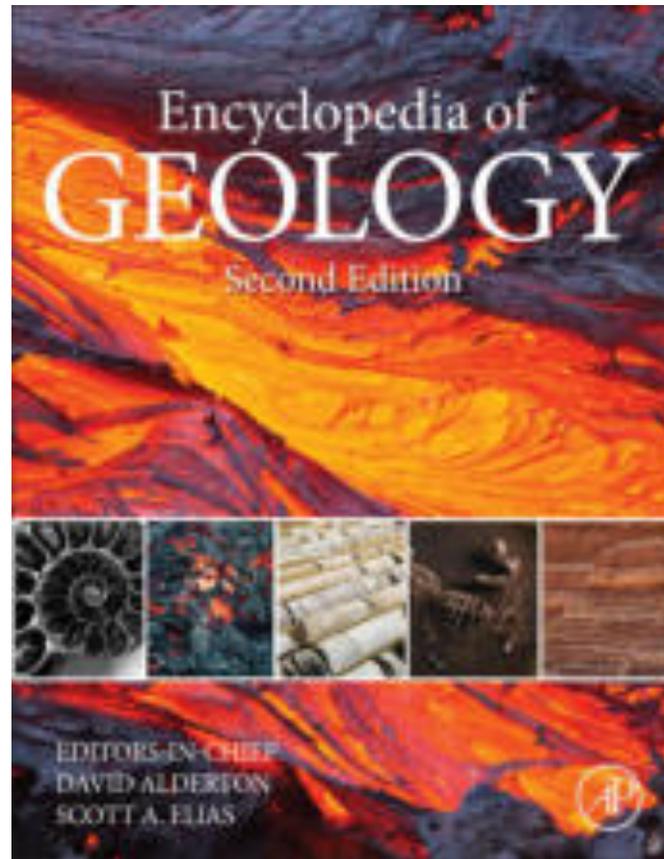


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## Dinosaur Origins

Júlio Cesar de Almeida Marsola and Max Cardoso Langer, Universidade de São Paulo, Ribeirão Preto, Brazil

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### Glossary

**Acetabulum** Concave articulation surface in the hip, formed by the ilium, pubis and ischium, which receives the femoral head.

**Air sac diverticula** Expansions of the respiratory system harbored by hollow surfaces of the bones, such as in cervical vertebrae.

**Apomorphies** Character states present in a monophyletic group that originated in its last common ancestor. Apomorphies are commonly regarded as evolutionary innovations that characterize a group. An example of an apomorphy is the hair of mammals.

**Carnian pluvial episode** An event of increased rainfall and perturbation of oceans and atmospheres around the world during the Carnian, in the early Late Triassic, which interrupted the common arid conditions of the time.

**Faunivorous** Animals that eat other animals, including vertebrates and invertebrates.

**Gondwanan** Related to what comes from Gondwana, a supercontinent that amalgamated what is now South America, Africa, Antarctica, Australia, Madagascar and India.

**Homologues** Structures that share the same ancestry, but do not necessarily perform the same function. Front flippers of whales, wings of bats, forelegs of cats and arms of humans are examples of homologous structures.

**Monophyly** The condition presented by groups sharing a single ancestor in a phylogenetic tree. A monophyletic group includes all descendants of that common ancestor.

**Pangaea** The last supercontinent of Earth, which congregated most landmasses from the Carboniferous to the Jurassic periods.

**Parasagittal** Any plane parallel to the sagittal plane. Limbs moving in the parasagittal plane are moving parallel to the medial plane of the body.

**Sister group** The monophyletic group that is closest to another monophyletic group in a phylogenetic tree.

**Temporal fenestrae** A fenestra is an opening between bones. The temporal fenestrae are two openings in the posterior region of the skull of diapsids, called the lower and the upper temporal fenestrae. In dinosaurs, the former is usually bordered by the jugal, postorbital, squamosal, and quadratojugal bones, whereas the latter is usually bordered by the postorbital, squamosal, and parietal bones.

**Transcontinental tetrapod biostratigraphy** Correlation of rock strata from different parts of the world by using their faunistic content, in this case, tetrapod fossils.

### Introduction

The Permo-Triassic mass extinction (ca. 250 million years ago) was the greatest biotic crisis Earth has experienced during the Phanerozoic. In the aftermath of this event, archosaurian reptiles became the dominant vertebrates in land ecosystems. Arguably the most notable group of archosaurs, the dinosaurs, emerged in the early Late Triassic in southern Pangaea, gradually spreading throughout the globe, with fossils found in every continent from the Early Jurassic onwards. The oldest unequivocal dinosaur fossils were collected from sedimentary rocks deposited on what is now South America, more specifically from southern Brazil and northwestern Argentina.

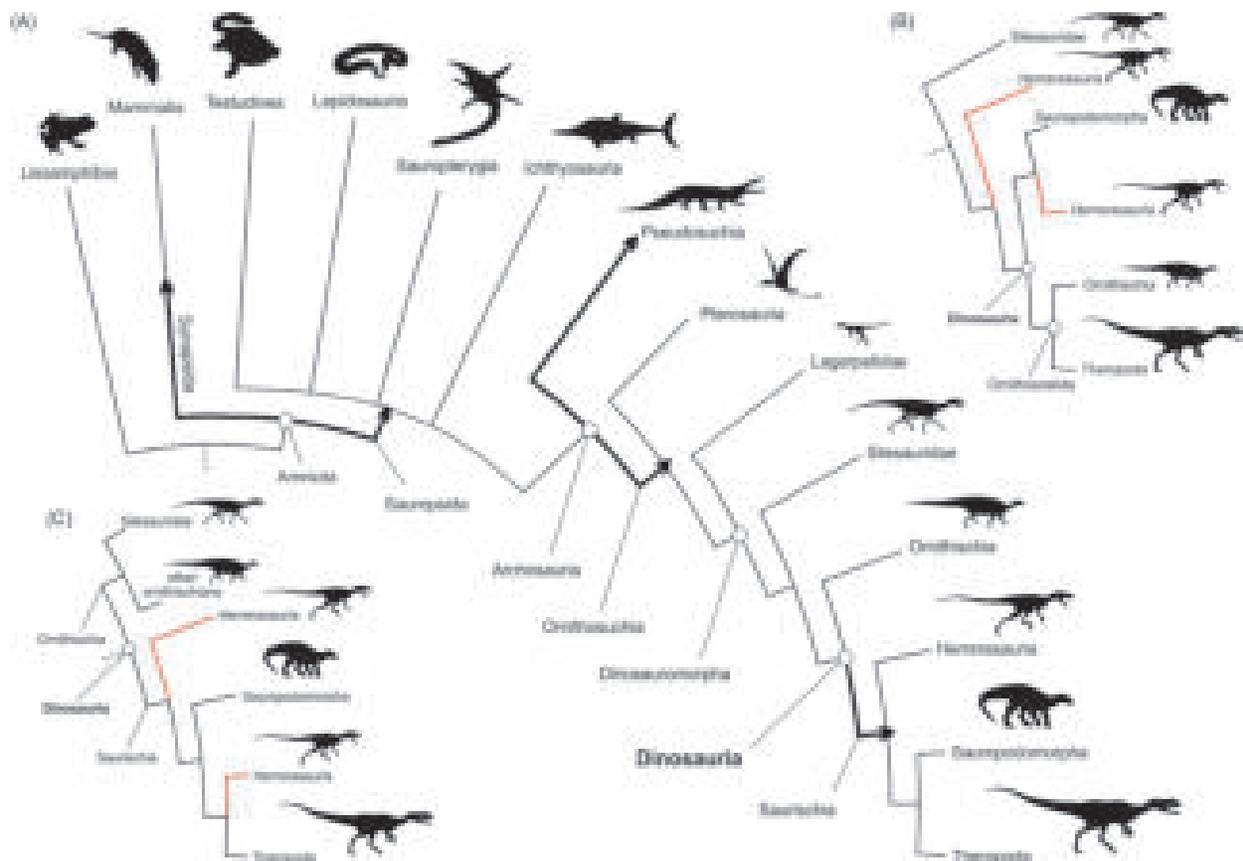
Although it was recently suggested that ornithischian dinosaurs emerged only during the Jurassic, the more orthodox (and still better supported) view is that the three main dinosaur lineages: Ornithischia, Sauropodomorpha, and Theropoda, were already part of Triassic ecosystems since slightly more than 230 Ma ago, during the Carnian stage. Ornithischians and theropods were very rare (perhaps even absent) at that time, and the first dinosaur radiation was characterized by a higher diversity of herrerasaurs, a predatory group with ambiguous affinities, and small-bodied sauropodomorphs. During the Norian (227–208 million years ago), dinosaurs became much more diverse and abundant, but only in the Jurassic did they achieve the ecological dominance that made

the group an example of evolutionary success. This event was likely triggered by another biotic crisis, the Triassic-Jurassic extinction (ca. 200 million years ago), that eliminated several therapsid lineages, such as dicynodonts and gomphodont cynodonts, as well as most pseudosuchians (members of the crocodile-line of archosaurs), such as aetosaurs, poposaurs, "rauisuchians," and phytosaurs. Those emptied niches were in part occupied by the dinosaurs, which flourished in the form of a great diversity of forms.

But what made dinosaurs resilient to the conditions that drove those other amniote lineages to extinction in the end of the Triassic, and what allowed their exceptional radiation on land ecosystems after that? The evolutionary success of dinosaurs is potentially explained by morphological and physiological traits, including bipedal locomotion with upright limbs moving in the parasagittal plane (made possible by additional sacral vertebrae, an open acetabulum, an in-turned femoral head, and a tarsal articulation that restricted rotational movements), a possibly an advanced breathing system with unidirectional flow and air sac diverticula (as indicated by pneumatized vertebrae), and a higher basal metabolism (as indicated by fast-growing juveniles and a body likely covered by filiform homologues of feathers). Much of these aspects have been recently reviewed in the specialized literature, but there is still much uncertainty regarding the origin of dinosaurs. Here, we aim to discuss some of those issues, highlighting the main evolutionary hypothesis and the directions that the research on the emergence of this fascinating group can take.

### Dinosaurs: A Unique Group of Archosaurs

Dinosaurs are archosaurs, the group that comprises living birds and crocodiles (Fig. 1). As such, they belong, along with other reptilian groups (i.e., turtles, lizards, snakes, and tuataras) in the amniote lineage known as Sauropsida, as opposed to the other main amniote lineage, the Synapsida, which includes mammals and their extinct relatives. Within Sauropsida, archosaurs, lepidosaurs (lizards, mosasaurs, snakes, and tuataras), and perhaps also turtles, belong into the Diapsida, a group generally characterized by the presence of two temporal fenestrae in the skull. Two other diapsid groups, the sauropterygians (including plesiosaurs) and the ichthyosaurs, thrived in the oceans during the Mesozoic, when dinosaurs dominated the terrestrial realm. Their evolutionary relationships are controversial, but they are surely not closely related to dinosaurs.



**Fig. 1** General cladograms depicting (A) a more conventional hypothesis of relationships for the major dinosaur groups and other main amniote lineages, the alternative (B) Ornithoscelida and (C) "silesaurid as ornithischian" hypotheses. Alternative positions for the herrerasaurs are indicated in red.

Archosaurs are divided into the crocodile (Pseudosuchia) and bird lineages, and dinosaurs consensually belong to the latter of these, which is referred to as Ornithosuchia or Avemetatarsalia. The bird lineage also includes the flying reptiles, the pterosaurs, which abounded during most of the Mesozoic, becoming extinct at the Cretaceous-Paleogene boundary; a temporal distribution much like that of the non-avian dinosaurs. Pterosaurs are the sister group to the Dinosauromorpha, a lineage that, beside the dinosaurs, includes also a series of small- to medium-sized archosaurs of Triassic age. Historically, these have been extensively sampled from the early Late Triassic Chanares Formation, in north-western Argentina, including forms such as *Lagerpeton*, *Lagosuchus*, *Marasuchus*, *Lewisuchus*, and *Pseudolagosuchus*. The former of those belong in the Lagerpetidae, one of the best-sampled lineages of non-dinosaurian dinosauromorphs and the sister group to all other members of that group, with records also in Late Triassic rocks of the western USA and Brazil. These are small, ca. 0.5 m long, probably bipedal animals that already exhibit many hind limb adaptations that characterize dinosaurs. In their turn, *Lewisuchus* and *Pseudolagosuchus* may belong to another relatively diverse group of dinosauromorphs, the Silesauridae, with occurrences also in Brazil (*Sacisaurus*), North America (*Eucoelophysis*), Europe (*Silesaurus*), and Africa (*Asilisaurus*, *Diodorus*, and *Lutungutali*), and a temporal record potentially stretching until the Middle Triassic in Africa. Silesaurids are medium-sized (about 1.5 m long in general) animals, with habits (quadrupedality, herbivory) that were, until their discovery, considered uncommon among early dinosauromorphs. Although heterodox, it has been suggested that silesaurids are, in fact, dinosaurs of the herbivorous Ornithischia branch. Dinosaurs are more distantly related to other Triassic archosaurs, which belong to the crocodile line. Yet, members of the Ornithosuchidae and “Rauisuchia” have been considered to be related to dinosaurs in the past. The monophyly of Dinosauria was established on modern roots around the end of the last century, by studies that also resurrected the notion that birds belong to the group. In fact, there is no present controversy that Aves belong to the Theropoda, the bipedal-carnivore branch of dinosaurs. As such, it is not possible to define Dinosauria as a natural group if birds are not included in it.

## The First Dinosaurs

The oldest undisputed dinosaur fossils are Gondwanan in origin, with a wealth of forms recorded from two stratigraphic units in South America, the upper Santa Maria Formation in southern Brazil and the Ischigualasto Formation in north-western Argentina (Table 1). These strata have been radiometrically dated as slightly older than 230 Ma, indicating a late Carnian age. The upper Santa Maria Formation has yielded the herrerasaur *Staurikosaurus pricei*, as well as the sauropodomorphs *Saturnalia tupiniquim*, *Buriolestes schultzi*, *Pampadromaeus barberenai*, and *Bagualosaurus agudoensis*, with the latter two coming from younger deposits. A more diverse dinosaur fauna has been unearthed from the Ischigualasto Formation, including the herrerasaurs *Herrerasaurus ischigualastensis* and *Sanjuansaurus gordilloi*, the sauropodomorphs *Panphagia protos*, *Chromogisaurus novasi*, and *Eoraptor lunensis*, as well as the putative theropod *Eodromaeus murphi* and the ornithischian *Pisanosaurus mertii*. Most of these come from the area of the Ischigualasto Provincial Park, in San Juan province, Argentina, but the latter taxon was collected from a different site, in La Rioja province, which may be younger in age. In addition, the dinosaur affinity of *Pisanosaurus mertii* was been recently challenged, with a Silesauridae affinity suggested instead. Outside South America, dinosaur remains have been recovered from stratigraphic units of putative Carnian age only in India and Zimbabwe, respectively from the Lower Maleri and the Pebbly Arkose formations, but these correspond to much more fragmentary specimens, and the inferred age of the strata in which they were found is based on poorly constrained transcontinental tetrapod biostratigraphy.

All dinosaur records from the Triassic of the northern continents (Eurasia and North America) are considered younger than those of the Ischigualasto and Santa Maria formations (Table 1). Large-bodied facultative-biped sauropodomorphs, informally called “prosauropods,” are the most abundant of them, in number of both specimens and species, and include iconic forms such as *Plateosaurus*, *Thecodontosaurus*, and *Riojasaurus*. Theropods are also relatively abundant in post-Carnian Triassic faunas, including taxa such as the European *Liliensternus*, the South American *Zupaysaurus*, and the North American *Coelophysis*, with the latter recognized on the basis of an impressive accumulation of hundreds of individuals from Ghost Ranch, New Mexico. Indeed, the consensually accepted theropod of possible oldest age, *Camposaurus arizonensis*, comes from the early Norian of the USA. Ornithischians, which are abundant in post-Triassic faunas, may lack a Triassic record. Two of the putative Triassic members of the group, the South African *Eocursor parvus* and the Argentinean “El Tranquilo” heterodontosaurid were collected from deposits that have been more recently considered Jurassic in age. On the other hand, the third of such taxa, *Pisanosaurus mertii*, as mentioned above, may not represent an ornithischian dinosaur.

An older than Carnian origin for dinosaurs has been inferred based on different lines of evidence. Fossil tracks suggest that dinosaurs, or animals that produce identical footprints, were present in Pangaea since the early Middle Triassic. In addition, a late Middle Triassic (Anisian: 247–242 million years ago) set of fossils collected in the Manda beds of Tanzania has been described as a putative dinosaur, named *Nyasasaurus parringtoni*. Its fragmentary nature, however, hampers a more precise assessment of its affinities. Finally, more complete skeletal remains from those same African strata have been assigned to the silesaurid *Asilisaurus kongwe*. The affinities of that taxon (i.e., whether it is a member of Silesauridae and whether silesaurids are dinosaurs or their sister group) may imply that the dinosaur lineage was present since the Middle Triassic. Therefore, although direct evidence, in the form of uncontroversial body fossils, is missing, there is a reasonable chance that dinosaurs already roamed southern Pangaea from the Middle Triassic.

**Table 1** Main early dinosaur and non-dinosaur dinosauriform records around the world

Taxa	Provenance	Age	Preserved material
<b>Dinosauromorpha</b>			
<b>Lagerpetidae</b>			
<i>Lagerpeton chanarensis</i>	Chañares Formation, northwest Argentina	early Carnian, Late Triassic	Partial skeleton
<i>Dromomeron</i> sp.	Chinle and Dockum groups, New Mexico and Texas, USA	Norian, Late Triassic	Isolated elements
<i>Ixalerpeton polesinensis</i>	Santa Maria Formation, south Brazil	late Carnian, Late Triassic	Partial skeleton
<b>Silesauridae<sup>a</sup></b>			
<i>Eucoelophysis baldwini</i>	Chinle Formation, New Mexico, USA	Norian, Late Triassic	Partial skeleton
<i>Silesaurus opolensis</i>	Drawno Beds, Krasiejów claypit, Opole, Poland	late Carnian, Late Triassic	Nearly complete skeletons
<i>Sacisaurus agudoensis</i>	Caturrita Formation, South Brazil	Norian, Late Triassic	Isolated elements
<i>Asilisaurus kongwe</i>	Manda Beds, Ruvuma, Tanzania	late Anisian, Middle Triassic	Nearly complete skeleton
<b>Dinosauria</b>			
<b>Ornithischia</b>			
<i>Pisanosaurus mertii<sup>b</sup></i>	Ischigualasto Formation, northwest Argentina	late Carnian, Late Triassic	Partial skeleton
<b>Herrerasauridae<sup>c</sup></b>			
<i>Herrerasaurus ischigualastensis</i>	Ischigualasto Formation, northwest Argentina	late Carnian, Late Triassic	Complete skeleton
<i>Staurikosaurus pricei</i>	Santa Maria Formation, south Brazil	late Carnian, Late Triassic	Partial skeleton
<b>Sauropodomorpha</b>			
<i>Eoraptor lunensis</i>	Ischigualasto Formation, northwest Argentina	late Carnian, Late Triassic	Complete skeleton
<i>Saturnalia tupiniquim</i>	Santa Maria Formation, south Brazil	late Carnian, Late Triassic	Nearly complete skeleton
<i>Panphagia protos</i>	Ischigualasto Formation, northwest Argentina	late Carnian, Late Triassic	Partial skeleton
<i>Pampadromaeus barberenai</i>	Santa Maria Formation, south Brazil	late Carnian, Late Triassic	Partial skeleton
<i>Buriolestes schultzi</i>	Santa Maria Formation, south Brazil	late Carnian, Late Triassic	Nearly complete skeleton
<b>Theropoda</b>			
<i>Eodromaeus murphi<sup>d</sup></i>	Ischigualasto Formation, northwest Argentina	late Carnian, Late Triassic	Nearly complete skeleton
<i>Tawa hallae<sup>d</sup></i>	Chinle Formation, New Mexico, USA	Norian, Late Triassic	Complete skeleton
<i>Camposaurus arizonensis</i>	Chinle Formation, Arizona, USA	Norian, Late Triassic	Incomplete epipodium and tarsal bones

<sup>a</sup>Possible ornithischian dinosaurs.

<sup>b</sup>Possible silesaurid.

<sup>c</sup>Possible theropod dinosaurs.

<sup>d</sup>Possible non-theropod dinosaurs.

## What Makes a Dinosaur?

To understand “what makes a dinosaur” it is necessary to go back to research carried out in the 19th century. In 1842, Sir Richard Owen first recognized that a set of fossils recently discovered in England, that is, *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*, formed a novel group of extinct reptiles he named Dinosauria. For him, these animals differed from all other reptiles by their much larger body-sizes and by uncommon traits of the hips and limbs related to an upright posture. Over the years, hundreds of new dinosaurs were discovered, disclosing a much greater variety of body plans than those originally imagined. Most dinosaurs were indeed gigantic, but several were small-bodied, to the point that some achieved the ability to fly. However, although currently accepted by the vast majority of paleontologists, birds were not included in the original conceptualization of the group by Owen. This is the case now because modern biology aims to establish monophyletic or “natural” groups, whose evolutionary history is unique and all encompassing, that is, including only organisms with a single origin, and all those sharing that single origin. This uniqueness is identified based on a set of novel traits that characterize the group, and several of such synapomorphies have been proposed to define Dinosauria in recent years. The problem is that these traits cannot be firmly establish unless the evolutionary patterns at the origin of the group are also firmly established, and, as seen below, there are doubts about the relationships between the three main dinosaur lineages and with two related Triassic groups (silesaurids and herrerasaurs).

Because the traditional understanding implies a composition of Dinosauria that includes ornithischians, theropods, and sauropodomorphs, the most recent common ancestor of these three groups corresponds to the first dinosaur. Yet, given the doubts about their relationships, we cannot clearly withdraw the morphology of this hypothetical form from such phylogenetic hypotheses. It is possible, however, to more broadly identify “typical” dinosaur features, present in the origin of the group, even though some will not be shared by all early dinosaurs, whereas others will in fact characterize slightly more encompassing groups. Some of the most distinctive of these features are a longer deltopectoral crest in the humerus, three sacral vertebrae, an open acetabulum in

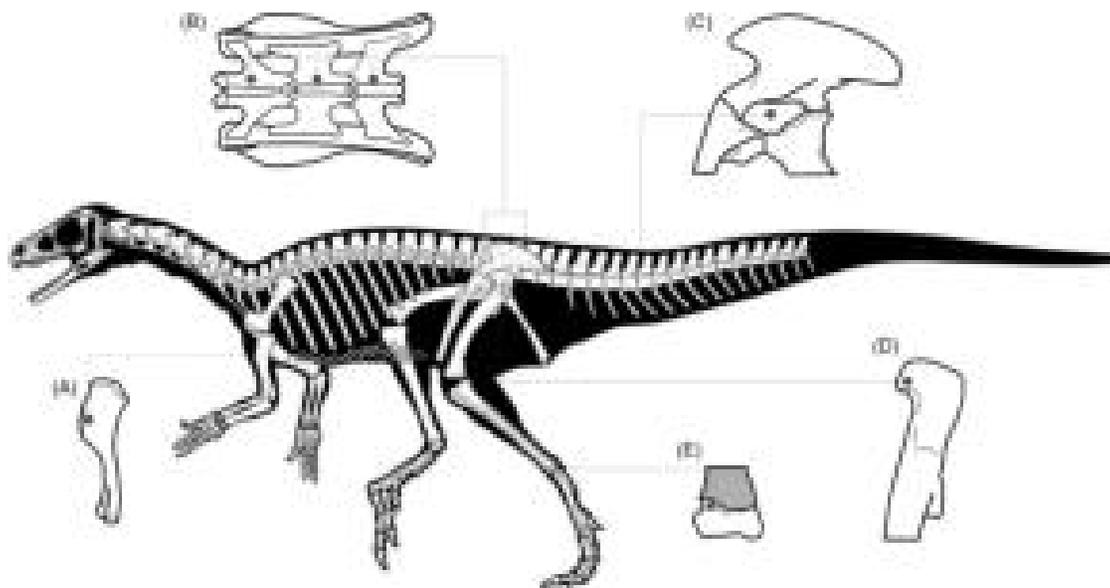
the pelvic girdle, an in-turned femoral head distinctly set from the femoral shaft, and a larger ascending process of the astragalus (Fig. 2).

All the features mentioned above are somehow related to the acquisition of upright posture and bipedal gait characteristic of early dinosaurs. Freeing the forelimbs from carrying the loads of the body mass allowed them to be used in other tasks, and a well-developed deltopectoral crest is indicative of powerful forelimb adduction. On the other hand, the increasing number of sacral vertebrae means that dinosaurs had a more robust connection between the vertebral column and the pelvic limb, which is required for effective bipedalism. That is also the case of the open acetabulum and the in-turned femoral head, structures that indicate a robust articulation in which the weight is loaded by the vertically positioned limbs. This constitutes a substantial change from the more sprawled ancestral condition, still seen nowadays in crocodiles, in which the acetabulum is fully closed by a bony wall and the femoral head is circular and smaller. The morphology present in dinosaurs creates a more stable rotational articulation between the hip and the femur. Together with those of the knee and ankle, which allow mostly fore-and-aft movements, this arrangement optimizes a parasagittal movement of the limbs, essential for an efficient bipedal gait. As for the ascending process of the astragalus, this provides dinosaurs a more tight articulation with the tibia, differing from the ancestral condition in which the tibia and the astragalus have a more planar articulation. This new condition constrains that junction to a hinge articulation between the proximal tarsals and the metatarsals, the so-called mesotarsal articulation, hampering rotational movements of the ankle. This skeletal configuration leads to more stable bipedal locomotion, especially at higher speeds.

### Dinosaurs' Family Tree

Beginning with the work of the British paleontologist Harry Seeley at the end of the 19th century, dinosaurs have been classified in two main lineages, Saurischia (or lizard-hipped dinosaurs, like *Tyrannosaurus* and *Apatosaurus*) and Ornithischia (or bird-hipped dinosaurs, like *Triceratops* and *Stegosaurus*). During most of the following century, although individually accepted as natural groups, these two kinds of dinosaurs were not considered very closely related to one another. Instead, they were considered to have been derived from different archosaur ancestors. Dinosaur monophyly, that is, the grouping of Saurischia and Ornithischia exclusive of other main archosaur groups, was hinted during the 1970s, firmly established by the first phylogenetic studies of the group in the 80s, and is now widely accepted. In fact, there are three major dinosaur groups: Ornithischia, Theropoda, and Sauropodomorpha (Fig. 1). The monophyly of each of them has never been seriously questioned, and the latter two are normally grouped into Saurischia. Yet, there is much uncertainty about the position of some Triassic forms relative to these three major groups. In addition, there were also recent challenging ideas on the traditional Saurischia-Ornithischia dichotomy, with the proposal that theropods are instead nested together with ornithischians in a group named Ornithoscelida, with sauropodomorphs placed as their immediate sister group (Fig. 1).

One of the Triassic dinosaur lineages with a more controversial phylogenetic position is the Herrerasauria. This consists of a group of medium- to large-sized predators with a few uncontroversial members, all from South America, with possible records also



**Fig. 2** Set of typical dinosaur features depicted by *Eoraptor lunensis*. (A) Humerus in medial view indicating a longer deltopectoral crest; (B) three sacral vertebrae shown in dorsal view; (C) pelvis in lateral view indicating an open acetabulum; (D) proximal part of the femur in anterolateral view indicating an in-turned head distinctly set from the shaft; (E) tibia (in gray) and astragalus in anterior view showing a large ascending process of the astragalus. Modified from Sereno, P.C., Martínez, R.N., and Alcober, O.A. (2012). Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). *Journal of Vertebrate Paleontology* 32(suppl. 1), 83–179.

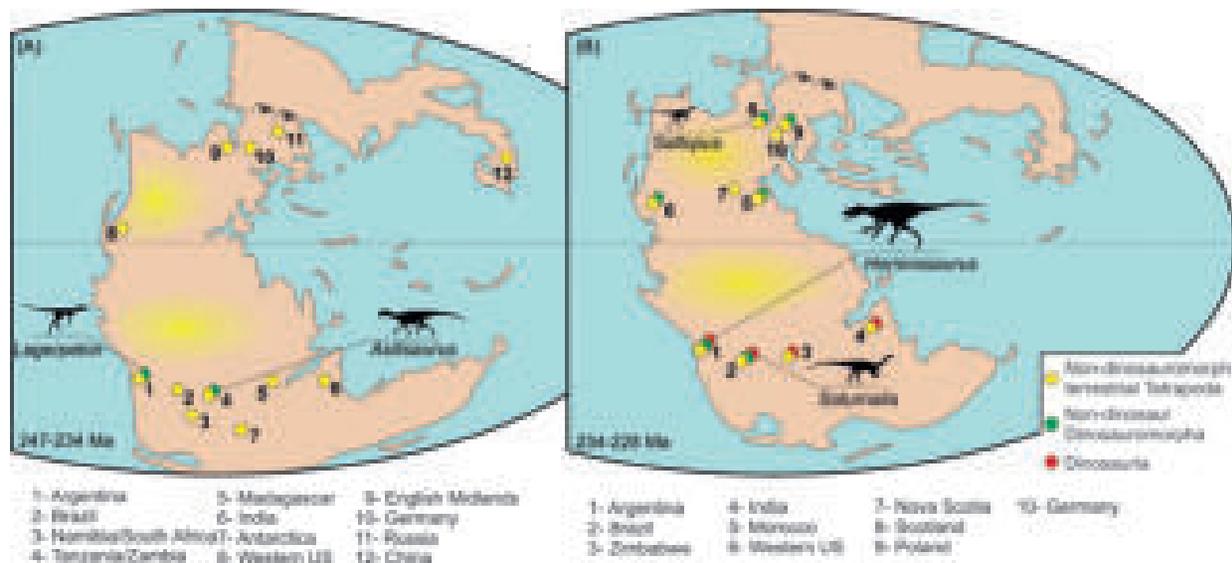
in the United States. They have been alternatively placed as one of the earliest branches of Theropoda, or as saurischians outside the Theropoda-Sauropodomorpha dichotomy. It has also been suggested that they are placed in the sauropodomorph lineage and even outside the smallest group to encompass Ornithischia, Theropoda, and Sauropodomorpha. In the latter case, herrerasaurs would not be considered dinosaurs *sensu stricto*, but would represent their immediate sister group. Yet, mainstream proposals hold the dinosaur sister group position to the Silesauridae, another lineage with a controversial position at the roots of Dinosauria. Although more commonly placed as non-dinosaur Dinosauromorpha, some studies have suggested that they actually belong into the ornithischian lineage, sharing with those dinosaurs the presence of an edentulous tip of the lower jaw. On the contrary, as mentioned above, the best-known possible ornithischian of Triassic age, *Pisanosaurus mertii*, may correspond to a Silesauridae, so that the dinosaur group Ornithischia could be absent from Triassic deposits. This matches a recent suggestion that ornithischians represent a younger lineage of Dinosauria, branching in the Jurassic from within theropods.

## Biogeography

Dinosaur fossils have been recorded on all continents, including Antarctica. This is a good metric of the evolutionary success of the group, which started back in the Triassic, probably in the region that eventually became South America. As aforementioned, the oldest and unequivocal dinosaur fossils come from deposits of that continent, which represented the southwestern portion of Pangaea (Fig. 3). For this reason, a long-standing hypothesis regards South America as the ancestral paleogeographical range of the group, preceding the gradual and successful expansion of their distribution over the supercontinent. Although it was recently proposed that dinosaurs could have originated in the northern part of Pangaea, where Europe is today, novel analyses have strongly supported the previous biogeographic scenario. Thus, the classic view of a southern origin for dinosaurs is currently better supported than before.

As previously discussed, new cladistic hypotheses for the origin of Dinosauria have not only provided alternative phylogenetic arrangements for its three main lineages, but also envisages the possibility that silesaurids belong in the group. However, recent biogeographic analyses consistently affirm southern Pangaea as the ancestral area of dinosaurs regardless of which phylogenetic hypothesis is employed, that is, considering silesaurids outside Dinosauria or as ornithischians, and considering the Saurischia-Ornithischia dichotomy or the newly proposed Ornithoscelida arrangement. Additionally, the analyses have also taken other variables in account, such as the increasing taxonomic sampling of early dinosaurs and the record of non-dinosaurian dinosauromorphs in the northern continents, with no effects on the results. This means that the southern Pangaeian hypothesis has been robust through time, with the many new early dinosaurs discovered in the last decades exerting no influence on the optimization of the ancestral area for the group. Further, such analyses discarded the idea that Late Triassic non-dinosaurian dinosauromorph body fossils and putative Middle Triassic dinosauromorph tracks from Europe could indicate that dinosaurs originated in northern Pangaea.

It is noteworthy that, despite the many Middle Triassic and early Carnian deposits worldwide that have been investigated, representing similar ecosystems as those later inhabited by dinosaurs and with numerous records of non-dinosauromorph



**Fig. 3** Palaeogeographic distribution indicating continental deposits with non-dinosauromorph Tetrapoda, non-dinosaur Dinosauromorpha, and Dinosauria during the Middle Triassic/early Carnian (A) and late Carnian (B), showing that the oldest undisputed dinosaur records come from the southern part of Pangaea. From: Marsola, J. C. A., Ferreira, G. S., Langer, M. C., Button, D. J., & Butler, R. J. (2018). Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. *Paleontology*. <https://doi.org/10.1111/pala.12411>.

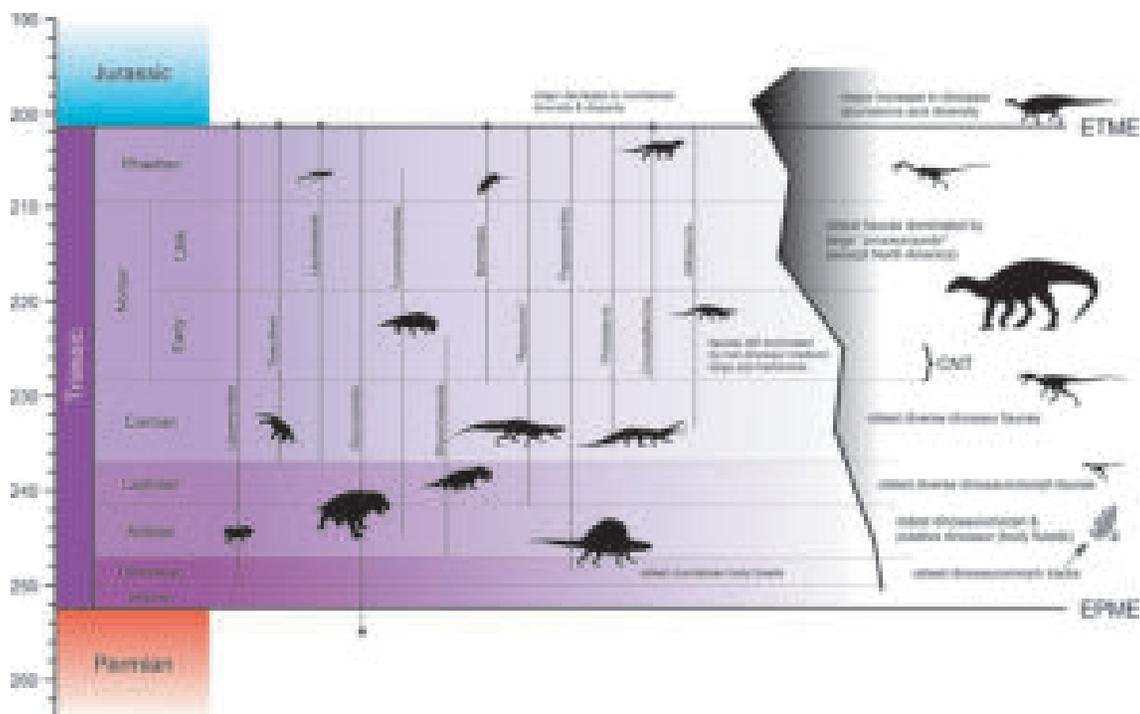
terrestrial tetrapods, none has yielded an uncontroversial dinosaur, whereas other dinosauromorphs were sampled only in Africa and South America (Fig. 3). Indeed, this also indicates that dinosaurs were restricted to the southern parts of Pangaea at the beginning of their evolutionary history.

### Paleoecology and Paleobiology of the Dinosaur Origins

Dinosaurs were not always as prevalent in Mesozoic ecosystems as they were during the Jurassic and the Cretaceous. Throughout the Late Triassic, the group played a more discrete role in terrestrial landscapes, with their initial radiation encompassing some key events. Most of the first dinosaurs were small animals, no more than 1.5 m long, highly contrasting with the terrestrial top-predators of the time, crocodylian-line archosaurs such as the “rauisuchians” *Saurosuchus*, *Batrachotomus*, and *Prestosuchus*, and the phytosaurs *Parasuchus*, *Leptosuchus*, and *Machaeroprotopus*, which reached up to 6–7 m long. Besides, the most common plant-eating animals of the time were the rhynchosaurs, a bizarre group of beaked archosauromorphs, as well as therapsids such as dicynodonts and gomphodont cynodonts. In this faunistic context, the emergence of dinosaurs may be seen as discrete. Although they were already relatively diverse in the Carnian, with about 10 species recognized so far, their fossils never represent more than 5% of the terrestrial tetrapod records of the stratigraphic units in which they occur. Although this hypothesis needs to be more deeply scrutinized, recent studies have shown that this initial dinosaur diversification was nearly synchronous with the Carnian Pluvial Episode, suggesting that both events could be somehow related.

Latter in the Triassic, in the Norian and Rhaetian (208–201 million years ago), dinosaurs continued to increase in diversity, but they most importantly became more abundant (Fig. 4). This may be related to climatic changes in the Pangaeian ecosystems following the Carnian Pluvial Episode, with a significant aridification of the supercontinent leading to the extinction of plants and key-herbivores at the Carnian-Norian boundary. Indeed, common plant-eating animals, like rhynchosaurs and some therapsids, became less diverse in the Norian, and the higher abundance of dinosaurs in that period was mainly achieved by the radiation of larger omnivore sauropodomorphs, the so-called “prosauropods.” Yet theropods also experienced an increase in diversity at that time, achieving larger sizes and sharing the ecological role of top predators with various pseudosuchians.

The Early Jurassic marks another important event in the early radiation of dinosaurs, which comprises the occupation of emptied niches (Fig. 4). Whereas dinosaurs and other modern sauropsid (crocodylians, turtles, lepidosaurs) and therapsid (mammals) lineages survived the Triassic-Jurassic extinction event, other terrestrial tetrapods, such as phytosaurs, poposaurs, “rauisuchians,” aetosaurs, gomphodont cynodonts, and probably dicynodonts became extinct at that time. This extinction event was likely related to climatic changes (global warming) triggered by extensive volcanic eruptions, which resulted in one of the largest igneous provinces on earth, the Central Atlantic Magmatic Province, which produced volcanic deposits measuring up to 300 m thick in



**Fig. 4** Macroevolutionary scenario for the origin and diversification of dinosaurs. Abbreviations: CNT, Carnian-Norian turnover; PTME, end-Permian mass extinction; ETME, end-Triassic mass extinction. From: Benton, M. J., Forth, J., and Langer, M. C. (2014). Models for the rise of the dinosaurs. *Current Biology*, 24(2), R87–R95.

the northern Atlantic coasts of North America and Africa. In the aftermath of this extinction, dinosaurs occupied part of the niches left empty by the above mentioned extinct tetrapods, leading to the emergence of diverse theropods and much larger sauropodomorphs, as well as armored groups of ornithischians. Following this opportunistic radiation, dinosaurs dominated terrestrial ecosystems for the next 135 millions of years.

Some physiological characters may have helped dinosaurs to thrive in such extreme conditions. Although it is hard to gather unequivocal evidence for such adaptations, an increasing number of studies have reinforced the hypothesis that dinosaurs had high metabolic rates. Evidence supporting this idea includes the presence of fibrolamellar bone tissues in early dinosaurs, indicating rapid growth, and phylogenetic reconstructions demonstrating that the ancestral dinosaur was probably covered by filamentous integumentary structures homologous to feathers, which would provide thermal insulation. In addition, pneumatic foramina for air sac diverticula, at least in cervical vertebrae, as seen in theropods such as *Coelophysis*, suggest the presence of a highly efficient respiration system, probably involving unidirectional flow as seen in modern birds today. Bipedalism, at least facultative in the case of early sauropodomorphs, was another important acquisition. Dinosauromorphs were the first vertebrate animals to walk bipedally and erect, and this ability was inherited by dinosaurs, allowing faster and more agile locomotion, and also freeing the forelimbs for other tasks.

As for the ancestral feeding behavior of dinosaurs, the few available lines of evidence suggest that most non-dinosaurian dinosauromorphs fed on small animals. One exception was the silesaurids, which had a modified dentition and a beak-like lower jaw tip that suggests that this group included plants in their diet. Among dinosaurs, the curved blade-like teeth of herrerasaurs and early theropods clearly indicate a strictly carnivorous diet, whereas ornithischians, are usually interpreted as full herbivores. As for sauropodomorphs, whereas sauropods were full herbivores, most “prosauropods” are considered to have had a mixed diet. Indeed, the earliest sauropodomorphs tended to have fewer herbivorous adaptations in their dentition, with taxa such as *Buriolestes schultzi* being most likely carnivores. This conclusion agrees with new studies on neuroanatomy, which demonstrate that these animals were capable of active hunting. In fact, defining the ancestral diet for dinosaurs requires a better understanding of their relationships than is currently available. However, only the more conventional scenario, with silesaurids outside Dinosauria and the classical Saurischia-Ornithischia dichotomy, allows the reconstruction of a diet other than carnivory as ancestral for the group. Therefore, the odds are that dinosaurs originally fed on other animals.

## Further Reading

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