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# Genomics of the semi-aquatic bugs (Heteroptera; Gerromorpha): recent advances toward establishing a model lineage for the study of phenotypic evolution

David Armisen and Abderrahman Khila

Gerromorpha, also known as semi-aquatic bugs, present the striking capability to walk on water surface, which has long attracted the interest of many scientists. Yet our understanding of the mechanisms associated with their adaptation and diversification within this new habitat remain largely unknown. In this review we discuss how new transcriptomic and genomic resources have contributed to establish the Gerromorpha as an important lineage to study phenotypic evolution. In particular we outline the impact of recent comparative transcriptomic analyses and first published genomes to advance our understanding of genomic basis of adaptations to water surface locomotion and sexual dimorphism.

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## Introduction

The semi-aquatic bugs (Hemiptera, Heteroptera, Gerromorpha) represent a monophyletic group of predatory insects characterized by the ability to live on the water-air interface [1]. Of the ~900 000 known insect species (representing approximately 80% of the world's species), Gerromorpha is the only lineage where the entire life cycle takes place in contact with the water surface. Gerromorpha's unique locomotory capabilities on the water-air interface has long attracted scientific interest to understand the biomechanical and evolutionary process of water walking — a long-standing question that raised curiosity every time someone has observed them walking on a pond or lake. Over 200 million years ago, the ancestor of the Gerromorpha transitioned from terrestrial habitats to the water surface, leading to a radiation that

culminated in over 2000 species classified into eight families [1]. Character state reconstructions suggested that the ancestral habitat of the Gerromorpha was either humid terrestrial or marginally aquatic [1–3]. Water striders subsequently became true water surface dwellers and colonized a diverse array of niches, including streams, lakes, ponds, marshes, and the oceans [1,4,5]. The invasion of these new habitats provided access to resources previously underutilized by insects and made the Gerromorpha the dominant group on water [1]. Because of this striking life history, they have fascinated scientists from various disciplines, including naturalists, applied mathematicians, ecologists, taxonomists, paleontologists and evolutionists. However, until recently, understanding the genetic mechanisms underlying their evolution and adaptation has been hindered by the lack of genomic resources, which were mostly limited to DNA barcoding to study geographical ecosystems and molecular diversity [6–9] and transcriptomic data for phylogeny reconstruction [10–12].

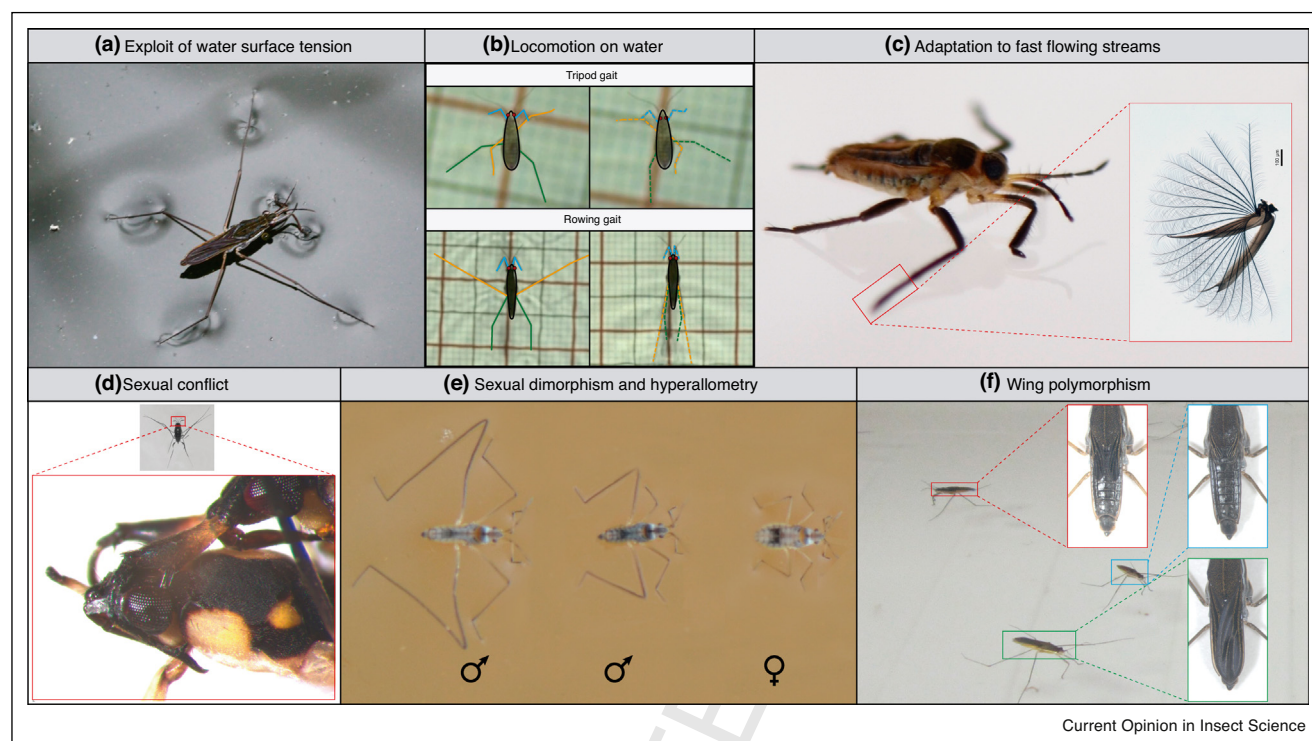
The development of new genomics and transcriptomics approaches based on next-generation sequencing (NGS) technologies and their decreasing cost in the last decade have permitted the sequencing of many non-model organisms. As a result, many long-standing evolutionary questions could be approached under the light of new study models offering the appropriate life history context. In this review we aim to illustrate how sequencing in various species of the Gerromorpha made it possible to explore the genomic basis of adaptations, such as water surface locomotion or sexual dimorphism and sexual conflict, and opened new paths to establish Gerromorpha as a model lineage to study phenotypic evolution.

## Developmental genetic basis of locomotion on the water surface

By living on water surface, the Gerromorpha face two primary challenges: how to remain afloat and how to generate efficient thrust forward on a fluid substrate [13–15]. The Gerromorpha evolved two main adaptations that are thought to be associated with these biomechanical challenges. On one hand, the hairs covering their legs act as non-wetting structures due to their specific arrangement and density. This adaptation allows to exploit water surface tension by trapping air between the leg and water [13–15,16\*] (Figure 1a). In the water strider *Gerris buenoi*, transcriptomic analyses showed that hydrophobic hairs

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Figure 1



**(a)** The semi-aquatic bugs exploit water surface tension due to increased leg length and bristle density. **(b)** Gerromorpha species can be classified according to their body plan, is tightly associated with the mode locomotion employed. Top: Species occupying transitional zones retain the ancestral body plan (hindlegs longer than midlegs) and move on water using a tripod gait (walking). In these species there is an alternate movement of both midlegs (orange) and hindlegs (green). Bottom: Species with a derived body plan (midlegs longer than hindlegs) move through a rowing gait and have specialized in open water zones. In this case hindlegs (green) barely move and are used as rudders while most of the propulsion is generated from simultaneous movement of the pair of midlegs (orange). **(c)** Some species inhabiting fast flowing streams evolved novel traits that increase their locomotion efficiency against water current. This is the case of all species of the genus *Rhagovelia*, such as *Rhagovelia antilleana* in the picture, which have developed a fan-like structure at the tip of the midlegs. The fan increases the contact surface between the leg and the water and therefore propulsion efficiency. **(d)** and **(e)** Most Gerromorpha species present conspicuous sexually dimorphic traits usually related to differences in body shape and size. In a few cases, trait modification can be extreme and the evolution of these elaboration are driven by conflict between the sexes or by competition between males. An example of extreme modification can be found in the antenna of *Rheumabates rileyi* males (d) which function to grasp females by the eyes during pre-mating struggles. In the case of *Microvelia longipes* male's (e), hindleg are strikingly long and are used as weapons to dominate egg laying sites and, therefore, access to females. **(f)** Many Gerromorpha species exhibit a rich variety of wing morphs such is the case of *Gerris buenoi* where macropterous (green), brachypterous (red), micropterous (blue) and apterous individuals can be found within the same population.

are innervated bristles under the control of the *achaete-scute homologue* (ASH) gene and changes in its regulation may have contributed to shaping these bristles [17]. On the other hand, an increase in relative leg length allows to effectively distribute weight without breaking the surface tension [15,16]. In Gerromorpha, the Hox gene *Ultra-bithorax* (Ubx) controls not only the growth of the hindlegs, as is the case in crickets and grasshoppers [18,19], but also the mid-legs through a novel domain of expression [20]. Changes in Ubx expression led to the evolution of a derived leg plan where mid-legs are longer than hindlegs. Basally branching lineages retain the ancestral body plan with hindlegs being the longest, occupy transitional zones, and move on the water using a tripod gait

with alternating leg movements which allows them to be versatile and walk both on water and on land (Figure 1b). Derived lineages which evolved a derived body plan have specialized in open water zones and use the rowing gait through simultaneous sculling motion of the pair of mid-legs [13–15] (Figure 1b). The hindlegs being shorter act as rudders. A combination of transcriptomic and experimental analyses showed that species with a derived leg plan have increased levels of Ubx expression in the hindlegs linked with a new growth-inhibiting function [21]. They also allowed to identify a previously unknown target gene of Ubx, named *Gamma-interferon-inducible lysosomal thiol reductase* (GILT), with a previously undescribed role in leg elongation that contribute to shape the

legs of water striders [22]. These findings show that novel interactions between ancient and highly conserved genes can contribute to the emergence of adaptive phenotypes.

### Impact of taxon-restricted genes on evolutionary innovations

Increased bristle density and leg elongation are modification of two ancestral traits shared by all insects. In addition to these modifications, novelties or key innovations have evolved and allowed the conquest of physically challenging niches, such as fast-flowing streams, by a strikingly speciose genus called *Rhagovelia*. Species from genus *Rhagovelia* have developed a unique structure, the propelling fan, which enabled this lineage to sustain permanent movement on fast flowing waters (Figure 1c). This structure folds and unfolds synchronously with leg movement, effectively acting like a propelling fan, which increases the propelling impulse with a high energetic efficiency [23<sup>••</sup>]. The family Veliidae contains 61 genera and about 900 species. Interestingly, half of these species are in the genus *Rhagovelia* and all of them have propelling fans (Polhemus). It is possible that this innovation contributed significantly to the impressive success of *Rhagovelia*. Comparative transcriptomic and experimental analyses found two taxon-restricted genes, *geisha* and *mother-of-geisha*, at the origin of this evolutionary innovation [23<sup>••</sup>]. More precisely, transcriptomic data links this new structure with a first emergence of *mother-of-geisha* in the Hemiptera, with an unknown function, followed by a taxon-specific duplication, leading to *geisha*, and a combined control of the fan development [23<sup>••</sup>]. With more than 400 known *Rhagovelia* species, the genus offers an exquisite model to further study the impact of taxon-restricted genes on rapid adaptive radiation.

### Semi-aquatic bugs as models to study sexual conflict and dimorphism

Semi-aquatic bugs represent an historically prominent model for the study of sexual selection and sexual conflict, which are known to drive phenotypic divergence of the sexes [24–26]. In many species, males are favoured to mate repeatedly but females pay increasing fitness costs for multiple mating [27]. This conflict is often illustrated with evasive or struggling behaviour in females [28–30]. As a result, escalation could drive the evolution of grasping traits in males [26,31,32<sup>••</sup>] and anti-grasping trait in females [26,33].

Males of the water strider *Rheumatobates rileyi* present one of the most spectacular trait modifications with a deep remodelling of their antenna morphology to grasp females' eyes during pre-mating struggles (Figure 1d). Study of this trait identified a novel function of the gene *distal-less (dll)* in male antennae morphogenesis due to a late expression during nymphal development [32<sup>••</sup>]. Other striking adaptations are the hyperallometric legs with relation to body size in the males of *Microvelia*

*longipes* (Figure 1e). Those exaggerated legs are used by males to fight other males and dominate egg-laying sites where they mate and guard females. Interestingly, sexual selection favouring longer legs conflicts with locomotion efficiency and, therefore, natural selection. Recent analysis confirmed the role of *Ubx* in leg elongation [34<sup>••</sup>]. A significant finding in this model was the determination that the gene *Bone Morphogenetic Protein 11* (BMP11) was a master regulator of growth for both body size and all three legs in *M. longipes* [34<sup>••</sup>]. More importantly, it regulates hyperallometry of the hindlegs by regulating the allometric slope. RNAi knockdown of BMP11 also showed a reduced fight intensity associated with decrease in legs length [34<sup>••</sup>]. This result showing a genetic correlation between several traits, including body and leg size and fighting behaviour, suggests that pleiotropy play a role in the evolution of adaptive sexually selected traits [35,36]. Future works could exploit the diversity of *Microvelia*, with a variable number of qualitative sexually dimorphic traits and fighting intensities, to further explore the impact of sexual selection and sexual conflict on genome evolution.

### Advances following the first published Gerromorpha genomes and their impact on future research

Transcriptomic data analyses have greatly contributed to the study of the genomics of evolutionary adaptations in Gerromorpha. However, they were limited to identifying the genes involved without further detail of the causal mutations and the role of selection. Recent advances in next generation sequencing and associated cost reduction made it possible to sequence the complete genomes of two Gerromorpha species named *G. buenoi* and *M. longipes*. These new resources opened the door to more in-depth analysis and laid the road for genomic research in the years to come.

An example of causal mutations identified thanks to genome data are the cumulative amino acid changes in *G. buenoi* opsins. Visual ecology of the water striders at the air-water interface has drawn considerable interest [37,38] with experimental works establishing their sensitivity to both green and blue wavelengths [39]. Yet blue opsin is consistently absent in Gerromorpha and other Heteroptera [40<sup>•</sup>]. Thanks to genome sequencing and analysis, a tandem repeat cluster of four green opsins genes was described, and one of the paralogs was identified as having accumulated all amino acid residue changes described in sensitivity shifts from green to blue in butterflies [40<sup>•</sup>,41,42]. This suggests that the sensitivity of *Gerris* to blue was regained through conversion of the green-sensitive sequence.

The genomes also revealed the presence of a significant number of gene duplication events, but their role remains unknown. One of such duplications is found in the Insulin



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Receptor (InR) family. Genomic and transcriptomic analyses suggest the the new InR copy was the result of retro-insertion, mostly because this copy lacks any introns [40<sup>\*</sup>], a mechanism also reported in Pyrrhocoroidea [43]. However, the insulin pathway and InR duplications have been described amongst other insects as having a role on controlling wing polyphenisms in planthoppers [44] and *Pyrrhocoris apterus* [43]. Future works should investigate the impact of duplications in such important gene families on the development and evolution of water striders.

Within the Gerromorpha, a conspicuous variety of wing lengths, apterous, micropterous and/or macropterous, and associated muscle development have been described [1,45] (Figure 1e). In species with wing polymorphism, population composition is associated with dispersal strategies as well as habitat quality [46] and will depend on a combination of both genetic factors and selective pressures [47–50] like population density [51,52], food scarcity [53], salinity [54], temperature [55], dryness [56], photoperiod [57], water quality [58] and sex ratio [59]. Combined with first published genomes, approaches such as epigenetics and population genetics open new research opportunities to study such highly plastic trait. Indeed, as development of each wing morphs is in many cases dependent on condition, epigenetic changes are expected to play a major role in regulating wing development. The availability of a high-quality genome will allow to map and detect those epigenetic changes and correlate them with genes either known to be involved in wing development pathway or identified through comparative transcriptomics analyses. Future studies could then explore the distribution of those modifications, as well as potential polymorphisms, between and within populations over time, effectively opening the door to study microevolutionary events.

The Gerromorpha can also be a model to study the role of epigenetic changes in the development and evolution of exaggerated sexually selected traits. The length of *M. longipes* males' hindlegs is dependent on both nutrition intake and genetic factors [60<sup>\*</sup>]. This interaction raises the question of what are the genes involved, what is the role of epigenetics, and how the combined action of polymorphism and epigenetic mechanisms impacts gene expression and phenotypic variation. While some advances were made on the genetic control of male leg length variation, nothing is known about potential epigenetic mechanisms. However, the recent publication of *M. longipes* genome laid the necessary foundation for the study of the role of epigenetic mechanisms in generating phenotypic variation within the same population.

Finally, other important adaptative traits, involving physiology, behaviour and morphology, are well described in various Gerromorpha species. These include adaptations

such as salinity tolerance [61,62], long distance signalling [63], adjustment of jumping behaviour in females [64<sup>\*</sup>] or coevolution of seminal receptacle and sperm morphology [65]. However, despite their importance to the study of phenotypic evolution, there are no works investigating the genomic basis of these adaptations. We believe that future works using a similar combined approach of transcriptomics, genomics and epigenetics as we described here, could be of great interest to further increase our understanding of adaptation using these traits as study models. To do so it will also be necessary to expand the currently limited number of molecular biology techniques available in Gerromorpha to include for example CRIPR-Cas9 genome editing.

## Conclusions

Recent advances in next generation sequencing technologies have made possible to overcome many of the limitations to study the genetic and genomic basis of adaptation in non-model organisms. In the semi-aquatic bugs, first transcriptomic data laid the foundations of comparative analyses that helped to understand the development of important adaptive traits. More recently, Gerromorpha genomes have opened new research opportunities and will allow to apply approaches such as epigenetics and population genetics. The Gerromorpha, due to the abundance of conspicuous adaptive phenotypes, can become a new model lineage to study various aspects of phenotypic evolution including morphology, physiology and behaviour.

## Conflict of interest statement

Nothing declared.

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