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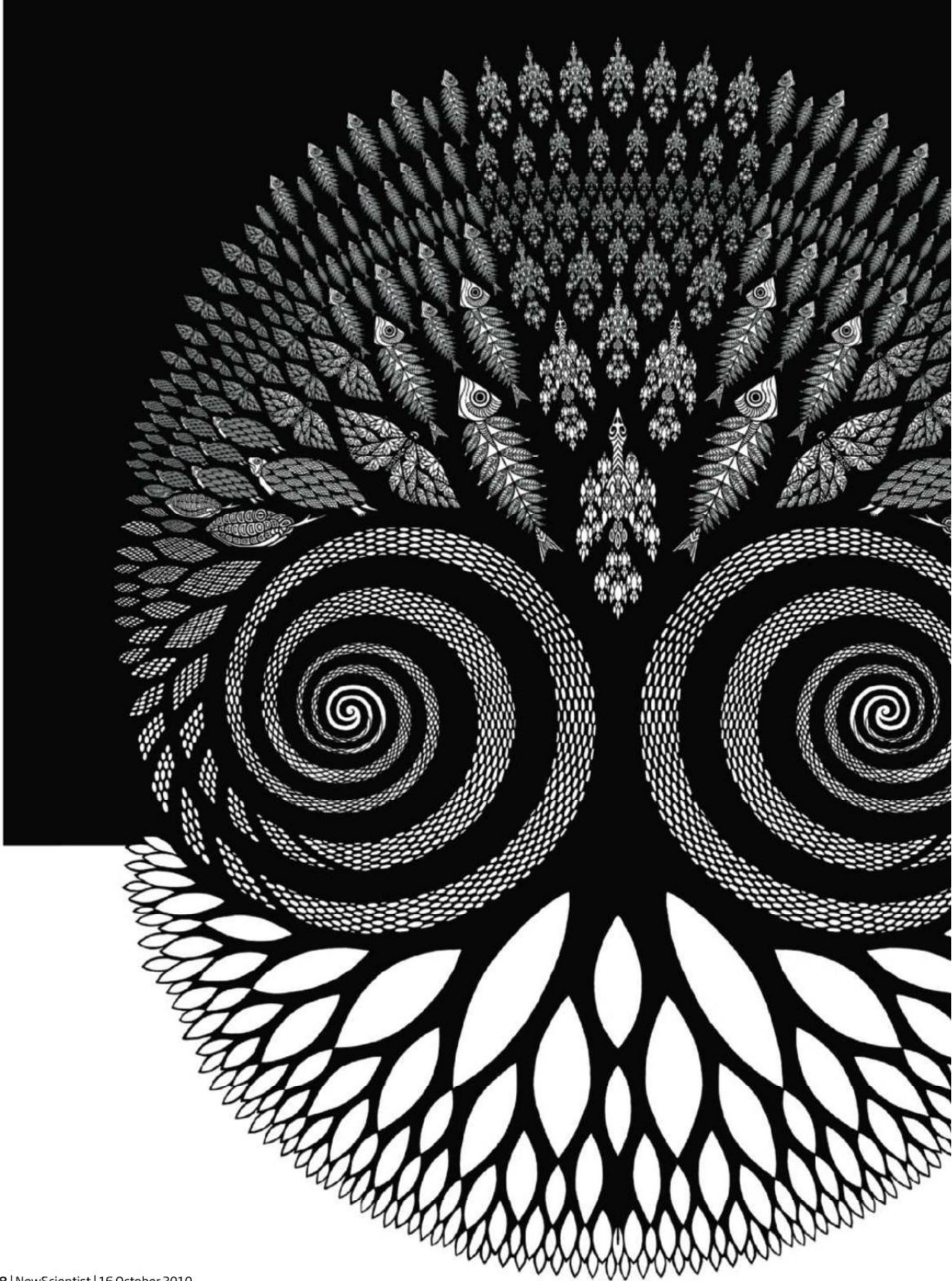
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IN 1856, geologist Charles Lyell wrote to Charles Darwin with a question about fossils. Puzzled by types of mollusc that abruptly disappeared from the British fossil record, apparently in response to a glaciation, only to reappear 2 million years later completely unchanged, he asked of Darwin: "Be so good as to explain all this in your next letter." Darwin never did.

To this day Lyell's question has never received an adequate answer. I believe that is because there isn't one. Because of the way evolution works, it is impossible to predict how a given species will respond to environmental change.

That is not to say that evolution is random – far from it. But the neat concept of adaptation to the environment driven by natural selection, as envisaged by Darwin in *On the Origin of Species* and now a central feature of the theory of evolution, is too simplistic. Instead, evolution is chaotic.

Darwin's argument was two-fold: First, life evolves from common ancestors. Second, it evolves by means of natural selection and adaptation. The first part has been accepted as a basic premise of biology since 1859. The second is more controversial, but has come to be accepted over the past 150 years as the principal mechanism of evolution. This is what is known as "adaptationism".

Adaptationism certainly appears to hold true in microevolution – small-scale evolutionary change within species, such as changes in beak shape in Galapagos finches in response to available food sources.

However, there is still huge debate about the role of natural selection and adaptation in "macroevolution" – big evolutionary events such as changes in biodiversity over time,

evolutionary radiations and, of course, the origin of species. Are these the cumulative outcome of the same processes that drive microevolution, or does macroevolution have its own distinct processes and patterns?

This is a long-running debate. In 1972, for example, Niles Eldredge and Stephen Jay Gould challenged the assumption that evolutionary change was continuous and gradual. Their "punctuated equilibrium" hypothesis argued that change happens in short bursts separated by long periods of stability, as distinct from the more continuous change over long periods expected to be the outcome of natural selection and adaptation.

Later, John Endler, an evolutionary biologist at the University of Exeter, UK, scrutinised claimed examples of natural selection but found a surprising lack of hard evidence (chronicled in his 1986 book *Natural Selection in the Wild*). More recently, and controversially, cognitive scientists Jerry Fodor of Rutgers University at New Brunswick, New Jersey, and Massimo Piattelli-Palmarini of the University of Arizona in Tucson have pointed out philosophical problems with the adaptationist argument (*New Scientist*, 6 February, p 28).

Palaeoecologists like me are now bringing a new perspective to the problem. If macroevolution really is an extrapolation of natural selection and adaptation, we would expect to see environmental change driving evolutionary change. Major climatic events such as ice ages ought to leave their imprint on life as species adapt to the new conditions. Is that what actually happens?

Our understanding of global environmental change is vastly more detailed than it was in Lyell and Darwin's time. James Zachos at ➤

Chaos THE THEORY OF EVOLUTION

Forget finding laws. The history of life is just one damn thing after another, says Keith Bennett

"The link between environmental change and evolutionary change is weak – not what Darwinists might have predicted"

the University of California, Santa Cruz, and colleagues, have shown that the Earth has been on a long-term cooling trend for the past 65 million years (*Science*, vol 292, p 686). Superimposed upon this are oscillations in climate every 20,000, 40,000 and 100,000 years caused by wobbles in the Earth's orbit.

Over the past 2 million years – the Quaternary period – these oscillations have increased in amplitude and global climate has lurched between periods of glaciation and warmer interglacials. The big question is, how did life respond to these climatic changes? In principle, three types of evolutionary response are possible: stasis, extinction, or evolutionary change. What do we actually see?

To answer that question we look to the fossil record. We now have good data covering the past 2 million years and excellent data on the past 20,000 years. We can also probe evolutionary history with the help of both modern and ancient DNA.

The highly detailed record of the past 20,000 years comes from analyses of fossilised tree pollen from lake and peat sediments. Tree pollen is generally recognisable to the level of genus, sometimes even species, and the sediments in which it is found can easily be radiocarbon dated.

In the 1970s and 1980s, palaeoecologist Margaret Davis at the University of Minnesota in Minneapolis created a map using this data which showed how North American tree taxa reached their respective present positions after the glaciers retreated at the end of the last ice age.

She found that the distribution shifts were individualistic, with huge variations between species in the rate, time and direction of spread. For example, larch spread from south-west to north-east, white pine from south-east to north-west. Rates vary from 100 metres a year to over 1000 metres (*Annals of the Missouri Botanical Garden*, vol 70, p 550). In other words, trees show no predictable response to climate change, and respond individually rather than as communities of species.

The fossil record also tells us that the make-up of modern forest communities differs from those of 20,000 years ago. Today we recognise various types of forest, such as boreal, deciduous and aspen parkland, each with a distinctive mix of tree species. Yet the fossil record tells us that these are just temporary groupings. Multi-species communities do not have long histories and do not shift their distributions in a coordinated way in response to climate changes, as Darwin supposed. We therefore cannot assume that the members of modern forest communities evolved together or are somehow dependent on each other.

The same appears to be true over longer timescales. Pollen data show that during earlier interglacial periods, when the climate was most similar to now, forest compositions were very different from today.

Research on animals has come to similarly unexpected conclusions, albeit based on sparser fossil records. For example, palaeontologist Russell Graham at Illinois State Museum has looked at North American mammals and palaeontologist Russell Coope

at the University of Birmingham in the UK has examined insects (*Annual Review of Ecology and Systematics*, vol 10, p 247). Both studies show that most species remain unchanged for hundreds of thousands of years, perhaps longer, and across several ice ages. Species undergo major changes in distribution and abundance, but show no evolution of morphological characteristics despite major environmental changes.

That is not to say that major evolutionary change such as speciation doesn't happen. But recent "molecular clock" research suggests the link between speciation and environmental change is weak at best.

Die hard

Molecular clock approaches allow us to estimate when two closely related modern species split from a common ancestor by comparing their DNA. Most of this work has been carried out in birds, and shows that new species appear more or less continuously, regardless of the dramatic climatic oscillations of the Quaternary or the longer term cooling that preceded it (*Trends in Ecology and Evolution*, vol 20, p 57).

What of extinction? Of course, species have gone extinct during the past 20,000 years. However, almost all examples involve some degree of human activity, either directly (think dodos) or indirectly (large mammals at the end of the last ice age, 12,000 years ago).

In fact, we only know of one recent extinction with no human involvement – a species of spruce, *Picea critchfieldii*, which was common in the lower Mississippi valley at the height of the last ice age but died out 12,000 years ago (*Proceedings of the National Academy of Sciences*, vol 96, p 13847). Others undoubtedly occurred, but extinction appears to be a surprisingly rare response to substantial climatic changes (see diagram, above right).

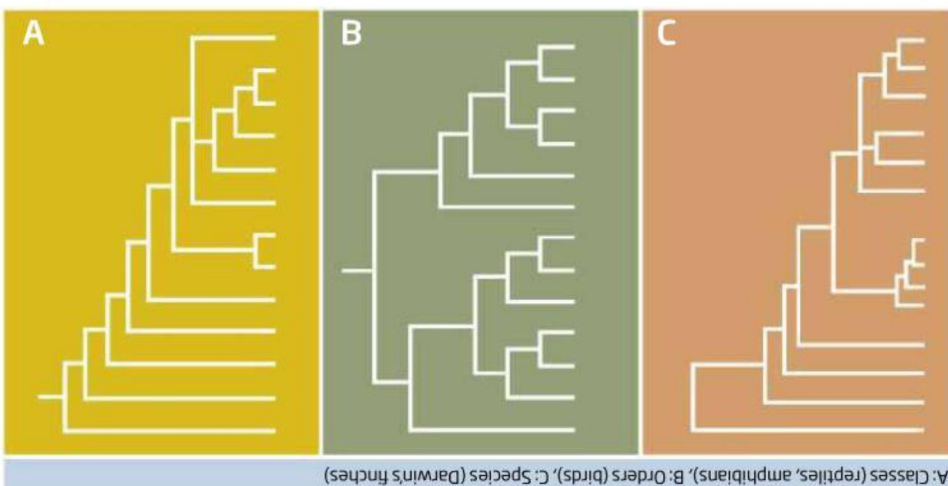
The overall picture is that the main response to major environmental changes is individualistic movement and changes in abundance, rather than extinction or speciation. In other words, the connection between environmental change and evolutionary change is weak, which is not what might have been expected from Darwin's hypothesis.

If environmental changes as substantial as continent-wide glaciations do not force evolutionary change, then what does? It is hard to see how adaptation by natural selection during lesser changes might then accumulate and lead to macroevolution.

I suggest that the true source of

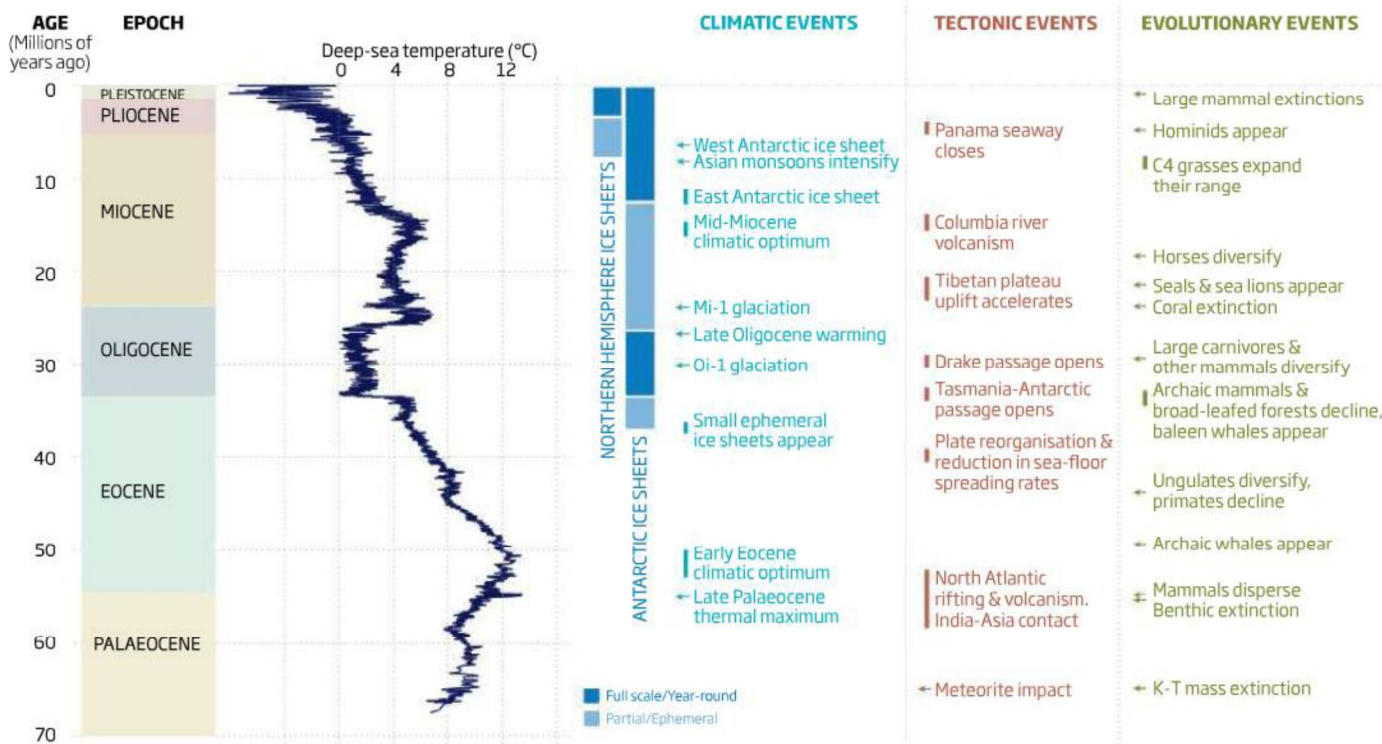
It's a fractal life

Phylogenetic trees, which illustrate evolutionary development and diversification, are "self-similar" – without labels it is impossible to tell what taxonomic level you are looking at. This is characteristic of a complex system



Roller-coaster Earth

The past 65 million years have seen major climatic and tectonic shifts, plus huge evolutionary changes, but connections between them are hard to discern



SOURCE: SCIENCE, VOL 282, P 698

macroevolutionary change lies in the non-linear, or chaotic, dynamics of the relationship between genotype and phenotype – the actual organism and all its traits. The relationship is non-linear because phenotype, or set of observable characteristics, is determined by a complex interplay between an organism's genes – tens of thousands of them, all influencing one another's behaviour – and its environment.

Not only is the relationship non-linear, it also changes all the time. Mutations occur continually, without external influence, and can be passed on to the next generation. A change of a single base of an organism's DNA might have no consequence, because that section of DNA still codes for the same amino acid. Alternatively, it might cause a significant change in the offspring's physiology or morphology, or it might even be fatal. In other words, a single small change can have far-reaching and unpredictable effects – the hallmark of a non-linear system.

Iterating these unpredictable changes over hundreds or thousands of generations will inevitably lead to evolutionary changes in addition to any that come about by the preferential survival of certain phenotypes. It follows that macroevolution may, over the longer-term, be driven largely by internally generated genetic change, not adaptation to a changing environment.

The evolution of life has many characteristics that are typical of non-linear systems. First, it is deterministic: changes in

one part of the system, such as the mutation of a DNA base, directly cause other changes. However, the change is unpredictable. Just like the weather, changes are inexorable but can only be followed with the benefit of hindsight.

Second, behaviour of the system is sensitive to initial conditions. We see this in responses to glaciations in the Quaternary period. The exact circumstances of the beginning of each interglacial determine the development of the whole period, leading to unpredictable differences between interglacials (*Quaternary Science Reviews*, vol 14, p 967).

Third, the history of life is fractal. Take away the labelling from any portion of the tree of life and we cannot tell at which scale we are looking (see diagram, left). This self-similarity also indicates that evolutionary change is a process of continual splitting of the branches of the tree.

Fourth, we cannot rewind, as Stephen Jay Gould argued in *Wonderful Life*. Were we to turn the evolutionary clock back to any point in the past, and let it run again, the outcome would be different. As in weather systems, the initial conditions can never be specified to sufficient precision to prevent divergence of subsequent trajectories.

Life on Earth is always unique, changing, and unpredictable. Even if certain patterns can be dimly discerned, our ability to do so diminishes with time, exactly as for the weather. Consider any moment of the geological record of life on Earth: to what extent were the changes of the next 10 or 100 million years predictable at that time? With the benefit of hindsight, we might

be able to understand what happened, and construct a plausible narrative for those events, but we have no foresight.

This view of life leads to certain consequences. Macroevolution is not the simple accumulation of microevolutionary changes but has its own processes and patterns. There can be no "laws" of evolution. We may be able to reconstruct the sequence of events leading to the evolution of any given species or group after the fact, but we will not be able to generalise from these to other sequences of events. From a practical point of view, this means we will be unable to predict how species will respond to projected climate changes over next century.

The question Lyell put to Darwin over 150 years ago is unanswerable because Lyell put it in terms of a particular group of organisms. Not even Darwin would be able to explain why that specific group behaved as it did.

In the last analysis, evolution can be likened to the description of human history as "just one damn thing after another", exactly as Fodor and Piattelli-Palmarini have argued.

We still have much to learn about how life evolved but we will not develop a full appreciation until we accept the complexity of the system. ■

Keith Bennett is professor of late-Quaternary environmental change at Queen's University Belfast, guest professor in palaeobiology at Uppsala University in Sweden, and author of *Evolution and Ecology: The Pace of Life* (Cambridge University Press). He holds a Royal Society Wolfson Research Merit Award