SYSTEMATICS OF LADYDIRD BEETLES (COLEOPTERA: COCCINELLIDAE)

by

JOSÉ ADRIANO GIORGI

(Under the Direction of Joseph V. McHugh)

ABSTRACT

Despite the familiarity and economic significance of Coccinellidae, the family has thus far escaped analysis by rigorous phylogenetic methods. As a result, the internal classification remains unstable and there is no framework with which to interpret evolutionary events within the family. We analyzed coccinellid phylogeny using a combined dataset of seven genes: 12S rDNA, 16S rDNA, 18S rDNA, 28S rDNA, Cytochrome oxidase I, Cytochrome oxidase II, and Histone 3. The entire dataset consists of 6565 aligned nucleotide sites, 1305 of which are parsimony informative. Our study included 20% of the generic-level diversity and 80% of the tribal-level diversity and 100% previously recognized subfamilies. We analyzed the dataset using parsimony and Bayesian methods. Our study supports the monophyly of Coccinellidae; however, most of the traditional subfamilies are not supported as monophyletic. Three recently proposed, but not widely accepted, subfamilies are recognized. A new subfamily is proposed to accommodate Monocoryni. We recognize eight subfamilies of Coccinellidae: Microweiseinae, Monocorynae (**new subfamily**), Coccinellinae, Chilocorinae, Sticholotidinae, Scymninae, Exoplectrinae, and Hyperaspidinae. The circumscription of Hyperaspidinae (Hyperaspidini Mulsant, Brachiacanthini Mulsant and Selvadiini Gordon) is extended to accommodate Platynaspidini Redtenbacher and Aspidimerini Mulsant. The tribe Coccinellini Latreille is paraphyletic with respect to Tytthaspidini Mulsant (**syn. nov.)** and Halyziini Mulsant (confirmed status). The tribes Noviini Mulsant, Cryptognathini Casey, Poriini Mulsant, and Diomini Gordon are treated as *incertae sedis*. The relationship between some of the subfamilies and the placement of several tribes remain ambiguous. We also utilized the phylogenetic hypothesis to provide an evolutionary perspective on the feeding preferences of coccinellids. Coccinellids exhibit a wide range of preferred food types, spanning kingdoms and trophic levels. Our study suggests that the ancestral feeding condition for the family is coccidophagy and that polyphagy served as an evolutionary stepping stone for primarily predaceous groups to adopt new feeding habits.

The Australian members of the ladybird beetle tribe Chilocorini are revised. Identification keys for genera and species are provided. Habitus and diagnostic characters from mouthparts, legs, and genitalia are illustrated. Major conclusions of the present study include recognition of the following: (1) five new species; (2) eleven junior synonyms at the species level; one junior synonym at the generic level; and (3) sixteen new lectotypes. According to our study, the Chilocorini in Australia consists of 23 species classified in 6 genera: *Brumoides, Chilocorus, Exochomus, Halmus, Orcus* and *Trichorcus*.

INDEX WORDS: Coleoptera, Cucujoidea, Cerylonid Series, Coccinellidae, ladybird beetle, lady beetle, ladybug, systematics, phylogeny, evolution, food preference, prey, trophic shift, taxonomic revision, Chilocorinae, Chilocorini, Australia.

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DEDICATION

I dedicate this dissertation to Dona Norma, my mom.

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CHAPTER 1

INTRODUCTION

This dissertation, written in article style, presents three separate research projects that aim to improve our knowledge about the evolution, phylogenetics and taxonomy of the ladybeetle family Coccinellidae.

In the first study (chapter 3), the evolution of feeding patterns for the family Coccinellidae is interpreted under the phylogenetic framework using molecular data from two ribosomal genes. Coccinellidae is remarkable for many of its feeding habits. While all their closest relatives from Cerylonid Series (C.S.) are primarily mycophagous, most coccinellids are predacious on other insects. In the C.S., isolated transitions to predation or parasitism are known for only a few species from the families Endomychidae and Bothrideridae. Strict phytophagy is another evolutionary step taken by the coccinellids that it is not seen in any other family of the C.S. Finally, the widespread mycophagous condition in the C.S., is rare in coccinellids and restricted to a group of advanced forms in the family. Given the fact that Coccinellidae represents more than 50% of the species diversity within the C.S., such ability to exploit a vast array of food items is possibly a key feature for the evolutionary success of Coccinellidae in terms of biodiversity.

The second study (chapter 4) is a high-level molecular phylogenetic analysis of Coccinellidae. The data set from the previous study is expanded to seven genes and many additional specimens. In this study we tested the previous systems of classification proposed for the family. The monophyly of the formally proposed subfamilies is tested and the relationships between the tribes investigated. To better represent the evolutionary history of Coccinellidae, some modifications in the classification of the family are proposed based on phylogenetic relationships suggested in this study.

Finally, in the last study, a taxonomic revision of the Australian Chilocorini is presented. This study constitutes part of a series of studies that aim to revise all the Australian species of ladybird beetle. In this study, identification keys for genera and species are provided and habitus and diagnostic characters from mouthparts, legs, and genitalia illustrated.

CHAPTER 2

LITERATURE REVIEW

Redtenbacher (1844) proposed the first subfamilial classification system for Coccinellidae by recognizing two biologically defined groups, the plant feeders and the aphid feeders. The phytophagous group corresponds to the current subfamily Epilachninae but the aphidophagous group spans the other currently recognized subfamilies. Mulsant (1846, 1850) also divided the family into two groups: the hairy species ("Trichoisomides") and the glabrous ones ("Gymnosomides"), but this system was even more artificial than its predecessor. Mulsant (1846; 1850), however, made an important contribution to coccinellid classification by recognizing supra-generic categories that correspond to the current tribes in Coccinellidae. In Korschefsky's (1931) classification three subfamilies are recognized: Epilachninae, Coccinellinae, and Lithophilinae. This system is consistent with that of Redtenbacher but it further subdivided the carnivores ("aphidophagous") on the basis of the tarsal structure. Despite these advances, the classification of Coccinellidae was still rudimentary and extremely artificial until the second half of the 20th century.

Sasaji (1968; 1971a, b) proposed a revised classification based on a careful investigation of larval and adult morphology. His system of six subfamilies (Sticholotidinae, Coccidulinae, Scymninae, Chilocorinae, Coccinellinae and Epilachninae) was widely accepted and remains the primary reference for the family (e.g., Booth et al., 1990; Pakaluk et al., 1994; Lawrence and Newton, 1995; Kuznetsov, 1997).

Additional subfamilies have since been recognized: Azyiinae and Exoplectrinae, elevated from tribal status (Gordon, 1994); Ortaliinae, for Ortaliini plus Noviini (Kovář, 1996); and Hyperaspidinae, for Hyperaspidini plus Brachiacanthini (Duverger 1989; 2001). In a work published posthumously, Duverger (2003), attached a distinct subfamily name to each of the 18 major groupings in Kovář 's dendrogram (1996), but unfortunately, a number of these names were invalid (based on junior synonyms), misspelled, or applied inconsistently within the different sections of the same paper. Ślipiński (2007) attempted to reverse current trends by suggesting a system based on only two subfamilies: Microweiseinae (=Scotoscymninae Duverger), for the "primitive" members of Sticholotidinae and a very broadly defined Coccinellinae for the remaining taxa. None of these various classifications has received a universal following.

Many regional taxonomic monographs have been published in the last three decades, including: Fürsch (1967) [European fauna]; Gordon (1985) [North America]; Hoang (1982; 1983) [Vietnam]; Iablokoff-Khnzorian (1982) [Palearctic and Oriental regions]; Kuznetsov (1997) [Russian Far East]; Pang and Mao (1979) [China]; Pope (1989) [Australian Coccinellinae]; Sasaji (1971a) [Japan]; and Savoiskaya (1983) [Central Asia and parts of the former USSR].

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CHAPTER 3

THE EVOLUTION OF FOOD PREFERENCE IN COCCINELLIDAE[2]

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Abstract

Despite the familiarity and economic significance of Coccinellidae, the family has thus far escaped analysis by rigorous phylogenetic methods. As a result, the internal classification remains unstable and there is no framework with which to interpret evolutionary events within the family. Coccinellids exhibit a wide range of preferred food types, spanning kingdoms and trophic levels. To provide an evolutionary perspective on coccinellid feeding preferences, we performed a phylogenetic analysis of 62 taxa based on the ribosomal nuclear genes 18S and 28S. The entire dataset consists of 3,957 aligned nucleotide sites, 787 of which are parsimony informative. Bayesian and parsimony analyses were performed. Host preferences were mapped onto the Bayesian tree to infer food preference transitions. Our results indicate that the ancestral feeding condition for Coccinellidae is coccidophagy. From the ancestral condition, there have been at least three transitions to aphidophagy and one transition to leaf-eating phytophagy. A second transition to leaf-eating phytophagy arose within an aphidophagous/pollinivorous clade. The mycophagous condition in Halyziini originated from aphidophagy. Our findings suggest that polyphagy served as an evolutionary stepping stone for primarily predaceous groups to adopt new feeding habits. The analyses recovered a clade comprising Serangiini plus Microweiseini as the sister group to the rest of Coccinellidae. The subfamilies Coccinellinae and Epilachninae are monophyletic; however, Sticholotidinae, Chilocorinae, Scymninae and Coccidulinae are paraphyletic. Our results do not support the traditional view of phylogenetic relationships among the coccinellid subfamilies. These results indicate that the current classification system poorly reflects the evolution of Coccinellidae and therefore requires revision.

Introduction

Of all the predaceous beetle groups, perhaps the most familiar to non-specialists is the lady beetle family, Coccinellidae. It is widely known that this charismatic group includes many beneficial species that are voracious predators of pestiferous aphids and scale insects. Indeed, the first successful classical biological control effort involved the introduction of the vedalia beetle, *Rodolia cardinalis* (Mulsant), to control cottony cushion scale, *Icerya purchasi* Maskell (Heteroptera: Margarodidae), on citrus plants in California during the late 1880's (Caltagirone and Doutt, 1989).

Despite this familiar stereotype of the family, Coccinellidae is far from homogeneous with respect to feeding behavior (Figs. 3.1-3.8, Table 3.1). While most coccinellids are predaceous, some are specialists on plant material (e.g., leaves), whereas others feed on fungi (Sutherland and Parrella, 2009, this issue). Even among the predaceous coccinellids, feeding preferences vary widely. Most of the preferred prey belong to the hemipteran suborder Sternorrhyncha (aphids, aldelgids, scales, mealybugs, whiteflies, and psyllids) (Hodek and Honěk, 2009; Obrycki et al., 2009, this issue), but there are significant deviations from this pattern. Some coccinellid species are known to feed on ants (Hymenoptera: Formicidae) (Harris, 1921; Pope and Lawrence, 1990; Samways et al., 1997; Majerus et al., 2007). Other coccinellid species are specialists on non-insects; for example, all members of the tribe Stethorini prey on tetranychid mites (Biddinger et al., 2009, this issue). Thus, the evolution of Coccinellidae includes feeding transitions that cross kingdoms of life (Plant, Animal, Fungus) and trophic levels (e.g., herbivore, primary carnivore).

Some feeding behaviors of Coccinellidae are especially interesting given the phylogenetic position of the family. Coccinellidae is part of a monophyletic group, the

Cerylonid Series (C. S.), which includes seven other families of cucujoid beetles: Alexiidae, Bothrideridae, Cerylonidae, Corylophidae, Discolomatidae, Endomychidae, and Latridiidae (Crowson, 1955; Robertson et al., 2008). The C. S. includes approximately 9,600 species divided among 646 genera (Robertson et al., 2008). Within this large and diverse clade, Coccinellidae is remarkable for many of its feeding habits. In the C. S. clade, strict phytophagy is extremely rare and possibly limited to the coccinellid subfamily Epilachninae and the coccinelline genus *Bulaea* Mulsant, although there is an isolated report of an endomychid, *Eumorphus quadriguttatus* (Illiger), inflicting damage on betel pepper plants, *Piper betel* (L.) (Piperaceae) (Mondal et al., 2003).

Even the predominantly predatory habit of Coccinellidae is odd because it constitutes a major exception to the general feeding patterns of the C. S. clade. The other seven C. S. families are primarily mycophagous, with isolated transitions to predation or parasitism being known for only two groups, the genus *Saula* Gerstaecker (Endomychidae) (Sasaji, 1978; Takagi and Ogata, 1985; Wen, 1995; Takagi, 1999; Leschen, 2000; Chien et al., 2002) and the subfamily Bothriderinae (Bothrideridae) (Crowson, 1981). *Saula japonica* Gorham preys mainly on scale insects, but is known to feed occasionally on Aleyrodidae (Hemiptera) and Acari (Sasaji, 1978). Bothriderinae are ectoparasites or predators of the immature stages of wood-dwelling Coleoptera and Hymenoptera (Crowson, 1981; Lawrence, 1991).

Given the relevance of coccinellids for biological control, much attention has been given to documenting feeding habits within the family. Although we now have a rudimentary understanding of the food preferences for many species of Coccinellidae, the broad scale evolutionary patterns of these traits remain unclear.

The lack of a phylogenetic framework for the family remains an impediment to understanding the general feeding patterns that have been observed. Since the advent of modern phylogenetic theory and practice, there have been a few attempts to address the higher-level phylogenetic relationships of Coccinellidae (Sasaji, 1971a; Yu, 1994; Kovář, 1996). Unfortunately, these studies lack a broad taxonomic representation and did not utilize modern phylogenetic methodologies.

The goal of this contribution is to conduct a rigorous phylogenetic analysis of Coccinellidae to provide a framework within which to interpret the evolution of feeding patterns for the family. A general overview of coccinellid classification, phylogeny, and food preferences is provided. Comprehensive treatments of these subjects have been published recently by Hodek and Honěk (1996) (food preferences and classification), Sloggett and Majerus (2000) (food preferences), Ślipiński (2007) (food preferences and classification), and Vandenberg (2002) (classification).

Food preference

Coccinellids consume many of the same foods as larvae and adults (Majerus, 1994; Hodek, 1996; Vandenberg, 2002). Indirectly, the female even selects the first meals for her offspring by ovipositing in the same area where she has been feeding (Seagraves, 2009, this issue). However, not all the foods regularly consumed by adult beetles are nutritionally adequate for reproduction, egg maturation, or larval development. Pollinivory, for example, is common in so-called “predatory” species but has been found to provide an adequate larval diet for only a few select genera (as discussed below; Lundgren 2009a, this issue).

Three major categories of feeding habits generally are recognized for coccinellids: predation (zoophagy), plant feeding (phytophagy) and fungus feeding (mycophagy) (Figs. 3.1-3.5). Most coccinellid species are predaceous on honeydew-producing insects from the hemipteran suborder Sternorrhyncha, although some prefer other arthropod prey. Departing from this predatory habit are the leaf-eaters, which are grouped within Epilachninae and the genus *Bulaea*, and the fungus feeders, which comprise two small groups from within Coccinellinae, Halyziini and some Tytthaspidini.

Many coccinellid species are known to utilize alternative food items (Figs. 3.6-3.9) (Lundgren, 2009a, this issue) in the absence of their preferred ones, leading to the distinction between "essential" food sources (i.e., those sufficient for larval development and adult oviposition) (Hodek, 1973; 1996) and merely facultative food sources. The use of honeydew, pollen, sap, nectar, and various fungi as alternative food sources is widespread among the predaceous groups (Pemberton and Vandenberg, 1993; Triltsch, 1997; Lundgren, 2009b), as is the exploitation of secondary or less favorable prey species (Hodek, 1973; 1996; Triltsch, 1997). In addition, studies by Moser et al. (2008) and Lundgren et al. (2009) suggest that species generally regarded as predaceous may regularly supplement their basic diet with small amounts of leaf material even in the presence of abundant prey and water (zoophytophagy).

Polyphagy also occurs among at least some mycophagous coccinellids which often complement their diet with pollen (Anderson, 1982; Ricci, 1982; 1986; Ricci et al., 1983). The most dietarily restricted coccinellids seem to be the Epilachninae. Thus far, there are no reports of these phytophagous species feeding on anything other than plant tissue.

The hemipteran suborder Sternorrhyncha is divided into four major divisions: Aphidoidea, Psylloidea, Aleyrodoidea, and Coccoidea (Gullan and Martin, 2003; Gullan and

Cook, 2007). All three families of Aphidoidea are essential foods for some predaceous coccinellids. Aphids are the preferred prey of most Coccinellini (Ślipiński, 2007), Platynaspidini (Sasaji, 1971a; Ślipiński, 2007), and most Aspidimerini (Poorani, 2001). In the Scymnini, aphids are the primary food source for species of *Apolinus* Pope and Lawrence (Anderson, 1981; as *Scymnodes* spp.) and most species of the large genus *Scymnus* Kugelann (Gordon, 1976). At least one instance of essential prey food in the Phylloxeridae has been reported. Wheeler and Jubb (1979) observed *Scymnus cervicalis* Mulsant preying on grape phylloxera (*Daktulosphaira vitifoliae* [Fitch]) in Pennsylvania, USA.

Psylloidea are an essential and possibly preferred food item for some Coccinellini (Hodek and Honěk, 2009, this issue) such as some species of *Calvia* Mulsant (Gordon, 1985) and *Olla* Casey (Michaud, 2001), although these predators also consume and reproduce on aphids. Psyllid-feeding has been reported in the myrmecophilous *Ortalia ochracea* Weise (Ortaliinae) (Samways et al., 1997).

Aleyrodidae are the preferred food choice for the Serangiini (Sticholotidinae). Two important sticholotidine predators of *Bemisia* whiteflies are *Serangium parcesetosum* Sicard (Al-Zyoud and Sengonca, 2004) and *Delphastus catalinae* (Horn) (Simmons et al., 2008). Within Scymninae, the genera *Zilus* Mulsant (Scymnillini) and *Nephaspis* Casey (Scymnini) also feed primarily on whiteflies (Gordon, 1985; 1994). *Nephaspis oculatus* (Blatchley) is another important predator of *Bemisia* whiteflies (Liu and Stansly, 1996; Crowder, 2006).

The vast majority of the Scymninae, Chilocorinae, Sticholotidinae and Coccidulinae prey on Coccoidea, and lady beetle predators of scale insects are represented disproportionately among the successful biological control programs that utilize introduced Coccinellidae (Drea and Gordon, 1990; Gordon, 1985). Although the Diaspididae (armored scales) are by far the most widely exploited prey group (Drea and Gordon, 1990), several other coccoid families are represented by known prey species, including Asterolecaniidae (pit scales), Cerococcidae (ornate pit scales), Coccidae (soft scales), Dactylopiidae (cochineal insects), Eriococcidae (felt scales), Kermesidae (gall-like coccids), Margarodidae (ground pearls), Monophlebidae (giant scales), Ortheziidae (ensign coccids), and Pseudococcidae (mealybugs).

A few coccinellids feed on bugs of the suborders Heteroptera and Auchenorrhyncha. Adults and larvae of *Synona melanaria* (Mulsant) (Coccinellini) feed on the eggs and nymphs of various species of *Coptosoma* Laporte (Heteroptera: Plataspidae) (Afroze and Uddin, 1998; Poorani et al., 2008). A relatively large African species of Coccinellini, *Anisolemnia tetrasticta* Fairmaire, preys on immatures of Plataspidae (Dejean et al., 2002). Some species of *Micraspis* Chevrolat (Coccinellini) are important predators of brown planthoppers (Auchenorrhyncha: Delphacidae) in rice (Shepard and Raspusas, 1989; Begum et al., 2002). *Naemia seriata* (Melsheimer) (Coccinellini) feeds on adults and nymphs of *Prokelisia* planthoppers (Delphacidae) (Finke, 2005). Adults and larvae of *Micraspis* and *Naemia* also feed extensively on the pollen produced by the host plants of their delphacid prey.

Among the predaceous Coccinellidae, there are relatively few departures from the widespread reliance on hemipteran prey. The greatest deviation occurs in Stethorini (Scymninae) which prey on spider mites and false spider mites (Acari: Tetranychidae and Tenuipalpididae) (Biddinger et al., 2009, this issue), the only non-insects regularly utilized as essential prey by lady beetles (Gordon and Chapin, 1983; Gordon, 1985). Ants represent another unusual prey item that is utilized by relatively few lady beetles (e.g., *Bucolus fourneti* Mulsant (Coccidulinae) (Ślipiński, 2007), *Ortalia ochracea, O. pallens* Mulsant (Ortaliini) (Harris, 1921; Samways et al., 1997; Majerus et al., 2007)*,* and *Scymnodes bellus* Pope and Lawrence (Scymnini) (Pope and

Lawrence, 1990). Majerus et al. (2007) provide an extensive review on the interactions between coccinellids and ants. Six species of Coccinellini (Coccinellinae) have been recorded as specialized predators of the immature stages of Chrysomelidae (Coleoptera): *Aiolocaria hexaspilota* (=*mirabilis*) Hope (Iwata, 1932; 1965; Savoiskaya, 1970), *Calvia quindecimguttata* L. (Kanervo, 1940), *Coccinella hieroglyphica* L. (Hippa et al., 1977; 1978; 1982; 1984), *Oenopia conglobata* (L.) (Kanervo, 1940; 1946), *Propylea quatuordecempunctata* L. (Iablokoff-Khnzorian, 1982), and *Neoharmonia venusta* (Melsheimer) (Whitehead and Duffield, 1982). In addition to the non-hemipteran hosts mentioned above, the larvae of Diptera, Lepidoptera, and Thysanoptera also are utilized as prey by some coccinellids (Hodek, 1973; 1996; Evans, 2009, this issue).

Some coccinellids have adopted an arthropod-free diet, relying instead on fungal or plant material for their primary source of nourishment. The conidia and hyphae of powdery mildews (Ascomycota: Erysiphales) appear to be the main food source for all members of Halyziini (e.g., *Psyllobora* Mulsant, *Halyzia* Mulsant, *Thea* Mulsant, *Illeis* Mulsant (=*Leptothea* Weise), and *Vidibia* Mulsant) (Turian, 1969; Hodek, 1973; Gordon, 1985; Vandenberg, 2002; Ślipiński, 2007; Sutherland and Parrella, 2009, this issue). Another tribe of Coccinellinae, Tytthaspidini, also includes species that favor mycophagy (e.g., *Tytthaspis sedecimpunctata* (L.) (Turian, 1969)); however, these species have not completely abandoned predation (Ricci, 1982).

All members of the subfamily Epilachninae are leaf-eating herbivores. Epilachnini feed on Aristolochiaceae, Curcubitaceae, Solanaceae (Gordon, 1975), Berberidaceae, Asteraceae (Hirai et al., 2006), Poaceae (Beyene et al., 2007; Igbinosa et al. 2007), and Fabaceae (Vandenberg, 2002). The Cynegetini have been reported to eat only Fabaceae (Kuznetsov, 1997). Outside Epilachninae, leaf-eating has been reported for *Bulaea lichatschovi* (Hummel)

(Coccinellinae: Tytthaspidini) (Savoiskaya, 1970). *Coleomegilla* Cockerell, *Micraspis*, and *Harmonia* Mulsant have been reported to feed on plant tissue. Moser et al. (2008) demonstrated that *Coleomegilla* and *Harmonia* larvae regularly ingest small amounts of plant tissue from the leaves and coleoptiles of corn seedlings even in the presence of abundant prey, and Pathak et al. (1994) found that, while *Micraspis* spp. generally play a beneficial role in controlling rice plant pests, both adults and larvae will damage leaf blades, hulls, and even developing rice grains in the absence of prey.

Pollen, honeydew, and nectar constitute a significant, if not essential, food item for most coccinellids (Hodek, 1973; Pemberton and Vandenberg, 1993; Lundgren, 2009a, this issue; 2009b). Pollen is a major component in the diet of *Tytthaspis sedecimpunctata* (L.) (Ricci et al., 1983; Ricci, 1986) and also has been reported to be an essential food for *Bulaea lichatschovi,* and some congeners (Capra, 1947; Savoiskaya, 1983). Among the carnivores, species of *Coleomegilla* and *Micraspis* feed extensively on pollen (Britton, 1914; Putman, 1964; Benton and Crump, 1981; Turner and Hawkeswood, 2003; Omkar, 2006; Lundgren et al., 2004; 2005; Lundgren, 2009b) and are among the few primarily predaceous species documented as capable of completing their life cycle on a pollen-only diet (Smith, 1960; Shepard and Raspusas, 1989; Lundgren and Wiedenmann, 2004).

Classification

Redtenbacher (1844) proposed the first subfamilial classification system for Coccinellidae by recognizing two biologically defined groups, the plant feeders and the aphid feeders. The phytophagous group corresponds to the current subfamily Epilachninae but the aphidophagous group spans the other currently recognized subfamilies. Mulsant (1846, 1850) also divided the family into two groups: the hairy species (“Trichoisomides”) and the glabrous ones (“Gymnosomides”), but this system was even more artificial than its predecessor. Mulsant (1846; 1850), however, made an important contribution to coccinellid classification by recognizing supra-generic categories that correspond to the current tribes in Coccinellidae. In Korschefsky’s (1931) classification three subfamilies are recognized: Epilachninae, Coccinellinae, and Lithophilinae. This system is consistent with that of Redtenbacher but it further subdivided the carnivores (“aphidophagous”) on the basis of the tarsal structure. Despite these advances, the classification of Coccinellidae was still rudimentary and extremely artificial until the second half of the 20th century.

Sasaji (1968; 1971a, b) proposed a revised classification based on a careful investigation of larval and adult morphology. His system of six subfamilies (Sticholotidinae, Coccidulinae, Scymninae, Chilocorinae, Coccinellinae and Epilachninae) was widely accepted and remains the primary reference for the family (e.g., Booth et al., 1990; Pakaluk et al., 1994; Lawrence and Newton, 1995; Kuznetsov, 1997).

Additional subfamilies have since been recognized: Azyiinae and Exoplectrinae, elevated from tribal status (Gordon, 1994); Ortaliinae, for Ortaliini plus Noviini (Kovář, 1996); and Hyperaspidinae, for Hyperaspidini plus Brachiacanthini (Duverger 1989; 2001). In a work published posthumously, Duverger (2003), attached a distinct subfamily name to each of the 18 major groupings in Kovář 's dendrogram (1996), but unfortunately, a number of these names were invalid (based on junior synonyms), misspelled, or applied inconsistently within the different sections of the same paper. Ślipiński (2007) attempted to reverse current trends by suggesting a system based on only two subfamilies: Microweiseinae (=Scotoscymninae Duverger), for the “primitive” members of Sticholotidinae and a very broadly defined

Coccinellinae for the remaining taxa. None of these various classifications has received a universal following (see Table 3.2 for a comparison of some of these contemporary classification systems).

Many regional taxonomic monographs have been published in the last three decades, including: Fürsch (1967) [European fauna]; Gordon (1985) [North America]; Hoang (1982; 1983) [Vietnam]; Iablokoff-Khnzorian (1982) [Palearctic and Oriental regions]; Kuznetsov (1997) [Russian Far East]; Pang and Mao (1979) [China]; Pope (1989) [Australian Coccinellinae]; Sasaji (1971a) [Japan]; and Savoiskaya (1983) [Central Asia and parts of the former USSR].

Because these treatments were geographically limited, many of the new genera and tribes proposed in them have ranges that are restricted to the geographical scope of the studies, even though the subfamilies are distributed worldwide (Vandenberg, 2002). This has resulted in many alternative classifications (see Table 3.2), none of which are easily reconciled (Vandenberg, 2002).

Phylogeny

Although the monophyly of the C. S. is well supported by molecular data (Hunt et al., 2007; Robertson et al., 2008), the closest relative of Coccinellidae remains unclear. Morphological considerations supported hypotheses that the sister-group was a clade comprising Endomychidae plus Corylophidae (Sasaji, 1971a; Crowson, 1981) or one comprising Endomychidae plus Alexiidae (Ślipiński and Pakaluk, 1991). These hypotheses were strictly intuitive, not based on formal phylogenetic analyses.

There have been formal phylogenetic studies of other C. S. taxa which provide insights about the closest relatives of Coccinellidae. Each of these studies, however, addressed different phylogenetic questions, so taxonomic sampling differed. In these studies, the following taxa were recovered as close relatives of Coccinellidae: Endomychidae (Tomaszewska, 2000), Anamorphinae (Endomychidae) plus Alexiidae (Hunt et al., 2007), and Corylophidae (Tomaszewska, 2005). In a parsimony analysis Robertson et al. (2008) found Leiestinae (Endomychidae) to be the sister taxon to Coccinellidae; however, a Bayesian analysis of the same data was ambiguous, suggesting that the sister group was either Endomychidae minus Anamorphinae, or Corylophidae plus Anamorphinae.

There have been a few attempts to address the higher-level phylogenetic relationships of Coccinellidae. Sasaji (1968; 1971a, b) and Kovář (1996) provided intuitive hypotheses (Figs. 3.10-3.11), not generated by formal phylogenetic methods. The relationships proposed by Sasaji (1968; 1971a, b) have received widespread acceptance. Under this hypothesis (Fig. 3.10), the subfamily Sticholotidinae is considered the most "primitive" group in the family, diverging from the rest of the coccinellids at the most basal split. On the main branch, two other major lineages were proposed: one including the subfamilies Scymninae and Chilocorinae, and the other including Coccidulinae, Coccinellinae and Epilachninae. In the latter group, Coccidulinae was considered the sister group to the Coccinellinae plus Epilachninae branch.

Kovář (1996) modified Sasaji's hypothesis by moving Coccidulinae to the base of the Scymninae plus Chilocorinae branch (Fig. 11) and by recognizing a new subfamily, Ortaliinae, which represented Noviini (previously in Coccidulinae) and Ortaliini (previously in Scymninae). Kovář considered the Ortaliinae to be the sister taxon to the Coccinellinae plus Epilachninae branch.

Yu (1994) conducted cladistic analyses using adult and larval morphological characters to address higher level relationships; however, the two data partitions (adult and larval characters) were analyzed separately and produced drastically conflicting topologies. The adult-based topology (Fig. 3.12) maintained Sticholotidinae at the base, but did not recover the subfamily as monophyletic. Epilachninae diverged from the rest of the family at the next highest node, followed by the Coccinellinae. In the sister group to the latter, Coccidulinae was recovered as paraphyletic with respect to Ortaliinae, Chilocorinae, and Scymninae. Chilocorinae and Ortaliinae were nested within Scymninae, rendering it paraphyletic. Epilachninae was recovered as basal in the larval analysis, and was the only monophyletic subfamily recovered. A close relationship between Serangiini and Sukunahikonini was the only point of similarity between the adult and larval topologies.

Materials and methods

Taxon sampling

For the purpose of this study, the tribal and subfamilial classification scheme of Kovář (1996) was followed because it represents the most recent, global treatment of the family. One synonymy adopted subsequently (Cynegetini = Madaini) is recognized in the current paper. Taxonomic exemplars for this analysis (Table 3.3) were obtained for 24 of 38 coccinellid tribes: Chilocorini, Platynaspidini, and Telsimini (Chilocorinae); Coccinellini, Discotomini, Halyziini, and Tytthaspidini (Coccinellinae); Azyini, Coccidulini, Cranophorini, Exoplectrini, and Poriini (Coccidulinae); Epilachnini and Cynegetini (Epilachninae); Ortaliini (Ortaliinae); Aspidimerini, Brachiacanthini, Diomini, Hyperaspidini, Scymnini, and Stethorini (Scymninae); and Microweiseini, Serangiini, and Sticholotidini (Sticholotidinae). This taxon sampling represents all 11 formally proposed subfamilies, excluding those elevated only by Duverger (2003). The outgroup taxa comprise five representatives from three C.S. families: Discolomatidae (1), Endomychidae (3), and Latridiidae (1). One representative of the family Erotylidae, a non-C. S. cucujoid, also was included in the analysis as a distant outgroup. Thus, a total of 62 (56 ingroup and 6 outgroup) taxa were represented in this study.

Nuclear sampling and laboratory procedures

Genomic DNA was extracted using the Qiagen DNeasy tissue kit (Valencia, CA). Target genes 18S rDNA and 28S rDNA were amplified via polymerase chain reaction (PCR). PCR primers and protocols are published elsewhere (Jarvis et al., 2004; Whiting, 2002). Primer combinations utilized for 18S include 1F + B3.9, a0.7 + bi and a2.0 + 9R (Whiting, 2002; Jarvis et al., 2004). Primer combinations used for 28S include 1a + 28Sb, 28Sa + 5b and 3.8a + 7b1 (Whiting, 2002). PCR product yield, specificity, and potential contamination were monitored by agarose gel electrophoresis. PCR products were purified using MANU96-well filtration plates, sequenced using D-rhodamine chemistry, and fractionated on an ABI3730 DNA analyzer at the Brigham Young University (BYU) DNA Sequencing Center. Assembly of contig sequences and editing of nucleotide fragments were performed using Sequencher 3.1.1 (Genecodes, 1999). Alignment of these data was performed in MAFFT (Edgar, 2004) using default parameters. Voucher specimens were deposited in the University of Georgia Coleoptera Tissue Collection and genomic DNA in the BYU Insect Genomics Collection. All novel sequences were submitted to GenBank (see Table 3.3 for accession numbers).

Phylogenetic analysis

Phylogenetic reconstruction of the concatenated 18S and 28S data was conducted under the parsimony criterion using TNT (version 1.1, Goloboff et al., 2003). Heuristic searches were performed under the "new technology search" (with sectorial searches, tree drifting, tree fusing, and ratcheting) implementing 5,000 replicates, holding 10 per replicate to a maximum of 10,000 trees. Multistate characters were treated as non-additive, gaps were treated as missing data, and all characters were weighted equally. All trees were rooted to *Pselaphacus nigropunctatus* (Coleoptera: Erolytidae). TNT was used to estimate branch support with nonparametric bootstrap values (Felsenstein, 1985) and Bremer support values (Bremer, 1994). To calculate bootstrap values we performed 1,000 replicates with 10 random sequence additions per replicate.

Bayesian analysis of the 18S and 28S data was performed in MrBayes (version 3.1.2, Ronquist and Huelsenbeck, 2003). Modeltest (Posada and Crandall, 1998) was used to select an appropriate model of sequence evolution for each gene under the AIC (Akaike Information Criterion) and these models were implemented in the Bayesian analysis. The partitioned Bayesian analysis comprised four separate runs each utilizing 5 million generations, flat priors, unlinked partitions, four chains (one cold and three hot), and trees sampled every 1,000 generations. Log-likelihood scores were plotted to determine stationarity and convergence of runs. Trees sampled after the ''burn-in'' from the four runs were combined and used to construct a 50% majority-rule consensus tree. Branch support was assessed with posterior probabilities determined via the 50% majority-rule consensus percentages.

Character scoring/ Mapping of food preferences

We scored prey/host association data for each terminal taxon included in the analysis based on records extracted from the literature. To score terminals identified only to genus or tribe, we combined all known food data for all member species. Sternorrhynchan prey were coded to the superfamilial level following the classification of Carver et al. (1991). Four superfamilies were represented: Aphidoidea, Psylloidea, Aleyrodoidea, and Coccoidea. Whenever evidence was provided, we constrained prey associations to essential food items only. Otherwise, we coded food preference based on all convincing records available. To enable character optimization and permit interpretation of the evolutionary sequence of feeding shifts, we constructed polymorphic character states for taxa that utilized more than a single category of food. Food preferences then were mapped on the Bayesian majority-rule consensus tree by simple, unambiguous character optimization with MacClade (version 3.06, Maddison and Maddison, 2003).

Results

Sequences and alignment

Sequences for the 18S ranged from 1,826 to 1,845 bp. For 28S, the sequences were larger and ranged from 2,116 to 2,209 bp. Some highly variable regions of 28S were removed and excluded from further analysis based on the premise that they were too variable in length to be reasonably aligned. These regions occurred at the nucleotide positions 401-493, 949-976, 1,612-1,648, and 1,859-2,029.

Phylogenetic analysis

Alignment of the molecular data yielded a matrix of 3,957 characters, 1881 for 18S and 2,076 for 28S. This combined matrix comprised 787 parsimony informative characters, 292 for 18S and 495 for 28S. The parsimony analyses resulted in six most parsimonious trees (4,069 steps, CI = 41, RI = 63). The strict consensus tree is shown in Fig. 3.13.

The hierarchical AIC as implemented in Modeltest yielded the General Time Reversible + Invariable Site + Gamma Distribution (GTR+I+G) model of sequence evolution as most appropriate for both the18S and 28S partitions. All Bayesian runs reached stationarity by 100,000 generations. The sampled trees from these first 500,000 generations (500 trees per run, 2,000 trees total) were discarded as ''burn-in'' and the remaining 18,000 sampled trees from the four runs were combined and used to construct the 50% majority-rule consensus tree (Fig. 3.14). Nodes in the cladograms are numbered for reference in the discussion below.

Discussion

Phylogenetic relationships of Coccinellidae

This study represents one of the few formal phylogenetic analyses for the higher-level taxa of Coccinellidae and is the first to utilize molecular data to address this issue. The resulting topologies from the parsimony and Bayesian analyses agree in many critical aspects (see Fig. 3.13 for points of agreement).

The analyses support the monophyly of Coccinellidae [Node 1, bootstrap (BS) = 82, Bremer (BR) = 13, Posterior Probability (PP) = 1.00] (Figs. 3.13-3.14). Although taxon sampling was broad, future analyses could improve on it by including representatives of Alexiidae and the endomychid subfamilies Anamorphinae and Leiestinae, since each of these taxa has recently been proposed as a close relative of Coccinellidae. The addition of exemplars for Mycetaeinae and Eupsilobiinae (both Endomychidae) also would strengthen this test because these taxa have conspicuous morphological similarities with some coccinellids (Pakaluk and Ślipiński, 1990; Ślipiński, 2007), but they have not yet been included in a phylogenetic study of the family.

The earliest divergence places the tribes Serangiini and Microweiseini as a well supported, monophyletic sister group [Node 2, BS = 100, BR = 53, PP = 1.00] of a large clade representing the remainder of the coccinellids [Node 3, BS = 75, BR = 10, PP = 1.00]. The placement of the Serangiini plus Microweiseini clade as the sister group to the remaining coccinellids is consistent with the hypotheses of Sasaji (1968; 1971a, b), Yu (1994), and Kovář (1996) (Figs. 3.10-3.12).

These analyses do not support the monophyly of Sticholotidinae as currently defined (Figs. 3.13-3.15). Vandenberg and Perez-Gelabert (2007) questioned the monophyly of Sticholotidinae since it appeared to include two distinctive lineages that differed significantly in the form of the apical maxillary palpomere. Vandenberg and Perez-Gelabert (2007) regarded the small sensory surface of the palp of Serangiini to be primitive and that of Sticholotidini to be more advanced, an observation supported by the findings of this phylogenetic study. Ślipiński (2007) provided other morphological arguments against the Sticholotidinae (*sensu* Sasaji) and erected the subfamily Microweiseinae to accommodate Serangiini, Microweiseini and Sukunahikonini. The establishment of Microweiseinae receives additional justification from the findings of this phylogenetic study.

One node higher on the phylogenetic tree, a second major division takes place, splitting the well supported subfamily Coccinellinae [Node 4, BS = 100, BR = 36, PP = 1.00] from the remaining coccinellids (Figs. 3.13-3.15). This finding contradicts the classical sister group relationship between Coccinellinae and Epilachninae as hypothesized by Sasaji (1968) and Kovář (1996). It also contradicts the hypothesis of Yu (1994), which placed Epilachninae as the sister group of the remaining coccinellids at the second major division.

Coccinellinae is recovered as monophyletic (Node 5, Figs. 3.13-3.15). Within Coccinellinae, the tribe Discotomini (here represented by *Pristonema* sp.) is recovered as the sister group of the remaining Coccinellinae. Members of Discotomini have very distinct serrate antennae but overall, share most of the characteristics of Coccinellinae (glabrous body, long and dorsally inserted antennae, and strongly securiform maxillary palpi).

The tribes Halyziini (here represented by the genera *Illeis* and *Psyllobora*, Node 6) and Tytthaspidini (here represented by *Bulaea anceps*) are nested within a well supported clade [Node 5, BS = 83, BR = 10, PP = 0.99], rendering Coccinellini paraphyletic. Given their specialized host preferences and distinct mandibular anatomy, these two groups have been given tribal level recognition (Hodek, 1973). The mandibles in Halyziini and Tytthaspidini have adaptations for scraping associated with their fungivorous and pollinivorous diets (Samways et al., 1997). Our study suggests that these tribes are derived lineages that arose within the two main branches of the generally aphidophagous tribe Coccinellini. In fact, despite differences in the shape of the mandible, both tribes have the distinct bifid incisive tooth characteristic of Coccinellini (Samways et al., 1997), providing further evidence for their placement within this clade.

A clade that includes Epilachninae, Coccidulinae, Ortaliinae, Scymninae, Chilocorinae, and the remaining Sticholotidinae (i.e., Sticholotidini) is supported by both the parsimony and Bayesian analyses [Node 8, BR = 4, PP = 0.56]. The support for this node is low; many of the relationships within it are poorly supported and show conflict between the two hypotheses, particularly at the deeper nodes. Nevertheless, there is some agreement between both topologies. The subfamilies Scymninae, Chilocorinae, and Coccidulinae are recovered as paraphyletic as presently defined. These results are not surprising given the lack of strong morphological or behavioral evidence to support these groups.

Despite the paraphyletic status of Chilocorinae, our study supported the sister group relationship between the tribes Telsimini and Chilocorini [Node 9, BS = 51, BR = 5, PP = 0.98]. The unifying characteristic of this subfamily, the lateral expansion of the clypeus, is suspected to have evolved independently many times in the Coccinellidae (Ślipiński et al., 2005). A similar modification is observed in members of the sticholotidine tribe Shirozuellini (e.g., *Ghanius*). Our study suggests that the lateral expansion of the clypeus has evolved at least twice within Coccinellidae. The tribe Chilocorini is supported as monophyletic [Node 10, BS = 52, BR = 5, PP = 1.00].

Our analysis supports the sister group relationship between *Cryptolaemus* and *Bucolus* suggested by Kovář (1996) [Node 11, BS = 66, BR = 4, PP = 0.74]. It is interesting that among the various authors who distinguished the subfamilies Coccidulinae and Scymninae (*sensu* Sasaji), all except Kovář placed *Cryptolaemus* in Scymninae. We suspect this may be based in part on the eye-catching orange and black color pattern and oval shape that make members of *Cryptolaemus* evoke a typical, if rather oversized, *Scymnus*. Antennal length is the first character used by Sasaji to distinguish the scymnine and cocciduline lineages, and by that single criterion (not to mention numerous other inconsistencies) the long, loosely articulated antenna of *Cryptolaemus* would disqualify it as a scymnine.

Food preference evolution

Coccidophagy: *The ancestral condition*

With the exception of Coccinellidae, the C. S. is primarily mycophagous. Although there are rare instances of predation known within the Series (e.g., *Saula* and Bothriderinae), those taxa have never been recovered as close relatives of Coccinellidae and thus they appear to have evolved the trait independently. Higher-level phylogenetic studies (Hunt et al., 2007; Robertson et al., 2008) have recovered Coccinellidae emerging from within mycophagous clades. Therefore, the ancestors of modern Coccinellidae made a transition from mycophagy to predation, specifically coccidophagy, according to these findings (Fig. 3.15).

Scales are the primary prey of most species of Chilocorinae, Coccidulinae, Scymninae and Sticholotidinae (Table 3.1, Fig. 3.15). According to our analyses, all exclusive scale-feeders are either in clades that have retained the ancestral state of coccidophagy or in clades that are ambiguous for feeding behavior at their basal node. None of the coccinellid taxa included in the current study represents an unambiguous reversal to exclusive coccidophagy from some other type of feeding behavior. In *Coelophora bisellata* Mulsant (Coccinellinae) scale-feeding has reappeared from an aphidophagous condition; however this species is not exclusively coccidophagous. The major transition to herbivory seen in Epilachnini is derived from scale-feeding (Fig. 3.15). Similarly, predation on Aphidoidea, Aleyrodoidea, Acari, and Formicidae each represent direct transitions from the ancestral scale-feeding condition or from an ambiguous condition. In our analyses, there is no evidence for an evolutionary stepping stone bridging the transition from coccidophagy to these other feeding behaviors.

Aphidophagy

Aphids have been documented as the primary food source for most members of the subfamily Coccinellinae (Ślipiński, 2007). Unfortunately, there are no available host data for the entire tribe Discotomini, so no food preference could be assigned for *Pristonema* sp., which is positioned as the sister taxon to the clade comprising the rest of Coccinellinae. As a result, the condition for the basal node of the subfamily is unclear. However, our analysis supports aphid-feeding as the ancestral condition for the node subtending the rest of this subfamily (Node 5, Fig. 3.15).

In addition to the widespread aphid-feeding observed in Coccinellini, exclusive aphidophagy appears in Coccidulini (in *Coccidula*), Aspidimerini (in *Aspidimerus*), Platynaspidini (all spp.), and Scymnini (in *Scymnus*) (Table 3.2, Fig. 3.15). Interestingly, Aspidimerini and Platynaspidini appear nested in an otherwise scymnine clade that includes the tribes Brachiacanthini and Hyperaspidini (Node B, Figs. 3.14-3.15), each of which includes taxa that are polymorphic for coccidophagy/aphidophagy (Table 3.2, Fig. 3.15). Clearly, there is an underlying tendency toward aphidophagy in this clade.

Some of the phylogenetic findings of this study contradict the current classification of Coccinellidae, yet are consistent with known food preference patterns. The genus *Platynaspis* (and perhaps the whole tribe Platynaspidini) does not form a monophyletic group with the rest of Chilocorinae. Platynaspidini (here represented by *Platynaspis* sp.) is the only member of Chilocorinae that does not feed on scales, so its placement in a clade of tribes (Aspidimerini, Hyperaspidini, and Brachiacanthini) with aphid-feeding tendencies is not surprising. In fact, a close relationship between Platynaspidini and Aspidimerini was suggested by Sasaji (1971b), who stated “The Aspidimerini are exactly similar to the Platynaspidini not only in adults but also in larvae. If these structural similarity [sic] were not caused by a secondary convergence, both tribes should be treated in a single phyletic stock."

Phytophagy (leaf-feeding)

Our analysis supports two independent shifts to phytophagy. All members of the subfamily Epilachninae feed on plant leaves (Hodek, 1996) and have completely abandoned carnivory. This is the only example of a major transition to strict phytophagy within the entire Cerylonid Series. According to our analysis, the leaf feeding condition observed in Epilachninae evolved from the ancestral scale feeding condition.

The genus *Bulaea* (Tytthaspidini) also includes phytophagous species and represents an independent shift to phytophagy according to our study (Fig. 3.15). *Bulaea lichatschovi* is known to eat leaves (Savoiskaya, 1970), as well as pollen (Capra, 1947; Savoiskaya, 1983), but unlike members of Epilachninae, the adults will consume aphids under laboratory conditions (NJV, unpublished data). The ancestral state in the transition to phytophagy seen in *Bulaea* is ambiguous, but was likely aphidophagy, pollinivory, or both. The mandible of adult *Bulaea* shows little change from the standard aphidophagous type, unlike the highly elaborated biting and grinding surfaces found in the epilachnine mandible (Samways et al., 1997).

According to our hypothesis, the phytophagy observed in *B. anceps* is nested in a predaceous/pollinivorous clade (Node A) that includes the genera *Coleomegilla* and *Micraspis* (Coccinellini). Although adults and larvae of *Coleomegilla* and *Micraspis* are primarily predaceous, both genera have a very diverse diet and are among the few predators known to consume substantial quantities of plant material (Pathak et al., 1994; Moser et al., 2008).

Thus, the relationships supported by our hypothesis (Node A, Fig. 3.15) are consistent with the food preferences observed in this group, even though they contradict the current classification system.

Phytophagy (pollen-feeding)

Pollen is an important alternative food source for many lady beetles regardless of their primary trophic relations, but it has been identified as an essential food for relatively few taxa (Lundgren, 2009b). It seems that a strict pollen diet does not provide adults with sufficient nutrients to promote reproductive behavior and egg maturation in most predatory species (Lundgren, 2009b; Majerus, 1994). Pollinivory may present other challenges to larvae. Some natural environments may not provide adequate free water to complement a dry, powdery diet. Also, in many species the larvae use extra-oral digestion (Hagen, 1962), which entails injecting their prey with hydrolytic enzymes and then sucking out the liquefied body contents. In these taxa the structure of the mouthparts (particularly the prostheca and mandibular dentition) (Samways et al., 1997) may be poorly configured for harvesting and ingesting dry particulate foods.

Although we are not aware of any strict pollinivores in the family Coccinellidae, some of the strongest tendencies in this direction are found among species belonging to node A (Fig. 3.15). Pollen has been identified as one of the preferred foods for the phytophagous genus *Bulaea* (Tytthaspidini) (Samways et al., 1997). In addition, the predatory genera *Coleomegilla* and *Micraspis* feed extensively on pollen (e.g., Britton, 1914; Putman, 1964; Benton and Crump, 1981; Turner and Hawkeswood, 2003; Omkar, 2006; Lundgren et al., 2004; 2005; Lundgren, 2009b), and are capable of completing their larval development on pollen alone (Smith, 1960;

Shepard and Raspusas, 1989; Lundgren and Wiedenmann, 2004). Although classically divided into two distinct tribes, the three exemplar genera in this clade share a number of attributes, including a pollen-rich diet, a strong tendency toward polyphagy, and the ability to successfully complete their life cycle in the absence of prey items. Thus, our findings suggest an interesting pattern where polyphagy serves as a stepping stone toward a more specialized arthropod-free diet in which pollen plays a critical role. These phylogenetic findings, despite contradicting the current classification, are consistent with the known feeding data for these taxa.

In reality, the terms "predation" and "phytophagy" do not represent absolute categories for coccinellids. Species in the primarily predaceous genera *Micraspis* and *Coleomegilla* are known to feed on leaves (Pathak et al., 1994; Moser et al., 2008) in addition to pollen during larval development. Similarly, although members of Tytthaspidini have specialized in mycophagy (i.e., *Tytthaspis*) and phytophagy (i.e., *Bulaea*), they are known to feed on some insects and mites (Ricci, 1982; NJV, unpublished data). The ability for larvae to cope with a dry pollen diet appears to be a significant development in this particular group of lady beetles.

Mycophagy

The evolution of the lady beetles seems to be closely associated with fungus feeding. It has been suggested that the preference for Sternorrhyncha might be a consequence of a previous diet on sooty mold that normally grows on honeydew produced by these hemipterans (see Leschen, 2000). Indeed, it appears that there is not a general physiological constraint against fungus consumption in lady beetles, since the use of conidia and spores by adult coccinellids is widespread (e.g., Fig. 3.5) (Hagen, 1962; Lundgren, 2009a, this issue; 2009b). However, only members of the tribe Halyziini and the genus *Tytthaspis* (Tytthaspidini) are regarded as fungus specialists (Sutherland and Parrella, 2009, this issue). In addition to having morphological adaptations of their mouthparts (Samways et al., 1997), these taxa are unique among lady beetles for having mycophagous larvae (Hodek, 1973; Gordon, 1985; Samways et al., 1997; Sutherland and Parrella, 2009, this issue).

Although this study does not include an exemplar of *Tytthaspis*, it includes another member of Tytthaspidini, *Bulaea anceps*. Assuming that Tytthaspidini is monophyletic, our findings would suggest that at least two independent shifts toward mycophagy have occurred in Coccinellidae. The mycophagous condition observed in *Tytthaspis* was derived from a polyphagous condition (Node A, Fig. 3.15). It should be noted that some *Tytthaspis* species have not completely abandoned predation, as mites and thrips have been found among the gut contents of *T. sedecimpunctata* (Ricci, 1982).

In contrast, Halyziini seems to be derived from a group of coccinellines with more normal predatory habits than the relatives of Tytthaspidini, but in reality not much is known about the actual prey preferences of these related taxa. Species of *Anatis*, for example, are not commonly found on low-growing herbs and grasses where their feeding behaviors could be easily scrutinized, but occur in the crowns of mature conifers and broad-leaved trees (Hodek, 1996). They are apparently habitat specialists, and although they are considered aphidophagous, they have been recorded on numerous other prey and alternative foods (Majerus, 1994; McKenzie, 1936). Members of the genus *Myzia* also are considered arboreal aphidophages, yet they seem to require prey from a select group of pine-feeding aphids in order to induce copulation and oviposition (Majerus, 1994). Clearly our understanding of the trophic requirements of this group is not comprehensive, and a more complete understanding would lend further insights into the transition from predatory to mycophagous habits within this clade.

Current limitations and future directions

In this study we acknowledge numerous shortcomings both in our taxon sampling and methodologies. We have under-represented certain geographical areas (e.g., Africa and Asia), some habitats (e.g., swamplands and upper canopies of tropical rain forests), and certain clades (e.g., the basal taxa (Sticholotidinae, in part = Microweiseinae, *sensu* Ślipiński), and the phytophagous subfamily Epilachninae). It would be desirable to expand our taxon sampling to get a more comprehensive representation of lady beetle diversity. This is particularly important because our understanding of the phylogenetic relationships of lady beetles is still rudimentary, and some of the recognized higher-level taxonomic categories for which we obtained exemplars may be largely artificial.

In presenting the evolution of feeding preferences we defined food categories taxonomically (e.g., Aphidoidea, Psylloidea, etc.). However, it is not clear that taxonomic classification is the most important criterion for determining trophic relations. In predatory species, for example, it may be that prey mobility, surface features (e.g., cuticular waxes, degree of sclerotization, etc.), or seasonal availability are of equal importance (Weber and Lundgren, 2009, this issue). Some lady beetles have very clear and narrowly defined feeding preferences, but for others the host plant or habitat may largely determine which prey species are consumed (Weber and Lundgren, 2009, this issue). For example, both *Naemia seriata* and *Anatis mali* (Say) feed on prey from various ordinal groups, but the former is restricted to grassy saltmarsh habitats, and the latter is nearly always found in the crowns of mature conifers. Even our decision to focus on essential foods may be flawed, since our preliminary results suggest the important role played by supplemental foods in allowing polyphagous species to begin to exploit new trophic niches.

Perhaps one of the greatest difficulties has been in assigning essential food preferences to our exemplar taxa. When possible, we have tried to represent the food choices of the actual species used in the investigation, but where no information was available for a particular genus or species, we assigned the most commonly recorded essential foods of related taxa. In a few cases the trophic relations of an entire genus or tribe were unknown or equivocal. Even for the better documented cases, we have been forced to rely on previously published records and lists reporting laboratory feeding studies, field observations, gut dissections, or merely casual observations of prey/host associations. We cannot determine which food items are essential for reproduction and development without laboratory studies. On the other hand, the results of laboratory feeding trials may misrepresent the actual foods available in the natural habitat and/or fail to realistically duplicate the normal context in which these foods are found (Weber and Lundgren, 2009, this issue). For example, many lady beetles do exceptionally well on processed moth eggs which have been sterilized to prevent hatching, removed from the ovipositional substrate, cleaned of obstructing debris, such as scales and webbing, and offered in unnatural densities. With these biases in mind, we sorted through available records to determine which items most likely represented the natural essential foods for the included taxa.

The two ribosomal nuclear genes used in this study proved to be of limited utility in resolving relationships among some of the main lineages in the family. The inclusion of additional genes and morphological data should contribute to a more robust phylogenetic hypothesis. Nevertheless, our analyses generally recovered generic and supergeneric groupings that historically were recognized and supported by morphological data. Where our results suggested novel relationships (e.g., the position of *Cryptolaemus* or Tytthaspidini), the findings are supported by morphological traits or published food preference data. Overall, we feel that the use of these molecular data to map the evolution of lady beetle feeding preferences is a significant step toward a better understanding of this interesting topic.

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Table 3.1. Summary of feeding preferences among Coccinellidae genera represented in the analysis. Foods which appear to be non-essential, occasional, or utilized by only a few species of the genus are placed in square brackets.

Taxon	**Feeding preferences**	**Reference**
Chilocorinae		
Chilocorus Leach 1815	Coccoidea	Gordon (1985)
Exochomus Redtenbacher 1843	Aphidoidea, Coccoidea	Gordon (1985)
Halmus Mulsant 1850	Coccoidea	Gordon (1985), Ślipiński and Giorgi (2006)
Orcus Mulsant 1850	Coccoidea	Froggatt (1903)
Platynaspis Redtenbacher 1844	Aphidoidea	Kaneko (2007)
Telsimia Casey 1899	Coccoidea	Ślipiński et al. (2005), Ślipiński (2007)
Coccinellinae		
Anatis Mulsant 1846	Aphidoidea, [various other insects]	Gordon (1985)
Bothrocalvia Crotch 1874	Unknown	
Bulaea Mulsant 1850	Plants (leaves), Pollen	Savoiskaya (1970, 1983), Capra (1947)
Coelophora Mulsant 1850	Aphidoidea, Coccoidea	Gordon (1985), Chazeau (1981)
Coleomegilla Cockerell 1920	Aphidoidea, pollen [Chrysomelidae & various other insects, mites (Tetranychidae), plants (leaves of corn seedlings)]	Smith (1960), Lundgren et al. (2004, 2005), Gordon (1985), Groden et al. (1990), Sebolt and Landis (2004), Moser et al. (2008), Putman (1957)
Cycloneda Crotch 1871	Aphidoidea	Gordon (1985)
Harmonia Mulsant 1850	Aphidoidea, [various other insects]	Gordon (1985), Sebolt and Landis (2004)

Hippodamia Dejean 1837	Aphidoidea	Hodek and Honěk (1996), Gordon (1985)
Illeis Mulsant 1850	Fungi (Erysiphaceae)	Ślipiński (2007), Anderson (1982)
Micraspis Chevrolat 1836	Aphidoidea, pollen, [Fulgoroidea, plants (rice panicles)]	Begum et al. (2002), Shepard and Raspusas (1989), Ślipiński (2007)
Myzia Mulsant 1846	Aphidoidea	Gordon (1985), Majerus (1994)
Olla Casey 1899	Psylloidea, Aphidoidea	Gordon (1985)
Pristonema Erichson 1847	Unknown	
Psyllobora Dejean 1836	Fungi (Erysiphaceae)	Gordon (1985)
Coccidulinae		
Azya Mulsant 1850	Coccoidea	Gordon (1985), Almeida and Carvalho (1996)
Bucolus Mulsant 1850	Formicidae (larvae)	Ślipiński (2007)
Chnoodes Chevrolat 1837	Unknown	
Coccidula Kugelann 1798	Aphidoidea	Majerus (1994)
Cranophorus Mulsant 1850	Unknown	
Cryptolaemus Mulsant 1853	Coccoidea	Gordon (1985)
Oridia Gorham 1895	Unknown	
Poria Mulsant 1850	Unknown	
Rhyzobius Stephens 1829	Coccoidea [Aphidoidea]	Gordon (1985)
Epilachninae		
Cynegetini Gordon 1975	Plants	Kuznetsov (1997)
Epilachna Costa 1849	Plants	Gordon (1975)
Ortaliinae		
Ortalia Mulsant 1850	Psylloidea, Formicidae (adult) [Fulgoroidea]	Harris (1921), Samways et al. (1997), Majerus et al. (2007)
Scymninae		
Aspidimerus Mulsant 1850	Aphidoidea	Takahashi (1921)

Brachiacantha Dejean 1837	Aphidoidea, Coccoidea	Gordon (1985)
Cryptogonus Mulsant *1850*	Coccoidea	Drea and Gordon (1990)
Diomus Mulsant 1850	Coccoidea (Aphidoidea)	Hall and Bennett (1994), Gordon (1999), Ślipiński (2007)
Hyperaspidius Crotch 1873	Coccoidea	Gordon (1985)
Hyperaspis Redtenbacher 1844	Coccoidea, Aphidoidea	Gordon (1985)
Scymnus Kugelann 1794	Aphidoidea	Lu and Montgomery (2001), Ślipiński (2007)
Stethorus Weise *1885*	Acari (Tetranychidae)	Gordon (1985)
Tiphysa Mulsant 1850	Unknown	
Sticholotidinae		
Sarapidus Gordon 1977	Unknown	
Serangium Blackburn 1889	Aleyrodoidea	Ślipiński and Burckhardt (2006), Gordon (1977), Hodek and Honěk (1996)
Sticholotis Crotch 1874	Coccoidea	Ślipiński (2007), Sasaji (1971)
Sulcolotis Miyatake 1994	Unknown	

Table 3.2. List of taxa used in the analysis including GenBank accession numbers. Dashes represent missing data.

Family	**Subfamily**	**Tribe**	**Species**	**18S**	**28S**
Erotylidae	Tritominae		*Pselaphacus nigropunctatus*	EU164627	EU164657
Discolomatidae	Aphanocephelinae		*Aphanocephalus* sp.	EU145628	EU145687
Endomychidae	Lycoperdininae		*Corynomalus laevigatus*	EU164639	EU164646
			Lycoperdina ferruginea	EU145637	EU145695
			Mycetina horni	EU145641	EU145699
Latridiidae	Latridiinae		*Latridius crenatus*	EU164623	EU164654
Coccinellidae	Chilocorinae	Chilocorini	*Chilocorus cacti*	EU145610	--------
			Exochomus quadripustulatus	FJ687695	FJ687736
			Halmus coelestris	FJ687687	FJ687728
			Halmus chalybeus	EU145607	EU145669
			Orcus lafertei	FJ687689	FJ687730
			Orcus bilunulatus	FJ687699	FJ687740
		Platynaspidini	*Platynaspis* sp.	EU145619	EU145678
		Telsimini	*Telsimia* sp.	FJ687697	FJ687738
	Coccidulinae	Azyini	*Azya orbigera*	FJ687666	FJ687707
		Coccidulini	*Coccidula* sp.	FJ687702	FJ687743
			Rhyzobius sp.	FJ687700	FJ687741
			Rhyzobius lophanthae	FJ687674	FJ687716
		Cranophorini	*Cranophorus* sp.	FJ687669	FJ687710
		Exoplectrini	*Chnoodes* sp.	EU145606	EU145668
			Oridia pubescens	FJ687693	FJ687734
		Poriini	*Poria* sp.	FJ687692	FJ687733

	Insertae Sedis	*Bucolus fourneti*	FJ687704	FJ687745
		Cryptolaemus	FJ687668	FJ687709
Coccinellinae	Coccinellini	*Anatis labiculata*	--------	FJ687714
		Bothrocalvia albolineata	FJ687688	FJ687729
		Coelophora bisellata	FJ687679	FJ687721
		Coleomegilla strenua	FJ687672	FJ687713
		Cycloneda sanguinea	FJ687681	FJ687723
		Harmonia axyridis	FJ687676	FJ687718
		Harmonia eucharis	EU145612	EU145672
		Hippodamia quinquesignata	FJ687673	FJ687715
		Hippodamia apicalis	FJ687683	--------
		Micraspis sp.	FJ687678	FJ687720
		Myzia pullata	FJ687671	FJ687712
		Olla v-nigrum	FJ687675	FJ687717
	Discotomini	*Pristonema* sp.	FJ687665	FJ687706
	Halyziini	*Illeis* sp.	FJ687680	FJ687722
		Psyllobora vigintimaculata	EU145604	EU145666
		Psyllobora sp.	FJ687691	FJ687732
	Tytthaspidini	*Bulaea anceps*	FJ687667	FJ687708
Epilachninae	Cynegetini	Cynegetini sp.	EU145608	--------
	Epilachnini	*Epilachna* sp.	EU145616	EU145675
Ortaliinae	Ortaliini	*Ortalia* sp.	EU145617	EU145676
		Ortalia horni	EU145614	--------
Scymninae	Aspidimerini	*Aspidimerus* sp.	FJ687696	FJ687737
		Cryptogonus sp.	FJ687698	FJ687739
	Brachiacanthin	*Brachiacantha* sp.	FJ687694	FJ687735

	i			
		Tiphysa sp.	EU145620	EU145679
	Diomini	*Diomus kamerungensis*	FJ687701	FJ687742
		Diomus notescens	FJ687703	FJ687744
	Hyperaspidini	*Hyperaspidius mimus*	FJ687684	FJ687725
		Hyperaspis lateralis	FJ687685	FJ687726
		Hyperaspis sp.		EU145671/
		.	EU145611	EU145714
	Scymnini	*Scymnus* sp. 1	EU145603	EU145665
		Scymnus sp. 2	FJ687682	FJ687724
	Stethorini	*Stethorus* sp.	EU145617	EU145676
Sticholotidinae	Serangiini	*Serangium* sp.	FJ687690	FJ687731
	Microweiseini	*Serapidus* sp.	FJ687670	FJ687711
	Sticholotidini	*Sticholotis* sp. 1	FJ687677	FJ687719
		Sticholotis sp. 2	FJ687686	FJ687727
		Sulcolotis sp.	FJ687705	FJ687746

Figure captions

Fig. 3.1. *Epilachna varivestis* Mulsant. Adult and larva feeding on soybean *Glycine max* (L.). Clemson University, USDA Cooperative Extension Slide Series, www.forestryimages.org.

Fig. 3.2. *Stethorus* sp. Larva feeding on spider mites. Sonya Broughton, Department of Agriculture & Food Western Australia, www.bugwood.org.

Fig. 3.3. *Cryptolaemus montrouzieri* Mulsant. Adults feeding on Hawthorn mealybug. Whitney Cranshaw, Colorado State University, www.bugwood.org.

Fig. 3.3. *Propylea quatuordecimpunctata* L. Adult feeding on aphids. Scott Bauer, USDA Agricultural Research Service, www.forestryimages.org.

Fig. 3.5. *Psyllobora vigintiduopunctata* (L.). Larva on powdery mildew. Stanislav Krejcik, www.meloidae.com.

Fig. 3.6. *Harmonia axyridis* (Pallas). Larvae cannibalizing a conspecific larva. Armin Hinterwirth, University of Washington.

Fig. 3.7. *Hyperaspis* sp. Adult feeding on spurge flower pollen. Whitney Cranshaw, Colorado State University, www.bugwood.org.

Fig. 3.8. *Coleomegilla strenua* (Casey). Adult feeding on eggs of the Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say). Whitney Cranshaw, Colorado State University, www.bugwood.org.

Fig. 3.9. Gut contents of "carnivorous" Exoplectrini spp. Adriano Giorgi, University of Georgia. 9A, gut contents including sternorrhyncan prey remains and fungal spores. 9B, gut contents including conidia of *Curvularia* sp. and *Cercospora* sp.

Fig. 3.10. Schematic phylogenetic tree interpreted from the dendrogram and accompanying text of Sasaji (1968, 1971a, b) showing only relationships among lady beetle subfamilies.

Fig. 3.11. Schematic phylogenetic tree interpreted from Kovář (1996) showing only relationships among lady beetle subfamilies.

Fig. 3.12. Schematic phylogenetic tree from cladogram published by Yu (1994) showing only relationships among lady beetle subfamilies.

Fig. 3.13. Strict consensus of the six most parsimonious tree topologies (4069 steps, CI = 41, RI = 63) resulting from analysis of two ribosomal nuclear genes. Bootstrap support values >50% are indicated above the branches. Bremer support values are indicated below the branches. Some nodes are numbered for further discussion. *Neda patula* image: courtesy of Guillermo González, www.coccinellidae.cl.

Fig. 3.14. Phylogenetic estimate of Coccinellidae based on Bayesian analysis of two ribosomal nuclear genes. Majority-rule consensus tree of the 18,000 trees sampled by the Markov chain. Posterior probabilities for each branch are shown close to the nodes. Some nodes are numbered for further discussion. *Curinus coeruleus* image: courtesy of Guillermo González, www.coccinellidae.cl.

Fig. 3.15. Host association data mapped on the lady beetle phylogeny resulting from the Bayesian analysis. Host type was scored at the superfamilial level for Sternorrhyncha. Lady beetles with multiple hosts were scored as polymorphic whenever a preferred food source could not be determined. Ambiguous optimizations are indicated on the nodes. *Adalia bipuncata* image: courtesy of Guillermo González, www.coccinellidae.cl.


3.1


3.2


3.3

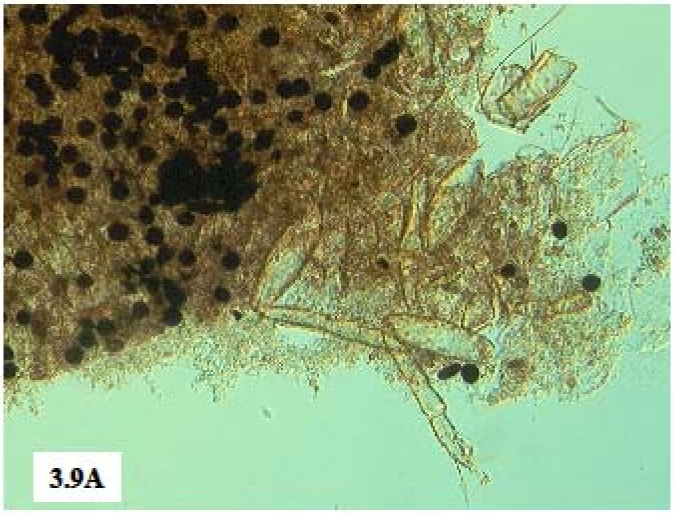

3.4

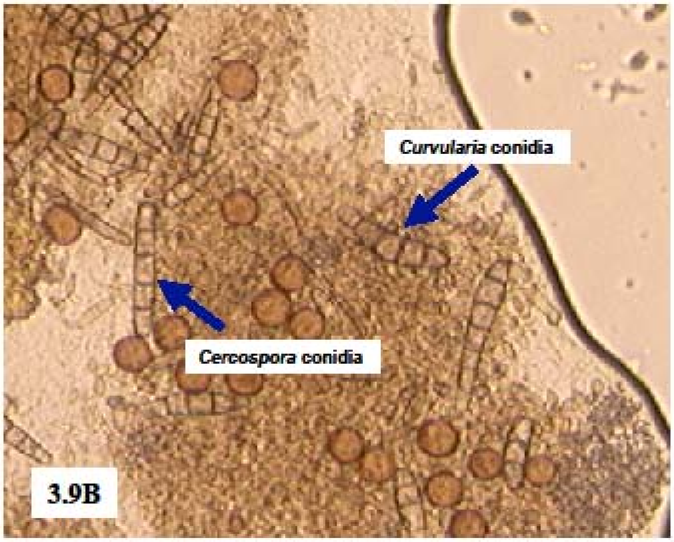

3.5


3.6


3.7


3.8


3.9A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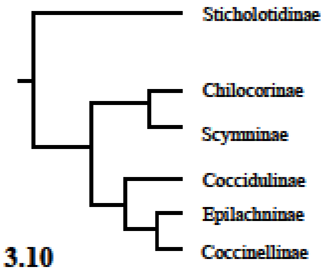
Cercospora conidia
3.9B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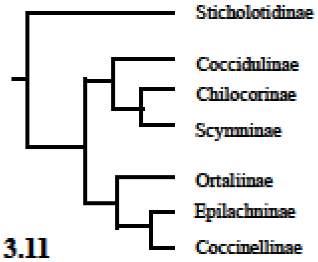
Scymninae
Coccidulinae
Epilachninae
Coccinellinae

3.10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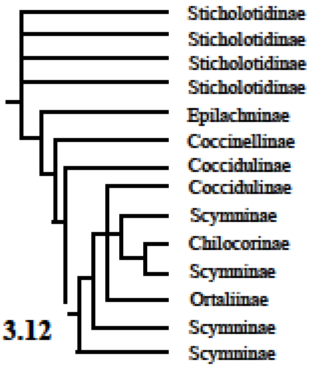
Scymninae
Ortaliinae
Epilachninae
Coccinellinae

3.11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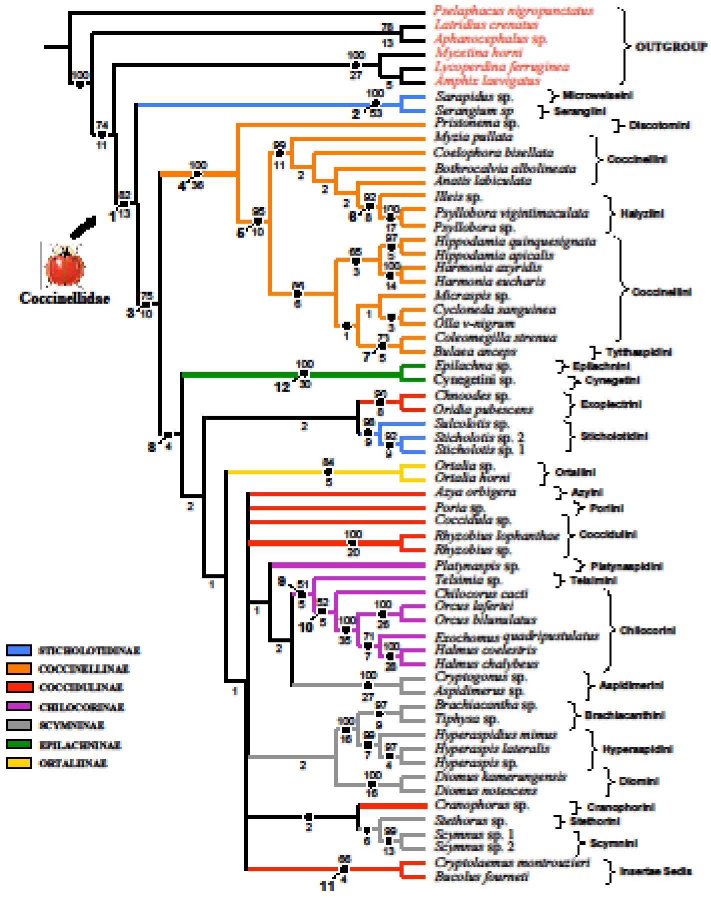
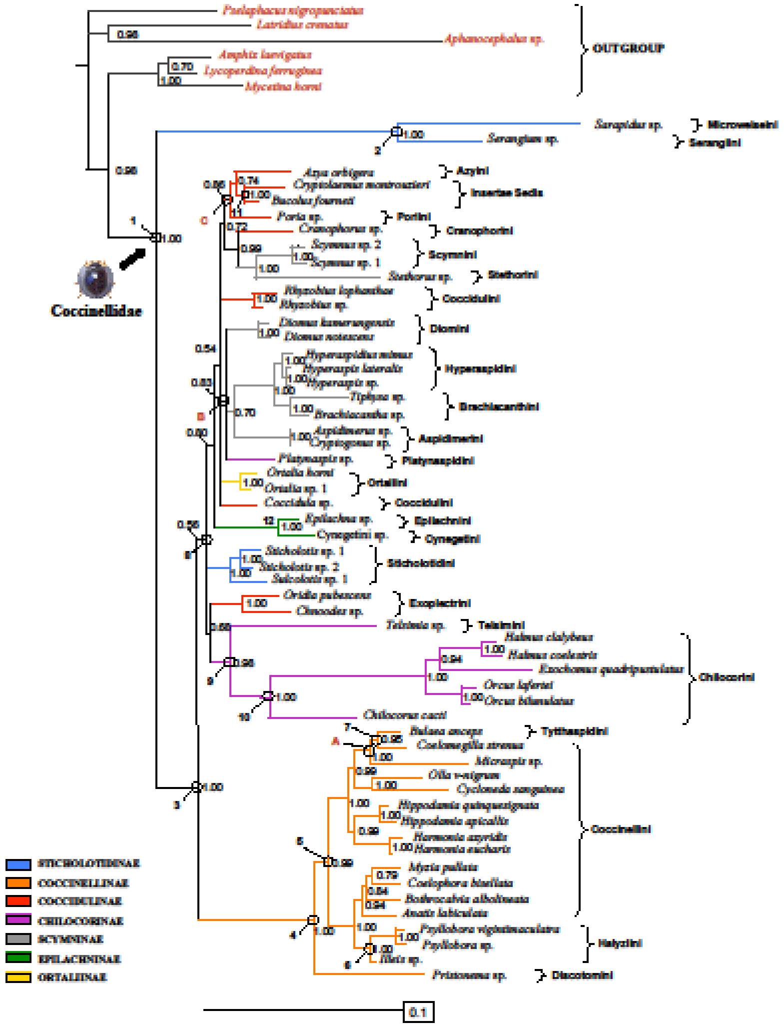
Sticholotidinae
Sticholotidinae
Sticholotidinae
Epilachninae
Coccinellinae
Coccidulinae
Coccidulinae
Scymninae
Chilocorinae
Scymninae
Ortaliinae
Scymninae
Scymninae

3.12


Coccinellidae
Pselaphacus nigropunctatus
Latridius crenatus
Aphanocephalus sp.
Mycetina horni
Lycoperdina ferruginea
Amphix laevigatus
OUTGROUP
Sarapidus sp.
Microweiseini
Serangium sp
Serangiini
Pristonema sp.
Discotomini
Myzia pullata
Coelophora bisellata
Bothrocalvia albolineata
Anatis labiculata
Coccinellini
Illeis sp.
Psyllobora vigintimaculata
Psyllobora sp.
Halyziini
Hippodamia quinquesignata
Hippodamia apicalis
Harmonia axyridis
Harmonia eucharis
Micraspis sp.
Cycloneda sanguinea
Olla v-nigrum
Coleomegilla strenua
Coccinellini
Bulaea anceps
Tytthaspidini
Epilachna sp.
Epilachnini
Cynegetini sp.
Cynegetini
Chnoodes sp.
Oridia pubescens
Exoplectrini
Sulcolotis sp.
Sticholotis sp. 2
Sticholotis sp. 1
Sticholotidini
Ortalia sp.
Ortalia horni
Ortaliini
Azya orbigera
Azyini
Poria sp.
Poriini
Coccidula sp.
Rhyzobius lophanthae
Rhyzobius sp.
Coccidulini
Platynaspis sp.
Platynaspidini
Telsimia sp.
Telsimini
Chilocorus cacti
Orcus lafertei
Orcus bilunulatus
Exochomus quadripustulatus
Halmus coelestris
Halmus chalybeus
Chilocorini
Cryptogonus sp.
Aspidimerus sp.
Aspidimerini
Brachiacantha sp.
Tiphysa sp.
Brachiacanthini
Hyperaspidius mimus
Hyperaspis lateralis
Hyperaspis sp.
Hyperaspidini
Diomus kamerungensis
Diomus notescens
Diomini
Cranophorus sp.
Cranophorini
Stethorus sp.
Stethorini
Scymnus sp. 1
Scymnus sp. 2
Scymnini
Cryptolaemus montrouzieri
Bucolus fourneti
Incertae Sedis
STICHOLOTIDINAE
COCCINELLINAE
COCCIDULINAE
CHILOCORINAE
SCYMNINAE
EPILACHNINAE
ORTALIINAE

3.13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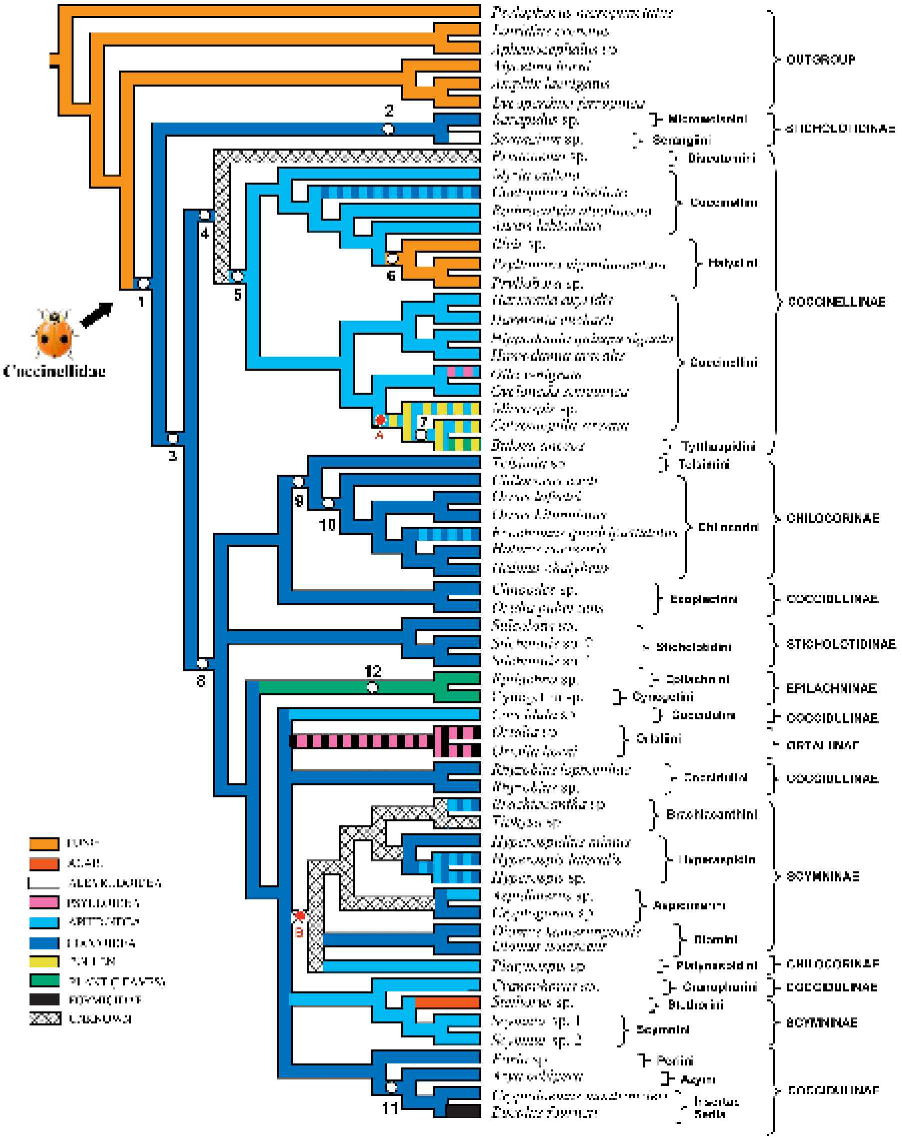
Latridius crenatus
Aphanocephalus sp.
Amphix laevigatus
Lycoperdina ferruginea
Mycetina horni
OUTGROUP
Sarapidus sp.
Serangium sp.
Microweiseini
Serangiini
Azya orbigera
Cryptolaemus montrouzieri
Bucolus fourneti
Azyini
Insertae Sedis
Poria sp.
Porini
Cranophorus sp.
Cranophorini
Scymnus sp. 2
Scymnus sp. 1
Scymnini
Stethorus sp.
Stethorini
Rhyzobius lophanthae
Rhyzobius sp.
Coccidulini
Diomus kamerungensis
Diomus notescens
Diomini
Hyperaspidius mimus
Hyperaspis lateralis
Hyperaspis sp.
Hyperaspidini
Tiphysa sp.
Brachiacantha sp.
Brachiacanthini
Aspidimerus sp.
Cryptogonus sp.
Aspidimerini
Platynaspis sp.
Platynaspidini
Ortalia horni
Ortalia sp. 1
Ortaliini
Coccidula sp.
Coccidulini
Epilachna sp.
Cynegetini sp.
Epilachnini
Cynegetini
Sticholotis sp. 1
Sticholotis sp. 2
Sulcolotis sp. 1
Sticholotidini
Oridia pubescens
Chnoodes sp.
Exoplectrini
Telsimia sp.
Telsimini
Halmus chalybeus
Halmus coelestris
Exochomus quadripustulatus
Orcus lafertei
Orcus bilunulatus
Chilocorus cacti
Chilocorini
Bulaea anceps
Tytthaspidini
Coleomegilla strenua
Micraspis sp.
Olla v-nigrum
Cycloneda sanguinea
Hippodamia quinquesignata
Hippodamia apicalis
Harmonia axyridis
Harmonia eucharis
Myzia pullata
Coelophora biselliata
Bothrocalvia albolineata
Anatis labiculata
Coccinellini
Psyllobora vigintimaculata
Psyllobora sp.
Illeis sp.
Halyziini
Prisonema sp.
Discotomini
Coccinellidae
A
B
C
1
2
3
4
5
6
7
8
9
10
11
12
STICHOLOTIDINAE
COCCINELLINAE
COCCIDULINAE
CHILOCORINAE
SCYMNINAE
EPILACHNINAE
ORTALIINAE
0.1

3.14


[illegible]
[illegible]
Aphanocephalus sp.
Mycetina horni
Amphix laevigatus
Lycoperdina ferruginea
Sarapidus sp.
Serangium sp.
[illegible] sp.
Myzia oblongata
[illegible]
[illegible]
Anatis labiculata
Illeis sp.
Psyllobora vigintimaculata
Psyllobora sp.
Harmonia axyridis
Harmonia [illegible]
Hippodamia quinquesignata
Hippodamia [illegible]
Olla v-nigrum
Coccinella [illegible]
Micraspis sp.
Coleomegilla maculata
Bulaea anceps
Telsimia sp.
Chilocorus cacti
Orcus [illegible]
Orcus [illegible]
Exochomus quadripustulatus
Halmus [illegible]
Halmus chalybeus
Chnoodes sp.
[illegible]
Sticholotis sp.
Sticholotis sp. 2
Sticholotis sp. 1
Epilachna sp.
Cynegetis sp.
Coccidula sp.
Ortalia sp.
Ortalia horni
Rhyzobius lophanthae
Rhyzobius sp.
Brachiacantha sp.
Tiphysa sp.
Hyperaspidius [illegible]
Hyperaspis lateralis
Hyperaspis sp.
Aspidimerus sp.
Cryptogonus sp.
Diomus [illegible]
Diomus [illegible]
Platynaspis sp.
Cranophorus sp.
Stethorus sp.
Scymnus sp. 1
Scymnus sp. 2
Poria sp.
Azya orbigera
Cryptolaemus montrouzieri
[illegible]
Microweiseini
Serangiini
Discotomini
Coccinellini
Halyziini
Coccinellini
Tytthaspidini
Telsimiini
Chilocorini
Exoplectrini
Sticholotidini
Epilachnini
Cynegetini
Coccidulini
Ortaliini
Coccidulini
Brachiacanthini
Hyperaspidini
Aspidimerini
Diomini
Platynaspidini
Cranophorini
Stethorini
Scymnini
Poriini
Azyini
Incertae
Sedis
OUTGROUP
STICHOLOTIDINAE
COCCINELLINAE
CHILOCORINAE
COCCIDULINAE
STICHOLOTIDINAE
EPILACHNINAE
COCCIDULINAE
ORTALIINAE
COCCIDULINAE
SCYMNINAE
CHILOCORINAE
COCCIDULINAE
SCYMNINAE
COCCIDULINAE
1
2
3
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5
6
7
8
9
10
11
12
A
B
Coccinellidae
FUNGI
ACARI
ALEYRODOIDEA
PSYLLOIDEA
APHIDOIDEA
COCCOIDEA
POLLEN
PLANT TISSUES
FORMICIDAE
UNKNOWN

3.15

CHAPTER 4

PHYLOGENETIC ANALYSIS OF THE LADYBIRD BEETLES (COLEOPTERA: COCCINELLIDAE) BASED ON MOLECULAR DATA[2]

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[2] Giorgi, J.A., N.J. Vandenberg, M. Moulton , J.V. McHugh, S.A. Ślipiński, K.B. Miller, and M.F. Whiting. To be submitted to *Systematic Entomology*.

Abstract

A phylogenetic analysis of the Coccinellidae was conducted using 92 taxa, including 19 outgroups. The density of taxon sampling allows for tests of relationships at the tribal level for most taxa. DNA was sequenced for four mitochondrial genes (12S rDNA, 16S rDNA, COI, COII,) and three nuclear genes (18S rDNA, 28S rDNA and Histone 3). The entire dataset consists of 6565 aligned nucleotide sites, 1305 of which are parsimony informative. Our study includes exemplars representing 20% of the genera, 80% of the tribes, and 100% of the currently recognized subfamilies. Analyses were performed using parsimony, maximum likelihood, and Bayesian methods. The relationships suggested by the two methods were largely congruent. Areas of incongruence correspond to one section of the topologies where support was limited. We use the results of these analyses to hypothesize a more natural, phylogenetically based classification of Coccinellidae. Our results corroborate some recently proposed ideas about the phylogeny and classification of the family, but strongly contradict the traditional arrangements. Our study supports the monophyly of Coccinellidae; however, most of the traditional subfamilies are not supported as monophyletic. Three recently proposed, but not widely accepted, subfamilies are supported. A new subfamily is proposed to accommodate Monocorynini. We recognize eight subfamilies of Coccinellidae: Microweiseinae, Monocoryninae (**new subfamily**), Coccinellinae, Chilocorinae, Sticholotidinae, Scymninae, Exoplectrinae, and Hyperaspidinae. The circumscription of Hyperaspidinae (Hyperaspidini Mulsant, Brachiacanthini Mulsant and Selvadiini Gordon) is extended to accommodate Platynaspidini Redtenbacher and Aspidimerini Mulsant. The tribe Coccinellini Latreille is paraphyletic with respect to Tytthaspidini Mulsant (**syn. nov.)** and Halyziini Mulsant (confirmed status). The tribes Noviini Mulsant, Cryptognathini Casey, Poriini Mulsant, and Diomini Gordon are treated as

incertae sedis. The relationship between some of the subfamilies and the placement of several tribes remain ambiguous.

Introduction

Coccinellidae, commonly known as ladybugs or ladybirds, is a charismatic group of insects that have long attracted attention due to their striking color patterns. Coccinellids are a worldwide cucujoid beetle family comprising approximately 6000 species. Together with seven other families, they form a monophyletic group called the Cerylonid Series ("C.S.") (Crowson 1955; Hunt et al. 2008; and Robertson et al. 2008). The great economic relevance of the family stems mostly from the fact that many coccinellids prey on insects that are serious pests in agriculture and forestry (scales, aphids, whiteflies, etc.). Many members of the family have been widely used in classical biological control programs (Obrycki and Kring 1998). Other aspects of coccinellid natural history that have attracted attention include male killing by maternally inherited bacteria (Majerus and Hurst 1997; Majerus et al. 1998; Hurst et al. 1992; 1997; 1999; Schulenburg et al., 2001; 2002), and utilization of chemical defenses (Pesteels et al. 1973; Tursch et al. 1973; Holloway et al. 1991; Holloway et al. 1993; Ayer and Browne 1997; de Jong et al. 1991). In contrast with the significant body of literature generated by these studies, the number of papers dealing with the phylogeny of Coccinellidae is remarkably small. As a consequence, the phylogenetic affinities between the main lineages of Coccinellidae are still poorly understood and the classification remains unsettled.

The most comprehensive paper on the classification and phylogeny of Coccinellidae is that of Sasaji (1968, 1971), which remains the primary reference for the family (e.g., Booth et al. 1990; Pakaluk et al. 1994; Lawrence and Newton 1995; Kuznetsov 1997) (Table 5). The traditional phylogenetic scheme proposed by Sasaji recognizes three major lineages. The most primitive lineage is represented by the subfamily Sticholotidinae, which is placed at the base of the dendogram. On the main branch, one lineage is formed by the coccinellids with reduced antennae (Chilocorinae and Scymninae), while the other comprises the coccinellids with terminal maxillary palpi that are strongly divergent and securiform (Coccidulinae, Epilachninae, and Coccinellinae). A closer relationship between Epilachninae and Coccidulinae is hypothesized based on the antennae which have a dorsal insertion and are relatively long and 11-segmented. Five subsequent studies have addressed high-level relationships of coccinellids (Yu 1994; Kovář 1996; Hunt et al. 2008; Robertson et al. 2008; Giorgi et al. 2009). Given either the lack of methodological rigor (Sasaji 1968; 1971; Yu 1994; Kovář 1996), inadequate taxon sampling (Robertson et al. 2008), or insufficient data (Giorgi et al. 2009), none of these studies have provided a well-supported phylogenetic hypothesis for the entire family.

This gap is reflected in the classification, especially at the subfamilial level. Coccinellidae *sensu* Sasaji (1968, 1971) comprises five subfamilies: Chilocorinae, Coccidulinae, Coccinellinae, Epilachninae, Scymninae and Sticholotidinae. While some of these subfamilies (Coccidulinae, Coccinellinae and Scymninae) are defined on the basis of suite of characters, none of them being exclusive, others (Chilocorinae, Sticholotidinae) are characterized solely on the basis of superficial similarity. Other subfamilial classifications have been proposed (Gordon 1994; Kovář 1996; Duverger 1989; 2001; 2003; and Ślipiński 2007) with the number of resulting subfamilies ranging from 2 to 18.

Recent taxonomic studies have pointed out major concerns with the current classification of coccinellids, especially the lack of morphological support for most of the currently recognized subfamilies. Vandenberg and Perez-Gelabert (2007) provided a detailed discussion on the taxonomic status of the subfamilies Coccidulinae and Sticholotidinae, addressing critical aspects of the current subfamilial concepts. According to these authors, the so-called “primitive” groups (Coccidulinae and Sticholotidinae) are particularly problematic and likely to be artificial assemblages of taxa. This study illustrated the problem with the misplacement of the Hispaniolan genus *Bura* Mulsant 1850, originally described in Coccidulinae and later transferred to Sticholotidinae. It should be mentioned that Sasaji was not familiar with the Neotropical coccinellid fauna, thus a significant amount of diversity was left out of his studies of 1968 and 1971. Ślipiński (2007) stated that many Australian coccinellids also do not fit within the definitions of Sasaji’s subfamilies. In that same paper, Ślipiński recognized a subgroup of Sticholotidinae (Microweiseini, Serangiini and Sukunahikonini) as a distinct subfamily; the Microweiseinae (= Scotoscymninae Duverger 2003). Other refinements of coccinellid classification were proposed in the same study, but no improvements were proposed to better define the subfamilies. The monophyly of Chilocorinae was questioned by Ślipiński (1994), who suggested that the diagnostic feature for the subfamily was actually the product of adaptative convergence. The hypothesized paraphyletic nature of both Chilocorinae and Sticholotidinae was later confirmed by molecular phylogenetic studies (Giorgi et al. 2009).

In the present study, we conducted a phylogenetic analysis of the family Coccinellidae based on molecular data from the mitochondrial ribosomal genes 12S rDNA and 16S rDNA, the nuclear ribosomal genes 18S rDNA and 28S rDNA, the mitochondrial protein-coding genes Cytochrome oxidase I (COI) and Cytochrome oxidase II (COII), and the nuclear protein-coding gene Histone 3 (H3). Our goal is to provide a robust phylogenetic framework to address current problems with the classification of the family.

Materials and methods

Taxon sampling

Of the 38 tribes recognized by Kovář (1996) (the most recent, global treatment of the family), only six are not represented in this study: Singhikalini (Coccinellinae), Epivertini, Eremochilini (Epilachininae), Scyminiliini, Pentilini (Scymninae), Argentipilosini, Limnichopharini, (Sticholotidinae). Of these tribes, Pentilini and Argentipilosini are synonyms of Cryptognathini (N.J. Vandenberg, in prep). Nineteen beetle species from seven other cucujoid families were selected as outgroups, six belonging to the C.S.: Alexiidae (1), Bothrideridae (1), Cerylonidae (1), Corylophidae (1), Discolomatidae (1), Endomychidae (11), and Latridiidae (2). One species of Erotylidae was chosen as a distant outgroup. We sampled within the Cerylonid Series because this group (to which Coccinellidae belongs to) has been consistently supported as a monophyletic. Thus, a total of 92 taxa (73 ingroup and 19 outgroup) were represented in this study (Table 1).

Molecular methods

Genomic DNA was extracted from single ethanol-preserved specimens following protocol described by Jarvis et al. (2004) and Whiting (2002). Voucher specimens were deposited in the University of Georgia Coleoptera Tissue Collection and genomic DNA in the BYU Insect Genomics Collection. PCR products were purified using MANU96-well filtration plates, sequenced using D-rhodamine chemistry, and fractionated on an ABI3730 DNA analyzer at the Brigham Young University (BYU) DNA Sequencing Center. The sequences were trimmed and assembled using Sequencher 3.1.1 (Genecodes 1999). Alignment of these data was performed in

MAFFT (Edgar 2004) using default parameters. The resulting alignment was checked by eye and edited manually in MACCLADE 4.08 (Maddison and Maddison 2000).

Phylogenetic analyses

Parsimony analysis

For the parsimony analysis we used TNT version 1.1 (Goloboff et al. 2003) to perform heuristic searches under the "new technology search" (with sectorial searches, tree drifting, tree fusing, and ratcheting) implementing 10,000 replicates, holding 10 per replicate to a maximum of 10,000 trees. Multistate characters were treated as non-additive, gaps were treated as missing data, and all characters were weighted equally. All trees were rooted to *Pselaphacus nigropunctatus* (Coleoptera: Erotylidae). To assess the confidence at each node, we calculated the bootstrap values (Felsenstein 1985), using TNT with 1000 replicates with ten random sequence additions per replicate. We also used TNT to evaluate the robustness of nodes with Bremer support (Bremer 1994). The maximum parsimony (MP) tree length was corroborated in NONA 2.0 (Goloboff 1999) using parameters similar to those in the TNT tree searches.

Bayesian analysis

To obtain an appropriate substitution model and model parameter values for the Bayesian analyses, each gene was separately analyzed under 56 evolution models using MRMODELTEST v. 2.2 (Nylander 2004; in MRMTGUI 1.01). Bayesian analysis was performed in MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). The partitioned Bayesian analysis comprised one run utilizing 10 million generations, flat priors, unlinked partitions, four chains (one cold and three hot), and trees sampled every 1,000 generations. Log-likelihood scores were plotted to determine stationarity and convergence of runs. Trees sampled after the ‘‘burn-in’’ from the four runs were combined and used to construct a 50% majority-rule consensus tree. Branch support was assessed with posterior probabilities determined via the 50% majority-rule consensus percentages.

Results

Sequences and Alignments

Introns and hyper variable regions from the alignments of the non protein-coding genes were excluded using Gblocks (Castresana 2000) on the server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). From the less stringent options we allowed only for gap positions within the final blocks; less strict flanking positions and smaller final blocks were not allowed. The amount of excluded characters for each gene ranged from 10% to 20% (Table 2).

Phylogenetic Analysis

Alignment of the molecular data yielded a matrix of 6565 characters. This combined matrix comprised 1305 parsimony informative. The parsimony analysis resulted in one most parsimonious trees (25852 steps, CI=40, RI=62) (Fig 1).

The General Time Reversible + Invariable Site + Gamma Distribution (GTR + I + G) was yielded by the hierarchical AIC as implemented in Modeltest as most appropriate model of sequence evolution for most of the genes (Table 3). The single Bayesian run was interrupted before reaching 4 million generations. The run reached stationarity by 300,000 generations. The sampled trees from the first 900,000 generations were discarded as ‘‘burn-in” and the remaining

913 trees were combined and used to construct the 50% majority-rule consensus tree (Fig. 2). Nodes in the cladograms are numbered for reference in the discussion below.

Overall the topological support for the TNT and Bayesian trees recover a similar pattern of support: high bootstrap values and posterior support nodes at every level of the tree, including the deepest nodes [nodes 1, 2, and 3] as well as most generic clades. Low support is particular evident in the deepest nodes within the "Scymninae" + Coccidulinae" + Epilachninae clade.

The analyses support the monophyly of Coccinellidae. The data further recover the subfamilies Epilachninae and Coccinellinae as monophyletic. Our analysis, however, indicates that most of the subfamilies defined by Sasaji (1968, 1971), including Sticholotidinae, Chilocorinae, Scymninae, and Coccidulinae, are not monophyletic.

Discussion

Coccinellidae Phylogeny

Some major taxonomic groupings and relationships were recovered by both analyses (Figs 1 and 2). Our study supports Coccinellidae as monophyletic [Node 1]. A clade comprising three tribes, Microweiseini Leng + Serangiini Pope + Sukunahikonini Kamiya [Node 2], is supported as sister group to the rest of the coccinellids [Node 4]. One node higher on the phylogenetic tree, a second major division takes place, splitting Monocorynini Gorham from the rest of the coccinellids [Node 5]. Above this node, one large clade is recovered in each analysis but with only moderate support. This clade includes part of Sticholotidinae (Plotinini and Sticholotidini) + Chilocorini Mulsant (including *Chilocorellus*) + Coccinellinae [Node 6]. Within this clade, Chilocorini is supported the sister group of Coccinellinae [Node 8]. Between this node [Node 6] and Monocorynini [Node 4] are the rest of Coccinellidae, including all of

Scymninae, Coccidulinae (except Monocorynini), Epilachninae, Platynaspidini, and Telsimini (Chilocorinae). In this section of the tree the support is weak and only a few clades are supported by both analyses. Among them are: Noviini + Cryptognathini [Node 26]; Brachiacanthini + Hyperaspidini [Node 27]; Scymnini Mulsant (*Nephaspis* Casey, *Sasajiscymnus* Gordon, *Scymnus* Mulsant, and *Nephus* Casey) + Stethorini Dobzhanski + *Blaisdelliana* Gordon [Node 21].

All the analyses conducted in this study, converged on very similar results. The major point of disagreement between the Bayesian and parsimony analyses occurs in one section of the tree where overall support is very low in all analyses, which is located between *Monocoryna* Gorham and Node 6 (Fig. 3). All members of the subfamilies Scymninae, Coccidulini Mulsant (excluding *Monocoryna*) and Epilachninae are recovered in that area. In conservative hypotheses of results, this area would be left unresolved, resulting in similar topologies for all analyses.

Because this section of the tree is located between well supported older and younger splits, this lack of resolution and support cannot be explained simply by saturation or too conservative sequences (Zwick 2008). Branch lengths between these taxa are extremely short (Figs 2 and 3, which could have resulted from an explosive radiation. Rapid radiations are difficult to track with any kind of marker due to the very short shared evolutionary histories (Whitfield and Lockhart 2007). The same lack of resolution in this region of the phylogeny was observed by Giorgi et al. (2009). In that study, however, a significantly smaller dataset was used. The present study has almost twice the number of analyzed nucleotides. In theory, we have also increased the quality of our data with the inclusion of three protein-coding genes. The taxonomic diversity in both the ingroup and outgroup have also been increased. However, the points of uncertainty in Giorgi et al. (2009) have not been greatly improved in the present study with the addition of data and taxa. This supports the prediction of Whitfield and Lockhart (2007) who stated that the addition of data or taxa could be of limited value in cases of ancient rapid radiation. During the course of our study, we noticed that small changes in the dataset have consistently affected the results, causing sometimes drastic topological changes in this one area of the tree. This could be another symptom of rapid radiation (Whitfield and Lockhart 2007).

Historically, phylogenetic studies based on molecular data have avoided addressing classification issues (Franz 2005). Apparently, the lack of morphological synapomorphies compromises the credibility of these studies. However, traditional anatomically-based studies on Coccinellidae have systematically failed to identify major lineages within the family on the basis of unique morphological features. If, in fact, we are dealing with a true case of ancient rapid radiation, both DNA and morphology should provide a limited amount phylogenetic signal in certain regions of the tree. As such, we are using the best supported aspects of our molecular phylogenetic hypothesis to propose a revised classification of Coccinellidae (Table 4 and 5) while making an effort to bring to the discussion any relevant morphological evidence.

Proposed classification of Coccinellidae

Sticholotidinae

The subfamily Sticholotidinae as defined by Sasaji (1968, 1971) comprises the coccinellids that are traditionally regarded as the most primitive. These ladybeetles are very small, cryptic and dull in coloration. Traditionally, the key diagnostic features for Sticholotidinae (*sensu* Sasaji) are the distinctly conical to elongate oval terminal maxillary palpomere and the mentum being narrowly articulated with the submentum. Sasaji's (1968, 1971) classification includes the tribes Serangiini Blackwelder, Shirozuelini Miyatake, Sticholotidini Weise, and Sukunahikonini Kamiya under the subfamily Sticholotidinae. Since Sasaji's studies, the subfamily was expanded to accommodate six additional tribes: Microweiseini Leng, Cephaloscymnini Gordon, Carinodulini Gordon, Pakaluk and Ślipiński, Argentipilosini Gordon and Almeida, Limnichopharini Miyatake, and Plotinini Miyatake.

Vandenberg and Perez-Gelabert (2008) raised two serious concerns about the classification of Sticholotidinae. First, Sasaji (1968, 1971) used characters that he considered to be primitive for defining the subfamily. Thus, if Sasaji's intuition about these characters was right, Sticholotidinae was defined on the basis of plesiomorphic characters, making it unlikely that the resulting group is a natural, monophyletic assemblage. Second, several of the genera and species that were subsequently added to Sticholotidinae no longer fit Sasaji's original diagnosis. The most relevant observation made by Vandenberg and Perez-Gelabert (2008) referred to the most distinctive and frequently cited feature of Sticholotidinae (Ślipiński 2004), the shape of the terminal maxillary palpomere, which differs by being elongate oval, rather than securiform as in the rest of the family. These authors point out that, in spite of the superficial similarity, two very distinct architectures of that palpomere apex occur within Sticholotidinae. In the "*Sticholotis* and allies", the terminal palpomere has a long obliquely oriented distal sensory surface that forms one side of the tapered apex. In "*Sukunahikona* and allies", the sensory surface is usually smaller, oval, and more distally positioned, with the taper beginning well in advance. This distinction suggested two main lineages in the subfamily, a division that had been suggested in Kovář's (1996) phylogeny.

Our study recovers Sticholotidinae as a polyphyletic group. These results are consistent with the findings of Giorgi et al. (2008) and opinions voiced in other studies (e.g., Ślipiński

2004; Ślipiński 2007; Vandenberg and Perez-Gelabert 2008). Our results are inconclusive regarding whether the subfamily (*sensu* Sasaji) comprises two or more independent lineages. The clade corresponding to the "*Sukunahikona* and allies" of Vandenberg and Perez-Gelabert (2008) is a well supported monophyletic group here recognized as a separate subfamily [Node 2, see discussion below].

The remaining Sticholotidinae corresponds to the "*Sticholotis* and allies" of Vandenberg and Perez-Gelabert (2008). Of this group, the tribes Cephaloscymnini, Carinodulini, and Limnichopharini are lacking in the present study. In our analyses, the remaining Sticholotidinae from this second group are recovered as a monophyletic group. A clade with *Sticholotis* Crotch, *Sulcolotis* Miyatake (Sticholotidini) and *Plotina* Kovář (Plotinini) was recovered in all analyses [Node 7]. *Ghanius* Ahmad (Shirozuelini), however, is nested within a Coccidulini clade in the parsimony analysis [Node L], and nested within Scymninae clade in the Bayesian analysis [Node J]. *Chilocorellus* Miyatake (Sticholotidini) is nested within the tribe Chilocorini (Chilocorinae) [Node 12]. The hypothesized position of Shirozuelini has only weak support and differs between the parsimony and Bayesian analyses. Strong morphological evidence suggests that this tribe belongs together with Sticholotidini. Thus, we believe that the phylogenetic position implied by our study does not provide convincing evidence against its placement in Sticholotidinae. Lacking any evidence to the contrary, we must leave Cephaloscymnini, Carinodulini, and Limnichopharini in Sticholotidinae for now.

Sticholotidini and Plotinini. Our study does not support the monophyly of Sticholotidini, one of the megadiverse groups of Coccinellidae. Even though its monophyly has never been challenged, this result is not particularly surprising. The tribe is here represented by the genera

Chilocorellus, *Sulcolotis* and *Sticholotis*. The genera *Sticholotis* and *Sulcolotis* are strongly supported as the sister group to *Plotina* (Plotinini) by all analyses [Node 7, BS=93, PP=0.96]. However, *Chilocorellus* is nested within Chilocorini, strongly supported as the sister group of *Chilocorus cacti* Linnaeus [Node 12, BS=100, PP=1]. It is noteworthy that *Chilocorellus* is one of the few genera of Sticholotidini that has a distinct lateral expansion of the clypeus. This modification also occurs in Chilocorini where it is considered a unifying feature of the tribe. Even though *Chilocorellus* exhibits some key Sticholotidini attributes (e.g., shape of the antennae and maxillary palp), its placement within Chilocorini is not only well supported by molecular data in both analyses but is also consistent with some morphological evidence. Thus, we propose the transfer of *Chilocorellus* from Chilocorini to Sticholotidinae (see Chilocorini section for additional discussion on the position of *Ghanius*). As mentioned before, a clypeal expansion also occurs in some other Sticholotidini genera (e.g., *Promecopharus* Sicard and *Glomerella* Gordon). Additional studies that include these taxa are required to determine their phylogenetic position.

Shirozuelini. This tribe comprises five genera occurring in Asia. Members of this tribe have elongated maxillary palps and relatively long and spindle-shaped antennae. Our study does not support a sister group relationship of Shirozuelini with any other members of the "Sticholotidini and allies" group that are represented in our analyses. In the parsimony analysis, *Ghanius* (Shirozuelini) is supported as the sister group of *Cranophorus* Mulsant (Coccidulinae) [Node L]. In the Bayesian analysis, it is supported as sister group of *Selvadius* Casey (Scymninae) [Node K]. We find no convincing morphological evidence to corroborate either of the relationships here hypothesized. Sasaji (1967), referred to *Shirozuella* Sasaji, the type genus, as being a "quite peculiar genus" in which "the structure of the head capsule with strongly expanded clypeus and the prosternal structure with a distinct anterior furrow are quite different from the rest of the subfamily". In spite of these differences, members of Sukunahikonini agree with Vandenberg and Perez-Gelabert's (2008) definition of the "*Sticholotis* and allies". Our results are inconclusive regarding the placement of *Ghanius*. The relationships recovered here are weakly supported and disagree between the parsimony and Bayesian analyses. Throughout the course of this study, the position of *Ghanius* has varied with the inclusion of additional taxa. Similar behavior was also observed for its suggested sister taxa, *Cranophorus* and *Selvadius*. Based on this observation, we consider our results regarding the position of *Ghanius* to be spurious. We suspect that the placement of *Ghanius* in the current study might be a result of long branch attraction. The terminal branch this taxon is particularly long. Since there is no convincing evidence that contradicts the placement of Shirozuelini together with Sticholotidini and Plotinini (excluding *Chilocorellus*) we keep this tribe within the subfamily Sticholotidinae.

Microweiseinae

A clade comprising the tribes Microweiseini, Serangiini and Sukunahikonini is well supported by all analyses as a distinct lineage from the remaining Sticholotidinae [Node 2, BS=90, PP=1]. These results are in agreement with previous findings of Giorgi et al. (2009). Morphological support for this group is well documented by Ślipiński (2007), who proposed a new family, Microweiseinae, to accommodate these tribes. Ślipiński (2007) defined Microweiseinae using the following characters: 1) tegmen asymmetrical with reduced and fused parameres, 2) spermatheca multi-cameral and sclerotised, 3) antennal insertions positioned close together between the eyes or in front of the eyes, and 4) antenna short, clubbed and comprising a maximum of 10 segments. Their larvae are characterized by the following features: 1) integument granulate, 2) mandible simple without a molar lobe, and 3) tibiotarsal apex with two spatulate setae. Another characteristic is that the pupa does not have urogomphi (Phuoc and Stehr 1974). Here, we recognize Microweiseinae Ślipiński as a valid subfamily of Coccinellidae.

Our study supports Microweiseini, Serangiini and Sukunahikonini as the sister group of the remaining coccinellids. This result is consistent with the previous hypotheses of Sasaji (1968, 1971), Yu (1994), and Kovář (1966). It also supports the hypothesis by Vandenberg and Perez-Gelabert (2008) that the obliquely oriented distal sensory surface of the terminal maxillary palpomere observed in the "advanced Sticholotidini" is a unique feature that characterizes all the coccinellids in the clade that forms the sister group to the Microweiseini + Serangiini + Sukunahikonini clade.

Sukunahikonini. This tribe is circumtropical and comprises five genera. Members are distinct from the other coccinellids by having a lateral carina along the external margin of the elytron and having the two basal abdominal sternites fused (incompletely) to each other. The present study strongly supports *Sukuhonikona* Kamiya (Sukunahikonini) as the sister group of Microweiseini (here represented by *Coccidophilus* Brèthes*, Parasidis* Brèthes*,* and *Sarapidus* Gordon) plus Serangiini (here represented by *Delphastus* Casey and *Serangium* Blackburn) [Node 2]. This result supports an hypothesis by Sasaji (1968) who proposed that Sukunahikonini was more primitive than Serangiini and Sticholotidini (which included *Microweiseia*, genus-type of Microweiseini, at the time).

Serangiini and Microweiseini. Serangiini is a small group of three genera with a circumtropical distribution. It is distinct from other coccinellids by its large one segmented, knife-shaped antennal club. Microweiseini is a group of five genera restricted to the New World, Africa and Australia whose members may be distinguished from other Microweiseinae by the following features: 1) sixth abdominal segment exposed beyond the apex of the preceding segment; 2) terminal maxillary palpomere elongated; and 3) labial palp terminally articulated.

A sister group relationship between Serangiini and Microweiseini receives strong supported by this study [Node 3, BS=85, PP=0.96]. These results support Kovář's (1996) hypotheses of a sister group relationship between the Microweiseini and Serangiini. In a discussion about the affinities of *Pseudosmilia* Brèthes (Microweiseini) with the other Sticholotidinae, Sasaji (1971) proposed a closer relationship to Serangiini than to any other tribe in the subfamily. He justified this hypothesis with the following characters: 1) presence of a subtriangular prosternum in the exposed part, 2) mesosternum short, and 3) the characteristic feature of the male genitalia.

Chilocorinae

The unifying characteristic of the subfamily has been the lateral expansion of the clypeus (Sasaji 1968; 1971; Kovář 1996; Vandenberg 2002). Apart from the clypeal expansion, these tribes have little in common other than their small antennae, which are very distinct anatomically from each other. The subfamily comprises the tribes Chilocorini Mulsant, Platynaspidini Redtenbacher and Telsimini Casey. In our study, Chilocorinae is recovered as a polyphyletic group. These results support Ślipiński et al. (2005), who questioned the monophyly of the subfamily. In that paper, the clypeal expansion (only unifying character of the tribe) was described as “an obvious anti-molestation device” and was proposed to be homoplastic.

A clade comprising most of the tribe Chilocorini (excluding *Chilocorellus*) is supported by all analyses as the sister group to Coccinellinae [Node 8, PP=0.77]. *Platynaspis* (Platynaspidini), however, is recovered as the sister group to Aspidimerini by the parsimony analysis [Node E] and recovered as the sister group to *Diomus* Blackburn (Diomini) in the Bayesian analysis [Node S]. *Telsimina* Casey (Telsimini) is recovered as the sister group to Noviini plus Cryptognathini in the parsimony analysis [Node D] and as the sister group of Cranophorini Casey plus Exoplectrini Crotch in the Bayesian analysis [Node G]. The evidence that supports the placement of Platynaspidini outside Chilocorinae is very convincing (see discussion below). Our analyses, however, cannot say for certain where Telsimini belongs. Since its placement with Chilocorini can be justified on morphological basis and has been supported in other studies (Giorgi et al. 2009) this subfamily should circumscribed to include the tribes Chilocorini and Telsimini.

In the present study, Chilocorini is moderately supported as sister group to Coccinellinae [Node 8]. This relationship is not supported by any obvious anatomical characters and greatly contradicts the classical view of coccinellid phylogeny, which suggests Chilocorinae as the sister taxon of Scymninae, and Coccinellinae as the sister taxon of Epilachninae. Sasaji (1968) advocates in favor of a Chilocorinae plus Scymninae clade based on the small, ventrally situated antennae, and exudation of a white wax-like substance by the larvae. The larval exudation is not a character universally present in either tribe, and the reduction of the antennae is a rather vague character. Besides, the adaptive value antennal reduction (presumably for anti-molestation) probably increases the likelihood of multiple independent origins. Thus, even though there are no obvious similarities to defend the position of Chilocorini supported by our data, the arguments in favor of a sister group relationship between Chilocorinae and Scymninae are weak. The Bayesian analysis of Giorgi et al. (2009) recovered Chilocorini and Coccinellinae as sister taxa, but the same relationship was not corroborated by the parsimony analysis in that study.

Chilocorini. Chilocorini is a relatively large, cosmopolitan group with around twenty genera. Members of this tribe are moderately large ladybeetles characterized by a dramatically hemispherical body, expanded clypeus, and short appendages received in fossae on the ventral surface (Ślipiński and Giorgi 2006). In the current study, *Chilocorellus* (Sticholotidini) is recovered within Chilocorini, and is strongly supported as the sister group of *Chilocorus* [12 BS 100, PP=1].

In this study this tribe is represented by the genera *Chilocorus* Leach*, Orcus* Mulsant, *Halmus* Mulsant, and *Exochomus* Redtenbacher. In both analyses the Sticholotidini genus *Chilocorellus* is the sister group of *Chilocorus*, rendering the tribe paraphyletic relative to *Chilocorellus*. *Chilocorellus* looks like a typical Sticholotidini in many regards (e.g., shape of antennae and terminal maxillary palpomere, see discussion on Sticholotidinae), but like the Chilocorini the clypeus is expanded laterally. This characteristic is also present in some other Sticholotidini (e.g., *Promecopharus*, *Chilocorellus,* and *Glomerella*).

Three other Chilocorini are included in this study. Our study strongly supports the clade *Orcus* + *Halmus* + *Exochomus* [Node 10, BS=100, PP=1] as the sister group of the clade *Chilocorus* + *Chilocorellus.* This result conflicts with the morphological evidence which suggests a distinction between *Exochomus* and the other three genera. In *Exochomus*, the last antennal segment is partially embedded in the previous one, the mid and hind tibiae bear an apical spur and the postcoxal line is completely recurved. In *Orcus*, *Halmus*, and *Chilocorus* the last antennal segment is “normal”, the mid and hind tibia lack an apical spur and the postcoxal line is incompletely recurved. In the clade *Exochomus* + *Orcus* + *Halmus*, the genus *Exochomus* is strongly supported as sister group of *Halmus* [Node 11, BS=77, PP=0.85]. This finding is unexpected because a sister group relationship was assumed for *Orcus* and *Halmus*. Beside the similarities already mentioned, *Orcus* and *Halmus* have a distinct marginal line at the base of the pronotum and reduced number of antennomeres.

Telsimini. This is a small group of two genera distributed in Africa, Micronesia, New Guinea, and Australia. In our study, Telsimini is supported as the sister taxon of Cranophorini + Exoplectrini in the Bayesian analysis [Node G], and as the sister taxon of Cryptognathini + Noviini in the parsimony analysis [Node D]. These results with the findings of Giorgi et al. (2009), who recovered a sister group relationship between Telsimini and Chilocorini. We find no convincing morphological evidence to corroborate the unexpected placement of this tribe in the current study. However, *Telsimina* Casey is another taxon that was sensitive to perturbations in the data. Because of the weak and conflicting support for the placement of *Telsimina* in this study and that fact that there is no strong evidence to support alternative relationships, we decide to leave Telsimini in Chilocorinae until more convincing evidence can be brought to bear on this subject.

Coccinellinae

All of the characteristics that make Coccinellidae a charismatic group are found in this subfamily. These are the relatively large, usually oval or hemispherical, colorful, and conspicuous ladybirds. Sasaji’s (1968) classification included the tribes Discotomini Mulsant, Halyziini (=Psylloborini Casey) and Coccinellini. Subsequently, the family was expanded to accommodate the tribes Singhikalini and Tytthaspidini. The members of Coccinellinae represented in our study, which did not include any representative of the tribe Singhikalini, were consistently recovered as a monophyletic group [Node 13, BS=100, PP=1]. These findings are in agreement with Giorgi et al. (2009). Singhikalini differs from the other Coccinellinae by having pronounced dorsal pubescence and more coarsely faced eyes. This tribe was originally assigned to Coccidulini (Coccidulinae) was but latter transferred to Coccinellinae by Miyatake (1972). The revised placement was supported by the form of the female genital plate. Also, the eyes (although somewhat coarsely facetted) are finer than those of most Coccidulinae. Despite these unusual features, Singhikalini has been regarded as being closer to the rest of the Coccinellinae than Discotomini (Kovář 1996; Duverger 2003). Given that view, the placement of Discotomini as the sister group of the remaining Coccinellinae, supported by our analyses, provides support for the monophyly of the subfamily as currently defined.

Discotomini. The genus *Pristonema* Erichson, is strongly supported in our analysis as the sister group of the rest of the Coccinellinae [Node 13]. This finding is in agreement with Giorgi et al. (2009). These results also support the contention of Sasaji (1968, 1971) and Kovář (1996), that the tribe was the most plesiomorphic ("primitive") in the subfamily. Members of Discotomini have very distinct antennae, in which antennomeres 4 and 6 to 9 are distinctly expanded medially forming serrate antennae (Sasaji 1971).

Coccinellini (=Halyziini and Tytthaspidini). Apart from the well supported sister group relationship between *Pristonema* (Discotomini) and the rest of the Coccinellinae, the topology supported by our study conflicts with the current classification. Nested in the sister group clade to *Pristonema* are the tribes Halyziini (here represented by *Illeis* Mulsant and *Psyllobora* Dejean) [Node 16] and Tytthaspidini (here represented by *Bulaea* Mulsant and *Tytthaspis* Mulsant) [Node 20], rendering Coccinellini paraphyletic. These results support the findings of Giorgi et al. (2009). Halyziini and Tytthaspidini are distinct from the other Coccinellinae by their unusual host preferences and distinct mandibular anatomy. However, despite the distinct morphological adaptations, the mandibles in both tribes have the distinct bifid incisor tooth characteristic of Coccinellini (Samways et al. 1997). The synonymy of Halyziini with Coccinellini has been already proposed by Ślipiński (2007). In the present study, *Illeis* + *Psyllobora* are strongly supported as sister group of a clade comprising *Coelophora* Mulsant + *Illeis* + *Psyllobora* + *Myzia* Mulsant+ *Anatis* Mulsant + *Bothrocalvia* Crotch [Node15, BS=99, PP=0.99]. Apart from the presence of *Coelophora*, this clade corresponds to the Halyziares of Mulsant (1850). In that classification, Halyziares was created to accommodate the Myziates and Halyziates. It is interesting that our study supports the very first classification scheme for the Coccinellini proposed by Mulsant (1850). *Bulaea* and *Tytthaspis* are nested in a strongly supported clade that also includes *Coleomegilla* Timberlake, and *Micraspis* Dejean [Node18, BS=87, PP=1]. The same relationships were recovered by Giorgi et al. (2009), but that study did not include *Tytthaspis*. With the inclusion of its type genus, *Tytthaspis,* we confirm the monophyly of Tytthaspidini. Based on this result, we synonymize Tytthaspidini **syn. nov.** with Coccinellini.

Scymninae

The monophyly of Scymninae in not supported in our study. These results are in agreement with the findings of Giorgi et al. (2009) and confirm the concerns of Pope (1989), Vandenberg (2002), and Ślipiński (2007), who questioned the monophyly of the subfamily. The subfamily was erected by Sasaji (1968) to accommodate the small-sized, hairy coccinellids, with reduced, ventrally inserted, antennae, and slightly securiform terminal maxillary palpomeres. From its original composition of seven tribes (Aspidimerini Mulsant, Cranophorini Casey, Hyperaspidini Mulsant, Ortaliini Weise, Scymnillini (=Zillini) Casey, Scymnini Mulsant, and Stethorini Dobzhanski), the subfamily grew to include four more (Brachiacanthini Mulsant, Cryptognathini Mulsant (=Pentilini) Mulsant, Diomini Gordon, Selvadiini Gordon) and lost one (Cranophorini) which was transferred to Coccidulinae. Even though some of these diagnostic features might still be common to all of them, Scymninae comprises an assemblage of very distinct forms.

Our findings indicate a polyphyletic condition for the subfamily as defined by Sasaji. In the Bayesian analysis, a major clade (J) includes Scymnini (including *Blaisdelliana* Gordon) plus Stethorini (21) as sister group of *Selvadius* + *Ghanius* (Shirozuelini) (K). This clade is supported as sister group of a clade (F) which includes the clade Ortaliini + Exoplectrini + Cranophorini + Telsimini. A major clade comprising Hyperaspidini + Brachiacanthini + Aspidimerini (T) is recovered as the sister group of Diomini + Platynaspidini (S). Together, the combined clade [Node L] is recovered as sister group of a primarily Coccidulinae (*sensu* Sasaji) clade (including *Cryptognatha* Mulsant). The parsimony analysis supports a clade (C) with Aspidimerini + Platynaspidini (D) as sister group of Noviini + *Cryptognatha* + Telsimini (E). Ortaliini is recovered as the sister group of Scymnini (including *Blaisdelliana*) + Stethorini. This clade is the sister group of a mixed clade that include Hyperaspidini + Brachiacanthini as sister group of Exoplectrini (excluding *Rodatus* Mulsant) as sister group of *Selvadius*.

These major clades are weakly supported and many different combinations were observed during our study. We believe, however, that there is a clear distinction between the *Scymnus*-like and the *Hyperaspis*-like groups (see discussion below). Thus, even if the sister group relationship between these two groups is supported in future studies, the subfamilial status for each of these clades would still be valid. We hold the same opinion about *Cryptognatha*. The placement of Cryptognathini within either of these two groups seems unlikely based on its morphology. In addition, some similarities occur between Cryptognathini and Noviini, which form a clade that is strongly supported in our analyses. We constrain the circumscription of Scymninae to include the tribes Scymnini, Stethorini and Ortaliini.

Stethorini. In the present study, *Stethorus* Weise (Stethorini) is recovered nested within Scymnini as the sister group of *Nephaspis* (Scymnini) [Node 22, PP=0.6]. These findings strongly contradict the opinion of many authors (e.g., Sasaji 1968; 1971; Gordon 1985; Kovář 1996) who regarded the tribe as the most primitive scymnine. Stethorini is distinct from the other coccinellids by being specialized for mite-feeding and was originally erected by Dobzhansky (1924) on the basis of the morphology of the female reproductive organs. However, Sasaji (1968, 1971) noted the similarities with Scymnini, which, in fact, had led some authors to place *Stethorus* into Scymnini. Thus, even though some authors believe that Stethorini should hold a more basal position in the subfamily (e.g., Sasaji 1968; 1971; Kovář 1996), its inclusion within Scymnini should not be surprising. Morphologically, both *Stethorus* and *Nephaspis* have a distinct anteriorly expanded prosternum that partially conceals the mouthparts. Within the Scymnini, this feature is restricted to these genera. Thus, this relationship is not necessarily a spurious one. However, given the length of these two terminal branches, longer than those of most of the other coccinellids, it is possible that this sister group relationship between *Stethorus* and *Nephaspis* is the result of long branch attraction or by chance similarity of third position caused by saturation. Given these concerns, we consider our study to be inconclusive regarding the sister group relationship between *Stethorus* and *Nephaspis*, and prefer to keep the current tribal status for this taxon. However, based on the concordance between the analyses and the similarities shared with some Scymnini, we consider Stethorini to be a member of Scymninae.

Scymnini. In our analysis, Scymnini is represented by the genera *Nephus*, *Sasajiscymnus*, *Scymnus* and *Nephaspis*. This tribe is not supported as monophyletic in our study. All analyses supported the same topology for these taxa. *Nephaspis* and *Stethorus* (Stethorini) are supported as sister taxa [Node 22, PP=0.6]. *Blaisdelliana* (Hyperaspidini) is recovered nested within Scymnini as sister group to *Scymnus* [Node 24, BS=100, PP=1]. *Blaisdelliana* is a typical Hyperaspidini and its position as sister group to *Scymnus* does not receive any outside support from morphological evidence. The sister group relationship between *Nephaspis* and *Stethorus* was discussed in the previous section. In the Bayesian analysis, the clade comprising the Scymnini (including *Stethorus* and *Blaisdelliana*) is supported as sister group of *Selvadius* (Selvadiini) + *Ghanius* (Shirozuelini) [Node J]. This same clade is supported as sister group of a clade comprising Exoplectrini, Hyperaspidini, Brachiacanthini, Selvadiini, Shirozuelini, and Cranophorini in the parsimony analysis [Node Q].

Our results regarding the placement of the clade comprising Scymnini (including *Stethorus* and *Blaisdelliana*) are inconclusive. Its placement is weakly supported and conflicting between the hypotheses. Since this clade mainly represents the tribe Scymnini and includes *Scymnus* (the type-genus of the tribe) it should represent the subfamily Scymninae.

Ortaliini. The placement of Ortaliini has been a matter of disagreement between classifications. In our study, the parsimony analysis supports *Ortalia* Mulsant (Ortaliini) as the sister group of a clade comprising Scymnini + *Stethorus* [Node M], a relationship proposed previously by Sasaji (1968, 1971). Although Ortaliini have long antennae, a condition that deviates greatly from one of the family's key characteristics, the occurrence of white wax-like larval exudation led Sasaji to placed Ortaliini in Scymninae without hesitation. An alternative classification for the tribe was proposed by Kovář (1996), who proposed the subfamily Ortaliinae to accommodate Ortaliini and Noviini (Coccidulinae). The Bayesian analysis, however, supports *Ortalia* as sister taxa of a clade comprising *Telsimina* (Telsimini), *Cranophorus* (Cranophorini) and Exoplectrini (here represented by *Chnoodes* Chevrolat and *Orydia* Gorham) [Node F]. This unusual placement has no support from morphological or biological evidence and has never been suggested in a previous classification scheme. Our study provides limited support for the placement of Ortaliini. The results are conflicting and weakly supported. However, we do not consider the placement of Ortaliini in Scymninae convincing enough either. Thus, we place this tribe as *incertae sedis*.

Hyperaspidinae

This clade represents a major lineage within Scymninae in terms of biodiversity. They are normally distinguished from the typical Scymnini by the lack of pubescence on the dorsal surface of the body and the fusiform antennal club, with a conical distal antennomere. The Scymnini are pubescent and have oval and asymmetrical antennal clubs, with quadrate or rounded distal antennomeres. Based on these distinctions, Duverger (1983) proposed

Hyperaspidinae to accommodate these two tribes. In addition to the morphological evidence, the topologies recovered in all analyses suggest this group to be a lineage distinct from Scymnini.

Our study suggests a close relationship between Hyperaspidini and Brachiacanthini. Aspidimerini has often been placed near Hyperaspidini because these taxa. These taxa share a very peculiar modification of the maxillary palps that are tucked underneath the mentum. Similar genital plates are also observed in these taxa and similar modifications of the mentum. Based on these concerns and observations, we place Platynaspidini and Aspidimerini in Hyperaspidinae.

Hyperaspidini and Brachiacanthini. A sister group relationship between Hyperaspidini and Brachiacanthini is strongly supported by all analyses [Node 27, BS=100, PP=1]. This was an expected result, since these two tribes are morphologically very similar. In fact, Brachiacanthini was erected by Duverger (1989) solely to accommodate the Hyperaspidini with an external spine on the anterior tibia. Our results, however, are inconclusive regarding the placement of this clade. The topologies supported by the Bayesian analysis suggest a sister group relationship with Aspidimerini [Node T, BS=50]. In the parsimony analysis, Hyperaspidini + Brachiacanthini was supported as the sister group to Exoplectrini (Coccidulinae) + Selvadiini [Node M]. Even though a close relationship with the Aspidimerini is not supported by all analyses, such a relationship is defensible on morphological grounds (see discussion below). No morphological evidence is available at the moment to support a sister group relationship to Exoplectrini.

Selvadiini. Selvadiini is a monotypic tribe endemic to North America. Given the obvious pubescence on the dorsal body surface, *Selvadius* was originally placed in Scymnini. Gordon (1985) created the tribe Selvadiini to accommodate *Selvadius* and placed the tribe in the subfamily Scymninae. That author pointed out the striking similarities with Hyperaspidini (the fusiform antennae and the shape of the head capsule) refering to *Selvadius* as a typical hyperaspidine. In our study, a sister group relationship between Selvadiini and Hyperaspidini + Brachiacanthini was not supported. In fact, *Selvadius* was never recovered as sister group of any of the "Scymininae" tribes. Our parsimony analysis supported *Selvadius* as the sister group to Exoplectrini [Node N] and the Bayesian analysis supported *Selvadius* as the sister group of *Ghanius* (Shirozuelini) [Node K]. The results concerning the placement of this tribe are inconclusive. Despite the pubescent dorsal surface, the morphological similarities shared with Hyperaspidini seem fairly convincing. We found no obvious similarities that provided morphological evidence for the sister group relationships recovered in the present study. It is worth mentioning, however, that Gordon (1985) found no support for the above mentioned relationship (Hyperaspidini + Selvadiini) on the basis of larval morphology. Based on the lack of evidence to the contrary, we place the tribe together with Hyperaspidini in the subfamily Hyperaspidinae.

Aspidimerini and Platynaspidini. Morphological similarities strongly support a close relationship between the tribes Platynaspidini and Aspidimerini (Sasaji 1971; 1979; 1992). In our study, this sister group relationship is recovered by the parsimony analysis [Node E]. This clade is not supported by the Bayesian analysis, in which *Platynaspis* was recovered as the sister taxon of *Diomus* [Node S] and Aspidimerini was recovered as the sister taxon of Hyperaspidini +

Brachiacanthini [Node T, PP=0.5]. This analysis, however, supports *Platynaspis* + *Diomus* as the sister group of Aspidimerini + Hyperaspidini + Brachiacanthini [Node R]. Thus, despite not being recovered as sister groups, some phylogenetic proximity between Platynaspidini and Aspidimerini is still suggested in the Bayesian topology.

The affinities between Platynaspidini and Aspidimerini were first suggested by Sasaji (1971), ‘‘The Aspidimerini are exactly similar to the Platynaspidini not only in adults but also in larvae. If these structural similarity [sic] were not caused by a secondary convergence, both tribes should be treated in a single phyletic stock”. A similar statement was made by Sasaji (1992), “although adult features [sic] very different between Aspidimerini and Platynaspidini, both lineages should be placed in sibling groups”. It is surprising that Sasaji decided to keep Platynaspidini in Chilocorinae, even though he was so confident about its close relationship with Aspidimerini. The following characters are the larval morphological similarities shared by Aspidimerini and Platynaspidini that were mentioned in Sasaji (1992): 1) body extremely flat, oval in outline, nearly smooth and without any dorsal spine or projection; 2) white wax exudation lacking; 3) antennal segments usually reduced; 4) maxillary palp reduced, 2-segmented; 5) maxillary lobe not well sclerotized; 6) legs very short and stout; 7) tibiotarsi with many or numerous apical clavate setae; 8) claw thick and distinctly appendiculate; and 9) mandible rather simple. We believe that our results, in addition to the morphological similarities mentioned above, provide enough evidence to place Platynaspidini together with Aspidimerini.

Coccidulinae

Sasaji’s (1968) classification includes the tribes Coccidulini Mulsant, Tetrabrachiini Mulsant (=Lithophilini), Noviini Mulsant and Exoplectrini Crotch. Subsequently, five tribes were added to the subfamily (Azyini Gordon, Cranophorini Casey, Monocorynini Gorham, Poriini Mulsant, and Oryssomini Gordon). The tribes Oryssomini and Tetrabrachiini are not represented in the present study. Our analyses do not support the Coccidulinae as a monophyletic group. These findings support the ideas of Pope (1988), Vandenberg (2002), and Vandenberg and Perez-Gelabert (2008), who questioned the monophyly of the subfamily. Sasaji (1968) erected this subfamily to accommodate the coccinellids that were weakly to moderately convex with long antennae, a pubescent dorsum, strongly securiform terminal maxillary palps and coarsely faceted eyes. Vandenberg and Perez-Gelabert (2008) proposed that the unifying characters of the subfamily were all plesiomorphic. In fact, Sasaji's (1968) own text suggested that the characters that he used to define the subfamily were plesiomorphic. As stated by Sasaji (1968), "Some of this [shared] characters show perhaps rather primitive phases and are also commonly observed in some other primitive groups or common to many groups…". The subfamily was not recovered as monophyletic in the molecular phylogenetic study by Giorgi et al. (2009).

In the Bayesian analysis, the cocciduline are distributed in three clades: 1) Exoplectrini + *Cranophorus* (Cranophorini) [Node H]; 2) Coccidulini + Noviini + Azya Mulsant (Azyini) + *Diomus* (Scymninae) [Node M]; and 3) *Rodatus* (Exoplectrini) + *Poria* Mulsant (Poriini) [Node C]. In the parsimony analysis, the cocciduline are distributed in four clades: 1) *Poria* (Poriini) is the sister group of Epilachninae (*Epilachna* Dejean and Cynigetini sp.) [Node A]; 2) *Rodatus* is the sister group of a clade comprising *Cryptognatha* (Cryptognathini) + Noviini [Node B]; 3) Exoplectrini [Node M]; and 4) *Monocoryna* occupies a more basal position in both analyses [Node 4].

Coccidulini. The monophyly of this tribe was not supported in the current study. This is the largest tribe in the subfamily with more than 30 valid genera currently. Coccidulini is represented in this study by the genera *Bucolus* Mulsant, *Coccidula* Mulsant, *Cranoryssus* Brèthes,, *Cryptolaemus* Mulsant, *Nothocolus* Gordon*, Orynipus* Brèthes, and *Rhyzobius* Erichson. The Bayesian analysis supports a primarily Coccidulinae clade that includes all the Coccidulini (excluding *Rodatus*), Noviini, *Cryptognatha* and *Azya* (Azyini) [Node M]. Within this clade, the first split divides *Coccidula* + *Cranoryssus* + *Nothocolus* + *Orynipus* + *Rhyzobius* [Node N] from the rest of the tribe [Node O]. In the second clade, Noviini + *Cryptognatha* is supported as sister group of *Azya* + *Bucolus* + *Cryptolaemus* [Node P, PP=0.8], where *Azya* is supported as sister group of *Cryptolaemus* [Node Q, PP=7.4]. In the same analysis, *Rodatus* is supported as sister group of *Poria* (Poriini) [Node C]. The parsimony analysis recovers *Azya* and *Diomus* nested within Coccidulini (excluding *Rodatus*) [Node F]. In this clade, *Azya* + *Diomus* (Diomini) [Node H] is supported as sister group of *Coccidula* + *Nothocolus* [Node G]. In the same analysis, *Rodatus* is at the base of node (B). In this node, a clade including Aspidimerini + Platynaspidini is supported as sister group of the clade (*Telsimina* + Cryptognathini + Noviini). These results are inconclusive regarding the circumscription of Coccidulini. Apart from the limited taxon sampling, the topologies are conflicting and most of the sister group relationships have low support. The data support a monophyletic group including *Coccidula*, *Cranoryssus*, *Nothocolus, Orynipus*, and *Rhyzobius* in the Bayesian analysis. The placement of *Rhyzobius* provides support for the recent synonymy proposed by Ślipiński (2007). The same analysis provides strong support for a clade comprising *Azya, Bucolus* and *Cryptolaemus*. The same clade was supported in the Bayesian analysis by Giorgi et al. (2009), but in that study, *Cryptolaemus* was supported as sister group of *Bucolus*. This is consistent with the taxonomic instability of the Australian *Cryptolaemus*. That genus was placed in Scymnini (Scymninae) by Sasaji (1968, 1971) and later transferred to Coccidulini by Kovář (1996). The same clades are not supported by the parsimony analysis. Despite that disagreement, a topological proximity between these taxa is supported by all analyses. In practice, these results suggest that these genera (*Bucolus*, *Coccidula*, *Cranoryssus*, *Cryptolaemus*, *Nothocolus, Orynipus, Rhyzobius,* and *Azya*) might or might not belong in the same tribe, but they are likely to belong to the same subfamily, which, given the inclusion of the type-genus *Coccidula*, would hold the name Coccidulinae. Whether Noviini + Cryptognathini would belong to this subfamily is less clear (see following paragraph). Another implication of the current study regards the subfamilial status of Azyini that was proposed by Gordon (1994) (see discussion below).

Azyini. This is a small group comprising only two genera with its distribution restricted to South America. Gordon (1994) justified the subfamilial rank for this tribe based solely on the thickened, obtuse anterior angles of the pronotum and the finely faceted eyes. Our study provides very limited support for that view. Even though the boundaries between Azyini and Coccidulini are not clarified by the present study, our results suggest, at least, a close relationship between these two tribes. Thus, a new subfamily for the accommodation of Azyini (and maybe some other genera currently classified in Coccidulini, such as *Cryptolaemus* and *Bucolus*) does not seem to be justifiable based on our current knowledge. Therefore, we feel that Azyini should remain in Coccidulinae.

Exoplectrinae

Gordon (1994) proposed subfamilial status for the tribe Exoplectrini. Our findings support the Exoplectrini as a distinct lineage apart from *Coccidula*, the type-genus of Coccinellinae. Exoplectrini (*Chnoodes*, *Oridia,* and *Neorhizobius* Crotch) may be distinguished from other coccinellids by the shape of the antenna, which has a distinct three-segmented club and a strongly expanded and flat scape. In our study, the placement of Exoplectrini is inconclusive. The tribe is weakly supported in the Bayesian analysis as the sister group of *Cranophorus* (Cranophorini) [Node H], in a clade that also includes *Telsimina* (Telsimini) and *Ortalia* (Ortaliini) [Node F]. In the parsimony analysis, it is recovered as the sister group of *Selvadius* (Selvadiini) [Node N]. A sister group relationship between Exoplectrini and Cranophorini can be justified on the basis of some shared "cocciduline" characters. The sister group relationship with Selvadiini, however, strongly contradicts the morphological evidence which suggests a close relationship of this tribe with Hyperaspidini and Brachiacanthini. Although our analyses provide weak and conflicting support for the precise position of Exoplectrini, our results suggest, with limited support, the placement of Exoplectrini outside the Coccidulinae (*sensu novo*), thus supporting the subfamilial status of this tribe, as suggested by Gordon (1994).

Monocoryninae Gorham*, new subfamily*

Among the best supported results in this study is the position Monocorynini, a monogeneric tribe restricted to Southeast Asia. The lone exemplar of this tribe, *Monocoryna* Gorham (Monocorynini), is consistently recovered near the base of the coccinellid phylogeny as the sister group of Microweiseinae [Node 4]. This tribe may be distinguished from other coccinellids by its very large, one segmented antennal club and the lack of a penis guide. Given the very distinct and well supported placement of this tribe, we propose a subfamilial status for the group, Monocoryninae **new subfamily**.

Epilachninae

The phytophagous lineage of ladybeetles corresponds to the subfamily Epilachninae. This is the only subfamily of Sasaji (1968, 1971) with reliable, unambiguous characteristics (viz, a distinct mandibular form with multiple teeth at the apex, and a mentum that is broader at the posterior margin). Members of the tribe Psylloborini (Coccinellinae) also have multidentate mandibles, but the architecture is different (Samways et al. 1997). In Sasaji's (1968, 1971) classification, only the tribe Epilachnini was recognized within the subfamily. Three other tribes have been added since then: Cynegetini Gordon (=Madaini), Epivertini Gordon, and Eremochilini Gordon and Vandenberg. Our analyses lend some support to the monophyly of Epilachninae; however, the tribes Epivertini and Eremochilini are not represented in the study. The inclusion of Eremochilini would provide a much more rigorous test for the monophyly of this subfamily. Members of the tribe Eremochilini are very distinct from the rest of the subfamily, which is otherwise morphologically homogeneous. Despite the dissimilarities, the morphological evidence supporting the monophyly of Epilachninae is very convincing.

Unfortunately, the placement of Epilachninae received limited support in our study. Our results contradict the traditional sister group relationship between Epilachninae and Coccinellinae that was hypothesized by Sasaji (1968, 1971) and Kovář (1996). The Bayesian analysis support Epilachninae plus Poriini as the sister group of a clade that comprises all the Scymninae, most the Coccidulinae (except Monocorynini and Poriini) and two Chilocorini tribes, Platynaspidini and Telsimini. In the parsimony analysis the Epilachninae + Poriini clade is recovered in a more basal position. According to the parsimony hypothesis, Epilachninae plus Poriini is at the base of the clade sister group to *Monocoryna*.

Incertae sedis

Noviini and Cryptognathini. In our study, Noviini is supported as sister group of *Cryptognatha* (Cryptognathini) [Node 26]. The placement of Noviini has been a matter of debate. Sasaji (1968, 1971) placed the tribe in Coccidulinae based on the anatomy of the pterothorax, maxillary palp, elytral epipleura, and femora. However, Sasaji (1968) notes morphological affinities with other tribes outside Coccidulinae, namely Ortaliini, Stethorini and Chilocorini. Kovář (1996) placed Noviini in Ortaliinae together with Ortaliini. Even though a close relationship between Noviini and Cryptognathini has never been suggested previously, these tribes share the following morphological similarities: 1) the prosternal shape at the central portion, 2) the very short antenna, 3) the robust cup-shaped last maxillary palpomere, 4) the compact body shape, 5) the broad flat legs, 5) and the recurved postcoxal line. The support for this clade is limited, but the relationship is corroborated by all topologies recovered in our study.

The placement of the Cryptognathini + Noviini clade is unclear. It has weak support and it is topologically unstable. In the Bayesian analysis this clade was always nested within the tribe Coccidulini [M]. These topologies suggest a classification of Coccidulinae that would include the tribes Coccidulini, Azyini, Noviini and Cryptognathini. In the parsimony analysis, Noviini plus Cryptognathini are supported as sister group of Telsimini. No obvious morphological similarities exist between these clades, which also received limited support in the analyses. Our results provide convincing evidence for a sister group relationship between the tribes Noviini plus Cryptognathini. Our findings, however, are not conclusive regarding the precise position of this clade. We believe that the topology recovered by the Bayesian analysis to be more convincing than the parsimony one. However, the decision of placing this clade in Coccidulinae would require the transfer of Cryptognathini from Scymninae. We believe that decision to be premature, given the level of support and limited morphological evidence that supports this clade as a member of Coccidulinae. Thus, until further studies provide more conclusive results, we place these two tribes as *incertae sedis*.

Cranophorini. This tribe is a small group, composed of two genera with distribution restricted to Australia and South Africa. In the present study, the placement of *Cranophorus* is very weakly supported and conflicts among analyses. This tribe was first treated by Sasaji (1968, 1971) under Scymninae. It was later transferred to Coccidulinae. *Cranophorus* is supported as sister group to *Ghanius* (Shirozuelini) in the parsimony analysis [Node L] and is recovered as the sister group to Exoplectrini in the Bayesian analysis [Node H]. As mentioned above, the close relationship with Exoplectrini which is supported by the Bayesian analysis is apparently not spurious, but no strong morphological evidence supports this clade either. A close relationship with *Ghanius* seems very unlikely as Shirozuelini has many characters shared with the *Sticholotis* (the type-genus of the Sticholotidinae). Given the long terminal branches of this clade, it is possible that this sister group relationship between *Ghanius* and the Exoplectrini is the result of long branch attraction. We believe our results are not conclusive enough to make a taxonomic decision about this group at this time. Thus, we consider the classification of the tribe Cranophorini as *incertae sedis*.

Poriini. This is a monotypic tribe of medium-sized, weakly convex ladybeetles from South America. Our study suggests a close relationship between Poriini and Epilachninae. In the parsimony analysis, Poriini is supported as the sister group of Epilachninae [Node A]. In the Bayesian analysis, it is supported as the sister group to *Rodatus* (Exoplectrini) [Node C] and this larger clade is recovered as the sister group to Epilachninae [Node B]. These results are surprising since no obvious similarities are shared between *Poria* and any members of Epilachninae. Although no host data are available, the mandibular shape in *Poria* and *Rodatus* is that of a typical predator, not like that of the phytophagous epilachnines. Apart from some characters used by Sasaji to define the subfamily Coccidulinae, there are no obvious morphological similarities between *Poria* and *Rodatus*. Poriini differ from the Coccidulini by the finely faceted eyes and the loose, very asymmetrical three-segmented antennal club. Members of Coccidulini have coarsely faceted eyes and a more compact, slightly asymmetrical three-segmented club. Overall, the placement of Poriini received weak and somewhat contradicting support in our analyses. A close relationship with *Rodatus* would suggest that Coccidulini was polyphyletic or that Poriini belong to the clade that comprises the Coccidulini and allies. The sister group relationship between Poriini and Epilachninae receives weak support in all of the analyses. Further studies should carefully investigate this relationship. We believe our results are not conclusive enough to make a taxonomic decision regarding this group. Thus, we place this tribe as *incertae sedis*.

Our study provides an alternative classification for Coccinellidae based on the best knowledge we have about the phylogenetic relationships within the family. This view strongly contradicts the traditional classification, as it does not support most of the Sasaji's subfamilies as monophyletic. Our findings, however, agree with many recent studies (Vandenberg 2000;

Vandenberg and Perez-Gelabert 2007; Ślipiński et al. 2005; Ślipiński 2007) and are well supported by morphological evidence. Unfortunately, our results were not conclusive regarding the position of some taxa. We place these taxa in *incertae sedis* (Table 4.4) until further studies provide more definitive answers.

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Table 4.1. Description of the molecular dataset. Numbers represent GenBank accession numbers. Dash mark represents missing data. Empty cells are existing sequences not yet submitted to GenBank.

		GenBank accession numbers						
Family/Tribe	**Species**	**12S**	**16S**	**COI**	**COII**	**18S**	**28S**	**H3**
EROTYLIDAE	*Pselaphacus nigropunctatus*					EU164627	EU164657	
CORYLOPHIDAE	*Clypastrea* sp.			________	________			________
LATRDIIDAE	*Cartodere* sp.							
	Akalyptoischion sp.		________		________			
DISCOLOMATIDAE	*Aphanocephalus* sp.					EU145628	EU145687	
BOTHRIDARIDAE	*Bothrideris* sp.	________			________			
CERYLONIDAE	*Cerylon* sp.							
ALEXIIDAE	*Sphaerosoma* sp.							________
ENDOMYCHIDAE	*Corynomalus laevigatus*					EU164639	EU164646	
	Lycoperdina ferruginea		________		________	EU145637	EU145695	________
	Mycetina horni					EU145641	EU145699	
	Bystus sp.							________
	Epipocus sp. 1	________	________	________		________		________
	Epipocus sp. 2							
	Endomychus sp.							
	Rhanidea sp.							
	Holoparamecus sp.							________
	Trochoideus sp.							________
	Chileolobius sp.		________	________				
	Stenotarsus sp.			________	________			
Chilocorini	*Chilocorus cacti*					EU145610	--------	________

	Exochomus quadripustulatus					FJ687695	FJ687736	
	Halmus chalybeus					EU145607	EU145669	
	Orcus bilunulatus					FJ687699	FJ687740	
Platynaspidini	*Platynaspis* sp.					EU145619	EU145678	________
Telsimini	*Telsimia* sp.					FJ687697	FJ687738	
Azyini	*Azya orbigera*					FJ687666	FJ687707	
Coccidulini	*Coccidula* sp.					FJ687702	FJ687743	
	Cranoryssus sp.	________		________	________			
	Nothocolus sp.	________						________
	Orynipus sp.	________	________	________	________			
	Bucolus fourneti					FJ687704	FJ687745	
	Cryptolaemus montrouzieri					FJ687668	FJ687709	
	Rhyzobius sp.					FJ687700	FJ687741	
Cranophorini	*Cranophorus* sp.					FJ687669	FJ687710	
Exoplectrini	*Chnoodes* sp.		________			EU145606	EU145668	
	Neorhizobius sp.					________		________
	Oridia pubescens					FJ687693	FJ687734	________
	Rodatus sp.	________	________		________			
Monocorynini	*Monocorina* sp.		________	________				
Noviini	*Anovia* sp.		________					________
	Rodolia sp.							________
Plotinini	Plotinini sp.		________					
Poriini	*Poria* sp.					FJ687692	FJ687733	
Coccinellini	*Anatis labiculata*					________	FJ687714	
	Bothrocalvia albolineata					FJ687688	FJ687729	
	Coelophora bisellata					FJ687679	FJ687721	
	Coleomegilla					FJ687672	FJ687713	

	strenua							
	Cycloneda sanguinea					FJ687681	FJ687723	
	Harmonia axyridis					FJ687676	FJ687718	
	Hippodamia quinquesignata					FJ687673	FJ687715	
	Micraspis sp.					FJ687678	FJ687720	
	Myzia pullata					FJ687671	FJ687712	
	Olla sp.							
	Olla v-nigrum					FJ687675	FJ687717	
Discotomini	*Pristonema* sp.					FJ687665	FJ687706	
Halyziini	*Illeis* sp.					FJ687680	FJ687722	
	Psyllobora vigintimaculata					EU145604	EU145666	
Tytthaspidini	*Bulaea anceps*					FJ687667	FJ687708	
	Tytthaspis sedecempuctata							
Cynegetini	Cynegetini sp.					EU145608		
Epilachnini	*Epilachna* sp.					EU145616	EU145675	
Ortaliini	*Ortalia* sp.					EU145617	EU145676	
	Ortalia horni					EU145614		
Aspidimerini	*Aspidimerus* sp.1					FJ687696	FJ687737	
	Aspidimerus sp.2							
	Cryptogonus sp.					FJ687698	FJ687739	
Brachiacanthini	*Brachiacantha* sp.					FJ687694	FJ687735	
	Tiphysa sp.					EU145620	EU145679	
Diomini	*Diomus kamerungensis*					FJ687701	FJ687742	
Hyperaspidini	*Blaisdelliana sexualis*							
	Hyperaspidius					FJ687684	FJ687725	

	mimus							
	Hyperaspis lateralis					FJ687685	FJ687726	
Scymnini	*Nephaspis* sp.							_________
	Nephus sp.		_________					
	Sasajiscymnus tsugae							
	Scymnus sp.					FJ687682	FJ687724	
Selvadiini	*Selvadius* sp.		_________					
Stethorini	*Stethorus* sp.					EU145617	EU145676	_________
Cryptognathini	*Cryptognatha* sp.							_________
Serangiini	*Delphastus* sp.							
	Serangium sp.					FJ687690	FJ687731	
Microweiseini	*Coccidophilus* sp.							
	Paradis sp.	_________						_________
	Sarapidus sp.					FJ687670	FJ687711	_________
Shirozuelini	*Ghanius* sp.							
Sticholotidini	*Chilocorellus* sp.							
	Sticholotis sp.		_________			FJ687677	FJ687719	
	Sulcolotis sp.					_________		_________
Sukunahikonini	*Sukunonahikona* sp.			_________		_________		

Table 4.2. Gblocks treatments.

GENES	TOTAL	GBLOCKS	% left
12S	344	277	80
16S	543	456	83
18S	1920	1740	90
28S	2244	1877	84

Table 4.3. Models of sequence evolution according to the AIC criterium.

GENE	12S	16S	18S	28S	COI	COII	H3
MODEL	GTR+I+G	TrN+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	TVM+I+G

Table 4.4. Proposed suprageneric classification of the Coccinellidae.

- **COCCINELLINAE**
  - Coccinellini Latreille 1807
  - Discotomini Mulsant 1850
  - Singhikalini Kapur 1963
- **CHILOCORINAE**
  - Chilocorini Mulsant 1846
  - Telsimini Casey 1899
- **SCYMNINAE**
  - Scymnini Mulsant 1846
  - Stethorini Dobzhanski 1924
  - Scymnillini Casey 1899
  - Diomini Gordon 1999
  - Ortaliini Weise 1902
- **HYPERASPIDINAE**
  - Hyperaspidini Mulsant 1850
  - Brachiacanthini Mulsant 1850
  - Aspidimerini Mulsant 1850
  - Platynaspidini Redtenbacher 1843
  - Selvadiini Gordon 1985
- **COCCIDULINAE**
  - Coccidulini Mulsant 1846
  - Azyini Mulsant 1850

Oryssomini Gordon 1974

Tetrabrachiini Mulsant 1850

EXOPLECTRINAE

Exoplectrini Crotch 1874

MONOCORYNINAE

Monocorynini Gorham 1885

MICROWEISEINAE

Microweiseini Leng 1920

Sukunahikonini Kamiya 1960

Serangiini Pope 1962

STICHOLOTIDINAE

Sticholotidini Weise 1901

Plotinini Miyatake 1994

Shirozuelini Miyatake 1994

Carinodulini Gordon, Pakaluk and Ślipiński 1989

Cephaloscymnini Gordon 1985

Limnichopharini Miyatake 1994

EPILACHNINAE

Epilachnini Mulsant 1846

Eremochilini Gordon and Vandenberg 1997

Cynegetini Gordon 1975

INCERTAE SEDIS

Cryptognathini Mulsant 1850

Noviini Mulsant 1846
Cranophorini Casey 1899
Poriini Mulsant 1846

Table 4.5. Sasaji's (1968) Coccinellidae classification. (Note that not all tribes listed in the table were included in the original treatment).

- **COCCINELLINAE**
    - Coccinellini Latreille 1807
    - Discotomini Mulsant 1850
    - Singhikalini Kapur 1963
- **CHILOCORINAE**
    - Chilocorini Mulsant 1846
    - Telsimini Casey 1899
    - Platynaspidini Redtenbacher 1843
- **SCYMNINAE**
    - Scymnini Mulsant 1846
    - Stethorini Dobzhanski 1924
    - Scymnillini Casey 1899
    - Diomini Gordon 1999
    - Ortaliini Weise 1902
    - Hyperaspidini Mulsant 1850
    - Brachiacanthini Mulsant 1850
    - Aspidimerini Mulsant 1850
    - Cryptognathini Mulsant 1850
    - Selvadiini Gordon 1985
- **COCCIDULINAE**
    - Coccidulini Mulsant 1846

- Azyini Mulsant 1850
- Oryssomini Gordon 1974
- Tetrabrachiini Mulsant 1850
- Exoplectrini Crotch 1874
- Noviini Mulsant 1846
- Cranophorini Casey 1899
- Poriini Mulsant 1846
- Monocorynini Gorham 1885

STICHOLOTIDINAE

- Microweiseini Leng 1920
- Sukunahikonini Kamiya 1960
- Serangiini Pope 1962
- Sticholotidini Weise 1901
- Plotinini Miyatake 1994
- Shirozuelini Miyatake 1994
- Carinodulini Gordon, Pakaluk and Ślipiński 1989
- Cephaloscymnini Gordon 1985
- Limnichopharini Miyatake 1994

EPILACHNINAE

- Epilachnini Mulsant 1846
- Eremochilini Gordon and Vandenberg 1997
- Cynegetini Gordon 1975

Figure captions

Fig. 4.1. Strict consensus of the six most parsimonious tree topologies resulting from the analysis of seven genes (25852 steps, CI=40, RI=62). Bootstrap support values >50% are indicated above the branches. Nodes that were recovered by all analyses are numbered. Some nodes that were specific to only some analyses are lettered to facilitate discussion. Classification follows Sasaji (1968, 1971).

Fig. 4.2. Phylogenetic estimate of Coccinellidae based on Bayesian analysis of seven genes. Nodes that were recovered by all analyses are numbered. Some nodes that were specific to only some analyses are lettered to facilitate discussion. Classification follows Sasaji (1968, 1971).

Fig. 4.3. Bayesian phylogenetic estimate showing region of short branches, possibly resulting from ancient rapid radiation.

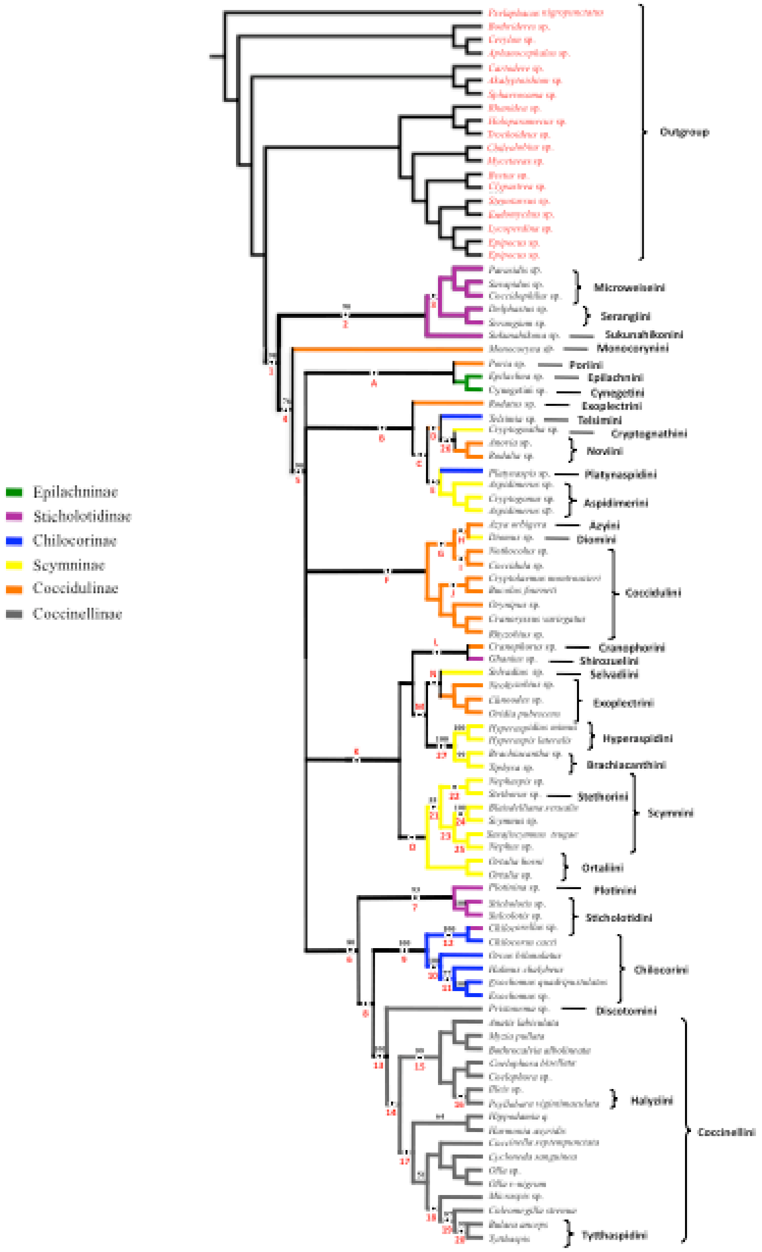
Epilachninae
Sticholotidinae
Chilocorinae
Scymninae
Coccidulinae
Coccinellinae
Outgroup
Microweiseini
Serangiini
Sukunahikonini
Monocorynini
Poriini
Epilachnini
Cynegetini
Exoplectrini
Telsimini
Cryptognathini
Noviini
Platynaspidini
Aspidimerini
Azyini
Diomini
Coccidulini
Cranophorini
Shirozuellini
Selvadiini
Exoplectrini
Hyperaspidini
Brachiacanthini
Stethorini
Scymnini
Ortaliini
Plotinini
Sticholotidini
Chilocorini
Discotomini
Halyzini
Coccinellini
Tytthaspidini

Fig. 4.1


Clypastraea sp.
Holoparamecus sp.
Stenotarsus sp.
Epipocus sp.
Sukunahikona sp.
Sukunahikonini
Coccidophilus sp.
Microweiseini
Delphastus sp.
Serangium sp.
Serangiini
Shirozuelini
Selvadius sp.
Selvadiini
Ortalia sp.
Ortaliini
Telsimia sp.
Telsimiini
Cynegetini sp.
Cynegetini
Epilachna sp.
Epilachnini
Cranophorus sp.
Cranophorini
Exoplectrini
Stethorus sp.
Stethorini
Scymnus sp.
Nephus sp.
Scymnini
Coccidula sp.
Coccidulini
Exoplectrini
Poriini
Rhyzobius sp.
Coccidulini
Platynaspis sp.
Platynaspidini
Diomus sp.
Diomini
Hyperaspis lateralis
Hyperaspidini
Brachiacantha sp.
Brachiacanthini
Aspidimerus sp.
Aspidimerini
Coccidulini
Azya orbigera
Azyini
Coccidulini
Cryptognatha sp.
Cryptognathini
Anovia sp.
Rodolia sp.
Noviini
Orcus bilunulatus
Halmus chalybeus
Exochomus quadripustulatus
Exochomus sp.
Chilocorini
Chilocorus cacti
Sticholotidini
Discotomini
Psyllobora vigintimaculata
Halyziini
Anatis labiculata
Hippodamia sp.
Harmonia axyridis
Cycloneda sanguinea
Olla v-nigrum
Olla sp.
Coccinella septempunctata
Coleomegilla
Tytthaspidini
Coccinellini
Sticholotis sp.
Sticholotidini
Plotinini
Monocorynini
Epilachninae
Stichololotidinae
Chilocorinae
Scymninae
Coccidulinae
Coccinellinae
1
2
3
4
5
6
7
8
9
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11
12
13
14
15
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17
18
19
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21
22
23
24
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26
27

Fig. 4.2

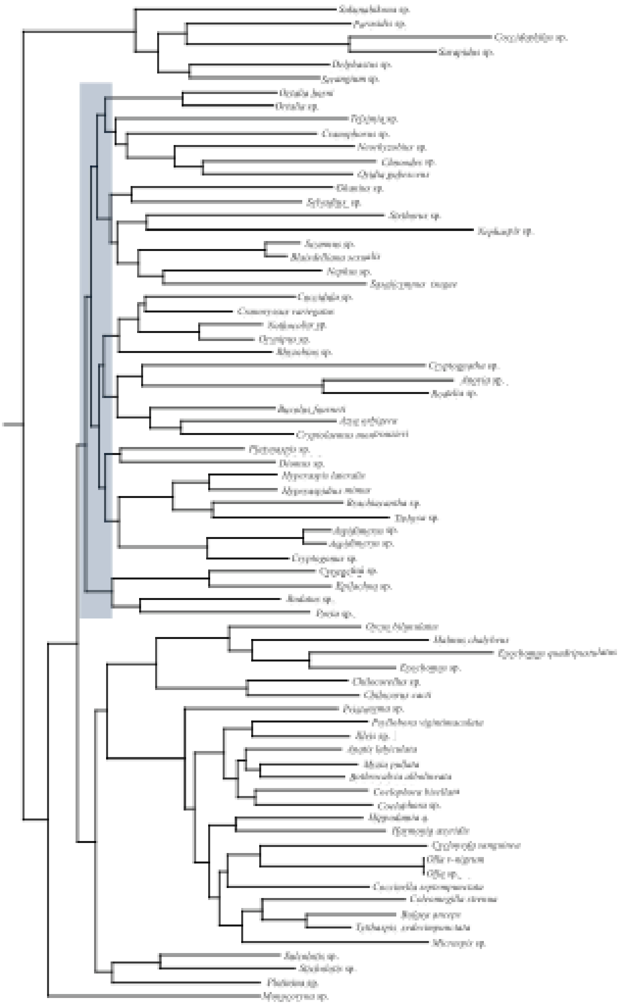
Coccidophilus sp.
Delphastus sp.
Serangium sp.
Ortalia sp.
Telsimia sp.
Stethorus sp.
Nephaspis sp.
Scymnus sp.
Nephus sp.
Rhyzobius sp.
Cryptognatha sp.
Bucolus fourneti
Azya orbigera
Cryptolaemus montrouzieri
Platynaspis sp.
Diomus sp.
Hyperaspis lateralis
Hyperaspidius mimus
Brachiacantha sp.
Cryptogonus sp.
Orcus bilunulatus
Halmus chalybeus
Exochomus quadripustulatus
Exochomus sp.
Chilocorus cacti
Psyllobora vigintimaculata
Anatis labiculata
Myzia pullata
Hippodamia sp.
Harmonia axyridis
Cycloneda sanguinea
Olla v-nigrum
Olla sp.
Coccinella septempunctata
Tytthaspis sedecimpunctata

Fig. 4.3

CHAPTER 5

REVISION OF THE AUSTRALIAN COCCINELLIDAE (COLEOPTERA)

PART 6. TRIBE CHILOCORINI[3]

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[3] A. Ślipiński, and Giorgi, J.A. 2006. Published in Annales Zoologici (Warszawa) 56(2): 265-304. Reprinted here with permission by Museum and Institute of Zoology, Polish Academy of Sciences.

Abstract

The Australian members of the coccinellid tribe Chilocorini are revised, keyed and illustrated. Chilocorini in Australia consists of 23 species classified in 6 genera: *Brumoides, Chilocorus, Exochomus, Halmus, Orcus* and *Trichorcus*. Five new species are described: *Brumoides piae*, *Chilocorus maculatus*, *Chilocorus micrus*, *Halmus hilli* and *Halmus viridis*. The following new synonyms are proposed: *Chilocorus malasiae* Crotch, 1874 (= *Chilocorus australasiae* Gadeau de Kerville, 1884; = *Chilocorus baileyi* Blackburn, 1890; = *Chilocorus flavidus* Blackburn, 1892b; = *Chilocorus diadema* Weise, 1898; = *Chilocorus meijerei* Weise, 1913; = *Chilocorus nasicornis* Korschefsky, 1944); *Orcus coelestris* Blackburn, 1891 (= *Orcus ovalis* Blackburn, 1892b; = *Orcus splendens* Blackburn, 1892b; = *Orcus clypeatus* Weise, 1923); *Orcus citri* Lea, 1902 (= *Orcus coxalis* Weise, 1917); *Orcus cyanocephalus* Mulsant, 1850 (= *Orcus lecanii* Blackburn, 1895; = *Orcus purpureocinctus* Lea, 1902); *Orcus punctulatus* Blackburn, 1892b (= *O. beneficus* Weise, 1913)**.** *Parapriasus* Chapin, 1965 is also considered as a synonym of *Orcus* Mulsant, 1850. Lectotypes are designated for: *Chilocorus australasiae* Gadeau de Kerville, 1884; *Ch. baileyi* Blackburn, 1890; *Ch. flavidus* Blackburn, 1892b; *Halmus cupripennis* Weise, 1923; *Orcus beneficus* Weise, 1913*; Orcus coelestris* Blackburn, 1891; *Orcus citri* Lea, 1902; *Orcus clypeatus* Weise, 1923; *Orcus coxalis* Weise, 1917; *Orcus evelynensis* Weise, 1923; *Orcus lecanii* Blackburn, 1895; *Orcus ovalis* Blackburn, 1892b; *Orcus punctulatus* Blackburn, 1892b, *Orcus purpureotinctus* Lea, 1902; *Orcus quadrimaculatus* Gadeau de Kerville, 1884 and *Orcus splendens* Blackburn, 1892b.

Key words— Coleoptera, Cucujoidea, Coccinellidae, Chilocorini, revision, Australia.

Introduction

Chilocorini is a moderately large, cosmopolitan group of ladybirds that is characterized by a distinctly hemispherical body, expanded clypeus and short appendages received in various fossae on the ventral side while in repose. Most of Chilocorini are coccid feeders but some feed on aphids and other sapsuckers (Hemiptera). This is an economically important group as many species have been used as biological control agents against many scales and aphids around the world (Drea and Gordon, 1990; Ponsonby and Copland, 1997).

Chilocorini is currently classified in the subfamily Chilocorinae (Sasaji, 1968) along with Platynaspidini and Telsimini, groups that share short antennae and a distinctly expanded clypeus, and comprises about 20 genera and 250 species (Korschefsky, 1932; Chapin, 1965, Kovář, 1995). The constitution of the subfamily and the classification of Chilocorini on a generic level are highly questionable. Ongoing research by Giorgi (revision of Chilocorini genera) and Ślipiński (classification of Coccinellidae) should solve some of the classification problems that will not be discussed here.

This article is the sixth in a series on the classification and phylogeny of Australian Coccinellidae that began by Bob Pope in 1989 (Pope, 1989) and reactivated by the senior author 15 years later (Ślipiński, 2004). Through the generous support of this research by the Australian Biological Resources Study (ABRS) the Australian members of the subfamilies Coccinellinae, Sticholotidinae and Chilocorinae received modern taxonomic treatments.

Australian Chilocorini is a small group consisting of a mixture of biogeographic elements. While *Orcus, Trichorcus* and *Halmus* represent endemic Australian elements in this fauna, the genera *Chilocorus* and *Brumoides* only recently arrived in Australia from the north. All very likely will be found in New Guinea and possibly in Indonesia. Apart from a paper by

Chapin (1965), with descriptions of two new Australian genera, there are no recent publications about Australian Chilocorini. This paper provides the first comprehensive treatment of the entire tribe in Australia with keys to the genera and species, and detailed morphological diagnosis.

Material and methods

Specimens were examined from the following institutions:

AM	Australian Museum, Sydney,
ANIC	Australian National Insect Collection, Canberra,
BMNH	The Natural History Museum, London,
BPBM	Bishop Museum, Honolulu,
CMN	The Canadian Museum of Nature, Ottawa,
CNC	Canadian National Insect Collection, Ottawa,
DARI	Insect Collection, New South Wales Department of Agriculture, Orange, New South Wales
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.,
MNHN	Muséum national d'Histoire naturelle, Paris,
NAQS	Northern Australia Quarantine Strategy, AQIS, Mareeba,
NHMB	Naturhistorisches Museum, Basel,
NRM	Naturhistoriska Riksmuseet, Stockholm,
NTMD	Northern Territory Museum and Art Gallery, Darwin,
NTDA	Northern Territory Department of Primary Industry and Fisheries, Darwin

QDPIB	Queensland Department of Primary Industries, Brisbane,
QDPIM	Queensland Department of Primary Industries, Mareeba,
QECB	Quarantine Entomological Collection, Broome
QMB	Queensland Museum, Brisbane,
SAM	South Australian Museum, Adelaide,
UQIC	University of Queensland Insect Collection, Brisbane,
USNM	United States National Museum, Washington DC,
VAIC	Victoria Agricultural Insect Collection, Department of Primary Industries, Knoxfield
ZMB	Zoologisches Museum, Humboldt Universität, Berlin.

Measurements were made using an ocular micrometer attached to a dissecting microscope as follows: (TL) total length, from apical margin of clypeus to apex of elytra; (PL) pronotal length, from the middle of anterior margin to margin of basal foramen; (PW) pronotal width at widest part; (EL) elytral length along suture, including scutellum; and (EW) elytral width across both elytra at widest part. Male and female genitalia were dissected, cleared in 10% solution of KOH and examined and photographed in glycerol. After examinations they were mounted in a drop of DMHF (dimethyl hydantoin formaldehyde) on a card and pinned with the specimen.

The photographs of the whole beetles, their genitalia, and other structures were executed on a digital camera. Composite images were generated using Auto-Montage software version 4.00 (Synoptics Ltd., http://www.syncroscopy.com). The distribution maps were produced from BioLink version 5.0 (CSIRO Entomology, http://www.biolink.csiro.au).

Taxonomy

Chilocorini Mulsant

Chilocoriens Mulsant, 1846: 28.

Exochomaires, Mulsant, 1850: 451.

Diagnosis. Body small to moderately large (2-8 mm), moderately to strongly convex with head in repose somewhat inserted into prothorax and usually directed downwards (Figs 5.7, 5.8); dorsum usually without apparent vestiture, rarely consisting of dense short hairs (Fig. 5.22). Head transverse, ventrally flattened; clypeus variously expanded laterally forming a shelf (Figs 5.183-5.188), entirely covering antennal insertions; ventral side without apparent antennal grooves. Mandible strong, triangular with single apical tooth and heavily developed retinaculum (Figs 5.53, 5.87, 5.101, 5.153, 5.173); maxillary palp moderately long, terminal palpomere parallel sided, weakly expanded to securiform (Figs 5.56, 5.65, 5.121-5.123); labial palp distinctly separated at base and inserted on ventral side of prementum. Antenna very short, 7-10-segmented with fusiform 3-segmented club. Pronotum transverse with anterior angles produced forward; pronotal base usually with bordering line; prosternum simple, moderately elongate in front of coxae; prosternal process narrow, parallel-sided, without carinae, completely separating procoxae; hypomeral fovea present or absent. Wings present, with large jugular lobe. Elytral punctures irregular, never in apparent rows; epipleuron broad and complete to apex (Fig. 5.189), often with foveae to receive apex of femora. Abdomen with 5 or 6 ventrites; postcoxal line at abdominal ventrite 1 variable, without associated pits and pores. Male genitalia: tegmen symmetrical, penis guide sometimes asymmetrical, parameres well developed and setose apically; penis a simple, single sclerite with large basal capsule. Female genitalia (Figs 5.90, 5.91, 5.94): coxite triangular, lightly sclerotised, usually bearing short styli; bursa copulatrix with infundibulum or fleshy lobe with sperm duct originating at the base of a sclerotised structure, duct composed of two parts of different diameters; spermatheca sclerotised, bean-shaped without ramus, with large accessory gland.

Distribution. Cosmopolitan.

Key to Australian genera of Chilocorini

1 Dorsal surfaces densely pubescent (Fig. 5.22); dull .... *Trichorcus* Blackburn

- Dorsal surfaces apparently glabrous and shiny...2

2 Mid and hind tibiae with apical spurs (Fig. 5.55); postcoxal line on abdominal ventrite 1 completely recurved (Fig. 5.58); apical antennomere very small and embedded in the penultimate one (Figs 5.51, 5.62) 3

- All tibiae without apical spurs; postcoxal line of abdominal ventrite 1 distinctly incomplete; apical antennomere larger and not embedded in the penultimate one..........4

3 Antenna 10-segmented; elytra dark brown with reddish maculae (Figs 5.15, 5.16)……………………………………………………………*Exochomus* Redtenbacher

- Antenna 8-segmented; elytra yellowish with dark longitudinal stripes or transverse patches (Figs 5.3-5.4)…………………………………………………………….*Brumoides* Chapin.

4 All tibiae dentate on outer margins (Figs 5.72, 5.79); pronotal base not margined……………………………………………………………..*Chilocorus* Leach.

- Tibiae not dentate along outer margins; pronotal base at least at the median part with marginal line (Figs 5.23, 5.26)……………………………………………………………5

5 Pronotum with marginal line along base broadly separated from the posterior edge (Fig. 5.26), the line continuing laterally and often forming arch posterio-laterally separated from

very fine marginal line (Fig. 5.191); antenna 9 (rarely 8)-segmented; elytral epipleuron almost always with deep foveae to receive femoral apex; coxite well developed with distinct styli…………………………………………………………..*Orcus* Mulsant

- Pronotum with marginal line along the base very close to the posterior edge, the line is uninterrupted and continues along posterior and lateral edges (Fig. 5.23); antenna 7-segmented with scape projecting apically (Fig. 5.100); elytral epipleuron without clearly defined foveae to receive femoral apex (Fig. 5.189); coxite reduced (Fig. 5.13……………. …………………………………………………...…………………*Halmus* Mulsant

BRUMOIDES CHAPIN

Brumoides Chapin, 1965: 237. Type species, original designation: *Coccinella suturalis* Fabricius, 1798 [= *Brumus daldorfii* Crotch, 1874: 21]

Diagnostic description. Dorsum glabrous; elytra yellowish or brown with dark markings (Figs 5.3-5.4). Head subquadrate or weakly transverse; eye distinctly emarginate; temple distinct, about as long as eye (Fig. 5.183). Antenna 8-segmented, short; scape symmetrical; terminal antennomere small and partially embedded in penultimate one (Figs 5.51, 5.62). Clypeus short, distinctly extending laterally; labrum entirely exposed. Maxillary palp relatively long, last palpomere somewhat expanded apically to weakly securiform with strongly oblique apex (Fig. 5.56); labial palp slender, terminal palpomere slightly shorter than the penultimate one. Pronotal base entirely bordered; prosternum long in front of procoxae; prosternal process very narrow, without carinae; hypomeral fovea absent. Protibia simple, narrow; meso- and metatibiae with 2 apical spurs (Fig. 5.55); tarsal claws appendiculate (Fig. 5.57) to weakly thickened at base (Fig. 5.61). Elytral margin very finely reflexed with complete bead; epipleural foveae absent.

Abdomen with 6th ventrite visible in male; postcoxal lines separated at middle, each arcuately recurving apically and reaching or almost reaching midpoint of lateral line (Figs 5.50, 5.58). Female genitalia: coxite sclerotised and distinctly elongate, bearing reduced styli; bursal appendix sclerotised and usually hook-like; spermatheca (Fig. 5.54) bean-shaped, cornu without a "beak". Male genitalia: penis guide weakly asymmetrical (Figs 5.47, 5.64); penis capsule well developed.

Discussion. With the description of *Brumoides*, Chapin (1965) restricted *Brumus* Mulsant to its type species. In his discussions and the key to the genera of Chilocorini he treated *Brumus* and *Exochomus* in various groups due to the differences in their tarsal claws. The obvious structural similarities were noticed by Kovář (1995) who discussed this generic complex and synonymized *Brumus* and *Exochomus*, but believed *Brumoides* was a separate genus. He also pointed out that these genera form a complex which is easily recognizable by having the pronotal base distinctly bordered.

Distribution. Worldwide.

Key to the Australian species of *Brumoides*

1 Each elytron in addition to somewhat darkened suture with 3 separate maculae or short transverse markings (Figs 5.4, 5.10); tarsal claws distinctly appendiculate (Fig. 5.57); larger species from western and northern coast .... *maculatus* Pope

\- Each elytron in addition to a sutural band with dark elongate area which is distinctly narrower at the level of hind legs (Figs 5.3, 5.9); tarsal claws simple (Fig. 5.61); smaller species, mostly from eastern coast..*piae* sp. nov.

Brumoides maculatus (Pope) comb. nov.

(Figures 4, 10, 47-56, 195)

Brumus maculatus Pope, 1954: 127.

Diagnosis. This species is easily distinguished from *B. piae* by its larger size, appendiculate tarsal claws and separate lateral maculae on elytra.

Description. Length 5.3-5.5 mm; TL/EW = 1.2-1.3; PL/PW = 0.4-0.5; EL/EW = 0.9-1.0. Surface predominantly yellowish; each elytron with 3 brownish maculae; a slightly transverse basal lateral one, a post-median transverse one, constricted medially or completely divided in some specimens, and a small rounded one at apical fifth of elytra (Figs 5.4, 5.10). Body slightly elongate and flattened. Head flat between eyes; micro reticulate between punctures; punctation smaller than eye facets, nearly 5.5 diameters apart. Eyes dorsally separated by about 3 times the width of an eye; inner ocular margin conspicuously diverging apically. Antenna (Fig. 5.51) with scape symmetrical, slightly larger at apex; pedicel barrel-shaped, about as long as scape; antennomeres 3 and 4 very similar in size and shape, somewhat trapezoidal; 5th 1.5 times as long as 4; 6th 1.5 times as long as 5th; 7th somewhat conical in lateral view, slightly shorter than 6th; 8th partially embedded in the 7th. Terminal maxillary palpomere weakly securiform (Fig. 5.56). Terminal labial palpomere robust, about 2 times as long as basal width; slightly shorter than preceding segment. Pronotal surface sculptured as on head; punctation almost obsolete, very shallow; prosternum relatively long in front of coxae, slightly more than 2 times longer than prosternal process widest width; tarsal claws distinctly appendiculate (Fig. 5.57). Elytral punctation stronger than on pronotum; epipleura narrowing abruptly medially. Abdomen with ventrite 6 slightly emarginate at apex; 5th wider than 4th; surface of ventrite 1 micro sculptured between postcoxal lines; postcoxal line almost reaching midpoint of lateral line (Fig. 5.50).

Tegmen (Figs 5.47, 5.48) relatively short about 1/2 the abdomen length; penis guide distinctly shorter than parameres; parameres densely setose at apex, the setae long; strut long, about 1.5 longer than tegmen; penis as in Figures 49 and 55. Spermatheca as in Fig. 5.54.

Types. Holotype male: "Monte Bello Is, Hermite I, viii-x.1952/ HMN Campania Collection, B.M. 1955.II/ Brumus maculatus Pope, DR Pope det 1955" (BMNH).

Other specimens examined. Northern Territory. Wessel Islands, Rimbija Is. (11.01S 136.45E), 3-14.ii.1977, T. Weir (1, ANIC); Black Point, Cobourg Peninsula (11.09S, 135.09E), 30.i.1977, ED. Edwards (1, ANIC); Birdum Creek nr Larrimah, 14.iv.1981, M. Malipatil, J. Hawkins (1, NTMD); Darwin (2, SAM). Queensland. Kowanyama, 10 mile swamp, d-vac on wild rice, 28.cvii.1982, J. Donaldson (3, QDPIB; 2, ANIC); Millaroo, sweep net in rice, 1.iv.1982, I. Kay (QDPIB). Western Australia. Queen's Islet, NW Australia (1, BMNH); Boebuck Bay, NW Australia, J. J. Walker (2, BMNH).

Biology. Unknown.

Distribution. Widely distributed along the coast of Western Australia, Northern Territory and Queensland, west to Cape York (Fig. 5.195).

Brumoides piae sp. nov.

(Figures 3, 9, 58-64, 183, 195)

Etymology. Dedicated to Dr Pia Laegdsgaard of the Department of Sustainable Natural Resources, NSW who collected a series of this interesting species and brought it for the first time to our attention.

Diagnosis. This species differs from *B. maculatus* by its smaller size, simple tarsal claws and joined lateral maculae on elytra.

Description. Length 5.5-5.7 mm; TL/EW = 1.2-1.3; PL/PW = 0.5-0.6; EL/EW = 0.9-1.0. Dorsal surface predominantly yellowish; head dark brownish around the eyes; each elytron (Figs 5.3, 5.9) with brownish sutural band, sometimes expanded laterally at apex and base; a second longitudinal brownish band running medially, not reaching any margin, distinctly expanded before its apex; meso-, metepimeron, meso-, metepisternum, meso-, metasternum, femora and abdominal ventrites (except the last one) usually dark brownish; the rest yellowish. Body slightly elongate oval and flattened; dorsal surface glabrous. Head flat between eyes; polished to weakly micro reticulate between punctures. Eyes dorsally separated by about 3 times the width of an eye; inner ocular margin conspicuously diverging apically. Antenna (Fig. 5.62) with scape symmetrical, slightly larger at apex; pedicel somewhat barrel-shaped, about as long as scape; antennomeres 3 and 4 very similar in size and shape, somewhat trapezoidal; 5th 1.5 times as long as 4th; 6th 1.5 times as long as 5th; 7th somewhat conical in lateral view, slightly shorter than 6th; 8th completely embedded in 7th. Terminal maxillary palpomere with sides nearly parallel (Fig. 5.60); terminal labial palpomere elongate, about 3 times as long as basal width; slightly shorter than preceding segment. Pronotal surface sculptured as on head; punctation smaller than eye facets, nearly 2 to 3 diameters apart; prosternum relatively short in front of coxae, about 1.5 times longer than prosternal process widest width; tarsal claws simple (Fig. 5.61). Elytral surface as on pronotum; punctation weaker than on pronotum, slightly shallower and sparser; epipleura gradually narrowing towards the apex. Abdomen with ventrite 6 truncate at apex; surface of ventrite 1 polished between postcoxal lines. Tegmen (Figs 5.63, 5.64) relatively short, about 1/2 the abdomen length; penis guide distinctly shorter than parameres; parameres densely setose at apex, the setae long; strut long, about 1.5 longer than tegmen; penis similar to *B. maculatus*, tip as in Figure 59.

Types. Holotype: New South Wales: Wallis Lake near Foster, salt marsh habitat, xi.2002, Pia Laegdsgaard (ANIC). Paratypes: same data as holotype (3, ANIC); Sydney, RC Perkins, 1942 (1, BMNH). Queensland: Lizard Island, Great Barrier Reef, 29.ix.1967, H. Heatwole (2, ANIC); Alva Beach 12 mi E Ayr, 26.ii.1975, H & A Howden (3, CNC; 1, ANIC); Kuranda, RCL Perkins, 1942 (1, BMNH); Cairns, 26.vi.1973, A & M Walford-Huggins (1, BMNH).

Biology. Unknown.

Distribution. This species has been found along the coastal salt marsh habitats in New South Wales and Queensland (Fig. 5.195).

CHILOCORUS LEACH

Chilocorus Leach, 1815: 116. Type species, monotypy: *Coccinella cacti* Linnaeus, 1767.

Diagnostic description. Dorsum glabrous; elytra black or brown with white or orange markings, sometimes elytra uniformly black or brown. Head transverse; eye distinctly emarginate; temple distinct, shorter than eye. Antenna 8-segmented, short; scape symmetrical; antennomere 8 as long as (Fig. 5.73) to distinctly longer than 7th (Fig. 5.78). Clypeus long and extending laterally into eyes; labrum partially exposed. Maxillary palp moderately long, last palpomere narrowing towards the apex (Fig. 5.65) to somewhat expanded apically with oblique apex (Fig. 5.86); labial palp slender, terminal palpomere as long as the penultimate. Pronotal base unbordered; prosternum moderately long in front of procoxae; prosternal process narrow, without carinae; hypomeral fovea absent. All tibiae flattened and angulated externally (Figs 5.72, 5.79), without apical spurs; claw strongly appendiculate. Elytral margin not reflexed with indistinct bead; epipleural foveae weak. Abdomen with 6th ventrite visible in male; postcoxal lines separated at middle, each running parallel to posterior margin of ventrite. Female genitalia

(Fig. 5.91): coxite weakly sclerotised and broadly triangular without styli; bursal appendix in a form of fleshy and not sclerotised protuberance; spermatheca bean-shaped (Fig. 5.88), cornu with a "beak". Male genitalia: penis guide weakly asymmetrical; penis capsule well developed.

Discussion. This is very large and economically important genus with approximately 80 species, most of them which are distributed in Palaearctic, Oriental and Afrotropical regions (Korschefsky 1932). The differences between many genera in this complex are very vague (e.g., number of antennomeres). It is likely that once a world wide revision of the species is completed, considerable changes will be made to the composition of currently recognized genera in Chilocorini. Many species of *Chilocorus* are hard to distinguish and some are based on karyological characters alone (Gordon, 1985). Primary hosts of *Chilocorus* are various scale insects (Gordon, 1985; Drea and Gordon, 1990) but some species seem to feed on aphids as well.

Distribution. Worldwide.

Key to the Australian species of *Chilocorus*

1 Elytra reddish brown or yellowish brown always with black margins (Fig. 5.5)…………... .... *circumdatus* Gyll.

\- Elytra variable but never reddish with black margins 2

2 Small, length less than 3 mm; elytra piceous, head and pronotum orange-yellow (Fig. 5.1) ....*micrus* sp. nov.

\- Much larger, length at least 5.5 mm; colour pattern almost always not as above 3

3 Head and anterior corners of pronotum yellow (Fig. 5.7); elytron with yellow humeral and apical maculae (Figs 5.6, 5.12); males with flat head and without clypeal projections or horns; aedeagus as in Figures 74-77 .... *maculatus* sp. nov.

- If head and pronotum similar as above, elytra entirely piceous (Fig. 5.2); males, especially the larger ones, with medially concave head and distinct clypeal projection (Fig. 5.14); aedeagus as in Figures 80, 81, 84 and 85.......................................*malasiae* Crotch

Chilocorus circumdatus (Gyllenhal)

(Figures 5, 13, 82, 83, 87, 88, 91, 93)

Coccinella circumdatus Gyllenhal in Schönherr, 1808: 155.

Diagnosis. The reddish elytra with dark borders will easily distinguish this species from the other Australian *Chilocorus*. Other distinctive characters are the presence of an almost complete bordering line at pronotal base, a densely pubescent metaventrite, discreet hypomeral fovea and a polished surface of the head.

Description. Length 4.2-5.9 mm; TL/EW = 1.0-1.1; PL/PW = 0.6; EL/EW = 0.8-0.9. Male. Surface predominantly yellowish brown or reddish brown, with a dark brown lateral margin of elytra (Figs 5.5, 5.13), from the humerus to the apex; a brownish "V" mark occurs on the metaventrite of some individuals. Head flat between eyes; polished between punctures; punctation about as large as eye facets, nearly 0.5 diameters apart. Eyes dorsally separated by slightly less than 2 times the width of an eye; inner ocular margin nearly parallel. Antennomere 8 long, about as long as 6th and 7th combined. Clypeus not projecting forward; slightly emarginate. Terminal maxillary palpomere slightly expanded toward apex; terminal labial palpomere long, about 4 times longer than basal width, longer than preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, shallower and sparser than on head, approximately 2 to 3 diameters apart, getting deeper and more concentrated on anterior angles; lateral borders oblique; bordering line present at base, the line visible only on outer margin of anterior angles; prosternum relatively short, about as long as to slightly shorter than prosternal process widest width; hypomeral fovea vestigial, drop-shaped; metaventrite densely covered with long pubescence. Elytral surface polished between punctures; punctation stronger than on pronotum, slightly deeper and more concentrated, about as large as eye facets, larger at the lateral margin; epipleura foveae discreet. Abdomen with ventrite 6 very short, broadly rounded; surface of ventrite 1 polished between postcoxal lines. Tegmen (Fig. 5.83) relatively short, about 1/2 the abdomen length; penis guide symmetrical (Fig. 5.83), about as long as parameres; parameres densely setose at apex, the setae long; strut as long as tegmen; penis similar to *C. malasiae*, apex as in Figure 85. Female externally similar to male.

Other specimens examined. Queensland. Brisbane, Eight Mile Plains Buschland, nr Bulimba Creek, on citrus tree, 5.i.2004, P. Chew (ANIC); Mount Molby, 25.v.1993, scales on peaches, J. Tunsted (QDPIM); Wakamin, 20.xi.1991, on maize, B. Pinese (QDPIM); ex DPI culture in Brisbane (QDPIM).

Remarks. This introduced species was first observed in Queensland in 1990 (Houston, 1991), feeding on citrus snow scale, *Unaspis citri* (Comstock). Apparently, previous unsuccessful attempts had been made to introduce it to Western Australia in 1902 (Wilson, 1960) and in 1960-1963 for control of California red scale, *Adonidiella auranti* (Maskell), and San José scale, *Quadraspilotus pernisiosus* (Comstock) (Hemiptera: Diaspididae). Since its discovery in Queensland it has been propagated and released in many citrus growing areas of the territory. It is credited with suppressing *U. citri* to sub economic levels in most of the orchards (Smith *et al.*, 1995).

Distribution. India, Sri Lanka, Indonesia, China, and Hong Kong. Introduced to Australia.

Chilocorus maculatus sp. nov.

(Figures 6, 7, 12, 69, 74-78, 204)

Etymology. The species name is derived from the Latin adjective *maculatus,* meaning spotted to acknowledge the maculate appearance of this handsome species.

Diagnosis. The piceous pronotum with only anterior angles yellowish, the 4 yellow well defined elytral maculae and the piceous thoracic sternites distinguish this species from the other Australian *Chilocorus*.

Description. Length 5.7-5.9 mm; TL/EW = 0.9-1.0; PL/PW = 0.45-0.55; EL/EW = 0.8-0.9. Male. Head entirely yellowish. Pronotum blackish with anterior angles yellowish (Figs 5.6, 5.7, 5.12); elytra predominantly piceous, each elytron with 2 large, somewhat rounded yellowish maculae, an antero-lateral one touching the lateral and anterior margin; a posterior one on apical fourth touching the lateral margin and suture. Head flat between eyes, polished between punctures; punctation somewhat obsolete, present only in the clypeal lateral extension. Eyes dorsally separated by approximately the width of an eye; inner ocular margin strongly diverging apically. Clypeus not projecting forward; slightly emarginate. Antennomere 8 long, about as long as 6th and 7th combined (Fig. 5.78). Terminal maxillary palpomere with sides nearly parallel; terminal labial palpomere slender, about 3 times longer than basal width, about as long as preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, shallow and sparse, approximately 2 diameters apart, obsolete on anterior angles; lateral border rounded; bordering line absent at base; prosternum short, slightly shorter than prosternal process widest width; hypomeral foveae absent. Elytral surface polished between punctures; punctation stronger in than on pronotum, slightly deeper and denser, about as large as to larger than eye facets, much larger at lateral margin, forming a irregular row across margin; epipleura foveae conspicuous. Abdomen with ventrite 6 very short, rounded at apex; surface of ventrite 1 polished between postcoxal lines. Tegmen (Figs 5.74, 5.75) relatively long, about 3/4 the abdomen length; penis guide symmetrical (Fig. 5.75), slightly shorter than parameres; parameres densely setose at apex, the setae short; strut about as long as tegmen; penis as in Figures 76 and 77. Female: abdominal ventrites 5th and 6th broadly rounded.

Types. Holotype: Queensland: Evelyn, 31.x.1965, R.J. Elder (ANIC). Paratypes: Mareeba, ex aleyrodids on *Hibiscus,* 28.iii.1976, K. Houston (11, QDPIB); Millaroo, 11.xi.1975, ex mango, J. Barrett (2, QDPIM); Mt. Bartle Frere, Broken Nose camp, 9-11.viii.1986, S. Kiener (2, NHMB); Cairns (2, SAM); Cairns, Baron River, Koebele (1, BPBM); Kuranda, iii.1909, G.E. Bryant (1, BMNH); Bushy Creek, Julatten (16.37S, 145.21E), 5.xiii.1968, Britton & Misko (1, ANIC); Julatten, 20-25.x.1980, milky bean, R.D. Pope (1, BMNH); Julatten, 1.viii.1987, Walford-Huggins (1, BMNH); Malanda, 17.viii.1978, P. McKeague (1, ANIC); Mt. Spec, 5-7.i.1956, J.G. Brooks (1, ANIC); Daintree, 15.iii.1989, K.H. Halfpapp (1, BMNH).

Biology. Nothing known beyond the label data listed above.

Distribution. Known from few localities in northern Queensland (Fig. 5.204).

Chilocorus malasiae Crotch

(Figures 2, 11, 14, 79-81, 84-86, 89, 203)

Chilocorus Malasiae Crotch, 1874: 187. Bielawski and Klausnitzer, 1970: 343-345.

Chilocorus australasiae Gadeau de Kerville, 1884: 71. New synonym.

Chilocorus Baileyi Blackburn, 1890: 1275. New synonym.

Chilocorus flavidus Blackburn, 1892b: 239. New synonym.

Chilocorus diadema Weise, 1898: 229. New synonym.

Chilocorus meijerei Weise, 1913: 445. New synonym.

Chilocorus nasicornis Korschefsky, 1944: 55. New synonym.

Diagnosis. The projecting clypeus will distinguish most males from all the other species of *Chilocorus.* The colour pattern of this species is very variable and can be very similar to *Ch. maculatus*, but the largely yellowish pronotum in combination with the almost entirely blackish elytra, where the yellow marks are not very well defined and usually absent at the apex, and the pale brownish venter distinguish this species from *Ch. maculatus.*

Description. Length 5.8-4.8 mm; TL/EW = 1.0-1.1; PL/PW = 0.5-0.6; EL/EW = 0.8-1.0. Male. Head entirely yellowish; pronotum entirely yellowish or with a distinct blackish or piceous area medially and along the posterior margin. Elytra variable from uniformly blackish to yellow with all intermediate stages (Figs 5.2, 5.11, 5.14); venter yellowish. Head strongly depressed between eyes; with a distinct set of long erected hairs across inner border of eyes; weakly micro reticulate between punctures; punctation obsolete, present only in the clypeal lateral extension. Eyes dorsally separated by slightly less than 2 times the width of an eye; inner ocular margin nearly parallel. Antennomere 8 long, about as long as 6th and 7th combined. In bigger males clypeus conspicuously projecting forward at middle, the projection somewhat bidentate at apex, but in smaller specimens clypeus without projection. Terminal maxillary palpomere slightly expanded toward apex (Fig. 5.86); terminal labial palpomere elongate, about 3 times longer than basal width, about as long as preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, approximately 2 diameters apart, obsolete on anterior angles; lateral border rounded; prosternum short, slightly shorter than prosternal process widest width. Elytral surface polished between punctures; punctation stronger than on pronotum, slightly deeper and denser, about as large as or larger than eye facets, much larger at lateral margin forming a irregular row across the margin; epipleural foveae conspicuous. Abdomen with ventrite 6 very short, slightly emarginate at apex; surface of ventrite 1 micro reticulate between postcoxal lines. Male genitalia as in Figures 80, 81, 84 and 85. Tegmen (Figs 5.84, 5.85) relatively short, about 1/2 the abdomen length; penis guide distinctly shorter than parameres; parameres densely setose at apex, the setae short; strut slightly longer then tegmen; penis as in Figures 80 and 81. Female differs from male by having the clypeus not projecting forward and for being conspicuously punctuated on head.

Types. Chilocorus malasiae: "Malasiae Mysol" Lectotype (Gordon, 1987:23), University of Cambridge. *Ch. baileyi.* "T3088 B.Ke/ Type/ Chilocorus Baileyi Black" (Lectotype, here designated, BMNH). *Ch. flavidus*: "4433 T Qu/ Chilocorus flavidus Blackb" (Lectotype, here designated, BMNH); the specimen at SAM bearing same data belongs to *Phrynocaria astrolabiana* (Weise). *Ch. australasiae*: Kerville gives Rockhampton and Moreton Bay as localities for *Ch. australasiae*. In the collection E. Sicard (MNHN) there are many specimens of this species some bearing handwritten labels "Rockhampton" or "Moreton Bay". The pinned male from Rockhampton is here designated as the lectotype; the other three specimens from the same series and one from "Moreton Bay" are paralectotypes. *Ch. diadema*: "Rockhampt. Mus. Hamb./Typus" (lectotype male, NRMS); "Rockhampton Mus Gadefroy/ diadema Wse/C.C. Eiffe ded. 29.viii.1893" (paralectotype female, NRMS). *Ch. nasicornis:* "Key Inseln Coll Schroder/ Typus/ Chilocorus nasicornis m det. R. Korschefsky 1944/ Korschefsky collection 1952" (holotype, USNM). *Ch. meijerei*. "Merauke Meijere/ Nieuw Guinea Merauke, Dr Koch 1904/ Chilocorus Meijerei m" (holotype, ZMB).

Other specimens examined. Queensland: (ZMB); 3 km NW Archer River crossing (15.24S, 145.55E), 11.iv.1989, G&A. Daniels (UQIC); Babinda, 1920, JF Illingworth (BPBM);

Deera I, JF Illingworth (BPBM); Badu Island, 16-25.xii.1976, H. Heatwole (AM); Bamaga (10.53S, 145.24E), 11.xii.1986, K.J. Houston, on tree with 3-4 spp. of bug nymphs, B59, adults and larvae (QDPIB); Batavia Downs (15.41S, 145.41E), 25.vi-25.viii.1982, Malaise trap, P. Zborowski & J. Cardale (ANIC) (3 km W of Batavia Downs (15.40S, 145.39E), 18.vi.-25.vii.1982, Malaise trap, P. Zborowski & E. Nielsen (ANIC); Boigu Island (09.17S, 145.13E), 11-15.ii.1991, J. Grimshaw (NAQS); Bowen, 1.x.1931 (QDPIB); Bucasia, 27.ix.1990, K. Sandery (SAM); Cairns (SAM, MVM, ANIC; SAM; CNC; BPBM); Cape York, xi.1891, O. Finish (ZMB); Kowanyama (15.28S, 141.45E), 18.ii.1991, J. Grimshaw (NAQS); Lockhart River, 8.iv.1992, J. Grimshaw (NAQS); Cardwell, 7.viii.1986, light, Kiener (NHMB); Claudie River, 16.xii.1971, D. Sands (ANIC); Cooktown (MVM); Danbulla, 11.15.1969, R. Parrott (CNC); Darun Island (09.25S, 145.32E), 4.iv.1990, J.F. Donaldson (NAQS); same locality 6-8.ii.1991, ex coconut palm, J. Grimshaw (NAQS); Domadgee, Gulf of Carpentaria, 25.iii.1999, J.F. Grimshaw, ex scale (NAQS); Giru, 9.x.1981, light, B. Lowery (ANIC); Good Island, 11.iii.1909, G. Bryant (BMNH); Green Island, 21.i.1973, J. Barret (QDPIM); Greenvale, 70 km SW, light, viii.1995, A.J. Watts (SAM); Heathlands (11.45S, 145.35E), 7.vi-25.vii.1992, Malaise trap, P. Zborowski & E. Nielsen (ANIC); Herberton, 21.vi, H.J. Carter (MVM); Hinchinbrook Island, viii.1951, J. Bechervaise (MVM); Kuranda, (SAM; BMNH; USNM; BPBM); Kurramine, 15.iii.1990, K. Halfpapp (QDPIM); Lizard Island, ix.1993, G. Pearce (QDPIM); Mackay, 24.vii.1934, M. Powell (QMB); Mackay (MVM); Magnet I. (MVM); Mareeba, 24.iii.1989, predator on oriental scale ex pawpaw, G.R. Dickson (QDPIM); Mareeba, 18.ii.1985, ex scales on palm, K.W. Halfpapp (QDPIM; 15 km E of Mareeba, 15.ii.1898, H&A Howden (CMN); 2 km SW of Mt. Inkerman (19.45S, 147.30E), 11.xii.1968, S. Misko (ANIC); Moa I, C. McNamara (SAM); Palm Park, 5.5 mi ESE of Byfield, 24.v.1969, T. Campbell & R. Jelous (ANIC); 12 km

W of Petford, 5.ii.1989, H.&A. Howden (CMN); 1 km N of Rounded Hill (15.17S, 145.13E), 5-6.x.1980, T. Weir (ANIC); Rockhampton, iv,1986, orange trees infested with scales, H. Jarvis (QDPIB); Saibai Island (09.22S, 145.30E), 5.iv.1990, J.F. Donaldson (NAQS); Seaview Range, Mt Fox Rd., 600 m, 15.xii.1986, Monteith, Thomson, Hamlet (QMB); South Johnstone, 5.vi.1990, on banana, K. Halfpapp (QDPIB); Southedge R.S., 29.v.2003, on mango, S. DeFaveri (QDPIM); same 25.i.1989, H&A Howden (CMN); Thursday Island, A.M. Lea & C.T. McNamara (SAM); Toolkoor (AM); Torres Straits, C.T. McNamara (SAM); Walkapun, xi.1988, larvae predators of mango scale (QDPIM); Weipa, 19.ii.1991, J. Grimshaw (NAQS); 13 km E by S of Weipa (15.40S, 145.00E), 15.ii.1994, P. Zborowski (ANIC); Yam Island (09.54S, 145.46E), 1.xiii.1986, ex diaspids on Cassava, K.J. Houston (NAQS); Yeppoon, 25.i.1975, H&A Howden (CNC); same 6.vi.1991, on palm with A. destructor, J. Grimshaw (NAQS); Yeppoon, 6.vi.1991, ex coconut with *Aspidorus destructor*, J. Grimshaw (NAQS). Northern Territory. Benjamin Lagoon, Coral Road, 14.ii.1994, ex *Aonidella orientalis* on *Carica papaya,*J.D. Duff (NTDA); Darwin, 11.xi.1979, 25.x.1981, 6.ii.1982, M.B. Malipatil (NTMD); Darwin, 9.iii.1981, on papaya, S. Pickering (NTDA); Darwin, 25.11.1966., CS.Li (1, NTMD); Darwin, G.F. Hill (SAM); Humpty Doo, lot 7, Collard Road, 15.ix.1998, ex *Nephelium lappaceum* fruit, H. Wallace (NTDA); Humpty Doo, 28.xii.1978, on papaya, L. Radunz (NTDA); Katama, 10.x.1982, C. Wilson (NTMD); Katherine Research Stat., 17.iv.1996, ex. *A. auranti* (Maskell) on *Citrus*, M. Hoult (NTDA); same locality, 9.xii.1999, grapefruit trees, M. Hoskins (NTDA); same locality and collector, 16.iii.2000, predating red scale on leaves of grapefruit tree (NTDA); "Leng's" Fox Road, 24 km SE Katherine, 8.iii.2001, ex *Citrus limon* fruit feeding on red scale *Aonidiella auranti*, M. Hoskins (NTDA); "J&C Etty" 2351 Edith Farms Rd., Katherine, 14.viii.2000, ex leaves of *Citrus paradisa*, grapefruit, feeding on black circular scale, M. Hoskins

(NTDA); “A. Cameron’s” Lot 4485, Katherine, 25.iii.2000, lemon foliage, M. Hoskins (NTDA); Keep River NP near Jarrnam (15.46S, 129.05E), 29.iv.1996, G.R. Brown (NTMD); Koongarra, 15 km E of Mt. Cahill, 24.v.1973, T.Weir & T. Angels (NTMD); same date bur E.G. Matthews (NTMD); Lambells Lagoon, Alphitonia Rd., lot 27, 19.viii.1998, ex *Mangifera indica,* D.Chin & H. Wallace (NTDA); Lee Point, 15 km NNE Darwin (15.20S, 130.54E), 17.xii.1979, T. Weir (ANIC); Litchfield NP, 20.i.1998, A. Zwick (1, ANIC); Roper R., N.B. Tindale (SAM).Western Australia: Wyndham, W. Crawshaw (BMNH); same locality, 24.x.1929, T.G. Campbell (ANIC); Mining Camp Mitchell Plateau (14.49S, 125.50E), 9-19.v.1983, Malaise trap, I. Naumann, J. Cardale (ANIC); Packsaddle via Kununurra, 6.iv.2001, ex *Ipomea* and pumpkin, A. Postle (QECB); Curtis’s via Kununurra, 4.iv.2001, ex papaya, A. Postle (QECB).

Biology. Label data shows that *Ch. malasiae* is associated with armoured scale insects. Along with *Ch. circumdatus* this species is commercially available from the Australasian Biological Control Inc. Association of Beneficial Arthropod Producers as “blue Chilocorus” to be used against many target scales mostly in citrus orchards.

Distribution. This is a widely spread species, commonly collected in northern Australia (Fig. 5.203), New Guinea and adjacent islands (Bielawski and Klausnitzer, 1970).

Chilocorus micrus sp. nov.

(Figures 1, 8, 65-68, 70-73, 204)

Etymology. This name has been derived from a Medieval Latin adjective, meaning small.

Diagnosis. The orange pronotum and the completely piceous elytra in combination with small size and broad protibia (Fig. 5.72) will distinguish this species from the other Australian *Chilocorus.*

Description. Length 5.8 mm; TL/EW = 1.2; PL/PW = 0.40; EL/EW = 0.9. Male. Head and pronotum orange to yellowish, elytra piceous (Figs 5.1, 5.8); venter yellowish. Head slightly depressed between eyes; polished between punctures; punctation obsolete, present only in the clypeal lateral extension. Eyes dorsally separated by approximately the width of an eye; inner ocular margin strongly diverging apically. Antennomere 8 short, about as long as 7th (Fig. 5.73). Terminal maxillary palpomere wider at basal half, slightly narrowing towards the apex (Fig. 5.65); terminal labial palpomere slender, about 2 times longer than basal width, about as long as preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, shallow and sparse, approximately 2 diameters apart, obsolete on anterior angles; lateral border rounded, somewhat acute; prosternum short, slightly shorter than prosternal process widest width. Elytral surface polished between punctures; punctation stronger, deeper and denser than on pronotum; about as large as eye facets, much larger at lateral margin, forming irregular row across margin; epipleural foveae vestigial. Abdomen with ventrite 6 somewhat truncate at apex; surface of ventrite 1 polished between postcoxal lines. Male genitalia as in Figures 66, 67, 70 and 71: Tegmen (Figs 5.70, 5.71) relatively long, about 3/4 the abdomen length; penis guide asymmetrical (Fig. 5.71), slightly shorter than parameres; parameres densely setose at apex, the setae long; strut as long as tegmen; penis as in Figures 66 and 67. Female: similar to male but differing by the having only 5 visible abdominal ventrites.

Types. Holotype: Northern Territory, Melville Island, W.D. Dodd (SAM). Paratype: same data as holotype; entirely dissected (ANIC).

Biology. Unknown.

Distribution. Known from two specimens collected on Melville Island (Fig. 5.204).

EXOCHOMUS REDTENBACHER

Exochomus Redtenbacher, 1843: 11. Type species, subsequent designation (Thomson, 1859: 160): *Coccinella quadripustulata* Linnaeus, 1758.

Diagnostic description. Dorsum glabrous; elytra black or brown with orange markings (Figs 5.15, 5.16). Head weakly transverse; eye distinctly emarginate; temple distinct, about as long as eye. Antenna 10-segmented, short; scape symmetrical; terminal antennomere small and partially embedded in penultimate one. Clypeus short, distinctly extending laterally; labrum almost entirely exposed. Maxillary palp (Fig. 5.99) relatively long, last palpomere somewhat expanded apically with strongly oblique apex; labial palp slender, terminal palpomere as long as the penultimate. Pronotal base entirely bordered; prosternum long in front of procoxae; prosternal process very narrow, without carinae; hypomeral fovea absent. Protibia simple, narrow; meso- and metatibiae with 2 apical spurs; claw strongly appendiculate. Elytral margin very finely reflexed with complete bead; epipleural fovea absent. Abdomen with 6th ventrite visible in male; postcoxal lines separated at middle, each arcuately recurving apically and reaching midpoint of lateral line (Fig. 5.98). Female genitalia: coxite sclerotised and distinctly elongate bearing reduced styli (Fig. 5.94); bursal appendix sclerotised and hook-like (Fig. 5.90); spermatheca bean-shaped; cornu without “beak” (Fig. 5.92). Male genitalia: penis guide weakly asymmetrical; penis capsule well developed.

Discussion. Kovář’s (1995) interpretation of the genus *Exochomus* and its type species were incorrect (R. Booth, personal communication), as explained by Poorani (2002). Once this correction is accepted, *Brumus* will probably become a junior synonym of *Exochomus.* That action does not solve the currently unsettled taxonomic status of many New World species described in *Exochomus* that have the pronotal base unbordered (Vandenberg, 2002).

Distribution. Worldwide, but the generic status of many species need to be verified.

Exochomus quadripustulatus (Linnaeus)

(Figures 15, 16, 90, 92, 94-99, 196)

Coccinella 4-pustulata Linnaeus, 1758: 367.

Description. Length 5.0-5.7 mm; TL/EW = 0.9-1.0; PL/PW = 0.4-0.5; EL/EW = 0.9-1.0. Male. Dorsal surface predominantly black; each elytra with 2 orange marks (Figs 5.15, 5.16): a anterolateral one, somewhat U-shaped, reaching the anterior margin but not the lateral one; a post-median one near the suture, not very well defined, somewhat transverse. Venter, predominantly dark-brownish to black; yellowish on epipleura basal half and last four abdominal ventrites. Body elongate, weakly convex. Head flat between eyes; punctation as large as eye facets, approximately 2 diameters apart. Eyes small, dorsally separated by more than 2 times the width of an eye; inner ocular margin slightly divergent. Antenna with scape asymmetrical, somewhat constricted in the base; pedicel barrel-shaped, about as long as scape; antennomere 3 trapezoidal, visibly shorter than pedicel; 3-8th transverse, gradually increasing in width; 8th somewhat quadrate; 9th strongly asymmetrical, about as long as 8th; 10th small and partially embedded in the 9th. Terminal maxillary palpomere slightly expanded toward apex; strongly oblique at apex, with outer side about 3 times longer than inner; terminal labial palpomere elongate, as long as penultimate segment. Pronotal surface sculptured as on head, the sculptures much weaker; punctation smaller than eye facets, shallower and sparser than on head, approximately 2 to 3 diameters apart; lateral borders truncate; pronotal base entirely bordered, the bordering line abruptly approaching the margin before it ends in a weak pronotal depression; prosternum long in front of procoxae, about 3 times longer than prosternal process widest width.

Elytral surface sculptured as on pronotum; punctures stronger than on pronotum, slightly deeper and more concentrated, about as large as eye facets; lateral margin finely reflexed. Abdomen with ventrite 6 weakly emarginate; surface of ventrite 1 micro reticulate between punctures. Tegmen (Fig. 5.95) relatively short, about 1/2 the abdomen length; penis guide asymmetrical (Fig. 5.95) visibly shorter than parameres; parameres densely setose at apex, the setae long; strut about as long as tegmen; penis as in Figures 96 and 97.

Specimens examined. Victoria: Mt. Dandenong; Baxter, 14.i.1981, RD Pope (BMNH); Western Australia: Tuart Forest, near Busselton; Perth: Swan River, N. Jarrah, Fremantle; Spearwood; Donnybrook; Sawyers Valley; Carmel; Mt Barker; Wilga; Mount Folly, Nannup.

Comments. A very detailed description and discussion of morphological variation and biology of this species is included in Kovář (1995: 101-113) under the name *Brumus quadripustulatus* (L.). This species has been imported to Australia to control *Chermes* sp. (Aphididae) on introduced conifers, mostly pine (*Pinus radiata*). It was released in ACT and New South Wales during 1934-1939 but no records of captures in these areas can be found. There are well established populations of this species in the south west of Western Australia. Recent material from Victoria also suggests an established population there. The sharply marked elytral pattern of red on black, typical of central and northern European specimens, is frequently blurred when the species breeds at temperatures of 20 centigrade or above, a condition frequently found during summer around Perth. Although adults have been taken on various trees and shrubs, including *Banksia* spp., *Eucalyptus* spp., and the imported conifer (*Pinus radiata*), there are no records of larval captures and so there is no definite information concerning essential or alternative prey in Australia. Schilder and Schilder (1928) list several species of aphids, including *Chermes*, on both conifers and deciduous trees while Ponsonby and Copland (1997) give references to a number of papers in which this species is claimed to feed on various soft scales (Coccoidea).

Distribution. Europe, Middle East, Mongolia, and Russian Far East. Introduced to USA (Gordon 1985) and Australia (Fig. 5.196).

Halmus Mulsant, 1850

Orcus (Halmus) Mulsant, 1850: 471. Type species, monotypy, *Coccinella chalybea* Boisduval, 1835.

Diagnostic description. Dorsum glabrous; elytra black to green, sometimes with metallic sheen, without markings. Head transverse; eye not emarginate; temple distinct, shorter than eye. Antenna 8-segmented, short; scape asymmetrical; terminal antennomere as long as (Fig. 5.100) to distinctly shorter than penultimate one (Figs 5.124, 5.129). Clypeus short, emarginate medially and extending laterally below eyes; labrum partially exposed. Maxillary palp moderately long, last palpomere somewhat expanded apically to securiform, with oblique apex (Figs 5.121-5.123); labial palp stout, terminal palpomere slightly shorter and narrower than the penultimate segment. Pronotal base entirely bordered (Fig. 5.23); prosternum moderately long in front of procoxae; prosternal process narrow, without carinae; hypomeral fovea absent. All tibiae simple externally, without apical spurs; claw strongly appendiculate (Fig. 5.92). Elytral margin weakly reflexed with reduced bead; epipleuron broad, strongly descending without foveae (Fig. 5.189). Abdomen with 6th ventrite visible in both sexes; postcoxal lines separated at middle, each running parallel to posterior margin of ventrite or recurving apically (Figs 5.107, 5.128). Female genitalia: coxite weakly sclerotised and broadly triangular, without styli (Fig. 5.102, 125); bursal appendix in form of a sclerotised spur (Fig. 5.104); spermatheca bean-shaped (Fig. 5.103), cornu without a "beak". Male genitalia: penis guide symmetrical; penis capsule well developed.

Distribution. Australia and New Guinea.

Discussion. In spite of the marked differences between the type species, *H. chalybeus*, and *H. coelestris* (=*ovalis*) mentioned by Chapin (1965), there is little doubt that they belong together along with *H. evelynensis* added by Weise (1923), agreeing in the principal structures of the head, pronotum and female genitalia.

Key to the Australian species of *Halmus*

1 Clypeus straight or barely emarginate medially (Fig. 5.185), entirely bordered.......... ....*H. coelestris* (Blackburn)

\- Clypeus distinctly emarginate medially and not bordered...2

2 Postcoxal line on ventrite 1 distinctly recurving apically (Figs 5.126, 5.128); body elongate oval and relatively flattened (Fig. 5.27); coloration of pronotum and head similar in both sexes..3

\- Postcoxal line on ventrite 1 not recurving apically (Fig. 5. 107); body shorter and more convex (Fig. 5.30); head and anterior part of pronotum yellowish to orange in males, monochromatic in females 4

3 Lateral borders of pronotum curved as in Figure 5.25; anterior angles relatively sharp, posterior angles almost obliterated. Queensland. ....*H. evelynensis* (Weise)

\- Lateral pronotal borders broadly curved; both anterior and posterior angles blunt but distinct. NSW...*H. viridis* sp. nov.

4 Pronotum with interspaces between punctures polished, disc almost always with metallic

reflection (Fig. 5.23); male genitalia as in Figures 5.114-5.117; North Queensland to New South Wales 5

\- Pronotum with interspaces between punctures reticulate, disc dark-coloured without metallic reflection; male genitalia as in Figures 5.112 and 5.113; Northern Territory...*H. hilli* sp. nov.

5 Male genitalia as in Figures 5.105, 5.115-5.117 ....*H. chalybeus* (Boisduval)

\- Male genitalia as in Figures 5.110, 5.114 ....*H. cupripennis* Weise

Halmus chalybeus (Boisduval)

(Figures 5.17, 5.23, 5.30, 5.100-5.107, 5.109, 5.115-5.117, 5.186, 5.189, 5.197)

Coccinella chalybea Boisduval, 1835: 595.

Halmus chalybeus: Weise, 1923: 134.

Diagnosis. This species is characterized by the combination of a distinctly convex body, metallic colour of dorsal surfaces, male having head and anterior corners of pronotum orange or yellowish, and the postcoxal line parallel to the hind margin of the first ventrite. From externally similar species, *cupripennis and hilli* it can be reliably separated based on male genitalia only.

Description. Length 5.2 – 4.1 mm; TL/EW = 0.9-1.1; PL/PW = 0.5-0.6; EL/EW = 0.8-0.9. Male. Dorsal surface metallic bluish to almost green except for most of the head and anterior corners of pronotum, which are yellowish (Fig. 5.23); venter predominantly dark brown, except antennae, mouthparts, hypomera, mesepimeron, mesepisternum, anterior femora and abdomen which are yellowish; first abdominal ventrite brownish medially. Body round, convex (Figs 5.17, 5.30). Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 diameters apart. Eyes dorsally separated by less than 2 times the width of an eye; inner ocular margin slightly diverging apically. Antennomeres 5, 6 and 7 about the same length (Fig. 5.100). Clypeus distinctly emarginate medially, with lateral extension markedly narrow (Fig. 5.186). Terminal maxillary palpomere with sides nearly parallel (Fig. 5.106); terminal labial palpomere somewhat conical; less than 2 times longer than basal width; about as long as the preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, shallow and sparse, approximately 2 to 3 diameters apart, obsolete on anterior angles; lateral borders broadly rounded to somewhat truncate; prosternum short in from of coxae, about as long as prosternal process widest width. Elytra surface polished between punctures; punctation stronger than on pronotum, about as large as to larger than eye facets, slightly deeper and more concentrated; lateral margin slightly reflexed. Abdomen with ventrite 6 conspicuous, shortly emarginate at apex; surface of f ventrite 1 polished between postcoxal lines; postcoxal line not recurving apically, running parallel to posterior margin for short distance (Fig. 5.107). Tegmen (Figs 5.115-5.117) relatively long, about 3/4 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres densely setose at apex, the setae long; strut as long as tegmen; penis as in Figures 5.105 and 5.109. Female similar to male but monochromatic and with abdominal ventrite 6 rounded, slightly pointed at apex.

Variation. There is a considerable colour variation on dorsal surfaces from dark bluish to almost green with interspaces between punctures mostly polished but sometimes showing some degree of cuticular reticulation as in *H. hilli*. Head in males is always bicoloured with upper surface darker but the extent of darkness varying from upper 1/5 to half the length of the head. There is also some clinal variation in male genitalia with the apical part of penis guide becoming narrower (Fig. 5.116) in specimens from northern Queensland as compared to a stouter penis (Fig. 5.115) in NSW and southern Queensland specimens.

Types. When describing *C. chalybea*, Boisduval gave as data “Nouvelle-Hollande. Collection de M. Dejean”. A single male occurs in the Dejean collection (Museum Lyon). It has a pink label inscribed with “Coccinella Chilocorus chalybea mihi Chilocorus cyaneus Macleay I in Nova Hollandia”. It agrees with the consistent interpretation of *chalybeus* from Mulsant onwards (R.D. Pope, personal information).

Other material examined (+800 specimens). New South Wales.19 km S Casino (29°02' S, 153°03' E) (3k N Lansdowne, via Taree (31°45' S, 152°32'); 4 km W Lansdowne, Lorien (31°45' S, 152°32'); approx. 24km NNW Gloucester (31°49' S, 151°52'); Barrington Tops (31°59' S, 151°27'); Barrington Tops SF. (32°00' S, 151°32'); Barrington Tops, Dilgry R. (31°53' S, 151°32'); Bawley Point (35°30' S, 150°24'); Bodalla (36°06' S, 150°03'); Bulladelah [Bulahdelah] (32°25' S, 152°12'); Cobark For. Pk. Barrington Tops (31°54' S, 151°36'); Cobark Forest Pk., Barrington Tops State Forest (31°54' S, 151°35'); Cumberland State Forest (33°43' S, 151°02'); Dilgry R. Loop, Barrington Tops State Forest (31°53' S, 151°32'); Dorrigo (30°20' S, 152°43'); Durras North, nr. Batemans Bay. Stop 16 (35°38' S, 150°18'); Ebor (30°24' S, 152°21'); Engadine (34°04' S, 151°01'); Erina (33°26' S, 151°24'); Gosford (33°26' S, 151°21'); Kenthurst (33°40' S, 150°59'); Kurmond (33°33' S, 150°41'); Kurrajong (33°33' S, 150°40'); Lindfield (33°47' S, 151°10'); Lismore (28°49' S, 153°16'); Mooney Mooney Creek, near Gosford (33°31' S, 151°12'); Murwillumbah (28°20' S, 153°24'); Otford (34°13' S, 151°00'); Ourimbah district (33°22' S, 151°22'); Oxford Falls (33°44' S, 151°14'); Peats Ridge (33°19' S, 151°14'); Putty Road, East Kurrajong (33°31' S, 150°46'); Richmond River (28°28' S, 152°55'); Rose Bay, Sydney (33°51'36"S, 151°15'36"E); Rydalmere (33°49' S, 151°02'); Sydney (33°53' S, 151°13'); Sydney dist., Oxford Falls (33°44' S, 151°14'); Tweed River (28°20' S, 153°20'); Wallacia (33°52' S, 150°38'); Wallacia (33°52' S, 150°38'); Wattle Flat, Styx River (30°35' S, 152°12');

Wingham (31°52' S, 152°22'); Wingham (31°52' S, 152°22'); Wingham (31°52' S, 152°22'); Yarramalong (33°14' S, 151°17'). Queensland. 10km NE Childers (25°10' S, 152°21') (19km S Bundaberg, Pine Creek [SW of Bundaberg] (25°04' S, 152°09') (19km S Bundaberg, Pine Creek [SW of Bundaberg] (25°04' S, 152°09') (2km NE of Mt. Coonowrin [Coonowrin] (26°53' S, 152°56') (3km NEbyN Julatten (16°35' S, 145°22'); 5km NW of Mount Molloy (16°39' S, 145°18'); 7-14 m. W of Herberton, via Watsonville (17°23' S, 145°19'); Bamboo Ck., nr. Miallo, N of Mossman (16°19' S, 145°23'); Bellenden Ker Range, Summit TV Stn (17°16' S, 145°51'); Biggenden (25°31' S, 152°03'); Blackall Ranges [Range] (26°34' S, 152°52'); Blackall Ranges [Range] (26°34' S, 152°52'); Brisbane (27°28' S, 153°02'); Brisbane (27°28' S, 153°02'); Bunya Mtns, 3 km from summit on Kingaroy Rd. (26°50' S, 151°33'); Bunya Mts., 2 km SE of Mt. Mowbullan (26°50' S, 151°33'); Burnett River nr. Biggenden (25°33' S, 151°39'); Bushy Ck., Julatten (16°37' S, 145°21'); Cairns (16°55' S, 145°46'); Cape Tribulation area (16°04' S, 145°28'); Cardwell (18°16' S, 146°01'); Cooroy (26°24'36"S, 152°54'36"E); Freshwater (16°53' S, 145°43'); Gatton (27°34' S, 152°17'); Goodna (27°36'36"S, 152°54'); Hann River (15°11' S, 143°52'); Indooroopilly, Brisbane (27°30' S, 152°58'); Ironside [Ironside Creek] (17°51' S, 144°21'); Jimboomba (27°50' S, 153°02'); Julatten (16°37' S, 145°21'); Kolan R. nr. Bundaberg (24°51' S, 152°21'); Kuranda (16°48'36"S, 145°37'48"E); Kuranda (16°48'36"S, 145°37'48"E); Lone Pine (19°08' S, 146°29'); Mackay (21°09' S, 149°11'); Meleney [Maleny] (26°46' S, 152°51'); Millaa Millaa Falls (17°30' S, 145°37'); Mt. Tamborine (27°55' S, 153°10'); Nat. Park [Lamington National Park] (28°19' S, 153°05'); Nipping Gully, Site 2 (25°40' S, 151°26'); Nipping Gully, Site 5 (25°42' S, 151°26'); Pine Ck. nr. Bundaberg (25°04' S, 152°09'); Queen Mary Falls, Killarney (28°20' S, 152°18'); Southedge Res. St., Mareeba (16°59' S, 145°19'); Springbrook (28°14' S, 153°16'); St. Lucia, Brisbane (27°30' S, 153°00'); Tambourine Mts.

[Tamborine Mountain] (27°55' S, 153°09'); Tanawah; Tinana, M'boro [Maryborough]; Toowoomba (27°33'36"S, 151°57'); Witches Falls N.P., Tamborine Mt. (27°56' S, 153°11'); Woody Point (27°16' S, 153°07').Victoria: Cann River (37°34' S, 149°09'); S Gippsland (38°14' S, 147°03' E).

Distribution. Widely distributed along the eastern coast from Victoria, New South Wales to northern Queensland (Fig. 5.197).

Notes. *Halmus chalybeus* might have travelled naturally to New Zealand. In 1892 Koebele introduced it into southern California where it became established (Gordon, 1985). Two years later, Koebele introduced the species to Hawaii (Fullaway, 1920). Recently, it was recorded as established on several islands in the Hawaii group (Leeper, 1976). Published accounts (e.g., Gordon, 1985) and label data show *H. chalybeus* to feed on several different species of scale insects, including *Anoidiella aurantii*, *Coccus viridis*, *Spodoptera mauritia*, *Parasaissetia oleae*, *Saissetia oleae*, *Icerya* spp. and *Pulvinaria* spp.

Halmus coelestris (Blackburn) comb. nov.

(Figures 5.18, 5.27, 5.118, 5.123, 5.124, 5.127, 5.131, 5.132, 5.134, 5.135, 5.185, 5.205)

Orcus coelestris Blackburn, 1891: 155.

Orcus ovalis Blackburn, 1892:241. New synonym.

Orcus splendens Blackburn, 1892b: 240. New synonym.

Orcus clypeatus Weise, 1923: 135. New synonym.

Diagnosis. This is a very distinctive species due to the presence of an obvious straight anterior border on the clypeus (Fig. 5.185).

Description. Length 5.5-5.9 mm; TL/EW = 1.25-1.45; PL/PW =0.5-0.6; EL/EW = 1.0-1.1. Male. Dorsal surface metallic bluish or greenish. Venter pale brownish, except thoracic and first abdominal ventrites, which are dark brownish. Body slightly elongate, somewhat flattened (Figs 5.18, 5.27). Head polished to weakly micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 diameters apart. Eyes dorsally separated by slightly more than 2 times the width of an eye; inner ocular margin slightly diverging apically. Antennomere 6 about 1.5 times longer than 5th and 7th. Clypeus straight, anteriorly bordered with lateral extension not conspicuously narrow. Terminal maxillary palpomere securiform (Fig. 5.123); terminal labial palpomere conical; less than 2 times longer than basal width; as long as the preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, approximately 2 diameters apart; obsolete on anterior angles; lateral borders slightly rounded. Prosternum relatively long in front of coxae, about 2 times longer than prosternal process widest width. Elytral surface polished between punctures; punctation stronger than on pronotum, about as large to larger than eye facets, slightly deeper; lateral margin slightly reflexed. Abdomen with ventrite 6 conspicuous, shortly emarginate at apex; surface of ventrite 1 polished between postcoxal lines; postcoxal line usually straight (Fig. 5.127) but sometimes recurving apically. Tegmen (Fig. 5.132) relatively long, about 3/4 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres densely setose at apex, the setae long; strut as long as tegmen; penis as in Figures 5.131 and 5.135. Female externally identical to male.

Types. Halmus ovalis is recorded by Blackburn as having been collected in north Queensland and sent to him by Mr Masters. The single female specimen, here considered as lectotype, from Blackburn collection (BMNH) bears the following data “4432 T N.Qu./ Type/ Australia Blackburn Coll. BM 1910-236”. No additional material of the original series could have been identified in SAM or at the Macleay Museum, Sydney. *H. coelestris* was described from unrecorded number of specimens said to come from "N. Territory of S. Australia". The single female lectotype in BMNH, bears the data "T 2476 N.T./ Type/ Australia Blackburn Coll. BM 1910-236/ Orcus coelestris Blackb". *H. splendens* was recorded by Blackburn from North Queensland and sent to him by Mr Masters. No material so labelled exists in the SAM, but a single male specimen in the BMNH bears the data "4431 T N. Qu/ type/ Australia Blackburn Coll. BM 1910-236/ Orcus splendens, Blackb" and it is considered as the lectotype. *H. clypeatus* was described from 39 specimens collected by Mjöberg at Alice River, Yarrabah, Laura and Bellenden Ker. There are 29 specimens of this series in the NRMS from Alice River, Bellenden Ker, Yarrabah and Laura; one specimen from Alice River is here designated as the lectotype.

Other material examined (+1000 specimens). New South Wales. Mt. Royal SF, nr. Singleton (32°11'S, 151°20'); Sydney (33°53'S, 151°13'). Northern Territory. Bathurst Is., Cape Fourcroy (11°48'S, 130°01'); Dhalinbuy (12°24'S, 136°23'19); Jabiru Town Lake (12°40'S, 132°53'); King River (12°03'S, 133°25'); Port Darwin (12°31'S, 130°48'); Stapleton (13°11'S, 131°02'); Wildman River Station Reserve (12°43'S, 131°48'). Queensland. 1 km N of Rounded Hill (15°17'S, 145°13'); 13km ENE of Mt. Tozer (12°42'S, 143°20'); 13km SE Herberton (17°27'S, 145°27'); 14km W by N Hope Vale Mission (15°16'S, 144°59'); 2mi. SW of Mt. Inkerman (19°45'S, 147°30'); 4 mi. S Atherton (17°19'S, 145°29'); 5km W by N of Rounded Hill (15°17'S, 145°10'); 8k W Kuranda (16°49'S, 145°34'); Ayr (19°35'S, 147°24'); Ayr (19°35'S, 147°24'); Black Mountain, Kuranda For. Sta. (16°24'S, 145°13'); Black Mt., Kuranda (16°24'S, 145°13'); Brandon, Lochinvar P.C. (19°33'S, 147°21'); Brisbane (27°28'S, 153°02'); Bundaberg (24°52'S, 152°21'); Burnett River, Bundaberg (24°53'S, 152°16'); Cairns (16°55'S, 145°46'); Cairns district (16°55'S, 145°46'); Claudie River (12°46'S, 143°17'); Darnley Island; 9°35'S, 143°46'); Dimbulah (17°09'S, 145°07'); Edmonton (17°01'S, 145°45'); Edmonton (17°01'S, 145°45'); Eureka Ck., Dimbulah (17°09'S, 144°59'); Fig Tree Creek, 39km S of Ingham (19°00'S, 146°10'); Freshwater via Cairns Gillies Highway, nr. Gordonvale (17°08'S, 145°45'); Harmer Creek (11°58'S, 142°55'); Holloways Beach Home Hill (19°40'S, 147°25'); Ingham (18°39'S, 146°10'); Ingham (18°39'S, 146°10'); Innisfail (17°32'S, 146°01'); Japoonvale (17°43'S, 145°54'); Julatten, nr. Mt. Molloy (16°36'S, 145°20'); Julatten (16°37'S, 145°20'); Kennedy (18°12'S, 145°57'); Kuranda (16°48'36"S, 145°37'48); Kuranda, Mareeba Rd., Goldmine creek (24°35'S, 148°13'); Kurramine Lake Barrine (17°15'S, 145°38'); Little Mulgrave River (17°07'S, 145°41'); Mandoo Mena Creek, 2km SSW (17°41'S, 145°58'); Mena Creek (17°40'S, 145°58'); Mission Beach (17°52'S, 146°06'); Mt. Bartle Frere, Broken Nose Camp (17°24'S, 145°49'); Murray Island, Torres Strait; 9°56'S, 144°03'); Murry Upper [Upper Murray] (18°05'S, 145°51'); Newell, 6.4km NE Mossman Redlynch, Cairns, Barron River (16°53'S, 145°42'); Redlynch (16°53'S, 145°42'); Rockhampton (23°22'S, 150°31'); Saibai Is., Torres Strait; 9°22'S, 142°36'); South Johnston (17°36'S, 146°00'); Tully (17°56'S, 145°56'); Weipa, Cape York (12°39'S, 141°53'). Western Australia. 3km NWbyN Mining Camp, Mitchell Plateau, Stop 21 (14°48'S, 125°49'); Kalgan River (34°39'S, 118°03'); Mining Camp, Mitchell Plateau (14°49'S, 125°50').

Distribution. Widely distributed in Australia (Fig. 5.205) and New Guinea

Notes. DeBarro (1990) recorded larvae and adults of this species as predators of pink sugarcane mealybug, *Saccharicoccus sacchari* (Cockerell).

Halmus cupripennis Weise

(Figures 5.21, 5.110, 5.114, 5.199)

Halmus cupripennis Weise, 1923: 135.

Diagnosis. Externally identical to *chalybeus*, however the male genitalia show significant differences from those of *chalybeus* (Figs 5.110, 5.114).

Types. Weise described *cupripennis* from 3 examples. "Evelyne [sic]/ Queensl. Mjöberg/ aug./ cupripennis m." (Lectotype male, and 2 paralectotypes, NRMS).

Biology. Unknown.

Distribution. Known only from type locality in northern Queensland (Fig. 5.199).

Halmus evelynensis (Weise) comb. nov.

(Figures 5.20, 5.25, 5.120, 5.122, 5.128, 5.29, 5.199)

Orcus evelynensis Weise, 1923: 135.

Diagnosis. The distinctly recurved postcoxal line combined with an elongated and weakly convex body, and the shape of the anterior angle of pronotum distinguish this species from the other *Halmus.*

Description. Length 5.4 mm; TL/EW = 1.0; PL/PW = 0.5; EL/EW = 0.9. Female. Dorsal surface bluish to purple, somewhat metallic (Fig. 5.20), venter dark brownish. Body elongate, somewhat flattened. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 to 2 diameters apart. Eyes dorsally separated by less than 2 times the width of an eye, inner ocular margin slightly diverging apically. Antennomere 6 about 2 times longer than 5th and 7th (Fig. 5.129). Clypeus distinctly emarginate medially, with lateral extension markedly narrow. Terminal maxillary palpomere nearly weakly securiform (Fig. 5.122); terminal labial palpomere somewhat conical; less than 2 times longer than basal width; conspicuously shorter than the preceding segment. Pronotal surface polished between punctures; punctation smaller than eye facets, shallow and sparse, 2 to 3 diameters apart, obsolete on anterior angles; lateral borders somewhat rounded with sharp angle on inner side (Fig. 5.25); prosternum short in front of coxae, about 1.5 times longer than prosternal process widest width. Elytral surface polished between punctures; punctation stronger than on pronotum, about as large as to larger than eye facets, slightly deeper and more concentrated; lateral margin slightly reflexed. Abdomen with ventrite 6 short; surface of ventrite 1 polished between postcoxal lines; postcoxal line distinctly recurving apically. Male externally identical to female; genitalia not studied.

Types. Weise erected this species on the basis of eight specimens from Evelyne [=Evelyn], Colosseum and Cedar Creek, all in Queensland. Seven of these are found in the collections of NRS. One of the Evelyn specimens bearing the data "Evelyne / Queensl. Mjöberg/ aug./ Typus/ Orcus evelynensis m." is here designated as a lectotype. Three specimens also bearing the data "Evelyne / Queensl. Mjöberg/ aug." are paralectotypes. Two further paralectotypes bear labels "Cedar Creek/ Queensl. Mjöberg/ april". The last specimen of the original type series with a label "Colosseum/ Queensl. Mjöberg" is not an example of *evelynensis* but is a specimen of *H. cupripennis*. All seven specimens are teneral and largely distorted. The male genitalia could not be here illustrated.

Other material examined. Australia: QLD. Cairns distr., A.M. Lea (1, SAM); Mount Lewis, 7.ii.1974, Walford-Huggins (2, BMNH).

Distribution. Known only from few localities in northern Queensland (Fig. 5.199).

Halmus hilli sp. nov.

(Figures 5.108, 5.111, 5.112, 5.113, 5.201)

Etymology. The species is dedicated to the collector of the oldest specimens of the type series, G.F. Hill.

Diagnosis. At first sight *H. hilli* might be mistaken for *H. chalybeus* and *H. cupripennis*. Apart from genital characters the distinctly reticulate surface of pronotum and the non-metallic blackish dorsal surface may serve as characters to separate these two species.

Description. Length 5.1-5.5 mm; TL/EW = 1.0-1.1; PL/PW = 0.5-0.6; EL/EW = 0.8-0.9. Male. Dorsal surface entirely blackish except for the head and anterior corners of pronotum, which are yellowish; venter yellowish brown. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 2 diameters apart. Eyes dorsally separated by less than 2 times the width of an eye; inner ocular margin slightly diverging apically. Antennomere 6 about 1.5 times longer than 5th and 7th. Clypeus distinctly emarginate medially with lateral extension markedly narrow. Terminal maxillary palpomere with sides nearly parallel to slightly securiform, moderately expanded toward apex; apex oblique with outer side about 2 times longer than inner; terminal labial palpomere somewhat conical; less than 2 times longer than basal width; shorter than the preceding segment. Pronotal surface sculptured as on head, the sculptures much weaker; punctation smaller than eye facets, shallow and sparse, approximately 2 to 3 diameters apart, obsolete on anterior angles; lateral borders slightly truncate; prosternum short, about as long as prosternal process widest width. Elytral surface polished between punctures; punctation stronger than on pronotum; about as large as to larger than eye facets, slightly deeper and more concentrated; lateral margin slightly reflexed. Abdomen with ventrite 6 conspicuous, shortly emarginate at apex; surface of ventrite 1 polished between postcoxal lines; postcoxal line not recurving apically, running parallel to posterior margin, almost reaching lateral margin. Tegmen (Figs 5.112, 5.113) relatively short, about 1/2 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres scarcely setose at apex, the setae short; strut visibly longer than tegmen; penis as in Figures 5.108 and 5.111. Female externally identical to male but with head and pronotum only slightly lighter than elytra.

Biology. Unknown.

Types. Holotype male: Northern Territory: Stapleton, G.F. Hill (SAM). Paratypes: same data as holotype (3, SAM; 1, ANIC; 1, BMNH); Melville Island, Rolla Plains, on *Acacia mangium*, 9.viii.2000, GR. Brown (1, NTDA); same data but 8.vi.2000 (1, ANIC; 1, NTDA); Melville Island, 2 km E of Three Ways, 4.x.2000, GR. Brown (1, NTDA); Wildman River, cashew plantation, ex foliage, 14.iii.1991, W. Houston (1, NTDA); 6 km E of Humpty Doo, 6-19.x.1990, UV light, R. Storey (1, QDPIM).

Distribution. Northern Territory (Fig. 5.199).

Halmus viridis sp. nov.

(Figures 5.19, 5.119, 5.121, 5.125, 5.126, 5.130, 5.133, 5.134, 5.136, 5.184, 5.199)

Etymology. The species name is formed from the Latin adjective *viridis* meaning green, referring to an unusual colour of this beetle.

Diagnosis. The elongate, somewhat flattened body in combination with the metallic greenish coloration, long prosternum and recurving postcoxal line distinguish this species from the other *Halmus*.

Description. Length 5.7-5.9 mm; TL/EW = 1.25-1.33; PL/PW = 0.5; EL/EW = 1.0-1.1. Male. Body metallic greenish (Fig. 5.19); epipleura, coxae, tarsi and last 3-4 last abdominal ventrites brownish. Body elongate, somewhat flattened. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 diameters apart. Eyes dorsally separated by slightly more than 2 times the width of an eye; inner ocular margin diverging apically. Antennomeres 5, 6 and 7 about the same length. Clypeus distinctly emarginate medially (Fig. 5.184), with lateral extension markedly narrow. Terminal maxillary palpomere securiform (Fig. 5.121); terminal labial palpomere conical; less than 2 times longer than basal width; distinctly shorter than the preceding segment. Pronotal surface polished between punctures on disc, micro sculptured on anterior angles, the micro sculpture somewhat rugose; punctation smaller than eye facets, shallower than on head, approximately 1.5 to 2 diameters apart, obsolete at anterior angles; lateral borders slightly rounded; prosternum relatively long in front of coxae, slightly more than 2 times longer than prosternal process widest width. Elytral surface polished between punctures; punctation stronger than on pronotum, about as large as to larger than eye facets, slightly deeper; lateral margin slightly reflexed. Abdomen with ventrite 6 relatively conspicuous, broadly emarginate at apex; surface of ventrite 1 polished between punctures; postcoxal line recurving apically (Fig. 5.126), the line fairly distant from the posterior margin. Tegmen (Figs 5.133-5.134) relatively short, about 1/2 the abdomen length; penis guide symmetrical, distinctly longer than parameres; parameres densely setose at apex, the setae long;

strut slightly shorter than tegmen; penis as in Figures 5.130 and 5.136. Female externally similar to male except having the ventrite 6 truncate at apex.

Types. Holotype: New South Wales. Lahey's Creek, Moombi, 15 mls NE of Tamworth, 5.vi.1966, Z. Liepa (ANIC). Paratypes: Snowy Mts, 6 m N Tom Groggin, sweep, iv.1982, P. Greenslade (2, ANIC); Tumut R, 1500', 4.i.1955, J. Sedlacek (1, BPBM; 1, MCZ); same locality and collector, xi.1956 (1, BPBM); MT. Royal SF near Sigleton, 15.xi.1986, B. Day, K. Khee, R. de Keyzer (5, AM; 2, ANIC); same locality, 20.xi.1988, B. Day (1, SAM); Werrikimbe NP, Upper Hastings R, 910 m, 7.xii.1986, D. Bickel (2, AM; 1, ANIC). Queensland: Cooktown ?? (1, ZMB).

Distribution. This species seems to be confined to the Snowy Mountains and adjacent areas of New South Wales (Fig. 5.199); a label of the specimen here reported as collected in "Cooktown" (northern Queensland) is illegible, hard to interpret and probably erroneous.

ORCUS MULSANT

Orcus Mulsant, 1850: 465. Type species, subsequent designation (Crotch, 1874: 188): *Orcus janthinus* Mulsant, 1850.

Orcus (Priasus) Mulsant, 1850: 467. Type species, subsequent designation (Chapin, 1965: 252): *Coccinella bilunulata* Boisduval, 1835.

Parapriasus Chapin, 1965: 254. Type species, original designation: *Coccinella australasiae* Boisduval, 1835. New synonym.

Diagnostic description. Dorsum glabrous; elytra black to blue or green sometimes with metallic sheen, in Australian species without markings. Head transverse; eye distinctly emarginate; temple distinct, shorter than eye. Antenna 9-segmented (rarely 8-segmented), short;

scape asymmetrical; terminal antennomere longer than penultimate one (except in *O. citri*, Fig. 5.170). Clypeus short, weakly emarginate medially and extending laterally into eyes (Fig. 5.188); labrum partially exposed. Maxillary palp moderately long, last palpomere somewhat expanded apically with oblique apex (Figs 5.166, 5.167); labial palp stout, terminal palpomere slightly shorter and narrower than the penultimate segment. Pronotal base entirely bordered medially, the bordering line continuing interrupted or uninterrupted laterally but always remaining separate from fine marginal line (Fig. 5.191); prosternum moderately long in front of procoxae; prosternal process narrow, without carinae; hypomeral fovea sometimes present near anterior angles of prosternum. All tibiae simple externally, without apical spurs; claw strongly appendiculate to almost simple. Elytral margin weakly reflexed usually without clear bead; epipleuron descending almost always with deep foveae. Abdomen with 6th ventrite usually visible in male; postcoxal lines separated or joined at middle, each running parallel to posterior margin of ventrite or recurving apically (Figs 5.145, 5.148, 5.146). Female genitalia: coxite well sclerotised and elongate with rudimentary styli; bursal appendix in a form sclerotised spur; spermatheca bean-shaped (Figs 5.151, 5.152, 5.164, 5.165), cornu without a “beak”. Male genitalia: penis guide symmetrical; penis capsule well developed.

Discussion. Both *Priasus* and *Parapriasus* share all important characters with *Orcus* including the peculiar form of antenna, pronotal border and the aedeagus morphology. The only character that distinguishes *Orcus* from *Priasus* and *Parapriasus* is the interrupted marginal line along pronotal base. As in other Chilocorini there is certain variation in the form of tarsal claws from simple to appendiculate and that character by itself does not seem to be of taxonomic significance at the generic level. Male genitalia in this group are very uniform and in most cases do not provide reliable characters to diagnose the species. Based on these observations we synonymize *Priasus* and *Parapriasus* with *Orcus*. The validity of currently recognized species will need to be further assessed using biological and molecular data.

Distribution. Oriental and Australian with a very large number of undescribed species from New Guinea and the Solomon Islands.

Key to the Australian species of *Orcus*

1 Elytra without distinct maculae 2

\- Elytra with yellowish or orange maculae... 5

2 Small species, length less than 3 mm; males with lateral parts of pronotum orange-yellow (Fig. 5.28); antenna 8-segmented..*O. citri* Lea

\- Larger species, length usually above 3 mm; males with pronotum monochromatic; antenna 9-segmented .... …3

3 Lateral margin of elytron thickened into a distinct border; lateral parts of pronotum near anterior angles with small and separate punctures, usually with clear additional inner line (Fig. 5.191); hypomeral fovea vestigial............................ ……*O. punctulatus* Blackburn

\- Lateral margins of elytron without thickened border; lateral parts of pronotum near anterior angles usually with distinct strigae and confluent punctation (Figs 5.26, 5.190), the inner line, if present, visible only posteriorly (Fig. 5.190); hypomeral fovea distinct.............. 4

4 Elytra with reddish or greenish metallic reflection; pronotum with at least lateral margin metallic green usually contrasting with discal colour; pro- meso- and metaventrites dark brown with abdominal ventrites pale; legs dark brown.. ....*O. lafertei* Mulsant

\- Elytra black, purple or green but without metallic reflection; if lateral pronotal margins greenish blue then not contrasting with the disc; pro- meso and metaventrite concolorous with pale abdominal ventrites; legs pale coloured.........……..*O. cyanocephalus* Mulsant

5 Elytron with single subbasal transverse macula (Fig. 5.34) .....*O. bilunulatus* (Boisduval)

- Elytron with at least 2 maculae 6

6 Elytron with 2 maculae (Fig. 5.46); antenna 8-segmented; body relatively flat................ .... *O. quadrimaculatus* de Kerville

- Elytron with 3 or 4 maculae; antenna 9-segmented; body distinctly convex 7

7 Elytron with 4 maculae (Fig. 5.32) .... *O. nummularis* (Boisduval)

- Elytron with 2 maculae anteriorly and a single, posterior macula (Figs 5.31, 5.33)........ 8

8 Tarsal claws barely widened at base; lateral margin of elytron distinctly bordered; elytral maculae distinctly smaller (Figs 5.33, 5.43); postcoxal line distinctly recurving apically (Fig. 5.148); Western Australia only. .... *O. obscurus* Blackburn

- Tarsal claws distinctly appendiculate; lateral margin of elytron without obvious border; elytral maculae larger (Fig. 5.31), the posterior one often very large and irregular, especially in specimens from WA; postcoxal line not recurving apically (Fig. 5.146) western and eastern coast. ....*O. australasiae* (Boisduval)

Orcus australasiae (Boisduval)

(Figures 5.31, 5.36, 5.39, 5.146, 5.187, 5.193)

Coccinella australasiae Boisduval, 1835: 595.

Orcus australasiae var. *quadrinotatus* Lea, 1902: 491.

Diagnosis. The presence of three maculae on each elytron in combination with the moderate size and strongly appendiculate tarsal claws distinguish this species from the other Australian *Orcus.*

Description. Description: Length 4.0-5.6 mm; TL/EW = 1.0-1.1; PL/PW = 0.5-0.6; EL/EW = 0.8-0.9. Male. Dorsal surface predominantly dark bluish, shiny; each elytron with 3 orange maculae arranged as in Figures 5.31, 5.36 and 5.39; first abdominal ventrite usually dark brown; intermediates abdominal ventrites usually black medially and yellowish laterally; antennae, labial palp and last abdominal ventrite yellowish; rest blackish. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, shallow, nearly 1.5 to 2 diameters apart. Eyes with inner margin slightly diverging apically. Antenna 9-segmented; pedicel slightly longer than wider; 3rd antennomere slightly shorter than pedicel; 9th broad, slightly longer than basal width. Terminal maxillary palpomere with sides nearly parallel; the apex moderately oblique with outer side about 1.5 times as long as inner; terminal labial palpomere elongate; about 3 times longer than basal width; about as long as preceding segment. Pronotal surface sculptured as on head; punctation about as large as eye facets, as shallow as on head, approximately 1.5 to 2 diameters apart; the punctures not confluent on anterior angles, getting only slightly deeper and sparser; anterior angles without distinct strigae; lateral borders slightly truncate; bordering line uninterrupted at base, the line slightly opening anteriorly, slightly bent on lateral border; prosternum short in front of coxae, about as long as prosternal process widest width; hind tibiae with outer tooth; tarsal claws distinctly appendiculate. Elytral surface polished; punctation stronger than on pronotum, slightly deeper and more concentrated; lateral margin slightly reflexed, usually only on apical half, without clear bead; epipleural foveae absent. Abdomen with 6 ventrites; 6th fairly evident; surface of ventrite 1 polished between postcoxal lines; postcoxal lines joined at middle, shortly recurving apically (Fig. 5.146); apical border of intercoxal process slightly swollen. Tegmen relatively long, about 2/3 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres sparsely setose, the setae short; strut as long as tegmen; penis similar to *O. nummularis*. Female externally similar to male, except for having only 5 visible abdominal ventrites, the 5th ventrite large and rounded, about 2 times longer than 4th.

*Types: "*Nouvelle-Hollande, coll. Dejean" (Museum Lyon, not examined).

Material examined (+1000 specimens). Australian Capital Territory. Canberra (35°18'S, 149°08'E); Australian National University, Canberra; Black Mountain (35°16'S, 149°06'E); Broken Bridge; Canberra, Botanic Gardens (35°16'S, 149°06'E); Commonwealth Park (35°17'S, 149°08'E); Cotter River (35°31'S, 148°50'E); Gungahlin (35°13'S, 149°08'E); Kingston (35°19'S, 149°09'E); Monash (35°24'S, 149°05'E); Mount Ainslie (35°16'S, 149°10'E). New South Wales. 5.5 km W Forest Reefs (33°27'S, 149°03'E); 2km SE of Goulburn (34°46'S, 149°44'E); 35k S Gunning (34°47'S, 149°17'E); 4 mls. NE of Goulburn (34°43'S, 149°46'E); 4km SW Morisset (33°08'S, 151°27'E); 5 km E Sutton (35°10'S, 149°18'E); 8km N Canberra, Federal Hwy (35°14'S, 149°08'E); 9.5 mi. E of Boomi (28°26'S, 152°46'E); Abercrombie R., 50mi. N Goulburn (34°11'S, 149°44'E); Budgong nr. Nowra (34°53'S, 150°36'E); Burra (35°33'S, 149°14'E); Cattai (33°33'S, 150°55'E); Clarence River (29°41'S, 152°56'E); Combogolong, Bathurst (33°17'S, 149°23'E); Congo, 8km SE by E of Moruya (35°58'S, 150°09'E); Cooranbong, Macquarie Lakes Dist. (33°05'S, 151°27'E); Dorrigo (30°20'S, 152°43'E); Dubbo (32°15'S, 148°37'E); Engadine (34°04'S, 151°01'E); Gosford (33°26'S, 151°21'E); Hawkesbury River (33°23'S, 150°59'E); Hoskintown [Hoskinstown] (35°25'S, 149°27'E); Kenthurst (33°40'S, 150°59'E); Mulgrave (33°37'S, 150°49'E); Murramurrang NP [Murramarang] (35°35'S, 150°21'E); Myall Lakes National Park (32°30'); N of Orange (33°17'S, 149°06’E); N.E. University, Armidale [New England University] (30°29'S, 151°40’E); Nelson Bay (32°43'S, 152°09’E); Oberon Prison Camp (34°01'S, 149°51’E); Pilliga (30°21'S, 148°53’E); Richmond R. (28°28'S, 152°55’E); Shoal Bay (32°44'S, 152°10’E); Sutton (35°10'S, 149°15’E); Sydney (33°53'S, 151°13’E); T'field [Tenterfield] (29°03'S, 152°01’E); Tea Tree Ck. Armidale (30°30'S, 151°30’E); Tenterfield (29°03'S, 152°01’E); The Gap, Sydney (33°51'S, 151°17’E); The Kurrajong, Blue Mts. (30°05'S, 150°54’E); The Ponds, Grafton Rd. (29°52'S, 152°27’E); Wahroonga (33°43'S, 151°07’E); Weetangera (28°43'S, 153°33’E). Queensland. Brisbane (27°28'S, 153°02’E); Brookfield, Bris. (27°30'S, 152°55’E); Cunnamulla (28°04'S, 145°41’E); Dalby (27°11'S, 151°15’E); Eidsvold (25°22'S, 151°07’E); Fletcher (28°46'S, 151°51’E); Jimboomba (27°50'S, 153°02’E); Palm Beach; Rockhampton (23°22'S, 150°31’E); Sunnybank (27°35'S, 153°03’E); Tambourine Mts. [Tamborine Mountain] (27°55'S, 153°09’E); Taringa (25°56'S, 148°39’E); Toowoomba (27°33'36"S, 151°57’E). South Australia. 25km S Kingscote, K I [Kangaroo Island] (35°52'S, 137°38’E); Lucindale (36°58'S, 140°22’E); Port Lincoln (34°44'S, 135°52’E); Pt. Pearce, Spencers Gulf (34°28'S, 137°26’E).Tasmania. 10mls. NNW of Sorell (42°39'S, 147°30’E); Beechford (41°02'S, 146°58’E); Cambridge (42°50'S, 147°26’E); Hobart (42°53'S, 147°19’E); Launceston (41°26'S, 147°08’E); Mt. Leslie Rd., Prospect, Launceston (41°28'S, 147°08’E); Newstead, Laun. [Launceston] (41°27'S, 147°10’E); Table C. [Table Cape] (40°57'S, 145°44’E); Trevallyn, Laun. [Launceston]; Hayes; Devonport. Victoria. Barwon Heads (38°17'S, 144°30’E); Baxter (38°12'S, 145°09’E); Birchip (35°59'S, 142°55’E); Dutson Downs (38°13'S, 147°19’E); Eildon Weir (37°14'S, 145°55’E); Eltham (37°43'S, 145°09’E); F.T. Gully [Ferntree Gully] (37°53'S, 145°18’E); Gippsland (37°50'S, 147°37’E); Grampians [The Grampians] (37°08'S, 142°31’E); Hexham (38°00'S, 142°42’E); Macedon (37°25'S, 144°34’E); Moe (38°11'S, 146°16’E); Morwell (38°14'S, 146°24’E);

Oakleigh (37°55'S, 145°07’E); Ringwood (37°49'S, 145°14’E); Victorian Alps; Warburton District (37°45'S, 145°42’E); Warburton (37°45'S, 145°42’E); Warragul (38°10'S, 145°56’E); Wattle Park (37°50'S, 145°06’E); Woori Yallock (37°47'S, 145°32’E); Yarra Bend, Boulevard Road [Yarra Bend Park] (37°48'S, 145°00’E). Western Australia. 11 km NW of Esperance (33°47'S, 121°48’E); 18km W of Balladonia (32°28'S, 123°40’E); 64km S Boyup Brook (34°25'S, 116°23’E); Albany (35°00'S, 117°52’E); Donnybrook & Collie on Sth Rd. (33°28'S, 115°59’E); Beverley (32°07'S, 116°56’E); Bunbury (33°20'S, 115°38’E); Cape Arid, Thomas River (34°01'S, 123°09’E); Cape Le Grand (34°01'S, 122°07’E); Coalmine Bch., Walpole Nornalup NP (34°59'S, 116°44’E); Coodanup nr. Madura (31°56'S, 126°58’E); Creek, 8km N of Osmington (33°48'S, 115°17’E); Deep Dene, Karridale (34°12'S, 115°06’E); Dongarra [Dongara] (29°14'S, 114°56’E); Eyre Bird Observatory, 40 km S of Cocklebiddy (32°25'S, 126°06’E); Furnissdale (32°34'S, 115°46’E); Garden Is. (32°12'S, 115°40’E); Harvey Est., West Shore (32°42'S, 115°41’E); Highway 1, 1 km W of Dalyup R. (33°39'S, 121°36’E); Hopetoun (33°57'S, 120°07’E); Juranda Rock Hole (33°13'S, 123°27’E); K.G.Sound [King George Sound] (35°00'S, 117°52’E); Katanning (33°41'S, 117°33’E); Lake Clifton, Yalgurup N.P. [Yalgorup] (32°48'S, 115°40’E); nr. Yalgurup N.P. [Yalgorup NP] (32°40'S, 115°38’E); Perth (31°57'S, 115°51’E); Pinjarra (32°38'S, 115°52’E); Preston Beach, Yalgorup Nat. Pk. (32°53'S, 115°39’E); Prevelly Park, 8km W Margaret R. (33°58'S, 114°59’E); Serpentine Falls (32°22'S, 116°02’E); Swan River (31°51'S, 116°00’E); Thomas R., Cape Arid N.Pk. (33°49'S, 123°02’E); Thomas River, 23 km NW by W of Mt. Arid (33°51'S, 123°00’E); Warren River, 10km S Pemberton (34°32'S, 116°02’E); Waterloo (33°20'S, 115°45’E); Wilga (33°42'S, 116°14’E); Yalgurup NP. [Yalgorup NP] (32°40'S, 115°38’E); Yanchep, 32mi. N Perth (31°33'S, 115°41'E).

Biology. Unknown but has been found several times feeding on casuarina mealybug, *Pseudoripersia turgipes* (Maskell), in ACT.

Distribution. Very common species in southern Australia, including Tasmania (Fig. 5.193).

Orcus bilunulatus (Boisduval)

(Figures 5.34, 5.37, 5.40, 5.138, 5.140, 5.141, 5.144, 5.147, 5.149, 5.154, 5.152, 5.153, 5.194)

Coccinella bilunulata Boisduval, 1835: 594.

Diagnosis. This is very distinctive species, immediately recognizable by its size and the presence of a single macula in each elytron (Fig. 5.34).

Description. Length 4.5-7.7 mm; TL/EW = 1.1-1.2; PL/PW = 0.5-0.6; EL/EW=0.9-1.0. Male. Dorsal surface predominantly metallic dark bluish; each elytron with a single macula anteriorly as in Figures 5.34, 5.37 and 5.40; first abdominal ventrite blackish between the postcoxal lines, yellowish laterally; second abdominal ventrite mainly yellowish with a median rather narrow dark brownish macula; antennae, labrum, labial palp, meso, and metepimeron, meso, and metepisternum yellowish; rest blackish. Body oval, convex. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 to 2 diameters apart. Eyes with inner margin nearly parallel. Antenna 9-segmented; pedicel about as long as wide; 3rd antennomere transverse, somewhat subquadrate; 9th elongate, about 2 times longer than basal width. Terminal maxillary palpomere with sides nearly parallel (Fig. 5.147); terminal labial palpomere elongate; about 3 times longer than basal width; about as long as preceding segment. Pronotal surface sculptured as on head; punctation about as large as eye facets, approximately 1.5 to 2 diameters apart; the punctures not confluent on anterior angles, getting only slightly deeper; anterior angles without distinct strigae; lateral borders rounded; bordering line uninterrupted at base, the line distinctly bordering the lateral border; prosternum short in front of coxae, about 1.5 times longer than prosternal process widest width; hind tibiae with outer tooth; tarsal claws simple (Fig. 5.154). Elytral surface sculptured as on pronotum, visibly weaker; punctation stronger than on pronotum, slightly deeper and more concentrated; lateral margin slightly reflexed, without clear bead; epipleural foveae absent. Abdomen with 6 ventrites; 6th very short, emarginate at apex; surface of ventrite 1 micro reticulate between postcoxal lines; postcoxal lines joined at middle; recurving apically (Fig. 5.149), reaching more than half the ventrite width, apical border of intercoxal process slightly swollen. Tegmen (Figs 5.140, 5.141) relatively short, about 1/2 the abdomen length; penis guide symmetrical, distinctly shorter than parameres; parameres sparsely setose, the setae short; strut about as long as tegmen; penis as in Figures 5.138 and 5.144. Female externally identical to male, except having only 5 visible abdominal ventrites, the 5th ventrite large and rounded, about 2 times longer than 4th.

*Types: "*Nouvelle-Hollande, coll. Dejean" (Museum Lyon, not examined).

Material examined (+1000 specimens): Australian Capital Territory. Australian National University, Canberra; Black Mt. (35°16'S, 149°06'E); Canberra (35°18'S, 149°08'E); Canberra nr. Div. of Entomology (35°18'S, 149°08'E); E of Aerodrome; Monash (35°24'S, 149°06'E); Turner (35°16'S, 149°07'E); Weston (35°20'S, 149°03'E); Westridge (35°18'S, 149°08'E). New South Wales. Araluen Valley (35°39'S, 149°49'E); Bantry Bay (33°47'S, 151°14'E); Blue Mountains (33°46'S, 150°26'E); Colo Vale (34°24'S, 150°29'E); Dalmeny nr. Narooma (36°13'S, 150°03'E); Dee Why (33°46'S, 151°18'E); Dorrigo (30°20'S, 152°43'E); Durras North (35°37'48"S, 150°18'E); Galston Gorge [general] (33°40'S, 151°05'E); Gerroa (34°46'S, 150°49'E); Hastings Range; Kioloa S.F. 15km NE Batemans Bay (35°30'S, 150°18'E); Macleay

Riv. (31°03'S, 152°50’E); Runnyford Ck., Nelligen (35°39'S, 150°08’E); Shoalhaven (34°51'S, 150°45’E); St. Georges Basin, nr. Jervis Bay (35°05'S, 150°35’E); Sydney (33°53'S, 151°13’E); Terry Hie Hie Sta. [Terry Hie HS] (34°58'S, 149°40’E); Tudibaring [Tudibaring Head] (33°30'S, 151°27’E); vicinity of Jenolan Caves (33°49'S, 150°01’E); Wattle Flat, Styx River (30°35'S, 152°12’E); Wollombi-Broke (32°56'S, 151°09’E); Wollomombi (30°31'S, 152°03’E); Yetholme (33°27'S, 149°49’E). Queensland. 2nd Palen Creek Crossing from Rathdowney (28°16'S, 152°48’E); Bakerville (17°23'S, 145°16’E); Gooburrum Shire, Moore Park, c.22km N of Bundaberg (24°43'S, 152°17’E); Indo'pilly [Indooroopilly] (27°30'S, 152°58’E); Yabba Creek, 10 km W of Imbil (26°28'S, 152°35’E). Tasmania. Hobart (42°53'S, 147°19’E); Launceston (41°26'S, 147°08’E); Punchbow Rd., Laun. [Launceston] (41°27'S, 147°10’E); Lindsforne. Victoria. Baxter (38°12'S, 145°09’E); Nowa Nowa (37°44'S, 148°06’E); Melbourne (37°49'S, 144°58'E).

Distribution. Very common species along the eastern coast of Australia, including Tasmania (Fig. 5.194).

Notes. Froggatt (1903) first reported this species feeding on casuarina mealybug, *Pseudoripersia turgipes* (Maskell), in New South Wales. This host supports large populations of *O. bilunulatus* in ACT, and both adults and larvae are found on *Casuarina* trees for most of the year.

Orcus citri Lea

(Figures 5.28, 5.158, 5.162, 5.163, 5.165, 5.167, 5.170, 5.174, 5.180, 5.201)

Ocrus citri Lea, 1902: 490

Orcus coxalis Weise, 1917: 221. New synonym.

Diagnosis. *Orcus citri* is a very distinctive species with its small, very convex, almost circular form and dark elytra. It is also distinctive in having 8-segmented antennae and middle and hind tibiae that lack the sharp outer tooth found in most of the *Orcus* species.

Description. Length 5.8-5.9 mm; TL/EW = 1.1-1.2; PL/PW = 0.5; EL/EW = 0.9-1.0. Male. Head and elytra metallic brownish; prothorax yellowish (Fig. 5.28), except central area of pronotum, which is brownish; antennae, labrum, labial palp, ventral surface of fore legs, meso- and metepimeron, meso- and metepisternum yellowish to pale brown; abdominal ventrites yellowish except in the area between the postcoxal lines. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1 diameter apart. Eyes with inner margin conspicuously diverging apically. Antenna 8-segmented (Fig. 5.170); pedicel about as long as greatest width; 3rd antennomere slightly shorter than pedicel; 8th broad, slightly longer than basal width. Terminal maxillary palpomere with side parallel (Fig. 5.167); terminal labial palpomere slightly elongate; about 2 times longer than basal width; shorter then preceding segment. Pronotal surface polished between punctures; punctation about as large as eye facets, as shallow as on head, approximately 1.0 diameters apart; the punctures not confluent on anterior angles, getting only slightly deeper and larger; anterior angles without distinct strigae; lateral borders rounded; bordering line uninterrupted at base, the line slightly opening anteriorly, then almost reaching lateral margin; prosternum short in front of coxae slightly longer than prosternal process widest width; hypomeral foveae absent; hind tibiae without outer tooth; tarsal claws weakly appendiculate. Elytral surface and punctation as on pronotum; lateral margin not reflexed, with clear bead; epipleural foveae absent. Abdomen with 6 ventrites; 6th very reduced, truncate to slightly emarginate at apex; surface of ventrite 1 micro reticulate between postcoxal lines; postcoxal lines separated at middle, running parallel to posterior margin of ventrite for a short distance (Fig. 5.174). Tegmen (Figs 5.162, 5.163) relatively long, about 2/3 the abdomen length; penis guide symmetrical, distinctly longer than parameres; parameres densely setose at apex, the setae relatively short; strut slightly shorter than tegmen; penis as in Figures 5.158 and 5.180. Female externally similar to male, except having monochromatic pronotum and only 5 visible abdominal ventrites; the 5th ventrite is rounded apically; spermatheca as in Figure 5.165.

Types. Lea did not mention how many specimens of *O. citri* he had before him but "on citrus trees" seems to suggest more than one. The two male examples mounted on a single card from the SAM are accepted as the lectotype and paralectotype bearing labels "Ty/ cirti Lea Type Tamworth/ Orcus citri Lea Ty 10366". The lectotype is the left specimen of the two. It also is in much better condition than the paralectotype. Weise also made no comment on the number of specimens of *O. coxalis* he had examined. A male specimen in the NRM labelled as "Queensland Staud. Cooktown/ Typus/ Orcus coxalis m" is accepted as the lectotype. The second male is accepted as a paralectotype.

Biology. Lea found this species on orange trees. The specimens from QDPIB were found on *Casuarina* sp. in association with larvae and probably when preying on the scale, *Pseudoripersia turgipes* (Maskell).

Other material examined: New South Wales: Booranong River, Bundarra Road near Armidale (1, BMNH). Queensland. 2nd Palen Creek Crossing from Rathdowney, K. Houston, 22-30.iii. 1975, K. Houston (2, QDPIB; 1, ANIC); Fletcher (1, ANIC); Kuranda, R. Perkins (1, BMNH); Mt. Tambourine, Lea (1, SAM).

Distribution: Known from few localities along the coast from central New South Wales to northern Queensland (Fig. 5.201).

Orcus cyanocephalus Mulsant

(Figures 5.26, 5.44, 5.155, 5.178, 5.206)

Orcus cyanocephalus Mulsant, 1850: 467.

Orcus Lecanii Blackburn, 1895: 239. New synonym.

Orcus purpureotinctus Lea, 1902: 490. New synonym.

Diagnosis. This species is separable from *O. lafertei* only by the lack of true metallic reflection on the elytra, which can be black, purple or green. Male genitalia are practically identical in this species complex.

Description. Length 5.5-4.5 mm; TL/EW = 0.9-1.0; PL/PW = 0.5-0.6; EL/EW = 0.8-0.9. Male. Dorsal surface varying from blue, purple or darkish-brown with varying degree of shine (Fig. 5.44); venter pale brown except for epipleura and lateral extremity of hypomera, which are dark brownish. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, not conspicuously deep and somewhat sparse, nearly 2 diameters apart. Eyes with inner margin slightly diverging apically. Clypeus weakly emarginate. Antennae 9-segmented, very similar to *O. lafertei* (Fig. 5.169). Maxillary and labial palpomeres also very similar to *O. Lafertei.* Pronotal surface sculptured as on head, the sculptures much weaker; punctation slightly larger than eye facets, as shallow as on head but more concentrated, approximately 1 diameter apart; the punctures confluent on anterior angles (Figs 5.26, 5.188); anterior angles with distinct strigae; lateral borders somewhat oblique; bordering line interrupted at base, the line slightly bent at the lateral border (in some specimens); prosternum moderately long in front of coxae about 1.5 times longer than the prosternal process widest width; hind tibiae with outer tooth; tarsal claws distinctly appendiculate. Elytral surface sculptured as on pronotum; punctation weaker than on pronotum, slightly shallower and sparser; lateral margin weakly reflexed, without clear bead; epipleural foveae conspicuous. Abdomen with 6 ventrites; 6th very reduced, straight to slightly emarginate at apex; surface of ventrite 1 polished between postcoxal lines; postcoxal lines joined at middle, running parallel to posterior margin of ventrite, almost reaching lateral margin; apical border of intercoxal process conspicuously swollen. Tegmen relatively short, about 1/3 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres densely setose at apex, the setae long; strut as long as tegmen; penis as in Figures 5.155 and 5.178. Female externally similar to male, except having only 5 visible abdominal ventrites, the 5th ventrite also rounded but longer than in male, about 2 times longer than 4th, somewhat oval.

Types. Orcus cyanocephalus: Lectotype in Oxford (Booth and Pope 1989); paralectotype in Crotch coll. “cyanocephalus ex Muls./ Guerin pt Essington” (Cambridge University). *O. lecanii* - Lectotype, "5899 Townsville, Type/ Australia Blackburn Coll. BM 1910-236”/ Orcus lecanii Black/ (BMNH). *O. purpureotinctus*: “purpureotinctus Lea BehnR/ 10367 Orcus purpureotinctus Lea Type, N.W. Australia (lectotype and paralectotype, SAM).

Material examined (+400 specimens). Northern Territory. 9 km N by E Mudginbarry H.S. [Mudginberri Homestead] (12°31'S, 132°54’E); Berrimah (12°26'S, 130°55’E); Darwin (12°27'S, 130°50’E); Groote Eylandt (14°02'S, 136°36’E); Howard Springs, 32km E Darwin (12°27'S, 131°03’E); Humpty Doo, 7 Collard Rd. (12°37'S, 131°15’E); J&C Etty, 2351 Edith Farms Rd., Katherine (14°28'S, 132°16’E); Kakadu NP, Saurcery Rock nr. Cannon Hill (12°23'S, 132°57’E); Katherine Research Station (14°28'S, 132°16’E); Ken Rayner's, Florina R. Katherine (14°27'S, 131°41’E); Lambells Lagoon, Lot 27 Alphatonia Rd. (12°33'S, 131°16’E); Malak Caravan Park, Darwin (12°27'S, 130°50’E); Melville Island (11°25'S, 131°31’E); Melville Islands, Rolla Plain (11°25'S, 131°31’E); Nguiu, Bathurst Is. (11°44'S, 130°37’E);

Obiri Rock area, Kakadu National Park (12°54'S, 132°38’E); Roper River, 5km E Mataranka (14°56'S, 133°07’E); Tipperary Station, Brocks Ck. (13°44'S, 131°03’E); Wildman River Cashew Plantation (12°40'S, 132°00’E); Yarrawonga Park nr Darwin (12°27'S, 130°50’E). Queensland: 10 km E Mareeba (17°00'S, 145°32’E); 10 km SW Clairview (22°15'S, 149°24’E); 12 km W of Petford (17°21'S, 144°49’E); 19 km S Mt. Molloy (16°51'S, 145°20’E); 23km E Mareeba, Kanervo Rd. (17°00'S, 145°39’E); 3km W Mt. Molloy (16°41'S, 145°18’E); 8km SW Kuranda (16°52'S, 145°35’E); Ayr (19°34'S, 147°24’E); Badu Island, Torres Strait (10°07'S, 142°07’E); Bartle Frere (17°27'S, 145°53’E); Batavia Downs HS (12°40'S, 142°40’E); Biboohra, River Rd. (16°55'S, 145°25’E); Burketown, Gulf of Carpentaria (17°45'S, 139°33’E); Burketown (17°45'S, 139°33’E); Cairns (16°55'S, 145°46’E); Cape Tribulation (16°05'S, 145°29’E); Charters Towers (20°05'S, 146°16’E); Davies Creek (16°59'S, 145°33’E); Heathlands (11°45'S, 142°35’E); Home Hill (19°40'S, 147°25’E); Koah Rd. via Mareeba (16°53'S, 145°33’E); Kowanyama, Cape York (15°28'S, 141°45’E); Leichhardt Ck. (19°54'S, 147°33’E); Nambour (26°38'S, 152°58’E); Parada (17°08'S, 145°15’E); Saibai Is.; 9°23'S, 142°40’E); South Johnston (17°36'S, 146°00’E); Southedge R.S. [Southedge Research Station] (16°49'S, 145°13’E); Station Ck., 10 m. S Mt. Carbine (16°37'S, 145°12’E); Thursday Island (10°35'S, 142°13’E); Townsville (19°16'S, 146°49’E); Tully (17°56'S, 145°56’E); Walkamin (17°08'S, 145°26’E). Western Australia: Carson Escarpment (14°49'S, 126°49’E).

Biology. Unknown.

Distribution. This species is widely distributed in northern parts of Australia (Fig. 5.206) and New Guinea.

Orcus lafertei Mulsant

(Figures 5.156, 5.162, 5.169, 5.175, 5.188, 5.190, 5.192, 5.202)

Orcus lafertei Mulsant, 1853: 190.

Diagnosis. This species is separable from *O. cyanocephalus* by its elytra with reddish or greenish metallic reflection.

Description. Length 4.0-4.7 mm; TL/EW =0.9-1.1; PL/PW = 0.5-0.6; EL/EW = 0.8-0.9. Male. Dorsal surface reddish, greenish or bluish; pronotum with anterior angles usually greenish, contrasting with the discal colour; elytra with metallic reflection; venter usually pale brownish, except for epipleura and hypomera, which are dark brownish; in some specimens pro-, meso-, and metaventrites and legs dark brownish. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, not conspicuously deep and somewhat sparse, nearly 2 diameters apart. Eyes with inner margin slightly diverging apically. Antenna 9-segmented (Fig. 5.169); pedicel about as long as its greatest width; 3rd antennomere slightly shorter than pedicel; 9th elongate, about 2 times longer than basal width. Terminal maxillary palpomere with sides nearly parallel; the apex moderately oblique with outer side about 1.5 times longer than inner; terminal labial palpomere elongate; about 3 times longer than basal width; about as long as preceding segment. Pronotal surface sculptured as on head, the sculptures much weaker; punctation slightly larger than eye facets, as shallow as on head but more concentrated, approximately 1 diameter apart; the punctures confluent on anterior angles; anterior angles with distinct strigae; lateral borders somewhat oblique; bordering line interrupted at base, the line slightly bent at the lateral border; prosternum moderately long in front of coxae, about 1.5 times longer than prosternal process widest width; hypomeral foveae conspicuous; hind tibiae with outer tooth; tarsal claws distinctly appendiculate (Fig. 5.192). Elytral surface sculptured as on pronotum; punctation slightly weaker than on pronotum, slightly shallower and sparser; lateral margin weakly reflexed, without clear bead; epipleural foveae conspicuous. Abdomen with 6 ventrites; 6th reduced, sometimes not very obvious in dry specimens, straight to slightly emarginate at apex; surface of ventrite 1 polished between postcoxal lines; postcoxal lines joined at middle, running parallel to posterior margin of ventrite, almost reaching lateral margin (Fig. 5.175); apical border of intercoxal process conspicuously swollen. Tegmen (Fig. 5.161) about 2/3 the abdomen length; penis guide symmetrical, as long as to slightly longer than the parameres; parameres densely setose at apex, the setae long; strut about as long as tegmen; penis as in Figures 5.156 and 5.178. Female identical to male, except for having only 5 visible abdominal ventrites, the 5th ventrite also rounded but longer than in male, about 2 times longer than 4th, somewhat oval.

Types. Lectotype, here designated: “75.36; Orcus Lafertei Muls T Moreton Bay/ Named by Mulsant/Type” (BMNH).

Material examined (+300 specimens). New South Wales: Tweed River (28°20'S, 153°20’E). Queensland: 10km E Mareeba (17°00'S, 145°32’E); 10km SW Clairview (22°15'S, 149°24’E); Baffle Ck, via Rosedale (24°31'S, 151°54’E); Brisbane (27°28'S, 153°02’E); Bundaberg (24°52'S, 152°21’E); Cairns (16°55'S, 145°46’E); Cleveland (27°32'S, 153°17’E); Eden Is., Southern Moreton Bay (27°45'S, 153°23’E); Halftide nr. Mackay [Half Tide] (21°18'S, 149°18’E); Maryborough (25°32'S, 152°42’E); Nambour (26°38'S, 152°58’E); Beenleigh (27°43'S, 153°12’E); Rockhampton (23°22'S, 150°31’E); Rocklea (27°33'S, 153°00’E); Southport (27°58'S, 153°25’E); Westwood (23°36'S, 150°10’E); Woody Point (27°16'S, 153°07’E); Yeppoon (23°07'S, 150°44’E).

Biology. Unknown.

Distribution. Common along the eastern coast from northern NSW to tropical Queensland (Fig. 5.202).

Orcus nummularis (Boisduval)

(Figures 5.32, 5.35, 5.38, 5.37, 5.139, 5.142, 5.143, 5.145, 5.150, 5.151, 5.198)

Coccinella nummularis Boisduval, 1835: 594.

Diagnosis. The presence of four maculae on each elytron distinguishes this species from the other Australian *Orcus.*

Description. Length 5.5-4.1 mm; TL/EW = 1.1; PL/PW = 0.5; EL/EW = 0.8-0.9. Male. Dorsal surface predominantly metallic brownish; each elytron with 4 yellowish or orange maculae arranged as in Figures 5.32, 5.35 and 5.38; antennae, labial palp, meso-, and metepimeron, meso-, and metepisternum and abdomen yellowish; rest dark brown. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, nearly 1.5 to 2 diameters apart. Eyes with inner margin slightly diverging apically. Antennae 9-segmented (Fig. 5.137); pedicel slightly wider than long; 3rd slightly shorter than pedicel; 9th relatively short, about as long as basal width. Terminal maxillary palpomere with sides nearly parallel; the apex moderately oblique with outer side about 1.5 times as long as inner; terminal labial palpomere slightly elongate; about 2 times longer than basal width; visibly shorter then preceding segment. Pronotal surface sculptured as on head, the sculptures much weaker; punctation about as large as eye facets, as shallow as on head; approximately 1.5 to 2 diameters apart; the punctures not confluent on anterior angles, getting slightly deeper; anterior angles without distinct strigae; lateral borders rounded to slightly truncate; bordering line uninterrupted at base; the line slightly opening anteriorly, then almost reaching lateral border.

prosternum short in front of coxae, about 1.5 times longer than prosternal process widest width; hypomeral foveae vestigial; hind tibiae with outer tooth; tarsal claws weakly appendiculate (Fig. 5.150). Elytral surface sculptured as on pronotum; punctation stronger than on pronotum, slightly deeper and more concentrated; about as large as eye facets, approximately 1.5 to 2 diameters apart; lateral margin slightly reflexed, without clear bead; epipleura foveae vestigial. Abdomen with 6 ventrites; 6th fairly evident; surface of ventrite 1 polished between postcoxal lines; postcoxal lines joined at middle, recurving apically without reaching the middle of the segment (Fig. 5.145); apical border of intercoxal process slightly swollen. Tegmen (Figs 5.142, 5.143) relatively long, slightly more than 2/3 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres sparsely setose, the setae short; strut as long as penis guide; penis similar to *O. bilunulatus*, tip as in Figure 5.139. Female similar to male, except having only 5 visible abdominal ventrites, the 5th ventrite large and rounded, about 2 times longer than 4th.

*Types: "*Nouvelle-Hollande, coll. Dejean" (Museum Lyon, not examined).

Material examined (+500): Australian Capital Territory. Narrabundah, Stevenson Orchard (35°21'S, 149°08'E); New South Wales. 24 mi. NW of Moree (29°13'S, 149°34'E); 9.5 mi. E of Boomi (28°26'S, 152°46'E); Blacktown, Old Quarry (33°46'S, 150°54'E); Bogan River (30°53'S, 147°04'E); Grenfell (33°54'S, 148°10'E); Greta (32°41'S 151°23'E); Gunnedah (30°59'S, 150°15'E); Mullaley (31°06'S, 149°55'E); Pilliga (30°21'S, 148°53'E); Sydney (33°53'S, 151°13'E); Whitton (34°31'S, 146°11'E); Queensland. 27km NW of Tambo (24°43'S, 146°04'E); 50km along Dalby-Moonie road; Brisbane (27°28'S, 153°02'E); Bundaberg (24°52'S, 152°21'E); Dalby (27°11'S, 151°15'E); Rockhampton (23°22'S, 150°31'E); Electra SF, nr. Bundaberg Marmor (23°41'S, 150°42'E); Maryborough (25°32'S, 152°42'E); Stradbroke Is.

(27°28'S, 153°28'E); Yeppoon (23°07'S, 150°44'E); South Australia. Lewiston Reserve nr. Two Wells (34°35'S, 138°31'E).

Biology. Unknown.

Distribution. This species is easily confused with *O. australasiae* and some series are mixed. It appears that this species is limited to the south-eastern part of Australia (Fig. 5.198) but does not occur in Tasmania.

Orcus obscurus Blackburn

(Figures 5.33, 5.43, 5.148)

Orcus Australasiae var. ? *obscurus* Blackburn, 1892b: 241.

Orcus obscurus: Blackburn, 1895: 240.

Diagnosis. The presence of 3 maculae on each elytron in combination with the relatively small size and tarsal claws with obsolete tooth distinguish this species from the other Australian *Orcus*.

Description. Length 5.7 mm; TL/EW = 1.5; PL/PW = 0.5; EL/EW = 1.0.

Female. Surface dark brownish, each elytron with 3 orange maculae arranged as in Figures 5.33 and 45. Head micro reticulate between punctures; punctation almost indistinct, smaller than eye facets, very shallow, nearly 2 diameters apart. Eyes with inner margin slightly diverging apically. Antenna 9-segmented; pedicel about as long as wide; 3rd antennomere slightly shorter than pedicel; 9th broad, slightly longer than basal width. Terminal maxillary palpomere with sides nearly parallel; the apex strongly oblique with outer side about 2 times longer than inner; terminal labial palpomere slightly elongate; about 2 times longer than basal width; visibly shorter than preceding segment. Pronotal surface sculptured as on head; punctation about as large as eye facets, approximately 1.5 to 2 diameters apart; the punctures obsolete on anterior angles; anterior angles without distinct strigae; lateral borders rounded; bordering line uninterrupted at base, the line slightly opening anteriorly, then almost reaching lateral border; prosternum short in front of coxae about as long as prosternal process widest width; hind tibiae with outer tooth; tarsal claws barely widened at base. Elytral surface somewhat coriaceous; punctation similar to pronotum, but difficult to see given the leathery nature of the surface; lateral margin slightly reflexed, without clear bead; epipleural foveae absent. Abdomen with 5 ventrites; 5th rounded at apex; surface of ventrite 1 micro reticulate between postcoxal lines; postcoxal lines joined at middle, weakly recurving apically (Fig. 5.148); apical border of intercoxal process flat. Male unknown.

Type. "T 7545, Yilg; type; var obscurus Blackb?/ Orcus obscurus, Blackb. Var? australasiae" (Lectotype, here designated, BMNH).

Biology. Unknown.

Material examined. Western Australia. 5 Km S Norseman (1, ANIC).

Distribution. Western Australia.

Orcus punctulatus Blackburn

(Figures 5.41, 5.42, 5.45, 5.177, 5.191, 5.207)

Orcus punctulatus Blackburn, 1892b: 240.

Orcus beneficus Weise, 1913: 444. New synonym.

Diagnosis. The bluish dorsal coloration in combination with a well developed elytral bead and vestigial hypomeral fovea distinguish this species from the other Australian *Orcus.*

Description: Length 5.8-4.7 mm; TL/EW =1.0; PL/PW = 0.4-0.5; EL/EW = 0.8-0.9. Male. Dorsal surface bluish or greenish, usually shiny (Figs 5.41, 5.42, 5.45); venter pale brown except epipleura and hypomera, which are dark brownish to somewhat purple in some specimens. Body rounded, convex. Head micro reticulate between punctures; punctation about as large as eye facets, shallow and sparse, nearly 2 diameters apart. Eyes with inner margin slightly diverging apically. Antenna 9-segmented very similar to *O. lafertei* (Fig. 5.169). Terminal maxillary palpomere with sides nearly parallel; the apex moderately oblique with outer side about 1.5 times longer than wide; terminal labial palpomere slightly elongate; about 2 times longer than basal width; slightly shorter than preceding segment. Pronotal surface micro sculptured between punctures; the sculptures somewhat different and much weaker than in head, rugose on disc and reticulate on anterior angles; punctation about as large as eye facets, as shallow as on head, approximately 1.5 to 2 diameters apart; the punctures not confluent on anterior angles, getting only deeper and sparser (Fig. 5.191); anterior angles without distinct strigae; lateral borders slightly oblique; bordering line interrupted at base, the line visibly bordering the entire lateral border in some specimens; prosternum very long in front of coxae, about 2 times the prosternal process widest width; hypomeral foveae vestigial; hind tibiae with outer tooth; tarsal claws distinctly appendiculate. Elytral surface sculptured as on pronotum; punctation more conspicuous than on pronotum; slightly deeper and sparser; lateral margin slightly reflexed; with clear bead; epipleural foveae conspicuous. Abdomen with 5 ventrites; 5th rounded at apex, somewhat oval; surface of ventrite 1 polished between postcoxal lines; postcoxal lines joined at middle, running parallel to posterior margin of ventrite (Fig. 5.177); apical border of intercoxal process conspicuously swollen. Tegmen relatively short, slightly longer than 1/2 the abdomen length; penis guide symmetrical, slightly longer than parameres; parameres densely setose at apex, strut as long as tegmen; penis as in *O. lafertei*. Female externally identical to male.

Types: Orcus punctulatus: lectotype: "4430 T Qu; Orcus punctulatus Black/" (BMNH); paralectotype: "N. Queensland, Blackburn coll.; 4430, Orcus punctulatus Blackb, co-type" (1, SAM). *O. beneficus*: lectotype, here designated: "Merauke Dr. Koth 1904/ Orcus beneficus m" (ZMB).

Material examined: Australia: H.J. Carter coll. (2, MVM). Northern Territory: Arnhem Land, Yirrkala, 3-6.viii.1948, R, Miller (1, USNM); Darwin (3, ANIC; 5, SAM); Darwin, Casuarina Beach Reserve (12°21'S, 130°52'E), 27.i.1991, Wells (1, NTMD); Limestone Gorge (16.02S 130.23E), 23-25.vi.1986, M. Malipatil (NTMD); Winnellie, Sandgroves Creek, feeding on *Silvestrapis* sp. on *Pandanus*, 15.iii.2000, L. Zhang (5, NTDA); Berry Springs, Lot 15 Southport Road, 14.xi.2002, D. Chin (1, NTDA); Jabiru, Town Lake (15.40S 135.53E), 16.ii.1991, Wells & Webber (1, NTMD); Tipperary Station Brock's Ck., 10.iv.1929, T. Campbell (1, ANIC); Matranka Homestead (14°55'S, 133°08'E), thermal springs, 25.viii.1981, palm leaf, B. Lowery (1, ANIC). Queensland: Cairns (16°55'S, 145°46'E), Lea (1, SAM); Heathlands (11.45S 145.35E), 15-26.i.1992, sweeping heath, T. Weir & I. Naumann (1, ANIC); Torres Strait: Moa Island, Kubin, (10.15S 145.18E), 7.vi.1990, ex. *Pandanus,* J. Grimshaw (5, NAQS); Badu Island (10°07'S, 142°07'E), 17.i.1997, J. Grimshaw (1, NAQS). Western Australia: H.J. Carter coll. (1, MVM); Broome (17.58S 135.14E), x.1994, T. Willing (QECB)

Biology. Nothing known beyond the label data listed above.

Distribution. Widely distributed in northern parts of Australia (Fig. 5.207) and New Guinea.

Orcus quadrimaculatus Gadeau de Kerville

(Figures 5.46, 5.157, 5.159, 5.160, 5.166, 5.171, 5.179, 5.200)

Orcus quadrimaculatus Gadeau de Kerville, 1884: 75.

Diagnosis. The presence of two maculae on each elytron (Fig. 5.46) immediately distinguishes this species from the other Australian *Orcus.*

Description. Length 4.7-5.3 mm; TL/EW = 1.1-1.2; PL/PW = 0.4-0.5; EL/EW = 0.9-1.0. Male. Dorsal surface predominantly metallic dark bluish; each elytron with 2 orange maculae as in Figure 5.46; antennae, labial palp, and last four abdominal ventrites yellowish; rest dark brown. Body elongate, somewhat flattened. Head micro reticulate between punctures; punctation smaller than eye facets, very shallow, almost indistinct, nearly 2 diameters apart. Eyes with inner margin slightly diverging apically. Antennae 8-segmented (Fig. 5.171); pedicel about as long as greatest width; 3rd antennomere longer than pedicel; 8th elongate, 2 times longer than basal width. Terminal maxillary palpomere very narrow (Fig. 5.166); sides nearly parallel; apex oblique with outer side about 2 times longer than inner; terminal labial palpomere slightly elongate, about 2 times longer than basal width, visibly shorter then preceding segment. Pronotal surface sculptured as on head; punctation about as large as eye facets; as shallow as on head, approximately 1.5 to 2 diameters apart; the punctures obsolete on anterior angles; anterior angles without distinct strigae; lateral borders rounded; bordering line uninterrupted at base, the line slightly opening anteriorly, ending in a weak depression before lateral border; prosternum short in front of coxae about 1.5 times longer than prosternal process widest width; hypomeral foveae absent; hind tibiae with outer tooth; tarsal claws weakly appendiculate. Elytral surface polished between punctures; punctation as on pronotum, slightly deeper; lateral margin slightly reflexed, without clear bead; epipleural foveae absent. Abdomen 6 ventrites; 6th short, straight to slightly emarginate at apex; surface of ventrite 1 somewhat microstriate between postcoxal lines; postcoxal lines joined at middle, running parallel to posterior margin of ventrite, almost reaching lateral margin; apical border of intercoxal process flat. Tegmen (Figs 5.159, 5.160) relatively long, about as long as abdomen length; penis guide symmetrical, distinctly longer than parameres; parameres densely setose at apex, the setae short; strut about 1/2 the tegmen length; penis as in Figures 5.157 and 5.179. Female externally identical to male, except having only 5 visible abdominal ventrites; 5th ventrite rounded, somewhat oval.

Types. Author gives “Rockhampton" as type locality. In the Sicard collection there are many specimens of this species apparently including the original “types” of Kerville. The pinned male from Rockhampton is selected as the lectotype (MNHN).

Comments. Orcus quadrimaculatus appears to be a rare species of very limited distribution in New South Wales. Most of the specimens so far seen are of considerable age and come from the Sydney area. Unpublished notes by R.D. Pope refer to specimens that were taken at Heathcote in 1970 by D. K. McAlpine, but that material has not been located at the Australian Museum. In view of currently known distribution the type locality “Rockhampton” must be regarded as erroneous.

Biology. Unknown.

Material examined. New South Wales. Sydney, Lea (SAM); Koebele (BISH); Wahroonga (ANIC); Cronulla, H. J. Carter (1, MVM); Maroubra (SAM); without locality (1, ANIC; 1, SAM; 1, BMNH).

Distribution. New South Wales (Fig. 5.200).

TRICHORCUS BLACKBURN

Trichorcus Blackburn, 1892a: 75. Type species, monotypy, *T. cinctus* Blackburn, 1892a.

Diagnostic description. The single included species is instantly recognized by its hirsute hemispherical form and brown-grey coloration (Fig. 5.22). Head transverse; eye not emarginate; temple distinct, shorter than eye. Antenna 10-segmented, short; scape asymmetrical; terminal antennomere longer than penultimate one (Fig. 5.172). Clypeus short, weakly emarginate medially and extending laterally below eyes (Fig. 5.29); labrum partially exposed. Maxillary palp moderately long, last palpomere securiform with oblique apex (Fig. 5.168); labial palp stout, terminal palpomere as broad and as long as the penultimate segment. Pronotal base bordered medially, the bordering line continues uninterrupted and is separate from fine marginal line; prosternum moderately long in front of procoxae; prosternal process narrow, without carinae; hypomeral fovea near anterior angles of prosternum absent. All tibiae simple externally; meso- and metatibiae with apical spurs; claw strongly appendiculate. Elytral margin weakly reflexed without clear bead (Fig. 5.24); epipleuron descending without foveae. Abdomen with 6th ventrite visible in male; postcoxal lines separated at middle, each running parallel to posterior margin and abruptly recurving apically (Fig. 5.176). Female genitalia: unknown. Male genitalia: penis guide symmetrical; penis capsule well developed.

Discussion. This genus is unlike any other member of Chilocorini due to the densely setose body.

Distribution. Monotypic genus known only from New South Wales.

Trichorcus cinctus Blackburn

(Figures 5.22, 5.24, 5.29, 5.168, 5.172, 5.173, 5.176, 5.181, 5.182)

Trichorcus cinctus Blackburn, 1892a: 73,

Description. Length 5.9 mm; TL/EW = 1.08; PL/PW = 0.42; EL/EW = 0.88. Male. Surface brownish. Pronotum yellowish on anterior angles and across anterior margin. Body hemispherical, densely covered by silky yellowish pubescence. Head somewhat flat between eyes; polished between punctures; punctation about as large as eye facets, very dense and relatively deep, nearly 1/2 diameters apart. Clypeus weakly emarginate; slightly reflexed laterally. Eyes dorsally separated by slightly less than 2 times the width of an eye; inner ocular margin nearly parallel. Antennomeres 3-8 transverse, gradually increasing in width; 9th 2 times longer than 8th; 10th very long, as long as 7th, 8th and 9th combined. Clypeus weakly emarginate; slightly reflexed laterally. Terminal maxillary palpomere subsecuriform, moderately expanded toward apex; apex strongly oblique with outer side about 2 times longer than inner; terminal labial palpomere broad, somewhat barrel-shaped, as long as penultimate segment. Pronotal surface polished between punctures; punctation smaller than eye facets, approximately 2 to 3 diameters apart, getting deeper and more concentrated on anterior angles; lateral borders truncate. Elytral surface coriaceous; the punctation stronger than on pronotum, slightly deeper and more concentrated, about as large as eye facets, larger on lateral margin; lateral margin not reflexed. Abdomen with ventrite 6 fairly visible, conspicuously emarginate. Tegmen (Fig. 5.182) very long, about as long as abdomen length; penis guide symmetrical; distinctly longer than parameres; parameres densely setose at apex, the setae long; strut short, about 1/2 the tegmen length; penis as in Figure 5.181. Female unknown.

Types. “Type/ 4242 NSW T [handwritten]/ Trichorcus cinctus, Blackb/ Australia Blackburn Coll. B.M. 1910-236” (Lectotype, here designated, BMNH). No more specimens have been located either in BMHH or SAM. A single example exists today among Koebele’s collection (BPBM), but there is no indication that is was actually seen by Blackburn.

Distribution. It was bred by Koebele from pupae found on Moreton Bay Fig (*Ficus macrophylla)* (Koebele, 1893), who considered it to be a coccid feeder. Blackburn recorded the locality as “near Sydney”, Koebele as “on the Clarence River, New South Wales”.

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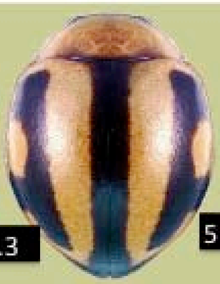

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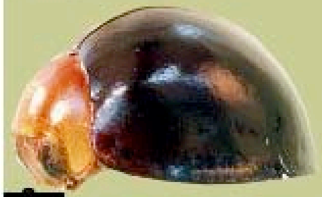

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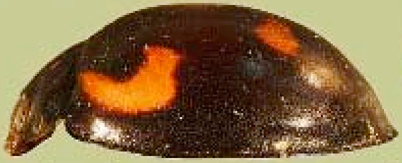

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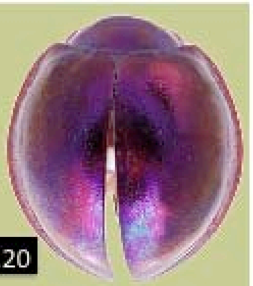
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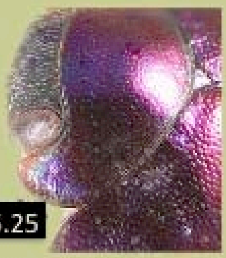
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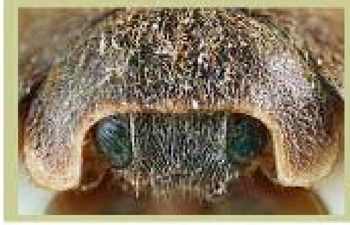
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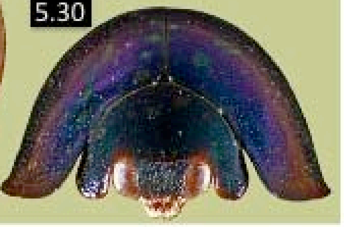
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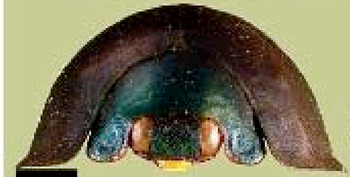
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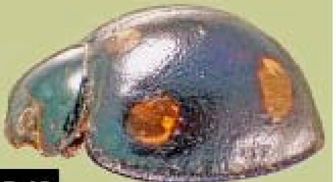
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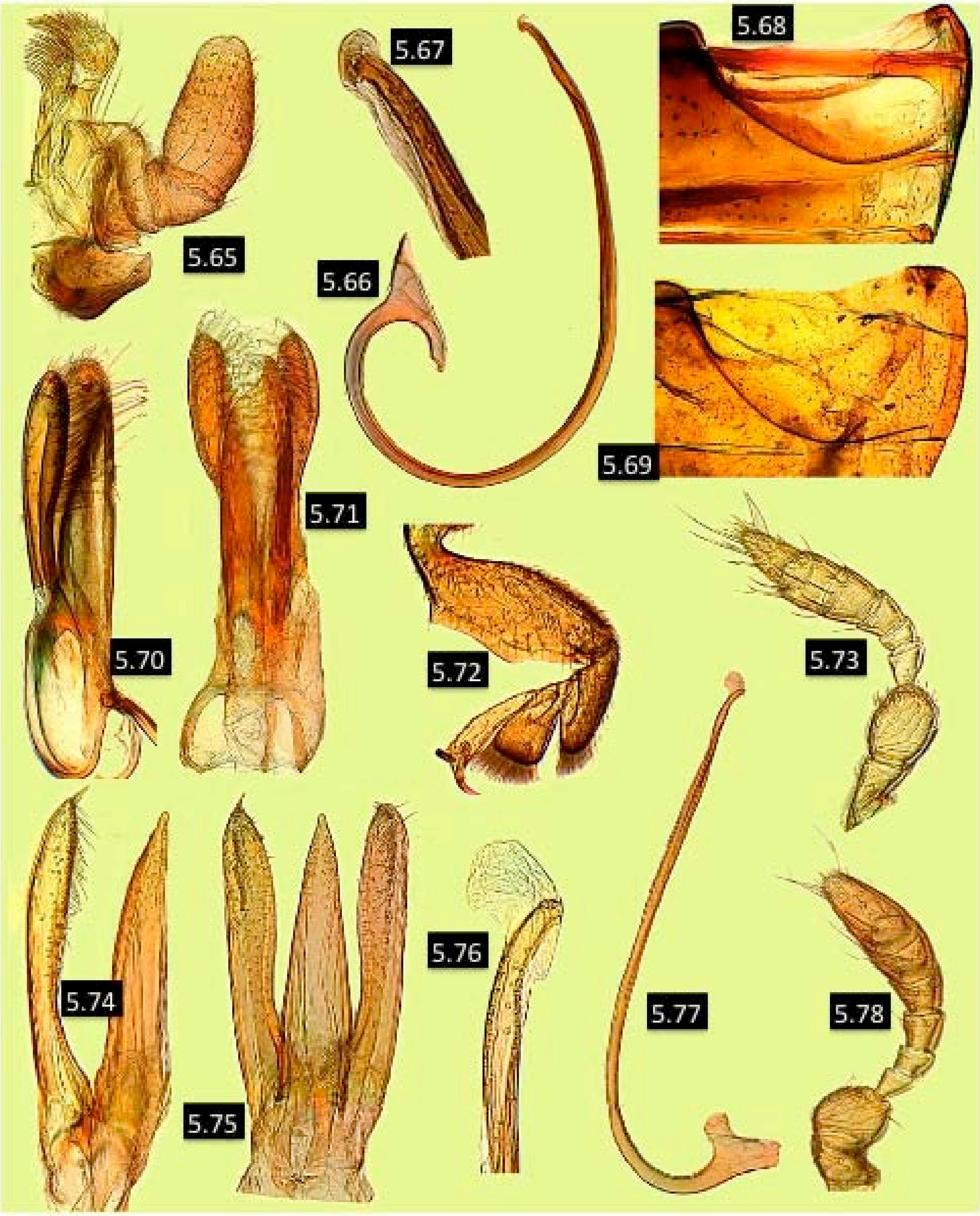
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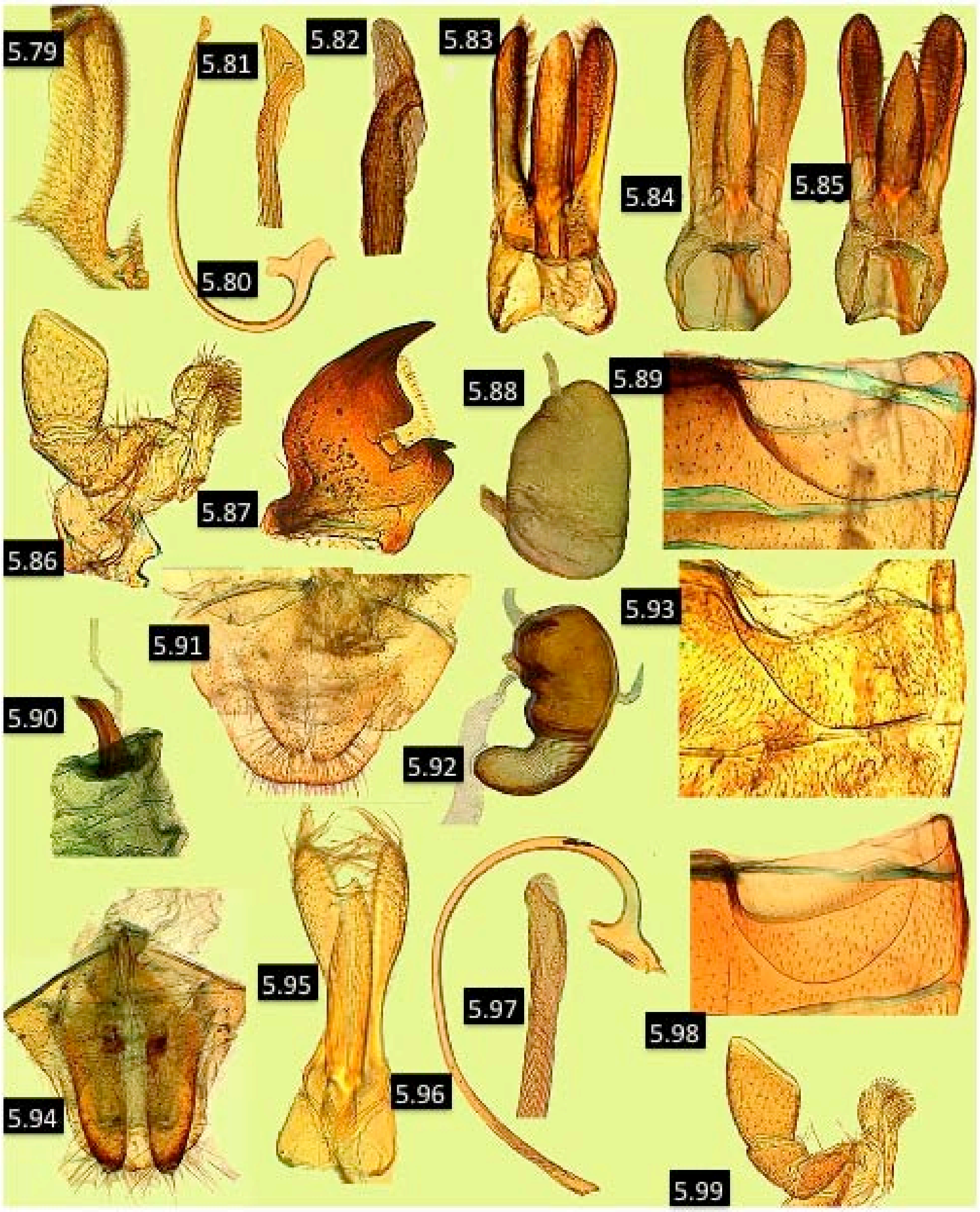
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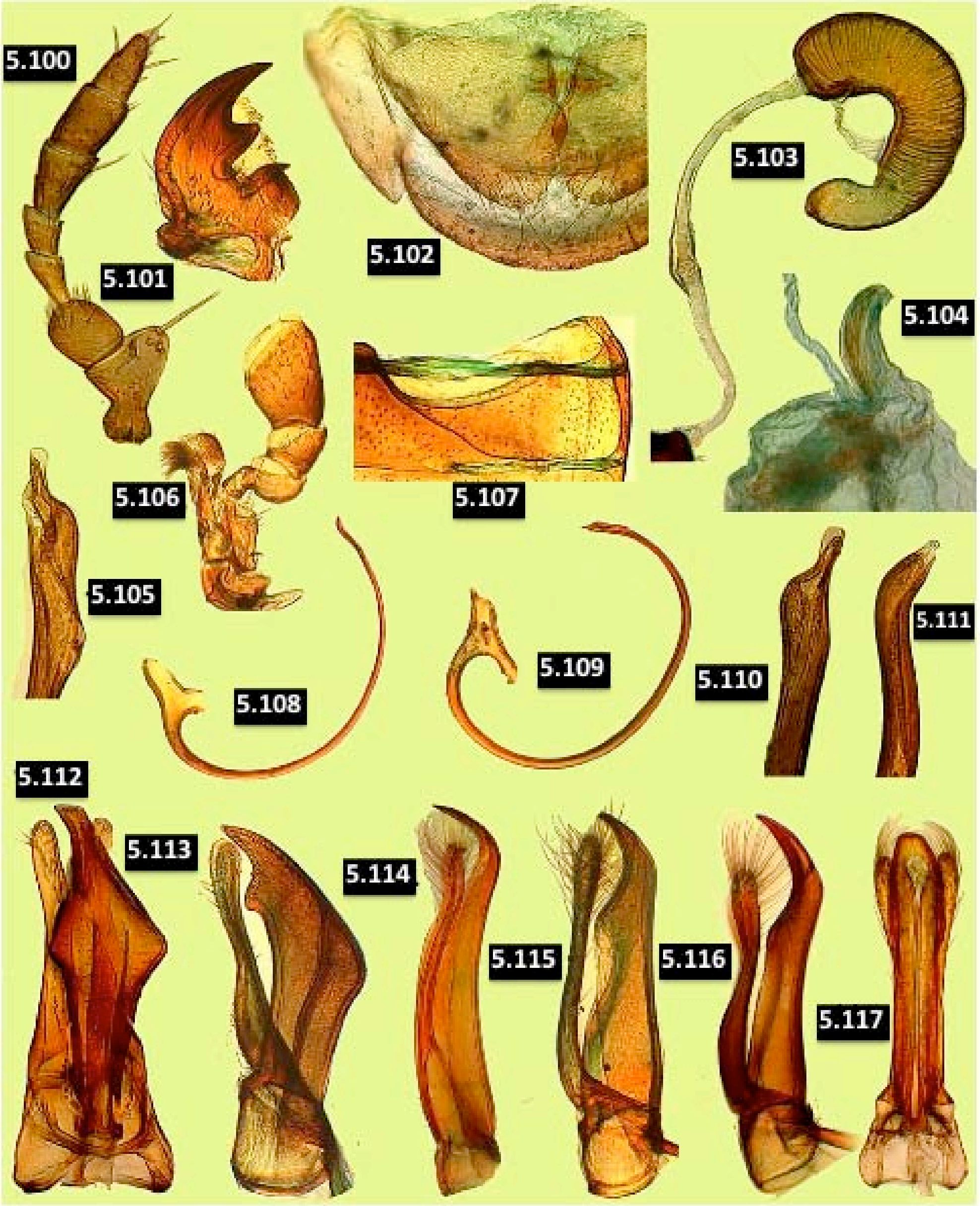
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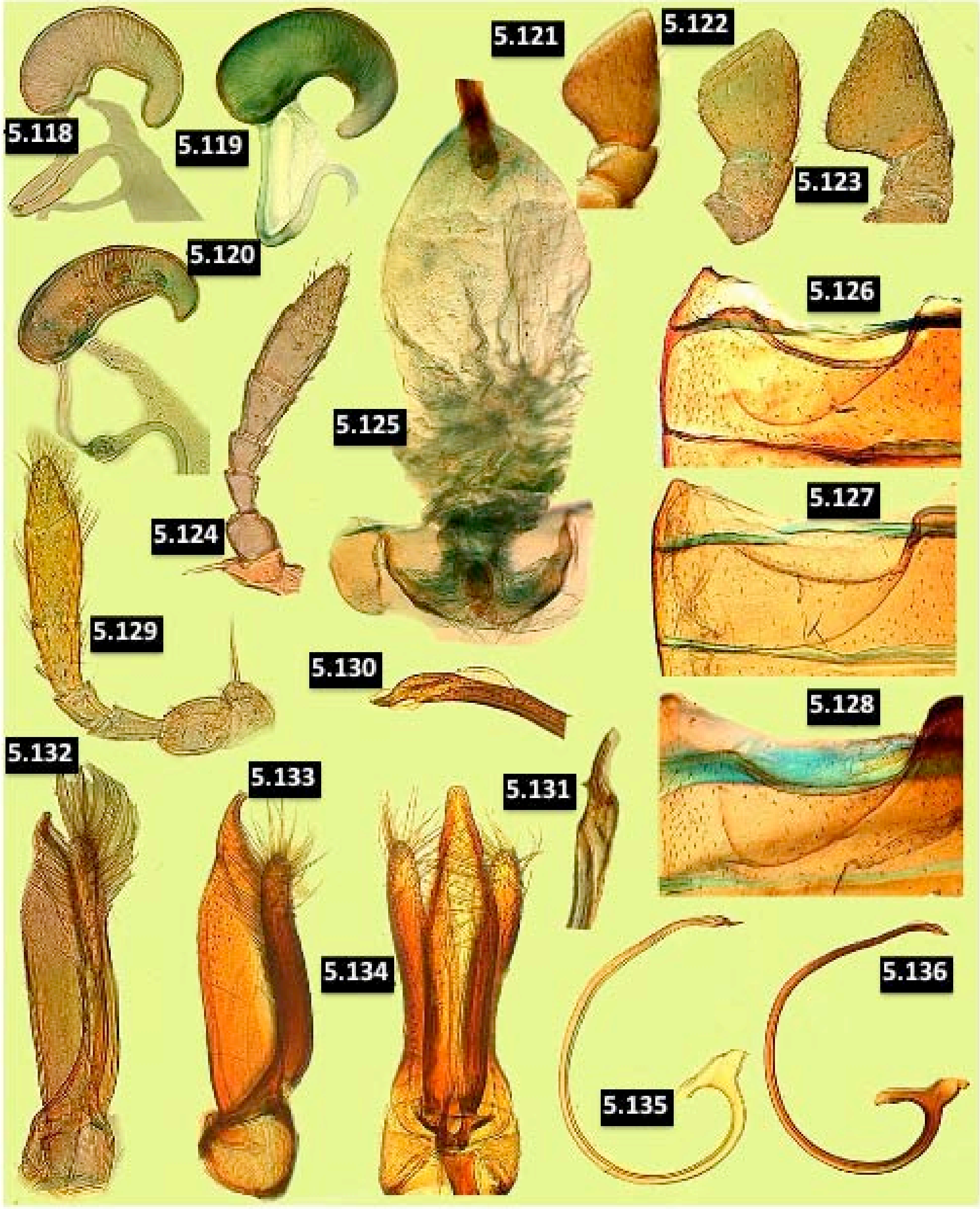
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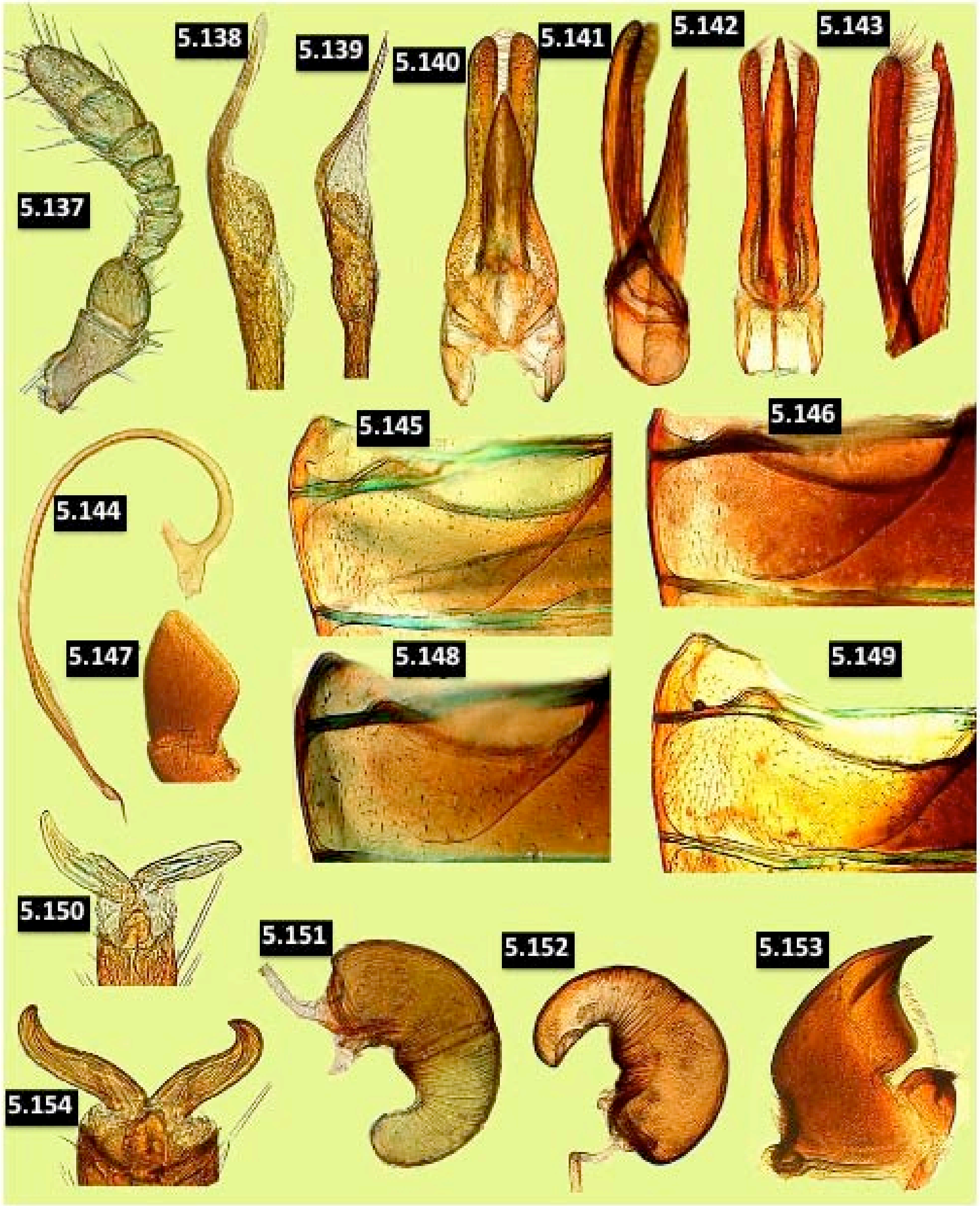
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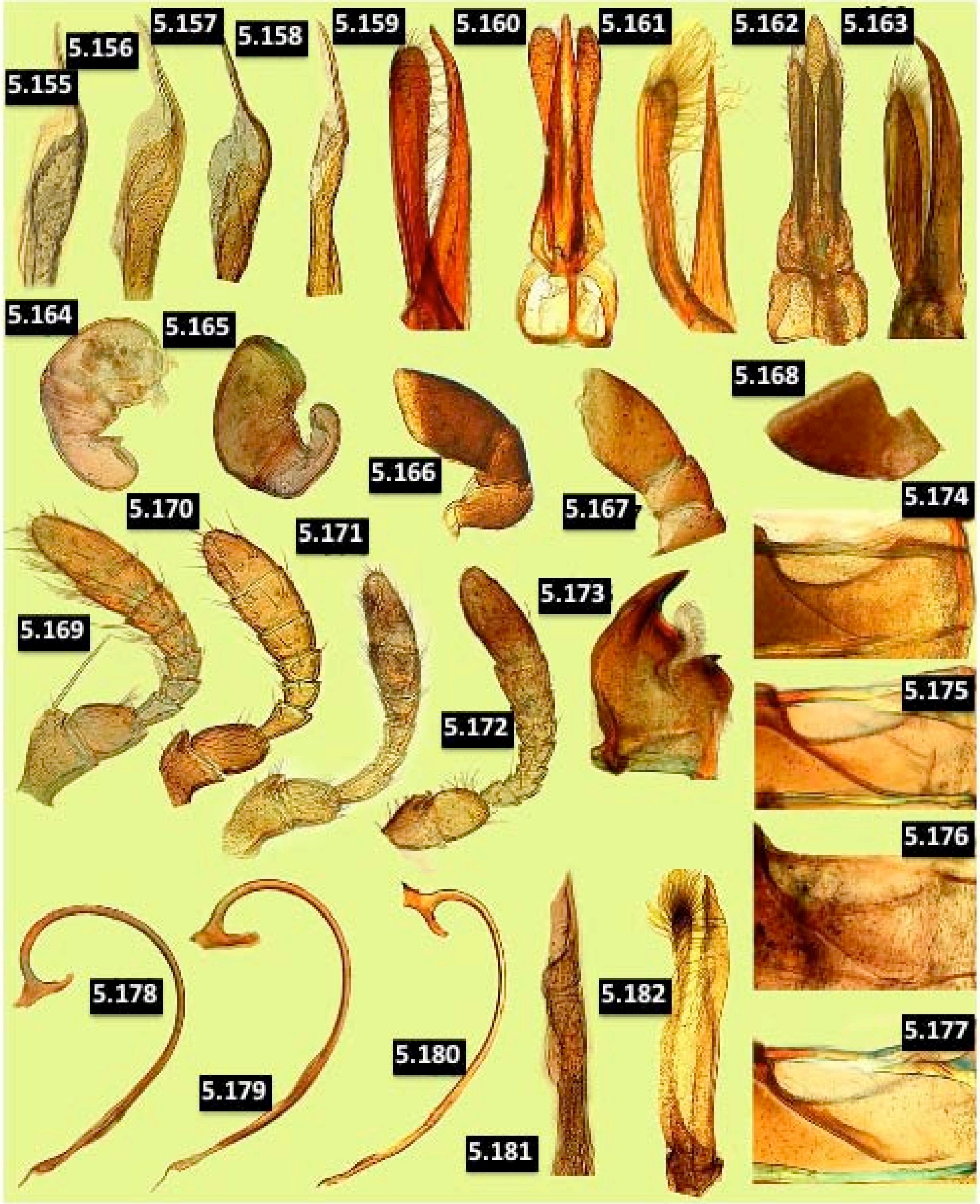
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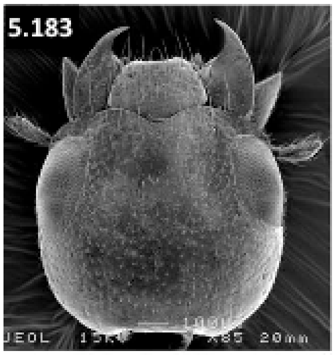

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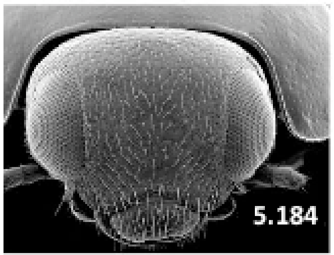

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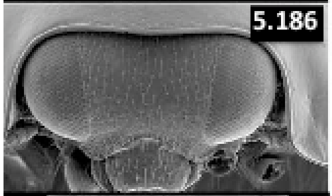

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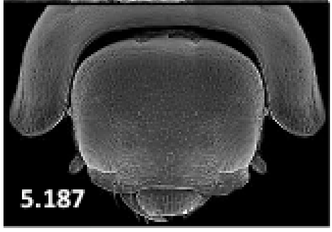

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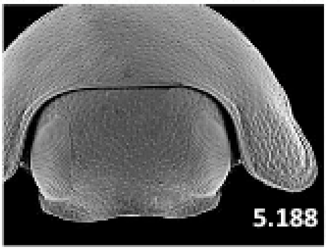

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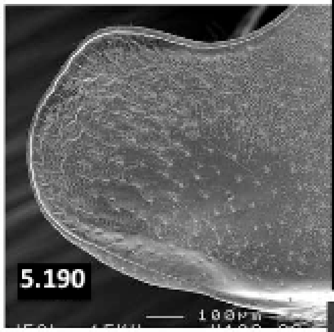

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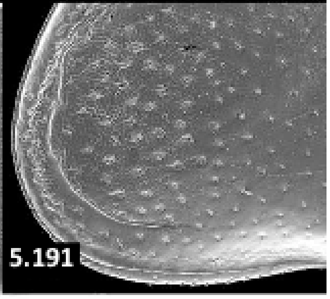

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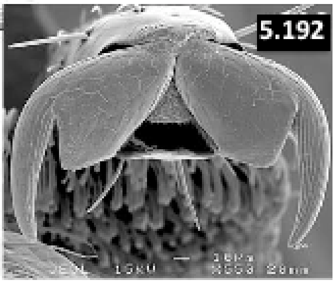

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CHAPTER 6

SUMMARY AND CONCLUSIONS

Despite the familiarity and economic significance of Coccinellidae, the family has thus far escaped analysis by rigorous phylogenetic methods. As a result, the internal classification remains unstable and there is no framework with which to interpret evolutionary events within the family. We analyzed coccinellid phylogeny using a combined dataset of seven genes: 12S rDNA, 16S rDNA, 18S rDNA, 28S rDNA, Cytochrome oxidase I, Cytochrome oxidase II, and Histone 3. The entire dataset consists of 6565 aligned nucleotide sites, 1305 of which are parsimony informative. Our study included 20% of the generic-level diversity and 80% of the tribal-level diversity and 100% previously recognized subfamilies. We analyzed the dataset using parsimony and Bayesian methods. Our study supports the monophyly of Coccinellidae; however, most of the traditional subfamilies are not supported as monophyletic. Three recently proposed, but not widely accepted, subfamilies are recognized. A new subfamily is proposed to accommodate Monocorynini. We recognize eight subfamilies of Coccinellidae: Microweiseinae, Monocoryninae (**new subfamily**), Coccinellinae, Chilocorinae, Sticholotidinae, Scymninae, Exoplectrinae, and Hyperaspidinae. The circumscription of Hyperaspidinae (Hyperaspidini Mulsant, Brachiacanthini Mulsant and Selvadiini Gordon) is extended to accommodate Platynaspidini Redtenbacher and Aspidimerini Mulsant. The tribe Coccinellini Latreille is paraphyletic with respect to Tytthaspidini Mulsant (**syn. nov.)** and Halyziini Mulsant (confirmed status). The tribes Noviini Mulsant, Cryptognathini Casey, Poriini Mulsant, and

Diomini Gordon are treated as *incertae sedis*. The relationship between some of the subfamilies and the placement of several tribes remain ambiguous. We also utilized the phylogenetic hypothesis to provide an evolutionary perspective on the feeding preferences of coccinellid. Coccinellids exhibit a wide range of preferred food types, spanning kingdoms and trophic levels. Our study suggests that the ancestral feeding condition for the family is coccidophagy and that polyphagy served as an evolutionary stepping stone for primarily predaceous groups to adopt new feeding habits.

The Australian members of the ladybird beetle tribe Chilocorini are revised. Identification keys for genera and species are provided. Habitus and diagnostic characters from mouthparts, legs, and genitalia are illustrated. Major conclusions of the present include recognition of the following: (1) five new species; (2) eleven junior synonyms at the species level; one junior synonyms at the generic level; (3) sixteen new lectotypes. According to our study, the Chilocorini in Australia consists of 23 species classified in 6 genera: *Brumoides, Chilocorus, Exochomus, Halmus, Orcus* and *Trichorcus*.