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THE ORIGINS OF DINOSAURIA: MUCH ADO ABOUT NOTHING

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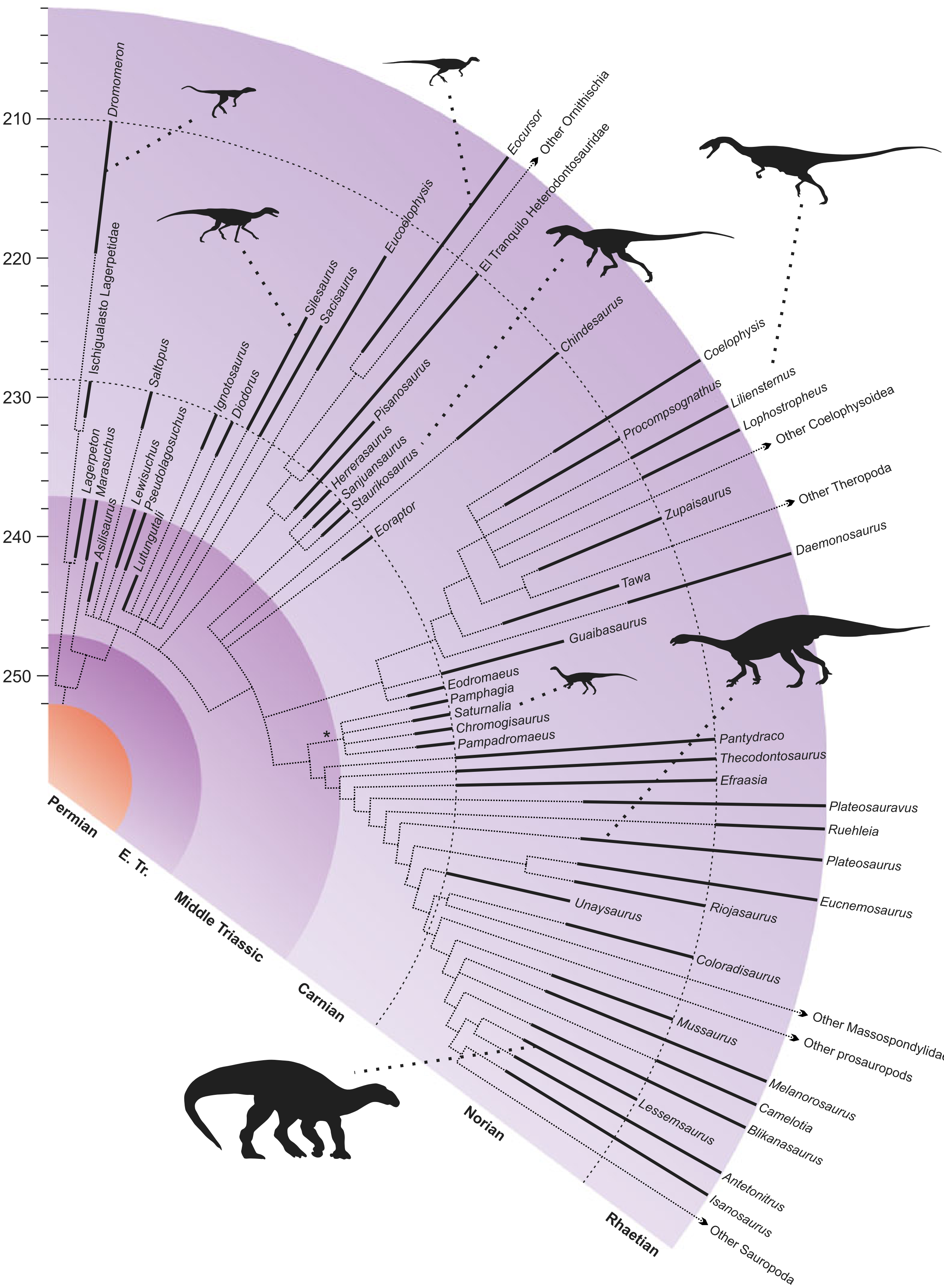
Abstract: Research this century has greatly improved our knowledge of the origin and early radiation of dinosaurs. The unearthing of several new dinosaurs and close outgroups from Triassic rocks from various parts of the world, coupled with improved phylogenetic analyses, has set a basic framework in terms of timing of events and macroevolutionary patterns. However, important parts of the early dinosauromorph evolutionary history are still poorly understood, rendering uncertain the phylogenetic position of silesaurids as either non-dinosaur Dinosauriformes or ornithischians, as well as that of various early saurischians, such as *Eoraptor lunensis* and herrerasaurs, as either noneusaurischians or members of the sauropodomorph or theropod lineages. This lack of agreement in part derives from a patchy distribution of traits among early members of the main dinosauromorph lineages and requires a more meticulous assessment of characters and homologies than those recently conducted. Presently, the oldest uncontroversial dinosaur records come from Late Triassic (Carnian) rocks of South America, southern Africa and India, hinting at a south-western Pangaea origin of the group. Besides, macroevolutionary approaches suggest that the rise of dinosaurs was a more gradual process than previously understood. Obviously, these tentative scenarios need to be tested by new fossil finds, which should also help close the major gaps recognized in the fossil record of Triassic dinosauromorphs.

Key words: Dinosauromorpha, Triassic, Saurischia, Ornithischia, evolution.

Coelophysis is a theropod. OK! *Plateosaurus* is a sauropodomorph. Fine! But in a broader context, few aspects of early dinosaur relationships are known for sure. Researchers are also comfortable (e.g. Ezcurra 2010*a*; Sues *et al*. 2011) with the allocation of several other Triassic dinosaurs to the theropod and sauropodomorph lineages. However, doubt pervades the relationships of various basal saurischians, including the herrerasaurs, a small but well-known group composed of at least three species and various complete specimens (Novas, 1993; Bittencourt and Kellner 2009; Alcober and Martinez 2010). In contrast, uncontroversial ornithischians of Triassic age are rare, but may include the silesaurids (Langer and Ferigolo, 2013), a diverse dinosauromorph group that are more commonly placed outside Dinosauria (Irmis *et al*. 2007). The timing of dinosaur origins is also contentious (Irmis *et al*. 2011; Martínez *et al*. 2011; Ramezani *et al*. 2011), with evidence of dinosaur near relatives in Early Triassic rocks (Brusatte *et al*. 2011*a*), but no well-accepted record of saurischians or ornithischians until the Late Triassic.

Following some considerations of the definition and diagnosis of the group, I shall here address two controversial aspects of early dinosaur systematics, the relationships of silesaurids and basal saurischians. This is followed by brief discussions of the biogeography, biodiversity and timing of the Triassic radiation of the group. Actually, if the evolution of dinosaurs as we know them today is seen from an end-Triassic standpoint, a single major lineage would be depicted, leading to the most diverse group of the time, the ‘prosauropods’ (basal sauropodomorphs), with less significant lagerpetid, silesaurid–ornithischian and herrerasaur–theropod radiations (Fig. 1). In this context, the current perceived importance of a particular dichotomy, the Saurischia–Ornithischia split, is clearly arbitrary and only meaningful in view of the great diversity both groups subsequently achieved during the Jurassic and Cretaceous. In the end, as with many other major groups, the origin of dinosaurs was probably an ordinary evolutionary event, bracketed by the dinosauromorph radiation earlier in the Triassic, when most significant dinosaur anatomical traits were



210
220
230
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Dromomeron
Ischigualasto Lagerpetidae
Lagerpeton
Marasuchus
Asilisaurus
Lewisuchus
Pseudolagosuchus
Lutungutali
Saltopus
Ignotosaurus
Diodorus
Silesaurus
Sacisaurus
Eucoelophysis
Eocursor
Other Ornithischia
El Tranquilo Heterodontosauridae
Pisanosaurus
Herrerasaurus
Sanjuansaurus
Staurikosaurus
Eoraptor
Chindesaurus
Coelophysis
Procompsognathus
Liliensternus
Lophostropheus
Other Coelophysoidea
Other Theropoda
Zupaisaurus
Daemonosaurus
Tawa
Guaibasaurus
Eodromaeus
Pamphagia
Saturnalia
Chromogisaurus
Pampadromaeus
*
Pantydraco
Thecodontosaurus
Efraasia
Plateosauravus
Ruehleia
Plateosaurus
Eucnemosaurus
Unaysaurus
Riojasaurus
Coloradisaurus
Other Massospondylidae
Other prosauropods
Mussaurus
Melanorosaurus
Camelotia
Blikanasaurus
Lessemsaurus
Antetonitrus
Isanosaurus
Other Sauropoda
Permian
E. Tr.
Middle Triassic
Carnian
Norian
Rhaetian

already acquired, and the general increase in diversity, disparity and abundance the group attained in post-Triassic times.

EARLY DINOSAUR SYSTEMATICS: DEFINITIONS AND CONTROVERSIES

Historical burden links the definition of many biological groups to a stereotyped anatomy, based on the identification of one or more diagnostic attributes. Classic examples include bird feathers, arthropod jointed appendages, tetrapod fingers and so forth. In many cases, cladistic studies have shown the putative unique features to be homoplastic, that is, present outside the scope of the defined group or absent in some of its members. In addition, an emphasis on taxon-based, rather than character-based, definitions (e.g. P. C. Sereno 2005, *Stem Archosauria*, version 1.0, http://www.taxonsearch.org/Archive/stem-archosauria-1.0.php), coupled with unstable phylogenetic scenarios (Dominguez and Wheeler 1997), has led to major variations in the inclusivity of clades, and hence in their diagnostic traits. As for dinosaurs, Owen (1842) created the name to encompass a group of large fossil reptiles that shared several unusual characters of the pelvis and hips. Yet, in the last century, the understanding of the group has been more strongly tied to a taxon-based reasoning (Ornithischia plus Saurischia; Seeley 1887) than to a unique inherited anatomy. Indeed, even when saurischians and ornithischians were believed to have independent origins among archosaurs, they remained under the 'Dinosauria' epithet (e.g. Romer 1966). The last 30 years has witnessed the establishment of the Saurischia–Ornithischia sister-grouping as an uncontroversial hypothesis (Gauthier 1986), leading to the current taxon-based definition of Dinosauria (Padian and May 1993) and attempts to identify the diagnostic traits of the group (Novas 1996; Sereno 1999; Langer *et al.* 2009; Brusatte *et al.* 2010*a*).

The following sections discuss two contentious aspects of early dinosaur phylogeny. The first corresponds to the position of silesaurids as either ornithischians or non-dinosaurian dinosauromorphs. This debate shows that the practice of identifying diagnostic anatomical traits for Dinosauria, as much as for any major clade, has faded to be of very limited value, both over time and under divergent scientific contexts. Indeed, if a group is defined based on an apomorphic trait (an ever less common practice in vertebrate palaeontology), that trait will in most cases end up being its only uncontroversial diagnostic feature, as the discovery of new fossils tends to spread other putative apomorphies to more inclusive clades. Otherwise, in a taxon-based definition, diagnostic traits will depend on the inclusivity of the named clade, which will vary greatly as new phylogenetic hypotheses and fossils come into light. Luckily for science, there is no sign that either of these will stop appearing in the short term.

Silesaurus*: quo vadis?*

In 2003, Jerzy Dzik described *Silesaurus opolensis*, a new archosaur with clear dinosaur affinities from the Late Triassic of Poland. At the time, he suggested possible ornithischian, 'prosauropod' and non-dinosaurian affinities, but most recent studies have supported the latter (Ezcurra 2006; Irmis *et al.* 2007; Brusatte *et al.* 2010*b*; Nesbitt 2011), or less frequently the first (Langer and Ferigolo 2013), hypothesis. Subsequently, several fossil taxa with proposed affinities to *S. opolensis* have been identified in various parts of the world, including Argentina, Brazil, Morocco, the USA, Tanzania and Zambia, ranging in time from the Anisian to the Norian–Rhaetian (Nesbitt *et al.* 2010; Kammerer *et al.* 2012; Martínez *et al.* 2012*a*; Langer *et al.* 2013; Peecook *et al.* 2013). Together with their unusually long forearms, which suggest at least facultative quadrupedality, *S. opolensis* and some other silesaurids bear a peculiar toothless tip to the lower jaw, which was probably covered by a keratinous 'beak'. This beak not only suggested an herbivorous or omnivorous diet, as also hinted at by the shape of silesaurid teeth, but also formed the basis of the proposed affinity of the group to ornithischian dinosaurs (Ferigolo and Langer 2007), which also bear a toothless tip to the lower jaw, formed by a midline predentary bone.

Despite similarities in general shape and some vascular features (Ferigolo and Langer 2007), the homology between the predentary bone and the silesaurid beak has been disputed, mostly because the latter is formed by a pair of bones that are not fully detached from the respective dentary. In addition, various phylogenetic studies (Ezcurra 2006; Langer and Benton 2006; Irmis *et al.* 2007; Brusatte *et al.* 2010*b*; Nesbitt *et al.* 2010; Nesbitt 2011)

FIG. 1. Time-calibrated phylogeny of Triassic dinosauromorphs. Relationships conservatively compiled from Langer (2004), Ezcurra and Novas (2007), Ezcurra and Cuny (2007), Smith *et al.* (2007), Langer *et al.* (2009), Nesbitt *et al.* (2009), Alcober and Martinez (2010), Ezcurra (2010*a*), Apaldetti *et al.* (2011*a, b*), Cabreira *et al.* (2011), Butler *et al.* (2011), Martínez *et al.* (2011), Sues *et al.* (2011), Langer and Ferigolo (2013), Peecook *et al.* (2013) and Otero and Pol (2013). Stratigraphic data compiled from Kozur and Bachmann (2008), Langer *et al.* (2010, 2013), Irmis (2011), Irmis *et al.* (2011), Martínez *et al.* (2011), Nesbitt (2011) and Peecook *et al.* (2013). Timescale from Gradstein *et al.* (2012). Asterisk indicates alternative position for *Guaibasaurus candelariensis*. *Abbreviations*: E. Tr., Early Triassic.

scored putative dinosaur synapomorphies as absent in silesaurids (Fig. 2A). Of these, few unambiguously endured scrutiny by Langer and Ferigolo (2013), including an expanded upper temporal fossa, epipophyses on vertebrae from the front part of the neck and an asymmetrical trochanter for the attachment of the caudofemoral musculature on the femur (reversed in theropods). The revision of Langer and Ferigolo (2013) not only suggested that some Late Triassic silesaurids may nest within Ornithischia, but also cast doubt on the inclusivity of the silesaurid clade (see also Bittencourt *et al.* in press), which may not include Mid-Triassic forms such as *Lewisuchus admixtus*, *Pseudolagosuchus major* and *Asilisaurus kongwe*. Excluding the possible homology of the ornithischian predentary and the silesaurid beak, some other features (Fig. 2A) also suggest that silesaurids may nest among ornithischians (Langer and Ferigolo 2013, p. 383), but these characters are highly homoplastic and do not provide strong evidence of this relationship.

The lack of agreement on establishing the patterns of a relatively short segment of evolutionary history, such as dinosaur origins, not only reflects the presence of ambiguous evidence, but also the concentration of effort dissecting a ‘trendy’ research topic. If dealing with a less explored clade, evidence on inclusivity and diagnoses would not be so scrutinized. Indeed, the more an evolutionary segment is investigated, the more aware authors are of ambiguous or homoplastic characters, as seen in the current debate over the phylogenetic positions of taxa around the origin of birds (e.g. Mayr *et al.* 2005; Turner *et al.* 2012). This is also the case with very well known anatomical parts: it is symptomatic that the informative characters indicated in Figure 2 are concentrated in the front half of the dinosauromorph body, even though the pelvic girdle and limb are probably the better known parts of their anatomy. This lack of agreement, coupled with the major ghost lineages recognized in the fossil record of Triassic dinosauromorphs (Irmis 2011; Nesbitt

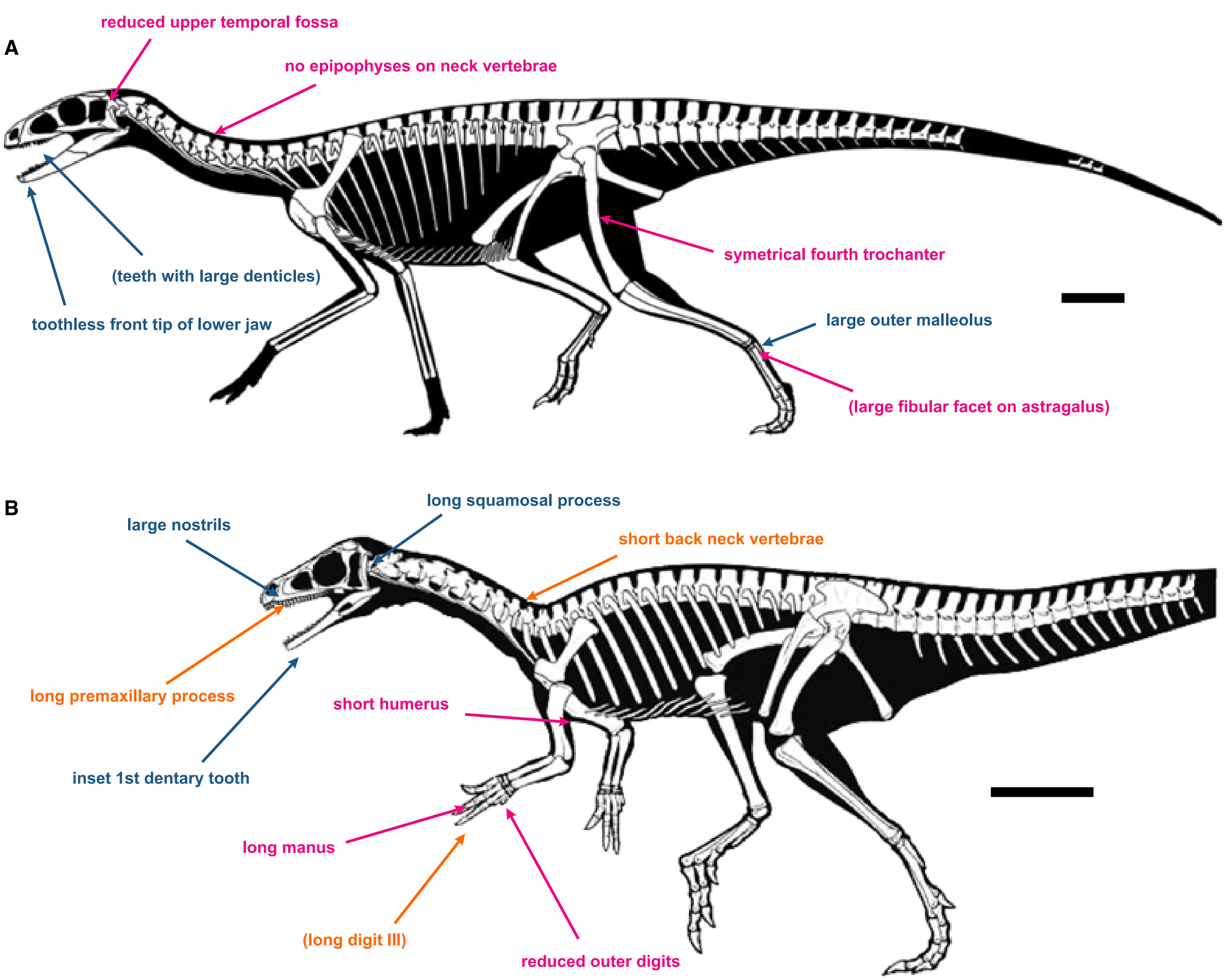

FIG. 2. Skeletal reconstructions of Triassic dinosauromorphs, with traits supporting alternative phylogenetic positions. A, *Silesaurus opolensis* (drawing by Scott Hartman); blue, ornithischian; magenta, non-dinosaur. B, *Eoraptor lunensis* (from Sereno *et al.* 2012); magenta, theropod; blue, sauropodomorph; orange, non-Eusaurischia. Less supported traits in brackets. Scale bars represent 10 cm.

et al. 2013), suggests the need to close those gaps as the great challenge for research on the origin of dinosaurs. Yes, more field work and new discoveries, abundant as they have been, are still needed.

Eoraptor *and basal saurischian relationships*

In the first edition of the compendium 'The Dinosauria', Hans-Dieter Sues was responsible for the first taxonomic chapter, '*Staurikosaurus* and Herrerasauridae' (Sues 1990). This was to some extent an outlier among the book's chapters, because it dealt with forms thought as likely falling outside of Saurischia and Ornithischia (Brinkman and Sues 1987), hence non-dinosaurian in the strict sense. More recently, as seen in the second version of the book (Weishampel *et al.* 2004), there has at least been agreement on the saurischian affinity of these South American forms (Sereno and Novas, 1992; Langer and Benton, 2006). In addition, many more basal saurischians have been since described from Late Triassic deposits (Bonaparte *et al.* 1999; Langer *et al.* 1999; Martinez and Alcober 2009; Nesbitt *et al.* 2009; Alcober and Martinez 2010; Ezcurra 2010*a*; Cabreira *et al.* 2011; Martinez *et al.* 2011). Although there is as yet no published disagreement as to the theropod nesting of *Eodromaeus murphi* and *Tawa hallae*, as well as on the sauropodomorph affinities of a group of small Carnian forms, including *Saturnalia tupiniquim*, *Panphagia protos*, *Chromogisaurus novasi* and *Pampadromaeus barberenai*, it is also true that most of these species were described in the last few years and their relationships have not yet been comprehensively revised by independent studies. In contrast, independent phylogenetic analyses continue to disagree on the position of the herrerasaurs as either theropods (Nesbitt *et al.* 2009; Nesbitt 2011) or as basal to the theropod–sauropodomorph dichotomy (Irmis *et al.* 2007; Ezcurra 2010*a*). The same is the case with *Eoraptor lunensis*, which was most recently suggested to belong to the sauropodomorph lineage (Martínez *et al.* 2011).

Twenty years after its original publication, we now have access to a very detailed account (Sereno *et al.* 2012) of the anatomy of *Eoraptor lunensis*, and it is possible to better assess its affinities. The nesting of *E. lunensis* within Theropoda was first proposed in the initial description of the taxon (Sereno *et al.* 1993) and subsequently supported by various authors (Novas 1996; Sereno 1999; Ezcurra 2010*a*; Nesbitt 2011; Sues *et al.* 2011). Of the many features once suggested to link *E. lunensis* to theropods, the few that endured recent scrutiny (Langer and Benton 2006; Martínez *et al.* 2012*b*; Sereno *et al.* 2012) are related to its raptorial arm, including a short humerus and long manus with reduced outer digits (Fig. 2B). Likewise, plesiomorphic features used to place *E. lunensis* basal to the sauropodomorph–theropod split (Langer 2004; Langer and Benton 2006) were reinterpreted by Sereno *et al.* (2012) as absent in the taxon, but minimally still include a long subnarial prong of the premaxillary bone and short vertebrae in the rear part of the neck (Fig. 2B). In contrast, characters proposed to link *E. lunensis* to Sauropodomorpha (Martínez *et al.* 2011, 2012*b*; Sereno *et al.* 2012) have yet to be independently reassessed. However, those listed by Martínez *et al.* (2012*b*) suffer from either poor definition, a highly homoplastic distribution, or their coding is dubious in *E. lunensis* (see Sereno *et al.* 2012) and cannot therefore be accepted as *prima facie* evidence of that affinity. Indeed, *E. lunensis* shares enlarged nostrils, a slender ventral prong of the squamosal bone and a slightly inset first tooth of the lower jaw with sauropodomorphs (Fig. 2B), but other features, such as a twisted first phalanx of the thumb and the cranial projection on the medial portion of the astragalus, are also seen in basal theropods, such as *Liliensternus liliensterni* and *Dilophosaurus wetherilli*, casting doubt upon their significance.

So what is behind such lack of agreement on the phylogenetic position of many basal saurischians? As with silesaurids, this may be in part due to the concentration of efforts on a popular research topic. Yet, it may also reveal peculiar aspects of that piece of evolutionary history, in which features that come to characterize the two main saurischian lineages occur more randomly among their basal members. These high homoplasy levels lead to ambiguous placement of taxa 'basal to' or 'at the base of' Theropoda and Sauropodomorpha. As a consequence, diagnostic traits are often only applicable within certain phylogenetic contexts, depending on the position of those taxa of uncertain affinities. For example, the status of various features that link *Eoraptor lunensis* to Neotheropoda depends on the position of herrerasaurs as their immediate outgroup, but could instead indicate just a eusaurischian affinity in the alternative scenario where herrerasaurs are not part of that group. Obviously, the more fossils we know, the better, but the description of more than one new basal saurischian per year for the last five years was not accompanied by a more stable scenario of relationships. Indeed, it seems that additional and better defined characters, as well as more comprehensive analyses of those characters already proposed (Sereno 2007), are more likely to help unravel basal saurischian evolution.

TIMING AND PATTERNS OF THE DINOSAUR RADIATION

Dinosaurs are the more diverse and better known components of a clade of gracile terrestrial archosaurs, the oldest records of which are inferred from footprints found in Olenekian (Early Triassic) rocks of Poland (Brusatte *et al.*

2011*a*). As such, dinosaurs are within a slightly larger radiation, Dinosauromorpha, that emerged less than 5 Ma after the great Permo–Triassic mass extinction (perhaps within 1 Ma if the Polish footprints are correctly attributed) and formed part of the ecosystem rebuilding that followed that event (Benton *et al.* 2014). In addition, the occurrence of *Asilisaurus kongwe* and *Nyasasaurus parringtoni* in the Manda beds of Tanzania (Nesbitt *et al.* 2010, 2013) suggests that close outgroups of dinosaurs, or even dinosaurs, arose shortly thereafter. In fact, the Anisian (Mid-Triassic) age of these taxa implies ghost lineages of about 5 Ma, spanning the entire Ladinian, in which dinosaurs or more closely related outgroups are to be identified. Considering the richness of deposits of that age in Brazil, Argentina, and possibly Namibia (Abdala *et al.* 2013), the search for dinosaurs in those rocks represents a major enterprise for the coming years. All this rests, however, on the assumption that the phylogenetic positions of *A. kongwe* and *N. parringtoni* as originally proposed are correct. Yet, both taxa are based upon specimens that are not directly associated, and the phylogenetic position of *A. kongwe* at least has been challenged (Langer and Ferigolo 2013). As for *N. parringtoni*, despite the comprehensive analysis of its anatomy and possible relationships provided by Nesbitt *et al.* (2013), the fact is that the material is too fragmentary and early dinosaur relationships too poorly constrained for a safe assessment of its affinities. Therefore, there is still no positive dinosaur record older than those of Carnian (Late Triassic) age from South America and elsewhere (Langer *et al.* 2009; Ezcurra 2012) and their immediate sister groups may be no older than the Ladinian (Langer and Ferigolo 2013), hinting at much less extensive ghost lineages than currently proposed.

As argued above, the Mid-Triassic record of dinosaurs is so uncertain that possible biogeographical patterns are not worth discussing. By contrast, their Carnian record is clustered in south Pangaea (Fig. 3), and the lack of dinosaurs in possibly coeval tetrapod-rich rocks of Europe and North America, such as the Lossiemouth Sandstone and Wolfville formations (Langer *et al.* 2009), corroborates the hypothesis of Late Triassic provinciality of faunas advocated by Ezcurra (2010*b*). It is also true, however, that north Pangaea deposits are not so abundant, and the above-mentioned not so well sampled or dated, possibly masquerading sampling biases as evolutionary or biogeographical patterns. Besides, more detailed patterns within south Pangaea, such as the cluster of dinosaurs within a subtropical to cool temperate arid belt (Ezcurra 2012), are harder to establish, mostly because the general distribution of all tetrapod bearing deposits is similar to that of dinosaurs. Nesbitt *et al.* (2009) suggested the South American protocontinent as the ancestral range of basal dinosaurs, but this result is surely in part driven by the superior (both more diverse and better preserved) record of South American basal dinosaurs, which form the bulk of early dinosaurs in phylogenetic analyses (Bittencourt and Langer, 2011). In turn,

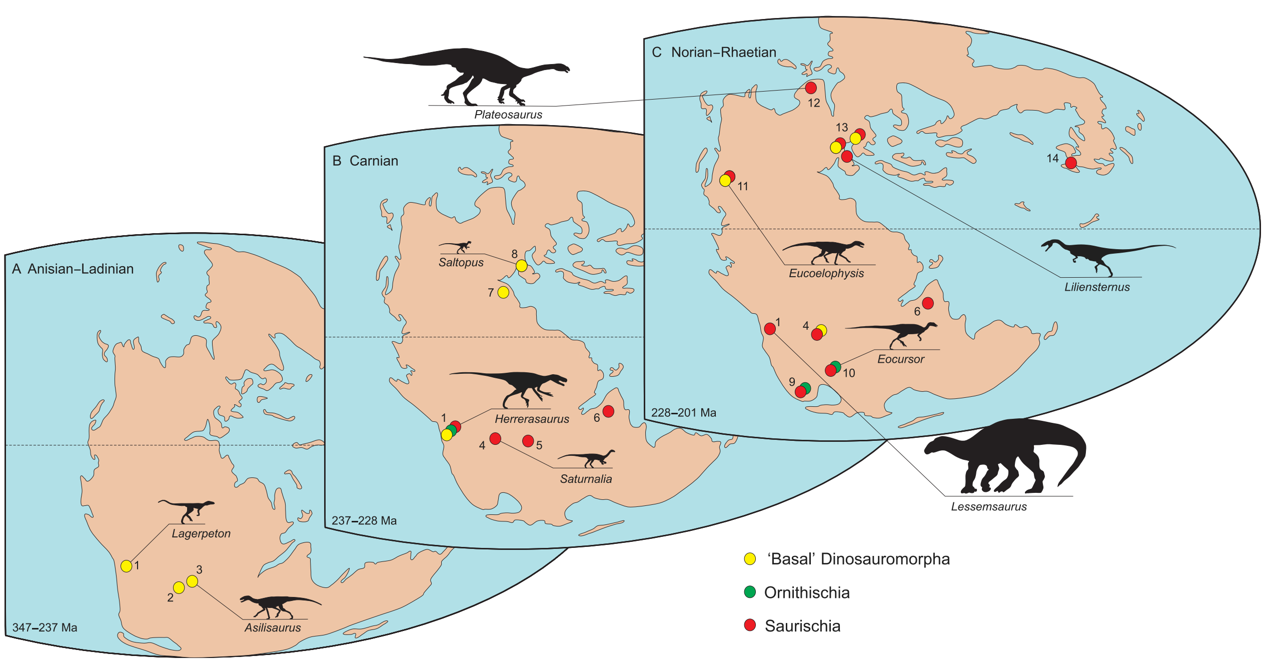

FIG. 3. Palaeogeographical distribution of dinosauromorph records. Mid- (A) and Late (B–C) Triassic maps from R. Blakey (*Mollewide plate tectonic maps*, http://jan.ucc.nau.edu/rcb7/mollglobe.html). Main occurrences are 1, north-western Argentina; 2, Zambia; 3, Tanzania; 4, south Brazil; 5, Zimbabwe; 6, India; 7, Morocco; 8, Scotland; 9, Patagonia; 10, South Africa; 11, western USA; 12, Greenland; 13, Europe (Germany, Poland, England and Wales); 14, Thailand.

this fossil richness, compared with that of other parts of the supercontinent (Ezcurra 2012), may, indeed, imply an origin of dinosaurs in south-western Pangaea. Later, during the Norian–Rhaetian (Fig. 3), dinosaurs spread across nearly the entire of Pangaea.

The strict assessment of taxa or fossils per geological period has been the base for most macroevolutionary studies of the patterns of the dinosaur radiation (Benton 1983; Ezcurra 2010*a*; Brusatte *et al.* 2011*b*), most of which concur on an abrupt increase in abundance or diversity of the group at some stage during the Late Triassic. Obviously, because no definite ornithischian or saurischian has yet been found prior to that stage, such an 'event' will always be identified during the Carnian. More recent studies, however, have attempted both to insert dinosaurs into a broader phylogenetic context and to employ more refined parameters to assess past diversity. Brusatte *et al.* (2008) and Irmis (2011), respectively, noted a continuous Mid–Late Triassic increase in the disparity of Avemetatarsalia (bird-line archosaurs, including dinosaurs and pterosaurs) and in the phylogenetic diversity of Dinosauromorpha (Fig. 4). By contrast, a notable size increase (a surrogate for diversity) was recognized only among sauropodomorphs in the early Norian (Irmis 2011), a pattern possibly related to the diversity loss of herbivorous dicynodonts (Sookias *et al.* 2012). Indeed, as dinosaur diversity and disparity appears to change at similar rates through the Triassic (Brusatte *et al.* 2008), there is no support for a disparity-first early burst model (Benton *et al.* 2014), and the rise of dinosaurs might have been a more gradual event than usually thought.

CONCLUSIONS: DIRECTIONS FOR FUTURE WORK

As with the study of the evolutionary (phylogenetic) patterns of perhaps all biological groups, the study of the dinosaur radiation suffers from the vicissitudes of modern science, while at the same time as, obviously, taking great advantage of it. Computers and algorithms are now capable of dealing with massive character–taxon phylogenetic data matrices; osteohistology permits ever more precise identification of the ontogenetic stage of fossil specimens; non-invasive image techniques (e.g. CT scanning, synchrotron) lead to anatomical studies in detail never imagined before. All these have allowed the leap in quality seen in works produced this century. However, prerequisites to all of these are laborious, small-scale aspects of anatomical and systematic research, such as carefully evaluation of morphological homologies, which have not been equally emphasized. As a mainly extinct group (ornithologists forgive me), the study of dinosaur relationships did not profit from the molecular phylogeny

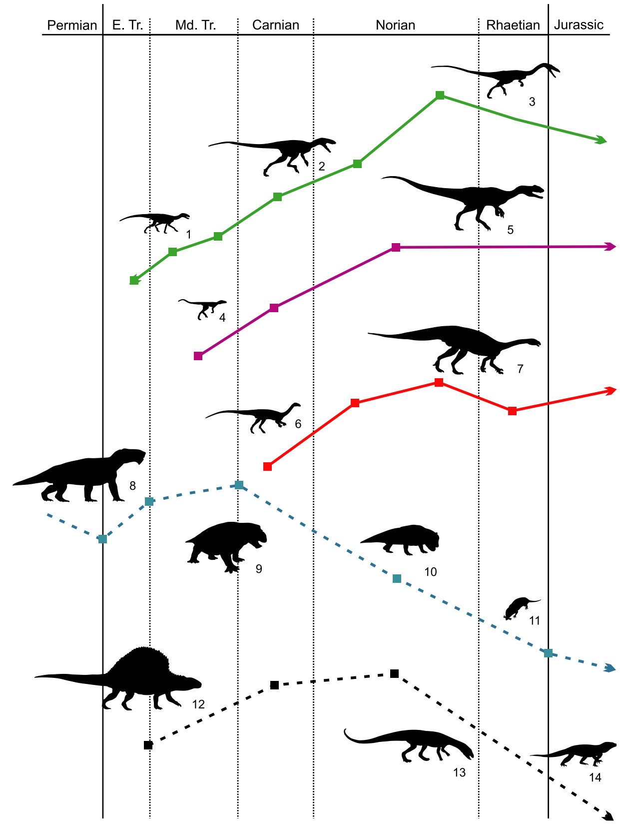

FIG. 4. Tetrapod macroevolutionary patterns through the Triassic. Green, dinosauromorph smoothed phylogenetic diversity (from Irmis 2011); purple, avemetatarsalian morphological disparity (from Brusatte *et al.* 2008); red, sauropodomorph body size estimate (from Irmis 2011); blue, therapsid body size estimate (from Sookias *et al.* 2012); black, crurotarsan morphological disparity (from Brusatte *et al.* 2008). *Silhouettes*: 1, silesaurid *Asilisaurus kongwe*; 2, herrerasaur *Staurikosaurus pricei*; 3, theropod *Coelophysis bauri*; 4, lagerpetid *Lagerpeton chanarensis*; 5, theropod *Zupaysaurus rougieri*; 6, sauropodomorph *Saturnalia tupiniquim*; 7, sauropodomorph *Plateosaurus engelhardti*; 8, gorgonopsian *Inostrancevia alexandri*; 9, dicynodont *Stahleckeria potens*; 10, cynodont *Scalenodontoides macrodontes*; 11, mammal *Adelobasileus cromptoni*; 12, ctenosauriscid *Arizonasaurus babbitti*; 13, poposaur *Effigia okeeffeae*; 14, crocodyliform *Protosuchus richardsoni*.

revolution. Hence, competent phylogenetic studies depend on time-consuming and non-state-of-the-art scoring of unambiguously defined anatomical characters and character states. Moreover, they depend on the correct identification of taxa, an issue only partially overcame by the sampling techniques of molecular studies.

As fossils are naturally incomplete, it is often more tricky for palaeontologists to assign specimens to well-defined species. Among Triassic dinosauromorphs, this happens in two different ways: isolated bones occurring in a single spot (e.g. Nesbitt *et al.* 2010; Langer and Ferigolo 2013) and partial skeletons occurring in the same site or stratigraphic unit (e.g. Novas 1993; Langer *et al*. 1999; Dzik 2003). In both cases, mistakes in the combination of specimens into taxa would be deadly harmful for phylogenetic inferences. Because it includes many taxa at the base of the dinosauromorph radiation (*Lagerpeton chanarensis*, *Marasuchus lilloensis*, *Pseudolagosuchus major* and *Lewisuchus admixtus*), some of them with several assigned specimens, the Mid-Triassic Chañares Formation, in Argentina, is a critical example of the second case (Langer *et al*. 2013). The choice here is to be as cautious as possible and only gather different specimens into terminal taxa for phylogenetic studies after comprehensive alpha-taxonomic revisions (which are usually lacking). The first case is slightly more complicated, as assembling isolated bones, in the absence of robust taphonomic evidence, always rests on indirect assumptions of 'phylogenetic signal' (Irmis *et al*. 2007; Kammerer *et al*. 2012). In these cases, one may run preliminary analyses without the 'putative chimera' operational taxonomic units and test their position or influence afterward. In the opposite direction is the description of similar taxa from coeval, or even the same deposits, as with Carnian members of the sauropodomorph lineage (Langer *et al*. 1999; Martínez and Alcober 2009; Ezcurra 2010*a*; Cabreira *et al*. 2011). In these cases, revisions of species level taxonomy (e.g. Novas 1993) are needed, to identify possible excessive splitting.

In sum, the radiation of dinosaurs can be said to be well understood at the broad scale, both considering its phylogenetic patterns and macroevolutionary processes. Obviously, there are various important issues still to be addressed, but several research groups are now firmly working on them. Indeed, the future of early dinosaur research is promising, and it will not be a surprise if, along with the recognition of new uncertainties, the current controversies are unravelled in the short term on the basis of new fossils and phylogenetic or macroevolutionary studies. For now, accumulated evidence suggests that, at the time of its occurrence, no extraordinary evolutionary changes accompanied the Saurischia–Ornithischia split at the origin of Dinosauria.

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