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Evolution: Out of the Ocean

New analyses suggest that animals colonized land sooner than previously thought, and maybe even before embryophytes (land plants). This has important implications for our understanding of the historical interactions of terrestrial organisms with each other and their physical environments.

Casey W. Dunn

The colonization of land by marine organisms took place many times — plants, animals, fungi, and many microbial lineages all made it here independently. These transitions are some of the most interesting and pivotal events in evolutionary history. They transformed the face of the Earth, its atmosphere, its oceans, and its geochemical cycles. It is clear that terrestrial organisms now depend on each other for their survival. They rely on each other for food, reproduction, dispersal, and many other services and resources. But if these organisms are now all so dependent on each other, how did the first arrivals survive? Their interactions with each other and with their new physical environments must have been very different from their interactions now.

In order to understand how the earliest terrestrial ecosystems were organized, we need to know who came first and when they arrived. Most hypotheses suppose that the food web as we know it now was assembled one element at a time, from the bottom up. First plants, then the animals that eat them, and so on. In a recent issue of *Current Biology*, Rota-Stabelli and colleagues [1] present analyses that contradict this classical perspective, suggesting that some animals colonized land at nearly the same time or even before plants. These results are consistent with other recent analyses that take a similar approach [2,3], indicating that these changes in our understanding of terrestrial life are robust across data sets and analyses.

All of these studies use time-calibrated phylogenies. These phylogenies are built with DNA sequence data, and the ages of a subset of internal nodes on the tree are then constrained so as to be no younger (though possibly older) than a known fossil taxon that belongs to that lineage [4]. The ages of the unconstrained nodes, such as those that are associated with transitions to land, can then be investigated with a variety of methods. Though molecular evolution has been used for decades as a clock to calibrate divergence events in the tree of life [5], this is a difficult business, and one that often leads to results that are inconsistent across studies and with the fossil record [6]. The challenges are many: results depend on inferring relationships between species, the homogeneity of rates of molecular evolution, the geological dating of fossils, and ascribing particular fossils to particular groups of organisms that are included in the phylogeny. Problems with any of these steps can have huge impacts on the results.

Rota-Stabelli and colleagues [1] focus on Ecdysozoa, the group of animals that includes nematodes, arthropods [7], and their relatives, while the other studies [2,3] focus on the arthropods. Many different ecdysozoan lineages have independently colonized land, including nematodes, onychophorans (velvet worms), tardigrades (water bears), and several groups of arthropods. The species that Rota-Stabelli and colleagues consider allow for assessments of six of these colonization events. All of these papers [1–3] make use of advanced statistical methods and software tools for building time-calibrated phylogenies. Well-sampled gene sequence data are available for a much broader diversity of organisms than only a few years ago, which is also improving our understanding of animal relationships [8]. In addition, our understanding of the fossil record has improved

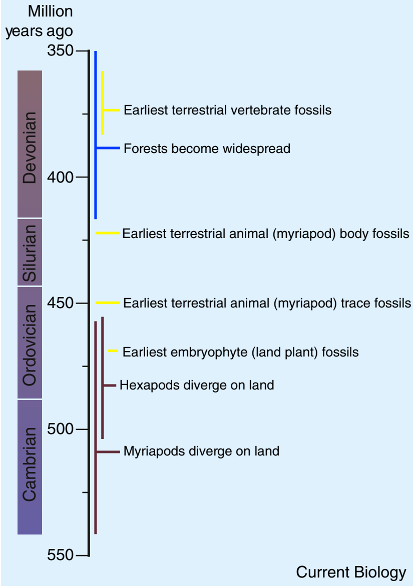

Figure 1. Timeline of the colonization of land in the early Paleozoic.

The first animals to arrive on land were the myriapods, the centipedes and millipedes. Direct fossil evidence for key events is indicated with yellow lines. These dates are drawn from the previous review of Garwood and Edgecombe [9], including the earliest terrestrial arthropod trace fossils [13], first terrestrial arthropod body fossils [14], and the earliest embryophyte fossils [11,17]. Selected results of Rota-Stabelli and colleagues [1] are indicated with brown lines. The vertical line indicates the minimum and maximum 95% credibility intervals across all their analyses, and the horizontal line is the mean value across their analyses.

considerably, allowing a more detailed calibration.

There are many fossils that speak directly to the colonization of land (Figure 1). The first evidence of embryophytes (the clade of land plants that includes liverworts, mosses, hornworts, and vascular plants) and land animals stems from the Paleozoic,the era that spans from 542–251 million years ago (mya) (Figure 1) [9]. The land was not sterile before they arrived. Other organisms lived on land long before the ancestors of modern-day terrestrial plants and animals joined them [10], though very little is known of these earlier terrestrial species. While many different animal lineages came to land independently, embryophytes are likely to have arrived only once. The earliest embryophyte fossils currently known date back to about 470 mya [11]. Early embryophytes lacked well-developed root systems and depended on fungal interactions to obtain nutrients [12], providing a compelling example of how important interactions between organisms were to the colonization of land.

The earliest known fossils of land animals are of millipedes. Trace fossils from about 450 mya have been interpreted as millipede footprints, followed by fossils of millipede bodies from about 423 mya [13,14]. Millipede fossils are followed by several other groups of terrestrial arthropods, but it isn't until much later that terrestrial vertebrates arrived on the scene in the upper Devonian (385–359 mya) [9].

How long have animals lived on land before leaving behind the first direct fossil evidence of their arrival? This is one of the central questions that Rota-Stabelli and colleagues tackle [1]. Their conclusion is that animals arrived on land much earlier than the fossil evidence suggests (Figure 1). Like the other recent studies [2,3], and in agreement with the fossil record, they find that myriapods, the group that includes millipedes and centipedes, were the first animals on land, around 544–457 mya. This range of dates overlaps with or precedes the first embryophyte fossils. Hexapods (the group that includes insects) are dated to 504–456 mya, and arachnids (spiders and relatives) to 515–407 mya.

Rota-Stabelli and colleagues [1] address many issues that are known to be problematic in calibrating phylogenies through analyses of multiple partial overlapping data sets, sensitivity tests, and the use of different subsets of fossil calibrations. These analyses indicate that the results are quite robust, which is reinforced by their congruence with the other recent studies [2,3].

Just as the work summarized here suggests that land animals are much older than their first fossils, embryophytes may be much older than their first fossils. This means we need to compare time-calibrated phylogenies of animals to those of embryophytes if we want to figure out who came first. In contrast to analyses of the first animals on land, however, there is wide variation across studies that date embryophytes [15]. This is in part due to differences in the rate of molecular evolution among different lineages of embryophytes [16]. A broadly sampled study [17] that attempted to address these issues estimated the first diversification of embryophytes to be in the interval of 490–425 mya. These overlapping windows for when animals (544–457 mya) and plants (490–425mya) arrived on land don't provide a definitive answer as to who got here first. But they do leave open the possibility that animals arrived first, as Rota-Stabelli and colleagues suggest [1].

The arrival of animals on land before plants would upend the classical notion that the order of community assembly reflected the structure of modern-day food webs, indicating that the first animals weren't dependent on plants, as they are now, for survival in their new habitat. Rota-Stabelli and colleagues [1] speculate that the earliest terrestrial animals might have fed on microbial mats or washed-up marine debris. This could be the case, but we will need to better understand complex communities that preceded plants and animals on land [10], and date the origin of embryophytes, before we can get an accurate picture of the early diet of terrestrial animals.

The questions that Rota-Stabelli and colleagues address [1] are not restricted to the colonization of land by animals. Like other recent analyses [18], they also find that some animal clades precede, by quite some time, the Cambrian Explosion seen in the fossil record. This indicates that many animal groups may be quite a bit older than previously thought. Though Rota-Stabelli and colleagues [1] do not definitively answer the question of whether plants or animals made it to land first, their results suggest that the two arrivals at least happened surprisingly closely.

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Memory Reconsolidation: Time to Change Your Mind

A new study shows that temporal expectations about threats are a key part of fear memories and that changing this temporal expectation is enough to trigger the updating and reconsolidation of a previously learned fear.

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and Peter D. Balsam[1,2,3]

When faced with new information there are some instances when old memories get updated, and some in which they do not. What factors specifically trigger this updating process? In this issue of *Current Biology*, Diaz-Mataix *et al.* [1] address this important unanswered question about our constantly evolving representation of the world. Imagine making a trip to revisit your childhood home. Your destination is your parents' house, and driving there feels almost automatic — you put little thought into what turns you must make and when to make them. The memories you have for the route home have been strongly formed and you access them with ease. Consider what would happen if you went to make the next turn only to discover that the street is no longer there. New road work since your last visit has altered the street layout. You must take a new route to get to your parent's home, and subsequently update your mental map to incorporate the new information so your future trips can follow the most efficient route. Ideally, we should benefit from our experiences — not remaining set in our ways, but rather being capable of flexibly adjusting our memories and representations as we encounter new information. It would be extremely inefficient to treat each experience as entirely unique and have to learn things *de novo* each time we encounter them.

Being able to form memories is ultimately what allows us to learn from experience and carry information about how the world works forward in time; being able to update memories allows us to continuously adapt to changes in the world, as is the case when road crews alter the street layout in your hometown. About 75 years ago the developmental psychologist Jean Piaget referred to the incorporation of new knowledge into our existing mental structures as assimilation, while the changing of cognitive structure based on new experience was called accommodation [2]. This became an enduring problem in the study of cognition, but it was not until fairly recently that we have begun to understand the neurobiological processes that underlie the formation and updating of memories.

Immediately following the formation of new memories there is a period of time in which the memory exists in a labile state, prone to several types of disruption. As more time passes, however, a process of progressive stabilization occurs — a process known as memory *consolidation* [3]. At one time it was believed that, once consolidation had occurred, memories were permanently fixed. Although several lines of earlier work suggested that following the reactivation of a previously formed memory it might reenter a labile state (see [4] for a review), little research was done on reconsolidation until Nader *et al.* [5] showed that reconsolidation is dependent on protein synthesis. These authors found that, if done immediately after reactivation of a fear memory, injection of a protein synthesis inhibitor into the basal lateral amygdala, a region now well established as crucial for Pavlovian threat (fear) conditioning [6], caused apparent erasure of the earlier learning.

Since that seminal study progress has been rapid, in part, because researchers converged on Pavlovian threat conditioning as the paradigm for studying learning, memory and reconsolidation. In this protocol a neutral stimulus, known as a conditioned stimulus (CS), is paired with some aversive stimulus, known as an unconditioned stimulus (US). This procedure commonly uses a tone as the CS and an electric foot shock as the US. What gets learned is a temporal expectation that, in the presence of a particular cue (tone), a specific event (electric foot shock) will happen at