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## Palaeontology: Dinosaurs, Boneheads and Recovery from Extinction

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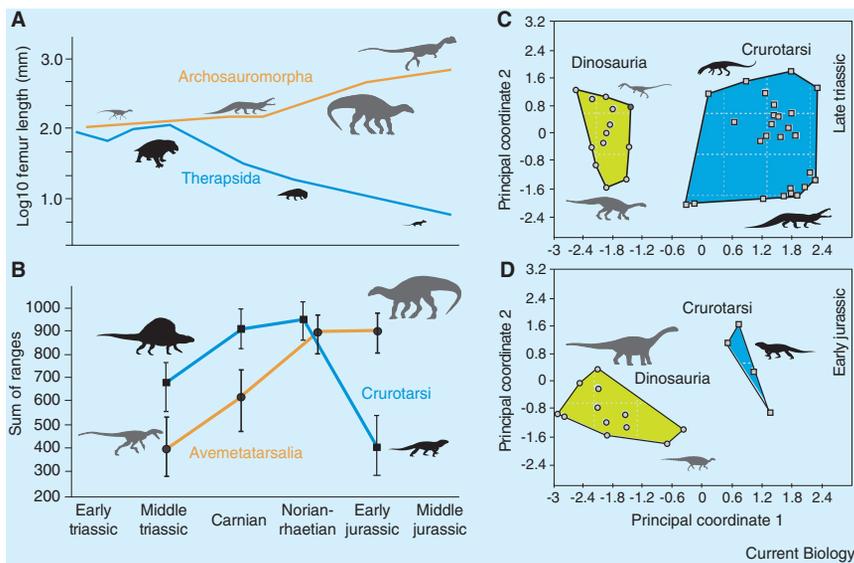
The Triassic was a time of turmoil, as life recovered from near-annihilation. Archosauromorph reptiles flourished and diversified as they filled empty ecological niches, and some of them presaged later dinosaurian inventions, such as thickened skull roofs.

The history of complex life on Earth began with the Cambrian explosion, 540 million years ago, and it was punctuated halfway through by the greatest crisis of all time, the Permo-Triassic mass extinction, 252 million years ago. As many as 90% of all animal species were wiped out, and the recovery of life was stuttering and unpredictable [1]. On land, the archosauromorph reptiles, including distant ancestors of modern crocodiles and birds, were first to explore the newly emptied landscapes, and they diversified into a broad range of forms, including the very first dinosaurs, appearing perhaps in the Middle Triassic [2–4]. By the Late Triassic, 237–201 million years ago, dinosaurs were going strong, together with other relatives, but the true range

of archosauromorph adaptations at that time has not been fully appreciated. In a new paper, in this issue of *Current Biology*, Michelle Stocker and colleagues [5] present a new archosauromorph, called ‘*Triopticus*’, which has an unexpected adaptation, a massively thickened skull roof, which is unexpectedly reminiscent of an invention of the pachycephalosaurs, dinosaurs of the Late Cretaceous.

Vertebrate life on land has sometimes been characterised as a to-and-fro relay between mammals and reptiles. In the Permian, synapsids (which include ancestors of mammals) dominated. The Permian ended with the mass extinction, and reptiles came to the fore, most

notably the archosauromorphs, including the dinosaurs, which dominated throughout the Mesozoic. And after they had died out 66 million years ago when an asteroid hit the Earth, the mammals came back. These two mass extinction events have long been viewed as important case studies for two macroevolutionary phenomena that were first highlighted by George Gaylord Simpson in his seminal book *Tempo and Mode in Evolution* [6], namely evolutionary relays and adaptive radiations. An evolutionary relay, in Simpson’s terms, is the replacement of one major clade by another, such as synapsids by archosauromorphs, or dinosaurs by mammals. Key questions concern the timing of the replacement,



**Figure 1. Macroevolution of tetrapods through the Triassic.**

(A) The relative fates of therapsids (derived synapsids) and archosauromorphs (archosaurs and close relatives) through the Triassic and the early part of the Jurassic, showing a long-term reduction of body size of therapsids and increase in body size of archosauromorphs. These trends were not driven by active selection for larger body sizes, based on [7]. (B) Changing fates of Avemetatarsalia (dinosaurs and relatives) and Crurotarsi (crocodile-line archosaurs), showing parallel changes in disparity (measured by sum of ranges) in the Triassic, and the crash in crurotarsan disparity through the end Triassic mass extinction, based on [8]. (C,D) Changing relative morphospace occupation by Dinosauria and Crurotarsi, suggesting a lack of impact of early dinosaurian evolution on crurotarsan morphospace in the Late Triassic, and a modest response by Dinosauria after extinction of Crurotarsi in the Early Jurassic, based on [10].

and whether it involves some form of competition or is mediated by environmental drivers. Adaptive radiations, or diversification events, are times when a clade expands rapidly. Key questions here concern the relative timing of the expansion and whether the diversification is driven by one or more key adaptations — special features that enable the group to occupy unique ecological niches — or by ecological opportunity, as it may arise when a species, or a group of species, goes extinct (Figure 1).

Archosauromorphs had evolved in the Late Permian but did not become particularly diverse or morphologically differentiated until the Triassic. A numerical study of evolutionary rates and models [7] found that archosauromorphs increased in mean body mass throughout the Triassic, while synapsid body size decreased, but the changes were evolutionarily passive, unlikely to be driven by these clades interacting (Figure 1A). There was no strong evidence for a trend towards larger size, sometimes called Cope's Rule, where evolutionary

rates were statistically faster than random (meaning passive change). A different study of rates of morphological change [8] also found that the rise of dinosaurs was gradual and they did not replace precursor groups rapidly (Figure 1B–D). These studies suggest that this Simpsonian evolutionary relay at least had been passive and long-term, with little evidence that the new groups, including dinosaurs, had burst onto the scene aggressively and rapidly vanquished the other clades.

But what was the balance of morphology and diversity in the diversification of archosauromorphs? Palaeontologists like to measure diversity (the number of species or genera) and disparity (the amount of morphological variation) and track the two through time. It has become clear that diversity and disparity are rarely coupled [9,10], which might come as a surprise — one might expect that morphological and ecological diversity would expand in concert with overall diversity of a clade. The patterns can go both ways, but the commonest finding in palaeontological studies has

been disparity-first, meaning that the new group, equipped with one or more novel characters, expands rapidly to the limits of morphospace (the numerical space that defines the sum total of morphologies seen in a sample of species), and subsequent evolution consists of specialisation of species to fill gaps in morphospace, not to expand it any further.

Stocker and colleagues [5] describe the new archosauromorph *Triopticus* based on a 9 cm long, rather solid lump of bone from the Otis Chalk (Dockum Group) of Texas, dated at 225 million years ago. At first sight it looks incomprehensible, a brownish handful, domed on top and covered with knobs and bumps, and with openings and hollows below. Once it is oriented, however, it becomes clear that this is a braincase with the arches over the eye sockets, and then an amazing thickening of bone above. In a normal archosaur of this size, the skull roof would be perhaps 5 mm thick, but in the *Triopticus* specimen it is over 50 mm thick. CT scanning reveals full details of the brain cast, including the semi-circular canals of the inner ear, all beautifully preserved inside. The name *Triopticus*, 'three eyes', refers to a third depression in the midline that looks like, but is not, an additional eye socket.

What is remarkable about *Triopticus* is that it increases the morphological disparity of Triassic archosauromorphs substantially, and provides an example of convergence with a clade of dinosaurs that lived 100 million years later, during the Cretaceous. The pachycephalosaurs are well known from Mongolia and North America as bipedal herbivorous dinosaurs that had a massively thickened cranium, used perhaps in male-on-male pre-mating combat, analogous to mountain sheep today. Such an adaptation was unexpected in basal archosauromorphs back in the Triassic.

In their morphometric analysis, which included 81 measurements of the shape and characteristics of skulls and skeletons, Stocker and colleagues [5] found *Triopticus* marking an extreme point, located further from the centroid of the overall sample of Triassic archosauromorphs and dinosaurs than even the pachycephalosaurs. In fact, to their surprise, the authors found that the Triassic sample occupied a larger area of morphospace than the dinosaur sample,



**Figure 2. The Otis Chalk menagerie.**

This single site from the Late Triassic (225 million years ago) has produced an amazing array of archosauromorphs, showing the extent of morphological variety achieved through the Triassic. Skulls of the long-snouted phytosaur *Angistorhinus* (top); the flat-headed temnospondyl *Buettneria* (bottom left), the newly discovered thick-skulled rauisuchian *Triopticus* (bottom middle) and snout of the beaked *Trilophosaurus* (bottom right). Courtesy of Michelle Stocker and Sterling Nesbitt.

although both comprised a similar number of species. Indeed, the Otis Chalk assemblage from Texas (Figure 2), as a single sample of the life of the Late Triassic, encompasses as much morphological disparity as all dinosaurs. It includes slender-snouted, fish-eating phytosaurs, armoured, snub-nosed, herbivorous aetosaurs, the bipedal, carnivorous rauisuchian *Poposaurus*, beaked shuvosaurids — and now the dome-headed *Triopticus*.

The new study by Stocker and colleagues [5] confirms earlier suggestions [8,10–12] that Triassic archosauromorphs experienced an early burst of evolution with an explosion of body forms. This burst was doubtless enabled by the huge opportunities for terrestrial vertebrates created by the mass extinction at the end of the Permian. Life in the Triassic seems to have accelerated in some way following the extinction, with a marked shift of all medium and large-sized animals from a sprawling posture, as seen today in lizards and salamanders, to an erect posture in both synapsids and archosauromorphs [13,14]. With faster, more sustained gaits, the new

archosauromorphs occupied morphospace and ecospace occupied before the crash by Late Permian synapsids, but they also evolved morphological and ecological adaptations never seen before. This enormous creativity in the morphology of the Triassic archosauromorphs presumably stimulated the origin of all modern tetrapod clades during the Middle and Late Triassic, such as the lissamphibians, turtles, lepidosaurs (lizards, snakes and relatives), crocodylomorphs, mammals, and even birds (in the form of the dinosaurs) [15]. This was a time of extraordinary invention in evolution.

Why did *Triopticus* and its disparate congeners not continue their remarkable early evolutionary success? A further mass extinction occurred at the end of the Triassic, 201 million years ago, and nearly all those groups found in the Otis Chalk succumbed. Dinosaurs somehow survived the crisis. They came to repeat some of the adaptations and designs already shown in the Late Triassic, but added many more, becoming a hugely successful group that dominated life on land for a further 135 million years.

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