
Chapter 12

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REPTILES

Michael J. Benton

INTRODUCTION

The fossil record of reptiles provides a rich supply of morphological and phylogenetic data, and many of its components have been interpreted as trends. Certain lineages show trends of increasing body size, increasing brain size, digital reduction or crest development. Larger-scale trends are indicated in the step-by-step acquisition by theapsids of mammalian characters, and in the apparently sequential modification of theropod dinosaurs into birds. At a larger scale, the reptiles show supposed trends of increasing diversity and increasing breadth of adaptation.

The term 'evolutionary trend' has a broad range of meanings (see Chapter 1 herein), ranging from a rather non-committal sense almost synonymous with 'change through time', to a strong sense of progressive impelled modification in a single direction, a meaning not far from the much-reviled teleological (goal-directed) interpretations of certain evolutionists earlier this century. In the present chapter, various kinds of trend will be described, and the term is used only to indicate a pattern of evolutionary change which, in retrospect, heads in one direction. Examples will be given of large-scale trends that lasted for hundreds of millions of years, and of small-scale trends that occurred over a few million years. Attempts will be made to identify the causes, extrinsic (competition, predator pressure, progressive habitat modification), intrinsic (heterochrony, canalisation) or non-existent (statistical artefact, imagination).

LARGE-SCALE TRENDS

The phylogeny of tetrapods

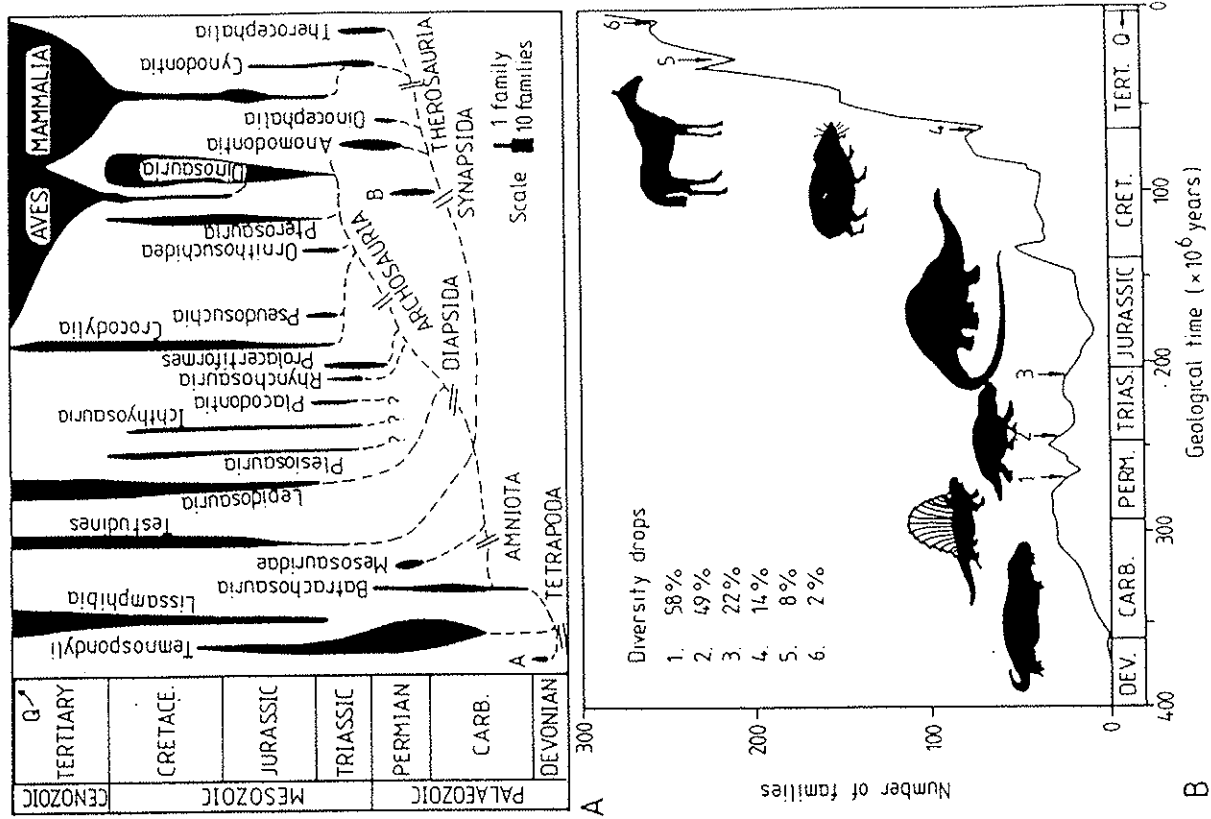
Reptiles are traditionally one of the four classes of four-limbed vertebrates, the tetrapods. The class Reptilia is, however, a paraphyletic group: it can be defined in such a way that it arose from a single common ancestor, an amphibian, but it excludes two major groups of descendants, the classes Aves (birds) and Mammalia. The lower boundaries of these two classes define the upper limits of Reptilia, boundaries that are arbitrary and defined, for the class Reptilia, by the absence of characters, rather than by their possession. Hence, large-scale trends in reptiles must be considered in terms of the Tetrapoda, or the Amniota (i.e. Reptilia, Aves and Mammalia) as a whole.

The broad pattern of tetrapod phylogeny, radiations and extinctions have been outlined elsewhere (Benton, 1989) and will only be summarised here in order to illustrate some large-scale trends. The simplified phylogenetic tree (Figure 12.1 A) shows several apparent phases of radiation. The amphibians, mainly 'temnospondyls' and batrachosaurs, dominated Carboniferous coal forests, and continued as important aquatic animals during the Permian and Triassic. Several major reptilian lineages radiated in Late Carboniferous times, but seemingly at low diversity and small size. The mammal-like reptiles dominated Permian landscapes, 'pelycosaur' in the Early Permian, and therapsids in the Late Permian.

Many new groups apparently arose and radiated in the Triassic: the archosaurs and cynodonts on land and the plesiosaurs, ichthyosaurs, and placodonts in the sea. Later in the Triassic, the turtles, crocodylians, pterosaurs, dinosaurs, and mammals began to radiate. The dinosaurs, pterosaurs, plesiosaurs and ichthyosaurs died out in the Late Cretaceous, and the birds and mammals became dominant.

When these phylogenetic data are plotted in the form of a graph of total familial diversity against time, some of the patterns become clearer (Figure 12.1 B). The most obvious feature is a marked rise in total diversity through time, which is interrupted by a number of declines. The key large-scale trend is diversity increase.

Figure 12.1 A. Phylogenetic tree of the Tetrapoda, showing the major groups of fossil and living amphibians and reptiles. Relationships (dashed lines), stratigraphic duration (vertical extent of balloon), and diversity (width of balloon) of each group are shown. Based on various sources given in Benton (1989). B. Standing diversity against time for tetrapods, with six postulated mass extinction events (nos. 1–6) shown, and their relative magnitudes (percentage falls in diversity) listed. Abbreviations: A, Ichthyostegidae; B, 'Pelycosauria'; Q, Quaternary; CARB, Carboniferous; CRET, Cretaceous; DEV, Devonian; PERM, Permian; TERT, Tertiary; TRIAS, Triassic.



All fossil records show increases in total diversity through time, whether they be records of marine invertebrates (Sepkoski *et al.*, 1981; Raup and Sepkoski, 1982), land plants (Niklas *et al.*, 1983), terrestrial vertebrates (Benton 1985a; see also Figure 12.1B). There are many possible explanations for this general large-scale trend (see also Benton, 1990):

- (a) The trend is an artefact of the patchy quality of the fossil record and the way in which we study it (Raup, 1972):
 - (i) the volume of sedimentary rock preserved unmetamorphosed increases towards the present;
 - (ii) the area of exposure of such fossiliferous rock increases towards the present;
 - (iii) palaeontologists devote much more attention to younger faunas and floras and hence name more species, genera, and families.
- (b) The trend is real and the result of genuine biological factors, such as:
 - (iv) fitness (Raup and Sepkoski, 1982), or reductions in levels of diffuse competition within communities (van Valen, 1984), or increases in the species: family ratio through time (Flessa and Jablonski, 1985);
 - (v) increase in the overall adaptive space occupied by a clade;
 - (vi) subdivision of niches, so that later forms occupy narrower niches and have more specialised adaptations;
 - (vii) increased endemicity as a result of abiotic changes;
 - (viii) 'cladistic inevitability': if the groups under study are all clades (i.e. monophyletic groups, those that include all of the descendants of a single common ancestor), their diversity is likely to increase above one if they are to survive.

Most palaeontologists now seem to accept that the trend of increasing diversity is real, that explanations (i)–(iii) may affect the pattern, but they do not account for every aspect of it. Three main lines of argumentation have been employed. First, Valentine (1973) argued that, although factors (i)–(iii) would probably seriously affect graphs of total global species diversity through time, they become less important as sources of error at higher taxic levels. In other words, figures for total species diversity would be severely affected by the availability of suitable rocks, and the intensity and nature of palaeontological study. However, there are fewer genera and even fewer families at any time, and the discovery of one species establishes the presence of a genus or a family just as well as the discovery of a hundred closely related species in rocks of the same age. In other words, families approximate more closely in taxic scale the stratigraphic acuity and completeness of most of the fossil record than do species which equate to time-scales measured in thousands of years and with more complete representation.

The second line of argument, that rising diversity trends are real, was advanced by Sepkoski *et al.* (1981). They noted that five different data bases on marine invertebrates all yielded similar graphs of increasing diversity

through time, even when the sources of data were semi-independent, such as marine trace fossil species, and families, genera, and species of body fossils compiled from different standard sources. The third argument was used by Signor (1982). He made estimates of the various postulated systematic sources of error in the known fossil record, such as (i)–(iii), and removed them as far as possible, by computer modelling, from the data. He found that the rising diversity trend was relatively little diminished by these manipulations, and that this was true for orders, families, genera and species.

Causes of diversity increase

If the rising diversity trend is real, is it possible to disentangle an explanation from hypotheses (iv)–(vii) noted above? Hypothesis (iv) may be true for marine invertebrates, since they appear to show a significant reduction in the probability of extinction through time (Raup and Sepkoski, 1982; van Valen, 1984; Flessa and Jablonski, 1985), whatever the reasons are for that. However, this is not the case for terrestrial tetrapods, in which Benton (1985a) found an overall rising trend in total extinction rates (0.008 more families dying out per million years; 5.0 per cent increase per stage; $p < 0.005$), and only a slightly declining per-taxon extinction rate (0.0001 fewer families dying out per family per million years; 0.08 per cent decline per stage; $p < 0.05$). The evidence does not suggest that tetrapods show a reduction in the probability of extinction.

Explanation (viii), the inevitability of an increase in diversity from a single ancestor, clearly plays a part, but this kind of stochastic, or random-walk type of model cannot account for the overall pattern. Hoffman (1986) developed a 'neutral' model for diversification, but had to maintain the rate of origination higher than the rate of extinction permanently in order to produce a realistic curve. A straightforward random-walk model with no such constraint would be as likely to decline as to increase.

This leaves three explanations, increase in adaptive space occupied (v), subdivision of niches (vi), and increasing endemicity (vii). These are all testable, and some preliminary analyses (Benton, 1990) suggest that all three factors have played a role in the diversification of the tetrapods.

The first known tetrapods, the families Ichthyostegidae and Acanthostegidae, were semi-aquatic piscivores that lived in and close to fresh waters. During the Carboniferous and Permian, many lineages of tetrapods became more fully terrestrial in habit, and various gliding and flying forms appeared in the Permian and Triassic. Fully marine forms arose in the Permian (mesosaurs), Triassic (ichthyosaurs, plesiosaurs, placodonts), Jurassic (crocodilians), Cretaceous (mosasaurs), Eocene (whales), and Oligocene (seals). Filters became more diverse after the evolution of birds in the Jurassic and bats in the Eocene. Arboreal and burrowing habitats were occupied at low diversity from the Permian and Triassic onwards (Figure 12.2A). Furthermore, diets broadened to include insectivory and carnivory in the Carboniferous, broadly adapted browsing herbivory in the Permian, omnivory after the Late Permian, and ever-more specialised herbivorous and

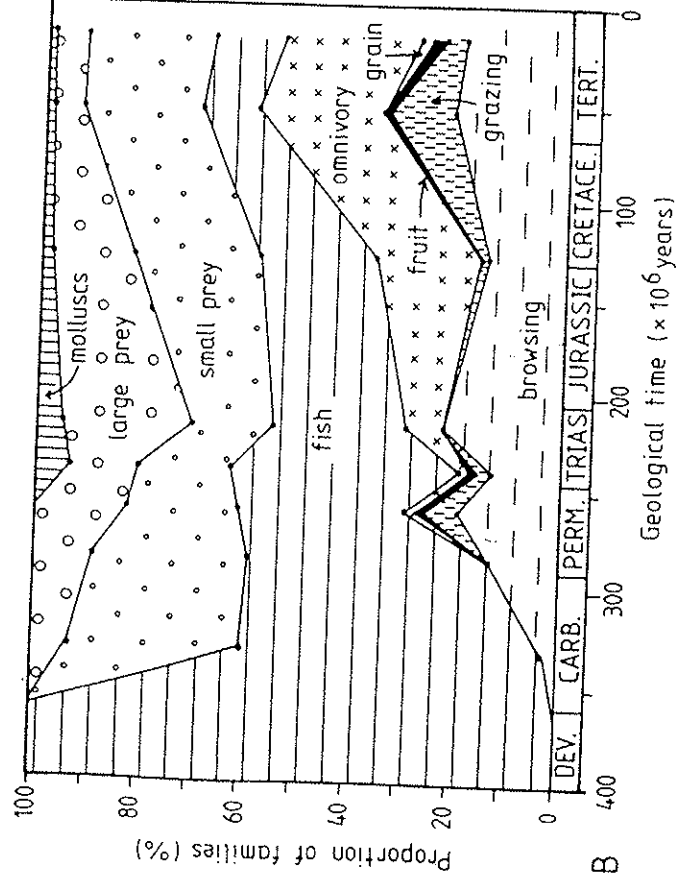
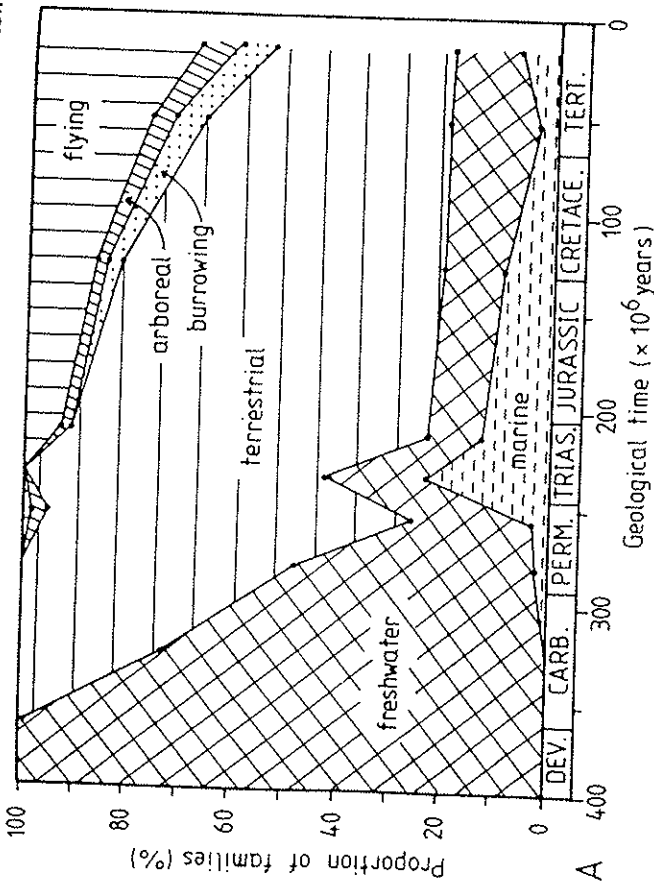


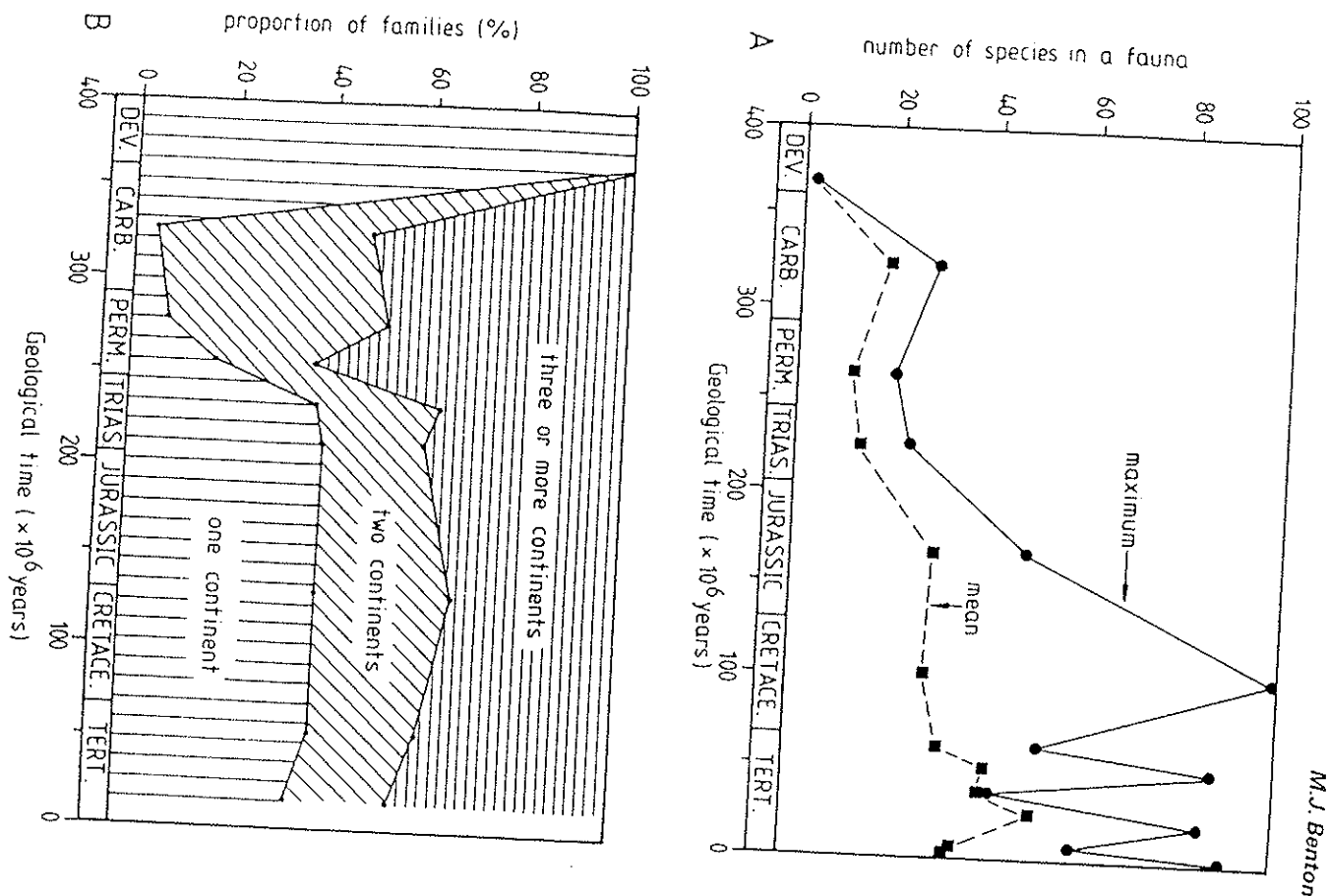
Figure 12.2. Proportions of (A) broad habitat types and (B) diets of terrestrial and marine tetrapod families through time. The habitats and diets were determined from the primary literature, and they represent the activities of all, or the majority of, species within a family. Families are grouped into broader time units than stages in order to provide large enough samples throughout (N = 44–360, mean = 146 families). Abbreviations as for Figure 12.1.

carnivorous modes (e.g., grazing, fruit, grain molluscs) after that (Figure 12.2B). These and other major adaptive expansions must have played a large part in increasing tetrapod diversity.

Subdivision of niches is suggested by an increase in the diversity of species within well-preserved tetrapod faunas. It is valid to compare an individual exceptionally preserved fauna (Lagerstätte) from the Carboniferous with one from the Eocene, since levels of preservation appear to be equivalent. In other words, Lagerstätten of all ages can show preservation of tiny animals, soft parts such as skin, scales and hair, and wholly soft-bodied organisms. A preliminary survey of 100 such faunas, spanning the past 350 million years in Europe and North America (Benton, 1990) shows a marked increase to mean faunal diversities of 18 in the Carboniferous and 35–51 in the Miocene and Pliocene (Figure 12.3A). In all cases, the species numbers are based on fossils found in a single locality or small fossil deposit, and the remarkable increase in standing diversity must in part be the result of specialisation and niche reduction.

Increasing endemism, as the third possible factor, has also played a part (Benton, 1985b). Particularly since the Carboniferous, with increasing north-south climatic differentiation, tetrapod families have become more restricted in their geographical distribution. In Permian, Triassic and Jurassic times, many families of terrestrial tetrapods were essentially global in distribution, and it was expected that the break-up of Pangaea after the Triassic would have led to increased endemism (Benton, 1985b). However, levels changed very little from Triassic times to the present (Figure 12.3B). It is likely that this large-scale increase in endemism has allowed global familial diversity to increase. Levels of endemism at lower levels (e.g. basin-basin) have yet to be investigated.

Global diversity increase is identified as a real trend in the evolution of tetrapods, and no doubt of most other major clades. This is a pattern that may be 'one-off' in all cases, dependent on specific historical circumstances, such as the break-up of Pangaea, latitudinal climatic diversification, the diversification of fishes (hence providing new adaptive space for predators), the diversification of angiosperms, and other major environmental changes. The specific effects of these events, and the relative roles of broad increases in adaptive space occupied, subdivision of niches, and increases in endemism have yet to be assessed. Explanations for the global rising trend in the diversity of marine invertebrates and plants may be different. There is no evidence for an inevitable motor of change that drives diversity ever upwards.



M. J. Benton

Reptiles

Size increase

A second major trend seen in reptilian evolution is body-size increase within all clades, at all levels of the taxonomic hierarchy. Among tetrapods as a whole, mean body size at any time has increased overall since the Devonian (Figure 12.4 A). The increase has, of course, been episodic, reset to lower levels by mass extinction events, which have generally affected large animals most. The overall increase in mean body size is not, however, as clear-cut as might have been expected, because the evolution of large animals has always been matched by diversification of smaller ones, too. Hence, the 'pulses' of evolution from modest to large size that follows major extinction events concern the largest taxa only and do not greatly affect the mean values. This is an example of a trend that is more to do with expansions of variance than with any genuine overall shift in mean body size (Gould, 1988).

Similar results are obtained from studies of particular major clades within the Tetrapoda, such as the Synapsida (Figure 12.4 B) and the Archosauria (Figure 12.4 C). The mean size of the synapsids declines with the advent of mammals, and that of the archosaurs declines with the advent of birds. The peak of maximum size represented by certain dinosaurs has not since been equalled.

The common finding of an evolutionary trend towards large body size in many lineages has become codified as Cope's Rule. Cope noted the tendency and he, and others, interpreted it as the expression of an inbuilt drive which could not be escaped. The trend has also been interpreted in terms of the selective advantages of large size, such as improved ability to capture prey or escape from predators, greater reproductive success, increased intelligence (large bodies have large brains), better stamina, expanded size range of possible food items, decreased annual mortality, extended individual longevity, and increased heat retention per unit volume (reviewed in Stanley, 1973). However, large animals suffer selective disadvantages, such as the need for large amounts of food, proneness to suffer when environments change, and small population sizes and restricted gene pools, all of which mean a great likelihood of extinction.

Stanley (1973) interpreted Cope's Rule in reverse: he argued that clades are always founded by small, often generalised, ancestors and hence the only way to evolve is up and towards specialization. Through time, the size ranges of clades extend to larger and larger values, an expansion of variance, even if not a real increase in mean size, as noted above. It is not easy to distinguish a

Figure 12.3. A: Maximum and mean number of tetrapod species in well-preserved terrestrial faunas. This graph is based on a sample of 100 faunas, with 1–20 faunas sampled per stratigraphic period (or epoch in the Caenozoic). Each 'fauna' is the species list of a single quarry or restricted sedimentary basin. Note the overall rise, with fluctuations in the maximum curve probably largely the result of variations in preservation quality. B: Variations in the geographic distribution of terrestrial tetrapod families arising during each time interval (as in Figure 12.2). Abbreviations as in Figure 12.1.

generally applicable explanation for increases in body size (reviewed by La Barbera, 1986).

SMALLER-SCALE TRENDS

Hundreds of examples of trends could be found from the fossil record of reptiles, some very small-scale, involving sequences of species within a genus, and others at a higher level, involving genera within a family, or families within an order. Four examples are given here, arranged in descending order of taxonomic and temporal scope.

Mammalian characters of synapsids

During the Late Carboniferous, Permian, and Triassic, the mammal-like reptiles were important terrestrial carnivores and herbivores; they included the ancestors of the mammals, which according to the traditional definition of Mammalia, arose in the latest Triassic (Kemp, 1982, 1988; Hopson and Barghusen, 1986). The mammal-like reptiles included a diversity of lineages during their history, all of which became extinct except for the one that eventually led to the mammals. In retrospect then, Kemp (1982; 1988) was able to show a progressive acquisition of mammal-like synapomorphies throughout the synapsid evolution, a 'trend' of increasing mammalness. His data are converted here into a statistical expression of the cumulative addition of mammal-like synapomorphies through time, plotted for the postulated 'direct line' to mammals (Figure 12.5 A).

The anatomical changes involved affected all parts of the skull and skeleton: reduction and differentiation of the teeth, formation of a secondary palate, fusion of the orbit and lower temporal fenestra, reduction in complexity of the lower jaw, shift from the reptilian articular-quadrate jaw joint to the mammalian dentary-squamosal joint, modifications to neck and trunk vertebrae, loss of lumbar ribs, and modification of the limbs and limb girdles for erect gait. Each of these broad anatomical changes took place in several steps, and each could be interpreted as a trend, or the whole complex of changes from reptiles to mammals can be regarded as an integrated mosaic trend or what Kemp (1985) calls a 'correlated progression'.

If this sequence of changes can be regarded as a trend or trend complex, then the mechanistic interpretation by Kemp (1985) and others has been adaptational. Each facet of the change towards mammalness is seen as part of a progressive change in feeding, locomotory, thermoregulatory and sensory efficiency, all driven by the forces of natural selection. Suggested extrinsic factors to account for such a trend have included direct competition with other contemporary animals, such as the early archosaurs (see, for example, Charig, 1984); diffuse biotic interaction ('weak competition'), including predation pressure; differential environmental response, in which successful groups become modified as a result of climatic, vegetational, and other changes (Benton, 1987a); and chance, especially in terms of the apparently undirected selective effects of mass extinctions (relevant events indicated in Figure 12.5 A) and the opportunistic radiation of survivors (Benton, 1983; 1987a).

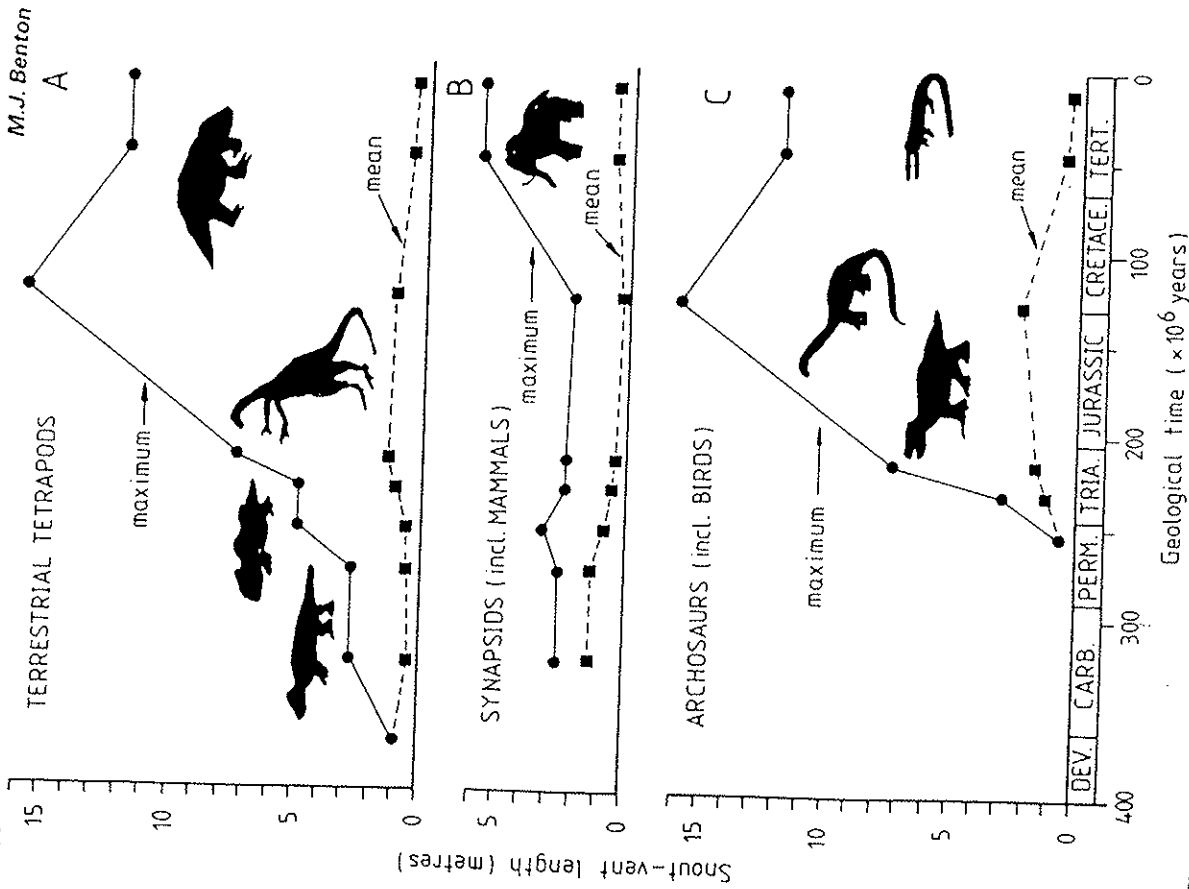
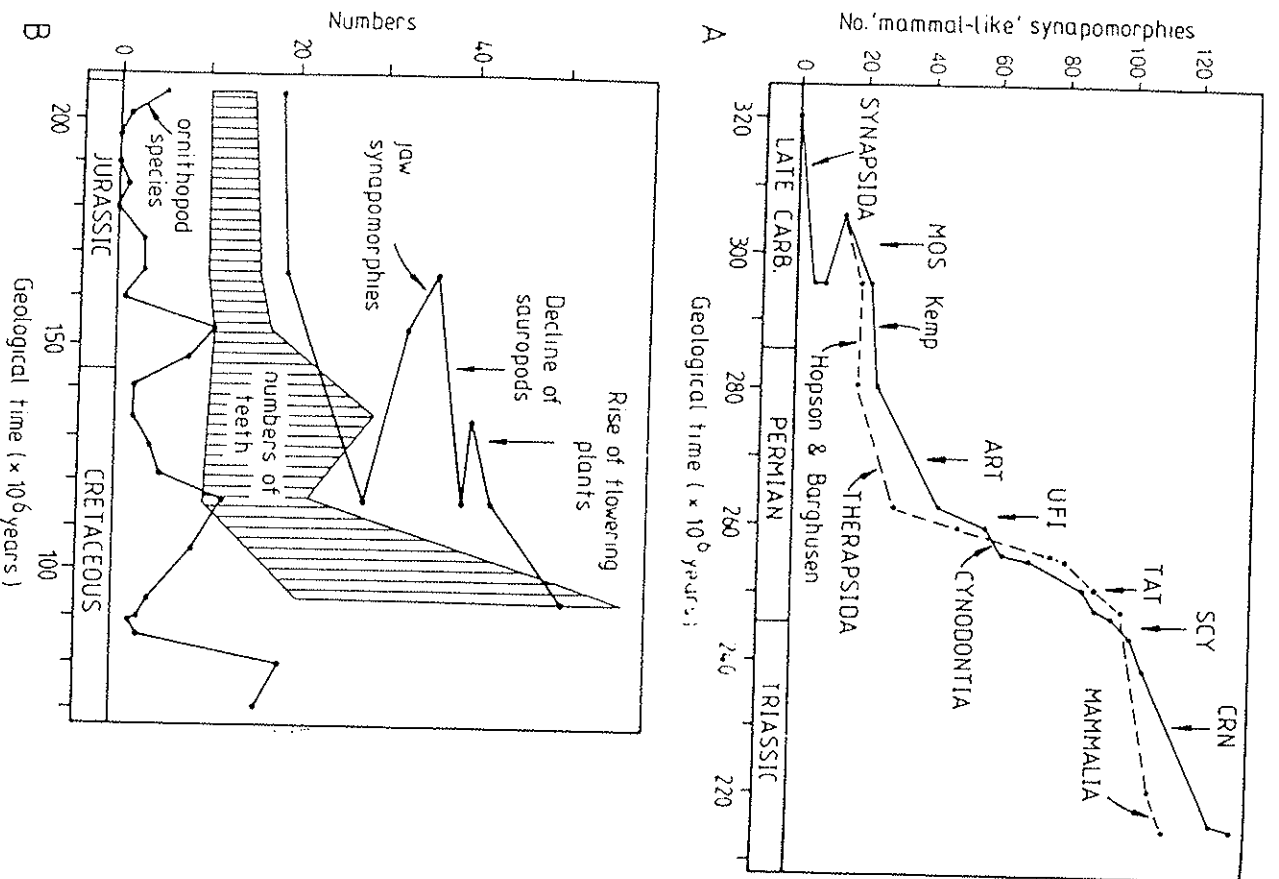


Figure 12.4. Size ranges of terrestrial tetrapods through time, plotted (A) for all taxa, (B) synapsids, including mammals, and (C) archosaurs, including birds. Maximum and mean measurements are indicated for grouped time intervals, as in Figure 12.2. Sizes are body lengths measured from the tip of the snout to the vent (i.e. excluding the tail), and they were recorded for each family according to a number of size classes. Mid-points of these size classes were used in the calculations (further details in Benton and Blacker, in prep.).



Reptiles

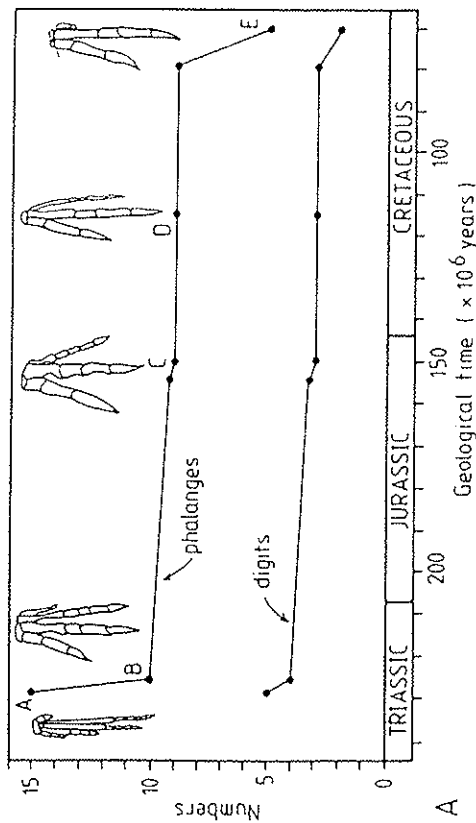
Herbivorous adaptation of ornithomorph dinosaurs

The ornithomorphs, bipedal plant-eating dinosaurs, arose in the Late Triassic or Early Jurassic, and radiated at low levels during the Jurassic and Early Cretaceous, but were spectacularly successful in the Late Cretaceous. This success, as the duckbilled dinosaurs, or hadrosaurs, has generally been attributed to their increasingly efficient jaws and tooth-batteries (see, for example, Norman and Weishampel, 1985). Whereas early forms had low snouts, few spaced teeth, and shallow jaws, the hadrosaurs had high horse-like snouts, powerful batteries of up to 2000 teeth, deep well-muscled lower jaws, and specialised skull joints that allowed a form of chewing. These anatomical changes occurred in several stages during the 140 million years of the Jurassic and Cretaceous, and could be termed a trend.

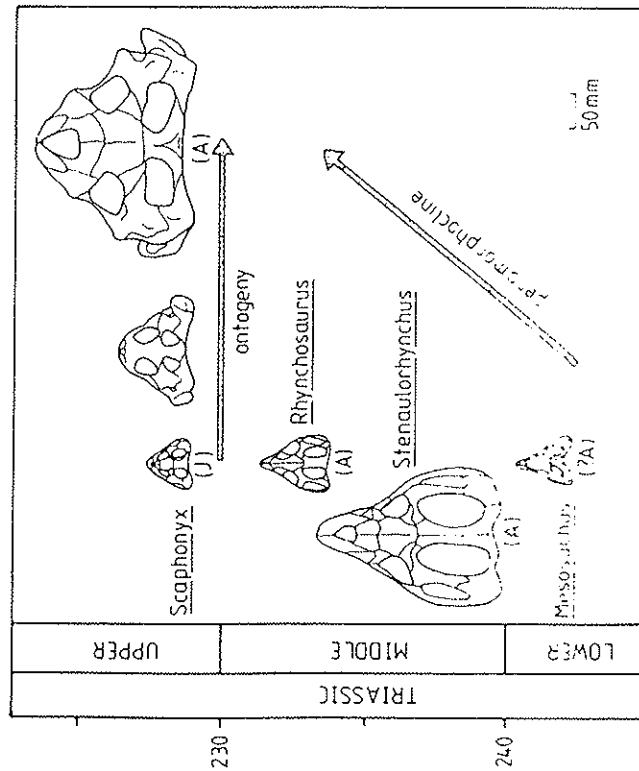
This trend can be represented in several ways (Figure 12.5 B). First, a statistical analysis of the acquisition of synapomorphies of the Ornithomorphs (cladistic analysis of Sereno, 1986) plotted against time, shows a pattern of jerky increase similar to the previous example. Unfortunately, the sequence of taxa as determined by the cladistic analysis does not match their temporal sequence, probably because of missing fossils, hence the zig-zag pattern of the graph. The second illustration of this trend is based on a single character: the range in numbers of tooth positions within each of the four jaw rami for key ornithomorph taxa (Weishampel, 1984). There is an overall increase, from 10–15 in Early Jurassic taxa to 20–57 in the Late Cretaceous hadrosaurs, but much of the increase is produced by increase in variance. The lower limit rises from 10 to 20, but the upper limit extends dramatically from 15 to 57. The acquisition of dental and jaw characters and the rise in numbers of teeth is matched to some extent by an episodic rise in ornithomorph species diversity (Weishampel and Norman, 1989), although much of this pattern merely reflects the distribution in time of dinosaur-bearing rock formations.

The trends in ornithomorph teeth and jaw mechanics throughout the Jurassic and Cretaceous are generally interpreted as the result of responses to environmental stimuli, particularly changes in the available plant food, (Weishampel and Norman, 1989), and possibly to extinctions of other herbivores. Peaks in the evolutionary rates of ornithomorph feeding

Figure 12.5. Two large-scale trends in reptilian evolution. A: The acquisition of mammal-like characters by synapsid reptiles of the Carboniferous, Permian and Triassic, based on the cumulative addition of synapomorphies at each node on the 'direct line' from the first synapsid to the first mammal. The taxa are those lettered A–H, J–R in Kemp (1982), with synapomorphies from Kemp (1982, 1988; solid line), and from Hopson and Barghusen (1986; dashed line). Dates are those of the oldest representative of the family, obtained from Benton (1987b). B: The trend to more specialised jaws and teeth (data from Sereno, 1986); ranges of the number of teeth in each jaw ramus of typical forms (data from Weishampel, 1984); and ornithomorph species diversity, plotted stage by stage (data from Weishampel and Norman, 1989).



A



B

mechanisms and in global diversity follow the decline of sauropods, in the Northern Hemisphere at least, at the end of the Late Jurassic, and the rise of the angiosperms (flowering plants) during mid- to Late Cretaceous times.

Loss of digits in the theropods

A smaller-scale trend is seen in the theropod dinosaurs in which digits and phalanges were lost from the hands (Figure 12.6 A). The first theropods in the Late Triassic, such as *Coelophysis*, had four fingers and ten phalanges in all, having lost the fifth finger (equivalent to our little finger) seen in the first dinosaurs. Digit 4 was already reduced, having only one phalanx. Most Jurassic theropods retained four fingers until Late Jurassic times, when the number fell to three. This was typical of most Cretaceous forms, until the latest Cretaceous, when large carnivores such as *Tyrannosaurus* lost the third finger as well, leaving only two fingers and five phalanges in all.

It is hard to discern reasons, extrinsic or intrinsic, for such a trend. The theropods ranged greatly in size, from that of a turkey to the 14-metre length of *Tyrannosaurus*. Further, different taxa presumably used their hands for very different activities: grappling with prey, picking at carcasses, grasping eggs, capturing insects, picking their teeth, and so on. Hence, it would be hard to find a simple all-encompassing adaptive explanation for digital reduction.

Digital reduction events in Theropoda seem to have been unique. Hence, the reduction to four digits occurred at the Tetanurae node in the cladogram (Gauthier, 1986). The reduction to two digits occurs only in the Late Cretaceous tyrannosaurids, and some retain a remnant of digit 3.

One embryological explanation for digital reduction in modern tetrapods (Alberch and Gale, 1985) relates to the body size of embryos and adults. Small animals have fewer cells available for differentiation of the limb bud at early developmental stages, and hence can lose elements. It is hard to see how this kind of explanation could apply to *Tyrannosaurus*!

It might be possible to discern a heterochronous cause for this trend. Evidence from the embryology of modern birds (which are tetanuran theropod derivatives) show that digits 3 and 4 appear in early developmental

Figure 12.6. Two smaller-scale trends in reptilian evolution. A: Digital and phalangeal reduction in theropod dinosaurs. Numbers of fingers and phalanges in the hand of a selection of theropod dinosaurs, and the ancestral *Lagosuchus* (A). Theropods are *Syntarsus* (B), *Allosaurus* (C), *Deinonychus* (D), and *Tyrannosaurus* (E). B: The postulated paramorphocline (extended ontogeny) seen in the evolution of the rhynchosaur skull. Adult skulls of three Early and Middle Triassic rhynchosaurs and an ontogenetic series of three of the skulls of *Scaphonyx fischeri* are shown. The skulls are positioned vertically according to their occurrence in time (stratigraphic column on the left), and horizontally according to the ratio of posterior skull-roof width to mid-line skull-roof length. Abbreviations: A, adult; J, juvenile. Based on Benton and Kirkpatrick, 1989.

stages, but digit 4 disappears, and digit 3 is much reduced in adults. Further, a juvenile theropod, *Ornitholestes*, shows a tiny nubbin of digit 4, which is lost in the adult (Gauthier, 1986). It seems likely that the trend of digital reduction is peramorphic (ancestral adult morphology present in juvenile phase of descendant; see McNamara, 1986). It is not clear whether the 'reduced and lost' has resulted from earlier initiation of digital development (predisplacement), acceleration of the rate of development (acceleration), or delay in the onset of sexual maturity (hypermorphosis).

Hypermorphosis is often associated with an increase in adult size, which was generally the case at times of digital reduction in the course of theropod evolution. However, more study of the developmental sequences of theropods will be needed in order to decide which peramorphic mechanism applies.

Rhynchosaur skulls

The rhynchosaur skulls were important herbivores in the Triassic of much of the world. They were distantly related to the archosaurs (Figure 12.1 A), and they died out just before the radiation of the dinosaurs. During their relatively short span of 17 million years or so, rhynchosaur skulls evolved some remarkable specialisations in their skulls and teeth in particular. One striking trend was expansion of the posterior part of the skull.

The first rhynchosaur had a typical reptilian skull shape, with a width to length ratio of 0.6 or 0.7. Later rhynchosaur skulls had much broader skulls, often broader than they were long, with width to length ratios of 1.0 to 1.2 (Figure 12.6 B). A developmental sequence of 13 skulls of the Late Triassic rhynchosaur *Scaphonyx fischeri* from Brazil demonstrated that this trend of skull expansion was peramorphic (Benton and Kirkpatrick, 1989). Although the youngest specimen in the sequence was six months to a year old, its skull width to length ratio of 0.8 was close to the ancestral adult condition. The peramorphic mechanism was identified tentatively as hypermorphosis since the adult Late Triassic rhynchosaur skulls are generally larger than those of the Early or Middle Triassic.

PARALLEL EVOLUTION

Large-scale and medium-scale trends in tetrapod history have been hard to interpret in a clear-cut way, whether as real progressive changes induced by competition, predation, environmental change or chance. Smaller-scale trends often seem to result from heterochrony. Is there another way of testing among the various causal mechanisms?

Parallel evolution, the evolution of similar features in two or more lineages along approximately the same pathways, has occurred several times in the evolution of reptiles. The character patterns may provide a test between extrinsic and intrinsic causes since the underlying principles differ: natural

selection/adaptation and heterochrony/canalisation, respectively. If parallel evolution is to be explained by extrinsic causes alone, the major morphological changes should occur roughly at the same time since they are presumably caused by particular new kinds of competitor or predator, or by particular changes in the physical environment. In detail, the morphological changes may seem very different, even though they have evolved towards the same function (i.e. analogies). Parallel evolution that is dominated by intrinsic constraints (heterochrony, canalisation) need not occur synchronously in all lineages, and the final results may be morphologically very similar (i.e. hard to distinguish from homologies) since they are channelled along a limited selection of developmental pathways. Two examples of large-scale parallel evolutionary trends among tetrapods will be considered: erect gait and skull-element reduction.

Erect gait

Erect (upright, parasagittal) gait is the derived posture seen in modern birds and mammals in which the limbs are held directly beneath the body and move backwards and forwards essentially in a vertical plane. It is not to be confused with bipedal (two-legged) gait. This posture is regarded as derived since living and fossil amphibians and most living and fossil reptiles have a sprawling gait, in which the limbs are held out to the sides and move in horizontal and vertical planes during walking.

The erect gait of mammals arose in ancestral mammal-like reptiles of the Triassic, while the erect gait of birds is traceable back through the dinosaurs to their Triassic thecodontian ancestors, the basal ornithosuchians. Erect gait arose at least twice in two other Triassic groups, the pseudosuchians (i.e. aetosaurs, rauisuchids, and poposaurids (?)) and the crocodylomorphs (the ancestors of crocodylians were small terrestrial bipedal insectivores with erect gait). How synchronous were these four parallel changes from sprawling to erect gait in the Triassic, and how morphologically similar were they?

The changes are not obviously synchronous. Time-span ranges from 240–235 million years ago for the achievement of erect gait in the hind limb of eynodont mammal-like reptiles (Kemp, 1982) to about 220 million years ago for the achievement of erect gait in the early crocodylomorph *Sallioapsuchus*. This part of the analysis reveals some problems of the kind palaeontologists always face. First, erect gait was achieved early on in the mammalian line, but only in the hindlimb—the first mammals of the latest Triassic still had a partially sprawling forelimb. Second, the first erect-limbed ornithosuchians and crocodylomorphs were essentially bipedal, during fast locomotion at least, and changes to the forelimbs may have been subject to different evolutionary forces. The first erect-limbed mammal-like reptiles and pseudosuchians were quadrupeds. Third, the origin of bipedality in crocodylomorphs may be much earlier than noted here if the poposaurids are the sister-group of crocodylomorphs (Benton and Clark, 1988). Conceivably, then, all dates would converge back on 235 million years ago. Hence, was the acquisition of erect gait synchronous or not?

Table 12.1 Evolution of erect gait in four reptilian lineages (based on data from Kemp, 1982; Benton and Clark, 1988)

Lineage	First appearance of erect gait	Type	Acetabulum	Primitive foot posture
Mammal-like reptiles	Middle Triassic	Buttress	Closed	Plantigrade
Ornithosuchians	Middle Triassic	Buttress	Open	Digitigrade
Pseudosuchians	Middle Triassic	Pillar	Closed	Plantigrade
Crocodylomorphs	Late Triassic	Buttress	Open	Digitigrade

In detail, the anatomical changes associated with the shift to erect gait are very different. Three groups share a 'buttress-erect' type of posture, in which the femur has an offset head that fits into the side of the near-vertical acetabulum (the hip socket) like the buttress of a church. The pseudosuchians, on the other hand, have a 'pillar-erect' posture (Benton and Clark, 1988), in which the femur does not have an offset head, and it fits straight into a near-horizontal acetabulum, like a pillar supporting a heavy roof. Further, ornithosuchians and crocodylomorphs have an open acetabulum, and this is surrounded by all three hip bones in the ornithosuchians, but only the ilium and ischium in crocodylomorphs. The mammals and pseudosuchians retain a primitive closed acetabulum. The last two groups primitively had a plantigrade foot posture, in which the sole of the foot touches the ground, while the other two had a digitigrade posture, in which the foot rests only on the tips of the toes.

In general, then, the acquisition of erect gait may have been a response largely to extrinsic factors. It seems to have occurred broadly synchronously in a few unrelated groups, and it has caused different anatomical modifications in general. An intrinsic element to the trend may be discerned, however, in some features of digital reduction, for example. The erect crocodylomorphs and ornithosuchians both show digital reduction, and the digit to become reduced in both cases is toe 5. This may suggest an element of canalisation.

Skull-element reduction

Most tetrapod lineages show some tendency to reduction in the number of skull bones. At the broad scale, the early amphibians had fewer skull elements than their fish ancestors, and the first reptiles had fewer than those amphibians. However, certain lineages of amphibians and reptiles lost further elements in comparison with their closest relatives. Examples include the extinct aistopods, living frogs, salamanders, and gymnophionans (caecilians), several lizard groups, amphisbaenians, and snakes (Table 12.2).

The reductions are obviously not synchronous, ranging in date from the Carboniferous (Viscan, c.340 million years ago) to the Tertiary (dates

Table 12.2 Loss of skull elements as a result of miniaturisation in diverse tetrapod groups. Data from Rieppel (1984), Benton (1987b), Carroll (1987), and Milner (1988)

Lineage	Origin of group (age in millions of years)	Mean adult skull length (mm)	Elements lost*
AMPHIBIA			
Aistopoda	Viscan (340)	15	pf, pp, sq, st, t
Anura (frogs)	Scythian (242)	15	ect, j, pf, prf, pp, t
Urodela (salamanders)	Bathonian (172)	10	ect, j, pf, pp, prf, t
Gymnophiona	Pliensbachian (195)	10	j, l, pl, po, prf, st
REPTILIA			
Acontinae	No fossils	15	l, po
Anguinae	Cambrian (79)	10	sq
Pygopodidae	No fossils	8	j, l, po, sq, st
Dibamidae	No fossils	15	j, l, pl, po, sq, st
Amphisbaenia	Paleocene (60)	15	j, l, pl, po, sq, st
Serpentes (snakes)	?Early Cretaceous (120)	30	ep, j, l, pf, sq

* Elements lost in extreme forms of the group in question.

Abbreviations: ect, ectopterygoid; ep, epipterygoid; j, jugal; l, lacrimal; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; sq, squamosal; st, supratemporal; t, tabular.

unknown, lizard groups with no fossil record; less than 60 million years ago). Anatomically, many of the changes are remarkably similar: elements such as the jugal, postfrontal, postorbital, prefrontal, and supratemporal are lost even in widely different lineages. The similarities are stronger within major clades, such as the Lissamphibia (living amphibians) and the Squamata (lizards and snakes) (Table 12.2).

These observations suggest broadly intrinsic causation, especially canalisation. Rieppel (1984) has observed that all of these groups showing reduction in numbers of skull elements are miniaturised. The biological constraints of keeping the brain, eye and jaws large enough to be functional are associated with changes in relative skull proportions and losses of non-essential bony elements. In small frogs and salamanders, which may lack many skull elements, those that ossify late in development tend to be lost first (see, for example, Hanken, 1984; Trueb and Alberch, 1985), examples of the paedomorphic process of progenesis (see Chapter 3 herein). There is, however, variation among taxa in many cases that suggests the additional involvement of selective forces on the nature of skull-element reduction.

It should be noted that the losses of skull elements noted in Table 12.2 are often used as apomorphies in cladistic analyses of the groups, and yet they may not be homologous at all!

CONCLUSIONS

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1. Trends occur in the fossil record of reptiles, and of tetrapods in general, at all scales, from their overall expansion in diversity, to changes in individual characters within lineages over a few million years.
2. Most large-scale trends seem to relate to major extrinsic causes, such as mass extinction events, changes in the physical environment, or the opening up of new adaptive space (e.g., new habitats, new sources of food).
3. Biotic factors such as competition and predation no doubt play a role in generating trends, but these are hard to imagine as remorseless driving forces on the geological time-scales involved (see also Benton, 1987a).
4. Most trends in tetrapods involve morphology and size at the lineage (species) level, but morphology, size and ecological strategies at higher taxic (major clade) levels.
5. Long-term trends, like the appearance of mammal-like characters in the ancestors of mammals, or modifications in herbivorous adaptations of ornithomimid dinosaurs, seem to occur sporadically rather than in a gradual progression, with key changes happening in bursts, often associated with an opportunistic radiation occurring after an extinction event of potential competitors.
6. Small-scale, species-level trends often involve clear evidence of heterochrony and canalisation constraining the pattern of change.
7. Parallel evolution may provide a test of the broad significance of extrinsic and intrinsic factors or trends. When extrinsic factors dominate, the parallel changes in more than one lineage may occur synchronously, and heterochrony and canalisation may show no synchrony at all, and changes should be morphologically similar. Examples of parallel evolution of erect gait (extrinsic) and of skull-element reduction (intrinsic) are given.

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