

The origin and early evolution of dinosaurs

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ABSTRACT

The oldest unequivocal records of Dinosauria were unearthed from Late Triassic rocks (approximately 230 Ma) accumulated over extensional rift basins in southwestern Pangea. The better known of these are *Herrerasaurus ischigualastensis*, *Pisanosaurus mertii*, *Eoraptor lunensis*, and *Panphagia protos* from the Ischigualasto Formation, Argentina, and *Staurikosaurus pricei* and *Saturnalia tupiniquim* from the Santa Maria Formation, Brazil. No uncontroversial dinosaur body fossils are known from older strata, but the Middle Triassic origin of the lineage may be inferred from both the footprint record and its sister-group relation to Ladinian basal dinosauromorphs. These include the typical *Marasuchus lilloensis*, more basal forms such as *Lagerpeton* and *Dromomeron*, as well as silesaurids: a possibly monophyletic group composed of Mid-Late Triassic forms that may represent immediate sister taxa to dinosaurs. The first phylogenetic definition to fit the current understanding of Dinosauria as a node-based taxon solely composed of mutually exclusive Saurischia and Ornithischia was given as “all descendants of the most recent common ancestor of birds and *Triceratops*”. Recent cladistic analyses of early dinosaurs agree that *Pisanosaurus mertii* is a basal ornithischian; that *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* belong in a monophyletic Herrerasauridae; that herrerasaurids, *Eoraptor lunensis*, and *Guaibasaurus candelariensis* are saurischians; that Saurischia includes two main groups, Sauropodomorpha and Theropoda; and that *Saturnalia tupiniquim* is a basal member of the sauropodomorph lineage. On the contrary, several aspects of basal dinosaur phylogeny remain controversial, including the position of herrerasaurids, *E. lunensis*, and *G. candelariensis* as basal theropods or basal saurischians, and the affinity and/or validity of more fragmentary taxa such as *Agnosphytys cromhallensis*, *Atwalkeria malerensis*, *Chindesaurus bryansmalli*, *Saltopus elginensis*, and *Spondylosoma absconditum*. The identification of dinosaur apomorphies is jeopardized by the incompleteness of skeletal remains attributed to most basal dinosauromorphs, the skulls and forelimbs of which are particularly poorly known. Nonetheless, Dinosauria can be diagnosed by a suite of derived traits, most of which are related to the anatomy of the pelvic girdle and limb. Some of these are connected to the acquisition of a fully erect bipedal gait, which has been traditionally suggested to represent a key adaptation that allowed, or even promoted, dinosaur radiation during Late Triassic times. Yet, contrary to the classical “competitive” models, dinosaurs did not gradually replace other terrestrial tetrapods over the Late Triassic. In fact, the radiation of the group comprises at least three landmark moments, separated by controversial (Carnian-Norian, Triassic-Jurassic) extinction events. These are mainly characterized by early diversification in Carnian times, a Norian increase in diversity and (especially) abundance, and the occupation of new niches from the Early Jurassic onwards. Dinosaurs arose from fully bipedal ancestors, the diet of which may have been carnivorous or omnivorous. Whereas the oldest dinosaurs were geographically restricted to south Pangea, including rare ornithischians and more abundant basal members of the saurischian lineage, the group achieved a nearly global distribution by the latest Triassic, especially with the radiation of saurischian groups such as “prosauropods” and coelophysoids.

Key words: Dinosauria, Dinosauroomorpha, Triassic, phylogeny, evolution, biogeography, Herrerasauria.

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I. INTRODUCTION

Dinosaurs originated in the Triassic period, and the Late Triassic represents the first 30 of the 165 million years of their “non-avian” history on Earth. Yet, of the 500-700 “well established” dinosaur genera (Wang & Dodson, 2006; Olshevsky, 2007), only about 30 (approximately 5%) were excavated from Triassic rocks, and the diversity/diversification of the group is mainly concentrated in the Jurassic (Rauhut, 2005b; Lloyd *et al.*, 2008) and/or Cretaceous (Wang & Dodson, 2006) periods. This is especially the case if one accepts the inference of Wang & Dodson (2006) that the Late Triassic represents the best sampled subperiod of the entire Mesozoic in terms of documented dinosaur diversity. Indeed, dinosaurs are rare in most Triassic fossil assemblages in which they occur, although by the end of the period they were already dominant members of various palaeocommunities.

Triassic dinosaurs were mostly bipedal, and not exceptionally large. The basal-most forms were probably omnivorous, but predatory and probably herbivorous dinosaurs also occurred during Late Triassic times. This includes *Herrerasaurus ischigualastensis*, a top predator up to 4 m long (Novas, 1997a), and *Riojasaurus incertus*, a plant-eater of about three tons (Seebacher, 2001). In taxonomic terms, most Triassic dinosaurs are regarded as members of one of the three major lineages of the group: Theropoda, Sauropodomorpha, and Ornithischia. Yet, despite representing well-known taxa, other Triassic dinosaurs have a debated phylogenetic position. This is particularly the case of the herrerasaurs, which were placed basal to the Ornithischia-Saurischia dichotomy,

nested within Theropoda, or regarded as non-eusaurischian saurischians.

Appealing inferences on dinosaur palaeobiology can be drawn from eggs and nestlings (Bonaparte & Vince, 1979; Moratalla & Powell, 1994), monospecific assemblages (Coombs, 1990; Schwartz & Gillette, 1994), visual-display-related morphological features (Vickaryous & Ryan, 1997), and “stomach contents” (Novas, 1997a; Nesbitt *et al.*, 2006) of Triassic dinosaurs. Yet, the most debated aspect of early dinosaur macroevolution corresponds to their first radiation, and various scenarios were invoked to explain the rise of the clade in a time interval during which most terrestrial tetrapods suffered important diversity losses. In fact, by Late Triassic times, dinosaurs arose and took their first steps along the evolutionary road, and the investigation of their obscure origins is crucial for the understanding of dinosaur interrelationships and palaeobiology as a whole.

(1) Historical background on early dinosaurs

Research on early dinosaurs can be said to have started with the work of the German palaeontologist Friedrich von Huene, and his descriptions of *Saltopus elginensis* Huene, 1910 (Fig. 1A), and *Spondylosoma absconditum* Huene, 1942. These two forms have completely different provenances, coming respectively from the Elgin area, in Northern Scotland, and Rio Grande do Sul, in South Brazil, but share curious similarities. Both were regarded as saurischian dinosaurs by Huene (1910, 1942) and were found in deposits considered the oldest dinosaur-bearing rocks known at the time. Huene (1932, 1942) identified various other putative Triassic dinosaurs as equivalent in age to either *Saltopus* or *Spondylosoma*, but most of these were shown to have doubtful

dinosaur affinities (Galton, 1985b; Benton, 1986b; Galton & Walker, 1996; Benton *et al.*, 2000; Rauhut & Hungerbühler, 2000; Parker *et al.*, 2005; Nesbitt, Irmis & Parker, 2007). Notable exceptions are *Thecodontosaurus antiquus* (Benton *et al.*, 2000) and the material Cope (1889) originally assigned to *Coelophysis bauri* (Nesbitt *et al.*, 2007), but these came from strata currently considered younger (Benton *et al.*, 2000; Langer, 2005b; Nesbitt *et al.*, 2007). Indeed, the older age of both the “*Stagonolepis*-beds” of Elgin (Huene, 1908) and the “Rio do Rasto” [sic] beds at Chiniquá (Huene & Stahlecker, 1931) was corroborated by recent work. The Lossiemouth Sandstone Formation has been dated as Carnian (Benton & Walker, 1985), whereas the *Dinodontosaurus* Assemblage-Zone of the Santa Maria Formation is considered of Ladinian age (Langer *et al.*, 2007c); or early-middle Carnian, following recent modifications on the Late Triassic time-scale (Muttoni *et al.*, 2004) and the corrections on the radiometric dating of the Ischigualasto Formation (Furin *et al.*, 2006).

Although the ages of the Lossiemouth Sandstone and Santa Maria formations were more securely established, the dinosaur affinities of *Saltopus elginensis* and *Spondylosoma absconditum* are still debated (Rauhut & Hungerbühler, 2000; Galton, 2000; Langer, 2004). This is in part due to the poor preservation of the specimens, which do not allow a comprehensive assessment of their morphological features. Therefore, it was not until Reig (1963) placed *Herrerasaurus ischigualastensis* (Fig. 1B) and *Ischisaurus cattoi* within Saurischia that unequivocal early dinosaurs were known to science. The described specimens were collected in 1961 from deposits of the Ischigualasto Formation, San Juan province, north-western Argentina, which have yielded remains attributable to dinosaurs since the late 1950s (Reig, 1963). With the discovery, in 1962, of the ornithischian *Pisanosaurus mertii* Casamiquela, 1967 (Fig. 1C), in that same stratigraphic unit, the presence of both main dinosaur lineages (i.e. Ornithischia and Saurischia), in the Triassic of South America was confirmed. Another important “early dinosaur” study of the time was the description of *Staurikosaurus pricei* Colbert, 1970 (Fig. 1D). Its type and only specimen, discovered in

1936 in the Santa Maria beds of South Brazil, was the first consensual early dinosaur to be collected.

While the 1980s were quiet times regarding the study of early dinosaurs, mainly witnessing the description of incomplete specimens (Galton, 1985b, 1986; Novas, 1986; Chatterjee, 1987; Murry & Long, 1989), the early nineties came with new and exciting discoveries. These include the unearthing, also from the Ischigualasto Formation, of a new basal dinosaur still to be fully described, *Eoraptor lunensis* (Serenio *et al.*, 1993; Sereno, 2007b), and of further material of *Herrerasaurus ischigualastensis* (Serenio & Novas, 1992, 1993; Novas, 1993; Sereno, 1993). In the late nineties, a new series of discoveries in Rio Grande do Sul, South Brazil, enlarged the knowledge of early dinosaur diversity. The then basal-most member of the sauropodomorph lineage, *Saturnalia tupiniquim* (Langer *et al.*, 1999; Langer, França & Gabriel, 2007b; Langer, 2003), was unearthed from the *Hyperodapedon* Assemblage-Zone of the Santa Maria Formation, whereas the overlying Caturrita Formation yielded the saurischian *Guaibasaurus candelariensis* (Bonaparte, Ferigolo & Ribeiro, 1999; Bonaparte *et al.*, 2007). Since the beginning of this century, some putative basal dinosaurs have been described (Fraser *et al.*, 2002; Ferigolo & Langer, 2007; Nesbitt *et al.*, 2007; Nesbitt & Chatterjee, 2008; Martinez & Alcober, 2009; Ezcurra, 2008), while the validity of others was evaluated in the light of new evidence (Remes & Rauhut, 2005; Yates, 2007b). More importantly, different evolutionary scenarios were proposed based on independent cladistic analyses, e.g. Langer & Benton (2006), Ezcurra (2006), Sereno (2007b), Irmis *et al.* (2007a), which attempted to sum up information in order to understand better the interrelationships of early dinosaurs.

(2) The dinosauriform radiation

For most of the last century, it was accepted that dinosaurs arose from “thecondont” precursors, either as a monophyletic group or, more frequently (Fig. 2), in the form of independent lineages (Huene, 1956; Colbert, 1964; Charig,

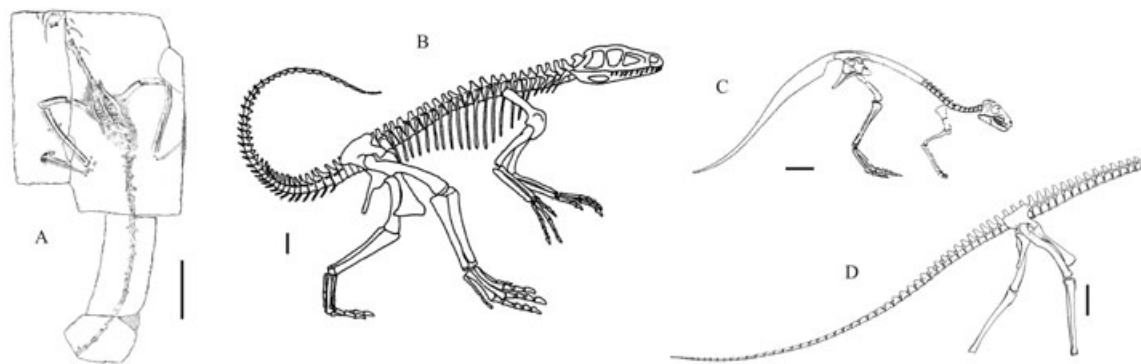


Fig. 1. Early images depicting some of the oldest putative dinosaurs. (A) Drawing of the slabs containing *Saltopus elginensis*, from Huene (1910). (B) Skeletal reconstruction of *Herrerasaurus ischigualastensis* as mounted in 1965 for exhibition at the Universidad Nacional de Tucumán, from Bonaparte (1997). (C) Skeletal reconstruction of *Pisanosaurus mertii*, from Bonaparte (1997). (D) Skeletal reconstruction of *Staurikosaurus pricei*, from Colbert (1970). Scale bars: A = 5 cm; B-D = 10 cm.

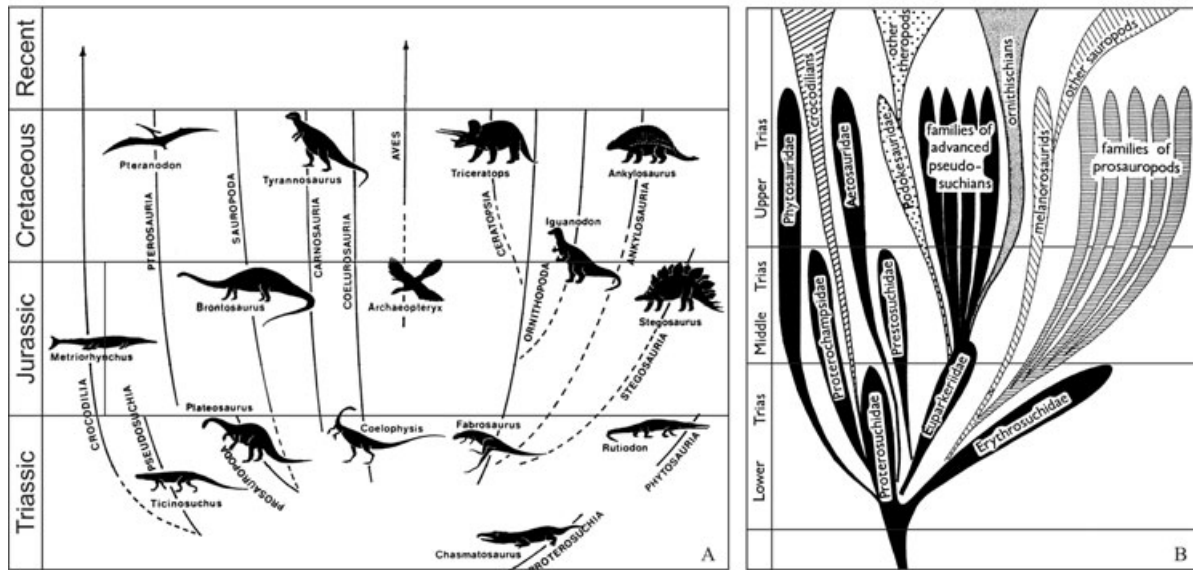


Fig. 2. Schemes of archosaur evolution depicting a polyphyletic Dinosauria. (A) Modified from Krebs (1974). (B) After Thulborn (1975).

Attridge & Crompton, 1965; Romer, 1966). “Thecodonts”, as composed of non-crown-group archosaurs, and basal members of both the bird and crocodile lines, are currently regarded as a paraphyletic group (Currie & Padian, 1997b; Benton, 2004). In his seminal paper on dinosaur phylogeny, Gauthier (1986) applied the name Ornithosuchia Huene, 1908, to designate a group composed of dinosaurs, pterosaurs (including *Scleromochlus*), ornithosuchids, *Euparkeria* (questionably), and “*Lagosuchus*”, a small archosaur from the Middle Triassic of Argentina (Romer, 1971; Bonaparte, 1975; Sereno & Arcucci, 1994). That clade was supposed to group all archosaurs that share a closer affinity to birds (within Dinosauria) than to crocodiles, which were placed in its sister group Pseudosuchia (Parrish, 1997; Senter, 2005). More recent work, however, excluded both *Euparkeria* (Benton & Clark, 1988; Sereno, 1991a; Juul, 1994; Benton, 2004) and ornithosuchids (Sereno, 1991a; Juul, 1994; Benton, 2004) from Ornithosuchia, restricting the inclusivity, and perhaps worthiness (Taylor, 2007) of the name. Indeed, alternative names were later proposed for the bird lineage of Archosauria, e.g. Avemetatarsalia Benton, 1999; Panaves Gauthier & De Queiroz, 2001. The inclusivity of this group could be even more reduced considering the labile position of pterosaurs, sometimes regarded as basal archosaurs (Bennett, 1996) or even outside Archosauria (Peters, 2000; Sobral & Langer, 2008). In this scenario, the non-dinosaur members of the bird-lineage of Archosauria would only include *Scleromochlus taylori* (a putative sister taxon to Pterosauria) from the Late Triassic of Elgin (Sereno, 1991a; Benton, 1999) and the so-called basal dinosauriforms.

The name Dinosauria was coined by Benton (1985) to include dinosaurs, birds, and ornithosuchids, but redefined by Sereno (1991a) to its current understanding, which excludes ornithosuchids. The basal (non-dinosaurian)

members of the group (Romer, 1971, 1972a, b; Arcucci, 1987) were for a long time known only from the Middle Triassic Chañares Formation of Argentina (Rogers *et al.*, 2001). These small, gracile forms were grouped within “Pseudosuchia”, but were soon recognized to have some bearing on the origin of dinosaurs (Romer, 1972a, b), which became evident with the works of Bonaparte (1975), Sereno & Arcucci (1993, 1994), and Novas (1996). Those authors identified typical dinosaur hind-limb traits on these taxa, including a distally tapering fibula, an anterior ascending process in the astragalus, a reduced calcaneum, a longer metatarsus with reduced outer elements, and a straight metatarsal V with reduced articulation area on the outer surface of the lateral distal tarsal (see also Irmis *et al.*, 2007a; Brusatte *et al.*, 2009). The taxonomy of the Chañares dinosauriforms has always been subject to some debate (Bonaparte, 1975, 1995; Sereno & Arcucci, 1994; Arcucci, 1987, 1998, 2005), and five names entered the literature: *Lagerpeton chanarensis* Romer, 1971; *Lagosuchus talampayensis* Romer, 1971 (*nomen dubium*; Sereno & Arcucci, 1994); *Marasuchus lilloensis* (Romer, 1972b, gen. Sereno & Arcucci, 1994); *Lewisuchus admixtus* Romer, 1972a (Arcucci, 1997); and *Pseudolagosuchus major* Arcucci, 1987.

Recent discoveries (Fraser *et al.*, 2002; Dzik, 2003; Irmis *et al.*, 2007a; Ferigolo & Langer, 2007) and interpretations (Novas & Ezcurra, 2005; Ezcurra, 2006; Nesbitt *et al.*, 2007) suggest that basal dinosauriforms were both more diverse in terms of anatomy and inferred habits, and more widely spread chronologically and geographically. *Dromomeron romeri* and *D. gregorii* (Irmis *et al.*, 2007a; Nesbitt *et al.*, 2009) were recognized in the Norian of western North America, which also yielded *Eucoelophysis baldwini*. The latter taxon, first described as a theropod dinosaur (Sullivan & Lucas, 1999), was reassigned to a non-dinosaur dinosauriform position,

as either the sister taxon to Dinosauria (Ezcurra, 2006) or forming a group with *Silesaurus opolensis* (Irmis *et al.*, 2007a). The latter form, collected in Carnian deposits of Poland (Dzik, 2003; Dzik & Sulej, 2007), provided the greatest breakthrough in the recent study of dinosaur origins. Its long fore limbs suggest that the animal was at least facultatively quadrupedal, while the edentulous front tip of its lower jaw apparently bore a corneous beak. This atypical set of traits revealed an unsuspected morphological diversity, hinting at how incomplete was, and certainly still is, our knowledge of the early stages of dinosauriform evolution. In addition, the record of *Silesaurus opolensis* extended the range of basal dinosauriforms into the Late Triassic of Europe, a possibility only hinted at before on the basis of controversial British taxa such as *Saltopus elginensis* (Rauhut & Hungerbühler, 2000) and *Agnosphitys cromhallensis* (Fraser *et al.*, 2002). Further, since the description of *Silesaurus opolensis*, newly and previously described Norian forms have been considered closely related to the taxon. This is the case for *Sacisaurus agudoensis* Ferigolo & Langer, 2007, from the Caturrita Formation of South Brazil, and a set of North American specimens (Nesbitt *et al.*, 2007), including material assigned to an unnamed *Silesaurus*-like form from the Petrified Forest Member, Chinle Formation, of New Mexico, and part of the original material of *Techosaurus smalli* Chatterjee, 1984, from the Bull Canyon Formation, Texas (Irmis *et al.*, 2007b). The latter taxon has been previously assigned to Ornithischia (Weishampel & Witmer, 1990; Sereno, 1991b; Hunt & Lucas, 1994), while *Sacisaurus agudoensis* might provide evidence that even *Silesaurus opolensis* represents a basal member of that dinosaur clade (Ferigolo & Langer, 2007).

The more complete non-dinosaurian dinosauriforms form a series of outgroups to Dinosauria, and they give clues about the origin of the clade (Ezcurra, 2006; Langer & Benton, 2006; Yates, 2007a; Irmis *et al.*, 2007a; Brusatte *et al.*, 2009). The long-held hypothesis of a more basal position for *Lagerpeton chanarensis* (Novas, 1992b; Sereno & Arcucci, 1993) was confirmed by independent studies (Irmis *et al.*, 2007a; Brusatte *et al.*, 2009), which allocated the genus *Dromomeron* as its sister taxon (Fig. 3A). Both *Lagerpeton* and *Dromomeron* lack several apomorphic features of Dinosauriformes such as a reduced medial lamina on the pubis, an antitrochanter expanding into the ilium, a lesser trochanter on the proximal femur, and a distal tibia bearing a lateral groove and a squared distal articulation (Irmis *et al.*, 2007a; Brusatte *et al.*, 2009). Within Dinosauriformes, most studies (Novas, 1992b, 1996; Ezcurra, 2006; Irmis *et al.*, 2007a; Brusatte *et al.*, 2009) place *Marasuchus lilloensis* as the basalmost member of the clade (Fig. 3A). More derived forms include *Pseudolagosuchus major* (Novas, 1992b, 1996) and its possible senior synonym *Lewisuchus admixtus* (Arcucci, 1998, 2005). Along with the identification of further dinosauriforms of equivalent grade (Dzik, 2003; Ezcurra, 2006), two alternative phylogenetic scenarios were proposed (Fig. 3A). Irmis *et al.* (2007a) suggested that *Eucoelophysis* and *Silesaurus* form the sister clade to Dinosauria, which may also include *Pseudolagosuchus* according to Nesbitt *et al.* (2007, p. 214).

Ezcurra (2006), on the other hand, placed all these taxa in a fully pectinated grade, where *Pseudolagosuchus*, *Silesaurus*, and *Eucoelophysis*, are respectively closer to Dinosauria. A somewhat intermediate view was adopted by Brusatte *et al.* (2009), in which *Pseudolagosuchus* has a basal position, and *Lewisuchus* forms, with other taxa, a more restricted sister clade to dinosaurs (Fig. 3A). In any case, all or some of these forms share with dinosaurs a number of apomorphic traits absent in *Marasuchus*, e.g. longer pubic shaft; femur with angular greater trochanter, “spike-like” lesser trochanter, and prominent trochanteric shelf; distal tibia with laterally expanded outer malleolus; astragalus with pyramid-shaped anterior ascending process; and sigmoidal metatarsal IV with deeper distal articular surface (Novas, 1996; Irmis *et al.*, 2007a; Brusatte *et al.*, 2009).

Regardless of their status as a clade or “grade”, these more derived basal dinosauriforms fill a gap (between *Marasuchus lilloensis* and dinosaurs) in archosaur evolution. More importantly, they fill that gap with the unsuspected diversity of forms that have been informally called “silesaurids”. This group may just include *Silesaurus*, and forms such as *Sacisaurus* and *Techosaurus*, which share with the Polish taxon dental/jaw features possibly related to a more herbivorous diet (Ferigolo & Langer, 2007; Irmis *et al.*, 2007b), but it could also encompass *Lewisuchus*, *Pseudolagosuchus*, and *Eucoelophysis*. Although the basis for this assignment lies on shared traits of the postcranium, there is no positive evidence that any of these forms was a facultative/full quadruped as *Silesaurus*. Yet, “herbivorous” teeth have been tentatively referred to *Eucoelophysis* (Irmis *et al.*, 2007a). The record of “silesaurids” and of the species of *Dromomeron* suggests that an extensive radiation of non-dinosaurian dinosauriforms preceded the Late Triassic dinosaur diversification, and that parallel to the first radiation of dinosaurs, that grade continued to flourish after the Ladinian (Irmis *et al.*, 2007a), extending their range into the northern part of west Pangea (Fig. 3B).

II. PHYLOGENY AND SYSTEMATICS

The name Dinosauria was erected by Owen (1842) to include three large terrestrial forms which he believed to compose a distinct group of extinct reptiles (Torrens, 1992; Padian, 1997a). In the following years, a sound concept of Dinosauria was established by the proposition of several classification schemes (Cope, 1866; Huxley, 1870; Marsh, 1882; Seeley, 1888). At that time, major taxa such as Sauropoda and Theropoda (Marsh, 1878, 1881), as well as Saurischia and Ornithischia (Seeley, 1888) were proposed. These names gained acceptance in the 20th Century (Huene, 1932; Romer, 1956) and still represent the major dinosaur subdivisions as currently understood (Fig. 4). However, for most of the last century these different dinosaur groups, and even some of their subgroups, were believed to have had independent origins (Fig. 2) from “thecodont” precursors (Huene, 1914, 1956; Colbert, 1964; Charig *et al.*, 1965; Romer, 1966; Reig, 1970; Krebs, 1974; Thulborn, 1975;

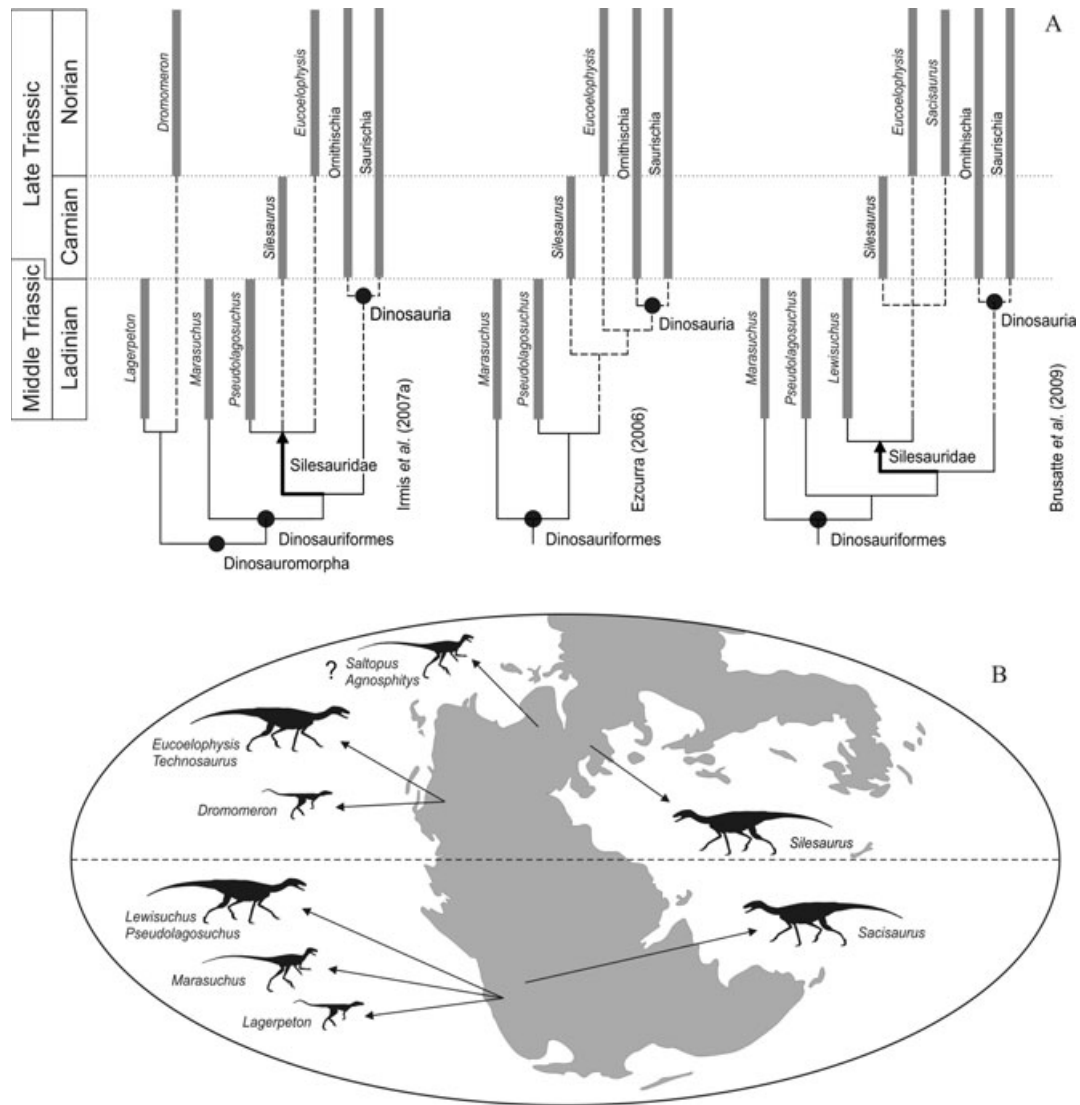


Fig. 3. Time-calibrated phylogenies and distribution of non-dinosaur Dinosauromorpha. (A) Recently proposed phylogenetic hypotheses; dotted lines indicate ghost lineages; names applied as in Table 1. Position of *Pseudolagosuchus* in the phylogeny of Irmis *et al.* (2007a) inferred from Nesbitt *et al.* (2007). (B) Geographic occurrence of taxa on a Late Triassic map redrawn from Blakey (2006). Black silhouettes adapted from various sources.

Cruickshank, 1975, 1979). The monophyly of Dinosauria was suggested by Bakker & Galton (1974) and Bonaparte (1975, 1976), firmly established by various pioneering cladistic works (Paul, 1984; Gauthier & Padian, 1985; Cooper, 1985; Brinkman & Sues, 1987), especially that of Gauthier (1986), and represents a consensual hypothesis nowadays (Novas, 1989; 1996; Sereno *et al.*, 1993; Sereno, 1999; Langer & Benton, 2006; Irmis *et al.*, 2007a).

(1) What makes a dinosaur?

Even if the monophyly of Dinosauria is consensually accepted, the issue of which morphological traits characterize the group continues to be debated (Novas, 1996; Langer & Benton, 2006; Sereno, 2007b). Several putative dinosaur

apomorphies were proposed in a variety of studies dealing with the phylogeny of the group, which frequently diverge upon the distribution of these same characters. This is epitomized by the continuing quarrel over one of the diagnostic features mentioned by Owen (1842) in the original proposition of the name: the number of vertebrae that compose the dinosaur sacrum. In the following text, most recent reviews of early dinosaur phylogeny (Novas, 1996; Sereno, 1999, 2007a; Fraser *et al.*, 2002; Benton, 2004; Langer & Benton, 2006; Ezcurra, 2006; Yates, 2007a, b; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a) are compared and evaluated, in a search for the set of traits that typically characterize the group. Obviously, a key point to set the diagnosis of Dinosauria is to determine whether some of the so-called basal dinosauriforms actually belong to the

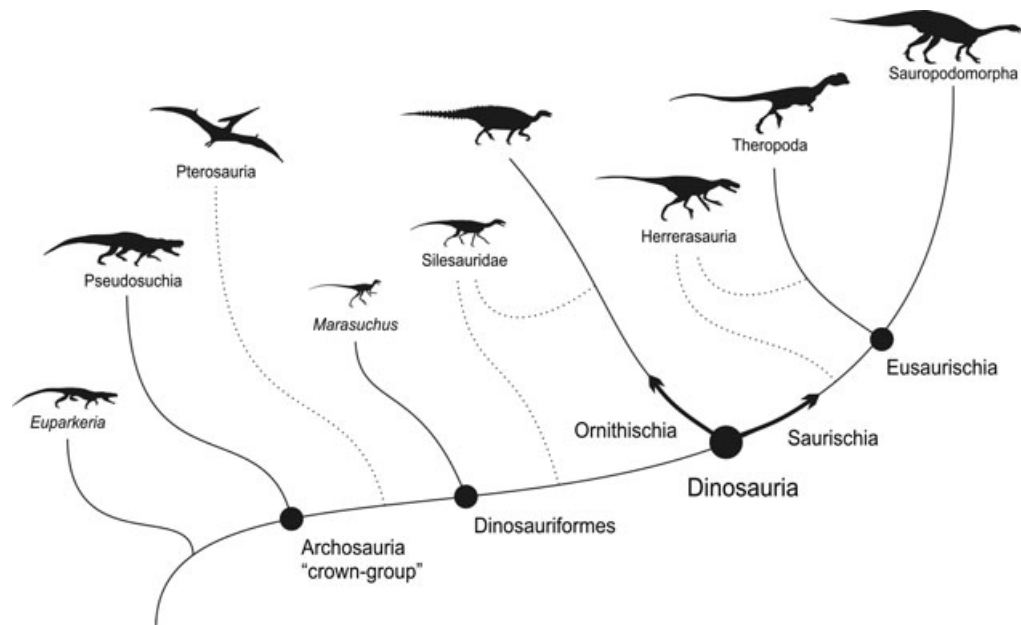


Fig. 4. Generalized phylogeny depicting the position of Dinosauria and its main groups within Archosauria. Dotted lines indicate major contentious placement of taxa; arrows indicate stem-based taxa; black circles indicate node-based taxa; names applied as in Table 1; black silhouettes adapted from various sources.

group. As reviewed by Langer & Benton (2006, pp. 316–317), various putative dinosaur apomorphies are seen in *Silesaurus opolensis*. These might represent true dinosaur apomorphies if the taxon is considered to represent a basal ornithischian (Ferigolo & Langer, 2007). Yet, current orthodoxy points towards the basal, non-dinosaurian position of *Silesaurus*, and this hypothesis of relationships represents the template based on which the unique dinosaur traits are discussed below.

Novas (1996) and Sereno (1999) respectively listed 17 and 18 characters as diagnostic for Dinosauria, while a modified version of one of their characters (presence of three or more sacral vertebrae) is the sole dinosaur apomorphy proposed by Fraser *et al.* (2002). Langer & Benton (2006) critically assessed these characters, questioning the apomorphic status of several of them. Features related to the cranial anatomy (Sereno & Novas, 1993) are particularly problematic because most basal dinosaurs and, especially, basal dinosauriforms lack good skull material. Indeed, traits such as the lack of the postfrontal bone, although typically absent in non-dinosaur archosaurs and present in dinosaurs (see Irmis *et al.*, 2007a, char. 14), can not be considered an unambiguous dinosaur apomorphy (Langer & Benton, 2006) given its equivocal occurrence in most forms placed at the very origin of the group. The same applies to other putative apomorphies of the dinosaur skull, such as the dorsal overlap of the transverse flange of the pterygoid by the ectopterygoid, and the lateral exposure of the quadrate head (Langer & Benton, 2006); see also Brusatte *et al.* (2008a, chars 10, 14, 38, 40, 67). The status of other putative apomorphies of the dinosaur skull is dependent on the position of *Silesaurus opolensis*, the cranial material of which is reasonably complete (Dzik, 2003; Dzik & Sulej, 2007). If not considered a dinosaur, some of its

cranial traits, e.g. frontal participating in the supratemporal fossa, are dismissed as dinosaur apomorphies. Yet, if its less consensual position as a basal ornithischian is accepted, these same traits continue potentially to represent dinosaur synapomorphies. On the contrary, plesiomorphic traits in the skull of *Silesaurus* such as a large post-temporal fenestra supports its non-dinosaurian affinity, and helps to define a reduced foramen-sized aperture (Fig. 5B) as apomorphic for dinosaurs (Irmis *et al.*, 2007a, char. 21). Other cranial features (Langer & Benton, 2006, char. 12; Ezcurra, 2006, chars 4, 20; Yates, 2007a, chars 26, 29; Irmis *et al.*, 2007a, chars 2, 25) suggested to represent possible dinosaur apomorphies, pending the criteria used for character optimization, have an erratic distribution among basal dinosaurs, and should not be considered *a priori* diagnostic traits of the group. A likely dinosaur apomorphy, related to the axial skeleton (Fig. 5C), is the presence of epipophyses on the cranial cervical vertebrae (Novas, 1996; Langer & Benton, 2006; Yates, 2007a; *contra* Ezcurra, 2006). This feature was previously considered a saurischian apomorphy, but more recently was recorded in basal ornithischians (Novas, 1996; Langer & Benton, 2006; Butler, Smith & Norman, 2007). Other putative apomorphies of the dinosaur vertebral column listed by Yates (2007a, chars 129, 142) have an inconsistent distribution, and should not be *a priori* considered as such.

As mentioned earlier, the increase in the number of vertebrae that forms the dinosaur sacrum (from two to more than two) continues to be listed as an apomorphy of the group (Novas, 1996; Sereno, 1999; Fraser *et al.*, 2002; Ezcurra, 2006). Recently, as discussed by Langer & Benton (2006), two main strategies of coding characters related to this transformation have been employed; but see Novas

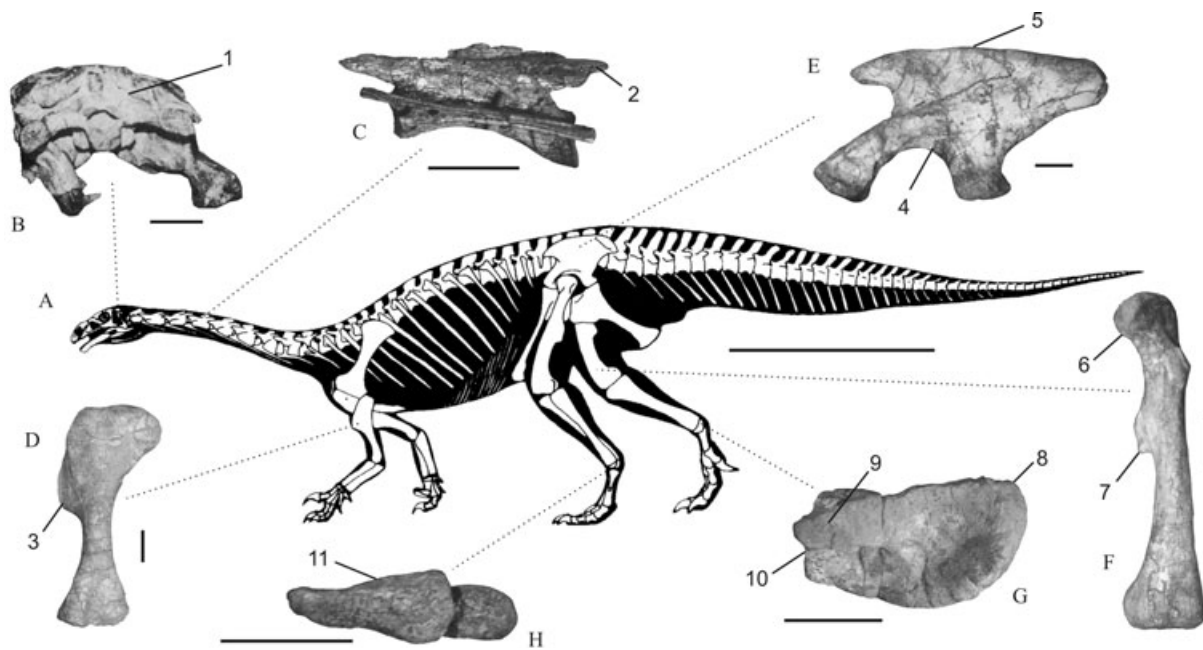


Fig. 5. The dinosaur *Plateosaurus engelhardti*. (A) Skeletal reconstruction (from Yates, 2003a), with indications of the better known apomorphic traits of Dinosauria. (B) Occipital view of the skull (from Galton, 1985a) indicating (1) a foramen-sized post-temporal fenestra. (C) Lateral view of a cervical vertebra, indicating (2) the presence of epiphyses. (D) Caudal view of the left humerus, indicating (3) a long deltopectoral crest. (E) Lateral view of the left ilium, indicating (4) an open acetabulum and (5) an arched dorsal margin. (F) Cranial view of the left femur, indicating (6) a femoral head inturned and distinctly offset from the shaft and (7) an asymmetrical forth trochanter. (G) Proximal view of the left astragalus, indicating (8) an acute anteromedial corner, (9) a broader ascending process, and (10) a reduced fibular articulation. (H) Cranial view of the distal tarsals, indicating (11) a proximally flat lateral distal tarsal. All figured material refers to the mounted skeletons (GPIT I and III) of the “Sauriersaal” at Institut für Geologie und Paläontologie, Tübingen (Weishampel & Westphal, 1986), except: B = SMNS 12949. Scale bars: A = 1 m; B-E, G-H = 5 cm; F = 10 cm.

(1996) for a combined approach. Some (Fraser *et al.*, 2002; Rauhut, 2003; Ezcurra, 2006; Irmis *et al.*, 2007a) adopted a topographic criterion, simply considering the number of sacral vertebrae, while others (Serenó *et al.*, 1993, Sereno, 1999; Langer, 2004; Langer & Benton, 2006, Yates, 2007a) attempted to recognize whether trunk or caudal elements have been incorporated into the sacrum. Evidence for a two-vertebrae sacrum within basal dinosaurs is limited, and restricted to incomplete specimens (Langer & Benton, 2006; Yates, 2007a; Sereno, 2007b). On the contrary, the sacrum of *Silesaurus* is clearly composed of three sacral vertebrae (Dzik & Sulej, 2007). Accordingly, based on the current evidence, and considering *Silesaurus* as closely related but outside Dinosauria, the statement that dinosaurs are apomorphic in having a sacrum composed of more than two vertebrae is misleading. A more detailed approach that attempts to recognize trunk or tail additions to the sacrum may provide further information. In a few basal dinosaurs, i.e. *Saturnalia tupiniquim*, *Herrerasaurus ischigualastensis*, *Staurikosaurus pricei*, *Guaibasaurus candelariensis*, and *Eoraptor lunensis*, the two primordial sacral vertebrae are readily recognized based on their much larger rib articulations. Other vertebrae may be incorporated into the sacrum from either the trunk (*Herrerasaurus*, *Eoraptor*) or the caudal (*Staurikosaurus*, *Saturnalia*) series, but none has a conspicuous sacral rib,

compared to the primordial elements. Such a robust third element is known in *Silesaurus opolensis*, and we agree with Dzik & Sulej (2007) that it is borne by a trunk vertebra added to the sacrum. Among the major dinosaur groups, all theropods and ornithischians have trunk vertebrae added to the sacrum, as is also the case in sauropodomorphs, except for *Plateosaurus* (Yates, 2003c) and, possibly, *Thecodontosaurus* (Yates, 2007a). Accordingly, even if a trunk vertebra added to the sacrum is seen in most basal dinosaurs, the presence of this character in *Silesaurus* dismisses its apomorphic status for the group. On the other hand, the incorporation of a caudal vertebra to the dinosaur sacrum seems more restricted, absent in various basal forms (i.e. *Herrerasaurus*, *Eoraptor*) and most basal sauropodomorphs (Yates, 2007a). Indeed, the presence of caudosacral vertebrae is also not accepted as a dinosaur apomorphy. It is evident that we are dealing with a highly homoplastic character, possibly affected by frame shift phenomena (Galton & Upchurch, 2000). It is also of misleading codification if one considers the ambiguous condition of vertebrae that bore small transverse processes/ribs that attach to the ilium and/or other sacral transverse processes/ribs; compare *Herrerasaurus* in Novas (1993) and Sereno (2007b). The increase in the number of sacral vertebrae is, generally speaking, surely a typical dinosaur trait. Yet, until more information, possibly derived

from better preserved specimens of key taxa, is available, the number of sacral vertebrae, and also the incorporation of either trunk or caudal elements in the sacrum cannot be unambiguously defined as dinosaur apomorphies. Besides, Langer & Benton (2006) considered a dorsally expanded cranial margin of the first primordial sacral rib as apomorphic for dinosaurs. Similarly, this condition was also recognized in *Silesaurus* (ZPAL Ab III/404/3), and can not be considered a dinosaur apomorphy in the phylogenetic framework adopted here.

Few characters of the pectoral girdle and limb have been considered apomorphic for dinosaurs. This may indicate that these parts of the dinosaur skeleton are not very modified relative to the basic archosaur condition. Yet, it may also reflect the lack of knowledge regarding these anatomical elements, especially the forearm and hand, in the outgroups to Dinosauria. This is particularly the case with the characters related to the reduction of the outer digits of the dinosaur manus (Gauthier & Padian, 1985; Novas, 1996; Sereno, 1999). Indeed, dinosaur digit IV is always subequal to or shorter than metatarsal III and never possesses more than three phalanges, none of which is an ungual (Langer & Benton, 2006). In addition, almost no dinosaur is known to possess more than two phalanges in manual digit V. On the contrary, manual digits IV and V of other archosauromorphs are elongated elements with three or more phalanges. More recently, Butler *et al.* (2007) claimed that an enlarged grasping manus (with elongated pre-ungual phalanges, prominent dorsal extensor pits and proximal intercondylar processes), previously considered typical of *Herrerasaurus ischigualastensis* and theropods (Sereno *et al.*, 1993; Sereno, 1999), may also be apomorphic for dinosaurs, due to its occurrence in basal ornithischians (*Eocursor parvus* and heterodontosaurids). However, the manus is unknown in non-dinosaur dinosauromorphs, and it is ambiguous at which point of basal dinosauromorph evolution these modifications occurred. Likewise, although no sternal plates have been recognized in basal dinosauromorphs, this may simply represent a preservation bias (Padian, 1997b), and their occurrence as paired ossifications (Sereno, 1999) can not be regarded as a trustworthy dinosaur apomorphy.

In fact, the single feature of the pectoral skeleton accepted by most previous studies as apomorphic for Dinosauria appears to be a long deltopectoral crest (Fig. 5D), which extends for more than 30–35% of the humeral length. Besides, as noted by several authors (Yates, 2007a; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a), contrasting with that of pseudosuchians and *Silesaurus opolensis*, the deltopectoral crest of dinosaurs is subrectangular, rather than subtriangular or rounded. Yet, although lacking its proximal margin, the deltopectoral crest of *Marasuchus lilloensis* (PVL 3871) seems of the subrectangular type (Bonaparte, 1975), implying a more inclusive distribution for that trait. Likewise, a shorter forearm relative to the humerus can not be accepted *a priori* as a dinosaur apomorphy (Irmis *et al.*, 2007a), given that a plesiomorphic longer forearm is retained in *Herrerasaurus ischigualastensis* and *Eoraptor lunensis* (Langer *et al.*, 2007b).

Most novel traits of the early dinosaur skeleton are seen in the pelvic girdle and limb. These were often related to the acquisition of an improved bipedal gait (Bakker & Galton, 1974), as typical of most basal members of the group. Further, some authors, e.g. Bakker (1971) and Charig (1972, 1984), have suggested that these traits represent key features that allowed, or even promoted, dinosaur radiation in Late Triassic times, while most other archosaurs were in decline. Regardless of their evolutionary consequences (see Sections IV.2,3), it is true that the dinosaur pelvic girdle and limb bear various apomorphic traits. Indeed, about half of the features presented by Novas (1996) and Sereno (1999) as diagnostic for dinosaurs are related to those elements (exclusive of the sacrum), and similar ratios are seen in other recent works: four out of 11 in Langer & Benton (2006); seven out of 11 in Ezcurra (2006); eighth out of 15 in Yates (2007a); and 10 out of 14 in Irmis *et al.* (2007a). Obviously, the fact that these anatomical parts are relatively well known in basal dinosauromorphs facilitates the recognition of dinosaur apomorphies.

Regarding the pelvic girdle, a perforated acetabulum (Bakker & Galton, 1974; Novas, 1996; Ezcurra, 2006; Yates, 2007a), better described as a straight to concave ventral acetabular margin of the ilium (Langer & Benton, 2006; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a), stands in most recent revisions as a valid synapomorphy of Saurischia plus Ornithischia (Fig. 5E), but that is not the case of a brevis fossa/shelf in the iliac postacetabular ala (Novas, 1996; Sereno, 1999; Fraser *et al.*, 2002; Benton, 2004; Yates, 2007a). Whereas a shelf is also present in *Marasuchus* (Fraser *et al.*, 2002; Langer & Benton, 2006; but see Novas, 1996), a fossa is not only seen in some basal dinosauriforms (e.g. *Silesaurus*), but is also lacking in herrerasaurids (Novas, 1992b, 1993, 1996; Langer & Benton, 2006). More recently, Ezcurra (2006) proposed a straight to convex dorsal margin of the ilium (Fig. 5E) as a dinosaur apomorphy. Indeed, basal dinosaurs lack a dorsally excavated ilium, which seems to be typical of basal dinosauromorphs (Sereno & Arcucci, 1993, 1994), although not well preserved in some (e.g. *Silesaurus*; ZPAL AbIII/361). On the contrary, other recently proposed apomorphies of the dinosaur ilium are either highly homoplastic (“long preacetabular process”; Yates, 2007a) or define a more inclusive clade (“acetabular antitrochanter present”; Irmis *et al.*, 2007a), i.e. Dinosauriformes (see Sereno & Arcucci, 1994). Irmis *et al.* (2007a) also suggested that a transversely compressed distal pubis is a dinosaur apomorphy, reversed in sauropodomorphs, but the definition and distribution of this feature is not so straightforward, as extensively discussed by Langer & Benton (2006, p. 338).

Irmis *et al.* (2007a, char. 73) newly proposed that the pubic process of the dinosaur ischium is apomorphic, because “separated from the ilial peduncle”. In fact, the surface connecting the iliac and pubic articulations of the ischium is simply excavated in many basal dinosaurs, especially theropods (*Coelophysis rhodesiensis*, QVM QG 1; *Liliensternus liliensterni*, MB R 2175) and ornithischians (*Scelidosaurus harrisoni*, BMNH1111; *Scutellosaurus lawleri*, UCMP 130580;

Butler *et al.*, 2007). On the contrary, in forms such as *Marasuchus lilloensis* (PVL 3870) and *Silesaurus opolensis* (ZPAL AbIII 1228, 404/1) that excavation does not reach the medial-most margin of the ischium, so that a medially displaced sheet of bone remains, filling the space between pubic process and iliac peduncle. This condition is reminiscent of more basal archosaurs, in which the ischium contributes significantly to the composition of the medial wall of a non-perforated acetabulum. *Herrerasaurus ischigualastensis* (PVL 2566) retains a much reduced medial sheet of bone, so that the acetabular surface of the ischium can be considered fully excavated, i.e. bearing the dinosaur apomorphy as defined by Irmis *et al.* (2007a). On the contrary, the condition among sauropodomorphs is variable (Yates, 2003c); e.g. in *Saturnalia tupiniquim* (MCP 3846-PV), although an extensive antitrochanter disrupts the clear observation of the character (but see *Liliensternus liliensterni*, MBR 2175), the medial sheet of bone occupies the space between that structure and the pubic articulation. Accordingly, the status of the character defined by Irmis *et al.* (2007a) awaits further investigation. Other previously proposed apomorphies of the dinosaur ischium include the presence of a reduced medioventral lamina (Novas, 1996; Langer & Benton, 2006) and a proximal dorsolateral sulcus (Yates, 2007a). Yet, both features are clearly present in *Silesaurus* (ZPAL AbIII 361, 404/1), so that their status as apomorphic for dinosaurs depends on the contentious position of that taxon.

The femur is possibly the most scrutinized bone in the study of early dinosaurs, with more than ten different characters found as apomorphic for the group in the phylogenies revised here. An inturned and subrectangular femoral head, that is distinctly set from the shaft, has been considered among the typical traits of dinosaurs by Bakker & Galton (1974) and Gauthier (1986). Yet, this general state was poorly dismembered into distinct and well-defined phylogenetic characters, in order to evaluate the apomorphic condition of each. Sereno (1999) defined an angular “greater trochanter” (i.e. nearly straight angle between the proximal articulation and the long axis of the shaft) as a dinosaur apomorphy, but that trait was also recognized in basal dinosauriforms (e.g. *Pseudolagosuchus major*, PULR 53; Ezcurra, 2006). This structure is a subrectangular femoral head, if the latter is distinctly offset from the shaft, as diagnostic of dinosaurs (Ezcurra, 2006, char. 231; Irmis *et al.*, 2007a, char. 81; Brusatte *et al.*, 2008a, char. 132). That condition appears along with an inturned femoral head (Fig. 5F), which can be also considered a dinosaur apomorphy.

Irmis *et al.* (2007a) claim that the femoral head of dinosaurs apomorphically bears a ligament sulcus and an asymmetrical fossa articularis antitrochanterica, but these traits have also been recorded in other basal dinosauriforms (Novas, 1996; Ezcurra, 2006). Likewise, the apomorphic condition of a reduced medial tuberosity (Novas, 1996; Sereno, 1999) and a prominent lesser trochanter (Novas, 1996) have been dismissed by most recent studies (Langer & Benton, 2006; Ezcurra, 2006; Irmis *et al.*, 2007a). Other features of the femoral head were considered apomorphic reversals of

Dinosauria (Ezcurra, 2006, char. 232; Irmis *et al.*, 2007a, char. 85; Brusatte *et al.*, 2008a, char. 135), but depend on character optimization. Besides, although reversed in theropods, the presence of an asymmetrical fourth trochanter (Fig. 5F) appears as a valid dinosaur apomorphy in most recent reviews (Langer & Benton, 2006; Ezcurra, 2006; Irmis *et al.*, 2007a), and has been recently recorded also in *Guaibasaurus candelariensis* (Bonaparte *et al.*, 2007; *contra* Langer & Benton, 2006) and *Chindesaurus bryansmalli* (GR 226; *contra* Yates, 2007a).

Previously defined tibial traits such as the presence of a cnemial crest (Novas, 1996; Sereno, 1999) and a transversely expanded distal articulation (Novas, 1996; Benton, 2004) are no longer believed to represent dinosaur apomorphies, given their erratic distribution among basal dinosaurs and dinosauriforms (Langer & Benton, 2006; Ezcurra, 2006; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a). Similarly, because also seen in *Silesaurus*, a descending process of the tibia that caudally overlaps the ascending process of the astragalus is also not regarded apomorphic for dinosaurs. According to Yates (2007a), a sub-quadratic distal tibia and a thinner fibula may represent dinosaur apomorphies, because the reverse condition is seen in *Silesaurus*. Yet, the record of the dinosaur condition in *Marasuchus lilloensis* jeopardizes that assumption. Accordingly, no unambiguous apomorphy is currently referred to the dinosaur pelvic epipodium. In addition, Ezcurra (2006) considered, under DELTRAN optimization, a tibia subequal to the femur as apomorphic for dinosaurs. Although the contrary was described for *Silesaurus opolensis* (Dzik, 2003), a longer tibia is not only typical of basal dinosauriforms (Sereno & Arcucci, 1993; 1994; *Pseudolagosuchus major*, PVL 4629), but was also retained in basal ornithischians (Santa Luca, 1980; Butler *et al.*, 2007). Indeed, among basal dinosaurs, only saurischians consistently bear a subequal or longer femur; but see *Staurikosaurus pricei* (Colbert, 1970).

The tarsal joint has also been the source of several anatomical traits believed to characterize dinosaurs. Yet, this is not the case of an astragalar ascending process and a lateral articulation between the calcaneum and the astragalar anterolateral process (Sereno, 1999), which were recently identified in other basal Dinosauriforma (Novas, 1996; Langer & Benton, 2006; Brusatte *et al.*, 2008a). Yet, a reduced fibular articulation (Langer & Benton, 2006; Brusatte *et al.*, 2008a), a broader ascending process (Yates, 2007a, char. 314), and an acute anteromedial corner (Irmis *et al.*, 2007a) apparently stand as apomorphies of the dinosaur astragalus (Fig. 5G). On the contrary, some putative apomorphies of the dinosaur calcaneum, such as a concave fibular articulation (Novas, 1996) and a rudimentary medial process (Sereno, 1999) have an erratic distribution among basal dinosauriforms, and can not be unambiguously considered as such (Langer & Benton, 2006; Ezcurra, 2006; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a). On the other hand, as far as the condition in the outgroups to Dinosauria can be accessed, a proximally flat lateral distal tarsal (Novas, 1996; Langer & Benton, 2006; Brusatte *et al.*, 2008a) stands as a

unique trait of the group (Fig. 5H). The single apomorphy of the dinosaur metatarsus proposed in the discussed studies of early dinosaur phylogeny is the so-called “sigmoid” metatarsal IV (Sereno, 1999), a condition given by the lateral displacement of the distal part of the bone (Novas, 1996; Brusatte *et al.*, 2008a). This condition is, however, also seen in some basal dinosauromorphs (Novas, 1996; Ezcurra, 2006), and disregarded as a dinosaur apomorphy.

(2) Phylogenetic definitions: naming early dinosaurs

With the advent of Phylogenetic Nomenclature (De Queiroz & Gauthier, 1990, 1992, 1994), systematists acquired an unprecedented tool to define taxon names in explicit phylogenetic context, setting their composition according to given hypotheses. A drawback of this revolution was the inflation of phylogenetic definitions for various names (Benton, 2000), as readily recognized in a brief inspection of Paul Sereno’s webpage *TaxonSearch*. Indeed, when dealing with these names, authors currently have to state which of the available definitions is adopted to translate them into the phylogenetic nomenclature system. The priority issue is expected to be settled with the publication of the “companion volume” of the *PhyloCode* (Cantino & De Queiroz, 2007). Yet, before this volume is published and, more importantly, accepted by the scientific community as the “Systema Naturae” of phylogenetic definitions, these will no doubt continue to proliferate in an unordered way. In the following paragraphs, the phylogenetic definitions pertinent to the discussion of dinosaur origins are treated in historical order and, in an attempt to emulate the “Principle of Priority” (ICZN, 1999), those first proposed, with small modifications added if absolutely required, are listed in Table 1 and employed throughout the text.

Because Jacques Gauthier was involved in the study of archosaurs, including dinosaurs, he presented some phylogenetic definitions for related groups (Gauthier & Padian, 1985; Gauthier, 1986) even before the publication of the paper that set the theoretical foundation of Phylogenetic Nomenclature (De Queiroz & Gauthier, 1990). Gauthier & Padian (1985) provided a phylogenetic definition for Ornithosuchia, while Gauthier (1986) explicitly defined Saurischia and Theropoda. Problematic aspects of these definitions include the use of supraspecific and/or informal specifiers (e.g. birds, archosaurs, crocodiles, dinosaurs, sauropodomorphs, Ornithischia) and their choice based on the phylogenetic orthodoxy of the time. Instead, we believe that, for the sake of precision, newly proposed phylogenetic definitions should use minimal groups as specifiers, and for historical coherence rely, as much as possible, on taxa mentioned in the original definition of the names. In any case, because first published, those definitions are adopted here for the names in question (Table 1). Alternative phylogenetic definitions for Saurischia (Padian & May, 1993; Padian, 1997d; Sereno, 1998; Holtz & Osmólska, 2004; Langer, 2004) just replace specifiers, either because these are more specific (Padian, 1997d; Sereno, 1998) or are quoted in the original proposition of the name (Langer, 2004). Yet, based

on current phylogenetic hypotheses, these circumscribe the same set of taxa as Saurischia *sensu* Gauthier (1986). Similarly, alternative specifiers in later definitions of Theropoda are more specific (Currie, 1997) and either more highly nested (Sereno, 1998) or first named (Padian, Hutchinson & Holtz, 1999; Holtz & Osmólska, 2004). Again, their use does not change the inclusivity of the group as defined by Gauthier (1986).

Further phylogenetic definitions pertinent to the discussed groups were proposed by Sereno (1991a), Novas (1992b), and Padian & May (1993). Sereno (1991a) gave node-based definitions for Ornithodira Gauthier, 1986, and Dinosauromorpha Benton, 1985. These had to be slightly modified (Table 1) to fit the logical basis of Phylogenetic Nomenclature and the updated taxonomy of Sereno & Arcucci (1994), but substitute definitions (Benton, 2004) are redundant. Especially problematic are the stem-based definitions of Dinosauromorpha (Sereno, 1991a, 2005; Benton, 2004) that use pterosaurs as the external specifier, given the uncertain phylogenetic position of these reptiles. In their current understanding, Ornithodira and Dinosauromorpha differ only by the inclusion of *Scleromochlus taylori* and possibly pterosaurs in the former. The least inclusive Dinosauriformes was node-based defined when first named by Novas (1992b). This was modified (Table 1) to fit the taxonomy of Sereno & Arcucci (1994), but equally requires no substitute definitions (Benton, 2004).

Apart from the equivocal list of taxa presented by Gauthier (1986, p. 44; see Padian, 1997a), Novas (1992b) provided the first phylogenetic definition of Dinosauria as “the common ancestor of Herrerasauridae and Saurischia + Ornithischia, and all of its descendants”. This is in agreement with the taxonomic orthodoxy of the time (Gauthier, 1986; Brinkman & Sues, 1987; Benton, 1990; but see Gauthier *et al.*, 1989), according to which: (1) saurischians plus ornithischians form a clade, contrary to the traditional view that these arose independently from “thecodont” precursors; (2) herrerasaurids, conventionally regarded as saurischian dinosaurs (Reig, 1963; Colbert, 1970), are basal to that clade. Indeed, in order to keep herrerasaurids as dinosaurs, Novas (1992b) used the former as an internal specifier of the latter. By contrast, Padian & May (1993) explicitly restricted the use of Dinosauria to the clade composed of Saurischia and Ornithischia, exclusive of “*Herrerasaurus* and its allies”. Despite the “priority” of Novas (1992b), the latter concept gained almost unconditional acceptance since (e.g. Sereno, 1998, 2005; Fraser *et al.*, 2002) and is employed here (Table 1). In any case, these alternate definitions only circumscribe different groups if herrerasaurids are placed outside the Saurischia + Ornithischia dichotomy, a hypothesis not supported by most recent studies (see below). Other authors (Holtz *in* Padian, 1997a; Olshevsky, 2000; Clarke, 2004) attempted phylogenetically to define Dinosauria using taxa included in the original proposition of the name. In this case, the best option may be using all names mentioned by Owen (1842) in a node-based fashion, and to define Dinosauria as “the most recent common

Table 1. Phylogenetic definition of names relevant in the context of early dinosaur evolution.

Name	Phylogenetic definition
ORNITHODIRA Gauthier, 1986	“Pterosauria, <i>Scleromochlus</i> , Dinosauromorpha (including birds), and all descendants of their most recent common ancestor” modified from Sereno (1991a); node-based
DINOSAUROMORPHA Benton, 1985	“ <i>Lagerpeton chanarensis</i> , <i>Marasuchus lilloensis</i> , <i>Pseudolagosuchus major</i> , Dinosauria (inc. Aves), and all descendants of their most recent common ancestor” modified from Sereno (1991a); node-based
DINOSAURIFORMES Novas, 1992b	“The most recent common ancestor of <i>Marasuchus lilloensis</i> , Dinosauria, and all taxa stemming from it” modified from Novas (1992b); node-based
SILESAURIDAE new name	“All archosaurs closer to <i>Silesaurus opolensis</i> , than to <i>Heterodontosaurus tucki</i> and <i>Marasuchus lilloensis</i> ”; stem-based
DINOSAURIA Owen, 1842	“All descendants of the most recent common ancestor of birds and <i>Triceratops</i> ” Padian & May (1993); node-based
ORNITHISCHIA Seeley, 1888	“Dinosaurs closer to <i>Triceratops</i> than to birds” Padian & May (1993); stem-based
GENASAURIA Sereno, 1986	“Thyreophora and Cerapoda and all descendants of their common ancestor” Currie & Padian (1997a); node-based
NEORNITHISCHIA Cooper, 1985	“All genasaurians closer to <i>Triceratops</i> than to <i>Ankylosaurus</i> ” Sereno (1998); stem-based
THYREOPHORA Nopcsa, 1915	“All genasaurians closer to <i>Ankylosaurus</i> than to <i>Triceratops</i> ” Sereno (1998); stem-based
SAURISCHIA Seeley, 1888	“Birds and all dinosaurs that are closer to birds than they are to Ornithischia” Gauthier (1986); stem-based
HERRERASAURIA Galton, 1985b	“All dinosaurs that share a more recent common ancestor with <i>Herrerasaurus</i> than with <i>Liliensternus</i> and <i>Plateosaurus</i> ” Langer (2004); stem-based
HERRERASAURIDAE Benedetto, 1973	“ <i>Herrerasaurus</i> , <i>Staurikosaurus</i> , their most recent common ancestor, plus all its descendants” modified from Novas (1992b); node-based
EUSAURISCHIA Padian <i>et al.</i> 1999	“The least inclusive group of Saurischia, containing <i>Cetiosaurus</i> and Neornithes” Langer (2004); node-based
SAUROPODOMORPHA Huene, 1932	“The clade including the most recent common ancestor of Prosauropoda and Sauropoda and all of its descendants” Salgado <i>et al.</i> (1997); node-based
MASSOPODA Yates, 2007a	“The most inclusive clade containing <i>Saltasaurus loricatus</i> but not <i>Plateosaurus engelhardti</i> ” Yates (2007a); stem-based
SAUROPODIFORMES Sereno, 2005	“The least inclusive clade containing <i>Mussaurus patagonicus</i> Bonaparte & Vince, 1979, and <i>Saltasaurus loricatus</i> Bonaparte & Powell, 1980” Sereno (2005); node-based
SAUROPODA Marsh, 1878	“The most recent common ancestor of <i>Vulcanodon karibaensis</i> and Eusauropoda and all of its descendants” Salgado <i>et al.</i> (1997); node-based
THEROPODA Marsh, 1881	“Birds and all saurischians that are closer to birds than they are to sauropodomorphs” Gauthier (1986); stem-based
NEOTHEROPODA Bakker, 1986	“ <i>Coelophysis</i> , Neornithes, their most recent common ancestor and all descendants” Sereno (1998); node-based
COELOPHYSOIDEA Nopcsa, 1928	“All ceratosaurs closer to <i>Coelophysis</i> than to <i>Carnotaurus</i> ” Sereno (1998); stem-based
AEROSTRA Paul, 2002	“ <i>Ceratopsaurus nasicornis</i> , <i>Allosaurus fragilis</i> and all the descendants of their most recent common ancestor” modified from Ezcurra & Cuny (2007); node-based

ancestor of *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*, and all its descendants”. Again, according to the current phylogenetic hypotheses, this definition circumscribes the same set of taxa as that of Padian & May (1993).

Novas (1992b) also proposed a node-based definition for Herrerasauridae, “emended” by Novas (1997a). Yet, both definitions are incomplete and a modified version of them is employed here (Table 1). There is no good reason to replace that definition with a stem-based Herrerasauridae (Sereno, 1998; Benton, 2004), especially because this is equivalent to Herrerasauria (see below). Further, Padian & May (1993)

provided a stem-based definition for Ornithischia, in a fashion that matches its mutual exclusivity in relation to Saurischia *sensu* Gauthier (1986). Subsequent definitions use more specific (Sereno, 1998) and also more “traditional” (Weishampel, 2004; Norman, Witmer & Weishampel, 2004a) specifiers, but are equally inclusive based on current phylogenies. Although the use of taxa mentioned in the proposal of Saurischia (e.g. *Allosaurus*, *Camarasaurus*) and Ornithischia (e.g. *Stegosaurus*, *Iguanodon*) may have been more desirable, all the previous definitions successfully translate Seeley’s (1888) dichotomous understanding of Dinosauria

into the Phylogenetic Nomenclature system. Likewise, it could also be argued that the use of apomorphy-based definitions for Saurischia and Ornithischia better represents that original proposition, given that the groups were defined on a character basis, i.e. opisthopic and propubic pelvis. Yet, this is problematic because only the ornithischian pelvic construction is apomorphic, whereas saurischians retain the general morphology seen in more basal archosaurs.

Salgado, Coria & Calvo (1997) first proposed a phylogenetic definition for Sauropodomorpha (Table 1). Their node-based definition preceded that (stem-based) given by Upchurch (1997b) by a couple of months, but both suffer from using Sauropoda and Prosauropoda as internal specifiers. Subsequent proposals attempt to replace those taxa by more specific, and deeply nested specifiers in either a node- (Serenó, 1998) or stem- (Galton & Upchurch, 2004; Sereno, 2007a) based fashion. Although lower rank specifiers are desirable, the same level of precision can be achieved using higher taxa that are, in turn, defined with direct reference (or by typification) to those minimal groups. Moreover, the adequacy of an either stem- or node-based Sauropodomorpha (Upchurch, Barrett & Galton, 2007) is minor in face of the primacy of the definition provided by Salgado *et al.* (1997).

More recently, Langer (2004) defined a stem-based Herrerasauria Galton, 1985b, and a node-based Eusaurischia Padian, Hutchinson & Holtz, 1999. The former group is potentially equivalent to Herrerasauridae *sensu* Sereno (1998), but the node-based original definition of Herrerasauridae is employed here. In that context, Herrerasauria (Table 1) can allocate dinosaurs closely related to, but outside the clade composed of *Herrerasaurus* plus *Staurikosaurus*. Eusaurischia, on the other hand, was first proposed to designate the clade composed of Sauropodomorpha plus Theropoda (Padian *et al.*, 1999). This is as inclusive as the stem-based Saurischia under certain phylogenetic schemes (Novas, 1996; Sereno, 1999), but excludes basal forms such as *Eoraptor* and herrerasaurs in alternative frameworks (Langer, 2004; Ezcurra, 2006) and remains a potentially useful name (Table 1). Finally, Silesauridae is here defined as a stem-based taxon that includes all archosaurs closer to *Silesaurus opolensis* than to *Marasuchus lilloensis* and *Heterodontosaurus tucki*. The latter form was chosen to represent Dinosauria because of its completeness (Santa Luca, 1980) and basal position within Ornithischia (Butler *et al.*, 2007), a group to which *Silesaurus* has been tentatively related (Frigolo & Langer, 2007).

III. DINOSAUR “TRAIL BLAZERS” IN SPACE, TIME, AND EVOLUTIONARY CONTEXT

(1) The oldest dinosaurs and the rocks that contain them

For most of the last century, except in a few important cases (Huene, 1926; Colbert, 1989; Sereno & Novas, 1992; Sereno *et al.*, 1993), the knowledge of Triassic dinosaurs was

based on incomplete and/or fragmentary skeletal remains. In the last decade, however, various studies (e.g. Rauhut & Hungerbühler, 2000; Langer, 2004; Parker *et al.*, 2005; Ezcurra, 2006; Nesbitt *et al.*, 2007) revised those early records, questioning the dinosaur affinity of several of them. On the other hand, the discovery of a variety of more complete basal dinosaurs (e.g. Langer *et al.*, 1999; Bonaparte *et al.*, 1999, 2007; Yates & Kitching, 2003; Butler *et al.*, 2007; Pol & Powell, 2007a, b; Martínez & Alcober, 2009; Ezcurra, 2008), allowed a more reliable picture to emerge. As detailed below, this accounts for the possible, but poorly supported Middle Triassic origin of the group, its first radiation during the Carnian, and the full establishment of the main dinosaur groups from the Norian onwards.

Usually, the oldest dinosaurs (Galton, 2000; Langer, 2004) are considered as coming from the Ischigualastian beds (Langer, 2005a) of northwestern Argentina and south Brazil (Fig. 6). These respectively include the Ischigualasto Sequence, Ischigualasto-Ischichuca depocenter, Bermejo Basin (Stipanovic & Marsicano, 2002; Currie *et al.*, 2009), and the Santa Maria Supersequence, Paraná Basin (Zerfass *et al.*, 2003), the continental sedimentation of which filled extensional rift basins related to the Gondwanides orogenesis (Zerfass *et al.*, 2004). Early works dated the Ischigualasto and Santa Maria formations as Middle Triassic (Romer, 1960, 1962; Reig, 1961, 1963), but a Late Triassic age, first proposed by Bonaparte (1966), has been supported by most recent biostratigraphic studies (Ochev & Shishkin, 1989; Lucas, 1998; Langer, 2005a, b). This was corroborated by the radiometric dating of the ‘Herr Toba’ bentonite (Fig. 6C), at the base of the Ischigualasto Formation (Rogers *et al.*, 1993), that provided a $^{40}\text{Ar}/^{39}\text{Ar}$ age of 227 ± 0.3 Mya. Yet, following the discrepancy between U-Pb and $^{40}\text{Ar}/^{39}\text{Ar}$ dates (Schoene *et al.*, 2006) and other comparative parameters, Furin *et al.* (2006) recalculated a date of $230.3\text{--}231.4 \pm 0.3$ Mya. This corresponds to the late Ladinian in most timescales (Ross, Baud & Manning, 1994; Remane *et al.*, 2000; Ogg, 2004; Ogg, Ogg & Gradstein, 2008), but recent works (Muttoni *et al.*, 2001, 2004; Gallet *et al.*, 2003; Kent, Muttoni & Brack, 2006; Kozur & Weems, 2007) assigned older ages for the Carnian boundaries. In that context, and considering the sedimentation rate of comparable rift basins (Rogers *et al.*, 1993; Currie *et al.*, 2009), the dinosaur-rich sites of the lower third of the Ischigualasto Formation can be placed in the latest Carnian. Yet, the middle third of that stratigraphic unit, that also yielded dinosaur remains, may rest within the middle Norian. This was recently corroborated by the dating of another bentonite, from above the middle sector of the Ischigualasto Formation (Currie *et al.*, 2009), which provided a $^{40}\text{Ar}/^{39}\text{Ar}$ age of 217.0 ± 1.7 Ma (Shipman, 2004), recalculated as $219.4\text{--}220.4 \pm 1.7$ Mya (M. Ezcurra, personal observations).

Ischigualastian dinosaurs (Fig. 6C) include *Herrerasaurus ischigualastensis*, along with its possible synonyms *Ischisaurus cattoi* and *Freguellisaurus ischigualastensis* (Novas, 1993), *Eoraptor lunensis* (Serenó *et al.*, 1993), and *Panphagia protos* (Martínez & Alcober, 2009), from the lower third of the Ischigualasto

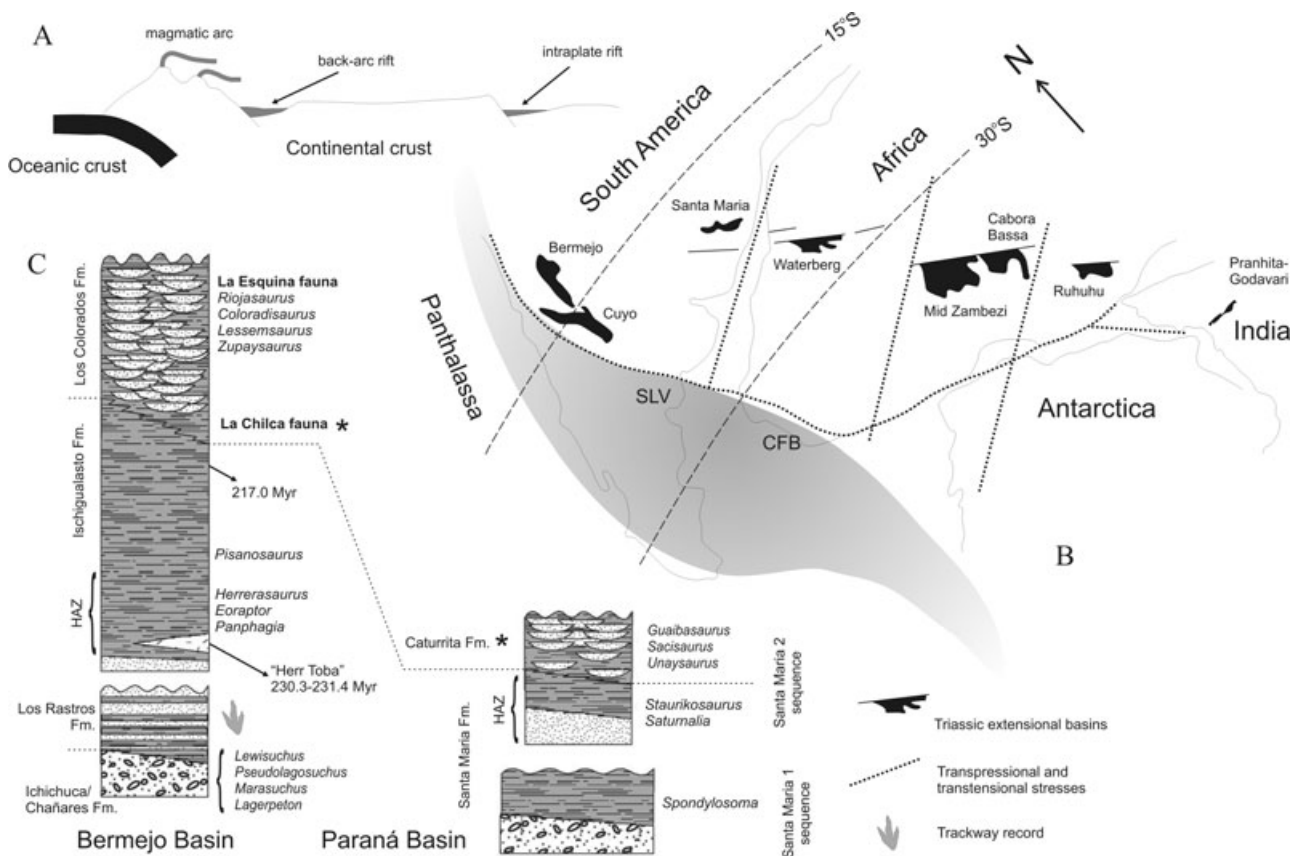


Fig. 6. Tectonic and sedimentary settings of southwestern Pangea during the Middle and Late Triassic, with emphasis on the South American dinosaur-bearing sequences (Zerfass *et al.*, 2004; Veevers, 2005). (A) Idealized east-west cross section from Santa Maria intraplate rift to the Cuyo back-arc rift and Gondwanides orogen. (B) Palaeogeographic reconstruction; note that the extensional basins are perpendicular to the transtensional stresses. Abbreviations as follows: SLV, Sierra de la Ventana; CFB, Cape Fold Belt. Gondwanides orogen in grey. (C) Stratigraphic charts of the Bermejo and Paraná Basins, depicting the dinosauriform/putative dinosaur record. Fm., Formation; HAZ, *Hyperodapedon* Acme Zone according to Langer *et al.* (2007c); Mys, million years before recent. Asterisks indicate possibly coeval faunas in which the dicynodont *Jachaleria* occurs.

Formation, and *Pisanosaurus mertii* (Bonaparte, 1976) from the middle third of that stratigraphic unit (Rogers *et al.*, 1993), as well as *Staurikosaurus pricei* (Colbert, 1970) and *Saturnalia tupiniquim* (Langer *et al.*, 1999) from the *Hyperodapedon* Assemblage-Zone of the Santa Maria Formation (Langer *et al.*, 2007b). More recently, the discoveries of two new herrerasaurids (Martinez & Alcober, 2007; Ezcurra & Novas, 2008), a *Saturnalia*-like animal (Ezcurra & Novas, 2008; Ezcurra, 2008), and a probable basal theropod (Martinez, Sereno & Alcober, 2008) have been announced from the Ischigualasto Formation. Outside South America, dinosaurs of similar age are much less conspicuous (Fig. 7). These mainly include fragmentary remains from Gondwanan areas such as the possible record of *Saturnalia* in the Pebbly Arkose Formation (Cabora Bassa Basin), lower Zambezi Valley, Zimbabwe (Raath, 1996; Langer *et al.*, 1999), and part of the specimens attributed to *Alwalkeria maliensis*, from the Lower Maleri Formation (Pranhita-Godavari Basin), in central Peninsular India (Chatterjee, 1987; Remes & Rauhut, 2005). The record of dinosaurs in other coeval deposits

such as the Timesgadiouine Formation (Argana Basin), in Morocco (Jalil, 1996; Gauffre, 1993), and the Isalo II beds (Morondava Basin), in Madagascar (Flynn *et al.*, 1999), has been dismissed (Jalil & Knoll, 2002; Flynn *et al.*, 2008). According to Langer (2005b) the Ischigualastian can be traced into northern Pangea to encompass the Lossiemouth Sandstone Formation, in northern Scotland. Yet, the only putative dinosaur from those strata, *Saltopus elginensis*, has doubtful affinities to the group (Rauhut & Hungerbühler, 2000; Langer, 2004).

All dinosaur osteological records from pre-Ischigualastian strata have been questioned, including *Spondylosoma absconditum* (Galton, 2000; Langer *et al.*, 2007c), from the Santa Maria 1 sequence in south Brazil (Fig. 6C). Further occurrences of the group in strata of equivalent age, mainly based on fragmentary European specimens (Huene, 1932), have also been dismissed (Benton, 1986b; Norman, 1990; Galton & Walker, 1996; Rauhut & Hungerbühler, 2000). On the other hand, suggestions that dinosaurs were already present in Middle Triassic times are backed up by two lines

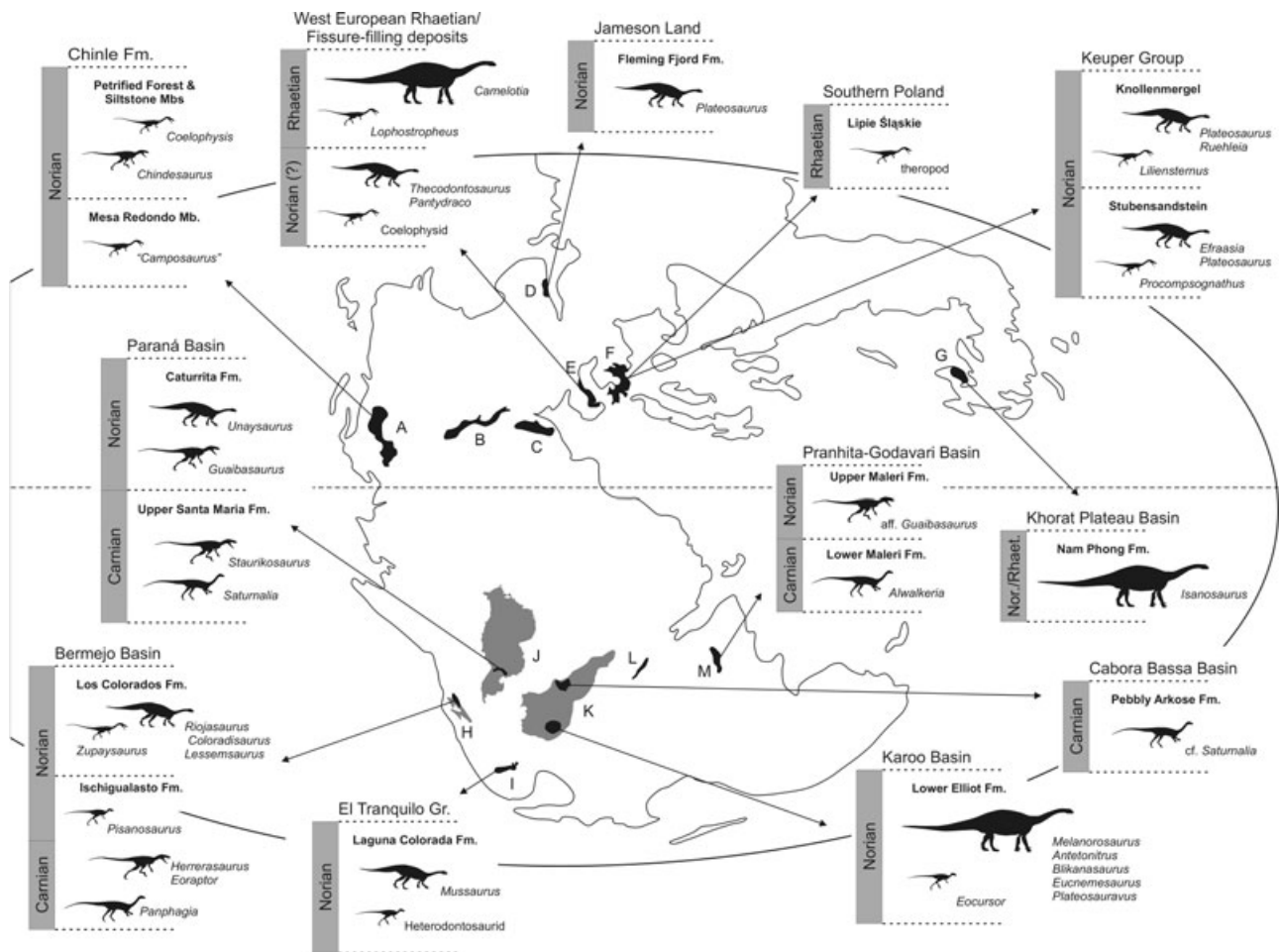


Fig. 7. Distribution of the main tetrapod-bearing deposits of Late Triassic age and their dinosaur record. (A) Chinle Formation and Dockum Group, western USA; (B) Newark Supergroup, North American Atlantic coast; (C) Argana Basin, Morocco; (D) Jameson Land, Greenland; (E) Fissure-filling and Rhaetian deposits, northwestern Europe; (F) Germanic Basin, Central Europe; (G) Khorat Plateau, Thailand; (H) Bermejo Basin, Argentina; (I) El Tranquilo Group, Argentina; (J) Paraná Basin, Brazil; (K) Karoo basins, south-central Africa; (L) Morondava Basin, Madagascar; (M) Pranhita-Godavari Basin, India. Late Triassic map redrawn from Blakey (2006). Generalized black silhouettes (not at the same scale) adapted from various sources. Fm., Formation; Mb., Member; Mbs, members.

of evidence: trackways and the stratigraphic calibration of phylogenetic hypotheses. Indeed, if silesaurids are accepted as an inclusive sister taxon to Dinosauria (Nesbitt *et al.*, 2007, p. 214; Brusatte *et al.*, 2008a; *contra* Ezcurra, 2006), encompassing Middle Triassic forms such as *Pseudolagosuchus* and *Lewisuchus*, then the dinosaur stem (although not necessarily dinosaurs) minimally arose at the same time, i.e. the Ladinian Stage. This is supported by evidence extrapolated from the palaeoichnological record. Tracks suggest the presence of dinosauriforms in the Middle Triassic of France (Lockley & Meyer, 2000), Italy (Avanzini, 2002), and Germany (Haubold & Klein, 2002). Some German tracks may correspond to dinosaurs, as is also the case for Middle Triassic footprints from various stratigraphic units in Argentina (Melchor & De Valais, 2006; Marsicano, Domnanovich & Mancuso, 2007), including the Los Rastros Formation (Fig. 6C). Although these may also represent basal dinosauriforms, the already

diversified and somewhat advanced fauna of saurischians found in the superposed Ischigualasto Formation, provides some basis to infer a Middle Triassic origin of dinosaurs.

In the scheme proposed by Langer (2005b), some tetrapod assemblages of the Newark Supergroup (Olsen, Schlichte & Gore, 1989), in the North American Atlantic coast (Fig. 7), albeit slightly younger than those of the Ischigualasto and Santa Maria formations, may correspond to the Late Ischigualastian. These include the faunas of the Wolfville (Fundy Basin, Nova Scotia) and Pekin (Deep River Basin, North Carolina) formations, the ornithischian records of which (Galton, 1983b; Hunt & Lucas, 1994) were considered unsubstantiated by Irmis *et al.* (2007b). In any case, during post-Ischigualastian times, dinosaurs became more abundant and widespread. Some of these taxa have been known for over a century (Meyer, 1837; Cope, 1889), but the diversity of Norian dinosaurs (Fig. 8) was greatly enhanced by

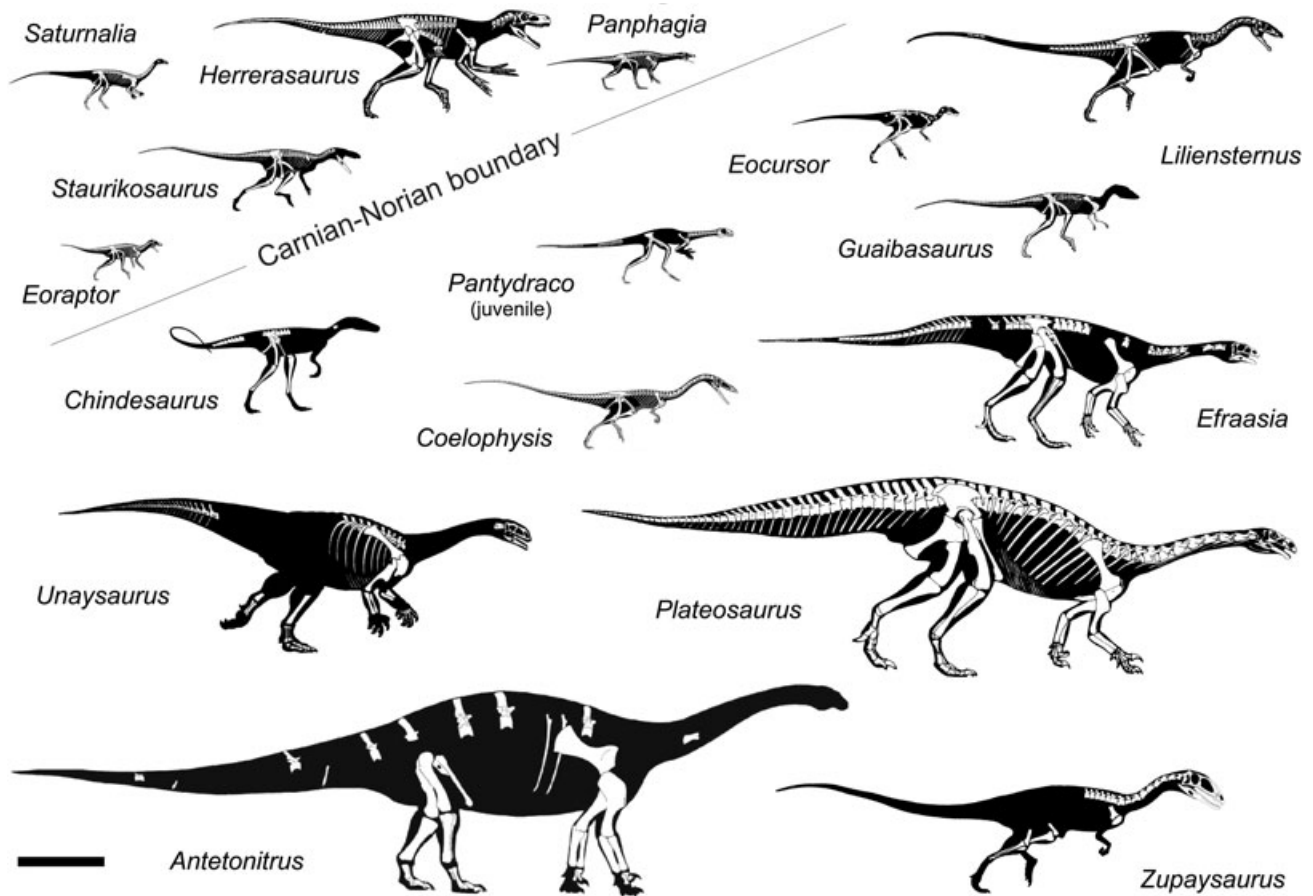


Fig. 8. Skeletal reconstructions (from various sources), at approximately the same scale, of selected Carnian and Norian dinosaurs, partially depicting the Late Triassic diversity of the group. Scale bar (lower left) = 1 m.

last-decade discoveries, especially from South America and South Africa, as outlined below.

Post-Ischigualastian dinosaur faunas in South America include those of the Los Colorados, Laguna Colorada, and Caturrita formations (Langer, 2005a). The latter stratigraphic unit, in south Brazil (Fig. 6C), has yielded the saurischian *Guaibasaurus candeleriensis* (Bonaparte *et al.*, 1999, 2007), as well as the “prosauropod” *Unaysaurus toletinoi* (Leal *et al.*, 2004). “Prosauropods” are well known in the La Esquina fauna of the Los Colorados Formation (Bonaparte, 1972). That stratigraphic unit covers the Ischigualasto Formation in northwestern Argentina (Fig. 6C), and includes *Riojasaurus incertus* (Bonaparte & Plumares, 1995), *Coloradisaurus brevis* (Bonaparte, 1978), and *Lessemsaurus sauropoides* (Pol & Powell, 2007a), along with theropods (Bonaparte, 1972) such as *Zupaysaurus rougieri* (Arcucci & Coria, 2003; Ezcurra & Novas, 2007a). In Patagonia, the Laguna Colorada Formation (El Tranquilo Group) has yielded the “prosauropod” *Mussaurus patagonicus* (Bonaparte & Vince, 1979; Pol & Powell, 2007b) as well as a heterodontosaurid ornithischian (Baez & Marsicano, 2001). Other dinosaur-bearing gondwanan deposits of similar age (Fig. 7) include the Lower Elliot Formation (Stormberg Group, Karoo Basin), in South Africa

(Knoll, 2005), and the Upper Maleri Formation, in peninsular India. The latter, along with the overlying Lower Dharmaram Formation, has yielded a diversified, but still undescribed fauna of basal saurischians (Kutty & Sengupta, 1989; Novas *et al.*, 2006), which may include a *Guaibasaurus*-like form (Kutty *et al.*, 2007). Basal sauropodomorphs are also well known in the Lower Elliot Formation, where *Melanorosaurus readi*, *Antetonitrus ingenipes*, *Blikanasaurus cromptoni*, *Eucnemesaurus fortis*, *Plateosaurus cullingworthi*, and a yet unnamed form (Yates, 2003a, 2007a, b, 2008; Yates & Kitching, 2003) were recorded along with the ornithischian *Eocursor parvus* (Butler *et al.*, 2007) and possible theropod teeth (Ray & Chinsamy, 2002).

In North Pangea, various Norian faunas of Europe and North America yielded dinosaur records (Fig. 7). These include the rich prosauropod fauna of the German Keuper, where *Efraasia minor* occurs in the Middle Stubensandstein (Löwenstein Formation) of Baden-Württemberg, along with *Procompsognathus triassicus* and other possible theropods (Hungerbühler, 1998; Rauhut & Hungerbühler, 2000; Yates, 2003a). Specimens/species attributed to *Plateosaurus* are much more widespread both geographically and stratigraphically (Yates, 2003c; Moser, 2003; Weishampel *et al.*, 2004),

also occurring in the overlying Knollenmergel (Trossingen Formation, and related stratigraphic units) of Baden-Württemberg, Bavaria, Lower Saxony, and Saxony-Anhalt, as well as in putative coeval faunas from France, Switzerland, and Greenland (Jenkins *et al.*, 1994; Galton & Upchurch, 2004). In addition, the Thuringian Knollenmergel has yielded the “prosauropod” *Ruehleia bedheimensis* and the theropod *Lilienstermus liliensterni* (Rauhut & Hungerbühler, 2000; Galton, 2001). The “lower” fissure-filling deposits of the British Isles (southwest England and south Wales) are also frequently regarded as Norian in age (Fraser, 1994; Benton & Spencer, 1995), although they might well spread into the late Carnian and/or Rhaetian (Benton *et al.*, 2000). Among these, the Pant-y-ffynnon site, in south Wales, is better known for its dinosaur fauna, which includes the basal sauropodomorph *Pantyraco caducus* (Kermack, 1984; Yates, 2003b; Galton, Yates & Kermack, 2007) and a small theropod possibly related to *Coelophysis/Syntarsus* (Rauhut & Hungerbühler, 2000). *P. caducus* was previously assigned to the genus *Thecodontosaurus*, the type species of which (*T. antiquus*) is also known from various other putatively coeval fissure-filling deposits (Benton & Spencer, 1995; Benton *et al.*, 2000). In addition, the Cromhall Quarry, in Avon, has yielded the specimens assigned to *Agnoosphitys cromhallensis*, the dinosaur affinity of which is controversial (Fraser *et al.*, 2002; Langer, 2004; Yates, 2007a). Perhaps, the youngest dinosaur-bearing deposits of the European Triassic are the Rhaetian beds of Normandy (northern France), Somerset-Avon (southwest England), Mid-Glamorgan (south Wales), and Belgium. These include the indeterminate theropod “*Zanclodon*” *cambrensis* (Rauhut & Hungerbühler, 2000; Galton, 2005a), the coelophysoid *Lophostropheus airelensis* (Ezcurra & Cuny, 2007), sauropodomorphs like *Camelotia borealis* (Storrs, 1994; see also Godefroit & Knoll, 2003), and the very unlikely record of a stegosaur (Galton, 2005a; Irmis *et al.*, 2007b). In addition, a possible theropod has been recovered recently from the Rhaetian beds of Lipie Śląskie, Poland (Dzik, Sulej & Niedzwiedzki, 2008). Isolated “dinosaur” teeth, mainly assigned to Ornithischia, have also been reported extensively from Norian-Rhaetian European strata (Weishampel *et al.*, 2004), none of which was recently confirmed (Butler, Porro & Heckert, 2006; Irmis *et al.*, 2007b). The “Eurasian” record of Norian-Raethian dinosaurs (Fig. 7) is completed by the basal sauropodomorphs of the Nam Phong Formation, Thailand, that include *Isanosaurus attavipachi* (Buffetaut *et al.*, 1995, 2000).

The record of Triassic dinosaurs in western USA was recently reviewed by Nesbitt *et al.* (2007; see also Parker *et al.*, 2005; Ezcurra, 2006; Nesbitt & Chatterjee, 2008). No compelling evidence of either sauropodomorphs or ornithischians was found, and only coelophysoids were positively identified, along with putative basal saurischians (herrerasaurs) and basal theropods (Fig. 7). Given that the Santa Rosa Formation ‘theropod’ (Heckert, Lucas & Sullivan, 2000) was considered an indeterminate archosaur (Nesbitt *et al.*, 2007), the oldest dinosaur from western USA, and possibly the oldest known neotheropod so far

is “*Camposaurus arizonensis*”, an indeterminate coelophysoid from the Placerias Quarry (Bluewater Creek Member, base of the Chinle Formation), northern Arizona (Hunt *et al.*, 1998). Younger records of coelophysoids include *Coelophysis bauri* (Colbert, 1989; Colbert *et al.*, 1992; ICZN, 1996; Spielmann *et al.*, 2007), the material described by Cope (1889) and Padian (1986), as well as other specimens (Ezcurra, 2006; Irmis *et al.*, 2007a; Spielmann *et al.*, 2007), along with some of those attributed to *Gojirasaurus quayi* (Carpenter, 1997; Nesbitt *et al.*, 2007). All these come from Norian deposits referred to the Chinle Formation (Petrified Forest Member and “siltstone member”), in central New Mexico and Arizona, and the Bull Canyon Formation (Dockum Group), in east New Mexico and west Texas (Nesbitt *et al.*, 2007). Among non-theropod dinosaurs, whereas *Caseosaurus crosbyensis* (Hunt *et al.*, 1998) was regarded as an indeterminate dinosauriform (Nesbitt *et al.*, 2007), putative herrerasaurs occur in the Petrified Forest Member (*Chindesaurus bryansmalli*) in Arizona, as well as in the Bull Canyon Formation, which also yielded a putative basal theropod (Nesbitt *et al.*, 2007; Nesbitt & Chatterjee, 2008). In terms of age, except for those of the Placerias Quarry, all reliable dinosaur occurrences in the Triassic of western North America are considered younger than the Blue Mesa Member of the Chinle Formation, in Arizona (Nesbitt *et al.*, 2007), which has been radiometrically dated as 219.2 ± 0.7 Myr (Irmis & Mundil, 2008).

In conclusion, although a Middle Triassic (Ladinian) origin of dinosaurs might be hypothesized, the oldest definitive records of the group date from about 230 million years ago. This corresponds to the Carnian stage of the Late Triassic. Radiometric dating of different levels of the Ischigualasto Formation, Argentina (Rogers *et al.*, 1993; Shipman, 2004) suggests that after about 20 million years, i.e. within the latest Triassic, a more diverse (Fig. 8), and specially more abundant and widespread dinosaur fauna was already present (Benton, 1983a; Ezcurra & Novas, 2008), as represented by the Los Colorados Formation and correlated assemblages from other parts of the world (Fig. 7).

(2) The evolutionary tree of early dinosaurs

“Early dinosaurs” are broadly understood here as all putative representatives of the group collected from Ischigualastian strata, as well as younger dinosaurs, the position of which within Ornithischia, Theropoda, or Sauropodomorpha, is yet to be firmly established (Table 2). These include reasonably well-known forms such as *Herrerasaurus ischigualastensis*, *Pisanosaurus mertii*, *Staurikosaurus pricei*, *Eoraptor lunensis*, *Saturnalia tupiniquim*, and *Panphagia protos*, as well as more fragmentary taxa (Huene, 1910, 1942; Chatterjee, 1987; Long & Murry, 1995; Bonaparte *et al.*, 1999; Fraser *et al.*, 2002; Langer, 2004; Nesbitt *et al.*, 2007). *Pisanosaurus* has always been considered an ornithischian dinosaur (Thulborn, 1971; Galton, 1972; Bonaparte, 1976), while *Herrerasaurus* and *Staurikosaurus* were assigned into the base of Saurischia by pre-cladistic works (Reig, 1963; Benedetto, 1973; Galton, 1977), although more specific affinities to either sauropodomorphs (Reig, 1970; Colbert, 1970; Van Heerden, 1978) or theropods

Table 2. Taxonomic assignment of “early dinosaurs”, as recently given by different authors.

Taxon	Proposed affinity
<i>Agnosphyys cromhallensis</i>	Non-dinosaur; Fraser <i>et al.</i> (2002) Dinosauria (<i>partim</i>); <i>nomen dubium</i> ; Langer (2004) Basal Theropoda; Yates (2007a) Basal Sauropodomorpha (Guaibasauridae); Ezcurra (2008)
<i>Aliwalia rex</i>	<i>Eucnemesaurus fortis</i> ; Yates (2007a)
<i>Alwalkeria maleriensis</i>	Basal Saurischia (<i>partim</i>); Remes & Rauhut (2005)
<i>Caseosaurus crosbyensis</i>	Dinosauriformes Nesbitt <i>et al.</i> (2007)
<i>Chindesaurus bryansmalli</i>	Herrerasauridae Irmis <i>et al.</i> (2007a) Basal Theropoda; Yates (2007a) Basal Saurischia (<i>partim</i>); Nesbitt <i>et al.</i> (2007)
<i>Eoraptor lunensis</i>	Basal Theropoda; Sereno (1999); Ezcurra (2006) Basal Saurischia; Langer (2004); Yates (2005)
<i>Guaibasaurus candelariensis</i>	Basal Saurischia (Guaibasauridae); Bonaparte <i>et al.</i> (2007) Basal Theropoda; Yates (2007a), Langer <i>et al.</i> (2007a) Basal Sauropodomorpha; Ezcurra (2008)
Herrerasauridae	Basal Theropoda; Novas (1996); Sereno (1999) Non-dinosaur; Fraser <i>et al.</i> (2002) Basal Saurischia, Langer (2004); Yates (2005); Ezcurra (2006)
<i>Herrerasaurus ischigualastensis</i>	Herrerasauridae Novas (1992b)
<i>Panphagia protos</i>	Sauropodomorpha Martinez & Alcober (2009)
<i>Pisanosaurus mertii</i>	Ornithischia Sereno (1999); Butler <i>et al.</i> (2007)
<i>Saltopus elginensis</i>	Dinosauriformes Rauhut & Hungerbühler (2000); Langer (2004)
<i>Saturnalia tupiniquim</i>	Stem-Sauropodomorpha; Langer & Benton (2006) Basal Saurischia (Guaibasauridae); Bonaparte <i>et al.</i> (2007)
<i>Sacisaurus agudoensis</i>	<i>cf.</i> Ornithischia; Ferigolo & Langer (2007) Non-dinosaur; Brusatte <i>et al.</i> (2008a)
<i>Silesaurus opolensis</i>	<i>cf.</i> Ornithischia; Ferigolo & Langer (2007) Non-dinosaur; Langer & Benton (2006)
<i>Spondylosoma absconditum</i>	Non-dinosaur; Galton (2000) <i>cf.</i> Herrerasauridae; Langer (2004)
<i>Staurikosaurus pricei</i>	Herrerasauridae Novas (1992b)
<i>Teyuwasu barberenai</i>	Dinosauria (<i>partim</i>); <i>nomen dubium</i> ; Langer (2004)

(Galton, 1973; Bakker & Galton, 1974) were also claimed. On the contrary, early cladistic studies (Fig. 9) depicted *Staurikosaurus* and *Herrerasaurus* basal to the Ornithischia+Saurischia dichotomy (Gauthier, 1986; Brinkman & Sues, 1987; Benton, 1990; Novas, 1992b), thus outside Dinosauria on its emerging monophyletic understanding (Gauthier *et al.*, 1989), whereas contemporaneous studies never questioned the ornithischian affinity of *Pisanosaurus* (Novas, 1989; Sereno, 1991b). These investigations set the basis to future research on basal dinosaur phylogeny, accepting the group as a monophyletic entity solely composed of Ornithischia and Saurischia, the latter including equally monophyletic Sauropodomorpha and Theropoda. Besides, Novas (1992b) placed *Herrerasaurus* and *Staurikosaurus* into a monophyletic Herrerasauridae, a hypothesis almost never contested since.

During the early nineties, new discoveries from the Ischigualasto Formation, including almost complete skeletons of *Herrerasaurus ischigualastensis* (Sereno & Novas, 1992, 1993; Novas, 1993, Sereno, 1993) and the first record of *Eoraptor lunensis* (Sereno *et al.*, 1993), were announced along with a new hypothesis of basal dinosaur relationships. This was advocated based on independent numerical analyses performed by Sereno *et al.* (1993; see also Sereno, 1999)

and Novas (1996) that found nearly identical results (Fig. 9). The Herrerasauridae was depicted as the sister-taxon of Neotheropoda, while *Eoraptor* was considered the basal-most theropod. Apomorphic traits supporting the theropod affinity of *Eoraptor* and Herrerasauridae were given as including caudally curved tooth crowns not expanded at the base, a broad axial intercentrum, elongated humerus and manus, deep extensor pits on the distal end of metacarpals I–III, and narrow metacarpal IV, as well as by typical predatory adaptations shared by herrerasaurids and theropods (Fig. 10), e.g. intramandibular joint, craniomandibular joint at about the same level as the tooth rows, and manual digits II and III with elongated penultimate phalanges and strongly curved unguals with enlarged flexor tubercles (Langer & Benton, 2006; Sereno, 2007b; but see Butler *et al.*, 2007). More recently, *Chindesaurus bryansmalli* was described as a herrerasaurid (Long & Murry, 1995; Novas, 1997a; Sereno, 1999), a phylogenetic hypothesis accepted by most authors up to the late nineties. However, the suggestions that *Chindesaurus* forms a clade with either *Herrerasaurus* (Novas, 1997a) or *Staurikosaurus* (Sereno, 1999) were not supported by recent

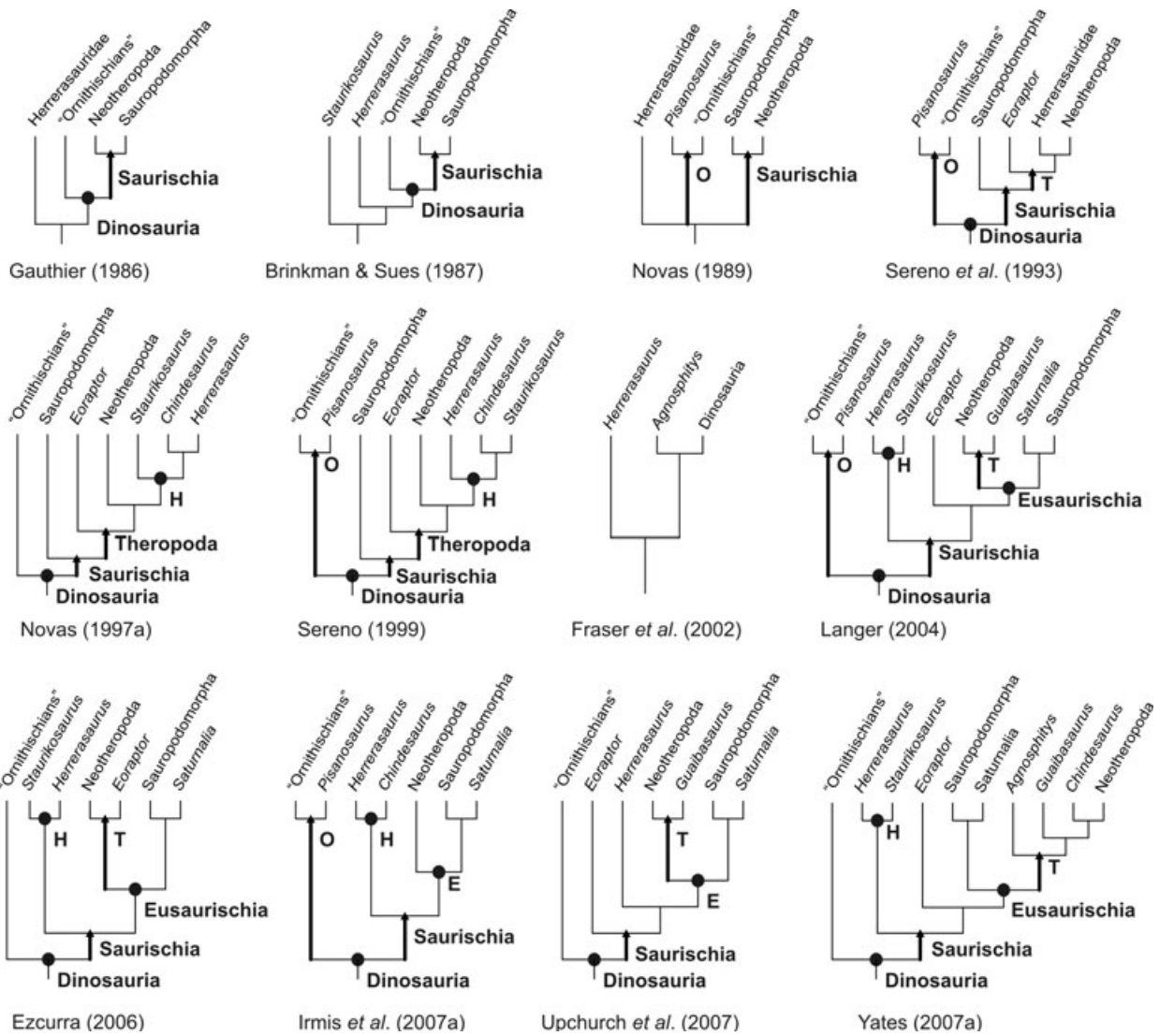


Fig. 9. Main alternative phylogenetic hypotheses depicting the interrelationships of “early dinosaurs”, modified from the cited sources. Arrows indicate stem-based taxa and black circles node-based taxa. Names applied as in Table 1, not as in the referred publications. Abbreviations as follows: O, Ornithischia; T, Theropoda; H, Herrerasauridae; E, Eusaurischia.

studies (Langer, 2004; Nesbitt *et al.* 2007; Bittencourt & Kellner, 2009), which place the North American taxon basal to the more “typical” herrerasaurids.

Around the turning of the 20th Century, the description of new basal dinosauriforms such as *Saturnalia tupiniquim* and *Agnosphytis cromhallensis*, led to the proposal of novel phylogenetic hypotheses of basal dinosaur relationships (Fig. 9). Langer *et al.* (1999) described *Saturnalia* as the basal-most sauropodomorph, within alternative phylogenetic arrangements depicting *Herrerasaurus* and *Staurikosaurus* as either saurischians basal to the Theropoda+Sauropodomorpha dichotomy, or as a monophyletic sister taxon to Dinosauria. Fraser *et al.* (2002) described *Agnosphytis* as the sister taxon to Dinosauria, favouring a position of *Herrerasaurus* outside that clade, but these results were not replicated by any quantitative analyses performed since then.

In a comprehensive analysis of basal theropod phylogeny, Rauhut (2003) recovered *Eoraptor lunensis* and herrerasaurids as basal theropods, as first proposed by Sereno & Novas (1992). However, most subsequent studies, including some focused on basal theropods (Yates, 2005; Smith *et al.*, 2007), contradicted that hypothesis of basal dinosaur relationships. Yates (2003b) conducted a cladistic study of basal sauropodomorphs, and found a new phylogenetic arrangement among saurischians where herrerasaurids were considered the sister group of all other components of the clade, termed Eusaurischia by Padian *et al.* (1999). Yates (2003b) also found *Saturnalia tupiniquim* as the most basal sauropodomorph, as previously claimed by Langer *et al.* (1999) and mainly accepted since. New comprehensive analyses by Langer (2004; see also Langer & Benton, 2006) independently came to similar results (Fig. 9). These corroborated

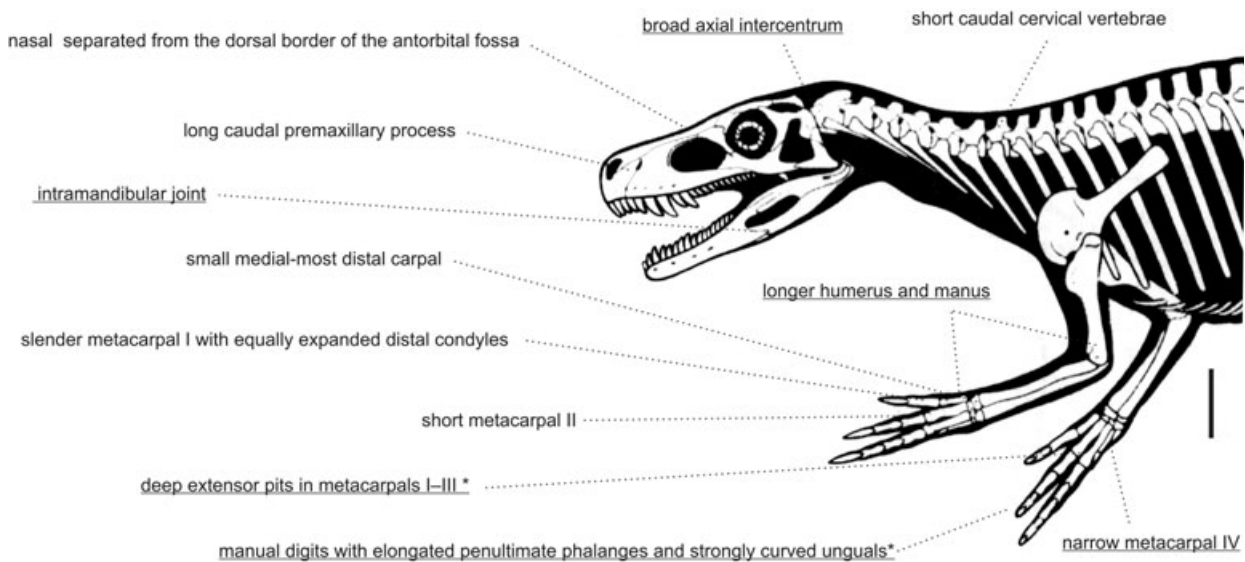


Fig. 10. Selected anatomical features of *Herrerasaurus ischigualastensis*, depicting a combination of apomorphic traits shared with Neotheropoda (underlined) and plesiomorphic states relative to the Eusaurischia condition (non underlined). Asterisks indicate traits also seen in basal ornithischians according to Butler *et al.* (2007). Skeletal reconstruction based on Sereno (1993). Scale bar = 10 cm.

the position of herrerasaurids as basal saurischians, adding *Eoraptor lunensis* as the sister taxon to Eusaurischia, and *Guaibasaurus candelariensis* as a basal theropod. Indeed, several eusaurischian apomorphies are lacking in herrerasaurids (Fig. 10) and/or *Eoraptor*, as exemplified by a short caudoventral premaxillary process, a nasal that possesses a caudolateral process and forms part of the dorsal border of the antorbital fossa, caudal cervical vertebrae longer than cranial trunk vertebrae, a large medial-most distal carpal, a stout metacarpal I with lateral distal condyle distally expanded, a long metacarpal II relative to metacarpal III, and an expanded distal end of the ischium (Langer & Benton, 2006).

Subsequent studies broadly agree with the above scenario (Irmis *et al.*, 2007a; Nesbitt & Chatterjee, 2008; Martinez & Alcober, 2009), but differ in minor details (Fig. 9). In a study focused on the non-dinosaurian affinity of the putative coelophysoid *Eucoelophysus baldwini* (Sullivan & Lucas, 1999), Ezcurra (2006) placed herrerasaurids as non-theropod saurischians, but *Eoraptor* as a basal theropod, sister taxon of Neotheropoda. In a study of basal sauropodomorph phylogeny, Upchurch *et al.* (2007) placed both Herrerasauridae and *Eoraptor* as non-theropod saurischians, but considered the former group as the sister taxon of Eusaurischia. Yates (2007a, b) expanded his previous studies, adding *Agnosphitys cromhallensis*, *Guaibasaurus candelariensis*, *Chindesaurus bryansmalli*, and *Eoraptor lunensis* to an analysis of basal sauropodomorphs. The former three taxa were found as basal theropods, with *Guaibasaurus* as the sister taxon of a clade including *Chindesaurus* plus Neotheropoda, and *Agnosphitys* as the most basal theropod. Yet, the theropod affinity of *Chindesaurus* was challenged by Irmis *et al.* (2007a), who supported its more traditional relation to *Herrerasaurus*, both lying basal to the sauropodomorph/theropod dichotomy, as also suggested

by Langer (2004) and Nesbitt *et al.* (2009). More recently, the diversity of basal members of the sauropodomorph lineage was increased by the discovery of *Panphagia protos* (Martinez & Alcober, 2009) and the undescribed sister-taxon of *Saturnalia tupiniquim* (PVSJ 845; Ezcurra, 2008), both from the Ischigualasto Formation, of Argentina. Further, Ezcurra (2008) also included *Agnosphitys* and *Guaibasaurus* in that dinosaur lineage. Indeed, Bonaparte *et al.* (2007) has already proposed a close relation between *Guaibasaurus* and *Saturnalia*, forming Guaibasauridae at the base of Saurischia. However, Langer (2004) suggested the theropod, possibly coelophysoid, affinity of *Guaibasaurus* (see also Upchurch *et al.*, 2007; Langer, Bittencourt & Schultz, 2007a; Bittencourt, 2008).

Several putative basal dinosaurs were never included in numerical phylogenetic analyses, and their affinities are open to scrutiny. Langer (2004) offered a comprehensive summary of these records, but this has to be updated with new information available since. Remes & Rauhut (2005) reassessed the affinity of *Alwalkeria malleriensis*, first described as a basal theropod (Chatterjee, 1987; Norman, 1990), but later regarded as a dinosaur of uncertain (Novas, 1989, 1997a) or eusaurischian (Langer, 2004) affinities. Those authors found that the holotype represents a chimera, including pseudosuchian and possible prolacertiform material, but also saurischian specimens. *Aliwalialia rex* Galton, 1985b, on the other hand, previously regarded as a herrerasaurid (Galton, 1985b; Paul, 1988) or a dinosaur of dubious affinities (Sues, 1990; Galton & Van Heerden, 1998; Langer, 2004) was shown to represent a junior synonym of *Eucnemesaurus fortis*, therefore a basal sauropodomorph (Yates, 2007a). Nesbitt *et al.* (2007) recently reviewed the status of the isolated ilium previously assigned to *Chindesaurus bryansmalli* (Long & Murry, 1995), which constitutes the holotype of *Caseosaurus*

crobyensis (Hunt *et al.*, 1998) and considered the material undiagnostic above Dinosauriformes. Other putative early dinosaurs such as *Saltopus elginensis*, *Spondylosoma absconditum*, and *Teyuwasu barberenai*, have not been studied recently. Indeed, their uncertain affinities as proposed by Langer (2004) are provisionally accepted here (Table 2).

In conclusion, recent cladistic analyses of basal dinosaur relationships agree in various aspects, which are accepted by most of the authors mentioned above: (1) dinosaurs represent a monophyletic group exclusive of forms such as *Lagerpeton chanarensis*, *Marasuchus lilloensis*, *Pseudolagosuchus major*, and *Silesaurus opolenis*; (2) Dinosauria is composed of two main lineages, Saurischia and Ornithischia; (3) *Pisanosaurus mertii* is a basal ornithischian; (4) *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* belong into a monophyletic Herrerasauridae; (5) *Eoraptor lunensis*, *Guaibasaurus candelariensis*, and herrerasaurids are saurischians; (6) Saurischia includes two main groups, Theropoda and Sauropodomorpha; and (7) *Saturnalia tupiniquim* and *Panphagia protos* are basal members of the sauropodomorph lineage.

On the contrary, several aspects of basal dinosaur phylogeny remain controversial. These include the position of herrerasaurids, *Eoraptor lunensis*, and *Guaibasaurus candelariensis* as basal theropods or basal saurischians, and the affinity and/or validity of various more fragmentary taxa such as *Agnosphitys cromhallensis*, *Alwalkeria malleriensis*, *Chindesaurus bryansmalli*, *Saltopus elginensis*, *Spondylosoma absconditum*, and *Teyuwasu barberenai*. Other equally incomplete forms have been more thoughtfully studied, but while the affinities of *Aliwalia rex* are better understood, *Caseosaurus crobyensis* continues to be problematic. In a reappraisal of the methodologies employed in recent analyses of basal dinosaur relationships, Sereno (2007b) highlighted that the lack of consensus regarding the same phylogenetic problematics is mainly due to differences in character/character-state choice and codification among authors. Indeed, it seems that more comprehensive studies, discussing these methodological issues, are necessary to achieve a better understanding of the phylogenetic relationships of basal dinosaurs. This is, in turn, essential to recognize the patterns leading to their early radiation and success during post-Triassic times.

(3) Geographical distribution of basal dinosaurs

The earliest records of dinosauromorphs and dinosauriforms based on body fossils, and also most of the trustworthy records of the earliest dinosaurs come from southern South America, especially Argentina (e.g. Bonaparte, 1975; Sereno & Novas, 1992; Sereno & Arcucci, 1993, 1994; Novas, 1992b, 1996; Langer *et al.*, 1999; Galton, 2000; Rogers *et al.*, 2001; Langer, 2004; Ferigolo & Langer, 2007; Martinez & Alcober, 2009). However, relatively few sites representative of terrestrial ecosystems of that time are known (Hammer, Collinson & Ryan, 1990; Lucas, 1998; Rogers *et al.*, 2001; Weishampel *et al.*, 2004) and no biogeographic hypothesis concerning the area of origin of the dinosaurian clades can be robustly tested (Parker *et al.*, 2005). Nonetheless, whereas almost all south-Pangean tetrapod-bearing deposits

of Carnian age (Langer, 2005b) bear undisputed, even if inconspicuous dinosaur records, the north-Pangean scenario is rather different, with no dinosaur positively identified in coeval tetrapod assemblages. Accordingly, an admittedly tentative scenario can be drawn, hinting at a southern Pangean origin of dinosaurs.

Obviously, any biogeographical picture of dinosaur origins has to be backed up by the current phylogenetic hypotheses depicting the relationships of the basal members of the group and its sister taxa. Accordingly, recent finds of basal dinosauromorphs in Europe (Fraser *et al.*, 2002; Dzik, 2003) and North America (Ezcurra, 2006; Irmis *et al.*, 2007a; Nesbitt & Chatterjee, 2008) came with new phylogenetic proposals, and indicate that those animals had a broader geographical and chronostratigraphic distribution than previously thought. Hypotheses that support an inclusive clade of basal dinosauriformes (i.e. Silesauridae) as the sister taxon to Dinosauria (Nesbitt *et al.*, 2007; Brusatte *et al.*, 2008a) face the problem of a Ladinian ghost-lineage of “stem-dinosaurs” (Fig. 3A), but are roughly in agreement with the southern origin scenario. *Spondylosoma absconditum*, from south Brazil, could fill that temporal gap, but its atypical morphology and uncertain affinity (Langer, 2004) prevent further scrutiny. The alternative pectinate topology (Ezcurra, 2006) overcomes the ghost-lineage problem, but suggests that north Pangean taxa represent the immediate outgroups to Dinosauria (Fig. 3A), jeopardizing the “out of south Pangea” model of dinosauromorph/dinosauriform/dinosaur radiation. The record of Ladinian-Carnian “dinosauriform/dinosaur” footprints in various parts of the world (Melchor & De Valais, 2006; Thulborn, 2006; Marsicano *et al.*, 2007) also hints at a broader distribution of these basal forms.

Late Triassic dinosaur records as a whole include body fossils from Europe, North and South America, India, Africa, and East Asia (Weishampel *et al.*, 2004), as well as putative tracks from Australia (Thulborn, 2000, 2006). This is congruent with the geographic configuration of the time (Fig. 7), when the Pangea Supercontinent and the lack of extensive oceanic barriers would favour biotic expansion (Shubin & Sues, 1991). Indeed, several non-dinosaur tetrapod clades also achieved a widespread distribution during the Late Triassic and Early Jurassic (Benton, 1993), but it is important to note that no dinosaur clade had a truly global distribution during Late Triassic times, especially in the Carnian Stage (Nesbitt *et al.*, 2007), even if only the areas with tetrapod-bearing sites are considered. The biogeographic patterns of early dinosaur radiation are, in fact, better analyzed having the proposed subdivisions of the group as a template.

The osteological record of Triassic ornithischians (Fig. 7) is restricted to three Norian forms: the South African *Eocursor parvus* (Butler *et al.*, 2007), an unnamed heterodontosaurid from Patagonia (Baez & Marsicano, 2001), and *Pisanosaurus mertii*, from northwestern Argentina (Casamiquela, 1967; Bonaparte, 1976), the latter of which may come from significantly older deposits. Various other remains, mostly isolated

teeth, from either Europe (Godefroit & Cuny, 1997; Godefroit & Knoll, 2003) or North America (Chatterjee, 1984; Hunt, 1989; Hunt & Lucas, 1994; Heckert, 2002, 2004) had been assigned to the group. Along with footprints from North America, Europe, and southern Africa, these may hint at a broader Norian-Rhaetian geographical distribution of ornithischians. Yet, neither the isolated teeth nor the footprints can be unequivocally assigned to the group (Parker *et al.*, 2005; Butler *et al.*, 2006; Irmis *et al.*, 2007b). Accordingly, as discussed by Irmis *et al.* (2007b), ornithischians do not seem to have been very diverse or abundant through the Triassic, and certain hypotheses of relationship (Sereno, 1991b, 1999; Xu *et al.*, 2006) imply large gaps in their fossil record. On the contrary, the usually accepted basal position of *Pisanosaurus* is in accordance with its older age, as is the possible basal position of heterodontosaurids (Butler, Upchurch & Norman, 2008) and *Eocursor* (Butler *et al.*, 2007) in relation to other ornithischians. The suggested heterodontosaurid affinity of *Pisanosaurus* (Bonaparte, 1976; Galton, 1986; Crompton & Attridge, 1986; Butler *et al.*, 2008) implies a minimal ghost-lineage for Genasauria *sensu* Butler *et al.* (2008), but is also in general agreement with a south Pangean origin of ornithischians. Indeed, Laurasian occurrences of the group can not be confirmed before the Early Jurassic (Irmis *et al.*, 2007b), when basal thyreophorans occur in North America, Europe, and Asia (Norman, Witmer & Weishampel, 2004a; Irmis & Knoll, 2008). A different picture emerges with the tentative placement of *Sacisaurus agudoensis* and especially *Silesaurus opolensis* as the most basal ornithischians (Ferigolo & Langer, 2007), but this hypothesis is still to be backed up by numerical phylogenetic analyses. In any case, the poorly documented early history of ornithischians prevents any accurate biogeographic approach. According to Irmis *et al.* (2007b), possible explanations for their rarity in Late Triassic rocks (e.g. sample bias, differential environmental occupation, systematic imprecision) are inconclusive.

Triassic saurischians have a much broader geographic distribution (Rauhut & Hungerbühler, 2000; Langer, 2004; Nesbitt *et al.*, 2007). Indeed, basal members of the group, and putative members of the theropod and sauropodomorph lineages occur as body fossils in various Carnian beds known from south Pangea (South America, southern Africa, and India) as well as in Norian-Rhaetian deposits of all continents except Australia and Antarctica (Fig. 7). However, most records of “basal saurischians” are, in fact, records of saurischians of uncertain affinities, and only *Eoraptor lunensis* and herrerasaurs have been, under certain phylogenetic hypotheses, positively placed basal to Eusaurischia. Well-known herrerasaurids are restricted to the South American Carnian (Langer, 2004; Bittencourt & Kellner, 2009), including *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei*. The clade remains unidentified in the relatively well-known post-Ischigualastian deposits of that continent, hinting at its restricted stratigraphic distribution. Yet, herrerasaurids have been identified in Norian beds of western USA (Long & Murry, 1995; Hunt *et al.*, 1998; Irmis *et al.*, 2007a; Nesbitt & Chatterjee, 2008), which would

represent the younger records of the group. In addition, given that the affinity of *Chindesaurus bryansmalli* to either of the South American herrerasaurids has been questioned (Langer, 2004; Bittencourt & Kellner, 2009), that North American herrerasaur would most probably represent the remnant of a lineage parallel to the typical members of the group, and not a more derived outcome of that radiation. On the contrary, the latter seems to be the case for the specimen described by Nesbitt & Chatterjee (2008), which bears herrerasaurid apomorphies.

If herrerasaurids and/or *Eoraptor lunensis* are treated as theropods, the group would fit the “out of South Pangea” radiation pattern, with a well-known record of basal forms in the Carnian of South America. In the alternative arrangement (Langer, 2004), the oldest theropod, i.e. the coelophysoid “*Camposaurus arizonensis*” (Nesbitt *et al.*, 2007), would not only come from North America, but also from Norian-age deposits. If not filled by herrerasaurids and/or *Eoraptor* this stratigraphic gap in theropod distribution is unexpected, given the occurrence of basal members of the sauropodomorph lineage in the Carnian (Langer *et al.*, 1999; Ezcurra, 2008; Martinez & Alcober, 2009), and the abundance of both saurischian groups later in the Triassic (Tykoski & Rowe, 2004; Galton & Upchurch, 2004). Indeed, mainly represented by coelophysoids (but see Nesbitt & Chatterjee, 2008), theropods become abundant during Norian-Rhaetian times (Fig. 7), with body fossils recorded in North America (Jenkins *et al.*, 1994; Nesbitt *et al.*, 2007), Europe (Rauhut & Hungerbühler, 2000; Ezcurra & Cuny, 2007), Argentina (Arcucci & Coria, 2003; Ezcurra & Novas, 2007a), India (F. E. Novas, personal observations), and perhaps South Africa (Ray & Chimsamy, 2002). The possible theropod affinity (Yates, 2007a, b) of controversial Norian taxa from Europe (*Agnosphitys cromhallensis*), North America (*Chindesaurus bryansmalli*), Brazil (*Guaibasaurus candelariensis*), and India (aff. *Guaibasaurus*) does not significantly change this distribution pattern. In comparison to the more abundant sauropodomorphs, osteological records of theropods are lacking in Norian-Rhaetian deposits from southwest Asia (Nam Phong Formation), suggesting that Pangean far-east was first reached by the herbivorous/omnivorous branch of Saurischia. Yet, this fossil assemblage is imperfectly known (Buffetaut *et al.*, 2000), and the absence of theropods might simply represent a circumstantial sample bias. The scarcity of theropod body fossils of Late Triassic age in southern Africa is somewhat filled by ichnological evidence (Ellenberger, 1974; Olsen & Galton, 1984; Raath *et al.*, 1990), and also inferred from their well-known Early Jurassic record (Raath, 1969; Bristowe & Raath, 2004; Yates, 2005). Possible theropod footprints are also known from Norian-Rhaetian deposits of other parts of the world (Gatesy *et al.*, 1999; Haubold & Klein, 2002; Demathieu & Demathieu, 2004; Thulborn, 2006), but several of them have been questioned (King & Benton, 1996; Marsicano *et al.*, 2007; Lucas, 2007; Nesbitt *et al.*, 2007), given their possible assignment to non-dinosaurian dinosauromorphs. In any case, the overall record leads to a scenario of low abundance of Carnian theropods, followed

by a significant Norian radiation, when the group occupied most parts of Pangea.

Sauropodomorphs are surely the most abundant dinosaur group of Triassic times. Basal members of the lineage, i.e. *Saturnalia tupiniquim* and its allies, come from Ischigualastian beds of South America (Langer *et al.*, 1999; Da Rosa *et al.*, 2006; Ezcurra, 2008; Martinez & Alcober, 2009), and possibly southern Africa (Raath, 1996). This record could be enhanced by the “prosauropods” of the Lower Maleri Formation referred to by Kutty & Sengupta (1989), but these have not been mentioned in more recent studies (Kutty *et al.*, 2007), which refer the Upper Maleri “prosauropods” to aff. *Guaibasaurus*. Assuming the above identifications as correct, a southern radiation of “*Saturnalia*-like” forms may have preceded the Norian diversification of true sauropodomorphs. The basal-most members of that group, *Pantyracosaurus caducus* and *Thecodontosaurus antiquus* (Yates, 2007a, b), come from fissure-filling deposits of England and Wales of alleged Carnian age, but this occurrence better fits the much broader distribution of later sauropodomorphs (Fig. 7). Indeed, the Norian-Rhaetian record of the group excludes only Antarctica, Australia, and continental North America (Vickers-Rich *et al.*, 1999; Galton & Upchurch, 2004; Nesbitt *et al.*, 2007). The former two areas, however, lack well-sampled tetrapod faunas of that age, and the absence of sauropodomorphs could represent a sampling bias. Indeed, the group can be said to have had a nearly global Norian distribution, but this was not uniform through time and space. Most of the basal, non-Plateosauria (*sensu* Yates, 2007a) taxa were recorded in Europe (Yates, 2003b,c; Galton & Upchurch, 2004; Galton, 2007), while more derived forms are widespread (Yates, 2007a, b; Galton & Upchurch, 2004; Leal *et al.*, 2004; Pol & Powell, 2007a). In this context, the lack of sauropodomorphs in the Norian of continental North America (Nesbitt *et al.*, 2007), though not in Greenland (Jenkins *et al.*, 1994), is intriguing. Indeed, this seems to represent a true biogeographic pattern, given the abundance of well-sampled tetrapod-bearing deposits of that age in the region. The occurrence of the latest basal dinosauriforms (Irmis *et al.*, 2007a) and probable herrerasaurs (Nesbitt & Chatterjee, 2008) in those faunas may also result from the causes that drove this pattern. As for basal sauropods, previous studies suggested that their distribution was initially restricted to southeastern Asia, expanding throughout Pangea by the Late Triassic-Early Jurassic (Gillette, 2003). Yet, recent phylogenetic hypotheses (Yates, 2007a, b; Smith & Pol, 2007; Upchurch *et al.*, 2007) have positioned south Pangean forms like *Antetonitrus ingenipes*, *Blikanasaurus cromptoni*, *Lessemisaurus sauropoides*, and *Melanorosaurus readi*, close to, or at the base of Sauropoda. This suggests a wider distribution of early members of the group, a pattern that seems to fit better the footprint record (Wilson, 2005). In any case, most Triassic ichnological evidence of sauropodomorphs was considered poorly substantiated (Lockley *et al.*, 1994; Rainforth, 2002, 2003).

IV. ECOLOGY OF THE DINOSAUR RADIATION

(1) The Triassic scene

During the Triassic, following the Late Permian maximum coalescence of Pangea, most continental areas remained forming a single landmass (Scotese, 2002; Golonka, 2002; Blakey, 2006). Towards the end of the period, major rift zones started to develop, especially along the Atlantic margins of North America and North Africa, accounting for the separation between Laurasia and Gondwana (LeTourneau & Olsen, 2003; Golonka, 2007). Besides, the climate experienced a trend towards higher instability compared to Paleozoic settings (Holser & Magaritz, 1987; Kent & Muttoni, 2003). The Triassic palaeoclimate was reviewed in various landmark publications (Tucker & Benton, 1982; Hallam, 1985; Parrish, 1993; Crowley, 1994; Golonka & Ford, 2000), which suggest a warm period, when polar ice caps were absent (Frakes, Francis & Syktus, 1992). Further, a latitudinal zonation seems to have been present, with an arid equatorial/tropical belt, a seasonally humid temperate zone, and mainly humid higher latitudes (Hallam, 1985; but see Fraser, 2006). In the second half of the period, a highly seasonal (monsoonal) humid climate prevailed over various parts of the supercontinent (Parrish, 1993). Triassic biotas reflect the transitional nature of the time interval (Anderson & Anderson, 1993; Fraser, 2006), particularly when terrestrial tetrapod faunas are considered. The period starts with the impoverished remaining diversity of the end-Permian mass extinction (Benton, 2003), ending up with an essentially modern fauna, that includes the first representatives of the chelonian, lepidosaur, crocodylian, avian (in the form of dinosaurs), and mammal lineages.

Part of the Triassic tetrapod diversity was inherited from the Permian, when dicynodonts and limnarchian temnospondyls reached their climax (King, 1988; Milner, 1993). These groups experienced a later diversification within the Triassic, along with the first radiation of lineages of latest Permian origin, like procolophonoids (Spencer & Benton, 2000), “protorosaurs” (Dilkes, 1998), archosaurs (Gower & Sennikov, 2000), and cynodonts (Botha, Abdala & Smith, 2007). These tetrapod groups diversified through the Early Triassic, composing the core of the Middle Triassic predinosaur terrestrial palaeocommunities; the “Kannemeyroid epoch” of Ochev & Shishkin (1989). An example of such faunas is known from the Chañares Formation, Argentina (Bonaparte, 1982; Rogers *et al.*, 2001) that is dominated by herbivorous cynodonts (*Massetognathus*) and dicynodonts (*Dinodontosaurus*), along with predatory cynodonts (*Chiniquodon*) and archosaurs (proterochampsids and “rauisuchians”). Nearly coeval faunas were recorded in Brazil, Russia, and Southern Africa, further including a variety of limnarchians, procolophonoids, and rhynchosaurs (Ochev & Shishkin, 1989; Lucas, 1998; Abdala & Ribeiro, 2003). In addition, as previously discussed, the Chañares fauna also includes the highest diversity of basal dinosauriforms (Romer, 1971, 1972a, b; Bonaparte, 1975; Sereno & Arcucci, 1993, 1994).

The oldest known dinosaurs are recorded in a particular faunal context, in which rhynchosaurs, especially the genus *Hyperodapedon*, became dominant primary consumers of various terrestrial faunas worldwide (Romer, 1962; Benton, 1983b). These were recorded in the *Hyperodapedon* Assemblage-Zone of the Santa Maria Formation (Fig. 11A), the lower part of the Ischigualasto Formation, the Lossiemouth Sandstone Formation, and the Lower Maleri Formation (Langer, 2005b). Apart from rhynchosaurs and the first dinosaurs, these faunas collectively encompass limnarchian temnospondyls (Marsicano, 1999; Sengupta, 2003), various archosaurs such as proterochampsids (Price, 1946; Sill, 1967), “rauisuchians” (Huene, 1942; Alcober, 2000), poposauroids (Alcober & Parrish, 1997), aetosaurs (Heckert & Lucas, 2002), phytosaurs (Chatterjee, 1978), crocodylomorphs (Bonaparte, 1982; Ezcurra, Lecuona & Irmis, 2008), and ornithosuchids (Benton & Walker, 1985), carnivorous (Martinez, May & Forster, 1996; Bonaparte & Barberena, 2001; Abadala & Gianinni, 2002) and herbivorous (Bonaparte, 1962; Chatterjee, 1982; Hopson, 1985) cynodonts; as well as dicynodonts (Cox, 1965). A similar faunal content was recorded in putatively coeval faunas that lack rhynchosaurs and dinosaurs such as that of Krasiejów, Poland (Dzik & Sulej, 2007), and the base of the Irohalene Member (Timesgadiouine Formation, Argana Basin), Morocco (Jalil, 1996). In fact, apart from the appearance of some archosaur groups, and the dominance of rhynchosaurs, the oldest dinosaur-bearing terrestrial faunas are not significantly different from those of Middle Triassic age.

Dinosaurs remain inconspicuous in younger faunas of Norian age, as seen at the base of the Los Colorados Formation (Caselli, Marsicano & Arcucci, 2001) and the Caturrita Formation (Langer *et al.*, 2007b), in South America, and in some possibly coeval North American fossil assemblages (Langer, 2005b), i.e. Sanfordian faunas of the Newark Supergroup; Camp Springs Member, Dockum Group; and Popo Agie Formation (Huber, Lucas & Hunt, 1993; Lucas, 1998). These faunas include metoposaurids, procolophonids, sphenodontians, *Hyperodapedon*, dicynodonts, traversodontid and mammal-like cynodonts, as well as various pseudosuchians (aetosaurs, phytosaurs, poposauroids, and possible “rauisuchids”). Later Norian deposits include a greater number of dinosaur records, within a slightly dissimilar faunal context; the “Prosauropod” Empire of Benton (1983a). As recorded from the top of the Los Colorados Formation, the fauna of La Esquina (Bonaparte, 1982; Caselli *et al.*, 2001) includes some of the oldest turtles, along with crocodyliforms, “remaining” pseudosuchian lineages (aetosaurs, ornithosuchids, “rauisuchians”), and mammal-like cynodonts (Fig. 11B). Putatively coeval faunas of other parts of the world, especially South Africa (Anderson, Anderson & Cruickshank, 1998), Europe (Benton, 1994a), and North America (Long & Murry, 1995), further include various temnospondyls and phytosaurs, inconspicuous dicynodonts (Dzik *et al.*, 2008), the latest traversodontids (Hopson, 1984), as well as the first mammals (Lucas & Luo, 1993).

(2) Lucky break?

Palaeoecological aspects of the early radiation of dinosaurs and its correlation to Late Triassic extinctions and corresponding biotic/environmental changes have been addressed by various classical and more recent studies (Colbert, 1958; Benton, 1983a; Charig, 1984; Olsen *et al.*, 2002; Tanner, Lucas & Chapman, 2004; Brusatte *et al.*, 2008a, b). Focus has been given to two inferred mass extinction events, at the Carnian-Norian and Triassic-Jurassic boundaries, and two alternative scenarios for the rise of the dinosaurs, the so-called “competitive” and “opportunistic” models. Studies from the mid-late 20th Century postulated that the replacement of various tetrapod groups, notably pseudosuchians and therapsids, by dinosaurs was a long-term affair driven by competition during the Late Triassic (Cox, 1967; Charig, 1980; Bonaparte, 1982). Its outcome would have been the dominance of dinosaurs over terrestrial ecosystems from Norian/Jurassic onwards, thanks to their “superiority” relative to the outcompeted contemporary tetrapods, pushed to extinction. Usually, the improved locomotory capability of the fully erect, bipedal early dinosaurs was considered the most notable advantage of the group (Charig, 1972, 1984), but their inferred advanced physiology has also been mentioned (Bakker, 1971). From the 1980s onwards, Benton (1983a, 1984, 1991) advocated an alternative model, based on which the Triassic radiation of dinosaurs was faster, opportunistically occupying adaptive zones emptied by the extinction of rhynchosaurs, therapsids (dicynodonts and some cynodonts), and pseudosuchians (phytosaurs, aetosaurs, rauisuchians). More recently, Brusatte *et al.* (2008a) demonstrated that Norian pseudosuchians occupied more morphospace and showed similar rates of character evolution compared to dinosauromorphs/dinosaurs. Indeed, this dismisses the classical “competitive” model, based on which those archosaurs were gradually replaced by dinosaurs. Yet, the scenario seems to be more complex in terms of patterns and timing of biotic turnovers, as discussed below.

Of the two proposed Late Triassic extinction events (Benton, 1986a, 1997), the end-Triassic is much better documented in the literature than the end-Carnian, which is often contested as minor or non-existent (Olsen & Sues, 1986; Olsen, Shubin & Anders, 1987; Hallam, 1990; Fraser & Sues, 1994; Hunt *et al.*, 2002). Classical studies reveal the final demise of conodonts and a severe reduction in the diversity of sponges, scleractinian corals, molluscs (ammonoids, gastropods, and bivalves), and brachiopods in the sea (Hallam, 1981; Raup & Sepkoski, 1982; Sepkoski, 1982, 1990), along with extinctions of insects (Benton, 1989) and tetrapods on land (Olsen & Sues, 1986; Benton, 1994b). Causes proposed for the end-Triassic mass extinction range from sea level change (Hallam, 1990), to the impact of one or more extraterrestrial bolides (Olsen *et al.*, 2002) and the establishment of the Central Atlantic Magmatic Province (Marzoli *et al.*, 1999). The latter two might have led to an increase in the levels of atmospheric CO₂, and so “greenhouse” warming (McElwain, Beerling & Woodward,

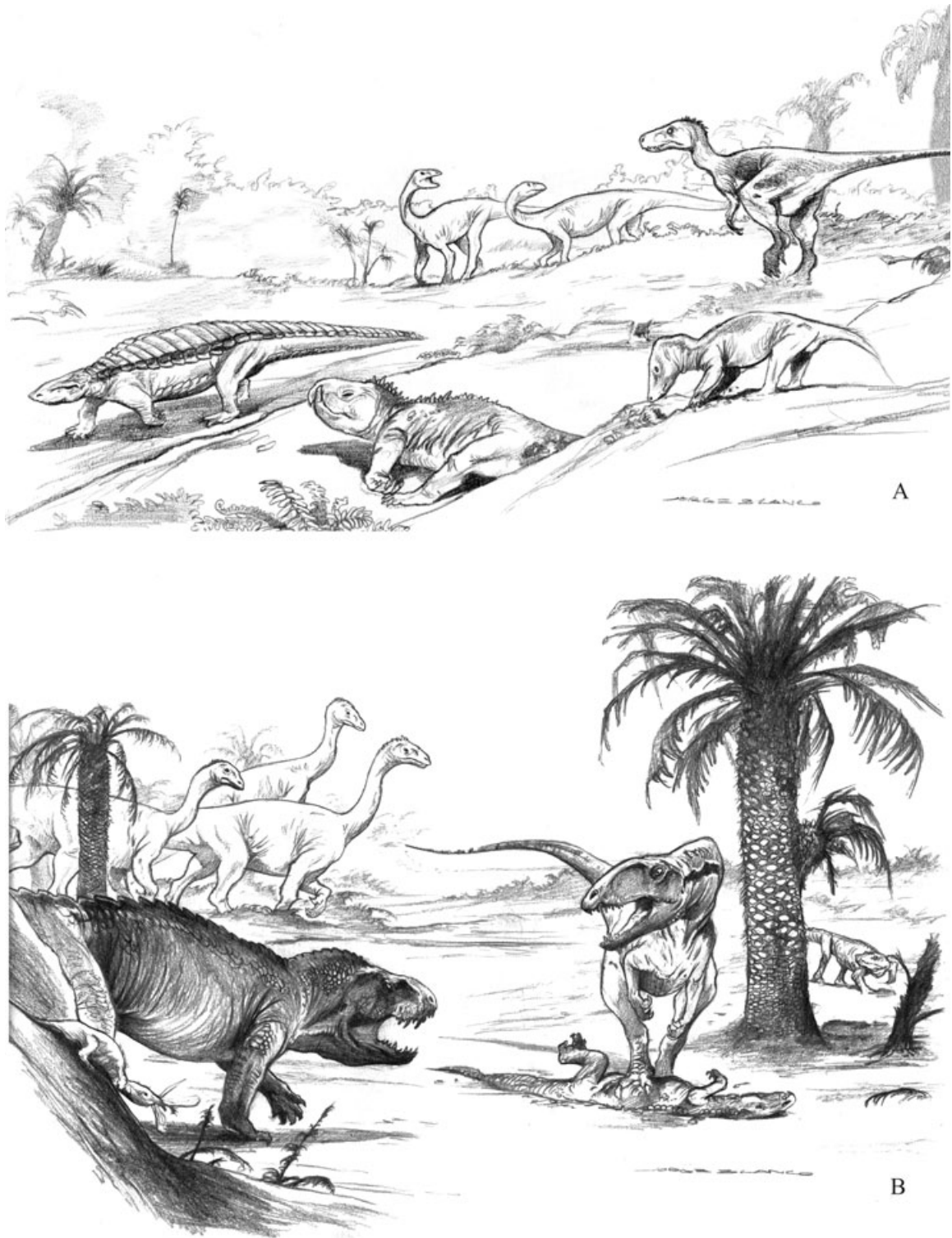


Fig. 11. Reconstruction of two dinosaur-bearing fossil assemblages of the South American Late Triassic. (A) Alemoa fauna (Santa Maria Formation), Carnian of south Brazil, depicting from left to right the aetosaur *Aetosauroides* sp.; the rhynchosaur *Hyperodapedon mariensis*; the stem-sauropodomorph *Saturnalia tupiniquim* (group on background); the cynodont *Prozoostrodon brasiliensis* (in front), and the herrerasaurid *Staurikosaurus pricei*. (B) La Esquina fauna (Los Colorados Formation), Norian of northwestern Argentina, depicting on the left (from back to front), a group of the sauropodomorph *Riojasaurus incertus*; the “rauisuchid” *Fasolasuchus tenax*, and the cynodont *Chalimimia musteloides*; on the right (from back to front), the crocodyliform *HemiprotoSuchus leali*, and the basal theropod *Zupaysaurus rougieri* subduing the ornithosuchid *Riojasuchus tenuiceps*. Drawings by Jorge Blanco.

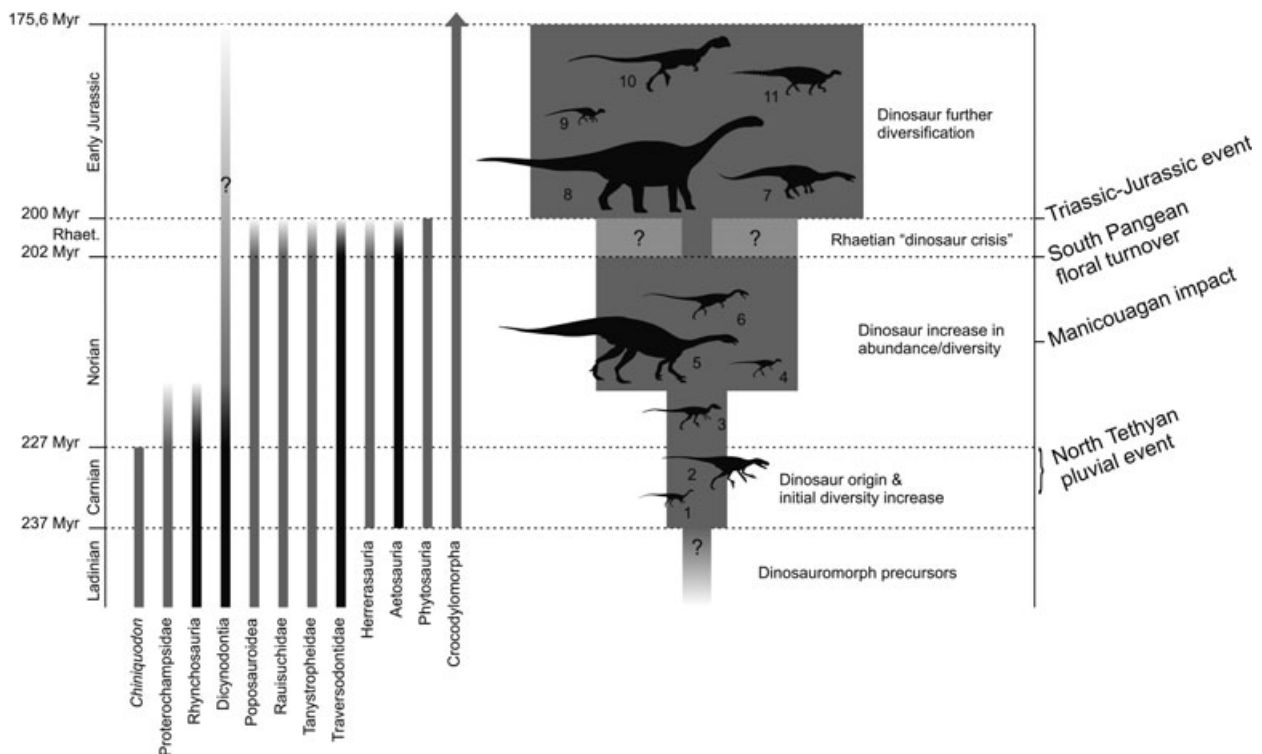


Fig. 12. Distribution of medium to large sized terrestrial amniotes along the Late Triassic and Early Jurassic and the rise of dinosaurs. Timeline from Gallet *et al.* (2003). Distribution of carnivorous (grey columns) and herbivorous/omnivorous (black columns) tetrapods modified from Benton (1994a), according to Dilkes (1998), Abdala & Giannini (2002), Abdala & Ribeiro (2003), Thulborn & Turner (2003), Lucas & Tanner (2005), Langer *et al.* (2007c), and Brusatte *et al.* (2008a). 1, *Saturnalia tupiniquim*; 2, *Herrerasaurus ischigualastensis*; 3, *Guaibasaurus candelariensis*; 4, *Eocursor parvus*; 5, *Plateosaurus engelhardti*; 6, *Liliensternus liliensterni*; 7, *Massospondylus carinatus*; 8, *Vulcanodon karibaensis*; 9, *Heterodontosaurus tucki*; 10, *Dilophosaurus wetherilli*; 11, *Scelidosaurus harrisoni*. Silhouettes (roughly at the same scale) adapted from various sources. Mys, million years before recent; Rhaet., Rhaetian.

1999). Yet, Tanner *et al.* (2004; see also Bambach, Knoll & Wang, 2004) compiled evidence to reject what they call “the myth of a catastrophic extinction at the Triassic-Jurassic boundary”. Indeed, as already hinted by some (Benton, 1994b; Cuny, 1995; Ezcurra & Cuny, 2007), although various well-known Triassic amniote groups have no Jurassic record, some might have gone extinct before the Triassic upper boundary (Fig. 12).

The pioneering studies of Benton (1983a, 1986a, 1989, 1994b), which first challenged the long-term “competitive” model of dinosaur radiation, also advocated that the main turnover of terrestrial faunas occurred at the Carnian-Norian, rather than at the Triassic-Jurassic boundary. This would have been characterized by the extinction of various tetrapod groups, connected to climatic/floral changes (Tucker & Benton, 1982). Problems related to that model include: (1) new data suggest the survival, at least until the initial stages of the Norian, of taxa believed to have gone extinct at the end of the Carnian (Fig. 12); (2) lack of synchronicity between the climatic/floral changes of north and south Pangea. Indeed, dicynodonts occur in Norian faunas of South (Langer *et al.*, 2007c) and North America (Long & Murry, 1995), in the latest Triassic of Poland (Dzik *et al.*, 2008), and perhaps in much younger

assemblages as well (Thulborn & Turner, 2003). In addition, the Caturrita Formation, of south Brazil, has yielded the latest (Norian) remains of proterochampsid archosaurs and rhynchosaurs (Langer *et al.*, 2007c), while lagerpetonids and herrerasaurids were recorded in the Norian of USA (Irmis *et al.*, 2007a; Nesbitt & Chatterjee, 2008; Nesbitt *et al.*, 2009). The diversity of chiniquodontid cynodonts, on the other hand, has been reduced to a single genus of Anisian-Carnian distribution in South America and southern Africa (Abdala & Giannini, 2002; Abdala & Smith, 2009). Accordingly, its absence in Norian strata does not represent the demise of a well-established lineage, as is also the case of single-genus “families” such as Pisanosauridae and Scleromochlidae (Benton, 1994b). On the other hand, it is important to stress that rhynchosaurs and dicynodonts get less common in Triassic faunas after the Carnian. This abundance shift, rather than their extinction, could indeed provide some evidence for a biological crisis at the Carnian-Norian boundary. In the marine realm, classical studies suggested that invertebrate extinctions were not conspicuous at the end of the Carnian (Simms & Ruffell, 1990), only few groups suffering a moderate loss of diversity (Schäfer & Fois, 1987; Smith, 1988). Yet, more recent data on the so-called Reingraben Turnover suggest that a major

restructuring of marine ecosystems occurred at the Carnian-Norian boundary (Hornung & Brandner, 2005; Stanley, 2006; Hornung, Krystyn & Brandner, 2007b).

Despite Cornet & Olsen's (1990) statement against significant floristic changes across the Carnian-Norian boundary, this is assumed in a climate-driven fashion by the biotic substitution model of Benton (1983a). Most authors agree on the occurrence of a monsoonal humid phase (Fig. 12), minimally affecting the northern Tethyan realm during the mid-late Carnian (Simms, Ruffell & Johnson, 1994; Hornung *et al.*, 2007a). Yet, although a humid phase was also recorded in the Late Triassic of other parts of the world, it seems to have lasted until later within the period in those areas. Prochnow *et al.* (2006) suggest that approximately during the deposition of the Petrified Forest Member of the Chinle Formation, presently considered of Norian age (Nesbitt *et al.*, 2007), western North America was experiencing a period of increasing humidity. Similarly, the Santa Maria Supersequence, in south Brazil, shows the progressive replacement of an ephemeral anastomosed fluvial-lacustrine system by a perennial braided fluvial system throughout the Carnian and Norian (Holz & Scherer, 2000; Zeffass *et al.*, 2003), whereas the Norian upper third of the Ischigualasto Formation bears evidence of a humidity peak, based on plant taphonomy and the occurrence of argillitic palaeosols (Colombi & Parrish, 2008). Besides, *Dicroidium*-floras occur through the entire sequence, as is also the case in other parts of south Pangea (White, 1990; Anderson & Anderson, 1993), while bennettitaleans and conifers only dominate after the Norian (Fig. 12).

What seems to occur during the Norian is a rise in the abundance of dinosaurs (Fig. 12). These are inconspicuous in Carnian faunas, representing about 5% of tetrapod fossils collected in the *Hyperodapedon* Assemblage-Zone of the Santa Maria Formation (Azevedo, Schultz & Barberena, 1990; Langer *et al.*, 2007c) and the lower third of the Ischigualasto Formation (Bonaparte, 1982; Rogers *et al.*, 1993). Carnivorous dinosaurs were proportionally more abundant, representing nearly 40% of all terrestrial meat-eaters, and half of the medium- to large-sized predators of the latter assemblage (Rogers *et al.*, 1993). By contrast, dinosaurs represent from 25 to 60% of the terrestrial tetrapods of classical Norian faunas (Benton, 1983a), notably in South Africa (Kitching & Raath, 1984), Argentina (Bonaparte, 1982), and Europe (Benton, 1994a). This is better documented for saurischians, especially with the notable radiation of "prosauropods". However, dinosaurs are still minor components of possibly older Norian faunas such as that of the Caturrita Formation (Langer *et al.*, 2007c), where they represent about 15% of the known diversity. Although the total number of dinosaurs registered in the Norian is at least three times higher than in the Carnian, Ezcurra & Novas (2008) emphasize that dinosaur diversity in the Ischigualasto Formation surpasses that of most Norian stratigraphic units (Fig. 7). This may imply that their radiation in the latter stage resulted in a more abundant and disparate (Brusatte *et al.*, 2008b), but not necessarily more diverse, dinosaur

fauna, leaving the greater total diversity of Norian dinosaurs to be explained based on the existence of more tetrapod-bearing sites of that age. Yet, various main dinosaur groups appear to have originated and/or radiated during the Norian, as is the case for heterodontosaurids, coelophysoids, and "prosauropods".

Moreover, as discussed by Novas (1997b; *contra* Benton, 1983a), the Late Triassic dinosaur rise did not occur in an empty ecospace. Instead, dinosaurs radiated during the Ischigualastian despite the high diversity and abundance of other tetrapods. Especially in the case of carnivores, it is difficult to deny a degree of overlap in the use of food resources by sympatric species of similar size (Glen & Dickman, 2008); whereas modern analogues suggest that feeding niche overlap is less significant among herbivores (Plumpton, 1996; Begon, Harper & Townsend, 1996, p. 778). In this context, it is possible to envisage strictly herbivorous Triassic dinosaurs, which were not many (see Section IV.3), using plant resources not previously exploited in full. Yet, counterevidence is given by the non-overlap of the rhynchosaur bearing Norian assemblages with younger faunas of that age (Fig. 12), in which dinosaurs are more abundant (Langer, 2005a). In this context, the Norian radiation of herbivorous dinosaurs could be linked to ecological release, given the extinction of rhynchosaurs (see also Brusatte *et al.*, 2008b). The corollary, as suggested by Novas (1997b), is that competitive pressure of non-dinosaur herbivores may account for the low abundance of herbivorous dinosaurs in the Carnian.

Whatever the physical causes of the end-Triassic event, direct "extermination" is unlikely to have been the only agent of the extinctions. Instead, the exacerbation of biotic interactions (including competition) in a changing environment probably also played a major role. In that context, the already abundant and diverse dinosaurs may have had the key adaptations to succeed and expand, within the shifting environment that drove various other tetrapods towards extinction. This is the second explanation offered by Brusatte *et al.* (2008a) accounting for the extinction of pseudosuchians, and not dinosaurs, at the Triassic-Jurassic boundary. It implies a circumstantial "superiority" of dinosaurs, while historical burden enforces the reference to a fully erect gait (Charig, 1972) and/or advanced physiology (Bakker, 1971; Ward, 2006) within the set of dinosaur "advantages". This explanation is preferred here, given that the first is based on "chance" (Brusatte *et al.*, 2008a), which just reflects cases "when our knowledge does not suffice for prediction" (Popper, 1959). In fact, as acknowledged by Popper (1959): we may not infer from the fact that an event is chance-like that its elements are 'due to chance'. This is because "chance" and lack of knowledge produce the same signatures, and can not be set apart in practice. In our understanding, opportunistic and competitive scenarios of dinosaurs rise are not mutually exclusive, and competition may have played an important role in that radiation episode. Not as a long-term affair, but triggered by the physical events ultimately linked to the end-Triassic extinction.

Although the Early Jurassic total diversity of dinosaur genera is not significantly higher than the Late Triassic (Wang & Dodson, 2006), it is usually accepted that another pulse of dinosaur radiation followed the Triassic-Jurassic extinction (Olsen *et al.*, 2002). This is better measured by the origin of certain lineages and exploitation of new ecological roles (Fig. 12). Among saurischians, large carnivores (Ezcurra & Novas, 2007a) and large quadruped herbivores (Yates & Kitching, 2003) were already known in the latest Triassic. In fact, the record of *Zupaysaurus* (Ezcurra & Novas, 2007a), and studies of Brusatte *et al.* (2008b), falsifies the hypothesis of theropod size increase due to ecological release after the Triassic-Jurassic boundary (Olsen *et al.*, 2002; Lucas & Tanner, 2005). Yet the Early Jurassic saw the radiation of the *Dilophosaurus*-clade (Smith *et al.*, 2007) and further acquisition of typical graviportal traits among sauropods (Barrett & Upchurch, 2007). The radiation of ornithischians was more notable, with heterodontosaurids attaining their diversity peak and the origin of both neornithischians and thyreophorans (Butler *et al.*, 2007). The latter represents the debut of quadrupedal armoured forms, within a morphospace previously unoccupied by dinosaurs.

In conclusion, the radiation of dinosaurs comprises at least three landmark moments (Fig. 12), mainly characterized by early diversification (Carnian); increase in diversity and, especially, abundance (Norian); and occupation of new niches (Early Jurassic). As previously mentioned, the Carnian diversification did not occur in an empty ecospace, but despite the abundance and diversity of contemporary tetrapods. The Norian increase in dominance might be connected to climatic/ floristic changes and to the extinction of herbivorous forms such as rhynchosaurs, but the timing of these events needs further investigation. The subtle Jurassic diversification, on the other hand, seems to have occurred in the aftermath of an extinction event (Brusatte *et al.*, 2008a). Indeed, this might be an example of opportunistic radiation into released ecospace (Benton, 1983a; Olsen *et al.*, 2002; but see Brusatte *et al.*, 2008b). Obviously, this does not fit the notion that the “end-Triassic” tetrapod extinctions were scattered over the end of the period (Tanner *et al.*, 2004). Indeed, the lack of various tetrapod groups in Rhaetian beds and the less than expected dinosaur diversity increase in the Early Jurassic seem to justify this latter scenario, but the “diversity loss” of dinosaurs and other tetrapods during the Rhaetian is likely to be due to sampling bias (Ezcurra & Cuny, 2007). In any case, post-Triassic tetrapod biodiversity can not be understood as the outcome of a single event, but seems modeled by long-term coexistence of different groups during the Late Triassic. Punctual events of environmental change may have enhanced interaction among lineages, leading to the extinction of some terrestrial forms. This was probably topped by a final historical contingency at the Triassic-Jurassic boundary, when dinosaur circumstantial “superiority” set the frame for the next 135 million years of archosaur evolution.

(3) Of legs and teeth: insights on the palaeobiology of early dinosaurs

Non-crown-group archosaurs were all quadrupedal and carnivorous (Charig, 1972; Parrish, 1986; Brusatte *et al.*, 2008a). This general pattern was retained in basal members of the crocodile-line (Bonaparte, 1984; Sereno, 1991a), although recent discoveries of bipedal (Nesbitt, 2007) and herbivorous/omnivorous (Parker *et al.*, 2005) pseudosuchians notably amplified the disparity of these archosaurs. The basalmost dinosaurs, instead, were all bipedal, but it is not clear if this was also the case for more basal dinosauromorphs, and several instances of reversion to full or facultative quadrupedalism are known within the group (Padian, 1997c). The feeding habit of basal dinosaurs is even more difficult to assess. Basal dinosauromorphs have a rather unspecialized dentition, but typical carnivores and herbivores occur early in dinosaur evolution (Barrett, 2000).

As seen in the previous section, bipedalism is often considered a key dinosaur feature that, along with a fully erect posture, favoured the radiation of the group during Late Triassic times. Yet, supporters of a polyphyletic origin of dinosaurs suggested that some quadrupedal lineages, particularly sauropods (Charig *et al.*, 1965), have never had bipedal ancestors, evolving directly from quadrupedal basal archosaurs (Fig. 2). The general acceptance of dinosaur monophyly, and the identification of its sister taxa within gracile, and presumably bipedal Middle Triassic archosaurs (Gauthier, 1986) settled the new orthodoxy of originally bipedal dinosaurs, which was in turn challenged by more recent data. This includes the discovery of a potentially quadrupedal basal dinosauromorph (Dzik, 2003), and new ichnological (Haubold & Klein, 2002) and biomechanical (Fechner, 2006) interpretations that hint at higher degrees of quadrupedalism among dinosaur precursors. It is consensual that herrerasaurs, basal theropods, and basal ornithischians were fully bipedal (Carrano, 2000; Butler *et al.*, 2007), but the condition among sauropodomorphs is less clear (Cooper, 1981; Barrett & Upchurch, 2007). In any case, only if all evidence in favour of basal dinosauromorph/dinosaur quadrupedalism is accepted, and optimized on a favourable phylogenetic framework (Fig. 13) does a quadrupedal/facultative bipedal origin of dinosaurs emerge as parsimoniously as a fully bipedal origin. Otherwise, the latter hypothesis is always favoured if herrerasaurs are regarded as basal saurischians (Yates, 2003b; Langer, 2004; Ezcurra, 2006; Irmis *et al.*, 2007a). In fact, a fully quadrupedal dinosaur origin is consistently ruled out, given that basal members of the sauropodomorph lineage, even if capable of walking on all fours, must have relied on bipedalism for higher speed locomotion (Christian & Preuschoft, 1996; Upchurch, 1997a; Langer, 2003). Actually, this may be the case also of *Silesaurus opolensis*, the unusual slender fore limbs of which may not have endured the same amount of stress as the hind limbs did (see Fariña, 1995). Evidently, more detailed biomechanical studies of basal dinosauromorphs are needed to recognize if dinosaurs originated from facultative or fully bipedal ancestors. At the moment, this is hampered by the scarce material

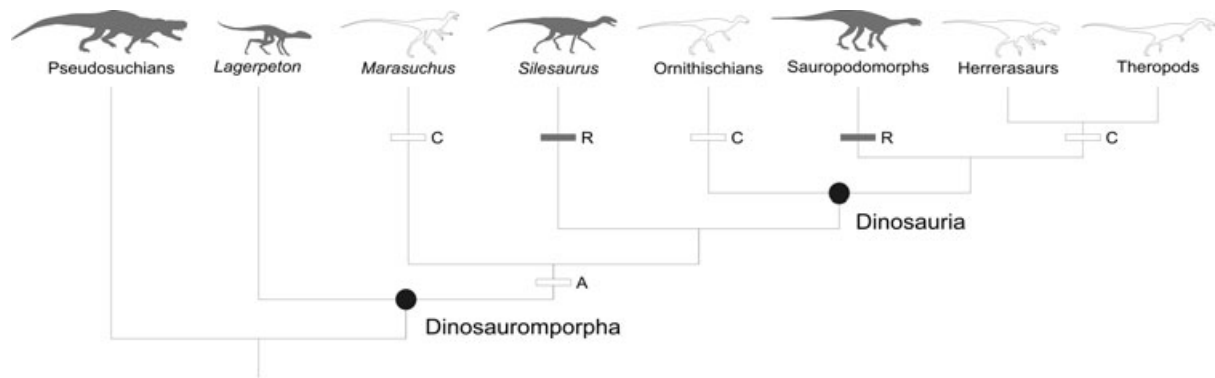


Fig. 13. Single hypothesis of basal dinosaur/dinosauromorph relationships in which the recognition of *Lagerpeton*, *Silesaurus*, and sauropodomorphs as quadrupedal/facultative bipedal (grey silhouettes) allows an equally parsimonious reconstruction of this gait, relative to a fully bipedal gait (white silhouettes), as ancestral to Dinosauria. White rectangles represent acquisition of bipedalism on either a quadrupedal/facultative bipedal (C = convergences) or fully bipedal (A = apomorphy) scenario of dinosaur origins. Grey rectangles (R = reversions) represent acquisition of facultative bipedalism/quadrupedalism on a fully bipedal scenario of dinosaur origins. Silhouettes adapted from various sources.

assigned to most of these forms, specially regarding their fore limb anatomy.

Classical scenarios of dinosaur dietary evolution (Charig *et al.*, 1965) depict independent origins of the major groups from carnivorous “thecondonts”. In fact, also in the cladistic paradigm, typical “carnivorous teeth”, i.e. pointed, caudally curved, labiolingually flattened, unexpanded at the base, and with finely serrated/denticulate keels, are usually accepted as plesiomorphic for dinosaurs (Gauthier, 1986; Langer & Benton, 2006, but see Barrett, 2000). Indeed, although more conical in likely piscivorous forms (Sill, 1967; Hungerbühler, 2000), teeth of basal archosaurs (Ewer, 1965; Gower, 2003) and pseudosuchians (Walker, 1964; Gower, 1999; Nesbitt, 2003) mainly fit into that pattern. Triassic exceptions are pseudosuchians that bear modified dentitions towards omnivory/herbivory/scavenging (Walker, 1961; Parker *et al.*, 2005). Given that known basal dinosauromorph teeth are all labiolingually flattened, there is a good case that the above described pattern is indeed ancestral to the group as a whole. Dinosaur dentitions are, however, more heterogeneous.

Until recently, the dentition of non-dinosaur dinosauromorphs was inferred from the rather fragmentary tooth-bearing bones referred to *Lewisuchus admixtus* (Romer, 1972a) and *Marasuchus lilloensis* (Bonaparte, 1975). The isolated partial jaw of *Lewisuchus* may not belong to the taxon, given that it was found disarticulated in a concretion with other archosaur taxa and seems larger in relation to the holotype skeleton (PULR 01). The maxilla of *Marasuchus* (PVL 3870) has been consensually attributed to the taxon (Serenó & Arcucci, 1994), but its teeth are not well preserved enough for an accurate inference of its diet. Most of the crowns fit into the plesiomorphic pattern described above, but more caudal elements seem slightly distally expanded at the base, making them somewhat “leaf-shaped” (Bonaparte, 1975). Yet, the lack of further dental modifications (see Barrett, 2000) precludes the assignment of an alternative diet to

Marasuchus, which probably fed on a variety of small animals. Lately, however, putative basal dinosauromorphs with herbivorous adaptations have been discovered (Dzik, 2003; Ferigolo & Langer, 2007; Irmis *et al.*, 2007a). *Silesaurus opolenensis* and *Sacisaurus agudoensis* bear an edentulous beak in the lower jaw, plus dental features usually associated with a more herbivorous diet in “prosauropods” and ornithischians (Galton, 1984; Crompton & Attridge, 1986; Sereno, 1991b), but lately given as evidence of omnivory (Barrett, 2000; Irmis *et al.*, 2007b). Accordingly, although a full herbivore ancestry of dinosaurs can be dismissed, there is some evidence that a strictly carnivorous origin was also not the case.

Barrett (2000) comprehensively reviewed early dinosaur feeding habits, remaining unsure about the ancestral diet of the group. There is full agreement, however, on the carnivorous habits of theropods and herrerasaurs (Barrett, 2000; Bittencourt, 2008), while basal ornithischians (Irmis *et al.*, 2007b) and typical “prosauropods” (Barrett & Upchurch, 2007) were most probably omnivorous. The condition in some small-sized basal saurichians such as *Eoraptor lunensis* and *Saturnalia tupiniquim* is more uncertain. *Eoraptor* bore “leaf-shaped” rostral teeth, but its diet was most probably still based on small animals. On the other hand, most teeth of *Saturnalia* are “leaf shaped”, and this animal is frequently referred to as bearing herbivorous adaptations (Barrett & Upchurch, 2007). However, the retention of finely serrated tooth keels (Yates, 2003b) suggests that *Saturnalia* was more carnivorous than any basal sauropodomorph.

The optimization of dental patterns into current hypotheses of early dinosaur phylogeny reveals various alternative scenarios. When forms with less modified dentition such as *Marasuchus* and *Eoraptor* are considered carnivores, the reconstruction of the ancestral dinosaur feeding habit is ambiguous in most cases. Yet, if *Eoraptor* plus herrerasaurs are considered basal theropods (Serenó, 1999), and *Silesaurus opolenensis* and *Sacisaurus agudoensis* placed in the sister clade to Dinosauria, then omnivory can be

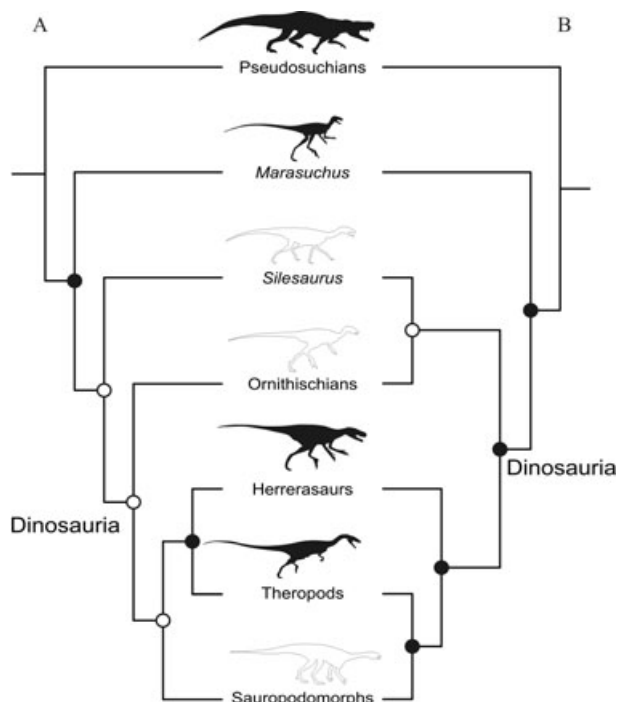


Fig. 14. Hypotheses of basal dinosaur/dinosauromorph relationships in which either omnivory (A) or carnivory (B) is unambiguously reconstructed as ancestral to Dinosauria. White and black silhouettes/circles, respectively, indicate omnivorous and carnivorous taxa/optimizations. Silhouettes adapted from various sources.

unambiguously regarded as plesiomorphic for the group (Fig. 14A). On the contrary, if *Silesaurus* and *Sacisaurus* are considered basal ornithischians (Ferigolo & Langer, 2007), and either *Eoraptor* or herrerasaurs basal saurichians (Langer & Benton, 2006), then dinosaurs are plesiomorphically carnivores (Fig. 14B). Yet, it is important to stress that the plesiomorphic dinosaur tooth morphology does not strictly compare to that of the typically carnivorous herrerasaurs and theropods, or to the omnivorous/herbivorous pattern of ornithischians and “prosauropods”. Teeth of basal forms as *Marasuchus*, *Saturnalia*, and *Eoraptor*, are less specialized, and this was most probably also the case for the dinosaur common ancestor, whether it was a strict carnivore or able to include plant material in its diet. In this context, each major dinosaur group seems to have independently acquired its typical dental traits, in some cases along with a significant increase in size. Indeed, the omnivorous/herbivorous dentition of basal ornithischians and sauropodomorphs are sufficiently different to preclude a common origin (Barrett, 2000). On the contrary, the carnivorous teeth of herrerasaurs and theropods are primary homologous (Bittencourt, 2008), and can be used as evidence for the nesting of the former within the latter group. Alternatively, they might have arisen independently, as adaptations to the predatory habits of these animals (Langer & Benton, 2006).

The skin of basal dinosaurs has always been thought as scaly, but this view was recently challenged by the discovery

of *Tianyulong confuciusi* (Zheng *et al.*, 2009), which provides the second evidence of an ornithischian with integumentary filaments (see also Mayr *et al.*, 2002). Its placement within Heterodontosauridae (Zheng *et al.*, 2009), i.e. the sister clade of all other ornithischians except *Pisanosaurus* (see Section V.1), shows that at least some very basal ornithischians bore integumentary filaments. Accordingly, if these are actually homologous to the “protofeathers” of theropod dinosaurs, the most recent common ancestor of saurischians and ornithischians would also likely bear this kind of epidermal coverage. Witmer (2009) is cautious about the dermal or epidermal origin of the integumentary structures of *Tianyulong*, and their homology with those of theropods. Yet, further research demonstrating the epidermal origin of those filaments, a hypothesis currently supported by their hollow structure (Zheng *et al.*, 2009), would suggest that early dinosaurs also bore integumentary filaments. If it was sufficiently abundant, the coverage could play a thermoregulatory function (insulation), probably implying a higher thermal inertia (Regal, 1975, 1985; Unwin, 1998; Wu *et al.*, 2004).

V. OUTCOMES OF A RADIATION

(1) Early ornithischian evolution

Although the concept of Ornithischia was defined only some twenty years later (Seeley, 1888), the first dinosaur classification schemes already congregated most members of the clade we now know within a “natural group”, e.g. Orthopoda Cope, 1866. Indeed, ornithischian monophyly remains one of the few uncontroversial issues in dinosaur taxonomy (Nopcsa, 1923, 1928; Huene, 1956; Romer, 1956, 1966; Steel, 1969; Thulborn, 1971, 1972; Galton, 1972; but see Maryańska, 1977), having been fully corroborated by cladistic studies (Serenó, 1999; Butler, 2005; Butler *et al.*, 2007, 2008). Traditional ornithischian diagnostic traits such as the opisthopubic pelvis (Seeley, 1888) and the preentary bone (Marsh, 1894) can not be unambiguously considered apomorphic for the group, because their occurrence in the suggested basalmost ornithischian, *Pisanosaurus mertii*, is equivocal (Butler *et al.*, 2008). Yet, various other features have been accepted as diagnostic for the clade, most of which correspond to modifications of the teeth and tooth-bearing bones, related to the acquisition of a more herbivorous diet. These include the presence of a buccal emargination on the maxilla, into which cheek musculature may have attached, and several changes in the shape and arrangement of the teeth, as recently reviewed by Irmis *et al.* (2007b) and Butler *et al.* (2008).

Five main ornithischian groups are traditionally recognized: Stegosauria, Ankylosauria, Ornithopoda, Pachycephalosauria, and Ceratopsia (Thulborn, 1972), but the relationships among these lineages remained ambiguous until the first cladistic analyses of the group were performed (Serenó, 1984, 1986; Norman, 1984; Maryańska & Osmólska, 1985; Cooper, 1985). Among these, the view advocated by Serenó (1986, 1991b, 1999) was highly influential for nearly two

decades, during which few other phylogenetic studies focusing on the basal radiation of Ornithischia were performed. Sereno (1998, 1999) recognizes two main ornithischian splits: Thyreophora and Neornithischia (Table 1). The former includes Stegosauria and Ankylosauria, whereas Ceratopsia and Pachycephalosauria compose Marginocephalia, the sister clade to Ornithopoda within Neornithischia. This general scheme is accepted by most recent studies (Xu *et al.*, 2006; Butler *et al.*, 2007, 2008), but details of basal forms nesting within each major group remain controversial.

Sereno (1986) combined neornithischians and thyreophorans within Genasauria, which encompasses the bulk of the Ornithischia. The first phylogenetic definition of the name (Table 1) employed the term Cerapoda in a connotation equivalent to Neornithischia *sensu* Sereno (1999). Indeed, Cerapoda was later defined by Weishampel (2004) as “genasaur more closely related to *Triceratops* than to *Ankylosaurus*”. The term was, however, more recently abandoned in favour of Neornithischia (Sereno, 1997, 1998, 1999, 2005), or used in a radically different node-based concept (Buchholz, 2002; Barrett, Butler & Knoll, 2005a; Butler *et al.*, 2008). Originally, non-Genasauria ornithischians included only *Lesothosaurus dignoticus*, from the Early Jurassic Upper Elliot Formation, southern Africa (Thulborn, 1970, 1972; Santa Luca, 1984; Knoll & Battail, 2001; Knoll, 2002a, b, c, 2005; Butler, 2005), and *Pisanosaurus mertii* (see Section III.1). Despite its plesiomorphic postcranial anatomy, the latter taxon has for a long time been regarded as the sole unequivocal Triassic ornithischian, based on traits of its partial skull and teeth (Sereno, 1991b; Butler *et al.*, 2007; Irmis *et al.*, 2007b). Historically, *Pisanosaurus* was related to “fabrosaurids” (Thulborn, 1971, 1972), heterodontosaurids (Charig & Crompton, 1974; Bonaparte, 1976; Cooper, 1985; Weishampel & Weishampel, 1983; Weishampel, 1984; Crompton & Attridge, 1986), and “hypsilophodontids” (Galton, 1972, 1986; Colbert, 1981), but later accepted as the most basal ornithischian (Novas, 1989; Weishampel & Witmer, 1990; Sereno, 1991b; Butler, 2005; Butler *et al.*, 2007, 2008; but see Norman *et al.*, 2004a). More recently, a non-Genasauria position was also inferred for the only other two ornithischian taxa with a Triassic record (Fig. 15A), Heterodontosauridae (Butler *et al.*, 2008) and *Eocursor parvus* (Butler *et al.*, 2007). This is partially based on the retention of several features otherwise atypical for the group such as a long hand with extensor pits on the metacarpals and phalanges, longer penultimate phalanges, and strongly recurved unguals with prominent flexor tubercles (Butler *et al.*, 2007). Heterodontosaurids are more extensively known from Early Jurassic strata (Fig. 15B), and were traditionally placed as the basalmost clade of Ornithopoda (Sereno, 1984, 1986; Norman, Witmer & Weishampel, 2004b), although unorthodox alternative placements were also proposed in the cladistic paradigm (Norman, 1984; Cooper, 1985; Maryańska & Osmólska, 1985; Buchholz, 2002; You, Xu & Wang, 2003; Xu *et al.*, 2006). The group is minimally composed of *Heterodontosaurus tucki*, from the Early Jurassic Upper Elliot (Santa Luca, 1980) and Clarens (Crompton &

Charig, 1962) formations of South Africa, and *Abrietosaurus consors*, from the former unit (Thulborn, 1974). Other post-Triassic heterodontosaurids may include *Lycorhinus angustidens* (Gow, 1975), also from the Upper Elliot Formation, unnamed forms from the Kayenta and Clarens formations (Irmis & Knoll, 2008), as well as younger records (Norman & Barrett, 2002; Galton, 2005b; Zheng *et al.*, 2009).

From the 1980s onwards, several putative ornithischians (e.g. *Galtonia gibbidens*, *Technosaurus smalli*, *Revueltosaurus callenderi*, *R. hunti*, *Lucianosaurus wildi*, *Pekinosaurus olseni*, *Tecovasaurus murreyi*, *Protecovasaurus lucasi*, *Crosbysaurus harrisae*) were reported from Late Triassic assemblages of North America (Hunt, 1989; Hunt & Lucas, 1994; Hunt *et al.*, 1998; Heckert, 2002, 2004) and Europe (Godefroit & Cuny, 1997; Cuny *et al.*, 2000; Galton, 2005b) mostly based on isolated teeth. Yet, recent studies demonstrated that the trustworthy Triassic record of the group is much more restricted. Parker *et al.* (2005) reported the first non-dental material of *R. callenderi*, showing that it represents a pseudosuchian rather than an ornithischian. Those authors also recognized notable convergences in the dental anatomy of ornithischians and some non-dinosaur archosaurs, e.g. low triangular tooth crowns with expanded base and carinae composed of large denticles. Indeed, in a comprehensive review of the Triassic ornithischian record, Irmis *et al.* (2007b) reinterpreted most of those isolated teeth as indeterminate archosauriforms. More recently, Ferigolo & Langer (2007) proposed the ornithischian affinity of the purported basal dinosauromorphs *Silesaurus opolensis* and *Sacisaurus agudoensis* (Fig. 15A). This was partially based on the suggested homology of the synapomorphic ornithischian prementary bone to the edentulous tip of the lower jaw seen in both taxa, which is formed by independent ossifications in the latter form. Yet, that proposition was not originally backed up by a numerical cladistic study, and further analyses failed to recover that hypothesis of relationships (Langer & Benton, 2006; Ezcurra, 2006; Irmis *et al.*, 2007a; Brusatte *et al.*, 2008a).

Until the early eighties, most authors accepted the “fabrosaurids” as a natural group of basal ornithischians, frequently depicted at the stem of either Ornithopoda or a more inclusive group of non-thyreophoran taxa (Galton, 1978; Norman, 1984). Yet, it became increasingly evident that “fabrosaurids” congregated a paraphyletic array of early, small-bodied forms (Weishampel & Witmer, 1990; Sereno, 1991b). In his phylogenetic studies, Sereno (1984, 1986, 1991b, see also Buchholz, 2002; Xu *et al.*, 2006) considered the archetypal “fabrosaurid” *Lesothosaurus dignoticus* as the sister taxon to Genasauria. More recently, however, this view was challenged by studies that placed that form within Genasauria (Butler *et al.*, 2007), either as a neornithischian (Butler, 2005) or a thyreophoran (Butler *et al.*, 2008). In the latter case, *Lesothosaurus* would represent the only thyreophoran to lack the typical cortical remodeling of cranial elements and osteoderms covering the dorsum of the body (Butler *et al.*, 2008). That genus was also reported from the Early Jurassic La Quinta Formation, in western Venezuela (Russell *et al.*,

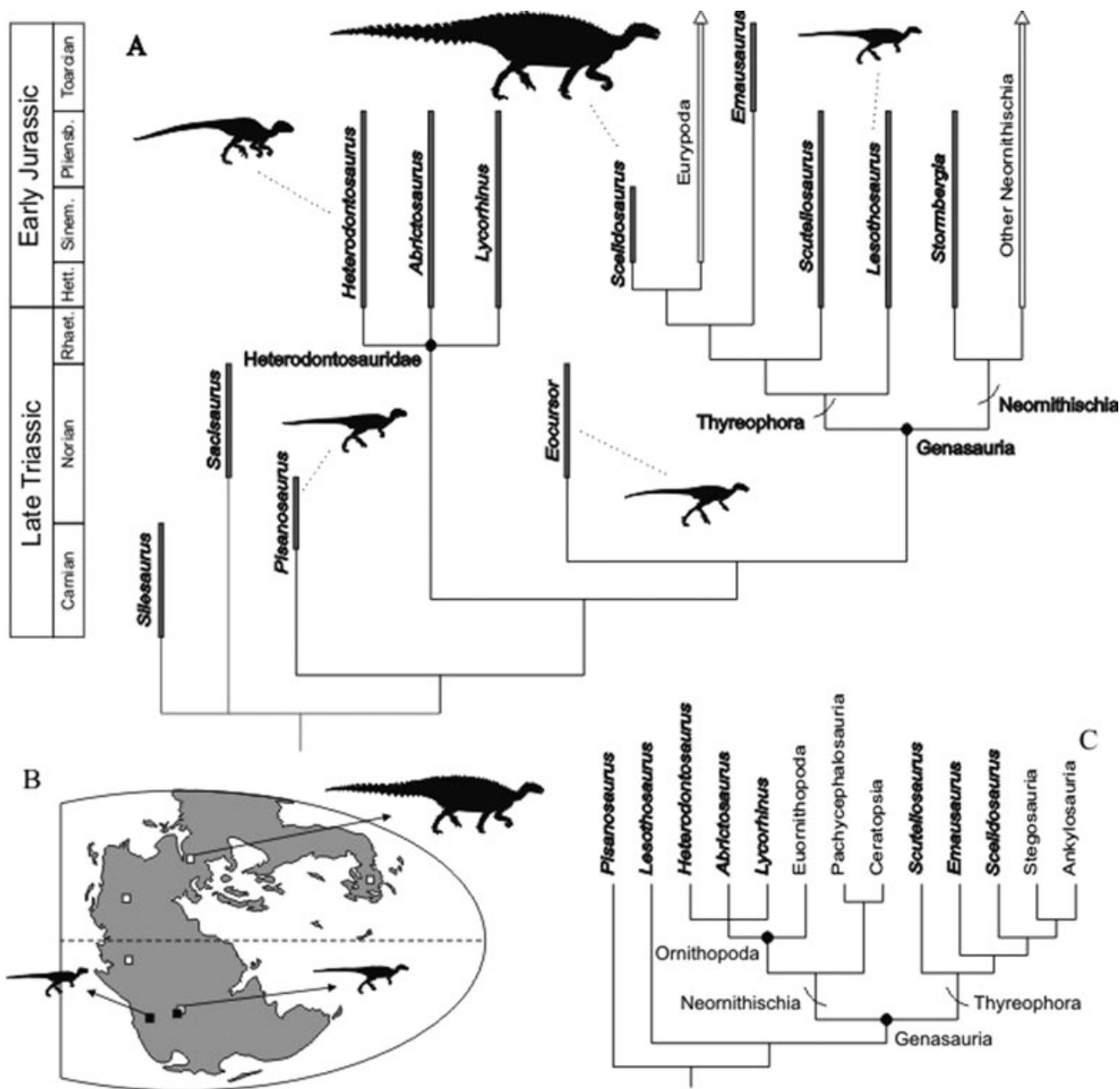


Fig. 15. Phylogenetic relationships and distribution of basal ornithischians. (A) Time-calibrated phylogeny depicting heterodontosaurids as the most basal clade of Ornithischia, based on Butler *et al.* (2007, 2008); dotted lines indicate uncertain position of *Silesaurus* and *Sacisaurus* according to Ferigolo & Langer (2007). (B) Geographic occurrences of Late Triassic (black squares) and Early Jurassic (white squares) taxa on a Late Triassic map redrawn from Blakey (2006). (C) More conventional phylogeny depicting heterodontosaurids as ornithopods, based on Sereno (1999); composition of Heterodontosauridae according to Butler *et al.* (2008). Black silhouettes (roughly at the same scale) adapted from various sources, names applied as in Table 1. In the cladograms, node- and stem-based taxa are respectively indicated by black circles and curved lines.

1992), but the specimens can only be referred to indeterminate non-cerapodan ornithischians (Barrett *et al.*, 2008). Other taxa previously regarded as “fabrosaurids” (Galton, 1978; Peng, 1997) have been considered of indeterminate affinity or placed within genasaurian subgroups (Sereno, 1991b; Norman *et al.*, 2004b, c; Butler, 2005).

Early Jurassic ornithischians other than *Lesothosaurus digonicus* have a less debated phylogenetic position (Fig. 15).

Scutellosaurus lawleri, from the Kayenta Formation of western USA (Colbert, 1981; Rosenbaum & Padian, 2000), *Emausaurus ernsti*, from Meckleberg, Germany (Haubold, 1991), and the genus *Scelidosaurus*, known from the Lower Lias of Dorset, England (Owen, 1861, 1863; Martill, Batten & Loydell, 2000; Norman, 2001) and possibly also from the Kayenta Formation (Padian, 1989), are consensually considered the basalmost thyreophorans (Sereno, 1999; Butler *et al.*, 2008). Early Jurassic thyreophorans are otherwise only

known from the Lufeng Formation of China (Irmis & Knoll, 2008). This includes the type specimens of *Bienosaurus lufengensis* (Dong, 2001) and *Tatisaurus oehleri* (Norman, Butler & Maidment, 2007), both of which lack autapomorphic features and may represent *nomina dubia* (Irmis & Knoll, 2008). Except for *Lesothosaurus*, heterodontosaurids, and thyreophorans, *Stormbergia dangershoeki*, from the Upper Elliot Formation (Butler, 2005; but see Knoll *et al.*, 2009), is the sole well known Early Jurassic ornithischian. Indeed, although much richer than during Triassic times, Early Jurassic ornithischian faunas are still poorly diverse. *Stormbergia dangershoeki* seems to represent the most basal Neornithischia, lacking typical features otherwise common to the group such as an elongated prepubic process (Butler, 2005; Butler *et al.*, 2007, 2008).

The divergence time of Ornithischia has been traditionally considered as Late Triassic, given the presence of *Pisanosaurus mertii* and various saurischian dinosaurs in South American deposits of that age. The phylogenetic hypothesis of Butler *et al.* (2007) better fits the stratigraphic data, restricting the Triassic record of ornithischians to non-Genasauria taxa. Instead, both traditional (Sereno, 1999) and more unusual (Buchholz, 2002; Xu *et al.*, 2006) arrangements require the existence of long ghost-lineages for Ornithopoda, Marginocephalia, and Thyreophora. The possible position of two South African forms at the base of both Thyreophora and Neornithischia (Butler *et al.*, 2008) suggests that the origin and early diversification of ornithischians is to be found in southwestern Gondwana (Rauhut & Lopez-Arbarello, 2008), where the Late Triassic record of the group is concealed (Fig. 15C). On the contrary, the bulk of Early Jurassic thyreophorans occur in North Pangea, particularly considering the uncertain affinity of the ankylosaur reported from the Kota Formation of India (Nath, Yadagiri & Moitra, 2002; Rauhut & Lopez-Arbarello, 2008).

The slightly more conspicuous Middle Jurassic record of ornithischians includes the first stegosaurs and ankylosaurs within Thyreophora and an array of basal neornithischians. The Lower Shaximiao Formation of China (Peng *et al.*, 2005) has yielded stegosaurs (Maidment & Wei, 2006) and neornithischians (Barrett *et al.*, 2005a), while the former group was recorded along with a possible pachycephalosaur from the Balabansai Formation of Kirghizia (Averianov, Martin & Bakirov, 2005; Averianov, Bakirov & Martin, 2007). In Europe, Middle Jurassic ornithischians are represented by basal ornithopods (Galton, 1980; Evans & Milner, 1994; Kriwet, Rauhut & Gloy, 1997; Ruiz-Omeñaca, Suberbiola & Galton, 2005), stegosaurs (Galton & Powell, 1983; Galton, 1990), and ankylosaurs (Galton, 1983a). Indeed, it was not until the Late Jurassic and Early Cretaceous that ornithischian faunas became abundant, with diverse thyreophorans, ornithopods, ceratopsians, and pachycephalosaurs, especially in Laurasian assemblages.

(2) Early sauropodomorph evolution

The sauropodomorph lineage includes dinosaurs with a small skull, a distally broad humerus, a relatively short hind limb, plus a series of other skeletal modifications

that support their monophyly in the cladistic paradigm (Sereno, 1999; Yates, 2003b; 2007a; Yates & Kitching, 2003; Langer & Benton, 2006; Upchurch *et al.*, 2007). On the contrary, as comprehensively reviewed by Sereno (2007a; see also Upchurch, 1997a; Galton & Upchurch, 2004), classical studies (Huene, 1929, 1956; Romer, 1956; Colbert, 1964) frequently allocated the basal sauropodomorphs known as “prosauropods” within a grade of saurischians from which both theropods and sauropods arose. The name Prosauropoda Huene, 1920, was coined in that context, in reference to a group lying at the base of the “herbivorous-omnivorous” branch of Pachypodosauria that, as the name implies, gave rise to sauropods. This included *Thecodontosaurus*, *Plateosaurus*, *Sellosaurus*, and *Anchisaurus*, but also *Poekilopleuron* “as a blind side stem” (Huene, 1920). On the contrary, forms at some point regarded as members of the sauropodomorph lineage such as *Paleosaurus* (Benton *et al.*, 2000) and *Gresslyosaurus* (Yates, 2007a) were allocated to the theropod-related branch (Huene, 1920). As often mentioned (Benton, 1986b), this was in part due to the mistaken association of carnivorous teeth with other “prosauropod” skeletal remains (Huene, 1932; Young, 1951). Charig *et al.* (1965; see also Galton, 1971, 1973) may be said to have settled the current concept of “Prosauropoda”, congregating various early saurischians of the sauropodomorph lineage. As properly put by Sereno (2007a), “prosauropods” represented the first grand radiation of dinosaurs sharing minimal morphological coherence. Basal sauropodomorphs radiated relatively fast during Late Triassic times, becoming the dominant terrestrial herbivores/omnivores from Norian to Early Jurassic landscapes (Upchurch, 1997a).

Sereno (2007a) selected from the universe of basal sauropodomorphs a subset of five taxa termed “core-prosauropods”, which should carry the name Prosauropoda, if found to represent a monophylum exclusive of sauropods. A comparable application is seen in Yates & Kitching (2003) and Upchurch *et al.* (2007). However, the first phylogenetic definition of the name was proposed under the orthodoxy of a monophyletic “Prosauropoda” as to include “Thecodontosauridae, Plateosauridae (Anchisauridae), Melanosauridae [sic], and all Sauropodomorpha closer to them than to Sauropoda” (Upchurch, 1997a; Sereno, 2005). Based on the type-genera of those family rank names, this definition is not applicable to the current framework of sauropodomorph evolution, since a clade that includes *Thecodontosaurus*, *Plateosaurus*, *Anchisaurus*, and *Melanorosaurus* also includes sauropods. Considering the criteria adopted here (Section II.2), that definition has precedence over following ones that arbitrarily select either a single (Sereno, 1998; Galton & Upchurch, 2004) or various “prosauropods” (Sereno, 2007a) as internal specifiers. Indeed, the definition of Upchurch (1997a) is to be kept and applied under an eventually revitalized framework of “prosauropod monophyly”, while newly proposed names should be used to designate major subgroups of Sauropodomorpha, as seen in Yates (2007a) and Smith & Pol (2007).

Early evolutionary studies of basal sauropodomorphs (Charig *et al.*, 1965; Galton, 1971, 1976) broadly discriminate three main “prosauropod” groups: one including more gracile forms, the so-called “narrow-footed prosauropods”, termed either Thecodontosauridae or Anchisauridae; a group of more “typical”, *Plateosaurus*-related forms; and a group of bulky quadrupeds, frequently termed Melanorosauridae. The sauropod affinity of the latter group was often advocated (Colbert, 1964; Cooper, 1981; Bonaparte, 1986), hinting at “prosauropod” paraphyly. Indeed, the first cladistic approach to sauropodomorph evolution reproduced that scheme (Gauthier, 1986), allocating *Thecodontosaurus antiquus* and *Efraasia minor* at the base of the clade, and the “broad-footed” forms, especially *Riojasaurus incertus*, closer to Sauropoda. The succeeding cladistic studies (Serenó, 1989, 1999; Galton, 1989; Benton *et al.*, 2000; Galton & Upchurch, 2004), however, failed to recover a similar paraphyletic array of “prosauropods”. Instead, they pointed towards a different picture, in which most, if not all “prosauropods” represented the monophyletic sister taxon to Sauropoda. This scheme is reminiscent of pre-cladistic approaches (Charig *et al.*, 1965; Cruickshank, 1975; Van Heerden, 1978) that partially relied on the supposed irreversibility of some features of the “prosauropod” foot, and on the uniqueness of their hand, in order to discard their bearing on the origin of sauropods (but see Yates, 2003b; Sereno, 2007a). More recently, “prosauropod” monophyly was deemed an analytical artifact derived from poor taxon sampling, that overlooked basal and near-sauropod sauropodomorphs (Yates, 2003b; see also Sereno, 2007a). Indeed, most recent studies (Yates & Kitching, 2003; Pol, 2004; Smith & Pol, 2007; Yates, 2007a, b), including those performed by previous proposers of “prosauropod monophyly” (Upchurch *et al.*, 2007; Sereno, 2007a) tend to agree that at least some forms previously assigned to “Prosauropoda” are basal to the bulk of sauropodomorphs, and that others are closely related to the sauropod radiation (Fig. 16A). Evidently, these hypotheses are not fully congruent with one another, but important common points are seen, as outlined below.

The most recently proposed basal sauropodomorph phylogenies (Pol, 2004; Yates, 2007a, b; Upchurch *et al.*, 2007) agree that the Late Triassic *Saturnalia tupiniquim*, *Pantyraco caducus*, *Thecodontosaurus antiquus*, and *Efraasia minor* are amongst the most basal members of the lineage, whereas *Panphagia protos* may be the basal-most member (Martinez & Alcober, 2009). Upchurch *et al.* (2007) also included *Mussaurus patagonicus* in that basal grade, but the taxon was given a more derived position by Pol (2004), Pol & Powell (2005, 2007b), and Sereno (2007a) based on first-hand examination of a more complete set of specimens. Such a basal position was also inferred, in an admittedly tentative fashion, to the newly described *Pradhania gracilis* from the Early Jurassic Upper Dharmaram Formation, India (Kutty *et al.*, 2007). The relative positions of the other forms are nearly consensual, with *Saturnalia* basal to *Thecodontosaurus* and *Pantyraco* (but see Galton & Upchurch, 2004), and

Efraasia closer to other sauropodomorphs (Fig. 16A). These taxa represent the first radiation of the sauropodomorph lineage, retaining various morphological traits of their basal saurischian/basal dinosauriform precursors (Barrett & Upchurch, 2007) such as the smaller size (adults are less than 4 m in length) and, at least facultative, bipedality. Other simplesiomorphies include a relatively long hand, a partially closed acetabulum, a distal femur lacking a well-developed extensor depression, metatarsals I and II closely appressed, plus several other skeletal features (Yates, 2003b; Yates & Kitching, 2003; Smith & Pol, 2007; Upchurch *et al.*, 2007). In addition, some of these forms possess novel herbivorous adaptations such as a higher number of coarsely denticulated teeth, although they might have retained an omnivorous diet (Barrett, 2000). The geographic distribution of these basal sauropodomorphs, along with that of slightly more derived forms (Pol, 2004; Yates, 2007a), suggests an initial radiation of the clade restricted to western Pangea (Fig. 16C). Considering the node-based definition of Sauropodomorpha and the (by typification) inclusion of *Thecodontosaurus* as an internal specifier of Prosauropoda, Langer (2002) proposed that *Saturnalia* should be excluded from Sauropodomorpha, and considered instead as a taxon on its stem lineage.

The relationships of sauropodomorphs more derived than *Efraasia minor* are far from consensual. In fact, several possible arrangements recently have been proposed (see various articles in Barrett & Batten, 2007; especially Sereno, 2007a). In most of them, however, a relatively stable set of taxa is placed closely related to traditional sauropods (Fig. 16A), minimally including Norian-Rhaetian forms such as *Camelotia borealis*, *Melanorosaurus readi*, *Blikanasaurus cromptoni*, and *Lessemsaurus sauropoides*, as well as *Antetonitrus ingenipes*, which was already first described as a sauropod. This roughly corresponds to the classical radiation of “melanorosaurids”, composed of usually larger (6.5–10 m), more herbivorous “prosauropods” (Barrett, 2000). Most of these may have adopted a fully quadrupedal gait (Yates & Kitching, 2003), although facultative bipedality is still suggested for several forms (Barrett & Upchurch, 2007). These taxa share a range of traits with eusauropods, including short and high dorsal centra, an increased number of sacral vertebrae, a longer manual digit I with a straighter ungual, broader non-terminal manual phalanges, and a straighter femur, elliptical in cross section and bearing distally displaced lesser and fourth trochanters (Yates & Kitching, 2003; Yates, 2007a, Upchurch *et al.*, 2007; Pol & Powell, 2007a). Some authors (Yates & Kitching, 2003; Smith & Pol, 2007; Yates, 2007a, b) include all or some of these forms within Sauropoda, given the stem-based definition of the taxon as to include forms closer to *Saltasaurus loricatus* than to the archetypal “prosauropod” *Plateosaurus engelhardti* (Wilson & Sereno, 1998; Sereno, 1999; Upchurch *et al.*, 2007), or alternative arbitrary attempts to mimic more traditional/current placement of forms either within or outside the group (Yates, 2007a; Sereno, 2007a). However, Sauropoda was first phylogenetically defined by Salgado *et al.* (1997) in a node-based fashion (Table 1) that may exclude forms regularly assigned to the

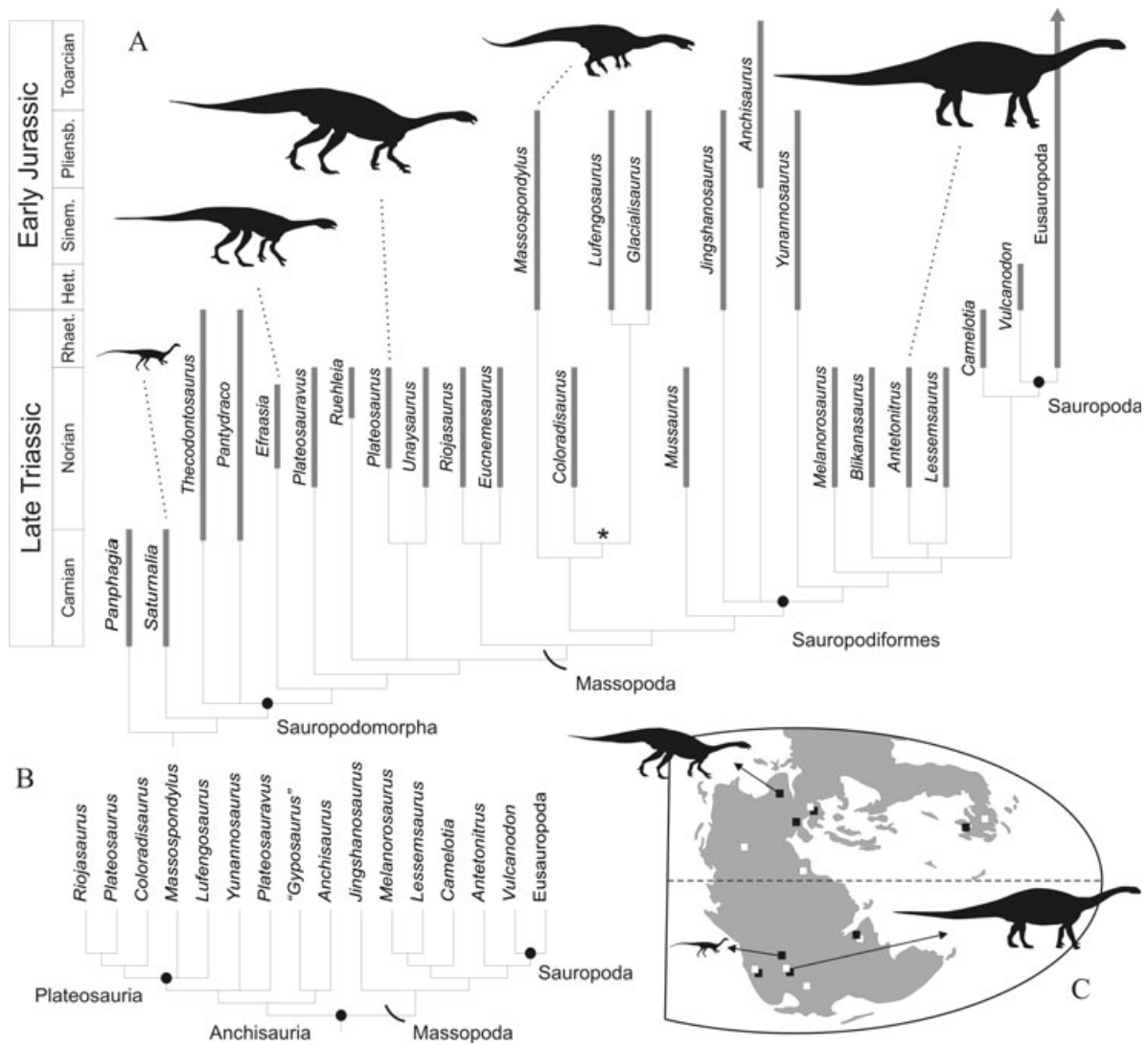


Fig. 16. Phylogenetic relationships and distribution of basal members of the sauropodomorph lineage. (A) Time-calibrated phylogeny depicting “core prosauropods” as a paraphyletic group, based on Yates (2007a, b), Smith & Pol (2007), and Martinez & Alcover (2009); asterisk indicates alternative placement of *Yunannosaurus* according to Pol (2004). (B) Alternative phylogeny depicting “core prosauropod” monophyly, based on part of the topology proposed by Upchurch *et al.* (2007). (C) Geographic occurrences of Late Triassic (black squares) and Early Jurassic (white squares) taxa on a Late Triassic map redrawn from Blakey (2006). Names applied as in Table 1; black silhouettes (roughly at the same scale) adapted from various sources. In the cladograms, node- and stem-based taxa are respectively indicated by black circles and curved lines.

clade such as *Isanosaurus attavipachi*, *Gongxianosaurus shibeiensis*, *Chinshakiangosaurus chuhghoensis*, and *Kotasaurus yamanpalliensis* (see table 2 in Upchurch *et al.*, 2007). The latter three taxa belong into the Early Jurassic (He, Li & Cai, 1988; Yadagiri, 2001; Upchurch *et al.*, 2007) radiation of sauropodomorphs that also includes some European (Wild, 1978) and North African (Allain *et al.*, 2004) forms. These are derived from an already widespread set of related Triassic taxa, leading to the well-established diversity of Mid-Late Jurassic sauropods (Rauhut & Lopez-Arbarelo, 2008).

Given such a more restrictive definition of Sauropoda, Yates (2007a) proposed the name Massopoda (= Sauropoda *sensu* Wilson & Sereno, 1998) also to encompass the

“prosauropod” stem leading to that group, exclusive of *Plateosaurus engelhardti*. In parallel, Sereno (2005) named a clade composed of sauropods plus some related “prosauropods” as Sauropodiformes (Table 1). Apart from the taxa discussed above, both Massopoda and Sauropodiformes probably also include *Mussaurus patagonicus* (Bonaparte & Vince, 1979; Pol & Powell, 2007b) and *Jingshanosaurus xinwaensis*, from the Early Jurassic Lufeng Formation of Yunnan, China (Zhang & Yang, 1994), a form accepted by most authors as sharing sauropod affinities (Pol, 2004; Upchurch *et al.*, 2007; Yates, 2007a). Additionally, newly discovered Early Jurassic forms as *Lamplughsaura dharmaramensis* from the Upper Dharmaram

Formation (Kutty *et al.*, 2007), and an undescribed Argentinian taxon (Pol & Garrido, 2007) may also belong to the sauropod stem. Other Early Jurassic forms such as *Yunnanosaurus huangi*, also from the Lufeng Formation (Young, 1942), and the “prosauropod” from the Portland Formation of eastern North America (*Anchisaurus polyzelus sensu* Yates, 2004; *Ammosaurus major sensu* Sereno, 2007a), have highly controversial affinities, and two antipodal scenarios have been presented (but see Pol, 2004). They may line up with other sauropod-related forms (Yates, 2007a, b) or belong to a clade of typical “prosauropods” (Upchurch *et al.*, 2007). There is limited evidence in favour of a monophyletic group of “core prosauropods” (Sereno, 2007a), minimally encompassing *Plateosaurus engelhardti*, *Riojasaurus incertus*, *Massospondylus carinatus*, *Lufengosaurus huenei*, and *Coloradisaurus brevis* (Fig. 16B). Potential apomorphic traits of this clade include modifications in the neurovascular foramina of the maxilla, the manus (carpal II does not completely cover the proximal end of metacarpal II, metacarpal V bears an expanded proximal end divided into two articular surfaces, first phalanx of manual digit I twisted by at least 60°), and foot (metatarsal IV with expanded proximal end). On the contrary, Pol (2004) and Yates (2007a, b) split that group into a successive array of three to five lineages on the stem to Sauropodiformes *sensu* Sereno (2007a), where forms related to *Plateosaurus* and *Riojasaurus* are considered more basal (Fig. 16A). Depending on the position of these forms relative to other sauropodomorphs is the application of names such as Plateosauria and Anchisauria, e.g. compare Yates (2007a) and Upchurch *et al.* (2007).

Either as a clade or grade, “core prosauropods” may represent a biological unit, playing similar roles in the Late Triassic–Early Jurassic ecosystems in which they occurred. Barrett & Upchurch (2007) reviewed the palaeobiology of these forms, highlighting some of their ecological adaptations. These include larger size (2.5–10 m) compared to more basal sauropodomorphs, and greater reliance on an herbivorous diet, although facultative omnivory was not discarded. “Core prosauropods” were also capable of bipedal locomotion (Cooper, 1981; Christian & Preuschoft, 1996; Bonnan & Senter, 2007), although larger forms were probably obligatory quadrupeds. This is the case for *Riojasaurus incertus*, previously connected to the origin of sauropods (Bonaparte, 1972; Gauthier, 1986). As a whole, that clade/grade congregates a relatively high diversity of Late Triassic forms, including *Ruehleia bedheimensis* and the species of *Plateosaurus* in Europe/Greenland, *Riojasaurus incertus* and *Unaysaurus tolentinoi* in South America, as well as *Eucnemesaurus fortis* and *Plateosaurus cullingworthi* in South Africa. Other “core-prosauropods” may fit into Massospondylidae, a clade that includes the Triassic *Coloradisaurus brevis* (Yates & Kitching, 2003), the Early Jurassic *Glacialisaurus hammeri* (Smith & Pol, 2007) from the Hanson Formation, Antarctica, and a possible set of Chinese forms (see Pol, 2004), minimally including *Lufengosaurus huenei* from the Lufeng Formation (Barrett, Upchurch & Xiao-Lin, 2005b). Its type genus *Massospondylus* (*M. carinatus*) is known from the Upper Elliot Formation

(Cooper, 1981; Gow, Kitching & Raath, 1990; Sues *et al.*, 2004; Reisz *et al.*, 2005) and other stratigraphic units in southern Africa (Cooper, 1981; Galton & Upchurch, 2004), but not in North America (Attridge, Crompton & Jenkins, 1985; Sues *et al.*, 2004). More recently, its sister taxon, *Adeopapposaurus mognai*, was described from the Lower Jurassic Cañon del Colorado Formation, Argentina (Martinez, 2009).

(3) Early theropod evolution

The name Theropoda was coined by Marsh (1881) as a new suborder of carnivorous dinosaurs, but its status as a “natural group” was rejected for the first half of the last century. At the time, gracile members of the group, the so-called “coelurosaurs”, were considered, along with “prosauropods”, the “basal stock” from which both sauropods and derived theropods evolved (Huene, 1914, 1920, 1932; Romer, 1956). Theropod monophyly was hinted at by Matthew & Brown (1922), firmly established by Colbert (1964), in an arrangement widely accepted since (Charig *et al.*, 1965; Romer, 1966; Colbert & Russell, 1969; Ostrom, 1978; Steel, 1970; Bakker & Galton, 1974), and corroborated by pioneering phylogenetic studies (Thulborn, 1984; Gauthier, 1986; Novas, 1992b; Holtz, 1994; Sereno, 1999). Indeed, taxa consensually assigned to the group share a series of typical traits, e.g. promaxillary foramen; well-developed pneumatization in cervical and cranial trunk vertebrae; manus with reduced metacarpal I, slender metacarpal III, and reduced/absent digits IV and V; ilium with prominent supracetabular crest and preacetabular ala; tibia with marked cnemial and fibular crests; transversely compressed calcaneum; foot with reduced outer digits (Rauhut, 2003; Ezcurra & Cuny, 2007; Ezcurra & Novas, 2007a).

As discussed in Section III.2, the most contentious aspect of early theropod evolution is the possible nesting of various Triassic forms within the group (Fig. 9). This is particularly the case for *Eoraptor lunensis* (Sereno *et al.*, 1993) and herrerasaurs (Sereno & Novas, 1992), but also for other taxa such as *Guaibasaurus candelariensis* (Langer *et al.*, 2007a), *Agnosphitys cromhallensis*, and *Chindesaurus bryansmalli* (Yates, 2007a). Indeed, these forms apart, the Norian coelophysoid “*Camposaurus arizonensis*” represents the oldest theropod (Hunt *et al.*, 1998; Nesbitt *et al.*, 2007), which would make Theropoda the only major dinosaur lineage lacking a well-defined Ischigualastian record. Moreover, based on the current knowledge of theropod diversity, and not considering the above-mentioned taxa as members of the group, the stem-based Theropoda would be as inclusive as the node-based Neotheropoda (Table 1). This name was first used by Bakker (1986) to combine theropods more derived than “podokesaurids”, but phylogenetically defined by Sereno (1998) as a more inclusive group. Yet, Neotheropoda remains a useful name under alternative arrangements (Fig. 9) and/or if new forms are found to belong to its stem (see Nesbitt & Chatterjee, 2008; Martinez *et al.*, 2008). Although a less inclusive Neotheropoda (Padian *et al.*, 1999; Wilson *et al.*, 2003) seems more useful in the current orthodoxy, and more properly translates the original meaning of the name (Bakker,

1986), the definition proposed by Sereno (1998) has historical “priority”.

Another controversial aspect of early theropod evolution is the possible monophyly of the oldest neotheropods, grouped within Ceratosauria and/or Coelophysoidea. Indeed, the first cladistic analyses of theropod relationships identified two main neotheropod lineages, Ceratosauria and Tetanurae (Gauthier, 1986; Rowe, 1989; Rowe & Gauthier, 1990). In turn, Ceratosauria was divided into two branches, the Late Triassic-Early Jurassic Coelophysoidea (i.e. *Coelophysus*, *Dilophosaurus*, and their kin) and the Jurassic-Cretaceous Neoceratosauria, including *Ceratosaurus* and abelisauroids (Novas, 1992a; Sereno, 1997, 1999; Holtz, 2000; Coria & Salgado, 2000). This arrangement was accepted during most of the 1990s, but the vast majority of more recent studies consider neoceratosaurs more closely related to tetanurans than to coelophysoids, challenging the monophyly of the traditional Ceratosauria (Carrano, Sampson & Forster, 2002; Carrano, Hutchinson & Sampson, 2005; Rauhut, 2003; Sereno, Wilson & Conrad, 2004; Yates, 2005; Ezcurra, 2006; Ezcurra & Novas, 2007a; Ezcurra & Cuny, 2007; Smith *et al.*, 2007; Carrano & Sampson, 2008; but see Tykoski & Rowe, 2004; Tykoski, 2005; Allain *et al.*, 2007). In fact, Ceratosauria was node-based defined by Rowe & Gauthier (1990) as “including *Ceratosaurus nasicornis*, *Dilophosaurus wetherilli*, *Liliensternus liliensterni*, *Coelophysus bauri*, *Syntarsus rhodesiensis*, *Syntarsus kayentakatae*, *Segisaurus halli*, *Sarcosaurus woodi*, and all other taxa stemming from their most recent common ancestor”, based on a phylogenetic framework in which these forms compose a monophylum exclusive of tetanurans. On the contrary, in the current orthodoxy (Fig. 17), Ceratosauria would point to the same node as Neotheropoda, circumscribing a much more inclusive group, and is not employed here. Instead, the term Averostra Paul, 2002, as phylogenetically defined by Ezcurra & Cuny (2007), designates the clade composed of Tetanurae plus Neoceratosauria (Table 1).

Early phylogenetic studies grouped all Triassic and Early Jurassic neotheropods within the Coelophysoidea clade. This included *Dilophosaurus wetherilli*, as the sister taxon to *Liliensternus liliensterni* plus Coelophysidae (Rowe & Gauthier, 1990; Holtz, 1994). The latter group is minimally composed of Late Triassic (Colbert, 1989; Rauhut & Hungerbühler, 2000) and Early Jurassic (Raath, 1969; Rowe, 1989) *Coelophysus*-“*Syntarsus*”-related forms (Paul, 1988; Bristowe & Raath, 2004), but may also include *Segisaurus halli* and *Procompsognathus triassicus* (Sereno, 1997, 1999; Tykoski & Rowe, 2004; Knoll, 2008). With the addition of newly described forms, such as *Zupaysaurus rougieri* and *Lophostropheus airelensis*, various cladistic analyses (Tykoski & Rowe, 2004; Carrano *et al.*, 2005; Tykoski, 2005; Ezcurra, 2006; Ezcurra & Novas, 2007a; Ezcurra & Cuny, 2007) also recovered a monophyletic Coelophysoidea *sensu lato* (Fig. 17B). As such, the group can be diagnosed by several craniomandibular features such as a flexible articulation between premaxilla and maxilla marked by a prominent subnarial diastema, an expanded rostral end of the dentary,

reduced serrations on premaxillary teeth, and enlarged (fang-like) teeth in the rostral portion of the dentary, as well as by a peculiar pattern of femoral dimorphism (Tykoski & Rowe, 2004; Ezcurra & Novas, 2007a; Ezcurra & Cuny, 2007). However, the monophyletic status of that group was questioned by Rauhut (2003), who found *Dilophosaurus* more closely related to tetanurans and neoceratosaurs than to coelophysids. Along with other forms, those taxa share cranial details such as a lacrimal fenestra, a dorsoventrally elongated orbit, and a reduced tooth count occupying a shorted portion of the maxilla, modifications in the retroarticular process of the lower jaw, and a higher astragalar ascending process (Smith *et al.*, 2007). A similar hypothesis of relationship was advocated by Yates (2005), which considered *Dracovenator regenti* as closely related to *Dilophosaurus wetherilli*. Smith *et al.* (2007) also found other Early Jurassic taxa such as *Cryolophosaurus ellioti* and “*Dilophosaurus*” *sinensis* as members of such a “*Dilophosaurus* clade” (Fig. 17A), partially characterized by the presence and/or differential configuration of the dorsal crests of the skull. Yates (2005) also assigned *Zupaysaurus* to that clade, but the phylogenetic position of that taxon is highly controversial within non-averostran neotheropods (Carrano *et al.*, 2005; Smith *et al.*, 2007; Ezcurra & Novas, 2007a). Clearly, as stem-based-defined by Sereno (1998), the inclusivity of Coelophysoidea is dependent on the adopted evolutionary framework. It may include only small to medium-sized forms similar to *Coelophysus*-“*Syntarsus*” (Fig. 17A), or also congregate an Early Jurassic radiation of large-bodied *Dilophosaurus*-like taxa (Fig. 17B).

Neotheropods experienced a rapid diversification during the Norian-Rhaetian and Early Jurassic, achieving a broad distribution over west Pangea (Fig. 17C). This early radiation was mostly represented by *sensu lato* “coelophysoids”, i.e. non-averostran neotheropods. Their Norian representatives include small to medium-sized forms reported from western USA (Colbert, 1989; Carpenter, 1997; Nesbitt *et al.*, 2007) and Europe (Sereno & Wild, 1992; Rauhut & Hungerbühler, 2000; Allen, 2004), most of which are also *sensu stricto* Coelophysoidea (Fig. 17B), and perhaps also larger forms such as *Zupaysaurus rougieri* (Arcucci & Coria, 2003). Close to the Triassic-Jurassic boundary, theropod remains become scarce and basically only *Lophostropheus airelensis* is known (Ezcurra & Cuny, 2007; but see Dzik *et al.*, 2008). Tetanurans previously have been reported from Late Triassic outcrops, but these records are not conclusive. The supposed bird *Protoavis texensis* (Chatterjee, 1991) has been recently reinterpreted as a chimaera (Nesbitt *et al.*, 2007), with some elements of “coelophysoid” affinities, but not of tetanuran nature. Otherwise, “*Zanclodon*” *cambrensis* was assigned to Tetanurae (Holtz, Molnar & Currie, 2004), but the available material does not differ from those of non-averostran theropods.

During the Early Jurassic (Fig. 17C), *sensu stricto* coelophysoids continue to be well represented in western USA, including *Segisaurus halli* from the Navajo Sandstone (Camp, 1936; Carrano *et al.*, 2005) and “*Syntarsus*” *kayentakatae* from

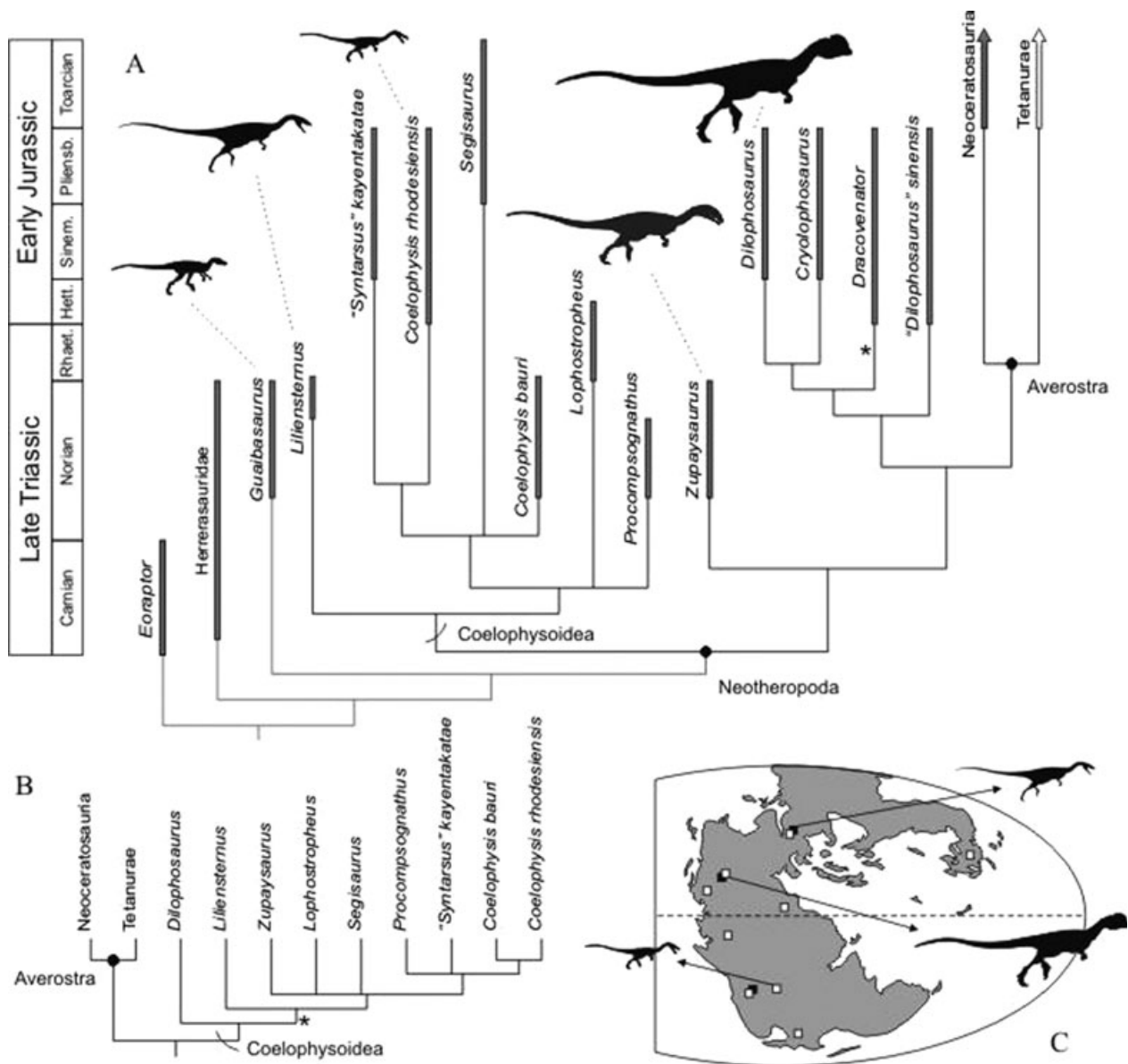


Fig. 17. Phylogenetic relationships and distribution of basal theropods. (A) Time calibrated phylogeny depicting “coelophysoids” as a paraphyletic group, based on Smith *et al.* (2007); position of *Lophostropheus* according to Ezcurra & Cuny (2007); position of *Procompsognathus* and relations within Coelophysidae according to Tykoski & Rowe (2004); asterisk indicates alternative placement of *Zupaysaurus* as sister taxon to *Dracovenator*, according to Yates (2005); dotted lines indicate uncertain position of herrerasaurids and *Eoraptor* according to Sereno (1999) and *Guaibasaurus* according to Langer & Benton (2006). (B) Alternative phylogeny depicting “coelophysoid” monophyly, based on Ezcurra & Cuny (2007) and Ezcurra & Novas (2007a); asterisk indicates alternative placement of *Zupaysaurus* according to Carrano *et al.* (2005). (C) Geographic occurrences of Late Triassic (black squares) and Early Jurassic (white squares) taxa on a Late Triassic map redrawn from Blakey (2006). Names applied as in Table 1; black silhouettes (roughly at the same scale) adapted from various sources. In the cladograms, node- and stem-based taxa are respectively indicated by black circles and curved lines.

the Kayenta Formation (Rowe, 1989), both in Arizona. In addition, “*Coelophysis*” *rhodesiensis* is known from the Upper Elliot Formation of South Africa (Raath, 1980) and especially from the Forest Sandstone of Zimbabwe (Raath, 1969). Further Jurassic records of “coelophysoids” are known from China (Irmis, 2004), Mexico (Munter & Clark, 2006), and possibly Europe (Andrews, 1921; Carrano & Sampson, 2004).

Larger forms attributed or not to the *Dilophosaurus*-clade also retain a broad distribution. These include *Dilophosaurus wetherilli* from the Kayenta Formation (Welles, 1984), *Dracovenator regenti* from the Upper Elliot Formation (Yates, 2005), *Cryolophosaurus ellioti* from the Hanson Formation of the Transantarctic Mountains (Hammer & Hickerson, 1994; Smith *et al.*, 2007), and “*Dilophosaurus*” *sinensis* from

the Lufeng Formation of China (Hu, 1993). In addition, the oldest averostrans are known from Early Jurassic assemblages. This includes *Berberosaurus liasicus*, a neoceratosaur from Morocco (Allain *et al.* 2007; but see Xu *et al.*, 2009), and the very dubious record of a therizinosauroid jaw in the Lufeng Formation (Zhao & Xu, 1998; Xu, Zhao & Clark, 2001; Rauhut, 2003). In any case, as sister taxon to Neoceratosauria, a tetanuran ghost lineage might be inferred for the latest Early Jurassic (Fig. 17A). Further Early Jurassic theropods were recorded from the La Quinta Formation of Venezuela (Moody, 1997) based on teeth that can not be allocated in a less inclusive clade.

Middle Jurassic dinosaur-bearing assemblages are rare (Rauhut & Lopez-Arbarello, 2008), but the available data show that the composition of theropod faunas changed drastically relative to those of Late Triassic and Early Jurassic age. “Coelophysoids” disappear completely from the fossil record, and tetanurans became the dominant forms. Apart from indeterminate theropod remains from North Africa (Monbaron, Russell & Taquet, 1999) and Madagascar (Flynn *et al.*, 2006), Middle Jurassic forms include a probable basal neoceratosaur from Australia (Long & Molnar, 1998; Rauhut, 2005a), and basal tetanurans from Argentina (Rauhut, 2005a), Europe, and China (Holtz *et al.*, 2004; Smith *et al.*, 2007). On the other hand, neoceratosaurs are better known from Late Jurassic and especially Cretaceous deposits (Carrano & Sampson, 2008; Xu *et al.*, 2009).

VI. CONCLUSIONS

(1) The oldest unequivocal records of Dinosauria are of Late Triassic age (approximately 230 Mya). These were unearthed from rocks accumulated over extensional rift basins in Argentina, Brazil, Zimbabwe, and India. The better known early dinosaurs are *Herrerasaurus ischigualastensis*, *Pisanosaurus mertii*, *Eoraptor lunensis*, and *Panphagia protos* from the Ischigualasto Formation, northwestern Argentina, and *Staurikosaurus pricei* and *Saturnalia tupiniquim* from the Santa Maria Formation, south Brazil. Other dinosaur records of equivalent age are either more fragmentary or of dubious affinities, hinting at a south Pangea origin of the group. No uncontroversial dinosaur body fossils are known from older strata, but a possible Middle Triassic origin of the lineage may be inferred from both the footprint record and its sister group relation to Ladinian basal dinosauromorphs.

(2) Dinosauria is by definition a monophyletic group that, in the present orthodoxy, combines saurischians and ornithischians to the exclusion of other major archosaur groups such as pterosaurs, phytosaurs, and crocodylomorphs. The first phylogenetic definition to fit the current understanding of Dinosauria as a node-based taxon solely composed of mutually exclusive Saurischia and Ornithischia was given as “all descendants of the most recent common ancestor of birds and *Triceratops*”. This definition should be followed until more specific provisions are given by the *PhyloCode*.

(3) Dinosaurs are nested within the bird-line of archosaurs along with pterosaurs (possibly), *Scleromochlus taylori*, and basal Dinosauromorpha, the phylogeny of which is in state of flux. It includes the archetypal *Marasuchus lilloensis*, a diversity of more basal forms such as *Lagerpeton* and *Dromomeron*, as well as silesaurids: a possibly monophyletic group that combines Mid-Late Triassic basal dinosauromorphs that may represent sister taxa to Dinosauria. Recent cladistic analyses of basal dinosaur relationships agree in various key points: (1) *Pisanosaurus mertii* is a basal ornithischian; (2) *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* belong in a monophyletic Herrerasauridae; (3) *Guaibasaurus candellar-ensis*, *Eoraptor lunensis*, and herrerasaurids are saurischians; (4) Saurischia includes two main groups, Sauropodomorpha and Theropoda; and (5) *Saturnalia tupiniquim* is a basal member of the sauropodomorph lineage, a position also inferred for the recently described *Panphagia protos*. On the contrary, several aspects of basal dinosaur phylogeny remain controversial, including the position of silesaurids as basal ornithischians or non-dinosaur dinosauromorphs; the position of herrerasaurids, *Eoraptor*, and *Guaibasaurus* as basal theropods or basal saurischians; and the affinity and/or validity of various fragmentary taxa such as *Agnosphitys cromhallensis*, *Alwalkeria maderiensis*, *Chindesaurus bryansmalli*, *Saltopus elginensis*, *Spondylosoma absconditum*, and *Teyuwasu barberenai*.

(4) The identification of dinosaur apomorphies is hampered by the incompleteness of the skeletal remains attributed to most basal dinosauromorphs, the skull and fore limb of which are particularly poorly known. Nonetheless, to the exclusion of silesaurids, Dinosauria can be diagnosed by a suite of derived traits, namely: foramen-sized post-temporal fenestra; epiphyses on cranial cervical vertebra; long deltopectoral crest; open acetabulum; arched dorsal iliac margin; femoral head inturned and distinctly offset from the shaft; asymmetrical fourth trochanter; astragalus with acute anteromedial corner, broad ascending process, and reduced fibular articulation; and proximally flat lateral distal tarsal. On the contrary, long-standing dinosaur apomorphies such as the absence of a postfrontal, the presence of more than two sacral vertebrae, reduced manual digits IV and V, modified “lesser trochanter”, and metatarsals II and IV subequal in length do not unambiguously diagnose the group. The prevalence of dinosaur diagnostic traits related to the pelvic girdle and limb may reflect the better preservation of these structures in their sister taxa, but may also suggest that these anatomical parts suffered most of the changes seen in the early dinosaur skeleton. Some of these traits can be related to the acquisition of an erect bipedal gait, which has traditionally been suggested to represent a key adaptation that allowed, or even promoted, dinosaur radiation in the Late Triassic.

(5) Contrary to the classical “competitive” model, dinosaurs did not gradually replace other terrestrial tetrapods over the Late Triassic. Yet, opportunistic and competitive scenarios are not mutually exclusive, and species interaction may have played a partial role in the rise of dinosaurs, which can be said to have consisted of three landmark

moments, separated by controversial (Carnian-Norian, Triassic-Jurassic) extinction events. The Carnian early diversification did not occur in an empty ecospace but despite the abundance and diversity of contemporary tetrapods. The Norian increase in dominance might be connected to climatic/floristic changes and to the extinction of herbivorous forms such as rhynchosaurs, but the timing of these events needs further investigation. The subtle Jurassic diversification seems to have occurred in the aftermath of an extinction event, and might be an example of opportunistic radiation into released ecospace, with the origin of neornithischians and thyreophorans, the heterodontosaurid diversity peak, the rise of the *Dilophosaurus*-clade, and further acquisition of typical graviportal traits among sauropods.

(6) It is traditionally believed that dinosaurs arose from bipedal and carnivorous forms, but evidence gathered from newly discovered basal dinosauromorphs indicate that quadrupedalism and omnivory/herbivory can not be discarded as possible ancestral traits of the group. At the moment, however, most evidence points towards a fully bipedal origin of dinosaurs. On the contrary, depending on the accepted hypothesis of relationships, the ancestral dinosaur diet can be reconstructed as either carnivorous or omnivorous. In any case, the plesiomorphic tooth morphology of dinosaurs does not strictly compare to the typical carnivorous or omnivorous/herbivorous patterns of more derived members of the group. Indeed, each major dinosaur group seems to have independently acquired its typical set of dental traits.

(7) The phylogenetic relationships of the basal members of each major dinosaur group have recently been reevaluated in the light of new evidence. Among ornithischians, unorthodox placements inside and outside Genasauria were proposed for *Lesothosaurus diagnosticus* and Heterodontosauridae, respectively. Within saurischians, both “Prosauropoda” and “Ceratosauria” were regarded as paraphyletic in their broader understanding. Yet, “core prosauropods” and coelophysoids may still represent smaller clades at the base of Sauropodomorpha and Theropoda, respectively.

(8) Whereas the oldest dinosaurs were geographically restricted to south Pangea, including rare ornithischians and more abundant basal members of the saurischian lineage, the group achieved a nearly global distribution by Norian/Rhaetian times, especially with the radiation of saurischian groups such as “prosauropods” and coelophysoids. This suggests an “out of south Pangea” model of dinosaur radiation, but no model is better than the evidence upon which it stands. In this case, the evidence is restricted to a handful of fossils from scattered areas around the world, and more prospection work is needed in order to build a more reliable scenario of dinosaur origins and basal radiation.

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VIII. APPENDIX 1. INSTITUTIONAL ABBREVIATIONS

BMNH, Natural History Museum, London, UK; GPIT, Institut für Geologie und Paläontologie, Tübingen, Germany; MB, Humboldt Museum für Naturkunde, Berlin, Germany; MCP, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; PULR, Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Fundación “Miguel Lillo”, San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan Argentina; QVM, National Museum of Natural History, Harare, Zimbabwe; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland.

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