

A novel hypothesis of dinosaur relationships and early dinosaur evolution

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For nearly 130 years dinosaurs have been divided into two distinct clades – Ornithischia and Saurischia. Here, we present a radical new hypothesis for the phylogenetic relationships of the major dinosaurian groups, one that challenges the current consensus concerning early dinosaur evolution and highlights problematic aspects of current cladistic definitions. Our study recovers, for the first time, a sister-group relationship between Ornithischia and Theropoda (Ornithoscelida), with Sauropodomorpha + Herrerasauridae 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 the independent acquisition of hypercarnivory in herrerasaurids and theropods, and offers an explanation for many of the anatomical features previously regarded as striking convergences between theropods and early ornithischians.

During the Middle–Late Triassic, the ornithodiran archosaur lineage split into a number of ecologically and phylogenetically distinct groups, including pterosaurs, silesaurids and dinosaurs, each characterised by numerous derived features¹. By the Carnian stage of the Late Triassic (~230 Ma), dinosaurs had diversified into three major lineages, Ornithischia, Sauropodomorpha and Theropoda, and, by the Norian (~208 Ma), some dinosaur groups had become species-rich and numerically abundant². Since 1887³ theropods and sauropodomorphs, which retain a classically ‘reptile-like’ pelvic anatomy, have been regarded as forming a natural group (Saurischia), distinct from the Ornithischia, which was characterised 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’ (= primitive archosaur) ancestors⁵. A formal hypothesis proposing dinosaur monophyly was proposed in 1974⁶, and consolidated in the 1980s⁷. 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 concentrating 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 included^{8,9,14}. Most recent studies on 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 include an adequate sample of early ornithischians and the majority also exclude pivotal taxa from other major dinosaur and dinosauromorph lineages^{2,10}. Furthermore, and possibly in part due to the unique anatomy of ornithischians, many studies on early dinosaur evolution tend to score ornithischian taxa only for characters that are thought to be either dinosaur symplesiomorphies or characters that are

related to discussions of ornithischian monophyly^{9,11,14}. As a result, these studies incorporate numerous, frequently untested, prior assumptions regarding dinosaur (and particularly ornithischian) character evolution and have overlooked the possibility that some of the characters exhibited by ornithischian taxa are homologues of those in saurischian dinosaurs, even though several authors have commented on the anatomical similarities shared by ornithischians and theropods¹³⁻¹⁶. In order to examine the possible effects of these biases on our understanding of dinosaur evolution, we undertook a novel phylogenetic analysis of basal Dinosauria and Dinosauromorpha, compiling the largest and most comprehensive dataset set of these taxa ever assembled. 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 a novel and unexpected tree topology that necessitates fundamental reassessment of current hypotheses concerning early dinosaur evolution, palaeoecology and palaeobiology.

We examined a wide range of dinosaurs and dinosauromorphs, including representatives of all known dinosauromorph clades. Our dataset included taxa providing wide spatiotemporal sampling (worldwide from the Middle Triassic–Cretaceous, with emphasis on Middle Triassic–Early Jurassic taxa), 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 unmatched by previous studies. For example, we are the first to score basal ornithischian taxa, such as *Lesothosaurus diagnosticus* and heterodontosaurids, for characters drawn from studies focused on early theropod or saurischian relationships^{10,11}. In this way, we tested rigorously for anatomical similarities and differences between all of the included basal dinosaur taxa for the first time. However, as in any study, some characters were inapplicable for some taxa and in these cases we scored each taxon as (-) for those characters. 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-beta¹⁷. Bremer support decay indices were also calculated using TNT 1.5-beta¹⁷. Constraint trees 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 striking and significant result is the recovery of an Ornithischia+Theropoda sister-taxon relationship. 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 recognised groupings of Compsognatha, Iguanodontidae, Megalosauridae and Scelidosauridae¹⁸. Ornithoscelida is strongly supported by 21 unambiguous synapomorphies (*) and other shared features, including: an anterior premaxillary foramen located on the inside of the narial fossa*; a diastema between the premaxillary and maxillary tooth rows of at least one tooth crown's length; 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 contact (appears convergently in some 'massospondylids')*; an anteroventrally oriented quadrate*; an extended contact between the quadratojugal and the squamosal; short and deep (length < twice dorsoventral height) paroccipital processes*; a post-temporal foramen that is entirely enclosed within the paroccipital processes*; a supraoccipital that is taller than it is wide*; a well-developed ventral recess on the parabasisphenoid*; an anterior tympanic recess (convergently acquired in *Plateosaurus*); a surangular foramen positioned posterolaterally on the surangular*; an entirely

posteriorly oriented retroarticular process, lacking 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 (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 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 (also lost in plateosaurids and more derived sauropodomorphs)*; a straight femur, without a sigmoidal profile (also acquired by more derived sauropodomorphs but absent in basal forms such as *Saturnalia*²⁰ and *Pampadromaeus*²¹, also absent in Herrerasauridae)*; a well-developed anterior trochanter that is broad and at least partly separated from the shaft of the femur*; a fibular crest on the lateral side of the proximal portion of the tibia (described as present in *Eoraptor*²² though we could not confirm its presence, 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)); a heavily 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* (Figure 1).

In addition to the 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 optimise as synapomorphies of any large clade within our trees, mostly due 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 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, Dinosauria²⁷ 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 revealed that a small number of poorly-known basal dinosauriform taxa had a tendency 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 >1734 steps). Excluding *Saltopus elginensis*, *Agnosphytis 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. Critically, Dinosauria and Saurischia exhibit Bremer support values of 3 and 4 respectively. Dinosauria+Silesauridae¹ was found to have a Bremer support value of 2 in this analysis (Extended Data Figure 1).

By producing a constraint tree in TNT¹⁷, we were able to calculate the number of additional steps it would take to recover a traditional Saurischia^{3,28} clade. We found that, with all taxa that are traditionally regarded as being saurischians included and forced into a single monophyletic group, 20 additional steps would be needed to recover Saurischia as previously defined²⁸. 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 Figures 2-4). These analyses are described in more detail in the Supplementary Information file.

(Figure 2)

The recovery of Sauropodomorpha outside the Ornithischia-Theropoda dichotomy is a novel and unexpected result, leading to the break-up of Saurischia as traditionally defined³. Sauropodomorpha exhibits much higher relative abundance and taxic diversity than ornithischians and theropods in the Triassic and Early Jurassic²⁹, a phenomenon that is yet to be explained adequately. It has been suggested previously that, for Ornithischia at least, the 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 hypothesised¹⁴. While our study suggests such an alternative origin for Ornithischia within Dinosauria, our hypotheses does not yet provide an explanation for the observed differences in species richness between the main dinosaurian clades during this time.

Herrerasauridae is recovered as the sister group to Sauropodomorpha, suggesting that some of the theropod-like features of their anatomy evolved independently of those found in theropods, most likely as 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 dinosaurs and so we are forced to interpret some of the similarities between herrerasaurids and theropods as convergences. This 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 or not? 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 likely, 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 sympleiomorphy 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, *Agnosphytis cromhallensis*, as a basal member of Silesauridae also provides some evidence for a northern hemisphere origin for Dinosauria+Silesauridae (silesaurids are also represented by a number of European and North American taxa¹), if not also of Dinosauria. This challenges over two decades of previous 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 dinosauriform localities in the Northern Hemisphere.

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 and elegant framework around which future studies can operate.

As Dinosauria²⁷ is currently defined as the least inclusive clade that includes *Passer domesticus* and *Triceratops 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 *Passer domesticus*, *Triceratops horridus* and *Diplodocus 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 basal forms, such as *Herrerasaurus* and *Eoraptor*, would then have no effect on the definition of Dinosauria, provided the new definitions that we propose are adopted (see Table 1).

The current definition of Theropoda – the most inclusive clade containing *Passer 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 prior to 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 sense³⁰, we propose a change in the definition – all taxa more closely related to *Passer domesticus* than to either *Diplodocus carnegii* or *Triceratops 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 definition³¹ and propose a new definition – all taxa more closely related to *Diplodocus carnegii* than to either *Triceratops horridus*, *Passer 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 as further work is carried out on this critical part of the tree.

Discussion. Our new 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 on 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 bauplan, size, stance, method of locomotion and diet, as well the clade's centre of origin³².

Recent studies have led to a general consensus that the earliest dinosaurs were relatively small and bipedal^{18,14,15,20-23,32}, and this idea finds further support within our hypothesis, as both basal sauropodomorphs and basal ornithoscelidans are small bipeds. 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 (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, furthermore, 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 ambiguous³⁵. 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*, also have heterodont dentitions. This suggests an omnivorous ancestral state for Ornithoscelida also. Taken together, this strongly suggests that ancestral dinosaurs were omnivorous, as the two largest clades within Dinosauria appear to be ancestrally omnivorous, bearing heterodont dentitions. The basal saurischian group Herrerasauridae evidently contains carnivores (e.g. *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 sister group to Dinosauria (or Dinosauria+*Saltopus*), Silesauridae, is largely composed of 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 *Agnosphytis*, 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. Due 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 age of the Triassic^{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 the Northern Hemisphere. Furthermore, our analyses places the origin of dinosaurs at the Olenekian-Anisian boundary (~247 Ma), slightly earlier than 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 Figure 5).

Our new hypothesis for dinosaur relationships and evolution, with the recovery of two new, major clades, reframes the debate about dinosaur origins. The timing and geographic 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 address fundamental questions regarding these important and iconic animals.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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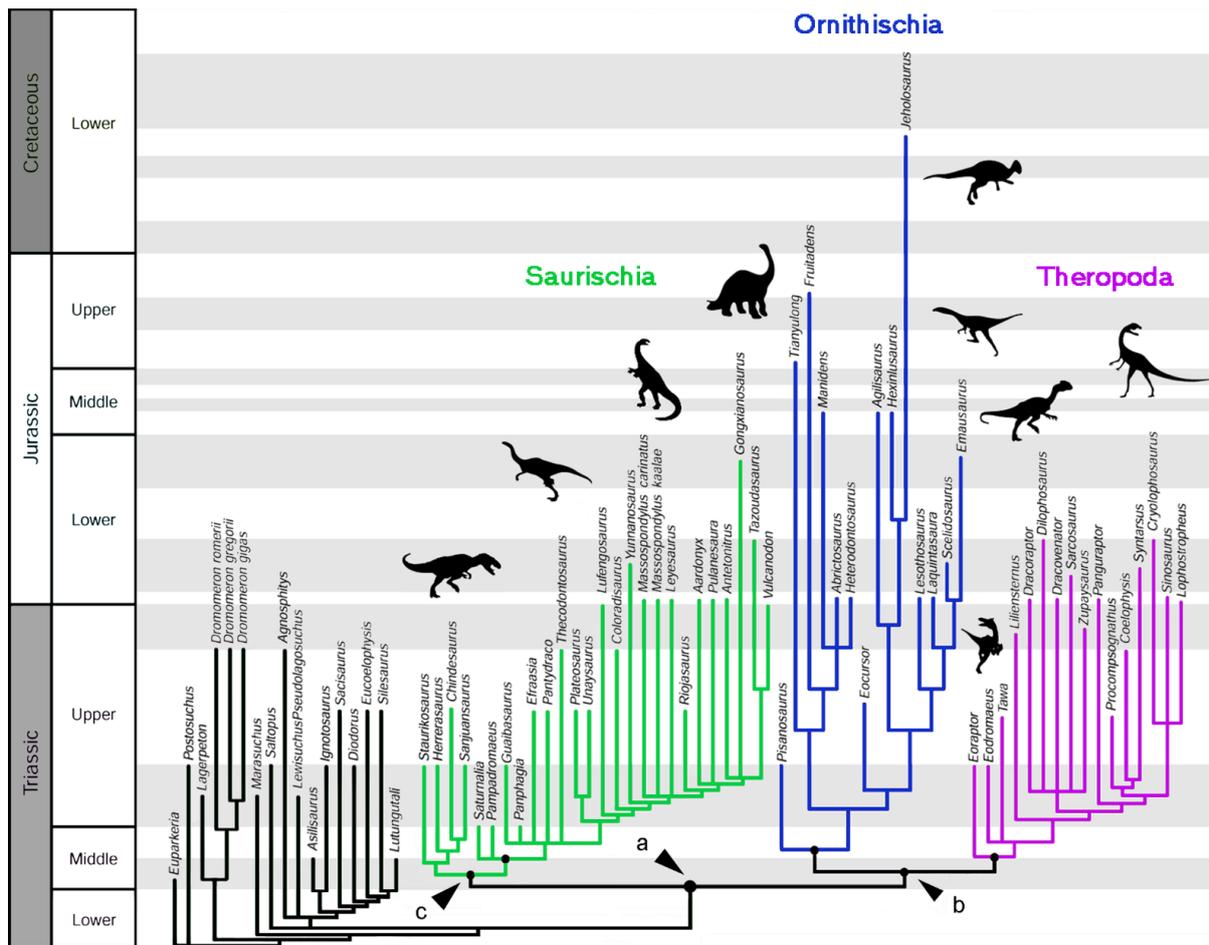


Figure 1. Phylogenetic relationships of early dinosaurs. Time-calibrated strict consensus of 94 trees of an analysis with 73 taxa and 457 characters (see Supplementary Information). a, The least inclusive clade that includes *Passer domesticus*, *Triceratops horridus* and *Diplodocus carnegii* = Dinosauria, as newly defined; b, The least inclusive clade that includes *Passer domesticus* and *Triceratops horridus* = Ornithoscelida, as defined; c, The most inclusive clade that contains *Diplodocus carnegii* but not *Triceratops horridus* = Saurischia, as newly defined. For further information on definitions see text and 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 (Lower Triassic), which has been expanded relative to the other subdivisions to better show the resolution within Silesauridae and among other non-dinosaurian dinosauromorphs.

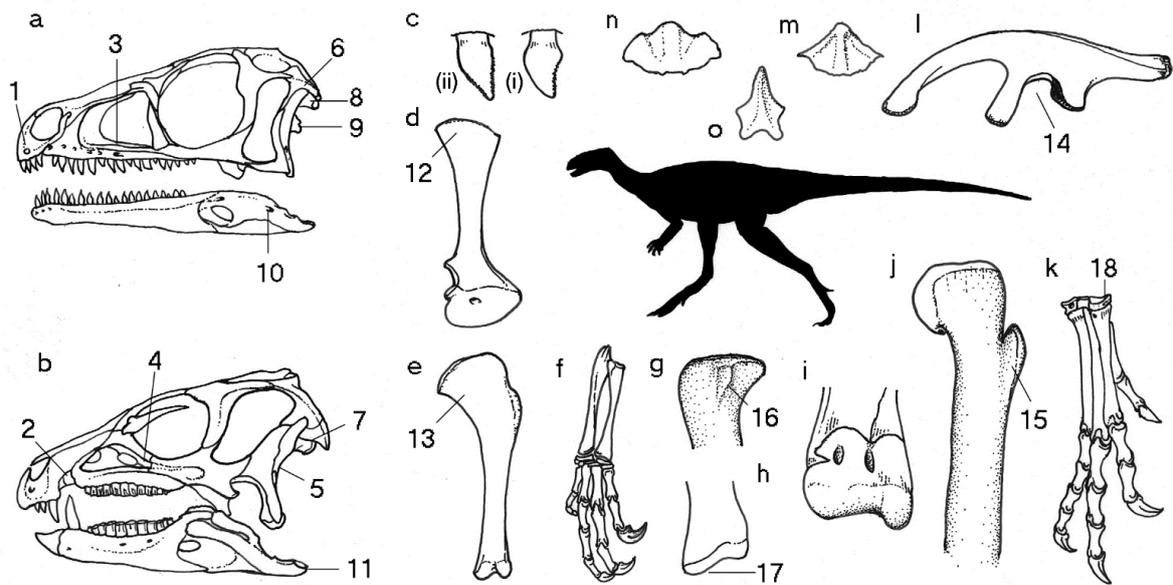


Figure 2. Skeletal anatomy of ornithoscelidans. a, Skull of *Eoraptor lunensis* (PVSJ 512)²²; b, Skull of *Heterodontosaurus tucki* (SAM-PK-K1332)¹⁶; c, Teeth of ornithoscelidans *Eoraptor lunensis* (PVSJ 512) and *Laquintasaura venezuelae* (MBLUZ P.1396); d, Scapula of *Lesothosaurus diagnosticus* (NHM UK PV R11000)²³; e, Humerus *Eocursor parvus* (SAM-PK-K8025); f, forelimb of *Heterodontosaurus tucki* (SAM-PK-K1332); g, Proximal end of tibia of *Lesothosaurus diagnosticus* (NHM UK PV RU B17); h, Distal end of tibia of *Lesothosaurus diagnosticus* (NHM UK PV RU B17); i, Fused distal end of 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 *Heterodontosaurus tucki* (SAM-PK-K1332); l, Ilium of *Heterodontosaurus 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, *Herrerasaurus ischigualastensis* (PVSJ 407) n, *Thecodontosaurus antiquus* (YPM 2192); o, *Heterodontosaurus tucki* (SAM-PK-K1332). 1-19 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 taller than wide; 10, foramen on lateral surface of dentary; 11, straight retroarticular process; 12, scapula, length > 3x 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. Scale bars = 20mm

Table 1. Newly proposed set of definitions for the major dinosaurian clades.

Clade	Definition
Dinosauria	The least inclusive clade that includes <i>Passer domesticus</i> , <i>Triceratops horridus</i> and <i>Diplodocus carnegii</i>
Ornithoscelida	The least inclusive clade that includes <i>Passer domesticus</i> and <i>Triceratops horridus</i>
Saurischia	The most inclusive clade that contains <i>Diplodocus carnegii</i> but not <i>Triceratops horridus</i>
Theropoda	The most inclusive clade that contains <i>Passer domesticus</i> but not <i>Diplodocus carnegii</i> or <i>Triceratops horridus</i>
Ornithischia	The most inclusive clade that contains <i>Triceratops horridus</i> but not <i>Passer domesticus</i> or <i>Diplodocus carnegii</i>
Sauropodomorpha	The most inclusive clade that contains <i>Diplodocus carnegii</i> but not <i>Triceratops horridus</i> , <i>Passer domesticus</i> or <i>Herrerasaurus ischigualastensis</i>
Herrerasauridae	The least inclusive clade that includes <i>Herrerasaurus ischigualastensis</i> and <i>Staurikosaurus pricei</i> ³⁷

Methods

Trees were produced and analysed in TNT 1.5-beta (Goloboff et al. 2008). 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:

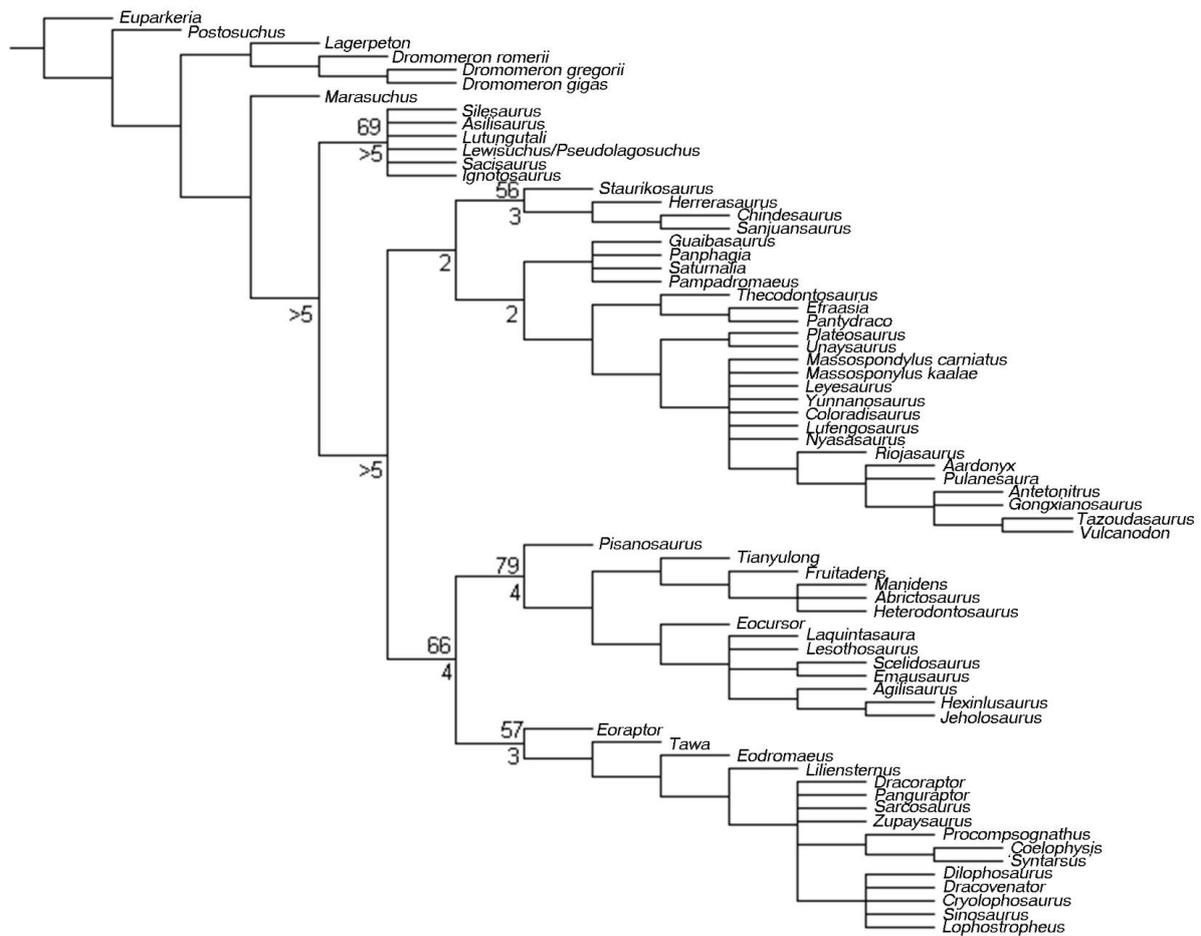
24, 35, 39, 60, 68, 71, 117, 145, 167, 169, 174, 180, 197, 199, 206, 214, 215, 222, 251, 269, 272, 286, 289, 303, 305, 307, 313, 322, 333, 334, 338, 353, 360, 376, 378, 387, 393, 442, 446

Bremer support values were calculated and constraint trees were produced using TNT 1.5-beta (Goloboff et al. 2008).

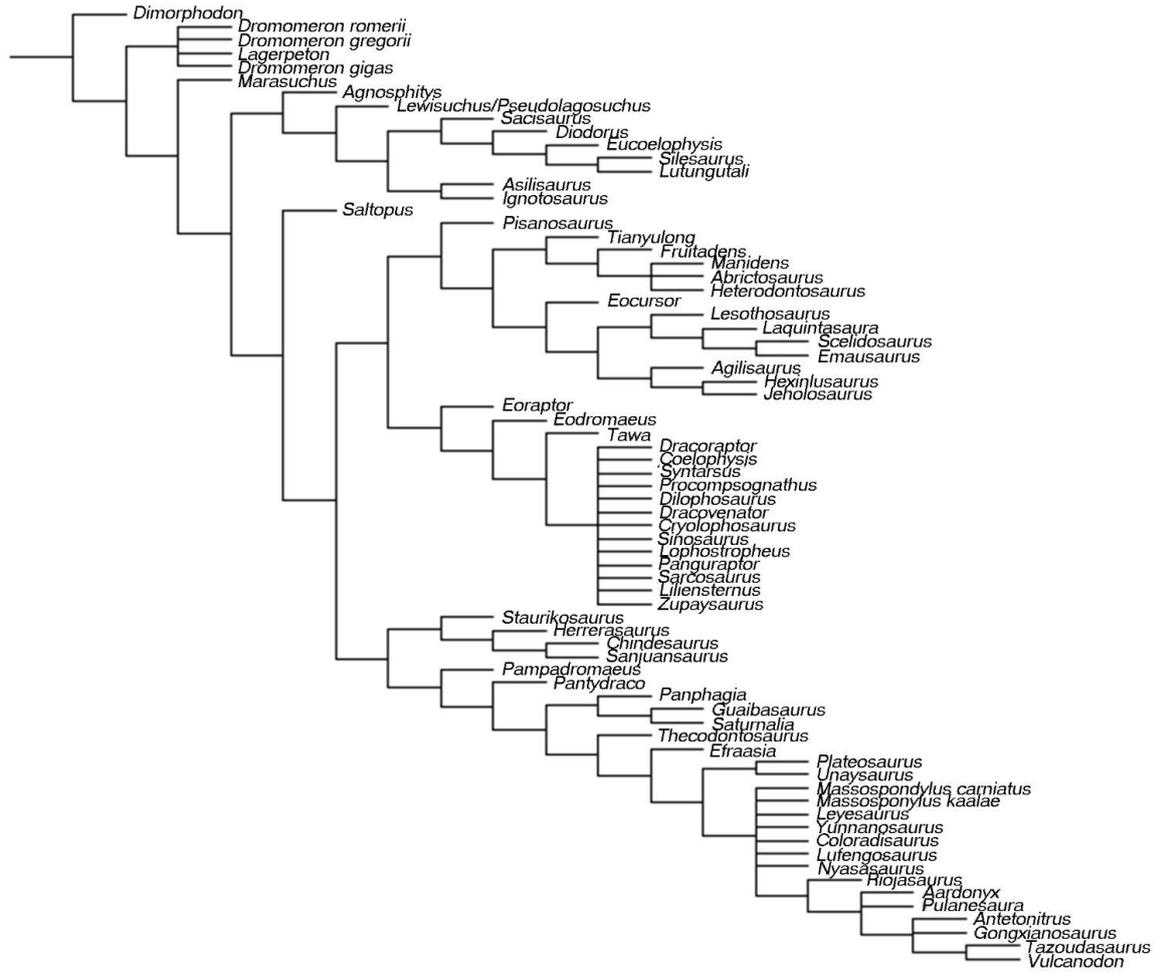
Data availability:

All data generated or analysed during this study are included in this published article (and its supplementary information files).

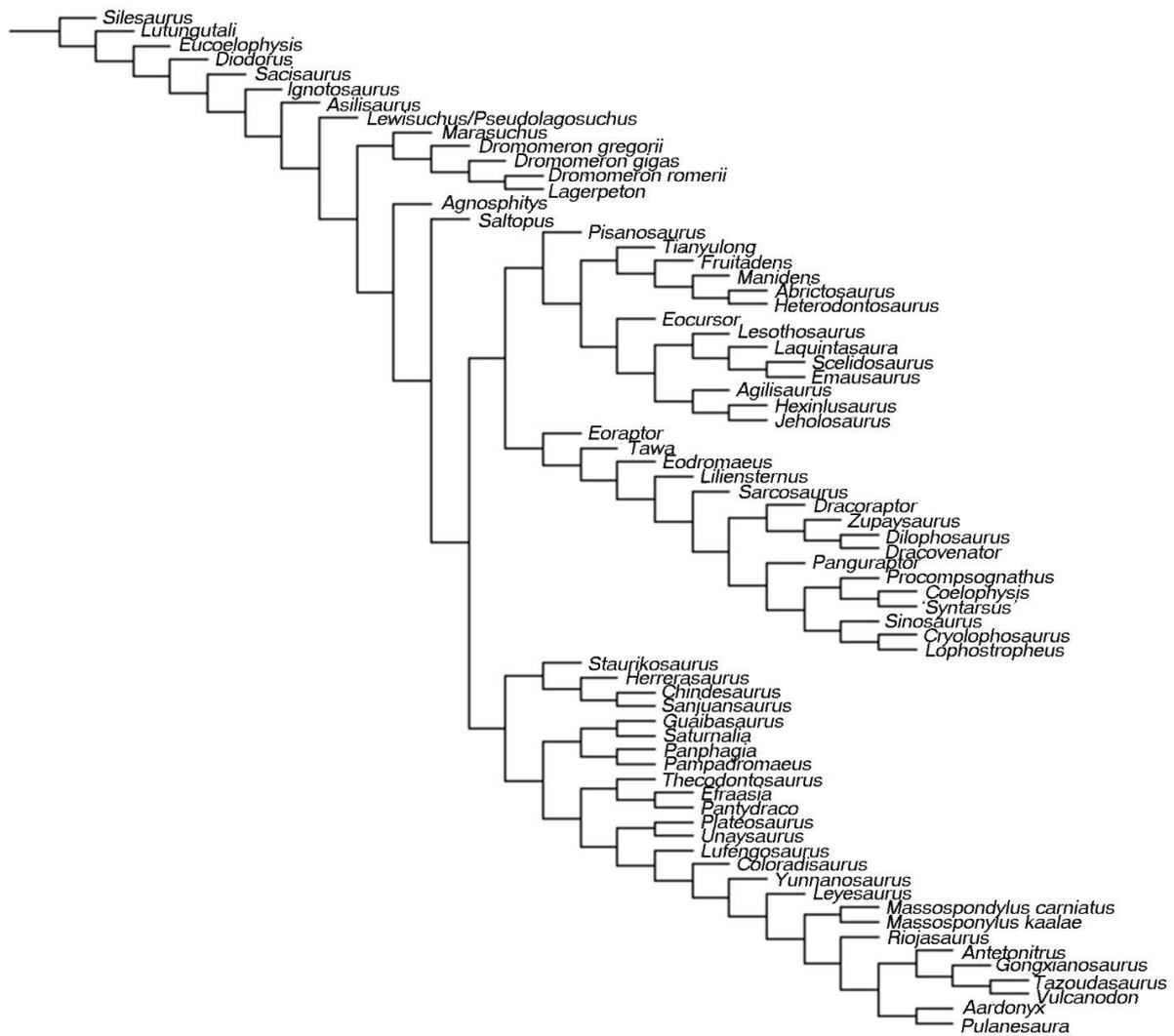
Extended Data Figure Legends



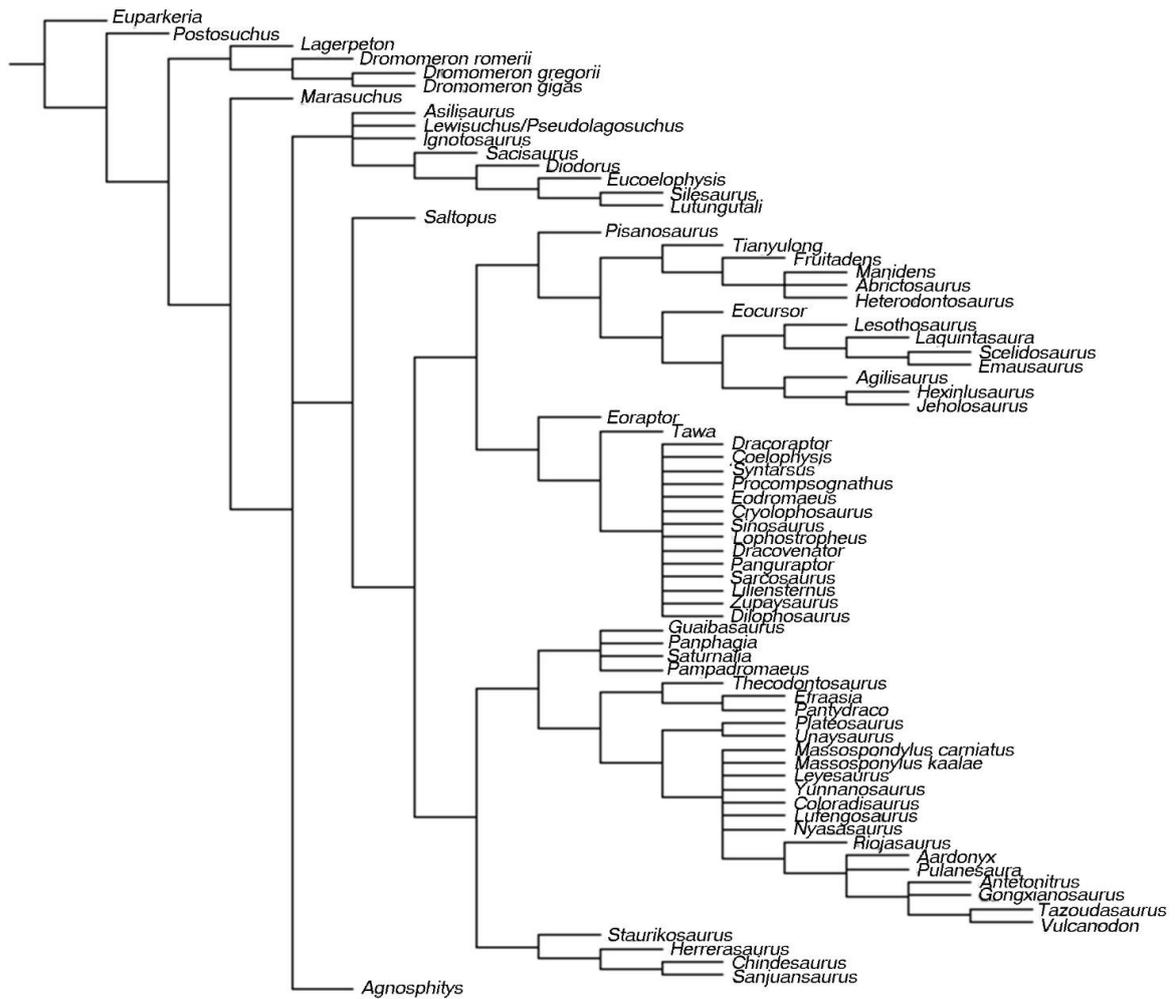
Extended Data Figure 1. Reduced strict consensus tree of the main analysis showing bootstrap frequencies (above) and Bremer support values (below) that were calculated for each of the major nodes, following the exclusion of *Saltopus elginensis*, *Agnosphytis cromhallensis*, *Eucoelophysis baldwini* 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.



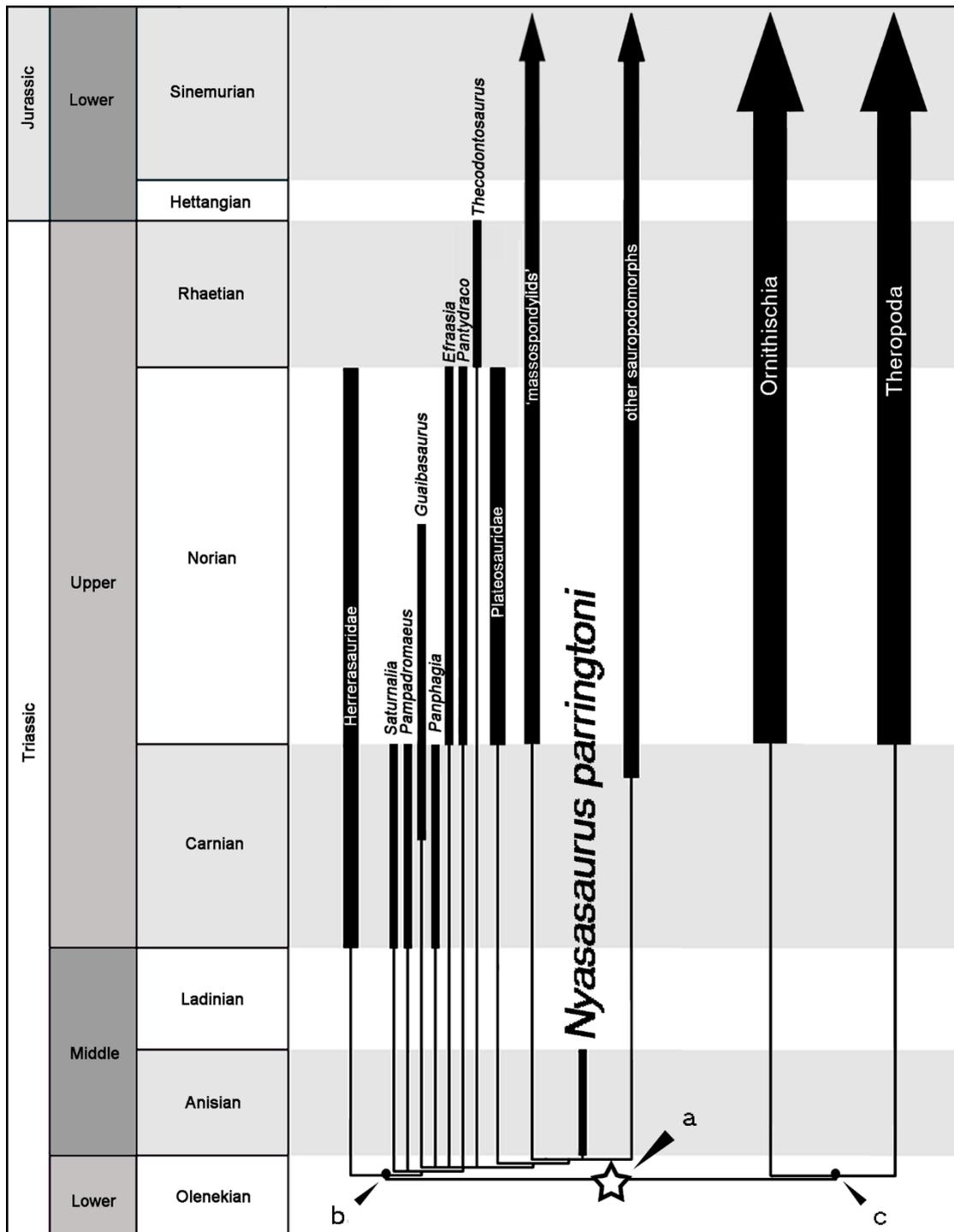
Extended Data Figure 2. Strict consensus tree produced when *Dimorphodon macronyx* was included in the dataset and chosen as the outgroup taxon (*Euparkeria capensis* and *Postosucus kirkpatricki* were not included). Tree was produced from 79 MPTs each of length 1627 steps. As in Extended Data Figure 1, the clades Ornithoscelida and Sauropodomorpha+Herrerasauridae (Saurischia, new definition) are both recovered. For further details of 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. Tree was produced from 83 MPTs each of length 1713 steps. For further details of 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 of length 1690 steps. The clades Ornithoscelida and Saurischia (new definition, see Table 1) are both recovered in this analysis. For further details of 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' saurpodomorph *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 of the additional analyses that were carried out as part of this study, see the Supplementary Information.