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Palaeontology

A dinosaur missing-link? *Chilesaurus* and the early evolution of ornithischian dinosaurs

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The enigmatic dinosaur taxon *Chilesaurus diegosuarezi* was originally described as a tetanuran theropod, but this species possesses a highly unusual combination of features that could provide evidence of alternative phylogenetic positions within the clade. In order to test the relationships of *Chilesaurus*, we added it to a new dataset of early dinosaurs and other dinosauromorphs. Our analyses recover *Chilesaurus* in a novel position, as the earliest diverging member of Ornithischia, rather than a tetanuran theropod. The basal position of *Chilesaurus* within the clade and its suite of anatomical characters suggest that it might represent a 'transitional' taxon, bridging the morphological gap between Theropoda and Ornithischia, thereby offering potential insights into the earliest stages of ornithischian evolution, which were previously obscure. For example, our results suggest that pubic retroversion occurred prior to some of the craniodental and postcranial modifications that previously diagnosed the clade (e.g. the presence of a predentary bone and ossified tendons).

1. Introduction

Chilesaurus diegosuarezi is from the Late Jurassic (Tithonian; *ca* 150 Ma) Toqui Formation of Chile and possesses a bizarre suite of anatomical features that, if considered individually, are usually thought to characterize distantly related dinosaur clades [1]. For example, *Chilesaurus* possesses features that appear 'classically' theropod-like, sauropodomorph-like and ornithischian-like, including a dolichoiliac ilium, similarities in ankle structure, and a retroverted pubis, respectively [1]. Given this melange of features, the authors who provided the original description of this taxon went to great lengths to determine its phylogenetic affinities using a variety of existing phylogenetic datasets representing a range of dinosaur clades [2–5]. Based upon their initial analyses, the authors concluded that this taxon represents an unusual tetanuran theropod [1]. This result implied that many of the features of *Chilesaurus* that are similar to those of ornithischians and sauropodomorphs were evolutionary convergences, which might have been related to the herbivorous diet that characterizes the majority of these taxa [1]. However, although the authors tested a number of alternative phylogenetic hypotheses, all of the datasets that they used were designed to test the interrelationships of either major clades within Archosauria or clades within Saurischia [2–5]. Hence, the full range of possible phylogenetic positions for *Chilesaurus* in Dinosauria has not yet been tested. Establishing the relationships of this taxon is critical for fully understanding the evolution of many major anatomical features, including those associated with herbivory, pelvic structure and locomotion [1].

Recently, a new large-scale dataset was assembled to investigate the interrelationships of early dinosaurs and other dinosauromorphs [6] that now

offers a tool for investigating dinosaur evolution and the relationships of problematic taxa. Unlike all previous datasets, it encompasses a broad range of taxa from each of the major dinosaurian clades [6]. Here, we use this novel dataset to reassess the systematic position of *Chilesaurus* within Dinosauria, in order to test whether it is nested within Theropoda or if an alternative placement is more strongly supported.

2. Material and methods

Character information on *Chilesaurus* was obtained from the original description [1] and added to the dataset presented in [6]. This modified dataset contained 76 taxa that were scored for 457 characters. It was analysed using TNT 1.5-beta [7]. Trees were searched for using the New Technology Search function, with ratchet and drift set to their default settings (10 iterations and 10 cycles, respectively) and with 100 random additional sequences. Following this first analysis, a second analysis was carried out using the Driven Search function. The search was run until the minimum tree length was hit 100 times. The most parsimonious trees (MPTs) produced in this search were then subjected to a further round of TBR branch swapping. Bremer support values (decay indices) were also calculated using TNT 1.5-beta [7]. Characters 24, 35, 39, 60, 68, 71, 72, 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, 386, 393, 442 and 446 were treated as ordered [6].

In contrast to [6], we scored the enigmatic British taxon *Agnosphitys cromhallensis* on the basis of the holotype material only, in order to remove any potentially adverse effects on the analysis that might result from the problematic nature of this taxon's hypodigm [8]. Constraint trees were produced in additional analyses that were conducted to force the inclusion of *Chilesaurus* within either a monophyletic Sauropodomorpha or Theropoda, as well as in derived positions within Theropoda, in order to determine the tree lengths associated with these alternative topologies.

3. Results

Our first analysis recovered 73 MPTs of length 1819 steps and our second, using TBR branch swapping, recovered 494 MPTs of the same length (figure 1). Both analyses recovered *Chilesaurus* as the earliest diverging member of Ornithischia. In our strict consensus tree, *Chilesaurus* falls stem-ward of all those taxa previously considered to represent the basal-most ornithischians, including the Late Triassic taxon *Pisanosaurus mertii*, which has long been regarded to be the first diverging ornithischian, and all heterodontosaurids [3,8].

Chilesaurus is united with ornithischians by the possession of the following features: a premaxilla with an edentulous anterior region (possibly for the support of a rhamphotheca); loss of recurvature in maxillary and dentary teeth; an anterior iliac process that is at least subequal in anteroposterior length to the posterior iliac process; a distinct brevis fossa that is not visible in lateral view, but is restricted to the ventral margin of the postacetabular process; a postacetabular process that is 25–35% of the total anteroposterior length of the ilium; possession of a retroverted pubis (opisthopubic pelvis); a pubis with a rod-like pubic shaft; a pubic symphysis that is restricted to the distal end of the pubis; a femur that is straightened in anterior view (no sigmoidal profile or medial bowing present); an anterior trochanter that extends almost as far proximally as the femoral head and is located near the lateral margin of the anterior face of the femur; and a fibula that is less than half of the width of the tibia in midshaft diameter. Although these character states optimize as ornithischian synapomorphies in this analysis, it should be noted that some of them also occur convergently in tetanuran theropods (although most are not present in non-tetanurans: see the electronic supplementary material), which would likely account for the phylogenetic position originally proposed by Novas *et al*. [1] (figure 2).

In addition to these characters, *Chilesaurus diegosuarezi* possesses a broadened, wing-like anterior trochanter on the femur that is at least partially separated from the femoral shaft. These two character states (wing-like anterior trochanter; anterior trochanter at least partly separated from the shaft) have both been listed as ornithischian synapomorphies by previous studies [2,8,9]. However, these features also appear in some theropods and have been interpreted as possible synapomorphies of Ornithoscelida [6].

Saltopus and *Agnosphitys* were found to be 'wildcard' taxa and these were removed from the strict consensus tree *a posteriori*. Following their removal, Bremer support values for each clade were low for many of the major clades (Dinosauria = 2; Saurischia = 1; Herrerasauridae = 4; Sauropodomorpha = 1; Ornithoscelida = 1; Ornithischia = 1; Theropoda = 2). However, removal of *Pisanosaurus mertii*, a taxon that has long frustrated attempts to understand early ornithischian evolution owing to its poor preservation, controversial interpretation and its mixture of highly derived and primitive anatomical features, improves Bremer supports for many clades (Sauropodomorpha = 2; Ornithoscelida = 3; Ornithischia = 3 (with Heterodontosauridae + Genasauria > 5); see the electronic supplementary material for further discussion).

When *Chilesaurus* was constrained to fall within a monophyletic Theropoda, 13 additional steps were added to the original strict consensus tree; when forced into a position more derived in Theropoda (Tetanurae), as originally suggested [1], 10 additional steps were required. Finally, 13 additional steps were needed to force the inclusion of *Chilesaurus* into Sauropodomorpha (see the electronic supplementary material).

4. Discussion

The results of our analyses suggest that *Chilesaurus* is not a tetanuran theropod, but a member of an early diverging and previously unknown lineage of ornithischian dinosaurs. The recovery of Theropoda and Ornithischia as sister taxa that are united by many shared features also offers a partial explanation for the initial recovery of *Chilesaurus* within Theropoda, especially in those cases where the datasets used to explore its relationships did not include an adequate ornithischian sample [2–5]. Features shared between ornithischians and theropods (but that are absent from sauropodomorphs), which had not previously been considered as synapomorphic, are present in *Chilesaurus* and offer further evidence in support of the ornithoscelidian hypothesis [6].

This new phylogeny highlights a unique combination of 'primitive' and 'derived' characters for *Chilesaurus* within Ornithischia. Moreover, it provides the first possible example

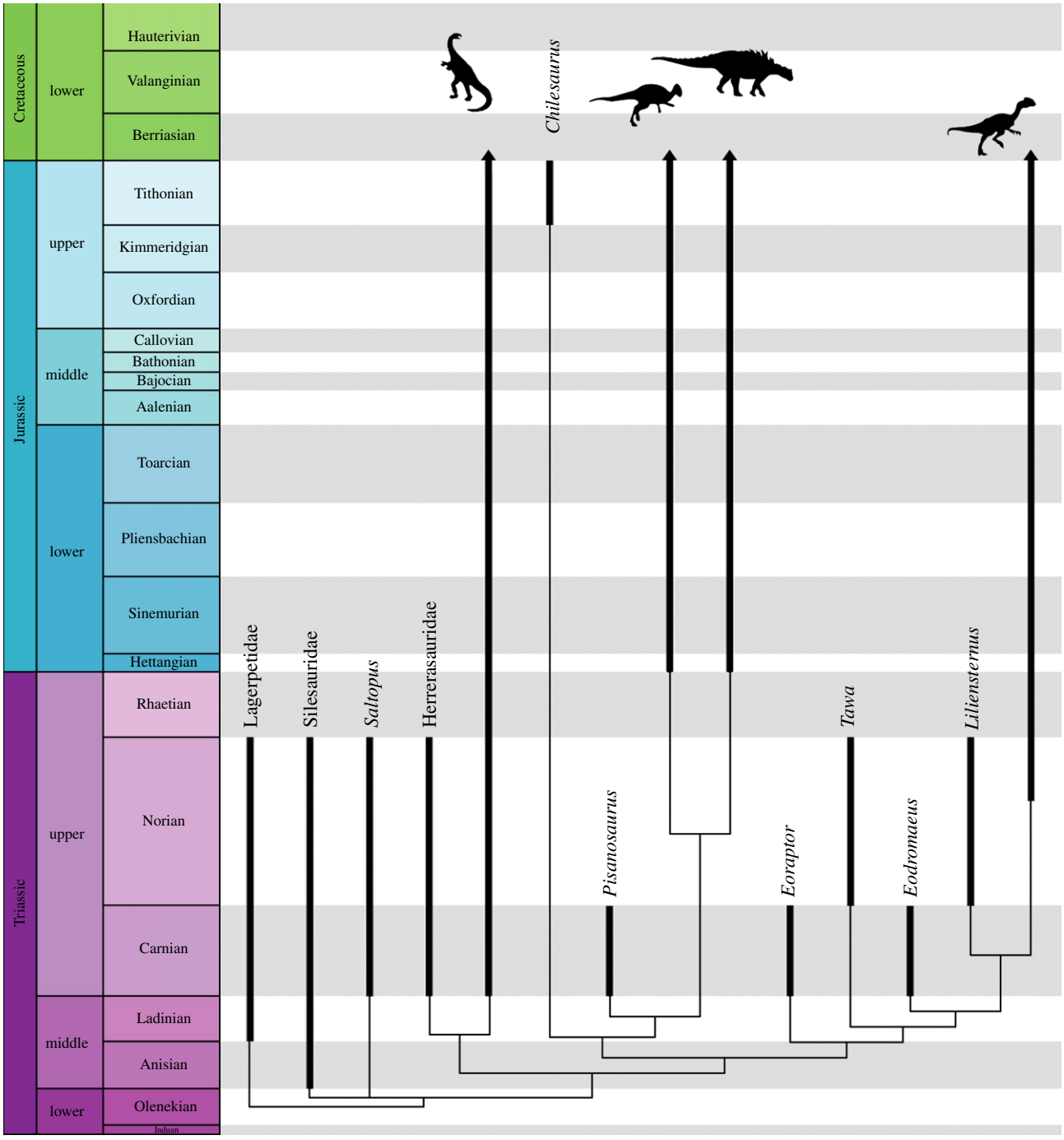

Figure 1. Simplified time-calibrated strict consensus tree in which *Chilesaurus* is recovered within Ornithischia. Silhouettes represent supraspecific taxa—from left to right: Sauropodomorpha, Heterodontosauridae, Genasauria and Neotheropoda.

of a 'transitional' ornithischian that has the potential to illuminate the order in which traditional ornithischian synapomorphies were acquired. As a result, the combination of characters present in *Chilesaurus* provides a new window through which to interpret the earliest stages of ornithischian evolution. For example, it is notable that *Chilesaurus* lacks a predentary bone, one of the features previously regarded as a fundamental ornithischian feature, although it possesses a retroverted pubis, demonstrating that opisthopuby preceded the evolution of some craniodental modifications. Furthermore, an edentulous anterior region of the premaxilla, for the support of a rhamphotheca, as well as the loss of recurvature in most maxillary and dentary teeth also precede the appearance of the predentary. As the presence of a rhamphotheca and the loss of cheek tooth recurvature are both directly related to omnivory/herbivory [10], this suggests that the ornithischians were already adapted to an obligate omnivorous/low-fibre herbivorous lifestyle prior to the acquisition of the predentary and that the appearance of this bone, which also bears a rhamphotheca, does not coincide with the onset of herbivory in this group. Opisthopuby has also been related to herbivory, as it has been suggested that pubic retroversion might be related to the evolution of a more complex, longer digestive tract. This would facilitate the processing of plant material while leaving the centre of mass unaffected in animals that were primitively bipedal [11]. Pubic retroversion is also present in other herbivorous dinosaur clades, such as therizinosaurids and birds, but is restricted to Ornithoscelida. Sauropodomorphs did not acquire this feature, which may have condemned them

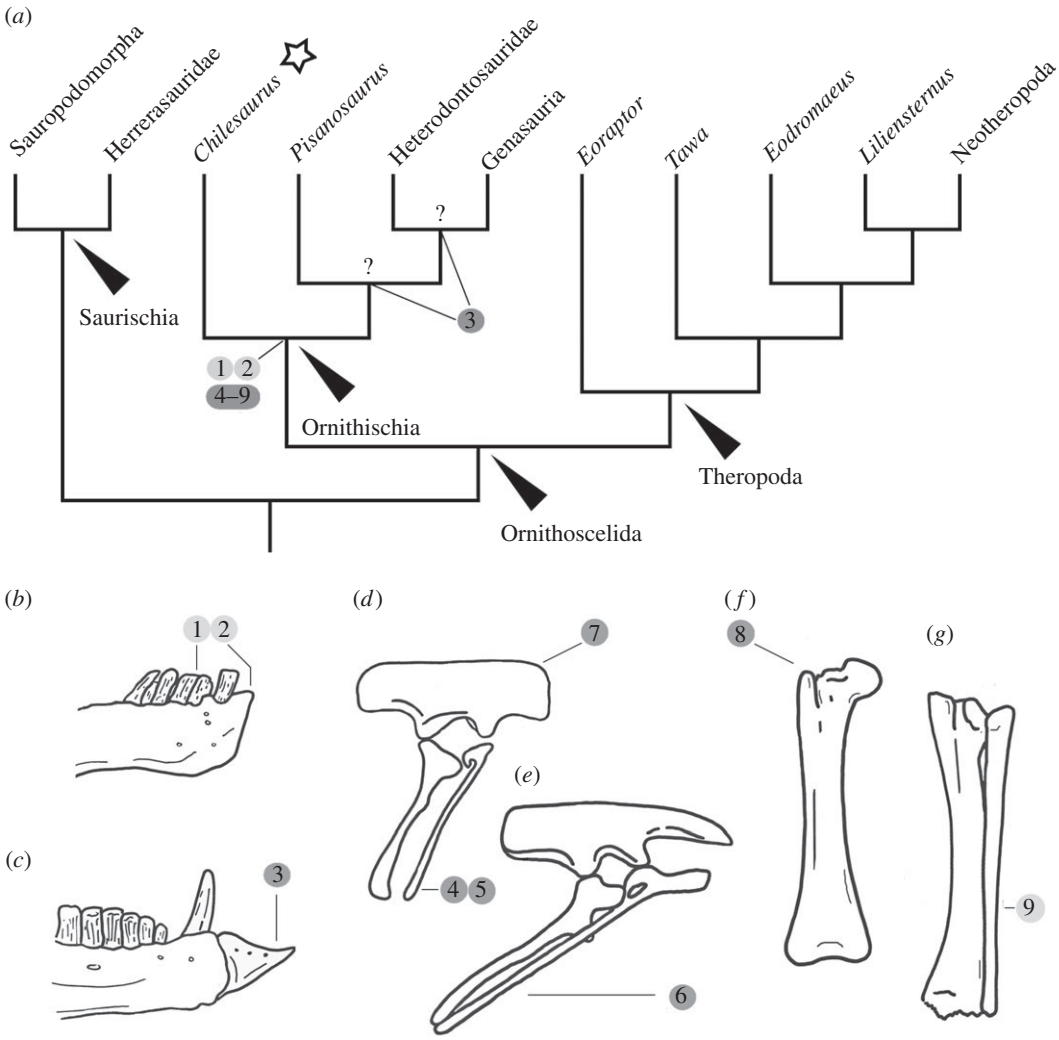

Figure 2. Ornithischian features of *Chilesaurus*. (*a*) Simplified tree with key acquisitions marked on; (*b*) right dentary of *Chilesaurus* (SNGM-1935) in lateral view; (*c*) right dentary of *Heterodontosaurus* (SAM-PK-K1332) in lateral view; (*d*) pelvic girdle of *Chilesaurus* SNGM-1936 in lateral view; (*e*) pelvic girdle of *Agilisaurus* (ZDM T6011) in lateral view; (*f*) right femur of *Chilesaurus* (SNGM-1935) in anterior view; (*g*) right tibia and fibula of *Chilesaurus* (SNGM-1935) in posterior view. Numbers indicate the acquisition of key ornithischian synapomorphies within the clade: 1, complete loss of recurvature in maxillary and dentary teeth; 2, edentulous anterior end of the dentary; 3, predentary bone at the anterior end of the lower jaw; 4, retroversion of the pubis; 5, rod-like pubic shaft; 6, pubic symphysis restricted to the distal end; 7, anteriorly elongate preacetabular process; 8, broadened, wing-like anterior trochanter; 9, fibula less than half the width of the tibia at midshaft. Dark grey circles denote unknown in *Pisanosaurus*.

to quadrupedality as any expansion of the gut anterior to the hips would have resulted in an anterior shift to the centre of mass. The epaxial ossified tendons in the vertebral column that are present in the majority of ornithischians are absent in *Chilesaurus*; the later evolution of this feature might have been related to a combination of diet and stance, providing additional axial support for the more complex digestive system that would be necessary in more derived, high-fibre herbivores (rather than the omnivorous, low-fibre diet that seems likely for *Chilesaurus* on the basis of its craniodental morphology). This absence in *Chilesaurus* further highlights the potentially transitional nature of this taxon from the ancestral dinosaurian condition to the more familiar ornithischian Bauplan.

5. Conclusion

This study identifies *Chilesaurus* as a transitional ornithischian taxon and suggests that the unique suite of anatomical features it possesses could be informative not only in unravelling dinosaur interrelationships, but also in shedding light on the evolution of the anatomical peculiarities that characterize ornithischians. Paradoxically, this early diverging lineage is of Late Jurassic age, implying an extensive ghost lineage between it and other ornithischians and basal theropods. If this hypothesis is correct, this ghost lineage suggests that other similar animals await discovery in Late Triassic–Middle Jurassic deposits. This study highlights the importance of broad taxon sampling when attempting to assess the phylogenetic affinities of enigmatic taxa such as *Chilesaurus* and also demonstrates the utility of this new early dinosaur dataset for testing the relationships proposed for other problematic dinosauromorph taxa [6].

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. M.G.B. designed the experiment, collected the data, ran the analyses, designed and produced the figure and co-wrote the manuscript. P.M.B. designed the experiment, collected the data, helped to design the figure and co-wrote the manuscript. Both authors gave final approval for publication.

Competing interests. We have no competing interests.

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