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Evolution of sideways locomotion in crabs

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eLife Assessment

This **valuable** study presents a comparative dataset on crab locomotion to examine the evolution of sideways walking. The evidence supporting the authors' claims is largely **convincing**. This work will be of interest to researchers in animal locomotion.

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Abstract

The evolutionary change in the mode of locomotion is often a major evolutionary event, triggering diversification. Sideways locomotion is a defining feature of true crabs (Brachyura) and may have contributed to their ecological success. Yet, the evolutionary origin of this unique behavior remains unknown. Here we show that the prevalence of sideways locomotion in true crabs reflects a single evolutionary origin from a forward-moving ancestor. Our behavioral analysis of 50 live crab species indicates that crab locomotion can be separated into two distinct types, sideways and forward locomotion, with no intermediates. The phylogenetic comparative analysis revealed a single origin of sideways locomotion, with multiple independent reversions to forward locomotion in ecologically specialized groups. The species richness data show that the lineage in which sideways locomotion originated is far more diverse than its nearest outgroups. These results suggest that sideways locomotion acted as a key innovation, potentially promoting adaptive radiation by enabling true crabs to exploit a wide range of ecological niches. Such a rare but innovative behavioral trait provides a framework for understanding how locomotor modes shape evolutionary diversification in animals.

Introduction

The evolution of novel functional traits can enable organisms to exploit previously inaccessible ecological niches (Stroud & Losos 2016; Miller *et al*. 2023). Such key innovations have shaped biodiversity on Earth by facilitating adaptive radiation within lineages. Because locomotion is a fundamental behavior that is involved in most survival and reproductive processes (Alexander 2003; Domenici 2010), innovations in locomotor mechanisms are often linked to adaptive radiations (Astudillo-Clavijo *et al*. 2015; Higham *et al*. 2015; Burress & Wainwright 2019; Hedrick *et al*. 2020; Feiner *et al*. 2021). For example, the evolution of flight in insects opened aerial niches globally and contributed to their enormous radiation (Grimaldi & Engel 2005), whereas modifications of the locomotor skeleton in *Anolis* lizards facilitated localized adaptive radiations within islands (Feiner *et al*. 2021). Most comparative studies on such innovations in locomotor behavior have taken a functional morphological approach. However, despite the recognized importance of behavioral aspects of key innovations (Miller *et al*. 2023), the actual locomotor behaviors have rarely been compared across species, largely due to the challenges of obtaining large, comparative datasets of animal behaviors.

True crabs (Infraorder Brachyura) are iconic for their sideways locomotion, enabling them to achieve fast bidirectional movements (Vidal-Gadea *et al*. 2008), which may be beneficial for escaping from predators (Wolfe *et al*. 2021). Sideways locomotion is associated with greater joint flexibility in the lateral direction and a thorax elongated along the preferred direction of locomotion (Vidal-Gadea *et al*. 2008). This unique locomotion could be a key innovation in decapod crustaceans, as it changes the behavioral axis through which animals interact with the environment (Miller 1949). Moreover, sideways locomotion could have contributed to the ecological success of true crabs. The number of species of true crabs (~7,904 species) far exceeds that of their sister group, Anomura (hermit crabs and others; ~3,437 species), or their closest relatives, Astacidea (clawed lobsters and crayfish; ~792 species) and Achelata (spiny and slipper lobsters; ~153 species), according to the World List of Decapoda, DecaNet (DecaNet eds. 2025). True crabs have also successfully colonized diverse habitats globally, including terrestrial, freshwater, and deep-sea environments (Wolfe *et al*. 2024; DecaNet eds. 2025). In addition, the crab-like body plan has evolved repeatedly among decapod crustaceans, a phenomenon known as carcinization (Morrison *et al*. 2002; Tsang *et al*. 2011; Keiler *et al*. 2017; Wolfe *et al*. 2021). Despite this rich diversity and extensive morphological information, however, data on actual locomotor behaviors of crabs are sparse, and no comparative studies based on large datasets have been conducted thus far, making it difficult to evaluate the role of this unique locomotor mode on crab evolution and diversity.

Although most true crabs use sideways locomotion, some groups—including raninids, majids, and mictyrids—move predominantly forward (Sleinis & Silvey 1980; Faulkes 2006; Vidal-Gadea *et al*. 2008). This raises key questions: when did sideways locomotion originate, how many times did it evolve, and how many times did it revert? With a recent comprehensive crab phylogeny based on genomic data (Wolfe *et al*. 2024), here, we conducted behavioral analyses of 50 live crab species. We aimed to (i) pinpoint the origin of the sideways locomotion within Brachyura, (ii) estimate the number of transitions and reversions between sideways and forward locomotion, and (iii) test whether the emergence of sideways locomotion is associated with species diversification. Our results highlight sideways locomotion as a rare but innovative behavioral trait, providing a framework to understand how locomotor modes shape evolutionary diversification in animals.

Methods

Experimental procedures

We obtained live crabs from multiple sources, including intertidal and subtidal field collections, public aquaria, and local fish markets. Animals were kept only as long as required to record locomotion and were returned to their habitat or handled according to institutional animal care guidelines. Animal care and experimental procedures were approved by the Animal Care and Use Committee of the Faculty of Fisheries, Nagasaki University (Permit No. NF-0060) in accordance with the Guidelines for Animal Experimentation of the Faculty of Fisheries and the Regulations of the Animal Care and Use Committee of Nagasaki University.

Locomotion was recorded in plastic circular arenas (diameter 80–140 cm) whose medium matched each species' native environment (dry, seawater, freshwater, or brackish, with or without bare sand) (Fig. 1a). Individuals were acclimated for 5 min in a bucket and then for 1 min inside a transparent cylinder placed at the arena center to minimize startle responses. After removing the cylinder, each trial was filmed for 10 min using a standard video camera (DSC-RX0, Sony Corporation, Tokyo, Japan) at 30 frames s^{-1}. The locomotion data were obtained from one representative individual per species due to logistical constraints and the low expected within-species variation. Our preliminary observations on several species for which many individuals were available suggest that locomotor direction is a species-level trait that is typically conserved. Thus, this limitation should have minimal effect on our goal of identifying broad interspecific patterns of locomotor direction.

Video analysis

Obtained videos were converted and downsampled to 5 frames s^{-1} for analysis using XMedia Recode 3.5 (*www.xmedia-recode.de*). For each frame, two landmarks along the longitudinal body axis (anterior and posterior carapace margins) were digitized using Kinovea 0.8.27 (*www.kinovea.org*) to estimate the instantaneous body axis and the centroidal position of the animal (Fig. 1b).

To standardize the evaluation of movement directions, we used a reference circle centered on the animal's starting position (Fig. 2). Each displacement bout was defined as the movement from the starting point to the point where the trajectory of the body center crossed the circle, with the next bout beginning once the reference circle was crossed. For each displacement bout, we computed the angle between the pre-movement body axis and the line to the crossed point as the movement direction (Fig. 2). Bouts were classified as forward (0–60° relative to the body axis), sideways (60–120°), or backward (>120°). Backward movements were rare and therefore excluded from the analyses (Fig. S1). To standardize the analysis, we classified both leftward and rightward movements as sideways motion, and movements occurring to the left of the body axis were mirrored to the right. We calculated behavior using the Forward–Sideways Index (FSI): $\mathrm{FSI} = (F - S) / (F + S)$, where F denotes the number of forward bouts and S denotes the number of sideways bouts. FSI values range from −1 (completely sideways) to +1 (completely forward). Species with $\mathrm{FSI} < 0$ were classified as sideways movers, and those with $\mathrm{FSI} > 0$ as forward movers.

The radius of the reference circle was determined systematically for each species (Table S1). For each species, we tested circle radii from 2 mm to 200 mm in 2-mm increments and computed the FSI at each radius. When the circle is too small, digitizing noise and body wobble near the start point tend to drive FSI toward 0. When the circle is too large, animals may turn within the circle before crossing, making the estimate unstable and unreliable. To capture the biologically meaningful motions, we selected the smallest radius at which the FSI showed a clear local maximum or minimum away from zero and then remained approximately stable as the radius increased further.

Ancestral state reconstruction

We extracted and pruned a recently published crab phylogeny (Wolfe *et al.* 2024), which was based on sequences of 10 genes (2 mitochondrial ribosomal RNA coding genes, 2 nuclear rRNA genes, and 6 nuclear protein-coding genes) and included 344 species across most major brachyuran lineages. Because our behavioral dataset did not always perfectly match the species included in (Wolfe *et al.* 2024), we reduced this tree to 44 genera, five families, and one superfamily, allowing closely related taxa to represent the observed species when the same species were unavailable. This approach enabled us to retain the terminals present in our dataset while preserving the placements of major clades relevant to this study (e.g., Eubrachyura, Raninoida).

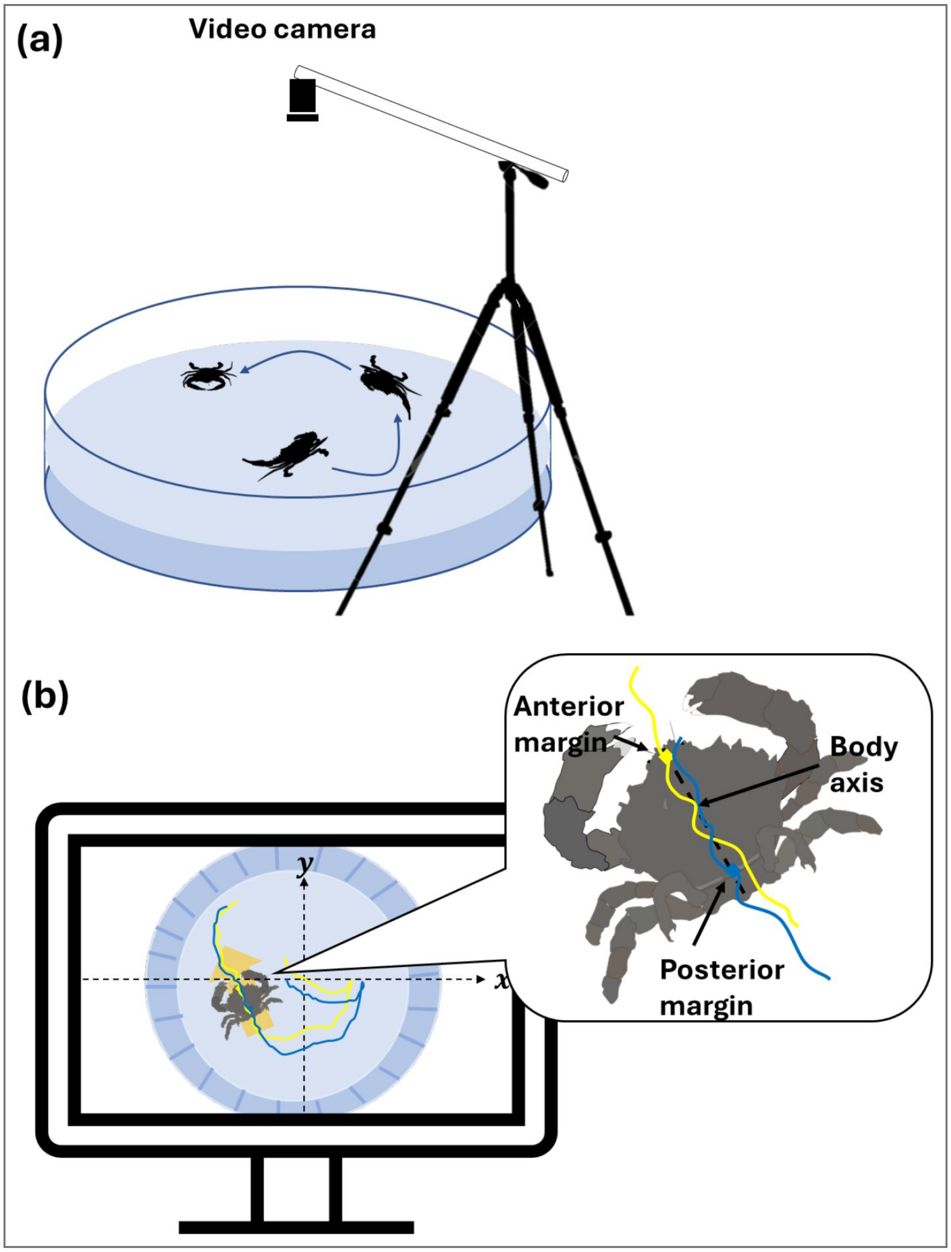


Figure 1. **Video acquisition and analysis workflow.**

(a) Experimental setup used to record each crab's behavior. (b) Extraction of two-dimensional position coordinates from video frames.

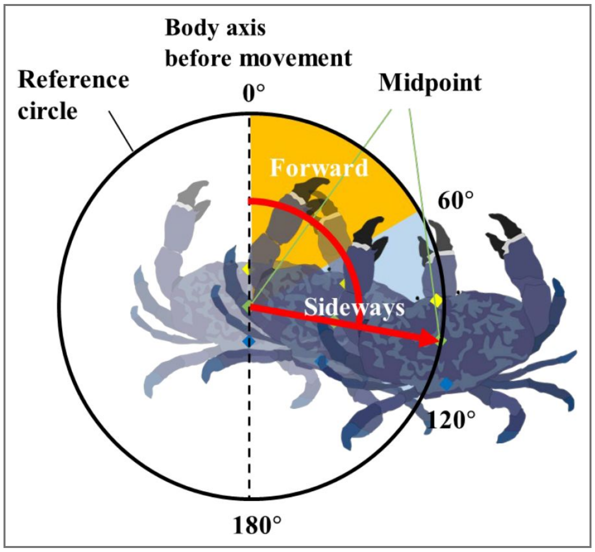


Figure 2. **Method for determining movement directions of each crab.**

For each movement bout, movement direction was defined as the angle between the previous body axis (from tail to head) and the displacement vector of the body's center (referred to as the midpoint). Displacement was measured when the midpoint reached the reference circle. These values across all movement bouts were then used to calculate the Forward–Sideways Index (FSI).

All terminals (44 genera, five families, and one superfamily) were coded as discrete states of either forward or sideways, based on the observed FSI values (positive: forward, negative: sideways). The tree was rooted with a hermit crab terminal (Anomura), for which we assigned the observed locomotor mode of *Coenobita purpureus* from our behavioral data. The node representing the common ancestor of Brachyura and Anomura (Meiura, starting/root node) was fixed to forward as a root prior. This assumption is based on the fact that further outer groups (e.g., crayfish, Astacidea) exhibit forward locomotion (Vidal-Gadea *et al*. 2008). Ancestral states were estimated on the pruned tree using maximum likelihood under equal-rates (ER) and all-rates-different (ARD) models, with model fit compared by Akaike Information Criterion (AIC). To summarize node-wise uncertainty and transition counts, we performed stochastic character mapping (500 replicates) and reported posterior probabilities at key nodes and the posterior distributions of transitions and reversals. All analyses were conducted in R version 4.3.2 (R Core Team 2023) using the packages *ape*, *phytools*, and *geiger*.

Results

Of the 50 species, 35 were classified as sideways movers and 15 as forward movers based on FSI (Fig. 3; Table S1). For example, *Ranina ranina* showed an FSI of 0.89, indicating forward movement, whereas *Geothelphusa dehaani* showed an FSI of -0.70, indicating sideways movement (Fig. 4). FSI values showed a clear separation between these locomotion modes, with little evidence for intermediates: forward movers had a median FSI of 0.82 (range: 0.24–0.94), while sideways movers had a median FSI of -0.80 (range: -1.00 to -0.39) (Fig. 3). This clear separation was supported by Hartigan's dip test (D = 0.083, n = 50, p = 0.007), indicating significant deviation from unimodality. All species-level circular histograms are provided in Supplementary Figure S1.

Model comparison favored the ARD model over the ER model (ΔAIC = 6.23; AIC weights = 0.957 vs. 0.043). Under the preferred ARD model, the transition rate from sideways to forward locomotion was estimated as 0.0029, slightly higher than the forward-to-sideways rate (0.0026). Ancestral state reconstruction placed the origin of sideways locomotion at the base of Eubrachyura (Fig. 5). Stochastic character mapping estimated the posterior probability of forward locomotion as 0.91 for the common ancestor of Brachyura, 0.79 for the common ancestor of Raninoida and Eubrachyura, and 0.24 for the eubrachyuran stem lineage. These results indicate that early-diverging lineages (i.e., Homoloida, Dromiacea, and Raninoida) retained the forward locomotion present in the common ancestor of Brachyura, and that sideways locomotion first appeared at the divergence between Raninoida and Eubrachyura. The ER model yielded a qualitatively similar placement, with only minor differences in the number of inferred transitions (Supplementary Figure S2).

To place these findings in a broader phylogenetic context, we examined locomotor states alongside species richness patterns in early-diverging brachyuran lineages. Cyclodorippoida is identified as the sister group of Eubrachyura, with Raninoida forming the next outgroup (Tsang *et al*. 2011; Wolfe *et al*. 2024). Behavioral data from Raninoida indicate that these crabs move forward (Fig. 3; Table S1). In contrast, the locomotor mode of Cyclodorippidae remains unknown because these crabs inhabit deep-sea environments that preclude direct behavioral observations. Based on DecaNet (World List of Decapoda) counts of accepted extant species (DecaNet eds. 2025), Eubrachyura contains approximately 7,468 described species, whereas Cyclodorippoida includes about 110 species and Raninoida only ~46 species. This sharp disparity highlights that the clade in which sideways locomotion is fixed—at the base of Eubrachyura or potentially in the common ancestor of Cyclodorippoida and Eubrachyura—is associated with far greater taxonomic diversity than the lineages retaining forward locomotion.

Our results also indicate that the sideways mode was largely retained across major eubrachyuran lineages. However, despite this overall stability, we inferred multiple independent reversions to forward locomotion distributed across the tree, including lineages leading to Majidae (*Hyas, Oregonia, Chionoecetes, Schizophrys, Tiarinia*), *Lybia, Arcania, Dorippe, Mursia*, Hymenosomatidae, *Arcotheres*, and *Mictyris*. Interestingly, within Majidae, *Chionoecetes* likely underwent a secondary

Figure 3. **Distribution of Forward–Sideways Index (FSI) values among crab species exhibiting forward and sideways locomotion.**

Orange bars represent species classified as forward movers, and blue bars represent species classified as sideways movers.

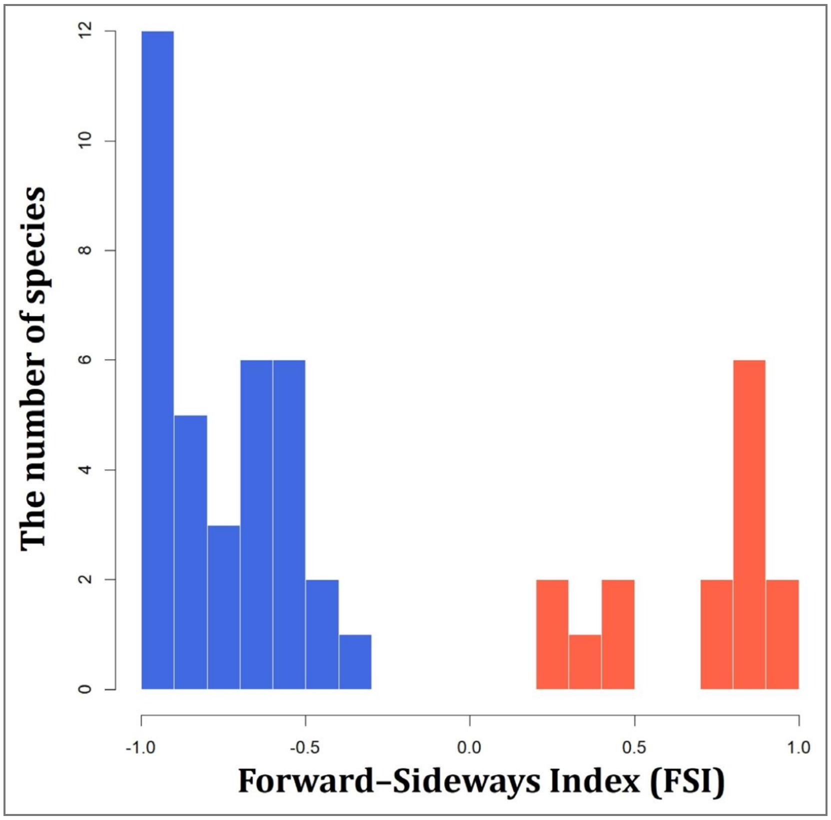
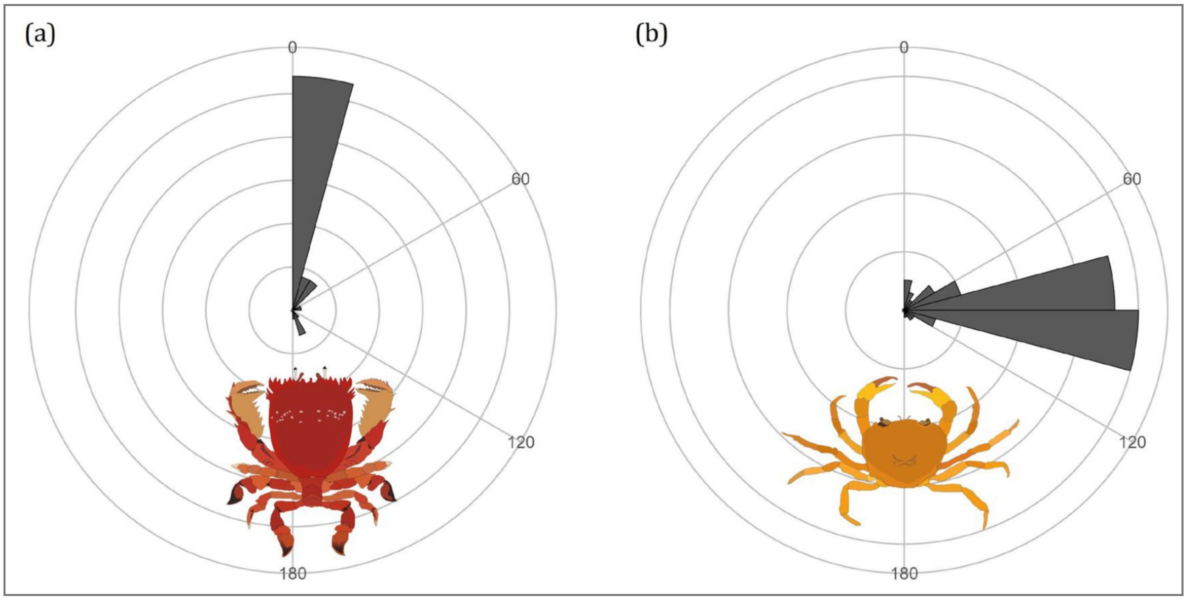


Figure 4. **Representative circular histograms of movement directions in crabs.**

(a) Forward movement in *Ranina ranina* (FSI = 0.89). (b) Sideways movement in *Geothelphusa dehaani* (FSI = -0.70). The 0°-180° axis denotes the crab's body axis before movement, with bars indicating the frequency of movement direction.



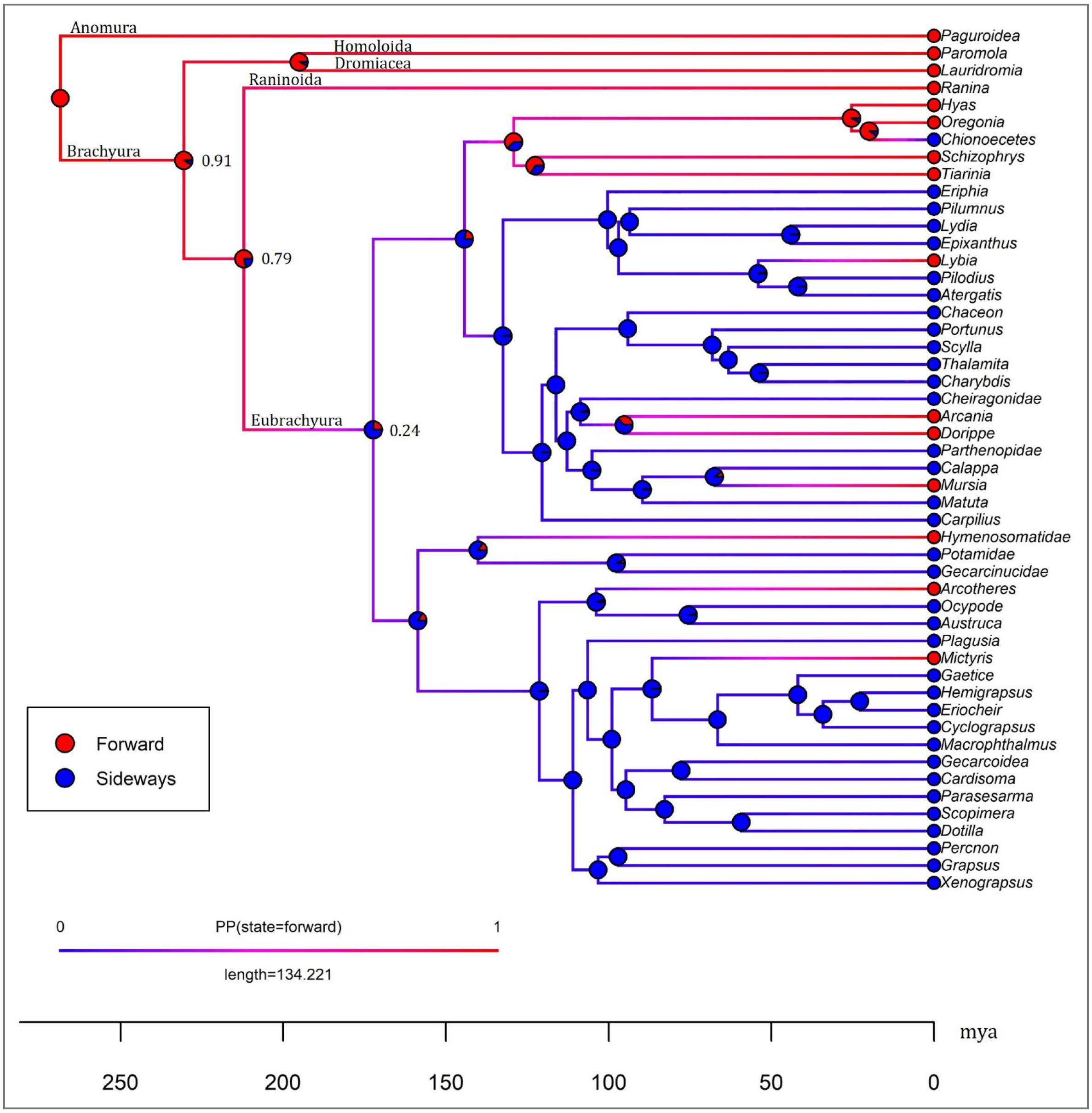


Figure 5. **Ancestral state reconstruction of locomotion in crabs under the all-rates-different (ARD) model.**

Red circles at the tips indicate forward locomotion, whereas blue circles indicate sideways locomotion. Pie charts at internal nodes and along branches represent the posterior probabilities of each locomotor state, estimated from 500 stochastic character maps. The x-axis shows geological time, scaled in millions of years before present (mya).

reversion back to sideways locomotion from a forward-moving ancestor within the group. Stochastic character mapping under the ARD model estimated sideways → forward reversions at a mean of 10.2 (interquartile range, IQR = 9–12) and forward → sideways gains at a mean of 4.1 (IQR = 3–5). Under the ER model, the corresponding estimates were 10.5 (9–12) and 4.6 (3–5), respectively.

These results indicate that the evolution of sideways locomotion is rare but, once established, tends to be stably retained. Reversions to forward locomotion (and subsequent reversions back to sideways locomotion) occur under particular ecological specializations, producing a complex evolutionary pattern across true crabs.

Discussion

Our ever-biggest behavioral dataset on crab locomotion reveals that sideways locomotion originated only once from the forward locomotion ancestor, rather than through multiple independent origins (Figure 5). In other words, the widespread sideways locomotion across true crabs is highly conserved after being inherited from the common ancestor at the base of Eubrachyura. This suggests that modern sideways-moving crabs likely share the same anatomical, neurological, and developmental mechanisms, such as the reduction of motor neurons that control muscles of proximal legs (Vidal-Gadea & Belanger 2013). The single transition event of sideways locomotion contrasts with carcinization, which has occurred repeatedly across decapods (Tsang *et al.* 2011; Keiler *et al.* 2017; Tan *et al.* 2018; Wolfe *et al.* 2021). Carcinization has produced crab-like morphologies in several lineages of Anomura, including porcelain crabs (Porcellanidae), king crabs (Lithodidae), and the coconut crab *Birgus latro*. However, our behavioral observations indicate that porcelain crabs move predominantly backward rather than sideways, and king crabs and the coconut crab move predominantly forward (unpublished data). These examples demonstrate that even when crab-like body forms evolve, the characteristic locomotor mode (i.e., moving sideways) does not necessarily accompany them. This highlights a distinction between morphological convergence and behavioral innovation: while body forms may converge multiple times, fundamental behavioral transitions can be rare.

The single origin and the remarkable diversity of Eubrachyura suggest that sideways locomotion is a key innovation that opened new ecological niches. The main adaptive advantage of sideways locomotion is the ability to move rapidly at similar speeds in both lateral directions (Vidal-Gadea *et al.* 2008; Wolfe *et al.* 2021), which is also supported by an experiment using crab-like robots (Chen *et al.* 2022). Having multiple locomotor directions is highly advantageous for escaping from predators, not only by making the escape direction unpredictable but also by providing multiple optimal escape routes (Domenici *et al.* 2011; Kawabata *et al.* 2023). Despite this advantage, sideways locomotion has clearly been difficult to evolve across the animal kingdom. This locomotor mode fundamentally changes the behavioral axis, affecting other behaviors such as burrowing, mating, and foraging (Atkinson & Eastman 2015; Crane 2015; Asakura 2016; Takeshita & Nishiumi 2022). The clear separation of FSI value distributions across species (Figure 3) indicates that forward and sideways locomotion are alternative modes; one cannot adopt both simultaneously. Thus, in the history of life, the evolution of sideways locomotion represents a unique event that has occurred only in true crabs (Figure 5), and potentially also in crab spiders (Wilcox 2017) and leafhopper nymphs (Chasen *et al.* 2014).

On the other hand, after the transition to sideways locomotion, crabs have experienced at least six independent reversions to forward locomotion (Figure 5). These reversions are particularly associated with major changes in life history traits. For example, soldier crabs (*Mictyris*) predominantly use forward walking (Figure S1; Table S1) in a way biomechanically similar to other forward-walking animals rather than sideways-walking crabs (Sleinis & Silvey 1980). Soldier crabs are unique for their gregarious nature and coordinated collective movements (Murakami *et al.* 2014), which may have brought them back to forward locomotion. Similarly, majoid crabs (e.g., *Oregonia, Tirarinia*) camouflage themselves with seaweed (Sato & Wada 2000; Hultgren & Stachowicz 2009), and pea crabs (e.g., *Arcotheres*) live hidden inside bivalves and other invertebrates, relying on their hosts for protection (de Gier & Becker 2020). Given that the major benefit of sideways locomotion is rapid escape from predators (Vidal-Gadea *et al.* 2008;

Wolfe *et al.* 2021), these examples with alternative strategies of predator avoidance may no longer need sideways locomotion, resulting in secondary losses. These exceptional forward-moving species imply that it is costly to maintain sideways locomotion in crabs, and that they retain evolutionary flexibility to lose this locomotor mode under certain ecological pressures.

Note that a key innovation is not the only process driving adaptive radiation, and the innovation may not always result in radiation (Fürsich & Jablonski 1984; Miller *et al.* 2023). External factors, such as ecological opportunity provided by mass extinction, are also critical for evolutionary diversification (Stroud & Losos 2016). Based on the divergence times reported by (Wolfe *et al.* 2024), the origin of sideways locomotion falls around ~200 Mya (earliest Jurassic, immediately post–Triassic–Jurassic extinction), a recovery interval marked by Pangaean rifting, expansion of shallow-marine habitats, and the early Mesozoic Marine Revolution—conditions that typically increase ecological opportunity (Buatois *et al.* 2016; Schoepfer *et al.* 2022). Disentangling the relative roles of intrinsic innovation and extrinsic environmental change will require trait-dependent diversification analyses (Maddison *et al.* 2007), fossil-informed timelines, and performance tests that link sideways movement to adaptive advantages.

Modes of locomotion—such as walking, swimming, and flying—fundamentally shape how animals interact with the environment, affecting behaviors related to foraging, predator avoidance, and reproduction (Alexander 2003; Domenici 2010). Sideways locomotion in true crabs is also a critical change in the mode of locomotion, whose evolutionary history is characterized by rarity, stability, and occasional reversions. Our case study illustrates how major innovations can open new adaptive opportunities, yet remain constrained by both phylogenetic history and ecological context. By integrating direct behavioral observations with a robust phylogenetic framework, this study expands our understanding of how animal locomotor modes diversify and persist through evolutionary time.

Data availability

Supplementary Figures and Tables contain the data used to generate the figures.

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Additional files

Supplementary Figures (Figures S1, S2)

Supplementary Table S1

Additional information

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Peer reviews

Reviewer #1 (Public review):

Summary:

This is an interesting and well-written manuscript in which the authors set out to answer a simple, old question with a modern toolkit: where in crab evolution did sideways walking arise, how often has it been lost or regained, and is it plausibly linked to the ecological and taxonomic success of true crabs. To do this, they record locomotion from 50 live species, convert each species' movements into a quantitative index that compares forward versus sideways bouts, and then map the resulting states onto a recent crab phylogeny to infer the most likely evolutionary history of locomotor direction.

Strengths:

The strongest part of the study is the dataset itself. Comparable behavioral measurements across dozens of crab species are rare. The authors have done the field and husbandry work needed to make this possible. The overall pattern they recover, that most true crabs are strongly biased toward sideways movement (while a smaller set of lineages move predominantly forward), is interesting and likely to be useful to others. The phylogenetic mapping is also a reasonable way to address the "how many times" question (although this is peripheral to my expertise). The manuscript makes a convincing case that sideways locomotion is not simply a trivial byproduct of a crab-like body plan.

Weaknesses:

Where I am less convinced is in how strongly the authors describe the discreteness of the behavioral categories and the absence of intermediates. The manuscript states that the Forward-Sideways Index shows a clear separation between two locomotor types with little evidence for intermediates, and it cites a statistical test rejecting a single peak in the distribution. However, the histogram in Figure 3 appears structured within each labeled category, with subclusters inside both the forward and sideways groups rather than a single tight peak per group. This matters because the index is built by first placing each movement bout into "forward" versus "sideways" bins using a fixed angle boundary and then collapsing the result into a single ratio. That approach is simple and transparent enough, but it can also hide mixed strategies. For example, a species that produces substantial amounts of both forward and sideways walking can still end up with a strongly positive or negative index, and therefore be classified as a pure "type," even though the underlying behavior is mixed. In that context, rejecting a single peak in the across-species distribution does not, by itself, justify the stronger claim that intermediates are rare or absent.

Related to this, a key methodological choice is the use of 60 degrees as the cutoff between forward and sideways bouts. This boundary may be reasonable as a convention, but the paper does not explain why it is the right place to draw the line, and there is a plausible biological concern that a fixed angular cutoff does not mean the same thing across taxa.

Crabs vary in body shape and in how the legs are arranged around the body. In my own comparative work, for example, some species show an elliptical stance pattern elongated along the preferred direction of travel, while others show a more circular leg arrangement, and the latter can express more mixed forward and sideways behavior. When limb arrangement and body geometry differ across species, the same measured angle can correspond to different underlying mechanics and different functional "degree of sidewaysness." The practical implication is that the reported binary separation may partly reflect the imposed classification rule, rather than a sharp biological divide.

Another limitation that affects interpretation is the decision to use one individual per species. I understand the logistics, and for some questions, a single representative individual can be a reasonable first pass. But it is not strong support for negative claims about intermediates, especially in a group where individuals can change substantially with growth and allometry. Crabs can grow dramatically, often with pronounced allometric shifts in limb proportions that can alter the center of mass location. Size alone can alter the kinematics and choice of locomotor behaviors in crustaceans. In species where appendage proportions change with size, or where certain legs become disproportionately large (or calcified), it is plausible that locomotor direction and the distribution of movement angles shift across ontogeny. That makes it hard to treat a single individual as a complete description of a species-level strategy, particularly for species that fall closer to the boundary between categories.

In sum, this is a valuable and useful behavioral comparative study with a dataset that many in the field will appreciate. The main conclusions about the likely evolutionary placement of sideways walking are plausible, but several of the stronger claims about discrete locomotor types, the absence of intermediates, and the relationship to diversification would be more convincing if the analysis were less dependent on a fixed angular cutoff and on single individuals per species, or if the manuscript framed those points more cautiously so the conclusions track the strength of the evidence.

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Reviewer #2 (Public review):

Summary:

The current work investigates the evolution of sideward locomotion in Brachyura in light of a single evolutionary origin. To this end, the authors first analysed the mode of locomotion in 50 crab species and observed mutually exclusive presence of sideways vs. forward movement. The phylogenetic analysis confirmed that there is indeed a single evolutionary origin for sideways movement, which was sometimes followed by several reversions to forward locomotion. This way, authors demonstrate how locomotor movement modes shape evolutionary diversification in animals by showing that species richness is much higher in side-ways-moving crabs than in the nearest groups. This is an interesting work that integrates behavioural analysis and phylogenetic relations, capitalising largely on crabs. I have a few suggestions and questions.

Firstly, I think the paper spends too much time on a straightforward analysis of the mode of locomotion. I was also wondering whether the phylogenetic analysis could be simply achieved by maximising an objective function in which the modes of movement are inversely coded for two putative groups, with all values calculated at all possible nodes.

Unfortunately, I find that the authors did not sufficiently discuss differences in the ecological niches of species with forward vs. sideways locomotion modes (including challenges of locomotion and substrate).

Likewise, what are the anatomic correlates of forward vs. sideways locomotion? For instance, how are the advantages assumed for sideways movement associated with a flattened body? Is it possible that the mode of motion is secondary to flattened/narrow body structure, which basically limits the distance between legs and thus makes the forward movement difficult - under this logic, the mode of movement would be a secondary phenomenon to body shape traits. How can one differentiate between this alternative and the one that puts the mode of movement in the centre of the story? On a related note, how do different modes of movement relate to the ability to fit into tight spaces - how does it relate to differences in leg joints?

Is it possible that the sideways movement maximises the scanned visual field per unit time/displacement, which may be beneficial for mostly forward-moving predators?

It is really difficult to decipher the information contained in the nodes (circles) in the printed black-and-white version of the manuscript.

Briefly, although I find the study interesting, the presented complexity may not be necessary given the endpoints; it can be achieved much more simply. Furthermore, the degree to which the conceptual analysis of different modes of locomotion was exercised was limited. The general approach may serve as a good model for the evolutionary analysis of other traits. The demonstration of traceability of the relations in question is a major contribution of the work.

Strengths:

The research question and the novel combination of different data types.

Weaknesses:

The complexity of the methods used, along with a limited discussion of the potential dynamics that may underlie the evolution of the sideways movement mode.

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