



# The Origin of the Dinosaurs

## El origen de los dinosaurios

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### Abstract

The origin of the dinosaurs has long been debated. There are two aspects, phylogenetic and ecological-evolutionary. Much of the phylogenetic confusion has been resolved by cladistic analysis of basal archosaurs which shows that the dinosaurs originated as part of a major clade Avemetatarsalia/ Ornithodira. Closest relatives of the dinosaurs are small Mid Triassic bipedal animals such as *Marasuchus* from Argentina. The basal avemetatarsalian is *Scleromochlus* from the Late Triassic of Scotland. The classic ecological-evolutionary model for the initial radiation of the dinosaurs had been that they competed gradually through the Triassic with precursor groups, and eventually prevailed. More detailed study of the timing of events suggests that the dinosaurs radiated opportunistically in a two-phase model, with expansion of herbivorous sauropodomorphs first in the early Norian, and expansion of large theropods and ornithischians in the Early and Mid Jurassic. Both expansion phases followed extinction events.

**Key words:** Dinosaur, Triassic, origin, opportunism, *Eoraptor*, *Herrerasaurus*.

### Resumen

El origen de los dinosaurios ha sido debatido durante mucho tiempo. Hay dos puntos de vista, el filogenético y el ecológico-evolutivo. La mayor parte de la confusión filogenética ha sido resuelta por análisis cladístico en arcosaurios basales. Éstos muestran que los dinosaurios se originaron como parte de un clado mayor Avemetatarsalia/Ornithodira. Los relativos más próximos a los dinosaurios son unos pequeños animales bípedos como el *Marasuchus* de Argentina. El avemetatarsaliano basal es *Scleromochlus* del Triásico Superior de Escocia. El modelo clásico ecológico-evolutivo de la radiación inicial de los dinosaurios ha planteado que éstos compitieron gradualmente durante el Triásico con grupos precursores y que finalmente prevalecieron. Un estudio más detallado de la datación de eventos sugiere que los dinosaurios radiaron oportunísticamente según un modelo de dos fases con una primera expansión de herbívoros sauropodomorfos en el Noriense basal y una expansión de grandes terópodos y ornitisquios en el Jurásico Inferior y Medio. Ambas fases de expansión sucedieron a eventos de extinción.

**Palabras clave:** dinosaurio, Triásico, origen, oportunismo, *Eoraptor*, *Herrerasaurus*.

## Introduction

When members of the public hear about dinosaurs, they always want to know why they died out. But the origin of the dinosaurs is an equally interesting question. Dinosaurs were a hugely successful group - they existed on the Earth for 165 million years (230-65 Myr ago) - and for most of that time they were the largest, the most abundant, and the most widespread land animals. For years, there has been confusion about the origin of the dinosaurs, for a variety of reasons: (1) uncertainty about what is a dinosaur, and what is not; (2) uncertainty about the validity of the taxon Dinosauria; (3) uncertainty about the timing of the initial radiation of the dinosaurs; and (4) lack of clarity concerning models for the radiation of major taxa.

The advent of cladistics into the study of the relationships of Archosauria about 1984 has largely answered points (1) and (2): many putative dinosaurs from the Early and Mid Triassic have been assigned to their proper places in the tree of life, and the clade Dinosauria is now well characterized by many unique synapomorphies. The timing of dinosaurian origin (point 3) is still debated, but repeated studies show the first dinosaurs are mid to late Carnian in age (c. 225 Myr ago), and the best known examples are from the Ischigualasto Formation of Argentina (notably *Eoraptor* and *Herrerasaurus*). There are some older supposed dinosaurian remains, but there are problems of identity or of dating. Models of radiation (point 4) have been clarified: the Carnian dinosaurs were relatively rare in their ecosystems, and did not exceed modest size. At the end of the Carnian, 217 Myr ago, the dominant herbivores died out – dicynodonts, chiniquodontids, and rhynchosaurs. The major lineages of dinosaurs, theropods, sauropodomorphs, and ornithischians, all appeared in the Carnian (228-217 Myr ago) and they radiated during the Norian and Rhaetian (217-204 Myr ago). There has been a heated debate about how this radiation happened, whether by successful competition with the synapsids, the basal archosaurs, and the rhynchosaurs, or by opportunistic radiation after an extinction event.

The aim of this paper is to review the first dinosaurs briefly, to place them cladistically among the early archosaurs, and to review the evidence for a competitive or opportunistic initial radiation of the group.

## Ornithodira: dinosaurs and relatives

The closest major outgroup of the dinosaurs is probably the pterosaurs (Fig. 1): Gauthier (1986) noted similarities between the two groups, particularly in the hindlimb. For example, the ankle joint is simplified to a hinge-like arrangement in which the astragalus and calcaneum act together as a kind of ‘roller’, and the middle three toes are elongated and held in an upright position so that the animal stands up on its toes, the digitigrade posture. Pterosaurs and dinosauromorphs together are termed the Ornithodira.

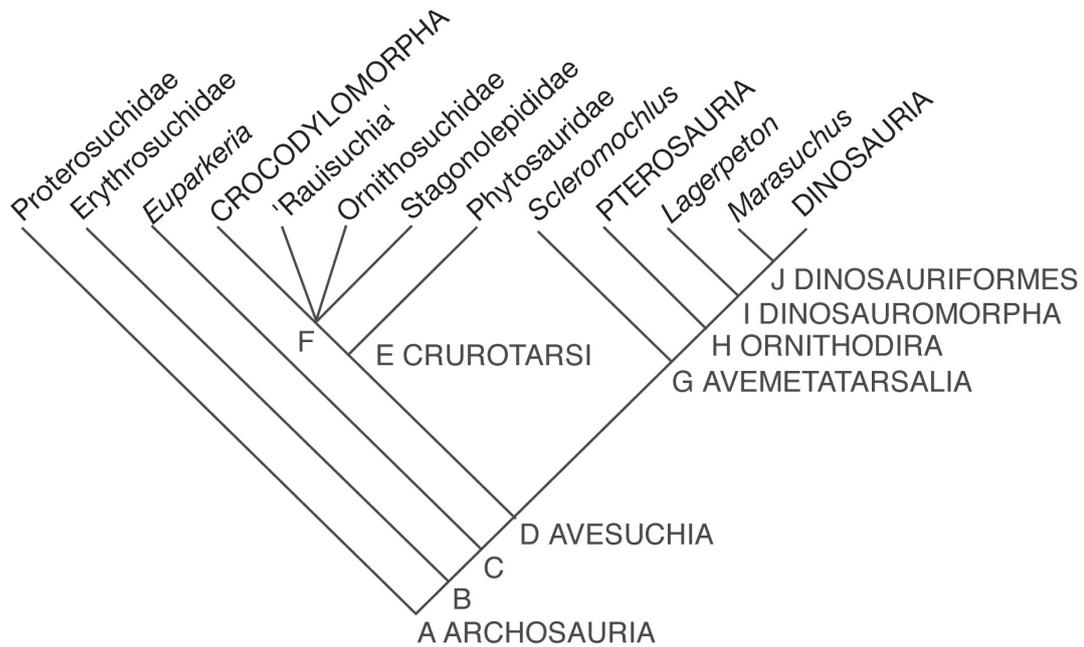


Figure 1. Cladogram showing the relationships of the Triassic archosaurs, based on the work of Gauthier (1986), Benton and Clark (1988), Sereno (1991), Benton (1999), and others. Synapomorphies of the various clades may be found in Benton (1999).

A small reptile from the Upper Triassic of Elgin, *Scleromochlus* (Fig. 2A), appears to be an outgroup to Ornithodira, the basal member of the dinosaur branch of archosaurian evolution, termed the Avemetatarsalia (Fig. 1). *Scleromochlus* has the bird-like features of a tibia that is longer than the femur, an adaptation seen in some running animals, and a closely bunched group of four elongate metatarsals. It lacks the elongate neck, reduced fibula, and the simplified ankle joint (astragalus and calcaneum closely attached to each other and to the tibia) seen in ornithodirans. *Scleromochlus* has sometimes been allied with Pterosauria (Sereno, 1991), but it appears more firmly located in the phylogeny at the base of Avemetatarsalia (Benton, 1999). This slender little reptile was only 170 mm long, the size of a blackbird, and it was certainly bipedal – its forelimbs are very much shorter than its hindlimbs. It had been interpreted as a climber or even a glider, and hence in some way ancestral to pterosaurs. *Scleromochlus* might even have been able to hop: it has the proportions of the desert-living jerboa, a small mammal that leaps around the sand dunes of North Africa and the Middle East at night.

Two small reptiles from the Mid-Triassic of Argentina fall closer to the dinosaurs than to the pterosaurs, *Lagerpeton* and *Marasuchus*. *Lagerpeton* is incompletely known, but is a

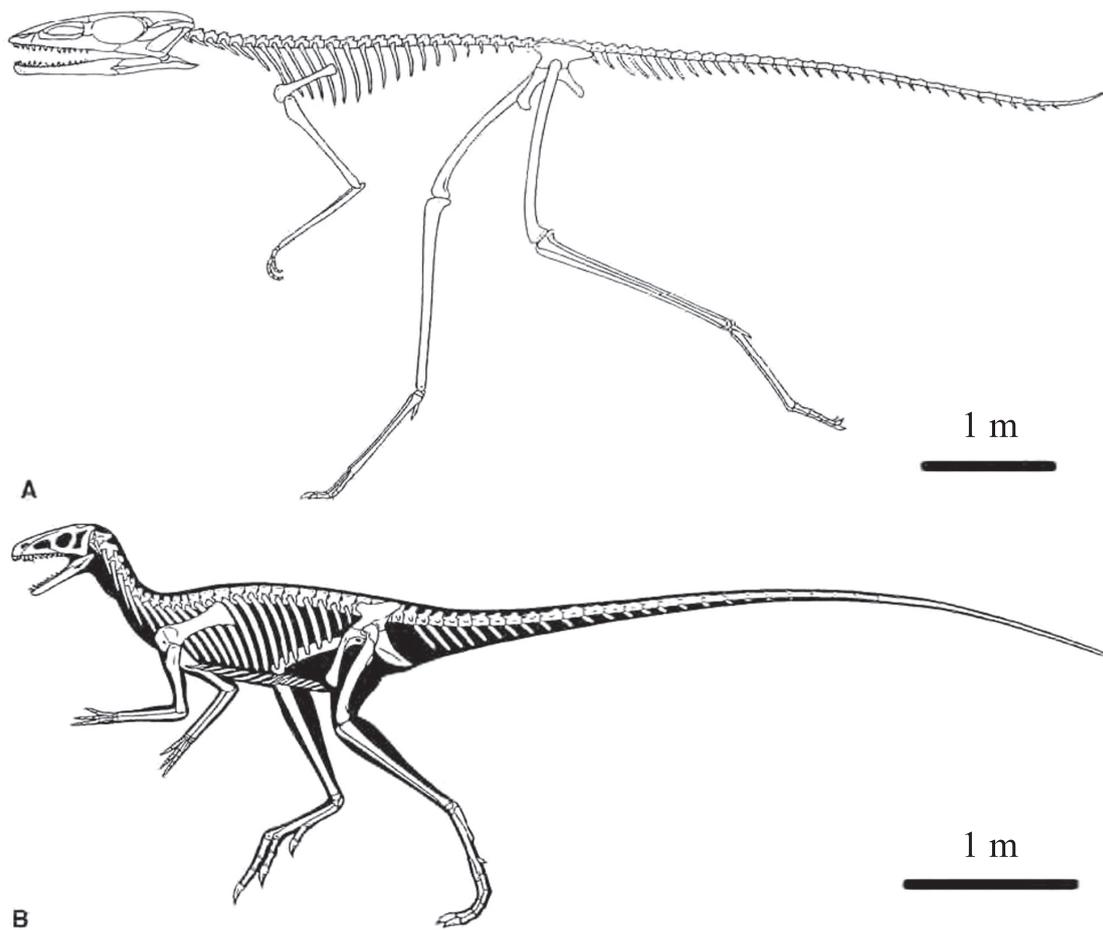


Figure 2. Basal avemetatarsalians: (A) *Scleromochlus*, skeleton in lateral view; (B) the basal dinosauromorph *Marasuchus*, skeleton in lateral view. [Figure A based on Benton (1999); B, courtesy of Paul Sereno and Carol Abraczinskas.]

basal dinosauromorph, whereas *Marasuchus* (Sereno and Arcucci, 1994) is a basal dinosauriform (Fig. 1), characterized by a number of shared characters (Sereno, 1991), such as: a ‘swan-neck’ in which the cervical vertebrae follow a strongly S-shaped curve, a forelimb less than half the length of the hindlimb, a much reduced calcaneum that is one-third or less of the size of the astragalus, and further specialized features of the foot.

*Marasuchus* (Fig. 2B) was a lightly built flesh-eater, some 1.3 m long, that presumably preyed on small fast-moving animals such as cynodonts and procolophonids, as well as perhaps worms, grubs, and insects. The skull is incompletely known, but the postcranial remains show many dinosaur-like characters, such as parallelogram-shaped cervical vertebrae (necessary for the S-curved neck), an arm that is less than half the length of the leg, the beginnings of an open acetabulum, and other features of the pelvis and limb bones associated with fully erect posture. *Marasuchus* was clearly a biped, running on its hindlimbs, and the long tail was presumably used as a balancing organ. It may have used its hands for grappling with prey and for passing food to its mouth.

## **The oldest dinosaurs**

Older accounts frequently state that dinosaurs arose early in the Triassic, and evidence in the form of skeletons and footprints is often quoted. The supposed skeletal remains of dinosaurs from before the Late Triassic turn out, though, to belong to prolacertiforms, rauisuchians, and other non-dinosaurian groups (Wild, 1973; Benton, 1986, 1994). Dinosaur footprints, generally showing three toes and no heels, because of their digitigrade posture, and the reduction of toes 1 and 5, had also been recorded from the Lower and Mid-Triassic of various parts of the world, but critical re-examination (Thulborn, 1990; King and Benton, 1996) shows that they have been wrongly identified.

The oldest true dinosaurs are known from the early part of the Late Triassic (the Carnian Stage, 228–217 Myr ago) from various parts of the world. The best specimens come from the Ischigualasto Formation of Argentina, source of a rich fauna of basal archosaurs, rhynchosaurs, and synapsids. The Ischigualasto dinosaurs, *Eoraptor* and *Herrerasaurus*, are relatively well known from nearly complete specimens, and they give an insight into the days before the dinosaurs rose to prominence.

*Eoraptor* (Serenó *et al.*, 1993) is a lightweight animal 1 m long (Fig. 3A), with a number of dinosaurian characters: the postfrontal is absent, there are three vertebrae in the sacrum, the deltopectoral crest runs a long way down the shaft of the humerus, the femur is modified for fully erect posture, and there are various dinosaurian characters in the ankle, including an ascending process on the astragalus.

*Herrerasaurus* (Serenó and Novas, 1992), is a larger, more heavily built animal 3 m long (Fig. 3B). It shows a number of synapomorphies of the Dinosauria, features that are not seen in *Marasuchus* or the pterosaurs: the acetabulum is fully open, and the head of the femur is bent inwards. *Herrerasaurus* has a short arm and a strong hand with three functional fingers (digits 4 and 5 are reduced to small bone splints), which it probably used for grasping and raking food. Both *Eoraptor* and *Herrerasaurus* were initially classed (Serenó and Novas, 1992; Serenó *et al.*, 1993) as basal theropods, although they may turn out either to be basal saurischians or even basal dinosaurs (Langer *et al.*, 1999).

At one time, most palaeontologists regarded the dinosaurs as a diverse assemblage of archosaurs that arose from several ancestors – a polyphyletic group. Recent cladistic analyses (e.g. Gauthier, 1986; Benton and Clark, 1988; Serenó, 1991) have indicated, however, that the Dinosauria is a monophyletic group, characterized by many features (Fig. 1). Other Carnian dinosaurs include a basal ornithischian and basal sauropodomorphs (Langer *et al.*, 1999), but they, *Eoraptor* and *Herrerasaurus*, were only rare elements in their faunas (1–3% of all skeletons). Before the end of the Triassic, however, the dinosaurs had radiated widely to become the most abundant vertebrates on land. How did this happen?

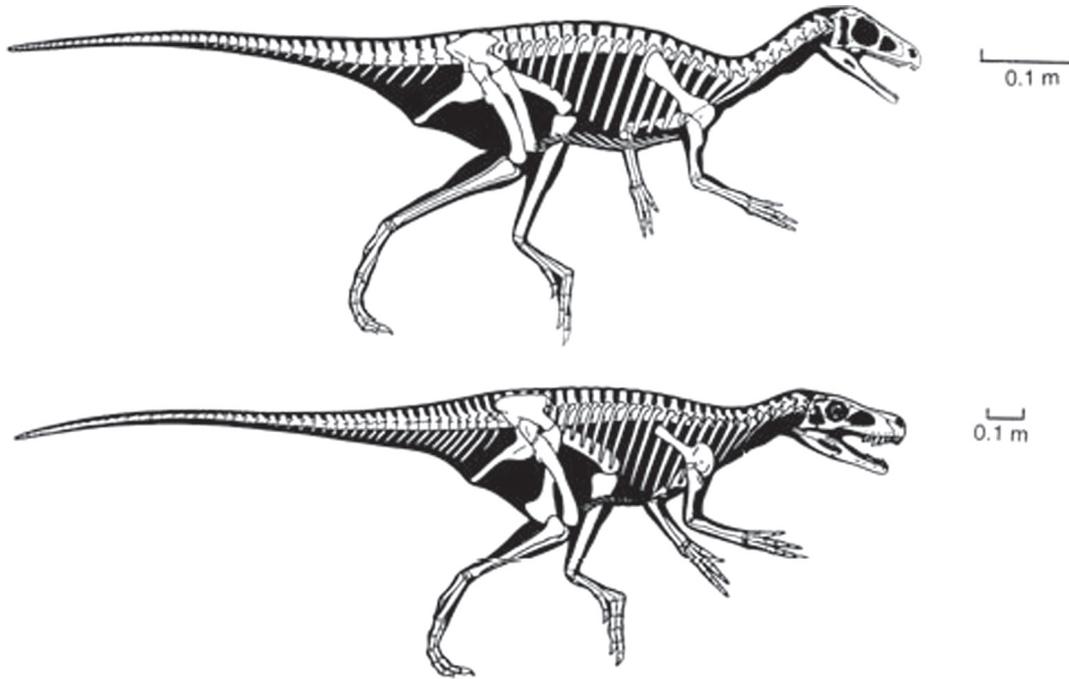


Figure 3. The first dinosaurs: (A) *Eoraptor*, skeleton in lateral view; (B) *Herrerasaurus*, skeleton in lateral view.  
[Figures courtesy of Paul Sereno and Carol Abraczinskas.]

### **Radiation of the dinosaurs – competition or mass extinction?**

There are currently two ways of viewing the radiation of the dinosaurs in the Late Triassic. Either they radiated opportunistically after a mass extinction event, or they competed over a longer time-span with the synapsids, rhynchosaurs, and basal archosaurs, and eventually prevailed.

Until recently, most authors (e.g. Bakker, 1972; Charig, 1984) favoured the competitive model for four reasons. First, as mentioned above, many considered that the dinosaurs were a polyphyletic assemblage, and hence that dinosaurs arose several times as a result of similar competitive pressures. Second, the origin of the dinosaurs was seen as a drawn-out affair, that started early in the Mid-Triassic, and involved extensive and long-term competition (Fig. 4). The dinosaur ancestors were regarded as superior animals, with advanced locomotory adaptations (erect gait) or physiological advances (warm-bloodedness, or cold-bloodedness: both cases have been argued!) that progressively competed with, and caused the extinction of, synapsids and basal archosaurs. Third, the appearance of the dinosaurs has often been regarded as a great leap forward in evolutionary terms.

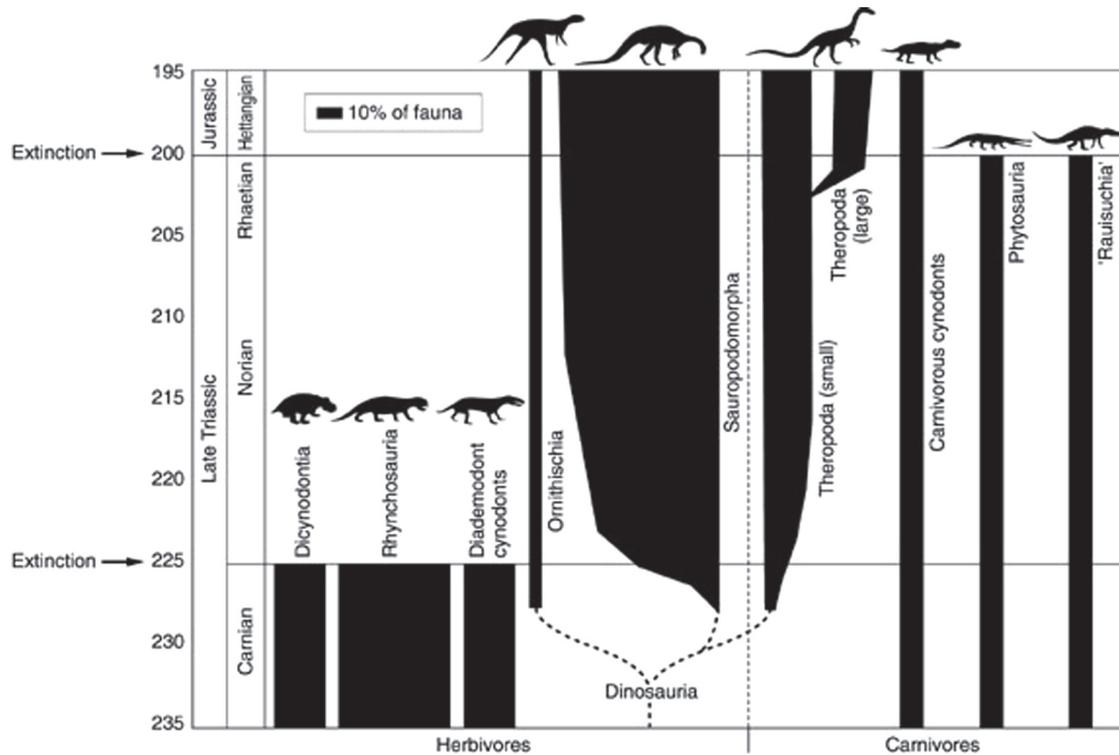


Figure 4. The expansion of the dinosaurs in two phases: (1) sauropodomorphs expanded in abundance and diversity at the beginning of the Norian, after the extinction of dominant herbivore groups (rhynchosaurs, dicynodonts, chiniquodontid cynodonts); (2) theropods diversified, with the appearance of large species, after the extinction of phytosaurs and 'rauisuchians' at the end of the Triassic. Note that the proposed expansion of large theropods only in the Early Jurassic has been questioned by Tanner *et al.* (2004).

Asterisks mark the end-Carnian and end-Triassic extinction events. Abbreviations: HET., Hettangian; SIN., Sinemurian.

A fourth reason why many palaeontologists accepted the competitive model for the radiation of the dinosaurs was more general. It had commonly been assumed that the evolution of life is in some way progressive, that more recent plants and animals are inevitably better than those that went before. So, modern mammals might be said to be better competitors than archaic mammals, archaic mammals might be better than dinosaurs, and dinosaurs might be better than their forerunners. This assumption of progress has never been demonstrated (Benton, 1987), and indeed the major changes in world floras and faunas might equally well be associated with expansions into new ecospace, involving no direct competition with pre-existing forms at all.

Several lines of evidence (Benton 1983, 1986, 1994) suggest that the dinosaurs radiated after ecospace had been cleared during the end-Carnian extinction event (Fig. 4), and that the dinosaurs did not establish their pre-eminence after a long period of competition with precursor groups.

1. The fossil record does not show a gradual take-over, but two rapid expansions after extinction events. The first dinosaurs in the Carnian were rare (1–3% of individuals). An extinction event at the end of the Carnian saw the disappearance of all dominant herbivore groups – the dicynodonts, most herbivorous cynodonts and the rhynchosaurs. Herbivorous dinosaurs then radiated seemingly rapidly in the early Norian, rising to 50–90% of individuals. Dinosaurs diversified further in the Early Jurassic after a second mass extinction at the very end of the Triassic when the remaining basal archosaurs and other groups died out.

2. The first dinosaurs had the key characters that assured their later success, but they did not take over at once (Serenó, 1999). During the Carnian, all three major dinosaurian lineages were present, but theropods and sauropodomorphs did not radiate for some 5–10 Myr after their origin, and ornithischians 20–25 Myr later, in the Early Jurassic.

3. The ‘superior adaptations’ of dinosaurs were probably not so profound as was once thought. Many other archosaurs also evolved erect gait in the Late Triassic, and yet they died out (e.g. aetosaurs, rauisuchians, ornithosuchids, and some early crocodylomorphs).

4. There were other extinctions at the end of the Carnian. The Dicroidium flora of the southern hemisphere gave way to a worldwide conifer flora about this time. There were turnovers in marine communities, particularly in reefs, and there was a shift from pluvial (heavy rainfall) climates to arid climates throughout much of the world (Simms and Ruffell, 1990). The climatic and floral changes may have caused the extinctions of the dominant herbivorous tetrapods.

5. The idea that simple competition can drive the replacement of one major group by another is an oversimplification. Competition between families or orders of animals is very different from the ecological observation of competition within or between species. In palaeontological examples such as this, competition has often been assumed to have been the mechanism, but the evidence has generally been shown to be weak (Benton 1987).

This kind of macroevolutionary debate is hard to set out in clearly testable form. Many palaeontologists would prefer not to investigate such questions, regarding them as story-telling of the worst sort. Intelligent people are bound to ask questions about major events, whether mass extinctions or evolutionary replacements; it would be unsatisfactory simply to say ‘we do not know, and never will’. And, as the quality of our understanding of the fossil record improves (more fossils, better dating, better geographical coverage), it is possible to home in on events and dissect them in increasing detail.

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