CONTENTS

CHAPTER 1

An Introduction to Dinosaurs

The Dinosauria represent an extremely successful group of tetrapods that were the dominant terrestrial group of most of the Mesozoic Era, and in the birds, have comfortably over 10,000 living species as descendants. (Throughout this book I will refer to dinosaurs and Dinosauria as a paraphyletic group, therefore excluding both Mesozoic and modern birds unless explicitly stated otherwise.) Although various fragmentary fossils that we now recognize as being dinosaurian were being discussed in the eighteenth century, they came to prominence with the naming of the British carnivore *Megalosaurus* in 1824[1] and herbivore *Iguanodon* in 1825[2] and the coining of the name "Dinosauria," or "fearfully great lizards," by Richard Owen in 1842.[3] The dinosaurs quickly grew in both numbers of species described and taxonomic ranks recognized, with ever more, ever better, and ever larger fossils being discovered. Dinosaurs soon became established as a major area of interest in the burgeoning field of paleontology and have become central to the study of the history of life on Earth (figure 1.1).

Dinosaurs are no longer considered the cold-blooded, tail-dragging, stupid, lizard-like monsters of the Victorian age, but are instead recognized as animals that were upright, active, fast-growing, and if not especially intelligent, certainly not stupid. Fossils of dinosaurs are now known from dozens of countries and from every continent, including Antarctica;[4] in life they occupied every ecosystem from mountains to deltas and deserts to forests,[5] and they included in their number the largest terrestrial animals of all time.[6] We have fossils of dinosaurs with their skin and feathers intact,[7] as well as other soft-tissue structures like cockscomb head crests,[8] and even traces of the original patterns and colors of the living animals.[9]

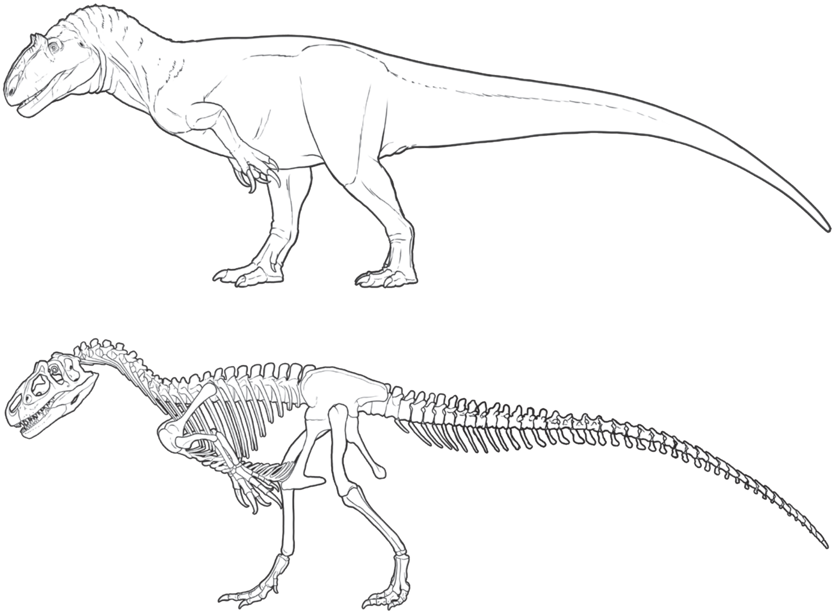

FIGURE 1.1 There is perhaps no such thing as a "typical" dinosaur given their huge range in shape, size, and, undoubtedly, behavior. Here, at least, is an exemplar: the large Late Jurassic theropod *Allosaurus*, by far the most common carnivore in its ecosystem, and both well represented in the fossil record and well studied. Shown are a restored skeleton and a life reconstruction of the animal. Artwork by Gabriel Ugueto.

These discoveries, coupled with two centuries of research, have enabled huge advances in the reconstruction of every aspect of the biology of dinosaurs. These ancient organisms are now firmly established in modern science, though there remain some large gaps and areas of uncertainty in our understanding of these incredible animals.

Origins and Relationships

Dinosaurs are members of the reptilian clade Archosauria that includes modern crocodilians (and their extinct ancestors and relatives), the Mesozoic flying reptiles the pterosaurs, and a number of other groups. (It is increasingly likely that the chelonians—turtles, terrapins, and tortoises—are also archosaurs or their closest relatives, though this is still a subject of academic debate and is not currently certain; for simplicity here they will be excluded from this clade.) The archosaurs are united in the presence of an antorbital fenestra (an opening in the skull between the naris and orbit, though this is secondarily lost in many groups), serrated teeth set in sockets in the jaws, and an upright stance with the limbs held under the body (though as with so many defining features, evolutionary history has modified these in various groups, most notably to give the semi-sprawling posture of modern crocodilians).[10]

Among these various archosaurs were a group of small (under 2 m in total length), bipedal carnivores or omnivores called the dinosauromorphs that ultimately gave rise to the dinosaurs. Sometime in the late part of the Middle Triassic around 240 million years ago,[11] the dinosaurs split from their dinosauromorph ancestors. At this time, there was a single major landmass, Pangea, that was largely hot and dry, although early dinosaurs may have favored the colder regions of this.[12] Inevitably, the early dinosaurs look extremely similar to their nearest relatives, and the exact point of separation and differentiation between the two is uncertain. The genus *Nyasasaurus* from the Middle Triassic of Tanzania, for example, may be either the oldest known dinosaur or the nearest dinosauromorph relative to the dinosaurs,[11] such is the closeness between the two at this point.

Early dinosaurs were small, bipedal carnivores. They were a relatively minor component of the early Late Triassic terrestrial ecosystems; though they diversified and grew in size, it was not until the extinction at the end of the Late Triassic that dinosaurs became the dominant terrestrial group of the Mesozoic.[12] The dinosaurs have long been split into three major clades: the theropods, which were bipedal and predominantly carnivorous and are the ancestors of birds; the sauropodomorphs, which were herbivorous and were long-necked and mostly large; and the ornithischians, which were herbivorous and produced a much greater diversity of body forms than the other groups.[10] The theropods and sauropodomorphs are united into the Saurischia ("lizard-hipped reptiles" because of their anteriorly directed pubis, though derived theropods and birds reverse this) as the sibling taxon to the Ornithischia (figure 1.2), though recently this interpretation has been challenged. Reinterpretation of

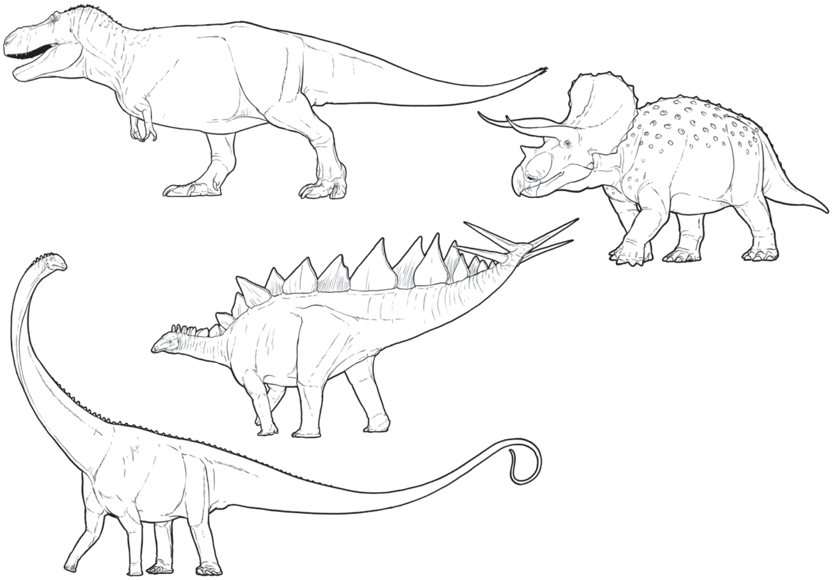

FIGURE 1.2 The major lineages of the dinosaurs, with Theropoda exemplified by *Tyrannosaurus* (top), Sauropodomorpha by *Diplodocus* (bottom), and Ornithischia by *Stegosaurus* (center) and *Triceratops* (right). Artwork by Gabriel Ugueto.

a number of traits coupled with new discoveries have suggested that in fact the theropods may lie with the ornithischians at the expense of the sauropodomorphs.[13] This is controversial, though certainly possible given the apparent absence of ornithischians in the Triassic (although see [14]). The exact nature of this split is largely irrelevant from the point of view of discussions of behavior, though for simplicity and clarity the "traditional" split into Saurischia and Ornithischia is used throughout.

Major Groups

Dinosaurs are known from around 1,500 valid genera, though this number is currently growing by 30 to 50 genera each year and has been for at least a decade. Each of the three main clades is well represented with several hundred taxa, though the theropods are the most numerous of these and the sauropodomorphs the least.

The theropods range from small animals that were perhaps as little as one kilo through to giants like the largest tyrannosaurs that were over 13 m long and weighed perhaps 7 tons or more. Although the basic bipedal form of theropods was essentially universal, they vary enormously in skull size and in the lengths of the neck, legs, and especially the arms.[15] Ancestrally, theropods were carnivorous, with sharp claws on the hands and feet, and all known truly carnivorous dinosaurs are theropods, although some were specialist fish or insect eaters, and members of a number of lineages in the Jurassic and Cretaceous switched to omnivory or even herbivory at various times.[16] Numerous derived theropods are preserved with feathers and also show various birdlike features, such as hollow bones (part of the system of extension of the pulmonary tracts termed air sacs), and extensive research demonstrates that the birds ultimately derived from a group of small theropods in the Middle Jurassic.[17] In particular, numerous small and feathered theropods are known from fossil beds of exceptional preservation, and so the transition to birds is one of the best studied and understood major evolutionary transitions in biology.

The sauropodomorphs are famous for producing the largest terrestrial animals of all time. In the Triassic, the early sauropodomorphs (often termed "prosauropods") were large for terrestrial animals at the time, but were small by the standards of those that came later.[6] The prosauropods were predominantly bipedal (though some were quadrupeds as juveniles) and were characterized by relatively long necks with small heads and a large body, all adaptations for herbivory,[6] though a handful of the very earliest species were probably omnivorous. In the Jurassic, these were replaced by the sauropods, quadrupedal animals that retained the small head, but now typically on an even longer neck,[18] and would go on to produce giants that could exceed 50 tons. Sauropodomorphs also had pneumatic vertebrae invaded by air sacs, and the largest of these animals had numerous vertebrae that were very light considering their size. As a consequence of this, however, large parts of their skeletons are often poorly preserved, although the apneumatic robust and massive limb bones are often found. Sauropods dominated the Jurassic landscapes, though they were rather less common in the Cretaceous, especially in the northern hemisphere.

It would mischaracterize the ornithischians to call them simply "all the other dinosaurs," though they do show considerable variation in general form, unlike the two saurischian lineages. The ornithischians range from small, 1-meter-long bipedal animals up to 15-meter-long giant quadrupeds; there were animals covered in armored plates and spikes, those with giant frills, crests, bosses, and horns on their heads (as well as plenty that were unadorned); and at least some also had feather-like filaments on the body in addition to scales.[19] Again, with the exception of perhaps a few of the earliest taxa which may have been omnivores, these were all herbivorous animals. Notably, we see some extraordinary adaptations to consume and process plants in the ornithischians (compared to the sauropodomorphs, who largely were bulk feeders on as much plant matter as possible), and this included the evolution of a beak at the front of the jaw with teeth behind.[16] Although rare early on, and currently absent in the Triassic, the ornithischians were important components of Jurassic faunas, and in the Cretaceous became the dominant herbivores in most terrestrial ecosystems.

For more information on the major clades within the Theropoda, Sauropodomorpha and Ornithischia see the guide in the Appendix (page 159).

Basic Biology

Although there are some serious gaps in the fossil record for dinosaurs, they appear to have occupied every major terrestrial ecosystem on Earth given their truly global distribution,[4] and this includes everything from sandy deserts[20] to Arctic ice.[21] As with many large modern animals, individual species are found across multiple environments, and there is strong evidence for migration of various dinosaurs;[22] annual migrations would have been the norm for at least some species.

As noted above, the dinosaurs include herbivores, omnivores, and carnivores,[23] but beyond this most general of statements about their feeding ecology, we have strong evidence for both generalist and specialist diets. Among herbivores, there are taxa known to have been selective or bulk feeders, and those that were high or low browsers. Among various theropods, there is evidence for long-distance pursuit predation, carnivory of other large animals, scavenging, piscivory, and insectivory. Evidence for these various patterns of behavior come from numerous sources, such as fossilized coprolites (feces) and regurgitated pellets, fossil stomach contents, tooth shape and wear on teeth, head shape and mouth sizes, and bite traces on bones, among others.[24]

The dinosaur fossil record is sufficient to trace some major evolutionary patterns through their history, and as such we have been able to identify important trends across their 180 million years of evolution. Notably, dinosaurs tended to get bigger over time, producing numerous large lineages, though the transition to birds came from a sustained reduction in size of theropods across tens of millions of years.[12] One other important transition is the repeated shift from bipedality to quadrupediality in various dinosaur lineages,[25] something that is notably seen in the various herbivores, but never (or at least, not yet) in the theropods.

In terms of locomotion, across the huge number of dinosaurs known and the variation in body plans from 1-kg bipedal theropods to >50-ton quadrupedal sauropods, there was a vast range of ability in terms of acceleration, top speed, and agility. Although dinosaurs were fundamentally terrestrial, many, if not all, could probably swim,[26] although few if any seem to have been even close to what might be termed semi-aquatic.[27] At least a few dinosaurs may have climbed trees,[28] and some could dig relatively well.[29] This is, of course, in addition to the flight of not just birds, but also various theropods close to the origins of birds that were at least gliders, and perhaps also included some capable of powered flight.[30]

Numerous dinosaurian taxa are known from mass mortality sites, suggesting that large numbers of individuals died together (see [31]), and there are also many extensive tracksites that show footprints of what are likely to be members of the same species moving and even foraging together (see [32]). Doubtless, many of these taxa were gregarious, or even social, and spent considerable amounts of time living in groups with the potential, at least, for complex social interactions. However, the evidence for sociality in dinosaurs has often been overstated;[33] almost any indication of two skeletons of a species found together has been used at times to infer complex behaviors in a species or even an entire clade.

There is strong evidence at least for sociosexual signals in dinosaurs,[34] so many species were signaling to each other (and to other species) even if they were not habitually living in groups. The most obvious of these signals include the many crests, frills, and horns of various lineages, but also include at least some of the feathers present on theropods, and display may have been an important component of early feather evolution.[34] The exact nature of any display behaviors is all but impossible to determine, though there is strong evidence of some large theropods engaging in ritualistic "scraping" courtships, in which, just as some modern birds do, pairs of animals would scrape the ground with their feet, leaving distinctive marks which have, rather incredibly, been preserved.[35]

Such interactions between dinosaurs would not always be simply about communication, as there is strong evidence of antagonist behavior in dinosaurs, especially between conspecific animals.[36, 37] Various preserved pathologies in fossil bones show that these animals fought one another, leaving serious injuries at times; numerous healed, and occasionally infected, bite marks (tyrannosaurs) and stab wounds (horned dinosaurs) are known. Although harder to diagnose, there is also some evidence for interspecific combat between dinosaurs, in particular for ornithischians fending off predatory theropods (see [38]). In addition to pathologies identified as resulting from combat, dinosaurs also inevitably accumulated injuries from daily living, and show evidence of a variety of deformities and pathological bones, including multiple different afflictions in a single individual.[39] Evidence of specific diseases or infections is harder to determine, though work has progressed in this area recently,[40] and in this light some modern diseases have been tentatively identified in dinosaur fossils[41] (figure 1.3).

As the dominant terrestrial animals for the majority of the Mesozoic, dinosaurs were key components of ancient ecosystems. They

FIGURE 1.3 Life reconstruction of *Tyrannosaurus* with infections in the jaw similar to those seen in modern carnivorous birds, following [41]. Artwork by Gabriel Ugueto.

would have had a profound effect on their local environments, and on the selection pressures on both other dinosaurs and other species. Exact interactions are effectively impossible to determine, but dinosaurs must have put severe browsing pressure on various plants and predation pressures on various animals (dinosaurian and otherwise), and they would have been host to gut bacterial floras, parasites, and so on. Similarly, there are many other aspects of dinosaur biology and behavior that we can infer from the fossil record only with considerable difficulty or have been able to ascertain for only a handful of specimens or species. Dinosaurs must have been competing with some other species for food and water, but which and to what extent is unknown. We know the colors of a handful of individuals (though there was doubtless intraspecific variation and at least in some species, dimorphism, with males and females differing in appearance). Issues like temperature tolerance, division of labor in parental care, water requirements, and so on are essentially unknown, and many might be unknowable (figure 1.4).

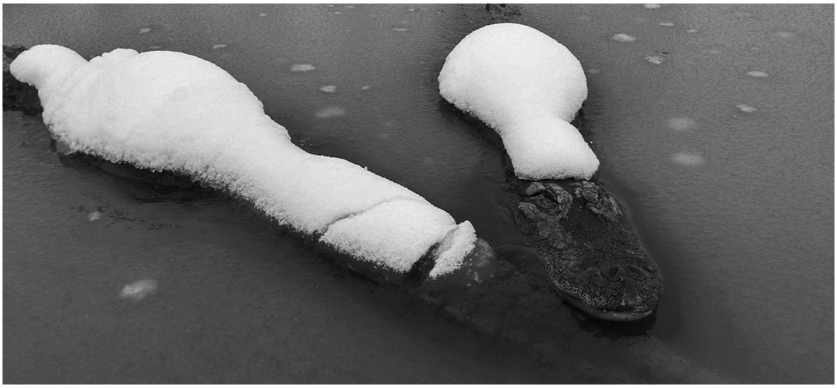

FIGURE 1.4 A relatively recent discovery is the tolerance for freezing temperatures by modern alligators (*Alligator mississippiensis*), suggesting a much greater range of physiology and behavioral options than previously recognized in the group. If such discoveries can be made in well-studied extant taxa, it naturally shows the difficulties of accurately reconstructing the physiology of ancient animals. Photograph courtesy of Jay Young and Jason McDonald.

Reproduction and Growth

Direct evidence of dinosaur sex has not been found, though clearly they must have mated. Although live birth is present in numerous extant reptile groups, no archosaurs are known to have given birth to live young (though it is suspected for one or two fossil clades), and so it is presumed that all dinosaurs laid eggs. Innumerable dinosaur eggs have been discovered, many in organized nests,[42] and even some entire nesting grounds are known. There is evidence for direct brooding by some of the most birdlike dinosaurs, including fossils of animals sitting directly on clutches of eggs.[43]

However, although post-hatching parental care is near-universal in extant archosaurs and was likely very common in dinosaurs, the extent of care, and the manner in which eggs and nests may have been incubated, and especially brooded, is uncertain.[42] The recent discovery of extremely long development times for some dinosaur embryos,[44] however, complicates this issue further, since it seems unlikely that large dinosaurs would have been capable of guarding nests for over three months at a time while still being able to forage and support themselves.

Given the limits of egg sizes, larger species would have grown through multiple orders of magnitude from hatchlings through to full-size adults, a pattern unusual among modern terrestrial vertebrates. In general, dinosaurs grew rapidly at a young age before growth slowed greatly as they reached larger sizes.[45] Unsurprisingly, dinosaurs did not start out as simply small-scale versions of adults, and changes during ontogeny, at least in some cases fairly dramatic,[46–48] would have resulted in their occupying multiple different ontogenetic niches as they grew.[49] Most notably, many structures that likely acted as socio-sexual signals were small in juveniles and only began to develop later in ontogeny, at or close to the onset of sexual maturity.[50] Growth in general was also non-uniform, and high plasticity in growth rates and great variation in size for a given age are seen in some;[51, 52] size is often not a good guide to the maturity of any single specimen.

A major issue for understanding the growth and development of dinosaurs is the general rarity of juvenile animals. Various biases work against the preservation and collection of small and juvenile fossils (they are harder for paleontologists to find, they are more likely to have been eaten by carnivores, and are more likely to decay), but even lineages of giants like sauropods are known from few small individuals. Compounding this problem is the difficulty in correctly identifying the age of a given specimen,[53] leading to conflicts over terms such as "adult," "subadult," "juvenile," and other age classes.[54] Combined with the differential growth trajectories and anatomical changes during ontogeny, this has led to considerable debate and/or confusion over the taxonomic identity of many juvenile dinosaurs (see [48]). Inevitably, therefore, examining the growth and development of dinosaurs is difficult when it is uncertain to which taxa various juvenile specimens may belong.

Brain and Senses

Most important, when considering dinosaur behavior, is their cranial capacity and the sensory input to their brain. Dinosaur brains are not preserved in the fossil record (bar one possible, and very notable, exception[55]). Data on dinosaur brain shape and structure is therefore derived from natural molds of the braincase or endocranium (the bony "inner skull" that encases the brain) or, more commonly now, digital models based on scans of dinosaurian skulls.[56] Since vertebrate brains have a largely stereotypical structure, major elements of the brain—most notably the olfactory bulb, cerebrum, optic lobe, and cerebellum—can be identified in dinosaurs, and give an approximate picture of their relative faculties. Paleontologists are therefore rapidly gaining an increasing understanding of dinosaurian senses.[57]

Dinosaurs lived in a complex world, and the variety of their ecologies inevitably led to a wide range of specializations in their capacity to sense and interact with their world. Dinosaurs were almost certainly tetrachromatic, and as with modern birds, would have been able to see into the UV spectrum.[58] This means that they would have seen a greater range of light frequencies than we do, and so a greater spectrum of colors. Work on the size of the olfactory bulb is also being used to determine the sense of smell in dinosaurs,[59] so it is becoming possible to begin to piece together the sensory systems of single species and the evolutionary history of these senses[60] based on the structures of their brains.

In addition to the components of the brain, the bony skull can also provide excellent evidence for the senses of dinosaurs. Some theropods, for example, had extraordinarily large eyes,[61] and this would have produced high visual acuity and/or the ability to see in low-light conditions. The shape and structure of the inner ears of some theropods have been elucidated and can be used to reconstruct the likely ranges of their hearing. Moreover, this reveals that some had asymmetric ears. This asymmetry allows animals to pinpoint the direction of sounds more effectively, and so would have been important for animals operating in low-light conditions,[62] thus giving further indications of the ecology of species. The presence of numerous complex foramina in the jaws of some large theropods has been used to argue for enhanced facial sensitivity in these species,[63] and although it is unclear quite how this would have been used or how sensitive it would have been, dinosaurs would have certainly had mechanoreceptors in their skin and so would have been receptive to touch.

FIGURE 1.5 Reconstructed brain of a *Triceratops* based on a 3D scan of the endocast. From this, major information about the size and structure of the brain, its component parts, and the inner ear can be determined. Figure courtesy of Ashley Morhardt.

Endocasts of sufficient quality to reconstruct the brain of dinosaurs in detail are rare, although some exceptional cases do exist, and while most are from larger, later species, this includes animals from the Triassic (see [64]) and tiny juveniles (see [65]) (figure 1.5). Studies of dinosaur brains have advanced significantly in recent years thanks to increasing attention being paid to these (see [66] for a recent review). Determining the intellectual capacity of even modern animals is difficult, and work on reptiles has been limited compared to that on birds and mammals, in turn limiting the scope for comparison with dinosaurs. Even so, it is possible to look at issues such as brain volume compared to body size and calculate the encephalization quotient (EQ) of dinosaurs for an estimate of their intelligence. (This can go awry, and the recent suggestion that *Tyrannosaurus* was comparable in intelligence to a chimpanzee has been subsequently squashed—see [67].) The EQ measure is a complex one and is not just a pure comparison of body size to brain volume, but scales with size—and different calculations are typically done for mammals, birds and reptiles.[68]

There are clearly major variations known in dinosaurs, and major uncertainties, too. For example, it has been noted that typical dinosaur braincases may have contained as little as 50 percent true brain tissues,[69] but Martin Brasier and colleagues[55] note that although iguanodontian dinosaurs had been given a reptile EQ range from 0.8–1.5, their specimen of an actual putative brain suggested that a much greater amount of brain tissue in an endocast could raise the EQ to as high as 5. For comparison, reptiles have an EQ from 0.4–2.4, extant crocodilians have an EQ of 0.9–1.1, and avians have a value that is typically 6 or above (though the range here is huge, running from 4 to over 28—all data from [68]), thus potentially putting some dinosaurs on a par with birds rather than reptiles.

Other values are of course known for various dinosaurs, calculated using various methods and differing brain-to-endocavity ratio (BEC) values. A good summary of this is given by David Evans,[70] who also provided some averaged estimates for various clades at the time. Among ornithischians, the hadrosaurs were at 2.8, horned dinosaurs 1.4, and armored dinosaurs 0.7. The Sauropodomorpha were 0.6, with various theropods ranging from 1.6 in allosaurs to 2.2 in tyrannosaurs and even as high as 7.1 and 8.6 for some of the most derived and bird-like clades. Some of these values come from only one or two studies of taxa, and some cover an enormous range of species and indeed an enormous range of values, but they are at least a good starting point. Collectively they suggest that, perhaps unsurprisingly, theropods (especially those closer to birds) were more intelligent than the sauropodomorphs and ornithischians. (See also [71] for a more recent list of dinosaurian taxa with EQ calculations.)

Uncertainty remains, though, as to how to calculate how much brain there is. Research by Daniel Jirak and Jiri Janacek[72] noted that the BEC ratio varies through ontogeny in crocodilians and could be as little as 29 percent in large adult tyrannosaurines, but a full 100 percent in the ancestral tyrannosaurs. In general, some of these lower values seem unlikely, and recent studies have pushed these values up and away from 29%–50% to more like 60%–70% and up (see [73]), so some of the older values given above that favored a 50 percent calculation are likely underestimates. In short, calculating an EQ or

BEC for any dinosaur is not easy. In addition to these varying values, quite how much an EQ tells you about the mental capacities of an animal is also questionable.[74] It is, though, probably safe to say that on average, dinosaurs were more intelligent than many extant reptiles, approximately as intelligent as living crocodilians and more intelligent squamates (lizards and snakes), but often less so than many modern birds.

For all that, brain size mostly simply correlates with body size, and this factor alone explains most variation in animal brain size. Thus any other extrapolations on intelligence immediately become problematic,[75, 76] while inconsistent considerations of variations in neuroanatomy and evolutionary trajectories can lead to misleading assumptions and mistaking noise for signals.[77] In short, dinosaur brains may be a leading clue to dinosaur behavior, but they can also be greatly misleading. The nature of dinosaur intelligence, therefore, and our ability to assay and even test hypotheses about aspects such as tool use (see [78]) are then inevitably challenging, to say the least.

Summary

It may sound trite to say that dinosaurs were real, living animals, but this point seems often overlooked because of the gaps in the fossil record that constrain researchers to focus on what we can work out from skeletons, footprints, and occasionally preserved soft tissues such as muscles and feathers, and far less on matters that are little known or unknown (figure 1.6). While it is difficult or even impossible to determine many aspects of dinosaur biology (or they are known from such limited data that broad inferences remain dubious), it should not be ignored that these were real animals that moved, mated, fed, excreted, competed, fought, died, and evolved. The gaps may be frustrating, but the rest of dinosaurian biology should not be forgotten, even if it is unknown. This brief overview should, though, provide a picture of the basics of dinosaur biology, and provide sufficient introduction to these animals to appreciate their diversity and disparity and to set the scheme for our basic knowledge of their lives.

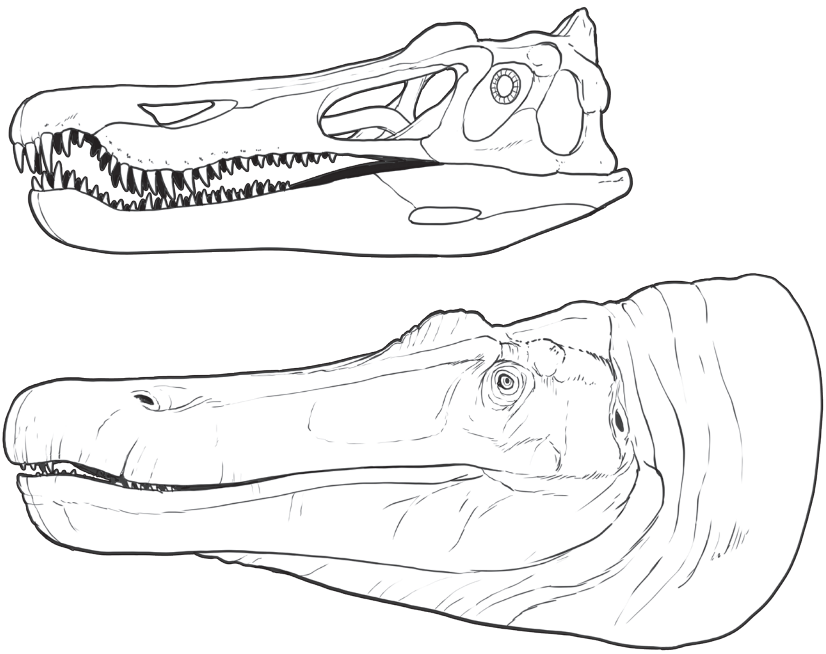

FIGURE 1.6 Skull and life restoration of the Lower Cretaceous British spinosaurid *Baryonyx*. Although known from a well-preserved and relatively complete skull, exactly how it looked and behaved is uncertain, with numerous questions outstanding, as the evidence remains limited. Artwork by Gabriel Ugueto.

INDEX

Page numbers in italics indicate figures and tables.