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The evolution of food preferences in Coccinellidae

José Adriano Giorgi [a,*], Natalia J. Vandenberg [b], Joseph V. McHugh [a], Juanita A. Forrester [a], S. Adam Ślipiński [c], Kelly B. Miller [d], Lori R. Shapiro [e], Michael F. Whiting [f]

[a] Department of Entomology, University of Georgia, 413 Biological Sciences Building, Athens, GA 30602, USA
[b] USDA-ARS, Systematic Entomology Lab, c/o National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC-168, Washington, DC 20013, USA
[c] CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia
[d] Department of Biology, University of New Mexico, 167 Castetter Hall, MSC03 2020, Albuquerque, NM 87131, USA
[e] Department of Entomology, The Pennsylvania State University, 509 Ag. Sciences & Industries Building, University Park, PA 16802, USA
[f] Department of Biology and M.L. Bean Life Science Museum, 693 Widtsoe Building, Brigham Young University, Provo, UT 84602, USA

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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 3957 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 1880s (Caltagirone and Doutt, 1989).

Despite this familiar stereotype of the family, Coccinellidae is far from homogeneous with respect to feeding behavior (Figs. 1–8 and 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). 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), 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). Thus, the evolution of Coccinellidae includes feeding transitions that cross kingdoms of life (plant, animal, and fungus) and trophic levels (e.g., herbivore and 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.),

* Corresponding author.
E-mail address: coccinellid@gmail.com (J.A. Giorgi).

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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 9600 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).

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.