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By land, air, and sea: hemipteran diversity through the genomic lens

Kristen A Panfilio^{1,2} and David R Angelini³

Thanks to a recent spate of sequencing projects, the Hemiptera are the first hemimetabolous insect order to achieve a critical mass of species with sequenced genomes, establishing the basis for comparative genomics of the bugs. However, as the most speciose hemimetabolous order, there is still a vast swathe of the hemipteran phylogeny that awaits genomic representation across subterranean, terrestrial, and aquatic habitats, and with lineage-specific and developmentally plastic cases of both wing polyphenisms and flightlessness. In this review, we highlight opportunities for taxonomic sampling beyond obvious pest species candidates, motivated by intriguing biological features of certain groups as well as the rich research tradition of ecological, physiological, developmental, and particularly cytogenetic investigation that spans the diversity of the Hemiptera.

Addresses

¹ School of Life Sciences, University of Warwick, Coventry CV4 7AL, United Kingdom

² Institute of Zoology: Developmental Biology, University of Cologne, 50674 Cologne, Germany

³ Department of Biology, Colby College, Waterville, ME 04901, United States

Corresponding author: Panfilio, Kristen A (Kristen.Panfilio@alum.swarthmore.edu)

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The Hemiptera: feeding, functional genetics, and hemimetabolous diversity

With an estimated 82 000 described species, roughly 9% of all known insects belong to the Hemiptera [1], making the bugs the fifth most diverse insect order after the holometabolous flies, butterflies, beetles, and ants. By contrast to those other four orders, the Hemiptera belong to the hemimetabolous insect radiation, a part of the insect family tree that retains many ancestral insect states that are just beginning to be investigated in the current genomics era. The Hemiptera, along with recently sequenced representatives of the lice (Psocodea, [2]) and thrips (Thysanoptera; i5K project: GCA_000697945.1),

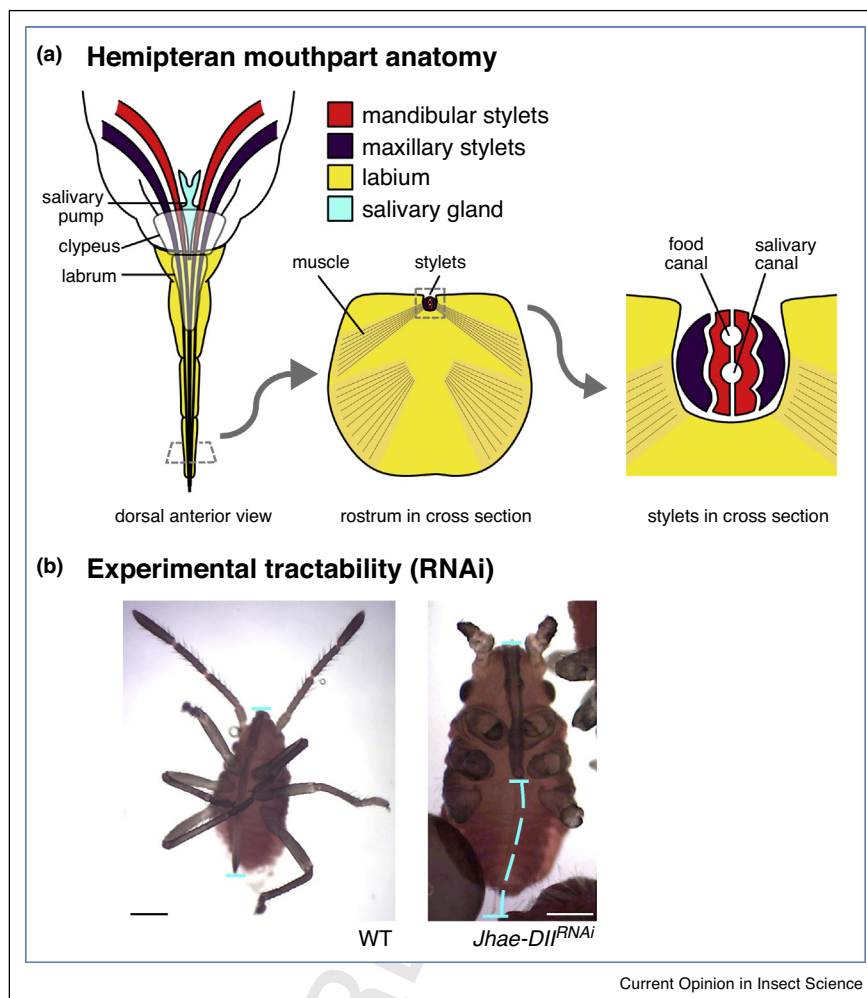
form the Paraneoptera. This superorder is also known as Acercaria and is traditionally considered the sister group clade to the Holometabola [3,4]. With phylogenetically-informed surveys already suggesting that the Hemiptera may be suitable outgroups to the Holometabola for a range of embryonic features [5,6], there is much to explore in this order that can inform larger patterns of development and evolution in the insects.

The Polyneoptera form the other major clade of hemimetabolous insects [4]. Published genome assemblies for this group include the large, repeat-heavy genome of the locust (Orthoptera) [7]. Investigations on eusociality within the Dictyoptera — independent from a later origin of eusociality within the holometabolous Hymenoptera — have compared the genomes of termites relative to the cockroach [8–10]. In this fast-moving field, there is even a recent first look at genomes of species among the ‘old wing’ orders Odonata and Ephemeroptera [11], outgroups to the Neoptera. Meanwhile, the Hemiptera currently comprise over half of the hemimetabolous species with sequenced genomes listed on the central insect genomics GitHub portal (as of October 2017, http://i5k.github.io/arthropod_genomes_at_ncbi).

Hemipterans have diversified into a variety of habitats where they make use of a range of food sources. Some members, such as aphids and planthoppers, have become notorious agricultural pests, while the evolutionary history of the group has been characterized by numerous shifts between predation and plant feeding [12]. Underlying these specializations is the defining feature of the Hemiptera: a common anatomy of piercing-sucking mouthparts (Figure 1a). Indeed, investigation of mouthpart development in the milkweed bug *Oncopeltus fasciatus* represents one of the earliest functional studies using RNA interference (RNAi) in the insects [13]. *O. fasciatus* has a long and active research tradition in developmental biology, genetics, and other fields, which had led to the recent sequencing and comparative analysis of its genome ([14], and see below). In general, RNAi is highly effective in the Heteroptera (‘true bugs’), with several species maintained as laboratory research models (Figure 1b, [13,15–18,19]). By contrast, to date there has been mixed success in using RNAi on mucivorous (sap feeding) agricultural pests of the Sternorrhyncha, both for environmental delivery and for systemic efficacy [20,21]. However, genetically and phenotypically detectable knockdown can be obtained with particularly high dsRNA concentrations via feeding

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Figure 1



Bugs suck: unique mouthpart anatomy underlies diverse feeding ecologies in the Hemiptera and highlights their experimental tractability. **(a)** All Hemiptera are characterized by conserved piercing-sucking mouthpart anatomy comprised of the labium, which acts as the outer support scaffold, and retractable, piercing stylets. These mouthparts can be deployed for feeding on a variety of fluid and solid substrates from diverse plants and animals (adapted from [24,101]). **(b)** The Heteroptera ('true bugs') are particularly amenable to functional molecular genetics techniques such as parental RNAi, here exemplified by knockdown of the *Distal-less* orthologue in the soapberry bug, *Jadera haematoloma*. By contrast with a wild type hatchling (WT, left), all appendages in a knockdown individual are severely truncated (right). This includes the labium (delimited by horizontal blue bars), such that the translucent stylets protrude substantially and are not supported (dashed blue line). Hatchlings (first instar nymphs) are shown in ventral aspect; scale bars are 200 μm .

91 or injection, with discretionary 'boost' secondary injections, in the pea aphid [22,23].

93 Here, we survey the hemipteran species that have been
 94 sequenced, looking at their value beyond their immediate
 95 sequencing justifications, and thereby establish the basis for
 96 our selection of future sequencing projects, sampling taxa
 97 from habitats as diverse as the land, air, and sea (Figure 2).

98 Holocentric chromosomes and karyotype evolution

99 In the mid-twentieth century, cytogenetics explored
 100 the diversity of chromosome structures and meiotic
 101

102 behaviors. Although most eukaryotes are typified by
 103 monocentric chromosomes, many lineages feature holo-
 104 centric chromosomes in which spindle microtubules con-
 105 nect at many points along the chromosome without a
 106 distinct kinetochore. This mode of cell division is seen in
 107 an estimated 16% of insect species [24], including the
 108 Odonata, Dermaptera, Psocodea, Lepidoptera, Trichop-
 109 tera, and Hemiptera, as well as in other arthropods such as
 110 some arachnids [25]. Holocentric chromosomes continue
 111 to segregate normally even when fragmented, perhaps
 112 explaining the resistance of species like *O. fasciatus* to
 113 mutation from ionizing radiation [26]. One prediction of
 114 the persistence of chromosomal fragments may be an

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