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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

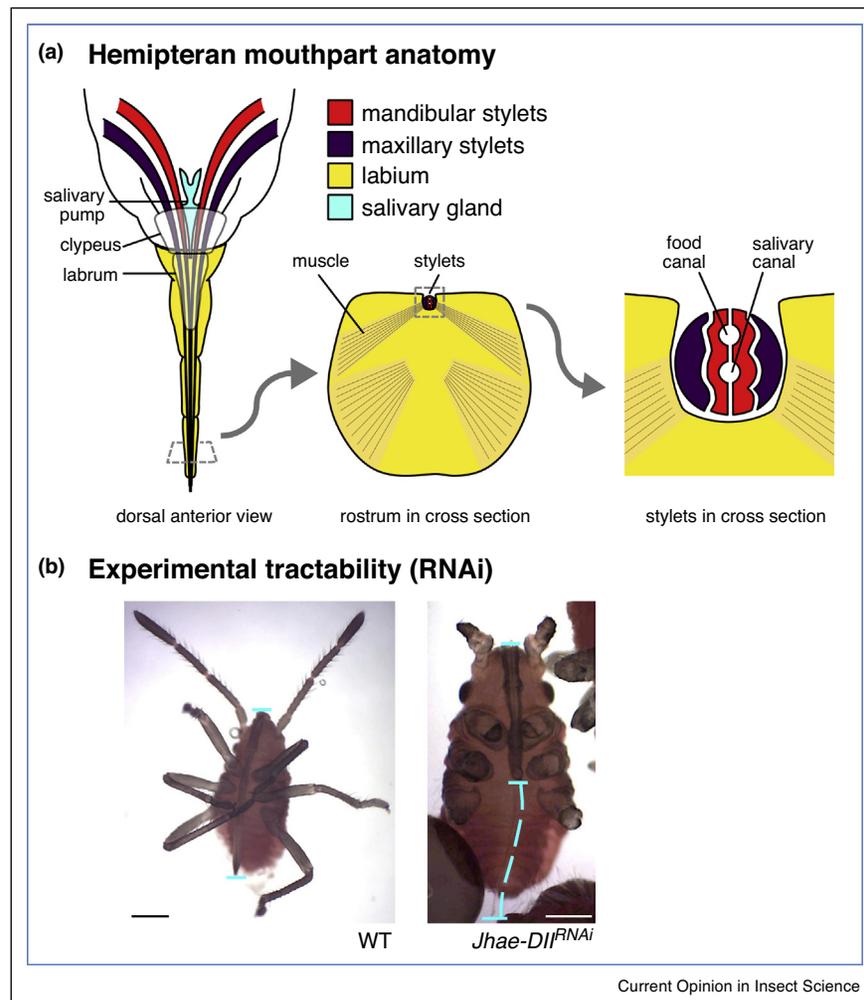
With an estimated 82,000 described species, roughly 9% of all known insects belong to the Hemiptera [1], making the bugs the fifth largest insect order after the holometabolous flies, butterflies, beetles, and ants. In contrast to those other four orders, the Hemiptera belong to the hemimetabolous insect 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 serve as 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 has 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^{••}]). In 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 or

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*. In 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 .

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

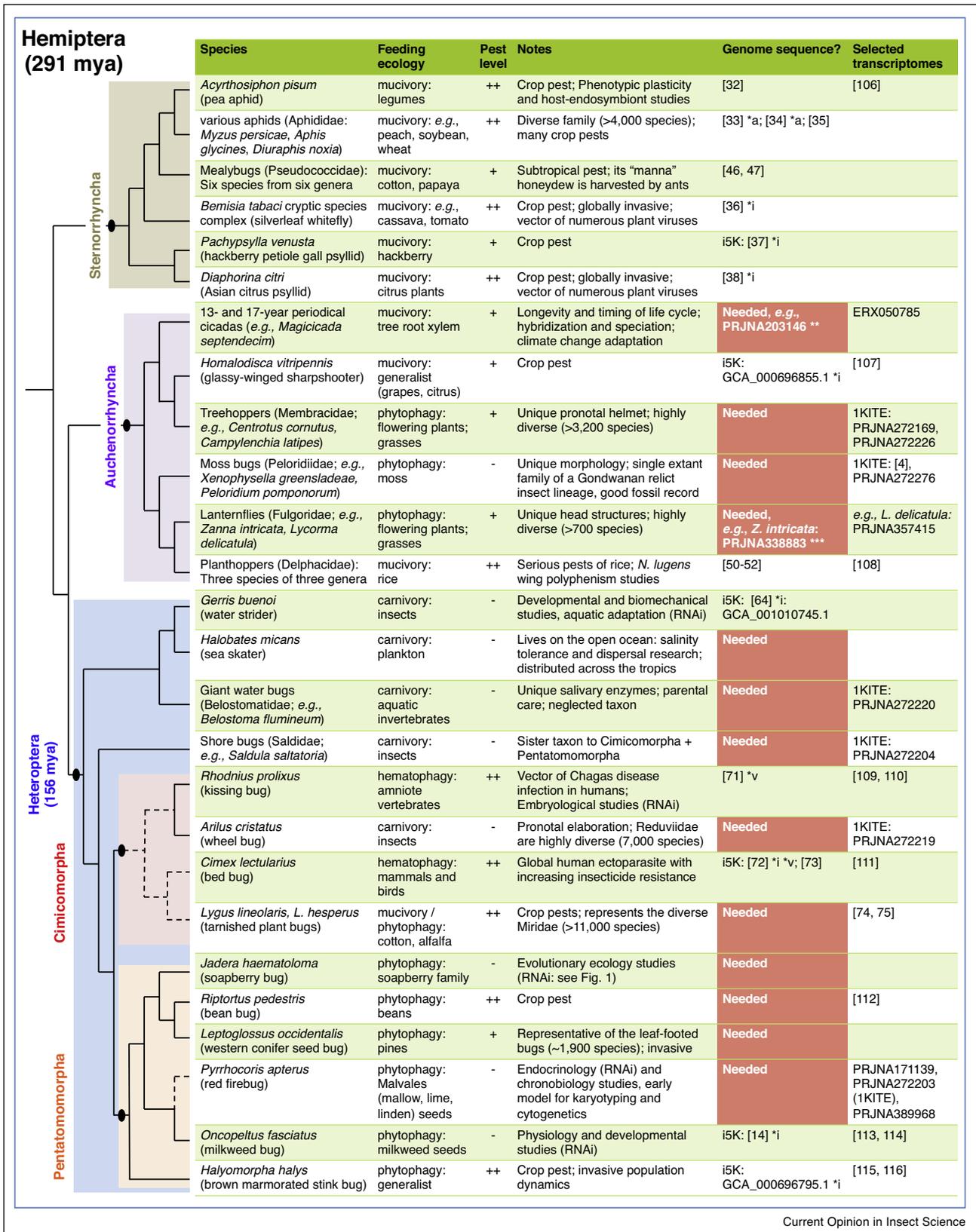
Here, we survey the hemipteran species that have been sequenced, looking at their value beyond their immediate sequencing justifications, and thereby establish the basis for our selection of future sequencing projects, sampling taxa from habitats as diverse as the land, air, and sea (Figure 2).

Holocentric chromosomes and karyotype evolution

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

behaviors. Although most eukaryotes are typified by monocentric chromosomes, many lineages feature holocentric chromosomes in which spindle microtubules connect at many points along the chromosome without a distinct kinetochore. This mode of cell division is seen in an estimated 16% of insect species [24], including the Odonata, Dermaptera, Psocodea, Lepidoptera, Trichoptera, and Hemiptera, as well as in other arthropods such as some arachnids [25]. Holocentric chromosomes continue to segregate normally even when fragmented, perhaps explaining the resistance of species like *O. fasciatus* to mutation from ionizing radiation [26]. One prediction of the persistence of chromosomal fragments may be an

Figure 2



elevated evolutionary rate of rearrangement, with some holocentric lineages prone to rapid karyotype evolution. As one affirmative example, the peach potato aphid undergoes rapid rearrangements, allowing selection for insecticide resistance [27].

Genomic insights from the Hemiptera and other insect groups suggest fundamental differences in the evolution of holocentrism among different lineages [28**]. The cell biology of holocentric cell division has been studied in detail in the nematode *Caenorhabditis elegans*, where the centromeric histone H3 variant CenH3 is required for mitosis. In contrast, all holocentric insect species lack CenH3 as well as the inner kinetochore protein CenpC [28**], and it remains unclear how diverse the mechanisms for kinetochore assembly and cell division may be in holocentric insects. There may also be genome structural differences, such as an absence or redistribution of the fixed length repetitive sequences that typify centromeric DNA in monocentric species such as *Drosophila melanogaster* [29].

The Hemiptera possess a remarkable diversity of meiotic processes, including apomictic parthenogenesis, non-chiasmatic segregation, and inverted meiosis [25]. The study of these poorly understood phenomena may provide fundamental insights into cell division. For example, holocentric chromosomes are often associated with inverted meiosis, in which the common order of reductional and equational cell divisions is reversed [30]. Although all Hemiptera possess holocentric chromosomes, inverted meiosis is known only from some groups, such as the soft scale insects (Coccidae), while others like the Heteroptera maintain the traditional meiotic order [30]. A better understanding of these diverse meiotic mechanisms may have relevance beyond insects, since non-canonical patterns of meiotic division, similar to inverted meiosis, have been inferred from SNP segregation in human oocytes [31]. Below, we highlight some of the extensive cytogenetic work that has been done in the Hemiptera, which will literally scaffold future genome sequencing efforts as well as

identify lineage-specific factors that regulate holocentric mitosis and meiosis.

Taxonomic survey of available and needed hemipteran genomes

Many species of **Sternorrhyncha** (aphids, psyllids, whiteflies) are serious agricultural pests. Therefore, they have received understandable research attention and remain prominent candidates for genome sequencing [32–35,36*,37,38]. Here, we focus on the larger diversity of the Hemiptera (Figure 2), a fascinating insect order that has a substantial basic research tradition extending over 100 years. Although two-thirds of currently sequenced hemipterans are high-status pests, most of the taxa we propose for future genome sequencing are rather justified by their use in basic research or by their unique biology.

Moreover, there is more to pest species' biology than their status as pests. Such species are effective at exploiting agricultural plant food sources in part because of underlying biological features such as developmental plasticity and microbial symbioses. For example, wing polyphenisms that underlie migratory behavior have been genetically dissected by global and candidate gene approaches in species such as the pea aphid [23,39] and the brown planthopper, *Nilaparvata lugens* (a member of the Auchenorrhyncha whose wing polymorphism is also reviewed in this issue, [40]). Meanwhile, given the low-nutrient diet of mucivores, sequencing of the hemipteran host has frequently garnered additional data for genomes of their bacterial endosymbionts. These microorganisms genetically and nutritionally complement the insects' physiology, enabling them to exploit host plants (e.g., [41–45]). Within the Sternorrhyncha, mealybugs, or scale insects, feature the intriguing situation of tripartite, nested symbioses wherein the insects' bacterial symbionts themselves have intrabacterial symbionts. Recent study of gene complementation and symbiont evolutionary histories has led to draft genome assemblies for six mealybug species and their bacterial constituents [46**,47]. These genomic resources also provide a foundation for future exploration of other biological features in these species.

(Figure 2 Legend) Hemiptera with sequenced genomes and those that would strongly augment biological and taxonomic diversity for comparative genomics. Most species sequenced to date are primarily agricultural pests and disease vectors. For many of the needed taxa, a wealth of transcriptomic data are already available, such as through the 1KITE initiative (e.g., [4]), while a pilot project of the i5K initiative [102] has made good headway in generating a critical mass of sequenced species for this most species-rich hemimetabolous insect order (e.g., [14**,37,64,72], and listed project accessions). Species suggested here for sequencing would then cover the major families of the Hemiptera and span a wide range of anatomical features (e.g., pronotal and head elaborations) and ecological niches (subterranean, aquatic, carnivorous). Furthermore, suggested species such as *Jadera haematoloma* and *Pyrrhocoris apterus* represent particularly tractable laboratory research models (e.g., Figure 1b). Phylogenetic relationships are primarily based on [62**], with further support for infraorder resolution for the Sternorrhyncha [103,104] and Cimicomorpha [61]. However, hemipteran relationships remain contested, in part reflected by dashed lines in the dendrogram. The Cimicomorpha have traditionally been recovered as a monophyletic clade with various internal topologies [24,61,77,105]. However, recent mitochondrial phylogenomic data — although problematic [79] — suggest that this infraorder may be paraphyletic with respect to the Pentatomomorpha [62**]. Furthermore, the position of *Pyrrhocoris apterus* within the Pentatomomorpha is unstable even across studies using comparable mitochondrial datasets (cf., [62**] vs. [78]). Divergence times are the median values reported in [4]. Accession numbers refer to projects in GenBank. Asterisks in the table indicate current sequence statuses, as of November 2017: (*) publicly accessible, BLASTable genome browser hosted by AphidBase (*a: <http://bipaa.genouest.org/is/aphidbase/>), i5K (*i: <https://i5k.nal.usda.gov/>), and/or VectorBase (*v: <https://www.vectorbase.org>); (**) no public data yet available; (***) unassembled, raw data thus far (SRA). In addition to those discussed in the main text, in this figure we highlight selected transcriptomes from the literature [106–116] or with GenBank project accessions.

As one example, mealybugs exhibit extreme sexual dimorphism, with flightless females and an unusual form of sex determination. Males may arise from unfertilized eggs or via differential epigenomic regulation that leads to the unusual process of heterochromatinization and elimination of the paternal genome [48,49].

The **Auchenorrhyncha** (cicadas, treehoppers, moss bugs) contain opportunities to investigate life cycle regulation and a range of lineage-specific anatomical elaborations (Figure 2). Although genomes have recently been published for planthoppers as major pests of rice [50–52], most Auchenorrhyncha have been sorely neglected. With over 1,300 species, cicadas (Cicadidae) represent a fascinating group for investigation of biological rhythms, from loud nightly singing to rare, gregarious emergences. In particular, the periodical cicadas of the genus *Magicicada* are among the longest lived insects, with a predominantly subterranean life style that culminates in a brief sexual adulthood on the surface in cycles of 13 or 17 years. Phylogenetic investigations with DNA from a rich, historical voucher collection revealed repeated, independent divergence to 13-year or 17-year cycles [53]. These changes may reflect geologic climatic fluctuations and environmental plasticity, rather than potential hybridization among sympatric species, but the need for genomic-scale analyses has already been recognized [53,54^{*}]. The requirements for cicadas' underlying molecular clocks — including both synchronization across populations and entrainment to the environment — provide an engaging challenge to unpick in terms of evolutionary lability, current cellular function, and potential scope for future adaptation to climate and habitat change [55]. Potential epigenomic regulation across the life cycle would be a key feature for future investigation. For example, while it is still early days, a range of epigenetic regulatory mechanisms has been implicated in the commitment to solitary or gregarious phases in swarming locusts (reviewed in [56^{*}]). Although cicada genomes are large by insect standards (~5–7 Gb), the wealth of SNP and RAD-seq data already available for closely related individuals and species within the *Magicicada* [54^{*}] provides a strong foundation for comparative genomics, more akin to the situation in mammals in terms of recent divergence times and dense sampling.

With their unique, flightless morphology and rich fossil record, moss bugs (Peloridiidae) are often described as living relicts from the Permian. The group is the subject of a handful of anatomical studies pertaining to their specialized cuticular secretions and exoskeletal functional properties within damp, temperate climates (e.g., [57,58]). Recent transcriptome sequencing and karyotyping (e.g., [4,59]) will support future genomic investigation of this ancient, seemingly unchanging lineage. Similarly, transcriptomes are already available for treehoppers (Membracidae) and lanternflies (Fulgoroidea), fellow

Auchenorrhyncha that would benefit from genomic investigation of their distinctive cuticular projections from the pronotum and head (Figure 2; e.g., [60]).

Many Hemiptera belong to the clade of 'true bugs', the Heteroptera. Relationships in this group remain uncertain, but the base of this radiation appears to be a paraphyletic assemblage of **aquatic Heteroptera**, whose habitats range from ponds to the open ocean [61,62^{**}]. Although aquatic insects are generally prone to fossilization, no stem group fossil Heteroptera have been found from the Permian, when the group is thought to have diversified [24]. Additional genomic resources will clarify the evolutionary origins and molecular basis of heteropteran diversification and aquatic adaptations. Within the infraorder Gerromorpha, both tissue-specific and species-specific transcriptomes have already supported developmental genetics investigations of male antennal modifications for grasping the female during mating on the water surface [63] and of the origin of the propelling leg fan used for locomotion in veliid species [19^{**}]. The recently sequenced genome of the water strider *Gerris buenoi* [64] represents a key first reference for these taxa and should help identify other lineage-specific adaptations. For example, the fellow gerrid *Halobates micans* is one of only a handful of insects of ecological challenges include dispersal, water pollution, and tolerance to salt, temperature, and UV exposure [65,66]. Genomic information for this species in comparison with that for the shore bugs (Saldidae), which dwell in the intertidal zone and face similar pressures [67], has the potential to reveal whether convergent molecular features underpin these lineages' independent adaptations to such environmental conditions.

The giant water bugs (Belostomatidae) are a striking taxon not only for their tremendous size, as the name *Giganometra gigas* implies [68], but also for their parental care. Males brood eggs to ensure their exposure to air [12] and deploy chemical defenses against potential predators such as ants [69]. 'Heteroptera' literally refers to the mixed composition of bugs' forewings, with both membranous and hardened regions ('hemelytra', [62^{**}]). Belostomids have uniquely taken advantage of the hemelytra to create air pockets that help them to stay afloat, through specialized abdominal modifications that channel air [70]. Building on recent transcriptomic work (Figure 2), genome sequencing within this family will open new avenues for research on respiratory physiology, chemical communication, and morphological innovation.

Within the **Cimicomorpha**, genomes have been sequenced for obligate blood-feeding human ectoparasites: the bed bug and the kissing bug [71–73], which represent evolutionarily independent instances of hematophagy in the Cimicidae and Reduviidae, respectively

[62**]. In contrast, with over 11,000 described species, genomic resources are greatly needed for the Miridae, a large family of mostly plant-feeding bugs. To date, work has focused on the polyphagous tarnished plant bugs of the genus *Lygus*. Transcriptome analysis of these prominent agricultural pests has explored how their salivary gland products facilitate the external digestion of plant tissues [74] and the molecular basis of insecticide resistance [75]. Interestingly, most other members of the tribe Mirini have high specificity for certain host plants (reviewed in [76]) and could provide the comparative framework for understanding the more generalist polyphagy of *Lygus* species. Moreover, phylogenetic relationships within the Cimicomorpha and even its monophyly remain controversial (Figure 2). The sequencing of mirids, as well as additional reduviids such as the wheel bug *Arilus cristatus*, will substantially expand phylogenomic information beyond the present molecular phylogenies based on rRNA and mitochondrial genes (e.g., [61,62**,77–79]). Indeed, phylogenies of concatenated, single-copy orthologues of protein-coding genes, based on official gene sets from genome sequencing, have proven robust and reliable for resolving deeper relationships among sequenced hemipterans and did preliminarily recover a cimicomorphan clade based on currently available taxa [14**].

Last, but certainly not least, are the **Pentatomomorpha**, which have one of the richest experimental traditions among the Hemiptera. For example, landmark mid-twentieth century work in the firebug *Pyrrhocoris apterus* demonstrated the potential impact of environmental phytochemicals on a species' endocrine system, which helped lead to development of juvenile hormone analogues [80,81]. Earlier, the first animal sex chromosomes were identified in this species in the 1890s (reviewed in [82]). In modern research, the firebug is readily amenable to RNAi [16]; it has a wealth of salivary gland and gut microbiome transcriptomic data (Figure 2); and an active research community has recently called for genomic resources to further advance work on this emerging model for chronobiology [83*]. Equally, the milkweed bug *Onco-peltus fasciatus* has served as a long-standing developmental and physiological research model (reviewed in [84]). Its recent genome sequencing has led to new insights and testable hypotheses on gene structure evolution and the molecular bases for feeding ecology differences across the Hemiptera [14**], and this resource is already being utilized by the community (e.g., [85,86]).

Future genome projects should build on this foundation in addressing topics such as feeding ecology. Invasive pests such as the polyphagous stink bug *Halyomorpha halys* (Pentatomidae, Figure 2) and the conifer seed bug *Leptoglossus occidentalis*, one of the diverse leaf-footed bugs (Coreidae), have rapidly expanded their geographical ranges in recent decades. *L. occidentalis* has spread

across North America and become introduced in Europe, where it can be a destructive pest of conifer trees [87]. Meanwhile, the crop pest *Riptortus pedestris* has emerged as a new model to examine hemipteran-bacterial symbiosis [88,89]. As in the Mirini, work on these invasive generalists can be contrasted with results from closely related phytophagous specialists. Many pentatomomorph specialists have achieved the metabolic feat of turning ingested plant toxins into warning pigmentation to deter predators (e.g., [14**,90]). For example, the red-shouldered soapberry bug, *Jadera haematoloma*, has served as a model for phenotypic evolution driven by adaptation to host plants [91,92]. Future genome sequencing would strengthen its ongoing development as a species for functional genetics (e.g., Figure 1b). Comparative genomics analysis on these groups will clarify a suite of related features pertaining to metabolism, chemical tolerance, and the molecular basis of feeding adaptation.

Large bug genomes and third generation sequencing approaches

Big genomes are challenging, but our computational capabilities are also growing. This will be important as comparative insect genomics ventures out from the known confines of the Holometabola to the wider diversity of hemimetabolous orders such as the Hemiptera. Although the cicadas' large genomes are a notable exception on par with the Orthoptera (e.g., [7]), the Hemiptera are a fair representation of genome size ranges among hemimetabolous insects [93]. At the larger end of the spectrum, a quarter of its 5.3-Gb genome was recently sequenced for the meadow spittlebug, *Philaenus spumarius* (Auchenorrhyncha: Aphrophoridae), a research species for phylogeographic studies of speciation and color polymorphism [94]. Although a substantial amount of sequence data (>1 Gb) was already assembled, there is still a long way to go with this species. As new genome sequencing projects are initiated for better taxonomic sampling, genome sizes much greater than 1 Gb will indeed need to be considered carefully in order to balance biological representation with tractability for generating useful draft-quality genomes. As a guide, the Animal Genome Size Database Release 2.0 from 2005 [95] has overestimated the genome sizes of some species. For example, the genome of *O. fasciatus* was initially estimated at 4.55 Gb [95], compared to recent flow cytometry measurements of 926 Mb [14**]. However, the Heteroptera in particular do have medium to large genomes.

Happily, such species will now benefit from recent innovations in sequencing approaches. Using long read data, high quality hybrid Illumina-PacBio assemblies have already been successfully generated for smaller-genome hemipterans (e.g., 300–600 Mb genomes, [34,36*]). Furthermore, optical mapping strategies have already substantially improved the assembly of large genomes for

vertebrates and plants [96–98]. Such approaches would also support future sequencing projects for large insect genomes. Given the painstaking cytogenetic work that underpins ongoing hemipteran research, such as karyotyping that has already been done in *P. spumarius* and congeners [99,100], the Hemiptera are well positioned to continue to thrive in and contribute to the modern comparative genomics era.

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