CONTENTS

Acknowledgments ix

1. Dinosaur Superstar 1
   - It's All in the Name 1
   - Unearthing *T. rex*: From Cretaceous to Celebrity 6
   - The Highs and Lows of Fame 36

2. What, in Actuality, Is a *T. rex*? 43
   - The Long Road to *Tyrannosaurus* 43
   - The Tyrannosaur Family Tree 53
   - *Tyrannosaurus rex*, the Species 65

3. Inside and Out 83
   - The Essence of Form: Bones and Muscles 83
   - A (Partial) Internal Tour 105
   - Clothing King Tyrants: The Life Appearance of *T. rex* 111

4. Breathing Life into Bones 131
   - Running Hot, Living Large 131
   - The Smarts, the Senses, the Voice 151
   - Cometh the Mechatyrants 162

5. Lands of the Tyrants 181
   - King Tyrants in Time and Space 181
   - Where the Rexes Roamed 188
   - Meeting the Neighbors 194

CONTENTS

6. Life, Food, Love, Death **217**

The King Tyrant Social Scene 217

Tyrannosaurus rex: Dinosaur Hunter 228

Love, Death, and *T. rex* 241

7. Death of a Species, End of an Era **257**

Approaching the Finish Line 257

Goodbye, *T. rex* 266

Afterlife 274

References 280

Image Credits 302

Index 303

masculine bias, noting that experienced, knowledgeable, and highly qualified female scientists avoid discussing *Tyrannosaurus* in public because certain men dislike being informed about their favorite dinosaur by non-male presenters. Outright dismissal or even abuse can follow. This politicization and toxification of science communication is surely the nadir of *Tyrannosaurus* hype, and a situation we can only push to change as soon as possible.

Academics are not immune to the hype of *Tyrannosaurus*, either. As noted above, *T. rex* is an intensely studied animal; so much so, in fact, that we might ask whether they are *over*-studied (Black 2022). This case has to be made against the counterargument that *T. rex* has become a "model organism" for dinosaurs, the likes of which are subjected to investigation precisely because we have so much data to contextualize new results. In the background of ongoing *T. rex* examination, however, are countless extinct organisms that have never been subjected to even elementary paleobiological investigations. Working on a popular fossil species like *Tyrannosaurus* can, of course, help to garner critical research funding and media attention, the likes of which can be essential to modern academic careers. Moreover, research involving king tyrants is often not exclusively focused on them: we learn much about other fossil organisms through studies that may have been funded because of a loose connection with *T. rex*. Such nuances are inevitably lost in news coverage of this science, however, which generally overemphasize any mention of *Tyrannosaurus* in dinosaur news stories or even crowbar king tyrants into news where they have no relevance. On those occasions when *T. rex* is the focus of a news story, the state of their science is often exaggerated and misleading. Contrary viewpoints are presented as sides in fierce arguments and debates, and unlikely "fringe" ideas are framed as overturning better-established hypotheses (e.g., the so-called "predator-scavenger debate" [chapter 6], or "the *Nanotyrannus* debate" [chapter 2]).

Whatever their rationale, our academic and media preoccupation with *Tyrannosaurus* creates an inflated sense of their importance to paleontological science and wider culture. In turn, this contributes to the private sales of *Tyrannosaurus* specimens and the debates about commercialization of fossils. This discussion has its own issues with hype as the strong feeling generated by high-profile fossil auctions, the likes of which sell *Tyrannosaurus* and similar-grade specimens, overshadows the nonproblematic, noncontroversial fossil sales that take place around the globe daily (Hippensteel and Condliffe 2013). Acknowledging this, however, does not exonerate fossil dealers from some of the tactics used to inflate *Tyrannosaurus* prices at auction, which include the application of dubious taxonomic labels to give specimens more prestige and value (e.g., listing specimens as the doubtful genus *"Nanotyrannus"*), or attaching paleobiological interpretations beyond those established by science (identifying specimens as male; see chapter 6). Another method, the sale of chimeric or very fragmentary skeletons with substantial amounts of replicated elements, is also now common, even as the transformation of *T. rex* bones into intellectual property makes selling replicated skeletons a risky business in itself: the auction house Christies rescinded a *Tyrannosaurus* specimen from sale in 2022 following unauthorized use of trademarked specimens in its reconstruction (Begum 2022; Neate 2022).

Hyping the sale of *T. rex* is not only unduly emptying the pockets of *T. rex* patrons; it is also having a measurable impact on the accessibility of *Tyrannosaurus* fossils to scientists and the public. As noted above, almost 50 substantial *T. rex* fossils, representing half our global inventory, have entered private ownership since the 1990s, setting a pace of acquisition that outstrips that of museums by roughly 17 percent (Carr 2021). That same figure, 17 percent, also accounts for the number of commercially-excavated *Tyrannosaurus* specimens that have found their way to museums, leaving most outside of the public trust (Carr 2021). If these rates remain steady, privately owned *Tyrannosaurus* will outnumber those accessioned to museums in the next few decades. Among them are rare and especially significant juvenile and subadult specimens that, as will be

FIGURE 1.23

The giant, North African theropod *Carcharodontosaurus saharicus* attacks a rebbachisaurid sauropod. Carcharodontosaurids were, by usual measures of evolutionary "success," a bigger deal than tyrannosaurids: this has not translated into greater cultural penetration for the group, however, perhaps owing to narrative stereotypes in our public discussion of dinosaur biology and evolution.

explored in later chapters, could tell us much about *T. rex* biology. As private *T. rex* ownership increases, concerns are growing not only about the immediate loss to science and our collective natural heritage, but also its longer-term implications. *Tyrannosaurus* is relatively abundant for a large dinosaur, and their fossils occur over a wide geographic area, but there are not infinite numbers of king tyrant fossils awaiting discovery. As a nonrenewable resource, continued collecting will, eventually, exhaust their supply. When that happens, will the bulk of *T. rex* specimens be in museums, or in private hands?

We could easily turn the rest of this book into a discourse purely on the curious culture that has developed around *T. rex*. This, however, is not our goal. Instead, our focus is on peeling back the sensationalism, politics, and controversy surrounding *Tyrannosaurus* to understand them as real, if long extinct, animals. Echoing the process a paleontologist may take to studying a *T. rex* specimen, we will learn where king tyrants fit into reptile evolution, describe their anatomy, and then, with this data in hand, make interpretations about their lifestyles. We will deconstruct hype and controversy where we find it, and put common assumptions about *T. rex* biology under the microscope to determine what, if anything, current science says about those topics. This myth-busting approach will reveal not only the sometimes genuinely amazing biology of *T. rex*, but also the wealth of human effort that has unraveled the details of their existence. Whatever opinion we have on the human history of *Tyrannosaurus*, the fact we know so much about them, and their capacity to shine a light on the biology of other dinosaurs, is something to celebrate.

2

WHAT, IN ACTUALITY, IS A *T. REX*?

THE QUESTION ABOVE has a seemingly obvious answer: everyone knows that *Tyrannosaurus* were enormous reptilian carnivores that pursued other large dinosaurs with great jaws and tiny arms. But to scientists looking to understand *T. rex* evolution, this assessment is far from sufficient. To understand king tyrants in detail, we must first learn what sort of dinosaurs they represented, where they fit in reptile evolution, and what, exactly, defines them as a species.

THE LONG ROAD TO *TYRANNOSAURUS*

T. REX DID not spring, fully formed, into existence from some primordial ether. They were the outcome of a long, complex evolutionary process, and their famous body plan was constructed not from entirely novel features, but by modifying traits that developed deep within their reptilian past. Indeed, if we consider king tyrant anatomy in the most general sense—as gigantic, large-headed, robust-bodied terrestrial reptiles adapted for predating other large animals (fig. 2.1)—we can appreciate that they were just one of several reptile groups to attain this form during the Mesozoic Era. The repeated appearance of these similar ecomorphs (that is, the expression between anatomical form and ecological role) is a consequence of evolutionary convergence; incidences where distantly related species develop similar adaptations to "solve" similar evolutionary challenges. Large, big-headed carnivorous reptiles began developing in the Early Triassic Period, some 180 million years before *Tyrannosaurus* evolved (fig. 2.2). Introducing some of these convergent species allows us to explore the deeper evolutionary pathways that ultimately led to the development of *T. rex*.

Considerable scientific effort goes into classifying evolutionary relationships between organisms, living and extinct. Doing so reveals how their anatomy was shaped through the process of natural selection, what extinctions their lineage endured, and what opportunities allowed them to diversify. Our means to classify organisms have, in the last few decades, diverged from the traditional means of discussing evolution and biological classification still taught in most schools, so appreciating where *Tyrannosaurus* fit in the tree of life might be aided by a brief primer on these methods. Many of us learn that organisms are categorized using a system established by Carl Linnaeus in the eighteenth century where species are placed in ranks: kingdoms, orders, families, and genera. These ranks have been all but abandoned by contemporary scientists in favor of modeling evolutionary trees, known as phylogenies, where organisms are placed in clades: groups of

FIGURE 2.1

The reconstructed holotype of *Tyrannosaurus rex*, as displayed at the Carnegie Museum, Pittsburgh. Holotypes are pivotal specimens in organismal classification as they define the characteristics of a species and are the remains to which a scientific name will be forever attached. No matter what other decisions occur in *T. rex* classification, this specimen, Carnegie Museum no. 9380, will always define the king tyrant species.

species with shared ancestry united by common anatomies. Clades are named and nested within one another, but are not ranked. After all, if life on Earth has evolved through a continuous, unbroken chain of natural selection, hierarchies are arbitrary and scientifically meaningless. Instead, we simply refer to taxonomic units: clades and "taxa" (or, singular, "taxon"), the latter being a name given to any named evolutionary unit, be it a single species or a clade of any size. "*Tyrannosaurus rex*" and "*Homo sapiens*" are taxa, and so are groups like "Tyrannosauridae" and "Hominidae." Evolutionary relationships between taxa are frequently expressed via branching diagrams known as phylogenetic trees.

The only holdovers of older Linnaean schemes are genera and species, the scientific binomials applied to discrete populations of organisms. Species are, generally speaking, the most fundamental taxonomic units, a population of organisms that are distinguishable in some way from all others. A genus may contain one or more species, and they are knowingly artificial; a taxonomic practicality that ensures consistency with hundreds of years of biological classification, as well as a means to more easily produce new taxonomic names. Each organism requires a unique name and, as we know from the names we give ourselves, a binomial system such as first name and surname, or genus and species, offers far greater variety than a single word.

ARCHOSAURIFORMES AND THE FIRST LARGE, GIANT-HEADED TERRESTRIAL PREDATORS: ERYTHROSUCHIDS

We might start our march toward the evolution of *Tyrannosaurus* by meeting the earliest successes in achieving a *T. rex*-like ecomorph: the erythrosuchids (figs. 2.2, 2.3A). These peculiar-looking reptiles were a widely distributed group of Early-Middle Triassic carnivores that resembled large lizards with enormous, deep heads (see Ezcurra et al. 2013 for an overview of this group). As members of the clade known as Archosauriformes, erythrosuchids were more closely related to archosaurs, the group that includes crocodylians and dinosaurs (the latter, of course, including birds), than they were to lizards and snakes. They were, nevertheless, a relatively archaic lineage only distantly related to any animals alive today (fig. 2.2). Archosauriformes were a major radiation of reptiles in the early Mesozoic Era. They are anatomically united by a unique hole in their snouts (the antorbital fenestra; see chapter 3), deeply rooted teeth set into sockets within their jaws, and appear to have been more energetic than other reptiles. They diversified across Triassic ecosystems emptied of their previous occupiers, our own distant mammalian relatives, by the mass extinction at the end of the Permian period 252 million years ago. This Triassic diversification of the archosaur line gave rise to many famous reptile types: the strange tanystropheids, the squat, beak-faced rhynchosaurs, the extremely diverse crocodylian lineage, the flying pterosaurs, and the dinosaurs. Following this rapid explosion in reptile form, the Triassic saw these lineages competing for the same niches within terrestrial ecosystems, from which dinosaurs emerged with the greatest stakes in herbivorous and carnivorous roles.

Erythrosuchids did not significantly overlap in geological time with dinosaurs as their 11-million-year evolutionary run, which spanned 251–242 million years ago, was largely concluded before dinosaurs appeared. Their Early and Middle Triassic habitats were still recovering from the Permian mass extinction and they lived among faunas and floras distinct from those that would develop later in the Mesozoic. Within this timeframe, erythrosuchids operated as predatory species that, in some cases, were arch-carnivores: giants reaching 5 m long. Scientific exploration of erythrosuchid ecology is still in its infancy, but they were evidently powerful animals equipped with strong bites. What they ate, and where they sourced their food is still uncertain, but most recent opinion has favored terrestrial carnivory over prey sourced in semi-aquatic roles (Ezcurra et al. 2013).

Our limited understanding of erythrosuchid paleoecology, and the fact that their bodies resembled

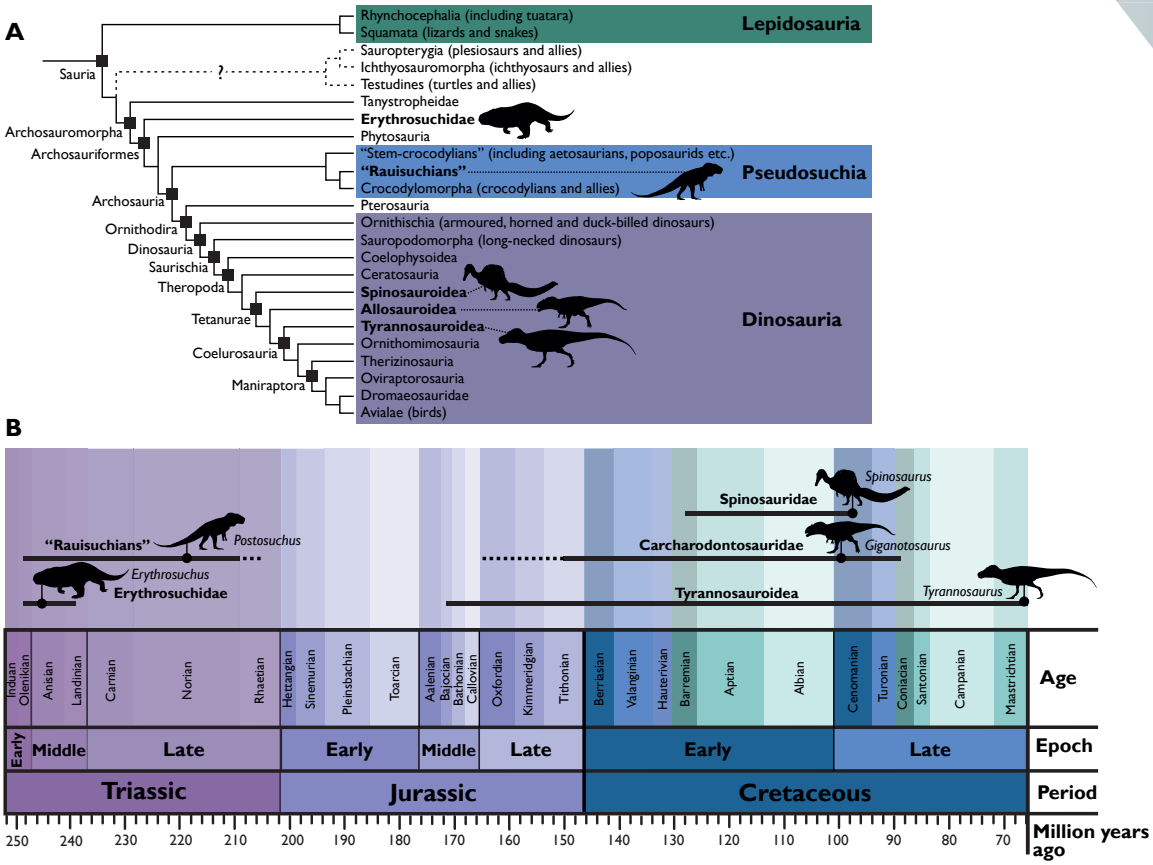


FIGURE 2.2

***Tyrannosaurus* in a broad evolutionary context. (A) Summary of reptile evolution; silhouettes and bold text denote clades discussed in this chapter; (B) temporal distribution of discussed groups and species across the Mesozoic Era.**

those of lizards or crocodylians mean that it is their enormous, well-built heads that make them primarily tyrannosaur-like. Despite their evolutionary distance, the fundamental similarities between tyrannosaur and erythrosuchid skulls are impressive, with shared solutions found for strengthening the neck-skull joint, increasing bite forces, and reinforcing the skull against stresses incurred during predation. Like *T. rex*, the posterior faces of erythrosuchid skulls were expanded to accommodate larger neck musculature, and their neck vertebrae were proportionally large. Their skulls also bore large spaces for jaw muscles, facilitating a strong bite. Broad skull bones and an associated reduction of skull openings likely increased the strength of their crania, although some vacuities, likely related to weight-saving, air-filled sinus tissues, remained. These same features underpin the morphology of the *Tyrannosaurus* head and neck (see chapters 3 and 4) and show that the genetic and functional potential for large-headed predators originated far outside of the tyrannosaur, or even dinosaur lines. Indeed, archosaurs appear to have been particularly well adapted to developing oversized heads, these appearing in several unrelated groups: erythrosuchids, predatory dinosaurs, horned dinosaurs, and the flying pterosaurs. In this sense, we can see that one of the most critical parts of *T. rex* anatomy, their enormous, powerful skulls, were not an evolutionary novelty, but pulled from evolutionary resources developed deep within their archosauriform ancestry.

FIGURE 2.3

Long before *Tyrannosaurus*, non-dinosaurian Triassic reptiles were experimenting with large-headed predatory body plans. These included (A) the 5–6 m long erythrosuchid *Erythrosuchus africanus* from South Africa; and (B) the superficially dinosaur-like *Postosuchus kirkpatricki*. More closely related to crocodylians than dinosaurs, *Postosuchus* is so convergent with tyrannosaurs that some initial interpretations posited that tyrant dinosaurs evolved from similar animals.

TWO-LEGGED, ROBUST-SKULLED, SHORT-ARMED CROCODILE RELATIVES: THE PREDATORY "RAUISUCHIANS"

Moving closer to *Tyrannosaurus* in reptile phylogeny introduces us to animals which, superficially speaking, looked a lot like predatory dinosaurs. These Triassic animals stood upright on two legs, had short arms and large skulls equipped with flesh-cutting teeth, but closer inspection reveals several obvious differences with dinosaurs. Their feet were short and compact rather than bird-like, and they were plantigrade: that is, they placed their ankle on the floor when walking and standing. Their legs were shorter and held in a more upright, columnar fashion, and some bore armor on their backs. Their necks were short and lacked the "S" shape so common to dinosaur predators, and their skulls were more massive. These were not dinosaurs

at all, but certain members of "Rauisuchia," a grade of reptiles from the crocodylian evolutionary line (figs. 2.2, 2.3B).

Modern crocodylians are often regarded as dinosaur-like animals or even living dinosaurs but, despite sharing a common ancestor, dinosaurs and crocodylians are not closely related. They are both part of Archosauria, the archosauriform group that includes crocodylians and their ancestors in one major clade, and the flying pterosaurs and the dinosaurs (including birds) in another. As a group, archosaurs elaborated on features already common to archosauriforms by further lightening their skulls and developing powerful hindlimb muscles, the latter of which allowed for deviation from the quadrupedal gaits of other reptiles. The crocodylian lineage is known as Pseudosuchia, a once-diverse group that, during the Triassic, were major competitors for the niches dinosaurs would eventually occupy. They included species that were radically different to living crocodylians, including gracile taxa that could run fast, others that adapted to eat plants, and even types that walked on two legs. The "rauisuchians" were some of the most dinosaur-like of all pseudosuchians, such that their fossils are often confused for one another (Nesbitt et al. 2013a). It's widely appreciated that "rauisuchian" evolutionary relationships are unresolved and, presently, this group acts as a taxonomic "wastebasket" for Triassic pseudosuchians that do not fit into other, better-defined lineages (Gower 2000; Nesbitt et al. 2013a). "Rauisuchia" is thus not considered a natural group but a collection of species with disparate sizes, lifestyles, and methods of locomotion, some of which may not be closely related to one another. In time, further study will tease out their evolutionary affinities.

Most "rauisuchians" were carnivores and among their diverse forms were the first truly large terrestrial reptilian predators, animals that reached or exceeded 7 m long. These giants included species like *Postosuchus kirkpatricki* (fig. 2.3B), which were among the first powerful, two-legged reptilian predators to adopt a *Tyrannosaurus*-like ecomorphology. Equipped with a stout, reinforced skull and large teeth adapted for tearing flesh (Weinbaum 2011), *Postosuchus* were arch-predators of the southern United States in the Late Triassic. Comparisons with this species and *Tyrannosaurus* are not merely casual as the original describer of *Postosuchus*, Sankar Chatterjee, felt that this Triassic carnivore was so *T. rex*–like that the two surely had close evolutionary affinities (Chatterjee 1985). Citing shared features of their skulls, hips, and limbs, Chatterjee felt that tyrannosaurs were not dinosaurs at all, but actually late-surviving descendants of *Postosuchus*-grade pseudosuchians (this idea, it's perhaps needless to say, has not endured). Whether *Postosuchus* was fully bipedal or not has been debated, but most authors have concluded that their short, slender arms would be of little use in terrestrial progression, as well as noting features optimizing two-limbed locomotion in their hips, spines, and legs (e.g., Chatterjee 1985; Weinbaum 2011; Nesbitt et al. 2013a).

As convergent on *T. rex* as *Postosuchus* was, comparing their anatomy highlights some important features that distinguish the *Tyrannosaurus* body plan from that of even the most formidable bipedal "rauisuchians." Chiefly, although the *Postosuchus* skeleton was lightly built compared to their close relatives (Chatterjee 1985), terrestrial pseudosuchians lacked adaptations to develop extremely large body sizes and fast locomotion (Nesbitt et al. 2013a). Their upright limbs and bipedal poses may have conferred some speed advantages over equivalently sized pseudosuchians with four, relatively sprawled limbs, but "rauisuchians" had relatively short, plantigrade legs that were less optimized for running than those of predatory dinosaurs. Their long bodies likely negatively impacted their agility at speed, too. It is thought that these properties limited "rauisuchian" predatory habits to ambushing prey rather than pursuing it over long distances, which was probably an option for at least some carnivorous dinosaurs. Additionally, they may have been relatively heavy compared to theropods, as pseudosuchians lack unambiguous evidence of the neck and torso air sacs that lightened dinosaur bodies (Butler et al. 2012; Weinbaum 2011). As with erythrosuchids and all other archosaur-line

reptiles, bony signatures of air sacs were present in "rauisuchian" skulls (e.g., Weinbaum 2011) and likely contributed to reducing the mass of the head, but the lack of weight-saving features elsewhere in their bodies may have precluded the attainment of *T. rex*–grade sizes and further impacted locomotion. We might view *Postosuchus*-like "rauisuchians" as demonstrating how close reptiles could get to a *Tyrannosaurus* ecomorph without developing those key anatomical and physiological properties that made dinosaurs well suited to developing gigantic, relatively fast predators.

DINOSAURS, THEROPODA, AND THE OTHER KING-SIZED DINOSAUR PREDATORS

One of the greatest archosaurian lineages were the dinosaurs, a major clade that is perhaps the most familiar group in the evolutionary address of *Tyrannosaurus rex*. Mesozoic dinosaurs were unique among terrestrial animals for their capacity to combine gigantic body sizes with particularly efficient terrestrial locomotion, with many adaptations to these traits distinguishing them from their pseudosuchian archosaur relatives. Historically, dinosaurs were characterized by features related to strengthening their skeletons and moving quickly, including reinforced pelves, hindlimbs adapted for upright postures with a specialized ball-and-socket joint between the femur and hip, and a hinge-like ankle. Learning more about the early origins of dinosaurs has smeared some of these features across other archosaurs, however (e.g., Brusatte et al. 2010a; Nesbitt 2011; Nesbitt et al. 2013b), and dinosaurs are today distinguished by minutiae of their skulls, vertebrae, and especially their limbs, the latter of which are also hallmarks of powerful locomotion (Coombs 1978; Nesbitt 2011; Cuff et al. 2022).

It is thought that this fast, low-cost movement was of particular utility to the first dinosaurs, which were predatory in habit (Benton 2004). In this respect, *Tyrannosaurus* and their carnivorous relatives represent continuations and refinements of the original dinosaur ecology, eschewing the evolutionary opportunities taken by omnivorous and herbivorous species elsewhere on the dinosaur tree. Indeed, as relatively long-legged bipedal reptiles with grasping hands, the first dinosaurs already had the fundamental foundation of the tyrannosaur body plan in place, and abundant evidence suggests that they already had fast metabolic rates (i.e., that they were endothermic, or "warm-blooded" animals with fast metabolisms, like birds and mammals, not ectothermic, or "cold-blooded," like living reptiles; see chapter 4). Although there is no fossil data indicating that the first dinosaurs had protofeathers (the fluffy skin covering that would eventually give rise to true feathers), such features are predicted in evolutionary models thanks to the presence of skin fibers in pterosaurs and several dinosaur groups (e.g., Campione et al. 2020; Benton 2021). Fluffy tyrannosauroids (see below) may have also inherited these features from early dinosaur ancestors (Xu et al. 2004, 2012).

Within Dinosauria are three well-established lineages: the ornithischians, or beaked herbivores, the sauropodomorphs, the long-necked dinosaurs and kin, and the theropods, exclusively two-legged, mostly predatory species. How these groups are related to each other has been largely unquestioned among researchers for the last century, with the saurischian group ("lizard-hipped" dinosaurs, with a forward-projecting pubic bone making for a triradiate pelvis; see chapter 3 for more on dinosaur anatomy) containing the sauropodomorphs and theropods, while Ornithischia ("bird-hipped," with a backward-angled pubic bone) stand independently. This long-standing model has been challenged through new studies of early dinosaur anatomy, however, as some features uniquely shared between theropods and ornithischians may indicate a closer affinity than previously appreciated. In this model, the theropod and ornithischian group is known as Ornithoscelida (Baron et al. 2017). Although the conventional view of dinosaur evolution has generally been upheld in subsequent study, the Ornithoscelida hypothesis and other revisions to the base of the dinosaur

tree have shown that traditional interpretations were not as concrete as previously thought. Discussions about the arrangement of the base of the dinosaur tree are ongoing (e.g., Langer et al. 2017; Müller and Garcia 2020; Norman et al. 2022).

Happily, this rocking of the dinosaur evolutionary boat does not affect our discussion as the composition of Theropoda, the predatory dinosaur line, is largely noncontroversial. Theropods first appeared in the Carnian stage of the Late Triassic Period (approximately 237–227 million years ago) and occupied most Mesozoic terrestrial predatory niches from the Early Jurassic onward (Brusatte et al. 2010a). A tremendously diverse group, they developed into gigantic and tiny forms during the Mesozoic, as well as fast runners and slow lumberers, carnivores, herbivores, and omnivores, and had skin covered in everything from scales to downy-fluff to fully developed, avian-grade feathers. In some other respects, theropods were evolutionarily conservative, never abandoning the two-limbed gaits of their ancestors, mostly retaining flesh-eating habits (at least in the Mesozoic), and never experimenting with extensive body armor. The origin of birds within Theropoda makes this the only dinosaur group to survive to modern times, as well as the most speciose of the three main dinosaur lineages. Living birds comprise something like ten thousand species, dwarfing the totality of Mesozoic dinosaurs known from fossils.

Amid this diversity arose several superficially tyrannosaur-like animals: species that combined large body size with big heads, short forelimbs, and rapid locomotion (fig. 2.2). Mesozoic theropods seem predisposed to developing large sizes because this was achieved by a variety of Cretaceous theropod types, including the noncarnivorous ornithomimosaurs (ostrich dinosaurs) and the bird–like oviraptorosaurs. Among the predatory lineages, however, the most tyrannosaur-convergent were members of the Allosauroidea and Spinosauridae: two diverse, geographically widespread Jurassic and Cretaceous lineages that evolved *T. rex*–grade stature and carnivorous capacity. These are the only non-tyrannosaurid species known that challenge *Tyrannosaurus* for the title of biggest terrestrial predator among Dinosauria or, indeed, any animals.

The interrelationships of large carnivorous theropods are somewhat uncertain (see below), but we can confidently assume that these gigantic species evolved independently of one another. One branch of theropod evolution gave rise to Spinosauridae, a group of long-snouted, low-skulled Cretaceous theropods that may (or may not) be allied with the famous Jurassic predators *Megalosaurus* and *Torvosaurus*. They ranged widely through the Mesozoic, spreading across Europe, Asia, Africa, and South America during the Early and mid-Cretaceous. Among the last and most spectacular of their kind was *Spinosaurus aegyptiacus*, a North African, Late Cretaceous (probably Cenomanian, 100–94 million years ago; Figure 2.2B; Ibrahim et al. 2020a) species famous for their tall, bony sails. This species needs little introduction to dinosaur aficionados as it has enjoyed a recent surge in popularity thanks to high-profile research (Ibrahim et al. 2014, 2020b) and a starring role in 2001's *Jurassic Park III*. Famously, the original *Spinosaurus* fossils were destroyed by Allied bombing during the Second World War, leaving this species recorded only through photographs and illustrations until relatively recently when, from 1990s onward, new fossils were finally unearthed in various North African nations (e.g., Dal Sasso et al. 2005; Ibrahim et al. 2014, 2020b).

The most significant of these new finds is a partial skeleton which has recast *Spinosaurus* as a short-legged theropod with a heightened, laterally compressed tail (Ibrahim et al. 2014, 2020b). They seem to have stood on four toes thanks to an enlarged first toe, or "hallux," that, unusually for a theropod, could reach the ground. How anatomically unusual *Spinosaurus* were remains controversial, and these matters may not be resolved until a more complete skeleton is found. Partial remains of key skeletal elements suggest that they bore the large, three-fingered hands and long, low snouts typical of all spinosaurids, but attempts to create whole-body reconstructions differ in subtle but important aspects of proportion and size, especially leg length (Evers et al. 2015; Paul 2016; Henderson 2018; Hartman 2020;

Sereno et al. 2022). Considerations of body proportions play into debates about virtually every interpretation of this animal, from their basic taxonomy, gait, and locomotive prowess to diet and lifestyle (e.g., Ibrahim et al. 2014, 2020b; Evers et al. 2015; Hone and Holtz 2017, 2021; Sereno et al. 2022). Taxonomic issues are perhaps the most crucial debates facing *Spinosaurus* at present because, currently, no consensus exists on how many spinosaurid species lived across North Africa and existing *Spinosaurus* reconstructions lean heavily on compiling specimens from across African countries. Are we are reconstructing the anatomy and lifestyle of one species, or creating a chimeric "Frankenstein" spinosaurid by combining several?

Uncertainty aside, *Spinosaurus* was clearly an aberrant species unlike any other giant theropod currently known. A wealth of evidence shows that spinosaurids obtained much of their food from aquatic settings (e.g., Ibrahim et al. 2014, 2020b; Hone and Holtz 2017, 2021), and *Spinosaurus* represents the furthest specialization of this evolutionary pathway. Some researchers have proposed that they adopted a pursuit-swimming predatory lifestyle (Ibrahim et al. 2014, 2020b; Fabbri et al. 2022), while others argue that they lived, as is generally assumed for other spinosaurids, somewhat like a mix of grizzly bear and heron: generalist foragers that waded into lakes and rivers to apprehend swimming prey (Hone and Holtz 2017, 2021; Henderson 2018; Sereno et al. 2022). Currently, the "wader" hypothesis seems more likely because several studies have shown that the *Spinosaurus* body plan was ill-suited to pursuing prey underwater (Henderson 2018; Hone and Holtz 2021; Sereno et al. 2022, see chapter 4 for more on theropod swimming) and, in this model, we can imagine *Spinosaurus* grabbing aquatic animals with their low, slender skulls and strongly clawed arms. *Spinosaurus* was further distinguished among predatory giants by their investment in enormous sails that ran along their backs and tails, structures that were almost certainly sociosexual display organs (Hone and Holtz 2021). These not only differentiate *Spinosaurus* from *T. rex*, which has reduced ornamentation (chapter 3) but other theropods in general. *Spinosaurus* was the peacock of the giant predatory dinosaurs (fig. 2.4).

In being such an unusual theropod, *Spinosaurus* has little else in common with *Tyrannosaurus* other than raw size. Since their discovery in the early twentieth century, *Spinosaurus* has been regarded as a giant that rivaled or exceeded *T. rex* in body length. Like all dinosaurs, *Spinosaurus* has evidence of mass-reducing air sacs within their bodies and necks that, along with other features, allowed them to grow very large. Our most substantial, but still far from entire, *Spinosaurus* skeleton perhaps measured nearly 11 m long when complete, not accounting for the natural curvature of the animal when standing. This individual may have massed around 4 tonnes (Ibrahim et al. 2020b), and scaling it to the largest *Spinosaurus* fossils implies a body length greater than that of the biggest *Tyrannosaurus*: 14–15 m. Estimated body masses were modest for such a long creature, however; just 7.4–9.5 tonnes (Ibrahim et al. 2020b; Sereno et al. 2022). This indicates that *Spinosaurus* may have been longer than the c. 12 m–long *T. rex*, but large king tyrants likely exceeded 8 or 9 tonnes, making them proportionally heavier (see chapter 4 for discussion of *T. rex* body mass). This assessment comes with the caveat that, without a complete, or even near complete *Spinosaurus* specimen, errors in our scaling assumptions, length estimates and mass predictions are near certain (Therrien and Henderson 2007; Persons et al. 2020). We need to learn a lot more about *Spinosaurus* before determining how it truly ranked in the Battle of the Biggest Theropods.

With *Spinosaurus* differing from *Tyrannosaurus* in virtually all attributes other than size, the group that converged most with giant tyrannosaurids are the carcharodontosaurids: a grand Cretaceous lineage of predatory dinosaurs that includes famous species like *Acrocanthosaurus atokensis*, *Giganotosaurus carolinii* (fig. 2.5) and *Carcharodontosaurus saharicus* (fig. 1.23). These theropods were probably the closest any group came to developing tyrannosaurine characteristics outside of the tyrannosaur line itself, and they are superficially similar in many attributes: large heads, small arms, and strongly

FIGURE 2.4

Longer than *Tyrannosaurus* but perhaps not as heavy, *Spinosaurus aegyptiacus* were among the most unusual of all theropods. A predator of aquatic prey, their anatomy contrasts markedly with that of king tyrants, not the least for the development of ostentatious sails on their torsos and tails. *T. rex*, in contrast, reduced their bony ornaments. In terms of fashion at least, there's no question who wins the battle between *Spinosaurus* and *Tyrannosaurus*.

FIGURE 2.5

The giant carcharodontosaurid *Giganotosaurus carolinii*. Large Cretaceous carcharodontosaurids such as this and *Carcharodontosaurus* are perhaps the only theropods that rivaled *Tyrannosaurus* in size and predatory scale.

built, massive bodies. In detail, however, they are quite different. Carcharodontosaurids lacked the elongate, narrow feet of tyrannosaurs, as well as their barrel-shaped chests and two-fingered hands. Their bite strengths were weaker, and their teeth better suited to tearing flesh than puncturing bone. In many respects, they resemble especially large versions of their Jurassic allosauroid ancestors, epitomized by the famous *Allosaurus*, and we might consider the giant Cretaceous carcharodontosaurids an archaic grade of predatory dinosaurs inflated to a new size class rather than, as with tyrannosaurs, a new kind of large-bodied predatory form (see below).

This is not, however, to imply that carcharodontosaurids should be regarded as somehow inferior to the tyrannosaur line. As noted in chapter 1, carcharodontosaurids were among the most widespread and longest-surviving groups of large theropods with a distribution across the Americas, Africa, Europe, and Asia, as well as an evolutionary history spanning much of the Cretaceous (fig. 2.2; Candeiro et al. 2018). They disappeared from the fossil record approximately 83 million years ago, and it was only after this that the tyrannosaur lineage, apparently in quick succession, developed large, robust forms (Brusatte et al. 2010b; Brusatte and Carr 2016). A patchy mid–Cretaceous dinosaur record obscures the specifics of this transition, but current data might indicate that the evolution of large tyrannosaurs was suppressed by the existence of giant carcharodontosaurids. Furthermore, the likes of the North African *Carcharodontosaurus* and South American *Giganotosaurus* were among the largest terrestrial predatory animals to ever live, equaling or surpassing *T. rex* in length and mass. Carcharodontosaurids were undoubtedly important theropods that shaped the development of Mesozoic terrestrial ecosystems.

As with *Spinosaurus*, working out exactly how big carcharodontosaurids could get remains challenging because their largest known skeletal remains are too incomplete for precise size estimates. The first-found specimen of *Giganotosaurus* has a thigh bone length surpassing that of the largest *T. rex* by 4 cm (Coria and Salgado 1995) and an estimated skull length of over 1.6 m (Canale et al. 2022), a value similar to that predicted for *Carcharodontosaurus* skulls (Sereno et al. 1996). These estimates are about 20 cm longer than the biggest complete *Tyrannosaurus* skull on record. Another *Giganotosaurus* specimen, an isolated fragment of lower jaw, hints at a 6.5–8 percent larger animal or, alternatively, a considerably more robust individual than the original specimen (Calvo 1998; Hartman 2013). If representing the former, this would equate to a skull surpassing 1.7 m long, almost 25 percent bigger than that of *T. rex*. How this translates to body length can only be coarsely estimated, but the 12 m attained by the biggest *T. rex* seems like a minimum value for such giants: 13 m or more seems plausible. Based on thigh bone proportions, they may have been heavier than *T. rex* as well (Persons et al. 2020). Attempts to compare the masses of big carcharodontosaurids and *Tyrannosaurus* have found that the robust chests of *T. rex* (chapter 3) make them relatively heavy for their size, but the greater stature of giant carcharodontosaurids may have out-massed *T. rex*, despite their more gracile construction (Hartman 2013; Paul 2016).

The above discussion should not be considered definitive, however. Our specimens of large carcharodontosaurids are even less complete than those of *Spinosaurus*, so any comparison between them and *Tyrannosaurus* is correspondingly imprecise. If we must force a winner in the contest for largest theropod, however, probability does not favor king tyrants. *T. rex* is a relatively well-sampled species and it has, thus far, presented a fairly consistent adult body length of 11–12.5 m. Large carcharodontosaurids, in contrast, are known by just a handful of bones that already hint at animals equaling or surpassing *T. rex* in magnitude. We may have lucked out by finding unusually big, exceptional carcharodontosaurids right away, but it's more statistically likely that these first discoveries represent averagely sized carcharodontosaurid adults, and that larger ones await excavation. It remains true that larger *Tyrannosaurus* may be discovered as well, but probability favors carcharodontosaurids having more surprises in store for us. Time, and further fieldwork, will reveal how accurate these predictions are.

THE TYRANNOSAUR FAMILY TREE

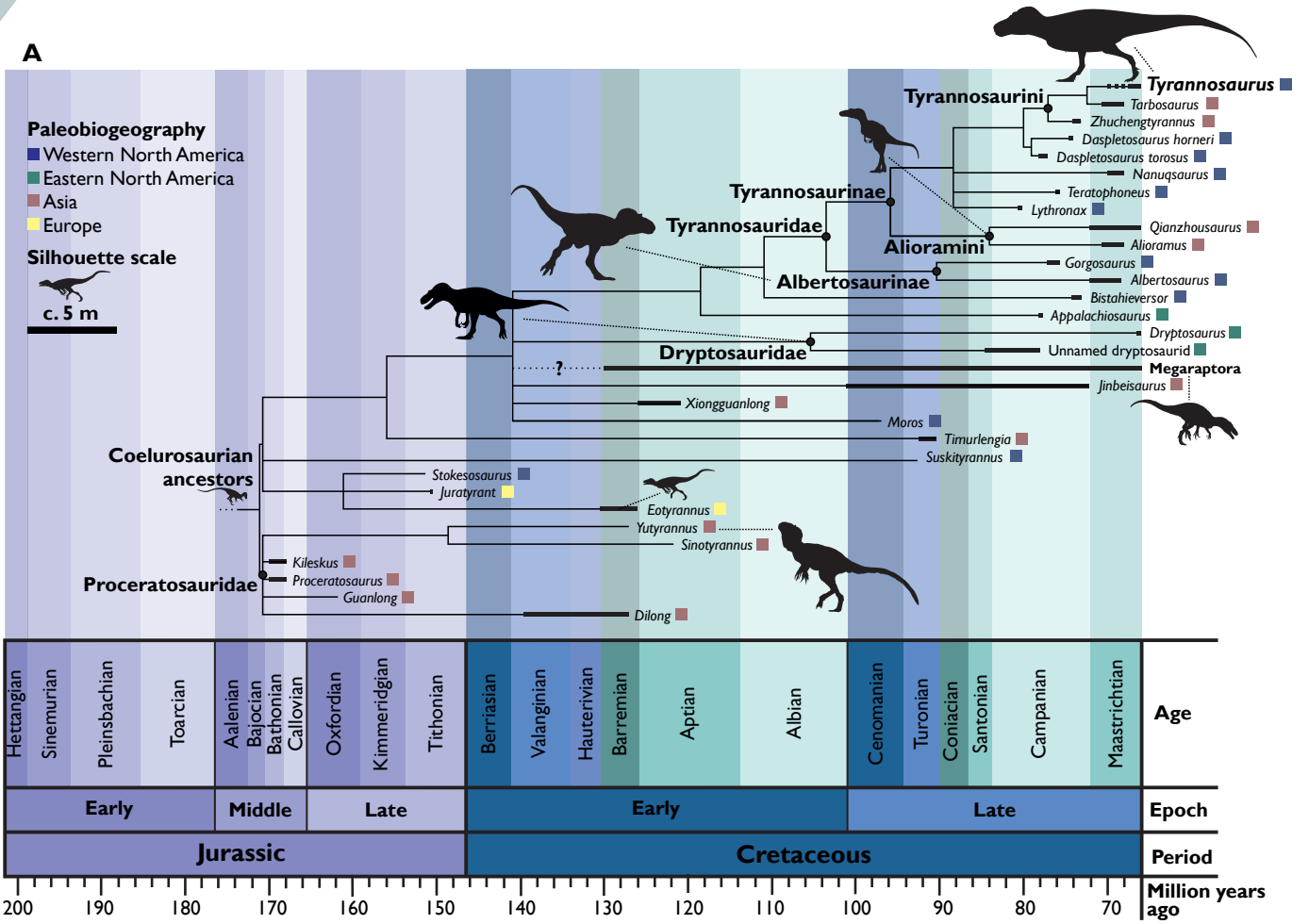
APPRECIATING HOW *TYRANNOSAURUS* arose from other dinosaurs, and distinguishing their true ancestry over mere convergent development of body plans, requires that we begin a more forensic examination of tyrannosaur evolution. In our discussion above we have already pinned down a broad phylogenetic address for *T. rex*: they belong to the reptile clades of Archosauriformes, Archosauria, Dinosauria, and Theropoda (fig. 2.2A). We have also mentioned that Mesozoic theropods were a particularly diverse and speciose bunch, and it is within this group that we should begin to narrow our focus. Theropod evolution has drawn particular interest among dinosaur researchers, and the broad structure of their phylogeny is now well established (e.g., Gauthier 1986; Holtz 1994, 2000; Rauhut 2003; Carrano & Sampson 2008; Carrano et al. 2012). Plenty of controversies and disagreements still exist over theropod interrelationships, but we can outline their evolution and place lineages, such as the *Tyrannosaurus* line, with some degree of confidence (fig. 2.2A).

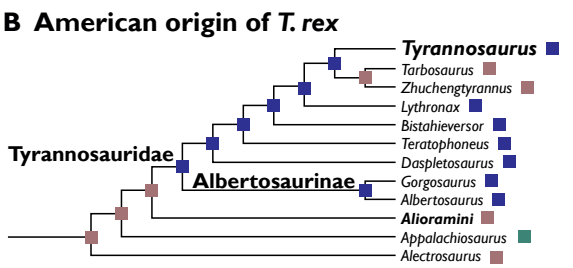
FINDING THE RIGHT BRANCH: TYRANNOSAUROIDEA

The basics of Mesozoic theropod evolution can be broadly understood with knowledge of a few major clades. Their first radiation were the Neotheropoda, which included coelophysoids and the incredibly diverse, long-ranging ceratosaurs (within which we find the eponymous *Ceratosaurus*, the frequently bizarre abelisaurs, and even some fast-running herbivores—see Delcourt 2018). The tetanurans were the next major clade, the first offshoots of which gave rise to three famous carnivorous lineages: megalosaurids, spinosaurids and allosauroids. As discussed above, the spinosaurids and allosauroids contain some of the largest theropod species known, but grand size developed independently several times within this clade and these giants were not closely related. This convergence on body size has only been appreciated relatively recently thanks to the advent of computerized means to identify animal clades. In the early and mid-twentieth century, in contrast, all large predatory theropods, including *Tyrannosaurus*, *Allosaurus*, *Spinosaurus*, and *Megalosaurus* were contained in a group known as "Carnosauria," a loose assortment of large and giant theropods that bore few shared anatomies. Today, we realize that *Allosaurus*, *Tyrannosaurus*, *Megalosaurus*, and so on only resemble one another in superficial features related to their great body sizes, and, in detail, their anatomy is too different to suggest close common ancestry. A clade known as Carnosauria survives in some phylogenetic schemes, but it is different in composition to its historic forebear, and no longer has any bearing on the *Tyrannosaurus* lineage (Rauhut 2003; Padian et al. 1999; Rauhut and Pol 2019).

The most diverse tetanuran clade was Coelurosauria, a group that, among other features, is marked by possessing the only incontrovertibly feathered (and protofeathered) theropods (Campione et al. 2020; Benton 2021). The coelurosaurs comprise the ornithomimosaurs, the ostrich dinosaurs, and their sister group, the Maniraptora. Maniraptorans were an extremely disparate group, including the giant, herbivorous therizinosaurs and the tiny insectivorous alvarezsaurs, as well as the Penneraptora, a collection of bird-like dinosaurs that eventually gave rise to avians themselves. The beaked oviraptorosaurs, omnivorous troodontids, and predatory dromaeosaurs (the group that houses *Velociraptor* and *Deinonychus*) are generally considered the closest non-avian dinosaur relatives of modern birds and their Mesozoic ancestors.

Within this scheme, *Tyrannosaurus* are placed at the base of Coelurosauria. This position makes them the closest relatives of birds among all of the giant predatory theropods, but they were not closely related to birds in any real sense. Their particular branch of coelurosaur evolution is the Tyrannosauroidea, a group of





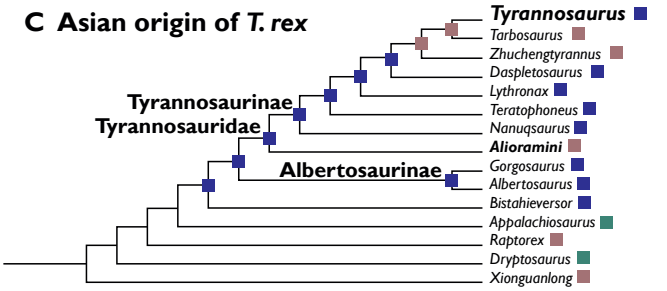


FIGURE 2.6

Tyrannosauroid evolution. (A) Chronogram (a time-calibrated phylogenetic tree) of Tyrannosauroidea with paleobiogeography indicated by colored boxes; (B–C) competing phylogenies of Tyrannosauroidea with different implications for the geographic origins of *Tyrannosaurus*. (A) Topology adapted from Brownstein (2021); (B) after Loewen et al. (2013); (C) after Brusatte and Carr (2016).

theropods that first appeared 170–165 million years ago, during the Middle Jurassic (fig. 2.6; Brusatte et al. 2010b; Brusatte and Carr 2016; Brownstein 2021; Naish and Cau 2022). Apparently restricted to the northern continents (though read on), they can be distinguished from other theropods by a number of features (Holtz 2004): a tall, blunted premaxillary bone (the bone at the front of the upper jaw, see chapter 3), "D"-shaped "incisor"-like teeth at the front of the mouth, fused nasal bones along the top of the snout, extensive air spaces in the skull and lower jaws, a prominent "shelf" on the outer rear surface of the lower jaw, upper pelvic bones (ilia) that almost touch over the hip, vertebrae that bear a central vertical muscle attachment ridge, and a uniquely shaped thigh bone head (Holtz 2004; Brusatte et al. 2010b).

The first tyrannosauroids were small, relatively generalized carnivores that hunted small game while larger megalosauroids and allosauroids occupied large-bodied predatory niches. Some analyses have placed the Late Jurassic North American coelurosaurs *Coelurus fragilis* and *Tanycolagreus topwilsoni* (fig. 2.7A) as early members of the tyrannosauroid line (Senter 2007). This interpretation has not been widely upheld, but, even so, these small species probably had a body plan similar to the most archaic tyrant dinosaurs. It is more widely agreed that the earliest-diverging and oldest lineage of the tyrannosauroids were the Proceratosauridae, a group presently known from Europe and Asia (fig. 2.7B; Rauhut et al. 2010; Brusatte and Carr 2016). The majority of proceratosaurid species are newly discovered, such that their place in tyrant dinosaur evolution and uniqueness are relatively fresh information. They still retained a lot of early coelurosaur features, most notably their relatively long, three-fingered forelimbs and relatively weak bites (Johnson-Ransom et al. 2024), but proceratosaurids were one of the longest-lived tyrannosauroid radiations, persisting for around 50 million years (Brusatte and Carr 2016). Some, such as *Proceratosaurus bradleyi* (fig. 2.8A), *Guanlong wucaii* and *Yutyrannus huali* developed prominent midline snout crests, also making them the most ostentatious species of the tyrannosaur line (Xu et al. 2006; Rauhut et al. 2010). Although generally small bodied, the 9–10 m long *Yutyrannus* and *Sinotyrannus kazuoensis* demonstrated that some proceratosaurids had graduated into larger predatory guilds by the Early Cretaceous (Ji et al. 2009; Xu et al. 2012). *Yutyrannus* and a fellow Cretaceous proceratosaurid, *Dilong paradoxus*, represent the only tyrannosauroids yet known to have definitely sported protofeathers (Xu et al. 2004, 2012).

THE MID-CRETACEOUS: TYRANNOSAUR WILDERNESS

Proceratosaurids appear to have gone extinct in the Early Cretaceous without any descendents, such that all their innovations in size and ornament had no bearing on further tyrant dinosaur evolution. It fell to their sister line of tyrannosauroids, which were at this point present in at least Europe and western North America, to carry the lineage forward. Our knowledge of early non-proceratosaurid tyrannosauroids is not extensive, but they are thought to be typified by small- to midsized (3–5 m long) species of the Jurassic and Early Cretaceous such as *Stokesosaurus clevelandi*, *Juratyrant langhami*, and *Eotyrannus lengi* (figs. 2.7C, 2.8B; Benson 2008; Brusatte and Benson 2013; Naish and Cau 2021). Tyrannosauroids of this grade were generally similar, if somewhat more robust and less ornamented, to proceratosaurids in appearance and ecology, with only the slender-snouted *Xiongguanlong baimoensis* hinting at anatomical diversification (D. Li et al. 2009). Compared to other exciting occurrences in theropod evolution at this time (including, for example, the proliferation of birds and other feathered dinosaurs, the development of fish-eating spinosaurids, the appearance of large carcharodontosaurids), Early Cretaceous tyrannosauroids might be regarded as relatively conservative. However, any generalizations about what tyrant dinosaurs were up to during this interval are tentative because a 20-million-year gap in the tyrannosauroid fossil record spans the middle duration of the Cretaceous (Brusatte and

A

B

C

FIGURE 2.7

Early tyrannosauroids. (A) The small (2 m long) Late Jurassic coelurosaur *Tanycolagreus topwilsoni*, a species that has been postulated as an early tyrannosauroid but may, instead, belong to another part of the theropod tree. The general form of *Tanycolagreus* was probably similar to the earliest members of the tyrannosaur lineage, in any case. (B) The 9 m long, crested proceratosaurid *Yutyrannus huali*, a large, protofeathered tyrannosauroid from colder regions of Cretaceous China; (C) *Eotyrannus lengi*, a small (4–5 m long) Early Cretaceous British tyrannosauroid.

Carr 2016). The recovery of fully formed, "advanced" tyrannosauroids on the other side of this intermission indicates that important developments in tyrant evolution must have taken place during this time: we simply lack the fossils to tell us what was happening.

Some authors posit that this gap in tyrant dinosaur evolution may be filled by an enigmatic theropod group: the Megaraptora (fig. 2.9A). The megaraptors were mid-to-large-sized predatory theropods that had a 60-million-year run lasting much of the Cretaceous, and their fossils occur across the Americas, Australia, and Asia. This apparent abundance contrasts with their relatively newly discovered status. The clade Megaraptora was only formally recognized in 2010 when Roger Benson and colleagues realized that several, hitherto difficult-to-place theropods such as *Aerosteon*

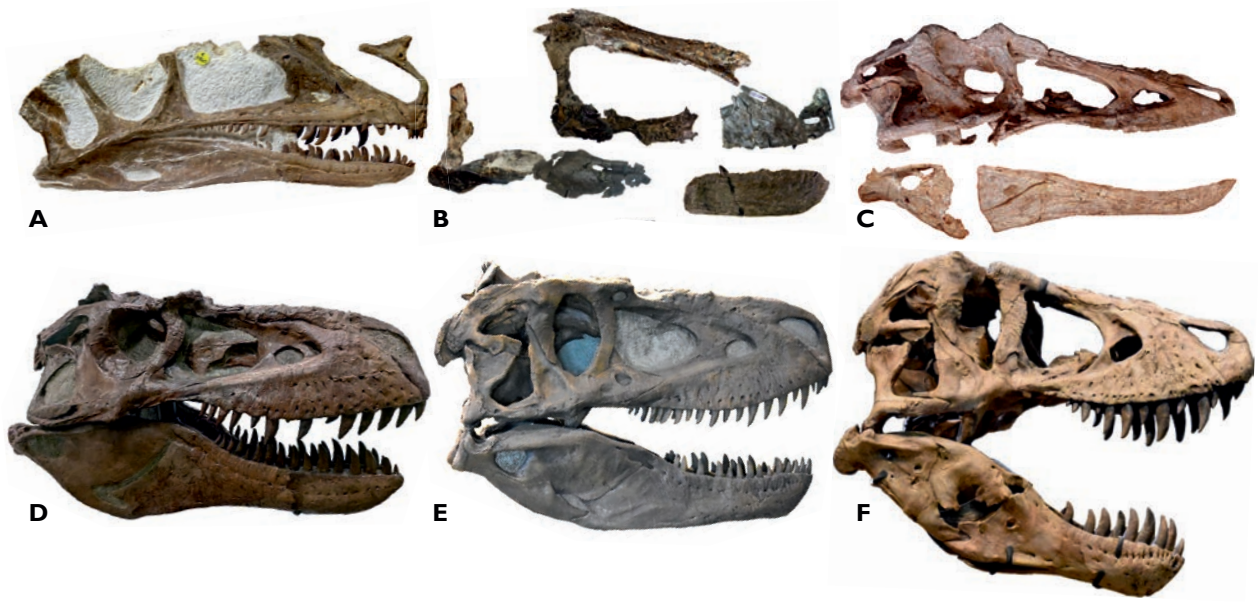


FIGURE 2.8

Skull material from select tyrannosauroids, representing the major grades of their evolutionary history. (A) The proceratosaurid *Proceratosaurus bradleyi*; (B) early tyrannosauroid *Eotyrannus lengi*; (C) alioramin *Qianzhousaurus sinensis*; (D) albertosaurine *Gorgosaurus libratus*; (E) tyrannosaurine *Daspletosaurus torosus*; (F) reconstructed holotype skull of *Tyrannosaurus rex*. Note the increasing skull depth in later tyrannosaurids, an adaptation to possessing longer, stronger tooth roots, increased skull rigidity, and larger jaw muscles. (B) Edited from Naish and Cau (2022). Images not to scale.

riocoloradensis, *Australovenator wintonensis*, *Fukuiraptor kitadaniensis*, and *Megaraptor namunhuaiquii* belonged to a unique theropod lineage. The delayed identification of this group represents, in part, a dearth of complete skeletons. Even the best-known megaraptorans such as *Megaraptor*, *Australovenator*, and *Murusraptor barrosaensis* are currently documented from very incomplete remains.

With scant fossils to work with, our understanding of megaraptoran anatomy, appearance, and ecology is relatively basic. Attaining up to 9 or 10 m body lengths, and with relatively long hindlimbs and shallow jaws

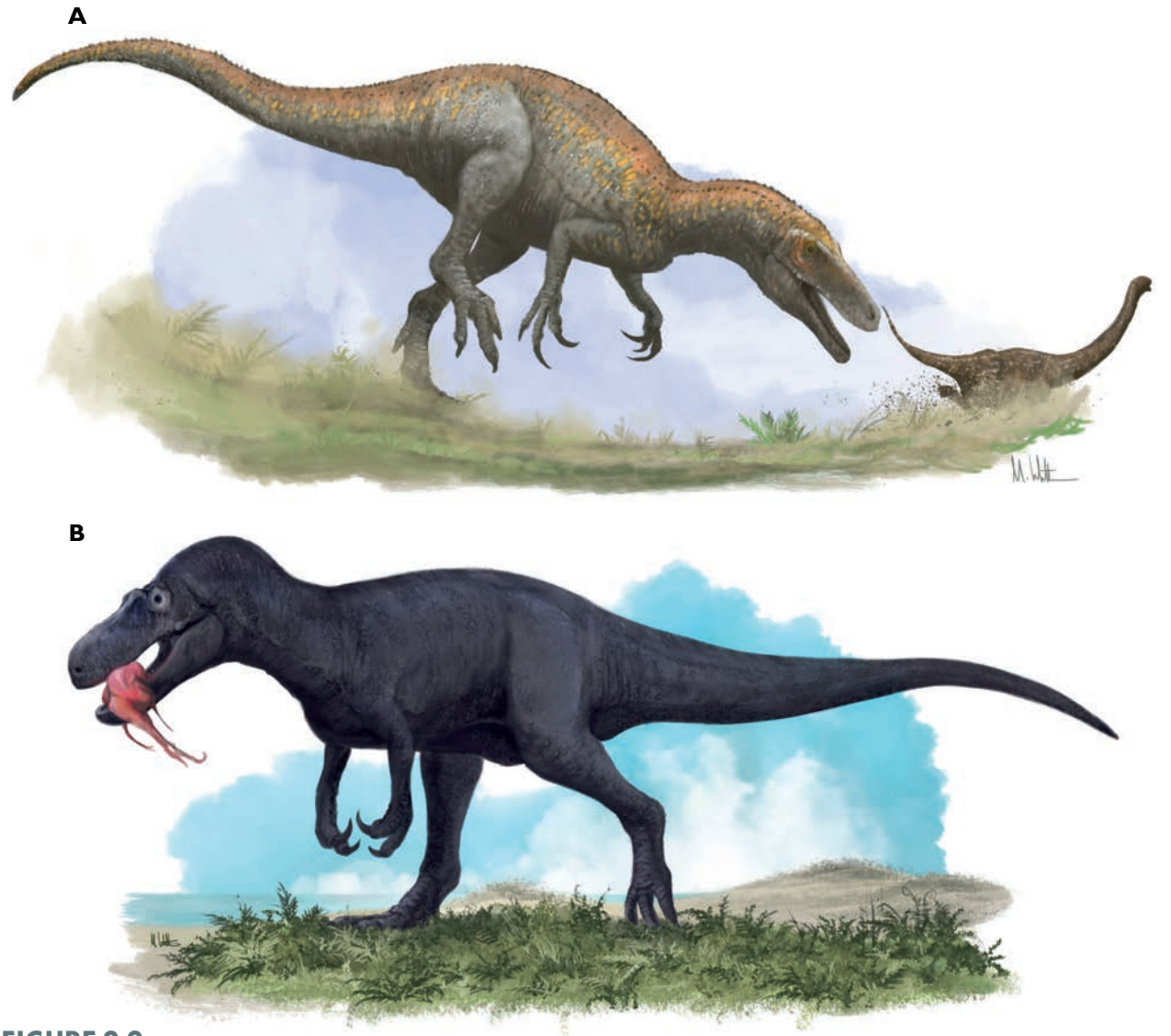


FIGURE 2.9

Possible and "intermediate" tyrannosauroids. (A) The megaraptoran *Australovenator wintonensis*. The affinities of megaraptorans are uncertain, but a number of researchers now hypothesize that they represent a lineage of unusual tyrannosauroids; (B) *Dryptosaurus aquilunguis*, a large-handed, late-surviving non-tyrannosaurid tyrannosauroid from the east coast of North America.

(Benson et al, 2010; Porfiri et al. 2014; White et al. 2015a; Aranciaga Rolando et al. 2022), their most characteristic features were long arms with enlarged, raptorial claws (White et al. 2015b; Novas et al, 2016). The relationships of megaraptorans to other theropods are controversial, with potential homes including Allosauroidea (Smith et al., 2008, Benson et al., 2010, Carrano et al., 2012; Zanno and Makovicky 2013; Coria and Currie 2016), the base of Coelurosauria (Apesteguía et al. 2016; Porfiri et al. 2018; Delcourt and Grillo 2018) or—of most interest to us here—as members or close relatives of the tyrannosaur line (Novas et al. 2016; Porfiri et al. 2014; Aranciaga Rolando et al. 2019, 2022; Naish and Cau 2022). If the latter is borne out, it would not only add a major, 60-million-year branch to tyrannosauroid phylogeny, but also place members of the tyrannosaur lineage in South America and Australia, continents hitherto considered beyond their reach. It would also demonstrate success with an unexpected body plan, the gracile skulls and long, powerful arms of megaraptorans being anatomically antithetical to the large heads and small arms that tyrant dinosaurs are famous for. As relatively large theropods, megaraptorans may also shed light on the evolution of larger size in later tyrannosauroids (Naish and Cau 2022). These implications must be regarded as provisional, however, as further discoveries and research are needed to elucidate exactly what sort of dinosaurs megaraptorans were, and where they fit in theropod evolution.

TYRANNOSAURIDAE: THE ROAD TO *T. REX*

The tyrannosauroid fossil record representing the final 25 million years of the Mesozoic is far superior to that of the mid-Cretaceous (Brusatte et al. 2010b; Brusatte and Carr 2016). Captured within this high-resolution window into tyrant dinosaur evolution were the last of the relatively archaic tyrannosauroids, *Suskityrannus hazelae* and *Moros intrepidus*, which occur in rocks of 100–90 million years old in western North America (Nesbitt et al., 2019; Zanno et al., 2019). *Jinbeisaurus wangi*, meanwhile, lived roughly contemporaneously in China (Wu et al. 2020). The future of tyrannosauroid evolution belonged to other clades, however. Different models of tyrant dinosaur evolution cloud the exact trajectory of anatomical development in this part of the tree (e.g., Brusatte and Carr 2016; Voris et al. 2020; Brownstein 2021), but all predict that features characterizing the final and most famous members of the group, such as greater size and longer, running-adapted hindlimbs, started development during that 20-million-year gap in the tyrant dinosaur record.

The path to tyrannosaurs becoming large, arch predators from their smaller Early Cretaceous relatives was via "intermediate" forms like *Appalachiosaurus montgomeriensis*, *Bistahieversor sealeyi* and the dryptosaurids, including *Dryptosaurus aquilunguis* (fig. 2.9B; Carr et al. 2005; Carr and Williamson 2010; Brusatte et al. 2011; Brownstein 2021). These tyrants remain relatively poorly known, and their basic proportions are only broadly understood. Ranging from 6 to 9 m in length, they had seemingly begun the trend of sustained body size increase evident during the final stages of tyrannosauroid evolution. The skulls and jaws of *Appalachiosaurus* and dryptosaurids were still shallow, but some of the more iconic aspects of tyrannosaur cranial shape were becoming apparent, including their ornamented snouts and the prominent, horn-like bones around their eyes (Carr et al. 2005). *Bistahieversor* sported deepened jaws, indicating development of this feature also began among "intermediate" tyrants (Carr and Williamson 2010). The hindlimbs of dryptosaurids possessed compressed, narrow foot bones (Brownstein 2021), perhaps hinting at increased running capacity (chapters 3 and 4). It remains unclear when the long, three-fingered forelimbs of tyrannosauroids shrank to their shorter, two-fingered variant, but *Dryptosaurus* hints at a halfway condition where the arm bones reduced to the proportions of later tyrannosaurs, but the hand (possibly now two fingered?) remained large (Brusatte et al. 2011). This "intermediate" phase of tyrant dinosaur evolution remains one of the most interesting

phases of their development, although further discoveries are needed to flesh out our knowledge of their anatomy and their roles in the emergence of their larger, later cousins.

The final major phase of tyrannosauroid evolution concerns the Tyrannosauridae (figs. 2.6, 2.10): the group of large, sometimes gigantic predators that, after tens of millions of years as small- and midsize carnivores, now filled top predatory roles in western North America and Asia. An excellent fossil record means that tyrannosaurid skeletal anatomy is understood in detail despite their geological longevity spanning a surprisingly short 15 million years (Brusatte and Carr 2016; Brownstein 2021). Phylogenetic predictions posit that tyrannosaurid origins occurred deep in the Cretaceous, perhaps over 100 million years ago (fig. 2.6; Loewen et al. 2013; Brusatte and Carr 2016; Brownstein 2021), but the early story of their evolution remains untold from fossils. Instead, our geological tyrannosaurid narrative starts with them already occupying vast regions across North America, from Alaska to Mexico, as well as in Asia, where their remains occur in Mongolia and China. By this point, tyrant dinosaurs were not only grand in stature (at least 6 m or more in length as adults, with most species reaching over 10 m), but they often represented the sole large predators in their respective environments (Holtz 2021). The circumstances behind their attainment of arch-predatory niches remains unknown: Did early tyrannosaurids drive their main competition, the carcharodontosaurids, to extinction? Or, alternatively, did they step into arch-predator niches after the carcharodontosaurid lineage ended through other means?

Along with grand body size, tyrannosaurids are defined by a number of features related to large-scale carnivory (Holtz 2004). Their jaws were deep and housed long-rooted teeth. These were no longer blade-like, as is the case for most predatory theropods, but thickened into lance- or spike-like shapes. Heightening and broadening the rear of the skull created enlarged spaces for jaw musculature, increasing their bite forces (Johnson-Ransom et al. 2024) to the extent that some skull regions had to be reinforced (e.g., Henderson 2003; Rayfield 2004; Snively et al. 2006). As a consequence of remodeling the posterior skull, tyrannosaurids had elevated degrees of forward-facing vision (Stevens 2006). Neck musculature was also enhanced, necessitating upward expansions of the rearmost skull bones to accommodate larger muscles. Elsewhere on their bodies, all tyrannosaurids possessed short, two-fingered arms, although some were smaller than others: the Asian giant *Tarbosaurus bataar* currently holds the record for the smallest tyrant dinosaur arms relative to body size (Brusatte et al. 2011). In contrast, their legs were especially long and bore the proportions of runners, even in species that likely exceeded the biomechanical capacity for rapid locomotion (Paul 1988a; Holtz 1995; Hutchinson and Garcia 2002; Persons and Currie 2016; Dececchi et al. 2020; also see chapter 4). Their feet, in particular, hinted at enhanced speed and agility through development of the arctometatarsal condition: the state where the ankle-end of the middle metatarsal (the long bones making the shaft of the foot; see chapter 3) was pinched between its neighbors (Holtz 1995; Snively et al. 2004). Shortened bodies and tails (Newman 1970) added to this unique configuration. This body plan combined adaptations for agility and speed with the strongest bites of any dinosaur (e.g., Johnson-Ransom et al. 2024) and a propensity for giant size: a predatory dinosaur group like no other.

Currently, thirteen to fourteen genera of tyrannosaurids are recognized, divided into a few tribes. The Albertosaurinae comprises *Gorgosaurus libratus* (figs. 2.8D, 2.10B) and *Albertosaurus sarcophagus*: two relatively gracile, although still very large (8–9 m long) tyrants that are known primarily from Alberta, Canada, but that also occur in the northern United States (Russell 1970; Currie 2003a). The albertosaurines have one of the best fossil records of any theropod, rivaling that of *Tyrannosaurus* for specimen abundance and quality. They appear to have died out before the end of the Cretaceous, with *T. rex* filling the void left by their departure. Another group, the Alioramini, is

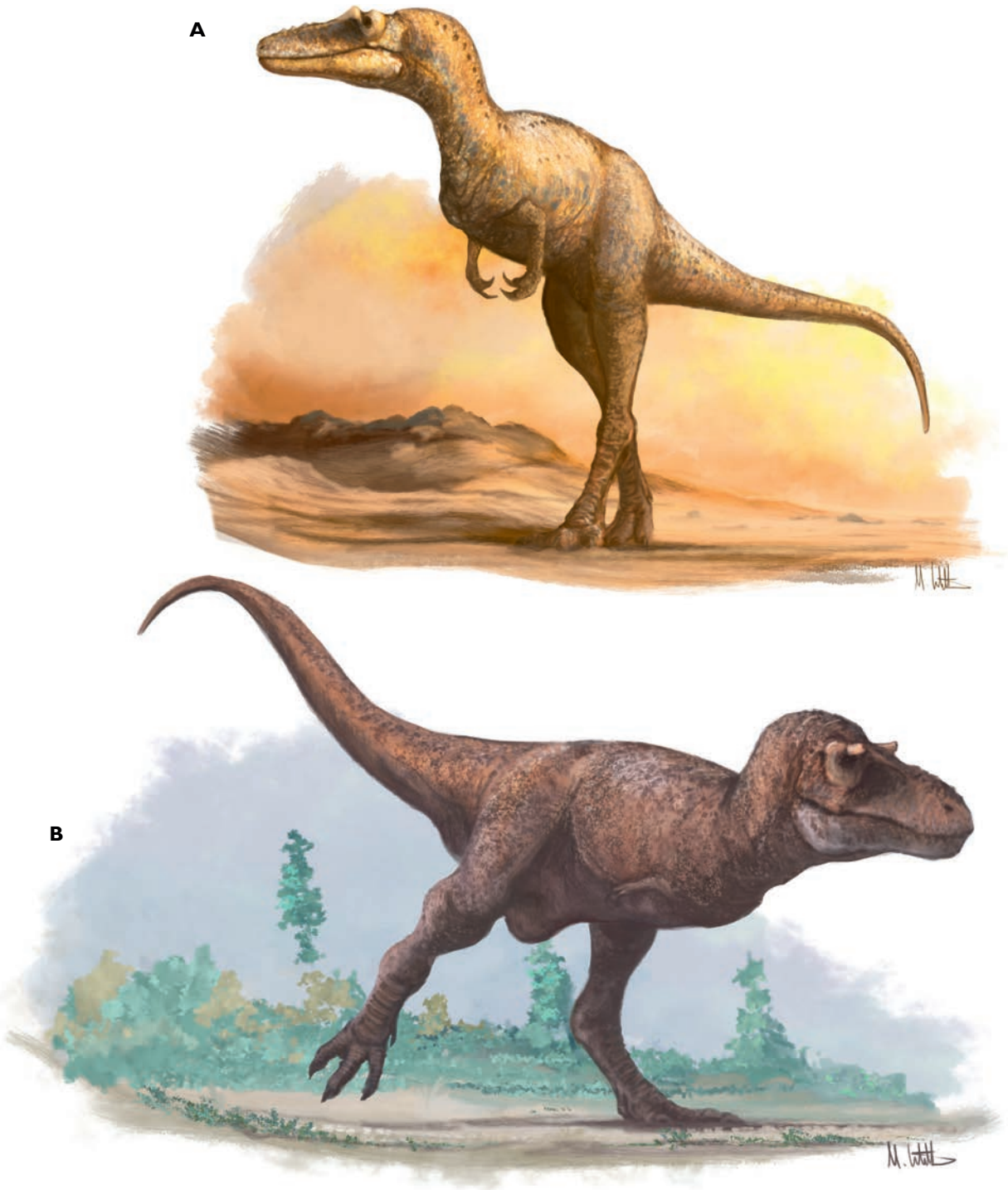


FIGURE 2.10

Examples of tyrannosaurids. (A) The Chinese *Qianzhousaurus sinensis*, representing the long-snouted alioramin branch of tyrannosaur evolution; (B) the albertosaurine *Gorgosaurus libratus*, a relatively gracile form of tyrannosaurid.

only known from Mongolia and China. Represented by two genera and three species, *Alioramus remotus*, *Alioramus altai* and *Qianzhousaurus sinensis*, the alioramins are perhaps the most unusual tyrannosaurids (fig. 2.10A; Brusatte et al. 2009, 2012; Lü et al. 2014; Foster et al. 2022). Smaller than their close relatives in only reaching 6–7 m in length, alioramins had especially low, long skulls that are, for their body size, 35 percent longer than expected. Their skulls were also unusually well decorated, with the ancestral tyrannosaur skull ornament exaggerated into large hornlets atop their snouts and around their eyes (fig. 2.8C). Their slender jaws indicate a departure from typical tyrannosaurid roles as arch-predators, perhaps better suiting mid-tier pursuers of small game. Larger prey was likely pursued by contemporary giant tyrannosaurids, such as *Tarbosaurus* and potentially *Zhuchengtyrannus magnus* (Lü et al. 2014). The co-occurrence of more than one tyrant species in a geological unit is unusual (Holtz 2021), further evidencing a deviant ecology for alioramins.

Where these strange tyrannosaurs fit within Tyrannosauridae is disputed (fig. 2.6B–C). Albertosaurines are generally regarded as the first branch to deviate from mainline tyrannosaurid evolution, but alioramins might represent a second early divergence of tyrannosaurids, forming a clade with the non-albertosaur tyrants, Tyrannosaurinae (fig. 2.6A and C; Lü et al. 2014; Brusatte and Carr 2016; Voris et al. 2020; Brownstein 2021). Alternatively, they might not be true tyrannosaurids at all, instead being close relatives (fig. 2.6B; Loewen et al. 2013; Dalman et al. 2024). These varied arrangements of tyrant clades affect hypotheses of tyrannosaur geographic origins. During the Late Cretaceous, North America was connected to Asia via a northern land bridge, forming a single landmass, Asiamerica, and, with a distribution across western North America and east Asia, it is clear that tyrannosaurid development involved dispersal across both continents. How often this occurred, however, is unclear. Some posit that tyrannosaurids arose in America and then moved across to Asia at least twice (e.g., Brusatte and Carr 2016; Voris et al. 2020; Brownstein 2021) if not on multiple occasions (Zheng et al. 2024), but others suggest that tyrannosaurid evolution began in Asia before shifting to North America, whereupon they developed distinct north-south faunas. Eventually, one branch then returned to Asia as the Cretaceous drew to a close (Loewen et al. 2013; Dalman et al. 2024).

This discussion has bearings on the origins of the *Tyrannosaurus* genus itself. The third main line of tyrannosaurid evolution consists primarily of North American species characterized by large size and particularly heavyset anatomy. It is from this line that *Tyrannosaurus* originated. The shape of this phase of tyrannosaurid evolution remains contested, with taxa from the southwestern United States, *Dynamoterror dynastes*, *Teratophoneus curriei*, *Lythronax argestes*, and the fragmentary Alaskan *Nanuqsaurus hoglundi* arranged differently in competing phylogenies (Carr et al. 2011; Fiorillo and Tykoski 2014; Brusatte and Carr 2016; McDonald et al. 2018; Voris et al. 2020; Brownstein 2021; Scherer and Voiculescu-Holvad 2023; Dalman et al. 2024). Some schemes consider the "intermediate" tyrannosauroid *Bistahieversor* a member of this lineage as well (Loewen et al. 2013), and others pull *Teratophoneus* outside of Tyrannosauridae (Naish and Cau 2022). A recently named Chinese species tentatively considered related to *Nanuqsaurus*, *Asiatyrannus xui*, looks set to complicate this arrangement further, not the least for implying that this phase of tyrannosaur evolution was not entirely confined to North America (Zheng et al. 2024). Some data also hints that *Asiatyrannus* may have been a "midsized" tyrannosaurid even as an adult, bucking the evolutionary convention of tyrannosaurids generally being large, arch carnivores. A mature specimen of this species is needed, however, to verify their actual adult proportions.

Dynamoterror, *Teratophoneus*, *Lythronax*, and *Nanuqsaurus* occupied large predator niches in western North America, from the northernmost regions down to southern states. From somewhere in this stock arose *Daspletosaurus* (fig. 2.8E), represented by three species, *D. torosus, D. wilsoni*, and *D. horneri* (Russell 1970;

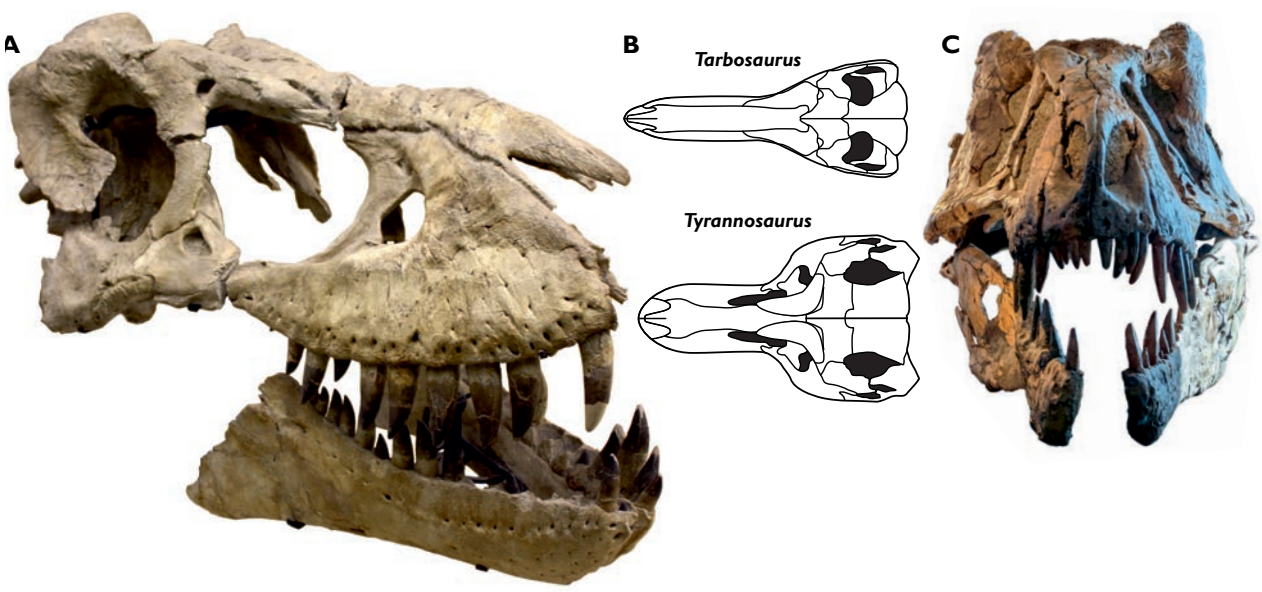


FIGURE 2.11

The closest known relative of *Tyrannosaurus*, the Mongolian tyrannosaurid *Tarbosaurus bataar*. (A) *Ta. bataar* holotype skull, demonstrating the strong similarity of this species to their American cousin; (B) comparison of *Tarbosaurus* and *Tyrannosaurus* skulls viewed from above; note the distinct bone arrangement as well as the difference in skull widths; (C) a large *Tyrannosaurus* skull housed in the Los Angeles Natural History Museum, demonstrating the extreme width of the posterior skull compared to the (also broadened) muzzle. (B) After Hurum and Sabath (2003).

Carr et al. 2017; Warshaw and Fowler 2022), as well as *Thanatotheristes degrootorum* (Voris et al. 2020). Together, these may form the clade Daspletosaurini. Their provenance in the northern United States, and the possibility that the three *Daspletosaurus* taxa represent a single evolving lineage (Warshaw and Fowler 2022, though also see Scherer and Voiculescu-Holvad 2023), hint at northern states having distinct tyrant faunas from the southern regions occupied by *Bistahieversor*, *Dynamoterror*, *Teratophoneus*, and *Lythronax*.

Daspletosaurus is considered a close relative of *T. rex* and may have been directly ancestral to the king tyrant lineage (fig. 2.8F). A twist in tyrannosaurid paleobiogeography complicates the origins of *Tyrannosaurus*, however. Despite being a North American taxon and the evidence of tyrannosaurids diversifying for millions of years in North America, the closest known relatives of the *Tyrannosaurus* genus are, in fact, the Asian giants *Tarbosaurus bataar* (Maleev 1955a, 1955b; Rozhdestvensky 1965) and *Zhuchengtyrannus magnus* (Hone et al. 2011a). Together, these three species form the clade Tyrannosaurini (Scherer and Voiculescu-Holvad 2023; Dalman et al. 2024). *Zhuchengtyrannus* is a very poorly known species, but *Tarbosaurus* (figs. 2.11–12) is represented by a number of excellent specimens, from great adults to tiny juveniles (Tsuihiji et al. 2011). A juvenile specimen of a Mongolian tyrannosaurid initially interpreted as an adult from a dwarf species, *Raptorex kriegsteini* (Sereno et al. 2009), may represent an early growth stage of *T. bataar* (Fowler et al. 2011a), or else might be a juvenile of a species unknown from adult remains (Carr 2023). At estimated body lengths of 12 m, both *T. bataar* and *Z. magnus* were especially large and robust tyrannosaurids that rivaled *T. rex* in size.

FIGURE 2.12

Tarbosaurus bataar **wanders home in the rain with a therizinosaur meal. Like** ***Tyrannosaurus*****,** ***Tarbosaurus*** **had a wide posterior skull, although it was not as broad as that of** ***T. rex*****.**

Tarbosaurus also approached, if not quite matched, king tyrants in bite power (Johnson-Ransom et al. 2024). Although similar in build and form, *Tarbosaurus* can be easily distinguished from *Tyrannosaurus* by their narrower skulls, and also their smaller arms (Hurum and Sabath 2003; Carr et al. 2023).

With close relatives occurring in Asia, some question exists over where *T. rex* originated (figs. 2.6B–C). Some researchers (Loewen et al. 2013; Dalman et al. 2024) propose that *Tarbosaurus* and *Zhuchengtyrannus* form a clade within Tyrannosaurini, representing an independent branch of giant Asian tyrannosaurids that split from the *Tyrannosaurus* line within North America almost 80 million years ago. Other phylogenies, however, point to *Tarbosaurus* and *Tyrannosaurus* forming an exclusive group that only diverged c. 70 million years ago, with *Zuchengtyrannus* their next closest relative (e.g., Brusatte and Carr 2016; Voris et al. 2020; Brownstein 2021; Zheng et al. 2024). This implies that the lineage begatting *T. rex* lived in Asia, and that the distribution of *Tyrannosaurus* represents king tyrants, or their immediate ancestors, returning to regions once occupied by other American tyrannosaurids. Fossil data suggests that the *Tyrannosaurus* lineage existed in the southwestern United States about 70 million years ago (Dalman et al. 2024; though also see chapter 5), but it remains to be seen whether these fossils represent innovations of American tyrannosaurs or recent immigrants from Asia. An improved understanding of early tyrannosaurins, including better resolution of their geological ages, are necessary to resolve this biogeographical conundrum.

TYRANNOSAURUS REX, THE SPECIES

WHEREVER IT ORIGINATED, North America eventually became home to the animal that we call *Tyrannosaurus rex*, and it is consideration of this species that will wrap up our assessment of king tyrant taxonomy. Paleontologists have a reputation for being fussy and indecisive about the names of organisms. Sometimes, it seems that we just can't seem to agree on what certain taxa should be called. Should *Suchomimus* be considered a variant of *Baryonyx*? Is *Torosaurus* a form of *Triceratops*? Are *Stygimoloch* and *Dracorex* junior names for *Pachycephalosaurus*? Other times, we resurrect archaic names after decades of suppression, with a famous recent example concerning the iconic *Brontosaurus*. After almost a century of being regarded as an invalid, subsumed name for *Apatosaurus*, scientists decreed it appropriate and necessary to start using *Brontosaurus* again in 2015 (Tschopp et al. 2015). To those not directly involved in dinosaur research, this fussiness can seem trivial, even neurotic. Do dinosaur names really matter *that* much?

This obsession with names reflects an important discussion about how best to catalog the history of life. The terms we give to species and clades have bearing on their uniqueness, and thus their relationships to other organisms. With our knowledge of the fossil record constantly growing, new data sometimes demands that the labels applied to certain specimens and species need to change, too. Such considerations are the fields of taxonomy (the identification of biological species, genera and higher groups) and systematics (understanding how species relate to one another). They operate within a series of rules and guidelines established by governing bodies to ensure practicality, stability, and fairness among the millions of names applied to living and extinct species. Because Mesozoic dinosaurs were animals, their names and classifications follow guidelines outlined by the International Commission on Zoological Nomenclature, or ICZN.

Within this system, *Tyrannosaurus rex* has proved to be a robust and noncontroversial species name. The *T. rex* label pertains to Carnegie Museum specimen 9380 (figs. 1.8, 2.1), the partial skeleton described and named by Henry Fairfield Osborn in 1905. CM9380 is the *T. rex* holotype: a specimen of an organism to which a scientific name is anchored, and upon which the species

is defined by a unique set of characteristics. Holotypes, sometimes called "type specimens" are critical to taxonomic practices as, once established, they act as permanent landmarks for specimen identification and categorization of their designated species. Accordingly, the fate of a species name is tied to the fate of its holotype. If a type specimen is found to be nondiagnostic (i.e., it is found to have no characters distinguishing it from other species), then the attached name becomes a *nomen dubium* (from Latin, "dubious name") and is no longer used by scientists. A name can also be invalidated if a holotype specimen is found to belong to another species. In this case, the older, more senior species name takes priority, and the younger, junior name is regarded as a synonym (this situation was, for a long time, considered the case for *Brontosaurus* until more detailed analyses showed that the *Brontosaurus* type material was anatomically distinct from *Apatosaurus*). Whatever the cause, these invalidated names tend to be written with quotation marks to stress their doubted nature (as with, for example, the defunct dinosaur genera "*Antrodemus*" [= *Allosaurus*] and "*Trachodon*" [= *Edmontosaurus*]).

The validity of holotypes constitutes a lot of discussion among paleontologists because experts frequently disagree over which are truly taxonomically distinct, which are over-interpreted variants of other taxa, and which are too poorly preserved to bear diagnosable features. Happily for *Tyrannosaurus* aficionados, CM9380 is a universally undoubted, reliable type specimen. It not only comprises multiple bones characterizing several parts of the *T. rex* skeleton, but represents an adult animal (Carr 2020), this being helpful because mature skeletons tend to bear more distinguished, diagnostic anatomy than juveniles. The properties that make *T. rex* unique have thus been known since the early 1900s, allowing us to diagnose the species through a unique combination of characters found on the holotype and, eventually, other specimens referred to the same species. This is not to imply that the defining characters of *T. rex* were an unchanging list of features written on stone tablets by Osborn when he first described the species in 1905. On the contrary, the diagnosis of *Tyrannosaurus rex* has been sharpened as we've learned more about theropod diversity, making our list of features that distinguish *T. rex* more exacting and detailed. Osborn's initial 1905 attempt to characterize *T. rex* was short and inaccurate, reflecting misunderstandings about the nature of tyrannosaurs as well as, of course, his insistence on rushing out a description before the holotype was fully prepared (chapter 1). He merely defined *T. rex* as:

> Carnivorous Dinosaurs attaining very large size. Humerus believed to be of large size and elongate (Brown). No evidence of bony dermal plates (Brown). (Osborn 1905, p. 262)

Within a year, and now with fully prepared bones to work with, Osborn (1906) was able to refine this into something more precise and useful. Although his diagnosis was still hampered by a lack of complete specimens, he was able to list defining particulars from the skull, dentition, forelimb, belly ribs, pelvic girdle, and hindlimb bones, as well as the number and form of the vertebrae. These features allowed Osborn and subsequent workers to establish *T. rex* as an unquestionably valid animal, and outlined criteria by which other *T. rex* specimens could be distinguished from other species (e.g., Bakker et al. 1988; Carpenter 1990; Molnar 1991; Carr and Williamson 2000, 2004; Hurum and Sabath 2003; Paul et al. 2022). The diagnosing features of *T. rex* have continued to evolve until, at the time of writing, their most recent iteration prepared by a team of tyrannosaurid experts led by Thomas Carr (2022). Today, we distinguish king tyrants from their close relatives by at least ten features, mostly pertaining to minutiae of skull anatomy, but also their tooth counts and the proportions of their arms and legs.

Thanks to this robust holotype and description during a pioneering era of dinosaur science, the *T. rex* name has never been in significant danger of invalidation or overwriting by a senior species. The most serious risks of the latter concern the two genera established for *Tyrannosaurus* material around the turn of the twentieth century: Edward Cope's 1892 "*Manospondylus gigas*"

and Osborn's second (1905) name for *Tyrannosaurus* material, "*Dynamosaurus imperiosus*." ICZN rules mean that the oldest name given to a species should take priority over any newer ones, and this would seem to give "*Manospondylus*" the advantage. However, whereas the *T. rex* holotype is very diagnostic, Cope's "*Manospondylus*" is not. Representing just two partial vertebrae, one of which is lost (fig. 1.5B), our remaining "*Manospondylus*"material is so badly weathered that we cannot even tell if it represents a part of the torso or the neck. Osborn first cast "*M. gigas*" as a *nomen dubium* in 1917 and any threat it presented to *T. rex* seemed over, at least until the year 2000. At this point, press reports suggested that the original "*Manospondylus*" quarry had been relocated, along with, potentially, more of the original "*M. gigas*" specimen (Brochu 2003). Would this have allowed "*M. gigas*" to rise from the grave and overthrow *T. rex*? As outlined by Brochu (2003), the answer to this is a straight "no." Not only would it be difficult to prove that the surviving "*M. gigas*" vertebra belonged to a newly unearthed specimen, but naming conventions dictate that scientific names can be abandoned if they have not been used in any meaningful manner for fifty years or more. Such a name is considered a *nomen oblitum*, Latin for "forgotten name." This situation clearly applies to "*M. gigas*."

"*Dynamosaurus imperiosus*" also poses no real nomenclatural threat to *T. rex*, on grounds of nomenclatural priority. Although Osborn named both *T. rex* and "*D. imperiosus*" in the same 1905 paper, *T. rex* was named on page 262, and "*D. imperiosus*" on page 263. That single page gives *T. rex* priority and means "*D. imperiosus*" has to be regarded as a synonym of *T. rex*, not the other way around. Furthermore, "*Dynamosaurus*" joins "*M. gigas*" in being considered a *nomen oblitum*. Neither of these historic names has a chance, therefore, of overthrowing the *Tyrannosaurus rex* label.

Stating that the *T. rex* name has been unchallenged by nomenclatural acts for the last century does not mean there has been no activity around king tyrant taxonomy, however. For the most part, *T. rex* has acted like a sponge, absorbing specimens initially identified as different tyrannosaurid taxa into an ever-expanding inventory of king tyrant remains. As our collections of *Tyrannosaurus* material have swollen, however, the tremendous variation in their remains has become apparent and some have doubted that all the fossils referred to *T. rex* truly represent a single species. This has led to several attempts to carve *T. rex* into different taxa, including the naming of potentially distinct tyrannosaurid species that lived alongside king tyrants. Simultaneously, some authors have treated the *Tyrannosaurus* genus as being expansive enough to encompass some Asian tyrannosaurs, chiefly, the Mongolian species *Tarbosaurus bataar*. Whether through new species or alternative means of generic classification, perhaps the name *Tyrannosaurus*, so long intimately associated with a single species, is due for expansion? This question is particularly pertinent as I finish editing this book in mid–2024. Following several years of relative stability, multiple studies have attempted, to greater and lesser success, to break *Tyrannosaurus rex* into more discrete taxonomic units since 2022 (Paul et al. 2022; Longrich and Saitta 2024; Dalman et al. 2024). At the time of writing, *T. rex* taxonomy is in an uncharacteristic state of flux, the outcomes of which will become apparent in years to come.

TYRANNOSAURUS BATAAR AND OTHER ASIAN *"TYRANNOSAURUS"*

Although *Tyrannosaurus* fossils are highly characteristic among those of other large theropods, they are not total anatomical outliers. Late Cretaceous Asia also housed gigantic, robust-skulled tyrannosaurids, some of which have been considered close relatives or even congeneric with *Tyrannosaurus* (fig. 2.6; Hurum and Sabath 2003). Among those to receive formal names are the Mongolian *Tyrannosaurus bataar* (Maleev 1955a) and the Chinese *Ty. lanpingensis* (Ye 1975), *Ty. luanchuanensis* (Dong 1979), *Ty. turpanensis* (Zhai et al. 1978), *Ty. zhuchengensis* (Hu et al. 2001) and *Zhuchengtyrannus magnus*

(Hone et al. 2011a). Most Chinese fossils labeled as "*Tyrannosaurus*" are fragmentary, nondiagnostic material such as teeth and portions of foot skeletons, and they are regarded as *nomina dubia* today (Holtz 2004; Hone et al. 2011a). They may represent pieces of more recently diagnosed taxa: "*Ty. zhuchengensis*" may belong to *Zhuchengtyrannus magnus* (Hone et al. 2011a), for example, and "*Ty. turpanensis*" is potentially a synonym of *Tarbosaurus bataar* (Shuonan et al. 1985; Holtz 2004).

The name *Tyrannosaurus bataar* has been more persistent in tyrannosaur literature. Named as part of a suite of new tyrannosaur taxa by E. A. Maleev in the mid-1950s (Maleev 1955a, b), *Tyrannosaurus bataar* was the original name for Mongolia's giant tyrannosaur, *Tarbosaurus*. The label *Tarbosaurus* was given to *Ty. bataar* in 1965 by A. K. Rozhdestvensky, who, simultaneously, interpreted all of Maleev's tyrannosaur "species" as growth stages of one, large-bodied taxon. Rozhdestvensky disagreed with Maleev's suggestion that this Mongolian tyrannosaurid was similar enough to *T. rex* to be placed in the same genus and instead used one of Maleev's other generic names, *Tarbosaurus*, to rehome the *bataar* lineage.

A somewhat complex taxonomic history followed, the technical details of which are unnecessary to relay here (Hurum and Sabath 2003 provide a review of the full history). We can instead summarize that most researchers have followed Rozhdestvensky's separation of *Tyrannosaurus* and *Tarbosaurus*, but not all, with some questioning whether *Tarbosaurus* should be kept as a distinct genus on grounds that it compares closely to *T. rex* in detailed anatomy (e.g., Paul 1988a; Carpenter 1992; Holtz 1994, 1995, 2001; Carr 1999, 2020; Carr and Williamson 2004). This view has some important implications for how we regard *Tyrannosaurus* evolution. If *Tyrannosaurus* and *Tarbosaurus* were congeneric, *Tyrannosaurus* would become an Asiamerican genus, not one restricted to North America. The geological range of *Tyrannosaurs* would also deepen thanks to *Tarbosaurus* possibly being slightly geologically older than *T. rex* (although also see below and chapter 5 for discussions of older *Tyrannosaurus* fossils in North America). In some phylogenies at least, *Zhuchengtyrannus magnus* would be captured into the *Tyrannosaurus* genus, too, such that there would be at least three (or four; see below) valid *Tyrannosaurus* species across two continents. The paleoecological breadth of *Tyrannosaurus* would also expand, the dinosaur communities and environments of latest Cretaceous Asia being distinguished from those of North America in a number of ways. In short, what seems like trivial taxonomic reconfiguration actually has a lot of implications for what the *Tyrannosaurus* genus is and was!

Because the question of *Tarbosaurus* vs. *Tyrannosaurus bataar* concerns genus-grade classification, however, there is no right or wrong answer to this conundrum, nor a taxonomic "truth" to uncover. Genera are holdovers from Linnaean forms of classification, and, unlike considerations of species, their names have no bearing on the branching structure of evolutionary trees. Nor are there firm rules about their application, such as how many species a genus should contain, or how much variation is permitted between species before a new genus is warranted. To that end, personal preference plays a role in genus formulation and there is little consistency in their content. Some genera are enormous, with dozens of species, while others contain just one. There is not even a consensus about the use of genera among researchers working on the same types of organisms. Gregory S. Paul (1988a, 2016), for instance, has argued that *Tyrannosaurus* should not only house *bataar*, but also species contained within the genera *Nanuqsaurus*, *Teratophoneus*, and *Daspletosaurus*. This scheme has not been adopted by other researchers, but Paul is not objectively "wrong": he simply has a differently calibrated "genericometer" than other paleontologists.

There is thus nothing "incorrect" about replacing *Tarbosaurus* with *Tyrannosaurus*, but we might also consider this issue from another angle: that good taxonomic practice emphasizes stability in our classifications of organisms. While it is accepted that the names we apply to animal species are an artificial means of organizing life, we cannot take a nihilistic, "anything goes" approach to classification. Changes to taxonomic labels

can be disruptive and confusing to researchers, especially if those names already have long, established, and widely understood meanings. Classification guidelines, therefore, suggest that specific and generic names should only be altered when there is good reason to do so, such as when resolving nomenclatural confusion or introducing new understanding to the evolution of a given clade. There are no such concerns to resolve with *Tarbosaurus* and *Tyrannosaurus*, however. Evolutionary studies repeatedly find them to be close relatives (e.g., Holtz 2004; Brusatte and Carr 2016; Voris et al. 2020; Brownstein 2021), but keeping the two as separate genera creates no complications for tyrannosaurid systematics. Neither is it peculiar for dinosaur genera to contain one species, as has traditionally been the case for both *Tarbosaurus* and *Tyrannosaurus*.

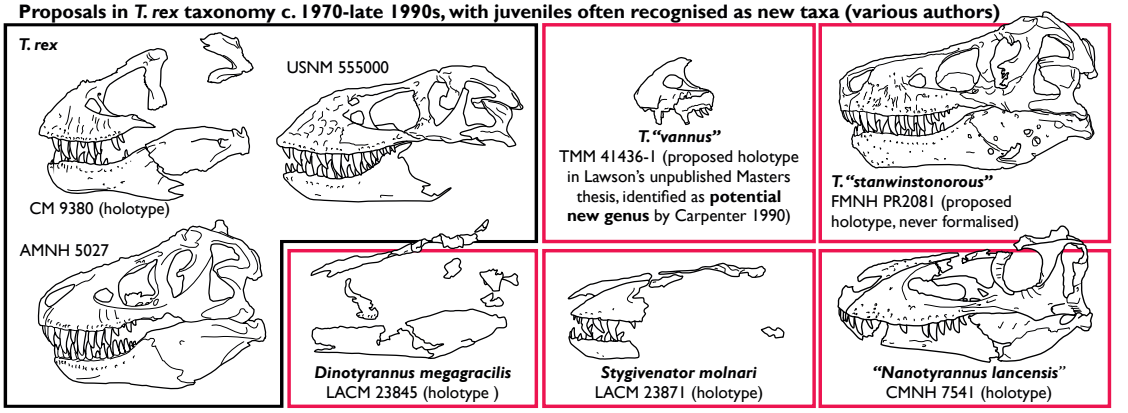
Such concerns, therefore, boil down to whether the benefits of expanding *Tyrannosaurus* to accommodate *bataar* outweigh any negatives. On one hand, such an act would leave no doubt about the close evolutionary affinities of *rex* and *bataar*. On the other, it clashes with the long-held understanding of *Tyrannosaurus* as an exclusively American genus, and means that more than fifty years of literature on *Tyrannosaurus* and *Tarbosaurus* requires a collective asterisk: "the classifications in these texts no longer apply." Perhaps there are more downsides to synonymizing *Tarbosaurus* and *Tyrannosaurus* than there are benefits, and, given that our application of the *Tyrannosaurus* label is ultimately arbitrary, it seems more sensible to retain their traditional uses. Such views may explain why the name *Tarbosaurus* remains widely used among contemporary tyrannosaurid researchers, while "*Tyrannosaurus bataar*" has only a few advocates.

"CRYPTIC" NORTH AMERICAN *TYRANNOSAURUS* SPECIES

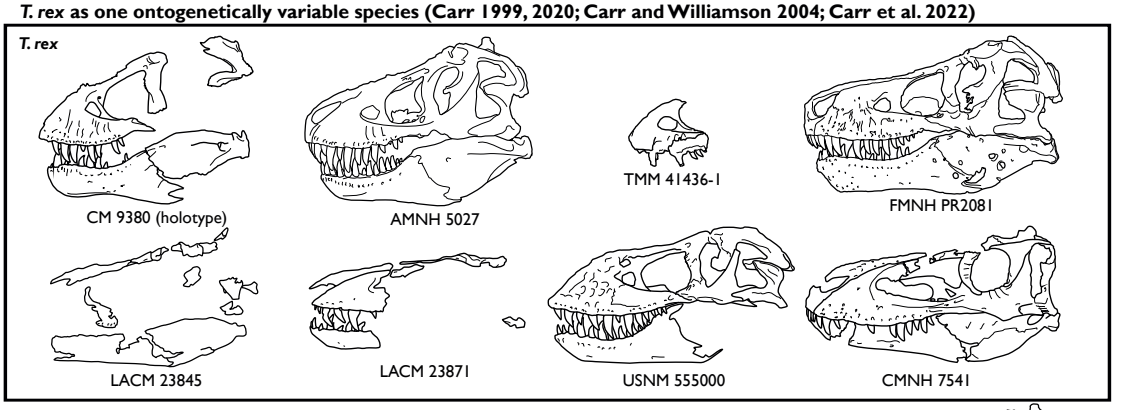
Less subjective taxonomic matters concern proposals that unusual *T. rex* fossils from North America might represent "cryptic" or hitherto unnoticed species (fig. 2.13). Such ideas have a long history, with perhaps the first occurring in an unpublished 1972 thesis by then-student Douglas Lawson, who would later attain fame for finding the giant azhdarchid pterosaur *Quetzalcoatlus northropi* (Lawson 1975). Lawson's thesis named "*Tyrannosaurus vannus*" for a small jaw bone from the Texan Tornillo Group that seemed distinct from other *T. rex* specimens. Because this name was never published in a peer-reviewed journal, it failed to meet criteria for establishment of a new species and never became "official" in the eyes of zoological nomenclature. In any case, Lawson revised his interpretation soon after, referring the same bone to *T. rex* itself a few years later (Lawson 1976). Different opinions have been expressed on this specimen ever since. Some have agreed with Lawson that the specimen is *T. rex* (Brochu 2003; Carr and Williamson 2014; Carr 2020) or at least a very close relative (Brochu 2003; Wick 2014). In his 1990 review of *T. rex* variation, Kenneth Carpenter opined that this specimen might represent a different southern *Tyrannosaurus* taxon, while Thomas Holtz (2021) lists the specimen as an indeterminate *Tyrannosaurus* species. Sampson and Loewen (2005) were more skeptical, questioning whether the specimen can be confidently identified as *Tyrannosaurus* at all. Over fifty years on, this maxilla remains an intriguing specimen because it probably stems from rocks older than most other *T. rex* material (Fowler 2017; also see chapter 5) and, as we shall see below, it is among these older sediments that the most promising evidence for novel *Tyrannosaurus* species is found.

More buzz circulated around *Tyrannosaurus rex* representing multiple species in the 1980s. Horner and Lessem (1993) and P. Larson (2008b) give Robert Bakker credit for noting features in *Tyrannosaurus* skeletons that might delineate new species during this decade and suggest that it was only a lack of specimens to verify these observations that prohibited the idea from progressing further. It was perhaps these conversations that prompted Gregory S. Paul (1988a) to muse on multiple *Tyrannosaurus* species in his 1988 book *Predatory Dinosaurs of the World*. Despite acknowledging variation in *T. rex* dentition and limb robustness, Paul

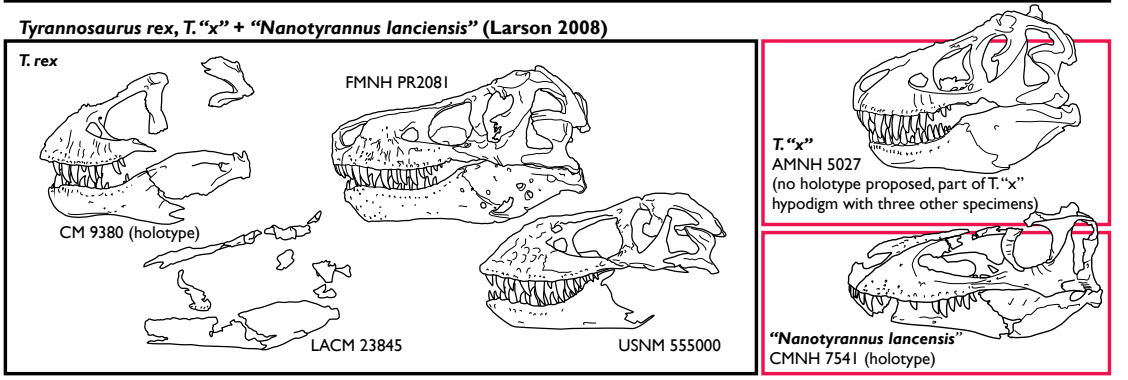
Proposals in *T. rex* taxonomy c. 1970-late 1990s, with juveniles often recognised as new taxa (various authors)



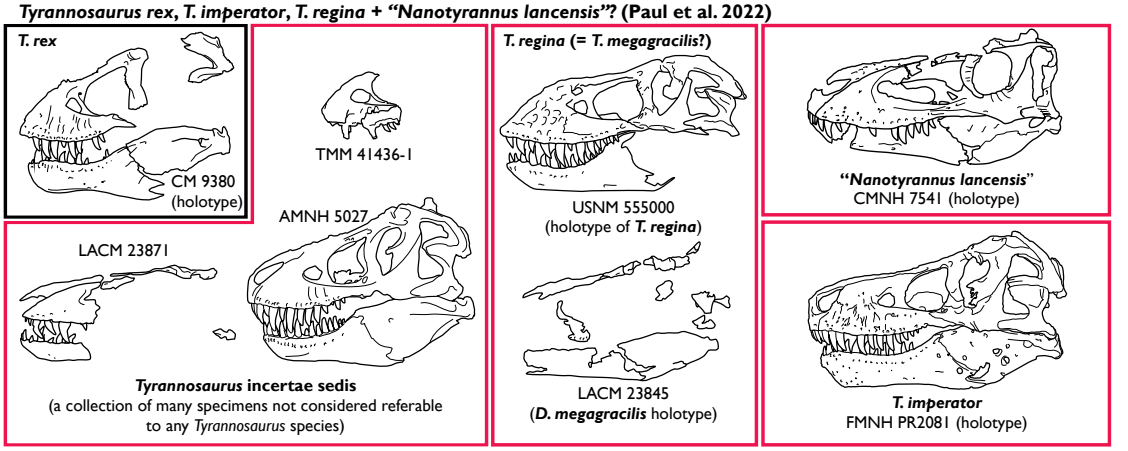
***T. rex* as one ontogenetically variable species (Carr 1999, 2020; Carr and Williamson 2004; Carr et al. 2022)**



***Tyrannosaurus rex*, *T. "x"* + *"Nanotyrannus lanciensis"* (Larson 2008)**



***Tyrannosaurus rex*, *T. imperator*, *T. regina* + *"Nanotyrannus lancensis"*? (Paul et al. 2022)**



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INDEX

Page numbers in *italics* indicate figures and tables.

abelisaurids, 53, 228
Abler, William, 236
Academy of Natural Sciences of Philadelphia, 7
Acheroraptor, 199
Acheroraptor temertyorum, *191*, 198
Acrocanthosaurus, forelimbs of, 175
Acrocanthosaurus atokensis, 21
Aerosteon riocoloradensis, 57–58
African buffalo, 212, 213, *214*
After Man (Dixon), 274
Age of Mammals, 258
Age of Reptiles, 6, 258, 259
air sacs, 47–48, 50; clavicular, 107, 159–60; in *T. rex*, 87, 105–8, 133
Alamosaurus, *210*, 210–11, 215, 255, *270*; characterizing dinosaur province, *184*, 209
Alamosaurus sanjuanensis: habitats, 209, *210*; stratigraphic distribution, *194*
Alberta, Canada, 60, 184, *184*, *185*, 188, 190–91
Albertosaurinae, *54*, 60, *61*, 62; facial ornament, 118
Albertosaurus, *54*, 71, 137, 253; skin impression, *113*; survivorship rates, *254*
Albertosaurus sarcophagus, 60; bonebed, 220, 253
Alioramini, *54*, *57*, 60, *61*, 62; facial ornament, 118
Alioramus, *54*
Alioramus altai, 62
Alioramus remotus, 62
alligator, *123*, 150, *152*, 153, 157, 161, 166, *167*, 242–43
alligatoroid, 196
Allosauroidea, *45*, 49, 53, 55, 59, 94; growth strategies, 137, *138*; forelimb function, 177; longevity, 255; pneumaticity, *106*
Allosaurus, 9, 22, 52, 53, 66, 156, 247, 248, 255; forelimbs of, 175; growth, 138; ribcage of, *95*; teeth of, *88*
Allosaurus fragilis, 1
alluvial plains, *T. rex* habitat, *184*, 188–91
Alvarez, Luis, 27
American Museum of Natural History (AMNH), 2, 7–10, 13–14, 18–19, 21–22, 24, 79, 278, *279*; classic *T.* rex mount in Dinosaur Hall, *16*; Department of Vertebrate Paleontology, 7, 8, 10; Hall of Fossil Reptiles, 10, 13, 18; modern *Tyrannosaurus* mount, *28*
AMNH 5027, *T. rex* specimen, 14, *16*, 17, 18, *16*, *18*, *70*, 79, 144, 184, *224*; *Jurassic Park* logo, 19, 32
anatomy, *T. rex*: brain, 151–55; bone, internal, *75*, 110–11, 142–43, *143*; color 126–29; cranial, 85–92; facial, 115–25; forelimb, 97–99, 175–77; gut, 108–10; hindlimb, 102–5, 163; integument, 32, 99, 105, 111–18, *119*; musculature, 87, 89–91, 93–94, *96*, 96, 99, 102, 108, 118–19, 122, 133, *134*, 140, 155–56, 164–65, 168–72, *169*, 172–73, 176, *176*, 233–34, *234*; pectoral, 97–99; pelvic, 99–102, 175–76, 242, *242*; pulmonary system, 105–8; reproductive, 244–45; ribs, 93–95; "robust" and "gracile" morphologies, 77, *77*, 78–79, 242; sensory, 155–58; size, 144–51; variation, 77–79, 241–43; vertebral column, 92–97; vocal, 158–61
Andrewsarchus mongoliensis, *5*
ankylosaurids, *159*, 160, 209, *209*, 211, 213–15, *215*, 220, 251, 262
Ankylosaurus, 194, 201, 209, 211, 214, 215; abundance in Hell Creek Formation, *182*; juvenile, *215*
Ankylosaurus magniventris, *209*, 209
Anning, Mary, 33
anteriorization, genetic, 173
anthropomorphism, 23
Anzu wyliei, *207*, 208
Apatosaurus, 65, 255
"Apex," *Stegosaurus* specimen, sale of, 33–34
Appalachia, 188
Appalachiosaurus montgomeriensis, *54*, 59
appearance. *See* life appearance of *T. rex*
Archaeopteryx, 27, 106
Archosauria, *45*, 47, 48, 53
Archosauriformes, *45*, 44–45, 53
archosaurs, 87; endothermy, 132, 133, *134*; evolution of facial anatomy, 45, 122, *123*, 157; models of floating, 167; reproduction, 245, 248, 249; vocalization, 160–62, *161*
arctometatarsal condition, 60, *103*, 104, 163, 208. *See also* hindlimb
armor, 10, 13, 46, 49, 157, 209, *209*, 211; absence of, 201, *215*; armored face of *T. rex*, 115, 125; as predator deterrent, 211–14
armored dinosaurs: *See* ankylosaurids
armadillos, 209, 213
arms. *See* forelimb
Asia, origin of *T. rex*, *54*, 62–63, 65, 80
Asiatyrannus xui, 62
asteroid, Cretaceous extinction, *256*, 257, 266–74
Australovenator, 58
Australovenator wintonensis, *58*, 58
Aves. *See* birds
Avisaurus archibaldi, *206*
Azhdarchidae, *25*, 69, 199, *200*, 201, *250*

"Baby Bob," *T. rex* specimen, 33
Bakker, Robert, 27, 29, 69, 72, 162
"Barnum," *T. rex* coprolite specimen, 109, *109*
Baryonyx, 65
behavior, predatory, 213; group foraging, tyrannosaurids, 219–23; Harris's hawks, 222, *223*; influence on color, 126–29; in Lancian ecosystems, 196–201; Komodo dragons, 221–22, 232–33; prey responses to, 166, 201, 202, 204, 208, 209, *210*, 211–15; senses, 155–58; role of *T. rex* arms, 172–77, *178–79*; *T. rex*, 96, 164–65, *166*, 168, 228–36; *T. rex* hatchlings, 248–49. *See also* toxic bite
behavior, *T. rex*: aggressive, 173, 223–28; clichéd, *37*, 38; complexity, 154–55; cooling; *134*; deducing from fossils, 217, 154–55; feeding, 237–41; gregariousness, 219–23; inferable from sensory anatomy, 118, 158; migratory, 218–19; parental, 248–50; predatory, 96, 164–65, *166*, 168, 228–36; reproductive, 135, 243–48; vocalization, *130*, 160–62. *See also* behavior, predatory; feeding
Bell, Phillip, 111
Benson, Roger, 57
Berthoud, Edward, 10, *11*
Big Five, mass extinctions, 257
birds: brains and intelligence, *152*, 153–55; bite forces, 172; color, 126, *127*; cranial kinesis, 170; evolution, *45*, 47, 49, 53, 55; eye anatomy, 87, 119; face biting, 226; feathers, 112, 114; growth, 137; hindlimb anatomy, 102, 163; in Lancian communities, 195, 196, 197, *206–7*, *249*, *264*; longevity, 253, 255; as models of dinosaur appearance, 118, 121, *123*; physiology, 114, 132–33; piratical behavior, 201; predatory behavior, 221–23, *223*, 234; pulmonary system, 105, 107–8, 133, 148; reproduction, 142–43, *143*, 243, 244–45, 247–49; sexual dimorphism, 243; talon use, 175, 177; *Trichomonosis*, avian infection, 252; use as models for dinosaur mass prediction, 147–48; vision, 156; vocal anatomy, *159*, 159–60, *161*. *See also* raptor (bird)
Bistahieversor, *54*, 63
Bistahieversor sealeyi, 59
bite(s): carcharodontosaurids, 52; erythrosuchids, 44; finches, 172; as predator deterrent, 213; as predatory tactic, 234–35; tyrannosauroids, 55, 60, 63, 80, 263; greatest strength, 171, 172
bite(s), *T. rex*: changes with growth, 92, 140–41, 236, 249; during predation, 29, 172–73, 177, 234–36, *235*; fossil evidence of, 202, 223–27, 230, *231*, 232, 237–41, 245, 252; influence on skull shape, 156, 263; jaw muscles, 169; as play behavior, 154; strength, 38, 80, 92, 162, 168–72, 229, 236; toxicity, 236. *See also* face biting

INDEX

Black, Riley, 39
"Black Beauty," *T. rex* specimen, 184
Black Hills Institute, South Dakota, 29
Bluth, Don, 30
body mass: *Alamosaurus*, 211; brain size, 153–54; carcharodontosaurids, 52; ecology, 232–33, *233*; egg and clutch size, 247–48; estimation methods, extinct animals, 145, 147, 148, *149*; *Spinosaurus*, 50; thermoregulation, 112–14
body mass, *T. rex*: estimates, 144–50; hypothetical maximum, 150; impact on locomotion, 163–65; increase during growth, 137, *138*, 140–41, 144
bonebeds, 202, 218, 220, 253
"Bone Wars," 7. *See also* Cope, Edward Drinker; Marsh, Othniel Charles
Bradbury, Ray, 25, 27
brains: dinosaurs, 132, 153–55, 201; intelligence and, 20, 30, 153–55; role in extinction, 258–59; size and structure, 85, 89–90, 105, 154–55; *T. rex*, 73, 151, *152*, 155–56; tyrannosaurids, 73, 151
British Columbia, tyrannosaurid tracks, *221*
British Museum (Natural History), 28
Brochu, Christopher A., 29, 84, 91
Brontosaurus, 8, 9, 22, 23, 65, 66; mentions in literature, *20*
Brontosaurus excelsus, 1, 8
Bronx Zoological Garden, 9
Brown, Barnum, *7*, 9, 10, 13, 17, 18, 22, 25, 33, 97, *109*, 172, 278
Burian, Zdeněk, 24
Burpee Museum, Illinois, 73

camouflage, 126–29, *127*
Campanian, *54*, *185*, 247, 259; dinosaur diversity, 260–62, *262*
Campione, Nicolás, 148
Carbone, Chris, 229
Carcharodontosauridae, 39, *41*, *45*, 50–52, *51*, 55, 60, 97, 278; facial sensitivity, 157–58; growth, 137, *138*; longevity, 255
Carcharodontosaurus, 21, 22, 51, 52
Carcharodontosaurus saharicus, 21, *41*, 50
Carnegie Museum, Pittsburgh, 8, 10, *11*, 24, 65; dinosaur hall, *25*; holotype *T. rex* skeleton, *42*
Carnian, 49
Carnosauria, 53
Carpenter, Kenneth, 30, 69, 73
Carr, Thomas, 34, 66, 73, 78, 79, 143
Carroll, Lewis, 211
cathedral, *3*
Cenozoic Era, 186–87, 258–59, 266, 274, *276*, *277*
Ceratopsia, horned dinosaurs, 204–5, *204*, *205*, 211, *212*, *215*, 213, 254, 262, *262*, *264*; bone beds, 218; gregariousness, 218–19; as prey and food for *T. rex*, 17, 230, *231*, 232–35, *234*, *235*, *237*, 238–41, *240–41*, 277; running speeds, 233–34, *234*
Ceratosauria, *45*, 53, *106*, *138*
Ceratosaurus, 53
Cerberophis, snake, 196
Champsosaurus, 196
Chatterjee, Sankar, 47
Chicxulub crater, Yucatan Peninsula. *See* K/Pg extinction
Chin, Karen, 109
China, *56*, 59, 60
claws, *T. rex*: feet, *103*, 104; hands, *98*, 99; use of manual claws in taxonomy, *75*, 76
cliché: dinosaurs, *41*; Mesozoic mammals, 196; *T. rex* depictions, 5, *37*, 38–39, 193, 279
climate. *See* paleoenvironments of *T. rex*
cloaca, anatomy, 109, 244–45, 246
CM9380, *T. rex* holotype specimen, *12*, *14*, 24, *25*, *42*, 65, 66, *70*; sale to Carnegie Museum, 24
Coelophysis, 156
Coelophysoidea, *45*, 53
Coelurosauria, *45*, 53, *54*, 55, *56*, 59; brains of, 153
Coelurus fragilis, 55
cold-blooded. *See* physiology
color: in predatory animals, 126, *127*; predictions for *T. rex*, 126, 128–29; reconstruction for extinct species, 126
Colorado, 17, *185*, *267*
Complete T. rex, The (Horner and Lessem), 29
Cooper, Merian C., 22
Cope, Edward Drinker, 7–8, 10, 17, 66, 67, 172, 174
coprolites, *T. rex*, 108–10
cornual process, *86*, 87–88, *89*, 118. *See also* facial appearance
cranial kinesis, 170
cranium, *T. rex*: awesomeness, 2, 83; changes with growth, 135, *136*, 138, 140–41, 144–45; differences to *Tarbosaurus*, *63*, 65; facial appearance, 113, 115–25; pathologies, 223–26, *224*, 245, 252; jaw function, 168–72; musculature, 89, *90*, 133, *134*; pneumaticity, *106*, 107–8; sensory anatomy, 155–58; skull and mandible, 5, 10, *11*, 13, *14*, *17*, 18, 35, *57*, *84*, 85–92, 94, 151, *152*; use in classification, 66, 71–80; use in predation, 177, 234–36. *See also* brains; dentition; face biting; headbutting
Cretaceous Period, *45*: climate, 132; environments and ecosystems, 126, 185, 188–211, 261–65; extinction, 256–74; fossil discoveries, 9, 10, 21, 245; fossil record, 52, 259–65; *Kulindadromeus*, 112; imagined post-Cretaceous dinosaurs, 274–77; large theropods, 49–52; temporal distribution of *T. rex*, 186–87; tyrannosauroid evolution within, *54*, 55, 57–65, 67, 68
Crichton, Michael, 30
Crocodylia: bite strength, 170–71; brains, *152*, 154; digestive process, 109; evolution, *45*, *45*, 46–48, 133, 157, 196; face biting, 226–27; growth, 137, 140; hunting strategies, 221–22, 234; jaw sensitivity, 157–58; as Lancian fossils, 196, 220, *264*, 265; as "living fossils," 274; as measures of ancient climates, 190; as models of dinosaur appearance, 112, 119, 121, 122, *123*, 125, 126, *127*; neck muscles, 94; physiology, 135; reproduction, 143, 244–45, 247–49, 247–48; sexual dimorphism, 242–43; temperature regulation, 133; vocal anatomy, *159*; vocal evolution, *159*, 160–62
Crocodylus porosus, 127, 170. *See also* saltwater crocodile
Currie, Phillip J., 30, 140, 220

Dakotaraptor steini, 199
Dalman, Sebastian G., 80
Daspletosaurus, *54*, 62, 63, 68, 137, 220; bite strength, *169*; facial skin, 115, 118; growth, *138*; survivorship rates, *254*; tooth wear, *123*
Daspletosaurus horneri, *54*, 62
Daspletosaurus torosus, *54*, 57, 62
Daspletosaurus wilsoni, 62
"*Deinodon*," 18
Deinonychus, 27, 30, 53, 198
Deinosuchus riograndensis, 196
dentition, *Allosaurus*, *88*
dentition, *T. rex*, *88*, 91–92, 236; replacement rate, 92; role in feeding, 238–29; strength, 168, 229, 234; "*Trix*," 219
Denver Formation, Colorado, *184*, 185; age, *185*, 187; environment, 191; site of oldest *T. rex* discovery, *11*, 17
Denversaurus schlessmani, 209
de Ricqlès, Armand, 27
Didelphodon vorax, 196, 197
diet, *T. rex*: appetite, 133, 135; confirmed prey species, 109, 202, 205, 230, *231*, *234*; feeding, 237–41; hunting, 230, 232–36; isotopic insights, 219
Dilong paradoxus, *54*, 55
Dino Hunters (TV series), 35
dinosaurs: as commercialized fossils, 33–36, 40–41; cultural appeal, 2, 4–6; defining anatomical characteristics, 48; discoveries in American West, 8–10; evolution, *45*, 48–49, extinction, 257–74; longevity, 254–55; popularity, 8, 10, 13, 19–27, *20*, 29–41; variation in integument, 111–12; visualization of, 36–38, 37; vocal anatomy, 160
Dinosaur 13 (film), 35
Dinosaur Heresies, The (Bakker), 29
Dinosaur Renaissance, *20*, 27–29, 30, 32, 228, 237
"*Dinotyrannus megagracilis*," 70, 71, 72, 80, *138*, *139*, 141, 220
Diplodocus, 8, 18, 19, *19*; auction value, 33; mentions in literature, *20*
Diplodocus carnegii, 1

INDEX

disease. *See* pathologies
Disney (film company), 22–24
Disney, Walt, 24
Dixon, Dougal, 274–76, *276*
Dollo's Law, 276
Doyle, Arthur Conan, 22, 274
Dracorex, 65
Dreadnoughtus schrani, *101*
Dromaeosauridae, *45*, 53, 71, *106*; as *T. rex* contemporaries, *191*, 198–99
Dryptosaurus, *54*, 172
Dryptosaurus aquilunguis, *58*, 59
"*Dynamosaurus*," 13, 17, 28, 185
"*Dynamosaurus imperiosus*," 10, *11*, 67
Dynamoterror, 63
Dynamoterror dynastes, 62

ears, 114, pneumaticity around, 107; in *T. rex*, *121*, 122. *See also* life appearance
ecology: predatory niches, 44, 47–49, 55, 60, 62; of *T. rex*, 129, 133, 198, 260–62
ectothermy, 48, 131–33, 162. *See also* physiology
Edmontonian faunal stage, *185*, *194*, 195, 205
Edmontosaurus, 66, 156, 197, 201, 215, 232, 263; abundance in Hell Creek Formation, *182*; musculature, 233, *234*; running speed, 233–34, *234*; as *T. rex* prey, 215, 230, 232, 263
Edmontosaurus annectens, 187, 194–95, 202, *203*, 211; as *T. rex* prey, *82*, *178–79*, *231*; stratigraphic distribution, 187, *194*
Edmontosaurus regalis, 202
elephant, 4, 83; body mass and size, 148, 150, 183, 247; color, 114, 128; eyeball size, *120*; longevity, 254; as prey species, 232; running, 162–63; thermoregulation, 114
emperor penguin, models of floating, *167*
enantiornithine, *206*. *See also* birds
encephalization quotient (EQ), 153, 155. *See also* brains
endocast, *T. rex*, 151–53, 155–56. *See also* brains
Eoneophron infernalis, 208
Eotyrannus lengi, *54*, 55, *56*, *57*
epidermal correlates, 115, *116*, *117*, 118
Erickson, Gregory M., 168, 253
erythrosuchids, 44–46
Erythrosuchus africanus, *45*, *46*
Evans, David C., 148
evolution: classification and methods, 43–44; influenced by *T. rex*, 211–15; "Red Queen arms race," 211; reptile, 43–48, *45*; success, 39; theropod, 48–52; tyrannosauroid, 53–59; tyrannosaurid, 59–65
"evolutionary teratology," 173
extinction, 43, 44, 60, 211; of dinosaurs, 6, 27, 256–74. *See also* K/Pg extinction; speculative evolution
extra-oral tissues: 32, 39, 115, 122–25. *See also* facial appearance

eye, anatomy: as restored in *T. rex*, 5, *31*, 32, 87–88, *89*, 115, 118–20, *120*; in tyrannosauroid evolution, 59, 62; sizes, *120*; sockets (orbits), *86*, 87; vision in *T. rex*, 155–56, 229

face biting: 223, *224*, 225–27, 252; among living animals, 226; theropods, 226
facial appearance: evolution in tyrannosauroids, 55, 59, 62; relation to aggressive behavior, 225–26, *227*, 228; *T. mcraeensis*, 80, *81*; *T. rex*, 4, 32, 50, *86*, 87–88, *89*, 115–25, 128, 144, 242–43. *See also* life appearance
Fantasia (movie), *20*, 22, 23–24
faunal stages, Cretaceous dinosaurs, 187, 188, 195
feathers: digestibility, 109; evolution, 48, 49, 111; insulative properties, 112, 114, 132; *See also* integument
feeding, *Tyrannosaurus*: as cause of arm reduction, 173; biting power, 168, *169*, 170; dental adaptations, 92, 237–41
Ferris Formation, *184*, 185, 191
fibers, skin, 48, 112, 114–15, *134*. *See also* feathers; protofeathers; integument
Field Museum of Natural History, Chicago, 8, 33; Charles Knight *T. rex* mural, *15*, 22; as Field Columbia Museum, Chicago, 8; ownership of "Sue" specimen, 33, *34*. *See also* "Sue," *T. rex* specimen
floodplains, *T. rex* habitat, 188, 190–92, 194, 204
foot. *See* hindlimb
footprints, *T. rex*, *104*, 105. *See also* hindlimb; trackways
forelimb: ornithischians, 201, 202; pneumatization, 107, 159; theropods, 49, 55, 59, 177
forelimb, *T. rex*: as characterizing anatomy, 66, 74, *75*, 76; discovery, 10, 13, 97; function, 172–77, *176*, 178–79, 245; musculature, 99, 176, *176*; osteology, 77, 84, 97, *98*, 99; pathologies, 177; range of motion of joints, 175, *176*; redundancy, 172–73, *174*, 275, *276*, 276; sexual dimorphism of, 242; size change through growth, 74, *75*, 76, 141–42, 175, *176*, 248, 249
forests, Cretaceous. *See* paleobotany
fossilization: biases against, 112, 150, 183, 195, 198; as distorting process, 83, *84*, 105, 109–10, *110*, 135, 220, 230, 238; of *T. rex* specimens, *84*, *182*, 198
fossil record: carcharodontosaurids, 52; identifying extinctions within, 257, 259; Lancian dinosaurs, *194*, 195, 232; limitations of, 215; pterosaurs, 199; *T. rex*, 34–35, 40–41, 65, 80, 141, 150, 181–83, 187, *194*, 253; tyrannosauroids, 55, 59, 60
Frenchman Formation, Saskatchewan, 184, *184*; age, 185; environment, 190–92
frontoparietal fossae, 133, *134*
Fukuiraptor kitadaniensis, 58

Gallus domesticus, *143*
Galton, Peter, 27
"*Ganeosaurus tardus*," speculative tyrannosaur, 275, *276*. *See also* speculative evolution
gastralia, 10, *14*, *85*, 94–95
Gauthier, Jacques, 27
geographic distribution, *T. rex*: 183–86, *184*; capacity for migration, 218–19; contemporary plants and animals, 194–210; paleoenvironments, 188–94
geological time: dating rocks, 186–87; dinosaur communities of, 194–95; distribution of *T. rex* in, *185*, 186–87, *194*; relationship to rock units, 183
geology, of ancient habitats, 218; of North American Late Cretaceous, 181–87; *T. rex* as an ambassador of, 36
Ghost of Slumber Mountain, The (O'Brien), 20, 22
Giganotosaurus, *45*, 52, 128; pelvis of, 101, *101*
Giganotosaurus carolinii, 50, *51*
Gilmore, Charles W., 72
Glut, Donald, 71
Godzilla (movie), 25
golden eagle, *127*
Gorgosaurus, *54*, 71, 72, 119, 187; bite force, 169; geological range, 187; growth, *138*; survivorship rates, *254*
Gorgosaurus lancensis, 72. See also "*Nanotyrannus lancensis*"
Gorgosaurus libratus, *57*, 60, *61*
great white shark, *127*
gregariousness, tyrannosaurids, 219–23
growth. *See* ontogeny
Guanlong wucaii, *54*, 55
Guinness World Records, 109
gut tissues, inferred for *T. rex*, 108–10

habitats. *See* paleoenvironments of *T. rex*
hadrosaurids, *203*, 254, 262, *262*, *264*; fossil abundance, 197, 202, 218; footprints, *104*, 105; gregariousness, 218–19; running speed, 233–34, *234*; as *T. rex* prey, *178–79*, 211, 214, 230, *231*, 232–35, 238, 247, 277. *See also Edmontosaurus*
Hall Lake Formation, New Mexico, *184*, 186; age, *185*, 187; environment, 192–93, *193*. *See also Tyrannosaurus mcraeensis*
Halstead, Beverly, 168
hand. *See* forelimb
Harris's hawk, 222, *223*
hatchling, *Ankylosaurus*, *215*
hatchling, *Tyrannosaurus*, *137*, 140, *142*, 165, *216*, 245, *246*; ecology, 195–96, 198–201, 248–51; survivorship, 253, *254*
Hatzegopteryx, 199. *See also* Azhdarchidae; pterosaurs, flying reptiles
Hay, Oliver P., 18–19; *Diplodocus*, *19*
head. *See* cranium
headbutting, *226–27*, 228
Hell Creek, Montana, 9

INDEX

Hell Creek Formation, Montana, North and South Dakota, 72, *184*; age, *185*, 187; botany, *191*, 192, 220; dinosaur abundance, 181–83; environment, 190–92; fauna, 196–99, 220, 262–63; preservation biases, 198; source of *T. rex* specimens, 184–85; stratigraphy, *78*, 181, *182*; 3 m gap, 263, *264*, 265
Henderson, Donald, 166
hindlimb: characterizing dinosaurs, 48; of theropods, 49, 58–59, 199, 208; of dinosaur herbivores, 201, 202, 233–34, *234*; pseudosuchians, 46–47
hindlimb, *T. rex*: as characterizing anatomy, 66; changes through growth, 135, *136*, 140–42, 144; discovery, 9, 10, 13, 17; functional morphology, 19, 96, *96*, 99, 102, 104–5, 145, 162–66, 177, 218, 232–34, 238, 244; medullary bone within, 243; musculature, *90*, *96*, 102; osteology, *14*, 99–105; pathologies, *250*, 252; position during copulation, 245; raptorial feet in *T. rex*, 13; role in predation, 172–73; *See also* arctometatarsal condition
holotype specimen: concept of, 65–67; of *Tyrannosaurus* species, *12*, *14*, *25*, *42*, 66–67, *70*, *71*, 72–73, 76–77, 80. *See also* CM9380
Holtz, Thomas, Jr. 69
Hone, David W. E., 30, 145, 150
horned dinosaurs. *See* Ceratopsia
horns, 4, 59, 62, 128, 204–5, 228, 258; in *T. rex*; 37, 88, 115, 118; use against predators, 211–15, *215*, 230
Hornaday, W. T., 9
Horner, Jack, 29, 181, 228. *See also* predator vs. scavenger controversy
Houston, David C., 229
Hoyt, Harry O., 22, 158
Hydrurga leptonyx, 1
hype, *T. rex*, 5–6, 19, 32–33. 36–41, 219, 229, 236, 258, 278

Iguanodon, 25
injuries. *See* pathologies
integument, *T. rex*, 32, 99, 105, 111–18, *119*; claw sheaths, 99, 105; facial skin, 115–18, *119*; feathers, 111, 112, 114; fossil evidence, 111–13; naked skin, 114–15; scales, 111–13; thermoregulatory concerns, 112–15
intelligence: as agent of dinosaur extinction, 258–59; dinosaur, 20, 30, 153–55, 215. *See also* brains
internal anatomy, *T. rex*, 105–11
International Commission on Zoological Nomenclature (ICZN), 65, 67
isotope(s): migration, 218–19; physiology, 132–33

"Jane," *T. rex* specimen, 73, *74*, *136*, 184, 241; age, 73, 141–42; bite strength of, 171; body mass, *147*; pathologies, *224*, 226, 253; taphonomy, *182*
Javelina Formation, Texas, 184, 186; age, *185*, 187; fauna, 196, 210
Jinbeisaurus wangi, 59
"Jordan theropod," *T. rex* specimen, 140, *141*. See also "*Stygivenator molnari*"
Judithian faunal stage, 195
Jurassic Period, 8, 9, *45*, 186; theropod communities, 49, 52, 260, 262; tyrannosauroid evolution in, 53, *54*, 55, *56*
Jurassic Park (novel), 30
Jurassic Park (movie), *20*, 71; logo, 19, 32; *T. rex*, 30–32, 122, 159, 162–63, 248. *Also see* AMNH 5027
Jurassic Park III (movie), 49
Juratyrant langhami, *54*, 55
juveniles: *Alamosaurus*, 211; *Ankylosaurus*, *215*; *Edmontosaurus*, 202, Komodo dragon, 222, 232, *233*; as theropod prey, 82, 109; *Triceratops*, *215*
juveniles, *T. rex*: 30, 191; anatomy, 85, 87–89, 91–92, 97, *136*, 138–42; in Cretaceous ecosystems, 195, *197*, 198–99, 208, 220, 232, 236, 248, *249*, 274; bite force, 169, 171; forelimb use, 172, 175, 176–77, 229; growth, 135–43, 248; life appearance, 114–15, *117*, 118, 129; locomotion, 164–66; mortality, 251, 253–54; private ownership and sale of specimens, 33, 40–41; scarcity of fossils, 247; taxonomic confusion, cause of, 66, *70*, *71*, 72–77; vocalization, 162

King Kong (movie): 1933, *20*, 22, 23, 274; 2005, 276
king tyrant, terminology, 39. *See also* *Tyrannosaurus rex*; tyrant king
Kirtlandian faunal stage, 195
Knight, Charles R., 13, 19, *21*, 22, 24; *Leaping Laelaps* (1897), 172, *174–75*; paintings of *T. rex*, *15*
Komodo dragon: as analogues for theropod biology, *127*, 128, 233, 238; predatory behavior, 221–22, *222*, 232, *233*, 236; skull, *123*, *124*; toxic bite of, 236. *See also* lizards
Koppelhus, Eva B., 30
K/Pg extinction: asteroid impact, *256*, 257–58, 266–74; Chicxulub impact site, 266, *267*, 268, 272, 275; historic considerations, 258–59; catastrophism vs. gradualism, 27, 259–62, *261*, *262*; dating of dinosaur extinction, 186–87, 195, 263–66; evidence of spring date, 266, 268; impact geography, *267*, 268; impact effects, 268–74; victims, 257
Kulindadromeus, 112

"*Laelaps*," 172, *174–75*. See also *Dryptosaurus*
Lakes, Arthur, 17
Lance Formation, Wyoming, 17, 182, *184*; age, *185*, 185, environment, 190–92
Lancian dinosaur community, *191*, 194–211; Cenozoic evolution of, 276; stratigraphic distribution of, *185*, *194*, 194–95; *T. rex* as the sole predator in, 258, 260–63
Land Before Time, *The* (movie), 30
Laramidia, landmass, *184*, 188; dinosaur communities, 194, 232, 238, 260
Larson, Peter, 30, 73, 77
larynyx, *159*, 160–61. *See also* syrinx; vocalization
Lawson, Douglas, 69
Leaping Laelaps (1897) (Knight), 172, *174–75*
legs. *See* hindlimb
Lepidosauria, *45*; vocal anatomy, *159*
Leptoceratops, *188*, *191*; characterizing dinosaur province, *184*, 204
Leptoceratops gracilis, 204, *204*; stratigraphic distribution, *194*
Lessem, Dom, 29
life appearance of *T. rex*, 111–29; color, 126–29; distortion in popular culture, 32, 36–37, *37*, 84; facial tissues, 115–25; of juveniles, 140, *142*. *See also* integument
lifespan. *See* longevity
lines of arrested growth (LAGs), 135, 137, *138*
Linnaeus, Carl, 43
Linnaean classification, 43–44
lion: color, *127*; cape buffalo, *214*; color, *127*; predatory behavior, 232
lips. *See* facial appearance
"living fossils," 274
lizards, *45*, 112, 170, 213; Cretaceous, 195, *196*, 220, *264*, 265; facial tissues, 122–24; as models for extinct reptiles, 19, 44, 45, 126, *127*, 140, 220–22, 238; physiology, 135, 137; reproduction, 244–45, 247, 249; toxic bites, 236; vocal anatomy, *159*, 160. *See also* Komodo dragon
Lockley, Martin, 173
locomotion, dinosaurs, 48–49, 60, 132, 220, *221*; "rauisuchians," 46–48; relation to longevity, 254
locomotion, *T. rex*, 96, *96*, 142, 162–65, *166*, 218–19, 232–34; sluggish, 28, 275. *See also* footprints, *T. rex*; trackways; swimming, *T. rex*
longevity: dinosaurs, 135, 254–55; large mammals, 254; theropods, 144, 211, 253–55, *254*
Longrich, Nicholas, 73
Lost World, *The* (movie): 1925, 22, *23*, 24, 25, 158, 274; 1960, 25
Lost World: Jurassic Park, *The* (Crichton), 248
Lost World: *Jurassic Park* (movie) 248
Lourinhanosaurus, 247, 248
lungs, 105–8, 159. *See also* air sacs; pneumaticity; pulmonary system
Lythronax, *54*, 62, 63
Lythronax argestes, *54*, 62

Maastrichtian, *54*, *185*, 186–87; dinosaur diversity decline, 259–63; Lancian biota, 194–211, 247; North American geography, *184*, 188–94; predator ecology, 197–201, 232
mammals: anatomy, 83, 89, 91, 92, 105, 107, 125, 126, *127*, 153–54, 160–61, 163; as dinosaur

INDEX

analogues, 148; evolution, 4, 20, 24, 44, 274; evolutionary success, 39, 187; face biting, 226; longevity, 253–55; Mesozoic, 8, 195–96, *197*, *249*, 264; physiology, 27, 29, 48, 114, 132–33, 135, 137; predator defenses, 212–14; predator ecology, *5*, 128, 198, 201, 213, 156, *214*, 220–23, *233*
McCrea, Richard T., 220
McRae Group, New Mexico, 80; McRae Formation, 186. *See also Tyrannosaurus mcraeensis*
Maleev, E. A., 68
Mallon, Jordan, 150
Maniraptora, 153, 156, 172; evolution, *45*, 53; feather use in display, 226; nests, 249
"*Manospondylus gigas*," 17, 66–67; holotype, *11*, *106*
Mapusaurus, 137, *138*
marine reptiles, 126, 188, 257
Marsh, Othniel Charles, 7–9, *11*, 17–18, 22. *See also* Osborn, Henry Fairfield; "*Ornithomimus grandis*"
masculinity, *T. rex*; 39–40, 258
mass extinctions. *See* extinction; K/Pg extinction
Matthew, William Diller, 10, *12*, 153, 162
medullary bone, 111, 142–43, 243
Megalodon. See *Otodus megalodon*
Megalosaurus, 49, 53
"*Megapubis acheirus*," speculative tyrannosaur, 275
Megaraptor namunhuaiquii, 58
Megaraptora, *54*, 57–59
melanosomes, 126. *See also* color
Mesozoic Era, 8, 9, *45*, 185–87, 238; birds, 159, 196–97; dinosaur evolution in, 48–49, 52, 155–56, 211–15, 257–74; ecosystems, 194–211, 260–63; flora, 188, 190, 192–93, 196, 260; marine ecosystems, 188; non-avian dinosaurs, 107, 112, 122, 137, 143, 153, 158, 160–61, 165, 167, 218, 229, 254–55; reptile evolution in, 43–47; tyrannosauroid evolution in, 53–59. *See also* K/Pg extinction
metabolism. *See* physiology
migrating behavior, dinosaurs, 218–19
Mitchell, Mary Mason, 19, *19*
model organism, *T. rex*, 30, 40, 278
Molnar, Ralph E., 30
Mongolia, 60, 63, *63*, 67–68, 204; as source of commercial fossils, 35. *See also Tarbosaurus*
monsterization, *Tyrannosaurus*, 19–24, 29, 36–39
Montana, 184, *185*; historic source of *Tyrannosaurus* fossils, 2, *7*, 9, 13, 17
Morhardt, Ashely, 155
Moros intrepidus, 59
morphodynamic compensation, 173
mountains, *T. rex* habitat, *180*, 188–90, 192–94, 205, 210. *See also* North American Cordillera
movies, *T. rex*; *20*, 22–25, 30, *31*, 32, 71, 122, 158, 159, 162, 163, 248, 274, 276
Murusraptor barrosaensis, 58
musculature, *Tyrannosaurus*: axial, 93–94, *96*, 96, 108; cranial, 87, 89–91, 118–19, 122, 133, *134*, 140, 155–56, 168–72, *169*; forelimb, 99, 172–73, 176, *176*; hindlimb, 102, 164–65, 233–34, *234*; caudofemoralis, 96, *96*, 102, 163, 233, *234*. *See also* anatomy
Museo del Jurásico de Asturias (MUJA), *244*
museums, *T. rex*: 2, *16*, *18*, *25*, *28*, *34*, *42*, *63*, 65, 73, *139*, 145, 181, *237*, 234, *244*, *275*, 278–79; as attraction, 2–4, *15*, 18, 19–22, 24, 28, 33–36, 258; collections, 40–41, 97, 253; research, 6–10, 13–14

"*Nanotyrannus lancensis*," 40, *70*, 72–77, 80; controversy, 73–77; holotype skull of, *71*, 140, 185; as pygmy species, 72, 197. *See also* "Jane," *T. rex* specimen; "Petey," *T. rex* specimen
Nanuqsaurus, *54*, 62, 68
Nanuqsaurus hoglundi, 62
Natural History Museum, Los Angeles, *38*, *63*, *139*, *275*. *See also* "Thomas," *T. rex* specimen
Natural History Museum, London, 28
Neotheropoda 53
Neovenator, 157–58
New Dinosaurs: An Alternative Evolution, *The* (Dixon), 274–76
Newman, Barney W., 28
New Mexico, 80, 183, *185*, 186, 210
Nightmare Before Christmas, *The* (movie), 140
North America: decline in dinosaur diversity, 259–63; impact of K/Pg event, 266–74; Lancian fauna, 194–211, 232, 247, 277; Maastrichtian geography, *184*, 188–94; paleontology, 6–19, 24; tyrannosaurids, *54*, 55, *58*, 59, 60, 62–63, 65, 68, 72, 220. *See also* Laramidia, landmass
North America, *T. rex*: fossil record, 65, 68, 69, 79; geological distribution, 183–87
North American Cordillera, *184*, 188, 190, 192, *193*, 204. *See also* alluvial plains; mountains
North Carolina Museum of Natural Sciences, 35
North Dakota, 185, *185*
North Horn Formation, Utah, *184*, 185; age, *185*, 187; environment, 192, 194; fauna, 210
nostrils, *T. rex*, 87, 115, *117*, *121*, 121–22, 156. *See also* life appearance; sensory capabilities, *T. rex*

O'Brien, Willis, 22
Observer, *The* (newspaper), 33
Ojo Alamo Formation, New Mexico, 198
One Million Years BC (film), 24
ontogeny: study of, dinosaur, 29, 137; relation to isotopes, 218–19; complications to tyrannosaurid taxonomy, 63, 68, 135; growth rates in theropods, *138*, 137; precociality vs. altriciality, 248–49
ontogeny of *T. rex*, 85, 87–89, 91, 92, 135–44, 171, 175, 198, 233, 243, 248–51, 253–55; adult growth stage, 144; body masses of growth stages, *147*; complications to taxonomy, 70–77; juvenile growth stage, 140–41, *172*, *246*, 249–51; late juvenile–subadult growth stage, 141–44; lines of arrested growth (LAGs), 74, *75*, 135, 137, *138*; physiology of, 132; reproductive maturity, 111, 135, *138*, 142–44, 226, 253. *See also* tyrannosaurid niche assimilation
Ornithischia: classification: *45*, 48; eggs, 247; integument, 112; medullary bone in, 143; pneumaticity, 107; remains in *T. rex* coprolite, 109; vocal anatomy, *159*, 160
Ornithomimidae, 104, 199, 208, 264
Ornithomimosaurs, *45*, 49, 53, *106*, 138
Ornithomimus, 17, 208; abundance in Hell Creek Formation, *182*; as prey of *T. rex*, 165, *166*; integument, 114–15, 208
"*Ornithomimus grandis*," 17, 185
Ornithomimus velox, 206
Ornithoscelida, 48
Osborn, Henry Fairfield, 2; classification of *T. rex*, 65, 66; early research on *T. rex*; 6–14, 17–19, 21, 22, 25, 278
osteoderm, 209, 211, 213, 215; as scutes in *Dynamosaurus*, 10, 13; in *T. rex*: 88, *89*, *117*, 118. *See also* armor
osteology, *T. rex*, 83–85; cranial, 85–92, 133, *134*; forelimb, 97–99, 175–77; hindlimb, 99–105, 163; vertebral and torso, 92–97, 105–8. See also *anatomy*
ostrich dinosaurs. *See* Ornithomimidae; ornithomimosaurs
Otodus megalodon, 171
Ostrom, John, 27

Pachycephalosauridae, 209
Pachycephalosaurus, 65; abundance in Hell Creek Formation, *182*
Pachycephalosaurus wyomingensis, *208*, 209; stratigraphic distribution, *194*
Padian, Kevin, 173
Palaeosaniwa, 196; as predator of *T. rex*, 249
paleobotany: extinction, 260, 268, 272; isotopes, 218; of *T. rex* paleoenvironments, 188, 190, 192–93, 195, 196, 220
paleoenvironments of *T. rex*, *184*, 188–94; alluvial plains, *184*, 188–91; biota, 194–211; floodplains; 188, 190–92, 194, 204; impact of Chicxulub impact on, 266–75; mountains, *180*, 188–90, 192–94, 205, 210
paleontology: commercialized, 29, 33–36, 40–41, 279; impact of world wars on, 19, 24; of Lancian North America, 180–211; popularization, 32, 36, 38; shift away from American dominance, 24; at turn of 20th century, 6–8; typological approach to taxonomy, 71; *T. rex* subculture, 2, 36–41, 181. *See also* dinosaurs: popularity

INDEX

Paleozoic Era, 186, 266
parenting, 245, 248–51
Parker, Neave, 24
Paronychodon, 198
Parrish, J. Michael, 30
pathologies: in herbivorous dinosaurs, caused by *T. rex*, 230, *231*, 237–41; in *T. rex*, *85*, 143, 144, 177, 223–27, *250*, 251–53, 255
Paul, Gregory S., 29, 68, 69, 79, 162, 163, 230, 275–76
Peabody Museum of Natural History, Yale, 7
"Peck's rex," *T. rex* specimen, *25*, 184; pathologies, *224*; taphonomy, *182*
Pectinodon, 198
pectoral girdle: pneumaticity, 107, 159; *T. rex*, 97, *98*, 99, 141, 175–77, 252
pelvic girdle, dinosaurs, 48, 55; bitten by *T. rex*, 168, *231*, 238–39; in speculative tyrannosaur descendants, 275. *See also* "*Megapubis acheirus*," speculative tyrannosaur
pelvic girdle, *T. rex*: anatomy, 83, 96, 99, 101–2, 111, *113*, 145, 150, *182*, 244; as characterizing anatomy, 66, 73; change through growth, *136*, 140, 144; discovery of, 10, 13, *14*, *16*, 18; incorrectly depicted, 32; sexual dimorphism of, 242
Permian extinction, 44, 257
Peterson, Olaf A., 10
"Petey," *T. rex* specimen, 241; as purported "*Nanotyrannus*," *75*, 76
Phanerozoic Eon, 186
physiology, 27, 29, 48, 128, 131–35, 144, 171, 215, 253; and growth, 135, 144; ectothermy, 48, 131–33, 162; endothermy, 48, 131–33, 218; in dinosaurs, 131–33; relevance to migration, 218. *See also* thermoregulation
Pickering, Stephen, 71
pigeon, closed-mouth vocalization, *161*
Pinacosaurus, larynyx, 160
Planet Dinosaur (documentary), 32
plant life, Cretaceous. *See* paleobotany
Platytholus clemensi, 209
play behavior, *T. rex*, 154
pliosaurid, marine reptile, 171
polar bear, *5*, *127*
popular culture, influence on *T. rex* depictions, 32, 36–37, *37*, 84, 228
population densities, *T. rex*, 133
poop. *See* coprolite
posture, *T. rex*, *15*, 19, 27–29, 102, 132, 156, 166; mating, 243–46
Postosuchus kirkpatricki, *45*, *46*, 48
pneumaticity, 106–8, *106*; in mammals, 107; functional implications, 107–8; relevance to vocalization, 159–60
predator vs. scavenger controversy, 5, 40, 228–30, 275, 277
Predatory Dinosaurs of the World (Paul), 29, 69
Prehistoric Planet (documentary), 248
Proceratosauridae, *54*, 55, *56*
Proceratosaurus bradleyi, *54*, 55, *57*
Protoceratops, 204
protofeathers, 32, 48, 55, *56*, 111, 112, 114, 132. *See also* integument
provincialism, dinosaur faunas, 195, 201, 204, 209. *See also Alamosaurus*; *Leptoceratops*; *Triceratops*
Pseudosuchia, *45*, 47. *See also* crocodylians
pterosaurs, flying reptiles, *25*, 69, 126; evolution, *45*, 44, *45*, 47, 48; fossil record, 199; as heroic champions against nasty tyrannosaurs, 199, *200*, 201, *250*; pneumaticity, 105, 107–8
pulmonary system: adaptive properties, 107–8, 133; evolution, 47–48, 50, 159–60; in *T. rex*; 87, 105–8, 133; vocalization, 159

Qianzhousaurus sinensis, *54*, 57, *61*, 62
Quetzalcoatlus, 199. See also Azhdarchidae
Quetzalcoatlus northropi, 25, 69, 199, *200*. See also Azhdarchidae

racial senility, extinction hypothesis, 258, 259
raptor (bird): use of talons 175, 177, 199; vision, 156
Raptorex, *54*, 63, 140, *141*
"Rauisuchia," *45*, 46–48
reproduction: copulation, 173, 243–45; Cretaceous, 196; eggs, nests and embryos, 245, 247–48
reptiles: anatomy, 87, 89, 94, 96, 102, 104, 115, 158, 236; brains, 153–55; as dinosaur substitutes on film, 25; evolution, 41, 43–48, 53, 105; facial anatomy, 118–25; food intake, 133; growth, 73, 135, 137, 139, 140; physiology, 132–33; predatory ecology, 221–22, 232–33, 249; reproduction, 244–45, 247; survivorship rate, 253; tail regeneration, 252; vision, 155; vocal evolution, 159–61
ribs, *Allosaurus*, *95*
ribs, *T. rex*, *85*; cervical, 14, 93, *93*; dorsal, 94–95, *95*; pathologies, *250*, 252
Richardoestesia, 198
Rite of Spring, *The* (Stravinsky), 22–24
roaring, *T. rex*, 2, 22–23, 38, *130*, 158–61. *See also* cliché: *T. rex* depictions
"robust" and "gracile" morphs, *T. rex*, 77, *77*, 78–80, 242
Rozhdestvensky, A. K., 68, 73
Ruxton, Graeme D., 229

Saitta, Evan T., 73
saltwater crocodile, *127*, 150, 170. *See also Crocodylus porosus*
"Samson," *T. rex* specimen, 35
Saskatchewan, 184, *184*, *185*, 190
Saurophaganax maximus, 21
"*Saurophagus*," 21
Sauropodomorpha, *45*, 48; eggs, 247
sauropods, long-necked dinosaurs; pneumaticity, 107–8; limbs and carriage, 150, 163; in Cretaceous North America, 209–11, 277; pelvic size, 101–2; as prey for *T. rex*, 211, 214, 232; longevity, 255
scales, skin covering: 22, 37, 49, 204; tyrannosaurids, 111–15, *117*, 118, *119*, 228. *See also* integument
scaling: body size, 50, 147–48, 150; muscle performance, 164; skeletal strength, 163–64. *See also* encephalization quotient (EQ)
scavenging: taphonomy, *182*, 183; *T. rex*, 178, 201, 228–30, 241, 274, 275, 277. *See also* predator vs. scavenger controversy
Schaeffer, Joep, 219
Schoedsack, Ernest B., 22
Schweitzer, Mary, 110
scientific names, 1–2, 67, 76. *See also* holotype specimen; taxonomy
sclerotic ring(s), *85*, 87; relationship to eye size, 119–20, *120*
Scollard Formation, Alberta, 184, *184*, 192; age, 185; environment, 188, 190
"Scotty," *T. rex* specimen, 184; body mass, *147*, 148, 150; maturity, 144
Second World War, 24
sensory capabilities, *T. rex*, 155–58
sexual dimorphism: relation to facial biting, 226–27; efforts to find in *T. rex*, 77, 78, 241–43; recognition among skeletons of living animals, 243; claims to increase value of *T. rex* specimens, 40
sharks, *126*, 171, 196
Short History of the World, *A* (Wells), 20
Sinotyrannus kazuoensis, 55
Signor-Lipps effect, 265
size, *T. rex*: adult, *5*, 144–45, *146*; maximum predicted, 150–51. *See also* body mass
skin. *See* integument
skull: *Andrewsarchus*, *5*; erythrosuchids, 45; pachycephalosaurs, 208; "rauisuchians," 47; theropods, 21, 52; *Triceratops*, *215*; tyrannosauroids, 55, *57*, 60, 62, *63*, 80, *81*, 141, 275
skull, *T. rex*, *5*, *57*, *84*, *116*, *120*, *141*, 145, 150, 220; anatomy, 85–92, 94, 107–8, 113, *117*, 121, *123*, 124, 151, 156, *157*, *169*; change with growth, *138*, 140–41; discovery, 10, *11*, 13, *14*, 17, 18, 22; iconic, 2; market value, 35; pathologies, *224*, 226; strength, 170–71, 228; use in classification, 66, *70*, 71–74, 76, *77*, 78, 80; variation, *77*, 243. *See also* brains; dentition; facial appearance
Smith, Joshua B., 91
Smithsonian National Museum of Natural History, Washington DC, *237*
snakes, *45*, 125, 126, 170, 257; Cretaceous, 196; reproduction, 244–45
social interactions, *T. rex*, 173, 219–28
Society of Vertebrate Paleontology, 35
soft tissues, 84, 105, 108, 126, 252; reconstruction of, *T. rex*, *90*, *96*, 111–25, 148, *149*, 150; non-mineralized in *T. rex*, 110–11; preservation of, 183. *See also* facial reconstruction; fossilization; musculature; taphonomy

INDEX

Sound of Thunder, A (Bradbury), 25, *26*, 27
South Dakota, 29, 185, *185*
speculative evolution, 274–77, *276*, *277*
speed, *T. rex*. *See* locomotion, *T. rex*
Sphaerotholus buchholtzae, 209
Spinosauridae, *45*, 49–50, *51*, 53, 55, 177, 278; growth, *138*; pneumaticity, *106*
Spinosaurus, 22, 32, *45*, 49–50, 52, 53, 128, 158; growth rate, *138*; mentions in literature, *20*; swimming, 166–67
Spinosaurus aegyptiacus, 21, 49, *51*
"Stan," *T. rex* specimen, *100*, 185, 241; body mass, *147*; pathologies, *224*, 245; maturity, *89*, 144; sale, 33, 35
Stegosaurus, 9, 23, 25, 33, 34; mentions in literature, *20*. *See also* "Apex," *Stegosaurus* specimen
Stenonychosaurus, 30
Sterling, Lindsey Morris, 13
Sternberg, Charles, 33
Stevens, Kent, 155
Stokesosaurus, *54*
Stokesosaurus clevelandi, 55
Stokowski, Leopold, 23–24
Stravinsky, Igor, 22, 23
Stromer, Ernst, 21
Struthiomimus, 208
Stygimoloch, 65
Stygimoloch spinifer, *194*
"*Stygivenator molnari*," *70*, 71, 72, 80; as juvenile *T. rex*, 140, *141*
Suchomimus, 65
"Sue," *T. rex* specimen, *34*, 83, *84*, *85*, *90*, *94*, *146*, *151*, *157*; body mass, 145, *147*, 148, *149*, 150; description of, 84, 91; discovery, 182, 185, 219–20; forelimbs, *98*, 176; maturity, *137*, 138, 144; pathologies, *224*, *250*, 251–53; sale, *20*, 33–35; use in classification, *70*, 71, *75*, 76. *See also* paleontology
survivorship, 253–55
Suskityrannus hazelae, *54*, 59
swimming, *T. rex*, 166–68
Swinton, W. E., 20
syrinx, 159–60. *See also* larynx; vocalization

tail: clubs, ankylosaurs, 209, 213, 215; *Edmontosaurus*, 230, *231*, *234*; reptile, complication to reproduction, 244–45; *Spinosaurus*, 49; *Stegosaurus*, 24; tyrannosaurid, 28, 80
tail, *T. rex*, 22, 28, *85*, 96–97, *96*, 102, 111, *113*, 132, 164, *234*; alleged sexual dimorphism, 242–43; as counterbalance to body, 108; discovery, 13; length, 18, 84, 92, 96–97, 145, 182; pathologies, 251–53. *See also* musculature, *Tyrannosaurus*
Tanycolagreus topwilsoni, 55, *56*
taphonomy, *182*, 183, 218–20. *See also* bonebeds; fossilization
Tarbosaurus, congeneric with *Tyrannosaurus*, 68–69; juvenile skulls, 140, *141*. See also *Tyrannosaurus bataar*
Tarbosaurus bataar, 35, 60, 62–65, 67
taxonomy, principles, 65–67, 68; *T. rex*, 65–81
teeth. *See* dentition
Teratophoneus, *54*, 62, 63, 68
Teratophoneus curriei, 62
territoriality, *T. rex*, 218–19
Texas, 69, 183, *185*, 186, 199, 210, 267
Thanatotheristes degrootorum, 62
thermoregulation, 112–14, 128, 131–33, *134*; thermal neutrality, 112–14
Theropoda, 2, 135; aggressive social behavior, 226, 228; anatomy, 19, 88, 91–92, 93, 94, *95*, 99, *101*, 102, 104–5, 122, 125; brains, 153–45; color, 128; evolution, *45*, 48–55, 58–59, 132, 276; evolutionary success, 39, 277; feeding, 229, 238; forelimbs, 97, 173–74, 177; gregariousness, 219; growth, 135, 137, *138*; Lancian diversity, *191*, 197–99, 206–9, 258–60, 262, *264*; locomotion, 163–65; longevity, 211, 255; pathologies, 251; pneumaticity, *106*, 107–8; reproduction, 142, 244–45, 247–48; senses, 155–58; size, 50, 52, 144, 277; swimming, 167; vocalization, 160
Thescelosaurus, 195, 201, *264*; abundance in Hell Creek Formation, *182*
Thescelosaurus neglectus, *202*
"Thomas," *T. rex* specimen, *139*, *275*; maturity, 144
Through the Looking Glass (Carroll), 211
tiger, *127*
tongues, 122
Tornillo Group, 69
Torosaurus, 65, 195, 205, 214, *235*, *264*
"*Torosaurus*" *utahensis*, 205
Torosaurus latus, 205, *235*
Torvosaurus, 49; eggs, 247, 248
toxic bite, *T. rex* 236
trackways: swimming, 166; tyrannosaurid, 220, *221*
Triassic Period, 43–47, *45*, 49, 186, 199
Triceratops, 1, 9, 13, *15*, 24, *38*, 65, 187, 194–95, 201, 204–5, 211, *212*, 214, 215, 232, *237*, 263; abundance in Hell Creek Formation, *182*, 197, 265; characterizing dinosaur province, 204; development of frills and horns, *215*; in film, 22, 24; market value of skull, 33; mentions in literature, *20*; predated and eaten by *T. rex*, 168, *200*, 230, *231*, 232, 234–35, *237*, 238–41, *240*; running speed of, 233–34, *234*; stratigraphic distribution of 187, *194*, 265; "*Triceratops* fauna," *184*, 187
Triceratops horridus, 1, *194*, 204, *205*, *264*
Triceratops prorsus, 194, 204
"Trix," *T. rex* specimen, 83, *116*, 185; dentition and diet, 219; maturity, 144; migration study, 219; pathologies, *224*, 253
Troodontidae, 53, 104, 198, 247, *264*
turtles, *45*, 132, *159*, 160, 177, 226, 274; Cretaceous, 196, 209, 220, 257, *264*, 265; reproduction, 244, 247, 248
Tyrannosaur Chronicles, The (Hone), 30
Tyrannosauridae, 44; alleged sexual dimorphism, 243; anatomy, 28, 72, 73, 90, 92, 94, 104, 107, *123*, 125, 233; bite force, 168, 169; brains, 151; distribution, 183, 186–87; ecology, 68, 128, 198, 260–62; evolution, *54*, *57*, 59–65, 80, 275, 277; evolutionary success, 39, 277; facial anatomy, 118, 119–20; forelimbs, 97, 99, 172–73; gregariousness, 220, *221*, 223; growth, 76, 137, *138*, 140, *141*, 142, 150; gut content, 108; integument, 112, 113, 126; locomotion, 163; longevity, 211, 253–55; predatory behavior, 228–30; reproduction, 247, 248; research on, 30; senses, 155–56; size, 49–50; social interactions, 226, 228; taxonomy, 66–77; tracks, *221*. *See also* tyrannosaurid niche assimilation; *Tyrannosaurus rex*
tyrannosaurid niche assimilation, 129, 198, 260–61
Tyrannosaurid Paleobiology (Parrish, Molnar, Currie and Koppelhus), 30
Tyrannosaurinae, 50, *54*, *57*, 62
Tyrannosaurini, *54*, 63, 65, 80
Tyrannosauripus pillmorei, track taxon, *104*, 105
Tyrannosauroidea, 172; anatomy, 55, *57*, 87, 163; bite force, 168–70; evolution, *45*, 48, 53–60, 62, 133; growth, 138; integument, 48, 55, 111, 113, 133; pneumaticity, 106; senses, 156
Tyrannosaurus: geographic origin, *54*, 62–63, 65, 80; holotypes of species, *12*, *14*, *25*, *42*, 66–67, *70*, *71*, 72–73, 76–77, 80; specimens of disputed affinity, 69–81, 186–87, 192–93; taxonomy, 65–81. *See also* "*Nanotyrannus lancensis*"; *Tyrannosaurus mcraeensis*; *Tyrannosaurus rex*; *Tyrannosaurus rex* specimens
Tyrannosaurus bataar, 67–69
"*Tyrannosaurus imperator*," *70*, 79–80; classification, *78*
"*Tyrannosaurus lanpingensis*," 67
"*Tyrannosaurus luanchuanensis*," 67
Tyrannosaurus mcraeensis, 80–81, *81*, 192, *193*; geological distribution, *184*, *185*, 186–87
"*Tyrannosaurus regina*," *70*, 79–80; classification, *78*
Tyrannosaurus rex, 1; abundance in Hell Creek Formation, 181–83; air sacs, 87, 105–8, 133, 159–60; anatomical variation, 77–79, 241–43; appetite, 133, 135; armored face, 115, 125; Asian origin of, *54*, 62–63, 65, 80; associated plants and animals, 194–210; brain(s), 73, 151, *152*, 155–56; bite strength, 38, 80, 92, 162, 168–72, 170–72, 229, 236; body mass, 144–50; bone, internal, *75*, 110–11; 142–43, *143*; celebrity status, 2–6, 19–24, 29–41; Charles Knight artworks of, *15*; classification, 65–67; clichéd depictions, 5, *37*, 38–39, 193, 279; color, predictions, 126–29; confirmed prey species, 109, 202, 205, 230, *231*,

INDEX

Tyrannosaurus rex continued:
234; coprolites, 108–10; cranial anatomy, 85–92, 133, *134*; ears, *121*, 122; ecology, 129, 133, 198, 260–62; endocast, 151–53, 155–56; evolution, 43–65; extinction, 257–74; eye anatomy, restored, 5, *31*, 32, 87–88, *89*, 115, 118–20, *120*; face biting, 223, *224*, 225–27, 252; facial appearance, 4, 32, 50, *86*, 87–88, *89*, 115–25, 128, 144, 242–43; feeding, 237–41; in fiction, 22–27, 158–59, 274–77; forelimb anatomy, 97–99, 175–77; forelimb redundancy, 172–73, *174*, 275, *276*, 276; fossil evidence of biting, 202, 223–27, 230, *231*, 232, 237–41, 245, 252; fossil record, 34–35, 40–41, 65, 80, 141, 150, 181–83, 187, *194*, 253; fossilization, *84*, *182*, 198; geographic distribution, 183–86, *184*; gregariousness, 219–23; gut anatomy, 108–10; hatchlings, *137*, 140, *142*, 165, 195–96, *216*, 245, *246*, 198–201, 248–51, 253, *254*; headbutting, *226–27*, 228; hindlimb anatomy, 102–5, 163; history of discovery, 6–19; holotype, *12*, *14*, 24, *25*, *42*, 65, 66, *70*; hype, 5–6, 19, 32–33, 36–41, 219, 229, 236, 258, 278; influence on dinosaur evolution, 211–15; integument, 32, 99, 105, 111–18, *119*; intelligence, 20, 30, 153–55, 215, 258–59; isotopic insights into diet, 219; *Jurassic Park* (movie) version, 30–32, 122, 159, 162–63, 248; K/Pg experience, 268–74; life appearance, 32, 36–37, *37*, 84, 111–29; lines of arrested growth (LAGs), 74, *75*, 135, 137, *138*; locomotion, 28, 96, *96*, 142, 162–65, *166*, 218–19, 232–34, 275; longevity, 135, 144, 211, 253–55; lungs, 105–8; masculinity, 39–40, 258; medullary bone, 111, 142–43, 243; migration, 218–19; model organism, 30, 40, 278; monsterization, 19–24, 29, 36–39; movie versions; 20, 22–25, 30, 31, 32, 71, 122, 158, 159, 162, 163, 248, 274, 276; musculature, 87, 89–91, 93–94, *96*, 96, 99, 102, 108, 118–19, 122, 133, *134*, 140, 155–56, 164–65, 168–72, *169*, 172–73, 176, *176*, 233–34, *234*; name, 2, 10, 13, 39; niche assimilation, 129, 198, 260–61; nostrils, 87, 115, *117*, *121*, 121–22, 156; ontogeny, 85, 87–89, 91, 92, 135–44, 171, 175, 198, 233, 243, 248–51, 253–55; Osborn, early research on; 6–14, 17–19, 21, 22, 25, 278; osteoderms, 88, *89*, *117*, 118; paleoenvironments of, *184*, 188–94; parenting, 245, 248–51; pathologies, *85*, 143, 144, 177, 223–27, *225*, *250*, 251–53, 255; pectoral anatomy, 97, *98*, 99, 141, 175–77, 252; pelvic anatomy, 99–102, 175–76, 242, *242*; physiology, 29, 128, 131–35, 171; play behavior, 154; pneumaticity, 106–8; population densities, 133; posture, *15*, 19, 27–29, 102, 132, 156, 166, 243–46; predatory behavior, 164–65, *166*, 168, 228–36, 248–49; pulmonary system, 105–8; reproduction, 173, 243–48; reproductive maturity, 111, 135, *138*; ribs, 14, *85*, 93–95, *95*, *250*, 252; roaring, 2, 22–23, 38, *130*, 158–61; "robust" and "gracile" morphologies, 77, *77*, 78–79, 242; sale of specimens, 24, 35–36, 40–41; scales, skin covering: 111–15, *117*, 118, *119*, 228; scavenging, 229; senses, 155–58; sexual dimorphism, efforts to find, 77, 78, 241–43; size, *5*, 144–45, *146*, 150–51; skull, *5*, *57*, *84*, 85–92, 94, 107–8, 113, *116*, *117*, *120*, 121, *123*, 124, *141*, 145, 150, 151, 156, *157*, *169*, 170–71, 220, 228; soft tissues, reconstruction of, *90*, *96*, 110–25, 148, *149*, 150; as sole predator of Lancian North America, 258, 260–63; survivorship, 253–55; tail, 22, 28, *85*, 96–97, 102, 108, 111, *113*, 132, 164, *234*, 242–43; *Tarbosaurus*, congeneric with, 68–69; taxonomy, 65–81; temporal distribution, *45*, 186–87; territoriality, 218–19; tongue, 122; toxic bite, 236; vertebral column, *14*, *15*, 28, 83, *85*, 90, 92–97, 102, 145, 182, 234, *250*, 251–53, 255; vocalization, 22–23, *130*, 158–62. *See also* juveniles, *T. rex*; museums, *T. rex*; *Tyrannosaurus*; *Tyrannosaurus rex* specimens
Tyrannosaurus rex (Bradbury), 27
Tyrannosaurus rex specimens: AMNH 5027, 14, *16*, 17, 18, 19, *16*, *18*, 32, *70*, 79, 144, 184, *224*; "Baby Bob," 33; "Barnum," coprolite, 109, *109*; "Black Beauty," 184; CM9380, holotype, *12*, *14*, 24, *25*, *42*, 65, 66, *70*; "Jane," 73, *74*, *136*, 141–42, *147*, 171, *182*, 184, 241, *224*, 226, 253; "Jordan theropod," 140, *141*; "Peck's rex," *25*, 184, *182*, *224*; "Petey," *75*, 76, 241; "Samson," 35; "Stan," 33, 35, *89*, *100*, 144, *147*, 185, *224*, 241, 245; "Sue," *20*, 33–35, *70*, 71, *75*, 76, 83–*85*, *90*, 91, *94*, 98, *137*, 138, 144, 145–51, *157*, 176, 182, 185, 219–20, *224*, *250*, 251–53; "Thomas," *139*, 144, *275*; "Trix," 83, *116*, 144, 185, 219, *224*, 253; "Wankel"/"Nation's *T. rex*," *3*, 144, *147*, *149*, *182*, 184–85, *237*; "Wyrex," *98*; 111, *113*; 252
"*Tyrannosaurus stanwinstonorous*," 71
"*Tyrannosaurus turpanensis*," 67–68
"*Tyrannosaurus vannus*," 69, 70
"*Tyrannosaurus* x," 77–79
"*Tyrannosaurus zhuchengensis*," 67–68
tyrant king, terminology, 39

United States, 47, 60, 62, 63, 65; Chicxulub impact, 266–75; commercial fossil laws, 35; dominance of early 20th century vertebrate paleontology, 6–9, 19–24; Lancian fauna, 194–211; Maastrichtian geography, 184, *184*, 188–94. *See also* North America
Utah, 185, *185*, 210

Valley of Gwangi (movie), 24
"*Vastatosaurus rex*," speculative tyrannosaur, 276
Velociraptor, 32, 53, 71, 198–99; mentions in literature, *20*
Velociraptor mongoliensis, 2
venom, used in predation, 236
vertebrae: adaptations to predatory lifestyles, 45; bitten by *T. rex*, 230, *231*, 238–39; hadrosaurid, *234*; posture, 47; records of Lancian fauna, 199; use in classification, 48, 55. *See also* tail
vertebrae, *T. rex*: anatomy, *14*, *15*, 83, *85*, 90, 92–97, 102, 145, 234; discovery, 9, 10, *11*, 13, *14*, *16*, 17; number of, 28, 145, 182; pathologies, *250*, 251–53, 255; pneumaticity, 106–8; posture, 28; scaling, 150; use in classification, 66, *67*, 78
vertebrate paleontology. *See* paleontology
vision, in predatory animals, 60, 155–56, 157, 229; in *T. rex*, 87, 118, 155–56, 158, 275. *See also* eyes
vocalization: closed-mouth, *130*, 161, *161*; evolution in reptiles, 158–62; *T. rex*, 22–23, *130*, 158–62
volcanoes, 22, 186, 192–93, *193*, 260
von Ebner lines, dentition, 92
von Fuehrer, Ottmar, 24

Walking with Dinosaurs (documentary), 248
"Wankel"/ "Nation's *T. rex*," *T. rex* specimen, *3*, 184–85, *237*; body mass *147*, *149*; maturity, 144; taphonomy, *182*
warm-blooded. *See* physiology
Wells, H. G., 20
Western Interior: geology, 183, *184*, 186–87, *194*, 259; Lancian biota, 195–211; Maastrichtian paleoenvironments, 188–94, 272
Western Interior Seaway, *184*, 188, 191–92, *267*, *271*, 272
whales, 83; eyeball size, *120*; longevity, 254
Williams, Maurice, 33
Willow Creek Formation, *184*; age, 185; paleoenvironment, 188, 190
Wilson, Maurice, 24
Woodward, Holly, 76
Wray, Fay, 22
"Wyrex," *T. rex* specimen, *98*; skin impressions, 111, *113*; tail trauma, 252
Wyoming, *185*, 185; historic *T. rex* discoveries, 10, *11*, 13, 17

Yutyrannus, *54*, 55, 111, 114, 169
Yutyrannus huali, 55, *56*

Zallinger, Rudolph, 24
Zhuchengtyrannus, *54*, 65
Zhuchengtyrannus magnus, 62, 63, 67–68