Zoological Journal of the Linnean Society, 2022, **196**, 1273–1309. With 11 figures.

Taxonomic, palaeobiological and evolutionary implications of a phylogenetic hypothesis for Ornithischia (Archosauria: Dinosauria)

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Received 1 October 2021; revised 25 June 2022; accepted for publication 19 July 2022

The origin and evolutionary relationships of ornithischian dinosaurs are topics that have undergone a series of substantial revisions. At present there are several competing hypotheses concerning the relationship between Ornithischia and the other principal clades of Dinosauria. Some hypotheses have posited a tree topology within Dinosauria that imply a 'ghost-lineage' for Ornithischia (whose representatives make their first unambiguous appearance in the Hettangian) that extends through a substantial portion of Triassic time. In contrast, other hypotheses have placed conventionally Triassic dinosauromorph (stem-lineage Dinosauria) taxa *within* the clade Ornithischia. Recently, a large-scale phylogenetic analysis recovered an array of taxa, known as 'silesaurids', as a paraphyletic assemblage of taxa (referred to in this article using the informal terms silesaurs or silesaurians) on the branch leading to the clade Ornithischia. This latter hypothesis of relationships would account for the apparent absence of Triassic ornithischians, because stem-lineage ornithischians (silesaurs in this article) are exclusively Triassic. However, the analysis that produced this novel topology used a dataset that, in its original form, did not include all early representatives of Ornithischia (*sensu lato*), and did not incorporate all the anatomical characters that have been suggested to unite Ornithischia with other dinosaurian clades (Theropoda and Sauropodomorpha). Nor did the initial study go on to expand upon some important taxonomic, palaeobiological and evolutionary implications of a topology that links a paraphyletic array of silesaurs to the clade Ornithischia. The present article addresses these latter issues by expansion and re-analysis of the original dataset. The results find further support for the hypothesis that silesaurs comprise a paraphyletic grouping of taxa on the stem of Ornithischia and that successive silesaur taxa acquire anatomical characters anagenetically in a process that culminates in the assembly of what may be described as a 'traditional' ornithischian. The overall topology of the consensus tree remains but little changed from the original analysis, despite the addition of new taxa and characters. To provide stability to this area of the tree and to preserve the most important of the relevant taxonomic names, we suggest a revised taxonomic framework for ornithischians that is consistent with this new topology. We retain the name Ornithischia for the total-group (traditional Ornithischia and its stem-lineage), while we resuscitate a name originally proposed by Richard Owen, Prionodontia (= 'coarse edged teeth') for the clade containing only the so-called traditional ornithischian (= 'bird-hipped') dinosaurs. We also erect Parapredentata as a more exclusive subclade in Ornithischia. This novel taxonomic framework is intended to provide phylogenetic clarity and a degree of stability in Ornithischia and Dinosauria as further analyses and new data continue to refine and re-shape the tree. The data presented in this study represent a stage in our attempt to establish an early dinosaur dataset in which character definitions and character scores are agreed upon and used consistently.

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ADDITIONAL KEYWORDS: anagenesis – dentition – Dinosauromorpha – herbivory – Heterodontosauridae – Jurassic – Neornithischia – postcranial anatomy – Prionodontia – silesaurs – systematics – Thyreophora – Triassic.

INTRODUCTION

Ornithischia has been long considered one of the two fundamental components of the Dinosauria – the other being Saurischia – with the arrangement of their pelvic bones being used as the primary criterion for this division, as implied by their names (Seeley, 1888; Charig, 1972, 1976; Bakker & Galton, 1974; Novas, 1996; see Fig. 1A). This dichotomy within the clade Dinosauria has proved to be well supported throughout the post-cladistic period of research (e.g. Gauthier, 1986; Sereno, 1999, 2005, 2007; Benton, 2004; Langer & Benton, 2006; Brusatte *et al.*, 2010; Langer *et al.*, 2010; Nesbitt, 2011; Cabreira *et al.*, 2016). A small number of studies have suggested alternate topologies: Paul (1984) and Bakker (1986) produced non-numerical propositions in favour of 'Phytodinosauria' (Fig. 1B); whereas Baron *et al*. (2017a, 2017b) conformed to the standard of data transparency associated with modern systematic studies when proposing 'Ornithoscelida' (Fig. 1C). In the past decade, the position of Ornithischia with respect to other clades in Dinosauria has proved to be unstable, with multiple competing hypotheses having emerged regarding their early evolutionary history (Cabreira *et al.*, 2016; Baron & Barrett, 2017; Baron *et al.*, 2017a, 2017b; Cau, 2018; Müller & Garcia, 2020a).

The results presented in a novel analysis (Baron *et al.*, 2017a) that challenged the fundamental dichotomy at the root of dinosaur relationships posited Ornithischia as the sister-taxon to Theropoda, rather than the unified Saurischia. This alternative topology was used to justify the resurrection of Huxley's clade name Ornithoscelida. Results of subsequent studies that used modified versions of the same dataset (e.g.

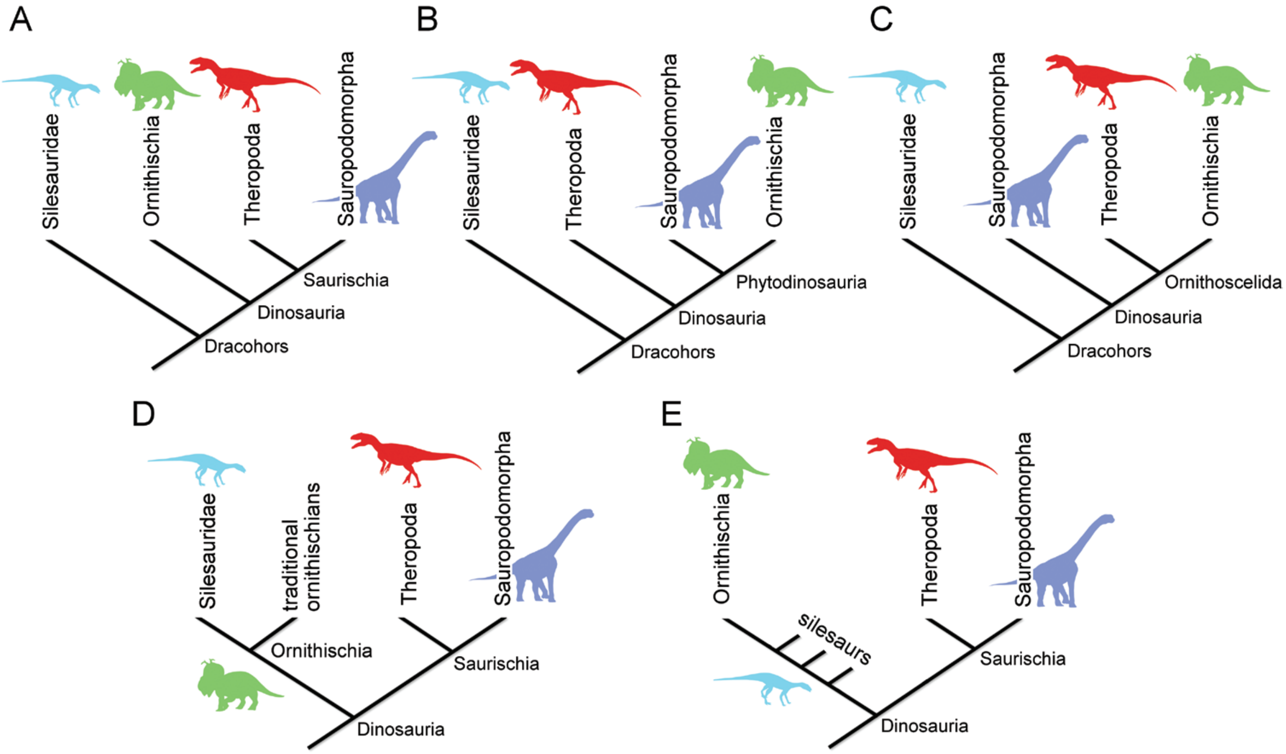

Figure 1. Hypotheses of the phylogenetic relationships of dinosaurs compared: A, the traditional ('Seeley') hypothesis (e.g. Nesbitt 2011; Langer *et al.*, 2017) incorporating the clade Silesauridae. B, the 'Phytodinosauria' hypothesis (e.g. Paul 1984; Bakker, 1986). C, the 'Ornithoscelida' hypothesis (e.g. Baron *et al.*, 2017a, 2017b; Cau, 2018). D, the 'Seeley' hypothesis with Silesauridae placed as the sister-taxon to traditional ornithischians (e.g. Langer & Ferigolo, 2013; Cabreira *et al.*, 2016). E, paraphyletic silesaurs as stem-lineage ornithischians (Müller & Garcia, 2020a). Silhouettes are based on artwork by Márcio L. Castro.

Langer *et al.*, 2017; Parry *et al.*, 2017; Lee *et al.*, 2019) found support for what can be termed both 'Seeley' and 'Ornithoscelida' models of dinosaurian relationships, with little difference in statistical support between these two alternatives or, in point of fact, the third alternative of a Sauropodomorpha–Ornithischia grouping – the 'Phytodinosauria' hypothesis advocated by Paul (1984) and Bakker (1986). Nevertheless, most comparatively recent phylogenetic studies recover topologies that accord with the 'Seeley' model (Nesbitt *et al.*, 2017b; Martz & Small, 2019; Ezcurra *et al.*, 2020; Novas *et al.*, 2021). Some recent analyses have also suggested that a grouping of Middle–Late Triassic species, usually referred to as members of the Silesauridae, are early diverging members of Ornithischia, enlarging on an earlier suggestion by Dzik (2003). The first of these proposals placed Silesauridae as the monophyletic sister-taxon to Ornithischia (Ferigolo & Langer, 2006; see Fig. 1D), although no formal phylogenetic analysis had been undertaken to support this suggestion. Their proposal focused on similarities drawn between the dental and mandibular anatomies in the silesaurid taxon (*Sacisaurus agudoensis* Ferigolo & Langer, 2006) and those seen in early ornithischians. Late Triassic silesaurs appear to have been herbivorous or possibly omnivorous animals and, consequently, display mandibulodental adaptations comparable to those seen among herbivorous ornithischians of the Early Jurassic. Their general proposition found support in the results of subsequent phylogenetic analyses (Langer & Ferigolo, 2013; Cabreira *et al.*, 2016; Pacheco *et al.*, 2019). However, a larger number of phylogenetic studies have continued to recover the Silesauridae as a discrete clade outside Dinosauria, usually found as the sister-taxon to Dinosauria (Nesbitt *et al.*, 2010, 2013, 2017a; Nesbitt, 2011; Baron *et al.*, 2017a, 2017b; Cau, 2018; Martz & Small, 2019; Ezcurra *et al.*, 2020), although most of these do not take into account several contributions that have considerably increased our knowledge about representatives of this group (e.g. Ezcurra *et al.*, 2019; Martz & Small, 2019; Nesbitt *et al.*, 2019).

One factor that confounds resolution of the silesaur–ornithischian relationship is the fragmentary nature and poor preservation of the Late Triassic taxon *Pisanosaurus mertii* Casamiquela, 1967. This taxon was originally described as the earliest known member of Ornithischia (Casamiquela, 1967) and this view gained widespread support (Bonaparte, 1976; Sereno, 1991, 2012; Butler *et al.*, 2007, 2008b; Irmis *et al.*, 2007a; Langer *et al.*, 2010; Boyd, 2015; Baron *et al.*, 2017a). Recent revisions of this material, and more comprehensive phylogenetic analyses, have resulted in this taxon moving around in the dinosauriform tree: from the ornithischian lineage to the silesaur lineage and back again (Baron *et al.*, 2017b; Agnolín & Rozadilla, 2018; Baron, 2019; Desojo *et al.*, 2020). Many other taxa originally interpreted as early ornithischians collected from Late Triassic outcrops (e.g. Hunt & Lucas, 1994) have also been reappraised in light of new discoveries, stratigraphic reassessments and phylogenetic analyses. These have been removed from Ornithischia, because they belong to other clades (e.g. Parker *et al.*, 2005; Irmis *et al.*, 2007b; Nesbitt *et al.*, 2007; McPhee *et al.*, 2017; Bordy *et al.*, 2020). Because of these reassessments, some of these authors have suggested that no Triassic ornithischians are known in the fossil record. This, in turn, implies that ornithischians may differ substantially from current understanding in terms of both the timing of their origin and topological placement in the dinosaur tree (Baron, 2019, 2020).

The phylogenetic status of the Late Jurassic taxon *Chilesaurus diegosuarezi* Novas *et al.*, 2015 from the Toqui Formation (Tithonian) of southern Chile, is of interest in the context of evolving ornithischian relationships. *Chilesaurus* (Novas *et al.*, 2015) has been posited as a derived theropod, a transitional 'missing-link' taxon between Ornithischia and Theropoda or even a sauropodomorph (Novas *et al.*, 2015; Baron & Barrett, 2017; Cau, 2018; Müller *et al.*, 2018a; Müller & Dias-da-Silva, 2019). The 'missing-link' interpretation of its placement (Baron & Barrett, 2017) is incongruent chronologically (Late Jurassic) and evolutionarily, in the context of the acquisition of the fundamental ornithischian bauplan, but its curious opisthopubic pelvic anatomy may point toward either iterative (the repeated theropodan acquisition of opisthopuby) or atavistic anatomical phenomena. It is clear that the relationship of *Chilesaurus* in Dinosauria needs clarification. Most recently, Federico Agnolín (pers. comm., 25 April 2022) has reaffirmed the theropod affinities of *Chilesaurus* on the basis of the presence of pleurocoels, complex laminae on the cervical vertebrae, the shape of the ilium and carpal anatomy.

Internal relationships in the ornithischian clade have also become unstable in recent years. For a long time, heterodontosaurids have been placed at the base of the ornithischian lineage as the earliest diverging clade (Butler *et al.*, 2008b; Boyd, 2015; Baron *et al.*, 2017c). The remaining non-heterodontosaurid ornithischians constituted a revised version of Genasauria (*sensu* Sereno, 1986). Genasauria include the osteoderm-bearing Thyreophora, as well as Neornithischia, the latter comprising Cerapoda and a long list of other ornithischian taxa whose relationships to one another have proved labile (e.g. Butler *et al.*, 2008b; Boyd, 2015; Dieudonné *et al.*, 2020). Discoveries such as those of *Eocursor parvus* Butler *et al.*, 2007 (Butler,

2010) and *Laquintasaura venezuelae* Barrett *et al.*, 2014, while not changing the overall topology of the traditionally recognized ornithischian clade, have added to the roster of ornithischian 'types' identifiable during the earliest stratigraphic stages (Hettangian–Sinemurian) that are known to contain *bona fide* ornithischian material. Prior to these latter discoveries, the earliest known ornithischians were recognized as 'lesothosaurs' (e.g. Galton, 1978), heterodontosaurids (e.g. Sereno, 2012) or extremely poorly preserved taxa based upon teeth alone (Hunt & Lucas, 1994), and the persistently problematic material referred to the taxon *Pisanosaurus* (Casamiquela, 1967).

The early ornithischian taxon *Lesothosaurus diagnosticus* Galton, 1978 has shifted between various subclades in Ornithischia, depending upon which anatomical characters and taxa have been included in analyses (e.g. Butler *et al.*, 2008a, 2008b; Boyd, 2015; Baron *et al.*, 2017c; Raven & Maidment, 2017, 2018; Raven *et al.*, 2019; Breeden & Rowe, 2020; Maidment *et al.*, 2020). Regardless, certain ornithischian taxa have invariably been chosen for use in broader phylogenetic analyses of dinosaurs and of archosaurs, on the supposition that they are appropriate early representatives of this large and highly diverse clade (e.g. Langer & Benton, 2006; Nesbitt, 2011; Cau, 2018). This informal but self-limiting 'protocol' constrains what such analyses can establish, both in terms of positioning ornithischians within Dinosauria and for resolving how stem-lineage dinosaurs (dinosauriforms) relate to them (Baron *et al.*, 2017a; Müller & Dias-da-Silva, 2019). Dieudonné *et al.* (2020) challenged current practices with regard to the anatomy of the earliest ornithischians. For example, they recovered heterodontosaurids nested in Cerapoda, rather than at the base of the ornithischian clade. This alternative topology implies that there may be fundamental misunderstandings concerning the composition of the earliest diverging ornithischian groupings, and about which anatomical features are representative of the earliest members of this clade. If heterodontosaurids prove to be correctly placed as topologically more derived ornithischians, then 'lesothosaurs', thyreophorans and other early genasaurians become the main source of information regarding the appearance of the ancestral ornithischian. As subclades in Ornithischia vary in their anatomy, the changes proposed by Dieudonné *et al.* (2020) need to be evaluated carefully in any future analyses that attempt to resolve early ornithischian (and, ultimately, dinosaurian) relationships.

Recent analyses of the relationship between early dinosaurs and their closest relatives have recovered silesaurs, previously considered to be a clade (Silesauridae) outside Dinosauria, as a paraphyletic assemblage of taxa *within* Dinosauria. Müller & Garcia (2020a) produced a phylogeny that placed silesaurians as successional taxa on the stem of Ornithischia (Fig. 1E). The implication drawn from this topology is that silesaurs occupy an evolutionary 'zone of transition' leading to the appearance of definitive ornithischian taxa, since silesaurs occur within the time-span of the otherwise substantial ghost-lineage for Ornithischia during much of the Middle–Late Triassic.

The placement of a variety of silesaur taxa on the stem of Ornithischia would have the effect of pushing back the timing of dinosaur divergences, and such profound phylogenetic issues need to be clarified and resolved so that the early phases of dinosaur evolution can be better understood. One corollary that develops from this proposition is the insight it might generate concerning the acquisition of the unique ornithischian bauplan.

The new topology has a bearing on the timing of divergence of the clades Theropoda and Sauropodomorpha. For example, the posited occurrence of the silesaurians *Lutungutali sitwensis* Peecook *et al.*, 2013 and *Asilisaurus kongwe* Nesbitt *et al.*, 2010 (Nesbitt *et al.*, 2019) in the Anisian (247–242 Mya), would push the stem-ornithischian–saurischian split as far back as the Early Triassic (Induan–Olenekian). This hypothesis is dependent on an Anisian age for the Manda Beds of Tanzania and the 'upper beds' of the Ntawere Formation of Zambia. However, recent work has posited a Carnian age (Marsicano *et al.*, 2016; Nesbitt *et al.*, 2017a; Peecook *et al.*, 2017). If a younger age of occurrence for *Lutungutali* and *Asilisaurus* were agreed, this would still push back the origin of the ornithischian stem-lineage from traditional hypotheses that have focused on the Latest Triassic–Early Jurassic interval (Crompton & Charig, 1962; Thulborn, 1971; Sereno, 1991; Norman *et al.*, 2004; Langer & Benton, 2006; Butler *et al.*, 2008b; Boyd, 2015; Baron, 2019).

Despite sampling a wide range of dinosauromorph taxa, the dataset developed by Müller & Garcia (2020a) did not include several early members of each of the major ornithischian subclades Thyreophora, Neornithischia and Heterodontosauridae. This omission reduces the quantity and quality of data available for the various analyses and, potentially, masks stepwise character acquisitions along branches in the trees that are recovered from such analyses. The suggestion that *Chilesaurus* may be a late-occurring yet anatomically 'transitional' theropod-like ornithischian that was topologically a basal sister-taxon to *Pisanosaurus* + *Heterodontosaurus*–Genasauria (Baron & Barrett, 2017: Fig. 2) implied that its anatomical characters might have some bearing on character acquisition and/or distribution during early stages of dinosaur evolution. *Pisanosaurus* has

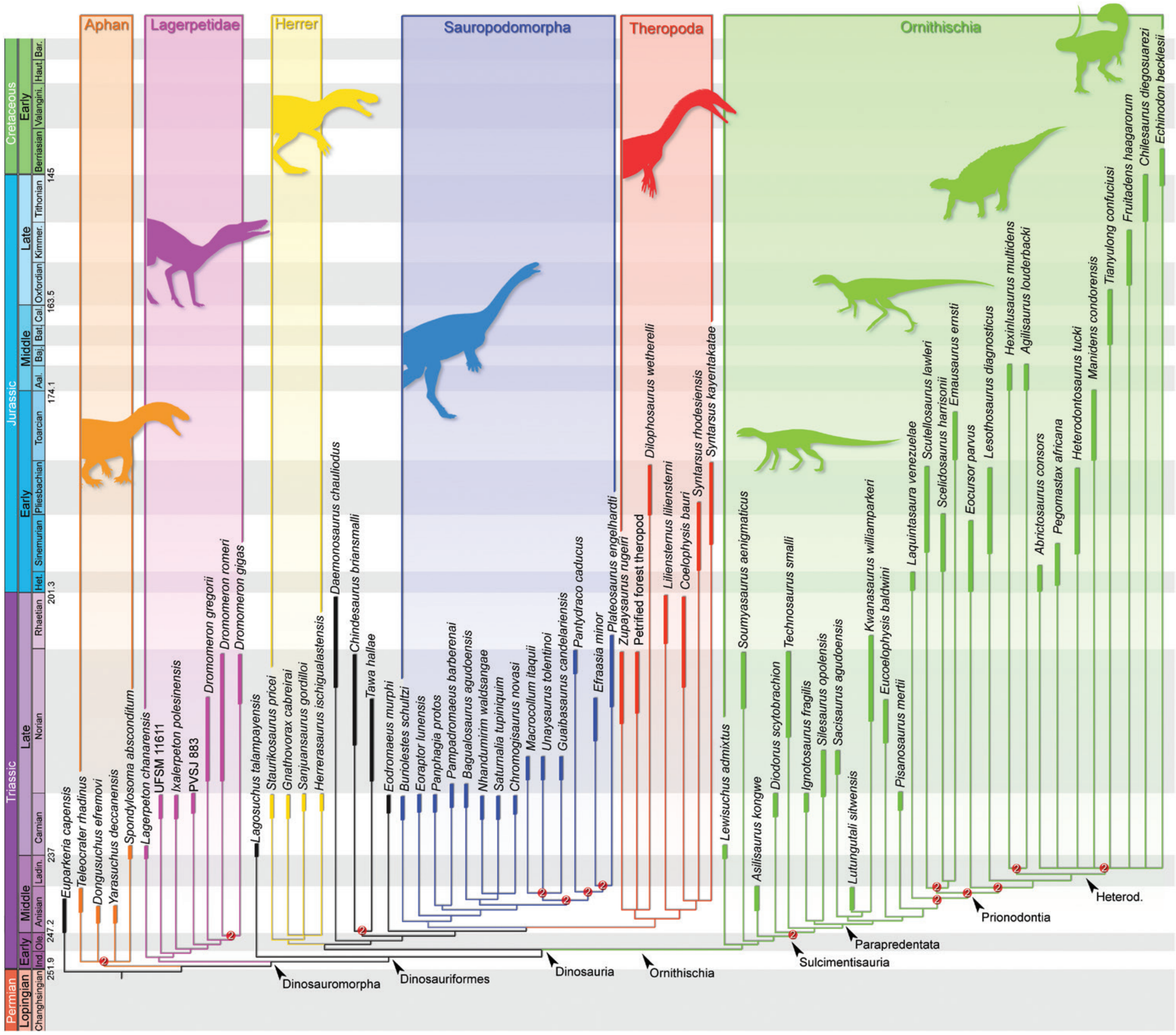

Figure 2. Time-calibrated strict consensus tree from the unconstrained analysis. Numbers on nodes represent Bremer support values higher than 1. *Saltopus elginensis* [Friedrich Freiherr] von Huene, 1910 was removed from the strict consensus tree after an iterPCR analysis (Pol & Escapa, 2009). Abbreviations: Aphan, Aphanosauria; Herrer, Herrerasauridae; Heterod., Heterodontosauridae. Silhouettes are based on artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia and John Sibbick.

also been posited as a silesaur, rather than a basal ornithischian (Baron *et al.*, 2017; Agnolín & Rozadilla, 2018; Baron, 2019).

The analyses presented here 'test' the effects that inclusion of early ornithischian taxa (including the enigmatic *Chilesaurus*) have on the recoverable topology at the base of the dinosaurian phylogeny. Particular attention is focused upon ornithischians and their interrelationship with silesaurians, theropods and saurischians more broadly. Building on the previous analysis of Müller & Garcia (2020a), we are able to describe, for the first time, a possible sequence by which the distinctive and unique anatomical traits observed in the ornithischian clade were assembled during Late Triassic times.

MATERIAL AND METHODS

Nine ornithischian taxa were added to the dataset of early dinosaurs assembled by Müller & Garcia (2020a). The additional taxa were drawn from a range of geographic and temporal settings spanning the Jurassic and Cretaceous periods. These include the Early Jurassic South American *Laquintasaura venezuelae* Barrett *et al.*, 2014, the North American *Scutellosaurus lawleri*

Colbert, 1981, the European *Scelidosaurus harrisonii* Owen, 1861 (Norman, 2020a, 2020b, 2020c, 2021) and *Emausaurus ernsti* Haubold, 1993; the Middle Jurassic Chinese *Hexinlusaurus multidens* (He & Cai, 1983) and *Agilisaurus louderbacki* (Peng, 1990), as well as heterodontosaurid taxa from the Early Jurassic of southern Africa and the Early Cretaceous of Europe (Butler *et al.*, 2008a, 2010; Norman *et al.*, 2011; Pol *et al.*, 2011; Sereno, 2012). *Chilesaurus diegosuarezi* from the Late Jurassic of Chile was included in this updated matrix to ensure that all currently competing sources of early ornithischian evolution and interrelationships were being evaluated. The majority of taxa were scored from direct observation of specimens by the authors. Additional anatomical information was taken from a combination of published and unpublished photographs of taxa, as well as from the published literature on these early species (Knoll, 2002a, 2002b; Butler, 2010; Butler *et al.*, 2007, 2008a, 2010, 2012; Knoll *et al.*, 2009; Pol *et al.*, 2011; Sereno, 2012; Barrett *et al.*, 2014, 2016; Galton, 2014; Novas *et al.*, 2015, 2021; Porro *et al.*, 2015; Baron *et al.*, 2017c; Breeden & Rowe, 2020; Norman, 2020a, 2020b, 2020c). Five new anatomical characters used in previous analyses of early dinosaurs and their close dinosaur relatives were added to the data matrix (see Supporting Information, File S1, for the complete list of characters and scores) as follows. Character 278 (from Nesbitt, 2011), palpebral: (0) present; (1) absent. Character 279 (from Butler *et al.*, 2008b), palpebral position: (0) above the orbit; (1) projects into the orbit. Character 280 (from Butler *et al.*, 2008b), femoral fourth trochanter orientation: (0) perpendicular to the axis; (1) pendent. Character 281 (Baron *et al.*, 2017a), tibial distal condyles: (0) condyles equally extensive; (1) medial condyle extends further distally; (2) lateral condyle extends further. Character 282 (Nesbitt, 2011), position of the Meckelian groove on the anterior-half of the dentary: (0) dorsoventral centre of the dentary; (1) restricted to the ventral border. All anatomical characters were selected because they appear in some, but not all, dinosauromorphs and are potentially informative regarding the interrelationships of the earliest taxa.

Analyses based on File S2 (see Supporting Information) were carried out using the software TNT v. 1.1 (Goloboff *et al.*, 2008) following the methodology used by Müller & Garcia (2020a). The phylogenetic analyses were based on equally weighted parsimony. Characters 4, 13, 18, 25, 63, 82, 84, 87, 89, 109, 142, 166, 174, 175, 184, 186, 190, 201, 203, 205, 209, 212, 225, 235, 236, 239, 250 and 256 were treated as additive (ordered). *Euparkeria capensis* Brown, 1913 (Ewer, 1965) was selected as the outgroup taxon and used to root the most parsimonious trees (MPTs) that were produced. The MPTs were produced using random addition sequence + tree bisection reconnection (TBR), which included 1000 replicates of Wagner trees (with random seed = 0), TBR and branch-swapping (holding 20 trees saved per replicate). Topologies retained as replicates were branch-swapped for MPTs using TBR. The strict consensus tree was generated using all trees recovered in the analysis and all OTUs. Decay indices (Bremer support values) and bootstrap values (1000 replicates) were also calculated using TNT, as in the analysis undertaken by Müller & Garcia (2020a).

Constrained analyses were then performed using the same search parameters as the first analyses to test various alternative hypotheses of early dinosaur interrelationships, as outlined above, and to assess the number of extra steps required to recover each of these. The first constrained analysis enforced a monophyletic Silesauridae apart from the 'traditional' ornithischians. Hence, in this analysis, the clade Dracohors (Silesauridae plus Dinosauria) is enforced (see: Cau, 2018). *Pisanosaurus* and *Chilesaurus* were set as floating taxa. The second constrained analysis enforced a monophyletic Ornithoscelida (see: Baron *et al.*, 2017a, 2017b). In this analysis, 'traditional' ornithischians and theropods were maintained as a clade distinct from Sauropodomorpha. *Chilesaurus, Chindesaurus bryansmalli* Long & Murry, 1995; *Daemonosaurus chauliodus* Sues *et al.*, 2011; *Eodromaeus murphi* Martinex *et al.*, 2011; *Guaibasaurus candelariensis* Bonaparte *et al.*, 1999; *Nhandumirim waldsangae* Marsola *et al.*, 2019; *Pisanosaurus mertii* and *Tawa hallae* Nesbitt *et al.*, 2009 were set as floating taxa. The third analysis enforced *Chilesaurus* within Theropoda, in accordance with the conventional view of this taxon (Novas *et al.*, 2015; Cau, 2018).

RESULTS

In the unconstrained analyses, 96 trees were recovered, each of 1107 steps (CI = 0.289; RI = 0.698). With the additional ornithischian taxa and *Chilesaurus* included in the dataset, the overall topology recovered in Dinosauria in the strict consensus tree (Fig. 2) remained unchanged from the initial analyses carried out by Müller & Garcia (2020a). The Dinosauria is divided into Ornithischia, incorporating the traditional forms and its stem-lineage taxa (silesaurs), and Saurischia (comprising herrerasaurids, theropods, sauropodomorphs and four taxa basal to Eusaurischia) (Fig. 2). The topology within the total clade (Ornithischia), as defined herein, is subtly different from the previous analysis (see Fig. 2). A succession of stem-lineage ornithischian taxa, in order: *Lewisuchus admixtus* Romer, 1972, *Soumyasaurus aenigmaticus* Sarıgül *et al.*, 2018 and *Asilisaurus kongwe*, leading to Sulcimentisauria is preserved, although the internal relationships within Sulcimentisauria are changed by the addition of new taxa. *Sacisaurus agudoensis* Ferigolo & Langer, 2006 is recovered in a clade with *Lutungutali sitwensis* and *Kwanasaurus williamparkeri* Martz & Small, 2019. This clade then forms the sister-taxon to a clade containing *Eucoelophysis baldwini* Sullivan & Lucas, 1999, *Pisanosaurus*, *Laquintasaura* (Barrett *et al.*, 2014) and the node-based clade Prionodontia (Ornithischia in traditional schemes; see below for the employed phylogenetic definition of Prionodontia). *Laquintasaura* was not included in the original study by Müller & Garcia (2020a), so this taxon's position as the proximal sister-taxon to Prionodontia is a novel result (see Figs 2, 6).

Within the historically conventional ornithischian clade (Prionodontia here), the Early Jurassic taxa *Scelidosaurus* (Owen, 1861b), *Emausaurus* (Haubold, 1990) and *Scutellosaurus* (Colbert, 1981) are recovered within a monophyletic Thyreophora (e.g. Butler *et al*., 2008; Arbour & Currie, 2016). This thyreophoran clade is then recovered as the sister-clade to all the remaining ornithischians, including the Early Jurassic southern African taxa *Eocursor* (Butler *et al.*, 2007) and *Lesothosaurus* (Galton, 1978), followed by Middle Jurassic neornithischians and an internally unresolved clade of heterodontosaurids. Interestingly, Heterodontosauridae is again recovered nested deeply in the clade Prionodontia, rather than in its more commonly recovered position as the earliest diverging subclade. We recover Heterodontosauridae in a sister-taxon relationship with the clade containing *Hexinlusaurus* (Barrett *et al*., 2005) and *Agilisaurus* (Peng, 1990). This result mirrors that produced by Dieudonné *et al.* (2020), in which heterodontosaurids are positioned away from the base of Ornithischia and close to the base of, or even within, Cerapoda. *Chilesaurus* was recovered in a deeply nested position in Prionodontia (formerly node-based Ornithischia). However, we recover *Chilesaurus* as a heterodontosaurid ornithischian (Figs 2, 6). It is important to note that an experimental analysis with *Chilesaurus* deleted (144 trees of 1069 steps each; CI = 0.299; RI = 0.713) recovered the same topology for the strict consensus tree, in which the internal relationships of Prionodontia remain unchanged. Silesaurians were once again recovered as a paraphyletic assemblage as stem-lineage ornithischians.

In the first of the constrained analyses (Fig. 3), which enforced a monophyletic Silesauridae, 1584 trees each of 1116 steps were produced (CI = 0.287, RI = 0.677); this represents nine extra steps compared with the MPTs produced in the initial unconstrained analyses. *Pisanosaurus* is recovered in Prionodontia (Fig. 3) rather than in Silesauridae (*contra* Baron *et al.*, 2017b; Agnolín & Rozadilla, 2018; Baron, 2019), as the sister-taxon to a clade comprising *Laquintasaura* and all more derived ornithischians. As in the unconstrained analyses, *Laquintasaura* is not recovered in the least inclusive clade containing thyreophorans and neornithischians. This again gives support to the result obtained in the first analysis, which suggests that *Laquintasaura* falls just outside Prionodontia. In this analysis, the relationships in Prionodontia are less well-resolved than in the unconstrained analyses. However, once again, the heterodontosaurids are not recovered as an early diverging clade in Prionodontia, but as a clade nested deeply in Neornithischia (*sensu* Dieudonné *et al.*, 2020). *Chilesaurus*, which was allowed to 'float' in this analysis, is recovered in Theropoda (*sensu* Novas *et al.*, 2015), as the sister-taxon to all other theropods (Fig. 3).

In the second constrained analysis (Fig. 4) that enforced the 'Ornithoscelida' hypothesis first proposed by Baron *et al.* (2017a), i.e. the Ornithischia–Theropoda sister-taxon relationship, the 220752 MPTs produced were each of 1145 steps (CI = 0.275, RI = 0.665), which is 38 steps longer than the MPTs of the initial analyses. The resolution in Dinosauria is poor in this analysis (Fig. 4), with the sauropodomorph, herrerasaurid and ornithoscelidan clades being found as a polytomy at the base of Dinosauria. Interestingly, *Chilesaurus* falls just outside of Ornithoscelida, as the sister-taxon to this clade. In this analysis, Silesauridae is recovered outside of Dinosauria, as part of Dracohors, and *Pisanosaurus mertii* is recovered as a silesaurid (*sensu* Baron *et al.*, 2017b; Agnolín & Rozadilla, 2018; Baron, 2019). This topology, and the placement of *Pisanosaurus*, is strikingly similar to the result presented by Baron *et al.* (2017b), in response to the revisions to the original dataset of Baron *et al.* (2017a) by Langer *et al.* (2017).

Finally, in the third constrained analysis (Fig. 5), which enforced *Chilesaurus* as a taxon in Theropoda, 144 MPTs each of length 1110 steps were recovered (CI = 0.288, RI = 0.680) (Fig. 5). As in the first constrained analysis (Fig. 3), *Chilesaurus* is recovered as the sister-taxon to all other theropods. The fundamental topology in Ornithischia is unchanged from the results of the unconstrained analyses. *Laquintasaura* is recovered as the proximal sister-taxon to the clade Prionodontia and *Pisanosaurus* is positioned as the sister-taxon to *Laquintasaura* (Fig. 5).

DISCUSSION

TAXONOMIC IMPLICATIONS

Several important taxonomic implications flow from the topology generated here (Figs 2, 6). The arrangement of taxa in what we refer to as the total ornithischian lineage necessitates revision, redefinition, addition or replacement of some clade names.

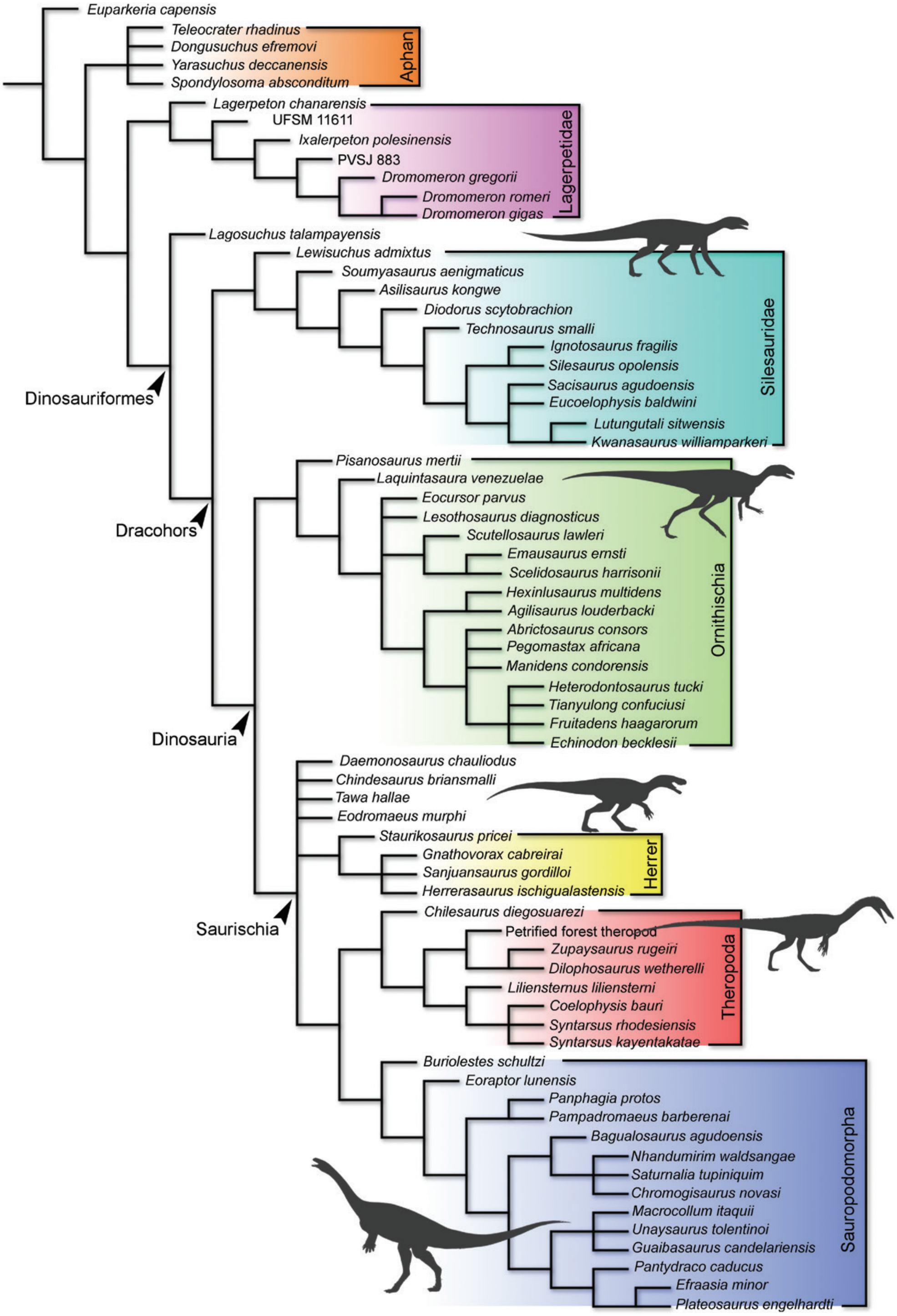

Figure 3. Strict consensus trees from the constrained analyses. First constrained analysis forcing a monophyletic Silesauridae apart from the 'traditional ornithischians'. Abbreviations: Aphan, Aphanosauria; Herrer, Herrerasauridae. Silhouettes are based on artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia, John Sibbick and Douglas M. Heman.

The definition and status of the clade Ornithischia is brought into focus by the results of this analysis. The inclusion of an array of silesaurs not just in the clade Dinosauria, but more specifically as members of the stem-lineage of Ornithischia, raises the questions: what, precisely, the clade Ornithischia

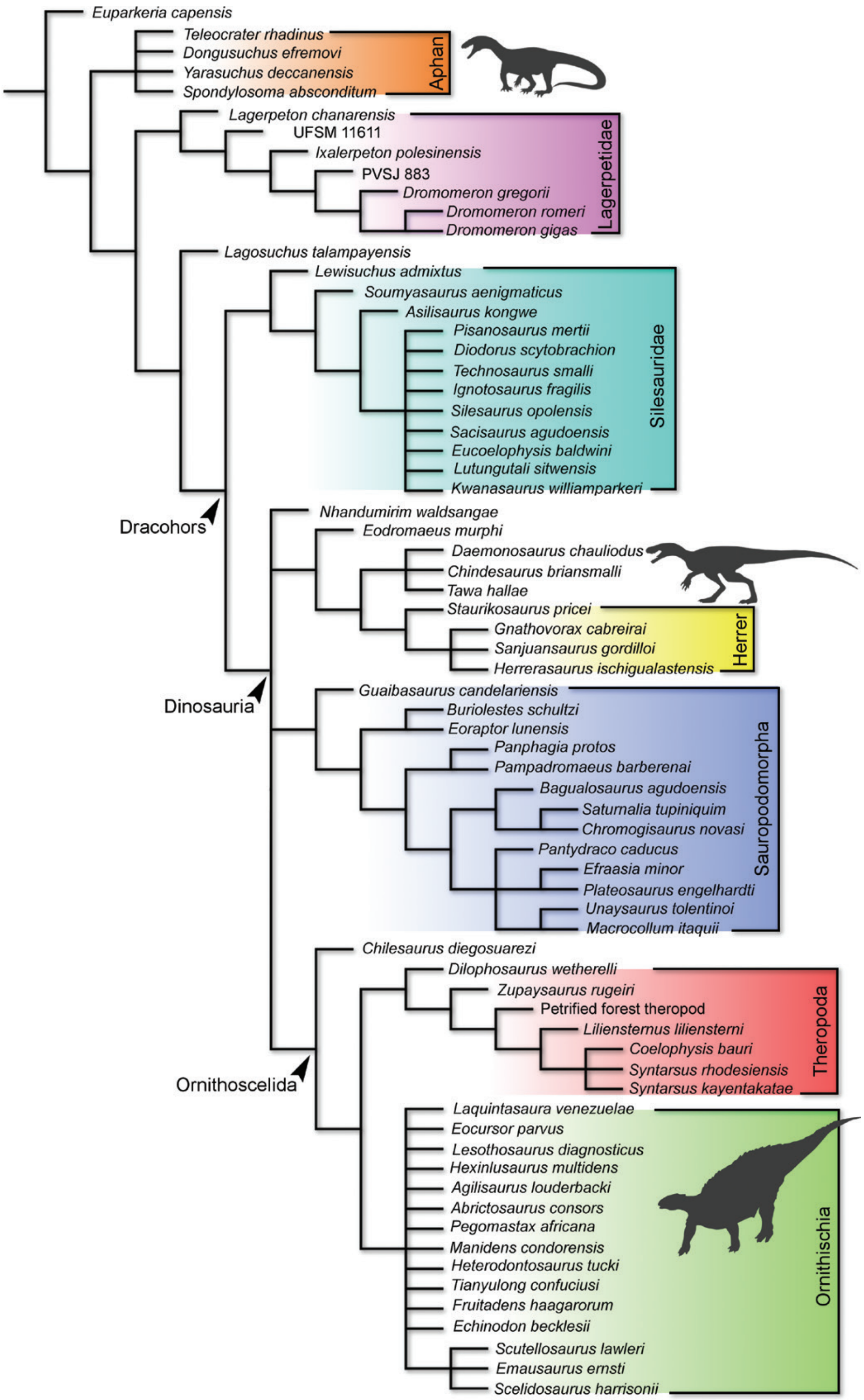

Figure 4. Second constrained analysis forcing a monophyletic Ornithoscelida. Abbreviations: Aphan, Aphanosauria; Herrer, Herrerasauridae. Silhouettes are based on artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia, John Sibbick and Douglas M. Heman.

is and what taxa should be included. As one of the two fundamental groupings of Dinosauria (Seeley, 1888) and recognized consistently since then, any dramatic shift in the composition of Ornithischia and its topological placement with respect to Saurischia has the potential to profoundly affect commonly used dinosaurian taxonomy. The new topology (Fig. 6) offers an opportunity for the taxon Ornithischia

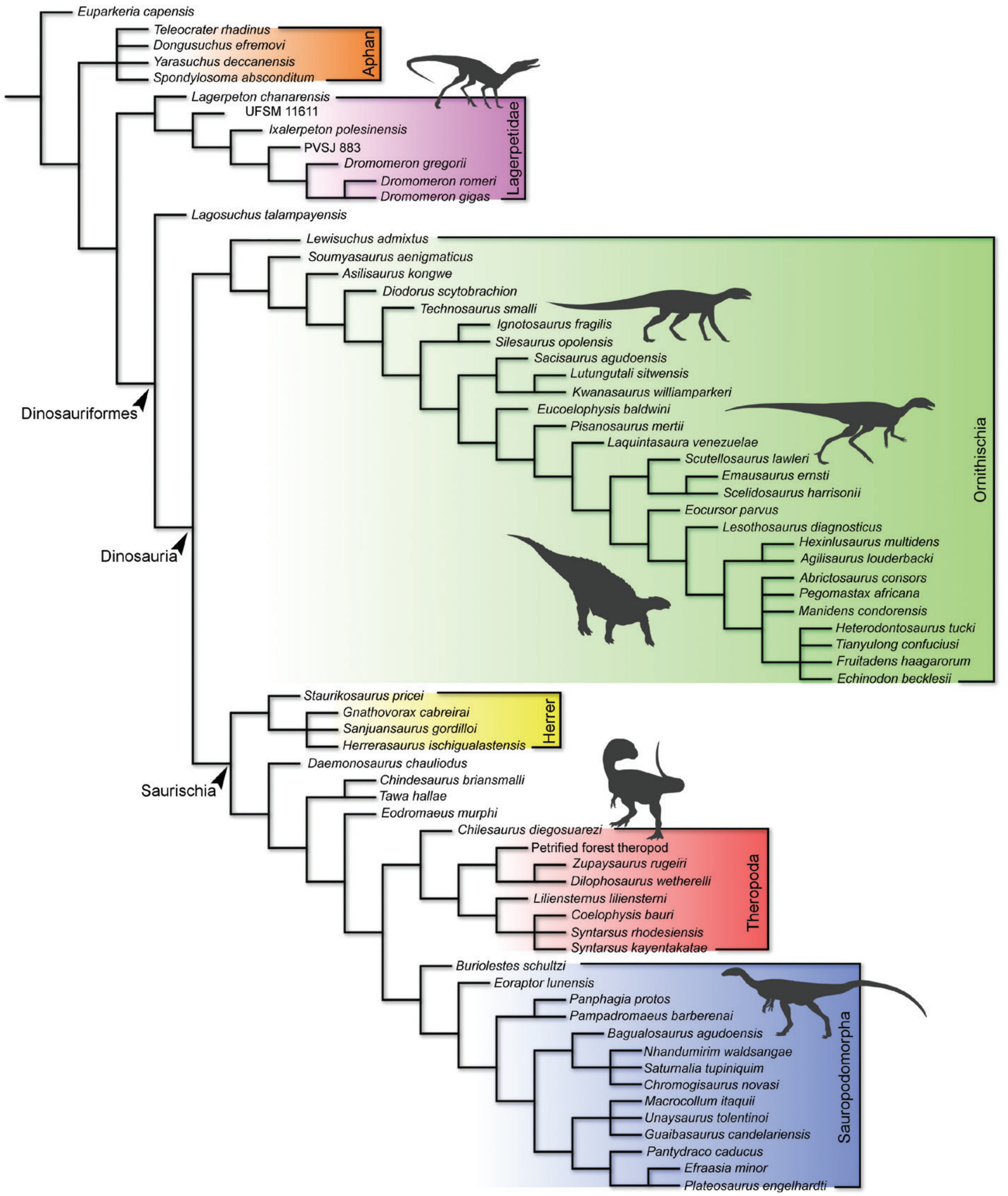

Figure 5. Third analysis forcing *Chilesaurus diegosuarezi* in Theropoda. Abbreviations: Aphan, Aphanosauria; Herrer, Herrerasauridae. Silhouettes are based on artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia, John Sibbick and Douglas M. Heman.

to become more inclusive, by the incorporation of a range of non-ornithischian taxa on its stem. The wording of the current stem-based phylogenetic definition of Ornithischia: 'the most inclusive clade that includes *Triceratops horridus* but not *Diplodocus carnegii* or *Passer domesticus*' (Baron *et al.*, 2017a) allows for this expansion, as recognized by Müller & Garcia (2020a). It is proposed herein

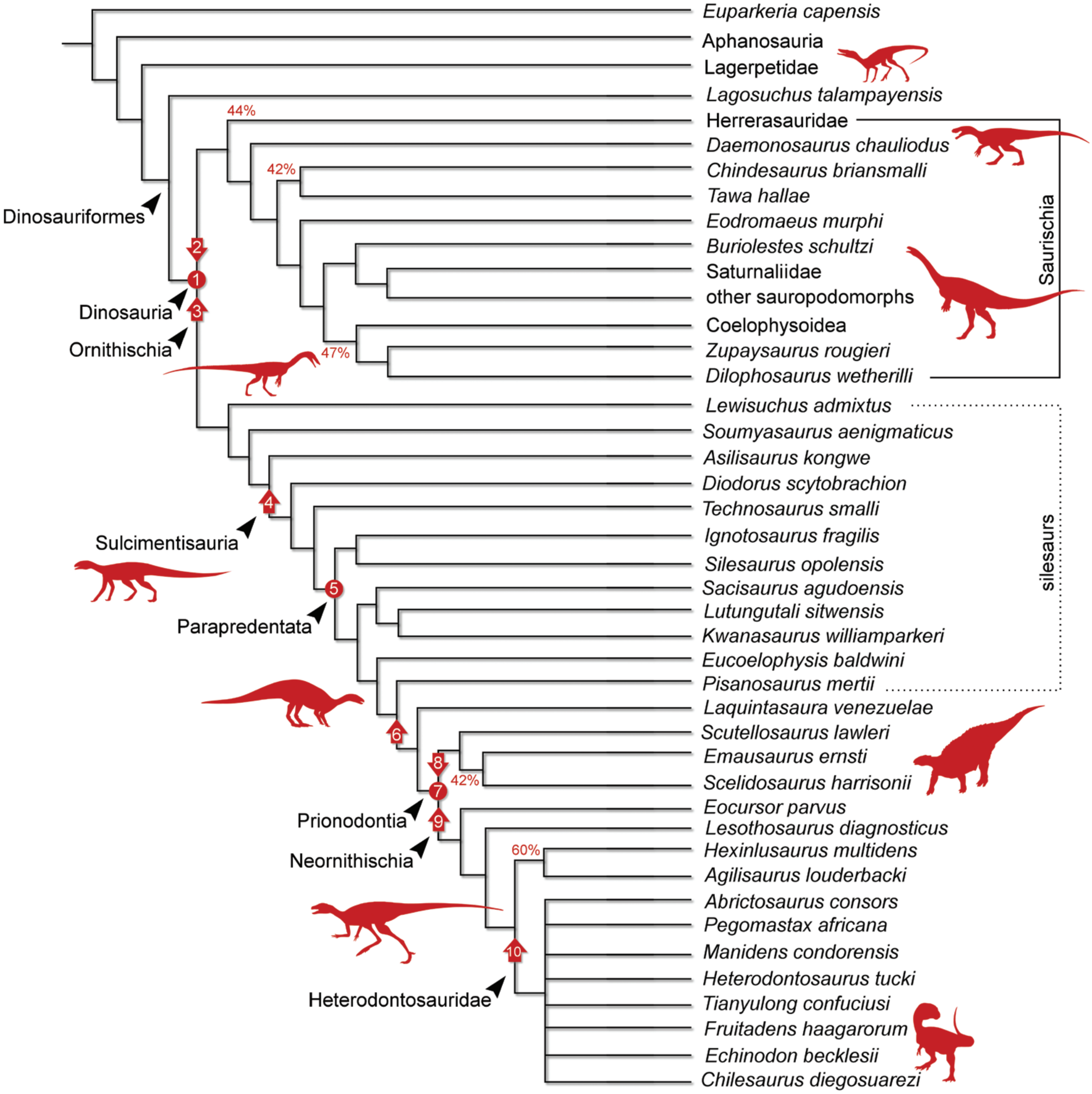

Figure 6. Strict consensus tree from the unconstrained analysis depicting node numbers mentioned in the text and bootstrap values equal to or higher than 40%. Node numbers: 1, Dinosauria; 2, Saurischia; 3, Ornithischia; 4, Sulcimentisauria; 5, Parapredentata; 6, Unnamed; 7, Prionodontia; 8, Thyreophora; 9, Neornithischia; 10, Heterodontosauridae. *Saltopus elginensis* was removed from the strict consensus tree after an iterPCR analysis (Pol & Escapa, 2009). Silhouettes based on the artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia and John Sibbick.

that the name Ornithischia be retained as the most inclusive clade in order to retain its status as one of the three principal dinosaur clades, even though its taxic composition and anatomical characteristics have been substantially broadened.

Historically, Ornithischia were defined and diagnosed (apomorphically) by the possession of a 'bird-like' opisthopubic pelvis as a consequence of the retroversion of the pubic shaft: this was the inspiration behind the name Ornithischia (hence 'bird hipped') coined by Seeley (1888). This group was distinguished from the Saurischia ('reptile hipped'), which contained all dinosaurian taxa that displayed the (plesiomorphic) forward-pointing pubis, as well as an apomorphic trait: the osteological markers associated with pneumatism. None of the currently known silesaurs possess either an ornithischian pelvic configuration or evidence of saurischian-like pneumatism.

One proposal regarding the taxonomy applicable to the silesaur–ornithischian lineage might be to retain a node-based definition of the Ornithischia: the common ancestor of *Scelidosaurus*, *Lesothosaurus* and *Heterodontosaurus* and all descendants, so that it excludes members of their stem-lineage and encompasses only those taxa that are anatomically ornithischian (in a classical sense). To do this would create substantial nomenclatural and taxonomical disturbance because it would become necessary to propose a new taxonomic name for the stem-based clade that is commonly understood to stand as the sister-taxon to Saurischia [notwithstanding Bakker (1986) or Baron *et al.* (2017a)].

Using phylogenetically derived definitions (de Queiroz & Cantino, 2020) to establish hierarchical taxonomies for fossil taxa means that clade names will change in their internal composition as new taxa are discovered and tree topologies alter in response. In this instance, the taxic composition of the stem-lineage of Ornithischia cannot be argued to be robust, given the range of competing hypotheses concerning the affinities and placement of currently known silesaurs and proximate taxa (Ezcurra, 2006; Irmis *et al.* 2007b; Nesbitt *et al.*, 2010; Langer & Ferigolo, 2013; Bittencourt *et al.*, 2014; Cabreira *et al.*, 2016; Baron *et al.*, 2017b; Agnolín & Rozadilla, 2018; Pacheco *et al.*, 2019; Ezcurra *et al.*, 2020; Müller & Garcia, 2020a). Conserving the taxon Ornithischia in a more inclusive sense does not preclude the possibility that other early diverging members of the clade may be discovered that retained the ancestral condition of a plesiomorphic 'saurischian' hip structure, but these would be positioned proximal to a more exclusive ornithischian node. The stem-based concept of Ornithischia will, necessarily, expand to encompass taxa that do not possess a bird-like hip morphology (or, indeed, some of the other apomorphies that pertain to the original conception of the ornithischian bauplan, e.g. predentary, palpebral bones and epaxial ossified tendons).

In their initial study, Müller & Garcia (2020a) chose to distinguish between the various 'silesaurids' (a paraphyletic grouping of taxa on the stem-lineage of Ornithischia) and the anatomically more derived ornithischian taxa; the latter group was referred to as 'traditional ornithischians'. The recognition of a more exclusive clade 'traditional ornithischians' implies that there is scope for a taxonomic term that recognizes this clade.

Exploring the historical literature associated with this topic, the term Ornithischia has not been the only name suggested for a group of exclusively opisthopubic (bird-hipped) dinosaurs. 'Predentata' was proposed by Marsh (1894), but is a junior objective synonym of Ornithischia (Seeley, 1888). The name Predentata was coined to recognize a feature that is unique and common to all of Seeley's then known ornithischians: the predentary bone that caps the dentary symphysis. An ossified predentary remains ubiquitous among known ornithischians [Nabavizadeh, 2016; Nabavizadeh & Weishampel, 2016; but note Norman (2020a) regarding the condition in *Scelidosaurus*; and the anatomical evidence for an ossified predentary is currently absent in *Scutellosaurus* and *Emausaurus*]. Until recently, the presence of a discrete ossified predentary has coincided consistently with the possession of a retroverted pubis.

In this context it should be noted that two taxa may have some bearing on early ornithischian relationships. *Laquintasaura* (Barrett *et al.*, 2014; see Figs 2, 6) may represent the earliest known (Hettangian) ornithischian taxon with a retroverted pubis. The anatomical evidence concerning the structure of the pubis was neither illustrated nor described in the original publication. Nevertheless, the existence of a pubis with a retroverted shaft has been confirmed by Júlio Marsola (pers. comm., 4 May 2022). However, the mandible is not preserved, so the presence/absence of a predentary bone cannot be verified. *Chilesaurus* (Novas *et al.*, 2015) is a much more dubious, taxon. Originally described as a Late Jurassic (Tithonian) herbivorous theropod dinosaur, it has poorly preserved teeth (blunt and evidently non-carnivore adapted) and there is no evidence to support the presence of a predentary (although the extreme rostral tip of the mandible seems to be edentulous and possibly possesses osteological correlates for a keratinous beak). This taxon has an ornithischian-like retroverted pubic shaft (a feature also recorded in a variety of stem-avian theropods). It has been suggested (Baron & Barrett, 2017) that this animal represents a late surviving 'missing link' between the Ornithischia and Theropoda. However, further study reveals that *Chilesaurus* displays a number of diagnostic theropod characteristics (Federico Agnolín, pers. comm., 25 April 2022).

Owen (1874) proposed the name 'Prionodontia' as a collective name for just three then-known dinosaur taxa: *Echinodon* (Owen, 1861a), *Iguanodon* (Mantell, 1825) and *Scelidosaurus*, which possess coarsely serrated, leaf-shaped teeth. Present-day taxonomies place these taxa in Heterodontosauridae, Neornithischia and Thyreophora, respectively. Owen's Prionodontia was encompassed by Seeley's much more appropriate, and utilitarian, Ornithischia. Prionodontia preceded Ornithischia by 14 years, but the name coined by Owen had little practical systematic value and no genuine phylogenetic intent:

it was a casual, descriptive grouping that blatantly ignored other, then known, dinosaur taxa that were similarly 'prionodontian' [*Hadrosaurus* (Leidy, 1859), *Hypsilophodon* (Huxley, 1869), *Hylaeosaurus* (Mantell, 1834), *Thecodontosaurus* (Riley & Stutchbury, 1836), *Trachodon* (Leidy, 1858) and *Troodon* (Leidy, 1856)]. Owen's contribution was ignored by contemporary practitioners because it lacked discriminatory sense and utility. In marked contrast, Ornithischia survived changes in systematic methods and the shift to using tree-based phylogenetic definitions, rather than apomorphy-based ones. We note that Prionodontia was listed with a membership of just *Echinodon*, *Iguanodon* and *Scelidosaurus*, which (inadvertently) conforms to a node-based phylogenetic definition supported by anchoring taxa. Seeley's apomorphy-based term Ornithischia, although needing regular revision, has remained comparatively stable (e.g. Gauthier, 1986; Sereno, 1986, 2005; Langer & Benton, 2006; Baron *et al*., 2017a, 2017b; Madzia *et al*., 2021).

As a node-based definition given in the terms set out above, Owen's Prionodontia (given its original membership) encompasses precisely the composition of the long-established clade Ornithischia. Owen's taxonomic name remains available and Prionodontia can be re-established as the clade name for the 'traditional ornithischians' of Müller & Garcia (2020a). It may be noted that the name proposed by Owen (1874), in its literal sense, could readily have been applied to the 'total group' (the 'traditional ornithischian' clade plus its stem-lineage) because all taxa within the total-group possess, literally, 'coarsely serrated teeth'. However, the precedent set by the general adoption of phylogenetically based taxonomic definitions allows the total group (paraphyletic silesaurs plus prionodontians) to retain the name Ornithischia [defined as all taxa more closely related to *Iguanodon bernissartensis* (Boulenger, 1881) than to either *Megalosaurus bucklandii* (Mantell, 1827) or *Diplodocus carnegii* (Hatcher, 1901)].

As constituted here, the clade Prionodontia contains both the thyreophoran and neornithischian subclades. With heterodontosaurids found within Neornithischia in this analysis, Prionodontia encompasses the same set of taxa as Genasauria (Sereno, 1986). Prionodontia (Owen, 1874) takes precedence for historical reasons, but it should be noted that Genasauria would continue to be valid and distinct from Prionodontia if heterodontosaurids were recovered outside of the Neornithischia–Thyreophora dichotomy, as they often have been (e.g. Butler *et al*., 2008b; Zheng *et al*., 2009; Nesbitt, 2011; Boyd, 2015; Baron *et al*., 2017a, 2017b).

If future analyses fail to recover such a close relationship between silesaurian ornithischians and more derived non-prionodontian taxa, the distinction between the clade names Ornithischia and Prionodontia would remain because they are stem- and node-based, respectively. Ornithischia would still include all taxa that fell outside the clade Prionodontia but were anatomically closer to these taxa than to saurischians and other dinosauromorphs.

NOMENCLATURE, DEFINITIONS AND CHARACTER STATES OF THE KEY NODES (FIG. 6)

Dinosauria (Fig. 6: node 1)

Definition adopted: The least inclusive clade containing *Iguanodon bernissartensis*, *Megalosaurus bucklandii* and *Cetiosaurus oxoniensis* Phillips, 1871 (Langer *et al*., 2020).

Characters in support (here): Basipterygoid process mediolaterally compressed (Char. 62: 0 → 1); post-glenoid process of the coracoid extending caudal to glenoid (Char. 140: 0 → 1); presence of a strong pillar caudal to the pre-acetabular embayment of the ilium (Char. 180: 0 → 1); pubis length more than 70% or more of femoral length (Char. 188: 0 → 1); more dorsally extensive contact between the medial surface of the ischia (Char. 197: 0 → 1); presence of a dorsolateral sulcus on the ischium (Char. 198: 0 → 1); rounded or elliptical outline of the distal portion of the ischium (Char. 199: 0 → 1); kinked transition from the femoral shaft to the femoral head (Char. 208: 0 → 1); angled 'greater trochanter' of the femur (Char. 216: 0 → 1); presence of a transverse groove on the proximal surface of the femur (Char. 217: 0 → 1); concave caudal margin of the distal end of the tibia (Char. 240: 0 → 1); and metatarsal IV subequal or shorter than metatarsal II (Char. 217: 0 → 1).

Saurischia (Fig. 6: stem / branch 2)

Definition adopted: The most inclusive clade containing *Allosaurus fragilis* (Marsh, 1877) and *Camarasaurus supremus* Cope, 1877 but not *Stegosaurus stenops* Marsh, 1887 (after Langer *et al*., 2020).

Characters in support: Subnarial foramen present (Char. 5: 0 → 1); premaxilla with a deep narial fossa at the rostroventral corner of the naris (Char. 19: 0 → 1); maxilla with significantly deeper rostrally than caudally surface ventral to the external antorbital fenestra (Char. 29: 1 → 0); caudal chonos of cranial cervical vertebrae as a shallow fossa (Char. 109: 0 → 1); epipophyses present in cervical vertebrae 6-9 (Char. 111: 0 → 1); neural arch of cervical vertebrae lower than caudal articular facet of the centrum (Char. 113: 0 → 1); articular surface of the rib of the first primordial sacral vertebra is C-shaped in lateral view (Char. 130: 0 → 1); transverse processes of sacral vertebrae roof the space between the ribs (Char. 131: 0 → 1); humerus + radius/femur + tibia length ratio less than 0.55 (Char. 141: 0 → 1); apex of deltopectoral crest between 30% and 43% down the length of the humerus (Char. 142: 0 → 1); expanded deltopectoral crest of the humerus (Char. 143: 0 → 1); humerus shorter than 0.6 of the length of the femur (Char. 145: 0 → 1); humerus sigmoid in lateral view (Char. 147: 0 → 1); average length of digits I–III of the manus more than 0.4 of the total length of humerus plus radius (Char. 153: 0 → 1); trenchant unguals on digits I–III of the manus (Char. 155: 0 → 1); deep extensor pits on distal/dorsal portion of metacarpals II-III (Char. 156: 0 → 1); width of the shaft of metacarpal IV significantly narrower than that of metacarpals I-III (Char. 167: 0 → 1); ventral margin of the acetabular wall of the ilium straight to concave (Char. 175: 0 → 1/2); distal end of the pubis slightly expanded (Char. 190: 0 → 1); kinked transition from the femoral shaft to the femoral head and expanded head (Char. 190: 1 → 2); deep groove between the lateral condyle and crista tibiofibularis on the distal end of the femur (Char. 231: 0 → 1); cnemial crest of the tibia arcs craniolaterally (Char. 234: 1 → 2); tibial articulation caudal to the ascending process of the astragalus with a markedly rimmed and elliptical fossa (Char. 249: 0 → 1); proximal articular facet for fibula of astragalus less than 0.3 of the transverse width of the bone (Char. 250: 0 → 1); cranial ascending process separated from the cranial surface of the astragalar body by a platform (Char. 256: 1 → 2); calcaneum with a concave articular surface for the fibula (Char. 261: 0 → 1); pointed caudal prong of the distal tarsal 4 (Char. 265: 0 → 1); distal tarsal 4 with a medial process (Char. 266: 0 → 1); and metatarsal IV with an expanded proximal portion (Char. 272: 0 → 1).

Ornithischia (Fig. 6: stem / branch 3)

Definition adopted: The most inclusive clade that includes *Iguanodon bernissartensis* but neither *Megalosaurus bucklandii* nor *Diplodocus carnegii* (after Baron *et al.*, 2017a).

Characters in support: Horizontal or only gently arched premaxillary palate (Char. 17: 0 → 1); strongly curved and hook-shaped jugal process of the ectopterygoid (Char. 57: 0 → 1; Fig. 5E); ventrally inclined dorsal surface of the rostrum of the dentary (Char. 74: 0 → 1); retroarticular is slightly upturned at its distal end (Char. 82: 0 → 1; Fig. 7F); premaxilla with four teeth (Char. 84: 0 → 1); teeth ankylosed into the alveoli (Char. 100: 0 → 1; Fig. 7G); and medial articular facet of the proximal portion of the femur is straight in caudomedial view (Char. 213: 0 → 1; Fig. 7J).

Sulcimentisauria (Fig. 6: stem / branch 4)

Definition adopted: The most inclusive clade that includes *Silesaurus opolensis* Dzik, 2003 but not *Asilisaurus kongwe* Martz & Small, 2019.

Characters in support: Serrations of middle maxillary/ dentary teeth are larger forming oblique angles with the margin of the tooth (Char. 89: 0 → 2; Fig. 7I); dentary teeth decrease in size significantly rostrally (Char. 97: 0 → 1; Fig. 7D); facies articularis antitrochanterica of the femur at the level of the greater trochanter (Char. 216: 1 → 0); fourth trochanter of the femur is mound-like with a subtle crest (Char. 220: 1 → 0); and a Meckelian groove restricted to the ventral border of the dentary (Char. 282: 0 → 1; Fig. 7H).

Parapredentata clade novum (see below) (Fig. 6: node 5)

Proposed definition: The least inclusive clade that includes *Silesaurus opolensis* and *Iguanodon bernissartensis* (see below).

Characters in support: Lateral dentary surface with a ridge posteriorly that borders an emargination that occupies half of the dentary width (Char. 77: 0 → 1; Fig. 7D).

Prionodontia (Fig. 6: node 7)

Definition adopted: The least inclusive clade that includes *Iguanodon bernissartensis* Boulenger in van Beneden, 1881, *Echinodon becklesii* Owen, 1861a and *Scelidosaurus harrisonii* (after Owen, 1874).

Characters in support: Buccal emargination separated from the ventral margin of the antorbital fossa in the maxilla (Char. 24: 0 → 1; Fig. 7N); neural spine shape of cervical vertebrae not twice as long (at the mid-height) as height (Char. 108: 1 → 0; Fig. 7O); ilium and pubis articular surfaces of the ischium separated by a non-articulating concave surface (Char. 201: 1 → 2; Fig. 7Q); and fibular condyle of the tibia offset cranially from the medial condyle (Char. 235: 1 → 0; Fig. 7P). In addition to the analysis output, members of this clade are characterized by the presence of a palpebral bone, a predentary bone, a strap-like pre-acetabular process, a pendent femoral fourth trochanter and epaxial ossified tendons.

Thyreophora (Fig. 6: stem / branch 8)

Definition adopted: The most inclusive clade that contains *Ankylosaurus magniventris* Brown, 1908 but not *Iguanodon bernissartensis* (after Sereno, 1998).

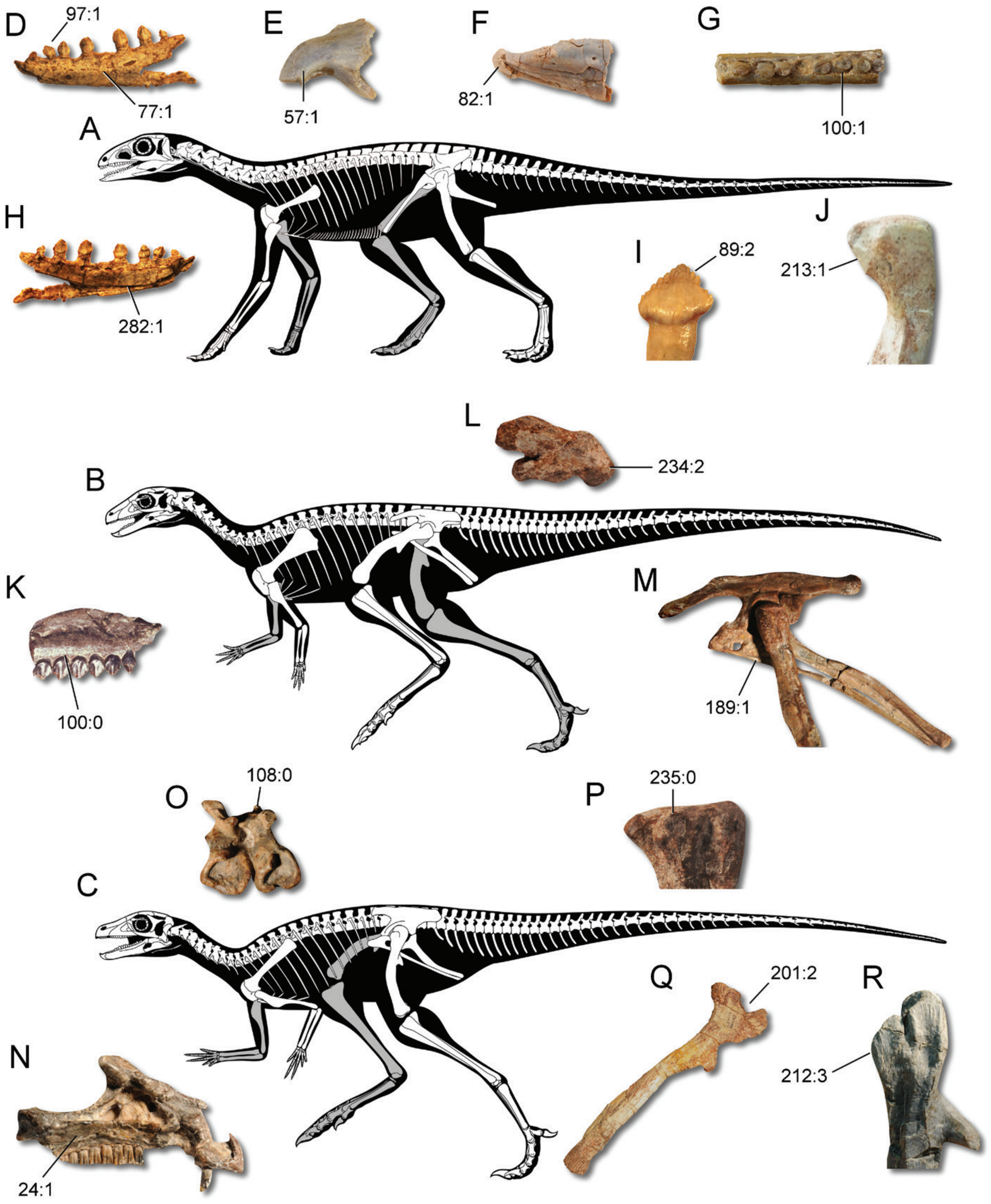

Figure 7. Body plan evolution within Ornithischia and character states with phylogenetic importance for the present hypothesis. A, skeletal reconstruction of *Silesaurus opolensis*, a parapredentatan (stem lineage) ornithischian (after Dzik, 2003). B, skeletal reconstruction of *Laquintasaura venezuelae*, a parapredentatan ornithischian (after Barrett *et al.*, 2014). C, skeletal reconstruction of *Eocursor parvus*, a prionodontian ornithischian (after Butler *et al.*, 2010). D, left dentary of *Kwanasaurus williamparkeri* (DMNH EPV.63136) in lateral view (modified from Martz & Small, 2019). E, left ectopterygoid of *Asilisaurus kongwe* (NMT RB159) in posterior (modified from Nesbitt *et al.*, 2019). F, posterior portion of the right hemimandible of *Asilisaurus kongwe* (NMT RB159) in lateral (modified from Nesbitt *et al.*, 2019). G, partial left dentary of *Asilisaurus kongwe* (NMT RB159) in occlusal view (modified from Nesbitt *et al.*, 2019). H, left dentary of *Kwanasaurus*

Characters in support: Height versus length of dentary less than 0.2 (Char. 73: 1 → 0); concave caudal margin of the distal end of tibia (Char. 240: 0 → 1); and presence of osteoderms on the vertebral column (Char. 277: 0 → 1).

Neornithischia (Fig. 6: stem / branch 9)

Definition adopted: The most inclusive clade that contains *Iguanodon bernissartensis* but neither *Ankylosaurus magniventris* nor *Stegosaurus stenops* (after Cooper, 1985).

Characters in support: Retroarticular process of articular longer than the height of the mandible ventral to the glenoid (Char. 81: 0 → 1); thicker portion of the supra-acetabular crest of the ilium closer to the pubic peduncle (Char. 172: 0 → 1); supra-acetabular crest of the ilium extends along the length of pubic peduncle (Char. 173: 0 → 1); brevis fossa of the ilium is directed ventrally (Char. 177: 1 → 0); anterior trochanter (or lesser trochanter) of the femur approaches the proximal articulation of the bone (Char. 212: 2 → 3; Fig. 7R); and facies articularis antitrochanterica of the femur is not 'ventrally inclined' (Char. 216: 1 → 0).

Heterodontosauridae (Fig. 6: stem / branch 10)

Definition adopted: The most inclusive clade containing *Heterodontosaurus tucki* Crompton & Charig, 1962 but not *Iguanodon bernissartensis*, *Pachycephalosaurus wyomingensis* Gilmore, 1931, *Triceratops horridus* Marsh, 1889, *Ankylosaurus magniventris* or *Stegosaurus stenops* (after Sereno, 1998, 2005).

Characters in support: Substantial diastema of at least one crown's length between maxillary and premaxillary teeth (Char. 21: 0 → 1); acute angle between ascending process and caudal process of jugal (Char. 50: 0 → 1); three premaxillary teeth (Char. 84: 2 → 0); maxillary/dentary teeth lack medial or lateral overlap of adjacent crowns (Char. 91: 1 → 0); distal margin of middle maxillary/dentary teeth never or subtly expanded at the base (Char. 94: 1 → 0); sacral ribs almost entirely restricted to a single sacral vertebra (Char. 129: 1 → 0); olecranon process of ulna enlarged and strongly striated (Char. 149: 0 → 1); fossa for the attachment of m. caudofemoralis brevis on the ventral surface of postacetabular part of ilium (Char. 174: 1 → 2); entirely convex dorsal margin of the ilium (Char. 180: 0 → 1); and astragalus-calcaneum co-ossified (Char. 258: 0 → 1).

SYSTEMATIC PALAEONTOLOGY: THE NEW CLADES

DINOSAURIA OWEN, 1842

ORNITHISCHIA SEELEY, 1888

PARAPREDENTATA (NOVUM)

Definition: Node-based. The least inclusive clade that includes *Iguanodon bernissartensis* and *Silesaurus opolensis*.

Etymology: Meaning 'like the predentary bearers', because members of this clade possess an edentulous (beak-like) tip of the dentary. Within Parapredentata, this beak takes two distinct forms: a tapering of the anterior end of the dentary in some silesaurs, such as *Kwanasaurus* (Fig. 7D, H), *Silesaurus* (Dzik, 2003 and *Sacisaurus* (Ferigolo & Langer, 2006); and as a separate ossification, such as in *Iguanodon* (Mantell), *Triceratops* (Marsh), *Stegosaurus* (Marsh) and many others (e.g. Romer, 1956; Nabavizadeh & Weishampel, 2016). This name also references Predentata, the unused and largely forgotten historic name for ornithischians erected by Marsh (1894). The silesaurs within this new clade resemble node-based ornithischians in the possession of an edentulous beak-like rostrum.

Range: Middle Triassic, Anisian (~242 Mya)/Carnian (~230 Mya) – Late Cretaceous, Maastrichtian (66 Mya).

Oldest known occurrence: Lutungutali sitwensis.

Remarks: Dzik (2003) described and illustrated an edentulous beak-like tip on the mandible of *Silesaurus*. When *Sacisaurus* was described by Ferigolo & Langer (2006), the beak-like tip of the dentary in the holotype of this smaller silesaur was remarked upon as possible evidence of a close link between silesaurians and the

williamparkeri (DMNH EPV.63136) in medial view (modified from Martz & Small, 2019). I, isolated tooth of *Kwanasaurus williamparkeri* (DMNH EPV.63843) in labial view (modified from Martz & Small, 2019). J, proximal portion of the right femur of *Sacisaurus agudoensis* (MCN PV100014) in caudomedial view. K, right maxilla of *Echinodon becklesii* (NHMUK OR48211) in lateral view (modified from Sereno, 2012). L, right tibia of *Eocursor parvus* (SAM-PK-K8025) in proximal view. M, left pelvic elements of *Heterodontosaurus tucki* (SAM-PK-K1332) in lateral view. N, skull of *Heterodontosaurus tucki* (SAM-PK-K1332) in right lateral view. O, cervical 6 and 7 of *Heterodontosaurus tucki* (SAM-PK-K1332) in left lateral view. P, proximal portion of the right tibia of *Eocursor parvus* (SAM-PK-K8025) in lateral view. Q, left ischium of *Lesothosaurus diagnosticus* (SAM-PK-K1105) in medial view (modified from Baron *et al.*, 2017a). R, proximal portion of the left femur of *Lesothosaurus diagnosticus* (BP/1/6582) in lateral view. Elements are not to scale.

ornithischians. Others dismissed this idea (e.g. Nesbitt, 2011), and some evidence was published to show the differences between the way that this beak formed in silesaurians and ornithischians (Holliday & Nesbitt, 2013). However, this doesn't preclude the possibility that a separate ossification started its 'evolutionary life' as part of the dentary that later became a separate bone in more derived taxa. Our new topology suggests that this could be the pattern of development of the anterior dentary of ornithischians, mirroring the appearance of the rostral bone in ceratopsians (You & Dodson, 2004). All taxa that possess a sharpened and edentulous anterior dentary within Prionodontia fall closer to Ornithischia than they do to all other silesaurs. This topology is supported by other anatomical characters and is recovered entirely in the absence of an assumption that these features are homologous (only Prionodontia are scored as having a true predentary in these analyses). Should future evidence be found that supports the possible homology of this feature, the strength of the topology recovered here would only increase.

DINOSAURIA OWEN, 1842
ORNITHISCHIA SEELEY, 1888
PARAPREDENTATA (NOVUM)
PRIONODONTIA OWEN, 1874

Definition: Node-based. The least inclusive clade that includes *Iguanodon bernissartensis*, *Echinodon becklesii* and *Scelidosaurus harrisonii*.

Range: Early Jurassic, Hettangian (~200 Mya) – Late Cretaceous, Maastrichtian (66 Mya).

Oldest known occurrence: *Eocursor parvus* Butler *et al.* (2007).

Remarks: Clade name stability and synonymy. The clade named Prionodontia in this article was referred to as 'traditional ornithischians' by Müller & Garcia (2020a). The lack of consensus regarding the topological position of heterodontosaurids (e.g. Butler *et al.*, 2008a; Dieudonné *et al.*, 2020; Yang *et al.*, 2020; Madzia *et al.*, 2021; and here) has important and disturbing taxonomic repercussions. For example, in this analysis, Prionodontia contains the principal subclades Thyreophora + Neornithischia (including heterodontosaurids); this is precisely equivalent, in terms of taxonomic content, to the recently proposed taxon Saphornithischia of Madzia *et al.* (2021: 64); the latter was defined as 'The smallest clade containing *Heterodontosaurus tucki* Crompton & Charig, 1962, *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Stegosaurus stenops* Marsh, 1887 and *Triceratops horridus* Marsh, 1889'. On this basis, the taxon name Prionodontia takes precedence over Saphornithischia by more than a century.

The revised consensus tree (Fig. 6), given that it incorporates heterodontosaurids within Neornithischia, similarly implies that the taxon Prionodontia is equivalent, in composition, to Genasauria as currently defined. Genasauria was first defined as '*Ankylosaurus*, *Triceratops*, their most recent common ancestor and all descendants' (Sereno, 1986). Madzia *et al.* (2021: 35) revised the definition of Genasauria as follows: 'The smallest clade containing *Ankylosaurus magniventris* Brown, 1908, *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Stegosaurus stenops* Marsh, 1887 and *Triceratops horridus* Marsh, 1889'. From a definitional perspective Prionodontia takes precedence by over a century.

Implementing the PhyloCode (de Queiroz & Cantino, 2020) establishes phylogenetic definitions for taxonomic names and promises logical consistency and long-term nomenclatural stability. As demonstrated here, nomenclatural consistency is dependent upon topological stability of fossil-based phylogenetic trees, which are inherently unstable given the incompleteness of the fossil record. The status of Prionodontia and the recently proposed Saphornithischia (Madzia *et al.*, 2021), as well as that of the long-established taxon Genasauria, are each matters of particular concern.

PALAEOBIOLOGICAL AND EVOLUTIONARY IMPLICATIONS

This revision of the topology within Dinosauromorpha, and reconstruction of Ornithischia in the light of its putative associated stem-lineage, generates several thought-provoking evolutionary interpretations. The changes in dental and mandibular anatomy (linked to feeding strategies) that can be seen to occur across the ornithischian clade challenge previous evolutionary models. Furthermore, changes in stance and gait, which are linked to forelimb, pelvic and hindlimb anatomy, appear to be cumulative if silesaurs represent a grade of early diverging stem-lineage ornithischians, rather than stem-lineage dinosaurs (non-dinosaurian dinosauriforms), as more commonly envisaged (Ezcurra, 2006; Irmis *et al.*, 2007b; Nesbitt *et al.*, 2010; Bittencourt *et al.*, 2014; Ezcurra *et al.*, 2020).

Dentition (Fig. 8)

Much attention has been paid to details of the dentition in Ornithischia and the role that these features played in developing an understanding of diet, feeding strategies and interpretations linked to the general notion of 'evolutionary success' (Mantell, 1825, 1848; Owen, 1861; Thulborn, 1970,

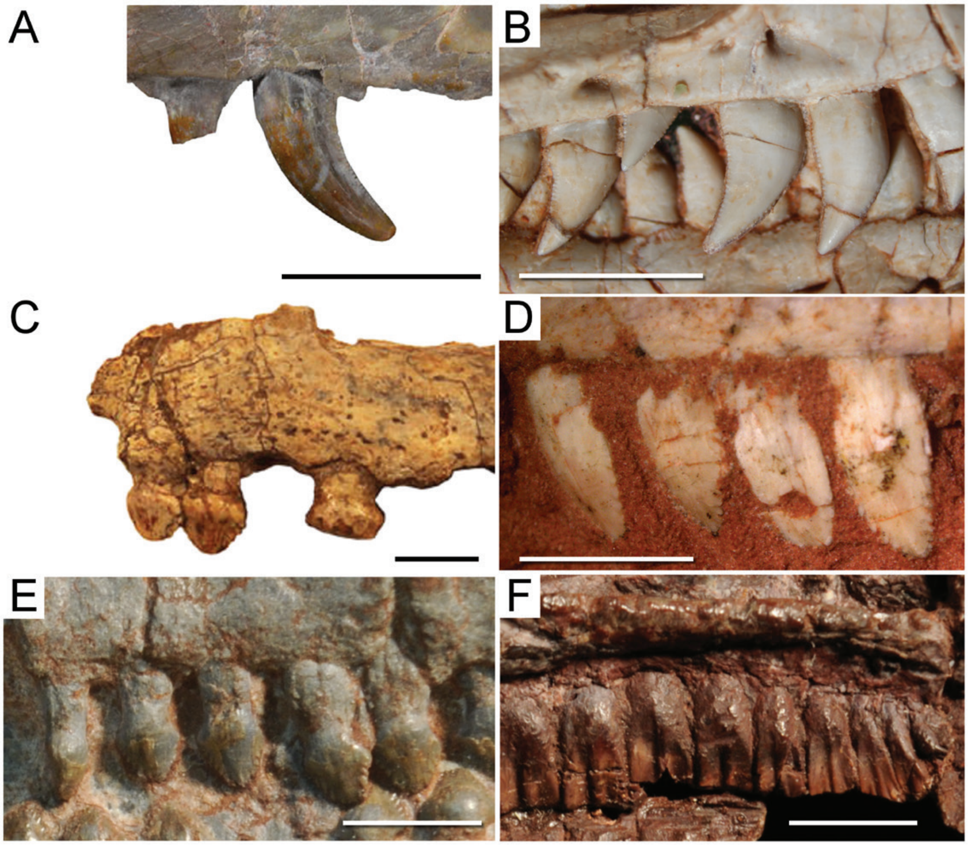

Figure 8. Maxillary teeth of selected dinosaurs described in this analysis, in labial view: A, left maxillary teeth of ornithischian *Lewisuchus admixtus* (CRILAR-Pv 552; modified from Ezcurra *et al.*, 2020). B, right maxillary teeth of the sauropodomorph *Buriolestes schultzi* (ULBRA-PVT280). C, left maxillary teeth of the parapredentatan *Kwanasaurus williamparkeri* (DMNH EPV.6587; modified from Martz & Small, 2019). D, left maxillary teeth of the sauropodomorph *Macrocollum itaquii* (CAPPA/UFSM 0001b). E, left maxillary teeth of the neornithischian *Lesothosaurus diagnosticus* (BP/1/6582). F, right maxillary teeth of the heterodontosaurid *Heterodontosaurus tucki* (SAM-PK-K 337). Scale bars = 5 mm.

1971; Norman, 1980, 1983, 1984, 2004, 2020a, 2021; Weishampel, 1984; Norman & Weishampel, 1985; Gow, 1990; Norman *et al.*, 2004b, 2011; Butler *et al.*, 2008b, 2012; Porro *et al.*, 2010, 2015; Pol *et al.*, 2011; Sereno, 2012; Becerra & Pol, 2020). Among the principal clades within Dinosauria, the ornithischians have commonly been thought to possess the most distinctive dental anatomy; and, within Ornithischia, it has equally been recognized that there is a high degree of variability among the major subclades (Norman *et al.*, 2004). Some clades are easily diagnosable based on their dentition alone, for example, heterodontosaurids, hadrosaurids and ceratopsids. Furthermore, large numbers of anatomical characters used in phylogenetic analyses of ornithischians describe features of their dental anatomy (e.g. Butler *et al.*, 2008b; Boyd, 2015; Dieudonné *et al.*, 2020). Much has also been said before about the distinction between ornithischian (prionodontian) dental anatomy and that seen in other dinosaurian clades (e.g. Sereno, 1991; Hunt & Lucas, 1994; Norman *et al.*, 2004); these distinctive features have been presumed to have been acquired during the earliest stages of prionodontian ornithischian evolution, as the group transitioned from an assumed carnivorous dinosaurian ancestor (Norman *et al.*, 2011; Müller & Garcia, 2020a). The latter possessed sharp, laterally compressed, recurved teeth with finely serrated margins, as seen in other dinosaurs, as well as non-dinosaurian dinosauromorphs such as *Lagosuchus talampayensis* (Sereno & Arcucci, 1994; Agnolín & Ezcurra, 2019).

Previous hypotheses have suggested that ornithischians must have slowly abandoned recurved teeth with finely serrated margins in favour of the more diamond-shaped crowns with coarsely denticulate margins seen in the earliest known prionodontian taxa (Owen, 1861, 1874; Thulborn, 1971; Nesbitt, 2011; Norman *et al.*, 2011; Baron & Barrett, 2017). In traditional hypotheses, this morphological transition was not well understood, because the earliest occurring (Hettangian), well-preserved prionodontian ornithischians (e.g. *Eocursor* and *Lesothosaurus*) already possessed the distinctive dental morphology. In some discussions, the heterodonty that characterizes contemporaneous heterodontosaurid ornithischians, which combines 'caniniform' teeth (suggestive of carnivory – see Fig. 7N) with chisel-shaped palisades of 'cheek' teeth (indicative of herbivory – Fig. 8F) was held up as evidence of this dietary transition (Crompton & Charig, 1962; Thulborn, 1971; Norman *et al.*, 2004, 2011). This idea gained added traction when the results of some phylogenetic analyses placed heterodontosaurids as the earliest diverging ornithischians (Butler *et al.*, 2008b; Boyd, 2015; Baron *et al.*, 2017a).

The initial discovery (Dzik, 2003) and subsequent increase in our understanding of the anatomy and diversity of Triassic silesaurs – many of which possess similarly diamond-shaped and denticulate tooth crowns mounted upon a waisted root, structurally akin to those seen in prionodontian ornithischians (see Figs 7D, H, I, 8C) – and this clade's initial placement as the sister-group to Dinosauria, did nothing to change the perception of how ornithischians acquired their unusual dental anatomy (Nesbitt, 2011; Baron *et al.*, 2017a). The prionodontian-like dental morphology seen in silesaurs was also described in other Triassic pseudosuchians and archosauromorphs (Parker, 2005; Sengupta *et al.*, 2017; Parker *et al.*, 2021). This led to a review of the assignments of Late Triassic taxa that had been determined solely upon the morphology of isolated teeth (e.g. Hunt & Lucas, 1994) and the suggestion of their being unreliably assigned, as reported by Parker (2005), Irmis *et al.* (2007b) and Nesbitt *et al.* (2007). Following the insightful observations made by Dzik (2003), Ferigolo & Langer (2006) expanded on Dzik's first suggestion (Dzik, 2003: 573) '… that *Silesaurus* is an early member of the ornithischian lineage' by suggesting that this interpretation applied to all known silesaurs (based on a combination of dental and mandibular characters), which were restricted to *Silesaurus* and *Sacisaurus* at that time; they later (Langer & Ferigolo, 2013) found support, albeit weak, in phylogenetic analyses that scored the characters that they had identified as putative silesaur–ornithischian homologies. This preliminary work was succeeded by analyses that placed silesaurs as a clade (Silesauridae) of dinosaurs and, more particularly, as the sister-taxon to Ornithischia (Cabreira *et al.*, 2016; Pacheco *et al.*, 2019). The analysis presented here (Figs 2, 6) places the silesaurs on the stem-lineage of Ornithischia, not as a sister-clade but as a paraphyletic assemblage of taxa that approach what are here termed the Prionodontia, in stepwise fashion (Müller & Garcia, 2020a). This topology suggests that the evolution of the dental anatomy of silesaurs might be traceable through successive taxa as they approach definitive ornithischian status. The earliest diverging members of the ornithischian stem-lineage (*Soumyasaurus* and *Lewisuchus* – see Figs 6, 8A) possess sharp, recurved, finely serrated teeth that are typical of the other non-dinosaurian dinosauromorph and dinosaur clades [Herrerasauridae, most members of Theropoda, early members of Sauropodomorpha (Fig. 8B) – Martínez *et al.*, 2011; Cabreira *et al.*, 2016; Pacheco *et al.*, 2019; Müller & Garcia, 2020b]. Equally some early sauropodomorphs (*Macrocollum* – Fig. 8D) display tall and spatulate, coarsely serrated maxillary teeth. Silesaurs positioned more proximate to Prionodontia [*Diodorus* (Kammerer *et al.*, 2012), *Silesaurus* and *Technosaurus* (Chatterjee, 1984); Fig. 6], possess more diamond-shaped tooth crowns. Finally, the silesaurs most proximate to Prionodontia, such as *Kwanasaurus* (Martz & Small, 2019: fig. 12; see Fig. 8C), possess teeth that closely resemble those of the earliest diverging members of each clade in Prionodontia, for example, *Lesothosaurus* (Sereno, 1991; see Fig. 8E) and *Scelidosaurus* (Norman, 2020a).

In summary, teeth of *Kwanasaurus* and those of taxa such as *Lesothosaurus* are practically indistinguishable: diamond/leaf-shaped and not strongly recurved, labiolingually and mesiodistally expanded above the root, and possessing comparatively large marginal denticles (compare Fig. 8C, E). Falling in the middle of the succession of taxa leading to Ornithischia, *Soumyasaurus*, *Asilisaurus* and *Diodorus* would, accordingly, represent intermediate stages in the transition from the *Lewisuchus*-like dental morphology to that displayed by *Technosaurus*, *Kwanasaurus* and Ornithischia (see Figs 6, 7).

With the heterodontosaurids recovered as more deeply nested with Prionodontia (Fig. 6), the earlier idea that the heterodontosaurid dentition represents a transitional stage between the ancestral (faunivorous) dinosaurian condition and that seen in more derived ornithischians (e.g. Norman *et al.*, 2011) is no longer supported. The new phylogenetic hypothesis implies that the characteristic dentition seen in heterodontosaurids represents a condition that is derived by comparison with the homodonty seen in early prionodontians. This interpretation also accords with the recovery of the Late Jurassic *Chilesaurus* in Heterodontosauridae (Figs 2, 6) because the dental anatomy of *Chilesaurus* (although poorly preserved) seems more generally similar in morphology to that seen in some heterodontosaurids than it is to the earliest diverging members of Prionodontia, such as *Lesothosaurus* and *Scelidosaurus* (Novas *et al.*, 2015; Baron & Barrett, 2017; Norman, 2020a).

A notable difference between the dentitions of the earliest diverging stem-lineage ornithischians (silesaurians) and the dentition in some members of the clades Parapredentata and Prionodontia, is the ankylothecodont tooth implantation seen in the former: their teeth are fused to the dentary and maxilla (Ferigolo & Langer, 2006; Nesbitt *et al.*, 2010; Nesbitt, 2011; Kammerer *et al.*, 2012; Baron *et al.*, 2017a, 2017b; Agnolín & Rozadilla, 2018; Baron, 2019; Desojo *et al.*, 2020; Mestriner *et al.*, 2021). This dental feature is not seen in any known members of Prionodontia, implying that this feature was either lost in more derived ornithischians or was only acquired sporadically among an early diverging subclade of silesaurians. *Pisanosaurus*, which, in this analysis, falls outside of Prionodontia, is too poorly preserved to offer evidence of its mode of tooth implantation; the appearance of the preserved dentition (obscured beneath a layer of tough haematite) has provided the scope for some authors to suggest that the teeth of *Pisanosaurus* are ankylothecodont (Baron *et al.*, 2017b; Agnolín & Rozadilla, 2018; Baron, 2019), while others disagree (Nesbitt, 2011; Desojo *et al.*, 2020). In this analysis, we have scored *Pisanosaurus* as missing data (?) for this anatomical character. It is currently not possible to pinpoint where precisely (or indeed *whether*), in this new hypothesis of ornithischian evolution, the ankylothecodont condition might have been acquired and/or lost.

Predentary (Fig. 7)

Prionodontians are characterized by the possession of a predentary bone (Fig. 7C), which is absent in stem-lineage ornithischians and all dinosauromorphs, and distinguishes prionodontians from all other dinosaurian taxa (Nabavizadeh, 2016; Nabavizadeh & Weishampel, 2016) and originally justified the creation of the taxon Predentata (Marsh, 1894). The predentary is a discrete, edentulous ossification that caps the symphyseal region of the dentaries; its sharp-edged margins would have supported a keratinous beak (rhamphotheca) for cropping vegetation (Dollo, 1882; Nabavizadeh & Weishampel, 2016). However, it should be noted that a predentary is not uniformly or consistently preserved among early prionodontians: the well-preserved, articulated remains of the basal thyreophoran *Scelidosaurus* (Norman, 2020a) have so far failed to recover an ossified predentary, although there are osteological correlates suggestive of its presence as an unossified element.

The identification and distribution of this anatomical feature among dinosauriforms (and stem-ornithischians) has been a source of interpretative confusion because silesaur taxa (e.g. *Silesaurus* and *Sacisaurus*) possess what has been referred to as a ‘predentary-like’ edentulous anterior portion of the dentary (Dzik, 2003; Ferigolo & Langer, 2006; Holliday & Nesbitt, 2013; Langer & Ferigolo, 2013). Silesaurs that have a well-preserved dentary now include *Asilisaurus*, *Silesaurus*, *Kwanasaurus* and *Sacisaurus*, and all show an anterior dentary ramus that is edentulous and tapers to a sharp point (see Fig. 7D, H). This feature is not unique among archosaurs: similar edentulous anterior dentary rami are also recorded in aëtosaurs, lagerpetids and pterosaurs (Nesbitt, 2011; Ezcurra *et al.*, 2020), as well as avian and some non-avian theropods (e.g. Lautenschlager *et al.*, 2014). According to the topology generated by this analysis, it can plausibly be inferred that the edentulous anterior portion of the dentary in silesaurs represents a precursor stage prior to the development of the discrete predentary bone in prionodontians, as suggested by Ferigolo & Langer (2006). A similar case of an additional ossification forming a novel edentulous bone on the anterior margin of the skull in prionodontians occurs in ceratopsians with the rostral bone, an unpaired element anterior to the paired premaxillae (You & Dodson, 2004).

A discrete predentary bone was originally reported to be present in silesaurs such as *Silesaurus* and *Sacisaurus* following the identification of suture-like features between the edentulous tip of the dentary and the remainder of the dentary ramus (Ferigolo & Langer, 2006), but this interpretation has proved to be erroneous (Dzik, 2003; Langer & Ferigolo, 2013). Traditional hypotheses positing silesaurs in a sister-taxon relationship with Dinosauria generate an ornithischian ghost-lineage across the Late Triassic; within that interpretative framework the origin of the predentary remains enigmatic because there are no Middle-to-Late Triassic dinosauriforms (except for silesaurs) that possess any osteological feature resembling an anatomical precursor of the predentary.

Pectoral girdle (Fig. 9)

The new tree topology (Fig. 6) brings into focus several other observable similarities and differences in the construction of the pectoral girdle between the silesaurs and prionodontians. The scapulae of early prionodontians, such as *Scutellosaurus*, *Scelidosaurus* and *Lesothosaurus* (Fig. 9F), and their nearest known relative, *Laquintasaura*, are comparatively robust and expanded at their distal ends (Santa Luca *et al.*, 1976; Barrett *et al.*, 2014; Breeden, 2016; Baron *et al.*, 2017c, Norman, 2020b). The distal expansion creates concave dorsal and ventral edges to the scapular blade. This condition contrasts with other early dinosaurs: the theropod *Tawa* (Nesbitt *et al.*, 2010; see Fig. 9C), and sauropodomorphs such as *Pampadromaeus barberenai* Cabreira *et al.*, 2011 and *Buriolestes schultzi* Cabreira *et al.*, 2016, which show only modest distal expansions. In herrerasaurids (Fig. 9B), an early diverging clade within Saurischia, the form of the scapula is narrow and strap-like, with no real distal expansion at all

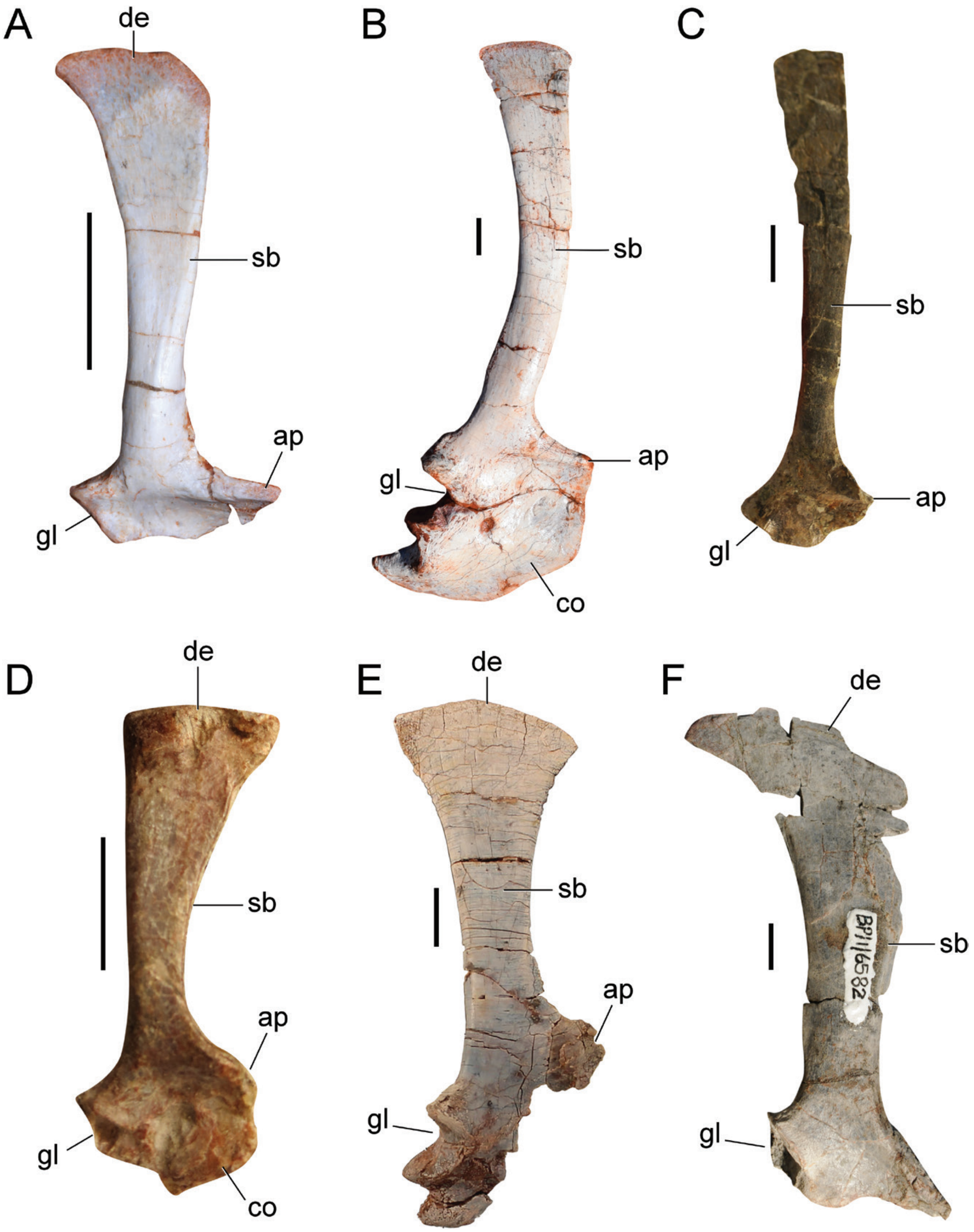

Figure 9. Pectoral girdle of selected ornithodirans in lateral view: A, right scapula of the lagerpetid *Ixalerpeton polesinensis* (ULBRA-PVT059). B, right scapula and coracoid of the herrerasaurid *Gnathovorax cabreirai* (CAPPA/UFSM 0009). C, right scapula of the early diverging saurischian *Tawa hallae* (GR 242). D, left (reversed) scapula and coracoid of the ornithischian *Lewisuchus admixtus* (PULR 01). E, left (reversed) scapula and coracoid of the ornithischian *Asilisaurus kongwe* (NMT RB159; modified from Nesbitt *et al.*, 2019). F, right scapula of the neornithischian *Lesothosaurus diagnosticus* (BP/1/6582). Abbreviations: ap, acromion process; co, coracoid; de, distal expansion; gl, glenoid; sb, scapular blade. Scale bars = 10 mm.

(Alcober & Martínez, 2010; Pacheco *et al.*, 2019). The scapulae in the stem-ornithischians *Lewisuchus* (Fig. 9D), *Silesaurus* and *Asilisaurus* (Fig. 9E) show a greater degree of distal expansion than that seen in the earliest saurischians and non-dinosaurian ornithodirans (Dzik, 2003; Nesbitt *et al.*, 2010, 2019; Bittencourt *et al.*, 2014; Piechowski & Tałanda, 2020). The silesaur *Asilisaurus* possesses a scapula that closely resembles that of *Lesothosaurus* (Fig. 9E, F). Our topology provides new evidence concerning the acquisition of the distinctively robust, distally expanded scapula seen in prionodontians.

Forelimb and posture (Fig. 7)

Another feature common to silesaurs (stem-ornithischians), but not generally observed in early prionodontians, is the small difference in the relative lengths of the forelimb and hindlimb (Dzik, 2003; Nesbitt *et al.*, 2010, 2019; Piechowski & Tałanda, 2020). Comparability between forelimb and hindlimb length is suggestive of quadrupedalism in known silesaurs (Dzik, 2003; Ferigolo & Langer, 2006; Nesbitt *et al.*, 2010, 2019; Ezcurra *et al.*, 2019; Grinham *et al.*, 2019; Piechowski & Tałanda, 2020). *Silesaurus*, for example, has a forelimb-to-hindlimb ratio that is close to 1 (Dzik, 2003), as does *Asilisaurus* (Nesbitt *et al.*, 2019). In comparison, the hindlimbs of many early prionodontians are considerably longer than their respective forelimbs, for example, *Lesothosaurus* (Fig. 7C) and *Heterodontosaurus* (Santa Luca, 1980). The only exceptions to this general trend are found in taxa that are recovered as the earliest members of Thyreophora (e.g. *Scelidosaurus*). *Scelidosaurus* is, and almost always has been, assumed to be quadrupedal (Owen, 1861; Norman, 2020b, 2021), and, therefore, more akin in its limb proportions to silesaurs.

Traditional hypotheses that placed *Eocursor* and *Lesothosaurus* along with heterodontosaurids as the first prionodontians (Norman *et al.*, 2004; Butler *et al.*, 2008b; Zheng *et al.*, 2009; Boyd, 2015; Baron *et al.*, 2017a, 2017b) advocated bipedal locomotion as the ancestral condition for dinosaurs more generally (Galton, 1972, 1978; Arcucci, 1987, 1989; Sereno, 1999). It has long been assumed that various clades within Prionodontia subsequently adopted quadrupedality independently multiple times, as changes in their overall size and anatomy dictated (Norman, 1980; Maidment & Barrett, 2011, 2012; Bates *et al.*, 2012; Maidment *et al.*, 2012, 2014; Barrett & Maidment, 2017). However, the phylogeny proposed here (Figs 2, 6) implies an evolutionary transition from the quadrupedal stance seen among stem-ornithischians, to the bipedal stance seen in the Early Jurassic prionodontians *Eocursor*, *Lesothosaurus* and heterodontosaurids. The new topology could be used to argue that the earliest thyreophorans based on associated skeletal material (e.g. *Scelidosaurus* – Norman, 2020b; *Yuxisaurus* Yao *et al.*, 2022) retained the ancestral quadrupedal stance seen in stem-Ornithischia, rather than having secondarily adopted a quadrupedal stance.

However, the clear exception to such a revised pattern of postural evolution is the North American taxon *Scutellosaurus*, which has often been posited as the most basal thyreophoran (Norman *et al.*, 2004; Butler *et al.*, 2008b; Maidment *et al.*, 2008; Thompson *et al.*, 2012; Baron *et al.*, 2017c; Norman, 2021). *Scutellosaurus* does not possess any convincing osteological correlates of quadrupedality (Maidment & Barrett, 2014; Maidment *et al.*, 2014); although *Scutellosaurus* was originally considered to be a facultative quadruped (Colbert, 1981). At present, the known material attributable to this taxon does not allow an accurate forelimb/hindlimb ratio to be calculated (Breeden & Rowe, 2020). Of the three thyreophorans analysed, the only taxon known from associated skeletal material (*Scelidosaurus*) indicates that adult individuals were quadrupedal, whereas juvenile individuals exhibit features (e.g. curved femur and a pendent fourth trochanter) suggestive of greater cursoriality and facultative bipedality (Norman, 2020b, 2021). All thyreophorans more derived than the taxa featured in this study are unequivocally quadrupedal. It is also true that the results of some phylogenetic analyses have placed *Lesothosaurus* as the earliest diverging member of Thyreophora (Butler *et al.*, 2008b; Maidment *et al.*, 2008; Raven & Maidment, 2017, 2018); this supports the hypothesis that the ancestral stance for Thyreophora was bipedal, and that this posture was abandoned subsequently in Stegosauria and Ankylosauria. Our new analysis failed to recover *Lesothosaurus* within Thyreophora, placing it in Neornithischia (*sensu* Baron *et al.*, 2017c; Langer *et al.*, 2017).

Contradictory observations concerning early dinosaurian posture arise from the fact that *Lesothosaurus* shows evidence that the forelimb-to-hindlimb ratio is higher in juvenile than in adult individuals (Sereno, 1991; Butler, 2010; Knoll *et al.*, 2009; Barrett *et al.*, 2016; Baron *et al.*, 2017c). This ontogeny is suggestive of a progressive shift in stance through an individual's life, with young individuals as facultative quadrupeds that become increasingly bipedal as they grew. A similar pattern of changing limb proportions with ontogeny has been recorded in the contemporaneous sauropodomorph *Massospondylus carinatus* Owen, 1854 (Neenan *et al.*, 2019). Although little more than speculative given the paucity of data, this leads to the intriguing possibility that the phylogenetic transition from quadrupedal to bipedal detected within the ornithischian stem is echoed in the ontogeny of some later ornithischian taxa, such as *Lesothosaurus* (see also: Nesbitt *et al.*, 2019).

Potential parallelisms in the evolutionary histories and growth patterns of ornithischians and sauropodomorph taxa across the Latest Triassic and Earliest Jurassic may justify further investigation.

Hindlimb and pelvis (Figs 10, 11)

The construction of the pelvis and hindlimb of prionodontian ornithischians has received much comment and analysis (Thulborn, 1971; Charig, 1972; Santa Luca, 1980; Norman *et al.*, 2004; Butler *et al.*, 2010; Galton, 2014; Baron & Barrett, 2017, 2018; Baron *et al.*, 2017a, 2017c). However, it is not just the retroversion of the pubis that makes them unique among the non-avialian dinosaurs; they also have distinctive ilia, with elongate, often strap-like, pre-acetabular processes (Santa Luca, 1980; Norman *et al.*, 2004; Langer & Benton, 2006; Butler *et al.*, 2008b; Nesbitt, 2011; Sereno, 2012; Baron *et al.*, 2017c; Norman, 2020b). Prionodontians also have unusual, often unique, characters in their femoral anatomy (e.g. Norman *et al.*, 2004; Maidment & Barrett, 2011; Maidment *et al.*, 2014; Baron *et al.*, 2017c). Examples include the presence of a pendent fourth trochanter (Fig. 10E, F: 4tr) [this structure differs from that of the (generally) asymmetric (non-pendent) fourth trochanter seen in all other dinosaurs (Langer & Benton, 2006; Nesbitt, 2011)]. The prominent, anterolaterally positioned and transversely compressed anterior trochanter is characteristic of ornithischian taxa (Fig. 10E, F: at). The anterior ('lesser') trochanter is also separated from the remainder of the proximal end of the femur by a clear gap or cleft. This latter morphology is only otherwise seen in the femora of neotheropods (Welles, 1984; Madsen & Welles, 2000; Nesbitt, 2011; Baron *et al.*, 2017a; Baron, 2019; Marsh & Parker, 2020; Marsh & Rowe, 2020), and has been proposed as a synapomorphy of Ornithoscelida in the analyses that recovered an Ornithischia–Theropoda sister-taxon relationship (Baron *et al.*, 2017a, 2017b). Most dinosaurian taxa possess a thin, spike-like, anterior trochanter that is entirely connected by a ridge to the proximal end of the femur (Fig. 10D).

Hindlimb anatomy (Fig. 10)

In contrast to prionodontian ornithischians, silesaurs lack a pendent (separated from the femoral shaft and finger-shaped) fourth trochanter (Fig. 10A–C: 4t). Moreover, some silesaurs also lack a transversely compressed anterior trochanter (at) that is separated from the rest of the femur by a distinct cleft (Dzik, 2003; Ferigolo & Langer, 2006; Griffin & Nesbitt, 2016; Marsh & Parker, 2020; Nesbitt *et al.*, 2009a). In *Asilisaurus kongwe* (Fig. 8B) the fourth trochanter forms a low crest (Nesbitt *et al.*, 2019) and the anterior trochanter is a low ridge that is connected with the shaft of the femur; the latter resembles that seen in basal saurischians (Galton, 1976; Sereno & Arcucci, 1994; Langer *et al.*, 1999; Langer & Benton, 2006; Langer *et al.*, 2010; Cabreira *et al.*, 2011, 2016; Martínez *et al.*, 2011; Nesbitt, 2011; Baron *et al.*, 2017a; Pacheco *et al.*, 2019).

The ontogenetic development of these femoral characters in silesaurs and various other ornithodirans has been considered (Griffin & Nesbitt, 2016; Müller *et al.*, 2019; Nesbitt *et al.*, 2009b). Griffin & Nesbitt (2016) observed polymorphism in the order of appearance and shape of bone scars, as well as changes in the overall morphology of the various femoral trochanters in femora of the silesaur *Asilisaurus*. They also suggested that the polymorphisms that they had observed in *Asilisaurus* may be equally applicable in unequivocal dinosaurs; their suggestion is reinforced by this analysis because it places silesaurs *within* Dinosauria. In the context of the present topology, it is interesting to note that predentatans, *Sacisaurus* (Fig. 8C, at), *Eucoelophysis* and *Kwanasaurus*, display femora with anterior trochanters that are transversely compressed and separated from the remainder of the proximal end of the femur by a distinct cleft, resembling the condition present in prionodontian ornithischians (Fig. 10E, F).

Silesaurs provide no meaningful information concerning the evolution of the fourth trochanter; indeed, some silesaur taxa barely possess a fourth trochanter (Kammerer *et al.*, 2012). In all silesaurs, the fourth trochanter forms a low mound or crest that is proximodistally symmetric when considered in medial and lateral views. By comparison, even in the femora of the earliest diverging members of Ornithischia, for example, *Eocursor* (Fig. 10E), *Lesothosaurus* (Fig. 10F) and *Scelidosaurus* (Norman, 2020b), the fourth trochanter is well developed, asymmetric, anteroposteriorly narrow and pendent (Butler *et al.*, 2007; Butler, 2010; Barrett *et al.*, 2016; Baron *et al.*, 2017c; Persons & Currie, 2019). In later diverging ornithischians, the degree to which the fourth trochanter is angled with respect to the femoral shaft and its proximodistal length becomes even greater (Butler *et al.*, 2010; Galton, 2014; Persons & Currie, 2019; Barta & Norell, 2021). This feature reaches an extreme form in heterodontosaurids, which possess a rod-like fourth trochanter that is narrow and has near parallel sides (Santa Luca, 1980; Sereno, 2012; Galton 2014). The new topology offers some insight concerning the evolution of the fourth trochanter within the ornithischian lineage. While it is worth noting that all prionodontians examined in this study have narrow, pendent fourth trochanters that project distally from the proximal posteromedial femoral shaft, this condition is not observed across all known

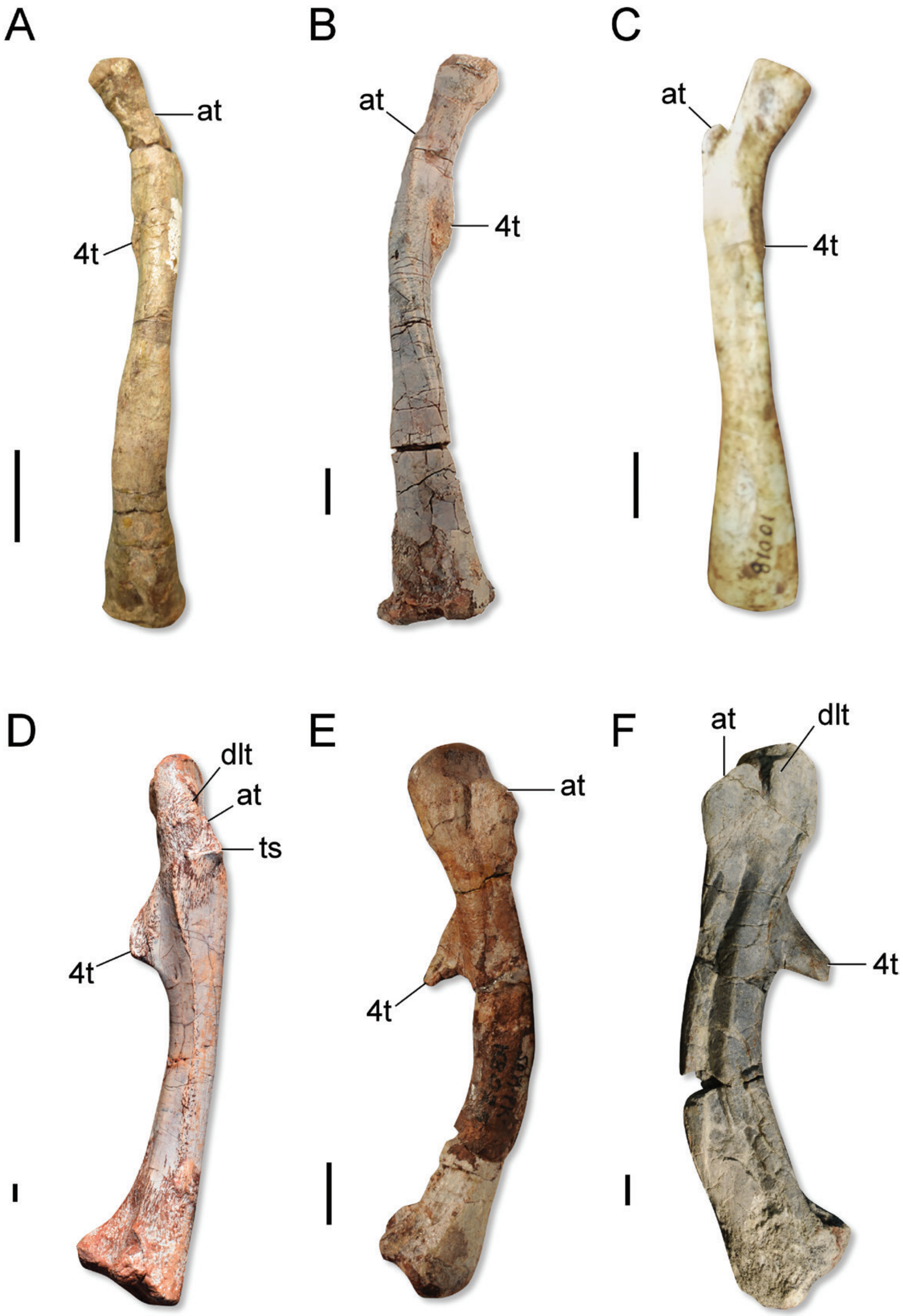

Figure 10. Femora of selected dinosaurs: A, left femur of the ornithischian *Lewisuchus admixtus* (PULR-PV 53) in anteromedial view. B, right femur of the ornithischian *Asilisaurus kongwe* (NMT RB159; modified from Nesbitt *et al.*, 2019) in anteromedial view. C, right femur of the parapredentatan *Sacisaurus agudoensis* (MCN PV10018) in anteromedial view. D, right femur of the herrerasaurid *Gnathovorax cabreirai* (CAPPA/UFSM 0009) in lateral view. E, right femur of the neornithischian *Eocursor parvus* (SAM-PK K 8025) in lateral view. F, left femur of the neornithischian *Lesothosaurus diagnosticus* (BP/1/6582) in lateral view. Abbreviations: 4t, fourth trochanter; at, anterior trochanter; dlt, dorsolateral trochanter; ts, trochanteric shelf. Scale bars = 10 mm.

members of a more inclusive clade. *Laquintasaura* (Fig. 7B) possesses a fourth trochanter that is more transversely expanded than in any early diverging prionodontian. Moreover, the distal portion of its trochanter is not clearly pendent (Barrett *et al.*, 2014: fig. 1). Given the position that *Laquintasaura* occupies in our tree (Figs 2, 6), this fourth trochanter morphology can plausibly be interpreted as transitional between the low mounded/crested form observed in silesaurs (stem-ornithischians) and the pendent morphology seen in early prionodontians.

This evolutionary hypothesis regarding the development of the form of the fourth trochanter in ornithischians has potentially wider implications for the evolution of the fourth trochanter in ornithodirans in general. Historically, the possession of an asymmetric fourth trochanter has been cited as a synapomorphy of the Dinosauria (Bakker & Galton, 1974; Sereno, 1999; Langer & Benton, 2006; Nesbitt, 2011; Baron *et al.*, 2017a). As noted above, the fourth trochanter in non-dinosaurians usually takes the form of a low mound or modest crest or is simply absent in, for example, specimens of *Dromomeron* Irmis *et al*., 2007 (Nesbitt *et al.*, 2009) and *Ixalerpeton polesinensis* Cabreira *et al.*, 2016, as well as early diverging members of the Avemetatarsalia such as *Teleocrater rhadinus* Nesbitt *et al*., 2017. In most early saurischians (Fig. 8D), the fourth trochanter, while being asymmetric, is more rectangular/trapezoidal in appearance than in *Laquintasaura* and does not project downward from the femoral shaft as it does in early Prionodontia.

With silesaurs recovered as stem-Ornithischia, the value of the fourth trochanter character as a potential synapomorphy of Dinosauria is challenged: the expanded and crested femoral fourth trochanter may have evolved independently in the saurischian (Fig. 10D) and ornithischian clades (Fig. 10E, F). While it is undeniable that the fourth trochanter in early diverging prionodontians is asymmetrical, it is implicit in the topology presented here (Fig. 6) that this trochanteric asymmetry was achieved independently of that seen in the femora of the earliest known sauropodomorphs and theropods.

Previous analyses that have included an anatomical character for fourth trochanter asymmetry, usually as a binary absent/present type character (e.g. Langer & Benton, 2006; Nesbitt, 2011; Cabreira *et al.*, 2016; Baron *et al.*, 2017a), tend to treat the distinguishable conditions in the ornithischians and saurischians that possess asymmetric trochanters as the same. In such analyses, Ornithischia/Prionodontia and most other dinosaurs have been scored as having asymmetry present (regardless of its form), which carries the assumption that this asymmetry is homologous; this is despite the clear differences in the overall shape of this trochanter between the ornithischians and saurischians that have been outlined above.

If the asymmetry of the fourth trochanter seen in ornithischians (Fig. 10E, F) and saurischians (Fig. 10D) was acquired independently, trochanteric asymmetry may have had an important functional locomotor correlate in early saurischians and prionodontians that did not apply in the case of stem-ornithischians (silesaurs). Currently known silesaurs are generally considered to be quadrupedal, whereas early prionodontians were largely bipedal. It is important to note, in this context, that most silesaurs are extremely fragmentary (*Silesaurus* is exceptional in this regard; see Fig. 7A) and this generalization needs to be tested against the discovery of new, more complete specimens. Similarly, the earliest saurischian dinosaurs currently known were also bipedal (e.g. Martínez *et al.*, 2011; Cabreira *et al.*, 2016). This hints at a possible correlation between stance, mode of locomotion, and the development of asymmetry and prominence of the fourth trochanter. This is perhaps unsurprising, given that the fourth trochanter would have served as an anchoring point for m. caudofemoralis longus et brevis and, therefore, been involved in the lever-arm mechanics associated with retraction of the hindlimb (Hutchinson, 2004; Maidment *et al.*, 2014; Persons & Currie, 2019).

Looking also at the ratio of the lengths of tibia to the femur in known silesaur and non-silesaurian ornithischians, there is a clear difference: in silesaurs the femur and tibia are roughly equivalent in length, or the femur is a little longer (Dzik, 2003; see Fig. 7A). In contrast, early prionodontians possess tibiae that are substantially longer than their femora (Santa Luca, 1980; Colbert, 1981; Galton, 2014; Baron *et al.*, 2017c). Many early saurischians demonstrate a similar relative elongation of the tibia with respect to the femur (Martínez *et al.*, 2011; Cabreira *et al.*, 2016). Just as in the case of the morphology of the fourth trochanter, this shared feature could, when working within previous phylogenetic hypotheses, have been interpreted as a synapomorphy of Dinosauria (e.g. Langer & Benton 2006; Baron *et al.*, 2017a). However, our analyses suggest that changes in hindlimb segment proportions arose independently in the ornithischian and saurischian lineages linked with the acquisition of bipedality.

The shape of the femoral head in silesaurian ornithischians differs from that described in prionodontians. *Silesaurus* and *Kwanasaurus* possess flat femoral heads that are not strongly medially directed (Dzik, 2003; Ferigolo & Langer, 2006; Ezcurra, 2006; Kammerer *et al.*, 2012; Nesbitt, 2011; Baron *et al.*, 2017a; Marsh & Parker, 2020). In contrast, the femoral heads of ornithischians are more typically globular/subspherical and off-set medially with respect to the long axis of the femoral shaft (Butler, 2010; Butler *et al.*, 2007; Nesbitt, 2011; Barrett *et al.*, 2016; Baron *et al.*, 2017c; Barta & Norell, 2021). *Laquintasaura* provides an example of a transitional femoral morphology: the medial face of the femoral head in this taxon is noticeably flatter than the heads of the femora of prionodontians (Barrett *et al.*, 2014: fig. 1), but the femoral head projects medially, unlike that seen in silesaurians.

The presence of a relatively well-developed, anteriorly expanded cnemial crest on the tibia in prionodontians, as seen in *Heterodontosaurus* (Santa Luca, 1980), *Lesothosaurus* (Baron *et al.*, 2017c) and *Scelidosaurus* (Norman, 2020b), reflects the adoption of a parasagittal gait and a uni-axial hinge-like extension-flexure at the knee joint. This feature, or more importantly a transitional morphological stage, is not seen in any of the currently known stem-ornithischians proximate to Prionodontia. Nor is the reduction of the fibula with respect to the tibia (linked to the shift away from torsion between the two shin bones during limb excursions). The suturing and subsequent fusion of parts of the tarsus observed in some early, structurally derived, heterodontosaurid prionodontians (Santa Luca, 1980; Sereno, 2012; Baron *et al.*, 2017a, 2017b) appears to be a clade-specific specialization that favours uni-axial flexure of the ankle joint.

Pelvic anatomy (Fig. 11)

Pre-acetabular process: The typical prionodontian ilium shows an elongate pre-acetabular process (prp) that forms a strap-shaped projection that extends anterior to the pubic peduncle of the ilium (Santa Luca, 1980; Butler, 2010; Butler *et al.*, 2008a; Galton, 2014; Baron *et al.*, 2017c; Norman, 2020b; see Fig. 11E, F). Most silesaurian ilia (Fig. 11C, D) have short pre-acetabular processes that do not project beyond the pubic peduncle (Dzik, 2003; Nesbitt *et al.*, 2010; Peecook *et al.*, 2013). In this respect, silesaur ilia resemble those of other non-dinosaurian dinosauromorphs and early saurischians (Fig. 11A, B). It is worth noting that the ornithischian taxon that is recovered closest to Prionodontia in this analysis, for which we have a near-complete ilium, is *Kwanasaurus* (Fig. 11C). The ilium of this taxon has a pre-acetabular process that projects *slightly* beyond the pubic peduncle when compared to other silesaurs (Martz & Small, 2019: fig. 14). The topology advocated here (Fig. 6) suggests that the ilium of *Kwanasaurus* demonstrates a plausible precursor stage in the process of elongation of the pre-acetabular process seen in prionodontians. It is worth noting that the pre-acetabular process and the dorsal iliac blade are often lost during fossil diagenesis or collection of the specimens (Müller *et al.*, 2018b), hindering the assessment of this structure in several silesaurs.

Acetabular fenestration: Phylogenetic analyses have consistently reported that dinosaurs are united by the shared presence of a perforated acetabulum (Charig, 1972; Bakker & Galton, 1974; Novas, 1996; Langer & Benton, 2006; Baron *et al.*, 2017a). By definition, the common ancestor of all dinosaurs possessed a perforate acetabulum (Fig.11E, F), in contrast to the condition seen in other non-dinosaurian ornithodirans, such as *Lagerpeton* (Romer, 1971), *Ixalerpeton* (Cabreira *et al.*, 2016; see Fig. 11A) and other taxa (Gauthier, 1986; Butler *et al.*, 2014; Sookias *et al.*, 2014; Ezcurra, 2006; Nesbitt *et al.*, 2017b).

Acetabular perforation is achieved in the various dinosaur clades by reduction in the extent of the ossified medial acetabular wall, so that there is little sutural contact with much (or any) between adjacent margins of the ilium, pubis and ischium. Herrerasaurids possess a partially perforate acetabulum (Fig.11B) with much of the medial acetabular wall ossified (Reig, 1963; Hunt *et al.*, 1998; Alcober & Martínez, 2010; Baron & Williams, 2018; Pacheco *et al.*, 2019). Many theropods show a similar morphology (Nesbitt *et al.*, 2009; Marsh & Rowe, 2020). Prionodontian ornithischians typically possess a perforate acetabulum, and several basal taxa show incomplete acetabular walls (Santa Luca, 1980; Norman *et al.*, 2004; Butler, 2010; Baron *et al.*, 2017c; Norman, 2020b; Barta & Norell, 2021). The same is true of the acetabular regions of early sauropodomorphs with the earliest diverging members of Sauropodomorpha displaying extensive acetabular walls (Langer *et al.*, 1999; Ezcurra, 2006; Cabreira *et al.*, 2016; Baron & Williams, 2018; Garcia *et al.*, 2019; Pretto *et al.*, 2019). Despite there being a well-developed wall, all these taxa retain a small 'dinosaurian' fenestra at what would otherwise be the sutural junction between pubis, ischium and ilium. In the new topology (Fig. 6), with silesaurs placed within Dinosauria, on the ornithischian stem, the acetabular fenestra seen in more derived ornithischians can be reinterpreted as having evolved independently of the condition seen in saurischian dinosaurs. *Lagosuchus talampayensis* Romer, 1971 (Agnolín & Ezcurra, 2019) and most silesaurs (and certainly the earliest diverging of these ornithischian taxa) possess closed acetabula (Dzik, 2003; Ferigolo & Langer, 2006; Nesbitt *et al.*, 2010, 2019; Peecook *et al.*, 2013). In some silesaurs, the iliac portion of the acetabular wall extends ventrally, beyond the level of the pubic and ischiadic peduncles of the ilium, creating a convex ventral margin of the acetabular ilium (*Asilisaurus*; see Fig. 11C). This condition resembles the condition in non-dinosaurian avemetatarsalians, such as *Teleocrater* (Nesbitt *et al.*, 2017b) and *Ixalerpeton* (Cabreira *et al.*, 2016;

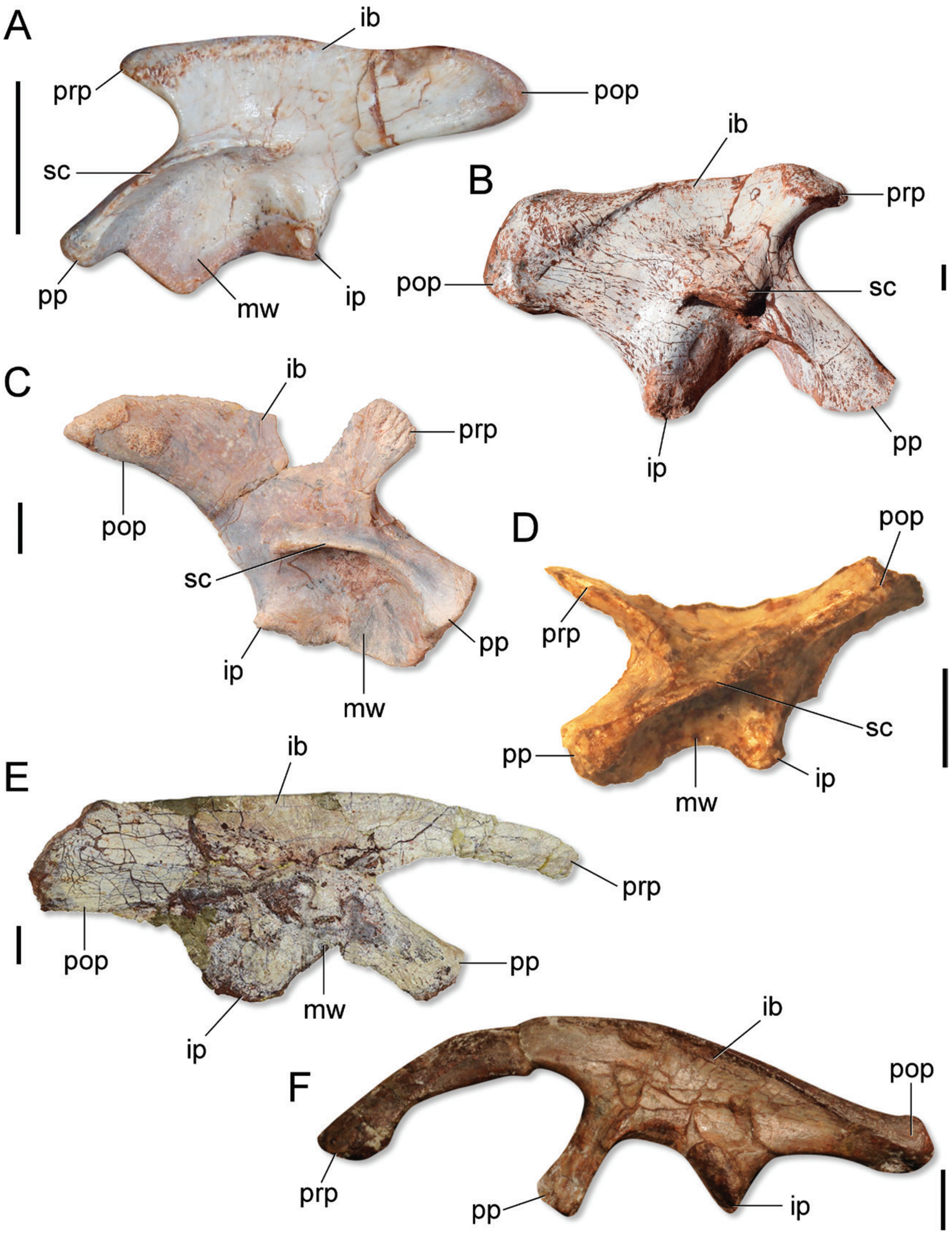

Figure 11. Ilia of selected ornithodirans: A, left ilium of the lagerpetid *Ixalerpeton polesinensis* (ULBRA-PVT059) in lateral view. B, right ilium of the herrerasaurid *Gnathovorax cabreirai* (CAPPA/UFSM 0009) in lateral view. C, right ilium of the prionodontian *Asilisaurus kongwe* (NMT RB159; modified from Nesbitt *et al*., 2019) in lateral view. D, left ilium of the parapredentatan *Kwanasaurus williamparkeri* (DMNH EPV.48506; modified from Martz & Small, 2019) in lateral view. E, left ilium of the neornithischian *Lesothosaurus diagnosticus* (SAM-PK-K1107; modified from Baron *et al*., 2017c) in medial view. F, left ilium of the heterodontosaurid *Heterodontosaurus tucki* (SAM-PK-K1332) in lateral view. Abbreviations: ib, iliac blade; ip, ischiadic peduncle; mw, medial wall; pop, postacetabular process; pp, pubic peduncle; prp, pre-acetabular process; sc, supracetabular crest. Scale bars = 10 mm.

see Fig. 11A). Following our topology, the inference is that the common ancestor of dinosaurs possessed a fully ossified acetabulum and that subsequent fenestration of this region in saurischians and ornithischians is another example of functionally correlated convergence. This interpretation gains some support from the observation of a substantial medioventral extent of the iliac acetabular wall (mw) in *Lesothosaurus* (Fig. 11E) and *Scelidosaurus* (Norman, 2020b), but this extent of the acetabular wall is not observed in more derived (neornithischian) taxa (Galton, 1974; Santa Luca, 1980; Barta & Norell, 2021).

Pubic retroversion: The oblique, posteroventral orientation of the pubic shaft appears close to, or coincidental with, the shift toward an overtly bipedal stance in ornithischians (see: Norman & Weishampel, 1991). Silesaurs, as stem-ornithischians, possess a conventionally anteroventrally orientated pubis and are commonly regarded as quadrupedal. The elongation of the pre-acetabular process of the ilium similarly appears to coincide with pubic retroversion in all known prionodontian ornithischians, as noted by Charig (1972). It is also the case that simultaneous changes occur in hindlimb/forelimb and femur/tibia ratios and the development of a pendent fourth trochanter in the transition from stem-ornithischian to prionodontian.

Summary

Given these apparently coincident changes in morphology (and implied function), the presence of silesaurs on the stem leading to Prionodontia (Fig. 6) offers a new insight into the order, timing and method of acquisition of key components of the derived ornithischian (prionodontian) bauplan; these interpretations undermine several character-states that have been regarded as uniquely dinosaurian. We hope that new discoveries will fill some of the gaps in our understanding of the anatomo-functional changes that occurred during the evolutionary history of Ornithischia and within dinosaurian lineages more broadly.

Evolutionary chronology

Prionodontian ornithischians appear in the fossil record in the Early Jurassic of Europe (Norman, 2020a), North America (Butler *et al.*, 2010; Breeden & Rowe, 2020) and southern Africa (Butler, 2010; Norman *et al.*, 2011; Sereno, 2012; Baron *et al.*, 2017c). The two most closely related stem-lineage ornithischians, *Pisanosaurus* Casamiquela, 1967 (Carnian, Late Triassic) and *Laquintasaura* Barrett *et al.*, 2014 (Hettangian, Early Jurassic) (see Fig. 6), are both from South America. This hints at a paleobiogeographic pattern involving a South American origin of Prionodontia, with a subsequent (Hettangian) establishment of prionodontians occurring in southern Africa. This pattern echoes that described in Sauropodomorpha: the earliest taxa occur in the Triassic of South America [as small faunivorous-to-omnivorous animals; Cabreira *et al.* (2016)], before producing more morphologically diverse forms (including specialist herbivores) in the Early Jurassic of South Africa (Langer *et al.*, 1999, 2010, 2022; Barrett, 2014; McPhee *et al.*, 2017; Lee *et al.*, 2019; Kent & Clemmensen, 2021).

There has been a re-evaluation of the status of *Pisanosaurus* (Casamiquela, 1967). Originally regarded as an early prionodontian ornithischian, it has since been referred to as a silesaurian (Agnolín & Rozadilla, 2018; Baron, 2019), but this latter interpretation has been further disputed (Desojo *et al.*, 2020; Müller & Garcia, 2020a). In addition, there has been chronostratigraphical reassessment (Bordy *et al.*, 2020) of the locality yielding the oldest undisputed record of the ornithischian *Eocursor* [from the Late Triassic (Norian) to the Early Jurassic (Hettangian)]. The latter re-dating creates a substantial Triassic ghost-lineage for the clade Ornithischia, if silesaurians are excluded from its stem (McPhee *et al.*, 2017; Baron, 2019, 2020; Müller & Garcia, 2020a). Considering the recent phylogenetic hypothesis proposed by Müller & Garcia (2020a), which positions silesaur taxa in a stepwise arrangement as stem-ornithischians, and reiterated in this contribution, the long Triassic ornithischian ghost-lineage has been removed.

Nevertheless, this hypothesis implies that an alternate ghost-lineage exists between the oldest currently known stem-ornithischian (*Lutungutali*, Middle Triassic, Upper Ntawere Formation; *Asilisaurus*, Middle Triassic, Lifua Member of the Manda Formation) from strata considered to be Anisian (Nesbitt *et al.*, 2010; see Fig. 2), and the oldest known saurischians (e.g. *Staurikosaurus pricei* Collbert, 1970, *Saturnalia tupiniquim* Langer *et al.*, 1999, Late Triassic, Upper Santa Maria Formation/Lower Candelária Sequence) from strata considered to be Carnian (Langer *et al.*, 2018; see Fig. 2). However, uncertainty also surrounds the dating of these 'earliest' records. Both *Asilisaurus* in the Lifua Member of the Manda Formation and *Lutungutali* in the Upper Ntawere Formation were thought to be Middle Triassic in age, based on the biostratigraphy of the cynodont genus *Cynognathus* (Seeley, 1895), but this estimation lacks support from radiometric dating (Nesbitt *et al.*, 2010; Peecook *et al.*, 2013; but see: Peecook *et al.*, 2017; Nesbitt *et al.*, 2019). On the other hand, Ottone *et al.* (2014) presented U-Pb dating, using zircons, from purportedly correlated strata in Argentina (Puesto Viejo Group) and reported that they can be dated as Early to Middle Carnian, similar in age to that of the dinosauromorph-bearing Chañares Formation of Argentina (Marsicano *et al.*, 2016; Ezcurra *et al.*, 2017). If this correlation is confirmed, the Lifua Member of the Manda Formation of Tanzania, as well as the Ntawere Formation of Zambia, may prove to be Carnian in age, removing the alternate ghost-lineage (Marsicano *et al.*, 2016; Nesbitt *et al.*, 2017; Peecook *et al.*, 2017). This revised dating would indicate that a split between the fundamental clades of dinosaurs occurred in the Early to Middle Carnian, rather than substantially earlier.

DISCUSSION: DINOSAUR RELATIONSHIPS IN FLUX

The dataset

The hypotheses, discussions and conclusions presented in this study are underpinned by the results of phylogenetic analyses that utilized an enlarged anatomical dataset of early dinosaurs and dinosaur close relatives. The dataset incorporates modifications derived from previous studies (Ferigolo & Langer, 2006; Yates, 2007; Cabreira *et al.*, 2011, 2016; Nesbitt, 2011; Bittencourt *et al.*, 2014; Baron *et al.*, 2017a, 2017b, 2017c; Langer *et al.*, 2017; Müller *et al.*, 2018b; Pacheco *et al.*, 2019; Müller & Garcia, 2020a). In its present form, it includes 71 taxa drawn from Dinosauria and proximate non-dinosaurian clades; this represents a substantial increase in sample size compared with that used in recent analyses focused in dinosauromorph affinities (e.g. Cabreira *et al.*, 2016; Pacheco *et al.*, 2019; Müller & Garcia, 2020a). The increase in taxon sampling follows the incorporation of several taxa not known at the time of more recent analyses (Cabreira *et al.*, 2016; Baron *et al.*, 2017a, 2017b; Langer *et al.*, 2017). In addition to increased taxon sampling, further anatomical characters used in this analysis have been drawn from existing datasets (Nesbitt, 2011; Baron *et al.*, 2017a; Martz & Small, 2019); in total, this study utilizes 282 anatomical characters.

Nevertheless, there is more that can be done to expand and improve both taxon and character sampling in this dataset. While this study included nearly all of the earliest known (Hettangian and Sinemurian) ornithischians (with the exception of the recently described *Yuxisaurus* Yao *et al.*, 2022, which may be Sinemurian or Toarcian) and all currently named silesaur genera, there is scope for future studies to expand this dataset through the addition of more saurischian dinosaurs and non-dinosaurian ornithodirans. Further expansion of the dataset will provide data that may strengthen the results of our phylogenetic analysis, as well as offering insights into the changes that have occurred along rapidly evolving branches of the dinosaurian tree during the Late Triassic to Early Jurassic. Similarly, the inclusion of more taxa and character-related data should permit greater accuracy in the correlation of stratigraphic occurrence with rates of anatomical character change within Dinosauria.

In terms of taxon sampling, a future source of additional anatomical and biogeographical data of dinosauromorph (stem-lineage Dinosauria) are recovered specimens that are not presently diagnosable and, therefore, do not bear names. These latter specimens are necessarily overlooked in phylogenetic analyses, even though they may add valuable data (Baron, 2020).

An aspiration arising from this research is the unification of anatomical character definitions, as well as consistency, in the scoring of their character states. Although many of the anatomical characters used in this study are similar to those used in other studies, there are many examples of fundamental differences between our own data matrix and others in terms of the descriptive construction of characters and interpretation of their character states. The novel analysis by Baron *et al.* (2017a) and the reply/rebuttal series by Langer *et al.* (2017) and Baron *et al.* (2017b) have provided an explicit example of how differences in character interpretation and scoring generate different results. This issue was highlighted by Müller & Dias-da-Silva (2019) through their demonstration that alterations in character coding can exert substantial influence upon the most unstable branches recovered in such analyses.

Prionodontia: a new dinosaurian subclade

The re-evaluation of a variety of taxa, previously considered to be dinosauromorphs, that places them on the stem of the dinosaurian clade Ornithischia necessitates a consequential taxonomic adjustment to reflect this topological alteration. Ornithischia, as a formal title, can be maintained because of its inclusive phylogenetic (PhyloCode) definition, which is phrased in such a way that it allows incorporation of these ‘non-ornithischian’ taxa on its stem. The continued recognition of the existence of a more exclusive subclade of taxa (previously named Ornithischia) that exhibit the range of anatomies associated with Seeley’s original ‘bird-hipped’ dinosaur grouping, necessitates the creation of a new taxonomic title for the latter group. Prionodontia is a taxonomic name that is available for the exclusive clade formerly known as Ornithischia. When this name was originally proposed by Richard Owen, he inadvertently selected just three dinosaur taxa that today act as appropriate specifiers and taxonomic anchors for the newly recognized subclade.

HYPOTHESES OF RELATIONSHIP: PROBLEMS

As mentioned earlier, there are three contrasting hypotheses concerning the fundamental relationships between what are understood to be the principal dinosaurian clades during the earliest phase of their evolution: Ornithischia–Saurischia (Seeley, 1888), Phytodinosauria (Bakker, 1986) and Ornithoscelida (Baron *et al.*, 2017a). No single hypothesis has been shown to be overwhelmingly better-supported statistically (Baron *et al.*, 2017a, 2017b; Langer *et al.*, 2017; Parry *et al.*, 2017) and this ambiguity persists. This lack of resolution highlights weaknesses in the cladistic-parsimony-based approach when applied to rapid (intense) diversification events. This problem is compounded by the absence of 'key' or maximally informative taxa due to the incompleteness of the fossil record of terrestrial taxa. Equally, the diversity of new (or resurrected) and disputed phylogenetic hypotheses concerning dinosaur groupings reflects the steadily rising number of new discoveries (many of which are far from complete) that have been recorded in recent years from the oldest known dinosaur-bearing strata [e.g. Novas *et al.* (2021), for a review of this topic].

The major dinosaur clades and earliest hypotheses of relationship were established on the basis of a small number of anatomically derived members of these clades (e.g. Seeley, 1888). In contrast, recent decades of research have revealed early diverging members of these lineages for example, *Eodromaeus murphi*, *Buriolestes schultzi* and *Gnathovorax cabreirai* Pacheco *et al.*, 2019, as well as several taxa that challenge our understanding of the dinosauromorph–dinosaur boundary, for example, *Silesaurus opolensis*, *Asilisaurus kongwe* and *Ixalerpeton polesinensis* (but see: Ezcurra *et al.*, 2020). The synapomorphies that typify the major clades are not clearly present in these animals and some of them *Buriolestes* (Cabreira *et al.*, 2016) present a mix of traits (Müller *et al.*, 2018c).

Steadily increasing numbers of novel taxa alter, or challenge, long-established synapomorphies and, as result, systematic analyses and phylogenetic interpretations have entered a period of intense disturbance. In this study, we have tested alternative topologies using the widest sample of early dinosaurs and their near relatives available and, perhaps not surprisingly, the results challenge orthodoxy. Nevertheless, we recognize that whereas some specimens are exquisitely preserved, early dinosaur relationships are mainly constructed (or affected by) data from a number of poorly preserved or incomplete specimens. Therefore, we recommend caution and circumspection when assessing the veracity of the present or indeed *any* of the currently advocated early-dinosaur phylogenetic trees.

More can still be done in the future to critically revise our anatomical character descriptors, character state choice and character scoring, as well as incorporating more data from new discoveries. Our dataset presents a synthesis of multiple, independently derived, data matrices and establishes a revised framework for the affinities among early dinosaurs and their close relatives. This, in turn, has led us to propose a novel interpretation of the origin, timing and sequence of acquisition of the anatomical features that constitute the unique ornithischian bauplan.

Pterosaurs and lagerpetids: One final caveat pertains to the recovery of a close phylogenetic linkage between pterosaurs and lagerpetids (Kammerer *et al.*, 2020; Ezcurra, 2020); this has the potential to influence current understanding of character optimization at the base of the ornithodiran tree and may equally have implications for early dinosauromorph evolution. Future iterations of this analysis will necessarily be broadened to include pterosaur taxa.

CONCLUSIONS

The addition of early (Jurassic) ornithischian taxa to the dataset developed by Müller & Garcia (2020a) generated a topology that necessitates the creation of a novel, and admittedly controversial, evolutionary history associated with the pattern of diversification among early ornithischian dinosaurs that probably started in the Latest Anisian or Early Carnian.

The results support a hypothesis of early dinosaur relationships that recovers a paraphyletic cluster of silesaurian taxa on the stem of the inclusively defined clade Ornithischia. Evolutionary changes on the stem of Ornithischia led, ultimately, to the appearance of a discrete subclade of the ornithischian lineage that has been recognized by using the resuscitated name Prionodontia. Prionodontians (formerly recognized as members of Seeley's original grouping Ornithischia) are identifiable in the fossil record by Hettangian time (the earliest Jurassic). The phylogenetics implied by the revised topology proposed here have necessitated alterations to the taxonomic content and names of clades. We have made these changes with the intention of minimizing opportunities for confusion, while maximizing informativeness. However, given the fundamental level at which these changes have taken place, some disturbance seems inevitable.

The order, timing and rate of several anatomical changes that occur during the transition from stem-lineage taxa to that seen in more derived (prionodontian) ornithischians had not been explored prior to this analysis. The topology generated by this fresh analysis offers novel insights into the stepwise acquisition of the anatomical characteristics associated with the unique ornithischian bauplan: specifically, the ornithischian mandibular construction, dentition (and implied diet), as well as pectoral, pelvic and femoral-hindlimb construction (and implied stance and gait). The new topology also generates novel interpretations of the time of origin, as well as the geographic distribution of the earliest dinosaurs.

In addition to the anatomo-functional implications that derive from the new topology, the phylogenetics necessitated a reconsideration of the taxonomy as it pertains to the clade Ornithischia within Dinosauria. There is a case made for the resurrection of the name Prionodontia (a taxon proposed by Richard Owen) in order to recognize 'traditional ornithischans'. This usage does not disturb the long-held taxonomy associated with the three principal dinosaurian clades: Theropoda, Sauropodomorpha and Ornithischia.

Assimilation and evaluation of data from this, as well as other, analyses, and supplemented by future discoveries and descriptions, is intended to establish a pathway leading to a universal dataset pertaining to the earliest known members of Dinosauria and their near relatives. The work presented here represents no more than a first step toward realizing that goal and lays a foundation upon which subsequent studies might be built.

ACKNOWLEDGEMENTS

We thank the Willi Henning Society for free access to the TNT software. The original research programme, focused on investigating the assembly of the ornithischian bauplan, was devised by DBN for a Natural Environment Research Council (NERC) - UKRI grant: NE/L501578/1, held at the Department of Earth Sciences, University of Cambridge and Christ's College Cambridge. DBN was financially and logistically supported by the Department of Earth Sciences Cambridge and Christ's College Cambridge. This study was also partially funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) scholarship for MSG, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 404095/2021-6 to RTM) and Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS 21/2551-0000680-3) to RTM. This article has benefitted from comments and corrections provided by two anonymous reviewers, as well as the informed guidance offered by Nick Fraser (National Museums of Scotland, Edinburgh) and the Editor (Maarten Christenhusz).

AUTHOR CONTRIBUTIONS

Originator of the intellectual problem: the origin of the ornithischian bauplan DBN. Data assembly and analytical processing was undertaken by RTM, MSG and MGB. All four authors were involved in the drafting of earlier versions of the manuscript. DBN made the final collation of multiple drafts and provided the editorial revision prior to the submission of the first version of this article. Subsequent submission of a revised version of this article was undertaken by DBN. All the final figures were compiled and created by RTM and MSG.

DATA AVAILABILITY

Data used in this article is presented in the Supporting Information section at the end of the paper and is freely available to download from the publisher's website.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

File S1. Data file with details of anatomical characters and scores used in the study.
File S2. TNT Nexus file.