Sample translation:

by the author

Prologue (pp. 11 – 13)

Since I was five years old, I have been fascinated by the giant dinosaurs of prehistoric times. I am very grateful that my passion and my destiny were revealed to me so early in life and that I was able to make this enthusiasm for dinosaurs my profession. Today, when I find a dinosaur bone in the field, I still have the same sparkle in my eyes as I did when I saw real skeletons of these giants for the first time at the Senckenberg Museum in Frankfurt. However, with the best will in the world, the path from dino-crazy child to vertebrate paleontologist was not straightforward. Nevertheless, I had the great fortune to be part of many, sometimes very important discoveries, even if I myself was not the center of attention. Some research projects I was involved in contributed to a better understanding of the evolution of dinosaurs and other prehistoric reptiles and fundamentally changed our image of dinosaurs. Some of it can be found in this book. Im happy to live in the golden age of palaeontology, when we use the latest technology to uncover new mysteries and unravel secrets that just a few years ago were thought never to be explained. One reason we've learned so much about the dinosaurs recently is the incredible speed with which new dinosaur species are being scientifically described. In the last 20 years alone, more new dinosaur species have been discovered than ever before. On average, around 45 new dinosaurs have been scientifically described each year since 2003, and there are currently no indications that the frequency will decrease in the foreseeable future. The reasons for this are more financial resources for science, more scientists, more teams in the field, better accessibility of remote sites and ever more accurate geological maps with exact coordinates of these sites. It is not uncommon for new fossils to be discovered at known locations during subsequent campaigns, and it is not uncommon for new species to emerge at these known sites. Another very important reason is the rapid advance in computing power and computing speed of computers and workstations, which make it possible to create simulations and three-dimensional models or to evaluate complex statistics and generate new family trees of dinosaurs.

But new dinosaur species not only provide new tongue twisters and not only fill the museums and expand the ancestral gallery of the dinosaurs, but also bring new insights into the relationship of these animals, their habitats and their survival strategies, paint an ever more accurate picture of their environment, their appearance and even help us to better understand the inner structure of the animals and the function of their internal organs. This is extremely important because some dinosaurs had such unusual physiques that we don't find anything comparable in nature today. It is also important because it helps us understand how dinosaurs were able to cope with drastic climate changes and adapt to new habitats.

Dinosaurs were fascinating creatures that can serve as model organisms to understand many mechanisms of nature and evolution. In this book, I use a few prominent examples to discuss the fact that there are always new discoveries to be made and that, despite our broad knowledge of dinosaurs, many questions still remain unanswered.

The Great Dying (pp. 15 – 24)
When the earth was burning, and the sea couldn't breathe.

In order to understand why the dinosaurs were able to become the most successful terrestrial vertebrate group in earth’s history, we first have to go back to the beginnings of the dinosaurian evolution and clarify which factors were necessary for the dinosaurs to be able to start their triumphant procession.
Today, every child knows that all dinosaurs, with the exception of modern birds, died out at the end of the Cretaceous period, around 66 million years ago when an asteroid hit the Earth and sealed their fate. This caused a mass extinction event, wiping out not only the dinosaurs, but many other animal species, including, for example, the ammonites in the oceans. The ammonites were Cephalopods related to today's nautilus and squid. They lived in the oceans of our planet for well over 300 million years and were an important part of the sometimes highly complex food webs in the marine ecosystems. Following the ammonites, which were often the main source of food for the bigger animals, large marine reptiles such as the paddle lizards (Plesiosaurs) and the monitor-like Mosasaurs also died out, leaving no surviving descendants.
As terrible as the consequences of this cosmic impact were, they were overshadowed by an event even more cataclysmic. An event widely considered to be the worst catastrophe ever for life on our planet, it was a cataclysm of apocalyptic proportions, so devastating that some authors refer to it as "The Great Dying": The Permian-Triassic mass extinction.
Michael Benton, one of the most important paleontologists of our time, even wrote a book about it with the striking title: "When Life Nearly Died". Taking place at the end of the Permian, it was the largest extinction event in Earth's history, resulting in about 90% of all species of that time becoming extinct. And for the first time in the history of the earth, many species of insects were also affected by the extinction.
During the Permian, food was still plentiful for all animals. Earth was a green planet. Plant growth had been so abundant for millions of years that the oxygen content in the atmosphere continued to rise and reached its highest level in the entire history of the earth. It is estimated that the atmospheric oxygen levels in the Permian were at about 30 percent. ((For comparison, oxygen levels in the atmosphere today are at only about 21 percent.))
But droughts, wildfires, air pollution and acid rain subsequently destroyed the lush forests, causing atmospheric oxygen levels to drop from 30 to about ten to fifteen percent and stayed there for millions of years throughout the entire Triassic period and even well into the Jurassic, never again reaching levels similar to those at the beginning of the Permian period. The effects were so far-reaching that it took nearly 15 million years for forests on Earth to recover fully from this catastrophe.

“The Great Dying”, and the subsequent collapse of the ecosystems, are thought to have been caused by mega-volcanism in Russia, observable still today by the remnants of the ancient lave streams, the so-called Siberian Traps, also called flood basalts (Russian: Сибирские траппы). These Siberian traps, or flood basalts, are gigantic lava sheets that stretch from the Barents Sea in the north-west to Kazakhstan in the Southwest. From there, they extend to

Novosibirsk and Irkutsk in the South. In the East, they extend beyond the Lena stream almost to Yakutsk. Some of you may recognise Irkutsk and Yakutsk from the board game “Risk”. The volcanic eruptions occurred in three waves over a 900,000-year period and covered an area of seven million square kilometers with magmatic (volcanic) rock. That is equivalent to almost the entire area of Australia!

The volcanic eruptions responsible for this event are considered to be among the largest-known volcanic events in Earth's history. The eruptions took place about 252 million years ago at the Permian-Triassic boundary and their consequences, as we have already seen, are causally linked to the mass extinction event at the end of the Permian.

The post-apocalyptic world after the Permian catastrophe must have come very close to our idea of hell. The mega-volcanism in Siberia released substantial amounts of carbon dioxide, fluorine, hydrogen chloride and sulfur dioxide, which combined with the rain to form sulfuric acid, causing lasting damage and destruction to marine and terrestrial habitats. Carbon dioxide emissions triggered global warming, increasing the global temperature by 5°C within a very short period of time. We now also suspect that the ozone layer too was severely damaged by the greenhouse gases and the fly ash, resulting in an increase in UV radiation, in turn hampering plant growth and causing pollen malformations. Massive forest fires accelerated the large-scale vegetation loss, and acid rain finished it off. It rained periodically, but only during the mega monsoon season, during which the celestial floodgates would open wide and pour forth torrents of caustic rain for days and weeks across the supercontinent of Pangea. The rest of the year was marked by terrible heat waves, droughts, fires and an average temperature of an unbearable 45°C. While there was still some isolated vegetation in the coastal regions, the interior land mass was dominated by vast deserts wider than even the Sahara or the Gobi. The consequences were devastating. The extreme conditions intensified the weathering processes (erosion) on the land, and the subsequent draining of the soil into the sea led to certain over-fertilization (eutrophication) effects such as the sudden proliferation of algae (algal blooms) in the marine habitats (biotopes). At the same time, there was an immense propagation of marine protozoa in oxygen-free (anoxic) environments, which released methane, halocarbons and considerable amounts of hydrogen sulphide (H_2S) into the atmosphere, in addition to all the gases from the volcanism.

Meanwhile the oceans too became oxygen-free (anoxic) causing all the reefs to die off, and with them all their inhabitants. We know about the momentous, oceanic, anoxic event because of the so-called black shales which only form under anoxic conditions. Once the anoxic ocean zones had formed, the pH had rapidly dropped, and the methane hydrate had released, a mass extinction began in the oceans. Methane escaped into the atmosphere, warming the Earth by a further 5°C and the upper water layers of the world's oceans by at least 8°C. The land was burning and the oceans were boiling. The constantly mounting greenhouse gas concentration initiated a domino effect which we call the galloping greenhouse effect. This explains why the mega-volcanism in Siberia lasted almost a million years, but the mass extinction probably for only about 30,000 years. At first, the changes were gradual, but as more habitats became damaged and destroyed and as more pollutants were emitted, temperatures rose faster, and the collapse of the ecosystems became unstoppable. In the end, about 95% of all marine species and about 75% of all terrestrial species became extinct in this event. Among the few survivors were the direct ancestors of dinosaurs and crocodiles: the so-called archosaurs!

Without this catastrophe, the triumphant rise of the dinosaurs would probably never have happened. It is, perhaps, an irony of Nature that, on the one hand, dinosaurs entered the world stage after a devastating mass extinction, while on the other, they themselves fell victim to such a mass extinction. There have been five such major mass extinction events in Earth's history. Three of these events are closely related to the formation of dinosaurs and were crucial to their unprecedented evolutionary success — but ultimately also responsible for their demise:

The Permian catastrophe around 252 million years ago favoured the development of archosaurs. The archosaurs, the so-called "ruling lizards" include all crocodiles and all dinosaurs. Birds also belong to this group, but there were no birds in the Triassic, yet. Archosaurs, and dinosaurs in particular, were so successful in the hostile world of the Triassic because they could survive in the low levels of oxygen with their efficient lungs, they could run faster with their long, straight legs tucked under their bodies, they could run farther than other reptiles and amphibians with their bodies away from the hot ground, and their scaly skins preventing their bodies from drying out much more efficiently than, for example, the moist skins of the large amphibians (Temnospondyli), an invaluable set of assets in the sweltering heat of the Triassic. This was advantageous in the frequently arid regions of the supercontinent. In this way, they were able to colonize habitats that were previously inaccessible to other creatures.

The end-Triassic mass extinction about 201 million years ago killed the conodonts in the sea, which had existed on Earth for about 340 million years and now disappeared without descendants. They appeared in the fossil record about 541 million years ago. As either the first vertebrates, or close relatives of today's vertebrates, they are among the earliest forms from which fish, amphibians, reptiles, mammals and birds later emerged. Their disappearance did not affect the evolution of dinosaurs, but it does show how momentous this catastrophe was. The extinction of many crocodile relatives at the end of the Triassic, however, did have an impact on dinosaur evolution: Rauisuchians, phytosaurs, aetosaurs and ornithosuchians. These four major groups within the crocodile lineage were as successful in the Triassic as the dinosaurs were, who initially faced considerable competition from them at the beginning of their evolution. At the same time, almost all Temnospondylids, that is, the huge amphibians, some of which could grow up to four metres long, died out. They are considered the sister group of today's frogs and salamanders. For the sake of simplicity though, you can imagine them as four-metre-long monster salamanders, some of which did not have the slippery skin of today's fire salamanders, but instead had dermal bones or even armour plates — so-called Osteoderms, still observable in crocodiles today. With the disappearance of the monster salamanders and most terrestrial crocodiles went also the dinosaurs’ main competition. With the loss of monster salamanders and most land-dwelling crocodiles, there was no longer any competition for the dinosaurs, and so they became the undisputed rulers of the earth at the beginning of the Jurassic.

The end-Cretaceous mass extinction about 66 million years ago finally sealed the fate of all non-avian dinosaurs, i.e. the dinosaurs which are not true birds and are not directly on the avian lineage. At the end of this book, I will explain why the dinosaurs did not survive this event. These three catastrophes did not happen in immediate succession, but many millions of years apart. The evolution of the dinosaurs took place over an unimaginably long time between the Permian catastrophe and the asteroid impact at the end of the Cretaceous period. These two events are about 186 million years apart.

To comprehend this incredibly long time, one has to realize that *Tyrannosaurus* and humans are a little over 65 million years apart. The last tyrannosaurs died out 66 million years ago and humans (Homo sapiens) emerged about 300,000 years ago. *Stegosaurus* on the other hand, became extinct almost 148 million years ago; hence, it lived around 80 million years before *Tyrannosaurus*. *Stegosaurus* and *Tyrannosaurus*, therefore, are further apart in time than *Tyrannosaurus* and humans (although phylogenetically, they are more closely related). But what is even more astonishing is that the very first dinosaurs existed around 90 million years before *Stegosaurus* — even further apart in time than *Stegosaurus* and *Tyrannosaurus*. The world in which *Plateosaurus* (an ancestor of the later, giant, long-necked dinosaurs) lived was a very different world from that in which Stegosaurus lived, and *Tyrannosaurus* in turn lived in a very different world from *Stegosaurus*. The reign of the dinosaurs has lasted so incredibly long that entire continents have broken up, seas have opened and closed, and entire oceans have formed. And this thrilling journey of the dinosaurs was sandwiched between two of Earth's greatest mass extinction events.

Both events were global catastrophes. Why is that important? The dinosaurs were the most successful land creatures in the long history of the Earth. No other group of animals has reigned on land as long as they have. But yet, by the end of the Cretaceous, they succumbed to a mass extinction characterized by large-scale changes in climate and vegetation. The asteroid that caused all this death and destruction only really killed a small number of the dinosaurs directly. All the rest perished in agony in the weeks and months after its impact, under darkening skies, dropping temperatures, dying forests, and the collapsing food chain.

If this scenario sounds somehow familiar, don't be surprised. Today humans are without doubt the most successful complex organisms on Earth. Just like the dinosaurs, we have colonized every continent, asserted our dominance over every enemy, and made use of every resource nature has provided, all the while Earth’s climate is changing faster than it ever has in the history of our planet. At the same time, most people are completely unaware that we are also dealing with an unparalleled species extinction. Never in Earth’s history have so many birds died. An article published in Science in 2019 estimated that the number of birds in North America had decreased by about 3 billion birds since 1970, which accounts for nearly 30% of the entire bird population in that area. In Germany, experts have estimated that bird breeding pairs have dropped from 97.5 million in 1998 to just 84.8 million in 2009, which is a decline of 15% in just 9 years (source: NABU). The number of flying insects has decreased even more dramatically. Their numbers have dropped by an alarming 76% in Germany’s nature reserves over the last 27 years. And while we might be glad that there are fewer mosquitoes at night, flying insects are the main pollinators for most crops and are a vital part of the diets of most bird species, bats, amphibians and small lizards.

The causes of climate change at the end of the Cretaceous are of course completely different than those of today, but that doesn't make the current climate change any less severe. The causes of the extinction of the dinosaurs were from the outside (extrinsic causes), whereas the causes of the current situation are from human activity (anthropogenic causes). Humans are driving climate change and species extinctions, but the devastating loss of species we are

witnessing barely even makes the headlines.
We often hear of people who do not believe in climate change, or who think that humans are not making any significant contribution to climate change. But it does not matter whether people believe in climate change or not, or in species loss or not. Opinions and personal views cannot interfere with facts, which are directly observable in nature: they are objectively measurable and verifiable by reproducible scientific experiments. Choosing to ignore the warning signs will not make the problems go away, they only get worse.

[…]

Chapter 10 (pp. 238 – 277)

Tyrannosaurus: The King of Tyrant-Lizards is the measure of all things!

The power of the brand: why *Tyrannosaurus* is so popular

Every child today knows *Tyrannosaurus rex*, the most popular and most easily recognized dinosaur of all time. The *T. rex* has its place not only in paleontology, but in the hearts of many children. It is a cultural phenomenon: after all, no other dinosaur has had as many depictions as *T. rex* has — whether portrayed on the screen or in books, on T-shirts or on bed linen, in jigsaw puzzles or in video games (including videos games that are not even about dinosaurs). Videos about *T. rex* abound on the internet, and many memes and jokes are based on it and its tiny arms. You'll find it in bags of dinosaur schnitzel, on birthday cakes and even on the lunchboxes of children as they skip to school. *T. rex* is also the most common type of dinosaur toy.
But what is so special about *Tyrannosaurus rex*? What makes it so popular, and why do we find it so fascinating? Much of it has to do with its name: *Tyrannosaurus rex*! That means "The King of Tyrant Lizards", an apt name for the undisputed ruler of the Late Cretaceous period of North America. Had *Tyrannosaurus* been given any other name, it might not have become so well-known.
Paleontologists first discovered individual teeth of *Tyrannosaurus* in Colorado in 1874 but could not yet assign them to any animal. In the 1890's, they discovered individual bones of the postcranial skeleton in eastern Wyoming. In 1892, Edward Drinker Cope, whom we already know from the "Bone Wars", described two poorly preserved vertebrae of *Tyrannosaurus*, which he mistakenly thought were the vertebrae of a horned dinosaur. He named the animal to which they belonged *Manospondylus gigas*, which means "giant porous vertebra". If these vertebrae had been diagnostic and much better preserved, Tyrannosaurus might be called *Manospondylus* today, but this name does not sound nearly as good.
After the deaths of Cope in 1897 and of Marsh in 1899, Barnum Brown found the first partial skeleton of a giant carnivore in eastern Wyoming — in the same region where Cope found his *Manospondylus* vertebrae, as well as the first complete fossil of *Triceratops*. Two years later, Barnum Brown found another partial skeleton in the Hell Creek Formation in Montana. Of this find, Brown wrote at the time: "I have never seen anything like it from the Cretaceous."

Henry Fairfield Osborn, president of the American Museum of Natural History in New York, named both animals in a publication in 1905. He named the find from Wyoming *Tyrannosaurus rex*. The animal from Montana he called *Dynamosaurus imperiosus*, a name combining both Latin and Ancient Greek meaning “powerful mighty lizard”. A year later, however, he realized that the bones from the two finds actually came from the same species and named them both *Tyrannosaurus*. The lower jaw of the animal, which he first described as *Dynamosaurus*, can still be seen in the Natural History Museum in London today. Since Osborn was the first to write about both animals in the same publication, he could have chosen the name *Dynamosaurus* instead, which is a cool name, but not nearly as good as *Tyrannosaurus*. We can be grateful that he chose the name we know and love today!

In total, just over 30 complete or almost complete skeletons are known today. Two of the most famous and most complete tyrannosaurs were discovered in the 1990's: "Stan", which had been on display at the Black Hills Institute in South Dakota for a very long time, and "Sue", which can still be admired at the Field Museum in Chicago. Both Stan and Sue got their nicknames from their respective discoverers, Stan Sacrison and Sue Hendrickson. Though called Sue, paleontologists do not yet know it was actually a female. Paleontologists can work out whether a dinosaur was male or female by checking for the presence of something called medullary bones, a special type of bone in which calcium is stored, and found only in female birds and dinosaurs when they are sexually mature and are able to lay eggs. As far as we know, this medullary bone has not yet been detected in Sue. One of the most beautiful of all skeletons of *Tyrannosaurus* is called “Tristan”. Discovered in Montana in 2012, its skull still contains 98% of its original elements, and is therefore the most complete skull we have of any tyrannosaur in the world. Tristan was on display at the Natural History Museum in Berlin from 2015 to 2020 before being moved to Copenhagen, and then back to Berlin again in 2022. What makes “Tristan” so special is that its bones are almost black — an effect caused by certain minerals in its fossilized bones that give them a glossy shine. In Leiden, Holland there has been on display since 2016 another tyrannosaur skeleton from Montana, nicknamed “Trix”. It was the main attraction of an exhibition tour through Europe from 2017 to 2019. I was lucky enough to see Trix at a conference in Paris in 2018.

A much smaller specimen discovered in 1946 contains a perfectly preserved skull of a small tyrannosaurid, to which the American paleontologist Robert Bakker and his colleagues in 1988 assigned the new species name: *Nanotryrannus lancensis*, which translates to “dwarf tyrant of the Lance Formation” which is rather strange since it actually came from the Hell Creek Formation. Since then, paleontologists have debated as to whether this is a new species or a mere juvenile *Tyrannosaurus rex*. Recent findings indicate that it was in fact a young *T. rex*, but the relatively long arms and the deviating tooth formula (it had more teeth in its jaw than an adult animal) make a proper assessment difficult. Why it still makes sense and what this has to do with allometry and variability, I'll get to in a moment. One of the most spectacular finds ever made was from Montana in 2006. There, a *Tyrannosaurus* and a *Triceratops* were found interlocked in agony. This is direct evidence that *Tyrannosaurus* hunted *Triceratops*. For a long time, the fossil remained in private hands and therefore inaccessible to science, until, fourteen years later, a museum in North Carolina finally bought this gem. It has been open to the public since 2022, and I can't wait to see it with my own two eyes. Thousands of people all over the world swarm to this exhibition just to catch a glimpse of a real dinosaur skeleton. But it is not just the public who are obsessed with *Tyrannosaurus*: paleontologists have studied it more thoroughly than any other dinosaur, and have discovered more about the biology of these giant animals in the last five years alone than ever before. For example, we now know why there were no other major predators in ecosystems where *Tyrannosaurus* was found, we know why its arms were so small, and we know whether *Tyrannosaurus* had feathers or not. Still, much is still uncertain, and the king of the dinosaurs does not cease to fascinate and intrigue us.

Record sum for the king

In the summer of 2019, I was at a dinosaur excavation in the Lance Formation in Wyoming. There, I met Pete Larson, president of the Black Hills Institute, a dinosaur museum in Hill City, South Dakota. Pete is an extraordinary person and a key figure in the discovery of tyrannosaur skeletons. For those of you who haven’t heard of him, look up his name and watch the film Dinosaur 13, a documentary about the discovery of Sue. Pete then invited the camera man, the photographer and me to visit him at his museum. I was desperate to visit that museum because I wanted to see Stan, which, as I have already mentioned above, is one of the largest and most complete tyrannosaur skeletons we have. Pete told us at the time that Stan was about to be sold. Pete and his brother — also a part owner of the institute — were at the time having a legal dispute. Part of the agreement was that Pete got to keep the museum, but his brother got to receive the proceeds from the sale of Stan. On the 6th of October 2020 Stan the *T. rex* was sold to an unknown bidder for the fabulous sum of 31.8 million US dollars — a record sum exceeding that of any previous fossil, and even the wildest estimates. The previous record for a fossil at an auction was for Sue, which had sold for the then enormous sum of 8.36 million US dollars in 1992. As exciting as Stan’s record was, the experts were worried: no one knew who the mystery bidder was and there were concerns that a private collector would withdraw the fossil from the public and thus prevent future research on it. From October 2020 until the end of March 2022, the bidder remained anonymous, the fossil remained “missing”, and speculation about its whereabouts ran wild. When Dwayne "The Rock" Johnson was seen with a tyrannosaur skull in the background during a television interview in January 2022, there were rumors that he was the bidder, but this turned out to be only a replica of Stan's head. Two months later, it was finally announced that the future Museum of Natural History in Abu Dhabi had bought the fossil. Paleontologists were relieved that a museum had acquired the animal and were happy to see it put on display in a part of the world where previously people rarely had access to natural history museums, fossils, and dinosaurs in particular.

How many tyrannosaurs have there been?

We know *Tyrannosaurus rex* only from the North American Midwest . Close relatives of the king of dinosaurs, such as *Tarbosaurus bataar* from Mongolia and *Zhuchengtyrannus magnus* are known from China, but the genus of *Tyrannosaurus* lived only in a restricted area of North America. Although so well-known and so popular, it had only lived for about the last 2 million years before the asteroid's impact at the end of the Cretaceous. But how many tyrannosaurs individuals have ever lived? This question cannot be answered with any certainty. There are simply too many things we do not know. But it is possible to get a rough idea of it, as the scientists at UC Berkeley have, by using a mathematical probability theory method called stochastics, and by applying something called the Monte Carlo simulation. In the Monte Carlo simulation, random samples of a distribution are drawn repeatedly using random experiments. With the help of the random samples, one can guess the solution to what is otherwise an unsolvable problem. To apply this method to our *Tyrannosaurus* problem well, we first need to ask a lot of questions. For example: in what period of Earth's past did *Tyrannosaurus* rex live? How much time passed from the first to the last occurrence of the species? How large was the area *Tyrannosaurus* inhabited? What was the population density? How many offspring did a single *Tyrannosaurus* produce? How many of these offspring survived to sexual maturity until they themselves could reproduce? On average, how old was it able to grow? How fast did it grow and was this rate faster or slower than the growth rate of mammals? Did it have an active metabolism? Was it ectothermic or endothermic (cold-blooded or warm-blooded)? How heavy was an adult *T. rex*? What position in the trophic pyramid did it occupy? What ecological niches did it occupy? Did its trophic level change throughout its ontogeny, that is, throughout the course of its life and development? How many generations of *Tyrannosaurus* have there been? What is the absolute number of skeletons preserved in the fossil record to this day? The answers to all these questions and more are then compared with the numbers from faunal assemblages of today's ecosystems. The question is therefore no small matter, and the answer will continue to change as new evidence comes to light. With the improvement of our data, such as more precise geographical range and more precise radiometric dating methods, our analysis can be even more refined. Nevertheless, it is astounding to see how a seemingly unsolvable problem might be approached. The scientists at UC Berkeley chose *Tyrannosaurus* of all animals because it is the best-studied dinosaur; it existed for a relatively short time (until the asteroid abruptly ended its reign); and because in comparison there are fewer of it, since it was at the top of the food chain in its ecosystem. So, what do the numbers tell us?

Tyrannosaurus lived on Earth for about 1.2 to 3.6 million years before the asteroid killed all non-avian dinosaurs outside the bird lineage. This gives us a mean value of 2.4 million years for its existence.

The scientists put the duration of one generation at about 19 years, calculated on the basis of the proportion of sexually mature individuals, the average number of offspring, their survival rate and the maximum lifetime. This leads to a calculation of some 127,000 generations of tyrannosaurs that ever lived.

The area which *Tyrannosaurus* inhabited is estimated by the scientists to be about 2.3 million square kilometers. The average body weight of a sexually mature *T. rex* is estimated to be about 5,200 kilograms — about 27 times the average weight of a lion and about 20 times the weight of a tiger. Because *Tyrannosaurus* was so much heavier but had a similarly active metabolism to modern mammals, its energy requirements must have been much higher. This means that there must have been far fewer mature animals in a given area than today's mammal predators. The vegetation can only feed a certain number of herbivores, which in turn can only feed a certain number of predators. And since an adult *Tyrannosaurus* cannot hunt small animals but is dependent on large herbivores, such as *Edmontosaurus* and *Triceratops*, its abundance is even further limited. The researchers assume that the population density of tyrannosaurs per square kilometer was only about 16% of the number of tigers and only about 7% of lions in their respective ecosystems. On a safari at the end of the Cretaceous period, you would have probably seen a tyrannosaur much less often than a tiger or a lion today. If you are a thrill seeker, you would have probably been disappointed by the scarcity of fully grown individuals and the difficulty to get a good snapshot of one of them, but you would have encountered a lot more babies and juvenile specimens and if we have learned anything from the Jurassic Park movies at all, then it’s that you really wouldn’t want to encounter any dinosaurs in the wild.

In absolute terms, the colleagues estimate that the population density of *T. rex* ranged from 0.00058 to 0.14 sexually mature individuals per square kilometer. With gives us an average value of around 0.0091 individuals/km2, or about 20,000 to 21,000 adult animals that lived contemporaneously on the total area. Multiplying these numbers, it follows that about 2.66 billion adult tyrannosaurs have existed through time. If you include hatchlings and young animals, the number is easily ten times higher and most likely even more than that. But if you are familiar with statistics and want to calculate the numbers yourself, you will find that the error bars are very, very high. If we follow the same calculation example but assume the smallest value (1.2 million years) for the reign of tyrannosaurs and for the smallest abundance of individuals per square kilometer (0.00058), then there were only about 84 million adult animals over the entire period of their existence. Conversely, if we assume a presence over 3.6 million years and an abundance of 0.14 individuals/km2, we end up with a staggering 61 billion adult tyrannosaurs. But these are of course not the only two variables with error bars – if we change the area size, the duration of a generation, the average age of sexual maturity, the number of offspring, or the average weight or any other variable, we could end up with completely new and vastly different numbers.

I want fresh meat: why *Tyrannosaurus* was not a scavenger.

Every now and then, there are people arguing that *Tyrannosaurus* may not have been an active predator at all, but rather a scavenger. One common argument for *Tyrannosaurus* being an obligate scavenger, is that its tiny forearms were completely useless for hunting prey. In a detailed scientific description of the forearms of *Tyrannosaurus*, paleontologists Kenneth Carpenter and Matt Smith clearly rejected this idea.

Since more and more evidence of their very active metabolism, rapid growth rates and their incredible biteforce have come to light, these voices have admittedly become quieter and rarer, but every now and then the scavenger argument still appears. A few years ago, a dear colleague of mine, Chris Carbone, impressively demonstrated that mathematics can actually prove unequivocally, that it is absolutely impossible to feed a tyrannosaur weighing five or six tons only by carrion. I first heard about the calculation model at a working group meeting in Flensburg. That was way back in 2010, and a year later his article was published in a journal. Although the lecture was so long ago, I still remember it well, because the computational model works more or less independently of whether *Tyrannosaurus* had a particularly high metabolism or rather a lower metabolism than today's predatory mammals. It also does not matter for the equation whether it was a scavenger, more of an ambush predator or a particularly zealous hunter, chasing its prey. The calculations are not easy, as they required a lot of research in advance. First of all, you have to estimate how many tyrannosaurs there were, how much prey was present and how much carrion occurred in its ecosystem and how long the carcasses usually remained accessible as a food source, and finally you have to figure out how large the area was in which prey and hunters coexisted. If you know these variables, however, the conclusions are conclusive and comprehensible. That's what makes this model so brilliant from my point of view. Some of the variables of this equation on the abundance of carrion, are the same as those that were important for the previous computational model. Similar to the question of the absolute number of *Tyrannosaurus* individuals, we must also assume values based on observations in today's nature. And just like in the previous section, we are looking for an approach for an unsolvable problem by proceeding analytically and solving individual components numerically.

Weighing the pros and cons of scavenging versus hunting is especially important if we want to understand the complex relationships in ecosystems. This is especially true of the interrelationships of carnivores of different trophic levels. As one of the largest terrestrial carnivores that ever lived, *Tyrannosaurus* is a particularly popular object of research and in the more than a hundred years since its discovery, its diet has been eagerly debated. Now, was *Tyrannosaurus* an active predator or an obligatory scavenger i.e., a scavenger that is solely dependent on carrion to survive?

To answer this question, it must be understood that almost all predators not only actively hunt, but also eat carrion when presented with the opportunity. Who turns down a free meal that doesn't require you to do anything? Sometimes even herbivores eat carrion to absorb important minerals when plant matter in their habitat is particularly nutrient-poor. Nevertheless, very few animals rely on carrion as the main component of their diet, since the appearance of carcasses is rather random and unpredictable and you cannot work out a reliable strategy on how to find food in short, recurring intervals, in sufficient quantities. In all today's ecosystems, the large, carnivorous mammals actively hunt mainly large vertebrates and so it is more than likely that an extremely large carnivorous dinosaur such as *T. rex* must have hunted as well, because with its enormous weight and the associated energy requirements, it simply would not have been able to compete with smaller predators as an obligate scavenger. To illustrate this, we need to look at the environmental conditions of North America's Late Cretaceous period and know the size distribution of concurrent herbivorous dinosaurs, as well as the abundance of competing, small carnivores. What makes the fauna of the late Upper Cretaceous period of North America so special is that we find almost no medium-sized predatory dinosaurs. Either we find small nimble predators with a body mass of less than 50 kilograms or giant tyrannosaurs with a huge body mass of one to seven or even eight tons. Why this is the case, I will explain in a moment. In the case of herbivores, the distribution was much more balanced. There were also very large and heavy representatives such as the horned dinosaur, *Triceratops*, which weighed up to 12 metric tons or the duck-billed dinosaur *Edmontosaurus*, with a body mass of up to 9 metric tons. *Triceratops* and *Edmontosaurus* are also the most common dinosaurs found in the Hell Creek Formation and Lance Formation. Club-tailed dinosaurs such as the well-known *Ankylosaurus* are much rarer to find but could also weigh up to 8 metric tons. Most tyrannosaurs have been found in the Hell Creek Formation and Lance Formation. These formations are found in Montana, Wyoming and South Dakota. In recent years, however, there have also been finds of these giant carnivores from New Mexico and Utah. There, the herbivore fauna was slightly different, and we see one of the last long-necked dinosaurs in North America: *Alamosaurus*. The mass estimates of these giant herbivores vary widely. In a publication from 2020, it was estimated to be around 38 metric tons. In addition to the giants, however, there were also many, much smaller herbivores and most of the animals of the time were juveniles (the reason being that dinosaurs produced many offspring and that the mortality rate was very high), which were many times more common than the adults. Hence, my colleagues assumed that almost 50 percent of the herbivores weighed only between 55 and 85 kilograms. If we now remember the last section, we know that on a huge area of 2.3 million square kilometers, only about 21,000 tyrannosaurs occurred at any given time. Based on the expected frequency of finding carrion and the fact that carcasses would have been quickly tracked down and consumed by smaller theropods even before a *Tyrannosaurus* would have found such a carcass, a primary diet consisting of carrion is very unlikely. Larger carcasses would have been very rare and highly contested, making them an unreliable source of food. My colleagues estimated the potential cadaver search rate of smaller theropods to be 14 to 60 times that of an adult *T. rex*. These results suggested that *T. rex* would not have been able to survive as an obligate scavenger and compete with small predators. Consequently, it has mainly hunted large vertebrate prey, similar to many large carnivorous mammals in modern ecosystems. But what are the numbers and considerations that go into this computational model?

First of all, we have to estimate how much carrion there could have been at all. Today, a productive modern ecosystem like the Serengeti produces 4.38 kg of carcasses per km^2, per day. Therefore, if we can assume that carcass abundance was similar in Mesozoic terrestrial ecosystems, a significant number of dinosaur carcasses would have been present in North America in the late Cretaceous period, enough to feed a single, adult *T. rex*. However, it becomes clear that finding these carcasses becomes a problem when we estimate the distributions of carcasses of different sizes in terms of the expected supply rate. Under the simplified assumption that all size classes of carcasses occur proportionately with the same frequency as the corresponding live animals, we can easily calculate an expected distribution. To do this, we use the Serengeti production rate and divide this rate among the size classes of herbivorous dinosaurs and then calculate how many animals are in each class. If each carcass existed for seven days before it was finally consumed, most carcasses would actually be very widely dispersed: on average, there would be only a single 75 kilogram carcass within a radius of 17 km^2; only once in an area of 160 km^2 there would be a 700 kilogram carcass and only once within a radius of 1,000 km^2, there would be a carcass with 5 tons. Carrion of a 25-ton herbivore would occur on average only once within a radius of 5,000 km^2. This makes it clear that these carcasses were difficult, if not impossible, for individual scavengers to find without having to travel very long distances at the same time. An animal alone would never have been able to travel such distances and, more importantly, the much more frequent, smaller predators would have long discovered and consumed the carcass in the meantime. Although the colleagues assumed a significantly lower population of tyrannosaurs in their calculations - if we follow this calculation model, the authors expect only about one third of the previously mentioned 21,000 tyrannosaurs (i.e., about 6,600 to 7,000 animals); but even with higher numbers, the chances of detecting fresh carrion would be almost forlorn.

One reason I'm talking about this older article, now, even though it dates back a few years,

is that the variables are similar and have recently regained relevance in understanding why there are no medium-sized hunters in the ecosystems dominated by *Tyrannosaurus*. This, from today's point of view, unnatural abundance distribution of very large and very small carnivores in the ecosystems, where medium-sized predators are completely absent, was noticed by paleontologists very early on. For a long time, colleagues tried to understand this phenomenon and did not have a good explanation for it. We cannot see this distribution in Jurassic ecosystems. On the contrary, in some of the most famous sites for Jurassic dinosaurs, such as the Morrison Formation in the Midwest of the USA, which we have already discussed, and in the Lourinhã Formation in Portugal, carnivores are more evenly spread over all size groups and lightweight and heavy animals are almost similarly common. This also applies to some ecosystems of the Lower Cretaceous period such as the Wessex Formation in England, where all the spinosaurids are from and the Sao Khua Formation in Thailand.
Particularly fascinating in this context is the Huincul Formation from the Upper Cretaceous period of Argentina. Here, there are huge charcharodontosaurs that, like *Tyrannosaurus*, weighed over five tons and yet medium sized predators were also represent. Only in the late Cretaceous period and only when tyrannosaurs become the dominant species, do we have a very clear separation of small predators, very large tyrannosaurs and no medium-sized predators at all. And therein may lie the secret of why the large non-avian dinosaurs, could no longer recover from the impact at the end of the Cretaceous period.

Like father, but not like son: Different prey for juvenile *T. rex*

In Chris Carbone’s article of 2011, he and his team compared different ecosystems of the late Upper Cretaceous period of North America. Various predatory dinosaurs lived in these ecosystems. But what is immediately noticeable is that, on the one hand, there are very small predators, where the body mass of an adult animal ranges from only 16 kilograms for dromeosaurs to about 63 kilograms for oviraptors and then there is a huge size gap, where the next larger carnivores was presumed to weigh at least 1,100 kilograms when fully grown. That's more than 17 times the body mass of the next smaller species. After these animals with a body mass of just over a ton, there is another huge gap, where the adult tyrannosaurs then weigh on average around 5,350 kilograms, which is almost five times as much. We do not know such a size distribution in any of today's ecosystems. What the authors did not know in 2011, however, is that the predatory dinosaur with a weight of 1,100 kilograms (it is *'Nanotyrannus'*) was not a genus of its own, but rather an immature tyrannosaur! This means that the actual body mass gap ranges from 63 kilograms to 5,350 kilograms; an almost 85-fold difference in mass! This makes this bimodal distribution all the more astonishing.
Initially, this phenomenon was explained by the incompleteness of the fossil record and for a long time it was assumed that the medium-sized predatory dinosaurs had simply not yet been found. The argument has always been a little thin but at least conceivable, since carnivores are much rarer in most ecosystems than herbivores and therefore you simply find fewer predators overall. However, since we have known many of the tyrannosaur sites for about 150 years now, it is clear that this is not the reason for the absence of medium-sized species. We see the same pattern in dozens of sites in North America and Asia and never do we find medium sized predatory species.
So, what is the answer to this mystery?

The cause of this uneven distribution lies in the completely different biology of tyrannosaurs and modern mammalian predators. Kruger National Park in South Africa has more than 15 different species of predatory mammals.

There are Lions, Cheetahs, Spotted- and Brown Hyenas, there are Leopards, African Wild Dogs and Wild Cats, there are Jackals, Caracals and Servals, there are Civets, Bat-Eared Foxes, Cape Foxes and Black-Footed Cats. And the body masses range from 150 to 250 kilograms for lions to only 1.3 to 1.9 kilograms for the Black-Footed Cats. In between, all weight classes are represented with a weight of Cheetahs and Leopards between 21 and 72 kilograms, in Hyenas between 38 and 64 kilograms and Caracal, Jackal and Serval between 6.4 and 19 kilograms and finally the small cats and foxes, which weigh between 1.3 and 6.4 kilograms. Many weight classes are even co-occupied by several different species.

In the dinosaur ecosystems of the Jurassic and until the early Lower Cretaceous, we also see a greater taxonomic diversity of larger predatory dinosaurs over 50 kilograms. Medium-sized predatory dinosaurs are also present there and the occurrence of different weight classes is evenly distributed. However, from about 83 million years before present until the extinction of the non-avian dinosaurs (from the Campanian to the Mastrichtian), this changes in faunal assemblages in Eastern and Central Asia and in western North America (Laramidia). Here, tyrannosaurs replace all, medium-sized predatory dinosaurs with a body mass between 50 and 500 kilograms. They are very rare or no longer present at all, although they still existed in these regions before the Campanian. Interestingly, these faunas dominated by tyrannosaurs, where far fewer other predatory dinosaur species appear, have no impoverishment of prey diversity. There is still a similar number of different prey species present. The supposedly missing food niches in the theropod assemblages, may have been occupied by juvenile and subadult tyrannosaur species that are functionally different from their adult parents.

And herein lies the fundamental difference between today’s large, carnivorous mammals and *Tyrannosaurus*:

Because mammalian cubs are suckled by their mother, they indirectly ingest the same food as the mother. In addition, the babies are relatively large and grow up quickly. Furthermore, the cubs of, for example, big cats, protected by the pack, do not have to hunt themselves until they are large and strong enough to do so. They are protected and fed by their pride of lions. This means that even if they are still too small to kill their own prey, they already feed on the same diet as their parents. Therefore, a lion occupies the same ecological niche since birth and always maintains the same trophic level.

For tyrannosaurs, this is quite different. Because dinosaurs hatch from eggs and eggs cannot be arbitrarily large, tyrannosaurs’ hatchlings are tiny compared to their parents. A tyrannosaur egg is about 40 to 45 centimeters long and the hatchling is about 70 to 80 centimeters long. A baby *T. rex* may have weighed about as much as a small to medium-sized dog. Thus, the mother of these babies may have weighed up to a thousand times more than her hatchlings. We now know that tyrannosaurs had an active metabolism and grew very quickly. But because the weight difference between a hatchling and an adult animal was so incredibly large, it still took almost 18 years for a *T. rex* to become large enough to become sexually mature. Because it took so long for tyrannosaurs to grow, we must assume that they also assimilated various food niches throughout their lives, some of which were otherwise occupied by medium-sized theropods. Instead, juvenile tyrannosaurs assimilated these niches and replaced other theropods in their ecosystem. Because it took a very long time for these animals to be fully grown and because the proportions of their bodies changed dramatically, they had to develop different hunting strategies and kill different prey in different ontogenetic stages of their lives. However, this also means that the new bauplan of tyrannosaurs was superior to that of other medium-sized predators. *Tyrannosaurs* would not have been able to replace these competitors otherwise. Hence, we can assume, that they outcompeted other predators during every stage of their growth. This means that even a juvenile *Tyrannosaurus*, which by far couldn't match the biteforce of an adult animal (the biteforce of the adult animals was about ten times greater than that of the adolescents), was nevertheless stronger and could run faster than other predators, thus guaranteeing the evolutionary success of its species and gradually replacing all other theropods. There are still very isolated occurrences of raptors, for example in the Hell Creek Formation; however, these are extremely rare and play no role when considering faunal assemblies as a whole. One of them is *Dakotaraptor*, which falls into the size cluster between 100 and 500 kilograms. It is roughly comparable to the size of the raptors from the Jurassic Park and Jurassic World Movies and looks fairly similar. In the sixth part of the film series, this species is even presented as an independent genus that differs from the other raptors. In the Hell Creek Formation, it may have occupied a very special ecological niche that was not occupied by the juveniles of the tyrannosaurs, or its hunting behaviour in the pack may have made coexistence with the much larger tyrannosaurs possible. Maybe, it killed prey that was still too big for juvenile *T. rex*. Furthermore, there are some troodontides that weighed between 50 and 100 kilograms. Whether they actually competed with tyrannosaurs for resources at all, is very questionable though, as they were most likely omnivores and may not have required large amounts of meat to meet their dietary needs. Overall, co-existence in an ecosystem that was dominated by *Tyrannosaurus* would only have been sustainable, if the patterns of prey selection had been different.

While we see a depletion of taxonomic diversity of predatory dinosaurs at the end of the Cretaceous period, we do not see a reduction of the number of ecological niches. This has to do, not only with the extreme increase in size of the top predators, but also with the strong ontogenetic change in their bodies. Some of the changes are so extreme that some colleagues even refer to them as a "secondary metamorphosis" in tyrannosaurs. They change their appearance so much that young animals are functionally differently from adults, which means that even though, they both belong to the same species, they functionally occupy different niches. This is also one of the reasons why some juvenile tyrannosaurs were not immediately recognized as such but were described as an independent species. The whole physique changes, and due to allometric growth, the proportions of their bodies change dramatically. While young tyrannosaurs initially have rather elongated skulls, which at a first glance look more like those of an *Allosaurus*, it becomes increasingly higher (expanding vertically, i.e. dorsoventral). This offers more space for larger and thicker jaw muscles and ensures that the biteforce increases more and more during ontogeny. The ratio of arm length to leg length changes; while the arms of the young animals are still relatively long, they basically stop growing at some point, while everything else continues to grow. This means that a juvenile animal may well have used its arms to hunt and to catch, injure or kill its prey because the jaws alone were not strong enough, yet. The amazing thing is that at some point in the development, the legs also grow slower than the rest of the body or the tail and thus the adult animals look beefier and more massive, while the young animals look more gracile, more nimble and long-legged. Nevertheless, the smaller individuals had proportionally longer arms, where the humerus bone corresponded to about 40 percent of the length of the thigh bone, whereas the upper arm in adults corresponds to only about 30 percent to the length of the thigh. However, as the jaws became stronger, it was no longer necessary for *Tyrannosaurus* to hold or injure prey with its hands during later growth stages. Basically, *Tyrannosaurus* occupied different food niches throughout the course of its life cycle. This is referred to as a "niche assimilation". We can observe this niche assimilation in all large dinosaurs. We have already experienced something similar with long-necked dinosaurs. But even the herbivores from the Hell Creek Formation, the prey of *Tyrannosaurus* so to speak, underwent a significant size increase of several orders of magnitude during ontogenesis. Thus, the animals were functionally different in different phases of their lives, too. In the case of the duck-billed dinosaur *Edmontosaurus*, this is as if one and the same animal had occupied all the food niches in the Serengeti, from the smallest grazing artiodactyl (even-toed ungulate), the dwarf antelope to the largest herbivore, the African elephant. This corresponds to the entire size range of ungulates and Proboscidea of Africa.

The same niche assimilation hypothesis also applies to that of tyrannosaurids. But here we find no analogy in today's animal kingdom. If we look again at the carnivorous mammals from Kruger National Park, it would be as if a tyrannosaur would grow up from a small jackal to an animal fifty times heavier than an adult lion over the course of its life!

However, these niche shifts must have happened abruptly in tyrannosaurids. Transitions from one phase to the next were short and transformations in the skeleton and physique were profound. This in turn, necessitated a rapid dietary shift with increasing size.

In summary, we can state that large carnivorous dinosaurs, unlike carnivorous mammals, have filled several niches over the course of their ontogeny. This led to a decrease in taxonomic diversity but not to a reduction in niche diversity, because juvenile predators were functionally independent, ecological morphospecies. This also explains the absence of medium-sized predators in the faunas of the Upper Cretaceous period. Their niches were filled by the growing mega carnivores. We can observe this gap on different continents, in different habitats and with different species, once the top predator niche of a habitat is filled by a member of the tyrannosaurids. This clearly shows that this phenomenon does not arise artificially through gaps in the fossil record or a collection bias but reflects the competition for resources.

This very specialized community structure of dinosaurs is related to their extreme size and the fact that they were egg-laying. These eggs were relatively small and small offspring hatched from them. Then, the hatchlings grew very quickly, and thus there were several ontogenetic niche shifts. The high number of offspring also created an environment where young animals were very abundant, yet where at the same time the mortality rate of the young animals was very high. Nevertheless, they dominated the ecosystem and morphologically and functionally replaced the role of meso carnivores. Their lack in biteforce was compensated with agility and speed, so that they even outcompeted their parents; also, the ability to run fast and enduringly, made them extremely dangerous for medium-sized herbivores and ensured that they could permanently replace other medium-sized predators in their ecosystems. This niche partitioning of juvenile and adult animals was also made possible by the fact that large tyrannosaurs could not have sustained on small prey alone, because smaller prey could not have provided enough energy to cover their requirements. In contrast, the young tyrannosaurids probably lacked the strength to kill the larger herbivores, such as the adult duck-billed dinosaurs or horned dinosaurs, which we know adult tyrannosaurids have fed upon. Hence, they didn’t get in the way of their parents, either.

I am the king of tyrant lizards and not a dicky: Did *T. rex* have feathers?

Some 20 years ago, when the discovery of feathered predatory dinosaurs in China were first reported and published, this was a huge sensation. More and more specimens came to light and more and more species showed signs of intensive plumage. This presence of feathers in theropod dinosaurs have led to speculations whether the largest tyrannosaurids, including *Tyrannosaurus rex*, may have been covered in feathers as well. This is an exciting question that, fortunately, we can answer today, as we have already found fossilized skin of tyrannosaurs. In biology and in palaeontology, the skin layers of animals (and humans), including the hair, feathers, spines, scales, and dermal armor that is formed inside the skin, are referred to as integument. Such fossil integument is known from Tyrannosaurus and other tyrannosaurids such as *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus* and *Tarbosaurus*. These finds confirm that these large and heavy tyrannosaurids had scaly, reptile-like skin and no feathers. At least this this is true for adult specimens and most regions of their bodies. We cannot completely rule out if these animals retained a few colourful display feathers at some highly visible parts of their bodies, to woo mates. However, there are other *Tyrannosaurus* relatives that were actually completely covered in feathers, such as *Yutyrannus* from China. The name is a mixture of Mandarin and Latinized Greek and translates to "feathered tyrant". It is the largest known, feathered predatory dinosaur, so far. Three almost completely preserved specimens of this animal are currently known. One of them, is a fully grown adult, one is a subadult animal and a third specimen is a juvenile. Although the name might imply this, *Yutyrannus* is not a direct relative of *Tyrannosaurus rex*, but rather evolved in a sister group. The fossils of *Yutyrannus* are around 130 million years old and show that gigantism has evolved at least twice and independently of each other (i.e., convergently) within these two theropod sister groups. I don't want to go into too much detail but in a nutshell, there is a superfamily, the so-called Tyrannosauroidea, which is part of the Coelurosauria, the so-called hollow-tailed lizards. The superfamily Tyrannosauroidea includes two families: the Proceratosauridae (they include *Yutyrannus*) and the Tyrannosauridae (which include *Tyrannosaurus rex*). The Tyrannosauridae are also commonly referred to as tyrannosaurids and they include all the other known tyrannosaurs mentioned above (*Tyrannosaurus*, *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus* and *Tarbosaurus*). All adult animals from the family Tyrannosauridae show no signs of plumage or any feathers so far. All these animals are uniformly covered by horny scales on their necks, abdomen, hips and tails. If these animals still had feathers in some areas, those were limited to the dorsal region. We currently assume that this family has lost its ancestral lush plumage in the late Lower Cretaceous (Albian) about 110 to 100 million years ago.

Why the tyrannosaurids did no longer have any plumage, but *Yutyrannus* still did, is probably due to a small but crucial detail. Some researchers had initially assumed that the loss of their gorgeous plumage may have had something to do with a milder paleoclimate in which the tyrannosaurids lived. However, this is now considered very unlikely. The geographical spread of the tyrannosaurids is vast and members of this clade lived under very different climatic conditions. A special example of this is *Nanuqsaurus*, whose name means “polar bear lizard”. The name is no coincidence, as remains of this animal were discovered in the Prince Creek Formation, in the far north of Alaska. Although at the end of the Cretaceous period Alaska was geographically not in the same place as it is today, it was still pretty far up North, and the climate was shaped by strong seasonal changes and must have been very cold and rough throughout the winter months. A plumage would have certainly been advantageous for *Nanuqsaurus*, but there is no evidence that these animals had feathers. Therefore, the loss of feathers cannot be explained with the paleoclimate.

Yutyrannus, the feathered tyrant from China, was about 9 meters long and weighed about 1,400 kilograms, according to the first description. Other authors assume, however, that this adult animal was probably only about 7.5 meters long and weighed around 1,100 kilograms. Now, at first glance, this may not necessarily make a big difference, but it may be the reason why the animal still had feathers while larger tyrannosaurids no longer did. In contrast, *Albertosaurus*, *Gorgosaurus* and *Daspletosaurus* each weighed about 2.5 tons (some estimates even assume up to 4 tons for the heaviest specimens for all of them). *Tarbosaurus* is even assumed to have weighed around 4 tons and *Tyrannosaurus* may have weighed an average of 5 to 6 tons, with the very largest animals weighing perhaps even 9 tons or more.

When certain groups of animals undergo an evolution towards gigantism, the ratio of body surface area to body mass changes dramatically. We have already seen this impressively with the long neck dinosaurs. As a reminder, this is due to the fact that the surface area increases as length squared, but the volume increases as length cubed. Such large and heavy animals then indirectly become gigantothermic, which means that the large body mass remains uniformly warm regardless of the outside temperature, because cooling through heat exchange from the inside to the outside takes longer and longer. If a thick or dense insulation layer, such as a dense plumage, is added, there is hardly any heat loss due to conduction. Conversely, this means that an animal with a large body mass and an active lifestyle, can overheat very quickly. In sauropods, this problem has been solved by a complex system of air sacs and mammals have sweat glands to regulate body temperature. In the case of heavy tyrannosaurids, this evolution towards gigantism during their evolution must have inevitably led to the loss of plumage.

Yutyrannus, on the other hand, which was fully covered in plumage, and in which no scales are known, had a body mass of about one ton (but certainly less than 1.5 tons). It may have hence not yet exceeded a threshold, where a complete plumage would have led to overheating. For *Yutyrannus*, it might have been advantageous to retain feathers because it lived in a more densely forested habitat than *Tyrannosaurus* and therefore perhaps needed more protection and more thermal insulation. In addition, the tyrannosaurids were more long-legged than their close relatives, which may indicate a way of life that can still be observed today in ratites, which travel long distances and can sometimes run very fast. Such a way of life is very energy-consuming and may also have increased the risk of overheating in long-lasting hunts.

However, because the tyrannosaurs are descended from feathered ancestors and because almost all hollow-tailed lizards (Coelurosauria) are feathered, we now assume that the horny scales of *Tyrannosaurus* are not comparable to the scales of crocodiles (i.e. not homologous), but have evolved secondarily from feathers. If anyone had said that 30 years ago, they would have simply thought this person was crazy. The same applies to the scales on the legs of some modern birds: they also evolved from feathers. In the case of today's birds, this secondary transformation of the leg feathers into scales is an adaptation to wading in the water (for example, in storks or herons) or to squatting and balancing on thin branches.
So, we know today that adult tyrannosaurs were scaly and not feathered; but what about the chicks? Were they feathered or also scaly? The fact that adult animals were covered with horny scales does not necessarily rule out the possibility that the young animals still had feathers and that these were lost during their ontogeny. However, such a change from feathers to horny scales within the life cycle of an animal, is unprecedented in the animal kingdom. Therefore, it remains super-exciting until we find the first remains of a baby *Tyrannosaurus* with integument! I would not be surprised if the loss of feathers is then related to one of the dramatic growth spurts and takes place at the same time, when the young animals transition from one ecological niche to another and perhaps also change their biotopes. The small, possibly feathered, hatchlings may have benefited from the protection of the dense forest, where they found their prey, and may have needed feathers, whereas juvenile tyrannosaurs might have hunted in open plains, and they might have not needed plumage anymore. To me, this is a plausible scenario since the juvenile tyrannosaurs had longer legs relative to their bodies than the adult animals and were certainly very fast runners.

Long legs, short arms: Short arms are normal and long arms are weird

Many jokes about *Tyrannosaurus* revolve around the fact that the king of the dinosaurs had very small arms. Almost tiny, relative to its otherwise enormous proportions.
When *Tyrannosaurus* rex was first discovered, only its upper arm was found and no forearm or fingers. At the first public display of the skeletal reconstruction in 1915, Osborn had even mounted three-fingered hands, as they were known from *Allosaurus*. But Osborne could have known better – the closely related *Gorgosaurus* was already known, and it only had two fingers on each hand. And although there was no longer any doubt that *Tyrannosaurus* also had only two fingers on each hand, only in 1989 a then newly found specimen, which is now exhibited in Montana, provided the first clear evidence, because it had complete forearms. Today it is clear that all tyrannosaurids had two fingers on each hand. We now know this from *Albertosaurus*, *Daspletosaurus*, and *Tarbosaurus* and most other representatives.
Nevertheless, I cannot deny the fact that *T. rex*'s arms were very small in relation to the overall body size. They were just one meter long and some of my colleagues describe them as rudimentary. But we shouldn't make fun of the tiny arms too early – muscle attachment sites on the humerus show that the biceps of *Tyrannosaurus* were very strongly formed. The forearm bones have extremely thick cortical bones, suggesting that they were able to withstand heavy loads. The biceps of an adult *T. rex* alone were strong enough to lift almost 200 kilograms; other muscles in the upper arm, such as the brachialis muscle, in combination with the biceps, would have made the elbow flexion even stronger. Not only would T. rex

have won every arm-wrestling match against any human – its raw muscle power would have easily enabled it to rip out the entire arm of a person. But while humans can rotate their upper arm 360 degrees at the ball joint of the shoulder, the freedom of movement of *Tyrannosaurus* was very limited. It could swivel its arm at the shoulder by just 40 degrees and at the elbow only by 45 degrees. The short but massive arm bones, the extreme muscle strength and the restricted range of motion suggest that the short arms evolved to cling on to its prey during a fight, despite massive resistance. This would have aided *Tyrannosaurus* to kill the prey with its huge jaws. This hypothesis is also supported by biomechanical analyses of the arms. Osborn noticed the large muscle attachment marks on the upper arm as early as 1906 and he also correctly concluded that the arms must have been very strong. He speculated that the arms had been used to hold a partner during mating. In the 1970s, it was also assumed that the arms were important when getting up from the ground after resting. They would have prevented the animal from slipping forward while pushing with the hind legs. All three considerations are conceivable and do not have to be mutually exclusive. Just last year, however, Professor Padian of Berkeley argued that reducing the arms in tyrannosaurids had no special functional purpose but was rather a secondary adaptation. In his opinion, the arms became smaller when the skulls of the animals became larger and the jaws became stronger. This helped avoiding bite wounds and serious injuries, for example, when a pack of tyrannosaurs fought over the same prey. Whether this argument is valid, however, remains to be seen. Despite seeing signs of pack behaviour in allbertosaurs, there is no evidence for such a behaviour for *Tyrannosaurus*, so far.

Another idea, suggesting that the arms were used as weapons in the hunt for prey and that the claws were used to slash its prey, is more than questionable. The arms are much too short for this and the radius of movement, as mentioned above, much too small. Although the finger claws could have inflicted long and deep cuts on the prey, *Tyrannosaurus* would probably not have been able to target vital and vulnerable areas with them.

But anyone who believes that the tyrannosaurs had the smallest forearm in the realm of the dinosaurs is mistaken. The arms of *Carnotaurus* and *Abelisaurus* from Argentina or *Majungasaurus* from Madagascar are much smaller than those of tyrannosaurs. The three carnivores all belong to a group we know as the abelisaurs and they occur predominantly in the southern hemisphere.

The extremely short arms seem strange to us because we no longer know any living non-avian dinosaurs. Therefore, short arms appear unfamiliar to us, when it is actually the bauplan of modern birds which is the unusual form. The blueprint of modern birds is characterized by a significant decrease in body size with a simultaneous increase in relative forearm length. Bird arms, or wings for that matter, are unusually long for dinosaurs. The evolution towards smaller body size and towards longer arms may be interconnected to enable powered flight. Conversely, there is an evolutionary trend towards a negative allometry of the forearms in non-avian theropods, so that larger non-avian species often have relatively shorter forearms. This seeming contradiction can be explained by the fact that early in the body development of the predatory dinosaurs, the forearm bones, i.e. the radius and the ulna, are disproportionately long. Hence, the longer a young animal lived, the longer the upper arm and thigh bones later became relative to the forearm bones. This was accompanied by a significant change in arm function, as we have already learned. Because tyrannosaurs were only fully grown at about 18 years of age, but the arm growth ended much earlier in development, the arms of the adult animals seem so small. With *T. rex* teenagers, this is not as noticeable, because a three or four-year-old *T. rex* already had arms of the same length as its adult parents, and they simply did not continue to grow afterwards. A large abelisaurid or tyrannosaur killed its prey with its jaw and no longer needed strong arms; consequently, the transition from one food niche to the next also controlled arm development. Conversely, small theropods needed the arms to catch prey and, in the case of birds, to be able to fly. The negative allometry of the arms is therefore a signal for evolutionary allometric trends. These evolutionary trends are then also reflected in ontogenetic allometric trends and vice versa.

In modern birds, the allometric growth of the arms is associated with changes in movement and behaviour along their ontogenesis – which means, it is associated with powered flight. The proportionally longer arms of birds are therefore a juvenile trait that adult birds retain. We have seen a similar retention of juvenile traits with the dwarfing of *Europasaurus*. This supports the idea that the underlying mechanism for the evolution of modern birds was pedomorphosis. By definition, pedomorphosis, is the retention of juvenile traits into later life stages. This can for one be achieved by acceleration of sexual maturation relative to the rest of development and secondly retardation of bodily development with respect to the onset of reproductive activity. As many birds in nature do not live to be older than three years and sexual maturity is accelerated, birds basically look like baby dinosaurs.

Boy or girl: Was the *Tyrannosaurus* Sue female?

The *Tyrannosaurus* Sue from the Field Museum in Chicago was named after its discoverer. But is the animal really a female? It's hard to say. Unique sexual characteristics in dinosaurs are usually lost during fossilization, along with many other aspects of their soft tissue anatomy. However, there is a certain bone tissue that only occurs in female birds and, as it turns out, also in dinosaurs outside the avian lineage. This is the so-called medullary bone tissue. This is a special, derived tissue that sticks to the inner wall of the compact bone that surrounds the inner medullary cavity. It is found in the midshaft region of long bones in female birds, when they are about to lay their eggs. Since medullary bone is found only in female birds, its discovery in extinct dinosaurs underpins the link between dinosaurs and birds. It suggests similar reproductive strategies and serves as an objective method for sex differentiation in dinosaurs. However, there is a catch: As already indicated, this only works in females who are already sexually mature and, at the time of their death, were in a phase shortly before egg laying. The medullary bone serves as a calcium reservoir, where calcium is stored before egg laying, which the females then need for eggshell mineralisation.

In Sue in Chicago, we don't find this type of bone tissue. But that doesn't necessarily mean that Sue was a male, either. It may also mean that Sue simply wasn’t about to lay eggs at the moment of its death. Medullary bone is known from two other tyrannosaurs. One animal is on display at the Museum of the Rockies in Bozeman, Montana. It is nicknamed "B. rex" and was about 18 years old at the time of her death and already weighed about 3 tons. " B. rex" is only less than 40 percent complete; but the skull is almost completely preserved. However, the medullary bones come from the medullary cavity of the thigh bone. And here more spectacular discoveries were made. Contrary to popular beliefs, this tyrannosaur has shown that fossil bones can, in fact, sometimes also contain original cells, blood vessels and even structural tissues, some of which still consist of their original proteins. But this was due to the extraordinary circumstances of the deposition and preservation of the animal after its death. The carcass of the tyrannosaur lady disintegrated after her death in a brackish estuarine channel and was buried in sand, in an oxygen-rich environment, which solidified shortly thereafter. As a result, there was no further chemical decomposition afterwards. Because of this extraordinary preservation of soft tissue in a dinosaur, many more studies will most certainly be carried out in the coming years.

The other female is housed in the Burpee Museum of Natural History, in Rockford, Illinois. She was about 15 years old at the time of death and thus still a teenager. Fossils of juvenile tyrannosaurs are extremely rare, but the Burpee Museum has two of them, both found in Montana, in the same region. The more complete specimen of the two teenagers, nicknamed "Jane," was slightly smaller and a little younger at about 13 years old. But we don't know if Jane was a female and sexually mature at all. Paradoxically, medullary bone has been detected in the larger animal and this animal bears the male nickname "Petey". It might be interesting to point out that “Jane” is this specimen, that was, at one point, believed to be a different species and had been assigned the name *Nanotyrannus*. It has since been re-named *Tyrannosaurus*, again, after it became evident, that it was in fact, just an immature *T. rex*.

[…]

Epilogue (pp. 324 – 325)

This book is intended to provide an overview of the latest incredible discoveries in vertebrate palaeontology and the fascinating new discoveries that my colleagues and I have made in recent years. Research in my field is more active than ever and we can use ever new methods to decipher mysteries that had previously been thought to be unsolvable. However, the book contains only a tiny fraction of what is currently being researched, but if it is well received, I’d happily tell you more some other time. For these stories, I have gathered information from different corners of the world. While 50 years ago research was dominated by North American and European palaeontologists, today the most exciting discoveries often come from South America, Asia, Africa, Australia, and even Antarctica. Dinosaurs are better understood than ever before, and yet there have never been so many unanswered questions. With every new find, we push open a new door, behind which we encounter many more questions, waiting to be deciphered by the next generation of researchers. By understanding the mechanisms responsible for the rise and fall of the dinosaurs we will better understand our own destiny and perhaps it will enable us to steer in the right direction for the benefit of our children.

Three of Earth's largest mass extinction events are related to the origin, the evolutionary success, and the demise of the non-avian dinosaurs. A constantly increasing concentration of greenhouse gases led to galloping greenhouse effects, which were barely noticeable at first but accelerated until these effects were irreversible. An ecological collapse was always followed by a massive species extinction, which subsequently triggered a trophic cascade and a collapse of the food web. The birds survived the last catastrophe, 66 million years ago, because they emerged in ecological niches that were least affected by the rapidly changing environmental conditions. Today, humans are destroying the habitats and the food sources for birds and threatening their biodiversity to such an extent that we may be responsible for the next great mass extinction. If we are not very careful, we will complete what the asteroid failed to do and wipe out the last dinosaurs on Earth. But that doesn't have to happen. We do know and we do understand what is happening around us. Now it is up to us to take the right measures and to finally listen to those who understand science and offer us solutions for the challenges we’re facing.