The idiosyncratic mammalian diversification after extinction of the dinosaurs

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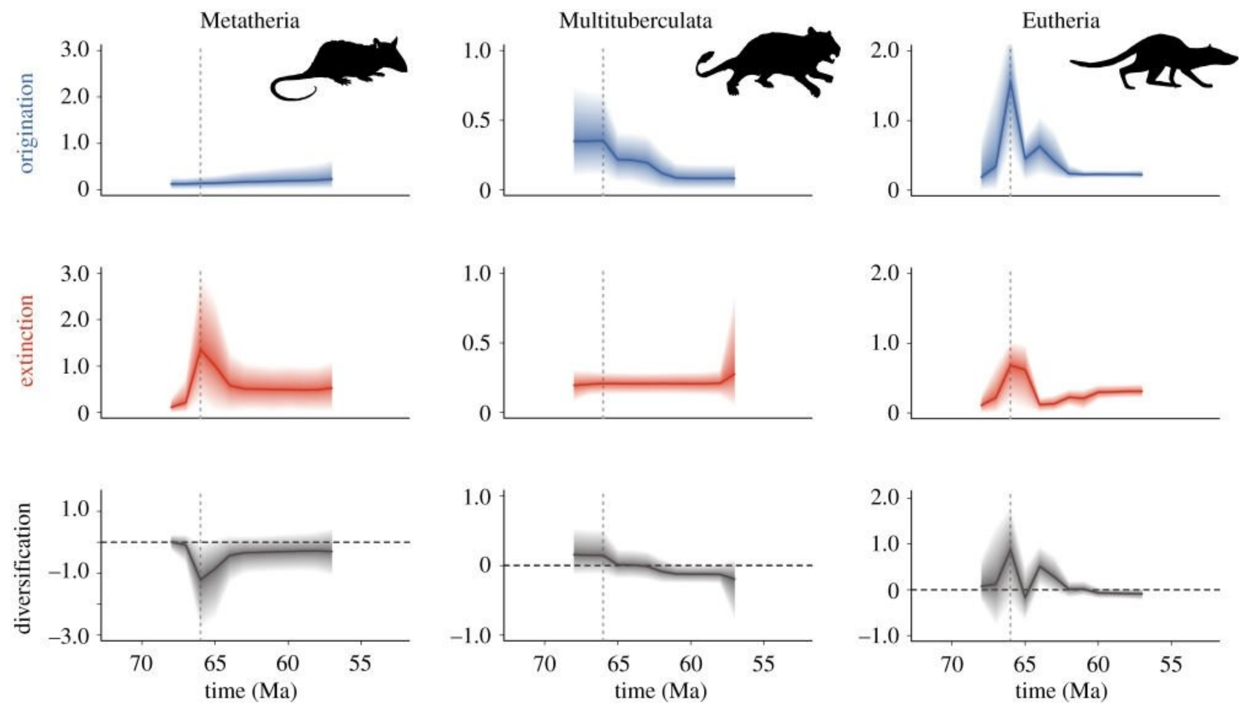

Researchers state that many mammals lineages coexisted with the dinosaurs before the end-Cretaceous mass extinction. Although many species of mammals also disappeared in the extinction event, several lineages survived (image: origination, extinction and diversification rates for the three mammalian clades in North America. Dotted lines denote the Cretaceous-Paleogene boundary. Credit: *Biology Letters*

Mass extinction typically conjures a picture of a meteor falling to Earth and decimating the dinosaurs along with everything else. However, this is not exactly what happened. Different groups of living beings were affected differently by the various mass extinctions that have occurred during the planet's history.

Consider mammals, a class of vertebrates that had already evolved during the dinosaur era and survived the mass extinction event that wiped out almost all the dinosaurs 66 million years ago, marking the end of the Cretaceous Period.

Four lineages of mammals were contemporaries of the giant reptiles. All four survived. Some were more adversely affected than others. In a study published in the journal *Biology Letters*, biologists Tiago Bosisio Quental of the University of São Paulo (USP) and Mathias Pires of the University of Campinas (UNICAMP), both from Brazil, set out to understand how groups of mammals survived the end-Cretaceous mass extinction. Their research was supported by São Paulo Research Foundation—FAPESP.

"When people talk about a mass extinction, it's assumed that they're referring to a single extinction event of exceptional magnitude during which a large number of species became extinct in a relatively short time," Pires said. Another way of looking at mass extinctions consists of observing the number of species in the fossil record. It can be inferred that a mass extinction occurred in a given geological period when the total number of species that disappeared from the fossil record was much higher than the number of new species that emerged.

"In other words, the extinction rate—the speed at which species are lost—surpasses the speciation rate—the speed at which species are created. This makes the diversification rate negative, since the diversification rate is given by the difference between the extinction and speciation rates," Pires said.

Five great mass extinctions have been identified in the fossil record in the last 500 million years (as well as many others on a smaller scale). They occurred for various reasons, such as magma spills lasting thousands or millions of years and releasing billions of tons of greenhouse gases that poisoned the atmosphere and blocked out the sun's rays.

This is what caused the worst of all mass extinctions, in which over 90 percent of species vanished. It happened 252 million years ago, marking the boundary between the Permian and Triassic Periods (and between the Paleozoic and Mesozoic Eras).

Mass extinctions have also been caused by greenhouse effects due to the release of billions of tons of carbon gas (CO_2) trapped under the seabed. One such episode is believed to have occurred at the end of the Triassic some 201 million years ago, killing 80 percent of all species.

The reverse has also happened, with billions of tons of CO_2 being sequestered from the atmosphere and causing temperatures to crash and ice to cover the planet. This was the case 444 million years ago, at the end of the Ordovician, when 86 percent of life forms disappeared.

The mass extinction that occurred 66 million years ago is known as the K-Pg event. The acronym refers to the end of the Cretaceous (Kreide in German) and the onset of the Paleogene (Pg).

On a larger time scale, the K-Pg event marks the boundary between the Mesozoic, the era dominated by dinosaurs, and the Cenozoic, the era extending from 66 million years ago to the present day during which mammals have been one of the dominant groups on the planet.

The K-Pg event was caused by a combination of two factors: devastating magma spills in what is now India and the impact of a comet or asteroid with a diameter of 10 km on the Yucatán peninsula in Mexico.

"All these mass extinction episodes are heterogeneous. They occurred for different reasons and unfolded in different ways. Their impact on life forms was not absolute but relative. Some groups suffered more, others less. Some disappeared, while others took advantage of the new environmental conditions after the catastrophe to diversify rapidly," Pires said.

In the new study, the researchers set out to investigate how the different lineages of mammals that existed at the end of the Cretaceous succeeded in emerging from the biotic bottleneck represented by the K-Pg event. Daniele Silvestro of the University of Gothenburg (Sweden) and Brian Rankin of the University of California Berkeley (USA) also participated in the study.

The great class of mammals emerged in the Triassic at least 220 million years ago. This is the age of the oldest known fossil. At the end of the Cretaceous, mammalian species were highly diversified. There were the Eutheria or placental mammals, the clade to which Homo sapiens belongs, as do all primates, rodents, bats, cetaceans, and ungulates, among others.

In addition, there were Metatheria or marsupials, the clade to which today's opossums, kangaroos, and koalas belong. They shared the planet with monotremes (egg-laying mammals) and multituberculates (an extinct taxon of rodent-like mammals named for the specific shape of their teeth, which had multiple tubercles).

The study by Pires and Quental stresses that mammals were particularly hard hit by the mass extinction in the Cretaceous. This does not mean that all four groups suffered equally. The mass extinction was more severe for some than for others.

During the Cretaceous, between 145 million and 66 million years ago, the multituberculates were the dominant and most diversified group of mammals. We know this because multituberculates are the vast majority in the fossil record prior to the K-Pg event. Fossils of placentals and marsupials are less numerous but also plentiful.

Monotremes are the exception. Today, they are few and far between. Indeed, they are comprised of just two families: one includes the duck-billed platypus while the other regards echidnas. Monotremes are also rare in the fossil record both before and after the Cretaceous, suggesting that the group has always been relatively marginal among mammals. For this reason, the researchers did not include monotremes in their study.

Given the knowledge that there were multituberculates, placentals, and marsupials, which group of mammals was most severely affected by the K-Pg event? Which had the most surviving genera? Which displayed the largest increase in diversity (or highest speciation rate) in the millions of years that followed the biotic bottleneck? Which group failed to recover from the cataclysm?

The only way to find answers to these questions is by analyzing the fossil record in a specific region of the planet to try to ensure that all groups of mammals were affected more or less to the same extent by the catastrophe 66 million years ago and in that region.

Quental and Pires chose North America as the focus for their study. One hundred and fifty years of continuous paleontological prospecting in the region have created a detailed picture of mammalian diversity before, during and after the K-Pg event.

"North America has a fossil record of sufficient quality for this kind of study. Other studies have been conducted to analyze how mammals as a whole survived the Cretaceous extinction, but as far we know, this is one of the first studies to analyze the dynamics of diversification in the different groups of mammals," Quental said.

Distinct diversification patterns

The scientists used a dataset containing 188 recent fossil assemblages from the Cretaceous and Paleocene (spanning from 69.9 million to 55 million years ago) located in the western interior of North America.

"The North American mammal fossil record has the richest and most extensively studied assemblages near the K-Pg event. Fossil occurrences are relatively well resolved, minimizing taxonomic uncertainty. This dataset includes information on nearly 290 genera of mammals, including multituberculates, eutherians, and metatherians," Quental said.

Several advanced statistical methods were used to estimate origination, extinction and diversification patterns before, during and after the K-Pg event. The results showed that the three groups emerged very differently from the mass extinction.

The origination rate for Methateria (marsupials), for example, remained approximately constant throughout the studied interval. However, a clear peak in extinction was identified during the K-Pg, generating a pulse of negative net diversification. After the K-Pg, the extinction rate gradually diminished, but negative net diversification persisted for more than 2 million years until approximately 64 million years ago.

Multituberculates were diversifying toward the end of the Cretaceous prior to the K-Pg boundary, showing high origination rates and relatively low extinction rates. Near the K-Pg boundary, the extinction rate remained low, but a drop in origination reduced the diversification of multituberculates to near zero. In other words, during the K-Pg, the diversification rate was in balance, as roughly the same number of genera were being created and becoming extinct.

According to the study, after the K-Pg boundary, the extinction rate for multituberculates continued to fall; however, the decrease in multituberculates' origination rate was even sharper, hence leading to negative diversification. Thus, the number of genera continued to diminish throughout the rest of the period analyzed, until 55 million years ago. The decline appears to have persisted for a long time, given that the multituberculates steadily disappear from the world fossil record. The clade ends approximately 35 million years ago.

Scientists believe the reason for the disappearance of the multituberculates may have been growing competition with rodents, a new eutherian lineage that originated shortly after the K-Pg in the Paleogene.

Eutherians (placentals) display high origination and high extinction near the K-Pg, resulting in high diversity turnover. Originations were higher than extinctions, except between 66 million and 64 million years ago.

Not long after this, there was a second origination pulse accompanied by a drop in the extinction rate, evidencing a short burst in diversification. Around 62 million years ago origination decreased and diversification remained around zero, suggesting diversity equilibrium.

"We found three diversification patterns among the mammalian groups. Metatheria (marsupials) conformed to the classic mass extinction response, with several temporally clustered extinctions leading to a sharp drop in diversification," Quental said.

Multituberculates underwent a reduction in diversity, with a decrease in diversification and subsequent diversity loss driven by declining origination rates rather than extinction. In other words, their diversity diminished because the creation of new species took a long time.

"Among eutherians there was a more complex rise-and-fall pattern due to rapid fluctuations in the speciation rate during and just after the K-Pg, while the extinction rate rose but not enough to cause negative diversification for long," Quental said.

According to Pires, the study shows that the K-Pg mass extinction was ecologically selective among mammalian lineages. "Extinctions were concentrated among the specialized carnivorous metatherians and insectivorous eutherians, whereas more generalized eutherians and multituberculates survived and maintained higher diversity," he said.

Although the results suggest eutherians suffered substantial losses at the K-Pg boundary, these losses were offset by increased origination. Diversification may have occurred among the survivors as other groups of eutherians came to North America from other continents.

"The dietary plasticity of multituberculates may have enabled some species to persist, explaining the low extinction rates. The ecological and taxonomic diversity of multituberculates increased during the late Cretaceous. However, our analysis shows that the multituberculates failed to offset extinction losses because they created less and less diversity, unlike the eutherians, whose losses were offset by high origination rates," Pires said.

In their conclusion, the authors note that when clades are assessed individually, mass extinction events may be seen as shifts in extinction, in origination, or in both regimes.

"This means that studies of macroevolutionary phenomena focusing on broad taxonomic groups may miss a much richer macroevolutionary history, which can be perceived only at finer taxonomic scales," Pires said.

More information: Mathias M. Pires et al, Diversification dynamics of mammalian clades during the K–Pg mass extinction, *Biology Letters* (2018). DOI: 10.1098/rsbl.2018.0458

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