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► To cite this version:

David Armiséen, Abderrahman Khila. Genomics of the semi-aquatic bugs (Heteroptera; Gerromorpha): recent advances toward establishing a model lineage for the study of phenotypic evolution. *Current Opinion in Insect Science*, 2022, 50, 10.1016/j.cois.2021.12.010 . hal-03836646

HAL Id: hal-03836646

<https://hal.science/hal-03836646>

Submitted on 2 Nov 2022

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Insect Science

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

David Armisén 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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Current Opinion in Insect Science 2021, 49:xx–yy

This review comes from a themed issue on **Insect genomics**

Edited by **Shuji Shigenobu**

<https://doi.org/10.1016/j.cois.2021.12.010>

2214-5745/© 2021 Published by Elsevier Inc.

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].

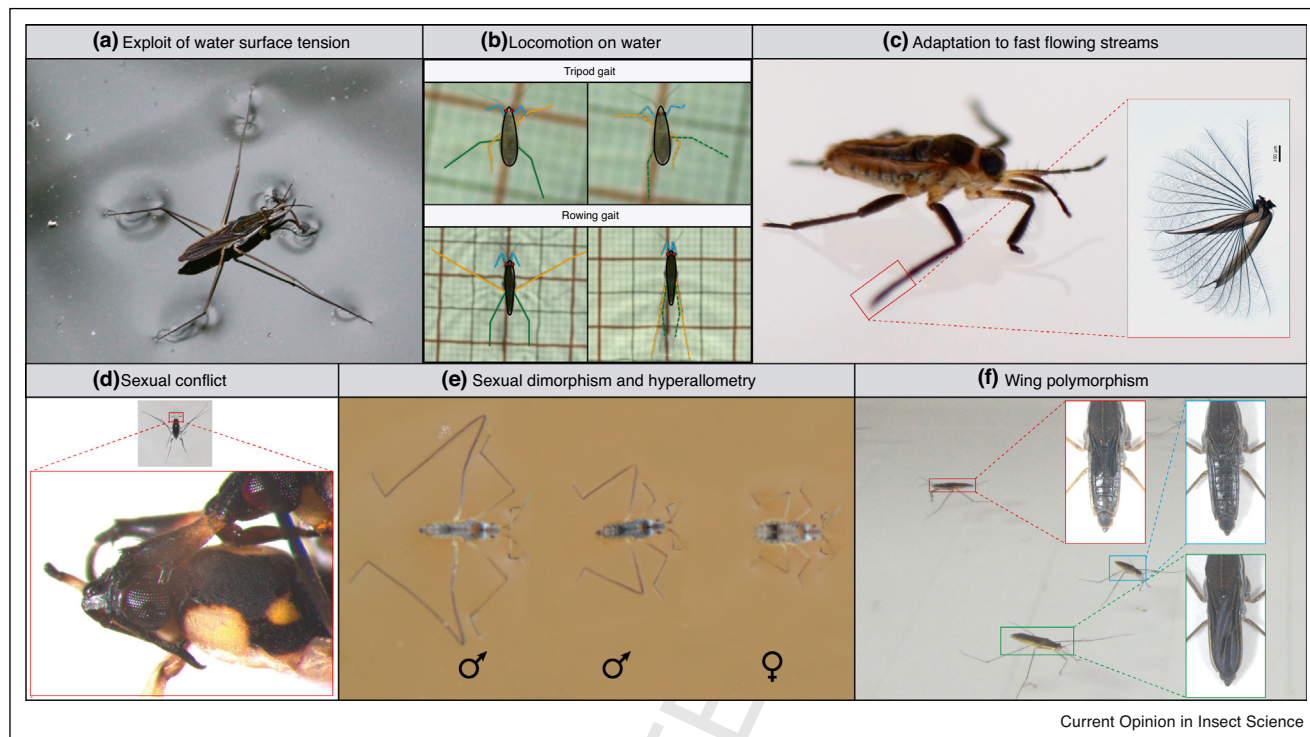
The development of new genomics and transcriptomics approaches based on next-generation sequencing (NGS) technologies and their decreasing cost in the last decade have permitted the sequencing of many non-model organisms. As a result, many long-standing evolutionary questions could be approached under 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.

88 are innervated bristles under the control of the *achaete-*
 89 *scute homologue* (ASH) gene and changes in its regulation
 90 may have contributed to shaping these bristles [17]. On
 91 the other hand, an increase in relative leg length allows to
 92 effectively distribute weight without breaking the surface
 93 tension [15,16]. In Gerromorpha, the Hox gene *Ultra-*
 94 *bithorax* (Ubx) controls not only the growth of the hind-
 95 legs, as is the case in crickets and grasshoppers [18,19],
 96 but also the mid-legs through a novel domain of expres-
 97 sion [20]. Changes in Ubx expression led to the evolution
 98 of a derived leg plan where mid-legs are longer than
 99 hindlegs. Basally branching lineages retain the ancestral
 body plan with hindlegs being the longest, occupy transi-
 tional 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 experi-
 mental analyses showed that species with a derived leg
 plan have increased levels of Ubx expression in the hind-
 legs 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 unde-
 scribed role in leg elongation that contribute to shape the

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

116 **Impact of taxon-restricted genes on** 117 **evolutionary innovations**

118 Increased bristle density and leg elongation are modifi-
119 cation of two ancestral traits shared by all insects. In
120 addition to these modifications, novelties or key innova-
121 tions have evolved and allowed the conquest of physically
122 challenging niches, such as fast-flowing streams, by a
123 strikingly speciose genus called *Rhagovelia*. Species from
124 genus *Rhagovelia* have developed a unique structure, the
125 propelling fan, which enabled this lineage to sustain
126 permanent movement on fast flowing waters (Figure 1
127 c). This structure folds and unfold synchronously with leg
128 movement, effectively acting like a propelling fan, which
129 increases the propelling impulse with a high energetic
130 efficiency [23**]. The family Veliidae contains 61 genera
131 and about 900 species. Interestingly, half of these species
132 are in the genus *Rhagovelia* and all of them have propel-
133 ling fans (Polhemus). It is possible that this innovation
134 contributed significantly to the impressive success of
135 *Rhagovelia*. Comparative transcriptomic and experimental
136 analyses found two taxon-restricted genes, *geisha* and
137 *mother-of-geisha*, at the origin of this evolutionary innova-
138 tion [23**]. More precisely, transcriptomic data links this
139 new structure with a first emergence of *mother-of-geisha*
140 in the Hemiptera, with an unknown function, followed by a
141 taxon-specific duplication, leading to *geisha*, and a com-
142 bined control of the fan development [23**]. With more
143 than 400 known *Rhagovelia* species, the genus offers an
144 exquisite model to further study the impact of taxon-
145 restricted genes on rapid adaptive radiation.

144 **Semi-aquatic bugs as models to study sexual** 145 **conflict and dimorphism**

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

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

longipes (Figure 1e). Those exaggerated legs are used
165 by males to fight other males and dominate egg-laying
166 sites where they mate and guard females. Interestingly,
167 sexual selection favouring longer legs conflicts with loco-
168 motion efficiency and, therefore, natural selection.
169 Recent analysis confirmed the role of *Ubx* in leg elonga-
170 tion [34**]. A significant finding in this model was the
171 determination that the gene *Bone Morphogenetic Protein 11*
172 (*BMP11*) was a master regulator of growth for both body
173 size and all three legs in *M. longipes* [34**]. More impor-
174 tantly, it regulates hyperallometry of the hindlegs by
175 regulating the allometric slope. RNAi knockdown of
176 *BMP11* also showed a reduced fight intensity associated
177 with decrease in legs length [34**]. This result showing a
178 genetic correlation between several traits, including body
179 and leg size and fighting behaviour, suggests that pleiot-
180 ropy play a role in the evolution of adaptive sexually
181 selected traits [35,36]. Future works could exploit the
182 diversity of *Microvelia*, with a variable number of qualita-
183 tive sexually dimorphic traits and fighting intensities, to
184 further explore the impact of sexual selection and sexual
185 conflict on genome evolution.

186 **Advances following the first published** 187 **Gerromorpha genomes and their impact on** 188 **future research**

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

199 An example of causal mutations identified thanks to
200 genome data are the cumulative amino acid changes in
201 *G. buenoi* opsins. Visual ecology of the water striders at the
202 air-water interface has drawn considerable interest [37,38]
203 with experimental works establishing their sensitivity to
204 both green and blue wavelengths [39]. Yet blue opsin is
205 consistently absent in Gerromorpha and other Heterop-
206 tera [40*]. Thanks to genome sequencing and analysis, a
207 tandem repeat cluster of four green opsins genes was
208 described, and one of the paralogs was identified as
209 having accumulated all amino acid residue changes
210 described in sensitivity shifts from green to blue in
211 butterflies [40*,41,42]. This suggests that the sensitivity
212 of *Gerris* to blue was regained through conversion of the
213 green-sensitive sequence.

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

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216 Receptor (InR) family. Genomic and transcriptomic anal-
 217 yses suggest the the new InR copy was the result of retro-
 218 insertion, mostly because this copy lacks any introns [40*],
 219 a mechanism also reported in Pyrrhocoroidea [43]. How-
 220 ever, the insulin pathway and InR duplications have been
 221 described amongst other insects as having a role on
 222 controlling wing polyphenisms in planthoppers [44]
 223 and *Pyrrhocoris apterus* [43]. Future works should investi-
 224 gate the impact of duplications in such important gene
 225 families on the development and evolution of water
 226 striders.

227 Within the Gerromorpha, a conspicuous variety of wing
 228 lengths, apterous, micropterous and/or macropterous, and
 229 associated muscle development have been described
 230 [1,45] (Figure 1e). In species with wing polymorphism,
 231 population composition is associated with dispersal strat-
 232 egies as well as habitat quality [46] and will depend on a
 233 combination of both genetic factors and selective pres-
 234 sures [47–50] like population density [51,52], food scar-
 235 city [53], salinity [54], temperature [55], dryness [56],
 236 photoperiod [57], water quality [58] and sex ratio [59].
 237 Combined with first published genomes, approaches such
 238 as epigenetics and population genetics open new research
 239 opportunities to study such highly plastic trait. Indeed, as
 240 development of each wing morphs is in many cases
 241 dependent on condition, epigenetic changes are expected
 242 to play a major role in regulating wing development. The
 243 availability of a high-quality genome will allow to map
 244 and detect those epigenetic changes and correlate them
 245 with genes either known to be involved in wing develop-
 246 ment pathway or identified through comparative trans-
 247 criptomics analyses. Future studies could then explore
 248 the distribution of those modifications, as well as potential
 249 polymorphisms, between and within populations over
 250 time, effectively opening the door to study microevolu-
 251 tionary events.

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

265 Finally, other important adaptative traits, involving phys-
 266 iology, behaviour and morphology, are well described in
 267 various Gerromorpha species. These include adaptations

such as salinity tolerance [61,62], long distance signalling
 [63], adjustment of jumping behaviour in females [64*] 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 tran-
 scriptomics, 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 techni-
 ques available in Gerromorpha to include for example
 CRIPR-Cas9 genome editing.

Conclusions

Recent advances in next generation sequencing technol-
 ogies 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 oppor-
 tunities and will allow to apply approaches such as epi-
 genetics 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, physiolo-
 gy and behaviour.

Conflict of interest statement

Nothing declared.

Acknowledgements

This work was supported by ERC Co-G WaterWalking #616346 and Labex
 CEBA grants to AK. We thank Severine Viala for her comments on the
 manuscript.

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