Biomechanics of terrestrial locomotion in fishes

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Abstract

Amphibious fishes employ diverse biomechanical strategies to navigate terrestrial environments, providing unique perspectives on locomotor evolution. These fishes use axial-based undulation, appendicular-based propulsion, and/or axial-appendicular coordination to generate forward motion on land. Although some of these behaviors resemble walking, they do not meet the biomechanical criteria for true walking gaits. Instead, walking-like behaviors have evolved across Chondrichthyes and Osteichthyes to facilitate energy efficiency, access to terrestrial resources, predator avoidance, and exploitation of novel habitats. Locomotor performance is highly variable across species and substrates, with kinematic variation enabling modulation of ground reaction forces, stride dynamics, and gait transitions in response to environmental challenges. Anatomical specializations, including reinforced pectoral girdles, modified fin articulations, and enhanced neuromuscular control, contribute to effective terrestrial

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propulsion and weight support. This chapter examines the biomechanical diversity of terrestrial locomotion in fishes, compares their locomotor strategies to those of tetrapods, and explores potential functional constraints shaping substrate-based in fishes during terrestrial movements.

1 Background

Most fishes are exclusively aquatic but amphibious behaviors – the natural tendency to spend part of their lives on land – evolved 87 times across 41 families and over 200 extant species (Damsgaard et al., 2020; Turko et al., 2021; Wright and Turko, 2016), comprising ~0.5 % of the 34,190 species of ray-finned fishes described to date (Dornburg and Near, 2021). A species' amphibious capacity is categorized based on their emersion tolerance, which spans from mere minutes to several months, and degree of preference for terrestrial habitats (Turko et al., 2021). This preference ranges from passive, forced emergence—driven by inhospitable conditions—to active emergence, where individuals seek terrestrial environments to gain fitness advantages such as enhanced reproductive success, access to novel food sources, and improved predator evasion (Turko et al., 2021). Examples of passive emersion include fishes becoming stranded after water levels decrease during low tides (Martin, 1995), droughts, or anthropogenic perturbations such as irrigation, water diversion, and hydroelectric dams (Nagrodski et al., 2012). Active emergence can be driven by the need to escape hypoxic water in intertidal fishes (Richards, 2011; Tigert et al., 2022), reproduce and deposit eggs on land in killifish and California grunion (Martin et al., 2004; Wells et al., 2015), and navigate natural or physical obstructions such as waterfalls or weirs in gobies, lamprey, and eels (reviewed in Ch. 7, Vol 41: Maie et al., 2025). Of the 87 lineages with amphibious species, harsh aquatic conditions promoted the evolution of amphibious behaviors in only 14 lineages so most fishes likely emerged onto land to access novel food, raise eggs in oxygen-rich environments, reduce competition, evade predators, bask in warmer temperatures to increase their metabolism, or obtain other direct benefits (Turko et al., 2021).

1.1 Terrestrial traits

While forced emersion or short forays over brief time periods can be accomplished with behavioral changes in even fully or primarily aquatic fishes (Minicozzi et al., 2020), fishes with higher degrees of amphibiousness exhibit morphological and physiological traits that improve their fitness and survival on land. In only two weeks, acclimatization to terrestrial environments in mangrove killifish (*Kryptolebias marmoratus*) resulted in an increased proportion and angiogenesis of red (slow-twitch) muscles to support slow and sustained locomotion through relatively fatigue-resistant muscle fibers and increased delivery of oxygen to those muscle fibers, respectively (Brunt et al., 2016). Gill lamellae typically have a high surface area for maximizing the diffusion of respiratory gases (oxygen and carbon dioxide) and are supported by buoyancy underwater, butcollapse on land and subsequently reduce the respiratory efficiency of the gills. However, *K. marmoratus* developed stiffer gill arches and calcified gill filaments to withstand the downward effects of gravity after only one week of terrestrial acclimatization (Turko et al., 2021, 2017). On the other hand, *Polypterus* fish had 28 % more white (fast-twitch) muscles when raised in terrestrial rather than aquatic environments, particularly in their pectoral fins that are used to produce short bursts on land, suggesting that phenotypically plastic responses can be linked to the way they move their propulsive structures during locomotor behaviors (Du and Standen, 2020). Increased ossification and lengthening of fin bones can result from terrestrial acclimation over several months (Du and Standen, 2020) and terrestrial adaptations over evolutionary timescales (Zhou et al., 2023), which can improve propulsion and weight support on land. The evolution and plasticity of phenotypic traits that enable amphibious behaviors is a burgeoning area of research that has many broader implications, such as identifying the anatomical changes required for vertebrates to become terrestrial.

The documented shifts in muscle composition and gill morphology in *Kryptolebias marmoratus* and *Polypterus* spp. underscore the role of phenotypic plasticity as a potential precursor to evolutionary change. These short-term, reversible modifications, such as increased red muscle fibers or stiffer gill structures, enhance performance on land without requiring fixed genetic alterations. From an Evo-Devo perspective, such plastic responses can expose cryptic genetic variation or alter developmental pathways in ways that bias evolutionary trajectories. Over time, repeated exposure to terrestrial conditions could canalize these plastic traits into heritable features, contributing to the stepwise anatomical innovations observed in the fin-to-limb transition (Standen et al. 2014). Thus, plasticity is not only a survival mechanism but may also act as a bridge between environmental challenge and evolutionary innovation. We recommend readers to read "*Micro- and Macroevolution of Fish Biomechanics*" in this volume for further discussion on the causes and consequences of evolutionary innovations (Ch. 10, Vol 41: Price and Evans, 2025).

1.2 Sustained vs. intermittent locomotion

Slow speed, substrate-based locomotion occurs across vertebrates, and can be broadly categorized as axial-based, axial-appendicular-based, and/or appendicular-based locomotion (Fig. 1). Extant fishes that employ fin-based locomotion to move along the substrate - whether underwater or on land – are often called "walking fishes", but these behaviors do not meet the criteria for a "true walking gait" and are, thus, more appropriately classified as walking-like movements (Struble and Gibb, 2022). These modes of terrestrial locomotion exhibit a high degree of interspecific and intraspecific variability, suggesting

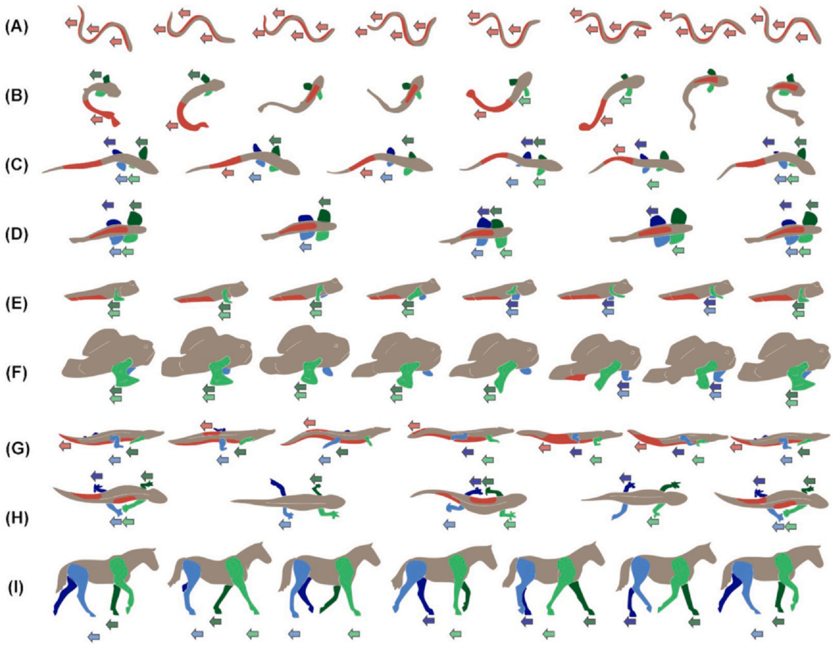

FIG. 1 Comparison of axial-based, appendicular-based, and axial-appendicular-based modes of substrate-based locomotion in extant vertebrates. Representative taxa include (A) ropefish (*Erpetoichthys calabaricus*), (B) "walking" catfish *Clarias batrachus*, (C) epaulette sharks (*Hemiscyllium ocellatum*), (D) blind cavefish (*Cryptotora thamicola*), (E) Atlantic mudskippers (*Periophthalamus koelreuteri = barbarus*), (F) giant frogfish (*Antennarius commerson*), (G) Nile crocodiles (*Crocodylus niloticus*), (H) lizards, and (I) domestic horses (Equus caballus). The locomotor structures involved in each taxon is represented in red for the axial system, blue for the pelvic appendages, and green for the pectoral appendages. The arrows represent the direction in which these locomotor structures would be moved to generate forward propulsion of the whole body. *Reproduced from Struble and Gibb (2022) with permission from Oxford University Press.*

they are far from *stereotyped* (*sensu* Wainwright et al., 2008). Axial-based locomotion is common in elongate fishes with paired fins that are reduced or absent, appendicular-based is currently only documented in mudskippers, and axial-appendicular-based locomotion is observed across a diverse range of ecologies, morphologies, and taxonomic groups. Moreover, fishes can switch between these locomotor modes, especially when traversing challenging terrain. Recent studies that have contributed towards a broader taxonomic sampling across fishes have revealed striking amounts of functional diversity between and within taxa and the application of 3D kinematics, 3D kinetics, mechanical properties, and/or phenotypic plasticity experiments have provided a finer lens to examine patterns of convergence and divergence in the phenotypic traits associated with terrestrial locomotion.

Amphibious fishes also employ intermittent modes of terrestrial locomotion that may shape their overall phenotype; while this is beyond the scope of this chapter, we briefly summarize some examples. Jumping biomechanics has been described in blennies (Hsieh, 2010), killifishes (Axlid et al., 2023; Bressman et al., 2016; McFarlane et al., 2019; Perlman and Ashley-Ross, 2016), mudskippers (Harris, 1960; Pace, 2017; Swanson and Gibb, 2004), galaxiids (Magellan, 2016), and other aquatic and amphibious fishes (Gibb et al., 2013, 2011; Sayer and Davenport, 1991). Some fishes will also temporarily emerge onto land to capture terrestrial prey (reviewed in Heiss et al., 2018). Examples of intermittent locomotion along the shoreline have been documented in eel-catfish (*Channallabes apus*), Wels catfish (*Silurus glanis*), moray eels (*Echidna nebulosa*), and four-eyed fish (*Anableps anableps*) (Cucherousset et al., 2012; Mehta and Donohoe, 2021; Michel et al., 2015; Van Wassenbergh, 2013). Readers should refer to the *"Biomechanics of adhesion in fishes"* (Ch. 7, Vol 41: Maie et al., 2025) in this volume to learn more about climbing behaviors in mudskippers (Hidayat et al., 2022; Wicaksono et al., 2018, 2016), gobies (Blob et al., 2023, 2006; Maie, 2022), lamprey (Kemp et al., 2009), *Anabas* perch (Davenport and Matin, 1990; Kuznetsov, 2022; Li et al., 2024), and many other species.

1.3 Emerging themes

General overviews of aquatic vs. terrestrial locomotion in fishes have been described in previous work (Pace and Gibb, 2014; Renous et al., 2011), so we focus on synthesizing the emerging patterns made in the past decade that have been largely attributed to compraisons across broader taxonomic diversity and/or environmental conditions. First, improvements in the accessibility and cost of 3D imaging techniques and machine learning have revolutionized our ability to achieve high-throughput analyses of morphology and behavior, providing the large datasets required for studying broadscale patterns and processes associated with the evolution of terrestrial locomotion in fishes. Other physiological data (e.g., electromyography, 3D kinetics) can be logistically difficult to collect in vivo but are crucial to understanding the internal and external forces, respectively, that could promote some of the anatomical changes (e.g., stiffer and longer bones) that are proposed to improve terrestrial locomotion in fishes. Consequently, empirical data has been limited to a relatively small proportion of the amphibious fishes that voluntarily sustain motion on land but these data sets have steadily increased in taxonomic diversity over the past decade. Another emerging pattern is that fishes using appendage-based locomotion to walk along substrates underwater or on land can possess phenotypic traits that are functionally comparable to tetrapods, suggesting that the terrestrial capabilities of fishes may have been previously underestimated. For instance, fishes are typically characterized by pelvic girdles that are completely detached from the vertebral column, but blind cavefish (*Cryptotora thamicola*) have robust pelvic girdles that are connected to the vertebral column, features that are more typical of tetrapods than fishes (Flammang et al., 2016).

In this chapter, our aims are to summarize the unique aspects of substrate-based locomotion of fishes on land versus underwater, identify the phenotypic features that enable effective terrestrial locomotion, highlight recent scientific advances achieved with genomics and evolutionary development ("Evo-Devo"), and then propose promising lines of inquiry to stimulate future research on the biomechanics of terrestrial locomotion in fishes.

2 Modes of sustained locomotion on land

2.1 Axial-based locomotion

Axial-based locomotion is characterized by lateral undulations that propagate down the body in an anteroposterior direction (Fig. 1A) – with negligible contributions of the (often reduced or lost) paired fins – and is primarily used by elongate fishes (Pace and Gibb, 2014). *Anguilla* is an iconic example for axial-based locomotion underwater ('body-caudal-fin swimming') and on land ('lateral undulations'), using standing waves of axial muscle contractions (Di Santo et al., 2021). Compared to body-caudal-fin swimming, lateral undulations on land exhibit higher amplitudes of bending that travel down the entire length of body while producing lower power output (Ellerby et al., 2001; Gillis, 1998; Gillis and Blob, 2001). African lungfish (*Protopterus annectens*) use a modified version of axial-based terrestrial locomotion that involves standing waves of muscle contractions in the trunk region – but not the caudal region of the axial system – that resembles terrestrial walking in salamanders, suggesting that neuromuscular control of lateral undulations may be conserved across vertebrates (Horner and Jayne, 2014). Other fishes that use axial-based terrestrial locomotion include: *Erpetoichthys calabaricus* ropefish (Mehta et al., 2021; Pace and Gibb, 2011; Ward et al., 2015), *Xiphister mucosus* pricklebacks (Clardy, 2012), *Lepidosiren* lungfish (Mehta et al., 2021), *Gymnallabes typus* catfish (Ward et al., 2015), *Monopterus albus* swamp eels (Bressman, 2022; Kuznetsov, 2022; Mehta et al., 2021), galaxiids (Magellan, 2016), and gunnels (Kawano pers. obs.; Renous et al., 2011).

2.2 Appendicular-based locomotion

The least common mode of terrestrial locomotion in fishes is appendicular-based and currently only known in the 'crutching' gait used by mudskippers (Family Oxuceridae; Fig. 1E). During the first half of stance, the pectoral fins are synchronously pushed down onto the substrate while their pelvic fins are retracted and then folded up against their venter to swing their center of mass upward and then forward. In the latter half of stance, the pectoral fins retract while the pelvic fins protract to act as a shock-absorber as the mudskipper lands its venter onto the substrate (Pace and Gibb, 2009; Quigley et al., 2022).

The antagonistic actions between the pectoral and pelvic fins act as a mechanical piston that improves the locomotor efficiency of crutching compared to the sand goby (*Istigobius ornatus*) that lacks retractable pelvic fins (Wicaksono et al., 2018). Although the pelvic fins are much smaller than the pectoral fins and do not contribute much towards accelerating the body, they do produce enough thrust to counteract their initial braking action (Harris, 1960). Typically, their body axis is held straight and balanced on the ventral aspect of their caudal fin to reduce frictional drag (Harris, 1960; Pace and Gibb, 2009). The anterior half of the body is pitched upwards at around 5–11° while yaw is maintained around 0° (Quigley et al., 2022). In appendicular-based gaits such as crutching, propulsion is produced exclusively by the paired fins while the body is dragged behind (Harris, 1960; Kawano and Blob, 2013).

2.3 Axial-appendicular-based locomotion

Axial-appendicular-based locomotion is powered by coordinated movements of the paired fins and body axis (Fig. 1B, C and D) but, in a large proportion of fishes, the pelvic fins are folded up against the body and do not directly contribute to terrestrial locomotion. Unlike axial-based locomotion where the amplitude of lateral bending remains consistent as it is propagated down the body axis, axial-appendage-based locomotion involves a standing wave of muscle contraction with higher amplitudes of lateral bending at the head and tail than at the center of mass (Pace and Gibb, 2014). The general sequence of events involves (1) curving the tail towards the head, (2) retracting and straightening the tail while lifting the anterior end of the body and pivoting the center of mass over one pectoral fin, (3) and then swinging the contralateral pectoral fin forward (Pace and Gibb, 2014). The pectoral fins of some species function primarily as structural supports – or biomechanical struts – that stabilize body posture and facilitate force transfer during terrestrial locomotion without directly generating mechanical work or propulsion, in contrast to motor-driven appendages that actively produce thrust (Bertram, 2016). Others may cycle between protraction and retraction to generate propulsion but, at least in *Polypterus*, the pectoral fins primarily act to lift the anterior body up rather than contributing towards propulsion or stabilization (Bhamra, 2022). Some examples of fishes that use axial-appendicular-based locomotion include walking *Clarias* catfishes, sculpins, *Channa* snakeheads, *Polypterus* bichirs, and *Arapaima* (Bressman, 2022; Bressman et al., 2019, 2018; Johnels, 1957; Kuznetsov, 2022; Pace and Gibb, 2014). Maie et al. (2025) describes how groups of catfishes (*Clarias* spp. and *Heteropneustes fossilis*) have extended spines on their pectoral fins that are used to push off the ground (Ch. 7, Vol 41), effectively lengthening the pectoral fin to potentially increase angular acceleration.

There are some distinct variations between species, however. Sculpins tend to slide their ventrum along the substrate rather than lifting their center of mass off the substrate, and, tidepool sculpins (*Oligocottus maculosus*) pivot their bodies over the base of their pectoral fins rather than the distal ends of the fin rays (Bressman et al., 2018). The same study found that two species of subtidal sculpins (*Leptocottus armatus* and *Icelinus borealis*) were less effective at producing forward movement because they do not protract-retract their pectoral fins whereas tidepool sculpins do. *Polypterus* switch between planting the lateral vs. medial side of the pectoral fins during stance based on the substrate type (Standen et al., 2016). Some species of Neotropical armored catfishes (Loricaridae) coordinate movements of their mouth with axial-pectoral-based locomotion (Bressman et al., 2021). Moreover, most fishes lift their bodies while using axial-appendage-based locomotion but snakeheads *(Channa* spp.) do not, likely due to constraints in lifting their relatively large bodies (Bressman et al., 2019). In Northern snakeheads (*Channa argus*), small individuals (less than 3.5 cm in total length) use ballistic jumps that resemble aerially-directed C-start escape responses also known as tail-flip jumps *sensu* (Gibb et al., 2011) whereas larger individuals perform a 'crawling' behavior where the body bends and rolls onto one pectoral fin while the tail is pushed against the ground to propel the animal forward and then bend the body to roll onto the contralateral pectoral fin (Bressman et al., 2019). However, the pectoral fins do not necessarily move in phase with one another, potentially because they primarily serve to reduce roll and thereby stabilize the body rather than produce propulsion.

Axial-appendicular-based locomotion can also combine lateral undulations with asynchronous movements of both the pectoral and pelvic fins in a walking-like behavior that resembles diagonal couplet walks in salamanders. Balitorid hillstream loaches (*Cryptotora thamicola*) use a lateral sequence, diagonal couplet gait to move through fast-flowing waters in their natural habitats and forward displacement is primarily driven by girdle rotation rather than protraction-retraction of their paired fins (Fig. 1D), which is facilitated by a robust pelvic girdle that is connected to the vertebral column (Flammang et al., 2016). Although there are other balitorids that use a diagonal couplet gait during terrestrial locomotion, *C. thamicola* advances the greatest distance forward and has the lowest stride frequency (Crawford et al., 2022). Species in Homalopteroidinae typically use a swimming-like behavior to slide across the substrate that is coordinated with short, fast cycles of the paired fins whereas species in Balitorinae (e.g., *C. thamicola*) have a steady and controlled speed with distinct swing vs. stance phases of the pectoral fins (Crawford et al., 2022). Epaulette sharks (*Hemiscyllium ocellatum*) use a "walk-trot" diagonal couplet (Fig. 1C) to emerge and crawl over exposed sections of coral reef (Pridmore, 1994). Initial observations suggest that walking-like behaviors are relatively conserved between aquatic and terrestrial locomotion in *H. ocellatum*, but kinematic comparisons between fully submerged vs. partially emerged individuals reveal distinct differences. Compared to fully submerged trials, the partially emerged walking-like behaviors of *H. ocellatum* have higher fin cycle frequencies, faster organismal speeds, wider rotation of the pectoral and pelvic girdles, and more extensive abduction and adduction of the pectoral fins (Travis, 2020). These amphibious fishes are also compelling models to compare and contrast the biomechanics of terrestrial locomotion between fish vs. tetrapod body plans, providing key insights into potential biomechanical constraints during the evolutionary transition from water to land in vertebrates during the Devonian period.

2.4 Cranial-axial-based

Some fishes use cranial-axial-based locomotion to sustain movements on land. Terrestrial locomotion in climbing perch (*Anabas testudineus*) may superficially resemble axial-appendicular locomotion but is distinct because subopercular spines on the skull act as surrogates for appendages (Davenport and Matin, 1990; Li et al., 2024). Unlike paired fins that can generate propulsion, the subopercular spines can only act as 'struts' that serve as shock absorbers and pivot points to rotate the body forward. The operculum is passively oriented to enable the subopercular spines to contact the substrate and has a limited range of motion, which is proposed to provide stable support without the need for stabilization from muscle contractions (Li et al., 2024). Although subopercular spines and paired fins can act as locomotor struts, the subopercular spines are less likely to be effective for forward displacement given that shorter struts typically have lower moments of inertia than long struts. Moreover, African lungfishes (*P. annectens*) use a 'head-crutching' behavior where they anchor their head into the substrate and then contract their axial muscles to vault their body forwards, with negligible contributions from the paired fins or tail (Falkingham and Horner, 2016). These and preceding examples underscore that behavioral flexibility can promote functional diversity without requiring major changes in morphological diversity.

3 Context-dependent variation on different terrain

The biomechanics and performance of animal locomotion depends on the environmental context, and fishes exhibit locomotor flexibility (*sensu* Wainwright et al., 2008) across compliant, inclined, and/or heterogeneous substrates. Fishes are generally slower on land than underwater, and more so on terrain that is inclined, deformable, and/or loose due to the lack of push points to gain purchase of the ground and generate propulsion. Push points are unstable on flowable substrates, such as loose pebbles, and more so when the angle of inclination becomes steeper. Studies on ecologically relevant substrates reveal far greater functional diversity and flexibility in the terrestrial locomotion of fishes than previously described.

Axial-based locomotion generally maintains lateral bending across terrestrial substrates, but can involve more exaggerated movements or gait transitions on particularly challenging terrain. *Anguilla* eels increase their amplitude of lateral bending on land by changing the activation intensity and duration in their axial muscles (Gillis, 1998; Gillis and Blob, 2001). The lateral bending of *A. rostrata* exhibits comparable kinematic profiles across substrate types (fixed pebbles, loose pebbles, packed sand) but is more effective on flat, sandy substrates and least effective on inclined, loose pebbles (Redmann et al., 2020). Forward displacement is a proxy for effective locomotion and increases when animals produce larger magnitudes of ground reaction forces to increase propulsion. When swamp eels (*Monopterus albus*) move on mud, they maintain forward propulsion in the absence of push points by switching from a traveling wave of lateral bending to sidewinding (Kuznetsov, 2022), which involves vertically lifting portions of the body that then make static contact with the substrate (Jayne, 2020). The benefit of gait transitions is evident in rock gunnels (*Pholis gunnellus*) which thrash when relying solely on lateral bending on smooth substrates, achieving effective locomotion only on heterogeneous substrates with push points (Renous et al., 2011). Obligate axial-based locomotors exhibit limited flexibility in terrestrial movement due to the absence or non-use of appendages, which restricts their ability to modulate propulsion and stability. This limitation helps explain why species capable of integrating paired fins into their locomotor repertoire via axial-appendage or appendage-based movements tend to exhibit greater locomotor flexibility across variable terrestrial substrates. The addition of fin-based support and propulsion can enhance maneuverability, improve postural control, and allow more effective substrate interaction compared to purely axial-based locomotion.

Fishes using appendage-based locomotion typically switch to axial-appendage-based locomotion on challenging terrain. Mudskippers will alternate between crutching with their pectoral fins and planting their tail side-to-side when moving on deformable substrates (e.g., loose sand), particularly when moving on inclines (McInroe et al., 2016). Positioning the tail broadside to the direction of travel helps to reduce slipping, and then primes the tail to increase forward displacement when it is straightened and pushes against the substrate (McInroe et al., 2016). Mudskippers also adjust their locomotor mechanics when moving on deformable, non-elastic substrates (Fig. 2). They increase both the duration and surface area of fin contact with the ground to compensate for energy loss. To extend their reach, they increase the protraction of their pectoral fins. They also grip the sand more effectively by arching the lepidotrichia of their pectoral fins, which helps reduce slipping. Finally, they negatively pitch their head toward the substrate and adopt a crouched posture to enhance stability (Naylor and Kawano, 2022). Axial-appendage-based locomotion in mudskippers still involves synchronous protraction-retraction cycles of the pectoral fins but can also be asynchronous in other fishes.

Axial-appendage-based locomotion can be highly variable and tends to be more effective on relatively complex rather than simple substrates. *Channa* fishes move longer distances and at faster speeds when navigating heterogeneous substrates (i.e., natural grass, smooth boat deck with rubber gripping

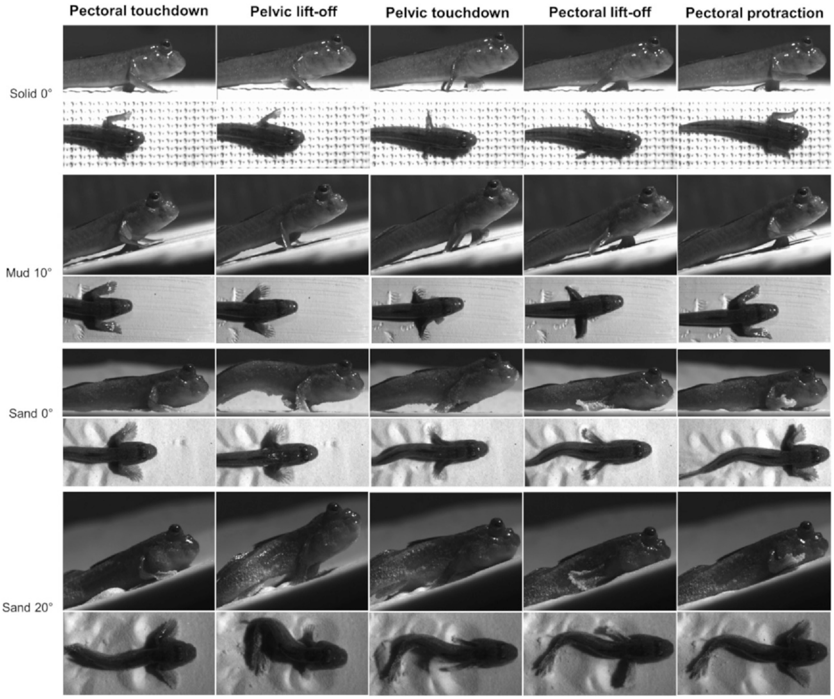

FIG. 2 Mudskippers shift from appendicular-based to axial-appendicular-based locomotion when traversing flowable sand but maintained appendicular-based locomotion on mud. When they apply weight to dry sand, mudskippers experience some sinking and slipping that they counteract by orienting their caudal fins broadside to the direction of movement, using their caudal fin as an anti-skid device and/or for propulsion, and arching their body axis vertically. These modifications were more pronounced when the sand was inclined at +20 degrees Naylor and Kawano (2022). *Reproduced with permission from Oxford University Press.*

points) compared to flat ones (i.e., artificial grass, bench liner) (Bressman et al., 2019). *Polypterus senegalus* use different gaits based on the environmental context: axial-based locomotion (gait I) on pebbles versus axial-appendicular based locomotion (gait II) on flat substrates, with the latter further subdivided based on whether the pectoral fin contacts the substrate with only the lateral/flexor side (gait IIa) or alternates between the lateral/flexor and medial/extensor sides (gait IIb) (Standen et al., 2016). Gait IIa has more consistent fin kinematics between steps on a given substrate compared to gait IIb, and modulates the magnitude of body and fin movements across flat substrates (mud, sand, plastic) whereas gait IIb does not. In both, the pectoral fins have highly variable kinematics that likely reflect their role in preventing the body from rolling while laterallly bending on land.

4 Functional comparisons between fins and limbs

4.1 Paleontological comparisons

Limbs were historically thought to be a key innovation that enabled the occupation of novel ecological niches and subsequent diversification of stem tetrapods but the earliest digit-bearing stem tetrapods were fully aquatic (Coates, 1996). As a result, there is substantial value in identifying the salient features that may have conferred digit-bearing stem tetrapods with the locomotor biomechanics to move more effectively on land compared to non-digit-bearing stem tetrapods (i.e., extinct lobe-finned fishes during the Devonian period). Early observations of fossil specimens from stem tetrapods proposed that there were physical limitations in the paired fins that precluded non-digit-bearing stem tetrapods from emerging out of the water. For instance, in the late 1800's, Huxley suggested that the angle and rotation of the pectoral fins during locomotion would have created an unrealistic amount of torsion ('twisting') in the humeri of fishes with tetrapod-like appendages, like the crossopterygian *Ceratodus* (Bowler, 2007).

The humeri in the appendages in non-digit-bearing stem tetrapods were short and stout, which would have prioritized strength and flexibility about the elbow to improve performance during swimming or substrate-based locomotion, whereas digit-bearing stem tetrapods had humeri that were flattened and L-shaped that would have presumably improved their substrate-based locomotion but not to the same extent as the cylindrical shapes of humeri in crown tetrapods (Dickson et al., 2021; Fig. 3). Despite these morphological differences, stem tetrapods were built for structural strength whereas crown tetrapods were built for increased stride length and greater range of motion (Dickson et al., 2021). Thus, Huxley's initial predictions may have been exaggerated because non-digit-bearing stem tetrapods could not attempt the extensive fin rotations that would have caused the failure that he proposed. Although the origin of terrestrial capacities emerged in digit-bearing tetrapods, recent analyses show that terrestrial adaptations for weight-bearing were already present in non-digit-bearing stem tetrapods such as the Devonian fish, *Eusthenopteron* (Clarac et al., 2024). Moreover, finite element analyses indicated that the non-digit-bearing stem tetrapod, *Tiktaalik rosae*, could stand, crawl, and walk on land and potentially lift its anterior end above the ground (Hohn-Schulte et al., 2013).

4.2 Adaptations in the girdles

An important anatomical shift during the evolution of terrestrial locomotion involves the transformation of the pectoral and pelvic girdles and their integration with the axial skeleton. In most fishes, the pectoral girdle is attached to the skull, forming a rigid complex with limited mobility, while the pelvic girdle is entirely free-floating, unattached to the vertebral column. This anatomical

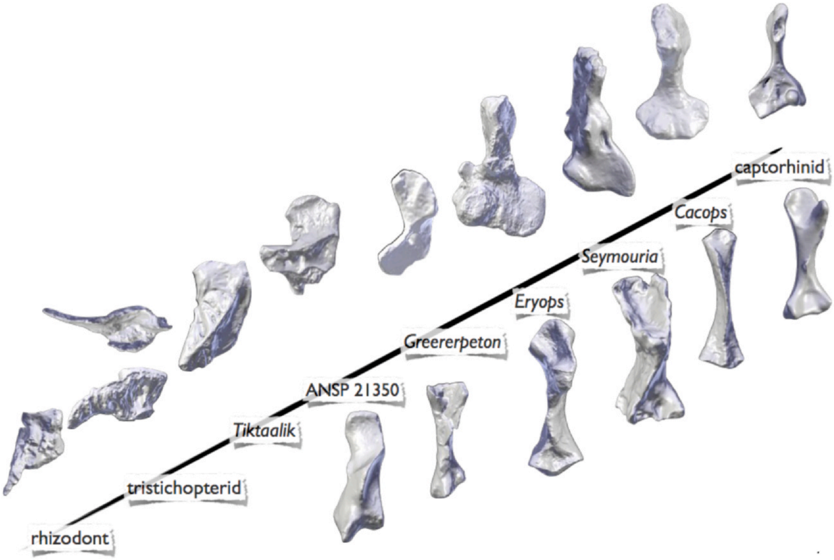

FIG. 3 Comparison of the ventral surfaces of stylopods from stem tetrapods and crown tetrapods, with humeri above the black diagonal line and femora below. Non-digit-bearing stem tetrapods include lobe-finned fishes from the Devonian that had relatively short, solid, and robust humeri that possessed a large flange-like process ('ventral ridge') for muscle attachment (e.g., rhizodonts, ristichopterid, elpistostegalids such as *Tiktaalik*). The humeri of *Tiktaalik* had a morphology that was somewhat intermediate to other non-digit-bearing stem tetrapods and the L-shaped humeri of digit-bearing tetrapods (e.g., ANSP 21350, *Greererpeton*). The humeri of crown tetrapods were more cylindrical than stem tetrapods and lacked the ventral ridge, and exhibited torsion ('twisting') of the distal end that would have presumably increased stride length. The femora of digit-bearing stem tetrapods were generally cylindrical but blockier than crown tetrapods. Images were produced from 3D surface scans of specimens from the Field Museum, Cleveland Museum of Natural History, Academy of Natural Sciences, and Smithsonian National Museum of Natural History. Images are not to scale. (Kawano, 2025a).

arrangement contrasts with that of tetrapods, where both girdles are decoupled from the skull and ultimately fused to the vertebral column, enabling more effective weight-bearing and force transmission during terrestrial locomotion. Components of the shoulder (i.e., clavicle and cleithrum) in *Polypterus* raised in terrestrial environments were longer and slender compared to those raised in aquatic terrestrials, helping to increase the range of motion in the pectoral fins in the former by reducing bony collisions with the skull (Standen et al., 2014). Notably, in sarcopterygian fishes like *Tiktaalik*, the pectoral girdle is partially decoupled from the cranium, allowing greater independence and limb-driven propulsion, while the pelvic girdle shows increased ossification and connection to the axial skeleton (Shubin et al., 2006). Similar structural changes have been observed in the extant cavefish *(Cryptotora thamicola)*, which possesses a robust pelvic girdle fused to the axial column—an adaptation previously thought to be unique to tetrapods for increasing mechanical stability (Flammang et al., 2016). Extant barred mudskippers (*Periophthalmus argentilineatus*) evolved robust shoulder girdles with enlarged scapula and coracoid to increase muscle attachment and thicker abductor muscles to produce larger locomotor forces compared to aquatic counterparts in a sister family (Ziadi-Künzli et al., 2024). These modifications underscore the evolutionary importance of girdle integration in facilitating the biomechanical demands of terrestrial life.

4.3 Modern analogs of early digit-bearing tetrapods

Computational models of the locomotor capabilities of extinct taxa can be substantially improved with a "total evidence" approach that incorporates empirical data from a range of functional analogs within extant taxa (Pierce et al., 2013), so we review key findings from some of the focal taxa. Biomechanical comparisons of fins and limbs in extant taxa have demonstrated that amphibious fishes use alternative strategies to move on land compared to salamanders, with the former being distinctly different but not necessarily inferior than the latter. Kinetic data conveys information about propulsion, maneuverability, and stability (Fig. 4), and represents the external forces that the ground applies to the appendage during locomotion (i.e., ground reaction force or GRF). During terrestrial locomotion, each appendage generally supports a net GRF equivalent to ~50 % of body weight in most quadrupeds and was 46 % and 47 % in the forelimbs and hindlimbs, respectively, of tiger salamanders (*Ambystoma tigrinum*), and 42 % in the pectoral fins of mudskippers (*Periophthalmus barbarus*) (Kawano and Blob, 2013). The magnitude of the net GRF is almost entirely (98.4 %) due to the vertical component of the GRF that lifts the body off the ground, 31.9 % due to the anteroposterior component that generates thrust, and 14.9 % by the mediolateral component that provides stability during locomotion. The only other amphibious fish with kinetic data during terrestrial locomotion that we are aware of at this time is *Polypterus*, which supports ~60 % of its body weight on its pectoral fins (Bhamra, 2022). Preliminary analyses revealed that the GRFs produced by the pectoral fins of *Polypterus* were almost entirely due to the vertical component of the GRF and equally small proportions from the other components of the GRF (Bhamra, 2022). Empirical data to directly compare the locomotor biomechanics of fins vs. limbs is relatively depauperate so further sampling of fishes and salamander is prudent to disentangle the effect of locomotor structure (i.e., fin vs. limb), degree of terrestriality, and gait.

Prior studies suggested that walking mechanics are largely conserved across tetrapods based on data from terrestrial amphibians and reptiles (Reilly et al., 2006); however, the earliest tetrapods were aquatic and recent biomechanical experiments reveal that terrestrial walking in semi-aquatic salamanders may serve as a valuable functional analog for a fish-like tetrapod. The Spanish

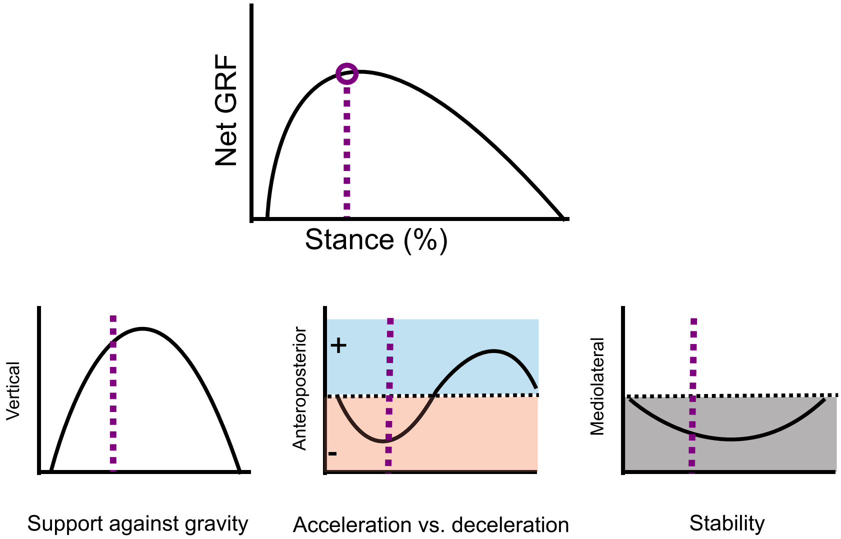

FIG. 4 Kinetics is the study of the forces and torques acting on structures to produce motion. Ground reaction forces (GRFs) are the equal-but-opposite reaction forces that are exerted onto locomotor structures when they contact the ground (i.e., during stance). The net GRF represents the total magnitude of the individual components in the vertical, anteroposterior, and mediolateral directions. The magnitude and sign of the mediolateral component quantify the lateral forces that are applied to the locomotor structure during stance and, thus, are related to stability. The anteroposterior component represents the horizontal forces that generate the fore-aft movements of the locomotor structure during stance and, thus, represent acceleration (when positive) and deceleration (when negative). The vertical component is the upward force exerted onto the locomotor structure and is often used to represent weight-support. The individual components are often compared at the percentage of the stance phase when the net GRF is maximal (also called the "peak net GRF"), which is represented by the dashed vertical line on each subpanel. (Kawano, 2025b)

ribbed newt (*Pleurodeles waltl*) is a multi-phasic, semi-aquatic salamander that has a terrestrial juvenile ('eft') phase but spends the majority of its life underwater (Karakasiliotis et al., 2013). Although *P. waltl* and *A. tigrinum* use a lateral sequence, diagonal couplet gait that is characteristic of terrestrial walking in tetrapods, the forelimbs and hindlimbs of semi-aquatic *P. waltl* support a lower proportion of body weight (40.4% and 36.2 %, respectively) than terrestrial *A. tigrinum* (45.8 % and 49.6 %, respectively) and even semi-aquatic *P. barbarus* (44.3 %) when the net GRF is at its maximum (Kawano and Blob, 2022). Although the lower values in semi-aquatic *P. waltl* salamanders may be interpreted to mean that it has poor weight-bearing capabilities, its limbs are loaded more slowly than *A. tigrinum* and *P. barbarus* which would reduce the impulse forces and, thus, risks of bone fracture in *P. waltl* (Kawano and Blob, 2022).

The 3D kinetics of semi-aquatic limbs exhibited a mosaic of fin-like and limb-like characteristics, where the forelimb data shared the most similarities with mudskipper pectoral fins and the hindlimb data shared the most similarities with the hindlimbs of terrestrial *A. tigrinum* (Kawano and Blob, 2022). The hindlimbs are the primary propulsors in salamanders which may have placed biomechanical constraints that limited kinetic variation between the semi-aquatic and terrestrial salamanders, whereas the forelimbs are often used for non-locomotor roles (e.g., burrowing, amplexus) that could promote functional versatility. For instance, the forelimbs of terrestrial *A. tigrinum* have a net acceleratory role at the beginning of stance – presumably to counteract the effects of tail drag – but are otherwise deceleratory during terrestrial walking; in contrast, the forelimbs of semi-aquatic *P. waltl* only have a deceleratory role that functionally resembles biomechanical struts in amphibious fish fins (Kawano and Blob, 2022). The medial orientation of the ground reaction force in terrestrial *A. tigrinum* was comparable to other tetrapods but more medial in the semi-aquatic mudskipper and intermediate in the semi-aquatic *P. waltl*, which could impose greater stresses to the appendicular bones in the latter (Kawano and Blob, 2022; Fig. 5). Broader comparisons across the aquatic-terrestrial continuum are needed and ongoing, but these findings provide compelling evidence that the biomechanics of terrestrial locomotion may be less conserved in vertebrates than previously thought.

Salamanders are often used to model the locomotion of early digit-bearing tetrapods but may be more appropriate for crownward tetrapods whereas amphibious fishes may be more appropriate models for at least some of the earliest tetrapods (Pierce et al., 2013). 3D digital reconstructions of one of the earliest digit-bearing tetrapods, *Ichthyostega,* demonstrated that it could not laterally bend its body like extant salamanders nor push off the ground with its hindlimbs so it could not perform a salamander-like walk, despite this being the prevailing theory for the earliest form of terrestrial locomotion in digit-bearing tetrapods (Pierce et al., 2012). Instead, *Ichthyostega* used synchronous movements of its forelimbs while maintaining a straight body axis and dragging its hindlimbs behind, in a similar fashion as mudskipper fishes (Pierce et al., 2013).

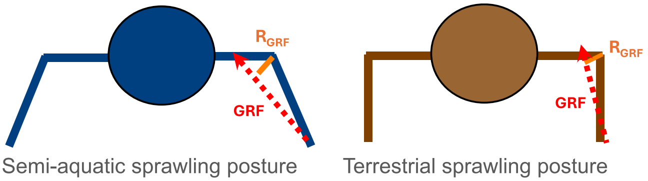

FIG. 5 Functional consequences of hyper-sprawling postures. Semi-aquatic *Periophthalmus barbarus* mudskippers and *Periophthalmus waltl* newts use hyper sprawling postures that extend their pectoral appendages more laterally than terrestrial tetrapods that use either sprawling or upright limb postures where the zeugopods (i.e., forearms, shins) are held vertically. Shifting the angle of the GRF would theoretically increase the moment arm of the GRF and consequently increase torques about the joint, which could impose greater stress about the joint and require stronger muscles to stabilize the joint (Kawano and Blob, 2013). (Kawano, 2025c).

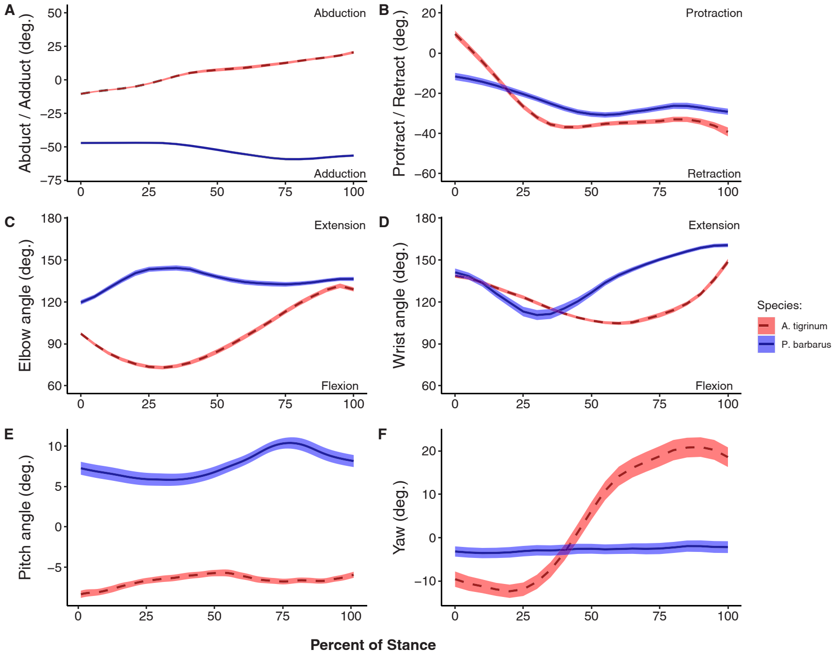

FIG. 6 Kinematic comparisons between the pectoral appendages of semi-aquatic Atlantic mudskippers (*Periophthalmus barbarus)* and primarily terrestrial tiger salamanders (*Ambystoma tigrinum*). During terrestrial locomotion the pectoral fins of mudskippers were primarily abducted and extended throughout stance while the anterior region of its body was pitched upward and remained straight (little to no yaw) whereas the forelimbs of the tiger salamander spent roughly comparable amounts of stance between abduction vs. adduction and flexion vs. extension, with a slight negative pitch and substantial yaw of the anterior portion of its body. (Quigley, 2022).

Moreover, *Ichthyostega* and other early tetrapods had limited abilities to protract their forelimbs whereas salamanders have an extensive range of motion about their shoulders that could mislead computational models to overestimate the locomotor capabilities of early tetrapods. (Molnar et al., 2021; Pierce et al., 2012). Mudskippers naturally have limited protraction about their shoulders (Fig. 6), serving as a valuable system to examine the functional consequences of biomechanical constraints that are not present in other functional analogs studied thus far (Quigley et al., 2022). In addition, long-axis rotation about the shoulder is extensive in extant salamanders (~85 degrees) (Nyakatura et al., 2019), but the maximum estimated values based on osteological measurements would only yield moderate long-axis rotation in stem tetrapods (*Eusthenopteron*: ~55 degrees, *Acanthostega:* ~40 degrees; *Ichthyostega:* ~50 degrees) (Molnar et al., 2021). Long-axis rotation has not been empirically measured in amphibious fishes in vivo, but is likely minimal due to the simple hinge joints in their paired fins. Thus, amphibious fishes may play a pivotal role in reconstructing the incipient stages during the evolution of terrestrial locomotion across vertebrates by providing key insights about how weight support and propulsion on land can be achieved despite potential biomechanical constraints in their musculoskeletal system.

5 Underwater walking in fishes as a precursor for terrestrial locomotion

Substrate-based locomotion plays a crucial role in enabling fishes to interact with complex benthic environments, conserve energy, and avoid predators (Di Santo, 2022; Di Santo and Goerig, 2025). In high-flow aquatic habitats, some species use modifications of the fins—such as suction cup-like pelvic fins or expanded fin spines—to maintain position against currents, minimizing energy expenditure compared to continuous swimming (Hale et al., 2022; Kano et al., 2012, Di Santo et al. 2025). These modifications emphasize balance, posture control, and station-holding, which likely represent functional precursors to more active forms of benthic locomotion. That is, the ability to resist displacement and stabilize the body on a substrate may have provided the biomechanical foundation for propulsion-based walking-like behaviors later. While adhesion-based strategies differ mechanically from terrestrial walking, they reflect an important stage in the evolutionary continuum of fin-substrate interactions and are reviewed in detail in "*Biomechanics of Adhesion in Fishes*" (Ch. 7, Vol 41: Maie et al., 2025). Here, we focus on fishes that use motions of the paired fins and axial system to generate forward propulsion across benthic surfaces. In these systems, paired fins are adapted not only for stability but also for modulating ground reaction forces and facilitating weight support (Foster et al., 2018; Foster and Higham, 2010; Webb, 2005). Understanding this progression from stabilization to locomotion is key to reconstructing the biomechanical pathways that enabled the transition from water to land (Ishida et al., 2024).

Walking-like and crawling-like movements enable fishes to exploit benthic habitats more effectively than continuous swimming. These precise substrate interactions facilitate navigation through complex environments, such as coral reefs, seagrass beds, and rocky substrates (Tatom-Naecker and Westneat, 2018). The gurnard (*Chelidonichthys lucerna*) demonstrates a six-legged walking behavior using its first three pairs of pectoral fin rays, which function as flexible and articulated limbs (Davenport and Wirtz, 2019). These rays exert forces on the substrate in a coordinated pattern, with contralateral rays moving almost in phase and ipsilateral rays showing a consistent coupling. This behavior was analyzed using a photoelastic gel technique, which revealed that the rays exert backward forces during more than 80 % of their stance phase, contributing to sustained forward propulsion (Jamon et al., 2007). The rays also exhibit a sensory role, detecting prey buried in sediments through chemosensory cells, highlighting their dual function in locomotion and foraging

(Bardach and Case, 1965; Petersen and Ramsay, 2020). The gurnard's walking is characterized by precise, controlled movements that allow effective exploration and exploitation of benthic habitats.

Despite its efficiency in aquatic environments, substrate-based locomotion presents distinct challenges on land. Buoyancy in water reduces the necessity for robust, weight-bearing skeletal structures, a requirement for terrestrial locomotion (Graham et al., 1997; Lutek et al., 2022; Standen et al., 2014). Transitioning from water to land introduces gravitational constraints, demanding mechanical and physiological adaptations (Shubin et al., 1997, 2006). For example, mudskippers must counteract their body weight by using modified pectoral fins with enlarged musculature and joint flexibility, adaptations absent in many obligately aquatic species (Kawano and Blob, 2013; Zhou et al., 2023; Ziadi-Künzli et al., 2024).

Paleontological and comparative evidence indicates that walking-like behaviors likely evolved underwater long before vertebrates moved permanently onto land. Underwater substrate-based locomotion in extant aquatic species such as skates, lungfish, and frogfish, reveals that many of the biomechanical and neural precursors for terrestrial locomotion first arose in benthic habitats. These behaviors conferred selective advantages, including precise navigation, predator evasion, and energetic efficiency at low speeds, by leveraging fin-substrate interactions instead of continuous swimming (Di Santo et al., 2017; Di Santo and Goerig, 2025). Over evolutionary time, these walking-like behaviors were likely co-opted and refined during the water-to-land transition, providing anatomical and functional scaffolding for limb-based gaits in tetrapods. Extinct taxa such as *Tiktaalik roseae*, *Acanthostega*, and *Ichthyostega* illustrate this gradual transition from fin-based propulsion to weight-bearing appendage use. Although these stem tetrapods lived in aquatic environments, they possessed limb-like or limb structures and robust girdles capable of supporting body weight during substrate-based movement (at least for short distances). Recent digital reconstructions suggest that *Ichthyostega*, for example, used synchronous forelimb-driven gaits that are more similar to mudskippers than to salamanders, challenging earlier hypotheses about the mechanics of terrestrial walking (Pierce et al., 2012, 2013). Fossils from these stem tetrapods suggest that the evolutionary shift toward terrestrial locomotion was not abrupt, but rather a stepwise process grounded in pre-existing aquatic behaviors. Extant amphibious fishes—such as mudskippers, lungfish, and walking cavefish—retain key elements of these ancestral locomotor strategies, offering functional analogs for how substrate-based walking may have evolved. Their behaviors help bridge the gap between extinct transitional forms and the emergence of limb-driven terrestrial locomotion in early tetrapods.

The biomechanical challenges of terrestrial environments highlight the substantial evolutionary modifications required to apply substrate-based aquatic locomotion for terrestrial environments, a transition exemplified by non-digit-bearing stem tetrapods and representing a pivotal event in vertebrate evolution (Ishida et al., 2024; Shubin et al., 2006; Stewart et al., 2024). Fossil evidence from stem tetrapods such as *Tiktaalik roseae* provides critical insights into the morphological adaptations that facilitated the shift from aquatic to terrestrial locomotion. *Tiktaalik* exhibits a suite of anatomical features that illustrate its dual functionality in swimming and substrate-based walking. For instance, its robust pectoral girdles were structurally adapted to support weight during substrate interactions, a key prerequisite for partial terrestriality (Shubin et al., 2006). Additionally, the presence of flexible, wrist-like articulations in its pectoral fins enabled precise and controlled movements on uneven substrates, bridging the functional gap between fins and true limbs (Shubin et al., 2006). These adaptations highlight the incremental and mosaic nature of evolutionary transitions, where there were gradual changes that refined features for load-bearing and maneuverability in vertebrates over millions of years (Shubin et al., 1997).

While the fossil record is fundamental to understanding the evolutionary changes that may have enabled the water-land transition, extant species that show similar locomotor structures can help us understand how these extinct species might have walked. Modern lungfish provide valuable insights as analogs for locomotion in non-digit-bearing stem tetrapods, shedding light on the evolutionary processes that facilitated the water-to-land transition (Falkingham and Horner, 2016; Horner and Jayne, 2014). Lungfish employ their pelvic fins in an alternating gait reminiscent of tetrapod locomotion, suggesting that substrate-based movement may have been an important selective pressure shaping stem tetrapod evolution (King et al., 2011). Beyond locomotion, lungfish physiology offers additional parallels to early tetrapods. Genetic studies reveal that lungfish express HoxD13, a pivotal regulatory gene involved in limb development, during pelvic fin morphogenesis (King et al., 2011). This finding underscores the evolutionary continuity of genetic pathways involved in fin-to-limb transitions, emphasizing the lungfish's role as a model for understanding the developmental and functional innovations underlying vertebrate terrestrialization (Shubin et al., 1997). Epaulette sharks (*Hemiscyllium ocellatum*) use substrate-based locomotion that informs our understanding of the evolution of walking-like behaviors. By using paired fins to traverse seafloors, particularly in hypoxic tidal pools, these sharks conserve energy and access oxygen-rich microhabitats (Porter et al., 2022; Pridmore, 1994). Detailed biomechanical analyses show that these sharks use a gait resembling tetrapod walking, with alternating pectoral and pelvic fin movements (Porter et al., 2022; Pridmore, 1994; Travis, 2020). This coordination allows them to sustain movement even in oxygen-depleted environments, reflecting a functional analog to stem tetrapod behavior.

Some fishes exhibit substrate-based walking behaviors even in fully aquatic environments where air exposure is not a concern, showing that walking may be useful for many ecological functions besides terrestriality (Di Santo and Goerig, 2025). Frogfish (*Antennariidae*), for example, possess modified pectoral and pelvic fins that are functionally analogous to limbs (Pietsch and Arnold, 2020). Frogfish fins possess joints that resemble tetrapod-like limb articulations, providing exceptional precision and control (Dickson and Pierce, 2018). Perhaps, frogfish walk instead of swimming to save energy at low speeds (Di Santo and Goerig, 2025; Di Santo and Kenaley, 2016). Similarly, skates (*Leucoraja erinacea*) provide a fascinating model for understanding the evolution of walking-like behaviors in aquatic vertebrates. Unlike many other fishes, skates move their pelvic fins in an alternating gait to "walk" along the seafloor (Giardina and Mahadevan, 2021). Recent research has demonstrated that skates possess central pattern generators (CPGs) in their spinal cords, which coordinate reciprocal activation of flexor and extensor muscles during fin movements, mirroring limb control in land-dwelling vertebrates (Jung et al., 2018). Furthermore, these neural circuits rely on conserved Hox transcription factors, which guide the development and organization of motor neurons responsible for appendicular locomotion (Jung et al., 2018; Shubin et al., 2009; Turner et al., 2019). Thus, the neural architecture underlying walking evolved in the common ancestor of vertebrates with paired appendages, long before the emergence of true limbs and terrestrial locomotion.

6 Broader significance and future opportunities

Walking behaviors observed in modern aquatic species suggest that the biomechanical precursors for terrestrial locomotion originated underwater. Substrate-based walking provided selective advantages, including enhanced foraging and predator evasion, in benthic habitats. Over evolutionary time, these behaviors and associated anatomical features were refined during the transition to land, forming the foundation for terrestrial locomotion. The shift from fins to limbs required balancing aquatic and terrestrial demands. Dorsoventral asymmetry in fin rays, as observed in *Tiktaalik*, may have facilitated lift and thrust generation, bridging the functional gap between swimming and walking (Stewart et al., 2020, 2017). These traits exemplify evolutionary compromises that enabled dual functionality in stem tetrapods living in semi-aquatic environments. Early tetrapods initially had weak limb joints but eventually evolved limbs with joint flexibility and weight-bearing capacities, driven by selective pressures in marginal aquatic-terrestrial habitats (Dickson and Pierce, 2018; Standen et al., 2014). Evo-devo studies have illuminated the genetic and developmental mechanisms underlying the fin-to-limb transition. Modularity in Hox gene expression and the role of signaling pathways such as Shh illustrate how small genetic changes can produce profound morphological innovations (Dahn et al., 2007; Letelier et al., 2021).

Recent work by Shubin and colleagues has advanced our understanding of fin-to-limb development through the application of CRISPR technologies (Nakamura et al., 2016). Using zebrafish as a model organism, these studies have pinpointed the role of Hox genes and other regulatory factors in shaping the skeletal structure of fins, demonstrating how small genetic modifications can lead to limb-like features. For instance, CRISPR manipulations targeting HoxD clusters have induced skeletal changes in zebrafish that mimic early stages of limb evolution, providing a functional blueprint for how fins transformed into limbs (Nakamura et al., 2021, 2016). Genomic studies of species like mudskippers and *Clarias* catfish have revealed specific genetic pathways that facilitate terrestrial locomotion. In mudskippers (*Periophthalmus spp.*), genes involved in fin development, such as those regulating joint articulation and enhanced muscle functionality, are upregulated during terrestrial activity (You et al., 2014). Additionally, these species exhibit adaptations in the expression of genes related to vascularization of the skin and respiratory structures, enabling efficient oxygen exchange in air. *Clarias* catfish (*Clarias spp.*) show similar patterns, with genes governing muscle fiber types and metabolic adjustments that are highly expressed during terrestrial excursions (Kushwaha et al., 2021).

Bio- and paleo-inspired robotics has leveraged insights from aquatic and terrestrial locomotion to develop efficient amphibious systems (Baines et al., 2024, 2019; Ishida et al., 2024). These technologies replicate biological gaits, offering applications in exploration and rescue operations. Robots modeled from fishes and tetrapods that use substrate-based locomotion replicate coordinated fin or limb movements for versatile locomotion in aquatic and terrestrial settings, showcasing the utility of biomechanical studies in advancing robotics (Lin et al., 2023; McInroe et al., 2016). Beyond these applications, the emerging field of paleo-robotics provides groundbreaking insights into extinct species' locomotion by employing robotic models to reconstruct evolutionary transitions, such as between aquatic and terrestrial environments (Ishida et al., 2024). This innovative approach bridges paleontology and engineering, allowing researchers to test biomechanical hypotheses and investigate the interplay of morphology and environment over evolutionary timescales (Ishida et al., 2024; Long, 2012). Advances in computer vision and machine learning enable large-scale analyses of locomotor patterns across phylogenetic frameworks, revealing evolutionary trends in biomechanics (Lauer et al., 2022; Mathis et al., 2018; Mathis and Mathis, 2020; Walter and Couzin, 2021). Behavioral ethograms combined with machine learning algorithms identify unique gaits, expanding our understanding of locomotor diversity in benthic locomotors (Bohnslav et al., 2021). CRISPR and transcriptomic technologies allow precise manipulation and analysis of genes associated with locomotor adaptations, offering transformative insights into evolutionary transitions (Carroll, 2012; Nakamura et al., 2021, 2016). By integrating these technologies, researchers can experimentally replicate evolutionary pathways, furthering our understanding of the genetic basis for terrestrial adaptations. Together, these biomechanical, evolutionary, and developmental insights suggest that terrestrial locomotion in fishes is not merely an evolutionary curiosity, but a key to understanding the diversity of movement strategies in vertebrates. As technologies advance, the integration of empirical, computational, and comparative approaches promises to reveal new dimensions of how vertebrate life moved from water to land.

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