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Patterns in Palaeontology: Who's there and who's missing?

by Simon Darroch[*1]

Introduction:

Sitting in the sweltering heat of southern Japan, I'm faced with a conundrum. The limestone cliff in front of me preserves the boundary between the Permian and Triassic periods, a point in time around 250 million years ago that witnessed the greatest mass extinction of the Phanerozoic eon. I'm collecting rock and fossil samples from around this boundary to study how the make-up of fossil communities changed in response to this extinction event: this ispalaeoecology. The boundary itself couldn't be easier to spot — the lower (and older) part of the cliff is composed of a pale white-yellow limestone packed full of fossils of shelled marine invertebrates including brachiopods, bivalves andgastropods, as well as microscopic sea-floor-dwelling (benthic) creatures called foraminifera. Some of these foraminifera have been found elsewhere in the world and are dated to the Permian period. The younger, higher rocks are an ominous-looking black, with fine layering and a blotchy texture that you might otherwise associate with old blue cheese. Fossils in this dark, rotten-looking limestone are extremely rare and dominated by one or two species of mollusc, but researchers have found fossilized teeth belonging to an eel-like animal called a conodont, of the species*Hindeodus parvus*, which unequivocally dates the rocks as Triassic in age. Somewhere at the boundary between these white and black limestones, 95% of all marine organisms with skeletons became extinct in the geological blink of an eye — currently thought to be less than 200,000 years. The palaeontological story would seem to be extremely simple: a diverse Permian benthic marine community suffered a mass extinction and was replaced by a community composed almost entirely of one or two species (Fig. 1). This pattern is broadly the same all over the world during this transition. So where is the conundrum?

The problem comes with deciphering the striking colour change between the Permian and Triassic limestones. The shift from white to black actually has very little to do with the extinction itself, but instead records a dramatic environmental change. The white Permian limestone was laid down in a shallow marine lagoon. The dark and mottled Triassic limestones record something very different — an algal marsh along a shoreline, very similar to that forming on the modern-day Andros Island in the Bahamas. The fine layering and mottled texture were produced through complex interaction between fast-growing algae and sediment carried in by storms. The algae formed flat, sticky mats in low-lying areas protected from the wind, and with surprising adhesive properties. During storms, sediment (made up mostly of clumps of carbonate mud, foraminifera and gastropod shells) was stirred up into the water column, and then transported onshore as part of the storm surge. A thin layer of this sediment was trapped on top of the mat, and became fixed as the algae grew through and around it. This is what produced the layering and unsettling 'blotchy' texture of the limestone.

The fundamental environmental change that occurred here across the Permian–Triassic boundary highlights two issues that complicate the interpretation of these bodies of limestone: 1) they represent very different environments that probably hosted very different original communities; and 2) these two settings probably preserve very different components of the community (one might

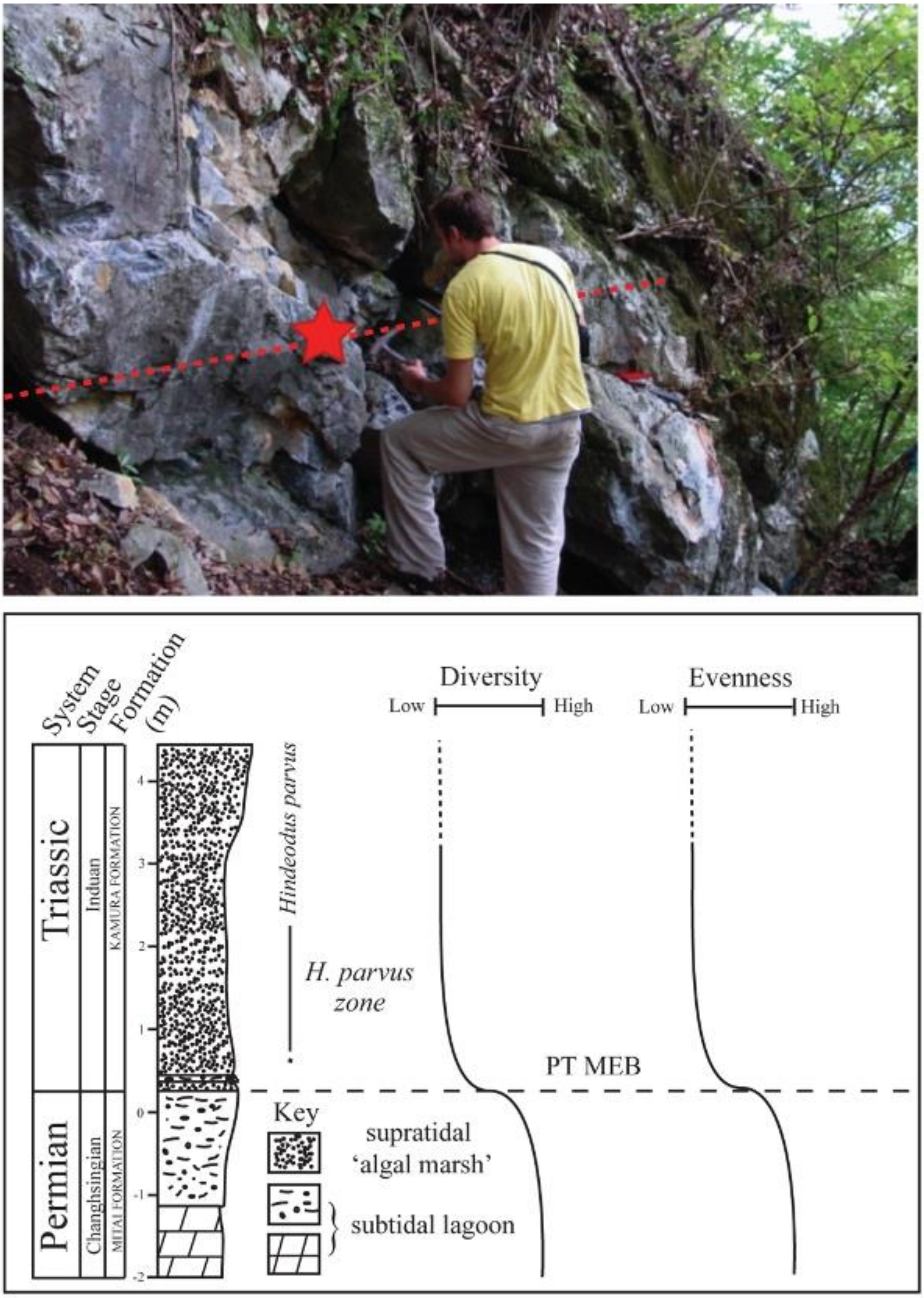

FIGURE 1 — TOP: SAMPLING THE PERMIAN–TRIASSIC BOUNDARY IN THE FIELD, IN KAMURA, KYUSHU (SOUTHERN JAPAN). DASHED LINE INDICATES POSITION OF THE BOUNDARY. BOTTOM: SCHEMATIC LOG SECTION OF THE BOUNDARY ('PT MEB' – PERMIAN-TRIASSIC MASS EXTINCTION BOUNDARY), WITH FOSSIL DIVERSITY (I.E. TOTAL SPECIES) AND EVENNESS (RELATIVE ABUNDANCE OF DIFFERENT SPECIES) CURVES.

preserve small creatures and the other big ones, for example, or one might preserve those with hard shells and the other those with soft bodies). As a result, the fossils record the original living communities with varying accuracy.

Palaeontology helps us to deal with the first problem by comparing fossils found in rocks representing similar environments at different times, so that we know what sort of things are recorded in each type of rock: we compare apples with apples and blotchy oranges with blotchy oranges. Dealing with the second problem is slightly more complex. Processes such as being shifted by water currents, winnowing (whereby small and light material is swept elsewhere), selective predation (where certain species are destroyed or taken elsewhere) and disarticulation (creatures' bodies breaking up after death) can strongly distort the appearance of the community and mask changes in community structure. Furthermore, the relative importance of these processes will vary between environments. As we go through different settings in the geological record, then, how do we know that the fossils that we find accurately represent the original make-up and ecologies of the living communities? Fortunately, live–dead studies conducted in modern environments offer a way to test the quality of the fossil record in a wide variety of sedimentary environments.

How do life–dead studies work?

On the face of it, live–dead studies are extremely simple. You choose a modern environment where sediment is being laid down and begin collecting members of the living and the dead communities (Fig. 2). In marine environments, the living community can typically be found: on or in the sediment (where you might find, for example, clams, sea urchins and soft-bodied worms); attached to blades of seagrass and other algae (many foraminifera and small gastropods); and at various heights in the water column (fish, squid and jellyfish, among thousands of others). Although some of these organisms may be rarer than others, and they may never interact, they all make up the living community in that environment, and in an ideal world would all enter the fossil record. The dead community, by contrast, is largely restricted to the sea floor, making up the sediment and organic debris scattered on and in the surface. This is the precursor or 'sub-fossil' record, and gives a good indication of what a palaeontologist might expect to see in the rock many millions of years later. Holding any handful of sediment under a microscope will reveal the typical contents: worn and broken shells, the broken up remains of sea urchin skeletons, and perhaps the withered cuticles of a few small arthropods.

How well these live and dead communities match ('live–dead agreement') is an effective measure of the potential quality of the fossil record in that environment. For clarity, palaeontologists refer to the living community and the death assemblage. The difference in terminology is due to the fact that the dead material is typically composed of biological remains both derived from the local environment and transported in from elsewhere (and potentially encompassing a large range of ages). Live–dead agreement can be calculated either on a presence/absence basis (who is there and who is missing?), or in terms of relative abundance (are the common species the most frequently preserved?). Both measures provide valuable information, and can be used to re-calibrate the fossil record in terms of how well the overall diversity and ecological make-up of original communities is being preserved.

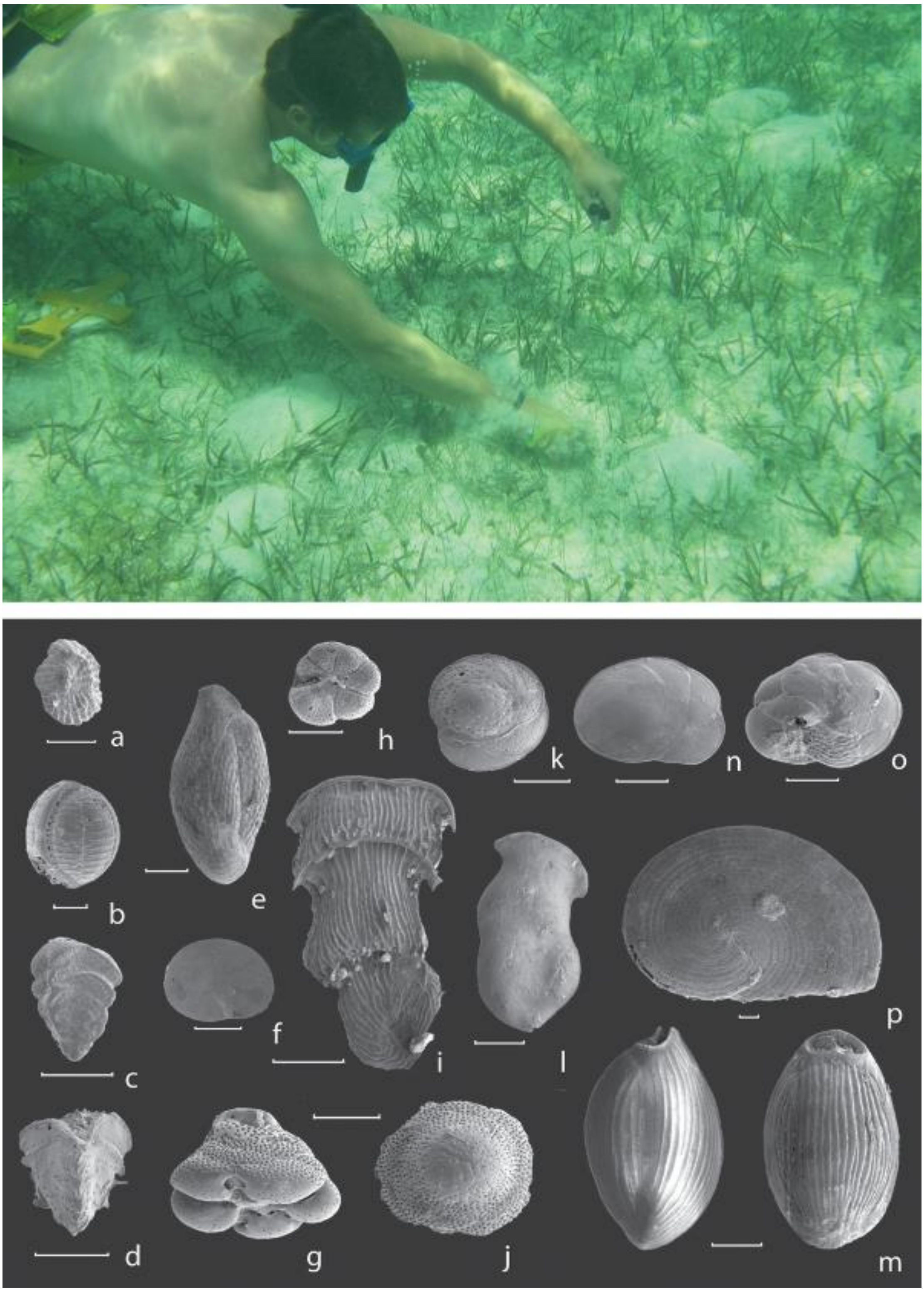

Figure 2 — Top: Testing the quality of the fossil record using benthic foraminifera; a live–dead study on San Salvador Island in the Bahamas. Bottom: Some common benthic foraminifera from this setting. Live–dead agreement is in general very poor, with only about 20% of species in the death assemblage also found in the living community, possibly as a result of recent human impact. Species are: a. Psuedohauerina sp.; b. Borelis pulchra; c. Chysalidinella dimporpha; d. Reusella spinulosa; e. Triloculina bicarinata; f. Amphistegina gibbosa; g,l. Cymbaloporetta squamosa; h. Rosalina floridiana; i. Vertebralina mucronata; l. Vertebralina sp.; m. Pyrgo comata; n,o. Asterigerina carinata; p. Archaias ungulatus. Figure modified from Darroch (2012 – reference below).

History and recent advances:

Although the field of taphonomy, or fossil preservation, has enjoyed more than 70 years of study, the analysis of live–dead agreement as a way to interpret the past was first thrust into the limelight by the palaeobiologist Thomas Schopf in the late 1970s. Schopf undertook a comprehensive live–dead study of the organisms in the area between high tide and low tide in Friday Harbor in the US state of Washington across three environmental settings (muddy, sandy and rocky substrates). He looked at 169 genera in a wide range of animal groups. The principal findings were encouraging: a relatively large proportion of invertebrates visible with the naked eye (the groups typically considered in paleoecological studies) had better-than-expected frequencies of preservation. But the study also highlighted what many palaeontologists had suspected for years: not a single wholly soft-bodied group (such as marine worms, sea slugs or jellyfish) observed in the living community was found in the death assemblage. This is perhaps the most obvious taphonomic 'megabias' in the fossil record — soft-bodied animals are almost never preserved, so compilations of fossil diversity through time only really represent the diversity of biomineralized animals and plants, which is far from a complete picture. This observation also highlights why fossil deposits that preserve the remains of soft-bodied organisms are so important; they represent snapshots in time when live–dead agreement is much higher than usual, providing a much more complete picture of the palaeocommunity (Fig. 3).

Fortunately, however, palaeontologists can achieve a great deal by looking at biomineralized organisms alone, and over the past 30 years studies in live–dead agreement have made huge advances in calibrating the accuracy of fossil assemblages, as well as isolating and quantifying the relative impacts of specific processes in different environments. More and more careful live–dead studies are providing powerful 'taphonomic vindication' for the study of fossil communities. For example, it has been demonstrated that in modern communities of benthic molluscs, the abundance of species is more often than not well preserved in death assemblages. Put simply, species that dominate the living community tend to be more common in the piles of dead shells that accumulate on the sea floor; that may seem a trivial finding, but it is great news for palaeontologists! In addition, whereas a single sample of the living community will typically contain only species that happen to be there at that ecological instant, death assemblages represent the accumulation of dead material over time, and so typically contain more of the rare species that you might otherwise miss; this means that death assemblages actually paint a better and more complete picture of a given community on reasonable ecological timescales (weeks to years). Finally, even within transects drawn through a single living community of molluscs across an area of sea floor, researchers have shown that measures such as evenness (the relative abundance of different species – a metric beloved by palaeontologists studying mass extinctions) can be replicated faithfully in their corresponding death assemblages. In these cases, death assemblages (and the 'sub-fossil' record) provide extraordinary records of the composition and distribution of the original communities. These studies therefore show that when we find these environments in the fossil record, we can trust the fossils in them to be an accurate record of what was once living there.

Even when live–dead agreement in easily preserved organisms is shown to be poor, palaeontologists can turn it to their advantage. One of the most important reasons why living communities and death assemblages might show little agreement involves a hot-button term — human impact. It is no secret that humans are having a detrimental impact on the oceans; as the concentration of carbon dioxide in the atmosphere rises, more is absorbed by the oceans, making them more acidic. In coastal areas next to big cities, the water is being contaminated with everything from heavy metals and plastic to nitrates and organic fertilizers. Organic material will decay, using up oxygen in the

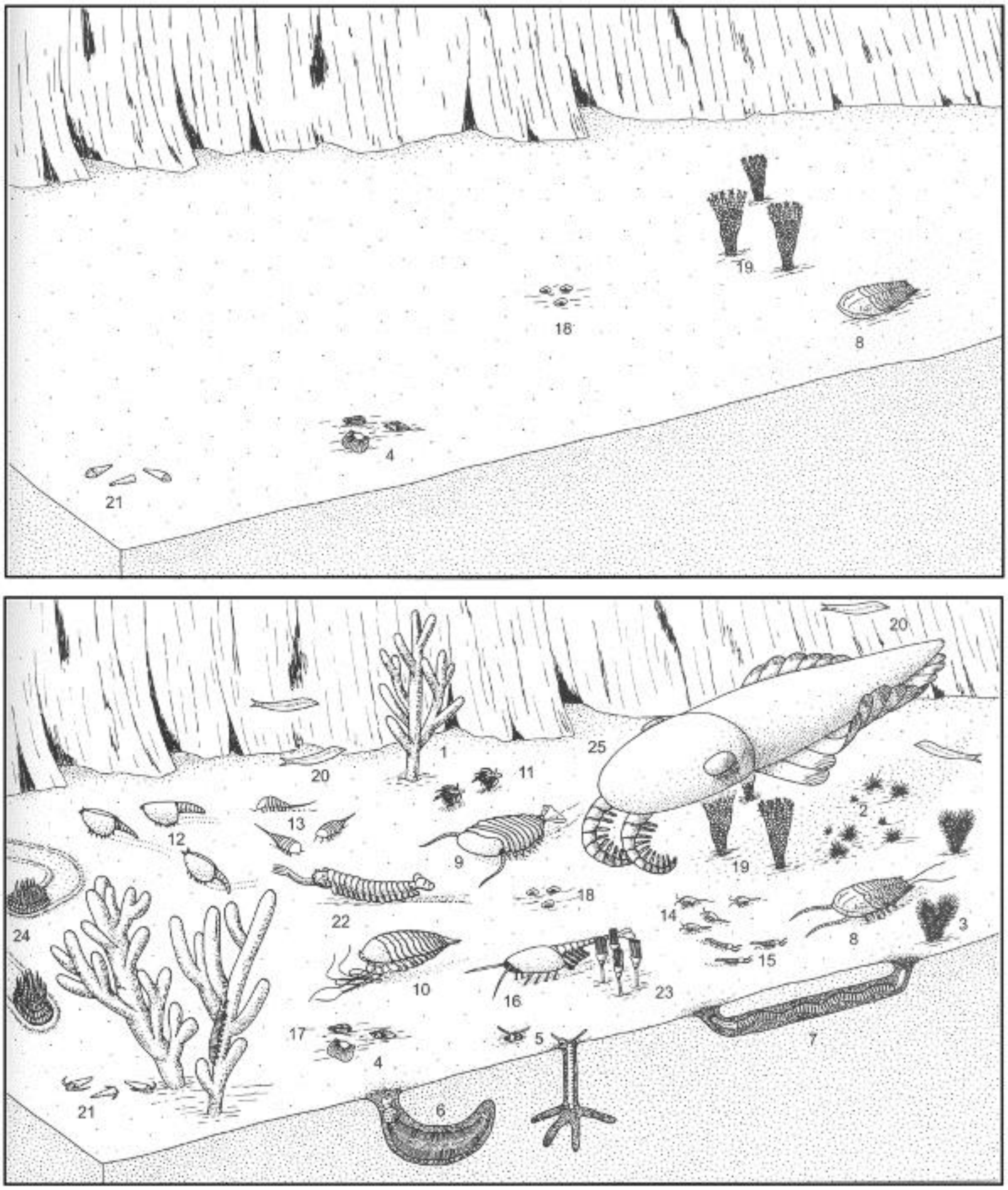

FIGURE 3 — POTENTIAL 'MEGABIAS' IN THE FOSSIL RECORD WHEN SOFT-BODIED ANIMALS ARE NOT PRESERVED. TOP: RECONSTRUCTION OF THE CAMBRIAN BURGESS SHALE DEPOSIT AS IT WOULD LOOK IF ONLY BIOMINERALIZED (SHELLY) ANIMALS WERE FOSSILIZED, AND NOT SOFT-BODIED ONES. BOTTOM: RECONSTRUCTION OF THE BURGESS SHALE AS IT MAY HAVE ACTUALLY APPEARED IN LIFE (I.E. WITH SOFT-BODIED ANIMALS). NOTE THAT LIVE–DEAD AGREEMENT IS ALMOST ALWAYS HIGHER WHEN SOFT-BODIED ANIMALS ARE FOSSILIZED. BOTH IMAGES FROM FOSSILS OF THE BURGESS SHALE, EDITED BY DEREK E.G. BRIGGS, DOUGLAS H. ERWIN, FREDERICK J. COLLIER AND CHIP CLARK (1995).

process and leaving none for invertebrates such as molluscs and crustaceans. Other pollutants may act as outright poisons. In these settings, living communities tend to contain few organisms, and to be dominated by one or two hardy species, similar to the Triassic limestones described above. The death assemblage, however, may contain an accumulation of shell material dating back before the arrival of humans and pollutants — a species-rich and high-evenness assemblage that records the make-up of the community in its original pristine state. Here, then, the living community and the death assemblage are *very* different. Live–dead agreement (specifically, poor live–dead agreement) acts as an indirect measure of pollution and human impact, and so is an important tool in the emerging field of conservation palaeobiology, in which palaeontological data is used to provide information about important issues in ecology and conservation. Ecologists and palaeontologists alike can use live–dead studies to measure human impact and ecosystem health, and, if necessary, can use them to work out where and how to try to reverse any damage to the environment.

Wrapping up:

So where does that leave me, apart from sitting and staring at my cliff section (still sweltering, and now scratching irritably at some insect bites)? The palaeoecological data show a transition over the Permian–Triassic boundary, from an assemblage bursting with fossils to one containing almost nothing, save for a few lonely bivalves. The story is the same the world over, but are the fossils faithfully recording the living community? The pale Permian limestones probably represent deposition in a warm shallow-water lagoon; live–dead studies in equivalent modern settings suggest that the sea floor here also played host to a rich community of plants, arthropods, and countless soft-bodied organisms. None of these have been preserved as fossils, but the biomineralized groups at least should provide a reasonable record of both the overall diversity and relative abundance of immobile molluscs and brachiopods. The dark Triassic limestones, by contrast, record periodic deposition and algal growth in a shoreline algal marsh; the fossil bivalve shells were probably swept onto shore during storms, but nothing living in the marsh itself stood much chance of being preserved. In the marsh, live–dead agreement was almost certainly extremely low. Sadly, in this instance there is very little we can say about the rate or pattern of Permian–Triassic extinction and recovery, because the environments represented by these two units did not preserve their original communities with equal quality. There is an interesting story here, but it doesn't involve pre- and post-extinction palaeoecology. Fortunately, not too far away there is another Permian–Triassic section composed of limestone from an area that was almost always submerged in water; there are still changes in the types of rock across the boundary, but they record palaeoenvironments that can be (and have been) studied in the context of their live–dead agreement. In the coming years, palaeontologists will attempt to calibrate all the settings we see in the fossil record, in terms of what is preserved and what isn't, so that when it comes to studying the composition of fossil communities, we can compare apples with apples across the boundary, rather than apples with blotchy oranges.

Further Reading:

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