ORIGINS OF BIODIVERSITY

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Abstract: Palaeontologists have always had something to say about the origins of biodiversity. However, until recently, most of what they had to say was somewhat speculative. Following the inspirational suggestions by Simpson in the 1940s, the American 'paleobiological revolution' of the 1970s encouraged palaeontologists to think numerically and in terms of hypothesis testing. What was lacking from that revolution was phylogeny, and this provides the basis of informative analyses that truly link deep time fossil data with molecular trees and extant taxa.

Key words: biodiversity, fossil record, 'paleobiological revolution', macroevolution, phylogeny.

THIS is the first of a series of virtual issues of *Palaeontology*, in which we present selections of articles published over the long history of the journal, since 1957. *Palaeontology* is frequently seen as a journal that is focused only on presenting descriptions and systematic accounts of fossils, but it has also been the venue for articles on wider topics, across themes in macroevolution, palaeoecology, functional morphology and taphonomy, for example. Admittedly, this role has not figured as highly as it might because authors tend to send such synoptic, synthetic and experimental studies to journals that specialize in palaeobiological and palaeoecological themes and indeed to cross-disciplinary journals in evolution, morphology and climate change, as well as to *Nature* and *Science*.

I have chosen the topic 'Origins of biodiversity' as a key theme in palaeontology that has clear cross-disciplinary impact and where palaeontologists have access to a unique data resource. There are of course continuing and serious debates about the quality of the fossil record, and these debates have at times led some nonpalaeontologists to doubt whether the fossil record has any merits at all. For example, eminent molecular biologists have from time to time suggested that the history of life in deep time may be understood satisfactorily from a study of living organisms alone; patterns in the past can then be extrapolated onto a molecular phylogeny by modelling notional speciation and extinction rates and rates of trait evolution. Others would see a more healthy approach in confronting the two signals, molecular and palaeontological, and in seeking agreement and conflict on the road to an understanding of how life originated and diversified, how diversity has been affected by intrinsic and extrinsic drivers and why some groups today are successful (i.e. species-rich) and others are not. Both the palaeontological and molecular data sources have their faults, but together

they may provide stronger insights into the past than can one or the other on its own.

In this brief review, I consider changes through research time in meanings of the history of biodiversity from Darwin, through the Modern synthesis of the 1940s, the 'paleobiological revolution' (PR) of the 1970s and 1980s, to today's phylogenetically oriented standpoint. I make a case that the PR was only in part the precursor of the most important currents in palaeobiological work on biodiversity, at present and in the future; indeed, the PR entirely missed the most important component of a complete understanding of the origins of biodiversity. I then present the 10 selected papers from *Palaeontology*, including some perhaps unexpected classics, ranging from the 1960s to the present century.

MEANINGS OF ORIGINS OF BIODIVERSITY

The topic of 'origins of biodiversity' has been a perennial theme for palaeontologists, and yet at different times, it has been construed in different ways. These phases may be divided into four stages in general thinking, namely the classic views of Darwin, the Modern synthesis, the paleobiological revolution and today.

1. Darwin's view. To Charles Darwin, the 'origin of biodiversity' was a major theme of the *Origin* (Darwin 1859) and much of his later writing. He is best known for having presented the crucial model of evolution by natural selection that is core to modern evolutionary understanding. It is sometimes forgotten that the second theme of his book was 'descent with modification', his important insight that evolution in deep time had occurred through

lineage splitting. Darwin's macroevolutionary model, visualized as a branching tree, contrasted with then-prevalent ideas of the 'chain of being', a linear succession of organisms from simple to complex. The branching tree, termed a 'Phylogenie' by Haeckel (1866), was a means of representing relationships between organisms living and fossil and of tracking all life back to a single common ancestor. The phylogenetic tree links such nineteenth century topics as embryology ('ontogeny recapitulates phylogeny') and classification, and it accounts for Darwin's main concern, shared with all the other Victorian explorers of tropical lands: just why is life so diverse? Why are there so many species on Earth?

In retrospect, there were two weak points in macroevolutionary understanding following Darwin. First, there was no method to test for the accuracy of any hypothesis of relationships and hence for the whole tree of life. Individual researchers could propose classifications and indeed trees that had various properties of convenience or adherence to their wider ideas about relationships of living organisms and where fossils might fit into the scheme. Second, and remarkably, many evolutionists, including Thomas Henry Huxley of all people, were equivocal about the importance of natural selection, and he, and perhaps most palaeontologists from 1860 to 1930, retained all kinds of unusual models of macroevolution, many of them, despite their fancy names, being squarely teleological (Bowler 1983).

2. The Modern Synthesis. The absence of method and dominance of metaphysical explanations in macroevolution continued in some traditions well past 1950, but was rather firmly rejected in most English-speaking countries thanks to the 'Modern synthesis' of the 1930s and 1940s. For palaeontologists, the turning point was George Gaylord Simpson's (1944) *Tempo and Mode in Evolution*, in which he focused on diversifications or radiations, times when clades expanded rapidly, and he saw that palaeontologists should investigate such events as key underpinnings of modern biodiversity. Simpson saw no methodological difference between neontology and palaeontology and that systematics and morphology could be explored seamlessly from modern to ancient taxa. His study group, the mammals, provided him with many excellent examples in which the fossil record was not necessarily grossly inferior to modern data, and questions of trait evolution and the role of intrinsic factors such as climate change could be explored from ancient to recent and without apology. Simpson (1944) did distinguish larger-scale macroevolutionary processes, termed by him variously megaevolution or quantum evolution, one of which was arguably a precursor of punctuated equilibria (Eldredge and Gould 1972) and the other of the Court Jester model (Barnosky 2000; Benton 2009). In the first,

Simpson envisaged times when evolving species lineages would jump from one evolving adaptive zone to another, marked by the appearance of rapid morphological change in some cases. In the other, he understood that major environmental crises might have had a substantial impact on the course of evolution and in ways that would counteract any species-level microevolutionary patterns. Both macroevolutionary models were, however, couched in purely Darwinian modes.

In his work, Simpson (1944) proposed statistical methods, then seen as quite revolutionary by many palaeontologists, to document rates and patterns of character change along lineages and during radiations. These methods were limited by the absence of a method to determine propinquity of relationships between taxa (as rectified by cladistics and molecular phylogenetics) and by the absence of a secure geological time scale (as rectified by international chronostratigraphic efforts and much improved radiometric dating). Nonetheless, most commentators agree that Simpson (1944) was a clearly influential precursor of all subsequent numerical and problem-oriented work in macroevolution.

3. The Paleobiological Revolution. Through the 'paleobiological revolution' (PR) of the 1970s, a small group of American palaeontologists, including James Valentine, David Raup, Tom Schopf, Steve Gould, Niles Eldredge and Jack Sepkoski, explored diversification in terms of species evolution models (punctuated equilibria vs phyletic gradualism), evolutionary directionality (directed vs stochastic patterns), evolutionary drivers (extrinsic/abiotic vs intrinsic/biotic) and diversity models (equilibrium vs exponential models). This episode of time, during which major books and papers were published, many of them remarkably highly cited, and during which the journal *Paleobiology* was launched, has acquired almost mythic status (Sepkoski and Ruse 2009; Sepkoski 2012). The impact and innovation were clearly huge, as the small group of enormously talented and ambitious researchers compiled and explored databases, brought new-fangled computers into play and for the first time began to propose evolutionary models against which their data might be tested. The PR has been tracked back to the work of Norman Newell and John Imbrie in the 1950s and 1960s, and a founding paper, although not focused on biodiversity, is Raup's (1962) remarkable discovery of unexplored morphospace. In this paper, Raup not only encompassed extinct and living gastropods in a single study, but applied a mathematically simplified model to their form and used computerized methods to generate hypothetical and real forms and then to analyse the results using multivariate statistics. No wonder the majority of palaeontologists at the time were terrified!

The revolutionary intentions of the young Americans, spearheaded by Steve Gould as their most vocal spokesman, have been thoroughly explored in recent histories of the subject (Sepkoski and Ruse 2009; Sepkoski 2012). Notable at the time was the disregard for this revolution by most working palaeontologists around the world, many of whom repeated the old mantras that we lacked data, we needed to find more fossils, we needed to specialize in a group to really understand it and that taxon counting and number crunching were exploitative and pointless. Such attitudes have diminished, but remain as a cogent criticism: numerically inclined researchers must always account for the vagaries of their data, while systematic specialists must understand that statistical approaches are designed to allow for a certain messiness in the raw data.

Did the PR of the 1970s set the scene for palaeontological work today and in the future? This theme is not fully explored in the recent histories (Sepkoski and Ruse 2009; Sepkoski 2012), which rather leave the impression that we are still working within the paradigms established at that time. A review of dominant research themes today suggests in fact that much of enormous value was established in the 1970s (e.g. punctuational species origins, the significance of mass extinctions, the role of extrinsic drivers in macroevolution, methodological acceptance of the use of synoptic databases and statistical analytical methods). However, other major efforts of the PR have been largely rejected (e.g. stochastic species evolution and the MBL model, periodicity of mass extinctions) and others are still debated (e.g. bias vs signal in palaeodiversity curves, equilibrial vs expansion models of diversification, species selection).

The key achievement of the PR was to force palaeontologists to behave like other scientists and to show courage. No other discipline permits its exponents to spend all their time simply describing phenomena, whether those phenomena are atoms, elements, spectra, stars, rocks, crevasses or plants. Gould's (1980) observation that the PR had forced the discipline to move from the ideographic ('descriptive') to nomothetic ('theory-testing') phase was correct. Funding and high-impact palaeobiological publications have burgeoned in recent decades as younger generations understand that their systematic, stratigraphic, ecological and morphological work must be couched in theory testing. But did the PR set out the grounds within which modern palaeobiology operates, and here specifically in the field of understanding the origins of biodiversity? The answer is firmly 'no'.

Ignored throughout the PR was phylogeny.

4. Biodiversity science today. To most biologists and especially those working on biodiversity and conservation biology issues, the meaning of the origins of biodiversity would

be interpreted as an entirely phylogenetic question rooted in molecular phylogenetic trees. The key mode of analysis is in terms of comparative phylogenetic methods (CPM; Felsenstein 1985; Harvey and Pagel 1991; Polly 2001; O'Meara 2012) used to explore the evolution of traits (= characters) derived from morphology, ecology and behaviour, seen as adaptations that ensured the success (= high biodiversity = high species richness) of some clades in comparison with others. At present, most standard CPM apply only to ultrametric trees, those with terminal taxa all of one age, but wider methods are being developed that can be used to process data across trees with extinct taxa (Polly 2001; Stadler 2011; O'Meara 2012; Thomas and Freckleton 2012). CPM are routinely used to ask questions such as (O'Meara 2012): what was the ancestral trait in a clade, how one trait (e.g. body size) affects another, how particular traits affect evolutionary rates, relative rates of evolution of different subclades in comparison with each other, whether the rate of evolution has decreased or increased through time, whether two subclades are evolving towards different evolutionary optima, how different traits relate to the likelihood of extinction, how population size has changed through time, whether there has been gene flow between particular species, when a species moved between land masses and the timings of accelerations and decelerations in trait evolution across clades and with respect to events such as climate changes or mass extinctions.

As will be outlined further below, current palaeontological research on the origins of biodiversity also focuses on the perennial debate about the shape of the global curves, whether sigmoid or exponential and what this means for the biological underpinnings, to what extent the shapes of palaeodiversity curves are driven by rock record bias, how important have been extrinsic drivers such as temperature and atmospheric composition in macroevolution, the interplay of diversity and disparity (i.e. morphological variance), the key broad evolutionary models underlying clade diversifications and the role of external drivers vs key adaptations (i.e. functional novelties) in triggering clade expansion.

It is intriguing that phylogeny barely figures in the PR and nor does it receive mention in many current overviews of macroevolution by marine palaeontologists. It could be then that most proponents of the PR and their intellectual successors today, unlike Simpson, were all experts trained in marine invertebrate palaeontology, and so, they were perhaps limited by their taxa and by their training. And yet, at the same time as the PR, the cladistic (Hull 1988) and later the CPM (Felsenstein 1985; Harvey and Pagel 1991) and molecular phylogenetic (Pagel 1999) revolutions were unfolding vigorously, all of which are key components of modern research in biodiversity (Purvis and Hector 2000; Purvis 2008).

Andrew B. Smith (pers. comm. 2012) suggested that there may have been more to the fact that the leaders of the PR did not use phylogenetic approaches and so missed many opportunities, and this was the debate about higher taxa as units of evolution. Jack Sepkoski and others often had to use families or genera to model diversity through time, and this was a convenience that enabled them to achieve some results; to compile global species-level data on the diversification of life would have been a huge chore and also probably subject to more error than compilations at higher taxic levels. The question then arose of how suitable a proxy were families and genera for species-level evolution. Linked with this was the fact that Steve Gould and others were keen to convert macro-evolutionary phenomena into higher levels of selection, an expansion of evolutionary theory (Gould 1985) in which genera and families might undergo sorting. And yet, many, if not most, of the families used in such PR studies turned out to be nonmonophyletic: most of the apparent periodic pattern of mass extinctions was founded on paraphyletic families and so was illusory (Smith and Patterson 1988), and the early appearance of higher taxa may have produced much of Sepkoski's logistic patterns and plateaux in global diversification (Benton 1997). Perhaps then, unease with these cladistic critiques meant that leaders of the PR shied away from the phylogenetic revolutions that were happening at the same time.

THE 10 PAPERS

Citations

In compiling the current virtual issue (Table 1), I was intrigued to find which was the most cited paper ever published in *Palaeontology*. It is hard to find a clear answer, however, because current bibliographic tools such as Web of Science, Scopus and Google Scholar have been indexing the journal only since 1985, 1995 and 2000, respectively. Hence, all three standard bibliometric tools miss citations up to those years and so severely underestimate citations of older papers.

According to Web of Science, the most cited paper from *Palaeontology* is a major compilation, a reference work on the past distributions of dinoflagellates (Harland 1983), with over 225 citations; this is rather high for the journal, but low for papers on biodiversity and even on macroevolution and palaeobiology in general; some classic publications (Gould 1977; Gould and Lewontin 1979) have accrued over 4000 citations each, for example.

Google Scholar gives a different answer, finding two papers from the 1960s, each with over 220 citations. These are Casey (1961), a classic on the stratigraphical palaeontology of the Lower Greensand, and the other being one of

TABLE 1. Contents of *Virtual Palaeontology* issue 1.

Original reference
ALROY, J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, **53**, 1211–1235.
BENTON, M. J. and EMERSON, B. C. 2007. How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology*, **50**, 23–40.
ERWIN, D. H. 2007. Disparity: morphological pattern and developmental context. *Palaeontology*, **50**, 57–73.
FRIEDMAN, M. and SALLAN, L. C. 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology*, **55**, 707–742.
HOFFMAN, A. 1985. Biotic diversification in the Phanerozoic: diversity independence. *Palaeontology*, **28**, 387–391.
JANIS, C. M. 1989. A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology*, **32**, 463–481.
McGOWAN, A. J. and SMITH, A. B. 2007. Ammonoids across the Permian/Triassic boundary: a cladistic perspective. *Palaeontology*, **50**, 573–590.
SMITH, A. B. and McGOWAN, A. J. 2007. The shape of the Phanerozoic marine palaeodiversity curve: how much can be predicted from the sedimentary rock record of Western Europe? *Palaeontology*, **50**, 765–774.
VALENTINE, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology*, **12**, 684–709.
VALENTINE, J. W. and JABLONSKI, D. 2010. Origins of marine patterns of biodiversity: some correlates and applications. *Palaeontology*, **53**, 1203–1210.

the papers on biodiversity that I selected, Valentine's (1969) first synopsis of marine invertebrate palaeodiversity patterns. The other biodiversity-themed papers, being considerably more recent, have been less cited.

The 1960s and 1970s

We include only one paper from the 1960s, Valentine (1969), a classic of the PR that was perhaps surprisingly published in *Palaeontology*. This was the first thorough documentation, using data assembled in the *Treatise on Invertebrate Paleontology*, to summarize the diversity of well-skeletonized marine invertebrates through the Phanerozoic, and it is an obvious immediate precursor of Jack Sepkoski's work on the same topic, largely published in *Paleobiology*. Valentine (1969) tried to circumvent the possible counterargument that his data were a demonstration of sampling bias by including only well-skeletonized organisms such as corals, arthropods, brachiopods, molluscs and echinoderms that were supposed to have 'good' or reliable fossil records.

Nonetheless, Valentine's 1969 paper was the basis on which Raup (1972) famously queried the merits of empirical palaeodiversity data and proposed instead a bias simulation model in which marine diversity had increased rapidly through the Cambrian and had then remained at more-or-less modern levels since then. The apparently lower levels of diversity in the Palaeozoic were then not real, but an artefact of poor sampling. Famously, the debate was apparently resolved by the 'consensus paper', Sepkoski *et al.* (1981), although the consensus was somewhat illusory. First, the five supposedly concordant data sets on marine palaeodiversity presented by these authors were hardly independent, because they were all drawn from the same fossil record. Second, the opposing protagonists, Valentine and Raup, really did not agree in their later reflections of the main points of the paper (Miller 2009); Valentine argued that it confirmed his view of a rather large increase in marine species diversity in the Cenozoic, and Raup felt it had confirmed his view of a modest rise.

The 1980s and 1990s

Very little of the large debates associated with the later history of the PR found their way into *Palaeontology*. Hoffman (1985) was a short paper that presented a counterpoint to Sepkoski (1984), and an argument that the patterns of marine animal diversification detected by Valentine (1969) and Sepkoski (1984) need not be explained by a diversity-dependent equilibrial model, but could be the result of a neutral model in which pre-existing species did not necessarily exert any particular damping effect on new originations.

In a different kind of contribution, Janis (1989) presented evidence that the ungulate mammals had varied in diversity through the Cenozoic largely as a result of climate change. The major climatic cooling of the past 30 myr is associated with massive spread of grasslands on most continents and a matching rise in diversity of large grazing mammals. This is probably the consensus view, but it has been vigorously disputed (e.g. Alroy *et al.* 2000). Such debates, in this case about a relatively well-documented portion of the fossil record, and for which well-studied living relatives exist, are crucial in the broader understanding of potential extrinsic drivers of diversification.

The twenty-first century

Partly by chance, and partly by design, 7 of the 10 selected papers are from years subsequent to 2000. After that time, the Palaeontological Association began to hold review seminars associated with their annual meetings and invited speakers provided texts of their papers for publication in *Palaeontology*. Several of the papers that follow emerged through this mechanism.

Benton and Emerson (2007) addressed a variety of topics concerning the macroevolution of biodiversity, at the phylogeographic (species) scale and at broader scale. They argued for a nonequilibrial view of the diversification of life, especially for life on land, emphasizing the evidence from studies of modern evolutionary ecology that speciation can beget speciation. In many cases, new species create unpredicted opportunities within their ecosystems for further new species, and so, there can be a positive feedback effect. Such ideas are hard to comprehend in a classic equilibrial-competitive model such as Darwin's 'barrel of apples', in which the origin of a new species can occur only if a pre-existing species goes extinct.

In the same year, Erwin (2007) provided a masterly overview of work since 1990 on disparity and macroevolution, highlighting the fact that most clade origins were associated with a disparity-first model, in which morphospace occupation typically expanded fast and species then emerged within that morphospace area. This would seem to suggest that during clade expansions, either an ecological opportunity or a key adaptation provided the clade with a chance to explore morphospace initially very widely and then the clade continued within that same portion of morphospace, but filled it with ever more specialized species that did not further expand the morphospace envelope.

McGowan and Smith (2007) presented a further important paper, a minute dissection of the recovery of ammonoids in the Early and Middle Triassic, following their near annihilation in the end-Permian mass extinction. Contrary to the normal pattern presented by Erwin (2007), these authors found that Early Triassic ammonoids showed major diversity fluctuations early and disparity expanded rather later. More importantly, McGowan and Smith (2007) also showed one very simple effect of the application of cladistics to biodiversity studies: such an analysis can provide a more complete diversity record than simple taxon counting. Their phylogenetically corrected diversity data, in which ghost ranges (i.e. missing, but implied basal ranges) were included, changed perspectives on the magnitude of the end-Permian event, with some 60 per cent of species going extinct rather than 85 per cent. This is because the cladistic analysis showed that several lineages must have originated in the latest Permian and yet are not represented by fossils.

The same authors (Smith and McGowan 2007) revisited the important and long-running debate that had been set off by Raup (1972), about whether the empirical palaeodiversity curve is broadly correct, the view of Valentine (1969), or whether it was much affected by rock record bias. These authors presented a *tour de force*

argument that ancient diversity is closely associated with map areas of rock units, suggesting that rock availability plays a major role in determining the apparent diversity documented within any time interval. Their map areas were restricted to north-west Europe, and so, it could be suggested that this was not an appropriate metric against which to assess the global diversity data set. However, their regional map areas were much more accurate than current global estimations of rock areas, and they argued that much of the global fossil record comes from north-west Europe in any case. Most notable is that Smith and McGowan (2007) presented a clear and novel means of statistically manipulating the empirical palaeodiversity signal to produce a corrected signal that excluded any possibility of influence from rock availability. Their numerical method has now been widely applied.

James Valentine has been blessed by a long life, and he was able to review the field of origins of biodiversity and macroecology with his student, David Jablonski (Valentine and Jablonski 2010). In numerous publications, these authors and their collaborators have long used marine bivalves as a major resource in exploring the history of ecosystems in different marine settings and across the globe. They were the first to demonstrate clear evidence for a latitudinal diversity gradient in bivalves through time, characterized by high tropical origination rates. Geographic variations in diversity have always been tied to trophic resources and planktonic modes, with planktotrophs dominating in tropical climes.

In another paper published in *Palaeontology* in 2010, Alroy (2010) presented a carefully reasoned argument in favour of his herculean efforts to lead a major community effort to recompile all the world's data on fossil distributions through the Paleobiology Database (PaleoDB). His series of synopses of the growing PaleoDB resource show close correlations of palaeodiversity with numbers of fossil collections and numbers of geological formations. He has been particularly innovative in developing novel and effective statistical procedures that attempt to remove the effects of sampling bias, and Alroy (2010) included the first detailed presentation of his innovative shareholder quorum subsampling method (SQS) that seeks to simulate even sampling across all samples and yet not to penalize rare taxa. His models for the evolution of biodiversity through time are in the classic, equilibrial framework proposed by Raup (1972) and championed by Sepkoski (1984), but opposed by Hoffman (1985), Valentine (1969) and Benton and Emerson (2007). The debate hinges importantly on the validity of sampling correction protocols, whether by SQS (Alroy 2010) or by modelling residuals from rock and fossil time series comparisons (Smith and McGowan 2007).

The final paper in the collection by Friedman and Sallan (2012) explored a variety of current numerical approaches in understanding aspects of macroevolution, but is largely a narrative account of the evolution of fishes. This might seem a somewhat old-fashioned or prosaic exercise. However, palaeoichthyologists have been rather sparse in number, and few have stepped back to take an overview of the broad-scale evolution of their group. These authors explored the patchy data on fish evolution during major biotic transitions and across mass extinction boundaries. They highlighted the need for comprehensive alpha taxonomic and cladistic study of all major fish groups. Some fish clades have been revised superbly well and the records are clear and reliable, but there are numerous murky portions of the piscine fossil record that urgently require detailed reworking. When it is recalled that fishes today account for half of the 60,000 species of vertebrates and yet there is probably a difference of two orders of magnitude in the numbers of systematists working on our finned and limbed relatives, the magnitude of the task becomes evident. Nonetheless, Friedman and Sallan (2012) are young and charismatic, and their *cri de coeur* may not go unanswered.

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