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The origin and early evolution of the ornithischian bauplan: evaluation and implications for the Dinosauria

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Abstract

The origin of the dinosaurian clade Ornithischia is a topic that has attracted little attention. There are currently three competing hypotheses concerning the relationship *between* the Ornithischia and the two other principal clades of Dinosauria: Theropoda and Sauropodomorpha. The two latter clades have fossil representatives that are well-documented in the Carnian (Late Triassic). However, each of the phylogenetic hypotheses support tree topologies within Dinosauria that imply the existence of a ghost-lineage for Ornithischia that extends through a substantial portion (~25 Ma) of Triassic time because Ornithischia make their first *unambiguous* appearance in the Hettangian (Early Jurassic).

Equally, little attention has been given to recent analyses that controversially have placed some Triassic dinosauromorph taxa (stem-lineage Dinosauria) *within* the clade Ornithischia. One large-scale phylogenetic analysis (Müller & Garcia, 2020a) recovered a preferred topology that featured an array of taxa (commonly referred to as silesaurids) as a paraphyletic assemblage of (dinosaurian) taxa placed along the branch leading to the clade Ornithischia. This latter hypothesis of relationships accounts for the apparent absence of Triassic ornithischians, because stem-lineage ornithischians (silesaurians in this article) have an exclusively Mid-Late Triassic stratigraphic distribution. The latter analysis used a dataset that did not include the diversity of known early representatives of Ornithischia (*sensu lato*) and did not incorporate all the anatomical characters that have been suggested to unite Ornithischia with the 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 silesaurians to the clade Ornithischia. This article addresses these latter issues by evaluating the published expansion and re-analysis of the original dataset (Norman *et al*., 2022).

The results supported the hypothesis that silesaurians comprise a paraphyletic grouping of taxa on the stem of Ornithischia and suggest that successive silesaur taxa acquire anatomical characters sequentially (potentially, anagenetically) in a process that culminates in the assembly of what may be described as the 'traditional' ornithischian bauplan. There are taxonomic consequences that arise if this new topology were to be accepted. For nomenclatural stability in this area of the tree, and to preserve the most widely recognised and relevant taxonomic names, we proposed a revised taxonomic framework for ornithischians that is consistent with this new topology. The name **Ornithischia** is retained for the cladistic 'total-group' (traditional *Ornithischia* of Seeley, plus its stem-lineage), and we resuscitated a name originally proposed by Richard Owen (**Prionodontia** = "coarse edged tooth") for the clade containing only what might be regarded as the 'traditional' ornithischian (objectively "bird-hipped") dinosaurs. The revised taxonomic framework provided a measure of phylogenetic clarity as well as a degree of stability with respect to the clades Ornithischia and Dinosauria. Consideration of the pattern of acquisition of pelvic and hind limb anatomical characters within the expanded clade Ornithischia has led to the suggestion that several of the supposedly 'key' anatomical traits that have been regarded as synapomorphies defining membership of the Dinosauria may alternatively have been acquired independently during the earliest phase of dinosaur diversification.

Keywords

Dinosauromorpha, systematics, silesaurians, anagenesis, dentition, anatomy, Triassic, Jurassic, Prionodontia.

N.B. This paper is a modified and abbreviated update based on the original publication: Norman *et al.* (2022). Taxonomic, palaeobiological and evolutionary implications of a phylogenetic hypothesis for Ornithischia (Archosauria: Dinosauria). *Zoological Journal of the Linnean Society*, 196(4): 1273-1309.

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INTRODUCTION

Since 1888, the taxa attributable to Dinosauria have been regarded as subdivisible into two principal groupings: Saurischia and Ornithischia (Fig. 1A), on the basis of the arrangement of their pelvic bones and the presence/absence of the anatomical correlates associated with pneumaticity (Seeley, 1888). This dichotomy has proved to be well supported throughout the pre- and post-cladistic eras (e.g. Romer, 1956, 1966; Gauthier, 1986).

A small number of studies have proposed alternate topologies: Bakker (1986) advocated a non-numerical proposition in favour of 'Phytodinosauria' (Fig. 1B); whereas Baron *et al.* (2017a, b) conformed to the standard of data transparency associated with modern systematic studies when proposing 'Ornithoscelida' (Fig. 1C). The position of Ornithischia with respect to other clades within Dinosauria has become unstable, with multiple competing hypotheses having emerged regarding their early interrelationships (Cabreira *et al.*, 2016; Baron *et al.*, 2017a, b; Baron & Barrett, 2017; Cau, 2018; Müller & Garcia, 2020a). Studies have found support for what can be termed both 'Seeley' (Fig. 1A) and 'Ornithoscelida' (Fig. 1C) patterns of dinosaurian relationships (e.g. Langer *et al.*, 2017; Parry *et al.*, 2017; Lee *et al.*, 2019). Little difference in statistical support lies between these two alternatives or, in point of fact, the third alternative of a Sauropodomorpha-Ornithischia grouping – the 'Phytodinosauria' hypothesis (Fig. 1B). Despite the equivocal nature of the fundamental datasets, most recent phylogenetic studies have tended to exhibit a preference for topologies that accord with the 'Seeley' model (Nesbitt *et al.*, 2017a; Martz & Small, 2019; Ezcurra *et al.*, 2020; Novas *et al.*, 2021).

Some recent analyses have suggested that a grouping of Middle-Late Triassic taxa, usually referred to as members of the Silesauridae, are early diverging members of Ornithischia (Fig 1D), enlarging on a tentative suggestion by Dzik (2003). These latter have focused particularly on similarities between the dental and mandibular anatomies in silesaurian taxa, notably *Silesaurus* (Dzik, 2003) and *Sacisaurus* (Ferigolo & Langer, 2006) and those seen in early ornithischians. Late Triassic silesaurians appear to have been herbivorous or possibly omnivorous animals and consequently display mandibulo-dental features comparable to those seen among herbivorous ornithischians of the Early Jurassic. The principal question that arises is: are these features *analogous* (Nesbitt, 2011; Nesbitt *et al.*, 2010, 2013, 2017a; Baron *et al.*, 2017a, b; Cau, 2018; Martz & Small,

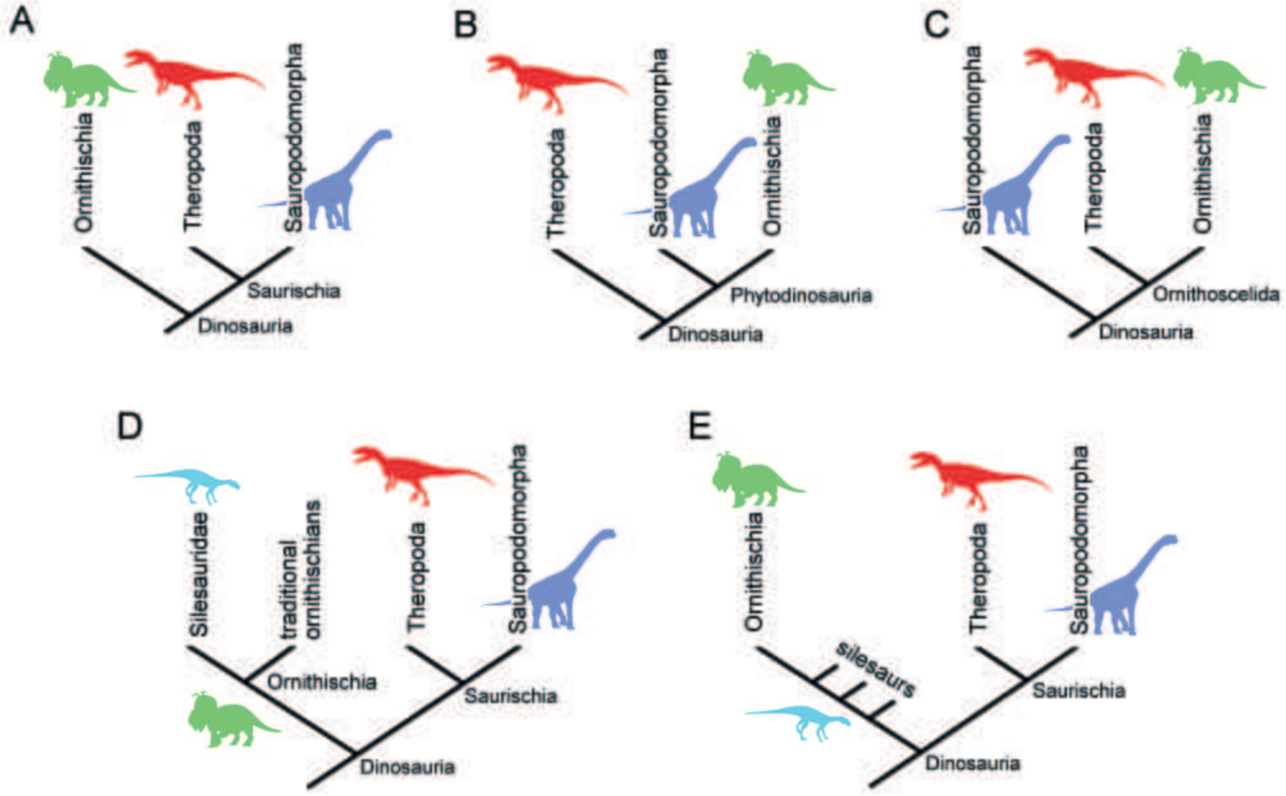

Fig. 1: Hypotheses of the phylogenetic relationships of dinosaurs compared: A) The traditional ('Seeley') hypothesis. B) The 'Phytodinosauria' hypothesis (Bakker; 1986). C) The 'Ornithoscelida' hypothesis (Baron *et al.*, 2017a). D) The 'Seeley" hypothesis with Silesauridae positioned as the sister-taxon to "traditional" ornithischians (Langer & Ferigolo, 2013; Cabreira *et al.*, 2016). E) Paraphyletic silesaurians positioned as a stem-lineage array of ornithischians (Müller & Garcia, 2020a). Silhouettes are based on artwork by Márcio L. Castro. (Modified from Norman *et al.,* 2022: fig. 1)

2019; Ezcurra *et al*., 2020) or *homologous* (Dzik, 2003; Langer & Ferigolo, 2013; Cabreira *et al*., 2016; Pacheco *et al*., 2019)?

The putative silesaurian-ornithischian relationship appears to be compromised stratigraphically by the existence of the Carnian (Late Triassic) taxon *Pisanosaurus mertii* Casamiquela, 1967. This taxon was described as the earliest known member of Ornithischia (Casamiquela, 1967) and this view gained widespread support (Bonaparte, 1976; Sereno, 1991, 2012; Irmis *et al*., 2007a; Butler *et al*., 2008b; Langer *et al*., 2009; Boyd, 2015; Baron *et al*., 2017a). Re-assessment of the holotype and more comprehensive phylogenetic analyses, have resulted in this taxon shifting within the dinosauromorph tree: from the ornithischian lineage to the silesaur lineage and back again (Agnolín & Rozadilla, 2018; Baron *et al*., 2017b; Baron, 2019; Desojo *et al*., 2020). Equally, many other taxa collected from Late Triassic outcrops and originally interpreted as early ornithischians (e.g. Hunt & Lucas, 1994) have also been re-appraised; this has led to their removal from Ornithischia (e.g. Parker *et al*., 2005; Irmis *et al*., 2007b; Nesbitt *et al*., 2007; McPhee *et al*., 2017; Bordy *et al*., 2020). These two factors have led to a general perception that no unequivocally Triassic ornithischians are currently known in the fossil record. Acceptance of this latter view implies that the timing of the origin of ornithischians, as well as their topological placement within Dinosauria, may differ substantially from the current consensus.

Müller & Garcia (2020a – see Fig. 1E) re-analysed the relationship between early dinosaurs and their closest relatives and recovered a succession of silesaurian taxa, previously considered to be a clade (Silesauridae) outside Dinosauria, as a paraphyletic grouping of taxa *within* Dinosauria and placed on the branch leading to Ornithischia. One implication that can be drawn from this topology, if it were to be accepted more widely, is that silesaurians are known to occupy a Middle-Late Triassic 'zone of transition' (filling the apparent ornithischian ghost-lineage) prior to the appearance of definitively ornithischian taxa. The placement of various silesaurian taxa on the stem of Ornithischia pushes back the timing of this dinosaur sub-clade divergence, and holds the prospect of offering anatomical insights concerning the acquisition of the uniquely ornithischian bauplan.

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 reduced the quantity and quality of data available for the various analyses and, potentially, masks step-wise character acquisitions along branches in the trees that are recovered from such analyses. These analyses (see Norman, *et al*., 2022) 'tested' the effect of inclusion and scoring of early ornithischian taxa on the recoverable topology at the base of the dinosaurian phylogeny. Attention was focused upon ornithischians and their possible interrelationship with silesaurians (with passing reference to theropods and saurischians more broadly). Building on the previous analysis of Müller & Garcia (2020a) an attempt was made to outline the anatomical evidence that supported a plausible sequence by which the anatomical traits observed in eponymous ornithischians were assembled during Late Triassic times.

The new topology also had a bearing on the timing of divergence of the dinosaurian 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), had the potential to push the ornithischian-saurischian split as far back as the Early Triassic (Induan-Olenekian). This timing is critically dependent on the accurate dating of the Manda Beds of Tanzania and the "Upper Beds" of the Ntawere Formation of Zambia. Recent work has however posited a Carnian age for these beds (Marsicano *et al*., 2016; Nesbitt *et al*., 2017b; Peecook *et al*., 2017). A younger age of occurrence for *Lutungutali* and *Asilisaurus* would still push back (to the Early Carnian) the time of divergence of the ornithischian stem-lineage; whereas most hypotheses that have tended to focus on the Norian (Crompton & Charig, 1962; Thulborn, 1971; Sereno, 1991; Norman *et al*., 2004; Langer & Benton, 2006; Butler *et al*., 2008b; Boyd, 2015; Baron, 2019).

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, 1861a and *Emausaurus ernsti* Haubold, 1990; the Middle Jurassic Chinese *Hexinlusaurus multidens* (He & Cai, 1983) and *Agilisaurus louderbacki* (Peng, 1990); plus heterodontosaurid taxa from the Early Jurassic of southern Africa and the Early Cretaceous of Europe (Butler *et al*., 2007, 2008b, 2010; Norman *et al*., 2011; Pol *et al*., 2011; Sereno, 2012). The dubious (theropod?) taxon *Chilesaurus diegosuarezi* Novas *et al*., 2015 from the Late Jurassic of Chile was included in the updated matrix to ensure that all currently competing sources of early ornithischian evolution and interrelationships were being evaluated.

Most 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, b; Barrett *et al*., 2014, 2016; Butler, 2005, 2010; Butler *et al*., 2007, 2008b, 2010, 2012; Knoll *et al*., 2009; Sereno, 2012; Galton, 2014; Novas *et al*., 2015, 2021; Pol *et al*., 2011; Porro *et al*., 2015; Baron *et al*., 2017c; Breeden & Rowe, 2020; Norman, 2020a, b, c, 2021). Five new anatomical characters, used in previous analyses of early dinosaurs and their close dinosaur relatives, were added to the data matrix (see Norman *et al*., 2022 – supplementary files). 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. The analytical protocols and the resultant topologies have been described in greater detail in Norman *et al*. (2022). A strict-consensus summary tree generated by the recent analysis is presented as Figure 2.

DISCUSSION

Taxonomic implications

Several important taxonomic implications flow from the resultant topology (Fig. 2). The arrangement of taxa in what we will refer to as the ‘total ornithischian lineage’ necessitates revision, re-definition and addition of some clade names.

The definition and status of the clade Ornithischia was brought into focus by the results of the analysis. The inclusion of an array of silesaurians not just in the clade Dinosauria, but more specifically as members of the stem-lineage of Ornithischia raised questions: what, precisely, is the clade Ornithischia? And, which taxa should be included? As one of the two fundamental groupings of Dinosauria (Seeley, 1888) and recognised consistently since that time, any dramatic shift in the topological placement of Ornithischia (and its composition) with respect to Saurischia, had the potential to profoundly affect commonly used dinosaurian nomenclature. The proposed topology (Fig. 2) offered an opportunity for the taxon Ornithischia to become more inclusive, through the incorporation of a range of ‘non-ornithischians’ (in a strictly literal sense = those animals without a ‘bird-like’ pelvic configuration) 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 carnegiei* or *Passer domesticus*” (Baron *et al*., 2017a) permits this expansion, as recognized by Müller & Garcia (2020a). It was proposed that the name Ornithischia be retained as an inclusive clade in order to retain its hierarchical status as one of the three principal dinosaur clades, even though its taxic composition and anatomical characteristics had been broadened substantially.

Historically, Ornithischia was 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 another apomorphic trait: osteological markers associated with pneumatism in living birds. N.B. None of the currently known silesaurian ornithischians possess either an opisthopubic pelvis or evidence of pneumatism.

One proposal regarding the taxonomy applicable to the silesaurian-ornithischian lineage might have been to retain a node-based definition of the Ornithischia: the common ancestor of *Scelidosaurus*, *Lesothosaurus* and *Heterodontosaurus* and all descendants; so that it excluded members of the stem-lineage and encompassed only those taxa that are anatomically ornithischian (in a classical sense). To do this risked creating substantial nomenclatural and taxonomical disturbance because it would have 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 meant that clade names may 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 could be argued to be robust, given the range of competing hypotheses concerning the affinities and placement of currently known silesaurians and proximate taxa (Ezcurra, 2006; Irmis *et al*., 2007a; Nesbitt *et al*., 2010; Langer & Ferigolo, 2013; Bittencourt *et al*., 2014; Cabreira *et al*., 2016; Agnolín & Rozadilla, 2018; Baron *et al*., 2017b; Pacheco *et al*., 2019; Ezcurra *et al*., 2020; Müller & Garcia, 2020a). Conserving the taxon Ornithischia in a more inclusive sense did not preclude the possibility that other early diverging members of this 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 phylogenetic concept of Ornithischia (as a ‘total group’) will, necessarily lead to an expansion of included 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, epaxial ossified tendons.

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

Exploring the historical literature associated with this general topic, revealed that the term Ornithischia had not been the only name suggested for a group of exclusively opisthopubic 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 was 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 anatomical evidence

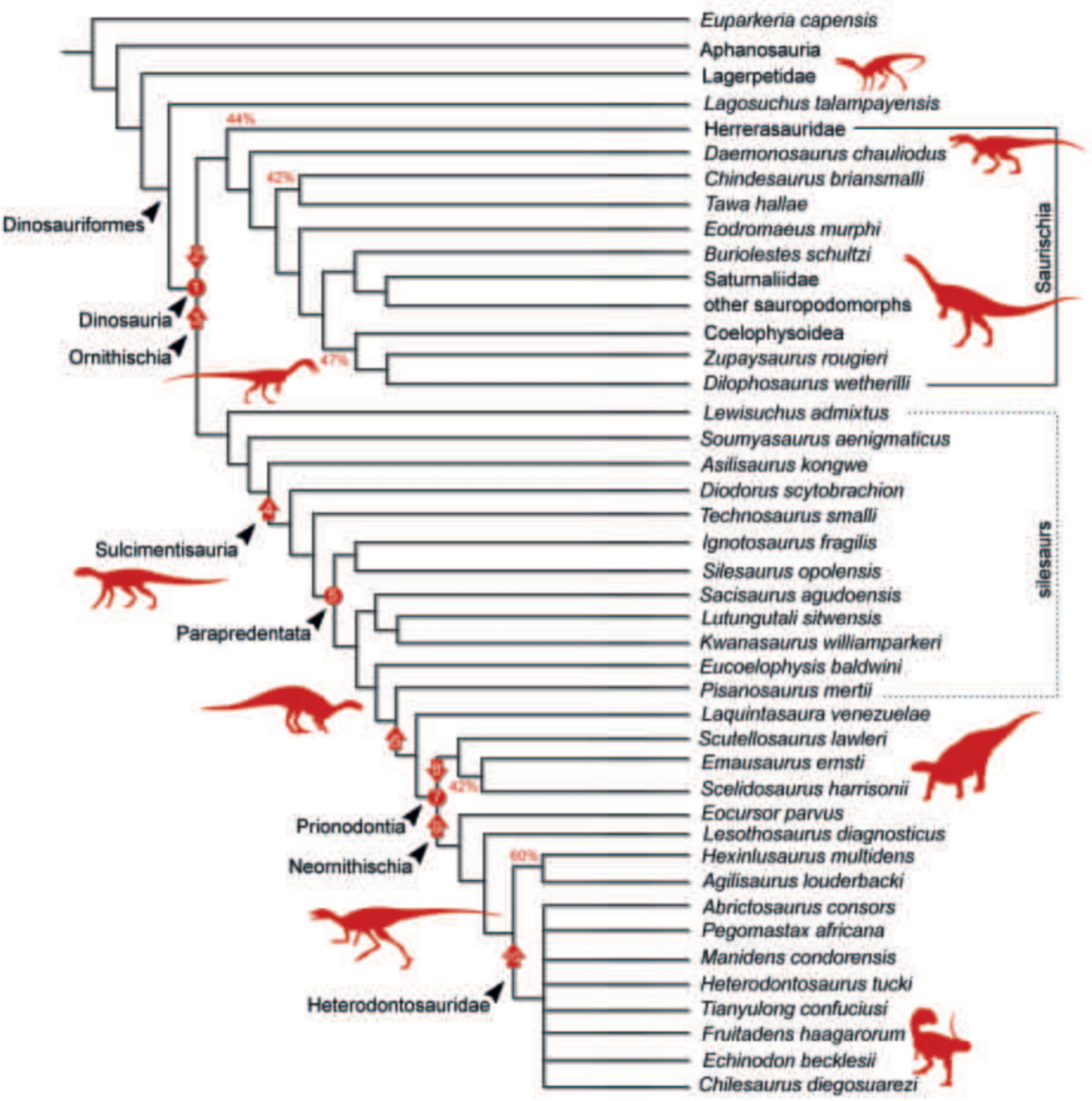

Fig. 2: Strict consensus tree from the unconstrained analysis. Node numbers: 1. Dinosauria, 2. Saurischia, 3. Ornithischia, 4. Sulcimentisauria, 5. Parapredentata, 6. Unnamed, 7. Prionodontia, 8. Thyreophora, 9. Neornithischia, 10. Heterodontosauridae. Silhouettes based on the artwork by Márcio L. Castro, Gabriel Lio, Rodrigo T. Müller, Maurício S. Garcia and John Sibbick. (Norman *et al.,* 2022: fig. 6)

for an ossified predentary is currently lacking in two other early thyreophorans: *Scutellosaurus* and *Emausaurus*)].

Owen (1874) proposed the name **Prionodontia** (for the bearers of 'coarse edged teeth') as a collective name for just three then-known dinosaur taxa: *Scelidosaurus* (Owen, 1861a), *Iguanodon* (Mantell, 1825) and *Echinodon* (Owen, 1861b), all of 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. Although Prionodontia preceded Ornithischia by 14 years, the name coined by Owen was of little practical systematic value and had no genuine phylogenetic intent; it appears to have been a casual/informal descriptive grouping that blatantly ignored other, then known, dinosaur taxa that were similarly 'prionodontian' e.g. *Hylaeosaurus* (Mantell, 1833), *Thecodontosaurus* (Riley & Stutchbury, 1836), *Troodon* (Leidy, 1856), *Trachodon* (Leidy, 1856), *Hadrosaurus* (Leidy, 1859), *Hypsilophodon* (Huxley, 1869). Owen's contribution was ignored by all contemporary practitioners because it lacked both discriminatory sense and utility. In marked contrast, Ornithischia survived subsequent changes in systematic methodology and the shift to using tree-based phylogenetic definitions rather than apomorphy based ones.

Prionodontia was listed by Owen with a membership of just *Echinodon, Iguanodon* and *Scelidosaurus*, which (inadvertently, and with hindsight) 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, b; Madzia *et al.*, 2021). As a node-based definition given in the terms set out above, Owen's Prionodontia (given its original membership) encompassed the composition of the long-established clade Ornithischia. Owen's taxonomic name remained available and Prionodontia was able to be established legitimately as the clade name for the "traditional ornithischians" of Müller & Garcia (2020a). It was 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 'coarsely serrated teeth'. However, the precedent set by the general adoption of phylogenetically-based taxonomic definitions allow 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 carnegiei* (Hatcher, 1901).

Should 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.

DISCUSSION: PALAEOBIOLOGICAL AND EVOLUTIONARY IMPLICATIONS

This revision of the topology within Dinosauromorpha, and reconstruction of Ornithischia in the light of its putative associated stem-lineage, generated several thought-provoking evolutionary interpretations. The changes in dental and mandibular anatomy challenge previous evolutionary models. Furthermore, changes in stance and gait, that are linked to forelimb, pelvic and hindlimb anatomy appeared also to be cumulative, provided that silesaurians can be agreed to represent a grade of early diverging stem-lineage ornithischians, rather than stem-lineage dinosaurs (i.e. proximate non-dinosaurians), as more commonly envisaged (Ezcurra, 2006; Irmis *et al*., 2007b; Nesbitt *et al.,* 2010; Bittencourt *et al*., 2014; Ezcurra *et al*., 2020).

Dentition (Figs 3, 4)

Much attention has been paid to details of the dentition in prionodontian ornithischians 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, 1861a; Thulborn, 1970, 1971; Norman, 1984, 2004, 2020a, 2021; Weishampel, 1984; Norman & Weishampel, 1985; Gow, 1990; Norman *et al*., 2004, 2011; Butler *et al*., 2008b, 2012; Porro, 2007; Porro *et al*., 2015; Pol *et al*., 2011; Barrett, 2014; Becerra & Pol, 2020). Among the principal clades within Dinosauria, the ornithischians have what has commonly been thought to possess the most distinctive dental anatomy and, within

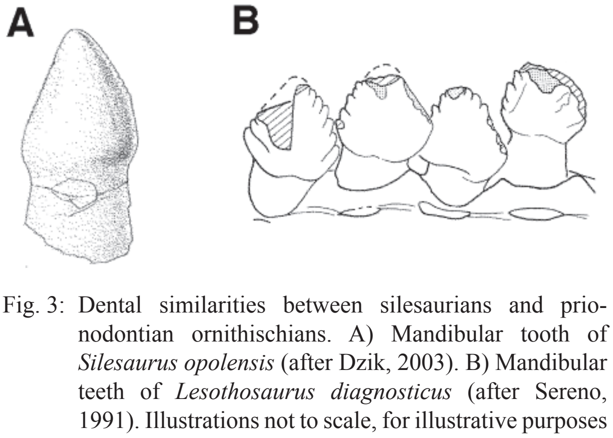

Fig. 3: Dental similarities between silesaurians and prionodontian ornithischians. A) Mandibular tooth of *Silesaurus opolensis* (after Dzik, 2003). B) Mandibular teeth of *Lesothosaurus diagnosticus* (after Sereno, 1991). Illustrations not to scale, for illustrative purposes only.

Prionodontia, it has always been recognised that there is a high degree of dental variability within the major subclades (Norman *et al*., 2004); although some clades are readily diagnosable based on their dentitions alone, e.g. heterodontosaurids, hadrosaurids and ceratopids. Furthermore, large numbers of anatomical characters used in phylogenetic analyses of ornithischians describe features of their dental anatomy (e.g. Butler *et al*., 2008a; Boyd, 2015; Dieudonné *et al*., 2020). Much has also been said before about the distinction between prionodontian ornithischian 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 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 (of the general morphology seen in Fig. 4A) with finely serrated margins, as seen commonly in theropod dinosaurs, as well as proximate stem-lineage dinosaurs 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, 1861a, b, 1874; Thulborn, 1971; Nesbitt, 2011; Norman *et al.,* 2004; 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 (Figs 3B, 4E). In some discussions, the heterodonty that characterizes contemporaneous

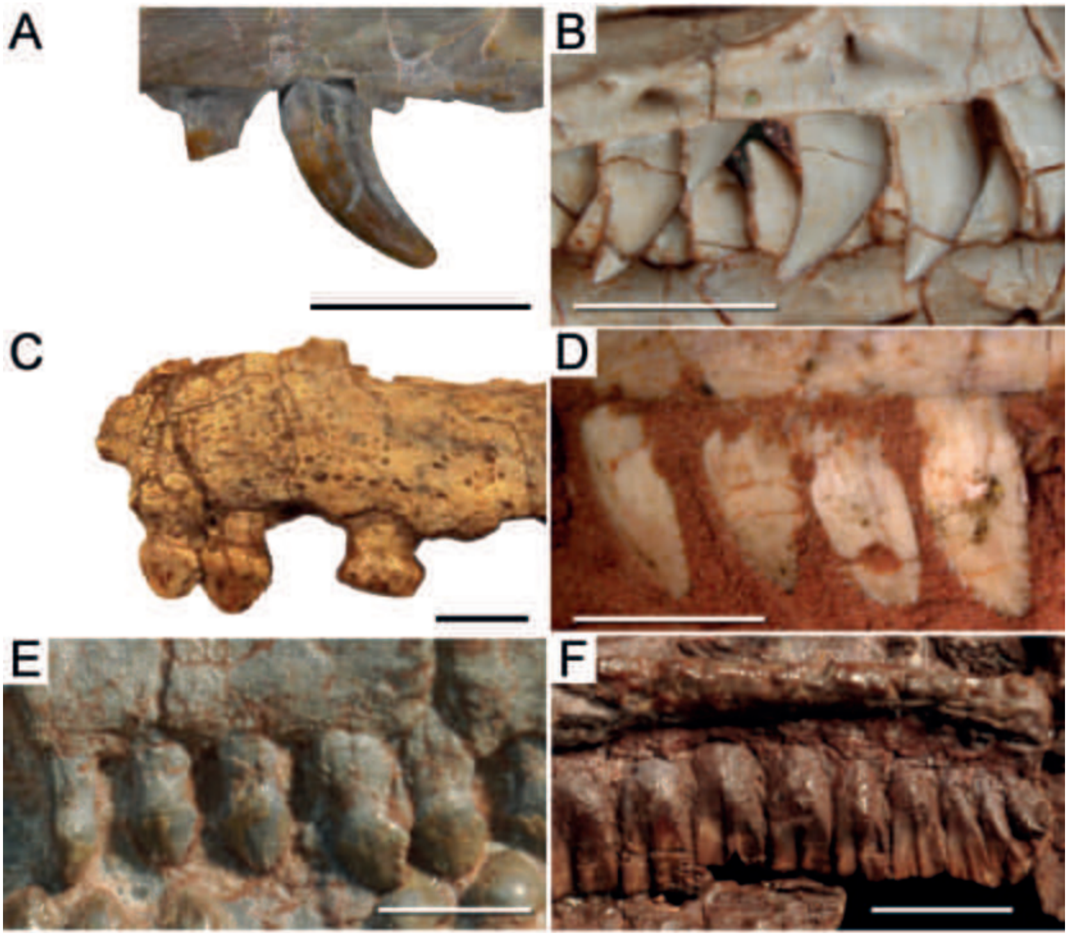

Fig. 4: Maxillary teeth of selected dinosauromorphs described in this analysis, in labial view: A) Left maxillary teeth of a basal silesaurian ornithischian *Lewisuchus admixtus* (CRILAR-Pv 552; modified from Ezcurra *et al*., 2020). B) Right maxillary teeth of the sauropodomorph *Buriolestes schultzi* (ULBRA-PVT280). C) Left maxillary teeth of the parapredentatan ornithischian *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 prionodontian *Lesothosaurus diagnosticus* (BP/1/6582). F) Right maxillary dentition of the heterodontosaurid prionodontian *Heterodontosaurus tucki* (SAM-PK-K 337). Scale bars = 5 mm. (Norman *et al.,* 2022: fig. 8)

heterodontosaurid ornithischians, which combines 'caniniform' teeth (suggestive of carnivory) with chisel-like palisades of 'cheek' teeth (indicative of herbivory – Fig. 4F) 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 prionodontian ornithischians (Butler *et al.*, 2008a; Boyd, 2015; Baron *et al.*, 2017a).

The initial discovery (Dzik, 2003) and subsequent increase in our understanding of the anatomy and diversity of Triassic silesaurians – 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 Fig. 4A) – 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 *Silesaurus* (Fig. 3A), was also described in other Triassic pseudosuchians and archosauromorphs (Parker *et al.*, 2005; Sengupta *et al.*, 2017; Parker *et al.*, 2021). These observations led to a review of the assignments of Late Triassic 'ornithischian' 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 *et al.* (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 (Fig. 4A) and mandibular characters (Figs 5, 6 'beak'), which were restricted to *Silesaurus* and *Sacisaurus* at that time. 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 silesaurians 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 (Fig. 2) places the silesaurs on the stem-lineage of Ornithischia, not as a sister-clade but as a paraphyletic assemblage of taxa that approach the clade Prionodontia, in stepwise fashion (Müller & Garcia, 2020a; Norman *et al.*, 2022). This topology suggests that the evolution of the dental anatomy of silesaurians might be traceable through successive taxa as they approach definitive prionodontian status. The earliest diverging members of the ornithischian stem-lineage (*Soumyasaurus* and *Lewisuchus* – see Figs 2, 3A) possess sharp, recurved, finely serrated teeth that are typical of the other non-dinosaurian dinosauromorphs and dinosaur clades (Herrerasauridae, most members of Theropoda, early members of Sauropodomorpha (Fig. 3B) – Martínez *et al.*, 2011; Cabreira *et al.*, 2016; Pacheco *et al.*, 2019; Müller & Garcia, 2020b). Equally, some early sauropodomorphs (*Macrocollum* – Fig. 3D) display tall and spatulate, coarsely serrated maxillary teeth. Silesaurians positioned more proximate to Prionodontia: *Diodorus* (Kammerer, Nesbitt & Shubin, 2012), *Silesaurus* and *Technosaurus* (Chatterjee, 1984) – see Fig. 2), possess more diamond-shaped tooth crowns. Finally, the silesaurs most proximate to Prionodontia, such as *Kwanasaurus* (Martz & Small, 2019: fig. 12 – see Fig. 3C), possess teeth that closely resemble those of the earliest diverging members of Prionodontia, e.g. *Lesothosaurus* (Sereno, 1991 – see Figs 3B, 4E) 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. 4C, 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 (Fig. 4A) to that displayed by *Technosaurus, Kwanasaurus* (Fig. 4C) and basal prionodontians (see Figs 2, 3B, 4E).

With the heterodontosaurids recovered as more deeply nested within Prionodontia (Fig. 2), 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 stem-lineage ornithischians and early prionodontians.

Predentary (Fig. 5C)

Prionodontians are characterised by the possession of a predentary bone (Fig. 5C) a single, 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). A discrete predentary is absent in stem-lineage ornithischians and all dinosauromorphs and distinguishes prionodontians from all other dinosaurian taxa (Nabavizadeh, 2016). However, it should be noted as a matter of caution that a predentary is not consistently preserved among early prionodontians: the well-preserved, articulated skeletal remains of the basal thyreophoran/basal ankylosauromorph *Scelidosaurus* (Norman, 2020a, 2021) and those of *Scutellosaurus* and *Emausaurus* have so far failed to recover an ossified predentary.

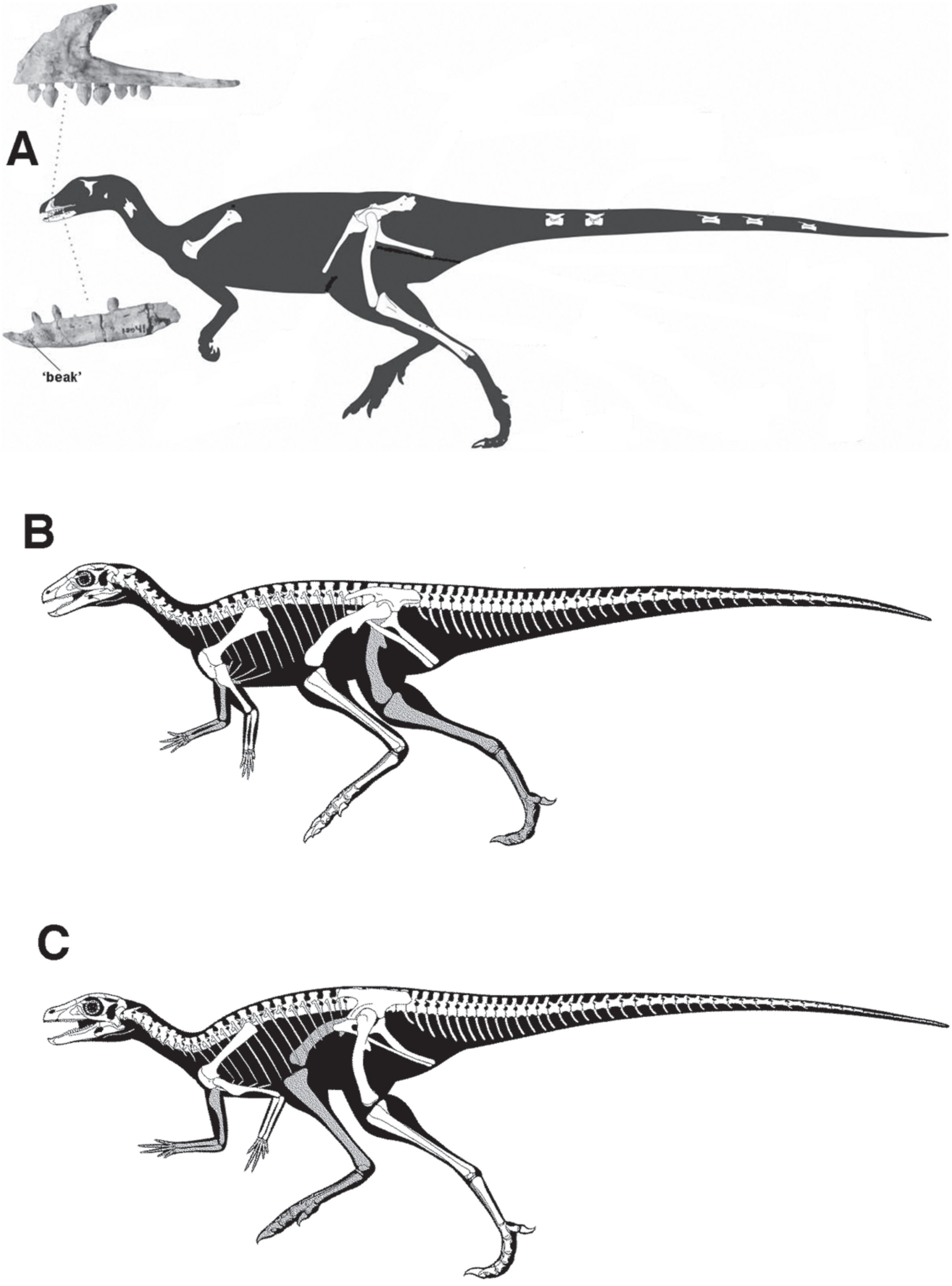

Fig. 5: Body plan evolution within Ornithischia and character states with phylogenetic importance for the present hypothesis. A) Skeletal reconstruction of *Sacisaurus agudoensis*, a silesaurian ornithischian (after Ferigolo & Langer, 2006) with insets of the preserved maxillary and mandibular anatomies – 'beak' refers to the toothless region at the anterior end of the mandible. B) Skeletal reconstruction of *Laquintasaura venezuelae*, the sister-taxon to all known prionodontian ornithischians (after Barrett *et al*., 2014). N.B. A predentary was restored on the mandible of *Laquintasaura,* but there is no proof that this bone was present. C) Skeletal reconstruction of *Eocursor parvus*, a prionodontian neornithischian (after Butler *et al*., 2010). Not to scale, for illustrative purposes alone.

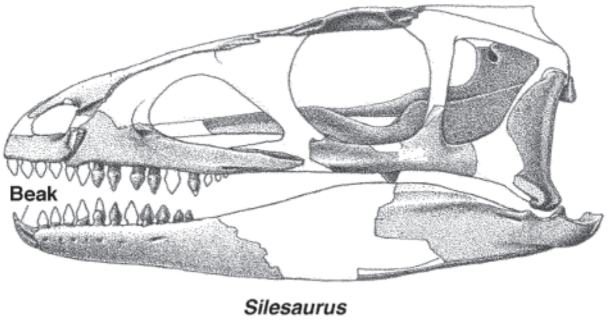

Fig. 6: The reconstructed skull of *Silesaurus opolensis* Dzik, 2003. 'Beak' refers to the toothless region at the anterior end of the mandible. N.B. Although it appears as though there is a clear suture between the 'Beak' and dentary there is no suture present in the original material. (From Dzik, 2003)

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. *Sacisaurus* and *Silesaurus* – see Figs 5A, 6 'beak') possess what has been referred to as a "predentary-like" edentulous anterior portion of the dentary (Dzik, 2003; Ferigolo & Langer, 2006; Langer & Ferigolo, 2013; Holliday & Nesbitt, 2013). Silesaurs that have a well-preserved dentary now include *Silesaurus*, *Sacisaurus, Asilisaurus* and *Kwanasaurus*. All show an anterior dentary ramus that is edentulous and tapers to a point. This morphology is not unique among archosaurs: similar edentulous anterior dentary rami are 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). Based upon the topology generated in the present 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 is known to occur in ceratopians (the rostral bone), as an unpaired element anterior to the paired premaxillae (You & Dodson, 2004). A discrete predentary bone was originally reported to be present in silesaurians 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). Previous hypotheses positing silesaurians 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 dinosauromorphs (except for silesaurians) that possess any osteological feature resembling an anatomical precursor of the predentary.

Pectoral girdle (Fig. 7)
The tree topology (Fig. 2) brought into focus other observable similarities and differences in the construction of the pectoral girdle between the silesaurians, prionodontians and other stem-lineage dinosaurs. The scapulae of early prionodontians, such as *Scutellosaurus, Scelidosaurus* and *Lesothosaurus* (Fig. 7F), and their nearest known relative, *Laquintasaura* (Fig. 4B) are comparatively robust and expanded at their distal ends (Santa Luca *et al*., 1976; Butler, 2005; 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. 7C), 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. 7B), an early diverging clade within Saurischia, the form of the scapula is narrow and strap-like, with no distal expansion (Alcober & Martínez, 2010; Pacheco *et al*., 2019). The scapulae in the stem-lineage ornithischians *Lewisuchus* (Fig. 7D), *Silesaurus* and *Asilisaurus* (Fig. 7E) show a greater degree of distal expansion than seen in the earliest saurischians and non-dinosaur ornithodirans (Dzik, 2003; Nesbitt *et al*., 2010, 2019; Bittencourt *et al*., 2014; Piechowski & Tałanda, 2020). *Asilisaurus* possesses a scapula that closely resembles that of *Lesothosaurus* (Fig. 7E, F).

Pelvis and hind limb (Figs 8, 9**)**
The construction of the pelvis and hind limb of prionodontian ornithischians has received much attention (Thulborn, 1971; Charig, 1972; Santa Luca, 1980; Norman & Weishampel, 1991; Butler *et al*., 2010; Baron *et al*., 2017a, c; Norman, 2021). 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 strap-like, elongate pre-acetabular processes (prp) – Fig. 8E, F (Santa Luca, 1980; Norman *et al*., 2004; Langer & Benton, 2006; Butler *et al*., 2008b; Nesbitt, 2011; Baron *et al*., 2017c; Norman, 2020b).

Prionodontians also have unusual, often unique, characters in their femoral architecture (e.g. Maidment & Barrett, 2011, 2014; Baron *et al*., 2017c). Examples include the presence of a pendent fourth trochanter (Fig. 9E, 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 prionodontian taxa (Fig. 9E, 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

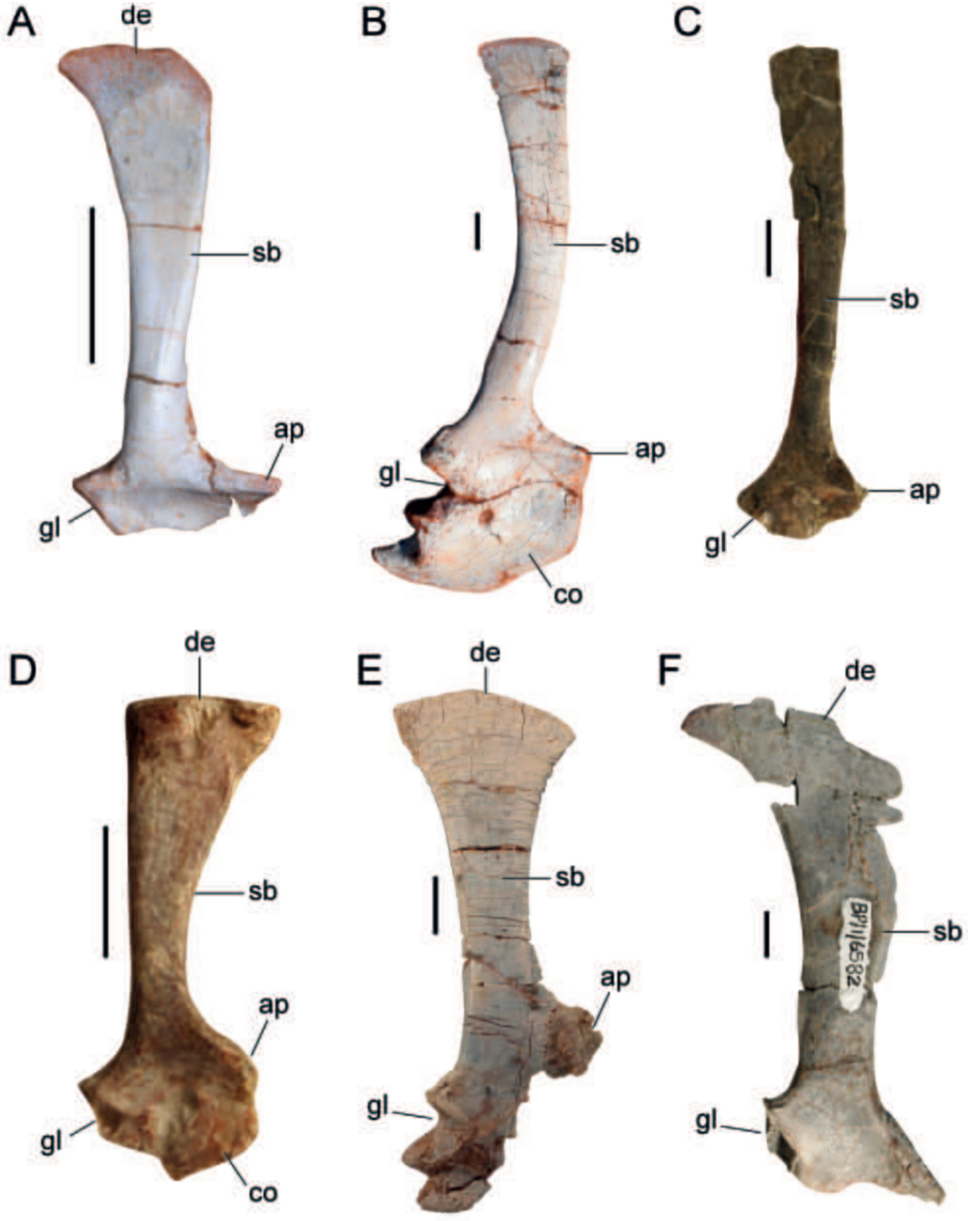

Fig. 7: Pectoral girdle of selected ornithodiran dinosauromorphs in lateral view: A) Right scapula of the lagerpetid *Ixalerpeton polesinensis* (ULBRA-PVT059). B) Right scapula and coracoid of the herrerasaurid *Gnathovorax cabreirai* (CAPPA/UFSM 0009). C) Right scapula of the early diverging saurischian *Tawa hallae* (GR 242). D) Left (reversed) scapula and coracoid of the silesaurian ornithischian *Lewisuchus admixtus* (PULR 01). E) Left (reversed) scapula and coracoid of the silesaurian ornithischian *Asilisaurus kongwe* (NMT RB159; modified from Nesbitt *et al.,* 2020); 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. (Norman *et al.,* 2022: fig. 9)

in the femora of neotheropods (Welles, 1984; Madsen & Welles, 2000; Nesbitt, 2011; Baron *et al*., 2017a; Baron, 2019; Marsh & Rowe, 2020; Marsh & Parker, 2020), and has been proposed as a synapomorphy of Ornithoscelida (Fig. 1C) in the analyses that recovered an Ornithischia-Theropoda sister-taxon relationship (Baron *et al*., 2017a, b). Most dinosaurian taxa possess a thin, spike-like, anterior trochanter that is connected by a ridge to the proximal end of the femur (Fig. 9D).

Pelvic anatomy (Fig. 8)

Preacetabular process. Most silesaurian ilia (Fig. 8C, D) have short preacetabular 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. 8A, 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. 8C). The ilium of this taxon has a preacetabular process that projects *slightly* beyond the pubic peduncle when compared to other silesaurs (Martz & Small, 2019: fig. 14). The topology proposed here (Fig. 2) suggests that the ilium of *Kwanasaurus* demonstrates a plausible precursor stage in the process of elongation of the preacetabular process seen in prionodontians. It is worth noting that the preacetabular process and the dorsal iliac blade seem to be insubstantial and are often eroded or lost during either diagenesis or excavation (Müller *et al*., 2018), hindering the assessment of this structure in several silesaurians.

Acetabular fenestration. Phylogenetic analyses have reported consistently that dinosaurs are united by the shared presence of a perforate 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. 8E, F), in contrast to the condition seen in other non-dinosaurian ornithodirans, such as *Lagerpeton* (Romer, 1971), *Ixalerpeton* (Cabreira *et al*., 2016 – see Fig. 6A) and other taxa (Gauthier, 1986; Sookias *et al*., 2014; Butler *et al*., 2014; Ezcurra, 2016; Nesbitt *et al*., 2017).

Acetabular perforation is achieved in dinosaur clades by reduction in the extent of the ossified medial acetabular wall so there is little sutural contact between adjacent margins of the ilium, pubis and ischium. Herrerasaurids (Fig. 8B) possess a 'partially perforate' acetabulum with much of the medial acetabular wall ossified (Reig, 1963; Hunt *et al*., 1998; Langer, 2004; Alcober & Martínez, 2010; Baron & Williams, 2018; Pacheco *et al*., 2019), and many theropods show a similar morphology (Nesbitt *et al*., 2009a; Marsh & Rowe, 2020). Prionodontian ornithischians typically possess a perforate acetabulum, similar to that seen in *Heterodontosaurus* (Santa Luca, 1980 – Fig. 8F); however, several basal taxa show a curtain like medial wall dorsomedially – forming what might be termed a partial ilial cupola (Norman *et al*., 2004; Butler, 2005, 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 (cupola-like) walls (Langer *et al*., 1999; Ezcurra, 2010; Cabreira *et al*., 2016; Baron & Williams, 2018; Pretto *et al*., 2019; Garcia *et al*., 2019). Despite there being a well-developed wall, all these taxa retain a small unossified 'dinosaurian' fenestra at what would otherwise be the sutural junction between ilium, pubis and ischium. With silesaurians placed within Dinosauria (Fig. 2), on the ornithischian stem, the acetabular fenestra seen in more derived ornithischians could be re-interpreted as having evolved independently of the condition seen in saurischian dinosaurs. *Lagosuchus talampayensis* Romer, 1971 (Agnolín & Ezcurra, 2019) and most silesaurians (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 silesaurians 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* – Fig. 8C). This condition resembles the condition in non-dinosaurian avemetatarsalians such as *Teleocrater* (Nesbitt *et al*., 2017b) and *Ixalerpeton* Cabreira *et al*., 2016 – Fig. 8A).

The inference that can be drawn from these observations is that the common ancestor of dinosaurs possessed a fully ossified acetabulum and that the subsequent fenestration of this region in saurischians and ornithischians is an 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. 8E) and *Scelidosaurus* (Norman, 2020b).

Pubic retroversion. The oblique, posteroventral orientation of the pubic shaft appears close to, or coincident with, the shift toward an overtly bipedal stance in ornithischians (see Norman & Weishampel, 1991). Silesaurians, as stem ornithischians, possess a conventionally anteroventrally orientated pubis and have been regarded variously as either bipedal or quadrupedal (compare Figs 5A, 10). The elongation of the preacetabular process of the ilium similarly appears to coincide with pubic retroversion in all known prionodontian ornithischians, as noted by Charig (1972). It is unfortunate that the details of the pelvic anatomy of silesaurians, that are placed proximate to definitive prionodontians (such as *Kwanasaurus*), are currently unclear. It is also the case that simultaneous changes seem to have occured in hindlimb/forelimb and femur/tibia ratios, as well as the development of a pendent fourth trochanter, during the transition between stem-lineage ornithischian and prionodontian (see below).

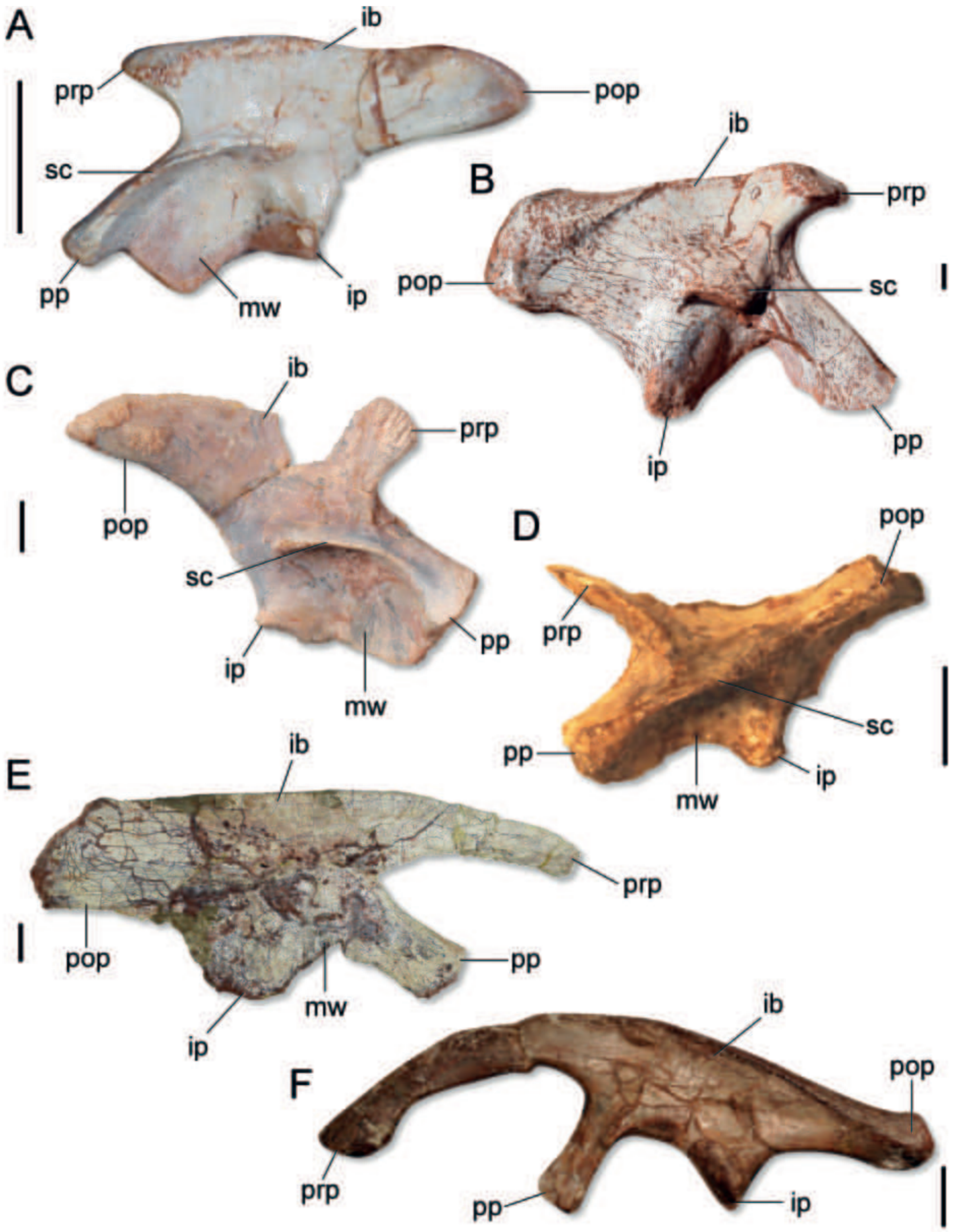

Fig. 8: Ilia of selected ornithodirans: A) Left ilium of the lagerpetid *Ixalerpeton polesinensis* (ULBRA-PVT059) in lateral view. B) Right ilium of the herrerasaurid *Gnathovorax cabreirai* (CAPPA/UFSM 0009) in lateral view. C) Right ilium of the silesaurian ornithischian *Asilisaurus kongwe* (NMT RB159; modified from Nesbitt *et al*., 2020) in lateral view. D) Left ilium of the derived silesaurian *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, preacetabular process; sc, supracetabular crest. Scale bars = 10 mm. (Norman *et al*., 2022: fig. 11)

Hind limb anatomy (Fig. 9)
In contrast to prionodontian ornithischians, silesaurians lack a pendent (i.e. projecting in a distal direction from the femoral shaft and finger-shaped) fourth trochanter (Fig. 9A-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, 2016b; Marsh & Parker, 2020; Nesbitt *et al*., 2019). In *Asilisaurus kongwe* (Fig. 9B) the fourth trochanter

Fig. 9: 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.*, 2020) 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. (Norman *et al*., 2022: fig. 10)

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; Nesbitt, 2011; Cabreira *et al.*, 2011, 2016; Langer *et al.*, 2010; Martínez *et al.*, 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, 2016a, b; Müller & Dias-da-Silva, 2019; Nesbitt *et al.*, 2019). Griffin & Nesbitt (2016a) 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 silesaurians *within* Dinosauria. In the context of the present topology it is interesting to note that *Sacisaurus* (Fig. 9C, 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. 9E, F).

Silesaurians 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 silesaurians, the fourth trochanter forms a low mound or crest that is proximodistally symmetric when considered in medial and lateral view. By comparison, even in the femora of the earliest diverging members of Prionodontia, for example *Eocursor* (Fig. 9E), *Lesothosaurus* (Fig. 9F) and *Scelidosaurus* (Norman, 2020b: fig. 79) the fourth trochanter is well developed, asymmetric, anteroposteriorly narrow and pendent. In later diverging prionodontians the degree to which the fourth trochanter is angled with respect to the femoral shaft and its proximodistal length becomes even greater (Barrett *et al.*, 2005; Butler *et al.*, 2010; 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; Galton, 2014).

The new topology offers some insight concerning the evolution of the fourth trochanter within the prionodontian lineage. *Laquintasaura* (Figs 2, 5B) is the most basal prionodontian and possesses a fourth trochanter that is more transversely expanded than in any early diverging prionodontian. Moreover, the distal portion of its trochanter is not pendent (Barrett *et al.*, 2014: fig. 1). Given the position that *Laquintasaura* occupies in our tree (Fig. 2), this fourth trochanter morphology can plausibly be interpreted as ‘transitional’ between the low mounded/crested form observed in silesaurians and the pendent morphology seen in all currently known early prionodontians.

This structural pathway 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. The possession of an asymmetrical 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 absent in, for example, specimens of *Dromomeron* Irmis *et al.*, 2007 (Nesbitt *et al.*, 2009a) and *Ixalerpeton polesinensis* Cabreira *et al.*, 2016 as well as early diverging members of the Avemetatarsalia such as *Teleocrater rhadinus* Nesbitt *et al.*, 2017b. In most early saurischians (Fig. 9D), 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 prionodontians.

With silesaurians recovered as stem-lineage ornithischians the status 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. 9D) and ornithischian clades (Fig. 9E, F). 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), treat the distinguishable conditions in the ornithischians and saurischians that possess asymmetric trochanters as homologous, despite the clear differences in the overall shape of this trochanter between the ornithischians and saurischians outlined here.

If the asymmetry of the fourth trochanter seen in prionodontian ornithischians (Fig. 9E, F) and saurischians (Fig. 9D) was truly acquired independently, trochanteric asymmetry may have had a functional correlation with locomotion in early saurischians and prionodontians that did not apply in the case of stem-lineage ornithischians (silesaurians). Currently known silesaurians are rarely well-preserved postcranially and consequently have been reconstructed in bipedal and quadrupedal poses (compare Figs 5 and 10) whereas early prionodontians were predominantly bipedal. Similarly, the earliest theropod and sauropodomorph dinosaurs currently known were 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 *mm. caudifemoralis longus* and *brevis*, and therefore involved in the lever-arm mechanics associated with retraction of the hind limb (Hutchinson, 2004; Maidment & Barrett, 2014).

Looking also at the ratio of the lengths of tibia to the femur in known silesaur and non-silesaurian ornithischians, there is a difference: in *some* silesaurians there is evidence that the femur and tibia are roughly equivalent in length, or the femur is a little longer (DZIK, 2003 – see Fig. 10 – but compare with Fig. 5A). Early prionodontians generally possess tibiae that are substantially longer than their femora – see Fig. 5B, C (Santa Luca, 1980; Colbert, 1981; Baron *et al*., 2017c – but note the exception provided by *Scelidosaurus* Norman, 2020b). Many early saurischians demonstrate a similar relative elongation of the tibia with respect to the femur (Martínez *et al*., 2011; Cabreira *et al*., 2016). As with 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). Our analysis *suggests* (but only equivocally) that changes in hind limb segment proportions might have arisen independently in the ornithischian and saurischian lineages, linked with an independent acquisition of bipedality. However, more complete skeletal remains associated with silesaurians are needed before this speculation can be substantiated.

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: fig. 82) reflects the adoption of a parasagittal gait with uni-axial hinge-like extension-flexure at the knee joint (and ankle). This feature, or more importantly a ‘transitional’ morphological stage, is not seen in any of the currently known stem-lineage ornithischians proximate to Prionodontia. Nor is the reduction of the fibula with respect to the tibia (linked to a shift away from torsion between the two shin bones during limb excursions).

Summary. Given these apparently coincident changes in morphology (and implied function), the presence of silesaurians on the stem leading to Prionodontia (Fig. 2) offers new insights into the order, timing and method of acquisition of key components of the derived ornithischian (prionodontian) bauplan. These interpretations (contingent upon acceptance of the topology proposed herein) pose questions concerning several character-states that have been regarded as uniquely dinosaurian. We anticipate that fresh discoveries will fill some of the anatomical gaps in our understanding of the anatomo-functional changes that occurred during the evolutionary history of Ornithischia and permit a detailed evaluation of how and when some key anatomical features were acquired within emerging dinosaur lineages.

DISCUSSION

Prionodontia: a new dinosaurian subclade

The re-evaluation of a variety of silesaurian taxa (previously considered to be non-dinosaur 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

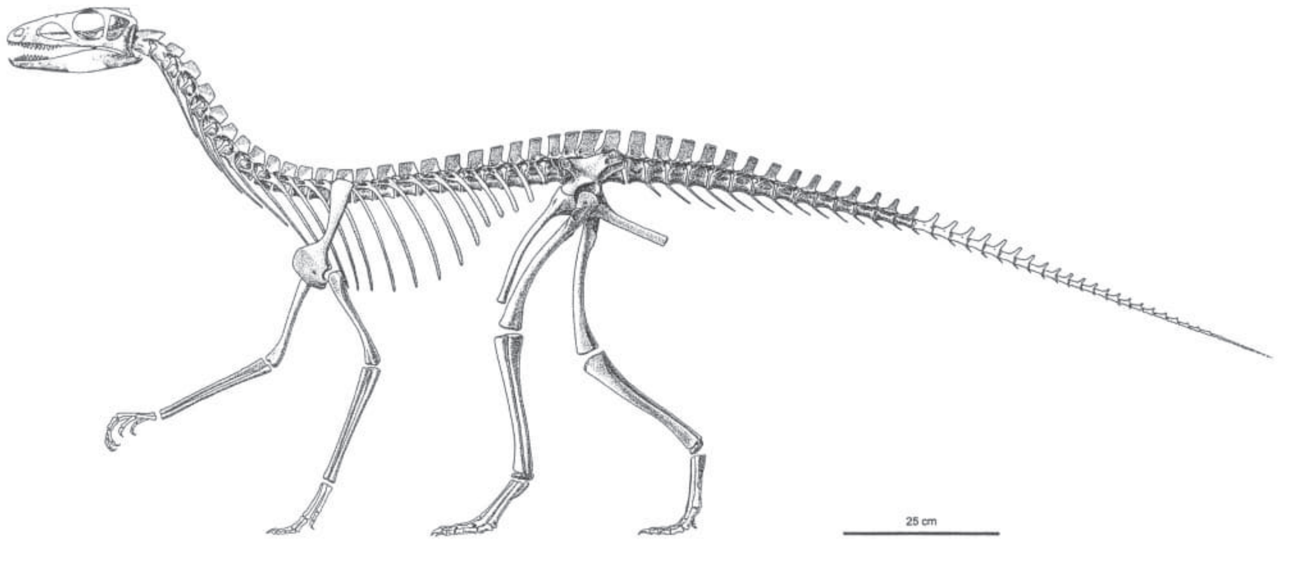

Fig. 10: The reconstructed skeleton and pose of *Silesaurus opolensis* (after Dzik, 2003). Contrast this with the original reconstruction and pose of the silesaurian ornithischian *Sacisaurus agudoensis* shown in Fig. 5A.

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 recognised sub-clade.

Hypotheses of relationship: problems

There are three contrasting hypotheses concerning the fundamental patterns of relationship between what are understood to be the principal dinosaurian clades (Fig. 1A-C): **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, b; Langer *et al*., 2017; Parry *et al*., 2017) therefore ambiguity persists. The lack of resolution highlights weaknesses in the cladistic parsimony-based approach to the naming and scoring of anatomical characters, when applied to evolutionarily rapid diversification events (such as the origin and early phases of diversification among Dinosauria during the Late Triassic). 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 hypothesis of relationship (or in Seeley's case, simply the convenient grouping of unrelated taxa) were established on the basis of a small number of anatomically derived members of these clades (Seeley, 1888). In contrast, recent decades of research have revealed early diverging members of these lineages, e.g. *Eodromaeus murphi* Martínez *et al*., 2011; *Buriolestes schultzi* Cabreira *et al*., 2016; *Gnathovorax cabreirai* Pacheco *et al*., 2019, as well as several taxa that challenge our understanding of the dinosauromorph-dinosaur boundary, e.g. *Silesaurus opolensis* Dzik, 2003; *Asilisaurus kongwe* Nesbitt *et al*., 2010; *Ixalerpeton polesinensis* Cabreira *et al*., 2016 (but see Ezcurra *et al*., 2020). The synapomorphies that typify the major clades are not clearly present in these animals and some of them such as *Buriolestes* (Cabreira *et al*., 2016) present a contradictory mix of traits (Müller & Dias-da-Silva, 2019).

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 article we examine the implications of the results an analysis that challenges orthodoxy. Unfortunately at present early dinosaur relationships are mainly constructed (or influenced) by data collected from a number of poorly preserved and 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.

CONCLUSIONS

The addition of conventionally ornithischian taxa to the dataset developed by Müller & Garcia (2020a) generated a topology that challenged the evolutionary history associated with the diversification of early ornithischian dinosaurs that in all probability commenced in the Early Carnian.

The analysis supported a hypothesis of early dinosaur relationships that recovers a paraphyletic cluster of silesaurian taxa on the stem of an inclusively defined clade **Ornithischia**. Anatomical changes identified among taxa on the stem of Ornithischia led, ultimately, to the appearance of a discrete subclade of ornithischians that has had to be recognised by resuscitating the name **Prionodontia**. Prionodontians (formerly recognised as members of Seeley's original grouping Ornithischia) are first identified reliably in the fossil record during the Hettangian (the earliest Stage of the Jurassic). The topology forces alterations to be made to the taxonomic content and names of some key clades. The changes were made with the intention of minimising 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 ornithischian taxa to those seen in more derived (prionodontian) ornithischians had not been explored prior to this analysis. Consideration of this analysis provokes novel insights (and questions) concerning the (apparent) step-wise 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 and mode of initial diversification of the earliest dinosaurs.

In addition to the anatomo-functional implications that derive from the new ornithischian topology, the phylogenetics necessitates a consideration of the possibility that some of the 'key' features regarded as unique to Dinosauria (notably those found in the pelvis and hind limb) might have been acquired independently. Such ideas need to be subjected to further critical assessment following (ideally) the discovery of new and better-preserved taxa. The work presented here represents no more than a tentative step toward clarification of the tempo and mode of dinosaur origins and early phases of their evolutionary history.

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