



Synchronous coevolution of behavior and morphology in cave-dwelling creeping invertebrates on rugged substrates

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Abstract. Subterranean environments impose extreme and highly specific selective pressures, including permanent darkness, structural heterogeneity, and limited resource availability. In creeping cave-dwelling invertebrates, these conditions promote coordinated evolutionary modifications of both morphology and behavior, resulting in integrated adaptive complexes optimized for tactile navigation and efficient locomotion on rugged substrates. This mini review synthesizes current evidence demonstrating that troglomorphic traits, such as eye reduction, depigmentation, elongation of appendages, and altered body proportions, are closely associated with functional and behavioral shifts, including modified locomotor strategies, spatial habitat selection, circadian organization, and exploratory activity. Comparative analyses across annelids, arthropods, crustaceans, and planarians reveal repeated patterns of convergence and parallelism, highlighting the predictable influence of substrate complexity and sensory constraints on organismal evolution. These morphological modifications enhance mechanical stability, tactile sensing, and performance in structurally complex cave systems, while behavioral adaptations optimize energy use and environmental interaction under resource-limited conditions. Evidence from phylogenetic, functional, and behavioral studies supports the concept that morphology and behavior evolve synchronously rather than independently, reflecting integrated responses to subterranean selective regimes. Despite significant advances, important gaps remain, particularly in biomechanical validation and high-resolution behavioral quantification. Addressing these gaps will improve understanding of the mechanisms driving coevolution in extreme environments and clarify general principles governing the evolution of organismal performance under spatial and sensory constraints.

Key Words: troglomorphy, cave invertebrates, behavioral evolution, morphological adaptation, locomotion, substrate complexity, convergent evolution, subterranean ecology, functional morphology, coevolution.

Conceptual framework: synchronous evolution of form and behavior in subterranean habitats. Cave and other hypogean habitats impose a distinctive combination of perpetual darkness, structural complexity, and resource scarcity. In crawling invertebrates, selection acts simultaneously on sensory and locomotor structures and on behavior, yielding coordinated shifts that can be regarded as synchronous coevolution of morphology and behavior. Troglomorphic traits such as eye loss,

depigmentation, elongation of appendages and sensory structures, and alterations of body proportions recur across unrelated lineages, indicating strong convergent selection in subterranean environments (Liu et al 2017; Gonzalez et al 2018; Gonzalez et al 2021). At the same time, behavioral changes in locomotion, spatial use, circadian activity, feeding, and stress responses modify how animals interact with rugged substrates and the three-dimensional cave matrix (de Souza et al 2024; Padmanaban et al 2025). Understanding these systems, therefore, requires integrating phylogenetic, functional-morphological, and behavioral perspectives rather than treating structures and behavior as independent.

The purpose of this mini review is to synthesize current knowledge on the synchronous coevolution of morphology and behavior in cave-dwelling creeping invertebrates and to highlight how substrate complexity and subterranean selective pressures shape integrated adaptive responses.

Classic troglomorphic syndromes in creeping invertebrates. Across annelids, arthropods, and other invertebrate groups, repeated colonization of caves has produced a recognizable troglomorphic syndrome. In scale worms (Aphroditiformia), cave-dwelling species show pronounced anophthalmia and depigmentation, coupled with significant elongation of sensory parapodial cirri relative to epigean congeners. Ancestral-state reconstructions indicate that cirrus elongation is associated with cave colonization. In contrast, eye reduction is more tightly related to deep-sea specialization, underscoring that distinct components of the troglomorphic phenotype can track different axes of environmental change (Gonzalez et al 2018). In cave millipedes from several orders and families, comparative analyses between troglobitic and epigean congeners show convergent evolution of a longer, more slender body, lighter coloration, and elongation of femora and tarsi of walking legs, with additional sex-specific antenna elongation in females. These changes plausibly enhance tactile exploration and mechanical stability on irregular cave floors, while reduced pigmentation reflects relaxed selection for photoprotection (Liu et al 2017). Troglobitic isopods and other crustaceans also display targeted modification of sensory and locomotor traits, including eye and pigment reduction and changes in body and limb morphology associated with life in saturated muds or semi-aquatic cave pools (Balázs et al 2021; de Souza et al 2024). Groundwater planarians exhibit high variability in troglomorphic characters such as blindness and depigmentation, often combined with specialized adhesive and feeding structures suited to structurally complex interstitial and cave habitats (Barzaghi et al 2021). Collectively, these examples indicate that creeping invertebrates repeatedly evolve body plans and appendages optimized for tactile sensing and efficient locomotion on uneven, obstacle-rich substrates, while vision and pigmentation are consistently reduced when not required.

Locomotion and functional morphology on rugged subterranean substrates. Rugged cave substrates, including rock breakdown, speleothems, and heterogeneous sediment, exert strong selection on the biomechanics of crawling and clinging. Comparative work on cave millipedes demonstrates that elongation of walking leg segments, especially femora and tarsi, is a convergent feature across lineages and is likely an adaptation to spanning gaps, negotiating crevices, and increasing contact points on irregular surfaces (Liu et al 2017). The elongation of dorsal cirri in cave scale worms, which are sensory and potentially assist in stabilization during crawling and swimming in anchialine caves, provides a similar example where appendage modifications serve mixed sensory and locomotor roles (Gonzalez et al 2018; Gonzalez et al 2021). Within the *Asellus aquaticus* species complex, repeated colonization of caves is associated with divergence in multiple functional morphological traits related to feeding, grooming, antipredator defense, and sensory systems, and with habitat-dependent modification of sexual dimorphism. Many of these traits, including changes in body proportions and limb structures, have obvious consequences for locomotion and substrate use in narrow fissures and on unstable cave floors (Balázs et al 2021). These subterranean examples parallel patterns documented in other systems where microhabitat and substrate properties strongly predict locomotor morphology, such as lizards evolving larger limb segments and toe structures in urban environments to better traverse smooth artificial surfaces (Winchell et al 2018), or fishes

showing clear associations between fin size, muscle mass, and benthic versus limnetic or substrate-specific niches (Colombo et al 2016). Although these latter studies are not subterranean, they reinforce a general principle: fine-scale variation in substrate structure repeatedly drives predictable shifts in locomotor morphology.

Behavioral shifts in cave invertebrates: locomotion, circadian rhythms, and space use. Cave environments also shape the temporal and spatial structure of activity. In semi-aquatic troglotic isopods (Styloniscidae), detailed chronobiological analyses under constant darkness, constant light, and light–dark cycles reveal predominantly infradian rhythms under constant conditions, with synchronization and clear day–night patterns emerging only when external cycles are present. This suggests that endogenous circadian organization persists but is decoupled from light in caves, leading to altered locomotor activity patterns that may optimize energy expenditure in resource-poor, temporally homogeneous environments (de Souza et al 2024). Behavioral plasticity in circadian output thus coevolves with life in non-cyclic habitats, even when the underlying clock is retained. Spatial habitat selection within caves provides another axis of behavioral adaptation. The highly troglomorphic carabid beetle *Dalyat mirabilis* is non-uniformly distributed along the cave, with higher abundances in chambers that maintain high and stable relative humidity and minimal climatic fluctuations. This pattern reflects behaviorally mediated microhabitat choice that interacts with morphological specializations such as extreme elongation and depigmentation described in this lineage, allowing persistence in the deepest, most buffered cave sectors (Mayoral et al 2022). Although focused on fish, studies in *Astyanax mexicanus* highlight how subterranean conditions can drive large shifts in locomotor and exploratory behavior, including modified stress responses and activity patterns (Yoshizawa 2015; Padmanaban et al 2025). Cave morphs show reduced “stress-like” behaviors and heightened exploration relative to surface conspecifics, with quantitative analyses revealing that distinct behavioral components co-segregate genetically (Padmanaban et al 2025). These data illustrate how integrated behavioral syndromes evolve under altered predation and resource regimes, and provide a framework readily transferable to invertebrate systems where analogous selective forces operate.

Evidence for coordinated evolution of morphology and behavior. The repeated covariation of morphological and behavioral traits across subterranean invertebrates supports the view that these traits evolve in a coordinated manner. In *Asellus aquaticus*, parallel morphological shifts between cave and surface populations are strongly trait- and function-specific, and are accompanied by habitat-dependent changes in sexual dimorphism, implying that both natural and sexual selection are reshaped in subterranean settings. Traits involved in mate competition and guarding in males and fecundity in females evolve differently in caves versus surface waters, reflecting altered behavioral interactions and densities (Balázs et al 2021). In scale worms, comparative phylogenetic analyses show that elongation of sensory cirri is statistically associated with cave occupation, while other traits, such as eye loss, correlate with deep-sea colonization. This pattern implies that specific structural modifications track distinct ecological challenges and associated behavioral demands: cirri likely support enhanced tactile exploration, prey detection, and navigation on complex cave substrates, whereas eye reduction is tied to persistent darkness and potentially energy economization (Gonzalez et al 2018). More broadly, reviews of cavefish emphasize behavior as the integrated outcome of multiple evolved morphological and physiological traits, arguing that subterranean selection pressures must be understood at the level of organismal performance rather than isolated structures (Yoshizawa 2015). Troglomorphic invertebrates align with this framework: elongated appendages and bodies, enhanced tactile and chemical sensing, and reduced visual investment co-occur with shifts in locomotor timing, microhabitat choice, and social or reproductive behaviors, creating coherent adaptive complexes.

The integration of morphological and behavioral adaptations forms a coordinated strategy that allows creeping cave-dwelling invertebrates to navigate rugged subterranean substrates efficiently while optimizing energy use under resource-limited conditions. This multi-level coordination is summarized conceptually in Table 1.

Table 1

Minimal integrative model of synchronous coevolution in cave-dwelling creeping invertebrates

<i>Level</i>	<i>Key concepts / Terms</i>	<i>Role</i>	<i>Explanation</i>
Base	Morphological adaptations: eye reduction, depigmentation, elongation of appendages and sensory structures, altered body proportions	Facilitate navigation on rugged subterranean substrates	These structural modifications enable creeping cave-dwelling invertebrates to move efficiently on uneven surfaces and enhance tactile sensing.
Level 2	Behavioral adaptations: modified locomotion, spatial habitat selection, circadian activity, exploratory behavior	Optimize energy use and environmental interaction under resource-limited conditions	Behavioral shifts allow organisms to navigate effectively and manage energy expenditure in caves with scarce resources.
Level 3	Integrated function: coordinated morphological and behavioral traits	Support efficient tactile navigation and overall performance	Morphological and behavioral traits work together to maintain performance and adaptability in complex subterranean habitats.
Apex	Synchronous coevolution: repeated patterns of convergence and parallelism across lineages	Demonstrate predictable evolutionary responses to subterranean selective pressures	Patterns across multiple lineages show that morphology and behavior evolve together in response to environmental constraints.

Note: Morphological and behavioral adaptations evolve in a coordinated manner to allow efficient navigation of rugged subterranean substrates while optimizing energy use under resource-limited conditions. Each level of the table represents a class of traits (morphological or behavioral) and their functional role in enhancing locomotion, tactile sensing, habitat use, or energy efficiency. This table summarizes the multi-level coordination described in the text.

Convergence, parallelism, and evolutionary pathways in subterranean lineages.

The subterranean biome is a natural laboratory for testing convergence and parallelism in the coevolution of form and behavior. Cave millipedes from four orders exhibit convergent elaboration of body length and leg segments, despite significant phylogenetic separation, indicating that similar locomotor challenges in caves canalize evolution toward a limited set of morphological solutions (Liu et al 2017). Cave scale worms show comparable convergence in sensory appendage hypertrophy between anchialine cave dwellers and holopelagic relatives that occupy the water column, even though the precise morphological pathways (cirrophore versus style elongation) differ. This convergence extends to behavioral traits, such as water-column swimming versus benthic crawling, which have evolved independently multiple times within Polynoidae (Gonzalez et al 2021). Parallel evolution is equally evident in cavefish, where numerous independent cave populations have repeatedly lost eyes and pigmentation through partially shared developmental mechanisms, yet with population-specific genetic contributions revealed by cave-cave hybrids (Sifuentes-Romero et al 2020). Such studies underscore that similar troglomorphic suites can arise via both shared and distinct developmental and genetic routes, with behavior likely following comparable patterns of constrained but not identical solutions. Planarian reviews reveal high morphological variability and scattered phylogenetic information among groundwater taxa, suggesting that repeated colonization events and local adaptation generate a mosaic of subterranean phenotypes whose behavioral correlates remain poorly documented (Barzaghi et al 2021). Together, these data reveal

that convergence in subterranean systems is strongest at the level of ecological function (tactile navigation, energy-efficient locomotion, cryptic coloration) and somewhat looser at the level of precise morphological or genetic implementation.

Substrate complexity beyond caves: insights from non-subterranean rugged habitats. Comparative evidence from non-subterranean but structurally challenging environments reinforces general principles relevant to creeping invertebrates. In urban lizards, individuals from city habitats with smooth, artificial substrates develop larger limb dimensions and related morphological traits that enhance sprint speed and reduce loss of traction, relative to forest conspecifics. This indicates rapid morphological evolution tied to novel locomotor demands of man-made surfaces (Winchell et al 2018). Similarly, in anuran amphibians, species using different microhabitats evolve distinct optimal limb morphologies and show corresponding differences in jumping performance, with arboreal and torrent species possessing relatively longer hindlimbs and superior jumping compared with terrestrial or fossorial taxa (Citadini et al 2018). In cichlid fishes, habitat use along benthic–limnetic and substrate axes predicts the size of pectoral and caudal fins and the mass of associated musculature, demonstrating that even within a single lineage, fine-scale habitat partitioning translates into functional divergence in locomotor morphology (Colombo et al 2016). These vertebrate examples, though outside caves, affirm that microhabitat structure and substrate properties consistently drive coordinated evolution of locomotor behavior and anatomy, a pattern mirrored in subterranean invertebrates facing rugged, discontinuous surfaces.

Future directions and research gaps. Despite growing comparative datasets, several gaps remain in understanding the synchronous coevolution of behavior and morphology in creeping cave invertebrates. First, most troglomorphic descriptions remain predominantly morphological; high-resolution behavioral phenotyping, akin to that applied in *Astyanax mexicanus* or in circadian studies of isopods, is rare in invertebrate cave lineages (de Souza et al 2024; Padmanaban et al 2025). Second, robust phylogenetic frameworks linking trait evolution to independent cave colonization events are available for only a handful of taxa, such as scale worms and *Asellus aquaticus*, limiting inference about the repeatability of coevolutionary trajectories (Gonzalez et al 2018; Balázs et al 2021; Gonzalez et al 2021). Third, the functional biomechanics of crawling and clinging on specific cave substrates have rarely been quantified experimentally, leaving many assumed links between elongation of appendages, body proportions, and locomotor performance untested (Liu et al 2017). Addressing these gaps will require integrative studies that combine comparative morphology, controlled behavioral assays, phylogenomics, and biomechanical modeling. Such work promises not only to clarify how invertebrates adapt to caves and other rugged substrates but also to illuminate general principles of how morphology and behavior coevolve under strong spatial and sensory constraints.

Conflict of interest. The authors declare that there is no conflict of interest.

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