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The evolution of food preferences in Coccinellidae

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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.

1. 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. 1-8, Table 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). 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).

1.1. 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. 1-5). 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. 6-9) (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).

1.2. 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 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 2), none of which are easily reconciled (Vandenberg, 2002).

1.3. 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. 10-11), not generated by formal phylogenetic methods. The relationships proposed by Sasaji (1968; 1971a, b) have received widespread acceptance. Under this hypothesis (Fig. 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. 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.

2. Materials and methods.

2.1. 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) 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.

2.2. 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 4.8a + 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 for accession numbers).

2.3. 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.

2.4. 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 4.06, Maddison and Maddison, 2003).

3. Results.

3.1. 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.

3.2. 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. 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. 14). Nodes in the cladograms are numbered for reference in the discussion below.

4. Discussion.

4.1. 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. 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. 13-14). 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. 10-12).

These analyses do not support the monophyly of Sticholotidinae as currently defined (Figs. 13-15). 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. 13-15). 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. 13-15). 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.

4.2. Food preference evolution.

4.2.1. 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. 15).

Scales are the primary prey of most species of Chilocorinae, Coccidulinae, Scymninae and Sticholotidinae (Table 1, Fig. 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. 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.

4.2.2. 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. 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 2, Fig. 15). Interestingly, Aspidimerini and Platynaspidini appear nested in an otherwise scymnine clade that includes the tribes Brachiacanthini and Hyperaspidini (Node B, Figs. 14-15), each of which includes taxa that are polymorphic for coccidophagy/aphidophagy (Table 2, Fig. 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."

4.2.3. 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. 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. 15) are consistent with the food preferences observed in this group, even though they contradict the current classification system.

4.2.4. 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. 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.

4.2.5. 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. 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. 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.

4.2.6. 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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Figure captions

Fig. 1. *Epilachna varivestis* Mulsant. Adult and larva feeding on soybean *Glycine max* (L.). Clemson University, USDA Cooperative Extension Slide Series, www.forestryimages.org.

Fig. 2. *Stethorus* sp. Larva feeding on spider mites. Sonya Broughton, Department of Agriculture & Food Western Australia, www.bugwood.org.

Fig. 3. *Cryptolaemus montrouzieri* Mulsant. Adults feeding on Hawthorn mealybug. Whitney Cranshaw, Colorado State University, www.bugwood.org.

Fig. 4. *Propylea quatuordecimpunctata* L. Adult feeding on aphids. Scott Bauer, USDA Agricultural Research Service, www.forestryimages.org.

Fig. 5. *Psyllobora vigintiduopunctata* (L.). Larva on powdery mildew. Stanislav Krejcik, www.meloidae.com.

Fig. 6. *Harmonia axyridis* (Pallas). Larvae cannibalizing a conspecific larva. Armin Hinterwirth, University of Washington.

Fig. 7. *Hyperaspis* sp. Adult feeding on spurge flower pollen. Whitney Cranshaw, Colorado State University, www.bugwood.org.

Fig. 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. 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. 10. Schematic phylogenetic tree interpreted from the dendrogram and accompanying text of Sasaji (1968, 1971a, b) showing only relationships among lady beetle subfamilies.

Fig. 11. Schematic phylogenetic tree interpreted from Kovář (1996) showing only relationships among lady beetle subfamilies.

Fig. 12. Schematic phylogenetic tree from cladogram published by Yu (1994) showing only relationships among lady beetle subfamilies.

Fig. 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. 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. 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.

Table 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 2. Comparison of higher-level classification systems of Sasaji (1971a), Kovář (1996) and Ślipiński (2007).

Sasaji (1971a)	Kovář (1996)	Ślipiński (2007) (Australian taxa only)
Sticholotidinae	**Sticholotidinae**	**Microweiseinae**
Serangiini	Serangiini	Serangiini
Sukunahikonini	Sukunahikonini	Sukunahikonini
	Microweiseini	Microweiseini
	Carinodulini	
		Coccinellinae
Sticholotidini	Sticholotidini	Sticholotidini
	Plotinini	
	Limnichopharini	
	Cephaloscymnini	
Shirozuellini	Shirozuellini	
	Argentipilosini	
Coccidulinae	**Coccidulinae**	
Coccidulini	Coccidulini	Coccidulini[2]
Exoplectrini	Exoplectrini	
Lithophilini	Lithophilini (as Tetrabrachini)	
	Azyini	
	Cranophorini[1]	
	Monocorynini	
	Ortaliinae	
Noviini	Noviini	Noviini
Scymninae		
Cranophorini		
Ortaliini	Ortaliini	
	Scymninae	
Scymnillini	Scymnillini	Scymnillini
Scymnini	Scymnini	
		Diomini
Aspidimerini	Aspidimerini	
	Selvadiini	
Hyperaspidini	Hyperaspidini	
	Brachiacanthini	
Stethorini	Stethorini	
	Cryptognathini (as Pentiliini)	
Chilocorinae	**Chilocorinae**	
Chilocorini	Chilocorini	Chilocorini
Platynaspidini	Platynaspidini	
Telsimini	Telsimini	Telsimini
Coccinellinae	**Coccinellinae**	
Coccinellini	Coccinellini	Coccinellini[3]
	Tytthaspidini	
Discotomini	Discotomini	
Halyziini (as Psylloborini)	Halyziini (as Psylloborini)	
	Singhikalini	
Epilachninae	**Epilachninae**	**Epilachninae**
Epilachnini	Epilachnini	Epilachnini
	Epivertini	
	Cynegetini (as Madaiini)	
	Eremochilini	

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[1] Includes Oryssomini

[2] Includes Exoplectrini, Scymnini, Stethorini, and taxa near Shirozuellini and Azyini

[3] Includes Halyziini

Table 3. 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
	Brachiacanthini	*Brachiacantha* sp.	FJ687694	FJ687735
		Tiphysa sp.	EU145620	EU145679
	Diomini	*Diomus kamerungensis*	FJ687701	FJ687742
		Diomus notescens	FJ687703	FJ687744
	Hyperaspidini	*Hyperaspidius mimus*	FJ687684	FJ687725
		Hyperaspis lateralis	FJ687685	FJ687726
		Hyperaspis sp. .	EU145611	EU145671/ 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


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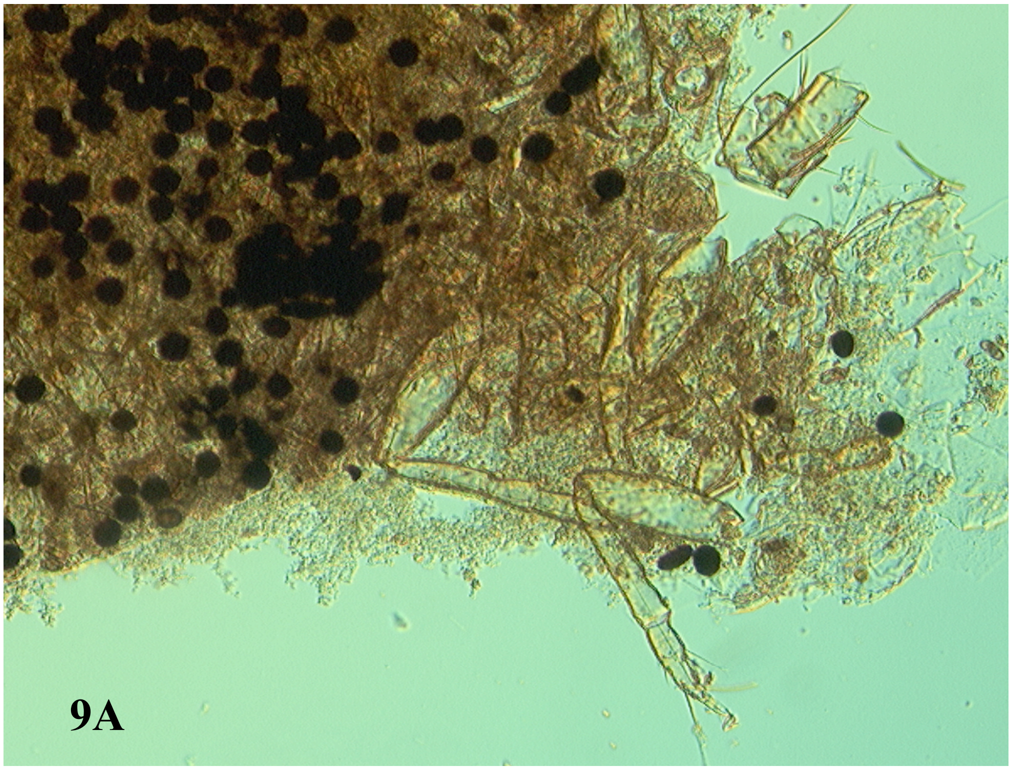
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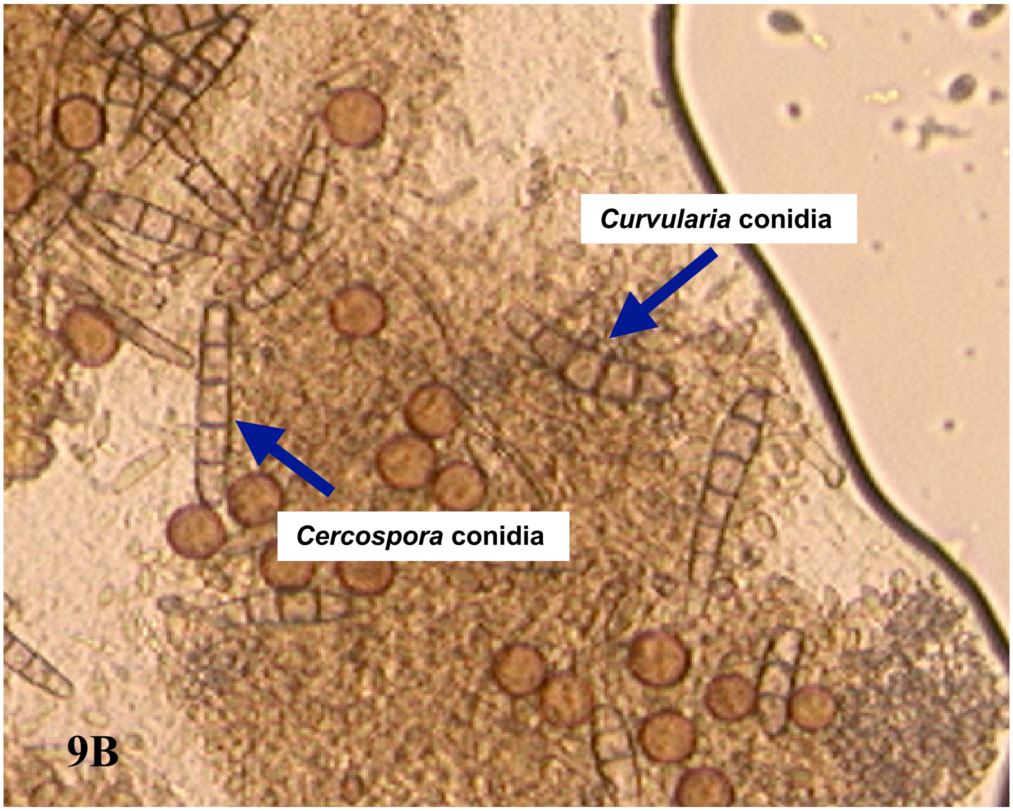
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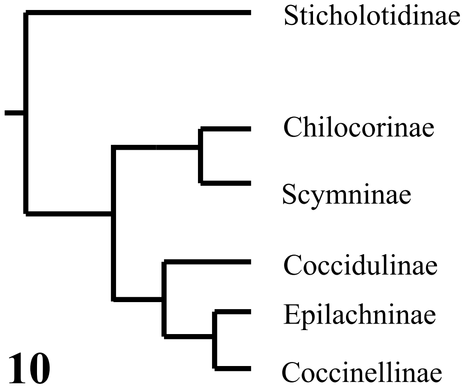
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Epilachninae
Coccinellinae

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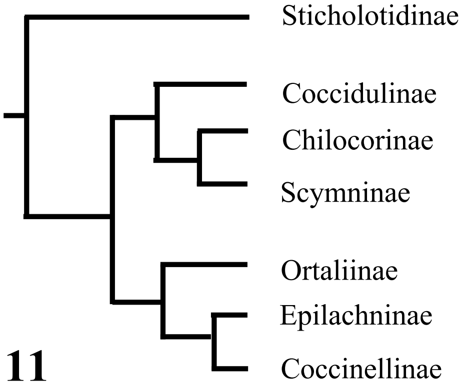
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Coccinellinae

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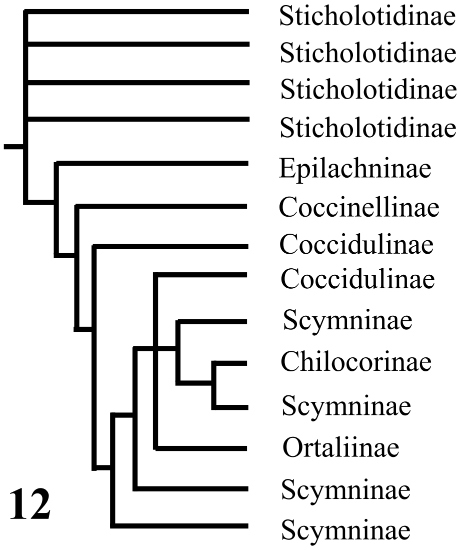
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Scymninae

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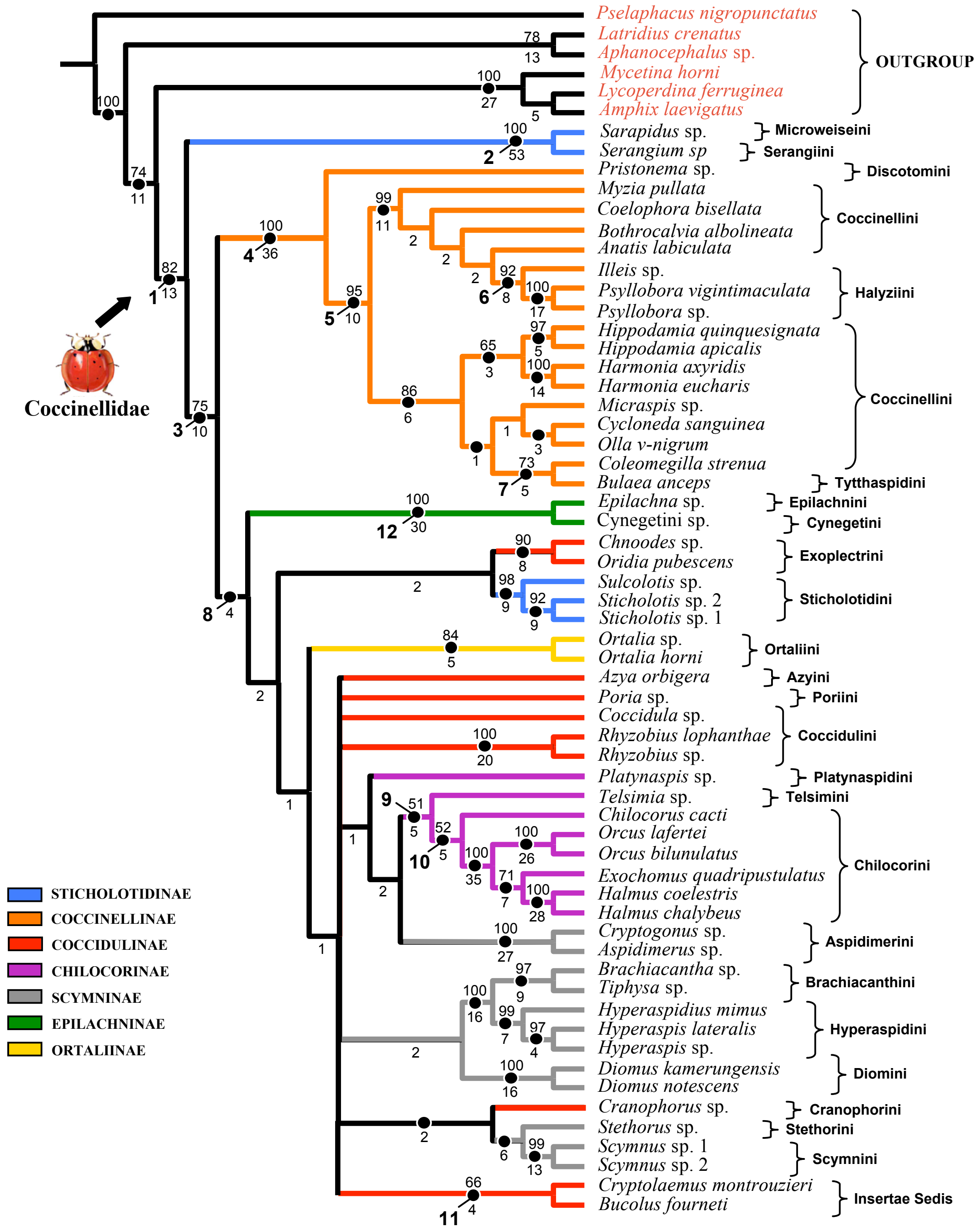
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Microweiseini
Serangium sp
Serangiini
Pristonema sp.
Discotomini
Myzia pullata
Coelophora bisellata
Bothrocalvia albolineata
Anatis labiculata
Coccinellini
Illeis sp.
Psyllobora vigintimaculata
Psyllobora sp.
Halyziini
Hippodamia quinquesignata
Hippodamia 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
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Orcus lafertei
Orcus bilunulatus
Exochomus quadripustulatus
Halmus coelestris
Halmus chalybeus
Chilocorini
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Aspidimerus sp.
Aspidimerini
Brachiacantha sp.
Tiphysa sp.
Brachiacanthini
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Hyperaspis lateralis
Hyperaspis sp.
Hyperaspidini
Diomus kamerungensis
Diomus notescens
Diomini
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Cranophorini
Stethorus sp.
Stethorini
Scymnus sp. 1
Scymnus sp. 2
Scymnini
Cryptolaemus montrouzieri
Bucolus fourneti
Insertae Sedis
Coccinellidae
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12
🟦 STICHOLOTIDINAE
🟧 COCCINELLINAE
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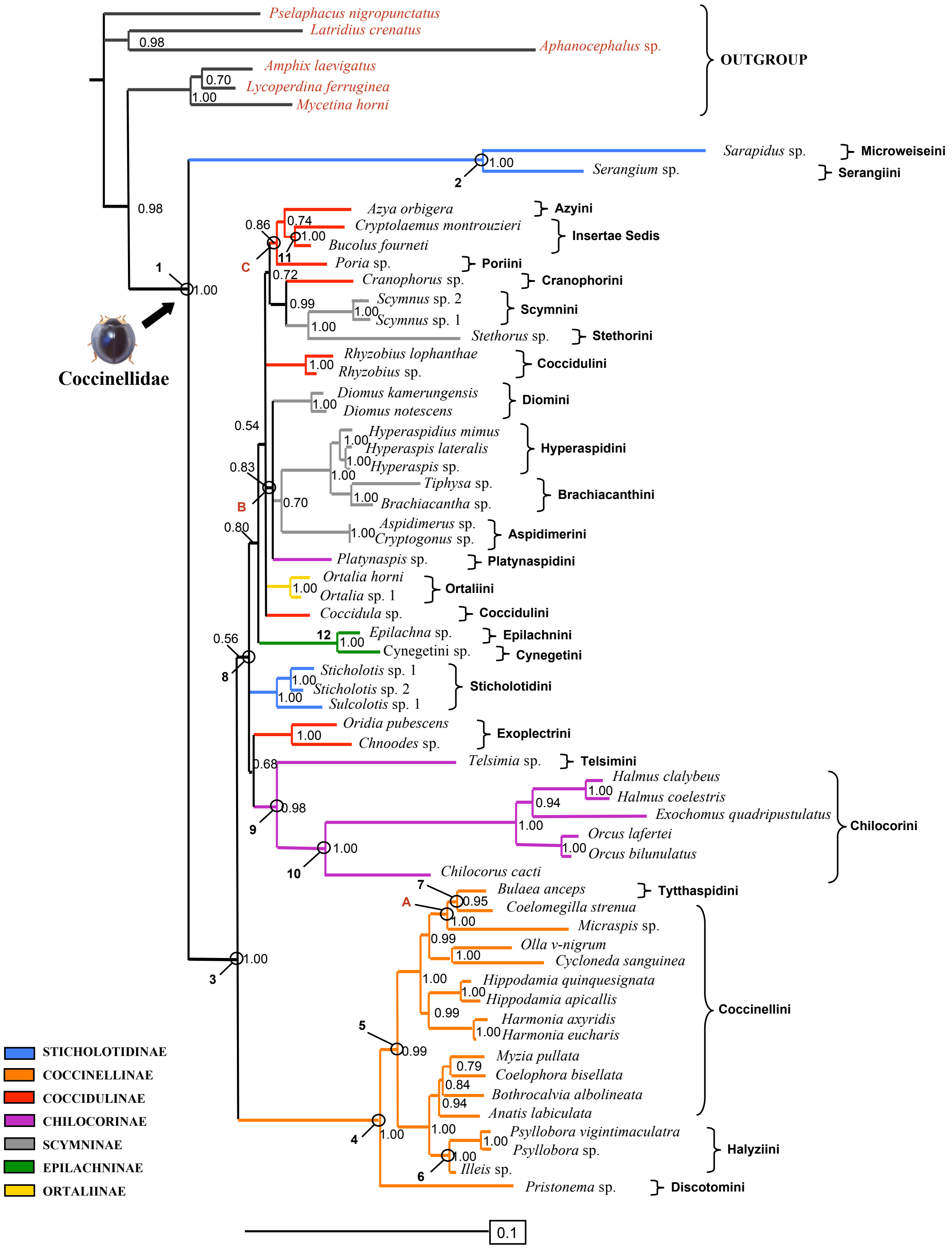
🟩 EPILACHNINAE
🟨 ORTALIINAE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Azyini
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Insertae Sedis
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Cranophorini
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Scymnini
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Stethorini
Coccinellidae
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Coccidulini
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Diomus notescens
Diomini
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Platynaspidini
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Coccidula sp.
Coccidulini
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Sulcolotis sp. 1
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Discotomini
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🟧 COCCINELLINAE
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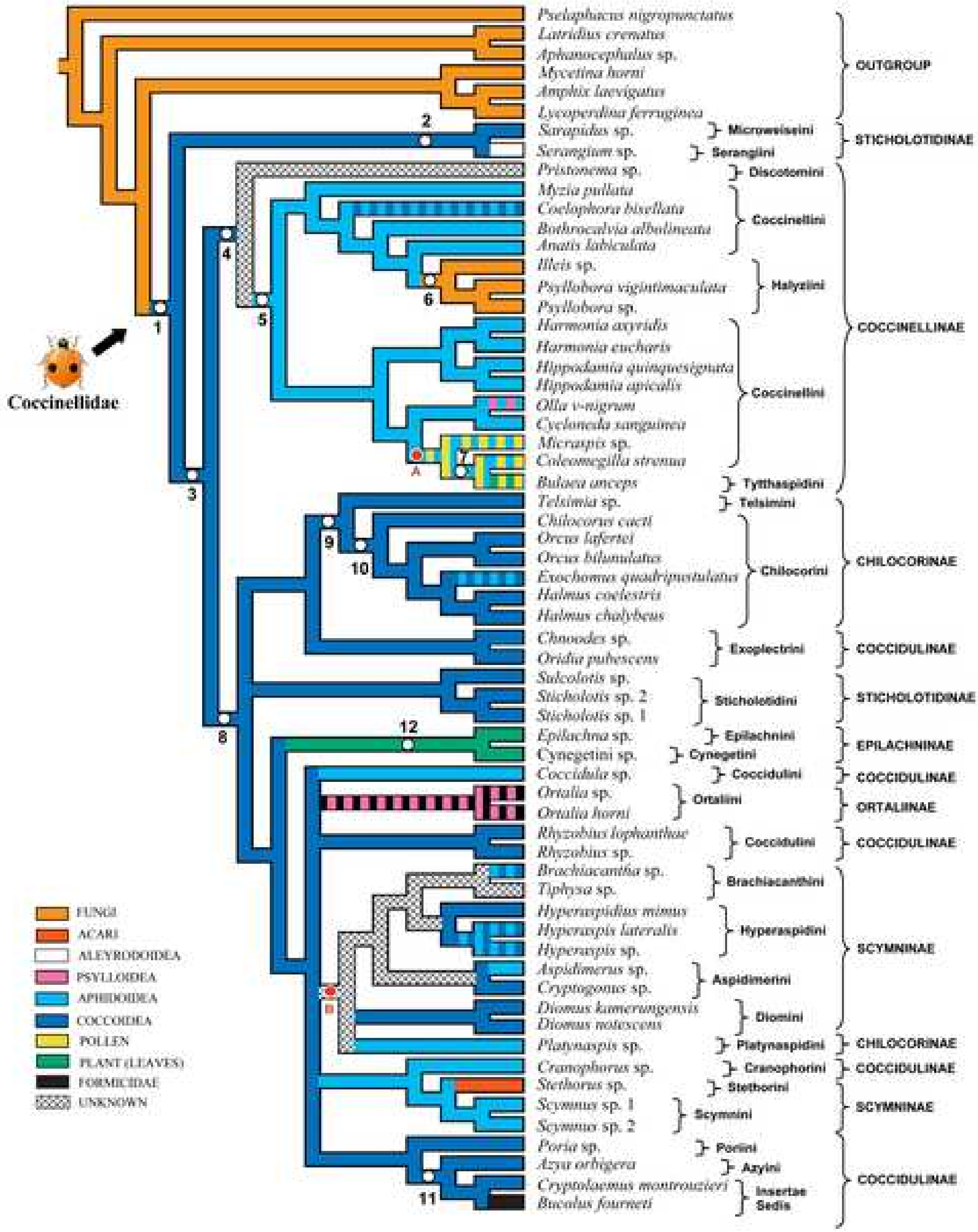
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Discotomini
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Cryptolaemus montrouzieri
Bucolus fourneti
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Azyini
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APHIDOIDEA
COCCOIDEA
POLLEN
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