I. and Klausnitzer, B. (1973) Morphology and taxonomy of the larvae with keys for their identification. *In:* I. Hodek (Ed.), *Biology of Coccinellidae*. Dr. W. Junk N. V. Prague, 260 pp.

Savoïskaya, G. I. (1983) Larvae of coccinellids (Coleoptera, Coccinellidae) of the USSR fauna. *Institute of the USSR Academy of Sciences* 243 pp.

Sasaji, H. (1968) Descriptions of the coccinellid larvae of Japan and the Ryukus (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science*, 18, 93-135.

Ślipiński, S. A. (2007) *Australian Ladybird Beetles (Coleoptera: Coccinellidae): their biology and classification*. Australian Biological Resources Study, Canberra. 141 pp.

Vandenberg, N. J. (2002) Family 93. Coccinellidae Latreille 1807. *In:* R. H. Arnett, Michael C. Thomas, Jr., P. E. Skelley, and J. H. Frank (Eds), *American Beetles Volume II: Scarabaeoidea through Curculionoidea*. CRC Press LLC Boca Raton, USA, pp. 371-389.

Weise, J. (1887) Ueber die Lebenweise von *Novius cruentatus* Muls. *Deutsche Entomologische Zeitschrift*, 31, 181-183.

Figure Legends

Figure 3.1. *Anovia circumclusa* (Gorham) egg.

Figures 3.2 - 3.4. *Anovia circumclusa* (Gorham), mature larva. **3.2.** Habitus, dorsal. **3.3.** Habitus, ventral. **3.4.** Habitus, lateral.

Figures 3.5 - 3.9. *Anovia circumclusa* (Gorham), larval head and appendages. **3.5.** Head, dorsal. **3.6.** Head, ventral. **3.7.** Head, anterior. **3.8.** Mandible, left, dorsal . **3.9.** Antenna, left, dorsal.

Figures 3.10 - 3.13. *Anovia circumclusa* (Gorham), larval legs. **3.10.** Prothoracic leg, left, dorsal. **3.11.** Mesothoracic leg, left, anterior. **3.12.** Metathoracic leg, left, anterior. **3.13.** Prothoracic tibia, left, anterior.

Figures 3.14 - 3.16. *Anovia circumclusa* (Gorham), pupa. **3.14.** Habitus, dorsal, clothed in last larval skin. **3.15.** Habitus, dorsal, last larval skin removed. **3.16.** Habitus, ventral, last larval skin removed.

Figures 3.17 - 3.22. *Anovia circumclusa* (Gorham), adult. **3.17.** Habitus, dorsal. **3.18.** Habitus, lateral. **3.19.** Habitus, dorsal. **3.20.** Habitus, lateral. **3.21.** Habitus, dorsal. **3.22.** Habitus, lateral.

Figures 3.23 - 3.29. *Anovia circumclusa* (Gorham), adult head and appendages. **3.23.** Head, dorsal. **3.24.** Head, ventral. **3.25.** Antenna, left, dorsal. **3.26.** Labrum, dorsal. **3.27.** Mandibles, dorsal. **3.28.** Maxilla, left, dorsal. **3.29.** Labium, ventral.

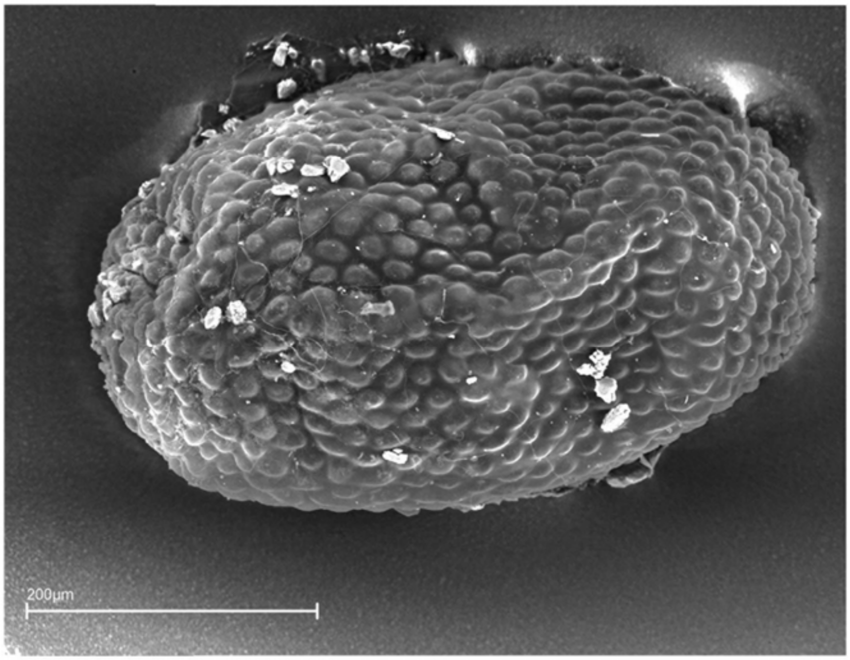
Figures 3.30 - 3.34. *Anovia circumclusa* (Gorham), adult prothorax and appendages. **3.30.** Pronotum, dorsal. **3.31.** Prosternum, ventral. **3.32.** Prothoracic leg, left, anterior. **3.33.** Mesothoracic leg, left, anterior. **3.34.** Metathoracic leg, left, anterior.

Figures 3.35 - 3.38. *Anovia circumclusa* (Gorham), adult pterothorax, abdomen, and appendages. **3.35.** Pterothorax, ventral. **3.36.** Pygidium, dorsal. **3.37.** Abdomen, ventral. **3.38.** Metathoracic tarsal claw, left, posterior.

Figures 3.39 - 3.41. *Anovia circumclusa* (Gorham), adult male genitalia, redrawn with permission from *Zootaxa* (Forrester and Vandenberg 2008). **3.39.** Aedeagus, dorsal. **3.40.** Aedeagus, lateral. **3.41.** Sipho, lateral.

Table 3.1. Summary of literature on immature stages of Noviini. e: egg; l: larva; p: pupa.

Table 3.2. Material examined.



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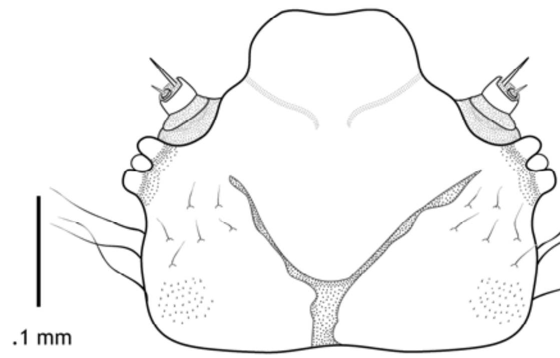

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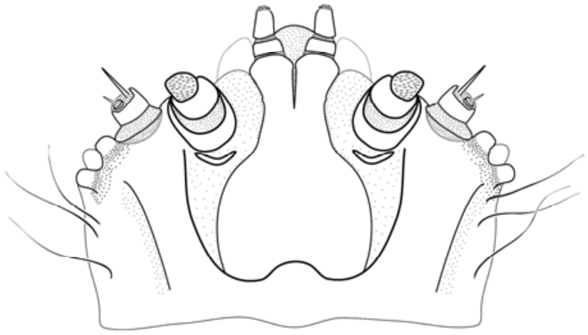

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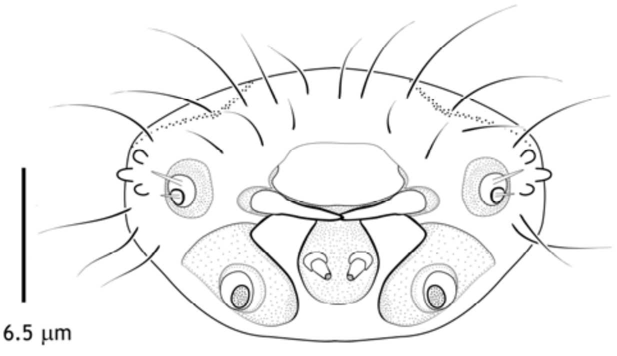

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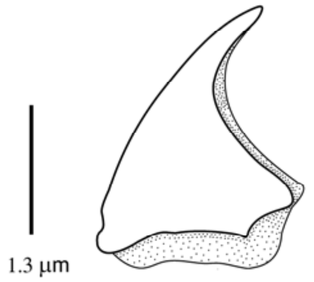

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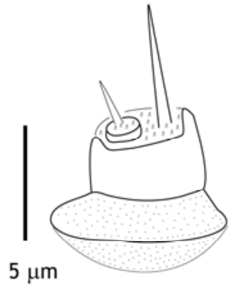

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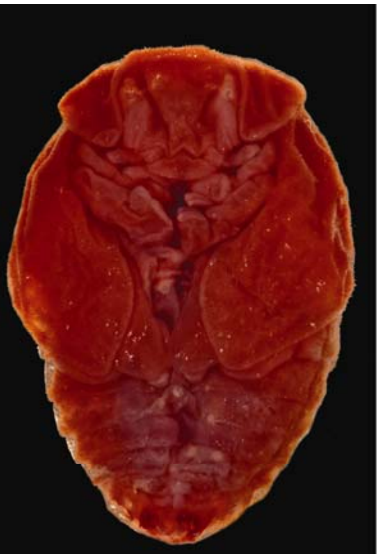

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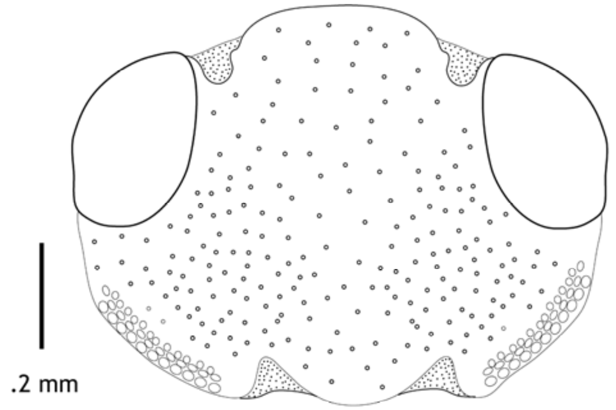

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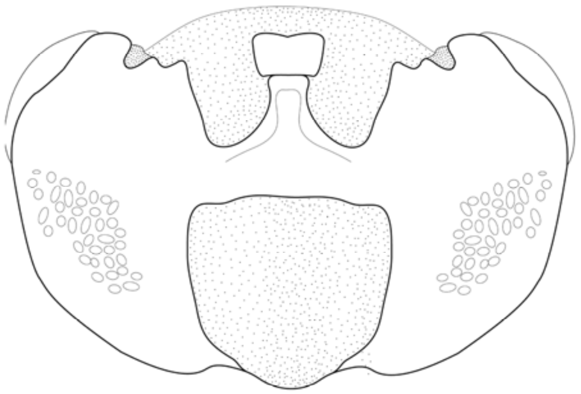

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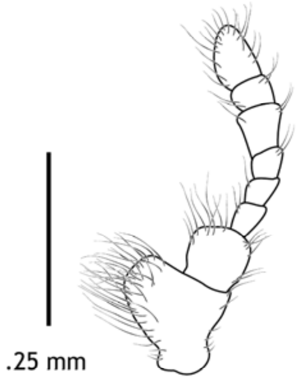

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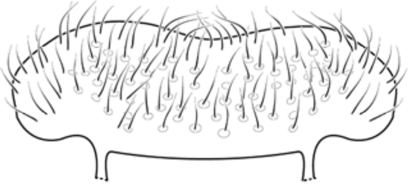

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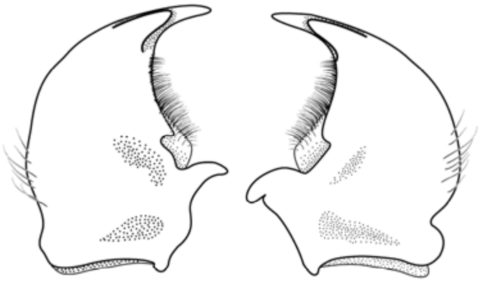

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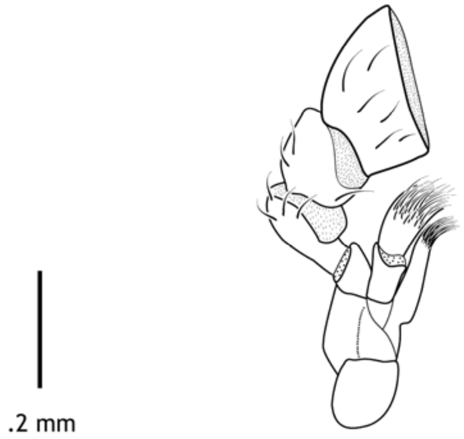

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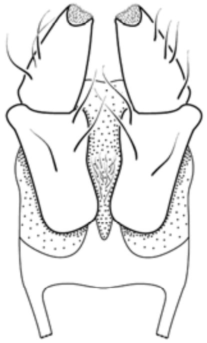

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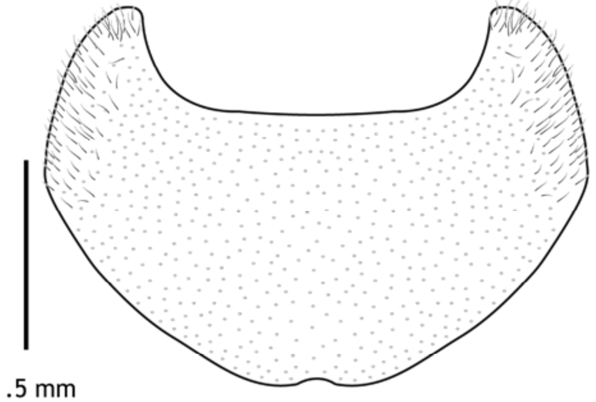

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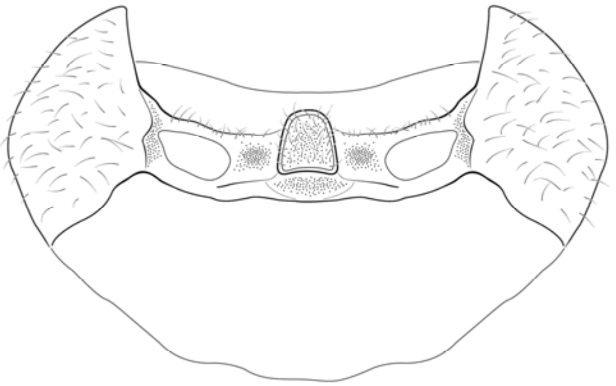

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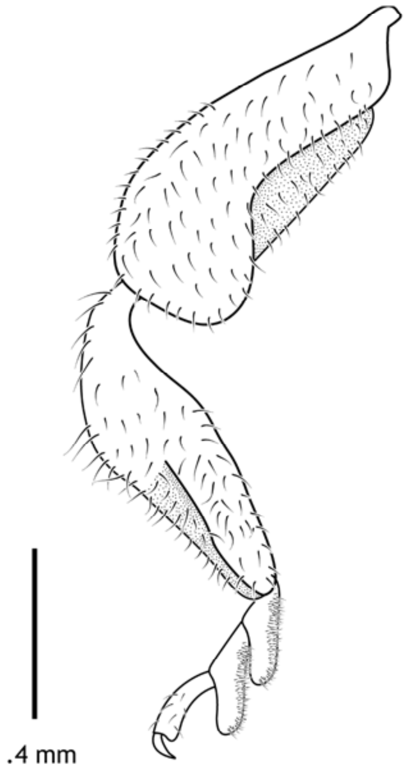

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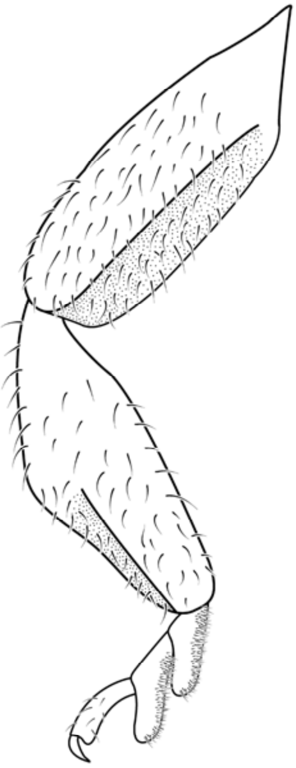

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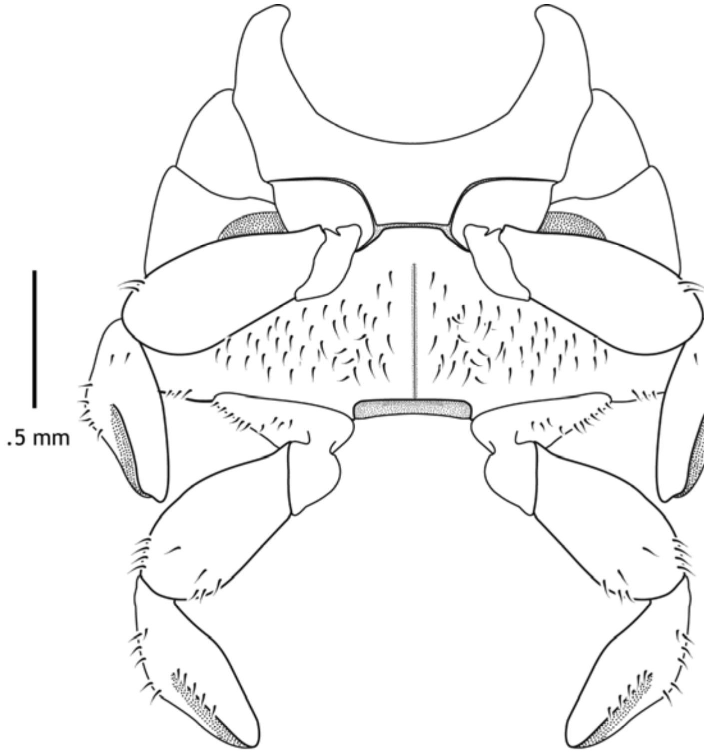

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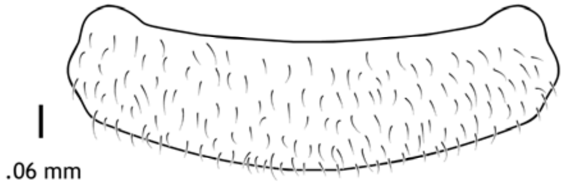

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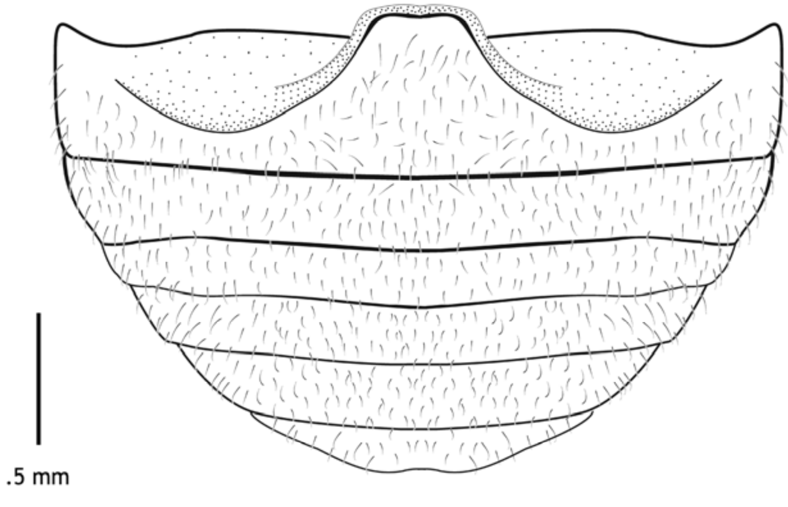

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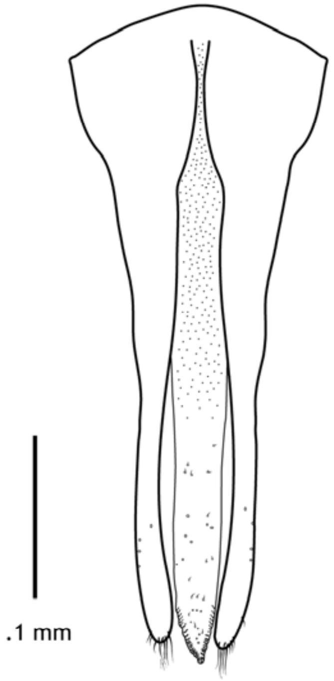
3.38



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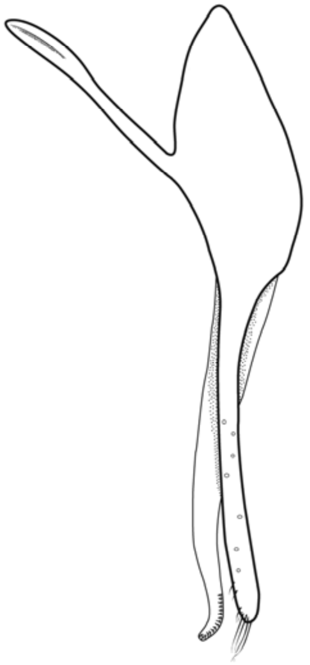

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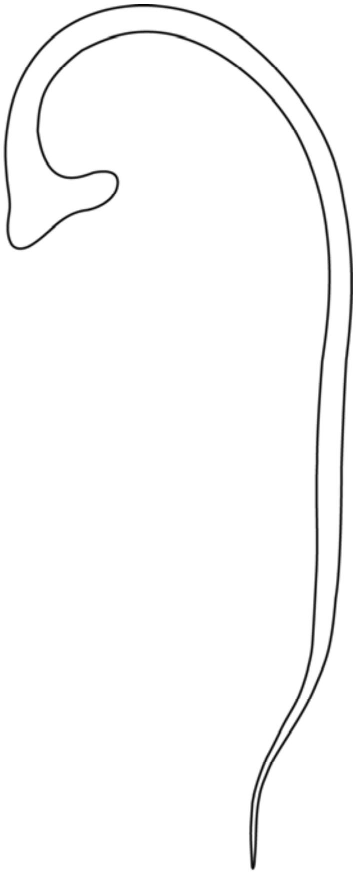

3.41

Table 3.1. Summary of taxonomic literature on immature stages of Noviini

Taxon	**Developmental stage, notes**	**Reference**	**Pages**
Noviini	(l, p) description, life history notes	Vandenberg (2002)	372
Noviini	(l) diagnosis	Emden van (1949)	278
Noviini	(l) diagnosis	Kamiya (1964)	86-93
Noviini	(l) key	Kamiya (1966)	82-83
Noviini	(l, p) description	Ślipiński (2007)	141
Noviini	(l) description, key	Savoiskaya (1983)	144
Noviini	(l) diagnosis, key	Sasaji (1968)	109-110
Noviini	(l) diagnosis, key	Savoiskaya (1973)	37, 40
Noviini	(p) description, key, illustrations	Phuoc & Stehr (1974)	6, 19, 43, 50
Anovia virginalis	(l) diagnosis	Gordon (1972)	25
Anovia virginalis	(l) description, illustration	Rees (1947)	118-119
Anovia virginalis	(l) diagnosis, illustration	Rees et al. (1994)	404, 410
Novius cruentatus	(l) description, illustrations	Klausnitzer & Shulz (1975)	359-361
Novius cruentatus	(e, l, p) development, life history	Weise (1887)	181-183
Novius cruentatus	(l) description, illustrations, biology	Perris (1862)	226-229, pl. 6
Rodolia cardinalis	(l) description, illustrations	Rees (1947)	117-118
Rodolia cardinalis	(e, l, p) development, life history	Balduf (1935)	139-146
Rodolia cardinalis	(e, l, p) description, illustrations	LeSage (1991)	485-490
Rodolia cardinalis	(e, l, p) description, illustrations	Priore (1963)	131-161
Rodolia cardinalis	(l) diagnosis	Gordon (1972)	25
Rodolia cardinalis	(l) diagnosis, illustration	Rees et al. (1994)	404, 410
Rodolia cardinalis	(l) description, illustration	Savoiskaya (1983)	144-148
Rodolia cardinalis	(l) diagnosis	Kamiya (1966)	82
Rodolia cardinalis	(l) diagnosis, illustration	Kamiya (1964)	86-93
Rodolia cardinalis	(l) description, illustration	Sasaji (1968)	110-111
Rodolia cardinalis	(l) diagnosis, illustration	Savoiskaya (1973)	43, 45
Rodolia cardinalis	(p) description, illustration	Phuoc & Stehr (1974)	6, 13
Rodolia cardinalis	(e, l, p) photographs, life history	Grafton-Cardwell (2002)	3
Rodolia concolor	(l) description	Kawaguchi (1935)	208
Rodolia concolor	(l) diagnosis	Kamiya (1966)	83
Rodolia concolor	(l) description, illustration	Sasaji (1968)	112-113
Rodolia concolor	(l) description, illustration	Savoiskaya (1983)	148
Rodolia fausti	(l) description, illustration	Savoiskaya (1983)	145
Rodolia fausti	(l) diagnosis, illustration	Savoiskaya (1973)	43, 45
Rodolia koebelei	(l) description	Rees (1947)	117-118
Rodolia limbata	(l) description, illustration	Savoiskaya(1983)	146
Rodolia limbata	(l) description, illustration	Sasaji (1968)	111-112
Rodolia limbata	(l) diagnosis, illustration	Savoiskaya (1973)	43, 45

Table 3.2. Material examined

Label 1	Label 2	Label 3	Label 4	#, gender	Depository
La Celba Honduras June 28	Chnodes sp.	FJ Dyer coll.	Anovia circumclusa (Gorham) det. R. Gordon	1 male	USNM
Tampico Mex 612	EA Schwarz Collector		Anovia circumclusa (Gorham) det. R. Gordon	2 males	USNM
Tampico Mex 2212	EA Schwarz Collector		Anovia circumclusa (Gorham) det. R. Gordon	1 female	USNM
Tampico Mex 1412	EA Schwarz Collector		Anovia circumclusa (Gorham) det. R. Gordon	1 female	USNM
Tegucigalpa Hond	June 23, 18	FJ Dyer coll.	Anovia circumclusa (Gorham) det. R. Gordon	1 male	USNM
Tegucigalpa Honduras VI. 12. 18	F. J. Dyer, Col. No. 40425	Anovia circumclusa (Gorham) det. R. Gordon		1 male	USNM
Tegucigalpa Honduras IV. 27. 18	F. J. Dyer, Col. No. 41319 41430	Anovia circumclusa (Gorham) det. R. Gordon		1 male 1 female	USNM
FLORIDA: Miami-Dade Co.	Miami S30 T53 R42	13-IX-2007 coll. O. Garcia	on *Quercus virginiana* [Fagaceae]. A *Diomus roseicollis* was in the same collection]	1 male	FSCA
Port Everglades, Fort Lauderdale, on leguminous weeds infested with *Icerya genistae*				1 male	USNM

CHAPTER 4

A REVISION OF THE WORLD NOVIINI (COLEOPTERA: COCCINELLIDAE)[2]

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[2] Forrester, J. A. and J. V. McHugh. To be submitted to *Zootaxa*.

Abstract

This paper treats the Noviini (Coleoptera: Coccinellidae) of the world. A review of the biology, ecology, and taxonomic history of the group is presented. The tribe is taxonomically treated, and a key to species, descriptions, illustrations, synonymies, type label data, and comparisons to similar species are provided. A list of all species names associated with Noviini, along with full citations is included.

A cladistic analysis based on adult morphological characters was employed to test the monophyly of Noviini and the three genera (*Anovia* Casey, *Novius* Mulsant, *Rodolia* Mulsant) included. Noviini is monophyletic, but *Rodolia* is polyphyletic with respect to *Anovia* and *Novius*. A new classification for Noviini is proposed: all species are included in a single genus, *Rodolia* Mulsant.

This revision treats 111 nominal species of Noviini. Of those, 46 are valid names: *Rodolia alluandi* Sicard 1909, *R. andamanica* Weise 1901, *R. apicalis* Sicard 1909, *R. argodi* Sicard 1909, *R. bella* (Blackburn) 1889, *R. canariensis* (Korschefsky)1937, *R. capucina* (Fürsch) 1975, *R. cardinalis* (Mulsant) 1850, *R. chapaensis* (Hoang) 1980, *R. cinctipennis* Weise 1912, *Anovia circumclusa* (Gorham) 1889, *R. concolor* (Lewis) 1879, *R. cruentata* (Mulsant) 1846, *R. delobeli* Chazeau 1981, *R. discoidalis* (Blackburn) 1895, *R. dubia* (Forrester & McHugh) 2008, *R. fulvescens* Hoang 1980, *R. fumida* (Mulsant) 1850, *R. iceryae* Janson in Howard 1889, *R. insularis* Weise 1895, *R. koebelei* (Gordon) 1892, *R. limbata* (Motschulsky) 1866, *R. lindi* (Blackburn) 1889, *R. marginata* Bielawski 1960, *R. mexicana* (Gordon) 1972, *R. minuta* Sicard 1909, *R. nigerrimus* Fürsch 1960, *R. nigra* Fürsch 1995, *R. obscuricollis* Sicard 1931, *R. occidentalis* (Weise) 1898, *R. podagrica* Wesie 1908, *R. prosternalis* Sicard 1909, *R. pumila* Weise 1892, *R. punica* (Gordon) 1972, *R. quadriplagiata* Sicard 1909, *R. rubea* Mulsant 1850,

R. rubra Blackburn 1889, *R. rufocincta* Lewis 1896, *R. severini* Weise 1895, *R. songchuana* Hoang 1980, *R. tamdaoana* Hoang 1980, *R. tripustulata* (Blackburn) 1895, *R. usambarica* Weise 1898, *R. virginalis* (Wickham) 1905, and *R. weisei* (Gordon) 1972.

Twenty of the valid names were found to be doubtful: *R. apicalis*, *R. canariensis*, *R. capucina*, *R. chapaensis*, *R. cinctipennis*, *R. concolor*, *R. delobeli*, *R. discoidalis*, *R. fulvescens*, *R. minuta*, *R. nigerrimus*, *R. obscuricollis*, *R. prosternalis*, *R. quadriplagiata*, *R. quadrispilota*, *R. rubra*, *R. rufocincta*, *R. severini*, *R. songchuana*, and *R. tamdaoana*.

Sixteen new synonymies were discovered: *Novius tridens* Lea 1901, placed under *R. cardinalis* (Mulsant) 1850; *N. immaculatus* Lea 1901, placed under *R. cardinalis* (Mulsant) 1850; *R. rufopilosa* Mulsant 1850, placed under *R. fumida* (Mulsant) 1850, *R. punctigera* Weise 1901, placed under *R. fumida* (Mulsant) 1850; *R. formosana* Korschefsky 1935, placed under *R. fumida* (Mulsant) 1850; *R. ferruginea* Weise 1900, placed under *R. iceryae* Janson in Howard 1889; *R. senegalensis* Weise 1913, placed under *R. iceryae* Janson in Howard 1889; *Novius Koebelei* Lea 1902, under *R. koebelei* (Gordon) 1972; *Macronovius limbatus* v. *fausti* Weise 1885, placed under *R. limbata* Motschulsky 1866; *R. breviuscula* Weise 1892, placed under *R. limbata* Motschulsky 1866; *R. cinctipennis* Weise 1912, placed under *R. limbata* Motschulsky 1866; *R. quadrimaculata* Mader 1939, placed under *R. limbata* Motschulsky 1866; *R. quadrimaculata* ab. *6-maculata* Mader 1939, placed under *R. limbata* Motschulsky 1866; *R. amabilis* Kapur 1949, placed under *R. podagrica* Weise; and *R. vulpina* Fürsch 1974, placed under *R. pumila* Weise 1892.

Ten new combinations are proposed: *Rodolia canariensis* (Korschefsky), 1937 (formerly *Novius*); *Rodolia circumclusa* (Gorham), (formerly *Anovia*); *Rodolia concolor* (Lewis), 1879 (formerly *Novius*); *Rodolia cruentata* (Mulsant), 1846 (formerly *N. cruentatus*); *Rodolia* *discoidalis* (Blackburn), 1895 (formerly *Novius*); *Rodolia limbata* (Motschulsky), 1866 (formerly *N. limbatus*); *Rodolia mexicana* (Gordon), 1972 (formerly *Anovia*); *Rodolia punica* (Gordon), 1972 (formerly *Anovia*); *Rodolia virginalis* (Wickham), 1905 (formerly *Anovia*); *Rodolia weisei* (Gordon), 1972 (formerly *Anovia*).

1 unnecessary replacement name is reported: *R. vitalisi* Mader 1955 (for *R. cardinalis*). 1 junior homonym is reported, and a new replacement name is given to it: *R. dubia* (Forrester & McHugh) 2008 (formerly *R.limbata* (Blackburn) 1895).

Introduction

"What fond inquiries filled my curious mind
How have I watched thy pastimes, Lady Flye,
And thought thee happiest creature of thy kind."

John Clare: "The Lady Flye"

When early Catholic farmers prayed for deliverance from aphids and other injurious pests, they were convinced that the colorful, dappled insects that saved their crops were sent directly from the heavens. The farmers referred to the insects as "beetles of Our Lady," believing that the red was symbolic of the Virgin Mary's red cloak and that the black spots were representative of her sorrows. Coccinellid systematics has advanced significantly since those times, but classification of lady beetles is still problematic.

Coccinellidae is one of the largest beetle families in the superfamily Cucujoidea, with over 6,000 nominal species. The family currently is placed within the Cerylonid Series, a monophyletic group of highly derived beetle families included in the superfamily Cucujoidea (Crowson 1955; Hunt *et al.* 2007; Robertson *et al.* 2007). The closest relatives of Coccinellidae are hypothesized to be Corylophidae and at least part of Endomychidae (Crowson 1955; Sasaji 1971). Morphological and molecular data supports a relationship between Coccinellidae and Anamorphinae + Corylophidae or with Leisestinae (Robertson *et al.* 2007). At least one study recovered a sister-group relationship between Coccinellidae and Alexiidae + Anamorphinae (Hunt *et al.* 2007).

Many lady beetles, particularly those in the tribe Coccinellini, are easily recognized because of their appealing coloration. They are usually shiny, and often bear spots, checkerboard patterns, or even stripes. The vast majority of coccinellids, though, strongly resemble moving dirt. They are small, furry, drably colored, and easily escape notice. The family is difficult to characterize, but most coccinellids can be distinguished by the convex, oval to hemispherical dorsum, flattened venter, and clubbed antennae. Most species have 4-4-4 tarsi, with the third tarsomere very small and concealed beneath the second (pseudotrimerous). Some have all four tarsomeres of equal length (true tetramerous) and others have tarsi reduced to 3-3-3 (true trimerous) (Vandenberg 2002).

I. What's In a Name?

"I belong to Our Lady, Your Mother
That isn't hard to believe
It's written in my name!"

Anon: "The Ladybird"

Catholic farmers were not the only group to believe that lady beetles were sacred. Coccinellids were considered divine in many societies, and their common names often reflected this association. In his book, *History of the Ladybird*, Exell (1991) reviews the colloquialisms associated with Coccinellidae. He lists 329 different names associated with 55 different languages; of those, approximately 25% are named in honor of the Virgin Mary (Exell 1991). Another 15% are also dedicated to religious figures, including Saint Catherine, Saint James, Saint John, Saint Nicolas, Saint Martin, Jesus, and the Pope (Exell 1991). One very notable exception is the Italian name "Galineta del Diablo," a black ladybird dedicated to Satan (Majerus 1994).

Non-Christian cultures also connected lady beetles to divinity. In Yiddish, lady beetles were often called *mashyiakhl* ("little Messiah") or *Moyshe rabbeynus beheymele* ("Moses' little cow") (Exell 1991, Philologos 2007). The reverence bestowed by the Catholics and the early

Christians was also mirrored by Yiddish common names. Like the Catholic names, the Yiddish names were the result of religious symbolism. In this case, dedication to the Virgin Mary was surpassed by dedication to the messiah or to Moses, who is one of the most esteemed figures in Judaism. According to Jewish tradition, Moses was a wealthy, and very humble, man. To him, worldly riches (in this case the multitude of cattle possessed by the children of Israel when they left Egypt) were no more significant than an insect. The name *Moyshe rebbeynus beheymele* was given to the lady beetle to signify the connection between God, man, and beauty (Philologos 2007).

The scientific name, Coccinellidae, is likely a derivative of the Latinized Greek *Kokkos*, meaning a seed or berry (Ślipiński 2007). Some authorities argue this point, insisting that the family name is derived from the Latin *coccinatus*, meaning clad in scarlet (Majerus 1994; Ślipiński 2007). Given their round, convex shape and often bright colorarion, Coccinellidae is a fitting name in either case.

Lady beetles have often been the subject of poetry, nursery rhymes, and folklore. Exell (1991), Gordon (1985), and Majerus (1994) provide a comprehensive summary of the lady beetle's inclusion in both ancient and popular cultures.

Taxonomic History

> "*Coccinellidae*
> *Are not birds and can be male;*
> *Spot the difference*."
>
> -Simeoni *in* Exell, 1991

I. Coccinellidae Latreille 1807

Lady beetle classification began with Linnaeus' *Systema Naturae* in 1758. He included 36 species in the genus *Coccinella*, many of which are still considered valid. Latreille (1804) recognized a group of lady beetles that all seemed to have trimerous tarsi; he referred to them as "Tridigités." Later, Latreille (1807) renamed the family "Coccinellidae," and provided the first available family group name for lady beetles. Redtenbacher (1843) attempted one of the first meaningful internal classifications of Coccinellidae, and divided the family into two groups: aphidophagous and phytophagous. Although the aphidophagous grouping proved to be artificial, the phytophagous group corresponds to the subfamily Epilachninae.

Mulsant's (1846, 1850) works are considered landmark classification events in the history of Coccinellidae. He focused only on the Coccinellidae of France, but in his later work Mulsant (1850) attempted to encompass the world fauna. His treatment was noteworthy because he proposed a new system of classification for lady beetles: he separated setose species from glabrous ones, and also attempted to include overall body shape (hemispherical vs. elliptical, dorsoventrally flattened vs. convex) and color patterns in his groupings (Mulsant 1846; Mulsant 1850). This system was quite unstable due to the subjectivity of the characters chosen for species diagnoses. As a result, many of his species were synonymized by subsequent authors.

Verhoeff (1895) and Dobzhansky (1926) were responsible for a major breakthrough in lady beetle classification. They performed extensive studies of male genitalia, proposed homologies, discussed functionality, and presented new classifications based on these findings. Today, the structure of the male genitalia is the most common way to differentiate lady beetle species.

In 1968, a new method for classifying lady beetles was devised. Sasaji (1968a) presented a phylogenetic hypothesis based on both larval and adult characters. He also provided a comprehensive review of lady beetle classification, with references to both authors and the structures they used to delineate subgroups within the family (Sasaji 1968a, 1971). He recognized six subfamilies of Coccinellidae: Sticholotidinae, Scymninae, Coccidulinae, Chilocorinae, Coccinellinae, and Epilachninae; this system is still followed by most contemporary authors (Gordon 1985; Booth *et al.* 1990; Pakaluk *et al.* 1994; Lawrence & Newton 1995; Kovár 1996; Vandenberg 2002). Alternative classifications were attempted by Chazeau *et al.* (1989), Fürsch (1996), and Ślipiński (2007);all researchers built upon Sasaji's classification by adding one or more subfamilies to the family group. Fürsch (1996) even solicited the help of coccinellid experts worldwide, but still no agreement was reached. As a result, current classifications are based on imprecise, subjective characters such as size, shape, color, and convexity, just as they were over a century ago. Although no agreement was ever reached, attempts to provide a sound classification scheme yielded several quality papers regarding the comparative morphology of coccinellid larvae (Gage 1920; Kamiya 1965; Sasaji 1968b; Savoiskaya 1973), pupae (Phuoc & Stehr 1974; Nakamura 1980), and adults (Gordon 1985; Kovár 1996; Vandenberg 2002).

II. Taxonomic Problems in Coccinellidae

If the subfamilial relationships and definitions within Coccinellidae are unstable, then the tribal ones are even more so. This is because most tribal and generic level revisions were conducted regionally, even though the subfamilies are cosmopolitan. The major consequence of these types of studies was that many proposed groups fell outside the revisionist's geographical area and were not considered at all for the taxonomic treatment (Vandenberg 2002). Even now, generic and higher level taxa are not rigorously defined, and new species descriptions are still based mainly on very labile characters, just as they were over a century ago. Coccinellid taxonomy seems to have been relegated to a small faction of "old school" experts: those who are comfortable describing a new species, creating a new genus, or even elevating a genus to tribal status for impact or convenience without any phylogenetic basis at all. As a result, countless synonymies have been created at all taxonomic levels within the family. That, combined with the sheer number of species (about 6000 worldwide), as well as the number of species imported to various places for biological control makes taxonomic endeavors within the family daunting to even the most seasoned coleopterist.

III. Noviini Mulsant

In 1850 Mulsant recognized a group of coccinellids he called *Noviaires.* They were covered with dense, short setae and had pubescent, entire eyes (no ocular canthus), antennae with 8 articles, trimerous tarsi, and 6 abdominal ventrites. Ganglebauer (1899) referred to this group as "Noviini." Currently included in the subfamily Coccidulinae, the tribe consists of approximately 80 nominal species divided among three genera: *Anovia* Casey, *Novius* Mulsant, and *Rodolia* (Mulsant) (Gordon 1972). The noviines are of particular interest because of their extensive use as biological control agents. The most famous example is undoubtedly *Rodolia cardinalis* (Mulsant). This beetle is especially well known for its ability to control the cottony cushion scale, *Icerya purchasi* Maskell, and is an introduced species on several continents, including North America.

The taxonomic problems in the tribe Noviini mirror those found within the family, especially the ambiguous generic definitions. Gordon (1972, 1985) noted that *Rodolia* and *Anovia* were virtually indistinguishable in the adult stage, and reported that only a difference in the number of larval antennomeres (Rees 1947) warranted the continued separation of the genera. Unfortunately, Rees's (1947) study only included one exemplar of *Anovia*. Forrester *et al.* (in prep) provides a new description of *Anovia* larvae and pupae, along with a review of the literature pertaining to immature stages of Noviini.

The extreme morphological similarity in Noviini does not end with the controversial *Rodolia/Anovia* matter. For over a century now, authors have used the generic names *Novius* and *Rodolia* almost interchangeably. Gordon (1972) remarked that "some species presently placed in *Novius* will have to be transferred to *Rodolia*." Ślipiński (2007) transferred all Australian species in the genus *Novius* to *Rodolia* in one sentence. Both authors were quite thorough in their studies of comparative morphology within the tribe, but neither Gordon (1972, 1985) nor Ślipiński (2007) attempted to classify noviine genera in light of their findings. Until now, no cladistic or revisionary treatment of this biologically important group was ever undertaken.

Biology

Although Coccinellidae is an extremely large beetle family (over 6000 species divided among 360 genera), several works encompassed biological and ecological aspects for the entire group. Reveiws of coccinellid biology and ecology are provided by Clausen (1940); Hagen (1962); Hodek (1973); Majerus (1994); Hodek & Honěk (1996); and Kuznetsov (1997).

I. Feeding Preferences

Most authors divide the family into two major groups based on feeding preference: phytophagous or predaceous. A few lady beetles supplement their diet with pollen or nectar, and at least one group (Halyziini) is primarily mycophagous (Gordon 1985; Ricci 1986). Many host records exist, but like the taxonomic information, studies of food preference were often limited to a particular geographic region; in many cases, only economically important lady beetles were studied (Balduf 1935; Klausnitzer & Klausnitzer 1986; Omkar & Pervez 2004).

Noviines are best known for their ability to effectively control scale insects, and the majority of literature pertaining to Noviini is focused on that issue. All members of the tribe are predaceous as both larvae and adults, and feed exclusively on scale insects in the family Monophlebidae, in particular, *Icerya aegyptiaca* (Douglas), *Icerya purchasi* Maskell, *Icerya seychellarum* (Westwood), *Monophlebus stebbingi* (Stebbing), *Crypticerya genistae* (Hempel), and *Paleococcus fuscipennis* (Burmeister) (Balduf 1935; Gordon 1985; Leeper 1976; Mendel *et al.* 1998; Samways *et al.* 1997; Dixon 2000). Most prey species are serious pests of citrus, legumes, or ornamentals. Noviines are usually found only where monophlebid scales are present. They are quite visible as both adults and larvae, crawling over the scale insects and substrate, feeding voraciously. In fact, their feeding is so voracious that obtaining and maintaining live cultures of noviines is extremely difficult (Divina Amalin, personal communication; Beth Grafton-Cardwell, personal communication).

Although noviines can decimate a scale population very quickly, individual feeding by the lady beetles is often a lengthy affair. Many times, adult noviines do not kill their prey readily, but impale the victim with their mandibles and then drag it around for up to a half hour (Stebbing 1904). Likewise, the larvae sometimes do not kill immediately. Once they pierce the scale with their sharp mandibles, they can anchor themselves to their substrate via their anal pore and feed for several hours (Stebbing 1904). Typically, gravid females consume more prey than unmated females or males; this may indicate a correlation between food consumption and oviposition rate (Balduf 1935).

II. Life History

Iperti (1999), Majerus (1994), and Hodek (1973) summarized general life history patterns for the family. Like other members of Coccinellidae, noviines reproduce prolifically. Field studies show that a female *Rodolia* can lay up to 330 eggs in a single season if conditions are favorable (Balduf 1935; Bodenheimer 1932). Noviine eggs are oval, magenta colored, and covered with a thin, waxy exudate (Forrester *et al.* in prep.). The surface of the egg is granular and contains many micropyles. These specialized pores probably allow for spermatozoa entrance as well as oxygen diffusion (Majerus 1994; Ricci & Stella 1998). Like other coccinellid eggs, the chorion of noviines is much stronger than that of other beetle eggs, presumably because noviines lay their eggs in exposed places, often in the vicinity of prey. Other times they oviposit directly underneath the prey item (Amalin, personal communication; LeSage 1991; Majerus 1994). The incubation period for *Rodolia cardinalis* eggs is approximately 6 days (Coquillet 1889); once they emerge, the young larvae feed immediately. Frequently, the first instars are found feeding in the egg sacs of *Icerya* species (Balduf 1935).

Coquillet (1889) provided the following account of the larval instar durations for *Rodolia cardinalis*: I: 6 days; II: 2 days; III: 5 days; IV: 7 days. The developmental time from egg to adult is, on average, about 35 days, with life cycle duration varying with temperature (Balduf 1935; Bodenheimer 1932). Developmental extremes occurred at 56° F (86 days) and 82° F (16 days) (Bodenheimer 1932). Noviine larvae are similar to those of Scymnini, Ortaliini, Hyperaspini, Coccidulini, Cryptognathini, Azyini and Telsimiini in that they produce a stringy, waxy exuvium that covers the dorsum. Pope (1979) provides a comprehensive investigation of wax production by coccinellid larvae, including Noviini.

Just before pupation, the last larval instar begins a prepupal stage that lasts from one to several days (Majerus 1994; Vandenberg 2002). This prepupal stage is a quiescent period when the larva ceases feeding and attaches itself to a substrate via a cauda (personal observation; Majerus 1994; Vandenberg 2002). The pupae are exarate and almost entirely covered by the last larval exuvium (Forrester *et al.* in prep.), and last approximately 8 or 9 days for Noviini (Balduf 1935; personal observation)

Eclosion can take several minutes, and often the beetle remains inside the pupal casing while the elytra and flight wings expand and dry (personal observation; Majerus 1994). At this point, the elytra are immaculate and pale; the deposition of pigments there can take several hours (personal observation; Majerus 1994; N. Vandenberg, personal communication). It is common for adults to mate very soon after eclosion. Bodenheimer (1932) notes that females of *Rodolia cardinalis* often mated immediately after emergence, with oviposition 3-4 days later during warmer seasons and 1-2 weeks later in cooler temperatures.

III. Aggregation

Some species of Coccinellidae are notorious for their ability to form large aggregations, particularly when overwintering. Although this phenomenon is well-known, studies pertaining to lady beetle aggregation are limited to a relatively small number of species, most of them in the subfamily Coccinellinae (Balduf 1935; Hodek 1973; Iperti 1999; Majerus 1994). Some of those species (e.g., *Harmonia axyridis* (Pallas)) have become such pests that control strategies are being considered for them (Kenis *et al.* 2008).

Only one study has addressed the aggregation behavior of noviines (Stebbing 1904). Interestingly, Stebbing's (1904) study showed that *Rodolia fumida* Mulsant (as *Vedalia guerinerii* Crotch) gathered in large numbers on the undersides of leaves during the warmest part of the day in summer. Larvae of this species also became gregarious just prior to pupation (Stebbing 1904). Stebbing (1904) also noted an aggregation of *V. guerinerii* in flight during the summer months, leading him to conclude that factors other than overwintering must be affecting this species.

IV. Color (Figs. 4.8 - 4.13)

Like the coccinellids of popular culture, noviines exhibit a wide variety of color patterns. Many of them display the familiar red background adorned with black markings. The black markings range from spots (e.g., *Rodolia cardinalis* (Mulsant)) to bands (e.g., *Rodolia bellus* (Blackburn)) to zonate regions (e.g., *Rodolia circumclusa* (Gorham)). Sometimes the entire posterior half of the elytra is piceous (e.g., *Rodolia circumclusa* (Gorham)), and in others, only the pronotum and head are darkly colored (e.g., *Rodolia koebelei* (Olliff)). Occasionally the entire beetle is shiny black with orange or red maculae (e.g., *Rodolia koebelei* (Olliff), *Rodolia lindi* (Blackburn)), and rarely with a narrow red or orange band around the lateral edge of the elytra (e.g., *Rodolia limbata* (Motschulsky)). The majority of noviines are monochromatic, with coloration ranging from pitchy black to rusty orange-brown to carmine red.

Much of the color variation (number of spots, spot position, spot size and shape) in lady beetles is genetic (Majerus 1994; Honěk 1996). Honěk (1996) provided a review of temporal and geographic variability in lady beetles, and noted that light colored populations tend to occur in arid regions while darker pigmentation is more common in humid areas. Gordon (1972) noted that in rare instances, some color patterns can be linked to specimen maturity.

V. Defense

Most authors agree that the bright orange, yellow, or red coloration of lady beetles is aposematic and that several different chemical compounds contribute to the various hues. The black pigment associated with the elytral maculae of coccinellids is probably melanin, the same pigment found in insect cuticle and wings (Honěk 1996; Stoehr 2006). The bright reds and oranges of the elytra are due to the presence of carotenoids and are exogenous, probably derived from aphidophagy (Bezzerides *et al.* 2006). In contrast, the defensive compounds tend to be endogenous alkaloids (Britton *et al.* 1977, Bezzerides *et al.* 2006). Studies involving the Asian lady beetle, *Harmonia axyridis* (Pallas) indicate that a larger proportion of red coloration (rather than hue intensity) signifies higher alkaloid content and a better defended beetle (Bezzerides *et al.* 2006). King and Meinwald (1996) provide a comprehensive review of lady beetle chemistry, listing 34 endogenous alkaloids associated with the beetles.

Not all coccinellids synthesize alkaloids for defense, though. Some are able to sequester chemical deterrents from their food sources (Daloze *et al.* 1994; King and Meinwald 1996; Pasteels 2007). Species of *Hyperaspis* Redtenbacher are notable examples, because these lady beetles are able to sequester and secrete carminic acid, a red pigment, from the cochineal scales that they eat (Daloze *et al.* 1994; Eisner *et al.* 1994; King & Meinwald 1996; Pasteels 2007). When *Hyperaspis* larvae are agitated, they secrete droplets of hemolymph containing carminic acid from the dorsal interstices (Eisner *et al.* 1994; King & Meinwald 1996). Rather than the oily yellow droplets associated with many other coccinellids, the secreted hemolymph of *Hyperaspis* larvae is the characteristic magenta color associated with carminic acid dye.

Interestingly, beetles in the tribe Noviini also secrete magenta-colored fluid if provoked (D. Amalin, personal communication; personal observation). Furthermore, when specimens of this group are placed in a weak KOH solution, the red color leaches out from the femorotibial junction and becomes concentrated in membranous areas such as the antennal club apex, maxillary palpi, and the spongy lobes beneath the tarsi (personal observation). Daloze *et al.*

(1994) showed that *Icerya purchasi*, the primary prey of noviines, produces carminic acid. It is unknown whether or not the magenta colored fluid secreted by noviines actually is carminic acid, but further inquiries into this phenomenon are certainly warranted.

VI. Biological Control

Beetles in the tribe Noviini are probably best known for their extensive use as biological control agents. In fact, one of the earliest and most successful ventures into the biocontrol realm involved a noviine: *Rodolia cardinalis*. Caltagirone & Doutt (1989) provide a complete review of the events leading up to the beneficial beetle’s importation into the United States. They also present a thorough literature review documenting the characteristics of successful control agents, illustrating clearly why beetles in the genus *Rodolia* are so well-suited for scale-insect control. Among the characteristics listed are: ability to disperse, ability to increase populations rapidly, ability to search, multivoltinism, narrow prey specificity, adult longevity, and high prey-searching efficiency (Caltagirone & Doutt 1989). They also point out that the limited dispersal ability of monophlebid scales favors the predator (Caltagirone & Doutt 1989). Additional studies of the efficacy of noviines as biological control agents is provided by DeBach & Rosen (1991), Dixon (2000), Hagen *et al.* (1976), and Quezada & DeBach (1973). Although the success of other lady beetles as control agents has been questioned, e.g., *Harmonia axyridis*, few if any, adverse environmental impacts have been reported as a result of widespread importation of *Rodolia* (Howarth 1991).

VII. Purpose of Study

"She came in fast, the ladybird,
Lowered her gear and made a spot landing.
She was almost a brand-new model
Three hundred million years ago."

Geoffrey Mostyn Lewis: "Advanced Technology"

Interest in noviines as biological control agents has been renewed by the recent introduction of scale pests into the United States (Hodges 2006). Noviines are very effective, species-specific predators. Unfortunately, they are very difficult to identify. This is due in part to the very ambiguous generic and species definitions associated with the group. To further complicate matters, many early species descriptions were based entirely on color patterns or geographic distribution; these characters are inadequate to diagnose species in Noviini.

Although several authors (Gordon 1972, 1985; Ślipiński 2007) have provided diagnostic characters at the tribal level, no formal cladistic analysis was ever undertaken to test the monophyly of the group. The purpose of this study is to: 1) test the monophyly of Noviini and included genera; 2) provide a classification for Noviini based on phylogeny; and 3) provide a taxonomic revision of the tribe.

Materials and Methods

I. Museum Material

No large scale revision can be completed without the aid of museum material. Many museums kindly loaned specimens, agreed to dissections, and provided assistance with label data and locality information. Others are referenced in the literature as being type depositories for various species. They are referenced by the following codens:

BMNH - British Museum of Natural History; London, United Kingdom (Dr. R.Booth)

ANIC - Australian National Insect Collection; Camberra. Australia (Dr. S. Ślipiński)

EMEC - Essig Museum of Entomology; Berkeley, United States (Dr. C. Barr)

MLAC - Natural History Museum of Los Angeles County; Los Angeles, United States (Dr. B. Brown)

MRAC - Musée Royal del'Afrique Centrale; Tervuren, Belgium (Dr. M. DeMeyer)

NHRM - Naturhistoriska Riksmuseet; Stockholm, Sweden (Dr. B. Viklund)

SAMA - South Australian Museum; Adelaide, Australia (Dr. E. Matthews)

UCRC - University of California at Riverside Entomology Museum; Riverside, United States (Dr. D. Yanega)

UMZC - University Museum of Zoology Cambridge, United Kingdom (Dr. W. A. Foster)

USNM - United States National Museum of Natural History; Smithsonian Institution; Washington, D. C., United States (Dr. N. Vandenberg)

ZIRS - Zooloigical Institute of the Russian Academy of Sciences (formerly Museum of Zoological Institute of the USSR in Leningrad); St. Petersburg, Russia (Dr. Boris Mikhaylovich Kataev)

ZMHB - Museum für Naturkunde; Berlin, Germany (Dr. B. Jaeger)

ZMHU - Zoological Museum at Helsinki University; Helsinki, Finland (Dr. H. Silfverberg)

It is important to note that many type specimens for Noviini are currently housed in the Musee d'Histoire Naturelle in Paris. Unfortunately, there currently is no curator for Coccinellidae there, and all material from this facility is inaccessible. Many descriptions are based upon reliably identified material, and many *nomina dubia* are reported.

II. Dissections

Dried, point- or card-mounted specimens were removed from their mounts via distilled water. Since many card-mounts included penmanship by the original author in ink, a paintbrush was used to apply the water; this way, the original handwriting was preserved. Once removed, specimens were heated in distilled water for softening.

For holotypes, only the beetle's abdomen was removed and placed in a warm KOH solution; then, genitalia removed. For specimens that were not part of a type series, the pronotum was removed and all parts were placed in a warm KOH solution. Then, the beetle was completely disarticulated, and all dissected parts were slide mounted and in glycerol. Prosterna required a bit more preparation, due to their odd 45° tilt. To eliminate movement, pronota were glued to a depression slide with a miniscule amount of water-soluble Elmer's glue. Once dried, they were then immersed in glycerol and viewed through a microscope.

III. Illustrations

All specimens were examined with a Meiji Techno RZ stereoscopic microscope. Illustrations were rendered using a camera lucida attached to a Leitz DMRB compound microscope (Leica Microsystems, Inc., Bannockburn, Illinois) in conjunction with Adobe Illustrator CS2 (Adobe Systems, Inc., 2003, San Jose, California). Pupae and adult habitus photographs were taken with a Microptics digital imaging system (Photografix, Inc., Richmond, Virginia) used with Helicon Focus and Combine Z software (http://www.hadleyweb.pwp.blueyonder.co.uk/ CZ4/Docs/combinez 4.htm). All photographs were edited with Adobe Photoshop (Adobe Systems, Inc., 2003, San Jose, California).

Phylogenetic Methods

I. Introduction

Although the tribe Noviini has been recognized as a natural group for over a century, no formal phylogenetic analysis of the tribe has ever been conducted. Although three genera are recognized, there is no current agreement regarding their definitions or boundaries. The names *Rodolia* (Mulsant) and *Novius* Mulsant have been used interchangeably in the literature for almost 30 years, and there is much disagreement regarding the separation of the two (Gordon 1972, 1985; Ślipiński 2007). Like *Rodolia* and *Novius*, *Rodolia* and *Anovia* Casey are extrememly similar morphologically. The separation of the two genera is contentious, and recent authors report that the two can only be distinguished by examination of the larval antennomeres (Rees 1947; Gordon 1972; Rees *et al.* 1994). Although the tribe is recognized on the basis of morphological characters, its monophyly has never been tested. Thus, before a worldwide revision of Noviini can be undertaken, it is necessary to determine whether or not Noviini, as currently recognized, is indeed a monophyletic group. In the present study, a phylogenetic analysis of Noviini based on morphological data is conducted in an attempt to: 1) test the monophyly of the tribe Noviini, 2) test the monophyly of the constituent noviine genera, and 3) investigate the relationships among these taxa. The results of the phylogenetic analysis are used as a framework upon which natural taxa may be identified, characterized via synapomorphy- and subsequently taxonomically revised at the species level.

II. Taxon Sampling

Over 2000 specimens of Coccidulinae were examined, representing five of eight tribes included in the subfamily. Taxon sampling was limited due to the rarity of some groups; hence, the remaining three cocciduline tribes were not included in this study. Since generic and tribal boundaries are particularly ambiguous in Coccidulinae (whose monophyly is also highly questionable), it was necessary to choose a broad range of outgroup taxa in order to test the monophyly of Noviini (Ślipiński 2007, Robertson *et al*. 2008). Representatives of hypothesized closely related tribes including Exoplectrini (4 genera), Ortaliini (1 genus), Coccidulini (2 genera), Azyini (1 genus), and Poriini (1 genus) were selected based on previous phylogenetic studies and classifications based upon comparative adult morphology (Gordon 1985; Kamiya 1965; Sasaji 1968; Sasaji 1971; Ślipiński 2007; Vandenberg 2002). Exemplars of all noviine genera were included in this sampling. Due to the ambiguous boundaries of Coccidulinae, one hypothesized "distant" outgroup was chosen: a species of *Anatis* Mulsant, a member of Coccinellinae. 28 total taxa were used in the phylogenetic analysis.

III. Morphological Data

Characters were scored after a thorough study of internal and external morphology; all characters were considered in light of "traditional" characters used in coccinellid taxonomy. Many of those have proven to be highly labile (e.g., color, size, convexity, and distribution), and were not included in this analysis. Likewise, descriptions of cocciduline genera found in the literature are based on the aforementioned subjective characters. For that reason, only characters that were directly observed were scored.

Characters

0. Dorsal habitus: hemispherical, widest at midlength (0); elongate, widest at humeral callus (1);
1. Lateral habitus: hemispherical (0); compressed (1)
2. Dorsal surface: glabrous (0); pubescent (1)
3. Eye canthus: present (0); absent (1)

4. Eye facets: glabrous (0); pubescent (1)
5. Clypeal apex: straight (0); arcuate (1)
6. Antennal grooves: present (0); absent (1)
7. Antennal segments: 8 (0); 10 (1); 11 (2)
8. Scape: laterally expanded on one side, strongly asymmetrical (0); cylindrical, symmetrical (1)
9. Pedicel: subglobose, as long as wide (0); cylindrical, longer than wide (1)
10. Antennal segments: asymmetrical (0); cylindrical, symmetrical (1)
11. Labrum: edges horizontally expanded just distal to clypeus (0); edges vertical just distal to clypeus (1); edges at 45° angle just distal to clypeus (2)
12. Apical maxillary palpomere: securiform, with distal edge > 2x as long as proximal edge (0); weakly expanded, with distal edge < 2x as long as proximal edge (1)
13. Pronotal margins: explanate (0); simple (1)
14. Posterior pronotal margin: sinuate (0); straight (1)
15. Posterior pronotal arch: present (0); absent (1)
16. Posterior pronotal angles apparent (0); obsolete (1)
17. Posterior margin of prosternal process: quadrate (0); rounded (1); acutely pointed (2)
18. Prosternal process: parallel sided (0); trapezoidal, widest posteriorly (1); trapezoidal, widest anteriorly (2)
19. Anterolateral margin of pronotum: thickened, with definite inner and outer edge (0); flattened, inner and outer margins not distinct (1)
20. Hypomeral fovea: present (0); absent (1)
21. Epipleural margin: complete to elytral apex (0); incomplete, not reaching elytral apex (1)

22. Epipleural fovea: absent (0); present (1)
23. Elytral margins: simple (0); explanate (1)
24. Lateral elytral margins: straight (0); sinuate (1)
25. Femur: uniformly wide (0); distinctly narrow at both apices (1); distinctly widest at one apex (2)
26. Prothoracic femoral lobe: long, extended distally beyond femoral apex (0); short, not extended distally beyond femoral apex (1)
27. Tibial spurs absent (0); apical (1); medial (2)
28. Protibial margins: straight (0); margins lobed, expanded medially (1); bilobed medially (2)
29. Tarsi 4-4-4 (0); 3-3-3 (1)
30. Abdominal ventrites: 5 (0); 6 (1)
31. Postcoxal lines: complete (0); incomplete
32. Transverse coxal line: present (0); absent (1)
33. Pronotal width: greatest near humeral angles (0); greatest anterior to humeral angles (1).

Cladistic Analysis

The data matrix for 28 terminal taxa (17 ingroup, 11 outgroup) and 34 adult morphological characters (Table 4.1) was assembled in WinClada version 1.00.08 (Nixon 1999-2000). For some exemplars, complete dissections were not permitted; therefore, some characters could not be scored for all taxa. For those characters, the missing data is indicated by a “?”. Tree searches were done via the parsimony ratchet in NONA as implemented by WinClada (Goloboff 1995; Nixon 1999-2000). Three repeated runs of 200 iterations each were performed; each time, 100% of the characters were sampled and 10 trees were held. In each run, characters were unordered and unweighted. WinClada was also used to both view trees and calculate the strict consensus tree (Nixon 1999-2000).

Tree searches for the same data matrix were also performed in TNT (Goloboff *et al.* 2003). Tree searches were done using the “traditional search” command in conjunction with the “tree bisection reconnection” (TBR) swapping algorithm (Goloboff *et al.* 2003). Three runs with 10 replicates each were performed, with 10 trees saved per replication. Bremer support values were calculated in TNT by using the “Analyze, Suboptimal” command. The suboptimal search was repeated to find trees that were 1 step longer than the most parsimonious tree, then 2 steps, etc. until 10 steps were reached. Then, the original TBR search was implemented again, and the “Trees, Bremer Supports” command was used with the default settings to obtain the support values. The cladogram presented was redrawn from the TNT output using Adobe Illustrator CS.

Results

The cladistic analysis in both WinClada and TNT recovered 3240 most parsimonious trees (MPTs) (tree length (L) = 88 steps; consistency index (CI) = .43, retention index (RI) = .66). Strict consensus of 3240 MPTs collapsed 23 nodes (Fig. 4.1). The monophyly of the tribe is well supported, with four uncontroverted synapomorphies and four homoplasious ones. The Noviini clade hada Bremer support value of 10. Very little can be inferred from the strict consensus tree due to lack of resolution, but these results are not surprising given the taxonomic level involved.

Although the tribe Noviini is clearly monophyletic, the same cannot be said for the genera comprising it. *Rodolia* appears to be paraphyletic with respect to at least some species of *Anovia*. This finding was not surprising given the morphological homogeneity of the tribe. The strong support for the monophyly of Noviini, along with the lack of support for separate noviine genera, necessitates a new classification. The most logical solution to this problem is to synonymize *Anovia* and *Novius* with *Rodolia,* leaving Noviini monogeneric. Although *Novius* has priority over *Rodolia*, the latter name has been used in well over 25 publications in the last 10 years. Furthermore, the applied entomological community and agricultural workers know this group only as *Rodolia*. It is therefore in the interest of stability that the name *Rodolia* takes precedence over *Novius* to refer to the single genus comprising the tribe Noviini.

Of the 8 synapomorphies supporting the monophyly of the tribe, 4 are uncontroverted with respect to the outgroups. First, Noviines have antennae composed of 8 articles (*Exoplectra* and *Aulis* have 10; all others have 11). Second, the structure of the labrum is unique to noviines. The lateral margins extend just beyond the clypeus and are directed outward at a 45° angle as opposed to being directed horizontally outward (*Exoplectra*) or not directed outward at all (all other outgroups). Third, noviines have femora that are distinctly widest at the distal apex, not narrow at both ends (*Poria*) or uniformly wide from end to end (all remaining outgroups). Fourth, noviines have tibiae that are lobed, or expanded at midlength. Both species of *Exoplectra* and the single exemplar of *Azya* have tibial groove edges that are bilobed; the remaining members of the outgroups have tibiae that are not expanded at all.

As expected with an analysis at the species level, many characters are homoplasious. Although these characters are poorly informative phylogenetically, in combination they are still reliably diagnostic for Noviini (Fig. 4.1). Members of the tribe are unique among coccidulines in that the eye canthus is absent. The only other genus whose members lack an eye emargination is *Coccidula.* When considered with the other taxonomic characters, entire eyes are reliably diagnostic for the tribe. Noviines also have a straight clypeal apex, as opposed to one that is raised at mid-width. The exception among outgroups is *Anatis*. Another diagnostic character for the tribe is the tarsal formula. Unlike most other coccinellids, noviines are truly trimerous. Again, a notable exception occurs in one of the outgroup members: representatives of *Ortalia* are also truly trimerous. Finally, noviines are distinguishable by the presence of 6 abdominal ventrites. All others have 5, except *Anatis* (also with 6). One very notable exception occurs in species of *Ortalia*. In this case, there is a sexual dimorphism: males have 6 ventrites and females have 5. Although the 6th ventrite of *Ortalia* males is very small and inconspicuous, it is present nevertheless.

The data used for this analysis recovered Poriini as the base of Coccidulinae and Noviini as a monophyletic group. Noviini remains unresolved with respect to sister-group candidates in the subfamily. Many authors e.g., Gordon (1972, 1985) and Rees (1947, 1994) believe that Noviini is most closely related to Exoplectrini; the basis for this assertion is the presence of the inflated, asymmetrical scape. Others place them near Coccidulini, Ortalini, or Scymnini based on their observation of morphological or feeding similarities. It is important to note that those authors did not base their classifications on a phylogenetic analysis; they also limited their work to a particular geographic region. Traditionally, Coccidulinae has been the dumping ground for small, pubescent, difficult-to-characterize lady beetles. Revisionary work that is global in scope is highly desirable for any tribe in that subfamily.

Tribe NOVIINI Ganglebauer, 1899

Noviini Ganglebauer, 1899: p. 954. Type genus: *Novius* Mulsant, 1850, by monotypy.

Noviaires Mulsant, 1850: p.938.

Novii Weise, 1895: p. 148; misspelling.

Noviina Jacobson, 1916: p. 969; misspelling.

Rodolia Mulsant, 1850

Rodolia Mulsant, 1850: p. 902. (Type species: *Rodolia ruficollis*, by subsequent designation).

Nomius Mulsant, 1846: p. 4, misspelling; corrected by the author in the 'Addenda et Errata,' issued at the same time as the original work, but not paginated.

Novius Mulsant, 1850: p. 942 (Type species: *Novius cruentatus* Mulsant, 1846, by monotypy).

Vedalia Mulsant, 1850: p. 905.

Macronovius Weise, 1885: p. 63.

Eurodolia Weise, 1895: p. 149. (Type species: *Eurodolia severini* Weise, 1895, by monotypy).

Anovia Casey, 1908: p. 408. (Type species: *Scymnus virginalis* Wickham, by monotypy).

For an exhaustive account of the internal and external morphology of *Rodolia*, please see Priore (1963).

Key to the World Noviini

1. Basal lobe of aedeagus expanded dorsally to form apical barb (Figs. 4.81, 4.82, 4.84, 4.85, 4.97, 4.98, 4.100, 4.101) 2

\- Basal lobe of aedeagus not expanded dorsally, apical barb absent (Figs. 4.69, 4.70, 4.72, 4.73, 4.75, 4.76, 4.78, 4.79) 9

2(1). Sipho narrow, less than or equal to 1 paramere width; length relative to aedeagus variable (Figs. 4.74, 4.77, 4.80, 4.83, 4.86, 4.90, 4.96, 4.99, 4.102) 3

\- Sipho stout, greater than 1 paramere width; length less than 2x aedeagus (Fig. 4.93) ....*R. koebelei*

3(2). Sipho short, < 2x length of aedeagus (Figs. 4.71, 4.77, 4.80, 4.90, 4.93, 4.99)....................4

\- Sipho long, > 2x length of aedeagus (Figs. 4.74, 4.86, 4.96, 4.102)...5

4(3). Median strut short, less than or equal to the length of the basal piece (Figs. 4.69, 4.70, 4.75, 4.76) 6

- Median strut long, greater than the length of the basal piece (Figs. 4.97, 4.98) ....*R. pumila*

5(3). Parameres parallel-sided or nearly so for entire length (Figs. 4.69, 4.72, 4.78, 4.81, 4.84, 4.94, 4.97, 4.100) 7

- Parameres abruptly constricted just proximal to midlength ....*R. insularis*

6(4). Prosternal process quadrate (Figs. 4.51-4.58)..*R. usambarica*

- Prosternal process cordate (Fig. 4.59) ....*R. cardinalis*

7(5). Parameres parallel to basal lobe or nearly so 8

- Parameres laterally arcuate, appearing to encircle the basal lobe ....*R. limbata*

8(7). Basal lobe with apical barb dorsally small, almost in same plane as basal lobe; ventrally with narrow, sharply pointed apex (Fig. 4.85)..*R. fumida*

- Basal lobe with apical barb dorsally prominent, ~ 45° from basal lobe; ventrally with wide, rounded apex (Fig., 4.101)...*R. rubea*

9(1). Sipho narrow, less than or equal to 1 paramere width, length relative to aedeagus variable (Figs. 4.74, 4.77, 4.80, 4.83, 4.86, 4.90, 4.96, 4.99, 4.102)...10

- Sipho stout, greater than 1 paramere width, length less than 2x aedeagus (Fig. 4.93)..... *R. nigra*

10(9). Base of sipho with apodeme present; size and shape variable (Figs. 4.74, 4.80, 4.86) 11

- Base of sipho with apodeme absent (Figs. 4.77, 4.88, 4.90) 12

11(10). Median strut long, > 2x length of basal piece (Figs. 4.97, 4.98).....................................13

- Median strut short, not as long as basal piece (Figs. 4.69, 4.70, 4.75, 4.76)............................16

12(10). Apex of sipho with small barb-like expansion present (Fig. 4.77) ....*R. bella*

- Apex of sipho simple, barb absent (Fig. 4.90)...*R. lindi*

13(11). Basal lobe apex bent downward in lateral view (Figs. 4.69, 4.73, 4.92, 4.95, 4.98) 14

- Basal lobe apex horizontal, not bent downward in lateral view (Fig. 4.80) ....*R. cruentata*

14(13). Siphonal apex narrow, threadlike, with bifurcation just proximal to apex (Figs. 4.74, 4.93) 15

- Siphonal apex narrow, threadlike, with bifurcation extending to apex, giving a 2-pronged appearance (Fig. 4.96)..*R. occidentalis*

15(14). Sipho straight for distal 3/4 (Fig. 4.74) .... *R. argodi*

- Sipho strongly recurved, circular for distal 3/4 .... *R. iceryae*

16(11). Basal lobe wide, > 1 paramere width, extending beyond internal margins of parameres for most of length (Figs. 4.69, 4.87) 17

- Basal lobe narrow, 1 paramere width or less, not extending beyond internal margins of parameres for most of length (Figs. 4.75, 4.78, 4.81, 4.84, 4.89, 4.91, 4.98, 4.100)...................19

17(16). Siphonal apex narrow, threadlike (4.74, 4.76, 4.80, 4.84, 4.86, 4.90, 4.99, 4.102) 18

- Siphonal apex wide, flattened (Fig. 4.71).. *R. andamanica*

18(17). Basal lobe gradually tapered to apex...*R. virginalis*

- Basal lobe abruptly narrowed to apex ....*R. mexicana*

19(16). Basal piece with length and width subequal or nearly so; if not subequal, then distal edge is longer (Figs. 4.69, 4.72, 4.75, 4.78, 4.81, 4.84, 4.87, 4.91, 4.94, 4.97, 4.100) 20

- Basal piece distinctly widest proximally ....*R. circumclusa*

20(19). Basal lobe with excavate region covering entire ventral surface; ventral surface very narrow; parameres widely separated from basal lobe..*R. alluandi*

- Basal lobe with excavate region covering only a small portion of ventral surface; ventral surface narrow, reaching, but not exceeding, internal margins of parameres ; parameres situated very close to basal lobe .... *R. weisei*

Species Accounts

Rodolia alluandi Sicard 1909 (Figs. 4.2, 4.51, 4.67)

Rodolia alluandi Sicard, 1909: p. 119.

Rodolia equestris Sicard, 1909: p. 120, synonym (Korschefsky, 1931: p. 98).

Diagnosis: The aedeagus is distinct for this species, with a very narrow basal lobe (subequal to the width of a paramere) and a short sipho. In all other representatives of *Rodolia*, the basal lobe is wider than the parameres. The sipho is slender, but only about as long as the aedeagus. In other congeners with a short sipho, the structure is much broader.

Description: Length 2.5 - 3 mm. Body hemispherical, widest just behind humeral angles, convex; black with one red spot on each elytron, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.2).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge deeply bilobed, with posterior width about 2x anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind (Fig. 4.51).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically (Fig. 4.67). Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin feebly sinuate. Parameres long, slender, excavate laterally, spatulate apically, widely separated from basal lobe; apical setae long; basal lobe very narrow, slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent. Median strut short, only about as long as basal piece. Sipho short, narrow, only about as long as aedeagus, apex simple; with asymmetrical basal capsule; basal capsule with apodeme present.

Female: unknown

Distribution: Madagascar

Remarks: Sicard's entire collection is housed in the Musee d'Histoire Naturelle in Paris. Unfortunately, there currently is no curator for Coccinellidae there, and all material from this facility is unaccessible. To further complicate matters, Sicard's original descriptions and keys are not sufficient to adequately diagnose species. However, this particular species is distinctive regarding both its morphology and its Madagascan distribution

Rodolia andamanica Weise 1901 (Figs. 4.3, 4.29, 4.52, 4.62, 4.69 - 4.71)

Rodolia andamanica Weise, 1901: p. 93.

Diagnosis: This species is similar to *R. podagrica* with its very short, very broad legs (Fig. 4.62); however, *R. andamanica* can be distinguished from *R. podagrica* and all other congeners by the size and position of the eyes as well as the structure of the male genitalia. *R.*

andamanica has unusually large eyes that cover much of the dorsal head surface (Fig. 4.29). Also, instead of a T-shaped apodeme, the basal capsule of the sipho is subhemispherical (Fig. 4.71). The species is also distinct in having a flat, broad siphonal apex (Fig. 4.71); remaining congeners have a threadlike siphonal apex.

Description: Length. 3 - 3.5 mm. Body subhemispherical, widest at humeral angles, convex; uniformly orange-brown, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.3).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation (Fig. 4.29); ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, covering much of the dorsal head surface, pubescent, not prominent, finely facetted (Fig. 4.29). Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical, with stout setae; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior and posterior edges feebly arcuate, with posterior width about 2x anterior width, setose; procoxal cavities slightly transverse, closed behind (Fig. 4.52).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad, almost as wide as long at widest point (Fig. 4.62). Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire (Fig. 4.62). Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate (Fig. 4.62). Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple (Fig. 4.62).

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid (Fig. 4.62). Aedeagus with basal piece length 1/2 width; proximal margin deeply cleft (4.69). Parameres long, slender, excavate laterally, spatulate apically, widely separated from basal lobe (at least a paramere width); apical setae short; basal lobe very wide, ~ 2 paramere widths, slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent (Figs. 4.69, 4.70). Median strut short, only about 1/2 as long as basal piece (Fig. 4.69). Sipho short, narrow, only about as long as aedeagus, dorsal edge abruptly ends at midpoint, apex flattened, not tapered to a point, simple; with subhemispherical basal capsule (Fig. 4.71).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: male, USNM. "Arroz; Philippinen; 28.8.7 / leg. G. Bëttcher; col. Korschefsky / Sicard det. / Korschefsky; Collection; 1952 / USNM; 2037254"

Distribution: India, Philippines

Remarks: Weise (1901) noted superficial similarity between *R. andamanica* and *R. punctigera* (now *R. fumida*); however, he did not examine the male genitalia. Instead, his diagnosis for *R. andamanica* was based only upon its small size. The size of the eyes relative to the head and the structure of the male genitalia both confirm *R. andamanica* as a valid species and provide sound diagnostic characters for identifying the species.

Rodolia apicalis Sicard 1909

Rodolia apicalis Sicard, 1909: p. 119; ***nomen dubium***.

Remarks: Sicard diagnosis *R. apicalis* solely on the basis of elytral coloration. Examination of the world's holdings of Noviini indicates that intraspecific color variation is quite common within the tribe, so diagnoses relying upon color are questionable, at best. In the case of *R. apicalis*, no reliably identified material is available, and the original description is insufficient to diagnose the species. Furthermore, Sicard's holotypes are presumed to be housed at the Musee d'Histoire Naturelle in Paris. Unfortunately, there is currently no curator for Coccinellidae there, and all material is unaccessible.

Rodolia argodi Sicard 1909 (Figs. 4.4, 4.53, 4.72 - 4.74)

Rodolia argodi Sicard, 1909b: p. 142.

Rodolia pallens Sicard, 1909b: p. 142; synonym (Korschefsky 1931: p. 99).

Rodolia plagiata Sicard, 1909b: p. 142; synonym (Korschefsky 1931: p. 99).

Diagnosis: This species is distinguishable by the structure of the aedeagus, particularly the sipho (Fig. 4.74). In *R. argodi*, the sipho is long and slender, with a deeply lobed siphonal capsule and a bifurcation just proximal to the apex (Fig. 4.74). *R. iceryae* and *R. occidentalis* also have a small bifurcation near the siphonal apex, but in *R. iceryae* the apex is recurved, not straight as in *R. argodi*. Both *R. iceryae* and *R. occidentallis* have a T-shaped apodeme present, but in *R. argodi* the structure is very deeply lobed, forming a V-shape (Fig. 4.74).

Description: Length 3.5 - 4 mm. Body hemispherical, widest just behind humeral angles, convex, shiny, black with red elytral border; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length > 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins not thickened; anterior and posterior edges horizontal, with posterior width about 2x anterior width; anterior edge with very short, stout setae; constricted at midlength; procoxal cavities slightly transverse, closed behind (Fig. 4.53).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsus 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequeal to width; proximal margin sinuate (Fig. 4.72). Parameres long, slender, excavate laterally, spatulate apically, apical 1/2 directed away from basal lobe; apical setae short; basal lobe about as long as parameres, excavate along midlength to receive sipho, distal 1/4 gradually tapering to glabrous apex; in lateral view, slightly curved ventrally, dorsal barb absent (Figs. 4.72, 4.73). Median strut slender, elongate, about half as long as aedeagus (Figs. 4.72, 4.73). Sipho elongate, narrow, about 2x as long as aedeagus, bifurcate just proximal to apex; with asymmetrical basal capsule; basal capsule with apodeme present (Fig. 4.74).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: male, USNM. "Ethiopia; Alemaya; Oct. 1, 1963 / B. G. Hill; collector/ USNM; 2037254"

Distribution: Ethiopia, Sudan

Remarks: Presumably, Sicard's entire collection is housed in the Paris Museum of Natural History. Unfortunately, there is currently no curator for Coccinellidae there, and all material from this facility is unaccessible. To further complicate matters, Sicard's original descriptions and keys are not sufficient to adequately diagnose species. Although no type material was available for this study, reliably identified specimens (det. Korschefsky) were used for the description. Like *R. alluandi* Sicard, this species is distinguished by both its morphology and Madagascan distribution, so a neotype for *Rodolia argodi* Sicard 1909 is hereby designated and deposited in the USNM.

Rodolia bella (Blackburn) 1889 (Figs. 4.5, 4.14, 4.75 - 4.77)

Novius bellus Blackburn, 1889: p. 188.

Rodolia bella Blackburn 1889: p. 143; new combination (Ślipiński 2007: p. 143).

Diagnosis: This species superficially resembles *R. lindi*, also from Australia. *R. bella* is distinguishable from *R. lindi* and all other congeners by the structure of the aedeagus (Figs. 4.75 - 4.77). In *R. bella*, the parameres are twisted 180 ° (Fig. 4.75, 4.76). Also, *R. bella* has a short sipho with a barbed apex (Fig. 4.77). *R. lindi* has a short sipho, but the siphonal apex is simple (Fig. 4.90). Finally, *R. bella* has a uniquely shaped siphonal capsule: it is semicircular mesally with a sinuate edge (Fig. 4.77). In all other congeners, the siphonal capsule has complete, smooth edges.

Description: Length 3.5 - 4 mm. Body hemispherical, widest just behind humeral angles, convex, shiny, black with red longitudinal stripes; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.5).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, with dorsal surface about as long as apical width, strongly securiform, distal edge > 2x as long as the proximal one, apical surface very narrow, length > 2x width, giving flattened appearance.

Pronotum widest anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge anterior to scutellum entire, not bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen longer than wide, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width, basal margin weakly arcuate (Fig. 4.75). Parameres long, slender, spatulate and twisted 180° apically; apical setae short; basal lobe about as long as parameres, excavate along midline to receive sipho, very broad basally, excavate with distal 1/4 gradually tapering to glabrous apex; in lateral view, slightly curved ventrally, dorsal barb absent (Figs. 4.75, 4.76). Median strut short, only about as long as basal piece (Figs. 4.75, 4.76). Sipho broad, short, only about as long as basal lobe, apically expanded to form small barb; basal capsule with apodeme absent; not bilobed or T-shaped (Fig. 4.77).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Holotype: male, BMNH. "Type / Australia; Blackburn Coll.; B. M. 1910 - 236. / Novius; bellus, Blackb."

Distribution: Australia

Remarks: Blackburn's original description notes that "this species does not appear to differ structurally from (*Novius*) *lindi* in any respect…apart from the totally different coloration" (Blackburn 1889). Dissection of both holotypes reveals that the male genitalia differs significantly between the two species. Although convexity is not a strong taxonomic character for the group, it is worth noting that *R. bella*, like many of its Australian congeners (e.g., *R. cardinalis*, *R. cruentata*, *R. koebelei*, *R. lindi*) is widest just posterior to to the humeral angles, making the habitus appear more elongate than in non-Australian *Rodolia.*

Rodolia canariensis Korschefsky 1937

Novius canariensis Korschefsky, 1937: p. 2.

Rodolia canariensis Korschefsky, 1937: p. 2; new combination; *nomen dubium*.

Remarks: In his original description, Korschefsky (1937) distinguishes (*Novius*) *canariensis* on the basis of color and notes, "This cute [beetle] is morphologically near the small Australian species." Unfortunately, this description is not sufficient to identify the species. There are additional complications: the type collection documented for many of Korschefsky's specimens is the "Uyttenboogaart Collection." According to museum curators (Dr. B. Jager (Berlin) and Dr. B. Viklund (Stockholm)), many of these types were split between the Museum für Naturkunde in Berlin and the Naturhistoriska Riksmuseet in Sweden. Others were either lost or destroyed in transit (Dr. B. Jager, personal communication). In the absence of an unambiguous species description, type material and reliably identified specimens, no neotype can be designated for *R. canariensis*.

Rodolia capucina Fürsch 1975

Rodolia capucina Fürsch, 1975: p. 649; ***nomen dubium***.

Fürsch remarks that this species bears close resemblance to *R. argodi*, but differs in both color and convexity. Unfortunately, both the original description and the subsequent diagnosis were based solely upon these factors. Examination of the world's holdings of Noviini shows that color and convexity varies significantly within species, so diagnoses based upon these factors are unreliable. The only definitive way to diagnose/identify noviine species is to examine the male genitalia. Unfortunately, the only two representatives of this species available for study are both females.

Rodolia cardinalis (Mulsant) 1850 (Fig. 4.6)

Vedalia cardinalis Mulsant, 1850: p. 906.

Rodolia cardinalis Mulsant, 1850: p. 906; new combination (Weise, 1905: p. 220).

Novius cardinalis Crotch, 1874: p. 283; synonym (Weise, 1895: p. 150)

Eurodolia cardinalis Weise, 1895: p. 150. synonym (Priore, 1963: p. 65).

Novius tridens Lea, 1901: p. 492; new synonym.

Novius immaculatus Lea, 1901: p. 492; new synonym.

Rodolia aegyptiaca Sicard, 1907: p. 67; synonym (Korschefsky, 1931: p. 99).

Macronovius cardinalis Weise, 1922: p. 104; synonym (Korschefsky, 1931: p. 99).

Macronovius cardinalis ab. *obnubilatus* Weise, 1922: p. 104; synonym (Korschefsky, 1931: p. 98)

Rodolia vitalisi Mader, 1955: p. 972; unnecessary replacement name.

Diagnosis: Like its congeners, *R. cardinalis* is identifiable by the structure of the male genitalia. This species has a basal lobe that is very wide (~2 paramere widths) and narrows gradually to the apex. Others, such as *R. fumida*, *R. virginalis*, and *R. weisei* also have a basal lobe that narrows gradually, but they are much narrower proximally (< 2 paramere widths). *R. cardinalis* is further distinguishable by the short (< 2x length of aedeagus), stout, sipho. The shape of the siphonal capsule is unique for *R. cardinalis* it is asymmetrical, but not T-shaped. *R. koebelei* also has a short, stout sipho, but the apex of the basal lobe is abruptly tapered, not gradually as in *R. cardinalis.* In other congeners with a short sipho, the structure is much narrower and has a T-shaped siphonal capsule with apodeme. Finally, in *R. cardinalis* the median strut is very short, subequal in length to the basal piece, and very large and square apically. In other congeners, the length of the median strut is variable, but the apex is always smaller than that of *R. cardinalis*.

Description: Length 3 - 3.5 mm. Body elongate-oval, widest at midpoint, convex, shiny; elytral color variable: sometimes uniformly rusty orange, head and pronotum black, usually carmine red with black maculae; dorsal surface covered with short, suberect, pale setae; head deflexed, not visible from above (Fig. 4.6).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical surface length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior margin sinuate, but not bilobed; laterally explanate. Prosternum narrow; tilted anteriorly; prosternal process abruptly raised, cordate; lateral and anterior margins thickened; anterior edge broadly rounded; posterior edge bilobed, with posterior width about 2x as long as anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, almost as wide as long; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present. Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin horizontal or nearly so. Parameres only as long as basal lobe, not twisted or spatulate apically; basal lobe very broad until abruptly narrowed apex, excavate along midline, but excavate region not entire to apex; apex slightly expanded dorsally and ventrally to form very small barb. Median strut stout and square, not elongate and narrow. Sipho broad, short, < 2x length of aedeagus, apex narrower and simple; siphonal capsule with apodeme absent, not T-shaped or expanded.

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Type not examined.

Distribution: Originally Australian, but due to its introduction as a biocontrol agent, this species is cosmopolitan.

Remarks: Although *R. fumida* has more synonyms associated with it, *R. cardinalis* certainly has the most convoluted taxonomic history. When Mulsant described the species in 1850, he included it and *sieboldii* in the genus *Vedalia*. In 1874, Crotch moved *cardinalis* to the genus *Novius*. Weise (1895) disagreed with Crotch's (1874) moving species from *Vedalia* to *Novius.* In the same paper, Weise (1895) described a new genus, *Eurodolia*, and noted that *Vedalia cardinalis* might actually belong in *Eurodolia*. He divided *Rodolia* into 2 groups based on the tarsal claw morphology: one group toothed and the other cleft, and synonymized *Macronovius* with *Rodolia*. Later, in 1905, Weise authored the new combination *Rodolia cardinalis* and included it in the "toothed claws" subgroup. Perhaps he was unsure, because in 1916, Weise again referred to *Eurodolia cardinalis*, then later (1922: p. 104) to *Macronovius cardinalis.* Finally, in 1931, Korschefsky synonymized *Macronovius* with *Rodolia*. Gordon (1985) noted that the tarsal claw character Weise (1895) used to define groups is, in fact, a sexual dimorphism. In all noviines, males have a tarsal claw that is cleft, while females have a well-developed basal tooth. Although not a diagnostic character for the group, it is worth noting that *R. cardinalis*, like many Australian-native congeners (e.g., *R. bella*, *R. cruentata*, *R. koebelei*, *R. lindi*) is widest just posterior to to the humeral angles, making the habitus appear more elongate than the non-Australian *Rodolia.*

Rodolia chapaensis Hoang 1980

Rodolia chapaensis Hoang, 1980: p. 13; ***nomen dubium***.

Remarks: Hoang described this new species after seeing only two female representatives. Although he briefly described the female exemplars, noviine females do not possess reliable diagnostic characters. Reliably identified material of *R. chapaensis* was not available for this study, but the differences in hemisternite morphology Hoang (1980) illustrated appear to be the result of a broken specimen. Hoang deposited his holotypes at the ZIRS in St. Petersburg, Russia (formerly the Zoological Institute of USSR in Leningrad). Unfortunately, that museum has no record of the specimens (Dr. Boris Mikhaylovich Kataev, personal communication).

Rodolia cinctipennis Weise 1912 (Fig. 4.7)

Rodolia cinctipennis Weise, 1912: p. 52. ***nomen dubium.***

Remarks: The only representative of this specimen is a female and the specimen includes only a determination label; no locality information is provided. The type is also a female; Weise's (1912) original description describes *R. cinctipennis* is being the "smallest variant of *iceryae*." The remainder of the diagnosis was based only on color and convexity. Neither color nor convexity is sufficient for diagnosing species in the tribe. Without a male specimen to dissect, no redescription for the species can be provided. *R. cinctipennis* is a doubtful name.

Rodolia circumclusa (Gorham)

Zenoria circumclusa Gorham, 1889, p. 262.

Anovia circumclusa Gorham, 1889: p. 262; new combination (Gordon, 1971: p. 1).

Rodolia circumclusa (Gorham), 1889: p. 262; new combination.

Diagnosis: Rodolia circumclusa, like its congeners, is diagnosable by the structure of the aedeagus. In *R. circumclusa*, the basal lobe is narrow (< 2 paramere widths) and has a ventrally-directed apex with no apical barb. Several congeners have a similar basal lobe: *R. iceryae* Janson in Howard, *R. lindi* (Blackburn), *R. mexicana* (Gordon), *R. nigra* Fürsch, *R. occidentalis* Weise, *R. punica* (Gordon), *R. virginalis* (Wickham), *and R. weise* (Gordon). *R. circumclusa* differs from those species in having a basal lobe that is narrow for the entire length; most similar species have a basal lobe that is much wider (> 2 paramere widths) basally. *R. cruentata* has a narrow basal lobe, but the apex is not bent downward as in *R. circumclusa.* Also, *R. circumclusa* has a basal piece that is widest proximally, with a feebly arcuate margin. *R. iceryae*, *R. lindi*, *R. mexicana*, *R. occidentalis*, *R. punica*, *R. virginalis*, and *R. weisei* all have a basal piece with a weakly curved proximal margin, but with length and width either subequal or widest distally.

Description: Length 4 - 4.5 mm. Body hemispherical, widest just behind humeral angles, convex; color variable; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge < 2x as long as the proximal one, apical sensory area with length > 2x width, lateral edge 2x length of mesal one.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge slightly cleft, with posterior width about 2x as long as anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin feebly arcuate. Parameres long, slender, spatulate apically; apical setae long; basal lobe narrow (< 2 paramere widths), not extending laterally beyond parameres; slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent. Median strut short, only about as long as basal piece. Sipho narrow, short, slightly longer than aedeagus, apex simple, with asymmetrical basal capsule; basal capsule with apodeme present.

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Type not examined.

Distribution: Guatemala, Honduras, Mexico, Panama, United States (Florida)

Remarks: *Anovia circumclusa* adults are best recognized by the structure of the male genitalia. In *A. circumclusa*, the basal lobe is slender and does not extend laterally beyond the internal margin of the parameres, while in all other *Anovia* species the basal lobe is quite broad, extending well beyond the internal margin of the parameres. Also, in *A. circumclusa* the basalpiece is widest basally, not distally as in *A. virginalis*.As is true for many representatives of Noviini, specimens of *R. circumclusa* exhibit a great deal of intraspecific color variation: some are red, or red with a discrete black ring, some have a posterior darkened area without a discrete border, and still others are entirely black. Forrester *et al*. (2008) summarizes color pattern variation for *R. circumclusa* and provides images illustrating each example.

Rodolia concolor (Lewis) 1879

Novius concolor (Lewis), 1879: p. 466.

Rodolia concolor Lewis, 1879: p. 466; new combination; ***nomen dubium***

Remarks: Lewis (1879) distinguished *Novius concolor* as being “Half as large again as *N. limbatus* Motschulsky, from which it may be known by its red thorax, scutellum, and elytra.” No type was available for this species, and no reliably identified material is available for it. The original description, based upon coloration, is insufficient to diagnose the species, so no neotype can be designated for it at this time.

Rodolia cruentata (Mulsant) 1846 (Figs. 4.11, 4.30, 4.38, 4.39, 4.48, 4.54, 4.68, 4.78 - 4.80)

Novius cruentatus Mulsant, 1846: p. 214.

Novius decempunctata Kraatz, 1862: p. 272; synonym (Crotch, 1874: p. 283).

Novius algiricus Crotch, 1874: p. 283; synonynm (Korschefsky, 1931: p. 97).

Novius conicollis Korschefsky, 1937: p. 1; new synonym.

Novius intermedius Günther, 1947: p. 86.

Rodolia cruentata (Mulsant), 1846: p. 214; new combination

Diagnosis: This species is distinguishable by the structure of both the male genitalia and the prosternal process. The aedeagus of this species is similar to *R. circumclusa* in having a basal lobe that is narrow (< 2 paramere widths) (Figs. 4.78, 4.79). However, the basal lobe of *R. cruentata* is remarkably straight, not bent downward as in other congeners (Figs. 4.78, 4.79). The structure of the prosternal process is also diagnostic for this species (Fig. 4.54). Instead of being tilted anteriorly (as in all other congeners), the prosternal process for *R. cruentata* is in the same plane as the pronotum (Fig. 4.54). This species is also unique in having the prosternal process quadrate with subequal anterior and posterior margins (Fig. 4.54). In other *Rodolia* species with a quadrate prosternal process, the structure is usually widest posteriorly.

Description: Length 4 - 4.5 mm. Body elongate-oval, widest at midpoint, dorsoventrally flattened, dull, orange or red with variable maculae; dorsal surface covered with short, sparse, suberect, golden setae; head deflexed, not visible from above (Fig. 4.11).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture (Fig. 4.30). Eyes large, pubescent, not prominent, finely facetted (Fig. 4.30). Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed (Figs. 4.38, 4.39). Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III with dorsal surface about as long as apical width, strongly securiform, distal edge > 2x as long as the proximal one, apical surface very narrow, length > 2x width, giving flattened appearance.

Pronotum widest anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge anterior to scutellum entire, not bilobed (Fig. 4.48). Prosternum narrow, not tilted anteriorly, parallel to pronotum; prosternal process abruptly raised, quadrate, very narrow, lateral edges thickened; anterior edge horizontal; posterior edge bilobed; procoxal cavities slightly transverse, closed behind (Fig. 4.54).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose.

Abdomen longer than wide, with broad, entire intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically (Fig. 4.68). Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin feebly bilobed. Parameres long, slender, spatulate apically; apical setae long; basal lobe about as long as parameres, broadest basally, excavate with distal 1/4 gradually tapering to glabrous apex; excavate along midline to receive sipho; in lateral view, very straight, dorsal barb absent (Figs. 4.78, 4.79). Median strut slender, apex slightly flattened (Figs. 4.78, 4.79). Sipho narrow, short, < 2x as long as basal lobe, apex abruptly narrowed, threadlike; basal capsule with apodeme absent, not bilobed or T-shaped (Fig. 4.80).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Type not examined.

Distribution: Known only from the Canary Islands

Remarks: Although habitus appearance is not a strong diagnostic character for any noviine, it is worth noting that *R. cruentata* is one of the few noviines that is very nearly parallel-sided (*R. limbata* and *R. cruentata* are the others). Because this character is very labile, it is not included in the diagnosis. The type depository for some of Korschefsky's specimens is listed as the “Uyttenboogaart Collection.” According to museum curators (Dr. B. Jager (Berlin) and Dr. B. Viklund (Stockholm)), these types were split between the Museum für Naturkunde in Berlin and the Naturhistoriska Riksmuseet in Sweden. Both museums have their specimens labeled “Paratypus,” although the specimens are not actual paratypes (personal communication). The description for *R. cruentata* was based upon reliably identified material from the USNM (det. Korschefsky) and the NHRM.

Rodolia delobeli Chazeau 1981

Rodolia delobeli Chazeau, 1981: p. 57; ***nomen dubium***.

Remarks: Chazeau (1981) diagnoses *Rodolia delobeli* by the length of the setae on the prosternal process; unfortunately, he does not directly compare the prosternal process of *R. delobeli* to any other species, noting only that the “general form…is similar.” The type depository for this species is the Musee d'Histoire Naturelle in Paris. This is unfortunate, because there is no curator for Coccinellidae there, and all material from that facility is inaccessible. To further complicate matters, there is no reliably identified material to confirm the species name.

Rodolia discoidalis (Blackburn) 1895

Rodolia discoidalis (Blackburn), 1895: p. 253; new combination; ***nomen dubium***.

Novius discoidalis Blackburn, 1895: p. 253.

Remarks: Blackburn (1895) differentiated *R. discoidalis* (then included in the genus *Novius*) from its Australian congeners by noting that *R. discoidalis*: “is a larger, broader, and more convex insect with elytral punturation certainly both finer and less close.” These highly labile characteristics are not sufficient to diagnose species in the genus *Rodolia*. Unfortunately, no type material of *R. discoidalis* was available for study, so no redescription can be provided. *R. discoidalis* is a doubtful name.

Rodolia dubia Forrester & McHugh 2008 new replacement name; *nomen dubium*

Novius limbatus Blackburn, 1895: p. 254 (Type: female, BMNH).

Rodolia limbata Blackburn, 1895: p. 254; new combination (Ślipiński, 2007: p. 143).

Rodolia limbata Blackburn, 1895: p. 254; junior homonym.

Remarks: Please see remarks for *R. limbata* (Motschulsky).

Rodolia fulvescens Hoang 1980

Rodolia fulvescens Hoang, 1980: p. 12; ***nomen dubium***.

Remarks: Hoang's (1980) original description of *R. fulvescens*, published in Vietnamese, translates as "Small, short oval, yellow…Male genitalia with stout, long, and strongly curved sipho." That assessment is true for many noviines, not just *R. fulvescens*. The lack of comparison between *R. fulvescens* and its congeners, along with the absence of reliably identified material, make this species name doubtful. Hoang deposited his holotypes at the ZIRS in St. Petersburg, Russia (formerly the Zoological Institute of USSR in Leningrad). Unfortunately, that museum has no record of the specimens (Dr. Boris Mikhaylovich Kataev, personal communication).

Rodolia fumida Mulsant 1850 (Figs. 4.9, 4.33, 4.42, 4.43, 4.46, 4.56, 4.64, 4.84- 4.86)

Rodolia fumida Mulsant, 1850: p. 904.

Vedalia fumida Mulsant, 1850: p. 904; synonym (Crotch, 1874: p. 281).

* Weise (1892) transferred this species back to *Rodolia*.

Rodolia roseipennis Mulsant 1850, p. 904; synonym (Crotch, 1874: p. 281).

Rodolia chermesina Mulsant 1850, p. 905; synonym (Crotch, 1874: p. 282).

Epilachna sexnotata Mulsant, 1850: p. 807; synonym (Booth & Pope 1989: p. 363).

Rodolia sexnotata (Mulsant), 1850; new combination (Booth & Pope 1989: p. 363).

Rodolia rufopilosa Mulsant, 1850: p.903; new synonym.

Rodolia formosana Korschefsky, 1935: p. 255; new synonym.

Epilachna arethusa Mulsant 1853, p. 126; synonym (Crotch, 1874: p. 281).

Epilachna testicolor Mulsant 1853, p. 127; synonym (Crotch, 1874: p. 281).

Vedalia Guerinii Crotch, 1874: p. 282; misspelling (Korschefsky 1931: p. 101).

Rodolia punctigera Weise, 1901: p. 93l; new synonym.

Rodolia dionysia Sicard 1909, p. 116; synonym (Korschefsky, 1931: p. 101).

Rodolia immsi Weise, 1912: p. 120; synonym (Korschefsky 1931: p. 101).

Rodolia guerini Korschefsky, 1931: p. 101; synonym (Booth & Pope 1989: p. 363).

Rodolia formosana Korschefsky, 1935: p. 255; new synonym.

Rodolia 6-maculata Korschefsky, 1940: p. 2; synonym (Kapur 1949: p. 535).

Diagnosis: R. fumida is diagnosable by the structure of the male genitalia (Figs. 4.84 - 4.86). In this species, the basal lobe is quite narrow (< 1 paramere width), with the apex expanded to form a very small dorsal barb (Figs. 4.84, 4.85). The sipho of this species has a T-shaped basal capsule with an apodeme (Fig. 4.86). Superficially, *R. fumida* resembles *R. insularis* and *R. rubea* in that all three have an apically barbed basal lobe and T-shaped siphonal capsule. Both *R. fumida* and *R. rubea* have parameres that expand gradually toward the apex, while *R. insularis* has parameres that are constricted at midlength. *R. fumida* can be further distinguished from *R. rubea* by the structure of the apical barb on the basal lobe (Figs. 4.84, 4.85). In *R. fumida*, the dorsal portion of the barb is narrowly pointed and very small (Figs. 4.84, 4.85). In *R. rubea* it is much larger, and the dorsal portion has a rounded apex (Figs. 4.100, 4.101).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad (Fig. 4.33). Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; apical teeth subequal in length; subprosthecal tooth and prostheca well-developed (Figs. 4.42, 4.43). Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III strongly securiform, dorsal surface about as long as apical width, distal edge > 2x as long as the proximal one, apical surface length < 2x width (Fig. 4.46).

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin slightly sinuate; posterior margin markedly so, feebly bilobed anterior to scutellum; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed, with posterior width about 2x as long as anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind (Fig. 4.56).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad (Fig. 4.64). Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire (Fig. 4.64). Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate (Fig. 4.64). Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple (Fig. 4.64).

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid (Fig. 4.64). Aedeagus with basal piece length subequal to width; proximal margin horizontal or nearly so (Fig. 4.84). Parameres long, slender basally, excavate laterally, spatulate and very wide (> 2x basal width) apically; apical setae long; basal lobe very narrow, slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho;; basal lobe about as long as parameres, excavate along midline to receive sipho, distal 1/4 tapering to setose apex; in lateral view, distal 1/4 curved ventrally, dorsal surface with small, posteriorly directed barb (Figs. 4.84, 4.85) Sipho elongate, narrow, < 3x as long as aedeagus, apical 1/4 abruptly threadlike, with asymmetrical basal capsule; basal capsule with apodeme present (Fig. 4.86).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Lectotype: male, UMZC

Distribution: Delhi, India, Pakistan

Remarks: R. fumida shares many characteristics with its congeners, one of which is an extensive list of synonyms. Some reasons for this include species descriptions based upon geographic region, color patterns, size, or convexity. Many of the synonyms for *R. fumida* are maculate, having 4 to 6 spots; although the color varies significantly within this species, the morphology is constant. Type material for this species was unavailable for this study, but a large series of reliably identified material (det. Korschefsky; det. Poorani) was used for the description and illustrations.

Rodolia iceryae Janson in Howard 1889

Rodolia iceryae Janson in Howard, 1889: p. 91.

Rodolia obscura Weise, 1898: p. 524; synonym (Raimundo, 1978: p. 35).

Rodolia ferruginea Weise, 1900: p. 130; new synonym.

Rodolia senegalensis Weise, 1913: p. 226; new synonym.

Diagnosis: R. iceryae, like all other noviines, is best diagnosed by the structure of the male genitalia. The parameres of this species are similar to those of *R. insularis*, in that they are medially constricted. However, *R. iceryae* does not have a basal lobe with a barbed apex as in *R. insularis. R. iceryae* has a very short, narrow sipho with a bifurcation just proximal to the siphonal apex. The only other species of *Rodolia* that have a similar sipho are *R. argodi* (Fig.

4.74) and *R. occidentalis* (Fig. 4.96). However, *R. iceryae* is readily distinguished from both of them in that the siphonal apex of *R. iceryae* is strongly recurved, so much so that the threadlike apex almost forms a complete circle.

Description: Length 3 - 3.5 mm. Body hemispherical, widest just behind humeral angles, convex; uniformly carmine-orange, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge < 2x as long as the proximal one, apical sensory area with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge feebly arcuate; posterior edge weakly bilobed, with posterior width about 2x as long as anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia weakly expanded medially, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin deeply cleft. Parameres long, slender, slightly constricted medially, excavate laterally, wide and spatulate apically, slightly overlapping basal lobe; apical setae on distal 1/3 short; basal lobe narrow, < 2 paramere widths, slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent. Median strut almost as long as aedeagus. Sipho short, narrow, only about as long as aedeagus, apex strongly recurved, almost forming complete circle, with asymmetrical basal capsule; basal capsule with T-shaped apodeme present.

Female: Tarsal claw with well-developed, square basal tooth.

Type material: Neotype: male, MRAC. "Coll. Mus. Congo; ex. coll. Dr. Breuning / Rodolia; iceriae Jans; det. H. Fürsch 1973 / MRAC"

***The first label attached to this specimen is undeciperable.

Distribution: Africa

Remarks: The original description for *R. iceryae* was done by O. E. Janson for L. O. Howard (1889). Raimundo (1978) synonymized *R. iceryae* with *R. obscura* Weise, but prioritized the wrong specific epithet. *R. iceryae* was described well before *R. obscura*, so the former name subsumes the latter. Weise distinguished *R. ferruginea* from congeners on the basis of finer punctation and slightly different coloration. He compared *R. senegalensis*, now a junior synonym of *R. iceryae*, to *R. occidentalis* and noted that *R. senegalensis* is "more yellow" and has "wider" legs. No genitalia were examined. The color in this species is variable, ranging from black to dark orange-brown, sometimes with a lighter region at the base of the elytra. The lighter region ranges from orange to carmine. In some representatives of *R. iceryae*, the lighter region is well defined, with a discrete margin. In others, the different colored regions blend together at their junction. The position of the lighter area varies within species, also. In some, it only covers the elytral bases. In others, it extends to the pronotum, and in at least one, it covers the scutellum. Since no type is available, a neotype is here designated based upon reliably identified specimens (det. Fürsch) and deposited in the MRAC.

Rodolia insularis Weise 1895

Rodolia insularis Weise, 1895: p. 55.

Diagnosis: Like its congeners, *R. insularis* is diagnosed reliably only by the structure of the male genitalia. *R. insularis* has wide parameres that are constricted basally. *R. insularis* is similar to *R. fumida*, *R. limbata*, and *R. rubea* in that all have an apically barbed basal lobe and a T-shaped siphonal capsule with apodeme (Figs. 4.81 - 4.86, 4.100 - 4.102). However, none of the others have the parameres medially constricted like *R. insularis*.

Description: Length 3 mm. Body elongate-oval, widest at midpoint, convex; uniformly orange with one red spot on each elytron, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge < 2x as long as the proximal one, apical sensory area with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly;

prosternal process abruptly raised, quadrate; lateral margins thickened; anterior and posterior edges horizontal; posterior width about 2x as long as anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin bilobed. Parameres short, only as long as median lobe, excavate along midline, spatulate apically, narrowed basally, but still with medial edge overlapping median lobe margins; apical setae long; basal lobe widest basally, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, expanded dorsally and laterally to form barb. Median strut about 2x length of basal piece. Sipho narrow, elongate, about 2x length of aedeagus, excavate, abruptly threadlike apically, with asymmetrical basal capsule; basal capsule with apodeme present.

Female: unknown

Type material: Syntype: male, ZMHB. "Mladag.; Sikora / insularis; Ws. / ex coll.; J. Weise / SYNTYPUS; Rodolia insularis; Weise, 1895; labelled by MNHUB 2006 / Museum für Naturkunde; Humboldt-Univ. Berlin; (MNHUB)"

Distribution: Madagascar

Remarks: In his original description, Weise (1895) described *R. insularis* as "round, convex, with dense, short pubescence, rusty in color, prothorax and elytra with fine punctures, prominent humeral calli, prosternum with elevated carina, curved, bifid claws." Unfortunately, this description is not sufficient to distinguish this species from remaining congeners. Like many other species of *Rodolia, R. insularis* is represented solely by the type specimen; however, the Madagascan distribution and unique structure of the aedeagus are sufficient to distinguish *R. insularis* from other members of *Rodolia*.

Rodolia koebelei (Gordon) 1972 (Figs. 4.49, 4.57, 4.87, 4.88)

Rodolia koebelei (Gordon), 1972: p. 26.

Rodolia koebelei (Olliff), 1895: pl. 1, new combination (Korschefsky, 1931: p. 101).

Novius Koebelei Olliff, 1895: pl. 1; ***nomen nudum.***

Diagnosis: R. koebelei is similar to *R. andamanica, R. bella*, *R. cardinalis*, *R. cruentata*, *R. lindi*, and *R. occidentalis* in having males with no barb on the apex of the basal lobe and no apodeme on the basal capsule of the sipho. Of those, only *R. koebelei* has a basal lobe that is abruptly narrowed for the distal 1/4 (Fig. 4.87).

Description: Length 3 - 3.5 mm. Body elongate-oval, widest at midpoint, convex, shiny; elytral color variable: sometimes uniformly rusty orange, head and pronotum black, usually carmine red with black maculae; dorsal surface covered with short, suberect, pale setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior margin sinuate, edge anterior to scutellum entire, not bilobed; laterally explanate (Fig. 4.49). Prosternum narrow; prosternal process abruptly raised, cordate; lateral and anterior margins thickened; anterior edge broadly rounded; posterior edge bilobed, moderately setose; procoxal cavities slightly transverse, closed behind (Fig. 4.57).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broad. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, almost as wide as long; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present. Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece longer than wide; proximal margin horizontal or nearly so (Fig. 4.87). Parameres only as long as basal lobe, not twisted or spatulate apically; basal lobe very broad until abruptly narrowed apex, excavate along midline, but excavate region not entire to apex; apex slightly expanded dorsally and ventrally to form very small barb (Fig. 4.87). Median strut square, very large (Fig. 4.87). Sipho short, < 2x length of aedeagus, excavate and broad to apex; siphonal capsule with apodeme absent, not T-shaped or expanded (Fig. 4.88).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: fourth instar larva, USNM

Distribution: Australia, United States (California)

Remarks: Novius koebelei was originally published as a *nomen nudum* by Olliff in 1895. He included a name and an illustration, but no description. Lea (1901) subsequently referred to the species, and noted, "This species was never described by the late Mr. A. Sidney Olliff, but as it is well known in the United Sates (where several coloured figures of it have been published) Mr. Olliff's name (unless the species should prove to be synonymous with *sanguinolentus*) will probably stand." Lea also synonymized *Novius lindi* (now *Rodolia*) with *R. koebelei*, but did not justify his decision. The morphology of the male genitalia of both *R. koebelei* and *R. lindi* is very different, indicating distinct species. Coquillett (1893) commented on the biology of the species and provided descriptions of the immature stages, but not the adult. Gordon (1985) referenced Coquillett's larval descriptions, and designated a neotype for the species based on a fourth instar larva, bearing the name *Rodolia koebelei* (Coquillett). Gordon (1972) said that adult specimens were present with the larvae, but he did not designate a neotype based upon adult material. According to Article 75.3 of the ICZN, a neotype is valid only when "data and description are sufficient to ensure recognition of the specimen designated." The larvae of Noviini are very homogeneous (Forrester *et al.* 2008), so it is unlikely that a name-bearing type attached to a larva will facilitate recognition of the species in the adult stage. The adult species description provided here is based upon reliably identified material (det. Coquillett), but a new neotype cannot be designated except by the Commission under the plenary power (Art. 78.1, ICZN). Although *Rodolia koebelei* was introduced in California, Gordon (1972, 1985) noted that this species has "disappeared" from California. There have been no records of *R. koebelei* from California in quite some time, but it is unknown whether this is a result of the beetle's absence or of poor collecting.

Rodolia limbata (Motschulsky) 1866 (Figs. 4.8, 4.40, 4.41, 4.55, 4.63, 4.81 - 4.83)

Novius limbatus Motschulsky, 1866: p. 178; synonym; (Lewis, 1896: p. 39)

Rodolia limbata Motschulsky, 1866: p. 178; new combination

Macronovius limbatus v. *fausti* Weise, 1885: p. 63; new synonym

Rodolia breviuscula Weise, 1892: p. 26; new synonym

Rodolia narae Lewis, 1896: p. 40; synonym (Kamiya, 1966: p. 89)

Rodolia cinctipennis Weise, 1912: p. 52; new synonym

Rodolia quadrimaculata Mader, 1939: p. 48; new synonym

Rodolia quadrimaculata ab. *6-maculata* Mader, 1939: p. 49; new synonym

Diagnosis: This species is distinguishable from all other members of *Rodolia* by the structure of the male genitalia (Figs. 4.81 - 4.83). In *R. limbatus* the basal lobe is narrow (< 2 paramere widths) (Fig. 4.81). *R. iceryae*, *R. lindi*, *R. mexicana, R. nigra*, *R. occidentalis*, *R. pumila*, *R. punica*, *R. virginalis*, *and R. weisei* also have a narrow basal lobe (Figs. 4.89, 4.91, 4.92, 4.94, 4.95, 4.97, 4.98), but *R. limbata* has a very narrow, posteriorly directed barb at the basal lobe apex (Figs. 4.81, 4.82). In other species with a barbed apex (*R. fumida*, *R. insularis*, and *R. rubea*), the size and shape of both the basal lobe apex and the posteriorly directed barb is very different (Figs. 4.84, 4.85, 4.100, 4.101). The shape and positioning of the parameres further distinguish *R. limbata*: they are curved away from the basal lobe medially and inward apically, making the basal lobe appear completely encircled (Figs. 4.81, 4.82).

Description: Length 3.5 - 4.5 mm. Body elongate-hemispherical, widest at humeral angles, convex, rusty orange-brown; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.8).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped tooth; tooth extending beyond subprosthecal tooth; subprosthecal tooth and prostheca well-developed; surface proximal to subprosthecal tooth with short, fairly dense setae (Figs. 4.40, 4.41). Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III with dorsal surface about as long as apical width, strongly securiform, distal edge > 2x as long as the proximal one; apical surface length < 2x width.

Pronotum widest just anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior and posterior margins slightly sinuate; laterally explanate. Prosternum narrow; prosternal process abruptly raised, quadrate, very narrow; lateral margins thickened, anterior and posterior edges horizontal or nearly so; procoxal cavities slightly transverse, closed behind (Fig. 4.55).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad (Fig. 4.63). Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire (Fig. 4.63). Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate (Fig. 4.63). Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple (Fig. 4.63).

Elytron convex, elongate, longer than wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid (Fig. 4.63). Aedeagus with basal piece length subequal to width; proximal margin feebly bilobed (Fig. 4.81). Parameres long, slender, excavate; arcuate laterally, appearing to encircle basal lobe; spatulate apically, apical setae short; basal lobe about as long as parameres, excavate along midline to receive sipho, distal 1/4 tapering to setose apex; in lateral view, tip curved ventrally, dorsal surface with posteriorly directed barb; barb narrow dorsally and ventrally (Fig. 4.81, 4.82). Sipho elongate, narrow, abruptly threadlike from midpoint to apex, with asymmetrical, T-shaped apodeme (Fig. 4.83).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: male, USNM. "N. Ussurisk, S. B. Reitter / Korschefsky, Collection, 1952 / USNM, 2037254"

Distribution: India, Japan, China

Remarks: Like many other representatives of Noviini, *R. limbata* enjoys a very convoluted nomenclatural history. Motschulsky (1866) first recognized and described *Novius limbatus* from Japan. Weise (1885) disagreed, including *limbatus* in his new genus, *Macronovius*; in that same paper, he described *Macronovius fausti*, a variation of *M. limbatus*. Later, in 1895, Blackburn, apparently unaware that the name already existed, recognized and described *Novius limbatus* from Australia. Both authors diagnosed their respective species on the basis of coloration, and reflected their assessments in the specific epithet (*limbus* = border, hem, or fringe). One year later, Lewis (1896) included Motschulsky's *limbatus* in the genus *Rodolia*. Korschefsky (1931) recognized both species in his catalogue, listing Blackburn's *limbatus* in *Novius* and Motschulsky's *limbatus* in *Rodolia*. Examination of Blackburn's holotype and material identified by Lewis shows that the Oriental *limbatus* is different from the Australian one. Unfortunately, the holotype for Blackburn's Australian species is a female, and although it is significantly different from Motschulsky's Oriental species, there are not sufficient characters for a definitive diagnosis. This presents a problem because of the name's status as a junior secondary homonym. To resolve the nomenclatural issue, a replacement name must be given for Blackburn's *limbatus*. However, the taxonomic problem still remains: the species is a *nomen dubium.* Dissection of type specimens shows that Weise's *fausti* (1885), *breviuscula*

(1892), and *pumila* (1892) are synonyms of Motschulsky's *limbatus* (1866). They are morphologically identical, and all are Oriental. Like many of its congeners, *R. limbatus* exhibits significant intraspecific color variation. The monochrome variants range from light brown-orange to dark orange-red. Sometimes, maculae are present in the form 4 to 6 irregularly shaped black spots; in some, these spots are often large and fused together to form black bands. In others, the bands are fused together, yielding entirely dark elytra with a red border (hence the specific epithet). A neotype is here designated and deposited at the USNM.

Rodolia lindi (Blackburn) 1889 (Figs. 4.16, 4.89, 4.90)

Novius lindi Blackburn, 1889: p. 188.

Rodolia lindi (Blackburn), 1889: p. 188; new combination (Ślipiński 2007: p. 143).

Diagnosis: R. lindi bears superficial resemblance to another Australian species, *R. bella* (Fig. 4.14). However, *R. lindi* can be distinguished by the structure of the aedeagus (Figs. 4.89, 4.90). In this species, the parameres are excavate for almost the entire length, and not twisted 180° as they are in *R. bella* (Figs. 4.75, 4.76, 4.89). The structure of the sipho is also unique: it is very short (shorter than the basal lobe), and does not have a T-shaped siphonal capsule (Fig. 4.90). *R. bella* also has a short sipho, but the siphonal apex is barbed in that species (Fig. 4.77). The siphonal capsule in *R. lindi* is also different: it is quadrate and narrow, not semicircular and abruptly expanded mesally as in *R. bella* (Figs. 4.77, 4.90). Finally, the basal piece of *R. lindi* is distinctly larger proximally, and has a sinuate basal margin (Fig. 4.90). The basal piece of *R. bella* has proximal and distal widths subequal; also, the basal margin is not sinuate (Fig. 4.75).

Description: Length 2.5 - 3 mm. Body elongate-oval, widest at midpoint, convex; shiny, dark brown with one orange spot on each elytron; dorsal surface covered with short, sparse, suberect, golden setae; head deflexed, not visible from above (Fig. 4.16).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III strongly securiform, distal edge > 2x as long as the proximal one.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior margin sinuate, edge anterior to scutellum entire, not bilobed; laterally explanate. Prosternum narrow; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, almost as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin sinuate (Fig. 4.89). Parameres long, slender, spatulate apically, twisted 180° apically, widely separated from basal lobe (at least a paramere width), apical setae long; basal lobe about as long as parameres, narrow basally, with distal 1/8 abruptly tapering to glabrous apex; excavate along midline to receive sipho; in lateral view, basal lobe slightly curved ventrally, dorsal barb absent (Fig. 4.89). Median strut very large, almost as long as basal piece (Fig. 4.89). Sipho short, only about as long as basal lobe, broad, apex simple; basal capsule with apodeme absent, not bilobed or T-shaped (Fig. 4.90).

Female: unknown

Type material: Holotype: male, BMNH. "Type / Australia; Blackburn Coll.; B. M. 1910 - 236. / Novius; lindi, Blackb."

Distribution: Australian; known only from the type locality.

Remarks: Blackburn's (1889) original description of *R. lindi* is quite generic and does not include a diagnosis for the species: "short, oval; convex; shiny; pubescent; dark with one red spot on each elytron." He references *R. lindi* in another species description (*Novius bellus;* now

Rodolia bella) in the same paper, and again distinguishes it on the basis of color, size, and convexity. Lea (1901) lists this species as a synonym of *Rodolia koebelei* (then included in *Novius*). Presumably, he made this decision based upon superficial color similarity. *R. lindi* and *R. koebelei* have similar coloration, but the morphology of each is quite distinct.

Rodolia marginata Bielawski 1960

Rodolia marginata Bielawski, 1960; ***nomen nudum***.

Remarks: One female specimen from the USNM bears a determination label that reads "*Rodolia marginata;* det. R. Korschefsky." There is no description in the literature, and the name does not occur in the Zoological Record. Poorani (2002) lists the species as "doubtful," but it is unknown whether she is in doubt about the presence of the species on the Indian subcontinent or the validity of the name. With no description accompanying the name, no type material available, and no male specimen to examine, no determination can be made for this specimen. Unfortunately, because the single exemplar is a female, no new description or diagnosis can be provided.

Rodolia mexicana (Gordon) 1972

Anovia mexicana Gordon, 1972: p. 29.

Rodolia mexicana (Gordon) 1972: p. 29; new combination.

Diagnosis: As is the case with all other noviines, *Rodolia mexicana* is only diagnosable by the structure of the male genitalia. *R. mexicana* resembles *R. pumila* in that both have a basal piece with length about 1/2 width. *R. mexicana* is also similar to *R. virginalis* in that both have a very wide basal lobe (> 2 paramere widths). However, in *R. mexicana* the basal lobe is abruptly narrow, while in *R. virginalis* and *R. pumila*, the basal lobe narrows gradually. *R. mexicana* also has an unusually narrow excavate region on the ventral side of the basal lobe.

Description: Length 3.0 - 3.5 mm. Body hemispherical, widest just behind humeral angles, convex; dark orange-brown, iridescent, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length > 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins slightly thickened; posterior and anterior width subequal, moderately setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length about 1/2 width; proximal margin horizontal or nearly so. Parameres long, slender, excavate laterally, spatulate apically; apical setae long; basal lobe very wide, extending beyond the external edges of the parameres, slightly longer than parameres, abruptly tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent. Median strut short, only slightly longer than basal piece. Sipho short, longer than aedeagus, but < 2x aedeagus length, broad to tapered apex, with asymmetrical basal capsule; basal capsule with apodeme present.

Female: unknown

Type material: Holotype: Canadian National Collection; Paratypes: USNM

Distribution: Mexico

Remarks: In his original description, Gordon (1972) diagnoses *R. mexicana* (then *Anovia mexicana*) by reporting that the sipho is "short and stout…the dorsal color is prdominantly black…and resembles *virginalis* but *mexicana* is larger and has the punctures on the head and pronotum denser than does *virginalis.*" Although color and size are variable for members of Noviini, these are not reliable diagnostic characters for species. Likewise, the size and density of punctures are variable both within species and between them. The basal lobe of *R. mexicana* is unique among other species of *Rodolia* and is unequivocally diagnostic for the species.

Rodolia minuta Sicard 1909

Rodolia minuta Sicard, 1909: p. 118; ***nomen dubium***.

Remarks: Sicard (1909) diagnosed *R. minuta* solely on the basis of elytral coloration; however, intraspecific color variation is quite common in *Rodolia*. Diagnoses relying upon color are questionable, at best. In the case of *R. minuta*, no reliably identified material is available, and the original description is insufficient to diagnose the species. An additional complication is the type depository for Sicard's holotypes. They are housed at the Musee d'Histoire Naturelle in Paris. Unfortunately, there is currently no curator for Coccinellidae there, and all material from that facility is unaccessible.

Rodolia nigerrimus Fürsch 1960

Rodolia nigerrimus Fürsch, 1960: p. 447; ***nomen dubium***.

Remarks: In his original description, Fürsch (1960) compareD *R. nigerrimus* to *R. cruentata*, and noted differences in both color and morphology of the female hemisternites. Unfortunately, color is not a reliable diagnostic character for any noviine species. Fürsch's (1960) illustration of the hemisternites is very difficult to interpret; there is no difference in structures of the two structures he has drawn. Finally, the type depository for this species is unknown and the author, though living, cannot be reached.

Rodolia nigra Fürsch 1995 (Figs. 4.58, 4.91 - 4.93)

Rodolia nigra Fürsch, 1995.

Diagnosis: Like others in the tribe Noviini, *R. nigra* is distinguished by the unique structure of the aedeagus (Figs. 4.91 - 4.93). Like *R. limbata* (Motschulsky), *R. nigra* has mesally directed parameres; however, in *R. nigra* they bend inward abruptly at the apex (Figs. 4.91, 4.92). In *R. limbata*, the parameres are not sharply bent, but laterally arcuate, encircling the basal lobe (Fig. 4.81). *R. nigra* is further distinguished from its congeners by both the sinuate mesal edge of the siphonal apodeme and the bifurcate siphonal apex (Fig. 4.93). *R. argodi* Sicard, *R. iceryae* Janson in Howard, and *R. occidnetalis* all have a siphonal apex that is bifurcate (Figs. 4.74, 4.96). *R. nigra* differs from both in having the basal capsule asymmetrical, almost semicircular, with a sinuate medial edge (Fig. 4.93). *R. argodi* and *R. iceryae* both have a sipho with a T-shaped basal capsule (Fig. 4.74).

Description: Length 2.0 - 2.5 mm. Body hemispherical, widest just behind humeral angles, convex; uniformly black, shiny; dorsal surface covered with short, suberect, pale setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI –

VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical sensory area with length ~ 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin arcuate; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge slightly bilobed, slightly wider than anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind (Fig. 4.58).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin feebly bilobed (Fig. 4.91). Parameres long, slender, excavate laterally, spatulate and curved mesad apically; apical setae short; basal lobe narrow, slightly longer than parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent (Figs. 4.91, 4.92). Median strut longer (< 2x) than basal piece (Figs. 4.91, 4.92). Sipho short, only about as long as aedeagus, broad to pointed, bifid apex, with asymmetrical basal capsule; basal capsule not T-shaped, but with apodeme present (Fig. 4.93).

Female: With well-developed, square, basal tooth.

Type material: Paratypes: 2 males, MNHUB. "ZIMBABWE: 10. iii. 2000 ~ 1260 m; 20°28'48, 7°S/29°24'38, 7°E; Strabe zw. Zvishavane und; Mbalabala Bushcamp ca. 60 km; WSW Zvishavane, leg. U. Göllner / Rodolia; nigra Fü; det. H. Fürsch 2002 / Museum für Naturkunde; Humboldt - Univ. Berlin; (MNHUB)

Distribution: Africa (Namibia)

Remarks: R. nigra is one of the few noviine species that does not have color variation. All exemplars of this species are uniformly black. This species is known only from the type locality.

Rodolia obscuricollis Sicard 1931

Rodolia obscuricollis Sicard, 1931: p. 229; ***nomen dubium***.

Remarks: Like many of Sicard's species descriptions, the one defining *R. obscuricollis* was solely based on color (Sicard 1931). Specifically, he noted the contrast between the color of the prothorax and the elytra. Color varies significantly within species of Noviini, so color is not a reliable diagnostic character for species. Sicard's holotypes are all housed in the Musee d'Histoire Naturelle in Paris. There is no curator for Coccinellidae there, so the material is inaccessible. To further complicate matters, no reliably identified material of this species was available.

Rodolia occidentalis Weise 1898 (Figs. 4.12, 4.94 - 4.96)

Rodolia occidentalis Weise, 1898: p. 122.

Rodolia marginalis Mader 1954: p. 34; aberration of *R. occidentalis*.

Diagnosis: R. occidenatalis is remarkable among noviines in that it can be distinguished not only by the structure of the aedeagus, but also by the structure of the tibia. The tibia of *R. occidentalis* is strongly lobed medially, rather than gradually expanded (as in all congeners). This species is further distinguishable by the structure of the basal lobe and the sipho (Figs. 4.94 - 4.96). The basal lobe for this species is quite distinct in having the excavate portion very narrow (< 1 paramere width) (Figs. 4.94, 4.95). The sipho of this species is similar to that of *R. argodi*, *R. iceryae*, and *R. nigra* in that it is bifurcate just proximal to the apex (Figs. 4.74, 4.93). In *R. occidentalis*, the bifurcation extends to the apex, giving the apex a 2-pronged appearance (Fig. 4.96).

Description: Length 3 - 3.5 mm. Body hemispherical, widest just behind humeral angles, convex; uniformly brownish orange, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.12).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; eyes large, covering much of dorsal head surface, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III securiform, distal edge less than twice as long as the proximal one, length < 2x width, sensory area with subequal length and width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior margin sinuate, edge anterior to scutellum weakly bilobed; laterally explanate. Prosternum narrow; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broad. Legs flattened, stout and broad. Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, with large medial expansion, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsus 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, almost as wide as long; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin feebly sinuate (Fig. 4.94). Parameres long, slender, spatulate, apical setae short; basal lobe almost as long as parameres, wide (~ two paramere widths), excavate along midline to receive sipho, excavate area very narrow (< 1 paramere width), gradually tapering to glabrous apex; in lateral view, basal lobe curved ventrally, dorsal barb absent (Figs. 4.94, 4.95). Median strut narrow, > 2x length of basal piece (Figs. 4.94, 4.95). Sipho elongate, about 2x aedeagus length, narrow to bifid, threadlike apex, basal capsule with T-shaped apodeme present (Fig. 4.96).

Female: Tarsal claw with well-developed, square basal tooth.

Type material: Neotype: USNM. “MUSÉE DU CONGO; Yaugarubi /“25” V - 1933; J. Vrydagh / Korschefsky; Collection; 1952 / USNM; 2037254”

Distribution: Africa

Remarks: As with much of Weise's material, type material for *R. occidentalis* is unavailable. Perhaps a type specimen was never designated. Many of Weise's holotypes were lost, particularly those that were deposited in Dresden. It is unknonwn whether or not a holotype for *R. occidentalis* ever existed, but it is certain that no type is available currently. Reliably identified material (det. Korschefsky) was used to describe the species. A neotype is here designated and deposited at the USNM.

Rodolia podagrica Weise 1908 (Figs. 4.13, 4.24, 4.34, 4.36, 4.59)

Rodolia podagrica Weise, 1908.

Rodollu amabilis Kapur, 1949: p. 536; new synonym.

Diagnosis: R. podagrica is the only species of *Rodolia* that is diagnosable based on a character other than the male genitalia. This species has very short, stout legs with subeuqual length and width. The structure of the male genitalia is most similar to *R. pumila*, but *R. podagrica* can be distinguished by the setae on the parameres: *R. podagrica* is the only species with setae on the inner margin extending the entire length of the parameres.

Description: Length 2.5 - 3 mm. Body hemispherical, widest just behind humeral angles, convex, uniformly orange; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Figs. 4.13, 4.24).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI –

VII expanded laterally; VIII longer than wide, apically rounded and broad (Fig. 4.34). Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus (Fig. 4.36). Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length about 2x width.

Pronotum widest anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward well beyond eye, anterior margin horizontal, straight; posterior margin sinuate, edge anterior to scutellum entire, not bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, cordate; lateral and anterior margins thickened; anterior edge broadly rounded; posterior edge bilobed, setae long and sparsely distributed; procoxal cavities slightly transverse, closed behind (Fig. 4.59).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broadly elongate, apical width subequal to entire length; deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsus 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple.

Elytron convex, about as wide as long at widest point; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral edge; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length shorter than width; proximal margin slightly sinuate. Parameres long, slender, widest apically; apical setae moderately long, extending the entire length of the parameres; basal lobe about as long as parameres, excavate along midline to receive sipho, excavation narrow, broad basally, distal 1/4 tapering to setose apex; in lateral view, distal 1/4 curved posteriorly, rounded apically, not sharply pointed; dorsal barb absent. Sipho short, < 3x length of aedeagus, narrow to threadlike apex; with asymmetrical basal capsule.

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Holotypes: BMNH, 1 female Sweden; Paratypes: BMNH, ZIL

Distribution: India, Sri Lanka, Manila

Remarks: Kapur (1949) noted that he deposited a holotype of *R. amabilis* in his personal collection. An exemplar of that species from his collection was compared with reliably identified exemplars of *R. podagrica* to determine the synonymy.

Rodolia prosternalis Sicard 1909

Rodolia prosternalis Sicard, 1909: p. 118; ***nomen dubium***.

Remarks: Sicard (1909) diagnosed *R. prosternalis* on the basis of elytral coloration and convexity. Intraspecific color variation is quite common within the tribe, so diagnoses relying upon color are questionable, at best. He also notes that *R. prosternalis* is defined by the "shape of the prosternum;" however, he does not state what that "shape" is. In the case of *R. prosternalis*, no reliably identified material is available, and the original description is insufficient to diagnose the species. A further complication is that Sicard's holotypes are housed at the Musee d'Histoire Naturelle in Paris. Unfortunately, there currently is no curator for Coccinellidae there, and all material is unaccessible.

Rodolia pumila Weise 1892 (Figs. 4.21, 4.60, 4.65, 4.97 - 4.99)

Rodolia pumila Weise, 1892: p. 26.

Rodolia okinawensis Miyatake, 1959: p. 127; synonym (Sasaji 1971, p. 239).

Rodolia vulpina Fürsch, 1974: p. 23; new synonym.

Diagnosis: R. pumila Weise, like its other noviine counterparts is distinguished by the structure of the aedeagus (Figs. 4.97 - 4.99). Several other noviines have the basal lobe narrow and gradually tapered toward the apex: *R. circumclusa* (Gorham), *R. iceryae* Janson in Howard, *R. lindi* (Blackburn), *R. nigra* Fürsch, *R. occidentalis* Weise, *R. punica* (Gordon), *R. virginalis* (Wickham), *and R. weise* (Gordon) (Figs. 4.89 - 4.94). *R. pumila* differs from those in having the basal lobe very deeply excavate; so much so that it is almost as deep as wide (Figs. 4.97, 4.98). The parameres of *R. pumila* are directed toward the basal lobe at midlength, then away from it apically (Fig. 4.97). The structure is similar to *R. insularis* Weise, but the parameres of *R. pumila* are not constricted.

Description: Length 4 – 4.5 mm. Body hemispherical, widest just behind humeral angles; convex, uniformly orange, occasionally with black pronotum, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above (Fig. 4.21).

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; apical teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III with dorsal surface about as long as apical width, strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length < 2x width.

Pronotum widest anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior margin sinuate, edge anterior to scutellum entire, not bilobed; laterally explanate. Prosternum narrow; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed; procoxal cavities slightly transverse, closed behind (Fig. 4.60).

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broad. Legs flattened, stout and broad (Fig. 4.65). Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire (Fig. 4.65). Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate (Fig. 4.65). Tarsus 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple (Fig. 4.65).

Elytron convex, about as wide as long at widest point; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid (Fig. 4.65). Aedeagus with basal piece length shorter than width; proximal margin deeply cleft (Fig. 4.97). Parameres long, slender, widest apically; apical setae long; basal lobe about as long as parameres, excavate along midline to receive sipho, very broad basally, dorsal edge curved, raised above basal piece, deeply excavate with distal 1/4 tapering to setose apex; in lateral view, distal 1/4 curved posteriorly, rounded apically, not sharply pointed; dorsal barb absent (Figs. 4.97, 4.98). Sipho short, < 3x length of aedeagus, narrow to threadlike apex; with asymmetrical basal capsule (Fig. 4.99).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Syntpe: 1 female, MHNUB

Distribution: China, Africa

Remarks: Like many of Weise's species, the descriptionfor *R. pumila* included a diagnosis that was based on labile characteristics such as color intensity and size (Weise 1892). No holotype was available for this study, so the species redescription above was based upon reliably identified material (det. Korschefsky).

Rodolia punica (Gordon) 1972

Anovia punica Gordon, 1972: p. 29.

Rodolia punica (Gordon), 1972: p. 29; new combination.

Diagnosis: R. punica is most similar to *R. circumclusa* and *R. virginalis* in having the basal piece subequal in length and width, no barb on the basal piece, and a T-shaped apodeme on the base of the sipho. *R. punica* differs from *R. circumclusa* and *R. virginalis* in having the basal lobe very wide, extending to the outer margin of the parameres; also, the excavation on the ventral side of the basal lobe is much narrower in *R. punica* than in either *R. circumclusa* or *R. virginalis*.

Description: Length 3 - 3.5mm. Body hemispherical, widest just behind humeral angles, convex; elytra entirely black or carmine red, with or without iridescent black ring, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna with 8 articles; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical sensory area with length > 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal or nearly so; posterior edge slightly arcuate, with posterior width slightly more than anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin horizontal or nearly so. Parameres long, very slender, excavate laterally, spatulate apically; apical setae long; basal lobe wide (> 2 paramere widths), slightly longer than parameres, apical 1/3 abruptly tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex directed downward, barb absent. Median strut short, slightly longer than basal piece. Sipho short, narrow, only about as long as aedeagus, apex simple; with asymmetrical basal capsule; basal capsule with apodeme present.

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Holotype: male, Venezuela: Edo. Aragua, Maracay, 22-VII-41, C. H. Ballou, eating *Icerya purchasi* (USNM).

Distribution: Venezuela, Panama

Remarks: Rodolia punica (Gordon) has color variation that is very similar to that of *Rodolia circumclusa* (Gorham): some are almost entirely a carmine red color, others have a dark ring and red zonate region, and still others are uniformly dark. Examination of the male genitalia is the only reliable way to differentiate these two species.

Rodolia quadriplagiata Sicard 1909

Rodolia quadriplagiata Sicard, 1909: p. 121; ***nomen dubium***.

Remarks: Sicard diagnosed *R. quadriplagiata* on the basis of elytral coloration. Color variation is quite common within and between species of the tribe, so diagnoses relying upon color are questionable, at best. Sicard also provided a rudimentary sketch of the antenna, but the drawing is not informative, much less diagnostic. In the case of *R. quadriplagiata*, no reliably identified material was available for this study, and the original description is insufficient to diagnose the species. To further complicate matters, Sicard's holotypes are housed at the Musee d'Histoire Naturelle in Paris. Unfortunately, there currently is no curator for Coccinellidae there, and all material is unaccessible.

Rodolia quadrispilota Sicard 1909

Rodolia quadrispilota Sicard, 1909: p. 120; ***nomen dubium***.

Remarks: Sicard diagnosis *R. quadrispilota* on the basis of elytral coloration and the shape of the prosternal process. Examination of the world's holdings of Noviini indicates that intraspecific color variation is quite common within the tribe, so diagnoses relying upon color are questionable, at best. He provides a rudimentary sketch of the prosternal process, but the artistic rendering is not informative. In the case of *R. quadrispilota*, no reliably identified material is available, and the original description is insufficient to diagnose the species. Furthermore, Sicard's holotypes are presumed to be housed at the Musee d'Histoire Naturelle in Paris. Unfortunately, there is currently no curator for Coccinellidae there, and all material is unaccessible.

Rodolia rubea Mulsant 1850 (Figs. 4.31, 4.32, 4.35, 4.37, 4.44, 4.45, 4.47, 4.50, 4.61, 4.66, 4.100 - 4.102)

Rodolia rubea Mulsant, 1850: p. 902.

Rodolia carneipellis Mulsant, 1853: p. 131; synonym (Korschefsky 1931: p. 102).

Rodolia carneipennis Mader, 1927: p. 763; misspelling (Korschefsky 1931: p. 102).

Diganosis: The structure of the male genitalia distinguishes *R. rubea* from all other members of the genus. It is similar to *R. fumida*, *R. insularis*, and *R. limbata* in having the basal lobe with a barbed apex and the sipho with a T-shaped apodeme (Figs. 4.81 - 4.86, 4.100 - 4.102). In *R. rubea* the sipho is very long, like that of *R. fumida* (Figs. 4.86, 4.102). However, the apical barb on the basal lobe is much larger in *R. rubea* (Figs. 4.84, 4.85, 4.100, 4.101). *R. rubea* can be distinguished from *R. insularis* by the parallel-sided parameres; they are not constricted at midlength as they are in *R. insularis* (Figs. 4.100, 4.101).

Description: Length 4 – 4.5 mm. Body hemispherical, widest just behind humeral angles, convex; dark red-orange, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture (Figs. 4.31, 4.32). Eyes large, pubescent, not prominent, finely facetted (Figs. 4.31, 4.32). Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad (Fig. 4.35). Clypeus narrow, apically horizontal. Labrum bilobed, expanded laterally beyond clypeus (Fig. 4.37). Mandible with bifid, sickle-shaped apical tooth; apical teeth subequal in length; subprosthecal tooth and prostheca well-developed (Figs. 4.44, 4.45). Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically; II trapezoidal; III with dorsal surface shorter than apical width, strongly securiform, distal edge > 2x as long as the proximal one, apical surface with length < 2x width (Fig. 4.47).

Pronotum widest anterior to posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward well beyond eye, anterior margin slightly sinuate; posterior margin markedly sinuate, edge anterior to scutellum entire; laterally explanate. Prosternum narrow; prosternal process abruptly raised, subrectangular; lateral margins thickened; narrowest anteriorly, bilobed posteriorly; procoxal cavities slightly transverse, closed behind (Fig. 4.61).

Scutellum small, triangular, impunctate (Fig. 4.50). Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broad. Legs flattened, stout and broad (Fig. 4.66). Prothoracic femur broadly elongate, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire (Fig. 4.66). Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate (Fig. 4.66). Tarsus 3-3-3; tarsomeres I and II elongate, bilobed with spongy pubescence ventrally; III, elongate, cylindrical; claw simple (Fig. 4.66).

Elytron convex, about as wide as long at widest point; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid (Fig. 4.66). Aedeagus with basal piece length subequal to width; proximal margin horizontal or nearly so (Fig. 4.100). Parameres long, slender, narrow basally, gradually expanding to setose apex; apical setae short, sparse; basal lobe about as long as parameres, excavate along midline to receive sipho; in lateral view, apex abruptly expanded and curved posteriorly both dorsally and ventrally to form barb; barb tip broadly rounded (Figs. 4.100, 4.101). Sipho elongate, narrow, >3x as long as aedeagus, apical 2/3 threadlike, basal capsule with apodeme present (Fig. 4.102).

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: male, ANIC. "Sandakan, Borneo, Baker"

Distribution: India, Indonesia

Remarks: Korschefsky (1931) correctly names *R. rubea* as the type species for the genus. Gordon (1972) claimed that Korschefsky (1931) was mistaken, and that the type species for *Rodolia* is *R. ruficollis*, by subsequent designation of Crotch (1874). Crotch (1874) did, in fact, designate *R. ruficollis* the type for the genus. In the same paper, though, he included *ruficollis* in *Vedalia*. Mulsant's original description for *R. rubea* was solely based upon color and therefore insufficient for diagnosing species.

Rodolia rubra (Blackburn) 1889

Novius ruber Blackburn, 1889: p. 148.

Rodolia rubra (Blackburn), 1889; new combination (Ślipiński 2007: p. 143); ***nomen dubium.***

Remarks: Blackburn (1889) described *R. rubra* (then *Novius*), as being "much like [other Australian species] but decidedly larger, and very differently coloured. The whole upper surface is a shining bright-red colour…" This inadequate description, along with Ślipiński's (2007) inclusion of the species in *Rodolia* is the only known reference for *R. rubra*. No type material was available for this study, so the species name remains doubtful.

Rodolia rufocincta Lewis 1896

Rodolia rufocincta Lewis, 1896: p. 40; ***nomen dubium***.

Remarks: Lewis's (1896) original description is the first and only reference to *R. rufocincta*. He diagnosed his new Japanese species on the basis of overall appearance: "This species is distinctly more oval than either *R. limbatus* [Motschulsky] or *R. concolor*." According to Lewis (1896), the color pattern of *R. rufocincta* is nearly identical to that of *R. limbatus* (Motschulskly). However, with no type specimen or other reliably identified material, the species cannot be determined or redescribed.

Rodolia severini (Weise) 1895

Rodolia severini (Weise), 1895: p. 150.

Rodolia severini (Weise), 1895: p. 150; new combination (Ślipiński 2007: p. 143); *nomen dubium*.

Remarks: Weise (1895) described the genus *Eurodolia* and included only one species: *E. severini*. He notes that *Vedalia cardinalis* and *Rodolia sanguinolentus* "probably belong in *Eurodolia* as well…" The genus *Eurodolia* was defined on the basis of color and "general appearance." Those features are very labile, and therefore unsuited for unequivocal species diagnoses. To further complicate matters, the holotype was originally deposited in the natural history museum in Dresden and was subsequently lost.

Rodolia songchuana Hoang 1980

Rodolia songchuana Hoang, 1980: p. 12; ***nomen dubium***.

Remarks: Hoang described this new species after seeing only female representatives. Unfortunately, female genitalia are not reliably diagnostic for members of Noviini. Reliably identified material of *R. songchuana* was not available for this study, and Hoang did not directly compare the morphology of *R. songchuana* to congeners. To further complicate matters, Hoang deposited his holotypes at the ZIRS in St. Petersburg, Russia (formerly the Zoological Institute of USSR in Leningrad) and that museum has no record of the specimens (Dr. Boris Mikhaylovich Kataev, personal communication).

Rodolia tamdaoana Hoang 1980

Rodolia tamdaoana Hoang, 1980: p. 12; ***nomen dubium***.

Remarks: Hoang diagnosed this species based upon the "very long and thin sipho bearing two minute thorns at the end." He did not directly compare his new species to existing ones: *R. argodi* Sicard and *R. iceryae* Janson in Howard also have a bifurcate siphonal apex. The color pattern Hoang describes for *R. tamdaona* is reminiscent of *R. iceryae.* However, in the absence of reliably identified or type material of *R. tamdaona*, the species name remains doubtful. To further complicate matters, Hoang deposited his holotypes at the ZIRS in St. Petersburg, Russia (formerly the Zoological Institute of USSR in Leningrad) and that museum has no record of the specimens (Dr. Boris Mikhaylovich Kataev, personal communication).

Rodolia tripustulata (Blackburn) 1895

Novius tripustulatus Blackburn, 1895: p. 254.

Rodolia tripustulata (Blackburn) 1895, comb. nov. (Ślipiński 2007: p. 143); ***nomen dubium.***

Remarks: Blackburn (1895) reported that *R. tripustulata* (then *Novius*) was similar to *R. cardinalis* (then *Novius*), but was distinguishable by the "closer, less fine puncturation." He provided no other diagnostic characteristics for the species. Unfortunately, no type or reliably identified material of this species was available for study, and the original description (and only reference) of *R. tripustulata* is insufficient to identify the species.

Rodolia usambarica Weise 1898

Rodolia usambarica Weise, 1898: p. 201.

Diagnosis: This species is recognizable by the structure of the male genitalia: the basal lobe is constricted basally and expanded medially, tapering to a barbed apex. Some congeners also have an apically barbed basal lobe (e.g., *R. fumida*, *R. insularis*, *R. limbata*, and *R. rubea*) but in those the basal lobe is not inflated at midlength. Also, in *R. usambarica* the excavate venter of the basal lobe is much narrower than that of congeners.

Description: Length 3.5 - 4 mm. Body hemispherical, widest just behind humeral angles, convex; uniformly orange, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge > 2x as long as the proximal one, apical sensory area with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior and posterior edges horizontal or nearly so, subequal in width, setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length subequal to width; proximal margin deeply cleft. Parameres long, slender, excavate laterally, spatulate apically; apical setae long; basal lobe constricted basally, expanded medially, subequal in length to parameres, gradually tapering to glabrous apex, excavate along midline to receive sipho; in lateral view, apex expanded dorsally and ventrally to form small barb. Median strut long and slender, almost as long as basal piece. Sipho short, narrow, only about as long as aedeagus, apex simple, flat and truncate; with asymmetrical basal capsule; basal capsule with apodeme present, but small.

Female: Tarsal claw with well-developed, square, basal tooth.

Type material: Neotype: male, ANIC. “Assab, 1907 / Africa or, Katona / Rodolia, usambarica, det. H. Fürsch / ex. coll. H. Fürsch / ANIC”

Distribution: Africa

Remarks: Weise (1898) diagnosed *R. usambarica* on the basis of “longer hair” and “more yellowish” coloration. He noted that the prosternum was “high,” but most *Rodolia* exemplars have a prosternum that is tilted and raised above the procoxae. The male genitalia characters unequivocally diagnose *R. usambarica*. In the absence of type material, a neotype is here designated on the basis of reliably identified material (det.Fürsch).*Rodolia virginalis* (Wickham) 1905

Scymnus virginalis Wickham, 1905: p. 166; synonym (Casey, 1908: p. 408).

Anovia virginalis (Wickham), 1905: p. 166; new combination (Casey, 1908: p. 408).

Rodolia virginalis (Wickham), 1905: p. 166; new combination.

Diagnosis: R. virginalis (Wickham) is distinguished by the structure of the male genitalia. In this species, the basal piece is narrowest at the proximal margin (please see Forrester & Vandenberg 2008). In all other *Rodolia* species, the basal piece is either subequal in proximal and distal width or widest proximally.

Description: Length 2.5 - 3 mm. Body hemispherical, widest just behind humeral angles, convex; color variable, shiny; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge < 2x as long as the proximal one, apical sensory area with length < 2x width; lateral edge ~ 2x as long as mesal one.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly;

prosternal process abruptly raised, quadrate; lateral margins only slightly thickened; anterior edge horizontal; posterior edge deeply bilobed, with posterior width about 2x anterior width, sparsely setose; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length greater than width; proximal margin horizontal or nearly so. Parameres long, slender, spatulate apically,; basal lobe very wide, extending beyond mesal edges of parameres, gradually tapering to apex, excavate along midline to receive sipho; in lateral view, apex curved slightly downward, barb absent. Median strut short, only about as long as basal piece. Sipho narrow, short, only about as long as aedeagus, apex tapered but not threadlike, with asymmetrical basal capsule; basal capsule with apodeme present.

Female: Tarsal claw with well-developed basal tooth.

Type material: USNM

Distribution: United States, Mexico

Remarks: Forrester & Vandenberg (2008) provided diagnostic characters and illustrations of the male genitalia for this species. As with many other noviine species, the elytral color patterns vary within *R. virginalis*: most are dark brown with one orange spot on each elytron, occasionally with orange on the humeral angles as well.

Rodolia weisei (Gordon) 1972

Anovia weisei Gordon, 1972: p. 30.

Rodolia weisei (Gordon), 1972: p. 30; new combination.

Diagnosis: R. weisei is unique in having a very narrow basal lobe; it does not extend beyond the outer edge of the parameres. It is similar to *R. circumclusa* in this regard, but *R. weisei* has a sipho that is much longer than the aedeagus (> 2x). Also, *R. weisei* has a basal piece that is longer then wide, not subequal in length and width as *R. circumclusa*.

Description: Length 3.5 - 4 mm. Body hemispherical, widest just behind humeral angles; convex; elytra, head, and medial 1/3 of pronotum dark orange brown, iridescent, shiny; lateral regions of pronotum lighter brown; dorsal surface covered with short, suberect, golden setae; head deflexed, not visible from above.

Head about twice as wide as long; dorsal surface covered with small, shallow punctules and pale setation; ventral surface narrow, with large, shallow, asymmetrical punctures; posterior margin slightly sinuate and excavate at pronotal juncture. Eyes large, pubescent, not prominent, finely facetted. Antenna inserted in front of the inner eye margin, insertion exposed. Antenna of 8 antennomeres; antennomere I laterally expanded, asymmetrical; II subglobose, about as long as wide; III – V more elongate, cylindrical, all of similar size; VI – VIII forming loose club; VI – VII expanded laterally; VIII longer than wide, apically rounded and broad. Clypeus narrow, apically horizontal. Labrum bilobed, convex, expanded laterally beyond clypeus. Mandible with bifid, sickle-shaped apical tooth; teeth subequal in length; subprosthecal tooth and prostheca well-developed. Lacinia slender, elongate, with setose apex. Maxillary palpus 3-segmented, with well-developed palpifer; sensory area visible on palpomeres I - III; I very wide apically, II trapezoidal, III strongly securiform, distal edge < 2x as long as the proximal one, apical sensory area with length < 2x width.

Pronotum widest at posterior angles; dorsal surface with shallow, small punctules; anterior edge extending forward just beyond eye, anterior margin horizontal, straight; posterior edge sinuate, weakly bilobed; laterally explanate. Prosternum narrow, tilted anteriorly; prosternal process abruptly raised, quadrate; lateral margins thickened; anterior edge horizontal; posterior edge bilobed, with posterior width about 2x as long as anterior width, moderately setose; setae long; procoxal cavities slightly transverse, closed behind.

Scutellum small, triangular, impunctate. Meso- and metaventrite flattened, pubescent. Mesothorax short, trapezoidal, narrowest posteriorly. Metaventrite longer, broader than mesothorax. Legs flattened, stout and broad. Prothoracic femur broad, stout, deeply grooved for tibial reception; groove sharply defined, bicarinate, extending entire length of femur; anterior edge lobed distally, posterior edge entire. Tibia widest at midlength, deeply grooved for reception of tarsus; groove bicarinate, posterior surface broader than anterior; posterior groove margin weakly sinuate. Tarsal formula 3-3-3; tarsomeres I and II elongate, bilobed ventrally with spongy pubescence; III, elongate, cylindrical; claw simple.

Elytron convex, about as long as wide; finely punctate, non-striate; epipleuron complete to posterior margin; ventral surface moderately rugose. Wing with cantharoid nervature, venation reduced, absent in distal half, with strong media and cubitus, one anal vein, and jugal lobe present.

Abdomen wider than long, with broad, cleft intercoxal process; postcoxal line complete to inner margin of lateral line; 6 slightly overlapping ventrites; I – V similar in shape, progressively narrowing to abdominal apex; VI rounded and feebly cleft apically. Pygidium trapezoidal, setose, broadly truncate apically.

Male: Tarsal claw bifid. Aedeagus with basal piece length greater than width; proximal margin horizontal or nearly so. Parameres long, slender, spatulate apically; basal lobe narrow, not extending beyond outside edges of parameres, gradually tapering to apex, excavate along midline to receive sipho; in lateral view, apex narrow, curved slightly downward, barb absent. Median strut short, only about as long as basal piece. Sipho slender, with asymmetrical basal capsule; basal capsule with apodeme present.

Female: unknown

Type material: 1 Paratype: male; USNM. “ex Guatemala,” N. Orleans 60-20819.”

Distribution: Guatemala

Remarks: This species is known from only two specimens, both of which are housed at the USNM. The paratype, whose dissected genitalia were used for Gordon’s (1972) study, was the only specimen available for the current study. Unfortunately, the genitalia vial contained only the sipho; the aedeagus was missing. The diagnosis and description above is based on Gordon's (1972) treatment along with the beetle parts that were present.

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Literature Cited

Arnett, R. H. (1963) *The Beetles of the United States*. Catholic University of America Press, Washington, D.C. 1112 pp.

Balduf, W.V. (1935) *Coccinellidae*, (13) Ladybeetles. Bionomics of Entomophagous Coleoptera. John S. Swift, Chicago, New York, 220 pp.

Bezzerides, A. L., McGraw, K. J., and Husseini, J. (2006) Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis. Behavioral Ecology and Sociobiology*, 61, 1401-1408.

Blackburn, T. (1895) Further notes on Australian Coleoptera, with descriptions of new genera and species. *Transactions of the Royal Society of South Australia*, 14, 201-255.

Blackburn, T. (1889) Further notes on Australian Coleoptera, with descriptions of new species. *Transactions and Proceedings and Report of the Royal Society of South* Australia, 11, 175-215.

Britton, G., Goodwin, T. W., Harriman, G. E., and Lockley, W. J. S. (1977) Carotenoids of the ladybird beetle, *Coccinella septempunctata*. *Insect Biochemistry*, 7, 337-345.

Bodenheimer, F. S. (1932) *Icerya purchasi Maskell und Novius cardinalis* Mulsant. Eine bevölkerungswissenschaftliche Studie über die Grundlagen der biologischen Bekämpfung. *Zeitschrift Für Angewandte Entomologie*, 19, 521-543.

Caltagirone, L. E. and Doutt, R. L. (1989) The history of the Vedalia Beetle importation into California and its impact on the development of biological control. *Annual Review of Entomology,* 34, 1-16.

Causton, C. E. (2004) Ensuring compatibility of biological control of *Icerya purchasi* Maskell with conservation in Galápagos: development of a procedure to evaluate risk. *In:*

R. G. V. Driesche (Eds), *Proceedings of the First International Symposium for the Biological Control of Arthropods*. USDA-FS Honolulu.

Chazeau, J. (1981) Presence du genre Rodolia Mulsant en Nouvelle-Caledonie, et description d'une nouvelle espece: *R. delobeli*. *Bulletin Entomologique Société Entomologique de France*, 56, 57-59.

Chazeau, J. H., Fürsch, H., and Sasaji, H. (1989) Taxonomy of coccinellids. *Coccinella*, 1, 6-8.

Clausen, C. P. (1940) *Entomophagous Insects*. McGraw-Hill, New York, 688 pp.

Coquillett, D. W. (1893) Report on some beneficial and injurious insects of California. *United States Department of Agriculture Entomology Bulletin*, 30, 9-33.

Coquillet, D. W. (1889) The imported Australian ladybird, *Vedalia cardinalis*. *Insect Life,* 2(8), 70-75.

Crotch, G. R. (1874) *A Revision of the Coleopterous Family Coccinellidae.* E. W. Janson, London. 311 pp.

Crowson, R. A. (1955) *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd & Co., Ltd., London. 187 pp.

Crowson, R.A. (1960). The phylogeny of Coleoptera. *Annual Review of Entomology.* 5, 111-134.

Daloze, D., Braekman, J., and Pasteels, J. M. (1994) Ladybird defence alkaloids: Structural, chemotaxonomic, and biosynthetic aspects (Col.: Coccinellidae). *Chemoecology*, 5, 173-183.

DeBach, P. and Rosen, D. (1991) *Biological control by natural enemies*. Cambridge University Press, Cambridge, 456 pp.

Dixon, A. F. G. 2000. *Insect predator-prey dynamics: Ladybird beetles and biological control*. Cambridge University Press, Cambridge, 257 pp.

Dobzhansky, T. (1926) Die paläarktischen Arten der Gattung *Coccinella L.* Rev. Russ. Ent. 20, 16-32.

Eisner, T., Ziegler, R., McCormick, J. L., Eisner, M., Hoebeke, E.R., and Meinwald, J. (1994) Defensive use of an acquired substance (carminic acid) by predaceous insect larvae. *Experientia*, 50, 610-615.

Exell, A. W. (1991) *The History of the Ladybird With some Diversions on This and That*. Erskine Press, Shotesham, 40 pp.

Freude, H., Harde, K. W., and Lohse, G. A. (1967) *Die Kafer Mitteleuropas*. Goecke & Evers, Krefeld.

Forrester, J. A. and Vandenberg, N. J. (2008) First Florida records for *Anovia circumclusa* (Gorham) (Coleoptera: Coccinellidae: Noviini): A natural enemy of *Icerya genistae* Hempel (Hemiptera: Margarodidae). *Zootaxa*, 1720, 66-68.

Forrester, J. A., Vandenberg, N. J., and McHugh, J. V. (2008) First description of the egg, pupa, and larva of *Anovia circumclusa* (Gorham) (Coleoptera: Coccinellidae: Noviini), with notes on intraspecific color variation. *In review.*

Fürsch, H. (1960) Neue palaearktische und afrikanische Coccinellide (Coleoptera). *Beiträge Zur Entomologie*,10, 442-451.

Fürsch, H. (1995) The ladybird beetles found by the Entomological Namibia Expedition of the Museum of Natural History Berlin 1992 with remarks on other African species (Coleoptera: Coccinellidae). *Mitteilungen-aus-dem-Zoologischen-Museum-in-Berlin*, 71, 327-340.

Fürsch, H. (1996) Taxonomy of coccinellids. *Coccinella,* 6, 28-30.

Gage, J. (1920) The larvae of the Coccinellidae. *Illinois Biological Monographs*, 6(4), 1-63.

Goloboff, P., S. Farris, and K. Nixon. (2000) TNT (Tree analysis using New Technology) (BETA) ver. xxx Published by the authors, Tucumán, Argentina.

Gordon, R. D. (1972) The tribe Noviini in the New World (Coleoptera: Coccinellidae). *Journal of the Washington Academy of Sciences*, 62(1), 23-31.

Gordon, R. D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society,* 93, 654-678.

Hagen, K. B. (1962) Biology and ecology of predaceous Coccinellidae. *Annual Review of Entomology*, 7, 289-326.

Hagen, K. S., Bombosch, S., and McMurtry, J. A. (1976) The biology and impact of predators. *In:* P. S. M. C. B. Huffaker (Eds), *Theory and Practice of Biological Control*. Academic Press, New York, 788 pp.

Hoang, D. N. (1980) Môt só loài bo rùa mói thuôc phân ho Coccidulinae (Coccinellidae, Coleoptera) ó Viêt Nam. *Tap chi Sinh Vat Hoc*, 2, 8-13.

Hodek, I. (1973) *Biology of Coccinellidae*. Academia, Prague, 266 pp.

Honěk, A. (1996) Variability and Genetic Studies. *In:* I. Hodek and I. Honěk (Eds.) *Ecology of Coccinellidae.* Kluwer Academic Publishers, Dordrecht, 464 pp.

Hodges, G. (2008) Pest Alert: *Crypticerya genistae* (Hemiptera: Monophlebidae), a new exotic scale insect for Florida. *Pest Alert,* 1-3.

Howard, L. O. (1889) Notes and descriptions of a few injurious farm and fruit insects of South Africa, 90-92.

Howarth, F. G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology,* 36, 485-509.

Iperti, G. (1999) Biodiversity of predeaceous Coccinellidae in relation to bioindication and economic importance. *Agriculture, Ecosystems, and Environment,* 74, 323-342.

Kamiya, H. (1964) Comparative morphology of larvae of the Japanese Coccinellidae, with special reference to the tribal phylogeny of the family (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science*, 14, 83-100.

Kapur, A. (1949) On the Indian species of *Rodolia* Mulsant (Coleoptera: Coccinellidae). *Bulletin of Entomological Research*, 39, 531-538.

Kenis, M., Roy, H. E., Zindel, R., and Majerus, M. E. N. (2008) Current and potential management strategies against *Harmonia axyridis*. *BioControl,* 53, 235-252.

King, A. G. and Meinwald, J. (1996) Review of the defensive chemistry of coccinellids. *Chemical Reviews*, 96, 1105-1122.

Korschefsky, R. (1931) Pars 118, Coccinellidae I. *In*: *Coleoptorum Catalogus*, vol. 16, pp. 1-224.

Korschefsky, R. (1937) Zwei neue *Novius*-Arten von den Canaren. *Societas Scientiarum Fennica. Commentationes Biologicae,* 6, 1-3.

Kovár, I. (1996). Phylogeny. *In:* I. Hodek and I. Honěk (Eds.) *Ecology of Coccinellidae.* Kluwer Academic Publishers, Dordrecht, 464 pp.

Kuznetsov, V. N. (1997) *Lady beetles of the Russian Far East. Memoir No. 1, Center for Systematic Entomology.* Sandhill Crane Press, Gainesville. 248 pp.

Latreille, P. A. (1804) *Histoire Naturelle, genérale et particuliere, des Crustacés et des Insectes. Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et partie du Cours complet* *d'Histoire naturelle rédigé par C. S. Sonnini, member de plusieurs Sociétes savants. Tome douzième*. F. Dufart, Paris, 424 pp.

Latreille, P. A. (1807) *Genera Crustaceorum et Insectorum secundum ordinem naturalem in families disposita, iconibus exemplisque plurimis explicate. Tomus tertius.* A. Koenig, Parisilis et Argentorati, 258 pp.

Lea, A. M. (1901) Descriptions of new species of Australian Coleoptera. *Proceedings of the Linnaean Society of New South Wales*, 36, 448-513.

Leeper, J. R. (1976) A Review of the Hawaiian Coccinellidae. *Proceedings of the Hawaiian Entomological Society,* 22, 279-306.

LeSage, L. (1991) Coccinellidae (Cucujoidea), the lady beetles, ladybirds. Pp. 485-494. *In*: F. W. Stehr, ed. Immature Insects. Vol. 2. Kendall/Hunt. Dubuque, Iowa.

Lewis, G. (1879) On certain new species of Coleoptera from Japan. *The Annals and Magazine of Natural History*, 4, 29-33.

Lewis, G. (1896) On the Coccinellidae of Japan. *Annals and Magazine of Natural History*, 17, 23-41.

Majerus, M. E. N. (1994) *Ladybirds.* Harper Collins, London. 367 pp.

Mendel, Z., Assael, F., Zeidan, S., and Zehavi, A. (1998) Classical biological control of Palaeococcus fuscipennis (Burmeister) (Homoptera: Margarodidae) in Israel. *Biological Control,* 12, 151-157.

Motschoulsky, V. (1866) Essai d'un catalogue des insectes de l'ile de Ceylan. Supplement. *Bulletin de la Societe Imperiale des Naturalistes de Moscou*, 39, 393-446.

Mulsant, M. E. (1846) Histoire naturelle des Coleopteres de France: Sulcicolles- Securipalpes. Paris, 280 pp.

Mulsant, M. E. 1850. Species de Coleopteres trimeres securipalpes. *Annales des Societe d'Agriculture, d'Histoire Naturelle et Arts Utiles de Lyon,* 2, 1-1104.

Nakamura, M. (1980) The pupae of some Japanese lady beetles, with reference to the phylogeny of the subfamily (Coleoptera: Coccinellidae). *New Entomologist,* 29(4), 15-25.

Nixon, K. C. (1999-2002) WinClada ver. 1.0000 Published by the author, Ithaca, NY, USA.

Olliff, M.S. (1895) Entomological notes-A friendly new ladybird. *Agricultural Gazette of New South Wales*, 6, 30-31.

Pasteels, J. M. (2007) Chemical defence, offence and alliance in ants-aphids-ladybirds relationships. *Population Ecology*, 49(1), 5-14.

Philologos (2007) On Language: The Adorable Moses Cow. *The Jewish Daily Forward*.

Phuoc, D. T. and Stehr, F. W. (1974) Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions of the American Entomological Institute* 10: 31-123.

Poorani, J. (2002) An annotated checklist of the Coccinellidae (Coleoptera) (Excluding Epilachninae) of the Indian subregion. *Oriental Insects* 36: 307-383.

Pope, R. D. (1979) Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology,* 4, 171-196.

Quezada, J. R. & DeBach, P. (1973) Bioecological studies of the cottony cushion scale, *Icerya purchasi* Mask., and its natural enemies, *Rodolia cardinalis* Mulsant and *Cryptochaetum iceryae* Will., in Southern California. *Hilgardia* 41, 631-688.

Raimundo, A. C. (1978) Contribuicao para o conhecimento dos coccinelideos de Angola - I. *Garcia de Orta; Serie de zoologia,* 4, 23-40.

Redtenbacher, L. (1843) *Abbildungen und Beschreibungen neuer und seltner Thiere und Pflanzen, in Syrien und im westlichen Taurus gesammelt von Th. Kotschy*. Schweizerbart, Stuttgart, 254 pp.

Rees, B. E. (1947) Taxonomy of the larvae of some North American Noviini (Coleoptera, Coccinellidae). *The Pan-Pacific Entomologist*, 23, 113-119.

Ricci, C. (1986) Seasonal food preferences and behaviour of *Rhizobius littura*. *In*: I. Hodek (Ed.) *Ecology of Aphidophaga 2*. Junk, The Hague, pp. 119-123.

Robertson, J. A., Whiting, M. F., and McHugh, J. V. (2008) Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea) *Molecular Phylogenetics and Evolution*, 46, 193 - 205.

Samways, M. J., Osborn, R., and Saunders, T. L. (1997) Mandible form relative to the main food type in ladybirds (Coleoptera: Coccinellidae). *Biocontrol Science and Technology*, 7, 275-286.

Sasaji, H. (1968a) Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia, Fukui*, 35, 1-37.

Sasaji, H. (1968b) Description of the coccinellid larvae of Japan and the Ryukus (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science* 18: 93-135.

Savoiskaya, G. I. and B. Klausnitzer (1973) Morphology and taxonomy of the larvae with keys for their identification. *In:* I. Hodek (Eds), *Biology of Coccinellidae*. Dr. W. Junk N. V. Prague, 36-55.

Sicard, A. (1909). Description d'une nouvelle espèce de Coccinellide d'Afrique. *Bulletin de la Societe Entomologique de France*, 112-113.

Sicard, A. (1931) Descriptions d'espèces nouvelles appartenant á la famile des Coccinellides (Coleoptera). *Annals and Magazine of Natural History*, 8, 228-234.

4, S. A. (2007) *Australian Ladybird Beetles (Coleoptera: Coccinellidae): Their Biology and Classification.* ABRS, Canberra. 286 pp.

Stebbing, E. P. (1904) On the life history of *Vedalia guerinii* Crotch, predaceous upon *M. stebbingi* Green. *The Journal of the Linnaean Society of London*, 24, 155-161.

Stebbing, E. P. (1914) *Indian Forest Insects of Economic Importance: Coleoptera*. J. K. Jain Brothers, Bhopal. 648 pp.

Stoehr, A. M. (2006) Costly melanin ornaments: the importance of taxon? *Functional Ecology*, 20, 276-281.

Unruh, C. M. and Gullan, P. (2008) Molecular data reveal convergent reproductive strategies in Iceryine scale inscts (Hemiptera: Coccoidea: Monophlebidae), allowing the re-interpretation of morphology and a revised generic classification. *Systematic Entomology,* 33, 8-50.

Vandenberg, N. J. (2002) Coccinellidae. *In:* P. E. S. Michael C. Thomas, J. Howard Frank (Eds), *American Beetles Vol. II: Scarabaeoidea through Curculionoidea*. CRC Press New York, 371-389.

Verhoeff, C. (1895) Beitrage zur vergleichenden Morphologie des Abdomens der Coccinelliden. *Archiv für Naturgeschichte*, 61, 1-80.

Weise, J. (1885) *Bestimmungs-Tabellen der Eeuropaischen Coleopteren. II. Heft. Coccinellidae. II. Auflage mit Berucksichtigung der Arten aus dem Nordlichen Asien*. Mdling, 83 pp.

Weise, J. (1892) Les Coccinellides du Chota-Nagapore. *Annales de la Societe Entomologique de Belgique*, 36, 19-27.

Weise, J. (1895) Uber die mit *Novius* Mulsant. *Annales de la societe Entomologique de Belgique*, 39, 147-151.

Weise, J. (1898) Coccinelliden aus Usambara. *Annales de la Societe Entomologique de Belgique*, 98, 191-201.

Weise, J. (1901) Contribution a l'etude de la faune entomologique de Sumatra. *Annales de la Societe Entomologique de Belgique*, 45, 91-96.

Weise, J. (1905) Ueber Chrysomeliden und Coccinelliden aus Rhodesia. *Deutsche Entomologische Zeitschrift*, 1905, 321-336.

Weise, J. (1912) Coccinellidae. *Wiss. Ergebnisse d. D. Zentral Afrika Exp., Bd. 4, Lfg. 3. Leipzig*, 43-52.

Weise, J. (1916) Results of Dr. E. Mjoberg's Swedish Scientific Expedition to Australia 1910-1913, II. Chrysomeliden und Coccinelliden aus West-Australien. *Arkiv for Zoologi Utgifvet af k. Svenska Vetenskapsakademien*, 10, 1-51.

Weise, J. (1922) Ueber einige amerikanische und australische, nach Südfrankreich eingeführte Coccinelliden. *Wiender Entomologische Zeitung*, 34, 104.

Figure Legends

Table 4.1. Matrix of adult morphological characters.

Figure 4.1. Strict consensus of 3240 most parsimonious trees. L = 122; CI = 31; RI = 43. Bremer support values greater than 5 are shown beneath the node.

Figures 4.2 - 4.7. Habitus, dorsal. **4.2.** *R. alluandi*. Sicard. **4.3.** *R. andamanica* Weise. **4.4.** *R. argodi* Sicard. **4.5.** *R. bella* (Blackburn). **4.6.** *R. cardinalis* (Mulsant). **4.7.** *R. cinctipennis* Weise.

Figures 4.8 - 4.13. Habitus, dorsal. **4.8.** *R. limbata* (Motschulsky). **4.9.** *R. fumida* Mulsant. **4.10.** *R. conicollis* (Korschefsky). **4.11.** *R. cruentata* (Mulsant). **4.12.** *R. occidentalis* Weise. **4.13.** *R. podagrica* Weise.

Figures 4.14 - 4.21. Type specimen labels. **4.14.** *N. bellus* Blackburn. **4.15.** *N. limbatus* Blackburn. **4.16.** *N. lindi* Blackburn. **4.17.** *N. simplicipennis* Blackburn. **4.18.** *R. cinctipennis* Weise. **4.19.** *R. insularis* Weise. **4.20.** *R. punctigera* Weise. **4.21.** *R. pumila* Weise

Figures 4.22 - 4.28. Type specimen labels. **4.22.** *R. guerini* Korschefsky. **4.23.** *R. quadrimaculata* Korschefsky. **4.24.** *R. podagrica* Weise. **4.25.** *R. senegalensis* Weise. **4.26.** *N. tridens* Lea. **4.27.** *R. 6-maculata* Korschefsky. **4.28.** *N. conicollis* Korschefsky.

Figures 4.29 - 4.32. Head capsules, dorsal and ventral. **4.29.** Head capsule, dorsal: *R. andamanica* Weise. **4.30** Head capsule, ventral: *R. cruentata* (Mulsant). **4.31.** Head capsule, dorsal: *R. rubea* Mulsant. **4.32.** Head capsule, ventral: *R. rubea* Mulsant.

Figures 4.33 - 4.37. Left antenna, dorsal. **4.33.** *R. fumida* Mulsant. **4.34.** *R. podagrica* Weise. **4.35.** *R. rubea*. **Figures 4.36, 4.37.** Labrum, dorsal. **4.36.** *R. podagrica* Weise. **4.37.** *R. rubea* (Mulsant).

Figures 4.38 - 4.41. Left and right mandibles, dorsal. **4.38, 4.39.** *R. cruentata* (Mulsant). **4.40, 4.41.** *R. limbata* (Motschulsky).

Figures 4.42 - 4.45. Left and right mandibles, dorsal. **4.42, 4.43.** *R. fumida* Mulsant. **4.44, 4.45.** *R. rubea* Mulsant.

Figures 4.46, 4.47. Left maxilla, dorsal. **4.46.** *R. fumida* Mulsant. **4.47.** *R. rubea* Mulsant.

Figures 4.48 - 4.50 . Pronota, scutellum. **4.48.** Pronotum: *R. cruentata* (Mulsant). **4.49.** Pronotum: *R. koebelei* (Gordon). **4.50.** Scutellum: *R. rubea* Mulsant.

Figures 4.51 - 4.53. Prosterna. **4.51.** *R. alluandi* Sicard. **4.52.** *R. andamanica* Weise. **4.53.** *R. argodi* Sicard.

Figures 4.54 - 4.56. Prosterna. **4.54.** *R. cruentata* (Mulsant). **4.55.** *R. limbata* (Motschulsky). **4.56.** *R. fumida* Mulsant

Figures 4.57 - 4.59. Prosterna. **4.57.** *R. koebelei* (Gordon). **4.58.** *R. nigra* Fürsch. **4.59.** *R. podagrica* Weise

Figures 4.60 - 4.61. Prosterna. **4.60.** *R. pumila* Weise. **4.61.** *R. rubea* Mulsant.

Figures 4.62 - 4.66. Left prothoracic leg, posterior. **4.62.** *R. andamanica* Weise. **4.63.** *R. limbata* (Motschulsky). **4.64.** *R. fumida* Mulsant. **4.65.** *R. pumila* Weise. **4.66.** *R. rubea* Mulsant.

Figures 4.67 - 4.68. Abdomen, ventral. **4.67.** *R. alluandi* Sicard. **4.68.** *R. cruentata* (Mulsant).

Figures 4.69 - 4.74. Male genitalia, dorsal and lateral. **4.69.** Aedeagus, dorsal: *R. andamanica* Weise. **4.70.** Aedeagus., lateral: *R. andamanica* Weise. **4.71.** Sipho, lateral: *R. andamanica* Weise. **4.72.** Aedeagus, dorsal: *R. argodi* Sicard. **4.73.** Aedeagus, lateral: *R. argodi* Sicard. **4.74.** Sipho, lateral: *R. argodi* Sicard.

Figures 4.75 - 4.80. Male genitalia, dorsal and lateral. **4.75.** Aedeagus, dorsal: *R. bella* (Blackburn). **4.76.** Aedeagus, lateral: *R. bella* (Blackburn). **4.77.** Sipho, lateral: *R. bella* (Blackburn). **4.78.** Aedeagus, dorsal: *R. cruentata* (Mulsant). **4.79.** Aedeagus, lateral: *R. cruentata* (Mulsant). **4.80.** Sipho, lateral: *R. cruentata* (Mulsant).

Figures 4.81 - 4.83. Male genitalia, dorsal and lateral. **4.81.** Aedeagus, dorsal: *R. limbata* (Motschulsky) **4.82.** Aedeagus, lateral: *R. limbata* (Motschulsky). **4.83.** Sipho, lateral: *R. limbata* (Motschulsky).

Figures 4.84 - 4.86. Male genitalia, dorsal and lateral. **4.84.** Aedeagus, dorsal: *R. fumida* Mulsant. **4.85.** Aedeagus, lateral: *R. fumida* Mulsant. **4.86.** Sipho, lateral: *R. fumida* Mulsant.

Figures 4.87 - 4.93. Male genitalia, dorsal and lateral. **4.87.** Aedeagus, dorsal: *R. koebelei* (Gordon). **4.88.** Sipho, lateral: *R. koebelei* (Gordon). **4.89.** Aedeagus, dorsal: *R. lindi* (Blackburn). **4.90.** Sipho, lateral: *R. lindi* (Blackburn). **4.91.** Aedeagus, dorsal: *R. nigra* Fürsch. **4.92 .** Aedeagus, lateral: *R. nigra* Fürsch. **4.93.** Sipho, lateral: *R. nigra* Fürsch.

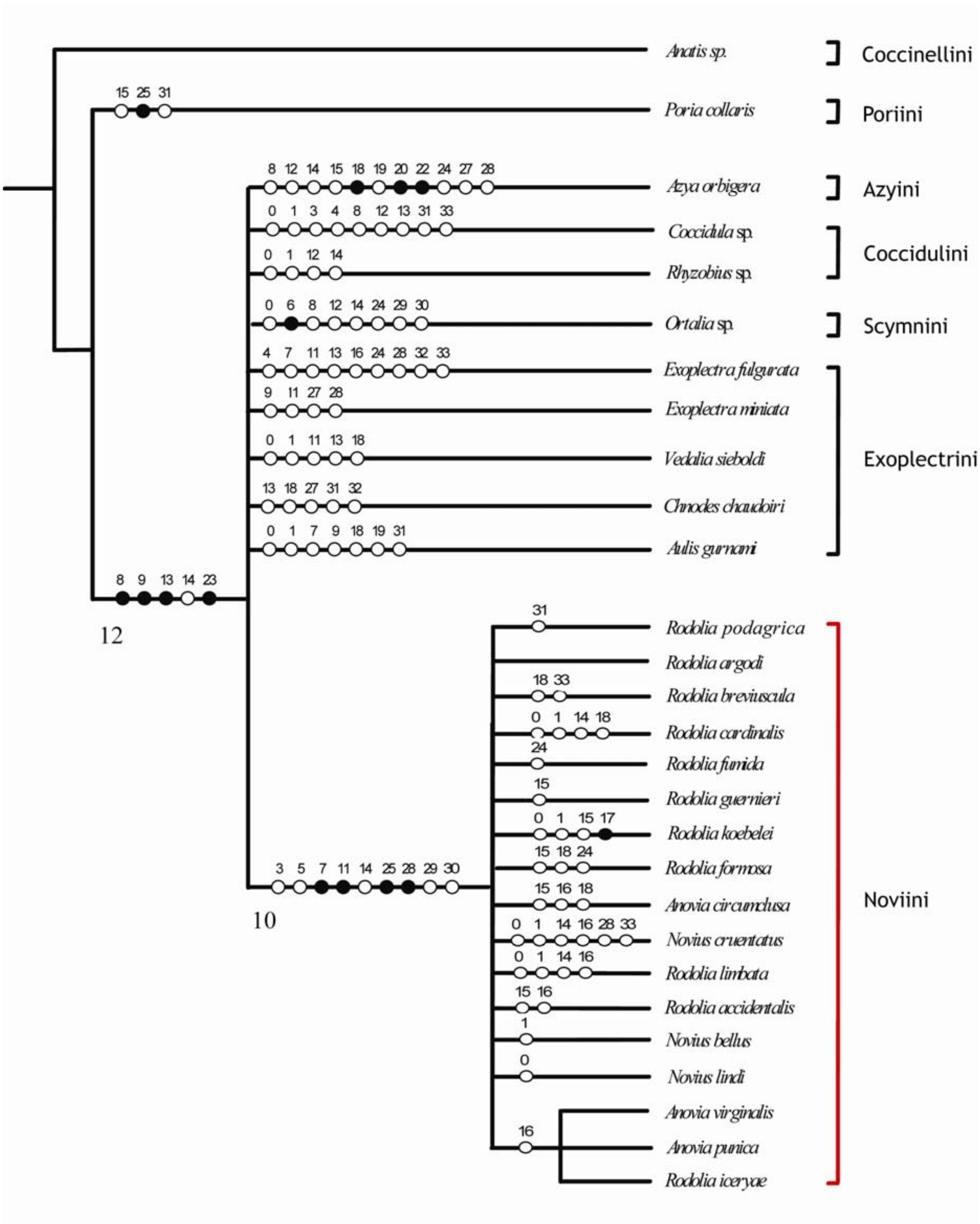
Figures 4.94 - 4.96. Male genitalia, dorsal and lateral. **4.94.** Aedeagus, dorsal: *R. occidentalis* Weise. **4.95.** Aedeagus, lateral: *R. occidentalis* Weise. **4.96.** Sipho, lateral: *R. occidentalis* Weise.

Figures 4.97 - 4.99. Male genitalia, dorsal and lateral. **4.97.** Aedeagus, dorsal: *R. pumila* Weise. **4.98.** Aedeagus, lateral: *R. pumila* Weise. **4.99.** Sipho, lateral: *R. pumila* Weise.

Figures 4.100 - 4.102. Male genitalia, dorsal and lateral. **4.100.** Aedeagus, dorsal: *R. rubea* Mulsant. **4.101.** Aedeagus, lateral: *R. rubea* Mulsant. **4.102.** Sipho, lateral: *R. rubea* Mulsant.

Table 4.1. Character matrix based on adult morphological data. Missing characters are coded as a ?.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Anatis sp.	0	0	0	0	0	0	0	2	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	0	1	1	1	0
Azya orbigera	0	0	1	0	1	1	0	2	1	0	0	1	1	1	0	0	0	0	2	0	0	1	1	0	0	0	1	1	2	0	0	1	1	0
Poria collaris	0	0	1	0	1	1	0	2	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0
Rhyzobius sp.	1	1	1	0	1	1	0	2	0	0	0	1	1	1	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0
Ortalia sp.	1	0	1	0	1	1	1	2	1	0	0	1	1	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0
Coccidula sp.	1	1	1	1	0	1	0	2	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	1	1
Exoplectra fulgurata	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	1	0	2	0	0	1	0	1
Exoplectra miniata	0	0	1	0	1	1	0	2	0	1	0	0	0	1	1	1	0	0	1	1	1	1	0	0	1	0	1	1	2	0	0	1	1	0
Vedalia sieboldi	1	1	1	0	1	1	0	2	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0
Chnodes chaudoiri	0	0	1	0	1	1	0	2	0	0	0	?	0	0	1	1	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0
Aulis gurnami	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0
Rodolia amabilis	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	1	1	0	0	1	2	1	0	1	1	1	0	1	0
Rodolia argodi	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia breviuscula	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	0	0	0	1	1	1	0	0	1	2	1	0	1	1	1	1	1	1
Rodolia cardinalis	1	1	1	1	1	0	0	0	0	0	0	2	0	1	1	1	0	0	0	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia fumida	0	0	1	1	1	0	0	0	0	0	0	?	0	1	0	1	0	0	1	1	1	1	0	0	0	2	1	0	1	1	1	1	1	0
Rodolia guernieri	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia koebelei	1	1	1	1	1	0	0	0	0	0	0	?	0	1	0	0	0	1	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia formosa	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	2	1	0	1	1	1	1	1	0
Anovia circumclusa	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	0	1	0	0	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Anovia virginalis	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Novius cruentatus	1	1	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	0	1	1	1	1	0	0	1	2	1	0	0	1	1	1	1	1
Rodolia limbata	1	1	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Anovia punica	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia occidentalis	0	0	1	1	1	0	0	0	0	0	0	?	0	1	0	0	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Rodolia iceryae	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	0
Novius bellus	0	1	1	1	1	0	0	0	0	0	0	?	0	1	0	1	0	0	1	1	1	1	0	0	1	2	1	0	?	1	1	1	1	0
Novius lindi	1	0	1	1	1	0	0	0	0	0	0	?	0	1	0	1	0	0	1	1	1	1	0	0	1	2	1	0	?	1	1	1	1	0


Anatis sp.
Coccinellini
15 25 31
Poria collaris
Poriini
8 12 14 15 18 19 20 22 24 27 28
Azya orbigera
Azyini
0 1 3 4 8 12 13 31 33
Coccidula sp.
0 1 12 14
Rhyzobius sp.
Coccidulini
0 6 8 12 14 24 29 30
Ortalia sp.
Scymnini
4 7 11 13 16 24 28 32 33
Exoplectra fulgurata
9 11 27 28
Exoplectra miniata
0 1 11 13 18
Vedalia sieboldi
Exoplectrini
13 18 27 31 32
Chnodes chaudoiri
0 1 7 9 18 19 31
Aulis gurnami
8 9 13 14 23
12
31
Rodolia podagrica
Rodolia argodi
18 33
Rodolia breviuscula
0 1 14 18
Rodolia cardinalis
24
Rodolia fumida
15
Rodolia guernieri
0 1 15 17
Rodolia koebelei
15 18 24
Rodolia formosa
3 5 7 11 14 25 28 29 30
15 16 18
Anovia circumclusa
Noviini
10
0 1 14 16 28 33
Novius cruentatus
0 1 14 16
Rodolia limbata
15 16
Rodolia accidentalis
1
Novius bellus
0
Novius lindi
Anovia virginalis
16
Anovia punica
Rodolia iceryae

4.1

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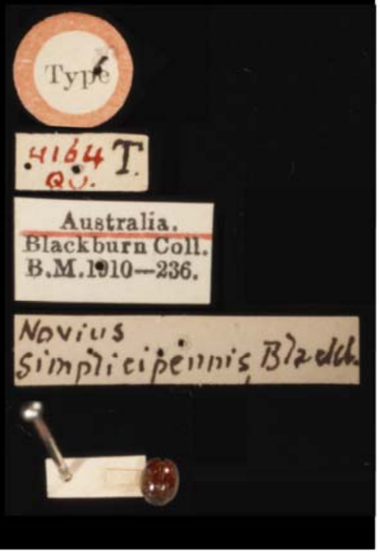

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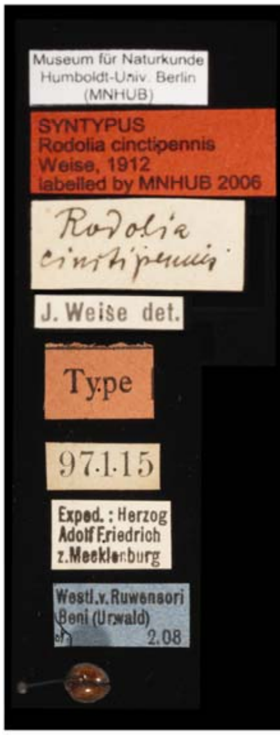

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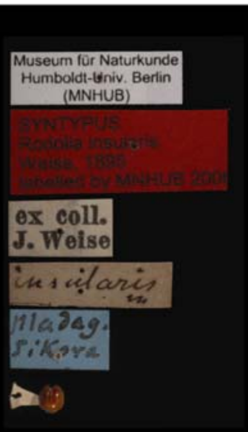

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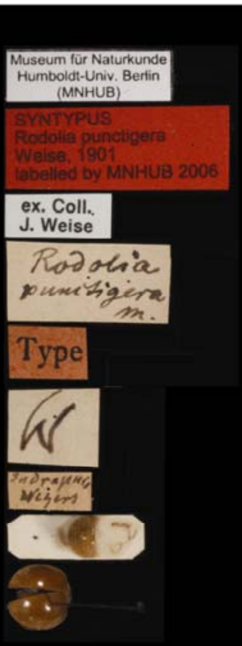

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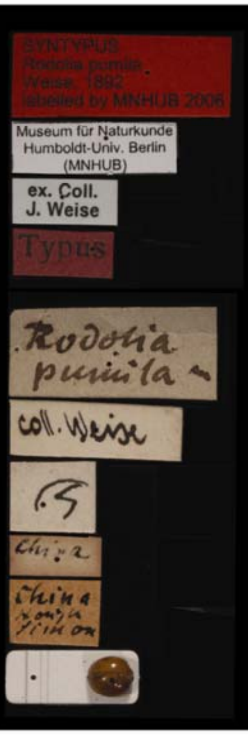

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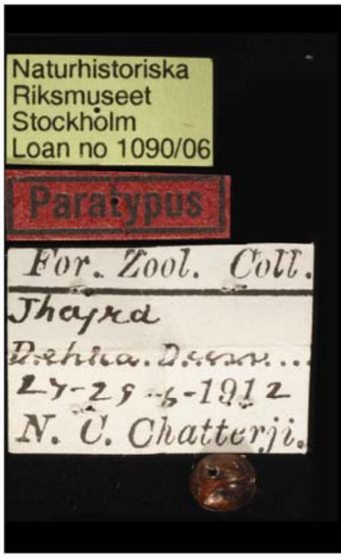

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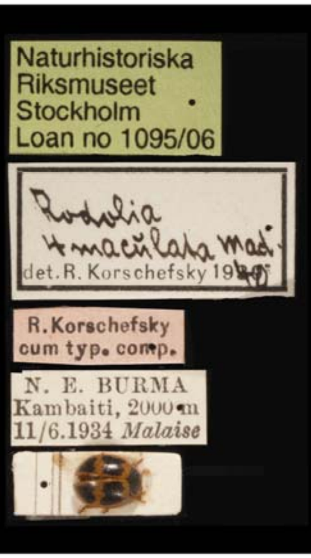

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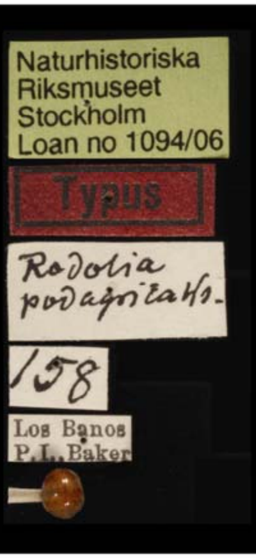

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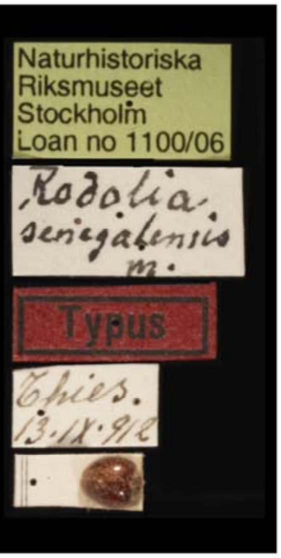

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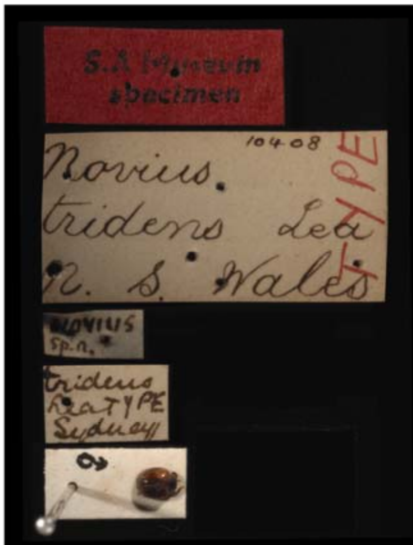

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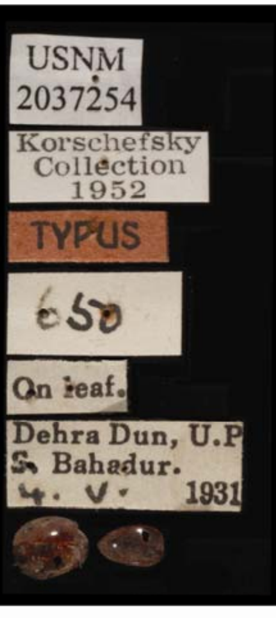

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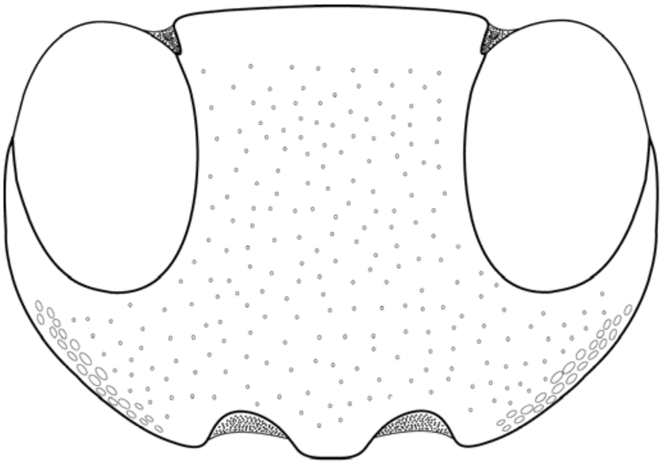

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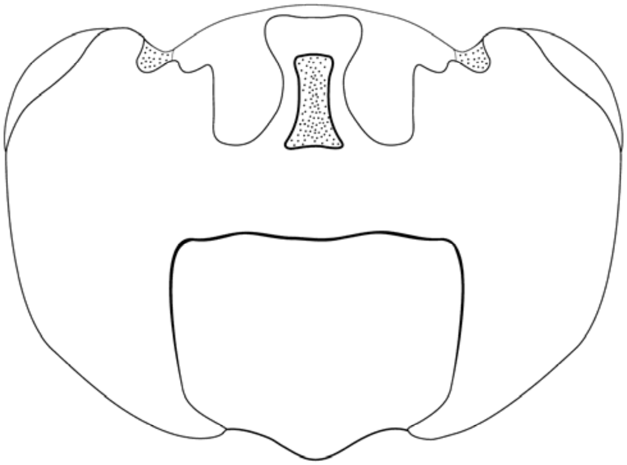

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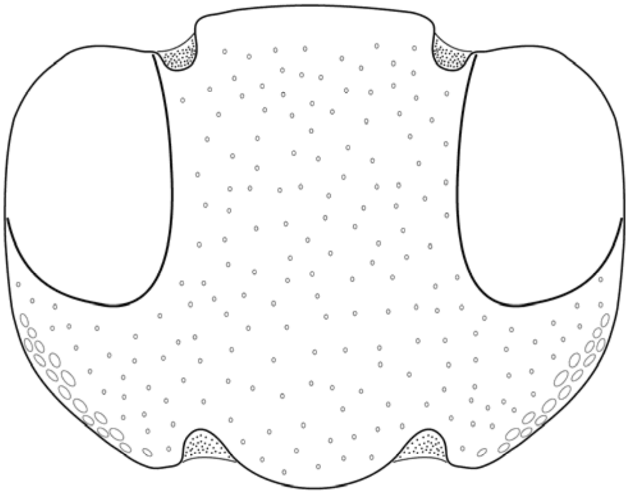

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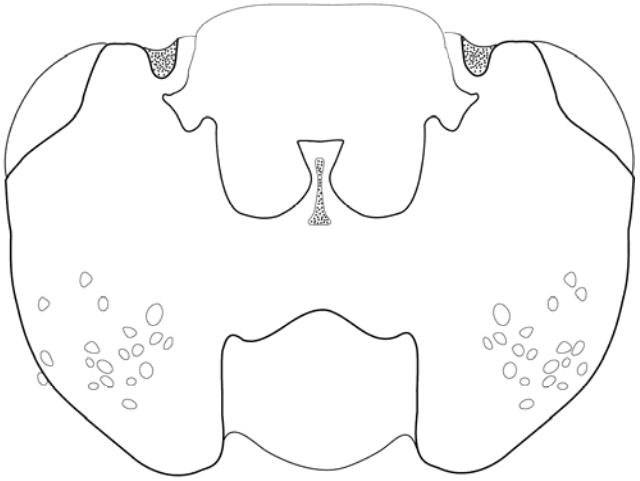

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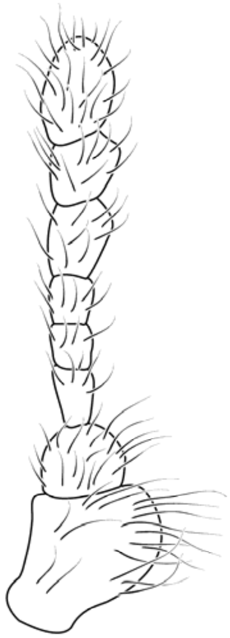
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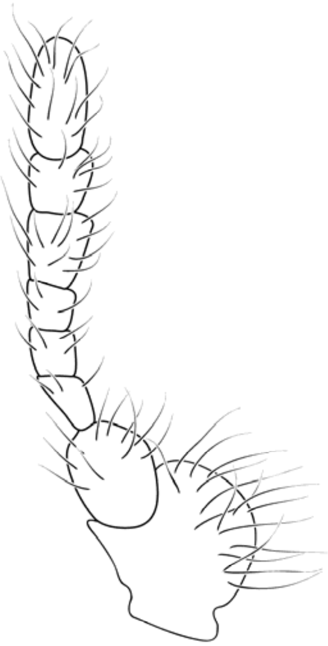
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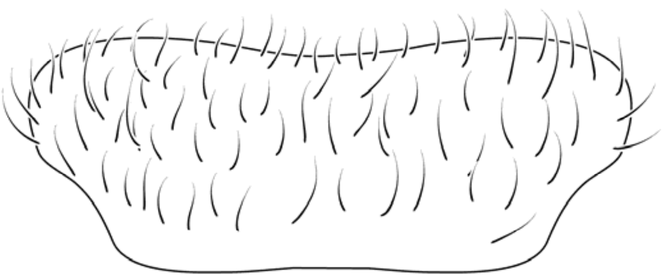
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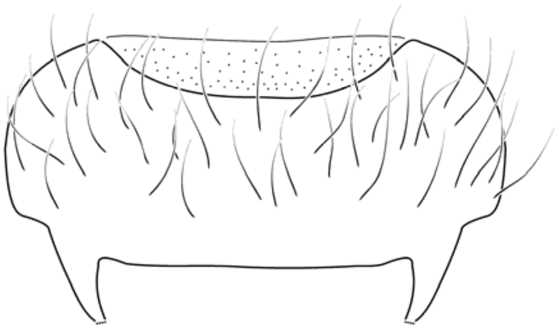
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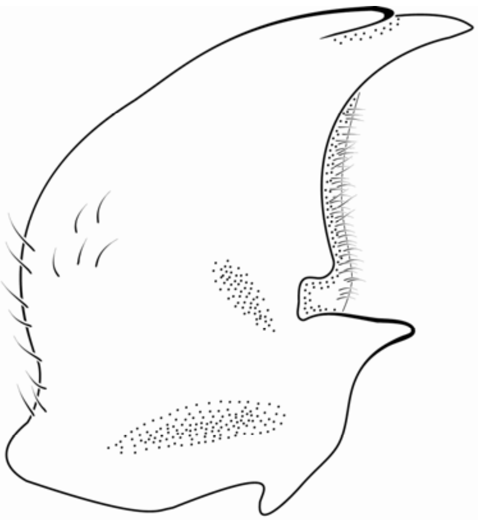

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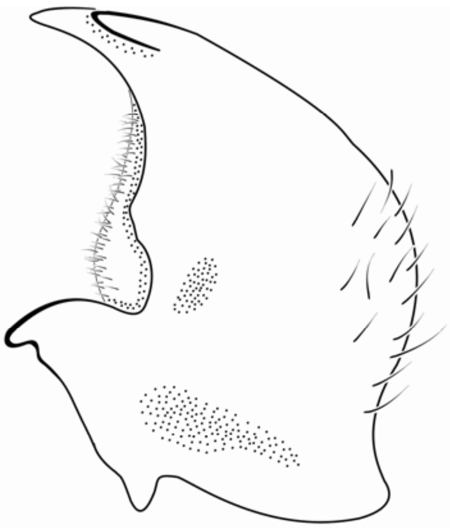

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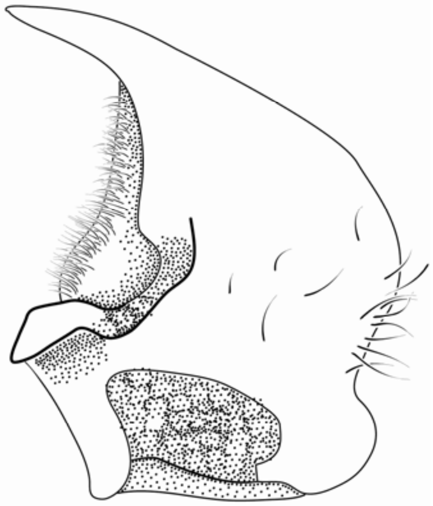

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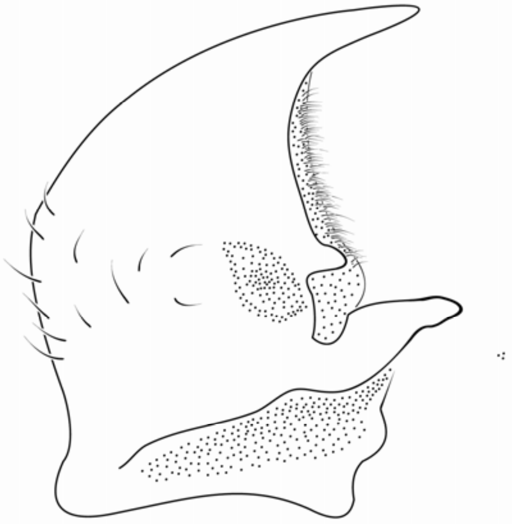

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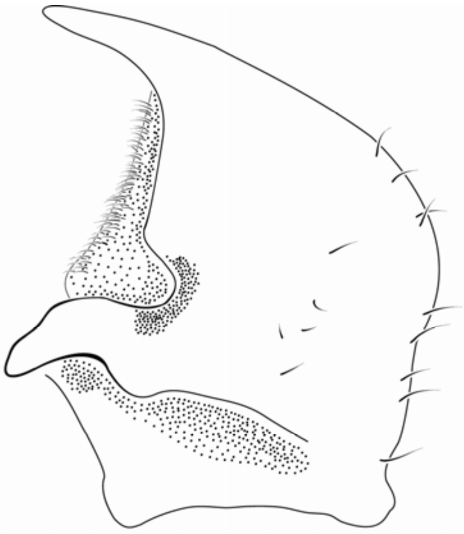

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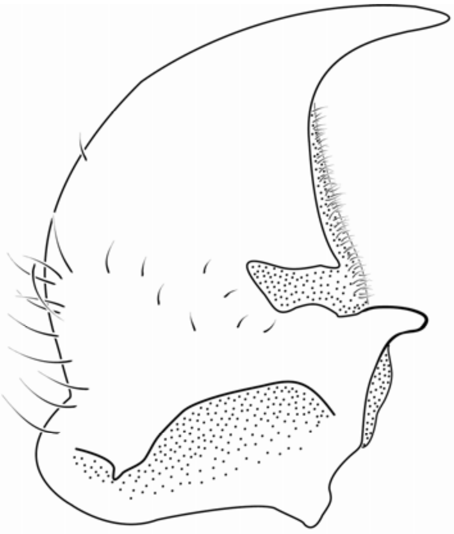

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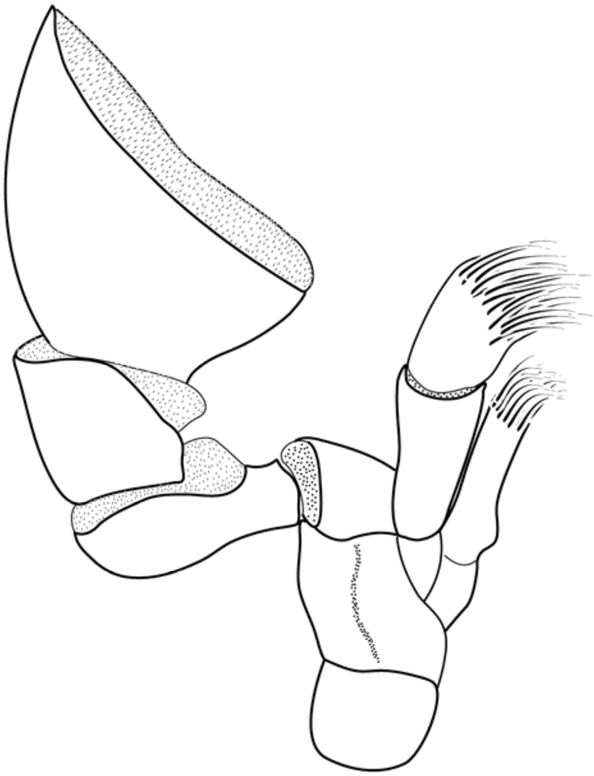

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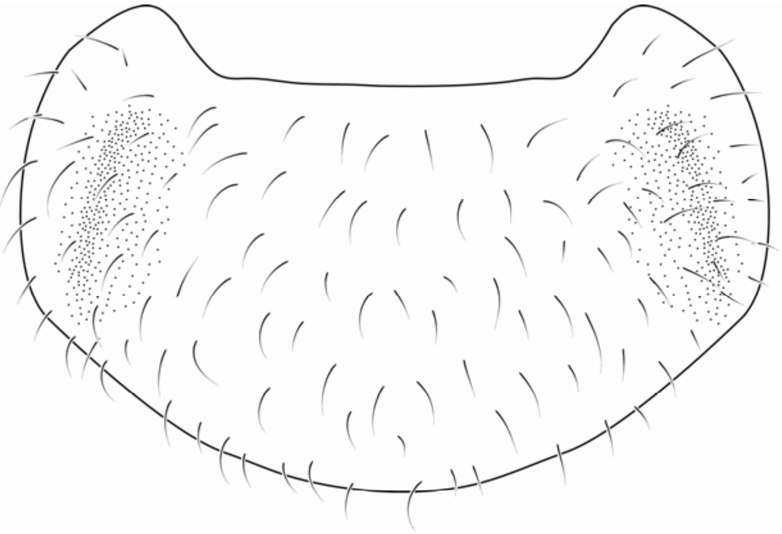

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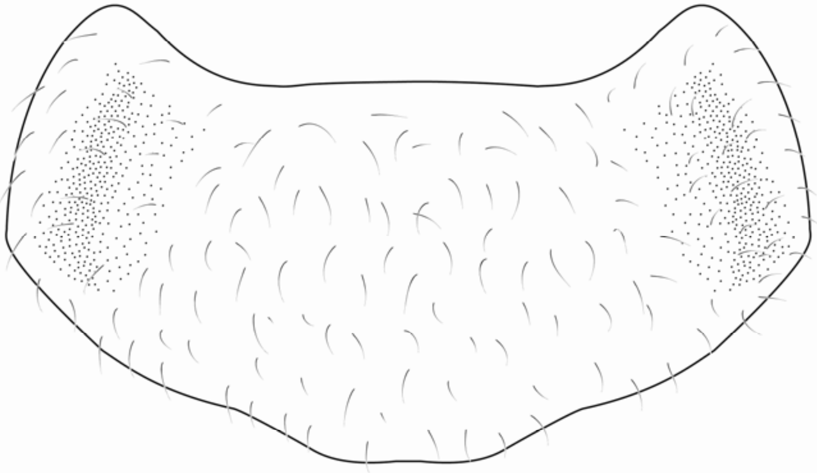

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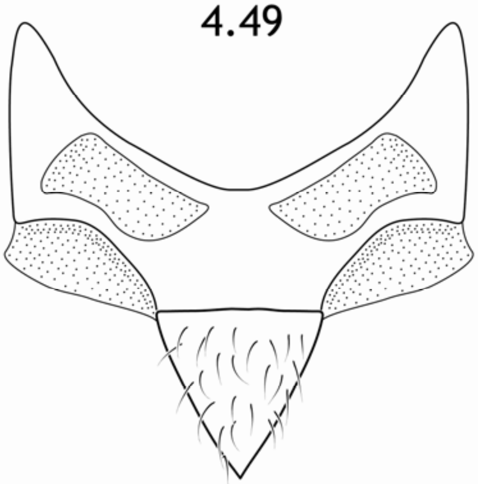

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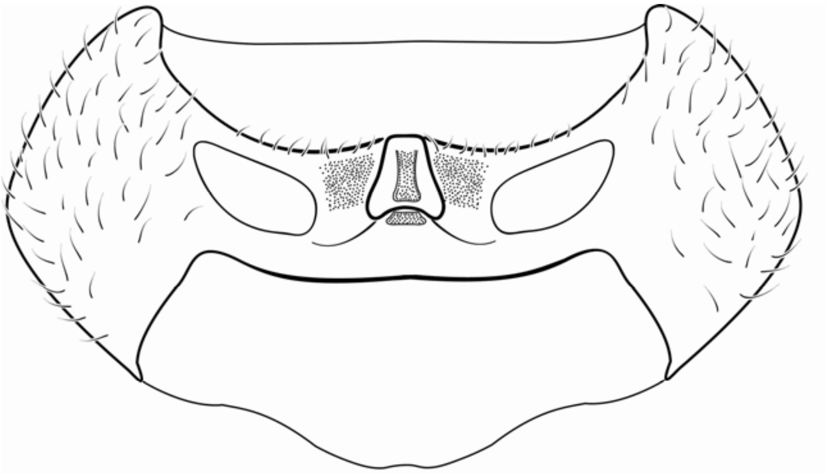

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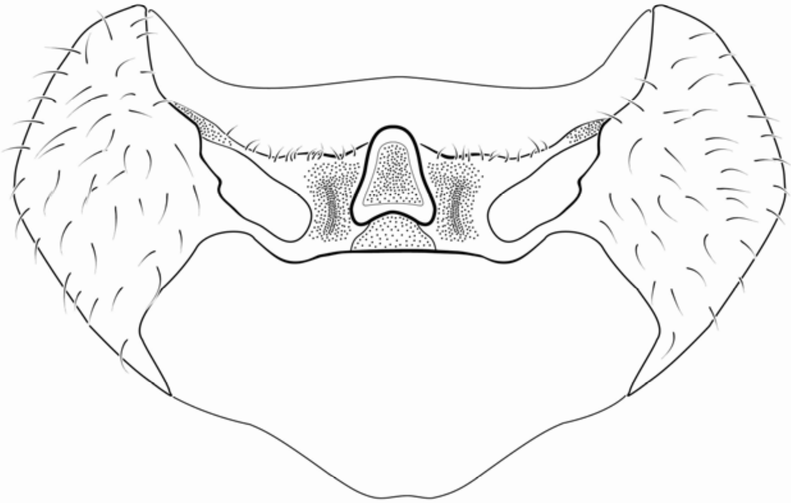

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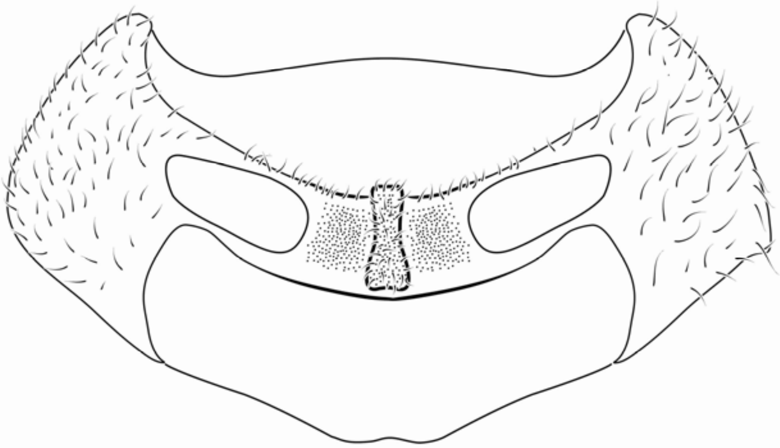

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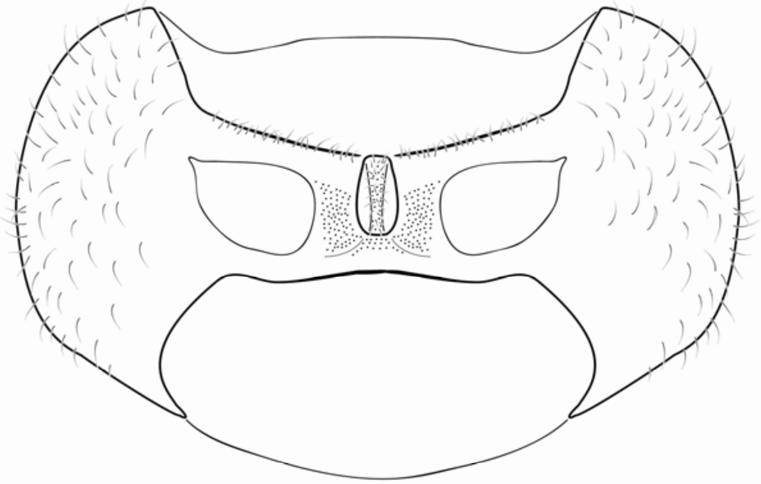

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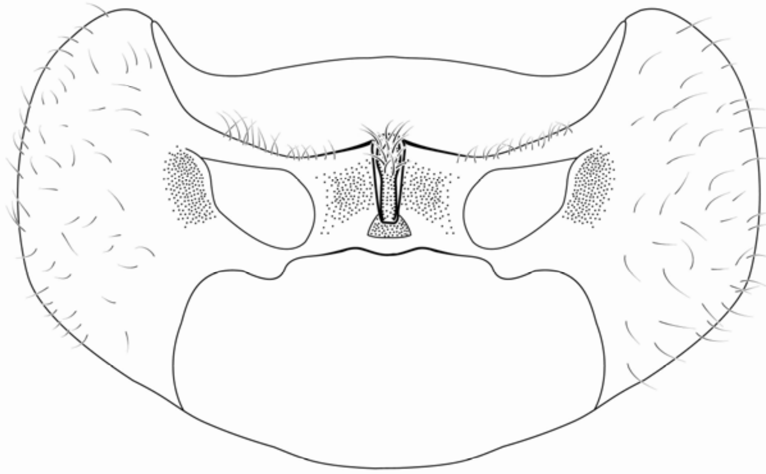

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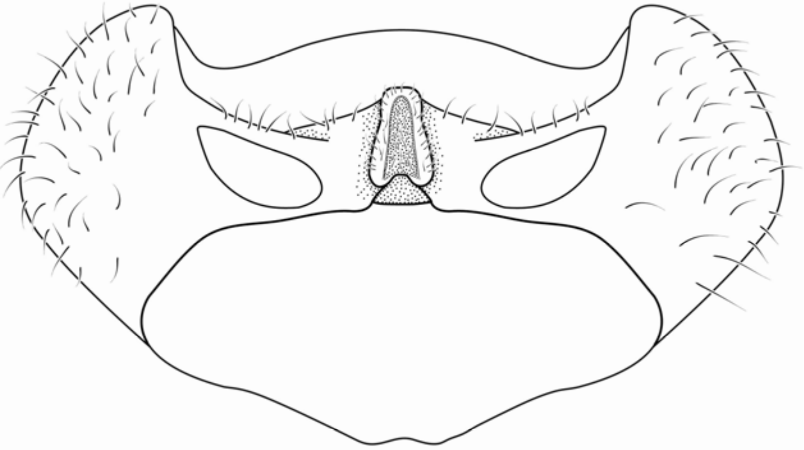

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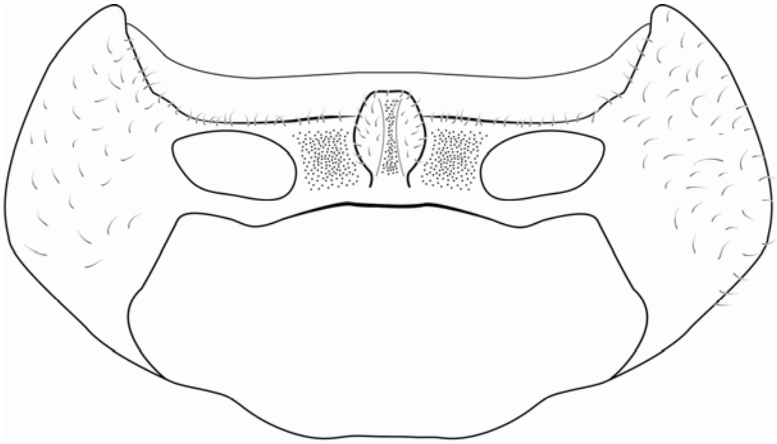

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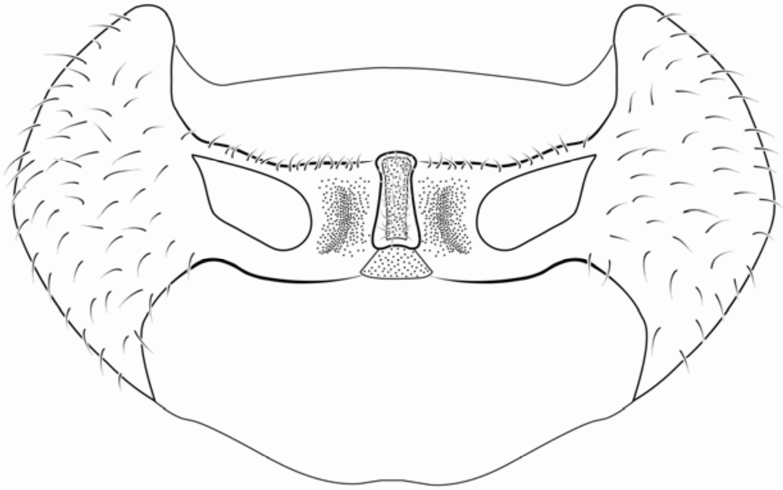

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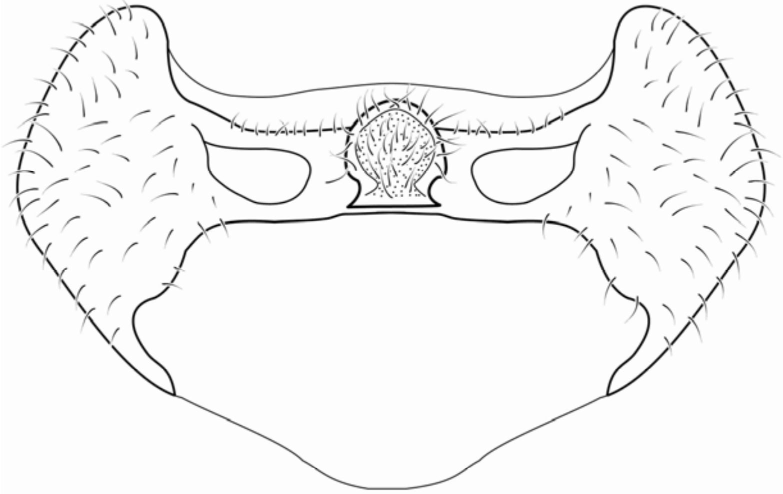

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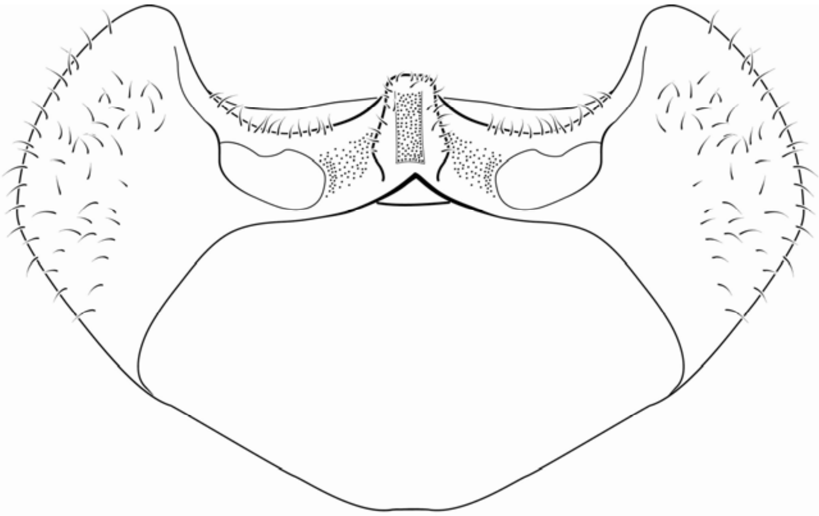

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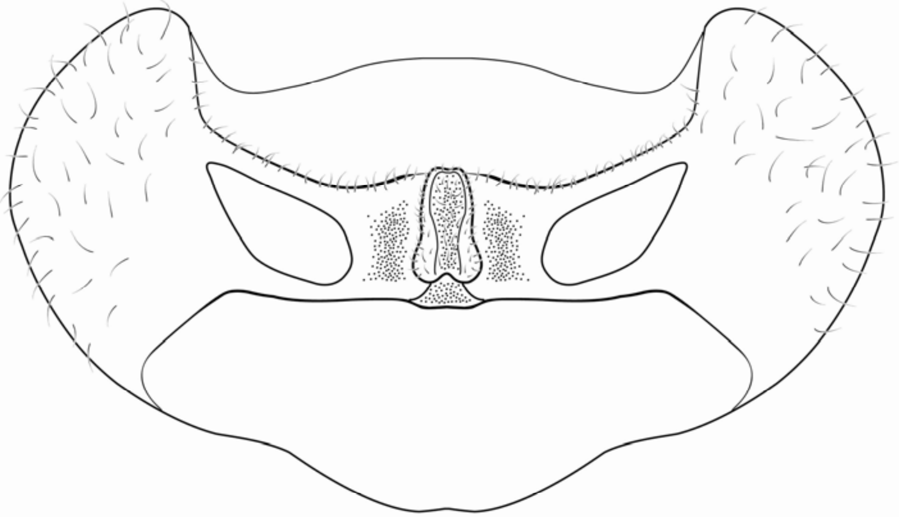

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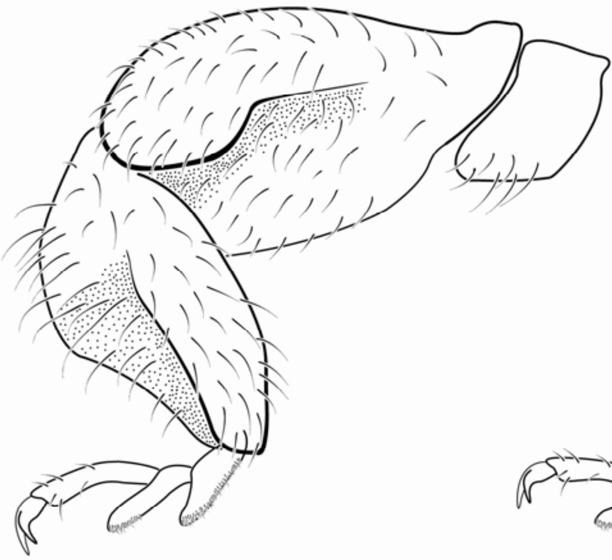

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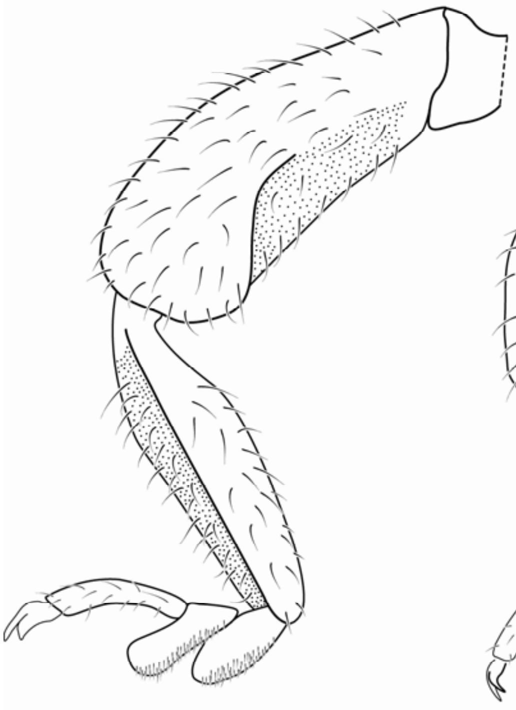

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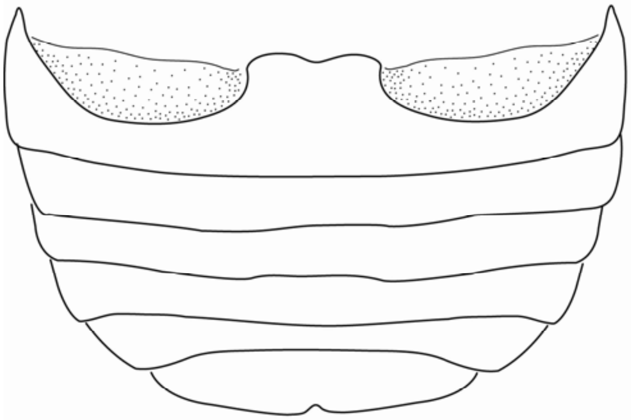

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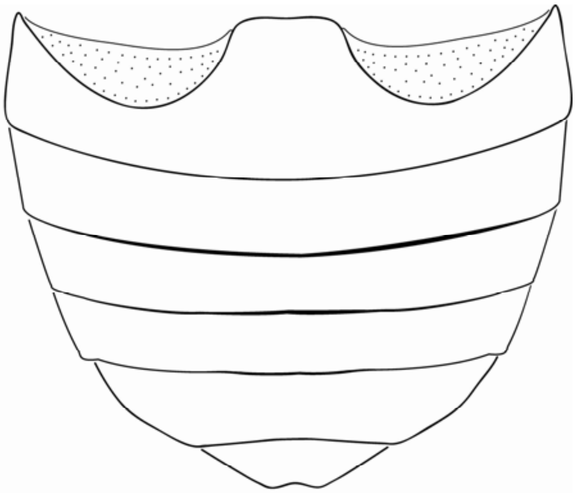

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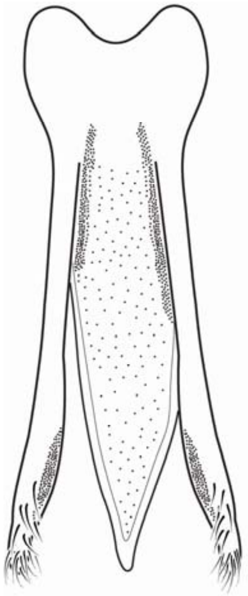

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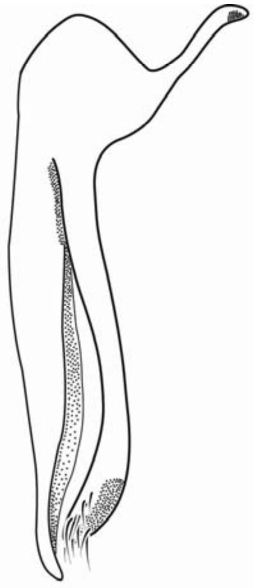

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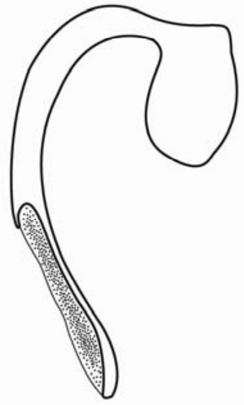

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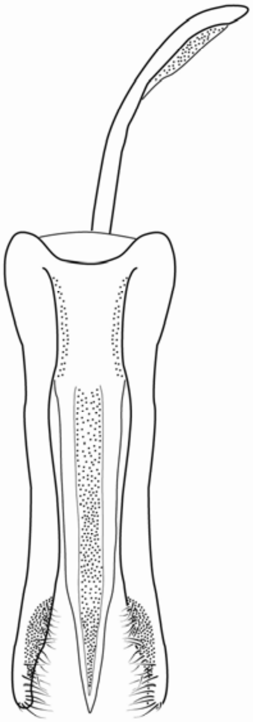

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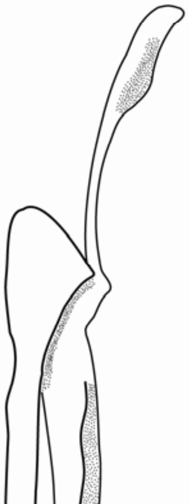

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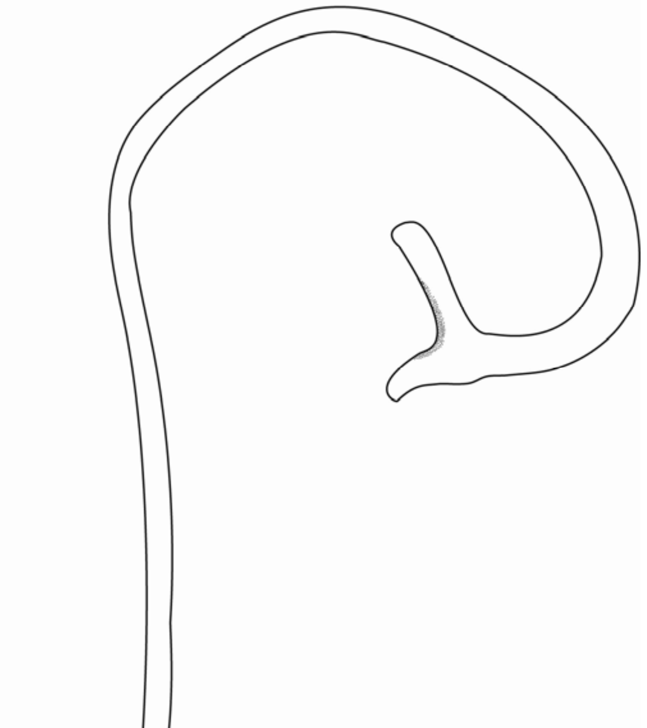

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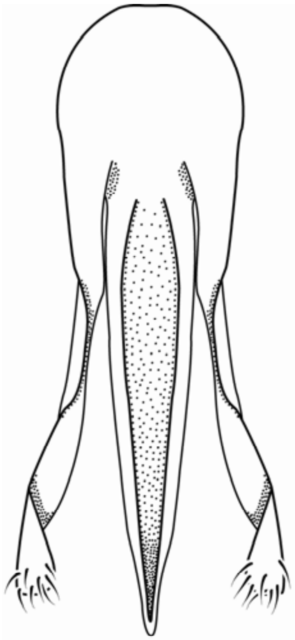

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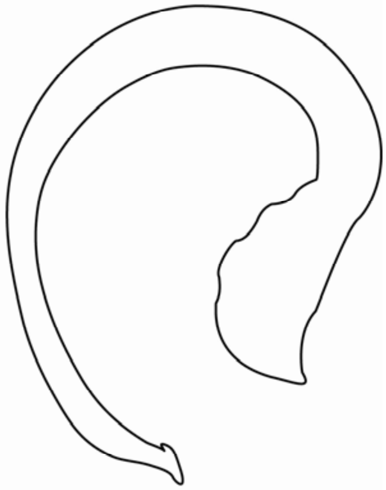

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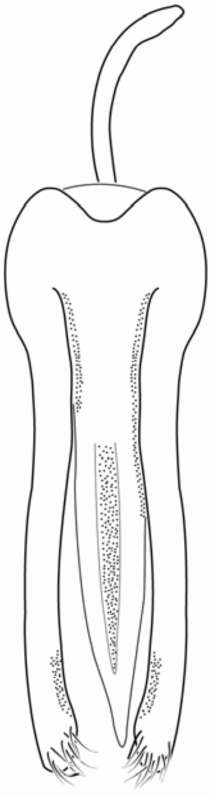

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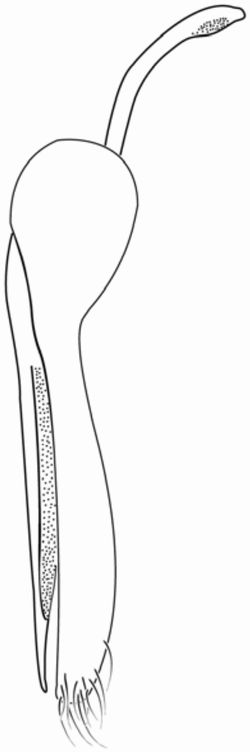

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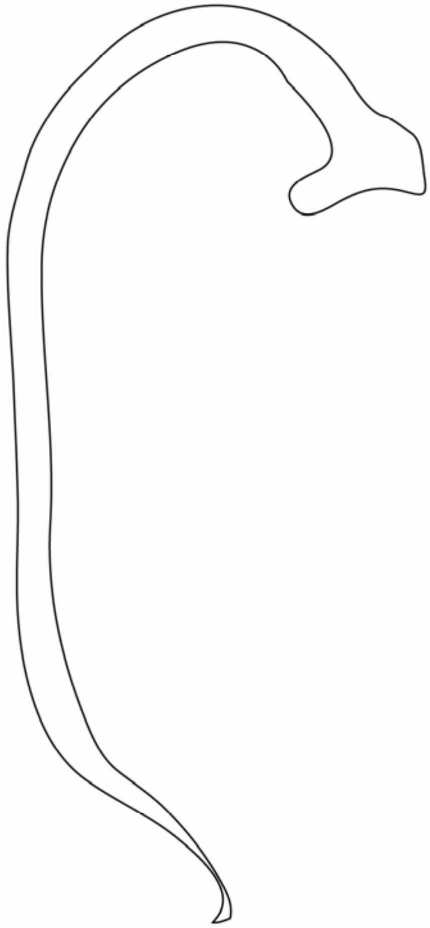

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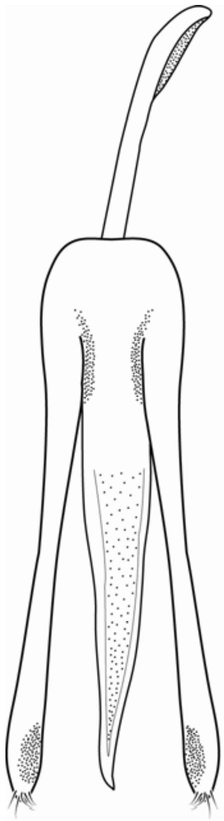

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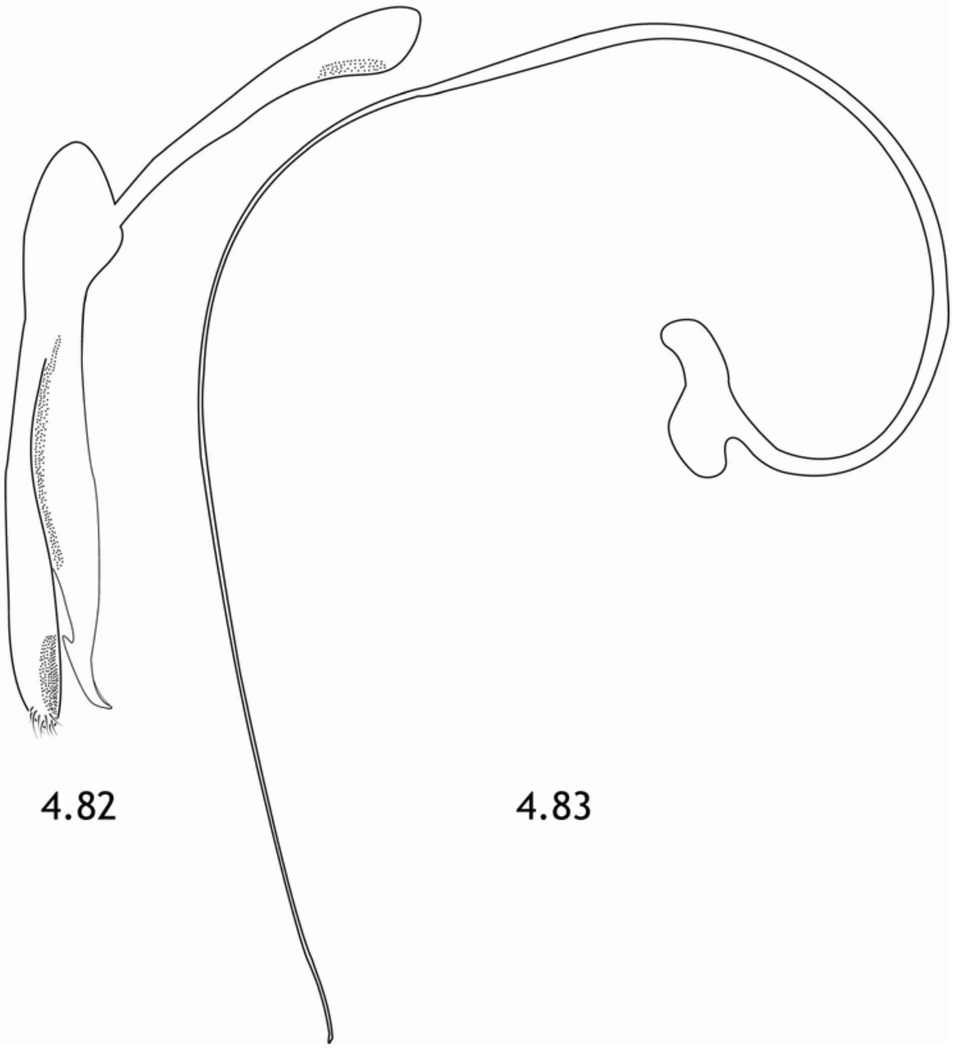

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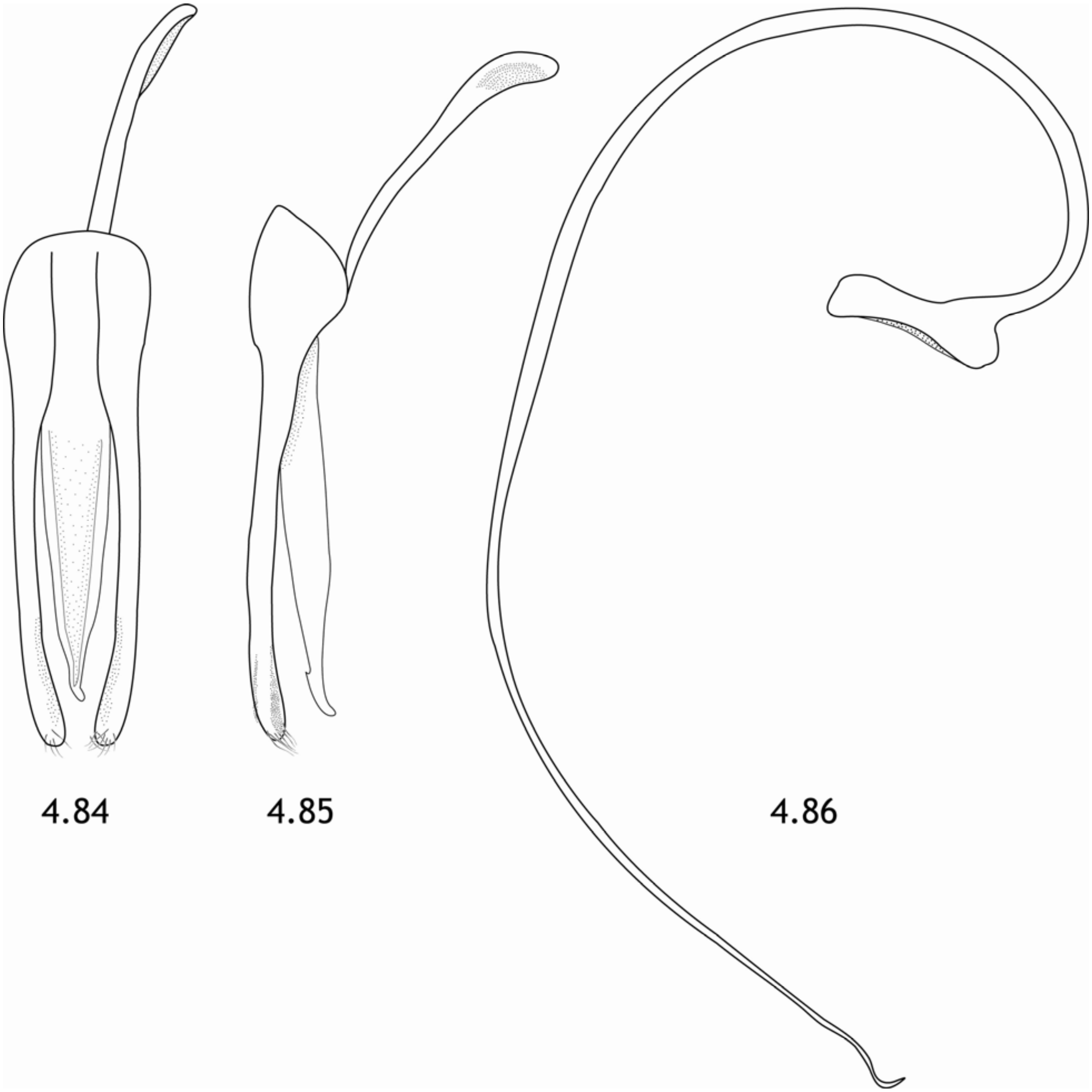

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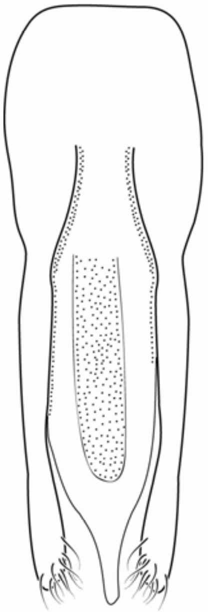

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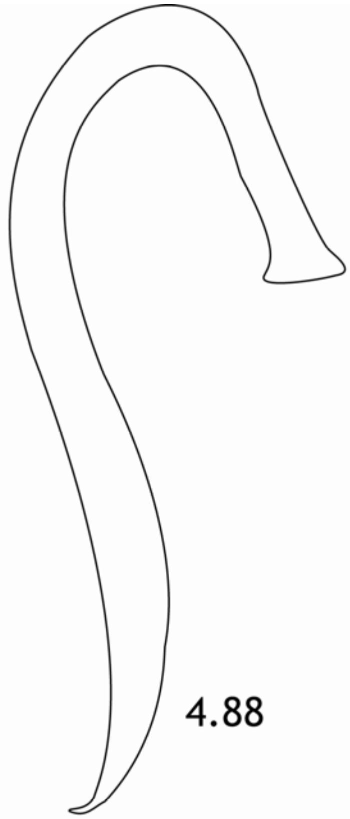

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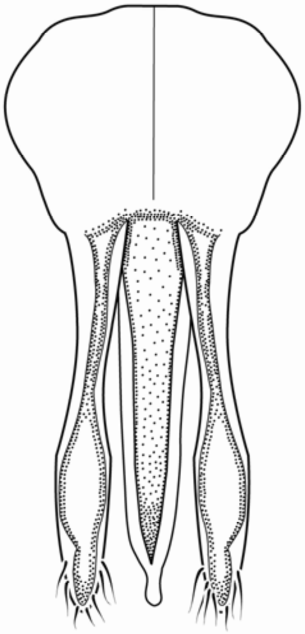

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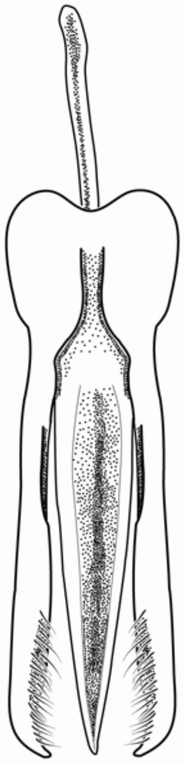

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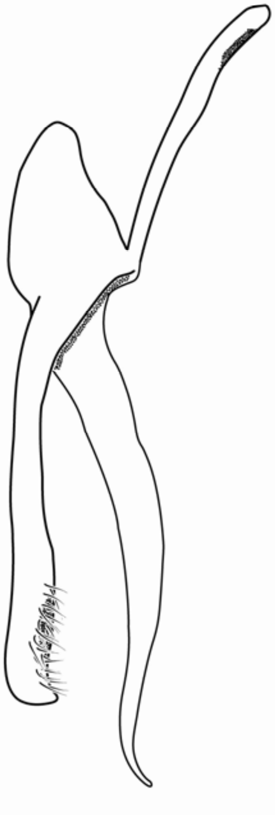

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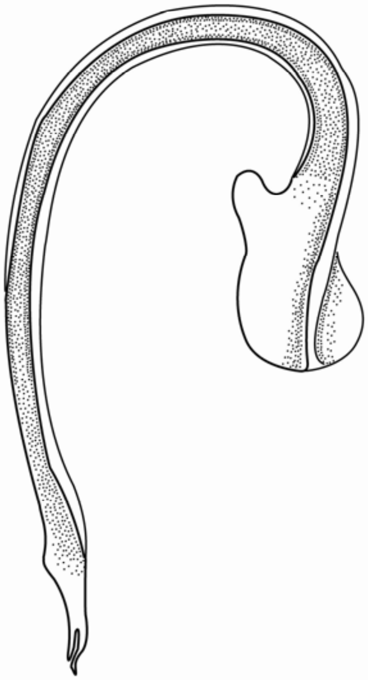

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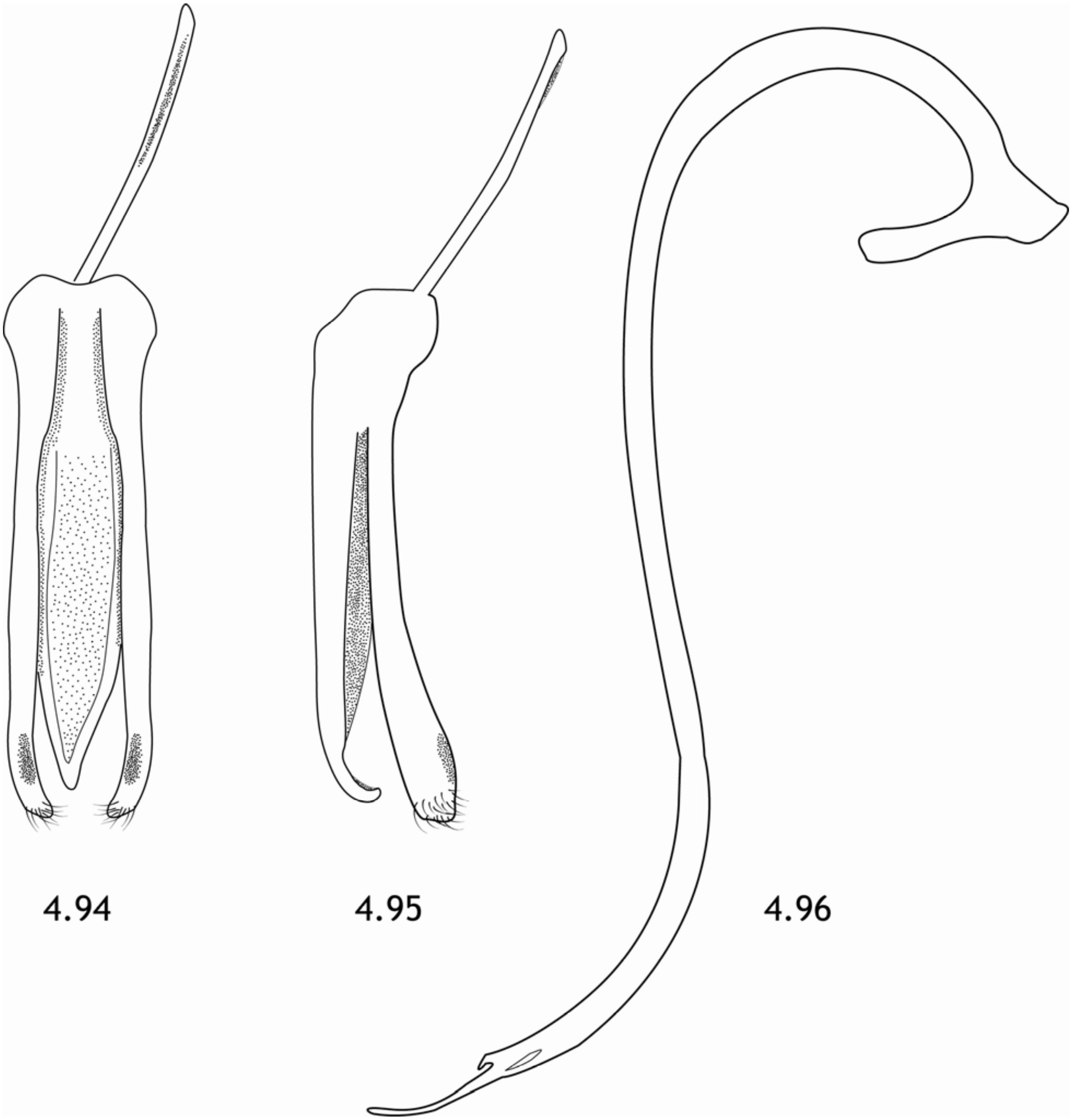

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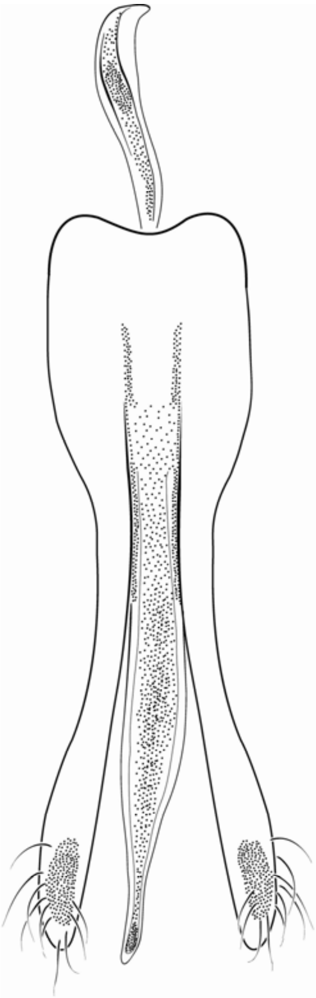

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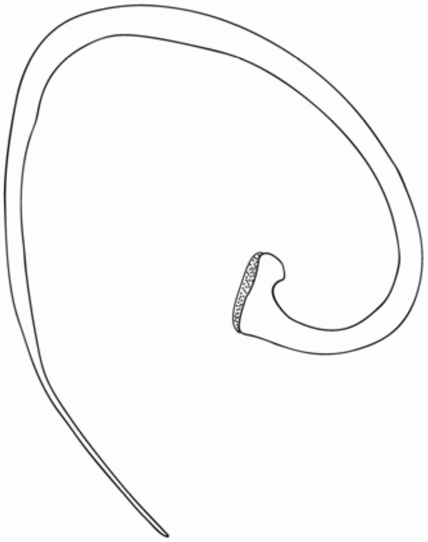

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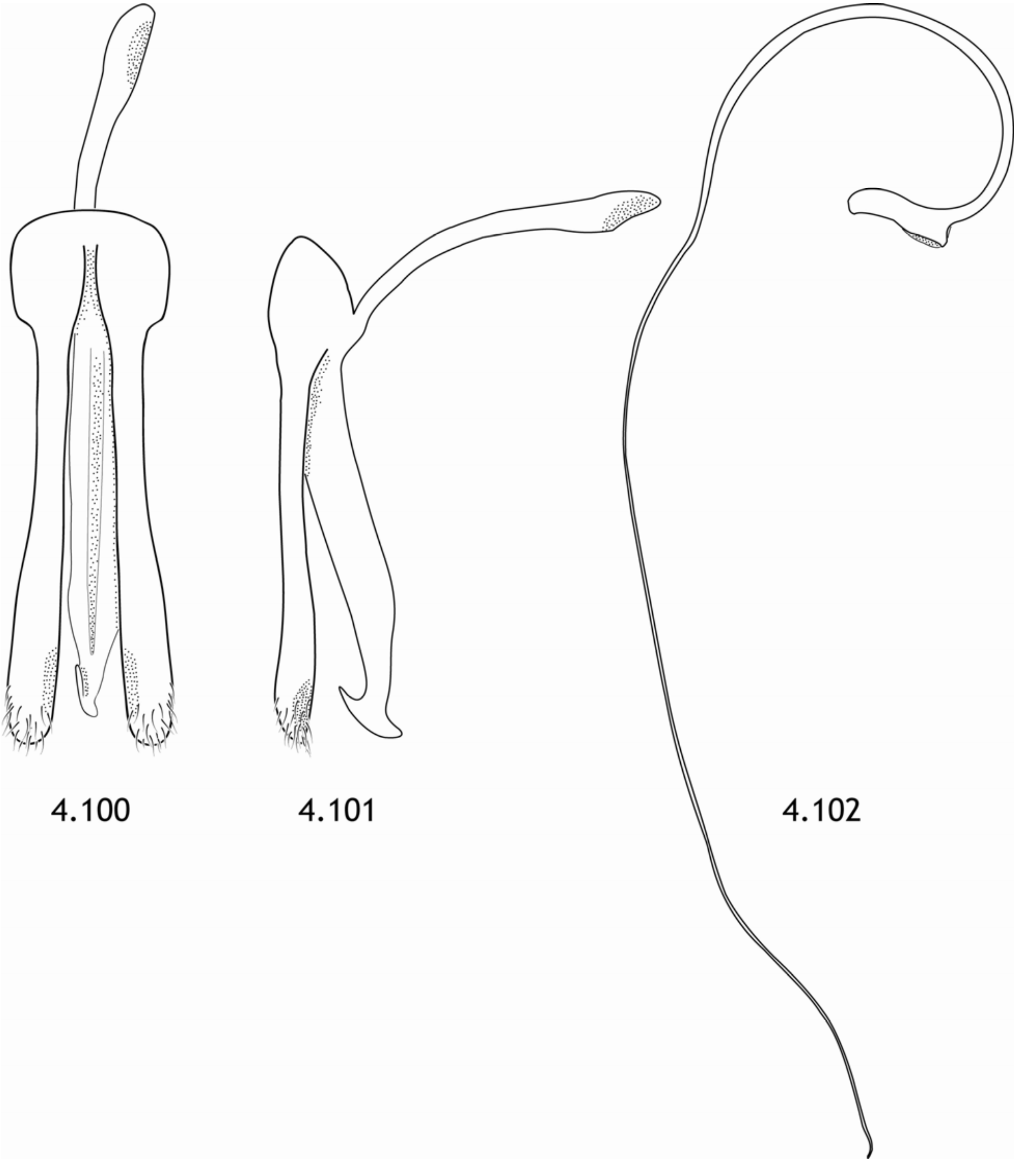

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CHAPTER 5

LADYBUGS STINK! A NOVEL CHEMICAL DEFENSE FOR NOVIINI (COLEOPTERA: COCCINELLIDAE)[3]

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[3] Forrester, J. A., Henderson, W. M., McLanahan, E. D., and J. V. McHugh. To be submitted to the *Journal of Chemical Ecology*.

Abstract

Many coccinellids are chemically defended; most species release endogenous alkaloids through reflex bleeding to thwart would-be predators. Some, such as *Coccinella septempunctata* L. and *Coccinella undecimpunctata* L. utilize chemicals sequestered from their aphid prey. In both cases, the deterrent chemical originates as a plant volatile that is sequestered first by the aphid, then sequestered by the lady beetle. *Hyperaspis trifurcata* Schaeffer is remarkable because it sequesters carminic acid from its cochineal scale prey. This chemical is present in the reflex blood of *H. trifurcata* larvae, and is a proven ant deterrent. *Rodolia cardinalis* (Mulsant) also secretes carminic acid in its reflex blood as both a larva and an adult. *Rodolia cardinalis* feeds almost exclusively upon monophlebid scales, which also may produce carminic acid. This study provides the first record of carminic acid sequestration by a noviine, *R. cardinalis*, and the first record of a lady beetle adult, sequestering and utilizing carminic acid in reflex blood.

Introduction

To races nurtured in the dark;--

How would your own begin?

Can blaze be done in cochineal,

Or noon in mazarin?

- Emily Dickinson: “I Found the Words to Every Thought”

In medieval times, lady beetles were thought to be sacred: they played a very important role as biological control agents. They were so important that early farmers believed that the colorful beetles were heaven-sent. They called them “Beetles of Our Lady,” and lady beetles have been considered harbingers of good luck ever since.

Even non-entomologists are familiar with coccinellids because of their appealing coloration. Most authorities agree that the bright orange, yellow, or red hues are aposematic, and that several different chemical compounds contribute to the color patterns. The black pigment on the elytra of coccinellids is probably melanin, the same pigment found in insect cuticle and wings (Honěk 1996; Stoehr 2006). The bright reds and oranges of the elytra are due to the presence of carotenoids and most likely are derived from aphidophagy (Bezzerides *et al.* 2007). In contrast, the defensive compounds of lady beetles tend to be endogenous alkaloids (Britton *et al.* 1977; Bezzerides *et al.* 2007; King & Meinwald 1996).

Three notable exceptions are *Coccinella undecempunctata* Linnaeaus 1758, *Coccinella septempunctata* Linnaeus 1758 (Coccinellinae) and *Hyperaspis trifurcata* Schaeffer 1905 (Scymninae) (Daloze *et al.* 1994; Hartmann *et al.* 1989; King and Meinwald 1996; Pasteels 2007). *Coccinella undecempunctata* sequesters cardiac glycosides by feeding upon *Aphis nerii* Boyer de Fonscolombe 1843 (Hemiptera: Aphididae), an aphid that is known to sequester glycosides from its host plant (Rothschild *et al.* 1970, 1973). *Coccinella septempunctata* sequesters pyrrolizidine alkaloids (PAs) by feeding upon *Aphis jacobaeae* Schrank 1801 (Hemiptera: Aphididae). *Aphis jacobaeae*, like *A. nerii*, sequesters deterrent chemicals from a host plant (*Senecio jacobaea* L.); the host plant synthesizes the alkaloids in its root system (Daloze *et al.* 1994; Hartmann *et al.* 1989; King and Meinwald 1996; Pasteels 2007). This chemical pathway linking plants, aphids, and lady beetles is an unusual example of tritrophic transmission of defenses: plant to herbivore to carnivore, with organisms at each level producing or sequestering repellent chemicals for their own benefit (Daloze *et al*. 1994).

Hyperaspis trifurcata Schaeffer 1905 also obtains defensive secretions via carnivory. However, *H. trifurcata* differs from all other coccinellid species in that it sequesters non-alkaloids. *Hyperaspis trifurcata* is also unique because it utilizes defensive chemicals that originate from an insect, rather than a plant source. Lady beetles in this group sequester and secrete carminic acid, an anthraquinone, from the cochineal scales (*Dactylopius* sp.) that they eat (Daloze *et al.* 1994; Eisner *et al.* 1994; King and Meinwald 1996; Pasteels 2007). Carminic acid produced by cochineal scales has been a well known source of red pigment for centuries. No other function was ascribed to it until Eisner (1980) showed that carminic acid is a very effective ant deterrent. He proposed that this deterrent might have evolved as a weapon against predation for the scale insect. Examples of insects sequestering chemicals that are synthesized by another insect (rather than a host plant) are rare (Chapman 1998; Eisner 1994).

Another unique aspect of carminic acid utilization by *H. trifurcata* representatives is that the chemical is only secreted during the beetle's larval stage (Eisner 1994). Eisner (1994) also showed that the concentration of carminic acid diminishes as the larva matures, and that the substance is absent altogether in the adults.

When *H. trifurcata* larvae are agitated, they secrete hemolymph containing carminic acid from the dorsal segmental interstices (Eisner *et al.* 1994; King & Meinwald 1996). Unlike the oily yellow droplets associated with all other coccinellids, the secreted hemolymph of *H. trifurcata* larvae is the characteristic magenta color associated with carminic acid dye (Eisner *et al.* 1994; King & Meinwald 1996).

Interestingly, beetles in the genus *Rodolia* (Mulsant) (Coccinellidae: Noviini) also secrete magenta-colored fluid when provoked (Dixon 2000; JAF, pers. obs.). Unlike *H. trifurcata*, *Rodolia cardinalis* (vedalia beetle) reflex bleeds carmine red during the larval, pupal, and adult stages. The egg does not reflex-bleed, but its color is consistent with carminic acid. This study was an effort to determine whether or not the reflex blood of *R. cardinalis* adults contains carminic acid. If it does, this would be the first record of a coccinellid adult sequestering and secreting a non-alkaloid chemical from another species of insect.

Materials and Methods

Live specimens of *R. cardinalis*, both male and female, were obtained from scale-infested trees in Parlier, California, for this study. Adult beetles were secured with a very small amount of water-soluble Elmer's glue on the end of a plastic pipette attached to the beetle's elytra. Once the glue was dry, the beetles were agitated with a dissecting needle, resulting in reflex bleeding. Discharged hemolymph was collected from the femorotibial junctures with micro-capillary tubes and immediately placed in HPLC-grade methanol. Due to the rapid coagulation of the hemolymph, the entire capillary was submersed in methanol. Adult beetles (n=3) as well as larvae were preserved in methanol and stored at -4 ºC until extraction. For this study, discharged hemolymph was analyzed along with whole beetle extracts.

Chemicals: Carminic acid (Figure 5.1, CAS Number 1260-17-9) was obtained from Sigma-Aldrich (Milwaukee, WI) and supplied with purity of 70-90%. All other analytical reagents were purchased from Fisher Scientific (Pittsburgh, PA) and were HPLC-grade or greater.

Carminic Acid Extraction: Carminic acid was extracted, with modifications, based on the solvent-based method of Méndez-Gallegos *et al.* (2004). Preserved specimens (described above) were homogenized for 20 minutes. After homogenization, the samples were centrifuged at 10,000 rpm for 10 minutes. The supernatant was removed and the extraction was repeated (n=3). All extracted fractions along with the preservation liquid were combined and evaporated to dryness under a gentle stream of nitrogen (approximately 4 hours). The dried extracts were reconstituted in 250 μL 30% acetonitrile/water (volume/volume) containing 0.1 % formic acid.

Mass Spectral Conditions: All conformational studies were performed on a Varian 1200L tandem mass spectrometer interfaced with a Varian 430 autosampler, a Varian 230 high-performance liquid chromatograph (HPLC) and an Alltech 631 column heater. All system operations were controlled by Varian MS Workstation version 6.0. Twenty (20) μL of sample were introduced using μL-pick-up mode to an Atlantis 3 μm T3 reversed-phase column (2.1 mm x 150 mm). The HPLC was operated in gradient mode with initial conditions of 95:5 mobile phase A (water/0.1% formic acid, volume/volume) and B (acetonitrile/0.1% formic acid, volume/volume) at a flow rate of 0.30 mL/min. A linear gradient was applied over 35 minutes to obtain mobile conditions of 5:95 (A:B) before being returned to starting conditions and held 10 minutes for equilibration. The column temperature was maintained at 30 ºC. Retention time of carminic acid was 2.15 minutes and the full scan chromatogram in positive ion mode is shown in Figure 5.2.

Results

Method development and characterization

Preliminary liquid chromatography-mass spectrometry (LC-MS) identification studies were performed to examine the fragmentation patterns of carminic acid with spectral scanning over 400-500 *m/z*. The capillary voltage was maintained at a temperature of 50 ºC and the drying gas temperature was 275 ºC. The predominant quadrupole 1 (Q1) MS-MS fragment of the carminic acid standard (70-90% purity, Sigma-Aldrich, Milwaukee, WI) was ion 493, corresponded to the expected parent ion [M+H] (shown in the inset of Figure 5.2).

Optimal collision induced dissociation (CID) experiments were then conducted. The CID at -12 eV resulted in the predominance of mass fragment 373 and an increased CID of -18 eV resulted in 355 as the most abundant mass fragment at quadrupole 3 (Q3). Mass fragments 373 and 355 were identified for LC-MS/MS confirmation experiments. The LC-MS/MS was then optimized at Q3 to monitor the transitions 493→373 (CID=-12 eV) and 493→355 (CID=-18 eV) (Figure 5.3).

Preliminary analysis of biological samples

Whole lady beetle extracts and hemolymph samples were analyzed via LC/MS-MS to determine whether or not carminic acid was present and a component of the reflex blood of lady beetles. The samples analyzed from both the whole lady beetle extract and the hemolymph, collected from reflex bleeding, were shown to contain measurable quantities of carminic acid (Figure 5.4). The results shown for the hemolymph extracts (Figure 5.4B) were obtained using 40 µL, or two times the volume (20 µL) of whole lady beetle extract analyzed (Figure 5.4A). The increase in volume was necessary to obtain a detectable response on the LC/MS-MS.

These results confirm that carminic acid is present in both whole lady beetle extracts and in the reflex blood of *R. cardinalis*. Hemolymph concentrations of carminic acid were not quantifiable due to the small amount of hemolymph acquired for this study.

Discussion

In early history, coccinellids were considered sacred for their efficacy as biological control agents. Insects were not valued solely for their abilities to control agricultural pests, though. Many were sought after as sources of natural pigments. One of those insects, the cochineal scale *Dactylopius coccus* Costa 1829 (Hemiptera: Coccidae), was considered extremely valuable because it was the main source for the most desirable colorant of all: red. The use of cochineal dye dates back to the early Aztecs. When Cortés arrived in Mexico in 1519, he was so taken aback by Montezuma's red robe that he sent cochineal dye back to Spain. A thriving industry was born, with the small, often sessile, insects as its hub (Eisner 2003). For several centuries, cochineal scales were the only source of red pigment, with no thought given to any other application for the substance.

Cochineal is also known as carminic acid, an anthraquinone (Baranyovits 1979; Thomson 1971). According to Eisner (2003), this chemical was isolated in 1819, but its structure was not elucidated until 1959. Eisner (1980) noted that other quinones, specifically, the benzoquinones and napthaquinones found in some opilionids, millipedes, and insects are powerful deterrents to predators. He hypothesized that the related anthraquinones might have the same deterrent effect. He was right, and during the course of his investigation, Eisner (1980) discovered the rare case of an insect, *Laetilia coccidivora* Comstock 1879 (Lepidoptera: Pyralidae), feeding exclusively upon carminic acid-laden prey: the coccid scale, *Dactylopius confusus* (Cockerell) 1893. *Laetilia coccidivora* is noteworthy because it is one of two species of

Lepidoptera that is carnivorous as a larva (*Feniseca tarquinius* (Fabricius) is the other). Eisner (1980) found that this cochineal feeder was remarkable in other ways, too: *Laetilia coccidivora* sequesters carminic acid and uses it for its own defense in the larval stage. In this case, the caterpillar regurgitates unaltered carminic acid, along with other gut contents, onto its would-be attackers (Eisner 1980, 2003).

In subsequent studies, Eisner *et al.* (1994) showed that two other coccid scale predators sequestered and used carminic acid in their larval stages: a fly, *Leucopis* sp. Malloch 1940 (Diptera: Chamaemyiidae), and a lady beetle, *Hyperaspis trifurcata* Schaeffer 1905 (Coleoptera: Coccinellidae). Both taxa shared commonality with *L. coccidivora* in that they only utilized carminic acid as a defense in the larval stage. However, the modes of chemical administration among the three chemical pirates were very different. *Laetilia coccidivora* regurgitated the deterrent, leading Eisner (1980) to believe that the chemical was not absorbed into the body of the caterpillar at all, much less incorporated into the later developmental stages and subsequently, the adult.

Leucopis larvae emit noxious droplets of fluid from the anus. Eisner (1994) dissected *Leucopis* larvae, and found that they had a large rectal pouch where the fluid was stored. He noted that the Malphigian tubules in *Leucopis* were always stained an intense red, and he proposed that carminic acid was absorbed in the midgut, and then passed back into the gut before being excreted through the anus (Eisner 1994, 2003).

Hyperaspis trifurcata, like many other coccinellids, is a reflex bleeder. When aggravated, the larva emits deep red hemolymph from the body surface at the point of disturbance. Eisner (1994) demonstrated that the hemolymph of *H. trifurcata* contained a concentration of carminic acid that was nearly identical to that of its cochineal prey. Because the chemical was emitted from virtually anywhere on the body surface, Eisner (1994, 2003) believed that the deterrent chemical passed through the midgut of *H. trifurcata* and then into the body cavity. There, it remained "at the ready," so to speak, until the larva was provoked (Eisner 1994, 2003).

Rodolia cardinalis is unique among all Coccinellidae in that it utilizes repellent carminic acid in all life stages. The preferred prey of *R. cardinalis* is monophlebid scales, usually species of *Icerya* Signoret 1876 or *Crypticerya* Cockerell 1895. It is unknown whether scale insects in the family Monophlebidae produce carminic acid; however, Gullan and Kosztarab (1997) hypothesized that the death of hymenopteran parasitoids in some monophlebids (then Margarodidae) might have been caused by defensive chemicals such as carminic acid. Representatives of both *I. purchasi* Maskell 1879 and *C. genistae* (Hempel) 1912 are bright magenta in color, just as species of *Dactylopius* are. All species of *Rodolia*, including *R. cardinalis*, feed voraciously on both *Icerya* and *Crypticerya* species. It is logical to think that *R. cardinalis*, like other carminic acid feeders, sequesters the chemical from its prey.

Hyperaspis trifurcata and *Rodolia cardinalis* share morphological commonality that might be associated with their similar chemical defenses. *Rodolia* larvae, like the scale insects they prey upon, are bright magenta in color, and covered with waxy threads. Eisner noted that the waxy covering of *H. trifurcata* prevented the reflex blood from sticking to the larva. This is very important because hemolymph containing carminic acid coagulates very quickly; if not for the waxy covering, the beetle larva would surely become stuck in its own defensive fluid (Eisner 1994). It is not clear how the chemical fluid is emitted from either larva. Eisner (1994) noted that representatives of *H. trifurcata* have no obvious pores or slits on the dorsum; however, the emission point was always close to the point of disturbance. The same is true for *R. cardinalis* larvae and pupae.

Rodolia cardinalis adults administer carminic acid by way of reflex bleeding. When provoked, the adult beetle first employs thanatosis. If it is further aggravated, the beetle emits a droplet of bright red fluid from the femorotibial juncture. As was the case with the larvae, the emission point was always from the leg that was closest to the point of disturbance.

It is interesting that lady beetles in the tribe Noviini share a unique chemical defense with those in the tribe Hyperaspidini. The tribes are classified into different subfamilies (Coccidulinae and Scymninae, respectively); however, the higher classification of Coccinelldae is in a state of flux. As more phylogenetic hypotheses are proposed, it is likely that the arrangement of coccinellid subfamilies and tribes will change. Molecular and morphological data currently provide the basis for ongoing phylogenetic studies of the family. Characterizing the chemical defense mechanisms employed by lady beetles may also play a key role in helping to connect the dots of lady beetle evolution.

Acknowledgements

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Literature Cited

Baranyovits, F. L. C. 1979. Cochineal carmine: an ancient dye with a modern role. *Endeavor*, 2, 85-92.

Bezzerides, A. L., McGraw, K. J., and Husseini, J. (2007) Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis. Behavioral Ecology and Sociobiology*, 61, 1401-1408.

Britton, G., Goodwin, T. W., Harriman, G. E., and Lockley, W. J. S. (1977) Carotenoids of the ladybird beetle, *Coccinella septempunctata*. *Insect Biochemistry*, 7, 337-345.

Chapman, R. F. (1998) The Insects: Structure and Function

Daloze, D., Braekman, J., and Pasteels, J. M. (1994) Ladybird defence alkaloids: Structural, chemotaxonomic, and biosynthetic aspects (Coleoptera: Coccinellidae). *Chemoecology*, 5, 173-183.

Dixon, A. F. G. (2000) *Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control*. Cambridge University Press, New York, 257 pp.

Eisner, T. and S. Nowicki (1980) Red cochineal dye (carminic acid): its role in nature. *Science* 208: 1039-1042.

Eisner, T., Ziegler, R., McCormick, J. L., Eisner, M., Hoebeke, E.R., and Meinwald, J. (1994) Defensive use of an acquired substance (carminic acid) by predaceous insect larvae. *Experientia*, 50, 610-615.

Eisner, T. (2003) *For Love of Insects*. Belknap Press of Harvard University Press, Cambridge, 448 pp.

Gullan, P. J. and Kosztarab, M. (1997) Adaptations in scale insects. *Annual Review of Entomology*, 42, 23-50.

Hartmann, T.; Toppel, G. (1987) Senecionine n-oxide, the primary product of pyrrolizidine alkaloid biosynthesis in root cultures of *Senecio vulgaris*. *Phytochemistry*, 26, 1639-1644.

Hartmann, T., Ehmke, A., Eilert, U., v.Borstel, K., and Theuring, C. (1989) Sites of synthesis, translocation and accumulation of pyrrolizidine alkaloid *N*-oxides in *Senecio vulgaris*. *Planta* 177, 98–107.

Hodek, I. and Honěk, A. (1996) Ecology of Coccinellidae. Kluwer, Dordrecht.

King, A. G. and Meinwald, J. (1996) Review of the defensive chemistry of coccinellids. *Chemical Reviews*, 96, 1105-1122.

Méndez-Gallegos, S. de J., Tarango-Arámbula, L.A. and González-González, M. (2004) Preliminary analysis of cochineal insects (*Dactylopius coccus* Costa) with High Liquid Chromatography (HPLC). *In*: Esparza-Frausto, G., Valdéz-Cepeda, R. and S. J. Méndez-Gallegos (eds.). *El Nopal: Tópicos de Actualidad. Universidad Autónoma Chapingo/Colegio de Postgraduados*. México, pp.223-234.

Lee, R. L. (1951) American Cochineal in European Commerce, 1526-1625 *The Journal of Modern History*, 23, (3), 205-224.

Pasteels, J. M. (2007) Chemical defence, offence and alliance in ants-aphids-ladybirds relationships. *Population Ecology*, 49(1), 5-14.

Rothschild, M. (1961) Defensive odours and Mullerian mimicry amongst insects *Transactions of the Royal Entomological Society of London*, 113, 101-21.

Rothschild M, von Euw J, Reichstein T (1970) Cardiac glycosides in the oleander aphid *Aphis nerii. Journal of Insect Physiology*, 16, 1141-1145.

Rothschild M, von Euw J, Reichstein T (1973) Cardiac glycosides in a scale insect *(Aspidiotus),* a ladybird *(Coccinella)* and a lacewing *(Chrysopa). Journal of Entomological Science* (A) 48, 89-90

Sasaji, H. (1968) Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia, Fukui*, 35, 1-37.

Stoehr, A. M. (2006) Costly melanin ornaments: the importance of taxon? *Functional Ecology*, 20, 276-281.

Thomson , R. H. (1971), Naturally Occurring Quinones Academic Press, New York. 760 pp.

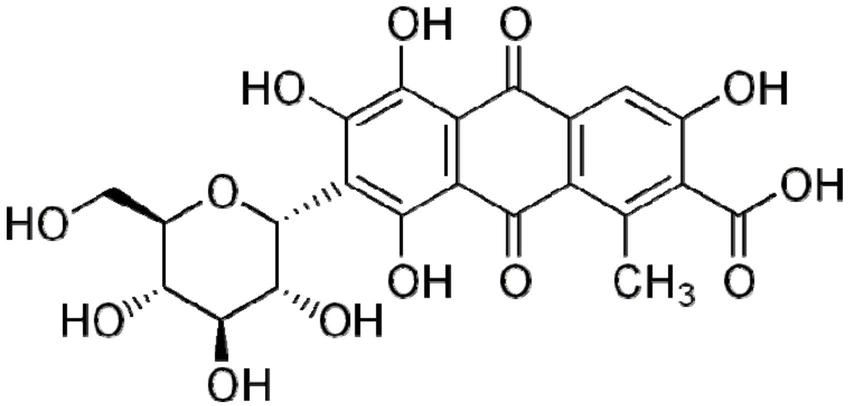
Figure Legends

Figure 5.1. Structural representation of carminic acid.

Figure 5.2. Full scan chromatogram of carminic acid (retention time equals 2.15 minutes) in positive ion mode. Inset represents mass break down (parent ion) present in quadrupole 1 of the MS-MS. The dominant ion observed is 493 m/z [M+H]+.

Figure 5.3. Mass fragmentation patterns obtained in quadrupole 3 at optimized conditions (please see "Materials and Methods"). In 3A, collision induced dissociation at -12 eV results in the predominance of mass fragment 373. Increasing the CID (-18 eV) results in mass fragment 355 as illustrated in 3B.

Figure 5.4. Preliminary analysis of whole lady beetle extracts (A) and hemolymph collected during gentle prodding inducing reflex bleeding (B). Note that the abundance scale is different for each representation. The injected amount of sample containing hemolymph extracts had to be increased to 40 uL in order to obtain an adequate response on the LC/MS-MS.



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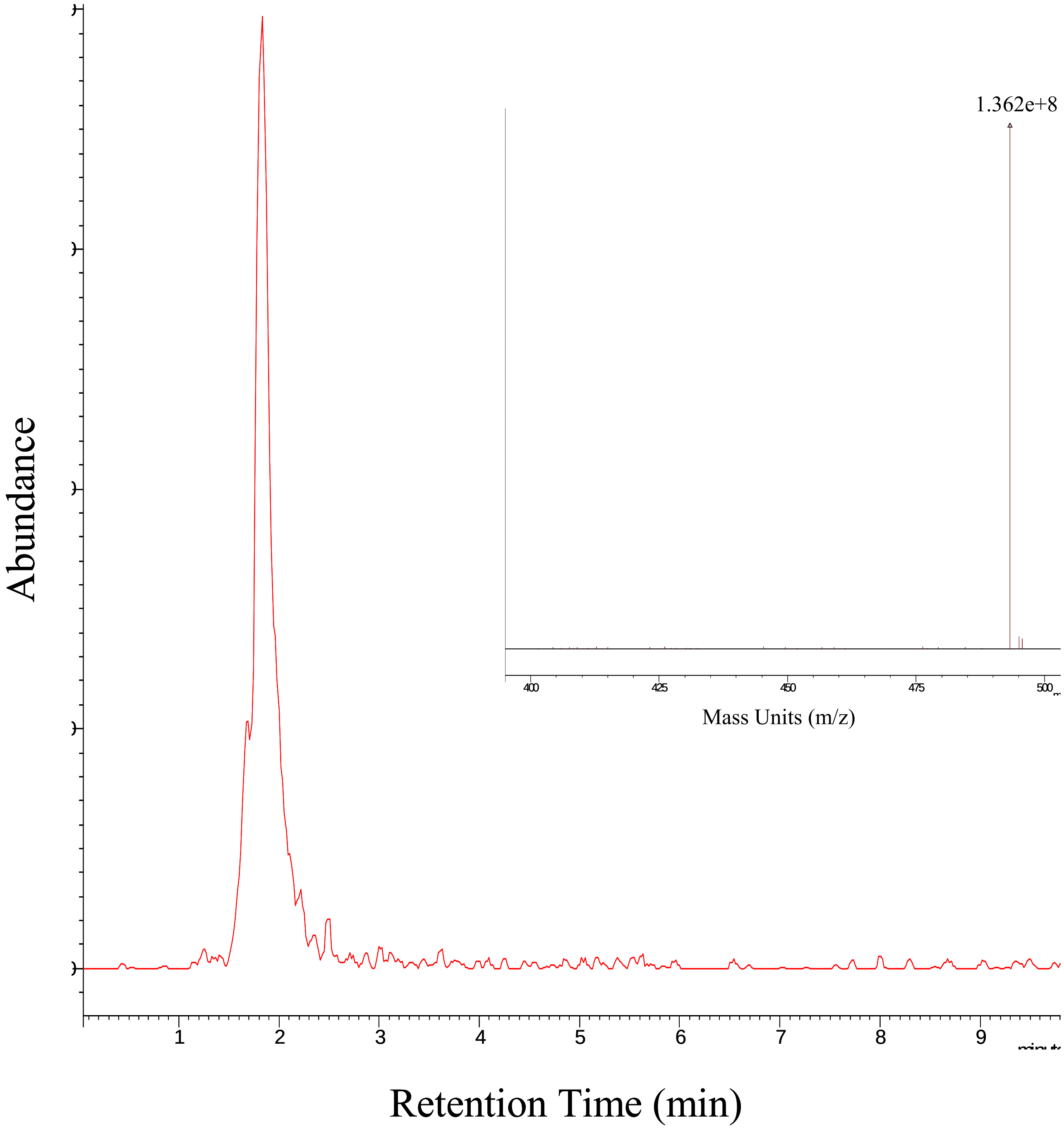
Abundance
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500
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Retention Time (min)

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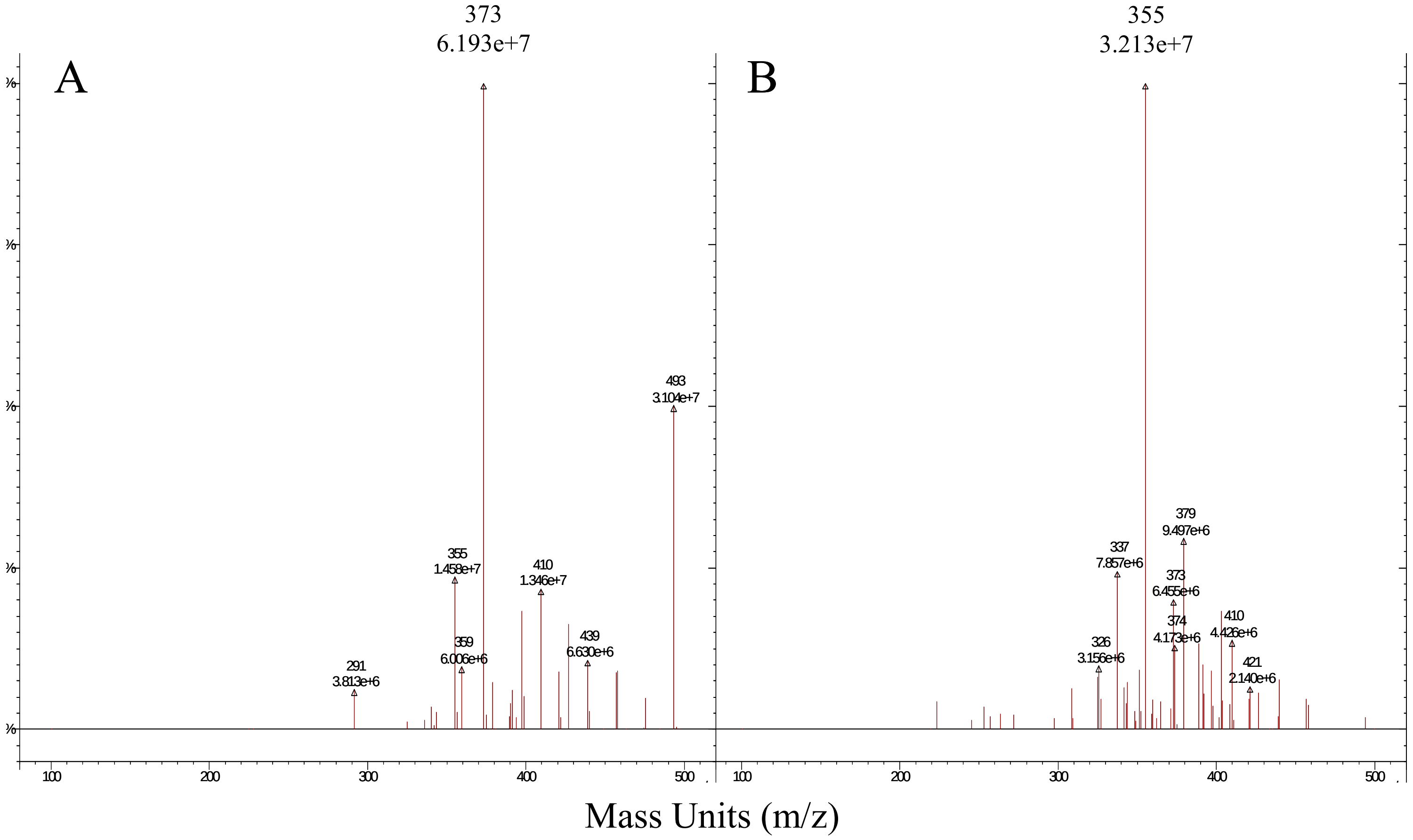
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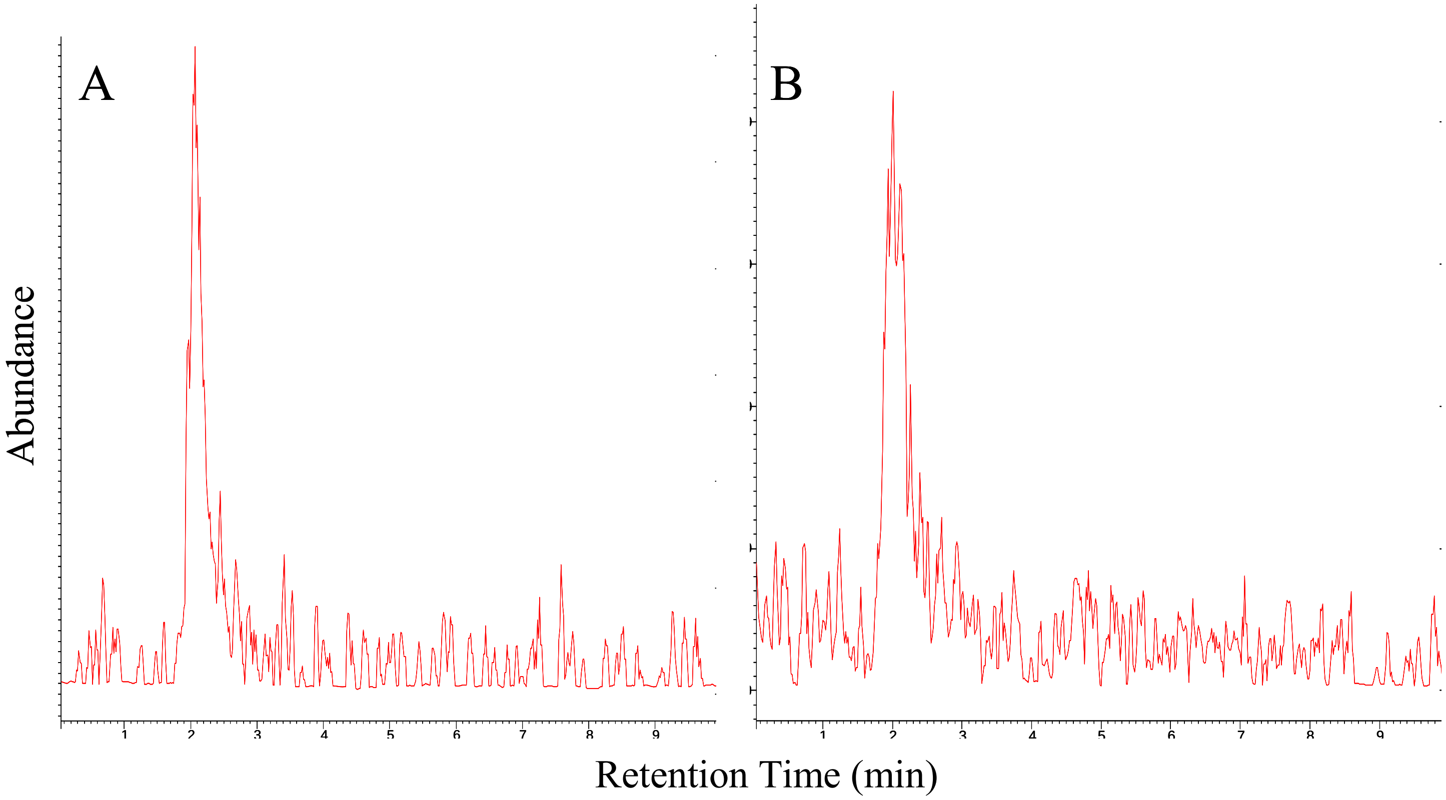
3.104e+7
355
3.213e+7
B
379
9.497e+6
337
7.857e+6
373
6.455e+6
374
4.173e+6
410
4.426e+6
326
3.156e+6
421
2.140e+6
100
200
300
400
500
100
200
300
400
500
Mass Units (m/z)

5.3



5.4

CHAPTER 6

CONCLUSION

"*Good little bug! Your name shall be*
Henceforth - My Lady's Bird!"

-Edward Blount: "The Story of the Ladybird"

The taxonomic problems that were so prevalent in Noviini mirror those found in the entire coccinellid family. The revision of Noviini is a significant contribution to the field of lady beetle systematics. Still, there is much to be done. Large groups of small, drably-colored coccinellids await revision on a global scale. Before those revisions can be undertaken, it is desirable to test the monophyly of the group being revised. Generic and tribal definitions are much more precise and unambiguous when they are based upon synapomorphy. Coccinellidae has a cosmopolitan distribution, so revisions should also be conducted on a global scale. To do otherwise is to repeat the mistakes of our predecessors.

Several researchers are actively working on projects involving Coccinelldae: molecular analyses of the entire family, morphological analyses of tribes and/or genera, and regional revisions of tribes and genera are active research projects now. Unfortunately, many workers continue to describe single species outside of any phylogenetic or revisionary context, while proposing new classifications without the benefit of any phylogenetic analysis. Coccinellidae is a very large group whose members appear to be evolving quite rapidly, so regional work and intuitive classifications are insufficient to resolve the taxonomic problems therein. Fortunately, many coccinellid workers have begun a united, multi-pronged approach to resolving the internal relationships in the family.

For my part, I plan to continue working on the subfamily Coccidulinae. Most authorities agree that this subfamily is not monophyletic; rather, it is a “dumping ground” for small, furry, and drably-colored lady beetles. Many economically important biological control agents are included in this group (*Cryptolaemus* Mulsant, *Sasajiscymnus* Vandenberg, *Scymnus* Kugelann, *Stethorus*), and their taxonomic problems are similar to those discussed for Noviini. In particular, the tribal and generic boundaries are not clear. Undoubtedly, countless synoymies exist in those groups, as well. Finally, no worldwide revision or natural classification for those groups has ever been attempted.

The sliver of light in the taxonomic darkness of Coccinellidae grows ever wider…

REFERENCES

Arnett, R. H. (1963) *The Beetles of the United States*. Catholic University of America Press, Washington, D.C. 1112 pp.

Balduf, W.V. (1935) *Coccinellidae*, (13) Ladybeetles. Bionomics of Entomophagous Coleoptera. John S. Swift, Chicago, New York, 220 pp.

Bezzerides, A. L., McGraw, K. J., and Husseini, J. (2006) Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis. Behavioral Ecology and Sociobiology*, 61, 1401-1408.

Blackburn, T. (1895) Further notes on Australian Coleoptera, with descriptions of new genera and species. *Transactions of the Royal Society of South Australia*, 14, 201-255.

Blackburn, T. (1889) Further notes on Australian Coleoptera, with descriptions of new species. *Transactions and Proceedings and Report of the Royal Society of South* Australia, 11, 175-215.

Booth, R. G., Cox, M. L., and Madge, R. B. (1990) *IIE guides to insects of importance to man. 3. Coleoptera*. University Press, Cambridge, 384 pp.

Britton, G., Goodwin, T. W., Harriman, G. E., and Lockley, W. J. S. (1977) Carotenoids of the ladybird beetle, *Coccinella septempunctata*. *Insect Biochemistry*, 7, 337-345.

Bodenheimer, F. S. (1932) *Icerya purchasi Maskell und Novius cardinalis* Mulsant. Eine bevölkerungswissenschaftliche Studie über die Grundlagen der biologischen Bekämpfung. *Zeitschrift Für Angewandte Entomologie*, 19, 521-543.

Caltagirone, L. E. and Doutt, R. L. (1989) The history of the Vedalia Beetle importation into California and its impact on the development of biological control. *Annual Review of Entomology,* 34, 1-16.

Causton, C. E. (2004) Ensuring compatibility of biological control of *Icerya purchasi* Maskell with conservation in Galápagos: development of a procedure to evaluate risk. *In:* R. G. V. Driesche (Eds), *Proceedings of the First International Symposium for the Biological Control of Arthropods*. USDA-FS Honolulu.

Chazeau, J. (1981) Presence du genre Rodolia Mulsant en Nouvelle-Caledonie, et description d'une nouvelle espece: *R. delobeli*. *Bulletin Entomologique Société Entomologique de France*, 56, 57-59.

Chazeau, J. H., Fürsch, H., and Sasaji, H. (1989) Taxonomy of coccinellids. *Coccinella*, 1, 6-8.

Clausen, C. P. (1940) *Entomophagous Insects*. McGraw-Hill, New York, 688 pp.

Coquillett, D. W. (1893) Report on some beneficial and injurious insects of California. *United States Department of Agriculture Entomology Bulletin*, 30, 9-33.

Coquillet, D. W. (1889) The imported Australian ladybird, *Vedalia cardinalis*. *Insect Life,* 2(8), 70-75.

Crotch, G. R. (1874) *A Revision of the Coleopterous Family Coccinellidae.* E. W. Janson, London. 311 pp.

Crowson, R. A. (1955) *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd & Co., Ltd., London. 187 pp.

Crowson, R.A. (1960). The phylogeny of Coleoptera. *Annual Review of Entomology.* 5, 111-134.

Daloze, D., Braekman, J., and Pasteels, J. M. (1994) Ladybird defence alkaloids: Structural, chemotaxonomic, and biosynthetic aspects (Col.: Coccinellidae). *Chemoecology*, 5, 173-183.

DeBach, P. and Rosen, D. (1991) *Biological control by natural enemies*. Cambridge University Press, Cambridge, 456 pp.

Dixon, A. F. G. 2000. *Insect predator-prey dynamics: Ladybird beetles and biological control*. Cambridge University Press, Cambridge, 257 pp.

Dobzhansky, T. (1926) Die paläarktischen Arten der Gattung *Coccinella L.* Rev. Russ. Ent. 20, 16-32.

Eisner, T., Ziegler, R., McCormick, J. L., Eisner, M., Hoebeke, E.R., and Meinwald, J. (1994) Defensive use of an acquired substance (carminic acid) by predaceous insect larvae. *Experientia*, 50, 610-615.

Freude, H., Harde, K. W., and Lohse, G. A. (1967) *Die Kafer Mitteleuropas*. Goecke & Evers, Krefeld.

Forrester, J. A. and Vandenberg, N. J. (2008) First Florida records for *Anovia circumclusa* (Gorham) (Coleoptera: Coccinellidae: Noviini): A natural enemy of *Icerya genistae* Hempel (Hemiptera: Margarodidae). *Zootaxa*, 1720, 66-68.

Forrester, J. A., Vandenberg, N. J., and McHugh, J. V. (2008) First description of the egg, larva, and pupa of *Anovia circumclusa* (Gorham) (Coleoptera: Coccinellidae: Noviini) with notes on intraspecific color variation. *In review*.

Fürsch, H. (1960) Neue palaearktische und afrikanische Coccinellide (Coleoptera). *Beiträge Zur Entomologie*,10, 442-451.

Fürsch, H. (1995) The ladybird beetles found by the Entomological Namibia Expedition of the Museum of Natural History Berlin 1992 with remarks on other African species

(Coleoptera: Coccinellidae). *Mitteilungen-aus-dem-Zoologischen-Museum-in-Berlin*, 71, 327-340.

Fürsch, H. (1996) Taxonomy of coccinellids. *Coccinella,* 6, 28-30.

Gage, J. (1920) The larvae of the Coccinellidae. *Illinois Biological Monographs*, 6(4), 1-63.

Ganglebauer, L. (1899). *Die Käfer von Mitteleuropa. Vol. 3, Familienreihe Staphylinoidea, 2. Theil: Familienreihe Clavicornia.* Wien, 1046 pp.

Goloboff, P., S. Farris, and K. Nixon. (2000) TNT (Tree analysis using New Technology) (BETA) ver. xxx Published by the authors, Tucumán, Argentina.

Gordon, R. D. (1972) The tribe Noviini in the New World (Coleoptera: Coccinellidae). *Journal of the Washington Academy of Sciences*, 62(1), 23-31.

Gordon, R. D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society,* 93, 654-678.

Hagen, K. B. (1962) Biology and ecology of predaceous Coccinellidae. *Annual Review of Entomology*, 7, 289-326.

Hagen, K. S., Bombosch, S., and McMurtry, J. A. (1976) The biology and impact of predators. *In:* P. S. M. C. B. Huffaker (Eds), *Theory and Practice of Biological Control*. Academic Press, New York, 788 pp.

Hoang, D. N. (1980) Môt só loài bo rùa mói thuôc phân ho Coccidulinae (Coccinellidae, Coleoptera) ó Viêt Nam. *Tap chi Sinh Vat Hoc*, 2, 8-13.

Hodek, I. (1973) *Biology of Coccinellidae*. Academia, Prague, 266 pp.

Honěk, A. (1996) Variability and Genetic Studies. *In:* I. Hodek and I. Honěk (Eds.) *Ecology of Coccinellidae.* Kluwer Academic Publishers, Dordrecht, 464 pp.

Hodges, G. (2008) Pest Alert: *Crypticerya genistae* (Hemiptera: Monophlebidae), a new exotic scale insect for Florida. *Pest Alert,* 1-3.

Howard, L. O. (1889) Notes and descriptions of a few injurious farm and fruit insects of South Africa, 90-92.

Howarth, F. G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology,* 36, 485-509.

Iperti, G. (1999) Biodiversity of predeaceous Coccinellidae in relation to bioindication and economic importance. *Agriculture, Ecosystems, and Environment,* 74, 323-342.

Kamiya, H. (1964) Comparative morphology of larvae of the Japanese Coccinellidae, with special reference to the tribal phylogeny of the family (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science*, 14, 83-100.

Kapur, A. (1949) On the Indian species of *Rodolia* Mulsant (Coleoptera: Coccinellidae). *Bulletin of Entomological Research*, 39, 531-538.

Kenis, M., Roy, H. E., Zindel, R., and Majerus, M. E. N. (2008) Current and potential management strategies against *Harmonia axyridis*. *BioControl,* 53, 235-252.

King, A. G. and Meinwald, J. (1996) Review of the defensive chemistry of coccinellids. *Chemical Reviews*, 96, 1105-1122.

Korschefsky, R. (1931) Pars 118, Coccinellidae I. *In*: *Coleoptorum Catalogus*, vol. 16, pp. 1-224.

Korschefsky, R. (1937) Zwei neue *Novius*-Arten von den Canaren. *Societas Scientiarum Fennica. Commentationes Biologicae,* 6, 1-3.

Kovár, I. (1996). Phylogeny. *In:* I. Hodek and I. Honěk (Eds.) *Ecology of Coccinellidae.* Kluwer Academic Publishers, Dordrecht, 464 pp.

Kuznetsov, V. N. (1997) *Lady beetles of the Russian Far East. Memoir No. 1, Center for Systematic Entomology.* Sandhill Crane Press, Gainesville. 248 pp.

Latreille, P. A. (1804) *Histoire Naturelle, genérale et particuliere, des Crustacés et des Insectes. Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et partie du Cours complet d'Histoire naturelle rédigé par C. S. Sonnini, member de plusieurs Sociétes savants.Tome douzième*. F. Dufart, Paris, 424 pp.

Latreille, P. A. (1807) *Genera Crustaceorum et Insectorum secundum ordinem naturalem in families disposita, iconibus exemplisque plurimis explicate. Tomus tertius.* A. Koenig, Parisilis et Argentorati, 258 pp.

Lawrence, J. F. and Newton, A. F., Jr. (1995). *Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names).* Pp. 779-1006. *In*: J. Pakaluk and S. A. Slipinski, eds. Biology, phylogeny and classification of Coleoptera; papers celebrating the 80th birthday of Roy A. Crowson. Museum Instytut Zoologii PAN, Warsaw.

Lea, A. M. (1901) Descriptions of new species of Australian Coleoptera. *Proceedings of the Linnaean Society of New South Wales*, 36, 448-513.

Leeper, J. R. (1976) A Review of the Hawaiian Coccinellidae. *Proceedings of the Hawaiian Entomological Society,* 22, 279-306.

LeSage, L. (1991) Coccinellidae (Cucujoidea), the lady beetles, ladybirds. Pp. 485-494. *In*: F. W. Stehr, ed. Immature Insects. Vol. 2. Kendall/Hunt. Dubuque, Iowa.

Lewis, G. (1879) On certain new species of Coleoptera from Japan. *The Annals and Magazine of Natural History*, 4, 29-33.

Lewis, G. (1896) On the Coccinellidae of Japan. *Annals and Magazine of Natural History*, 17, 23-41.

Majerus, M. E. N. (1994) *Ladybirds.* Harper Collins, London. 367 pp.

Mendel, Z., Assael, F., Zeidan, S., and Zehavi, A. (1998) Classical biological control of Palaeococcus fuscipennis (Burmeister) (Homoptera: Margarodidae) in Israel. *Biological Control,* 12, 151-157.

Motschoulsky, V. (1866) Essai d'un catalogue des insectes de l'ile de Ceylan. Supplement. *Bulletin de la Societe Imperiale des Naturalistes de Moscou*, 39, 393-446.

Mulsant, M. E. (1846) Histoire naturelle des Coleopteres de France: Sulcicolles-Securipalpes. Paris, 280 pp.

Mulsant, M. E. 1850. Species de Coleopteres trimeres securipalpes. *Ann. Sci. Phys. Nat. Lyon,* 2, 1-1104.

Nakamura, M. (1980) The pupae of some Japanese lady beetles, with reference to the phylogeny of the subfamily (Coleoptera: Coccinellidae). *New Entomologist,* 29(4), 15-25.

Nixon, K. C. (1999-2002) WinClada ver. 1.0000 Published by the author, Ithaca, NY, USA.

Olliff, M.S. (1895) Entomological notes-A friendly new ladybird. *Agricultural Gazette of New South Wales*, 6, 30-31.

Pakaluk, J., Ślipiński, S. A., and Lawrence, J. F. (1994). Current classification and family-group names in Cucujoidea (Coleoptera). *Genus*, 5: 223-268.

Pasteels, J. M. (2007) Chemical defence, offence and alliance in ants-aphids-ladybirds relationships. *Population Ecology*, 49(1), 5-14.

Phuoc, D. T. and Stehr, F. W. (1974) Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions of the American Entomological Institute* 10: 31-123.

Poorani, J. (2002) An annotated checklist of the Coccinellidae (Coleoptera) (Excluding Epilachninae) of the Indian subregion. *Oriental Insects* 36: 307-383.

Pope, R. D. (1979) Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology,* 4, 171-196.

Quezada, J. R. & DeBach, P. (1973) Bioecological studies of the cottony cushion scale, *Icerya purchasi* Maskell, and its natural enemies, *Rodolia cardinalis* Mul. and *Cryptochaetum iceryae* Will., in Southern California. *Hilgardia* 41, 631-688.

Raimundo, A. C. (1978) Contribuicao para o conhecimento dos coccinelideos de Angola I. *Garcia de Orta; Serie de zoologia,* 4, 23-40.

Redtenbacher, L. (1843) *Abbildungen und Beschreibungen neuer und seltner Thiere und Pflanzen, in Syrien und im westlichen Taurus gesammelt von Th. Kotschy.* Schweizerbart, Stuttgart, 254 pp.

Rees, B. E. (1947) Taxonomy of the larvae of some North American Noviini (Coleoptera, Coccinellidae). *The Pan-Pacific Entomologist*, 23, 113-119.

Robertson, J. A., Whiting, M. F., and McHugh, J. V. (2008) Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea) *Molecular Phylogenetics and Evolution*, 46, 193-205.

Samways, M. J., Osborn, R., and Saunders, T. L. (1997) Mandible form relative to the main food type in ladybirds (Coleoptera: Coccinellidae). *Biocontrol Science and Technology,* 7, 275-286.

Sasaji, H. (1968a) Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia, Fukui*, 35, 1-37.

Sasaji, H. (1968b) Description of the coccinellid larvae of Japan and the Ryukus (Coleoptera). *Memoirs of the Faculty of Fukui University, Series II, Natural Science* 18: 93-135.

Sasaji, H. 1971. *Coccinellidae (Insecta: Coleoptera). Fauna Japonica* Academic Press of Japan, Keigaku Publishing, Tokyo. ix+344 pp.

Savoiskaya, G. I. and B. Klausnitzer (1973) Morphology and taxonomy of the larvae with keys for their identification. *In:* I. Hodek (Eds), *Biology of Coccinellidae*. Dr. W. Junk N. V. Prague, 36-55.

Sicard, A. (1909). Description d'une nouvelle espèce de Coccinellide d'Afrique. *Bulletin de la Societe Entomologique de France*, 112-113.

Sicard, A. (1931) Descriptions d'espèces nouvelles appartenant á la famile des Coccinellides (Coleoptera). *Annals and Magazine of Natural History*, 8, 228-234.

Ślipiński, S. A. (2007) *Australian Ladybird Beetles (Coleoptera: Coccinellidae): Their Biology and Classification.* ABRS, Canberra. 286 pp.

Stebbing, E. P. (1904) On the life history of *Vedalia guerinii* Crotch, predaceous upon *M. stebbingi* Green. *The Journal of the Linnaean Society of London*, 24, 155-161.

Stebbing, E. P. (1914) *Indian Forest Insects of Economic Importance: Coleoptera*. J. K. Jain Brothers, Bhopal. 648 pp.

Stoehr, A. M. (2006) Costly melanin ornaments: the importance of taxon? *Functional Ecology*, 20, 276-281.

Unruh, C. M. and Gullan, P. (2008) Molecular data reveal convergent reproductive strategies in Iceryine scale inscts (Hemiptera: Coccoidea: Monophlebidae), allowing the re-interpretation of morphology and a revised generic classification. *Systematic Entomology,* 33, 8-50.

Vandenberg, N. J. (2002) Coccinellidae. *In:* P. E. S. Michael C. Thomas, J. Howard Frank (Eds), *American Beetles Vol. II: Scarabaeoidea through Curculionoidea*. CRC Press New York, 371-389.

Verhoeff, C. (1895) Beitrage zur vergleichenden Morphologie des Abdomens der Coccinelliden. *Archiv für Naturgeschichte*, 61, 1-80.

Weise, J. (1885) *Bestimmungs-Tabellen der Eeuropaischen Coleopteren. II. Heft. Coccinellidae. II. Auflage mit Berucksichtigung der Arten aus dem Nordlichen Asien*. Mdling, 83 pp.

Weise, J. (1892) Les Coccinellides du Chota-Nagapore. *Annales de la Societe Entomologique de Belgique*, 36, 19-27.

Weise, J. (1895) Uber die mit *Novius* Mulsant. *Annales de la societe Entomologique de Belgique*, 39, 147-151.

Weise, J. (1898) Coccinelliden aus Usambara. *Annales de la Societe Entomologique de Belgique*, 98, 191-201.

Weise, J. (1901) Contribution a l'etude de la faune entomologique de Sumatra. *Annales de la Societe Entomologique de Belgique*, 45, 91-96.

Weise, J. (1905) Ueber Chrysomeliden und Coccinelliden aus Rhodesia. *Deutsche Entomologische Zeitschrift*, 1905, 321-336.

Weise, J. (1912) Coccinellidae. *Wiss. Ergebnisse d. D. Zentral Afrika Exp., Bd. 4, Lfg. 3. Leipzig*, 43-52.

Weise, J. (1916) Results of Dr. E. Mjoberg's Swedish Scientific Expedition to Australia 1910-1913, II. Chrysomeliden und Coccinelliden aus West-Australien. *Arkiv for Zoologi Utgifvet af k. Svenska Vetenskapsakademien*, 10, 1-51.

Weise, J. (1922) Ueber einige amerikanische und australische, nach Südfrankreich eingeführte Coccinelliden. *Wiender Entomologische Zeitung*, 34, 104.

APPENDIX A

World Checklist of Noviini

Tribe NOVIINI Ganglebauer, 1899

Noviini Ganglebauer, 1899: p. 954. Type genus: *Novius* Mulsant, 1850, by monotypy.

Suppressed for stability in family group names.

Noviaires Mulsant, 1850: p.938; alternate but accepted spelling.

Novii Weise, 1895: p. 148; misspelling.

Noviina Jacobson, 1916: p. 969; misspelling.

Rodolia Mulsant, 1850

Rodolia Mulsant, 1850: p. 902. (Type species: *Rodolia ruficollis*, by subsequent designation).

Nomius Mulsant, 1846: p. 4, misspelling; corrected by the author in the 'Addenda et Errata,' issued at the same time as the original work, but not paginated.

Novius Mulsant, 1850: p. 942 (Type species: *Novius cruentatus* Mulsant, 1846, by monotypy).

Macronovius Weise, 1885: p. 63; synonym (Korschefsky, 1931: p. 98).

Eurodolia Weise, 1895: p. 149. (Type species: *Eurodolia severini* Weise, 1895, by monotypy).

Anovia Casey, 1908: p. 408. (Type species: *Scymnus virginalis* Wickham, by monotypy).

1. *alluandi* Sicard

    Rodolia alluandi Sicard, 1909a: p. 119

    Rodolia equestris Sicard, 1909a: p. 120, synonym (Korschefsky, 1931: p. 98)

    Distribution: Madagascar

2. *andamanica* Weise

    Rodolia andamanica Weise, 1901: p. 93

    Distribution: India, Philippines

3. *apicalis* Sicard

    Rodolia apicalis Sicard, 1909: p. 119; *nomen dubium*

    Distribution: Madagascar

4. *argodi* Sicard

    Rodolia argodi Sicard, 1909: p. 142

    Rodolia pallens Sicard, 1909b: p. 142; synonym (Korschefsky, 1931: p. 99)

    Rodolia plagiata Sicard, 1909b: p. 142; synonym (Korschefsky 1931: p. 99)

    Distribution: Africa (Somalia)

5. *bella* (Blackburn)

    Novius bellus Blackburn, 1889: p. 188

    Rodolia bella Blackburn, 1889; new combination (Ślipiński, 2007: p.143)

    Distribution: Australia (New South Wales)

6. *canariensis* Korschefsky

    Novius canariensis Korschefsky, 1937: p. 2

    Rodolia canariensis Korschefsky, 1937: p. 2; new combination; *nomen dubium*

    Distribution: Spain (Canary Islands)

7. *capucina* Fürsch

Rodolia capucina Fürsch, 1975: p. 649; *nomen dubium*

8. *cardinalis* (Mulsant)

Vedalia cardinalis Mulsant, 1850: p. 906

Rodolia cardinalis Mulsant, 1850: p. 906; new combination (Weise, 1905: p. 220)

Eurodolia cardinalis Weise, 1895: p. 150; synonym (Priore, 1963: p. 65)

Novius tridens Lea, 1901: p. 492; new synonym

Novius immaculatus Lea, 1901: p. 492; new synonym

Rodolia aegyptiaca Sicard, 1907: p. 67; synonym (Korschefsky, 1931: p. 99)

Macronovius cardinalis Weise, 1922: p. 104; synonym (Korschefsky, 1931: p.98)

Macronovius cardinalis ab. *obnubilatus* Weise, 1922: p. 104; synonym (Korschefsky, 1931; p. 98)

Rodolia vitalisi Mader, 1955: p. 972; unnecessary replacement name.

Distribution: worldwide

9. *chapaensis* Hoang

Rodolia chapaensis Hoang, 1980: p. 13; *nomen dubium*

Distribution: India (Bangladesh)

10. *cinctipennis* Weise

Rodolia cinctipennis Weise, 1912: p. 52; *nomen dubium*

Distribution: Africa (Uganda)

11. *circumclusa* (Gorham)

Zenoria circumclusa Gorham, 1889, p. 262

Anovia circumclusa Gorham, 1889: p. 262; new combination (Gordon, 1971: p. 1)

Rodolia circumclusa Gorham, 1889: p. 262; new combination

Distribution: South America (Guatemala, Honduras); North America (Florida)

12. *concolor* (Lewis)

Novius concolor Lewis, 1879: p. 466.

Rodolia concolor Lewis, 1879: p. 466; new combination; *nomen dubium*

13. *cruentata* (Mulsant)

Novius cruentatus Mulsant, 1846: p. 214

Novius decempunctata Kraatz, 1862: p. 272; synonym (Reitter, 1906: p. 367)

Novius algiricus Crotch, 1874: p. 283

Novius intermedius Günther, 1947: p. 86

Rodolia cruentata Mulsant, 1846: p. 214; new combination

Distribution: Europe (France, Germany)

14. *delobeli* Chazeau

Rodolia delobeli Chazeau, 1981: p. 57; *nomen dubium*

Distribution: New Caledonia

15. *discoidalis* (Blackburn)

Novius discoidalis Blackburn, 1895: p. 253

Rodolia discoidalis Blackburn, 1895: p. 253; new combination; *nomen dubium*

Distribution: Australia

16. *dubia* Forrester & McHugh

Novius limbatus Blackburn, 1895: p. 254; junior homonym

Rodolia limbata Blackburn, 1895: p. 254; new combination (Ślipiński, 2007: p. 143)

Rodolia dubia Forrester & McHugh, 2008; new replacement name

Distribution: Australia

17. *fulvescens* Hoang

Rodolia fulvescens Hoang, 1980: p. 12; *nomen dubium*

Distribution: India (Bangladesh)

18. *fumida* (Mulsant)

Rodolia fumida Mulsant, 1850: p. 904

Vedalia fumida Mulsant, 1850: p. 904; synonym (Crotch, 1874: p. 281)

* Weise (1892) transferred this species back to *Rodolia*

Rodolia roseipennis Mulsant 1850, p. 904; synonym (Crotch, 1874: p. 281)

Rodolia chermesina Mulsant 1850, p. 905; synonym (Crotch, 1874: p. 282)

Epilachna sexnotata Mulsant, 1850: p. 807; synonym (Booth & Pope 1989: p. 363)

Rodolia sexnotata (Mulsant), 1850; new combination (Booth & Pope 1989: p. 363)

Rodolia rufopilosa Mulsant, 1850: p.903; new synonym

Epilachna arethusa Mulsant 1853, p. 126; synonym (Crotch, 1874: p. 281)

Epilachna testicolor Mulsant 1853, p. 127; synonym (Crotch, 1874: p. 281)

Vedalia Guerinii Crotch, 1874: p. 282; misspelling (Korschefsky 1931: p. 101)

Rodolia punctigera Weise, 1901: p. 93l; new synonym

Rodolia dionysia Sicard 1909, p. 116; synonym (Korschefsky, 1931: p. 101)

Rodolia immsi Weise, 1912: p. 120; synonym (Korschefsky 1931: p. 101)

Rodolia guerini Korschefsky, 1931: p. 101; synonym (Booth & Pope 1989: p. 363)

Rodolia formosana Korschefsky, 1935: p. 255; new synonym

Rodolia 6-maculata Korschefsky, 1940: p. 2; synonym (Kapur 1949: p. 535)

Distribution: China, India

19. *iceryae* Janson in Howard

Rodolia iceryae Janson in Howard, 1889: p. 91

Rodolia obscura Weise, 1898: p. 524; synonym (Raimundo, 1978: p. 35)

Rodolia ferruginea Weise, 1900: p. 130; new synonym

Rodolia senegalensis Weise, 1913: p. 226; new synonym

Distribution: Africa, India

20. *insularis* Weise

Rodolia insularis Weise, 1895: p. 55

Distribution: Madagascar

21. *koebelei* (Gordon)

Novius Koebelei Olliff, 1892: pl. 1 (published as a *nomen nudum*)

Rodolia koebelei Olliff, 1892: pl. 1, new combination (Ślipiński, 2007: p. 143)

Novius Koebelei Lea, 1902: p. 493; new synonym

Distribution: Australia

22. *limbata* (Motschulsky)

Novius limbatus Motschulsky, 1866: p. 178; synonym; (Lewis, 1896: p. 39)

Rodolia limbata Motschulsky, 1866: p. 178; new combination

Macronovius limbatus v. *fausti* Weise, 1885: p. 63; new synonym

Rodolia breviuscula Weise, 1892: p. 26; new synonym

Rodolia narae Lewis, 1896: p. 40; synonym (Kamiya, 1966: p. 89)

Rodolia cinctipennis Weise, 1912: p. 52; new synonym

Rodolia quadrimaculata Mader, 1939: p. 48; new synonym

Rodolia quadrimaculata ab. *6-maculata* Mader, 1939: p. 49; new synonym

Distribution: Africa (Uganda), China, India, Japan

23. *lindi* (Blackburn)

Novius lindi Blackburn, 1889: p. 188

Rodolia lindi Blackburn, 1889: p. 188; new combination (Ślipiński 2007: p. 143)

Distribution: Australia

24. *marginata* Bielawski

Rodolia marginata Bielawski, 1960; *nomen nudum*

25. *mexicana* (Gordon)

Anovia mexicana Gordon, 1972: p. 29

Rodolia mexicana Gordon 1972: p. 29; new combination

Distribution: MIddle America (Mexico)

26. *minuta* Sicard

Rodolia minuta Sicard, 1909: p. 118; *nomen dubium*

Distribution: Madagascar

27. *nigerrimus* Fürsch

Rodolia nigerrimus Fürsch, 1960: p. 447; *nomen dubium*

Distribution: Africa

28. *nigra* Fürsch

Rodolia nigra Fürsch, 1995.

Distribution: Africa (Zimbabwe)

29. *obscuricollis* Sicard

Rodolia obscuricollis Sicard, 1931: p. 229; *nomen dubium*

Distribution: Europe (United Kingdom)

30. *occidentalis* (Weise) 1898

Rodolia occidentalis Weise, 1898: p. 122.

Rodolia marginalis Mader 1954: p. 34. (aberration of *R. occidentalis*)

Distribution: Africa (Cameroon)

31. *podagrica* Weise

Rodolia podagrica Wesie, 1908: p. 307.

Rodolia amabilis Kapur, 1949: p. 536; new synonym

Distribution: India

32. *prosternalis* Sicard

Rodolia prosternalis Sicard, 1909: p. 118; *nomen dubium*

Distribution: Madagascar

33. *pumila* Weise

Rodolia pumila Weise, 1892: p. 26

Rodolia okinawensis Miyatake, 1959: p. 127; synonym (Sasaji 1971, p. 239)

Rodolia vulpina Fürsch, 1974: p. 23; new synonym

Distribution: Africa, China, Japan

34. *punica* (Gordon) 1972

Anovia punica Gordon, 1972: p. 29

Rodolia punica Gordon, 1972: p. 29; new combination

Distribution: Middle and South America

35. *quadriplagiata* Sicard

Rodolia quadriplagiata Sicard, 1909: p. 121; *nomen dubium*

Distribution: Madagascar

36. *quadrispilota* Sicard

Rodolia quadrispilota Sicard, 1909: p. 120 *nomen dubium*

Distribution: Madagascar

37. *rubea* Mulsant

Rodolia rubea Mulsant, 1850: p. 902

Rodolia carneipellis Mulsant, 1853: p. 131; synonym (Korschefsky 1931:p. 102)

Rodolia carneipennis Mader, 1927: p. 763; misspelling (Korschefsky 1931: p. 102)

Distribution: India

38. *rubra* (Blackburn)

Novius ruber Blackburn, 1889: p. 148

Rodolia rubra Blackburn, 1889; new combination (Ślipiński 2007: p. 143); *nomen dubium*

Distribution: Australia

39. *rufocincta* Lewis

Rodolia rufocincta Lewis, 1896: p. 40; *nomen dubium*

Distribution: Japan

40. *severini* (Weise)

Rodolia severini Weise, 1895: p. 150.

Rodolia severini Weise, 1895: p. 150; new combination (Ślipiński 2007: p. 143); *nomen dubium*.

41. *songchuana* Hoang

Rodolia songchuana Hoang, 1980: p. 12; *nomen dubium*

Distribution: India (Bangladesh)

42. *tamdaoana* Hoang

Rodolia tamdaoana Hoang, 1980: p. 12; *nomen dubium*

Distribution: India (Bangladesh)

43. *tripustulata* (Blackburn)

Novius tripustulatus Blackburn, 1895: p. 254.

Rodolia tripustulata Blackburn, 1895, new combination (Ślipiński 2007: p. 143).

44. *usambarica* Weise

Rodolia usambarica Weise, 1898: p. 201

Distribution: Africa (Tanzania)

45. *virginalis* (Wickham)

Scymnus virginalis Wickham, 1905: p. 166; synonym (Casey, 1908: p. 408)

Anovia virginalis Wickham, 1905: p. 166; new combination (Casey, 1908: p. 408)

Rodolia virginalis Wickham, 1905: p. 166; new combination

Distribution: Middle America (Mexico); North America (Utah)

46. *weisei* (Gordon)

Anovia weisei Gordon, 1972: p. 30

Rodolia weisei Gordon, 1972: p. 30; new combination

Distribution: Middle America (Guatemala)