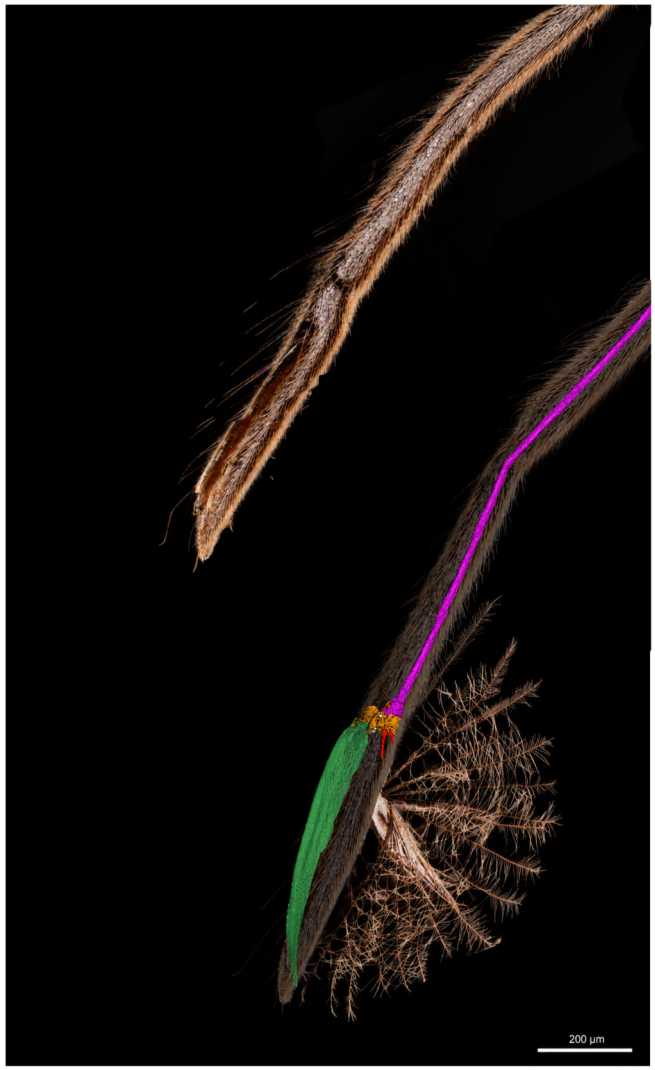

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SYMPOSIUM ARTICLE

Evolution of Distal Swimming Structures in Gerromorpha: Functional Use of Claws and Fan

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Abstract Distal leg structures of some species of Gerromorpha are highly modified, with unique fan and blade-like structures. Within Gerromorpha, we explore the evolutionary transformations of tarsomeres based on detailed morphological documentation, to clarify the complex morphology and function of the legs. In this infraorder, plesiomorphic conditions of the tarsi are maintained in Mesoveliidae, Hebridae, Hydrometridae, "Macroveliidae" and Hermatobatidae, with apical claws and without specialized tarsal or pretarsal structures. In contrast, highly specialized deeply and symmetrically cleft apical mesotarsomeres, with blade-like claws and a feather-shaped empodium, are apomorphic features of *Chenevelia stridulans* and *Rhagovelia antilleana* (Veliidae). Using X-ray microtomography, we document to anatomy and infer the function of middle leg tarsomere swimming apparatus for *Rhagovelia antilleana*, *Callivelia conata* (Veliidae), *Chenevelia stridulans*, and *Gerris buenoi* (Gerridae). We also propose a hypothetical two-component explanation for the release of the fan in *Rhagovelia* and *Chenevelia* based on video and scan observations. For *Rhagovelia* and *Chenevelia*, the contraction of the femuro-pretarsalis muscle, which is attached by a very long and thin tendon to the conspicuously curved unguitractor plate, releases actively the leaf-like claws from the cleft, as well as the fan-shaped structure. The latter is folded in its resting position but unfolds passively outside of the cleft. The combination of deployable fan and modified claws is a locomotory system driven by a hybrid active-passive mechanism enabling species of these genera to improve their propulsion and colonize fast-running water habitats. These structural changes were a unique evolutionary innovation in Gerromorpha, enabling them to cope with specialized habitats and to access new ecological niches.

Introduction

Only few taxa able of moving on the water surface have managed to colonise this challenging habitat. Referring to its harshness, Omer-Cooper (1934) called this habitat "a world of the dead and the dying" in a study on the surface-swimming whirligig beetles (Gyrinidae). Gyrinidae have evolved flat oar-like mid and hind legs, allowed a lift-based propulsion on water surface (Sun et al. 2024). While the anatomy and functional morphology of these surface-swimming Gyrinidae have been

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intensively investigated (e.g., Nachtigall 1961; Larsén 1966; Voise and Casas 2010; Liu et al. 2018; Sun et al. 2024), studies on the leg anatomy of Gerromorpha are scarce (Andersen 1976a, 1976b, Bang et al. 2025; Lee et al. 2025). In contrast to the fast-swimming, speed-boat-like Gyrinidae, Gerromorpha (Heteroptera) have conquered this environment by walking or gliding on the surface film with long and mostly thin legs, sometimes using the mid-legs as oars. Some of these water striders have acquired striking adaptations and innovations, especially affecting leg morphology, thus improving locomotion at the air-water interface. Species that live on the margin of water bodies—the ancestral niche—have an ancestral body plan, with hind legs being longer than middle legs, which, in turn, are longer than the forelegs (Andersen 1982). Species of basal lineage, such as representatives of Mesoveliidae, for instance, run on land and water surface with the so-called alternative tripod gait, involving alternative movements of all three pairs of legs (Crumière et al. 2016). In contrast, species that specialize on open and even turbulent waters—the derived niche of water striders (Gerridae)—evolved a crucial innovation, with middle legs that are longer than both fore and hind legs. Among more specialized lineages, rowing evolved as a novel mode of locomotion through simultaneous sculling motion of the middle legs (Crumière et al. 2016; Armisén et al. 2022; Ortega-Jimenez et al. 2025). Synchronous striking movements of long middle legs propel the body forward like oars. Forelegs support the body, play a role in prey manipulation, copulation and in body balance during locomotion. The hind legs are used for orienting, steering, and supporting the body when the middle legs are lifted off the surface and protracted (Andersen and Polhemus 1976c). Other adaptive traits of water strider's legs have been investigated in detail, such as the complex vestiture of hairs (Finet et al. 2022; Andersen 1976a), or some leg features including muscles (Andersen 1976b). Nevertheless, important morphological aspects of the legs are still unknown. For example, the alternating tripod gait of species of *Microvelia* in both aquatic and terrestrial terrains was recently investigated by O'Neil et al. (2024) even though morphological details of the movements of the terminal tarsomeres were lacking.

Some species of riffle bugs have specialized on fast flowing, unsteady streams, where they move on the surface with agility and maneuvrability (Crumière et al. 2016; Santos et al. 2017). Species from the genera *Rhagovelia*, *Chenevelia* and *Tetraripis,* e.g. have evolved a propelling fan on the tip of their legs. This morphological innovation is composed of several branches, that opens once in the water and acts as paddle by extending the surface area in contact with water. This additional surface area, compared to a normal tarsal ending, provides an increased thrust and enables these species to cope with faster flowing waters and thus thrive in a new ecological niche (Santos et al. 2017; Steinmann et al. 2026). How exactly the formation of these fans has affected internal structures (e.g., muscles and tendons) of the legs, and how their movement is coordinated relative to other structures, such as the unguitractor and claws, remains an open question. To address these issues, we mainly focus on two species of the Veliidae, *Rhagovelia antilleana* and *Chenevelia stridulans,* where a plumy fan-shaped structure is present on the apical mesotarsomere (Santos et al. 2017;Badiane et al. 2024).

Three different functional interpretations were presented in previous works: a passive opening and closing of the fan via elastocapillarity dominance, an active one via muscular control, or both via a hybrid passive-active model (Cheng and Fernando 1971; Andersen 1982 ; Santos et al. 2017, Bang et al. 2025; Ortega-Jimenez et al. 2025). In a passive deployment scenario, the flat-ribbon fans would open in $<$ 10 ms via surface tension as a "surface tension battery" upon tarsus-water contact, independent of muscles, relying instead on physical interactions with the water surface and enabling ultrafast propulsion without neural input (Cheng and Fernando 1971; Andersen 1983). This interpretation was based on dissection, merged with high-speed imaging and robotic replication. Contrasting evidence based on intact legs of *Rhagovelia distincta* suggests an active muscle-driven expansion/retraction in natural cleft positions, arguing that strict passivity is an artifact of dissection. According to that, Bang et al. (2025) argue, based on observations of intact insects, that both protraction and retraction involve active muscular control, while elastocapillarity contributes mainly to fan conformation once submerged. A hybrid mechanism involves a passive opening, while the claw retractor muscle actively re-folds the fan (∼50 ms) for recovery. This integrates active and passive movements, resulting in enhanced interfacial agility. Ortega-Jimenez et al. (2025), e.g. proposed a hybrid passive-active model, in which fan opening is predominantly passive via elastocapillarity while fan closing may be passive or active depending on whether the fan exits the water or remains submerged.

The objective of our study is to clarify the complex morphology and function of middle leg tarsomeres in water strider species from the two largest families, namely the paraphyletic riffle bugs ("Veliidae") and the water striders (Gerridae). We place the documented structural features and analysed mechanism into an evolutionary framework using a comparative approach. We carry out a formal reconstruction of the character evolution, with a sampling including four focal species: *Rhagovelia antilleana*, *Chenevelia stridulans*,

Callivelia conata ("Veliidae") and *Gerris buenoi* (Gerridae), as well as additional terminals of Gerromorpha genera and an outgroup based on data from the literature. We also evaluated similar but distinctive morphological adaptations, such as for instance blade-like claws combined with two similar blade-like structures in *Husseyella* and *Euvelia* (Andersen and Polhemus 1976c, fig. 8.11). To understand how exactly these morphological innovations function at the organismal level, we provide an overview of the internal and external structures of the tarsomere of the three species of "Veliidae" and *Gerris buenoi* (Gerridae). Finally, based on X-ray microtomography (μ-CT) scan reconstructions, we propose a mechanism for the deployment of the fan in *Rhagovelia* and *Chenevelia* in comparison with tarsal and pretarsal specializations in related taxa and data in the literature (e.g., Andersen 1976a, 1976b; Andersen and Polhemus 1976c).

In summary, our study spans morphological adaptations from a relatively unmodified Gerromorpha tarsomere to a very complex one with specialized structures such as a deep cleft, blade-like claws and a feather-like empodial fan. The reconstruction of character transformations highlights evolutionary changes in Gerromorpha species to overcome physical barriers and access new ecological niches.

Material and methods

Biological material

This study is based on adult male specimens of *Rhagovelia antilleana, Callivelia conata, Chenevelia stridulans, and Gerris buenoi*, raised at the Institute of Functional Genomics (Lyon) collection following the protocol of Santos et al. (2017). These samples of "Veliidae" and Gerridae include species with different degrees of mesotarsal specializations, with and without the fan-like structure according to Armisén et al. (2022). We fixed each specimen in an increasing concentration of ethanol (70:80:90:99%) to prevent soft structures shrinkage. The specimens were stained in a 2M iodine solution one week before the scanning date and were washed in 99% ethanol solution two days prior to the scanning date (based on the protocol of Katzke et al. 2022). During sample preparation, we saw a contraction of the animal's leg coupled with and closing of the fan. According to the literature (Resh, 2009 ; Beutel et al. 2014), we wanted to see whether this was because of the contraction of M. femuro-pretarsalis. To do that, we dissected a sample to record this behaviour (Supplementary materials V1). We chose to not manually pull the tendon for the μ-CT scan to not damage the leg, less than 1 mm wide. We also wanted to provide an explanation of the use of the fan using the two fixed states ("fan open" and "fan close") in *Rhagovelia* and *Chenevelia* to better understand the different steps of the fan opening. One individual of each species was used for μ-CT scanning of the whole body. Then, to achieve a higher quality scan of the structures of the tarsus and pretarsal structures, the middle leg of one individual per species was detached from the body and the tarsi were scanned individually. Five individuals of *Rhagovelia and Chenevelia* were chosen according to the state of their middle leg tarsomere: fan open or closed. For these two states, one tarsomere of the middle leg of two different samples was scanned.

Phylogenetic analyses and reconstruction of character evolution

Based on data from literature, we built a character matrix using WinClada (Nixon 1999). We then performed a reconstruction of character state evolution using the packages "ape" (Paradis et al. 2004) and "phytools" (Revell 2012) in Rstudio (v4.5.2). To do so, we used the tree topology and branch length from Armisén et al. (2022) and added missing taxa as follows. We placed *Hermatobates* as sister to all other taxa (Raupach et al. 2026; Jin et al. 2026). We placed *Macrovelia*, *Chenevelia*, and *Xenobates* according to Damgaard (2008), and we placed *Pseudovelia* according to Andersen 1983 and Jin et al. (2026). When we added missing taxa to a branch, we divided the given branch length by two to assign half of the branch length value to the newly added taxa. We then used "phytools: make.sinmap" function to perform character map simulations on the phylogenetic tree. It allowed us to reconstruct the evolution of discrete traits using an equal-rates model (ER) as done by Armisén et al. (2022).

Micro-CT scanning and three-dimensional reconstruction

The μ-CT Scanner used was an EasyTom160 (RX Solutions, France) operated with the XAct rev software (v.22.11). The scanning parameters chosen consisted of a tube voltage of 50 kV, a current of 200 μA, with air filter obtained with a LaB6 X-ray source (filament Ø: 0.35 mm). We obtained 1120 to 1504 scan projections from 1 to 4 vertical stiches, which resulted in a voxel size of 2–3.7 μm for the whole body and 0.6 μm for the tarsomeres (*Callivelia*, *Gerris*, *Rhagovelia* state open and close, *Chenevelia* state open). using a flat-panel detector. The resulting scan projection data were reconstructed in 3D with the XAct rev software (v.22.11, RX Solutions, Chavanod, France) and saved as tiff files. The tiff data were then postprocessed with Avizo (v.2025.1, Thermo Fisher Scientific, USA) software to segment the internal structures of L2 left leg last tarsomere into separate

materials to create volume renders from the tiff image series. Each structure was manually segmented from 2D views, with an interval between two segmented slices of 20, 10, or 5 slices, according to the complexity of the structure. The segmented slices were then extrapolated to obtain a 3D structure and manually cleaned to overlap with the focus structures in each 2D view. Renderings were provided using the "generate surface" tool of Avizo.

Results

Morphology of tarsi

A glossary and 3D renderings of the fore, middle and hind legs of the following four species are provided in the Supplementary materials (Figs. S1–S4) to illustrate the following description.

Gerris Buenoi

Tarsal formula 2–2-2 (corresponding to 2 tarsomeres for fore-middle-hind legs respectively, Supplementary materials S1). Forelegs: Short, with two long cylindrical tarsomeres of the same size, both three times longer than wide. Unmodified curved and symmetrical claws inserted subapically, overtopped by short apical dorsal projection of tarsomere 2. An arolium or pulvilli or other attachment devices are missing, like on the other legs, and an empodium is not visible (Fig. 1A). Midlegs: Middle tarsus strongly elongated, almost 5 times as long as protarsus, very slender compared to fore leg, and cylindrical. Both tarsomeres are about equally long, more than 10 times longer than wide. Claws unmodified, slender, slightly curved; also inserted subapically and overtopped by dorsal tarsal projection. Empodium not visible (Figs. 1A and 2A). Hindlegs: Tarsus similar to mesotarsus, but only about half as long. Both tarsomeres are very thin compared to fore leg, cylindrical and about equally long. The claws, including insertion, are similar to those of the middle leg (Fig. 1A).

Callivelia conata

Tarsal formula 3–3-3 (Supplementary materials S2). Forelegs: Protarsus much smaller than other tarsi, about half as long. Tarsomeres 1 and 2 are very short; the latter is distinctly wider than longer. Tarsomere 3 is almost twice as long as tarsomeres 1 and 2 combined. It is approximately spindle-shaped and widened in the middle region. The claws are curved, slender, about as long as the segment, and inserted in a wide and strongly asymmetrical notch. Adhesive devices are absent. An empodium is not visible (Figs. 1B and 2B). Midlegs: Mesotarsomere 1 is very short, about as long as wide. Tarsomere 2 is about 4 times as long and cylindrical. Tarsomere 3 is about as long as 2, with a fairly

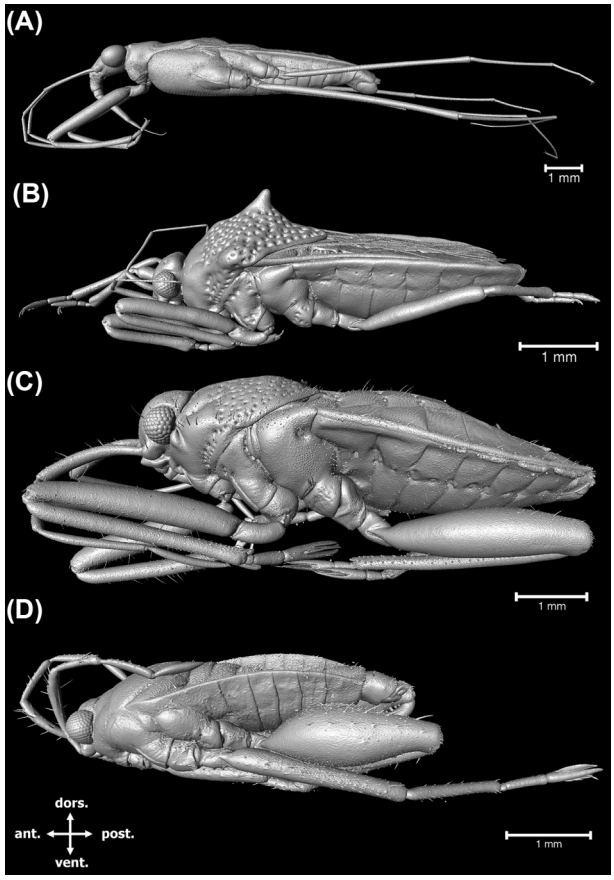

Fig. 1 Side view of *Gerris buenoi* (A), *Callivelia conata* (B), *Chenevelia stridulans* (C), and *Rhagovelia antilleana* (D). The images are based on 3D rendering from μ-CT scans.

short, strongly asymmetrical notch containing an unmodified subapical claw. The lateral lobe enclosing the notch is much longer than mesal one; both are apically subacuminate. The empodium is not visible. The claws are about half as long as tarsomere 3, with very distinct basal extensions, otherwise unmodified, slightly curved, symmetrical (Figs. 1B and 2B). Hindlegs: Very similar to midlegs but with a very slightly larger width (Fig. 1B).

Rhagovelia Antilleana

Tarsal formula 3–3-3 (Supplementary materials S4). Forelegs: Protarsus club-shaped, with very short tarsomeres 1 and 2. Protarsomere 3 with long curved claws inserted in deep asymmetrical notch. Empodium is not visible (Figs. 1D and 2D). Midlegs: Tarsus slender, slightly less wide than tibia. Mesotarsomere 1 very short, wider than long, with oblique apical articulatory area; mesotarsomere 2 about 5 times as long, cylindrical; mesotarsomere 3 about as long as 2, divided by a deep cleft into nearly symmetrical halves of distal 2/3 of segment; the apices of halves are rounded and rather flat; a group of three small setae is

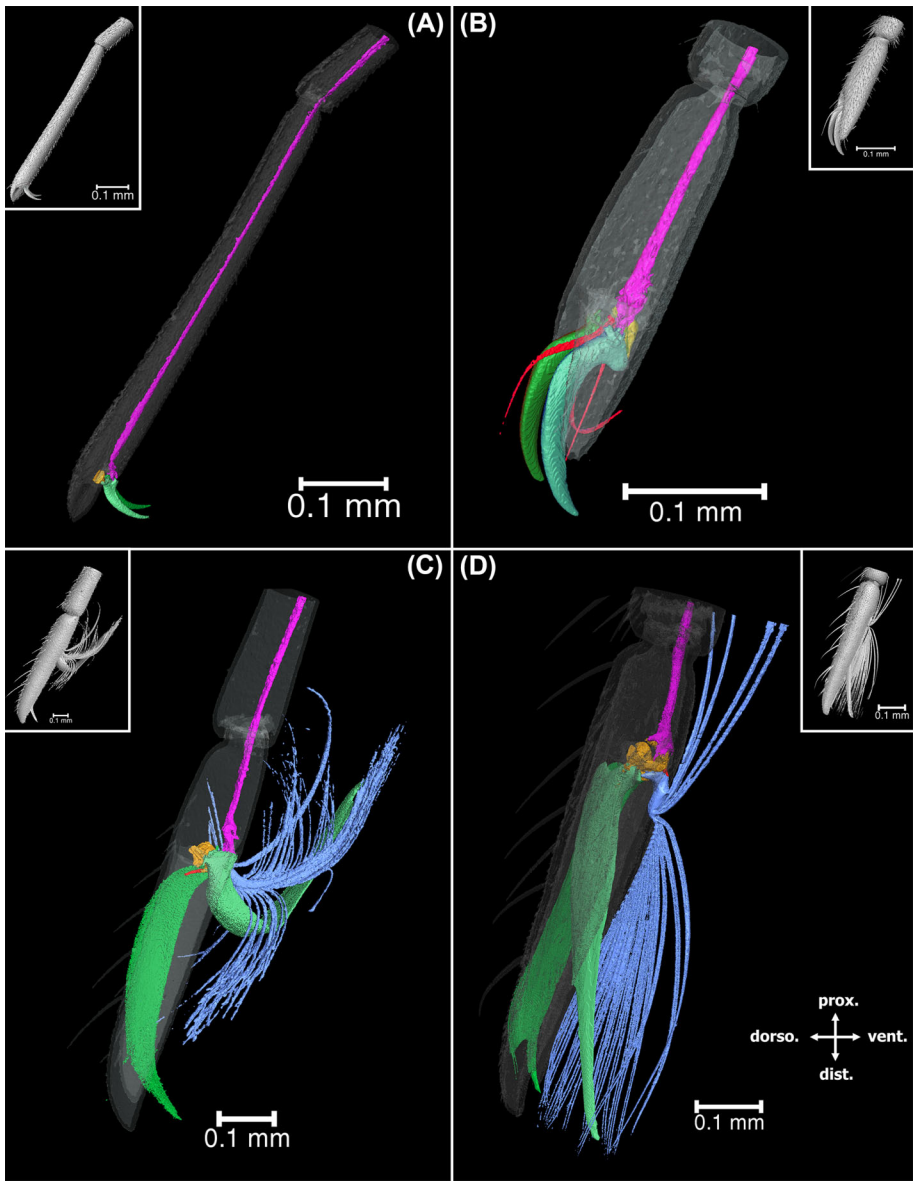

Fig. 2 External and internal views of the last tarsomere of the left middle leg of Gerris buenoi (A), Callivelia conata (B), Chenevelia stridulans (C), and Rhagovelia antilleana (D). Each equivalent structure was segmented with the same color to indicate homology: tendon (pink), unguitractor plate (orange), setae (red), fan (blue), left claw (light green), right claw (dark green), cuticle of tarsomere (gray transparent). The claws are partly similar to those of other insects (A, B), then widened into a leaf-like structure (C, D). The tendon is directly attached to inguitractor (A, B) or has dual attachment points, one in a dorsal position on the tarsal cuticle and the other one on the unguitractor plate (C, D). There is also an increasing structural complexity of the unguitractor plate with a positional shift from apical (A) to a ventral orientation (B, C, D).

present at the base of the cleft. The claws are strongly enlarged, blade-like, and basally articulated with an apical part of the unguitractor plate. The unguitractor is massive, strongly curved in lateral view; the bifid basal part bears the insertion of the very long and thin tendon of the femuro-pretarsalis muscle (IIfpm1; Aibekova et al. 2022); distolaterally the unguitractor is connected with the inner wall of the apical tarsomere 3; at its apical margin it is connected with a highly modified empodium ("ventral arolium"). The base of the empodium is solid, curved in the opposite direction than the unguitractor plate; its distal part forms a conspicuous fan- or feather-like swimming plume, ca. seven to eight times longer than the curved basal stalk; the plume is composed of ca. 20 individual branches with numerous very fine secondary barbules (Figs. 1D and 2D). The barbules were visible in µ-CT data set but not reconstructed in the present study because of their anatomical entanglement making renderings meaningless (Supplementary materials Fig. S5). Hindlegs: The

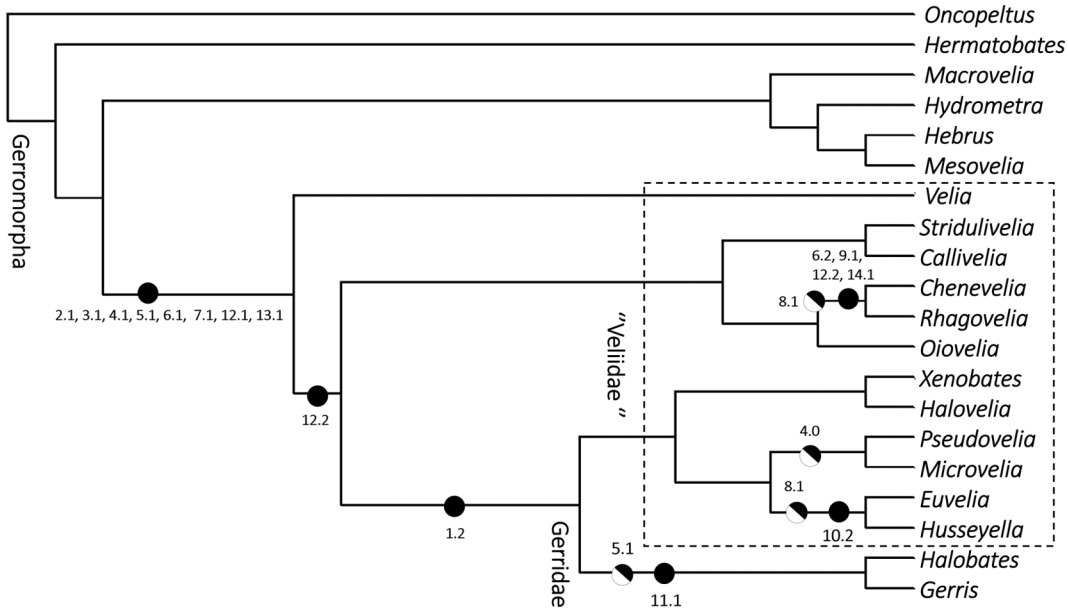

Fig. 3 Tree based on the topology of Armisén et al. 2022 and Jin et al. (2026). Apomorphic character states (full circle: unambiguous, half circle: ambiguous, with reversals and/or parallel evolution) were mapped on branches using ancestral state reconstruction based on Rstudio (v4.5.2) packages "ape" (Paradis et al. 2004) and "phytools" (Revell 2012). More details on the character in the section "Selected leg characters of Gerromorpha (see also Table 1).

tarsus is very similar to the mesotarsus, but distinctly smaller and slenderer. A deep and nearly symmetrical cleft is also present, with similar but smaller claws, and with a long hair-like empodium with a row of spines along one margin, thus appearing serrated (Fig. 1D).

Chenevelia Stridulans

Tarsal formula 3–3-3 (Supplementary materials S3). All three pairs of legs are very similar to the condition described for *Rhagovelia*, including the deep cleft of the middle and hind legs, the modified blade-like claws. *Chenevelia* fan is a bush-shape swimming plume formed by the empodium of mesotarsomere 3, and present a serially homologous serrated empodium of the metatarsomere 3. The branches of the fan are successively divided in two in a fractal manner (Fig. 1C and 2C).

Selected leg characters of Gerromorpha, with a main focus on "Veliidae"

While the former section dealt with the four focal species, we now present a comparative approach with a broader sample of 20 representative species of Gerromorpha (Fig. 3) to carried out a formal reconstruction of the leg character evolution (Table 1).

1. Tarsal segmentation: (0) 3; (1) 2; (2) 3–2-2; (3) 1–2-2. Three on all legs in *Rhagovelia* and *Chenevelia* (Zettel 1996) and most other genera. Tarsi two-segmented in *Husseyella* (Herring 1955) and some other genera, for instance *Halovelia*, and also in *Hydrometra*, *Gerris* and *Halobates* (Andersen 1976b). An unusual tarsal formula 3–2-2 occurs in one species of *Rhagovelia* (Drake 1966: described as *Trochopus*). A one-segmented protarsus is an apomorphy of Microveliinae according to Damgaard (2008).
2. Asymmetric notch of apical protarsomere: (0) absent; (1) present. Absent in *Mesovelia* and in Hebridae and Hydrometridae (e.g., Andersen and Weir 1999). An asymmetrical notch is present in *Velia*, *Callivelia*, *Rhagovelia* and *Chenevelia* (Andersen 1976a ; Zettel 1996), and also in other genera traditionally placed in Veliidae. A shallow notch (coded as 1) is formed by a small projection overtopping the claws in *Gerris* and *Halobates* (coded as 1).
3. Position of foreclaw: (0) apical; (1) shifted proximal. Apical in Mesoveliidae, Hebridae, and Hydrometridae (Andersen and Weir 1999; Morales et al. 2020). Shifted proximal in *Callivelia*, *Rhagovelia* and *Chenevelia* (Zettel 1996), also in other genera traditionally assigned to Veliidae (e.g., Herring 1955; Matsushima et al. 2021: Fig. 4 ; Rodrigues and Moreira 2024). Also inserted preapically in *Gerris* and *Halobates* (Anderson and Cheng 2004).
4. Relative length of middle and hind legs: (0) about equally long or middle legs shorter; (1) middle legs longer. Hind leg longest in *Mesovelia*, *Austrovelia*, *Microvelia* and *Pseudovelia*, and also in Hebridae and

Table 1 Matrix of leg characters of Gerromorpha, with a main focus on "Veliidae."

Characters	Tarsal segmen-tation	Protar-sal notch	Position of foreclaw	Longer leg	Subapical mesotar-somere	Cleft/notch meso-tarsomere 3	Position of middle claws	Shape of middle claws	Feather-like empodium	Additional blade-like appendages	Subapical meta6 tarsomere	Cleft/notch meta-tarsomere 3	Position of hind claw	Appendages meta-tarsomere 3
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Taxa														
Oncopeltus	3–3–3	–	Apical	Hindleg	Normal	Absent	Apical	Normal	Absent	Absent	Normal	Absent	Apical	Absent
Hermatobates	3–3–3	–	Apical	Hindleg	Normal	Absent	Apical	Normal	Absent	Absent	Normal	Absent	Apical	Absent
Macrovelia	3–3–3	–	Apical	Hindleg	Normal	Absent	Apical	Normal	Absent	Absent	Normal	Absent	Apical	Absent
Mesovelia	3–3–3	–	Apical	Hindleg	Normal	Absent	Apical	Normal	Absent	Absent	Normal	Absent	Apical	Absent
Hebrus	2–2–2	–	Apical	Hindleg	Normal	Absent	Apical	Normal	Absent	Absent	Normal	Absent	Apical	Absent
Hydrometra	3–3–3	–	Apical	Hindleg	Slender, not elongated	Absent	Apical	Normal	Absent	Absent	Slender, not elongated	Absent	Apical	Absent
Velia	3–3–3	+	Subapical	Midleg	Normal	Notch	Subapical	Normal	Absent	Absent	Normal	Absent	Subapical	Absent
Chenevelia	3–3–3	+	Subapical	Midleg	Normal	Cleft	Subapical	blade-like	Present	Absent	Normal	Cleft	Subapical	Serrated
Stridulivelia	3–3–3	+	Subapical	Midleg	Normal	Notch	Subapical	Normal or blade-like	Absent	1 blade-like empodium	Normal	Notch	Subapical	Absent or paired
Oiovelia	3–3–3	+	Subapical	Midleg	Normal	Notch	Subapical	Normal	Absent	Absent	Normal	Notch	Subapical	Absent
Callivelia		+	Subapical	Midleg	Normal	Notch	Subapical	Normal	Absent	Absent	Normal	Notch	Subapical	Absent
Rhagovelia	3–3–3	+	Subapical	Midleg	Normal	Cleft	Subapical	Blade-like	Present	Absent	Normal	?	Subapical	Serrated
Trochopus	3–2–2	+	Subapical	Midleg	Normal	Cleft	Subapical	Blade-like	Present	Absent	Normal	Notch	Subapical	empodium ?
Husseyella	2–2–2	+	Subapical	Midleg	Normal	Notch	Subapical	Blade-like	Absent	2 blade-like	Normal	Notch	Subapical	Absent
Microvelia	1–2–2	+	Subapical	Hindleg	Normal	Shallow notch	Subapical	Normal	Absent	Absent	Normal	Shallow notch	Subapical	Absent
Halovelia	2–2–2	+	Subapical	Midleg	Normal	Absent	Subapical	Normal	Absent	Absent	Normal	Shallow notch	Subapical	Absent
Xenobates	2–2–2	+	Subapical	Midleg	Normal	Absent	Subapical	Normal	Absent	Absent	Normal	Shallow notch	Subapical	Absent
Euvelia	1–2–2	+	Subapical	Midleg	Normal	Deeply cleft?	Subapical	leaf-like	2 blade-like	2 blade-like	Normal	Notch	Subapical	Absent
Pseudovelia	2–2–2	+	Subapical	Hindleg	Normal	Shallow notch	Subapical	Normal	Absent	Absent	Normal	Shallow notch	Subapical	Absent
Halobates	2–2–2	+	Subapical	Midleg	Elongated	Shallow notch	Subapical	Normal	Absent	Absent	Elongated	Shallow notch	Subapical	Absent
Gerris	2–2–2	+	subapical	Midleg	Elongated	shallow notch	Subapical	normal	Absent	Absent	Elongated	Shallow notch	Subapical	Absent

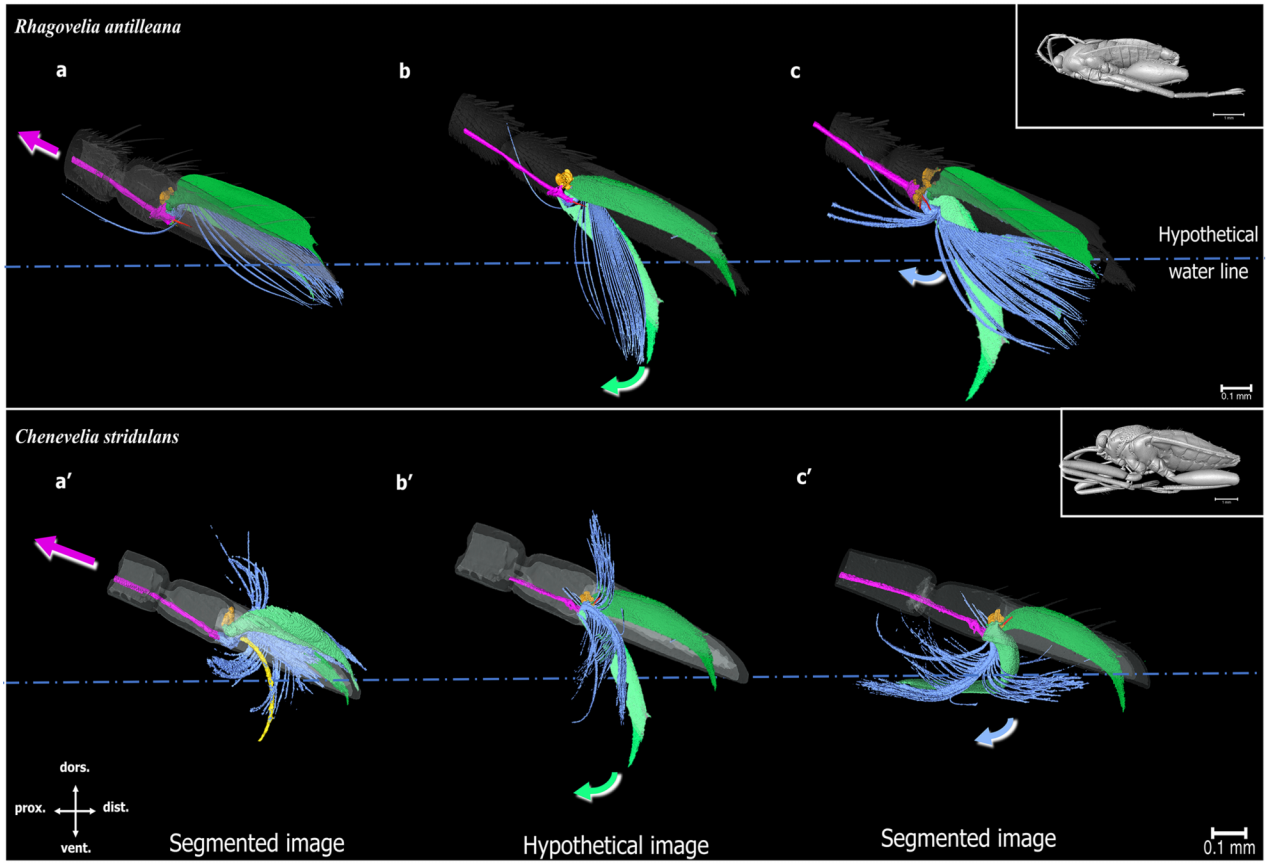

Fig. 4 Fan opening in Rhagovelia antilleana (a, b, c) and Chenevelia stridulans (a', b', c') as a hybrid passive and active process. Model showing the fan and claw movement when pulling the middle-leg tendon in the proximal direction. (a, a') Contraction of M. femuro-pretarsalis during adduction. (b, b') Pull of the tendon caused by contraction of M. femuro-pretarsalis, claws and fan are pushed out of the last tarsomere (Supplementary materials Fig. S7). (c, c') Fan opens passively after contact with the water. Arrow represents the direction of the movement of each involved structure; Dashed line indicates the water surface. Images a, a', c and c' are based on direct reconstructions of the fan from two different samples. Images b and b' are hypotheticals reconstructions made from sample observation and interpolation from images a, a', c and c'.

Hydrometridae, and in outgroup taxa like *Oncopeltus* (Andersen and Weir 1999; Morales et al. 2020). Middle legs longer in other genera of Gerromorpha (e.g., Andersen and Weir 1999; Zettel 1996).

5. Length of subapical mesotarsomere: (0) less than 10 times longer than wide; (1) more than 10 times longer than wide. The very slender subapical mesotarsomeres are conspicuously thin and elongated in *Gerris* and *Halobates* (Anderson and Cheng 2004), arguably an autapomorphy of Gerridae. Thin mesotarsomeres are also present in Hydrometridae and *Xenobates* (Andersen and Polhemus 1976c; Andersen and Weir 1999), but distinctly less elongated than in Gerridae.
6. Notch or cleft of apical mesotarsomere: (0) absent; (1) asymmetric notch; (2) deep longitudinal cleft. A deep cleft is present in *Chenevelia* (Zettel 1996) and *Rhagovelia,* resulting in nearly symmetrical halves of the distal 2/3 of the tarsomere. A deep cleft is also present in *Euvelia* according to Morales et al. 2020 . An asymmetrical, often rather shallow notch is present in other genera, e.g. *Velia* (Andersen and Polhemus 1976c, fig. 16), *Microvelia* (Matsushima et al. 2021: Fig. 4) or *Husseyella* (Andersen and Polhemus 1976c, fig. 8.11; in contrast to Herring 1955: Fig. 1E). Notches or clefts are completely absent in non-Gerromorpha outgroups, and also in Mesoveliidae, Hebridae and Hydrometridae (Andersen and Weir 1999).
7. Position of claws of middle leg: (0) apical; (1) shifted proximal. Apical in Mesoveliidae, Hebridae and Hyrometridae (Andersen and Weir 1999; Damgaard 2013). Shifted proximad in other genera of Gerromorpha including *Callivelia*, *Rhagovelia* and *Chenevelia,* but only slightly in *Pseudovelia* and some other genera including *Gerris* and *Halobates* (Andersen and Polhemus 1976;

Andersen and Weir 1999; Zettel 1996; Matsushima et al. 2021).

8. Shape of claws of middle leg: (0) unmodified; (1) blade-like. Blade-like and enlarged in some species of *Strudivelia* but unmodified in others (Floriano et al. 2017). Unmodified in Mesoveliidae and *Velia*, and also in some other genera such as *Microvelia*, *Halovelia*, *Xenobates*, or *Shaverdinia* (Andersen and Weir 1999; Matsushima et al. 2021 : Fig. 4; Zettel and Laciny 2021). Blade-like in *Rhagovelia* and *Chenevelia* (Andersen and Polhemus 1976c; Zettel 1996), and also in *Huseyella* and *Euvelia* of Microveliinae (Herring 1955; Molano et al. 2016: Fig. 1; Morales et al. 2020).
9. Specialized feather-like empodium of apical mesotarsomere in addition to claws: (0) absent or simple bristle-like "arolia"; (1) fan-like (or plumose) appendage. Single feather-shaped appendage present in *Rhagovelia* and *Chenevelia* (*Andersen and Polhemus 1976c* ; Zettel 1996).
10. Propeller-like propulsive structure on mesotarsus: (0) absent; (1) present, with one blade-like appendage in addition to blade-like claws; (2) present, with two blade-like appendages in addition to blade-like claws. One additional blade-like element is present in some species of *Stridulivelia* but absent in others (Floriano et al. 2017). Two blade-like additional appendages are present in *Husseyella* (Andersen and Polhemus 1976c, fig. 8. 11) and *Euvelia*, but not in *Microvelia* species examined by Matsushima et al. (2026).
11. Length of subapical metatarsomere: (0) less than 10 times longer than wide; (1) more than 10 times longer than wide. Like the mesotarsomeres strongly elongated in *Gerris* and *Halobates* (e.g., Andersen and Polhemus 1976c).
12. Notch or cleft of metatarsomere 3: (0) absent; (1) with asymmetrical notch; (2) with deep nearly symmetrical deep cleft. A notch or cleft is missing in Mesoveliidae, Hebridae and Hydrometridae (Andersen and Weir 1999). A deep cleft is present in *Rhagovelia* and *Chenevelia* (Andersen and Polhemus 1976c ; Zettel 1996). An asymmetrical notch is present in *Callivelia* and other Gerromorpha genera, also including *Gerris* and *Halobates* (Anderson and Cheng 2004; Floriano et al. 2017), in some cases very shallow.
13. Position of claws of hind leg: (0) apical; (1) shifted proximal. Apical in Mesovelidae, Hebridae and Hydrometridae (Andersen and Weir 1999; Moreira et al. 2008). Shifted proximal in other Gerromorpha genera (e.g., Herring 1955;Rodrigues and Moreira 2024), but only slightly in *Pseudovelia*, *Halovelia* and *Xenobates* (Andersen and Weir 1999: Fig. 4,). Also inserted subapically in *Gerris* and *Halobates* (Anderson and Cheng 2004).
14. Specialized empodium of apical metatarsomere in addition to claws: (0) absent; (1) single serrated empodium. A single serrated empodium is present in *Rhagovelia* and *Chenevelia* (Zettel 1996), considering the deep cleft of the apical metatarsomere. A specialized appendage is absent on the hind leg of *Husseyella* (Herring 1955) and other genera. Drawings in Floriano et al. (2017: Figs. 3 and 4) suggesting the presence of blade-like appendages on the hind legs of some species of *Stridulivelia* apparently refer to the middle legs as indicated by the text in that study.

Phylogenetic analyses

For a preliminary evaluation of character evolution, we conducted equal-rates analysis of the 14 scored features of the distal legs (Supplementary materials Fig. S6). The following clades were obtained on the character map simulation on the phylogenetic tree:

Gerromorpha excl. Hebridae, Mesoveliidae and Hydrometridae, char. states 4.1, middle leg longest (reversal in *Pseudovelia* and *Microvelia*).

Gerromorpha excl. Hermatobatidae, "Macroveliidae," Hebridae, Mesoveliidae and Hydrometridae, char. states 2.1, notch of apical protarsomere, 3.1, claw of proleg inserted subapically, 6.1, notch or cleft of apical mesotarsomere, 7.1, middle claw subapical, 12.1, cleft or notch of apical metatarsomere; 13.1, hind claw subapical.

Gerridae (*Gerris* and *Halobates* included), char. states 5.1, 11.1, subapical meso- and metatarsomeres strongly elongated.

Callivelia, *Husseyella*, *Euvelia* + (*Chenevelia* and *Rhagovelia*), char. state 8.1, middle claws elongated and blade-like.

Chenevelia and *Rhagovelia*, char. states 9.1, feather-shaped empodium of middle leg, 12.1 deep and nearly symmetrical cleft of apical metatarsomere, 14.1. empodium of hind leg with serrated edge.

For a more reliable reconstruction of character evolution, we used the phylogenetic topology of Armisén et al. (2022) and Jin et al. (2026). The reconstruction of character evolution (ancestral state reconstruction based on parsimony) with Rstudio yielded the following apomorphies:

Gerromorpha excl. Hermatobatidae, "Macroveliidae," Microveliidae, Hebridae and Hydrometridae: char. states, 2.1, notch of apical protarsomere, 3.1, claw of

foreleg inserted subapically; 4.1, middle legs longer than hind leg (ambiguous, several reversals, e.g., *Microvelia* and *Pseudovelia*); 6.1, notch of apical mesotersomere; 7.1, middle claws inserted subapically; 12.1, notch of apical metatarsomere; 13.1, claws of hind leg inserted subapically.

Gerromorpha: char. state 4.1, middle legs longer than hind leg (ambiguous, several reversals, e.g., *Microvelia* and *Pseudovelia*). Gerromorpha excl. Hermatobatidae, "Macroveliidae," Microveliidae, Hebridae and Hydrometridae: char. states, 2.1, notch of apical protarsoemere, 3.1, claw of foreleg inserted subapically; 6.1, notch of apical mesotarsomere; 7.1, middle claws inserted subapically; 12.1, notch of apical metatarsomere; 13.1, claws of hind leg inserted subapically.

Haloveliinae (*Xenobates*, *Halovelia*) + Microveliinae (*Huseyella*, *Euvelia*, *Microvelia*, *Pseudovelia*) + Gerridae: char. states 1.1. Tarsal formula 2–2-2 (with secondary modifications and parallel evolution in several other groups, e.g., Hebridae).

Gerridae (*Gerris*, *Halobates*), char. states 5.1, 11.1, subapical meso- and metatarsomeres strongly elongated.

Oiovelia, *Callivelia*, *Chenevelia* and *Rhagovelia*, char. states 8.1, blade-like middle claws (reversal in *Oiovelia*, parallel evolution in *Euvelia* and *Husseyella*, also in some species of *Stridulivelia*).

Euvelia and *Huseyella*, char. state 10.1, two additional blade-like structures on middle leg, forming propeller-like propulsive organ together with blade-like claws (one additional blade-like structure in some species of *Stridulivelia*).

Chenevelia, and *Rhagovelia*, char. states 6.2., deep cleft of apical mesotarsomere, 9.1, feather-like empodium of middle leg; 14.1, serrated empodium of hind leg.

Functional interpretations of the opening of *Rhagovelia* and *Chenevelia* fan

Our reconstruction of the middle leg of *Rhagovelia antilleana* shows highly specialized distal mesothoracic tarsi, divided deeply and nearly symmetrically by a cleft, containing the enlarged blade-like claws and a tightly folded fan-shaped or feather-like structure. Contraction of the M. femuro-pretarsalis (IIfpm1; Aibekova et al. 2022) tilts the conspicuously curved unguitractor plate to which a very long and thin tendon attaches. This releases the blade-like claws from the cleft, and also the fan-shaped structure, which unfolds outside of the cleft after contact with water by elastocapillarity (Ortega-Jimenez et al. 2025).

Discussion

In order to clarify the complex morphology and use of the tarsomeres in Gerromorpha, we mainly focused on the anatomy of the last tarsomere of the middle leg of four species in a phylogenetic context. Despite the diversity of locomotion strategies, a shared principle is that animals must exert a force on a dynamic environment to propel their bodies and all their segments in the desired direction (Dickinson et al. 2000). This force is generated by the acceleration of the body segments due to the internal forces of agonist and antagonist muscles controlled by the nervous system. On a short timescale, locomotion results from a complex interaction between neural processes, muscle activity, biomechanical properties and morphology of the body parts involved (Dickinson et al. 2000; Holmes et al. 2006). In a bigger one, functionally related traits and characters such as tarsal form differences may reflect ecological adaptation, contribute to reconstructing evolutionary relationships, or highlight potential convergences driven by similar functional requirements. Our work provides morphological evidence of the skeletomuscular elements of this distal leg region and its modified structures, enabling improved locomotion at the air–water interface.

Phylogenetic implications of the leg morphological adaptations

The features of the legs examined are largely consistent with the phylogenetic concept of Armisén et al. (2022) and Jin et al. (2026), especially with a clade Gerromorpha excl. Hermatobatidae,"Macroveliidae." Mesoveliidae, Hebridae and Hydrometridae. This large subunit of Gerromorpha, which comprises most of the traditional "Veliidae" (not "Macroveliidae" and Mesoveliidae) and Gerridae, is supported by several modifications of the legs, such as proximal shifts of the claws of all three pairs, with more or less distinct notches of the apical tarsomeres, and middle legs longer than the hind legs (Fig. 3).

The most ancestral condition among the traditional "Veliidae" is found in "Macroveliidae" and Mesoveliidae, with apically inserted unmodified claws, a long and apically acuminate empodium ("ventral arolium"), with two empodial setae (parempodium), and a simple dorsal hair-like structure ("dorsal arolium") (Andersen 1976a, fig. 14). Notches or a cleft of the apical tarsomeres are missing, and also empodial specializations. We consider this complex of features, which is also found in Hermatobatidae, Hebridae and Hydrometridae, as part of the groundplan of Gerromorpha. Moving on the water surface is mainly or exclusively enabled by the dense and complex hydrophobic hairs on the apical leg region, which appears to be generally present in Gerromorpha (Andersen 1976b).

The aim of our evaluation of a limited number of tarsal features (and a limited taxon sampling) was not to resolve the phylogeny of the Gerromorpha, but rather the reconstruction of evolutionary transformations of a specific character system in the group. However, aside from the suggested ground plan configuration and monophyletic Gerromorpha excl. Hermatobatidae, "Macroveliidae," Mesoveliidae, Hebridae and Hydrometridae, we can confidently identify a clade comprising *Rhagovelia* and *Chenevelia* sharing unique and conspicuous apomorphies of the middle and hind tarsi, a deep, nearly symmetrical cleft of both tarsomeres 3, a fan-like empodium of mesotarsomere 2, and a serrated empodium of metatarsomere 3 (Fig. 3). Even though a clade *Euvelia* + *Husseyella* was not unambiguously supported analyses (only in some trees obtained), we assume that both genera are sister taxa in agreement with Armisén et al. (2022). Furthermore, we show how an enhanced complexity of existing structures, such as setae or empodia, may explain important aspects of the evolution of Gerromorpha (Fig. 2). The specialized subgroup of Heteroptera is by now well supported as a clade by a recent study based on transcriptome analyses, whereas the traditional family "Veliidae" or riffle bugs, is clearly paraphyletic (Armisén et al. 2022; Raupach et al. 2026; Jin et al. 2026). Mesoveliidae is now treated as a separate family, and a subgroup including for instance the genus *Microvelia* is more closely related to Gerridae (Armisén et al. 2022), while in Raupach et al. (2026) Haloveliinae and Microveliinae are more basal in the ("Veliidae" + Gerridae) clade. No formal taxonomic decision (re-classification) has been made, probably due to limited/bias taxon sampling in each of these studies.

Interestingly, a highly advanced mesotarsal apparatus has evolved in *Euvelia* and *Husseyella*. This structure, a propeller-like propulsive organ, is formed by an enlarged blade-like claws (like in *Rhagovelia* and *Chenevelia*), plus two additional blade- or leaf-like appendages (Andersen and Polhemus 1976c , fig. 8.11). A clade comprising our terminals of Gerridae and a subgroup of the traditional "Veliidae," Haloveliinae and Microveliinae (Armisén et al. 2022), is only very tentatively supported by our data, with a tarsal formula 2–2-2 as a groundplan apomorphy (Fig. 3). This interpretation implies secondary modifications (e.g., tarsal formula 3–2-2) and events of parallel evolution. Even if gene expression seems to be one of the most powerful criteria for homology, its reliability decreases with phylogenetic distance. Related taxa like *Tetraripis* and taxa with blade-like claws, i.e. *Papuavelia* and *Xiphovelia* not included in this study should be investigated to complete this study. To get a better overview of the actual phylogeny, those data should be also integrated with palaeontological and morphological data (Klementz et al. 2025). Combining both datasets could therefore increase the overall amount of phylogenetic signal and improve the robustness of the inferred tree. It could also help to reduce the risk that one data source dominates the analysis simply because it contains more characters.

Last tarsomere role in locomotion in insects, and in particular fan-less Gerromorpha

Like in other groups of insects, the midleg tarsus in Gerromorpha (with three or two tarsomeres) dominates propulsion through the coxa-trochanter-femur-tibia-tarsus extension sequence with tripod cycles. The femurotibial joint provides primary thrust leverage and tibial-tarsal articulation, enabling surface tension modulation via hydrophobic setae (Crumière et al. 2016). The femuro-pretarsalis muscle generally plays a critical role in pretarsal positioning and grip modulation during locomotion, prey capture, and substrate adhesion, as shown in Orthoptera (Snodgrass 1942) and Hymenoptera (; Aibekova et al. 2022). This muscle generally originates on the upper femoral region and inserts via an apodeme on the pretarsal base, i.e. the unguitractor plate, enabling precise claw depression/extension (Gorb 1996; Beutel et al. 2014). During walking, it depresses the claws to interlock with microstructured surfaces. In the case of species of Gerromorpha, dense arrays of short setae on the tarsomere push against the water surface tension and help to keep the legs afloat with their waterproof wax coat. In our four species, similar structures are present (Fig. 2) with a tendon going through the leg up to a femoral muscle suggesting a quite similar use of the claws. However, in *Rhagovelia* and *Chenevelia*, the claw can fold in or out, which does not appear to be the case in *Gerris* and *Callivelia*. Other structural features, such as the shape of the unguitractor plate, which appear to have a more complex morphology in *Rhagovelia* and *Chenevelia*, should be investigated to determine a potential link with the possible angle of the claw relative to the tarsomere. In many cases the muscle is combined with a dual-tipped apex of the leg facilitates a reversible grip. It includes the arolium-claw complex in Hymenoptera and Lepidoptera, or the paired pulvilli plus claws in Diptera (Beutel and Gorb 2001). The extension penetrates compliant substrates while the depression recruits compliant pads for smooth detachment, governed by Hill-type force-velocity (Federle et al. 2001; Labonte and Federle 2013). Further investigations should focus on *in vivo* characterization of all leg segments (angles, orientation, and location) and leg muscles to determine muscles-related parameters (muscle volume, fiber length, muscle strengh) and compare them to the forces required for insect rowing movement. Understanding these mecha-

nisms is a key to compare motion at the insect scale but also for the development of insect-inspired robots.

Last tarsomere role in locomotion in fan-bearing species

Some Gerromorph species have evolved specialized structures enabling improved locomotion at the air-water interface. A tight control of the insect over the opening-closing of the fan is important for optimizing maneuvrability, which is essential to escape predators or secure mates and prey. In *Rhagovelia* and *Chenevelia*, this enhanced maneuvrability could be enabled by coordinating the claw-fan synchronization that operates via the presence of femoral–pretarsal depressor muscle. This muscle is linked to a tendon inserted on the unguitractor plate (Federle et al. 2001), and its contraction leads to the synchronous release of the blade-like claws and the folded fan. The trochanter-femoral joints initiate sweeping sculling arcs, while distal tarsal segments maintain stability, complemented by the asymmetric thrust generated by the unfolded fan (Ortega-Jiménez et al. 2025). Recovery stroke repositions the leg chain anteriorly, allowing the proximal–distal coordination. Our morphological data suggest the presence of an active mechanism with the presence of the tendon allowing the contraction of the femoro-pretarsal muscle, whereas no evidence of active process on the unfolding of the fan is shown on µ-Ct data. According to Ortega-Jiménez et al. (2025) data (Figs. S1 and S3) and our data (Supplementary materials V1 and V2), we assumed that the unfolding of the fan should be achieved by a passive elastocapillarity mechanism, with an active claw deployment, synchronized with fan opening at 4200°/s for interfacial propulsion (120 body lengths/s). Active muscular control thus blends proximally with passive distal mechanics (Ortega-Jiménez et al. 2025). It remains uncertain how important the active and passive components are in relation to each other, and whether the opening and closing mechanisms Aibekova et al. 2022 differ. High-speed imaging revealed claw-arolium cycles < 40 ms ($\sim$25 Hz maximum) during reversible grip in ants and bees (Federle et al. 2001), with fast synchronous fibers enabling rapid deployment (Swank et al. 2006). Same cycles are expected in our species. However, we know that water striders' claw extension likely anchors the pretarsus against water due to surface tension while the unfolded fan is mainly used for rapid escape movements, creating thrust (magnitude of the force transfer between the fan and the fluid) asymmetry for sharp turns (Steinmann et al. 2026). Resilin-mediated elastic recoil in tarsal cuticle could then facilitate detachment without energetic cost, complementing the fan's passive mechanics. Due to viscous shear stress, a resistive force, the lamellate fan, similar to a leaky paddle, acts as an equivalent of a membrane oar able to produce 80% of the hydrodynamic drag force (Steinmann et al. 2026). At the end of the rowing process (leg flexion), the femuro-pretarsalis muscle contraction should allow the return of the unguitractor and the claws to their initial position (Fig. 4). The re-folding of the fan to its baseline configuration may occur via interfacial capillary forces at the air–water boundary at the end of the gait cycle, highlighting a passive mechanical solution analogous to other insect locomotor structures in which biomechanical trade-offs favor efficiency over power; e.g. claws amplify muscle output through lever arms (gear ratio $\sim$4:1), generally minimizing metabolic cost during sustained clinging in insects (Federle et al. 2001). The combined functions of both the the fan and of this hybrid system—active proximal musculature driving passive distal structures—may explain *Rhagovelia*'s and *Chenevelia*'s higher maneuvrability over other water striders lacking elaborated pretarsal fans.

Conclusion

Our study sheds new light on the origin of key innovations in Gerromorph. We demonstrate that incorporating characters of the legs, especially tarsomeres into a transcriptome-based phylogeny can provide useful information to help resolve the phylogeny when several nodes remain poorly resolved, such as that of the "Veliidae." It also highlights the fact that both morphology and transcriptomic support the same evolutionary hypothesis. We also show that the emergence of this innovation seems to require the use of internal structures such as the tendon to unfold and refold the claw into the tarsomere. A key point of our work effectively separates what has previously been treated more generally as "fan opening/closing" into two distinct components. In this interpretation, the feather-like part may open through elastocapillarity, whereas the claw-associated part may be under active control via the tendon, two components not distinguished so far. However, there are no internal structures suggesting an active aperture of the fan, supporting a passive mechanism hypothesis. More investigations are needed to understand the proportion of active or massive mechanisms under the use of the claw-fan complex. Investigations with hight-speed camera for instance, could highlight which claw is used, if it is always the same one or if it changes according to behaviour. Finally, biomechanical models, coupling 3D high-speed leg movement (Arroyave et al. 2022), fan-opening kinematics and µ-CT muscle fiber models, should help to improve the understanding of the observed maneuvrability and increased thrust performance across the Gerromorpha.

Author contributions

Conceptualization: J.D., R.B. and J.C., Data curation: J.D., R.B., M.U., and Q.N.X., Formal analysis: J.D., R.B., and A.B., Funding acquisition: J.C., Investigation: J.D., R.B., and A.B., Methodology: J.D., R.B., M.V., A.B., and J.C., Project administration: M.V., Q.N.X., A.K., and J.C., Resource: M.V., Q.N.X., A.K., and J.C., Software: J.D., R.B., M.V. and AB, Supervision: M.V., A.K. and J.C., Validation: RB, AK and JC, Visualization: JD, RB and AB, Writing original Draft: J.D., R.B. and A.B., Writing, review and editing: J.D., R.B., M.V., M.U., A.B., Q.N.X., A.K., and J.C.

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Supplementary data

Supplementary Data available at *ICB* online.

Data availability

The data and scripts, which support the findings of this study, are available in the supplementary materials.

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