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An Introduction to Dinosaurs

It is necessary to begin with a straightforward, if not pedantic, question: what is a dinosaur? In popular parlance a dinosaur is often anything that is old, big, or frightening. Any kindergartner could identify *Tyrannosaurus* or *Triceratops* as dinosaurs, and they would be correct, but newspapers will often sloppily use the term "dinosaur" to refer to flying reptiles (pterosaurs), marine reptiles (plesiosaurs, ichthyosaurs, etc.), or even large mammals (such as the woolly mammoth). "Dinosaur" has become a cultural and political idiom as well: out-of-touch politicians or washed-up celebrities are often mockingly ridiculed as "dinosaurs," a synonym for lethargy, obsolescence, and inevitable extinction.

Although the term "dinosaur" is firmly established in the popular lexicon, it is also a scientific term that refers to a specific group of organisms that shared particular anatomical features and lived during a certain period of time. While the popular definition of "dinosaur" is amorphous, the scientific definition is precise. We will get to that definition in a moment, but first it is necessary to review exactly where dinosaurs fit in the tree of life – when they evolved, what they evolved from, and who their closest relatives are – so it is easier to comprehend the explicit distinction between dinosaur and non-dinosaur. Some of the following discussion may seem elementary to more advanced readers, and I intentionally use a more conversational tone in this introduction to appeal to non-specialists and younger students. It is important, however, to set the stage for this book by first painting in broad strokes, before progressing to a more nuanced discussion of dinosaur anatomy, ecology, behavior, and function.

Dinosaurs: A Brief Background

Dinosaurs are one of the best-known, most intensively studied, and most successful groups of tetrapods: animals with a backbone that have limbs with digits (fingers and toes) (Fig. 1.1). Within the tetrapod group, dinosaurs are members of a speciose subgroup of reptiles called the Archosauria, which literally means “ruling reptiles” in Greek (Cope, 1869; Romer, 1956; Carroll, 1988; Benton, 2005) (Figs 1.1–1.6). This is a fitting moniker, as archosaurs have been a major component of terrestrial ecosystems since the early Mesozoic, and for large swaths of time have been ecologically dominant and incredibly diverse (Benton, 1983; Fraser, 2006). Living archosaur subgroups include two major clades, birds and crocodylomorphs, which are among the most familiar and successful groups of extant vertebrates (note that a “clade” refers to a group of animals that includes an ancestor and all of its descendants; Fig. 1.5) (Gauthier, 1986; Sereno, 1991a; Nesbitt, 2011). However, the great majority of archosaur diversity is extinct, and the two main

living groups merely represent two highly aberrant body types (fliers and semiaquatic sprawlers) that were able to endure several mass extinction events that pruned most other lineages on the archosaur family tree. Dinosaurs, without a doubt, are the most familiar of these extinct archosaurs.

The archosaur clade is an ancient group that originated approximately 250 million years ago (Nesbitt, 2003, 2011; Brusatte et al., 2010a, 2011a; Nesbitt et al., 2011). Some of the closest archosaur relatives are known from the Late Permian (e.g. Dilkes, 1998; Nesbitt et al., 2009a), and archosaurs themselves arose within the first few million years after the devastating Permo-Triassic mass extinction, the largest instance of mass death in earth history, estimated to have eradicated 75–95% of all species (Raup, 1979; Stanley and Yang, 1994; Benton, 2003; Erwin, 2006; Clapham et al., 2009). The Permo-Triassic extinction interval was a time of death and destruction on a massive scale, but its aftermath was a time of equally large-scale rebirth: ecosystems were reshuffled, organisms that were once overshadowed had the freedom to flower, and entirely new groups originated and

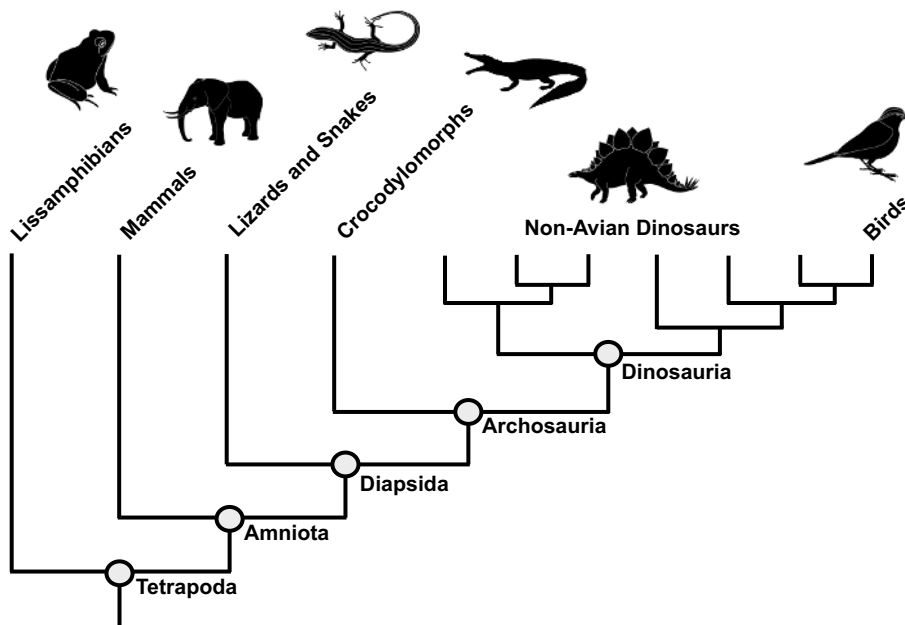


Figure 1.1 A simplified genealogical tree (cladogram) of tetrapods (limbed vertebrates) showing the position of dinosaurs and their closest relatives. Artwork by Simon Powell, University of Bristol.

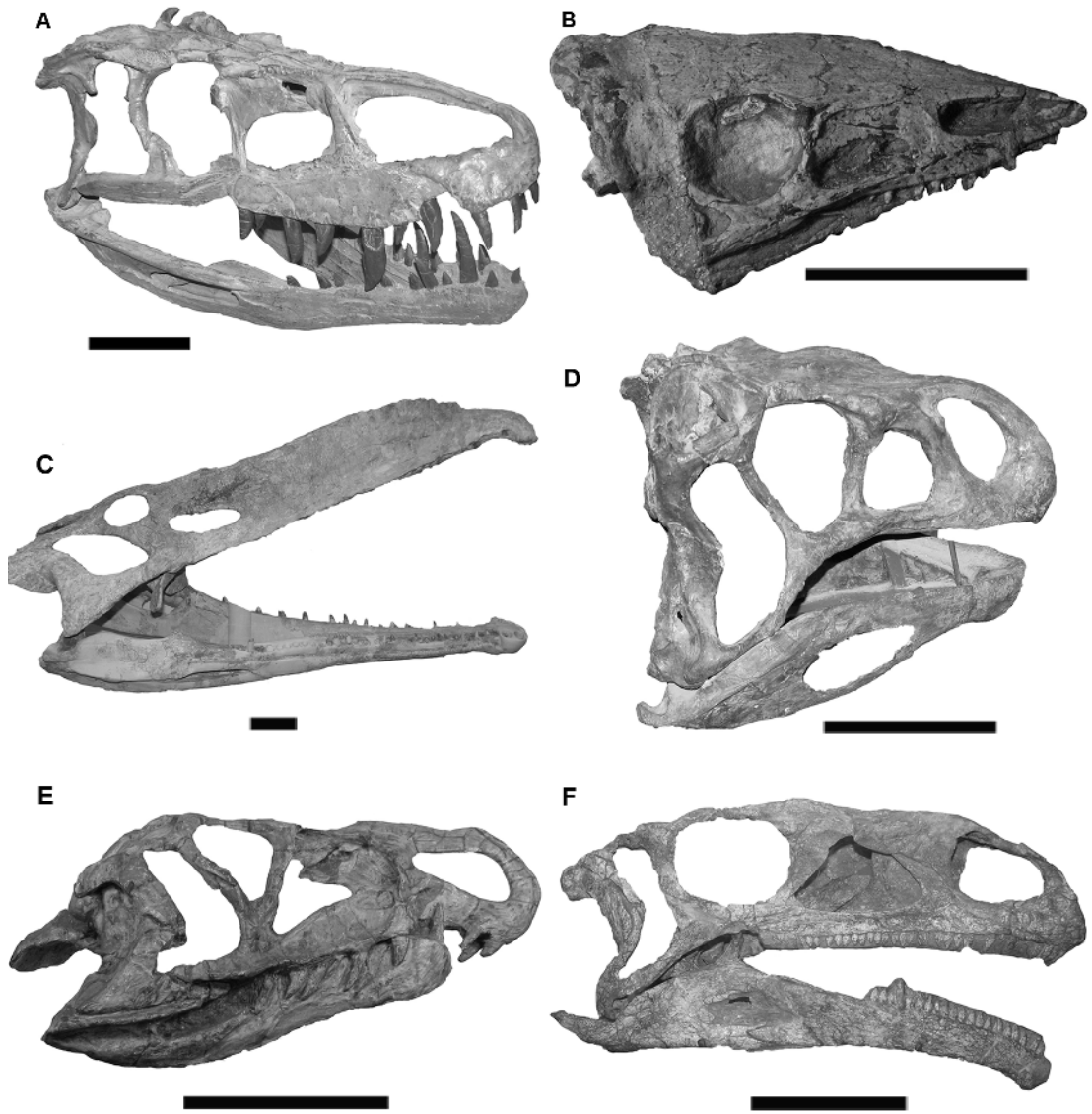


Figure 1.2 A montage of the skulls of various archosaurs, including the rauisuchian crurotarsan *Batrachotomus* (A), the aetosaurian crurotarsan *Aetosaurus* (B), the phytosaurian crurotarsan *Nicrosaurus* (C), the poposauroid crurotarsan *Lotosaurus* (D), the ornithosuchid crurotarsan *Riojasuchus* (E), and the sauropodomorph dinosaur *Plateosaurus* (F).

diversified in the barren, post-extinction landscape (Benton et al., 2004; Sahney and Benton, 2008). Among these entirely new groups were “modern” lineages such as turtles, mammals, lepidosaurs (lizards and their relatives), lissamphibians (frogs and

salamanders), and archosaurs. It is no wonder that the Triassic Period is often called the “birth of modern ecosystems,” as so many of today’s most distinctive and successful clades originated during this time.

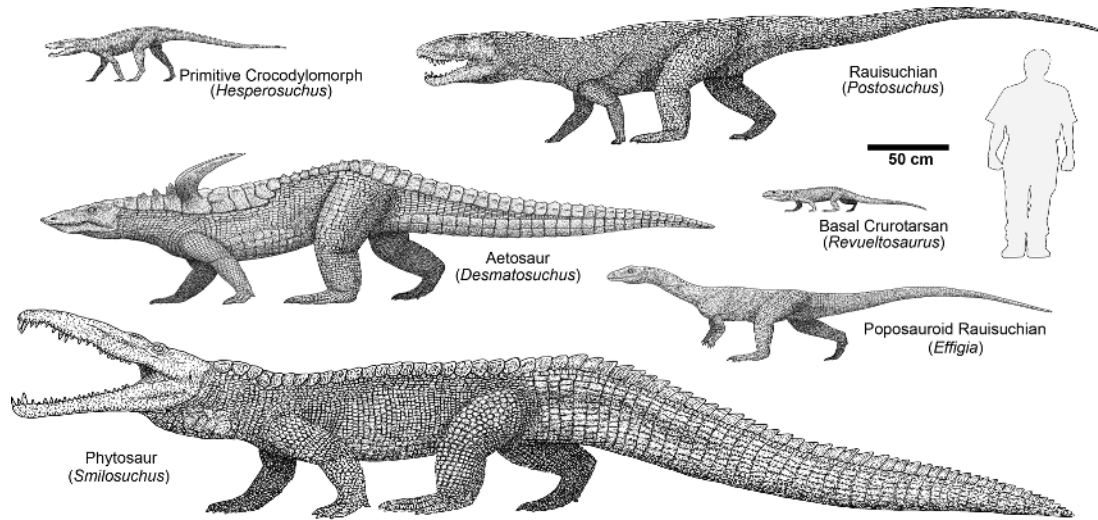


Figure 1.3 A montage of life reconstructions of various crurotarsan (crocodile-line) archosaurs. Illustrations courtesy of Dr Jeff Martz, National Park Service.

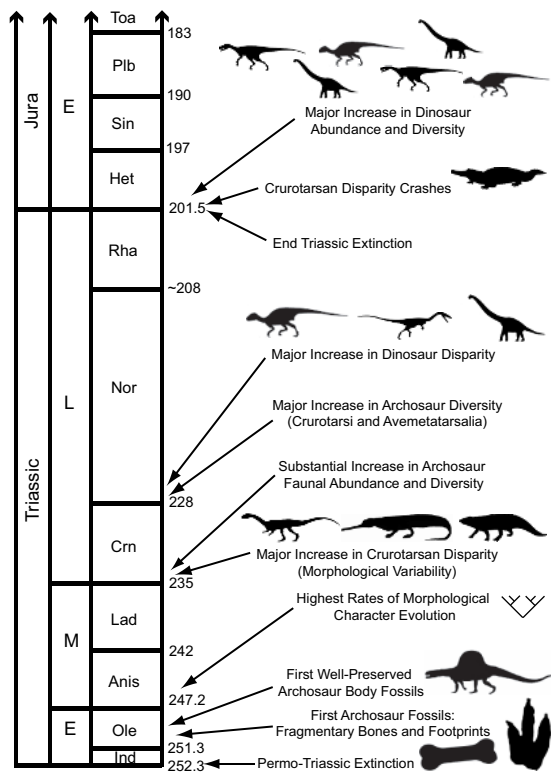


Figure 1.4 A general timeline of important events during the first 70 million years of archosaur evolution during the Triassic and early Jurassic. Image based on illustration in Brusatte et al. (2011a).

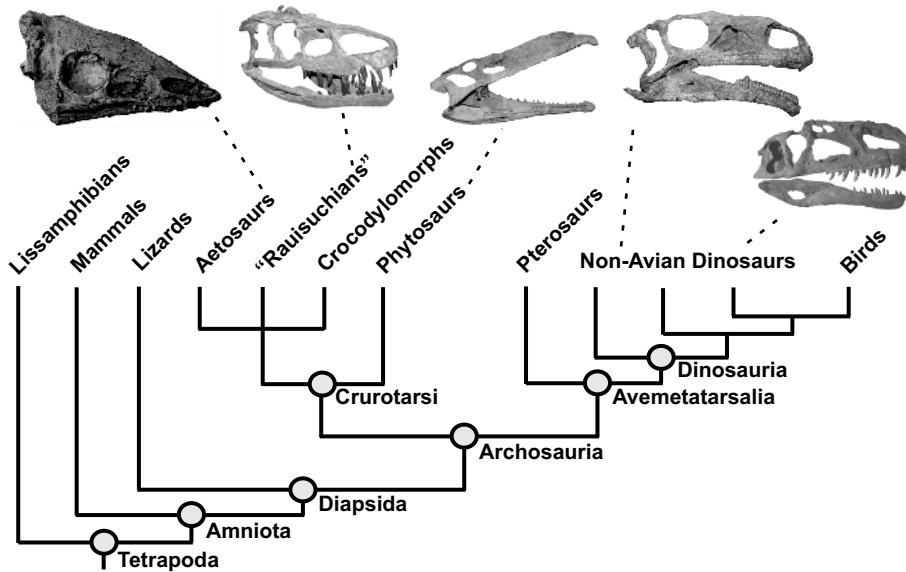


Figure 1.5 A simplified genealogical tree (cladogram) of archosaurs, showing the position of dinosaurs and their closest relatives. Artwork by Simon Powell, University of Bristol.

The archosaur clade diversified rapidly after its origination, as most of the major archosaur subclades and body plans were established by the end of the Early Triassic, a mere 5 million years after the mass extinction (Brusatte et al., 2011b) (Fig. 1.4). The oldest unequivocal archosaur body fossil with a well-constrained age and phylogenetic position is *Xilousuchus*, from the late Olenekian/early Anisian (c.247–248 million years ago) of China

(Nesbitt et al., 2011). This species is a derived member of the “crocodile line” of archosaur phylogeny, which is properly referred to as Crurotarsi (also sometimes called Pseudosuchia). Crurotarsi includes crocodylomorphs and their closest extinct relatives, whereas the other half of the archosaur clade, the “bird-line” group Avemetatarsalia (sometimes also called Ornithodira), includes birds, dinosaurs, and pterosaurs (the familiar flying

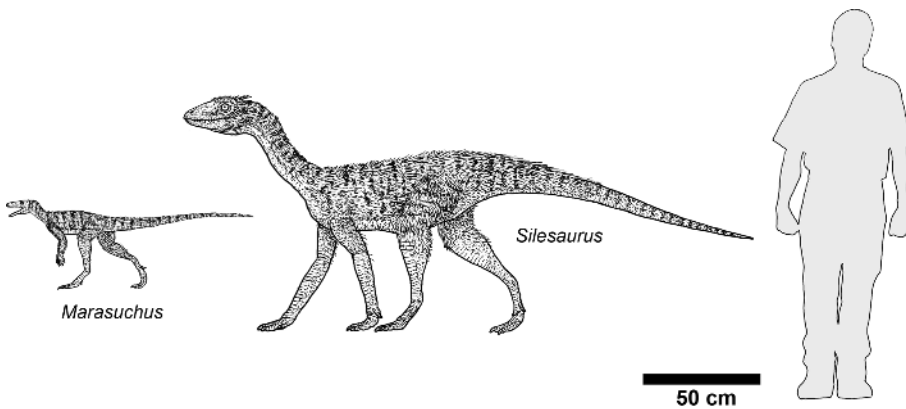


Figure 1.6 Life reconstructions of the basal non-dinosaurian dinosauriforms *Marasuchus* and *Silesaurus*, two of the closest relatives to dinosaurs. Illustrations courtesy of Dr Jeff Martz, National Park Service.

reptiles) (Gauthier, 1986; Sereno, 1991a; Benton, 1999, 2004; Irmis et al., 2007a; Brusatte et al., 2010a, 2011b; Nesbitt, 2011) (Fig. 1.5). Because *Xilousuchus* is a member of the crocodile lineage, then the bird line (but not true birds themselves) must have also been present by approximately 248 million years ago, because these two lineages are each other's closest relative, and the presence of one implies the contemporary existence of the other (see Norell, 1992, 1993 for details of such "ghost lineages," which will be discussed later in the text).

Although the bird lineage, of which dinosaurs are a part, must have been present by the Early Triassic, the first body fossils of truly dinosaur-like animals are not known until the late Anisian (c.243–244 million years ago) (Nesbitt et al., 2010). These fossils do not belong to true dinosaurs, as will become clear below, but are among the handful of closest relatives to dinosaurs, and likely resembled and behaved like their more famous cousins (Fig. 1.6). More properly, they are members of the "dinosaur stem clade," technically known as Dinosauromorpha (Sereno, 1991a; Benton, 1999, 2004;

Ezcurra, 2006; Brusatte et al., 2010a; Nesbitt, 2011). Among the best known species are *Lagerpeton* (Sereno and Arcucci, 1993), *Marasuchus* (Sereno and Arcucci, 1994), *Dromomeron* (Irmis et al., 2007a), *Silesaurus* (Dzik, 2003), and *Asilisaurus* (Nesbitt et al., 2010). Middle to Late Triassic dinosauromorphs were small animals, no bigger than a small dog, and were incredibly rare in their ecosystems. The tiny fragile footprints of some of these close dinosaur cousins are known from several fossils sites in the western United States (Peabody, 1948) and Europe (Haubold, 1999; Ptaszynski, 2000; Klein and Haubold, 2007; Brusatte et al., 2011a), and these are remarkably scarce compared with the footprints of other characteristic Triassic animals, especially crocodile-line archosaurs (Fig. 1.7). It seems therefore that these dinosaur stem taxa were small, rare, only represented by a few species, and overshadowed by other contemporary reptiles. From such a humble beginning came the dinosaurs.

True dinosaurs likely originated some time in the Middle Triassic, although it is difficult to pinpoint the exact time. The first dinosaur body fossils

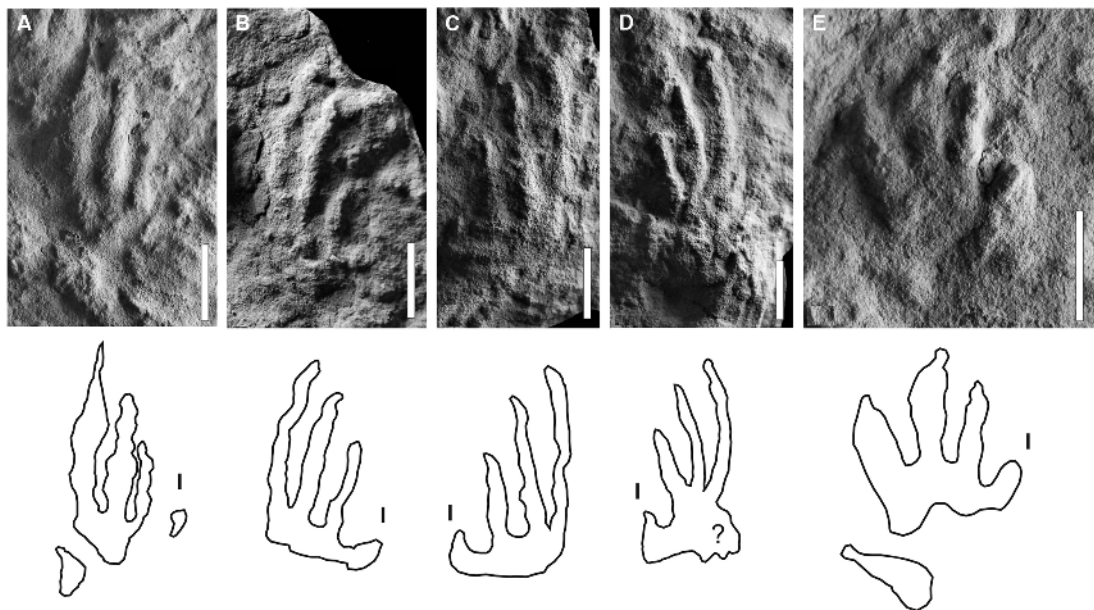


Figure 1.7 A montage of photographs and illustrations of the footprints (A–D) and handprint (E) of a small-bodied quadrupedal dinosauromorph from the Early Triassic of Poland. These fossils are currently the oldest known fossil evidence of the dinosauromorph lineage. Scale bars equal 1 cm. Images by Grzegorz Niedźwiedzki and modified from Brusatte et al. (2011a).

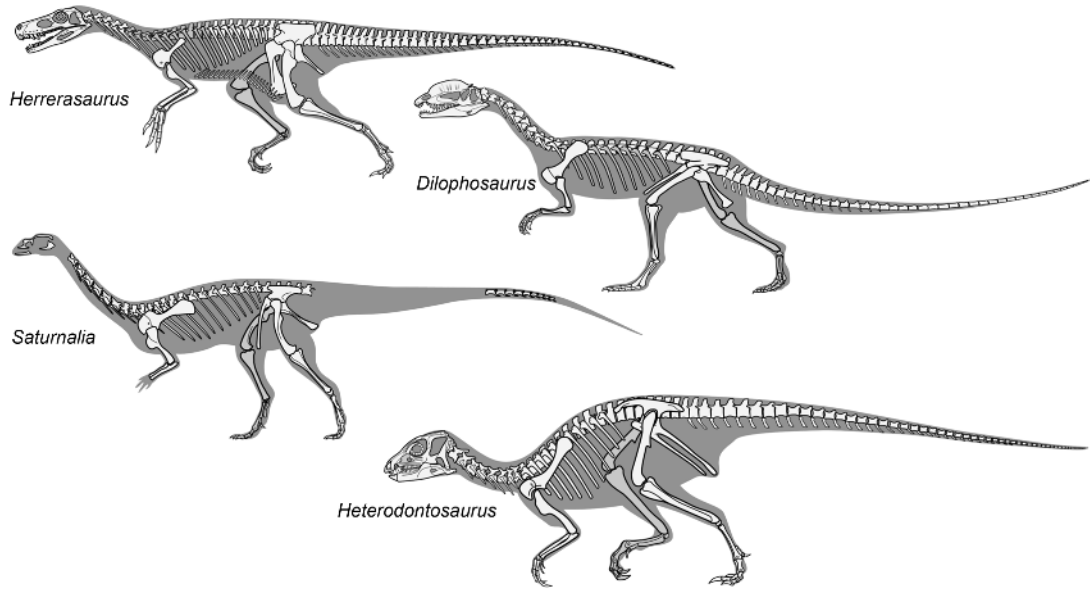


Figure 1.8 Skeletal reconstructions of four early dinosaurs from the Late Triassic to Early Jurassic: the theropod *Herrerasaurus*, the theropod *Dilophosaurus*, the sauropodomorph *Saturnalia*, and the ornithischian *Heterodontosaurus*. Illustrations by Frank Ippolito (American Museum of Natural History) and modified from Brusatte et al. (2010b).

are known from rocks that were deposited in Argentina at approximately the Carnian–Norian boundary (c.228 million years ago) (Rogers et al., 1993; Shipman, 2004; Brusatte et al., 2010b; Ezcurra, 2010a; Langer et al., 2010; Martinez et al., 2011) (Figs 1.8 and 1.9). However, it is almost certain that dinosaurs arose several million years earlier. First, the closest relatives of dinosaurs were clearly present by at least 243 million years ago, as outlined above, and it is reasonable to hypothesize that dinosaurs originated around this time (Nesbitt et al., 2010). Second, there are a number of provocative footprints, which closely match the feet of primitive dinosaurs, that have recently been described from the Ladinian (c.242–235 million years ago) of Europe and South America (Gand and Demathieu, 2005; Melchor and de Valais, 2006). Regardless of the exact timing of dinosaur origins, which will surely become clearer as new fossils are found, it is undeniable that dinosaurs began to diversify quickly once they originated. By the time the first dinosaur body fossils appear in the fossil record, representatives of the three major subgroups of dinosaurs – the carnivorous theropods, long-necked

sauropodomorphs, and herbivorous and often armored or crested ornithischians – are already present (Sereno and Novas, 1992; Sereno et al., 1993; Langer et al., 1999, 2010; Butler et al., 2007; Martinez and Alcober, 2009; Brusatte et al., 2010b; Ezcurra and Brusatte, 2011; Martinez et al., 2011).

Therefore, by the Late Triassic, the Age of Dinosaurs was in full swing, and over the course of the next 50 million years dinosaurs would continue to diversify into new species and body types, before ultimately becoming the dominant mid-to-large size vertebrates in terrestrial ecosystems globally in the Early Jurassic, about 176 million years ago (Benton, 1983; Brusatte et al., 2008a, 2008b, 2010b) (Fig. 1.4). From this point on, throughout the remainder of the Jurassic and the Cretaceous, from approximately 175 to 65 million years ago, dinosaurs truly were “ruling reptiles” in every sense of the phrase. They lived in all corners of the globe, including the Arctic highlands, and reached some of the most stupendous sizes ever seen in land-living animals. Some species developed absurdly long necks, others extravagant horns and armor that would make a medieval

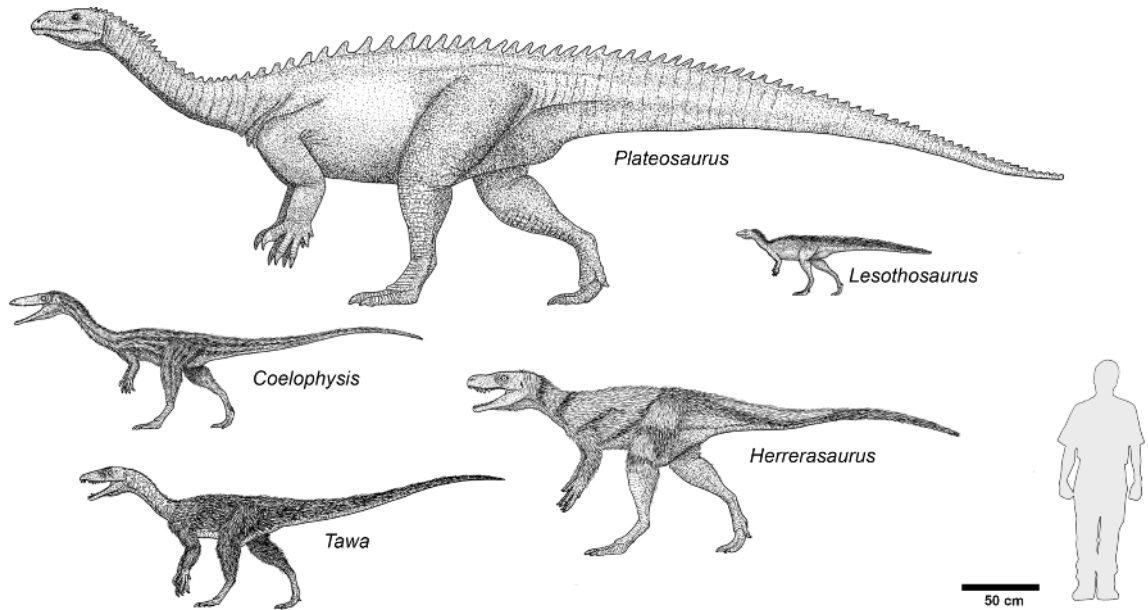


Figure 1.9 Life reconstructions of early dinosaurs from the Late Triassic. Illustrations courtesy of Dr Jeff Martz, National Park Service.

knight blush, and yet others grotesque skulls, longer than an average man is tall and packed with dagger-like teeth, perfect for delivering bone-crunching bites. This fantastic array of dinosaurs – predators and herbivores, dwarves and 50-m long behemoths and all sizes in between – continued to evolve in concert with the slow drift of the continents and the roller-coaster wiggles of climate change, until an unexpected visitor from outer space smashed into the planet 65 million years ago, snuffing out the Age of Dinosaurs and permitting the survival of only one marginal, aberrant dinosaur subgroup: the birds.

The Scientific Definition of Dinosaurs

The above review liberally used terms like “true dinosaur” and “close dinosaur cousin.” Vague terminology like this can often be maddening, and can sadly obstruct communication between scientists. Thankfully, however, there is an explicit definition of what constitutes a dinosaur (the “true dinosaurs”). Dinosaurs are defined by

scientists as “members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus* (the living house sparrow)” (Padian and May, 1993; Sereno, 1998; Sereno et al., 2005). At first this definition may seem confusing, and perhaps even counterintuitive, but in fact it is quite straightforward.

Most modern biologists define groups of organisms, such as dinosaurs or mammals or birds, based on ancestry, not on the possession of certain characteristics (e.g. de Queiroz and Gauthier, 1990, 1992; Sereno, 2005). An animal is a dinosaur if it falls in a certain place on the family tree of life, in this case that group of organisms that includes *Triceratops*, the living sparrow (*Passer*), and all descendants of their common ancestor. This hypothetical common ancestor can be visually traced on a family tree (properly called a cladogram, or a phylogeny) of reptiles: simply find *Triceratops*, then *Passer*, and then trace the branches leading to both species down to their common meeting point (Fig. 1.10). Any species that can also be traced down to this common ancestor – in other words, any species that descended from this ancestor – is by definition a dinosaur.

Phylogenetic definitions may seem confusing, but they can be understood with analogies to our own family histories. Some of my ancestors, for instance, immigrated to the United States from northern Italy. As the story goes, my great grandfather, upon hearing distressing rumors of anti-Italian sentiment in his soon-to-be new homeland, decided to change his surname from the obviously Italian “Brusatti” to the somewhat more ambiguous “Brusatte” when registering as a new citizen. This name change can be thought of as the origin of a new group of organisms, in this case the Brusatte family, and anybody who has descended from my great grandfather is by definition a Brusatte. It doesn’t matter what we look like – whether we are tall, short, fat, thin, or bald – or when or where we live. We are simply Brusattes by definition.

The definition of Dinosauria given above is called a phylogenetic definition, and it is a general definition that can be applied to any cladogram. Clearly, however, this definition needs a phylogeny for context, and it is unintelligible without a cladogram to refer to. The first scientists to study dinosaurs did not define them this way, which is unsurprising given that these pioneering paleontologists were working in a pre-Darwinian world in which evolution (and hence common ancestry) was regarded as heresy. The man who named Dinosauria, Richard Owen (1842), followed the custom of the time and defined dinosaurs as those

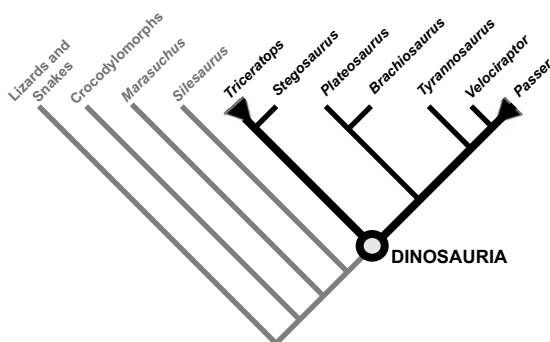


Figure 1.10 A schematic illustration showing how a group (such as Dinosauria) is defined in a phylogenetic sense. Dinosauria is formally defined as “members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus*.” This definition requires a genealogical tree, or phylogeny, to make sense. In this case, locate *Triceratops* and *Passer* on the tree and then trace both branches back to their common ancestral meeting point (denoted by a circle). All species that also descended from this common ancestor are dinosaurs by definition (those species shown in black), whereas other species that fall outside this group are not dinosaurs by definition (those species shown in gray).

animals possessing a certain set of anatomical features, which included various traits relating to body size, posture, and locomotion (see below). Owen saw these features as essential characteristics – an unchangeable blueprint that set dinosaurs apart from other reptiles – but today we simply recognize them as products of common ancestry, as traits that all dinosaurs inherited from that distant ancestor that unites *Triceratops* and *Passer*. These are so-called synapomorphies: shared derived characters – evolutionary novelties – that unite a group on the tree of life.

This clarifies an important point: animals such as dinosaurs are not strictly defined by their anatomical features, but every group on the tree of life possesses a characteristic set of traits inherited from their common ancestor and thus absent in other organisms. These features are said to diagnose dinosaurs, rather than define them. An analogy can be seen in medicine: cancer is defined as a disease in which cells grow uncontrollably (a process), but is diagnosed by symptoms such as headaches, swelling, or abnormal breathing. Doctors never rigidly define a disease based on symptoms, but a certain disease usually has a characteristic set of symptoms, and by noticing and studying these symptoms a doctor can pinpoint the disease that is causing them. Dinosaurs, therefore, are defined based on ancestry, but share a common set of features, and by identifying and studying these features scientists can be sure that a certain specimen or organism is truly a dinosaur.

Characteristic Features of Dinosaurs

With the above semantics out of the way, we can now focus on those features that distinguish dino-

saurians. After all, these anatomical features, and their biological and ecological significance, are much more interesting than the subtleties of cladograms, and the mundane quibbles about whether a certain species did or did not descend from a certain common ancestor. This criticism is not to trivialize phylogenetic definitions – their strength is in their explicitness and stability – but unfortunately tedious debates have raged over whether a certain species is a proper dinosaur or falls just outside of the group defined by *Triceratops* and *Passer*. These academic quarrels can be maddening, because the focus is on a technicality of nomenclature rather than much more illuminating discussions of biology, function, and evolution. And in one sense these debates miss the point, because even if an animal is not quite a dinosaur by definition, it may still have many features common to other dinosaurs, and may have resembled and behaved like true dinosaurs.

A prime example concerns a recently described group of peculiar Middle to Late Triassic archosaurs called the silesaurids. There is no question that these animals were very similar to dinosaurs, as they share several derived features with species that are unequivocally part of the *Triceratops*–*Passer* group. But there is debate over whether they are true dinosaurs: whether they descended from the common ancestor of *Passer* and *Triceratops*, or whether they are the closest relatives of true dinosaurs (i.e., are immediately outside the *Triceratops*–*Passer* group) (Dzik, 2003; Ferigolo and Langer, 2007; Irmis et al., 2007a; Brusatte et al., 2010a; Nesbitt et al., 2010; Nesbitt, 2011). This debate is indeed important for that narrow group of specialists which focuses on reptile phylogeny, and does have important ramifications for understanding patterns of character evolution, but is of little concern even for most dinosaur paleontologists. Therefore, in this section, I take a more catholic view of dinosaurs and focus not only on those features that precisely diagnose Dinosauria, but also features that are seen in a handful of the closest dinosaur relatives, which are not dinosaurs by definition but likely were very similar to dinosaurs in a biological sense. Throughout the remainder of this book the focus will be on true dinosaurs, but close dinosaur cousins (“stem dinosaurs”) will sometimes be discussed for context or to flesh out exploration of biology, function, or large-scale evolutionary patterns.

When outlining features common to all dinosaurs, it is wise to begin with some historical background. Dinosauria was first established as a distinctive group by Owen (1842), who recognized that three extinct genera of large reptiles – *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus* – shared several unusual features that were unknown in other reptiles, both living and extinct. These included features of the hips, limbs, and body posture, which generally indicated that dinosaurs had a more upright stance than other reptiles (see review in Cadbury, 2002). Discoveries of new fossils continued at a frenzied pace during the remainder of the 19th century, and by the dawn of the 20th century paleontologists had recognized that not only did all known dinosaurs share many features – including several additional hallmarks revealed by the new finds – but that they could be divided into two major subgroups: the “lizard-hipped” saurischians, which include theropods and sauropodomorphs, and the “bird-hipped” ornithischians (Seeley, 1887). These groups are recognized to this day as the two major subdivisions of dinosaurs. Over the next several decades, however, scientists gradually changed their conception of dinosaurs. For much of the 20th century, paleontologists considered saurischians and ornithischians to be separate lineages, which independently diverged long ago from separate “thecondont” (primitive archosaur) ancestors. Therefore, all the features common to saurischians and ornithischians were not seen as the product of common ancestry – characteristics that united all dinosaurs relative to other animals – but rather as insignificant nuances of the anatomy that evolved in parallel in both groups. The very idea of a single, distinctive dinosaur group had fallen out of favor.

This view began to change in the mid 1970s and within a few years was widely dismissed as outdated and incorrect. A new generation of paleontologists, motivated by new discoveries and conceptual advances, resurrected Owen’s (1842) original notion of a single, unique group of Mesozoic reptiles – Dinosauria – that could be distinguished from all other organisms based on their possession of shared derived characters. This revolution in thinking was driven by two major factors. First, if saurischians and ornithischians were descended from separate ancestors, then the most primitive members of both groups should look very different from each other.

However, as new fossil finds of early saurischians and ornithischians were discovered in Triassic rocks across the world, this prediction was utterly rejected (Welles, 1954; Crompton and Charig, 1962; Reig, 1963; Colbert, 1970). Instead, primitive theropods, sauropodomorphs, and ornithischians were remarkably similar to each other, exactly as would be predicted if they diverged from a single common ancestor. Second, the advent of an explicit, numerical methodology for inferring genealogical relationships—cladistics—swept through the field of biology in the 1970s and 1980s (Hennig, 1965, 1966). Cladistic principles hold that a lengthy roster of shared anatomical features between two groups is much more likely to indicate close relationship than parallel evolution, and it would take quite a bit of special pleading to retain saurischians and ornithischians as separate entities that evolved so many eerily similar features independent of each other.

It was more plausible, therefore, that the myriad similarities between saurischians and ornithischians meant that these two groups descended from a common ancestor, and could be united as a single, larger group: Dinosauria. This view was persuasively articulated in a seminal 1974 paper by Robert Bakker and Peter Galton. In doing so, Bakker and Galton (1974: 168–169) highlighted a surprisingly long list of characteristic dinosaur features, many of which had been revealed by new discoveries during that long dark period when saurischians and ornithischians were assumed to be nothing but distant, convergent relatives. These features included an upright and fully erect posture, an enlarged deltopectoral crest on the humerus (which anchors large shoulder and chest muscles), a perforated hip socket for articulation with the head of the femur, a well-developed fourth trochanter and lesser trochanter on the femur (which anchor hindlimb muscles), and an ankle joint in which the proximal tarsals (astragalus and calcaneum) were “fixed immovably on the ends of the tibia and fibula [resulting in a] simple unidirectional hinge between the astragalus–calcaneum and distal tarsals.” As is evident, many of these features have to do with the posture, strength, and range of motion of the forelimbs and hindlimbs: compared with their closest relatives, dinosaurs had a more upright stance and stronger, more muscular legs, which moved in a more restricted fore–

aft direction, ideal for fast running and keen balance. Importantly, Bakker and Galton (1974) acutely recognized that many of these hallmark dinosaur features are also present in living birds, and thus support a close relationship between dinosaurs and birds. This was not a new idea, but one that was rapidly gaining traction in the field at the time. It had been proposed as early as the 1860s (Huxley, 1868, 1870a, 1870b), but had largely been ignored until the pioneering studies of John Ostrom in the 1960s and 1970s (Ostrom, 1969, 1973).

It is a great testament to the work of Bakker and Galton (1974) that many of the features they described as dinosaur trademarks are still considered valid today. This is no small feat, as the exact characteristics that diagnose a clade on the tree of life, such as Dinosauria, are constantly changing as new fossils are discovered and ideas are reinterpreted. At one point in time a certain character, such as a large deltopectoral crest, may only be known in one group, such as dinosaurs. It is easy to envision, however, how a single new fossil discovery, such as a new close dinosaur cousin with a large crest, could reveal that this feature is more widely distributed. This has, in fact, happened to several of Bakker and Galton’s diagnostic characters but, importantly, most of the features they described are still only known in dinosaurs and a handful of their closest cousins, and their general argument that dinosaurs are distinguished from other reptiles by their posture and hindlimb anatomy still stands. But perhaps most important of all, Bakker and Galton’s (1974) paper was a catalyst for future studies, and authors continue to actively debate exactly what characters unite dinosaurs.

Over the past four decades, beginning with Bakker and Galton’s (1974) paper, approximately 50 characters have been identified as potential dinosaur synapomorphies. Many of these have emerged from detailed, higher-level cladistic analyses of archosaur phylogeny (Benton, 1984, 1999, 2004; Gauthier, 1986; Benton and Clark, 1988; Novas, 1989, 1992, 1996; Sereno, 1991a, 1999; Sereno and Novas, 1994; Fraser et al., 2002; Ezcurra, 2006, 2010a; Langer and Benton, 2006; Irmis et al., 2007a; Nesbitt et al., 2009b, 2010; Brusatte et al., 2010a; Martinez et al., 2011; Nesbitt, 2011). Of course, different phylogenies may imply different patterns of character evolution, and the exact

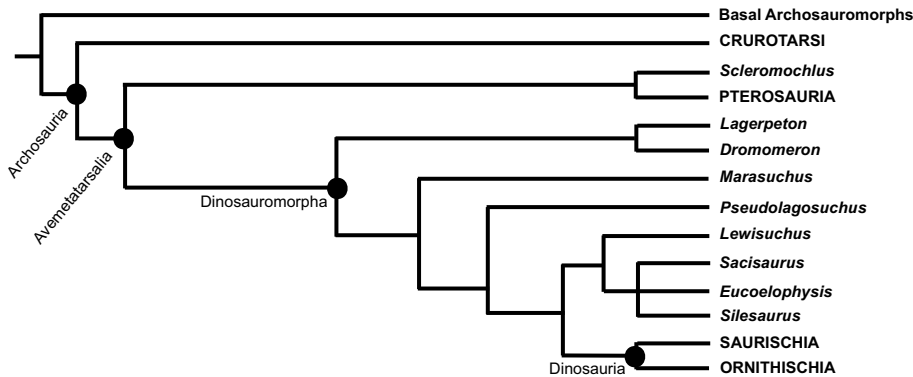


Figure 1.11 The genealogical relationships of “bird-line” archosaurs (Avemetatarsalia) based on the phylogenetic analysis of Brusatte et al. (2010a).

characters that diagnose Dinosauria often differ depending on the phylogeny being considered. To avoid the risk of getting mired in a tedious catalogue of different phylogenies, the discussion here uses the recent phylogeny of Brusatte et al. (2010a) and the review of dinosaur origins by Brusatte et al. (2010b) as guides. This phylogenetic context is graphically shown in Fig. 1.11.

Taking at first a reductionist view, seven features are currently recognized as unequivocal synapomorphies of Dinosauria. In other words, these characters are only known in true dinosaurs, and are absent even in the closest dinosaur cousins. These bona fide dinosaur hallmarks are known from across the skeleton, and include the following.

1 Temporal musculature that extends anteriorly onto the skull roof. The mandibular adductors (temporal muscles) are among the fundamental muscles of mastication in vertebrates: when they contract they elevate the lower jaw, allowing the mouth to close. Dinosaurs have an unusually large and extensive set of mandibular adductor muscles, which expand anteriorly onto the top of the skull (see Holliday, 2009 for review). Although muscle tissue is rarely preserved in dinosaur fossils, the location and size of the mandibular adductors can be deduced based on the position and size of a smooth fossa on the skull roof, to which these muscles attached. In most reptiles, including most archosaurs and even close dinosaur kin such as *Silesaurus*, the

fossa is restricted to the parietal bone, and is only expressed as a narrow depression in front of the supratemporal fenestra (one of the main diapsid skull openings, which will be described in more detail below) (Dzik, 2003). In dinosaurs, however, the fossa extends further anteriorly onto the frontal bone, and is a much deeper and more discrete depression (Fig. 1.12A,B). This indicates that the mandibular adductor muscles were larger and more powerful in dinosaurs than in close relatives, and probably implies that dinosaurs had a stronger bite than most other archosaurs.

2 Posterior process of the jugal bifurcates to articulate with the quadratojugal. The jugal bone forms the lateral “cheek” region of the skull underneath the eye and articulates posteriorly with the quadratojugal bone. Together these two bones define the ventral margin of the lateral temporal fenestra, the second of the two main diapsid skull openings. In all archosaurs other than dinosaurs, including *Silesaurus*, the posterior process of the jugal tapers and meets the quadratojugal at a simple overlapping joint (Dzik and Sulej, 2007). In dinosaurs, by contrast, the posterior process bifurcates into two prongs, which clasp the anterior process of the quadratojugal (Fig. 1.12C,D). The biological significance of these two conditions is uncertain, but it is likely that dinosaurs had a stronger jugal–quadratojugal articulation, and this may be functionally associated with their larger mandibular adductor musculature and inferred stronger bite force.

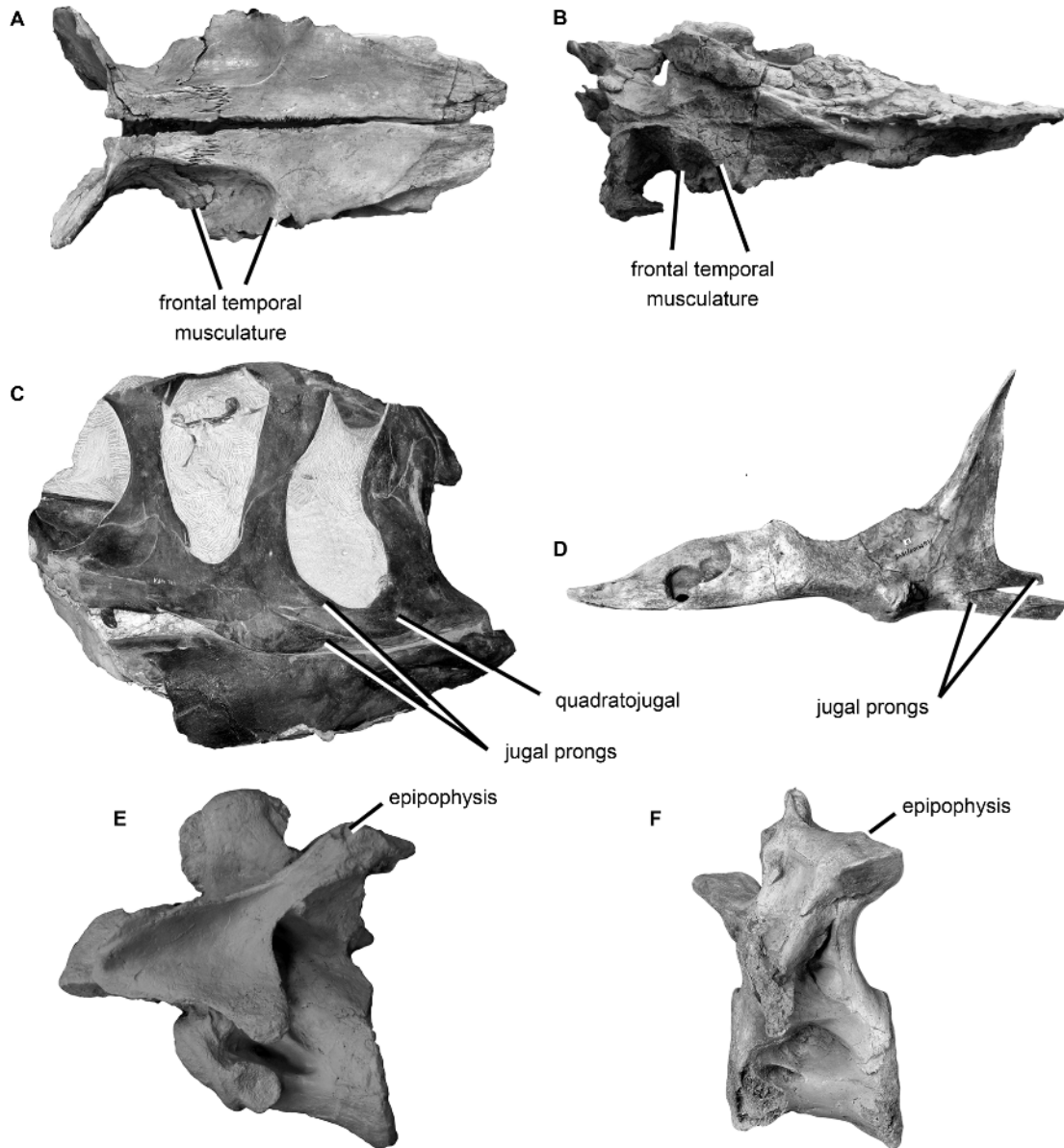


Figure 1.12 Distinctive features of dinosaurs. (A, B) Portions of the skulls of two theropod dinosaurs in dorsal view (*Dubreuillosaurus* and *Guanlong*) showing the anterior extension of the fossa for the temporal jaw muscles onto the frontal. (C, D) The bifurcated posterior process of the jugal, for articulation with the quadratojugal (jugal and quadratojugal of the theropod *Allosaurus* shown in articulation in C, only the jugal of the tyrannosaurid theropod *Alioramus* shown in D). (E, F) The epiphysis, a bump-like projection of bone on the dorsal surface of the postzygapophysis of the cervical vertebrae of the large theropod *Aerosteon* (E) and the tyrannosaurid *Alioramus* (F). Photographs (D) and (F) by Mick Ellison; image (E) courtesy of Dr Roger Benson.

3 Epiphyses on the cervical vertebrae. Epiphyses are projections of bone, which range from small mounds to more elaborate flanges, that protrude from the dorsal surfaces of the postzygapophyses of the cervical vertebrae (those parts of the vertebra that articulate with the following vertebra) (Fig. 1.12E,F). These are present in all dinosaurs, but not close relatives such as *Marasuchus* (Serenó and Arcucci, 1994) or *Silesaurus* (Dzik, 2003; Piechowski and Dzik, 2010). Various muscles of the neck would have attached to these structures, as well as some muscles that may have extended onto the back and thorax (Tsuihiji, 2005; Snively and Russell, 2007a, 2007b). The primary function of these muscles is to extend, rotate, and reinforce the neck and back. Although these muscles would have been present in other archosaurs, the epiphyses in dinosaurs would have increased their available attachment area, perhaps indicating that these muscles were stronger or capable of a greater range of motion (see Snively and Russell 2007a, 2007b for functional considerations).

4 Elongate deltopectoral crest. The deltopectoral crest is a ridge of bone on the humerus, the upper bone of the arm, that anchors the deltoid muscle of the shoulder and the pectoralis muscle of the chest (Coombs, 1978a; Nicholls and Russell, 1985; Dilkes, 2000; Jasinowski et al., 2006). Its primary purpose is to support the latter muscle, whose contraction brings the arm closer to the body. A discrete deltopectoral crest is present in many animals, but it is especially prominent and elongate in dinosaurs, in which it is expressed as an offset flange that extends for 30–40% of the length of the entire humerus (Fig. 1.13). In most other archosaurs, including close dinosaurian relatives such as *Marasuchus* (Serenó and Arcucci, 1994) and *Silesaurus* (Dzik, 2003), the deltopectoral crest is shorter, less offset, and restricted to the proximal portion of the humerus. The large deltopectoral crest of dinosaurs indicates that forelimb motion, particularly adduction towards the body, was especially powerful.

5 Open acetabulum in the pelvis. The acetabulum is the joint surface on the pelvis that articulates with the femur (thigh bone). In humans this is a ball-and-socket joint: the globular head of the femur fits into a deep depression on the pelvis.

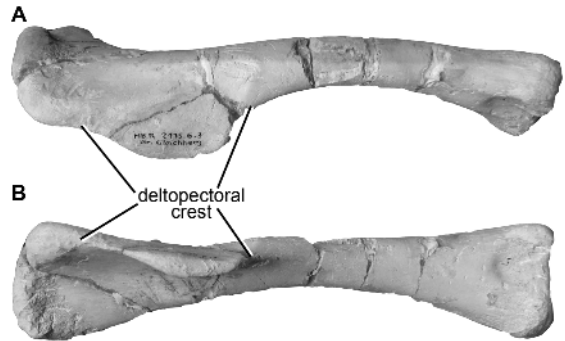


Figure 1.13 Distinctive features of dinosaurs. The humerus of the Late Triassic theropod *Liliensternus* in lateral (A) and anterior (B) views showing the expanded deltopectoral crest.

A similar condition, although with a much shallower socket and a less spherical head of the femur, is present in most reptiles, including most archosaurs. In these animals, the acetabulum is always a discrete socket, which is backed by a medial wall of bone. Dinosaurs, by contrast, have a very different morphology (Fig. 1.14). In all primitive dinosaurs, and most species of more derived dinosaurs, the acetabulum is “open” like a window, because there is no medial wall. This condition is readily apparent in even fragmentary fossils, as a concave ventral margin of the ilium (the most dorsal of the three pelvis bones) is a surefire hallmark of an open acetabulum. The closest relatives of dinosaurs, including *Marasuchus* and *Silesaurus*, have a ventral ilium that is essentially straight, but punctuated by a small concave divot (Serenó and Arcucci, 1994; Dzik, 2003). This is often referred to as an “incipiently open” acetabulum, and is hypothesized to be a transitional morphology that was later elaborated into the fully open condition of dinosaurs.

The opened and closed acetabular morphologies have clear functional significance (Fig. 1.15). Many reptiles, including primitive archosaurs, have a sprawling posture. In these sprawling forms, of which crocodiles are a prime example, the femur is angled outwards to a near horizontal inclination, and during locomotion the full weight of the body is transmitted medially, directly between the femur and the medial wall of the acetabulum. Therefore, it is no surprise that

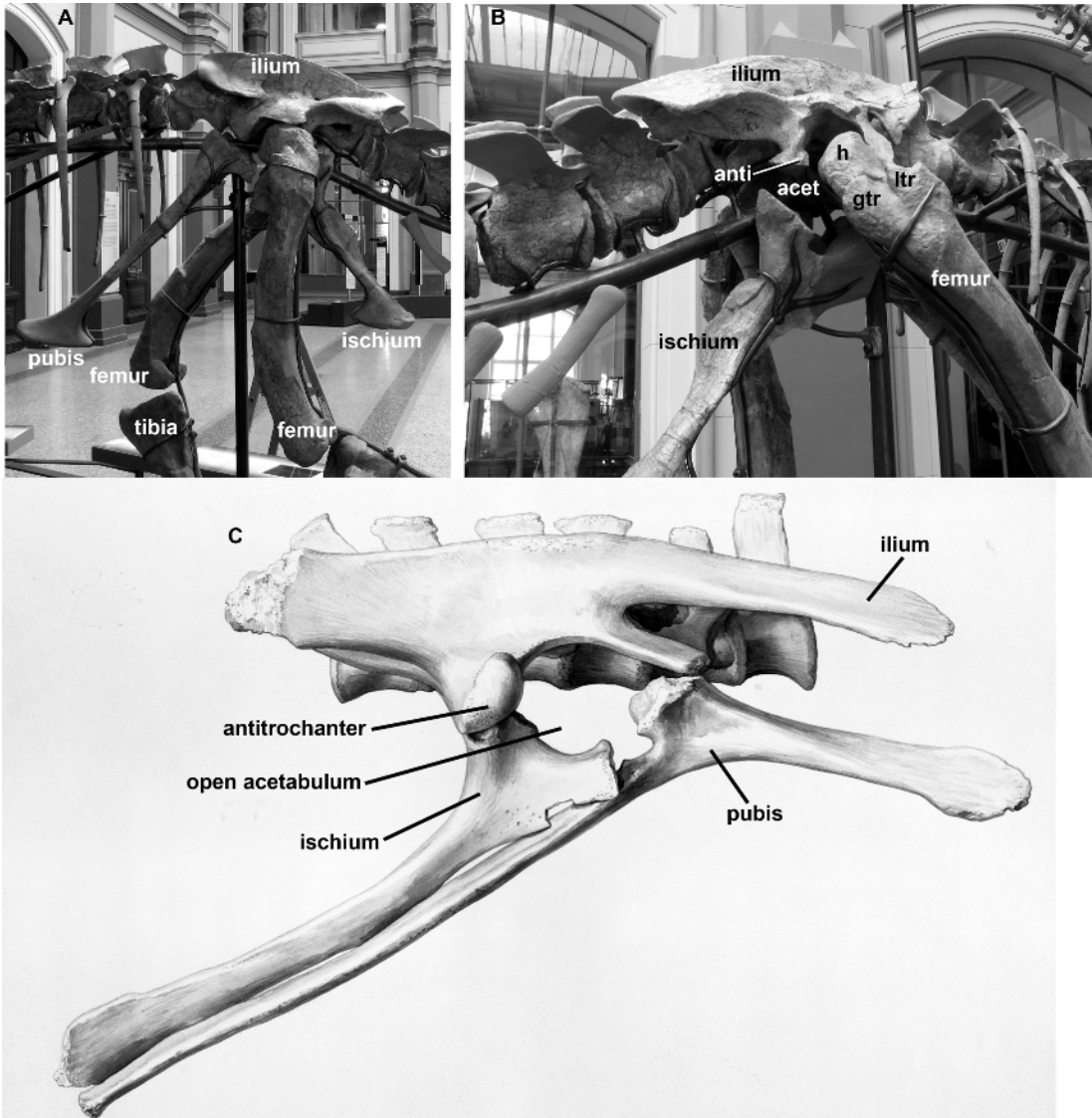


Figure 1.14 Distinctive features of dinosaurs. (A, B) The pelvis of the basal theropod *Elaphrosaurus* in left lateral (A) and oblique right lateral/posterior (B) views showing the articulation of the various bones of the pelvis and the distinctive open acetabulum of dinosaurs. (C) The articulated pelvis of the ornithischian dinosaur *Thecelosaurus* showing the open acetabulum and antitrochanter. Image (C) courtesy of the American Museum of Natural History Library (image #338613). acet, acetabulum; anti, antitrochanter; gtr, greater trochanter; h, head; ltr, lesser trochanter.

the acetabulum has a bony medial wall to provide reinforcement and dissipate stress. Dinosaurs and close relatives, however, have a more upright posture in which the hindlimbs are positioned directly underneath the body. This is facilitated

by a modified femur, which has a head offset approximately 90° from the shaft, thus allowing the shaft to reposition itself in a vertical orientation (Fig. 1.15). As a result, the brunt of the body weight is transmitted between the top of the

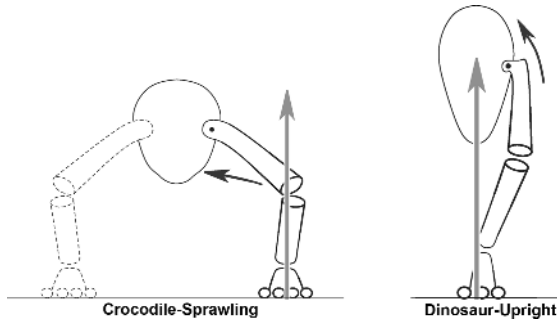


Figure 1.15 Schematic of force vectors in a sprawling animal (a crocodile) and an upright-walking dinosaur. The gray arrows indicate the major forces created when the foot impacts the ground during locomotion and the black arrows indicate the direction that this force is transmitted within the body of the animal (between the femur and pelvis). Note that the main internal force in sprawling animals is directed inward, explaining the bony medial wall of the acetabulum (used to dissipate stress), whereas that of the upright-walking dinosaur is directed mostly upward, explaining why a bony medial wall is not necessary to dissipate stress in these animals (but a robust lip of bone above the acetabulum is necessary to dissipate stress). Modified from Hutchinson and Gatesy (2000). Used with permission from the Paleontological Society.

femur and only the very top surface of the acetabulum, and is not deflected medially into the acetabulum itself. This likely explains why the bony wall, so important for stress reduction in sprawling taxa, is absent in dinosaurs. It also explains why, in comparison to crocodiles and other sprawling taxa, dinosaurs and their closest upright-walking relatives have a robust lip of bone along the top of the acetabulum. And, perhaps most reaffirming, this explains why a handful of aberrant crocodile-line archosaurs that stood fully upright in a dinosaur-like fashion, such as *Effigia* (Nesbitt and Norell, 2006) and *Poposaurus* (Weinbaum and Hungerbühler, 2007; Schachner et al., 2011a), have an almost identical open acetabulum in their pelvis.

- 6 Fourth trochanter of the femur asymmetrical. The fourth trochanter is a ridge on the posterior surface of the femur and is present in all archosaurs. It anchors the caudofemoralis musculature, a large set of muscles that extends from the

tail to the femur and primarily acts to retract, or pull back, the leg during locomotion. Many archosaurs have either a subtle trochanter, indicating weak caudofemoral muscles, or a symmetrical and rounded trochanter. Dinosaurs, on the other hand, possess an asymmetrical crest-like trochanter in which the more distal portion of the crest is expanded relative to the proximal portion (Fig. 1.16D). This asymmetry is best seen in lateral or medial views, where it is apparent that the distal part of the trochanter forms a steeper angle to the femoral shaft than the more proximal trochanter. The functional significance of an asymmetrical, as opposed to symmetrical, fourth trochanter is unclear. In general, it is hypothesized that the large trochanters of many archosaurs, including dinosaurs and their closest relatives, were related to more powerful and efficient limb motions, in comparison to other species with delicate trochanters (Gatesy, 1990; Farlow et al., 2000).

- 7 Articular facet for the fibula occupies less than 30% of the width of the astragalus. The astragalus and calcaneum are the two proximal tarsal bones in archosaurs, and they play an integral role in hindlimb motion by forming the primary articulation between the lower leg (tibia and fibula bones) and the foot (Figs 1.17 and 1.18). In crocodile-line archosaurs, as well as many other reptiles, the astragalus and calcaneum are approximately the same size, and the primary line of motion in the ankle is between these two bones, which rotate against each other and fit together like a peg and socket (Cruickshank and Benton, 1985; Sereno and Arcucci, 1990; Sereno, 1991a). This suite of features is generally referred to as a “rotary joint” or a “crurotarsal joint” (Fig. 1.18A,B).

However, dinosaurs and their closest relatives are immediately recognized by a modified condition, in which the astragalus is much larger than the calcaneum (Fig. 1.18C). In these taxa, the astragalus is firmly braced against both the calcaneum and the tibia and fibula, and these four bones essentially form a single functional complex with no rotary motion between any of the individual elements (Fig. 1.17). Most strikingly, the astragalus has a long, thin, tongue-like flange called the ascending process that sits

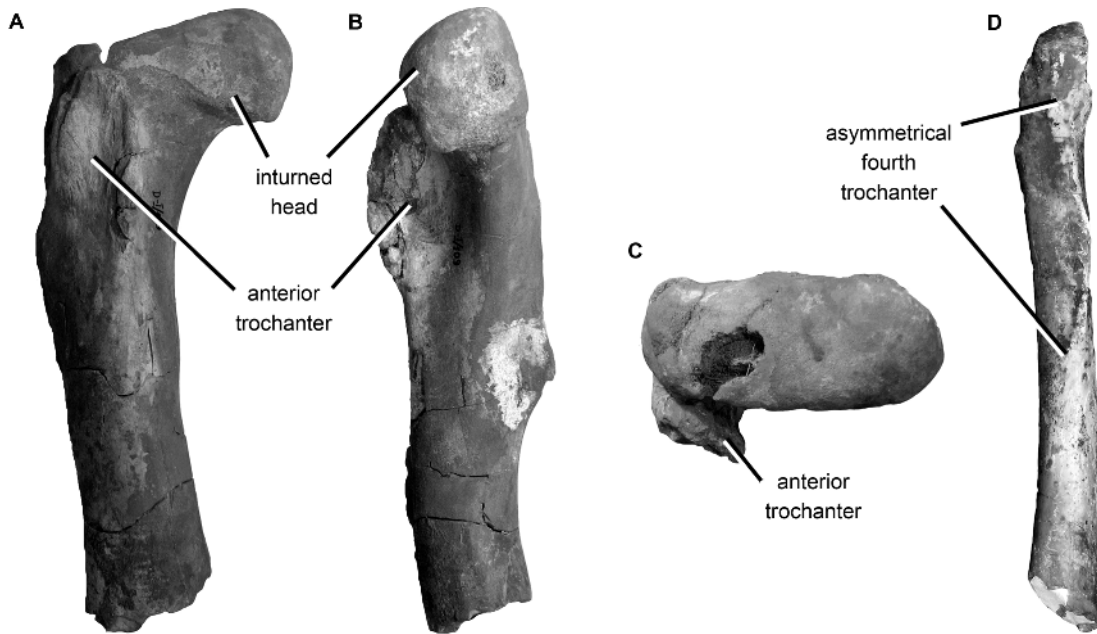


Figure 1.16 Distinctive features of dinosaurs. The left femur of the tyrannosaurid theropod *Tarbosaurus* in anterior (A), medial (B), and proximal (C) views illustrating the diagnostic inturned femoral head and anterior trochanter of dinosaurs. (D) The left femur of the small theropod *Miragaia* in posterior view illustrating the asymmetrical fourth trochanter of dinosaurs.

against the anterior surface of the distal tibia, firmly uniting the two bones. As a result, the primary line of motion is between the leg plus proximal tarsals complex and the foot itself. This is the so-called “hinge joint,” or “mesotarsal” condition of bird-line archosaurs, which clearly differs from the crurotarsal condition of crocodile-line archosaurs.

Although these general ankle types – crurotarsal versus mesotarsal – distinguish crocodile-line archosaurs from bird-line archosaurs, true dinosaurs do have a further unique condition of the ankle that even mesotarsal “stem dinosaurs” such as *Silesaurus* do not possess. In dinosaurs, the fibula makes only a restricted contact with the astragalus, such that the smooth articular facet for the fibula on the astragalus is less than 30% of the width of the astragalus (Fig. 1.17B). In functional terms, this means that the fibula of dinosaurs is reduced and the tibia is the dominant bone of the lower leg. This probably relates to the general dinosaurian condition of upright

posture and fast locomotion, as a limb can move faster and more efficiently as a simpler structure, with less range of motion between individual bones and one dominant bone to the expense of others.

In summary, true dinosaurs are distinguished from all other reptiles by the seven features discussed above. There are also a number of additional features that, while not strictly diagnostic of Dinosauria itself, are only seen in dinosaurs and a few of their closest relatives: “stem dinosaurs” such as *Lagerpeton*, *Marasuchus*, *Silesaurus*, and *Asilisaurus*, which lived during the Early to Late Triassic (Sereno and Arcucci, 1993, 1994; Dzik, 2003; Nesbitt et al., 2010). Unsurprisingly, most of these features are also indicative of upright posture, fast locomotion, and a muscular reinforced skeleton. The most distinctive and important of these features include the following.

- 1 Three or more sacral vertebrae. The sacral vertebrae articulate with the pelvis, fitting tightly

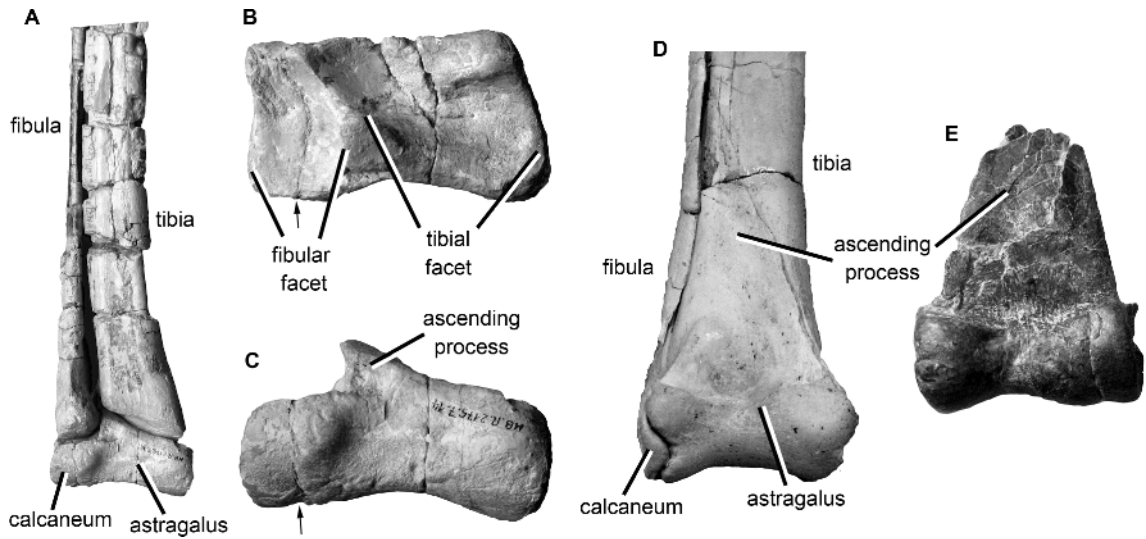


Figure 1.17 Distinctive features of dinosaurs. The articulated ankle of the Late Triassic theropod *Liliensternus* (A) and the Late Cretaceous ornithomimosaurian theropod *Gallimimus* (D) showing the characteristic mesotarsal ankle condition in which the calcaneum is reduced to a small spool of bone that is firmly attached to the large astragalus. The ankle bones of *Liliensternus* are also shown in proximal (B) and anterior (C) views, and the ankle of *Deinonychus* is shown in anterior (E) view. Note that the arrow in (B) points to the calcaneum–astragalus contact: only a small portion of the astragalus contributes to the fibular facet (another distinctive feature of dinosaurs). Image (E) taken by the author but copyright of the Peabody Museum of Natural History.

between the left and right ilium bones, and therefore are important in rigidly connecting the vertebral column and the hindlimbs. Whereas many archosaurs have only two sacral vertebrae, dino-

sosaurs and some of their closest relatives have three or more sacral vertebrae. In fact, some derived dinosaurs have more than six sacral vertebrae. The increased sacral count is reflective of a

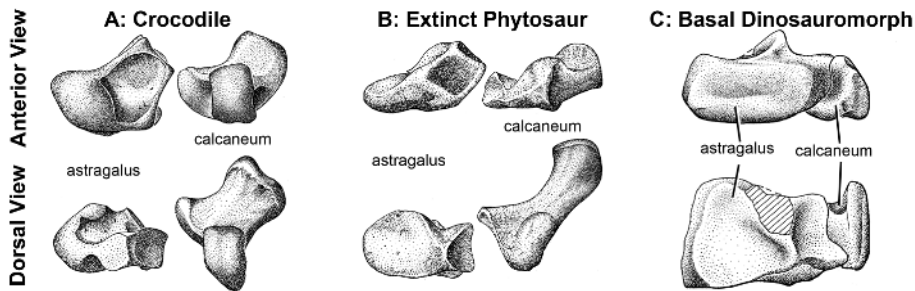


Figure 1.18 Mesotarsal vs. crurotarsal ankles. Crurotarsal ankles in a crocodile (A) and a phytosaur (an extinct member of the crocodile-line of archosaur phylogeny) (B), and a mesotarsal ankle in the basal dinosauromorph *Marasuchus* (C). In crurotarsal ankles the astragalus and calcaneum are approximately equal in size and articulate together at a mobile ball-in-socket joint. Mesotarsal ankles, however, are characterized by a proportionally enlarged astragalus and a tiny calcaneum, which articulate at a firm contact that permits no motion between them. Reproduced with permission from Sereno (1991a).

stronger, reinforced articulation between the backbone and pelvis, and would have helped brace the more muscular and swifter hindlimbs of dinosaurs.

- 2 Elongate pubis and enlarged antitrochanter. The pubis is the most anterior of the three bones of the pelvis, and in dinosaurs and close relatives this bone is extremely elongate relative to the shorter squatter morphology in other archosaurs. A major pelvic muscle, the puboischiofemoralis, originated along the pubis, and stretched onto the ischium (the most posterior pelvic bone) and the proximal part of the femur (Hutchinson and Gatesy, 2000; Carrano and Hutchinson, 2002; Hutchinson, 2001a, 2002). Therefore, a longer pubis would have increased the attachment area of this muscle, a consequence whose functional significance is not immediately clear. It is likely, however, that this muscle rearrangement was related to the upright posture of dinosaurs and the general strengthening of their legs (see Fig. 1.14). Another plausibly related feature is seen in the posterior part of the pelvis. The antitrochanter is a rough articular surface where the greater trochanter of the femur, the spur that the puboischiofemoralis muscle attaches to, makes contact with the pelvis (Hutchinson and Gatesy, 2000; Hutchinson, 2001b, 2002). This contact zone is limited to a narrow corner of the ischium in most archosaurs, but in dinosaurs and close relatives it is greatly expanded, and extends across parts of both the ischium and ilium (see Fig. 1.14). Once again, the precise functional significance of the enlarged antitrochanter is unclear, but at the very least it is indicative of a broader, and perhaps tighter, articulation between the femur and pelvis. This may have helped strengthen and rigidify the leg, and would have restricted the range of motion of the femur such that it primarily moved in a single plane, which is important for fast-running animals.
- 3 Anterior trochanter on the femur. The puboischiofemoralis muscles, which bring the hindlimb forward and towards the body, attach to the anterior surface of the femur, immediately below the head that articulates with the pelvis (Hutchinson and Gatesy, 2000; Hutchinson, 2001b, 2002). This attachment site is generally smooth in most archosaurs, but in dinosaurs and close

relatives is expanded into a rugose flange called the anterior trochanter (see Fig. 1.16). Therefore, dinosaurs and their kin would have had larger and more powerful hindlimb muscles, consistent with their upright posture and rapid locomotion.

- 4 Elongate, compact metatarsus with reduced lateral and medial digits. All bird-line archosaurs, including dinosaurs, stem dinosaurs, and pterosaurs, share a unique condition in which the metatarsal bones of the foot are bunched together and elongated (Gauthier, 1986) (Fig. 1.19). Furthermore, dinosaurs and their closest relatives have greatly reduced the size of the first and fifth metatarsals and their corresponding digits – the toes on the inside and outside of the feet – such that the central three metatarsals dominate the foot and form a simplified, paddle-like structure (Fig. 1.19). In sum, these modifications allow the metatarsus to act as a single unified structure, which is essentially a third major long bone of the hindleg (along with the femur and tibia). Unlike the metatarsals of humans and many other animals, including most archosaurs, these bones did not contact the ground during locomotion in bird-line archosaurs. Instead, only the toes themselves would have touched the substrate. Similar lengthening, strengthening, and simplifying of the metatarsus is seen in living animals that run rapidly, such as horses and gazelles. The bunched metatarsus of bird-like archosaurs is so unusual, and functionally significant, that it clearly registers in footprints of these species, including the oldest known members of the clade from the early Olenekian of Poland (Brusatte et al., 2011a) (see Fig. 1.7). In these footprints, as well as hundreds of other footprints from later in the Triassic and throughout the Mesozoic, only the toes are impressed in the sediment, and the digits themselves are nearly parallel due to the bunched construction of the foot (see also Ptaszynski, 2000; Carrano and Wilson, 2001).

With the above exhaustive list in mind, there should be no confusion between dinosaurs and other archosaurs. The dinosaur clade, as well as slightly more inclusive clades that also include “stem dinosaurs” and pterosaurs, are strikingly modified relative to crocodiles and other reptiles. More than 10 distinctive features are known only in

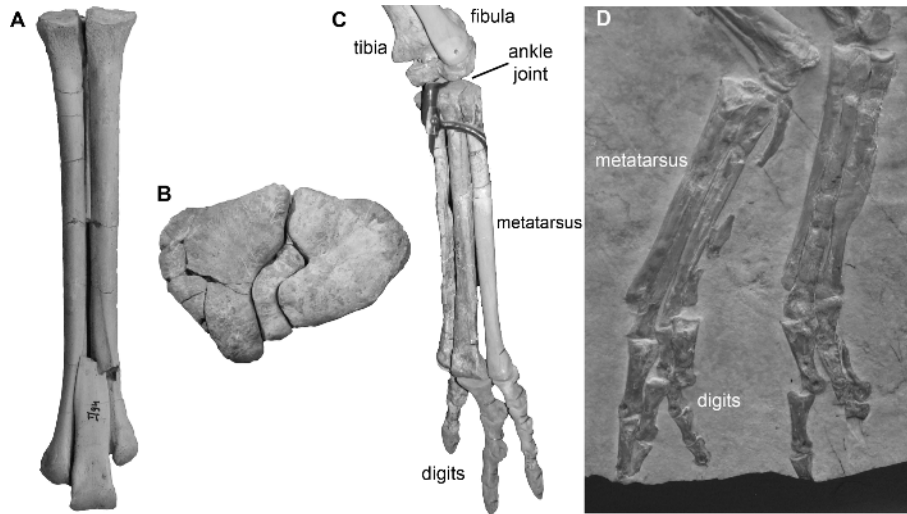


Figure 1.19 Distinctive features of dinosaurs. The metatarsus of the ornithomimosaurian theropod *Gallimimus* in anterior view (A), the metatarsus of the tyrannosaurid *Tarbosaurus* in proximal view (B), the metatarsus of early theropod *Elaphrosaurus* in posterior view (C), and the feet of the small theropod *Compsognathus* (D). All illustrate the “bunched” morphology characteristic of dinosaurs, in which the individual metatarsals are clustered close together and not splayed apart (as in crocodiles and other close dinosaurian relatives).

dinosaurs and their closest relatives, and possession of these characters is a surefire indication that a fossil specimen is a dinosaur. But these characters are not merely typological badges of honor that label specimens as dinosaurs, but also dynamic features of the skeleton that had clear functional and biological significance. Most of these characters are related to posture and muscle function: dinosaurs walked more upright and were faster than their closest relatives, and they had particularly strong jaw, neck, and forearm muscles and a rigid skeleton ideal for withstanding the rigors of a fast, active lifestyle.

The Major Dinosaur Subgroups

All dinosaurs evolved from a common ancestor and share a common set of skeletal features. With this said, a mere glance at any dinosaur museum exhibit—say, a *Tyrannosaurus* locked in aggressive battle with the deadly horns of *Triceratops*—is a dazzling reminder of just how different dinosaurs can be from one another. This remarkable diversity of size,

shape, diet, ornamentation, and lifestyle is one reason that the public is so fascinated with dinosaurs, and is surely a primary reason why dinosaurs were able to dominate terrestrial ecosystems for over 100 million years.

As briefly touched on above, dinosaurs can principally be divided into two major subgroups, the “lizard-hipped” saurischians and “bird-hipped” ornithischians, each of which can be further divided, finer and more finely, into less inclusive subgroups (see Fig. 1.21). This is, of course, because the family tree of life is hierarchical: a human is a primate, primates are one of many groups of mammals, mammals are tetrapods, tetrapods are vertebrates, vertebrates are one of numerous groups of animals, and so on. Chapter 4 will provide a detailed overview of the dinosaur family tree, and a discussion of the most comprehensive and up-to-date phylogenetic analyses used to construct it. First, however, it is necessary to provide a summary outline of the major dinosaur subgroups, to introduce the fundamental splits in dinosaur evolution and build a framework for the remainder of this narrative.

One of the great ironies of dinosaur paleontology is that the name Ornithischia is derived from the

Greek for “bird hip,” even though birds are actually direct descendants of saurischian dinosaurs, and thus technically members of the “lizard-hipped” clade itself! This confusion, however annoying, is justified with a bit of historical context. When Seeley (1887) first recognized and named the ornithischian clade, the idea that birds evolved from dinosaurs, and particularly the more specific hypothesis that they derived from small carnivorous saurischians, was little more than a fringe speculation. Seeley was one of the first scientists to present a detailed classification of dinosaurs: an attempt to make order out of the exasperating diversity of shape, size, and diet among the ever-expanding pantheon of dinosaur species. As a keen anatomist, Seeley recognized a fundamental difference between two clusters of dinosaurs. Many species, such as the large carnivore *Allosaurus* and the long-necked herbivore *Diplodocus*, had a pelvis in which the pubis bone projected forward, just as in most living reptiles (Fig. 1.20A). He referred to these dinosaurs as saurischians: the “lizard-hipped” group. A few other species, though, had a bizarre condition in which the pubis was rotated backwards, so that it paralleled the ischium (Fig. 1.20B). These dinosaurs included the plated *Stegosaurus* and herbivorous *Iguanodon*, and Seeley collectively referred to them as ornithischians,

or “bird-hipped” dinosaurs, because living birds have a similar pelvic configuration. Seeley, therefore, was not proposing that ornithischian dinosaurs evolved from birds, but merely that their most distinguishing feature – their retroverted pubis bone – was similar to that of birds.

More than a century after Seeley’s (1887) initial classification, ornithischians are today recognized as an incredibly diverse group, which includes a whole range of herbivorous species, many of which are armored or ornamented, and which run the gamut from fleet-footed to plodding, dog-sized to larger than elephants (Serenó, 1997, 1999; Weishampel, 2004) (Fig. 1.21). Ornithischians are primarily united by two sets of characteristics: those relating to the “bird-like” pelvis morphology and others closely tied to herbivory. The pubis is retroverted, as originally noted by Seeley (1887), and there is a novel flange of bone, called the prepubic process, that projects forward at the articular surface between the ilium and pubis. Furthermore, there are additional sacral vertebrae to brace the pelvis, and the anterior wing of the pelvis (the preacetabular process) is long, thin, and strap-like (Serenó, 1997, 1999; Weishampel et al., 2004; Butler et al., 2007, 2008a; Irmis et al., 2007b; Butler, 2010). Many of these pelvic features relate to the reconfiguration of muscles and the accommodation of a larger gut, essential for herbivorous species

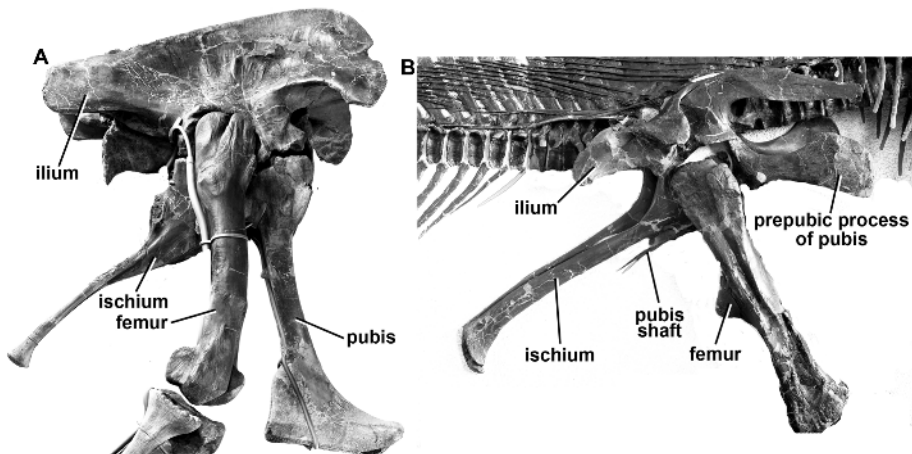


Figure 1.20 Saurischian and ornithischian pelvises. (A) The pelvis of the theropod *Tyrannosaurus*, which exhibits the saurischian condition in which the pubis projects forward. (B) The pelvis of a hadrosaurid, which exhibits the ornithischian condition in which the pubic shaft projects backward (paralleling the ischium) and a novel prepubic process projects forward. Images courtesy of the American Museum of Natural History Library (image #35423, 4267).

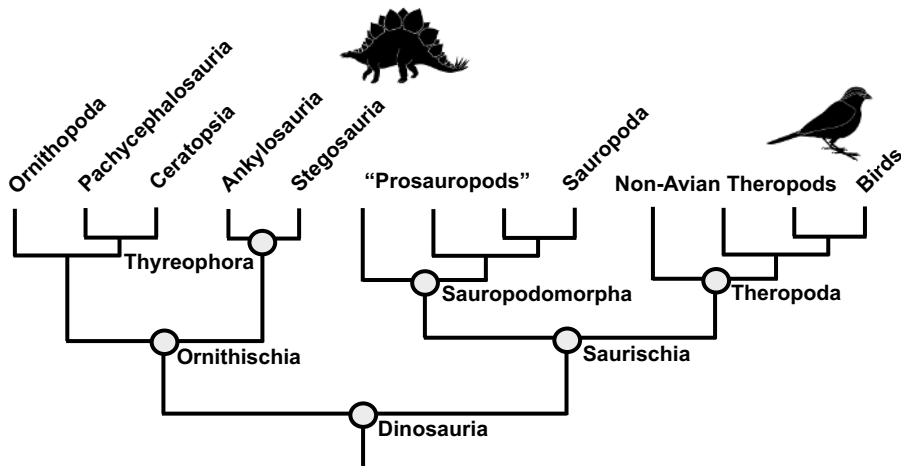


Figure 1.21 The general genealogical relationships of the major groups of dinosaurs.

that must ingest large quantities of plant matter. Other unique characters relating to herbivory include well-developed wear facets on leaf-shaped teeth, a large and strong dentary bone in the lower jaw, and the inferred presence of cheeks, which are vital for retaining chewed food in the mouth (Norman, 1984; Weishampel, 1984; Weishampel and Norman, 1989; Sereno, 1997, 1999; Butler et al., 2007).

The ornithischians that shared these characters persisted from the Late Triassic until the end of the Cretaceous, a span of some 165 million years. The oldest ornithischians, which include the puzzling and frustratingly poorly preserved *Pisanosaurus*, are known from the rock horizons in Argentina that preserve the world's oldest dinosaurs (Bonaparte, 1976; Sereno, 1991b; Butler et al., 2007, 2008a; Irmis et al., 2007b). Although they were present from the inception of the dinosaur clade, ornithischians remained rare and marginal during the Late Triassic, and only a handful of specimens are known from across the globe (Bonaparte, 1976; Butler et al., 2007; Irmis et al., 2007b; Butler, 2010). After the end-Triassic extinction, however, ornithischians exploded in diversity (number of species), faunal abundance, and geographic distribution, and became, along with the long-necked sauropod dinosaurs, the pre-eminent herbivores in most terrestrial ecosystems across the world (Butler et al., 2007, 2008a; Brusatte et al., 2008b). Many of the fundamental ornithischian subgroups arose and diversified during

the Jurassic: the plate-backed stegososaurs, the armored and tank-like ankylosaurs, and the beaked ornithopods (Galton and Upchurch, 2004a; Norman et al., 2004a; Vickaryous et al., 2004; Maidment et al., 2008; McDonald et al., 2010). One subgroup of the ornithopods, the duck-billed and fabulously crested hadrosaurids, flourished during the Cretaceous, along with two other fantastically ornamented ornithischian subgroups, the horned ceratopsians and dome-headed pachycephalosaurs (Dodson et al., 2004; Horner et al., 2004; Maryanska et al., 2004; You and Dodson, 2004; Prieto-Márquez, 2010a; Ryan et al., 2010a). No ornithischians, however, were able to endure the Cretaceous–Paleogene extinction.

The other major subgroup of dinosaurs, the saurischians, were also remarkably diverse, both in the number of species that lived during the Mesozoic and the variability in their size, anatomy, and diet (Fig. 1.21). Of course, saurischians also survive today as birds, meaning that this major subgroup has persisted for the past 65 million years in a world that is otherwise barren of dinosaurs. Seeley (1887) differentiated saurischians from ornithischians based on pelvic anatomy, but we now know that the “lizard-like” condition of saurischians is a primitive character that was retained from distant ancestors. After all, as its descriptive moniker implies, a lizard-like pelvis is present not only in saurischians but also in crocodiles and many other reptiles. This raises a problem. Because only shared,

derived characters that are inherited from a common ancestor – in this case, the common ancestor of saurischians to the exclusion of all other reptiles – are useful in diagnosing a clade, scientists must recognize discrete evolutionary novelties of saurischians in order to retain this subgroup as a true division of Dinosauria. Otherwise, saurischians would simply be a nebulous assemblage of primitive dinosaurs, not their own unique group united by derived features. This is not a problem for ornithischians, because their highly peculiar pelvis is clearly modified from the primitive reptilian condition, and thus represents an undisputable evolutionary novelty. Yet, do saurischians possess any of their own novelties?

Fortunately, such characters do indeed exist, and the roster of saurischian novelties is being continuously refined as new fossils of Triassic dinosaurs emerge. All saurischians share derived features of the neck, hand, and feet (Serenó, 1997, 1999; Langer and Benton, 2006; Nesbitt et al., 2009b; Martínez et al., 2011). The neck is elongate, due to the increased length of individual vertebrae, and the epiphyses – the projections on the cervical vertebrae for muscle attachment that are present in all dinosaurs – are not limited to only the first few vertebrae as in ornithischians, but are present along the entire neck. The hand is long, nearly half the length of the arm, and the first finger is especially large and projects strongly medially relative to the remainder of the hand. All together, these features allowed the hand to function as a strong grasping organ, perfect for claspng prey. The metatarsals of the feet lie against each other in an overlapping, en echelon arrangement, and do not simply abut each other as in ornithischians and other archosaurs. Although some of these shared novelties have been revealed by new fossils, other discoveries have dismissed several previously held saurischian features as more widely distributed among dinosaurs. For instance, it was long considered that saurischians uniquely possessed a subnarial foramen between the premaxilla and maxilla, pneumatic openings and laminae on the vertebrae, and hyposphene–hypantrum articulations to reinforce the contact between vertebrae. These features, and many others, are now known to be present in some primitive ornithischians (Butler et al., 2007), and sometimes even in stem dinosaurs and crocodile-line archos-

saurs (Gower, 2001; Dzik, 2003; Nesbitt and Norell, 2006; Nesbitt, 2007; Weinbaum and Hungerbühler, 2007; Brusatte et al., 2010a).

The first saurischian fossils are also known from the same Late Triassic Argentine units that yield the first ornithischian fossils. In fact, the two major saurischian subgroups – the carnivorous theropods and long-necked herbivorous sauropodomorphs – are already present by this time (Serenó and Novas, 1992; Serenó et al., 1993; Langer et al., 1999; Bittencourt and Kellner, 2009; Martínez and Alcober, 2009; Ezcurra, 2010a; Ezcurra and Brusatte, 2011; Martínez et al., 2011). Unlike ornithischians, however, saurischians quickly diversified, became ecologically dominant, and spread across the globe soon after their origination. Theropods and sauropodomorphs are common fossils in Late Triassic rocks around the world, and in many ecosystems primitive sauropodomorphs were the most common, and the largest, herbivores (Benton, 1983).

Most Triassic sauropodomorphs were “prosauro-pods,” an informal name for a nebulous grade of primitive species that did not comprise their own unique group distinguished by novel characters (Galton and Upchurch, 2004b; Upchurch et al., 2007; Yates, 2007; Pol et al., 2011). Prosauro-pods were the ancestors and closest relatives of the sauropods, the distinctive long-necked, small-headed, plant guzzlers typified by *Brachiosaurus* and *Diplodocus* (Upchurch, 1995, 1998; Wilson and Serenó, 1998; Wilson, 2002; Upchurch et al., 2004; Curry-Rogers and Wilson, 2005). These behemoths, which originated in the Late Triassic but reached their zenith in the Late Jurassic and Early Cretaceous, included the largest land animals to ever live. Compared to such giants, however, the Triassic and Early Jurassic “prosauro-pods” were much smaller and had shorter necks, and many species were likely omnivorous and could alternate between walking on two or four legs (Barrett, 2000; Barrett and Upchurch, 2007; Bonnan and Senter, 2007; Langer et al., 2007).

The earliest theropods were mostly small animals, dwarfed in comparison with their later, more familiar Jurassic and Cretaceous cousins such as *Tyrannosaurus* and *Allosaurus* (see Plates 1, 2, and 3). Most Triassic theropods belonged to a primitive grade of small species, the “coelophysoids,” which like the “prosauro-pods” was not a unique group united by derived characters. These primitive ther-

opods are exemplified by *Coelophysis*, a kangaroo-sized species overshadowed by much larger crocodile-line predators when it was alive (Colbert, 1989; Brusatte et al., 2008a). Some Triassic theropods, however, grew up to 5–6 m in length, and were surely apex predators in their ecosystems (Huene, 1934). A sudden and pronounced increase in theropod size is recorded across the Triassic–Jurassic boundary, immediately after the extinction of many crocodile-line archosaurs that filled top predator niches (Olsen et al., 2002), and throughout the Jurassic and Cretaceous theropods would diversify into a stupefying array of different subgroups. The most familiar of these are probably the tyrannosauroids, typified by the iconic *Tyrannosaurus rex*, and the dromaeosaurids, which include the sleek scythe-clawed predators *Deinonychus* and *Velociraptor* of *Jurassic Park* fame (see Plates 4–11). Regardless of their size or when they lived, theropods are united by a fairly conservative body plan: they are bipedal predators, most of which could run quickly and had a multitude of weapons, sharp teeth and claws included, to take down prey. Only some very aberrant, derived Late Jurassic and Cretaceous species, such as the beaked ornithomimosaurs, the toothless oviraptorosaurs, and the barrel-chested therizinosauroids, would deviate from this fast-running, predatory lifestyle; instead, these theropods were omnivorous or, in some cases, completely herbivorous (Kobayashi et al., 1999; Barrett, 2005; Zanno et al., 2009; Zanno and Makovicky, 2011).

Birds: Living Dinosaurs

The most atypical theropods, however, are undoubtedly the birds. One of the great revelations of dinosaur research, and perhaps the single most important fact ever discovered by dinosaur paleontologists, is that birds are descended from small carnivorous theropods. This idea was originally proposed by Thomas Henry Huxley, the acerbic 19th century advocate of evolution known as “Darwin’s Bulldog,” in the 1860s. This was a revolutionary decade in science. Darwin had published his *Origin of Species* in 1859, which persuasively and decisively laid out the evidence for evolution by natural selection. Rational thinkers had no

recourse: organisms evolved over great lengths of time, and shared characteristics were indicative of a close genealogical relationship. The public was a bit more skeptical, however, and pundits like Huxley were on the lookout for so-called “missing links” – transitional fossils that captured, like a freeze frame, the evolution of one group into another – that could viscerally demonstrate the reality of evolution to the masses.

It did not take very long for a convincing “missing link” to appear. In 1861, a mere two years after Darwin’s groundbreaking publication, quarry workers in the Bavarian hillsides of Germany discovered the fossilized bones of a peculiar bird (Fig. 1.22A). This fossil had to be a bird: the fine preservation revealed an unmistakable halo of feathers around the body, it had a wishbone at the front of its chest, and the wrists and feet were almost identical to those of living birds. But something was amiss. This bird had teeth in its skull and a long bony tail, features that are not present in any living bird. And, even more puzzling, the skeleton of this bird, especially the form of its tail and skull, was eerily similar to another fossil discovered in the same lithographic limestone beds: a small predatory theropod called *Compsognathus*. To keen observers like Huxley this fossil was the Holy Grail: a “missing link” that possesses features of both dinosaurs and birds, and therefore captures an evolutionary transition between the two groups.

This fossil bird was named *Archaeopteryx*, and it immediately became a public sensation and still remains one of the most important and iconic fossils in the history of paleontology (Chambers, 2002). In a series of publications, and more important in a whirlwind sequence of public lectures, Huxley ebulliently argued that *Archaeopteryx* was proof positive that birds were descended from dinosaurs (Huxley, 1868, 1870a, 1870b). In an ironic twist, the strikingly half-bird, half-dinosaur skeleton of *Archaeopteryx* helped sway public perception in favor of evolution, but Huxley’s specific idea that birds evolved from small carnivorous dinosaurs fell out of favor among scientists (Heilmann, 1926). It was not until the 1960s that a small, vocal group of paleontologists resurrected Huxley’s ideas, buoyed largely by the discovery of spectacular fossils of the very bird-like dinosaur *Deinonychus* (Ostrom, 1969). Today, the hypothesis that birds evolved from theropod dinosaurs – nay, that

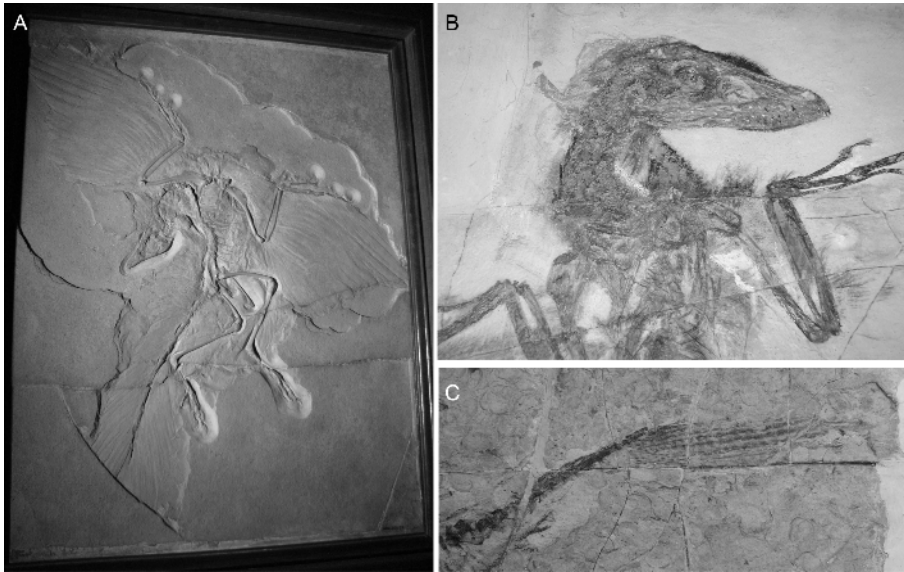


Figure 1.22 The evolutionary relationship between dinosaurs and birds. (A) The iconic Berlin specimen of *Archaeopteryx*, the oldest known bird; (B) the feathered non-bird dinosaur *Sinornithosaurus*, a dromaeosaurid closely related to *Velociraptor*, and (C) the tail of the feathered non-bird theropod dinosaur *Caudipteryx*. All photos by the author.

birds actually *are* theropod dinosaurs, since they are firmly nested within the group – enjoys nearly universal acceptance in the scientific community (Gauthier, 1986; Padian and Chiappe, 1998; Chiappe and Witmer, 2002; Chiappe, 2007).

The theory that birds descended from dinosaurs is so widely accepted because it is supported by a preponderance of evidence. Grand ideas demand strong evidence, and the dinosaur–bird link, which might be dismissed as too fanciful to be true by some critics, foots the bill. Living birds share hundreds of skeletal features with dinosaurs, and many characteristics that are unique to birds among living animals – a wishbone, a long S-shaped neck, a mesotarsal ankle joint, a wrist that enables the arm to fold against the body, and a retroverted pelvis being some of the most conspicuous – are also present in bona fide Mesozoic dinosaurs such as *Tyrannosaurus* and *Velociraptor* (see Padian and Chiappe, 1998; Shipman, 1998; Chiappe and Witmer, 2002; Chiappe 2007). Ditto for soft tissues: sinuses in the skulls and internal chambers in the vertebrae conclusively show that many dinosaurs had an extensive system of air sacs, a critical component of the bellows-like respiratory system un-

ique to modern birds, and proteins from a *Tyrannosaurus* skeleton that miraculously survived the rigors of 66 million years of fossilization share uncanny structural and molecular similarities with proteins of living birds (Britt, 1993; O’Connor and Claessens, 2005; Schweitzer et al., 2005a; Organ et al., 2008; Sereno et al., 2008; Benson et al., 2011). There is behavioral evidence as well: spectacularly preserved dinosaur fossils have been found in the characteristic sleeping and egg brooding postures of living birds (Norell et al., 1995; Xu and Norell, 2004), bone histology and texture indicate that dinosaurs grew rapidly like living birds (Padian et al., 2001; Erickson et al., 2007), and medullary bone – a novel tissue that provides calcium for the shelling of eggs – is known only among birds and dinosaurs (Schweitzer et al., 2005b).

Most extraordinary of all, thousands of spectacularly preserved dinosaur specimens, all of which have been discovered in northeastern China during the past 20 years, are unmistakably sheathed in a coat of feathers (Chen et al., 1998; Norell and Xu, 2005) (Fig. 1.22B,C; see Plates 5–7). Some of these feathers, with their central quill and radiating barbs, are identical to those of modern birds (Norell

et al., 2002), and their preservation is so astounding that one could easily be fooled into thinking that they had just been plucked from a living, breathing species. Intensive molecular sampling demonstrates that many of these feathers preserve remnants of the melanosomes, the pigment-containing structures that give feathers their radiant (or in some cases drab) hues (Li et al., 2010; Zhang et al., 2010; Wogelius et al., 2011). And it wasn't only the closest relatives of birds that had feathers, but also much more distant cousins such as the herbivorous therizinosauroids (Xu et al., 1999) and, most incredible, the tyrannosauroids (Xu et al., 2004). Emerging evidence provocatively suggests that non-theropods had feathers, as a number of basal ornithischian specimens have also been found with a downy coat (Mayr et al., 2002; Zheng et al., 2009), and it is therefore possible that the common ancestor of dinosaurs was a feathered species.

Birds, therefore, are surviving members of the dinosaur clade. They are every bit as much a "dinosaur" as *Tyrannosaurus*, *Stegosaurus*, or *Brachiosaurus*, and their main distinction from other dinosaurs, aside from their novel flying lifestyle, is that they were able to survive the global meltdown at the Cretaceous–Paleogene boundary. Among dinosaurs, birds are most closely related to dromaeo-

saurids (*Velociraptor* and kin) and the troodontids, an intriguing subgroup of small, sleek, intelligent, and perhaps omnivorous theropods (Makovicky and Norell, 2004). These genealogical relationships – the nesting of birds within theropod dinosaurs and the particularly close relationships between birds, dromaeosaurids, and troodontids – are consistently recovered in phylogenetic analyses, and therefore these branches of the dinosaur family tree are on solid footing (Gauthier, 1986; Sereno, 1999; Norell et al., 2001a; Clark et al., 2002; Senter, 2007; Turner et al., 2007a; Csiki et al., 2010; Xu et al., 2011a).

The World of the Dinosaurs

It is difficult, if not impossible, to understand the biology and evolution of dinosaurs without an appreciation for the physical world they inhabited. Disregarding birds, which will not be the subject of this book, dinosaurs lived during the Mesozoic Era (from about 252 to 65 million years ago), an extraordinary time in earth history that witnessed the birth and death of a supercontinent and experienced some of the highest temperatures and sea levels in the geological record (Fig. 1.23). Indeed, as eloquently described by Sellwood and Valdes (2006), in an

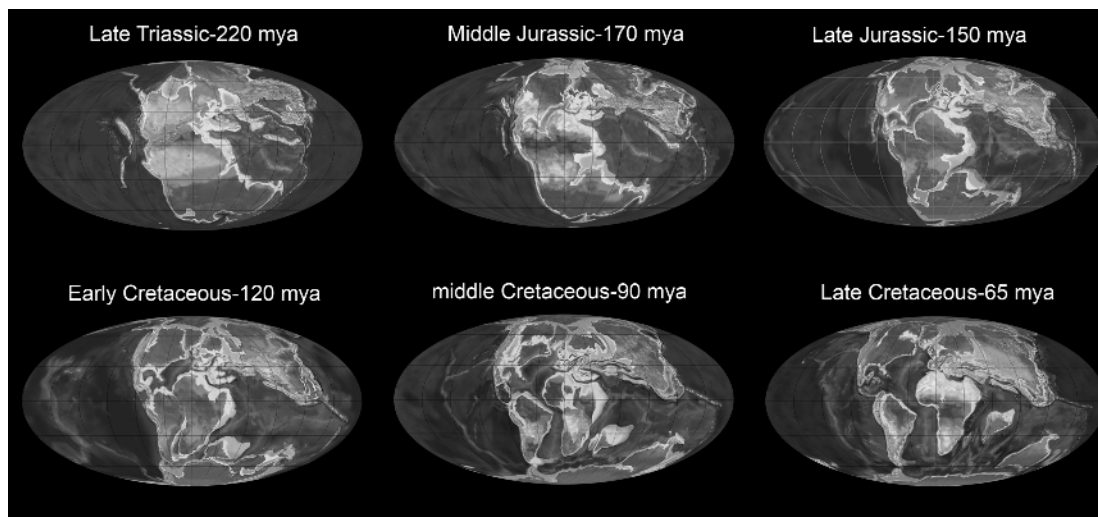


Figure 1.23 Paleogeographic maps, showing the configuration of the continents and oceans during six intervals throughout the Mesozoic history of dinosaurs. All images courtesy of Dr Ron Blakey (<http://www2.nau.edu/rcb7/globaltext2.html>).

important overview of Mesozoic climates that should be referred to for more specific information, “the Mesozoic earth was, by comparison with the present, an alien world.”

Dinosaurs and their closest relatives originated in the Triassic Period (c.252–201 million years ago; see Sues and Fraser, 2010 for a general overview). The physical geography of this time was remarkable: most of the world’s land was sutured together into a single landmass, the supercontinent Pangaea, which was centered on the equator and surrounded by a single giant ocean (Wegener, 1924; Smith et al., 1994; Scotese, 2004) (Fig. 1.23). Climates on this supercontinent were warm and arid, especially in the continental interior of Pangaea, which was far from the ameliorating effects of the coasts (Sellwood and Valdes, 2006). It is generally thought that temperatures became warmer and more arid throughout the Triassic, and by the time the first dinosaurs evolved much of the planet may have been covered in deserts (Tucker and Benton, 1982). Climate change during the Triassic may not have been gradual, however, as the rock record chronicles an abrupt transition from somewhat cooler and wetter conditions to substantially warmer and more arid climates during the Norian, the lengthy Triassic substage (c.228–208 million years ago) during which dinosaurs began their rise to dominance (Simms and Ruffell, 1990). Moreover, the most abrupt climatic change occurred at or near the Triassic–Jurassic boundary. Global temperatures and greenhouse gas levels spiked at this time, almost certainly the result of widespread volcanism associated with the initial rifting of Pangaea, and it is probably not coincidental that major extinctions in the terrestrial and marine realm occurred almost synchronously (McElwain et al., 1999; Whiteside et al., 2010).

Many of the extremes of Triassic geography and climate would dampen during the ensuing Jurassic Period (c.201–146 million years ago). Pangaea began to fragment during the Late Triassic, as an influx of heat from the deep interior of the earth tore open rift basins along what is currently the Atlantic coast of North America and Europe. These basins grew wider with time, and by the Middle Jurassic the nascent Atlantic Ocean separated Pangaea into northern and southern blocks (Fig. 1.23). The northern landmass, called Laurasia, contained North

America, Asia, and Europe, the latter of which was flooded by high sea levels and reduced to a series of islands. The southern landmass, called Gondwana, was a still-giant block of crust that included South America, Africa, Australia, Antarctica, and India. The Jurassic was still a time of warm climates, but conditions were much wetter than during the arid Late Triassic and, as a result, a great diversity of plants (especially gymnosperms) were able to flourish at all latitudes (Rees et al., 2000; Sellwood and Valdes, 2006). The extreme peaks of Late Jurassic temperature are best illustrated by a simple comparison: geological evidence indicates that atmospheric carbon dioxide levels, a proxy for temperature, were up to four times higher in the Late Jurassic than in today’s world (Berner, 2006; Fletcher et al., 2008).

The physical world continued to change, and to assume a more modern feel, during the final stanza of dinosaur evolution, the Cretaceous Period (c.145–65 million years ago). Laurasia and Gondwana, the two great remnants of Pangaea, further disintegrated during the Cretaceous, and by the end of the period the continents were positioned, more or less, in their current configuration (Smith et al., 1994; Scotese, 2004) (Fig. 1.23). Continental rifting was especially vigorous in Gondwana: what began as a single large landmass in the Late Jurassic fragmented into today’s characteristic southern continents within a time frame of only a few tens of millions of years. Most remarkably, India began the Cretaceous as a wedge of crust between Africa and Antarctica, but steadily moved northeast until it had just begun colliding with Asia at the time the dinosaurs went extinct. This collision, of course, would be fully realized several million years later, with the Himalayas rising skyward as a consequence.

The Cretaceous world was still a hothouse, with high global temperatures and little evidence for polar ice caps, but temperatures fluctuated more wildly than during the Triassic and Jurassic (see Skelton et al., 2003). Temperatures were especially high throughout the middle Cretaceous, probably driven by intensive volcanism that belched large volumes of carbon dioxide into the atmosphere. High temperatures resulted in high sea levels, because little water was locked up in glaciers, and warm shallow seas lapped the continents. During the Late Cretaceous, for instance, North America

was bisected by one such seaway, which stretched from the Gulf of Mexico to the Arctic. Global temperatures probably reached a peak approximately 100–120 million years ago, approximately at the same time as a middle Cretaceous extinction event thought to have been caused by rapid stagnation of the oceans (Jenkyns, 1980; Fletcher et al., 2008). Whether dinosaurs and other terrestrial organisms were affected by this brisk interval of climate change is uncertain. From this point on, however, atmospheric carbon dioxide levels, and thus global temperature, decreased throughout the remainder of the Cretaceous (Fletcher et al., 2008). Our modern climates, which are relatively cool compared with other intervals in earth history, come at the tail end of this long-term, 100-million-year decline. This being said, although current temperatures are cool compared with the Mesozoic, human-induced climate change is a pressing source of concern because of its rapid pace and its potential to alter physical environments that humans have become accustomed to.

Conclusions

Dinosaurs are an iconic group of archosaurian reptiles, whose living descendants include about 10 000 species of modern birds. Although the term “dinosaur” is part of the popular vocabulary, and is often used to denote anything that is old, huge, or frightening, the scientific concept of dinosaurs is precise: dinosaurs are defined as the clade on the family tree of life that encompasses *Triceratops*, the

living sparrow (*Passer*), and all descendants of their most recent common ancestor. This group, formally referred to as Dinosauria, is diagnosed by several shared derived characters, or evolutionary novelties, that all dinosaurs inherited from their common ancestor. Most of these features relate to posture, locomotion, and musculature: dinosaurs stood upright, were likely faster than their closest relatives, and had a skeleton and associated musculature that were well adapted to endure a fast active lifestyle. Dinosaurs can be divided into two major subgroups, the “lizard-hipped” saurischians and “bird-hipped” ornithischians, each of which can be further subdivided more finely into other subgroups. The principal saurischian subgroups are the carnivorous theropods and long-necked sauropodomorphs, whereas familiar ornithischians include the armored ankylosaurs, plated stegosaurs, duck-billed hadrosaurs, horned ceratopsians, and dome-headed pachycephalosaurs. The evolutionary history of dinosaurs is a gripping narrative that took place against a backdrop of drifting continents, climate change, and mass extinction events. Dinosaurs originated in the Middle Triassic, gradually became more diverse and abundant during the Late Triassic, and were able to endure the end-Triassic mass extinction that decimated many competitor groups. During the Early Jurassic dinosaurs truly became dominant on a global scale, and for the remainder of the Mesozoic were the pre-eminent vertebrates, both carnivore and herbivore, at mid-to-large size in terrestrial ecosystems across the globe.