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A palaeoequatorial ornithischian and new constraints on early dinosaur diversification

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Current characterizations of early dinosaur evolution are incomplete: existing palaeobiological and phylogenetic scenarios are based on a fossil record dominated by saurischians and the implications of the early ornithischian record are often overlooked. Moreover, the timings of deep phylogenetic divergences within Dinosauria are poorly constrained owing to the absence of a rigorous chronostratigraphical framework for key Late Triassic–Early Jurassic localities. A new dinosaur from the earliest Jurassic of the Venezuelan Andes is the first basal ornithischian recovered from terrestrial deposits directly associated with a precise radioisotopic date and the first-named dinosaur from northern South America. It expands the early palaeogeographical range of Ornithischia to palaeoequatorial regions, an area sometimes thought to be devoid of early dinosaur taxa, and offers insights into early dinosaur growth rates, the evolution of sociality and the rapid tempo of the global dinosaur radiation following the end-Triassic mass extinction, helping to underscore the importance of the ornithischian record in broad-scale discussions of early dinosaur history.

1. Introduction

Dinosaurs originated by the early Late Triassic (approx. 230 Ma), but achieved global ecological dominance during the earliest Jurassic (30 Myr later) [1–5], following the end-Triassic mass extinction (ETE; approx. 201.6 Ma [6]). Recent discoveries have illuminated the earliest evolutionary history of saurischian dinosaurs [7,8], but comparable material for the other major dinosaur clade, Ornithischia, is scarce [9,10] and has not been fully incorporated into phylogenetic analyses of early dinosaurs [2,11]. This has left a substantial gap in our understanding of early dinosaur interrelationships, diversification and palaeobiology. Moreover, poor geochronological control on many of the Late Triassic–Early Jurassic rock units yielding early dinosaur material places severe limits on our ability to constrain accurately the timing and tempo of the dinosaur radiation [3], hindering attempts to examine rates of faunal change, character evolution and morphospace occupation.

Here, we describe a new early ornithischian dinosaur on the basis of abundant material from a monodominant bonebed in the La Quinta Formation of the Venezuelan Andes. In addition, we provide a well-constrained maximum radioisotopic age for this locality, based on analysis of detrital zircon crystals found in direct association with the specimens, thereby providing one of only a few absolute age estimates available for Late Triassic–Early Jurassic terrestrial faunas worldwide [3,12]. Taken in combination, these new data open a critical new window on early dinosaur evolution by (i) identifying a new taxon that substantially increases the amount of available early ornithischian material, (ii) extending the

palaeogeographical distribution of early dinosaurs, and (iii) providing a new absolute time constraint for understanding the tempo of the early dinosaur radiation. The remains of this new taxon give critical new insights into the global diversification of ornithischians that occurred in the wake of the ETE [9], an event that fundamentally altered the trophic structure of terrestrial ecosystems for the remainder of the Mesozoic Era.

2. Systematic palaeontology

Dinosauria Owen, 1842.

Ornithischia Seeley, 1887.

Laquintasaura venezuelae, taxon nov.

(a) Etymology

'Laquinta-', after the type horizon, and '-saura', Greek for lizard (fem.); *venezuelae*, for the country and people of Venezuela.

(b) Holotype

Museo de Biología de la Universidad del Zulia, Maracaibo (MBLUZ) P.1396, an isolated maxillary or dentary tooth.

(c) Paratypes

MBLUZ P.5017, distal part of a left femur; MBLUZ P.5018, proximal part of a left ischium; MBLUZ P.5005, a left astragalocalcaneum.

(d) Referred material

Hundreds of individual elements (some isolated, some in dense accumulations), including teeth, cranial elements (premaxilla, maxilla, jugals, parietals, frontal, postfrontal, exoccipital/opisthotic, pterygoid, quadrates), cervical, dorsal, sacral and caudal vertebrae, ribs, scapulae, pelvic girdle elements, and hindlimb material; no forelimb material is known and pedal material is rare. See [13] and the electronic supplementary material, table S1 for a full list of prepared material referred to this taxon: large amounts of additional material currently await preparation in the collections of MBLUZ.

(e) Locality and horizon

Road-cut between the towns of La Grita and Seboruco, Táchira State, Venezuela [13,14]. La Quinta Formation, Lower Jurassic (see electronic supplementary material, figure S1). Previous age estimates for this unit, which were based primarily on biostratigraphical and some limited radioisotopic data, were poorly constrained and ranged from Late Permian–Lower Cretaceous. However, our new analyses based on CA-TIMS U–Pb zircon analysis demonstrate that the bonebed has a maximum depositional age of 200.91 ± 0.55 Ma placing it in the earliest Jurassic (Hettangian) within as little as 0.5 Ma of the ETE [6]. See the electronic supplementary material for full details of the radioisotopic analyses.

(f) Diagnosis

Laquintasaura can be differentiated from other early ornithischians by the following autapomorphic combination of dental characters: cheek tooth crowns have isosceles-shaped outlines, which are apicobasally elongate, taper apically, are mesiodistally widest immediately apical to the root/crown

junction, possess coarse marginal denticles extending for the full lengths of the crown margins, and possess prominent apicobasally extending striations on their labial and lingual surfaces. Postcranial autapomorphies include: sharply inflected dorsal margin of ischium dorsal to the obturator process; femoral fibula epicondyle medially inset in posterior or ventral views; and astragalus with a deep, broad, 'U'-shaped notch in anterior surface. See the electronic supplementary material for additional comparative comments.

3. Description

Laquintasaura is represented by abundant teeth, ribs and girdle elements, and scarcer cranial, limb and vertebral remains (figure 1). The specimens were found in a single monodominant bonebed, either isolated or in dense, jumbled, disarticulated associations, with a minimum of four (and possibly many more) individuals preserved. The largest femur is 90 mm in length, consistent with a total body length of approximately 1 m based on comparisons with other bipedal ornithischians (see comparative measurements in the electronic supplementary material). Previous brief reports of isolated material from the bonebed provided alternative identifications for several elements [13]; however, restudy and the examination of new specimens indicate that, with the exception of two theropod teeth, all bonebed material is consistent with referral to a single early ornithischian taxon.

This is the first reported early ornithischian bonebed containing multiple individuals. Preliminary taphonomic observations suggest that the specimens exhibit no signs of prolonged subaerial exposure but some evidence of low-energy transport, as suggested by the lack of damage, but the rarity of articulated specimens. These observations suggest that the bonebed contains the remains of a potentially gregarious group of small dinosaurs that died in a single event, though it is unclear whether they died as a result of the same process that transported the fossils, or whether this transport occurred after death. Further taphonomic and sedimentological work is needed in the field to provide additional data on this issue. If confirmed this would provide the earliest-known evidence for the evolution of complex social behaviours in Ornithischia, which are currently confirmed for Late Jurassic and Cretaceous taxa only [15].

Most of the cranial elements (e.g. jugal, postorbital, quadrate, braincase elements) are similar to those of other early ornithischians. A partial maxilla (MBLUZ P.5016) lacks a buccal emargination, possesses a shallow antorbital fossa and small antorbital fenestra and exhibits 'special foramina' [16]. Its poorly preserved *in situ* teeth are comparable to the many isolated teeth found in the bonebed. These teeth are unique among ornithischians (and dinosaurs more generally), with exceptionally elongate, apically tapering crowns that are sometimes slightly recurved (MBLUZ P.1369, P.5007, P.5010, P.5039: ratio of apicobasal crown height to mesiodistal crown width = 1.5–1.7). The crowns are labiolingually expanded with respect to the root, and the base of the crown is asymmetrically expanded in mesial view, forming a 'cingulum', a combination of features regarded an ornithischian synapomorphy [10,17]. Both crown margins bear coarse serrations along their full lengths, and the crown is broadest mesiodistally almost immediately apical to the root/crown constriction. Crowns possess prominent apicobasally extending striations on their

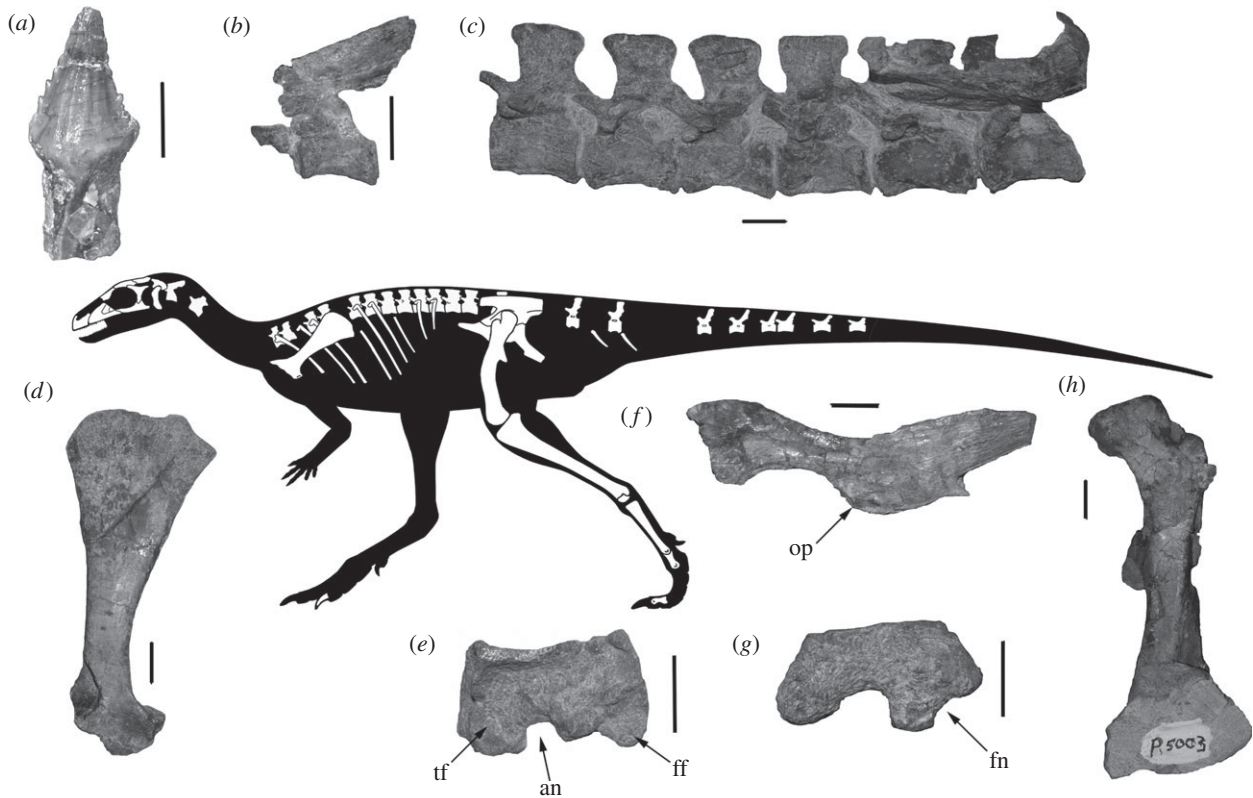


Figure 1. Composite reconstruction of *Laquintasaura venezuelae* gen. et sp. nov., with representative skeletal elements: (a) cheek tooth (MBLUZ P.1396: holotype) in labial view, (b) atlas–axis complex (MBLUZ P.1350) in left lateral view, (c) articulated middle and posterior dorsal vertebrae (MBLUZ P.5009) in right lateral view (reversed), (d) left scapula (MBLUZ P.5000) in lateral view, (e) left astragalocalcaneum (MBLUZ P.5005: paratype) in proximal view, (f) left ischium (MBLUZ P.5018: paratype) in lateral view, (g) left femur (MBLUZ P.5017: paratype) in distal view and (h) left femur (MBLUZ P.5003) in anterior view. Anterior notch, an; notch in fibular epicondyle, fn; fibular facet, ff; obturator process, op and tibial facet, tf. Scale bars, 2 mm (a) and 10 mm (b–h).

labial and lingual surfaces (figure 1a). This combination of dental features is unknown in the maxillary or dentary dentitions of any other ornithischian (see the electronic supplementary material for detailed comparisons).

Ornithischian synapomorphies in the postcrania [17] include the presence of an elongate preacetabular process of the ilium (MBLUZ P.5039) and a retroverted pubis (MBLUZ P.5008). The inflection of the dorsal ischial margin (MBLUZ P.5018) is much more pronounced than in other basal ornithischians (*Eocursor*, *Heterodontosaurus*, *Lesothosaurus*, *Stormbergia*) (figure 1f). In contrast to *Heterodontosaurus* and *Lesothosaurus*, an obturator process is present in *Laquintasaura*, whereas the obturator process of *Stormbergia* is anteroposteriorly shorter than in the new taxon. In *Laquintasaura*, the fibular epicondyle of the distal femur is inset from the femoral lateral margin by a distinct notch (MBLUZ P.5017; figure 1g), which is absent or weakly developed in other basal ornithischians (*Pisanosaurus*, *Eocursor*, heterodontosaurids, *Lesothosaurus*, *Stormbergia*). The astragalus and calcaneum of *Laquintasaura* are fused (MBLUZ P.5005), as in *Fruitadens* and *Heterodontosaurus*, but in contrast to other early ornithischians. The deep, 'U'-shaped notch in the anterior margin of the astragalus (figure 1e) is absent in other basal ornithischians (*Abrictosaurus*, *Fruitadens* and *Pisanosaurus*). Further comparative and descriptive comments can be found in the electronic supplementary material, figures S2–S4.

4. Osteohistology

Osteohistological analysis of several *Laquintasaura* specimens reveals the presence of parallel-fibred bone tissue that is well

vascularized by simple vascular canals (figure 2 and see also the electronic supplementary material, figures S6–S9). In long bones, the latter change from an overall longitudinal arrangement early in development to a reticular pattern dominated by laminar organization in older specimens. No secondary osteons are present in any of the long bones, and woven-fibred bone was absent.

Laquintasaura exhibits a similar growth pattern to the geologically younger small-bodied ornithischians *Scutellosaurus* and *Fruitadens*, which each possess a 'lamellar-zonal' pattern, and that lack evidence for elevated bone growth rates in early ontogeny [18–20]. Osteohistological analysis also indicates that the *Laquintasaura* bonebed contains individuals of different ages. One individual shows multiple (at least nine) tightly spaced lines of arrested growth in the scapula, which are interpreted as an external fundamental system that, together with the very high rate of bone remodelling in this specimen, indicates it is from a skeletally mature adult individual, with a minimum age of 10–12 years. In contrast, other specimens show no signs of slowing growth and presumably belong to juvenile or subadult individuals (see electronic supplementary material for full details).

5. Phylogenetic analysis

Character data for *Laquintasaura* were incorporated into a recent comprehensive ornithischian dataset [17,21]. The resulting matrix included 227 characters scored for 55 taxa and was analysed in TNT [22] (see the electronic supplementary material for details and figure S10). The analysis recovered

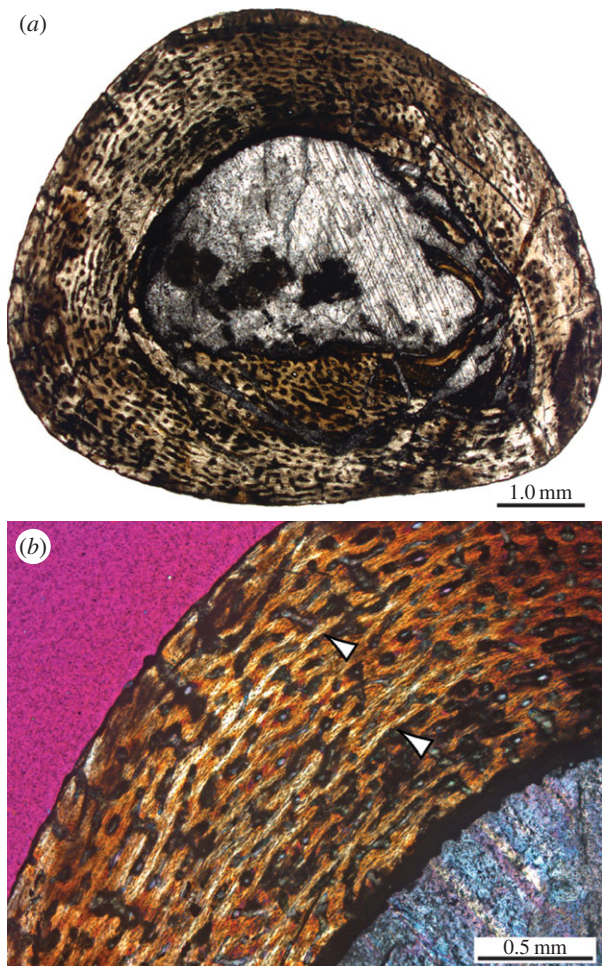


Figure 2. Osteohistological section of small tibia (MBLUZ P.5021), from a juvenile individual: (a) complete section in normal-polarized transmitted light and (b) close-up of cortex in cross-polarized light using lambda compensator. The entire compacta consists of parallel-fibred bone subdivided by two growth annuli (marked by arrowheads). The bone tissue is vascularized by simple primary canals and woven bone is absent.

2160 most parsimonious trees of length 585 steps (consistency index = 0.434; retention index = 0.697; rescaled consistency index = 0.303). A strict consensus of these places *Laquintasaura* in an unresolved polytomy with the major ornithischian clades Heterodontosauridae, Neornithischia and Thyreophora along with other early ornithischian taxa, such as *Lesothosaurus*. An unusual character combination and the scarcity of cranial material currently prevent definitive resolution of its phylogenetic position (figure 3a).

6. Discussion

Ornithischians were the dominant large-bodied herbivores of many Late Mesozoic terrestrial ecosystems, but their early evolution has been obscured by a dearth of material [9,10], with Late Triassic dinosaur assemblages characterized by an overwhelming preponderance of saurischian taxa and specimens [1–5,7,8]. Ghost lineages derived from phylogenies indicate that numerous ornithischian lineages must have been present at this time [17], but only three Late Triassic taxa are known from the first 30 Myr of the clade's history (*Eocursor*, from South Africa; and *Pisanosaurus* and an unnamed heterodontosaurid from Argentina), each based on incomplete singleton specimens [9,23,24]. In each case, either the phylogenetic

affinities of the taxon or its geological age have been challenged: for example, it has been suggested that one of these specimens (*Pisanosaurus*) is not an ornithischian at all, whereas *Eocursor* and the unnamed Argentinean heterodontosaurid have been suggested to be derived from strata of Early Jurassic age [25]. Consequently, ornithischians have been regarded as exceptionally rare faunal components during the Late Triassic and restricted geographically to the middle–high latitudinal regions of southern Pangaea [1–3,9].

The Early Jurassic ornithischian record is substantially richer than that of the Triassic, with a species-rich southern African assemblage (more than 60 known specimens of several heterodontosaurid taxa, *Lesothosaurus* and *Stormbergia*), remains of early armoured dinosaurs in Europe and western North America (multiple specimens of *Scelidosaurus* and *Scutellosaurus*), and indeterminate fragments from other regions [26–32]. However, age determinations for the southern African and North American assemblages are controversial and based almost exclusively on poorly constrained vertebrate biostratigraphy [33,34], the utility of which is debatable and problematic for age correlations over wide geographical areas [35]. Moreover, the better-dated European records comprise monotoxic occurrences in marine sediments [31] and are younger in age than *Laquintasaura*. Although it has been hypothesized that a major ornithischian radiation took place in the Early Jurassic [9,28,30], the timing, dynamics and palaeobiogeography of this radiation have been obscured by poor geochronological constraints on early ornithischian assemblages and the limited geographical distribution of terrestrial tetrapod assemblages from this interval.

Laquintasaura demonstrates unequivocally that, at least locally, ornithischians were relatively abundant soon after the ETE, perhaps within as little as 0.5 Ma of the extinction. *Laquintasaura* also indicates a significant and unprecedented palaeogeographical range expansion for the early ornithischian record (figure 3b,c), which now extends to the palaeoequator, contrary to recent predictions made by hypotheses of climatically driven latitudinal variation in early dinosaur biogeography and diversity, which have suggested that these regions were inhospitable for early dinosaurs [3,36]. The rapid increases in ornithischian abundance and distribution in the ETE aftermath [3,9] potentially resulted from ecological release following the sharp diversity declines or extinctions in other herbivorous tetrapod clades (synapsids, pseudosuchians, silesaurids) that occurred near to or across the Triassic/Jurassic boundary or the amelioration of climatic barriers that might have limited Triassic ornithischian diversity. This set the stage for ornithischians to become one of the most abundant and speciose terrestrial herbivore clades of the Mesozoic. The small size and conservative anatomy of *Laquintasaura*, which also characterizes other early ornithischians, suggests that these changes were not accompanied by immediate increases in disparity and body size. The onset of these trends occurred later in the Jurassic, as indicated by the appearance of larger, quadrupedal and armoured taxa [31], and a major body plan diversification evident from the Middle Jurassic onwards (the appearance of ankylosaurs, stegosaurs, ornithomimids and ceratopsians) [17]. Hence, although the ETE might have created conditions that favoured dramatic increases in ornithischian abundance and distribution, presaging the establishment of 'typical' Mesozoic ecosystems, there was a considerable lag before ornithischians responded to this event with the appearance of radically new body plans.

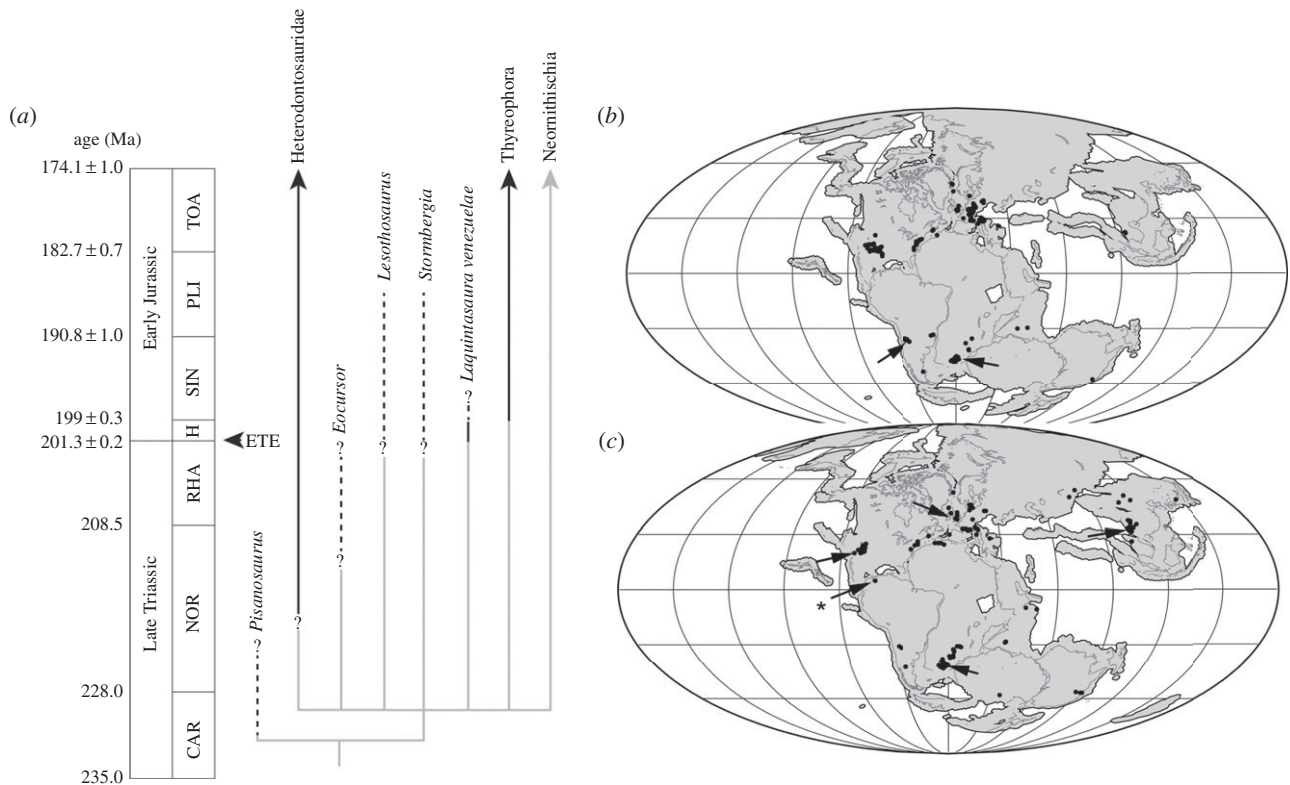


Figure 3. Phylogeny and temporal and spatial distributions of early ornithischians. (a) Simplified time-calibrated phylogeny. Lines in black are known ranges; grey lines are inferred (ghost) lineages; dashed lines and question marks indicate taxa with poorly constrained stratigraphic ranges; arrowheads signify clades that continue into the Middle Jurassic. Dinosaur localities in the Late Triassic (b) and Early Jurassic (c). Arrows indicate ornithischian localities; the asterisk signifies the *Laquintasaura* locality. Note the scarcity of palaeoequatorial dinosaur localities and limited palaeobiogeographical distribution of ornithischians in the Late Triassic and their subsequent spread in the Early Jurassic. Carnian, CAR; end-Triassic extinction event, ETE; Hettangian, H; Norian, NOR; Pliensbachian, PLI; Rhaetian, RHA; Sinemurian, SIN; Toarcian, TOA. See the electronic supplementary material for full details.

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Data accessibility. The original phylogenetic data matrix and high-resolution versions of the histological images used in this study can be downloaded from Dryad (doi:10.5061/dryad.51248), and other supporting data are available in the electronic supplementary material.

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