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THE EVOLUTION OF OMNIVORY IN HETEROPTERAN INSECTS

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Abstract. Although omnivory is common and widespread across many animal taxa, the evolutionary origin of omnivory, the selective forces that promote or constrain omnivory, and the morphological, physiological, and behavioral hurdles that animals have to overcome to become omnivores have not been studied. The goal of this paper is to stimulate the development of ideas concerning the evolution of omnivory. We focus on the terrestrial lineages of the insect order Heteroptera and use published life history data and recent phylogenies to test two hypotheses concerning the evolutionary origin of feeding on both plants and prey: (1) that the propensity to feed on seeds and pollen is correlated with the evolution of omnivory, and (2) that broad host range (polyphagy) is correlated with the evolution of omnivory. In order to test these hypotheses, we mapped the plant part consumed and host plant range of insect species in two heteropteran suborders onto their respective phylogenies and used phylogenetically independent contrasts to test for correlations of these traits with omnivory. We found evidence that seed and pollen feeding and broad host ranges are correlated with the evolution of omnivory within both ancestrally herbivorous and ancestrally predaceous lineages of terrestrial heteropterans.

Key words: feeding habits; herbivory; Heteroptera; omnivory; predation; seed and pollen feeding; sister-group comparisons.

INTRODUCTION

Feeding on both prey and plant food is a widespread feeding habit in insects (Whitman et al. 1994, Alomar and Wiedenmann 1996, Coll and Guershon 2002). Thousands of omnivorous insect species occur throughout a broad range of insect taxa, including grasshoppers, earwigs, thrips, true bugs, beetles, and ants. These insects represent a unique blend of morphological, physiological, and behavioral adaptations found in their predaceous and herbivorous relatives. Omnivorous insects in the order Heteroptera (true bugs), for example, possess digestive tracts and accessory salivary glands that are intermediate in length, size, and placement of those found in their herbivorous and predaceous relatives (Slater and Carayon 1963, Goodchild 1966). In addition, many species of omnivorous heteropterans produce protein-digesting enzymes (proteinases and phospholipases) and plant-digesting enzymes (amylases and pectinases) whereas their strictly herbivorous and predaceous cousins produce only a subset (Baptist 1941, Goodchild 1966, Kahn and Ford 1967, Miles 1972, Varis et al. 1983, Cohen 1990, 1996, Schaefer and Panizzi 2000, Wheeler 2001). Omnivorous heteropterans also have piercing-sucking mouthparts (stylets) with characteristics of both herbivorous heteropterans (smooth stylets to penetrate plants) and predaceous heteropterans (toothed or curved stylets for holding prey) (Faucheux 1975, Cobben 1979, Cohen 1996).

The ecological significance of omnivory has historically received little attention. Recent studies, however, suggest that omnivory can deny prey density-related refugia from predation, dictate the strength of top-down control and resulting trophic cascades, alter the stability of food webs, and profoundly influence the movement of energy and nutrients through ecosystems (Polis et al. 1989, Polis 1991, Polis and Strong 1996, Fagan 1997, Holt and Polis 1997, Ostrum et al. 1997, Holyoak and Sachdev 1998, McCann et al. 1998, Rosenheim 1998, Eubanks and Denno 1999, 2000).

Studies of the evolution of omnivory, in contrast, are almost nonexistent in the literature (but see Cooper 2002, Denno and Fagan 2003, Diehl 2003). We know relatively little about the adaptive advantages of omnivory and the selective forces that favor or constrain the evolution of omnivory. The evolution of the morphological, physiological, and behavioral traits associated with omnivory have not been studied and we do not know if these traits evolve as a suite of correlated characters. Further, we know very little about the evolutionary consequences of evolving the ability to feed on both plants and prey. For example, the evolution of omnivory might influence the diversification rate of omnivorous taxa, but questions such as this have not been raised in the literature.

The goal of this paper is to stimulate the development of ideas concerning the evolution of omnivory. Insight into the evolutionary origin of omnivory will help us understand the adaptive significance of

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omnivory and elucidate the morphological, physiological, and behavioral hurdles that animals must overcome to consume both prey and plant food. We focus on the terrestrial lineages of the insect order Heteroptera and use published life history data and recent phylogenies to test two hypotheses concerning the evolutionary origin of feeding on both plants and prey: (1) that the tendency to feed on seeds and pollen is correlated with the evolution of omnivory, and (2) that broad host range (polyphagy) is associated with the evolution of omnivory.

In the evolution of omnivory from an ancestral state of herbivory, the propensity of an herbivorous species to evolve the ability to capture and consume prey may be related to the plant part consumed by the species (Sweet 1979, Cobben 1979). Different parts of the same host plant can vary tremendously in concentrations of nitrogen and nitrogen is an important limiting nutrient for most insects (Strong et al. 1984). Seeds and pollen frequently contain up to 10% nitrogen whereas leaves often contain as little as 0.7% nitrogen. Phloem and xylem tissues contain even less nitrogen than leaves (0.005% and 0.0002%, respectively) (Andrews 1935, Evans 1982, Murray and Cordova-Edwards 1984, Strong et al. 1984, Douglas and Weaver 1989). Plant parts also vary in the concentrations of other nutrients, carbohydrates, defensive allelochemicals, and the type and degree of antiherbivore mechanical defenses (Tamas et al. 1979, Strong et al. 1984, Thomison et al. 1988). As a result, herbivorous insects are usually adapted to feed on a particular part of their host plant or plants (Janzen 1979, Kirk 1985). For example, foliage-feeding species do not produce the digestive enzymes that would allow them to digest the proteins found in seeds and pollen, but these enzymes are produced by their seed and pollen-feeding relatives (Houseman et al. 1984, Kirk 1985, Cohen 1996, Schaefer and Panizzi 2000, Wheeler 2001). Some authors have hypothesized that seed and pollen-feeding herbivores may be preadapted to consume nitrogen-rich prey and, consequently, that lineages of seed or pollen-feeding herbivores will give rise to omnivores more frequently than lineages of foliage-feeding herbivores (Sweet 1979, Cobben 1979). This is predicted on the basis of a nutritional match between nitrogen-rich plant parts and nitrogen-rich prey. Conversely, predaceous lineages of insects are hypothesized to be more likely to give rise to omnivores that feed on seeds and pollen than omnivores that feed on plant foliage because high nitrogen plant parts (seeds and pollen) are nutritionally more similar to prey (Sweet 1979, Cobben 1979). Feeding on seeds and pollen is, therefore, hypothesized to be a transitional state in the evolution of omnivory from both herbivory and predation.

The host range of herbivorous insect species may also affect their propensity to evolve the adaptations necessary for prey feeding (Sweet 1979, Cobben 1979). Host range is defined by the diversity of plant taxa consumed by an herbivorous or omnivorous insect species. The morphological, physiological, and behavioral adaptations associated with polyphagy (feeding on diverse plants representing two or more plant families) may lend themselves to an omnivorous lifestyle. For example, polyphagous insects produce the enzymes necessary to digest a variety of plant species and have the ability to detoxify a variety of allelochemical-based plant defenses (Bernays and Minkenberg 1997). Some authors have suggested that adaptations such as detoxifying enzymes make polyphagous species more likely to consume prey than monophagous species (Sweet 1979, Cobben 1979). Polyphagous herbivores may also have behavioral traits that make it more likely that they will be omnivorous than their monophagous or oligophagous relatives. Polyphagous herbivores move among plants far more often than their monophagous relatives and this may affect their nutrient requirements as well as their predisposition to attack and consume prey (Wheeler 2001). Lineages of polyphagous herbivores, therefore, may be more likely to evolve omnivorous species than are their monophagous relatives. Conversely, omnivorous species that have recently evolved within predaceous lineages are also likely to be polyphagous. Until they undergo selection for specialization on specific plant taxa, these omnivores are unlikely to be very specific about the host plants they consume.

We evaluated these hypotheses by focusing on the life histories and evolutionary history of several terrestrial lineages of the insect order Heteroptera. Terrestrial heteropterans are an ideal group for studying the evolution of feeding habits because they have diverse feeding habits, contain many omnivorous species, have well-known biologies, and have relatively well-established taxonomic and evolutionary relationships. In addition, the three feeding habits have evolved multiple times within this order, with herbivorous lineages giving rise to predators and predaceous lineages giving rise to herbivores (Cobben 1979, Sweet 1979, Schuh 1986, Schuh and Slater 1995, Coll 1998). Heteropterans, therefore, provide a rich biological and historical framework to test ideas regarding the evolution of omnivory.

In order to test our two hypotheses concerning the evolutionary origin of omnivory, we mapped the plant parts consumed and host plant range of insects in two heteropteran suborders onto their respective phylogenies and used phylogenetically independent contrasts to test for correlations between these traits and omnivory.

METHODS

We extracted life history information for 398 species of terrestrial heteropterans distributed in 232 genera, 22 families, and two suborders from 146 published sources (see Appendices). We focused on the terrestrial heteropterans in the suborders Cimicomomorpha and Pentatomomorpha because they include large numbers of herbivores, omnivores, and predators, and because strict herbivory, omnivory, and strict predation have evolved independently multiple times within these groups (Cobben 1979, Sweet 1979, Schuh 1986, Schuh and Slater 1995, Alomar and Wiedenmann 1996). We used the most recent phylogenies for each suborder, Schuh and Stys (1991) for the Cimicomomorpha (Appendix A) and Henry (1997) for the Pentatomomorpha (Appendix B), for our analyses. Both of these phylogenies are based on morphological characters. These two lineages are particularly useful for this study because the Cimicomomorpha is ancestrally predaceous and the Pentatomomorpha is ancestrally herbivorous (Sweet 1979, Cobben 1979, Schuh 1986, Schuh and Stys 1991, Henry 1997). The correlation of seed and pollen feeding and broad host range with the evolution of omnivory in both lineages would suggest that these traits play a pivotal role in the evolutionary transition from herbivory to omnivory and from predation to omnivory.

For each heteropteran species surveyed, we scored the family and subfamily classification, the plant part consumed by the species, and whether or not the species consumed prey. From this information, we characterized the species' feeding habit as strictly herbivorous (consumes only plants), omnivorous (consumes plants and prey), or strictly predaceous (consumes only prey). We also characterized the species host range as monophagous (consumes plants belonging to one genus), oligophagous (consumes plants in two or more genera within the same plant family), or polyphagous (consumes plants in two or more families).

We used two analyses to control for possible phylogenetic nonindependence among heteropteran species. Our approach follows that of Fagan et al. (2002) and all methods are based on the principal of phylogenetically independent contrasts (Felsenstein 1985). The two tests represent each end of the continuum between strictness of correction for similarity due to common ancestry and potential statistical power (Mazer 1998, Ackerly and Reich 1999). We used both liberal and conservative techniques to control for phylogenetic constraints because omnivory has evolved multiple times within multiple heteropteran lineages and is unlikely to be highly conserved (i.e., is phylogenetically labile).

The first analysis partitioned species into a set of family-level groups each containing at least one phylogenetically independent contrast between herbivores and omnivores (sensu Fagan et al. 2002). These groupings corresponded to single, monophyletic taxa in the case of the superfamily Pentatomoidea, the families Berytidae, Miridae, Pyrrhocoridae, and Rhopalidae, and the subfamily Lygaeinae. In other cases, these family-level groups consisted of pairs of sister taxa with different feeding life histories (omnivorous vs. herbivorous; Table 1). This procedure reduced our data to eight family-level groups (Table 1). We then conducted a logistic regression analysis with family group, plant part consumed (foliage or reproductive), and host range (restricted or polyphagous) as predictor variables and feeding habit (herbivory or omnivory) as the dependent variable (SAS version 8.2, Proc Logistic with class statement; Stokes et al. 2000).

TABLE 1. Numbers of omnivores and herbivores used in eight independent contrasts to test for correlations of feeding habit with plant part consumed (foliage vs. reproductive parts) and with host range (monophagy or oligophagy vs. polyphagy).

Taxa	No. omnivores in contrast	No. herbivores in contrast
Miridae	54	66
Pentatomoidea†	28	64
Alydidae + Coreidae	1	14
Rhopalidae	1	3
Pyrrhocoridae	2	7
Berytidae	7	4
Ishnorhynchinae + Orsillinae	1	8
Lygaeinae	3	7

† Includes families Acanthosomatidae, Cydnidae, Pentatomidae, Scutelleridae, and Thyreocoridae.

This analysis corrects for phylogenetic nonindependence among family-level groups, but treats species within these groups as independent and does not control for phylogenetic non-independence at levels above family. The second analysis controls for phylogenetic nonindependence at all levels and is considered a conservative test of correction for similarity due to common ancestry. In this analysis, we reduced the data set further to include only phylogenetically independent contrasts among sister taxa (Ridley 1983, Felsenstein 1985, Harvey and Pagel 1991). This required that we assign a feeding habit to each family-level group. If all species within a group were herbivorous, then we scored that group as herbivorous. If some or all species within the group were omnivorous, then we scored that group as omnivorous. We identified four meaningful phylogenetically independent contrasts using the phylogenies of Schuh and Stys (1991) and Henry (1997): Miridae (omnivorous) vs. Tingidae (herbivorous), Coreidae (herbivorous) vs. Alydidae (omnivorous), Berytidae (omnivorous) vs. Colobathristidae (herbivorous), and Ischnorhynchinae (omnivorous) vs. Orsillinae (herbivorous). We used two 2 × 2 contingency table analyses to test the hypotheses that evolutionary changes in feeding habit were independent of plant part consumed and host range. A significant *G* is evidence that pairs of character states are not independent, but that some combinations of characters are more or less common than expected by chance (Ridley 1983, Harvey and Pagel 1991).

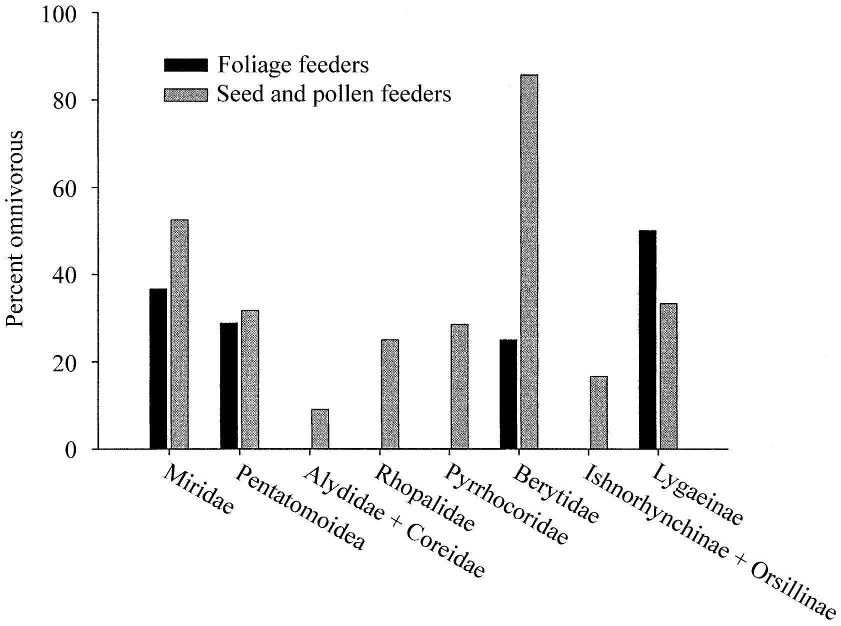

FIG. 1. Percentages of species that are omnivorous among species that feed on foliage or on seeds and pollen, in each of the eight family-level groups used in our logistic regression analysis. Missing bars indicate ''zero'' values.

RESULTS

Feeding on seeds and pollen is correlated with omnivory.—We found strong support for the hypothesis that the evolution of omnivory is correlated with the consumption of seeds and pollen. There was a significant effect of plant part on feeding habit in the analysis that controlled for phylogenetic nonindependence at the level of family group (Wald $\chi^2 = 4.01$, df = 1, $P = 0.045$). Overall, heteropteran species that consumed seeds and pollen were more likely to be omnivorous than foliage-feeding species (Fig. 1). In the Miridae, for example, 53% of the species that fed on reproductive plant parts were omnivorous whereas only 37% of the species that fed on foliage were omnivorous (Fig. 1). This pattern was even more striking in the Berytidae: 85% of the species that fed on seeds and pollen were omnivorous and only 25% of the species that fed on foliage were omnivorous (Fig. 1). The effect of family group in this analysis was not significant (Wald $\chi^2 = 11.10$, df = 7, $P = 0.134$).

We found the same pattern in the analysis that controlled for phylogenetic nonindependence at all levels. In this analysis, taxa that fed on seeds and pollen were significantly more likely to be omnivorous than their foliage-feeding sister taxa ($G = 6.1$, df = 1, $P < 0.025$). In addition, feeding on seeds and pollen appeared to be correlated with omnivory in both the ancestrally predaceous lineage (Cimicomomorpha) (e.g., Miridae in Fig. 1) and the ancestrally herbivorous lineage (Pentatomomorpha) (e.g., Berytidae in Fig. 1).

Polyphagy is correlated with omnivory.—We also found evidence that the host range of a heteropteran species affects its propensity to be omnivorous. There was a statistically significant affect of host range on feeding habit in the analysis that controlled for phylogeny at the family-group level (Wald $\chi^2 = 26.52$, df = 1, $P < 0.001$). This was evident in the Miridae, the Pentatomoidea, the Alydidae + Coreidae, the Berytidae, the Ischnorhynchinae + Orsillinae, and the Lygaeinae (Fig. 2). The opposite pattern was evident in the Rhopalidae and the Pyrrhocoridae (Fig. 2). These results suggest that there may be an interactive effect of family group and host range such that in some groups polyphagous species are more likely to be omnivorous and in other groups monophagous species are more likely to be omnivorous, but our data set was neither large enough nor balanced enough to test this hypothesis statistically. There was a statistically significant effect of family group (Wald $\chi^2 = 14.83$, df = 7, $P = 0.038$), indicating that there was an effect of phylogeny on the distribution of omnivores.

We saw the same pattern in the analysis that controlled for phylogenetic nonindependence at all levels: polyphagous taxa were significantly more likely to contain omnivorous species than their monophagous or oligophagous sister taxa ($G = 6.0$, df = 1, $P < 0.025$). Host range and omnivory appeared to be correlated in both the ancestrally predaceous lineage (Cimicomomorpha) (e.g., Miridae in Fig. 2) and the ancestrally herbivorous lineage (Pentatomomorpha) (e.g., Berytidae in Fig. 2).

DISCUSSION

Our results support the hypotheses that seed and pollen feeding and broad host plant range are correlated with the evolution of omnivory in terrestrial heterop-

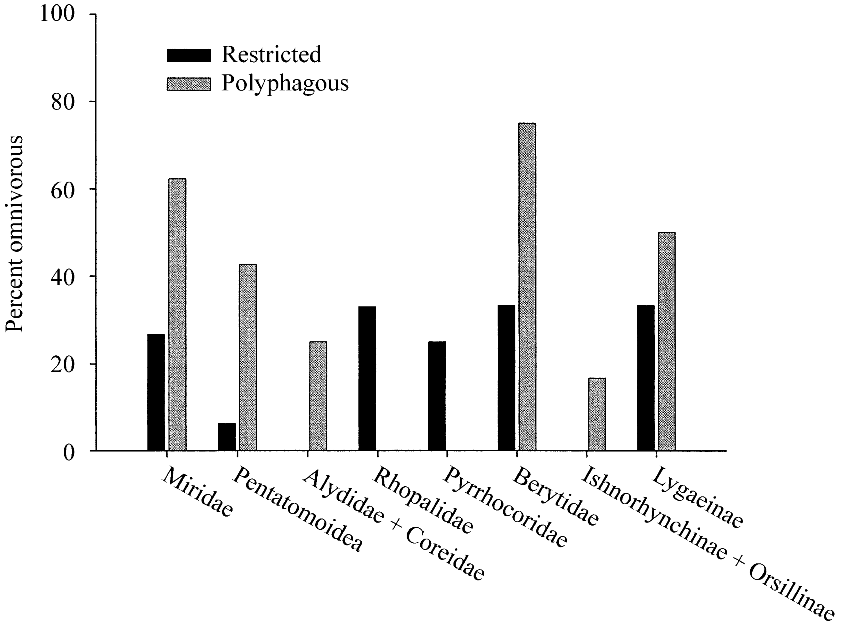

FIG. 2. Percentage of species that are omnivorous among species with restricted host ranges (monophagous + oligophagous) or broad host ranges (polyphagous) in each of the eight family-level groups used in our logistic regression analysis. Missing bars indicate "zero" values.

terans. Heteropteran species that fed on seeds and pollen were significantly more likely to be omnivorous than their foliage-feeding relatives (Fig. 1). Likewise, polyphagous species were significantly more likely to be omnivorous than their relatives with restricted host ranges (monophagous or oligophagous), although this effect may vary to some extent among family-level groups (Fig. 2). These patterns were apparent when we used both liberal and conservative methods to control for the effects of phylogeny on the evolution of omnivory and were apparent in both ancestrally predaceous (Cimicomomorpha) and ancestrally herbivorous (Pentatomomorpha) lineages.

We suggest that seed and pollen-feeding insects are preadapted to consume prey and that predaceous insects are similarly predisposed to consume nitrogen-rich plant parts. Preadapation may be associated with physiological traits. For example, the digestive enzymes produced by seed and pollen-feeding herbivores may be able to digest prey. Similarly, the digestive enzymes produced by predators may be able to digest seeds and pollen. Further, some morphologies or behaviors of seed and pollen-feeding herbivores and predators may be functionally interchangeable. For example, how similar do the mouthparts of omnivores have to be to their herbivorous and predaceous relatives to function adequately in both prey and plant consumption? Do host-plant identification behaviors and mobility associated with polyphagous heteropterans allow them to track prey? To our knowledge, these hypotheses have never been tested; however, questions like these could be addressed by comparative studies of closely related herbivores, omnivores, and predators.

Ecological consequences

The consumption of seeds and pollen as well as polyphagy could dramatically affect the spatial and temporal abundance of omnivorous insects. Omnivores that consume seeds and pollen may be forced to track changes in the abundance of these plant resources in space and time (Eubanks and Denno 1999, 2000). Omnivorous insects are noted for their attraction to pollen and seeds (Kiman and Yeargan 1985, Read and Lampman 1989, Coll and Bottrell 1991, 1992) and some studies even suggest that omnivorous "predators" actually track variation in the production of seeds and pollen more than they track variation in the population size of prey (Cottrell and Yeargan 1998, Eubanks and Denno 2000). The impact of these omnivores on prey is largely dictated by variation in the abundance of seeds and pollen because the presence of high quality plant food not only affects omnivore abundance, but also alters the per capita consumption of prey by omnivores (Cottrell and Yeargan 1998, Eubanks and Denno 2000). Likewise, the abundance of polyphagous plant feeders is affected by spatial and temporal variation in host plants, and polyphagous herbivores are frequently more widespread and abundant than monophagous relatives, especially if the monophagous insects specialize on relatively rare plants (Ehrlich and Raven 1964).

Evolutionary consequences

Omnivory may be a key innovation that leads to taxonomic diversification if the ecological flexibility provided by the ability to consume both prey and plant food allows omnivorous species to be more ''successful'' than their strictly herbivorous or predaceous relatives. We did not have enough data to test this hypothesis statistically, but our preliminary results are intriguing. We found three independent contrasts of omnivorous and herbivorous sister taxa for which we could readily find the number of described species and/or estimates of the number of extant species: Miridae (omnivorous) vs. Tingidae (herbivorous), Coreidae (herbivorous) vs. Alydidae (omnivorous), and Berytidae (omnivorous) vs. Colobathristidae (herbivorous). In two out of the three contrasts, the omnivorous taxa were dramatically more diverse than their herbivorous sister taxa (Miridae vs. Tingidae and Berytidae vs. Colobathristidae). This interesting result suggests that the evolution of omnivory may have profound consequences for the generation of biodiversity.

In conclusion, we found evidence that the evolution of omnivory is correlated with the consumption of seeds and pollen and broad host range within heteropteran insects. Our results suggest that herbivorous species that consume these nitrogen-rich, reproductive plant parts are far more likely to evolve the adaptations necessary to include prey in their diet than their foliage-feeding relatives. Likewise, polyphagous species are more likely to evolve the ability to include prey in their diet than their relatives that specialize on a single or few plant species. Conversely, predators may be pre-adapted to feed on seeds and pollen and may be pre-adapted to have a broad host range. We hope our assessment of the evolution of omnivory in heteropteran insects stimulates the development of ideas concerning the evolutionary origin and consequences of this important feeding habit.

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APPENDIX A

The phylogeny of family relationships in the heteropteran suborder Cimicimomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A1.

APPENDIX B

The phylogeny of family relationships in the heteropteran suborder Pentatomomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A2.

APPENDIX C

Taxonomic placement, host range, plant part feeding preference, and feeding habit of 398 terrestrial heteropteran insects in suborders Cimicimomorpha and Pentatomomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A3.