Underrated Champions

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Asst. Prof. Jacek Szwedo studies the evolution and phylogeny of *Hemiptera*, in particular *Fulgoromorpha, Cicadomorpha and Coleorrhyncha*), the evolution, classification, paleobiology, paleodiversity, paleogeography, and evolutionary scenarios of *Hemiptera* and their relatives *Paraneoptera*. He also conducts research in comparative morphology of modern and fossil *Hemiptera*, based on present-day and extinct faunas, the latter preserved as inclusions in fossilized resin and sedimentary rocks.

The *Hemiptera* order, sometimes known as the "bugs," includes herbivorous aphids and cicadas, as well as certain predatory species of true bugs that feed on the blood of humans and domestic animals (such as bedbugs). In evolutionary terms, *Hemiptera* are some of the most successful insects among all present-day fauna

Their history is long and complex, dating back at least 330 million years. Present-day hemipterans are descended from just a few past evolutionary lines. They differ from other

***Aafrita biladalshama* Szwedo et Azar, 2013 – representative of the extinct *Perforissidae (Fulgoromorpha)* family – preserved in Early Cretaceous amber found in Lebanon. *Perforissidae* were widespread and highly diverse during the Cretaceous, extending as far as Gondwana and Laurasia**

insect orders in that they do not undergo full metamorphosis between larval and adult phases. Instead, their youngsters – known as nymphs – hatch directly from eggs in a form that largely resembles adults; in the majority of cases, the main difference is that nymphs do not have fully developed wings (although in some species the nymphs do not resemble the adult forms).

Hemiptera can be found in all environments: deserts, tropical rainforests, freshwater reservoirs and open oceans, mountain ranges, forest floors, soil, and deep caverns. They include herbivorous, mycetophagous, predatory and hematophagous animals which can act as vectors for plant, animal and human diseases. They vary greatly in size, from 1 mm (such as certain *Heteroptera*: *Anthocoridae* and *Sternorrhyncha*) to very large, such as the empress cicada *Megapomponia imperatoria* (Westwood, 1842), which can reach lengths of 7 cm with a wingspan of over 20 cm. What all insects in the order have in common is the structure of their mouthparts and how they feed. Their mandibles and maxillae are sheathed within a modified labium to form a rostrum – a proboscis capable of piercing tissues and sucking out the liquids.

Representative of the *Hylicellidae (Cicadomorpha)* family from Middle Jurassic strata in Daohugou in China. They are one of the extinct *Clypeata* groups – highly diverse and abundant, and the only evolutionary lineage representing the *Cicadomorpha* suborder in contemporary fauna

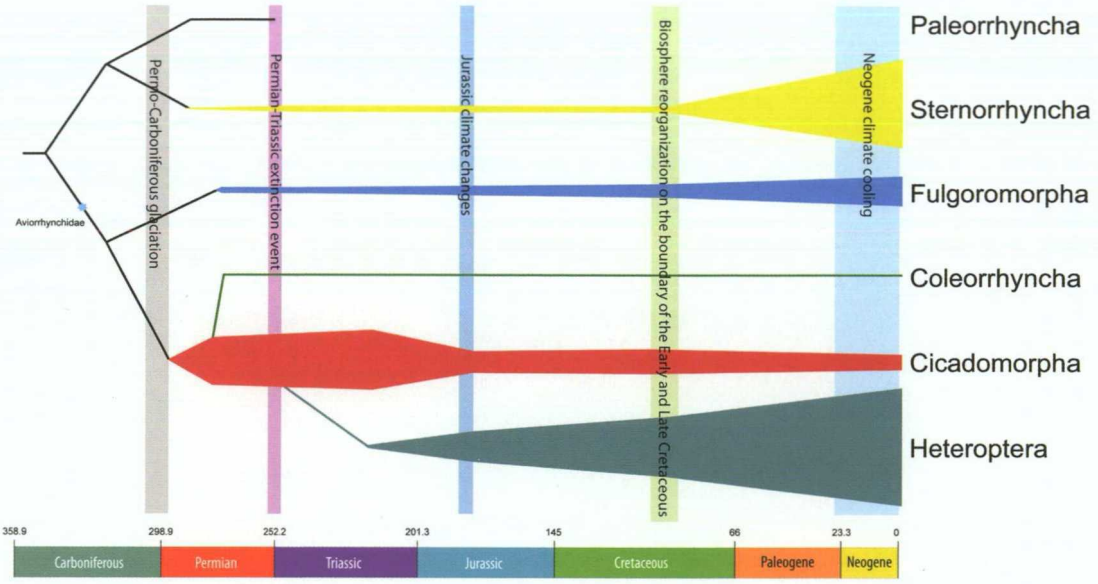
The order comprises six suborders: *Sternorrhyncha*, *Fulgoromorpha*, *Cicadomorpha*, *Coleorrhyncha* and *Heteroptera*, and the extinct *Paleorrhyncha*.

Ancient beginnings and the great boom

The earliest *Hemiptera* date back to the Serpukhovian (lower subsystem of the Carboniferous). They were related to the now extinct *Hypoperlidae*, whose mouthparts were already sufficiently extended and adapted to collecting pollen from seed ferns and early gymnosperms, while their wings resembled those found in the earliest *Hemiptera*. Carboniferous *Hemiptera* specialized in feeding on liquid found in sieve tube elements of plants. Various *Paleorrhyncha* were present during the Permian; they were small insects with an elongated proboscis and ovipositor and simple wings. The most rapid development was seen in the *Hemiptera* lineages, whose diversity and present-day forms arose during the Triassic. At these times ancestors of *Heteroptera* shifted from phytophagy via scavenging to predation. Also *Clypeata* – the only *Cicadomorpha* surviving to the present day characteristic by a developed clypeus and salivary pump muscles, which allowed them to transition to feeding on the contents of the xylem – appeared and diversified during the Triassic. Their symbionts likely specialized around the same time. The Jurassic marks the rapid development of aphids, *Fulgoromorpha* and *Clypeata*. *Heteroptera* include all infraorders, as well as secondary herbivorous forms; while *Nepomorpha* have always been aquatic, representatives of the *Gerromorpha* infraorder evolved to become aquatic quite independently.

Environmental changes essential for present-day *Hemiptera* lineages occurred during the biocenotic crisis on the boundary between Early and Late Cretaceous, when land habitats became dominated by angiosperms, while several Palaeophytic evolutionary lines of gymnosperms – which had been host plants to numerous *Hemiptera* – became extinct. In the wake of this, strictly phytophagous aphids, scale insects and whiteflies underwent a rapid diversification. The period also witnessed the development of present-day *Cicadomorpha*: *Clypeata* families.

Changes of the flora forced herbivorous species to adapt to new conditions and new trophic niches. During the Paleogene, aphids, scale insects, whiteflies, *Psylloidea*, *Fulgoromorpha* and *Cicadomorpha*, as well as herbivorous *Heteroptera* all underwent extensive specialization. The next evolutionary challenge faced by the *Hemiptera* was the cooling and drying that occurred during the early Oligocene, and the appearance of open grassy and herbaceous habitats. The



Simplified chronophylogram of the evolution of *Hemiptera* suborders. Time in millions of years

new environments were quickly inhabited by specialized groups of phytophages from all suborders.

Why so prevalent?

Hemiptera include 290 contemporary and fossil families, making them the most differentiated insect order. They show extensive taxonomic, morphological, ecological and behavioral diversity. In spite of the close similarities of the mouth apparatus in all species, they feed on a wide range of vegetable and animal matter; this has allowed them to take many diverse ecological niches with a wide distribution around the globe. Most herbivorous *Hemiptera* excrete excessive sugars ingested with food, forming a type of wax used as a material shielding their bodies, protecting deposited eggs or holding sacs of eggs carried by females, and waxy strands or "feathers" which serve as protection and to stabilize flight. *Cicadellidae* form structures known as brochosomes which also perform a protective function. Numerous *Hemiptera* shelter their eggs by laying them within plant tissues. Some species exhibit forms of caring for their offspring, such as covering the eggs with a waxy substance, carrying eggs, looking after the larvae, or viviparity.

The insects have close bonds with internal bacterial symbionts; we could go as far as saying that they undergo evolutionary processes as "extended organisms" (in the Dawkinsian sense of the extended phenotype). The symbionts evolve with their hosts and are transmitted generation to generation. They supplement the insects' diet by supplying them with essential nutrients such as amino acids and vitamins, and they are found in herbivorous, predatory and hematophagous species. Many Hemiptera coexist with ants, "hiring" them to look after their larvae in exchange for honeydew secretions. Larvae of the Australian endemic leafhopper *Kahaono montana* Evans, 1966 (*Cicadomorpha*: *Cicadellidae*) conceal themselves from predators by secreting silky strands – the only known species of Hemiptera to do so. *Myndus chazeaui* Bourgoin, 2012 (*Fulgoromorpha*: *Cixiidae*) from New Caledonia hide in cocoons made of silk strands secreted by spiders from the *Clubionidae* family.

The *Hemiptera* present a high adaptability and a broad trophic spectrum, and they have evolved to make use of a range of food sources through a variety of feeding mechanisms. They have excellent adaptability, rapid taxonomic and morphological differentiation, and they are able to recover their diversity after major biotic crises. They also enter into numerous symbiotic and mutualistic interactions. All this contributes to the order's abundance and great evolutionary success. ■

Further reading:

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