Dinosaur Evolution: From Where Did They Come and Where Did They Go?

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The rhetorical and two-part question “From where did dinosaurs come and where did they go?” encourages the asking of many more questions, but such questions will inevitably relate to two intertwined phenomena experienced by all life: evolution and extinction. Dinosaurs, like all living things, originated through evolutionary processes, diversified as a result of those very same processes, and most of their lineages went extinct. In this chapter, I will focus on the processes and products of evolution in dinosaurs, but with emphasis on the beginning of that history. Hypotheses for dinosaur extinctions 65 million years ago and the evolution of some dinosaur lineages into birds are discussed in detail by other authors in this volume (see Currie, page 89; and Archibald, page 99).

Scientific studies of dinosaur evolution exemplify that science is a work in progress. Its practitioners often acknowledge that once-stated certainties are liable to be proven wrong, once-outlandish ideas may be closer to reality than originally thought, or, alternatively, only minor tweaking is needed to clarify some previously accepted hypotheses. For example, the statement “Dinosaurs evolved from reptiles in the latter part of the Late Triassic Period and went extinct at the end of the Cretaceous Period” has been amended in the past 20 years to “Dinosaurs evolved from archosaur lineages in the earliest part of the Late Triassic and some of them are still with us today as birds.” Such shifts illustrate how scientists revise or disprove hypotheses more than affirm them (and often are delighted when they do so!), and dinosaurs in particular constitute excellent subjects for revisionist thinking. Each new discovery of dinosaur remains or dinosaur trace fossils provides yet more evidence for testing whether previously accepted concepts about dinosaurs and their evolution (especially their origins) are still justified.

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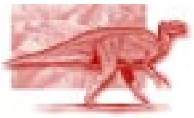


Dinosaur Ancestors and the Origins of Dinosaurs

What were the most likely ancestors of dinosaurs? Intrinsic to this question is the dilemma facing a paleontologist, which is how to define the "first dinosaur" from the fossil record. For example, *Stegosaurus stenops* of the Late Jurassic Period and *Triceratops horridus* of the Late Cretaceous were certainly dinosaurs (just ask any five-year-old), but what about *Eoraptor lunensis* and *Herrerasaurus ischigualasto* of the Late Triassic? Some paleontologists think that *Eoraptor* was a dinosaur,[1, 2] whereas others do not,[3] and similar dissent is expressed about *Herrerasaurus*.[4] Additionally, given the transitional nature of evolution, any declaration made by a paleontologist that he or she found evidence for the "first dinosaur" might be analogous to stating that a shade of gray is exactly between white and black. The fossil evidence for the evolutionary lineage for dinosaurs, particularly in their early history, is not well known. Does this situation mean that no hypotheses about the origins of the first dinosaurs can be made? Of course not—paleontologists can still hypothesize, because after all, a little bit of evidence is better than none. Moreover, paleontologists acknowledge that although they can only hypothesize on the basis of what evidence they have now, they also optimistically remind themselves that the fossil record gets better every day as more discoveries are made and studied. As a result, a definition of the "first dinosaur" can be given here, but with the understanding that undoubtedly it will be refined and clarified later.

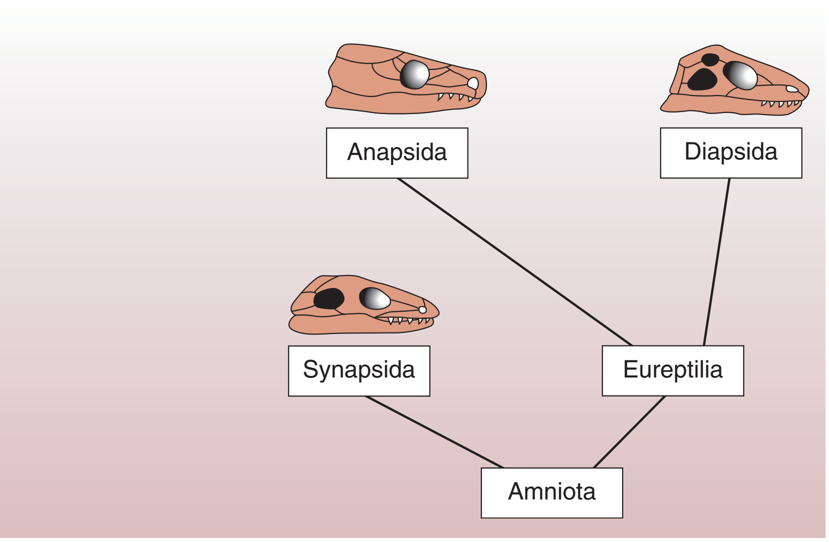


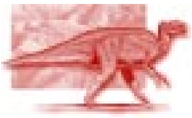
Fig. 1. Synapsid, anapsid, and diapsid skull types in a showing their hypothesized evolutionary relationships. Temporal fenestra indicated by blackened areas; orbits (eye sockets) are shaded. Adapted from Martin (2001: Fig. 10.5).

Origin of Dinosaur Ancestors

The ancestors and origin of dinosaurs could be traced back to the origin of life itself. However, for the sake of brevity, let us begin with amniotes—four-legged vertebrates (tetrapods) that evolved enclosed (cleidoic) eggs for reproduction. Amniotes appeared by the beginning of the Pennsylvanian Period, about 310 million years ago.[5, 6] The evolution of a cleidoic egg was a huge step for tetrapods because it allowed them to inhabit areas that were dry or distant from bodies of water. No longer were tetrapods bound to certain terrestrial ecosystems. One of the predictions of evolutionary theory is that they should have undergone relatively rapid diversification as a reflection of adapting to these different ecosystems. Indeed, this was the case, and this diversification can best be seen by looking at changes in their skulls and limbs through the latter part of the Paleozoic Era.

Amniotes are broadly divided into three evolutionarily related groups—Anapsida, Synapsida, and Diapsida, based on the number of temporal fenestrae they possess (Fig. 1). Place a couple of fingers behind your eye socket on the side of your skull. You will feel a soft area there. Your hand is feeling a temporal fenestra, which is a hole in the structure of your skull caused by your cheekbone: the cheekbone flares out around the fenestra. Anapsids lack temporal fenestrae; synapsids have one on each side of the skull; and diapsids have two on each side of the skull. (Using this definition, you are a synapsid.) Based on current data, diapsids and anapsids probably evolved from a common ancestor, hence they are put in the same group (Eureptilia) and separated from synapsids.

The diapsid group, or , is where we will find dinosaurs. During the later part of the Permian Period (about 260 million years ago), diapsids diverged into two clades: Lepidosauria (lizards and snakes) and Archosauria. Archo-



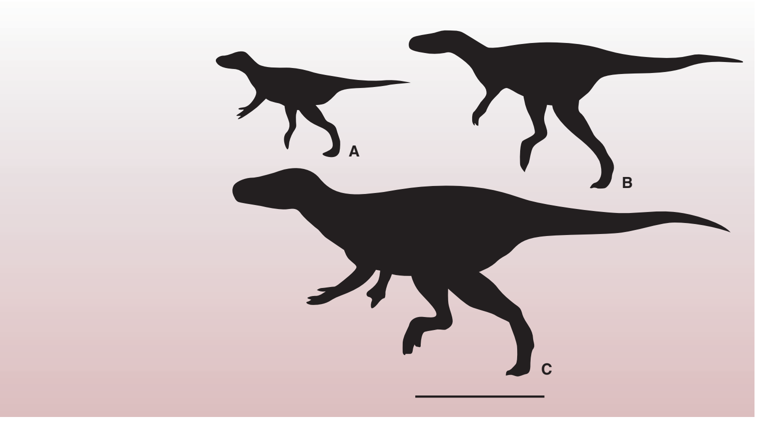


Fig. 2. Profiles of three Late Triassic ornithodirans defined as primitive dinosaurs. **A.** *Eoraptor lunensis.* **B.** *Staurikosaurus pricei.* **C.** *Herrerasaurus ischigualasto.* Adapted from Martin (2001: Fig. 10.10). Bar scale = 1 m.

saurs are distinguished by the following traits: openings in the skull in front of the eye sockets, laterally compressed and serrated teeth, holes in the front of the lower jaw (dentary), modified ankle bones, and longer bones in the pelvis.[7] Archosaurs show up in the fossil record in the Early Triassic and evolved into crocodiles, pterosaurs, dinosaurs, and birds. A fossil that is a likely candidate for a common ancestor to these archosaurs is a one-meter long animal—*Euparkeria*, of the Early Triassic of South Africa.[8]

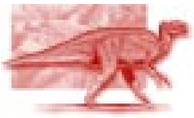
Archosaurs then diverged into two s during the Triassic Period: Pseudosuchia, which included many fossil forms, as well as the living crocodilians,[9] and Ornithodira. Dinosaurs are ornithodirans, originating from that either during the latest part of the Middle Triassic or the earliest part of the Late Triassic, about 230 million years ago. Although pterosaurs are not "flying dinosaurs," they are also ornithodirans, and thus are closely related to dinosaurs; that is, they share a common ancestor.

First Dinosaurs: What, When, and Where?

So what did the "mother of all dinosaurs" look like? Based upon features common to the earliest dinosaurs and pterosaurs, this ancestor would have been bipedal, had hind limbs longer that its forelimbs, had four (or five) digits on its hand, long metatarsals and digits on its foot, a uniquely hinged ankle, and a tibia and fibula longer than its femur.[10, 11] Thus far, the best fits to this description are represented by *Marasuchus* (synonomized with *Lagosuchus* by some paleontologists) and *Lagerpeton*, which both occur in Middle Triassic strata of Argentina.[12, 13] *Marasuchus* and *Lagerpeton* apparently originated very close to the divergence time of ornithodirans, meaning that their descendants could have become either pterosaurs or dinosaurs.

Three fossils from the earliest part of the Late Triassic (~227.8 mya) can be considered candidates for the oldest known dinosaur (Figs. 2, 3): *Eoraptor lunensis* and *Herrerasaurus ischigualasto* from the Ischigualasto Formation of Argentina, and *Staurikosaurus pricei* from the Santa Maria Formation of Brazil.[14, 6, 17, 1, 18, 19, 2] Of these species, the one that causes the most arguments among paleontologists is *Eoraptor*. Its primitive traits, such as the lack of a joint within its mandible, as well as hindlimb and pelvic bones that differ slightly from those of all other dinosaurs,[2] prompted skepticism as to whether it is indeed a dinosaur.[3] Whichever may be the best candidate, most paleontologists agree that these "first" dinosaurs were saurischians ("lizard-hipped" dinosaurs) and that they were evolutionarily connected with theropods.[20, 21, 22] However, the exact evolutionary relationships with ancestor and descendant species are still the subject of debate.[23]

Fig. 3. *Herrerasaurus ischigualasto* of the Late Triassic of Argentina, interpreted as one of the first dinosaurs. Specimen in The Field Museum, Chicago, IL.



Competing with these fossils for the title of "oldest known dinosaur" are a few recent finds of prosauropod fragments in Madagascar, which some paleontologists assert were in strata older (230–235 mya) than those of *Eoraptor* and *Herrerasaurus*.[24] Unfortunately, no radiometric ages are yet calculated for the Madagascar rocks and the age estimate, which dips into the Middle Triassic, is currently based only on associated fossils. Nevertheless, this exciting find has helped to show how the beginning of dinosaur evolution is likely to be pushed back slightly in geologic time.

Supplementary evidence for the advent of dinosaurs comes not from skeletal evidence, but from tracks. Some tracks in the latest part of the Middle Triassic and earliest part of the Late Triassic closely resemble what most paleontologists agree are dinosaur tracks.[25, 26] Because the anatomy of probable dinosaur ancestors points toward bipedal walking and a foot with three prominent toes, their tracks should reflect this two-legged walking and a three-toed compression shape. Considering the large number of tracks left by a living and moving animal in comparison to its single body, early dinosaur tracks may be more common than their fossilized bodies. However, skepticism about what animals made what tracks is necessary and good skeletal data correlations are needed before making any conclusions about dinosaurs walking in the Middle Triassic.[26]

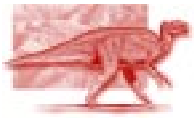
Early Dinosaur Diversification

Finds of primitive dinosaurs and their probable ancestors in South America, in addition to those recently found in Madagascar, currently point toward an origin of dinosaurs from the southern continent of Gondwana during the Middle to Late Triassic. How they diversified immediately after their origin is a good question. One hypothesis is that early dinosaurs successfully competed with other archosaurs for habitats and resources throughout the latter part of the Triassic, which caused some pseudosuchians to go extinct and ornithodirans to endure.[27] However, this hypothesis is not very well supported by the fossil evidence, in that inverse trends between dinosaur abundance and extinctions of other archosaurs are not clear. Indeed, some archosaur lineages show signs of going extinct well before dinosaurs were established, suggesting that environmental factors were primarily affecting their natural selection, rather than interspecific competition with dinosaur ancestors.[28, 29] The latest addition to this hypothesis invokes a meteorite-linked extinction of pseudosuchians that opened the way for the 140-million-year dinosaurian hegemony that began in the last part of the Triassic.[30]

For a broad overview of how a changing world may have contributed to the development of dinosaurs, we must look at what was happening during the Late Triassic. About 220 million years ago, the supercontinent Pangea began to break up, resulting in major sea level fluctuations.[31] Evidence of environmental change and its effects on flora and fauna during the Late Triassic includes major extinctions of marine invertebrates. The splitting of Pangea no doubt triggered changes in the ocean and atmosphere, which in turn would have altered global climate. Geologic evidence of such climate change includes thick and widespread Triassic evaporite deposits, formed by the evaporation of seawater in restricted basins during extended times of aridity.[32, 33, 34, 35]

The arid Triassic climates impacted terrestrial communities. Selection favored drought-resistant plants, which became dominant during this time. With a change in the availability of food sources to herbivorous tetrapods, picky eaters would have gone extinct and generalists would have survived to spread their genes to a new generation. Is this mere speculation? No, the fossil record of plants from the Late Triassic shows such a shift in correspondence with climate change,[36, 37] and this change also roughly correlates with changes in terrestrial archosaur assemblages. Of course, correlation is not necessarily causation, thus much more data are needed before making a more definitive linkage of climatic and ecologic factors with pseudosuchian extinctions and dinosaur evolution. Nevertheless, this evidence provides a starting point for review or revision of such hypotheses.

The breakup of Pangea, in combination with sea-level fluctuations, also caused habitat



fragmentation on a massive scale, meaning that dinosaur and other archosaur faunas became geographically isolated. Such a situation would have been conducive for speciation as isolated populations adapted to their new ecosystems. This scenario is also backed by geologic and paleontologic evidence. Diversification in the fossil record shows an approximate correlation with continental breakups during the Phanerozoic Eon, long before the Mesozoic.[38] One of the hypotheses to explain this diversification is that new ecosystems provided new niches for species with the genetic ability to adapt. Dinosaurs thus would have had new adaptations in the Late Triassic that likely interrelated with newly available niches caused by both continental rifting and the abandonment of niches as other archosaurs went extinct.[39]

As mentioned earlier, a new revelation contrasting with (or augmenting) the preceding gradual scenario concerns a possible meteorite impact near the end of the Triassic Period. The evidence cited for this hypothesis is multifaceted, drawn from archosaur body fossil assemblages, dinosaur tracks, iridium concentrations, and fern spores in sediments spanning the Triassic-Jurassic boundary.[30] The gist of this hypothesis is that pseudosuchians already had depleted numbers when a meteorite (sufficiently large enough to cause ecological damage) struck the Earth. Then they quickly became extinct. Meanwhile, ferns, as typical "first colonizers" after an ecological catastrophe, became more abundant after the impact, and the surviving ornithodirans (including dinosaurs) were left with ecological niches newly unoccupied by other archosaurs. The idea of a meteorite impact near or at the end of the Triassic that had an adverse effect on global ecosystems is not new,[40, 41] but the subsequent refining of this hypothesis illustrates a progress of the science behind it.

Early Evolutionary Trends in Dinosaurs

Dominance in Size and Number

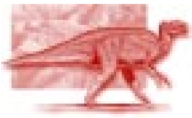
Regardless of the large- and small-scale evolutionary factors that shaped dinosaur evolution, their ascent to being the dominant land animals of terrestrial ecosystems within only about 25 million years is certainly noteworthy. The overall evolutionary trends observed in dinosaurs after their early evolutionary history include an increase in larger body sizes (especially in theropods and sauropodomorphs), increased diversity (i.e., more species), and a higher representation within terrestrial faunas. As represented by the skeletal record, dinosaurs went from about 6 percent of terrestrial amniote species to as much as 60 percent by the end of the Triassic Period.[42] The switch from relatively uncommon and small theropods to abundant and much larger theropods toward the end of the Triassic is also well reflected by dinosaur tracks.[43, 30]

Changes in Body Plans

More specific evolutionary trends include changes in other aspects of body plans, such as how some prosauropods (e.g., *Plateosaurus*), became adapted to a quadrupedal lifestyle, despite all indications that the most immediate ancestors of dinosaurs were bipedal.[44] This change in locomotion was likely a consequence of increased body size in prosauropods toward the end of the Triassic, in which they became the largest land herbivores of that time.

A Shift to Herbivory

Dinosaurs showed rapid diversification with respect to feeding, considering that carnivorous and herbivorous dinosaurs show up at nearly the same time in the geologic record. This early shift to herbivory for dinosaurs can be illustrated by prosauropod teeth from the Late Triassic, teeth that must have evolved in accordance with the availability of certain plants as food.[17] Prosauropod teeth were certainly a departure from the pointed and bladelike teeth of early theropods that were used for meat-eating. Prosauropod herbivory was apparently augmented by the use of gastroliths ("stomach stones") that were probably used to grind tough-to-digest food.[45, 46, 47] The use of gastroliths by terrestrial vertebrates for processing plant material was rare until the evolution of herbivorous dinosaurs. Throughout the remainder of the Mesozoic, sauropodomorphs, in particular, used them as aids to digestion.[48, 49]



Parenting

Reproductive behaviors may have been similar to those of later generations of dinosaurs, but only two Late Triassic dinosaur nests (containing dinosaur egg clutches) have been found so far.[50, 51] Thus, much is still unknown about whether dinosaur parents brooded or cared for their young, behaviors proposed for some Late Cretaceous dinosaurs (see Horner, page 71).[52]

Thermoregulation

Changes in thermoregulation ("cold-blooded" versus "warm-blooded") in archosaur lineages leading to dinosaurs are likewise poorly understood, but remain as intriguing areas for future research, considering current controversies about dinosaur thermoregulation (see de Ricqlès, page 79).[53, 54]

The fact that dinosaurs survived environmental factors that caused the extinctions of other archosaurs means that dinosaur ancestors had genes that favored their selection. These genes were later modified considerably during the successive 140-million years of the Jurassic and Cretaceous periods, but the persistence and diversification of dinosaurs during such a long span of time bespeaks of the successes of their initial adaptations. Their long story, still incomplete, began with their seemingly humble and obscure origins in the Triassic.

Where Did Dinosaurs Go?

Any ally inclined paleontologist will gleefully inform you that dinosaurs never went extinct, they are still here as birds. For those who do not know the "secret handshake" shared by cladists, one might think that such pronouncements are attributable to an unquestioning acceptance of what is printed in tabloid newspapers. As odd as the statement "birds are dinosaurs" may sound, it is just as apt as saying "humans are mammals." The key to understanding why birds are dinosaurs is related to hypotheses concerning ancestor-descendant relationships, just as was demonstrated for archosaurian ancestors of dinosaurs. Thus far, the hypothesis that modern birds descended from theropod ancestors in the Mesozoic Era (likely in the Middle or Late Jurassic) has not been falsified, despite its thorough testing for nearly 140 years. This line of inquiry into bird origins with relation to dinosaurs began when a skeleton of *Archaeopteryx* was discovered in 1861 and was immediately noted as an intermediate form between reptiles and birds by naturalist T.H. Huxley (see Currie, page 89).[55]

But to tell anything more about this story would be preemptory. Rest assured that a combination of genetic and environmental factors were involved, and we can observe those factors today. Birds represent some of the best examples of animals we have actually watched evolve (such as the famous "Darwin's finches" of the Galapagos [56, 57]). As a result, data pertinent to the evolution of dinosaurs will continue to be collected as birds and other archosaurs (such as crocodiles) are studied today, and given enough time, major parts of this chapter will have to be amended. The foundation of evolution is change, and the same goes for our knowledge of evolution. In this sense, the evolution of dinosaurs is no exception.

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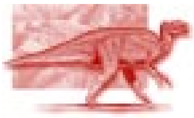

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