The origin and early radiation of dinosaurs

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ABSTRACT

Dinosaurs were remarkably successful during the Mesozoic and one subgroup, birds, remain an important component of modern ecosystems. Although the extinction of non-avian dinosaurs at the end of the Cretaceous has been the subject of intense debate, comparatively little attention has been given to the origin and early evolution of dinosaurs during the Late Triassic and Early Jurassic, one of the most important evolutionary radiations in earth history. Our understanding of this keystone event has dramatically changed over the past 25 years, thanks to an influx of new fossil discoveries, reinterpretations of long-ignored specimens, and quantitative macroevolutionary analyses that synthesize anatomical and geological data. Here we provide an overview of the first 50 million years of dinosaur history, with a focus on the large-scale patterns that characterize the ascent of dinosaurs from a small, almost marginal group of reptiles in the Late Triassic to the preeminent terrestrial vertebrates of the Jurassic and Cretaceous. We provide both a biological and geological background for early dinosaur history. Dinosaurs are deeply nested among the archosaurian reptiles, diagnosed by only a small number of characters, and are subdivided into a number of major lineages. The first unequivocal dinosaurs are known from the late Carnian of South America, but the presence of their sister group in the Middle Triassic implies that dinosaurs possibly originated much earlier. The three major dinosaur lineages, theropods, sauropodomorphs, and ornithischians, are all known from the Triassic, when continents were joined into the supercontinent Pangaea and global climates were hot and arid. Although many researchers have long suggested that dinosaurs outcompeted other reptile groups during the Triassic, we argue that the ascent of dinosaurs was more of a matter of contingency and opportunism. Dinosaurs were overshadowed in most Late Triassic ecosystems by crocodile-line archosaurs and showed no signs of outcompeting their rivals. Instead, the rise of dinosaurs was a two-stage process, as dinosaurs expanded in taxonomic diversity, morphological disparity, and absolute faunal abundance only after the extinction of most crocodile-line reptiles and other groups.

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1. Introduction

Dinosaurs are icons of prehistory, and remain an important part of the modern world in the form of some 10,000 living species of birds. Although the extinction of non-avian dinosaurs at the end of the Cretaceous Period (~65 Ma) has long been a focus of fascination and debate, the origin and early diversification of dinosaurs is not nearly as well understood. During the past 25 years, numerous new fossils, reinterpretations of long-forgotten specimens, and numerical analyses have significantly revised our understanding of this major macroevolutionary event, which is one of the most profound and important evolutionary radiations in the history of life.

In particular, new fossil material from Argentina (Sereno and Novas, 1992; Sereno et al., 1993; Martinez and Alcober, 2009), Brazil (Langer et al., 1999; Leal et al., 2004; Ferigolo and Langer, 2007), Africa (Yates and Kitching, 2003; Butler et al., 2007; Nesbitt et al., 2010; Yates et al., 2010), Europe (Dzik, 2003), and southwestern North America (Irmis et al., 2007a; Nesbitt et al., 2009b) has clarified the relationships of the first dinosaurs and their close relatives. Reanalysis of existing specimens has improved our understanding of character evolution on the lineage leading to Dinosauria (e.g., Sereno and Arcucci, 1994a,b; Langer and Benton, 2006; Brusatte et al., 2010b) and has changed our understanding of the distribution of early dinosaurs in time and space (Parker et al., 2005; Irmis et al., 2007b; Nesbitt et al., 2007). Most recently, quantitative analyses, which take into account this avalanche of new morphological and geological data,

have examined in unprecedented detail the macroevolutionary, biogeographical, and paleoecological changes associated with the rise of dinosaurs (e.g., Brusatte et al., 2008a,b; Nesbitt et al., 2009b, 2010).

In this paper, we summarize current knowledge on the origin and early diversification of dinosaurs during the first 50 million years of their evolutionary history, from the Triassic through the Early Jurassic. Our aim is to provide a comprehensive synopsis of early dinosaur evolution, which may be of interest not only to specialists on dinosaurs or early Mesozoic earth history, but paleontologists, geologists, evolutionary biologists, and educators in general. As such, we frame our review in broad strokes, and provide information on the biological, geological, and evolutionary backdrop to early dinosaur history. We review the relationships of dinosaurs to other reptiles, define dinosaurs and discuss the anatomical features that distinguish them from other groups, summarize the early history of the major dinosaur clades, and discuss the physical and climatic background of early dinosaur faunas. We close by integrating this information into a comprehensive picture of the large-scale macroevolutionary patterns that characterize the origin and ascent of dinosaurs.

While our paper was in review, an independent summary of dinosaur origins was published by Langer et al. (2010). As these two manuscripts were written independently and at the same time, we do not discuss the conclusions of Langer et al. (2010) here, but note that the two papers largely complement each other in the discussion of early dinosaur evolution.
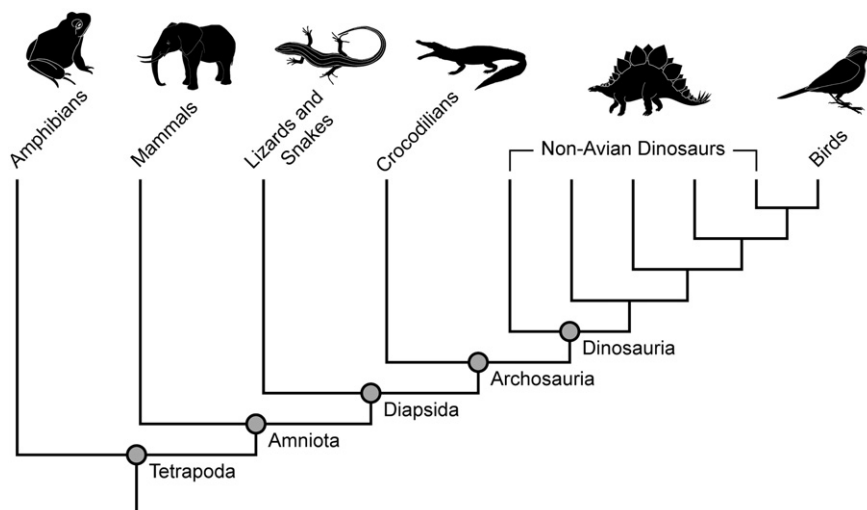
Fig. 1. A cladogram (phylogenetic or genealogical tree) of the major groups of tetrapods, the land-living vertebrates. Dinosaurs, including their avian descendants, are deeply nested within the Archosauria, a group that also includes crocodiles and their kin. Silhouettes not to scale. Cladogram delineated by Simon Powell, University of Bristol.

2. The biological setting for the origin of dinosaurs

2.1. Archosauria: the ruling reptiles

Dinosaurs are members of a speciose clade of vertebrates called the Archosauria (the "ruling reptiles": Cope, 1869), which includes birds, crocodylians, and their extinct relatives (note that we follow the definition of Archosauria as a crown group, consisting of birds, crocodiles, and all descendants of their most recent common ancestor, sensu Gauthier, 1986). Archosaurs are deeply nested within the radiation of land-living vertebrates, and themselves are a subgroup of diapsid reptiles (a more inclusive clade that also includes lizards, snakes, and possibly turtles: Fig. 1; Benton, 2005). The archosaur lineage originated approximately 245 million years ago, just a few million years after the devastating Permo-Triassic mass extinction. This extinction was the most profound period of mass death in geological history and is estimated to have wiped out up to 75–95% of all species (Raup, 1979; Stanley and Yang, 1994; Benton, 2003; Erwin, 2006; Clapham et al., 2009). In its aftermath, ecosystems reshuffled and entirely new groups of organisms arose and diversified, including "modern" lineages such as turtles, mammals, lepidosaurs, and archosaurs (e.g., Benton et al., 2004; Sahney and Benton, 2008).

The archosaur lineage diversified rapidly after its origination at the beginning of the Triassic (Nesbitt, 2003 see also Kubo and Benton, 2009). One of the oldest unequivocal archosaurs, *Arizonasaurus*, is known from the Anisian (ca. 243 Ma) of the southwestern United States (Nesbitt, 2003, 2005). It is a derived member of the "crocodile line" of archosaur phylogeny (Crurotarsi, also known as Pseudosuchia), which along with the "bird line" (alternatively known as Avemetatarsalia, Ornithodira, or Ornithosuchia) is one of the two major subdivisions of the archosaur clade (Fig. 2). The derived position of *Arizonasaurus* within Crurotarsi indicates that several other archosaur lineages extend back into the Middle Triassic, but the archosaur fossil record of this time is poor. During the Late Triassic, archosaurs of both major subgroups were exceptionally abundant in ecosystems across the globe. This period of time, from approximately 235–201 million years ago, witnessed the evolution of several morphologically distinctive archosaur clades that filled a variety of ecological roles (Nesbitt, 2007; Brusatte et al., 2008a; Nesbitt et al., 2010). Most of these groups, such as the long-snouted and semi-aquatic phytosaurs, the heavily armored aetosaurs, the sleek and predatory ornithosuchids, and the predatory and omnivorous "rauisuchians," became extinct by the end of the Triassic. Only the pterosaurs and dinosaurs, from the bird line, and the crocodylomorphs, derived members of the crocodile line, survived into the Jurassic.
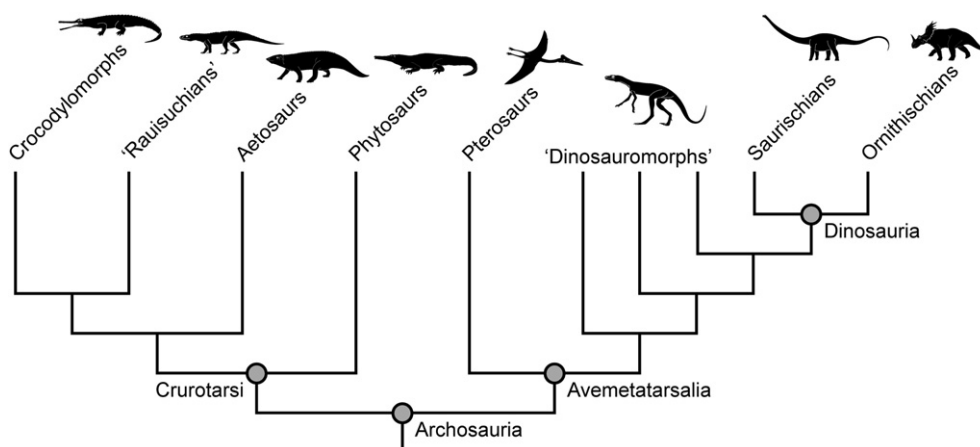
Fig. 2. A cladogram of the major groups of archosaurs. Archosauria is divided into two major groups, the crocodile line (Crurotarsi) and the bird line (Avemetatarsalia). The crocodile line is further subdivided into several subgroups (the long-snouted and semi-aquatic phytosaurs, the heavily armored aetosaurs, the mostly predatory rauisuchians, and true crocodylomorphs), whereas the bird line includes dinosaurs, birds, and a handful of close "dinosauromorph" cousins. Silhouettes not to scale. Cladogram delineated by Simon Powell, University of Bristol.

2.2. Avemetatarsalia: the "bird-line" of archosaur phylogeny

Dinosaurs belong to Avemetatarsalia (an essentially equivalent group is also known as Ornithodira, or in the older literature, Ornithosuchia), the "bird line" of archosaur phylogeny. Extant birds, the only living members of this subgroup, are descended from theropod dinosaurs (e.g., Gauthier, 1986; Padian and Chiappe, 1998). However, several extinct Mesozoic taxa also belong to the bird-line lineage, including the non-avian dinosaurs, pterosaurs (flying reptiles), and a handful of early non-dinosaurian dinosauromorphs that are the closest relatives of dinosaurs (herein referred to as "basal dinosauromorphs"). Only a small sample of basal dinosauromorphs has been discovered. These range in age from the Middle–Late Triassic and are known primarily from small, fragmentary, and incomplete specimens often missing entire regions of the skeleton. Most of these taxa resemble small predatory dinosaurs in their overall anatomy (e.g., *Lagerpeton* and *Marasuchus*: Sereno and Arcucci, 1994a,b), whereas recently discovered taxa such as *Silesaurus* (Dzik, 2003), *Sacisaurus* (Ferigolo and Langer, 2007), and *Asilisaurus* (Nesbitt et al., 2010) were quadrupedal herbivores or omnivores whose teeth superficially resemble those of ornithischian dinosaurs. Phylogenetic analyses indicate that these herbivorous taxa form their own distinct clade, Silesauridae, which is the immediate sister taxon (closest relative) of Dinosauria (Irmis et al., 2007a; Brusatte et al., 2008a, 2010b; Nesbitt et al., 2009b, 2010; Langer et al., 2010). The recent discovery of Late Triassic representatives of these groups (e.g., Dzik, 2003 and Irmis et al., 2007a) demonstrates that they co-existed with dinosaurs for at least 15 million years.

2.3. Dinosauria: definition

As with any group of organisms, the designation of what does and does not constitute a dinosaur (Fig. 3) is a matter of definition. Traditional taxonomists, beginning with Owen (1842), defined Dinosauria based on a set of shared anatomical features. Fossil reptiles were considered dinosaurs if they possessed these characteristics, which historically have related to size, posture, and locomotion (see below). However, most modern systematists define groups of organisms based on ancestry instead of the possession of "essential" characters (e.g., de Queiroz and Gauthier, 1990, 1992; Sereno, 2005). Under such a system, known as phylogenetic taxonomy, an animal is a dinosaur only if it falls out in a certain place on the tree of life. Anatomical characteristics are used to reconstruct the genealogical tree, and serve to diagnose groups, but their possession is not an essential requirement for group membership.
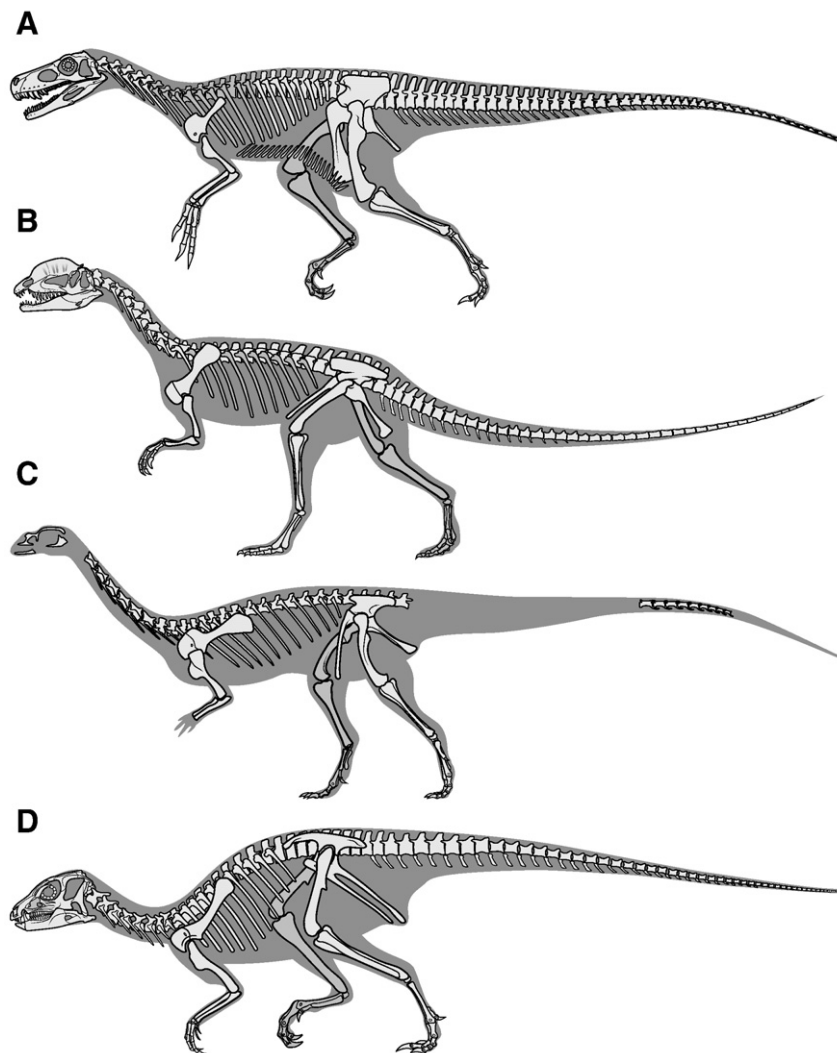
Fig. 3. Skeletal reconstructions of four Late Triassic–Early Jurassic dinosaurs, representing the major subgroups of early dinosaurs. These reconstructions are designed to provide a general guide to early dinosaur skeletal anatomy, and should not be used for fine-scale anatomical comparison or character state scoring in phylogenetic analysis. A, *Herrerasaurus ischigualastensis* (Dinosauria incertae sedis, possibly a theropod or stem saurischian outside the theropod + sauropodomorph clade); B, *Dilophosaurus wetherilli* (Theropoda); C, *Saturnalia tupiniquim* (Sauropodomorpha); D, *Heterodontosaurus tucki* (Ornithischia). Reconstructions delineated by Frank Ippolito, American Museum of Natural History.

Under the phylogenetic taxonomy system, Dinosauria is defined as the least inclusive clade containing *Triceratops horridus* and *Passer domesticus* (Padian and May, 1993; Sereno, 1998; Sereno et al., 2005). This definition is sometimes phrased as: "*Triceratops horridus*, *Passer domesticus*, and all descendants of their most recent common ancestor." Under this definition, an organism is only a dinosaur if it is a member of the group on a phylogeny (cladogram) that can be traced down to the node representing the common ancestor of *Triceratops* and modern birds (of which *Passer* is an exemplar). Such a definition is not specific to a certain phylogenetic tree–which is always a hypothesis that can be overturned by new discoveries and interpretations–but rather can be applied to any phylogeny. However, under different phylogenies, different organisms may or may not be dinosaurs depending on their relationships. It is important to remember that this has nothing to do with anatomical features (other than the fact that anatomy is usually used to reconstruct the phylogeny). Most current phylogenetic analyses find silesaurids to fall just outside of the defined dinosaur group, even though both possess many features that were once thought to be unique to dinosaurs. However, in the future, newer phylogenetic work may show these genera to fall inside the dinosaur group, thus necessitating their classification as dinosaurs. In this way, the phylogenetic taxonomy system is flexible in dealing with revised hypotheses of relationships.

Some researchers use a slightly different definition of Dinosauria: "the least inclusive clade containing *Megalosaurus* and *Iguanodon*." In essence this definition replaces *Triceratops* and *Passer* with two alternative specifier taxa. *Megalosaurus* and *Iguanodon* are preferred by some because they were the first two dinosaurs named, and were instrumental in shaping Richard Owen's (1842) concept of Dinosauria. However, we prefer using *Triceratops* and *Passer* for two reasons: these specifiers were used in the first phylogenetic definition of Dinosauria (Padian and May, 1993) and *Megalosaurus* is a poorly understood and fragmentary taxon that has only recently been redescribed in detail (Benson et al., 2008; Benson, 2010b).

2.4. Dinosauria: diagnosis

Although Dinosauria is defined on ancestry and not anatomical characters, there is still a diagnostic set of features that is characteristic of dinosaurs and unknown in other organisms. These characters are said to diagnose dinosaurs rather than define them, just as medical symptoms can be diagnostic of a disease but no disease is rigidly defined by a set of symptoms. In a cladistic sense, these diagnostic features are shared derived characters (synapomorphies) that support Dinosauria as a unique natural group (a monophyletic clade) on the tree of life.

Owen (1842) first recognized Dinosauria as a distinctive group, containing *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*, based on several shared features of the hips (three sacral vertebrae), limbs, and body posture (upright stance) (Cadbury, 2002). Over time, nearly a thousand new non-avian dinosaurs have since been added to this original triumvirate. In doing so, new characters were identified as additional distinctive dinosaur features whereas some of Owen's original characters were dismissed as inaccurate or also observed in other non-dinosaur fossil reptiles. By the end of the 19th century paleontologists recognized two major groups of dinosaurs: the "lizard-hipped" saurischians, which include carnivorous dinosaurs such as *Megalosaurus* and the long-necked herbivorous sauropods, and the "bird-hipped" ornithischians, which include an array of armored, ornamented, and large-bodied herbivores such as *Iguanodon* and *Triceratops* (Seeley, 1888). These groups are still recognized as the two major subdivisions of dinosaurs. However, for much of the 19th and 20th centuries paleontologists considered saurischians and ornithischians to represent separate lineages, which independently diverged long ago from separate "thecodont" (a term applied to an ill-defined assemblage of primitive archosaurs) ancestors and thus were

not particularly closely related (e.g., Colbert, 1964; Charig et al., 1965; Romer, 1966). Thus, in a cladistic sense, dinosaurs were seen as a polyphyletic (non-natural) group.

In a seminal paper published in 1974, Bakker and Galton persuasively argued that saurischians and ornithischians were not distant relatives, but rather could be united within a monophyletic Dinosauria. In essence, they resurrected Owen's (1842) original concept of a single, unique natural group of Mesozoic vertebrates that could be distinguished from all other organisms based on their possession of shared derived characters. Several anatomical features shared by saurischians and ornithischians were recognized by Bakker and Galton (1974:168–169), including upright and fully erect posture, an enlarged deltopectoral crest on the humerus, a "specialized" hand, a perforated acetabulum (hip socket), a well-developed fourth trochanter on the femur, a lesser trochanter on the femur, 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." To Bakker and Galton (1974), these shared skeletal features were unlikely to have arisen by convergent evolution, but rather are shared characters that ornithischians and saurischians inherited from a common ancestor. Under Bakker and Galton's (1974) conception, Dinosauria also included a living group of descendants: the birds. This was not a new idea: it had been proposed as early as the 1860s (e.g., Huxley, 1868, 1870a,b), but had fallen out of favor until the pioneering studies of John Ostrom in the 1960s (e.g., Ostrom, 1969, 1973).

Although dinosaur monophyly was controversial to some (e.g., Charig, 1976a,b; Thulborn, 1975; Chatterjee, 1982; Charig, 1993), most vertebrate paleontologists enthusiastically accepted Bakker and Galton's (1974) evidence as overwhelming (e.g., Bonaparte, 1975; Benton, 1984, 1985; Cruickshank and Benton, 1985; Padian, 1986; Sereno, 1986). The advent of numerical cladistic analyses in the mid 1980s crystallized support for both dinosaur monophyly and the hypothesis that birds evolved from theropod dinosaurs (e.g., Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991a). Today, higher-level phylogenetic analyses continue to find robust support for dinosaur monophyly (e.g., Juul, 1994; Benton, 1999, 2004; Sereno, 1999; Ezcurra, 2006; Langer and Benton, 2006; Irmis et al., 2007a; Brusatte et al., 2008a; Nesbitt et al., 2009b; Brusatte et al., 2010b; Nesbitt et al., 2010), although the exact characters diagnosing the dinosaur group continue to change as new fossils are found and old ideas are reinterpreted.

Over 50 characters have been cited as dinosaur synapomorphies in both pre-cladistic and cladistic studies (Bakker and Galton, 1974; Benton, 1984; Gauthier, 1986; Benton and Clark, 1988; Novas, 1989; Sereno, 1991a; Novas, 1992; Sereno and Novas, 1994; Novas, 1996; Benton, 1999; Sereno, 1999; Fraser et al., 2002; Langer and Benton, 2006; Irmis et al., 2007a; Nesbitt et al., 2009b, 2010; Brusatte et al., 2010b). Potential dinosaur characteristics are distributed throughout the body. However, very few characters of the skull diagnose Dinosauria as a whole, and most unique dinosaur features relate to the limbs and girdles. This pattern reflects two factors. First, the limbs and girdles are heavily modified compared to close relatives, presumably a result of a transition from a facultative quadrupedal to an obligate bipedal posture on the lineage leading to dinosaurs. Second, many close dinosaur outgroup fossils are missing skulls and hands but preserve nearly complete limbs and girdles, thus enabling detailed study of these structures.

Of the pool of potential dinosaur synapomorphies, characters can be partitioned into three categories: (1) character states that consistently diagnose Dinosauria; (2) character states that might diagnose Dinosauria, but whose distribution in close outgroup taxa remains unknown or ambiguous; and (3) character states that clearly do not diagnose Dinosauria, usually because they have subsequently been identified in other organisms. Recently, a striking pattern has

emerged. Few characters are unique to Dinosauria, and many long-standing dinosaur synapomorphies are actually found in other archosaur taxa. Most of these seem to represent independent acquisitions (convergences), underscoring the remarkable similarity of distantly related archosaurs that lived during the Triassic Period (e.g., Nesbitt and Norell, 2006).

In the following sections we briefly discuss and review the most frequently cited character states that may or may not diagnose Dinosauria (Fig. 3).

2.4.1. Character states that consistently diagnose Dinosauria

2.4.1.1. Elongated deltopectoral crest. The deltopectoral crest of the humerus, a muscle attachment site for the deltoid and pectoralis muscles of the arms and chest, extends along 30–40% of the humerus in both saurischians and ornithischians. In nearly all other archosaurs, including the close dinosaur outgroups *Marasuchus* and silesaurids, the deltopectoral crest is shorter and restricted to the proximal region of the humerus. An elongated deltopectoral crest is also convergently present in the basal archosauriform *Erythrosuchus* (Gower, 2003) and the crurotarsan archosaur *Yarasuchus* (Sen, 2005).

2.4.1.2. Open acetabulum. The acetabulum, the joint surface on the pelvis that articulates with the femur, is backed by a medial wall of bone in most reptiles. However, in most dinosaurs the acetabulum is "open" like a window, with no bounding wall. An open acetabulum has long been cited as a dinosaur synapomorphy and is clearly present in ornithischians, theropods, and nearly all sauropodomorphs (except for the basal sauropodomorphs *Panphagia* and *Saturnalia*, which have a "partially" open acetabulum). This character is often specified in phylogenetic analysis by reference to the ventral margin of the ilium (e.g., Irmis et al., 2007a: character 65). In taxa with an open acetabulum the ventral margin of the ilium is distinctly concave. In the closest relatives of dinosaurs, *Silesaurus* and *Marasuchus*, the ventral margin of the ilium is essentially straight, with at most a small concave divot, and this condition has been referred to as an incipiently open acetabulum (e.g., Sereno and Arcucci, 1994b; see discussion in Novas, 1996). Although rare among archosauriforms, a concave ventral margin of the ilium is present in some crurotarsan archosaurs (e.g., *Poposaurus*: Weinbaum and Hungerbühler, 2007), including nearly all basal crocodylomorphs (e.g., Crush, 1984).

2.4.1.3. Temporal musculature extends anteriorly onto skull roof. The frontals of all early dinosaurs have a distinct fossa anterior to the supratemporal fenestra, which likely was an attachment site for the upper temporal musculature used to adduct (close) the lower jaw (Gauthier, 1986). Although most close dinosaur relatives lack cranial material, the well-preserved frontals of the early dinosauromorph *Silesaurus* do not have a fossa (Dzik, 2003), thus indicating that the extensive fossa is a dinosaur character. However, basal crocodylomorphs also bear a distinct fossa on the frontal anterior to the supratemporal fenestra.

2.4.1.4. Epipophyses on the cervical vertebrae. Epipophyses are projections of bone, likely for muscle and ligament attachment, which protrude from the dorsal surfaces of the postzygapophyses of the cervical vertebrae. All basal dinosaurs possess epipophyses (Langer and Benton, 2006), although the size, shape, length, and projection angle of these processes vary considerably (e.g., compare *Coelophysis* (Colbert, 1989) with the more derived theropod *Majungasaurus* (O'Connor, 2007)). Basal ornithischians (e.g., *Heterodontosaurus*) only have epipophyses on the anterior cervical vertebrae, whereas saurischians have epipophyses in nearly all cervical vertebrae (Langer and Benton, 2006). Epipophyses are not present in the closest relatives of dinosaurs (e.g., *Marasuchus*, *Silesaurus*), but are present in some crurotarsans (e.g., *Lotosaurus* and *Revueltosaurus*).

2.4.1.5. Articulation facet for fibula occupying less than 30% of the transverse width of the astragalus. Both bones of the lower hind limb, the tibia and the fibula, articulate with the astragalus bone of the ankle in archosaurs. In dinosaurs, the fibula only makes a restricted contact with the astragalus, such that the fibular articular facet of the astragalus is less than 30% of the transverse width of the astragalus itself. This feature is unique to dinosaurs and unknown in other archosaur groups.

2.4.1.6. Femoral fourth trochanter asymmetrical, with distal margin forming a steeper angle to the shaft. The caudofemoralis, one of the major muscles controlling the hindlimb, attaches to a rugose scar on the shaft of the femur called the fourth trochanter. Bakker and Galton (1974) first suggested that a modification of the fourth trochanter represents a shared derived character for dinosaurs. Although their original concept is not specific and no longer valid, basal dinosaurs do share an asymmetrical, crest-like fourth trochanter, in which the ventral portion of the scar is medially expanded relative to the dorsal portion. This morphology contrasts with the rounded, symmetrical fourth trochanter of *Silesaurus*, *Marasuchus*, and crurotarsan archosaurs, and thus is only present in dinosaurs. Theropod dinosaurs later re-evolve a symmetrical fourth trochanter, but this is independent of the condition seen in early dinosauromorphs.

2.1.4.7. Posterior process of the jugal bifurcated to articulate with the quadratojugal. The jugal bone, which forms the lateral "cheek" region of the skull underneath the eye, has a bifurcated posterior process in dinosaurs. This bifurcation receives the anterior prong of the quadratojugal, and presumably strengthens the contact between the two bones. In other archosaurs, including *Silesaurus* (Dzik and Sulej, 2007:fig. 18A), the single posterior process of the jugal either lies above or below the anterior process of the quadratojugal.

2.4.2. Character states that might diagnose Dinosauria

Fossil specimens of the closest relatives of Dinosauria, such as *Lagerpeton*, *Marasuchus*, *Silesaurus*, and early pterosaurs, are often incomplete and poorly preserved. Most of these lack skulls and hands, and when present these structures are often eroded, crushed, or fragmentary. Therefore, although dinosaurs possess many interesting and potentially diagnostic characters of the skulls and hands, these are difficult to evaluate because we cannot determine if the characters are present in the closest dinosaur relatives. They may represent true dinosaur synapmorphies, or they may characterize a more inclusive group but are currently unrecognized in other taxa due to missing data alone. The following characters fall into this category: postfrontal absent, ossified and paired sternal plates, reduced manual digits IV and V, three or fewer phalanges in the fourth manual digit, and post-temporal foramen present.

In a similar vein, the following potential synapomorphies are absent in the proximal outgroups to dinosaurs, but their distribution within Dinosauria remains complicated. They may represent dinosaur synapomorphies, but further study is required.

2.4.2.1. Brevis fossa/shelf. In archosaurs, a portion of the caudofemoralis musculature, the caudofemoralis brevis, attaches to either the lateral or ventral portion of the posterior process of the ilium, just posterior to the acetabulum (Carrano and Hutchinson, 2002). Only a slight attachment scar for this muscle is present on the ilia of crurotarsans, whereas most dinosaurs have a distinct scar or fossa (=pocket) on either the lateral or ventral surface of the ilium. This fossa is usually referred to as the "brevis fossa," and its medial bounding rim the "brevis shelf" (Novas, 1996). However, the distribution of this character among dinosaurs and close outgroups is complex, and it is possible that not all conditions are homologous. For instance, the basal dinosaur *Herrerasaurus* lacks any kind of brevis fossa (contra Novas, 1993), whereas the non-dinosaur *Silesaurus* possesses a distinct fossa,

which was likely acquired independently from that of dinosaurs since the basal silesaurid *Asilisaurus* lacks a fossa (Nesbitt et al., 2010). Furthermore, the basal condition among ornithischians is unclear: *Heterodontosaurus* lacks a lateral expression of the fossa, *Eocursor* has a shallow fossa on the ventral surface of the ilium, and *Lesothosaurus* has a distinct scar on the lateral surface of the ilium. Similarly, the condition in sauropodomorphs is unsettled: the basal taxon *Panphagia* has a deep fossa, the basal *Saturnalia* possesses a small fossa, and *Plateosaurus* lacks even a rudimentary fossa. Clearly this character deserves further study, and detailed comparisons of the brevis fossa are needed in order to assess its homology among taxa.

2.4.2.2. At least three sacral vertebrae. The number of sacral vertebrae, those vertebrae that articulate with the pelvis, has often been used as a character in phylogenetic analyses (e.g., Gauthier, 1986; Benton and Clark, 1988; Novas, 1996; Benton, 1999). The dinosauromorphs *Lagerpeton* and *Marasuchus* have two primordial sacral vertebrae, a character state that is usually optimized as the primitive condition among archosaurs. The recently discovered *Silesaurus*, a member of the sister taxon of Dinosauria, has three sacral vertebrae, whereas the basal dinosaurs *Herrerasaurus* and *Staurikosaurus* have only the two primordial sacrals, which has been considered as a reversal to the primitive condition (Novas, 1996). Basal ornithischians have as many as six (*Heterodontosaurus*), sauropodomorphs have at least three, and neotheropods have at least five sacral vertebrae. The identity of individual sacrals is often complex. Novas (1996) and Langer and Benton (2006) attempted to identify each sacral vertebra as a dorsosacral (a dorsal vertebra incorporated into the sacrum), a primordial sacral (a sacral homologous to the plesiomorphic two of *Marasuchus* and other tetrapods), or a caudosacral (a caudal vertebra incorporated into the sacrum). However, their methods for identifying sacral vertebrae have recently been questioned (Nesbitt, 2008). Given the varying numbers of sacrals in early dinosaurs and outstanding questions over the identification of individual sacrals, the number of sacral vertebrae at the root of Dinosauria has yet to be accurately determined.

2.4.3. Character states that clearly do not diagnose Dinosauria

Many characters once thought to diagnose dinosaurs have moved down the stem and now represent synapomorphies of more inclusive clades. This is a direct result of the discovery of several close dinosaur relatives, such as *Asilisaurus* (Nesbitt et al., 2010), *Silesaurus* (Dzik, 2003), *Sacisaurus* (Ferigolo and Langer, 2007), and *Dromomeron* (Irmis et al., 2007a; Nesbitt et al., 2009a), as well as the redescription of *Marasuchus* (Sereno and Arcucci, 1994b), *Lagerpeton* (Sereno and Arcucci, 1994a), and *Eucoelophysis* (Ezcurra, 2006; Nesbitt et al., 2007). These characters include: ectopterygoid dorsal to transverse flange of the pterygoid; posteroventrally oriented glenoid on the scapula and coracoid; reduced pubis/ischium contact; reduced ischiadic medioventral lamina; inturned femoral head; proximal femur with reduced medial tuberosity; anterior trochanter of the femur present; tibial descending process that fits posterior to the astragalar ascending process; flat to concave proximal calcaneum; presence of mesotarsal ankle; metatarsals II and IV subequal in length; and a distal end of metatarsal IV that is taller than wide.

As additional dinosauromorph taxa are discovered and redescribed and archosaur anatomy and phylogeny is studied in more detail, it is possible that some of the characters listed above as "consistent" dinosaur synapomorphies will also move down the stem. However, keeping in mind the large number of discoveries of the past 30 years, it is remarkable that many of Bakker and Galton's (1974) original diagnostic characters of Dinosauria still remain valid.

2.4.4. Feathers: a dinosaur innovation?

Without question, one of the largest surprises in paleontology in the last 15 years has been the discovery of feathers and feather-like structures in non-avian dinosaurs. These structures were first reported in small compsognathid theropods from the Early Cretaceous Yixian Formation of northern China (Ji and Ji, 1996; Chen et al., 1998). These structures are not true feathers, but rather small filamentous integumentary structures termed "protofeathers," a presumed evolutionary precursor to true feathers. Their nature had been disputed until the recent report that they contain color-bearing melanosomes exactly as in modern bird feathers (Zhang et al., 2010; see also Li et al., 2010). These finds were soon followed by the announcement of feathers of modern aspect, nearly indistinguishable from those in living birds, in a number of close bird relatives (Ji et al, 1998). The geologically oldest specimens to show feather-like structures include the theropod *Pedopenna* (Xu and Zhang, 2005) and two taxa belonging to the bizarre and poorly-known theropod clade Scansoriopterygidae (Zhang, et al., 2002; Zhang et al., 2008) from the Daohugou Formation, which may be as old as Middle Jurassic (Liu et al, 2006)."Feathered" non-avian dinosaurs, including tyrannosauroids (Xu et al., 2004), compsognathids (Goehlich et al., 2006; Ji et al., 2007), dromaeosaurs (Xu et al., 1999a,b; Ji et al., 2001), therizinosaurs (Xu et al., 1999a,b) and troodontids (Ji et al., 2005), continue to be described regularly.

Currently, the key question is: "how deep in the dinosaur family tree do feathers, or integumentary structures homologous with feathers, go?" Until recently, the occurrence of integumentary structures in dinosaurs outside Theropoda has been controversial. In 2002 an unusual specimen of the common Yixian ornithischian *Psittacosaurus* was described as possessing a comb-like structure of wavy bristle-like filaments on the tail (Mayr et al., 2002). Although the identity of these structures has been contested (one author even suggested they were a fossil plant associated with the specimen), observation of the specimen (by MAN) validates Mayr et al.'s (2002) interpretation. Unfortunately, the provenance of this specimen (removed from China illegally and in a foreign museum) makes it difficult and unethical to incorporate it into any informed scientific discussion (see Dalton, 2001; Long, 2003). Yet, recently another specimen, this time a heterodontosaurid ornithischian, was reported as possessing feather-like structures (Zheng et al., 2009). This taxon, *Tianyulong*, displays both the thick, wavy, bristle-like tail structures of *Psittacosaurus*, as well as more enigmatic integument (perhaps "protofeathers") in the neck area. Finally, it is worth pointing out that filamentous integumentary coverings have been reported in a variety of pterosaurs, flying reptiles which are close relatives of dinosaurs but outside of Dinosauria proper. These fossils, including specimens of *Sordes pilosus* (Sharov, 1970; Bakhurina and Unwin, 1995) and several specimens from the Yixian and Daohugou Formations (Lu, 2002; Wang et al., 2002; Ji and Yuan, 2002; Kellner et al., 2009; see Norell and Ellison, 2005) show incontrovertible evidence for such structures, but it is unclear whether these are homologous to bird feathers or even dinosaurian "protofeathers."

The earliest fossils that physically preserve integumentary structures, which are difficult to fossilize except in remarkable conditions, have been found in Middle Jurassic rocks. However, because these structures are found in a diversity of ornithischian and saurischian dinosaurs, there is little doubt that they were present in the ancestor of all dinosaurs, and probably the ancestor of dinosaurs and pterosaurs as well (and therefore present primitively in Ornithodira). Thus, filamentous, feather-like structures (true feathers or protofeathers) must have been present in Late Triassic dinosaurs. Could feather-like structures extend much deeper in the reptile phylogenetic tree? This is one of the most exciting questions of modern vertebrate paleontology, and its answer depends on both the discovery of additional remarkable fossils and the investigation of molecular and developmental evidence of structural feather proteins in extant non-dinosaurian archosaurs (e.g., crocodiles). Therefore, in summary, although more research needs to be completed, the hypothesis that keratinous feather-like coverings are homologous

for Dinosauria and beyond seems reasonable at this time. The evolutionary (physiologic, sociobiologic, biomechanical and developmental) aspects of this are only beginning to be studied.

3. Geological setting for the origin of dinosaurs

3.1. Dating the origin of dinosaurs

Dinosaurs likely originated during the Middle Triassic (Nesbitt et al., 2010) and the first unequivocal dinosaur fossils are known from the late Carnian. However, much about the geological and temporal backdrop of early dinosaur history remains poorly understood (Fig. 4). A well-resolved chronostratigraphic framework is necessary to answer questions successfully about the tempo and mode of the origin of dinosaurs. This requirement has been one of the many challenges to developing a consensus on how and why dinosaurs became so successful during the early Mesozoic. In particular, there have been three major outstanding questions: (1) what are the ages and durations of the marine stages of the Late Triassic Period?; (2) how can these stages, which are defined using marine invertebrate biostratigraphy, be correlated to terrestrial dinosaur-bearing formations?; and (3) what are the numerical absolute ages of the principal terrestrial vertebrate assemblages that contain early dinosaurs?

The uncertainty surrounding the age and duration of the Carnian, Norian, and Rhaetian stages is a direct result of the lack of precise radioisotopic dates (Mundil, 2007). Although the most recent estimates indicate that the Late Triassic Epoch is over 30 million years long (e.g., Muttoni et al., 2004; Furin et al., 2006), there are only four published precise radioisotopic ages (Rogers et al., 1993; Riggs et al., 2003; Furin et al., 2006; Schaltegger et al., 2008) for this time

period. The base of the Late Triassic is poorly dated: there are no precise radioisotopic ages from near the Ladinian–Carnian boundary and there is no published magnetostratigraphic record that crosses the boundary. An approximate age of 235 Ma for the Ladinian–Carnian boundary has been interpolated using records from earlier in the Ladinian (e.g., Mundil et al., 1996; Muttoni et al., 1997; Mundil et al., 2003; Brack et al., 2005). The Carnian–Norian boundary is constrained by a new U–Pb single crystal zircon age of 230.91 ±0.33 Ma from the Upper Carnian marine section at Pignola, Italy (Furin et al., 2006). Biostratigraphic correlation of this section to magnestratigraphic records from elsewhere in the Tethys region place the Carnian–Norian boundary at between 227 and 228 Ma (Furin et al., 2006: fig. 1), consistent with the Newark Astrochronological Polarity Timescale from eastern North America (Muttoni et al., 2004). The Norian is very poorly dated: there is only one published precise radioisotopic age (Riggs et al., 2003), and it is from terrestrial strata that cannot be directly correlated to the marine biostratigraphic events that define stage boundaries. Calibration of magnetostratigraphic records using palynomorph assemblages (e.g., Kent and Olsen, 1999; Muttoni et al., 2004) and magnetostratigraphy from a key marine section (Muttoni et al., 2010) indicate an age of 208–209 Ma for the Norian–Rhaetian boundary. Taken together, these data suggest that the Norian Stage has a duration of approximately 20 Ma, two-fifths the length of the entire Triassic Period. The end of the Rhaetian (Triassic–Jurassic boundary) is well constrained to between 202 and 201 Ma by U–Pb ages and magnetostratigraphic data (e.g., Kent and Olsen, 1999; Schoene et al., 2006; Schaltegger et al., 2008; Jourdan et al., 2009), with an estimated age of 201.3 Ma based on cyclostratigraphy (Whiteside et al., 2010).

The earliest known dinosauromorph-bearing assemblage is from the ?late Anisian Manda Formation of Tanzania (Nesbitt et al., 2010),
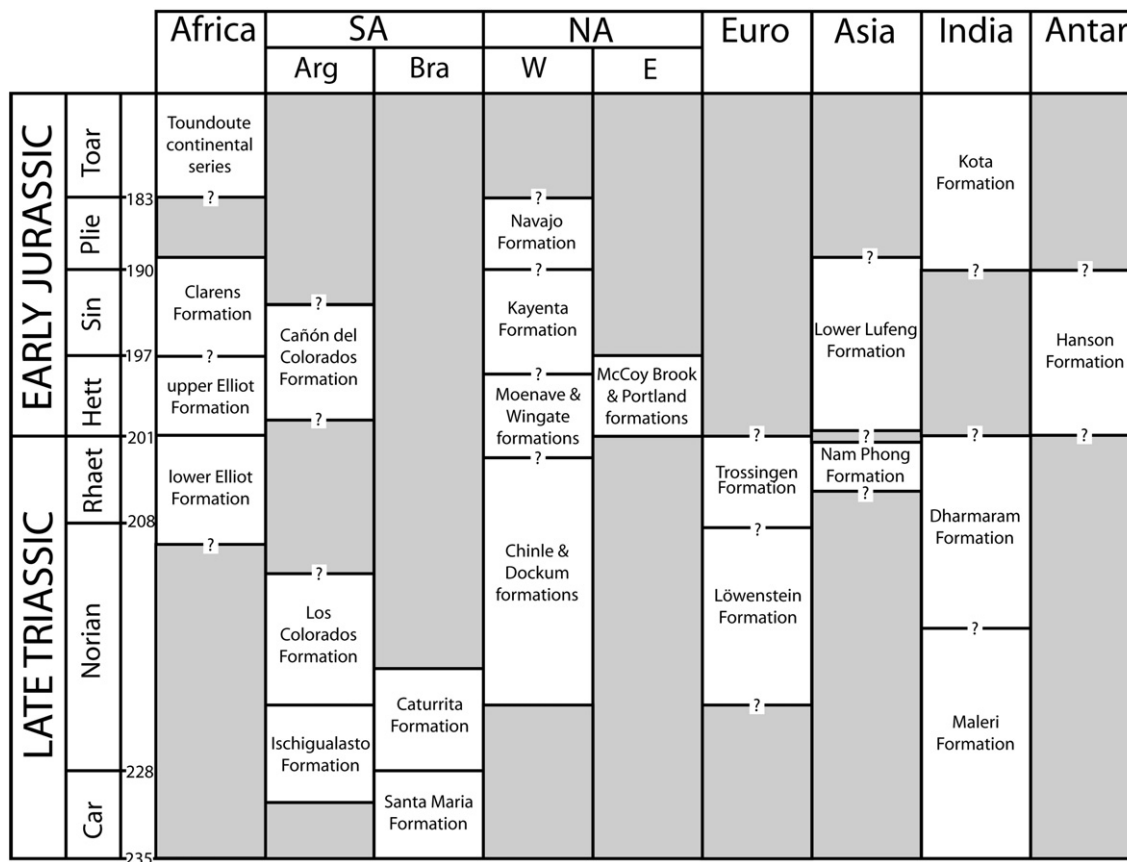
Fig. 4. A generalized geological correlation chart for the major Late Triassic and Early Jurassic dinosaur-bearing formations across the globe. The Triassic timescale at left is a modified version of Walker and Geissman (2009), with a longer Rhaetian following Muttoni et al. (2010). Note that most boundaries between formations, as well as global correlations, are imprecise due to many reasons discussed in the text. This is designed to provide a coarse guide of important early dinosaur faunas, not a precise correlation chart. Abbreviations: Arg = Argentina; Bra = Brazil; E = Eastern North America; W = Western North America. Chart delineated by Randall Irmis and Sterling Nesbitt.

whose age is based solely on vertebrate biostratigraphy. The slightly younger Middle Triassic Los Chañares Formation of northwestern Argentina has been better sampled, and has yielded several basal dinosauromorph taxa, including at least one lagerpetid and silesaurid (Nesbitt et al., 2010) (Fig. 4). These strata are dated as Ladinian based on vertebrate biostratigraphy and the age of overlying strata (e.g., Rogers et al., 1993; Bonaparte, 1997; Rogers et al., 2001; Langer et al., 2007a). The oldest well-dated dinosaur-bearing assemblage is from the lower Ischigualasto Formation in northwestern Argentina. Rogers et al. (1993) reported a ^{40}Ar/^{39}Ar radioisotopic age of 227.8 ± .3 Ma from the lower portion of the formation. This age was recently revised to 231.4 Ma by Furin et al. (2006) to account for re-calibration of the age standard used in the original analysis as well as the bias in the Ar/Ar system that systematically yields ages ~1% too young (e.g., Min et al., 2000; Mundil et al., 2006; Kuiper et al., 2008). Unpublished ^{40}Ar/^{39}Ar ages indicate the top of the Ischigualasto Formation is between 223 and 220 Ma (Shipman, 2004). Taken together, these data indicate that the formation spans the Carnian–Norian boundary. Therefore, the oldest dinosaurs from the Ischigualasto Formation are late Carnian in age, not early Carnian as previously reported (e.g., Rogers et al., 1993; Martinez and Alcober, 2009), and some Ischigualasto dinosaurs, notably *Pisanosaurus*, may be Norian in age (Irmis et al., 2007b; Langer et al., 2010).

Early dinosaur-bearing strata from southern Brazil are probably of similar age based on correlations to the Ischigualasto Formation using vertebrate biostratigraphy (e.g., Schultz et al., 2000; Langer, 2005; Langer et al., 2007a). The Chinle Formation of the Colorado Plateau in western North America is traditionally considered late Carnian–Norian in age (e.g., Litwin et al., 1991; Lucas, 1998), but new U–Pb radioisotopic age constraints indicate that even the oldest fossiliferous strata are Norian in age (Riggs et al., 2003; Irmis and Mundil, 2008; Mundil et al., 2008). Footprint assemblages from the Newark Supergroup of eastern North America (e.g., Olsen et al., 2002) are tied to a high-resolution magnetostratigraphic record that is calibrated using palynomorph biostratigraphy (Kent and Olsen, 1999). Most other classic early dinosaur assemblages from the Late Triassic are dated primarily using biostratigraphic methods (conchostrachans, palynomorphs, vertebrates). These biochronologies have yet to be comprehensively calibrated with radioisotopic ages, so correlations to marine stages or the numerical Late Triassic timescale should be approached with caution.

3.2. The paleoenvironment of early dinosaurs

Global general circulation models for the Late Triassic Period predict warm and seasonal climates for most of Pangaea (Fig. 5). Lower latitude areas of Pangaea experienced summer temperatures above 35 °C, with slightly cooler winter temperatures. In contrast, high-latitude areas were warm during the summer (>20 °C), but near or below freezing during the winter (Sellwood and Valdes, 2006). These models predict very low levels of annual precipitation for low-latitude Pangaea. These areas predominantly experienced summer-wet precipitation (Sellwood and Valdes, 2006), though some mid-latitude areas were arid throughout the year. The poles are assumed to have experienced cool temperate conditions (Sellwood and Valdes, 2006: fig. 2b).

Global syntheses suggest that there was a long-term decrease in atmospheric oxygen during the Late Triassic, but there is considerable disagreement about the duration and intensity of this event (e.g., Bergman et al., 2004; Berner, 2006; Algeo and Ingall, 2007). These data also suggest major fluctuations in atmospheric CO_2 during the early Mesozoic (e.g., Berner, 2006). The general interpretation of these data is an increase in temperature and aridity through the Triassic, which is consistent with the general circulation model data. One complicating factor is that Laurasia moved progressively northward during the Late Triassic (Kent and Tauxe, 2005), but this would also explain an increase in aridity and seasonality as the landmass moved out of the tropics.

Previous authors have suggested linkages between climate change through the Triassic and terrestrial vertebrate evolution (e.g., Robinson, 1971; Tucker and Benton, 1982; Benton, 1983; Simms and Ruffell, 1990a). There was an overall change through three major

Fig. 5. A generalized reconstructed scene from the Late Triassic (Norian) of central Pangea, a dry and arid environment inhabited by the earliest dinosaurs and other archosaurs. A herd of the primitive theropod dinosaur *Coelophysis* congregates near a watering hole in the foreground. In the background a duo of *Coelophysis* stalks two herbivorous prosauropod dinosaurs, while a giant rauisuchian (quadrupedal crurotarsan predator) lurks in the distance and primitive pterosaurs (flying reptiles) soar overhead. Scene reconstructed using CGI and taken from Brusatte (2008), *Dinosaurs* (Quercus Publishing, London). Note that this is an artistic interpretation of a hypothetical Late Triassic community, not a scientifically accurate portrayal of a specific fossil assemblage.

facies associations indicating increasing aridity. Deposition of typical red bed sediments in which tetrapods were preserved began in the Early Triassic of Gondwana and Russia. These beds are dominated by fluvio-lacustrine sandstones and mudrocks with coal seams and abundant plant material, indicating a mild and moist temperate regime. Middle Triassic and "Carnian" tetrapod sites worldwide are dominated by sediments indicating warm to hot climates, with variable humid and dry annual cycles, represented by fluvio-lacustrine sandstones and mudrocks with rare coals, some red beds and calcretes, occasional gypsum, and common plant fossils. The final facies association, fluvio-lacustrine red beds with calcrete, playa mudrocks, gypsum and halite deposits and aeolian sandstones, is seen in Norian to Early Jurassic successions in Gondwana, North America, and Europe. These units indicate hot sub-tropical arid/semi-arid climates with rare or erratic rainfall—essentially deserts, with alluvial fans and ephemeral streams, sand seas, playas, sabkhas and salt lakes.

The transition from the Carnian to Norian, or early to middle Norian if the successions are re-dated (see above), was also marked by a substantial shift from pluvial to arid conditions throughout the Tethyan realm (Simms and Ruffell, 1990a), and these major climatic changes may have been associated with floral changes from a predominantly *Dicroidium*-dominated flora in Gondwana to one based around arid-adapted conifers. Such climatic and floral changes might have precipitated extinctions of herbivorous rhynchosaurs and dicynodonts. These changes may coincide with the independently documented Reingraben Turnover/Raibl Event, which was a major restructuring of marine ecosystems during the middle and late Carnian (Furin et al., 2006; Stanley, 2006; Hornung et al., 2007). These consistent changes to more arid conditions could either be caused by global climate change, movement of continents through different climatic zones (e.g., Kent and Tauxe, 2005), or a combination of both factors.

Finally, a variety of evidence indicates severe environmental stress on land and in the ocean at the Triassic–Jurassic boundary, with a sharp increase in atmospheric CO_2 levels (e.g., Smith and Kitching, 1997; McElwain et al., 1999; Cohen and Coe, 2007; Michalík et al., 2007; Hautmann et al., 2008; Whiteside et al., 2010). These environmental changes may have been associated with a mass extinction near the Triassic–Jurassic boundary, which is recognized as one of the "big five" mass extinctions in earth history (e.g., Raup, 1986; Benton, 1995). New work using records of compound-specific stable carbon isotopes from the Triassic–Jurassic boundary interval of the Newark Supergroup in eastern North America indicates that the eruption of flood basalts caused a massive input of greenhouse gases into the atmosphere, and that the release of this greenhouse gas and the earliest basalt flows are synchronous with biotic extinctions both on land and in the ocean (Whiteside et al., 2010). These data are the strongest evidence yet indicating flood volcanism caused the end-Triassic mass extinction.

Aside from this general information on Triassic and Jurassic climate and environments, published paleoenvironmental proxy data for specific early dinosaur-bearing strata are limited (Fig. 5). Sedimentological, geochemical, and paleobotanical evidence indicates that the earliest known dinosaurs from the upper Carnian Ischigualasto Formation of Argentina lived in a dry seasonal climate that later fluctuated with wetter conditions during the early Norian (Moore, 2002; Shipman, 2004; Tabor et al., 2004, 2006; Colombi and Parrish, 2008; Currie et al., 2009). Multi-proxy evidence from the Norian Chinle Formation of western North America indicates that it was deposited under humid, wet, sub-tropical conditions during the early Norian, but that the paleoenvironment gradually became drier and more seasonal during the later Norian (e.g., Dubiel et al., 1991; Parrish, 1993; Dubiel, 1994; Prochnow et al., 2006), consistent with the northward drift of Laurasia (Kent and Tauxe, 2005). Data from northern New Mexico indicate that during the late Norian to Rhaetian the environment was semi-arid to arid, with moderate to severe

fluctuations in a variety of environmental parameters (Cleveland et al., 2008a,b; Dunlavey et al., 2009).

3.3. Early dinosaur-bearing formations

Early dinosaurs are distributed across Pangaea. Footprints and body fossils are known from several sedimentary basins in Argentina, most notably the Ischigualasto and Los Colorados formations of the Ischigualasto–Villa Union Basin in northwestern Argentina (e.g., Rogers et al., 1993; Bonaparte, 1997; Zerfass et al., 2004). Similarly aged strata (Santa Maria and Caturrita formations) in southern Brazil preserve an extensive tetrapod assemblage, including basal dinosauromorphs, basal saurischians, and early sauropodomorphs (e.g., Langer et al., 2007a). Late Norian to Early Jurassic rocks of the Stormberg Group (primarily the lower and upper Elliot Formation) in southern Africa preserve diverse assemblages that are dominated by sauropodomorph dinosaurs (e.g., Olsen and Galton, 1984; Knoll, 2004, 2005). Basal saurischians and sauropodomorphs are known from Late Triassic sediments in the Pranhita–Godavari Valley in India (e.g., Kutty et al., 2007). Late Triassic dinosaurs are unknown from Madagascar, Antarctica, and Australia, but the Early Jurassic Hanson Formation in Antarctica preserves theropod and sauropodomorph dinosaurs (Smith and Pol, 2007; Smith et al., 2007).

Extensive early dinosaur assemblages are also known from Laurasia. In western North America, basal dinosauromorphs, basal saurischians, and theropods are known from the Norian Chinle Formation and Dockum Group. Overlying Early Jurassic strata preserve a diverse assemblage of ornithischians, sauropodomorphs, and theropods in the Glen Canyon Group (e.g., Tykoski, 2005). The dinosaur record of eastern North America is primarily documented by footprints, with extensive late Carnian, Norian, and Rhaetian dinosauromorph assemblages from the Newark Supergroup (Olsen and Huber, 1998; Olsen et al., 2002), but it also includes Early Jurassic body fossils of the sauropodomorph *Anchisaurus* (e.g., Yates, 2004) and theropods (Talbot, 1911; Colbert and Baird, 1958). Norian and Rhaetian terrestrial strata from the Germanic Basin in Europe are dominated by basal sauropodomorphs (e.g., Yates, 2003b), but theropods are also present (Schoch and Wild, 1999). Similar assemblages have been reported from Greenland (Jenkins et al., 1994), and Dzik et al. (2008) recently reported theropod dinosaurs from the latest Triassic of Poland. Poorly dated fissure fills from western Europe record the presence of sauropodomorphs and possible theropods (e.g., Benton et al., 2000; Yates, 2003a); these are generally thought to be latest Triassic to Early Jurassic in age (Whiteside and Marshall, 2008). Dinosaurs are conspicuously absent from the Late Triassic of Asia, but an extensive sauropodomorph-dominated assemblage is known from the Lower Jurassic Lufeng Formation of Yunnan, China; this assemblage also includes rare ornithischians and theropods (e.g., Luo and Wu, 1994).

4. Dinosaurs of the Late Triassic and Early Jurassic

The following is a summary of the evolution and distribution of the major dinosaur subgroups during the Late Triassic and Early Jurassic (Fig. 3). A complete list of all valid dinosaur taxa known from this time span is given in Table 1. A framework cladogram showing the general phylogenetic relationships of early dinosaurs is given in Fig. 6.

4.1. Ambiguous taxa: Eoraptor and Herrerasauridae

Two taxa from the Ischigualasto Formation of Argentina, *Herrerasaurus ischigualastensis* (Fig. 3A) and *Eoraptor lunensis*, are represented by some of the most complete specimens of any early dinosaur, yet their phylogenetic position has been the source of vigorous debate. Emerging evidence, most notably a revised understanding of dinosaur character evolution buoyed by the discovery of the nearly

Table 1
A list of Late Triassic and Early Jurassic dinosaur species, divided into the three major dinosaur subgroups (Theropoda, Ornithischia, Sauropodomorpha), as well as six taxa that are clearly dinosaurs but of uncertain position. All named and valid species are included, as well as a number of unnamed specimens that are likely diagnostic and represent valid species-level taxa.

Taxon	Geographic area	Formation	Age	References
Dinosauria *incertae sedis*				
Chindesaurus bryansmalli	Southwestern USA	Chinle and Tecovas formations	Middle Norian	Long and Murry (1995)
Herrerasaurus ischigualastensis	Argentina	Ischigualasto Formation	Late Carnian–early Norian	Reig (1963); Sereno and Novas (1992); Sereno (1993); Sereno and Novas (1994); Novas (1993)
Eoraptor lunensis	Argentina	Ischigualasto Formation	Late Carnian–early Norian	Sereno et al. (1993)
Staurikosaurus pricei	Brazil	Santa Maria Formation	Late Carnian–early Norian	Colbert (1970); Bittencourt and Kellner (2009)
Guaibasaurus candelariensis	Brazil	Caturrita Formation	Norian	Bonaparte et al. (1999); Langer and Benton (2006)
Agnosphitys cromhallensis	United Kingdom	Cromhall Quarry	Norian–Rhaetian	Fraser et al. (2002)
Sauropodomorpha				
Anchisaurus polyzelus	Connecticut, USA	Portland Formation	Pliensbachian–Toarcian	Hitchcock (1865); Galton (1976); Yates (2004); Fedak and Galton (2007)
"*Massospondylus sp.*"	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Attridge et al. (1985)
Unnamed basal sauropodomorph(s)	Arizona, USA	Navajo Formation	Pliensbachian–Toarcian	Brady (1935, 1936); Galton (1971, 1976); Yates (2004); Irmis (2005)
Seitaad ruessi	Utah, USA	Navajo Formation	Pliensbachian–Toarcian	Sertich and Loewen (2010)
Panphagia protos	Argentina	Ischigualasto Formation	Late Carnian–early Norian	Martinez and Alcober (2009)
Coloradisaurus brevis	Argentina	Los Colorados Formation	Norian–?Rhaetian	Bonaparte (1978)
Lessemsaurus sauropoides	Argentina	Los Colorados Formation	Norian–?Rhaetian	Bonaparte (1999); Pol and Powell (2007a)
Riojasaurus incertus	Argentina	Los Colorados Formation	Norian–?Rhaetian	Bonaparte (1969)
Mussaurus patagonicus	Argentina	Laguna Colorada Formation	?Norian	Bonaparte and Vince (1979); Pol and Powell (2007b)
Adeopapposaurus mognai	Argentina	Cañón del Colorado Formation	Early Jurassic	Martínez (2009)
Saturnalia tupiniquim	Brazil	Santa Maria Formation	Carnian–early Norian	Langer et al., 1999; Langer (2003)
Unaysaurus tolentinoi	Brazil	Caturrita Formation	Norian	Leal et al. (2004)
Glacialisaurus hammeri	Antarctica	Hanson Formation	Sinemurian–Pliensbachian	Smith and Pol (2007)
Melanorosaurus readi	South Africa	Lower Elliot Formation	Norian	Haughton (1924); Yates (2007a)
Eucnemesaurus fortis	South Africa	Lower Elliot Formation	Norian	Haughton (1924); Yates (2007b)
Plateosauravus cullingworthi	South Africa	Lower Elliot Formation	Norian	Haughton (1924)
Blikanasaurus cromptoni	South Africa	Lower Elliot Formation	Norian	Galton and van Heerden (1985)
Antetonitrus ingenipes	South Africa	Lower Elliot Formation	Norian	Yates and Kitching (2003)
Massospondylus carinatus	South Africa/Lesotho	Upper Elliot Formation and Clarens Formation	Hettangian–Pliensbachian	Owen (1854)
Massospondylus kaalae	South Africa	Upper Elliot Formation	Hettangian–Sinemurian	Barrett (2004, 2009b)
Ignavusaurus rachelis	Lesotho	Upper Elliot Formation	Hettangian–Sinemurian	Knoll (in press)
Aardonyx celestae	South Africa	Upper Elliot Formation	Hettangian–Sinemurian	Yates et al. (2010)
Vulcanodon karibaensis	Zimbabwe	Vulcanodon Beds	?Hettangian	Raath (1972)
Tazoudasaurus naimi	Morocco	Toundoute Continental Series	Toarcian	Allain et al. (2004)
Lamplughsaura dharmaramensis	India	Upper Dharmaram Formation	?Sinemurian	Kutty et al. (2007)
Pradhania gracilis	India	Upper Dharmaram Formation	?Sinemurian	Kutty et al. (2007)
Barapasaurus tagorei	India	Kota Formation	Hettangian–Pliensbachian	Jain et al. (1975)
Kotasaurus yamanpalliensis	India	Kota Formation	Hettangian–Pliensbachian	Yadagiri (1988, 2001)
Plateosaurus gracilis	Germany	Lowenstein Formation	Early Norian	von Huene (1908); Yates (2003b)
Efraasia minor	Germany	Lowenstein Formation	Mid-late Norian	von Huene (1932); Galton (1973); Yates (2003b)
Plateosaurus engelhardti	Germany	Lowenstein Formation and Trossingen Formation	Mid Norian–Rhaetian	von Meyer (1837); Yates (2003b)
Plateosaurus ingens	Germany	Trossingen Formation	Rhaetian	Rutimeyer (1856); Galton (2001)
Ruehleia bedheimensis	Germany	Trossingen Formation	Rhaetian	Galton (2001)
Thecodontosaurus antiquus	United Kingdom	Magnesian Conglomerate	Norian–?Rhaetian	Riley and Stutchbury (1836)
Pantydraco caducus	United Kingdom	Pant-y-ffynnon Quarry	Norian–?Rhaetian	Yates (2003a); Galton et al. (2007)
Lufengosaurus huenei	China	Lower Lufeng Series	Early Jurassic	Young (1941); Barrett et al. (2005)
Jingshanosaurus xinwaensis	China	Lower Lufeng Series	Early Jurassic	Zhang and Yang (1994)
Yunnanosaurus huangi	China	Lower Lufeng Series	Early Jurassic	Young (1942): Barrett et al. (2007)
Yimenosaurus youngi	China	Fengjiahe Formation	Pliensbachian or Toarcian	Bai et al. (1990)
Chinshakiangosaurus chunghoensis	China	Fengjiahe Formation	Pliensbachian or Toarcian	Upchurch et al (2007b)
Gongxianosaurus shibeiensis	China	Ziliujing Formation	Early Jurassic	He et al. (1998)
Isanosaurus attavipachi	Thailand	Nam Phong Formation	Late Norian–Rhaetian	Buffetaut et al. (2000)
Theropoda				
Tawa hallae	New Mexico, USA	Chinle Formation	Norian–?Rhaetian	Nesbitt et al. (2009b)
Coelophysis bauri	New Mexico, USA	Chinle Formation	Norian–?Rhaetian	Cope (1889),Colbert (1989)
Unnamed coelophysoid	New Mexico, USA	Chinle Formation	Norian	Heckert et al. (2000, 2003)
Gojirasaurus quayi	New Mexico, USA	Bull Canyon Formation	Norian	Carpenter (1997); Nesbitt et al (2007)
Coelophysoidea indet. ("*Camposaurus*")	Arizona, USA	Chinle Formation	Early Norian	Long and Murry (1995); Hunt et al (1998); Nesbitt et al (2007)
Dilophosaurus wetherilli	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Welles (1954, 1970, 1984)
"*Syntarsus*" *kayentakatae*	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Rowe (1989)
Unnamed theropod ("Shake-N-Bake Theropod")	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Tykoski (1997, 2005); Tykoski and Rowe (2004)
Segisaurus halli	Arizona, USA	Navajo Formation	Pliensbachian–Toarcian	Camp (1936); Carrano et al. (2005)
Podokesaurus holyokensis	Massachusetts, USA	?Portland Formation	Pliensbachian–Toarcian	Talbot (1911)
Zupayasaurus rougieri	Argentina	Los Colorados Formation	Norian–?Rhaetian	Arcucci and Coria (2003); Ezcurra (2007); Ezcurra and Novas (2007)

Table 1 (*continued*)

| Taxon	Geographic area	Formation	Age	References
Theropoda				
Cryolophosaurus ellioti	Antarctica	Hanson Formation	Sinemurian–Pliensbachian	Hammer and Hickerson (1994); Smith et al. (2007)
Coelophysis rhodesiensis	Zimbabwe, South Africa	Forest Sandstone and upper Elliot formations	Hettangian–?Sinemurian	Raath (1969)
Dracovenator regenti	South Africa	Upper Elliot Formation	Hettangian–Sinemurian	Yates (2005)
Berberosaurus liassicus	Morocco	Toundoute continental series	Pliensbachian–Toarcian	Allain et al. (2007)
Unnamed theropod	Morocco	Wazzant Formation	Toarcian	Jenny et al. (1980); Taquet (1984)
Procompsognathus triassicus	Germany	Lowenstein Formation	Norian	Fraas, 1913; Sereno and Wild (1992); Rauhut and Hungerbühler, 2000; Knoll (2008)
Liliensternus liliensterni	Germany	Knollenmergel	Norian	von Huene (1934); Welles (1984); Rauhut and Hungerbühler, 2000; Rauhut (2003)
Lophostropheus airelensis	France	Moon-Airel Formation	?Rhaetian–Hettangian	Cuny and Galton (1993); Rauhut and Hungerbühler (2000); Ezcurra and Cuny (2007)
Unnamed theropod	Poland	Lipie Śląskie clay-pit	?Norian–Rhaetian	Dzik et al. (2008)
Sarcosaurus andrewsi	England	Lower Lias	Late Sinemurian	Andrews (1921); Carrano and Sampson (2008)
Unnamed theropod	England	Lower Lias	Late Sinemurian	Newman (1968); Carrano and Sampson (2004, 2008)
?Dilophosaurus sinensis	China	Lower Lufeng Series	Early Jurassic	Hu (1993)
Eshanosaurus deguchiianus	China	Lower Lufeng Series	Hettangian	Zhao and Xu (1998); Xu et al. (2001)
Ornithischia				
Scutellosaurus lawleri	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Colbert (1981); Rosenbaum and Padian (2000)
Unnamed thyreophoran ("*Scelidosaurus* sp.")	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Padian (1989); Tykoski (2005)
Unnamed heterodontosaurid	Arizona, USA	Kayenta Formation	Hettangian–Sinemurian	Attridge et al. (1985)
Pisanosaurus mertii	La Rioja, Argentina	Ischigualasto Formation	Early Norian	Casamiquela (1967); Bonaparte (1976); Sereno (1991a,b); Irmis et al. (2007b)
Unnamed heterodontosaurid	Santa Cruz, Argentina	Laguna Colorada Formation	?Norian	Báez and Marsicano (2001)
Unnamed ornithischian	Venezuela	La Quinta Formation	Early or Middle Jurassic	Barrett et al. (2008)
Eocursor parvus	South Africa	Lower Elliot Formation	Norian	Butler et al. (2007)
Lycorhinus angustidens	South Africa	Upper Elliot Formation	Hettangian–Sinemurian	Haughton (1924); Hopson (1975); Gow (1990)
Abrictosaurus consors	Lesotho	Upper Elliot Formation	Hettangian–Sinemurian	Thulborn (1970b); Hopson (1975)
BMNH A100	Lesotho	Upper Elliot Formation	Hettangian–Sinemurian	Thulborn (1970b); Hopson (1975); Butler et al. (2008a,b)
Heterodontosaurus tucki	South Africa	Upper Elliot Formation and Clarens Formation	Hettangian–Pliensbachian	Crompton and Charig (1962); Santa Luca (1980); Butler et al. (2008a,b)
Lesothosaurus diagnosticus	South Africa/Lesotho	Upper Elliot Formation	Hettangian–Sinemurian	Thulborn (1970a, 1971, 1972); Galton (1978); Sereno (1991b); Butler (2005)
Stormbergia dangershoeki	South Africa/Lesotho	Upper Elliot Formation	Hettangian–Sinemurian	Butler (2005)
Emausaurus ernsti	Mecklenberg, Germany	Unnamed unit	Early Toarcian	Haubold (1990)
Scelidosaurus harrisonii	Dorset, England	Lower Lias	Late Sinemurian	Owen (1861, 1863)
Bienosaurus lufengensis	Yunnan, PR China	Dark Red Beds of the Lower Lufeng	Sinemurian	Dong (2001)
Tatisaurus oehleri	Yunnan, PR China	Dark Red Beds of the Lower Lufeng	Sinemurian	Simmons (1965); Norman et al. (2007)

complete basal theropod *Tawa* (Nesbitt et al., 2009b), suggests that both taxa are true theropods, as originally argued by Sereno and colleagues in the early 1990s (see below). However, given the continued limited character support for this phylogenetic placement (e.g., Nesbitt et al., 2009b: SOM), it is probable that the relationships of *Herrerasaurus* and *Eoraptor* will remain contentious.

Herrerasaurus is a bipedal carnivore that reached lengths of up to 4 m. It was originally hypothesized to be the immediate sister taxon (closest relative) to Dinosauria (as defined in this paper) (Gauthier, 1986; Brinkman and Sues, 1987; Novas, 1992). Some subsequent authors regarded *Herrerasaurus* as a true dinosaur, but of uncertain phylogenetic position (Novas, 1989). The discovery of more complete specimens in the late 1980s demonstrated that *Herrerasaurus* is a true dinosaur, but also gave rise to two opposing viewpoints on its affinities: some authors regard it as a stem saurischian outside of the theropod + sauropodomorph group (Langer, 2004; Langer and Benton, 2006; Irmis et al., 2007a), whereas others argue that it is a basal member of the theropod lineage (Sereno et al., 1993; Novas, 1996; Sereno, 1997, 1999; Rauhut, 2003; Sereno, 2007a; Nesbitt et al., 2009b). This debate is currently one of the most important unresolved questions regarding early dinosaur phylogeny and evolution.

Herrerasaurus is usually grouped with another carnivorous dinosaur, *Staurikosaurus pricei*, within a subclade of early dinosaurs

called the Herrerasauridae, which is supported by a number of unique derived characters (Langer and Benton, 2006; Nesbitt et al., 2009b). *Staurikosaurus* is known from the Santa Maria sequence in Brazil, which is approximately the same age as the Ischigualasto Formation (Langer, 2005; Langer et al., 2007a). *Staurikosaurus* is represented by a single partial skeleton, which is substantially less complete than specimens of *Herrerasaurus*, including the mandible, most of the vertebral column, pelvic girdle, and partial hindlimbs (Colbert, 1970). A comprehensive redescription of *Staurikosaurus* has recently been undertaken, and should help clarify its anatomy and phylogenetic position (Bittencourt and Kellner, 2009).

The phylogenetic position of the much smaller *Eoraptor*, a predator or omnivore that reached lengths of 1–2 m, is equally controversial. Although all phylogenetic analyses have placed *Eoraptor* as a member of the saurischian lineage, there is debate over whether it is a true theropod or a more primitive stem saurischian dinosaur outside of the theropod + sauropodomorph clade. Sereno et al. (1993) found *Eoraptor* as the most primitive theropod, outside of a more derived group that includes *Herrerasaurus* and all other theropods; this result was also found by Novas (1996), Sereno (1999), and Rauhut (2003). However, Langer and Benton (2006) found *Eoraptor* as more derived than *Herrerasaurus* but outside of the theropod + sauropodomorph clade. Thus, neither *Eoraptor* nor *Herrerasaurus* is a true theropod in
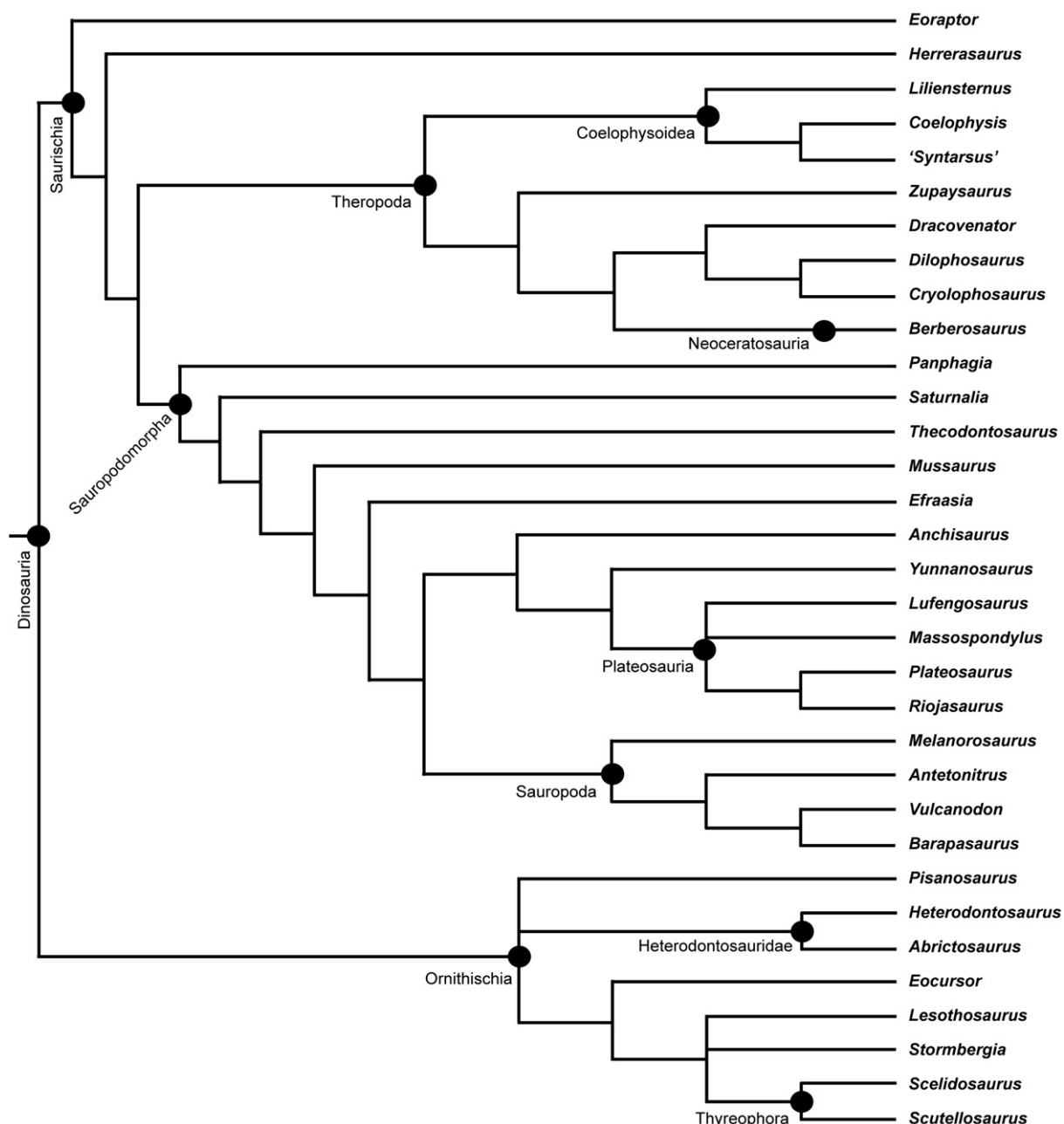
Fig. 6. A framework phylogeny (cladogram) of several of the most complete and important Triassic and Jurassic dinosaurs, with major clades denoted. This phylogeny does not result from a novel cladistic analysis, but is a summary cladogram that relies heavily on the analyses of Langer and Benton (2006) for overall dinosaur relationships, Smith et al. (2007) for theropod relationships, Butler et al. (2007) for ornithischian relationships, and Upchurch et al. (2007a) for sauropodomorph relationships. Please refer to the original cladistic analyses for further details. Cladogram delineated by Stephen Brusatte.

Langer and Benton's (2006) phylogeny. Most recently, Nesbitt et al. (2009b) recovered *Eoraptor* as a theropod, but more derived than *Herrerasaurus*. Much of this instability may relate to the fact that *Eoraptor* has yet to be fully described, though Langer (Langer and Benton, 2006: p. 311), Irmis (Irmis et al., 2007a,b), and Nesbitt (Nesbitt et al., 2009b) did examine the specimen first-hand.

Chindesaurus bryansmalli and *Guaibasaurus candelariensis* are two other enigmatic saurischian dinosaurs from the Late Triassic. *Chindesaurus* is from the Upper Triassic (Norian) Chinle Formation of Arizona (Long and Murry, 1995; Nesbitt et al., 2007). It reached lengths of 2–3 m, and is mainly known from the incomplete skeleton of the holotype specimen, which preserves a partial vertebral column, pelvis, and hindlimbs. Clearly a saurischian (Nesbitt et al., 2007), *Chindesaurus* has been included in the clade Herrerasauridae as a theropod (Long and

Murry, 1995; Hunt, 1996; Novas, 1996; Hunt et al., 1998; Nesbitt et al., 2009b) and as a stem saurischian outside of the theropod + sauropodomorph group (Langer, 2004; Irmis et al., 2007a). New material of *Chindesaurus* from the Hayden Quarry (Irmis et al., 2007a) may help clarify its ambiguous systematic position. *Guaibasaurus*, from the Caturrita Formation of southern Brazil, is known from three specimens that together preserve most of the skeleton, except for the skull (Bonaparte et al., 1999, 2007). Unfortunately, the articular ends of the bones are poorly preserved; thus, important character states of the femur, tibia, and ankle cannot be scored using available material. *Guaibasaurus* has been considered either the sister taxon to saurischians (Bonaparte et al., 1999, 2007) or a basal theropod (Langer, 2004; Langer and Benton, 2006; Yates, 2007a,b). Its phylogenetic position is still unresolved, but it can be confidently placed within Saurischia (Langer et al., 2007a,c).

All of these controversial taxa share skeletal features with unequivocal carnivorous theropods, such as recurved and serrated teeth and elongate hands with recurved claws (Fig. 3A,B; Sereno et al., 1993; Sereno, 1999; Langer, 2004). Some authors suggest that these common features are homologous between all of these taxa and neotheropods (e.g., Sereno, 1999), whereas others consider such characteristics to be convergent, usually based on character optimization in a phylogenetic analysis (Langer, 2004; Langer and Benton, 2006). Nevertheless, the distribution and interpretation of some "predatory" features among basal dinosaurs is complicated. For example, one of the basal-most ornithischians, *Heterodontosaurus* (see below), has an elongated manus with clearly recurved claws, characters present in *Herrerasaurus* and unequivocal theropods. Thus, these features may simply represent the plesiomorphic condition for Dinosauria rather than derived specialization indicative of preferential relationship to theropods. These characters are also difficult to interpret phylogenetically. For example, the proposed homology of the intramandibular jaw joint that allows motion between bones of the lower jaw for *Herrerasaurus* and theropods is unclear, given that the joint is constructed differently in these two taxa (Sereno, 1999; Langer and Benton, 2006).

These character conflicts, along with many others, help explain why the phylogenetic positions of *Eoraptor*, *Chindesaurus*, *Guaibasaurus*, *Herrerasaurus*, and *Staurikosaurus* remain unresolved to date. As with many paleontological debates, it is likely that new fossil discoveries of these dinosaurs or closely related taxa will help resolve this puzzle. Indeed, the recent discovery of *Tawa*, a remarkably complete basal theropod, may prove instrumental, as its combination of primitive and derived characters help pull *Herrerasaurus*, *Chindesaurus*, *Staurikosaurus*, and *Eoraptor* into the theropod clade in the largest and most up-to-date phylogenetic analysis of basal dinosaurs yet published (Nesbitt et al., 2009b).

4.2. Theropods

4.2.1. Late Triassic theropods — fossil record and distribution

The first definitive theropods are known from the Norian. Previous records of Carnian theropods, such as the coelophysoid "*Camposaurus*" (Hunt et al., 1998), have been recently re-dated as Norian (Nesbitt et al., 2007; Irmis and Mundil, 2008). However, if *Eoraptor*, *Herrerasaurus*, or *Staurikosaurus* are basal members of Theropoda, as hypothesized by Sereno et al. (1993), Sereno (1999), Nesbitt et al. (2009b), and others, then this clade would extend into the Carnian. Regardless, the presence of Carnian sauropodomorphs–members of the sister taxon of Theropoda–imply that the theropod lineage also extends into the Carnian by virtue of its ghost lineage (e.g., Langer et al., 1999; Martinez and Alcober, 2009).

Theropods are generally rare in Late Triassic assemblages and exhibit low taxonomic diversity and a relatively restricted range of morphology compared to Early Jurassic members of the group. Most known definitive Late Triassic theropods may belong to a major clade called Coelophysoidea (e.g., Sereno, 1999; Carrano et al., 2002; Rauhut, 2003; Tykoski and Rowe, 2004; Carrano et al., 2005; Ezcurra and Novas, 2007; Smith et al., 2007). The most basal major clade of theropod dinosaurs, Coelophysoidea includes a range of mostly small-bodied predators such as *Coelophysis*, "*Syntarsus*," *Liliensternus*, *Lophostropheus*, *Gojirasaurus*, and *Procompsognathus* (Table 1). Several indeterminate coelophysoids are also known, and it is clear that this clade was geographically widespread during the Late Triassic and possibly abundant in some ecosystems (e.g., Ghost Ranch: Colbert, 1989). Recently, however, it has been proposed that Coelophysoidea, as traditionally considered, is a paraphyletic grade on the line to more derived theropods (Smith et al., 2007; Nesbitt et al., 2009b). It may be that Coelophysoidea is a restricted clade that only includes *Coelophysis* and close relatives (known as Coelophysidae), but this awaits further testing and corroboration. What is clear, however, is that the

recently described *Tawa* from the Norian of New Mexico is more basal than taxa traditionally regarded as coelophysoids, and thus outside the clade Neotheropoda (Nesbitt et al., 2009b).

The puzzling Argentine theropod *Zupaysaurus* was initially described as the oldest tetanuran theropod (see below), but has been reinterpreted as a more basal taxon (e.g., Ezcurra, 2007). However, whether it falls within the coelophysoid clade or is outside of this clade and more closely related to tetanurans is a matter of debate (e.g., compare the phylogenies of Ezcurra and Novas (2007) with Smith et al. (2007) and Nesbitt et al. (2009b)). Definitive tetanuran and/or neoceratosaurian theropods are still unknown from the Late Triassic, and neither lineage can be confidently extended into this time using ghost lineages.

One final specimen deserves comment. Dzik et al. (2008) briefly described a number of well-preserved fossils from the latest Triassic (?Rhaetian) of Poland, which they interpreted as representing a large theropod dinosaur (~3 m in length). They argued that this specimen extends the fossil record of large theropods, otherwise known from the Early–Middle Jurassic, into the Late Triassic. However, Triassic theropods of the same general size of the new Polish material are already known (*Gojirasaurus*, *Liliensternus*). Although two of us (SLB, RJB) have examined the specimens, we await a full description of the material before commenting on its phylogenetic and evolutionary importance. Regardless of the affinities of these large specimens, there are unequivocal small theropod vertebrae (described as coelophysoids by Dzik et al., 2008) in the same quarry.

4.2.2. Late Triassic theropods — paleobiology

Most Late Triassic theropods were small-bodied and gracile. The familiar *Coelophysis bauri*, which reached an average length of about 2 m and a mass of 10–40 kg (Peczkis, 1994), is a useful general model for Late Triassic theropod size and morphology. However, the coelophysoid *Liliensternus* reached much larger body sizes, and may have approached about 6 m in length and up to 400 kg in mass (Peczkis, 1994). The same is also true of *Gojirasaurus*, which is estimated at 5.5 m in length (Carpenter, 1997). Truly colossal theropods, in the size range of *Allosaurus* (~8 m in length) and greater, are unknown from the Late Triassic.

Late Triassic coelophysoids, as well as *Tawa*, possessed the specializations seen in most predatory theropods. The skull was elongate, filled with an array of serrated and recurved teeth, and well constructed to withstand the high stresses of biting prey (Rayfield, 2005). The feet and hands were capped with sharp claws. The skeleton itself was light and gracile and the tail was long and stiff for balance, features that enabled speed and maneuverability. These theropods were most likely active predators. *Coelophysis* has long been described as a cannibal that fed on the remains of its own young (e.g., Colbert, 1989), but recent reinterpretation reveals that the supposed infant *Coelophysis* bones in the gut of one specimen belong to an early crocodylomorph (Nesbitt et al., 2006).

The spectacular fossil assemblage of Ghost Ranch, New Mexico, gives an unprecedented view of dinosaur community and population structure. This assemblage includes the remains of hundreds of *Coelophysis* individuals, ranging from small juveniles to adults (Colbert, 1989). Many skeletons are complete, articulated, and exceptionally well preserved, and are buried within abandoned channel deposits that indicate rapid burial after minor transport (Schwartz and Gillette, 1994). It is likely that this assemblage preserves a group of individuals that was overtaken by a rapid environmental crisis, such as a drought or flood (Colbert, 1989; Schwartz and Gillette, 1994). As such, it is one of the few sites in the Mesozoic fossil record where a potential theropod dinosaur community is well represented (Irmis, 2009; Rinehart et al., 2009).

Although hundreds of skeletons of *Coelophysis* are known from Ghost Ranch, theropods are generally rare components of other Late Triassic ecosystems (e.g., Rauhut and Hungerbühler, 2000; Nesbitt

et al., 2007). Carnivorous theropods are much rarer (in an absolute faunal abundance sense) and less diverse (in a taxonomic sense) than contemporary carnivorous crurotarsans such as phytosaurs, ornithosuchids, and rauisuchians (e.g., Welles, 1986). This is borne out by Benton's (1983) compilation of absolute faunal abundance in Late Triassic fossil sites, although careful studies of crurotarsan taxonomic diversity have yet to be undertaken. Similarly, carnivorous theropods are much less morphologically disparate than carnivorous crurotarsans in the Late Triassic (Brusatte et al., 2008a,b).

4.2.3. Early Jurassic theropods — fossil record and distribution

Early Jurassic theropods are much more common, taxonomically diverse, and exhibit a greater range of morphologies than Late Triassic members of the group. Whereas only coelophysoids and similar taxa–mostly small-bodied and primitive theropods–were present in the Late Triassic, the Early Jurassic witnessed the evolution of more derived theropod clades characterized by larger body size and more disparate morphology. Most importantly, two major theropod clades, each of which would persist until the end of the Cretaceous, originated during the Early Jurassic.

The first of these clades, Ceratosauria (also called Neoceratosauria), would later give rise to the familiar Late Jurassic *Ceratosaurus* and the speciose Cretaceous clade Abelisauroidea (e.g.., Tykoski and Rowe, 2004; Carrano and Sampson, 2008). The oldest known putative ceratosaur is *Berberosaurus*, which comes from the Pliensbachian–Toarcian of Morocco (Allain et al., 2007). Allain et al. (2007) interpreted the fragmentary remains of *Berberosaurus* to represent the oldest abelisauroid, which would place it in a quite derived position within Ceratosauria. However, Carrano and Sampson (2008) instead argued that this taxon is the most basal ceratosaur, concordant with its stratigraphic position as the oldest unequivocal fossil of Ceratosauria. More recently, the phylogenetic analysis of Xu et al. (2009) found *Berberosaurus* as a more basal theropod, outside the Ceratosauria + Tetanurae clade. If correct, this would prompt a reinterpretation of neoceratosaur origins and early evolution.

The second of these major clades, Tetanurae, includes the largest carnivorous dinosaurs in most post-Early Jurassic ecosystems and later gave rise to birds (e.g., Sereno, 1999; Rauhut, 2003; Holtz et al., 2004; Smith et al., 2007). The oldest unequivocal tetanuran fossils are known from the early Middle Jurassic (Bajocian) of England (Waldman, 1974; Benson, 2008; Benson, 2010a). Carrano and Sampson (2004) suggested that a fragmentary knee joint from the late Sinemurian of England, included in the holotype of *Scelidosaurus* and figured by Owen (1861), may represent the oldest known tetanuran. However, there is no definitive anatomical evidence that this specimen is a tetanuran (Benson, 2010a). Nonetheless, because ceratosaurs and tetanurans are sister taxa, the presence of *Berberosaurus*, if a ceratosaur, implies that the tetanuran lineage also extends into the Early Jurassic.

Another possible clade of theropod dinosaurs also flourished during the Early Jurassic. The phylogenetic analysis of Smith et al. (2007) recovered a monophyletic "dilophosaurid" clade consisting of several medium-large-bodied Early Jurassic theropods, including *Dilophosaurus* (Fig. 3B), *Cryolophosaurus*, and *Dracovenator*. Each of these taxa possesses some form of distinctive cranial ornamentation, and features of these crests were important characters uniting the group in the phylogenetic analysis. However, Brusatte et al. (2010a) argued that Smith et al.'s (2007) character list too finely atomizes details of the cranial ornamentation, effectively over-representing the crest in the dataset and biasing the analysis towards finding a distinct clade of crested forms. As a result, when Brusatte et al. (2010a) reran the analysis using their own preferred system of scoring cranial crests the "dilophosaurid" clade disappeared. Additionally, this clade was not recovered by the comprehensive phylogenetic analysis of Nesbitt et al. (2009b), which samples a range of basal dinosaurs and theropods. Thus, the existence of a distinct "dilophosaurid" clade is currently a matter of debate among basal theropod workers. However,

both groups of workers agree that none of these taxa (with the possible exception of *Dilophosaurus*) belongs to a coelophysoid clade, and therefore are theropods more closely related to ceratosaurs and tetanurans than to coelophysoids.

Alongside these more derived groups, coelophysoids remained common through the Early Jurassic before going extinct at or near the end of this time interval (Carrano et al., 2005; Ezcurra and Novas, 2007). Some of the most familiar coelophysoids, such as *Coelophysis rhodesiensis*, "*Syntarsus*" *kayentakatae*, and *Segisaurus*, are known from the Early Jurassic.

Finally, one puzzling specimen deserves comment. Zhao and Xu (1998) and Xu et al. (2001) described an incomplete lower jaw from the Early Jurassic Lufeng Formation of China as the oldest known therizinosauroid. Therizinosauroids are a bizarre clade of derived coelurosaurian theropods that, in the grand scheme of dinosaur evolution, are one of the closest relatives of birds (e.g., Sereno, 1999; Clark et al., 2004). If this jaw, which was described as a new genus (*Eshanosaurus*), does represent a therizinosauroid, then it would drag numerous derived theropod lineages into the Early Jurassic by virtue of ghost range extensions. None of these lineages is currently known from even fragmentary Early or Middle Jurassic fossils. However, the systematic affinities of *Eshanosaurus* have generated substantial controversy among dinosaur workers (e.g., Rauhut, 2003; Irmis, 2004; Barrett, 2009a). Most striking, Barrett (2009a) made a compelling argument that this specimen is poorly dated, and could be as young as Early Cretaceous in age. Therefore, the resolution of this enigma probably depends on the discovery of more complete, unambiguously associated, and well-dated material of *Eshanosaurus*, as well as additional discoveries of other Early Jurassic coelurosaur fossils.

4.2.4. Early Jurassic theropods — paleobiology

Relative to the Late Triassic, the Early Jurassic was a time of increased theropod diversity and morphological disparity. Several distinct theropod groups co-existed, and these differed in body size and general morphology. The remaining coelophysoids were mostly small, similar in body size to the familiar Late Triassic *C. bauri*. However, the Early Jurassic *Dilophosaurus* reached lengths of about 6 m and a mass of 400 kg (e.g., Welles, 1984; Peczkis, 1994). *Cryolophosaurus* was even larger, and is estimated at 6.5 m in length and 465 kg in mass (Smith et al., 2007). The fossil remains of *Berberosaurus* are fragmentary, but its femur is approximately 90% as large as that of *Dilophosaurus* (Allain et al., 2007).

Despite the large range in size and overall anatomy, all Early Jurassic theropods (with the possible exception of *Eshanosaurus* if indeed it is an Early Jurassic theropod) were likely carnivorous, judging from their shared arsenal of serrated teeth, sharp claws, and skeletons adapted for speed (e.g., long hindlimbs). The evolution of dietary diversity in theropods–which included piscivorous spinosauroids, omnivorous ornithomimosaurs, herbivorous therizinosauroids, and the bizarre oviraptorosaurs and alvarezsaurids–did not occur until later in the group's history. The preponderance of cranial ornamentation in Early Jurassic theropods suggests that visual display was important for these animals, but whether this is unusual compared to the normal range of archosaur cranial ornamentation is difficult to evaluate (Smith et al., 2007).

4.2.5. Theropods across the Triassic/Jurassic boundary

Theropods probably had a global distribution in the Late Triassic, because their remains are known from all regions with a good Late Triassic fossil record (southwestern USA, Germany, Poland, France, Argentina). Theropod distribution was clearly global in the Early Jurassic, with specimens known from North America, Europe, Asia, North Africa, and South Africa. Unfortunately, theropod remains are scarce enough that it is difficult to say much about latitudinal or other regional diversity patterns during the Late Triassic or Early Jurassic.

A literal reading of the fossil record, as well as phylogenetic corrections that extend taxa back in time with ghost lineages, both indicate that there was a significant shift in theropod evolution across the Triassic–Jurassic boundary. Theropods were more taxonomically diverse in the Early Jurassic and evolved into a range of major clades and body plans during this time. How this diversification may relate to the Triassic–Jurassic extinction is unclear, but it is possible that theropods expanded in diversity, morphological disparity, and possibly ecological roles after the extinction of many carnivorous crurotarsan lineages (phytosaurs, ornithosuchids, rauisuchians) at or near the Triassic–Jurassic boundary (Olsen et al., 2002; Benton, 2004, 2005; Brusatte et al., 2008b). In any case, the overall picture of theropod rarity and morphological conservatism during the Late Triassic, and expansion in diversity and disparity in the Early Jurassic, argues against the hypothesis that theropods radiated rapidly soon after they originated (e.g., Hunt, 1991; Heckert and Lucas, 1995; Hunt et al., 1995; Carpenter, 1997).

4.3. Sauropodomorphs

4.3.1. Late Triassic sauropodomorphs — fossil record and distribution

Among Triassic dinosaurs, sauropodomorphs have one of the best fossil records in terms of taxonomic diversity and specimen abundance. Approximately twenty taxa are known from Late Triassic deposits on four continents (South America, Europe, Africa, Asia). These taxa fall into two general categories, which may or may not refer to discrete phylogenetic clades (see below). First, basal sauropodomorphs, commonly known as "prosauropods," were large, bipedal or quadrupedal herbivores or omnivores. Second, the more derived true sauropods were gigantic, fully quadrupedal, long-necked, barrel-chested herbivores.

The earliest sauropodomorphs are known from the late Carnian of South America. Martinez and Alcober (2009) recently described *Panphagia protos* based on a single well-preserved partial skeleton from the lower Ischigualasto Formation of northwestern Argentina. This taxon is currently the most basal sauropodomorph known, and lacks many of the derived characters present in other, more derived sauropodomorphs. An additional undescribed sauropodomorph is also present in the Ischigualasto Formation (Ezcurra, 2008). Until the discovery of *Panphagia*, *Saturnalia tupiniquim* from the upper Santa Maria Formation of southern Brazil (Langer et al., 1999, 2007c; Langer, 2003) was the most basal sauropodomorph known. This taxon is from strata that are biostratigraphically correlative with the Ischigualasto Formation (Langer, 2005; Langer et al., 2007b). *Saturnalia* is known from several specimens that together preserve most of the skeleton. This material provides our most complete look at the earliest sauropodomorphs and shows conclusively that *Saturnalia* shares many features with the rest of Sauropodomorpha.

By the end of the Norian, sauropodomorphs were both abundant and diverse in South America, Africa, and Europe. It is not uncommon for late Norian and Rhaetian formations from these continents to contain 3–6 penecontemporaneous sauropodomorph taxa (e.g., Los Colorados Formation: Galton and Upchurch, 2004). In contrast, no unquestionable sauropodomorph remains are known from North America until the Early Jurassic (Nesbitt et al., 2007).

The Triassic sauropodomorph species are phylogenetically diverse and include both basal forms as well as close relatives of the true sauropods. Unfortunately, the specific interrelationships of these taxa are still controversial, and two main competing phylogenetic hypotheses have been proposed. The first hypothesis suggests that most or all basal sauropodomorphs (i.e., non-sauropod sauropodomorphs) form a monophyletic group that is the sister taxon to Sauropoda (e.g., Sereno, 1999; Benton et al., 2000; Yates and Kitching, 2003; Galton and Upchurch, 2004; Sereno, 2007b; Upchurch et al., 2007a). In contrast, other studies find these taxa as a largely paraphyletic grade where some basal sauropodomorphs are closer

to sauropods than they are to each other (e.g., Yates, 2003a,b, 2007a,b; Smith and Pol, 2007; Yates et al., 2010). Despite these disagreements, recent phylogenies agree in several aspects: that *Panphagia*, *Saturnalia*, *Thecodontosaurus*, *Pantydraco*, and *Efraasia* form successive branches at the base of Sauropodomorpha; that *Coloradisaurus* from the Late Triassic of Argentina forms a monophyletic clade with several Early Jurassic taxa including *Massospondylus* and *Lufengosaurus*; and the Late Triassic taxa *Blikanasaurus*, *Lessemsaurus*, *Melanorosaurus*, and *Antetonitrus* are more closely related to neosauropods ("true" sauropods) than to other basal sauropodomorphs (Smith and Pol, 2007; Upchurch et al., 2007a; Yates, 2007a,b; Yates et al., 2010).

4.3.2. Late Triassic sauropodomorphs — paleobiology

The earliest sauropodomorphs were small: *Saturnalia* has a femur length of 15 cm (Langer, 2003) and *Panphagia* was only slightly larger (Martinez and Alcober, 2009). Body size increased fairly early in sauropodomorph evolution. *Efraasia* and a majority of more derived sauropodomorphs have femur lengths above 50 cm (Carrano, 2006). The basal sauropods *Antetonitrus* and *Lessemsaurus* have femoral lengths of approximately 75 cm (Yates and Kitching, 2003; Pol and Powell, 2007a,b). Although *Isanosaurus attavipachi* from the Late Triassic of Thailand was about the same size, a 1.04-meter-long indeterminate sauropod humerus from the same strata demonstrates that sauropods reached truly gigantic sizes, equal to their Jurassic relatives, prior to the Triassic–Jurassic boundary (Buffetaut et al., 2002).

Associated with this increase in body size was a transformation from bipedal (the putative primitive dinosaurian condition) to quadrupedal locomotion. Although there is evidence that the earliest sauropodomorphs may have been facultatively quadrupedal (Langer et al., 2007b), most basal sauropodomorphs were unable to pronate their manus, which restricted their ability to walk quadrupedally (Bonnan and Senter, 2007). Nonetheless, more derived basal sauropodomorphs such as *Aardonyx* show specializations towards pronation (Yates et al., 2010) and the earliest sauropods were able to pronate their hands (e.g., *Melanorosaurus* and *Antetonitrus*), which along with a variety of other specializations indicates that these taxa were habitual if not obligate quadrupeds (Yates and Kitching, 2003; Bonnan and Yates, 2007; Yates et al., 2010). More derived Late Triassic sauropods like *Isanosaurus* were obligate quadrupeds, show a variety of graviportal specializations, and are very similar to other sauropods from the Early Jurassic (Buffetaut et al., 2000; Yates et al., 2010).

The final major functional change in early sauropodomorph evolution was the transformation from the primitive archosaurian state of carnivory to herbivory. Basal sauropodomorphs were traditionally interpreted as browsing herbivores based on their iguana-like teeth, long necks, and large body size (e.g., Galton, 1985). However, as pointed out by Barrett (2000), most of these features are ambiguous indicators of true herbivory. If comparisons with iguanid lizards are appropriate, it is likely that basal sauropodomorphs were omnivores (Barrett, 2000; Barrett and Upchurch, 2007). This view was strengthened by the discovery of the basal-most sauropodomorph, *Panphagia*, which shows few feeding specializations other than non-recurved teeth with large serrations/denticles (Martinez and Alcober, 2009). The teeth of *Saturnalia* show a similar condition (R.B.I., personal observation), and in fact are similar to those of the Triassic saurischian *Eoraptor* (Sereno et al., 1993). An increase in body size and the development of obligate quadrupedality through the evolution of basal sauropodomorphs is consistent with a trend towards a more herbivorous diet (Barrett and Upchurch, 2007). Specializations for obligate herbivory such as U-shaped jaws, spatulate tooth crowns with reduced denticles, and a lateral plate on the dentary only appear in the most basal sauropods (Barrett and Upchurch, 2007; Upchurch et al., 2007b). Although these features are only documented in Early Jurassic taxa (e.g., Upchurch et al., 2007b), they are present in taxa more basal than the Triassic *Isanosaurus*,

indicating that obligate herbivory in sauropodomorphs must have evolved during the Late Triassic.

4.3.3. Early Jurassic sauropodomorphs — fossil record and distribution

Sauropodomorphs achieved a worldwide distribution during the Early Jurassic, and both basal sauropodomorphs ("prosauropods") and true sauropods thrived during this time. *Anchisaurus* is the earliest known sauropodomorph from North America (Yates, 2004), and Smith and Pol (2007) recently described *Glacialisaurus* from Antarctica. *Glacialisaurus*, *Massospondylus* from southern Africa, and *Lufengosaurus* from China are all part of a clade of basal sauropodomorphs that had its origins in the Late Triassic, with the Argentine *Coloradisaurus* (Smith and Pol, 2007; Yates, 2007a,b). *Anchisaurus*, along with *Seitaad* from western North America (Sertich and Loewen, 2010), *Jingshanosaurus* and *Yunnanosaurus* from China, and *Aardonyx* from South Africa appear to be typical "prosauropods", but may in fact be closely related to the true sauropods (Yates, 2004, 2007a,b; Yates et al., 2010). Basal sauropods also had a cosmopolitan distribution during the Early Jurassic, and include *Chinshakiangosaurus* and *Gongxianosaurus* from China, *Vulcanodon* from southern Africa, *Tazoudasaurus* from Morocco, and *Barapasaurus* from India. Although many of these lineages originated in the Late Triassic, the non-sauropod sauropodomorphs appear to have gone extinct at the end of the Early Jurassic. Indeed, no "prosauropods" are known from after this time period, and during the Middle Jurassic–Late Cretaceous large sauropods dominated the megaherbivore niche in most terrestrial ecosystems.

4.3.4. Early Jurassic sauropodomorphs — paleobiology

The discovery of Triassic sauropods demonstrated that most of the major changes in early sauropodomorph evolution, such as the development of quadrupedal locomotion and obligate herbivory, occurred prior to the Triassic–Jurassic boundary (see above). Thus, Early Jurassic sauropodomorphs represent further diversification of lineages that had already acquired these specializations earlier in their evolutionary history. In other words, the Early Jurassic was not a period of major new bodyplan evolution, but rather saw the modification of body types and lineages that had evolved much earlier.

During the Early Jurassic, sauropodomorphs continued to become more graviportal and increased in body size. Taxa such as *Vulcanodon*, *Tazoudasaurus*, and *Barapasaurus* had femoral lengths of well over a meter (Carrano, 2006; Allain and Aquesbi, 2008). The poor terrestrial fossil record during the latest Early and Middle Jurassic has limited our understanding of neosauropod origins and diversification, but it is likely that neosauropods originated in the late Early Jurassic. Perhaps the most significant paleobiological event in Early Jurassic sauropodomorph evolution is the disappearance of "prosauropod" type basal sauropodomorphs by the end of the epoch.

4.3.5. Sauropodomorphs across the Triassic/Jurassic boundary

Sauropodomorphs had a nearly cosmopolitan distribution by the end of the Norian (South America, Europe, Greenland, South Africa, southeast Asia, but not North America), and were present on all continents by the end of the Early Jurassic. Sauropodomorph remains are usually easily identifiable given that they are the largest terrestrial vertebrates during the Late Triassic–Early Jurassic. All recent phylogenetic hypotheses outlined above indicate that much of the diversification of basal Sauropodomorpha occurred in the Norian. Both typical "prosauropods" and early sauropods were present in the Late Triassic, and most of these lineages continued into the Early Jurassic. Thus, the Triassic–Jurassic extinction seemed to have little effect on sauropodomorph diversification, distribution, and abundance, even though the poor global terrestrial rock record of the latest Triassic (Rhaetian) limits conclusions about sauropodomorph evolution during this time.

4.4. Ornithischians

4.4.1. Late Triassic ornithischians — fossil record and distribution

Our understanding of Triassic ornithischians has undergone a radical revision in recent years. Prior to 2005, the Triassic ornithischian record was believed to include a number of taxa, including eight monospecific genera erected on the basis of isolated teeth from North America alone (Table 2). However, Parker et al. (2005) described the first non-dental material referable to one of these taxa, *Revueltosaurus callenderi*. These cranial and postcranial specimens lacked dinosaur features and were conclusively shown to belong to an herbivorous crurotarsan (crocodile-line) archosaur. Thus, any dental similarities between *Revueltosaurus* and ornithischians were independently acquired, and the preponderance of ornithischian-like teeth common in the Late Triassic of North America could no longer be definitely ascribed to ornithischians. This possibility had already been raised by the description of the basal dinosauromorph *Silesaurus* from the Carnian of Poland, which possessed low leaf-like teeth reminiscent of those of ornithischians (Dzik, 2003).

In combination, these two discoveries prompted a comprehensive reassessment of the Late Triassic ornithischian record (Irmis et al., 2007b; see also Butler et al., 2006a), which is summarized in Table 2. Following this reassessment, only three Late Triassic body fossil specimens are currently considered ornithischian, and all are from a relatively small geographical area in southern Gondwana.

First, *Pisanosaurus* is known from a partial skeleton that includes limited cranial material (Casamiquela, 1967; Bonaparte, 1976). Sereno (1991b) suggested that the holotype was a chimera of at least two taxa, but there seems to be little basis for this proposal (Irmis et al., 2007b). The phylogenetic position of *Pisanosaurus* is highly controversial: it has been identified as the most basal known ornithischian (Sereno, 1991b, 1999; Butler, 2005; Irmis et al., 2007a; Butler et al., 2008a), or as a possible heterodontosaurid (Bonaparte, 1976), and even its ornithischian affinities have been questioned (Thulborn, 2006; Irmis et al., 2007b). This uncertainty results from character conflict in the holotype: cranial material shares derived character states with ornithischians and specifically heterodontosaurids (e.g., the degree and pattern of occlusal wear facets) whereas the postcranial skeleton contains numerous plesiomorphic character states, including possibly an anteriorly directed pubis (seen in no other ornithischian: e.g., Sereno, 1986, 1999; Butler et al., 2008a; but see Irmis et al., 2007b).

Second, Báez and Marsicano (2001) described a tooth-bearing fragment of maxilla from Patagonia as a heterodontosaurid closely related to *Heterodontosaurus* from the Early Jurassic of South Africa (Fig. 3D). Although this fragment is poorly preserved, its heterodontosaurid identity has been tentatively accepted (Irmis et al., 2007b). Finally, Butler et al. (2007) and Butler (2010) described *Eocursor* from the lower Elliot Formation of South Africa, based upon a relatively complete skeleton of a single individual. *Eocursor* is the most completely known Triassic ornithischian and was identified as the sister taxon to Genasauria, a clade comprising most post-Triassic ornithischian diversity (Butler et al., 2007; Butler, 2010).

Tridactyl footprints from the Late Triassic of the USA, Europe and Africa have been identified as having been made by ornithischians (e.g., Biron and Dutuit, 1981; Mietto, 1985; Olsen and Baird, 1986; Dal Sasso, 2003; Knoll, 2004; Milàn and Gierlinski, 2004; Weishampel et al., 2004). However, a tridactyl pedal morphology similar to that of early ornithischians was present in many Triassic taxa, including basal saurischians, theropods, the earliest sauropodomorphs (e.g., *Saturnalia*: Langer, 2003), and dinosauromorphs (e.g., *Silesaurus*: Dzik, 2003). Thus, it is not possible to confirm the ornithischian identity of any of the reported footprints (Irmis et al., 2007b).

4.4.2. Late Triassic ornithischians — ghost lineages and diversity

Triassic ornithischian fossils are scarce, limiting our understanding of the early diversity of the clade. However, ghost lineages derived

Table 2

A list of Late Triassic taxa that were once thought to represent ornithischian dinosaurs, but are now regarded as belonging to other reptilian clades. Taxa erroneously thought to be dinosaurs, but not ornithischians, are listed in Table 3.

Taxon	Material	Formation and age	Original reference	Current placement	Current reference
Revueltosaurus callenderi	Teeth, partial skeleton including skull, postcrania	Bull Canyon Formation, New Mexico and Chinle Formation, Arizona, USA (Norian)	Hunt (1989); Padian (1990)	Valid taxon of Pseudosuchia	Parker et al. (2005), Irmis et al. (2007a,b)
Revueltosaurus (=*Krzyzanowskisaurus*) *hunti*	Teeth	Chinle Formation, Arizona (Norian)	Heckert (2002, 2005)	*Revueltosaurus* sp.	Irmis et al. (2007a,b)
Galtonia gibbidens	Teeth	New Oxford Formation, Newark Supergroup, Pennsylvania, USA (?upper Carnian)	Hunt and Lucas (1994)	*Revueltosaurus* sp.	Irmis et al. (2007a,b)
Pekinosaurus olseni	Teeth	Pekin Formation, Newark Supergroup, North Carolina, USA (?upper Carnian)	Hunt and Lucas (1994)	*Revueltosaurus* sp.	Irmis et al. (2007a,b)
Tecovasaurus murryi	Teeth	Tecovas Formation, Dockum Group, Texas, USA (?upper Carnian)	Hunt and Lucas (1994)	Valid taxon, Archosauriformes incertae sedis	Irmis et al. (2007a,b)
Lucianosaurus wildi	Teeth	Chinle Formation, New Mexico (Norian)	Hunt and Lucas (1994)	Valid taxon, Archosauriformes incertae sedis	Irmis et al. (2007a,b)
Protecovasaurus lucasi	Teeth	Tecovas Formation, Dockum Group, Texas, USA (?upper Carnian)	Heckert (2004)	Valid taxon, Archosauriformes incertae sedis	Irmis et al. (2007a,b)
Crosbysaurus harrisae	Teeth	Tecovas Formation, Dockum Group, Texas, USA (?upper Carnian)	Heckert (2004)	Valid taxon, Archosauriformes incertae sedis	Irmis et al. (2007a,b)
Technosaurus smalli	Cranial/postcranial fragments	Bull Canyon Formation, Dockum Group, Texas, USA (Norian)	Chatterjee (1984)	Non-dinosaurian *Silesaurus*-like taxon (in part)	Irmis et al. (2007a,b); Nesbitt et al. (2007)
"Wolfville ornithischian"	Maxilla	Wolfville Formation, Nova Scotia, Canada (Norian)	Galton (1983)	Archosauriformes incertae sedis	Irmis et al. (2007a,b)
Ornithischia indet.	Teeth	Late Triassic of USA and Western Europe	Tatarinov (1984); Galton (1986); Kirby (1991); Godefroit and Cuny (1997); Godefroit et al. (1998); Cuny et al. (2000); Godefroit and Knoll (2003)	Archosauriformes incertae sedis	Butler et al. (2006a); Irmis et al. (2007a,b)
Stegosauria indet.	Fragments of limb bones	Westbury Formation, England, (Rhaetian)	Galton (2005)	Tetrapoda indet.	Butler et al. (2006a); Irmis et al. (2007a,b)
Footprints including *Atreipus* spp.	Footprints	Late Triassic of USA, South Africa and Western Europe	Biron and Dutuit (1981); Mietto (1985); Olsen and Baird (1986); Dal Sasso (2003); Knoll (2004); Milàn and Gierliński (2004); Weishampel et al. (2004)	Dinosauriformes incertae sedis	Irmis et al. (2007a,b)

from phylogenies may indicate the presence of additional lineages for which fossil evidence has not yet been identified. The number of additional lineages that can be inferred depends upon the phylogeny chosen, as well as on interpretations of the phylogenetic position of fragmentary Late Triassic specimens.

Assuming that the maxilla described by Báez and Marsicano (2001) can be accurately referred to Heterodontosauridae (and/or *Pisanosaurus* ultimately proves to be a heterodontosaurid), the phylogeny of Sereno (1986, 1999) suggests that the major ornithischian clades Genasauria, Thyreophora, Neornithischia, Ornithopoda, Euornithopoda and Marginocephalia were also present prior to the Triassic/Jurassic boundary, implying a major Triassic ornithischian phylogenetic diversification despite apparent low numerical abundance (based on a dearth of fossils). Similarly, early origins of major ornithischian clades and high Triassic diversities are predicted by phylogenies that position heterodontosaurids as the sister taxon to Marginocephalia (e.g., Xu et al., 2006). However, if the Laguna Colorado maxilla does not represent a heterodontosaurid ornithischian, then the phylogenies of Sereno (1986, 1999) and Xu et al. (2006) would instead suggest that this diversification may have occurred in the earliest Jurassic.

An alternative view of ornithischian phylogeny differs primarily by positioning heterodontosaurids as non-genasaurian basal ornithischians (Butler, 2005; Butler et al., 2007, 2008a, 2010). This phylogeny implies an Early Jurassic origination date for Genasauria. In general, this phylogeny predicts later appearances for major ornithischian clades than do previous phylogenetic hypotheses, and a lower diversity of ornithischian clades present in the Late Triassic. As a result, this phylogeny fits the observed stratigraphic record more closely than do previous phylogenies (Wills et al., 2008).

4.4.3. Late Triassic ornithischians — paleobiology

The earliest ornithischians, such as *Pisanosaurus* and *Eocursor*, were small-bodied, with known specimens reaching just over a meter in body length (Bonaparte, 1976; Butler et al., 2007; Butler, 2010). Distal elements of the hindlimb (tibia, metatarsals) are elongate, suggesting well-developed cursorial abilities. Tooth-to-tooth occlusion and a buccal emargination were both present in *Pisanosaurus* (Sereno, 1991b). This latter character, which refers to the inset placement of the maxillary and dentary teeth, suggests the presence of a fleshy 'cheek', which has been viewed as a key ornithischian innovation (Galton, 1973; Sereno, 1997), and dental wear indicates a rapid acquisition of sophisticated jaw mechanics. By contrast, the cranial morphology of *Eocursor* is similar to that of *Lesothosaurus* (Sereno, 1991b) or *Scutellosaurus* (Colbert, 1981), with a low coronoid process of the lower jaw, a weakly inset dentary tooth row, a jaw joint which is only slightly offset below the level of the tooth row, and low, triangular teeth which lack systematic wear facets and possess enlarged denticles on mesial and distal surfaces. Barrett (2000) suggested that early ornithischians such as *Lesothosaurus* and heterodontosaurids may have been facultatively omnivorous, rather than strictly herbivorous, and this interpretation is also plausible for *Pisanosaurus* and *Eocursor*.

4.4.4. Early Jurassic ornithischians — fossil record and distribution

In stark contrast to the Late Triassic, Early Jurassic ornithischians are taxonomically and phylogenetically diverse, and are known from locally abundant and often excellently preserved material. The most diverse and important Early Jurassic ornithischian fauna is known from the upper Elliot Formation and overlying Clarens Formation of South Africa and Lesotho. This fauna includes the basal ornithischians *Lesothosaurus* (Thulborn, 1970a, 1971, 1972; Galton, 1978; Sereno, 1991b; Butler, 2005) and *Stormbergia* (Butler, 2005), and five named monospecific genera of heterodontosaurids (*Heterodontosaurus*, *Abrictosaurus*, *Lycorhinus*, *Lanasaurus*, *Geranosaurus*: Broom, 1911; Haughton, 1924; Crompton and Charig, 1962; Thulborn, 1970b, 1974;

Gow, 1975; Hopson, 1975; Santa Luca et al., 1976; Santa Luca, 1980; Gow, 1990; Butler et al., 2008b). Recent reviews consider only three of the heterodontosaurid genera to be valid (Weishampel and Witmer, 1990; Norman et al., 2004c). However, the taxonomy of the Southern African heterodontosaurids is problematic: additional taxa may be present (RJB pers. obs.) and further work is needed. Although Early Jurassic ornithischian material is often described as rare, specimens representing over 60 southern African individuals (many undescribed) are known (RJB pers. obs.).

Within North America, substantial material of the early thyreophoran *Scutellosaurus* is present in the Kayenta Formation (Sinemurian– Pliensbachian) of Arizona (Colbert, 1981; Rosenbaum and Padian, 2000), and is the most commonly recovered dinosaur from this formation (Tykoski, 2005). Large postcranial osteoderms indicate the presence of a second, larger, thyreophoran, and were referred to the genus *Scelidosaurus* by Padian (1989; see also Tykoski, 2005). An undescribed heterodontosaurid specimen (Attridge et al., 1985) is also known. The only other reported ornithischians from the Early Jurassic of North America are undescribed teeth from the McCoy Brook Formation of Nova Scotia (Shubin et al., 1994).

Thyreophoran ornithischians are well represented in the Early Jurassic of Europe. *Scelidosaurus* is known from multiple articulated and often nearly complete specimens from the Lower Lias (late Sinemurian) of England (Owen, 1861, 1863; Barrett, 2001), and *Emausaurus* is known from a single specimen from the Toarcian of Germany (Haubold, 1990).

Asian Early Jurassic ornithischians are known primarily from the Dark Red Beds of the Lower Lufeng Formation (Sinemurian) of China. Recent revisions of material from this formation have recognized only three specimens as ornithischian: the fragmentary holotypes of *Tatisaurus* (Simmons, 1965; Norman et al., 2007) and *Bienosaurus* (Dong, 2001), and an indeterminate fragmentary hindlimb (Irmis and Knoll, 2008). *Tatisaurus* and *Bienosaurus* are tentatively considered to represent basal thyreophorans (Norman et al., 2007). In contrast with the upper Elliot and Kayenta formations, ornithischians are exceptionally scarce components of the Lower Lufeng assemblage.

Early Jurassic terrestrial faunas from South America are poorly known. However, Barrett et al. (2008) described teeth and a distal tibia referable to Ornithischia from either the Early or Middle Jurassic of Venezuela.

4.4.5. Early Jurassic ornithischians — paleobiology

Heterodontosaurids were more abundant and diverse in the Early Jurassic than at any other time in their evolutionary history, and a range of cranial morphologies were present (e.g., Hopson, 1975; Weishampel and Witmer, 1990). This suggests that a variety of cranial mechanisms and feeding styles may have been important in enabling a number of heterodontosaurid genera to coexist (e.g. in the upper Elliot Formation of southern Africa). Among other Early Jurassic ornithischians, an orthal mechanism with some interlocking of the upper and lower dentitions has been postulated for *Lesothosaurus* (Thulborn, 1971), whereas Barrett (2001) suggested a 'puncture-crushing' mechanism for *Scelidosaurus*. It is possible that most Early Jurassic ornithischians were omnivorous (Barrett, 2000), rather than strictly herbivorous.

Most Early Jurassic ornithischians (e.g. heterodontosaurids, *Lesothosaurus*, *Scutellosaurus*) were apparently small-bodied, with the largest known individuals reaching around 1–1.5 m in length. However, the Early Jurassic marks the appearance of the first moderately large ornithischians. Adults of *Scelidosaurus* were at least 4 m in length, and *Stormbergia* probably reached lengths of around 3 m. Ornithischians of similar size were probably also present in the Kayenta Formation of Arizona (Padian, 1989; RJB pers. obs.).

Most Early Jurassic ornithischians probably utilized both quadrupedal and bipedal gaits, as argued for heterodontosaurids (Santa Luca, 1980; Weishampel and Witmer, 1990), *Lesothosaurus* (Norman et al., 2004a), and *Scutellosaurus* (Colbert, 1981; Norman et al., 2004b), and as

suggested by the probable ornithischian ichnogenus *Anomoepus* (Olsen and Rainforth, 2003). *Scelidosaurus* is generally regarded as an obligate quadruped (Norman et al., 2004b), suggesting that a reversal to this condition had occurred in the thyreophoran lineage by the Sinemurian. However, Gierlinski (1999) has suggested, based upon ichnological evidence, that large basal thyreophorans such as *Scelidosaurus* may have been capable of at least occasional bipedal locomotion.

4.4.6. Ornithischians across the Triassic/Jurassic boundary

During the Early Jurassic, ornithischians achieved a global distribution, with definite body fossils known from Africa, Europe, North America, and Asia. Although poorly dated, body fossils may indicate the existence of ornithischians in South America in the Early Jurassic. Ornithischians are both relatively abundant and diverse within the upper Elliot Formation of southern Africa and the Kayenta Formation of the USA (see above). In contrast, ornithischian fossils remain highly scarce relative to saurischians in the Lower Lufeng Formation of China, suggesting that ornithischian abundance varied geographically (Irmis and Knoll, 2008). Early armored dinosaurs (thyreophorans) were diverse and are known from North America, Asia, and Europe, but are absent from the southern African record, suggesting some degree of provinciality in early ornithischian faunas.

There was undoubtedly a dramatic increase in ornithischian abundance across the Triassic–Jurassic boundary. By the Early Jurassic ornithischians are relatively diverse, abundant, and globally distributed. Major ornithischian clades such as Genasauria, Thyreophora and Neornithischia can be identified. The exact timing of this diversification is problematic, because of the poorly constrained dating of many Late Triassic and Early Jurassic sequences, but it does appear that ornithischians are scarce in, or absent from, most latest Triassic (Norian/Rhaetian) assemblages, but relatively abundant in earliest Jurassic (Hettangian/Sinemurian) assemblages. How this diversification might relate to proposed extinction events at the Triassic–Jurassic boundary remains uncertain. However, a number of herbivorous clades went extinct at this time, which may have vacated ecological niches into which ornithischians were able to radiate (Olsen et al., 2002; Butler et al., 2007; Brusatte et al., 2008b).

4.5. Taxa often mistaken as dinosaurs

Throughout the Late Triassic dinosaurs evolved alongside their close relatives, the crurotarsan (crocodile-line) archosaurs (Fig. 7). These two groups were heavily convergent on each other, in some cases eerily so (Nesbitt and Norell, 2006), and as a result many fragmentary specimens of crurotarsans have been mistaken for dinosaurs, and vice versa (Tables 2 and 3). Many such specimens, especially isolated teeth, were formally assigned to various dinosaurs in the pre-cladistic era of archosaur systematics. However, Benton (1986b) demonstrated that many of these so-called dinosaur specimens from the Triassic actually represent crurotarsans (Fig. 7). Additionally, Benton (1986b) showed that putative Early and Middle Triassic dinosaur footprints, identified across Europe, could not be unambiguously identified as dinosaur tracks.

"Dinosaur-like" crurotarsans can still be problematic. For example, Chatterjee (1993) announced the discovery of *Shuvosaurus* from the Late Triassic of Texas, which he interpreted as the oldest member of the ornithomimid lineage, a group of theropods mostly restricted to the Cretaceous. As ornithomimids are deeply nested within Theropoda, this discovery suggested that many lineages of carnivorous dinosaurs were present, but unknown from fossils, in the Late Triassic. However, Nesbitt and Norell (2006) and Nesbitt (2007) demonstrated that *Shuvosaurus* and its close relative *Effigia* are actually members of the crurotarsan lineage.

Other studies have mistaken even more basal reptiles as among the 'oldest dinosaurs.' For example, Flynn et al. (1999) reported two new sauropodomorph dinosaurs from the early Late Triassic of Madagascar.
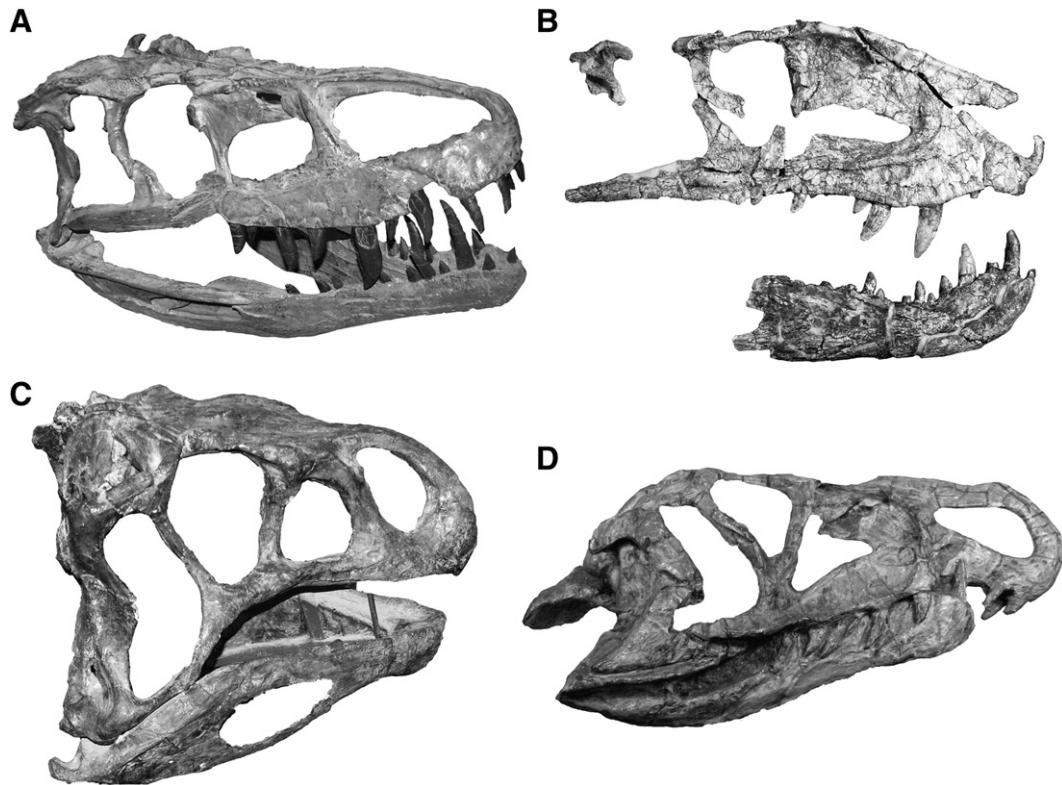
Fig. 7. A montage of crurotarsan (crocodile-line) archosaurs convergent on the earliest dinosaurs. A, *Batrachotomus*, a large, quadrupedal, rauisuchian predator from the Ladinian of Germany; B, *Postosuchus*, a large, quadrupedal, rauisuchian predator from the Norian of the United States; C, *Lotosaurus*, a mid-sized, quadrupedal, sail-backed omnivore from the Anisian of China; D, *Riojasuchus*, a mid-sized, quadrupedal or bipedal, swift predator from the Norian of Argentina. Figure delineated by Stephen Brusatte.

Additional material and a careful reevaluation of the specimens demonstrate that the purported 'sauropodomorph' material belongs to a taxon only distantly related to dinosaurs that shares uncanny modifications of the skull with plant-eating, large-bodied dinosaurs (Flynn et al., 2008; Flynn et al., 2010). Similarly, Nesbitt et al. (2007) demonstrated that several supposed dinosaurs from the Late Triassic of North America actually represent dinosauromorphs, the closest relatives to dinosaurs rather than bona fide members of the group.

This historical review, although brief, testifies to both a practical problem in identifying Late Triassic specimens and a remarkable fact about evolution during this period. Although most large-bodied terrestrial reptiles of the Jurassic and Cretaceous were dinosaurs, a number of different Triassic groups converged on the same general body plans, including animals closely related to modern crocodylians (Fig. 7). Although this often makes it difficult to identify fragmentary specimens, it suggests that the Late Triassic was a unique time in terrestrial vertebrate evolution during which different groups iteratively evolved the same generalized morphologies (Nesbitt and Norell, 2006; Nesbitt, 2007).

5. The dinosaur radiation: a historical review

Until the 1980s, most authors (e.g., Colbert, 1964; Romer, 1966; Bakker, 1972; Charig, 1972, 1984) pictured the radiation of the dinosaurs as part of an evolutionary relay of successive faunal replacements throughout the Triassic. This was the favored viewpoint for three main reasons:

(1) As noted earlier, most authors considered that the dinosaurs were a polyphyletic assemblage and hence that dinosaurs arose several times, essentially convergently, as a result of similar competitive pressures.

(2) The origin of the dinosaurs was seen as a drawn-out affair that started early in the Middle Triassic and involved extensive and long-term competition. The dinosaur ancestors were regarded as superior animals, with advanced locomotory adaptations (erect gait: Charig, 1972, 1984) or physiological advances (e.g., warm-bloodedness: Bakker, 1972) that progressively competed with, and caused the extinction of, all of the synapsids and basal archosaurs, that lacked such superior features.

(3) The first appearance of dinosaurs was seen as a great advance that must have been the mark of some kind of competitive process. It had commonly been assumed that the evolution of life was in some way 'progressive,' and that more recent plants and animals are inevitably better than those that went before. We discuss this further, below.

Table 3
A list of Late Triassic taxa that were once thought to represent dinosaurs, but are now regarded as belonging to other reptilian clades. Taxa erroneously thought to be ornithischian dinosaurs are listed separately in Table 2. *Technosaurus* is listed in both tables, as its holotype is a chimaera (Nesbitt et al., 2007).

Taxon	Current placement	Reference
Azendohsaurus	Basal archosauromorph	Flynn et al. (2008)
Eucoelophysis	*Silesaurus*-like dinosauromorph	Nesbitt et al., 2007; Ezcurra (2007)
Ornithosuchus	Crurotarsan archosaur	Gauthier (1986); Sereno (1991a)
Postosuchus	Crurotarsan archosaur	Long and Murry (1995)
Protoavis	Numerous taxa	Nesbitt et al. (2007)
Saltopus	Dinosauromorph	Rauhut and Hungerbühler (2000)
Shuvosaurus	Crurotarsan archosaur	Nesbitt and Norell (2006)
Spinosuchus	Basal archosauriform	Nesbitt et al. (2007)
Spondylosoma	Crurotarsan archosaur?	Galton (2000)
Technosaurus	*Silesaurus*-like dinosauromorph	Nesbitt et al. (2007)
Teratosaurus	Crurotarsan archosaur	Benton (1986b)

Beginning in the 1980s, many scientists began to take a different view. Benton (1983, 1986a, 1994) argued that the dinosaurs radiated after ecospace had been cleared during the end-Carnian extinction event (which now is likely dated within the Norian, because of the redating of strata discussed above), and that the dinosaurs did not establish their pre-eminence after a long period of competition with precursor groups. This view was supported by several lines of evidence:

(1) The fossil record does not show a gradual takeover, but apparently two expansions after extinction events, the first at the end of the Carnian (or early Norian) when the dominant herbivores, the rhynchosaurs and dicynodonts, became dramatically depleted, and were replaced in the Norian by basal sauropodomorphs, and then at the end of the Triassic, when most crurotarsans died out, and large theropods and armored dinosaurs radiated in the Early Jurassic.

(2) The first dinosaurs had all or most of the supposed "key characters" (upright stance, etc.) that were thought to help them outcompete other groups, but they did not take over at once (Sereno, 1999). During the Carnian, all three major dinosaurian lineages were present, but they did not radiate until much later.

(3) The "superior adaptations" of dinosaurs were probably not so profound as was once thought. For instance, many other archosaurs also evolved erect gait in or by the Late Triassic, and yet they died out (e.g. aetosaurs, rauisuchians, ornithosuchids, and some early crocodylomorphs).

(4) There were other extinctions at the end of the Carnian or within the early Norian. The *Dicroidium* flora of the southern hemisphere gave way to a worldwide conifer flora about this time (see above). There were turnovers in marine communities, particularly in reefs, and there was a shift from pluvial (heavy rainfall) climates to arid climates throughout much of the world (Simms and Ruffell, 1990b). The climatic and floral changes may have caused the extinctions of the dominant herbivorous tetrapods.

(5) The idea that simple competition can drive the replacement of one major group by another is an oversimplification. Competition between higher taxa ("families" or "orders") of animals is very different from the ecological observation of competition within or between species in an ecosystem. In paleontological examples such as this, competition has often been assumed to have been the mechanism, but the evidence has generally been shown to be weak (Benton, 1987).

Ideas of competition and superiority stemmed from the deep-seated views of many distinguished architects of the Modern Synthesis (e.g., Theodosius Dozhansky, George Gaylord Simpson, Julian Huxley) that evolution was progressive (Gascoigne, 1991). Dobzhansky et al. (1977, p. 508) defined progress in evolution as "systematic change in a feature belonging to all members of a sequence in such a way that posterior members of the sequence exhibit an improvement of that feature." Such views emerged naturally from Darwin's world view that evolution was competitive, and that a new species could arise only by supplanting a pre-existing species. Darwin, in his unpublished *Natural Selection* manuscript (see Stauffer, 1975, p. 208), compared the present-day diversity of species to a number of apples floating on the surface of a barrel filled with water. The surface of the water is packed with floating apples, and it is impossible to add a new apple without displacing one that is already there. Such ideas were at the base of many branches of ecological theory, including the classic Lotka–Volterra models of the 1930s, the theory of island biogeography (MacArthur and Wilson, 1967), and the logistic models of global marine biodiversity (Sepkoski, 1996).

The tension between selection and contingency, or, as Darwin put it, between selection and environment, goes on today. The Red Queen model of evolution (Van Valen, 1973) sees most of macroevolution (long-term evolution of large clades) driven by biotic interactions, although the physical environment is allowed a place. An opposing view, termed the Court Jester model (Barnosky, 2001), is that changes in climate and topography, and unpredictable events (contingency), contribute much more to the larger patterns, and especially to wholesale extinctions and many major diversifications following such crises. The question is how much of the tree of life, of modern biodiversity, and large-scale geographic patterns of distribution are mediated by physical environmental factors, and how much by competition and predation in ecosystems (Benton, 2009)?

In exploring classic examples of diversifications and biotic replacements (Gould and Calloway, 1980; Benton, 1987; Roy, 1996), most turned out to be best explained as responses to contingent events such as mass extinctions. Competition was rarely invoked as a simplistic clade vs. clade process, but rather at a more refined level of, for example, differential response to a crisis. Whatever the final outcome of these debates about the most influential drivers of large-scale evolution, a key lesson has been not to make unsupported assumptions, and to focus on quantifiable data (taxonomic diversity, faunal abundance, morphological disparity), and to do so within a sound chronologic, stratigraphic, and phylogenetic framework. Because dinosaurs are a major group that has been well studied, and for which an abundance of phylogenetic, stratigraphic, and morphological data exist, they are an ideal test case for examining macroevolutionary patterns over time.

6. The macroevolutionary pattern of the dinosaur radiation

6.1. Introduction

There is a rich historical legacy of debate regarding the early evolutionary history of dinosaurs. The Triassic fossil record and the toolkit of analytical methods available to paleontologists have changed greatly over the course of this debate. Many of the first scientists to offer hypotheses on the dinosaur radiation based their ideas on a literal reading of the fossil record combined with intuition based on experience and assumptions about how macroevolution works over long time scales. Over the past decade scientists have aimed to understand biases in the fossil record, worked to incorporate a phylogenetic framework into their studies, and begun to utilize a wide array of analytical techniques to quantify macroevolutionary patterns.

Many of these methods have been used to examine the radiation of dinosaurs. Perhaps the most important result of these studies is an understanding that the dinosaur radiation is more complex than often assumed (e.g., Brusatte et al., 2008b). Evolutionary radiations are not single events that can be described with broad platitudes, but have many different components that are often decoupled from each other. For instance, a clade may originate long before it speciates into a number of lineages, becomes numerically abundant in its ecosystem(s), or evolves into a wide range of different body types or ecological roles. These various components–lineage origination (cladogenesis), faunal abundance, taxonomic diversity, and morphological disparity– are distinctive measures of biodiversity that may or may not be related to each other. Each has been used to describe the radiation of dinosaurs in some form or another, but they must be considered side-by-side for an integrative picture of the early history of dinosaurs.

6.2. Lineage origination, cladogenesis, and phylogeny

The oldest unequivocal dinosaur fossils are known from the Carnian (see above) and are approximately 230 million years old. However, as with any observed fossil occurrences, this is only a minimum estimate for the origination of the dinosaur lineage. In reality, it is likely that dinosaurs extended further back in time, and the duration of this missing record can be estimated by ghost lineages on the phylogenetic tree of dinosaurs and their closest relatives (e.g., Norell, 1992). Because dinosaurs and their sister taxon had to originate at the same point in time (by definition), the discovery of

a sister taxon fossil older than the oldest known dinosaur will in effect extend the range of dinosaurs (or more accurately, their stem lineage) earlier in time (Norell, 1992, 1993).

Most recent phylogenetic analyses recover a sister group relationship of Dinosauria and a clade of mostly herbivorous dinosauromorphs centered on *Silesaurus*, *Sacisaurus*, and *Eucoelophysis* (e.g., Irmis et al., 2007a; Brusatte et al., 2008a; Nesbitt et al., 2009b, 2010; Brusatte et al., 2010b). Most members of Silesauridae are Carnian–Norian in age (e.g., Sullivan and Lucas, 1999; Dzik, 2003; Ezcurra, 2007; Ferigolo and Langer, 2007). However, Nesbitt et al. (2010) recently reported the discovery of a new member of the silesaurid clade, *Asilisaurus*, in the ?late Anisian of Tanzania. Thus, the presence of *Asilisaurus* in the Anisian implies that the lineage leading to Dinosauria originated by this time (Sidor et al., 2008; Nesbitt et al., 2010).

Within Dinosauria, the oldest ornithischian (*Pisanosaurus*: Bonaparte, 1976; Irmis et al., 2007b) and sauropodomorph (*Saturnalia*: Langer et al., 1999) are from the Carnian. The oldest unequivocal theropods, including *Coelophysis*, *Zupaysaurus*, and *Liliensternus*, are from the Norian. *Coelophysis* has long been considered to extend into the Carnian (e.g., Tykoski and Rowe, 2004), but revised radioisotopic dates for the Chinle Formation of the southwestern United States indicate that all localities where *Coelophysis* fossils are found are Norian in age at the oldest (Irmis and Mundil, 2008). However, as theropods are the sister taxon to sauropodomorphs, their ghost lineage extends into the Carnian. Indeed, if the controversial basal dinosaurs *Herrerasaurus* and *Eoraptor* do represent true theropods (see above), then Carnian specimens are already known (Rogers et al., 1993). Ghost lineages are unable to extend the ornithischian and sauropodomorph lineages back further from the Carnian, but it would not be surprising if unequivocal ornithischians, sauropodomorphs, theropods, or stem saurischians, do eventually come to light in Middle Triassic assemblages.

A phylogenetic perspective also gives insight into the pace of the dinosaur radiation. Recent discoveries of non-dinosaurian dinosauromorphs in Norian assemblages have greatly increased the stratigraphic range of the closest dinosaurian cousins (Irmis et al, 2007a). Previously these animals were thought to have gone extinct at or around the time that dinosaurs themselves originated (e.g., Sereno and Arcucci, 1994a,b). The new discoveries show that dinosaurs and their closest cousins persisted side-by-side for up to 20 million years, indicating that the rise of dinosaurs–the process by which dinosaurs became the preeminent terrestrial vertebrates at the expense of closely related groups–was a prolonged affair.

In summary, dinosaurs are first known from the Carnian but their stem lineage extends at least into the Anisian (Middle Triassic) based on ghost lineages. The major subgroups of dinosaurs are first known from the Carnian and early Norian, and none of these lineages can yet be confidently extended earlier than the Carnian. Thus, the current picture is one of early dinosaur origination (possibly in the Middle Triassic) followed by a delayed splitting of major dinosaur subgroups sometime during the Carnian. The dinosaur radiation itself was gradual, and proceeded in many steps, not sudden.

6.3. Taxonomic diversity and significant diversification shifts

In macroevolutionary studies "diversity" refers strictly to the number of taxa (usually species, genera, or higher taxa such as families), usually within a certain time bin or a certain area. This is different from lineage origination: a group can be present but contain very few species, and thus exhibits low diversity. Measuring diversity is normally quite straightforward, as it necessitates nothing more than counting taxa over time or space, and in some cases correcting for missing lineages unknown in the fossil record but implied by phylogeny (ghost lineages: Norell, 1992).

On the other hand, "diversification" is a broad, and often vague, umbrella term that is used in many different ways. Oftentimes researchers will refer to "significant diversification events" in a

group's evolutionary history. These are moments in time when a group speciates (or avoids extinction) at a pace or in a pattern that differs from the more normal "background" tempo of evolution. Although seemingly vague, these events can be identified by statistical tests that compare an observed phylogeny or diversity profile with a null expectation for how groups *should* split and speciate over time if splitting is random. This null expectation is usually based on a "birth–death" model that assumes each lineage has an equal, but independent, probability of splitting at any given time over the course of a group's evolution (see Chan and Moore, 2002; Nee, 2006; Ricklefs, 2007; Purvis, 2008 for more details). In essence, a certain time interval or a certain part of a cladogram can be identified as exhibiting "significant diversification" if it differs from the null model.

The taxonomic diversity of dinosaurs over time has long been a subject of interest, especially for those scientists studying the duration and magnitude of the extinction of non-avian dinosaurs at the end of the Cretaceous (e.g., Dodson, 1990). Diversity measurements continually change as new fossils are discovered and specimens are reinterpreted (for instance, compare the dinosaur diversity measurements of Dodson (1990) and Wang and Dodson (2006)). A profile of dinosaur diversity over time was recently provided by Lloyd et al. (2008), who were also the first authors to provide a phylogenetic correction to diversity measures across all Dinosauria (based on a supertree of dinosaur phylogeny, which as a "summary tree" is a broad and inexact proxy for a correction) and examine the potential sampling biases implicit in the dinosaur fossil record. Their diversity curves, based both on observed fossils ("taxic estimate") and observed counts corrected for ghost lineages ("phylogenetic estimate"), indicate a steady increase in diversity from the Carnian through the Early Jurassic (Table 4). Their statistical subsampling technique, which attempts to standardize sampling in order to remove biases that result from temporal variation in the quality of the fossil record, suggests that diversity was steady across the Carnian and Norian but jumped in the Early Jurassic (Lloyd et al., 2008: fig. 2b). (See also the recent phylogenetically-corrected diversity analysis presented by Barrett et al. (2009)).

Lloyd et al. (2008) also used their dinosaur supertree to ask two important questions: (1) which specific nodes (branching events) represent significant diversification shifts?; and (2) are significant diversification shifts concentrated in any specific interval of time? By comparing their cladogram to one expected under the null "birth–death" model, Lloyd et al. (2008) identified several nodes that exhibit significant diversification shifts. These are essentially nodes that are significantly more speciose than their sister taxon, which is a violation of the null model that assumes random splitting over time (see Chan and Moore, 2002, 2005; Jones et al., 2005). Importantly, these significant nodes are concentrated in the first third of dinosaur history, and most of them in the Late Triassic and Early Jurassic (Lloyd et al., 2008: fig. 3a,c), a result corroborated by statistical tests. Thus, the Late Triassic and Early Jurassic was a critical interval for dinosaur diversification, especially compared to the remainder of the history of dinosaurs.

Table 4
Dinosaur diversity by time (data from Lloyd et al., 2008; Brusatte et al., 2008b).

	Carnian	Norian	Early Jurassic[1]	Early Jurassic[2]
Taxic	9	22	26	27
Phylogenetic	14	9	8	13
Total	23	31	34	40

"Taxic" indicates observed fossil occurrences, with dates taken from Weishampel et al. (2004). "Phylogenetic" indicates the observed data plus a correction for ghost lineages (phylogenetic history of a taxon unpreserved in the fossil record but implied by the supertree of Lloyd et al., 2008). "Total" is a summation of taxic and phylogenetic measures. Early Jurassic estimates are calculated without (1) and with (2) inclusion of *Eshanosaurus*, a controversial derived theropod that, if correctly identified, drags several lineages into the Early Jurassic.

6.4. Morphological disparity and morphospace occupation

Morphological disparity refers to the range of morphologies and body types exhibited by a group of organisms. Disparity measures something quite different from lineage origination and diversity: a group could be present and/or taxonomically diverse, but may only exhibit a narrow array of body types and anatomical variability. Alternatively, a group could have very few species (low diversity), each characterized by a highly unique morphology (high disparity).

Disparity can be measured in several ways, using either morphometric data or discrete characters, such as those used in phylogenetic analyses (Wills et al., 1994). The goal in each case is to represent the overall morphology of a set of organisms. These morphological measurements or characters are then subjected to multivariate statistical analysis, which ordinates taxa in a multidimensional space (a "morphospace": Raup, 1965; McGhee, 1999; Erwin, 2007). In essence, a morphospace is akin to a morphological "map," which graphically represents how similar and different taxa are from each other in their body plans. Statistical tests can then be used to determine if certain groups of organisms (usually binned either taxonomically or by time) have a greater diversity of morphologies than other groups. In statistical terms, morphological diversity can be quantified in many ways, but the two most common methods calculate range and variance statistics for the different bins (Wills et al., 1994; Ciampaglio et al., 2001). Range measures denote the entire spread of morphological variation (the size of morphospace occupied by the group), whereas variance measures indicate average dissimilarity among members of the group (the spread of the group in morphospace).

The morphological disparity of Late Triassic and Early Jurassic dinosaurs, as well as other contemporaneous archosaur groups, was measured by Brusatte et al. (2008a,b) (Figs. 8 and 9). These studies indicate that dinosaur disparity increased over time, from the Carnian through the Early Jurassic (Fig. 9). The main jump in disparity was between the Carnian and Norian, which is deemed significant by statistical te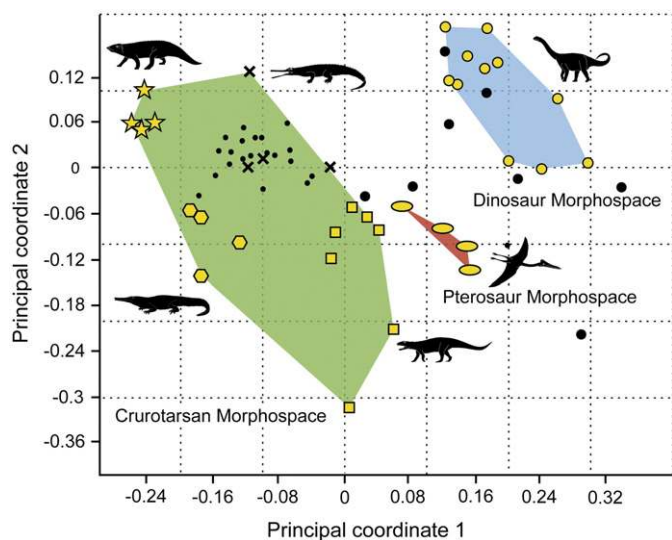sts, whereas there was only a slight and non-significant increase from the Norian to the Early Jurassic despite the extinction of many supposed dinosaur competitors at the Triassic–Jurassic boundary.

Brusatte et al. (2008a,b) also calculated the disparity of the crurotarsan archosaurs, which were exceptionally abundant and diverse in the Late Triassic, lived alongside early dinosaurs for tens of millions of years, and in many cases were eerily morphologically convergent with dinosaurs (Fig. 7). These facts suggest that crurotarsans and dinosaurs were "competitors" during the Late Triassic, in the sense that they were similar animals that lived alongside each other and probably competed for similar resources (e.g., Nesbitt and Norell, 2006; Nesbitt, 2007; Brusatte et al., 2008a,b). Importantly, crurotarsans were significantly more disparate than dinosaurs throughout the Late Triassic, and it was only after the Triassic–Jurassic extinction that dinosaur disparity overtook crurotarsan disparity (Figs. 8 and 9). In other words, crurotarsans were exploring a wider range of body plans, morphologies, and diets than Triassic dinosaurs. These results hold if strict sister taxa–in this case Avemetatarsalia and Crurotarsi, the two main lines of archosaur phylogeny–are compared. Brusatte et al. (2008a) used this result to argue that early dinosaur history was more a matter of contingency than prolonged, gradual outcompetition of competitor groups.
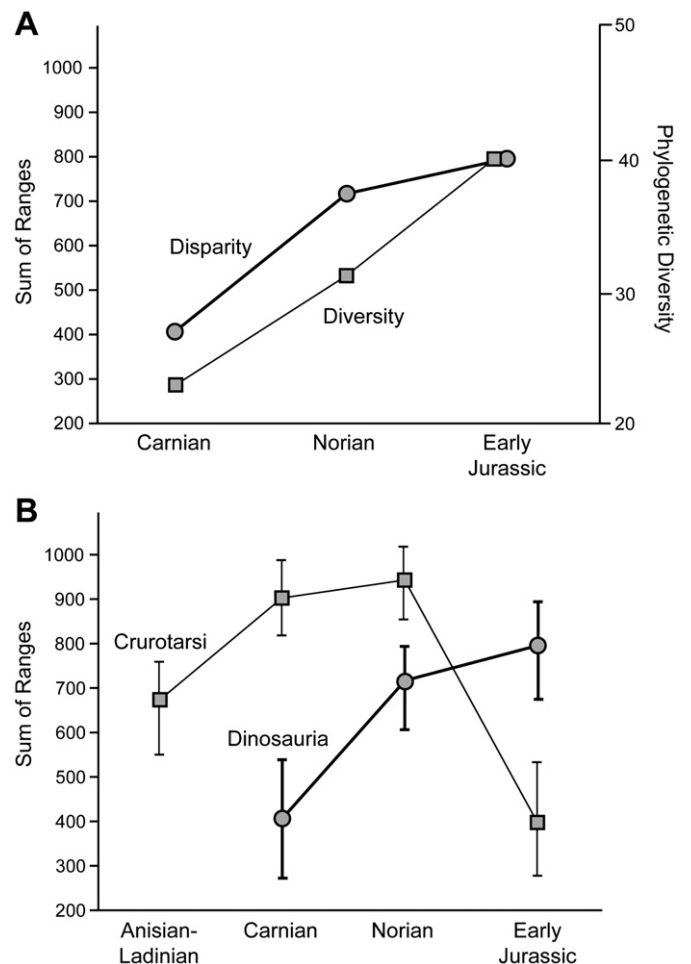

Fig. 8. A morphospace for Triassic archosaurs, based on Brusatte et al. (2008a). Three general clusters of taxa are denoted: crurotarsans (crocodile-line archosaurs), pterosaurs, and dinosaurs. Crurotarsan morphospace is significantly larger than dinosaur morphospace, as well as avemetatarsalian (dinosaur + pterosaur + dinosauromorph morphospace), meaning that crurotarsans were occupying a larger range of body plans and morphologies than dinosaurs during the Late Triassic. Large outlined circles, dinosaurs; ovals, pterosaurs; squares, poposauroid rauisuchians; hexagons, phytosaurs; stars, aetosaurs; crosses, crocodylomorphs; small solid circles, "rauisuchid" rauisuchians; large solid circles, non-dinosaurian dinosauromorphs and *Scleromochlus*. Plot delineated by Stephen Brusatte and Simon Powell (University of Bristol).

Fig. 9. A plot of archosaur taxonomic diversity and morphological disparity over time, based on Brusatte et al. (2008b). A, diversity and disparity for dinosaurs across the Late Triassic and Early Jurassic; B, disparity for dinosaurs and crurotarsans across the Late Triassic and Early Jurassic. Morphological disparity (Norian) peaked earlier than taxonomic diversity (Early Jurassic) in the evolutionary radiation of dinosaurs. Crurotarsans had a significantly higher disparity (occupied more morphospace) than dinosaurs across the Late Triassic, but after the Triassic–Jurassic extinction dinosaurs occupied significantly more morphospace. Plots delineated by Stephen Brusatte and Simon Powell (University of Bristol).

However, it must be noted that the decrease in crurotarsan disparity in the Early Jurassic may partially be an artifact of sampling, because Brusatte et al. (2008b) did not include several morphologically disparate crocodylomorphs from the Kayenta Formation: the *Edentosuchus*-like form (Sues et al., 1994: fig. 16.3) and the goniopholid *Calsoyasuchus* (Tykoski et al., 2002).

One aspect of Brusatte et al.'s (2008a,b) study deserves further comment. Dinosaurs and crurotarsans were shown not to overlap in morphospace (Fig. 8), which could be conceived as evidence against direct competition. However, this conclusion is premature for three reasons. First, the figured morphospace plots only depict the first two (of many) multivariate axes, and dinosaurs and crurotarsans do overlap on most of these axes. Second, disparity analyses have a phylogenetic bias, and the separation of dinosaurs and crurotarsans on the first (most important) multivariate axis is likely the result of phylogeny alone, just as the separation of taxon clusters in some morphometric analyses is due to size alone. Third, as outlined by Stayton (2006), the mere overlap or non-overlap of taxa in morphospace is inadequate for assessing convergence.

6.5. Faunal abundance

Absolute numerical abundance is a straightforward measure: the percentage of individuals or biomass belonging to a certain species or group in an ecosystem. Once again, this need not be tied to lineage origination, diversity, or disparity. For instance, it is easy to imagine a situation in which a certain group is exceptionally abundant in an ecosystem, but all of this abundance is due to a single species (low diversity) with a single body plan (low disparity).

Unfortunately, measuring absolute faunal abundance in fossil assemblages is exceptionally difficult. First, preserved fossil assemblages are rarely unbiased records of extinct ecosystems, but rather represent a collection of specimens that has passed through numerous taphonomic and preservational filters. Second, the time and resources needed to undertake a complete census of a fossil assemblage can be astronomical, especially if specimens are spread across different museums and have been collected by different groups. Understandably, abundance studies (at least of fossil vertebrates) are rare and play only a small role in current Mesozoic vertebrate paleobiological research programs.

Only one study has attempted to measure the absolute abundance of early dinosaurs and other Triassic and Jurassic vertebrates from many sites across the globe. Benton (1983) relied on detailed databases of museum collections and correspondence from local experts to chart the abundance of early dinosaurs and their contemporaries. The most important results from this study are: (1) that dinosaurs were rare in the Carnian but their abundance spiked in the Norian; (2) crurotarsan archosaurs were more numerically abundant than dinosaurs in many Late Triassic ecosystems; (3) the relative abundance of dinosaurs and crurotarsans varied by latitude during the Late Triassic; and (4) by the Early Jurassic dinosaurs were the most abundant large terrestrial vertebrates in ecosystems across the globe. Although Benton's (1983) database is by now severely outdated and geographically restricted, we see no reason to doubt these general patterns he observed for the regions studied given our own experience with fieldwork and collections work worldwide. However, there are clear deviations from this trend, particularly in North America, where dinosaur abundance remains low throughout the Norian (Irmis et al., 2007a).

6.6. Rates of morphological change

Evolutionary biologists utilize many different measures of evolutionary rate, which aim to quantify the "speed" of evolution. The most common approach is to measure the rates of origination and extinction of lineages over time, which gives an overall rate of diversification (e.g., Ricklefs, 2007; Fröbisch, 2008; Ruta and Benton, 2008). Other rate metrics quantify the rate of molecular sequence change (e.g., Mindell and Thacker, 1996; Lavin et al., 2005) or various aspects of continuous phenotypic change, such as body size (e.g., Garland, 1992; Gingerich, 1993; Pagel, 1998; Roopnarine, 2003; O'Meara et al., 2006).

An additional rate metric, which is seldom used but potentially illuminating, is the rate of discrete morphological character change over time. Measuring this rate necessitates the optimization of discrete morphological characters onto a cladogram, which allows for the calculation of a rate of change (characters changing/time) for each branch on the tree (Wagner, 1997). This procedure is still in its infancy, and awaits a formalized statistical protocol for hypothesis testing (Oakley, 2003), but has been used to examine the early evolutionary history of tetrapods (Ruta et al., 2006) and dinosaurs (Brusatte et al., 2008a).

Brusatte et al. (2008a) used a framework phylogeny of Triassic archosaurs and a database of over 400 anatomical characters to measure the average rate of change for different taxonomic groups and time intervals. They found that dinosaurs and their crurotarsan "competitors" had statistically indistinguishable rates of change, a sign that neither group was outpacing the other during the Late Triassic. Additionally, they found that the rate of change within dinosaurs was significantly higher in the Carnian than in the Norian, consistent with a long-hypothesized prediction that evolutionary rates are highest during the earliest part of a clade's history (Valentine, 1980; Schluter, 2000; Gould, 2002).

7. The evolutionary radiation of dinosaurs: current status

The five macroevolutionary measures described above–lineage origination, taxonomic diversity, morphological disparity, faunal abundance, and evolutionary rates–give an integrated and synthetic picture of the evolutionary radiation of dinosaurs. Quantitative studies of the dinosaur radiation, which subject observed fossils, morphological features, and phylogeny to rigorous statistical protocols, are still in their infancy. However, the message that has emerged from recent studies is clear and consistent: the radiation of dinosaurs was a prolonged affair, not a sudden takeover, and was much more complex than often assumed.

Most importantly, the radiation of dinosaurs (or any group for that matter) must be viewed as a patchwork quilt comprised of many components. Traditionally paleontologists have treated the rise of dinosaurs–either explicitly or implicitly–as a single event (e.g., Bakker, 1971, 1972; Bakker and Galton, 1974; Charig, 1984), which is often explained by generalized mechanisms such as "competition," "opportunism," or "superiority." In other words, the prevailing debate has long been whether the rise of dinosaurs resulted from some sort of innate superiority, which enabled dinosaurs to outcompete other reptiles, or was a matter of contingent good luck on a grand scale (see review in Benton, 2004). As is often the case, such debates inevitably result in simplification and polarization: complex concepts are distilled down to buzzwords and researchers retreat to their own corners instead of generating new data.

The new quantitative toolkit unmistakably exposes the dinosaur radiation as a complex process that unfolded over tens of millions of years. Dinosaurs originated long before they became taxonomically diverse, morphologically disparate, or numerically abundant in their ecosystems (Fig. 9). Morphological disparity and high rates of character change spiked early in dinosaur history, long before and out-of-step with taxonomic diversity. This decoupling of disparity and diversity, and the burst of disparity before diversity, is typical for many evolutionary radiations (Erwin, 2007). Likely competitors to early dinosaurs explored a larger range of body types throughout the Late Triassic and evolved at indistinguishable rates, and even the closest cousins of dinosaurs persisted alongside their better-known

relatives for up to 20 million years. Very clearly, different components of the dinosaur radiation proceeded at different paces and were decoupled from each other, as has also been seen in many other groups (see review in Erwin, 2007). With this pattern now unmasked, it is foolish to try to reduce the first 50 million years of dinosaur history into a single platitude.

With that being said, and keeping in mind the intricacies of the debate, most of us still favor a more-or-less "opportunistic" view of the evolutionary radiation of dinosaurs. This view itself is much more complex than its one-word slogan may imply, and unfortunately is often condensed by the press (and in some cases by our own misguided words) into an argument for random "good luck" and nothing more. The argument boils down to a dichotomy between contingency and continuity, a view of evolution that has been well articulated by Gould (1989), Alvarez (1997), and others. Both contingency and continuity play a role in the history of life, but the fundamental question in the current paper is this: which process was more important in the early history of dinosaurs? Was the rise of dinosaurs a gradual process by which things changed incrementally over time? In other words, were dinosaurs destined to become dominant and preeminent vertebrates, by virtue of certain characteristics or abilities, once they originated? Or, did dinosaurs take advantage of one or several contingencies of earth history, which could have never been predicted when the first dinosaur arose sometime in the Middle Triassic?

Our view of the dinosaur radiation is in line with Jablonski's (1986, 1991, 2001, 2005, 2008) view of macroevolution: that "successful" organisms must navigate both background and mass extinction events in order to survive and prosper. The dinosaurs were clearly successful during the first 30+ million years of their history in the Middle and Late Triassic. But so were the crurotarsan archosaurs and the close dinosauromorph cousins to dinosaurs. In fact, based on their larger morphospaces, greater range of body types and diets, and numerical dominance in many ecosystems, it could be argued that the crurotarsans were doing better than the dinosaurs during the Late Triassic. It was only after the Triassic–Jurassic mass extinction that dinosaurs could truly stake a claim as the preeminent terrestrial vertebrates, as it was during the Early Jurassic when they achieved numerical dominance in terrestrial ecosystems across the globe and enjoyed their most significant period of diversification. The same cannot be said of the crurotarsans, which were hit hard by the mass extinction and truncated to only a single lineage, the crocodylomorphs (although this lineage re-radiated later in the Jurassic and Cretaceous into a range of body forms that have yet to be investigated by disparity analysis).

Thus, there was nothing "inevitable" or "predestined" about their later success when dinosaurs first arose: they had to traverse both a prolonged journey throughout the Late Triassic and a sudden period of global devastation at the Triassic–Jurassic extinction. Although debatable, dinosaurs also appear to have weathered a more minor extinction at the Carnian–Norian boundary or in the early Norian. Dinosaurs only had "good luck" in the sense that they were able to endure the extinction(s) whereas some of their contemporary competitors were not. We do not deny that dinosaurs may have survived because one or several "important" characters—indeed, it is likely that the marked asymmetry in dinosaur and crurotarsan survival into the Early Jurassic was due to differences in growth, metabolism, or locomotion. The important distinction is that these characters were not "key innovations" that allowed, or drove, dinosaurs to either rapidly blossom when they first originated or gradually outcompete other groups over long time scales. They were simply features that came in handy when an unpredictable global meltdown struck.

In closing, we distill our view of the dinosaur radiation into the following statement: there was nothing predestined or superior about dinosaurs when they first arose, and without the contingency of various earth-history events during the early Mesozoic, the Age of Dinosaurs might have never happened.

8. The evolutionary radiation of dinosaurs: future directions

The origin and early evolution of dinosaurs have long been subjects of fascination and continue to be a central focus of research in the paleontology community. Current work on early dinosaur history is proceeding at a rapid pace, with particular emphasis on both primary data collection and synthetic studies that aim to place early dinosaurs in a phylogenetic, paleoenvironmental, and macroevolutionary context.

Over the past 25 years, perceptions of dinosaur origination and early history have changed with the discovery of new specimens, both new taxa and fossils of previously described species. There is no reason to think that this trend will change, especially as Triassic and Jurassic rocks are being explored at a remarkable rate, new localities are consistently being discovered, and localities known for over a hundred years are still producing new and exciting specimens. In particular, field exploration in Tanzania (Sidor et al., 2008; Nesbitt et al., 2010), Madagascar (Flynn et al., 2008), Poland (Dzik and Sulej, 2007; Dzik et al., 2008), the southwestern United States (Irmis et al., 2007a; Nesbitt et al., 2009a,b), Argentina (Martinez and Alcober, 2009), and Brazil (Ferigolo and Langer, 2007) has already yielded important new material, and should continue to do so throughout the near future. Additional fieldwork is underway across western and central Europe, South America, and Asia, and these regions–or other as yet unknown areas–may prove to be the next frontier of early dinosaur discovery.

Similarly, perceptions of early dinosaur evolution have changed in concert with changing views on the phylogeny of dinosaurs and their closest relatives. Several large-scale analyses of archosaur and dinosaur phylogeny are underway (e.g., Brusatte et al., 2008c; Nesbitt et al., 2009b, 2010; Brusatte et al., 2010b; SJN, unpublished data; RBI, unpublished data), and paleontologists are just beginning to experiment with large phylogenetic datasets. These analyses will be instrumental in reconstructing the pattern of anatomical character change on the line to dinosaurs (e.g., Nesbitt et al., 2009a,b), as well as the biogeographic distribution of dinosaurs during the Triassic and Jurassic (e.g., Upchurch et al., 2002; Butler et al., 2006b; Nesbitt et al., 2009b).

A robust understanding of early dinosaur evolution also relies on geological data. It is essential to not only understand the climatic and environmental backdrop of early dinosaur history, but also the absolute and relative ages of dinosaur fossils and entire dinosaur assemblages. Such temporal information is critical to large-scale macroevolutionary studies, such as those that examine the diversity and evolutionary rates of dinosaurs over time. The Triassic and Early Jurassic are notoriously lacking in precise radioisotopic dates, and correlations between formations on both local and global scales is extremely difficult (e.g., Furin et al., 2006; Mundil, 2007). Previously, scientists have relied on organisms themselves to date and correlate the rocks, but many of these correlations have proved to be unreliable (Rayfield et al., 2005; Martz and Small, 2006; Irmis and Mundil, 2008; Rayfield et al., 2009). Perhaps more so than new specimens, precise radioisotopic dates of units within key dinosaur-bearing Triassic and Jurassic formations, such as the Chinle and Elliot Formations, are of the utmost importance.

Finally, the fundamental goal for paleontologists working on early dinosaur history is to understand exactly how dinosaurs ascended from a marginal group of small Triassic reptiles to the dominant terrestrial vertebrates of the Jurassic and Cretaceous. Questions such as these are difficult to answer, and perhaps intractable, but if solved may go a long way in helping scientists understand large-scale evolutionary processes and the dynamics of evolutionary radiations. For workers interested in these big-picture questions, there is perhaps no more ideal group to focus on than dinosaurs. Broad-scale

macroevolutionary analyses must be based on a firm foundation of anatomical, phylogenetic, and geological data. These types of study are in their infancy (e.g., Brusatte et al., 2008a,b), and so far have looked at the diversity, evolutionary rates, and morphospace occupation of dinosaurs over time. Large-scale studies of early dinosaur biogeography, lineage-level dinosaur and archosaur extinctions during the early Mesozoic, and regional faunal and ecological differences remain to be done. It is these types of study, in association with new fossil discoveries and renewed phylogenetic and geological analyses, which promise an exciting future for dinosaur research.

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