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Our shallow-water origins

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Vertebrates encompass all animals with a backbone, from fish to humans. How and when they evolved are questions that have been studied for centuries, revealing the origins and processes involved in anatomical innovations such as jaws, teeth and paired appendages (*1*). A less explored, but equally important question is *where* they evolved. Indeed, the environmental context of vertebrate evolution remains a gap in our knowledge. Understanding the habitat constraints faced when key traits evolved is necessary to answering fundamental questions in macroevolution such as the extent to which the environment can drive anatomical transformations. Reaching this level of understanding has been limited mostly by a lack of data in available compendia (*2*).

[On page x of this issue] Sallan *et al*. compiles a new database of early occurrences (mid-Paleozoic, 490-360 Ma) and site-specific environmental information to reconstruct vertebrate ancestral habitats. They found that all major vertebrate clades originated in restricted, shallow-water environments. Indeed, the fossil record of mid-Paleozoic fish is known from rocks that accumulated in shallow-waters (*3*). However, it has been recognized that this might be an artifact of a poor fossil record; in other words, the habitats from where ancient fish have been recovered might reflect outcrop availability rather than true origins. Sallan *et al.* explicitly test this possibility and demonstrate that while most early fish fossils are found in rocks coming from depths between 60 and 200 meters (*4*), the early diversification of vertebrates was restricted to shallower environments, of less than 60 m of depth. Accordingly, the ancestral habitats of early fish are not a sampling artifact.

Importantly, Sallan *et al.* show that the use of shallow-water habitats as a cradle for diversification was robust and persistent over time. Similar to what has been found in benthic invertebrates (*5*), vertebrates continued to originate there even long after they had diversified, dispersed or evolved anatomic innovations (e.g., jaws). Evolutionary shifts to deeper waters were far more difficult than to other nearshore environments, or to freshwater. Nevertheless, early fish managed to occupy different aquatic environments along the depth gradient. Interestingly, dispersal into habitats outside the protected cradle were not necessary to evolve new phenotypes. Instead, the major body forms (e.g., benthic and pelagic) originated in shallow waters before expanding to new habitats.

What was so special about the shallow-water habitats where vertebrates diversified? The mid-Paleozoic nearshore environments were somewhat different from today. Seagrasses, mangroves and modern coral-reefs were yet to appear. Nevertheless, habitat-forming species such as stromatolites, sponges and early corals, occurred (*4*). These habitats experienced fundamental evolutionary changes during this time, as the water column gradually filled up with newly evolved nektonic forms (*6*). The exploitation of the vertical habitat dimension was likely driven by competition in the saturated benthic zone, and by increased productivity resulting from riverine influx when arborescent flora evolved on the land (*7*). Although these transformations took place in all coastal habitats, most origination was located in lagoon-like systems, and therefore in protected areas. Was the combination of heterogeneity, structure and protection the foundations for the diversification of major vertebrate clades?

Today, protected shallow-water ecosystems are not only biodiversity hot-spots, but also serve as essential nurseries for fish (e.g., coral reefs, estuaries and mangroves). These ecosystems offer physical structure, habitat heterogeneity and trophic complexity, ultimately providing abundant food and refuge to marine fauna, as well as important services to humans (*8*). It is known that nearshore systems have supported fish diversity for at least 66 million years (*9*). The study of Sallan *et al.* not only extends this association to the very origins of vertebrates, but also highlights the role of shallow-waters as a persistent cradle for their diversification. Nevertheless, just as these environments can support biodiversity, their reduction can also result in their loss. Not long ago (geologically speaking), marine vertebrates suffered a significant extinction as shallow-water habitats contracted due to dramatic sea-level oscillations (*10*). Before they had time to recover, modern humans started degrading these ecosystems not only by over-exploiting their fauna, but by destroying the structure that provides the foundations of biodiversity (*11*). The work of Sallan *et al.* shows us that without shallow-water habitats, vertebrates like us would probably not have evolved. Worryingly, it is precisely these ecosystems the ones that have been altered the most by human activities (*12*).

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Figure ideas
3D image showing the different types of nearshore envioroments and their depths divided in 2, one showing the enviroments from the past (left), and the other (right) showing the enviroments today.