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The rise of the mammals

Fossil discoveries combined with dating advances give insight into the great mammal expansion

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More than 70 million years ago, dinosaurs ruled the Earth and the furry ancestors of the mammals were nothing but lunch for the dominant species. This all changed dramatically when 66 million years ago an asteroid impacted on Earth. The resulting climate change drove the large dinosaurs to extinction and thus created large ecological niches for mammals to rapidly evolve and take over. At least, that was the interpretation of what happened after the impact. But it was only recent discoveries of extensive fossils from that era, combined with advances in accurate dating techniques, that have dispelled most lingering doubts about the rise of the mammals in the wake of the Cretaceous–Paleogene mass extinction (KPgE). These advances have also achieved what earlier looked impossible by extracting more granular detail about the events and behavioural adaptations that occurred during the million years after the KPgE.

This interest in the evolution of mammals and plants at the end of the Cretaceous period has only arisen quite recently, although some mammal relics were already described in the original discovery of the dinosaurs in 1824 when naturalist William Buckland presented bones from one of the first known dinosaurs, Megalosaurus, at the Geological Society of London. At the same time, Buckland revealed some small jaws from the same group of fossils, but these attracted far less interest than the discovery of the huge dinosaurs. Over the next 160 years, further mammalian bones turned up alongside dinosaur fossils, but it was only in 1997 with the discovery of a more complete mammal fossil in north-eastern China that the great mammalian radiation hypothesis began to take root. This has been followed by discovery of nearly 60 almost complete specimens from that same area.

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Climate change as driver of evolution

Still lacking though was an understanding of what happened during that rapid expansion or the selective forces behind the rapid increase in size and changes in behaviour such as a switch from nocturnal to diurnal living for some species. That deficit has now at least partially been allayed by analysis of an unusually complete record of not just mammals but also reptiles and plants found in the state of Colorado, USA (Lyson *et al*, 2019). According to the authors, it has provided the first clear elucidation of the drivers and tempo of biotic recovery after the KPgE, and their calibration against climate change.

Mammalian taxonomic richness doubled over the first 100,000 years. Mammals also recovered to the size of the pre-extinction period, that is up to 7 kg in weight compared with the 0.5 kg of the immediate survivors of the asteroid impact. At the same time, the richness of megafloral species also increased rapidly, which in turn drove an equally dramatic increase in the body mass of the largest mammals. After 300,000 years these had increased by 30 times up to 15 kg. The next major development was emergence of the bean family about 700,000 years after the KPgE that further stoked the evolution of additional large mammals, according to the study. By now, mammals up to 50 kg weight were present. Furthermore, it appeared that each of the concurrent plant and mammal bursts in diversity seemed to coincide with global warming.

It was the combination of an extensive cross section of fossils covering this period and highly accurate sources of dating that enabled the researchers to lift the bonnet on the events within this million year period for the first time, commented Tyler Lyson, Curator of Vertebrate Palaeontology at the Denver Museum of Nature and Science and lead author on that paper. “We were very fortunate to not only have fantastic plant and animal fossils, but we were able to date the rocks in which the fossils were found”, he said. “Other areas from this time period lacked one or more of these critical pieces, that is time, plants, and animals. We determined that, perhaps not surprisingly, these elements were correlated. We noticed three distinct warming intervals and at each warming interval we saw a change in the plants and a subsequent change in the mammalian fauna. Specifically, the warming intervals were important for the reestablishment of the forests, which were devastated by the asteroid impact. The reestablishment of the forests impacted mammalian diversity and overall larger body size by providing new food sources”.

As so often, the study raised further questions, one being the cause of the warming periods that drove the spurts in mammalian evolution. Surprisingly, a likely cause may have been the major volcanic events called the Deccan Traps in what is now southern India that had been considered as causes of the dinosaur mass extinction. However, a

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study published in June 2020 presented evidence through computer simulations that the impact of a 12 km asteroid was almost certainly the cause of the mass extinction rather than the volcanic events (Chiarenza *et al*, 2020). The gist of the argument is that while the volcanic events resulted in temperature changes around 2C which, although significant, were too small to trigger mass extinctions, the asteroid impact might have temporarily crashed average global temperatures by as much as a 30°C. However, those smaller warming events driven by the volcanoes would have been sufficient to trigger temporary accelerations in mammalian and plant evolution. After the extinction of the dinosaurs, the volcanoes sparked small temperature increases coinciding with those spikes in evolution. As Lyson concluded, "these warming intervals likely played a role in the rapid evolution and re-diversification of the ecosystems post extinction".

Elucidating behaviours from the fossil record

Such rapid evolution in size and diversity appears to have coincided with equally dramatic behavioural changes in mammals. The most fundamental change was the emergence of diurnal mammals active during the daytime, after they had been confined to more furtive nocturnal foraging or hunting by the dominance of the dinosaurs. Yet, this is the more challenging part as identifying behaviour from the fossil record alone is notoriously difficult, commented Roi Maor who studies evolution of mammalian behaviour at Tel Aviv University in Israel. "This is a behavioural trait that leaves little trace in fossils other than sometimes the shape, size, and orientation of the eye sockets, but their correlation with actual activity pattern is loose and often inconclusive in mammals", he explained. Partly for that reason, Maor and his team conducted a phylogenic analysis of extant mammals based on various nuclear and mitochondrial genes and correlated that with current behaviour traits to infer when major behavioural changes might have occurred.

In 2017, around two years before the Lyson paper, Maor's team reported that the first ancestral mammal species to be active in the daytime probably lived around 65.8 million years ago, just 200,000 years after the dinosaur mass extinction (Maor *et al*, 2017). "This exact timing was based on calculations of the likely activity pattern for each ancestral mammal whose living descendant species were among the 2,415 species in our activity data set, and on the phylogenetic relationships linking all those species", Maor explained. "Such reconstructions of ancestral character incorporate uncertainty from trait data of extant species and uncertainty in phylogenetic relationships". This uncertainty relates to how long a given species existed before becoming extinct or evolving into another species and topology, which reflects the closeness of relationships between species. "While we are highly confident in our activity data, the mammal phylogeny is much less certain, and at least three alternative phylogenetic models, as a phylogenetic tree or set of trees, have been published since we performed our analyses", Maor added. However, his team was able to narrow uncertainty over the key event—the evolution of diurnal activity of the relevant species, the Artiodactyl—to levels below 2%. "That is, the probability that the ancestral Artiodactyl that lived 65.8 Ma was not active during the day, that is nocturnal, is very small", Maor commented.

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Rapid evolution of placental mammals

Mammals then were predominantly small and nocturnal before the great mass extinction, but there had already been sudden increases in diversity. However, prior to the mass extinction, those appeared to be in groups that had evolved in parallel to the placental mammals that are dominant today. "The explosion in mammal diversity 65.8 Ma occurred mainly on the placental branch of the mammal tree", Maor said. "Although recent discoveries show that Mesozoic (252 million to 66 million years ago) mammals were more diverse than previously thought, this diversity was in groups that are not ancestral to placental mammals, and that later became extinct", he added, referring to a recent paper (Grossnickle *et al*, 2019). "So one can average overall mammalian diversity and thus get a slightly less dramatic change in mammal diversity post K-Pg, but the 'explosive' pattern in placentals remains".

This distinction between early mammalian groups—the therians that give birth to live young without a shelled egg and the non-therians—is crucial to understanding their evolution and change across around the Cretaceous–Paleogene, argues Gregory Wilson Mantilla at the University of Washington, Seattle, USA. "Rather than thinking of mammals as one monolithic group, we can view them as the major modern groups, with eutherians leading to placentals and metatherians leading to marsupials, and monotremes who are minor players, then the non-therian groups that have no living members", he said. "Some of those non-therian groups, such as multituberculates, seem to have been diversifying along with the early episodes of the angiosperm ecological diversification in the latest Cretaceous 85 mya and into the Cenozoic. The therians, that is eutherians plus metatherians, seem to have been a bit slower to diversify and perhaps requiring the extinction of non-avian dinosaurs".

The multituberculates are an extinct taxon of rodent-like mammals, while the Eutheria is one of two mammalian clades with extant members that diverged in the Early Cretaceous or perhaps the Late Jurassic. All current mammals indigenous to Europe, Africa, Asia and North America north of Mexico are eutherians. Metatheria is the other clade that includes all mammals more closely related to marsupials.

The underlying point is that rapid evolutionary changes are not evenly distributed across all taxa: some evolved faster with variations in timing and geography. As Maor pointed out, "the larger your focal clade, the less dramatic patterns you can expect to observe. This is because speciation and extinction occur all the time, but are, presumably, unevenly distributed among taxa, and ecological factors determine the odds for extinction or speciation. Looking at larger clades, which are more diverse ecologically, has an averaging effect on observed evolutionary trends". In this case, the changes around the great dinosaur mass extinction are more exceptional across placentals than mammals as a whole. Indeed, placental mammals largely took over, to the extent they account for nearly all living mammalian species today.

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David Grossnickle from the University of Washington, USA, emphasized that despite recent progress, the fossil record before the dinosaur extinction remains woefully incomplete. "So the 'spurts' of mammalian diversification are simply our hypotheses based on our current information, and they'll likely be revised with future fossil discoveries", he commented. "But, based on the current fossil record, early mammals seem to have experienced three distinct diversification events, starting with very early mammals (and mammalian 'cousins', often called mammaliaforms) during the Early or Middle Jurassic, or about 180-160 million years ago. Many mammal groups arose during that time. Several of these groups survived past a time of environmental turmoil in the mid-Cretaceous (ca. 100 million years ago) and seemed to have diversified afterwards".

The third spurt Grossnickle referred to was the Cretaceous–Paleogene mass extinction of non-avian dinosaurs 66 million years ago. "This third diversification event was the most profound, resulting in the incredible diversity of mammals that are on Earth today", Grossnickle said. "And thus it has gained the most research interest, and it's the most widely accepted among my peers".

Mammals co-evolved with plants

Another question has centred around the co-evolution of mammals and plants, since changes in each have in turn driven expansions in the other with mutual feedback. As Grossnickle commented, Lyson's paper significantly strengthened the argument that plants and mammals co-diversified after the K-Pg mass extinction event, but he cautions that further evidence is needed. "Finding strong evidence for co-evolutionary diversifications of plants and mammals (or any animals) remains challenging, because we can't observe ecological interactions of extinct species", he explained. "In contrast, in modern ecosystems, we know which plants are eaten by herbivores, which mammals act as seed dispersers of plants by eating their fruits, etc. But the plant-mammal interactions in extinct lineages have to be roughly inferred from a limited number of clues. And, unfortunately, fossil animals and fossil plants are rarely found at the same fossil localities - different types of preservational environments tend to be associated with animals, for example river-beds, and plants, such as swamps".

Grossnickle conceded though that it was fairly clear that flowering plants, the angiosperms, diversified in the Late Cretaceous—the period between 145 Mya to 66 Mya—and after the K-Pg mass extinction. "This is congruent with two of the three 'spurts' of mammalian diversification, which provides some evidence that many mammals and plants co-evolved with each other", he said. "For instance, fleshy fruits appear in the fossil record shortly after the K-Pg boundary, and at about that same time there was a diversification of primate ancestors (plesiadapiforms) that likely lived in trees and ate those fleshy fruits. Recent fossil discoveries of limb bones have helped to confirm that these primate ancestors were able to climb in trees. Attracting mammals with fleshy fruits benefited the plants because the mammals would disperse the seeds by pooping them out elsewhere around the forest. Therefore, it's likely that the mammal and plant diversifications are linked, but this is still an active research topic".

Grossnickle agreed that, like the fossil evidence, the phylogenetic hypotheses from Maor and others offer further indirect evidence that plants and mammals diversified in tandem. "Basically, there's rapid branching of plant phylogenetic trees at the same time as there's rapid branching of mammal phylogenetic trees in the Late Cretaceous and after the K-Pg boundary, so this is used as indirect evidence that plants and mammals diversified together".

However, it is not the smoking gun that links the two events irrevocably beyond all doubt. "We need more fossils, so it's imperative for us as palaeontologists to continue to do fieldwork to help fill in the gaps in the fossil record", Grossnickle said. "Traditionally, much of what we know about the lead-up to and recovery from the K-Pg mass extinction is based on fossil sites in western North America. However, recently there have been many spectacular fossil discoveries in countries like China, India, and Madagascar, and I'm sure that these regions will continue to produce exciting fossils for the foreseeable future".

Advances will also come through greater collaboration and integration between the two key disciplines involved, that is palaeontology and evolutionary biology. "Traditionally, palaeontologists have studied fossils, and evolutionary biologists have studied modern organisms, including using DNA to produce phylogenetic trees", Grossnickle commented. "Because the two groups of researchers are relying on different lines of evidence, the evolutionary stories told by the two groups are often in conflict. However, in recent years there has been a greater push to merge data from fossil organisms and modern organisms into more holistic studies, thus providing a more complete picture of the evolutionary histories of different groups of organisms".

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