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## Biogeochemistry

### Oxygen burrowed away

*Multicellular animals likely evolved at the seafloor after a rise in oceanic oxygen levels. Biogeochemical model simulations suggest that as these animals started to rework the seafloor, they triggered a negative feedback that reduced global oxygen.*

Filip J. R. Meysman

When Charles Darwin visited the family estate of his future wife Emma Wedgwood in 1837, her father, Josiah Wedgwood showed Darwin an agricultural field where just 15 years earlier, the surface had been covered with lime and cinders<sup>1</sup>. These materials were now buried at considerable depth below the surface, and Wedgwood believed that earthworms were the responsible agents<sup>2</sup>. This discussion with his father-in-law to be triggered a lifelong interest in the mixing of soil by animals – bioturbation –, and in later years, Darwin devoted an entire monograph to the subject stating that “Worms have played a more important role in the history of the world than most persons would at first suppose”<sup>3</sup>. Boyle *et al.*<sup>4</sup> in *Nature Geoscience* take this idea now to such a scale and level, that even Darwin - although not afraid of a grand idea himself - would most likely be genuinely surprised. These authors suggest that the evolution of bioturbation some 540 million years ago affected the oxygenation of oceans and atmosphere.

Until now, ideas about the co-evolution of life on earth typically put geochemistry and microbiology in the driver's seat: interactions between microbes and rocks are determining global biogeochemistry, and setting the stage upon which biological evolution unfolds. Yet, since the emergence of multicellular life in the Neoproterozoic, microbes are not the only players around, and so the question can be raised whether the evolution of plants or animals induced any feedbacks on global geochemistry, steering the co-evolution of life on earth. To date the best studied ‘macro-organism’ feedback is the evolution of vascular plants in the Devonian, which introduced a potent biotic feedback on global biogeochemistry, increasing atmospheric O<sub>2</sub> levels, by stimulating the burial of carbon in oceanic sediments through production of refractory lignin [5]. But what about that other defining moment in the evolution of life, the rise of animals?

Animals may not have been passive players amidst changing atmospheric or oceanic conditions either. It is generally held that an increase of oceanic oxygen at the end of the Neoproterozoic allowed the development of multicellular organisms with higher metabolic demands. This biotic expansion culminated in the Cambrian explosion 540 million years ago, when a wide variety of animals appeared in the fossil record over a relatively short time<sup>7</sup>. Originally living on top of the seafloor, early animals soon colonized the subsurface as well, looking for shelter from predators and tapping into organic food resources buried in the sediments. These activities dramatically altered the appearance of the ocean floor<sup>2</sup>. Before the rise of bioturbation, most of the seafloor was covered with microbial mats. As animals burrowed into and under the mats, regular layers of matted sediments were replaced by a heterogeneous reworked sediment layer intersected with animal burrows. In recent years, new speculative ideas start have surfaced, forwarding scenarios how this “burrowing revolution” could have influenced atmospheric or oceanic variables. One idea is that the onset of bioturbation may have increased sulfate concentrations in the ocean, as bioturbation stimulates sulfide re-oxidation in marine sediments [6].

Boyle *et al.*<sup>4</sup> now suggest that the effects of the “burrowing revolution” went even further. They propose that the onset of bioturbation triggered a series of feedbacks, which counteracted the global oxygenation in the late Neoproterozoic, and subsequently stabilized atmospheric O<sub>2</sub> at lower levels. To support their idea, they simulated the effects of sediment mixing on phosphorus and organic carbon burial in a simplified model of global biogeochemistry. In their simulations, bioturbated sediments retain more phosphorus relative to carbon as compared to unmixed sediments, a signature also observed in present day bioturbated sediments<sup>8</sup>. Higher organic phosphorus burial lowers the availability of the limiting nutrient phosphorus, and hence decreases oceanic productivity, which leads to reduced organic carbon burial and lower oceanic and atmospheric O<sub>2</sub> concentrations. This subsequently promotes the expansion of ocean anoxia, which then restricts the distribution of bioturbating animals. The overall result is a negative feedback process that stabilizes atmospheric oxygen at a lower level, compared to the initial Neoproterozoic concentrations.

Boyle *et al.* also show that redox conditions, as reconstructed from proxy data, are largely consistent with the expansion of ocean anoxia that their model predicts. Still, it should be noted that there are few proxy datasets with sufficiently high temporal resolution, and that there is considerable debate on how bioturbation developed through the early Phanerozoic. For example, the current model simulations assume a rapid increase in the depth and intensity of bioturbation in the early Cambrian, which may not necessarily have been a global phenomenon<sup>9</sup>.

Much is still unknown about the redox structure of the ocean and atmosphere during the late Neoproterozoic and early Cambrian (800 to 400 million years ago) and its relationship with evolving life.

Boyle *et al.*<sup>4</sup> now propose that the advent of digging and burrowing animals set up a feedback loop that regulated atmospheric oxygen and oceanic phosphorus levels. Although we are still far from knowing to what extent worms and their ilk influenced the geochemical history of our planet, this is a novel and testable hypothesis, which will inspire novel thinking and incite engaging discussions – maybe even with your prospective father-in-law.

## References

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