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DEALING WITH EXTINCT LIFE FORMS

by Stefan Bengtson

It's kind of fun to be extinct.
Ogden Nash, "Carnival of the Animals"

One legacy of the late Jack Sepkoski is a widespread interest in extinctions, in particular the mass extinctions which at various times have finished off large numbers of existing lineages of organisms. Extinctions are an integrated part of the dynamics of the biosphere, a shaping force as much as a destructive one. Sad for the extinguished, but an unavoidable part of evolution, as necessary – and heartbreaking – as individual death.

Yet we often seem to reason as if organisms seldom did become extinct, as if evolution was teleologically channelled towards the extant forms of life. Why else do we not recognize a single extinct phylum? Why else is just about any radially symmetrical macrofossil interpreted as a cnidarian or possibly poriferan? Why else are the three billion years of Precambrian history populated with microorganisms predominantly belonging to extant taxa? Why else do we take the thermophilic basal roots of the Tree of Life of extant organisms to tell us that life originated in hot environments?

The reasons for this actualistic view of the fossil record can be described in positive terms as a reflection of sound scientific methods: Reliance on knowledge of living organisms when interpreting fossil ones, use of rigorous and repeatable methods of analysis, abstaining from untestable speculations, adherence to parsimony when choosing between alternative hypotheses, etc. They may also be described negatively, however: Lack of imagination or courage, intellectual laziness, misapplication of methodologies, confusing models with reality, etc.

Which description is closer to the truth?

Harnessing the imagination

Science fiction epics named "Star This" or "Star That" can be annoying. Anyone who has ever marvelled at the almost unfathomable disparity expressed even in the DNA-bound life forms on our own

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planet will be disheartened to see that the wider expanses of the galaxy do not seem to house much greater disparity than can be produced with pieces of latex between the eyes of terrestrial *Homo sapiens* var. *hollywoodensis*.

To be sure, there are some practical reasons for this. Human actors are easier to find and direct (at least before they themselves have become "stars") than sapient shoestrings, and the general audience may relate less congenially to an intelligent shade of blue (thanks to Douglas Adams for that example) than to something that looks more or less like uncle Bert on a bad day. But, most importantly, most of us can only imagine that which is similar to what we already know. Hence the run-of-the-mill Roswell alien is distinctly humanoid, and so are images of gods in most religions (unless they be monkeys, snakes, or similarly mundane creatures). Call it lack of imagination if you will, but there's a deeper principle at work here: even a creative imagination needs stuff to work on, something to tinker with. It's just like evolution. New concepts don't just materialize out of nothing, they build on something that already exists. Even when the new negates the old, the new owes its existence to that which was before.

Science is a good example of this principle. Imagination is indispensable in science, but without the harness of known reality it is of little use. The remarkable power of science lies in its building on what's known in order to understand the unknown. Merely imagining something is of little help – it must in the end connect in some specific way with what's already known.

Thus it's a sound scientific principle that whatever is postulated must be testable through observations and potentially falsifiable. Yet even sound scientific principles may lead us astray if wrongly applied. I suggest that our usual practices in dealing with extinct life forms often do just that.

A little about probabilities

We don't know how many species have lived on Earth, not even how many are alive today. Common estimates, however, end up with something like 40–50 million living ones and perhaps a thousand times as many extinct ones. This could be expressed as "one per mill of species have survived", but as these figures lump real extinctions with "pseudoextinctions" (by anagenesis or cladogenesis) and do not describe changes through time, they are not particularly revealing. A more specific and telling example would be to take the situation in, say, the Cambrian. The Sepkoski curve of generic diversity of marine animals suggests that when the Middle Cambrian plateau had been reached, the number of fossilizable genera was about one-tenth of that in the recent (Pleistocene) past. Applying this ratio to all species, the present number of species would translate to 4–5 million in the Cambrian. Since present diversity is very much land-based (insects being an overwhelmingly dominant group) and the estimates include non-animals as well, the number of animal species in the Cambrian may be perhaps an order of magnitude smaller. Say, then, that there were some half million animal species by the Middle Cambrian. How many of these were ancestors of anything living today? At least some paleontologists believe that few if any crown-group phyla of animals existed at that time. If true, this would bring the number of surviving animal lineages in the Cambrian to around 50 (the number of recognized phyla plus some allowance for Cambrian crown-group representatives).

In other words: Pick a species at random in the Cambrian, and you have a

1:10,000 chance of having picked one representing a now living lineage.

Unparsimonious parsimony

Does it matter? Most of the 499,950 extinct Cambrian lineages probably share some characters with the extant ones anyway. We should be able to analyze the relationships of taxa whether or not there are unknowns between them. All earthly life is related by common descent. Or, is it? Actually, this is an assumption based on our analyses of the few surviving lineages. The conclusion that all known living forms are related is well supported by their sharing the same genetic code. This comes as close to a fact as anything in science. The assumption that all fossil forms are similarly related, however, is based on parsimonious reasoning – why postulate multiple origins of life if it isn't necessary? The assumption of a single origin may well be correct, but it need not be. (Obviously I'm not talking dinosaurs or trilobites here, but rather blobs in Archean or Proterozoic rocks.)

The principle of parsimony, "Occam's Razor", is tightly connected with the fact alluded to above, that science builds on what's known in order to understand the unknown. Our reasoning shouldn't take wider turns than the data allow us. It's a heuristic principle, however, not a law of Nature. We use it as a rule-of-thumb to decide between competing hypotheses: If they are equal in everything except complexity, we choose the simplest one. Yet what is parsimonious at one level of analysis may not be so at another one. If you hold two pieces of a 30-piece jigsaw puzzle and they appear to fit, it's a reasonable guess that they belong together. If the puzzle has 10,000 pieces, however, you will want to make very sure that you're not pounding two almost-fitting pieces into place by sheer force, particularly if they are of a simple, general shape and if the jigsaw puzzle is so old that the colours on most pieces have worn out. In that situation, the interpretation that the first two pieces you happen to pick up fit together is not particularly parsimonious. The more pieces in the puzzle, the more important it is to study them carefully before putting it together.

If misapplied, the principle of parsimony may lead to serious bias. For example, an a priori assumption (i.e. based on character analysis rather than on distribution in a cladogram) that similar characters in different taxa are convergent rather than homologous is generally considered "scientifically unsound", "methodologically doubtful", etc. Our best-established phylogenetic trees, such as the molecular Tree of Life, are based on living organisms, because of the abundance of well-accessible characters, including molecular ones. When similar characters in fossils are treated as potentially homologous in a phylogenetic analysis, convergences will either end up as false homologies or be interpreted as homoplasies. In the former case, they will bias the analysis towards acceptance into the known phylogenetic tree; in the latter case they will have no effect at all. The methodology is lopsided: Heads – I win; tails – nobody wins. A recipe for bias.

With fossils having many and complex characters, this may be less of an issue. There may be enough truly homologous characters available to drown the homoplasies. However, when we are dealing with fossils having simple and poorly preserved characters, particularly in the earlier parts of the geologic column where the ratio of extant to extinct lineages may be very low, we will almost invariably, by our choice of method, affix them closely to the tree of extant life, using the glue of parsimony. Misapplication of the parsimony principle may thus lead us fundamentally astray.

Extinct lineages in extant genomes

Look at another fossil record. Molecular biologists have come to realize that at least among prokaryotic organisms lateral gene transfer (the transfer of genetic material between evolutionary lineages by close interactions between unrelated organisms) has occurred repeatedly in evolutionary history. There is still considerable controversy regarding the frequency and importance of this process – the problem is to recognize where it has happened. Is an anomaly between different gene phylogenies due to incorrectly reconstructed phylogenies or to lateral gene transfer? Even with perfect methods, lateral gene transfer can presently only be determined when it has occurred between two lineages having at least partly known genomes.

But what if the donor of the gene material is extinct? Given the frequency of extinctions in geologic time, this should be the rule rather than the exception. In such a case there is presently no way of recognizing it – a novel set of genes in a lineage will look about the same whether it has been acquired by lateral transfer from a now extinct organism or has evolved afresh in the lineage where it is seen. Nonetheless, what is impossible today may not be so tomorrow, and maybe with other algorithms or markers such transfers from ghosts will become recognizable. They are not likely to be so, however, if molecular systematists (mis)apply Occam's Razor to the effect that invoking unknown organisms is always "non-parsimonious", "scientifically unsound", or whatever the damning phrase in vogue may be. I would rather suggest that, if lateral transfer has happened numerous times in the early evolution of life, Occam's Razor suggests that most cases of such transfer will have been from now extinct organisms. In other words, a giant fossil record of extinct lineages may be laid down in extant genomes, we just do not see it as yet.

Life unbounded

Coming back to the topic of life in the (non-Hollywood) universe: Astrobiology is currently a field of science where even the existence of the ultimate study object, extraterrestrial life, is still not proven to general satisfaction (other parallels to theology are probably unjust). As always, the value is in the journey, not the destination. Whether or not we will ever be able to document that life has arisen elsewhere in the universe, however, the methods and theories being developed promise to give us a new understanding of life on Earth. The astrobiological approach forces us to look beyond the familiar expressions of life: to life in extreme environments, to life at its edges and beginnings, to life outside that which we know and form part of. It may be no coincidence that a number of prominent palaeontologists are deeply involved in astrobiological pursuits. When we probe life on this planet back towards its origins we are getting beyond the limit where we can safely apply the pattern given us by modern life as a key to the past. Trying to develop an understanding for possible conditions of life outside Earth, we are also forced to look at life on Earth with new glasses. Our actualistic reading glasses are great for many purposes, but they occasionally need to come off. Then we may also see the masses of extinct life forms for what they are – something dramatically more than mere ornaments on the molecular Tree of Life.