


## Hypothesis

# A Subsurface Stepping Stone Hypothesis for the Conquest of Land by Arthropods

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**Abstract:** The conquest of land by arthropods is commonly believed to be a surface phenomenon associated with the arrival of photosynthetic plants, atmospheric oxygenation, and an ozone shield in the mid-Paleozoic Era. However, recent molecular and fossil evidence suggests terrestrial fauna may have first appeared in the Cambrian, before the proliferation of plants and ozone, which are thought to be essential for survival. This raises the question—how could arthropods survive on land without established plants and an ozone shield? We propose a hypothesis that chemolithoautotrophic cave ecosystems, independent of photosynthesis, may have served as a subsurface stepping stone, providing a possible explanation for the land invasion enigma. Chemolithoautotrophic caves have offered abundant food and radiation protection, enabling ancient arthropods to evolve strategies to adapt to new frontiers through gradual dispersion from the sea to shielded cave waters, then to cave hygroscopic margins of cave waters, and, finally, to the surface.

**Keywords:** subterranean habitat; cave fauna; early Palaeozoic; terrestrial colonization; arthropods; shielded caves; chemolithoautotrophy



**Citation:** Frumkin, A.; Chipman, A.D. A Subsurface Stepping Stone Hypothesis for the Conquest of Land by Arthropods. *Diversity* **2024**, *16*, 6. <https://doi.org/10.3390/d16010006>

Academic Editors: Srećko B. Ćurčić and Gordan S. Karaman

Received: 5 November 2023

Revised: 1 December 2023

Accepted: 20 December 2023

Published: 22 December 2023



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## 1. Introduction

### 1.1. The Terrestrialization Problem

The terrestrialization of plants and arthropods represents a major milestone in the diversity, evolution, and adaptations of Earth's ecosystems. Understanding how species colonized the land surface would shed new light on the links between the evolution of life and the environment, as well as how biology affects the physical and chemical environment and vice versa.

In order for animals living in the sea to colonize the land surface, a number of physiological and environmental barriers need to be overcome. These include aerial respiration and gas exchange, water management and osmoregulation, digestion, temperature control, terrestrial locomotion without the benefit of buoyancy, aerial sensory perception, reproduction outside of water, including water resistance of eggs and embryos, utilization of new food sources, and protection against environmental and other stresses such as desiccation, rapid temperature fluctuations, and increased exposure to ultraviolet radiation [1–3]. Water is essential to life in several ways, such as a medium for biochemical reactions, for the transport of cell solutes, for the maintenance of cell turgor, and for inter-cellular transport and signaling. The variability of water availability on land is problematic for terrestrial life—dehydration can be as fatal as inundation by floods for land organisms.

Adaptations caused by changes in anatomy, physiology, and sensory systems allowed the colonizing species to overcome the terrestrial environmental challenges. In extant animals, degrees of terrestrial adaptation can be determined from their ecology, behavior, anatomy, and physiology. Comparing the anatomical and physiological features of aquatic and terrestrial organisms has helped scientists understand the underlying mechanisms

responsible for the transition from sea to land. Understanding the evolutionary changes in body structure, respiratory system, and locomotion of aquatic versus terrestrial animals sheds light on the adaptations for living on land and provides insights into the development of these traits in different lineages [1–4]. The fossil record helps track some of the evolutionary changes that occurred during the transition to land, but this record is partial and unsatisfactory in most terrestrial environments.

By comparatively examining the ways in which animals respond to the challenges and opportunities presented by the land, we can gain a better understanding of ecological dynamics and how ecosystems have evolved over time. On the other hand, understanding paleohydrology, paleoclimate, and ancient geomorphology can shed light on the possible routes from sea to land that allowed transition and adaptation to living on the land.

### 1.2. The Earliest Terrestrial Ecosystems

Precambrian Metazoa are known only from the marine environment, and there is no evidence of higher plants in the fossil record until much later in the Palaeozoic. Nevertheless, probable prokaryotic colonizers would have been extremely important in developing soil profiles and contributing towards a terrestrial environment that was amenable to later colonization by higher plants and animals.

The fossil record holds only a few clues for the sequence and timing of events during the major phase of terrestrialization in the Palaeozoic. Four phases of plant terrestrialization were recognized by Edwards and Selden [4], based mainly on the plant fossil record. Exceptional examples of invertebrate animal fossils appear in the later phases, with the first terrestrial animals almost undoubtedly being arthropods [2]. Complex terrestrial biotas, based mainly on arthropods and plants, had developed by the Devonian period; colonizations by vertebrates and molluscs followed these early pioneers much later, into already well-established ecosystems.

In spite of the many attempts to decipher the terrestrialization process, details of the journey from water to land remain obscure, with the precise timing of the water-to-land transition being disputed for different animal taxa. Molecular clocks may reliably date evolutionary timescales only if ground-truthed by fossils, which are rare for early terrestrial organisms [5–7].

Land colonization by plants and arthropods is commonly considered together, assuming arthropod terrestrialization was associated with the arrival of photoautotrophic multicellular plants. Early plants increased terrestrial food availability and generated a more effective ozone shield. With low early atmospheric O<sub>2</sub> levels, stratospheric ozone was low, enabling short-wavelength ultraviolet light to enter the troposphere and trigger photochemical reactions [8]. Strong feedback exists between ozone formation, atmospheric chemistry, and biospheric oxygen production [9]. Thus, the ozone shield was likely strengthened as atmospheric oxygen rose since ~450 Ma in the Late Ordovician [10].

The oldest undisputed land plant fossils are Ordovician cryptospores [11,12] and spore-bearing plant fragments [13,14], although signs of fungus-like fossils have been known in paleo-caves since the Ediacaran [15,16]. Molecular clocks date crown group plants to the mid-Cambrian to early Ordovician [17–19]. However, molecular clocks suggest arthropods may have colonized land as early as the mid-Cambrian ~510 Ma [20,21], probably earlier than macroscopic terrestrial plants that produce significant amounts of oxygen and provide adequate shelter.

### 1.3. Arthropod Terrestrialization

Arthropods underwent at least three independent terrestrializations in the Paleozoic [5], but relevant body fossils from the first stages of terrestrialization are almost nonexistent. Notably, arthropod trace (trackways) fossils do not definitively indicate full land ‘colonization’—brief forays into upper tidal or other paralic zones for feeding, reproduction, or molting while still remaining largely marine cannot be excluded [22–24].

Definitive proof of terrestrialization requires finding fossils of terrestrial crown-group members with terrestrial taphonomy, and these are few and far between.

Molecular phylogenies show that myriapods—an entirely terrestrial group—diverged from other mandibulates and started diversifying in the Cambrian [5], but see [2]. Some late Cambrian trace fossils may have myriapod or euthycarcinoid (a stem-group lineage of myriapods) origins, likely made by a semi-terrestrial arthropod [2,22]. The earliest undisputed crown-group myriapod body fossils are much younger, from the Silurian [2].

Hexapods (including insects), the largest modern terrestrial arthropod group, have an extremely poor early terrestrial fossil record. Molecular dating suggests that the hexapod diversification slightly postdated the diversification of myriapods, both during the Ordovician [5], with their closest relatives being remipede crustaceans [25–29]. No consensus exists as to which are the earliest fossil hexapods [27–30], but they are Devonian at the earliest.

Arachnids—the land members of Chelicerata—constitute the third arthropod terrestrialization event in the Paleozoic. While chelicerates diverged from mandibulates in the Precambrian based on molecular trees, the terrestrial members only started diversifying in the Ordovician, suggesting a later transition to land [2,5]. However, recent phylogenetic [31] and morphological-developmental [3] data raise the possibility of two independent terrestrialization events—one in pulmonate arachnids and one in non-pulmonates. Silurian trigonotarbid represents the earliest known terrestrial arachnids [32], although their precise phylogenetic position is unclear.

Although the major arthropod groups probably invaded land independently, they faced similar challenges and developed analogous, sometimes identical, adaptations once established [33]. The conundrum is whether early arthropod terrestrialization could occur before suitable plants developed, associated with habitats sheltered from UV radiation, and if it did, what did they feed on and where did they shelter? If molecular clocks are reliable, myriapod and possibly other arthropod diversification began before plants significantly populated land and while ozone levels were apparently too low to adequately shield against damaging UV radiation outside of water. The amount of damage caused by UV radiation to extant arthropods is highly variable and context-dependent [34,35], and it is difficult to assess how it would have affected Cambrian–Ordovician arthropods. However, it is likely that the UV radiation they would have sustained before the establishment of an adequate ozone layer would have reached levels that are lethal to extant arthropods.

#### 1.4. Previous Hypotheses

Some previous hypotheses stressed the anatomical and physiological modifications that could facilitate terrestrialization [36]: The tracheal hypothesis suggests that the evolution of tracheal respiratory systems in arthropods allowed them to breathe air and invade land. Tracheal systems allow for direct gas exchange, bypassing the need for breathing through gills or across moist surfaces typical of marine arthropods. This hypothesis proposes that tracheal breathing was what enabled mandibulate arthropods like millipedes, centipedes, and primitive insects to move onto land during the Silurian and Devonian periods [37]. Note that this hypothesis does not cover the terrestrialization of pulmonate arachnids.

The general terrestrialization hypothesis focuses more broadly on adaptations that allowed arthropods to deal with the stresses of the terrestrial environment, not just respiratory adaptations [38]. Evolutionary innovations like thickened cuticles, waxy coatings, spine-like outgrowths, sensory organs, and hardened exoskeletons may have enabled the first terrestrial colonizations [38,39].

The herbivory hypothesis suggests that feeding on primitive vascular plants provided an attractive nutritional resource that may have pulled some arthropods towards terrestrial life [40]. Fossil evidence of terrestrial arthropod feeding marks on early land plants provides some support for this idea. The availability of abundant, nutritious food on land could have facilitated some of the early dispersals from marine environments.

Some combination of tracheal breathing, structural adaptations to the stresses of land, and the availability of new terrestrial food sources likely worked together to enable early arthropods like myriapods to migrate from coastal and tidal environments to inland terrestrial habitats [32]. All of these co-evolving adaptations likely played a role in the process at different points in time.

In this paper, we focus on the optimal environmental route that could facilitate terrestrialization. Previous hypotheses relating to this question included scenarios such as the marine–interstitial route [1], the freshwater-to-terrestrial route [41,42], mycotrophic plant colonization associations [43], the aerial plankton/wind transportation hypothesis, and the assembling ecosystem hypothesis [44–46].

The freshwater-to-terrestrial route hypothesis proposes that the ancestors of terrestrial animals evolved originally in freshwater habitats like rivers and lakes. Gradual adaptation occurred from aquatic to moist terrestrial environments like river banks. This is supported by some genetic similarities between freshwater and terrestrial taxa [1,46].

The marine interstitial hypothesis suggested that terrestrial animal groups evolved from ancestors adapted to marine intertidal zones, especially moist spaces between sand/soil particles. This habitat buffered climate change while allowing adaptation to terrestrial life. Some modern intertidal invertebrates display relevant adaptations [47]. A similar hypothesis suggests that terrestrialization occurred via interstitial terrestrial soil spaces [48,49]. The mycotrophic hypothesis proposes that fungal symbioses were key to the first terrestrial animals providing nutritious food sources in plant-absent environments. Modern fungal farming invertebrates showcase how fungi could facilitate terrestrial transition. The co-evolution of land fungi and animals was postulated [37,50].

The aerial plankton/wind transportation hypothesis suggested that some marine organisms, propagules, or dormant life stages evolved to become part of aerial plankton, passively carried by wind to land [44,45]. Some modern aerial plankton show that such dispersal is possible from the ocean to land.

None of the previous land invasion scenarios provided a complete explanation covering all aspects. Here we propose a subsurface stepping stone hypothesis (Figure 1), attempting to provide a full explanation, or at least a complementary one to previous hypotheses. In this model, a first step towards terrestrialization is life in a self-sufficient subterranean cave ecosystem. The term ‘cave’ refers here to subsurface systems of interconnected voids that can be penetrated by arthropods. Our hypothesis builds upon recent advances in the study of chemoautotrophic caves, discussed shortly below.

### 1.5. Advances in the Study of Chemoautotrophic Caves

Chemoautotrophic ecosystems were first discovered in the 1960s in an underwater cave in Israel [51]. Such caves contain chemoautotrophic bacteria that derive energy from inorganic molecules in the cave systems and fix carbon dioxide into organic compounds. This provides the basis for the complex food webs within the caves [52].

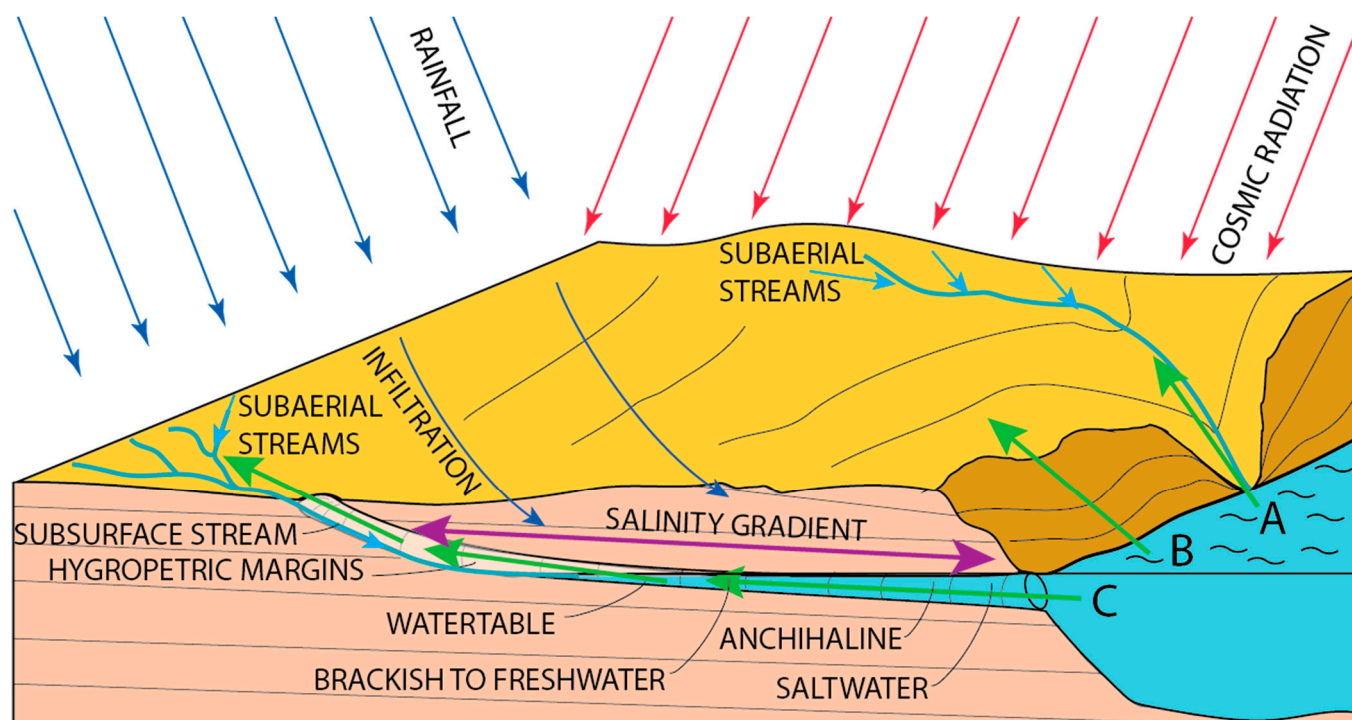
Since their discovery, over 300 large chemoautotrophic cave systems (accessible to humans) have been documented around the world, especially along continental margins. The diversity of bacteria involved has expanded greatly beyond initial discoveries, including new phyla and metabolic pathways [53].

Recent advances in techniques for studying such ecosystems have progressed from initial morphological observations to include genetic sequencing, isotopic tracing, microbial activity measurements, and modeling. This has revealed complex interdependencies between bacterial primary producers, metazoan consumers at multiple trophic levels, and abiotic factors in marine and cave environments [54,55].

Notable chemoautotrophic cave ecosystems studied in depth include Movile Cave in Romania, which contains rich sulfur-oxidizing communities with over 50 endemic species [52,56], and Ayyalon Cave, whose entire chemoautotrophic ecosystem is endemic [55,57].

There is evidence that some chemoautotrophic cave ecosystems receive a substantial nutrient supply from marine photosynthetic primary production or breakdown of

aboveground organic matter. However, many ecosystems appear capable of functioning independently, representing unique extreme habitats [55,58].



**Figure 1.** Diagram of three potential routes for the colonization of land by arthropods (green arrows). A. Colonization from sea to land through subaerial rivers, with exposure to physiological challenges such as ultraviolet radiation, lack of food sources, and other terrestrial stresses [1,46]. B. Direct colonization from sea to land, possibly using the soil interface [48], with exposure to physiological challenges. This route involves arthropods migrating directly from the ocean onto land, requiring adaptation to harsh conditions including UV exposure, lower humidity, a lack of food sources, and other terrestrial stresses. C. Gradual, stepwise colonization via caves containing anchialine water, hygropetric margins (where a thin film of water covers the rock surface), and subsurface streams (this paper). This route provides a more incremental pathway to land through brackish zones and freshwater inside caves. Adaptation to terrestrial life could occur gradually by first exploiting food sources in cave water sheltered from UV radiation. Eventually, arthropods could emerge from caves to colonize land after suitable habitats developed with abundant plant food sources, high oxygen levels, and protective ozone. The cave environment allows for incremental adaptation before facing the selection pressures on land.

Recent phylogenetic and biogeographic studies show that chemoautotrophic cave ecosystems, which had also acted as anchialine systems connected with the sea, have supported arthropod communities based on sulfur-oxidizing microorganisms for millions to tens of millions of years [59–61]. This demonstrates the long-term stability and robustness of such cavities and their ecosystems.

Overall, chemoautotrophic caves provide models for studying life in durable, extreme environments in the partial or complete absence of sunlight. Continued research promises to reveal more about subsurface biomes and the fundamentals of carbon and nutrient cycling. Here, we suggest that such caves could have served as a stepping stone for the transition of arthropods from sea to land prior to the appearance of terrestrial photosynthetic plants.

## 2. Discussion

The accepted prerequisites for the arthropod land conquest, including a well-developed land flora and an effective ozone shield against UV radiation, were irrelevant for under-



ground self-sustaining systems. Such a subsurface system of terrestrial chemosynthetic microbial life could provide a reliable long-term trophic basis without the need for a land flora and without the hazards of UV radiation. Microbial chemolithoautotrophy is indeed ancient in Earth's history and predates photolithotrophy. The oldest known chemotrophic organisms are Archaean thermophilic prokaryotes, which inhabited sub-sea-floor volcanogenic–hydrothermal environments [62]. Anoxygenic forms of photosynthesis and chemoautotrophy played dominant roles in primary production for much of the Archaean era [63]. Biomats producing energy from sulfur compounds have been known since the Archean [64] and likely thrived in cave systems during the Paleozoic as they do today (Figure 2). Therefore, it is reasonable to hypothesize that the faunal invasion into cave systems could have taken place prior to and independently of the evolution of terrestrial ecosystems. Such an invasion would have been possible during early Paleozoic times of relatively low atmospheric oxygen concentrations and without terrestrial plants, utilizing terrestrial, highly productive sulfidic groundwater, where microbial biomats provided the needed resources for the food web. Under low-oxygen conditions, appropriate faunal adaptations would be necessary [65]. Some cave crustaceans and arachnids possess the hemocyanin copper protein, which functions as an oxygen carrier in the blood, allowing them to extract small amounts of dissolved oxygen under hypoxic conditions [66].

Species can rapidly colonize caves if sufficient variability and phenotypic plasticity are present in the population, as has been demonstrated to be possible within a few generations [67]. Species already adapted to detritivorous life below the photic zone could have switched to cave habitats with almost no special adaptations. Troglomorphic features and behaviors, such as loss of eyes and pigments or elongated sensory organs, could be caused by changes in the expression of developmental genes within the available time frame.

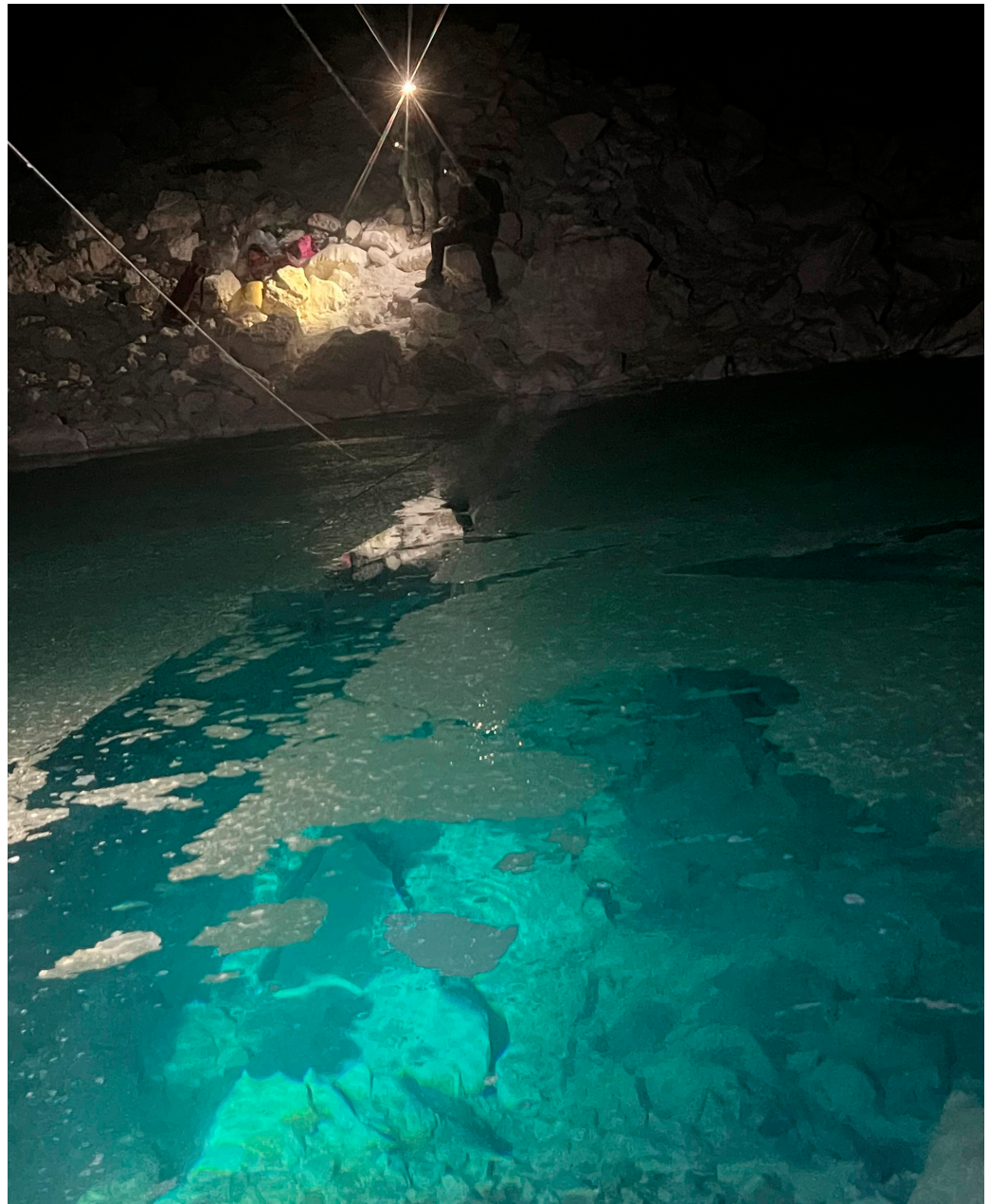
Caves provide gradual transitions from saltwater through anchihaline brackish to freshwater and from water-inundated voids through the hygropetric environment at the water margins to dry habitats (Figure 1). This is and has been promoted by the natural water cycle: Rainfall can infiltrate the subsurface and reach caves, and it can also be drained in subaerial catchments as runoff, collecting into streams that can form large cave systems and become subsurface rivers. Any form of this groundwater, while flowing into the sea, may create freshwater in anchihaline brackish environments. These can provide transitional routes, allowing arthropods to gradually adapt and move from salt water to freshwater. The subsurface rivers also carry food, such as fungus, from land into caves. Thus, cave arthropods could benefit from several food sources, including sea-sourced materials, chemosynthetic microorganisms, and terrestrial materials.

Metazoans with terrestrial surface locomotion, such as arthropods, could develop amphibious foraging behavior on the hygropetric borders of water bodies in caves to access biofilms stranded by changes in water levels or to hunt smaller organisms utilizing these stranded biofilms. Such foraging would be a first step towards venturing into drier subsurface voids. This hypothetical behavior is consistent with the ecology of the Ayyalon Cave arachnids—the pseudoscorpion *Ayyalonia dimentmani* and the scorpion *Akrav israchanani* [68,69], as well as the observation of an amphibious Mexican cave chactoid scorpion, *Alacran* [70].

Following improved adaptation to subaerial locomotion, feeding, and breathing, which could have all taken place within the isolated and self-sufficient cave system, some species could have ventured out of caves, initially relying on chemoautotrophic biofilms extending out through cave streams. Once there was enough photoautotrophic food on the surface, these pioneering arthropods could have stayed out of caves, taking advantage of the increasing surface resources.

Leaving the caves and surviving in exposed environments could have taken place during the Ordovician to Devonian periods, coupled with the rise of terrestrially productive photosynthetic plants and concomitantly with the increase in atmospheric oxygen and ozone levels [71–73]. This could occur many millions of years after the adaptation to cave

systems. Upon emergence from the cave systems, the pioneering arthropods could lose their troglomorphic adaptations due to changes in the expression of developmental genes.



**Figure 2.** Chemoautotrophic microbial mat over the water of Ayyalon Cave, Israel, during the recent research expedition of 30 November 2023. This cave site sustains an endemic ecosystem with arthropods for millions of years [60–62]. Photo: A. Frumkin.

This scenario is consistent with modern observations, which show repeated recolonization of surface habitats by cave-dwelling arthropods. These include troglobitic arachnids [74] and groundwater arthropods [75], indicating that the adaptation to the subsurface is not a one-way evolutionary route. We do not claim that the first steps to terrestrialization had to have taken place in deep, isolated chemoautotrophic systems. There is no reason to assume that the stepping-stone caves were necessarily as isolated as some known current sulfidic karst systems [52,55]. Indeed, we would expect some light to have penetrated a few of the caves; otherwise, we would expect visual sense organs to have degenerated irreversibly, as seen in some subterranean arthropods [76].

Our hypothesis requires the existence of cave systems of karst or volcanic origin during early Paleozoic times, a known feature of this period [77,78]. Volcanic caves may have been more common than karst caves in ancient terrestrial environments, but other cave-forming processes are possible, as in other planetary systems, e.g., tectonic fracturing [79,80].

Chemolithoautotrophic systems exist in karst caves today and can be used as field models for the hypothesis presented here [52,55]. These examples are relatively independent of atmospheric oxygen levels. Recent studies show that microbial life is common at great depths [81]. Sulfuric caves connected to the sea can accommodate chemolithoautotrophic microbial mats, supporting chemosynthetic primary production [82]. Modern lava tubes that accommodate lava flows in Hawaii demonstrate terrestrial thermal sulfidic water connected with seawater via anchihaline environments. The lava-tube basaltic bedrock contains reduced sulfur, iron, and manganese, which can serve as energy sources for chemolithoautotrophic biomats [83]. Prior to limestone cave development, lava tubes could thus be the earliest caves to support a subsurface haven for life and possibly a terrestrialization route as well. As noted above, because light is not available beyond the twilight zone of caves, the dark-zone inhabitants have to adapt to alternative food sources, such as chemolithotrophic bacteria [82–84].

Finding supporting fossil evidence for our hypothesis is not easy, as Paleozoic arthropod fossils in caves are rare [85,86], and Paleozoic caves are not well preserved [77,78,87]. The lack of fossilization of cave fauna is demonstrated by the isopod suborder Phreatoicoidea, which is currently exclusive to caves, but whose fossils are commonly found in late Carboniferous marine sediments. After moving into freshwater environments during the Permian [88], their fossils are unknown after the Triassic, during or after which they became subterranean. The low preservation potential of cave fauna is consistent with the almost complete lack of terrestrial or semi-terrestrial fossils of stem-group terrestrial taxa.

Perhaps the most suggestive evidence for caves being stepping stones to terrestrialization is that the closest living sister group to terrestrial insects are the obligatory cave-dwelling remipedes. While there is no a priori reason to assume that the common ancestor of remipedes and insects resembled remipedes in its ecology and habitat, such a reconstructed ancestor would be fully consistent with our hypothesis.

Finally, the highly disjunct distribution of crustaceans adapted specifically to the poorly oxygenated water of anchihaline caves, including Spelaeogriphaceae and Remipedia, suggests a Pangean origin, possibly of Paleozoic age [89]. This should be carefully evaluated on a comparative phylogenetic level, which could potentially reveal multiple independent adaptations to cave habitats. This is again consistent with a very early shift to cave-dwelling habitats in some arthropod taxa.

### 3. Conclusions

The development of complex terrestrial arthropod life on Earth required overcoming several major hurdles. First, the challenges of transitioning from an aquatic environment onto dry land were immense. Arthropods needed to evolve adaptations to overcome UV radiation, prevent desiccation, move on solid substrates, obtain oxygen, and find new food sources outside of water when no vegetation was available.

Direct colonization from the ocean onto land would require rapid, radical adaptations to the harsh conditions on land. Arthropods would need to quickly evolve solutions for various problems all at once.

We propose an alternative route—gradual adaptation through cave environments. Such a subsurface stepping stone hypothesis provides an answer to the conundrum of early Paleozoic arthropod terrestrialization, which took place before suitable surface habitats formed with abundant plants, oxygen, and ozone shielding. Coastal caves could have provided a more stepwise pathway to terrestrial life. The cave habitat shielded arthropods from UV radiation, while they gradually adapted to drier conditions through brackish and freshwater (Figure 1). Food sources could be obtained from chemolithoautotrophic microbial mats, as well as other cave organisms such as fungi. Once pre-adapted through



cave life, emerging onto land would be less difficult after abundant plants, oxygen, and increased ozone developed outside. Traits needed in caves could have been discarded later, as surface conditions improved.

In conclusion, the proposed terrestrialization route would have allowed one or more arthropod taxa to adapt to new frontiers via a stepwise and gradual dispersion from the sea into anchihaline cave waters, hygropetric margins of water bodies in caves, and finally to the surface. This hypothesis is consistent with modern cave observations [52,61] and phylogenetic reconstructions from DNA data [49].

As the complex problem of terrestrialization has produced several persuasive hypotheses, our hypothesis may stand alone or be complementary to former scenarios of terrestrialization. Several available routes could be used for the colonization of land by various taxa diachronically across the heterogenic coastal terrain. In any particular case, a specific hypothesis may correspond better to reality than others, and future studies can address the question of which scenario corresponds best to the available key evidence.

Our new hypothesis can potentially be supported by several possible types of additional data or analysis:

- Look for geological and fossil evidence of suitable ancient coastal/cave/paleokarst habitats existing in the Cambrian through Ordovician periods when molecular data suggests early arthropod diversification on land. The recovery of early Paleozoic fossils representing crown group or upper-stem group terrestrial arthropod taxa with identifiable adaptations to cave life or to bacterial mat feeding would help to substantiate the new hypothesis.
- Identify fossils with signs of incipient troglomorphy (eye/pigment loss, sensory elongation) that do not show full adaptation to caves. Transitional forms would be expected.
- Use modeling approaches to determine if subsurface habitats could have supported arthropod nutritional and respiratory needs before surface habitats developed. Energetic feasibility modeling could be informative.

**Author Contributions:** Conceptualization, A.F.; Validation, A.F. and A.D.C.; Investigation, A.F.; Writing—Original Draft Preparation, A.F.; Writing—Review and Editing, A.F. and A.D.C. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest.

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