DISPATCH

Palaeobiology: The enzymes that made soft-tissue fossils scarce[OK?]

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Fossilised soft tissues offer exceptional glimpses of ancient biology. However, a new study of the evolution of decay enzymes suggests their proliferation over 500 million years ago contributed to the decline of soft tissue preservation, leaving the animal fossil record dominated by shells and skeletons.

When we think of animal fossils, we probably think of tyrannosaur bones, the ancient shells of ammonites or the calcitic exoskeletons of trilobites. We are less likely to imagine soft, unarmoured worms making their way into the fossil record, or the internal organs and skin of *T. rex*. That's because the vast majority of fossils preserve only the hard mineralised body parts of ancient animals[1,2]. Soft tissues, and entirely soft-bodied animals, like worms, do fossilise, but only in rare circumstances, and the fossil record suggests these circumstances have become rarer through geological time[3]. A new study by Philip Vixseboxse and colleagues[4] in this issue of *Current Biology* argues that this decline may reflect the proliferation of decay enzymes, specifically bacterial collagenases.

Geological sites that exceptionally preserve soft tissues provide unprecedented windows onto the biology of ancient ecosystems. For example, in the famous ~505-million-year-old Burgess Shale in British Columbia, over 80% of the fossil animal genera are soft-bodied[5]. Those soft-bodied fossils reveal diverse animal life-styles, including swimming predators and burrowing taxa, and showcase the complexity of such an ancient ecosystem. In fact, as the first unambiguously biomineralised animal skeletons only appeared around 550 million years ago[6], our understanding of much of the early history of animals relies on soft-bodied fossils [AU this sounds a bit odd, they are still visible as soft bodied fossils]. Yet the importance of soft-tissue preservation is not only peculiar to the early animal fossil record. A seminal study of the modern ecosystem in Friday Harbor, Washington, showed that >50% of

its fauna are entirely soft-bodied[7], meaning we would also need soft-bodied fossils to accurately record its biodiversity.

Interestingly, there appears to be a major decline in the number of geological sites with soft tissue preservation starting around 500 million years ago[3]. This exacerbated the degree to which the animal fossil record was biased toward biomineralised organisms. Most studies explain the decline as a consequence of environmental change[3], often pointing to long-term increases in marine oxygen levels around that time[OK?][8,9]. Oxygen fuels aerobic decay, so greater oxygen availability may allow decay to proceed more efficiently. However, other hypotheses have also been proposed, including the changing composition of ancient seawater: Palaeozoic (539–252 million years ago) changes in marine silica[10] or calcium concentrations[11] may have diminished the cementation of sediments, removing physical barriers that protected soft tissue fossils from degraders and oxidants.

However, at its core, soft-tissue preservation requires the suppression of a biological process: decay. Microbial degraders consume animal soft tissues. In this process, the fibrous animal molecule collagen presents an important obstacle. It plays a vital role in maintaining the integrity of animal soft tissues[12,13]. Therefore, breaking it down is a crucial step in soft tissue decay and, today, enzymes are key catalysts in this process. Specifically, microbial collagenases can accelerate the breakdown of collagen by cleaving the molecule into more accessible monomers[14]. The central role collagenases play in collagen breakdown led Jerzy Dzik to propose, in 1999, that the decline of soft tissue preservation in the fossil record reflected the evolution of collagenases, enabling decay to proceed more efficiently[12]. Yet Dzik had no means to determine the evolutionary history of collagenases to test this idea.

In their paper, Vixseboxse and colleagues[4] do just that. They reconstruct the history of genes encoding collagenases across prokaryotic lineages. This is no trivial task, as the history of these genes is littered with lateral gene transfer, in which genes move between lineages rather than being inherited from parent to offspring. To disentangle this complex history, Vixseboxse and colleagues[4] compared phylogenetic trees of collagenase genes from modern taxa with a reference tree of prokaryotic relationships. This reference tree was time calibrated using fossil occurrences. By doing so, they were able to see how and when the genes, and thus collagenases, proliferated between prokaryotic lineages.

Their results support Dzik's theory, although not in the way he originally envisaged. Collagenases did not, as Dzik had postulated[12], originate at the point at which the soft tissue fossil record entered decline. Instead, they originated hundreds of millions of years earlier, at least as far

back as the Palaeoproterozoic era (2,500–1,600 million years ago). At this time, they were confined to anaerobic prokaryotic groups. It was not until the Neoproterozoic (1,000–539 million years ago) that they spread via lateral gene transfer to aerobic bacterial clades that are the major players in the decay of animal tissues today (such as Bacteroidetes and Gammaproteobacteria)[15,16]. This result, then, suggests aerobic decay bacteria acquired collagenases and became much more efficient at breaking down collagen just before the soft tissue fossil record entered decline[3] and as environmental oxygen levels likely increased[17]. Could this finally explain why soft tissue preservation becomes scarcer through geological time?

Perhaps, but marine animals do not always decay aerobically. This potentially limits the importance of aerobic degradation pathways in explaining the pattern. In fact, sites of exceptional soft tissue preservation are commonly associated with local anoxia[11]. The findings of Vixseboxse and colleagues[4] suggest that within anoxic settings, the anaerobic prokaryotic lineages that break down collagen have remained relatively unchanged since the Palaeoproterozoic. If soft tissue fossilisation was confined to anoxic settings, the Neoproterozoic proliferation of collagenases among aerobic bacteria might be inconsequential to the long-term distribution of soft tissue fossils. A fruitful line of inquiry will be to reexamine the record of exceptionally preserved fossil sites[3] to determine whether those in oxygen-rich[OK?] settings specifically decline from the early Palaeozoic onwards. This is a pattern that would be predicted by the acquisition of collagenase among aerobic bacterial lineages.

The analyses of Vixseboxse and colleagues[4] further prompt the question of why collagenases proliferated within aerobic bacterial lineages during the Neoproterozoic in the first place. As already highlighted, this expansion occurred broadly at the same time that oxygen likely increased in the oceans[17], but it also occurred as animals rapidly diversified across the Ediacaran and Cambrian periods (635–487 million years ago)[18]. These correlations raise the tantalising possibility that aerobic bacterial lineages acquired collagenases in response to a more oxygenated Ediacaran–Cambrian world or because diversifying collagen-rich animals provided a newly abundant source of food. Unfortunately, the timing of the spread of collagenase given by the authors remains imprecise, spanning tens of millions of years. It also relies on fossil calibrations despite few prokaryotic lineages having a useful fossil record. Only a more precise timeline for collagenase proliferation would enable these proposed links with oxygenation and animal diversification to be tested.

Regardless of the drivers of collagenase expansion or the importance of oxygen-rich versus anoxic settings, Vixseboxse and colleagues[4] demonstrate how biological tools, such as phylogenetic

analysis, can complement geological observations to probe the mechanisms of fossilisation. Such approaches may ultimately reveal how the biases of the fossil record vary through time, across environments, and among organisms.

Declaration of interests

The author declares no competing interests.

Figure 1. Collagenase spread alongside fossil record decline.

Acquisition of collagenase genes by aerobic bacterial lineages and temporal correlation with soft tissue preservation decline[3], Ediacaran and Cambrian fossil assemblages, and marine oxygen levels (O_2 curve adapted from[17] (CC BY 4.0); fossil silhouettes from phylopic.org)

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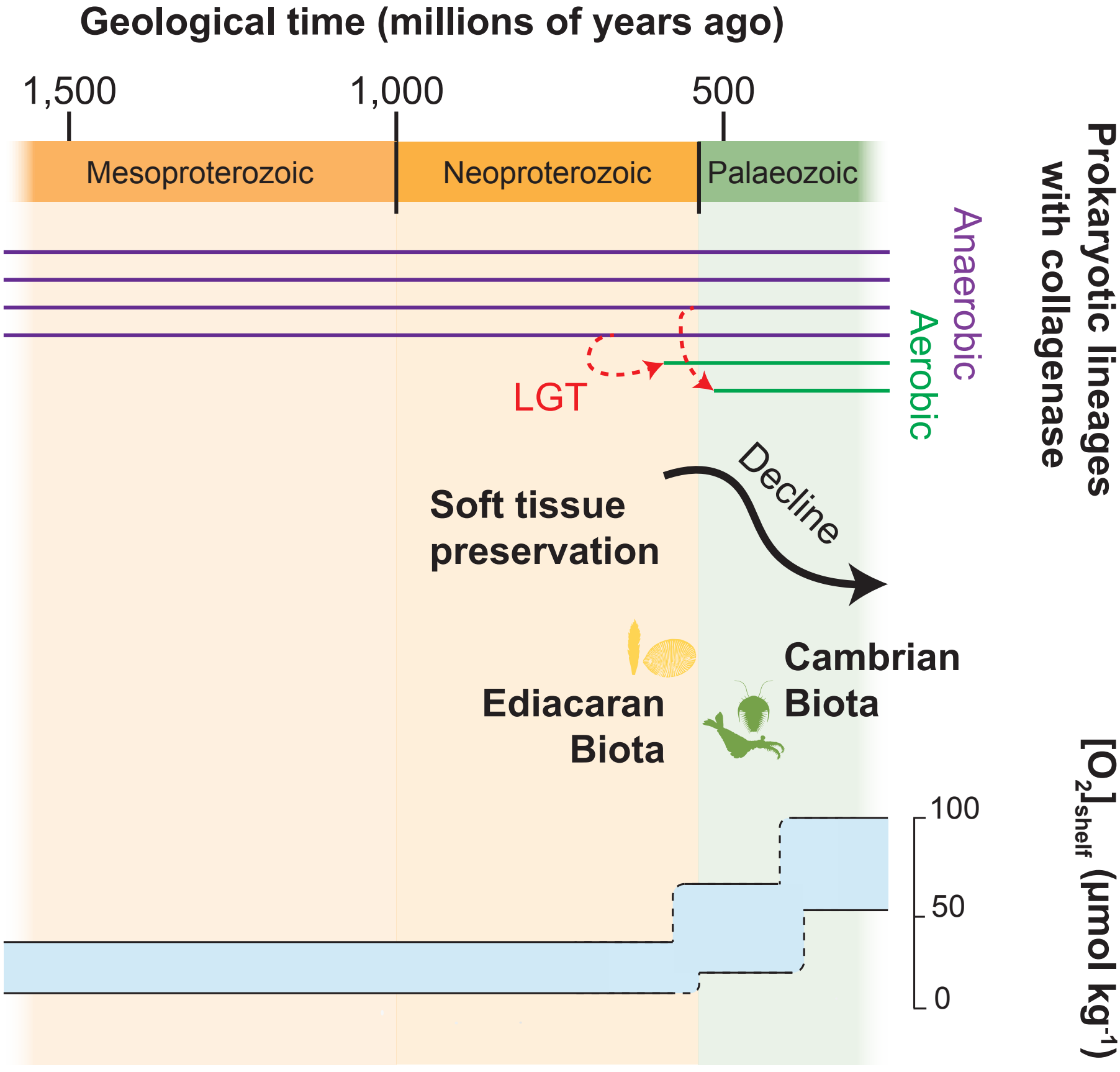
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Geological time (millions of years ago)
1,500
1,000
500
Mesoproterozoic
Neoproterozoic
Palaeozoic
Anaerobic
Aerobic
Prokaryotic lineages with collagenase
LGT
Soft tissue preservation
Decline
Ediacaran Biota
Cambrian Biota
100
50
0
[O2]shelf (µmol kg-1)