SEDIMENTOLOGY

Digging deeper

The Cambrian evolution of burrowing species is thought to have facilitated sediment mixing. However, sediment fabrics suggest that bioturbation remained insignificant until the appearance of more efficient sediment mixers in the Silurian.

Murray Gingras and Kurt Konhauser

Throughout the Precambrian, marine sediments passed into the rock record largely undisturbed unless subjected to processes such as slope collapse, seismicity or rapid dewatering. In near-shore environments, chemical exchange between bottom ocean waters and sediments were primarily limited to pore-water advection and diffusion. These processes were hindered by the broad distribution of biofilms and microbialites, which effectively served as a physical barrier between the ocean and the deeper sediments. The evolution of mobile animals capable of mixing the sediment through burrowing behaviours occurred by the late Ediacaran and early Cambrian. Writing in *Nature Geoscience*, Tarhan and colleagues[1] show that the transition to well-mixed and well-oxygenated sediments — and hence modern redox-driven nutrient cycles — did not occur until at least 120 million years after burrowing animals first appeared.

Early animals burrowed across and through sedimentary layers, mixing them in a process known as bioturbation. Sediments were homogenized through the mixing of fresh and older layers, and grazing also led to increased decomposition of sedimentary organic material. Bioturbation also influenced the solid-phase and pore-water properties of sediment by increasing the transport of diagenetic reactants and products across the sediment–water interface. This transport also affected the spatial distribution of redox-sensitive nutrients.

In particular, the impact of oxygen penetrating below the sediment–water interface has been linked to the oxidation of sedimentary sulfides (Fig. 1), resulting in a several-fold increase in seawater sulfate concentrations[2] as well as establishing a phosphorus sink in the oceans[3]. From a biological perspective, increased sediment oxygenation also permitted widespread colonization of the upper sediments by aerobic bacteria and animals at the expense of the previous occupants, the anaerobically respiring bacteria. These anaerobic bacteria were thus marginalized to the deeper sedimentary layers where they reside today.

MURRAY GINGRAS

Figure 1 | Burrows and oxygen. Animals capable of burrowing into the sediments evolved by the Early Cambrian. However, Tarhan and colleagues show that sediments did not become well mixed until the Silurian. Burrows, like that of a spionid polychaete seen here, introduce oxygen into marine sediments, and thereby generate an oxidized zone (the orange halo). A lack of a deep, well-oxygenated mixed layer in early Palaeozoic sediments could explain the low seawater sulfate concentrations that persisted through this interval. Photo taken in Willapa Bay, Washington, USA.

The advent of biological mixing is coupled with a greater diversity of trace fossils, and is referred to as the Agronomic Revolution[4]. As animals radiated physiologically and evolved behaviours capable of exploiting different types of food resources, the thickness of bioturbated zones within marine sediments, and quite possibly the amount of biological reworking, increased. However, it is unclear how this zone developed and expanded over time.

Tarhan and colleagues[1] propose that the biogenically mixed layer slowly increased in thickness throughout the Cambrian and into the Silurian, based on a dataset with outstanding temporal and spatial coverage. They present data from twenty-two sites from North America, Europe and Australia that span the lower Palaeozoic. They attribute the rise in bioturbation to an increase in the bulldozer effect: vigorously grazing animals move rapidly through sediment, mixing it. The authors also propose that the increase in the thickness of the mixed layer through the Palaeozoic corresponds to small increases in marine sulfate concentrations, as more oxygenated sediments would promote sulfide oxidation. Correspondingly, a dramatic increase in bioturbation in the Devonian would have reduced the burial of sulfide and organic carbon, and might be a way of explaining a drop in atmospheric oxygen level at that time.

A protracted development of marine bioturbation challenges long-held views of the Ediacaran–Cambrian transition. For example, grazing and burrowing animals are considered to have led to the extinction of Ediacaran fauna, as well as the limitation of microbialite colonization during the Palaeozoic. A gradual expansion of animal activity contradicts this explanation. However, the link between grazing animals and the restriction of microbialite biomes has become less certain in the past decade. In upper Cambrian and Ordovician strata, microbially induced sedimentary structures are commonly observed alongside bioturbated sediment[5]. Furthermore, animals known from the early Cambrian may not have engaged in burrowing activities, despite their body plans being indicative of such behaviour — according to this theory, grazing behaviours more emblematic of the Phanerozoic did not appear until the middle of the Cambrian[6]. Nevertheless, the Agronomic Revolution is most often viewed as a Cambrian event[6,7], and not, as this study shows, a prolonged cultural evolution.

If the demise of the Ediacaran biome was not, in fact, a consequence of the rapid spread of bioturbation, it may instead have resulted from nutrient or other chemical factors that have yet to be identified. It is also curious that most forms of grazing behaviours were well-established by the end of the Cambrian, yet deep sedimentary mixing is severely limited until well into the Silurian. Tarhan and colleagues suggest that this represents the absence of very mobile deposit feeders; however, arthropods, molluscs and annelids already existed by the Ordovician. Low dissolved oxygen concentrations may have encouraged animals to stick close to local oxygen oases associated with microbial mats[8] instead of burrowing deep in the sediments. Alternatively, the development of the mixed layer may instead reflect the evolution of the community structure of infaunal organisms living within the sediment column.

Tarhan and colleagues[1] have shown that the development of the mixed layer occurred well after animals capable of mixing the sediment appeared. When biogenically mixed layers analogous to Mesozoic and Cenozoic mixed layers actually arose, and how this development relates to marine geochemical and infaunal ecological changes, remains to be determined. ❐

Murray Gingras and Kurt Konhauser are in the Department of Earth and Atmospheric Sciences, 1-26 Earth Science Building, University of Alberta, Edmonton, Alberta T6G 2E3, Canada.
e-mail: mgingras@ualberta.ca

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