

Investigating Evolutionary Radiations

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About the Author

Michael J. Benton is currently head of the Palaeobiology & Biodiversity Research group at the University of Bristol. He was head of the Department of Earth Sciences from 2001–2008, and president of the Geologists' Association from 2006–2008. He typically has three or four funded postdoctoral workers and five or six doctoral students in his laboratory, and 47 of his graduate students have completed a doctorate, and most have proceeded to postdocs and employment (23 have secured permanent posts in universities, museums, and other academic institutions). He founded the MSc in Palaeobiology, at the University of Bristol in 1996, and since then over 200 students have now completed the degree. He was elected a Fellow of the Royal Society of Edinburgh in 2008, and was Bass Distinguished Visiting Scholar at Yale University in 2009. He has over 500 publications, including over 200 refereed scientific papers, with 16 in *Nature* and *Science*, and more than 50 books, including the leading textbooks *Vertebrate Palaeontology* (in many editions) and *Introduction to Paleobiology and the Fossil Record* (with David Harper, 2009). His current research focuses on major events in the history of life. He is currently pursuing two major themes: (1) the end-Permian mass extinction and subsequent recovery, and (2) the Cretaceous explosion of birds and other taxa. In the first, new work on long stratigraphic sections in the continental red beds of Russia has revealed much about climate change and the numerous blows to biodiversity through the largest mass extinction of all time, and the long, drawn-out recovery phase in the Triassic. In the second, new numerical work on dinosaurian evolution shows that they did not participate in the Cretaceous Terrestrial Explosion, when flowering plants, insects, lizards, and birds radiated explosively. Further, ultrastructural study of dinosaur and bird feathers from Liaoning (125 Ma) shows melanosomes and other astonishing detail that will hugely enhance our understanding of the initial radiation of birds and their acquisition of novelties. For both themes, new work in China offers enormous promise.

Representative Articles

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Abstract

Life today is hugely diverse and yet the origins of that biodiversity are only dimly understood. Charles Darwin saw the temporal and geographic linkages between modern and ancient organisms, and he argued that life arose from a single ancestor, and major groups arose by “descent with modification”. We must thank Darwin for the tree metaphor in evolution. Modern studies are beginning to reveal the relationship between diversity (species richness) and disparity (variation in form), and the importance of both factors in generating modern biodiversity. Classic models of adaptive radiation suggest that major clades expand initially rapidly, and that a great deal of change in disparity happens before the major diversity jump. The Cretaceous Terrestrial Revolution, from 120–80 Ma ago, marked the dramatic rise of angiosperms in terrestrial ecosystems and their role triggering massive diversifications among arthropods and vertebrates. New data sets and new statistical tools show patterns of diversification as well as the piecemeal manner in which many key innovations, or novelties, were constructed and their seemingly ad hoc genomic regulation.

Key Words

Macroevolution; evolutionary radiation; biodiversity; evolutionary novelty

Introduction

Life today is hugely diverse, the result of billions of years of evolution. This biodiversity, critical to our understanding of evolutionary processes, is now under threat as a result of the burgeoning human population and modification of the environment. Much of the great richness of modern biodiversity is founded on a relatively limited number of highly diverse groups, such as beetles, social insects, flowering plants, lizards, birds, and mammals. These appear to owe their success to particular adaptations that enabled or drove rapid, even explosive, phases of evolution in the geological past. Understanding these evolutionary radiations and the role of the unique characters, or novelties, of successful groups of organisms are issues of deep interest to scientists and the public in terms of understanding nature, how evolution works, and the past, present, and future conservation of biodiversity. Remarkably, our current understanding of such large-scale radiations is still imprecise and often anecdotal.

Most large-scale evolution happens during evolutionary radiations, sometimes called adaptive radiations, a model that was developed in the twentieth century (Simpson 1944; Stanley 1979; Benton 1987, 1997; Gould 2003), but which

tracks back to the work of Charles Darwin (Darwin 1859). The classic, textbook model of an adaptive radiation, as expounded by George Gaylord Simpson (Simpson 1944), and essentially supported ever since, is that a group expands, often relatively rapidly, and this expansion is driven or enabled by a key innovation, a feature of anatomy or behavior that adapts the new organisms particularly well to be successful.

There are four approaches to studying evolutionary radiations (Gavrilets and Losos 2009): fossils, phylogenetic comparative methods, microevolutionary studies of extant taxa, and laboratory experiments. Most recent work has focused on the third and fourth approaches (Schluter 2000; Gavrilets and Losos 2009; Rundell and Price 2009), and key findings include ten observations (Gavrilets and Losos 2009): much speciation and divergence happens early in a radiation, species diversity may initially overshoot and then reduce, initial divergence may relate to habitats and then divergence is controlled by other traits, speciation may be enhanced by larger geographic areas, speciation may occur in the absence of allopatry, selection gradients of intermediate slopes promote speciation, one-dimensional geographic areas such as

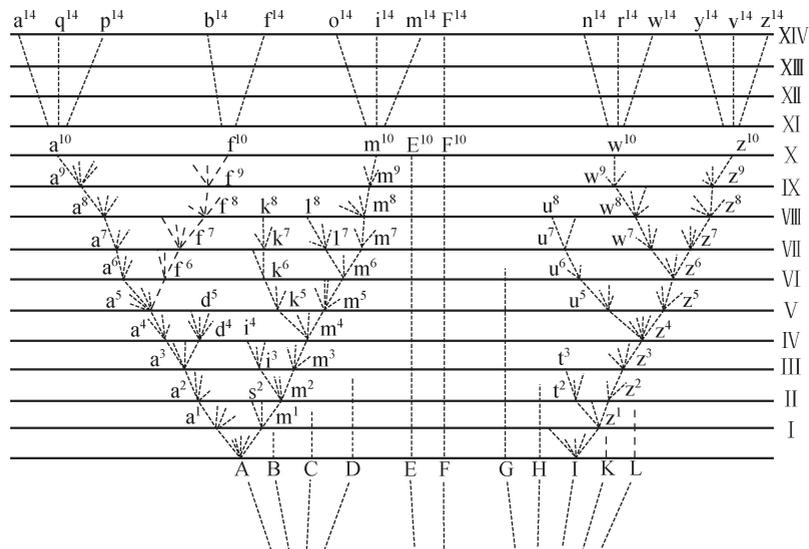
rivers or shores promote speciation more than two-dimensional spaces such as lakes or oceans, speciation after the initial burst usually involves minimum phenotypic change, rapid and extensive diversification is most likely if the number of underlying genetic loci is small, and species can stably maintain their divergence in the face of gene flow and hybridization.

Some of these findings from the phylogeographic study of small-scale radiations lend themselves to exploration at larger scales, most notably the observation of initial explosive radiation followed by overshooting and lineage reduction. Larger-scale studies might lack the fine-scale genetic analysis possible when studying species within a genus, but they open up opportunities to explore lineage sorting on a large scale, to compare changes in morphology and species richness, and especially to track the origin of key novel characters.

1. Darwin and Diversification

Famously, the only illustration in Darwin's *On the Origin of Species* was a hypothetical phylogenetic chart (Fig. 1), showing the fates of 12 lineages after their origin. Of these 12, two (A and I) successfully radiate, whereas the other ten lead to nothing. Clade A branches in a balanced manner, with roughly equal splitting to left and right, whereas clade I is unbalanced, with branching preferentially to the right, and perhaps illustrating a trend. Darwin called these patterns of evolution descent with modification, and this was his explanation of all phenomena we might group together today as macroevolution, all the aspects of evolution from speciation upwards.

Darwin's (1859) *On the Origin of Species* is generally remembered for its exposition of the principles of natural selection, the entirely original idea that explained how small-scale



▲ Fig. 1

Darwin's concept of descent with modification. This is the only illustration in Charles Darwin's *On the Origin of Species* (Darwin 1859), and it shows twelve lineages, lettered A-L, evolving upwards through time. Two of the lineages (A, I) radiate and diversify, whereas the others do not prosper. This kind of tree-like diagram is commonplace today, but it was a revolutionary idea in the 1850s when most people did not believe in any kind of evolutionary change, let alone splitting of species and regular extinction.

competition and predation could modify organisms at the population level from generation to generation: this aspect of his work has probably attracted most attention. However, Darwin regarded his discovery of descent with modification as equally important: like evolutionists today, he was astounded by modern biodiversity, and by the extraordinary detail of the history of life revealed by fossils. Natural selection clearly worked at the *microevolutionary* level, in other words, over short time scales and at population level, but Darwin sought an explanation of larger phenomena.

In fact, the history suggests that Darwin had always wished to explore these two concepts – natural selection and descent with modification – as two sides of the same coin. Famously, on the voyage of the *Beagle* (1831–1836), Darwin had started as an Anglican liberal creationist, assuming that species were fixed, and that God had created life as we know it in all its diversity and wonder, but that there had perhaps been past creations that accounted for the numerous divisions of geological time, each with their characteristic fossils. During the *Beagle* voyage, Darwin observed two things that made him doubt the fixity of types: vertical (temporal) and horizontal (geographical) genealogical links between taxa.

First, in Argentina, he collected fossils of giant ground sloths and giant armadillos that were clearly anatomically similar to modern sloths and armadillos. Why, he asked, was there apparently continuity of descent between the fossils and living forms in a particular region unless those forms had evolved, the older into the newer, and without intervening creative acts? Under a model of creation, there is no reason why successively created assemblages of organisms would show any vertical connections.

Second, and more famously, Darwin observed the phenomenon of geographic variation on the Galápagos Islands: the giant tortoises on each island were distinctive enough that the locals could identify the source of any specimen because of differences in the carapace and head shapes. Later, when he returned to England and received expert ornithological advice from John

Gould, Darwin also realised that the diverse small birds he had collected all shared an ancestor with the modern grassquit, *Tiaris obscura*, from Ecuador. In the course of a relatively short time, geological speaking, what had presumably been a small population of finches, perhaps blown from the mainland 1000 km away, had diversified into the 14 species we recognize today (6 species of *Geospiza*, 6 species of *Camarhynchus*, and one species each of *Certhidea* and *Pinaroloxias*; in Darwin's day, 12 species were recognized). Darwin recognized the Galápagos islands as volcanic, and so he knew they had emerged through the waters of the Pacific in the Cenozoic, and modern radiometric dating confirms this, providing dates from 3 million years (Ma) ago, to less than 1 Ma for different islands in the archipelago.

In his chapter on “Geographical distribution”, Darwin wrote (*On the Origin of Species*, pp. 398-399):

Why should the species which are supposed to have been created in the Galapagos Archipelago, and nowhere else, bear so plain a stamp of affinity to those created in America? There is nothing in the conditions of life, in the geological nature of the islands, in their height or climate, or in the proportions in which the several classes are associated together, which resembles closely the conditions of the South American coast: in fact there is a considerable dissimilarity in all these respects. On the other hand, there is a considerable degree of resemblance in the volcanic nature of the soil, in climate, height, and size of the islands, between the Galapagos and Cape de Verde Archipelagos: but what an entire and absolute difference in their inhabitants! The inhabitants of the Cape de Verde Islands are related to those of Africa, like those of the Galapagos to America. I believe this grand fact can receive no sort of explanation on the ordinary view of independent creation; whereas on the view here maintained, it is obvious that the Galapagos Islands would be likely to receive colonists, whether by occasional means of transport or by

formerly continuous land, from America; and the Cape de Verde Islands from Africa; and that such colonists would be liable to modification;—the principle of inheritance still betraying their original birthplace.

In exploring descent with modification, Darwin made many statements in *On the Origin of Species*. For example, on pages 333-334, he explains the vertical, or geological, aspect: “Thus, on the theory of descent with modification, the main facts with respect to the mutual affinities of the extinct forms of life to each other and to living forms, seem to me explained in a satisfactory manner. And they are wholly inexplicable on any other view. On this same theory, it is evident that the fauna of any great period in the earth’s history will be intermediate in general character between that which preceded and that which succeeded it.” He goes on to link this to geographic variation on page 351, where he says: “On these views, it is obvious, that the several species of the same genus, though inhabiting the most distant quarters of the world, must originally have proceeded from the same source, as they have descended from the same progenitor.” These principles explain shared resemblances among organisms, the basis of an evolutionary view of taxonomy, as he noted on page 420, “All the foregoing rules and aids and difficulties in classification are explained, if I do not greatly deceive myself, on the view that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking.”

It is often said that Darwin was first to propose, in *On the Origin of Species*, that all of life descended from a single ancestor, and yet that claim has been disputed. In Darwin’s day, there were no Precambrian fossils, and the fossil record seemingly ended in the Cambrian rocks that had yielded brachiopods, trilobites, and other primitive forms. In the final pages of the first edition of *On the Origin of Species*, he wrote

(Darwin 1859, pp. 488-489): “When I view all beings not as special creations, but as the lineal descendants of some few beings which lived long before the first bed of the Silurian system was deposited, they seem to me to become ennobled”. In later editions, with increasing paleontological knowledge, Darwin substituted “Cambrian” for “Silurian”. But did he really believe that the origin of life was in fact the “origins” of life from many unknown Precambrian ancestors? His illustration (Fig. 1) might suggest many lines of descent, and yet on page 419 of the 1869 edition of *On the Origin of Species* he wrote, in the context of this missing Precambrian record: “We now know that at least one animal did then exist”, meaning the ancestor of the known Cambrian forms. Most importantly, in the first edition (Darwin 1859, p. 484) he wrote: “...I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed”, although later, on page 490, he clearly leaves open the possibility of multiple origins of life. Note that Darwin strengthened this statement in the second edition by adding “by the Creator” to the end of the sentence. He removed this last phrase in later editions, but did not enter into further detail about how the one “primordial form”, or several forms, might have arisen. Close reading of Darwin’s correspondence, and his discussions with Thomas Huxley and others, make it clear (Strick 2003) that Darwin was happy with the idea of a naturalistic origin of life, in “some warm pool”, as he wrote to his friend Joseph Hooker, and that he simply avoided an explicit statement that life had originated naturally from nonliving matter, and once only, and that all species living and extinct descended from that one ancestor, to avoid causing unnecessary offence to the Christian people of Britain and the world.

Most of what Darwin said about diversification, radiations, and the origins of biodiversity is largely in tune with modern thinking. It is ironic that other evolutionists of Darwin’s day, including Thomas Huxley, had difficulties with his views on descent with modification, and found it hard to abandon the pre-Darwinian theory of archetypes – Huxley saw *Archaeopteryx* as

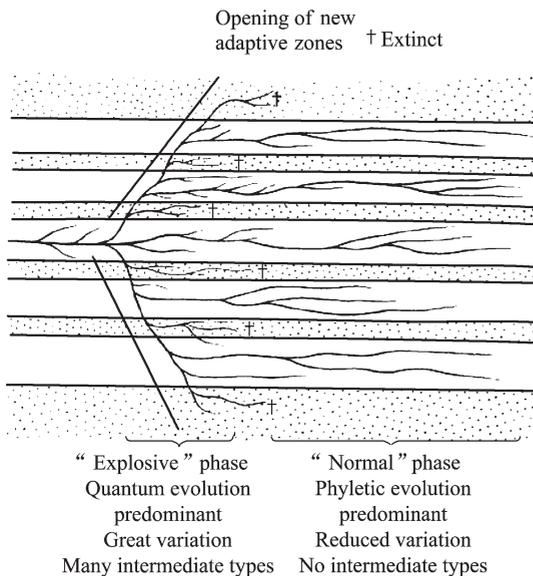
intermediate between dinosaurs and birds, but looked for a deeper ancestry of birds to allow what he saw as the enormous leap from one archetype to another (Di Gregorio 1982; Bowler 1992). Nonetheless, despite the sometimes forgotten difficulties and lack of understanding of Darwinism in Europe and North America from 1860–1930 (Bowler 1992), the Neodarwinian Synthesis of the 1930s provided a clearer understanding of Darwin’s views on macroevolution, and George Gaylord Simpson was instrumental in combining paleontological and neontological evidence.

2. The Ecospace Model for Adaptive Radiation

There are two models for evolutionary radiations, the ecospace model and the genome or developmental model. The ecospace model (Simpson 1944; Stanley 1979; Gavrilets and Losos 2009) suggests that variations in ecological opportunity control the success of major new morphologies and this produces a pattern that mimics differential introduction of innovations (Fig. 2). Simpson (1944) identified several

aspects: radiations are “driven” by key adaptations/innovations (Gavrilets and Losos 2009), whether they enter previously vacated ecospace, or conquer new habitats (Simpson 1944, pp. 210-214; Stanley 1979, p. 102); they rapidly fill and overshoot, and then there is extinction/weeding out as many early lineages fail, so leaving gaps in ecospace/morphospace. Simpson (1944) also argued that taxa that radiate rapidly in this way might often be “preadapted” in having acquired many of the crucial elements of the key innovation before the radiation.

The genomic reorganization model (Erwin *et al.* 1987; Erwin 1992; Valentine 1995, 2004; Crepet and Niklas 2009) posits a mutation-driven model of evolutionary change. The early burst of radiation in a clade could suggest that genetic opportunities were less canalized early on, and regulatory pathways were repatterned and redeployed (Erwin 1992; Valentine 1995, 2004). These two models need not be mutually exclusive and indeed both could operate in tandem (Erwin 2007), but most evolutionists would probably assume that the ecospace model is the norm.



◀ Fig. 2
Simpson’s (1944) ecospace model for adaptive radiation. It shows initial explosive evolution into new sectors of ecospace, followed by an “overshoot” as the clade diversifies excessively, and then extinction of intermediates as the clade settles to a more stable format.

3. Deep-Time Evolutionary Radiations

The need for an integrated programme of macroecological and morphological-developmental studies of evolutionary radiations on geological time scales has been highlighted several times. In his seminal text on adaptive radiations, Schluter (2000, p. 181) notes that “Most tests of key innovation hypotheses attempt to correlate appearance of a novelty with change in the net rate of speciation rather than with adaptive radiation, of which speciation is only part. The lack of attention to effects of novel traits on ecological and phenotypic expansion is an outstanding gap in the study of key innovations.” In other words, little has been done to map clades and characters to identify patterns of timing, shapes of clades and subclades over millions of years, and the distribution of anatomical characters, including putative key innovations.

Evolutionary biologists and paleontologists may explore various aspects of a radiation event. The group in question must be monophyletic, meaning it had a single ancestor and includes all descendants of that ancestor, in other words the group is a clade. In such a case, the unique characters, the apomorphies or homologies, of the clade may include features that are associated with the radiation, whether in driving it in some sense, or in combining to provide the novelties, or unique adaptive features that presumably explain the success of the group. In describing a radiation, the investigator ought to have available a complete tree, that is a numerically determined pattern of relationships of all species living and extinct, and ideally complete and dated tree – that is, a tree that is calibrated against geological time using all available fossil and branch length data. A key means of describing a radiation is by assessing diversity through time, typically the number of species or lineages in each identifiable time bin from the origin of the clade and forwards in time. In paleontological examples, the diversity measure may be founded on genera, as a proxy for species, reflecting the patchiness of the fossil record, except in cases of marine plankton and other exceptionally complete examples. It is also of crucial interest to consider disparity, the variance in morphology, and this

may be assessed from shape measurements or from discrete characters, often apomorphies. Simple organisms, such as unicells, may be described adequately by shape measures, such as lengths, widths, and outlines, but more complex organisms are often better represented by sets of discrete characters. Further, if those discrete characters are apomorphies, they may be used to define patterns of character acquisition through time, and especially the rates and patterns of acquisition of different character complexes, including novelties.

At least four criticisms have been made of current understanding of large-scale evolutionary radiations.

- (1) First, most studies of large-scale radiations have been poorly defined in terms of phylogeny (Smith 1994): without a strong and independently derived phylogenetic tree, the evolutionary radiation cannot be placed precisely in time, quantified, or associated with particular organisms or groups. Earlier accounts by leading paleontologists (Simpson 1944; Stanley 1979; Raikow 1986), for example, lacked an explicit cladistic framework.
- (2) Second, key innovations (or “key adaptations”, “adaptive breakthroughs”, or “novelties”) are hard to define and hard to identify (Heard and Hauser 1995; Donoghue 2005; Gavrillets and Losos 2009). They can only be recognized retrospectively once they are associated with a particular speciose clade. Many key innovations are based on anecdotal evidence (“birds are successful because they can fly, or because they are warm-blooded, or because they can exploit new food sources”), and few have been tested. Sometimes, when a speciose clade, such as Passeriformes (the songbirds), is investigated, there is no obvious, single major novelty, or even substantial cladistically unique character of the clade (Raikow 1986). Some definitions of key innovations (Rosenzweig and McCord 1991, p. 204) explicitly include a claim that key adaptations are progressive in characterizing or specifying a competitively superior clade,

whereas most investigators (e.g., Benton 1983, 1987; Hunter 1998; Gould 2002) would explicitly rule that out. Brooks and McLennan (2002) defined key innovations as apomorphic characters that may be demonstrated to have adaptive value in comparison with their precursors and to have played a role in initiating speciations. These tests may be hard to carry out, and there is a circularity in selecting traits associated with diverse groups and identifying those as key innovations, in that other characters not listed in the cladistic data matrix might be missed (Guyer and Slowinski 1993); there is no demonstration that these characters actually had a role in promoting speciation; and characters accumulated in stem organisms that were crucial innovations are ignored (Hunter 1998). As an example, most of the unique features of birds that are claimed to be key innovations (feathers, endothermy, wings, flight, 3D vision and enhanced optic lobes, pneumaticity of bones and air sacs) are now known to have arisen at numerous points among the theropod dinosaurs in the stem lineage to Aves/Avialae and yet some or all of these probably were responsible for the initial radiation of birds (see below).

- (3) Third, it has often been said (e.g., Schluter 2000; Gavrillets and Losos 2009; Rundell and Price 2009) that the classic association of radiation and key innovation may not always apply. Indeed, many radiations may lack evidence of a key innovation, and in others, substantial novelties did not lead to a major increase in diversity. Erwin (1992) distinguished five hypothetical kinds of “adaptive radiations” that vary in the role of novelty, diversity increase, and disparity increase.
- (4) Fourth, it is inappropriate to scale up the findings of laboratory and field studies to the macroevolutionary level because different processes might have operated in the past (Erwin *et al.* 1987), and certainly the behavior of subspecies and species on islands may not reflect precisely the patterns of global diversifications over millions of years. Further, taking models and observations from the level of evolution within and between

species and scaling them up to larger clades consisting of dozens or hundreds of species over long spans of time is probably fruitless because the patterns and processes are separated by many orders of magnitude.

New programmes of study of evolutionary radiations on the larger scale have become feasible recently because of a combination of circumstances: (1) development of well-revised phylogenetic trees of major clades, many of them complete at species level; (2) publication of extensive cladistic character data matrices; (3) new numerical methods for analysing evolution and adaptation in phylogenetic trees; (4) improvements in geological dating; (5) new methods to assess completeness of paleontological data sets (Foote *et al.* 1999; Benton *et al.* 2000; Smith 2007; Jablonski 2008); and (6) rapid development of techniques in the field of evolutionary developmental biology (“evo-devo”), most notably the identification of genomic controls of morphology (Müller 2007; Wagner 2007; Carroll 2008).

Interdisciplinary work that crosses the boundary from the modern biota to the past, combining fossils with comparative phylogenetic methods, is essential if we are to disentangle the most substantial questions about evolution, not least the relative roles of biotic and physical factors (Benton 2009) and the nature and likely outcomes of the current biodiversity extinction threat (Davies *et al.* 2008). Many earlier studies of the diversity of life through time focused on the simple summation of species, or higher taxa, through units of geological time, but phylogenetic approaches add considerable richness to such analyses. They allow the identification of ghost ranges, and other times when fossils are missing, but more importantly, a suite of comparative phylogenetic methods (see below) may be applied to explore the relative timing of expansions and contractions of clades, and the nature of character evolution through time and across the phylogenetic tree.

There are a number of key questions about major clade expansions:

- (1) Is there an early phase of explosive evolution? What are typical time scales and magnitudes, and does disparity expand first, and diversity second?
- (2) Is there then an overshooting phase, where diversity may expand substantially, and then fall back? How does this affect disparity?
- (3) Do novelties typically arise in one burst, associated with massive clade expansion (a simplistic “key adaptation model”), or are they compiled piecemeal over longer spans of time, and passing through many precursor stages?
- (4) Which characters come first? Wagner (1995) found that environmentally controlled innovations preceded anatomically deeper characters.
- (5) If a clade re-radiates, perhaps following an extinction event, is the second radiation a weak reflection of the first?
- (6) Do the initial lineages fill morphospace more completely than the set of lineages that perhaps survive an initial ‘weeding out’ phase? In other words, are there gaps in morphospace in the later history of large clades, as predicted by Simpson (1944; see Fig. 2)?
- (7) Do individual subclades show limited disparity, with closer coupling of disparity and diversity in their later history than in the explosive phase?
- (8) Do rapidly evolving clades partition disparity early, whereas slowly evolving clades show more within-clade disparity?

4. Numerical Studies of Radiations

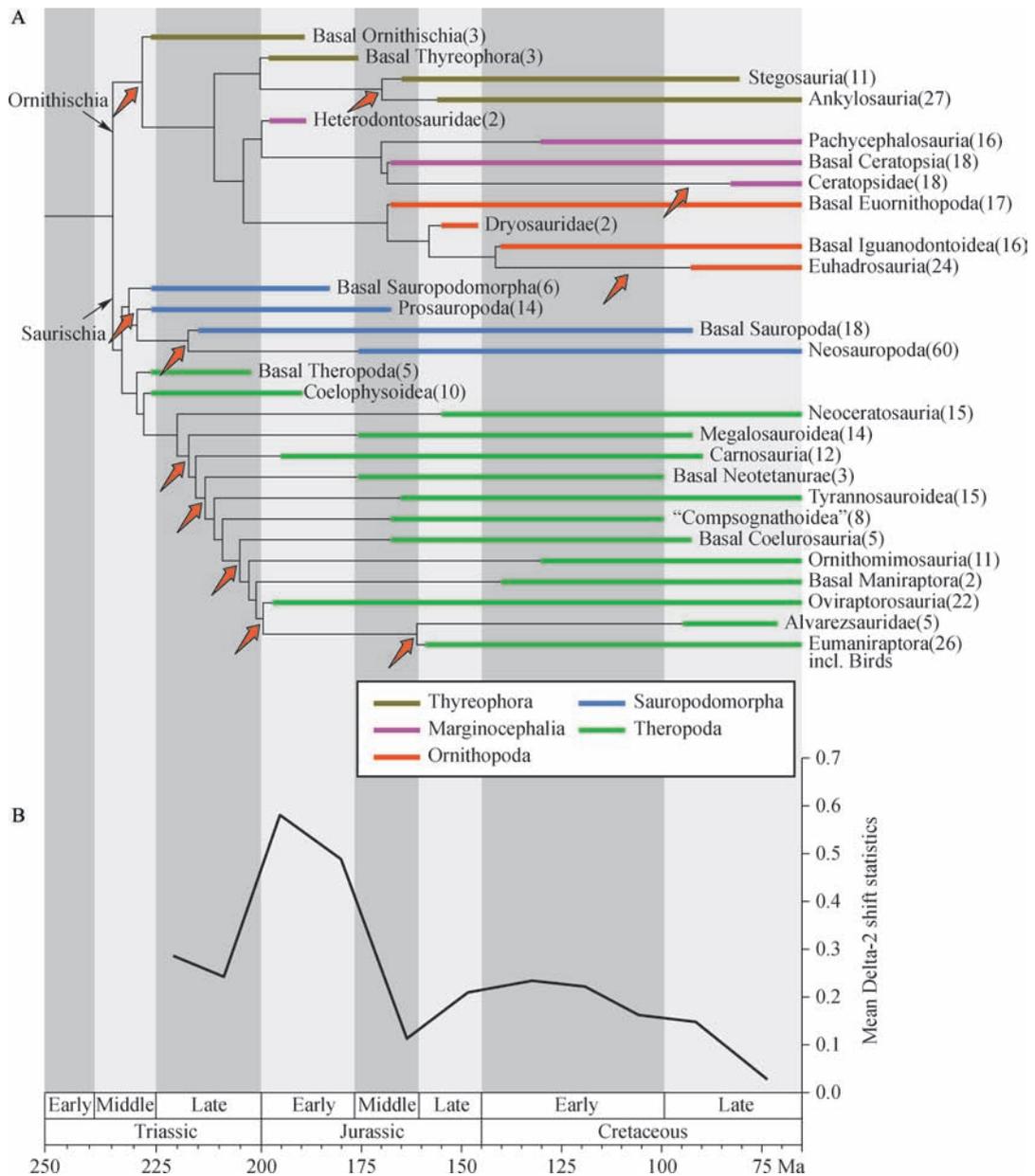
The study of large-scale evolutionary radiations requires complete phylogenetic trees based on both extant and fossil taxa, a high quality geological time scale, and appropriate comparative phylogenetic methods (Felsenstein 1985, 2004; Harvey and Pagel 1991). These comparative methods allow analysts to test for correlated evolutionary changes in two or more traits, and to distinguish phylogenetic inheritance from adaptive aspects of characters. For example, flightless birds may be generally large in body size, as a shared feature of the clade, not a unique character of each species in the clade; proper phylogenetic comparative methods will distinguish

what component of their body size is a result of group inheritance, and what is unique to the species or genus in question.

Some biologists (Harvey *et al.* 1994; Paradis 1998) have argued that molecular trees are better than morphological trees, especially those involving fossils, for large-scale studies of evolution. However, as one delves deeper into geological time, the accuracy of molecular trees diminishes, and this is especially significant when considering clade origins. Despite efforts to argue that deep-time events can be reconstructed from mathematical analysis of trees based on extant taxa (Paradis 1998), fossils remain the only valid source of information for quantifying the tempo and mode of evolutionary change through time (Smith 1994; Mayhew 2003). Intelligent approaches to combining fossils and phylogenetic comparative techniques include an awareness of the bias and gaps in the fossil record (Smith 1994, 2007; Foote *et al.* 1999; Benton *et al.* 2000).

Examples of the new combined approaches are emerging. Lloyd and colleagues (Lloyd *et al.* 2008) used phylogenetic comparative methods with a supertree of dinosaurs, based on 155 source trees and 440 species, to show that dinosaurs had not diversified substantially in their last 50 Ma (Fig. 3). This suggests that dinosaurs were not part of the Cretaceous Terrestrial Revolution (KTR), the time when angiosperms took over terrestrial ecosystems, coincident with the rise of leaf-eating, pollinating, and social insects, as well as new groups of lizards, birds, and mammals, and they plodded about seeking the ever-rarer gymnosperms, puzzled perhaps by the balmy scent of angiosperms and the buzzing of bees and beetles. In a study of character evolution in angiosperms, Crepet and Niklas (2009) report a good correlation between early angiosperm diversity and the acquisition of new floral characters as well as with the rise in insect family numbers.

Looking deeper in time, Brusatte and colleagues (Brusatte *et al.* 2008) showed that synapomorphies of dinosaurs and crurotarsans, the two major archosaur groups on land in the Middle and



▲ Fig. 3

Phylogeny of the dinosaurs, showing times of unusually high diversification rate. This diagram shows a simplified outline of dinosaurian relationships based on several cycles of cladistic analyses and revisions, and summarized from a supertree of 420 of the 550 or so currently valid dinosaurian species. Major groups are plotted against time, highlighting the known fossil record (thick line) and inferred earlier unknown record ("ghost range"). Numbers of species included in the supertree are indicated for each clade. Red arrows indicate 11 statistically significant diversification shifts, which are clustered in the first one-third of dinosaurian evolution (A), as highlighted in the summary of probability of significant diversification shifts through time (B). A full-scale version of the 2008 dinosaur supertree may be seen at <http://palaeo.gly.bris.ac.uk/macro/supertree/>. (Based on Lloyd *et al.* [2008], and drafted by Simon Powell.)

Late Triassic, were acquired at equivalent rates, and that crurotarsan morphospace remained substantial through the initial 30 Ma of dinosaurian evolution (Fig. 4). This suggests strongly that these early dinosaurs were not competing wholesale with the crurotarsans, as had been suggested, and that the origin of the major clade Dinosauria was characterized, unusually perhaps, by slow expansion of disparity and more rapid increase in diversity. This study, based on disparity analysis of discrete apomorphies, shows the ability of the approach to represent static estimates of relative morphospaces occupied by different subclades at different times, to compare different regions of the body, and to look at rates of morphological evolution through time.

5. The Origin of Birds

The origin and diversification of birds is a classic example of a radiation that has repeatedly attracted attention. Birds (Class Aves) are a diverse group today, with some 10,000 species, they are heavily studied, and the fossil record has improved substantially. If we are to understand the origins of modern biodiversity, speciose groups such as birds are key. Birds have been heavily studied because they are obvious animals in human landscapes, and, as visual animals themselves, they have always attracted attention because they are colorful. Finally, we see them as hugely successful today largely because of their suite of specializations for flight, such as their wings, feathers, lightweight skeleton, enhanced eyesight, advanced parental care, and complex visual displays. Until recently, paleobiologists often despaired of being able to reconstruct bird evolution from the fossils, but spectacular discoveries from China, Spain, Argentina, and other parts of the world have enormously enhanced our knowledge, not only by adding species to the roster of fossil forms, but also by adding some spectacularly well preserved materials (Fountain *et al.* 2005; Benton *et al.* 2008; Xu *et al.* 2009; Zhang *et al.* 2010).

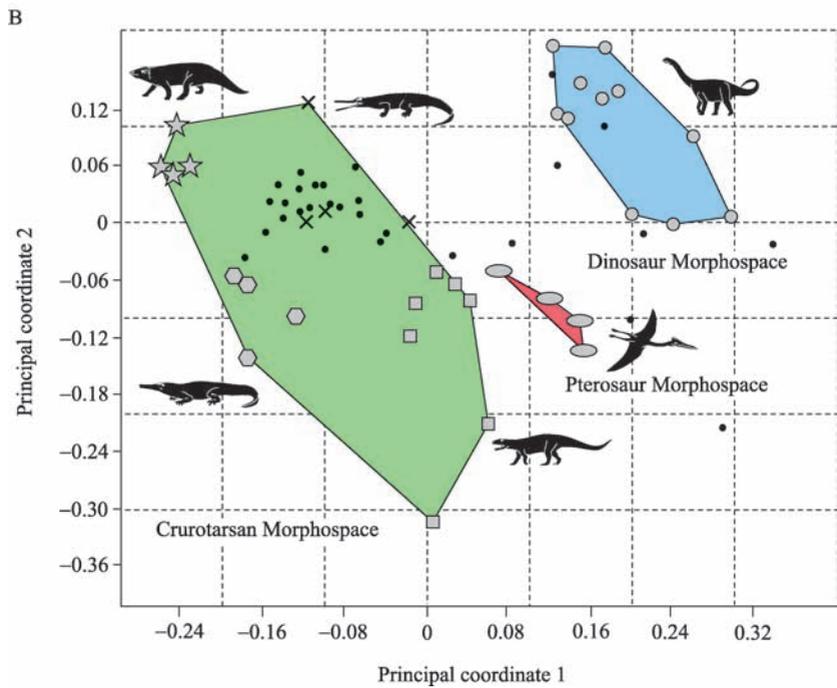
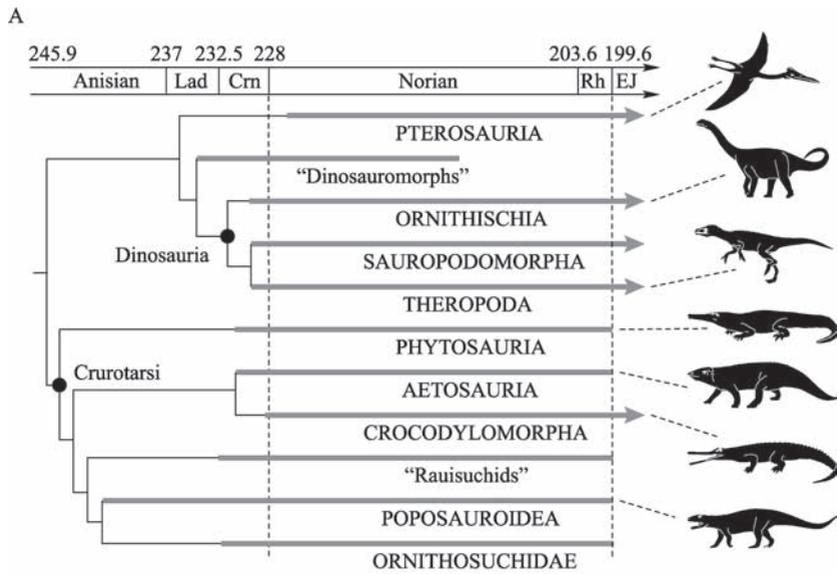
New work on bird evolution has revealed one startling fact: the clade did not acquire its key adaptations or novelties in one event, or even over a short span of intense evolution, but rather

over some 50–100 Ma. At one time (e.g., Ostrom 1976), the origin of birds in the Late Jurassic, equivalent to the branching point in the cladogram of *Archaeopteryx* and all subsequent birds, was associated with the acquisition of numerous morphological innovations, such as feathers, wings, massive pectoral flight muscles, the furcula (“wishbone”), pneumatic (= hollow) bones, expanded eyes and optic lobe of the brain, and many other characters that, together, constitute a classic set of novelties that form a package of flight adaptations. Subsequent discoveries of small theropod dinosaurs, and most notably the feathered birds and dinosaurs from the Early Cretaceous and the Middle-Late Jurassic of Liaoning, in China (Zhou *et al.* 2003; Benton *et al.* 2008; Xu *et al.* 2009; Zheng *et al.* 2009; Zhang *et al.* 2010) have smeared this impressive list of synapomorphies of Aves back down the stem of the cladogram.

The effects can be measured readily. Whereas in 1986, Jacques Gauthier (Gauthier 1986) was able to list 20 synapomorphies of birds (= Avialae = Aves), the list was reduced to a mere three in revised studies in 2001 (Norell *et al.* 2001): humerus is longer than scapula (i.e., elongate forearm or wing), pubic apron less than one-third of shaft length, and shortened tail (no more than 25 caudal vertebrae). This is a rather limited number of characters to diagnose the branching point that gave rise to birds, and really the elongate wing (and so inferred powered flight) is the only substantial functional feature left.

The rapid reduction in unique avian characters was partly a geometric side effect of adding many more fossils into the cladogram – each branching point in a cladogram is likely to be marked by one or more unique character acquisitions, and so the more branches there are, the more the existing character lists are spread out. However, intense study of the morphological transition from theropods to birds has revealed many new characters (Norell *et al.* 2001; Turner *et al.* 2007), and this should partly offset the inevitable dilution of character lists.

The key change has been that many of the characters listed by Ostrom, Gauthier and others as uniquely



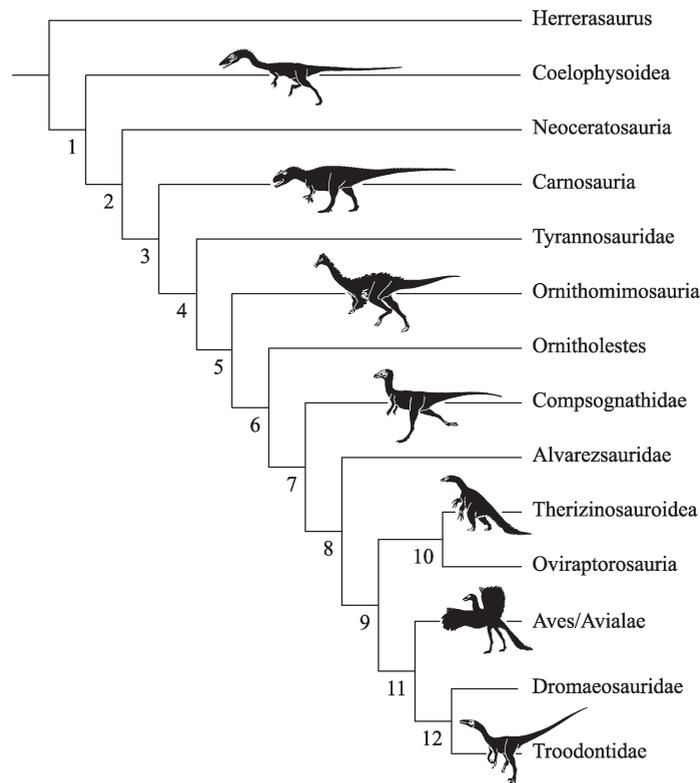
avian in the 1970s and 1980s have moved down the cladogram (Fig. 5), some, such as the furcula (= fused clavicles; "wishbone") right to the base of the theropod dinosaurs, and various kinds of feathers also well down the theropod stem, or even to the base of Dinosauria or lower if ornithischians

also had dermal filaments (Zheng *et al.* 2009). This backwards smearing down the phylogenetic stem resulted from new fossils that revealed feathers, as well as from close study of existing fossils.

Subsequent bird evolution, from *Archaeopteryx*

◀ Fig. 4

A. Simplified phylogeny for Triassic archosaurs scaled to the Triassic time scale. Numbers at top refer to millions of years before present; grey bars represent the observed durations of major lineages; vertical dashed lines denote two hypothesized extinction events; arrowheads indicate lineages that survived the Triassic-Jurassic event. Lad, Ladinian; Crn, Carnian; Rh, Rhaetian; EJ, Early Jurassic. **B.** Empirical morphospace for *Triassic archosaurs*, based on the first two principal coordinates, derived from the same data set, showing that dinosaurs were not broadly outcompeting crurotarsans, as predicted by former ‘competitive’ models for biotic replacement. This study (Brusatte *et al.* 2008) was based on a data matrix of 64 taxa and 437 characters of the skull and skeleton of crurotarsans and dinosaurs, analysed in a series of steps. Disparity studies such as this are still rather novel, and yet there is considerable potential to use the new numerical techniques to dissect many other such radiations. The techniques (Wills *et al.* 1994; Wills, 2001) are as follows: (1) take a taxon/character data matrix; (2) calculate intertaxon distances (pairwise Euclidean distances), using the software MATRIX (Wills); (3) carry out a Principal Coordinates Analysis (PCO) of these distance measures, using the software Ginkgo or PAST; (4) calculate disparity measures from the Euclidean distances, expressed as sums and products of ranges and variances, using the software RARE (Wills); (5) correct these measures for samples of different sizes by rarefaction to take account of the possibility that disparity α sample size, also using the software RARE (Wills); (6) results may be shown as morphospace plots (PCO axes) for whole the sample, for subclades, by time slices, or by character sets – these partitions of the data allow numerous comparative questions to be explored; (7) disparity measures may also give rates of evolution if partitioned by time divisions, and these allow comparisons of changes in diversity and disparity through time, changes in both measures for different subclades, and the effects of major physical perturbations.



▲ Fig. 5

Cladogram of theropod evolution, showing the timing of appearance of avian characters down the theropod stem. The silhouetted animals, from top to bottom, are *Coelophysus*, *Allosaurus*, *Garudimimus*, *Compsognathus*, *Nothronychus*, *Archaeopteryx*, and *Saurornithoides*. Formerly ‘avian’ characters appeared at the numbered nodes, or lower, as follows: 1, furcula (‘wishbone’); 4, simple filamentous ‘feathers’; 6, semilunate carpal; 9, true feathers; 11, unserrated teeth, maxilla participates in external naris, straplike scapula, scapula with acromion process, ischium elongate, elongate pennaceous feathers. This leaves the following characters of Aves: inferred flapping flight, no more than 25 caudal vertebrae, humerus is longer than scapula, pubic apron less than one-third of shaft length. (Based on Norell *et al.* [2001] and Turner *et al.* [2007].)

to modern birds, saw the shortening of the tail to a pygostyle, the loss of teeth, deepening of the sternum, and other changes to the fully-fledged modern bird. *Archaeopteryx* could fly, and presumably squawk, with the best of them, but it took 50 Ma of theropod evolution and a further 50 Ma of early bird evolution for the various novelties of birds to be honed to their present state.

A complete phylogenetic tree, with apomorphies mapped to nodes, will allow detailed investigations of a range of questions concerning radiations and the evolution of novelties:

- (1) Was the diversification of birds driven by the origin of flight, as a key character complex? Is it the case that different morphofunctional systems were involved and to what extent.
- (2) Did the clade expansion happen in one smooth process, or in several steps? This could be tested by looking at character acquisition by time slices, and profiles of character-based evolutionary rates through the Cretaceous.
- (3) Does expansion of one clade affect others? Are sister clades affected, and are ecological competitors driven to extinction? This could be assessed by comparing bird evolution with other theropods (sister clades) and with pterosaurs (potential competitors).
- (4) Do successful clades expand equally in all directions, or is the expansion driven by particular sub-clades? Comparisons of enantiornithine and ornithurine bird clades, for example, should show this.
- (5) How did birds respond to the end-Cretaceous mass extinction event? Is there any evidence for lineage sorting or a bottleneck across this catastrophic extinction. How did modern bird clades expand, and how does this second expansion compare with the initial radiation?

Further, such studies that use discrete apomorphic characters, should allow exploration of links between evolution and development. Current molecular developmental studies are exploring the nature of the genomic control of particular morphological attributes (Müller 2007; Wagner

2007; Carroll 2008), and it turns out that particular morphological attributes, including adaptive features of organisms, may depend on a series of genomic switches, some enhancing a phase in development, others silencing a gene. As more and better fossils show paleontologists where particular avian characters appeared and, importantly, the order in geological time in which they appeared, it will be possible to compare those deep-time sequences with sequences of gene action during development to see whether there are any explicable linkages. Such studies may shed light on how, why, and when particular adaptations of birds, or other clades, emerged, and how they are regulated today.

Much of this new work will require a thorough rethinking of terminology and basic assumptions. For example, zoologists have always taught their classes that the cephalopod eye and the vertebrate eye may look startlingly similar, but they are clearly convergent structures because the ancestry of each clade is so ancient, and most cephalopods at least lack such complex eyes. Taken a step further, the camera-like eye of the cephalopod or vertebrate is clearly entirely different from the multiple-unit arthropod eye, and so their structures can barely even be said to be convergent because they are constructed so differently. Startlingly, it now turns out that the vertebrate eye and the arthropod eye share genomic control by the transcription factors *Eyeless* and *PAX6*. The morphologist is left with the conundrum of deciding whether these two such widely different morphologies that share a function are in fact convergences or even homologies. Shubin and colleagues (Shubin *et al.* 2009) have termed these deep homologies, being based on aspects of genomic control that date back to the origin of metazoans.

6. Conclusions

- (1) Perhaps most of modern biodiversity arose through discrete and relatively rapid evolutionary radiations.
- (2) We have a golden opportunity now to combine molecular and paleontological trees, to date them using a combination of fossil distributions and Bayesian methods (Benton

and Donoghue 2007) and to apply numerical methods to investigate the evolution of disparity.

- (3) There should be no more squabbling about whether molecular or paleontological trees are best – indeed, neither method can work without the other. Further, trees without fossils can never be complete, and fossils can be accommodated without compromising the quality of trees and evolutionary studies (disparity studies do not require a complete fossil record).
- (4) Perhaps novelties did not arise instantly, and they may partly precede evolutionary radiations (“preadaptation”). In the case of birds, it took 50 Ma for their tightly coordinated set of unique novelties to evolve.
- (5) Exploring genomic control of novelties has

thrown up real surprises, and more needs to be done to track the role of natural selection and genomic tinkering in forming the link between evolutionary radiations and novelties.

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