doi:10.1038/nature21700

A new hypothesis of dinosaur relationships and early dinosaur evolution

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For 130 years, dinosaurs have been divided into two distinct clades—Ornithischia and Saurischia. Here we present a hypothesis for the phylogenetic relationships of the major dinosaurian groups that challenges the current consensus concerning early dinosaur evolution and highlights problematic aspects of current cladistic definitions. Our study has found a sister-group relationship between Ornithischia and Theropoda (united in the new clade Ornithoscelida), with Sauropodomorpha and Herrerasauridae (as the redefined Saurischia) forming its monophyletic outgroup. This new tree topology requires redefinition and rediagnosis of Dinosauria and the subsidiary dinosaurian clades. In addition, it forces re-evaluations of early dinosaur cladogenesis and character evolution, suggests that hypercarnivory was acquired independently in herrerasaurids and theropods, and offers an explanation for many of the anatomical features previously regarded as notable convergences between theropods and early ornithischians.

During the Middle to Late Triassic period, the ornithodiran archosaur lineage split into a number of ecologically and phylogenetically distinct groups, including pterosaurs, silesaurids and dinosaurs, each characterized by numerous derived features[1]. By the Carnian stage of the Late Triassic (around 230 million years ago (Ma)), dinosaurs had diversified into three major lineages, Ornithischia, Sauropodomorpha and Theropoda, and, by the Norian stage (around 208 Ma), some dinosaur groups had become species-rich and numerically abundant[2]. Since 1887 (ref. 3) theropods and sauropodomorphs, which retain a classically reptile-like pelvic anatomy, have been regarded as forming a natural group (Saurischia), distinct from Ornithischia, which was characterized by 'bird-hipped' pelvic anatomy[3,4]. For nearly a century, ornithischians and saurischians were regarded as unrelated, each descended from a different set of 'thecodont' (a primitive archosaur) ancestors[5]. A formal hypothesis proposing dinosaur monophyly was proposed in 1974 (ref. 6), and consolidated in the 1980s[7]. As a direct result of these and other analyses, Ornithischia and Saurischia came to be regarded as monophyletic sister-taxa: this hypothesis of relationships has been universally accepted ever since[2,8–13].

Recent phylogenetic analyses of early dinosaurs have also supported the traditional scheme (Saurischia and Ornithischia), but those studies that concentrated on the earliest divergences within the clade have been limited to include only a handful of the relevant taxa and incorporate numerous a priori assumptions regarding the relationships within and between the higher taxonomic groups[8,9,14]. Most recent studies of basal dinosaur relationships have tended to focus on a handful of taxa contained within one or two dinosaur clades (usually Saurischia), with Ornithischia represented only as either a single supraspecific taxon or by a small number of basal forms, such as *Heterodontosaurus* and *Pisanosaurus*[2,10–12]. No studies on early dinosaur relationships have included an adequate sample of early ornithischians and the majority of studies have also excluded pivotal taxa from other major dinosaur and dinosauromorph (near dinosaur) lineages[2,10]. Furthermore, and possibly in part owing to the unique anatomy of ornithischians, many studies of early dinosaur evolution have tended to score ornithischian taxa only for either anatomical characters that are thought to be dinosaur symplesiomorphies (ancestral traits or characters shared by two or more taxa) or characters that are related to discussions of ornithischian monophyly[9,11,14]. As a result, these studies have incorporated numerous, frequently untested, prior assumptions with regard to dinosaur (and particularly ornithischian) character evolution, and have overlooked the possibility that some of the characters found in ornithischian taxa are homologues of those in saurischian dinosaurs, even though several authors have commented on the anatomical similarities shared by ornithischians and theropods[13–16]. In order to examine the possible effects of these biases on our understanding of dinosaur evolution, we carried out a phylogenetic analysis of basal Dinosauria and Dinosauromorpha and compiled, to our knowledge, the largest and most comprehensive dataset of these taxa to date. Although this study has drawn upon numerous previous studies, no prior assumptions were made about correlated patterns of character evolution or dinosaur interrelationships. The results of this study challenge more than a century of dogma and recover an unexpected tree topology that necessitates fundamental reassessment of current hypotheses concerning early dinosaur evolution, palaeoecology and palaeobiology.

We analysed a wide range of dinosaurs and dinosauromorphs, including representatives of all known dinosauromorph clades. Our dataset included taxa that allowed wide spatiotemporal sampling worldwide, from the Middle Triassic to Cretaceous, with particular emphasis on taxa from the Middle Triassic to Early Jurassic, with varied body sizes, morphologies and levels of skeletal completeness. We attempted, as objectively as possible, to score all taxa for all characters (where applicable), a level of inclusivity that is unmatched by previous studies. For example, we are, to our knowledge, the first to score basal ornithischian taxa, such as *Lesothosaurus diagnosticus* and heterodontosaurids, for characters obtained from studies that focused on early theropod or saurischian relationships[10,11]. In this way, we rigorously tested for anatomical similarities and differences between all of the included basal dinosaur taxa. However, some characters were inapplicable in some taxa and these were treated as uncertainties using the notation (−) in this analysis. Taxa were scored from a combination of personal observations, information from the literature and a small number of unpublished photographs.

In total 74 taxa were scored for 457 characters. Phylogenetic trees were produced and analysed in TNT 1.5-beta[17]. Bremer support decay indices were also calculated using TNT 1.5-beta[17]. Constraint trees

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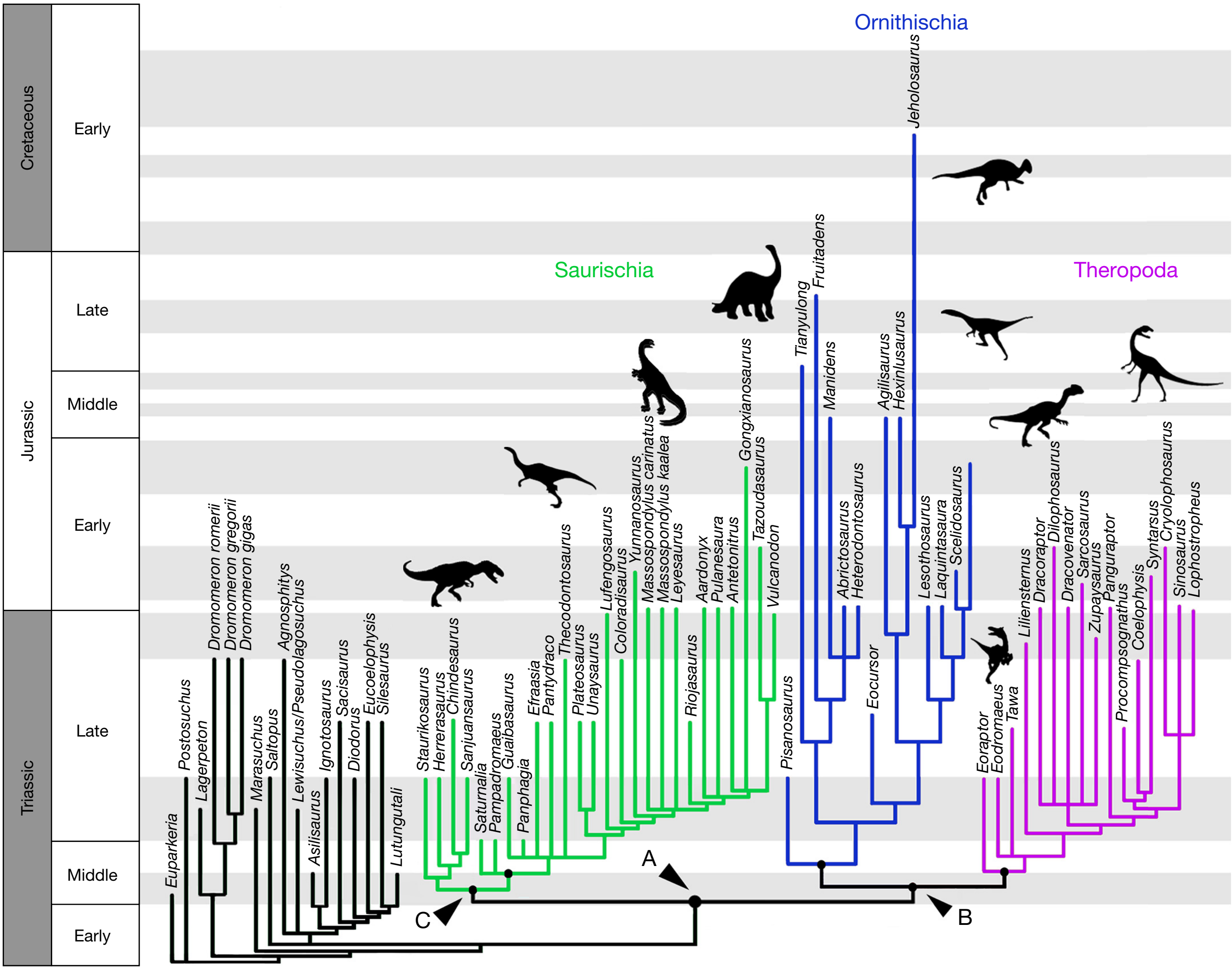

Figure 1 | Phylogenetic relationships of early dinosaurs. Time-calibrated strict consensus of 94 trees from an analysis with 73 taxa and 457 characters (see Supplementary Information). A, the least inclusive clade that includes *Passer domesticus*, *Triceratops horridus* and *Diplodocus carnegii*—Dinosauria, as newly defined. B, the least inclusive clade that includes *P. domesticus* and *T. horridus*—Ornithoscelida, as defined. C, the most inclusive clade that contains *D. carnegii*, but not *T. horridus*—Saurischia, as newly defined. For further information on definitions see Table 1. All subdivisions of the time periods (white and grey bands) are scaled according to their relative lengths with the exception of the Olenekian (Early Triassic), which has been expanded relative to the other subdivisions to better show the resolution within Silesauridae and among other non-dinosaurian dinosauromorphs.

were produced in order to investigate the differences in tree lengths between competing hypotheses of group interrelationships. For more information on the analyses, see the Supplementary Information.

Results

Our most notable result is the recovery of a sister-taxon relationship between Ornithischia and Theropoda (Fig. 1). This clade has not been recovered by any other numerical cladistic analysis of archosaur interrelationships and the implications of this result are important and far-reaching. For this clade, we propose reviving the name Ornithoscelida, which was originally proposed by Huxley for a group containing the historically recognized groupings of Compsognatha, Iguanodontidae, Megalosauridae and Scelidosauridae[18]. The formation of the clade Ornithoscelida is strongly supported by 21 unambiguous synapomorphies (see Fig. 2), including: an anterior premaxillary foramen located on the inside of the narial fossa; a sharp longitudinal ridge on the lateral surface of the maxilla; a jugal that is excluded from the margin of the antorbital fenestra by the lacrimal–maxilla bone contact (this appears convergently in some 'massospondylids'); an anteroventrally oriented quadrate; short and deep (length of more than twice the dorsoventral height) paroccipital processes; a post-temporal foramen that is entirely enclosed within the paroccipital process; a supraoccipital that is taller than it is wide; a well-developed ventral recess on the parabasisphenoid; a surangular foramen positioned posterolaterally on the surangular; an entirely posteriorly oriented retroarticular process, which lacks any substantial distal upturn; at least one dorsosacral vertebra anterior to the primordial pair; neural spines of proximal caudals that occupy less than half the length of the neural arches (which are also present in some sauropodomorphs, but absent in Herrerasauridae, *Guaibasaurus*[19], and nearly all sauropodomorphs as or more derived than *Plateosaurus*); scapula blade more than three times the distal width (also found in *Guaibasaurus*[19]); humeral shaft that has an extensively expanded ventral portion of the proximal end, creating a distinct bowing (convergently acquired in plateosaurids and more derived sauropodomorphs); absence of a medioventral acetabular flange (which was also lost in plateosaurids and more derived sauropodomorphs); a straight femur, without a sigmoidal profile (which was also acquired by more derived sauropodomorphs, but

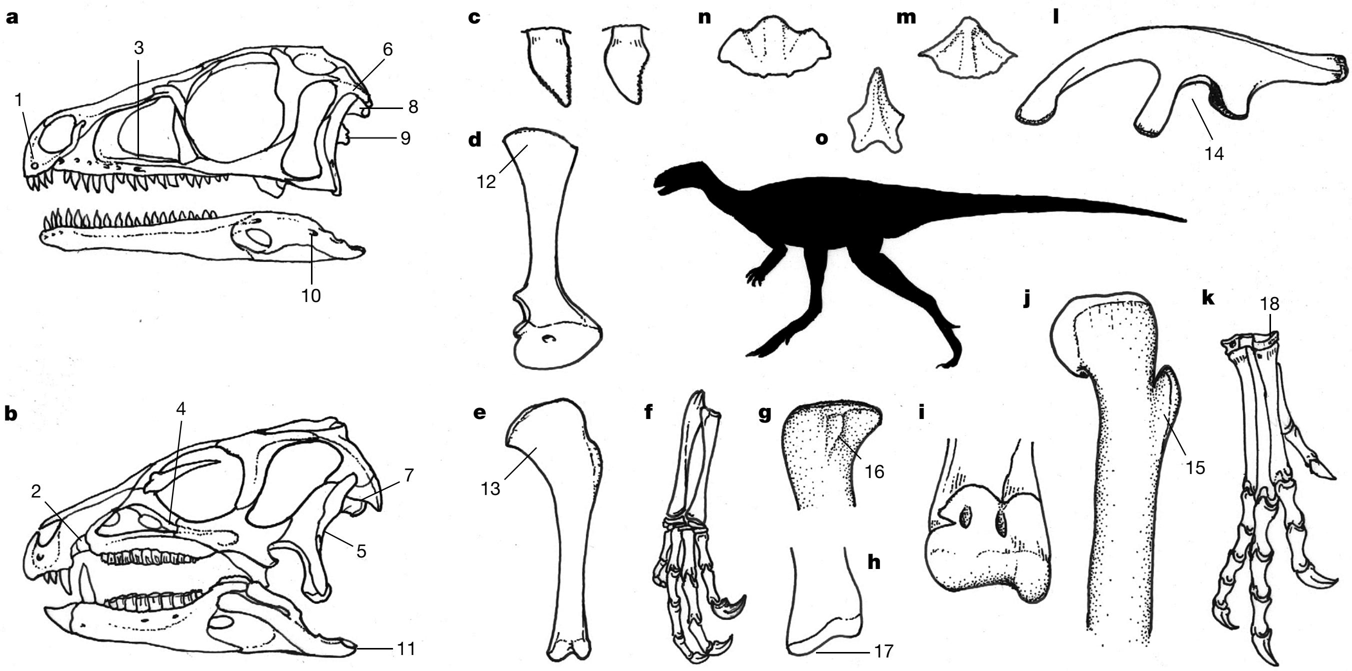

Figure 2 | Skeletal anatomy of ornithoscelidans. **a**, Skull of *Eoraptor lunensis* (PVSJ 512)[22]. **b**, Skull of *Heterodontosaurus tucki* (SAM-PK-K1332)[16]. **c**, Teeth of ornithoscelidans *E. lunensis* (PVSJ 512) (left) and *Laquintasaura venezuelae* (MBLUZ P.1396) (right). **d**, Scapula of *Lesothosaurus diagnosticus* (NHM UK PV R11000)[23]. **e**, Humerus of *Eocursor parvus* (SAM-PK-K8025). **f**, forelimb of *H. tucki* (SAM-PK-K1332). **g**, Proximal end of the tibia of *L. diagnosticus* (NHM UK PV RU B17). **h**, Distal end of the tibia of *L. diagnosticus* (NHM UK PV RU B17); **i**, Fused distal end of the tibia, fibula and proximal tarsals of *Fruitadens haagarorum* (LACM 115727)[15]. **j**, Femur of neotheropod *Dracoraptor hanigani* (NMW 2015.5G.1-11). **k**, Distal tarsals and pes of *H. tucki* (SAM-PK-K1332). **l**, Ilium of *H. tucki* (SAM-PK-K1332). **m**–**o**, Supraoccipitals of saurischian (**m**, **n**) and ornithoscelidan (**o**) dinosaurs showing the difference in height:width ratios observed in these clades. **m**, *H. ischigualastensis* (PVSJ 407). **n**, *Thecodontosaurus antiquus* (YPM 2192). **o**, *H. tucki* (SAM-PK-K1332). 1–18, select synapomorphies of Ornithoscelida: 1, anterior premaxillary foramen; 2, diastema; 3, sharp ridge on maxilla; 4, jugal excluded from antorbital fenestra; 5, anteroventrally oriented quadrate; 6, elongate quadrate–squamosal contact; 7, elongate paroccipital processes; 8, post-temporal foramen enclosed within paroccipital processes; 9, supraoccipital that is taller than it is wide; 10, foramen on lateral surface of dentary; 11, straight retroarticular process; 12, scapula, length $> 3\times$ distal width; 13, ventrally bowed humerus; 14, open acetabulum; 15, broadened anterior trochanter, partially separated from femoral shaft; 16, fibular crest; 17, oblique distal surface of tibia; 18, fusion of distal tarsals to metatarsals.

absent in basal forms such as *Saturnalia*[20] and *Pampadromaeus*[21], and is also absent in Herrerasauridae); a well-developed anterior trochanter that is broad and at least partly separated from the shaft of the femur; a strongly reduced fibular facet on the astragalus; a transversely compressed calcaneum with reduced posterior projection and medial process; a first metatarsal that does not reach the ankle joint, but that is instead attached ventrally to the shaft of metatarsal II; and fusion of the distal tarsals to the proximal ends of the metatarsals (Fig. 2). Other shared features included: a diastema between the premaxillary and maxillary tooth rows of at least one tooth crown's length; an extended contact between the quadratojugal and the squamosal bones; an anterior tympanic recess (convergently acquired in *Plateosaurus*); a fibular crest on the lateral side of the proximal portion of the tibia (described as present in *Eoraptor*[22], although we could not confirm its presence, which is also absent in *Tawa*[11]); an oblique articular end of the tibia in which the outer malleolus extends further distally than the inner malleolus (although this appears to be absent in *Pisanosaurus*; PVL 2577 (Instituto Miguel Lillo, Tucumán, Argentina)).

In addition to the characters described above, several other unusual anatomical features are shared by some members of Ornithoscelida including fusion of the sacral neural spines (as in *Lesothosaurus*[23] and *Megalosaurus*[24]); the presence of an antitrochanter on the ilium (in *Heterodontosaurus*[15] and numerous theropods); reduction of the distal end of the fibula (in *Heterodontosaurus, Tianyulong, Fruitadens*[15,25] and numerous theropods); fusion of the tibia, fibula and proximal tarsals into a tibiotarsus (as in *Heterodontosaurus*[15], *Coelophysis* and '*Syntarsus*'[26]); and fusion of the metatarsals (as in *Heterodontosaurus*[14] and *Syntarsus*[25]). Together, these characters seem to suggest a more complex relationship among basal dinosaurs than can be explained by traditional models. However, these characters do not currently optimize as synapomorphies of any large clade within our trees, mostly owing to a lack of information on some taxa, which stems from the incompleteness of the fossil record. Future studies and, critically, new discoveries, may yet reveal the nature of these characters and their distribution within Dinosauria.

The new clade Ornithoscelida is well supported, with a Bremer support of 4. Additionally, Ornithischia, Theropoda, Sauropodomorpha and Herrerasauridae are also well supported with Bremer support values of 4, 3, 3 and 3, respectively. With all taxa included, Saurischia (new definitions—see below) has a relatively low Bremer support value of 2. Further to this, Dinosauria[27] is also poorly supported, with a Bremer support value of 1. However, further investigation of the causes of the decay values of Dinosauria, Sauropodomorpha and Saurischia showed that a small number of poorly known basal dinosauromorph taxa tended to move out of the groups that they are more traditionally associated with and into various positions within Sauropodomorpha and Saurischia in a small number of suboptimal trees (trees with overall length >1,734 steps). Excluding *Saltopus elginensis*, *Agnosphitys cromhallensis*, *Eucoelophysis baldwini* and *Diodorus scytobrachion*, all of which have relatively low levels of skeletal completeness, when compared to most of the other taxa in our study, increases the Bremer support values for each of the major clades. Notably, Dinosauria and Saurischia exhibit Bremer support values of 3 and 4, respectively. Dinosauria + Silesauridae[1] were found to have a Bremer support value of 2 in this analysis (Extended Data Fig. 1).

By producing a constraint tree in TNT[17], we were able to calculate the number of additional steps it would take to recover a traditional clade Saurischia[3,28]. We found that, with all taxa that are traditionally regarded as saurischians included and forced into a single monophyletic group, 20 additional steps would be needed to recover Saurischia as previously defined[28]. This gives strong support to our recovery of a paraphyletic Saurischia and a monophyletic Ornithoscelida. Furthermore, additional analyses that experimented with alternative outgroup taxa and character ordering also produced the same results as in the main analysis (Extended Data Figs 2–4). These analyses are described in more detail in the Supplementary Information.

The recovery of Sauropodomorpha outside the Ornithischia–Theropoda dichotomy is an unexpected result, leading to the break-up of Saurischia as it has been defined traditionally[3]. Sauropodomorpha exhibit much higher relative abundance and taxic diversity than ornithischians and theropods in the Triassic and Early Jurassic[29], a phenomenon that is yet to be explained adequately. It has previously been suggested that, for Ornithischia at least, their later appearance in the fossil record and relatively low abundance in the Triassic and Early Jurassic, especially when compared with that of Sauropodomorpha, might be a direct result of a different origin of Ornithischia than traditionally hypothesized[14]. Although our study suggests that there may be an alternative origin for Ornithischia within Dinosauria, our hypothesis does not yet provide an explanation of the observed differences in species richness between the main dinosaurian clades during this time.

Herrerasauridae is recovered as the sister clade to Sauropodomorpha, suggesting that some of the theropod-like features of their anatomy have evolved independently of those found in theropods. This is most likely a direct result of their fully carnivorous feeding strategy; in our hypothesis a fully carnivorous feeding strategy is not recovered as the plesiomorphic condition for Dinosauria and we are forced to interpret some of the anatomical similarities between herrerasaurids and theropods as convergences. The convergent evolution of hypercarnivore morphology within Dinosauria raises interesting questions about the drivers of early dinosaur evolution. For example, did a dentition composed exclusively of sharp, recurved and serrated teeth, such as those that are present in representatives from both of these clades, evolve independently of each other? The earliest representatives of each of the major dinosaur clades often possess at least some recurved, serrated teeth, most commonly as part of a heterodont dentition. However, no known members of Sauropodomorpha or Ornithischia exhibit dentitions that are exclusively composed of recurved, serrated teeth, nor does the early theropod *Eoraptor*. Hence, it seems probable, within our new framework, that at least some of the recurved, serrated teeth that make up the dentition of derived theropods and herrerasaurids have convergently adopted this morphology. Furthermore, the rostral extension of the dentary tooth row appears also to be convergent between theropods and herrerasaurids; in members of both clades, the dentary tooth row extends to the rostral tip of the dentary. It is also possible, however, that this character represents a dinosaur symplesiomorphy and its functional significance is unknown.

Dinosauria is recovered in a polytomy with Silesauridae and the enigmatic Late Triassic British taxon *Saltopus elginensis*. This, along with the placement of another enigmatic British taxon, *Agnosphitys cromhallensis*, as a basal member of Silesauridae also provides some evidence for a Laurasian origin for Dinosauria and Silesauridae (silesaurids are represented by European and North American taxa[1]). This challenges over two decades of thinking on dinosaur origins and evolution, which placed these events firmly within Gondwana, and suggests that more attention should be focused on the discovery of new Middle–Late Triassic dinosauromorph-yielding localities in the Laurasian landmass.

Table 1 | The proposed set of definitions for the major dinosaurian clades

Clade	Definition
Dinosauria	The least inclusive clade that includes *P. domesticus*, *T. horridus* and *D. carnegii*
Ornithoscelida	The least inclusive clade that includes *P. domesticus* and *T. horridus*
Saurischia	The most inclusive clade that contains *D. carnegii*, but not *T. horridus*
Theropoda	The most inclusive clade that contains *P. domesticus*, but not *D. carnegii* or *T. horridus*
Ornithischia	The most inclusive clade that contains *T. horridus*, but not *P. domesticus* or *D. carnegii*
Sauropodomorpha	The most inclusive clade that contains *D. carnegii*, but not *T. horridus*, *P. domesticus* or *H. ischigualastensis*
Herrerasauridae	The least inclusive clade that includes *H. ischigualastensis* and *Staurikosaurus pricei*[37]

Definitions

Our tree topology requires new definitions for several clades within Dinosauromorpha. Following previous suggestions, we use three well-known, deeply nested species as the specifiers within our new definitions—*Passer domesticus* (a theropod), *Triceratops horridus* (an ornithischian) and *Diplodocus carnegii* (a sauropodomorph). The consistent use of these three taxa, in various combinations, provides a simple framework around which future studies can operate.

As Dinosauria[27] is currently defined as the least inclusive clade that includes *P. domesticus* and *T. horridus*[28], our newly proposed topology would result in the exclusion of Sauropodomorpha from Dinosauria. To circumvent this and to maintain taxonomic stability, we redefine Dinosauria as the least inclusive clade that includes *P. domesticus*, *T. horridus* and *D. carnegii*. The addition of *Diplodocus* to the definition of Dinosauria guarantees that Sauropodomorpha, Ornithischia and Theropoda will remain within the higher-level clade irrespective of changes to future phylogenetic hypotheses. The fundamental interrelationships of the major dinosaurian lineages, as well as the position of basally positioned taxa such as *Herrerasaurus* and *Eoraptor*, would then have no effect on the definition of Dinosauria, provided that the new definitions, which we propose, are adopted (see Table 1).

The current definition of Theropoda—the most inclusive clade containing *P. domesticus* but not *Saltasaurus loricatus*[28]—is problematic as it would, within our new hypothesis, force the inclusion of ornithischians. Ornithoscelida was coined 11 years before Theropoda[17,30] and so it could be argued that Theropoda should become obsolete by reason of priority when definitions result in these two names encompassing the same set of taxa. In order to maintain Theropoda in its more traditional sense[30], we propose a change in the definition—all taxa more closely related to *P. domesticus* than to either *D. carnegii* or *T. horridus*. We also propose a new definition of Sauropodomorpha, in order to better maintain the stability of this clade through future amendments to the dinosaur tree. We modify the currently held definition[31] and propose a new definition—all taxa more closely related to *D. carnegii* than to *T. horridus*, *P. domesticus* or *Herrerasaurus ischigualastensis*.

We revive the name Ornithoscelida to encompass the clade defined by *Triceratops* and *Passer* because the name, as originally coined in 1870, was designed to reflect the very bird-like hindlimbs of dinosaurs such as *Megalosaurus* and *Iguanodon*[18]. Given the number of features of the hindlimb that are shared exclusively among members of this new clade, it seems an appropriate choice; not only this, but its junior status with respect to Dinosauria[18,27] provides an element of taxonomic stability, while further work is carried out on this critical part of the tree.

Discussion

Our hypothesis forces a re-evaluation of previous scenarios of early dinosaur evolution and diversification. The recovery of two distinct clades, Ornithoscelida and Saurischia, provides several challenges to established hypotheses concerning the anatomy, palaeobiology and palaeobiogeography of early dinosaurs. For example, there has been much debate concerning the appearance of the common ancestor of the dinosaurs and its way of life, and recent discoveries[11,19–22] have shed some light on these matters. However, a number of key issues remain hotly contested, including the ancestral dinosaur's body plan, size, stance, method of locomotion and diet, as well the clade's centre of origin[32].

Recent studies have led to a general consensus that the earliest dinosaurs were relatively small and bipedal[8,14,15,20–23,32], and this idea finds further support within our hypothesis, as both basal sauropodomorphs and basal ornithoscelidans are small bipeds (Fig. 2, silhouette). Manus anatomy in many early dinosaurs also appears to be very similar, with supinated, non-weight-bearing, 'grasping' hands appearing in basal saurischians such as *Herrerasaurus* (PVSJ 373 (Museo de Ciencias Naturales, San Juan, Argentina)) and basal ornithoscelidans such as *Heterodontosaurus* (SAM-PK-K1332 (Fig. 2f) (Iziko South African Museum, Cape Town, South Africa)) and *Eoraptor* (PVSJ 512). As pointed out in several previous studies[15,33,34], these similarities were often considered to represent convergences given the supposedly distant relationship between taxa such as *Heterodontosaurus* and *Herrerasaurus*. Within our new framework, the supinated, grasping hands seen in some early taxa are interpreted as the primitive dinosaurian condition. It may be that the ability to grasp with the manus played an important role in early dinosaur evolution, perhaps related to feeding, and it is possible that the evolution of bipedality (and the removal of the manus from locomotion) allowed this grasping ability to evolve in early dinosaurs, conferring some sort of evolutionary advantage over contemporary ornithodiran and archosaurian groups, eventually leading to the dinosaurs' increase in prominence during the Mesozoic era.

In terms of diet, carnivory, herbivory and omnivory have all been suggested for early dinosaurs, but current hypotheses of dinosaur relationships render this issue ambiguous[35]. The heterodont dentition of basal sauropodomorphs such as *Pampadromaeus*[21], *Panphagia* and *Pantydraco*[8] suggest that members of basal Sauropodomorpha experimented with omnivory in the group's early stages. In our model, Theropoda and Ornithischia are united into a clade, the basal members of which, such as *Heterodontosaurus* and *Eoraptor* (Fig. 2a, b), have heterodont dentitions. This also suggests an omnivorous ancestral state for Ornithoscelida. Taken together, this suggests strongly that ancestral dinosaurs were omnivorous, as the two largest clades within Dinosauria appear to be ancestrally omnivorous. The basal saurischian group Herrerasauridae evidently contains carnivores (for example, *Herrerasaurus*: PVSJ 407 and *Sanjuansaurus*: PVSJ 605), but given the condition in Sauropodomorpha and Ornithoscelida, this now appears to be more likely a derived condition. In addition, the proximate sister taxon to Dinosauria (or Dinosauria and *Saltopus*), Silesauridae, comprises mostly herbivores such as *Silesaurus*, *Asilisaurus* and *Diodorus*, adding further weight to this interpretation. However, it should be noted that the most basal members of Silesauridae in our hypothesis, *Lewisuchus*/*Pseudolagosuchus*[1,36] and *Agnosphitys*, show anatomical features that are indicative of carnivory[35,36]. New discoveries relating to this part of the dinosauromorph tree may shed further light on this issue, but within our new hypothesis omnivory seems to be the most likely feeding strategy of early dinosaurs.

Our hypothesis also presents a challenge to previous thinking on dinosaur origins, in terms of its geographic and temporal setting. Owing to the discovery of numerous early and basally diverging dinosaurs and their dinosauromorph outgroups in southern South America and eastern Africa, previous work on dinosaur origins has favoured a Gondwanan origin for Dinosauria, sometime during the Anisian stage of the Triassic period[1,2,11,13,19–22,32]. Our new model suggests that, as a result of the position of a number of key taxa (see Supplementary Information), the origin of dinosaurs may not have been Gondwana, but rather somewhere in Laurasia. Furthermore, our analyses places the origin of dinosaurs at the boundary of the Olenekian and Anisian stages (around 247 Ma), slightly earlier than has been suggested previously and, similarly, some of the key divergences within the clade may also have occurred in the late Middle and very earliest Late Triassic[2,32] (Extended Data Fig. 5).

Our hypothesis for dinosaur relationships and evolution, with the recovery of two new, major clades, reframes the debate about dinosaur origins. The timing and geographical setting of dinosaur evolution may require reappraisal and our proposal raises numerous questions about the ancestral dinosaur's body plan, the sequence of evolution of key anatomical features within the clade, and the timing of this radiation. This work provides a new framework for addressing fundamental questions regarding these iconic animals.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 13 September 2016; accepted 10 February 2017.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We thank S. Chapman (Natural History Museum, London, UK), R. Smith (Iziko South African Museum, Cape Town, South Africa), E. Butler (National Museum, Bloemfontein, South Africa) B. Zipfel (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa), J. Powell (Instituto Miguel Lillo, Tucumán, Argentina), R. Martinez (Museo de Ciencias Naturales, San Juan, Argentina) and D. Pol (Museo Paleontológico Egidio Feruglio, Trelew, Argentina) for access to specimens in their care, R. Butler, J. Choiniere, B. McPhee, C. VanBuren and K. Chapelle for helpful discussion, M. Williams for assisting with the production of figures, and C. Baron for helpful comments on the manuscript, and the Willi Hennig Society for making TNT 1.5-beta software freely available. Funding for M.G.B. was provided by a NERC/CASE Doctoral Studentship (NE/L501578/1).

Author Contributions M.G.B., P.M.B. and D.B.N. designed this research project. M.G.B., D.B.N. and P.M.B. contributed data. M.G.B. conducted the phylogenetic analyses. M.G.B, D.B.N. and P.M.B. wrote the manuscript. M.G.B. and D.B.N. produced the figures.

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Reviewer Information *Nature* thanks K. Padian, H.-D. Sues and the other anonymous reviewer(s) for their contribution to the peer review of this work.

METHODS

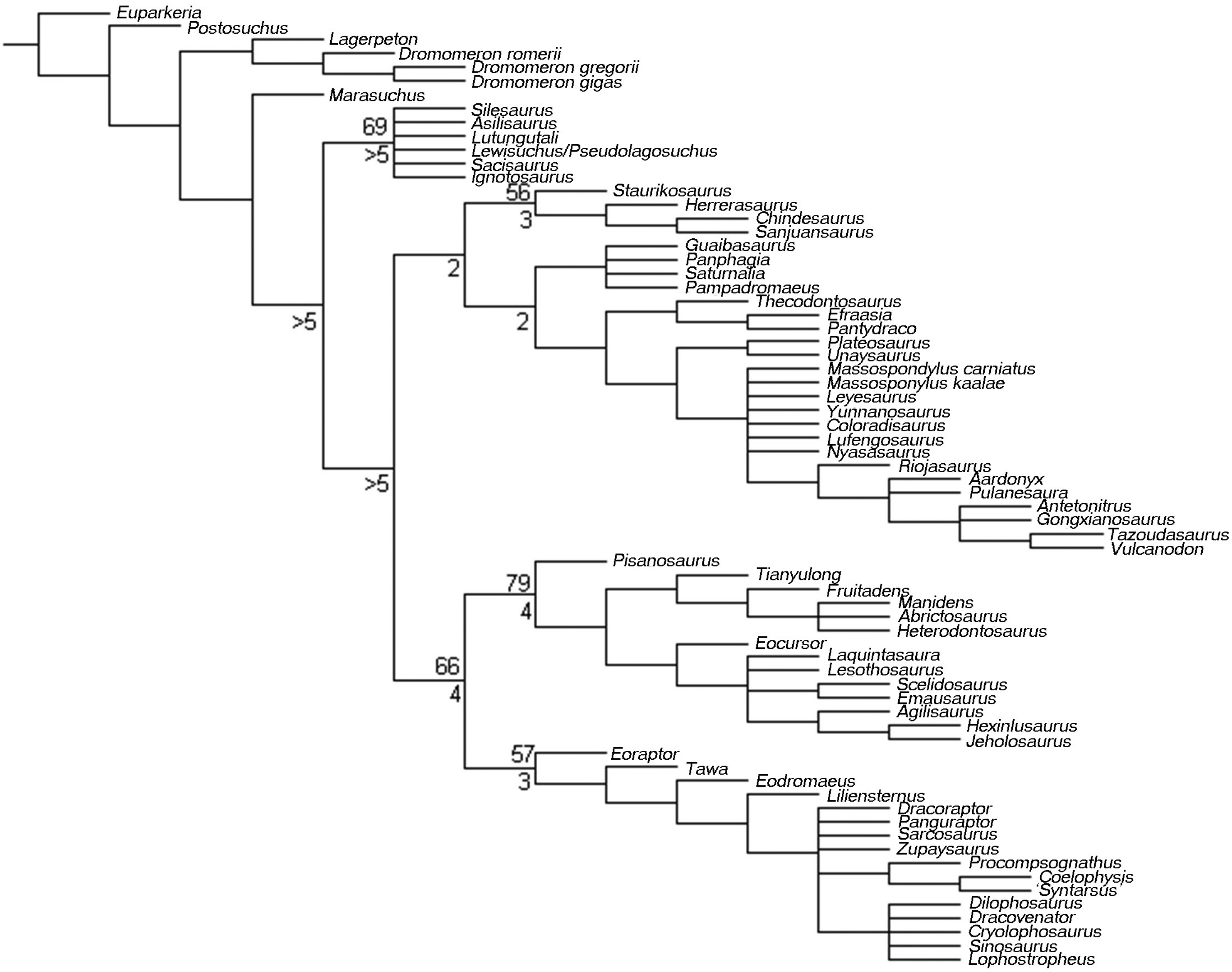
Trees were produced and analysed in TNT 1.5-beta[17]. In total 74 taxa were scored for 457 characters. Using the new technology search function, with ratchet and drift set to their defaults (10 iterations and 10 cycles, respectively) and with 100 random additional sequences.

The following characters were treated as ordered: 24, 35, 39, 60, 68, 71, 117, 145, 167, 169, 174, 180, 197, 199, 206, 214, 215, 222, 251, 269, 272, 286, 289, 303, 305, 307, 313, 322, 333, 334, 338, 353, 360, 376, 378, 387, 393, 442, 446.

Bremer support values were calculated and constraint trees were produced using TNT 1.5-beta[17].

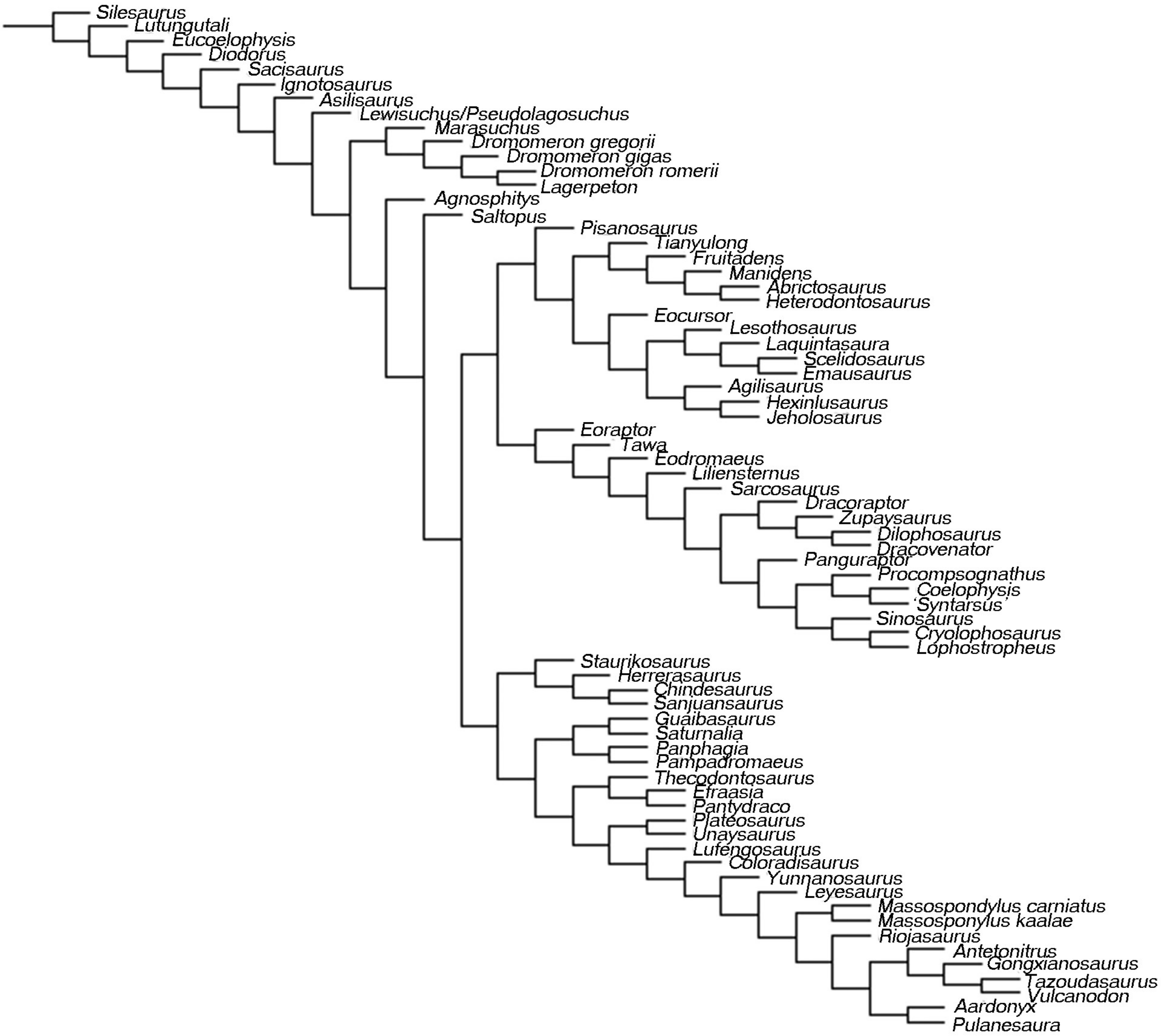
No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Data availability. All data generated or analysed during this study are included in this published article (and its Supplementary Information).

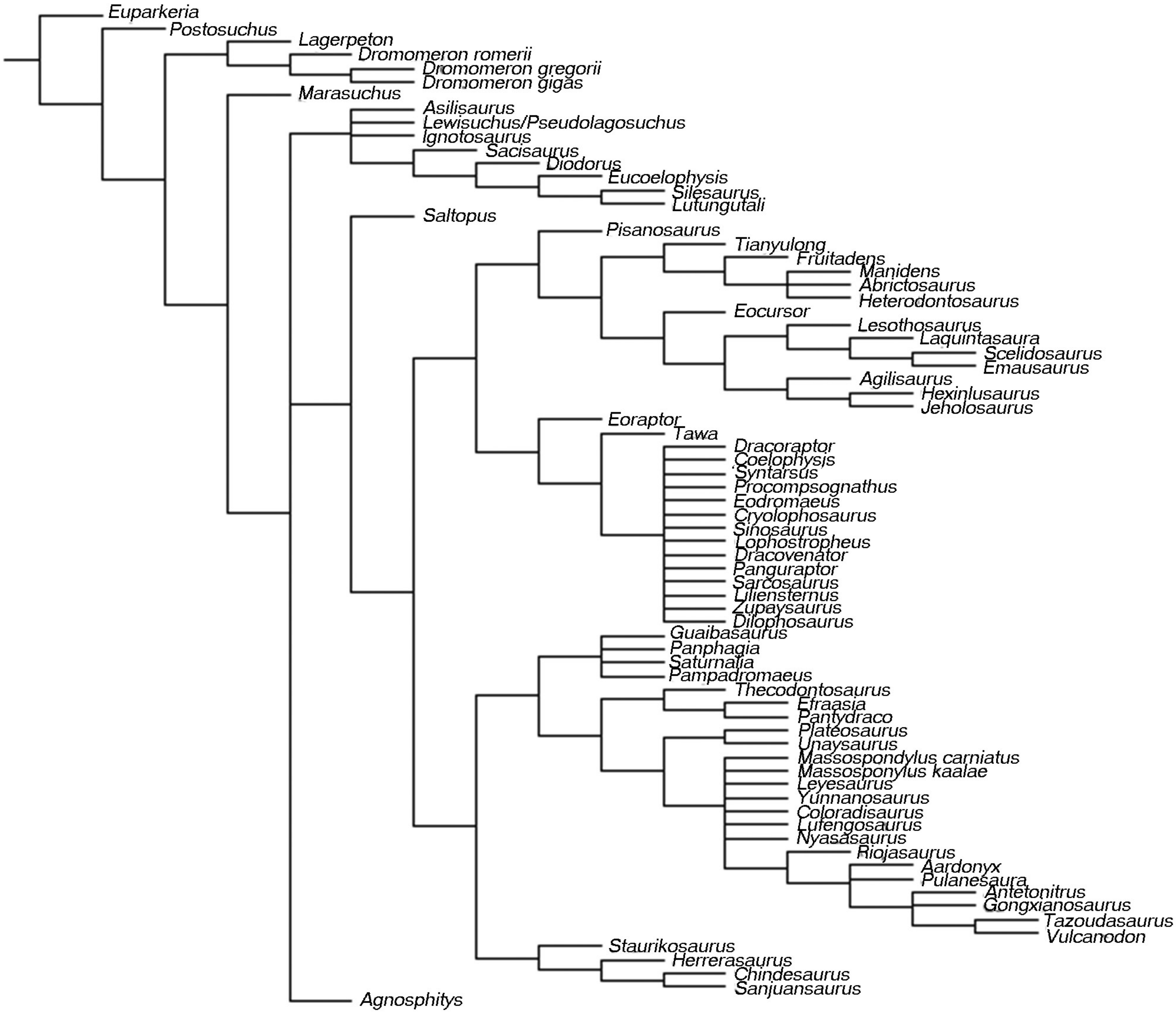


Extended Data Figure 1 | Reduced strict consensus tree of the main analysis showing bootstrap frequencies (above node) and Bremer support values (below node) that were calculated for each of the major nodes, after the exclusion of *Saltopus elginensis*, *Agnosphitys cromhallensis*, *Eucoelophysis baldwini* and *Diodorus scytobrachion*. Ornithoscelida, Ornithischia, Theropoda, Herrerasauridae, Dinosauria and Silesauridae are all very well supported, with Bremer support values of 3 or more. Saurischia (new definition) and Sauropodomorpha are less well supported, with Bremer support values of 2. Bootstrap frequencies below 50 are not shown.

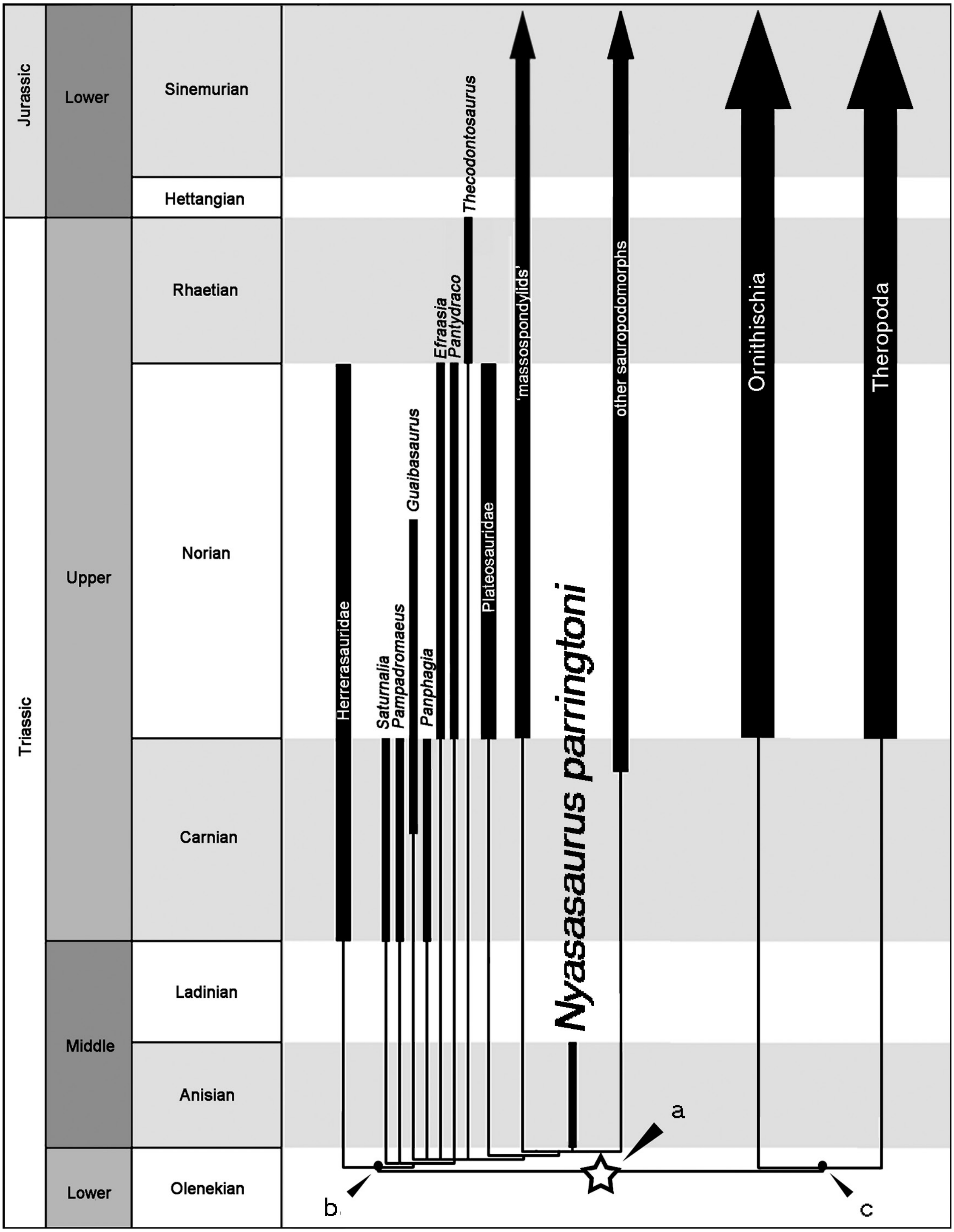
Extended Data Figure 2 | Strict consensus tree produced when *Dimorphodon macronyx* was included in the dataset and chosen as the outgroup taxon (*Euparkeria capensis* and *Postosucus kirkpatricki* were not included). The tree was produced from 79 MPTs (most parsimonious trees) each with a length of 1,627 steps. As in Extended Data Fig. 1, the clades Ornithoscelida and Sauropodomorpha plus Herrerasauridae (Saurischia, new definition) are both recovered. For further details on the additional analyses that were carried out as part of this study, see the Supplementary Information.



Extended Data Figure 3 | Strict consensus tree produced when the non-dinosaurian silesaurid taxon *Silesaurus opolensis* was chosen as the outgroup taxon. The tree was produced from 83 MPTs each with a length of 1,713 steps. For further details on the additional analyses that were carried out as part of this study, see the Supplementary Information.



Extended Data Figure 4 | Strict consensus tree produced when no characters were treated as ordered. Tree was produced from 83 MPTs each with a length of 1,690 steps. The clades Ornithoscelida and Saurischia (new definition, see Table 1) are both recovered in this analysis. For further details on the additional analyses that were carried out as part of this study, see the Supplementary Information.



Extended Data Figure 5 | Strict consensus tree set against the geological timescale, showing the predicted Early Triassic divergence dates of Dinosauria (star) and of the major dinosaurian lineages when the potential 'massospondylid' sauropodomorph *Nyasasaurus parringtoni* is included in the analysis. **a**, Origin of Dinosauria (new definition) when *Nyasasaurus* is considered. **b**, Origin of Saurischia (new definition) when *Nyasasaurus* is considered. **c**, Origin of Ornithoscelida when *Nyasasaurus* is considered. For further details on the additional analyses that were carried out as part of this study, see the Supplementary Information.