Chapter 1

New Perspectives on the Evolution of Late Palaeozoic and Mesozoic Terrestrial Tetrapods

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Abstract Palaeobiology, like all sciences, progresses by a combination of the discovery of new information, in this case fossils, the application of new techniques, and the development of new concepts with which to generate novel kinds of hypotheses. Research in the field of Late Palaeozoic and Mesozoic terrestrial tetrapods has involved major advances in all three of these over the last decade or so. Several new discoveries fill in gaps in the evolution of higher tetrapod taxa such as Tetrapoda, Dicynodontia, and birds, while others add significantly to the understanding of patterns of faunal turnover and palaeo-community structure.

The molecular revolution in biology is having a profound effect on several aspects of palaeobiology, in particular the use of large amounts of sequence data for phylogenetic studies and estimating branching dates. In some cases, notably placental mammals, this has produced results that highlight the limitations of purely morphological evidence in this, and probably other cases, and points to the desirability of seeking other kinds of evidence of relationships. Molecular developmental biology is starting to suggest new evolutionary hypotheses about the molecular genetic basis of the evolutionary transitions that can be inferred from the fossil record, such as how the tetrapod limb arose. In the field of functional analysis of fossils, CT scanning has opened the way to the application of such methods as finite element analysis for studying the mechanical design of fossil tetrapod skulls and skeletons. Geochemistry has also introduced new methods, notably stable isotope analysis, that have a direct bearing on the interpretation of the palaeoenvironmental background of major evolutionary events such as mass extinctions.

The principal new concept in palaeobiology arises from a shift towards the systems view that it is the interactions of the parts of a complex system, rather than the nature of the parts themselves that provide the main key to understanding how the system works. Correlated progression is a model based on this concept which offers a more realistic view of major evolutionary transitions such as the origins of tetrapods, mammals, and potentially all the higher taxa of tetrapods. Earth sciences are also moving more towards a systems way of thinking, such as when seeking explanations for mass extinctions.

1. 1 Introduction

Palaeobiology contributes in principle to evolutionary theory by providing evidence about several phenomena of long-term evolution that are only revealed at all by the fossil record. Any theory about the mechanism of evolution that claims to be comprehensive must be able to account for such geological-timescale events, including: the several million years of stasis that is typical of palaeospecies; the great kaleidoscopic pattern of taxonomic turnover at every level from species and genera to orders and classes; the occasional periods of mass extinction during which anything up to 90% of the Earth's species disappear; and the environmental circumstances surrounding the major morphological transitions represented by the appearance of new higher taxa. The fundamental issue is whether simple extrapolation of mechanisms known to occur at the level of the interbreeding population -- Darwinian natural selection in particular -- provides a sufficient explanation for the long term course of phylogenetic change, or whether rare events or extremely slow processes that are unobservable in field or laboratory are also at work over this timescale. There has been a regrettable failure even to take seriously this possibility on the part of some authors (e.g. Charlesworth 1996; Bell 2000); others however are well aware of the issue (e.g. Gould 1994; Kemp 1999; Grantham 2007).

The fossil record of Late Palaeozoic and Mesozoic terrestrial tetrapods offers some of the most important evidence of all concerning aspects of long term evolutionary patterns. During this time,

several major evolutionary transitions occurred that resulted in new higher taxa, and for which several intermediate grades between the ancestral and the descendant are represented as known fossils. Following the origin of the taxon Tetrapoda itself during the Late Devonian, there duly appeared the lineages leading to such radically new kinds of tetrapods as the amphibians, turtles, mammals, snakes, dinosaurs, and birds. This period of time is also uniquely important for palaeobiogeographical study, because great changes in the continental configurations coincided with the diversification of several of these new tetrapod taxa, which throws light upon the relationship between patterns of phylogeny and patterns of biogeographic vicariance (e.g. Upchurch et al. 2002).

Like all sciences, progress in palaeobiology may be described as occurring on three distinguishable though intimately interrelated fronts. First there is the accumulation of new, empirically derived information resulting from the discovery of new fossils, and new data about their palaeobiogeographical distribution and palaeoecological setting. Second there are new techniques for studying existing material that are capable of generating more detailed, accurate answers to palaeobiological questions than hitherto possible. Third there is the development of new concepts or frameworks for thinking about the fossil record, leading to the generation of novel hypotheses and theories about evolution at this scale.

1. 2 New Fossils

Without doubt, the most spectacular new fossils of the Mesozoic are the tetrapods of the Yixian Formation of China (Zhang 2006). This remarkable locality is dated as Early Cretaceous, probably Hauterivan to Aptian, and according to Zhou et al. (2003), the palaeofauna resulted from a combination of a shallow lacustrine environment and rapid volcanic ashfall. A series of small tetrapods are superbly preserved, often including impressions of pelt or feathers. There are small nonavian theropod dinosaurs, including feathered specimens, and basal birds. Complete mammalian skeletons of several taxa are found including, importantly, the early metatherian *Sinodelphys*

(Luo et al. 2003) and early eutherian *Eomaia* (Ji et al. 2002). These two fossils helpfully place the latest divergence date of the marsupials from the placentals at about 120 million years ago.

However aesthetically pleasing these specimens are, from the perspective of evolutionary theory the most important recent finds of Late Palaeozoic and Mesozoic tetrapods are firstly those that are stem members of lineages leading to major new taxa, and secondly those that significantly expand the known diversity, morphological disparity, and temporo-spatial distribution of ecologically important extinct taxa. Among the many discoveries of the last few years bearing on these questions, the following are particularly illustrative.

1.2.1 Sequence of acquisition of characters: stem tetrapods

Until the early 1990's, almost everything known from the fossil record about the transition from ancestral fish-grade tetrapodamorph to fully limbed tetrapod was based on the comparison of the Late Devonian *Eusthenopteron* as an 'ancestral fish' with *Ichthyostega* as a basal tetrapod (Save-Soderbergh 1932; Jarvik 1980), although a certain amount was also known about the more progressive 'fish' grade form *Panderichthys* (Vorobyeva and Schultze 1991; Boisvert 2005). The next important addition came from the detailed description of *Acanthostega* (Clack 1994; Coates 1996), which is more basal than *Ichthyostega*. Meanwhile, several other Late Devonian tetrapod or near tetrapod genera have been described from much more fragmentary material, such as *Ventastega* from Latvia, *Tulerpeton* from Russia, and *Elginerpeton* from Scotland, as reviewed by Clack (2002).

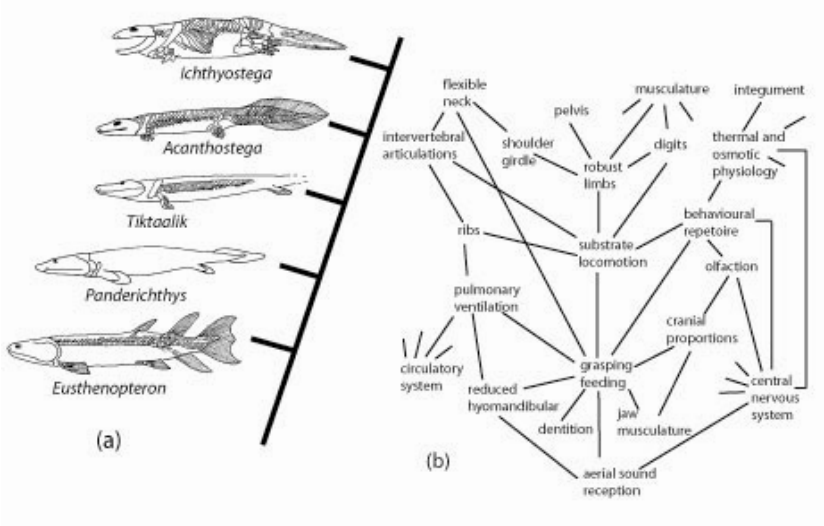

Fig. 1.1 (a) Cladogram of the best known stem tetrapods. (b) Functional and structural integration between the parts of an evolving tetrapod, to show the principle of the correlated progression model of the origin of major new taxa. From Kemp (2007a).

Cladistic analysis of these various forms gave a good deal of information about the sequence of acquisition of tetrapod characters within the hypothetical lineage of ancestors and descendants, but there remained a substantial morphological gap between what were still essentially finned ‘fish’ and digit-bearing tetrapods. Therefore the recent description of *Tiktaalik* (Daeschler et al. 2006; Shubin et al. 2006), which partially spans this gap, adds another highly informative stage in the sequence, refining yet further what can be inferred about the morphological evolution of tetrapods (Fig. 1.1a). Indeed, *Tiktaalik* has been compared with *Archaeopteryx* in the importance of its particular combination of ancestral and derived characters, and therefore in its role of further resolving the sequence of acquisition of tetrapod traits. Any comprehensive account of the origin of tetrapods and their transition from aquatic to terrestrial habitat must necessarily start with this information.

1.2.2 Sequence of acquisition of characters: stem dicynodontian therapsids

The dicynodontian therapsids of the Late Permian were of enormous evolutionary significance because they were the first highly abundant terrestrial, herbivorous, often herd-dwelling tetrapods, a mode of life that was to be pursued successively in the Mesozoic by the ornithischian dinosaurs, and in the Tertiary by the ungulate placentals and diprotodont marsupials. Like these taxa, dicynodontians were also highly diverse, with numerous species showing relatively minor differences in feeding and locomotory structures from one another. Morphologically, dicynodontians were highly modified from the basal therapsid form, and a series of recently described mid-Permian fossils from the South African Karoo and Russia have gone far towards illustrating the manner in which they achieved their specialisation (Fig. 1.2). The most basal of these is *Anomocephalus* (Modesto et al. 1999), which is relatively long-snouted and lacks the extensive re-modelling of the adductor musculature seen in more derived forms. *Patronomodon* (Rubidge and Hopson 1996) has an enlarged temporal fenestra, and depressed jaw articulation region of the skull. *Suminia* (Rybczynski 2000) has taken these trends further, with a dorsally bowed zygomatic arch and a jaw hinge allowing antero-posterior shifts of the lower jaw. *Eodicynodon* (Rubidge 1990), which has been known for some time, is more or less fully dicynodontian in structure, having evolved the characteristic reorganisation of the jaw musculature and lost the anterior teeth apart from a pair of upper tusks.

The importance of this sequence is that it greatly increases the understanding of how, anatomically and functionally, the uniquely novel dicynodontian feeding structures evolved (Reisz and Sues 2000; Kemp 2005).

1.2.3 Sequence of acquisition of characters: other tetrapods

The anatomical and functional evolution of birds is beginning to be better understood as a consequence of a plethora of relevant discove-

ries of feathered dinosaurs, stem-birds and early avians, notably in the Early Cretaceous Jehol fauna (Zhou 2004; Xu and Norrell 2006; Turner et al. 2007: Hu et al. 2009)).

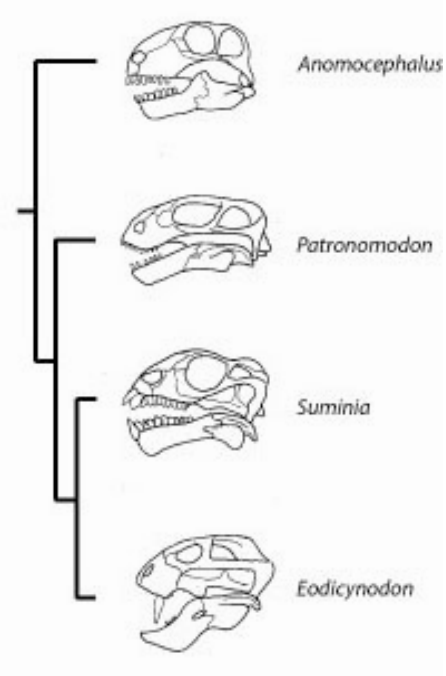

Fig. 1.2 Cladogram of three basal anomodonts and the dicynodontian *Eodicynodon*. Redrawn from Reisz and Sues (2000), Modesto et al. (1999), and Rubidge (1990).

Another major tetrapod taxon for which Mesozoic intermediate stages have recently come to light is the snakes. *Pachyrachis* (Caldwell and Lee 1999), for example, has small but distinct hind limbs, while the more recently discovered *Najash* (Apesteguía and Zaher 2006) has even larger ones, here associated with a pelvis still connected to the sacral vertebrae and apparently capable of a degree of locomotory function. Even more remarkable is *Odontochelys*, a Late Triassic turtle in which the carapace is represented only by expanded ribs and neural plates, evidently an intermediate stage towards the definitive chelonian structure (Li et al. 2008).

1.2.4 Morphological disparity: new kinds of dinosaurs

One of the ways to throw light upon the nature, laws, and potential of morphological structure is to increase the range of known actual morphologies, and from time to time strange new fossil forms perform this purpose. No extinct taxon is more prone to this than the dinosaurs, and descriptions of new, highly aberrant species continue to appear regularly. The 3-4 metre high giant, ostrich-like theropod *Gigantoraptor* (Xu et al. 2007), and *Nigersaurus*, a sauropod with an extraordinary, paper-thin skull and transversely oriented rows of fine teeth (Sereno et al. 2007) are just such surprises. Even more unpredictable, the four-winged, bird-like *Microraptor* from the Yixian has challenged theories on the origin of flight (Padian and Dial 2005; Chatterjee and Templin 2007).

1.2.5 Pattern of ecological replacement: the rise of the dinosaurs

The origin and early diversification of dinosaurs in the Upper Triassic is an area of perennial interest, given the Mesozoic dominance of the group from the Jurassic onwards. Most of the new work on dinosaurs has actually been re-description and exceedingly detailed phylogenetic analysis of existing material (e.g. Rauhut 2003; Butler 2005; Langer and Benton 2006; Upchurch et al. 2007). Additional to this, however, other recent discoveries bear on the more general palaeobiological question concerning the process of replacement of the basal archosaurs and other terrestrial taxa such as rhynchosaurs and cynodonts by Dinosauria during the Late Triassic. It has long been debated whether this was a competitive process in which dinosaur species were in some way competitively superior, or an opportunistic one whereby dinosaurs only diversified after an environmental perturbation had caused the extinction of the other groups (Benton 1996; Kemp 1999). Testing between these two models is not easy, and depends on an estimate of the exact temporal relationship between the decline of the old and the increase of the new taxa, and whether the event was accompanied by palaeoecological signals of an ecological perturbation that could feasibly account for an initial

extinction event. The evidence from the time course of the replacement has tended to support the opportunistic model, in which an extinction event at the close of the Carnian saw the end of the hitherto dominant non-dinosaur herbivore groups, while dinosaurs did not radiate extensively until the succeeding Norian (Benton 1994). However, this interpretation is disturbed by the recent discovery of North American Upper Triassic representatives of several taxa of basal dinosauriforms that were previously known only from the Middle Triassic (Irmis et al. 2007). This evidence for a significant overlap between these basal groups and the dinosaurs indicates that a much longer, more gradual process was involved, suggesting that a form of competitiveness played a greater role. One attractive possibility is that it was a case of "incumbent replacement", lasting throughout the Upper Triassic, in which the rate of taxon replacement was controlled by the rate of background extinction of individual species of the pre-existing community, rather than by direct species to species competition (Rosenzweig and McCord 1991). Other recently described fossil evidence from both North America (Lucas and Tanner 2006) and India (Bandyopadhyay and Sengupta 2006) indicates that the replacement was completed by about the close of the Norian.

1.2.6 Ecological potential: the disparity of Mesozoic mammals

The mammals of the Jurassic and Cretaceous (Kielan-Jaworowska et al. 2004) have always been believed to be an ecologically conservative taxon of small, insectivorous and omnivorous animals, analogous in habits to the modern insectivores, rodents, and small opossums of the modern world, but vastly less diverse and abundant. However, in the last few years a most surprising range of adaptive types has been described. With an estimated body weight of 13 kg and a presacral length of 700mm, *Repenomamus giganticus* (Hu et al. 2005) was considerably larger than was thought possible for Mesozoic mammals, and indeed shows evidence of having fed on young dinosaurs. *Fruitafossor* (Luo and Wible 2005) is adapted for a fossorial existence with powerful, mole-like limbs. *Castorocauda* (Ji

et al. 2006) pursued a beaver-like aquatic life, and *Volticotherium* (Meng et al. 2006) was a gliding mammal. It is thus becoming clear that most of the range of habitats occupied by modern small mammals also occurred in the archaic Mesozoic groups, and that during this Era small mammals had a far more significant ecological role in the terrestrial community than hitherto supposed (Jin et al. 2006).

1.3 New Techniques

1.3.1 The molecular revolution: phylogenetic reconstruction

No area of biology has been left untouched by the last decade's avalanche of data resulting from the development of routine sequencing of nucleic acids. For phylogenetic studies, the sheer amount of information contained in DNA, the objectivity of defining a unit character as a single nucleotide, and the availability of ever-more sophisticated statistical methods for analysing it lead to far more resolved and precisely dated phylogenetic branching points than morphology has proved capable of revealing. Of course molecular systematics applies directly only to recent organisms, but it can have an indirect effect on the phylogenetic analysis of the extinct members of modern taxa whose stem-groups and early divergencies are represented in the fossil record. Moreover, molecular techniques necessarily have an effect on the confidence that can be placed on phylogenies of taxa that are entirely fossil. In several cases, such as the interrelationships of placental mammals and modern birds, the molecular evidence has shown that morphology alone is incapable of recapturing the phylogeny. By analogy, this should greatly increase our scepticism about the reliability of the morphological-based phylogenies of certain entirely fossil groups where the morphological support is not great.

The rise to dominance of molecular over morphological data for phylogenetic reconstruction and its effect on interpretation of the Mesozoic tetrapod fossil record is illustrated most comprehensively

by the case of the placental mammals. The earliest member of the Eutheria, which includes the stem-group plus the crown-group placentals, is *Eomaia* (Ji et al. 2002). It is probably Barremian in age, around 125Ma, and occurs in the Yixian Formation of China, so is Laurasian in distribution. A considerable variety of taxa of eutherians are known from the Aptian-Albian and onwards into the Late Cretaceous, most abundantly in Asia and North America but also including a small number in Africa and India. However, no undisputed member of any of the modern placental orders (crown placentals) has been described prior to the Cretaceous-Tertiary boundary, and almost all make their appearance in the fossil record in a window of time between about 65Ma and 55Ma, from Early Palaeocene to Early Eocene. Concerning the interrelationships between the placental orders, morphological analysis generated relatively few supraordinal groups (Fig. 1.3), and even the monophyletic status of these was always subject to dispute (e.g. Novacek et al. 1988; McKenna and Bell 1997; Rose 2006). Otherwise, the phylogeny was dominated by a large, unresolved polytomy of up to ten lineages.

From the late 1990's onwards, rapidly accumulating molecular sequence data has resulted in a totally unpredicted, radical modification to the morphological-based view of placental interrelationships (Springer et al. 2003; 2005). Most of the morphological-based monophyletic groups have been either rejected outright, or had their membership altered, whilst the central polytomy has been fully resolved (Fig. 1.3). Beyond all reasonable doubt, the placental orders fall into the now familiar four superorders Afrotheria, Xenarthra, and the boreotherian sister groups Laurasiatheria and Euarchontoglires. Equally unpredicted, the estimated dates of most of the ordinal divergences based on the molecular evidence and using a variety of clock-like and relaxed clock-like models (Fig. 1.4), have been pushed back into the Cretaceous, some by a mere 10Ma or so, others much farther (Springer et al. 2003; Springer et al. 2005; Bininda-Emonds et al. 2007).

The immediate response to the new phylogeny by a number of palaeobiologists was, predictably enough, that the molecular evidence must be incorrect, and particularly as regards the new estimates of the divergence dates. However, given the volume of data now supporting it, the molecular-based phylogeny itself is by far the

best supported hypothesis of relationships: mammalian palaeobiologists now have the exciting task of reinterpreting the anatomical evolution as inferred from the new cladogram, including seeking morphological characters that are congruent with the molecular-based groupings (Asher et al. 2003), and elucidating the historical biogeography of placental mammals (Archibald 2003; Kemp 2005; Hunter and Janis 2006)

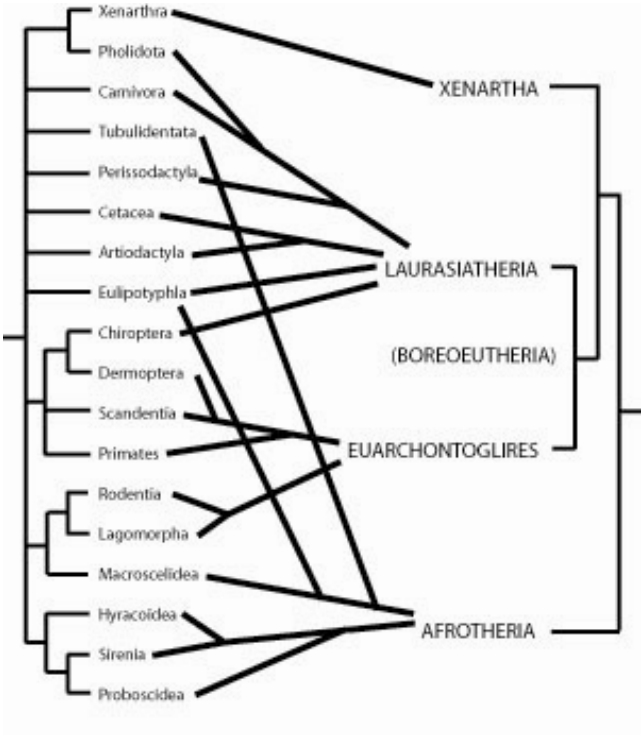

Fig. 1.3 A comparison of Novecek et al.'s (1988) morphological based interrelationships of placental mammalian orders (left), with Springer et al's (2003; 2005) molecular-based phylogeny (right), showing how radical a modification the molecular data caused.

More problematic, and therefore more challenging is the matter of the divergence dates. If the molecular-based dates are anything like correct, then why are no placental orders represented prior to the end of the Cretaceous? But if the fossil-based divergence dates are more accurate, then the rate of molecular evolution must be variable

to an as yet inexplicable extent. It is always possible that crown placentals were too rare to have been discovered as fossils, or that they were diversifying in a region of the world not represented by Late Cretaceous continental sediments, such as part of Gondwana, but there are good statistical arguments against these explanations (Foote et al. 1999; Donaghue and Benton 2007). A more interesting possible explanation is the “Long Fuse” hypothesis that crown placentals were in fact present in the Late Cretaceous and are indeed represented by known fossils, but that so

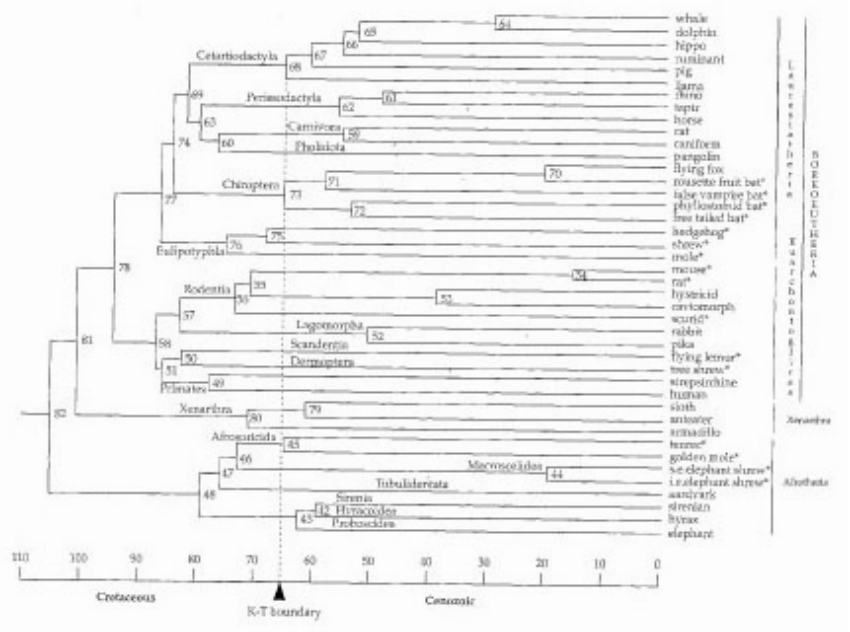

Fig. 1.4 Molecular-based estimates of dates of divergence of placental superorders and orders (redrawn from Murphy and Eizirik 2009).

little morphological divergence had occurred that their affinities are difficult to recognise. At least three possible Cretaceous crown placentals have been suggested: zalambdalestids as members of Glires (rodents plus lagomorphs), zhelestids as assorted ungulate orders, and palaeoryctids as members of the Carnivora and Creodonta (Archibald et al. 2001). If the long-fuse hypothesis is true, then it raises the challenging question of why the original lineage splitting was separated from major morphological evolution. Perhaps rapid

diversification at a low taxonomic level in the Late Cretaceous was associated with a new ecological opportunity to divide the small, nocturnal insectivore/omnivore habitat into many niches occupied by a series of relatively similar, dentally progressive mammals. The much more rapid and extensive evolution of the characters diagnostic of the living members of the lineages must have been triggered later by a substantially larger environmental perturbation which created radically new ecological opportunities for mammals immediately after the end of the Cretaceous.

The case of the placental mammals is important because it raises the questions of why the morphology failed adequately to reveal their phylogenetic interrelationships, why the fossil record fails to correspond to the molecular-based estimates of the dates of divergence, and what is the relationship between the supraordinal groupings and the historical geology of the continental masses, which latter is actually a more accurate predictor of the main superorders than is morphology.

However, its importance extends further because the lessons to be learned from the molecular taxonomy of placental mammals can be applied by analogy to fossil taxa that lack living members. Where the cladogram of such a taxon is based on a level of morphological support that is no greater than that for the old, discredited placental mammal cladogram, then its accuracy must be in doubt. The response to such a suggestion may be that, in the absence of molecular data, the best supported morphological cladogram is the best hypothesis possible, however weak that support may be, and that there is no way of improving on it. There are, though, other possible sources of phylogenetically relevant information that have not always been as extensively explored as they deserve. One is palaeobiogeography, which relates branching points in the phylogeny to vicariant or dispersal events that can sometimes be correlated with tectonic movements of land masses, or opening up of potential dispersal routes, as revealed by the geological record (e.g. Upchurch et al. 2002). Another potentially independent source of phylogenetic information is functional analysis. A given cladogram implies a particular sequence of transformation of characters between the nodes, which themselves can be taken to represent the sequence of hypothetical ancestors and descendants. In so far as each such hypotheti-

cal ancestor had to be a fully integrated, functionally coherent phenotype, then one cladogram may be judged better than another because it implies a functionally more plausible sequence of evolutionary transitions (Kemp 1988). To give an example, different authors have produced very different phylogenies of the therapsids of the Late Permian. Focussing on the Anomodontia that were mentioned earlier, this therapsid taxon has been claimed to be the sister group of, respectively, Dinocephalia, Therocephalia, Eutheriodontia (Therocephalia+Cynodontia), and Theriodontia (Gorgonopsia+Eutheriodontia) (Kemp 2009). In every case, the proposed synapomorphies supporting the respective relationship are few and mostly trivial or poorly defined. However, if the sequence of increasingly derived basal members of the Dicynodontia (Fig. 1.2) are interpreted functionally in terms of increasingly modified adaptations of the skull, dentition and jaw musculature for dealing with a herbivorous diet, then the most plausible hypothetical ancestral structure resembles a generalised primitive therapsid that possessed none of the derived characters of any of those other therapsid taxa (Kemp 2005, pages 79-80). Therefore the functional analysis resolves the phylogenetic position of Anomodontia as a basal therapsid divergence, unrelated to any of the other groups.

1.3.2 The molecular revolution: molecular developmental genetics

It has long been a hope of evolutionary biologists that the molecular genetic basis underlying phenotypic evolutionary change will eventually be understood in enough detail to complete the connection between genetics and evolution that began with the synthetic theory. The still very young discipline of evolutionary developmental genetics, “EvoDevo”, is explicitly concerned with the causal relationship between what the fossil record and comparative morphology show to have been the course of phenotypic change and what molecular genetics shows to have been the molecular basis for it. One of the most intensively studied cases is the origin of tetrapod limb, which is particularly promising because of the combination of fossil evidence about its evolution with its role over many decades as a model sys-

tem for embryology, traditional and latterly molecular (Hall 2007). The broad features of the morphological transition from fish fin to tetrapod limb are illustrated by the sequence of Upper Devonian fossils from *Eusthenopteron* to *Ichthyostega* mentioned earlier (Shubin et al. 2006; Coates and Ruta 2007). Meanwhile, techniques for demonstrating the timing and regions of gene expression in both normal and mutant individuals, to date mainly of mice, chick and zebrafish, are beginning to unravel the molecular basis of the development (Tanaka and Tickle 2007). Exciting as the prospect is, however, there is a very long way to go before there are comprehensive hypotheses about how mutations in particular genes caused particular aspects of the transition from fin to limb. A bewilderingly large number of genes and gene products have been shown to act in the overall development of the vertebrate paired appendages (e.g. Arias and Stewart 2002; Tanaka and Tickle 2007). At present there is little agreement even on the fundamental question of whether the tetrapod autopodium (hand and foot) evolved by modification of pre-existing structures in the fish fin, or is neomorphic (Wagner and Larsson 2007). It is possible only very tentatively to suggest certain steps that might have occurred in the sequence of genetic evolution, based on simple comparisons between modern fish and tetrapods. Wagner and Larsson (2007), for example, have recently proposed that a general autopodial developmental module evolved as a consequence of the separation of the domains of expression of two homeobox genes, Hoxa 11 and Hoxa 13. Subsequent evolution of digits within this new autopodial field was related to the acquisition of new functions by HoxD genes (e.g. Kmita et al. 2002). At some point the genes known to be involved in the identity of specific digits, such as the Shh (sonic hedgehog) and Gli3, were recruited into the system.

A second potentially illuminating example concerning late Palaeozoic and Mesozoic tetrapods is that of the synapsid jaw. Depew and his colleagues (Depew et al. 2005; Depew and Simpson 2006) have studied the expression of genes involved in patterning of the mandibular arch, and the effects of their mutations in mutant mice. In attempting to account for different proportions of the elements of the mandibular arch amongst vertebrates, and the maintenance of functional integration between maxillary and mandibular compo-

nents, they propose a “hinge and caps” model. The hinge region is presumed to be the first source of positional information for the developing mandibular arch, and integration of signals from the hinge and from their own respective attachments leads to the correct registration of upper and lower jaws. As in the limb, a very large number of genes are expressed during mandibular development, and presumably variations in the timing, position and strength of their expressions is responsible for variation in the morphology amongst different vertebrates. In the case of mammals, reduction of the posterior component of the maxillary and mandibular elements as the hinge bones gradually reduced and eventually converted into ear ossicles is assumed to have been one such outcome. The hope is that eventually it will be possible to hypothesise just what sequence of genetic mutations caused this condition, but again evolutionary developmental biology is a long way off this goal.

Indeed, given the complexity of the network of integrated gene activity involved in these examples, it is not even certain that the information available from the fossil record will ever have the resolution to test hypotheses about the genetic basis of evolutionary transition. Undoubtedly however, there is a great deal yet to be learned about the relationship between genotype and phenotype that will bear on the question.

1.3.3 Computed tomography and finite element analysis

A serendipitous consequence of the widespread introduction of CT scanning in medicine has been the availability of equipment for scanning fossil material. With varying degrees of resolution, a fossil can effectively be non-invasively sectioned, visually reconstructed in three dimensions, and the reconstruction can even be corrected for post-mortem damage and distortion. As use of the technique spreads, a rapid increase in anatomical knowledge can be expected, complete with computerised descriptions and atomisation into characters for multivariate and phylogenetic analysis.

CT scanning also lends itself to the application of engineering techniques for analysing mechanical structure. Finite element analy-

sis (FEA) is a computational method for visualising the patterns of stress and strain in a structure that is subjected to a regime of applied forces. It is beginning to be used in palaeobiology to investigate the stresses generated within skeletal elements by the estimated forces of the reconstructed muscles. It is then possible to relate the biological design of the anatomical structure to its mechanical function as a transmission system for the stresses generated by feeding, locomotion etc. Rayfield et al. (2001) applied the method to the jaw mechanics of the large theropod dinosaur *Allosaurus*. By revealing the pattern of stresses within the reconstructed cranium induced by the action of inferred jaw muscles during biting, they could demonstrate the relationship between aspects of the skull design and the force pattern. For example, they showed that the large antorbital fenestrae in the skull do not weaken it significantly, because the bars of bone surrounding them act as compressive struts, effectively distributing the stress between the maxillae and the robust skull roof. In a later study, Rayfield (2005) compared the skull mechanics of three different theropods, *Coelophysis*, *Allosaurus* and *Tyrannosuarus*, and showed that aspects of the morphological differences between them correlate with differences in the stress patterns. In the first two forms, the fronto-parietal region of the skull roof is strongly built and it is in this region that the compressive and shear stresses peak. In contrast, the nasal region of *Tyrannosaurus* receives the highest stresses, and here it is this part that is the more robust region. Presumably the differences reflect different diets and modes of jaw use during feeding. As with all phenotypic differences, these may be mapped onto a phylogeny of the theropods in order to generate hypotheses of the functional significance of the inferred evolutionary divergencies in cranial anatomy (Barrett and Rayfield 2006).

There are other aspects of tetrapod evolution that are amenable to FEA analysis, though always bearing in mind Alexander's (2006) caution about the extent of the uncertainty about the anatomy and properties of the soft tissue components in fossil vertebrates. By applying the assumed locomotory muscle forces to a 3D reconstruction of the limb of a tetrapod that is placed in a variety of possible orientations relative to the ground, it will be possible to discover which posture and gait minimises the stresses generated in the bones, with the implication that these reflect the animal's normal mode of loco-

motion in life. Again, as with dinosaur cranial mechanics, the technique will illuminate the functional significance of transitions to radically new modes of locomotion, for example the origin the bipedality of dinosaurs (Hutchinson 2004), parasagittal gait of mammals (Kemp 1978), and the flight of birds (Garner et al. 1999; Clarke et al. 2006) and pterosaurs (Wilkinson 2007).

Another example is the application of FEA by Srivastava et al. (2005) to dinosaur eggshells, where comparison with birds' eggs suggests that thin-shelled species such as *Megaloolithus, jabalpurensis*, were adapted for more arid conditions. They were able to relate the magnitude of the stresses on the egg shell to its microstructure in different species. Those with thinner shells experience higher stresses, as would be expected, but thinness is also correlated with the presence of additional subspherolith elements in the structure, which compensates by increasing the strength.

1.3.4 New techniques for analysing the geochemical record

Methods for measuring extremely small quantities of rare stable isotopes and trace elements have revolutionised the study of the palaeoenvironmental setting of fossils, and the search for the causes of the great events in the history of the Earth's biota. Of no part of the fossil record is this more true than that of the Late Palaeozoic and Mesozoic, during which the evolution and diversification of tetrapods was intimately tied up with four of the "big five" mass extinction events of the Phanerozoic. The Late Devonian crisis occurred around the time that the tetrapods originated, while the Mesozoic itself is, of course, bounded by the end-Permian and end-Cretaceous events that so affected tetrapod history. In between these two, the late Triassic event occurred around the time of the extinction of several archosaur, synapsid, and rhynchosaur taxa, the origin of the mammals, and the beginning of the great dinosaur radiation.

In particular, the last couple of decades have witnessed the development of techniques for estimating several potentially critical environmental parameters, such as palaeotemperatures on the basis of O_2 isotope ratios. There are a number of methods for estimating

atmospheric CO_2 levels, including boron and carbon isotopes, and calculated volumes of buried organic carbon in palaeosols (Royer et al. 2004), and this also gives an indirect guide to palaeotemperatures on the basis of the greenhouse effect. The atmospheric O_2 level can be measured by the extent of sulphur bacterial and therefore anaerobic activity determined from sulphur isotopes, among other methods (Berner et al. 2000). The severity of continental weathering and therefore aspects of the climate are indicated by measures of strontium isotopes. Biologically, photosynthesising organisms preferentially fix ^{13}C over ^{12}C, so the proportions of these isotopes in fossil marine shells give an indirect measure of the primary productivity. The ratio of these isotopes also differs in different kinds of plants, and therefore analysing the enamel of teeth can give a clue to the diet of herbivorous tetrapods.

As an example of the way in which this more detailed palaeoenvironmental evidence may help account for significant evolutionary events, Kemp (2006) considered the conditions of the mid-Permian, the time when the basal "pelycosaur-grade" synapsids were replaced by the more progressive early therapsids. There is no evidence for a major environmental perturbation such as a mass extinction event, but the geochemical indicators do reveal a period in which the temperature had been gradually rising from the level during the Permo-Carboniferous glaciation to about 3^oC higher than today. The estimated O_2 level, though declining, was still 27% above modern levels, and the CO_2 level had risen to about three times the present-day value. He proposed a model in which the origin of the therapsids, a taxon whose morphology indicates substantially higher metabolic rates and activity levels than "pelycosaurs", was correlated with the higher oxygen availability. This higher energy budget was itself associated with the evolution of physiological regulatory mechanisms that adapted therapsids for maintaining their activity throughout the increased seasonality brought on by the rising global temperature.

1.4 New Concepts

New information, whether from discovering new fossils or from applying new methods to existing material, leads to more detailed answers to the questions about long-term patterns and processes of evolutionary change and the environmental conditions under which they occurred. This continual process of development is occasionally accompanied by the spread of a radical new concept, or way of thinking about the major evolutionary events that are illustrated by the fossil record. For the last half a century, most of the palaeobiological interpretation of fossils and its associated stratigraphic information has been dependent on a pair of simplifying concepts. The first is in a general sense atomism (Rieppel 2001), where it is assumed that an organism consists of many discrete, more or less mutually independent characters. This assumption was found to be necessary for tractable phylogenetic analysis, and remains as important for modern computerised cladistic methodology as it ever was for traditional, non-mathematical systematic methods. Furthermore, it allows evolutionary change to be described and accounted for solely in terms of morphological shifts in discrete, identifiable traits.

The second simplifying concept is reductionism, in which it is assumed that evolutionary changes, even major morphological transitions, are caused by a simple, potentially identifiable natural selection force acting on the lineage of successive phenotypes. This is the widely accepted and rarely disputed view that the major evolutionary events of macroevolution are caused by no more than extrapolation of population level processes of microevolution acting for long enough. Therefore all that is required to account for a particular evolutionary transformation is that the one single dimension of the environment guiding the direction of the evolutionary change be identified.

Comparable atomistic and reductionist concepts have also been applied to much of the study of the palaeoecological background to major evolutionary events, such as mass extinctions and explosive radiations, and the rise of radically new kinds of community. It is usually assumed that in effect the environment consists of more or less independent parameters, and that a perturbation of one of these

alone can be the cause of some great event. As far as palaeocommunity structure and dynamics are concerned, the reductionist assumption allows the processes known from studies of modern ecology, such as interspecific competition, population regulation mechanisms by predator-prey interactions, etc, can be offered as the sole cause of even those major changes that are only revealed on the geological time scale.

Of course, from Aristotle through Goethe onwards there has never been a shortage of critics of the simplification inherent in these twin concepts, and in more recent years they have been represented by the writings of, for example, Dullemeijer (1974; 1980), Riedl (1977; 1978), and Gould (2002). Nor has there been an absence of apologists for atomism and reductionism pointing out, quite reasonably, that however much atomism and reductionism may simplify the real world, they do actually provide a framework for testable hyopotheses – they work. More complex "scenarios" are claimed to be effectively untestable, because a model based on a more realistically large number of variables rapidly descends into chaotic behaviour, and therefore explains nothing.

The conceptual shift that is presently spreading into palaeobiology is actually yet another consequence of the molecular revolution in biology, namely what has come to be termed 'systems biology' (Kirschner 2005; Konopka 2007). Once it became clear to molecular biologists that cellular control mechanisms, and genetic developmental modules consist of confusingly large numbers of different interacting molecules, it was obvious that neither the atomistic assumption that each molecular species can be treated as an independent entity, nor the reductionist assumption that the action of each different molecule can be predicted from its structure alone could explain these cellular-level processes. Rather, it is the nature of the interactions between the many different molecules that determine the properties of the integrated system as a whole. For a long time engineers have used a systems approach to such things as control mechanisms for highly complex machinery, and molecular biology is adopting the same general methods (Ceste and Doyle 2002). Such interactive phenomena within networks as signalling, feedback, inhibition, synergy, parallel pathways, and so on are more use-

ful for explaining the properties of a system than merely describing the nature of the interacting entities themselves.

The current shift in the direction of a systems approach to palaeobiology may be illustrated by two different areas of investigation.

1.4.1 The origin of major new taxa: correlated progression

One of the ultimate quests of evolutionary biology is surely elucidation of the mechanism by which an evolving lineage undergoes the kind of long trek through morphospace that involves large changes in numerous traits, and that therefore culminates in a radically new kind of organism – a new higher taxon. It is therefore surprising how little attention has been paid to this problem by the evolutionary biology community at large. As explained, the inhibition is primarily due to the atomistic and reductionist concepts. These underwrite a model of evolution in which even the most extensive of evolutionary change is due to 'normal', that is to say microevolution, driven by natural selection acting on one, or at most perhaps two or three characters at a time within an interbreeding population. Corollaries of this model include the concept of key innovation – the idea that an evolutionary modification of some particular "key" character on its own opens up a new adaptive zone, and the familiar idea of preadaptation – which again attributes special significance to certain specified characters. From the environmental perspective, the model assumes that there was a relatively very simple selective force involved, such as for a new food source, a more effective means of escaping predators by increasing running speed, or whatever.

Such a simple view of how lineages and their characters undergo large evolutionary transformation is manifestly unrealistic. The phenotypic characters of an organism are certainly not independent of one another, but are structurally and functionally inter-dependent parts of a highly integrated system. Nor does natural selection actually act on individual characters, but on organisms as a whole, for fitness is a property of an organism that results from the integrated action of all its traits. At times it may appear that the available varia-

tion of some particular character has a more critical effect on an organism's fitness than the variation in others. However, the actual fitness of an individual bearing such a favourable character still depends on the integrated relationship of this character to many other characters within the organism.

An alternative model (Fig. 1.5) that is much more realistic can be derived from the concept of correlated progression (Thomson 1966; Kemp 2007a; 2007b). The main assumption is that all the traits are functionally interlinked in such a fashion that the phenotype acts as an integrated system, but that there is a sufficient degree of flexibility in the functional and structural connections between traits that any one of them can change to a small extent, without losing its integration within the phenotype as a whole. No further change in that trait is presumed possible unless and until appropriate, comparably small changes have occurred in all the other traits to which it is functionally connected: in this way the integration of the phenotype is maintained as the lineage traverses even very long distances through morphospace.

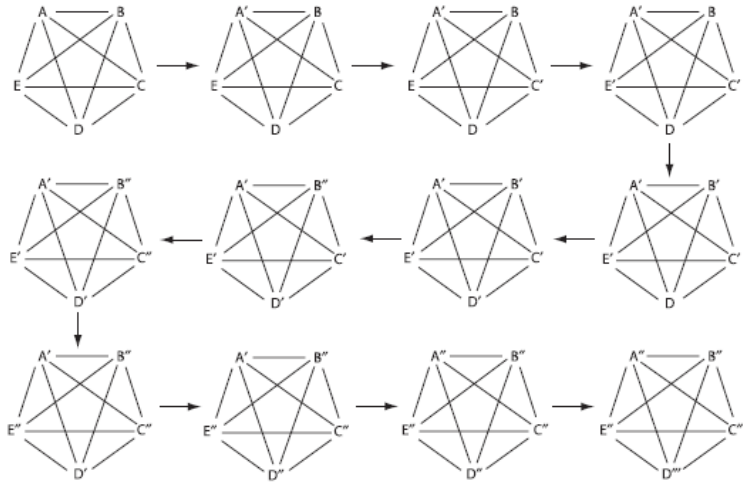

Fig. 1.5 The correlated progression model, illustrated by a five-trait phenotype in which all the traits are functionally interlinked. No more than a small incremental change in any one trait, such as. A' to A'', is possible unless and until correlated small changes in the others have occurred. (From Kemp 2007b).

The model also has implications for the nature of the selection force driving long term evolutionary change, which is assumed to act on the phenotype as a whole, and not on individual, atomised traits. Therefore, over significant evolutionary time, the selection force must be regarded as a complex of many ecological parameters: indeed, in principle all the parameters that affect the organism's life. In consequence, a long-term evolutionary trend from an ancestral to a highly derived phenotype results from the evolving lineage tracking a very general ecological gradient, rather than as a response to any single identifiable aspect of it. In essence, the correlated progression model is a systems approach, because it is based on the nature of the integrated interactions between the parts of the organism, rather than on the nature of the individual parts as such.

The correlated progression model is particularly appropriate in the context of interpreting the evolution of Late Palaeozoic and Mesozoic tetrapods, for it is here that a fossil record implying sequences of acquisition of traits can be combined with a detailed interpretation of the functional significance of those traits, and how they are integrated in the whole organism. The model has been applied in some detail to the synapsid fossil record and the origin of mammals (Kemp 1985, 2005, 2007b), and in outline to the origin of tetrapods in the light of the new evidence about the sequence of acquisition of tetrapod characters (Fig. 1.1), and to turtles in the light of their extremely modified morphology (Kemp 2007a). Time is ripe for an explicit application of the correlated progression model to the origin of those other Mesozoic tetrapod higher taxa for which there is a growing fossil record of intermediate grades, such as dinosaurs, birds, and snakes.

1.4.2 The causes of mass extinctions: Earth Systems Science

Mass extinctions are one of the most important discoveries that palaeontogists have ever made, and solving the problem of what causes them is fundamental to earth science. It is also fundamental to evolutionary biology because of the dramatic effect these crises had on the course of the history of life on Earth. Most of the past literature on

the subject has been predicated upon a belief that mass extinctions are caused by a relatively simple, single change in the environment, one that required little imagination to see how it would devastate a wide swathe of different kinds of organisms. For example, different authors have attributed the end-Permian mass extinction event to, respectively, nutrient collapse, a bolide impact, high CO_2 level and a greenhouse effect, anoxia, volcanism, methane extrusion, and hydrogen sulphide (Bambach 2006). However, such single-trigger models, even allowing for a cascade of subsequent effects, fail to account adequately for all the geochemical and geophysical signals associated with the event. Certainly there is some supporting evidence for each of these proposed causes (Hallam and Wignall 1997; Erwin and Jin 2002; Benton 2003; Bambach 2006; Twitchett 2006). Reduced primary productivity is indicated by carbon isotope ratios; massive volcanism by the formation of the Siberian Traps; a bolide impact by the geochemistry of deposits in Meishan, China; anoxia by shifts in stable isotope ratios of carbon and sulphur, and also black shale deposits; temperature increase by a shift in oxygen isotope ratios and the nature of preserved terrestrial palaeosols; high methane levels by the magnitude of the carbon isotope ratio shift; a rise in CO_2 by various of these signals. In addition to these, there is stratigraphic evidence for a major regression of the sea, followed by a rapid transgression, and for active tectonic events as Pangaea was commencing its break up. Because of the low temporal resolution of the stratigraphic record, and the globally dispersed occurrence of strata, there is also a highly incomplete biological picture of the time-course of mass-extinctions (Bambach 2006). From start to completion of the end-Permian event may have taken anywhere between the order of 10^{-2} years (*i.e.* days) to 10^{6} years and may have been a single catastrophic, a gradual, or a stepped process, and yet still appear in fossil record to have been an instantaneous event. Whether all the geochemical, stratigraphic, and biotic signals are contemporaneous or sequential is not even determinable.

The second major mass extinction associated with the Mesozoic occurred in the Late Triassic. It is associated with a comparable plethora of abiotic signals, and is therefore as shrouded in mystery as to its timing, course, and cause as is the end-Permian event (Tanner et al. 2004).

The observation that all mass extinctions are accompanied by a considerable variety of different signals, and that no two mass extinction events are ever associated with exactly the same combination of such signals is not of course new. A number of authors have proposed flow-diagrams for particular cases to illustrate possible interrelationships between the different environmental perturbations, and how these might have affected the biota. However, these have all tended to be based on the assumption that there was a potentially identifiable, single trigger that led, directly or indirectly, to a cascade of secondary effects. For the end-Permian event, Hallam and Wignall (1997) and Wignall (2001) suggested that the trigger was the gaseous content of the volcanic output associated with the formation of the Siberian traps, and that this had a series of consequences (Fig. 1.6). This model certainly can account for a number of the abiotic signals, but it is not at all clear whether all of them, including those indicating sea level change, tectonic activity, or a possible bolide impact are coincidental or causally related.

The traditional twin concepts of reductionism and atomism, shown to be inadequate in the context of macroevolution, are similarly under challenge here. The reductionist view that the causes of extinction of species in ecological time can simply be extrapolated to geological time is difficult to sustain. Bambach (2006, quoting a personal communication from J. Payne and W. Fischer) pointed out that for a species whose population size was of the order of 10^{15}, if the death rate differed from the birth rate by only 0.1%, then the species would be extinct within 30,000 generations. For a typical fossil species, or a very large number of such species simultaneously, the extinction would appear instantaneous, because this time course is so far below the temporal resolution of the vast proportion of the fossil record. For a typical fossil species, or a very large number of such species simultaneously, the extinction would appear instantaneous, because this time course is so far below the temporal resolution of the vast proportion of the fossil record. Yet a differential of such small magnitude would be impossible to detect even in a modern ecological setting. If the actual time course for the extinction event was, say, 100,000 years or more, which would still appear instantaneous, then the death rate to birth rate differential would be so minute that it is difficult to imagine an environmental perturbation

that was actually small enough to be the determinate cause. In this light, the complex perturbations demonstrable during mass extinctions would seem to be vastly greater in magnitude than necessary.

The atomistic approach to the causes of mass extinction assumes that the parameters of the palaeoenvironment – temperature, levels of the different atmospheric gases, sea level, and so on - can be treated as discrete elements, as also can the various elements of the biota. Yet realistically, the various environmental and biotic elements must always have been interacting as a complex, integrated system. In this context therefore, study of large scale patterns of diversity changes such as mass extinctions is ripe for a systems approach, in which it is assumed to be the nature of the interactions between several palaeoenvironmental factors that determines the effect on the biota. The cause of a mass extinction need not be a discrete, identifiable trigger like volcanic activity, causing a cascade of secondary events such as changes in CO_2 level, temperature, and degree of anoxia. Rather, it might be more fruitful if a mass extinction was assumed to result from the interactions amongst several coincidental environmental perturbations, elucidation of which is a problem for systems analysis.

So far rather little thought has been given to this conceptual shift that parallels the shift towards systems thinking in macroevolution. James Lovelock's variously celebrated and reviled "Gaia Hypothesis" (Lovelock 1979; 2000) is essentially a systems approach to the Earth and its biota, and Lawton (2001) has defined the general field of what he terms 'Earth System Science'. More recently Wilkinson (2003; 2006) has discussed and applied such systems concepts as feedbacks, autocatalysis, hierarchical levels, and emergence of new properties, in a novel interpretation of the earth's biosystem. As this way of thinking spreads, it may be predicted that within the next couple of decades understanding of the relationship between evolutionary patterns and environment over geological time will become far greater. It is likely that there are long-term, and extremely infrequent ecological processes that apply only on a geological timescale, and that cannot be discovered from ecological time-scale study alone. It is only in this light that such events as mass extinctions and major episodes of evolutionary radiation may eventually be understood.

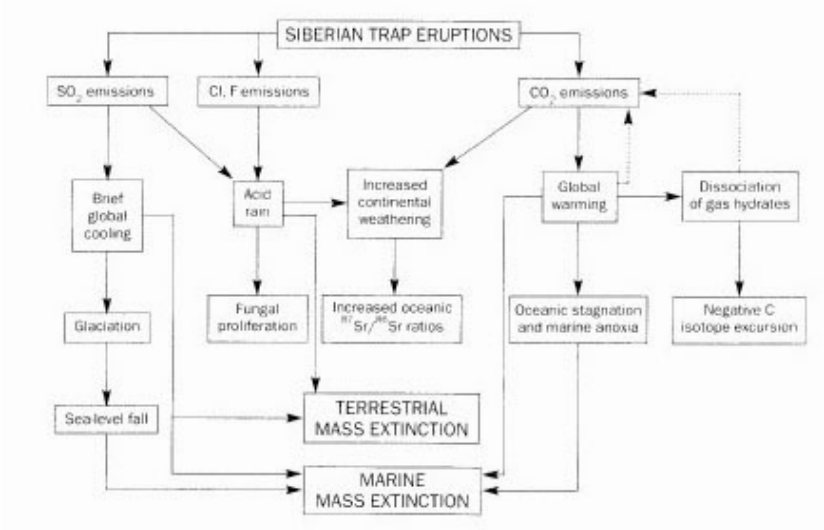

Fig. 1.6 Wignall's proposed scheme of the interrelationships of the abiotic factors associated with the end-Permian mass extinction. (reproduced from Benton 2003).

1.5 Conclusion

The most radical new perspectives on the evolution of Late Palaeozoic and Mesozoic terrestrial tetrapods are indirectly due to the revolution in molecular biology, in which very large amounts of DNA of many modern species has been sequenced, alongside the development of powerful computer programmes and sophisticated statistical methods for its interpretation. This has thrown a great deal of new light on the evolutionary patterns and processes of living organisms, insights that can increasingly be applied by analogy to fossil organisms. Highly robust molecular-based phylogenies of taxa like birds and mammals, whose early branchings were closely spaced morphologically, have exposed the very limited extent to which morphological characters reliably reveal relationships in such cases. In turn, this is generating caution about accepting the accuracy of the purely morphological-based phylogenies of comparable extinct taxa, such as therapsids and dinosaur subgroups, and correspondingly more at-

tention must be paid to potentially corroborating biogeographical and functional evidence of relationships.

Increasing understanding of the relationship at the molecular level between genes, developmental processes, and phenotyopic structure is leading to a greater understanding of how gene mutations in known regulatory gene families might have caused particular morphological transitions that are inferred from the fossil record of stem tetrapods, mammals and other higher taxa. This aspect of molecular biology has as yet generated much less in the way of firm palaeobiological results than the systematics aspect, but promises eventually to be at least as profound.

The third new perspective also owes its origin to the molecular biology revolution, though even more indirectly. Systems biology is being developed for analysing and understanding how complex, dynamic molecular systems work. A comparable systems approach can be applied to large scale phenotypic evolution, and to the complex environmental circumstances associated with major evolutionary events. In the near future, computer simulations of evolving sequences of characters as inferred from stem group fossils will lead to a deeper understanding of the evolutionary causes of the origin of such major taxa as tetrapods, amphibians, chelonians, snakes, dinosaurs, birds and mammals. Similarly, viewing the palaeoenvironment and its perturbations in geological time as a system of integrated parameters will allow a greater understanding of how the environment is implicated in the great evolutionary events of mass extinction, ecological replacement, explosive radiation, and origin of new higher taxa, as uniquely revealed in the fossil record.

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