

**THE SYSTEMATIC RELATIONSHIPS,
PHYSIOLOGY AND LIFE HABITS OF THE
'HYPHSILOPHODONTID' DINOSAURS**

by

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Publications

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Additionally, during the course of my PhD, I have been involved in several research papers not directly related to the research topics investigated in this thesis:

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Abstract

The ‘hypsilophodontids’ are an informal group of ornithischian dinosaurs that share a similar *bauplan*: being bipedal, small to medium-bodied (~1–2 m), and relatively conservative in their morphology. These dinosaurs are known from Antarctica, Asia, Australasia, Europe, North America and South America, and have a temporal range from the Middle Jurassic to the latest Cretaceous. The phylogenetic relationships of the ‘hypsilophodontids’ remains one of the key questions in ornithischian dinosaur research, with recent phylogenetic studies recovering these taxa in one of two highly conflicting positions: (1) primarily within Cerapoda (Ornithopoda+Marginocephalia), as a paraphyletic assemblage of early ornithopods; and (2) primarily outside of Cerapoda, within the clade Thescelosauridae. This uncertainty has impeded our understanding of ornithischian evolutionary history and consequently, our interpretation of some of the major transitions in these groups, such as the acquisitions of obligate high-fibre herbivory and quadrupedality.

In this thesis, I use multiple palaeontological approaches to improve our understanding of non-cerapodan neornithischians and early-diverging ornithopods (‘hypsilophodontids’). Three recent phylogenetic studies that have recovered contrasting placements for the ‘hypsilophodontids’ were subject to in-depth character and taxon manipulation, with the aim of identifying the cause of these conflicting topologies. Results find that matrices which originally recovered the ‘hypsilophodontids’ within Cerapoda were comparably more stable in response to this manipulation, perhaps suggesting these relationships are more robust. These three data matrices were further used to evaluate the morphological disparity within ‘hypsilophodontids’, finding that

this group represents a diverse assortment of taxa. Disparity-through-time results show that the pelvic girdle and hind limb morphologies of ornithischians were comparatively diverse in the Middle Jurassic, indicating that important locomotory adaptations were evolving at this time. The long bone histology of the namesake ‘hypsilophodontid’, *Hypsilophodon foxii*, was examined to give insight into the growth patterns of these dinosaurs. Five histological ontogenetic stages were distinguished; however no unambiguous lines of arrested growth (LAGs) were recovered, suggesting *Hypsilophodon foxii* maintained uninterrupted growth even during periods of seasonal stress. The presence or absence of regular developing LAGs in other ‘hypsilophodontids’ implies that two distinct growth strategies were adopted by these taxa. Lastly, digital techniques were used to investigate the neuroanatomy and tooth replacement cycle of a new genus of ornithopod from Antarctica. Endocranial reconstructions reveal a large floccular lobe that extends considerably through the anterior canal of the endosseous labyrinth, suggesting this animal had enhanced gaze stabilisation and was capable of rapid eye, head and neck movements. Digital segmentation of the dentary provides an in-depth assessment of an alternative ornithopod dental condition, compared to the more widely researched dental batteries of hadrosaurian ornithopods.

This thesis provides a significant contribution to our understanding of the ‘hypsilophodontids’, showing that these dinosaurs exhibited disparate morphologies, neuroanatomies and even distinct patterns of growth. The phylogenetic affinities of the ‘hypsilophodontids’ remain contentious, but I hope the recommendations suggested in this thesis will aid future studies looking to resolve these relationships.

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Chapter 1

INTRODUCTION

1.1. The ‘hypsilophodontids’

The two main sub-clades of Dinosauria, Ornithischia (“bird-hipped”) and Saurischia (“lizard-hipped”), were erected by Seeley (1888), based primarily on differences observed in the pelvic anatomy. These groups remain widely accepted over a century later, although dinosaur intrarelationships have been the subject of recent debate (e.g. Baron *et al.* 2017b; Langer *et al.* 2017). Within Ornithischia, five main clades are traditionally recognised — Ankylosauria, Stegosauria, Ceratopsia, Pachycephalosauria and Ornithopoda — each of which exhibits highly distinctive morphologies. The interrelationships between these five clades have been largely stable within the literature over the last two decades (Butler *et al.* 2008; Boyd 2015; Han *et al.* 2018): Ankylosauria and Stegosauria are united within the early-diverging clade Thyreophora; Ceratopsia and Pachycephalosauria are grouped together within Marginocephalia; and Ornithopoda + Marginocephalia together form the clade Cerapoda (Figure 1.1). However, the phylogenetic positions of many ornithischians that either fall outside, or are potentially early-diverging members, of these five clades (e.g. heterodontosaurids, ‘hypsilophodontids’), remain highly uncertain and fluid between analyses (Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021). These taxa generally share a similar bauplan, being small to medium-bodied (~1–2 m), bipedal, and “conservative” in

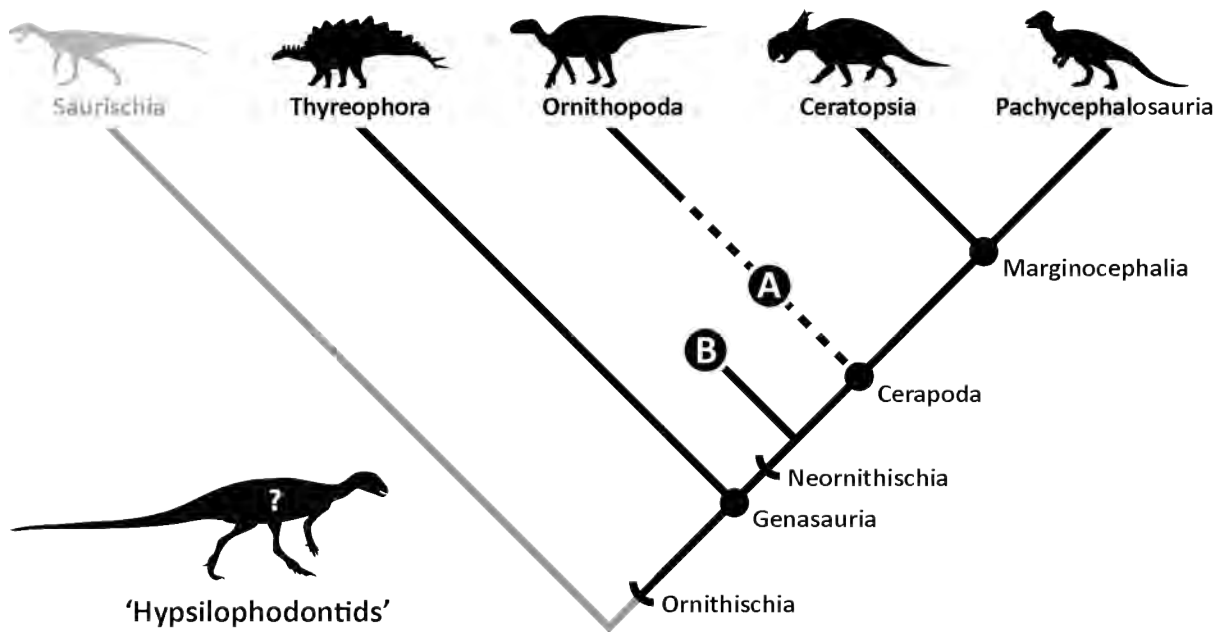


Figure 1.1. Simplified cladogram of ornithischian relationships showing the two positions where the majority of ‘hypsilophodontids’ have been recovered in recent independent phylogenetic analyses: **A**, as early-diverging ornithopods (e.g. Butler *et al.* 2008; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018); and **B**, within the non-cerapodan neornithischian clade, Thescelosauridae (e.g. Boyd 2015; Herne *et al.* 2019). Silhouettes from <http://phylopic.org>: S. Hartman, I. Reid, E. Willoughby.

their morphologies, lacking the ornamentation and elaborate features often found in derived ornithischian groups (e.g. body armour, horns, frills, crests; Norman *et al.* 2004).

Historically, taxa that shared these bauplans and were of uncertain phylogenetic affinities were frequently referred to the family Hypsilophodontidae (e.g. Sternberg 1940; Thulborn 1971; Galton 1972; Rich & Rich 1989), which was originally erected by Dollo (1882) to include ornithopods closely related to the British dinosaur

Hypsilophodon foxii (Weishampel & Heinrich 1992). The comparatively unspecialised morphologies of the ‘hypsilophodontids’ led Thulborn (1971) to hypothesise that these taxa represented the ‘basal stock’ from which several major ornithischian groups (e.g. ceratopsians, pachycephalosaurians, iguanodontians) may have descended. Galton (1972, 1978) generally agreed with the main themes put forward in Thulborn (1971), but proposed that taxa he considered to be the basal-most ornithischians (e.g. *Echinodon*, *Lesothosaurus*, *Nanosaurus*), be removed from Hypsilophodontidae to form the new family Fabrosauridae (Galton 1972).

The introduction of cladistic methods saw the publication of numerous ornithischian phylogenies within a relatively short period of time (e.g. Milner & Norman 1984; Norman 1984; Sereno 1984; Cooper 1985; Maryanska & Osmólska 1985; Sereno 1986). In those analyses where Hypsilophodontidae, or a ‘hypsilophodontid’ (e.g. *Hypsilophodon*), were included, these taxonomic units were recovered within Ornithopoda (Norman 1984; Sereno 1984; Cooper 1985; Sereno 1986), often in a sister-group relationship to the iguanodontians (e.g. Sereno 1986; =Euornithopoda sensu Weishampel & Heinrich 1992). Additionally, several of these studies highlighted anatomical differences between *Dryosaurus* and *Valdosaurus* (which were both assigned to Hypsilophodontidae by Galton 1977, 1981, 1983; Galton & Taquet 1982), and other ‘hypsilophodontids’ (Milner & Norman 1984; Norman 1984; Sereno 1986). Milner & Norman (1984) proposed that *Dryosaurus* and *Valdosaurus* be instead included in a separate family, which the authors named Dryosauridae.

At this time, a monophyletic Hypsilophodontidae was widely accepted within the literature (e.g. Norman 1984; Sereno 1984; Sereno 1986; Sues & Norman 1990; Weishampel & Heinrich 1992), however this would change towards the turn of the

century, with almost all subsequent studies finding little support for their monophyly (e.g. Scheetz 1999; Buchholz 2002; Weishampel *et al.* 2003; Liu 2004; Butler 2005; Butler *et al.* 2008; Boyd *et al.* 2009; Brown *et al.* 2011; Boyd 2015; Dieudonné *et al.* 2016; Han *et al.* 2018; although see Spencer 2007). The lack of support for Hypsilophodontidae brought into question the taxonomy and relationships of taxa traditionally assigned to this group, with most authors instead referring to them as ‘basal ornithopods’ or ‘basal euornithopods’ (e.g. Scheetz 1998; Weishampel *et al.* 2003; Norman *et al.* 2004).

Butler *et al.* (2008) tested the phylogenetic framework of Ornithischia by focusing on the relationships of early-diverging members of the major ornithischian clades (Figure 1.2a). This analysis included 11 ‘hypsilophodontids’, which – at the time – was the most to be ever included within a single dataset: however, up to five were removed from these analyses *a posteriori* to improve tree resolution (Butler *et al.* 2008). These authors recovered most of the ‘hypsilophodontids’ as a paraphyletic assemblage of early-diverging ornithopods (e.g. Figure 1.1, A); however, *Agilisaurus*, *Hexinlusaurus* (formerly *Yandusaurus multidentis*, Barrett *et al.* 2005) and *Othnielia* (now referred to as *Nanosaurus*: Carpenter & Galton 2018) were recovered outside of Cerapoda as basal neornithischians (Butler *et al.* 2008; Figure 1.2a), in agreement with findings from several other studies around this time (Lui 2004; Barrett *et al.* 2005; Butler 2005; and subsequent studies, e.g. Makovicky *et al.* 2011; Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021). In the following year, a study by Boyd *et al.* (2009) revising the taxonomy of the *Thescelosaurus*, recovered significantly different results from those of Butler *et al.* (2008) and all prior analyses (e.g. Scheetz 1999; Weishampel *et al.* 2003; Norman *et al.* 2004), finding most ‘hypsilophodontids’ to

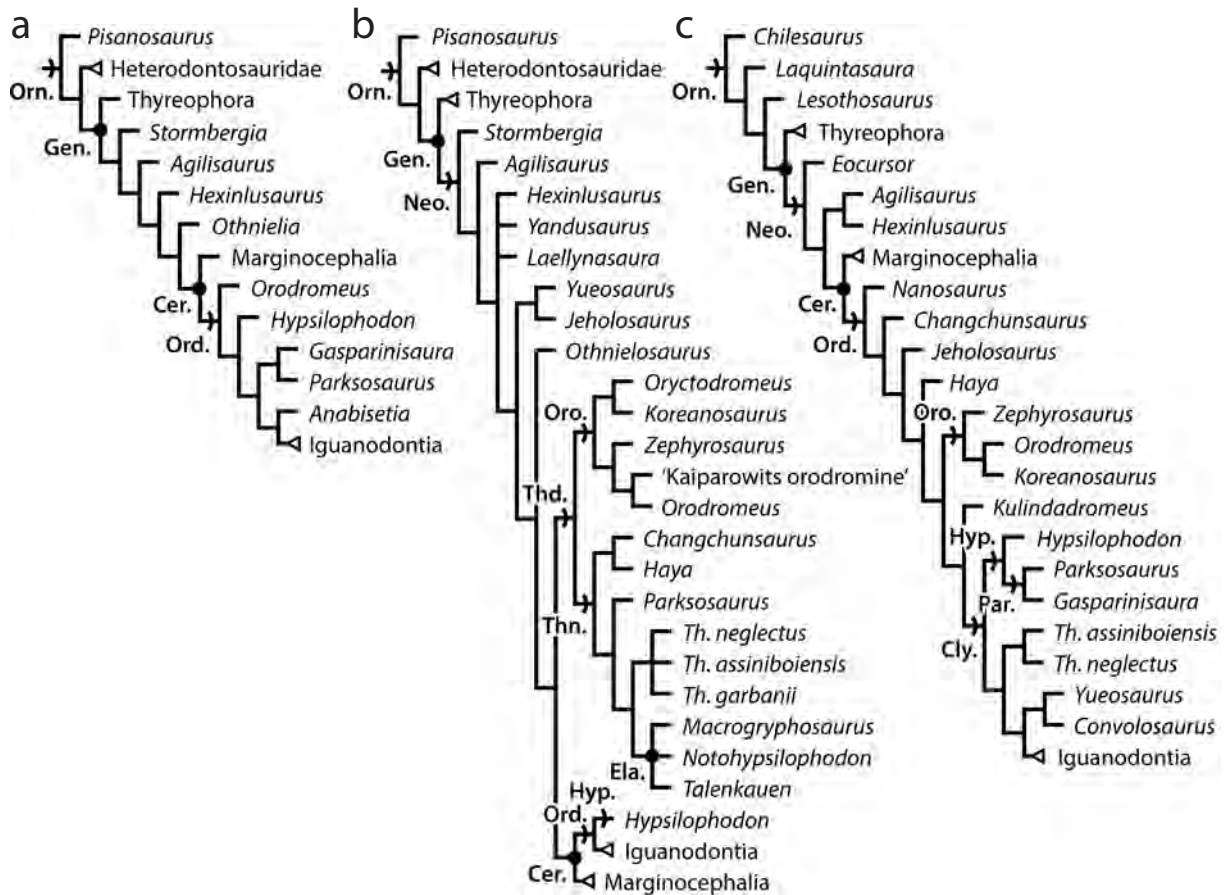


Figure 1.2. Simplified tree topologies from phylogenetic analyses of ornithischian relationships: **a**, Butler *et al.* (2008); **b**, Boyd (2015); **c**, Dieudonné *et al.* (2021). **Abbreviations:** **Cer.**, Cerapoda; **Cly.**, Clypeodonta; **Ela.**, Elasmaria; **Gen.**, Genasauria; **Hyp.**, Hypsilophodontidae; **Igu.**, Iguanodontia; **Neo.**, Neornithischia; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Oro.**, Orodrominae; **Par.**, Parksosauridae; **Th.**, *Thescelosaurus*; **Thd.**, Thescelosauridae; **Thn.**, Thescelosaurinae.

nest within a monophyletic clade, exclusive of *Hypsilophodon*. This new clade included a dichotomy at its base, separating *Orodromeus*, *Oryctodromeus* and *Zephyrosaurus* (Orodrominae; Brown *et al.* 2013b) from the Maastrichtian-aged taxa *Parksosaurus* and *Thescelosaurus* (Thescelosaurinae; Brown & Druckenmiller 2011). The

clade encompassing these two groups was later referred to as Thescelosauridae Sternberg, 1937 (see Brown *et al.* 2013b), but its placement relative to Cerapoda remained somewhat ambiguous due to the absence of marginocephalian taxa in the datasets of Boyd *et al.* (2009) and, later, Brown *et al.* (2013b).

In what was the largest ornithischian dataset compiled at the time, Boyd (2015) tested the relationships of the ‘hypsilophodontids’ relative to cerapodans (Figure 1.2b). As in previous analyses (Boyd *et al.* 2009; Brown *et al.* 2013b), Boyd (2015) recovered most of the ‘hypsilophodontids’ within Thescelosauridae, exclusive of *Hypsilophodon*. However, importantly, Boyd (2015) recovered Thescelosauridae in a sister group relationship with Cerapoda (Figure 1.1, B), leaving *Hypsilophodon* as the only ‘hypsilophodontid’ remaining within Ornithopoda (Figure 1.2b). Furthermore, as *H. foxii* was the internal specifier of Hypsilophodontidae (Dollo 1882; Sereno 2005), Boyd (2015) reported *Hypsilophodon* as the sole member of the clade (Figure 1.2b, ‘Hyp.’). Similar topologies were later recovered by Madzia *et al.* (2018) using a modified version of the Boyd (2015) matrix, although in this study, *Hypsilophodon* was recovered outside Ornithopoda, as the sister taxon of Cerapoda.

Subsequent phylogenetic analyses have not recovered tree topologies congruent with Boyd (2015) and Madzia *et al.* (2018), except with the use of implied character weighting (Herne *et al.* 2019). Most recently, Dieudonné *et al.* (2021) conducted a large-scale analysis of ornithischian relationships, with the aim of resolving cerapodan relationships (Figure 1.2c). The authors found results congruent with those of Butler *et al.* (2008) and a more recent analysis by Han *et al.* (2018; which aimed to clarify the positions of the basal ceratopsians *Yinlong* and *Psittacosaurus*), recovering most ‘hypsilophodontids’ within Cerapoda as early-diverging ornithopods (Figure

1.1, A; Figure 1.2c). Additionally, this study was the first in recent decades to recover a monophyletic Hypsilophodontidae that included more taxa than just *Hypsilophodon*, which also included *Gasparinisaura* and *Parksosaurus* (Figure 1.2c, ‘Hyp.’).

These recent cladistic analyses have provided two highly incongruent hypotheses concerning the phylogenetic position of ‘hypsilophodontids’, with studies finding these taxa either: (1) mainly within Cerapoda (Marginocephalia+Ornithopoda) as early-diverging ornithopods (Figure 1.1, A: e.g. Butler *et al.* 2008; Han *et al.* 2018; Dieudonné *et al.* 2021); or (2) primarily as non-cerapodan neornithischians, within the clade Thescelosauridae (Figure 1.1, B: e.g. Boyd 2015). There is currently no consensus within the literature as to which hypothesis is best-supported.

1.2. Chapter summary and aims

This thesis focuses on non-cerapodan neornithischians and early-diverging ornithopods that share the traditional ‘hypsilophodontid’ bauplan. These taxa are known from Antarctica, Asia, Australasia, Europe, North America and South America (Figure 1.3), and have a temporal range extending from the Middle Jurassic to the latest Cretaceous (see Appendices A1.1 for a summary of focal taxa). Here, I use multiple approaches commonly applied in palaeontological studies to investigate the palaeobiology and relationships of these enigmatic dinosaurs.

The phylogenetic relationships of taxa traditionally referred to as ‘hypsilophodontids’ remains enigmatic, with recent phylogenetic analyses recovering the taxa primarily within one of two conflicting placements: (1) primarily within Cerapoda (Ornithopoda+Marginocephalia), as a paraphyletic assemblage of early ornithopods;

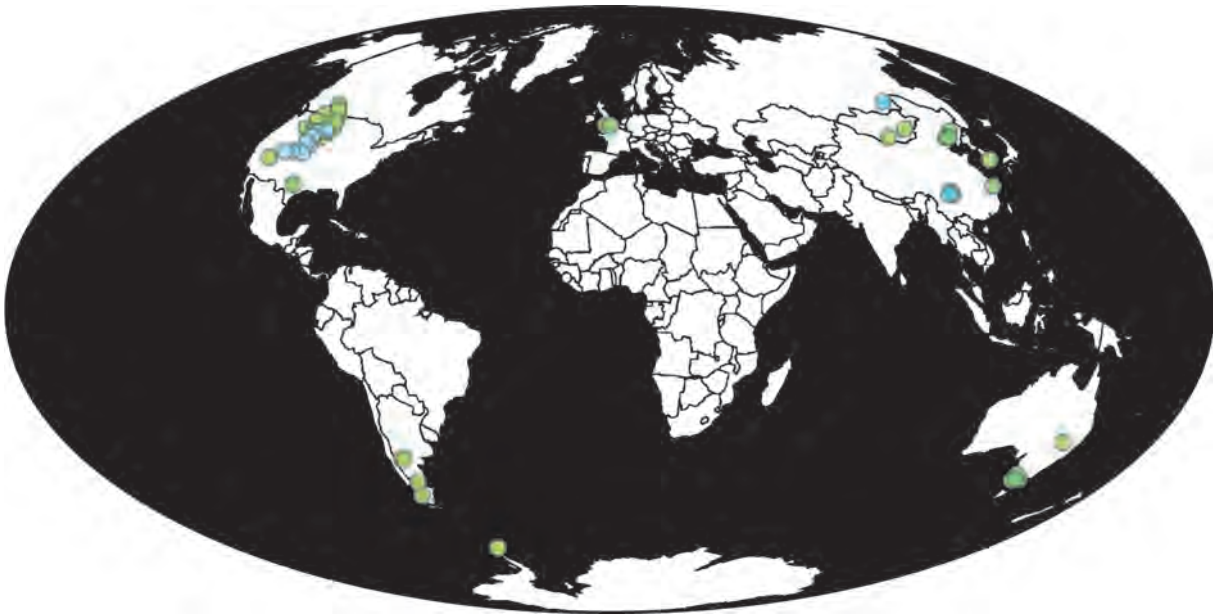


Figure 1.3. Occurrence data for taxa of interest in this thesis. Data retrieved from the Paleobiology Database (paleobiodb.org; accessed: 20/08/23). Colour code follows the International Chronostratigraphic Chart (stratigraphy.org, v 2023/06): Jurassic (blue); Cretaceous (green).

and (2) primarily outside of Cerapoda, within the clade Thescelosauridae. In Chapter 2, I compare three recent neornithischian data matrices, which have recovered topologies congruent with one of these placements, to test how each responds to manipulation of taxa and characters. The aim of this study is to provide insight for future assessments of neornithischian relationships.

The ‘hypsilophodontids’ are traditionally considered to be conservative or unspecialised in their morphologies; however, their phenotypic diversity has yet to be formally examined. In Chapter 3, I use character-based methods to assess changes in the morphological disparity of ornithischian dinosaurs through time, as well as the

morphospace distribution of the ‘hypsilophodontids’ relative to other ornithischian clades. The main aim of this chapter is to determine the phenotypic diversity of the ‘hypsilophodontids’, and determine whether patterns of evolution differ throughout the skeleton.

Hypsilophodon foxii is a small bipedal ornithopod from the Early Cretaceous of the Isle of Wight, UK. To date, dozens of partially complete *H. foxii* specimens have been recovered from the ‘*Hypsilophodon* Bed’, a kilometre-long exposure along the southwest coast of the island. However, relatively little is known about the taphonomy of the bed. In Chapter 4, I use histological methods to determine the ontogenetic distribution of individuals within the *Hypsilophodon* Bed. This research aims to investigate the growth patterns and strategies of *Hypsilophodon* and other neornithischian dinosaurs.

In 1989, the partial skeleton of a new genus of ornithopod dinosaur was discovered during a British Antarctic Survey expedition to the James Ross Island area, about 30 km east of the Antarctic Peninsula. The material was dated as Late Cretaceous in age, and included a partial braincase and near-complete dentaries and maxillae. In Chapter 5, I use micro-computed tomographic (μ CT) methods to describe the endocranial anatomy, inner ear anatomy, tooth replacement cycle and dentary neurovasculature of this new ornithopod. The primary aim of this study is to investigate the sensory capabilities and life habits of this Antarctic dinosaur.

1.3. Institutional abbreviations

NHMUK, Natural History Museum, London, UK

IWCMS, Isle of Wight Council Heritage Collections, Dinosaur Isle Museum, Sand-
own, UK

The following chapter has been published as Brown, E. E., Butler, R. J., Barrett, P. M. and Maidment, S. C. 2022. Assessing conflict between early neornithischian tree topologies. *Journal of Systematic Palaeontology*, **19**, 1183–1206.

Chapter 2

ASSESSING CONFLICT BETWEEN EARLY NEORNITHISCHIAN TREE TOPOLOGIES

The phylogenetic relationships of the species commonly referred to as ‘hypsilophodontids’ remain one of the key questions in ornithischian dinosaur research, having profound implications for understanding the origin, evolution and taxonomical compositions of several more recently evolved neornithischian clades. Recent phylogenetic analyses have recovered two conflicting placements for these taxa: (1) primarily within Cerapoda (Ornithopoda+Marginocephalia), as a paraphyletic assemblage of early ornithopods; and (2) primarily outside of Cerapoda, within the clade Thescelosauridae. Here I assess three recent independent neornithischian phylogenetic studies that have recovered topologies congruent with one of these placements. I compare the compositions of these data matrices and test how each of them responds to manipulation of taxa and characters. The positions in which controversial clades are recovered is shown to be highly dependent on the sample of taxa analysed; however, taxon incompleteness or instability is not a contributing factor in altering topology. Character completeness and homoplasy is shown not to significantly alter tree topology either, although these factors can affect resolution. In one matrix investigated, femoral and dental characters are found to provide disproportionate support for the placement of key taxa outside of Cerapoda, and the exclusion of a small number of these characters results in ‘hypsilophodontids’ falling within Ornithopoda. In contrast, matrices that originally recovered ‘hypsilophodontids’ within Cerapoda are comparably more stable, with this

array of taxa remaining in a consistent position throughout all analyses. There is still much work to be done to resolve these relationships, but this study provides several suggestions for future analyses with the aim of resolving areas of conflict within the neornithischian tree.

2.1. Introduction

2.1.1. Neornithischia

Neornithischians were a diverse and highly successful clade of ornithischian dinosaurs with a fossil record extending from the Middle Jurassic to the end of the Maastrichtian (Sereno 1999; Butler *et al.* 2008; Boyd 2015; Baron *et al.* 2017a; Dieudonné *et al.* 2021). Throughout their evolutionary history, neornithischians gained a worldwide distribution and gave rise to three of the five main ornithischian clades: Ceratopsia, Pachycephalosauria and Iguanodontia (Norman 1984; Cooper 1985; Maryanska & Osmolska 1985; Sereno 1999; Butler *et al.* 2008; Boyd 2015). Although the relationships of these three clades to each other are largely accepted (with ceratopsians and pachycephalosaurs usually united in Marginocephalia, which in turn is the sister clade of Ornithopoda), the relationships of neornithischian taxa that fall outside, or close to the roots, of these main groups are poorly resolved. These taxa tend to be bipedal, small to medium-bodied, and lack the distinctive and often ornate morphological features (e.g. horns, crests, frills) seen in later branching cerapodan clades (Norman *et al.* 2004).

Traditionally, taxa that shared this bauplan and were of uncertain phylogenetic affinities were often assigned to ‘Hypsilophodontidae’ (e.g. Thulborn 1971; Galton 1973), which became a diverse taxonomical ‘waste-basket’ with wide temporal and spa-

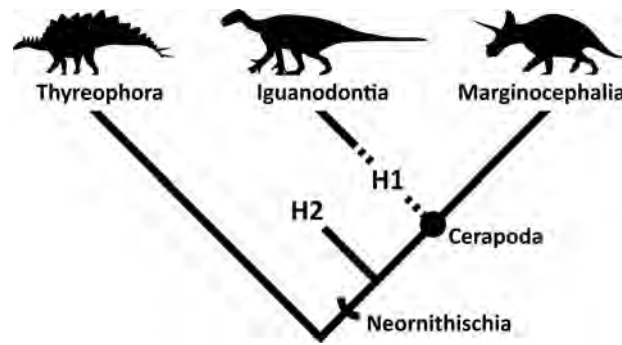


Figure 2.1. Simplified cladogram showing the two positions where ‘hypsilophodontids’ have been recovered in recent independent phylogenetic analyses: H1, hypothesis 1 (e.g. Butler *et al.* 2008; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018); H2, hypothesis 2 (e.g. Boyd 2015; Herne *et al.* 2019). Silhouettes from <http://phylopic.org>; S. Hartman.

tial distributions. Although modern cladistic analyses generally agree that this group is para- or polyphyletic (e.g. Scheetz 1999; Sereno 1999; Buchholz 2002; Butler *et al.* 2008; Boyd 2015), this leaves questions as to the phylogenetic placements of these ‘hypsilophodontids’ (as I will refer to them here) within Neornithischia.

The last decade saw several large-scale independent phylogenetic studies focusing on neornithischian relationships (e.g. Butler *et al.* 2011; Boyd 2015; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018). However, these analyses do not agree on the phylogenetic positions of the ‘hypsilophodontids’, generally recovering these taxa in two strongly contrasting positions, either diverging before (e.g. Boyd 2015; Madzia *et al.* 2018; Herne *et al.* 2019) or after (e.g. Sereno 1999; Buchholz 2002; Butler 2005; Butler *et al.* 2008; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018) the origins of Marginocephalia and Ornithopoda in the Middle–Late Jurassic. This lack of resolution has im-

peded our understanding of important character changes throughout the evolutionary history of neornithischians and, consequently, our interpretation of some of the major transitions seen in more deeply nested cerapodan groups, such as the acquisitions of obligate high-fibre herbivory (Barrett 2014; Mallon & Anderson 2015) and quadrupedality (Maidment & Barrett 2012a).

Here, I assess the two main current hypotheses (Figure 2.1) concerning the phylogenetic position of the ‘hypsilophodontids’: hypothesis 1 (H1), that these taxa primarily fall within Cerapoda (Marginocephalia+Ornithopoda) as early-diverging ornithopods; and hypothesis 2 (H2), that the majority are non-cerapodan neornithischians, within the clade Thescelosauridae (Orodrominae+Thescelosaurinae). I investigate how character and taxon sampling has influenced the recovery of these two contrasting hypotheses by comparing and contrasting three recent datasets compiled to examine neornithischian phylogeny, with the aim of aiding future assessments of early neornithischian relationships.

2.1.2. Previous analyses

Most large-scale studies looking at ornithischian and neornithischian relationships over the past two decades have recovered ‘hypsilophodontids’ in a position congruent with H1 (Figure 2.1), as a paraphyletic assemblage within Ornithopoda (e.g. Sereno 1999; Buchholz 2002; Butler 2005; Butler *et al.* 2008; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018), with several of the stratigraphically earliest ‘hypsilophodontids’ (e.g. *Agilisaurus*, *Hexinlusaurus*) placed outside Ornithopoda as non-cerapodan neornithischians.

Although a few older studies recovered a monophyletic ‘Hypsilophodontidae’

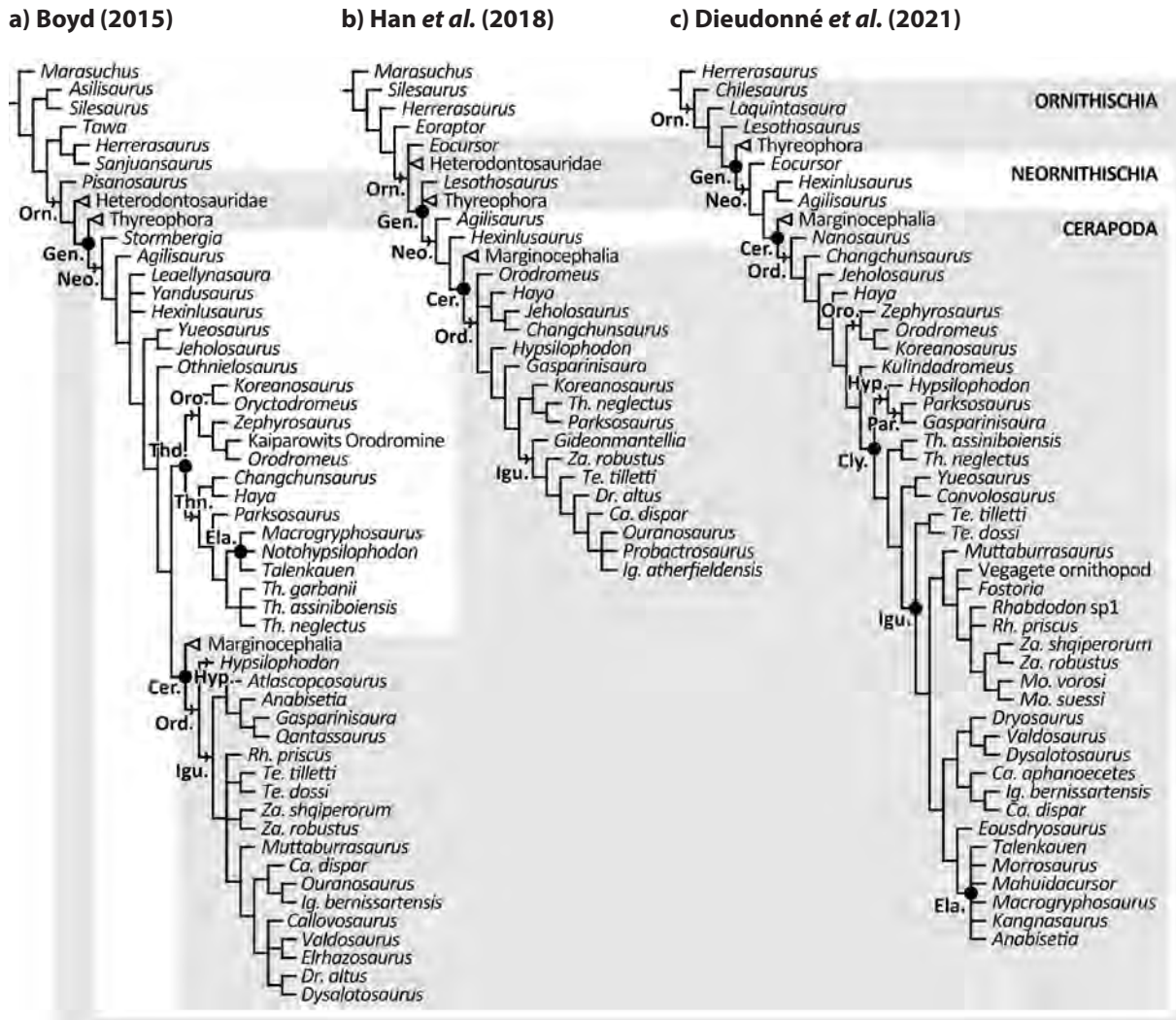


Figure 2.2. Simplified tree topologies from recent phylogenetic analyses of neornithischian relationships. **a**, strict consensus of the 36 most parsimonious trees (MPTs) generated from the matrix of Boyd (2015); **b**, reduced consensus produced by pruning eight unstable taxa from the 53,376 MPTs generated from the matrix of Han *et al.* (2018); and **c**, reduced consensus produced by pruning *Yandusaurus* from the 176 MPTs generated from the matrix of Dieudonné *et al.* (2021). See Supplemental material 4, Table A2.1 for clade definitions. **Abbreviations:** **Ca.**, *Camptosaurus*; **Cer.**, Cerapoda; **Cly.**, Clypeodonta; **Dr.**, *Dryosaurus*; **Ela.**, Elasmaria; **Gen.**, Genasauria; **Hyp.**, Hypsilophodontidae; **Ig.**, *Iguanodon*; **Igu.**, Iguanodontia; **Mo.**, *Mocholodon*;

Neo., Neornithischia; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Oro.**, Orodrominae; **Par.**, Parksosauridae; **Rh.**, *Rhabdodon*; **Te.**, *Tenontosaurus*; **Th.**, *Thescelosaurus*; **Thd.**, Thescelosauridae; **Thn.**, Thescelosaurinae; **Za.**, *Zalmoxes*. (Fig. 2.2, cont.)

(e.g. Sereno 1986; Weishampel & Heinrich 1992), a study by Boyd *et al.* (2009), revising the taxonomy of *Thescelosaurus*, was the first to recover many of these taxa as a clade, but independent of *Hypsilophodon* and other more deeply nested ornithopods. This new clade included a dichotomy at its base, separating *Orodromeus*, *Oryctodromeus* and *Zephyrosaurus* (Orodrominae; Brown *et al.* 2013b) from the Maastrichtian taxa *Parksosaurus* and *Thescelosaurus* (Thescelosaurinae; Brown & Druckenmiller 2011). The clade encompassing these two groups was later referred to as Thescelosauridae Sternberg, 1937 (see Brown *et al.* 2013b), but its placement relative to Cerapoda remained somewhat ambiguous due to the absence of marginocephalian (Ceratopsia+Pachycephalosauria) operational taxonomical units (OTUs) from the analyses of Boyd *et al.* (2009) and Brown *et al.* (2013b). Presenting the largest phylogenetic dataset of basal neornithischians compiled at the time (255 characters; 65 OTUs), Boyd (2015) recovered Thescelosauridae (incorrectly referred to as Parksosauridae in Boyd [2015]) as a sister group to Cerapoda (Figure 2.1: H2 position; Figure 2.2a). With respect to taxa usually regarded as either non-cerapodan neornithischians or ornithopod cerapodans, Boyd (2015) recovered: (1) *Stormbergia*, *Agilisaurus*, *Hexinlusaurus*, *Yandusaurus*, *Leaellynasaura*, *Yueosaurus*, *Jeholosaurus*, *Othnielosaurus* and the clade Thescelosauridae as non-cerapodan neornithischians; (2) *Koreanosaurus* as the sister-taxon to *Oryctodromeus*, within the thescelosaurid clade Orodrominae; (3) a clade

of Gondwanan elasmarians (*Macrogyphosaurus*, *Notohypsilophodon*, *Talenkauen*) outside of Cerapoda within Thescelosauridae, as the sister clade to *Thescelosaurus*; (4) *Hypsilophodon* as the only noniguanodontian ornithopod; and (5) a Gondwanan clade of early-diverging iguanodontians (*Atlascopcosaurus*, *Anabisetia*, *Gasparinisaura* and *Qantassaurus*). This matrix was later updated by Madzia *et al.* (2018), adding a further 10 OTUs and modifying character scorings for 14 OTUs. Madzia *et al.* (2018) also recovered Thescelosauridae outside of Cerapoda, but with several key differences from the results of Boyd (2015) concerning the taxa of interest: (1) *Hypsilophodon* was placed outside of Cerapoda; (2) *Changchunsaurus* and *Haya* were recovered as orodromines rather than thescelosaurines, within Thescelosauridae; and (3) Elasmaria was placed inside Cerapoda as a clade of early-branching ornithopods, inclusive of the unnamed clade of Gondwanan ornithopods recovered in Boyd (2015).

Subsequent phylogenetic analyses have not recovered the ‘hypsilophodontids’ in a position congruent with Boyd (2015) and Madzia *et al.* (2018), except with the use of implied character weighting (Herne *et al.* 2019). To date, the largest morphological dataset of neornithischian taxa (380 characters; 72 OTUs) is the study presented by Han *et al.* (2018), based on their description of the early ceratopsian *Yinlong downsi* (Figure 2.2b). This analysis recovered the ‘hypsilophodontids’ in a position congruent with H1, primarily within Ornithopoda. More specifically, among basal neornithischians and ornithopod cerapodans, Han *et al.* (2018) recovered: (1) *Agilisaurus* and *Hexinlusaurus* as the only non-cerapodan neornithischians; (2) *Haya*, *Jeholosaurus* and *Changchunsaurus* as a monophyletic group of Asian basal ornithopods (Jeholosauridae); and (3) *Koreanosaurus*, *Parksosaurus* and *Thescelosaurus* in a monophyletic group of non-iguanodontian ornithopods (?Thescelosaurinae). Most recently, Dieu-

donné *et al.* (2021) presented a new independent analysis of cerapodan relationships (342 characters; 72 OTUs) that also recovered the ‘hypsilophodontids’ within a position consistent with H1. Concerning basal neornithischians and ornithopod cerapodans, Dieudonné *et al.* (2021) recovered: (1) *Eocursor*, *Agilisaurus* and *Hexinlusaurus* as the only non-cerapodan neornithischians; (2) *Nanosaurus* as the earliest-branching ornithopod; (3) *Zephyrosaurus*, *Orodromeus* and *Koreanosaurus* as an early-branching ornithopod clade, Orodrominae; (4) Parksosauridae within a Hypsilophodontidae clade together with *Hypsilophodon*; (5) Hypsilophodontidae, *Thescelosaurus* and *Yueosaurus* + *Convolosaurus* as non-iguanodontian clypeodont ornithopods; and (6) *Elasmaria* within Iguanodontia.

Whereas matrices that produce a topology consistent with a H2 placement for the ‘hypsilophodontids’ (Boyd 2015; Madzia *et al.* 2018) seem to be the exception, recent descriptive papers of basal neornithischians, ‘hypsilophodontids’ and iguanodontians have used both H1 (e.g. Baron *et al.* 2017a; Salgado *et al.* 2017; Andrzejewski *et al.* 2019; Herne *et al.* 2018; Bell *et al.* 2019; Li *et al.* 2019; Yang *et al.* 2020) and H2 matrices (e.g. Herne *et al.* 2018; Madzia *et al.* 2018; Barta & Norell 2021), showing that both topologies are considered plausible within the literature and that there is no consensus on these relationships.

2.2. Methods

2.2.1. Data matrices

The matrices from Han *et al.* (2018) and Dieudonné *et al.* (2021) were chosen to represent hypothesis 1 (H1), while Boyd (2015) was used for hypothesis 2 (H2). While

Dieudonné *et al.* (2021) is the most recent phylogenetic analysis to recover a topology congruent with H1, this analysis is contentious because it recovered heterodontosaurids within Pachycephalosauria, in contrast to many previous studies that identified the former as the earliest diverging ornithischian clade (e.g. Butler *et al.* 2008; Boyd 2015; Han *et al.* 2018; but see Xu *et al.* [2006] for an alternative view). However, testing hypotheses concerning the phylogenetic position of heterodontosaurids is beyond the scope of this study. To ensure that the results are not influenced by the differing positions of heterodontosaurids in Boyd (2015) and Dieudonné *et al.* (2021), the data matrix from Han *et al.* (2018; which recovers heterodontosaurids as basal ornithischians, as in Boyd [2015]), was also analysed. The matrix from Han *et al.* (2018) was chosen rather than Butler *et al.* (2008), because (1) it is the largest ornithischian character matrix to date, (2) it largely builds on the characters from Butler *et al.* (2008), and (3) the phylogenetic positions of the ‘hypsilophodontids’ are more poorly resolved in Butler *et al.* (2008) than Han *et al.* (2018). The original data matrix presented in Boyd (2015) was selected to test H2 rather than the updated version of the matrix in Madzia *et al.* (2018) because the original Boyd (2015) matrix produced consensus trees with more resolved relationships for the taxa of interest. The matrix from Herne *et al.* (2019; a modified version of the Dieudonné *et al.* [2016] matrix) was not included in my analyses, despite recovering a H2 topology, because the H2 topology was only recovered using implied character weighting, which would make it an inappropriate comparator as all characters are weighted equally in the other analyses under consideration.

The data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) provide the basis for all of the analyses in this study. All three of these matrices were originally analysed using the traditional (heuristic) search option in TNT (Tree

Table 2.1. Summary of the three data matrices analysed in this study and methods originally used to analyse them. Abbreviations: H1, hypothesis 1; H2, hypothesis 2; MPTs, most parsimonious trees; OTU, operational taxonomical unit; TBR, tree bisection reconnection.

	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
No. of OTUs	65	72	72
No. of characters	255	380	342
Character weighting	Equal	Equal	Equal
No. of ordered characters	0	21	4
Tree search methods	Traditional tree search using TBR swapping algorithm with 10,000 replications, holding 10,000 trees per replication.	Traditional tree search using TBR swapping algorithm with 1,000 replications, holding 100 trees per replication. Subsequent TBR swapping of trees in RAM.	Traditional tree search using TBR swapping algorithm with 1,000 replications, holding 10 trees per replication. Subsequent TBR swapping of trees in RAM.
MPTs generated	36	53,376	176
Phylogenetic position of the ‘hypsilophodontids’	H2	H1	H1

Analysis using New Technology: v. 1.5; Goloboff & Catalano 2016). The data matrices and original methods used by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) are summarized in Table 2.1. The original tree search from Boyd (2015) produced 36 most parsimonious trees (MPTs) and a relatively well-resolved strict consensus tree (Figure 2.2a). The original tree searches from Han *et al.* (2018) and Dieudonné *et al.* (2021) produced 53,376 MPTs and 176 MPTs, respectively, both with relatively poorly resolved strict consensus trees, lacking resolution at the base of Cerapoda. Han

et al. (2018) identified eight unstable taxa (*Albalophosaurus*, *Koreaceratops*, *Laquintasaura*, *Micropachycephalosaurus*, *Pisanosaurus*, *Yandusaurus*, *Yueosaurus* and *Zephyrosaurus*) that were subsequently removed using the 'Pruned trees' function in TNT to give a well-resolved reduced strict consensus tree (Figure 2.2b). *Yandusaurus* was also identified as unstable in Dieudonné *et al.* (2021) and subsequently pruned to give a well-resolved reduced strict consensus (Figure 2.2c). The original strict consensus trees from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) are referred to hereafter as BSCT, HSCT and DSCT, respectively. Han *et al.* (2018) and Dieudonné *et al.* (2021) also produced and reported reduced consensus trees (described above), which are referred to in this study as HRSCT and DRSCT, respectively.

I performed an additional 92 phylogenetic analyses (Analyses A–K; Table 2.2) to test how character and taxon sampling may have influenced the relationships recovered by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). All taxa and character manipulation was implemented in TNT. Raw TNT files were downloaded from the supplementary material of Han *et al.* (2018) and Dieudonné *et al.* (2021). The supplement for Boyd (2015) only provides the character matrix as a .doc file, so scorings were inputted manually into Mesquite (v. 3.61, Maddison & Maddison 2019) and exported as a TNT file for this study. The TNT files from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) are included in the supplement for this study (see Supplemental material 1–3, Brown *et al.* 2022: <https://doi.org/10.6084/m9.figshare.19385540.v1>). Analyses A–K were all conducted using a traditional search algorithm in TNT, with 10,000 replications and TBR swapping algorithm (holding 100 trees per replication). Strict consensus trees were generated and reported in all analyses. In some analyses, the TNT function *prunnelsen* or *IterPCR* (Pol & Escapa 2009) was used to identify un-

Table 2.2. Summary of phylogenetic analyses conducted in this study. ‘X’ denotes the data matrix being analysed, either: B2015, Boyd (2015); H2018, Han *et al.* (2018); or, D2021, Dieudonné *et al.* (2021).

Analysis Name	Description
Analysis A.1	Excluding OTUs from Boyd (2015) and Han <i>et al.</i> (2018) that are not common in both matrices
Analysis A.2	Excluding OTUs from Boyd (2015) and Dieudonné <i>et al.</i> (2021) that are not common in both matrices
Analysis B.X.1	Excluding OTUs under 10% complete from X
Analysis B.X.2	Excluding OTUs under 20% complete from X
Analysis B.X.3	Excluding OTUs under 30% complete from X
Analysis C.X	Safe taxonomic reduction of OTUs from X
Analysis D.X	Removal of unstable OTUs from X
Analysis E.X	Unordering all characters from X
Analysis F.X.1	Excluding craniodental characters from X
Analysis F.X.2	Excluding postcranial characters from X
Analysis G.X.1	Excluding rostral characters from X
Analysis G.X.2	Excluding palatal characters from X
Analysis G.X.3	Excluding cranial roof characters from X
Analysis G.X.4	Excluding skull base characters from X
Analysis G.X.5	Excluding braincase characters from X
Analysis G.X.6	Excluding mandible characters from X
Analysis G.X.7	Excluding dentition characters from X
Analysis G.X.8	Excluding vertebral column & rib characters from X
Analysis G.X.9	Excluding pectoral girdle & sternum characters from X
Analysis G.X.10	Excluding forelimb characters from X
Analysis G.X.11	Excluding pelvic girdle characters from X
Analysis G.X.12	Excluding hind limb characters from X
Analysis H.X	Excluding the most character-rich skeletal element from X
Analysis I.X.1	Implied character weighting $k=1$ of X
Analysis I.X.2	Implied character weighting $k=3$ of X
Analysis I.X.3	Implied character weighting $k=5$ of X
Analysis J.X.1	Excluding characters homoplasy > 95th percentile from X
Analysis J.X.2	Excluding characters homoplasy > 85th percentile from X
Analysis J.X.3	Excluding characters homoplasy > 75th percentile from X
Analysis K.X.1	Excluding characters under 10% complete from X
Analysis K.X.2	Excluding characters under 20% complete from X
Analysis K.X.3	Excluding characters under 30% complete from X

stable taxa that were pruned subsequently. When interpreting phylogenetic relationships derived from the re-analysis of matrices by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021), I used the clade definitions as outlined in each of the original given studies (see Appendix, A2.1).

2.2.2. Stratigraphical congruence

All three matrices were re-analysed in TNT, replicating the original methods outlined in Table 2.1. The stratigraphical congruence of all of the MPTs, strict consensus trees and reduced strict consensus trees (if applicable) produced using the original methods of Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were assessed using the R-package *strap* (v. 1.4; Bell & Lloyd 2015), applying the command *StratPhyloCongruence* (with 1000 permutations). First and last appearance dates were retrieved from the Paleobiology Database (PBDB, <https://paleobiodb.org/>), checked against recent literature, and updated where necessary (see Appendices, A2.2). The as-yet undescribed North American orodromine ‘Kaiparowits orodromine’ from the Boyd (2015) matrix was given the full stratigraphical range of the Kaiparowits Formation (76.6–74.5 Ma; Roberts *et al.* 2013). Stratigraphical congruence was assessed using the following metrics: Stratigraphical Consistency Index (SCI: Huelsenbeck 1994); modified Manhattan Stratigraphical Measure (MSM: Siddall 1998; Pol & Norell 2001); Gap Excess Ratio (GER: Wills 1999); and Minimum Implied Gap (MIG: Benton & Storrs 1994; Wills 1999). MIG was reported in millions of years. Time-calibrated strict and reduced strict consensus trees were produced using the R-packages *strap* (v. 1.4; Bell & Lloyd 2015) and *paleotree* (v. 3.3.25; Bapst & Wagner 2019).

2.2.3. Taxon sampling

2.2.3.1. Shared taxa. The matrix from Boyd (2015) shares 39 and 45 OTUs with the matrices from Han *et al.* (2018) and Dieudonné *et al.* (2021), respectively (see Appendices, A2.2). To control for the effects of these studies using different OTUs, the relationships among these shared OTUs were re-analysed using a traditional tree search in TNT, with 10,000 replications and TBR swapping algorithm (holding 100 trees per replication). OTUs that were not scored in matrices from Boyd (2015) and Han *et al.* (2018), or Boyd (2015) and Dieudonné *et al.* (2021) were removed prior to these tree searches. IterPCR was used to identify unstable taxa to prune them from the strict consensus trees.

2.2.3.2. Taxon completeness. In order to determine if taxon completeness was a factor in the differing relationships recovered, the OTUs coded by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were assessed using an iteration of the Character Completeness Metric (CCM). The CCM was originally devised by Mannion & Upchurch (2010) as a method of assessing specimen completeness based on the proportion of phylogenetically informative characters preserved. Although initially developed to assess the sauropodomorph fossil record (Mannion & Upchurch 2010), it has since been used to quantify completeness in a range of extinct groups (e.g. Walther & Frobisch 2013; Dean *et al.* 2016; Verriere *et al.* 2016; Tulin & Butler 2017).

Davies *et al.* (2017) used an alternative method to calculate CCM in fossil eutherian mammals, instead assessing the proportion of characters scored to a taxon relative to the total number of characters in the cladistic matrix. This is the iteration I use in this study to quantify completeness by taxon. Completeness was assessed in all three data matrices in R (v. 3.6.2) using the R-package TreeTools (v. 1; Smith 2019a)

and *ape* (v. 5.4-1; Paradis *et al.* 2019). Unsourced characters include unknown character states (?) and characters inapplicable to a taxon (–). The R-script used to compute completeness is provided in the supplement to this paper (see Supplemental material 5, Brown *et al.* 2022: <https://doi.org/10.6084/m9.figshare.19385540.v1>). The distribution of completeness scores across taxa from each character matrix was mapped onto the corresponding strict consensus tree using the R-packages *ape* (v. 5.4-1; Paradis *et al.* 2019), *phytools* (v. 0.7-47; Revell 2012) and *maps* (v. 3.3.0; Becker *et al.* 2016).

Tree searches of all three matrices were re-run excluding OTUs with varying low completeness: <10% complete (Analysis B.1); <20% (Analysis B.2); and <30% (Analysis B.3). All tree searches were undertaken in TNT using a traditional search with 10,000 replications and TBR swapping, holding 100 trees per replication (with a maximum of 100,000 trees held).

2.2.3.3. *Taxon stability.* Safe taxonomical reduction (Wilkinson 1995) identifies unstable OTUs that lack unique combinations of character scores, which can be removed *a priori* from a data matrix. This method reduces the number of MPTs generated and therefore increases the resolution of the resulting consensus trees, without affecting the inferred relationships of other OTUs in subsequent phylogenetic analyses. Safe taxonomical reduction was applied to all three data matrices using the R-package *Claddis* (v. 0.6.3; Lloyd 2016), applying the command *safe_taxonomic_reduction*. Unstable taxa identified using this method were removed from the respective data matrix subsequently using the *taxcode* command in TNT. These data matrices were re-analysed using a traditional tree search in TNT, with 10,000 replications and TBR swapping algorithm (holding 100 trees per replication) as Analysis C.

IterPCR was used to identify unstable taxa to be pruned *a posteriori* from the

strict consensus trees produced from tree searches of the Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) matrices (Analysis D). To identify their impact on resulting tree topologies, these unstable taxa were pruned from the strict consensus trees.

The positional congruence (reduced; PCR) of taxa from all three data matrices was identified using the *tcomp* function in TNT, following Pol & Escapa (2009). PCR values and completeness values of taxa from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were logged and tested for a significant correlation using Pearson's rank.

2.2.4. Character sampling

2.2.4.1. Shared characters. The character list from Boyd (2015) was manually compared with that from Han *et al.* (2018) and Dieudonné *et al.* (2021), respectively, to identify equivalent and shared characters in both analyses. These characters were also categorised based on whether they differed in character description and/or in the character states used. Characters that support the clades Thescelosauridae, Cerapoda or Ornithopoda in either the strict consensus from Boyd (2015) or the reduced strict consensus from Han *et al.* (2018) and Dieudonné *et al.* (2021) were identified using the *apo* function in TNT. Characters found to support one of these clades in Boyd (2015), that are also characters identified as present in either Han *et al.* (2018) or Dieudonné *et al.* (2021), were mapped in TNT to identify whether their phylogenetic signals differ due to inconsistent scoring or taxon sampling.

2.2.4.2. Character ordering. The impact of ordering multi-state characters on tree resolution is debated within phylogenetics (Hauser & Presch 1991; Lipscomb 1992; Wilkinson 1992; Brazeau 2011; Grand *et al.* 2013; Rineau *et al.* 2015). All three

of the data matrices analysed in this study include multi-state characters. Of these, 21 and four characters from Han *et al.* (2018) and Dieudonné *et al.* (2021), respectively, are ordered. No characters were ordered in Boyd (2015). Here I re-analysed the matrices from Han *et al.* (2018) and Dieudonné *et al.* (2021) in TNT with all characters unordered. This analysis (Analysis E) was implemented using a traditional tree search in TNT, with 10,000 replications and TBR swapping algorithm (holding 100 trees per replication).

2.2.4.3. Character partitions. In this study, characters from all three matrices were grouped by: (1) skeletal element (e.g. femora); (2) into one of 12 skeletal regions (e.g. hind limb); and (3) as either craniodental or postcranial. The 12 skeletal regions (including seven craniodental and five postcranial sub-regions) are outlined in the Appendices, A2.3–2.4. Characters not attributed to a specific skeletal element/region (e.g. H1, head shape in dorsal view), were excluded from subsequent analyses involving those partitions.

To identify the relative importance of characters from different skeletal regions, a series of 15 tree searches were run for each matrix, whereby characters from the following partitions were excluded: (1) either all craniodental or all postcranial characters (Analysis F); (2) each of the 12 skeletal regions (Analysis G); and (3) characters pertaining to the most character-rich postcranial element from each data matrix (Analysis H). All tree searches were undertaken in TNT using a traditional search with 10,000 replications and TBR swapping, holding 100 trees per replication (with a maximum of 100,000 trees held). The *prunenelsen* and *pcrprune* TNT functions were used to identify unstable taxa to prune from the resulting strict consensus trees. Reduced strict consensus trees reported when pruning resulted in increased resolution to taxa of in-

terest, but without pruning over 10% of OTUs. Taxa were removed prior to the analysis if excluding characters from a specific partition in turn excluded all characters scored for that taxon.

2.2.4.4. Character completeness. The completeness of each character from all three matrices was assessed as the proportion of taxa scored per character. Completeness of characters was calculated using an R-script provided in the supplement to this paper (see Supplemental material 5, Brown *et al.* 2022: <https://doi.org/10.6084/m9.figshare.19385540.v1>). Character completeness was also compared between the 12 different skeletal regions used previously. Tree searches of all three matrices were re-run excluding characters with varying low completeness to see if resulting topologies began to converge: 15% complete (Analysis I.1); 25% complete (Analysis I.2); and 35% complete (Analysis I.3). All tree searches were undertaken in TNT using a traditional search with 10,000 replications and TBR swapping, holding 100 trees per replication (with a maximum of 100,000 trees held).

2.2.4.5. Homoplasy. Data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were re-run using the original methods outlined above, but with implied weighting to see if their topologies converged. Implied weighting downweights characters based on how homoplastic the model considers them to be. The strength of this weighting is based on the concavity constant, k , with lower values (e.g. $k=1$) more strongly downweighing homoplastic characters. The *piwe* function in TNT was used to activate implied weighting prior to the tree search with the following k values: 1 (Analysis J.1); 3 (Analysis J.2); and 5 (Analysis J.3).

Character homoplasy was calculated from the strict consensus trees produced in the replicated tree searches of Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.*

(2021) using the *chomo* function in TNT. This function expresses homoplasy as the number of extra steps required to explain state changes of a character throughout a given tree topology as homologous rather than homoplastic. The relative distribution of homoplasy throughout different skeletal regions was presented as the percentage difference between the relative proportion of homoplasy (%) and relative proportion of total characters (%), for a given partition.

Tree searches were re-run for all three data matrices excluding characters of varying levels of homoplasy to see if the topologies would begin to converge. The cut-offs used were 95th percentile (Analysis K.1), 85th percentile (Analysis K.2) and 75th percentile (Analysis K.3). All tree searches were undertaken in TNT using a traditional search with 10,000 replications and TBR swapping, holding 100 trees per replication (with a maximum of 100,000 trees held).

2.3. Results

2.3.1. Stratigraphical congruence

The data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were re-analysed using their original search parameters (Table 2.1). The resulting consensus trees were also time-calibrated (see Appendices, A2.5a–e). Tests of stratigraphical congruence show that the 36 MPTs from Boyd (2015) and 53,367 MPTs from Han *et al.* (2018) are generally equally congruent, while the 176 MPTs from Dieudonné *et al.* (2021) (Table 2.3) are the least congruent. The strict consensus tree from Boyd (2015) (see Appendices, A2.5a) is more congruent than that from Han *et al.* (2018) (see Appendices, A2.5b); however, the reduced strict consensus from Han *et al.* (2018) (see

Table 2.3. Results of stratigraphic congruence tests of maximum parsimony trees (MPTs) from re-analysis of matrices by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Abbreviations: SCI, Stratigraphical Consistency Index; GER, Gap Excess Ratio; MSM*, modified Manhattan Stratigraphical Measure; MIG, Minimum Implied Gap.

	SCI	GER	MSM*	MIG
Boyd (2015; 36 MPTs)				
Median	0.5317	0.8298	0.1344	1337.52
Range	0.5238–0.5397	0.8160– 0.8304	0.1256–0.1349	1333.32– 1431.52
Han <i>et al.</i> (2018; 53,367 MPTs)				
Median	0.5143	0.8352	0.1291	1316.62
Range	0.4714–0.5714	0.8094– 0.8484	0.1136–0.1388	1224.87– 1496.12
Dieudonné <i>et al.</i> (2021; 176 MPTs)				
Median	0.5	0.8201	0.1121	1429.33
Range	0.4714 – 0.5286	0.8181 – 0.8248	0.1109 – 0.1147	1396.43– 1444.03

Appendices, A2.5c) is generally more congruent than the strict consensus from Boyd (2015) (Table 2.4). The strict consensus tree from Boyd (2015) is more stratigraphically congruent than both the strict and reduced strict consensus trees from Dieudonné *et al.* (2021; Table 2.4; see Appendices, A2.5d–e).

2.3.2. Taxon sampling

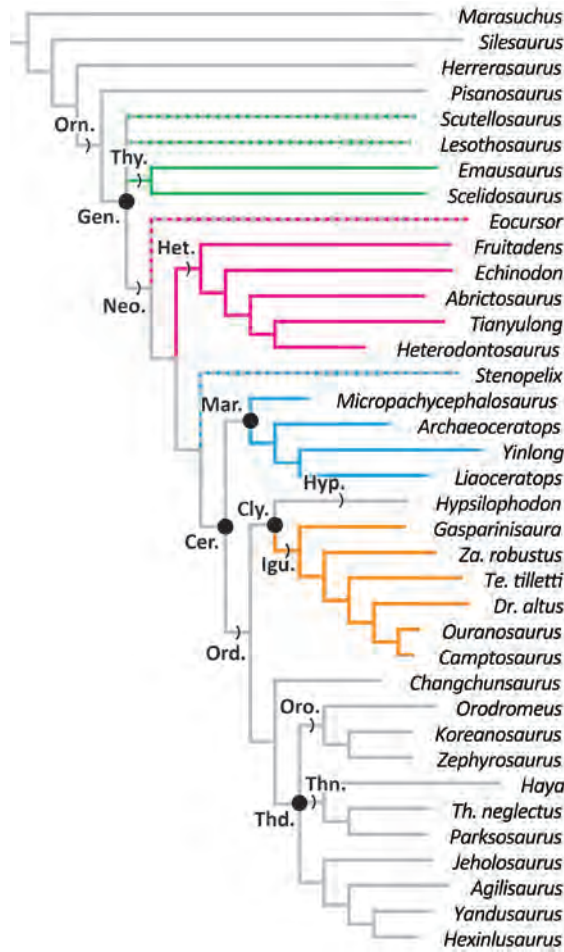
2.3.2.1. Shared taxa. Including only the 39 taxa shared by both Boyd (2015; 60% overlap) and Han *et al.* (2018; 54.2% overlap) in a tree search of the pruned Boyd

Table 2.4. Results of stratigraphic congruence tests of strict consensus trees (SCT) and reduced censuses trees (RCT) from re-analysis of matrices by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Abbreviations as in Table 2.3.

	SCI	GER	MSM*	MIG
Boyd (2015; 36 MPTs)				
SCT	0.5317	0.8298	0.1344	1337.52
Han <i>et al.</i> (2018; 53,367 MPTs)				
SCT	0.6364	0.7531	0.0901	1887.42
RCT	0.5455	0.8266	0.1365	1245.73
Dieudonné <i>et al.</i> (2021; 176 MPTs)				
SCT	0.5455	0.7917	0.0983	1630.03
RCT	0.5082	0.8177	0.1116	1436.03

(2015) matrix results in 66 MPTs and a poorly resolved strict consensus tree (see Appendices, A2.6a; Analysis A.1). However, two unstable taxa (*Yueosaurus* and *Wannanosaurus*) were identified and pruned subsequently, giving a well-resolved reduced strict consensus tree (Figure 2.3a) that possesses a number of differences from BSCT: (1) heterodontosaurids were resolved as basal neornithischians; (2) Thescelosauridae was found within Ornithopoda; (3) *Changchunsaurus*+Thescelosauridae were found as the sister group of Clypeodonta (*Hypsilophodon*+Iguanodontia); and (4) *Jeholosaurus*, *Agilisaurus*, *Yandusaurus* and *Hexinlusaurus* formed a clade within Thescelosauridae. Removing taxa from the matrix by Han *et al.* (2018) that are not scored in Boyd (2015) produced 164 MPTs and a poorly resolved strict consensus tree (see Appendices, A2.6b). Following pruning of three unstable taxa (*Abriktosaurus*, *Yueosaurus* and *Micropachycephalosaurus*) a well-resolved reduced strict consensus tree was ob-

a) Boyd (2015)



b) Han et al. (2018)

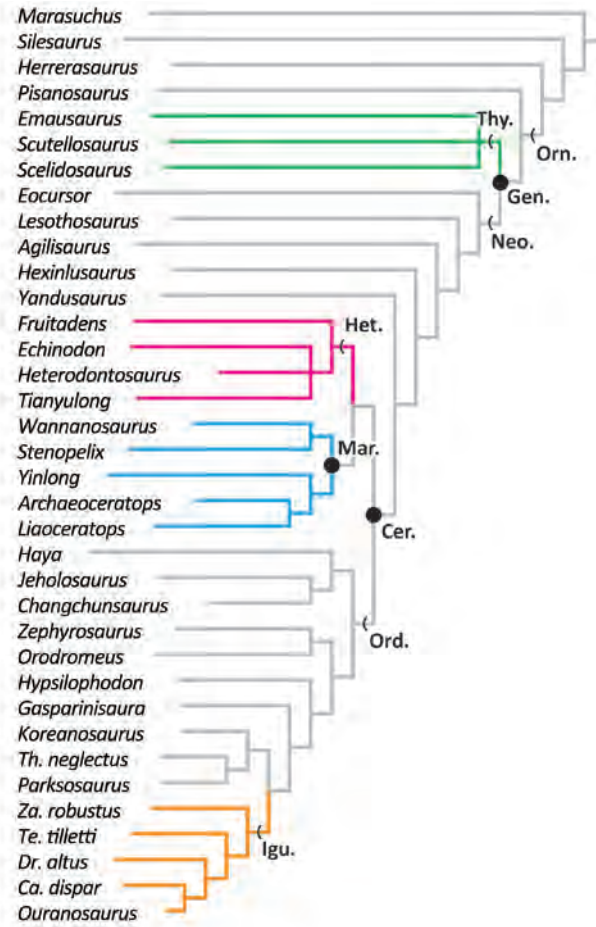


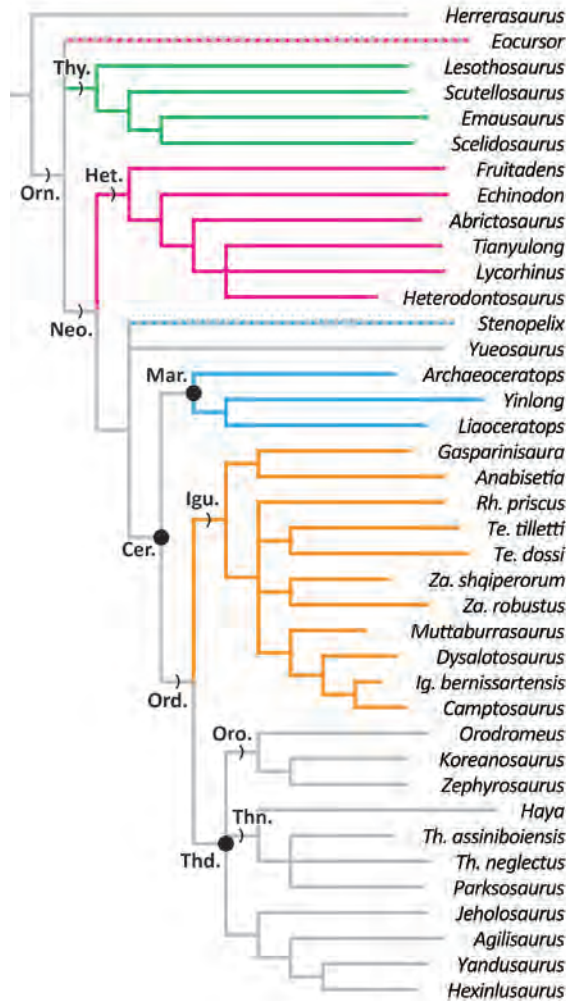
Figure 2.3. Reduced consensus trees produced using only shared taxa ($n=39$), following: **a**, pruning of two unstable taxa (*Yueosaurus*, *Wannanosaurus*) from the 66 most parsimonious trees (MPTs) generated from the matrix by Boyd (2015); and **b**, pruning of three unstable taxa (*Abrictosaurus*, *Yueosaurus* and *Micropachycephalosaurus*) from the 164 MPTs generated from the matrix by Han *et al.* (2018). See A2.1 for clade definitions. **Abbreviations:** **Ca.**, *Camptosaurus*; **Cer.**, Ceratopsia; **Cly.**, Clypeodontia; **Dr.**, *Dryosaurus*; **Gen.**, Genasauria; **Het.**, Heterodontosauridae (pink); **Hyp.**, Hypsilophodontidae; **Igu.**, Iguanodontia (yellow); **Mar.**, Marginocephalia (blue); **Neo.**, Neornithischia; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Oro.**, Orodrominae; **Te.**, *Tenontosaurus*; **Th.**, *Thescelosaurus*; **Thd.**, Thescelosauridae; **Thn.**, Thescelo-

saurinae; **Thy.**, Thyreophora (green); **Za.**, *Zalmoxes*. Dashed lines indicate the group in which a taxon was recovered in the original analyses of Boyd (2015) and Han *et al.* (2018), respectively. (Fig. 2.3, cont.)

tained (Figure 2.3b), which recovered several differences in topology from HRSCT: (1) heterodontosaurids are found within Cerapoda in a sister-group relationship with Marginocephalia; and (2) *Eocursor* and *Lesothosaurus* are recovered within Neornithischia, but in earlier-branching positions than *Agilisaurus* and *Hexinlusaurus*; (3) *Yandusaurus* is identified as the sister group of Cerapoda; and (4) *Orodromeus* forms a clade with *Zephyrosaurus* (Orodrominae sensu Brown *et al.* 2013b).

Including only the 45 taxa coded in both Boyd (2015; 69.2% overlap) and Dieudonné *et al.* (2021; 62.5% overlap) when conducting a tree search of the Boyd (2015) matrix, produces 180 MPTs and a poorly resolved strict consensus (see Appendices, A2.7a; Analysis A.2). IterPCR identified six unstable taxa (*Changchunsaurus*, *Hypsilophodon*, *Macrogryphosaurus*, *Talenkauen*, *Valdosaurus*, *Wannanosaurus*) and pruning these resulted in a well-resolved reduced strict consensus (Figure 2.4a) that shows several differences compared with BSCT: (1) heterodontosaurids recovered as basal neornithischians; (2) *Stenopelix* found to be a non-cerapodan neornithischian; (3) Thescelosauridae nested within Ornithopoda in a sister-group relationship with Iguanodontia; (4) *Jeholosaurus*, *Agilisaurus*, *Yandusaurus* and *Hexinlusaurus* found within Thescelosauridae; and (5) *Gasparinisaura* recovered as an iguanodontian. Excluding taxa from Dieudonné *et al.* (2021) that are not coded in Boyd (2015) results in two MPTs and a well-resolved strict consensus (Figure 2.4b; see Appendices, A2.7b).

a) Boyd (2015)



b) Dieudonné et al. (2021)

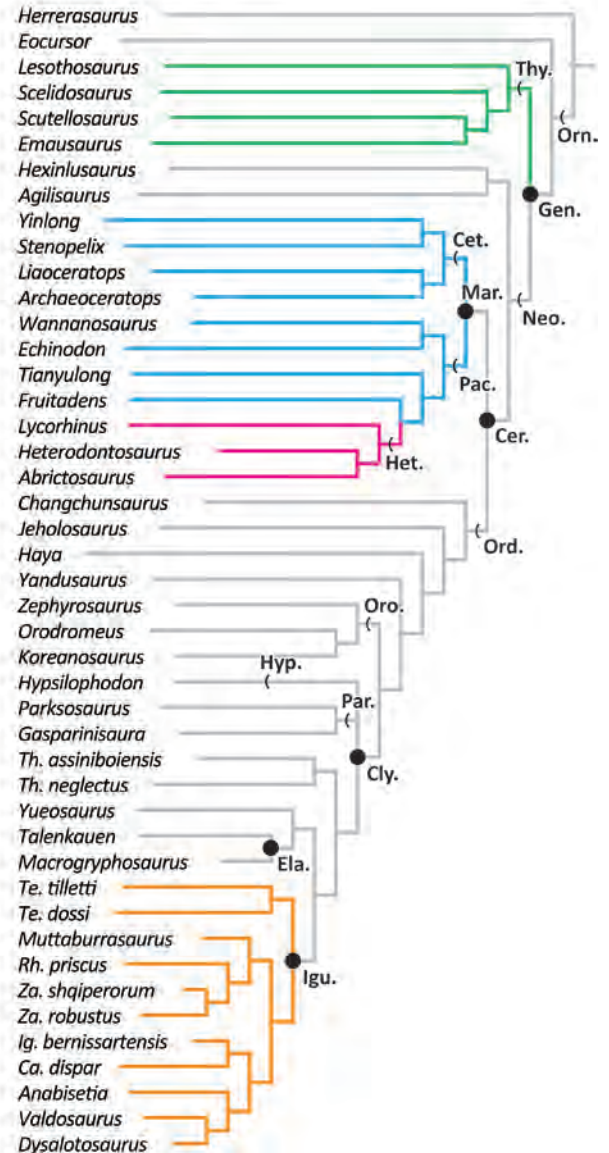


Figure 2.4. Consensus trees produced using only shared taxa ($n=45$): **a**, following pruning of six unstable taxa (*Changchunsaurus*, *Hypsilophodon*, *Macrogyphosaurus*, *Talenkauen*, *Valdosaurus*, *Wannanosaurus*) from the 180 most parsimonious trees (MPTs) generated from the matrix of Boyd (2015); and **b**, the strict consensus of the two MPTs generated from the matrix of Dieudonné *et al.* (2021). **Abbreviations:** **Ca.**, *Camptosaurus*; **Cer.**, Cerapoda; **Cly.**, Clypeodonta; **Ela.**, Elasmaria; **Gen.**, Genasauria; **Het.**, Heterodontosauridae (pink); **Hyp.**, Hypsilophodontidae;

Igu., Iguanodontia (orange); **Ig.**, *Iguanodon*; **Mar.**, Marginocephalia (blue); **Neo.**, Neornithischia; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Oro.**, Orodrominae; **Par.**, Parksosauridae; **Rh.**, *Rhabdodon*; **Te.**, *Tenontosaurus*; **Th.**, *Thescelosaurus*; **Thd.**, Thescelosauridae; **Thn.**, Thescelosaurinae; **Thy.**, Thyreophora (green); **Za.**, *Zalmoxes*. Dashed lines indicate the group in which a taxon was recovered in the original analyses of Boyd (2015) and Dieudonné *et al.* (2021), respectively. (Fig. 2.4, cont.)

This consensus differs from DSCT in recovering: (1) *Eocursor* as a basal ornithischian; (2) *Yandusaurus* within Ornithopoda; (3) Parksosauridae+Hypsilophodontidae in a polytomy at the base of Clypeodonta; and (4) Elasmaria outside of Iguanodontia and forming a clade with *Yueosaurus*. Taxon sampling is shown here to substantially alter the implied relationships recovered across all three matrices. Boyd (2015) and Han *et al.* (2018) are particularly impacted by taxon inclusion, with numerous changes identified concerning the taxa of interest and clades that are frequently considered to have ambiguous affinities (e.g. heterodontosaurids, thescelosaurids).

2.3.2.2. Taxon completeness. Taxa coded in the Boyd (2015) matrix are generally less complete (average = 41.1%) than those scored in both Han *et al.* (2018; average = 50.9%) and Dieudonné *et al.* (2021; average = 46.8%) (Figure 2.5).

Neornithischian taxa with very low completeness in Boyd (2015) are found throughout the tree (see Appendices, A2.8a) and tend to fall within polytomies (e.g. *Yandusaurus*, *Macrogyphosaurus*, *Notohypsilophodon*, *Micropachycephalosaurus*, *Stenopelix*, *Callovosaurus*). The few highly complete taxa in Boyd (2015) are consistently recovered in resolved positions (e.g. *Dryosaurus*, *Dysalotosaurus*, *Hypsilopho-*

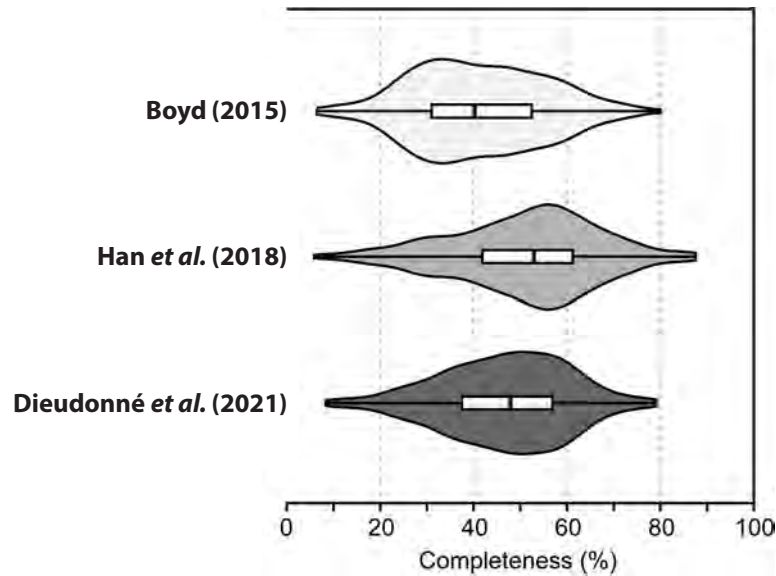


Figure 2.5. Distribution of completeness scores for scored taxa in the data matrices of Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021).

don, *Orodromeus*).

In the strict consensus tree from Han *et al.* (2018; see Appendices, A2.8b), the polytomy at the base of Cerapoda contains both highly incomplete (e.g. *Micropachycephalosaurus*, *Yueosaurus*, *Koreanosaurus*) and highly complete taxa (e.g. *Orodromeus*, *Jeholosaurus*, *Hypsilophodon*, *Haya*). All eight of the taxa pruned in HRSCT have <25% completeness.

The polytomy at the base of Cerapoda in the strict consensus tree from Dieudonné *et al.* (2021; see Appendices, A2.8c) contains moderately complete taxa (>50%), with the exception of *Yandusaurus* (22%), which was pruned from the original analysis after being identified as unstable. Taxa of moderate completeness generally occur throughout the tree, although areas within Iguanodontia in particular have taxa that are both highly incomplete (e.g. the elasmarians, which are recovered as a polytomy)

and highly complete (e.g. *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon*).

Removing the most incomplete OTUs from Boyd (2015) reduces the resolution of inferred relationships for the taxa of interest in this study compared to BSCT (Analyses B1–3.B2015; see Appendices, A2.9–11). The thescelosaurines are particularly affected, falling as a polytomy at the base of Thescelosauridae when OTUs <30% complete (n=28) are removed prior to the tree search (Analysis B.3.B2015; see Appendices, A2.11). Removing highly incomplete taxa from Boyd (2015) also recovers *Jeholosaurus* within Thescelosauridae, rather than as a non-thescelosaurid neornithischian as in BSCT. Excluding OTUs <10% complete prior to the tree search of Han *et al.* (2018; Analysis B.1.H2018; see Appendices, A2.12) and Dieudonné *et al.* (2021; Analysis B.1.D2021; see Appendices, A2.15) does not impact the resulting tree topology, perhaps due to the small number of highly incomplete taxa in both matrices (n=3 and n=2, respectively; compared to n=7 in Boyd [2015]). Removing taxa <20% complete from Han *et al.* (2018; Analysis B.2.H2018; see Appendices, A2.13) largely improves the resolution of implied relationships, but further removal of incomplete taxa (<30% complete; Analysis B.3.H2018; see Appendices, A2.14) fully resolves the polytomy at the base of Cerapoda. Analysis B.2–3. H2018 (see Appendices, A2.13–14) also recovers *Lesothosaurus* within Thyreophora (consistent with Butler *et al.* [2008] and Boyd [2015]), rather than as a basal genasaurian, as in HSCT. Removing taxa <20% complete from Dieudonné *et al.* (2021; Analysis B.2.D2021; see Appendices, A2.16) resolves the polytomy at the base of Cerapoda in DSCT, but many ‘hypsilophodontids’ remain poorly resolved within Ornithopoda. Further excluding taxa <30% complete (see Appendices, A2.17) resolves the relationships of the remaining ‘hypsilophodontids’, but other groups (e.g. thyreophorans) become less resolved.

Taxa from Boyd (2015) are generally more incomplete than those from Han *et al.* (2018) and Dieudonné *et al.* (2021). Removing incomplete taxa from Boyd (2015) reduces tree resolution, while the same action increases tree resolution for the Dieudonné *et al.* (2021) and, especially, the Han *et al.* (2018) datasets. Relationships of the taxa of interest generally remain consistent with those presented in the original studies.

2.3.2.3. Taxon stability. Application of safe taxonomical reduction to the Boyd (2015) matrix identified *Thescelosaurus garbanii* as taxonomically equivalent to *Thescelosaurus neglectus*. *Th. garbanii* was removed from the Boyd (2015) matrix prior to re-analysis, which generated 36 MPTs with a well-resolved strict consensus tree (see Appendices, A2.18; Analysis C.B2015). Apart from the absence of *Th. garbanii*, this strict consensus tree is identical to BSCT. When applied to the matrix of Han *et al.* (2018), *Yueosaurus tiantaiensis* was identified as taxonomically equivalent to *Hypsilophodon foxii* and *Orodromeus makelai*. *Y. tiantaiensis* was removed from the matrix, which was then re-analysed in TNT, producing 3439 MPTs and a poorly resolved strict consensus tree (see Appendices, A2.19; Analysis C.H2018) identical to HSCT, except in recovering *Jeholosaurus* as the sister-taxon to *Changchunsaurus*. No OTUs were identified as safe to remove from the Dieudonné *et al.* (2021) dataset.

IterPCR identified *Lycorhinus* as an unstable taxon that could be pruned to improve the resolution of the strict consensus tree generated from the Boyd (2015) matrix. When this taxon is pruned from the strict consensus tree (see Appendices, A2.20; Analysis D.1.B2015) the relationships of heterodontosaurids and thescelosaurines are better resolved. Excluding *Lycorhinus* prior to the tree search produces 12 MPTs with a strict consensus (see Appendices, A2.21; Analysis D.2.B2015) that is equally well re-

solved as that resulting from Analysis D.2.B2015, but with several minor branch swaps.

Eight unstable taxa (*Yueosaurus*, *Pisanosaurus*, *Yandusaurus*, *Zephyrosaurus*, *Albalophosaurus*, *Laquintasaura*, *Micropachycephalosaurus* and *Koreaceratops*) were pruned in the original reduced strict consensus of 53,376 MPTs derived from Han *et al.* (2018). Here, IterPCR identifies nine taxa (*Yueosaurus*, *Pisanosaurus*, *Yandusaurus*, *Zephyrosaurus*, *Albalophosaurus*, *Laquintasaura*, *Micropachycephalosaurus*, *Aquilops* and *Yamaceratops*) that could be pruned to improve the tree resolution; however, the additional pruning of *Aquilops* and *Yamaceratops* only increases the resolution among neoceratopsian taxa (see Appendices, A2.22; Analysis D.1.H2018). These nine taxa were also excluded prior to the tree search replication, producing 660 MPTs (Analysis D.2.H2018). The strict consensus of these trees is relatively well resolved (see Appendices, A2.23), similar to HRST, but comparably lacking in resolution among the heterodontosaurids, basal neornithischians and basal ceratopsians. Dieudonné *et al.* (2021) pruned *Yandusaurus* to increase the resolution of the original strict consensus of 176 MPTs. Here, IterPCR identified *Macrogryphosaurus*, *Mahuidacursor* and *Yandusaurus* as unstable in the tree search. Pruning these three taxa (see Appendices, A2.24; Analysis D.1.D2021) resolves the polytomies at the base of Cerapoda and Elasmaria recovered in the original strict consensus from Dieudonné *et al.* (2021). Excluding these three taxa prior to the tree search replication produces 40 MPTs and a strict consensus tree (see Appendices, A2.25) similar to Appendix Figure A2.25, but lacking resolution among the iguanodontians (Analysis D.2.D2021).

Taxa from the 36 MPTs generated from the Boyd (2015) matrix are generally far more positionally congruent than those from the 53,376 MPTs and 176 MPTs generated from the matrices by Han *et al.* (2018) and Dieudonné *et al.* (2021), respectively

(see Appendices, A2.26). The least positionally congruent taxa from Boyd (2015) are *Hexinlusaurus*, *Leaellynasaura* and *Yandusaurus* (PCR = 0.958), which are all recovered in a polytomy at the base of Neornithischia in the strict consensus tree (Figure 2.2A). In the data matrix from Han *et al.* (2018), there are seven taxa that are outliers in their poor positional congruence, with PCR values ranging from 0.557 to 0.784 (*Pisanosaurus*, *Laquintasaura*, *Micropachycephalosaurus*, *Yueosaurus*, *Yandusaurus*, *Lesothosaurus* and *Eocursor*). All of these taxa (except for *Lesothosaurus*) have low completeness scores (<30%). Taxa from Dieudonné *et al.* (2021) are highly positionally congruent (PCR = >0.976), with the exception of one outlier taxon, *Yandusaurus*, which has a PCR value of 0.596. PCR values and completeness are not correlated significantly in taxa from either Boyd (2015) or Dieudonné *et al.* (2021; Table 2.5). PCR values and completeness are significantly positively correlated in taxa from Han *et al.* (2018), but do not significantly correlate when those seven PCR-outlier taxa are excluded.

Safe taxonomical reduction has little impact on tree resolution in Analysis C, but at least in Han *et al.* (2018) *a priori* exclusion of taxa identified as safe to remove significantly reduced the number of MPTs generated from 53,376 to 3439, which should improve consensus tree resolution. Following a tree search, IterPCR finds unstable taxa in each of the three matrices, although considerably more in Han *et al.* (2018). When these unstable taxa are pruned following a tree search analysis, the resulting reduced strict consensus trees generated are generally better resolved than if those taxa were excluded *a priori*. IterPCR identifies *Yandusaurus* as unstable in both Han *et al.* (2018) and Dieudonné *et al.* (2021). *Yandusaurus* is consistently identified as unstable across all three matrices, being recovered in a polytomy in all three original

Table 2.5. Results of Pearson’s r correlation test between logged character completeness and logged positional congruence (reduced; PCR) of taxa from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Significant p -values are italicised.

	Pearson’s r	p -value
Boyd (2015)	-0.0647	0.6084
Han <i>et al.</i> (2018)	<i>0.3168</i>	<i>0.0067</i>
Han <i>et al.</i> (2018; minus outliers)	0.1801	0.1512
Dieudonné <i>et al.</i> (2021)	0.0975	0.4153

strict consensus trees and identified as having low PCR values. Taxa from Han *et al.* (2018) are less positionally congruent than those from Boyd (2015) and Dieudonné *et al.* (2021). Generally, there is no relationship between completeness and positional congruence (although the two values significantly correlate in Han *et al.* [2018]), which is particularly evident in several taxa that are highly incomplete in two or all of the matrices investigated but have vastly different PCR values following tree searches (e.g. *Micropachycephalosaurus*, *Yueosaurus*).

2.3.3. Character sampling

2.3.3.1. Shared characters. The matrix from Boyd (2015) shares 79 characters with Han *et al.* (2018); however, only 38 of those shared characters use the same character states (including those where the states are reversed) and thus capture the same morphological variation (see Brown *et al.* 2022; Supplementary material, Table S4). Boyd (2015) shares more characters with Dieudonné *et al.* (2021; $n=118$), 58 of which use the same character states (see Appendices, A2.27).

The clade Thescelosauridae in Boyd (2015) is supported by state changes in seven characters. None of these characters are coded in Han *et al.* (2018), but five are coded in Dieudonné *et al.* (2021). Of these, only character B255 (=D21; unfused/fused premaxillae) uses the same character states in both matrices and are thus equivalent. In addition, there is no conflict in the coding of this character between the two matrices. In several of the remaining shared characters, the state partitioning has been subtly reworked in Dieudonné *et al.* (2021) (e.g. B98=D122; angle between the base and long axis of the braincase), which has in turn caused substantial changes to how these characters have been coded and therefore how they infer evolutionary change.

Cerapoda is supported by state changes in seven characters in Boyd (2015). Three of these characters are also coded in Han *et al.* (2018), and three are coded in Dieudonné *et al.* (2021). B123 (distribution of enamel on maxillary and dentary teeth) is found in both Han *et al.* (2018; H226) and Dieudonné *et al.* (2021; D171). D171 is equivalent to B123 (although uses slightly different wording) but is not supportive of Cerapoda in Dieudonné *et al.* (2021). H226 is not equivalent to B123 as it has an extra state, but both H226:1 and B123:1 (asymmetrical distribution of enamel on maxillary and dentary teeth) are supportive of Cerapoda in their respective phylogenetic analyses.

In Boyd (2015), the clade Ornithopoda is supported by state changes in seven characters. Two of these characters are also coded in the matrix by Han *et al.* (2018), while three are coded in Dieudonné *et al.* (2021). Two of these shared characters are equivalent to each other (B28=H44, maxilla/jugal suture; B250=D219, absence/presence of ossified hypaxial tendons along the tail); however, neither are supportive of Ornithopoda in their respective phylogenetic analyses.

2.3.3.2. Character ordering. Unordering all characters in Han *et al.* (2018) (Analysis E.H2018) generated 47,801 MPTs. The strict consensus of these MPTs (see Appendices, A2.28) is slightly more poorly resolved than when 21 characters are ordered, particularly in the resolution of the ceratopsians.

Unordering all characters in Dieudonné *et al.* (2021) (Analysis E.D2021) produced 100 MPTs and a relatively poorly resolved strict consensus tree (see Appendices, A2.29). This strict consensus recovers several ‘hypsilophodontids’ (*Koreanosaurus*, *Kulindadromeus*, *Orodromeus*, *Parksosaurus*, *Yueosaurus*, *Zephyrosaurus*), originally recovered in resolved positions within Ornithopoda, in a clade at the collapsed base of Cerapoda. These results show how even minimal use of character ordering (e.g. the four ordered characters in Dieudonné *et al.* [2021]) can have an impact on the resulting tree topology and inferred relationships of taxa.

2.3.3.3. Character partitions. As is typical for many morphological matrices (Mounce *et al.* 2016), craniodental characters are more abundantly represented than postcranial characters in Boyd (2015; 55.7%), Han *et al.* (2018; 59.5%) and Dieudonné *et al.* (2021; 56.4%) (Table 2.6). Of these craniodental characters, those relating to the dentition make up a larger proportion of the total characters in Boyd (2015; 12.2%) than in Han *et al.* (2018; 8.4%) and Dieudonné *et al.* (2021; 10.5%). In Boyd (2015) and Dieudonné *et al.* (2021), the hind limb region contains the highest proportion of characters from the postcranium (16.5% and 12.9%, respectively; compared to 8.7% in Han *et al.* 2018). The pelvic girdle is the best represented postcranial region in the matrix of Han *et al.* (2018), comprising 11.3% of all characters, compared to 10.2% and 10.8% in Boyd (2015) and Dieudonné *et al.* (2021), respectively. Of the main postcranial regions, the pectoral girdle is the most poorly represented in all three

Table 2.6. Proportion of characters relating to a specific skeletal region relative to all characters, from the matrices by Boyd (2015; n=255), Han *et al.* (2018; n=380) and Dieudonné *et al.* (2021; n=342).

	Relative proportion of total characters (%)		
	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
Craniodental vs. Postcranial			
Craniodental	55.69	59.47	56.43
Postcranial	44.31	40.53	43.57
Skeletal region			
Rostrum	10.59	10.53	10.53
Palate	0	2.63	1.46
Cranial roof	4.71	7.89	6.43
Lateral skull base	14.12	12.11	11.11
Braincase	4.71	4.21	6.14
Mandible	8.24	11.05	8.77
Dentition	12.16	8.42	10.53
Vertebral column	6.67	8.42	7.60
Pectoral girdle & sternum	3.14	2.89	3.51
Forelimbs	6.67	6.84	7.02
Pelvic girdle	10.20	11.32	10.82
Hind limbs	16.47	8.68	12.87
N/A	2.35	5.00	3.22

matrices (Boyd 2015, 3.1%; Han *et al.* 2018, 3.2%; Dieudonné *et al.* 2021, 3.5%). The most character-rich postcranial element in Boyd (2015) is the femur, making up 7.8% of all characters (for comparison: Han *et al.* 2018, 3.2%; Dieudonné *et al.* 2021, 5%). In both Han *et al.* (2018) and Dieudonné *et al.* (2021) the ilium is the most character-rich postcranial element, making up 5.5% and 6.1% of total characters, respectively (compared to 4.7% in Boyd 2015).

Excluding all craniodental characters (n=142) from Boyd (2015; Analysis F.1.B2015) produced 33,800 MPTs and a poorly resolved strict consensus (see Appendices, A2.30) with a polytomy of cerapodan and some basal neornithischian and ornithischian taxa. Removing postcranial characters (n=113; Analysis F.2.B2015) produced 6800 MPTs with a strict consensus tree consisting of a large polytomy of all ingroup taxa (see Appendices, A2.31). Excluding craniodental characters (n=226) from the analysis by Han *et al.* (2018; Analysis F.1.H2018) produced 44,600 MPTs and a polytomous strict consensus tree (see Appendices, A2.32), while removing postcranial characters (n=154; Analysis F.2.H2018) produced 600 MPTs with a strict consensus consisting of a large polytomy at the base of Neornithischia (see Appendices, A2.33). Excluding craniodental characters (n=193) from Dieudonné *et al.* (2021; Analysis F.1.D2021) results in 6800 MPTs and a strict consensus consisting of a large polytomy of all ingroup taxa (see Appendices, A2.34). When postcranial characters were excluded (n=149) prior to the reanalysis of Dieudonné *et al.* (2021; Analysis F.2.H2018), 16,900 MPTs were produced, with a strict consensus tree characterized primarily by a very large polytomy (see Appendices, A2.35).

When excluding character partitions pertaining to different skeletal regions from Boyd (2015; Analysis G.1–12.B2015; see Appendices, A2.36–46), Thescelosauridae remained in a non-cerapodan neornithischian position in only five of the 11 analyses (character partitions excluded: braincase; mandible; vertebral column; pectoral girdle; pelvic girdle). When either all dental (n=31) characters or all hind limb (n=42) characters were excluded from the Boyd (2015) matrix, Thescelosauridae was recovered nested within Ornithopoda (see Appendices, A2.41b, A2.46a–b). In Han *et al.* (2018), the ‘hypsilophodontids’ remain within Cerapoda when each of the 12 parti-

tions are excluded (Analysis G.1–12.H2018; see Appendices, A2.47–58). Most of the strict consensus trees produced following exclusion of character partitions from Han *et al.* (2018) present topologies and inferred relationships very similar to those in the original strict consensus (rostral; palatal; cranial roof; skull base; mandibular; dental; vertebral column; pectoral girdle; forelimb). However, excluding some of the character partitions from Han *et al.* (2018) recovers controversial placements for clades, such as the inclusion of heterodontosaurids within Cerapoda (braincase; hind limb). ‘Hypsilophodontids’ also remained within Cerapoda when each of the 12 character partitions were excluded from the Dieudonné *et al.* (2021) matrix (Analysis G.1–12.D2021; see Appendices, A2.59–70).

Removing femoral characters (the most character-rich postcranial element, $n=20$) from the analysis by Boyd (2015) resulted in 1700 MPTs and the recovery of Thescelosauridae within Ornithopoda following pruning of six unstable taxa from the strict consensus (Analysis H.B2015; see Appendices, A2.71b). Femoral characters B212 (presence/absence of a trench between the greater trochanter and the head of the femur), B213 (convex/flat lateral surface of the greater trochanter) and B223 (form of the anterior intercondylar groove) were identified as particularly problematic in their effects on tree topology. Excluding these three characters from the Boyd (2015) data matrix prior to tree searching produces 600 MPTs and a relatively well-resolved strict consensus tree (Figure 2.6), recovering Thescelosauridae within Ornithopoda. Excluding iliac characters from the Han *et al.* (2018, $n=21$) matrix resulted in 2696 MPTs and a poorly resolved strict consensus tree (Analysis H.H2018; see Appendices, A2.72). This strict consensus is largely the same as HSCT, but removing iliac characters resolves the polytomy at the base of Ornithischia. Removing iliac characters from Dieu-

donné *et al.* (2021, n=21) prior to the tree search recovers the clades Orodrominae, Marginocephalia and Clypeodonta in a polytomy at the collapsed base of Neornithischia (Analysis H.D2021; see Appendices, A2.73).

Excluding either cranial or postcranial character partitions from each of the three analyses produced consensus trees with poor resolution. Removing craniodental characters from Boyd (2015) had less negative impact on the resulting tree resolution than removing postcranial characters, in contrast to the results from Han *et al.* (2018) and Dieudonné *et al.* (2021) where the opposite was found. Excluding specific character regions affected the outputs of the three matrices differently, but seemed to impact the inferred relationships of Dieudonné *et al.* (2021) the least. Removing certain skeletal partitions from Boyd (2015) and Han *et al.* (2018) recovered controversial placements for some taxa (e.g. thescelosaurids in Boyd [2015]; heterodontosaurids in Han *et al.* [2018]), differing significantly from the results of their original analyses.

2.3.3.4. Character completeness. Character completeness scores are generally highest in Han *et al.* (2018; average = 50.9%), followed by Dieudonné *et al.* (2021; average = 46.7%) and lastly Boyd (2015; average = 41.1%) (Figure 2.7). In Boyd (2015), postcranial characters (average = 43.9%) have higher completeness scores than cranial characters (average = 38.7%). In contrast, cranial character completeness scores (average = 54.6%) were far higher than those for postcranial characters (average = 45%) in Han *et al.* (2018), while both partitions had equal completeness in Dieudonné *et al.* (2021; craniodental average = 46.2%; postcranial average = 46.7%).

Dental characters have the highest completeness scores of any craniodental partition for each of the three matrices (see Appendices, A2.74). Palatal characters comprise the cranial partition with the lowest completeness scores in Han *et al.* (2018) and

Boyd (2015) - excluding three femoral characters

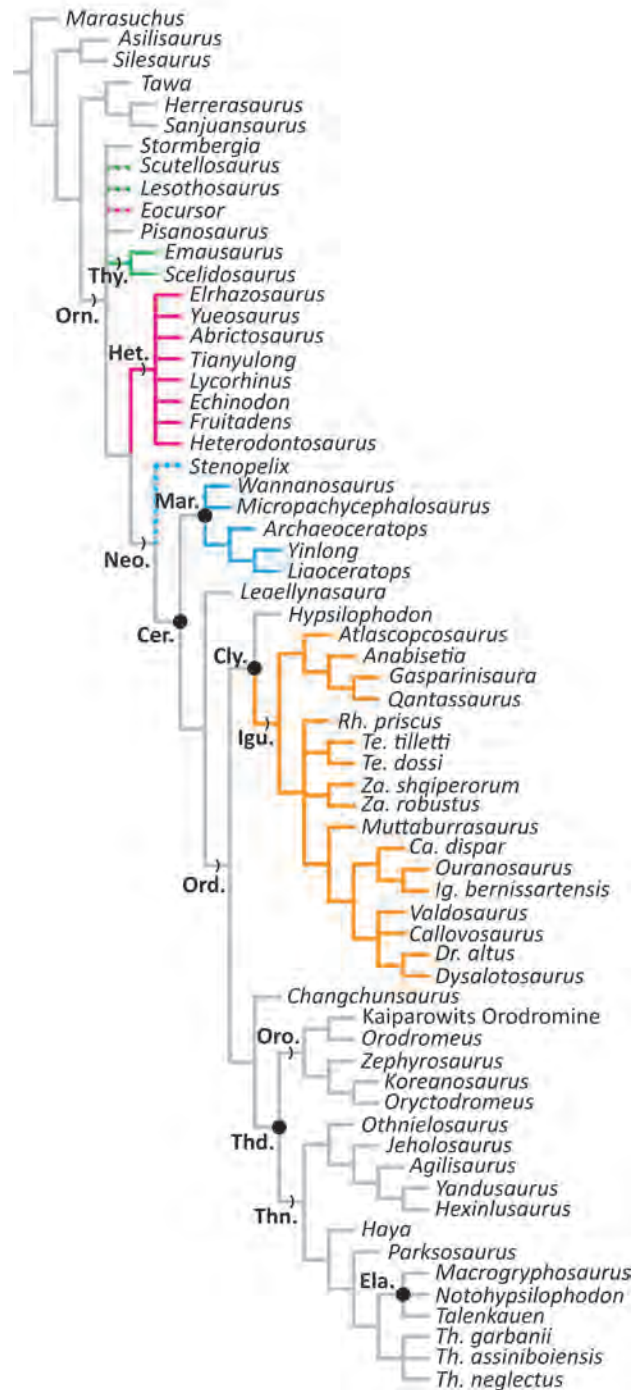


Figure 2.6. Strict consensus tree of 600 most parsimonious trees generated from Boyd (2015) when femoral characters 212, 213 and 223 are removed. **Abbreviations:** **Cer.**, Cerapoda; **Cly.**, Clypeodonta; **Ela.**, Elasmaria; **Hyp.**, Hypsilophodontidae; **Ig.**, Iguanodon; **Igu.**, Iguanodontia (orange); **Mar.**, Marginocephalia (blue); **Neo.**, Ne-

ornithischia; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Oro.**, Orodrominae; **Te.**, *Tenontosaurus*; **Th.**, *Thescelosaurus*; **Thd.**, Thescelosauridae; **Thn.**, Thescelosaurinae; **Thy.**, Thyreophora (green); **Za.**, *Zalmoxes*. Coloured dashed lines indicate the group an OTU was recovered in the original analysis of Boyd (2015). Dashed lines indicate the group in which a taxon was recovered in the original analysis of Boyd (2015). (Fig. 2.6, cont.)

Dieudonné *et al.* (2021), whereas in Boyd (2015) braincase character scores are lowest (although no palatal characters are scored in Boyd [2015]). In the matrix of Boyd (2015), hind limb elements exhibit the highest character completeness scores of all postcranial regions (see Appendices, A2.74b). Pelvic characters are generally the most complete postcranial partition in Han *et al.* (2018) and Dieudonné *et al.* (2021). The forelimb region has the lowest character completeness scores across all three matrices.

Excluding characters with scores of less than 25% (Analysis I.1–2.B2015; see Appendices, A2.75–76) from the Boyd (2015) matrix prior to the tree search produces a well-resolved strict consensus with tree topologies very similar to the original strict consensus from Boyd (2015). Excluding characters whose scoring is 35% complete (n=93) prior to the tree search of Boyd (2015; Analysis I.3.B2015) results in 1300 MPTs and a poorly resolved strict consensus tree with the contents of Thescelosauridae and Cerapoda in a large polytomy (see Appendices, A2.77).

When characters that were scored for less than 15% (n=6) and 25% (n=22) were excluded from Han *et al.* (2018) prior to the tree search, 37,644 and 14,015 MPTs were produced, respectively, both with poorly resolved strict consensus trees (see Appen-

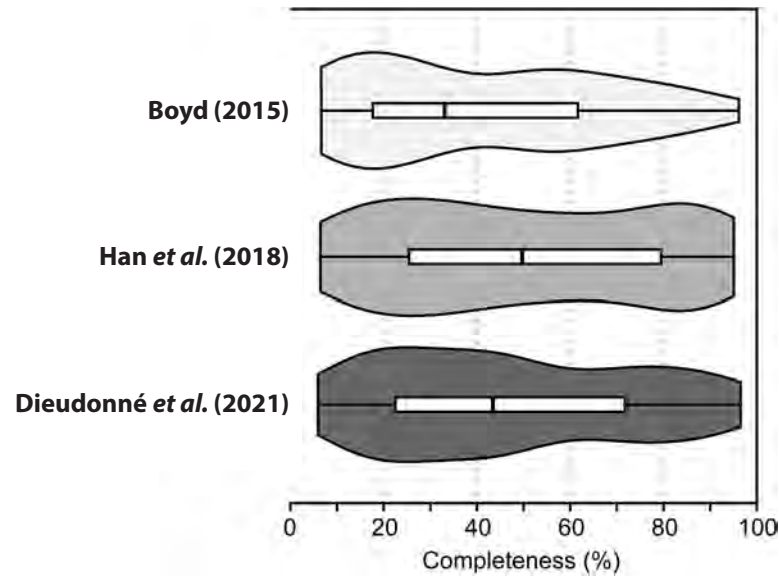


Figure 2.7. Distribution of completeness scores for individual characters in data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021).

trices, A2.78–79) very similar to the original analysis from Han *et al.* (2018). Further excluding characters scored with up to 35% completeness ($n=68$) produced 5361 MPTs and a similar poorly resolved strict consensus tree (see Appendices, A2.80), but with slightly better resolution among basal ornithischian taxa.

Excluding characters whose scoring is less than 15% complete ($n=7$) from Dieudonné *et al.* (2021; Analysis I.1.D2021) produced 1780 MPTs and a poorly resolved strict consensus tree (see Appendices, A2.81) very similar to DSCT, but with a polytomy of basal ornithopods. When further characters with scores that are under 25% ($n=22$) and 35% ($n=74$) complete are excluded from Dieudonné *et al.* (2021), 4559 and 1981 MPTs are produced, respectively, both with much more poorly resolved strict consensus trees (see Appendices, A2.82–83).

These results demonstrate that removing characters with low completeness

scores has a negative effect on tree resolution in all three matrices, but does not result in major changes to inferred relationships.

2.3.3.5. Homoplasy. The tree search of the Boyd (2015) matrix with an implied weighting of $k=5$ (Analysis J.1.B2015), produced 538 MPTs with a relatively well-resolved strict consensus tree (see Appendices, A2.84) that showed several topological differences to the original Boyd (2015) strict consensus tree produced where all characters were equally weighted: (1) the ‘elasmarian thescelosaurids’ *Notohypsilophodon*, *Talenkauen* and *Macrogryphosaurus* are recovered within Cerapoda as ornithopods; (2) the basal marginocephalian *Stenopelix* is placed as a basal neornithischian; (3) *Hypsilophodon* and *Micropachycephalosaurus* are recovered outside of Cerapoda as basal thescelosaurids; and (4) the Asian taxa *Yueosaurus* and *Jeholosaurus* are recovered within Thescelosauridae. As the concavity constant is reduced ($k=3$ and $k=1$; Analysis J.2–3.B2015) the resolution of the resulting tree topologies decreases, with larger polytomies at the base of Cerapoda, but the contents of Thescelosauridae and Cerapoda remain the same (see Appendices, A2.85–86).

A tree search of the matrix by Han *et al.* (2018) with implied weighting using a high concavity constant ($k=5$) produced 384 MPTs with a poorly resolved strict consensus tree (see Appendices, A2.87). This strict consensus showed very few differences to that produced when all characters were weighted equally, but is generally better resolved: (1) the polytomy at the base of Ornithischia is resolved; (2) Marginocephalia (Ceratopsia+Pachycephalosauria) is recovered; (3) iguanodontian relationships are fully resolved; (4) *Yandusaurus* is recovered as an early-branching pachycephalosaurid; and (5) the possible ceratopsian *Albalophosaurus* is placed in a polytomy at the base of Genasauria. Reducing the concavity constant to $k=3$ does not impact the topol-

ogy of the strict consensus tree, and further reducing it to $k=1$ only results in the movement of *Stenopelix* to the base of Marginocephalia (see Appendices, A2.88–89).

When an implied weighting of $k=5$ was applied prior to a tree search of the Dieudonné *et al.* (2021; Analysis J.1.D2021) matrix, three MPTs were produced with a well-resolved strict consensus tree (see Appendices, A2.90). This strict consensus tree showed several differences concerning ‘hypsilophodontid’ taxa to that of the DSCT, recovering: (1) *Hexinlusaurus* within Ornithopoda in a sister-taxon relationship with *Kulindadromeus*; (2) *Haya* and *Changchunsaurus* + *Jeholosaurus* in an Asian clade ‘Jeholosauridae’ sensu Han *et al.* (2012); (3) ‘Jeholosauridae’ in a sister-group relationship with Orodrominae; (4) *Yandusaurus* in a resolved position within Ornithopoda, as a sister-group to *Gasparinisaura* + *Parksosaurus*; and (5) *Gasparinisaura* + *Parksosaurus* basal to *Hypsilophodon* and outside of Clypeodonta and Hypsilophodontidae. Reducing the concavity constant to $k=3$ (Analysis J.2.D2021) does not significantly impact the relationships of the strict consensus tree (see Appendices, A2.91), but further reduction to $k=1$ (Analysis J.3.D2021) recovers controversial relationships: Marginocephalia is not recovered and Pachycephalosauria falls out as an early branching ornithischian clade (see Appendices, A2.92).

Characters from Dieudonné *et al.* (2021) are far more homoplastic than those from both Boyd (2015) and Han *et al.* (2018) (see Appendices, A2.93). The distribution of homoplasy throughout the skeleton differs among all three matrices (see Appendices, A2.94). In Boyd (2015), pelvic girdle characters are the most homoplastic relative to their weighting. Dental characters are highly homoplastic across all three matrices, but especially so in Han *et al.* (2018) relative to the rest of the skeleton. The most homoplastic dental characters in Boyd (2015; B137) and Dieudonné *et al.* (2021; D150)

concern the number of dentary teeth, while in Han *et al.* (2018) the most homoplastic character relates to the number of maxillary teeth (H203). For Han *et al.* (2018) and Dieudonné *et al.* (2021) these dental characters are also the most homoplastic of all characters in the given matrix. In all three matrices, rostral characters are the least homoplastic.

Excluding characters with varying degrees of homoplasy did not cause the topologies to converge. Excluding homoplastic characters in each of the three ranges (>95th, >85th, >75th percentile) investigated from Boyd (2015; Analysis K.1–3.B2015) generates highly unresolved strict consensus trees consisting of a polytomy at the base of Ornithischia (see Appendices, A2.95–97). Excluding characters in the top 95th percentile from the matrix by Han *et al.* (2018; Analysis K.1.H2018) generated 44,900 MPTs and a poorly resolved strict consensus with a polytomy at the base of Ornithischia, but recovered the clades Thyreophora, Iguanodontia and Neoceratopsia (see Appendices, A2.98). Exclusion of homoplastic characters in the top 85th percentile (Analysis K.2.H2018) produced 40,500 MPTs with a poorly resolved strict consensus (see Appendices, A2.99) very similar to HSCT, but better resolved, recovering Marginocephalia and Genasauria. Further exclusion of homoplastic characters (Analysis K.3.H2018) generates a highly unresolved strict consensus from 99,100 MPTs consisting of a polytomy at the base of Ornithischia (see Appendices, A2.100). Excluding characters with homoplasy over the 95th percentile from Dieudonné *et al.* (2021; Analysis K.1.D2021) resulted in 3779 MPTs and a poorly resolved strict consensus tree (see Appendices, A2.101), similar to DSCT, but with a polytomy at the base of Ornithopoda and poorer resolution among pachycephalosaurians. Further exclusion of homoplastic characters (Analysis K.2–3.D2021) produces an even more poorly resolved strict con-

sensus (see Appendices, A2.102–103), with a polytomy at the base of Ornithischia and Neornithischia.

Use of implied weighting does not impact the topology of Han *et al.* (2018), while in Dieudonné *et al.* (2021) only the strongest use of implied weighting ($k=1$) causes significant topological changes to the ornithischian tree (e.g. recovering pachycephalosaurians at the base of Ornithischia). The use of implied weighting in the Boyd (2015) matrix results in a strict consensus that is less well resolved than BSCT and contains several major changes in topology concerning the taxa of interest. Excluding highly homoplastic characters from all three matrices does not alter the topologies or relationships observed from the original studies but does significantly reduce the resolution of the consensus trees produced.

2.4. Discussion

2.4.1. Taxon sampling

Studies investigating phylogenetic methods agree overwhelmingly that more extensive taxon sampling, including the addition of highly incomplete taxa, is beneficial to analyses (e.g. Kearney 2002; Zwickl & Hillis 2002; Kearney & Clark 2003; Wiens 2006; Butler & Upchurch 2007; Heath *et al.* 2008; Prevosti & Chemisquy 2010; Wiens & Morrill 2011; but see Rosenberg & Kumar [2001] for an alternative view). However, it is also clear that unstable taxa can have a negative effect on tree resolution and obscure inferred relationships, with reduced consensus methods being utilized in several recent analyses of ornithischian relationships (e.g. Maidment 2010; Thompson *et al.* 2012; Baron *et al.* 2017a; Han *et al.* 2018; Dieudonné *et al.* 2021).

In addition, I find here that the choice of taxa included within an analysis can significantly impact the inferred relationships, particularly concerning ‘wildcard’ groups with controversial or disputed phylogenetic placements (e.g. heterodontosaurids, thescelosaurids) (Brusatte 2010; Raven & Maidment 2018). Although there is a reasonable amount of overlap between taxa in Boyd (2015) and either of the two H1 matrices (>60% overlap), removing unique taxa in Analysis A resulted in several substantial changes from the original reported tree topologies. The sampling of OTUs was found to have the most influence on the tree topologies recovered from the Boyd (2015) dataset, followed by Han *et al.* (2018), and lastly Dieudonné *et al.* (2021), whose topology remained very consistent with DRSCT (original Dieudonné *et al.* [2021] reduced strict consensus tree) when unique taxa were removed (n=27/72; Figure 2.4b).

Excluding unique taxa (not found in Boyd [2015]) from Han *et al.* (2018) and Dieudonné *et al.* (2021) did not impact the phylogenetic position of the ‘hypsilophodontids’ and these taxa remained in a placement consistent with H1 (Hypothesis 1; Figure 2.1), within Ornithopoda. In contrast to the results from BSCT (original Boyd [2015] strict consensus tree), removing unique taxa from Boyd (2015) recovers the ‘hypsilophodontids’ within Cerapoda, as ornithopods (the H1 position), in both Analysis A.1 (taxa shared with Han *et al.* 2018; Figure 2.3) and A.2 (taxa shared with Dieudonné *et al.* 2021; Figure 2.4), but still primarily within a monophyletic Thescelosauridae. This suggests that the H2 position of ‘hypsilophodontids’ found in Boyd (2015) is at least partially related to taxon sampling.

Additionally, the original phylogenetic analyses from Boyd (2015) and Han *et al.* (2018) both recovered Heterodontosauridae as an early branching ornithischian clade (in contrast to Dieudonné *et al.* [2021], where the group is recovered within Mar-

ginocephalia), but in Analysis A.1 the heterodontosaurids are recovered as neornithischians (and even in a sister-group relationship to Marginocephalia in Analysis A.1b). From my results it is clear that OTU choice is capable of significantly altering the position of controversial clades. In particular, it leads us to question the phylogenetic placement of the heterodontosaurids, which seems to be highly dependent on the other taxa included, although it is noteworthy that in analyses of larger-scale dinosaur matrices, heterodontosaurids remain close to the root of Ornithischia (Baron *et al.* 2017b).

While removing unique taxa from the analyses caused numerous changes in topology from the original consensus trees reported, the same is not found when taxa were excluded based on their completeness or instability. Excluding taxa with low completeness scores prior to tree searches (Analysis B) recovered tree topologies very similar to the original studies. The most significant difference is that removing highly incomplete taxa from Han *et al.* (2018) and (to a lesser degree) Dieudonné *et al.* (2021) increased tree resolution. Unstable taxa identified and pruned in the original studies from Han *et al.* (2018) and Dieudonné *et al.* (2021) to increase tree resolution were all found here to be <25% complete, which is likely to explain why *a priori* exclusion of incomplete taxa in Analysis B.2–3 increased the resolution of the strict consensus trees produced. This suggests a relationship between instability and completeness, which is supported by a correlation between completeness values and PCR (positional congruence reduced) values in taxa from the Han *et al.* (2018) matrix. Within a tree search, a greater proportion of missing data for a taxon (i.e. lower taxon completeness) generates more potential placements for that taxon, which find less consensus, and consequently are typically recovered in a poorly resolved position (Kearney 2002). This relationship is not found in Boyd (2015), which generally has more incomplete taxa

than either H1 matrix (Figure 2.5), but fewer unstable taxa (see Appendices, A2.26). Instead, this result demonstrates how taxa with relatively few characters scored can still be highly phylogenetically informative and so should not be excluded from analyses (Kearney & Clark 2003).

2.4.2. Character sampling

The data matrix from Boyd (2015) shares relatively few characters with either Han *et al.* (2018; 30%) or Dieudonné *et al.* (2021; 46%) and it is therefore unsurprising that enigmatic taxa such as ‘hypsilophodontids’ have been recovered in such conflicting placements within the neornithischian tree. Of those characters that are shared, the majority use different character states and do not capture the same morphological variation. Some of these differences in state partitioning are very subtle, but significantly change how the characters infer evolutionary change and, in some cases, whether these characters are supportive of specific clades.

Character ordering increased the resolution of the strict consensus trees generated from the datasets of Han *et al.* (2018) and Dieudonné *et al.* (2021), without significantly altering the inferred relationships. Ordering multi-state characters where appropriate has been found similarly to increase tree resolution in several previous studies (Slowinski 1993; Grand *et al.* 2013; Rineau *et al.* 2015).

Analysing craniodental and postcranial character partitions in isolation often recovers different relationships (Mounce *et al.* 2016) and this effect has been shown to be especially marked in non-avian dinosaurs (Li *et al.* 2020). My analyses demonstrate significant differences between the tree topologies produced from craniodental and postcranial character partitions of the three neornithischian datasets I exam-

ined. Across all three matrices, removing either craniodental or postcranial character partitions greatly reduced tree resolution compared to the original consensus trees of Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). However, in Boyd (2015), postcranial characters were found to yield a more resolved tree topology compared to craniodental characters. This is in contrast to results found for Han *et al.* (2018) and (to a much lesser extent) Dieudonné *et al.* (2021), and also ornithischian phylogenies as a whole (Li *et al.* 2020), in which craniodental characters seem to have more impact on resulting topology. These contrasting results further demonstrate the extent to which the data matrix from Boyd (2015) differs from that of Han *et al.* (2018) and Dieudonné *et al.* (2021).

Character partition exclusion does not affect the position of the ‘hypsilophodontids’ in Han *et al.* (2018) and Dieudonné *et al.* (2021) and the results of these parsimony analyses remain in agreement with H1. This suggests that characters throughout the skeleton in both H1 matrices have generally congruent phylogenetic signals concerning the position of the ‘hypsilophodontids’. Removing dental or hind limb characters from Boyd (2015) recovers the ‘hypsilophodontids’ within Ornithopoda, in an H1 position and in conflict with the H2 placement originally recovered in Boyd (2015). This would suggest that dental and hind limb partitions both contain characters that are disproportionately more supportive of a H2 topology than characters from other skeletal regions. This was also found to be the case more specifically in individual skeletal elements and characters; excluding only three femoral characters from the Boyd (2015) matrix recovered Thescelosauridae within Cerapoda (an H1 position; Figure 2.6), in contrast to results from BSCT. These three femoral characters have completeness scores that are relatively high (range = 29–71%; average = 53%), are not particularly homoplastic

(range = 1–3 extra steps), and pertain to distinct morphological features at the proximal (B212, presence/ absence of a trench between the greater trochanter and the head of the femur; B213, convex/flat lateral surface of the greater trochanter) and distal end (B223, form of the anterior intercondylar groove) of the femur. B213 is also found to be a synapomorphy of Thescelosauridae, both in this study and in Boyd (2015). In Boyd (2015), this character did not support the clade Jeholosauridae (*Changchunsaurus* + *Haya*, *Jeholosaurus*; Han *et al.* 2012), with *Jeholosaurus* being coded B213:0 (convex lateral surface of the greater trochanter) and *Haya* being coded B213:1 (flat lateral surface of the greater trochanter). This character was later excluded from the modified Boyd (2015) matrix by Madzia *et al.* (2018) and reformulated in Dieudonné *et al.* (2021), where it was found to support Jeholosauridae. These characters, as defined and coded in Boyd (2015), have a strong influence on the topology produced in BSCT and their inclusion significantly alters the inferred interrelationships of ornithischian taxa. The distribution of these characters, the definition of their character states, and the way they are scored should therefore be a focus of future work.

My results suggest that excluding highly homoplastic or incompletely scored characters does not significantly alter the tree topology or relationships recovered, but reduces the resolution of the consensus trees that are generated. Implied weighting of characters at all strength levels ($k=1-5$) does not alter the position of ‘hypsilophodontids’ within Han *et al.* (2018) and Dieudonné *et al.* (2021), although in the latter, the strongest level of weighting ($k=1$) does recover Pachycephalosauria (inclusive of Heterodontosauridae, as in DSCT) in a controversial placement, separate from Ceratopsia, at the base of Ornithischia (see Appendices, A2.92). The use of implied weighting in Boyd (2015) results in several major changes compared to the BSCT concerning taxa of

interest, most notably recovering: (1) *Hypsilophodon* outside of Cerapoda, rather than as a basal ornithopod; and (2), the elasmarians inside Cerapoda as ornithopods, rather than as a clade of thescelosaurines. These results are more congruent with the updated iteration of the Boyd (2015) matrix by Madzia *et al.* (2018), which also recovers both of these topological features. The Madzia *et al.* (2018) iteration of the Boyd (2015) matrix, along with my own study, demonstrates the labile relationships of these taxa, with numerous changes in relationships possible between Thescelosauridae and Cerapoda, which seem to be particularly marked with elasmarians. The use of implied character weighting is contentious within parsimony analyses (Congreve & Lamsdell 2016; Goloboff *et al.* 2018; Smith 2019b), but it is important to note the effect that homoplastic characters have on these matrices.

2.4.3. Recommendations for future studies

I find that recent analyses that have recovered one of two conflicting placements for the ‘hypsilophodontids’ are largely distinct in character composition. The independence of these matrices has been beneficial to our understanding of ornithischian phylogenetics, with areas of consensus adding credence to the validity of those common relationships, and areas of disagreement identifying unresolved clades that need more attention (e.g. ‘hypsilophodontids’, heterodontosaurids). However, I propose that rather than continuing to develop largely independent character matrices that predictably recover either a H1 or H2 placement for ‘hypsilophodontids’, characters from recent neornithischian data matrices should be combined, critically assessed and updated to reflect current understanding of ornithischian character evolution. Characters should be widely sampled from throughout the skeleton and over-representation of a specific

element (e.g. femoral characters in Boyd [2015]) should be limited if possible, although consideration should be given to how character rich a particular element is. The characters that support particular clades of interest (e.g. ‘Thescelosauridae’, Cerapoda and Ornithopoda) or have been shown to be problematic in this study should be assessed to understand how their character construction and state partitioning influence their evolutionary signal.

As the relationships of ‘hypsilophodontids’ remain relatively fluid with respect to those of ‘core’ cerapodans, future studies should cast a wide net regarding OTU choice, sampling a broader array of basal forms from the major genasaurian clades and potentially incorporating representatives of other dinosaur clades. Testing whether outgroup choice substantially influences tree topology was beyond the scope of this study, but this is also an important consideration for future studies with several recent major changes to the base of the ornithischian tree (Baron & Barrett 2017; Agnolín & Rozadilla 2018; Müller & García 2020; Dieudonné *et al.* 2021). The phylogenetic analysis from Boyd (2015) was the first to include several poorly known enigmatic neornithischian taxa (e.g. *Atlascopcosaurus*, *Koreanosaurus*, *Leaellynasaura*, *Notohypsilophodon*, *Qantassaurus*) in a large-scale ornithischian matrix. Several of these taxa (particularly those from the Southern Hemisphere) have not been included in an independent phylogenetic analysis subsequently, possibly due to the incompleteness of some of this material, inadequate published descriptions, their uncertain systematics, or outdated reference material. It is important for future analyses to be as inclusive of these enigmatic taxa as possible, as well as recently described taxa (e.g. Li *et al.* 2019; Yang *et al.* 2020). Importantly, future matrices should include characters representative of the large range of ornithischian taxa included. Characters from Boyd

(2015) were predominately (37%; n=120) derived from Scheetz (1999), which focused on the phylogenetic position of *Orodromeus makelai* and did not include any marginocephalian taxa. Because characters derived from these two matrices were not formulated for use on marginocephalian taxa, they may not be appropriate for discerning the phylogenetic positions of taxa that are relatively labile around the base of Cerapoda, to the extent that they are in Boyd (2015).

Prior to the tree search, safe taxonomical reduction should be utilized to identify taxa that can be excluded without impacting the relationships of the remaining taxa. Here, safe taxonomical reduction identified one taxon to remove from both Boyd (2015; *Thescelosaurus garbanii*) and Han *et al.* (2018; *Yueosaurus tiataiensis*), which in the case of the latter significantly reduced the number of MPTs generated in the tree search. Where it can be justified, characters should be ordered. Although increased resolution does not necessarily increase the accuracy of the resulting topology, it is crucial to discerning phylogenetic relationships (Smith 2019b). Therefore, following the tree search, if the resolution of the strict consensus tree is poor, unstable taxa should be identified and pruned to give a reduced strict consensus (Wilkinson 1994; Pol & Escapa 2009). Taxa should not be removed *a priori* (unless using safe taxonomical reduction), even if they have been identified as being unstable within the topology. Here, removing taxa identified by IterPCR (Pol & Escapa 2009) as unstable *a posteriori* (i.e. pruning), resulted in increased tree resolution compared to *a priori* removal. In addition to the recommendations outlined in this study, new computational methods are also being developed to assess conflict between competing topologies derived from morphological datasets (Goloboff & Sereno 2021).

2.5. Conclusions

This study presents the first in-depth assessment and comparison of three recent neornithischian analyses that recover one of two conflicting placements for the ‘hypsilophodontids’: hypothesis 1 (H1), primarily within Cerapoda as a paraphyletic assemblage of basal ornithopods (Han *et al.* 2018; Dieudonné *et al.* 2021); and hypothesis 2 (H2), primarily within the non-cerapodan neornithischian clade, Thescelosauridae (Boyd 2015). Taxon and character manipulation of each data matrix was performed to identify how these factors influenced the recovered topologies.

In all of the analytical permutations applied in this study, the H1 matrices I investigated (Han *et al.* 2018; Dieudonné *et al.* 2021) recovered ‘hypsilophodontids’ within Cerapoda, in a position consistent with their original H1 placement. By contrast, in the H2 matrix investigated (Boyd 2015), the positions of ‘hypsilophodontids’ were found to be far more susceptible to the influences of both character and taxon sampling, with several analyses recovering the majority of ‘hypsilophodontids’ within Cerapoda, in positions more congruent with H1 than H2. Within the Boyd (2015) dataset, characters from femoral and dental regions were found to be disproportionately more supportive of a H2 topology, compared to characters from other regions of the skeleton. Furthermore, removing only three femoral characters from Boyd (2015) resulted in Thescelosauridae being recovered within Ornithopoda. This result emphasises how influential individual characters can be in a data matrix, and how they can have a major impact on our understanding of major evolutionary changes. While the phylogenetic positions of the ‘hypsilophodontids’ remain contentious and require much further study, my results tend to favour a placement consistent with H1, within Cerapoda.

Chapter 3

MORPHOLOGICAL DISPARITY OF THE 'HYPSILOPHODONTIDS' AND OTHER ORNITHISCHIAN DINOSAURS

The 'hypsilophodontids' are an informal assemblage of ornithischian dinosaurs that have been traditionally united by a shared bauplan: bipedal, small to medium-bodied, and lacking distinctive and ornate morphological features. The phylogenetic affinities of these dinosaurs are highly controversial, with recent cladistic analyses recovering the taxa in conflicting positions within Ornithischia. Here, I performed discrete character-based disparity analyses on three recent character-taxon matrices to visualise and quantify the morphological variation between the 'hypsilophodontids' and other ornithischian groups. Anatomical regions were investigated separately to determine how patterns of evolution differ throughout the skeleton. My results show that ornithischian disparity declined to its nadir in the Middle Jurassic, before increasing dramatically into the Late Jurassic. Most anatomical partitions follow this evolutionary pattern: however, pelvic girdle and hind limb morphologies were comparatively diverse in the Middle Jurassic, indicating that important locomotory adaptations were evolving at this time. Principal coordinate plots show that the 'hypsilophodontids' have a large morphospace distribution, demonstrating that this group represents a highly diverse assortment of taxa. When different anatomical partitions are analysed, some of these taxa frequently overlap with derived ornithischian clades, such as iguanodontians, while others often occupy unique morphospace. Although the affinities of the

‘hypsilophodontids’ remain uncertain, the broadly disparate signals observed in this study imply that these taxa likely occupy different branches of the ornithischian tree, rather than being united within a monophyletic group.

3.1. Introduction

Assessing the morphological variation (disparity) among species and higher taxa has been fundamental in developing our understanding of macroevolutionary trends within the fossil record, giving insight into adaptive radiations, evolutionary rates, and morphological innovation (Foote 1993; Wills 2001; Hopkins & Gerber 2021). As a result, several methods of quantifying disparity have been developed and implemented in palaeobiological studies over the last half a century. In some of the earliest disparity studies, higher taxonomic ranks (e.g. families, orders) were used as proxies for morphological distinctiveness (Valentine 1980; Erwin *et al.* 1987; Foote 1997; Erwin 2007). Changes in the number of higher taxa through time provided a relatively easy way of evaluating patterns of diversification and extinction (Valentine 1980; Erwin *et al.* 1987; Foote 1997), although the artificial and subjective nature of taxonomic ranks led to this approach being criticised (Smith and Patterson 1988; Forey *et al.* 2004; Erwin 2007).

Modern disparity studies typically measure the morphological variation amongst fossil taxa using traditional morphometric measurements (e.g. Foote 1993; Lefebvre *et al.* 2006; Dyke *et al.* 2009; Campione & Evans 2011; Gutarra *et al.* 2023), geometric morphometrics (e.g. Friedman 2010; Young *et al.* 2010; Campione & Evans 2011; Brusatte *et al.* 2012a; Foth *et al.* 2012; MacLaren *et al.* 2017; Maiorino *et*

al. 2018; Ruta *et al.* 2019; Schaeffer *et al.* 2020) and discrete character analyses (e.g. Foote 1984; Brusatte *et al.* 2008; Young *et al.* 2010; Prentice *et al.* 2011; Butler *et al.* 2012b; Fischer *et al.* 2017; Ezcurra & Butler 2019; Ruta *et al.* 2019; Moon & Stubbs 2020; Schaeffer *et al.* 2020; Apaldetti *et al.* 2021; Raven 2021; Müller 2022; Casali *et al.* 2023). Discrete character analyses tend to be the preferable option in palaeobiological studies, particularly when being applied to diverse taxonomic samples, as homologous morphometric variables can often be difficult to find in highly divergent taxa (Hetherington *et al.* 2015). Additionally, morphometric methods are highly intolerant to missing data, which proves particularly problematic when analysing fossil taxa that are regularly fragmented, deformed and eroded (Brown *et al.* 2012; Arbour & Brown 2014; Kammerer *et al.* 2020).

Of the studies that employ discrete character methods, most re-purpose data from cladistic matrices originally constructed for assessing phylogenetic relationships (e.g. Brusatte *et al.* 2008; Young *et al.* 2010; Prentice *et al.* 2011; Butler *et al.* 2012b; Fischer *et al.* 2017; Ezcurra & Butler 2019; Moon & Stubbs 2020; Schaeffer *et al.* 2020; Apaldetti *et al.* 2021; Raven 2021; Müller 2022; Casali *et al.* 2023). Once these character-taxon matrices have been converted into a pairwise distance matrix, results can be subjected to ordination and various disparity metrics, in order to unravel trends through time and between taxonomic groups (Lloyd 2016). In addition, recent disparity analyses have also been used to investigate the unique evolutionary patterns of different anatomical regions (e.g. Müller 2022; Casali *et al.* 2023). Morphological changes in the vertebrate skeleton are known to be highly modular (Mitteroecker & Bookstein 2007; Clark & Middleton 2008; Klingenberg 2008; Mounce *et al.* 2016). As different anatomical regions are subject to differing selective pressures (e.g. feed-

ing, locomotion), distinct regions of the skeleton often exhibit different evolutionary rates (Mitteroecker & Bookstein 2007; Clark & Middleton 2008; Klingenberg 2008; Mounce *et al.* 2016). Partitioning datasets in this way can reveal morphologies that are high specialised or that have evolved convergently in multiple groups (Müller 2022; Casali *et al.* 2023).

Ornithischian (“bird-hipped”) dinosaurs were a highly successful and diverse group that dominated late Mesozoic ecosystems. Today, they are well-known for their elaborate and often ornate morphologies, which include horns, frills, crests, and body armour (Farlow & Dodson 1975; Weishampel *et al.* 2007; Prieto-Márquez *et al.* 2016). In contrast, the group of ornithischians informally termed the ‘hypsilophodontids’ are comparatively conservative in morphology. These taxa are bipedal, small to medium-bodied, and tend to lack distinctive and ornate morphological features (Norman *et al.* 2004).

As discussed in Chapter 2 (Brown *et al.* 2022), there is currently little consensus on the position of ‘hypsilophodontids’ with Ornithischia, with recent phylogenetic analyses recovering these taxa in one of two conflicting positions: primarily within Cerapoda, as early-diverging ornithopods (e.g. Butler *et al.* 2008; Dieudonné *et al.* 2016; Han *et al.* 2018; Dieudonné *et al.* 2021); or primarily as non-cerapodan neornithischians, within the clade Thescelosauridae (Boyd 2015; Herne *et al.* 2019). It is also uncertain how closely related the ‘hypsilophodontids’ are to each other, with most modern cladistic analyses generally agreeing that the group is para- or polyphyletic (e.g. Scheetz 1999; Sereno 1999; Buchholz 2002; Butler *et al.* 2008; Boyd 2015).

While discrete character-based disparity analyses have been widely applied to fossil groups (e.g. Prentice *et al.* 2011; Butler *et al.* 2012; Ruta *et al.* 2013; Ezcurra and

Butler 2018, Schaeffer *et al.* 2019; Moon and Stubbs 2020), work on ornithischians has been relatively limited, focusing on key periods in dinosaur evolution (e.g. end-Cretaceous mass extinction event, Brusatte *et al.* 2012b), or particular groups, including the thyreophorans (Romano 2017; Raven 2021; Romano 2021), hadrosaurs (Stubbs *et al.* 2019; Takasaki *et al.* 2020) and ornithomimid dentition (Strickson *et al.* 2016). To date, the study by Strickson *et al.* (2016) is the only disparity analysis to include ‘hypsilophodontid’ taxa, in which the authors found these taxa had low dental disparity and a slower evolutionary rate compared to derived ornithomimids.

Here, I assess the disparity of the ‘hypsilophodontids’ and other ornithischians using character-taxon matrices from three recent phylogenetic analyses. I investigate how ornithischian disparity as a whole has changed over time and the areas of the skeleton that may have been driving these changes. I also reconstruct the morphospace occupation of different anatomical partitions to observe the position of ‘hypsilophodontids’ relative to other ornithischian clades. The main aim of this study is to determine how diverse the ‘hypsilophodontids’ were, and to see if morphospace occupation can reveal subtle signals in the cladistic matrices that are the basis for assessing the phylogenetic affinities of these dinosaurs.

3.2. Methods

3.2.1. Matrices

The character-taxon matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were chosen for this study. These three matrices were investigated in Brown *et al.* (2022; Chapter 2) and a full summary of each can be found in Table 2.1. They are

ideal for this study because they are largely independent of each other and find conflicting phylogenetic placements for several key ornithischian taxa (including ‘hypsilophodontids’) that substantially alter our understanding of the origin and evolution of Cerapoda (Brown *et al.* 2022; Chapter 2).

3.2.2. Comparative taxonomic groupings

To understand where ‘hypsilophodontids’ (or thescelosaurids/early-diverging ornithopods, as they will be referred to herein) plot relative to derived ornithischian clades, all operational taxonomic units (OTUs) were assigned to one of seven groups: early-diverging ornithischian/early-diverging neornithischian (EDO/EDN); heterodontosaurid; thyreophoran; thescelosaurid/early-diverging ornithopod (T/EDO); iguanodontian; ceratopsian; pachycephalosaurian. These assignments were based on phylogenetic proximity in recent analyses (Butler *et al.* 2008; Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021).

The group ‘EDO/EDN’ encompasses all ornithischian taxa that have not been recently recovered within any of the following clades: Heterodontosauridae, Thyreophora, Thescelosauridae, or Cerapoda. I decided to lump together early-diverging ornithischians and early-diverging neornithischians because some taxa are relatively fluid between these positions (e.g. *Eocursor parvus*, Han *et al.* 2018; Dieudonné *et al.* 2021). Additionally, the putative thyreophorans *Isaberrysaura*, *Laquintasaura* and *Lesothosaurus* were assigned to EDO/EDN to assess their distance in morphospace from other thyreophorans. There is currently little consensus on the phylogenetic affinities of *Laquintasaura* and *Lesothosaurus*, with recent analyses recovering these taxa either near the base of either Genasauria, Thyreophora or Neornithischia (Butler *et al.*

2008; Boyd 2015; Baron *et al.* 2017a; Han *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021). In contrast, the inclusion of *Isaberrysaura* within Thyreophora is largely uncontroversial (Han *et al.* 2018; Dieudonné *et al.* 2021) and the taxon likely represents the stratigraphically earliest-known stegosaur (Raven *et al.* 2023). However, as the original phylogenetic analyses by Salgado *et al.* (2017) failed to recover *Isaberrysaura* as a thyreophoran (with *Isaberrysaura* being recovered by Salgado *et al.* [2017] in various phylogenetic positions, including as a basal neornithischian, non-cerapodan thescelosaurid, and as an early-diverging ornithopod, depending on the ornithischian character matrix used [Butler *et al.* 2007; Godefroit *et al.* 2014; Boyd 2015; Baron *et al.* 2017a]), I decided to exclude the taxon from the thyreophoran group in this study, to test how *Isaberrysaura* plots relative to thyreophorans and other ornithischians.

All taxa that have been recovered as either a non-cerapodan thescelosaurid or non-iguanodontian early-diverging ornithopod in Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) were assigned to T/EDO (Table 3.1; n = 19).

Here, ceratopsians and pachycephalosaurians were investigated as two separate groups, rather than together within a marginocephalian group. Considering the broadly different bauplans of ceratopsians and pachycephalosaurians (e.g. with the former being mainly quadrupedal and latter being entirely bipedal), lumping these taxa together may result in marginocephalians occupying a large distribution of morphospace. Investigating these clades separately also allowed me to assess the morphospace distribution of these clades relative to both each other, and to other ornithischian clades. In the recent analysis by Dieudonné *et al.* (2021), heterodontosaurids were recovered as a paraphyletic group near the base of Pachycephalosauria. Grouping ceratopsians and pachycephalosaurians would limit the ability of this study to visually and statistically

Table 3.1. OTUs assigned as thescelosaurid/early-diverging ornithopod (T/EDO) in this study and how they have been recovered in recent phylogenetic analyses by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021).

OTUs	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
<i>Changchunsaurus parvus</i>	Thescelosaurid	Early-diverging ornithopod	Early-diverging ornithopod
<i>Convolosaurus marri</i>	-	-	Non-iguanodontian clypeodont
<i>Gasparinisaura cincosaltensis</i>	Iguanodontian	Early-diverging ornithopod	Non-iguanodontian clypeodont
<i>Haya griva</i>	Thescelosaurid	Early-diverging ornithopod	Early-diverging ornithopod
<i>Hypsilophodon foxii</i>	Early-diverging ornithopod	Early-diverging ornithopod	Non-iguanodontian clypeodont
<i>Jeholosaurus shangyuensis</i>	Early-diverging neornithischian	Early-diverging ornithopod	Early-diverging ornithopod
<i>Kaiparowits orodromine</i>	Thescelosaurid	-	-
<i>Koreanosaurus boseongensis</i>	Thescelosaurid	Early-diverging ornithopod	Early-diverging ornithopod
<i>Kulindadromeus zabaikalicus</i>	-	-	Early-diverging ornithopod
<i>Macrogyrophosaurus gondwanicus</i>	Thescelosaurid	-	Elasmarian iguanodontian

Table. 3.1. (cont. on following page)

Table 3.1. (cont.)

OTUs	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
<i>Nanosaurus agilis</i>	-	-	Early-diverging ornithopod
<i>Notohypsilophodon comodensis</i>	Thescelosaurid	-	-
<i>Orodromeus makelai</i>	Thescelosaurid	Early-diverging ornithopod	Early-diverging ornithopod
<i>Oryctodromeus cubicularis</i>	Thescelosaurid	-	-
<i>Parksosaurus warreni</i>	Thescelosaurid	Early-diverging ornithopod	Non-iguanodontian clypeodont
<i>Talenkauen santacrucensis</i>	Thescelosaurid	-	Elasmarian iguanodontian
<i>Thescelosaurus assinihoiensis</i>	Thescelosaurid	-	Non-iguanodontian clypeodont
<i>Thescelosaurus garbanii</i>	Thescelosaurid	-	-
<i>Thescelosaurus neglectus</i>	Thescelosaurid	Early-diverging ornithopod	Non-iguanodontian clypeodont
<i>Yueosaurus tiantaiensis</i>	Early-diverging neornithischian	Unresolved neornithischian	Non-iguanodontian clypeodont
<i>Zephyrosaurus schaffi</i>	Thescelosaurid	Unresolved neornithischian	Early-diverging ornithopod

investigate these hypotheses further.

Some marginocephalians included in this study have uncertain or conflicting placements in the phylogenetic analyses by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) (e.g. *Micropachycephalosaurus*, *Stenopelix*, *Wannanosaurus*; see Butler & Zhao [2008] and Butler & Sullivan [2009] for discussion on the affinities of these taxa). For consistent comparisons between analyses, these problematic taxa were assigned to either Ceratopsia or Pachycephalosauria: *Micropachycephalosaurus* was assigned to Ceratopsia, following Butler *et al.* (2008), despite being recovered in a polytomy at the base of Marginocephalia in Boyd (2015) and in a polytomy at the base of Cerapoda in Han *et al.* (2018); *Stenopelix* was assigned to Ceratopsia following Han *et al.* (2018) and Dieudonné *et al.* (2021); and finally, *Wannanosaurus* was assigned to Pachycephalosauria, following Han *et al.* (2018) and Dieudonné *et al.* (2021).

It is worth noting that in each of the three matrices investigated, the proportion of taxa from each taxonomic grouping is not representative of the true diversity of ornithischians (Figure 3.1a–d). Furthermore, the matrices include relatively few shared taxa (see Chapter 2: 2.3.2.1) and vary in how many taxa from each group they sample (Figure 3.1b–d). While Boyd (2015) and Dieudonné *et al.* (2021) were aimed at resolving neornithischian relationships, the purpose of the Han *et al.* (2018) analysis was primarily to clarify the positions of the basal ceratopsians, *Yinlong* and *Psittacosaurus*. The matrices from Boyd (2015) and Dieudonné *et al.* (2021) therefore contain a higher proportion of T/EDOs and iguanodontians than Han *et al.* (2018), while Han *et al.* (2018) contains a much higher proportion of ceratopsian taxa than either Boyd (2015) or Dieudonné *et al.* (2021). The differing aims of these matrices also influenced their creation and composition, with Han *et al.* (2018) including a higher proportion of

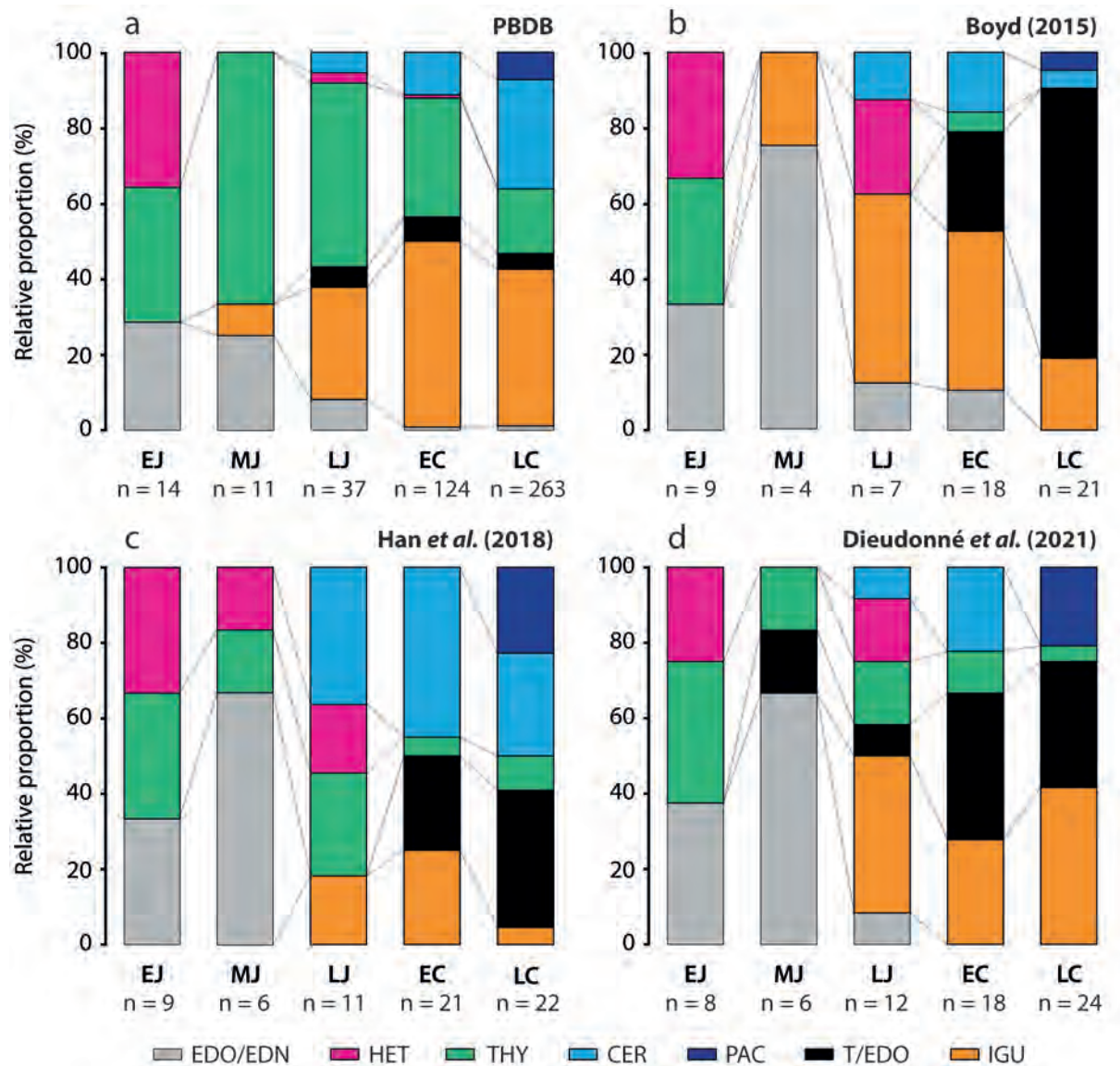


Figure 3.1. Relative diversity of ornithischian taxonomic groups over geological time (a, pbdb: paleobiodb.org, accessed 17/08/23) compared to the representation of those groups in recent morphological matrices from Boyd (2015, b), Han *et al.* (2018, c) and Dieudonné *et al.* (2021, d). Time bin abbreviations: EC, Early Cretaceous; EJ, Early Jurassic; LC, Late Cretaceous; LJ, Late Jurassic; MJ, Middle Jurassic. **Abbreviations:** CER, ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); IGU, iguanodontian (orange); HET, heterodontosaurid (pink); PAC, pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod

(black); **THY**, thyreophoran (green). (Fig. 3.1, cont.)

characters dedicated to polarising relationships within Ceratopsia. This will inherently affect the disparity results of the ceratopsians derived from the Han *et al.* (2018) matrix, likely showing this group as more disparate relative to other clades. These caveats are important to consider when trying to assess the disparity within neornithischian and where taxa often recovered as T/EDOs fit in the tree.

3.2.3. Disparity analyses

There are a number of different methods of assessing disparity from a character-taxon matrix, each of which quantify slightly different aspects of morphological variation. Prior to analyses, these matrices must be converted into a pairwise distance matrix (Lloyd 2016) using one of the four following metrics: Generalised Euclidean Distance (GED; Wills 1998), Gower's Coefficient (GC; Gower 1971), Maximum Observable Rescaled Distance (MORD; Lloyd 2016) or Raw Euclidean Distance (RED). While GED and GC are often used in the literature (e.g. Deline *et al.* 2012; Ezcurra & Butler 2018), Lloyd (2016) tentatively recommended the use of the MORD, finding that this metric generally outperforms the alternatives. MORD has also been shown to better alleviate the effects of missing data compared to the other distance metrics (Flannery Sutherland *et al.* 2018; Lehmann *et al.* 2019), making it highly suitable for use in palaeontological datasets that often contain numerous unobservable (?) or inapplicable (-) character scorings. Most disparity analyses require ordination, which is a statistical method of mapping observed variables into a reduced dimension, while still retain-

ing the same degree of similarity and dissimilarity between variables (Guillerme *et al.* 2020a). The Principal Coordinate Analysis (PCoA) is the most commonly used method of ordination for character-based disparity analyses (e.g. Moon & Stubbs 2020; Apaldeti *et al.* 2021; Müller 2022; Casali *et al.* 2023), and allows the morphological variation between observations (i.e. OTUs) and groups of observations (i.e. taxonomic bins) to be visualised in morphospace when plotted.

When investigating changes in disparity through time, several metrics are commonly used in palaeobiology studies, each of which can be broadly categorised into one of three measures: size, which represents the amount of space occupied (e.g. sum of variance, sum of ranges); density, which represents the distribution and quantity of observations in space (e.g. pairwise distances/dissimilarity); and position, which represents the location of observations in space (e.g. distance from centroid) (Guillerme *et al.* 2020b). It is beneficial to consider multiple measures when assessing disparity, as these metrics can be used to investigate different macroevolutionary signals (e.g. radiations; Halliday & Goswami 2016; Guillerme *et al.* 2020b).

In this study, I chose to investigate morphological disparity using the following methods: (1) PCoA; (2) sum of variance; (3) median distance from centroid; and, (4) weighted mean pairwise dissimilarity. These metrics cover each of the three disparity indices (size, density and position), ensuring that results capture a full picture of morphological change. To measure ‘size’, the sum of variance metric was favoured over sum of ranges, as range-based measures have been shown to be volatile and easily biased by sample size (Guillerme *et al.* 2020a; Smith *et al.* 2021). Disparity analyses 1–3 require ordination of the data, while analysis 4 (weighted mean pairwise dissimilarity), is a pre-ordinate analysis. Ordination often requires the removal of taxa with high

proportions of unscored characters, as distances are not calculable in pairs of OTUs where there are no coded characters in common (Smith *et al.* 2014; Apaldetti *et al.* 2021; Lloyd *et al.* 2022). This pre-ordination metric is therefore advantageous when assessing fossil taxa, as it allows the incorporation of highly incomplete OTUs.

Disparity analyses were conducted in R (R Studio, 2023.06.0), using the R-packages *Claddis* (v 0.6.3, Lloyd *et al.* 2020) and *DispRity* (v 1.7.0, Guillaume 2018). Following recommendations from Lloyd (2016) and Smith *et al.* (2021), outgroup taxa were removed prior to each analysis using the *prune_cladistic_matrix* function from *Claddis* (v 0.6.3, Lloyd *et al.* 2020). The *Claddis* function *ordinate_cladistic_matrix* was used to compute the morphological distances and perform a PCoA on each of the three trimmed cladistic character datasets (Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021; 3.2.1.). The Maximum Observable Rescaled Distance (MORD) distance metric was chosen for this computation, following recommendation from Lloyd (2016). OTUs removed during the ordination of each distance matrix are outlined in the Appendix, see A3.1.

The ordinated distance matrices were imported into the software PAST (Hammer *et al.* 2001), where the first three principal coordinate axes were plotted (PCo1 vs PCo2; PCo1 vs PCo3). Taxa were colour-coded following the taxonomic groupings outlined in 3.2.2. Convex hulls were drawn where two or more taxa from a clade were present in a plot. Additionally, to test whether morphological disparity was significantly different between taxonomic groups, the non-parametric one-way PERMANOVA test was used with 9999 permutations.

To investigate how morphological distances vary throughout the skeleton, six additional PCoAs were run using anatomically-partitioned versions of each of the three

matrices. Matrices were partitioned prior to each analysis to include only characters from each of the five anatomical regions: skull (excluding dentition); dentition; vertebrae; pectoral girdle and forelimb; and pelvic girdle and hind limb. Characters not attributed to a specific skeletal region (e.g. Dieudonné *et al.* 2021: #253, presence/absence of postcranial osteoderms), were excluded from subsequent analyses involving those partitions. Each of the anatomically-partitioned distance matrices also underwent a PERMANOVA test in PAST (Hammer *et al.* 2001; using 9999 permutations) to test for significant differences between taxonomic groupings.

To assess disparity through time, data were sub-sampled using two approaches: chronostratigraphic bins at epoch-level (Early Jurassic, Middle Jurassic, etc.) and equally sized bins of 20 Ma (66–86 Ma, 86–106 Ma, etc.). These two methods were used to account for the potential biases introduced when using time bins of variable lengths (Guillerme and Cooper 2018; for reference, epoch-level time bins used in this study range in length from 13.2 Ma [Middle Jurassic] to 44.5 Ma [Early Cretaceous]). Operational taxonomic units (OTUs) were assigned to time bins based on first and last appearance dates retrieved from the Paleobiology Database (PBDB, paleobiodb.org) checked against recent literature, and updated where necessary (see Appendices, A2.2).

Once subsets of the ordinated distances matrices were created, the data were bootstrapped 100 times using the *boot_matrix* function in the R-package *DispRity* (v 1.7.0, Guillerme 2018). The *dispRity* function (R-package *DispRity*, v 1.7.0) was then used to apply two disparity metrics to the bootstrapped data: the sum of variance and the median Euclidean distance from centroid. The results were plotted through time as box and whisker plots in R Studio.

Disparity was also assessed through time using a pre-ordinated method, the weighted mean pairwise dissimilarity metric. The *Claddis* function *calculate_morphological_distances* was used to convert the cladistic character datasets by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) into pairwise distance matrices. As above, the data were sub-sampled using two approaches: chronostratigraphic bins at epoch-level (e.g. Early Jurassic, Middle Jurassic, etc.) and equally sized bins of 20 Ma. Subsequently, the weighted mean pairwise dissimilarity of the pre-ordinate distance matrices was computed using a R-function from Apaldetti *et al.* (2021). The function also calculated 95% confidence intervals from 9999 bootstrap replicates. Mean values and confidence intervals were plotted through time in R Studio.

To investigate how disparity through time has changed between different regions of the skeleton, the weighted mean pairwise dissimilarity metric was also applied to anatomically partitioned versions of each of the three cladistic matrices. Matrices were partitioned prior to each analysis to include only characters from each of the five anatomical regions: skull (excluding dentition); dentition; vertebrae; pectoral girdle and forelimb; and pelvic girdle and hind limb. As with the anatomically-partitioned principal component analysis, characters not attributed to a specific skeletal region were excluded from analyses involving those partitions. To compute and visualise weighted mean pairwise dissimilarity through time, the partitioned datasets were subject to the same methods as the full dataset (see above). The weighted mean pairwise dissimilarity metric was chosen to look at disparity through time between different regions of the skeletons (rather than the sum of variance and median distance from centroid metrics) because this metric allows the incorporation of OTUs that were trimmed during the ordination of the distance matrix (see Appendix A3.1 for a list of OTUs

excluded during ordination). This incorporation provides a sufficient sample size for OTUs to be subsampled by both time bin and anatomical partition.

3.2.4. Comparative data

Ornithischian diversity through time was plotted for comparison with disparity results in this study. Two measures were used to assess diversity changes: raw species richness; and number of collections. Data were retrieved from the Paleobiology Database (paleobiodb.org, accessed 17/08/23). Diversity was time sub-sampled using three approaches: chronostratigraphic bins at epoch-level (e.g. Early Jurassic, Middle Jurassic, etc.) and age-level; and equally sized bins of 20 Ma. The age-level data could not serve for direct comparison with disparity through time results, as these analyses did not have sufficient sample size to allow for bins of this resolution. Raw species richness and number of collections was plotted through time in PAST (Hammer *et al.* 2001).

3.3. Results

3.3.1. Morphospace occupation

Across the three matrices, the variance in this analysis accounted for by the first three PCo axes ranges from: 3.9% to 8.8% in PCo1; 3.4% to 6.9% in PCo2; and 3.3% to 6% in PCo3. The total number of axes for each matrix ranges from: 34 to 49 for Boyd (2015); 43 to 62 for Han *et al.* (2018); and 47 to 62 for Dieudonné *et al.* (2021). The full range of variances across all axes can be found in the Appendices, see A3.2.

3.3.1.1. Boyd (2015) PCoA. In the first analysis, which includes all anatomical partitions, many of the thescelosaurids/early-diverging ornithopods (T/EDOs) lie

within or close to ceratopsian morphospace along PCo1 and PCo2 (Figure 3.2a; A3.3a). None of the T/EDOs are recovered inside of iguanodontian morphospace in the PCo1/PCo2 plot, but *Talenkauen* and *Gasparinisaura* sit adjacent to it. In the PCo1/PCo3 plot (A3.4a), *Gasparinisaura* does lie within iguanodontian morphospace. This disparity between T/EDOs and iguanodontians is shown to be significant in PERMANOVA analyses (A3.5a). The early-diverging neornithischian *Othnielosaurus* lies relatively separate from the rest of the early-diverging ornithischians/neornithischians (EDO/Ns), amongst the T/EDOs. *Lesothosaurus* sits in proximity to thyreophorans in the analysis, as well as the basal neornithischians *Stormbergia* (which has been suggested to be an adult synonym of *Lesothosaurus*; Knoll *et al.* 2010) and *Eocursor*. In the PCo1/PCo2 plot (Figure 3.2a; A3.3a), the only pachycephalosaurid in the analysis, *Wannanosaurus*, lies within heterodontosaurid morphospace, but in the PCo1/PCo3 plot (A3.4a), the taxon does not overlap with other clades.

When only skull characters are included in the analysis, T/EDOs become far more dispersed within morphospace (Figure 3.2b; A3.3–4b). In the PCo1/PCo3 plot, most of the T/EDOs either overlap with iguanodontian morphospace or lie adjacent to it (A3.4b). Along PCo2, T/EDOs tend to plot more disparately from the iguanodontians. *Lesothosaurus* plots disparately from thyreophorans in the analysis, and is positioned among T/EDOs such as *Changchunsaurus* and *Jeholosaurus*.

The inclusion of only dental characters results in most T/EDOs clustering outside of the morphospace of any particular clade, primarily in a single quadrant (Figure 3.2c; A3.3c). In the PCo1/PCo2 plot, *Talenkauen* and *Gasparinisaura* reside within iguanodontian morphospace, while *Hypsilophodon* lies within ceratopsian morphospace (Figure 3.2c; A3.3c). In the PCo1/PCo3 plot (A3.4c), *Gasparinisaura* also lies

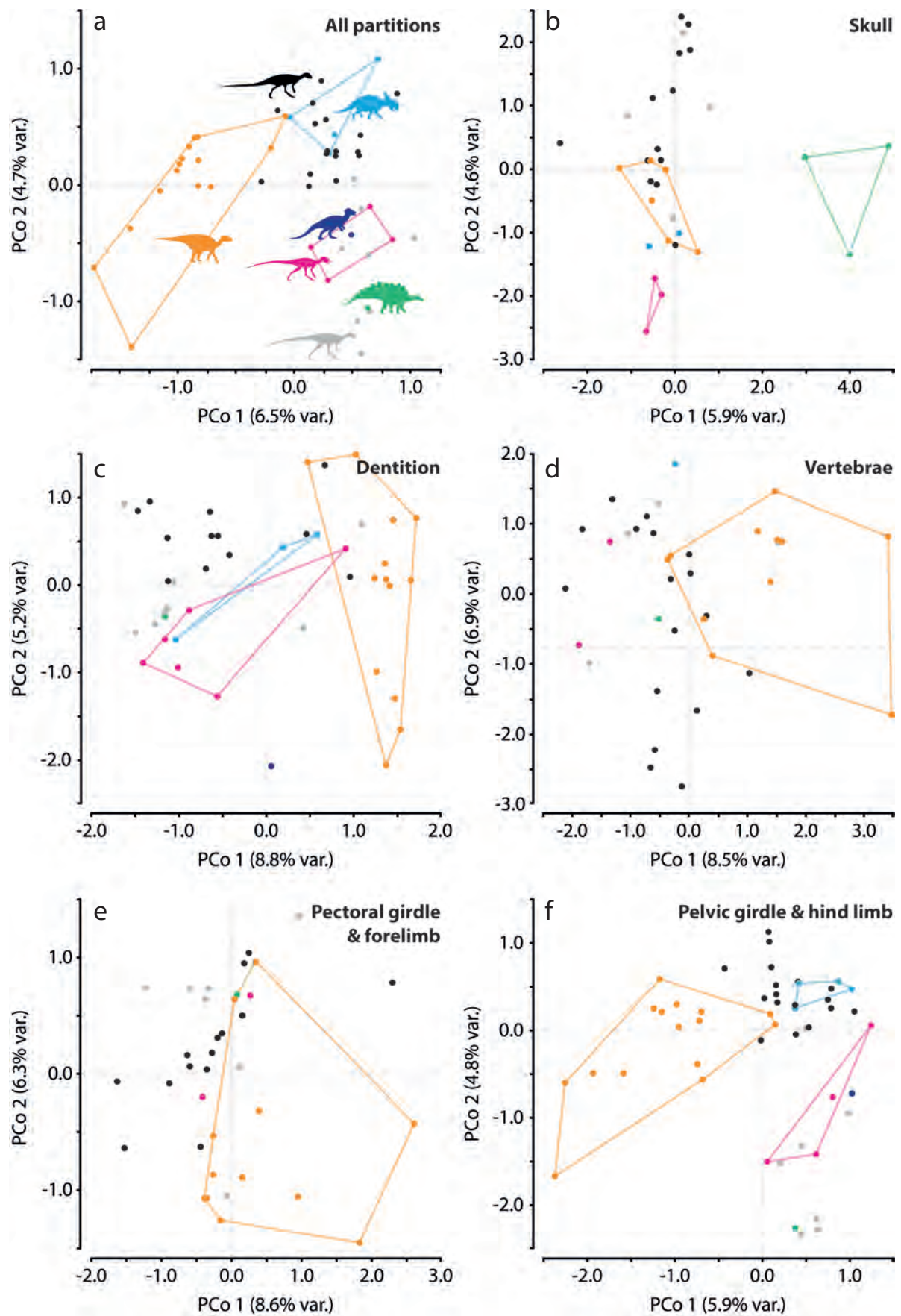


Fig. 3.2 (caption on following page)

Figure 3.2. Morphospace plot showing the results of principal coordinate analyses derived from the morphological matrix by Boyd (2015), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). For a version of the figure with taxa labelled, see Appendix A3.3. Silhouettes from <http://phylopic.org>: M. Dempsey, S. Hartman, E. Willoughby.

within iguanodontian morphospace, but *Talenkauen* and *Parksosaurus* reside within heterodontosaurid morphospace. The heterodontosaurids are disparate throughout both plots, with *Heterodontosaurus* lying proximal to the iguanodontians (Figure 3.2c; A3.3–4c). Many of the EDO/Ns (including *Lesothosaurus*) lie close to heterodontosaurid morphospace and the thyreophoran *Scutellosaurus*, but *Agilisaurus* and *Othnielosaurus* lie among T/EDOs. Ceratopsian and heterodontosaurid morphospace overlaps, but the pachycephalosaurid *Wannanosaurus* lies far from both, in unique morphospace (Figure 3.2c; A3.3–4c).

When only vertebral characters are investigated, the T/EDOs are highly dispersed within morphospace, but generally in the negative portion of the PCo1 plot (Figure 3.2d; A3.3–4d). Of the T/EDOs, only *Gasparinisaura*, *Thescelosaurus neglectus* and *Zephyrosaurus* are recovered within iguanodontian morphospace in the PCo1/PCo2 plot (Figure 3.2d; A3.3d). In the PCo1/PCo3 plot, the orodromines *Orycto-*

dromeus and the Kaiparowits orodromine also overlap with iguanodontians (A3.4d).

In the analysis of pectoral girdle and forelimb characters, the T/EDOs are highly dispersed along the PCo1 and PCo2 axes (Figure 3.2e; A3.3e), but are more constrained along PCo3 (A3.4e). *Parksosaurus* is the only T/EDO to occupy iguanodontian morphospace in the PCo1/PCo2 plot (Figure 3.2e; A3.3e): however, in the PCo1/PCo3 plot, *Hypsilophodon*, *Jeholosaurus*, *Haya* and *Yueosaurus* also overlap with iguanodontians (A3.4e). *Yueosaurus* is very disparate from all other T/EDOs along the PCo1 axis (Figure 3.2e; A3.3e). The iguanodontians are widely dispersed through morphospace and occupy a large proportion of both plots (Figure 3.2e; A3.3–4e).

When considering only pelvic girdle and hind limb characters, most T/EDOs occupy morphospace between the iguanodontians and ceratopsians (Figure 3.2f; A3.3–4f). In the PCo1/PCo2 plot (Figure 3.2f; A3.3f), none of the T/EDOs overlap with iguanodontian morphospace: however, in the PCo1/PCo3 plot, *Changchunsaurus* does (A3.4f). The iguanodontians dominate the negative morphospace along PCo1 (Figure 3.2f; A3.3f). The Kaiparowits orodromine is the only T/EDO to lie within ceratopsian morphospace. The pachycephalosaurid *Wannanosaurus* sits outside, but adjacent to, heterodontosaurid morphospace in PCo1/PCo2 (Figure 3.2f; A3.3f). However, *Wannanosaurus* is highly disparate from all other taxa along the PCo3 axis (A3.4f). The heterodontosaurids are moderately dispersed across all three axes plotted (Figure 3.2f; A3.3–4f), particularly *Tianyulong*. The only thyreophoran in the analysis, *Scutellosaurus*, lies close to the EDO/Ns *Eocursor*, *Stormbergia* and *Lesothosaurus* in PCo1/PCo2 (Figure 3.2f; A3.3f). The other EDO/Ns are relatively dispersed along PCo2, with *Othnielosaurus*, for example, sitting among the T/EDOs (Figure 3.2f; A3.3–4f). In the PCo1/PCo3 plot, both *Scutellosaurus* and the EDO/Ns are relatively concentrated in

the centre of the plot (A3.4f).

3.3.1.2. Han et al. (2018) PCoA. When all character partitions are included in the analysis, all of the T/EDOs are relatively clustered and sit outside of all of the morphospace occupied by other clades, between the iguanodontians, thyreophorans and heterodontosaurids (Figure 3.3a; A3.6–7a). Along PC2, iguanodontians do not overlap with any other taxa (Figure 3.3a; A3.6a). The putative ceratopsian *Micropachycephalosaurus* lies within heterodontosaurid morphospace, leading to a relatively significant overlap in occupied morphospace between the ceratopsians and heterodontosaurids. The pachycephalosaurids are relatively clustered, but overlap with both ceratopsians and heterodontosaurids. The EDO/Ns *Lesothosaurus* and *Agilisaurus* lie just adjacent to thyreophoran morphospace.

Including only skull characters in the analysis results in both T/EDO and the iguanodontians being clustered at the positive end of PCo1 (Figure 3.3b; A3.6–7b). By contrast, the ceratopsians mostly occupy the negative end of PCo1 and do not overlap with any other taxa along this axis. Most T/EDOs overlap or lie very close to the iguanodontians in both the PCo1/PCo2 plot (Figure 3.3b; A3.6b) and PCo1/PCo3 plot (A3.7b). In PCo1/PCo2, the T/EDO *Changchunsaurus* lies within heterodontosaurid morphospace, whereas *Orodromeus* and *Thescelosaurus neglectus* occupy thyreophoran morphospace (Figure 3.3b; A3.6b). However, none of the T/EDOs overlap with the heterodontosaurids or thyreophorans along PCo3 (A3.7b). The morphospace occupation of heterodontosaurids and pachycephalosaurids overlaps, but PERMANOVA analyses suggests that the skull morphologies of these groups are significantly different (A3.8b). Across all three plotted axes, the EDO/N *Isaberrysaura* lies within thyreophoran morphospace (Figure 3.3b; A3.6–7b). Along PCo2, *Laquintasaura* is disparate

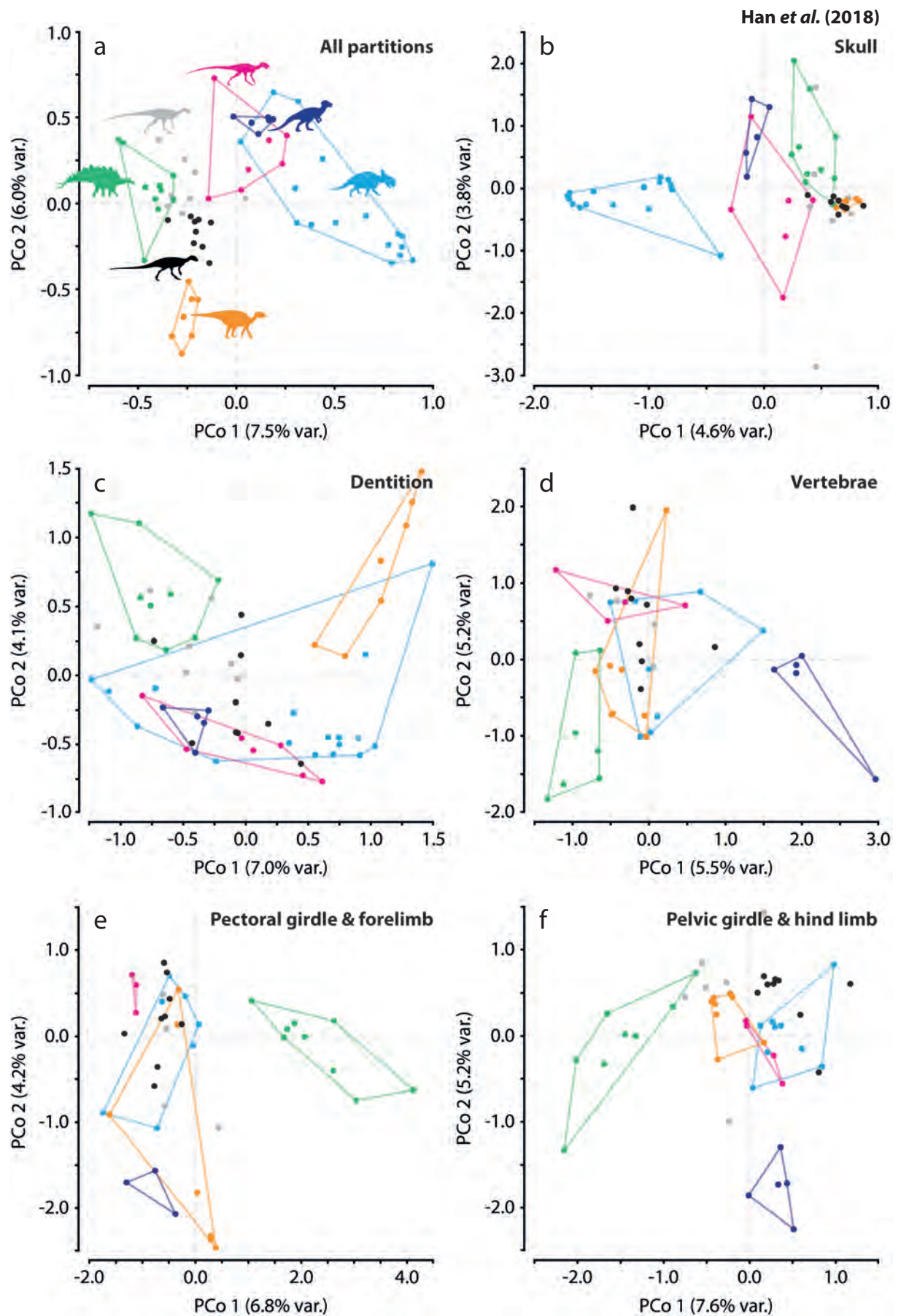


Fig. 3.3 (caption on following page)

Figure 3.3. Morphospace plot showing the results of principal coordinate analyses derived from the morphological matrix by Han *et al.* (2018), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). For a version of the figure with taxa labelled, see Appendix A3.6. Silhouettes from <http://phylopic.org>; M. Dempsey, S. Hartman, E. Willoughby.

from all taxa, occupying unique area of morphospace (Figure 3.3b; A3.6b): however, in PCo1/PCo3, this taxon overlaps with the thyreophorans (A3.7b). The EDO/Ns *Agilisaurus*, *Hexinlusaurus* and *Lesothosaurus* sit amongst the T/EDOs and iguanodontians in both PCo1/PCo2 (Figure 3.3b; A3.6b) and PCo1/PCo3 (A3.7b), but do not reside within a particular morphospace.

When only dental characters are tested, T/EDOs are moderately dispersed throughout the PCo1/PCo2 plot and are relatively distant from all iguanodontian taxa (Figure 3.3c; A3.6c). Most T/EDOs lie within ceratopsian morphospace, which occupies a large proportion of both plots, and overlaps with iguanodontians, heterodontosaurids and pachycephalosaurids (Figure 3.3c; A3.6–7c). Pachycephalosaurid morphospace overlaps with the heterodontosaurids in the PCo1/PCo2 plot (Figure 3.3b; A3.6b), but in PCo1/PCo3 there is no overlap between these groups (A3.7c). Across both plots, the EDO/Ns *Agilisaurus*, *Hexinlusaurus*, *Lesothosaurus* and *Yandusaurus*

lie close to the T/EDOs, while *Isaberrysaura*, *Laquintasaura* and *Pisanosaurus* sit within or adjacent to thyreophoran morphospace (Figure 3.3c; A3.6–7c).

In the analysis including only vertebral characters, T/EDOs are, again, relatively dispersed (Figure 3.3d; A3.6d), although less so along PCo3 (A3.7d). In both PCo1/PCo2 (Figure 3.3d; A3.6d) and PCo1/PCo3 (A3.7d), there is a large amount of overlap between iguanodontian, ceratopsian and heterodontosaurid morphospace. Most T/EDOs occupy this heavily overlapped area of the plot. *Changchunsaurus* is highly disparate from the other T/EDOs, being the only taxon within the group to have a positive PCo1 value (Figure 3.3d; A3.6–7d). *Yueosaurus* is the only T/EDO to occupy unique morphospace in PCo1/PCo2 (Figure 3.3d; A3.6d). The pachycephalosaurids are disparate from all other clades and do not overlap along PCo1 with any other taxa (Figure 3.3d; A3.6–7d).

When only pectoral girdle and forelimb characters are included in the analysis, T/EDOs are constrained along the PCo1 axis but more dispersed along PCo2 and PCo3 (Figure 3.3d; A3.6–7e). In PCo1/PCo2 (Figure 3.3d; A3.6e), most T/EDOs are recovered in both iguanodontian and ceratopsian morphospace: however, in the PCo1/PCo3 plot (A3.7e), most T/EDOs occupy unique morphospace. Most EDO/EDNs are recovered amongst T/EDOs, overlapping in morphospace with the ceratopsians and iguanodontians. PERMANOVA analyses find that EDO/EDNs are significantly different from the thyreophorans in this anatomical partition (A3.8e). Compared to all other partitions, heterodontosaurids are highly concentrated within morphospace. There is no morphospace overlap between pachycephalosaurids and heterodontosaurids (Figure 3.3d; A3.6–7e), although the two groups do lie adjacent to each other in the PCo1/PCo3 plot (A3.7e). The thyreophorans occupy unique morphospace in both PCo1/PCo2

(Figure 3.3d; A3.6e) and PCo1/PCo3 (A3.7e), and do not overlap with any other taxa along the PCo1 axis.

Including only pelvic girdle and hind limb characters results in most T/EDOs plotting in a cluster (Figure 3.3f; A3.6–7f). The exceptions are *Yueosaurus*, *Changchunsaurus* and *Koreanosaurus*, which are disparate from all other T/EDOs along the PCo1 axis. In the PCo1/PCo2 plot (Figure 3.3f; A3.6f), most of the EDO/Ns are concentrated in a single quadrant and are distinct from other clades. However, in PCo1/PCo3 (A3.7f), most T/EDOs lie within ceratopsian and/or pachycephalosaurian morphospace. The pachycephalosaurids are distant from the heterodontosaurids along both the PCo2 and PCo3 axis (Figure 3.3f; A3.6–7f).

3.3.1.3. Dieudonné et al. (2021) PCoA. Including all partitions in the analysis results in T/EDOs being relatively dispersed, particularly along PCo1 and PCo3 (Figure 3.4a; A3.9–10a). In the PCo1/PCo2 plot, most T/EDOs overlap with or are adjacent to morphospace occupied by iguanodontians or ceratopsians: however, in PCo1/PCo3, many occupy unique morphospace. *Koreanosaurus* and *Zephyrosaurus* plots consistently with other T/EDOs along PCo1, but are set apart from the rest of this group along the PCo2 and PCo3 axes. There is no overlap between heterodontosaurids and pachycephalosaurids in either plot.

When only skull characters are included, T/EDOs are generally clustered within or adjacent to iguanodontian morphospace (Figure 3.4b; A3.9–10b). However, *Nanosaurus* lies relatively distant from the other T/EDOs along the PCo2 and PCo3 axes. In the PCo1/PCo2 plot, all of the EDO/Ns, apart from *Laquintasaura* and *Lesothosaurus*, plot among the cluster of T/EDOs. However, in PCo1/PCo3, the EDO/Ns are more spread out from each other. Ceratopsians are relatively concentrated and overlap with

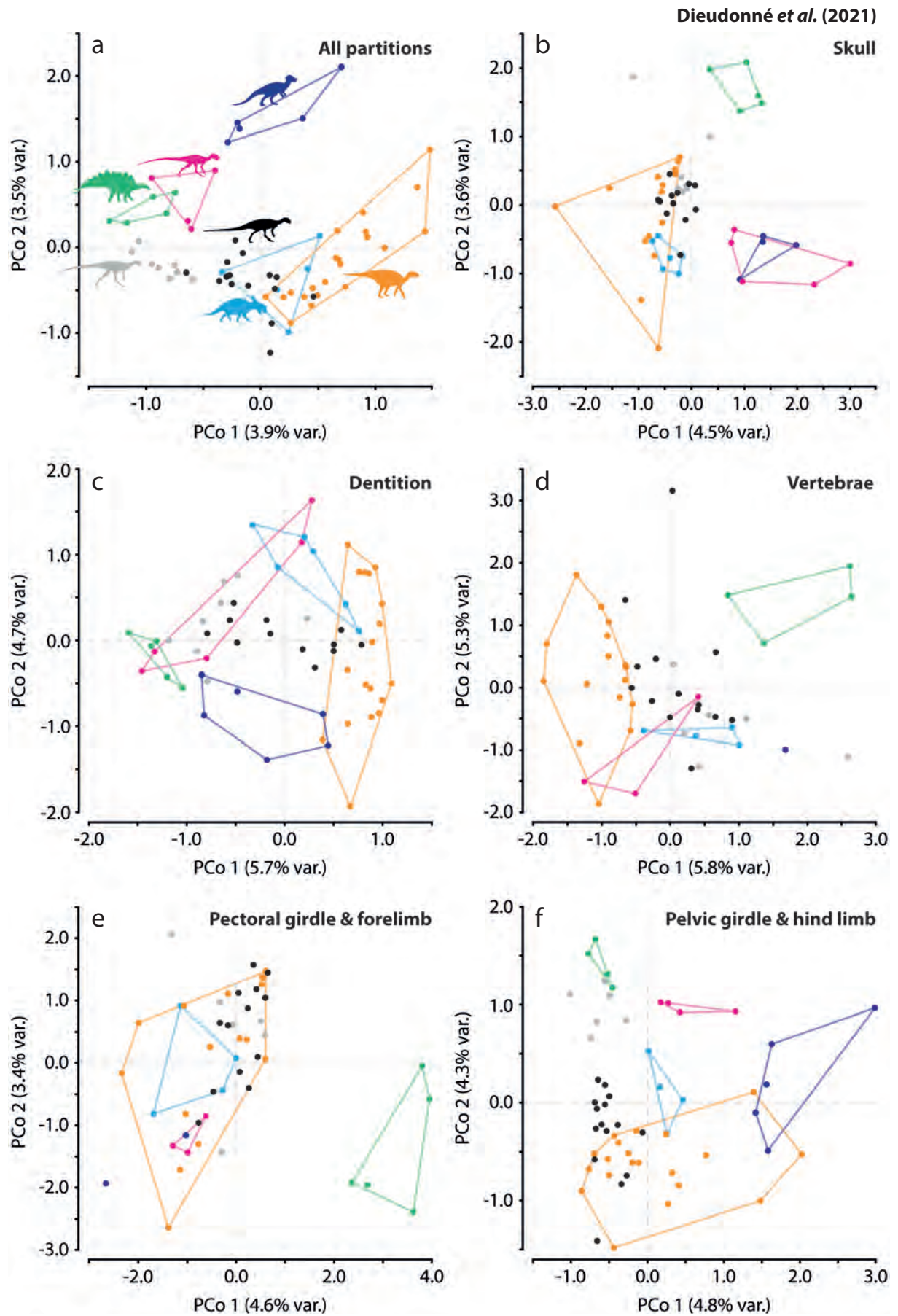


Fig. 3.4 (caption on following page)

Figure 3.4. Morphospace plot showing the results of principal coordinate analyses derived from the morphological matrix by Dieudonné *et al.* (2021), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). For a version of the figure with taxa labelled, see Appendix A3.9. Silhouettes from <http://phylopic.org>: M. Dempsey, S. Hartman, E. Willoughby.

iguanodontians. There is also significant overlap between heterodontosaurids and pachycephalosaurids in both the PCo1/PCo2 (Figure 3.4b; A3.9) and PCo1/PCo3 plot (A3.10). PERMANOVA results find that heterodontosaurids and pachycephalosaurians are the only groups to not be significantly different (A3.11), further emphasising the overlap between these groups in this partition.

Including only dental characters results in T/EDOs plotting disparately along PCo1, but comparably concentrated along PCo2 and PCo3 (Figure 3.4c; A3.9–10c). *Gasparinisaura* and *Parksosaurus* occupy iguanodontian morphospace, while *Changchunsaurus*, *Haya* and *Nanosaurus* occupy heterodontosaurid morphospace (Figure 3.4c; A3.9c). The heterodontosaurids and pachycephalosaurids are both very disparate in their distributions (Figure 3.4c; A3.9–10c), and only overlap with each other in the PCo1/PCo3 plot (A3.10c). All EDO/Ns except for *Yandusaurus*, plot negatively along PCo1, predominately within morphospace occupied by the heterodontosaurids.

When only vertebrae characters are included in the analysis, T/EDOs are widely dispersed in both PCo1/PCo2 (Figure 3.4d; A3.9d) and PCo1/PCo3 (A3.10d). None of the T/EDOs lie within iguanodontian morphospace, but *Convolosaurus* and *Parkosaurus* lie adjacent to it. There is overlap between the heterodontosaurids and both ceratopsians and iguanodontians. *Macrogyphosaurus* is notably disparate from all other taxa along the PCo2 axis (Figure 3.4d; A3.9d). The only pachycephalosaurid included in this analysis, *Wannanosaurus*, is highly disparate from other cerapodans along both the PCo1 and PCo3 axes (Figure 3.4d; A3.9–10d).

In the analysis including only pectoral girdle and forelimb characters, T/EDO are relatively dispersed from each other, particularly along PCo2 (Figure 3.4e). The iguanodontians are highly disparate in their distribution, and overlap with ceratopsian, heterodontosaurid and pachycephalosaurid morphospace occupation. In both the PCo1/PCo2 (Figure 3.4e; A3.9e) and PCo1/PCo3 plot (A3.10e), most T/EDOs lie within iguanodontian morphospace. Most of the EDO/Ns (excluding *Isaberrysaura*) are recovered amongst the T/EDOs, within or adjacent to iguanodontian morphospace. The thyreophorans are highly distant from the other clades and do not overlap with any other taxa along PCo1 (Figure 3.4e; A3.9–10e).

When only pelvic girdle and hind limb characters are investigated, T/EDOs are recovered relatively clustered, with the exception of a few outliers (Figure 3.4f; A3.9–10f). *Thescelosaurus assiniboensis* and *Yueosaurus* consistently occupy iguanodontian morphospace in both PCo1/PCo2 (Figure 3.4f; A3.9f) and PCo1/PCo3 (A3.10f), however most other T/EDOs plot nearby, largely adjacent to it across both plots. The thyreophorans are relatively concentrated along PCo1 (4.8% var.) and PCo2 (4.3% var.), but along PCo3 (3.5% var.) *Scutellosaurus* plots disparately from the other thyre-

ophorans, within iguanodontian morphospace. In PCo1/PCo2 (Figure 3.4f; A3.9f), the EDO/EDNs are recovered in largely unique morphospace, relatively close to the thyreophorans. Along PCo3 the EDO/EDNs are found amongst the T/EDOs (A3.10f): however, *Lesothosaurus* remains close to the thyreophoran *Scutellosaurus*. Iguanodontian morphospace overlaps minimally with the ceratopsians and pachycephalosaurids. The pachycephalosaurids are relatively restrained along PCo1, except for *Prenocephale*, which plots at the positive end of PCo1 (Figure 3.4f; A3.9f). The heterodontosaurids are highly constrained along PCo2 and PCo3 (Figure 3.4f; A3.9–10f), but *Tianyulong* is relatively dispersed from the others in PCo1, and plots just within iguanodontian morphospace in PCo1/PCo3 (A3.10f). There is no overlap between the pachycephalosaurids and heterodontosaurids.

3.3.2. Disparity through time

3.3.2.1. Sum of variances. The disparity through time of all three cladistic datasets using the median sum of variances metric is shown in Figure 3.5. Results show that disparity is generally low in the Early and Middle Jurassic, but increases into the Late Jurassic. Results derived from the Boyd (2015) dataset show disparity peaks in the Early Cretaceous before declining in the Late Cretaceous (Figure 3.5a–b). Whereas in results generated from the Han *et al.* (2018) and Dieudonné *et al.* (2021) matrices, disparity continues to rise in the Cretaceous, peaking in the most recent time bin (Figure 3.5c–f).

3.3.2.2. Median distance from the centroid. Figure 3.6 shows disparity through time using the median Euclidean distance from the centroid metric. Results are similar to those using the sum of variances metric. When epoch-level time bins are used, disparity dips into the Middle Jurassic (Figure 3.6a, c, d), however this signal is

error bars; and outliers. Time bins: epoch-level (a, c, e) and equal slices of 20 Ma (b, d, f). (Fig. 3.5, cont.)

not retained when equally sliced time bins were used in Boyd (2015, Figure 3.6b) and Dieudonné *et al.* (2021, Figure 3.6f). Disparity increases in the Late Jurassic. In results derived from the Boyd (2015) dataset, disparity declines through the Cretaceous (Figure 3.6a–b), whereas results from Han *et al.* (2018) and Dieudonné *et al.* (2021) peak in the Late Cretaceous (Figure 3.6c–f).

3.3.2.3. Weighted mean pairwise dissimilarity. Disparity through time using the weighted mean pairwise dissimilarity metric is shown in Figure 3.7. Results show broadly similar disparity patterns to those using the sum of variances (Figure 3.5; 3.3.1.1) and median distance from centroid metrics (Figure 3.6; 3.3.1.2). Disparity is lowest during the Middle Jurassic (Figure 3.7a–c), or during the 166–186 Ma time bin (Figure 3.7d–f), which corresponds to the latest Early Jurassic and the early Middle Jurassic. Across all three datasets, disparity increases sharply between the Middle Jurassic and Late Jurassic time bins (Figure 3.7a–c). When using epoch-level time bins, the Late Jurassic shows the highest disparity across all matrices, before declining into the Cretaceous. Similarly, this increase is also observed in the 146–166 Ma time bin (Figure 3.7d–f), although in Boyd (2015), disparity does not peak until the 126–146 Ma time bin. In results derived from the Boyd (2015) matrix, disparity declines considerably between the Early and Late Cretaceous, similar to results computed using the sum of variances (Figure 3.5a–b) and median distance from the centroid (Figure 3.6a–b) metrics. In results derived from both the Han *et al.* (2018) and Dieudonné *et al.* (2021)

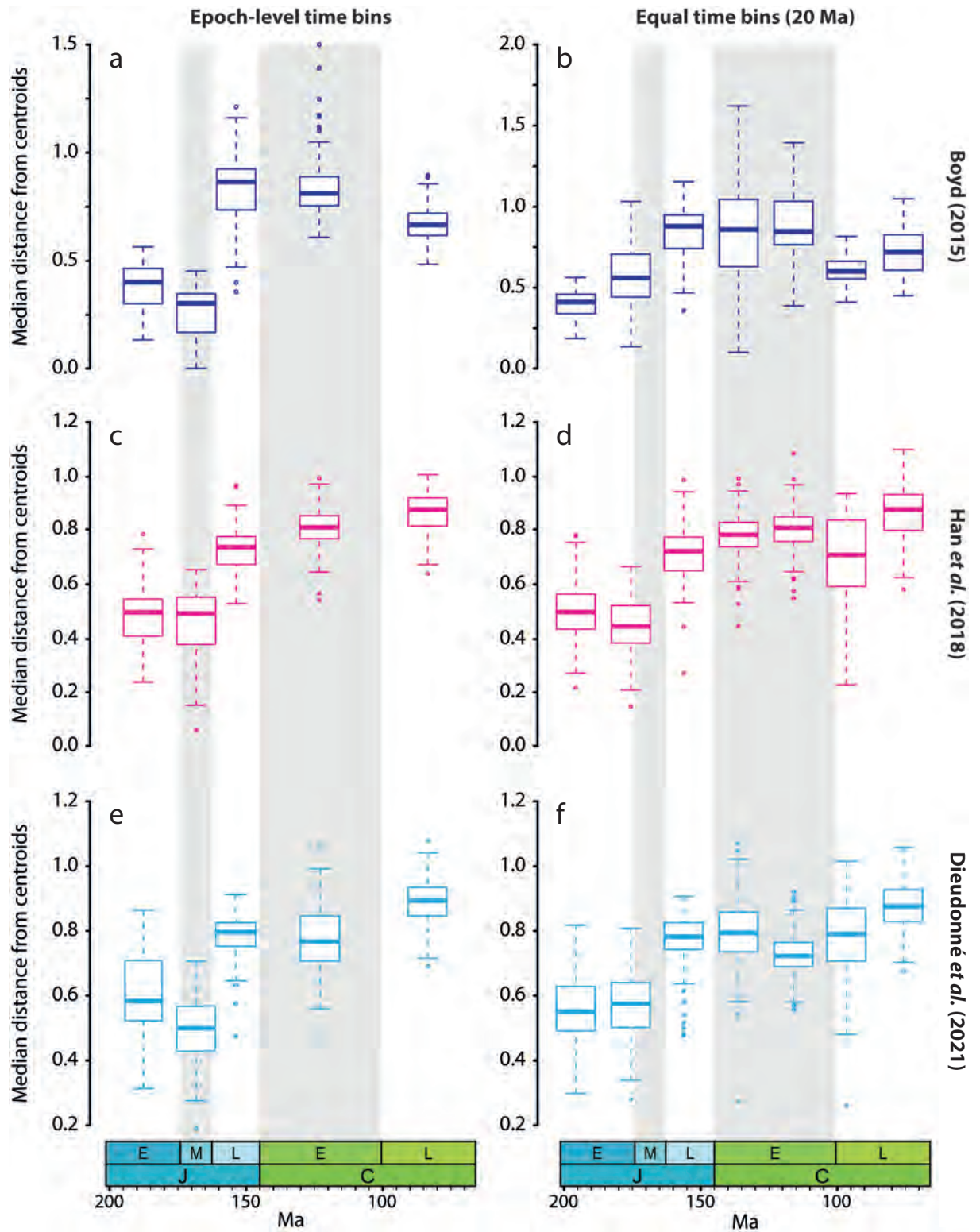


Figure 3.6. Disparity through time using the median Euclidean distance from the centroid metric. Generated from matrices by Boyd (2015, **a–b**), Han *et al.* (2018, **c–d**) and Dieudonné *et al.* (2021, **e–f**). Box and whisker plots include: the median; 25% and

75% quartiles; 2.5% and 97.5% error bars; and outliers. Time bins: epoch-level (a, c, e) and equal slices of 20 Ma (b, d, f). (Fig. 3.6, cont.)

datasets, disparity generally remains level through the Cretaceous (Figure 3.6c–f). When data is subsampled using equally-sized slices, the most recent bin (66–86 Ma) sees disparity increase in Boyd (2015, Figure 3.6b) and Han *et al.* (2018, Figure 3.6d), but decline in Dieudonné *et al.* (2021, Figure 3.6f). This decline is incongruent with disparity measures computed using the sum of variances (Figure 3.5e–f) and median distance from the centroid (Figure 3.6e–f) metrics, where disparity is observed to peak in the most recent time bin.

Weighted mean pairwise dissimilarity was also used to measure disparity through time from anatomical partitioned versions of the Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021) datasets. Results are shown in Figure 3.8–9. When only skull characters were included in the pre-ordination analysis, disparity is lowest in the Middle Jurassic across all matrices (Figure 3.8a–c). Disparity increases steeply into the Late Jurassic, and remains largely level into the Cretaceous. In results derived from the Boyd (2015) and Dieudonné *et al.* (2021) datasets, disparity declines into the Late Cretaceous (Figure 3.8a, c), whereas in Han *et al.* (2018) disparity remains stable (Figure 3.8b). When equal time bins are used (Figure 3.9a–c), trends remain largely consistent for both Han *et al.* (2018, Figure 3.9a) and Dieudonné *et al.* (2021, Figure 3.9c). However, in Boyd (2015), there is no dip during time bins spanning the Middle Jurassic, with disparity being at its lowest during between 86–106 Ma (Figure 3.9a). Additionally, in contrast to the epoch-level time bins, disparity sharply increases in the

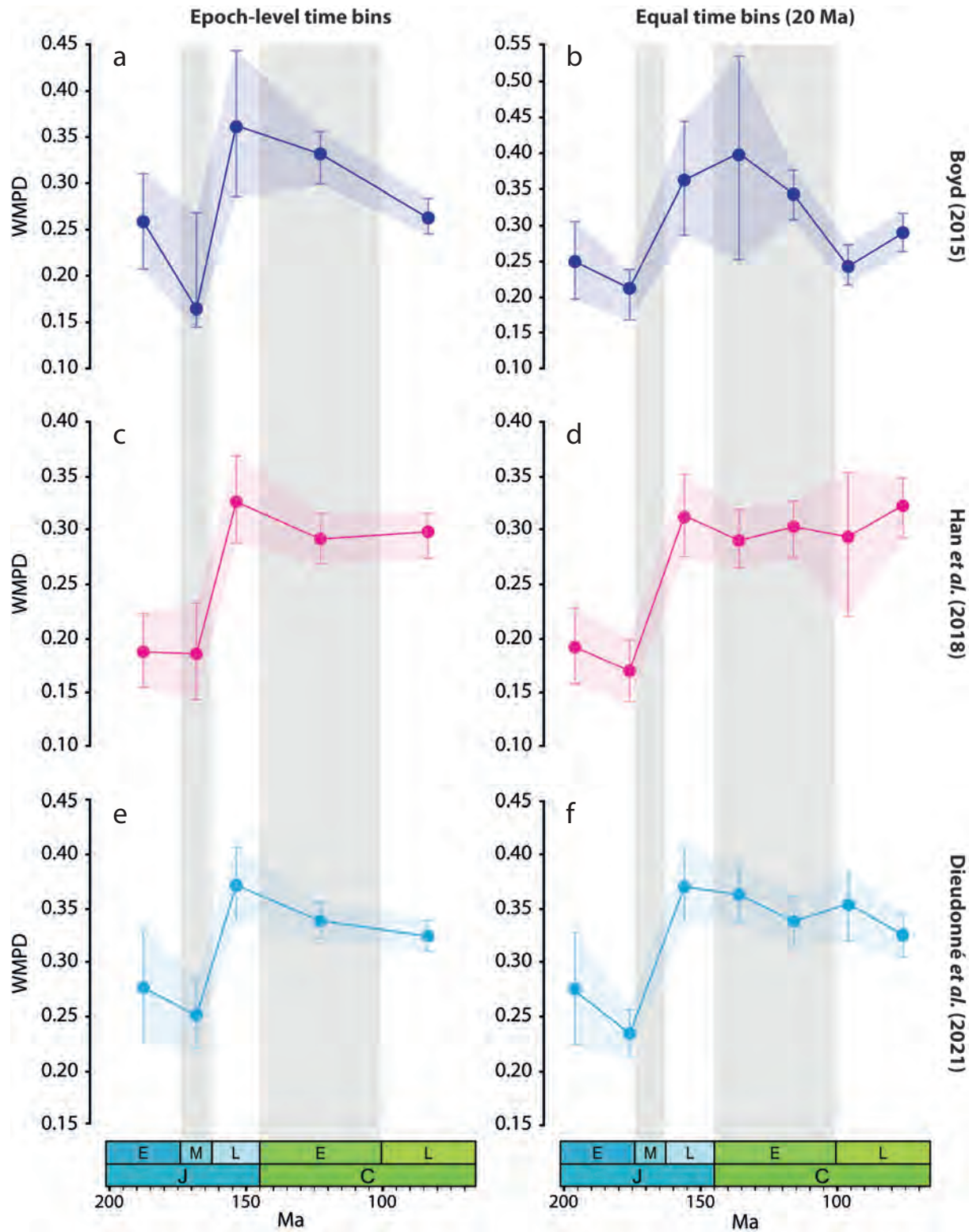


Figure 3.7. Disparity through time using the weighted mean pairwise dissimilarity (WMPD) metric. Generated from matrices by Boyd (2015, **a–b**), Han *et al.* (2018, **c–d**) and Dieudonné *et al.* (2021, **e–f**). Upper and lower limits represent 95% confidence

levels from 9999 bootstrap replicates. Time bins: epoch-level (a, c, e) and equal slices of 20 Ma (b, d, f). (Fig. 3.7, cont.)

most recent time bin (66–86 Ma, Figure 3.9a).

In the analysis including only dental characters, a dip in disparity is observed in the Middle Jurassic across all matrices (Figure 3.8d–f), although in results derived from Boyd (2015) this dip is far more exaggerated (Figure 3.8d). Dental disparity peaks in the Late Jurassic, before declining through to the Late Cretaceous. Results are largely consistent with those where equal time bins were used (Figure 3.9d–f), with the main difference being that in Boyd (2015), disparity increases in the most recent time bin (66–86 Ma, Figure 3.9d).

When including only vertebral characters, disparity generally increases from the Early Jurassic to Late Cretaceous across all three matrices (Figure 3.8g–i). In results computed from the Dieudonné *et al.* (2021) dataset, disparity dips in the Middle Jurassic, before steeply increasing in the Late Jurassic, similar to in other partitions. In contrast, in Boyd (2015) and Han *et al.* (2018), vertebral disparity does not dip in the Middle Jurassic. Results are generally consistent when equal time bins were used (Figure 3.9g–i).

In the forelimb and pectoral girdle analysis, disparity dips in the Middle Jurassic in both Boyd (2015) and Dieudonné *et al.* (2021, Figure 3.8j, l). While in Han *et al.* (2018), disparity increases to its peak in the Late Jurassic before declining into the Late Cretaceous (Figure 3.8k). Disparity also peaks in the Late Jurassic in Boyd (2015), before declining and levelling off into the Late Cretaceous (Figure 3.8j), whereas in

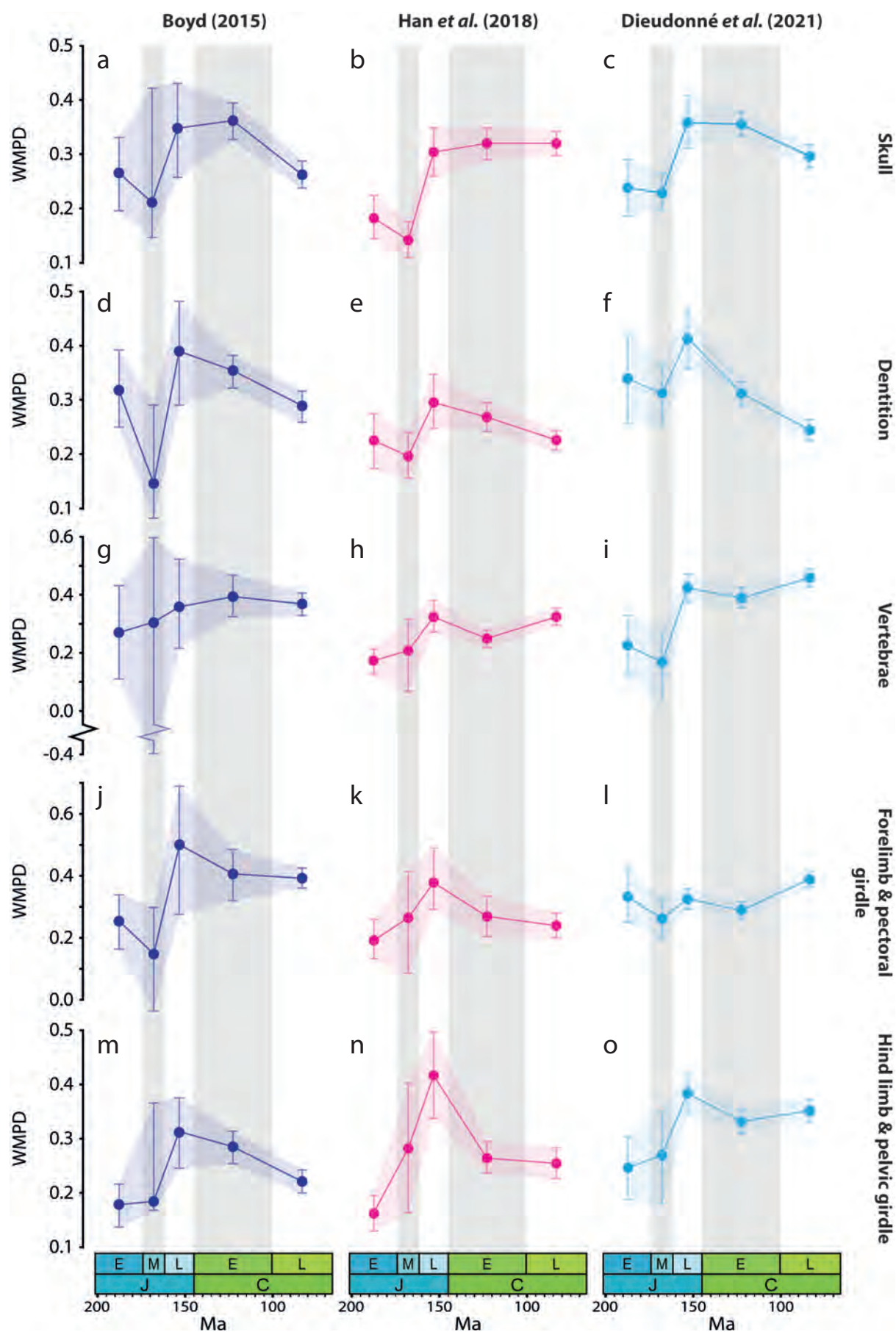


Fig. 3.8 (caption on following page)

Figure 3.8. Disparity through time by anatomical region using the weighted mean pairwise dissimilarity (WMPD) metric. Generated from matrices by Boyd (2015: **a, d, g, j, m**), Han *et al.* (2018: **b, e, h, k, n**) and Dieudonné *et al.* (2021: **c, f, i, l, o**). Data was partitioned into epoch-level time bins. Anatomical regions: skull (**a–c**); dentition (**d–f**); vertebrae (**g–i**); pectoral girdle and forelimb (**j–l**); pelvic girdle and hind limb (**m–o**). Upper and lower limits represent 95% confidence levels from 9999 bootstrap replicates.

Dieudonné *et al.* (2021), disparity peaks in the Late Cretaceous (Figure 3.8l). Results are highly consistent with those where equal time bins have been used (Figure 3.9j–l), however one main difference is a sharp dip in disparity in Han *et al.* (2018) between 86–106 Ma (Figure 3.9k).

When only hind limb and pelvic girdle characters are included in the ordination, disparity is lowest in the Early Jurassic across all matrices, and increases to its peak in the Late Jurassic (Figure 3.8m–o). Disparity then declines into the Early Cretaceous, although much more steeply in Han *et al.* (2018) than the other two matrices. In Boyd (2015) and Han *et al.* (2018), disparity continues to decline in the Late Cretaceous (Figure 3.8m–n), whereas in Dieudonné *et al.* (2021), disparity increases slightly (Figure 3.8o). When equal time bins were used, disparity in Boyd (2015) increases to its peak between 126–146 Ma (=Early Cretaceous), before declining to its lowest at 86–106 Ma (= ~earliest Late Cretaceous, Figure 3.9m). Unlike where epoch-level time bins were used, here in Boyd (2015), disparity increases into the most recent time bin (66–86 Ma, Figure 3.9m). Results from analysis of the Han *et al.* (2018) and Dieudonné *et al.*

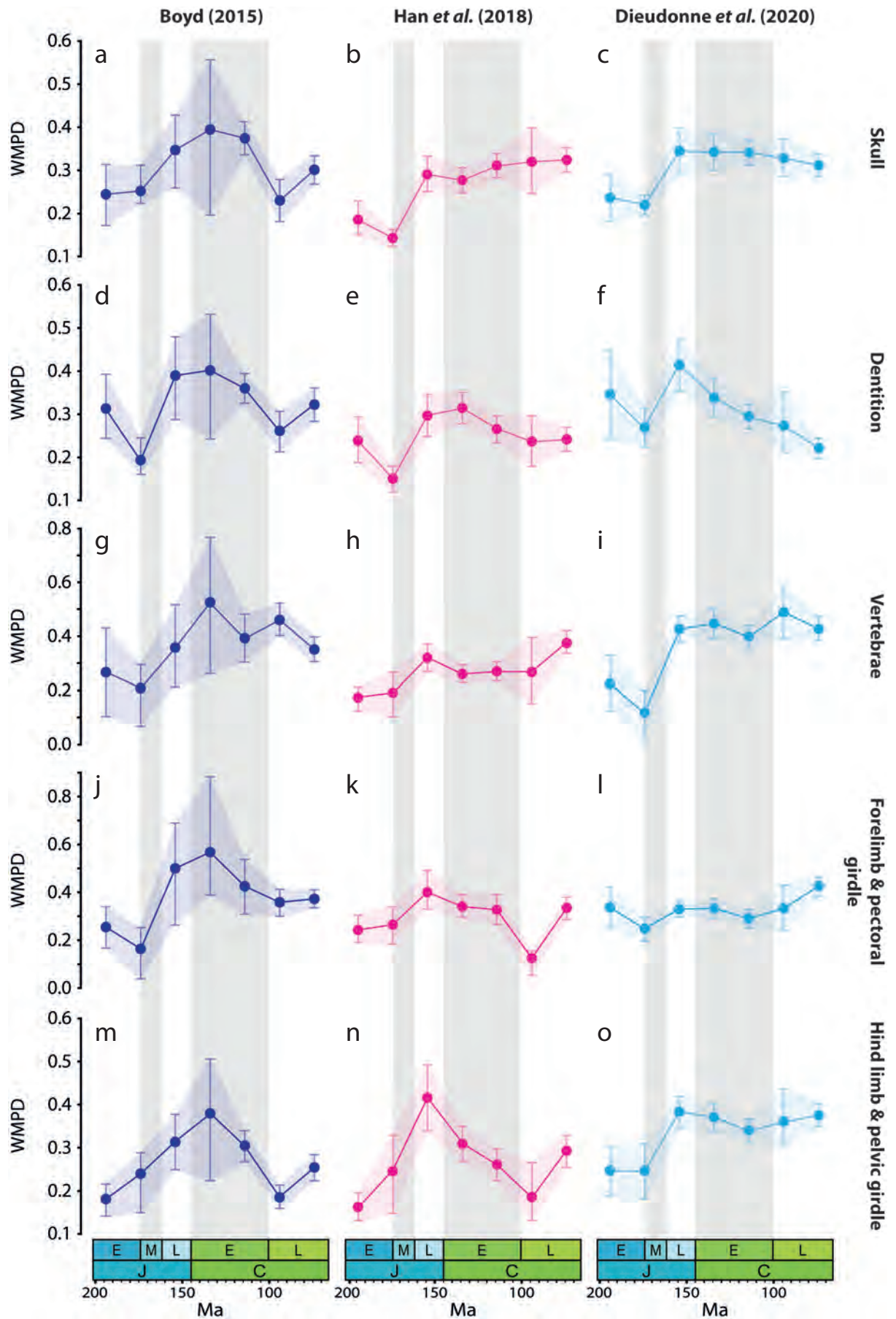


Fig. 3.9 (caption on following page)

Figure 3.9. Disparity through time by anatomical region using the weighted mean pairwise dissimilarity (WMPD) metric. Generated from matrices by Boyd (2015: **a**, **d**, **g**, **j**, **m**), Han *et al.* (2018: **b**, **e**, **h**, **k**, **n**) and Dieudonné *et al.* (2021: **c**, **f**, **i**, **l**, **o**). Data was partitioned into equal time bins of 20 Ma. Anatomical regions: skull (**a–c**); dentition (**d–f**); vertebrae (**g–i**); pectoral girdle and forelimb (**j–l**); pelvic girdle and hind limb (**m–o**). Upper and lower limits represent 95% confidence levels from 9999 bootstrap replicates.

(2021) matrices using equal time bins show results very consistent to when epoch-level time bins were used (Figure 3.9n–o). However, in Han *et al.* (2018), disparity is observed to increase sharply in the most recent time bin (66–86 Ma, Figure 3.9n), unlike where epoch-level time bins were used.

3.3.3. Comparative data

Ornithischian diversity through time was approximated from raw species richness and number of collections. Results are shown in Figure 3.10. Diversity is very low throughout the Early and Middle Jurassic, apart from a small peak in the Sinemurian (Figure 3.10a–b, Si), which corresponds to the upper Elliot Formation of southern Africa, where a number of the earliest ornithischians have been recovered (*Abriktosaurus*, *Eocursor*, *Heterodontosaurus*, *Lesothosaurus*, *Lycorhinus* and *Pegomastax*; Bordy *et al.* 2020). At epoch-level, number of collections sees a significant drop of almost 60% between the Early and Middle Jurassic (Figure 3.10b), whereas raw species richness declines by only 20% over the same time span (Figure 3.10a). Over 90% of the species

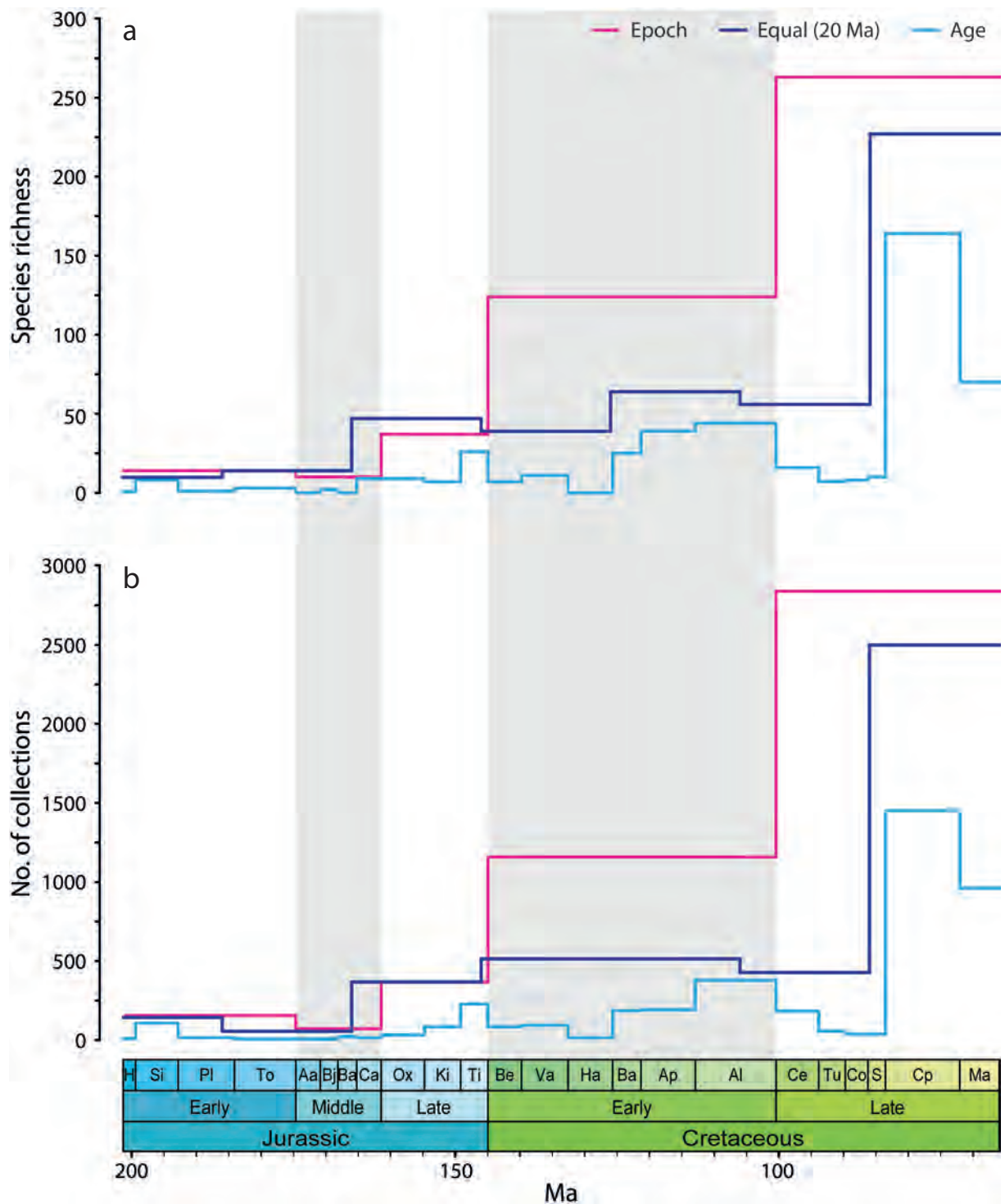


Figure 3.10. Raw species richness (a) and number of collections (b) for ornithischians during the Jurassic and Cretaceous. Data retrieved from the Paleobiology Database (paleobiodb.org, accessed 17/08/23). Data was time-sliced into the following bins: epoch-level (pink); equal slices of 20 Ma (dark blue); age-level (light blue).

richness in the Middle Jurassic comes from the Callovian (Figure 3.10a, Ca), however this age makes up less than 30% of Middle Jurassic ornithischian collections data (Figure 3.10b). The Late Jurassic sees a moderate increase in diversity (Figure 3.10a–b). However, age-level data shows that this is predominately the result of a peak in the Tithonian (Figure 3.10a–b, Ti), which corresponds to the most recent parts of the Morrison Formation (western United States), where over a dozen valid ornithischian taxa have been recovered (e.g. *Camptosaurus*, *Dryosaurus*, *Fruitadens*, *Hesperosaurus*, *Stegosaurus*; Carpenter & Galton 2018; Maidment & Muxworthy 2019; Paleobiology Database, paleobiodb.org). When the data is sub-sampled by epoch, diversity is observed to increase greatly into the Early Cretaceous (Figure 3.10). However, when equally-sized time slices are used, diversity remains relatively stable between the Late Jurassic and early Late Cretaceous (Figure 3.10a–b), particularly the number of collections. Age-level data shows that diversity in the Early Cretaceous is much higher in the latter ages (Figure 3.10a–b). Diversity greatly increases into the Late Cretaceous (Figure 3.10a–b), with both raw species richness and collection numbers increasing by 112% and 144% respectively from their levels in the Early Cretaceous. Age-level data shows that diversity is relatively low throughout the early Late Cretaceous, but peaks in the Campanian (Figure 3.10a–b, Cp), before declining into the Maastrichtian (Figure 3.10a–b, Ma).

3.4. Discussion

3.4.1. Patterns of disparity within Ornithischia

Disparity-through-time analyses suggest that the phenotypic diversity of ornithischi-

ans declined into the Middle Jurassic, where it reached its nadir (Figure 3.5–7). This reduction also corresponds with ornithischian species-richness and sampling patterns, with the number of collections, in particular, declining substantially into the Middle Jurassic (Figure 3.10). A similar trend was also recovered when using equally-sized time bins of 20 Ma, showing that this result is not just an artefact of the comparatively short length of the Middle Jurassic compared to the other epoch-level time bins sampled (although see Figures 3.5b, f & 3.6b). It is worth noting, however, that the Middle Jurassic is notoriously poorly sampled, particularly considering the number of dinosaur-bearing formations of this age (Barrett *et al.* 2009). When the disparity-through-time analysis (weighted mean pairwise dissimilarity) was applied to anatomically partitioned iterations of each character-taxon matrix, disparity was also shown to decline into the Middle Jurassic across most partitions. An exception to this was in the pelvic girdle and hind limb partition, where across all three matrices, disparity is lowest in the Early Jurassic, and increases into the Middle Jurassic (Figure 3.8j–l). This may suggest that pelvic girdle and hind limb morphologies were changing at a faster evolutionary rate than other anatomical regions at this time, perhaps in association with locomotory adaptations. Future studies could investigate this further using musculoskeletal biomechanical models of Jurassic ornithischian taxa to quantify changes in locomotory ability (e.g. by measuring pelvic girdle and hind limb muscle moment arms; Bates *et al.* 2012; Maidment & Barrett 2012a; Maidment *et al.* 2014b) during this time period.

Throughout all matrices and measures, disparity tends to increase greatly during the Late Jurassic (Figure 3.5–7). This increase in disparity also coincides with a substantial increase in ornithischian species-richness during the Late Jurassic (Figure 3.10; Barrett *et al.* 2009). It is, however, difficult to know how much of this trend re-

flects true evolutionary innovation, with changes in disparity through time likely highly influenced by taxon sampling. Across the three cladistic matrices investigated, the Late Jurassic time bin sees the introduction of several groups (e.g. ceratopsians, thecelosaurids/early-diverging ornithopods, iguanodontians; Figure 3.1), so it would be expected that morphological disparity would increase during this interval.

While disparity-through-time trends derived from each of the three cladistic matrices were broadly similar in the Jurassic, these patterns diverge in the Cretaceous. In results derived from Boyd (2015), disparity tends to decline substantially through the Cretaceous (Figure 3.5–7a), whereas in results generated from Han *et al.* (2018) and Dieudonné *et al.* (2021), disparity tends to plateau or subtly increase in these later time bins (Figure 3.5–7c, e). The only exception to the Cretaceous decline observed in results derived from Boyd (2015), is in the size-based disparity measure (Figure 3.5a), where disparity peaks in the Early Cretaceous, before declining into the Late Cretaceous. However, this measure is known to be highly influenced by outliers, of which there are many in the Early Cretaceous time bins (Figure 3.5a–b; Guillerme *et al.* 2020). Overall, the Cretaceous disparity trends observed in this study are likely to be highly inaccurate, given that the number of Cretaceous taxa included in either of the three matrices investigated comprises only a fraction of the known Cretaceous species richness for ornithischians (~10%; Figure 3.1, 3.10a).

3.4.2. Implications for the systematics of the thecelosaurids/early-diverging ornithopods

Morphospace analyses demonstrate that although ‘hypsilophodontids’ are often considered to be anatomically conservative, they are actually morphologically diverse,

regularly plotting disparately from each other (Figure 3.2–4). This disparity seems to be most pronounced when calculated using the matrix of Boyd (2015), where thescelosaurids/early-diverging ornithopods (T/EDOs) are widely distributed when all character partitions are investigated (Figure 3.2, A3.3–4). This is likely due to the taxon sampling in this cladistic matrix, which includes more T/EDOs than Han *et al.* (2018) and Dieudonné *et al.* (2021), but proportionally fewer taxa from other ornithischian clades (i.e. ceratopsians, iguanodontians, pachycephalosaurians; Figure 3.1). Results also show some thescelosaurids/early-diverging ornithopods (T/EDOs) regularly plot closer to other ornithischian clades than they do to other T/EDOs. For example, the T/EDOs *Gasparinisaura* and *Talenkauen* regularly plot close to, or overlap with, iguanodontian morphospace, even in results derived from the matrix of Boyd (2015; A3.4a, c), in which *Talenkauen* was originally recovered phylogenetically distant from the iguanodontians, outside of Cerapoda within Thescelosauridae (Boyd 2015). Additionally, some T/EDOs (e.g. *Changchunsaurus*, *Koreanosaurus*, *Yueosaurus*) frequently plot particularly distant from other T/EDOs (e.g. A3.3e; A3.6d, f; A3.9a), often in unique areas of morphospace, suggesting that these taxa had highly specialised morphologies.

These disparate signals imply that the ‘hypsilophodontids’ do not represent a monophyletic clade (i.e. Thescelosauridae), but perhaps a paraphyletic assemblage of taxa occupying one or multiple branches of the neornithischian tree. This is generally congruent with findings from multiple recent phylogenetic analyses where T/EDOs were predominately recovered within Cerapoda as early-diverging ornithopods (Butler *et al.* 2008; Dieudonné *et al.* 2016; Han *et al.* 2018; Dieudonné *et al.* 2021). It is also congruent with results from Chapter 2, which found this hypothetical placement more stable to taxon and character manipulation (Brown *et al.* 2022).

Morphospace analyses generated using the Boyd (2015) matrix consistently recover most T/EDOs in unique morphospace across all anatomical partitions (Figure 3.2), which does suggest that these taxa are highly specialised and distinct from derived clades. This is in line with results from the phylogenetic analysis conducted by Boyd (2015; and subsequently in Madzia *et al.* 2018; Herne *et al.* 2019), which recovered most of these T/EDOs outside of Cerapoda, within the clade Thescelosauridae. By contrast, investigations of the Han *et al.* (2018) and Dieudonné *et al.* (2021) matrices reveal that T/EDOs frequently plot within ornithopod or ceratopsian morphospace, suggesting these taxa generally have cerapodan-like morphologies (Figure 3.3–4). These results are consistent with phylogenetic analyses from Han *et al.* (2018) and Dieudonné *et al.* (2021), in which T/EDOs were recovered primarily within Cerapoda as early-diverging ornithopods. An exception to this is in the pelvic girdle and hind limb partition (Figure 3.2–4f), and to a lesser extent, the dental partition (Figure 3.2, 3.4b; A3.7b), where T/EDOs were found to largely occupy unique areas of morphospace across all three matrices, suggesting these anatomical regions were relatively specialised and distinct in most T/EDOs. In Chapter 2 (section 2.4.2; Brown *et al.* 2022), dental and hind limb characters in the Boyd (2015) matrix were found to be disproportionately more supportive of the exclusion of T/EDOs from Cerapoda than characters from other anatomical partitions. It is worth noting that pelvic girdle characters in Chapter 2 did not have an effect on the tree topology of Boyd (2015; section 2.3.3.3): however, as pelvic girdle and hind limb characters were grouped together in this study, it is uncertain which region (or both) is responsible. Results here seem to agree with findings from Chapter 2 that hind limb and dental morphologies in ‘hypsilophodontids’ do have a non-cerapodan signal, and even more so, that this signal is not just

restricted to the Boyd (2015) cladistic matrix, but in the matrices of Han *et al.* (2018) and Dieudonné *et al.* (2021). This further emphasises the importance of investigating these regions when trying to resolve neornithischian relationships.

3.4.3. Comments on non-focal group taxa

3.4.3.1. Early-diverging ornithischians. The origin and early evolution of Ornithischia is poorly understood (Irmis *et al.* 2007; Baron *et al.* 2017b; Baron 2019; Müller & Garcia 2020; Norman *et al.* 2022). While large-scale analyses of dinosaur relationships suggest that ornithischians originated during the Middle to Late Triassic, the earliest definitive members of the clade are Early Jurassic in age (Butler 2005; Butler *et al.* 2007; Irmis *et al.* 2007; Olsen *et al.* 2010; Baron 2019). The phylogenetic positions of these early ornithischians (e.g. *Eocursor*, *Laquintasaura*, *Lesothosaurus*) are also controversial, and it remains unclear whether some of these taxa represent either early-diverging ornithischians or the earliest members of derived ornithischian clades (e.g. heterodontosaurids, thyreophorans; Butler 2010; Boyd 2015; Baron *et al.* 2017a; Salgado *et al.* 2017; Han *et al.* 2018; Dieudonné *et al.* 2021).

One such taxon is *Eocursor* from the upper Elliot Formation of South Africa (Butler *et al.* 2007; Butler 2010; Bordy *et al.* 2020). In its original description, Butler *et al.* (2007) noted a number of similarities between *Eocursor* and the heterodontosaurid *Heterodontosaurus*, particularly in the manus, but recovered *Eocursor* as the sister-taxon of Genasauria. Subsequent phylogenetic analyses have been unable to find consensus on the placement of *Eocursor*, recovering the taxon in a polytomy at the base of Ornithischia (Han *et al.* 2018), as an early-diverging heterodontosaurid (Boyd 2015), and as an early-diverging neornithischian (Dieudonné *et al.* 2021).

These phylogenetic positions are moderately congruent with the morphospace results. The unresolved polytomous position of *Eocursor* within the original Han *et al.* (2018) analysis is demonstrated by the fluidity in how the taxon plots across different principal coordinate axes or anatomical partitions (Figure 3.3; A3.6–7). *Eocursor* is generally recovered either within a unique region of morphospace (e.g. PCo1/PCo2, all partitions, dental partition: A3.6a, c), amongst basal ornithischians (e.g. pelvic girdle and hind limb partition: A3.6–7f) or within the morphospace of Cerapoda (e.g. PCo1/PCo3, all partitions, dental partition: A3.7a,c). *Eocursor* plots similarly in results derived from the Dieudonné *et al.* (2021) dataset: however, here the taxon plots even more regularly within or adjacent to cerapodan morphospace, namely when only dental (Figure 3.4c; A3.9–10c) or pectoral girdle and forelimb characters (Figure 3.4e; A3.9–10e) are included in analyses. This mix of cerapodan-like and basal ornithischian-like morphologies illustrates why this taxon was recovered comparatively far up the tree, within Neornithischia, in the original phylogenetic analysis by Dieudonné *et al.* (2021). Morphospace results find little evidence to suggest *Eocursor* has heterodontosaurid affinities, even in data derived from the Boyd (2015) matrix, where *Eocursor* often plots amongst early-diverging ornithischians or basal thyreophorans within the morphospace (e.g. Figure 3.3a, c, f). Results generated from Boyd (2015) also show *Eocursor* plotting within cerapodan morphospace when certain anatomies are analysed in isolation (e.g. pectoral girdle and forelimbs, A3.4f). These inferred cerapodan-like morphologies in the dental, pectoral girdle and forelimb regions may be the result of evolutionary convergence.

In this study, the putative thyreophorans *Isaberrysaura*, *Laquintasaura* and *Lesothosaurus* were included within the group ‘EDO/N’ to assess where in morphos-

pace they plotted, relative to the thyreophorans. In the three ornithischian matrices investigated in this study, these taxa have been recovered in the following positions: *Isaberrysaura* has been recovered within Thyreophora by both Han *et al.* (2018) and Dieudonné *et al.* (2021); *Laquintasaura* has been recovered as an early-diverging ornithischian by Dieudonné *et al.* (2021) and in a polytomy at the base of Ornithischia by Han *et al.* (2018); and *Lesothosaurus* has been recovered as an early-diverging ornithischian by Dieudonné *et al.* (2021), in a polytomy at the base of Genasauria by Han *et al.* (2018), and as an early-diverging thyreophoran by Boyd (2015).

Here, morphospace results derived from the Han *et al.* (2018) matrix support the inclusion of *Isaberrysaura* within Thyreophora, with the taxon being consistently recovered within, or proximal to, thyreophoran morphospace across all partitions (A3.6–7a–c). However, in results generated from Dieudonné *et al.* (2021) the relationship is much less clear, with *Isaberrysaura* only plotting moderately close to the thyreophorans when dental characters were analysed in isolation (A3.9–10c). In the remaining iterations, *Isaberrysaura* and other EDO/EDNs tend to fall close to the T/EDOs and iguanodontians (e.g. in the skull partition analysis, A3.9–10b). This result is somewhat surprising, considering that the same matrix recovered *Isaberrysaura* as well-nested within Thyreophora as the sister taxon to Stegosauria when subject to phylogenetic analysis by Dieudonné *et al.* (2021). The contrast between the results derived from these two cladistic matrices highlights how interpretations of discrete character analyses should be treated with caution.

Han *et al.* (2018) originally recovered *Laquintasaura* in an unresolved polytomous position at the base of Ornithischia. The taxon was subsequently pruned *a posteriori* to improve tree resolution. In morphospace results generated using the Han

et al. (2018) data matrix, *Laquintasaura* often plots in either a unique region of morphospace (e.g. in the skull partition analysis PCo1/PCo2 plot, A3.6b), or within, or adjacent to, thyreophoran morphospace (e.g. in the dental partition analysis PCo1/PCo2 plot, A3.6c). By comparison, in results derived from Dieudonné *et al.* (2021), *Laquintasaura* most often plots in a unique area of morphospace, disparate from all other taxa. This is particularly apparent in the skull (e.g. A3.9b) and pelvic girdle and hind limb partitions (A3.9–10f), and suggests that *Laquintasaura*, or these morphologies specifically, were likely highly specialised.

Finally, concerning *Lesothosaurus*, the morphospace results from all three cladistic matrices tend to suggest that the skull, pectoral girdle and forelimb morphologies of this taxon are more similar to those of early-diverging neornithischians, T/EDOs and iguanodontians than to thyreophorans (A3.3–4b, e; A3.6–7b, e; A3.9–10e; although see A3.9–10b, where *Lesothosaurus* instead plots between the T/EDOs and thyreophorans when skull characters were investigated in isolation). In contrast, when the matrices were partitioned to include only pelvic girdle and hind limb characters, *Lesothosaurus* was found to be comparably disparate to the early-diverging neornithischians, T/EDOs and iguanodontians, instead plotting close to early-diverging ornithischians (e.g. *Eocursor*) or thyreophorans (A3.3–4f; A3.6–7bf; A3.9–10f). As most thyreophorans are quadrupeds, it may not seem surprising that there is a large amount of disparity between the pectoral girdle and forelimb morphologies of this clade and the bipedal *Lesothosaurus*. However, it is worth noting that one of the thyreophorans within the analyses, *Scutellosaurus*, is bipedal (Maidment & Barrett 2012b; Breeden III *et al.* 2021; Anderson *et al.* 2023), so this result is not purely indicative of locomotory mode. In morphospace analyses of the pelvic girdle and hind limb morphologies,

Lesothosaurus and other early-diverging ornithischians (which are also bipedal) often plot far closer to *Scutellosaurus* than other thyreophorans, which likely reflects their similar locomotory abilities (A3.6–7f; A3.10f). Overall, my results tend to undermine the inclusion of *Lesothosaurus* in Thyreophora.

3.4.3.2. Early-diverging neornithischians. The stem-based clade Neornithischia comprises all genasaurians more closely related to the hadrosaur *Parasaurolophus walkeri*, than to the thyreophorans *Ankylosaurus magniventris* and *Stegosaurus stenops* (Cooper 1985). Typically, Neornithischia includes three of the five major ornithischian clades: Ceratopsia, Ornithopoda and Pachycephalosauria, which are all united within the node-based clade Cerapoda. Traditionally, Neornithischia and Cerapoda were largely similar in composition, as very few or no neornithischian taxa were recovered outside of Cerapoda (e.g. Sereno 1986; Sereno 1999; Buchholz 2002). However, in the last two decades various phylogenetic analyses investigating ornithischian relationships have recovered several non-thyreophoran genasaurians outside of Cerapoda (e.g. Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016; Han *et al.* 2018; Madzia *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021). Many of these taxa are recovered as early-diverging neornithischians (Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016; Han *et al.* 2018; Madzia *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021), but in a few analyses, some taxa also fall out within the clade Thescelosauridae (Boyd 2015; Madzia *et al.* 2018; Herne *et al.* 2019). Here I focus on the former, which includes the taxa *Agilisaurus*, *Hexinlusaurus*, *Leaellynasaura*, ‘*Othnielosaurus*’ (which is now considered to be *Nanosaurus*, sensu Carpenter & Galton 2018), *Stormbergia* and *Yandusaurus*.

Agilisaurus, *Hexinlusaurus* and *Yandusaurus* were traditionally considered to

be ‘hypsilophodontids’, but are now consistently recovered as non-cerapodan early-diverging neornithischians (Galton 1973; Weishampel & Heinrich 1992; Barrett *et al.* 2005; Butler *et al.* 2008; Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021). *Leaellynasaura* was also originally described as a ‘hypsilophodontid’ (Rich & Rich 1989), but unlike the aforementioned taxa, there is currently little consensus on its phylogenetic position, owing to its incompleteness. Recent (albeit limited) phylogenetic analyses have recovered *Leaellynasaura* in two highly conflicting positions, as an early-diverging neornithischian (Boyd 2015) or as an elasmarian ornithopod (Herne *et al.* 2019; see Appendix, A1.1 for more details). Lastly, *Stormbergia* has been recovered as the basal-most neornithischian in both Butler *et al.* (2008) and Boyd (2015), however some authors question the validity of this taxon and suggest that *Stormbergia* may represent an ontogenetically older stage of *Lesothosaurus* (e.g. Knoll *et al.* 2010; Baron *et al.* 2017a).

Results here find that early-diverging neornithischians typically plot close to the thescelosaurids/early-diverging ornithopods (T/EDOs) across different anatomical partitions. An exception to this is observed in the pelvic girdle and hind limb partition, where most early-diverging neornithischians (e.g. *Agilisaurus*, *Hexinlusaurus*, *Leaellynasaura*, *Stormbergia*) plot disparately from T/EDOs, often close to early-diverging ornithischians, heterodontosaurids, thyreophorans and ornithopods. ‘*Othnielosaurus*’ consistently places close to the T/EDOs throughout all analyses, which supports recent interpretations by Carpenter & Galton (2008) that this taxon is a junior synonym of the T/EDO *Nanosaurus*.

Due to incompleteness, the Australian taxon *Leaellynasaura* was only included in the dental and pelvic girdle and hind limb partition analyses. When the dental

partition is assessed, *Leaellynasaura* plots disparately from all other early-diverging neornithischians and moderately close to other Gondwanan taxa (*Gasparinisaura* and *Talenkauen*; A3.3–4c). In contrast, when the pelvic girdle and hind limb partition is analysed in isolation, *Leaellynasaura* plots disparately from the Gondwanan taxa, close to heterodontosaurids and marginocephalians (A3.3–4f). Results of the dental partition analyses are somewhat congruent with those from Herne *et al.* (2019), which recently recovered *Leaellynasaura* as an elasmarian ornithopod along with a number of Gondwanan taxa (including *Gasparinisaura* and *Talenkauen*). The data matrix used by Herne *et al.* (2019) to recover this topology was a modified version of the Boyd (2015) matrix and used implied character weighting. Prior to analyses, Herne *et al.* (2019) updated the scoring of *Leaellynasaura* in the Boyd (2015) dataset to reflect recent assessments by Herne *et al.* (2016) that all postcranial material assigned to the taxon was inconclusive. Results of this chapter seem to tentatively agree with concerns from Herne *et al.* (2016) that the inclusion of dubious specimens within *Leaellynasaura* could have resulted in a taxonomic chimera. Furthermore, results here suggest the pelvic girdle and hind limb material formerly attributed to *Leaellynasaura* could actually be that of an early marginocephalian, given its proximity to *Stenopelix* (A3.4f) and *Wannanosaurus* (A3.3f).

3.4.3.3. Heterodontosaurids and marginocephalians. Although heterodontosaurids and marginocephalians are not the focal group of this thesis, the recovery of heterodontosaurids within Pachycephalosauria during a recent re-evaluation of cerapodan relationships (Dieudonné *et al.* 2021) has major implications for the origins of both Cerapoda and Ornithopoda, and on taxa that remain relatively fluid around these clades (i.e. the ‘hypsilophodontids’). While the placement of both Pachycephala-

losauria and Marginocephalia within Ornithischia has remained consistent since the mid-1980s (Serenio 1984; Cooper 1985; Maryńska & Osmólska 1985), the same cannot be said for the heterodontosaurids. Even in the last two decades, cladistic analyses have recovered heterodontosaurids near the base of Ornithischia (Figure 3.11, H1; e.g. Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016; Baron *et al.* 2017a,b; Han *et al.* 2018), as the sister group to Marginocephalia + Ornithopoda (Figure 3.11, H2; Cerapoda sensu Butler *et al.* 2008; e.g. Butler 2005; Spencer 2007), as the sister-group to Marginocephalia (Figure 3.11, H3; e.g. Buchholz 2002; You *et al.* 2003; Xu *et al.* 2006), and most recently, as a paraphyletic assemblage within Pachycephalosauria (Figure 3.11, H4; Dieudonné *et al.* 2021). Analyses in Chapter 2 further attest to this fluidity, with results finding the phylogenetic placement of Heterodontosauridae to be highly dependent on taxon and character sampling (see Chapter 2; sections 2.3.2.1. and 2.3.3.3).

In most of the morphospace analyses in this study, the heterodontosaurids often plot disparately from each other, particularly considering the relatively small number of taxa included in this group. Furthermore, some heterodontosaurids are consistently placed within, or adjacent to, iguanodontian morphospace (e.g. *Heterodontosaurus*), while others more often overlap with the ceratopsians (e.g. *Fruitadens*). The dental partition consistently shows the greatest distribution of heterodontosaurids, with the taxa dispersed along PCo1 in all three matrices (A3.3–4c; A3.6–7c; A3.9–10c). These results are not supportive of a monophyletic Heterodontosauridae, incongruent with the recent phylogenetic analysis by Dieudonné *et al.* (2021). In addition, the large distribution and disparity in signal relative to other ornithischian clades could also imply that some of these heterodontosaurids actually occupy different branches of the tree

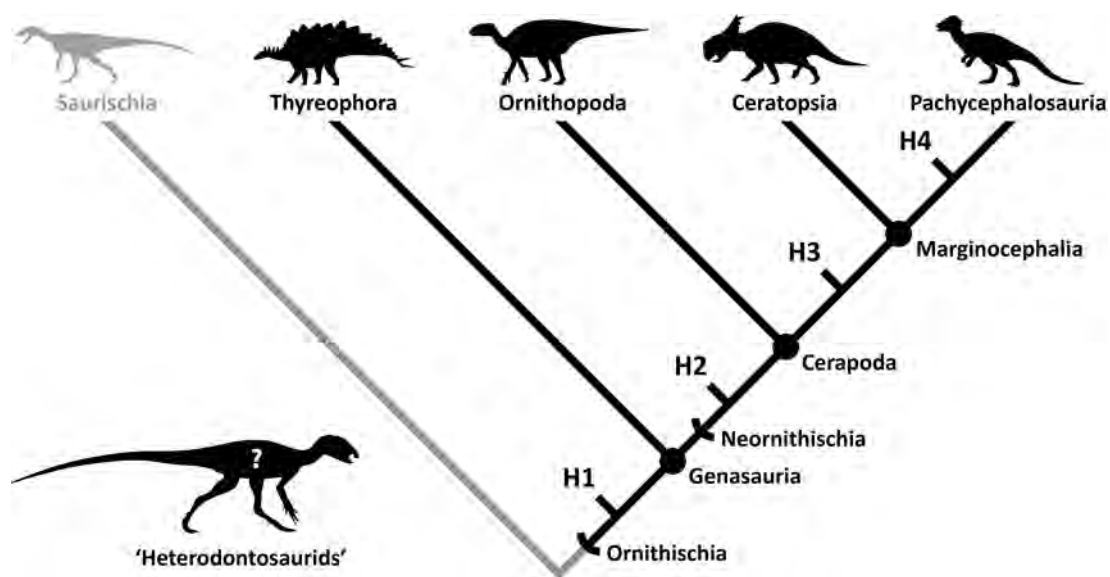


Figure 3.11. Simplified cladogram showing the four positions where 'heterodontosaurids' have been recovered in recent phylogenetic analyses: H1, hypothesis 1 (e.g. Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016; Baron *et al.* 2017; Han *et al.* 2018); H2, hypothesis 2 (e.g. Butler 2005; Spencer 2007); H3, hypothesis 3 (e.g. Buchholz 2002; You 2003; Xu *et al.* 2006); H4, hypothesis 4 (e.g. Dieudonné *et al.* 2021). Silhouettes from <http://phylopic.org>: S. Hartman, I. Reid, E. Willoughby.

Concerning the inclusion of heterodontosaurids within Pachycephalosauria, analyses using the data matrices from Han *et al.* (2018) and Dieudonné *et al.* (2021) suggest that these two groups have shared skull morphologies (Figure 3.6b, 3.7b;

A3.6–7b, A3.9–10b). There is also more limited evidence of an overlap in dental (Figure 3.7c; A3.6c, A3.10c) and pectoral girdle and forelimb morphologies (Figure 3.7e; A3.9e). In contrast, I find that vertebral (Figure 3.6d, 3.7d; A3.6–7d, A3.9–10d) and pelvic girdle and hind limb morphologies (Figure 3.6f, 3.7f; A3.6–7f, A3.9–10f) in heterodontosaurids and pachycephalosaurids are largely distinct from each other. These shared morphologies may be suggestive of a close phylogenetic relatedness between these two groups, but also could be the result of evolutionary convergence in these particular morphologies. Interpretations were limited in results derived from the Boyd (2015) matrices due to the inclusion of only one putative pachycephalosaurian in the analysis, *Wannanosaurus* (Figure 3.1; see section 3.2.2), which did overlap with heterodontosaurid morphospace when all partitions were included (PCo1/PCo2: Figure 3.2a; A3.3a), but otherwise was recovered in unique morphospace disparate from all other taxa in the analysis (e.g. A3.3–4c, A3.3–4d).

In summary, these findings show that even in phylogenetic studies that recover heterodontosaurids at the base of Ornithischia (i.e. Boyd 2015; Han *et al.* 2018) there is still evidence of potential cerapodan affinities within these character matrices. This is congruent with results from Chapter 2 (see sections 2.4.1.), where removing unique taxa from Boyd (2015) and Han *et al.* (2018) resulted in heterodontosaurids being recovered as neornithischians (Figure 2.3–4), and even within Cerapoda as the sister-group of Marginocephalia (Figure 2.3). These disparate signals and fluid results do not provide much insight into the phylogenetic affinities of the heterodontosaurids (which remain highly contentious), but may suggest that the group is not monophyletic. Further research is required to confirm these interpretations.

3.4.4. Limitations

The re-purposing of cladistic matrices for use in disparity analyses has recently been brought into question, with studies demonstrating that results should be treated with caution (Flannery Sutherland *et al.* 2019; Smith *et al.* 2021). The sampling of both characters and taxa within cladistic matrices has been shown to be highly influential on the resulting disparity trends (Flannery Sutherland *et al.* 2019; Smith *et al.* 2021). Furthermore, certain aspects of the tree topologies produced by cladistic matrices (e.g. branch length) can reflect the distribution of taxa within morphospace, suggesting that the results of disparity analyses are not entirely decoupled from phylogenetic signal (Smith *et al.* 2021).

Here, I assessed the morphological disparity of the neornithischians using three recent cladistic datasets by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). These matrices are largely independent from each other in both character and taxon sampling (Chapter 2; Brown *et al.* 2022). Additionally, when subject to phylogenetic analysis they each recovered conflicting phylogenetic placements for several key ornithischian taxa (Chapter 2; Brown *et al.* 2022).

Despite differences in character and taxon sampling between the three matrices, the disparity-through-time results find several similarities, most notably that disparity was lowest in the Middle Jurassic and then increased greatly into the Late Jurassic (Figure 3.5–7). The observation of this trend across all three cladistic matrices and disparity-through-time metrics may suggest that it does represent a true evolutionary signal. However, there are also vast differences between the disparity results generated from these different matrices. During the Late Cretaceous, disparity tends to sharply decline in the results derived from the Boyd (2015; Figure 3.5–7) matrix, whereas in

the results derived from Han *et al.* (2018) and Dieudonné *et al.* (2021) disparity increases (Figure 3.5–6), or at least remains stable (Figure 3.7). This difference may be the result of uneven taxon sampling between both time bins and character-taxon matrices. For example, in Boyd (2015), the Late Cretaceous time bin is dominated by T/EDOs, comprising 71% of taxa in this bin ($n = 15$), compared to 36% and 33% in Han *et al.* (2018; $n = 8$) and Dieudonné *et al.* (2021; $n = 8$) respectively (Figure 3.1).

While this demonstrates that uneven taxon sampling can have a strong influence on disparity-through-time results, the similar trends in the results derived from the Han *et al.* (2018) and Dieudonné *et al.* (2021) matrices show that matrices with different character and taxon sampling, as well as different overall aims, can still produce broadly similar disparity signals.

Several recent studies have used morphospace disparity plots, derived from cladistic matrices, to elucidate patterns of morphological evolution in different anatomical regions (e.g. Müller *et al.* 2022; Casali *et al.* 2023). Many of these studies use a single cladistic matrix as the data source for these analyses (e.g. Müller *et al.* 2022; Casali *et al.* 2023). Here, I used three largely independent character-taxon matrices to assess the relative placement of ornithischian taxa within morphospace across five separate anatomical partitions. Following the ordination of these matrices, the first three principal coordinate axes were plotted. Unfortunately, these three axes only captured a small amount of the total morphological variance (A3.2; avg. total variance in PCo1–3 across all partition iterations: Boyd 2015 = 17.6%; Han *et al.* 2018 = 15.4%; Dieudonné *et al.* 2021 = 12.6%), significantly limiting the value of any interpretation. Additionally, each ordination involved the removal of OTUs where distances could not be calculated by the algorithm (Lloyd *et al.* 2022; see A3.1 for a full list of removed taxa). In the

vertebral and pectoral girdle and forelimb partitions, this removal was particularly extensive, equating to up to 38% of total OTUs in a given data matrix (A3.1). While many of these excluded OTUs tend to include a large proportion of missing characters, their exclusion undoubtedly omits a considerable number of informative observations.

When comparing the morphospace plots of a given anatomical partition between the cladistic matrices they were derived from, the placement of taxa is often varied or conflicting. For example, the PCo1/PCo2 plot generated from the Han *et al.* (2018) matrix suggests that the pelvic girdle and hind limb morphologies of the T/EDOs *Changchunsaurus* and *Koreanosaurus* are highly disparate from all other T/EDOs (A3.6f); whereas in the same plot using the Dieudonné *et al.* (2021) matrix, these taxa are recovered among other T/EDOs (A3.9f), suggesting shared pelvic girdle and hind limb morphologies. This demonstrates how interpretations based on the position of taxa within morphospace and their distance from other taxa/clades should be treated with caution, as results can differ significantly between matrices. Assessing morphospace distribution using multiple different cladistic matrices, as in this study, adds credence to common trends where they are found.

Smith *et al.* (2021) suggested that the cladistic matrices used in disparity analyses should be constructed with that purpose in mind, rather than re-purposed from studies assessing phylogenetic relationships. This is because the aims of these phylogenetic studies have an influence on the taxon and character sampling, and therefore on the disparity results (Smith *et al.* 2021). The three cladistic matrices utilised in this study were re-purposed from recent phylogenetic analyses of ornithischian relationships: however, each of these had different aims. The matrices developed by Boyd (2015) and Dieudonné *et al.* (2021) were created to resolve the systematic relation-

ships of ornithischians and cerapodans, respectively, whereas the aim of the Han *et al.* (2018) matrix was primarily to clarify the positions of the basal ceratopsians, *Yinlong* and *Psittacosaurus*. These different aims are reflected in the morphospace results obtained in this study, particularly in those derived from the Han *et al.* (2018) matrix, where the ceratopsians generally appear far more disparate than in results derived from the Boyd (2015) and Dieudonné *et al.* (2021) matrices, often occupying a large proportion of the total morphospace (e.g. PCo1/PCo2 dental partition, Figure 3.3c; A3.6c). This led to far more taxa overlapping with ceratopsian morphospace in these iterations, obscuring occupation patterns. It also likely caused other non-ceratopsian clades to appear more clustered: for example, in results derived from Han *et al.* (2018), iguanodontian skull morphology is highly constrained (Figure 3.3b; A3.6–7b), whereas in results generated from Boyd (2015) and Dieudonné *et al.* (2021) it is far more widely dispersed (Figure 3.2b, 3.4b; A3.3–4b, A3.9–10b). The comparatively high ceratopsian disparity in results derived from Han *et al.* (2018) is because this cladistic matrix contains both a higher proportion of characters dedicated to resolving relationships within Ceratopsia, and more ceratopsian taxa, than the Boyd (2015) and Dieudonné *et al.* (2021) matrices. These results highlight the importance of considering the original intent of a cladistic matrix when re-purposing it for use in disparity analyses.

3.5. Conclusions

In this study, I used three recent phylogenetic analyses of ornithischian relationships to investigate changes in morphological disparity through time and the morphospace occupation of the ‘hypsilophodontids’ relative to other ornithischian clades. While tra-

ditionally considered morphologically conservative, this study shows that the ‘hypsilophodontids’ actually represent a highly diverse assortment of taxa, which is evident from their disparate distribution throughout morphospace. Some of these focal taxa frequently plot closer to more derived ornithischian clades (e.g. iguanodontians), whereas others often inhabit unique regions of morphospace. These results tend to agree with recent phylogenetic analyses, and the findings presented in Chapter 2, that the ‘hypsilophodontids’ likely represent a paraphyletic assemblage of taxa, rather than a suite of animals (mostly) united within a monophyletic group (i.e. Thescelosauridae). Analyses do, however, find that the dental, pelvic girdle and hind limb morphologies of the thescelosaurids/early-diverging ornithopods occupy largely unique areas of morphospace, suggesting that these anatomical regions were highly specialised.

Although not the main focus of this thesis, the morphospace analyses in this study also gave insights into other ornithischians with uncertain phylogenetic affinities. Results show that the ‘heterodontosaurids’ and pachycephalosaurids have shared skull morphologies, which could suggest close relatedness, as recovered in a recent phylogenetic analysis by Dieudonné *et al.* (2021), or be the result of evolutionary convergence. The monophyly of Heterodontosauridae is brought into question due to the extensive distribution of these taxa in morphospace, implying that the ‘heterodontosaurids’ may in fact occupy different branches of the ornithischian tree.

When looking at ornithischian disparity through time, I find that phenotypic diversity generally declined into the Middle Jurassic, before exploding into the Late Jurassic. This spike was preceded by a diversification of pelvic girdle and hind limb morphologies, which may indicate that important locomotory adaptations were evolving at this time, and possibly driving this burst of evolutionary innovation in the Late

Jurassic.

The limitations discussed highlight how results of disparity analyses should generally be treated with caution, as they are highly influenced by both the character and taxon sampling of the cladistic matrices investigated. When making interpretations from character-based disparity analyses, it is preferable to use multiple cladistic matrices, as areas of congruence give credence to results.

Chapter 4

LONG BONE HISTOLOGY OF *HYPSILOPHODON FOXII* (ORNITHISCHIA: ORNITHOPODA) FROM THE ISLE OF WIGHT, UK

Hypsilophodon foxii is a small bipedal ornithopod from the Early Cretaceous of the Isle of Wight, UK, which hails from a single bed at the top of the Wessex Formation, the ‘*Hypsilophodon* Bed’. Here, I examined the long bone histology of six individuals across various size classes. I distinguished five histological ontogenetic stages, broadly summarised by the change from fast growing well-vascularised woven-fibred bone at the juvenile stage, to slower growing poorly-vascularised parallel-fibred bone in the outer cortex of sub-adults. The cortices of the most ontogenetically mature individuals were subject to extensive secondary remodelling and periosteal cortical drift, but show periods of faster and slower growth demonstrated by the presence of annuli and zones. No unambiguous LAGs were recovered in any section, suggesting *Hypsilophodon foxii* maintained uninterrupted growth even during periods of seasonal stress. The presence or absence of regular developing LAGs in other small to medium-sized cerapodans implies that two distinct growth strategies were adopted by these taxa, possibly due to differences in developmental plasticity. No external fundamental system was observed; however, a similar, highly avascular periosteal layer was found in the tibia of the largest individual, suggesting it was approaching skeletal maturity. Both inter-elemental and intra-specific variation was noted, with the latter implying distinct growth trajectories, possibly reflecting sexual dimorphism. Used in conjunction with

our ontogenetic interpretations, size distribution profiles tentatively suggest that the *Hypsilophodon* Bed was catastrophic in origin, possibly capturing a genuine population consisting primarily of juveniles and sub-adults.

4.1. Introduction

Amprino (1947) was the first to identify a relationship between bone microstructure and its rate of deposition. To this day, “Amprino’s rule” remains a cornerstone for making palaeohistological interpretations (de Buffrénil *et al.* 2021a). These methods have been widely applied to dinosaurs, revealing insights into the growth rate, physiology, ontogenetic status, and life histories of numerous non-avian theropods (e.g. Chinsamy 1990; Horner & Padian 2004; Schweitzer *et al.* 2005; Lee & O’Connor 2013; Skutschas *et al.* 2017; Barta *et al.* 2022), sauropodomorphs (e.g. Curry 1999; Sander 2000; Klein & Sander 2008; Woodward & Lehman 2009; Company 2011; Cerda *et al.* 2022), and ornithischians (e.g. Horner *et al.* 2000; Redelstorff and Sander 2009; Hayashi *et al.* 2009; Horner *et al.* 2009; Knoll *et al.* 2010; Cerda & Chinsamy 2012; Werning *et al.* 2012; Woodward *et al.* 2015; Fostowicz-Frelik & Slowiak 2018; Cerda *et al.* 2019; Kitchener *et al.* 2019; Zhao *et al.* 2019; Garcia-Marsà *et al.* 2020; Han *et al.* 2020; Hübner *et al.* 2021; Skutschas *et al.* 2021; Wosik & Evans 2022). Dinosaurs displayed faster growth rates than many modern reptiles, with some of the largest dinosaurs growing at accelerated speeds comparable to those of mammals and birds (Erickson *et al.* 2001; Padian *et al.* 2004). However, this rapid development is often interrupted by temporary pauses in growth, marked by lines of arrested growth (LAGs; de Buffrénil *et al.* 2021b). In extant vertebrates, LAGs have been shown to have annual periodicity

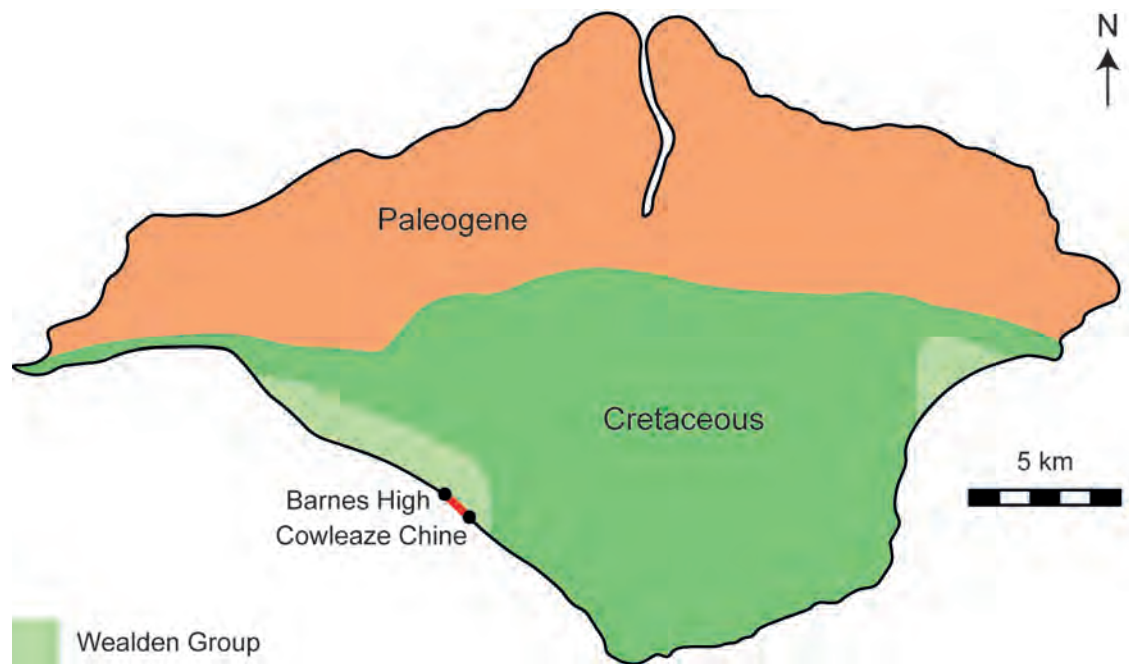


Figure 4.1. Simplified geological map of the Isle of Wight showing the extent of the Wealden Group (light green) and the extent of the '*Hypsilophodon* Bed' (red line), which is exposed between Barnes High and Cowleaze Chine. Modified from Sweetman & Insole (2010).

and, consequently, these features have been used frequently to estimate the ontogenetic ages of fossil specimens (Peabody 1961; Reid 1985; Horner *et al.* 1999; Köhler *et al.* 2012; Zhao *et al.* 2013a; Woodward *et al.* 2015; Han *et al.* 2020; Botha *et al.* 2022).

Ornithopoda is a diverse clade of ornithischian dinosaurs that attained a world-wide distribution during the Cretaceous, with specimens found on all seven continents. The group has been well-sampled histologically, permitting the creation of comprehensive ontogenetic series and growth curves for *Dysalotosaurus* (Hübner *et al.* 2012), *Edmontosaurus* (Wosik & Evans 2022), *Maiasaura* (Woodward *et al.* 2015) and *Tenontosaurus* (Werning 2012).

Hypsilophodon foxii (Huxley 1869) is a small, early-diverging ornithopod from the Early Cretaceous Wessex Formation (Wealden Group) of the Isle of Wight, UK. The species is among one of the most well-studied and well-sampled British dinosaurs, with dozens of partially complete specimens recovered from the ‘*Hypsilophodon* Bed’, a kilometre-long exposure along the southwest coast of the island (Figure 4.1; Galton 1974; Coram *et al.* 2017). Work on the taphonomy of the bed has been limited, but current hypotheses (Coram *et al.* 2017) suggest that this large accumulation is the result of a mass mortality event (e.g. a flash flood), implying that *Hypsilophodon* may have lived in large groups.

Here, I examine the long bone histology of six individuals of *Hypsilophodon foxii* from the NHMUK collections. The main aim of this study is to determine the ontogenetic distribution of individuals within the *Hypsilophodon* Bed. This will allow me to understand the growth patterns utilised by *H. foxii*, as well as inform on the population dynamics of the taxa and origin of the bed.

4.2. Methods

4.2.1. Material

4.2.1.1. Sampled *Hypsilophodon foxii* specimens. Over two dozen *Hypsilophodon foxii* femora and tibiae are accessioned within the NHMUK collection; however, many of these are incomplete proximal or distal ends. In histological studies, limb bones are typically sectioned midway along the diaphyseal region. This is because the diaphyseal region generally undergoes the least remodelling and erosion, and there is less chance of the inclusion of uninformative bone and tissues that have migrated from

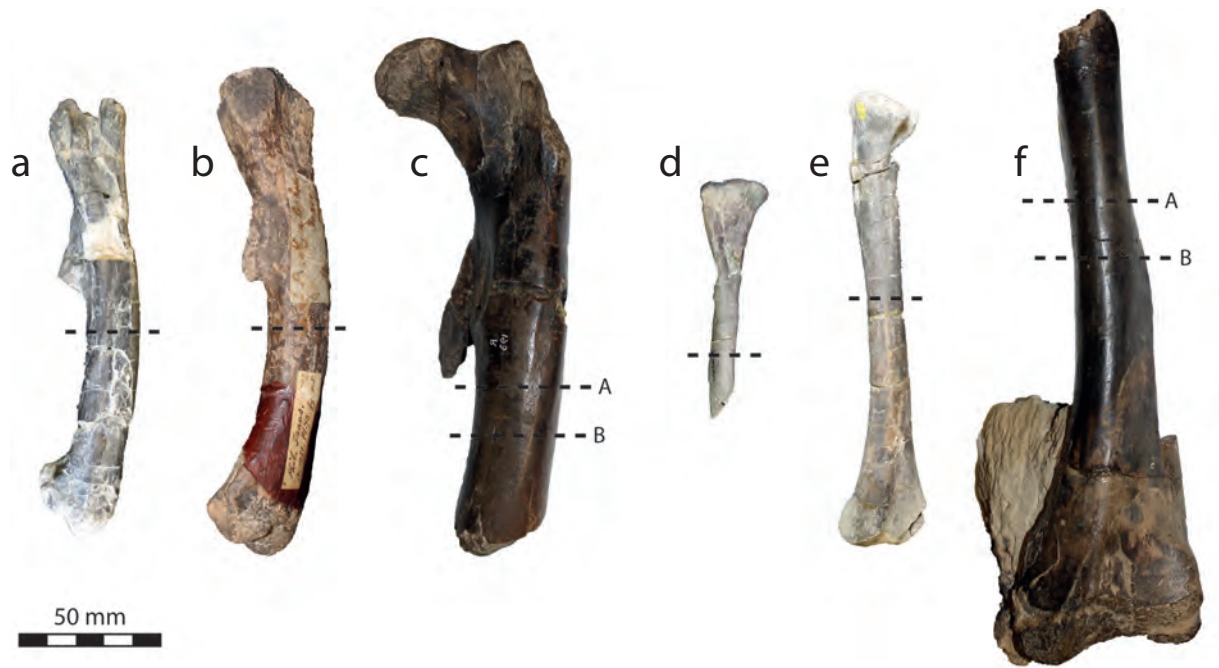


Figure 4.2. Specimens of *Hypsilophodon foxii* sampled in this study. Femora: **a**, NHMUK PV R 196 (right); **b**, NHMUK PV R 192a (left); **c**, NHMUK PV R 193 (right, partial proximal end). Tibiae: **d**, NHMUK PV R 5830 (left, partial distal end); **e**, NHMUK PV R 752 (right); **f**, NHMUK PV R 193 (right, partial distal end). Dashed lines indicate the approximate position along the long bone that the thin section originates. Views: anterior (a–c); posterior (d–e).

the metaphyseal region (Padian *et al.* 2013a). Suitable specimens were selected based on their mid-section circumference, ensuring the analysis included a varied range of limb bone sizes.

Three femora and three tibiae were histologically sampled from five unassociated NHMUK *Hypsilophodon foxii* specimens (Figure 4.2; Table 4.1). Both the femur and tibia were sectioned in NHMUK PV R 193, which is the largest known individual referred to *Hypsilophodon foxii* in the collections of both the NHMUK and IWCMS.

Table 4.1. Limb bones of *Hypsilophodon foxii* histologically examined in this study.

Specimen no.	Element	Mid-diaphyseal circumference (mm)	No. of thin sections
NHMUK PV R 196	Femur (r)	54.2	1
NHMUK PV R 192a	Femur (l)	72.2	1
NHMUK PV R 193	Femur (r)	82.0	2
NHMUK PV R 170	Femur (r)	62.1*	1
NHMUK PV R 5830	Tibia (l)	34.1	1
NHMUK PV R 752	Tibia (r)	43.5	1
NHMUK PV R 193	Tibia (r)	61.0	2

*Measured proximal to the fourth trochanter

All long bone sections were cut transversely in the diaphyseal regions, approximately at the mid-shaft. The development of midshaft trochanters (e.g. the fourth trochanter in femora) can result in cortical drift and the development of radially-oriented vascular canals in the region (Padian *et al.* 2013a). To avoid the influence of the fourth trochanter on bone histology (Padian *et al.* 2013a), femoral sections were taken at a distance from this feature. In both the femur and tibia of NHMUK PV R 193, a second thin-section was taken due to damage at the mid-shaft which resulted in the cortex in the first sections being largely incomplete. This also allowed me to examine histological variation throughout the diaphysis. Samples were prepared following the techniques outlined in Padian & Lamm (2013).

These five individuals are all recorded as originating from the *Hypsilophodon* Bed, although precise stratigraphical details are unknown or ambiguous. None of the specimens are associated with cranial material, but all have hind limb characters that



Figure 4.3. *Hypsilophodon foxii*, NHMUK PV R 170 (proximal end of right femur). Imaged in anterior view.

support their referral to *Hypsilophodon foxii* (Galton 1974). However, one of the tibiae, NHMUK PV R 752, was considered by Galton (1975) to be indeterminate generically and specifically, although the reasons for this assessment were not stated.

4.2.1.2. Other samples. I also re-examined a thin-section of NHMUK PV R 170, originally described by Reid (1984b), and later figured in Chinsamy *et al.* (1998). This thin-section is derived from the proximal end of a right femur (Figure 4.3; Table 4.1).

NHMUK PV R 170 is associated with a number of postcranial fragments from the *Hypsilophodon* Bed. Lydekker (1888; pp. 194, 234, 236) catalogued most of this material as juvenile *Iguanodon* sp.. However, Galton (1974) later assigned all of it to *Hypsilophodon*, and then subsequently referred to it as generically and specifically indeterminate ‘hypsilophodontids’ (Galton 1975). Some of the material originally cat-

alogued as NHMUK PV R 170 has since been referred to other taxa and assigned new catalogue numbers (e.g. NHMUK PV R 8421, NHMUK PV R 12440; Galton 1975; Barrett 1996; Barrett *et al.* 2011).

The remaining postcranial material catalogued as NHMUK PV R 170, including the thin-section used in our study, is currently assigned to *Hypsilophodon foxii* (Barrett 1996). This femoral section was sampled transversely, approximately at the mid-section of the diaphysis, but as the fourth trochanter is visible, it was sectioned more proximally than the thin-sections prepared specifically for this study.

4.2.2. Imaging

Specimens were imaged in both plain-polarised and cross-polarised light using an AxioImager M3 at NHMUK. Images were post-processed in Adobe Photoshop CC (v24.1.1, adobe.com) to improve the contrast and brightness.

4.2.3. Measurements

Features of interest were measured in ImageJ (v. 1.53c, imagej.nih.gov/ij). Cortical thickness was calculated as the mean percentage of cortex along the a-axis (the longest measurable length) and b-axis (perpendicular to the a-axis; Figure 4.4). Where specimens were considerably crushed, sections were first reconstructed using Adobe Photoshop CC (v. 24.1.1, adobe.com; Figure 4.5). Where large segments of the periosteal margin were missing, the boundary was first extrapolated (Figure 4.5). Body mass estimates of femoral specimens were calculated from femoral circumference measurements using the R-package *Masstimate* (Campione 2020), following the equation in Campione *et al.* (2014).

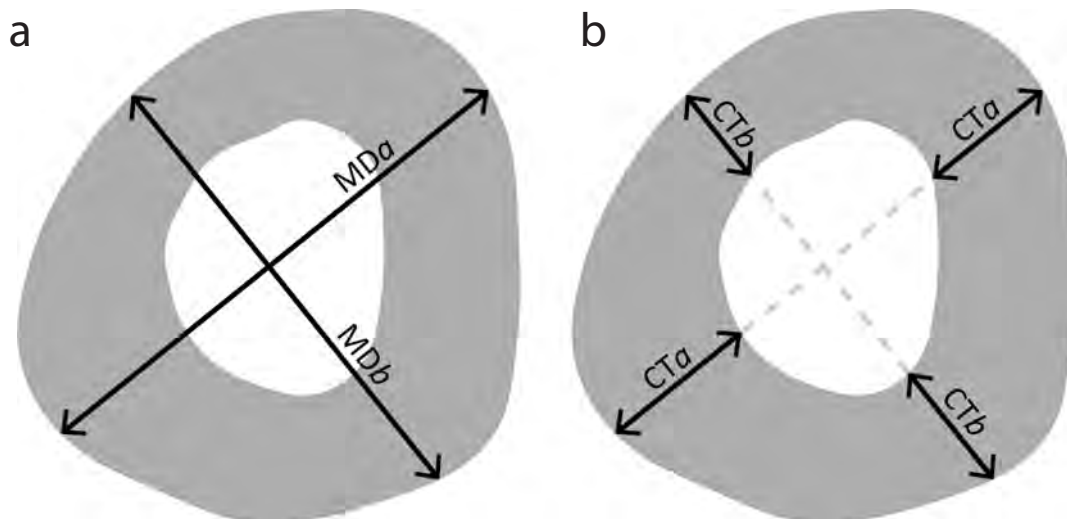


Figure 4.4. Diagram showing how midshaft diameter (**a**; MD) and cortex thickness (**b**; CT) was measured across the a- and b-axis of the thin sections in this study.

4.2.4. Size distribution

Femoral and tibial lengths were used as proxies for body size in order to evaluate the size distribution of *Hypsilophodon* individuals from the *Hypsilophodon* Bed. Much of the material analysed was incomplete, so I used linear regressions to estimate the original complete lengths of these elements. The regressions plotted limb bone length against one of three measurements: proximal end width (femora, $n = 5$; tibiae, $n = 4$), distal end width (femora, $n = 4$; tibiae, $n = 5$), and the length from the proximal tip to the distal base of the fourth trochanter (femora, $n = 4$; Figure 4.6; see Appendices A4.1). Measurements were collected from 18 femora and 19 tibiae at NHMUK and IWCMS. The linear regressions were plotted in R (R Studio, 2023.03.1,) allowing the lengths of nine femora and 13 tibiae to be estimated. Histograms visualising the size distribution of the bone bed (mortality profiles), using both true and estimated lengths, were generated in PAST (Hammer *et al.* 2001). Additionally, PAST was used to compute

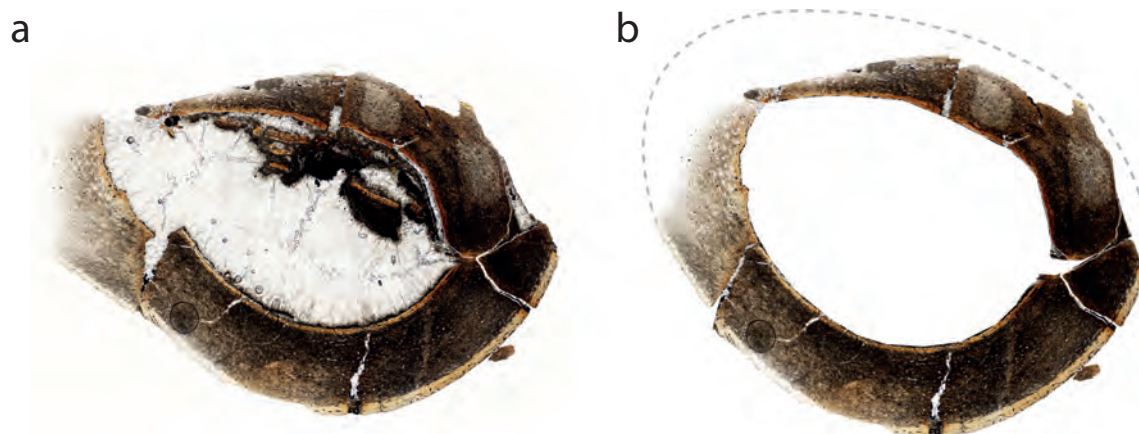


Figure 4.5. Reconstructed medullary cavity in NHMUK PV R 5830: **a**, original; **b**, reconstructed. Dashed lines indicate extrapolated periosteal margin.

normality tests to determine whether the distribution was normal. The Shapiro-Wilk and Anderson-Darling test were selected, as these tests are highly recommended when looking at smaller sample sizes (e.g. $n = <50$; Yazici & Yolacan 2007).

4.2.5. Descriptive methods

Histological terminology follows Francillon-Vieillot *et al.* (1990), Padian & Lamm (2013), Prondvai *et al.* (2014) and de Buffr  nil *et al.* (2021a). Here, I describe each of the nine long bone sections by identifying the bone matrix type, vascular canal type/arrangement, osteonal development, osteocyte morphology/arrangement, and the presence of growth marks. I decided not to identify bone complexes (e.g. fibrolamellar), which are made up of a suite of different histological features, as these complexes can often vary in how they are defined and diagnosed throughout the literature, making cross-study comparisons more difficult (Werning 2012; Stein & Prondvai 2013; Prondvai *et al.* 2014; Shapiro & Wu 2019).

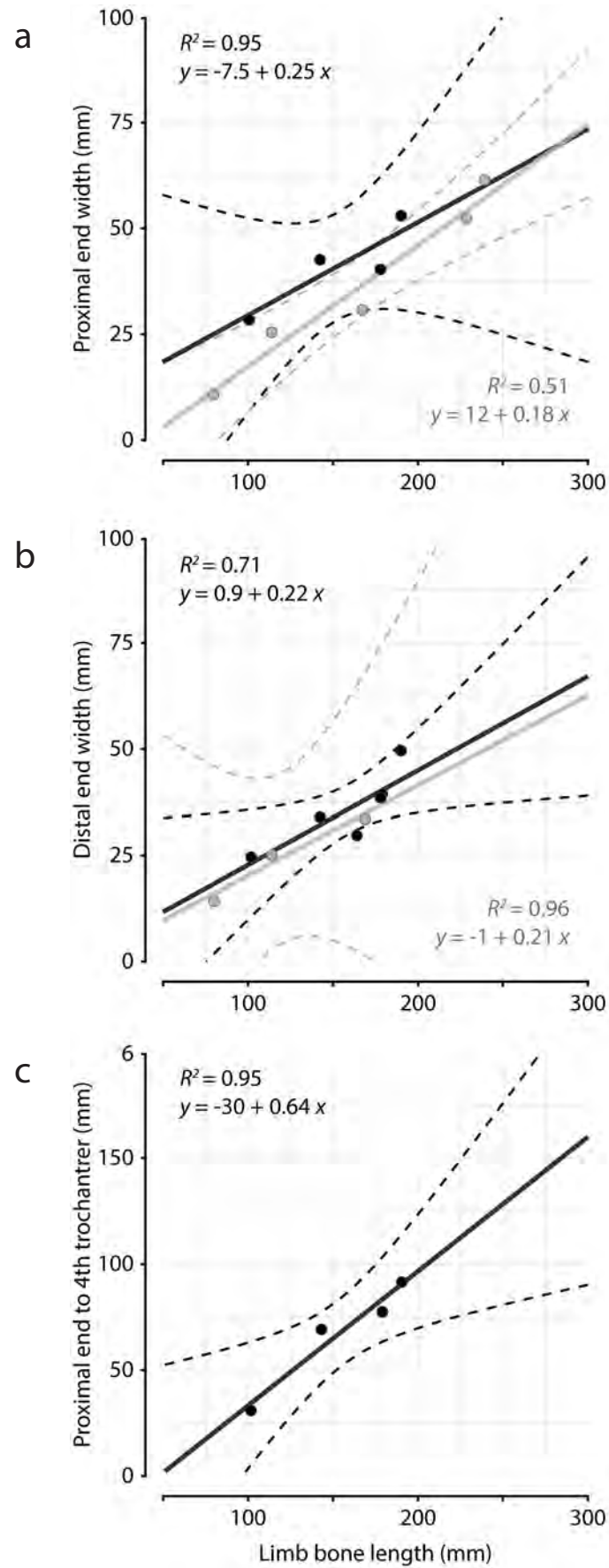


Fig. 4.6 (caption on following page)

Figure 4.6. Regression plots used to estimate the limb bone lengths of incomplete *Hypsilophodon foxii* specimens: **a**, proximal end width; **b**, distal end width; **c**, length from the proximal end of the femur to the base of the fourth trochanter. R^2 value and regression equation: top left (femora); bottom right (tibiae). Colour key: femora (black); tibiae (grey).

4.2.6. Histological features of interest

4.2.6.1. Bone matrix. Bone matrix primarily consists of collagenous proteins secreted by osteoblasts, which assemble together to form collagen fibres (Lin *et al.* 2020; Senter 2022). The structure and orientation of these collagen fibres within the bone matrix reflects the rate at which the bone was synthesised: slower growing bone tends to be laid down in organised layers, while faster growing bone results in a more haphazard arrangement (Huttenlocker *et al.* 2013; Shapiro & Wu 2019; de Buffr  nil & Quilhac 2021). Bone matrix can be differentiated into three distinct types based on the arrangement of collagen fibres observed: lamellar; parallel-fibred; and woven-fibred (de Buffr  nil & Quilhac 2021). These three types can be easily distinguished from each other under cross-polarised light (Figure 4.7). All three of these bone matrix types can be present throughout a single section of cortex.

Lamellar bone matrix is deposited at the slowest rate, and consists of thin layers of collagen fibres (lamellae) that are stacked in a parallel array. Adjacent layers are deposited in opposing directions, which causes the lamellae to alternate between extinguished and illuminated bands under cross-polarised light (Huttenlocker *et al.* 2013). As in lamellar bone, parallel-fibred bone also consists of collagen fibres that

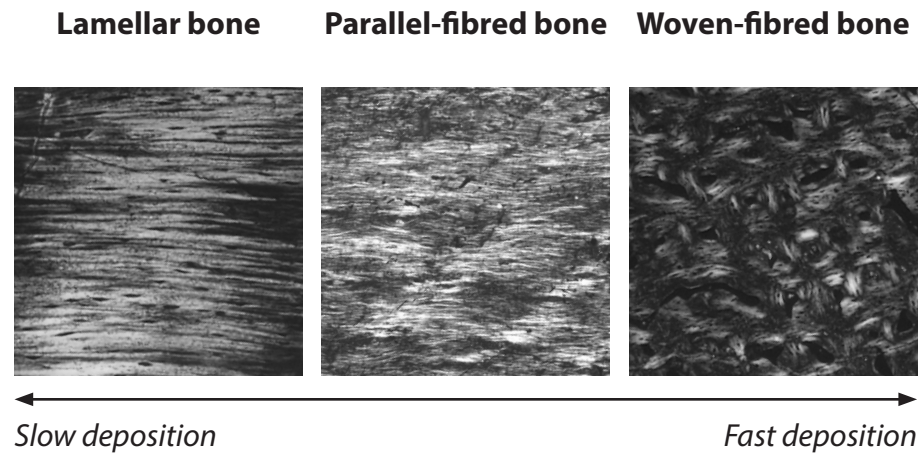


Figure 4.7. Bone matrix types and their relative deposition rates. Examples shown are *Hypsilopodon foxii* thin sections from this study, imaged in cross-polarised light and edited to black & white in Adobe Photoshop CC (adobe.com; 2022). Modified from McFarlin *et al.* (2016).

are arranged in parallel. Parallel-fibred bone can be easily distinguished from lamellar bone by its mass birefringence under cross-polarised light, which has an anisotropic pattern (Huttenlocker *et al.* 2013; de Buffr  nil & Quilhac 2021). Woven-fibred bone matrix is the most rapidly deposited bone type, and is made up of randomly arranged collagen fibres. Because of the lack of organisation, woven-fibred bone often appears darker under cross-polarised light than other bone types.

4.2.6.2. Vascular canals. In life, blood vessels and nerves travel through networks of vascular canals in bone. These vascular canals are termed as either simple canals, primary osteons, or secondary osteons. Simple canals are observed as unlamellated tunnels. Primary osteons are formed when canals become ossified, becoming surrounded by concentrically deposited lamellar bone. Secondary osteons are formed through remodelling of an existing vascular canal. Osteoclasts cut into and resorb bone

surrounding the canal, and osteoblasts subsequently deposit bone as cylindrical (or conical; Doube 2022) lamellae. Secondary osteons are generally much bigger than primary osteons, and often have a distinct cementing line around their circumference (Huttenlocker *et al.* 2013).

In this study, the orientations of the vascular canals were described as either longitudinal, laminar (or circumferential), radial, or reticular, following Francillon-Vieillot *et al.* (1990; Figure 4.8). Normally one of these orientations predominates throughout the matrix.

4.2.6.3. Osteocytes. Osteocytes are formed when osteoblasts become encased within small holes (lacunae) in the bone matrix, following osteogenesis (Franz-Odenaal *et al.* 2006; Dallas & Bonewald 2010; de Buffr  nil & Quilhac 2021). In life, osteocytes tend to conform to one of two types: (1) stellate or multipolar in morphology, within a random arrangement; and, (2) spindle-like or flat in morphology, within an organised arrangement that generally follows the alignment of the collagen fibres in the bone matrix (de Buffr  nil & Quilhac 2021). Unlike osteocytes, lacunae are well preserved in fossils, and are thought to accurately reflect the morphology of the osteocytes once encased within (Organ *et al.* 2007; Montanari *et al.* 2013; D’Emic & Benson 2013; de Buffr  nil & Quilhac 2021; Haridy *et al.* 2021).

In this study I assess the form, arrangement and density of osteocytes (lacunae) within the bone matrixes observed. Here, osteocyte orientation was inferred from the alignment of the long axis of the lacunae within the bone matrix. Organised arrangements, where the dominant osteocyte orientation aligns with the direction of collagen fibres with the bone matrix, are characteristic of parallel-fibred and lamellar bone, whereas random osteocyte arrangements are characteristic of woven-fibred bone (de

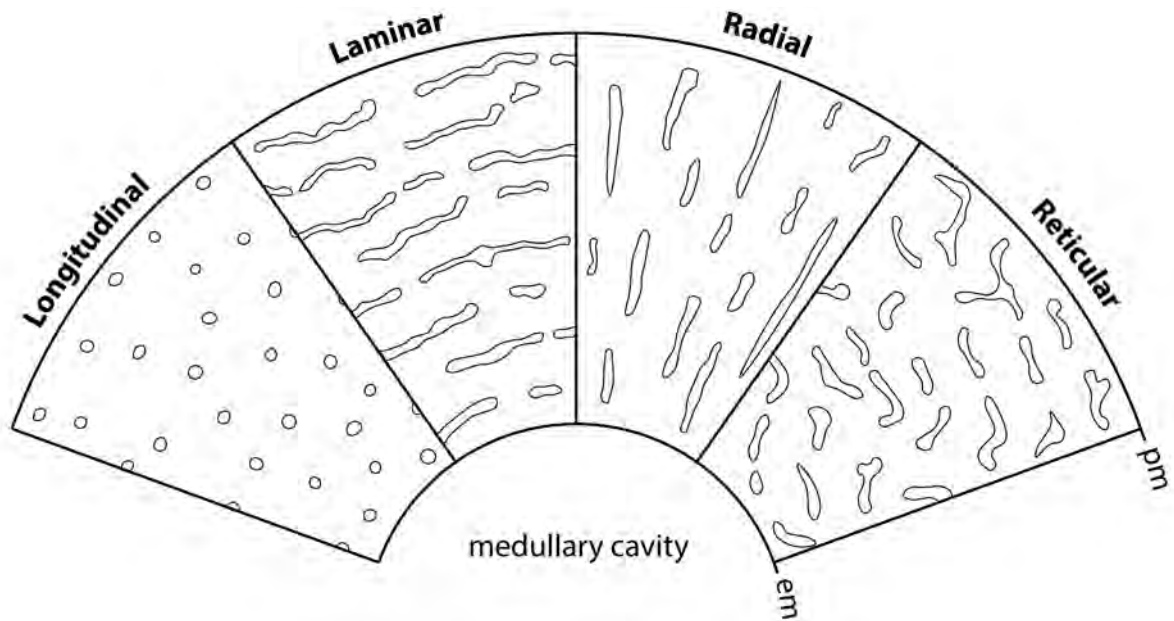


Figure 4.8. Schematic visualising the different orientations that vascular canals can appear within a transverse histological section: longitudinal, laminar (or circumferential), radial and reticular. **Abbreviations:** **em**, endosteal margin; **pm**, periosteal margin.

Buffr nil & Quilhac 2021). Osteocyte morphology is also often characteristic of bone matrix type: with woven-fibred bone containing multipolar/stellate osteocytes (observed in fossils as round/oval lacunae); and parallel-fibred and lamellar bone containing flat or spindle-like osteocytes (de Buffr nil & Quilhac 2021). Additionally, there is some evidence to suggest that high osteocyte density may be linked to faster rates of bone formation, with woven-fibred bone generally containing more osteocytes than other types of bone matrix (Padian *et al.* 2013b; Hernandez *et al.* 2004).

4.2.6.4. Growth marks. Cyclical growth marks indicate a change in bone deposition rate within the cortex. Three types of cyclical growth marks are traditionally

recognised: zones, which reflect a period of relatively increased growth; annuli, which reflect a period of reduced growth; and lines of arrested growth (LAGs), which reflect a temporary full cessation of growth (de Buffr  nil *et al.* 2021b). In fossils, LAGs often appear as black lines that can be traced around the circumference of the cortex (Lee and O'Connor 2013; de Buffr  nil & Quilhac 2021). In modern tetrapods, the presence of LAGs has been linked to the slowdown in development during colder or dryer seasons where resources tend to be scarcer. In many studies on dinosaur palaeohistology, LAGs have been used to estimate the age of an individual at death (e.g. Reid 1985; Horner *et al.* 1999; Zhao *et al.* 2013a,b; Woodward *et al.* 2015; Han *et al.* 2020; Botha *et al.* 2022). Annuli are often observed as layers (> ca. 10 μm in thickness; de Buffr  nil & Quilhac 2021) of parallel-fibred or lamellar bone that are poorly vascularised, while zones are typically thicker layers of woven-fibred bone, but can also be formed from parallel-fibred bone. Unlike LAGs, annuli and zones are not typically recognised as indicators of annual cyclicity, however Hutton (1986) found that in Nile crocodiles, annuli were deposited during cool seasons, while zones were deposited during hot seasons.

4.3. Results

4.3.1. Histological descriptions

4.3.1.1. Femur. Femoral sections are described in ascending order of mid-diaphyseal periosteal circumference.

NHMUK PV R 196. The femur NHMUK PV R 196 is sub-triangular in shape, with a midshaft diameter of 17.9 mm x 13.7 mm and cortical thickness of 36.4% (Figure

4.9a–b). The medullary cavity is infilled with calcite crystals that have broken up much of the endosteal margin. The medullary cavity contains broken trabeculae as well as a large triangular segment of cortex. These trabeculae are lined with lamellar bone and are obscured by bacterial invasion, along with much of the inner cortex. Much of the endosteal margin is lined with lamellar bone tissue, up to 0.2 mm thick, which forms an inner circumferential layer (ICL; Figure 4.9c–d). The inner and mid-cortex is dominated by lamellar-lined resorption bays up to 0.8 mm in diameter (Figure 4.9e–f). Smaller resorption bays are also found in the inner cortex throughout the section, but are significantly smaller. Throughout the entire cortex, parallel-fibred bone seems to be the underlying matrix (Figure 4.9g–h). Osteocytes are flattened and organised in parallel. The inner cortex is dominated by secondary osteons, some of which appear to overlap with each other, suggesting multiple generations. In the middle and outer cortex longitudinal primary osteons become most prevalent, but in one region secondary osteons extend into the outer cortex. Throughout the cortex, only a few canals anastomose. Vascularisation decreases towards the periphery. In the outer cortex, a black line can be observed. This line is non-cyclical and seems to be constrained to the medial region of the section. I interpret this as a cortical drift line (Figure 4.9i–j), formed due to anisometric bone growth and the resulting shift of the medullary cavity (Francillon-Vieillot *et al.* 1990; Woodward *et al.* 2013). This cortical drift line might have been caused by the developing fourth trochanter (Padian *et al.* 2013a; Woodward *et al.* 2013), which serves as a muscle attachment site for the *M. caudofemoralis longus* (Maidment & Barrett 2011). In *Hypsilophodon foxii*, the fourth trochanter is relatively large (compared to other similarly-sized ornithopods), pendant, and sits on the medial side of the femur, proximal to the midshaft. Cortical drift is also known to

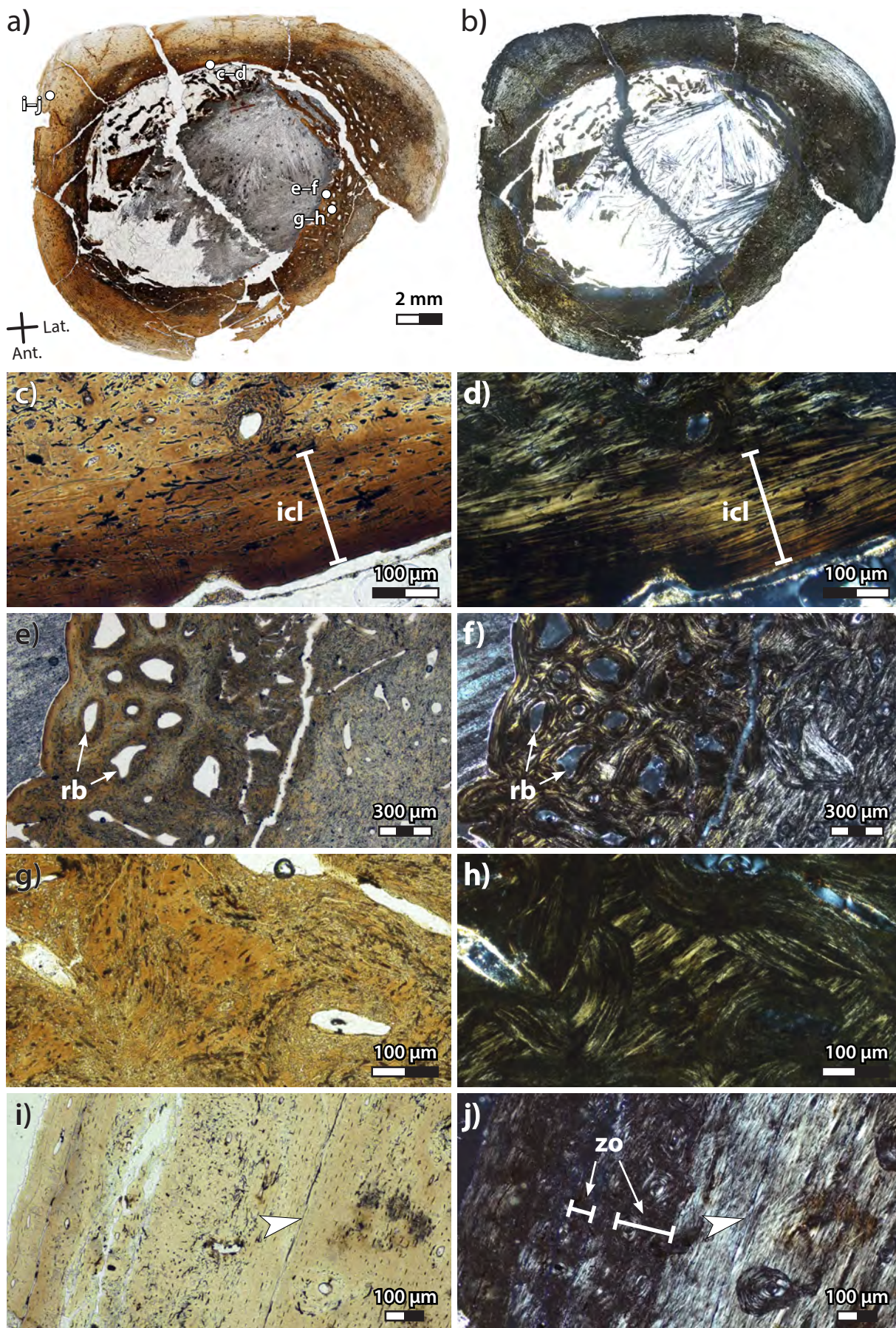


Fig. 4.9 (caption on following page)

Figure 4.9. Femoral section of *Hypsilophodon foxii* (NHMUK PV R 196): **a–b**, whole section; **c–d**, inner circumferential lamella (icl) in the inner cortex; **e–f**, extensive remodeling in the inner and mid-cortex with lamellar-lined resorption bays (rb); **g–h**, secondary osteons and underlying parallel-fibred bone, in the inner cortex; **i–j**, two zones (zo) of woven-fibred bone and a cortical drift line (white arrow) in the outer cortex. Left, plain polarised light; right, cross polarised light.

be prevalent in the diaphyses of long bones that are curved along the long axis (Enlow 1962). The femoral shaft of *Hypsilophodon foxii* is bowed anteriorly in medial/lateral view, so is likely susceptible to cortical drift. Peripheral to this cortical drift line, two thin zones of highly-vascularised woven-fibred bone can be observed (Figure 4.9i–j). A thin layer of parallel-fibred bone separates the two zones (Figure 4.9i–j). These zones are only observable in a limited section of the outer cortex due to extensive periosteal cortical drift.

NHMUK PV R 192a. The femur NHMUK R 192a is sub-ovate in cross-section, with a midshaft diameter of 21.8 mm x 21.1 mm and cortical thickness of 25.8% (Figure 4.10a–b). The medullary cavity is entirely infilled with matrix, which has damaged much of the endosteal margin and inner cortex. The cortex is heavily altered by extensive bacterial invasion, which obscures much of the bone fabric and osteocyte density. Large resorption cavities (up to ~0.5 mm) are observed in one region of the inner cortex. Some of these cavities appear to be surrounded by layers of lamellar bone (Figure 4.10c–d). A small number of secondary osteons are also observed in this localised area. The rest of the middle and outer cortex is highly-vascularised with simple canals and

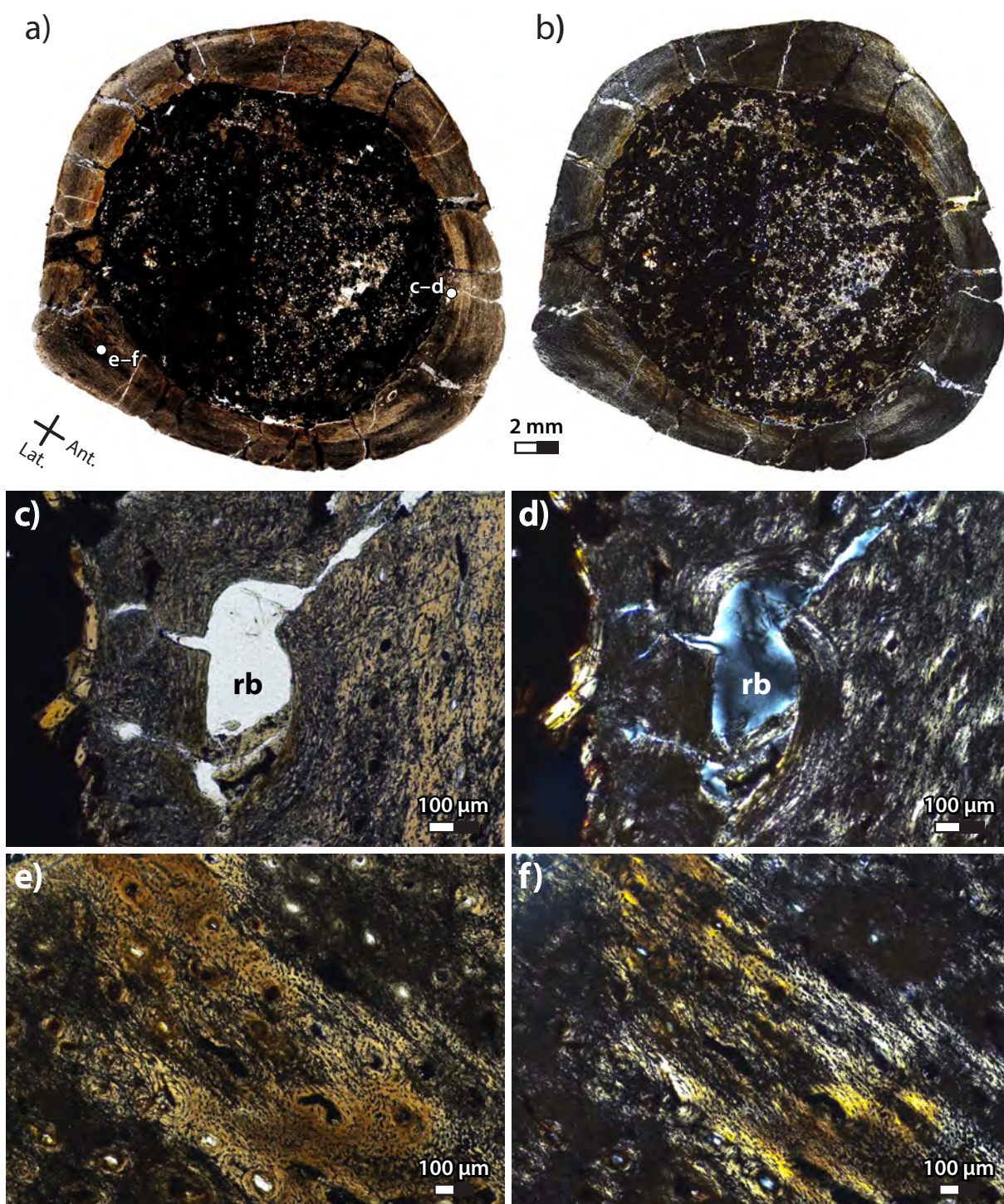


Figure 4.10. Femoral section of *Hypsilophodon foxii* (NHMUK PV R 192a): **a–b**, whole section; **c–d**, lamellar-lined resorption bays (rb) in the inner cortex; **e–f**, primary osteons in the inner cortex. Left, plain polarised light; right, cross polarised light.

some primary osteons. These canals are mainly longitudinal in orientation, but many anastomose circumferentially, particularly on the medial side near the fourth trochanter. Osteocytes and bone matrix can be observed relatively unobscured in a couple of patches of throughout the cortex. The middle and outer cortex consist of parallel-fibred bone, with flattened osteocytes arranged in parallel. Some areas of woven-fibred bone are visible in the inner cortex. In these areas, osteocytes are rounded/oval in shape and are found in much higher density (Figure 4.10e–f).

NHMUK PV R 170. The femur NHMUK PV R 170 is ovate in cross-section, with a midshaft diameter of 25.3 mm x 16.7 mm and a cortical thickness of 56% (Figure 4.11a–b). The medullary cavity is infilled with matrix around the periphery and calcite crystals internally, but the endosteal margin is minimally impacted. The cortex is highly vascularised and dominated by primary osteons. Vascular canals throughout the cortex are longitudinal and highly reticular in orientation, and many anastomose with three or more other canals (Figure 4.11c–d). Strongly radially oriented canals are observed in localised areas in both the posterior region and at the level of the fourth trochanter (Figure 4.11e–f). Some canals open to the surface of the bone, but this occurs primarily immediately adjacent to the fourth trochanter. The matrix is composed entirely of woven-fibred bone, dense in osteocytes. These osteocytes show no particular organisation and occur primarily at the interstices between vascular canals. There is no evidence of secondary remodelling or growth marks in this sample.

NMHUK PV R 193. Two femoral sections were taken from NHMUK PV R 193: A and B. Both sections are triangular in shape. Measurements were taken from the most complete section (B): midshaft diameter of 26.7 mm x 22.6 mm and cortex thickness of 43.2%.

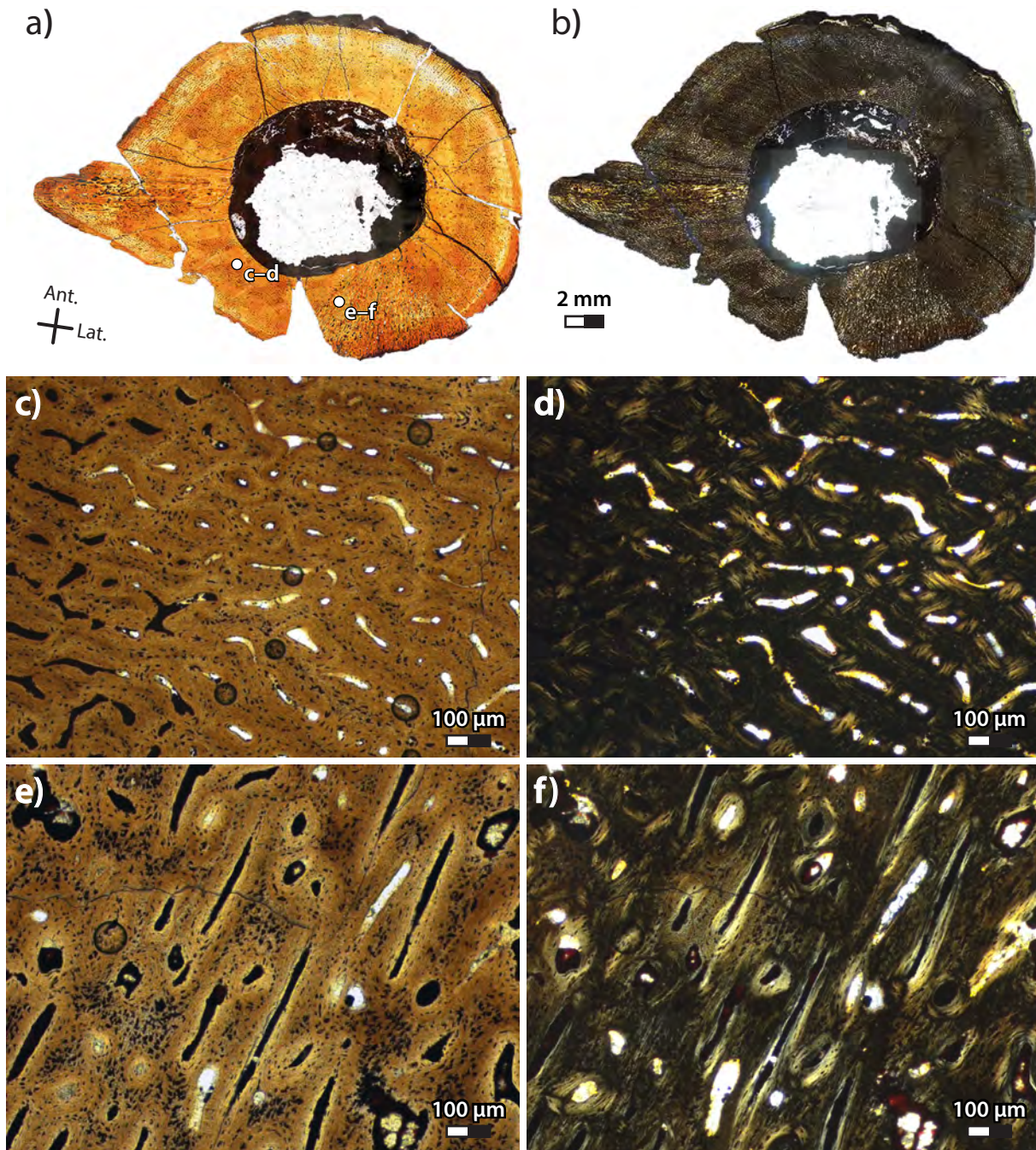


Figure 4.11. Femoral section of *Hypsilophodon foxii* (NHMUK PV R 170): **a–b**, whole section; **c–d**, woven bone dominated by primary osteons with longitudinal and reticular orientations; **e–f**, radially oriented canals in the posterior region of the mid-cortex. Left, plain polarised light; right, cross polarised light.

In section A of NMHUK PV R 193 (Figure 4.12a–b), the medullary cavity is infilled with calcite crystals, which have damaged the endosteal margin of the cortex. The medullary cavity includes broken pieces of the endosteal margin, all of which are densely packed with osteocytes. This thin-section is missing much of its lateral and anterior regions. The lateral region of the inner cortex contains large reabsorption cavities up to 1 mm in diameter. Much of the bone fabric in the inner cortex is obscured by bacterial invasion, but in areas where this underlying matrix is visible many of the resorption cavities are lined with lamellar bone and surrounded by secondary osteons. In some cases, these secondary osteons overlap the lamellar bone that surrounds the resorption cavities. In the lateral region of the inner cortex, the resorption cavities are far fewer in number and smaller in size and there is a mix of both primary and secondary osteons. Throughout the inner and middle cortex consists of a mix of well-vascularised woven-fibred and parallel-fibred bone, primarily with longitudinal canals, some of which anastomose circumferentially. In the anterolateral region, the canals are primarily radially oriented. Radially projecting Sharpey's fibres are observed through the inner to outer cortex in this region. These Sharpey's fibres cross-cut and overlie the parallel-fibred bone matrix in the inner cortex (Figure 4.12c–d). In addition, two growth lines were identified in this anterolateral region. In a few instances in this area, these growth lines have been remodelled and overlain with secondary osteons. Both growth lines are observed as distinct dark lines in this localised area, but are not consistent throughout the rest of the cortex (Figure 4.12e–f). I interpret these non-cyclical lines as cortical drift lines.

In section B of NMHUK PV R 193 (Figure 4.13a–b), the medullary cavity is infilled with calcite crystals which, as in section A, have damaged the endosteal margin of

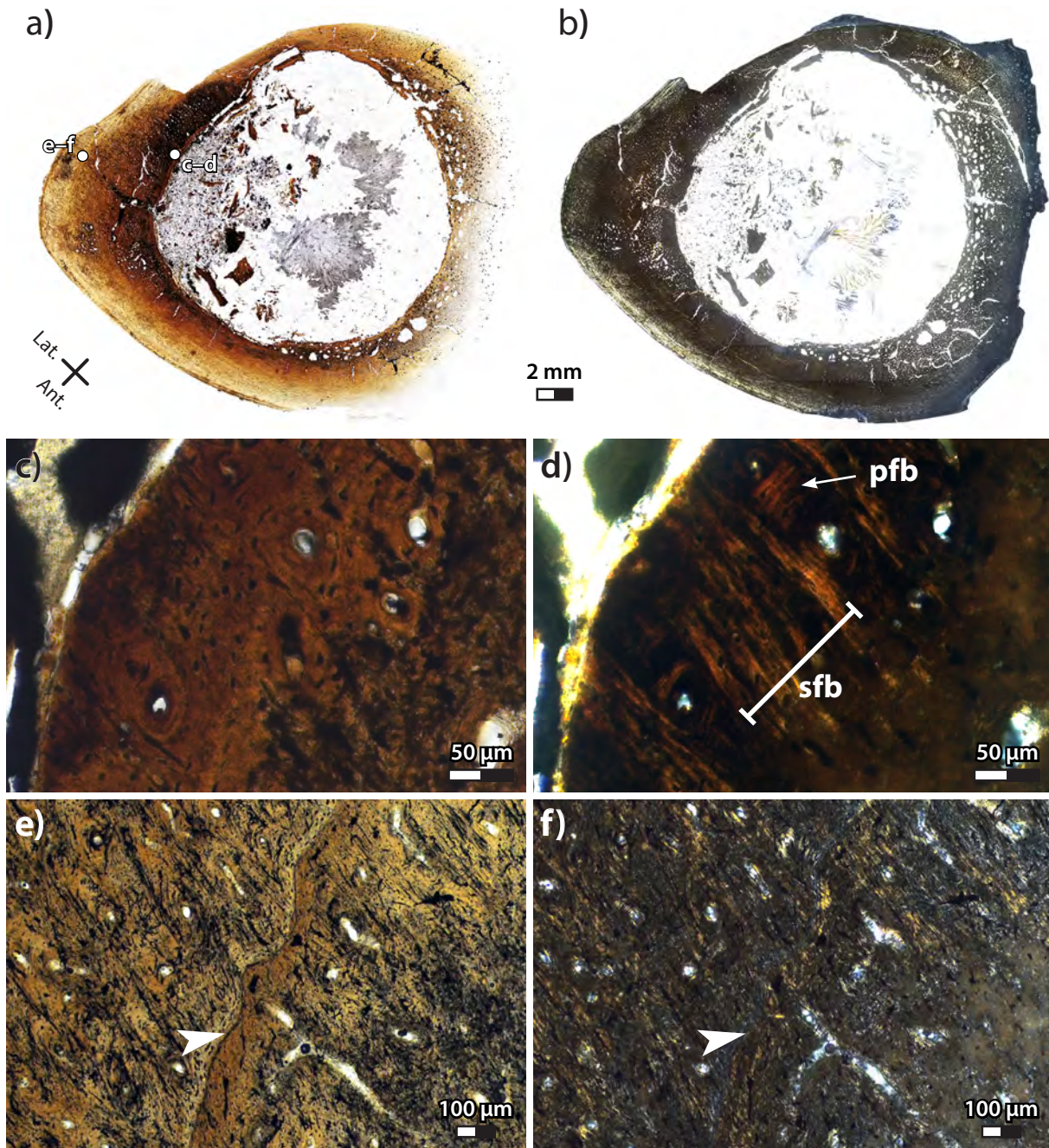


Figure 4.12. Femoral section of *Hypsilophodon foxii* (NHMUK PV R 193; Section A): **a–b**, whole section; **c–d**, Sharpey's fiber bundle (sfb) radially cross-cutting the underlying parallel-fibred bone (pfb) in the inner cortex; **e–f**, outermost cortical drift line in the outer cortex (white arrow). Left, plain polarised light; right, cross polarised light.

the cortex. This thin-section is more complete than section A, but is still lacking much of the outermost cortex and lateral region. Resorption cavities are observed in the inner cortex in the lateral and medial regions; however, they are considerably smaller (up to 0.2 mm) than those in section A. Most of these small resorption cavities do not seem to be surrounded by layers of lamellar bone, but several crescents of lamellar bone are seen to connect to the endosteal margin, suggesting that lamellar-lined resorption cavities might have been destroyed by the calcite crystals within the medullary cavity. Both primary and secondary osteons are found in the lateral and medial region, with secondary osteons and extensive remodelling extending out into the mid-cortex of both regions (Figure 4.13c–d). The inner and middle cortex consists primarily of well-vascularised woven-fibred bone (Figure 4.13e–f). Vascular canals throughout much of cortex are primarily longitudinally oriented, but there are also some circumferential and reticular canals. Some of the vascular canals in the anterolateral region of the sample are radially oriented, but less so and to a lesser degree than in section A. Vascularisation decreases towards the periphery. The outer cortex is dominated by parallel-fibred bone with very low vascularisation (Figure 4.13g–h). Two non-cyclical growth lines are also identified in the anterolateral region of the section, here interpreted as cortical drift lines (Figure 4.13i–j). Both growth lines are distinct dark lines in the anterolateral region. Throughout the rest of the section, the innermost growth line quickly fades into an annulus-like layer of largely avascular parallel-fibred bone. The outermost growth line is even more restricted in its extent. As in section A, Sharpey's fibre bundles extend radially throughout the cortex in the anterolateral region (Figure 4.13i–j).

4.3.1.2. Tibia. Tibial sections are described in ascending order of mid-diaphyseal periosteal circumference.

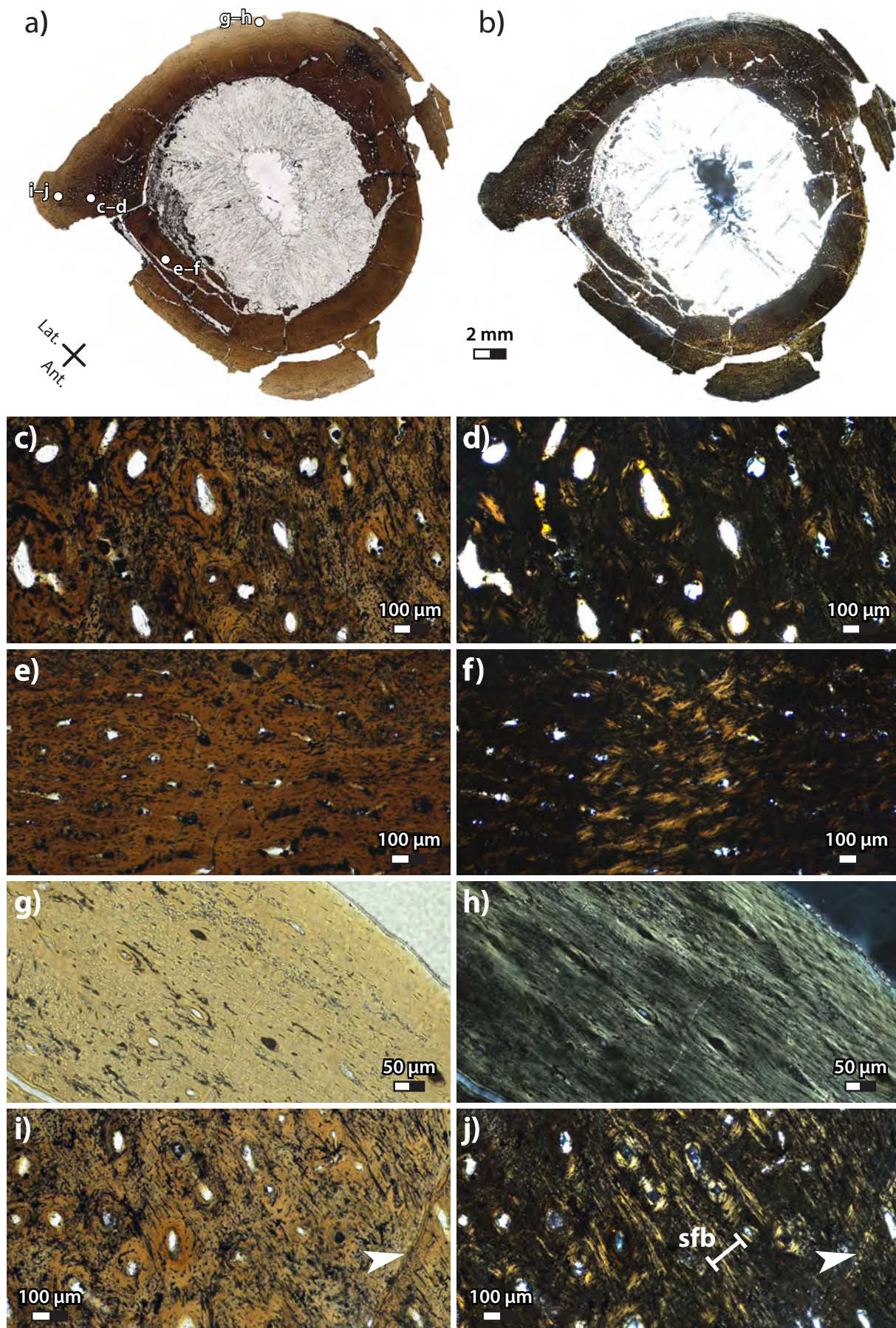


Fig. 4.13 (caption on following page)

Figure 4.13. Femoral section of *Hypsilophodon foxii* (NHMUK PV R 193; Section B): **a–b**, whole section; **c–d**, secondary osteons in the mid-cortex; **e–f**, woven bone in the mid-cortex; **g–h**, poorly vascularised parallel-fibred bone in the outer cortex. Left, plain polarised light; **i–j**, innermost cortical drift line (white arrow) and bundles of Sharpey's fibers (sfb) in the mid-cortex; right, cross polarised light.

NHMUK PVR 5830. The tibia NHMUK PV R 5830 (Figure 4.14a–b) is lateroventrally compressed, but reconstruction of the thin-section suggests that its cross-section was originally elliptical in outline, with an estimated midshaft diameter of 9.9 mm x 7.8 mm and cortex thickness of 39.3%. The medullary cavity is infilled with calcite crystals, which contains broken pieces of the endosteal margin. Most of the cortex has been altered by bacterial invasion, obscuring the arrangement of osteocytes and the matrix type present throughout much of the section. Thin layers of the innermost and outermost cortex are not obscured, and show a moderately dense distribution of osteocytes. Most of these osteocytes are flattened and are not organised around the circumference of canals. Vascular canals within the section consist of both longitudinal simple canals and primary osteons, many of which anastomose circumferentially. Vascularisation remains high from the inner to outer cortex. Some vascular canals open out onto the periosteal surface. Parallel-fibred bone is found throughout most of the section (Figure 4.14c–d): however, a localised area of woven-fibred bone can be found in the lateral region (towards the fibula). Vascular canals are also larger in this lateral region of the tibia. No growth marks are present.

NHMUK PV R 752. The tibia NHMUK PV R 752 (Figure 4.15a–b) is ovate/

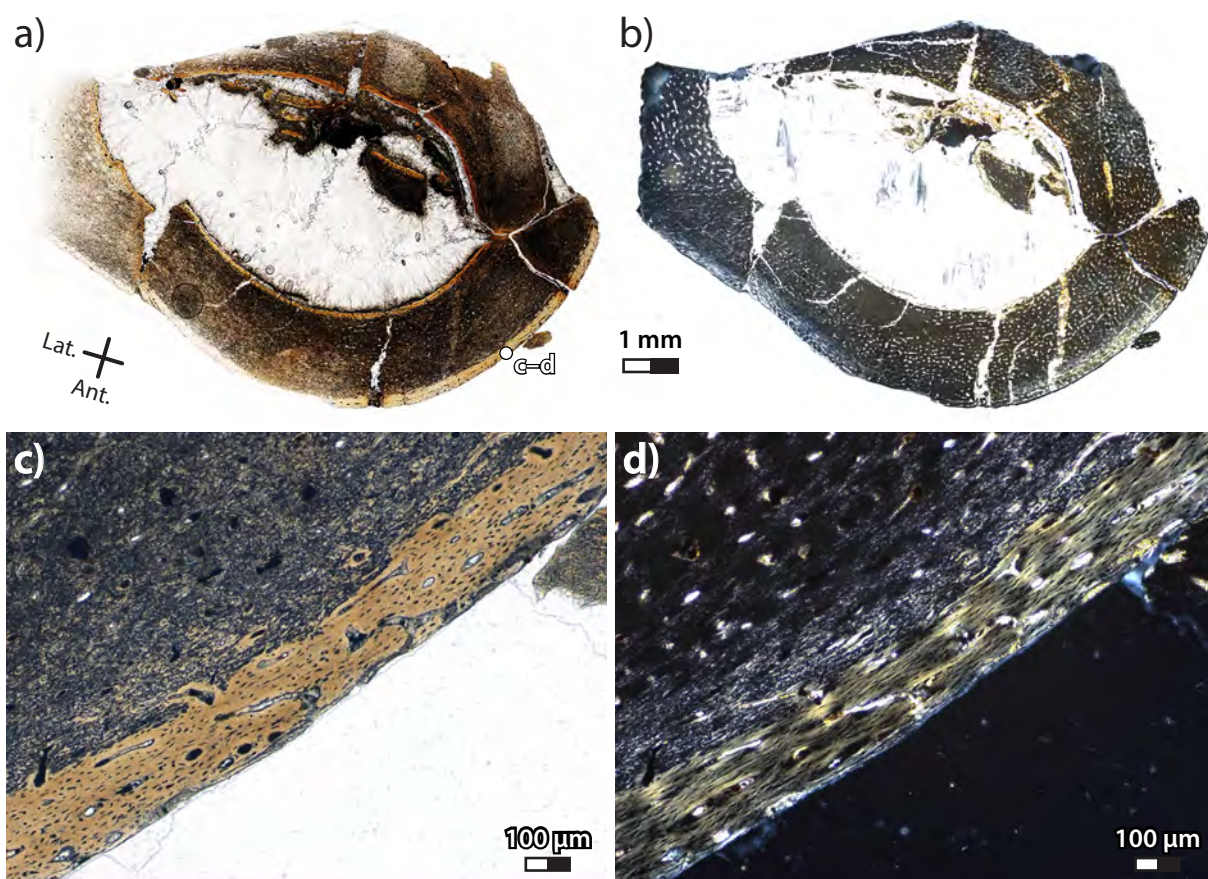


Figure 4.14. Tibial section of *Hypsilophodon foxii* (NHMUK PV R 5830): a–b, whole section; c–d, parallel-fibred bone in the outer cortex. Left, plain polarised light; right, cross polarised light.

sub-triangular in shape, with a midshaft diameter of 12.6 x 12.3 mm and cortex thickness of 51.6%. The medullary cavity is infilled with calcite crystals, but these have caused relatively minor damage to the endosteal margin. The outer cortex is obscured by bacterial invasion. At the endosteal margin on the lateroanterior side of the section, there is a thick layer of lamellar bone tissue, which forms an inner circumferential layer (ICL; Figure 4.15c–d). Within the inner cortex, close to the ICL, are a number of secondary osteons that vary in size. The inner cortex is composed primarily of highly-vas-

cularised woven-fibred bone, which has densely packed oval osteocytes that are often randomly aligned. A few resorption cavities can be found in the inner cortex. The middle and outer cortex consists of parallel-fibred bone with flattened osteocytes aligned in parallel. Most of the vascular canals in this region are longitudinally oriented primary osteons, although some anastomose circumferentially across several canals. A thick zone of woven-fibred bone can be found within the middle cortex, sandwiched between parallel-fibred bone (Figure 4.15e–f). Peripheral to this zone, vascularisation decreases towards the outer margin. A sharp dark line is visible near the periosteal margin in the lateral region (Figure 4.15g–h), although its extent is untraceable far beyond this region, likely obscured by bacterial invasion. This line might represent a line of arrested growth (LAG), but remains ambiguous.

NHMUK PV R 193. Two tibial sections were taken for NHMUK PV R 193: A and B. Both sections are ovate/sub-triangular in shape. Measurements were taken from the most complete section (B): midshaft diameter of 26.7 mm x 22.6 mm and cortex thickness of 51.6%.

In section A (Figure 4.16a–b), the medullary cavity is infilled with calcite crystals, which includes broken trabeculae, some with large resorption bays. These trabeculae are obscured by bacterial invasion, along with much of the inner cortex. The anterior region of the inner cortex contains resorption bays up to ~300 µm in diameter. The inner cortex consists of highly-vascularised woven bone and includes a mixture of both primary and secondary osteons. Many of the primary osteons in this region have a single cement line. Vascular canals are primarily longitudinal in orientation, but some anastomose circumferentially. The middle cortex has a large number of secondary osteons, but the outer cortex exhibits primary osteons almost exclusively. A cyclical layer

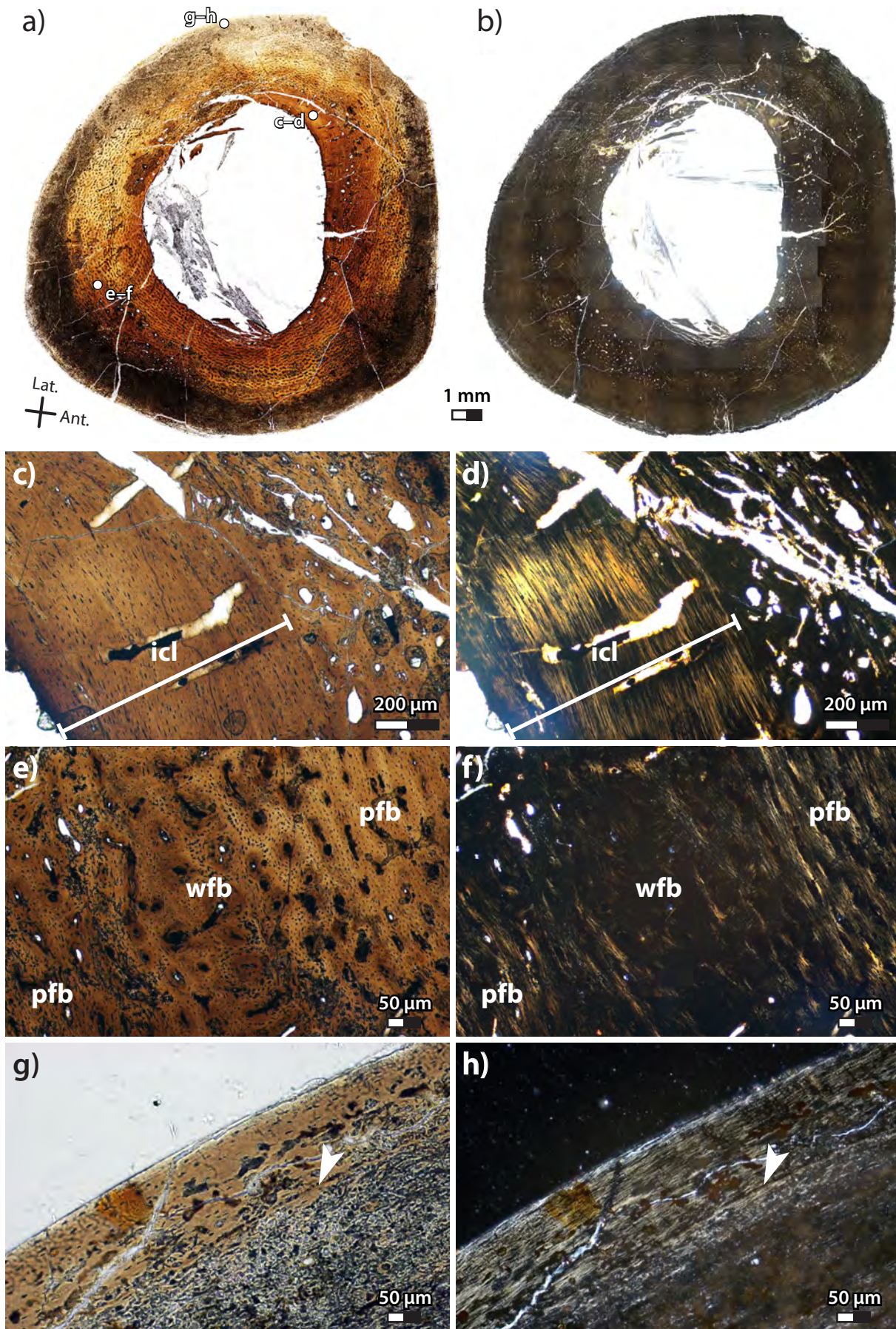


Fig. 4.15 (caption on following page)

Figure 4.15. Tibial section of *Hypsilophodon foxii* (NHMUK PV R 752): **a–b**, whole section; **c–d**, inner circumferential lamella (ICL) in the inner cortex; **e–f**, zone of woven-fibred bone (WFB) sandwiched between parallel-fibred bone (PFB) in the mid cortex; **g–h**, low vascularisation in parallel-fibred bone in the outer cortex, and a possible line of arrested growth (LAG; white arrow). Left, plain polarised light; right, cross polarised light.

of avascular parallel-fibred bone is visible in the middle cortex. This layer is interpreted as an annulus, which suggests a period of decreased growth activity. In one region, this annulus splits into two layers separated by woven-fibred bone, and a single row of circumferentially aligned primary osteons (Figure 4.16c–d). Vascularisation and osteocyte density both decrease towards the outer cortex, where the fabric transitions to parallel-fibred bone. In the anterolateral region of the outer cortex there is a zone of well-vascularised woven-fibred bone, ranging from 150–500 μm in width, which is highly distinct from the parallel-fibred bone that sandwiches it when viewed under cross-polarised light (Figure 4.16e–f). A thin layer ($\sim 150 \mu\text{m}$) of largely avascular fine parallel-fibred bone (possibly intermediate parallel-fibred/lamellar bone) is observed at the periosteal margin (Figure 4.16e–f). This layer is distinct from the parallel-fibred bone elsewhere in the section, as the collagen fibres of the bone matrix are considerably finer, suggesting very slow growth at time of death. No LAGs are present.

In section B (Figure 4.17a–b), the medullary cavity is infilled with calcite crystals, which have caused minor damage to the endosteal margin. A thin layer of lamellar bone lines most of the endosteal margin on the anterior and medial sides. The in-

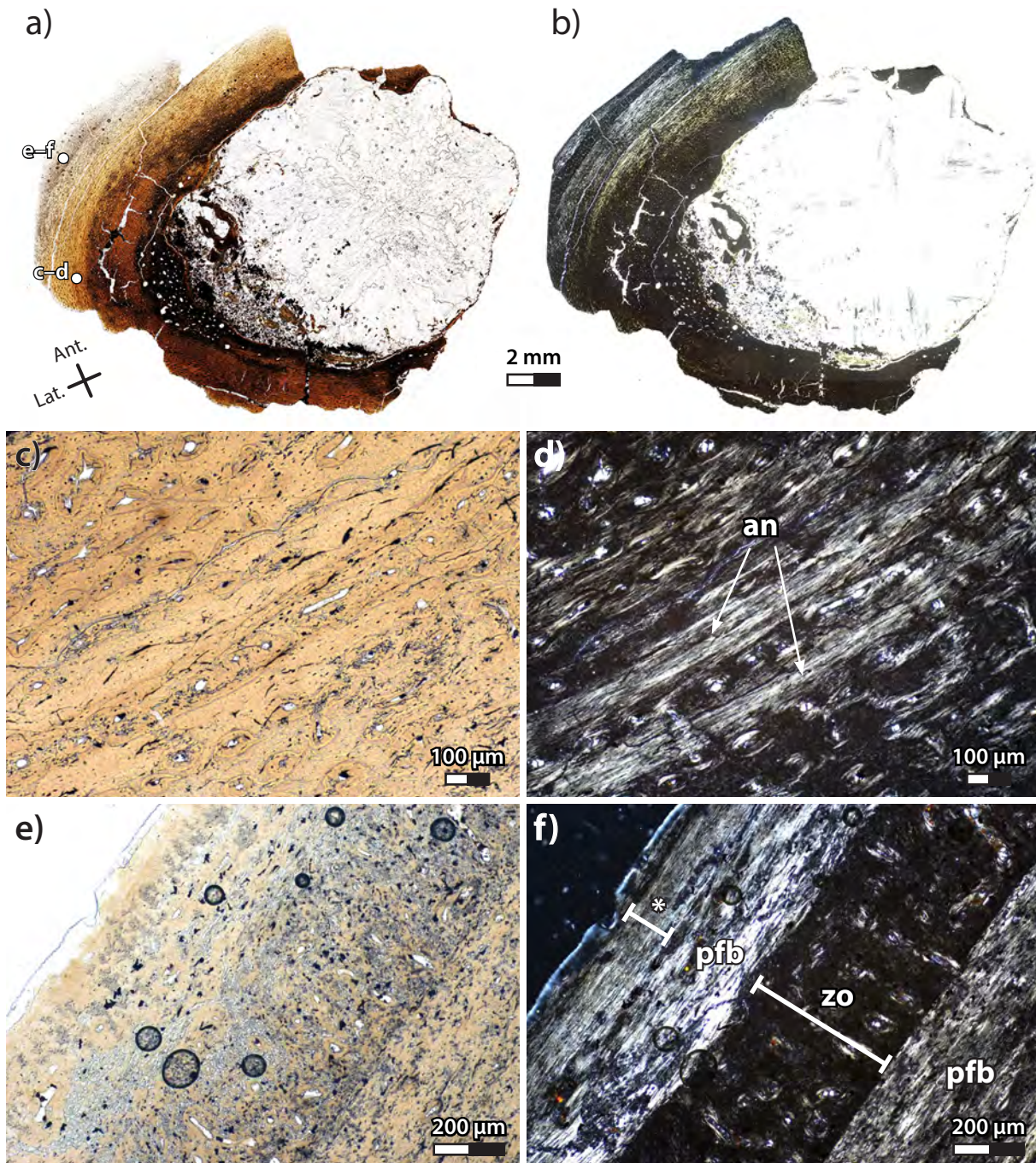


Figure 4.16. Tibial section of *Hypsilophodon foxii* (NHMUK PV R 193; Section A): **a–b**, whole section; **c–d**, split annulus (an) in the mid cortex; **e–f**, layer of fine avascular parallel-fibred bone (pfb) at the periosteal margin (asterisk) and a zone (zo) of woven-fibred bone. Left, plain polarised light; right, cross polarised light.

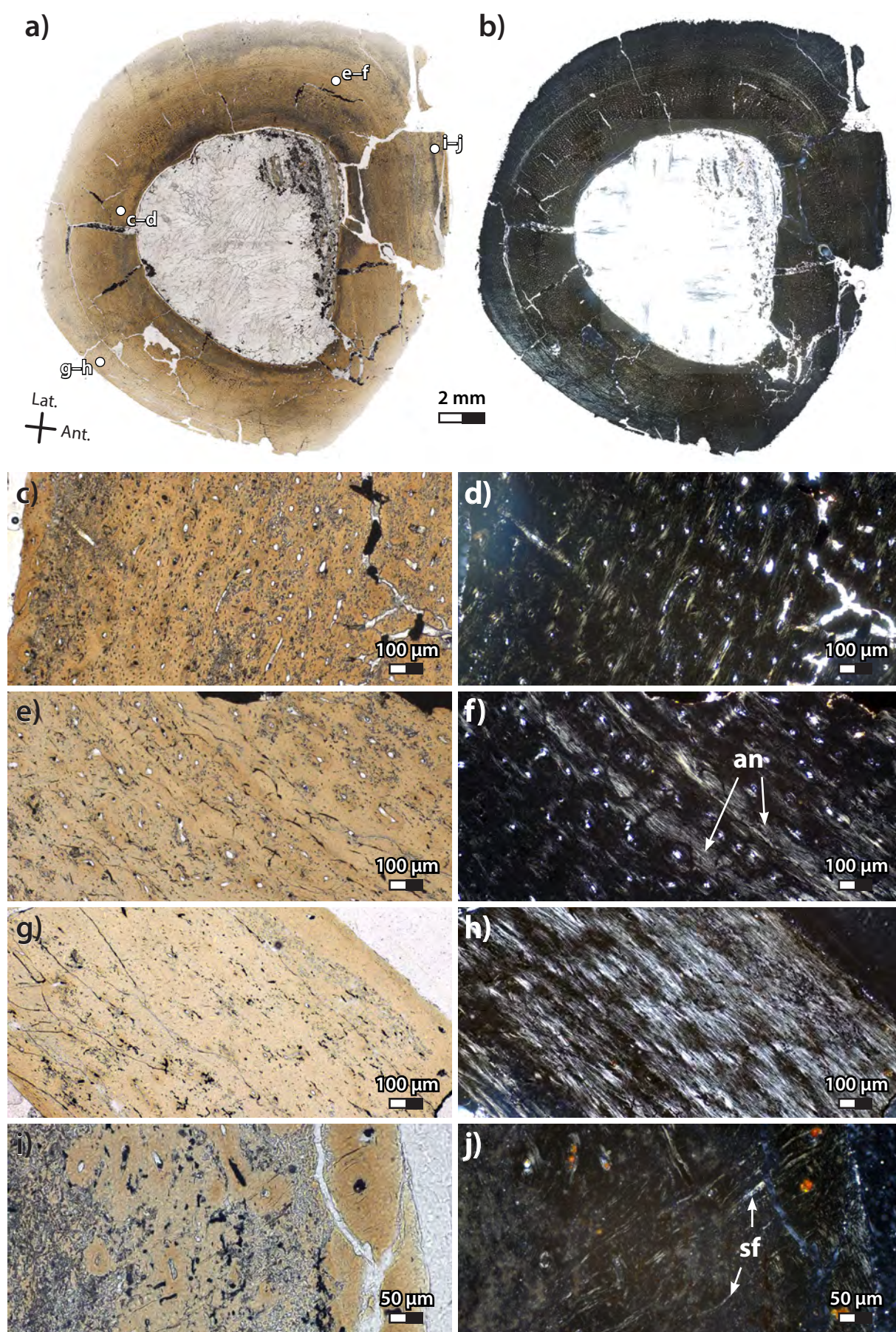


Fig. 4.17 (caption on following page)

Figure 4.17. Tibial section of *Hypsilophodon foxii* (NHMUK PV R 193; Section B): **a–b**, whole section; **c–d**, woven-fibred bone in the inner cortex dominated by primary osteons; **e–f**, split annulus (an) in the mid-cortex; **g–h**, parallel-fibred bone in the outer cortex; **i–j**, radially oriented structural fibres (sf) in the anterolateral region of the outer cortex. Left, plain polarised light; right, cross polarised light.

ner and middle cortex consists predominately of woven-fibred bone matrix, which is well-vascularised with longitudinal primary osteons (Figure 4.17c–d). Some of these primary osteons have a single cement line. The osteocytes in this region are generally oval in shape and random in orientation, but some are arranged around the osteons. Osteocyte density is high in the inner cortex, but reduces in the middle cortex. A few resorption bays can be found in the inner cortex, but they are much smaller than those in section A, and most of these are not lined with lamellae. As in section A, a thin layer of parallel-fibred bone that forms an annulus, can be observed in the middle cortex. This annulus also splits at the anterolateral side of the section (Figure 4.17d–e). The outer cortex consists primarily of poorly-vascularised parallel-fibred bone with flattened osteocytes that are aligned parallel to the fibres of the bone matrix. However, well-vascularised woven-fibred bone persists into the outer cortex in the anterior region of the section. Short, radially-oriented Sharpey’s fibres cross-cut this woven-fibred bone near the periosteal margin (Figure 4.17f–g). As in section A, a zone of woven-fibred bone is visible in a localised area on the anterolateral side of the section: however, in this section the width of this zone is much thinner (~250 µm) and its extent is heavily eroded by periosteal cortical drift. No LAGs are present.

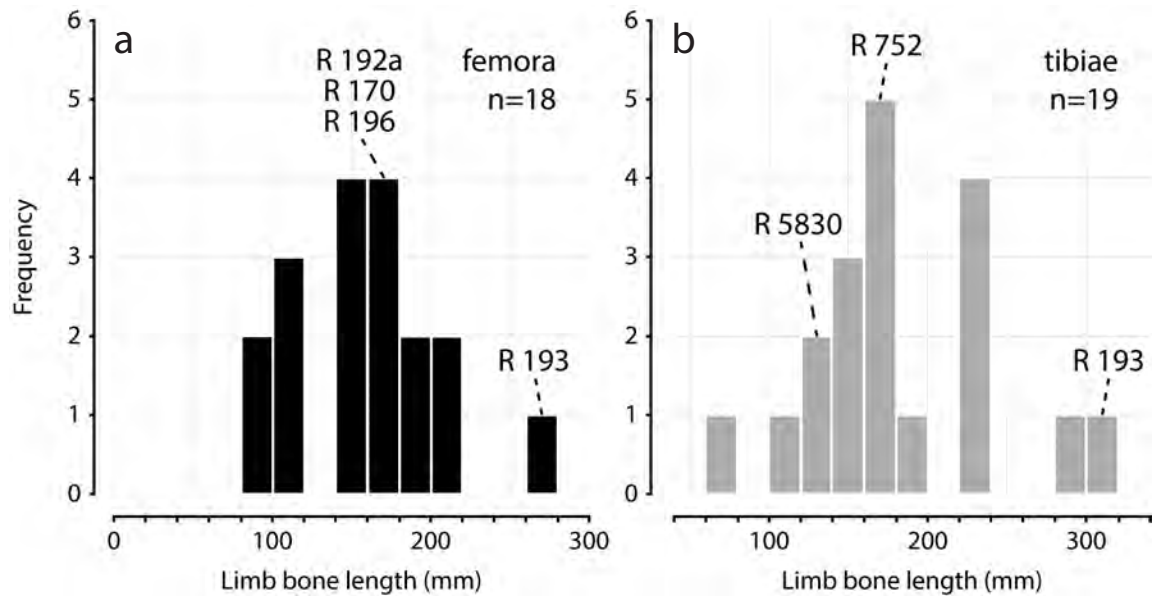


Figure 4.18. Size distribution of *Hypsilophodon foxii* individuals from the *Hypsilophodon* Bed based on limb bone lengths: **a**, femora; **b**, tibiae. Specimens sampled in this study are labelled. Specimens have the prefix 'NHMUK PV'.

4.3.2. Mortality profiles

A mortality profile for the *Hypsilophodon* Bed was created using femoral and tibial length as a proxy for body size (Figure 4.18). Visually, both profiles appear to have normal distributions, with a higher proportion of medium-sized individuals, and a comparatively lower number of the very smallest and very largest individuals. Shapiro-Wilk and Anderson-Darling tests confirm that both distributions are normal (Table 4.2).

4.4. Discussion

4.4.1. Ontogenetic summary

Here, I differentiate each studied specimen into one of five histological ontogenetic

Table 4.2. Results of Shapiro-Wilk and Anderson-Darling normality test for the distribution of *Hypsilophodon foxii* long bone lengths from the *Hypsilophodon* Bed.

	Shapiro-Wilk test	p-value	Anderson-Darling test	p-value
Femoral length	0.961	0.615	0.265	0.653
Tibial length	0.924	0.137	0.658	0.071

stages (HOS) based on the distinct histological features observed (Table 4.3). These HOS increase ontogenetically from juvenile stage (HOS 1) to near skeletally mature adults (HOS 5).

4.4.1.1. HOS 1. I assign the femur NHMUK PV R 170 to HOS 1. The entire cortex is composed of highly vascularised woven-fibred bone, which is dominated by primary osteons. Most of these canals are reticular in orientation, but at the level of the fourth trochanter and within the posterior region of the section a high proportion of radially-oriented canals is observed throughout the cortex. Multiple studies using modern birds have suggested that woven-fibred bone with radially-oriented canals might be the most rapidly growing bone tissue (Castanet *et al.* 2000; de Margerie *et al.* 2002; de Margerie *et al.* 2004; Pratt & Cooper 2018), indicating that these localised areas in NHMUK PV R 170 were growing faster than the surrounding bone. Some vascular canals open on to the periosteal surface. Vascularity is uniformly high throughout the section, similar to that seen in early juveniles of *Orodromeus*, *Dryosaurus* and *Tenontosaurus* (Horner *et al.* 2009; Werning 2012). There is no evidence of LAGs or secondary remodelling. The bone histology observed in NHMUK PV R 170 suggests that the individual had a continuous and rapid growth rate.

Table 4.3. Summary of histological ontogenetic stages (HOS) outlined in this study.

	HOS 1	HOS 2	HOS 3	HOS 4	HOS 5
Primary bone matrix	Woven-fibred bone	Parallel-fibred bone	Parallel-fibred bone	Woven-fibred bone and parallel-fibred bone in cortex, lamellar bone lining the medullary cavity	Woven-fibred bone and parallel-fibred bone in cortex, lamellar bone lining the medullary cavity
Vascular canal primary orientation	Reticular	Longitudinal	Longitudinal	Longitudinal	Longitudinal
Anastomosing canals	Many	Some	Some	Some	Few
Secondary remodelling	No	No	Resorption bays and secondary osteons in inner cortex	Resorption bays and secondary osteons in inner to mid-cortex	Resorption bays and multiple generations of secondary osteons throughout cortex
Zonation	Azonal	Azonal	Azonal	Zonal	Zonal – defined zones and annuli
Reduced vascularity towards periphery	No	No	No	Yes	Yes – periphery is almost avascular
Referred specimens	NHMUK PV R 170 (femur)	NHMUK PV R 5830 (tibia)	NHMUK PV R 192a (femur)	NHMUK PV R 752 (tibia)	NHMUK PV R 196 (femur); NHMUK PV R 193 (femur & tibia)

4.4.1.2. HOS 2. The tibia NHMUK PV R 5830, which has the smallest diameter of any of the long bones in our sample, is assigned to HOS 2. This stage is differentiated from HOS 1 by a change from well-vascularised woven-fibred bone to slower growing parallel-fibred bone. Vascular canals are predominately longitudinal primary osteons, many of which anastomose circumferentially. Some vascular canals open on the periosteal surface. As in HOS 1, there is no change in vascularity from the inner to the outer cortex. There is no evidence of LAGs or secondary remodelling. This bone histology suggests that NHMUK PV R 5830 was undergoing continuous, but relatively slow, growth.

4.4.1.3. HOS 3. The femur NHMUK PV R 192a is assigned to HOS 3. The cortex here is primarily parallel-fibred bone with longitudinal primary osteons, some of which anastomose circumferentially. This stage differs from HOS 2 as there is evidence of secondary remodelling from resorption bays and a few secondary osteons are present, which are confined to the inner cortex. The presence of resorption bays suggests that the medullary cavity was in the process of expanding. As in HOS 1-2, vascularity does not change throughout the cortex. There is no evidence of LAGs, although it is possible that LAGs in NHMUK PV R 192a might have been obscured or destroyed by extensive bacterial invasion and/or the matrix infilling the specimen.

4.4.1.4. HOS 4. I assign the tibia NHMUK PV R 752 to HOS 4. Unlike prior stages, the cortex in HOS 4 is zonal and consists of areas of woven-fibred and parallel-fibred bone that represent periods of differing growth rate. Vascular canals are primarily longitudinal in orientation, with some that anastomose. As in HOS 3, resorption bays are found in the inner cortex, many of which are lined with multiple lamellae, suggesting that at the time of death the medullary cavity was not undergoing

expansion. The medullary cavity is also lined with lamellar bone in the form of an inner circumferential layer (ICL; also known as an internal fundamental system). Unlike an external fundamental system, where lamellar bone is deposited at the periosteum, ICL do not suggest a specific growth stage (de Buffr  nil & Quilhac 2021), but ICLs are rare in juvenile bones (Padian *et al.* 2013a). The presence of an ICL suggests a pause in medullary cavity expansion at this growth stage. Secondary osteons can be found in the inner and middle cortex. The key difference between HOS 4 and all prior stages, is that vascularisation decreases towards the periphery, suggesting that growth was decelerating significantly before death.

4.4.1.5. HOS 5. I assign the two remaining individuals in our sample to HOS 5: NHMUK PV R 193 (tibia and femur) and NHMUK PV R 196 (femur). Across all three elements, the inner cortex consists primarily of well-vascularised woven-fibred bone, which contains dense, randomly aligned osteocytes. The bone matrix changes in the middle cortex to parallel-fibred bone with osteocytes aligned in parallel. Vascular canals are primarily longitudinal in orientation, with fewer anastomoses than prior stages. In HOS 5, remodelling is extensive. Secondary osteons are found in the inner and middle cortex of all specimens, and may extend into the outer cortex in some regions. In the inner cortex, some of these secondary osteons overlap, suggesting multiple generations of remodelling. In all specimens assigned to this growth stage, a layer of almost avascular parallel-fibred bone lines the periosteum, suggesting that growth was continuing but at a greatly reduced rate. As in HOS 4, the histology observed is zonal, however in HOS 5 these zones are far more distinct and appear as cyclical growth marks (e.g. annuli and zones).

Femora of this stage (NHMUK PV R 193 and NHMUK PV R 196) show cortical

drift lines constrained to one region of the section. Cortical drift lines in the femora of larger *Hypsilophodon foxii* individuals might be related to the development of the fourth trochanter (Padian *et al.* 2013a; Woodward *et al.* 2013), but could also be caused by cortical drift due to the curved shape of the femora (Enlow 1962). In the largest individuals of this stage (NHMUK PV R 193; both elements), Sharpey's fibres can be observed. At the endosteal margin of the femora, these appear as thick bundles of fibres, but in both elements, these fibres are thin cross-cutting lines at the periosteum. These fibres imply the presence of strong muscle attachments (Canoville *et al.* 2021). In the largest tibia, NHMUK PV R 193, Sharpey's fibres are localised to the anterolateral region near the periosteal margin, and are possibly associated with the membrana interossea cruris (Bishop *et al.* 2021). In the femora, Sharpey's fibres are localised to the anterolateral region and found alongside a few radially oriented canals, both are likely associated with the *M. femorotibialis medialis* (Maidment & Barrett 2011). The presence of a small number of radial canals in this localised region suggests the continued growth of bone in this area, which might have reinforced the muscle attachment site.

4.4.2. Skeletal and reproductive maturity

In most vertebrates, growth is determinate and ceases well before the maximum possible age of an individual is reached (Woodward *et al.* 2011; Frýdlová *et al.* 2020; Rothschild & Witzmann 2021). This cessation of growth is indicated by the presence of an external fundamental system (EFS; also known as an outer circumferential lamella, OCL) at the bone periphery (Cormack 1987; Woodward *et al.* 2011). An EFS is defined as a sub-periosteal layer of avascular and acellular parallel-fibred or lamellar bone tis-

sue, often containing a number of tightly packed LAGs (Ponton *et al.* 2004; Woodward *et al.* 2011; de Buffr  nil & Quilhac 2021b). This feature has been found in several ornithopods (Horner *et al.* 2000; Cooper *et al.* 2008; Kitchener *et al.* 2019; S  lowiak *et al.* 2021), indicating the attainment of skeletal maturity (full adult size) in these taxa and confirming determinate growth. In our sample, a ~120 µm layer of avascular and acellular parallel-fibred bone can be found at the periphery of the tibia of the largest individual, NHMUK PV R 193 (Figure 4.16e-f). Extensive periosteal cortical drift in this specimen has eroded much of this layer’s extent around the cortex. This feature is similar to possible EFSs reported in other non-avian dinosaurs (e.g. Horner *et al.* 2009; Barta *et al.* 2022), but regardless of whether or not it represents a true EFS, its presence suggests that this individual was likely nearing skeletal maturity.

In contrast to skeletal maturity, definitive indicators of reproductive maturity are rarely observed in fossil taxa. Among non-avian dinosaurs, these indicators include the preservation of eggs within the body cavity (Chen *et al.* 1998; Sato *et al.* 2005; Jin *et al.* 2019) and the presence of medullary bone (Schweitzer *et al.* 2005; Lee & Werning 2008; H  bner *et al.* 2012; Skutschas *et al.* 2017; Prondvai 2017), neither of which have been observed in *Hypsilophodon foxii*.

The timing of reproductive maturity relative to skeletal maturity varies considerably among modern diapsids. In extant squamates (lizards, snakes, and amphisbaenians) and crocodilians (alligators and crocodiles), reproductive maturity is attained far before the animal has reached its full size, and coincides with the start of a significant slowdown in growth rate, as energy is reallocated from growth to reproduction (Erickson *et al.* 2007; Lee & Werning 2008; Boukal *et al.* 2014). This is very different to extant birds, where reproductive maturity is attained only after full adult size has been

reached (Erickson *et al.* 2007; Lee & Werning 2008; however, see e.g. kiwi, Bourdon *et al.* 2009). Independent studies suggest that the timing of maturation in non-avian dinosaurs followed the reptilian model, with reproductive maturity preceding skeletal maturity (Erickson *et al.* 2007; Lee & Werning 2008). Lee & Werning (2008) produced growth curves for three dinosaur taxa (*Allosaurus*, *Tyrannosaurus*, and *Tenontosaurus*) including sexually mature individuals (with medullary bone present) and confirmed that, as in modern reptiles, reproductive maturity coincides with the onset of a significant deceleration in growth.

In palaeohistology, several features are considered indicative of declining growth rate: more longitudinal vascular canals; fewer anastomosing canals; a change to more organised bone matrix (i.e. parallel-fibred or lamellar); reduced vascularity towards the periphery; reduced distance between growth marks towards the periphery; and the formation of an EFS (Amprino 1947; Castanet *et al.* 2000; Horner *et al.* 2000; Padian & Horner 2007; Padian & Lamm 2013; de Buffr  nil *et al.* 2021a). In *Hypsilophodon*, HOS 1 shows none of these features, indicating rapid and continuous growth prior to the attainment of reproductive maturity. In contrast, the dominance of slower-depositing parallel-fibred bone in HOS 2 suggests that sexual maturity has been reached and growth has begun to decelerate. The vast size difference in size between the reproductively mature HOS 2 tibia (NHMUK PV R 5830; circumference = 34 mm) and the HOS 5 tibia (NHMUK PV R 193; circumference = 61 mm), which is likely nearing skeletal maturity, is consistent with findings from Lee & Werning (2009) that suggest reproductive maturity in dinosaurs is often reached at one-third to one-half of full adult size. Other factors such as harsh environmental conditions could also be responsible for the comparatively slow growth seen in HOS 2 onwards, but this is

difficult to test. HOS 4 shows multiple features that indicate decreasing growth rates, demonstrating that individuals of this stage are undoubtedly sexually mature.

4.4.3. Age estimation

In extant vertebrates, lines of arrested growth (LAGs) have been shown to correspond to an annual temporary cessation in growth, independent of metabolic rate and climatic stress (Peabody 1961; de Buffrénil & Castanet 2000; Snover & Hohn 2004; Köhler *et al.* 2012). As a result, counting the number of LAGs has frequently been used to estimate the age of individuals in fossil samples (e.g. Horner & Padian 2004; Horner *et al.* 2009; Werning 2012; Zhao *et al.* 2019; Han *et al.* 2020). In *Hypsilophodon*, I found no definitive or unambiguous LAGs in any of the individuals sampled, suggesting this dinosaur underwent continuous and uninterrupted growth throughout its life. However, it cannot be ruled out that LAGs may have been: 1) lost due to cortical drift or extensive remodelling; 2) obscured by bacterial invasion; or 3) misinterpreted as non-cyclical cortical drift lines. Only further sampling will confirm my findings.

The absence of LAGs is common in many sauropods (Curry 1999; Sander 2000; Cerda *et al.* 2017), but has also been observed in several large hadrosaurids (e.g. *Edmontosaurus*, Chinsamy *et al.* 2012; *Saurolophus*, Słowiak *et al.* 2020) and the small ornithopod *Convolosaurus* (Winkler 1994; Andrzejewski *et al.* 2019). *Dryosaurus*, *Dysalotosaurus* and an unnamed Early Cretaceous ornithopod from Australia were formerly considered to lack LAGs, but this feature has subsequently been documented in all three taxa, albeit rarely (Chinsamy 1995; Chinsamy *et al.* 1998; Horner *et al.* 2009; Hübner *et al.* 2012; Woodward *et al.* 2018). In sauropods and hadrosaurids, the continuous growth demonstrated by the lack of LAGs is thought to have enabled

them to achieve gigantism (Słowiak *et al.* 2020). This reasoning is not applicable to the small ornithopods *Convolosaurus* or *Hypsilophodon*. Chinsamy (1998) proposed that the absence of LAGs in *Dryosaurus* (= *Dysalotosaurus*; although LAGs were later found, Hübner *et al.* 2012) may imply the taxa had indeterminate growth, meaning that development did not cease during the lifespan of the individual (Woodward *et al.* 2011; Rothschild & Witzmann 2021). However, the relationship between LAGs and determinate/indeterminate growth is tenuous, with LAGs being found in extant taxa with indeterminate growth (e.g. starred agama: Kumaş & Ayaz 2014). Horner *et al.* (2009) suggested that the absence of LAGs in *Dryosaurus* and *Dysalotosaurus* (again, LAGs were later found in both taxa: Hübner *et al.* 2012) could indicate that an adult specimen has yet to be discovered, having implications for the taxonomy of both. While the absence of an EFS in my sample implies that a skeletally mature *Hypsilophodon foxii* has not yet been found, the EFS-like feature near the periosteal margin in NHMUK PV R 193 suggests that the specimen was nearing full size, implying that *H. foxii* is not a juvenile synonym of another taxon. Another possible explanation for the lack of LAGs could be that all individuals sampled are less than one-year old; however, I reject this hypothesis due to the presence of zones and annuli in HOS 5, which are also considered to be indicators of annual cyclicity (Hutton 1986).

It has been hypothesised that the scarcity or complete lack of LAGs in multiple small to medium-bodied ornithopods (i.e. *Convolosaurus*, *Dryosaurus*, *Dysalotosaurus*, *Hypsilophodon*), might imply a shared growth pattern among early-diverging ornithopods (Winkler 1994; Hübner *et al.* 2012; Woodward *et al.* 2018; Andrzejewski *et al.* 2019). Hübner *et al.* (2012) suggested that lower food demands and alternative adaptations to surviving seasonal stresses (e.g. fossoriality) may have negated the need

for smaller ornithopods to cease growth annually. *Orodromeus* was considered an exception to this trend, as LAGs are present from juvenility (Horner *et al.* 2009; Hübner *et al.* 2012). However, over the last decade, LAGs have been recovered in several more small ornithopods/thescelosaurids, including *Oryctodromeus* (Krumenacker 2017), *Jeholosaurus* (Han *et al.* 2020) and taxonomically indeterminate polar ‘hypsilophodontids’ (Woodward *et al.* 2018). This demonstrates that both growth patterns can be observed in small- to medium-sized ornithopods/thescelosaurids, although it remains uncertain what has driven this dichotomy. With the exception of the polar taxa, the aforementioned species have all been recovered from similar palaeolatitudes within the temperate zone (paleobiodb.org) and were therefore likely exposed to broadly comparable climatic conditions and environmental stresses (Hay & Floegel 2012; Varela *et al.* 2018). Additionally, as *Oryctodromeus* has been found in burrows and exhibits several anatomical features consistent with digging habits (Varricchio *et al.* 2007), fossoriality does not seem to be a viable explanation for a lack of LAGs. Instead, differences might reflect a disparity in the degree of developmental plasticity. Bone is a plastic tissue and its formation rate is known to be significantly affected by external environmental factors and internal physiological factors (Hutton 1986; Starck & Chinsamy 2002; Sander & Klein 2005). Developmental plasticity is the ability of an organism to respond to these factors, resulting in the expression of different phenotypes later in development (Smith-Gill 1983; Starck & Chinsamy 2002). The presence of regularly deposited LAGs suggests strong developmental plasticity, as individuals are not wasting energy on bone growth during times of seasonal stress. In addition to functional influence, variation in the bone histology of vertebrates has also been shown to have a significant phylogenetic component (Montes *et al.* 2010). Recent cladistic analyses

have recovered *Orodromeus*, *Oryctodromeus* and *Jeholosaurus* as earlier-diverging than *Convolosaurus*, *Dryosaurus*, *Dysalotosaurus* and *Hypsilophodon* (Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021), which suggests that the presence of annually-deposited LAGs might be the plesiomorphic condition for Neornithischia.

4.4.4. Growth variation

4.4.4.1. Intraspecies variation. Although my interpretations are limited by a small sample size, histological observations of femora in *Hypsilophodon* show significant growth variation that might hint at the presence of multiple growth trajectories (Figure 4.19). NHMUK PV R 196 is the smallest femur included within my analysis, but its bone microstructure leads me to assign it to the most ontogenetically mature stage, HOS 5, likely equivalent to a late sub-adult. Body mass estimates suggest this individual weighed 11.9 kg. By contrast, NHMUK PV R 170 has an estimated body mass of 17.3 kg, but a bone microstructure indicative of a rapidly growing juvenile. Furthermore, body mass estimates imply that individuals assigned to HOS 5 ranged up to 37.2 kg (NHMUK PV R 193).

This marked variation could reflect sexual size dimorphism in *Hypsilophodon*, like that observed in many extant archosaurs (Thorbjarnarson 1994; Wilkinson & Rhodes 1997; Navarro *et al.* 2005; Cox *et al.* 2007; Székely *et al.* 2007; Platt *et al.* 2009; Hone & Mallon 2017). Sexual dimorphism is difficult to test in fossil taxa without the presence of definitive female indicators (e.g. medullary bone or gravidity), but has been proposed for several non-avian dinosaurs where variable growth trajectories have been implied from long bone histology (e.g. Klein & Sander 2008; Cerda & Chinsamy 2012; Han *et al.* 2020; Barta *et al.* 2022). Another possible explanation could be that this

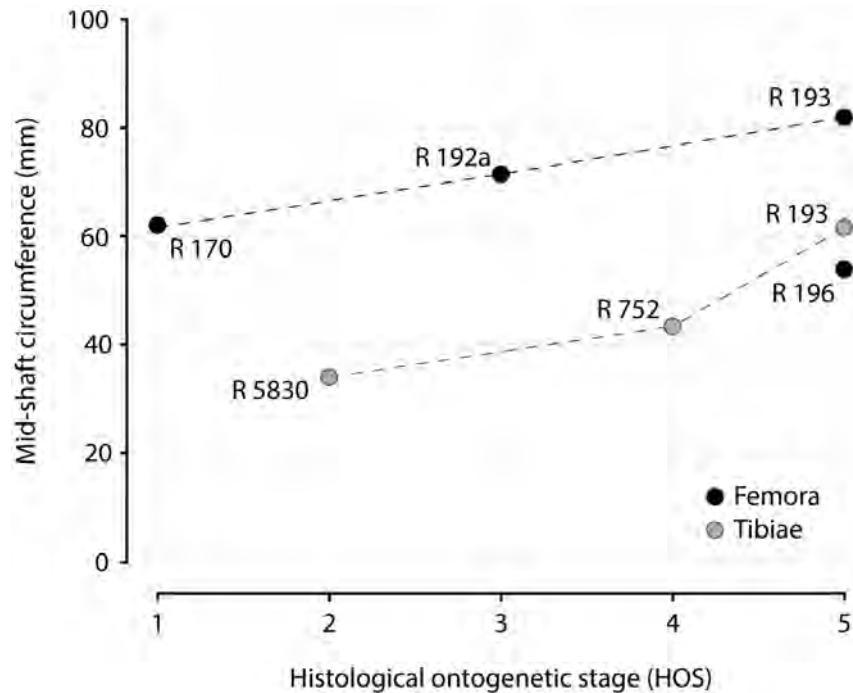


Figure 4.19. Growth curve of *Hypsilophodon foxii* based on the histological ontogenetic stages (HOS) outlined in this study. Specimens have the prefix 'NHMUK PV'. Dashed lines indicate possible growth patterns. **Key:** femora (black); tibiae (grey).

variation reflects strong developmental plasticity, which is considered to be the ancestral state within archosaurs, and has been inferred in several early dinosaurs (Sander & Klein 2005; Klein & Sander 2007; Griffin & Nesbitt 2016; Griffin 2018; Chapelle *et al.* 2021; Barta *et al.* 2022). In the early sauropodomorph *Plateosaurus*, fully grown individuals ranged in body length from 4.8 m to 10 m (Sander & Klein 2005). Authors rejected sexual dimorphism as a possible cause, due to the unimodal distribution in terminal body size, and concluded that strong plasticity was present (Sander & Klein 2005). The final hypothesis I consider is that variation may indicate that the specimens studied represent two or more distinct species. This is certainly a possibility,

considering that several specimens from the *Hypsilophodon* Bed originally referred to *Hypsilophodon foxii* were subsequently re-assigned to other Wealden taxa, such as *Valdosaurus*, or found to be generically and specifically indeterminate (Galton 1975; Galton 1977; Barrett *et al.* 2011). Taxonomic re-evaluation of all of the specimens referred to *H. foxii* is required to determine whether multiple species are present.

4.4.4.2. Inter- and intra-elemental variation. My study focuses on the histology of two hind limb elements, the femur and tibia. In the largest specimen (NHMUK PV R 193), both elements were sectioned twice, giving an insight into the histological variation between different elements of the same individual and the variation found within a single element.

I find that inter-elemental variation is significant. In the tibial sections of NHMUK PV R 193, an annulus and a zone are present in the middle and outer cortex, respectively, but neither feature is found in the femoral section. A disparity in the number of growth marks found in different limb elements of the single individual has been observed in several ornithopods (e.g. Horner *et al.* 2000; Hübner 2012; Cerda & Chinsamy 2012). This inter-elemental variation is often attributed to the relative size of the different elements, with larger elements tending to grow faster (Woodward *et al.* 2014; Cerda *et al.* 2019). Another likely factor is the significant periosteal cortical drift (=osseous drift) observed in more mature limb bones of *Hypsilophodon* in this study. This is particularly clear in the tibial section of NHMUK PV R 193, where the zone in the outer cortex has been extensively eroded by drift (Figure 4.20). It is possible that these cyclical features formed in both the femur and tibia, but have eroded away in the former. This variation between different elements highlights the importance of sampling multiple bones when investigating the histology of an individual (Horner *et al.*

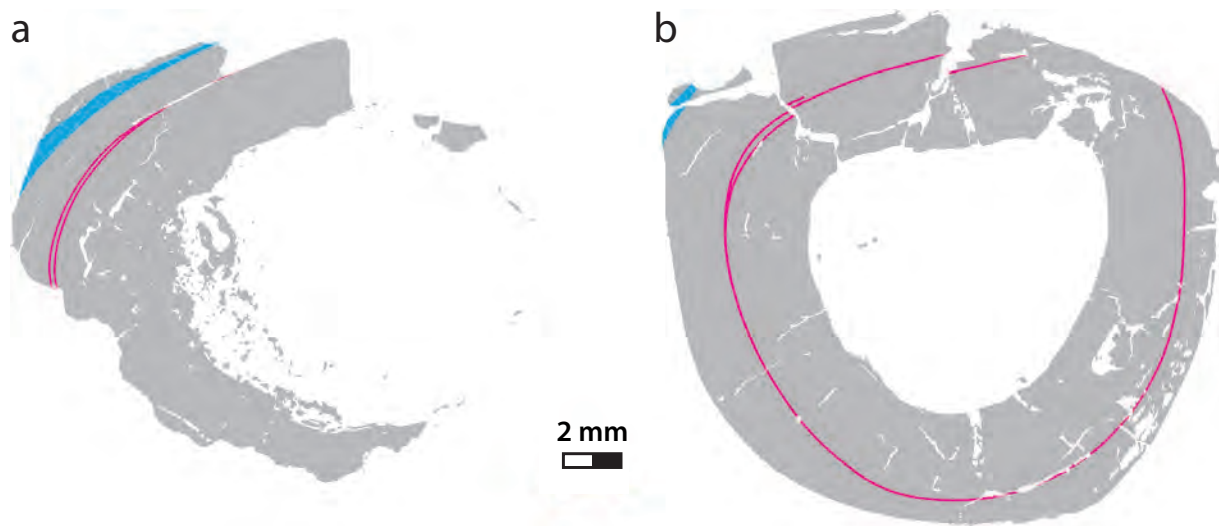


Figure 4.20. Erosion of zones in tibial sections of NHMUK PV R 193 due to periosteal cortical drift: **a**, Section A; **b**, Section B. Colour key: annulus (pink); zone (blue).

2000).

Intra-elemental variation in the two femoral sections is minimal, with section A having comparably larger and more numerous resorption bays in the inner cortex than section B. Femoral section A was sampled more proximally than section B, closer to the fourth trochanter. The increased medullary cavity resorption observed in section A is likely due to its proximity to this dynamic muscle attachment site. The histological variation observed between the two tibial sections is due to periosteal cortical drift, with the zone in the outer cortex being almost entirely eroded in the more distal section B (Figure 4.17).

4.4.5. Population structure

Sedimentological observations led Coram *et al.* (2017) to conclude that the *Hypsilo-*

phodon Bed was deposited in two or more mass mortality events, such as a flash flood. The implication is that these individuals were part of groups that lived and died at the same time, rather than a time-averaged accumulation of individuals that died at different times. The monodominant nature of the bone bed also supports the idea that this was a single mass mortality event, with most monospecific and monodominant bone beds frequently interpreted as catastrophic in origin (e.g. Bell and Campione 2014; Chiba *et al.* 2015; Hübner *et al.* 2021; however see e.g. Lauters *et al.* 2008). Mortality profiles are useful for interpreting the causes of bone bed accumulations (Varricchio & Horner 1993; Lyman 1994). These profiles are often created using the size or age distribution of individuals within a bonebed. Distributions are then compared to hypothetical profiles for catastrophic or attritional death assemblages. Catastrophic distributions are typically right-skewed ('L-shaped') and represent the death of a living population, which would primarily consist of juvenile and subadult individuals (Lyman 1994; Berger *et al.* 2001; e.g. Erickson *et al.* 2009, Varricchio *et al.* 2008; Barta *et al.* 2022; Wosik & Evans 2022). In contrast, attritional accumulation distributions are often bimodal ('U-shaped'), reflecting the greater mortality rates of the youngest and oldest individuals within a population (Lyman 1994; e.g. Hübner *et al.* 2021).

Here, I created a mortality profile for the *Hypsilophodon* Bed from the size distribution of *Hypsilophodon* hind limb bones (Figure 4.18). It was found that neither profile is consistent with a typical catastrophic or attritional death assemblage: however, these hypothetical profiles can be ambiguous (Klein 1982). Both profiles indicate that the bone bed was composed predominately of medium-sized individuals, followed by fewer small individuals and with even fewer large individuals. Results from our histological analyses allow me to infer the maturation of individuals within the distribu-

tion. Unfortunately, the limited juvenile material within our histological sample limits understanding of their distribution within the assemblage. Additionally, the high plasticity and distinct growth patterns identified within samples further obscures trends between size and ontogenetic stage. This is exemplified by the juvenile femur, NHMUK PV R 170, which occupies the same size bin as two sexually mature sub-adults (Figure 4.18a). Nevertheless, the size distribution still indicates underrepresentation of hatchlings and early juveniles in the bone bed, as found in several other bone bed studies representing both catastrophic and attritional assemblages (Varricchio *et al.* 2008; Hübner *et al.* 2021; Wosik *et al.* 2020; Wosik & Evans 2022). This absence could suggest that younger individuals formed independent groups separate to the main herd (Forster 1990; Lauters *et al.* 2008; Varricchio *et al.* 2008; Erickson *et al.* 2009; Zhao *et al.* 2013a; Hübner *et al.* 2021), but may also reflect taphonomic and/or sampling biases, with smaller individuals more likely to undergo post-mortem transportation and being generally less likely to be preserved and discovered (Cooper *et al.* 2006; Lauters *et al.* 2008; Brown *et al.* 2013a).

The high proportion of medium-sized individuals in our size distribution likely represents an abundance of juveniles and sexually mature sub-adults, as would be expected in a standing crop population. This notion is further supported by the scarcity of large, nearly skeletally mature adults (e.g. NHMUK PV R 193), which likely reflects the increased probability of death expected with increased age (Hübner *et al.* 2021). As the size distribution is consistent with a standing crop population, I interpret the *Hypsilophodon* Bed as catastrophic in origin (Lyman 1994; Berger *et al.* 2001). Mortality profiles that have been interpreted as representing catastrophic assemblages have also been constructed for several non-avian dinosaurs, including the ornithomimid

Sinornithomimus dongi (Varricchio *et al.* 2008), the early ceratopsian *Psittacosaurus lujiatunensis* (Erickson *et al.* 2009) and the hadrosaurid *Edmontosaurus annectens* (Wosik & Evans 2022).

Although the size distribution is congruent with a living population, it remains uncertain whether these individuals were part of the same population (i.e. living within a herd). Other dinosaur bone bed studies have found evidence suggesting that individuals found within represented a group in life. In *E. annectens*, all sectioned elements showed layering of laminar bone near the periosteal surface, suggesting that the individuals likely died at the same time during a period of slow growth (Wosik & Evans 2022). In *C. dongi*, the aligned arrangement and close proximity of individuals within the bone bed indicated that they were part of a single herd that died as a result of miring (Varricchio *et al.* 2008). Here, we find no corresponding growth marks between multiple specimens of *H. foxii*: in fact, the periosteal surface is notably varied between samples, suggesting the individuals may not have been experiencing the same climatic stresses near the time of death. Additionally, there is little to no information about the arrangement of *H. foxii* specimens within the bed, with many isolated specimens being discovered *ex situ* (Galton 1974). Further investigation of the sedimentology of the *Hypsilophodon* Bed is required to verify the cause of death, which will hopefully shed further light on the population dynamics of this taxa.

4.5. Conclusions

The histology of *Hypsilophodon foxii* suggests that this taxon experienced rapid, continuous growth during the juvenile stage, followed by slower but largely uninterrupted

growth after the attainment of sexual maturity. This constant growth is evidenced by the absence of unambiguous lines of arrested growth (LAGs) in our sample, although the presence of annuli in the most ontogenetically mature specimens does indicate temporary slowdowns in growth. The growth strategy observed in *H. foxii* is similar to that reported in other early-diverging ornithopods (e.g. *Convolosaurus*), but contrasts with that in other early-diverging ornithopods/thescelosaurids (e.g. *Orodromeus*), demonstrating histovariability within Neornithischia.

Sections from mature individuals are highly asymmetrical, and show both inter- and intra-elemental variation, primarily as a result of extensive periosteal cortical drift (=osseous drift). Inter-specific variation is also observed and might be the result of either sexual dimorphism, high plasticity, or the inclusion of multiple distinct taxa within the sample (and none of these explanations are mutually exclusive). These results highlight the importance of sampling multiple specimens and multiple elements when making histological inferences.

I found that our sample consists of one juvenile and five sexually mature sub-adults, one of which is likely very close to skeletal maturity, as shown by an almost avascular layer of parallel-fibred bone at the periosteum. The body-size distribution of specimens (and their inferred sub-adult ontogenetic stage) suggests that the *Hypsilophodon* Bed may be catastrophic in origin, although it remains unclear whether these individuals represented a herd in life.

Chapter 5

TOOTH REPLACEMENT CYCLES AND NEUROANATOMY OF A NEW ORNITHOPOD FROM THE LATE CRETACEOUS OF ANTARCTICA

Ornithopods are a highly successful clade of ornithischian dinosaurs that had a cosmopolitan distribution during the Cretaceous Period, being found on every continent. Here I use micro-computed tomographic (μ CT) scan data to investigate the dentary and partial braincase of a new, unnamed ornithopod from the Late Cretaceous of Antarctica. Using digital segmentation techniques, the dentition and neurovasculature were reconstructed from the dentary μ CT data, while the internal cavities that would have housed the endosseous labyrinth, cranial nerves and floccular lobe were reconstructed from the braincase μ CT data. The relationships between functional, replacement and non-functional old teeth at each tooth family was examined to investigate the different stages of tooth replacement in this new ornithopod. Reconstructed Zahnreihen patterns suggests an average Z-spacing of 2.4, consistent with several similar ornithischians. The neurovascular anatomy is found to be relatively simple throughout most of the length of the dentary, but becomes more complex at the predentary-dentary margin. The inner ear could not be completely reconstructed, but the endosseous labyrinths are sub-triangular in outline, similar to those of other ornithopods. The morphology of the digitally reconstructed floccular lobe is unusual in that it is forked, but also in how far it extends through the anterior canal of the endosseous labyrinth. Enlarged floccular

lobes have been linked to gaze stabilisation and rapid head movements in both extinct and extant theropods, indicating that this ornithopod may have had similar specialisations. These results inform us on the evolution of sensory abilities and dental systems within both ornithopods and other major dinosaur groups.

5.1. Introduction

Ornithopods are a group of herbivorous dinosaurs that were highly successful and diverse during the Cretaceous Period (Sereno 1999; Weishampel *et al.* 2004). Fossil remains from this group have been found on all seven continents, demonstrating that ornithopods had a worldwide distribution at their acme (Butler & Barrett 2012).

The dental complexity of ornithopods is exemplified by the dental batteries of hadrosaurs, which consist of multiple generations of vertically-stacked and interlocking teeth (Erickson *et al.* 2012). The development of these impressive batteries increased the efficiency of food processing in these dinosaurs and is often considered to be the main reason hadrosaurs were so successful in the Late Cretaceous (Horner *et al.* 2004; Erickson *et al.* 2012; LeBlanc *et al.* 2016; Bramble *et al.* 2017). However, while there have been multiple studies investigating these batteries, we have little understanding of how this dental morphology evolved, due to the lack of comparative examples from early-diverging ornithopods (Erickson *et al.* 2012; LeBlanc *et al.* 2016; Bramble *et al.* 2017; Chen *et al.* 2018).

Accurately evaluating tooth formation and replacement requires observing the relationships between functional and growing replacement teeth in-situ within the jaw. Previous dinosaur studies have done this using histological (e.g. Erickson 1996;

D’Emic *et al.* 2013; LeBlanc *et al.* 2016; Bramble *et al.* 2017; Chen *et al.* 2018) or computed tomographic (CT) methods (e.g. Butler *et al.* 2012; Sciscio *et al.* 2017; He *et al.* 2018; D’Emic *et al.* 2019; Becerra *et al.* 2022; Chang *et al.* 2021; Hu *et al.* 2022). Histological analyses of dentition are useful, particularly when estimating replacement rate or investigating modes of implantation or attachment, as various features involved in these processes cannot be observed in CT data (e.g. von Ebner lines; Erickson 1996). However, when looking at tooth replacement cycles, the use of CT is highly preferable to histology, as it is not only non-destructive, but also allows teeth to be visualised in three-dimensions, potentially allowing identification of important features that may be missed in two-dimensional histological sections.

Within Ornithischia, there has been limited research into tooth formation and replacement cycles, with CT methods so far applied only to heterodontosaurids (Porro *et al.* 2011; Butler *et al.* 2012; Sciscio *et al.* 2017; Becerra *et al.* 2022) and ceratopsians (He *et al.* 2018; Hu *et al.* 2022). Histological methods have recently been used to look at in-situ tooth replacement in the early-diverging ornithopod/thescelosaurid *Changchunsaurus* (Chen *et al.* 2018) and several hadrosaurs (LeBlanc *et al.* 2016; Bramble *et al.* 2017). Results from Chen *et al.* (2018) give us an important insight into what is likely the ancestral condition for tooth replacement in Ornithopoda, however a broader comparative framework is required to understand how complex dentitions evolved in the clade.

In contrast to the aforementioned dentition studies, CT data has been widely used to investigate the palaeoneurology of ornithopod dinosaurs (e.g. Evans *et al.* 2009; Farke *et al.* 2013; Lauters *et al.* 2013; Lautenschlager & Hübner 2013; Thomas 2015; Becerra *et al.* 2018; Knoll *et al.* 2021). The morphology of the endocranium is

generally considered to be closely associated with the morphology of the soft tissues held within (Fabbri *et al.* 2017; Watanabe *et al.* 2019). This association has enabled palaeontologists to examine the endocranial anatomy of fossil taxa for over a century, initially by observing natural or artificial endocasts (often obtained using highly destructive methods), and more recently by studying digital endocasts reconstructed from CT data (Witmer *et al.* 2008). The morphology of digitally segmented endocranial features of interest (e.g. the brain cavity, endosseous labyrinth, cranial nerve canals) have shed light on the sensory capabilities and life habits of numerous dinosaur taxa (e.g. Franzosa & Rowe 2005; Witmer *et al.* 2008; Witmer & Ridgely 2008; Evans *et al.* 2009; Miyashita *et al.* 2011; Knoll *et al.* 2012; Lautenschlager *et al.* 2012; Farke *et al.* 2013; Lauters *et al.* 2013; Lautenschlager & Hübner 2013; Lautenschlager *et al.* 2014; Thomas 2015; Becerra *et al.* 2018; McKeown *et al.* 2020; Paulina-Carabajal *et al.* 2020; Ballell *et al.* 2021; Müller *et al.* 2021; Button & Zanno 2023). While hadrosaurs and iguanodontians are well-sampled in these analyses (e.g. Evans *et al.* 2009; Farke *et al.* 2013; Lauters *et al.* 2013; Lautenschlager & Hübner 2013; Lautenschlager *et al.* 2014; Thomas 2015; Becerra *et al.* 2018; Knoll *et al.* 2021), early-diverging ornithopods have been largely neglected (e.g. Button & Zanno 2023), impeding our understanding of how these taxa lived and the evolution of the clade.

Here I use micro-computed tomographic (μ CT) methods to describe the endocranial anatomy, inner ear anatomy, tooth replacement cycle and dentary neurovasculature of a new genus of ornithopod dinosaur from the Late Cretaceous of Antarctica. To date, several ornithopod fossils have been recovered from the Antarctic continent (e.g. Case *et al.* 2000; Coria *et al.* 2013; Rozadilla *et al.* 2016), but so far none have included cranial material, apart from an isolated hadrosaur tooth (Case *et al.* 2000).

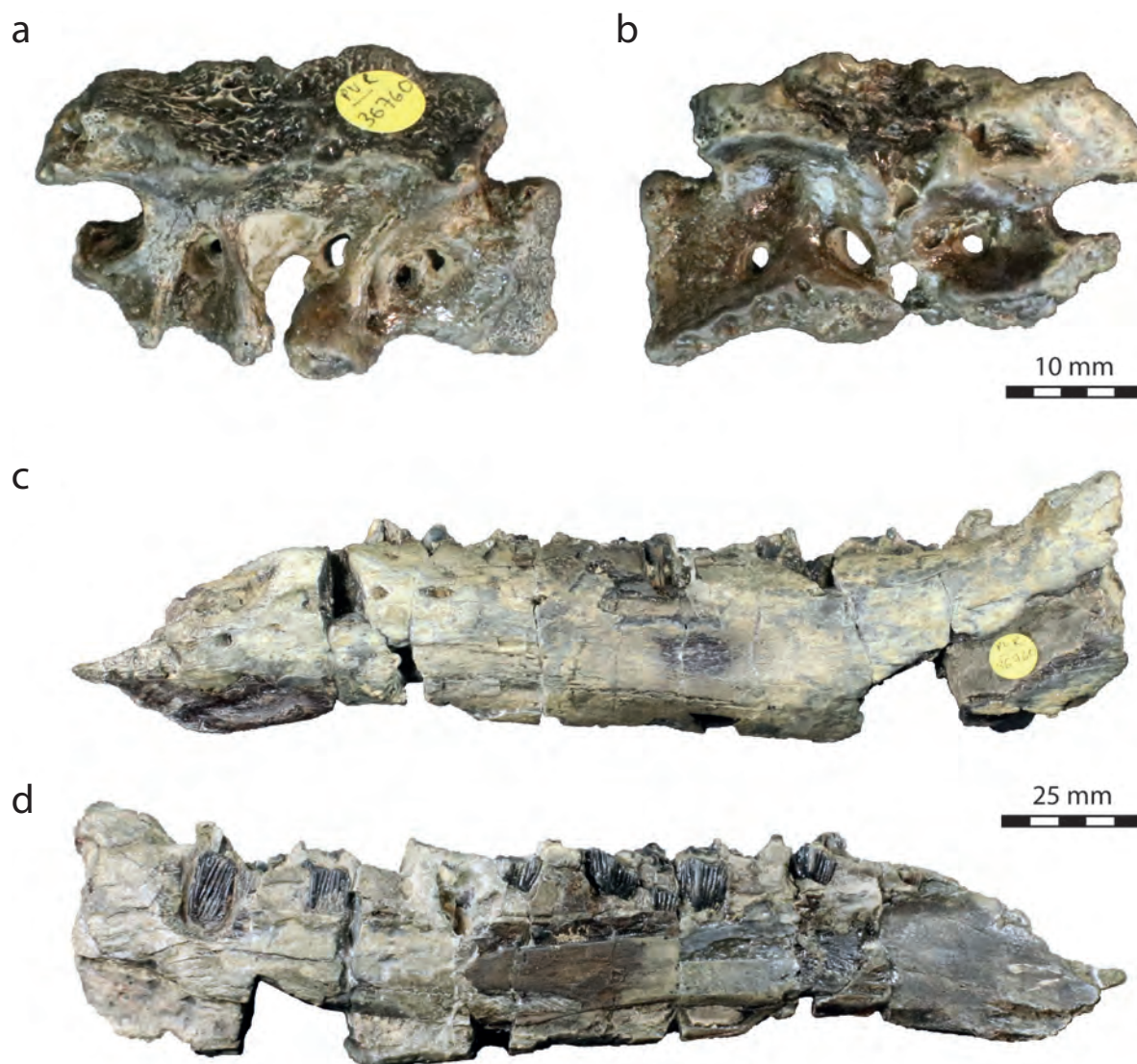


Figure 5.1. Specimens of NHMUK PV R 36760 analysed in this study: left partial braincase, **a—b**; and left mandible, **c—d**. Specimens shown in lateral (a, c), and medial view (b, d).

5.2. Methods

5.2.1. Specimen

NHMUK PV R 36760 is a partial skeleton recovered from the Cape Lamb Member of

the Lopez de Bertodano Formation (Campanian–Maastrichtian) on Vega Island, Antarctica. This material was discovered during a British Antarctic Survey expedition in 1989 (Hooker *et al.* 1991) and later accessioned by the Natural History Museum (London, NHMUK). While much of the partial skeleton is well preserved, several bones had been shattered due to freeze thaw following prolonged exposure on the cold polar surface. All of the material is considered to represent a single individual.

The left wall of the partial braincase (Figure 5.1a–b) and the left dentary (Figure 5.1c–d) of NHMUK PV R 36760 were μ CT scanned. The partial braincase consists of the left prootic-opisthotic complex. All of the functional tooth crowns along the left dentary investigated in this study were lost due to this frost action, mostly leaving just the roots. The dentary itself has also been heavily fractured, revealing several unerupted replacement teeth along its lingual surface. The dentary was fragmented into several portions, but was restored to its original length prior to this study at NHMUK.

5.2.2. Scanning

NHMUK PV R 36760 was μ CT scanned using a Nikon Metrology XT H 225 ST scanner at the Natural History Museum, London (NHMUK). Scanning parameters are outlined in A5.1. The braincase dataset consisted of 3723 coronal slices (1460 x 1737 x 2850 pixels, voxel size 0.02 mm). The dentary dataset consisted of 5205 coronal slices (1100 x 1429 x 2538 pixels, voxel size 0.035 mm).

5.2.3. Digital reconstruction

The μ CT data were imported in SPIERSedit (3.1.0, <https://spiers-software.org>). Areas of interest were manually segmented using the Masks and Curves tools following Bal-

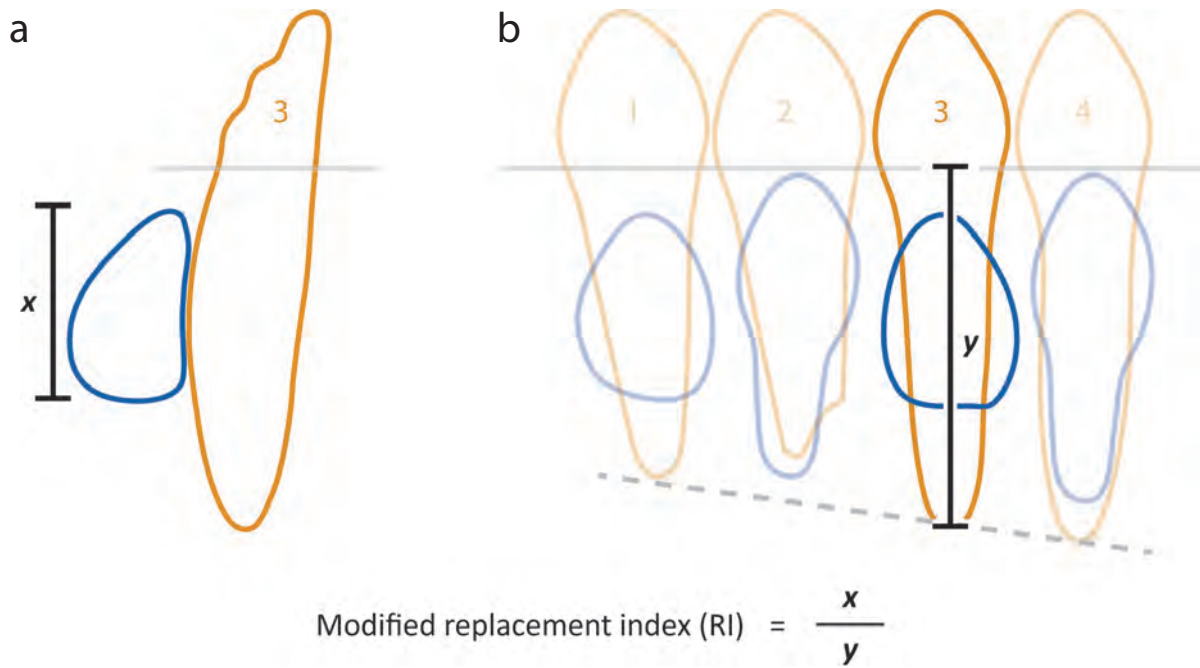


Figure 5.2. Schematic showing how the modified replacement index (RI) of a given replacement tooth was calculated in this study, using: **a**, the sub-oral height of the replacement tooth (= x); and, **b**, the estimated maximum root length (dashed line) of the functional tooth it is replacing (= y). Numbers indicate the hypothetical tooth positions. Views: rostral (a); labial (b). Key: functional tooth (yellow); replacement tooth (blue).

anoff *et al.* (2016) and Lautenschlager (2017).

5.2.4. Tooth Replacement

Most non-mammalian gnathostomes are polyphyodont, meaning that they replace their teeth continuously throughout life (Whitlock & Richman 2013). In diapsid reptiles, tooth replacement often occurs in regular alternating sequences along the jaw, in repeating patterns termed Zahnreihen (Woerdeman 1921; Edmund 1962; Whitlock

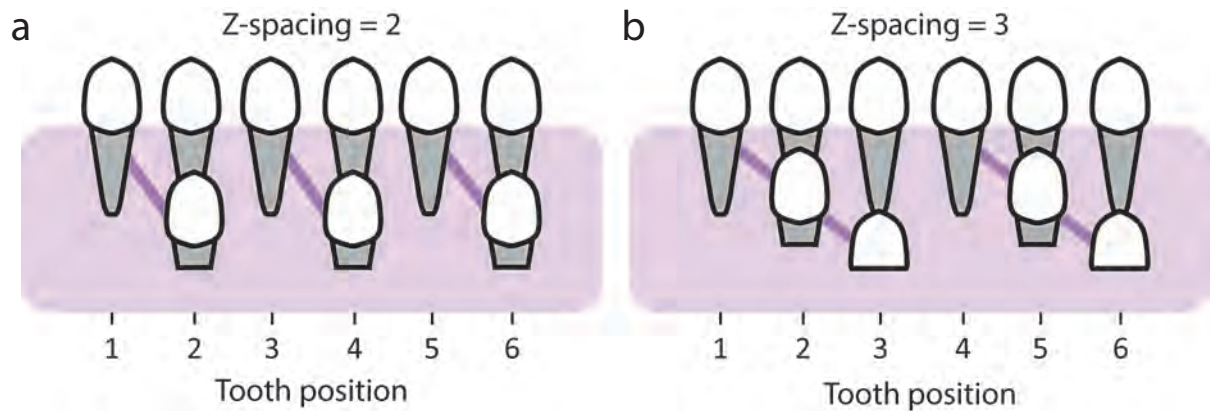


Figure 5.3. Diagram demonstrating different Zahnreihen patterns (purple lines) along hypothetical jaws: **a**, Z-spacing = 2; **b**, Z-spacing = 3.

and Richman 2013). This staggered growth ensures that some new replacement teeth are always close to being fully developed, should a number of neighbouring functional teeth become lost at once.

In this study, two methods were used to quantify the relative developmental stage of reconstructed teeth. The first is a categoric approach, which assigns each tooth family (defined as a functional tooth and all of its predecessors and successors) to one of several predetermined developmental stages (Hanai & Tsuihiji 2019). These values were then plotted for each tooth family. These developmental stages were determined based on observations from the digital segmentation of the dentary (NHMUK PV R 36760), and are outlined in the Results section (see 5.3.2.1).

The second method modifies the replacement index (RI) developed by Fastnacht (2008) and subsequently used by He *et al.* (2018). Unlike the categoric method, this approach plots multiple teeth at each tooth family separately, rather than one plot per tooth family. An RI value of 1.0 is given to a fully erupted tooth without an associat-

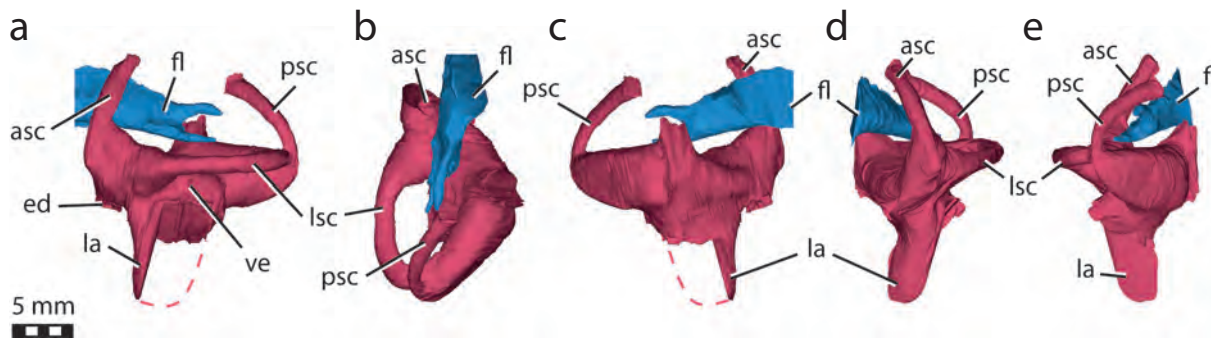


Figure 5.4. Partial left endosseous labyrinth (pink) and brain cavity (blue) process of NHMUK PV R 36760. Endocranial reconstructions are shown in (a) lateral, (b) dorsal, (c) medial, (d) anterior and (e) posterior views. **Abbreviations:** **asc**, anterior semi-circular canal; **ed**, endolymphatic duct canal; **fl**, floccular fossa; **la**, lagena; **lsc**, lateral semi-circular canal; **psc**, posterior semi-circular canal; **ve**, vestibule.

ed replacement tooth. If a replacement tooth is present, its RI equals its sub-oral length divided by the estimated maximum root length of the functional tooth it is replacing (Figure 5.2). This differs from Fastnacht (2008), in which replacement tooth RI was measured as the height of the replacement tooth relative to the height of the functional tooth. However, as the crowns of all of the functional teeth in NHMUK PV R 36760 have been lost due to frost shattering, this method had to be modified. If a replacement tooth is present in a tooth family, the RI of the functional tooth being replaced would be 1.0 more than the replacement tooth RI. Should a remnant of old functional tooth also be present in a tooth family, the RI of that tooth would be 1.0 more than the current functional tooth RI. Therefore, RI values: <1 = replacement teeth; ≥ 1 but <2 = functional tooth; ≥ 2 = remnant of previous generation functional tooth.

By quantifying and plotting the replacement stages of teeth along the dentary,

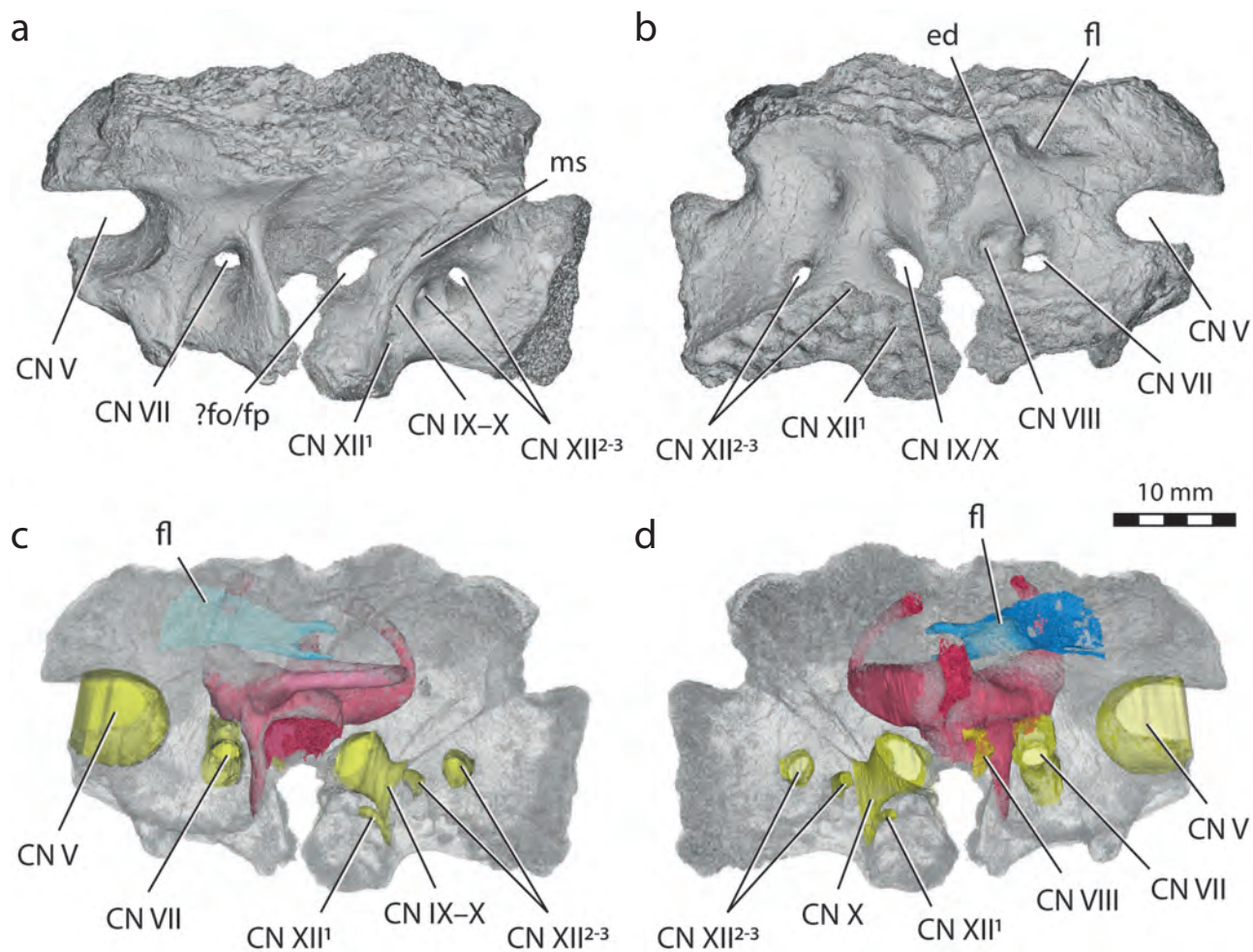


Figure 5.5. Neuroanatomy of NHMUK PV R 36760. Surface model of partial braincase derived from CT scan data: with labelled foramen (**a**, **b**); with digital reconstructions of the endocranial neuroanatomy (**c**, **d**). Partial braincase shown in lateral (**a**, **c**) and medial view (**b**, **d**). **Abbreviations:** **CN V**, trigeminal nerve canal; **CN VII**, facial nerve canal; **CN VIII**, vestibulocochlear nerve canal; **CN IX**, glossopharyngeal nerve canal; **CN X**, vagus nerve canal; **CN XII¹⁻³**, hypoglossal nerve canals 1–3; **ed**, endolymphatic duct; **fl**, flocculus fossa; **?fo/fp**, ?fenestra ovalis/fenestra pseudorotunda; **ms**, metotic strut. Key: pink, endosseous labyrinth; light blue, brain cavity; yellow, cranial nerve canal.

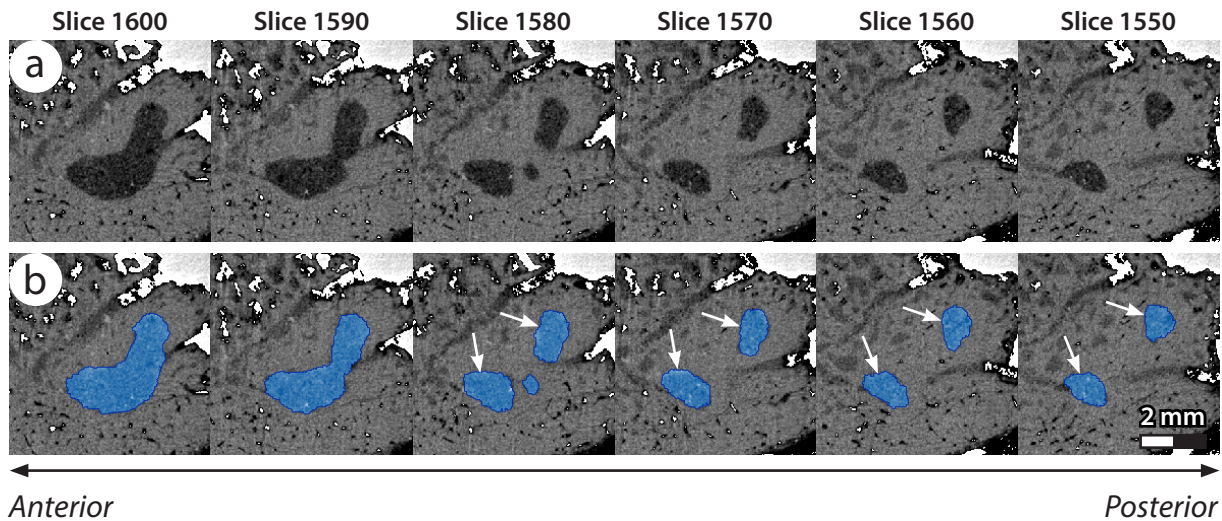


Figure 5.6. Segmentation of the floccular fossa between slices 1600–1550, showing the bizarre forked morphology of the posterior end: **a**, raw CT data of the braincase (NHMUK PV R 36760), zoomed in on the area where the floccular fossa can be observed; **b**, area interpreted and segmented as the floccular fossa in the software 'SPI-ERSedit' (blue). White arrows show the two 'prongs' of the forked feature.

using both the categoric and RI methods, the Zahnreihen could be inferred. A Zahnreihe can be defined as a group of neighbouring teeth that are at different developmental stages (Figure 5.3) (Fastnacht 2008; Whitlock and Richman 2013). The anterior-most tooth in a Zahnreihe is the most developed, while the posterior-most is the least developed. By measuring the distance between adjacent Zahnreihen in NHMUK PV R 36760, the Z-spacing of this new ornithopod can be determined (DeMar 1972).

5.3. Results

5.3.1. Endocranial reconstructions

5.3.1.1. Brain cavity. Due to the partial preservation of the braincase, much of the brain cavity of NHMUK PV R 36760 could not be reconstructed, except for the left floccular lobe of the cerebellum (Figure 5.4, 5.5). The flocculus in NHMUK PV R 36760 projects posterolaterally through the space between the anterior semicircular canal (ASC) of the endosseous labyrinth to form a large mediolaterally compressed lobe. Rostrally, this lobe is sub-oval in cross-section but it becomes more triangular posteriorly, before forking into distinct dorsal and ventral processes, that end in-line with the crus communis. A forked floccular lobe has not been reported in previous studies, and it is possible that either one of these processes is a preservational artefact or taphonomic feature (e.g. an internal crack). However, examination of the raw CT data (Figure 5.6.) does appear to suggest that this forked morphology is likely a unique feature of the new taxon. The presence of a floccular lobe (or associated recess) distinct from the cerebellum has been found in taxa from all of the major ornithischian clades, however most of these lobes are observed as small convex impressions that do not extend much, if at all, through the anterior semi-circular canal, unlike the condition in NHMUK PV R36760 (Galton 1989; Galton 2012; Lautenschlager & Hubner 2013; Leahey *et al.* 2015; Miyashita *et al.* 2011; Thomas 2015; Stocker *et al.* 2016; Paulina-Carabajal *et al.* 2018; Becerra *et al.* 2022; Dunfee 2022; Yang *et al.* 2023).

In contrast, an elongate floccular lobe that extends substantially through the space between the anterior semi-circular canal (ASC) is widespread among non-ornithischian avemetatarsalians, having been digitally reconstructed in several pterosaurs (Witmer *et al.* 2003; Codorníu *et al.* 2016), non-dinosaurian dinosauriforms (Piechowski *et al.* 2019; Ezcurra *et al.* 2020), herrerasaurids (Stocker *et al.* 2016; Pacheco *et al.* 2019), non-avian theropods (Franzosa & Rowe 2005; Lautenschlager *et al.*

2012; Balanoff *et al.* 2014; Paulina-Carabajal & Succar 2015; Paulina-Carabajal & Currie 2017; Paulina-Carabajal & Filippi 2018; King *et al.* 2020; Schade *et al.* 2020) and early sauropodomorphs (Bronzati *et al.* 2017; Ballell *et al.* 2021; Müller *et al.* 2021).

5.3.1.2. Endosseous labyrinth. The left endosseous labyrinth of NHMUK PV R 36760 could only be partially reconstructed due to the absence of other constraining braincase elements (Figure 5.3, 5.4). The lateral semicircular canal (LSC) was the only semicircular canal to be reconstructed completely. The posterior semicircular canal (PSC) is largely complete, whereas the anterior semicircular canal (ASC) is approximately 50% complete, and both the PSC and ASC lack their dorsolateral regions. The visible section of the PSC extends from the posterior ampullae at an acute angle ($\sim 25^\circ$), giving this section of the labyrinth a triangular outline in lateral view. By contrast, the ASC extends from the anterior ampullae at an obtuse angle ($\sim 110^\circ$), suggesting that it produced a broader, oval outline to the anterior part of the labyrinth. The ventral region of the crus communis is visible, allowing for the posterior and anterior margins of the ASC and PSC, respectively, to be estimated. The lagena was poorly constrained and only the anterior margin could be reconstructed here. The visible region suggests that the lagena extends at least 7 mm ventromedially from the vestibule. The endolymphatic duct extends ventromedially from the anterior margin of the vestibule into the brain cavity, just dorsally to the facial nerve canal (CN VII). Anterior to the crista interfenestralis (Figure 5.5, cf) there is a large auditory recess, which in life would likely have held the fenestra ovalis (= fenestra vestibuli) or fenestra pseudorotunda (Figure 5.5, fo/fp). This feature was poorly constrained and could not be digitally reconstructed.

5.3.1.3. Cranial nerves. Several cranial nerves are discernible from the foramina exposed on the lateral surface of the partial braincase, but microcomputed

topographical analyses provide greater understanding of their 3D morphology and positioning relative to each other (Figure 5.5). The trigeminal nerve canal (CN V) is positioned at the anterior margin of the specimen, but its lateral extent is incomplete due to taphonomic damage. CN V is considerably larger than the other cranial nerve canals, with the foramen expanding into a funnel-shaped opening as it extends laterally from the endocranial cavity, which would have housed the trigeminal ganglion and the mandibular and maxillary branches of this nerve (CN V₂₊₃). The ophthalmic branch of this nerve (CN V₁) is not observed. The facial nerve canal (CN VII) exits the brain cavity just ventral to the endolymphatic duct. CN VII is relatively small and tubular, but as it continues laterally, its diameter slightly expands. The vestibulocochlear nerve canal (CN VIII) exits the brain cavity and immediately splits into two distinct branches that enter different parts of the endosseous labyrinth: the vestibular nerve, which extends posteriorly into the medial margin of the vestibule; and the cochlear nerve, which extends ventrally to enter the dorsal region of the lagena. The glossopharyngeal nerve (CN IX) and the vagus nerve (CN X) exit the brain cavity via a large, shared foramen, the metotic foramen. It is likely that the jugular vein and accessory nerve (CN XI) also exited the brain cavity through the metotic foramen along with CN IX and CN X, although the morphologies of neither could be discerned here. CN XI in particular, is often not distinct in archosaurs (Gower & Weber 1998; Sampson & Witmer 2007). CN IX–X (and other accessory nerves/veins associated with the metotic foramen) leave the lateral side of the braincase via a large posterolaterally-directed foramen, just posterior to the metotic strut. This metotic strut separates the CN IX–X opening from the auditory recess described in section 5.1.2. The hypoglossal nerve canal (CN XII) leaves the brain cavity as three separate canals (CN XII_{1–3}, from anterior to posterior). The

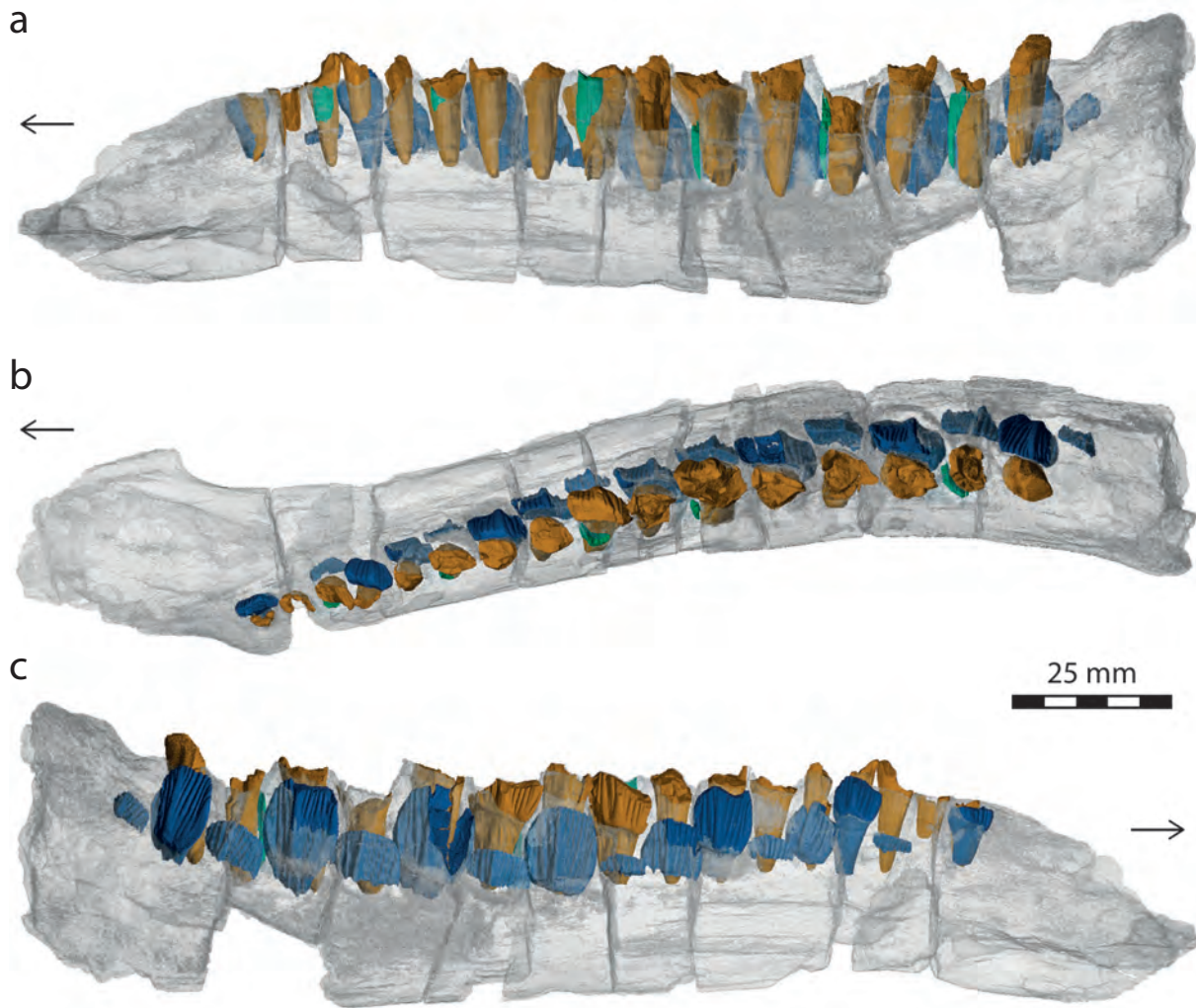


Figure 5.7. Digital reconstructions of mandibular dentition in NHMUK PV R 36760. Mandible shown in lateral (a); dorsal (b); and medial (c) view. Arrow indicates the mesial direction. Key: yellow, functional tooth; blue, replacement tooth; green, resorbed old tooth.

anterior-most hypoglossal nerve canal (CN XII1) is the smallest in diameter, but longest in length, and exits the braincase just ventral to the metotic foramen. CN XII1 is also the most lateroventrally-directed of the three hypoglossal nerve canals. CN XII2 leaves the braincase posterior to CN X. CN XII3 has a significantly larger diameter than

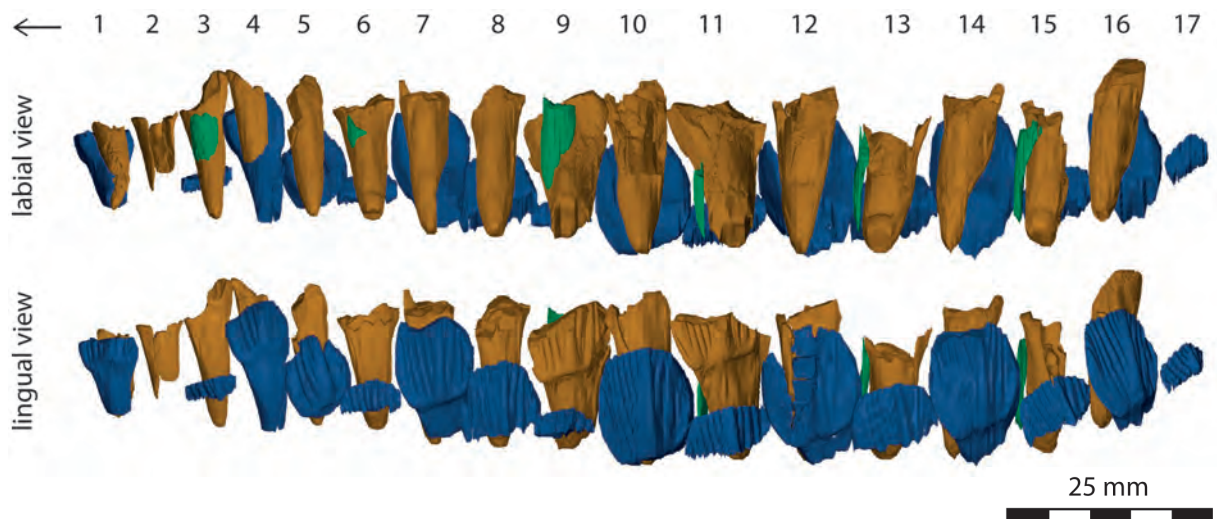


Figure 5.8. Digitally reconstructed and extracted mandibular dentition in NHMUK PV R 36760. Lingual view reversed. Numbers indicate the position of the tooth family along the tooth row. Arrow indicates the mesial direction. Key: yellow, functional tooth; blue, replacement tooth; green, resorbed old tooth.

both CN XII1&2, but also the shortest length. CN XII3 exits the braincase dorsoposterior to CN XII2. Within Ornithischia, three hypoglossal nerve canals have been observed in ceratopsians (Hopson 1979; Forster 1996; Witmer & Ridgely 2008a), thyreophorans (Averianov 2002; Miyashita *et al.* 2011; Paulina-Carabajal *et al.* 2018), and the ornithomimid *Gryphosaurus* (Hopson 1979; Prieto-Marquez 2010).

5.3.2. Segmentation of the dentary

5.3.2.1. Dentition. The dentary of NHMUK PV R 36760 contains 16 functional teeth, 16 developing replacement teeth and six remnants from the previous generation of functional teeth, across 17 tooth families (Figure 5.7, 5.8). These tooth families show teeth at varying stages of replacement along the dentary. Each functional tooth (FT)

has an associated replacement tooth (RT) developing lingually to it, except for FT 2, where CT scans reveal an empty tooth crypt where a replacement tooth would be expected. The lack of a functional tooth or corresponding alveolus lingual to RT 17, the posterior-most tooth in the dentary, suggests that RT 17 represents a newly developing tooth family. This shows that the jaw of this animal was still growing at time of death.

Extensive resorption of the functional teeth is found in only FT 1 and FT 4, while FT 5, 7, 10, 12, 14 and 16 show signs of minimal resorption (Figure 5.7, 5.8). Remnants from the previous generation of functional teeth were found labial to FT 3, 6, 9, 11, 13 and 15 (Figure 5.7, 5.8). These remnants are observed as thin layers of dentine, with most being crescent-shaped in horizontal cross-section.

The relationships between functional teeth, replacement teeth, and, if applicable, the previous generation of functional teeth, were examined at each tooth family. Throughout the dentary, various stages of tooth development were represented, allowing a complete replacement cycle to be reconstructed.

The cycle of tooth replacement starts with the development of a new replacement tooth germ lingual to the functional tooth it will eventually replace (e.g. Figure 5.8; tooth family [TF] 3). This replacement tooth germ consists of just the very apex of the crown, but already, the primary ridge and denticles are distinguishable. At this early stage, absorption by the current functional tooth of its predecessor is still ongoing. This is evident from the fragments of partially absorbed previous generation functional teeth that are found labially to six of the 16 functional teeth. The crown of the replacement tooth continues to develop, while moving closer towards the functional tooth and up towards the surface of the dentary (e.g. Figure 5.8; TF 5). By this stage, all remnants of the previous generation of functional teeth have been fully resorbed. Next, the root

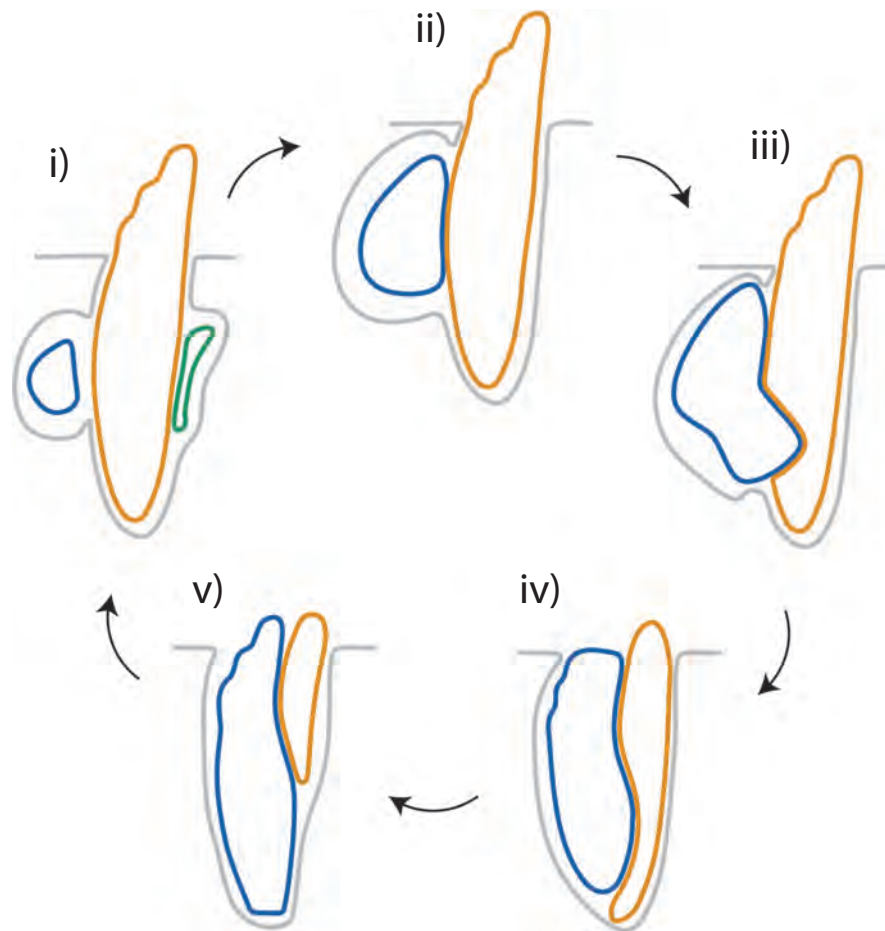


Figure 5.9. Schematic transverse sections showing the five tooth replacement stages used in this study: **i)** Replacement tooth small and lying lingually to, but separated from, the functional tooth. Old resorbed tooth remains still visible labially to the functional tooth; **ii)** Replacement tooth close to lingual surface of functional tooth. No evidence of reabsorption of the functional tooth. Old tooth completely resorbed; **iii)** Reabsorption of the functional tooth by the replacement tooth present, but restricted to the lower portion of the functional tooth; **iv)** Extensive reabsorption present throughout the full length of the functional tooth, but the functional tooth still remains longer than the replacement tooth; **v)** Functional tooth significantly shorter than the replacement tooth reabsorbing it. Key: functional tooth (yellow); replacement tooth (blue); resorbed old tooth (green).

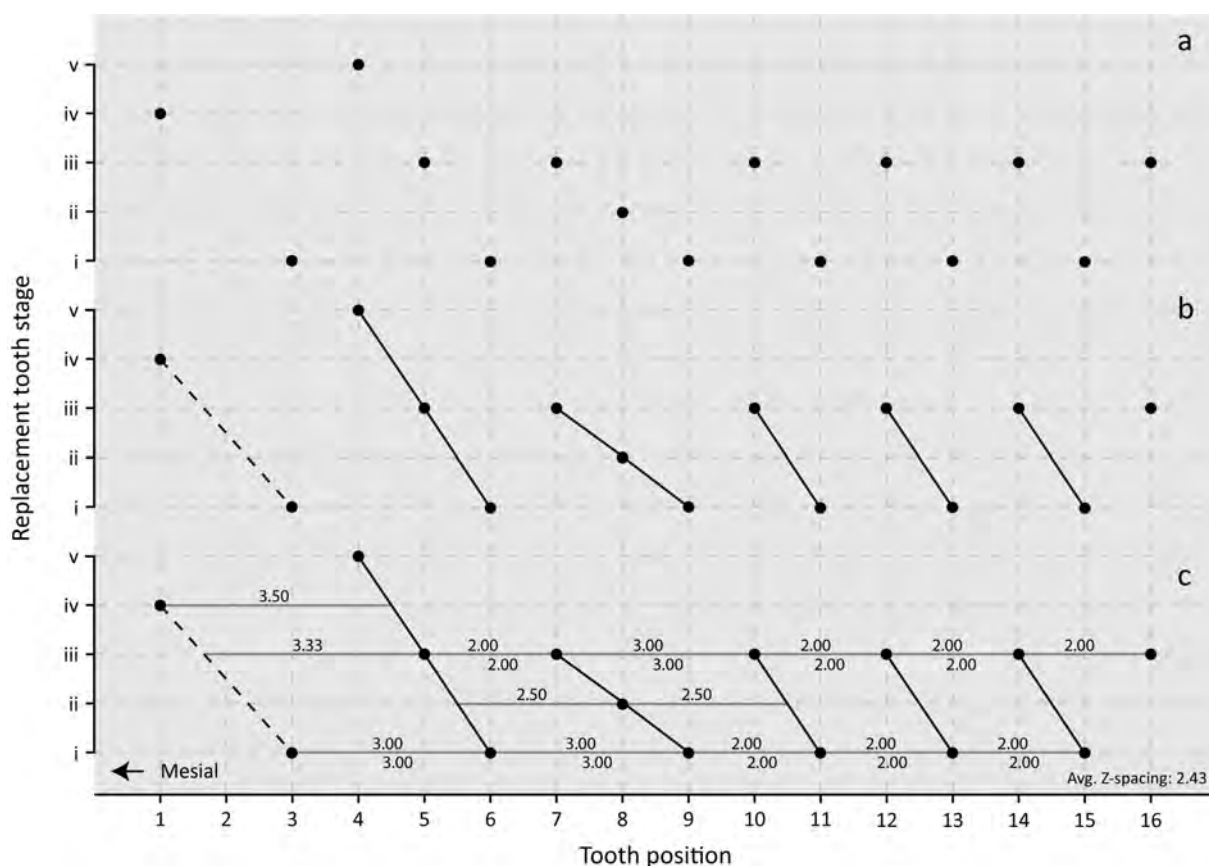


Figure 5.10. Quantification of tooth replacement patterns among reconstructed teeth in the left mandible of NHMUK PV R 36760: **a**, Plotted replacement stages (black plots); **b**, Zahnreihen patterns (black lines); **c**, Z-spacing (grey horizontal lines). Dashed lines indicate extrapolated Zahnreihen patterns over missing teeth.

of the replacement tooth begins to grow, cutting diagonally into the ventral region of the functional tooth root (e.g. Figure 5.8; TF 10). Later, the replacement tooth begins to straighten and the full length of the functional tooth undergoes significant resorption (e.g. Figure 5.8; TF 7). Due to frost action of the oral margin of the dentary in NHMUK PV R 36760, it is difficult to determine at which point the replacement tooth erupted from the surface, but it is likely the replacement tooth would have begun to

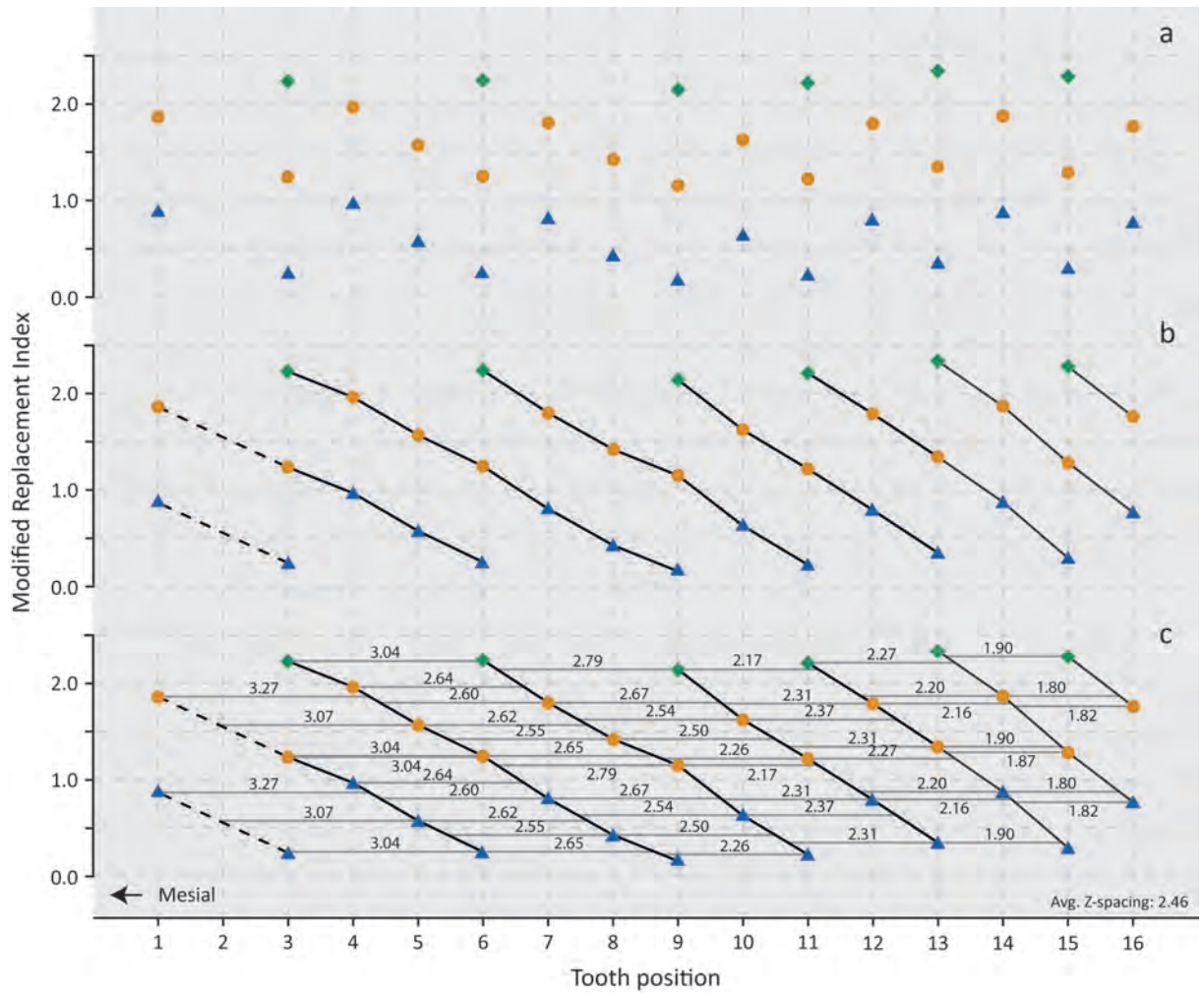


Figure 5.11. Quantification of tooth replacement patterns among reconstructed teeth in the left mandible of NHMUK PV R 36760: **a**, Plotted modified Replacement Index; **b**, Zahnreihen patterns (black lines); **c**, Z-spacing (grey horizontal lines). Plot key: green diamond, previous functional tooth; yellow circle, functional tooth; blue triangle, replacement tooth. Dashed lines indicate extrapolated Zahnreihen patterns over missing teeth.

erupt around this stage. At this point, the crown of the functional tooth would likely detach from the root, and the remnants of this root would continue to be resorbed.

The replacement cycle observed in NHMUK PV R 36760 can be separated into five distinct developmental stages (Figure 5.9), which were utilised in our categoric approach to quantify the relative developmental stages of teeth throughout the dentary, following methods outlined in section 5.2.4.

The categoric (Figure 5.10) and modified replacement index (Figure 5.11) methods of quantifying tooth development find that the left dentary of NHMUK PV R 36760 had average Z-values of 2.43 and 2.46, respectively. Both approaches also find that the anterior portion of the dentary (tooth families 1–9) has higher Z-values (Z-values = ~ 3.0), compared to the posterior portion of the dentary (tooth families 10–16: Z-values = ~ 2.0). Plots also demonstrate front-to-back replacement, as observed in other ornithischians (He *et al.* 2018).

5.3.2.2 Dentary cavities. Digital reconstructions of void spaces within NHMUK PV R 36760 show the internal dentary morphology of this ornithopod. Computed tomographical analyses reveal a single internal cavity (Figure 5.12), with two regions that separate and become distinct from each other anterior to tooth family 16: the upper region, a neurovascular canal stretching the entire length of the specimen; and the lower region, a cavity that is restricted to the posterior of the mandible, interpreted to have held Meckel's cartilage. The posterior portion of the neurovascular canal is simple, running parallel and lingual to the roots of the functional teeth. The anterior portion of the neurovascular canal becomes deflected ventromedially, and substantially more complex, with numerous bulbous branches expanding and diverging antero-dorsally towards the predentary-dentary junction. Several elongate simple branches also expand medially from the anterior region of the primary neurovascular canal. In this anterior region of the mandible, the neurovascular canal instead sits ventral to

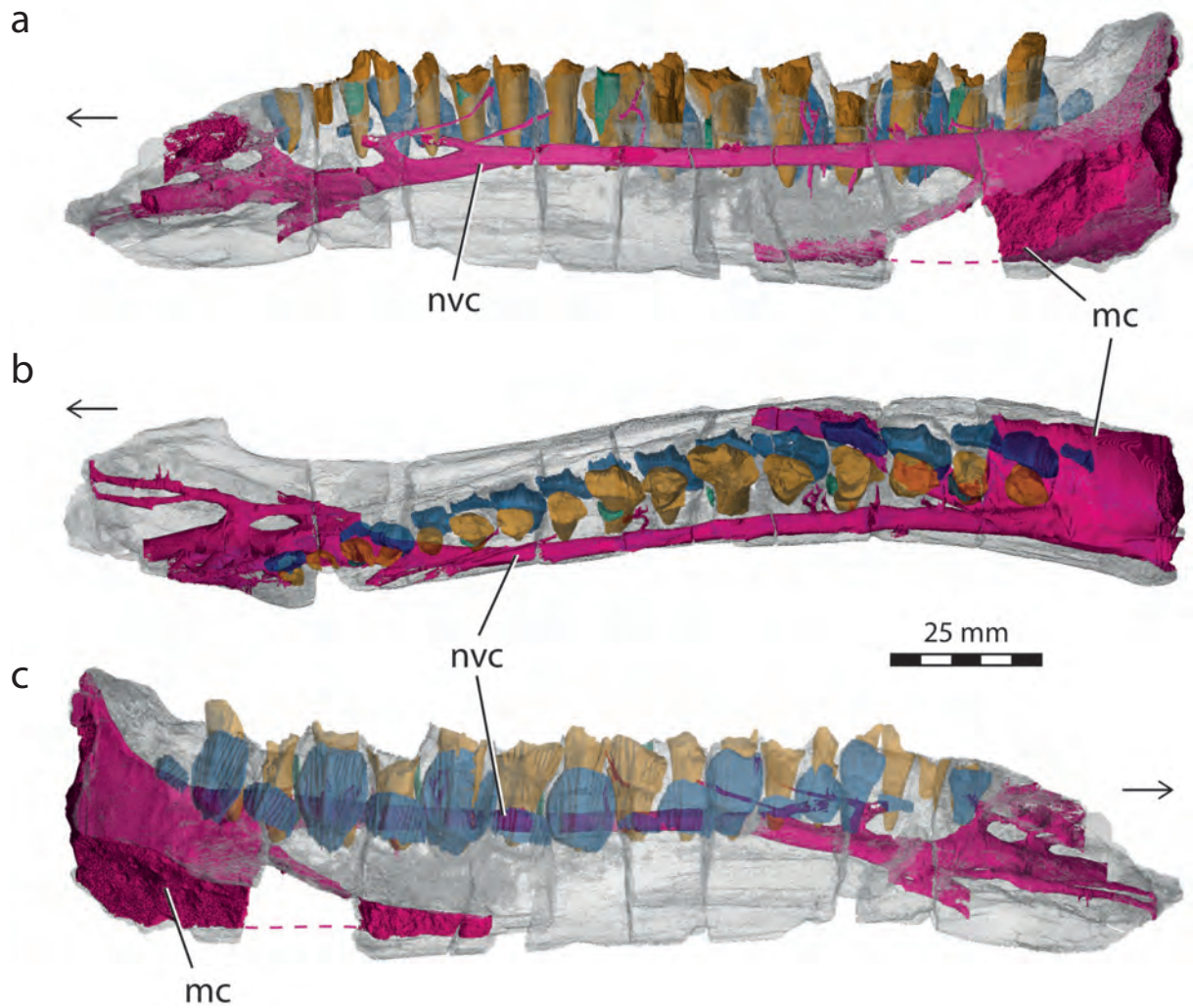


Figure 5.12. Digital reconstructions of endomandibular cavities (pink) in NHMUK PV R 36760. Mandible shown in lateral (a); dorsal (b); and medial (c) view. **Abbreviations:** **mc**, Meckel's cartilage; **nvc**, neurovascular canal. Arrow indicates the mesial direction. Dentition shown at opacity: 100% (a); 75% (b); and 50% (c).

the dentary teeth. Along the full length of the neurovascular canal, numerous small branches (many of which could not be reconstructed or only partially reconstructed due to their small size) radiate, predominately from points between teeth, towards the surface of the alveoli. Many of these branches expand dorsoventrally from the neuro-

vascular canal, but several towards the anterior portion of the mandible extend posteriorly.

5.4. Discussion

5.4.1. Sensory abilities of NHMUK PV R 36760

In extant vertebrates, the floccular lobe of the cerebellum interprets both visual inputs from the eye and vestibular signals from the endosseous labyrinth to co-ordinate two important reflexes: the vestibulo-collic reflex (VCR), which acts to stabilise the head; and the vestibulo-ocular reflex (VOR), which acts to stabilise the image on the retina (Witmer *et al.* 2003; Voogd & Wylie 2004; Walsh *et al.* 2013). NHMUK PV R 36760 exhibits a well-developed floccular lobe, that extends substantially through the space between the anterior semi-circular canal. It is important to note that the size of the floccular lobe reconstructed here is reflective of the size of the floccular fossa (fossa subarcuata), and not of the true size of the floccular lobe, as in life this fossa may also have housed other soft tissues such as blood vessels (Walsh *et al.* 2013; Ferreira-Cardoso *et al.* 2017). However, the volume of the floccular fossa is likely still correlated with the volume of the floccular lobe, so can, albeit tentatively, be used to infer behaviours and other specialisations (Witmer *et al.* 2003; Walsh *et al.* 2013). The well-developed floccular lobe described here suggests that NHMUK PV R 36760 was capable of rapid eye, head, and neck movements and advanced gaze stabilisation. These specialisations have been linked to behaviours such as predation and flying in other taxa (e.g. Witmer *et al.* 2003; Bronzati *et al.* 2017; King *et al.* 2020; Müller *et al.* 2020), but in the case of NHMUK PV R 36760, these specialisations may be associated with cursorial ability,

as well as other behaviours, such as courtship and territoriality (Lautenschlager *et al.* 2012; Ballel *et al.* 2021).

Within Ornithopoda, a floccular lobe that is distinct from the rest of the endocranial cavity has been observed in *Hypsilophodon* (Galton 1989; 2012), *Dysalotosaurus* (Lautenschlager & Hubner 2013), *Dryosaurus* (Galton 1989; Dunfee 2022) and *Tenontosaurus* (Thomas 2015). Of these taxa, *Dryosaurus*, *Hypsilophodon* and *Tenontosaurus* have a well-developed floccular lobe that extends posteriorly through the opening formed by anterior semi-circular canal, as described in NHMUK PV R 36760 (Galton 1989; Galton 2012; Thomas 2015; Dunfee 2022). This is in contrast to more derived ornithopods, where the floccular lobe is indistinguishable from the rest of the brain endocast (e.g. hadrosaurs: Chavèz *et al.* 2006; Evans *et al.* 2009; Lauters *et al.* 2012; Farke *et al.* 2013; Cruzado-Caballero *et al.* 2015; Becerra *et al.* 2018; non-hadrosaurid iguanodontian: Knoll *et al.* 2021). In addition to the aforementioned taxa, a floccular recess is observed in the braincases of the early-diverging ornithopods *Zephyrosaurus* (Sues 1980), *Orodromeus* (Scheetz 1999), *Thescelosaurus assiniboensis* (Brown *et al.* 2011), *Thescelosaurus neglectus* (Boyd 2014), *Oryctodromeus* (Krumenacker 2017), *Convolosaurus* (Andrzejewski *et al.* 2019) and *Parksosaurus* (Sues *et al.* 2023), showing that these taxa also had distinct floccular lobes. Many of these taxa share a similar bauplan, being bipedal, small to medium-bodied and relatively morphologically conservative. Additionally, hind limb anatomy and proportions suggest that many were cursorial (Carrano 1999; Norman *et al.* 2004). There is currently little consensus on the phylogenetic placement of these taxa, with multiple independent phylogenetic studies recovering them either outside or inside Cerapoda (Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016, 2021; Han *et al.* 2018). Discussion in Chap-

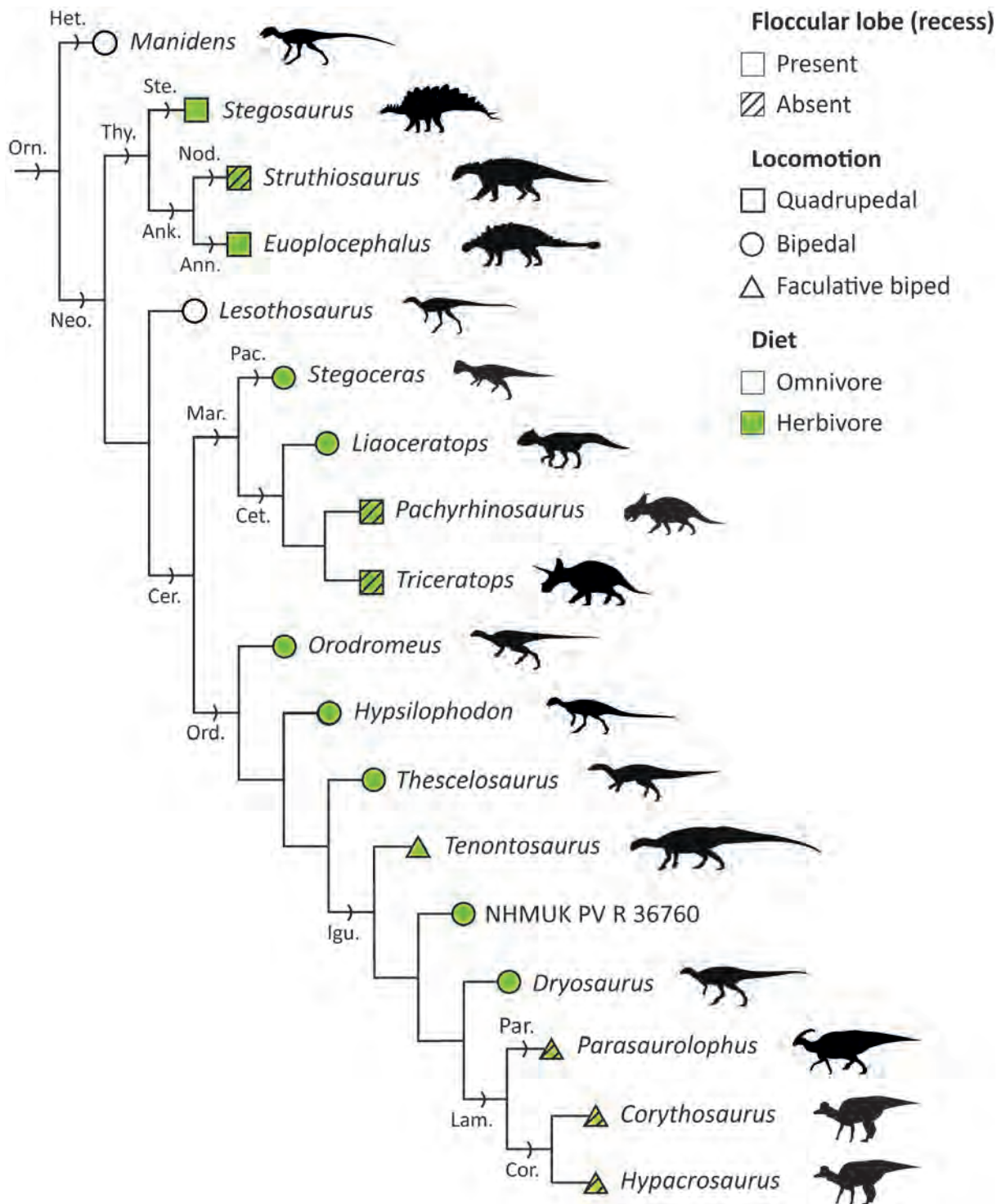


Figure 5.13. Simplified cladogram demonstrating the presence of a distinct floccular lobe (or associated recess) throughout Ornithischia. Relationships based on phylogenetic analyses from Cruzado-Caballero *et al.* (2013), Han *et al.* (2018) and Maidment *et al.* (in prep.). Taxa (top-down): *Manidens* (Becerra *et al.* 2022); *Stegosaurus*

(Galton 2001); *Struthiosaurus* (Schade *et al.* 2022); *Euoplocephalus* (Miyashita *et al.* 2011; Leahey *et al.* 2015); *Lesothosaurus* (Porro *et al.* 2015); *Stegoceras* (Stocker *et al.* 2016); *Liaoceratops* (Yang *et al.* 2023); *Pachyrhinosaurus* (Witmer & Ridgely 2008); *Triceratops* (Sakagami & Kawabe 2020); *Orodromeus* (Scheetz 1999); *Hypsilophodon* (Galton 1989; 2012); *Thescelosaurus* (Boyd 2014); *Tenontosaurus* (Thomas 2015); NHMUK PV R 36760 (this study); *Dryosaurus* (Galton 1989; Dunfee 2022); *Parasaurolophus* (Farke *et al.* 2013); *Corythosaurus* (Evans *et al.* 2009); *Hypacrosaurus* (Evans *et al.* 2009). Key: Floccular lobe/recess: present (blank), absent (striped); mode of locomotion: quadrupedal (square), bipedal (circle), facultative biped (triangle); diet: omnivore (white), herbivore (green). **Abbreviations:** **Ank.**, Ankylosauria; **Ana.**, Ankylosaurini; **Cet.**, Ceratopsia; **Cer.**, Cerapoda; **Cor.**, Corythosaurini; **Het.**, Heterodontosauridae; **Igu.**, Iguanodontia; **Lam.**, Lambeosaurinae; **Mar.**, Marginocephalia; **Neo.**, Neornithischia; **Nod.**, Nodosauridae; **Ord.**, Ornithopoda; **Orn.**, Ornithischia; **Pac.**, Pachycephalosauria; **Par.**, Parasaurolophini; **Ste.**, Stegosauria; **Thy.**, Thyreophora. Silhouettes from <http://phylopic.org>: C. Brown, P. Buchholz, M. Dempsey, C. Dylke, A. Farke, S. Hartman. (Fig. 5.13, cont.)

ter 2 (Brown *et al.* 2022) favours the placement of these taxa as early-diverging ornithopods, as recovered by Butler *et al.* (2008), Han *et al.* (2018) and Dieudonné *et al.* (2021). In this case, it seems that the presence of a well-developed floccular lobe is the ancestral condition in Ornithopoda, restricted to early-diverging ornithopods and early-diverging iguanodontians (*Dysalotosaurus*, *Dryosaurus*, *Tenontosaurus*), and was not retained in later diverging ornithopods (Figure 5.13). The well-developed floccular

lobe observed in NHMUK PV R 36760 could suggest it is likely to be an early-diverging ornithopod or early-diverging iguanodontian, rather than a derived ornithopod. Preliminary phylogenetic analyses conducted by Maidment *et al.* (in prep.) recover NHMUK PV R 36760 as an early-diverging iguanodontian when run using the Dieudonné *et al.* (2021) character matrix or as part of the non-cerapodan neornithischian clade, Thescelosauridae, when using the Boyd (2015) matrix. The findings of this study are generally congruent with either placement.

Among non-ornithopod ornithischians, distinct floccular lobes (or recesses) have been observed in the heterodontosaurid *Manidens* (Becerra *et al.* 2022), several thyreophorans (Galton 1988; Galton 2001; Miyashita *et al.* 2011; Leahey *et al.* 2015; Paulina-Carabajal *et al.* 2018; see Paulina-Carabajal *et al.* 2016 for discussion on this feature in ankylosaurs), *Lesothosaurus* (Porro *et al.* 2015), the pachycephalosaurid *Stegoceras* (Stocker *et al.* 2016) and the basal ceratopsian *Liaoceratops* (Yang *et al.* 2023). The presence of this trait across all five major ornithischians clades (Figure 5.13) suggests that a well-developed floccular lobe is likely the ancestral condition within Ornithischia, subsequently lost in derived ornithopods, ceratopsians and some thyreophorans (e.g. Chavèz *et al.* 2006; Evans *et al.* 2009; Lauters *et al.* 2012; Farke *et al.* 2013; Cruzado-Caballero *et al.* 2015; Becerra *et al.* 2018; Paulina-Carabajal *et al.* 2018; Sakagami & Kawabe 2020; Knoll *et al.* 2021).

A well-developed floccular lobe is also thought to be the ancestral condition in sauropodomorphs (Serenó *et al.* 2007; Balanoff *et al.* 2010; Knoll *et al.* 2012; Paulina-Carabajal 2012; Bronzati *et al.* 2017; Müller *et al.* 2020; Ballell *et al.* 2021). It has been suggested that this may be related to the shift early in Sauropodomorpha from bipedality to quadrupedality, with quadrupedality being considered to require less so-

phisticated balance control than bipedality (Chatterjee and Zheng 2002; Balanoff *et al.* 2010; Paulina-Carabajal 2012). More recently, this reduction in floccular lobe size has been tentatively linked to the adoption of a herbivorous diet in more derived sauropodomorphs (Bronzati *et al.* 2017; Müller *et al.* 2020).

Ornithischians were primitively bipedal, but within the group, quadrupedality is known to have evolved independently at least three times, in thyreophorans, ceratopsians and hadrosaurs (Maidment *et al.* 2014a; Barrett & Maidment 2017). Within Ornithischia, the presence or absence of a distinct floccular lobe does appear to roughly correlate with locomotion (Figure 5.13). An obvious exception is in thyreophorans, where well-developed floccular lobes have been observed in multiple quadrupedal taxa, including stegosaurs and late-diverging ankylosaurids (e.g. Galton 1988; Galton 2001; Miyashita *et al.* 2011; Leahey *et al.* 2015; Paulina-Carabajal *et al.* 2018). The larger floccular lobe in these quadrupeds are instead thought to be linked to the neurological involvement in VCR/VOR required to use their defensive tail clubs and spikes (Schade *et al.* 2022). It is also possible that this tentative relationship between floccular size and locomotion is more generally related to cursorial ability, considering that advanced gaze stabilisation would be highly beneficial to agile cursors (Ballel *et al.* 2021). While many early-diverging forms from ornithischian clades are widely accepted as cursorial, there is still debate concerning the cursorial ability of many derived ornithischian dinosaurs (Carrano *et al.* 1999; Maidment *et al.* 2012). Carrano *et al.* (1999) stated that no large ornithischians (both bipedal and quadrupedal) displayed the morphological features of a cursorial mode of locomotion. However, Maidment *et al.* (2012) found that quadrupedal hadrosaurs showed more cursorial morphologies than other quadrupedal ornithischians (ceratopsians and thyreophorans) and may have been capable of

running. More palaeoneurology and locomotory studies involving ornithischian taxa are required to investigate this relationship further.

Regarding dietary change, there does not seem to be a relationship between floccular lobe reduction and herbivory in Ornithischia (Figure 5.13). Early ornithischians, including those with distinct floccular lobes such as *Manidens* and *Lesothosaurus*, were likely omnivorous (Ballell *et al.* 2022). However, as many ornithischians with well-developed floccular lobes (including NHMUK PV R 36760) are considered obligate herbivores, it seems unlikely that floccular lobe size is associated with dietary change in these clades (Figure 5.13).

The vestibular region of the endosseous labyrinth, consisting the vestibule and semi-circular canals, is responsible for balance and contributes to the vestibulocollic (VCR) and vestibulo-ocular (VOR) reflexes. In life, endolymph fluid moves back and forth through each of the canals as the skull rotates, triggering receptors in the ampullae that send signals to the brain through the vestibulocochlear nerve (CN VIII) (Clack 2016). This region could only be partially reconstructed in NHMUK PV R 36760, which is missing the dorsal-most portion of the anterior and posterior semi-circular canals. However, the inner ear of NHMUK PV R 36760 is superficially similar in its sub-triangular outline to those of other ornithopods that have been investigated previously (e.g. Galton 1989; Norman *et al.* 2004; Evans *et al.* 2009; Lautenschlager & Hübner 2013; Cruzado-Caballero *et al.* 2015; Thomas 2015). In NHMUK PV R 36760, the anterior semi-circular canal exits the ampullae at a considerably higher angle ($\sim 110^\circ$) than the posterior semi-circular canal ($\sim 25^\circ$), suggesting that, when complete, the anterior canal would have formed a taller ovate shape compared to the shorter triangular outline of the posterior canal. This would be congruent with several ornithopods that have

been observed to have a taller anterior semi-circular canal compared to the posterior semi-circular canal (Galton 1989; Norman *et al.* 2004; Evans *et al.* 2009; Lautenschlager & Hübner 2013; Cruzado-Caballero *et al.* 2015; Thomas 2015).

The lower portion of the endosseous labyrinth contains the lagena, which is responsible for housing the organ of hearing. In life, the lagena contains sound-detecting cells that are stimulated by sound waves transmitted from the middle ear (Sobral *et al.* 2016). The length of the lagena (or ‘endosseous cochlear duct’) relative to basicranial length is often used as a proxy for the auditory abilities in extinct taxa (e.g. Walsh *et al.* 2009; Brusatte *et al.* 2016; Sobral *et al.* 2016; Serrano-Martínez *et al.* 2019; Brown *et al.* 2020). Only the anterior margin of the lagena could be reconstructed in NHMUK PV R 36760, however this gives a minimum length of ~7 mm. This minimum length is considerably smaller than the lagena length (= cochlear length) measured in other adult ornithopod specimens investigated (9.7–16.7 mm: Evans *et al.* 2009; Lautenschlager & Hübner, 2013; Cruzado-Caballero *et al.* 2015), suggesting that around a third of the length of the lagena is missing from our reconstruction in NHMUK PV R 36760.

Digital techniques have been used to investigate the jaw neurovasculature of several dinosaur taxa, providing insights into thermoregulation, facial sensitivity and edentulism (Porter 2015; Barker *et al.* 2017; Wang *et al.* 2018; Porter & Witmer 2020; Kawabe & Hattori 2022). In NHMUK PV R 36760, a large neurovascular canal was reconstructed extending the full length of the dentary (Figure 5.10). This canal is interpreted as the inferior alveolar nerve canal (= mandibular canal), which in life would have held the mandibular artery, mandibular vein and mandibular nerve (Porter 2015; Lessner 2021). The morphology of this canal is relatively simple throughout

much of its length, with very small canal branches radiating dorsally towards the alveoli of the teeth. This differs from those observed in *Triceratops*, *Fukuisaurus* and *Edmontosaurus*, in which relatively large branches radiate anterodorsally (and also anteroventrally in *Triceratops*) from along the length of the main canal (Kawabe & Hattori 2022). This difference may be explained by the large dental batteries present in *Triceratops*, *Fukuisaurus* and *Edmontosaurus*, which require more blood supply than the comparatively simple tooth replacement methods in NHMUK PV R 36760 (Porter 2015; Kawabe & Hattori 2022). The dentary neurovasculature in NHMUK PV R 36760 becomes far more complex at the anterior tip of the mandibular canal, with several bulbous branches radiating anteriorly towards the predentary-dentary margin. This more complex neurovascular network may infer the presence of a sensitive predentary rhamphotheca (Nabavizadeh & Weishampel 2016). A sensitive ‘bill’ may have enabled NHMUK PV R 36760 to use remote touch when foraging, as seen in several modern bird families (e.g. kiwi, Apterygidae; ibises, Threskiornithidae; Cunningham *et al.* 2010). *Fukuisaurus* also shows this increased complexity in neurovasculature towards the predentary-dentary margin (Kawabe & Hattori 2022), which may indicate that *Fukuisaurus* and NHMUK PV R 36760 employed similar forging behaviours that required enhanced sensitivity of the predentary rhamphotheca. In contrast, the neurovasculature in *Edmontosaurus* and *Triceratops* becomes simpler towards its anterior tip (Kawabe & Hattori 2022), which may imply that the predentary was not particularly sensitive, especially compared to *Fukuisaurus* and NHMUK PV R 36760. However, as the predentary was not included in the analyses by Kawabe & Hattori (2022), it is also possible that the predentary in *Edmontosaurus* and *Triceratops* may have housed complex neurovasculature pertaining to a sensitive predentary rhamphotheca. Den-

tary neurovasculature has been not been widely studied in ornithopods, so it is uncertain how widespread these morphologies are within the clade.

5.4.2. Tooth replacement cycle

Previous studies on tooth replacement in ornithopods have focused primarily on the complex dental batteries found in hadrosaurs (Erickson *et al.* 2012; LeBlanc *et al.* 2016; Bramble *et al.* 2017). As a result, we have little understanding of how these dental batteries evolved. Here, I segmented the dentition within NHMUK PV R 36760 in order to understand how this ornithopod replaced its teeth (Figure 5.7, 5.8). As in many dinosaurs (e.g. Porro *et al.* 2011; Butler *et al.* 2012; Schwarz *et al.* 2015; Fong *et al.* 2016; Chen *et al.* 2018; He *et al.* 2018; Hanai & Tsuihiji 2019; Becerra *et al.* 2022; Hu *et al.* 2022), NHMUK PV R 36760 exhibits lingual tooth replacement, where the new replacement tooth germ emerges lingually to the functional tooth and migrates labially towards the functional tooth. This is in contrast to the subdental replacement found in mammals, crocodiles, ceratopsids and hadrosaurs, in which the replacement tooth germ migrates dorsally from below the functional tooth (LeBlanc *et al.* 2016).

The tooth replacement cycle in NHMUK PV R 36760 is broadly similar to that in *Changchunsaurus* (Chen *et al.* 2018) and some early-diverging ceratopsians and neoceratopsians (He *et al.* 2018; Hu *et al.* 2022). As in *Changchunsaurus*, the replacement tooth of NHMUK PV R 36760 did not fully invade the pulp of the functional tooth until it was almost fully erupted (Chen *et al.* 2018). This is advantageous as it ensures the functional tooth is not shed until the replacement tooth is ready to replace it. If the replacement tooth were to breach the pulp cavity of the functional tooth early in development, this would disrupt the vascular supply to the pulp, and lead to the function-

al tooth being shed before the new replacement tooth was fully developed (Edmund 1960; LeBlanc *et al.* 2016).

Fragments of previous generation functional teeth (PGFT) were found labial to several functional teeth in both NHMUK PV R 36760 and *Changchunsaurus* (Chen *et al.* 2018). Within Dinosauria, these PGFT fragments have also been observed in the theropod *Coelophysis* (LeBlanc *et al.* 2017), the heterodontosaurid *Heterodontosaurus* (Porro *et al.* 2011), a hadrosaurid (Bramble *et al.* 2017), the early-diverging ceratopsian *Yinlong* (Hu *et al.* 2022), and the neoceratopsian *Liaoceratops* (He *et al.* 2018). In Hu *et al.* (2022), fragments from just two PGFT were reconstructed in only the largest of the four *Yinlong* specimens studied. Like in NHMUK PV R 36760 and *Changchunsaurus*, these remnants represent a single prior generation of functional teeth (Chen *et al.* 2018; Hu *et al.* 2022). This is considerably fewer than in *Liaoceratops*, where root fragments from up to four prior generations of functional teeth were preserved as a result of extensive tooth migration between replacement cycles (He *et al.* 2018). Chen *et al.* (2018) suggested that the continued presence of these PGFT remnants in *Changchunsaurus* may be the result of gradual lingual migration of the tooth row, similar, but less extreme than that seen in *Liaoceratops* (Chen *et al.* 2018; He *et al.* 2018). In contrast, the PGFT remnants in NHMUK PV R 36760 become fully resorbed before the new replacement crown has reached 40% of its full length, suggesting the migration seen in *Liaoceratops* and *Changchunsaurus* does not occur. Resorption of the functional tooth in NHMUK PV R 36760 is found to initiate considerably later than in other cerapodans with lingual tooth replacement. In *Changchunsaurus* this reabsorption begins soon after the replacement tooth germ emerges (Chen *et al.* 2018), and in *Chaoyangsaurus* and *Yinlong*, it begins even before the new replace-

ment germ emerges (Hu *et al.* 2022).

Results also show evidence of the formation of a new tooth family at the posterior end of the dentary. This suggests that the individual was still growing at time of death and confirms that the number of dentary teeth in this taxon increased throughout ontogeny. This is a common ontogenetic feature in ornithopods (Hübner & Rauhut 2010) and highlights the potential issues of using the number of teeth as a taxonomic character in morphological matrices (e.g. Boyd 2015: #112; #126; #137; Han *et al.* 2018: #196, #203, #204; Dieudonné *et al.* 2021: #150, #159).

5.4.3. Implications for diet and mastication

Tooth replacement rate can be assessed based on the number of replacement tooth generations present per tooth family, with more generations indicating a faster replacement rate (Erickson 1996; D’Emic *et al.* 2013; LeBlanc *et al.* 2016). Here I interpret that NHMUK PV R 36760 likely had a relatively slow rate of tooth replacement, as indicated by the single generation of replacement teeth present. Heterodontosaurids (*Heterodontosaurus*, Norman *et al.* 2011; *Fruitadens*, Butler *et al.* 2012; *Manidens*, Becerra *et al.* 2022), early-diverging ceratopsians (*Psittacosaurus*, Averianov *et al.* 2006; *Yinlong*, *Chaoyangsaurus*, Hu *et al.* 2022) and the early-diverging ornithopod *Changchunsaurus* (Chen *et al.* 2018), have similarly been found to have a single generation of replacement teeth and likely also had slow tooth replacement rates. This is in contrast to more derived cerapodans, which tend to have two or more generations of replacement teeth per tooth family, and likely had comparably faster tooth replacement rates (Brown and Schlaikjer 1940; Edmund 1960; Tanoue *et al.* 2012; Bramble *et al.* 2013; Chen *et al.* 2018; Morschhauser *et al.* 2019; Hu *et al.* 2022). While a slow

tooth replacement rate may give us insight into the phylogenetic affinities of NHMUK PV R 36760 as an early-diverging ornithopod, it may also point towards the diet of this animal. Slower rates of tooth replacement imply relatively low levels of dental wear, which may indicate that this ornithopod may have processed foods less before swallowing, ate softer foods, or employed strategies other than mastication to process tougher foods (e.g. gastroliths).

The Z-values of NHMUK PV R 36760 are higher in the anterior region of the dentary compared to its posterior region. This suggests that posterior teeth were being replaced at a faster rate than those anteriorly. Similar Z-value distributions were found in *Yinlong* (Hu *et al.* 2022), where it was suggested that this early-diverging ceratopsian primarily used the posterior region of its jaw to chew food. Teeth that are used more frequently are subject to increased wear and therefore need to be replaced more frequently. The reverse condition to NHMUK PV R 36760 (this study) and *Yinlong* (Hu *et al.* 2022) has been observed in the early-diverging neoceratopsians *Liaoceratops* and *Chaoyangsaurus*, where it has been suggested that the anterior region of the jaw had higher replacement rates and was therefore used more frequently in mastication (He *et al.* 2018; Hu *et al.* 2022). Hu *et al.* (2022) suggested that these changes may represent a transfer in the main chewing region during the evolution of early ceratopsians. Further research is required to determine whether the regionalisation of replacement rates throughout the dentary is an adaptation widespread throughout both ornithopods and marginocephalians.

5.5. Conclusions

The use of μ CT data has enabled me to investigate the endocranial anatomy, inner ear morphology, tooth replacement cycle and dentary neurovasculature of a new genus of ornithopod dinosaur. This has revealed much about the sensory capabilities and life habits of the taxon, but perhaps most importantly, the position of this taxa as an early-diverging ornithopod or non-cerapodan neornithischian (Maidment *et al.* in prep) makes it of high importance in future studies of ornithopod evolution for comparative purposes.

Endocranial reconstructions reveal that the new ornithopod had an elongate floccular lobe that extended into the space between the anterior semi-circular canal. This feature suggests that NHMUK PV R 36760 had enhanced gaze stabilisation and was capable of rapid eye, head and neck movements, perhaps to avoid predation, for visual communication or to navigate complex environments. The presence of a distinct floccular lobe is likely the ancestral condition within Ornithischia, being found in taxa from each of the five major clades. Floccular lobe reduction in some later-diverging ceratopsians and ornithopods may be linked to the reversion to quadrupedality or the loss of cursoriality in these taxa, although wider sampling is required to further assess this.

Digital segmentation of the dentary has allowed the tooth replacement cycle of NHMUK PV R 36760 to be fully reconstructed and visualised in three-dimensions. Lingual to the functional teeth sits a single generation of replacement teeth, suggesting a generally slow rate of replacement. Investigation of Zahnreihen patterns reveal that teeth at the posterior end of the jaw were being replaced more frequently than those at the anterior of the jaw, which may indicate that the posterior region was primarily used in mastication. The morphology of the dentary neurovasculature is relatively simple

throughout much of its length, but becomes more complex at the predentary-dentary margin, which suggests that NHMUK PV R 36760 may have had a sensitive ‘bill’, perhaps used in particular foraging behaviours. This study provides an in-depth assessment of an alternative ornithopod dental condition compared to the more widely researched dental batteries of hadrosaurs. Further sampling throughout the ornithopod tree is required to determine the ancestral dental condition within the clade and how complex dental batteries evolved.

Chapter 6

CONCLUSIONS

This thesis focuses on the enigmatic ‘hypsilophodontids’, an informal group of ornithischian dinosaurs that share a similar bauplan: bipedal, small to medium-bodied (~1–2 m), and conservative in morphology. Across four research chapters, I explore the controversial relationships of the ‘hypsilophodontids’, as well as some of the physiological and behavioral adaptations exhibited by these taxa. Here I present some of my main results, with suggestions for future work.

6.1. Chapter overview and main findings

Chapter 2 presents a novel suite of analytical methods for assessing the causes of phylogenetic conflict in the neornithischian tree. Three recent ornithischian data matrices were subject to in-depth character and taxon manipulation to determine why these matrices recover the ‘hypsilophodontids’ in one of two conflicting placements: hypothesis 1 (H1), primarily within Cerapoda as a paraphyletic assemblage of basal ornithopods (Han *et al.* 2018; Dieudonné *et al.* 2021); and hypothesis 2 (H2), primarily within the non-cerapodan neornithischian clade, Thescelosauridae (Boyd 2015). Results of this study found that the positions in which controversial groups (e.g. ‘hypsilophodontids’, heterodontosaurids) are recovered is highly dependent on the sample of taxa included within the analysis, demonstrating the importance of selecting representative taxa

when assessing phylogenetic relationships. Taxon completeness and character completeness were both found not to be contributing factors in altering topology, showing how operational taxonomic units (OTUs) with high proportions of missing data should still be included within cladistic matrices. Across all of the analytical permutations applied, the H1 matrices I investigated consistently recovered ‘hypsilophodontids’ within Cerapoda, in a position consistent with their original H1 placement. By contrast, the H2 matrix investigated was found to be far more susceptible to the influences of both character and taxon sampling. The exclusion of unique OTUs, dental characters, hind limb characters or femoral characters from the H2 matrix resulted in the majority of ‘hypsilophodontids’ placing within Cerapoda, in positions more congruent with H1 than H2. Furthermore, the exclusion of just three femoral characters from Boyd (2015) was found to recover Thescelosauridae within Ornithopoda, demonstrating the huge impact that individual characters can have on our understanding of major evolutionary changes.

For Chapter 3, I performed discrete character-based disparity analyses on the same three cladistic matrices investigated in Chapter 2. The purpose of this chapter was to quantify the morphological variation in ‘hypsilophodontids’ to compare this to that seen in other ornithischian groups. Data matrices were additionally partitioned by anatomical region, allowing me to identify patterns of modular evolution within the ornithischian skeleton. Morphospace results find that the ‘hypsilophodontids’ often displayed a large distribution, with some of these focal taxa regularly plotting close to other ornithischian clades. This suggests that the ‘hypsilophodontids’ represent a diverse paraphyletic assemblage of taxa, that likely occupy multiple branches of the ornithischian tree, rather than being united within a monophyletic clade (i.e. Thesce-

losauridae). The dental, pelvic girdle and hind limb regions of the ‘hypsilophodontids’ were found to be comparatively specialized, occupying largely unique morphospace in all matrices investigated. When looking at ornithischian disparity changes through time, the pelvic girdle and hind limb partitions were found to be of further significance, exhibiting comparably high levels of phenotypic diversity in the Middle Jurassic, suggesting important locomotory adaptations may have been evolving at this time.

In Chapter 4, I examined the long bone histology in six individuals of *Hypsilophodon foxii*. This study aimed to identify the ontogenetic status of these specimens and investigate patterns of growth within these animals. In *H. foxii*, no unambiguous lines of arrested growth (LAGs) could be recovered, suggesting that this taxon underwent rapid and uninterrupted growth. The scarcity or complete absence of LAGs has also been observed in several other ornithopods (e.g. *Convolosaurus*, *Dryosaurus*, *Dysalotosaurus*), suggesting this may be a shared growth pattern among these dinosaurs. By contrast, the presence of extensive LAGs in earlier-diverging ‘hypsilophodontids’ (e.g. *Jeholosaurus*, *Orodromeus*, *Oryctodromeus*) demonstrates the histovariability of growth strategies among these taxa. Furthermore, the presence of annually-deposited LAGs might be the plesiomorphic condition for Neornithischia.

Chapter 5 used μ CT techniques to examine the neuroanatomy and tooth replacement cycle of a new genus of ornithopod from the Late Cretaceous of Antarctica. The morphology of the floccular lobe, partial endosseous labyrinth and five of the 12 cranial nerves could be reconstructed from the partial braincase specimen; while the neurovasculature and 38 teeth could be segmented from a near complete dentary. The segmented dentition included: 16 functional teeth, 16 developing replacement teeth and six remnants from the previous generation of functional teeth. The relationships

between functional, replacement and non-functional old teeth at each tooth family enabled me to visualise the full cycle of tooth replacement in three-dimensions, something which has not previously been achieved in an ornithopod dinosaur. This study represents an important example of an alternative ornithopod dental condition compared to the more well-studied dental batteries of the hadrosaurs. Concerning the endocranial anatomy, the endosseous labyrinths could not be completely reconstructed, but superficially resemble other ornithopods in the sub-triangular outline of the anterior and posterior labyrinths. The morphology of the digitally reconstructed floccular lobe was found to extend for a considerable distance through the anterior canal of the endosseous labyrinth. The size of this feature suggests that this new ornithopod had enhanced gaze stabilisation and was capable of rapid head, eye and neck movements.

6.2. Future work

Resolving the phylogenetic relationships of the ‘hypsilophodontids’ remains a priority within ornithischian research, with current uncertainty limiting our understanding of major transitions throughout the evolutionary history of these dinosaurs. Results from Chapter 2 tend to favour the placement of ‘hypsilophodontids’ primarily within Cerapoda as early-diverging ornithopods, while insights from Chapter 3 suggest that the ‘hypsilophodontids’ were a diverse assemblage of taxa. These findings do not tend to support the proposal that most ‘hypsilophodontids’ fall within a monophyletic group (i.e. Thescelosauridae): however, only a large-scale reassessment of neornithischian relationships, and the discovery of new material, can confirm this. Future studies looking to clarify these relationships should combine characters from recent neornithis-

chian data matrices. They should also aim to incorporate some of the new “hypsilophodontid-grade” taxa that have been described following the most recent analysis of neornithischian relationships by Dieudonné *et al.* (2021), which hail from Asia (Yang *et al.* 2020; Manitkoon *et al.* 2023), Europe (Longrich *et al.* 2024) and North America (Bonde *et al.* 2022; Tykoski *et al.* 2023). Chapter 2 (section 2.4.3.) provides a number of more technical recommendations for future studies looking to resolve these relationships and emphasises the importance of combining character/taxon matrices and re-evaluating characters. The impact of outgroup choice was not investigated during Chapter 2, but is an important consideration for future reassessments of ornithischian relationships. I would also encourage the application of the methods outlined in Chapter 2 to other controversial groups with major phylogenetic conflicts (e.g. testudines, eutherian mammals).

In Chapter 2, the phylogenetic position of the heterodontosaurids was found to be highly dependent on the sample of taxa included within the analysis. Furthermore, in Chapter 3, the heterodontosaurids were found to plot within a wide region of morphospace, with some of these taxa frequently lying within, or close to, the morphospace occupied by derived cerapodan groups (e.g. iguanodontians). These results bring in to question the proposed placement of heterodontosaurid at the base of Ornithischia and the validity of a heterodontosaurid monophyly. A thorough re-assessment of heterodontosaurid relationships is required to resolve these concerns, supplemented by the discovery of new material.

In Chapter 4, two distinct growth strategies were identified among the ‘hypsilophodontids’, with taxa exhibiting either continuous uninterrupted growth (demonstrated by the absence/lack of LAGs, e.g. *Convolosaurus*, *Hypsilophodon*) or spo-

radic growth (demonstrated by the presence of frequent LAGs, e.g. *Jeholosaurus*, *Orodromeus*). It remains uncertain whether these patterns reflect behavioural (e.g. migration) or physiological (e.g. degree of developmental plasticity) differences between these taxa. It would be interesting to explore these hypotheses, as well as to more broadly investigate the diversity of growth patterns within Neornithischia. Further histological sampling of neornithischian taxa is required to build a comparative framework of the bone microstructure and growth strategies found within the group.

While there has been extensive research effort into the adaptive significance of dental batteries in hadrosaurs and ceratopsians, the origins and evolution of these features remain uncertain. Chapter 5 presents a novel contribution to our understanding of tooth replacement cycles in neornithischian dinosaurs, representing an alternative dental condition to the more widely studied dental batteries. This alternate condition could represent a primitive form of dental replacement from which the complex batteries of the hadrosaurs originated, however the lack of comparative studies currently hinders these interpretations. Future work should focus on describing models of tooth replacement in other neornithischians, particularly early-diverging ornithopods. While histological methods are often utilised in studies of dinosaur dentition (e.g. Chen *et al.* 2018), the use of CT methods is often highly preferable, being both non-destructive and allowing the relationships between teeth at a single tooth family to be visualised in three dimensions.

The presence of a distinct floccular lobe seems to be the ancestral condition within Ornithischia, being found in early-diverging forms from each of the five major clades. In Chapter 5, I hypothesised that the floccular lobe reduction observed in some later-diverging ceratopsians and ornithopods may be linked to the reversion to

quadrupedality or the loss of cursoriality in these groups. Further sampling of a broad range of neornithischian taxa is required to confirm this. Neornithischians that share a ‘hypsilophodontid’ bauplan are generally found to have distinct floccular lobes, however the diversity in size and extent between these taxa is considerable. It would be very interesting to investigate the functional significance of comparatively well-developed floccular lobes in dinosaurs such as NHMUK PV R 36760 and *Hypsilophodon* (Galton 1989, 2012).

6.3. Final thoughts

The phylogenetic affinities of the ‘hypsilophodontids’ remain contentious, but results of this thesis tend to favour a placement primarily within Cerapoda as early-diverging ornithopods. Resolving these relationships is crucial to our understanding of some of the major transitions that occurred during the early evolutionary history of Neornithischia. I hope that the recommendations suggested in this thesis will aid future studies looking to reassess these relationships. The multifaceted approaches used here demonstrate that the ‘hypsilophodontids’ comprise a diverse assemblage of taxa, which shared a highly successful bauplan that persevered for ~100 million years. Herein, the ‘hypsilophodontids’ are shown to exhibit disparate morphologies, neuroanatomies and even distinct patterns of growth, in contrast to more traditional ideas that have considered many of these taxa as largely homogenous and unspecialised. This thesis provides new data that add to our understanding of the palaeobiology and relationships of the ‘hypsilophodontids’, but there is still much to learn about these enigmatic dinosaurs.

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Appendices

A1.1. Taxa of interest

A summary of the focal taxa in this thesis.

***Agilisaurus louderbacki* Peng, 1990**

Age: Middle Jurassic (Barrett *et al.* 2005; Zhou *et al.* 2022).

Geology: Lower Shaximiao Formation of the Sichuan Province, China (Barrett *et al.* 2005)

Systematics: This taxon has been traditionally assigned to Fabrosauridae (Peng 1990, 1992) and Hypsilophodontidae (Sues & Norman 1990), which are now both widely considered to be para- or polyphyletic assemblages (e.g. Butler 2005; Butler *et al.* 2008). Phylogenetic analyses have previously recovered *Agilisaurus* as a basal euornithopod (Buchholz 2002; Weishampel *et al.* 2003), but more recently tend to agree that this taxon is a non-cerapodan neornithischian (Butler 2005; Butler *et al.* 2008; Boyd 2015; Han *et al.* 2018; Dieudonné *et al.* 2021). In several analyses, *Agilisaurus* is recovered as the basal-most neornithischian (e.g. Dieudonné *et al.* 2016; Han *et al.* 2018).

***Albertadromeus syntarsus* Brown *et al.*, 2013b**

Age: Campanian, Late Cretaceous (Brown *et al.* 2013b).

Geology: Upper Oldman Formation of Alberta, Canada (Brown *et al.* 2013b).

Systematics: The limited inclusion of *Albertadromeus* in phylogenetic analyses suggests that the taxon was a thescelosaurid orodromine (Brown *et al.* 2013b; Bell *et al.* 2018b; Madzia *et al.* 2018).

***Atlascopcosaurus loadsi* Rich & Rich, 1989**

Age: Albian, Early Cretaceous (Agnolín *et al.* 2010).

Geology: Eumeralla Formation of Victoria, Australia (Agnolín *et al.* 2010).

Systematics: *Atlascopcosaurus* was originally assigned to the clade Hypsilophodontidae by Rich & Vickers-Rich (1999), but has since also been referred to as a non-dryomorph ornithopod (Agnolín *et al.* 2010) and basal euornithopod (Norman 2004). To date, *Atlascopcosaurus* has been included in a limited number of phylogenetic studies, owing to its incompleteness. Bell *et al.* (2018b) recovered *Atlascopcosaurus* as the sister-taxon of Iguanodontia, whereas Boyd (2015) and Madzia *et al.* (2018) recovered the taxon within Iguanodontia, as part of a clade of several other Gondwanan taxa.

***Changchunsaurus parvus* Zan *et al.*, 2005**

Age: Aptian–Cenomanian, ‘middle’ Cretaceous (Butler *et al.* 2011).

Geology: Quantou Formation of the Jilin Province, China (Jin *et al.* 2010).

Systematics: The phylogenetic position of *Changchunsaurus parvus* is contentious within the literature. Several analyses have supported a sister-taxa relationship with *Jeholosaurus*, both within Ornithopoda (Han *et al.* 2012; Dieudonné *et al.* 2016; Han *et al.* 2018) and at the base of Neornithischia (Herne *et al.* 2019), with Han *et al.* (2012) proposing the formation of a new clade Jeholosauridae to include the Asian taxa *Changchunsaurus*, *Haya* and *Jeholosaurus*. However, phylogenetic analyses that predominately follow the Boyd (2015) matrix tend to recover *Changchunsaurus* as phylogenetically distant from *Jeholosaurus*, outside of Cerapoda, either as a thescelosaurine thescelosaurid (Boyd 2015) or as an orodromine thescelosaurid (Bell *et al.* 2018b; Madzia *et al.* 2018). More recently, Dieudonné *et al.* (2021) recovered *Changchunsaurus* within Cerapoda as an early-diverging ornithopod, phylogenetically close to both *Haya* and *Jeholosaurus*.

***Changmiania liaoningensis* Yang *et al.*, 2020**

Age: Barremian, Early Cretaceous (Yang *et al.* 2020).

Geology: Yixian Formation of the Liaoning Province, China (Yang *et al.* 2020).

Systematics: *Changmiania* has only been included in one phylogenetic analysis, a modified version of the Dieudonné *et al.* (2016) matrix by Yang *et al.* (2020), in which it was recovered as the basal-most ornithopod.

***Convolosaurus marri* Andrzejewski *et al.*, 2019**

Age: Aptian, Early Cretaceous (Andrzejewski *et al.* 2019).

Geology: Twin Mountains Formation of Texas, U.S.A. (Andrzejewski *et al.* 2019).

Systematics: Limited phylogenetic analyses have suggested that *Convolosaurus* is a non-iguanodontian ornithopod (Andrzejewski *et al.* 2019; Dieudonné *et al.* 2021).

***Diluvicursor pickeringi* Herne *et al.*, 2018**

Age: Albian, Early Cretaceous (Herne *et al.* 2018).

Geology: Eumeralla Formation of southern Victoria, Australia (Herne *et al.* 2018).

Systematics: In the original description by Herne *et al.* (2018), the phylogenetic position of *Diluvicursor* could not be resolved beyond a large polytomy of ornithopods. Subsequently, Herne *et al.* (2019) recovered the taxon as a non-iguanodontian ornithopods, within a clade of other Gondwanan taxa, Elasmaria. Bell *et al.* (2019) recovered the taxon in a polytomy with *Changchunsaurus*, *Hypsilophodon*, and *Macrogryphosaurus*, within a large polyphyly of basal neornithischians and cerapodans.

***Gasparinisaura cincosaltensis* Coria & Salgado, 1996**

Age: Campanian, Late Cretaceous (Coria & Salgado 1996; Dingus *et al.* 2000).

Geology: Anacleto Formation of Patagonia, Argentina (Armas & Sanchez 2011).

Systematics: Recent phylogenetic analyses all agree on the inclusion of *Gasparinisaura* within Ornithopoda, however there is disagreement on whether the taxon is a non-iguanodontian ornithopod (Han *et al.* 2018; Madzia *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021), iguanodontian (Butler *et al.* 2008; Boyd 2015), or euig-

uanodontian (Coria & Salgado 1996). *Gasparinisaura* is commonly recovered in close association with other Gondwanan taxa (Calvo *et al.* 2007; Boyd 2015; Madzia *et al.* 2018; Herne *et al.* 2019), but has most recently been found within the clade Hypsilophodontidae, with *Parksosaurus* and *Hypsilophodon* (Dieudonné *et al.* 2021).

***Haya griva* Makovicky *et al.*, 2011**

Age: Santonian–Campanian, Late Cretaceous (Barta & Norell 2021).

Geology: Javkhlant Formation of Mongolia (Makovicky *et al.* 2011).

Systematics: The original placement of *Haya griva* as an early-diverging ornithomorph (Makovicky *et al.* 2011) has been supported by several subsequent analyses (Dieudonné *et al.* 2016; Han *et al.* 2018; Andrzejewski *et al.* 2019; Li *et al.* 2019; Dieudonné *et al.* 2021). These phylogenetic analyses tend to recover *Haya* as part of the clade, Jeholosauridae (Han *et al.* 2012), along with *Changchunsaurus* and *Jeholosaurus* (Dieudonné *et al.* 2016; Han *et al.* 2018; Andrzejewski *et al.* 2019; Li *et al.* 2019). However, *Haya* has also been recently recovered outside of Cerapoda (Boyd 2015; Madzia *et al.* 2018; Barta & Norell 2021). *Haya* was recovered as a thescelosaurine thescelosaurid by Boyd (2015), and later as an orodromine thescelosaurid by Madzia *et al.* (2018). In the recent redescription of *Haya* by Barta & Norell (2021), the taxon was found to be either a thescelosaurid or the closest sister taxon to Thescelosauridae.

***Hexinlusaurus multidens* He & Cai, 1984**

Age: Middle Jurassic (Barrett *et al.* 2005; Zhou *et al.* 2022).

Geology: Lower Shaximiao Formation of the Sichuan Province, China (Barrett *et al.* 2005).

Systematics: This taxon was originally described as a new sub-species of *Yandusaurus*, (*Yandusaurus multidens*, He & Cai 1984), but later Barrett *et al.* (2005) found sufficient differences to warrant the creation of a new genus,

Hexinlusaurus. Prior to this reassignment, *Y. multidens* (= *H. multidens*) was considered a ‘hypsilophodontid’ (Sues & Norman 1990). The phylogenetic position of *Hexinlusaurus* is relatively stable between different matrices, with results tending to recover the taxon as an early-diverging neornithischian (e.g. Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2021). In many of these analyses *Hexinlusaurus* is usually recovered in a more derived position than *Agilisaurus*, also from the Lower Shaximiao Formation of China (Butler *et al.* 2008; Ösi *et al.* 2012; Han *et al.* 2012; Boyd 2015; Dieudonné *et al.* 2016; Han *et al.* 2018); however, in Dieudonné *et al.* (2021), *Hexinlusaurus* was recovered in a basal neornithischian clade with *Agilisaurus*.

***Hypsilophodon foxii* Huxley, 1869**

Age: Barremian, Early Cretaceous (Galton 1974; Galton 2009).

Geology: Wessex Formation of the Isle of Wight, U.K. (Galton 1974).

Systematics: *Hypsilophodon* was traditionally part of the clade Hypsilophodontidae (Dollo 1882), which became a waste-basket group of small bipedal ornithischians. This clade has become largely obsolete in modern systematics (Butler *et al.* 2008), with Boyd (2015) recovering *Hypsilophodon* as the sole member of Hypsilophodontidae. More recently, Dieudonné *et al.* (2021) recovered Hypsilophodontidae as a monophyly within Clypeodonta, consisting of *Hypsilophodon*, *Parksosaurus* and *Gasparinisaura*. *Hypsilophodon* is widely considered to be a non-iguanodontian ornithopod, as supported by several recent phylogenetic analyses (e.g. Butler *et al.* 2008; Boyd 2015; Dieudonné *et al.* 2016; Han *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021), although it has also been recovered outside of Ornithopoda, as the sister taxon to Cerapoda (Madzia *et al.* 2018).

***Jeholosaurus shangyuanensis* Xu *et al.*, 2000**

Age: Barremian–Aptian, Early Cretaceous (Xu *et al.* 2000).

Geology: Yixian Formation of the Liaoning Province, China (Han *et al.* 2012).

Systematics: Recent phylogenetic studies have recovered *Jeholosaurus* as an early-diverging neornithischian (Boyd 2015; Bell *et al.* 2018b; Barta & Norell 2021) or early-diverging ornithopod (Butler *et al.* 2005; Butler *et al.* 2008; Han *et al.* 2012; Han *et al.* 2018; Andrzejewski *et al.* 2019; Li *et al.* 2019; Dieudonné *et al.* 2021). A phylogenetic analysis from Han *et al.* (2012) found that *Jeholosaurus* formed a clade of East Asian taxa, including *Changchunsaurus* and *Haya* (=Jeholosauridae; Han *et al.* 2012). Jeholosauridae has been subsequently recovered in several phylogenetic analyses (Dieudonné *et al.* 2016; Han *et al.* 2018; Andrzejewski *et al.* 2019; Li *et al.* 2019), although others have found *Jeholosaurus* as phylogenetically distant from both *Changchunsaurus* and *Haya*, and instead, in a clade with *Yuesaurus* (Boyd 2015; Bell *et al.* 2018b; Barta & Norell 2021).

***Koreanosaurus boseongensis* Huh, 2010**

Age: Santonian–Campanian, Late Cretaceous (Huh 2010).

Geology: Seonso Conglomerate of the Chollanam-do Province, South Korea (Huh 2010).

Systematics: Huh (2010) originally referred to *Koreanosaurus* as a basal ornithopod and sister taxon of the North American taxon *Orodromeus*, but performed no formal analysis due to the lack of available characters. Subsequently, phylogenetic analyses have recovered *Koreanosaurus* as an orodromine within the non-cerapodan clade Thescelosauridae (Boyd 2015; Krumeracker 2017; Bell *et al.* 2018b; Herne *et al.* 2019), or within Cerapoda, as an early-diverging ornithopod (Dieudonné *et al.* 2016; Han *et al.* 2018) or orodromine (Dieudonné *et al.* 2021).

***Kulindadromeus zabaikalicus* Godefroit *et al.*, 2014**

Age: Bathonian, Middle Jurassic (Cincotta *et al.* 2019).

Geology: Ukureyskaya Formation of Chita, Russia (Godefroit *et al.* 2014).

Systematics: Limited phylogenetic analyses have recovered *Kulindadromeus* as an early-diverging neornithischian (Godefroit *et al.* 2014; Salgado *et al.* 2017; Bell *et al.* 2018b) or early-diverging ornithopod (Dieudonné *et al.* 2021).

***Leaellynasaura amicagraphica* Rich & Rich, 1989**

Age: Early Cretaceous (Rich & Rich 1989).

Geology: Eumeralla Formation of Victoria, Australia (Rich *et al.* 2010).

Systematics: Rich & Rich (1989) originally assigned *Leaellynasaura* to the clade Hypsilophodontidae. Norman (2004) considered the taxon to be a basal ornithopod, while in a later reassessment of Australasian non-avian dinosaurs, Agnolín *et al.* (2010) described *Leaellynasaura* as non-iguanodontian ornithopod. Owing to its low completeness, *Leaellynasaura* has been included in limited phylogenetic studies. Furthermore, the analyses that have included this taxon find little congruence on its placement within Neornithischia. Boyd (2015) recovered *Leaellynasaura* in a polytomy with *Hexinlusaurus* and *Yandusaurus* near the base of Neornithischia, phylogenetically distant from other Gondwanan taxa. In contrast, Herne *et al.* (2019) recovered the *Leaellynasaura* within a clade of other Gondwanan taxa (Elasmaria) near the base of Ornithopoda. Madzia *et al.* (2018) found that the inclusion of *Leaellynasaura* in their analysis was causing a large polytomy near the base of Neornithischia.

***Macrogyphosaurus gondwanicus* Calvo *et al.*, 2007**

Age: Turonian–Coniacian, Late Cretaceous (Calvo *et al.* 2007; Ibiricu *et al.* 2010).

Geology: Portezuelo Formation of Patagonia, Argentina (Calvo *et al.* 2007).

Systematics: The first phylogenetic analysis to include *Macrogyphosaurus* recovered the taxon in a basal euiguanodontian clade with *Talenkauen*, coined Elasmaria by the authors (Calvo *et al.* 2007). Subsequently, *Macrogyphosaurus* has been recovered both outside of Cerapoda, as a thescelosaurine (Boyd 2015), and within Cerapoda, as a non-iguanodontian ornithopod (Madzia *et al.* 2018; Herne *et al.* 2019)

or iguanodontian (Dieudonné *et al.* 2021). As in the original analysis by Calvo *et al.* (2007), *Macrogryphosaurus* is consistently recovered within the monophyletic clade Elasmaria (Madzia *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021).

***Morrosaurus antarcticus* Rozadilla *et al.*, 2016**

Age: Maastrichtian, Late Cretaceous (Rozadilla *et al.* 2016).

Geology: Snow Hill Island Formation of James Ross Island, Antarctica (Rozadilla *et al.* 2016).

Systematics: *Morrosaurus* has been included in limited phylogenetic analyses to date. Rozadilla *et al.* (2016) recovered the taxon as a non-iguanodontian ornithopod, within a clade of other Gondwanan ornithopods (*Anabisetia*, *Gasparinisaura*, *Macrogryphosaurus*, *Notohypsilophodon*, *Talenkauen*, *Trinisaura*).

***Nanosaurus agilis* Marsh, 1877**

Age: Kimmeridgian–Tithonian, Late Jurassic (Galli *et al.* 2018).

Geology: Morrison Formation of Colorado, U.S.A. (Norman 2004).

Systematics: Norman (2004) considered *Nanosaurus agilis* to be nomen dubia, however some authors have suggested it is valid (Galton 2007) and may also represent an adult synonym of several other Morrison Formation taxa (*Drinker nisti*, *Othnielosaurus consors* and *Othnielia rex*; Carpenter & Galton 2018). As a result of its uncertain validity, *Nanosaurus* has been excluded from many large-scale analyses of ornithischian relationships (e.g. Butler *et al.* 2008; Boyd 2015). *Nanosaurus* was however including in a recent phylogenetic analysis by Dieudonné *et al.* (2021), where the taxon was recovered as an early-diverging ornithopod. Additionally, Herne *et al.* (2019) replaced *Othnielosaurus consors* with *Nanosaurus agilis* (following revisions from Carpenter & Galton 2018), recovering the OTU outside of Cerapoda as the sister taxon to a clade comprising Jeholosauridae + Thescelosauridae.

***Nevadadromeus schmitti* Bonde *et al.*, 2022**

Age: Cenomanian, Late Cretaceous (Bonde *et al.* 2022).

Geology: Willow Tank Formation of Nevada, U.S.A. (Bonde *et al.* 2022).

Systematics: *Nevadadromeus* has yet to be formally included in any phylogenetic analyses, but taxonomic comparisons suggest it is a thescelosaurine (Bonde *et al.* 2022).

***Notohypsilophodon comodorensis* Martínez, 1998**

Age: Cenomanian, Late Cretaceous (Martínez & Novas 2006; Ibricu *et al.* 2014).

Geology: Bajo Barreal Formation of Patagonia, Argentina (Martínez 1998).

Systematics: Martínez (1998) originally described *Notohypsilophodon* as an ornithopod within the clade Hypsilophodontidae. *Notohypsilophodon* was recently reassessed by Ibricu *et al.* (2014) and coded into the Han *et al.* (2012) character matrix, however the resulting placement was unstable, owing to its incompleteness. Few subsequent phylogenetic analyses have included *Notohypsilophodon*, and results have been largely incongruent. Boyd (2015) recovered *Notohypsilophodon* outside of Cerapoda, within a clade of elasmarian thescelosaurines, while Bell *et al.* (2018b) recovered the taxon as an early-diverging ornithopod, despite using a modified version of the Boyd (2015) matrix. Analyses by Rozadilla *et al.* (2016) found *Notohypsilophodon* within a clade of Gondwanan ornithopods.

***Orodromeus makelai* Horner & Weishampel, 1988**

Age: Campanian, Late Cretaceous (Horner & Weishampel 1988; Freimuth & Varricchio 2019).

Geology: Two Medicine Formation of Montana, U.S.A. (Horner & Weishampel 1988).

Systematics: Most phylogenetic analyses agree that *Orodromeus* resides within Cerapoda as an early-diverging ornithopod (Butler *et al.* 2008; Dieudonné *et al.* 2016;

Han *et al.* 2018; Dieudonné *et al.* 2021), however several recent phylogenetic analyses have recovered *Orodromeus* outside of Cerapoda, within the clade Thescelosauridae (Boyd 2015; Bell *et al.* 2018b; Madzia *et al.* 2018; Herne *et al.* 2019). While these analyses provide two very different hypotheses for the placement of the *Orodromeus* within Neornithischia, *Orodromeus* is consistently found within the monophyly Orodrominae (Brown *et al.* 2013b; Boyd 2015; Madzia *et al.* 2018; Dieudonné *et al.* 2021), or in a sister-taxon relationship with *Zephyrosaurus* (e.g. Boyd *et al.* 2009; Brown *et al.* 2011; Andrzejewski *et al.* 2019; Li *et al.* 2019).

***Oryctodromeus cubicularis* Varricchio *et al.*, 2007**

Age: Albian–Cenomanian, ‘middle’ Cretaceous (Varricchio *et al.* 2007; Krumeacker *et al.* 2019).

Geology: (1) Blackleaf Formation of Montana, U.S.A.; (2) Wayan Formation of Idaho, U.S.A. (Varricchio *et al.* 2007; Krumeacker 2010).

Systematics: In phylogenetic analyses conducted by Varricchio *et al.* (2007), the authors found that *Oryctodromeus*, *Zephyrosaurus* and *Orodromeus* formed a distinct clade from the other basal ornithopods in the analysis. Brown *et al.* (2013b) recovered similar results, coining the clade Orodrominae. In the same analysis, Orodrominae was recovered as the sister group of Thescelosaurinae, which united formed the clade coined Thescelosauridae (Brown *et al.* 2013b). Boyd (2015) subsequently recovered Thescelosauridae outside of Cerapoda and *Oryctodromeus* as an orodromine thescelosaurid.

***Parksosaurus warreni* Parks, 1926**

Age: Maastrichtian, Late Cretaceous (Eberth & Braman 2012)

Geology: Horseshoe Canyon Formation of Alberta, Canada (Eberth & Braman 2012)

Systematics: Recent analyses of neornithischian relationships have recovered *Parksosaurus* as a non-cerapodan thescelosaurine thescelosaurid (Boyd 2015; Bell *et*

al. 2018b; Madzia *et al.* 2018;) or a non-iguanodontian ornithopod (Han *et al.* 2018; Herne *et al.* 2019; Dieudonné *et al.* 2021). *Parksosaurus* has previously been recovered as the sister taxon of *Hypsilophodon* (Weishampel & Heinrich 1992), *Thescelosaurus* (Weishampel *et al.* 2003; Boyd *et al.* 2009; Brown *et al.* 2011; Bell *et al.* 2018b; Han *et al.* 2018), and *Gasparinisaura* (Buchholz 2002; Butler *et al.* 2008; Butler *et al.* 2009; Butler & Han 2009; Makovicky *et al.* 2011; Godefroit *et al.* 2014; Andrzejewski *et al.* 2019; Li *et al.* 2019; Dieudonné *et al.* 2021). Most recently, Dieudonné *et al.* (2021) found *Parksosaurus* as the sister taxon to *Gasparinisaura* within the clade Hypsilophodontidae.

***Qantassaurus intrepidus* Rich and Vickers-Rich, 1999**

Age: Aptian, Early Cretaceous (Rich and Vickers-Rich 1999; Agnolín *et al.* 2010).

Geology: Wonthaggi Formation of Victoria, Australia (Rich and Vickers-Rich 1999).

Systematics: *Qantassaurus* was originally described by Rich and Vickers-Rich (1999) as part of the clade Hypsilophodontidae. Subsequently, Agnolín *et al.* (2010) categorised the taxon as a non-dryomorph ornithopod. Recent phylogenetic analyses have recovered *Qantassaurus* within a clade of other Gondwanan taxa near the base of Ornithopoda (Madzia *et al.* 2018) and near the base of Iguanodontia (Boyd 2015).

***Talenkauen santacrucensis* Novas *et al.*, 2004**

Age: Maastrichtian, Late Cretaceous (Rozadilla *et al.* 2019).

Geology: Pari Aike Formation of Patagonia, Argentina (Novas *et al.* 2004).

Systematics: Initial analyses by Novas *et al.* (2004) recovered *Talenkauen* as a basal euiguanodontian. Subsequent phylogenetic studies have recovered the taxon outside of Cerapoda as a thescelosaurine thescelosaurid (Boyd 2015), within Cerapoda as a non-iguanodontian ornithopod (Madzia *et al.* 2018; Andrzejewski *et al.* 2019; Herne *et al.* 2019) and most recently, as an elasmarian iguanodontian (Dieudonné *et al.* 2021).

***Thescelosaurus assiniboensis* Brown *et al.*, 2011**

Age: Maastrichtian, Late Cretaceous (Boyd *et al.* 2009).

Geology: Frenchman Formation of Saskatchewan, Canada (Brown *et al.* 2011).

Systematics: Recent phylogenetic analyses have recovered *Thescelosaurus assiniboensis* outside of Cerapoda as a thescelosaurine thescelosaurid (Boyd 2015; Madzia *et al.* 2018) and within Cerapoda, as a non-iguanodontian ornithopod (Dieudonné *et al.* 2021).

***Thescelosaurus garbanii* Morris, 1976**

Age: Maastrichtian, Late Cretaceous (Boyd *et al.* 2009).

Geology: Hell Creek Formation of Montana, U.S.A. (Boyd *et al.* 2009).

Systematics: Owing to its poor completeness, *Thescelosaurus garbanii* has been included in limited phylogenetic analyses to date. Boyd *et al.* (2009) recovered *T. garbanii* in a clade with *Thescelosaurus neglectus*, confirming its referral to *Thescelosaurus*. Subsequently, *T. garbanii* has been consistently recovered in a clade with other species of *Thescelosaurus* (Brown *et al.* 2011; Boyd 2015; Madzia *et al.* 2018). A large-scale analysis of ornithischian relationships by Boyd (2015) recovered *T. garbanii* outside of Cerapoda, as a thescelosaurine thescelosaurid.

***Thescelosaurus neglectus* Gilmore, 1913**

Age: Maastrichtian, Late Cretaceous (Boyd *et al.* 2009).

Geology: Lance Formation of Wyoming, U.S.A. (Boyd *et al.* 2009).

Systematics: Recent phylogenetic analyses have recovered *Thescelosaurus neglectus* in one of two highly conflicting positions, either as a non-cerapodan thescelosaurid (Boyd 2015; Madzia *et al.* 2018; Herne *et al.* 2019) or within Cerapoda, as a non-iguanodontian ornithopod (Dieudonné *et al.* 2016; Dieudonné *et al.* 2021).

***Trinisaura santamartaensis* Coria et al., 2013**

Age: Campanian, Late Cretaceous (Coria et al. 2013).

Geology: Snow Hill Island Formation of James Ross Island, Antarctica (Coria et al. 2013).

Systematics: Phylogenetic analyses conducted in the original description of *Trinisaura* recovered the taxon as a non-dryomorph ornithopod (Coria et al. 2013). *Trinisaura* has subsequently been recovered as a non-iguanodontian ornithopod (Rozadilla et al. 2016; Bell et al. 2018b). Rozadilla et al. (2016) recovered *Trinisaura* within a clade of other Gondwanan ornithopods (*Anabisetia*, *Gasparinisaura*, *Macrogryphosaurus*, *Morrosaurus*, *Notohypsilophodon*, *Talenkauen*), while in Bell et al. (2018b) this taxon was found in a sister group relationship with *Anabisetia*.

***Vectidromeus insularis* Longrich et al., 2024**

Age: Hauterivian–Barremian, Early Cretaceous (Longrich et al. 2024).

Geology: Wessex Formation of the Isle of Wight, U.K. (Longrich et al. 2024).

Systematics: *Vectidromeus* has yet to be included within phylogenetic analyses, however Longrich et al. (2024) have assigned the new taxon to the family Hypsilophodontidae.

***Weewarrasaurus pobeni* Bell et al., 2018**

Age: Cenomanian, Late Cretaceous (Bell et al. 2018b).

Geology: Griman Creek Formation of New South Wales, Australia (Bell et al. 2018b).

Systematics: The original phylogenetic analysis by Bell et al. (2018b) recovered *Weewarrasaurus* as a non-iguanodontian ornithopod. This taxon was recovered in a polytomy along other Gondwanan taxa, including *Talenkauen* and *Macrogryphosaurus*.

***Yandusaurus hongheensis* He, 1979**

Age: ?Oxfordian, Upper Jurassic (Barrett *et al.* 2005).

Geology: Upper Shaximiao Formation of the Sichuan Province, China (Barrett *et al.* 2005).

Systematics: *Yandusaurus* was originally referred to the family Hypsilophodontidae (He 1979; He & Cai 1983). Early phylogenetic analyses recovered the taxon within a monophyletic Hypsilophodontidae, in a sister group with *Othnielia* (= *Nanosaurus agilis*, *sensu* Carpenter & Galton 2018; Weishampel & Heinrich 1993). More recently, Boyd (2015) recovered *Yandusaurus* in a polytomy with *Hexinlusaurus* and *Leaellynasaura* near the base of Neornithischia. In phylogenetic analyses from Han *et al.* (2018) and Dieudonné *et al.* (2021), *Yandusaurus* had to be pruned from the strict consensus trees to improve resolution.

***Yueosaurus tiantaiensis* Zheng *et al.*, 2012**

Age: Albian–Cenomanian, ‘middle’ Cretaceous (Zheng *et al.* 2012).

Geology: Liangtoutang Formation of the Zhejiang Province, China (Zheng *et al.* 2012).

Systematics: In the first phylogenetic analysis to include *Yueosaurus*, Boyd (2015) recovered the taxon in a clade with *Jeholosaurus* near the base of Neornithischia. Subsequently, *Yueosaurus* has been recovered as a non-cerapodan thescelosaurid (Herne *et al.* 2019), and a non-iguanodontian ornithopod (Dieudonné *et al.* 2016; Dieudonné *et al.* 2021).

***Zephyrosaurus schaffi* Sues, 1980**

Age: Albian, Early Cretaceous (Sues 1980; Michael *et al.* 2019).

Geology: Cloverly Formation of Montana, U.S.A. (Sues 1980).

Systematics: Recent phylogenetic analyses have recovered *Zephyrosaurus* as either a non-cerapodan thescelosaurid (Boyd 2015; Madzia *et al.* 2018; Herne *et al.* 2019)

or within Cerapoda, as an early-diverging ornithopod (Dieudonné *et al.* 2016; Han *et al.* 2018; Dieudonné *et al.* 2021). *Zephyrosaurus* frequently falls out within the clade Orodrominae (Brown *et al.* 2013b; Boyd 2015; Madzia *et al.* 2018; Dieudonné *et al.* 2021).

A2.1. Definitions of clade names as they are used in Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Clade definitions are not specifically outlined in Han *et al.* (2018), so are inferred. References for definitions used: 1, Butler *et al.* (2008); 2, Sereno (1998); 3, Norman (2015); 4, Calvo *et al.* (2007); 5, Rozadilla *et al.* (2016); 6, Sereno (2005); 7, Sereno (2012); 8, Madzia *et al.* (2018); 9, Marsh (1881); 10, Boyd (2015); 11, Brown *et al.* (2013b); 12, Sereno (1998).

Clade name	Original author	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
Cerapoda	Sereno (1986)	<i>Parasaurolophus walkeri</i> Parks 1922, <i>Triceratops horridus</i> Marsh 1889, their most recent common ancestor and all descendants. (node) ¹		
Ceratopsia	Marsh (1890)	N/A	All marginocephalian closer to <i>Triceratops</i> Marsh 1889 than to <i>Pachycephalosaurus</i> Brown and Schlaikjer 1943. (stem) ²	
Clypeodontia	Norman (2015)	<i>Hypsilophodon foxii</i> Huxley 1869, <i>Edmontosaurus regalis</i> Lambe 1917, their most recent common ancestor, and all of its descendants. (node) ³	N/A	<i>Hypsilophodon foxii</i> Huxley 1869, <i>Edmontosaurus regalis</i> Lambe 1917, their most recent common ancestor, and all of its descendants. (node) ³
Elasmaria	Calvo <i>et al.</i> (2007)	<i>Talenkauen santacrucensis</i> Novas <i>et al.</i> 2004 and <i>Macrogyrophosaurus gondwanicus</i> Calvo <i>et al.</i> 2007, their most recent common ancestor and all descendants. (node) ⁴	N/A	<i>Talenkauen santacrucensis</i> Novas <i>et al.</i> 2004 and <i>Macrogyrophosaurus gondwanicus</i> Calvo <i>et al.</i> 2007, their most recent common ancestor and all descendants. (node) ^{4,5}
Genasauria	Sereno (1986)	<i>Ankylosaurus magniventris</i> Brown 1908, <i>Stegosaurus stenops</i> Marsh 1877, <i>Parasaurolophus walkeri</i> Parks 1922, <i>Triceratops horridus</i> Marsh 1889, <i>Pachycephalosaurus wyomingensis</i> Gilmore 1931, their most recent common ancestor and all descendants. (node) ^{1,6}		
Heterodontosauridae	Romer (1966)	All ornithischians more closely related to <i>Heterodontosaurus tucki</i> Crompton & Charig 1962 than to <i>Parasaurolophus walkeri</i> Parks 1922, <i>Pachycephalosaurus wyomingensis</i> Gilmore, 1931, <i>Triceratops horridus</i> Marsh 1889, or <i>Ankylosaurus marginiventris</i> Brown 1908. (stem) ⁶		The most inclusive clade containing <i>Heterodontosaurus tucki</i> Crompton & Charig 1962 but not <i>Tianyulong confuciusi</i> Zheng <i>et al.</i> 2009, <i>Fruitadens haagarorum</i> Butler <i>et al.</i> 2010, <i>Echinodon becklesii</i> Owen 1858. (stem) ⁷

A2.1. (cont.)

Clade name	Original author	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
Hypsilophodontidae	Dollo (1882)	All neornithischians more closely related to <i>Hypsilophodon foxii</i> Huxley 1869 than to <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ⁶	N/A	All neornithischians more closely related to <i>Hypsilophodon foxii</i> Huxley 1869 than to <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ⁶
Iguanodontia	Dollo (1888) / Baur (1891)	All ornithopods more closely related to <i>Parasaurolophus walkeri</i> Parks 1922 than to <i>Hypsilophodon foxii</i> Huxley 1869 or <i>Thescelosaurus neglectus</i> Gilmore 1913. (stem) ⁶		<i>Iguanodon bernissartensis</i> Boulenger 1881, <i>Dryosaurus altus</i> Marsh 1878, <i>Rhabdodon priscus</i> Matheron 1869, <i>Tenontosaurus tilletti</i> Ostrom 1970, their common ancestors and all of their descendants. (node) ⁸
Marginocephalia	Sereno (1986)	<i>Triceratops horridus</i> Marsh 1889, <i>Pachycephalosaurus wyomingensis</i> Gilmore 1931, their most recent common ancestor and all descendants. (node) ¹		
Neornithischia	Cooper (1985)	All genasaurians more closely related to <i>Parasaurolophus walkeri</i> Parks 1922 than to <i>Ankylosaurus magniventris</i> Brown 1908 or <i>Stegosaurus stenops</i> Marsh 1877. (stem) ¹		
Ornithischia	Seeley (1887)	All dinosaurs more closely related to <i>Triceratops horridus</i> Marsh 1889 than to either <i>Passer domesticus</i> Linnaeus 1758, or <i>Saltasaurus loricatus</i> Bonaparte & Powell 1980. (stem) ¹		
Ornithopoda	Marsh (1882)	All genasaurians more closely related to <i>Parasaurolophus walkeri</i> Parks 1922, than to <i>Triceratops horridus</i> Marsh 1889. (stem) ^{1,9}		
Orodrominae	Brown <i>et al.</i> (2013b)	All neornithischians more closely related to <i>Orodromeus makelai</i> Horner & Weishampel 1988 than to <i>Thescelosaurus neglectus</i> Gilmore 1913 or <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ¹⁰	N/A	All 'thescelosaurids' [ornithopods] closer to <i>Orodromeus makelai</i> Horner & Weishampel 1988 than to <i>Thescelosaurus neglectus</i> Gilmore 1913. (stem) ¹¹
Pachycephalosauria	Maryanska & Osmolska (1974)	N/A	All marginocephalians closer to <i>Pachycephalosaurus</i> than to <i>Triceratops</i> Marsh 1889. (stem) ¹²	

A2.1. (cont.)

Clade name	Original author	Boyd (2015)	Han <i>et al.</i> (2018)	Dieudonné <i>et al.</i> (2021)
Parksosauridae	Buchholz (2002)	All neornithischians more closely related to <i>Parksosaurus warreni</i> Parks 1926 than to <i>Hypsilophodon foxii</i> Huxley 1869, <i>Dryosaurus altus</i> Marsh 1878, or <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ¹⁰	N/A	All neornithischians more closely related to <i>Parksosaurus warreni</i> Parks 1926 than to <i>Hypsilophodon foxii</i> Huxley 1869, <i>Dryosaurus altus</i> Marsh 1878, or <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ¹⁰
Thescelosauridae	Brown <i>et al.</i> (2013b)	<i>Thescelosaurus neglectus</i> Gilmore 1913, <i>Orodromeus makelai</i> Horner & Weishampel 1988, their most recent common ancestor, and all of its descendants. (node) ¹¹	N/A	N/A
Thescelosaurinae	Sternberg (1937)	All neornithischians more closely related to <i>Thescelosaurus neglectus</i> Gilmore 1913 than to <i>Orodromeus makelai</i> Horner & Weishampel 1988 or <i>Parasaurolophus walkeri</i> Parks 1922. (stem) ¹⁰	N/A	N/A
Thyreophora	Nopcsa (1915)	All genasaurians more closely related to <i>Ankylosaurus magniventris</i> Brown 1908 than to <i>Parasaurolophus walkeri</i> Parks 1922, <i>Triceratops horridus</i> Marsh 1889, or <i>Pachycephalosaurus wyomingensis</i> Gilmore 1931. (stem) ¹		

A2.2. First (FAD) and last appearance dates (LAD) of operational taxonomic units (OTUs) from data matrices by Boyd (2015; B), Han *et al.* (2018; H) and Dieudonné *et al.* (2021; D). Ages obtained from the Paleobiology database (PBDB; <https://paleobiodb.org/>) checked against recent literature and updated where necessary.

OTU	B	H	D	FAD	LAD	Reference
<i>Abriotosaurus consors</i>	X	X	X	201.3	190.8	Bordy <i>et al.</i> (2020)
<i>Agilisaurus louderbacki</i>	X	X	X	170.3	168.3	Barrett <i>et al.</i> (2005)
<i>Albalophosaurus yamaguchiorum</i>		X		129.4	113	Matsuoka <i>et al.</i> (2016)
<i>Anabisetia saldivai</i>	X		X	93.5	89.3	PBDB
Ankylosauria			X	163.5	66	Dieudonné <i>et al.</i> (2021)
<i>Aquilops americanus</i>		X		109.9	103.6	Michael <i>et al.</i> (2019)
<i>Archaeoceratops oshimoi</i>	X	X	X	112.03	105.3	PBDB
<i>Asilisaurus kongwe</i>	X			247.2	242	PBDB
<i>Atlascopcosaurus loadsi</i>	X			113	100.5	Boyd (2015)
<i>Auroraceratops rugosus</i>		X		113	100.5	Suárez <i>et al.</i> (2016)
<i>Bagaceratops rozhdestvenskyi</i>		X		83.6	72.1	PBDB
<i>Callovosaurus leedsi</i>	X			166.1	163.5	Boyd (2015)
<i>Camptosaurus aphanoecetes</i>			X	150.8	145	PBDB
<i>Camptosaurus dispar</i>	X	X	X	156.3	146.8	Trujillo <i>et al.</i> (2006)
<i>Changchunsaurus parvus</i>	X	X	X	125	93.9	PBDB
<i>Chaoyangsaurus youngi</i>		X	X	156	139	Liu <i>et al.</i> (2012)
<i>Chilesaurus diegosuarezi</i>			X	148.7	147	Suárez <i>et al.</i> (2016)
<i>Convulosaurus marri</i>			X	125	113	PBDB
<i>Dryosaurus</i> (composite)			X	152.1	145	Carpenter & Lamanna (2015)
<i>Dryosaurus altus</i>	X	X		156.3	146.8	Trujillo <i>et al.</i> (2006)
<i>Dysalotosaurus lettowvorbecki</i>	X		X	157.3	152.1	Boyd (2015)
<i>Echinodon backlesii</i>	X	X	X	145	139.8	Boyd (2015)
<i>Elrhazosaurus nigeriensis</i>	X			125	113	PBDB
<i>Emausaurus ernsti</i>	X	X	X	183	182	PBDB
<i>Eocursor parvus</i>	X	X	X	201	196	Bordy <i>et al.</i> (2020)
<i>Eoraptor lunensis</i>		X		231.4	228	PBDB & Sereno <i>et al.</i> (2012)
<i>Eousdryosaurus nanohallucis</i>			X	155.7	152.1	Escaso <i>et al.</i> (2014)
<i>Euoplocephalus tutus</i>		X		76.7	76.4	Penkalski (2018)
<i>Fostoria dhimbangunmal</i>			X	100.2	96.6	Bell <i>et al.</i> (2019)
<i>Fruitadens haagarorum</i>	X	X	X	151.88	150.02	Maidment & Muxworthy (2019)
<i>Gargoyleosaurus parkpinorum</i>		X		157.3	152.1	PBDB
<i>Gasparinisaura cincosaltensis</i>	X	X	X	83.5	79.5	Dingus <i>et al.</i> (2000)
<i>Gideonmantellia amosanjuanae</i>		X		129.4	125	Ruiz-Omeñaca <i>et al.</i> (2012)
<i>Goyocephale lattimorei</i>		X	X	86.3	72.1	PBDB
<i>Haya griva</i>	X	X	X	86.3	83.6	Boyd (2015)

A2.2. (cont.)

OTU	B	H	D	FAD	LAD	Reference
<i>Herrerasaurus ischigualastensis</i>	X	X	X	229.2	227.94	Langer <i>et al.</i> (2018)
<i>Hesperosaurus mjosi</i>		X		161.2	150.8	PBDB
<i>Heterodontosaurus tucki</i>	X	X	X	201.3	190.8	PBDB
<i>Hexinlusaurus multidens</i>	X	X	X	170.3	168.3	Barrett <i>et al.</i> (2005)
<i>Homalocephale calathoceros</i>		X	X	83.6	66	PBDB
<i>Hualianceratops wucaiwangensis</i>		X		162.2	159.7	Han <i>et al.</i> (2015)
<i>Huayangosaurus taibaii</i>		X		170.3	168.3	Barrett <i>et al.</i> (2005)
<i>Hypsilophodon foxii</i>	X	X	X	129.4	125	Butler & Galton (2008)
<i>Iguanodon atherfieldensis</i>		X		125.45	122.46	PBDB
<i>Iguanodon bernissartensis</i>	X		X	129.4	125	Butler & Galton (2008)
<i>Isaberrysaura mollensis</i>		X	X	171.6	168.4	PBDB
<i>Jeholosaurus shangyuanensis</i>	X	X	X	126	125.8	Chang <i>et al.</i> (2017)
<i>Kaiparowits orodromine</i>	X			76.6	74.5	Roberts <i>et al.</i> (2013)
<i>Kangnasaurus coetzeei</i>			X	100.5	66	PBDB
<i>Koreaceratops hwaseongensis</i>		X		113	103	PBDB & Lee <i>et al.</i> (2011)
<i>Koreanosaurus boseongensis</i>	X	X	X	86.3	72.1	PBDB
<i>Kulindadromeus zabaikalicus</i>			X	168.3	166.1	Cincotta <i>et al.</i> (2019)
<i>Laquintasaura venezuelae</i>		X	X	200.91	199.3	Raven <i>et al.</i> (2019)
<i>Leaellynasaura amicagraphica</i>	X			113	100.5	Boyd (2015)
<i>Leptoceratops gracilis</i>		X		66.97	66	Arbour & Evans (2019)
<i>Lesothosaurus diagnosticus</i>	X	X	X	201.3	190.8	Bordy <i>et al.</i> (2020)
<i>Liaoceratops yanzigouensis</i>	X	X	X	125	122.46	Hailu <i>et al.</i> (2007)
<i>Lycorhinus angustidens</i>	X		X	201.3	190.8	Bordy <i>et al.</i> (2020)
<i>Macrogryphosaurus gondwanicus</i>	X		X	89.8	86.3	Boyd (2015)
<i>Mahuidacursor lipanglef</i>			X	85.8	83.6	PBDB
<i>Manidens condorensis</i>		X		171	167	Pol <i>et al.</i> (2011)
<i>Marasuchus lilloensis</i>	X	X		236	234	Marsicano <i>et al.</i> (2016)
<i>Micropachycephalosaurus hongtuy-anensis</i>	X	X		83.6	72.1	Butler & Zhao 2008
<i>Minmi paravertebra</i>		X		125	113	Bell <i>et al.</i> (2018a)
<i>Mochlodon suessi</i>			X	83.6	72.1	Ösi <i>et al.</i> (2012)
<i>Mochlodon vorosi</i>			X	86.3	83.6	PBDB
<i>Morrosaurus antarcticus</i>			X	72.1	66	PBDB & Garcia-Marsà <i>et al.</i> (2020)
<i>Mosaiceratops azumai</i>		X		93.9	72.1	PBDB & Jackson <i>et al.</i> (2018)
<i>Muttaborrasaurus langdoni</i>	X		X	113	100.5	Boyd (2015) & Dieudonné <i>et al.</i> (2021)
<i>Nanosaurus agilis</i>			X	150.208	149.43	Galli <i>et al.</i> (2018)
<i>Notohypsilophodon comodorensis</i>	X			100.5	86.3	Boyd (2015)
<i>Orodromeus makelai</i>	X	X	X	80.044	74.076	Freimuth & Varricchio (2019)

A2.2. (cont.)

OTU	B	H	D	FAD	LAD	Reference
<i>Oryctodromeus cubicularis</i>	X			100.5	93.9	PBDB
<i>Othnielosaurus consors</i>	X			156.3	146.8	Trujillo <i>et al.</i> (2006)
<i>Ouranosaurus nigeriensis</i>	X	X		125	113	Boyd (2015)
<i>Pachycephalosaurus wyomingensis</i>			X	72.1	66	PBDB
<i>Parksosaurus warreni</i>	X	X	X	70.4	68.4	Ogg <i>et al.</i> (2004)
<i>Pegomastax africanus</i>		X		201.3	199.3	PBDB
<i>Pinacosaurus grangeri</i>		X		83.6	72.1	PBDB
<i>Pisanosaurus mertii</i>	X	X		229.2	227.94	Langer <i>et al.</i> (2018)
<i>Prenocephale prenes</i>		X	X	83.6	66	PBDB
<i>Probactrosaurus gobiensis</i>		X		129.4	100.5	PBDB
<i>Protoceratops andrewsi</i>		X		83.6	72.1	PBDB
<i>Psittacosaurus lujiatunensis</i>		X		125.45	122.46	PBDB
<i>Psittacosaurus major</i>			X	130	122.5	PBDB
<i>Psittacosaurus mongoliensis</i>		X	X	125	113	PBDB
<i>Qantassaurus intrepidus</i>	X			127.2	125	PBDB
<i>Rhabdodon priscus</i>	X		X	72	71.5	Fondevilla <i>et al.</i> (2016)
<i>Rhabdodon</i> sp1			X	72.1	70	Dieudonné <i>et al.</i> (2021)
<i>Sanjuansaurus gordilloi</i>	X			229.2	227.94	Langer <i>et al.</i> (2018)
<i>Scelidosaurus harrisonii</i>	X	X	X	199.3	190.8	PBDB
<i>Scutellosaurus lawleri</i>	X	X	X	199.3	182.7	PBDB
<i>Silesaurus opolensis</i>	X	X	X	237	208.5	Drózdź (2018)
<i>Stegoceras validum</i>		X	X	83.5	70.6	Schott <i>et al.</i> (2011)
<i>Stegosauria</i>			X	170.3	125	Dieudonné <i>et al.</i> (2021)
<i>Stegosaurus stenops</i>		X		157.3	145	PBDB
<i>Stenopelix valdensis</i>	X	X	X	145	139.8	Butler & Sullivan (2009)
<i>Stormbergia dangershoeki</i>	X			201.3	190.8	Bordy <i>et al.</i> (2020)
<i>Talenkauen santacrucensis</i>	X		X	93.9	89.8	Rozadilla <i>et al.</i> (2019)
<i>Tawa hallae</i>	X			215	213	Nesbitt <i>et al.</i> (2009)
<i>Tenontosaurus dossi</i>	X		X	125	113	Andrzejewski <i>et al.</i> (2019)
<i>Tenontosaurus tilletti</i>	X	X	X	125	100.5	PBDB
<i>Thescelosaurus assiniboensis</i>	X		X	72.1	66	PBDB
<i>Thescelosaurus garbanii</i>	X			67.4	66	Renne <i>et al.</i> (2013)
<i>Thescelosaurus neglectus</i>	X	X	X	69	66	Lehman <i>et al.</i> (2006)
<i>Tianyulong confuciusi</i>	X	X	X	163.5	157	Gao & Shubin (2012)
<i>Valdosaurus canaliculatus</i>	X		X	129.4	125	Barrett <i>et al.</i> (2011)
<i>Vegagete ornithopod</i>			X	129.4	113	Fernández-Baldor <i>et al.</i> (2017)
<i>Wannanosaurus yansiensis</i>	X	X	X	72.1	66	PBDB
<i>Xuanhuaceratops niei</i>		X		163.5	145	PBDB
<i>Yamaceratops dorn gobiensis</i>		X		86.3	83.6	PBDB
<i>Yandusaurus hongheensis</i>	X	X	X	161.5	154.8	Barrett <i>et al.</i> (2005)

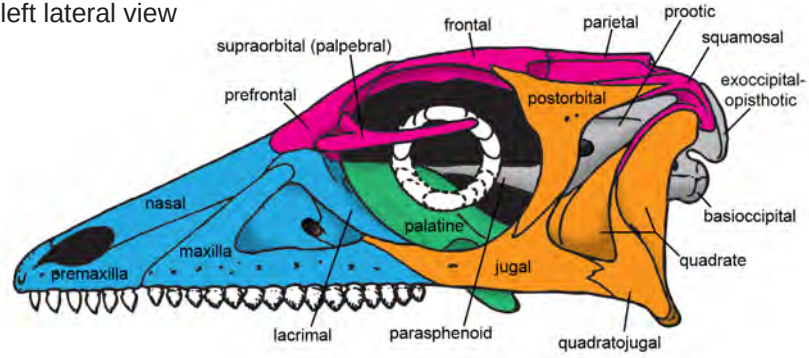
A2.2. (cont.)

OTU	B	H	D	FAD	LAD	Reference
<i>Yinlong downsi</i>	X	X	X	163.5	157.3	Han <i>et al.</i> (2018)
<i>Yueosaurus tiantaiensis</i>	X	X	X	105.9	96	Wang <i>et al.</i> (2000)
<i>Zalmoxes robustus</i>	X	X	X	72.1	66	Brusatte <i>et al.</i> (2017)
<i>Zalmoxes shqiperorum</i>	X		X	72.1	66	Brusatte <i>et al.</i> (2017)
<i>Zephyrosaurus schaffi</i>	X	X	X	109.9	103.6	Michael <i>et al.</i> (2019)

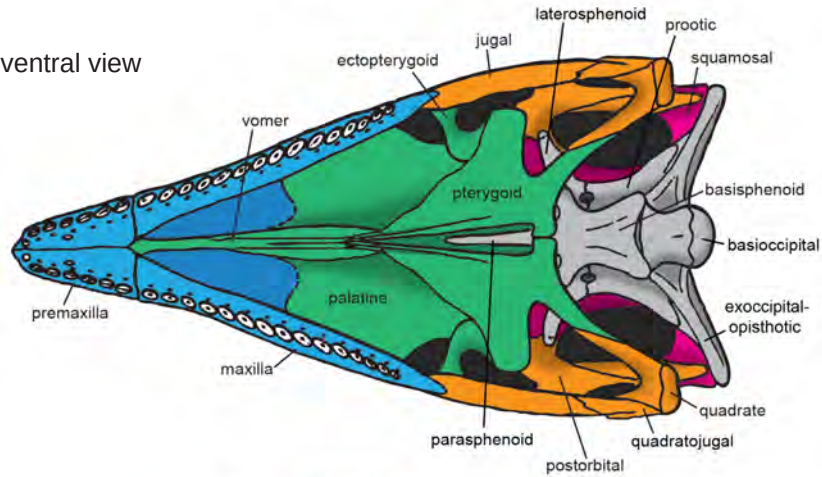
A2.3. Character partitions and their contents.

Partition	Contents
<i>Craniodental -</i>	
Rostrum	antorbital fenestra; lacrimal; maxilla; nares; nasal; premaxilla; rostral bone
Palate	ectopterygoid; palatine; pterygoid; vomer
Cranial roof	frontal; palpebral (supraorbital); parietal; parietosquamosal; post-temporal fenestra; prefrontal; squamosal; supratemporal fenestra
Skull base	infratemporal fenestra; jugal; postorbital; quadrate; quadratojugal
Braincase	basioccipital; basal tubera; basisphenoid; laterosphenoid; occiput; opisthotic; paraoccipital; prootic; supraoccipital
Mandible	angular; coronoid; dentary; mandibular fenestra; post-dentary bones; prementary; retroarticular process; surangular
Dentition	dentary teeth; maxillary teeth; premaxillary teeth
<i>Postcranium -</i>	
Vertebral column & ribs	caudals; cervicals; dorsals; sacrals
Pectoral girdle & sternum	clavicle; coracoid; parascapula; scapula; sternum
Forelimb	carpals; humerus; intermedium; manual digits; metacarpals; radius; ulna
Pelvic girdle	ilium; ischium; pubis
Hindlimb	astragalus; calcaneum; femur; fibula; metatarsals; pedal digits; tarsals; tibia

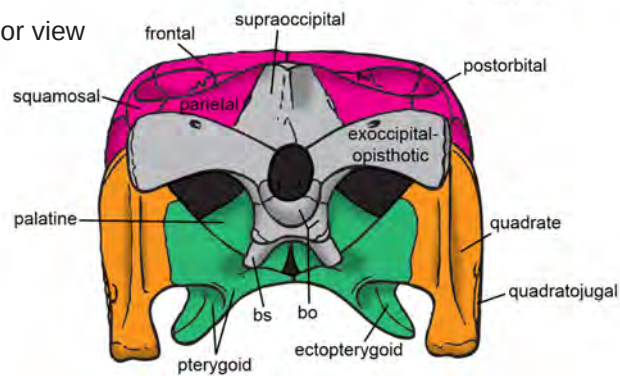
left lateral view



ventral view

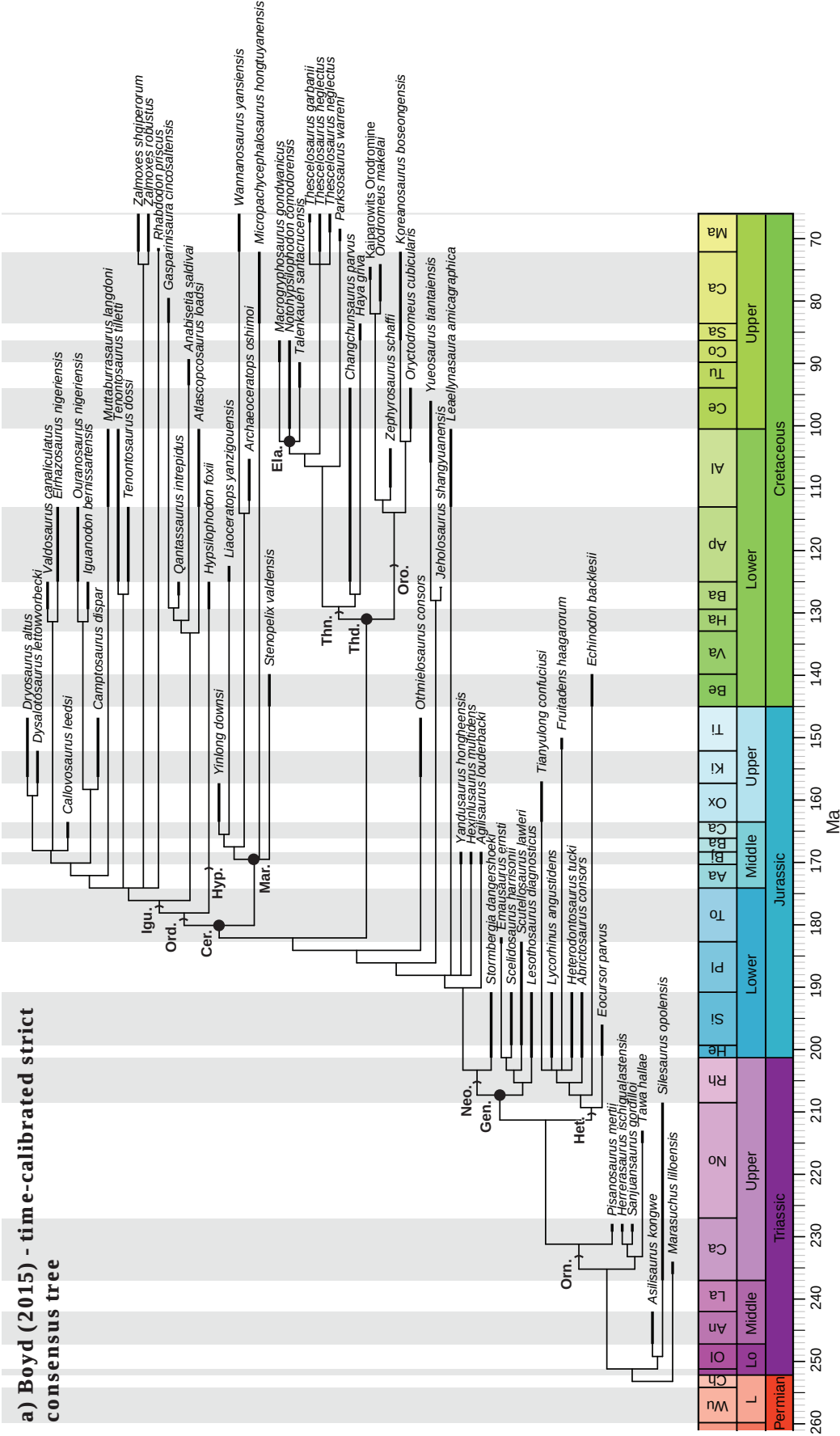


posterior view

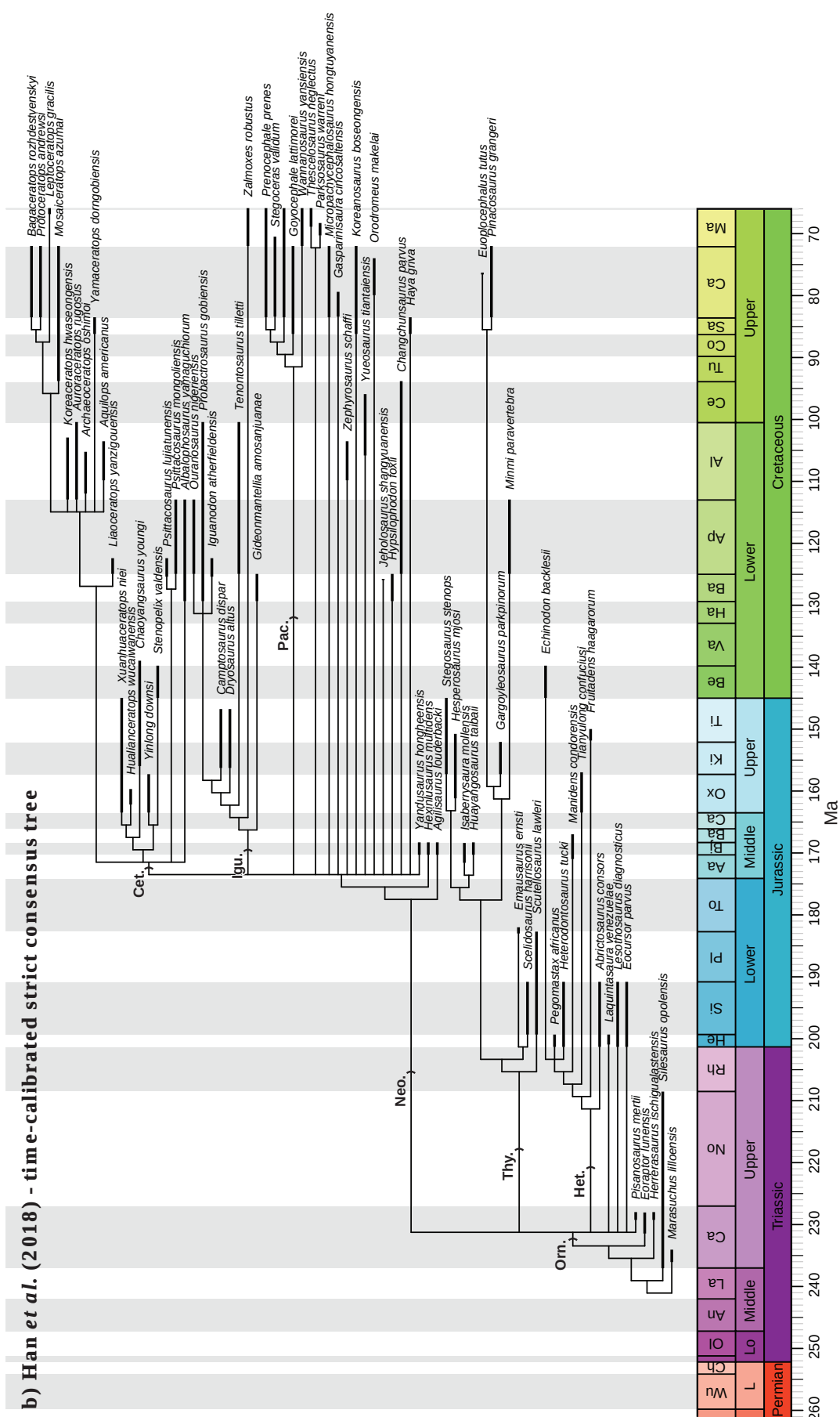


A2.4. Diagram illustrating the cranial partitions used: rostrum (blue); palate (green); cranial roof (pink); skull base (orange); braincase (grey). Diagram of *Lesothosaurus diagnosticus* modified from Sereno (1991). Abbreviations: **bs**, basisphenoid; **bo**, basoccipital.

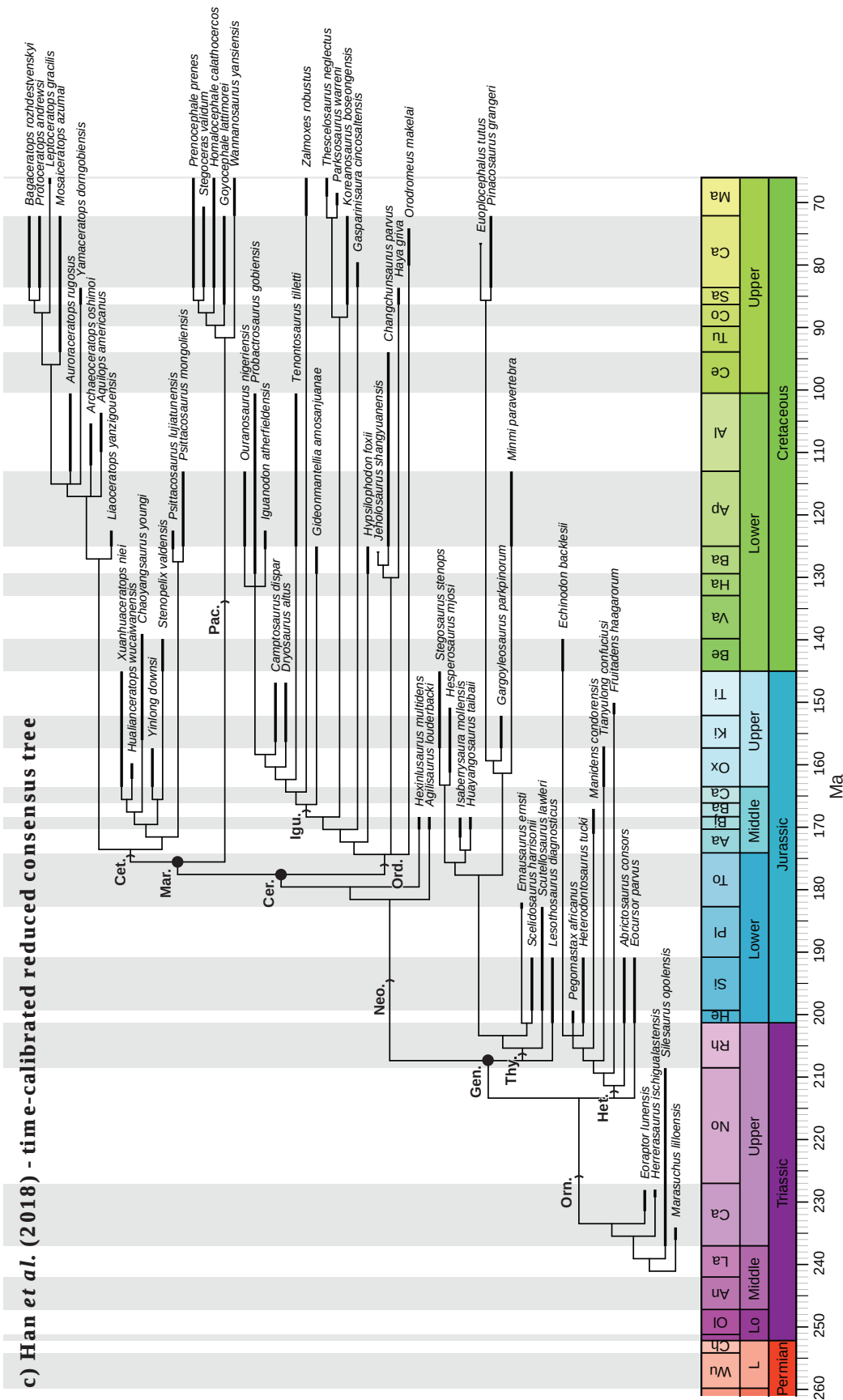
a) Boyd (2015) - time-calibrated strict consensus tree



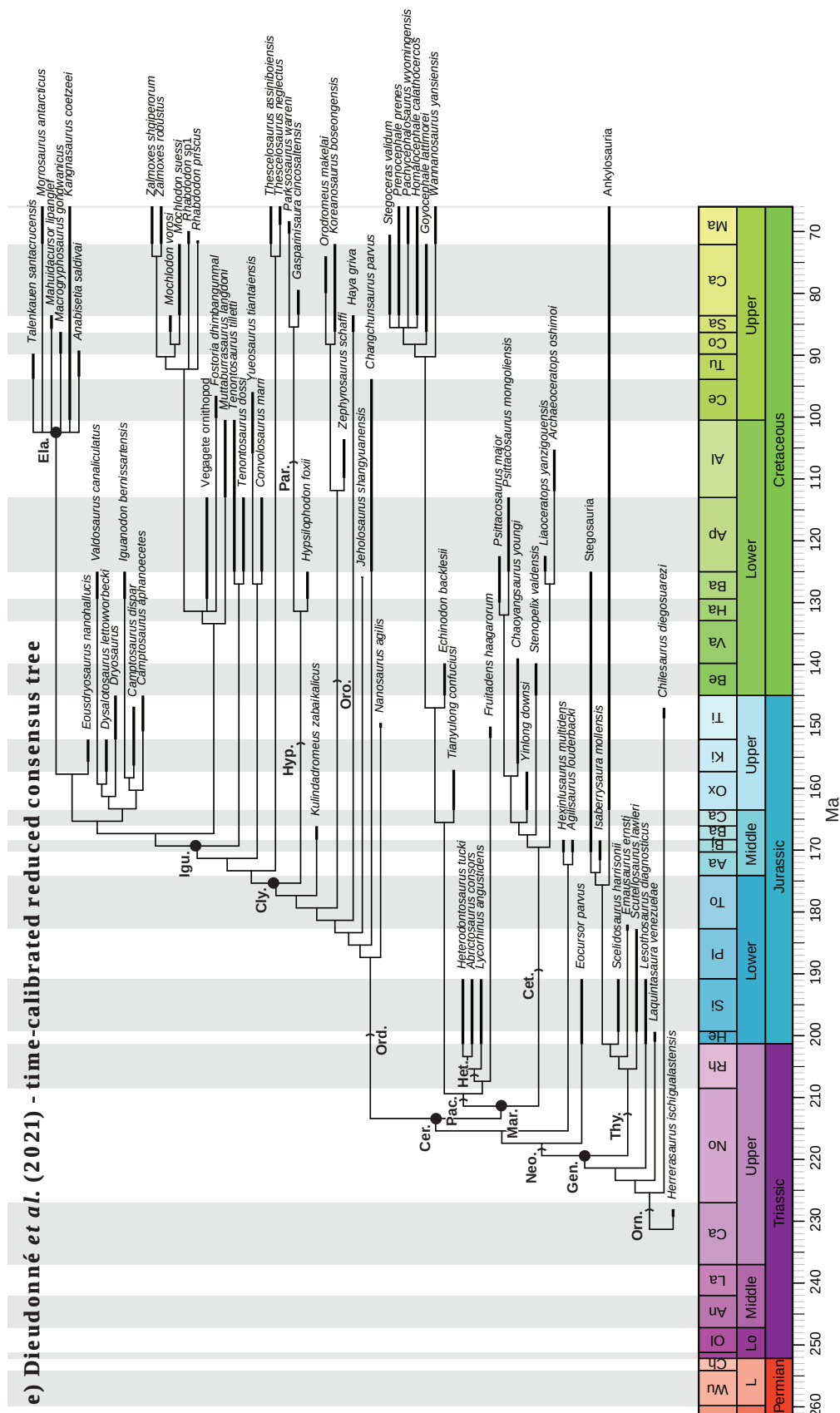
A2.5a. Time-calibrated strict consensus tree produced from 36 MPts generated from the matrix by Boyd (2015). Minimum branch length set to 2 million years. Abbreviations: Cer., Cerapoda; Ela., Elasmaria; Gen., Genasauria; Het., Heterodontosauridae; Hyp., Hypsilophodontidae; Igu., Iguanodontia; Mar., Marginocephalia; Neo., Neornithischia; Ord., Ornithomimidae; Orn., Ornithischia; Oro., Orodrominae; Par., Parksosauridae; Thn., Thescelosauridae; Thd., Thescelosaurinae; Thy., Thyreophora.



A2.5b. Time-calibrated strict consensus tree produced from 53,376 MPTs generated from the matrix by Han *et al.* (2018). Minimum branch length set to 2 million years. Abbreviations: Cer., Ceratopsia; Cet; Ceratopsia; Het., Heterodontosauridae; Igu., Iguanodontia; Neo., Neornithischia; Orn., Ornithischia; Pac., Pachycephalosauria; Thy., Thyreophora.



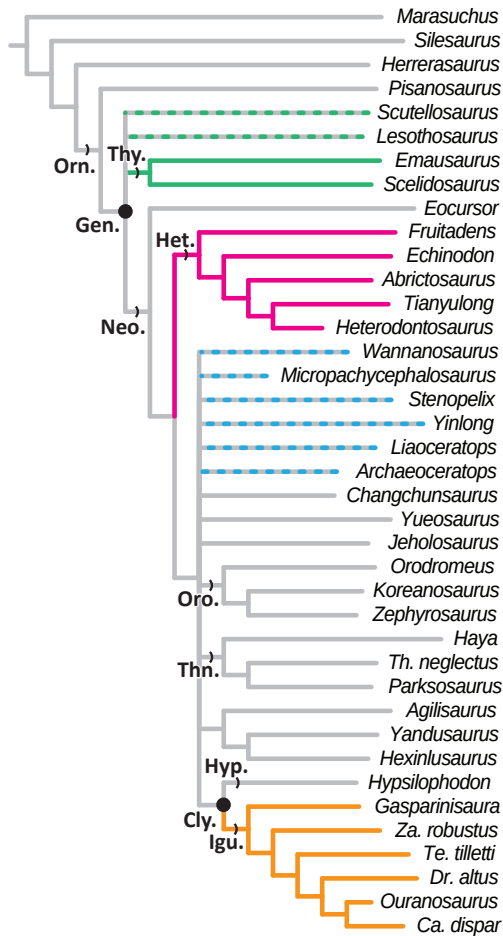
A2.5c. Time-calibrated reduced consensus tree produced by pruning eight unstable taxa from 53,376 MPTs generated from the matrix by Han *et al.* (2018). Minimum branch length set to 2 million years. Abbreviations: Cer., Ceratopsia; Gen., Genasauria; Het., Heterodontosauridae; Igu., Iguanodontia; Mar., Marginocephalia; Neo., Neornithischia; Ord., Ornithischia; Pac., Pachycephalosauria; Thy., Thyreophora.



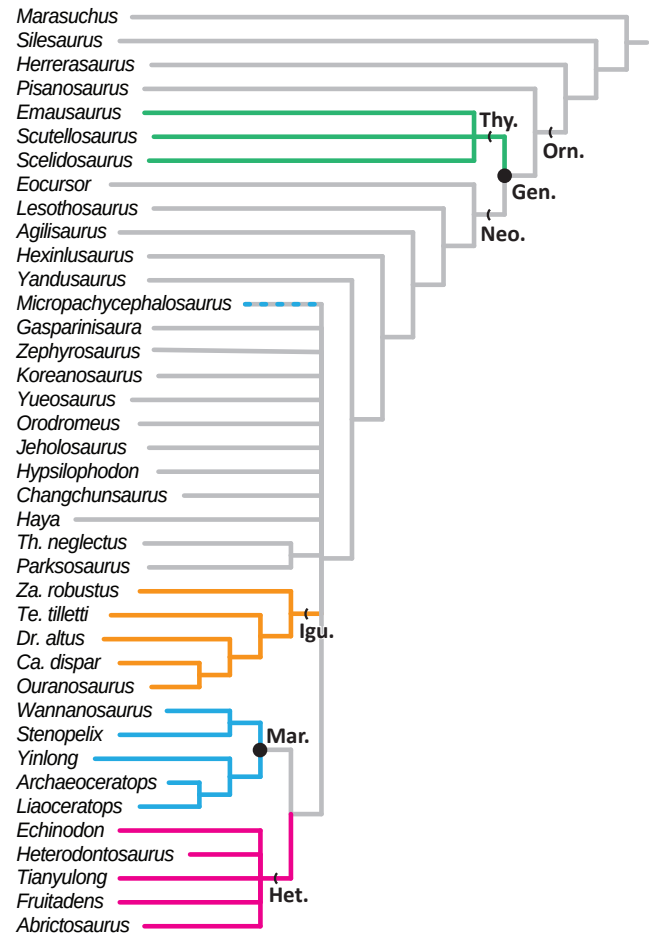
A2.5e. Time-calibrated reduced consensus tree produced from pruning of *Yandusaurus* from the 176 MPTs generated from the matrix by Dieudonné *et al.* (2021). Minimum branch length set to 2 million years. Abbreviations: Cer., Cerapoda; Cet; Ceratopsia; Cly., Clypeodonta; Ela., Elasmaria; Gen., Genasauria; Het., Heterodontosauridae; Hyp., Hypsilophodontidae; Igu., Iguanodontia; Mar., Marginocephalia; Neo., Neornithischia; Ord., Ornithopoda; Orn., Ornithischia; Oro., Orodrominae; Pac., Pachycephalosauria; Par., Parksosauridae; Thy., Thyreophora.

Analysis A.1 - shared OTUs

a) Boyd (2015)



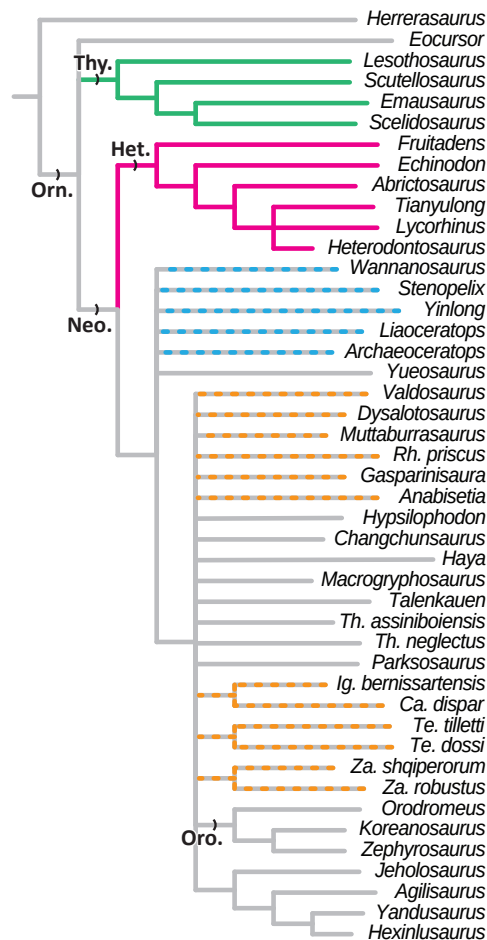
b) Han *et al.* (2018)



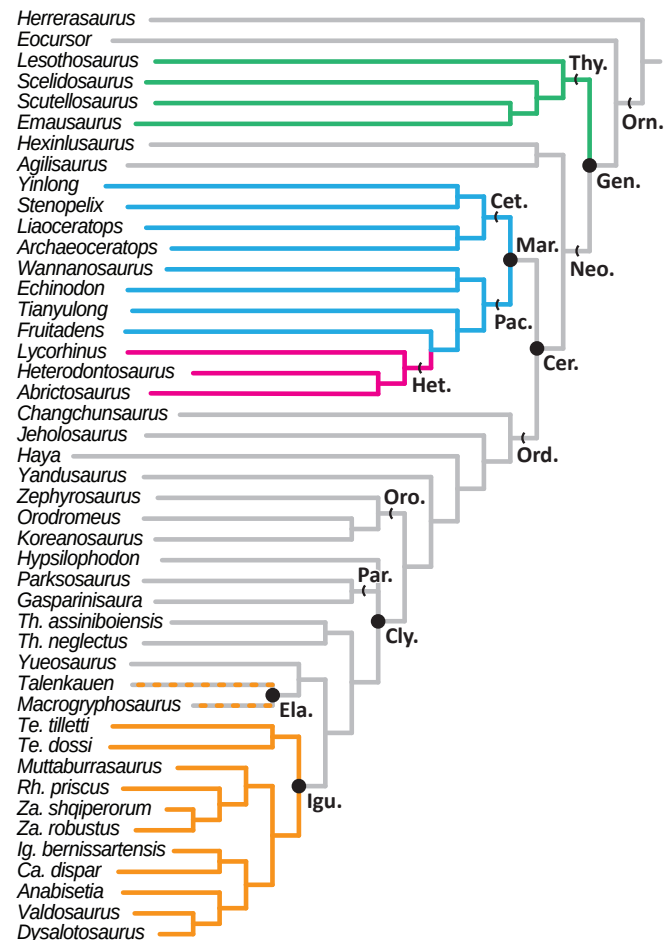
A2.6. Strict consensus trees produced using only shared taxa ($n=39$) in Boyd (2015) and Han *et al.* (2018). a) Strict consensus of 66 MPTs produced from Boyd (2015); and, (b) strict consensus of 164 MPTs from Han *et al.* (2018). Abbreviations: *Ca.*, *Camptosaurus*; *Cly.*, *Clypeodonta*; *Gen.*, *Genasauria*; *Het.*, *Heterodontosauridae* (pink); *Igu.*, *Iguanodontia* (orange); *Mar.*, *Marginocephalia* (blue); *Neo.*, *Neornithischia*; *Orn.*, *Ornithischia*; *Oro.*, *Orodrominae*; *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Thy.*, *Thyreophora* (green); *Za.*, *Zalmoxes*. Coloured dashed lines indicate the group an OTU was recovered in the original respective analysis by Boyd (2015) or Han *et al.* (2018).

Analysis A.2 - shared OTUs

a) Boyd (2015)



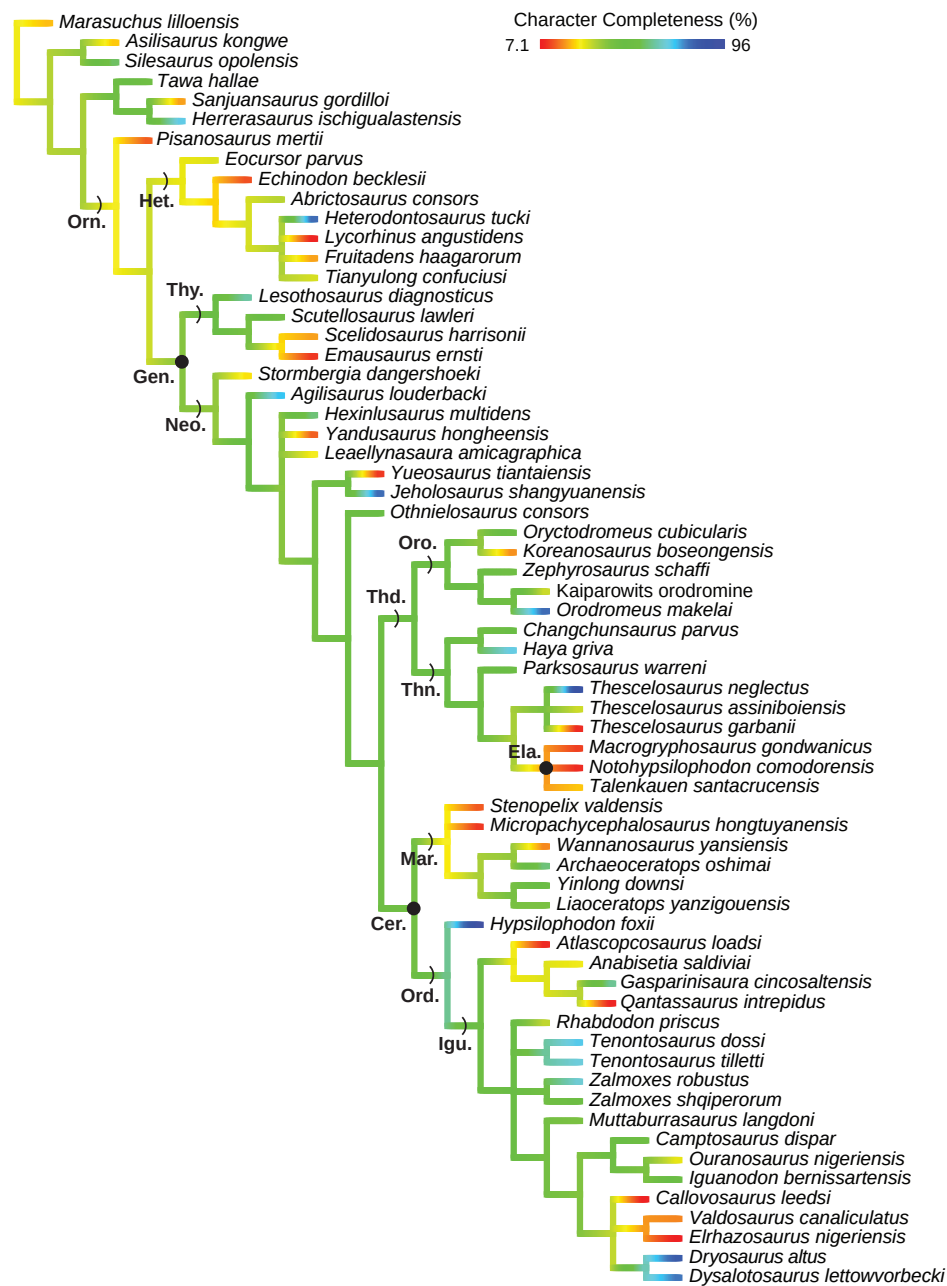
b) Dieudonné *et al.* (2021)



A2.7. Strict consensus trees produced using only shared taxa ($n=45$) in Boyd (2015) and Dieudonné *et al.* (2021). a) Strict consensus of 180 MPTs produced from Boyd (2015); and, (b) strict consensus of 2 MPTs from Dieudonné *et al.* (2021). Abbreviations: *Ca.*, *Camptosaurus*; *Cer.*, *Cerapoda*; *Cet.*, *Ceratopsia*; *Cly.*, *Clypeodonta*; *Ela.*, *Elasmaria*; *Gen.*, *Genasauria*; *Het.*, *Heterodontosauridae* (pink); *Ig.*, *Iguanodon*; *Igu.*, *Iguanodontia* (orange); *Mar.*, *Marginocephalia* (blue); *Neo.*, *Neornithischia*; *Ord.*, *Ornithopoda*; *Orn.*, *Ornithischia*; *Oro.*, *Orodrominae*; *Pac.*, *Pachycephalosauridae*; *Par.*, *Parksosauridae*; *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Thy.*, *Thyreophora* (green); *Za.*, *Zalmoxes*. Coloured dashed lines indicate the group an OTU was recovered in the original respective analysis by Boyd (2015) or Dieudonné *et al.* (2021).

Taxon Completeness

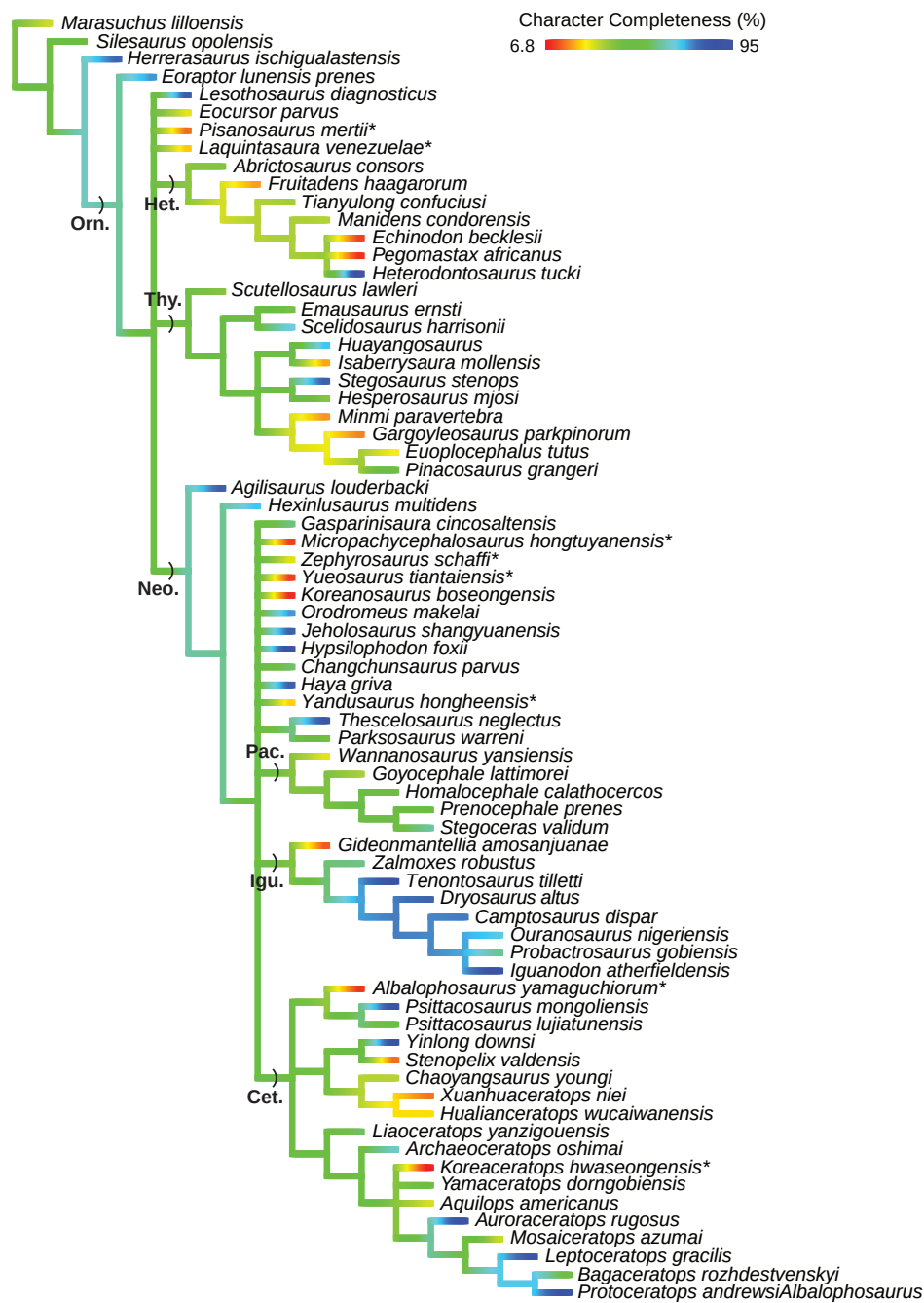
a) Boyd (2015)



A2.8. Character completeness scores of taxa mapped onto the strict consensus trees of: (a) the 36 most parsimonious trees generated from the matrix by Boyd (2015); (b) the 53,376 most parsimonious trees generated from the matrix by Han *et al.* (2018); and (c) the 176 most parsimonious trees generated from the matrix by Dieudonné *et al.* (2021). Asterisks indicate taxa pruned for the reduced consensus trees in Han *et al.* (2018) and Dieudonné *et al.* (2021). Abbreviations: Cer., Cerapoda; Cet., Ceratopsia; Ela., Elasmaria; Gen., Genasauria; Het., Heterodontosauridae; Igu., Iguanodontia; Mar., Marginocephalia; Neo., Neornithischia; Orn., Ornithischia; Ord., Ornithopoda; Pac., Pachycephalosauria; Thd., Thescelosauridae; Thn., Thescelosaurinae; Thy., Thyreophora.

Taxon Completeness

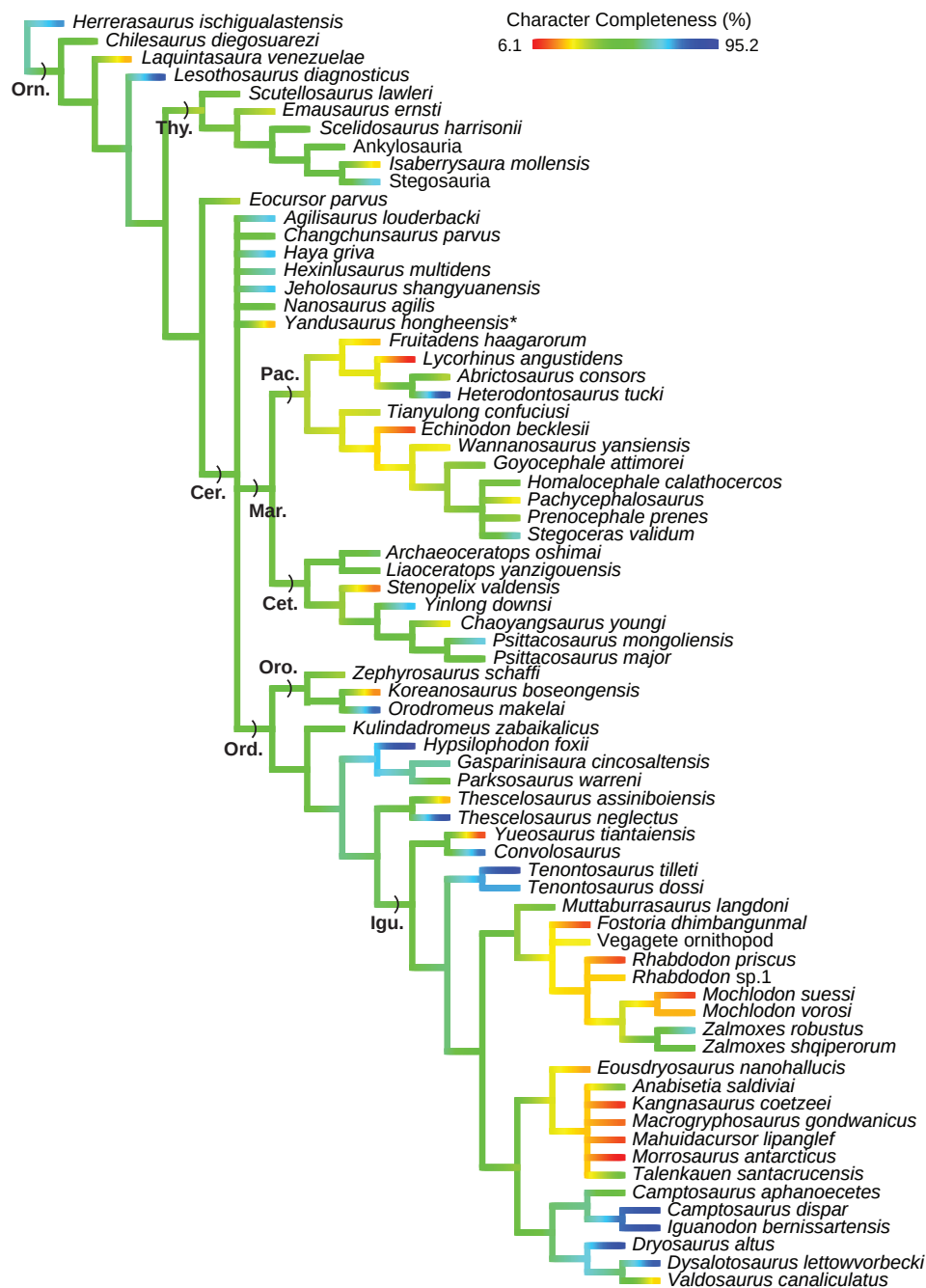
b) Han *et al.* (2018)



A2.8. (cont.)

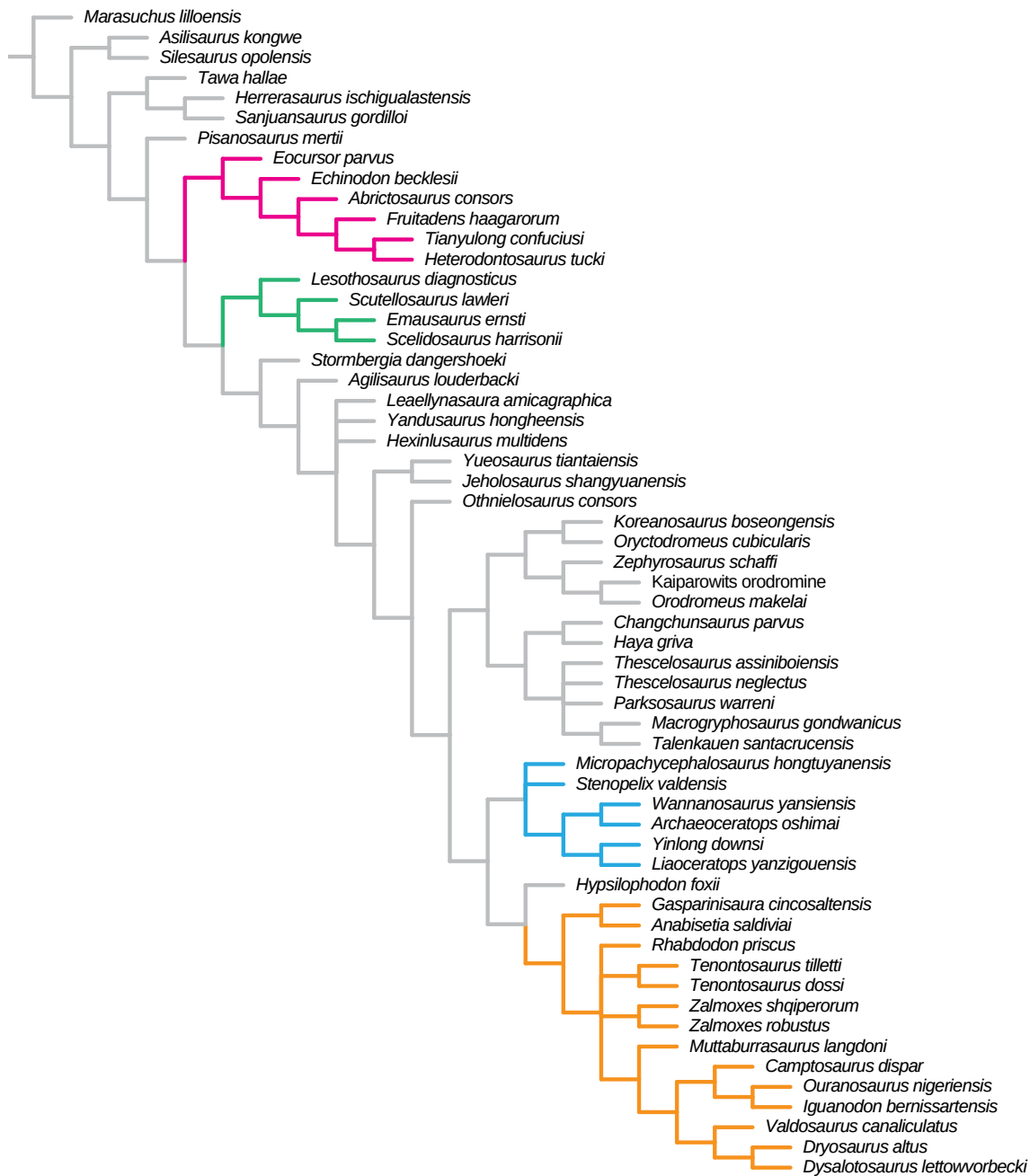
Taxon Completeness

c) Dieudonné *et al.* (2021)



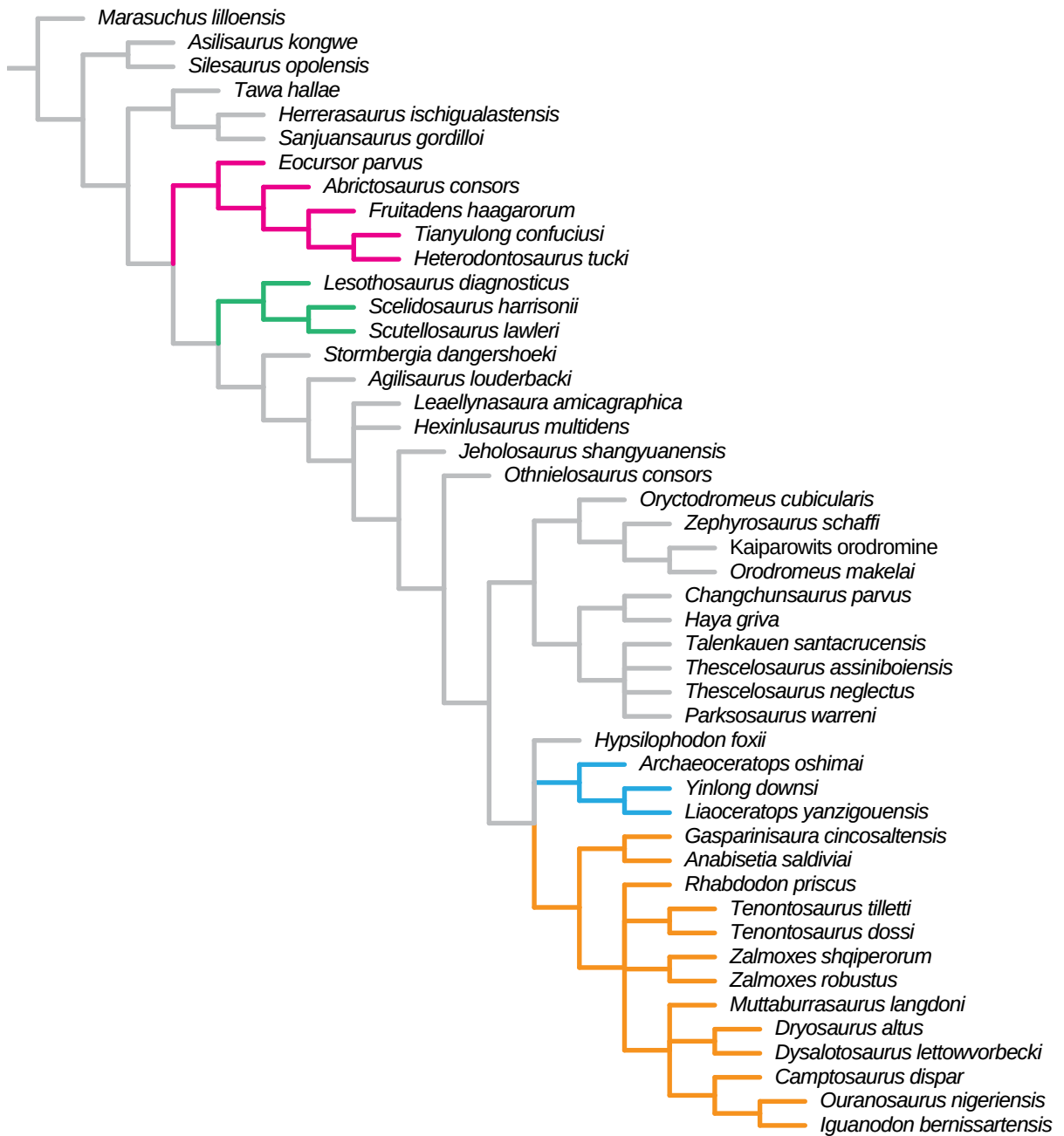
A2.8. (cont.)

Analysis B.1.B2015 - excluding OTUs <10% complete



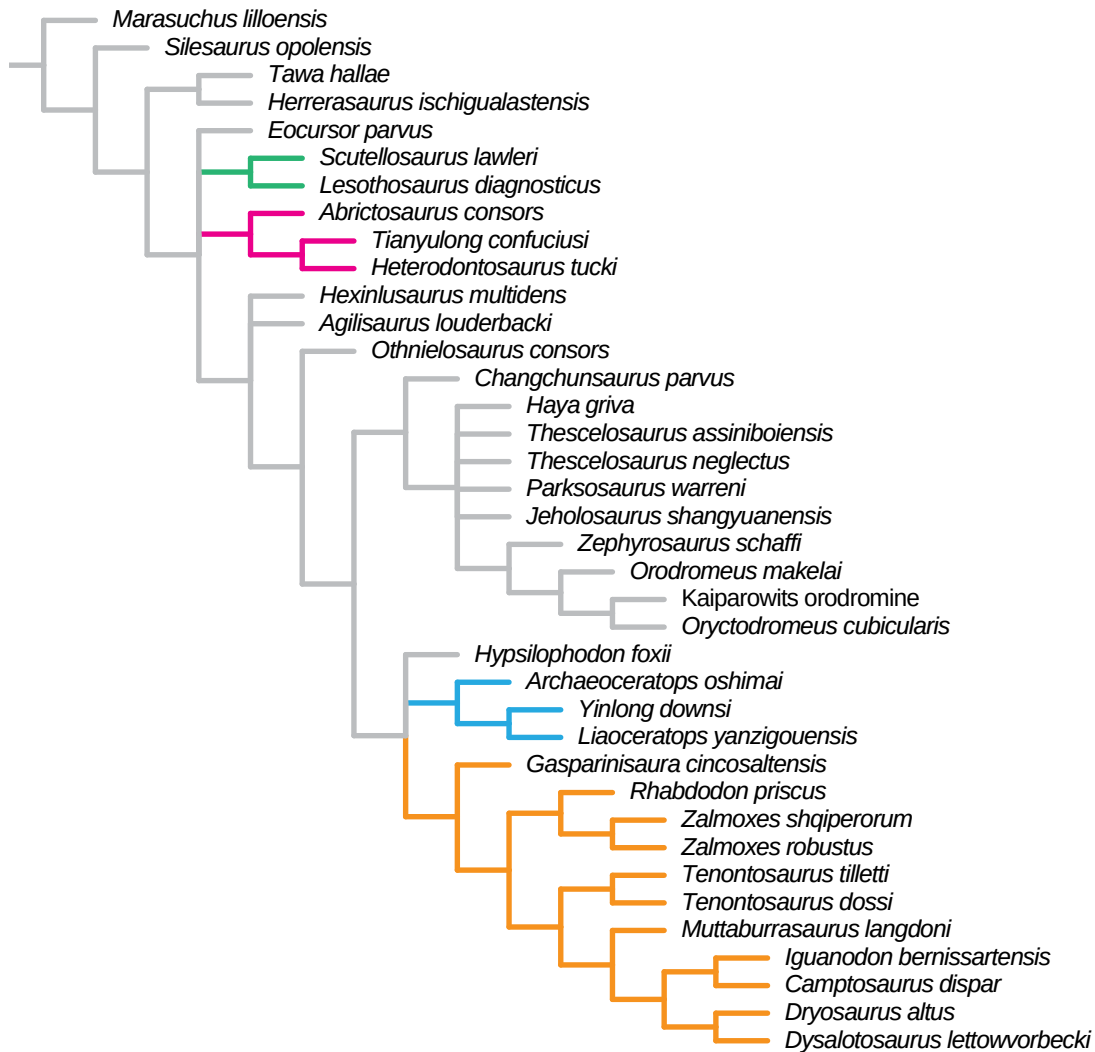
A2.9. Strict consensus tree of 24 MPTs produced from Boyd (2015) when OTUs <10% complete are excluded *a priori* (n=7). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis B.2.B2015 - excluding OTUs <20% complete



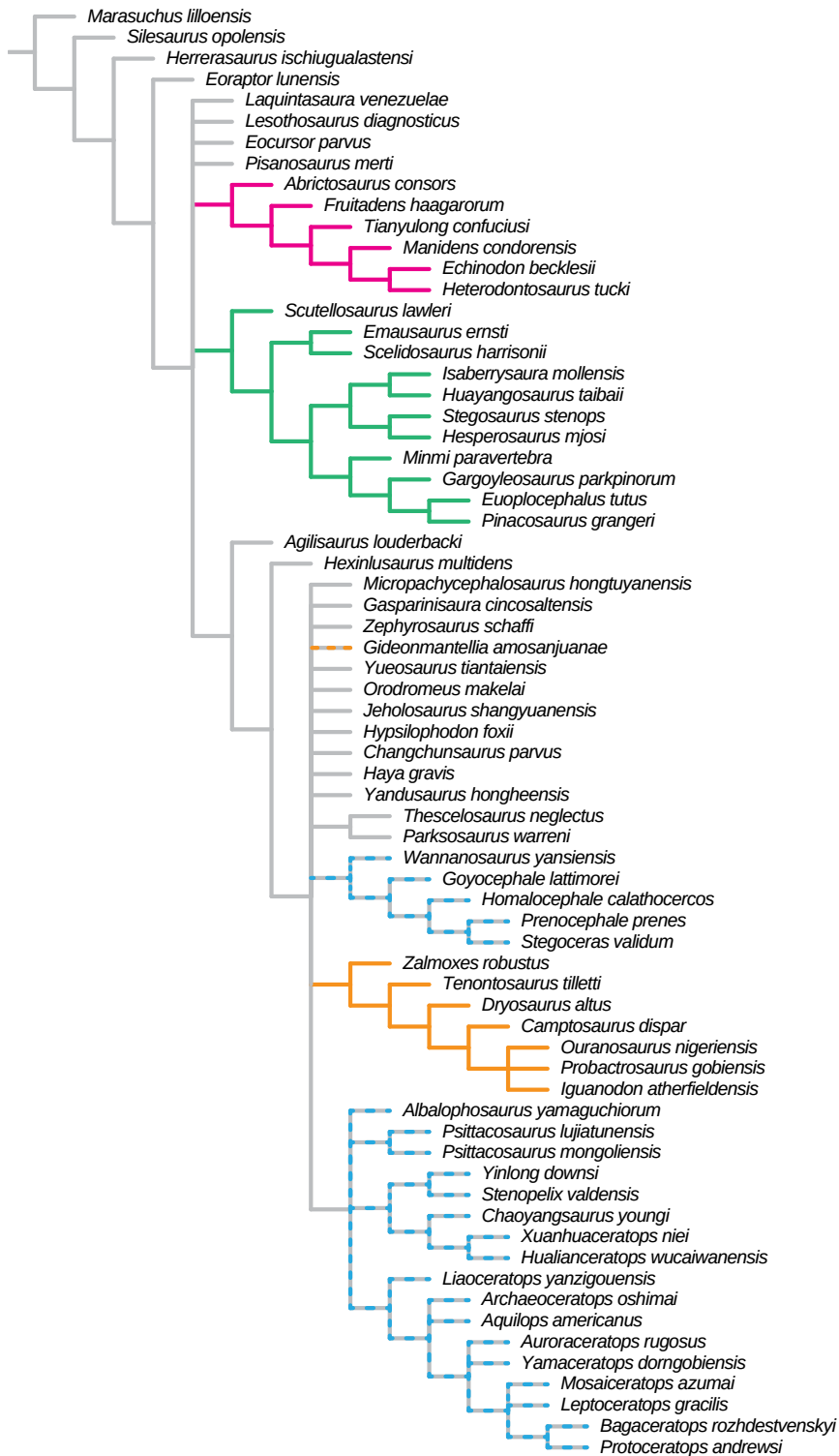
A2.10. Strict consensus tree of 28 MPTs produced from Boyd (2015) when OTUs <20% complete are excluded *a priori* (n=18). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis B.3.B2015 - excluding OTUs <30% complete



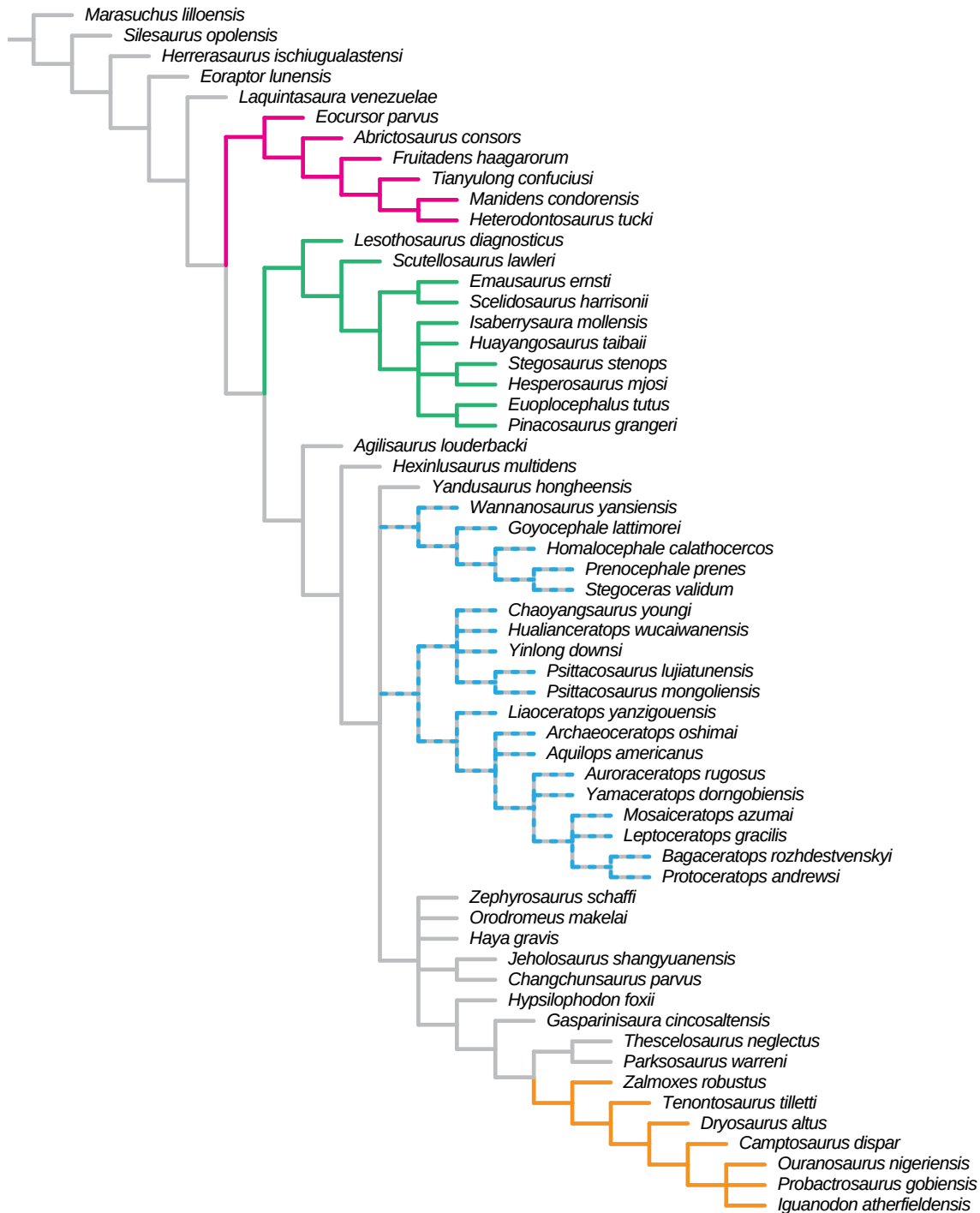
A2.11. Strict consensus tree of 8 MPTs produced from Boyd (2015) when OTUs <30% complete are excluded *a priori* (n=27). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis B.1.H2018 - excluding OTUs <10% complete



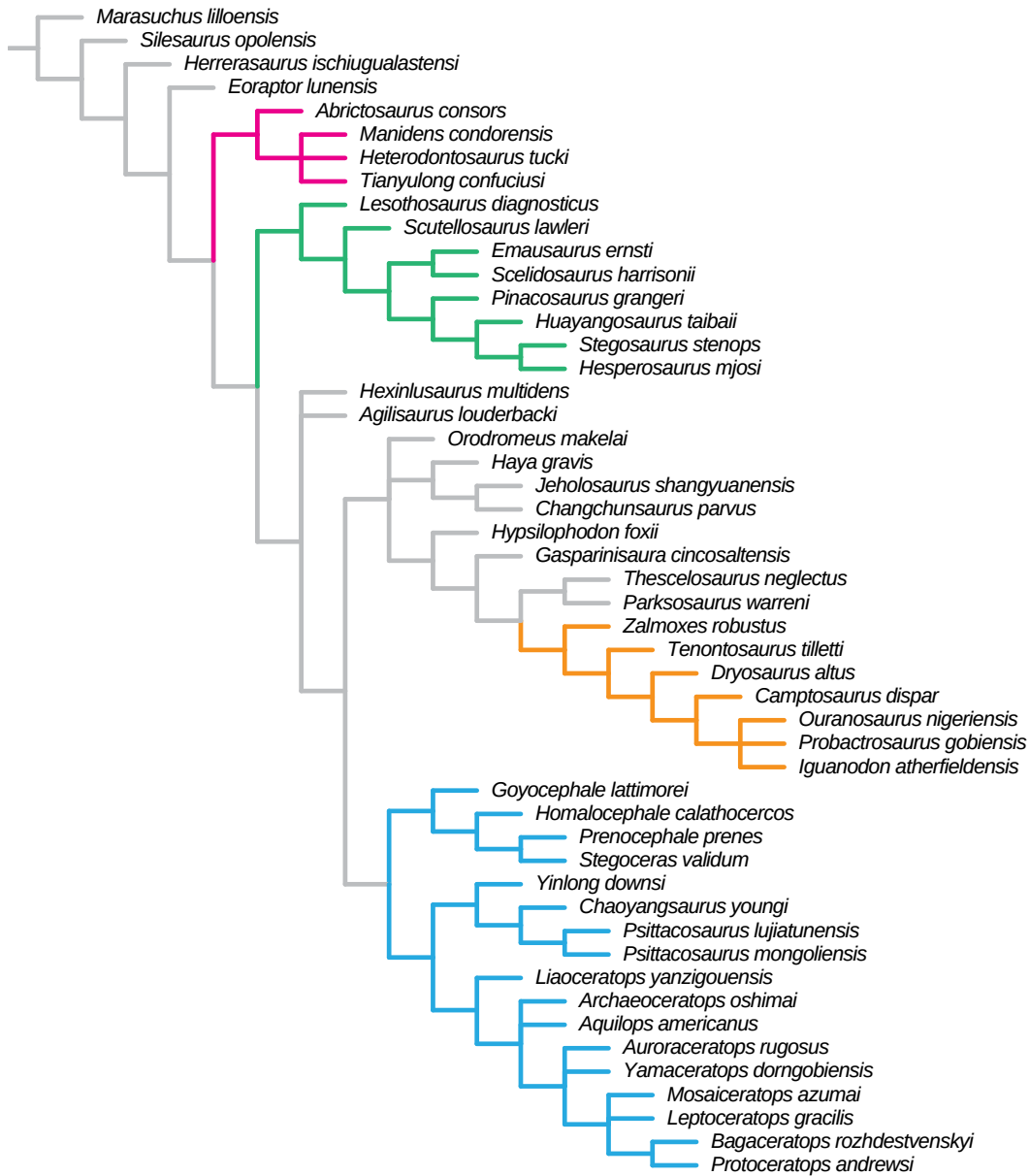
A2.12. Strict consensus tree of 52,700 MPTs produced from Han *et al.* (2018) when OTUs <10% complete are excluded *a priori* (n=3). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis B.2.H2018 - excluding OTUs <20% complete



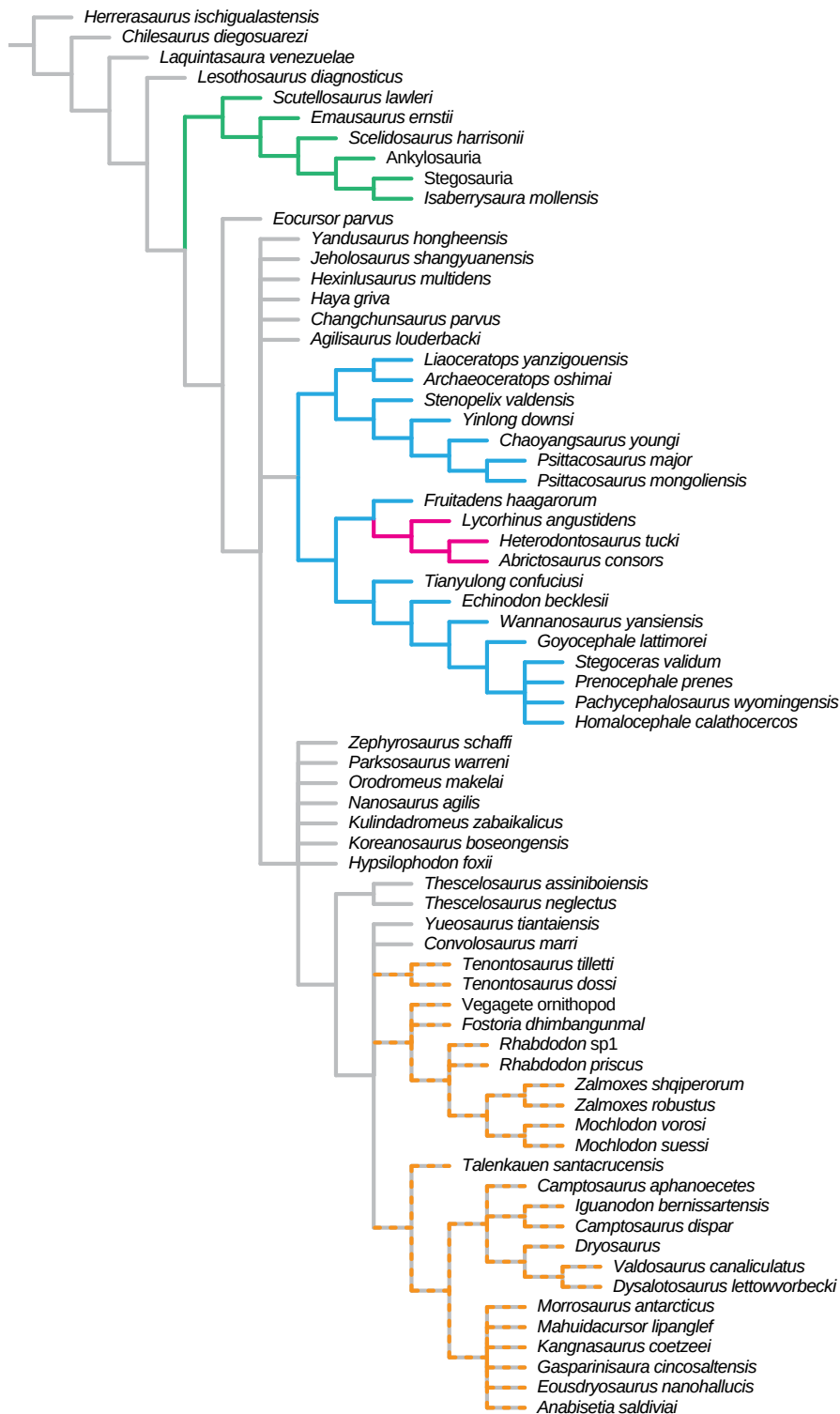
A2.13. Strict consensus tree of 720 MPTs produced from Han *et al.* (2018) when OTUs <20% complete are excluded *a priori* (n=13). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis B.3.H2018 - excluding OTUs <30% complete



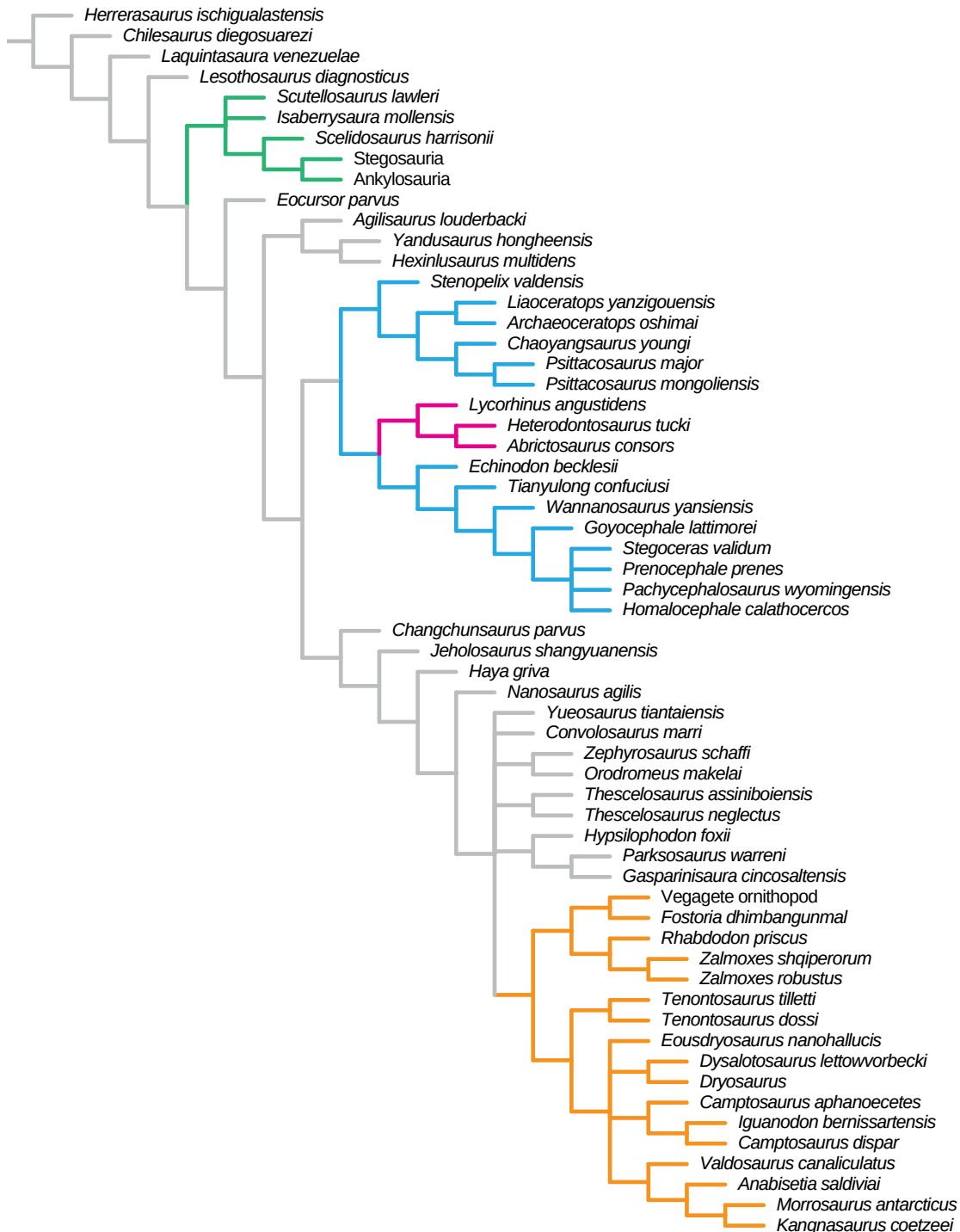
A2.14. Strict consensus tree of 72 MPTs produced from Han *et al.* (2018) when OTUs <30% complete are excluded *a priori* (n=22). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis B.1.D2021 - excluding OTUs <10% complete



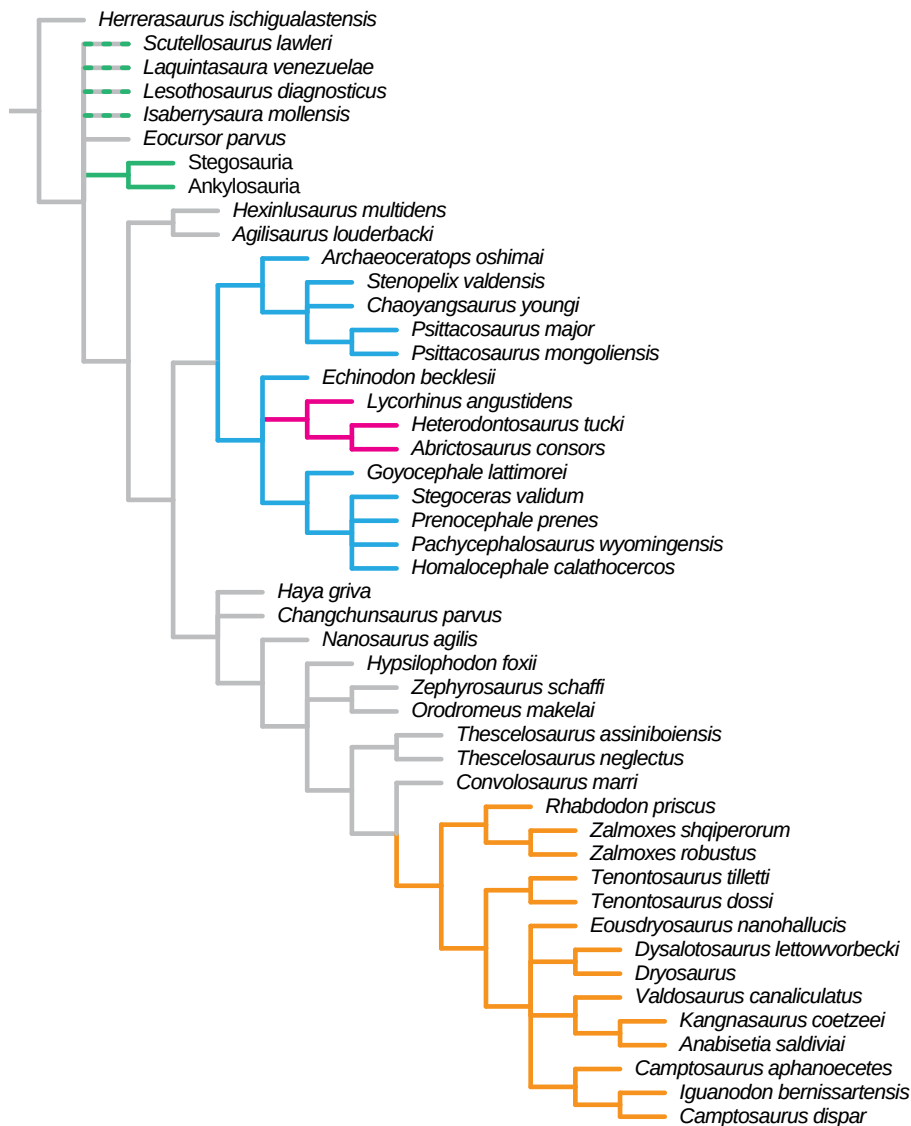
A2.15. Strict consensus tree of 264 MPTs produced from Dieudonné *et al.* (2021) when OTUs <10% complete are excluded *a priori* (n=2). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis B.2.D2021 - excluding OTUs <20% complete



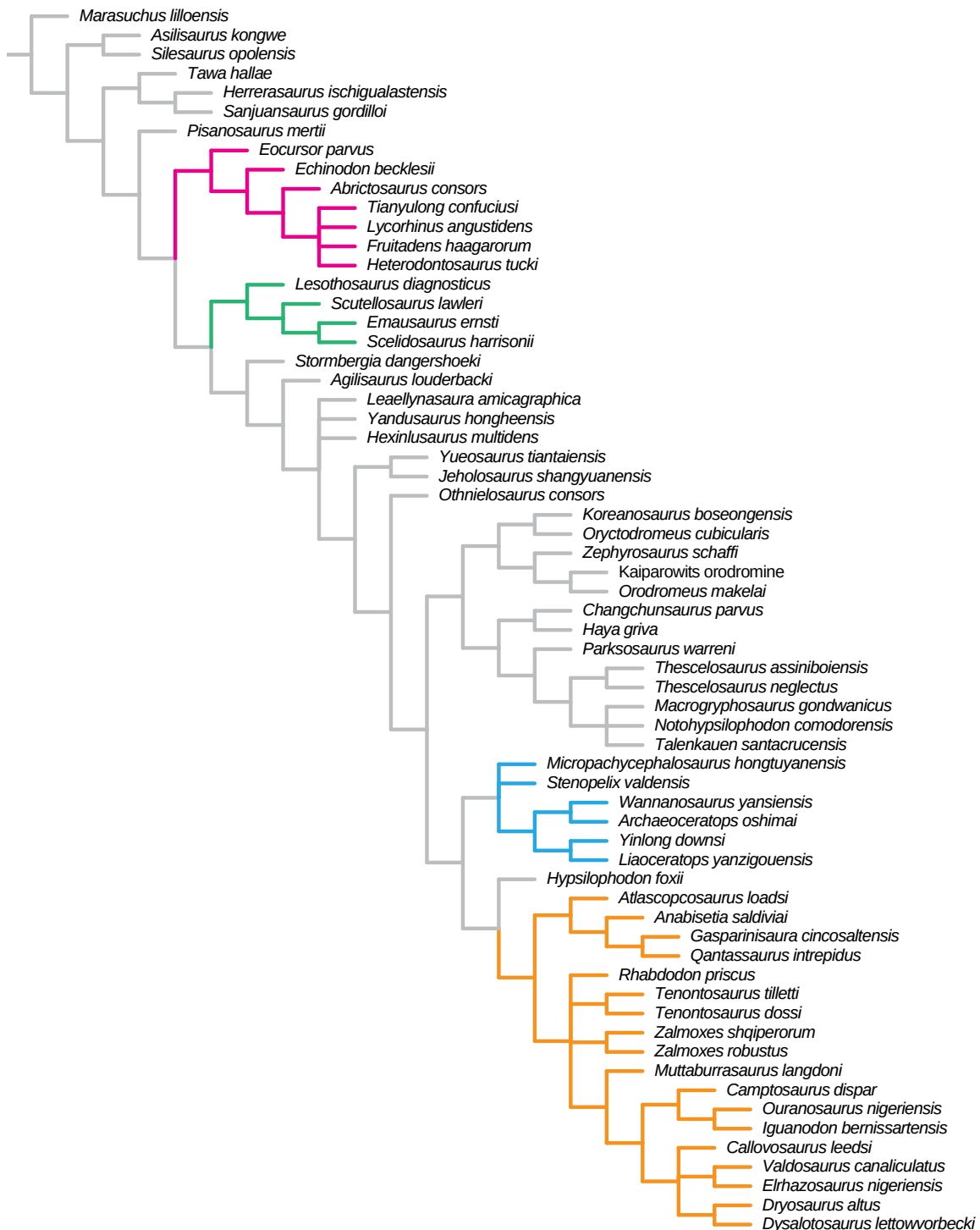
A2.16. Strict consensus tree of 48 MPTs produced from Dieudonné *et al.* (2021) when OTUs <20% complete are excluded *a priori* (n=12). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis B.3.D2021 - excluding OTUs <30% complete



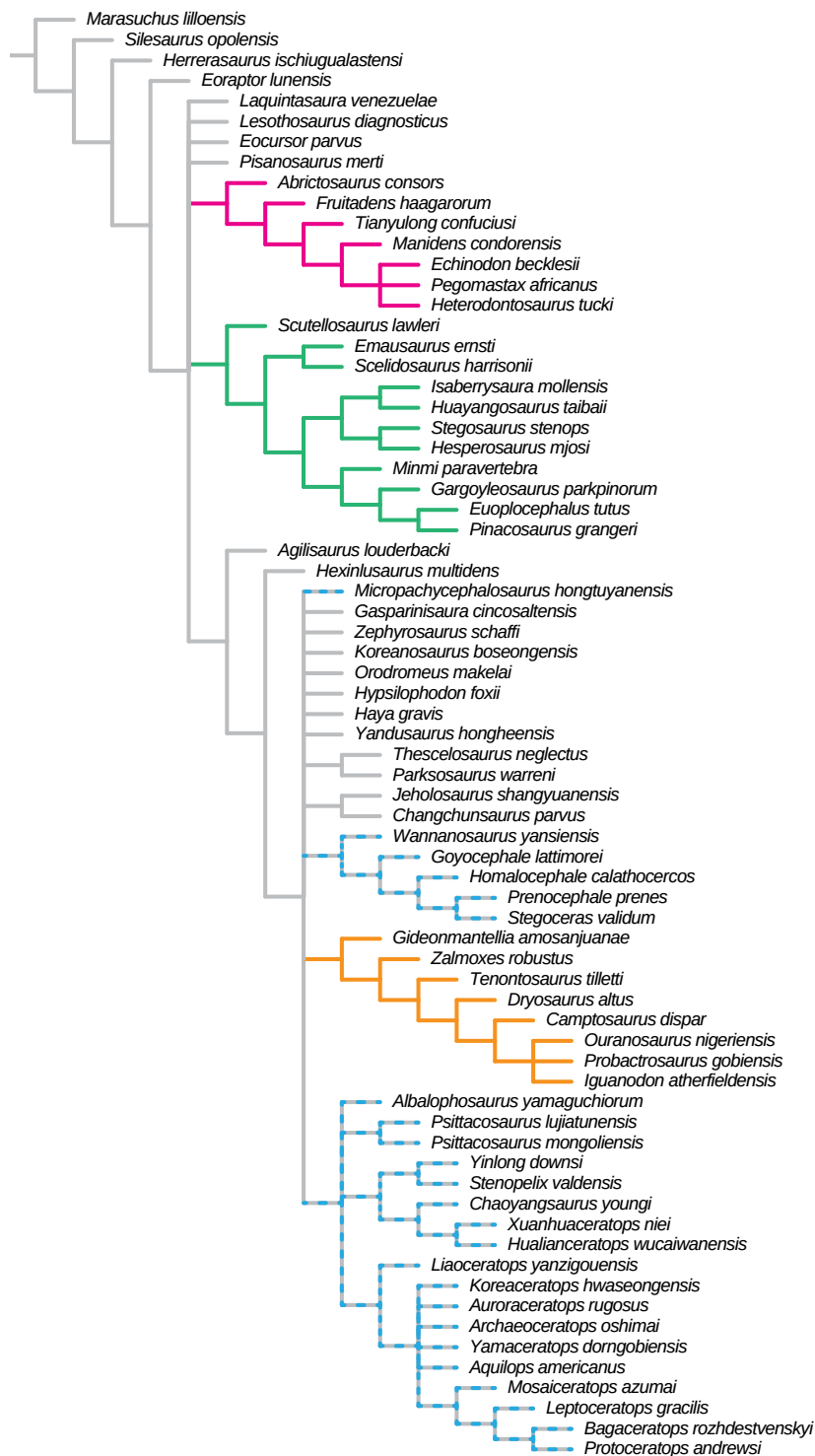
A2.17. Strict consensus tree of 114 MPTs produced from Dieudonné *et al.* (2021) when OTUs <30% complete are excluded *a priori* (n=25). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis C.B2015 - safe taxonomic reduction



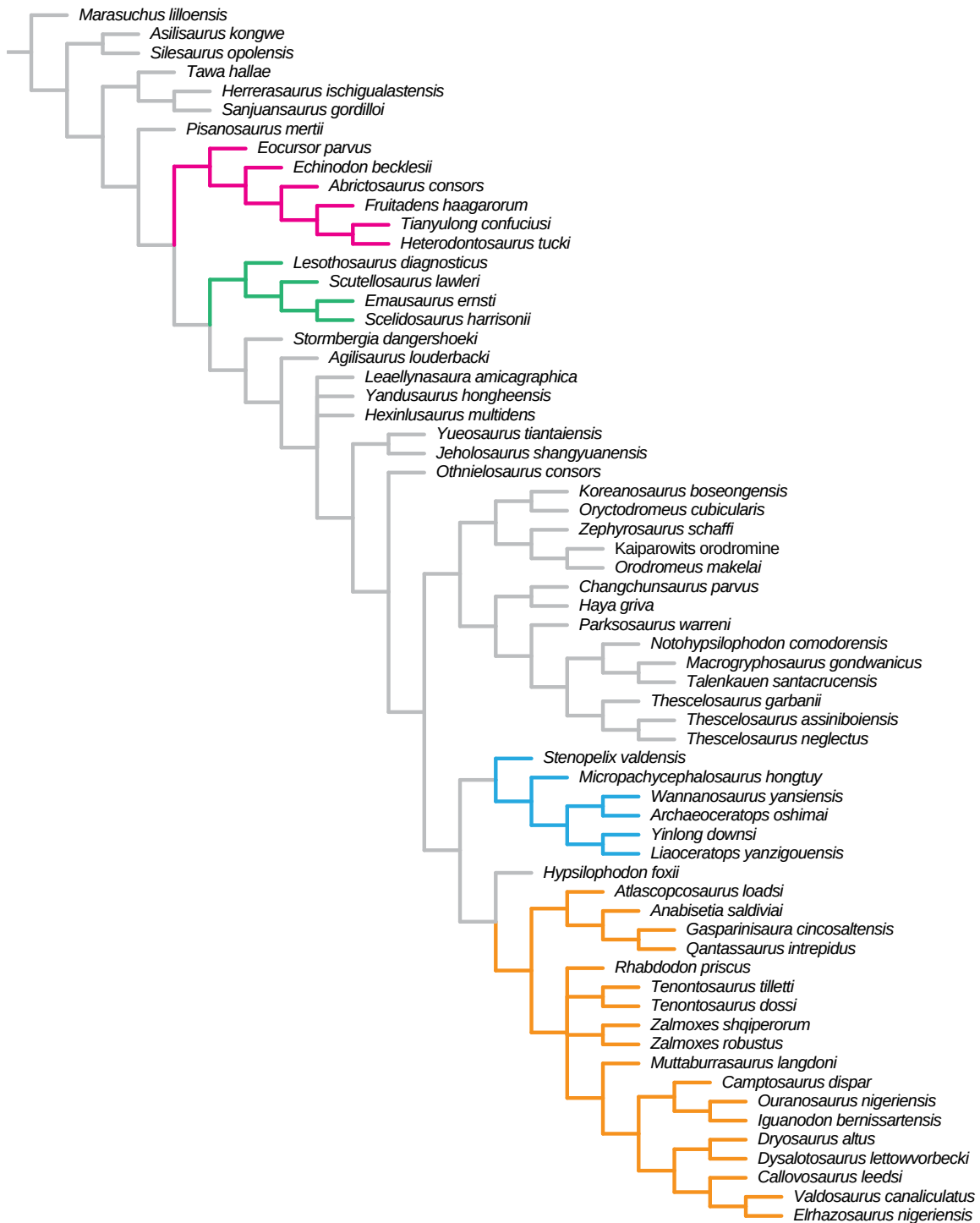
A2.18. Strict consensus tree of 36 MPTs produced from Boyd (2015) following *a priori* exclusion of unstable OTUs (*Thescelosaurus garbanii*) identified using safe taxonomic reduction. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis C.H2018 - safe taxonomic reduction



A2.19. Strict consensus tree of 3439 MPTs produced from Han *et al.* (2018) following *a priori* exclusion of unstable OTUs (*Yueosaurus*) identified using safe taxonomic reduction. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis D.1.B2015 - reduced strict consensus tree



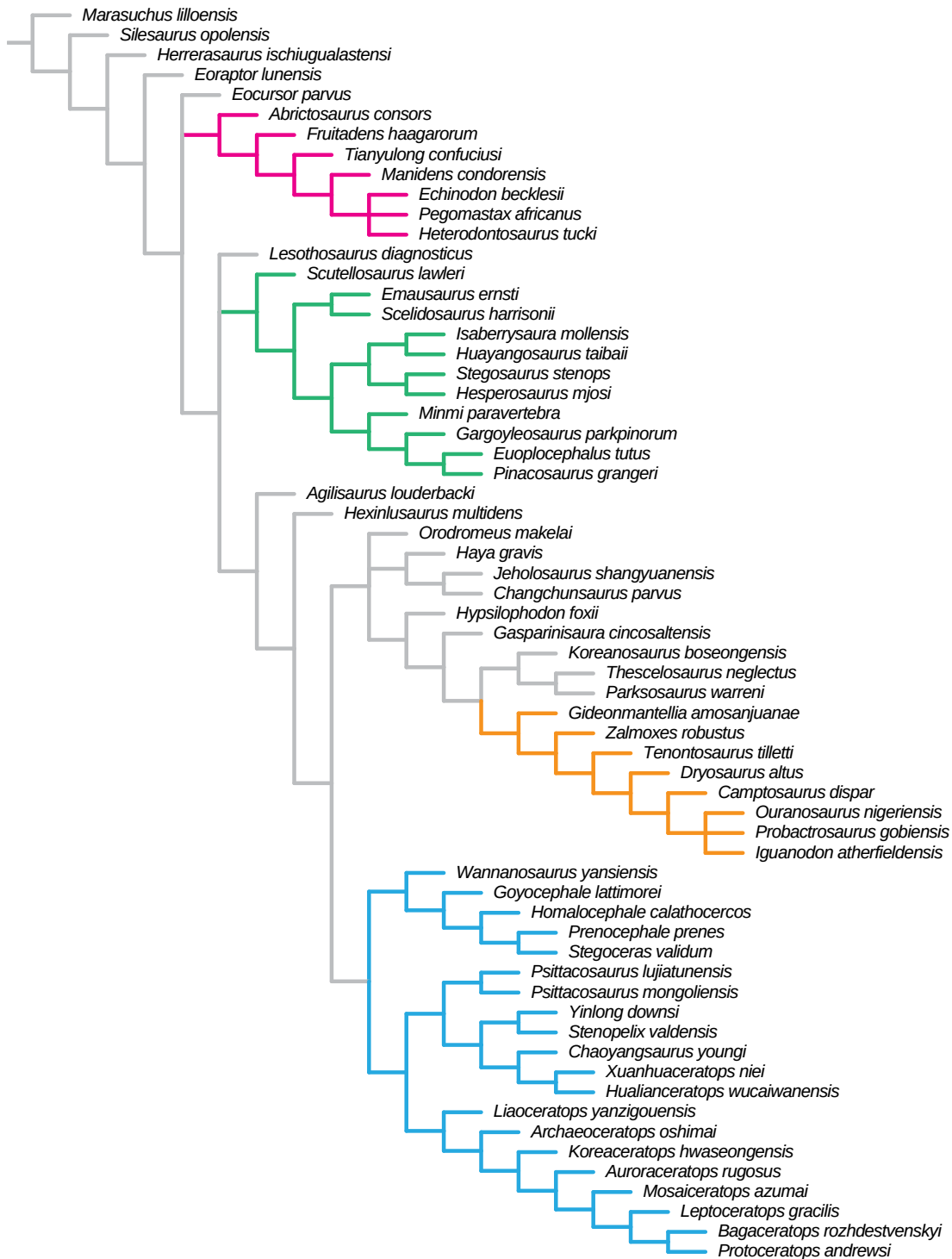
A2.20. Reduced strict consensus tree of 36 MPTs produced from Boyd (2015) following pruning of one unstable OTU (*Lycorhinus*) identified using IterPCR. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis D.2.B2015 - *a priori* exclusion of unstable OTUs



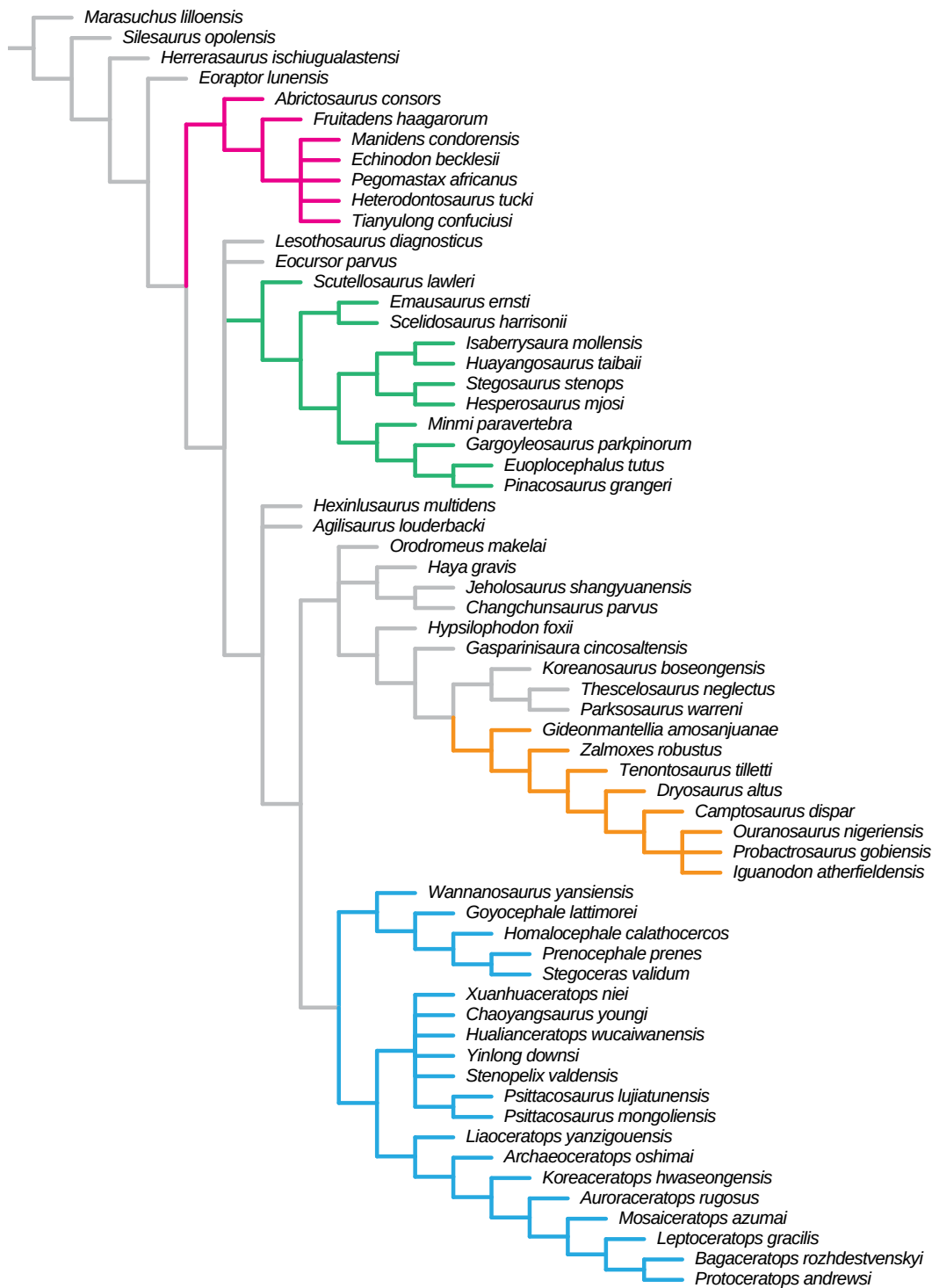
A2.21. Strict consensus tree of 12 MPTs produced from Boyd (2015) following *a priori* exclusion of OTUs identified as unstable by IterPCR (*Lycorhinus*). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis D.1.H2018 - reduced strict consensus tree



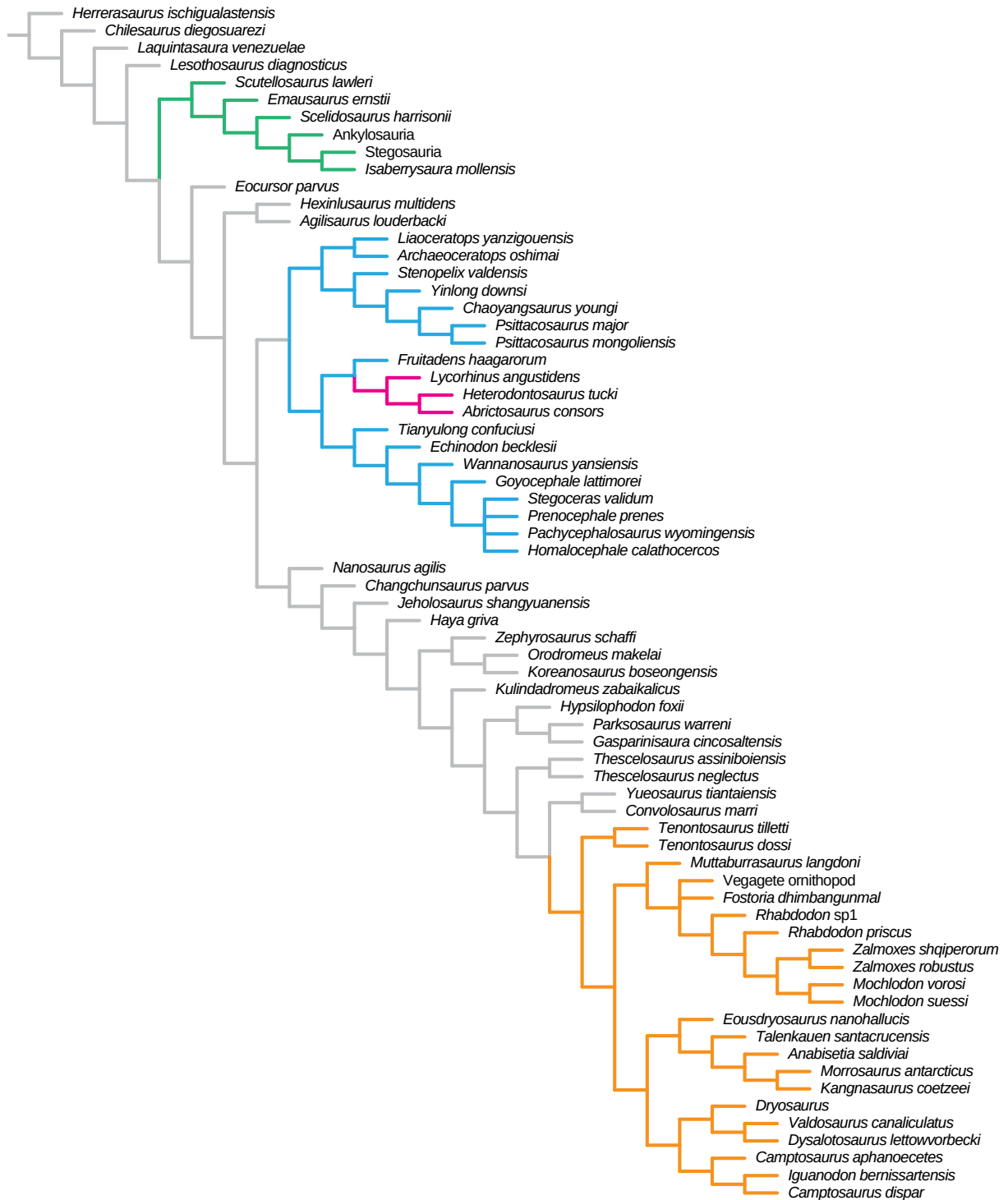
A2.22. Reduced strict consensus tree of 53,376 MPTs produced from Han *et al.* (2018) following pruning of nine unstable OTUs (*Albalophosaurus*, *Aquilops*, *Laquintasaura*, *Micropachycephalosaurus*, *Pisanosaurus*, *Yamaceratops*, *Yandusaurus*, *Yueosaurus*, *Zephyrosaurus*) identified using IterPCR. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis D.2.H2018 - *a priori* exclusion of unstable OTUs



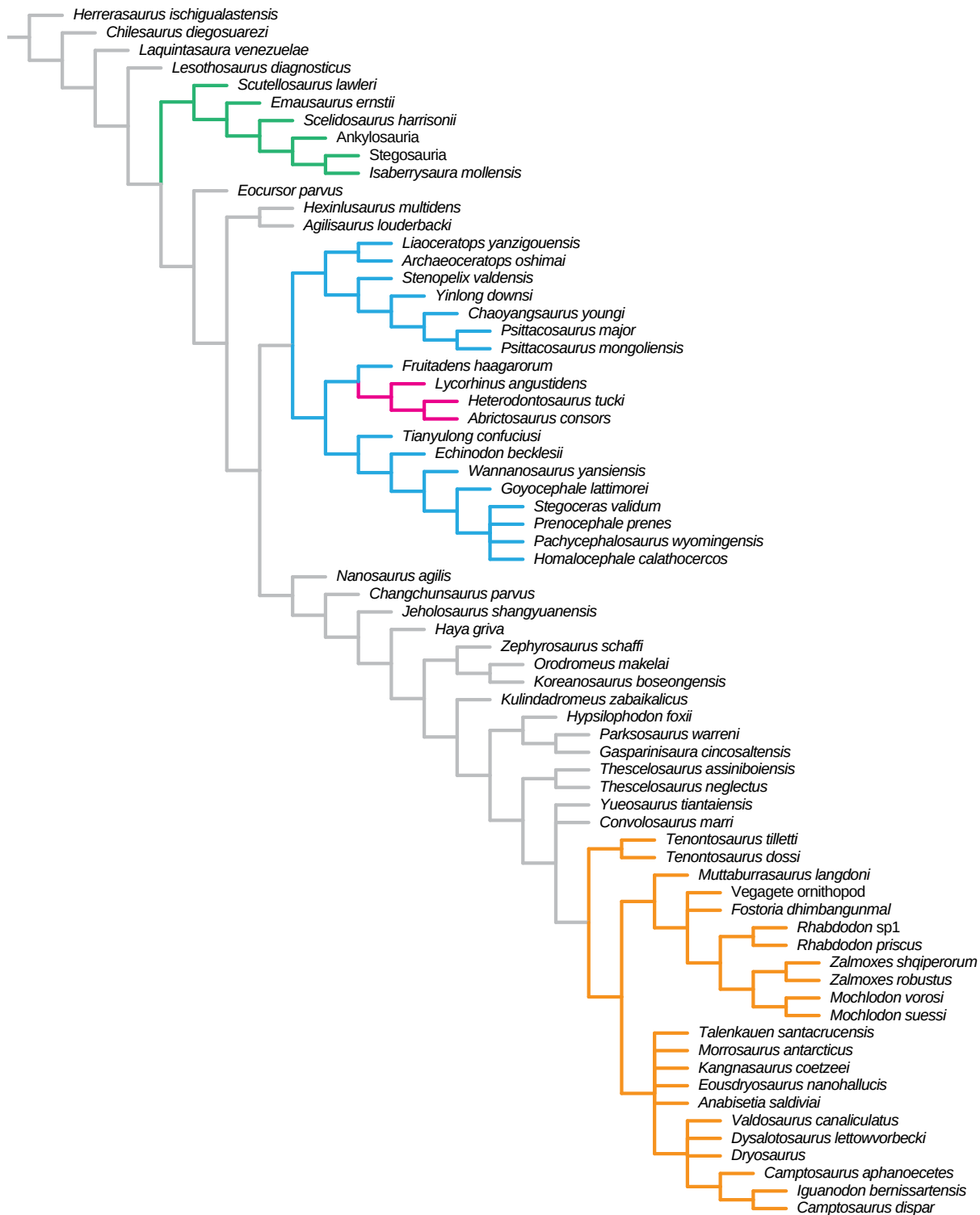
A2.23. Strict consensus tree of 660 MPTs produced from Han *et al.* (2018) following *a priori* exclusion of nine OTUs identified as unstable by IterPCR (*Albalophosaurus*, *Aquilops*, *Laquintasaura*, *Micropachycephalosaurus*, *Pisanosaurus*, *Yamaceratops*, *Yandusaurus*, *Yueosaurus*, *Zephyrosaurus*). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis D.1.D2021 - reduced strict consensus tree



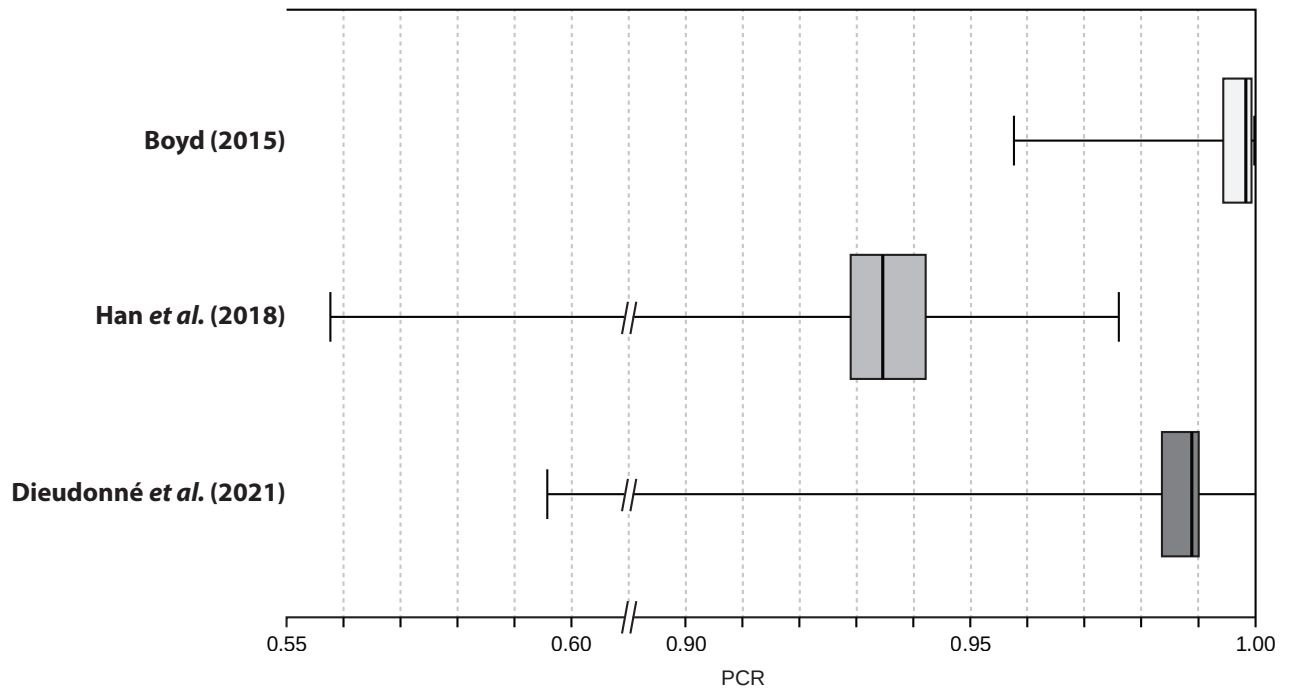
A2.24. Reduced strict consensus tree of 176 MPTs produced from Dieudonné *et al.* (2021) following pruning of three unstable OTUs (*Macrogrypusaurus*, *Mahidacursor*, *Yandusaurus*) identified using IterPCR. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis D.2.D2021 - *a priori* exclusion of unstable OTUs



A2.25. Strict consensus tree of 40 MPTs produced from Dieudonné *et al.* (2021) following *a priori* exclusion of three OTUs identified as unstable by IterPCR (*Macrogyphosaurus*, *Mahuidacursor*, *Yandusaurus*). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Positional congruence (reduced; PCR)



A2.26. Distribution of positional congruence (reduced; PCR) values for taxa in data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021).

A2.27. Characters in Boyd (2015) that are also found in Han *et al.* (2018) and Dieudonné *et al.* (2021). Key: *, different character states used; ~, reversed states. **Abbreviations:** **equi.**, equivalence; **no.**, number.

Boyd (2015) charac- ter No.	Boyd (2015) character also found in:				Boyd (2015) charac- ter No.	Boyd (2015) character also found in:			
	Han <i>et al.</i> (2018)		Dieudonne <i>et al.</i> (2021)			Han <i>et al.</i> (2018)		Dieudonne <i>et al.</i> (2021)	
	No.	Equi.	No.	Equi.		No.	Equi.	No.	Equi.
1	2	*	2	*	52	88	*		
2	153		131		57			113	*
3	5		8		58	110			
4			15	*	59	70	*		
6	12	*	14		63			43	*
7	19		16		65			46	
8			28	*	66	94	*		
9	16	*			67			44	*
10	13		19		68	154	*	132	*
12			13		69	155	~	133	
15	14				70	156		135	
16	10	*	17		71	158	*	138	
19	41	*	33		72	159		137	
21	43				73	162		141	*
22	15				74			142	*
23	45 & 46	*	53	*	75	168	*	145	*
24	47		51		77			140	*
25	48	*	54	*	82	175	*		
28	44				83			130	*
30	50	*			85	181			
31			90	*	86	184	*	153	
32			85		87	92	*	104	
33			93	*	88			26	
34	101				89	22	*		
35	66	*	95	*	93	33		35	
36			82		95			55	
38	56 & 57		87	*	97	179		154	
39			83	*	98			122	*
40			84		101			111	
41	78		98		103			106	*
42	80	~			105			118	
47			102		107			120	*

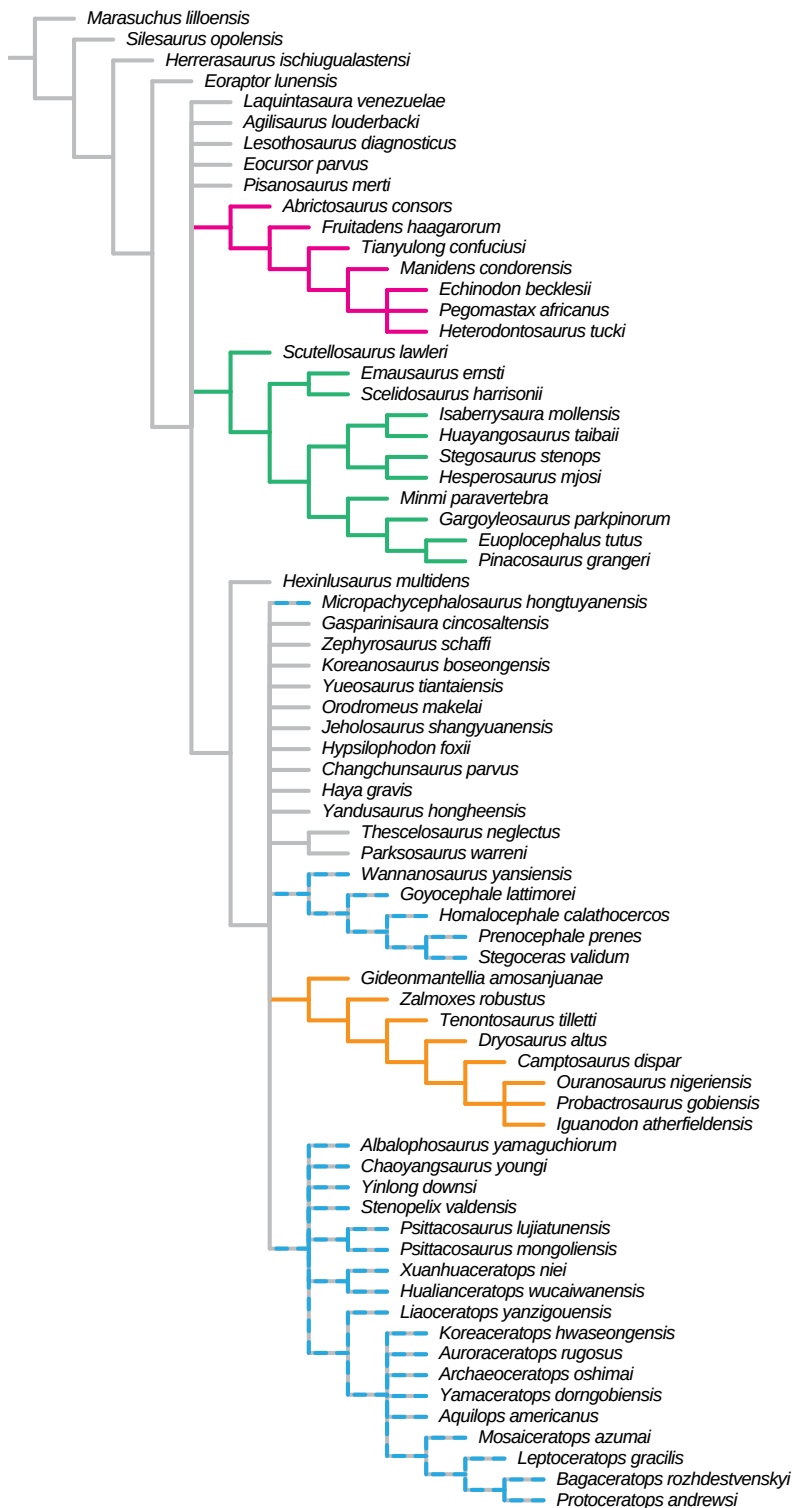
A2.27. (cont.)

Boyd (2015) charac- ter No.	Boyd (2015) character also found in:				Boyd (2015) charac- ter No.	Boyd (2015) character also found in:			
	Han <i>et al.</i> (2018)		Dieudonne <i>et al.</i> (2021)			Han <i>et al.</i> (2018)		Dieudonne <i>et al.</i> (2021)	
	No.	Equi.	No.	Equi.		No.	Equi.	No.	Equi.
109	130	*	125	*	159			224	*
111	195				160			229	*
112	196	*	159	*	161			230	
113			184		162			231	*
116	197	*	160		164			232	*
118			187		165	267	*		
119			183		166	275	*		
122			177	*	167	280	*		
123	226	*	171		169			243	
124			191	*	173			246	
126	203	*			174	287		251	
127					175	292	*		
128			182	*	176	295	*		
129	129 130		174		177	297			
130			174		179	296	*	256	*
132	132 133	*	178	*	181	302	*		
135			193	*	182			277	*
137	204	*	150	*	183	322		265	
138			188	*	184	323	*	266	
141	227	*	202	*	188	320	*	273	*
142			198	*	190			208	
143			199		193			207	*
144	234	~	200		194	336	*	279	*
146			204		196	346		283	*
147	238	*	203	*	198			282	*
148	243	*	205		200			288	*
149			206		202	332			
151	248		210		203	333		292	*
152			209	*	204			292	*
153			216		205	329	*	293	*
154			217		206	335		294	
156			211		212	352	*		
157	264		215		213			301	*

A2.27. (cont.)

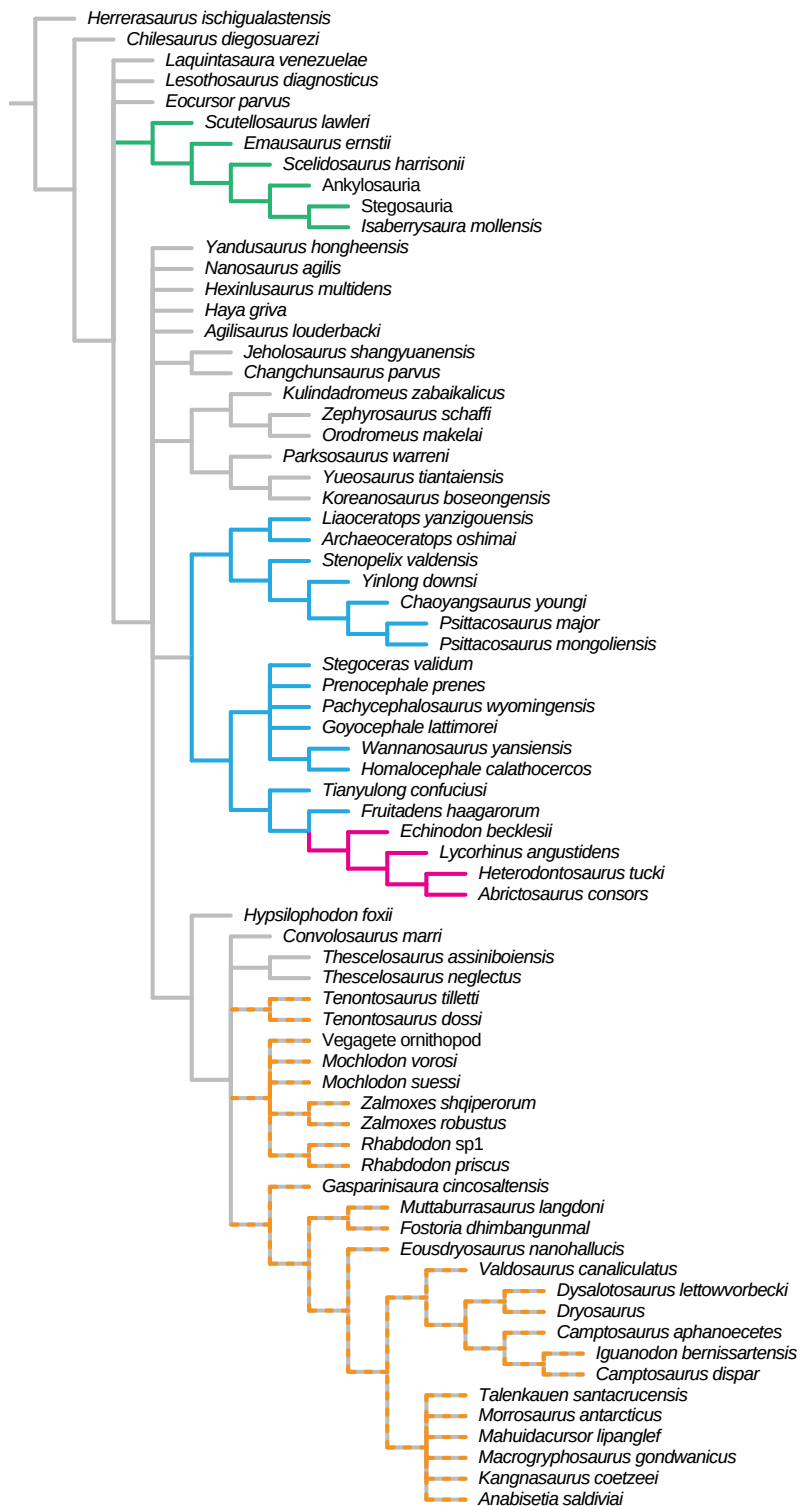
Boyd (2015) charac- ter No.	Boyd (2015) character also found in:			
	Han <i>et al.</i> (2018)		Dieudonne <i>et al.</i> (2021)	
	No.	Equi.	No.	Equi.
214				
215			299	*
216			300	*
220			305	
221	357		303	
222	358		306	*
224	359		307	
226	349	*		
229	361	*		
233			316	
235			320	
236			319	*
237			321	*
238			323	*
240			324	*
242			326	*
245	374	*	333	*
248	377			
250			219	
254	147			
255			21	

Analysis E.H2018 - all characters unordered



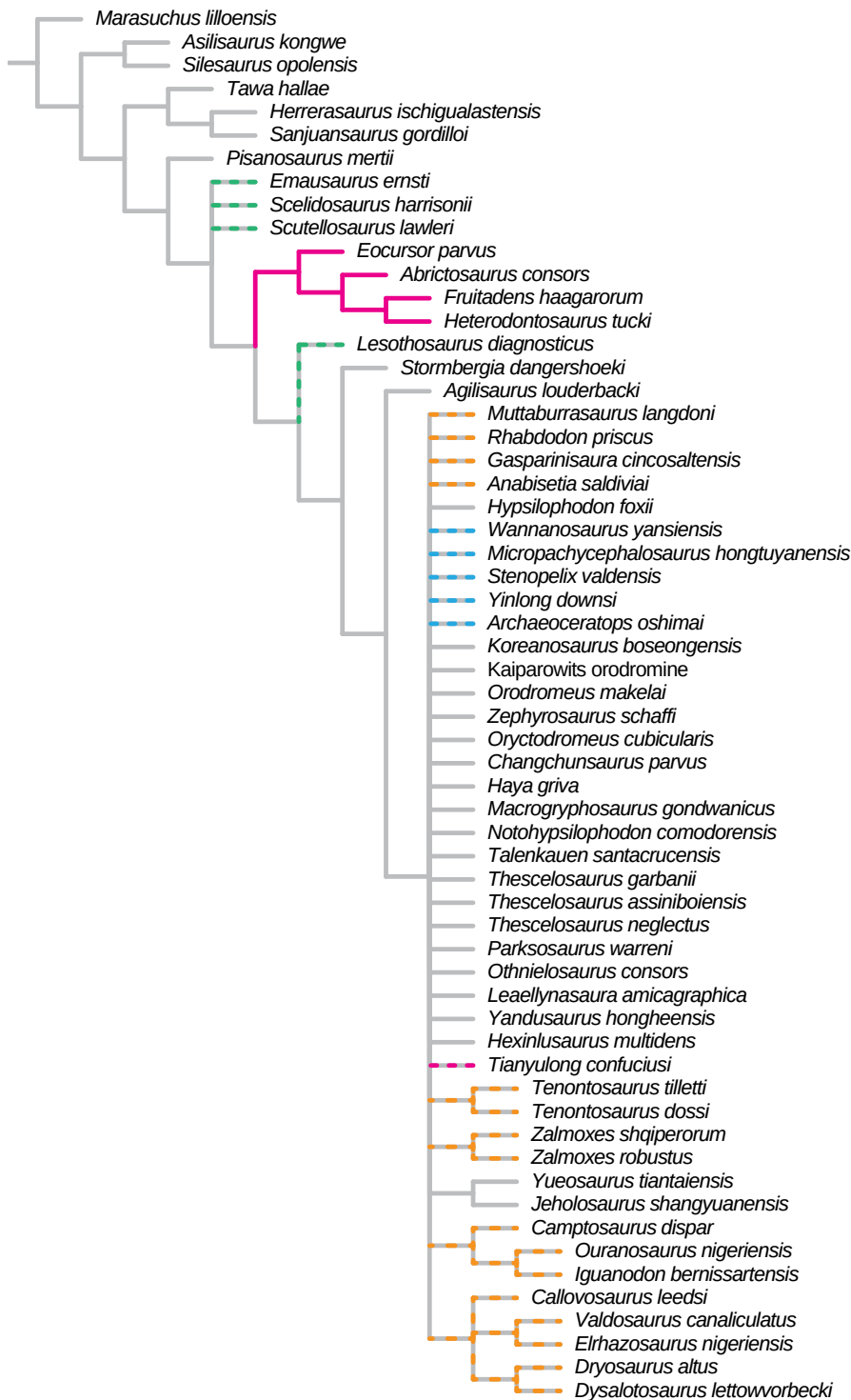
A2.28. Strict consensus tree of 47,801 MPTs produced from Han *et al.* (2018) with all characters ordered. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis E.D2021 - all characters unordered



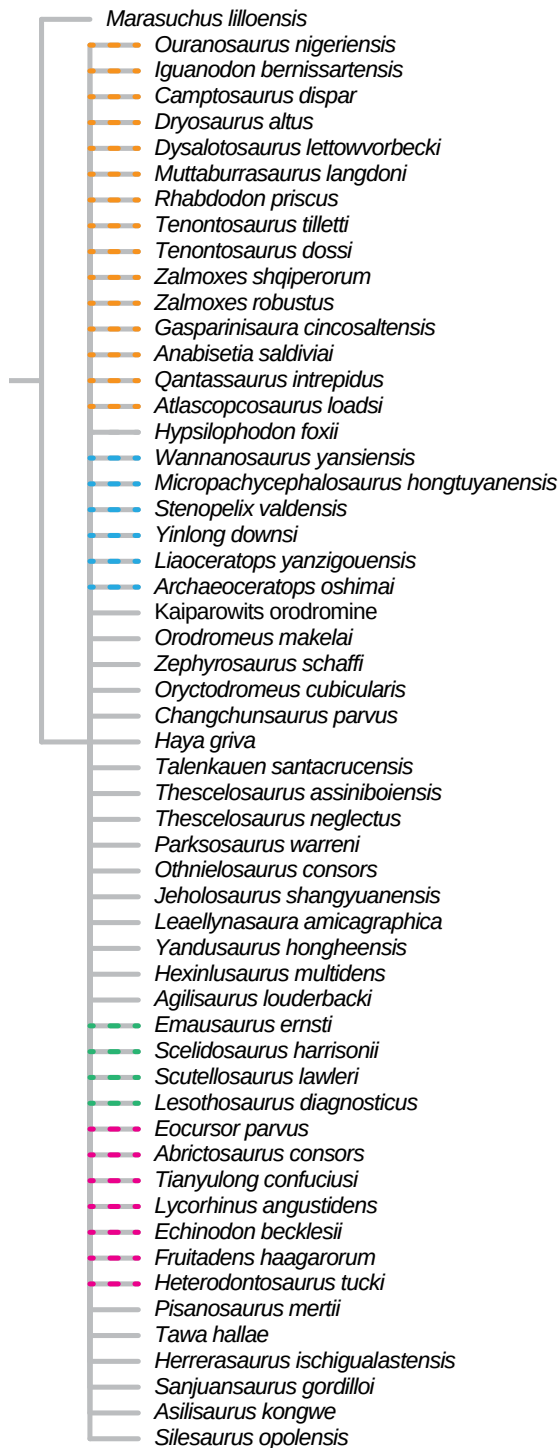
A2.29. Strict consensus tree of 100 MPTs produced from Dieudonné *et al.* (2021) with all characters ordered. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis F.1.B2015 - craniodental characters excluded



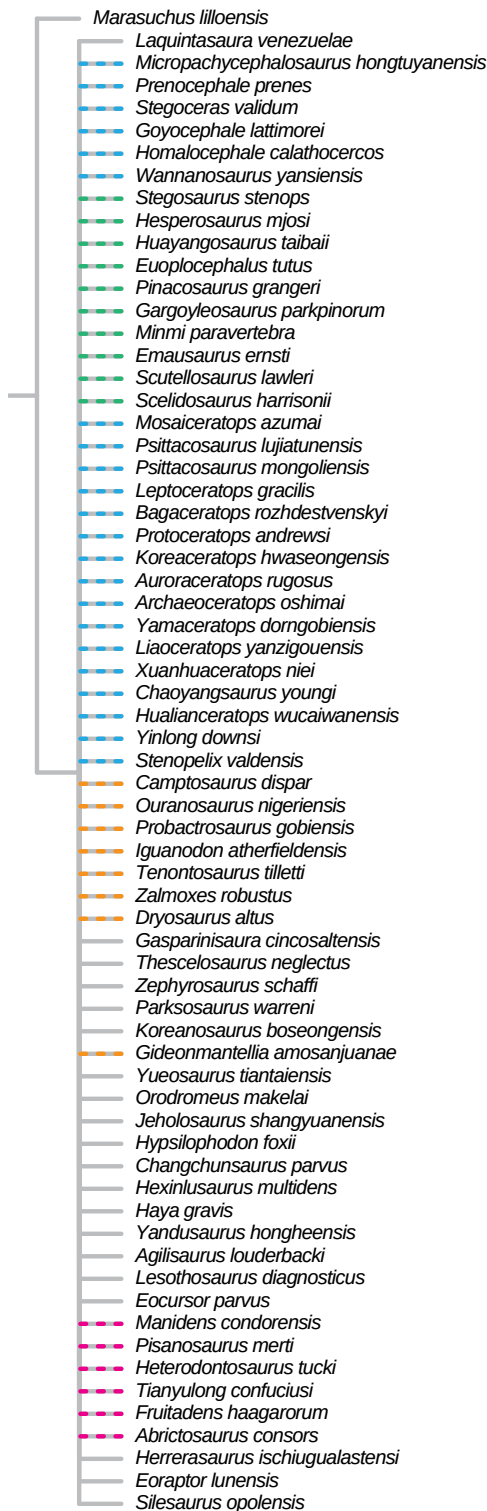
A2.30. Strict consensus tree of 33,800 MPTs produced from Boyd (2015) when all craniodental characters are removed. Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Five taxa were removed prior to the tree search (*Echinodon*, *Lycorhinus*, *Liaoceratops*, *Atlascopcosaurus*, *Qantassaurus*). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis F.2.B2015 - postcranial characters excluded



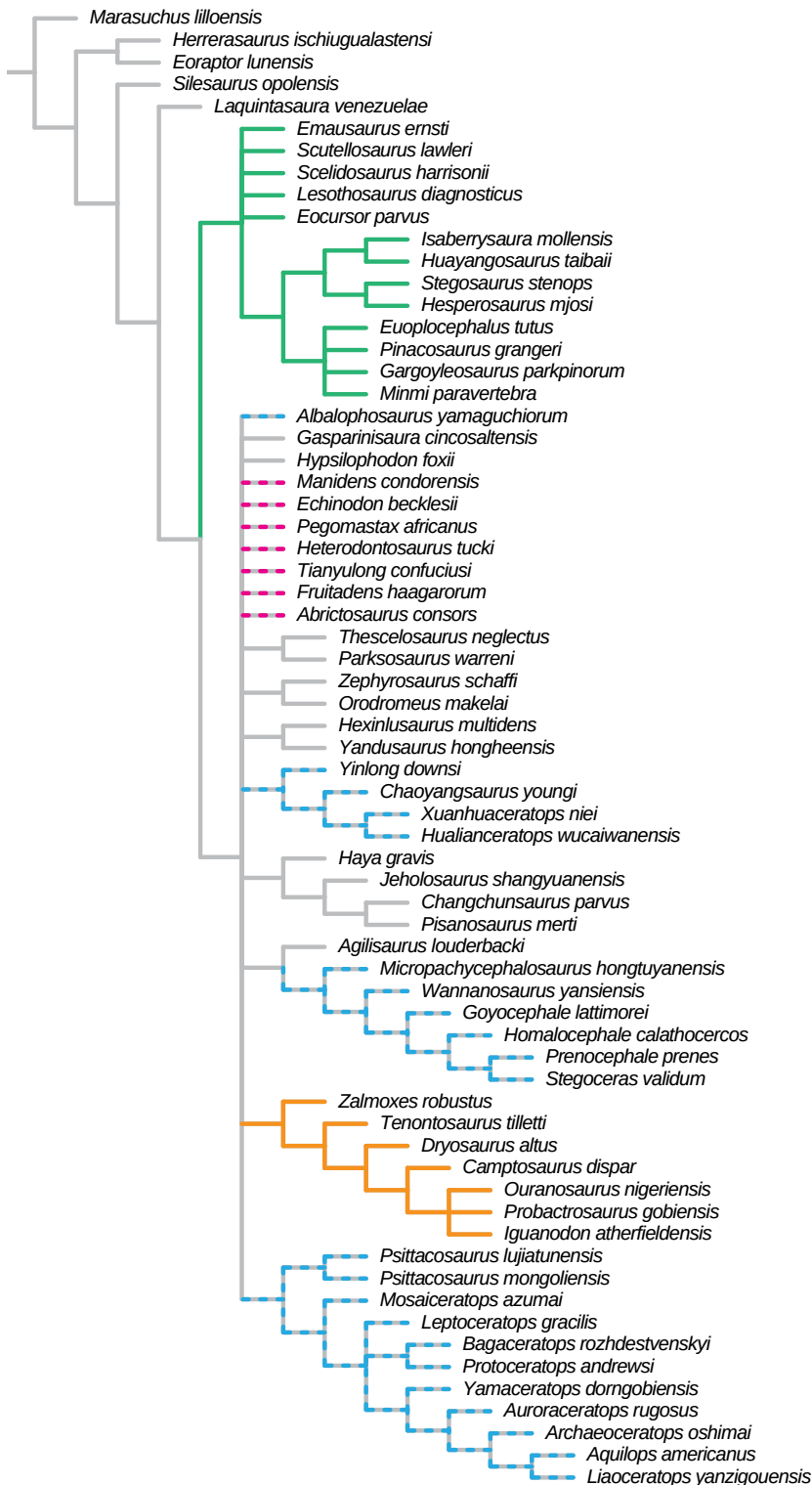
A2.31. Strict consensus tree of 6,800 MPTs produced from Boyd (2015) when all postcranial characters are removed. Nine taxa were excluded prior to the tree search (*Callovosaurus*, *Elrhazosaurus*, *Koreanosaurus*, *Macrogyrophosaurus*, *Notohypsilophodon*, *Stormbergia*, *Thescelosaurus garbanii*, *Valdosaurus*, *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Five taxa were removed prior to the tree search (*Echinodon*, *Lycorhinus*, *Liaoceratops*, *Atlascopcosaurus*, *Qantassaurus*).

Analysis F.1.H2018 - craniodental characters excluded



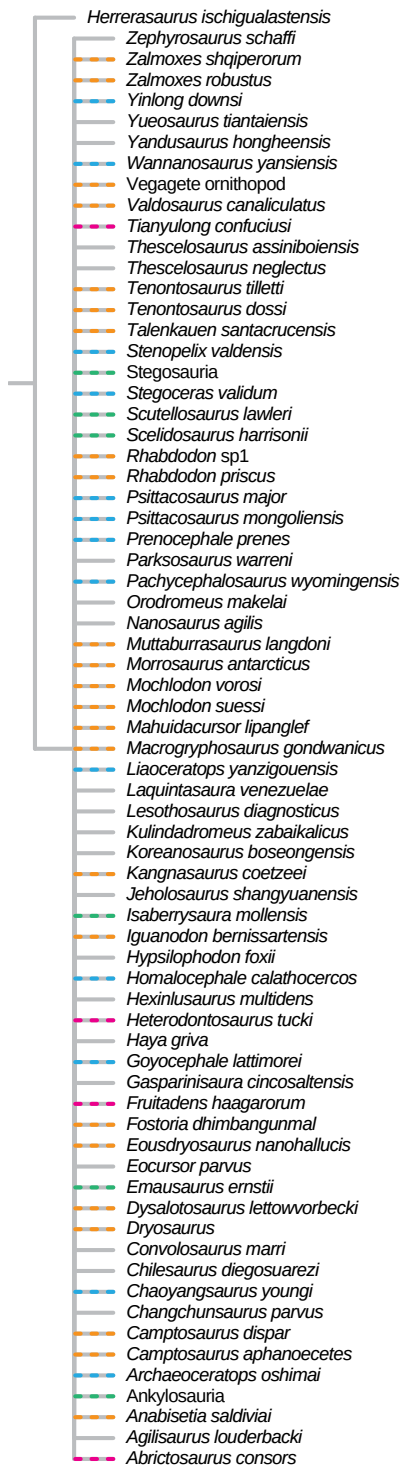
A2.32. Strict consensus tree of 44,600 MPTs produced from Han *et al.* (2018) when all craniodental characters are removed. Five taxa were removed prior to the tree search (*Pegomastax*, *Echinodon*, *Aquilops*, *Albalophosaurus*, *Isaberrysaura*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis F.2.H2018 - postcranial characters excluded



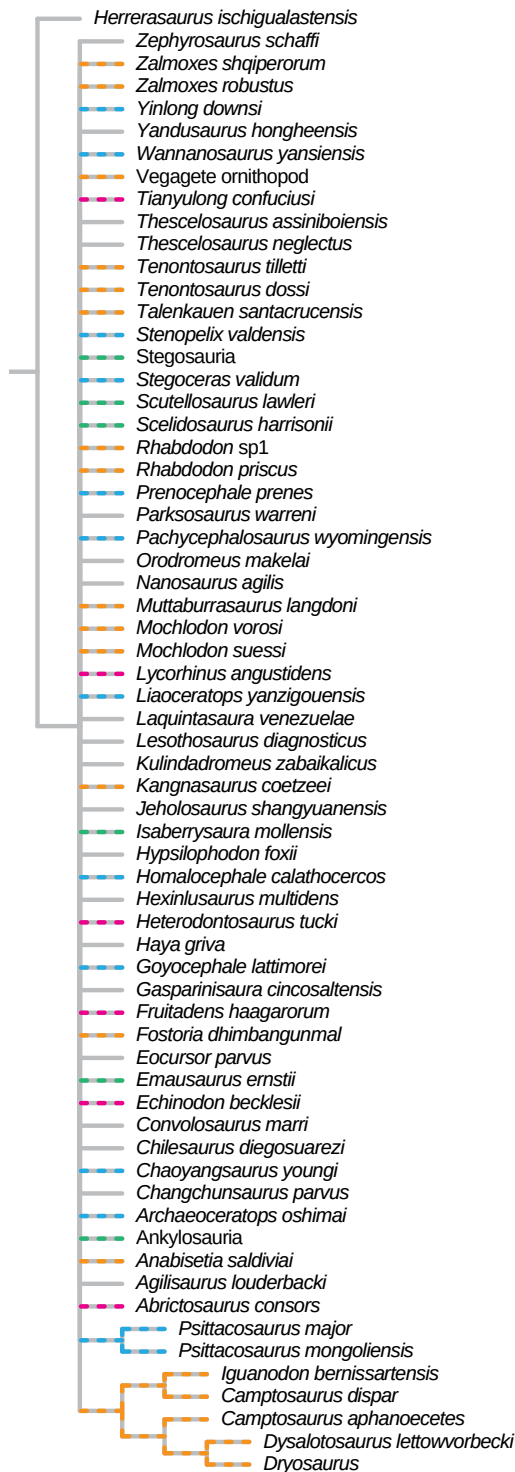
A2.33. Strict consensus tree of 600 MPTs produced from Han *et al.* (2018) when all postcranial characters are removed. Five taxa were removed prior to the tree search (*Gideonmantellia*, *Koreaceratops*, *Koreanosaurus*, *Stenopelix*, *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis F.1.D2021 - craniodental characters excluded



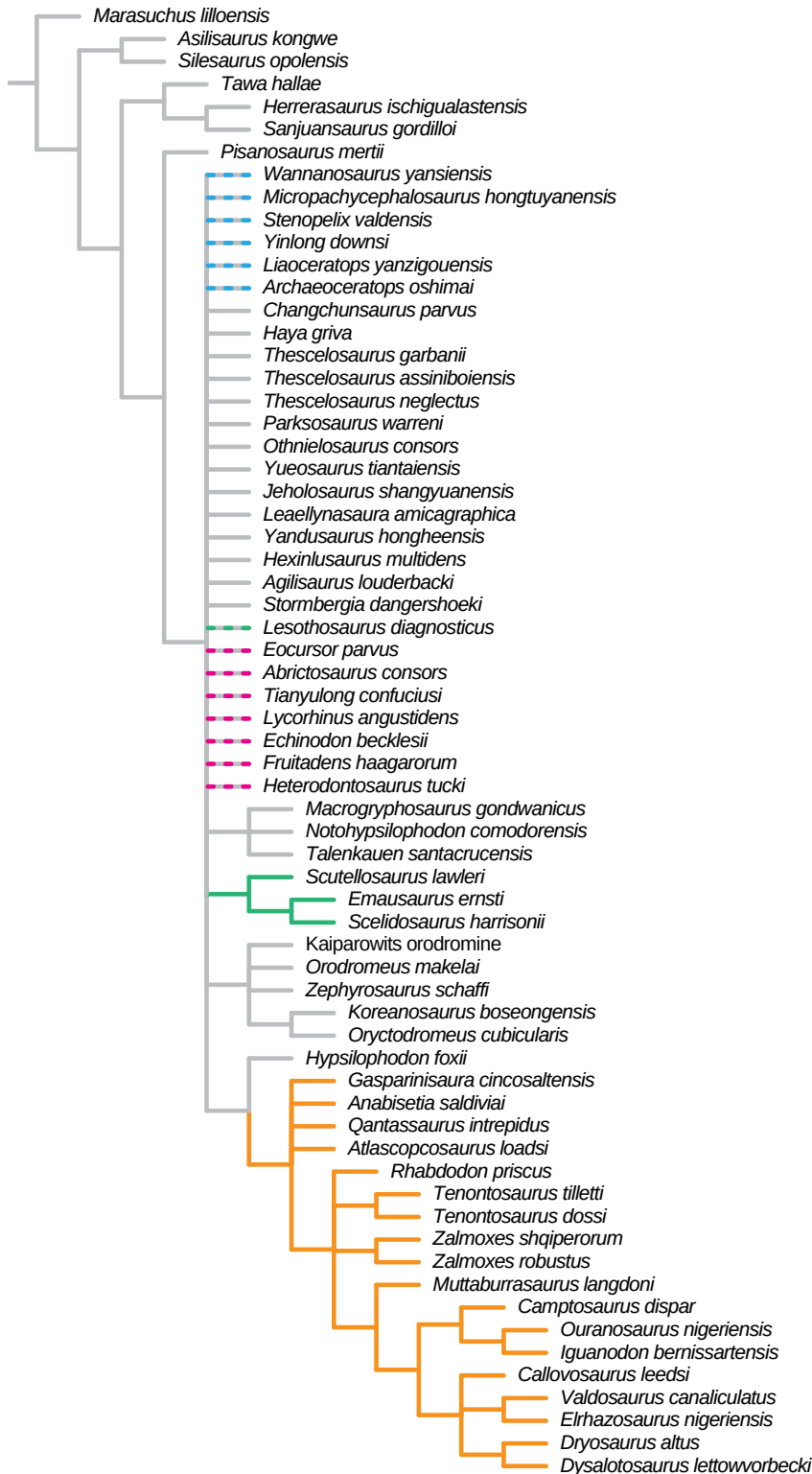
A2.34. Strict consensus tree of 6,800 MPTs produced from Dieudonné *et al.* (2021) when all craniodental characters are removed. Two taxa were removed prior to the tree search (*Echinodon*, *Lycorhinus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis F.2.D2021 - postcranial characters excluded



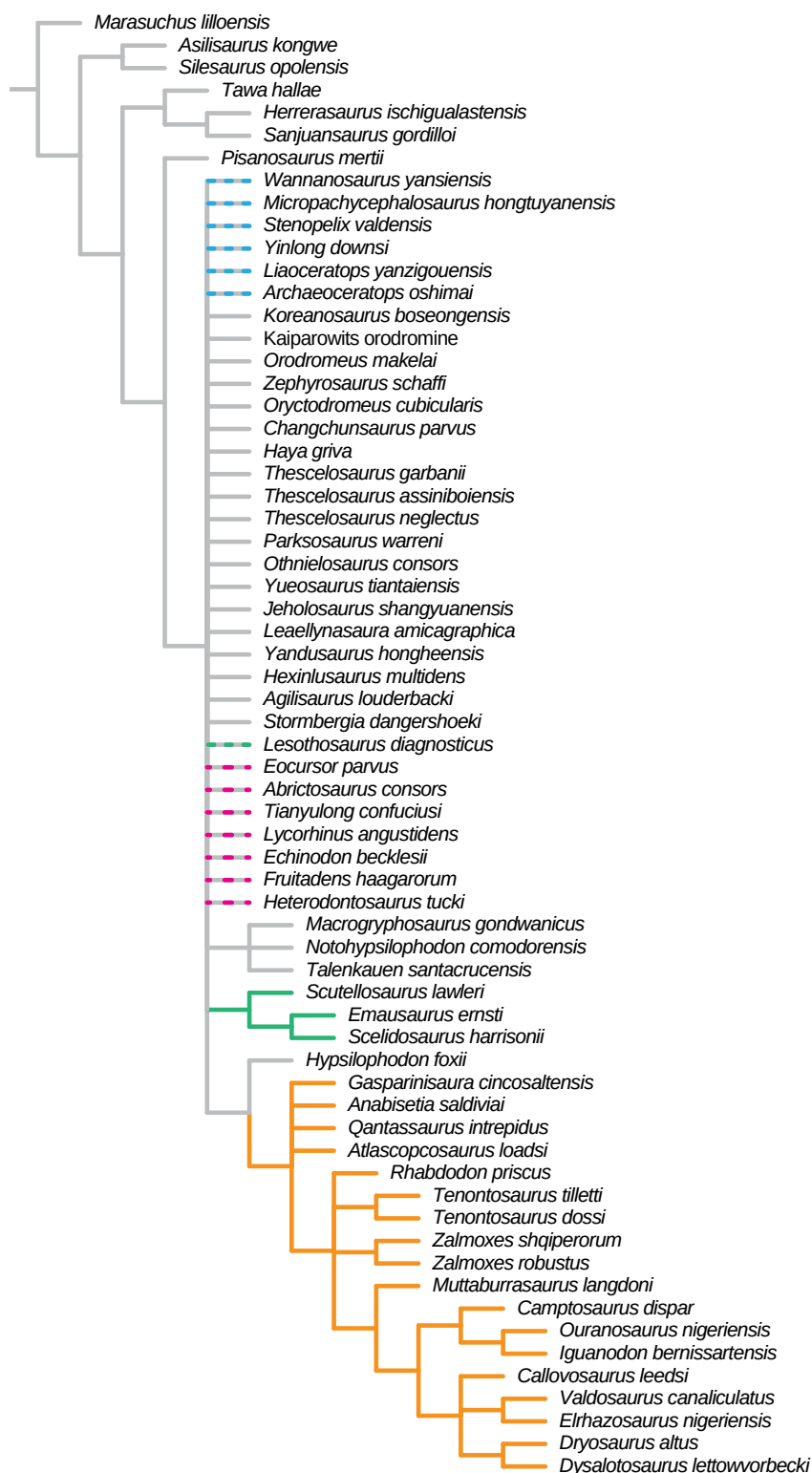
A2.35. Strict consensus tree of 16,900 MPTs produced from Dieudonné *et al.* (2021) when all postcranial characters are removed. Two taxa were removed prior to the tree search (*Echinodon*, *Lycorhinus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis G.1.B2015 - excluding rostral characters



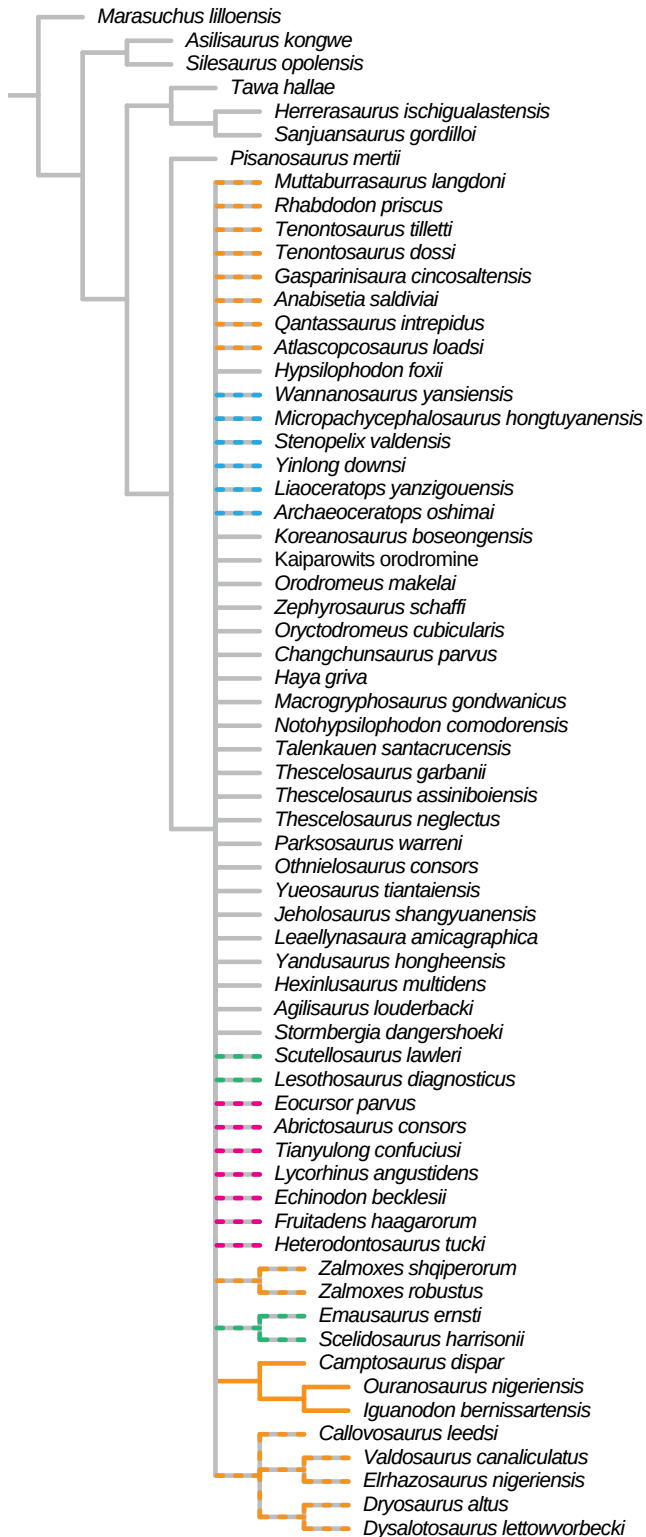
A2.36. Strict consensus tree of 2,436 MPTs produced from Boyd (2015) when all rostral characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.2.B2015 - excluding cranial roof characters



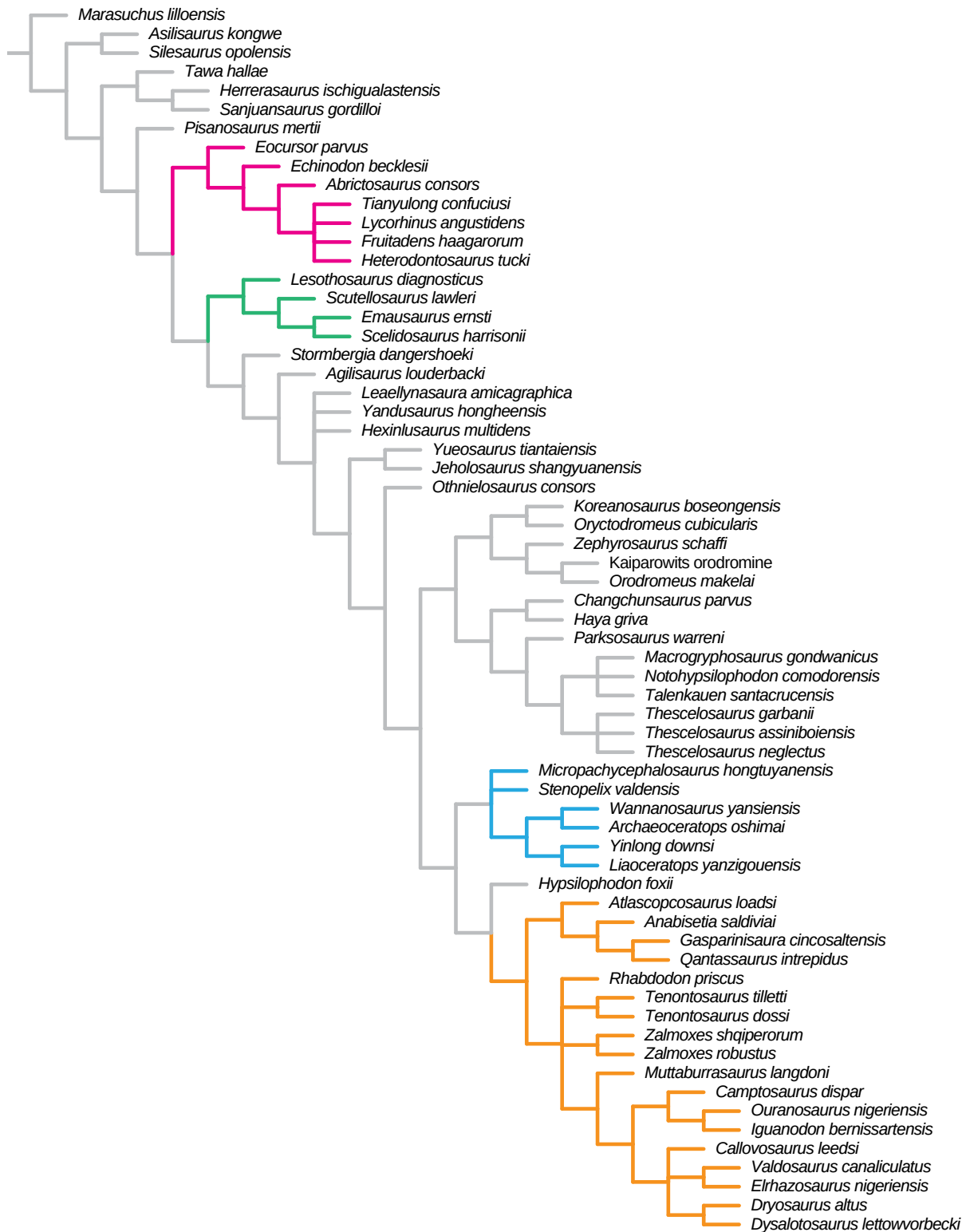
A2.37. Strict consensus tree of 1,548 MPTs produced from Boyd (2015) when all cranial roof characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.4.B2015 - excluding skull base characters



A2.38. Strict consensus tree of 23,500 MPTs produced from Boyd (2015) when all skull base characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

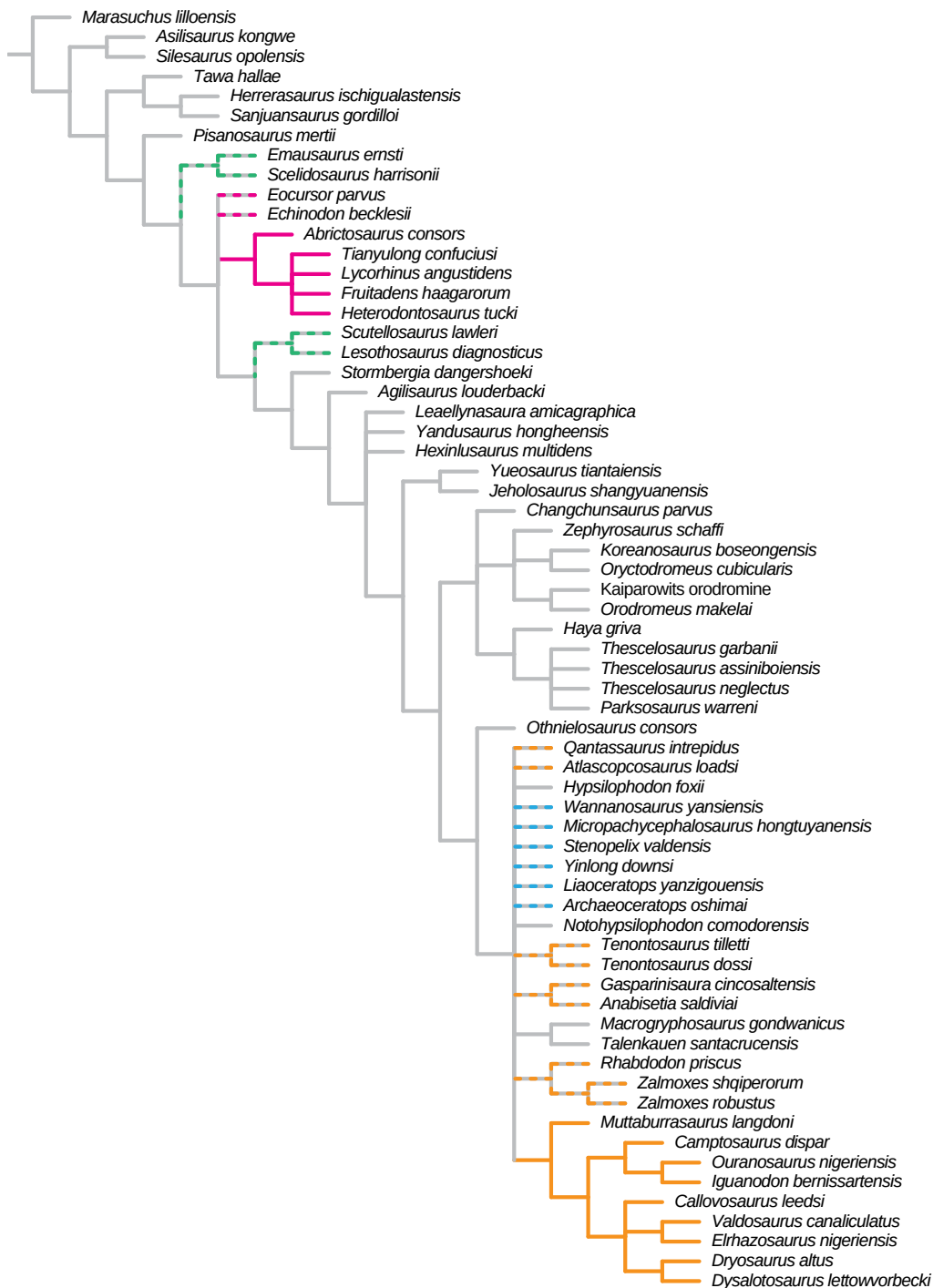
Analysis G.5.B2015 - excluding braincase characters



A2.39. Strict consensus tree of 36 MPTs produced from Boyd (2015) when all braincase characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis G.6.B2015 - mandible characters excluded

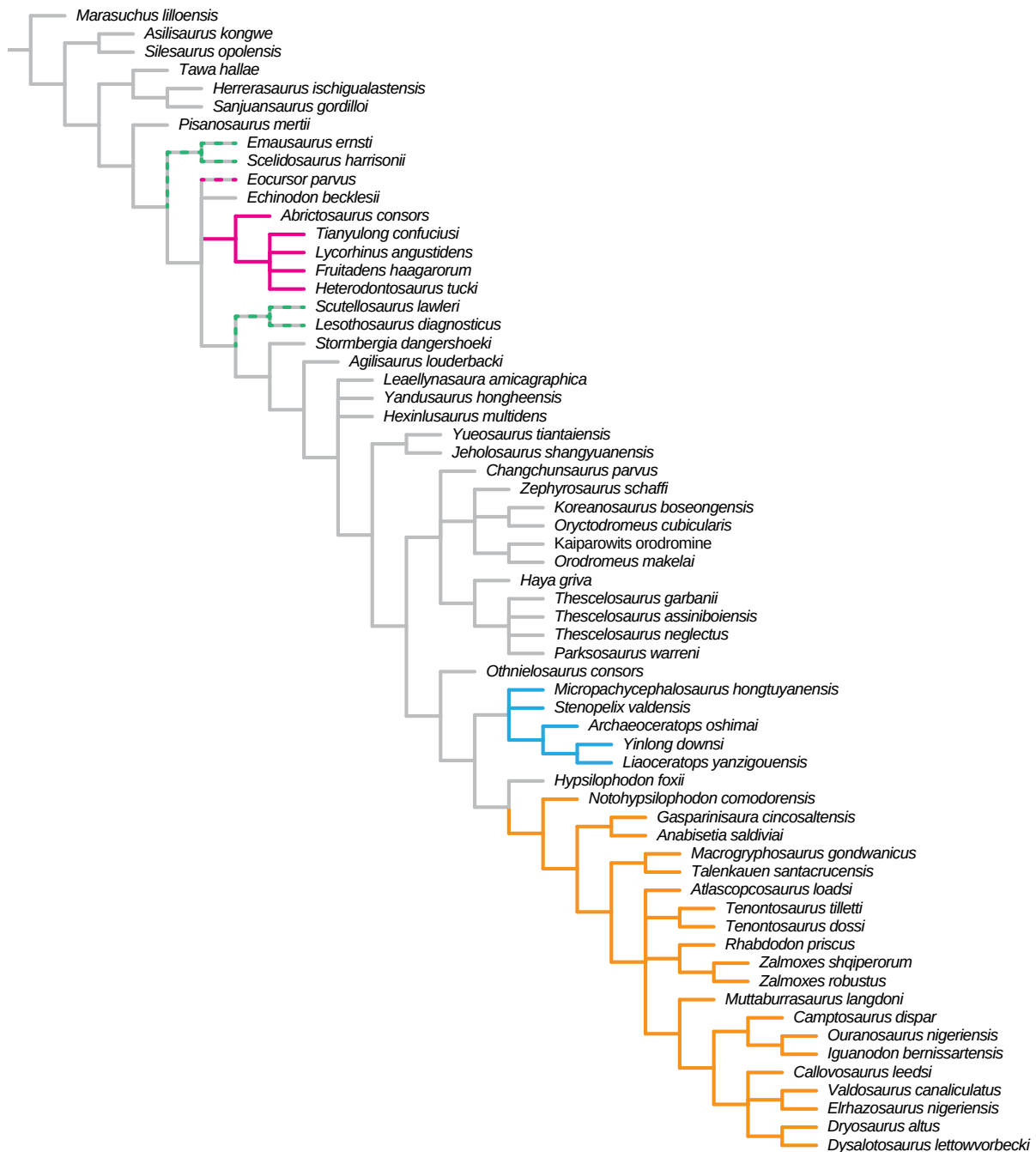
a) strict consensus tree



A2.40. Boyd (2015) tree topology when all mandibular characters are removed: (a) strict consensus of 2,302 MPTs; (b) reduced strict consensus tree following pruning of two unstable taxa (*Qantassaurus*; *Wannanosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.6.B2015 - mandible characters excluded

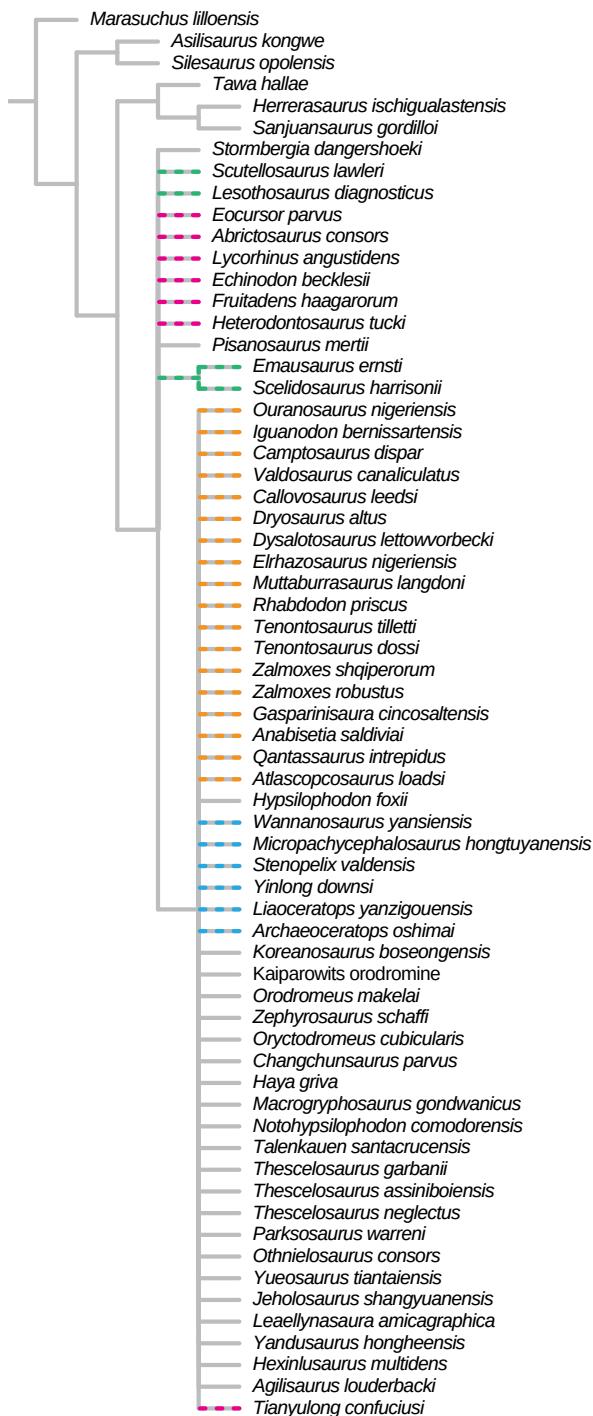
b) reduced strict consensus tree



A2.40. (cont.)

Analysis G.7.B2015 - dental characters excluded

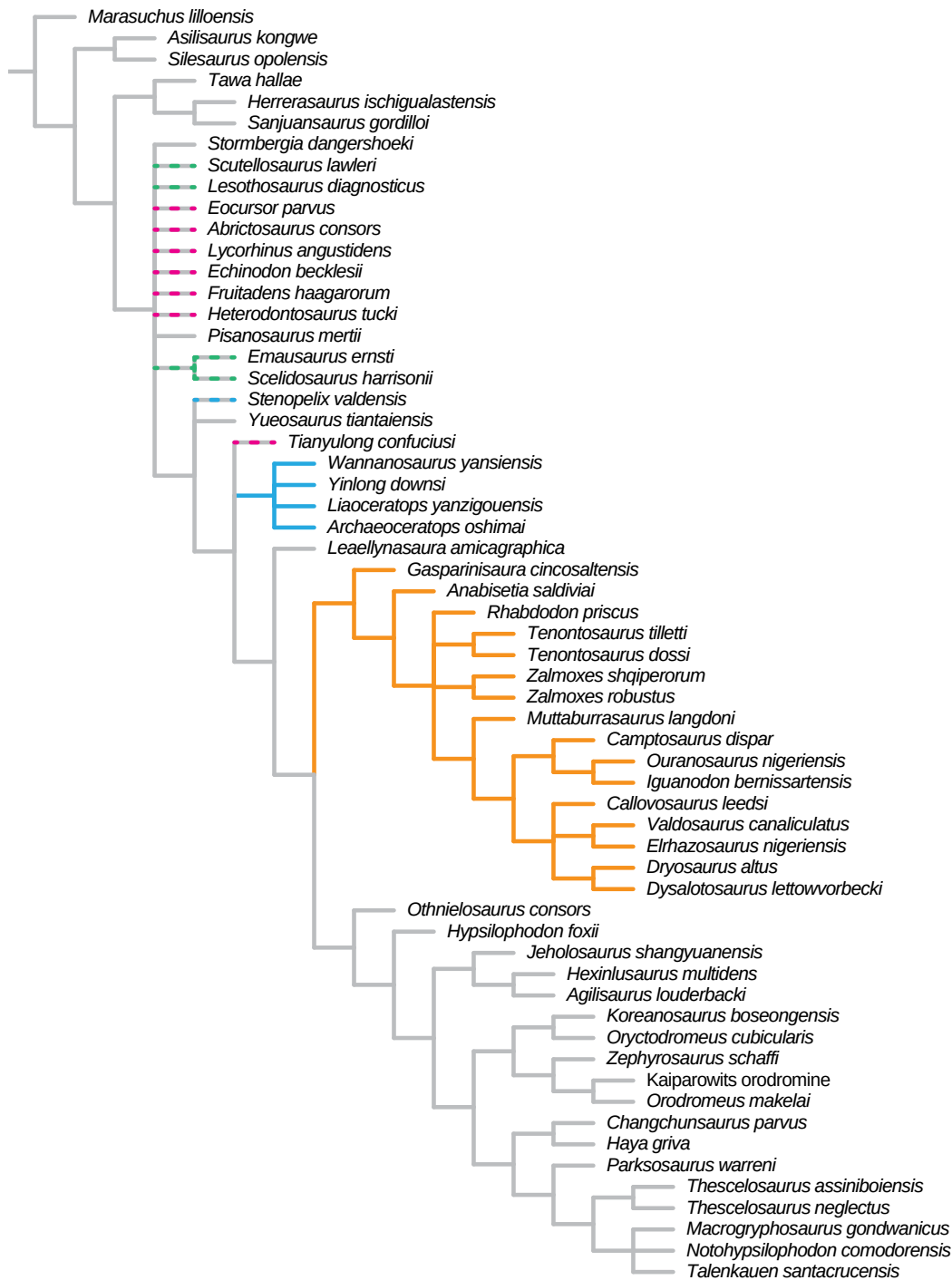
a) strict consensus tree



A2.41. Boyd (2015) tree topology when all dental characters are removed: (a) strict consensus of 6,800 MPTs; (b) reduced strict consensus tree following pruning of five unstable taxa (*Atlascopcosaurus*; *Micropachycephalosaurus*; *Qantassaurus*; *Thescelosaurus garbanii*; *Yandusaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

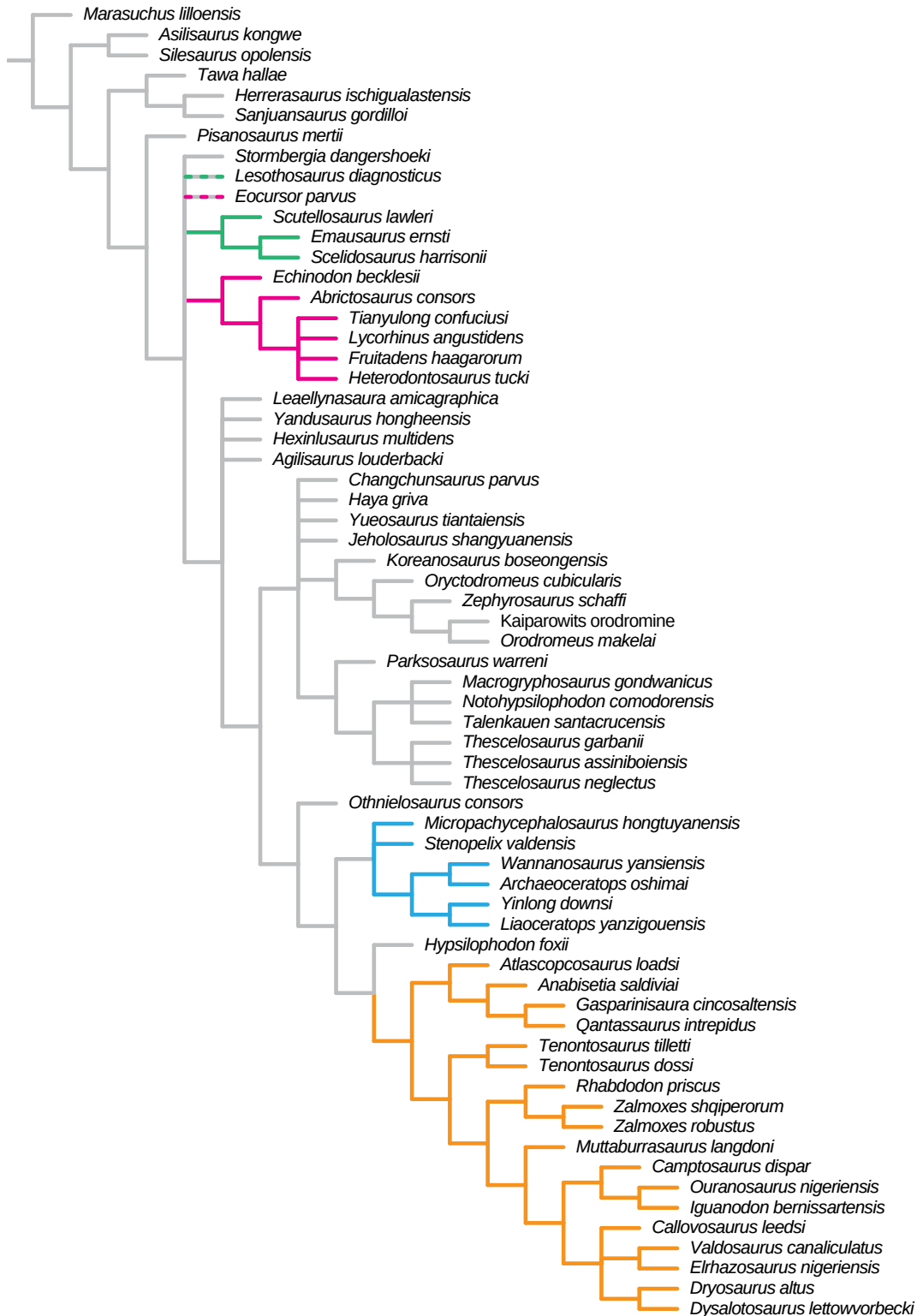
Analysis G.7.B2015 - dental characters excluded

b) reduced strict consensus tree



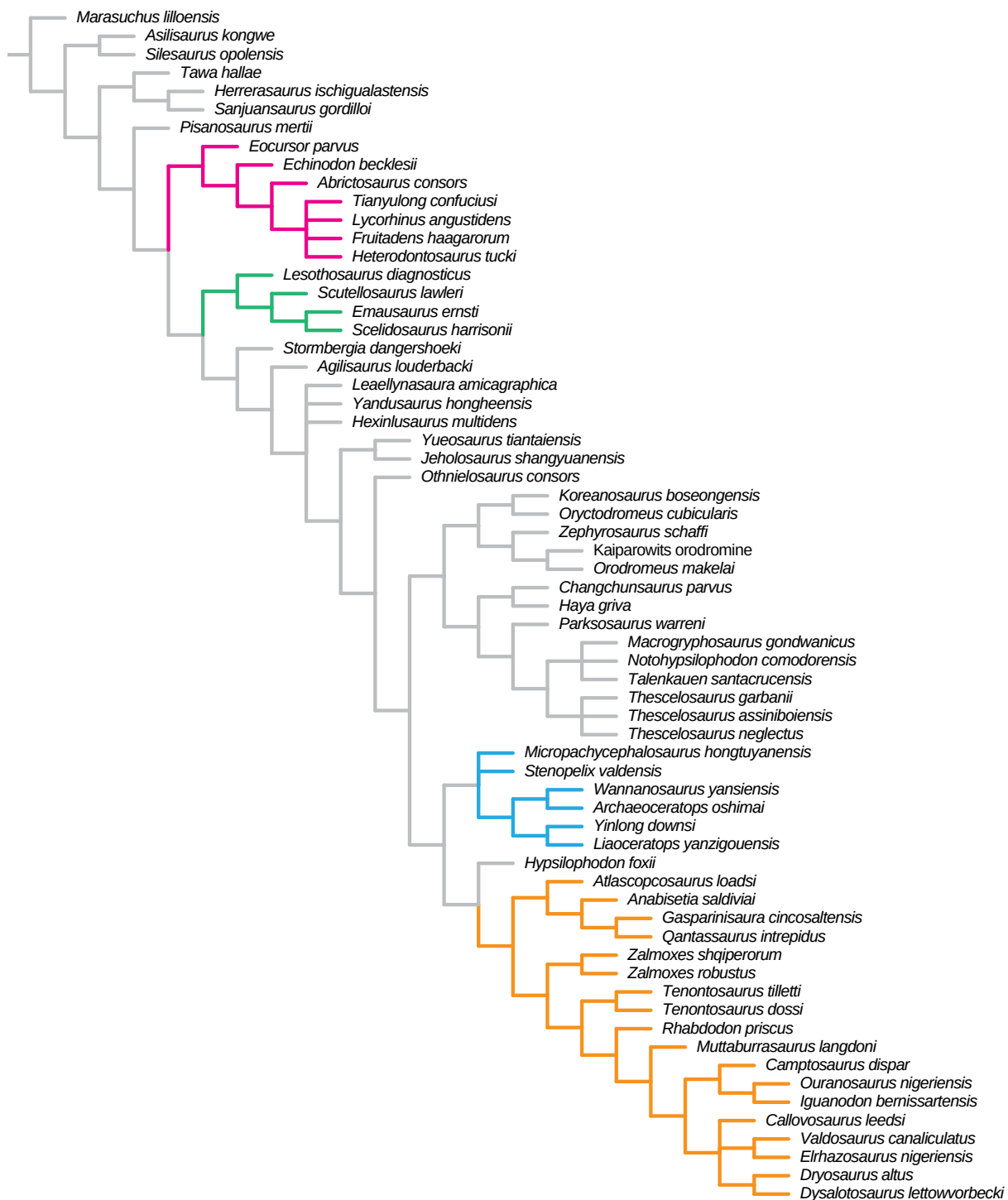
A2.41. (cont.)

Analysis G.8.B2015 - vertebral column & rib characters excluded



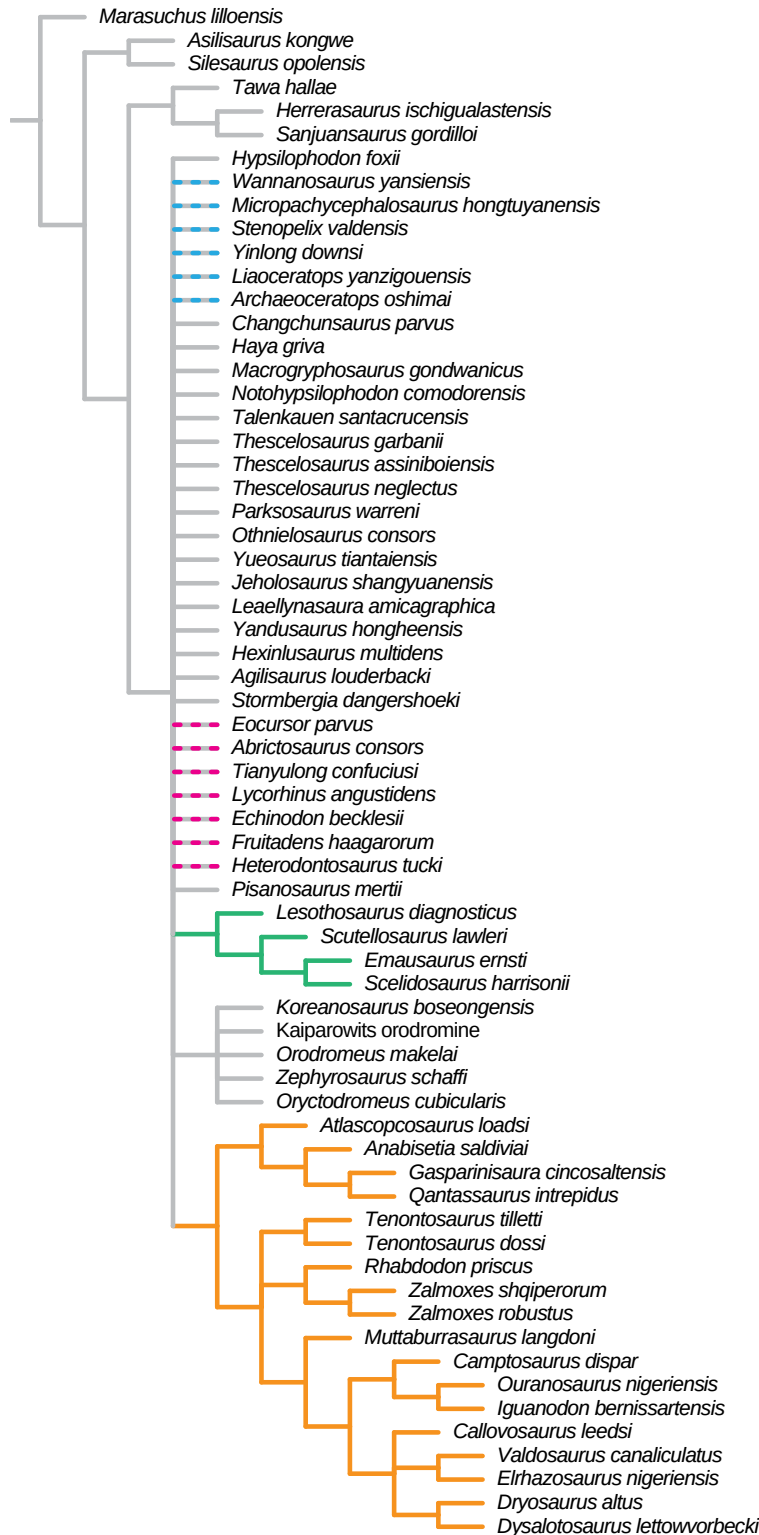
A2.42. Strict consensus tree of 42 MPTs produced from Boyd (2015) when vertebral column & rib characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.9.B2015 - pectoral girdle & sternum characters excluded



A2.43. Strict consensus tree of 12 MPTs produced from Boyd (2015) when all pectoral girdle & sternum characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

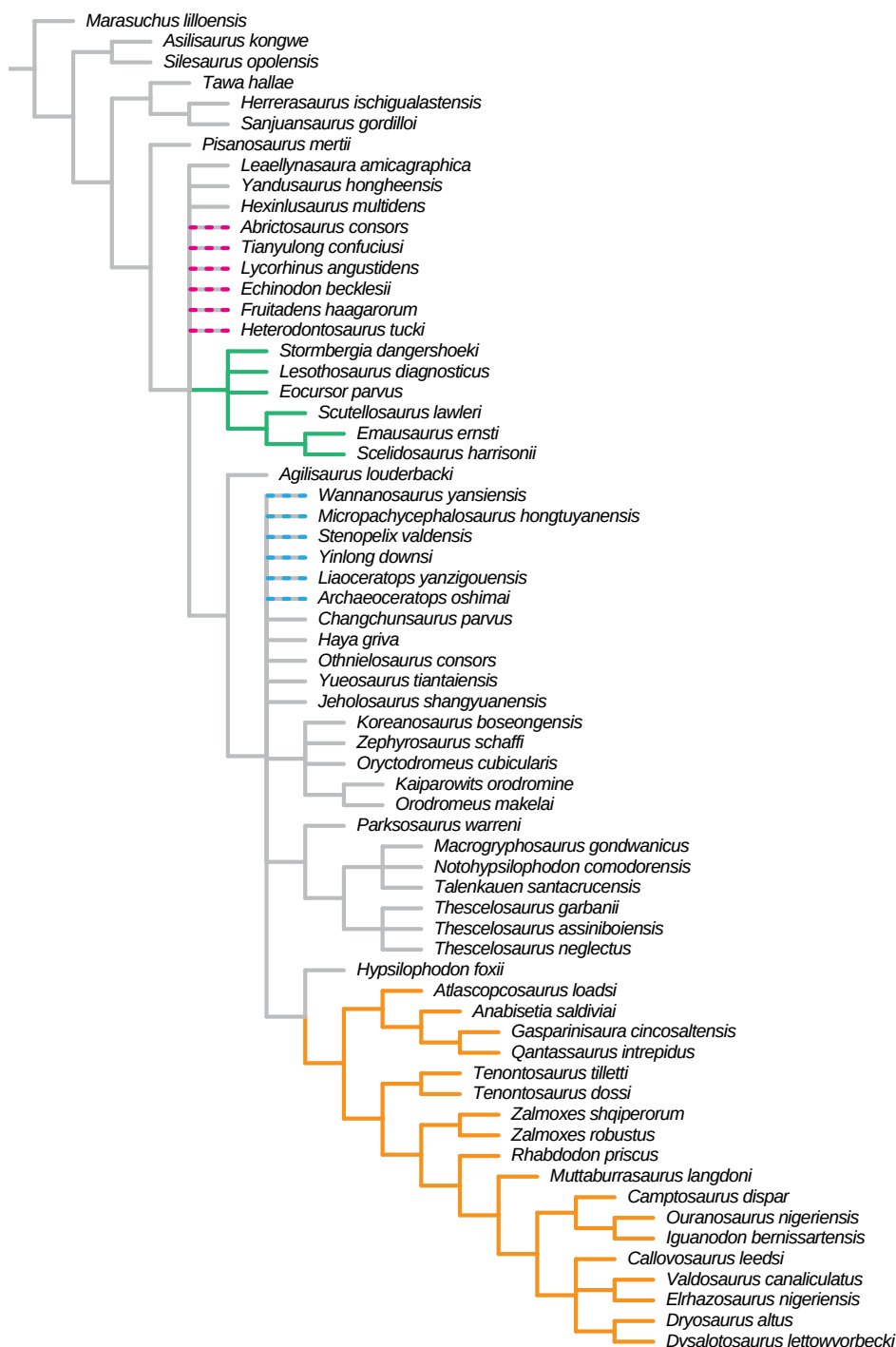
Analysis G.10.B2015 - forelimb characters excluded



A2.44. Strict consensus tree of 3,700 MPTs produced from Boyd (2015) when all forelimb characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.11.B2015 - pelvic girdle characters excluded

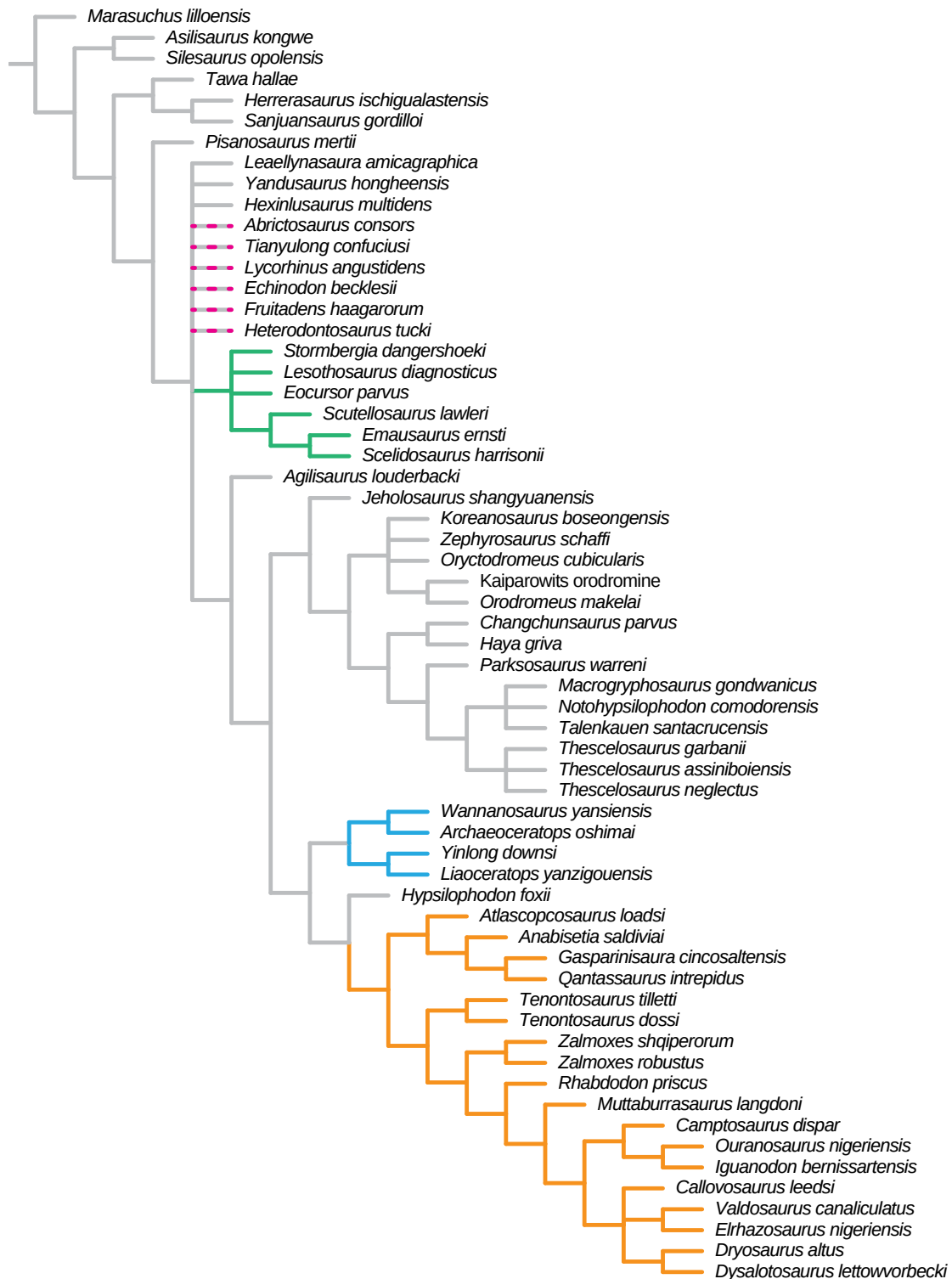
a) strict consensus tree



A2.45. Boyd (2015) tree topology when all pelvic girdle characters are removed: (a) strict consensus of 3,046 MPTs; (b) reduced strict consensus tree following pruning of four unstable taxa (*Micropachycephalosaurus*; *Othnielosaurus*; *Stenopelix*; *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.11.B2015 - pelvic girdle characters excluded

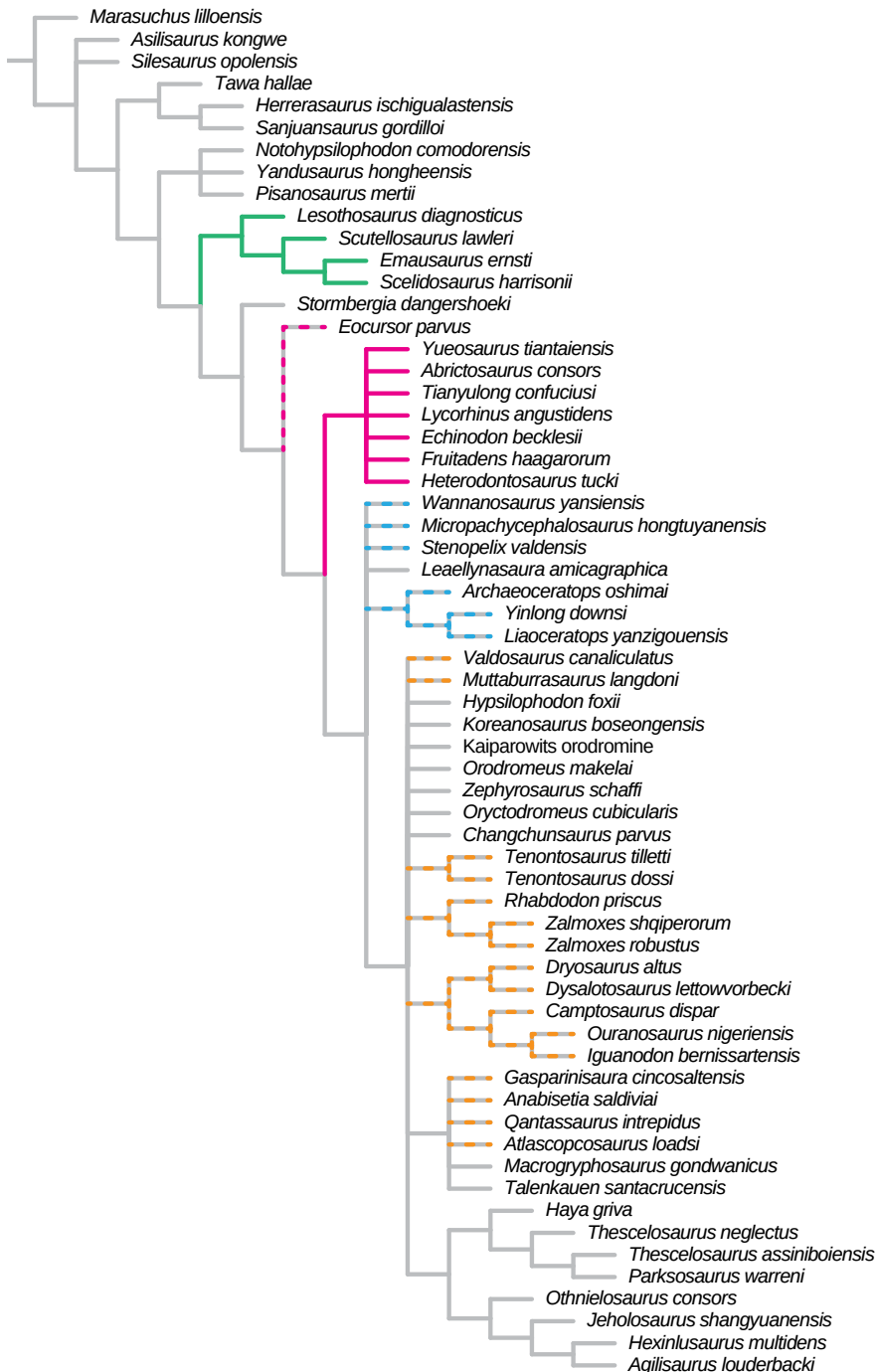
b) reduced strict consensus tree



A2.45. (cont.)

Analysis G.12.B2015 - hind limb characters excluded

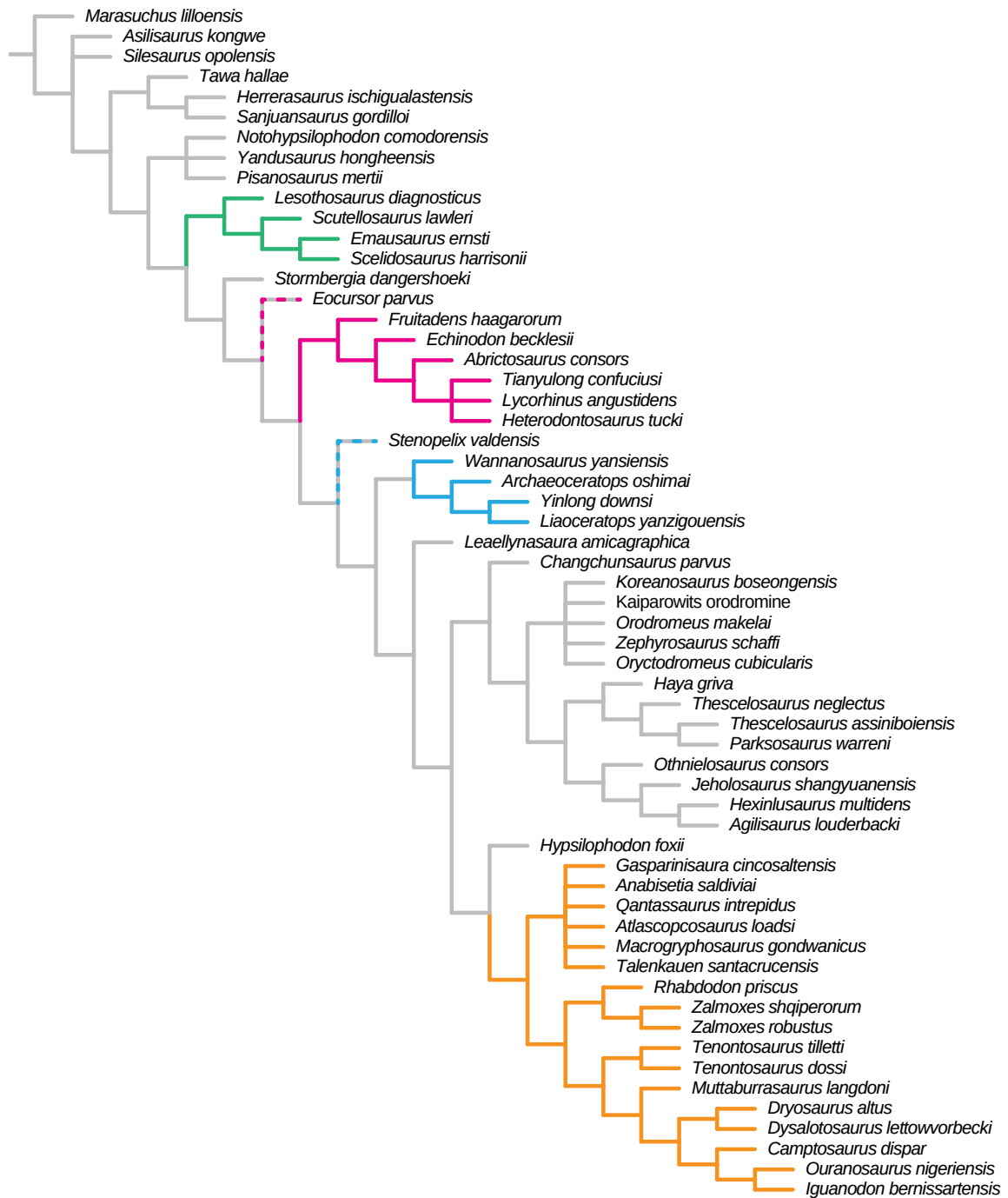
a) strict consensus tree



A2.46. Boyd (2015) tree topology when all hind limb characters are removed: (a) strict consensus of 2,200 MPTs; (b) reduced strict consensus tree following pruning of three unstable taxa (*Micropachycephalosaurus*; *Valdosaurus*; *Yueosaurus*). Three taxa were excluded prior to the tree search (*Callovosaurus*; *Elrhazosaurus*; *Thescelosaurus garbanii*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis G.12.B2015 - hind limb characters excluded

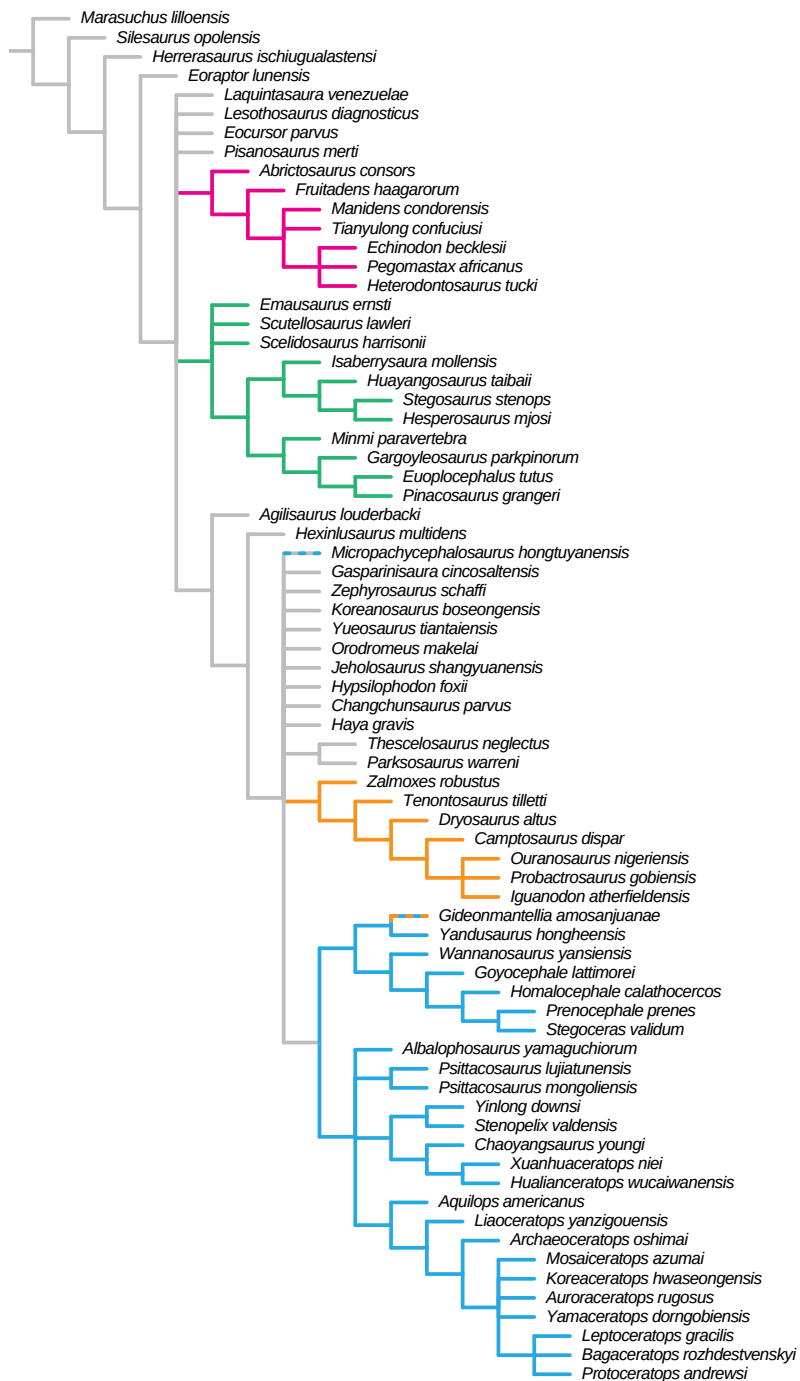
b) reduced strict consensus tree



A2.46. (cont.)

Analysis G.1.H2018 - rostral characters excluded

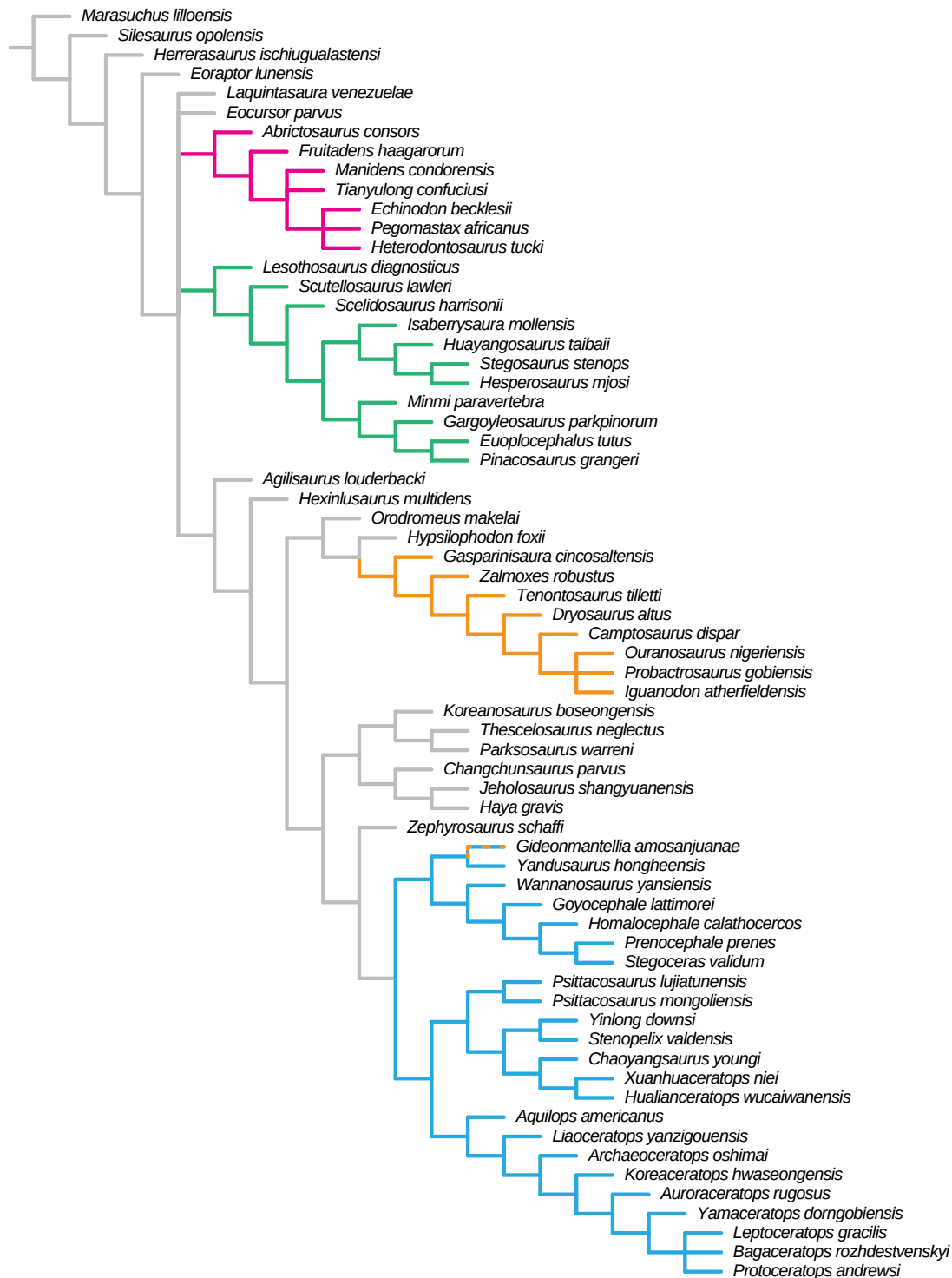
a) strict consensus tree



A2.47. Han *et al.* (2018) tree topology when all rostral characters are removed: (a) strict consensus of 1,500 MPTs; (b) reduced strict consensus tree following pruning of six unstable taxa (*Albalophosaurus*; *Emausaurus*; *Micropachycephalosaurus*; *Mosaiceratops*; *Pisanosaurus*; *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

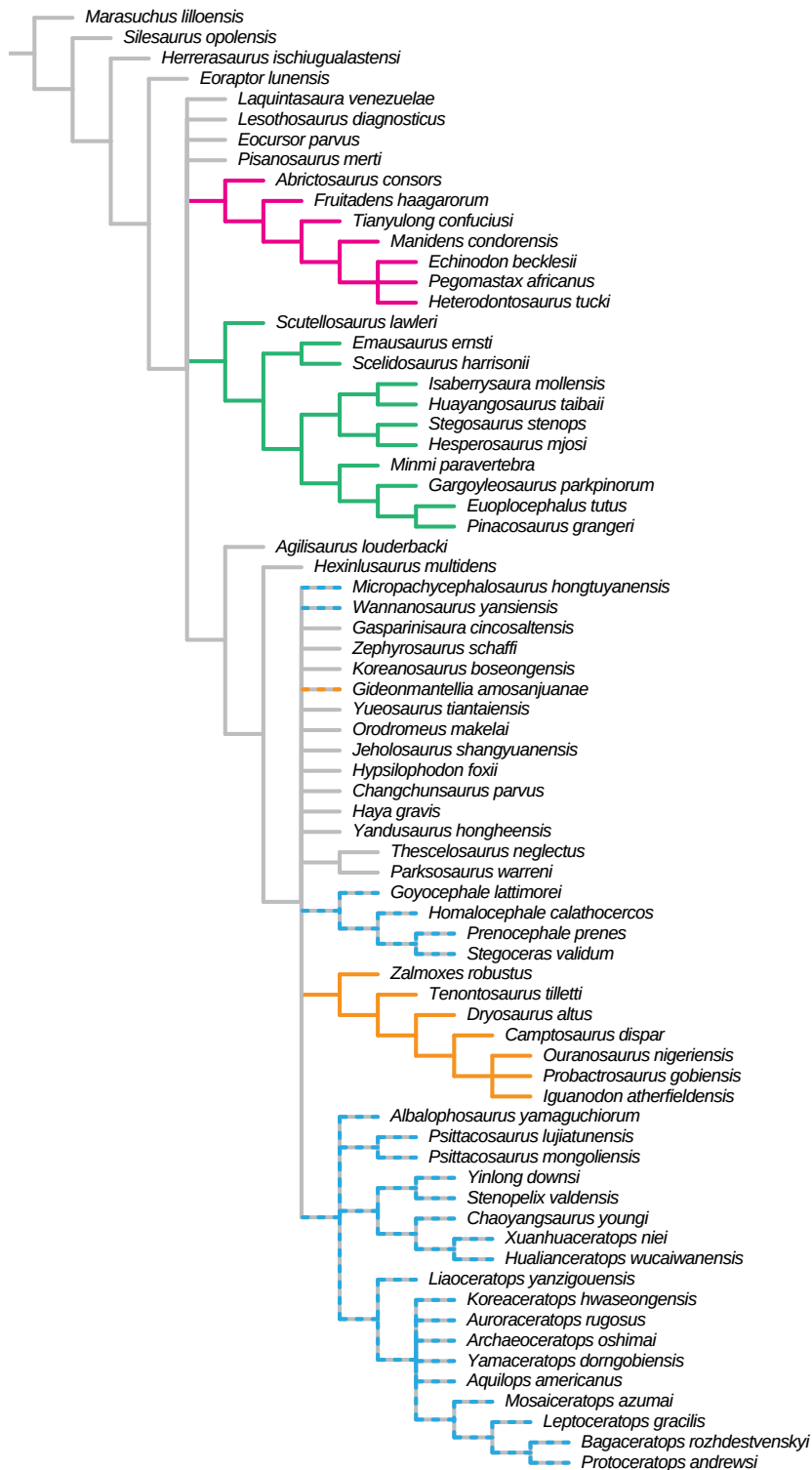
Analysis G.1.H2018 - rostral characters excluded

b) reduced strict consensus tree



A2.47. (cont.)

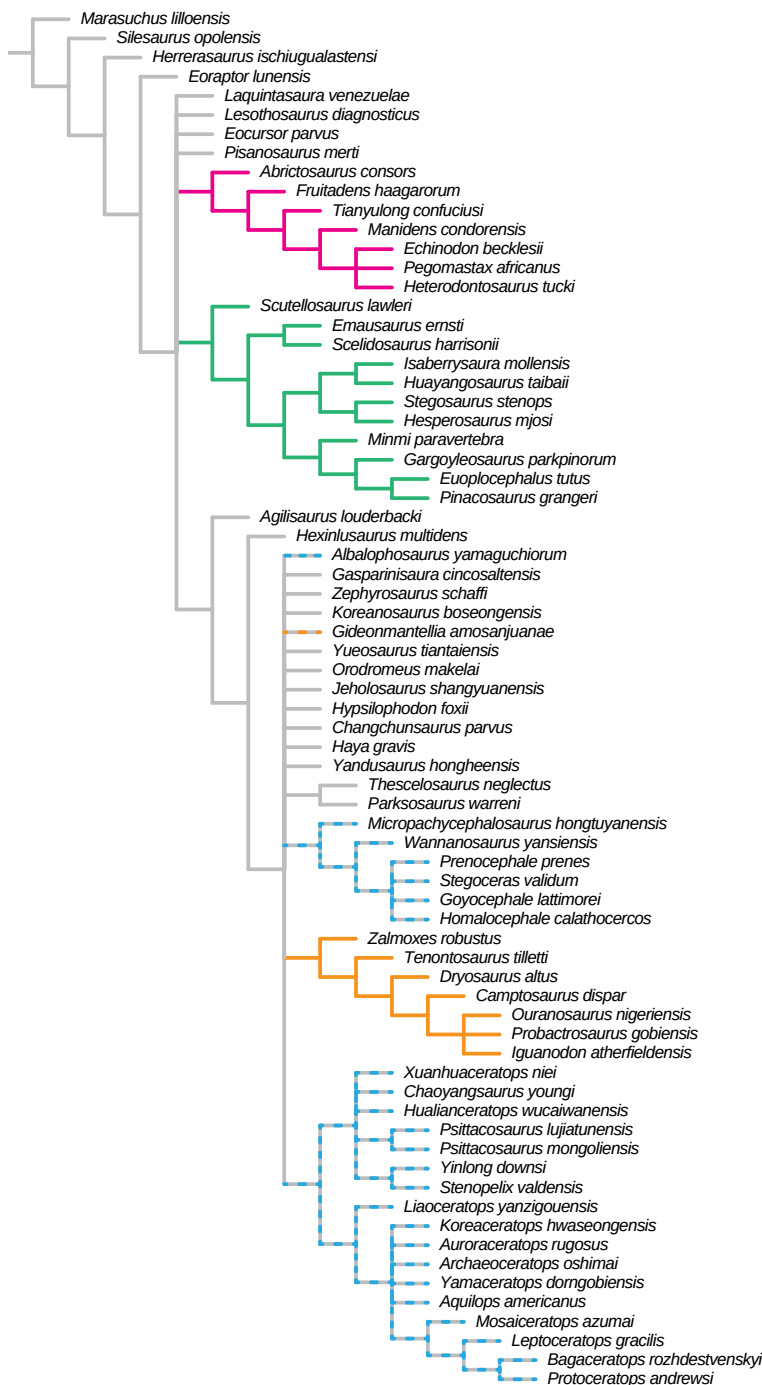
Analysis G.2.H2018 - palatal characters excluded



A2.48. Strict consensus tree of 39,262 MPTs produced from Han *et al.* (2018) when all palatal characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.3.H2018 - cranial roof characters excluded

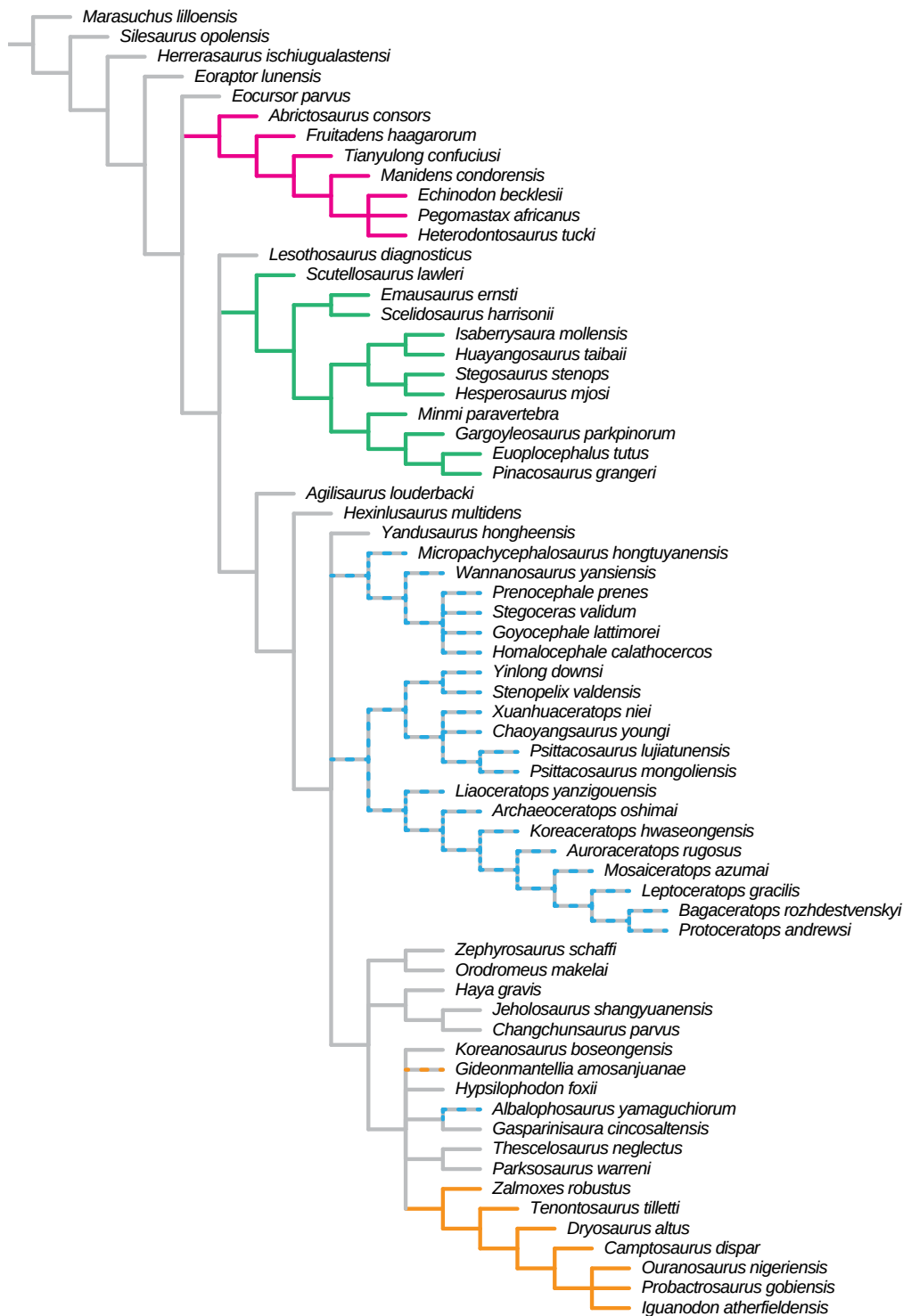
a) strict consensus tree



A2.49. Han *et al.* (2018) tree topology when all cranial roof characters are removed: (a) strict consensus of 42,600 MPTs; (b) reduced strict consensus tree following pruning of six unstable taxa (*Aquilops*; *Hualianceratops*; *Laquintasaura*; *Pisanosaurus*; *Yamaceratops*; *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

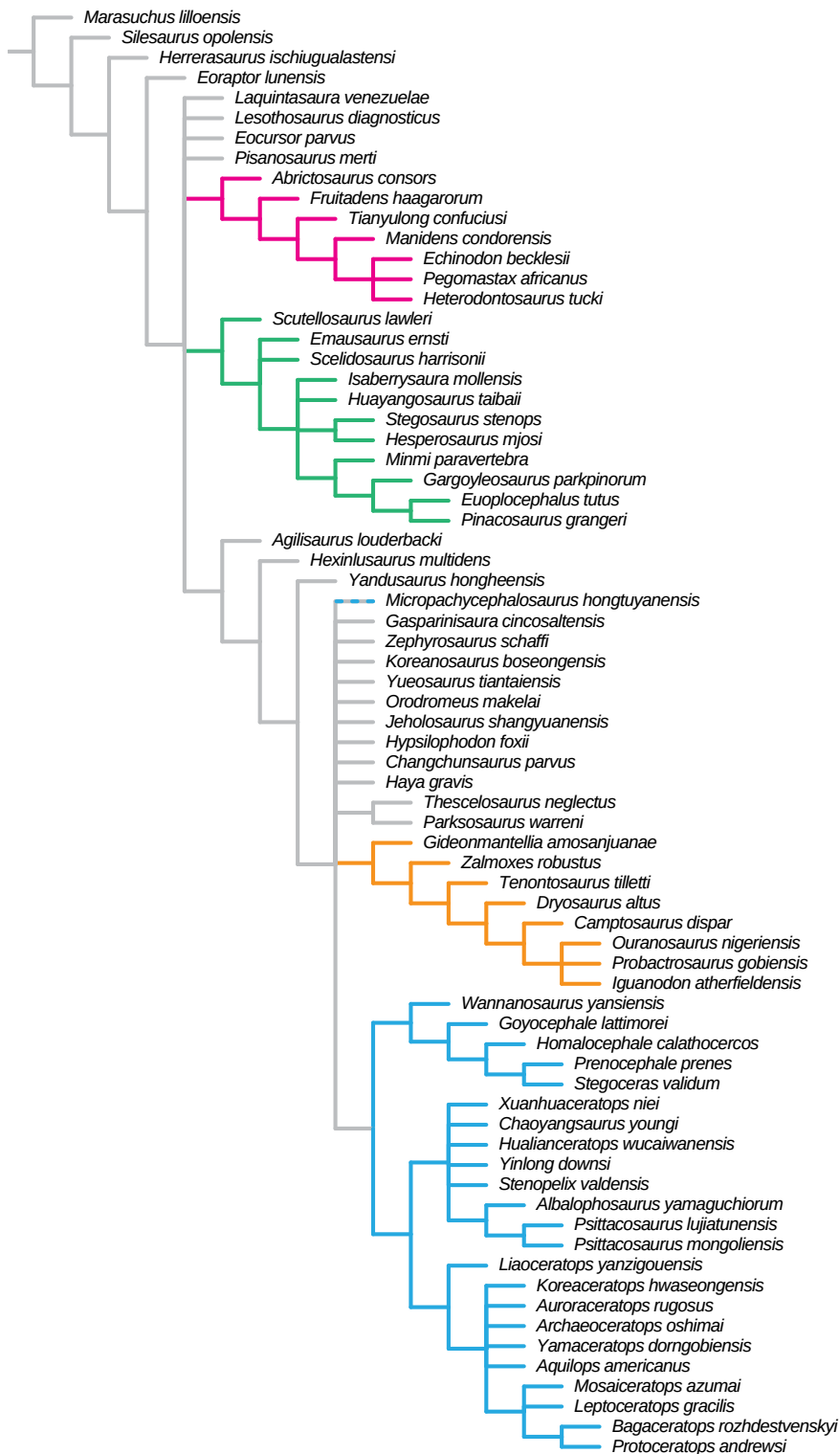
Analysis G.3.H2018 - cranial roof characters excluded

b) reduced strict consensus tree



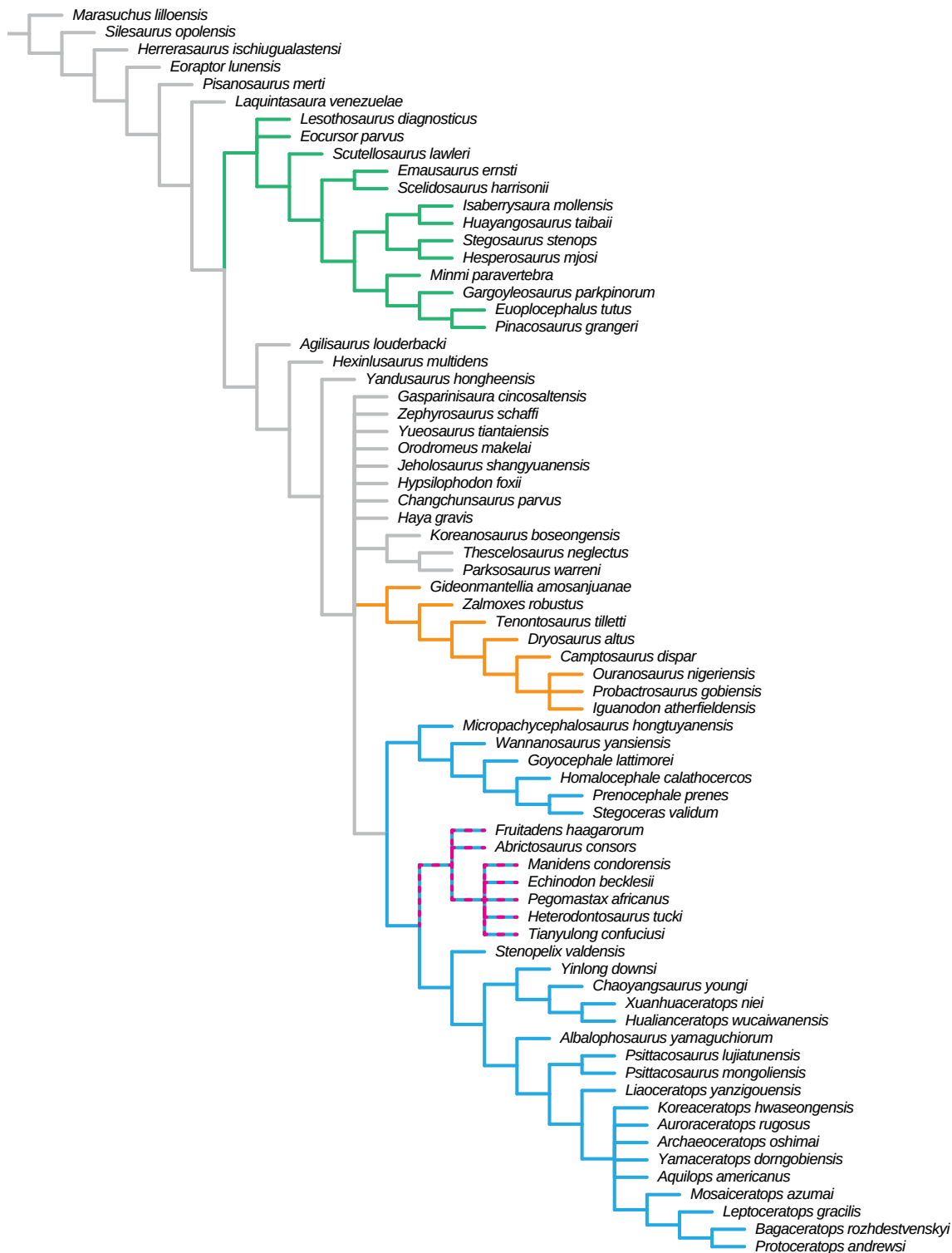
A2.49. (cont.)

Analysis G.4.H2018 - skull base characters excluded



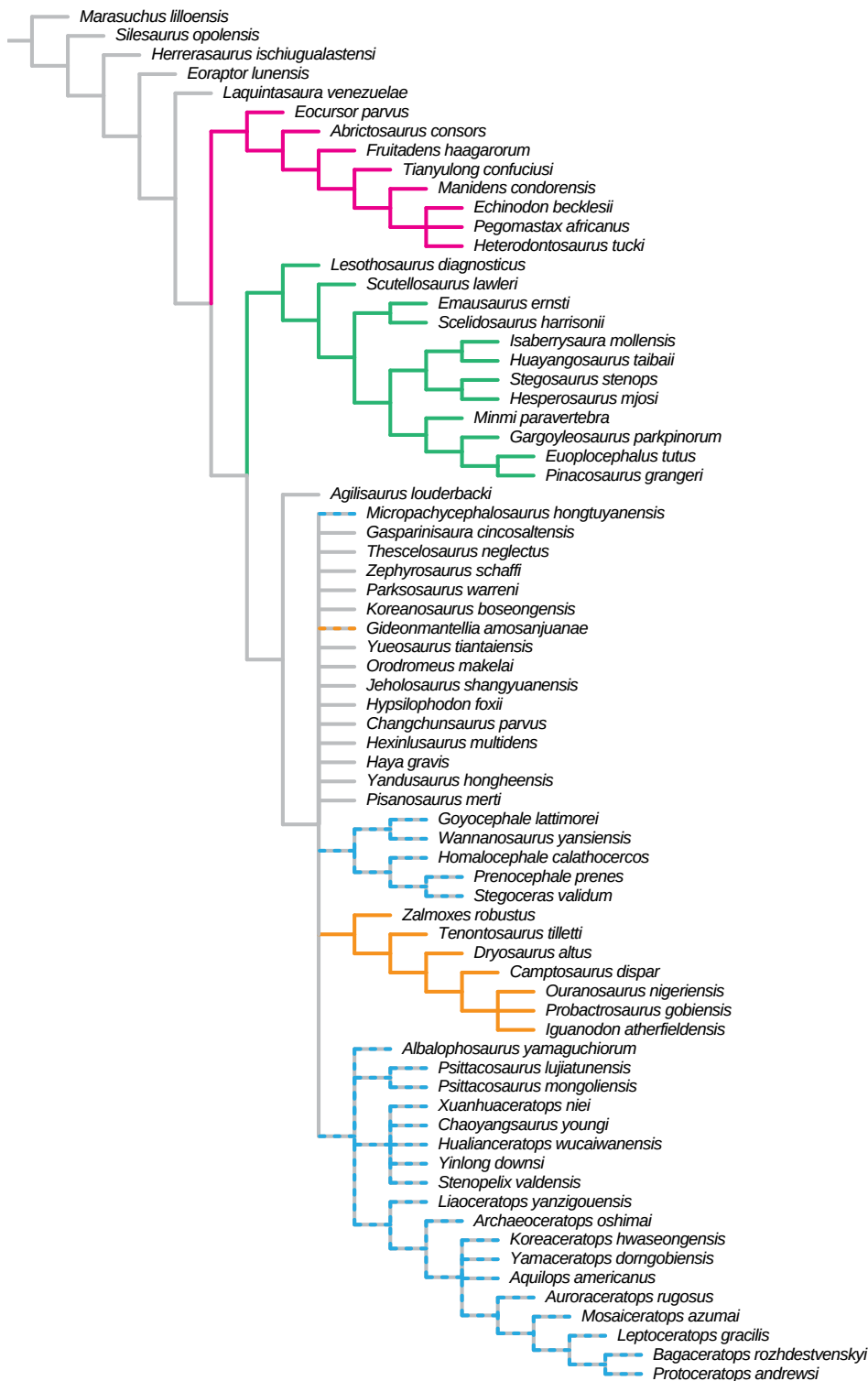
A2.50. Strict consensus tree of 7,100 MPTs produced from Han *et al.* (2018) when all skull base characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.5.H2018 - braincase characters excluded



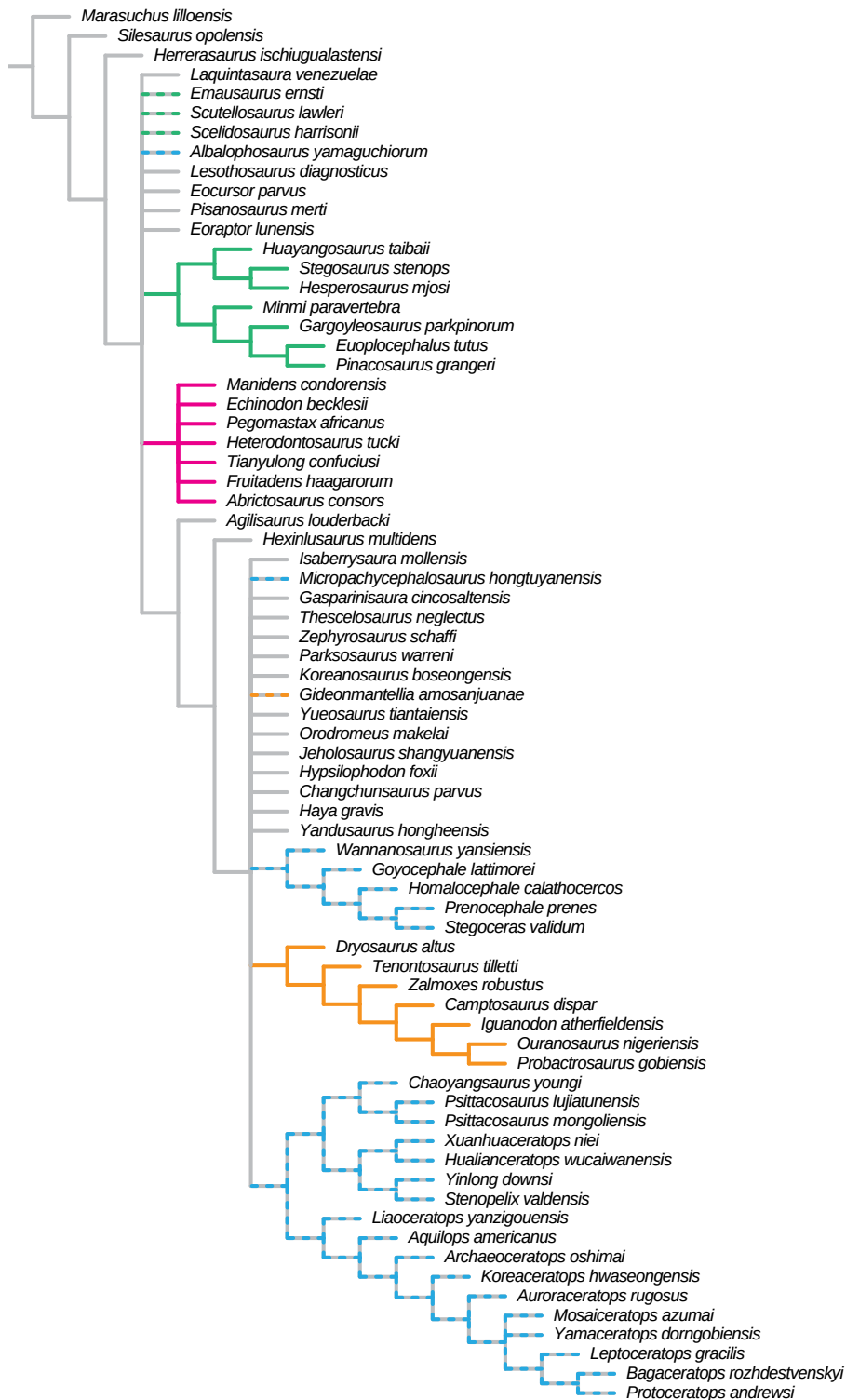
A2.51. Strict consensus tree of 1,342 MPTs produced from Han *et al.* (2018) when all braincase characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.6.H2018 - mandibular characters excluded



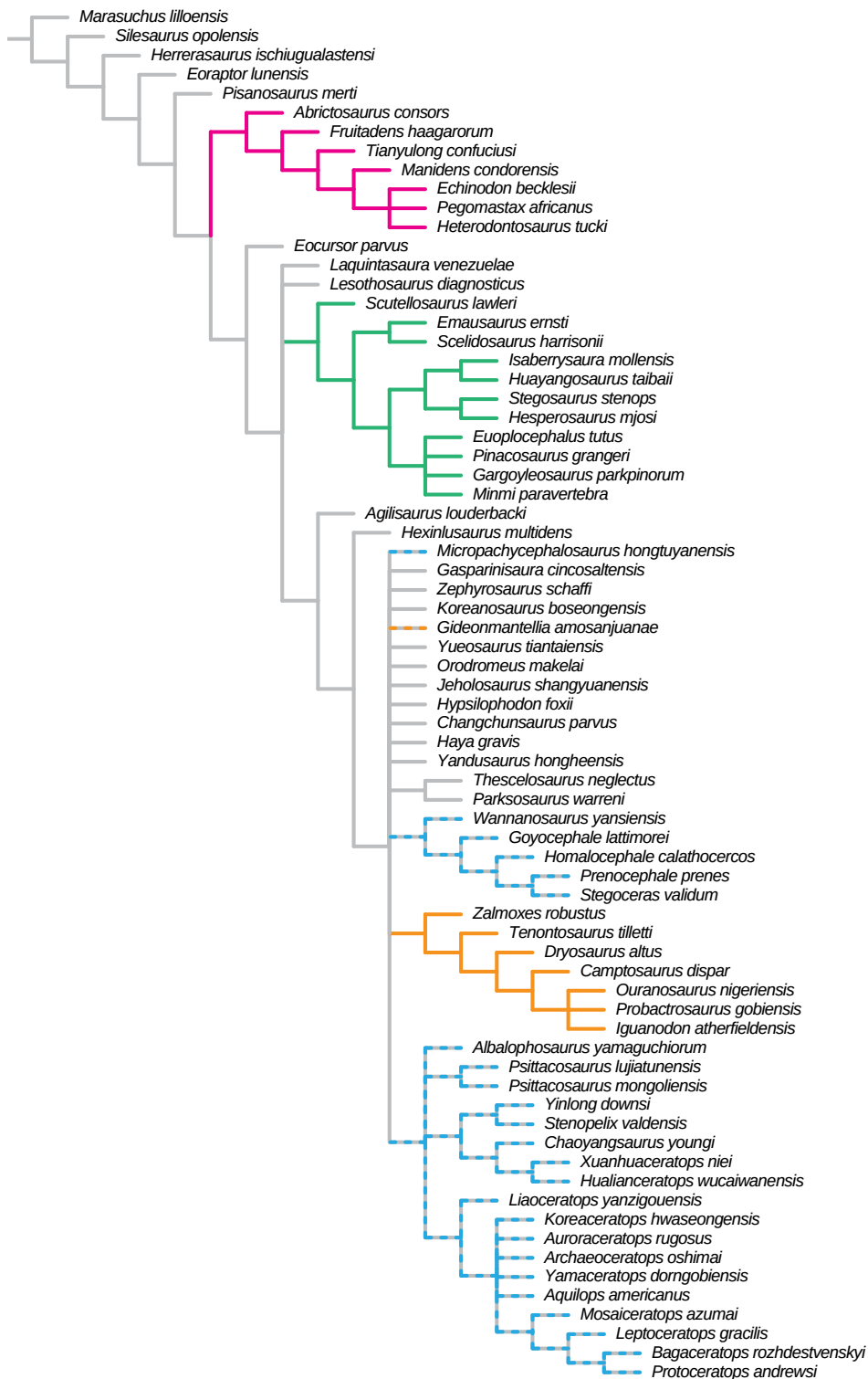
A2.52. Strict consensus tree of 5,100 MPTs produced from Han *et al.* (2018) when all mandibular characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.7.H2018 - dental characters excluded



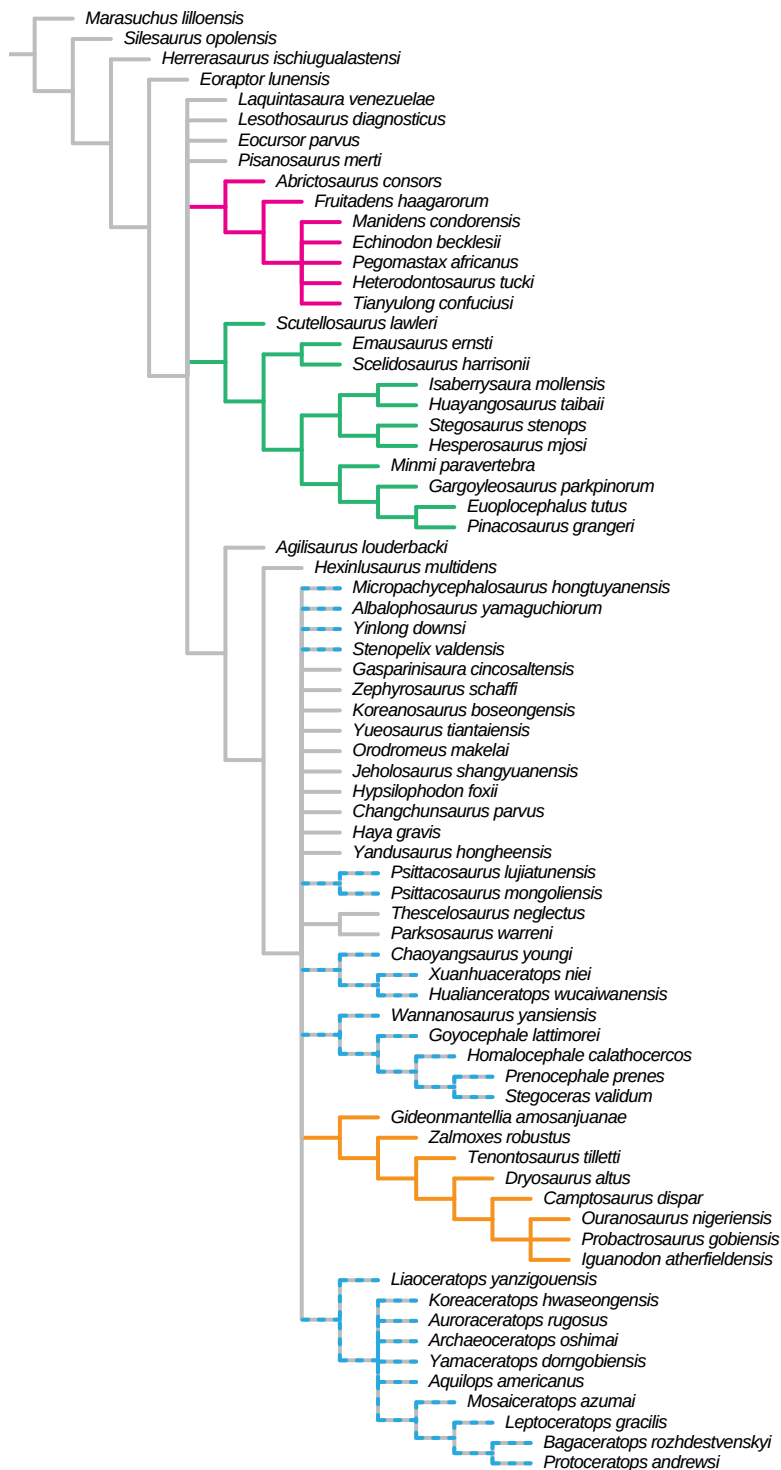
A2.53. Strict consensus tree of 52,500 MPTs produced from Han *et al.* (2018) when all dental characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.8.H2018 - vertebral column & rib characters excluded



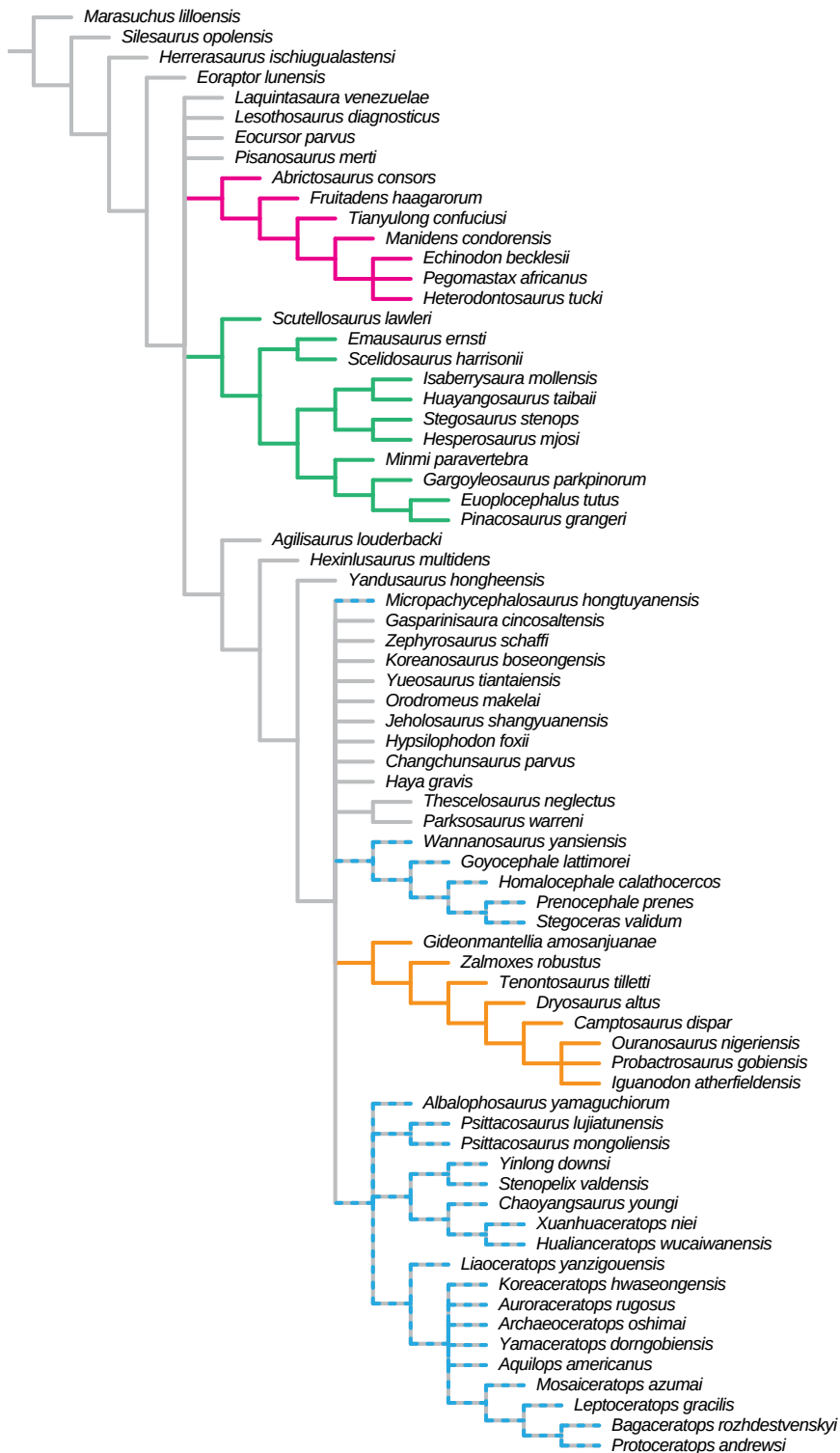
A2.54. Strict consensus tree of 9,911 MPTs produced from Han *et al.* (2018) when all vertebral column and rib characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.9.H2018 - pectoral girdle & sternum characters excluded



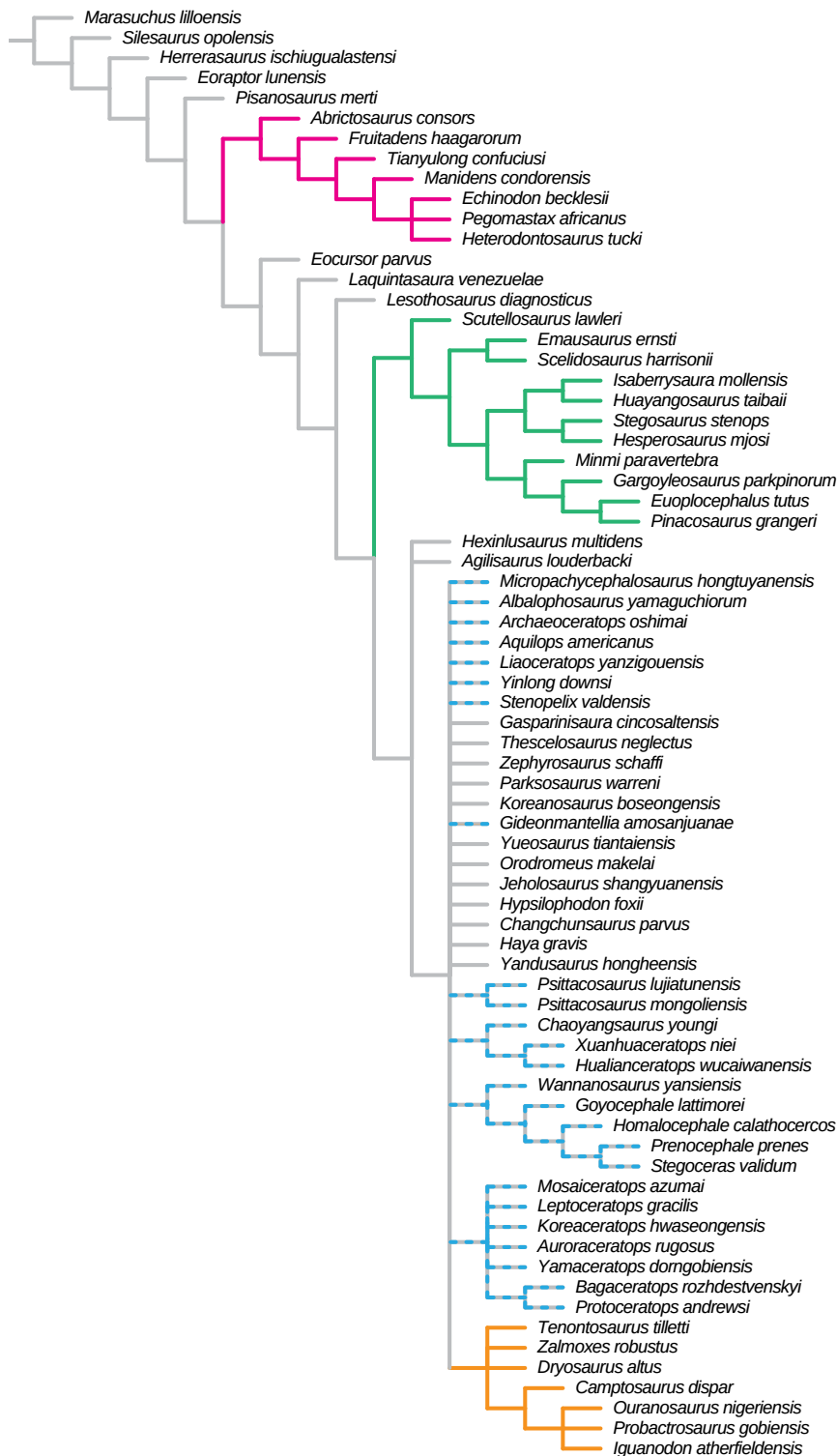
A2.55. Strict consensus tree of 28,000 MPTs produced from Han *et al.* (2018) when all pectoral girdle and sternum characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.10.H2018 - forelimb characters excluded



A2.56. Strict consensus tree of 11,159 MPTs produced from Han *et al.* (2018) when all forelimb characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

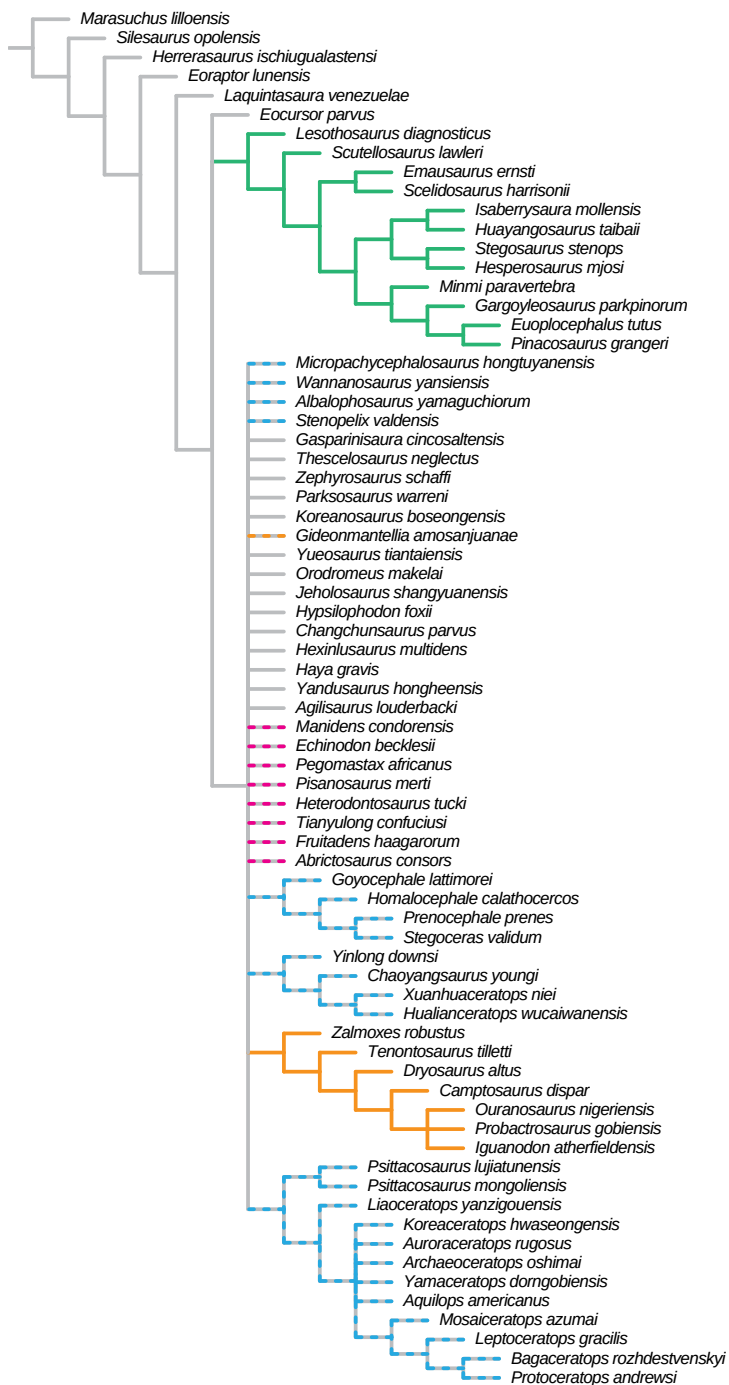
Analysis G.11.H2018 - pelvic girdle characters excluded



A2.57. Strict consensus tree of 36,400 MPTs produced from Han *et al.* (2018) when all pelvic characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.12.H2018 - hind limb characters excluded

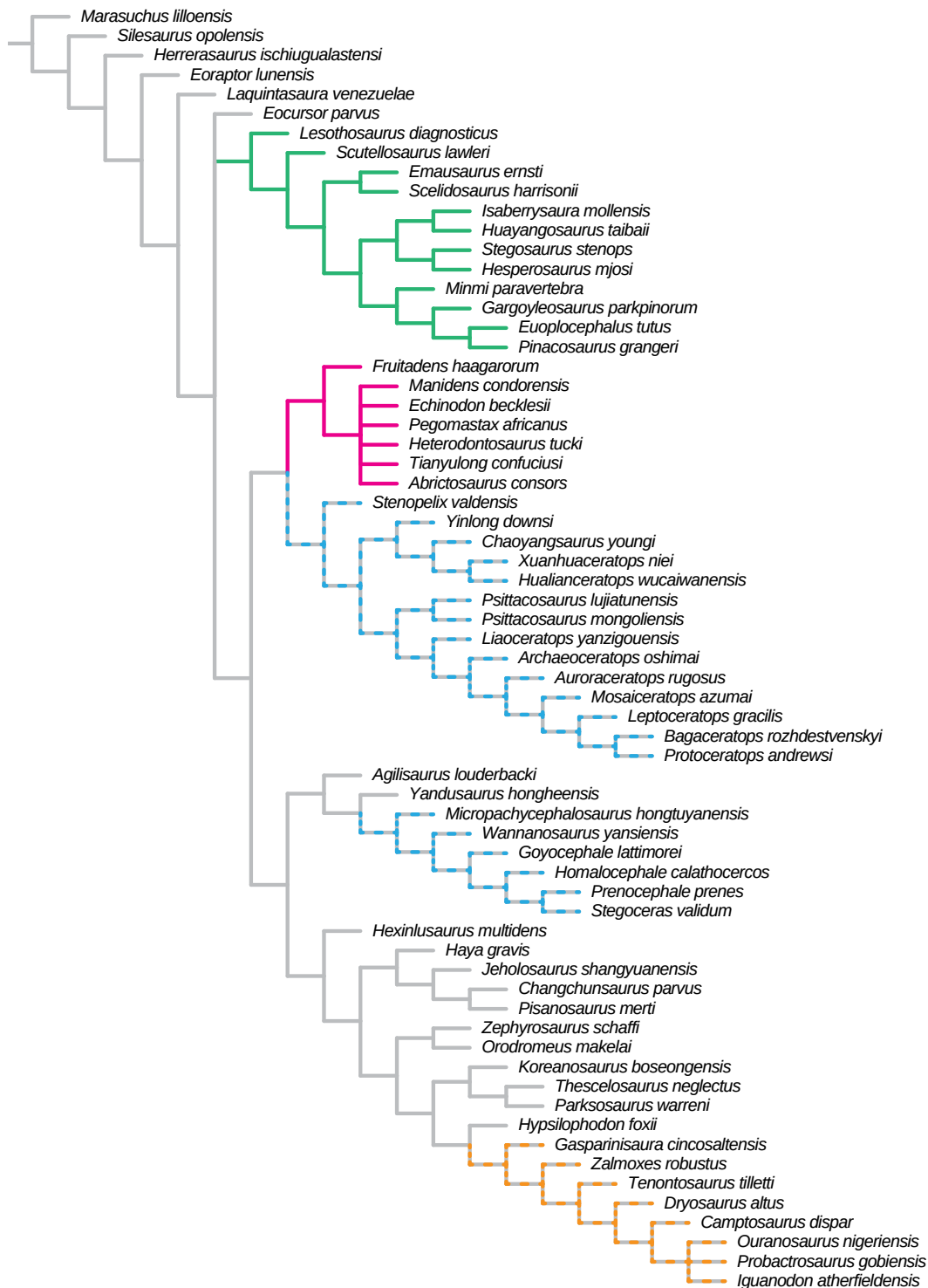
a) strict consensus tree



A2.58. Han *et al.* (2018) tree topology when all hind limb characters are removed: (a) strict consensus of 13,800 MPTs; (b) reduced strict consensus tree following pruning of six unstable taxa (*Albalophosaurus*; *Aquilops*; *Gideonmantellia*; *Koreaceratops*; *Yamaceratops*; *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis G.12.H2018 - hind limb characters excluded

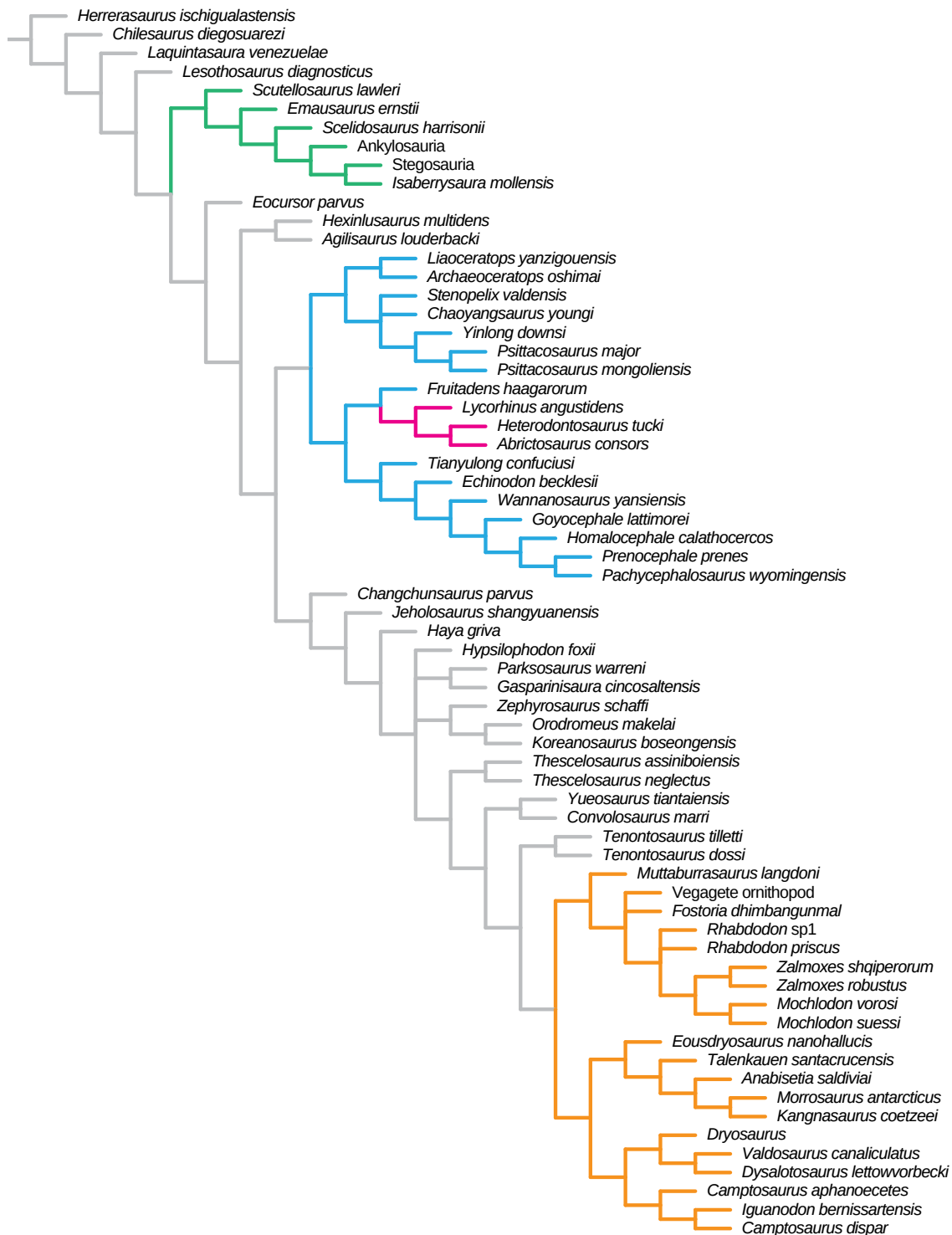
b) reduced strict consensus tree



A2.58. (cont.)

Analysis G.1.D2021 - rostral characters excluded

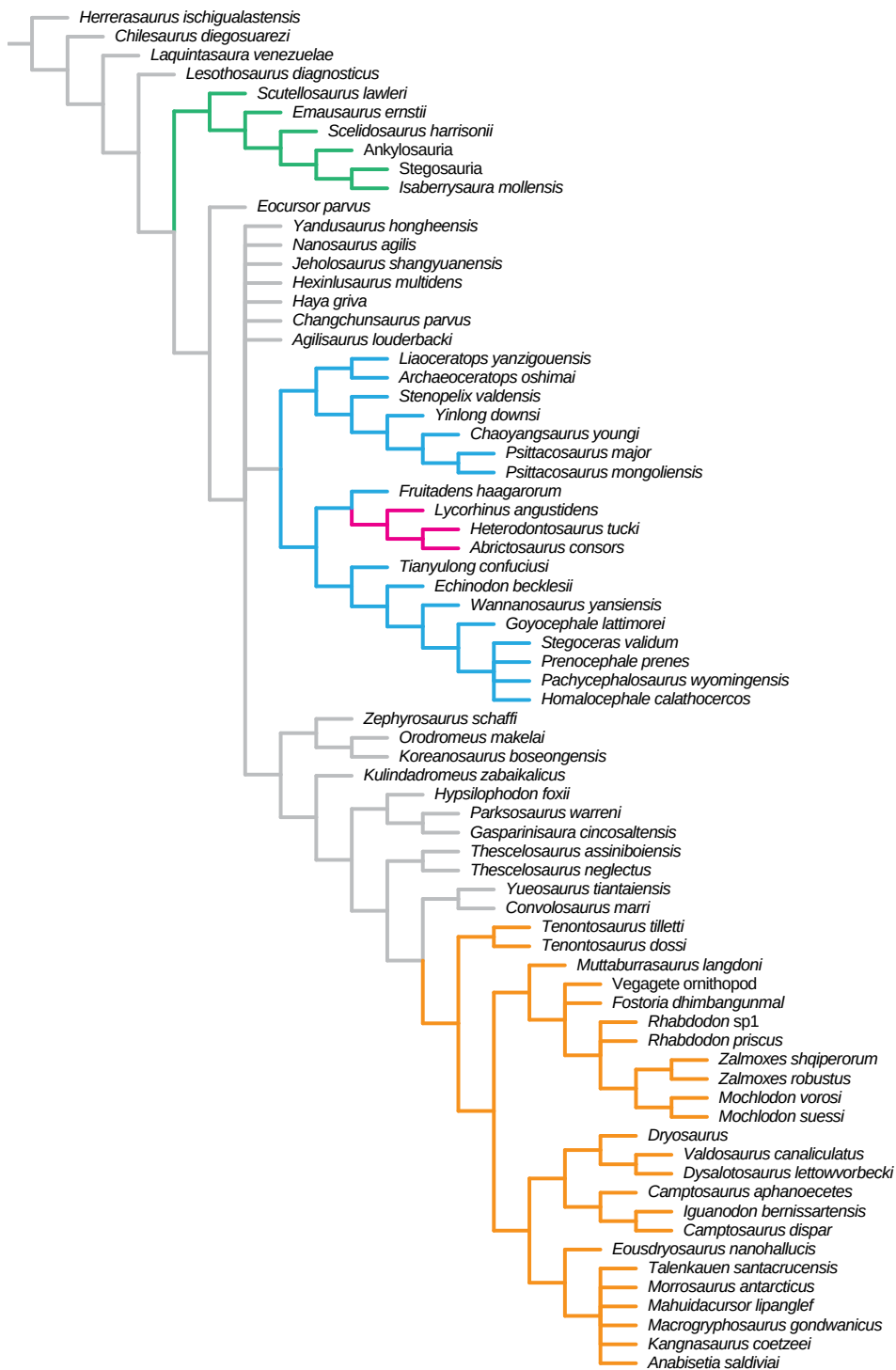
b) reduced strict consensus tree



A2.59. (cont.)

Analysis G.2.D2021 - palatal characters excluded

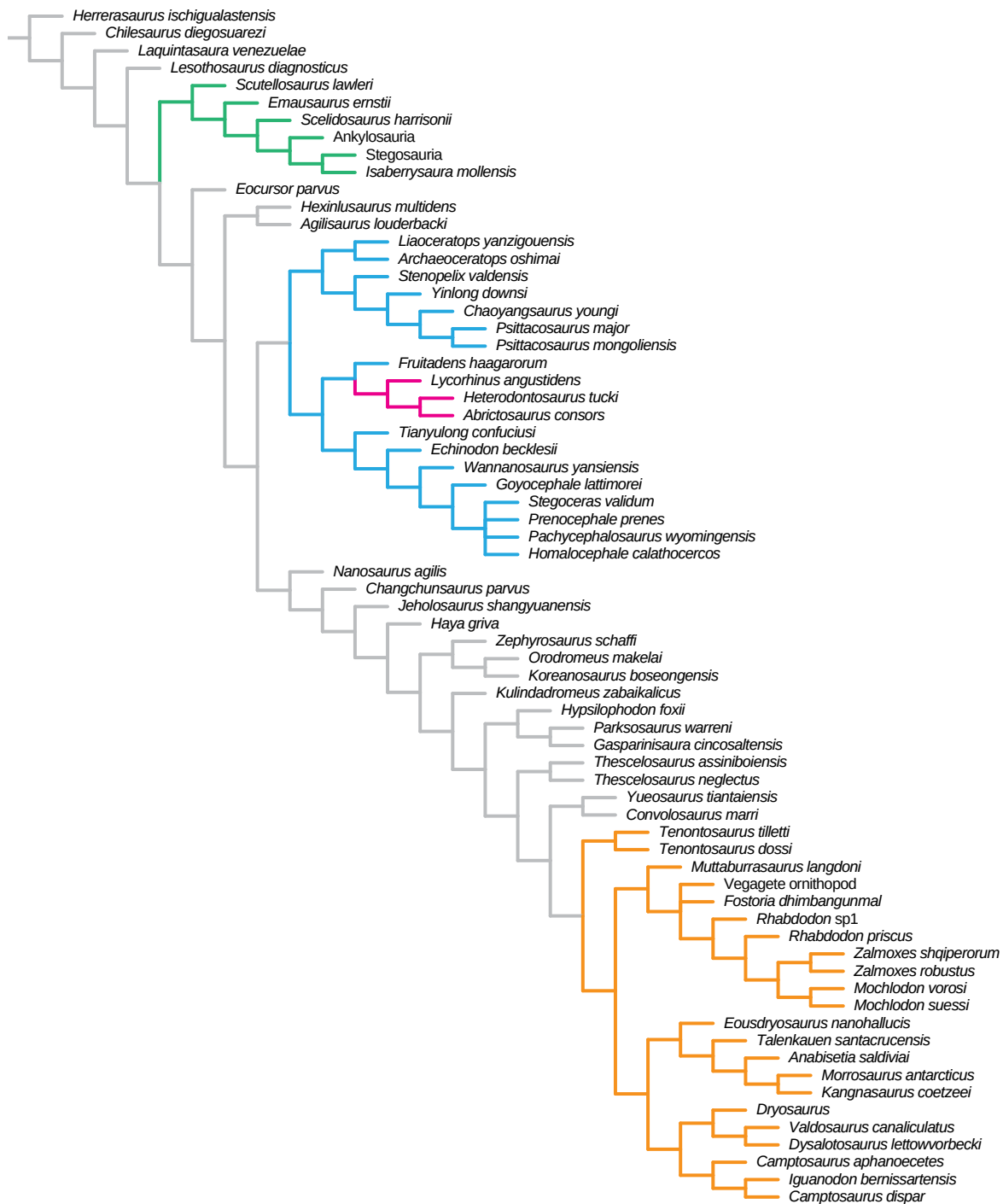
a) strict consensus tree



A2.60. Dieudonné *et al.* (2021) tree topology when all palatal characters are removed: (a) strict consensus of 176 MPTs; (b) reduced strict consensus tree following pruning of three unstable taxa (*Macrogyphosaurus*, *Mahuidacrusor*, *Yandusaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis G.2.D2021 - palatal characters excluded

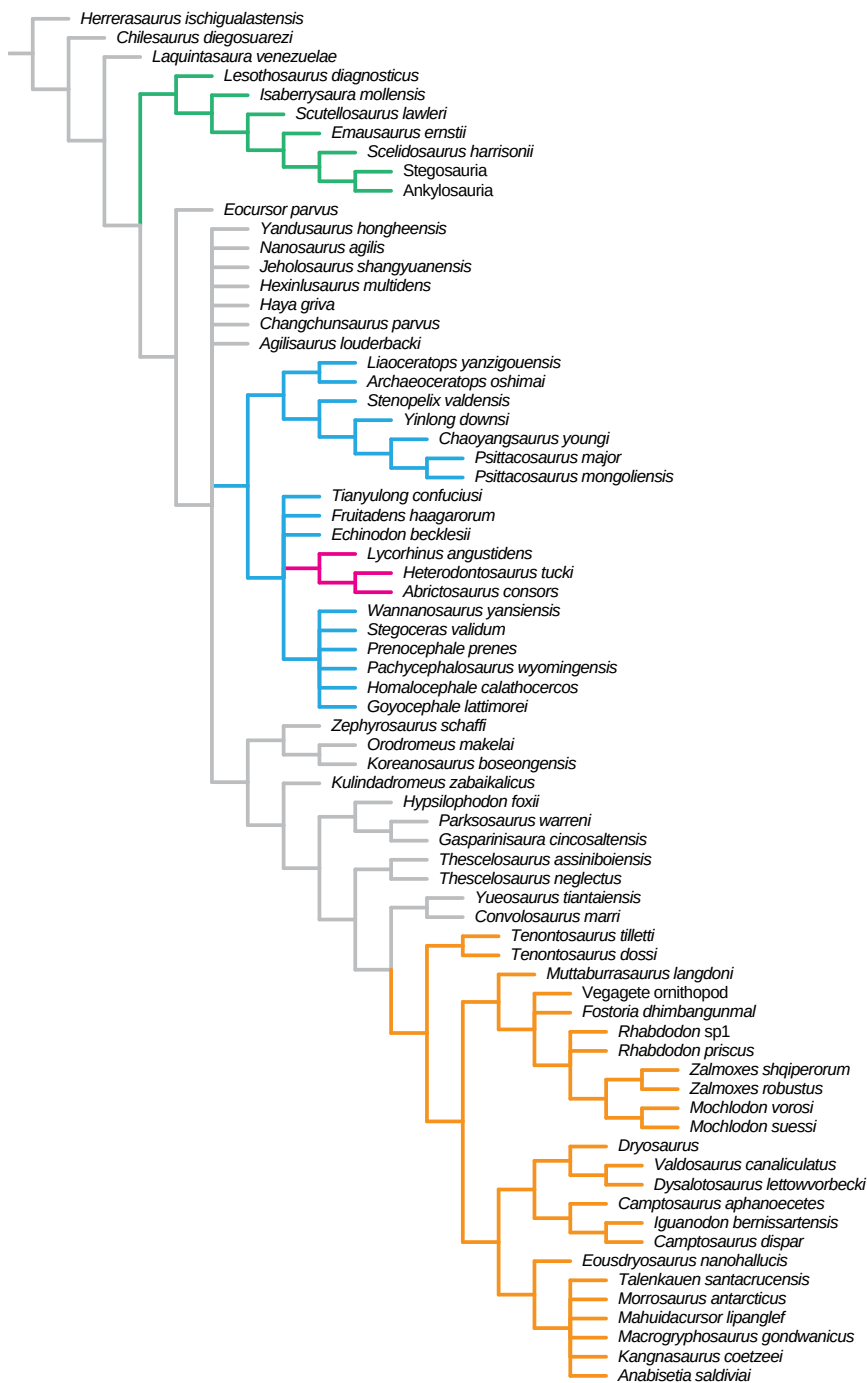
b) reduced strict consensus tree



A2.60. (cont.)

Analysis G.3.D2021 - cranial roof characters excluded

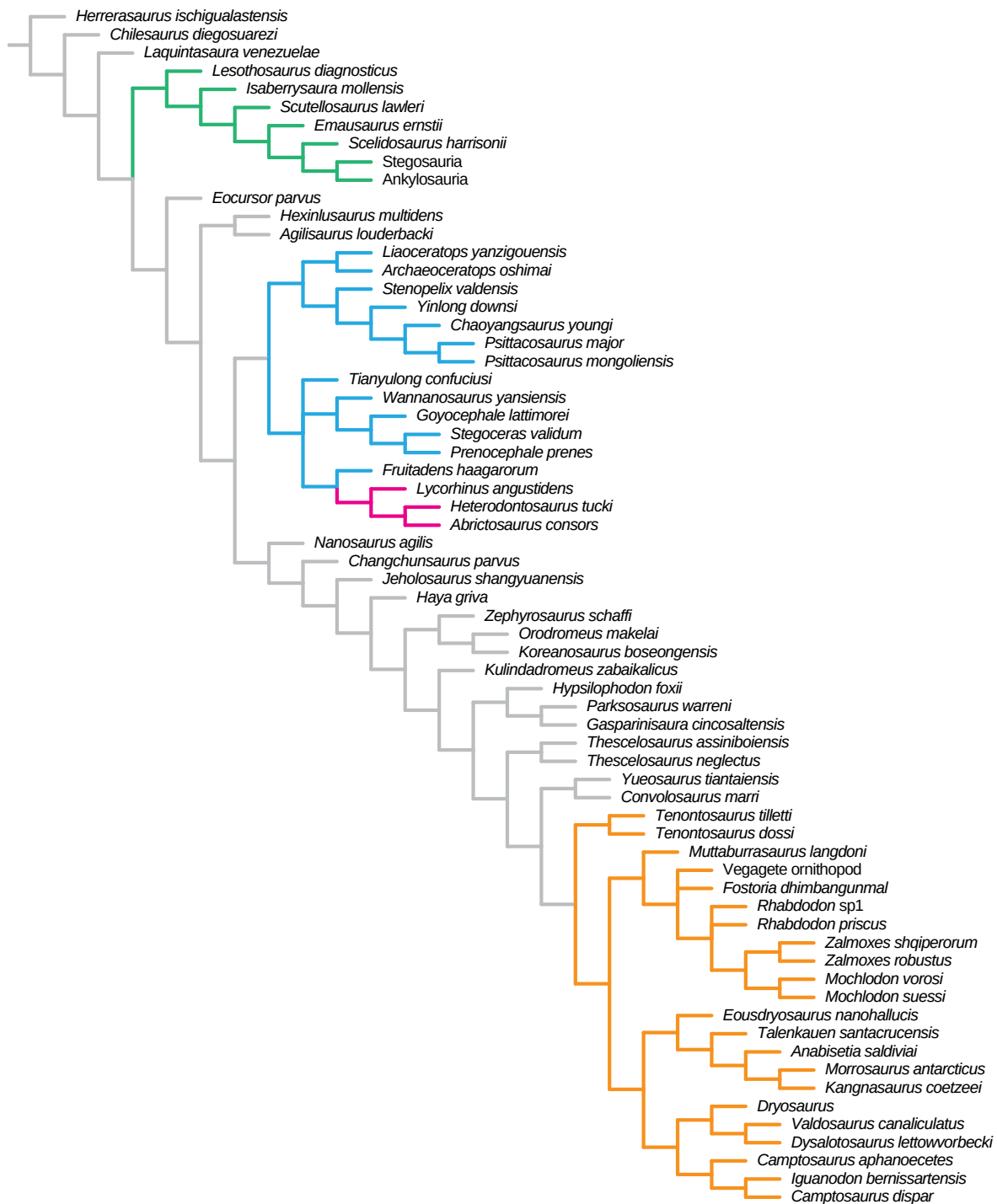
a) strict consensus tree



A2.61. Dieudonné *et al.* (2021) tree topology when all cranial roof characters are removed: (a) strict consensus of 132 MPTs; (b) reduced strict consensus tree following pruning of six unstable taxa (*Echinodon*, *Macrogyphosaurus*, *Mahuidacrusor*, *Pachycephalosaurus*, *Yandusaurus*). Strict consensus tree of 132 MPTs produced from Dieudonné *et al.* (2021) when all cranial roof characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis G.3.D2021 - cranial roof characters excluded

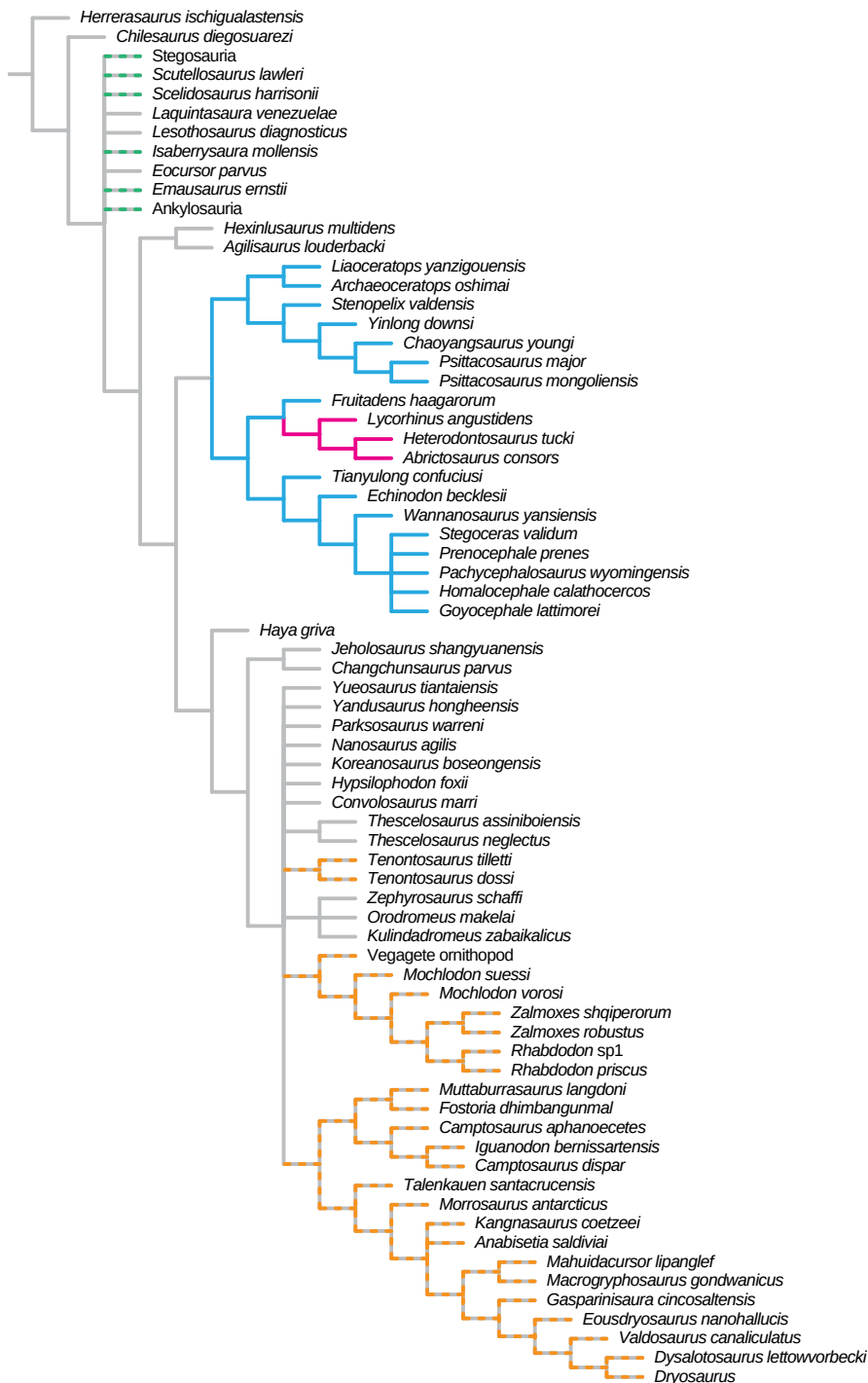
b) reduced strict consensus tree



A2.61. (cont.)

Analysis G.4.D2021 - skull base characters excluded

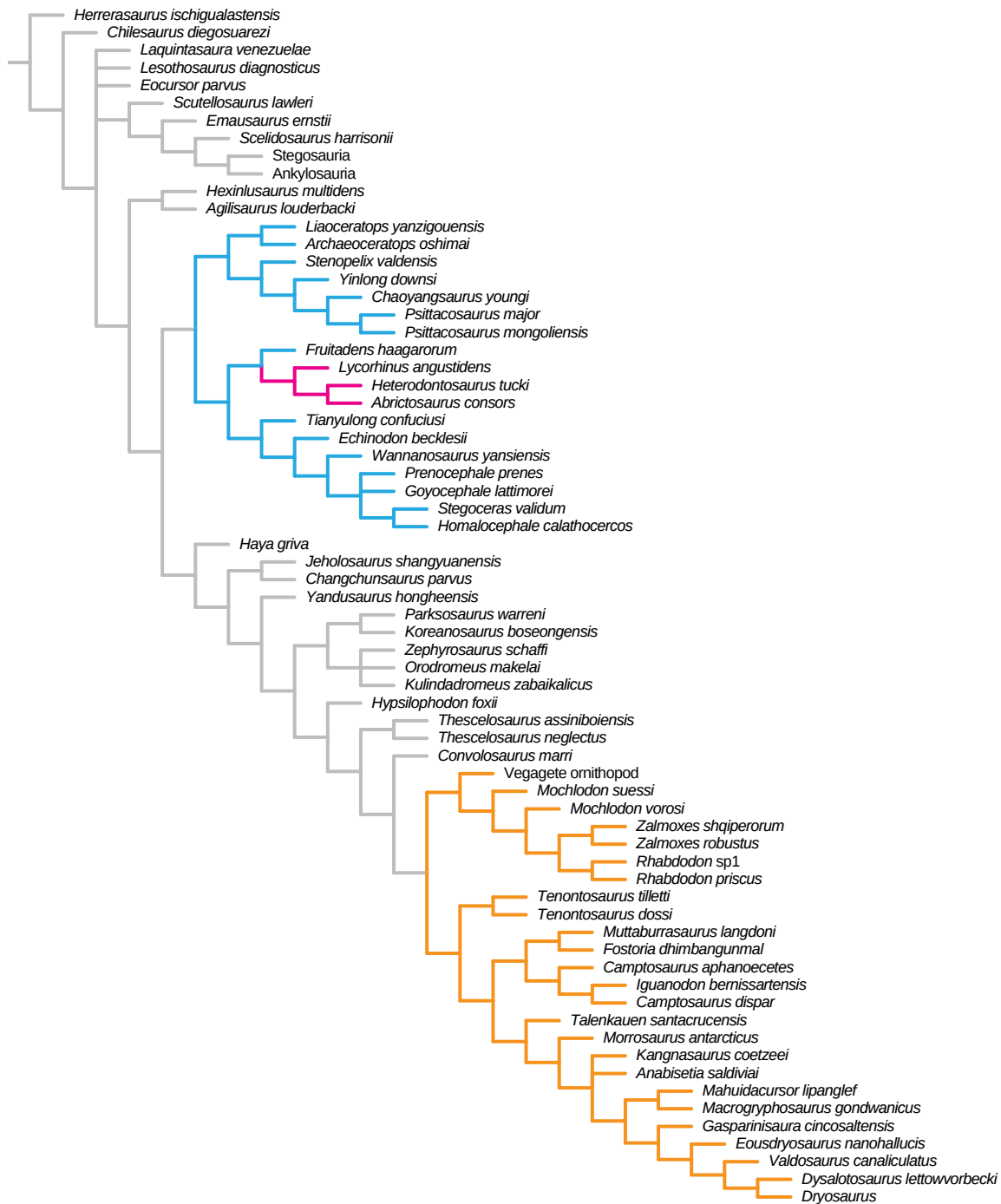
a) strict consensus tree



A2.62. Dieudonné *et al.* (2021) tree topology when all skull base characters are removed: (a) strict consensus of 354 MPTs; (b) reduced strict consensus tree following pruning of four unstable taxa (*Isaberrysaura*, *Nanosaurus*, *Pachycephalosaurus*, *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis G.4.D2021 - skull base characters excluded

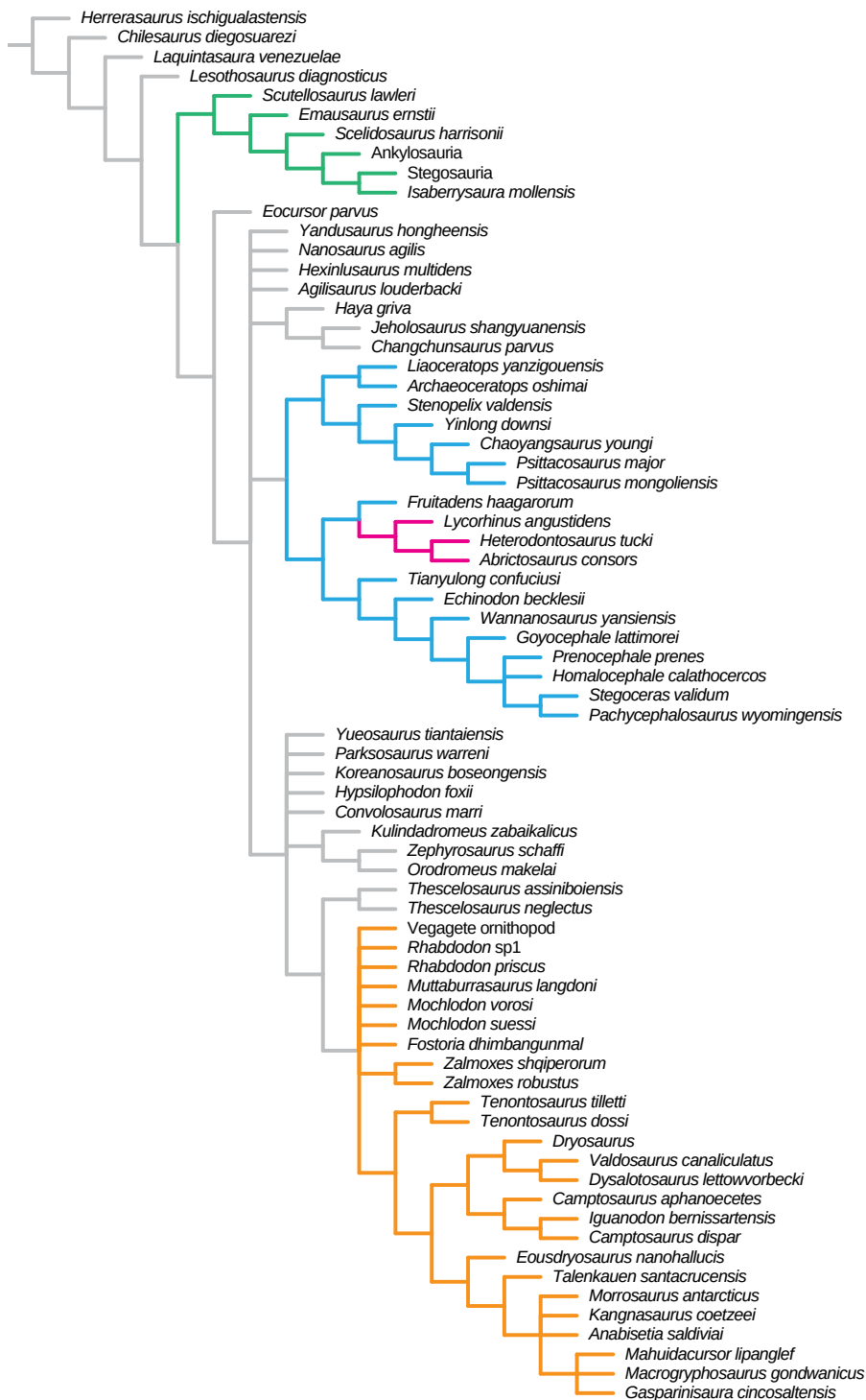
b) reduced strict consensus tree



A2.62. (cont.)

Analysis G.5.D2021 - braincase characters excluded

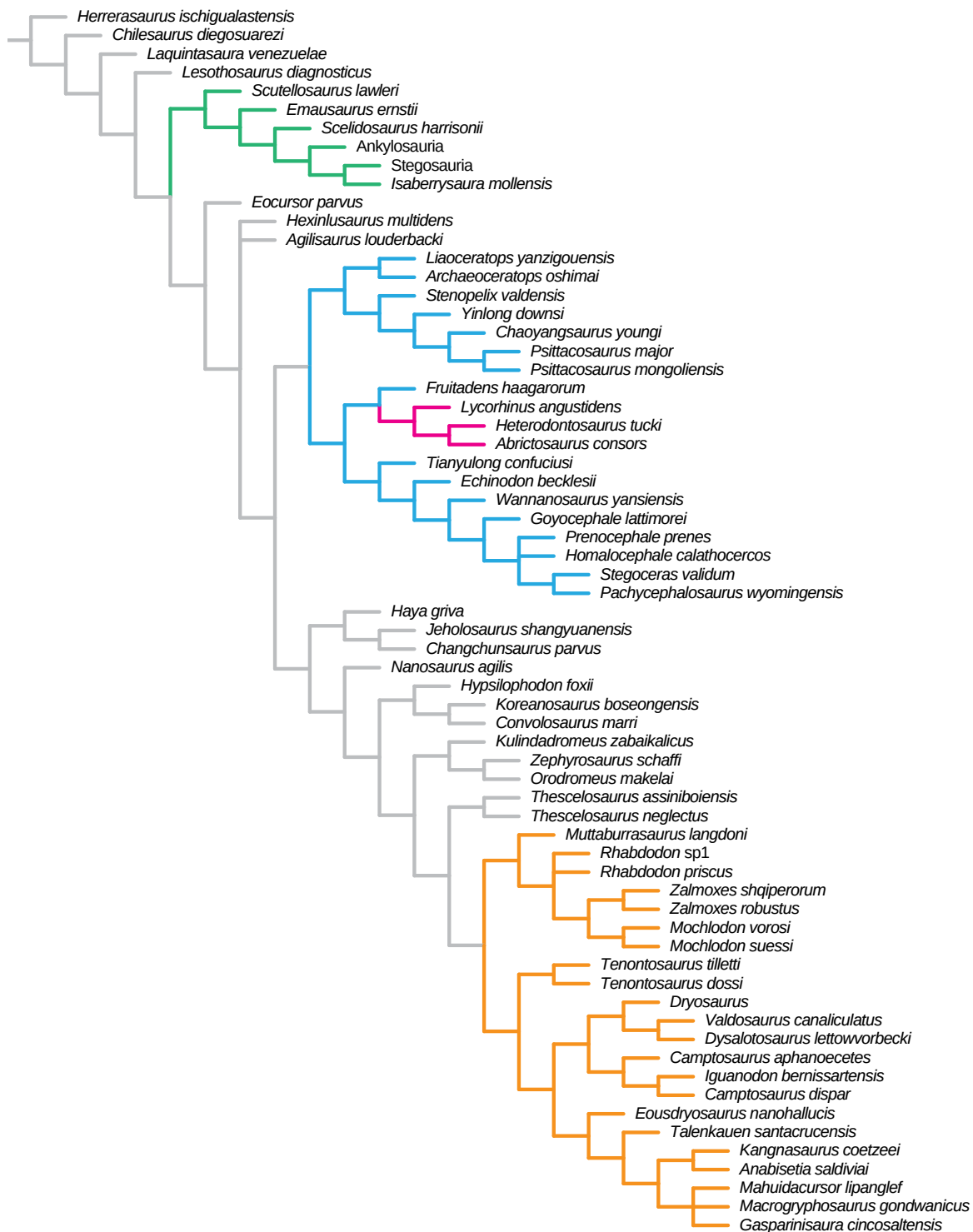
a) strict consensus tree



A2.63. Dieudonné *et al.* (2021) tree topology when all braincase characters are removed: (a) strict consensus of 367 MPTs; (b) reduced strict consensus tree following pruning of six unstable taxa (*Fostoria*, *Nanosaurus*, *Morrosaurus*, *Vegagete ornithopod*, *Yandusaurus*, *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

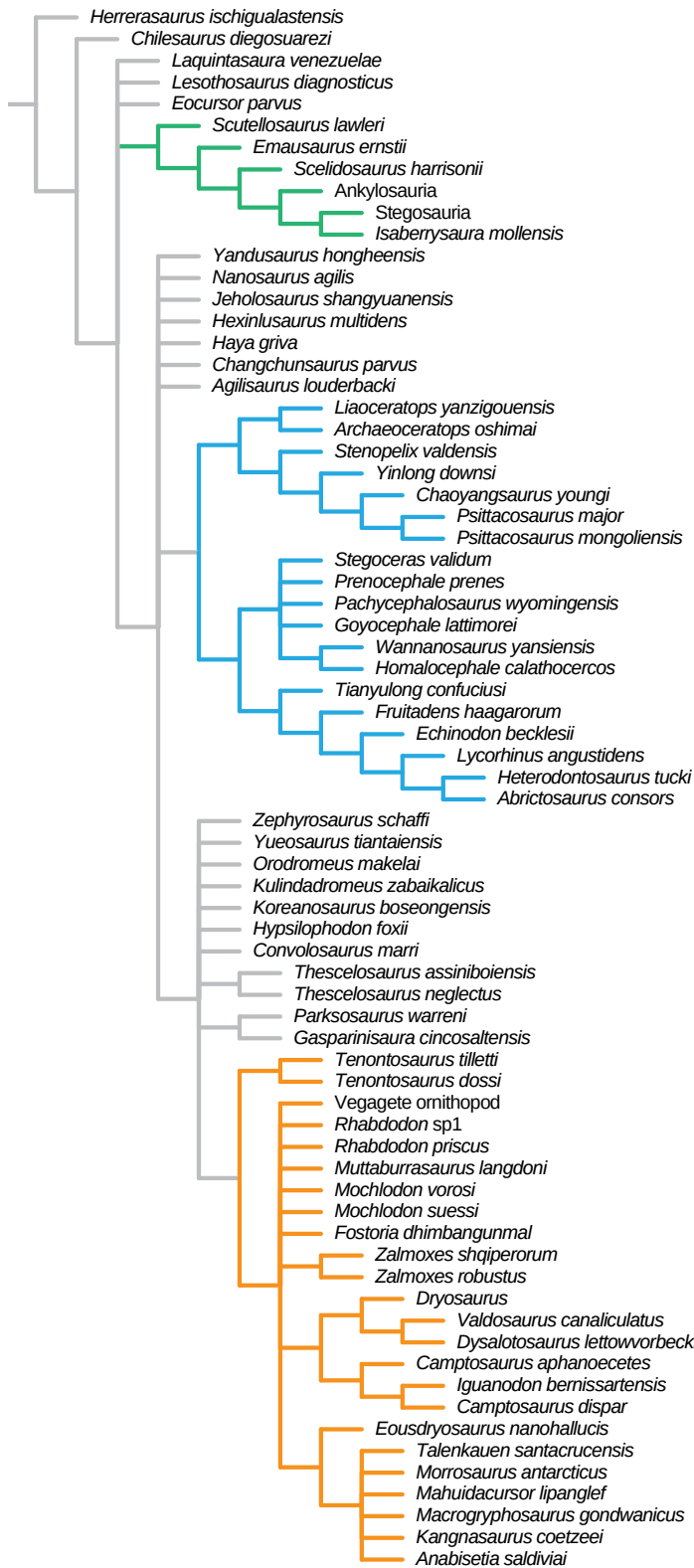
Analysis G.5.D2021 - braincase characters excluded

b) reduced strict consensus tree



A2.63. (cont.)

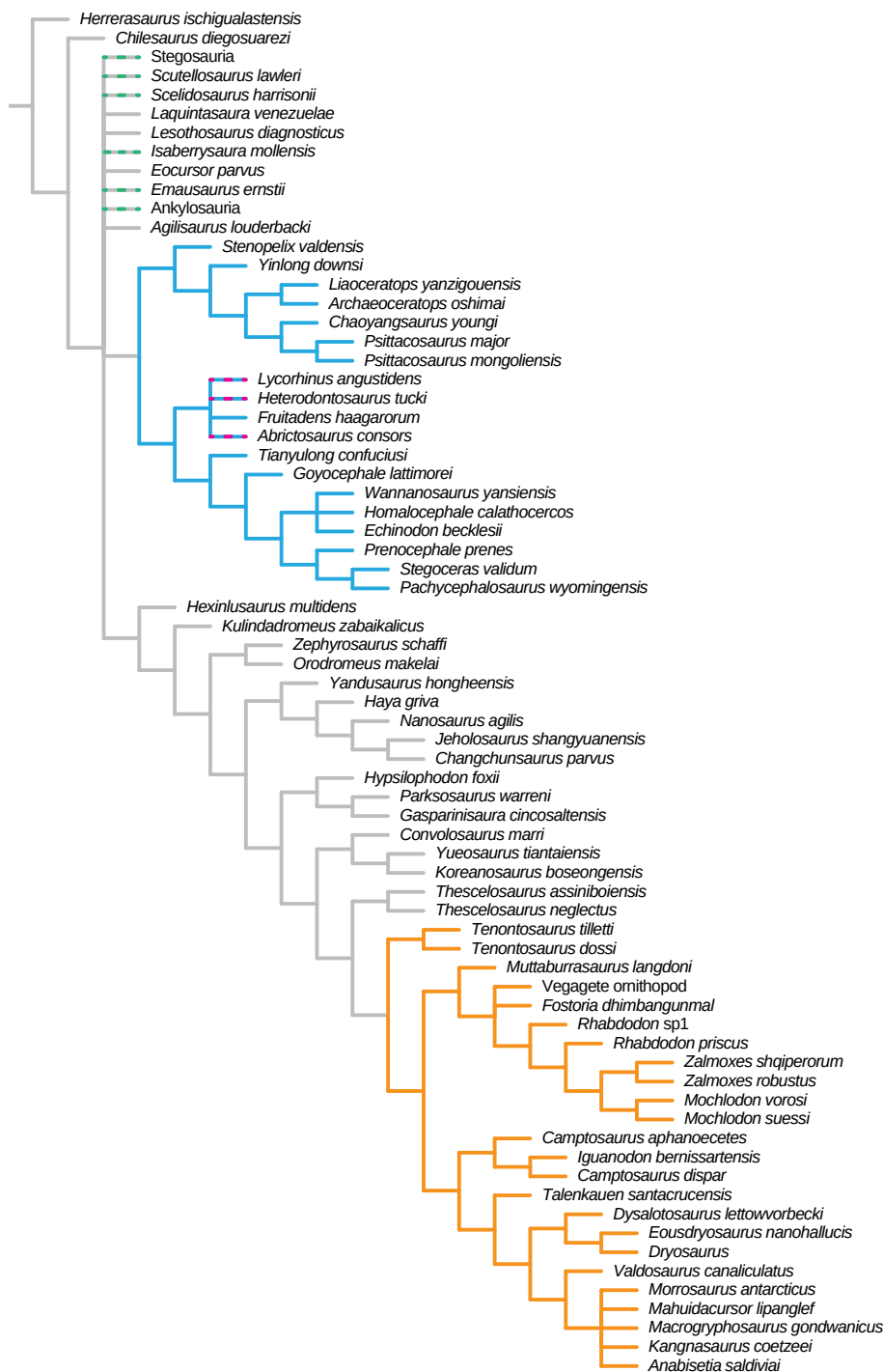
Analysis G.6.D2021 - mandible characters excluded



A2.64. Strict consensus tree of 18,800 MPTs produced from Dieudonné *et al.* (2021) when all mandibular characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis G.7.D2021 - dental characters excluded

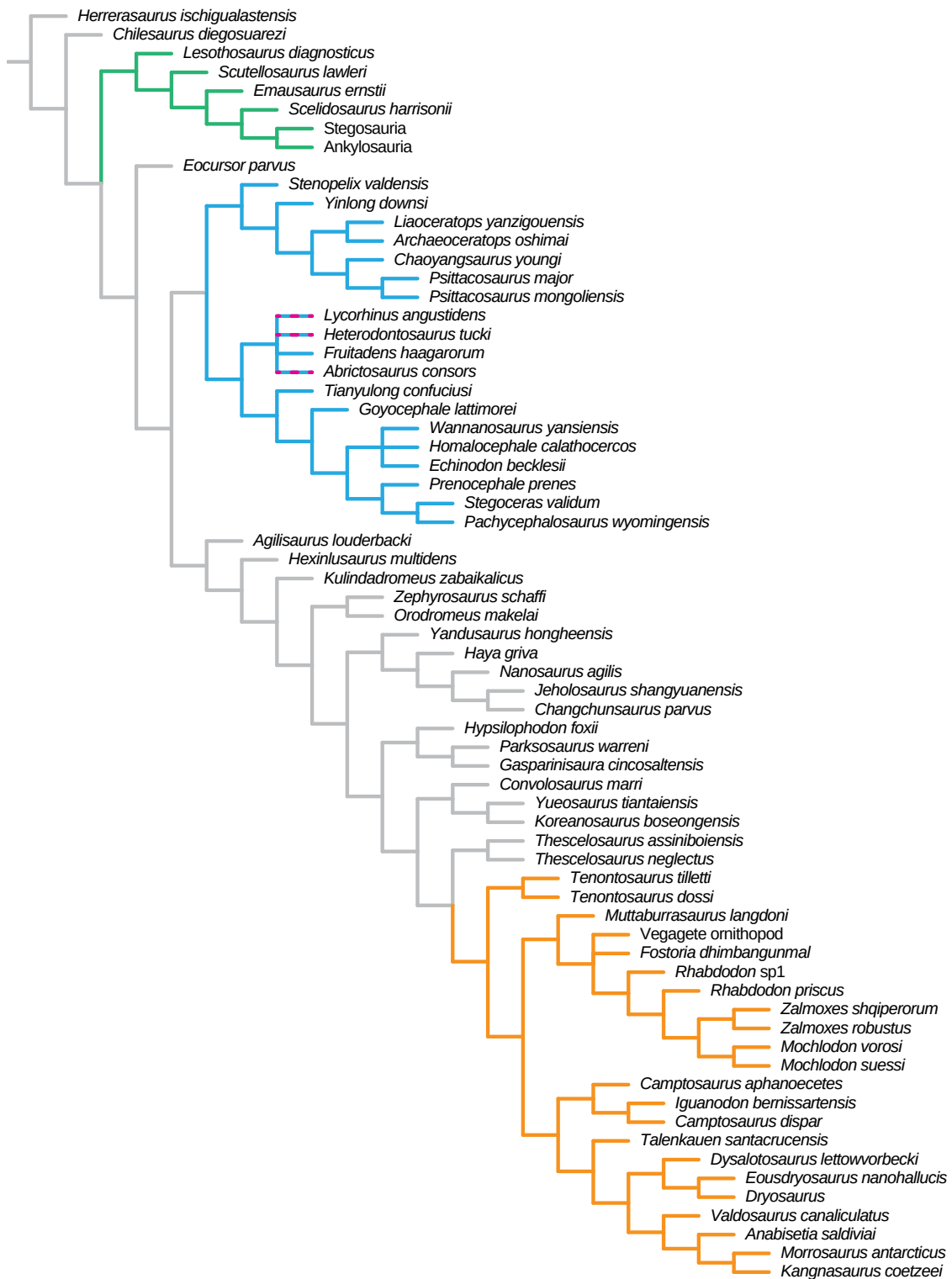
a) strict consensus tree



A2.65. Dieudonné *et al.* (2021) tree topology when all dental characters are removed: (a) strict consensus of 160 MPTs; (b) reduced strict consensus tree following pruning of four unstable taxa (*Isaberrysaura*, *Laquintasaura*, *Macrogyphosaurus*, *Mahuidacursor*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

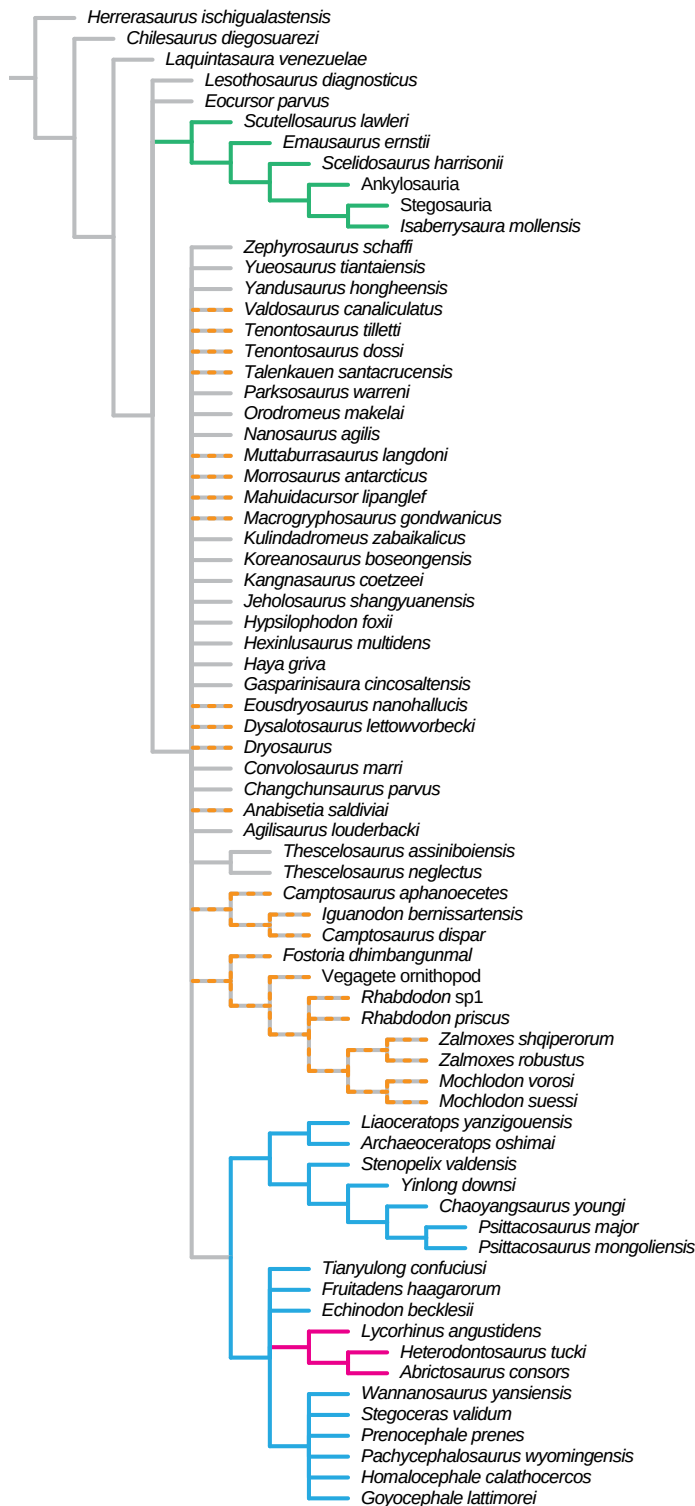
Analysis G.7.D2021 - dental characters excluded

b) reduced strict consensus tree



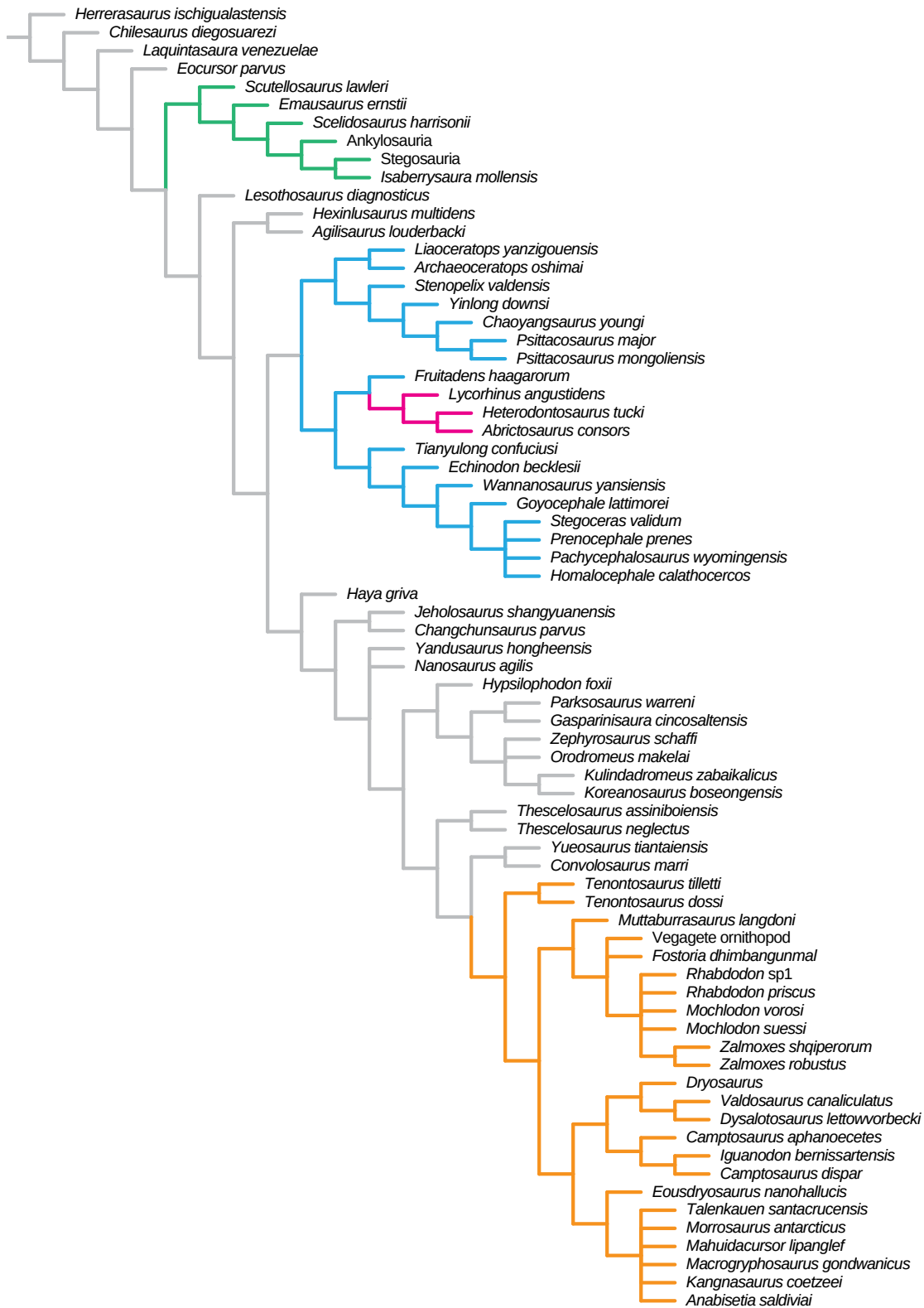
A2.65. (cont.)

Analysis G.8.D2021 - vertebral column & rib characters excluded



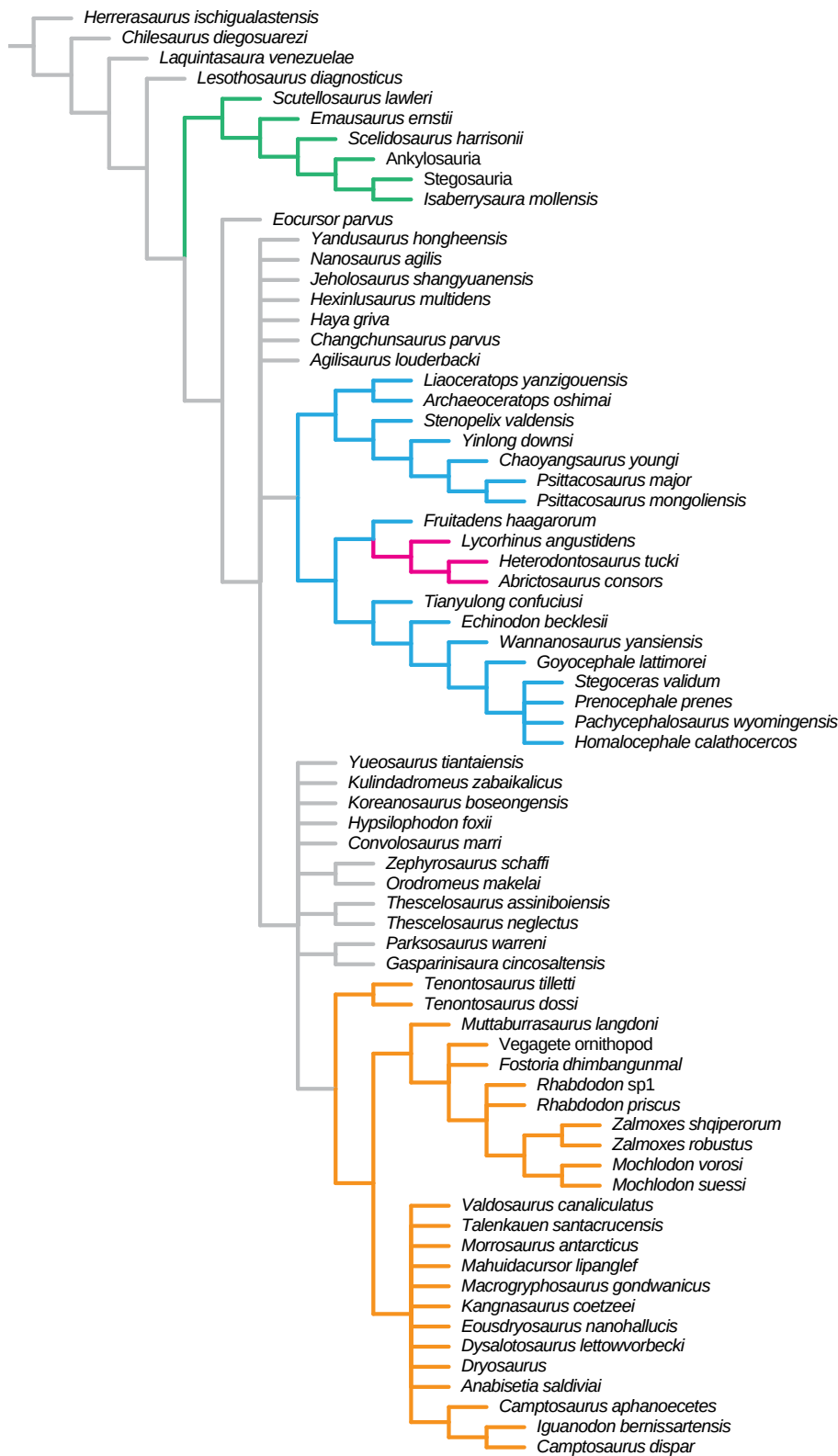
A2.66. Strict consensus tree of 1,057 MPTs produced from Dieudonné *et al.* (2021) when all vertebral column and rib characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis G.9.D2021 - pectoral girdle & sternum characters excluded



A2.67. Strict consensus tree of 690 MPTs produced from Dieudonné *et al.* (2021) when all pectoral girdle characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

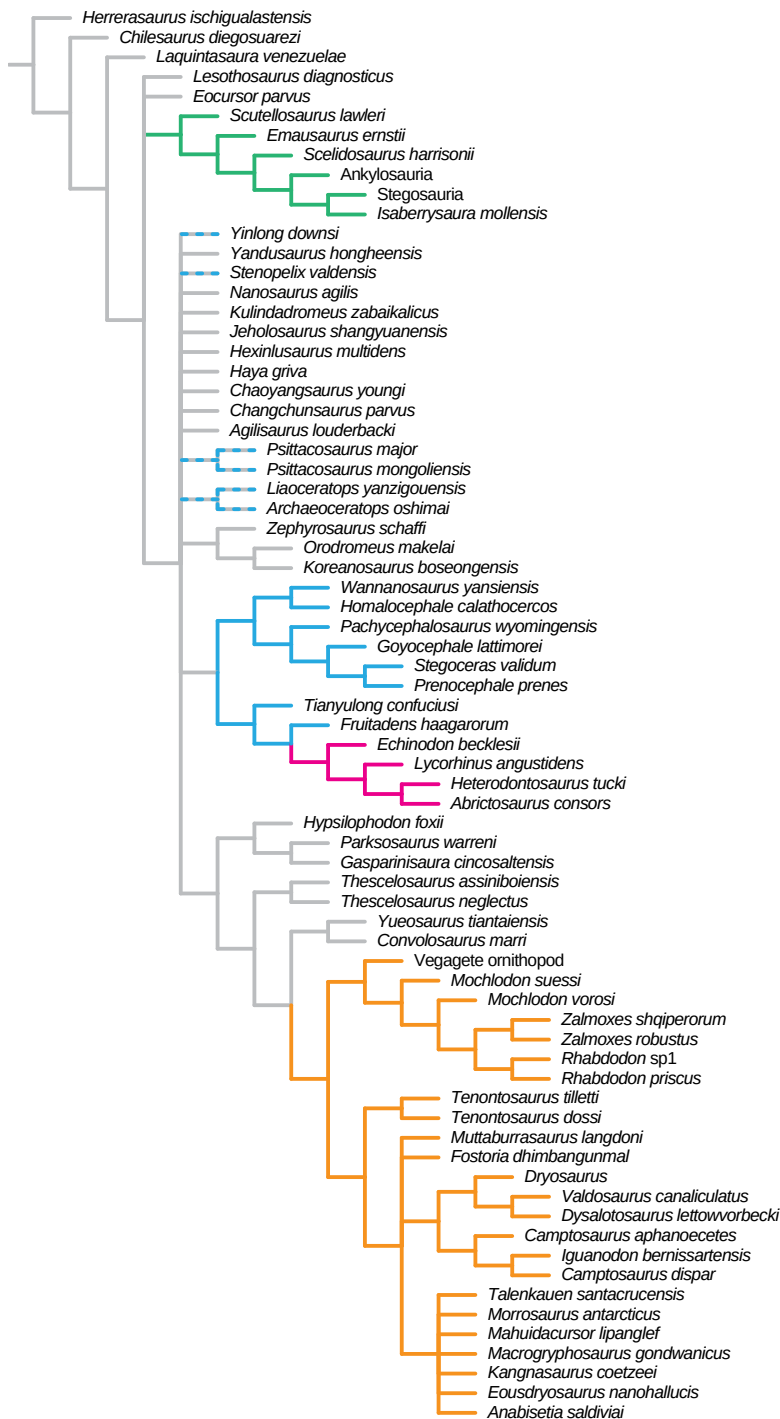
Analysis G.10.D2021 - forelimb characters excluded



A2.68. Strict consensus tree of 397 MPTs produced from Dieudonné *et al.* (2021) when all forelimb characters are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis G.11.D2021 - pelvic girdle characters excluded

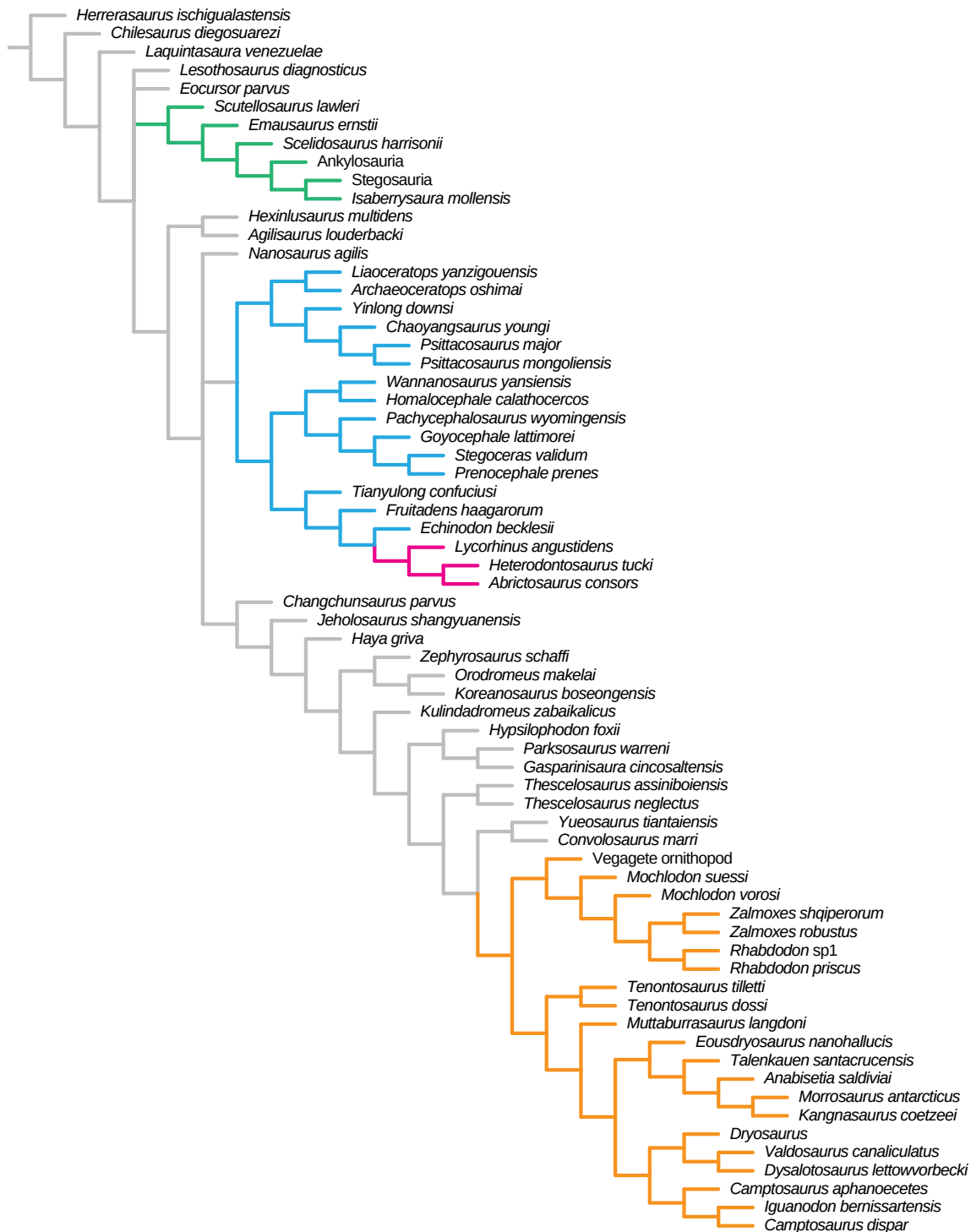
a) strict consensus tree



A2.69. Dieudonné *et al.* (2021) tree topology when all pelvic characters are removed: (a) strict consensus of 1,300 MPTs; (b) reduced strict consensus tree following pruning of five unstable taxa (*Fostoria*, *Macrogyphosaurus*, *Mahuidacursor*, *Yandusaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

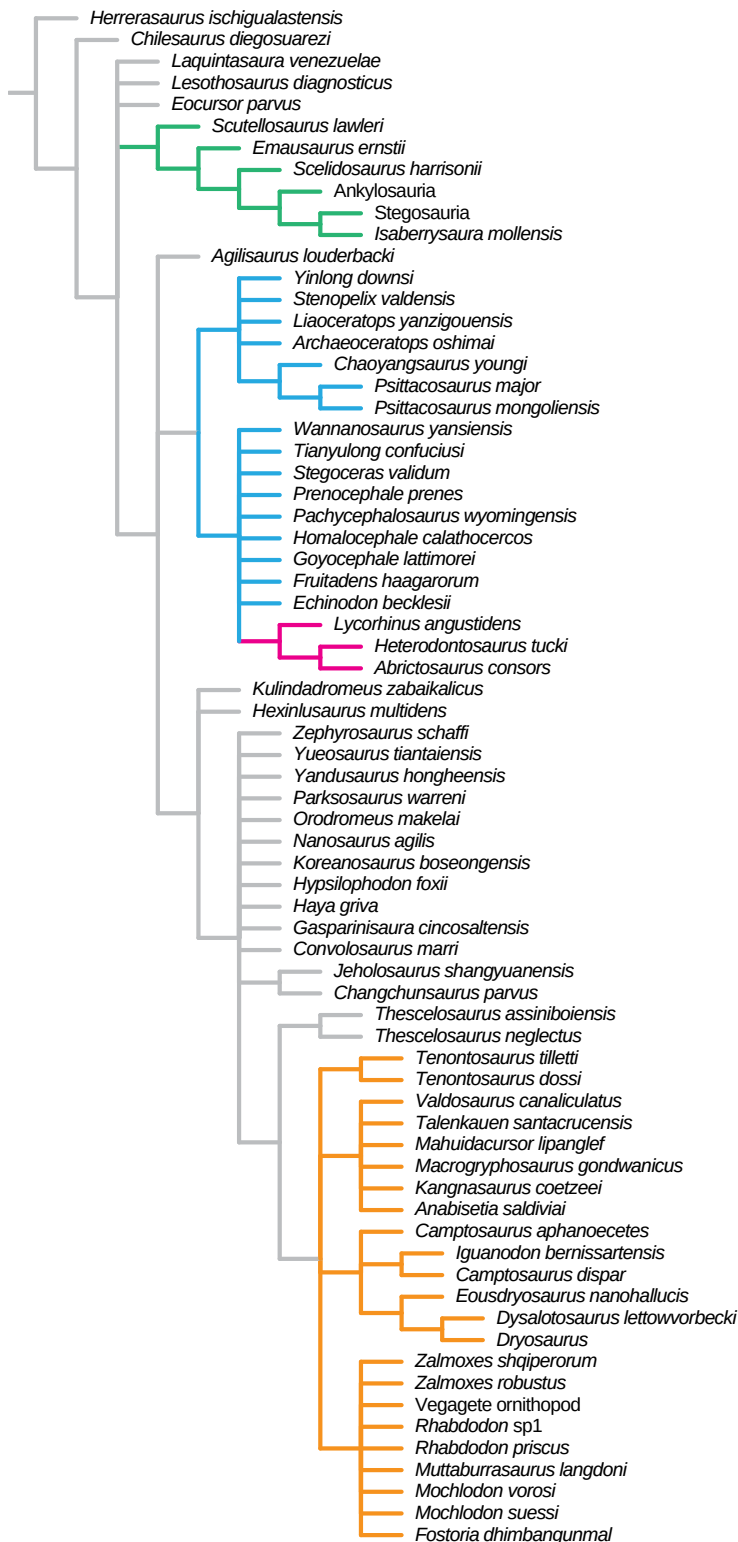
Analysis G.11.D2021 - pelvic girdle characters excluded

b) reduced strict consensus tree



A2.69. (cont.)

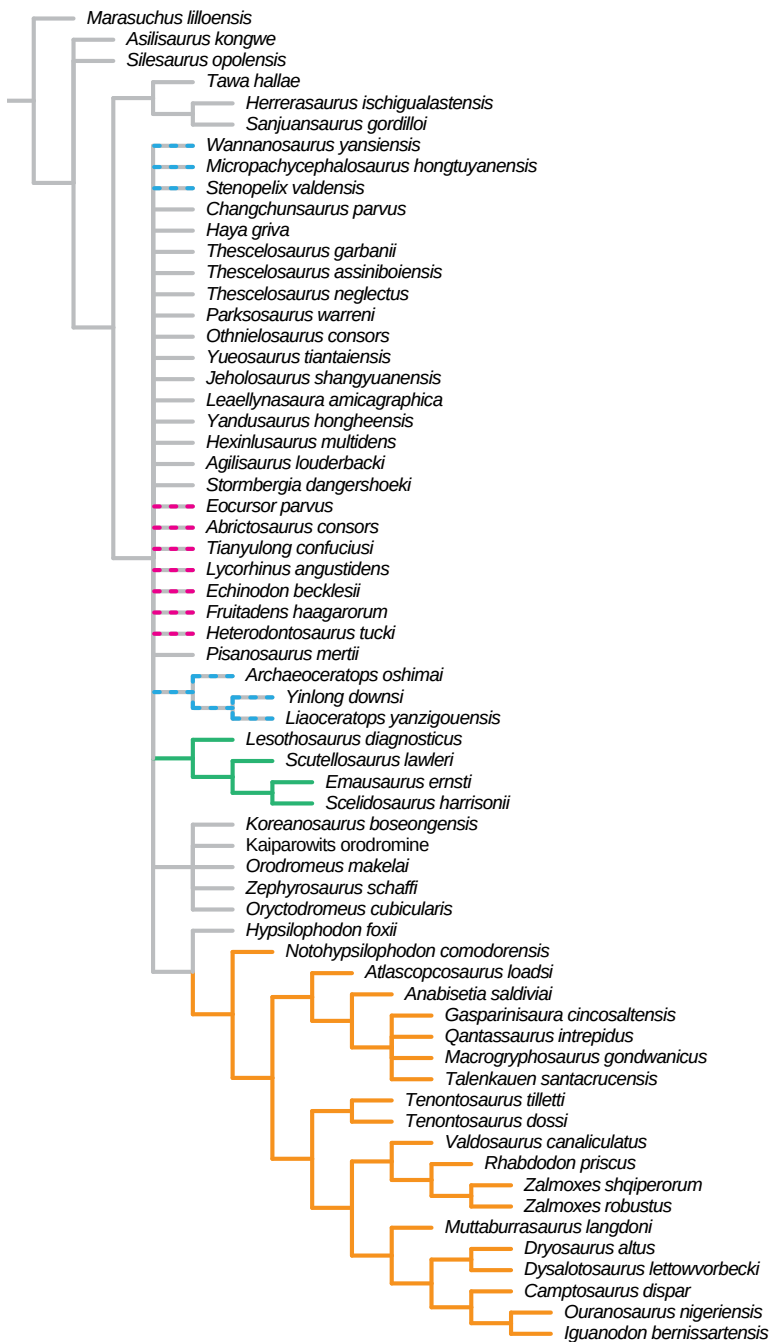
Analysis G.12.D2021 - hind limb characters excluded



A2.70. Strict consensus tree of 24,600 MPTs produced from Dieudonné *et al.* (2021) when all hind limb characters are removed. *Morrosaurus* was removed prior to tree search. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis H.B2015 - excluding the most character-rich skeletal element (femur)

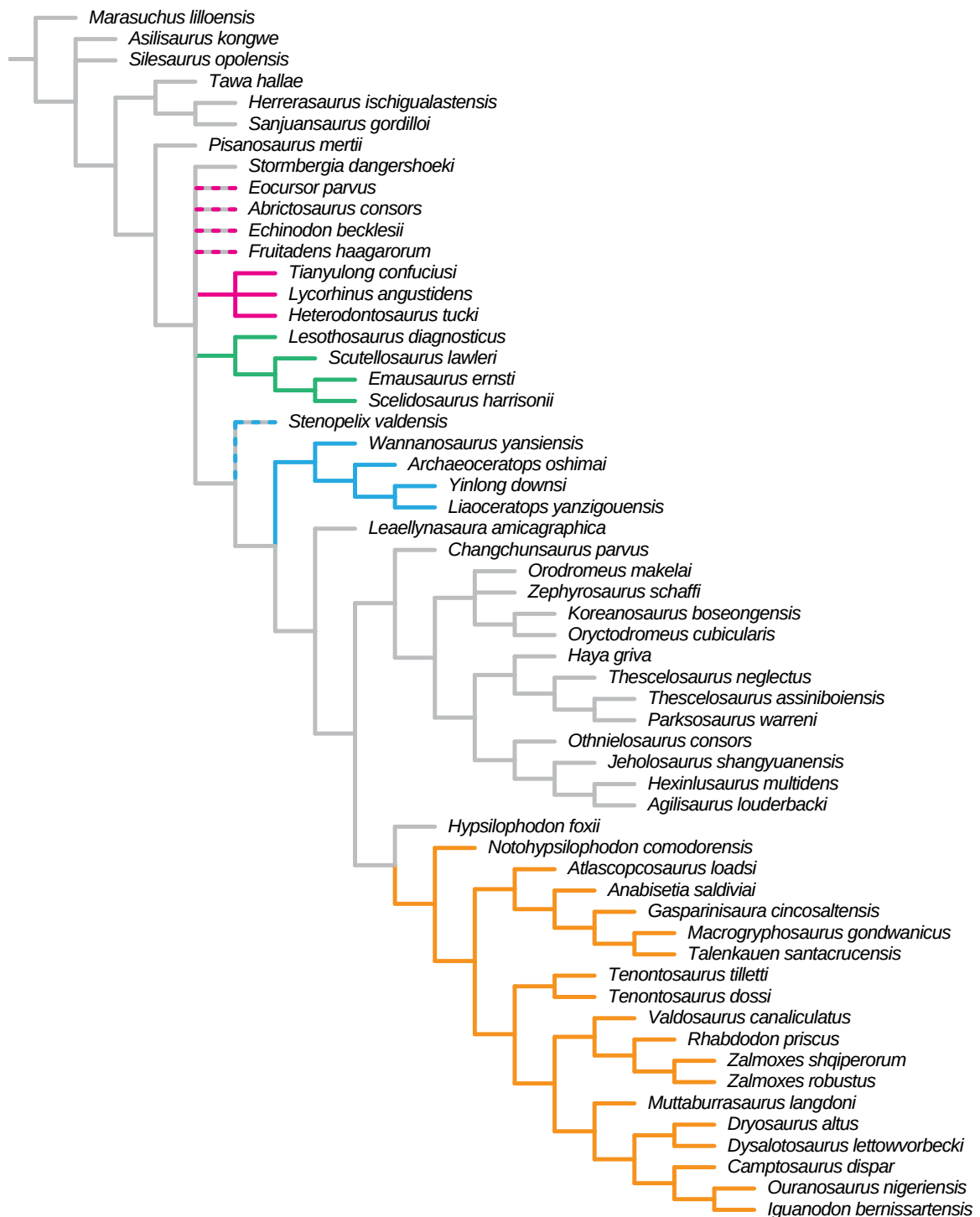
a) strict consensus tree



A2.71. Boyd (2015) tree topology when all femoral characters are removed: a) strict consensus of 1,700 MPTs; (b) reduced consensus tree following pruning of six unstable taxa (*Kaiparowits orodromine*, *Thescelosaurus garbanii*, *Micropachycephalosaurus*, *Qantassaurus*, *Yandusaurus*, *Yueosaurus*). Two taxa were removed prior to the tree search (*Callovosaurus*, *Elrhazosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis H.B2015 - excluding the most character-rich skeletal element (femur)

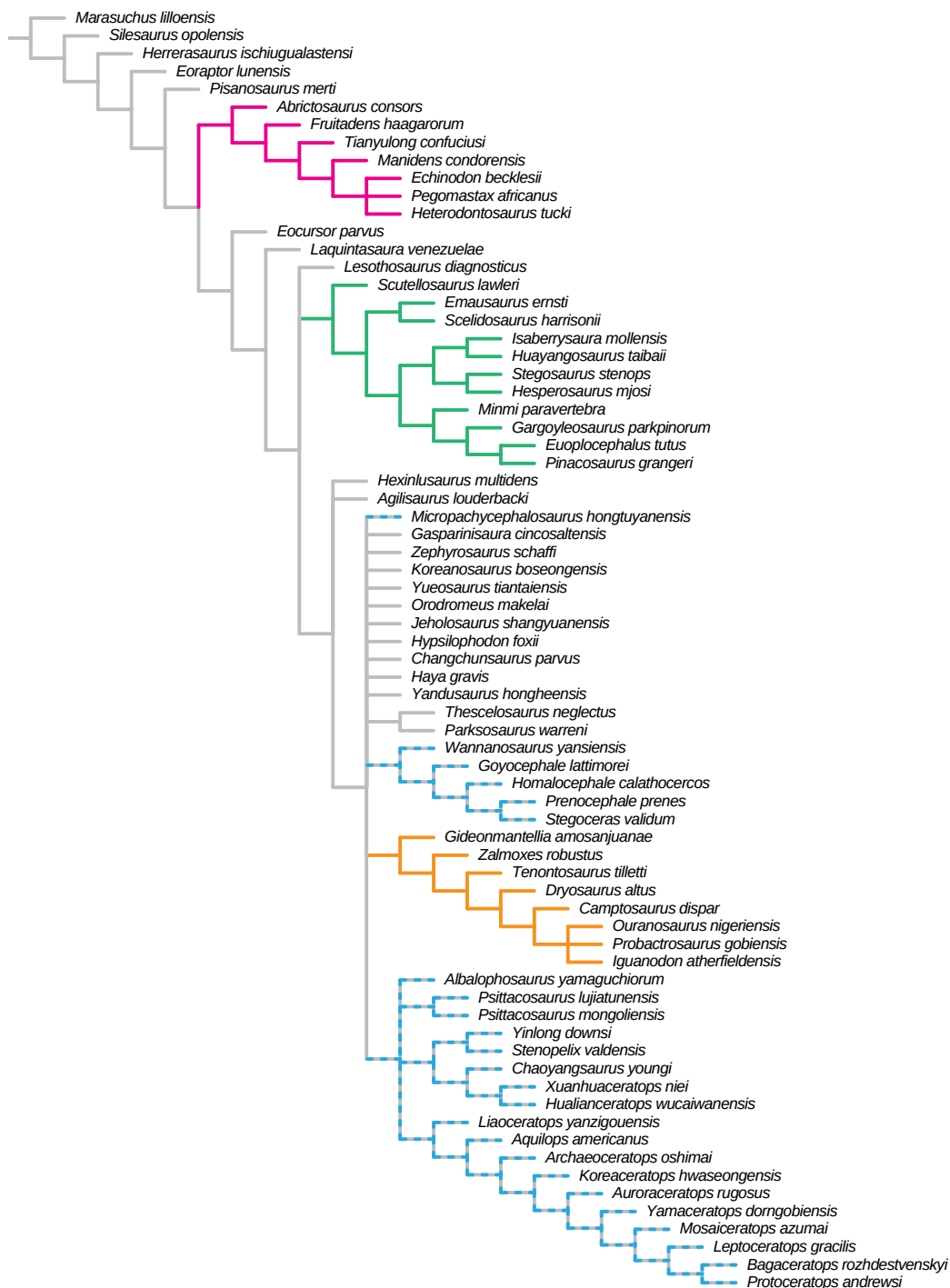
b) reduced strict consensus tree



A2.71. (cont.)

Analysis H.H2018 - excluding the most character-rich skeletal element (ilium)

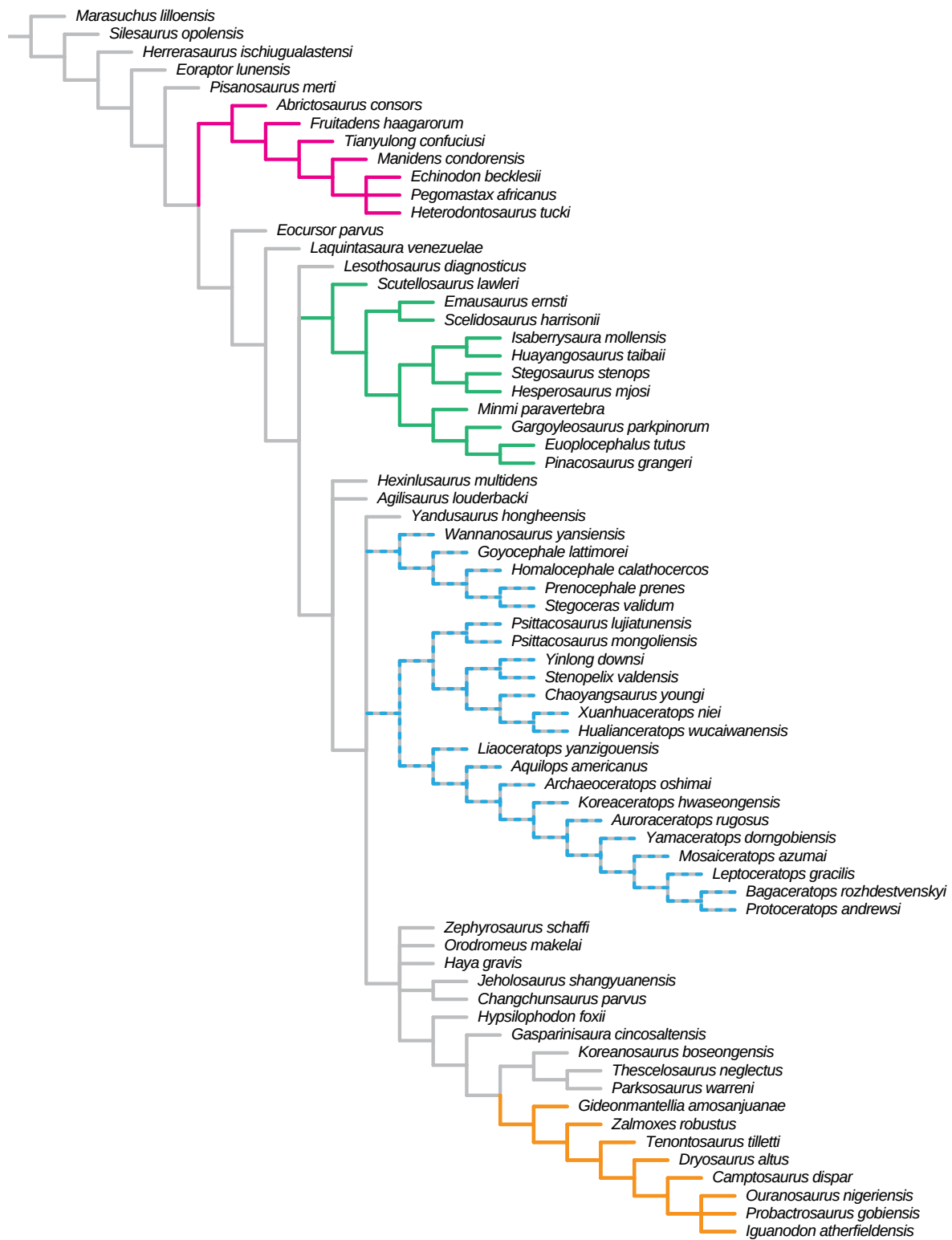
a) strict consensus tree



A2.72. Han *et al.* (2018) tree topology when all iliac characters are removed: a) strict consensus of 2,696 MPTs; (b) reduced consensus tree following pruning of three unstable taxa (*Albalophosaurus*, *Micropachycephalosaurus*, *Yueosaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis H.H2018 - excluding the most character-rich skeletal element (ilium)

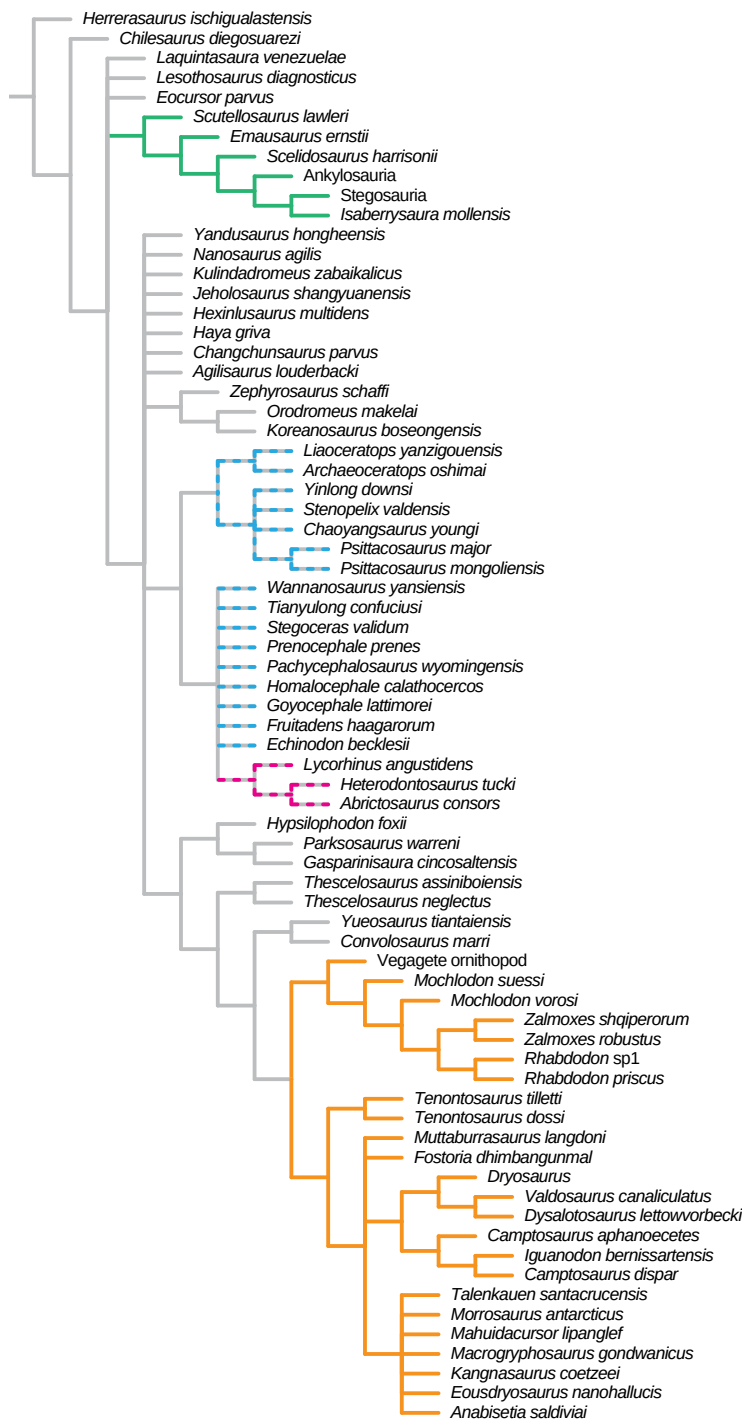
b) reduced strict consensus tree



A2.72. (cont.)

Analysis H.D2021 - excluding the most character-rich skeletal element (ilium)

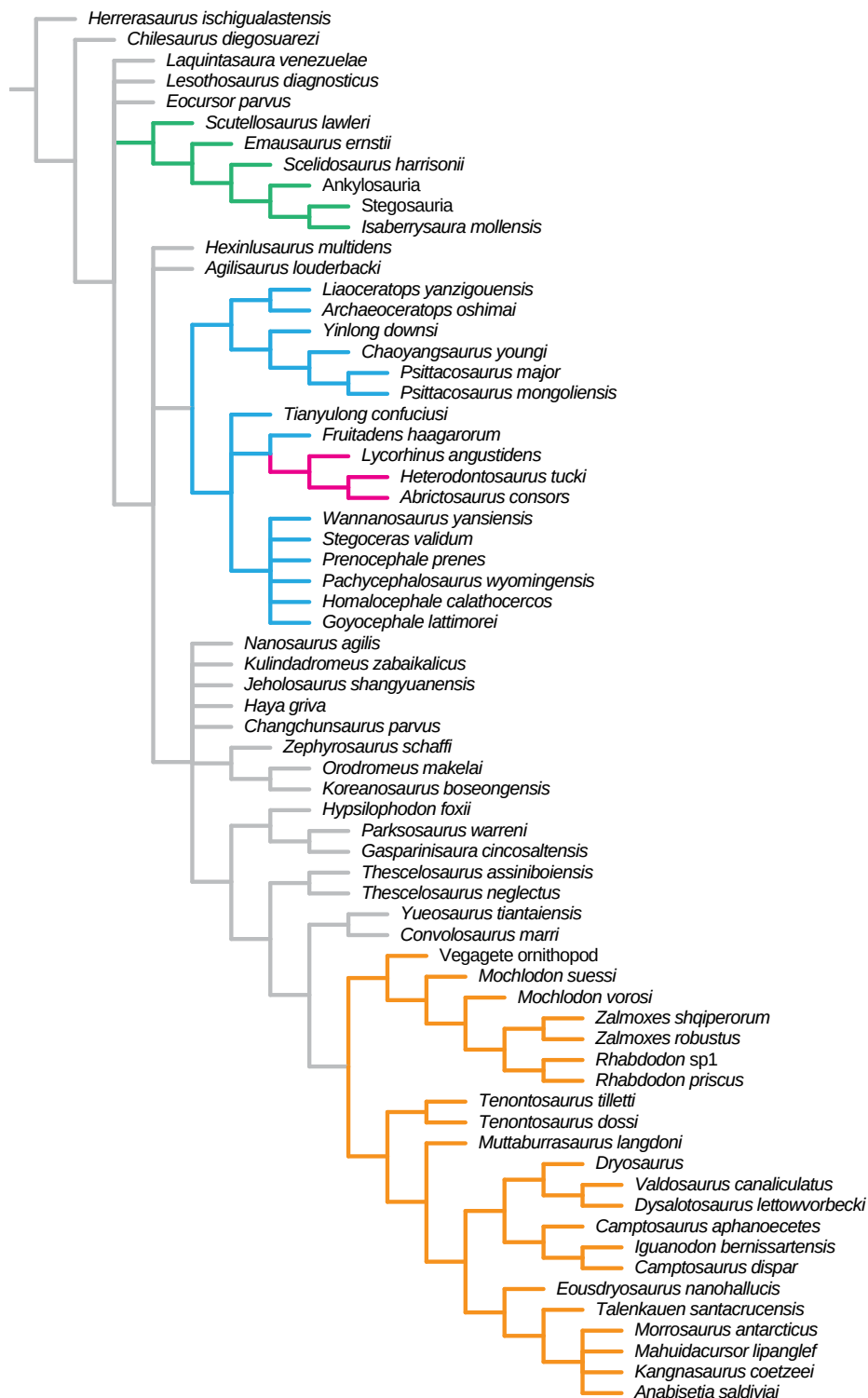
a) strict consensus tree



A2.73. Dieudonné *et al.* (2021) tree topology when all iliac characters are removed: a) strict consensus of 3,337 MPTs; (b) reduced consensus tree following pruning of five unstable taxa (*Echinodon*, *Fostoria*, *Macrogyphosaurus*, *Stenopelix*, *Yandusaurus*). Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis H.D2021 - excluding the most character-rich skeletal element (ilium)

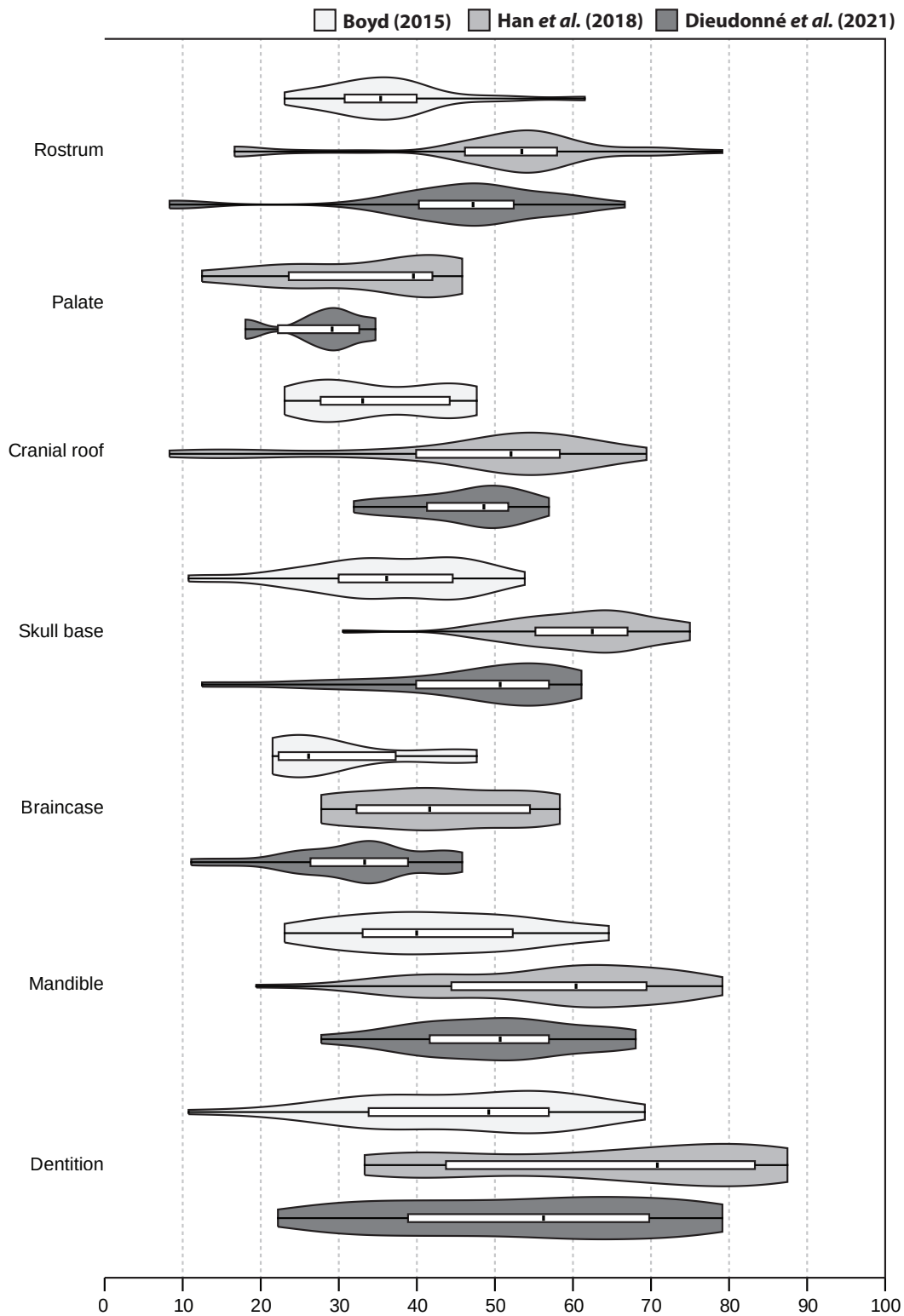
b) reduced strict consensus tree



A2.73. (cont.)

Character completeness

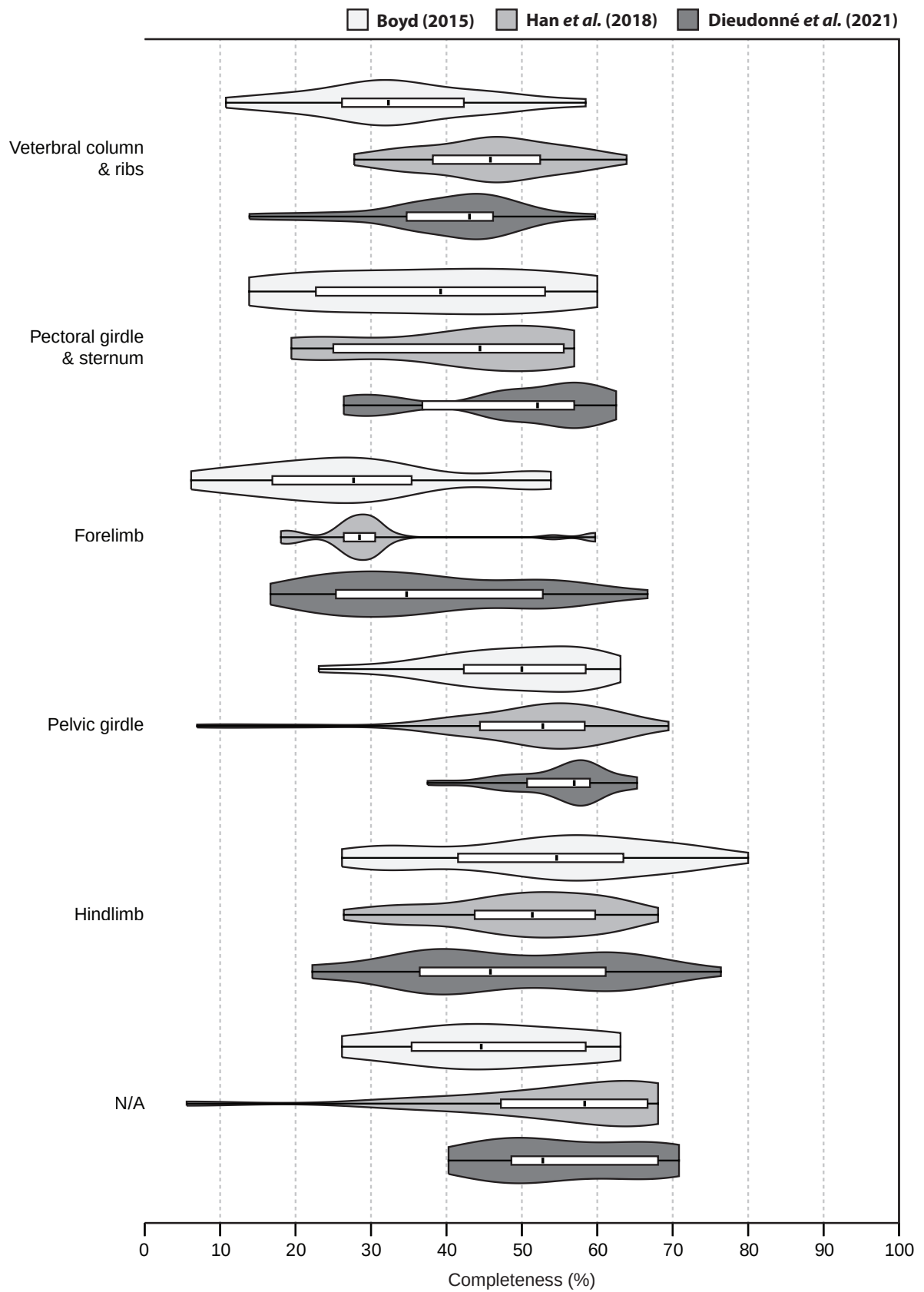
a) craniodental



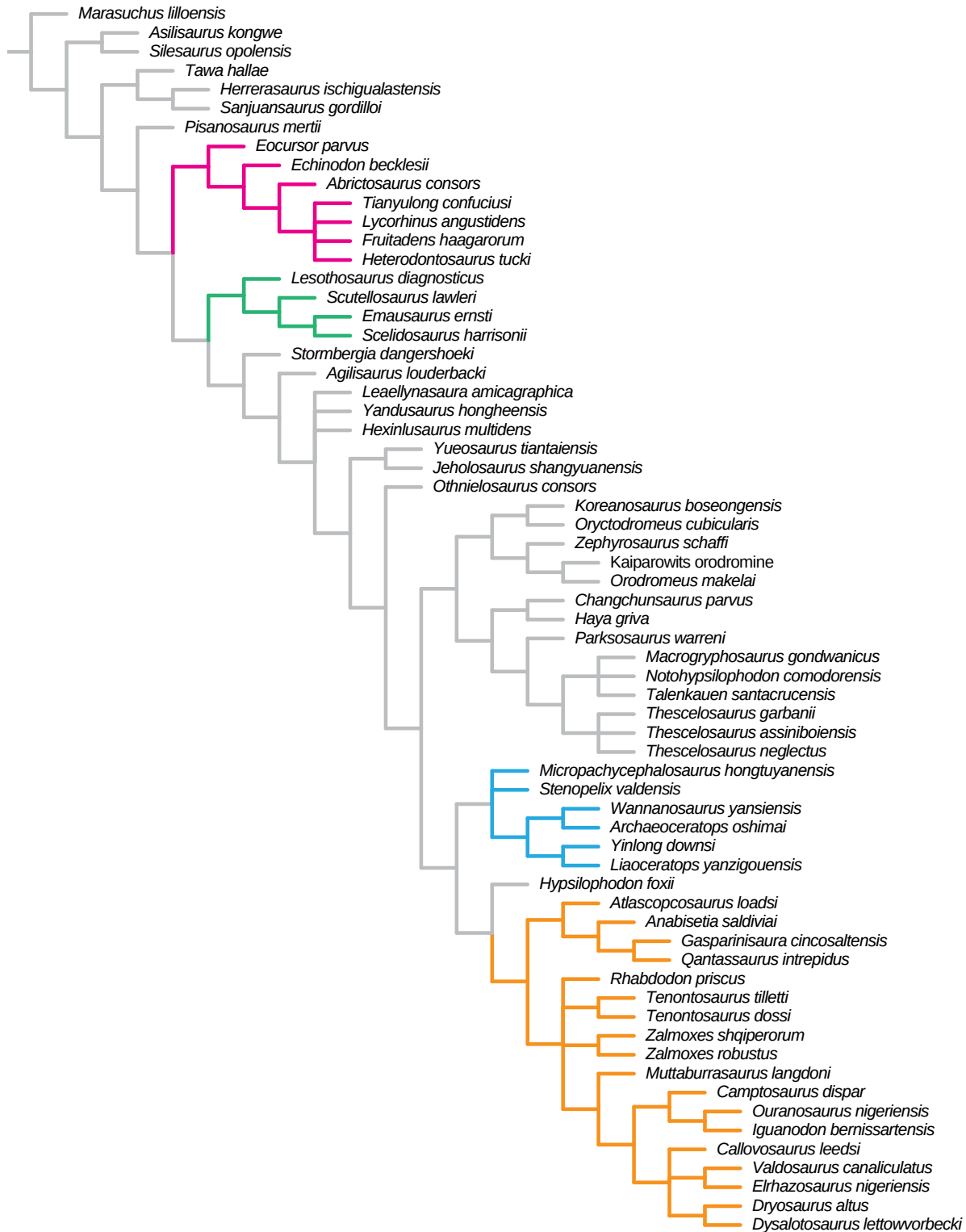
A2.74. Distribution of completeness scores from individual characters across (a) craniodental regions and (b) postcranial regions, in data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). No palatal characters in Boyd (2015).

Character completeness (cont.)

b) postcranial

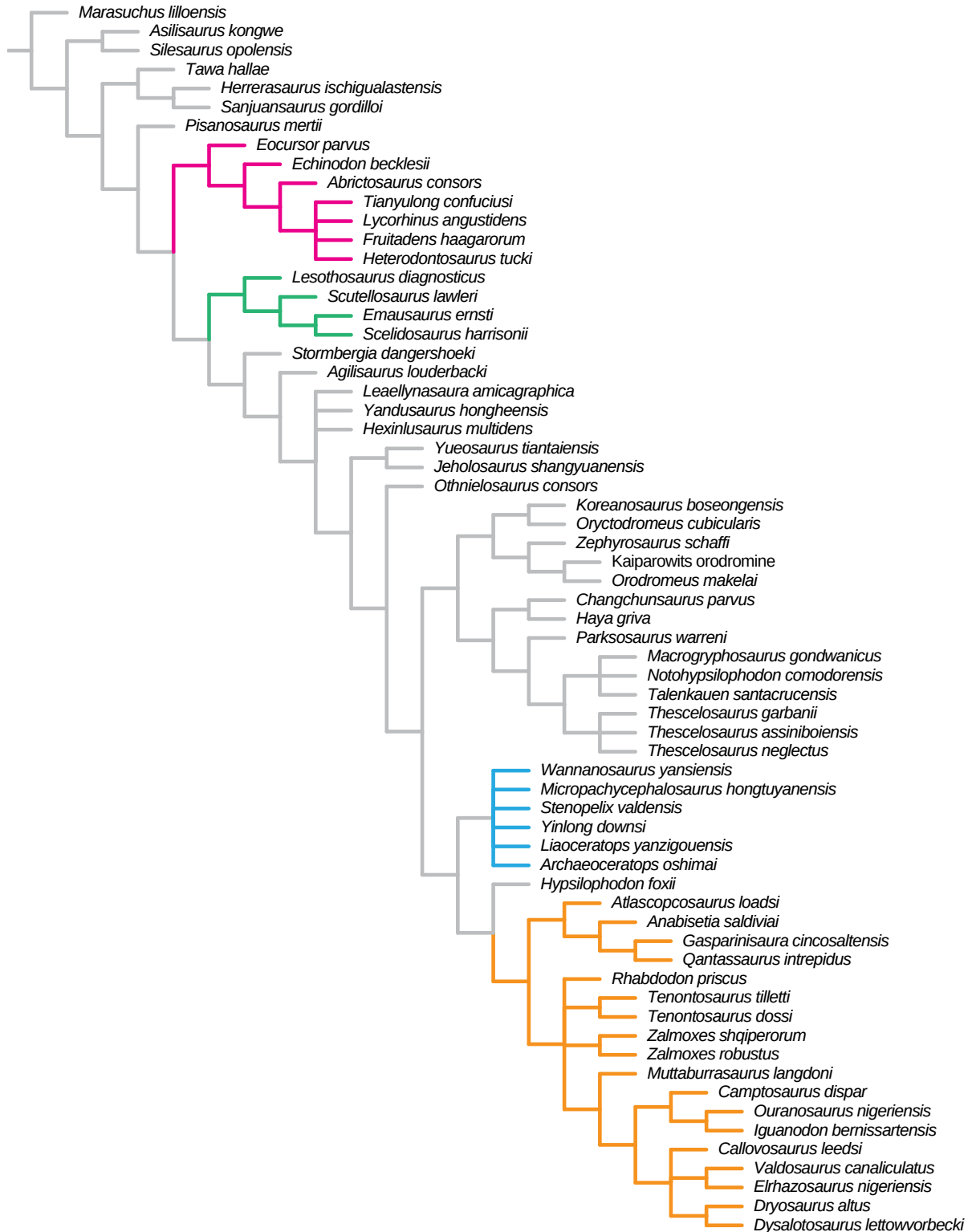


Analysis I.1.B2015 - excluding characters <15% complete



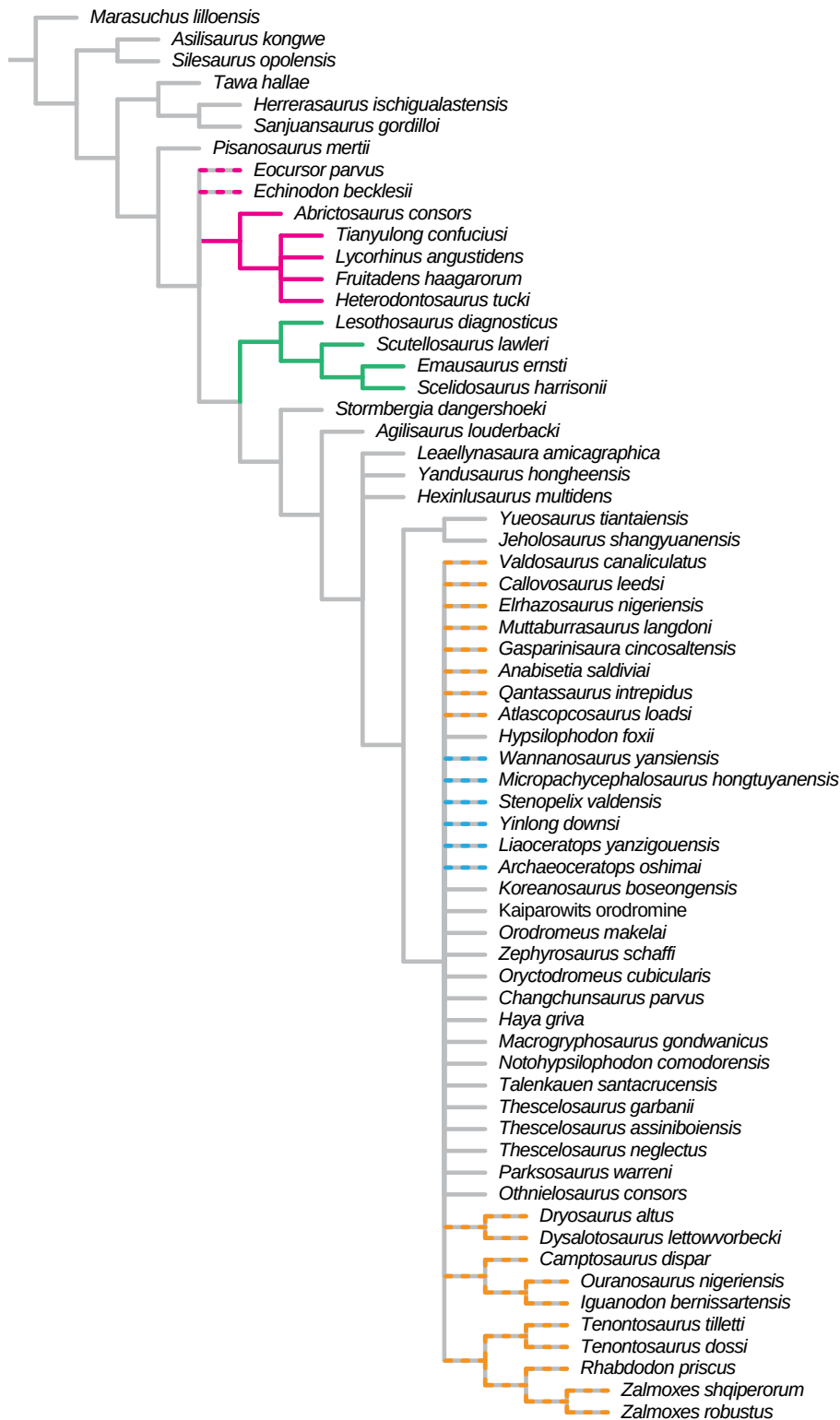
A2.75. Strict consensus tree of 36 MPTs produced from Boyd (2015) when characters <15% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis I.2.B2015 - excluding characters <25% complete



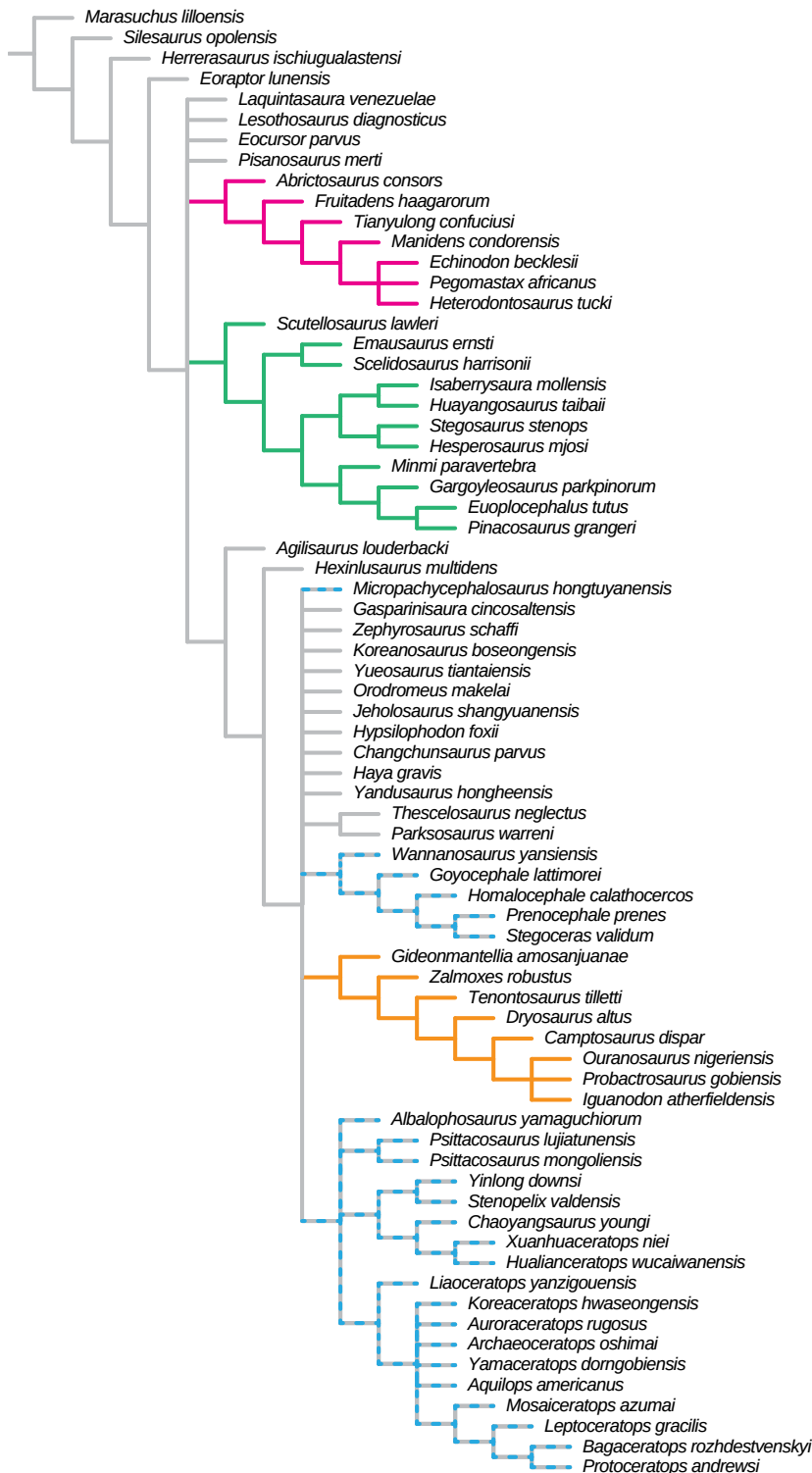
A2.76. Strict consensus tree of 108 MPTs produced from Boyd (2015) when characters <25% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis I.3.B2015 - excluding characters <35% complete



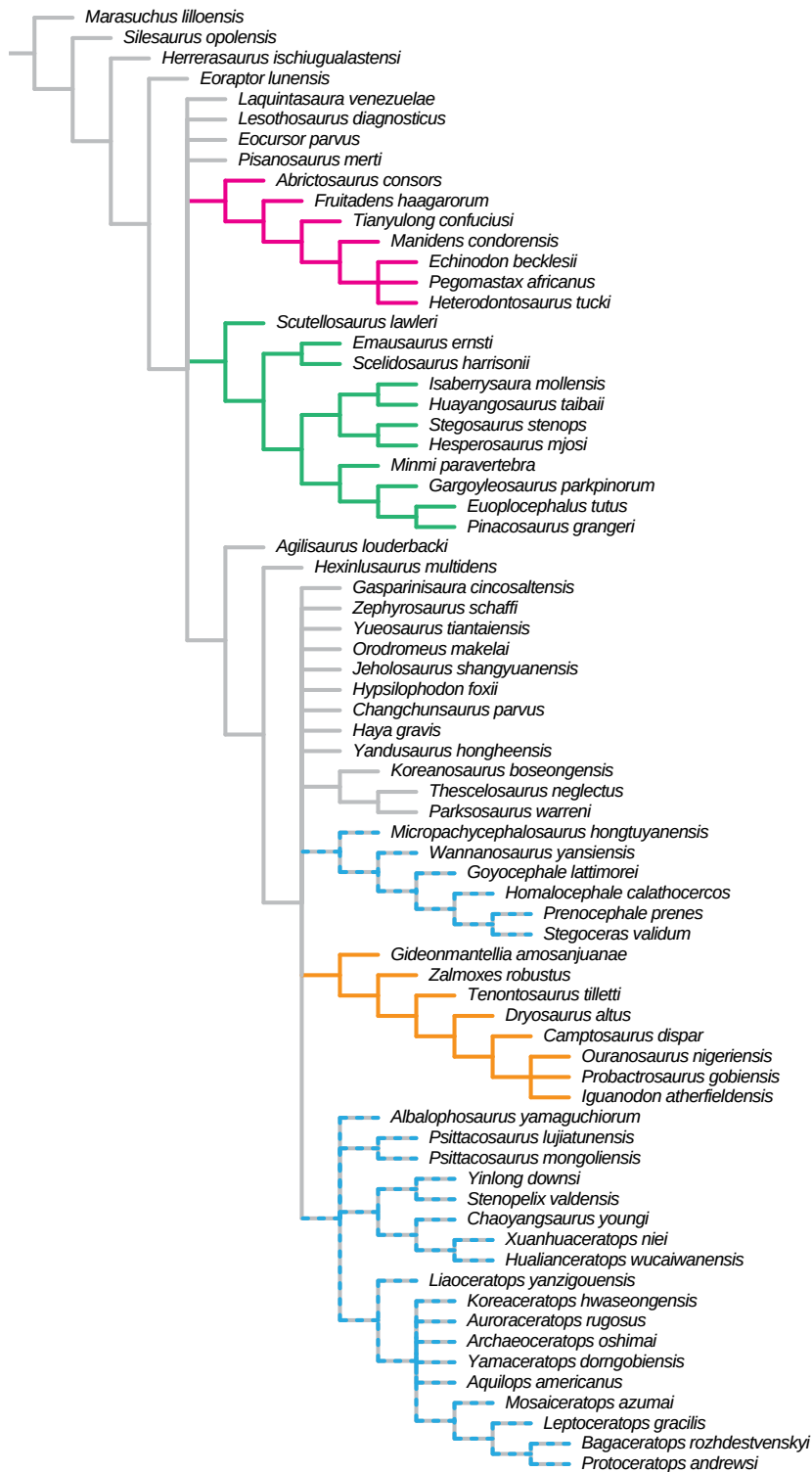
A2.77. Strict consensus tree of 1,300 MPTs produced from Boyd (2015) when characters <35% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis I.1.H2018 - excluding characters <15% complete



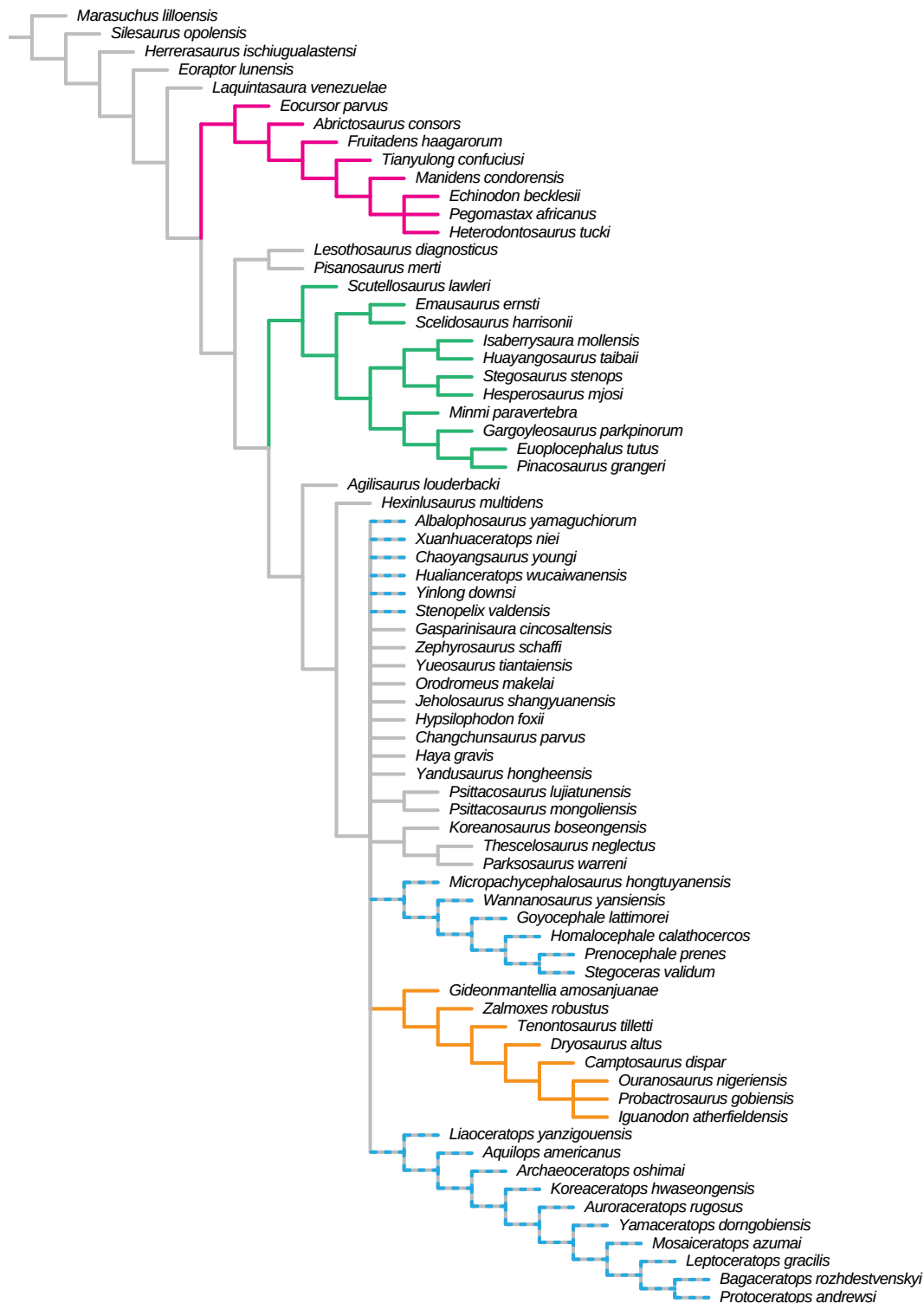
A2.78. Strict consensus tree of 37,644 MPTs produced from Han *et al.* (2018) when characters <15% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis I.2.H2018 - excluding characters <25% complete



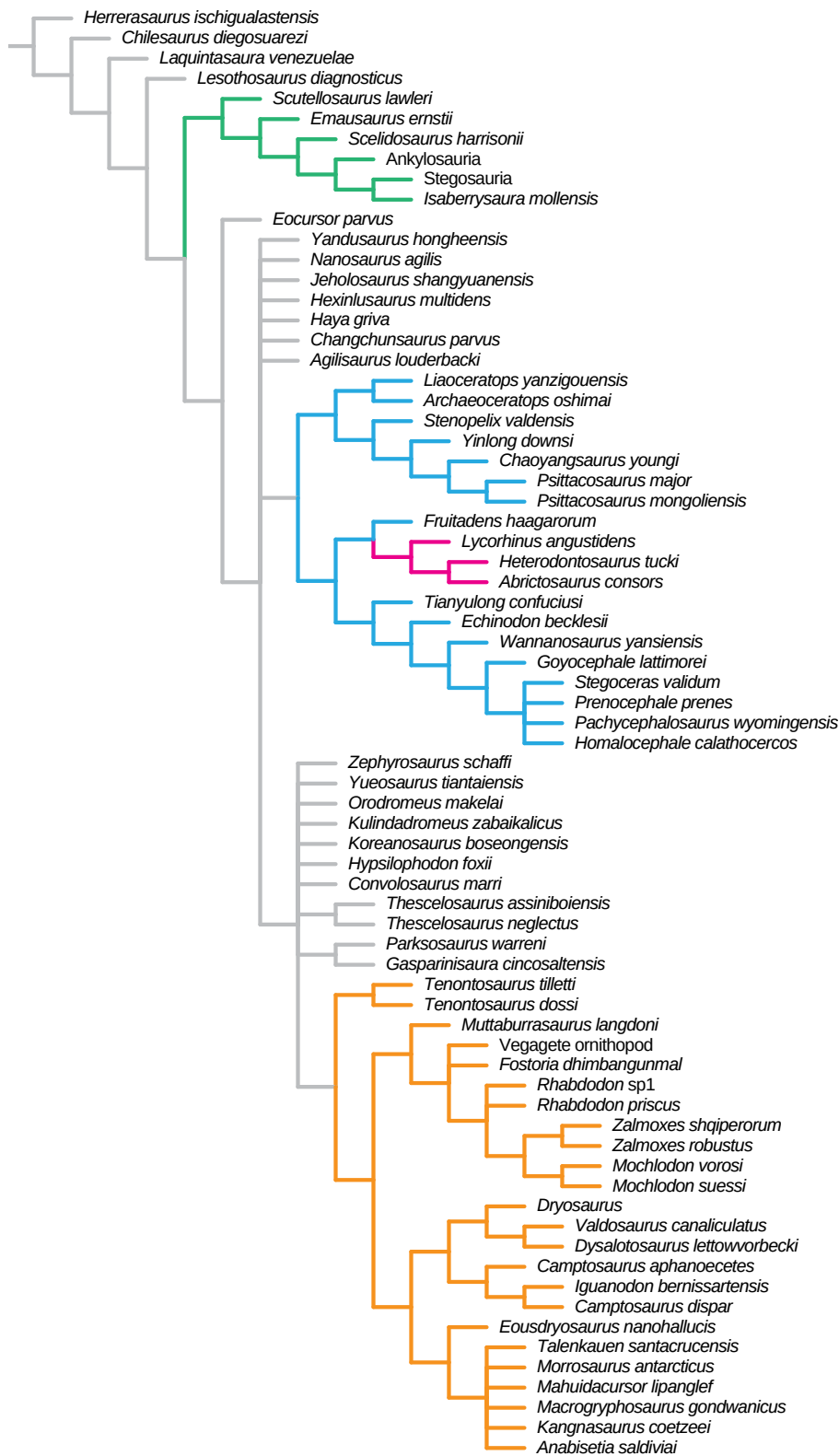
A2.79. Strict consensus tree of 14,015 MPTs produced from Han *et al.* (2018) when characters <25% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis I.3.H2018 - excluding characters <35% complete



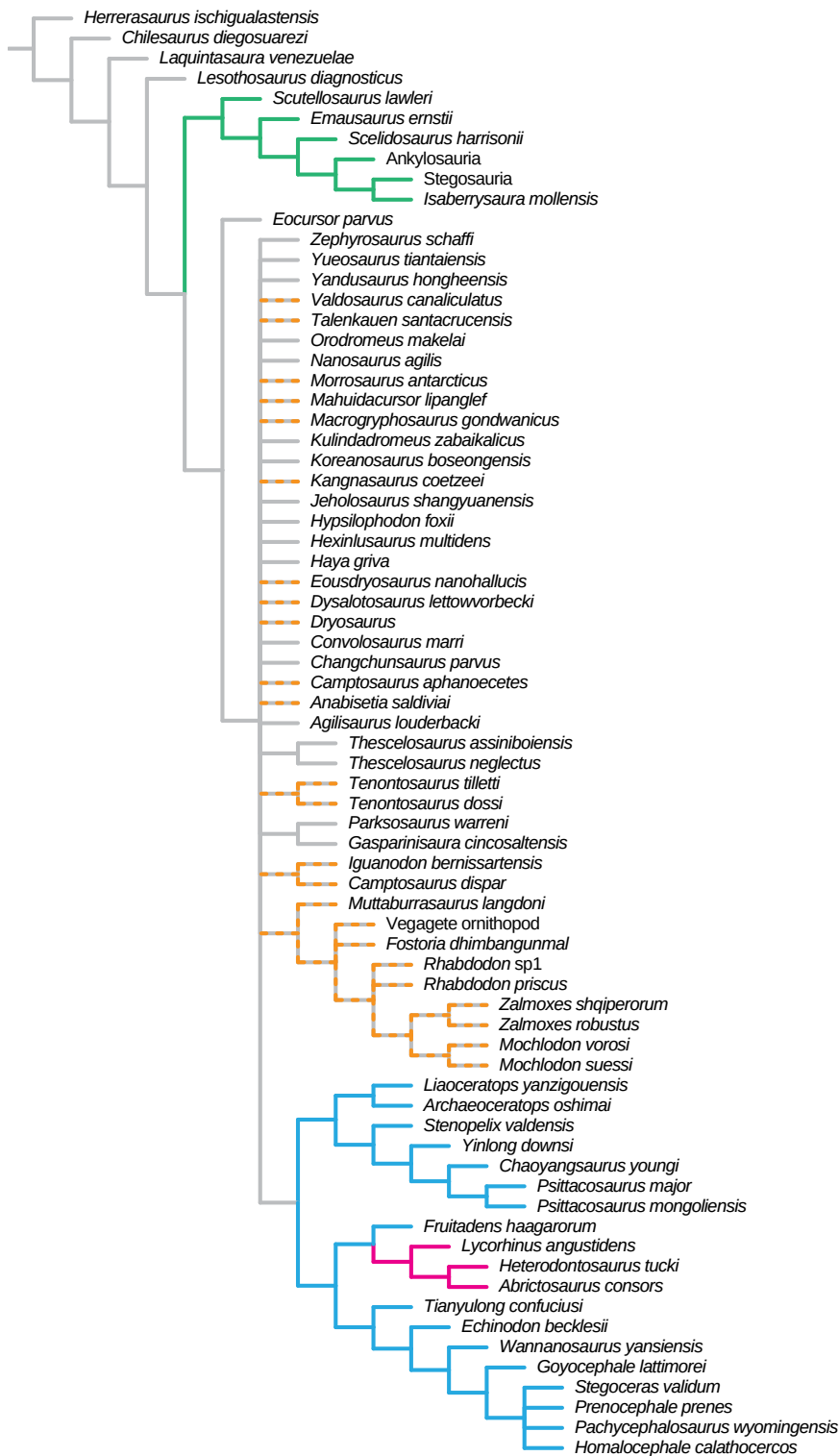
A2.80. Strict consensus tree of 5,361 MPTs produced from Han *et al.* (2018) when characters <35% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis I.1.D2021 - excluding characters <15% complete



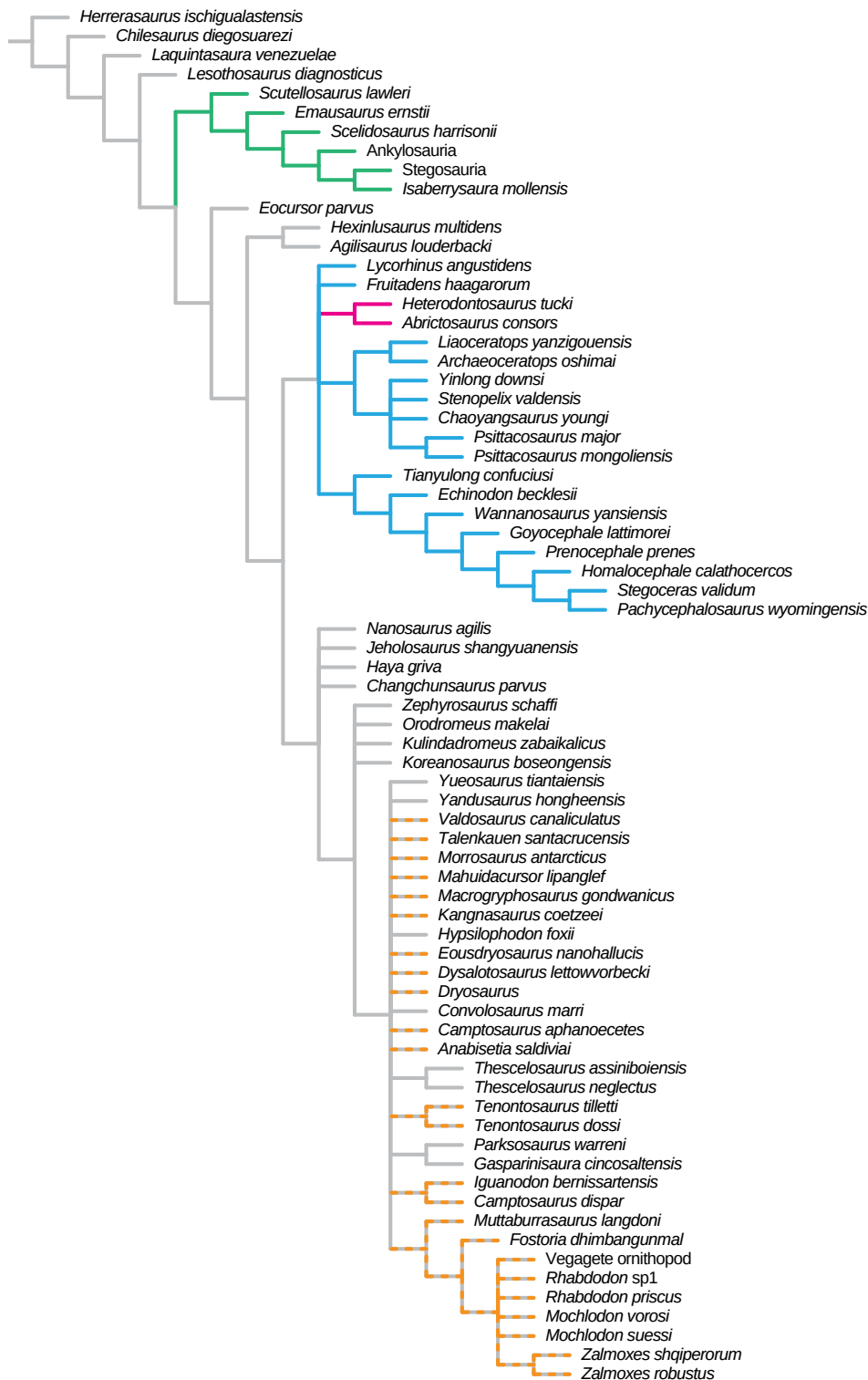
A2.81. Strict consensus tree of 1,780 MPTs produced from Dieudonné *et al.* (2021) when characters <15% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green).

Analysis I.2.D2021 - excluding characters <25% complete



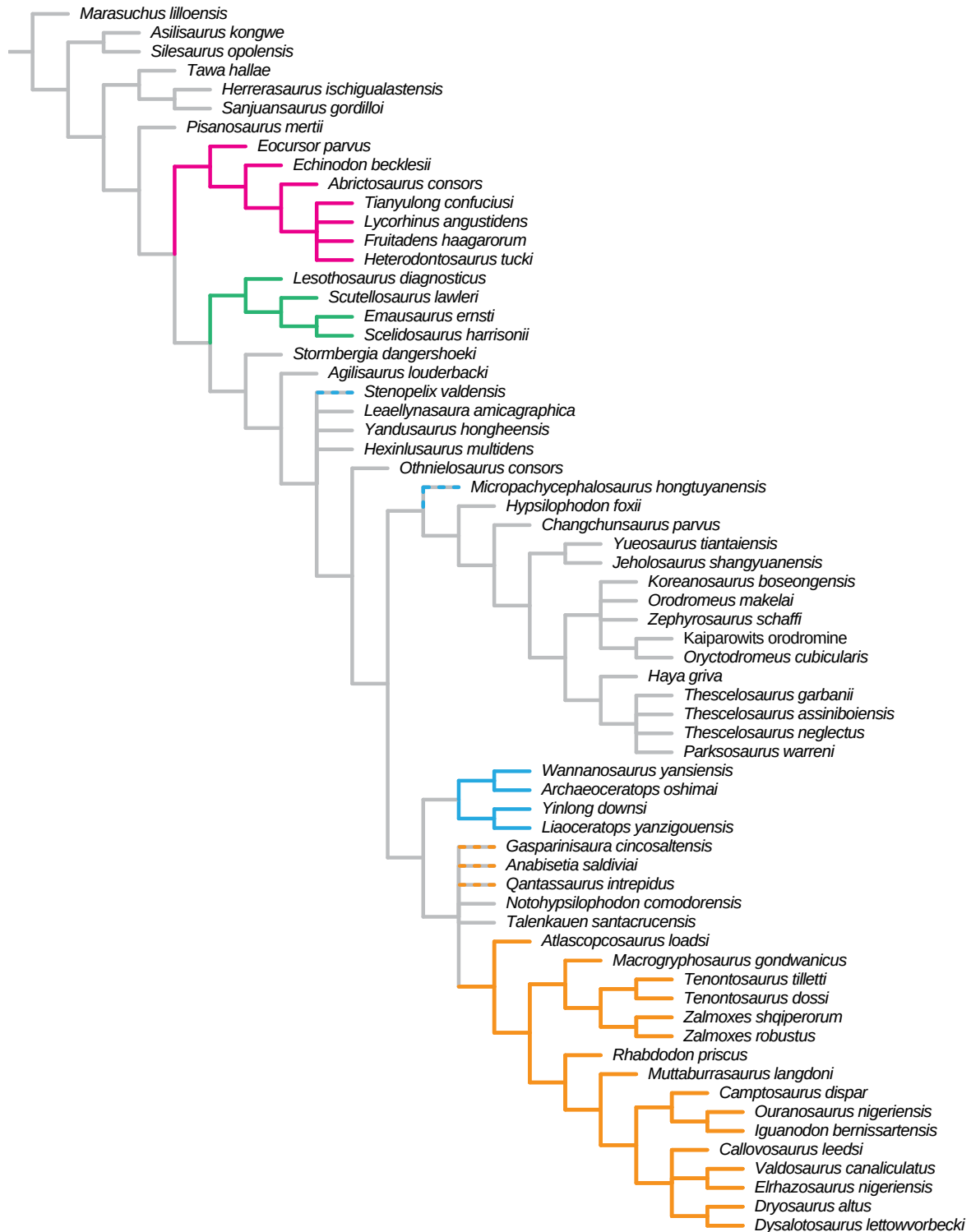
A2.82. Strict consensus tree of 4,559 MPTs produced from Dieudonné *et al.* (2021) when characters <25% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis I.3.D2021 - excluding characters <35% complete



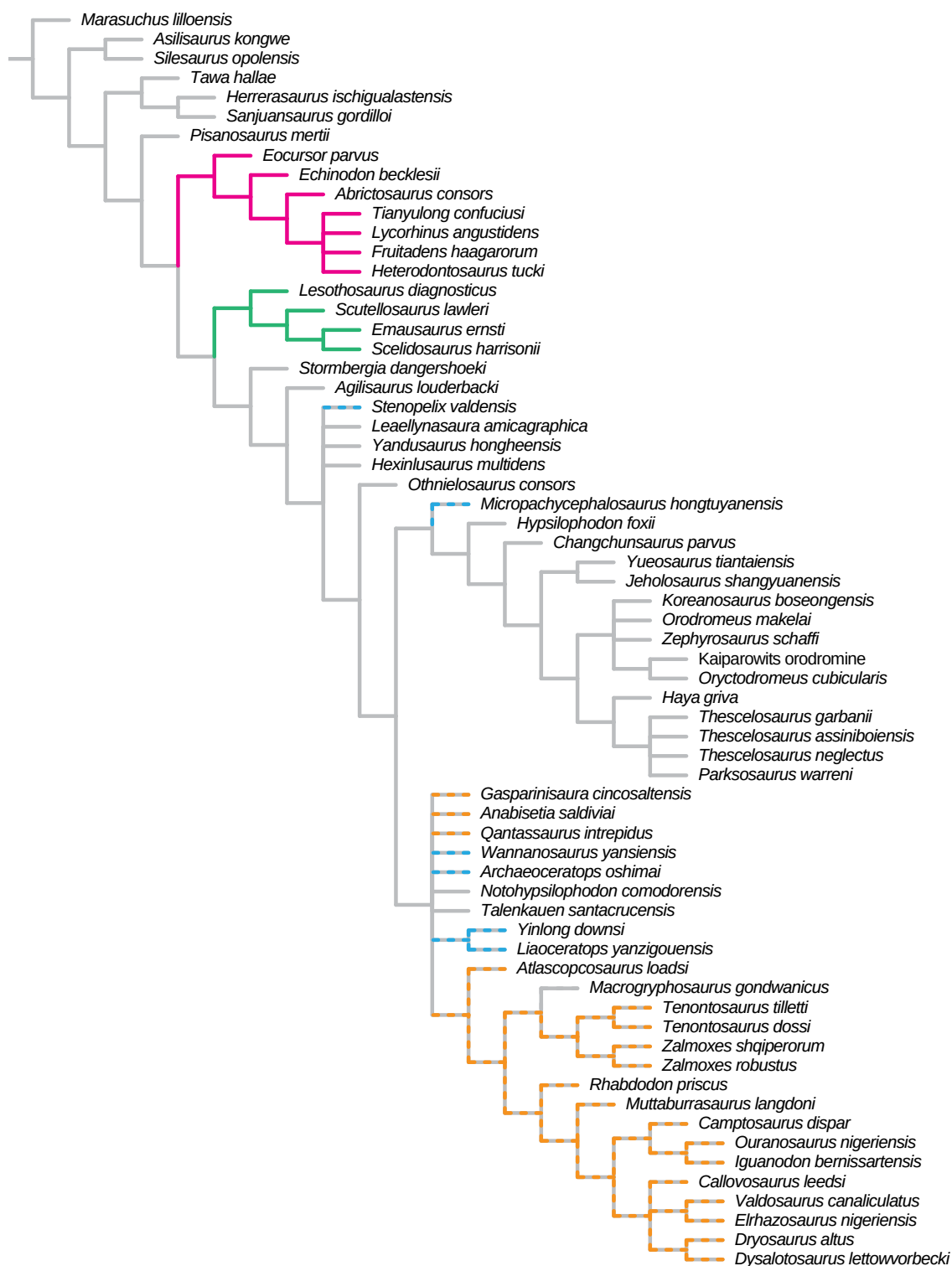
A2.83. Strict consensus tree of 1,981 MPTs produced from Dieudonné *et al.* (2021) when characters <35% complete are removed. Key: Het., Heterodontosauridae (pink); Iguanodontia (orange); Marginocephalia (blue); Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis J.1.B2015 - implied weighting $k=5$



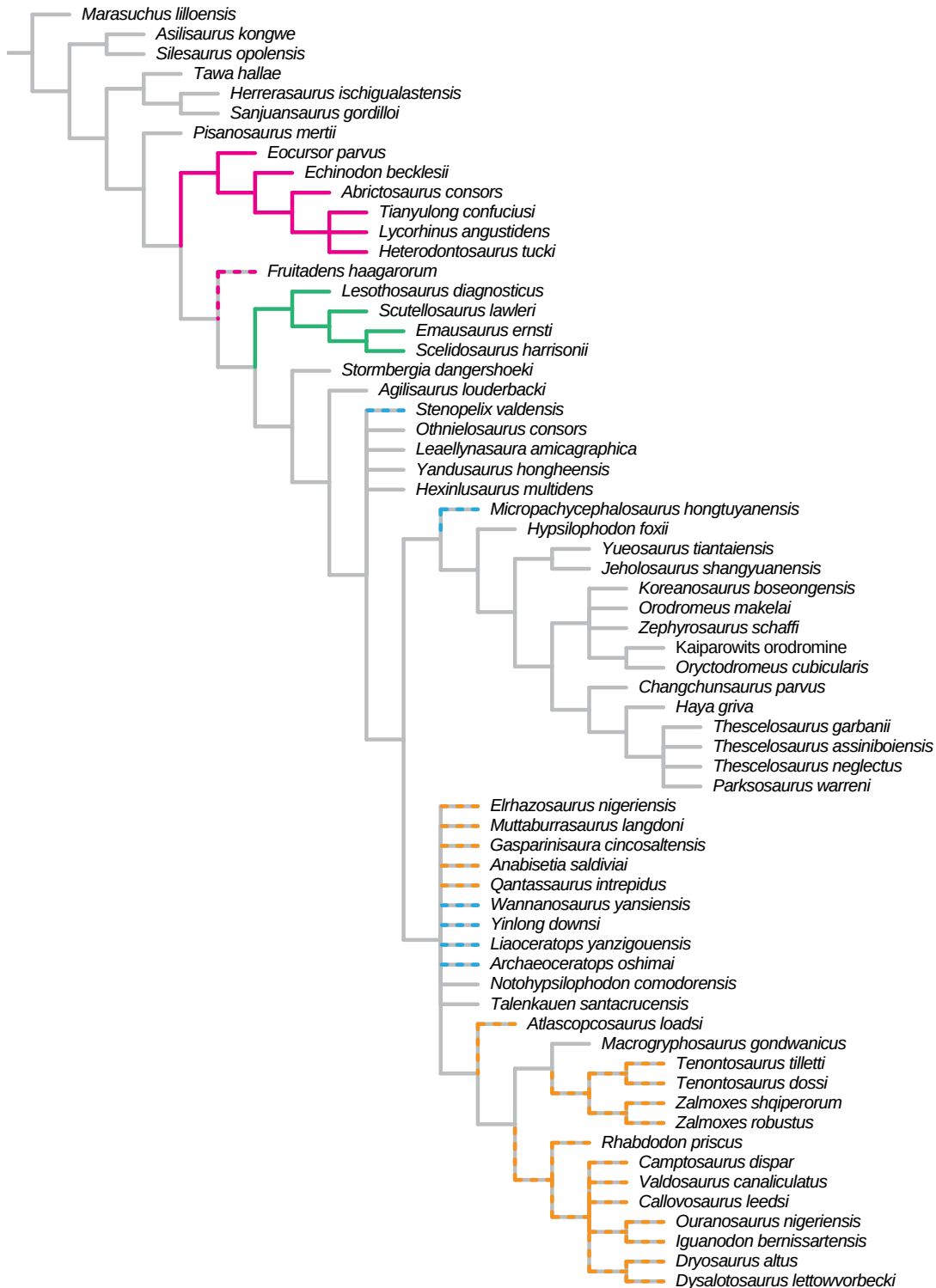
A2.84. Strict consensus tree of 538 MPTs produced from Boyd (2015) using implied character weighting ($k=5$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis J.2.B2015 - implied weighting $k=3$



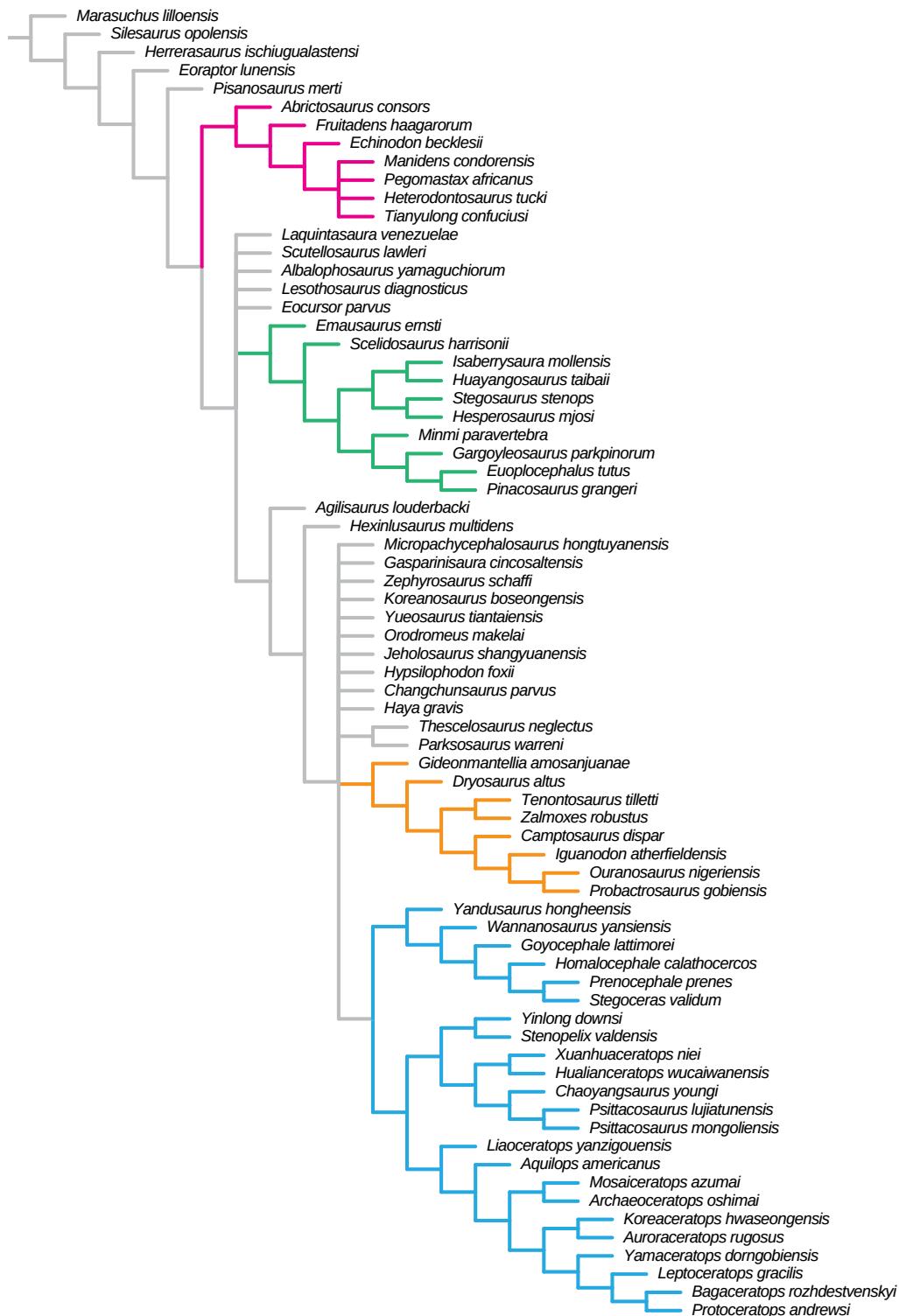
A2.85. Strict consensus tree of 629 MPTs produced from Boyd (2015) using implied character weighting ($k=3$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis J.3.B2015 - implied weighting $k=1$



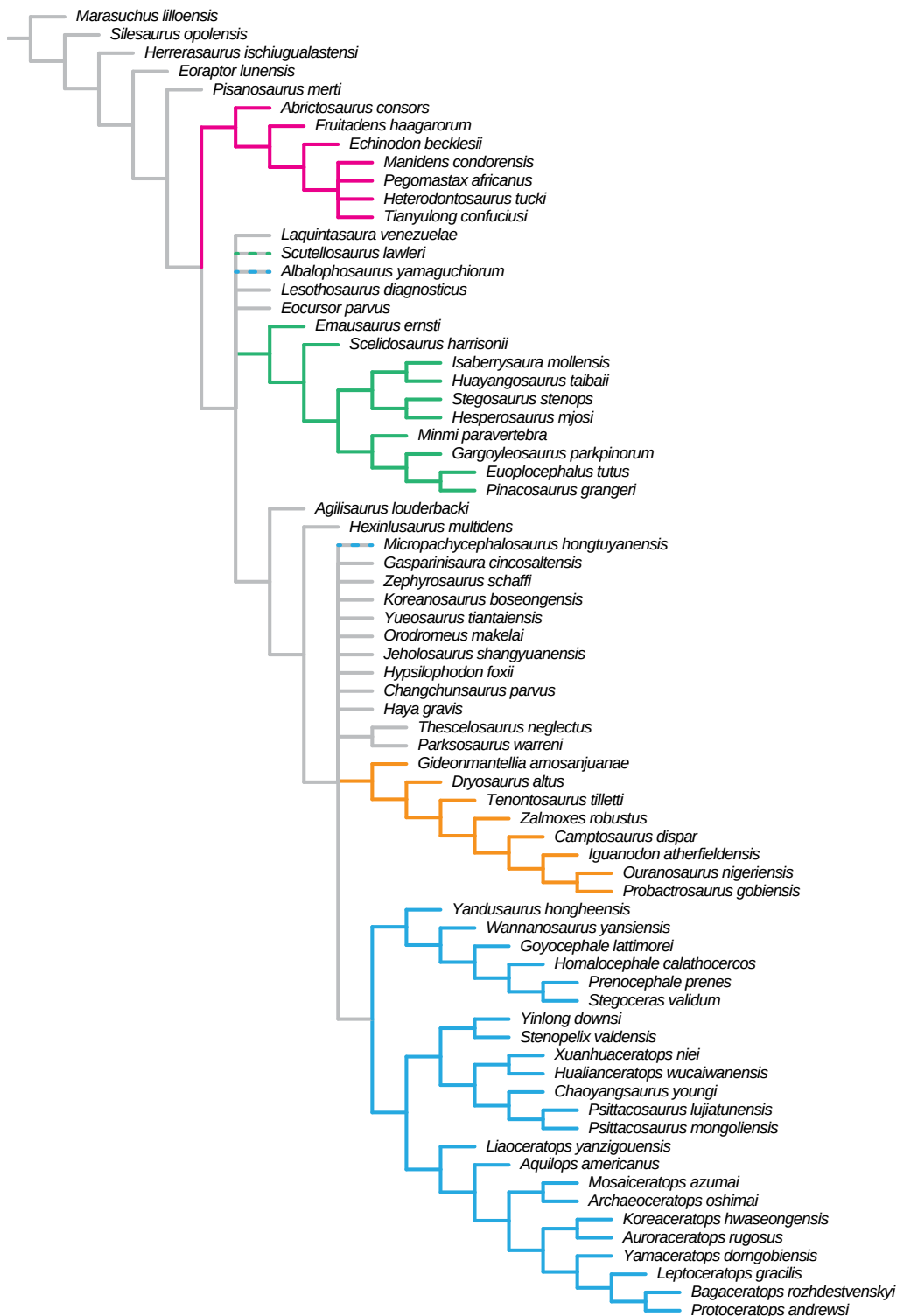
A2.86. Strict consensus tree of 863 MPTs produced from Boyd (2015) using implied character weighting ($k=1$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Boyd (2015).

Analysis J.1.H2018 - implied weighting $k=5$



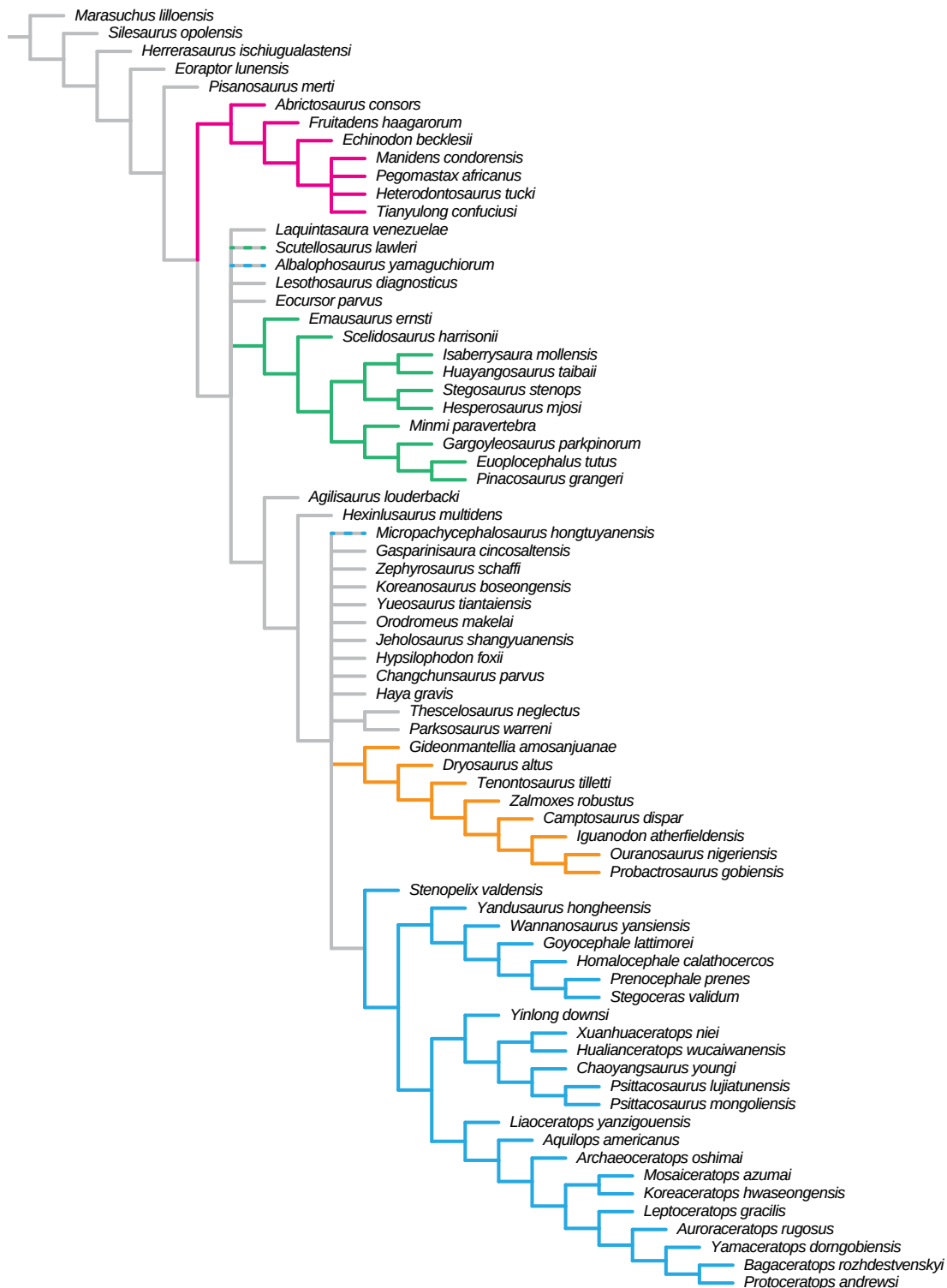
A2.87. Strict consensus tree of 384 MPTs produced from Han *et al.* (2018) using implied character weighting ($k=5$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis J.2.H2018 - implied weighting $k=3$



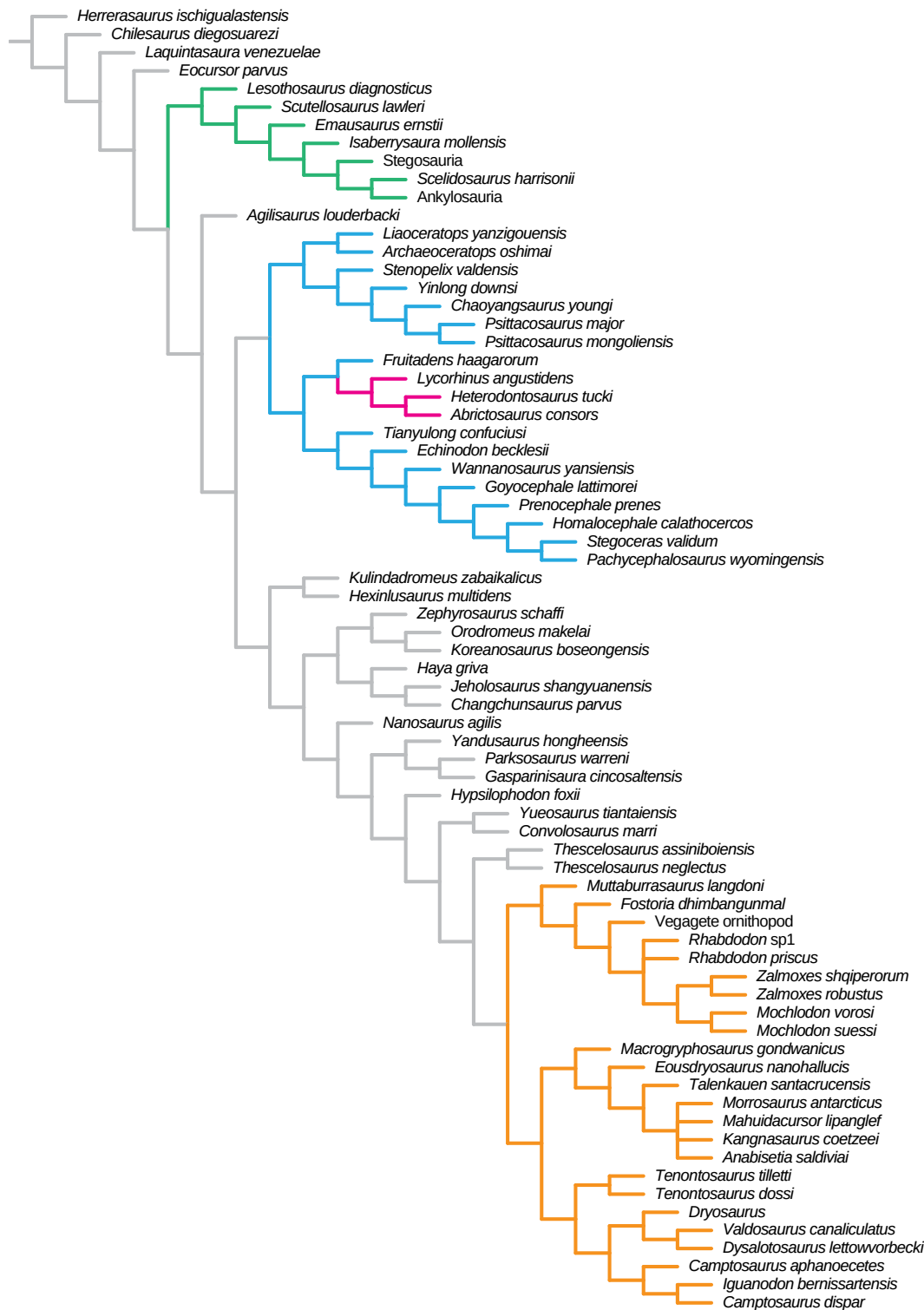
A2.88. Strict consensus tree of 384 MPTs produced from Han *et al.* (2018) using implied character weighting ($k=3$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis J.3.H2018 - implied weighting $k=1$



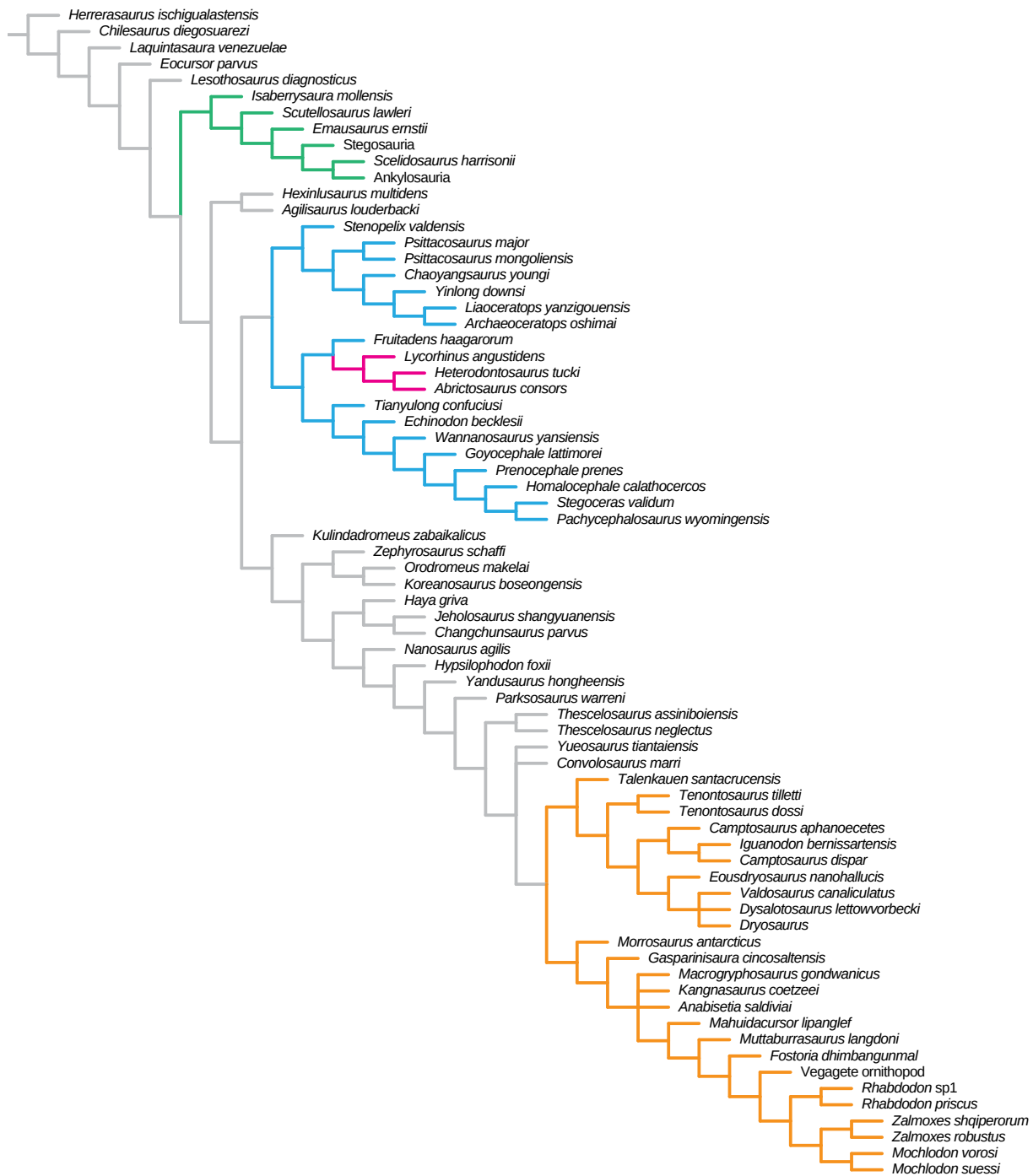
A2.89. Strict consensus tree of 384 MPTs produced from Han *et al.* (2018) using implied character weighting ($k=1$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Han *et al.* (2018).

Analysis J.1.D2021 - implied weighting $k=5$



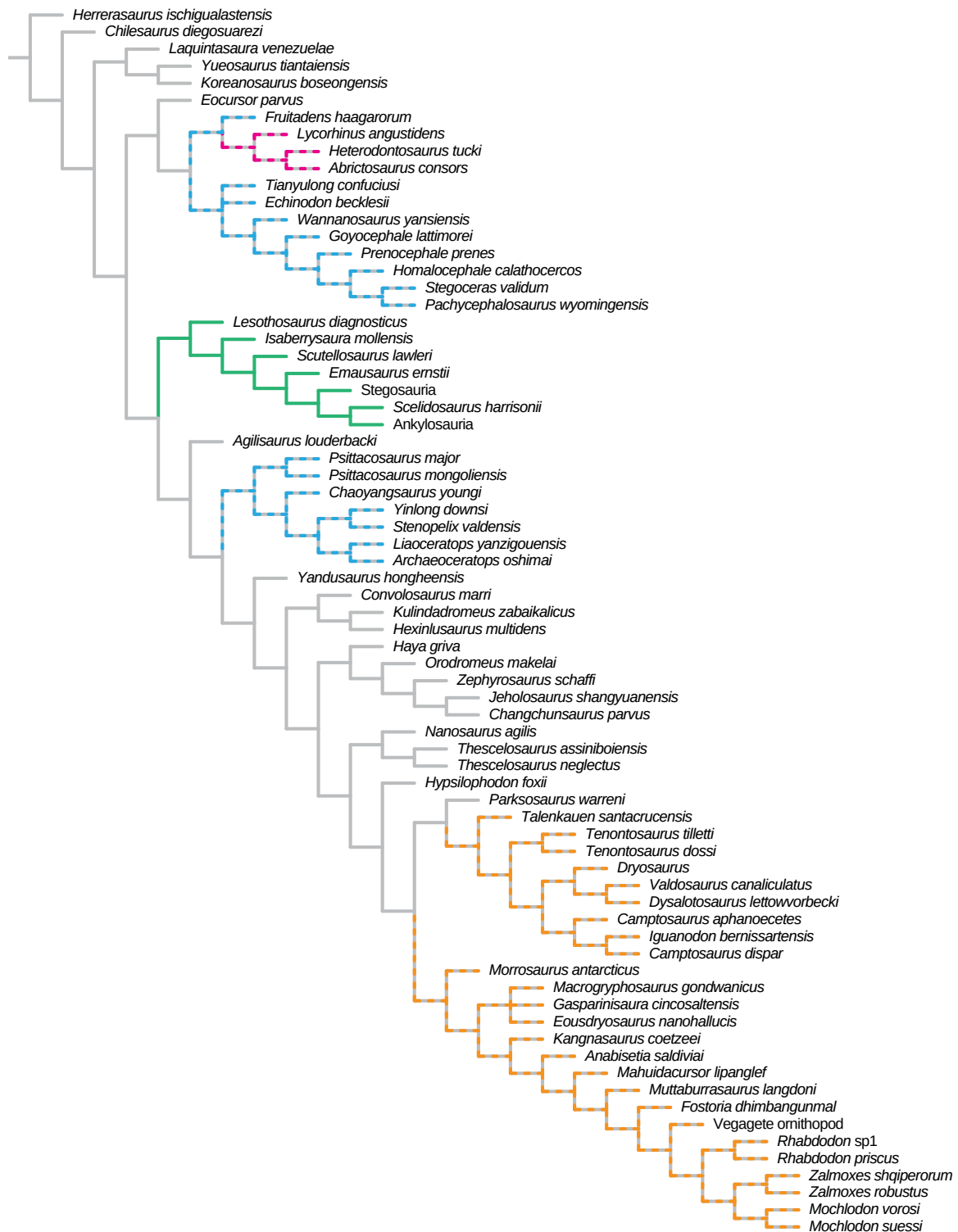
A2.90. Strict consensus tree of 3 MPTs produced from Dieudonné *et al.* (2021) using implied character weighting ($k=5$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis J.2.D2021 - implied weighting $k=3$



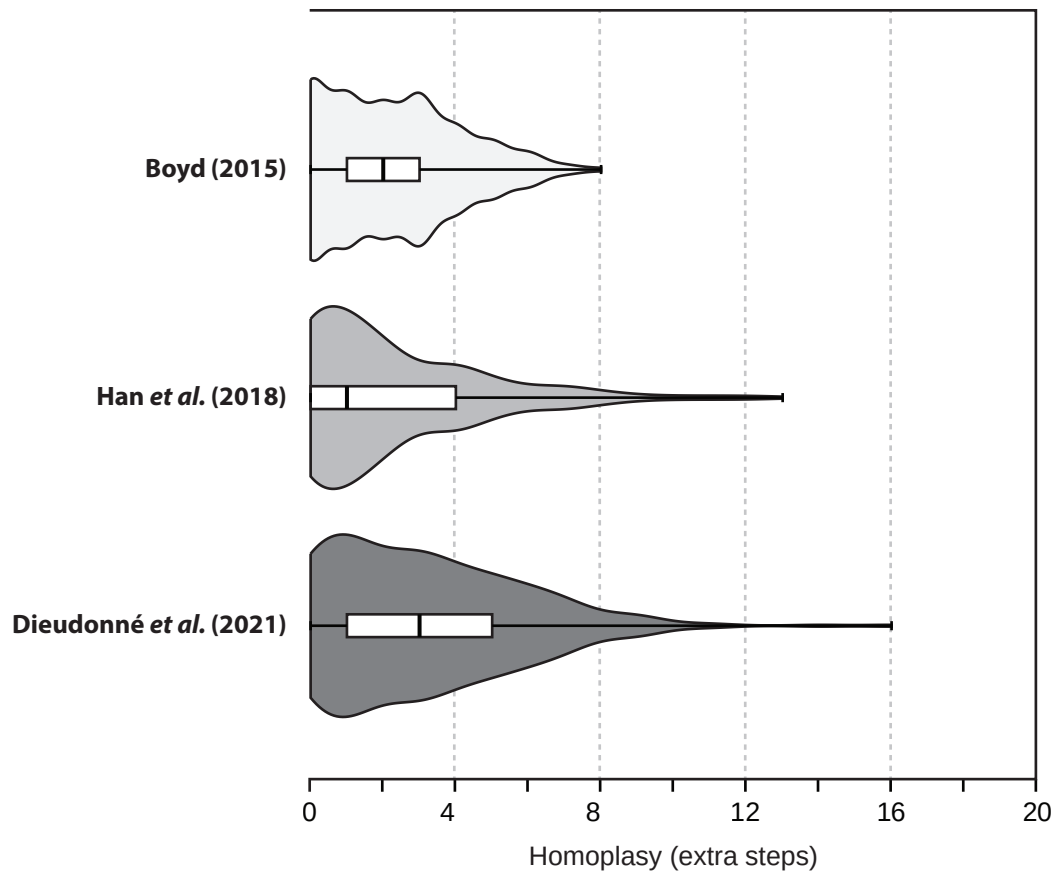
A2.91. Strict consensus tree of 2 MPTs produced from Dieudonné *et al.* (2021) using implied character weighting ($k=3$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Analysis J.3.D2021 - implied weighting $k=1$



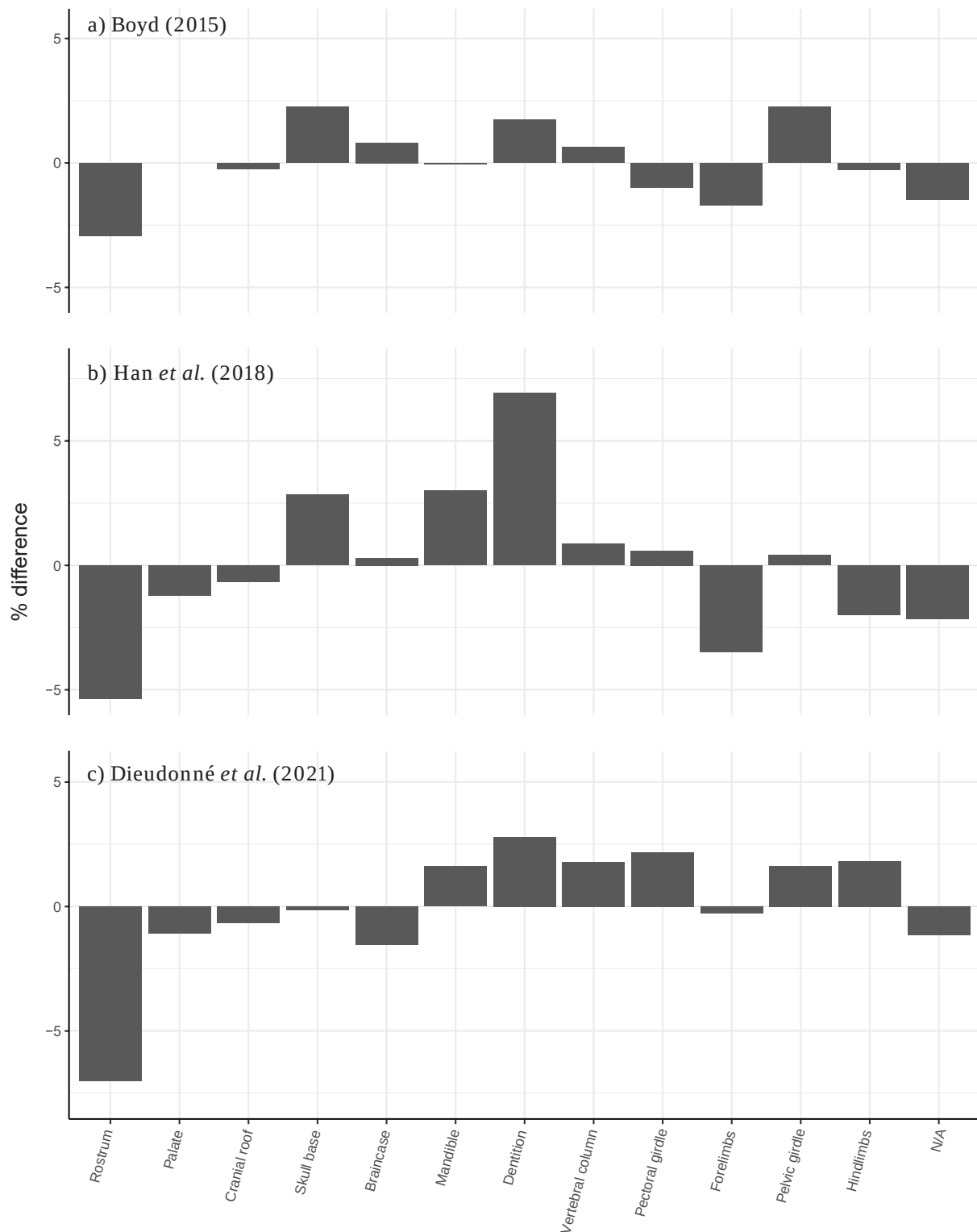
A2.92. Most parsimonious tree produced from Dieudonné *et al.* (2021) using implied character weighting ($k=1$). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green). Coloured dashed lines indicate the group an OTU was recovered in the original analysis by Dieudonné *et al.* (2021).

Homoplasy



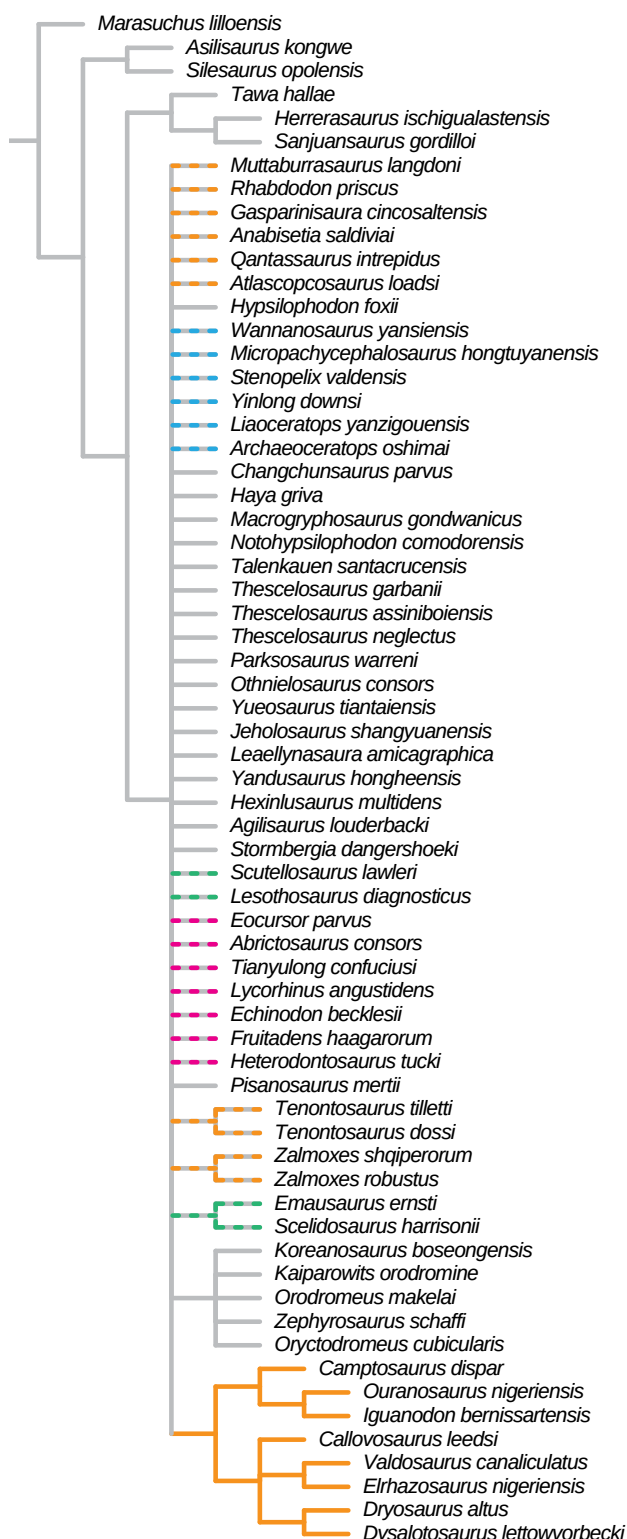
A2.93. Distribution of homoplasy for characters in data matrices from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021).

Homoplasy



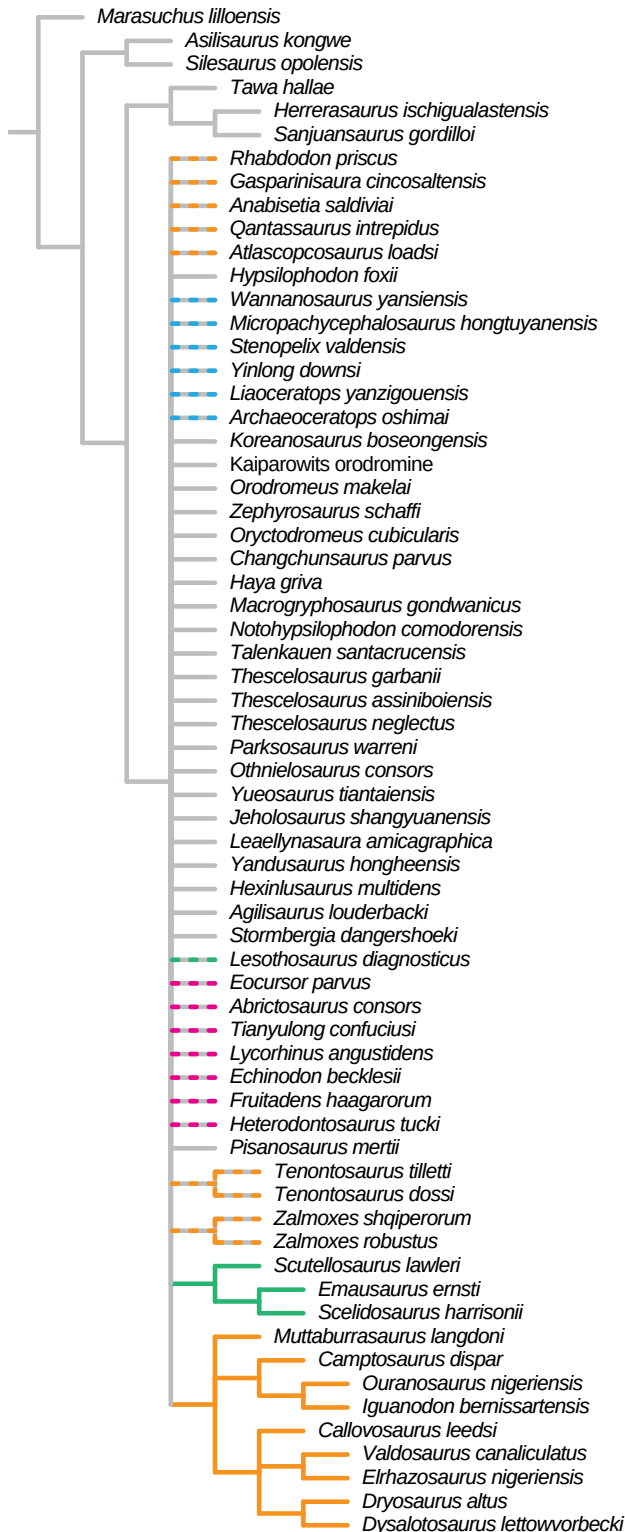
A2.94. Percentage difference between character homoplasy (%) and the proportion of total characters (%) per skeletal region in: (a) Boyd (2015); (b) Han *et al.* (2018); (c) Dieudonné *et al.* (2021). No palatal characters in Boyd (2015).

Analysis K.1.B2015 - excluding characters with homoplasy >95th percentile



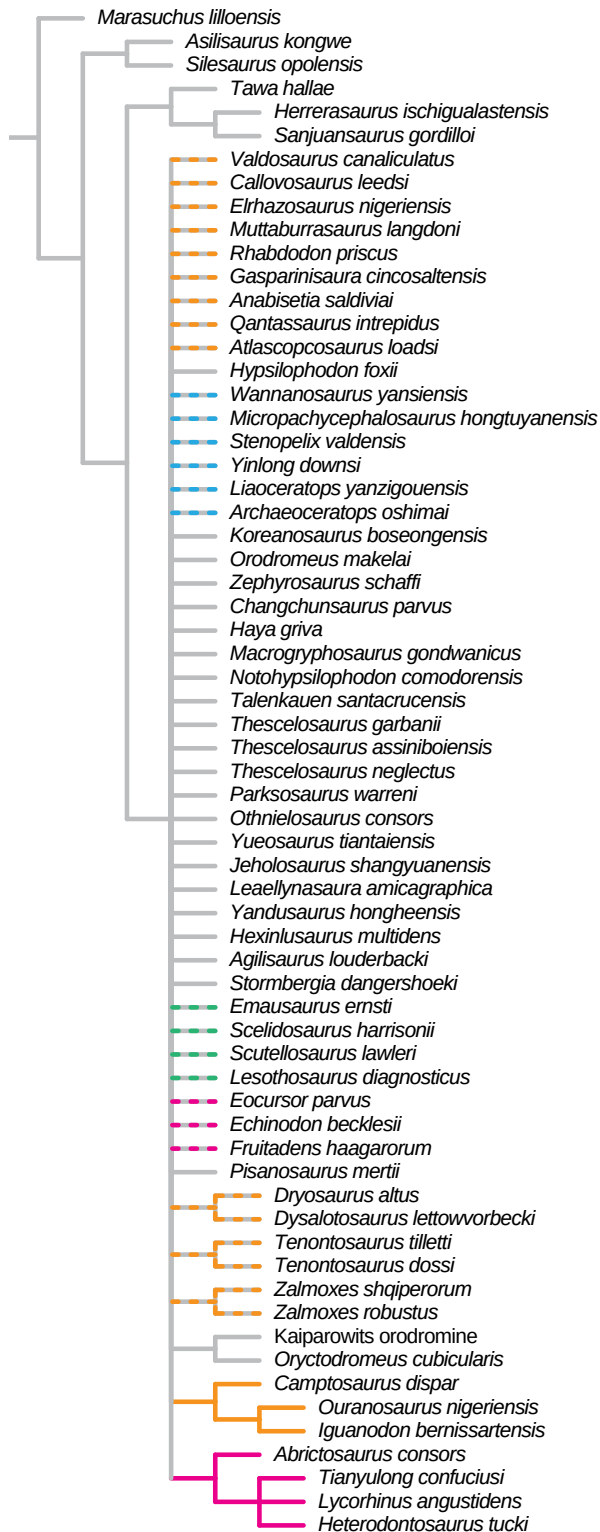
A2.95. Strict consensus tree of 37,500 MPTs produced when characters with homoplasy >95th percentile are removed from Boyd (2015). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.2.B2015 - excluding characters with homoplasy >85th percentile



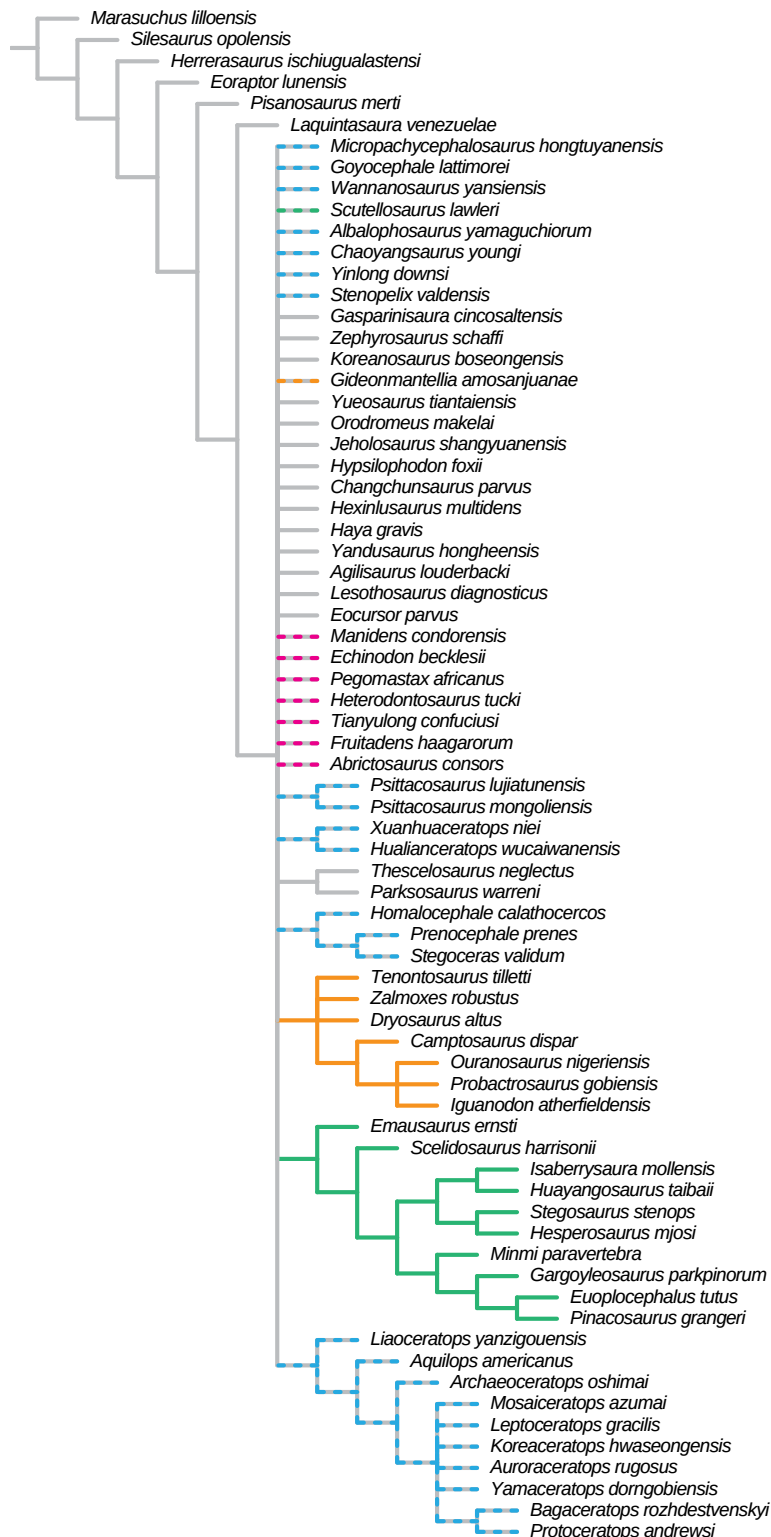
A2.96. Strict consensus tree of 44,800 MPTs produced when characters with homoplasy >85th percentile are removed from Boyd (2015). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.3.B2015 - excluding characters with homoplasy >75th percentile



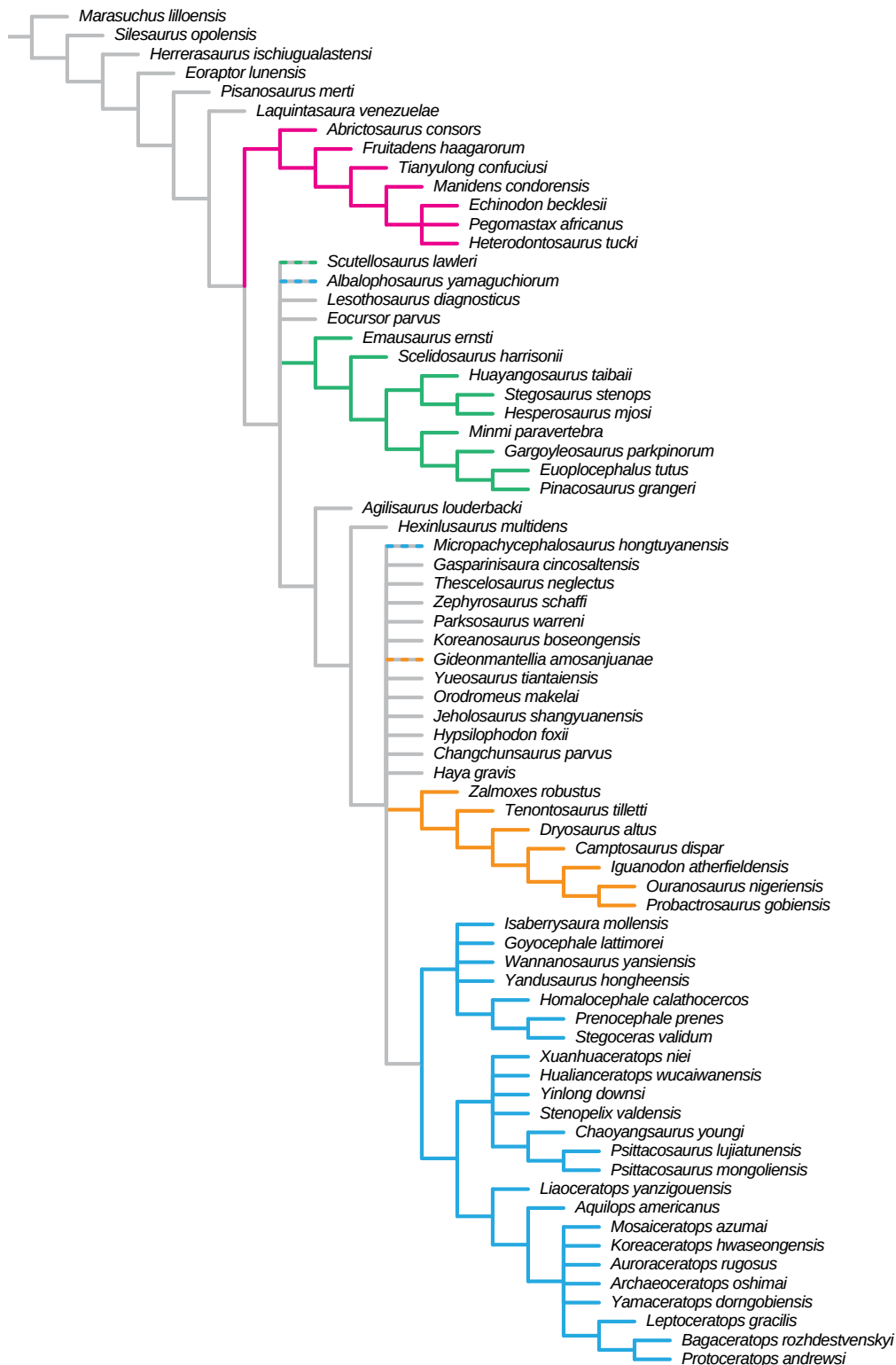
A2.97. Strict consensus tree of 7,700 MPTs produced when characters with homoplasy >75th percentile are removed from Boyd (2015). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.1.H2018 - excluding characters with homoplasy >95th percentile



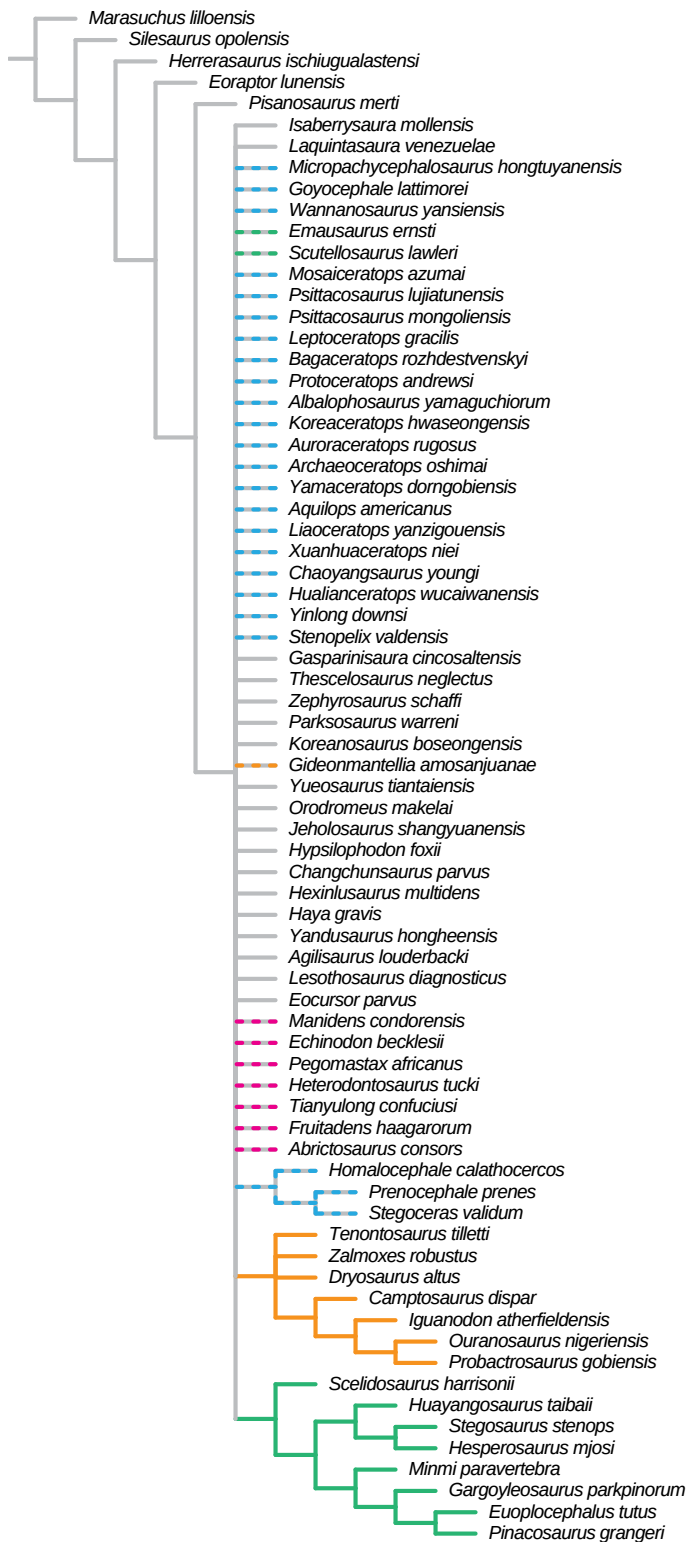
A2.98. Strict consensus tree of 44,900 MPTs produced when characters with homoplasy >95th percentile are removed from Han *et al.* (2018). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.2.H2018 - excluding characters with homoplasy >85th percentile



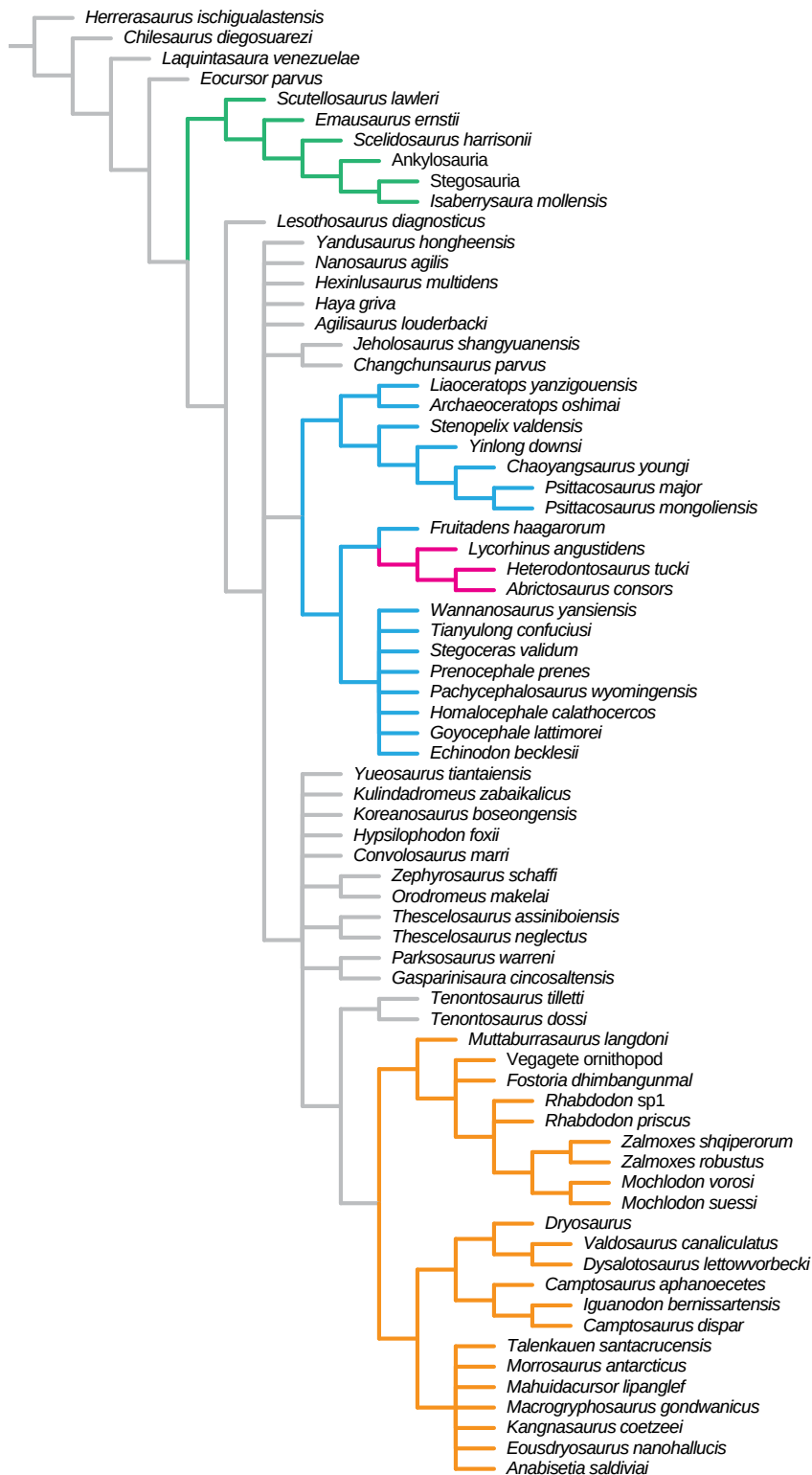
A2.99. Strict consensus tree of 40,500 MPTs produced when characters with homoplasy >85th percentile are removed from Han *et al.* (2018). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.3.H2018 - excluding characters with homoplasy >75th percentile



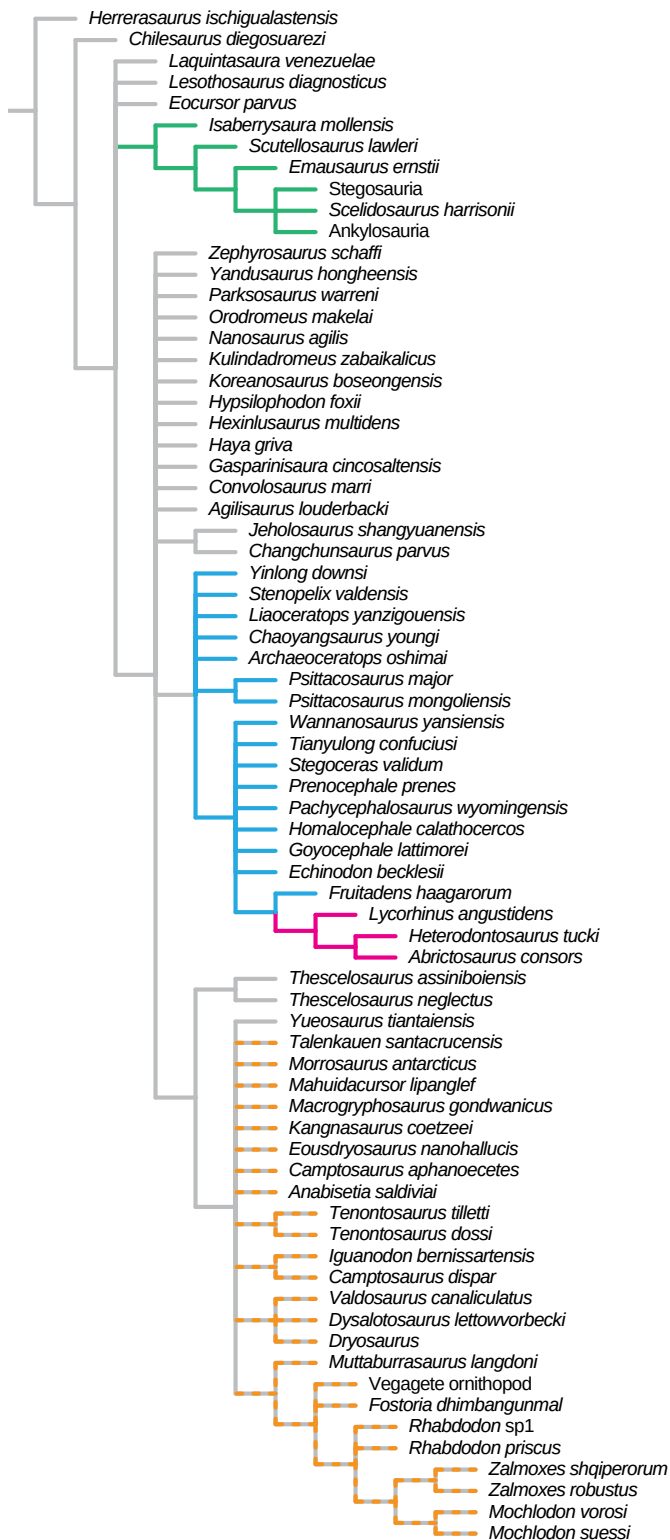
A2.100. Strict consensus tree of 99,100 MPTs produced when characters with homoplasy >75th percentile are removed from Han *et al.* (2018). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.1.D2021 - excluding characters with homoplasy >95th percentile



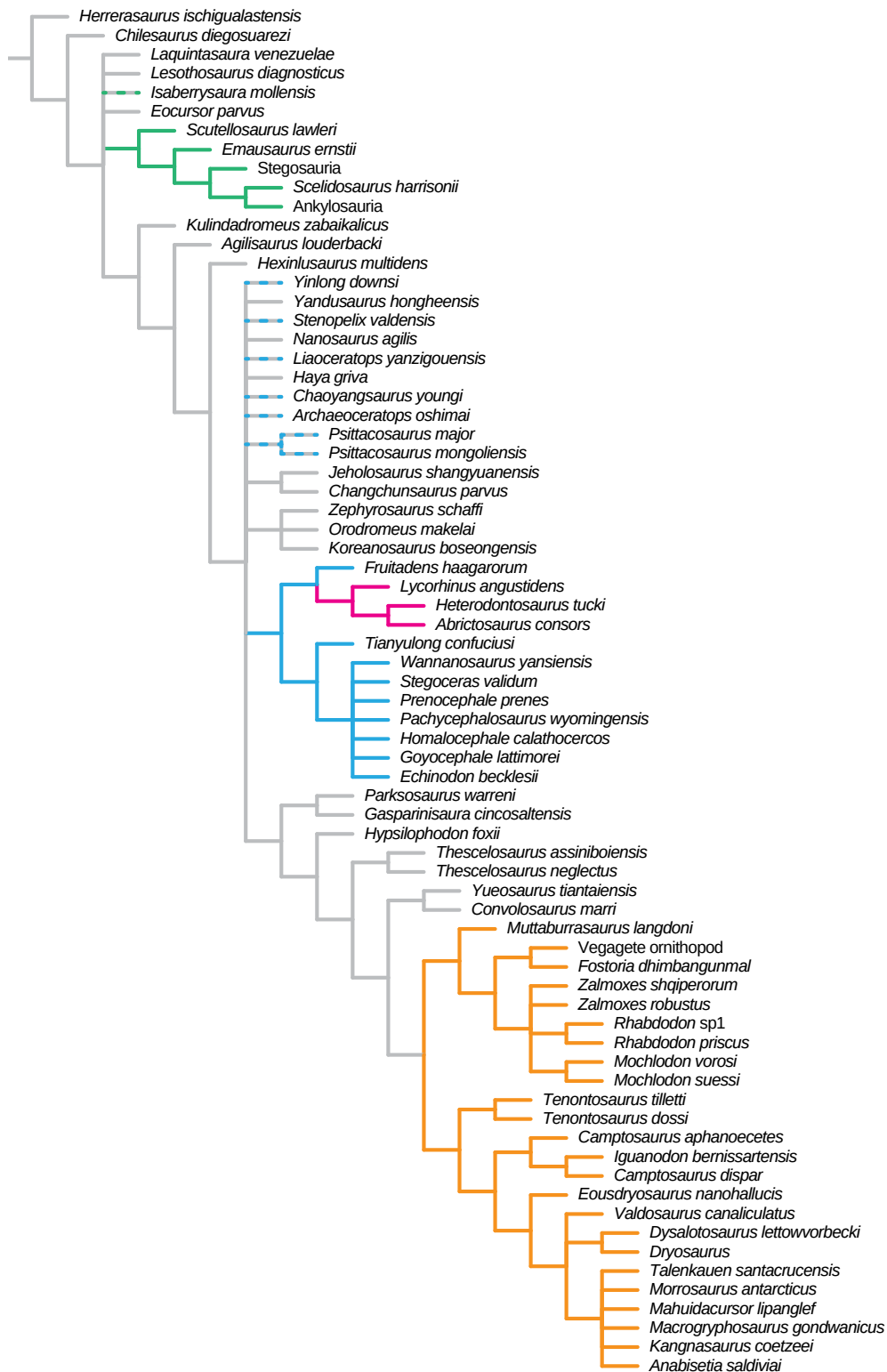
A2.101. Strict consensus tree of 3,779 MPTs produced when characters with homoplasy >95th percentile are removed from Dieudonné *et al.* (2021). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.2.D2021 - excluding characters with homoplasy >85th percentile



A2.102. Strict consensus tree of 21,400 MPTs produced when characters with homoplasy >85th percentile are removed from Dieudonné *et al.* (2021). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

Analysis K.3.D2021 - excluding characters with homoplasy >75th percentile



A2.103. Strict consensus tree of 6,000 MPTs produced when characters with homoplasy >75th percentile are removed from Dieudonné *et al.* (2021). Key: Het., Heterodontosauridae (pink); Igu., Iguanodontia (orange); Mar., Marginocephalia (blue); Thy., Thyreophora (green).

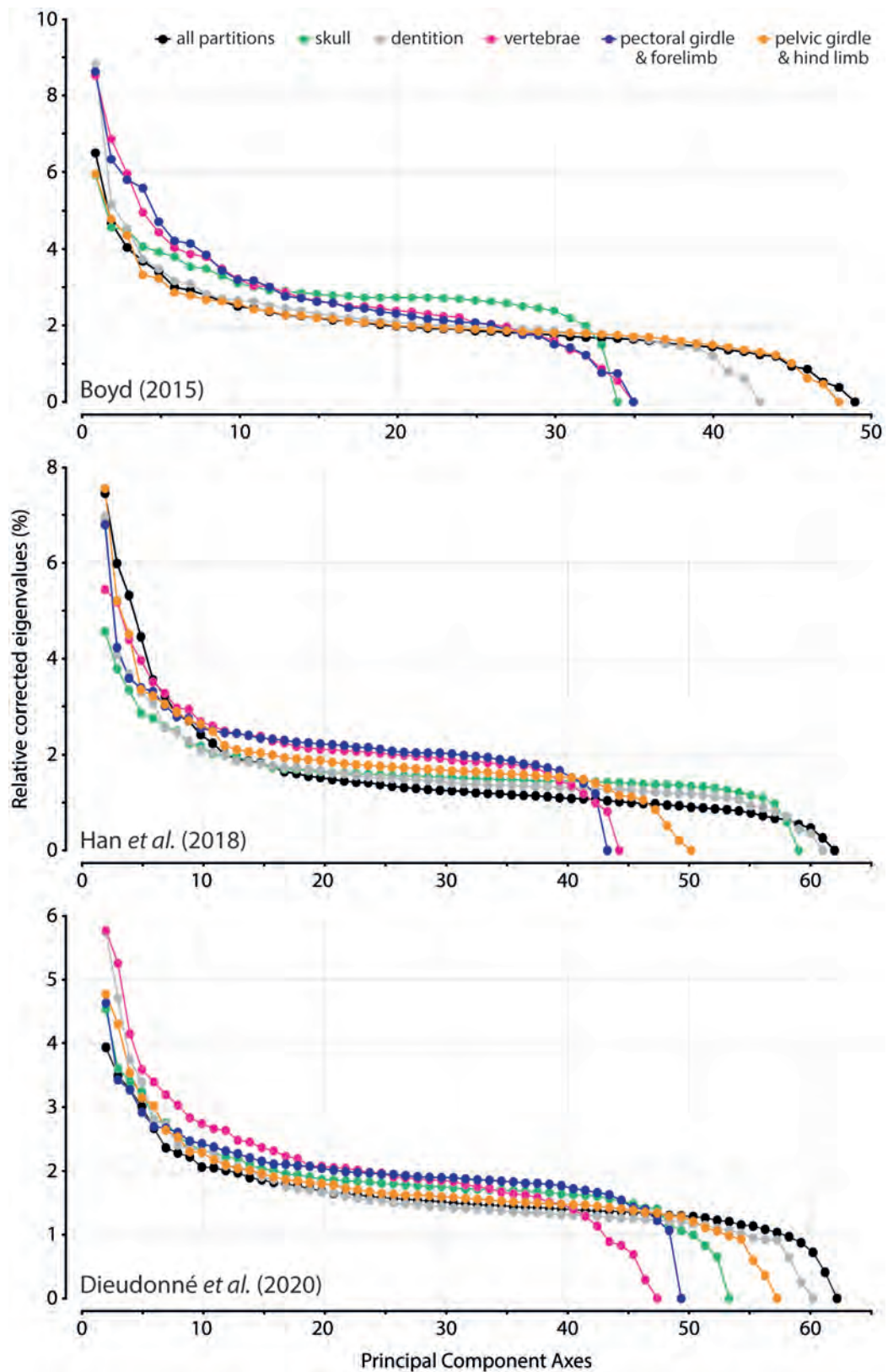
A3.1. OTUs removed during the ordination of distances matrices generated in this study from character matrices by Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Abbreviations: *Mo.*, *Mochlodon*; *Ps.*, *Psittacosaurus*; *Rh.*, *Rhabdodon*; *Th.*, *Thescelosaurus*.

Boyd (2015) matrix	
All partitions	<i>Atlascopcosaurus</i> , <i>Echinodon</i> , <i>Emausaurus</i> , <i>Liaoceratops</i> , <i>Lycorhinus</i> , <i>Macrogyphosaurus</i> , <i>Qantassaurus</i> , <i>Scelidosaurus</i>
Skull	<i>Atlascopcosaurus</i> , <i>Callovosaurus</i> , <i>Elrhazosaurus</i> , <i>Fruitadens</i> , <i>Koreanosaurus</i> , <i>Leaellynasaura</i> , <i>Lycorhinus</i> , <i>Macrogyphosaurus</i> , <i>Micropachycephalosaurus</i> , <i>Notohypsilophodon</i> , <i>Stenopelix</i> , <i>Stormbergia</i> , <i>Th. assiniboensis</i> , <i>Th. garbanii</i> , <i>Valdosaurus</i> , <i>Yandusaurus</i> , <i>Yueosaurus</i>
Dentition	<i>Callovosaurus</i> , <i>Elrhazosaurus</i> , <i>Koreanosaurus</i> , <i>Macrogyphosaurus</i> , <i>Micropachycephalosaurus</i> , <i>Notohypsilophodon</i> , <i>Stenopelix</i> , <i>Stormbergia</i> , <i>Th. assiniboensis</i> , <i>Th. garbanii</i> , <i>Valdosaurus</i> , <i>Yueosaurus</i>
Vertebrae	<i>Abrictosaurus</i> , <i>Anabisetia</i> , <i>Atlascopcosaurus</i> , <i>Callovosaurus</i> , <i>Echinodon</i> , <i>Elrhazosaurus</i> , <i>Emausaurus</i> , <i>Eocursor</i> , <i>Gasparinisaura</i> , <i>Leaellynasaura</i> , <i>Lesothosaurus</i> , <i>Liaoceratops</i> , <i>Lycorhinus</i> , <i>Micropachycephalosaurus</i> , <i>Ouranosaurus</i> , <i>Qantassaurus</i> , <i>Scelidosaurus</i> , <i>Stenopelix</i> , <i>Th. garbanii</i> , <i>Tianyulong</i> , <i>Yandusaurus</i> , <i>Yinlong</i>
Pectoral girdle & forelimb	<i>Abrictosaurus</i> , <i>Archaeoceratops</i> , <i>Atlascopcosaurus</i> , <i>Callovosaurus</i> , <i>Echinodon</i> , <i>Elrhazosaurus</i> , <i>Emausaurus</i> , <i>Eocursor</i> , <i>Fruitadens</i> , <i>Leaellynasaura</i> , <i>Liaoceratops</i> , <i>Lycorhinus</i> , <i>Macrogyphosaurus</i> , <i>Micropachycephalosaurus</i> , <i>Qantassaurus</i> , <i>Scelidosaurus</i> , <i>Stenopelix</i> , <i>Th. assiniboensis</i> , <i>Th. garbanii</i> , <i>Talenkauen</i> , <i>Valdosaurus</i> , <i>Wannanosaurus</i> , <i>Tianyulong</i> , <i>Yinlong</i>
Pelvic girdle & hind limb	<i>Atlascopcosaurus</i> , <i>Echinodon</i> , <i>Emausaurus</i> , <i>Liaoceratops</i> , <i>Lycorhinus</i> , <i>Macrogyphosaurus</i> , <i>Qantassaurus</i> , <i>Scelidosaurus</i> , <i>Yandusaurus</i>
Han <i>et al.</i> (2018) matrix	
All partitions	<i>Gideonmantellia</i> , <i>Koreaceratops</i> , <i>Koreanosaurus</i> , <i>Stenopelix</i> , <i>Yueosaurus</i>
Skull	<i>Eocursor</i> , <i>Gideonmantellia</i> , <i>Koreaceratops</i> , <i>Koreanosaurus</i> , <i>Marasuchus</i> , <i>Micropachycephalosaurus</i> , <i>Pegomastax</i> , <i>Stenopelix</i> , <i>Yueosaurus</i>
Dentition	<i>Euoplocephalus</i> , <i>Gideonmantellia</i> , <i>Koreaceratops</i> , <i>Koreanosaurus</i> , <i>Stenopelix</i> , <i>Yueosaurus</i>
Vertebrae	<i>Abrictosaurus</i> , <i>Albalophosaurus</i> , <i>Aquilops</i> , <i>Bagaceratops</i> , <i>Chaoyangsaurus</i> , <i>Echinodon</i> , <i>Emausaurus</i> , <i>Eocursor</i> , <i>Euoplocephalus</i> , <i>Gargoyleosaurus</i> , <i>Goyocephale</i> , <i>Hualianceratops</i> , <i>Isaberrysaura</i> , <i>Koreaceratops</i> , <i>Liaoceratops</i> , <i>Micropachycephalosaurus</i> , <i>Mosaiceratops</i> , <i>Pegomastax</i> , <i>Pisanosaurus</i> , <i>Ps. lujiatunensis</i> , <i>Stenopelix</i> , <i>Wannanosaurus</i> , <i>Xuanhuaceratops</i> , <i>Yamaceratops</i> , <i>Zephyrosaurus</i>
Pectoral girdle & forelimb	<i>Albalophosaurus</i> , <i>Aquilops</i> , <i>Archaeoceratops</i> , <i>Bagaceratops</i> , <i>Echinodon</i> , <i>Euoplocephalus</i> , <i>Gargoyleosaurus</i> , <i>Gideonmantellia</i> , <i>Hesperosaurus</i> , <i>Homocephale</i> , <i>Hualianceratops</i> , <i>Isaberrysaura</i> , <i>Koreaceratops</i> , <i>Laquintasaura</i> , <i>Liaoceratops</i> , <i>Manidens</i> , <i>Micropachycephalosaurus</i> , <i>Mosaiceratops</i> , <i>Parksoosaurus</i> , <i>Pegomastax</i> , <i>Pisanosaurus</i> , <i>Prenocephale</i> , <i>Ps. lujiatunensis</i> , <i>Stenopelix</i> , <i>Yamaceratops</i> , <i>Zephyrosaurus</i>
Pelvic girdle & hind limb	<i>Albalophosaurus</i> , <i>Aquilops</i> , <i>Bagaceratops</i> , <i>Chaoyangsaurus</i> , <i>Echinodon</i> , <i>Emausaurus</i> , <i>Euoplocephalus</i> , <i>Fruitadens</i> , <i>Hualianceratops</i> , <i>Isaberrysaura</i> ,

Koreaceratops, Liaoceratops, Pegomastax, Pisanosaurus, Ps. lujiatunensis, Xuanhuaceratops, Yamaceratops, Yandusaurus, Zephyrosaurus

Dieudonné et al. (2021) matrix

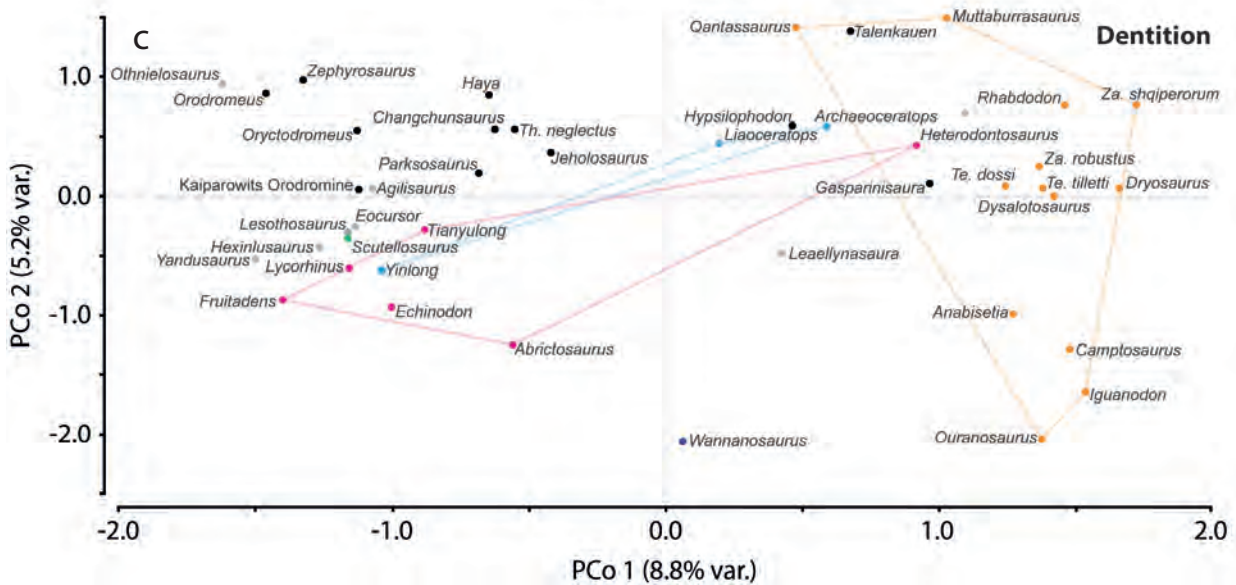
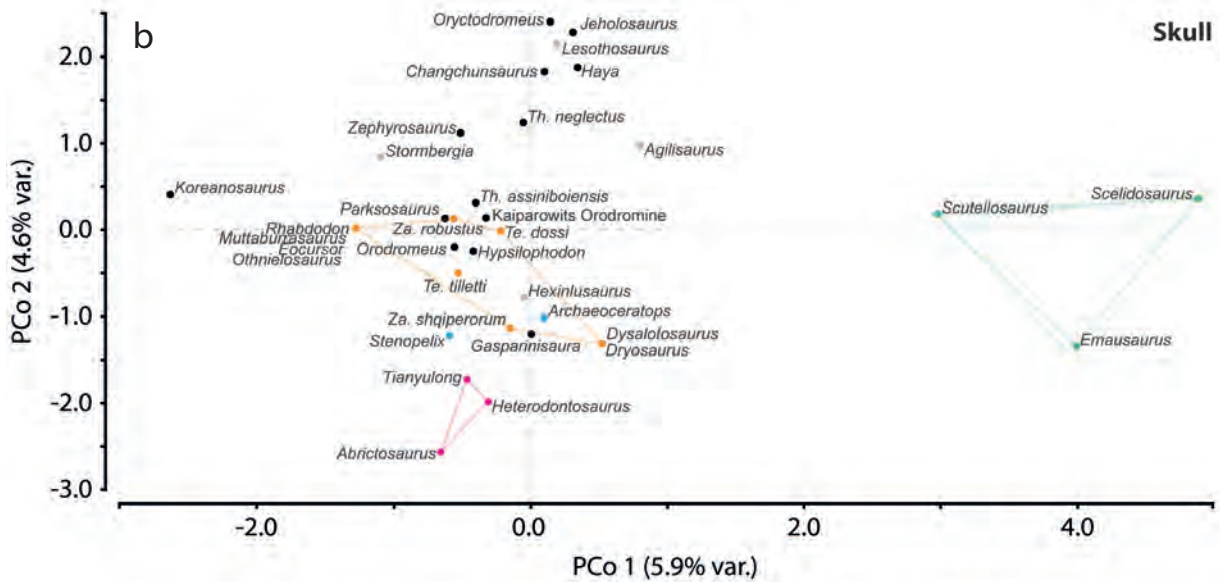
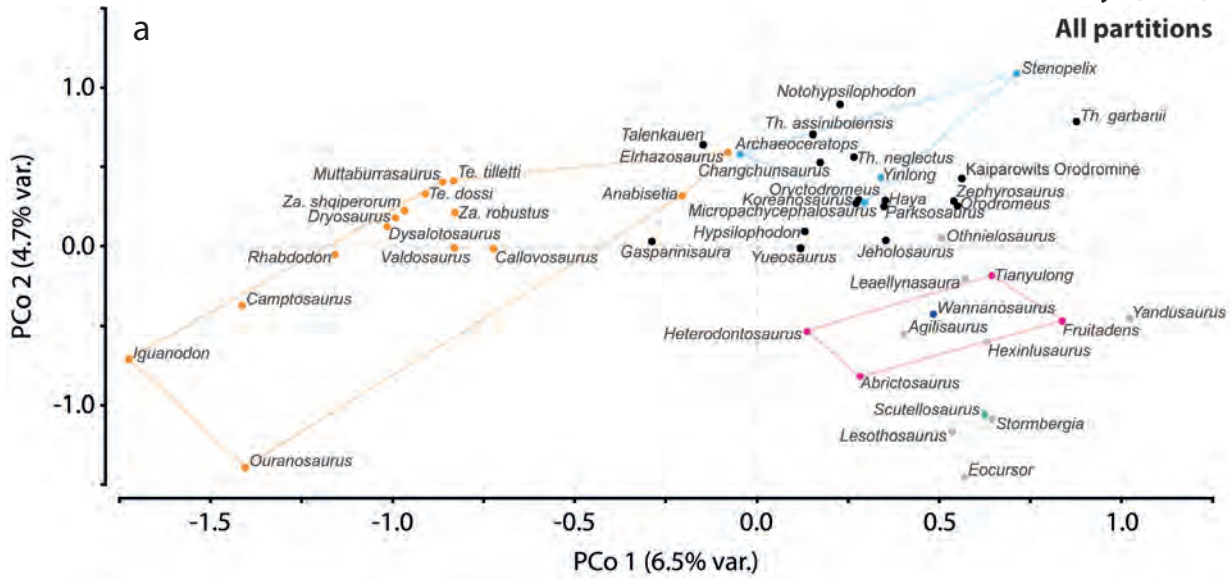
All partitions	<i>Chaoyangsaurus, Echinodon, Liaoceratops, Lycorhinus, Macrogyphosaurus, Mahuidacursor, Morrosaurus, Pachycephalosaurus</i>
Skull	<i>Ca. aphanoecetes, Eocursor, Eousdryosaurus, Fostoria, Homalocephale Isaberrysaura, Kangnasaurus, Koreanosaurus, Lycorhinus, Macrogyphosaurus, Mahuidacursor, Mo. suessi, Morrosaurus, Pachycephalosaurus, Prenocephale, Stenopelix, Th. assiniboensis, Valdosaurus, Yueosaurus</i>
Dentition	<i>Eousdryosaurus, Fostoria, Koreanosaurus, Macrogyphosaurus, Mahuidacursor, Morrosaurus, Stenopelix, Th. assiniboensis, Valdosaurus, Yueosaurus</i>
Vertebrae	<i>Abriktosaurus, Ankylosauria, Archaeoceratops, Chilesaurus, Echinodon, Emausaurus, Eousdryosaurus, Goyocephale, Homalocephale, Isaberrysaura, Kangnasaurus, Kulindadromeus, Laquintasaura, Liaoceratops, Lycorhinus, Mo. suessi, Mo. vorosi, Morrosaurus, Pachycephalosaurus, Prenocephale, Ps. major, Rh. priscus, Scelidosaurus, Stegoceras, Stenopelix, Th. assiniboensis, Tianyulong</i>
Pectoral girdle & forelimb	<i>Abriktosaurus, Archaeoceratops, Chaoyangsaurus, Echinodon, Emausaurus, Eousdryosaurus, Homalocephale, Isaberrysaura, Kangnasaurus, Laquintasaura, Liaoceratops, Lycorhinus, Macrogyphosaurus, Mo. suessi, Morrosaurus, Pachycephalosaurus, Prenocephale, Ps. major, Rh. priscus, Rh. sp., Stenopelix, Th. assiniboensis, Valdosaurus, Zephyrosaurus</i>
Pelvic girdle & hind limb	<i>Chaoyangsaurus, Echinodon, Emausaurus, Goyocephale, Isaberrysaura, Liaoceratops, Lycorhinus, Macrogyphosaurus, Mahuidacursor, Mo. suessi, Pachycephalosaurus, Ps. major, Zephyrosaurus</i>



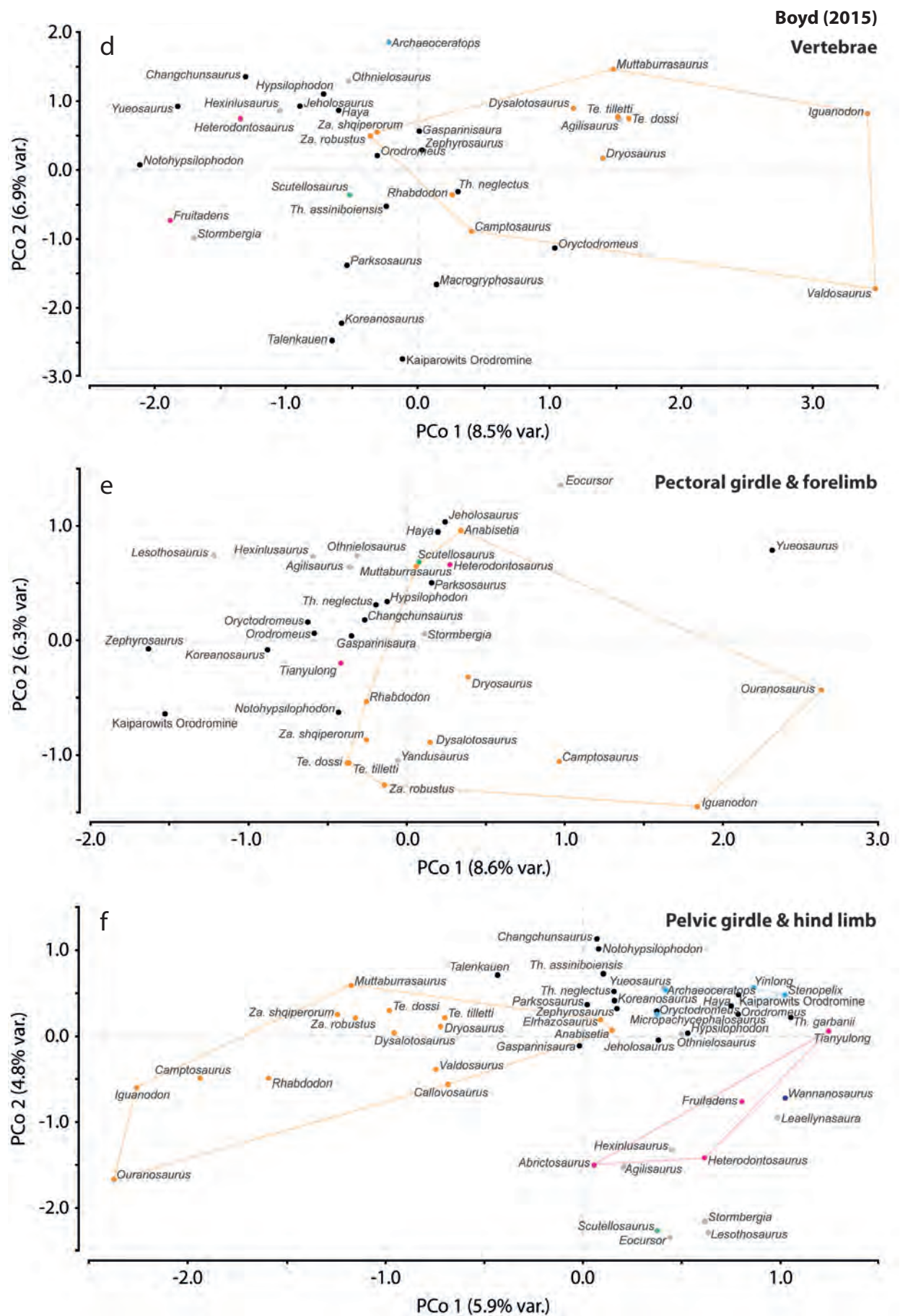
A3.2. Variance across all principal component axes for distances matrices computed from Boyd (2015), Han *et al.* (2018) and Dieudonné *et al.* (2021). Key: all partitions (green); skull (orange); dentition (purple); vertebrae (pink); pectoral girdle and forelimb (green); pelvic girdle and hind limb (yellow).

Boyd (2015)

All partitions

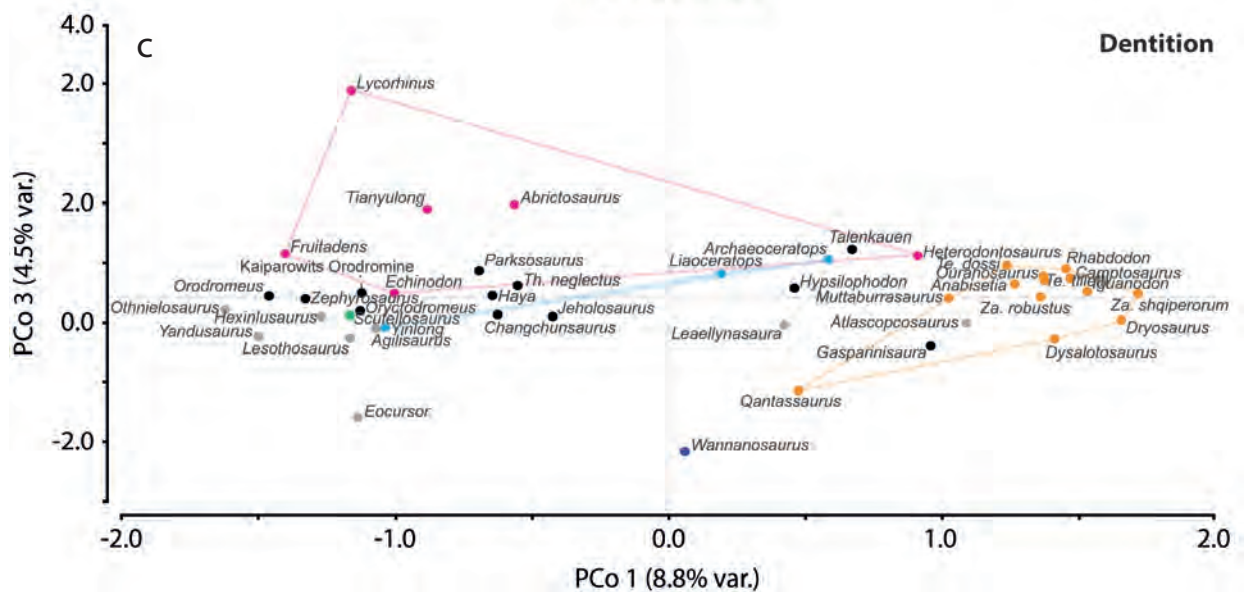
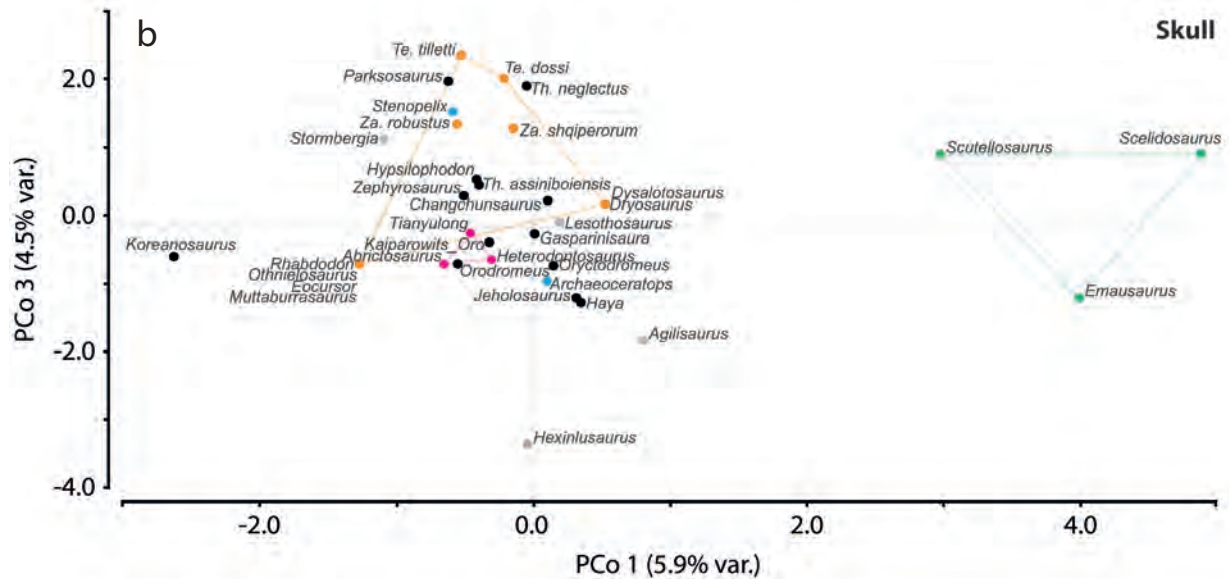
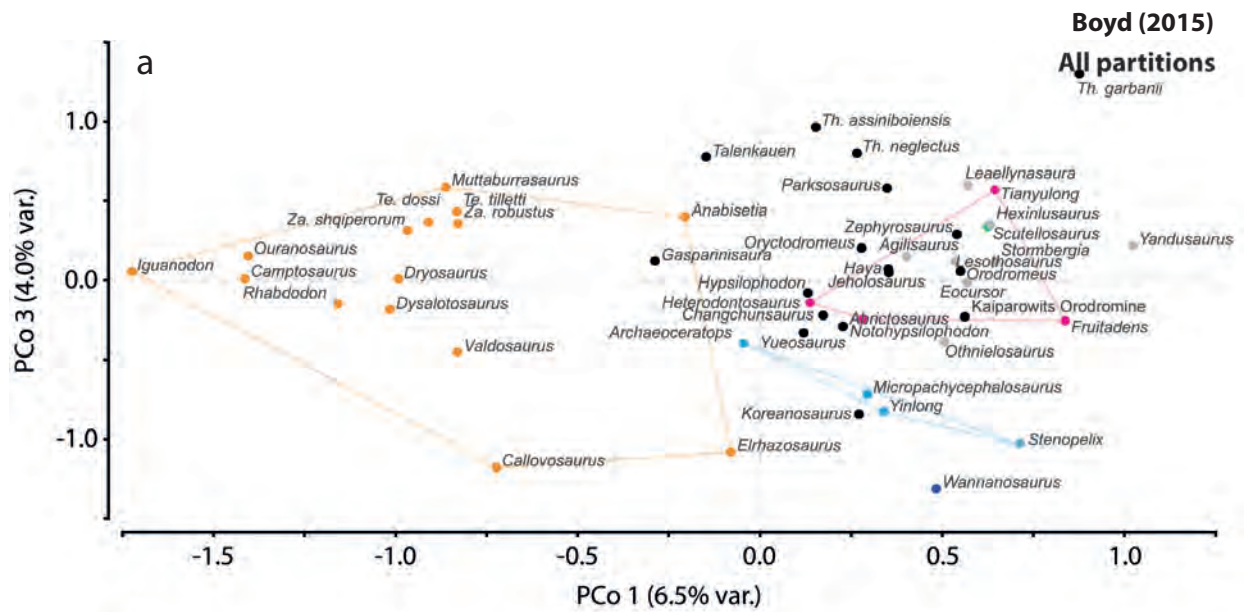


A3.3 (cont. on following page)



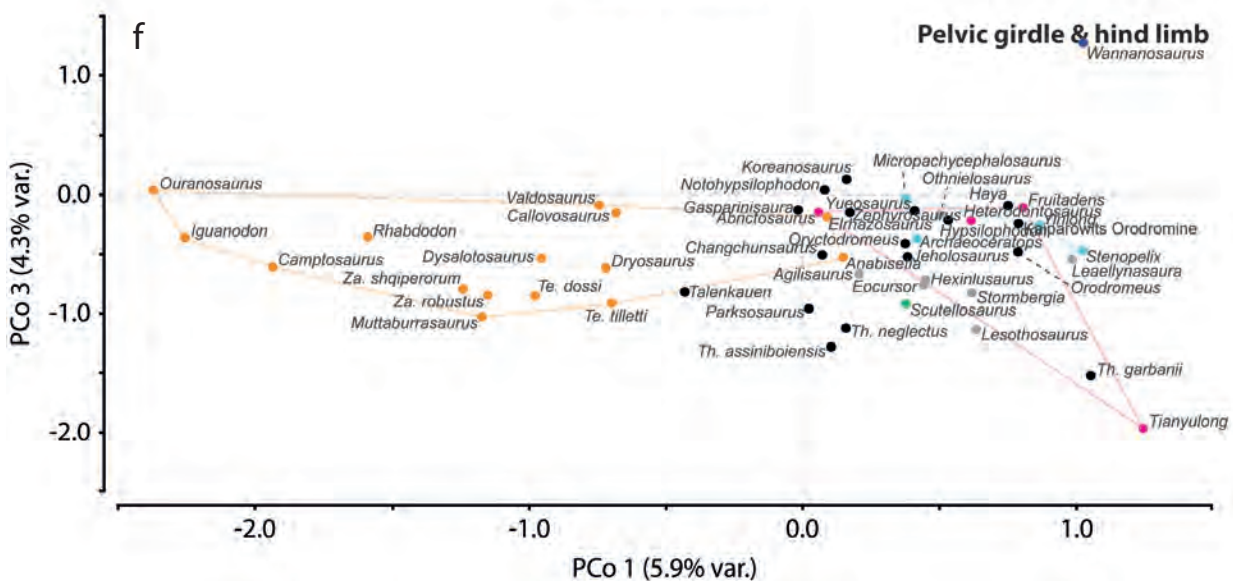
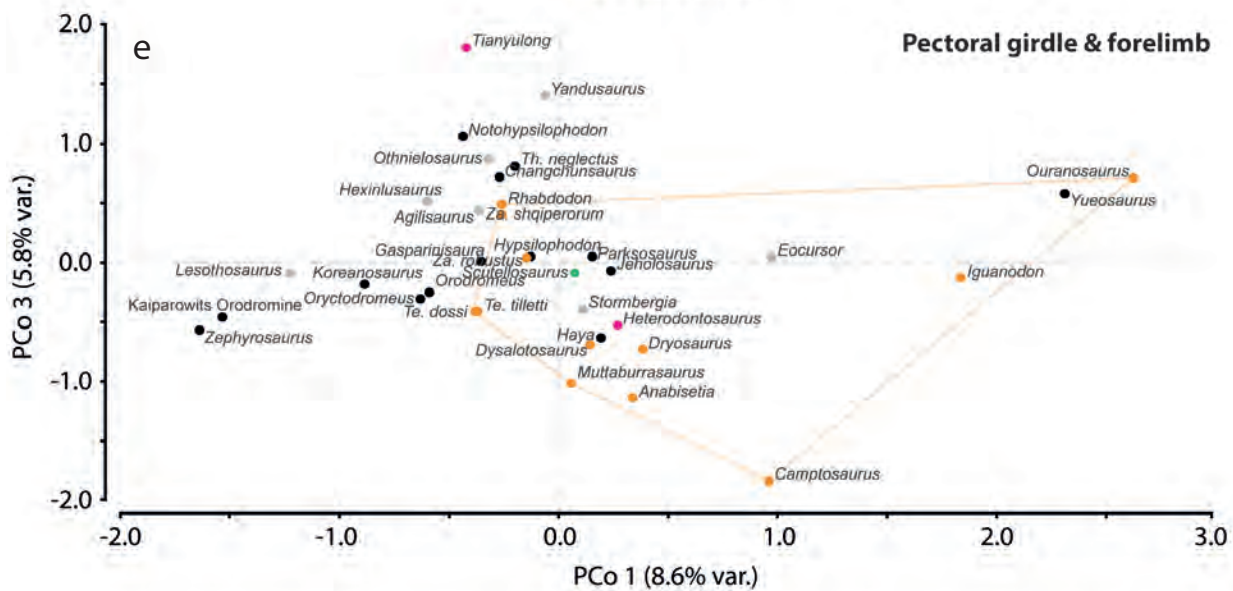
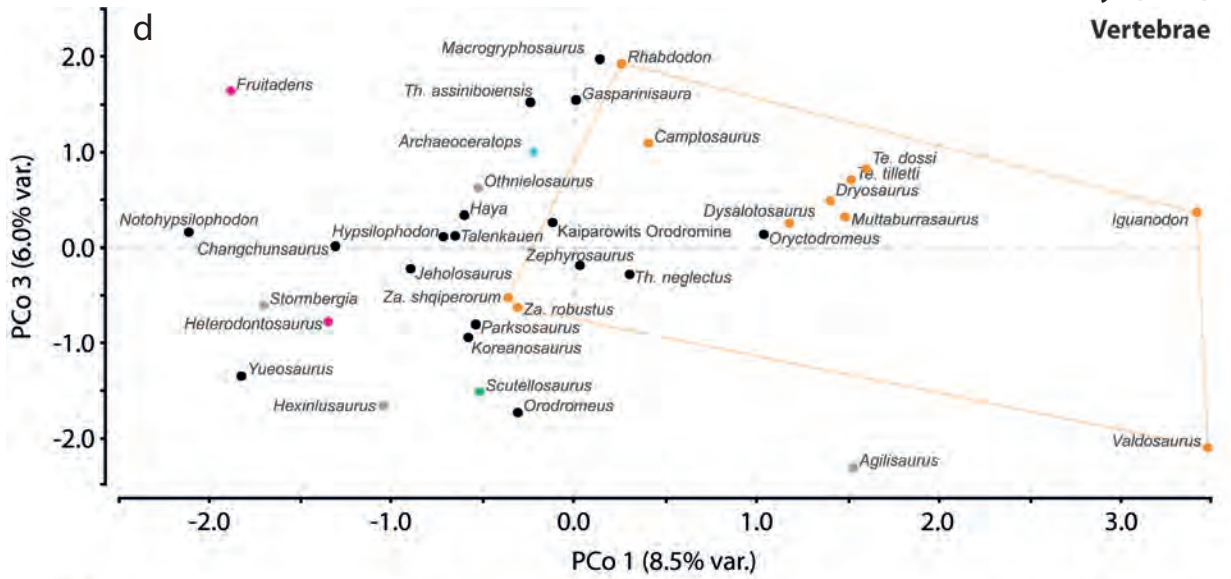
A3.3 (caption on following page)

A3.3. Morphospace plot (PCo 1 vs. PCo 2) showing the results of principal coordinate analyses derived from the morphological matrix by Boyd (2015), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Za.*, *Zalmoxes*.



A3.4 (cont. on following page)

Vertebrae



A3.4 (caption on following page)

A3.4. Morphospace plot (PCo 1 vs. PCo 3) showing the results of principal coordinate analyses derived from the morphological matrix by Boyd (2015), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Za.*, *Zalmoxes*.

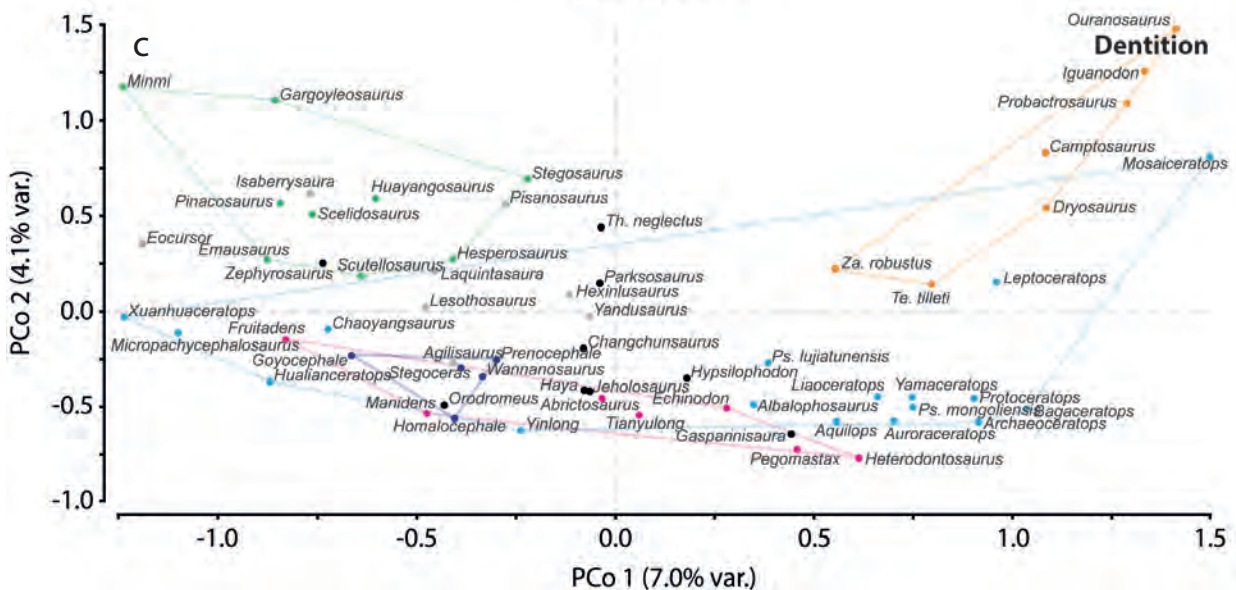
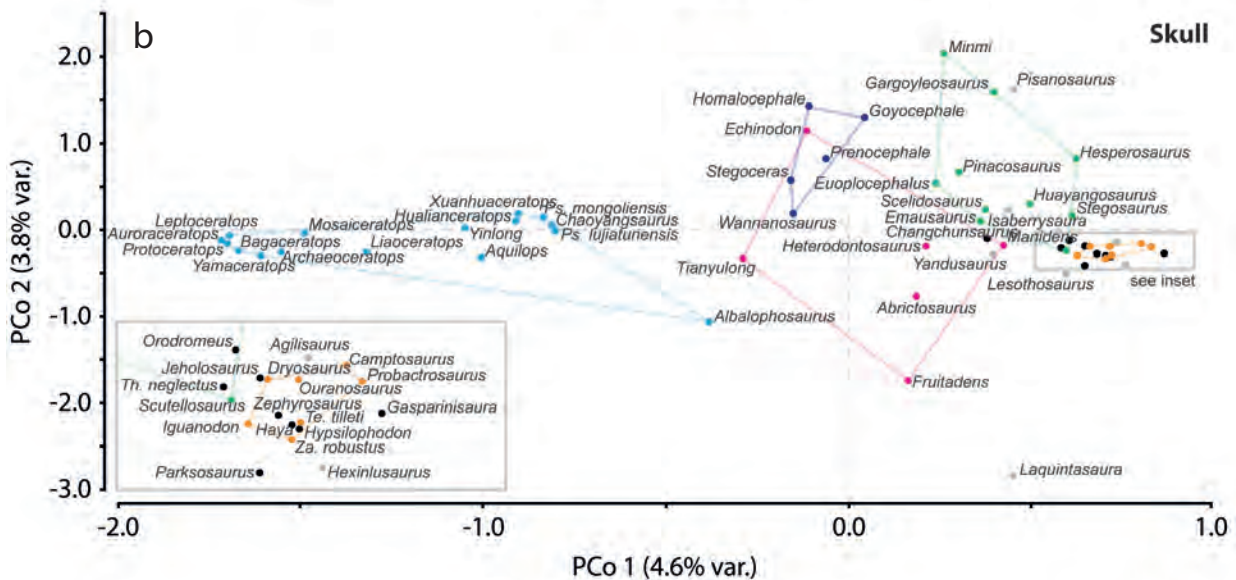
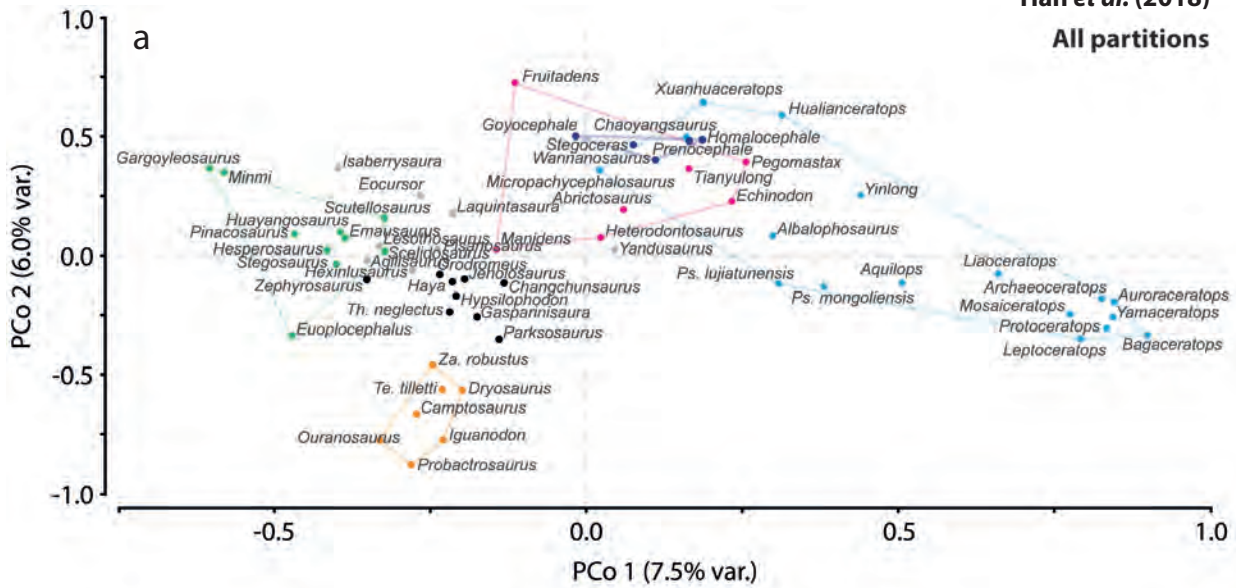
A3.5. Results of one-way PERMANOVA test on distance scores derived from partitioned versions of the Boyd (2015) matrix between phylogenetic groupings using all axes. Partitions: **a**, all partitions; **b**, skull; **c**, dentition; **d**, vertebrae; **e**, pectoral girdle & forelimb; **f**, pelvic girdle & hind limb. Abbreviations: EDO/EDN, early-diverging ornithischian/neornithischian; THY, thyreophoran; T/EDO, thescelosaurid/early-diverging ornithopod; CER, ceratopsian; PAC, pachycephalosaurian; IGU, iguanodontian. Results in bold italics show statistical significance at $p = 0.05$.

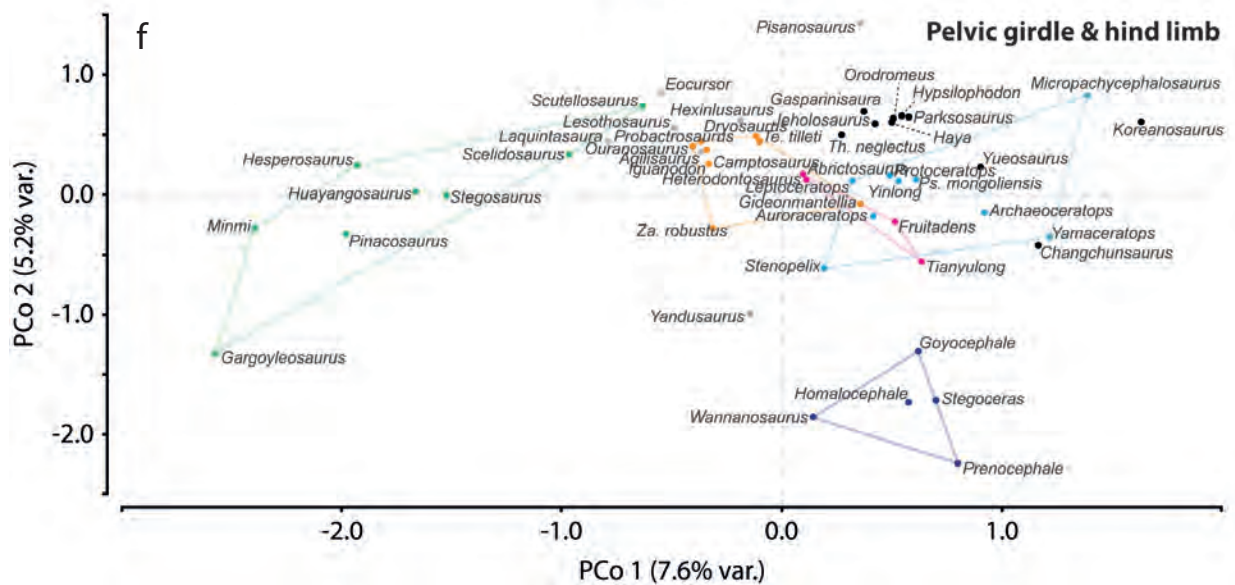
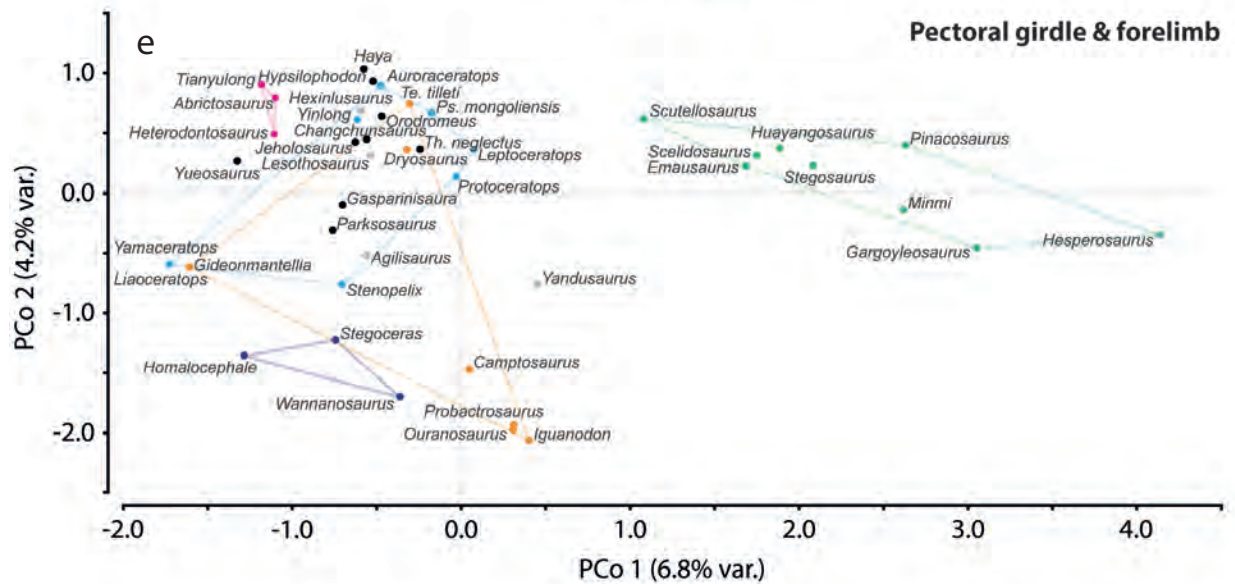
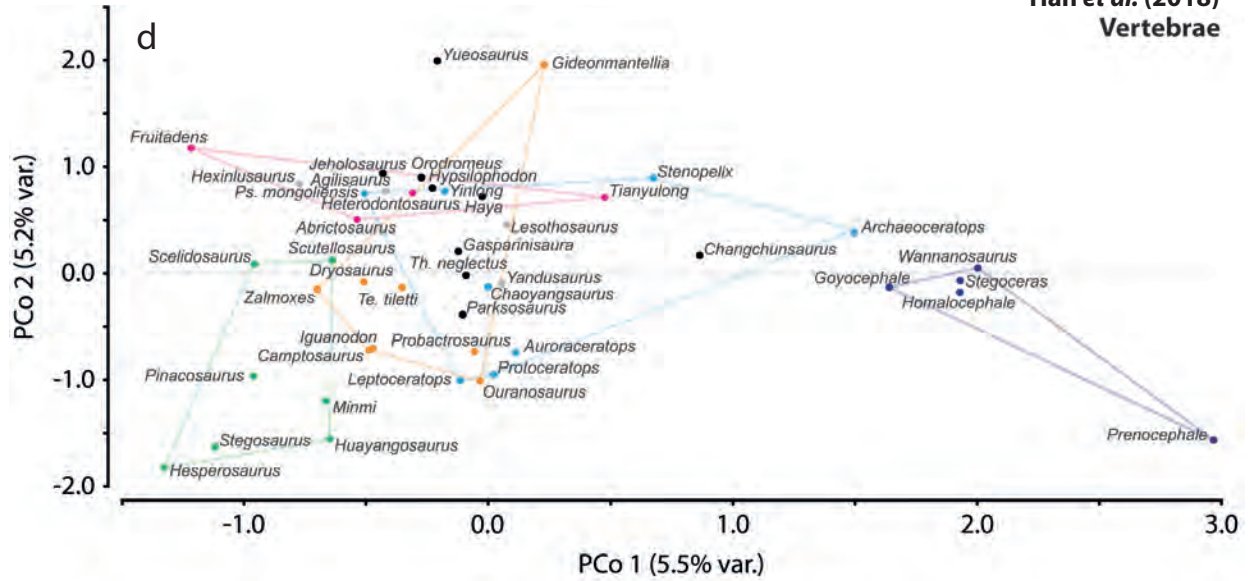
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0187	0.1964	0.0019	0.0591	0.3965	0.0001	a) all partitions
EDO/EDN		0.6598	0.0001	0.0023	0.4353	0.0001	
THY			0.0559	0.2003	1	0.0587	
T/EDO				0.1651	0.0574	0.0001	
CER					0.6032	0.0019	
PAC						0.0606	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0234	0.0951	0.002	0.1005	N/A	0.006	b) skull
EDO/EDN		0.0115	0.7474	0.2593	N/A	0.0649	
THY			0.0024	0.1004	N/A	0.0049	
T/EDO				0.0604	N/A	0.003	
CER					N/A	0.1139	
PAC						N/A	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0015	0.2857	0.0002	0.0353	0.1398	0.0001	c) dentition
EDO/EDN		0.3376	0.0536	0.0173	0.5594	0.0001	
THY			0.0887	0.196	1	0.0724	
T/EDO				0.0892	0.0881	0.0001	
CER					0.2028	0.0011	
PAC						0.0729	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.3366	0.3301	0.4231	0.666	N/A	0.0232	d) vertebrae
EDO/EDN		0.8046	0.2766	1	N/A	0.1672	
THY			0.4637	1	N/A	0.0242	
T/EDO				0.6613	N/A	0.0001	
CER					N/A	0.4115	
PAC						N/A	

A3.5 (cont. on following page)

A3.5. cont.

	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.1356	0.663	0.8283	N/A	N/A	0.0874	e) pectoral girdle & forelimb
EDO/EDN		0.2483	0.802	N/A	N/A	0.005	
THY			0.3309	N/A	N/A	0.235	
T/EDO				N/A	N/A	0.0048	
CER					N/A	N/A	
PAC						N/A	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.2686	0.2012	0.0027	0.2947	0.3991	0.0005	f) pelvic girdle & hind limb
EDO/EDN		1	0.0001	0.0064	1	0.0001	
THY			0.0558	0.2009	1	0.0619	
T/EDO				0.1267	0.7146	0.0001	
CER					1	0.0028	
PAC						0.0613	

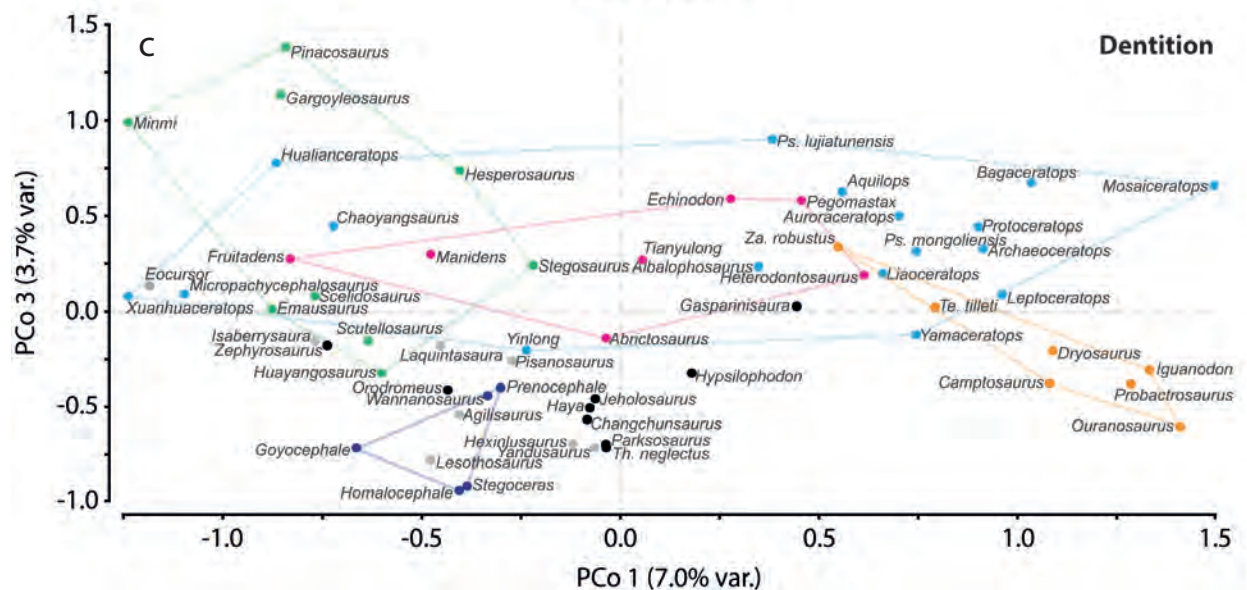
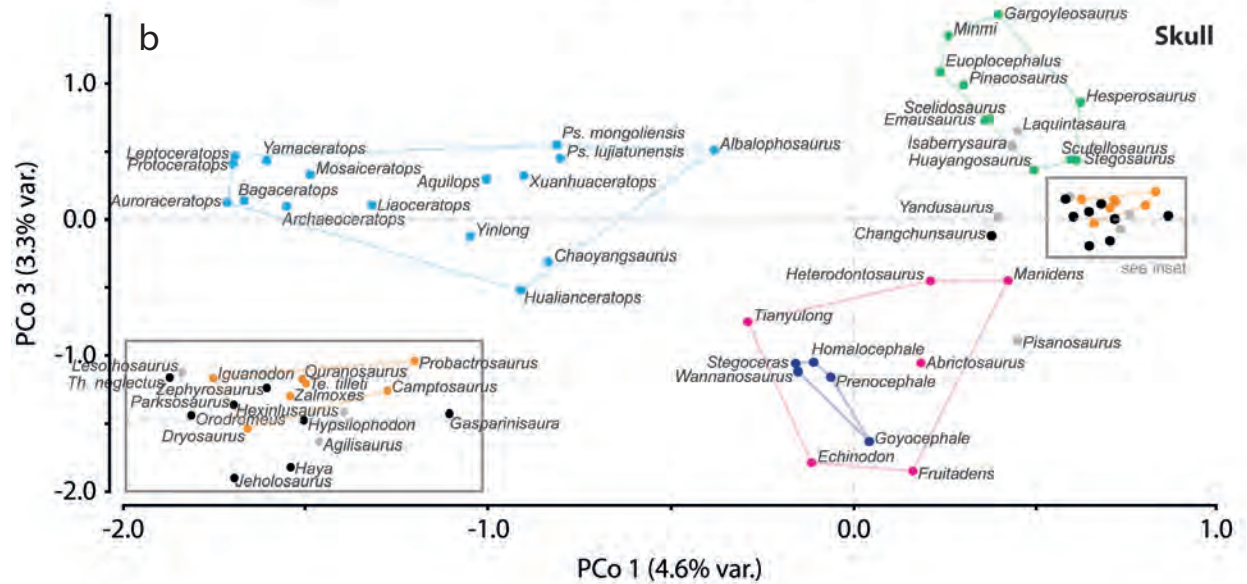
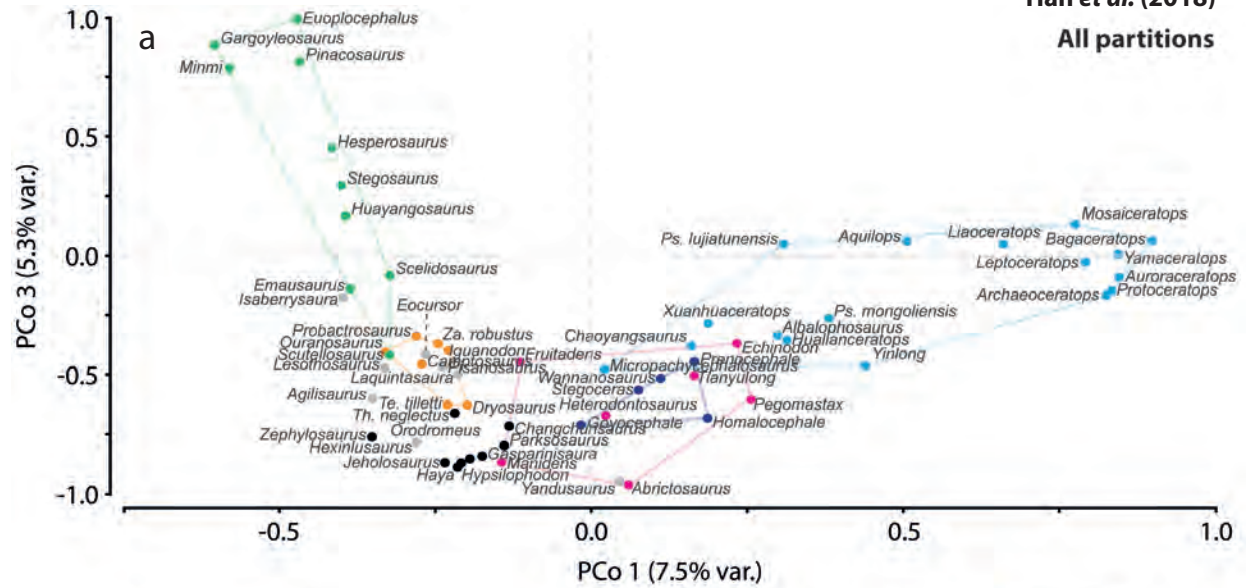




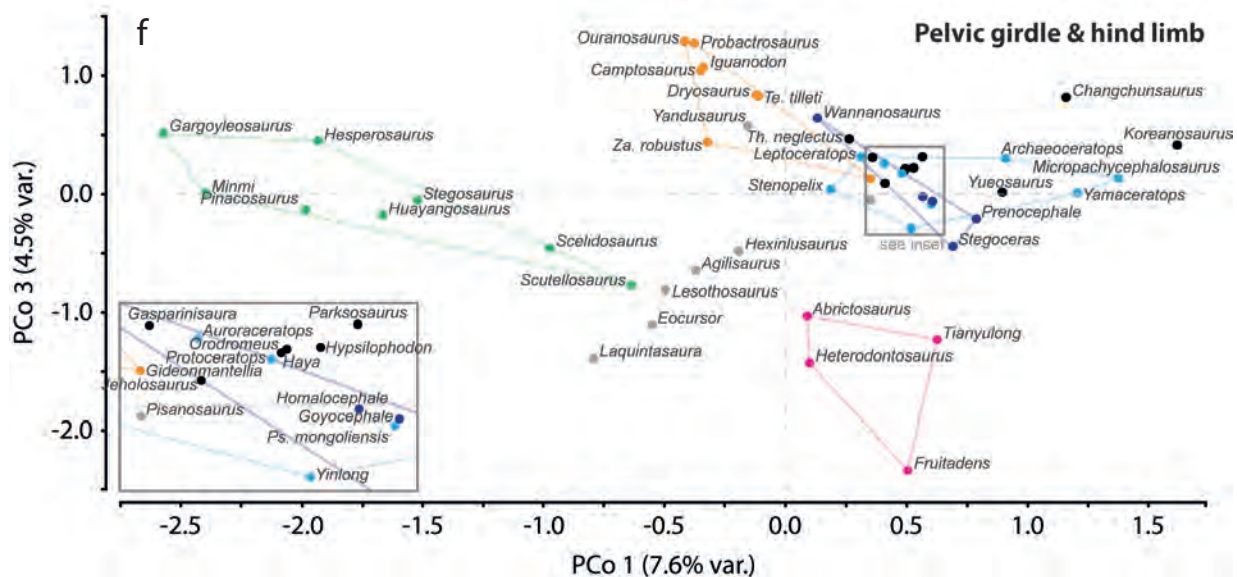
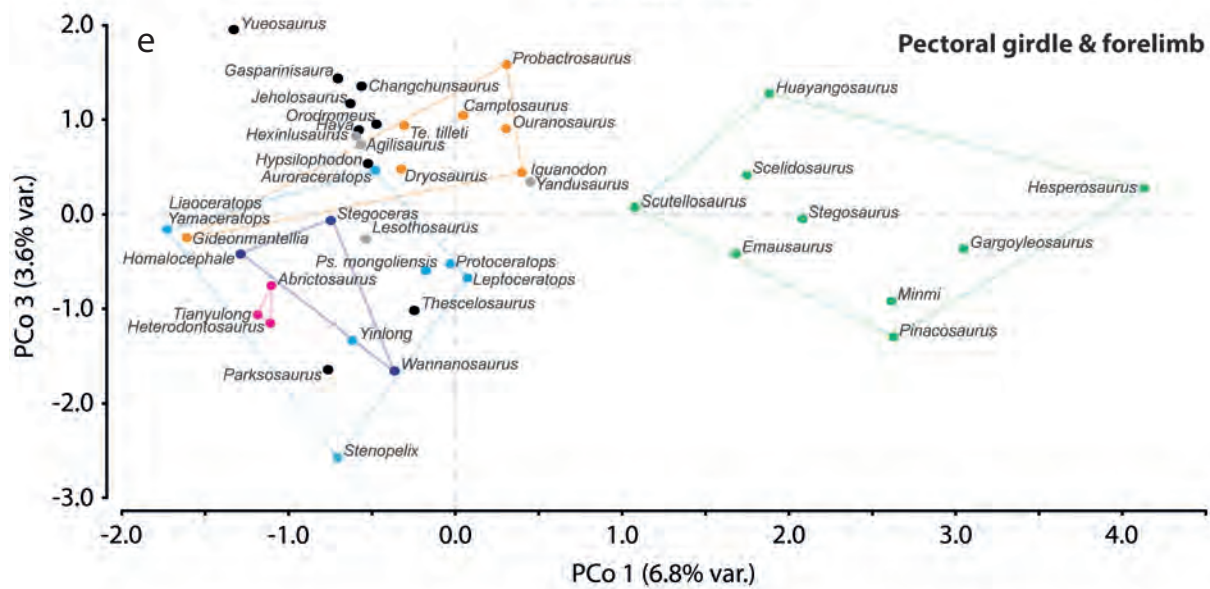
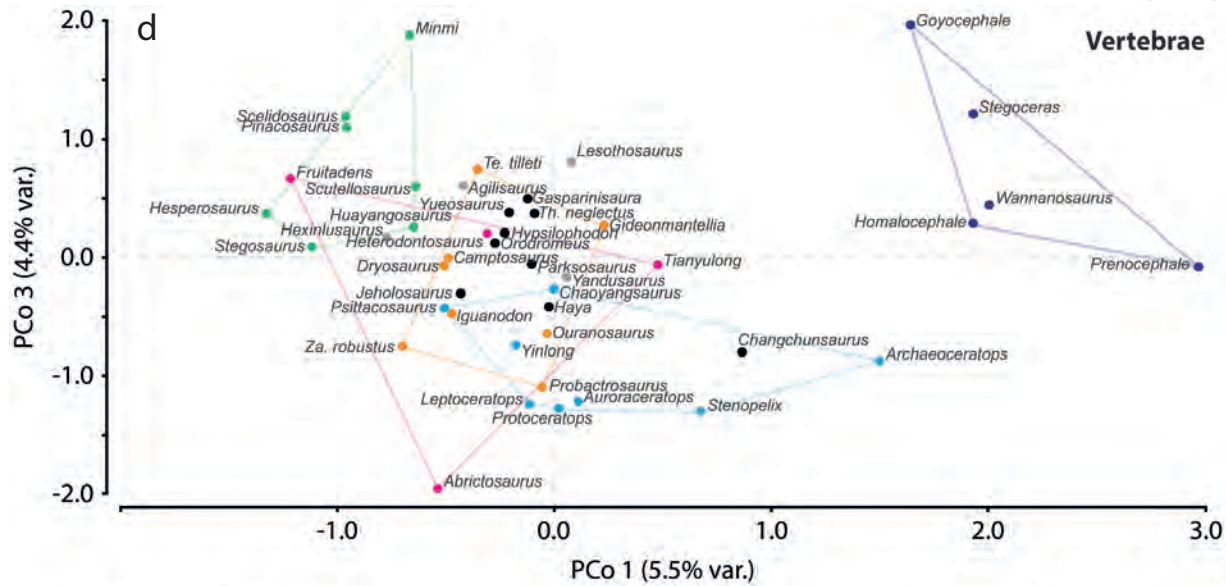
A3.6 (caption on following page)

A3.6. Morphospace plot (PCo 1 vs. PCo 2) showing the results of principal coordinate analyses derived from the morphological matrix by Han *et al.* (2018), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Ps.*, *Psittacosaurus*; *Za.*, *Zalmoxes*.

All partitions



A3.7 (cont. on following page)



A3.7 (caption on following page)

A3.7. Morphospace plot (PCo 1 vs. PCo 3) showing the results of principal coordinate analyses derived from the morphological matrix by Han *et al.* (2018), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Ps.*, *Psittacosaurus*; *Za.*, *Zalmoxes*.

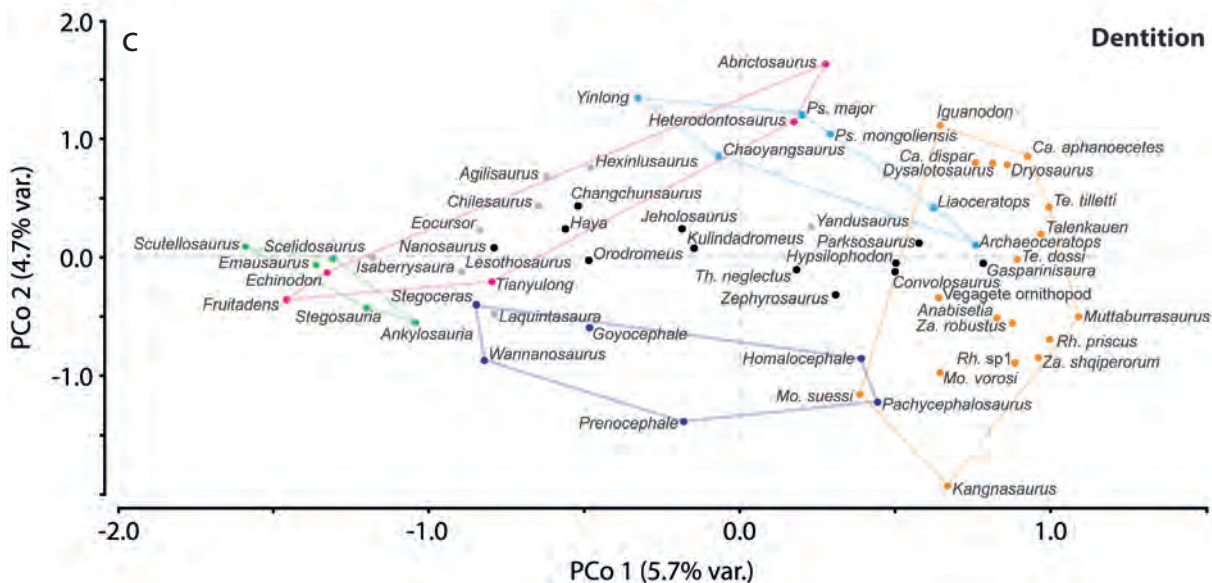
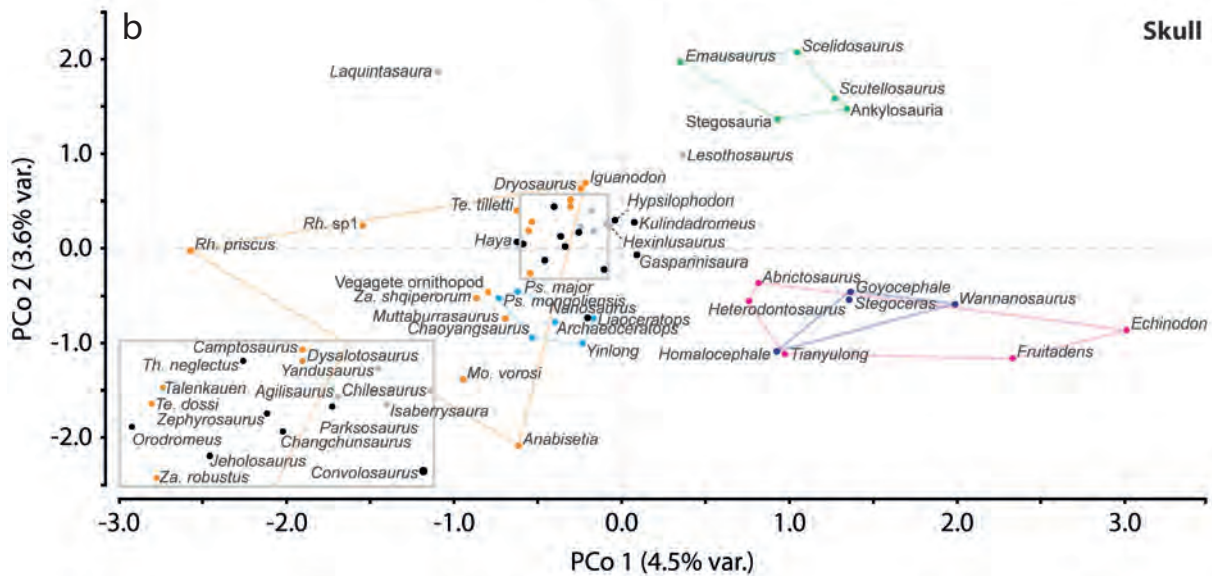
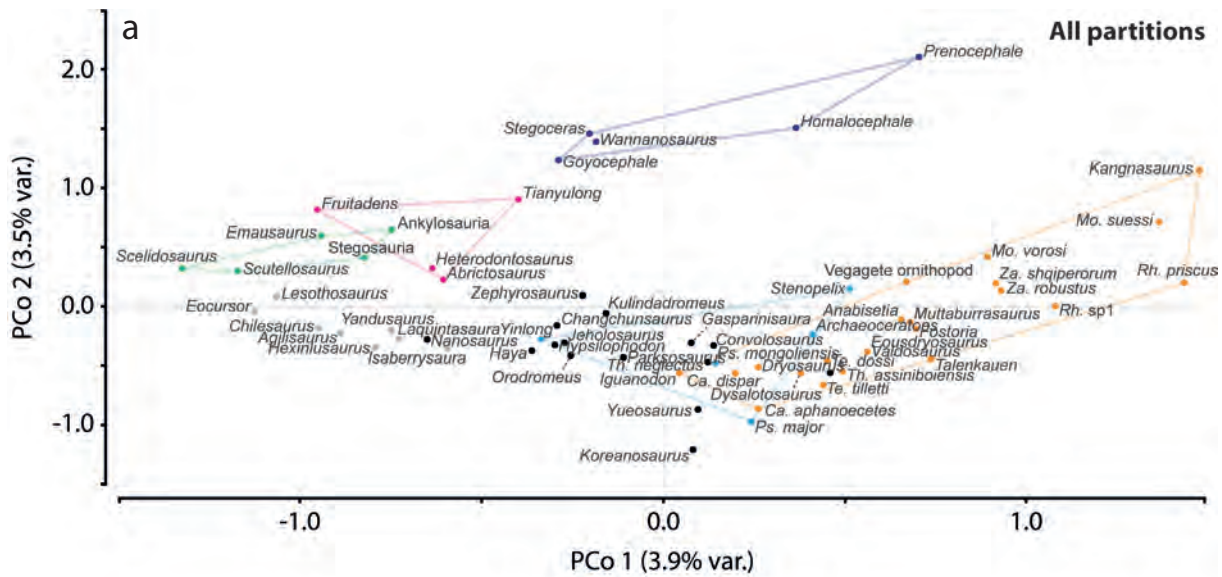
A3.8. Results of one-way PERMANOVA test on distance scores derived from partitioned versions of the Han *et al.* (2018) matrix between phylogenetic groupings using all axes. Partitions: **a**, all partitions; **b**, skull; **c**, dentition; **d**, vertebrae; **e**, pectoral girdle & forelimb; **f**, pelvic girdle & hind limb. Abbreviations: EDO/EDN, early-diverging ornithischian/neornithischian; THY, thyreophoran; T/EDO, thescelosaurid/early-diverging ornithopod; CER, ceratopsian; PAC, pachycephalosaurian; IGU, iguanodontian. Results in **bold italics** show statistical significance at $p = 0.05$.

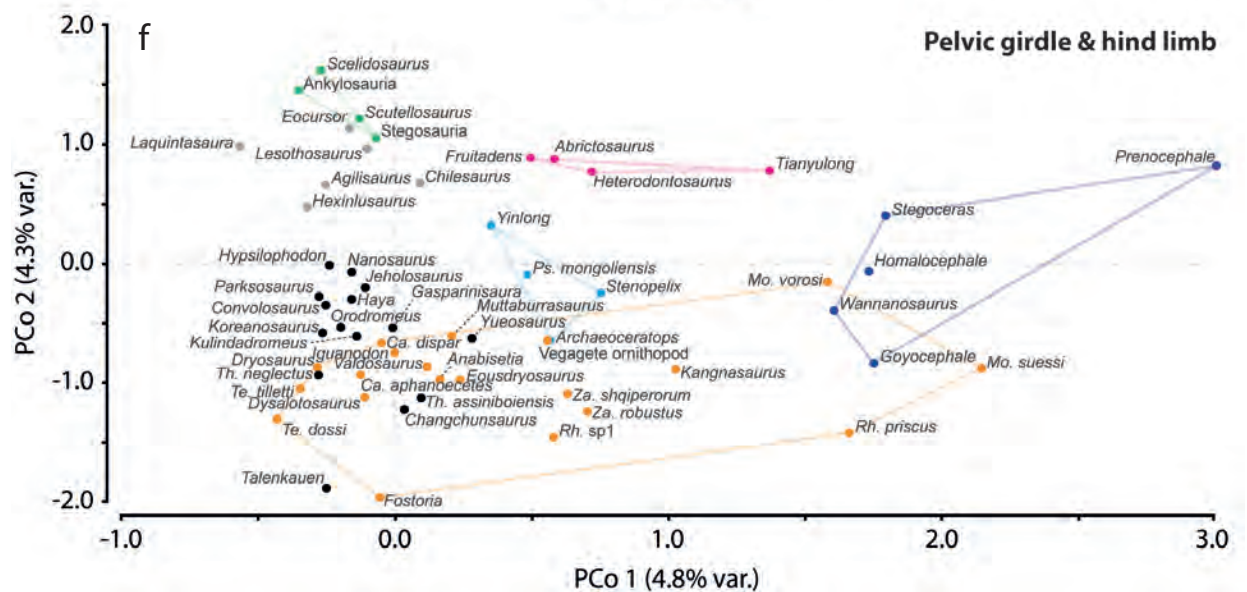
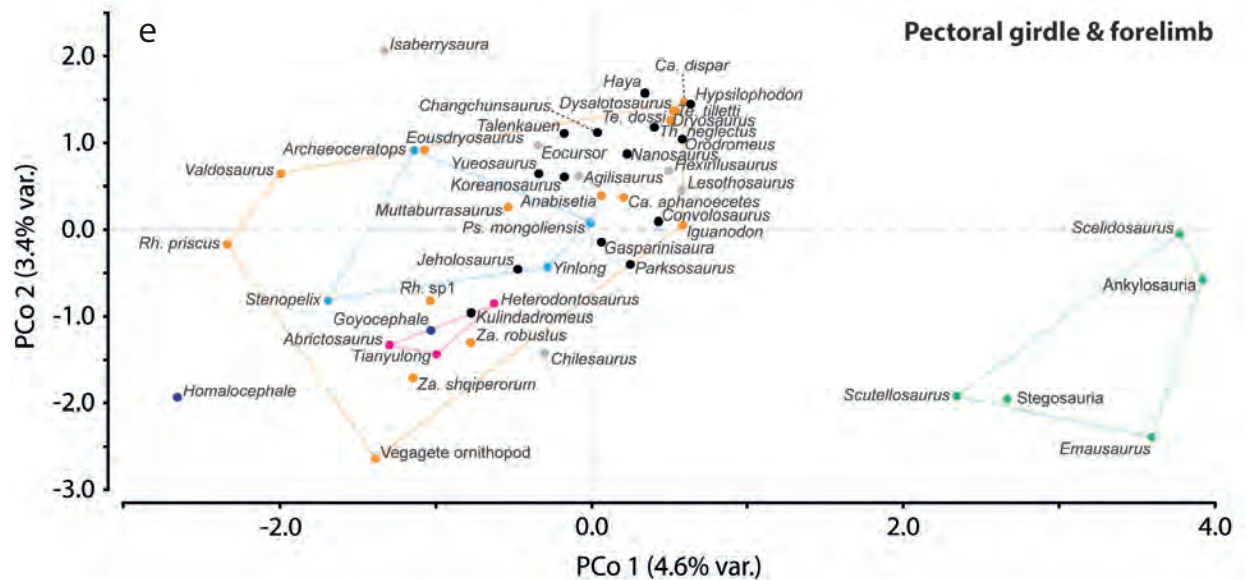
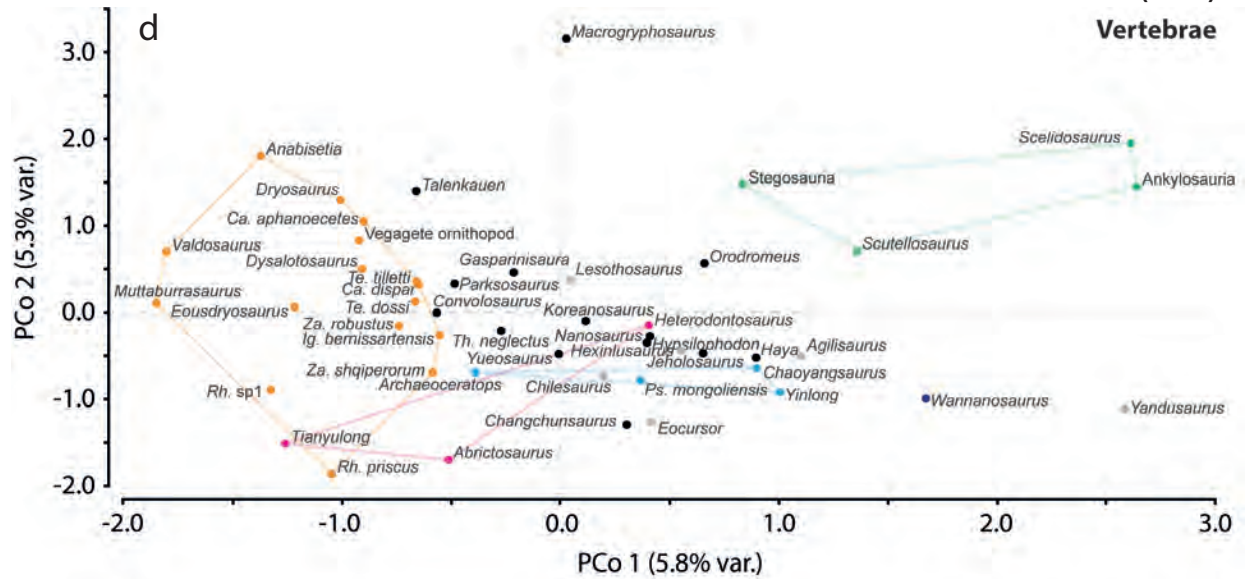
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0002	0.0001	0.0001	0.0001	0.0007	0.0005	a) all partitions
EDO/EDN		0.0009	0.0003	0.0001	0.0009	0.0001	
THY			0.0001	0.0001	0.0005	0.0001	
T/EDO				0.0001	0.0007	0.0002	
CER					0.0001	0.0001	
PAC						0.0014	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0169	0.0002	0.0003	0.0001	0.0017	0.0008	b) skull
EDO/EDN		0.0126	0.0936	0.0002	0.0097	0.0041	
THY			0.0001	0.0001	0.0006	0.0004	
T/EDO				0.0001	0.0005	0.0002	
CER					0.0001	0.0001	
PAC						0.0021	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0004	0.0003	0.0001	0.0009	0.0018	0.0004	c) dentition
EDO/EDN		0.028	0.0328	0.0007	0.0008	0.0002	
THY			0.0002	0.0002	0.0007	0.0001	
T/EDO				0.0017	0.0002	0.0002	
CER					0.0004	0.0001	
PAC						0.0008	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0284	0.0025	0.1349	0.1925	0.0073	0.0197	d) vertebrae
EDO/EDN		0.0131	0.2677	0.0218	0.009	0.0276	
THY			0.0001	0.0007	0.0004	0.0001	
T/EDO				0.0107	0.0003	0.0006	
CER					0.0014	0.0007	
PAC						0.0008	

A3.8 (cont. on following page)

A3.8. cont.

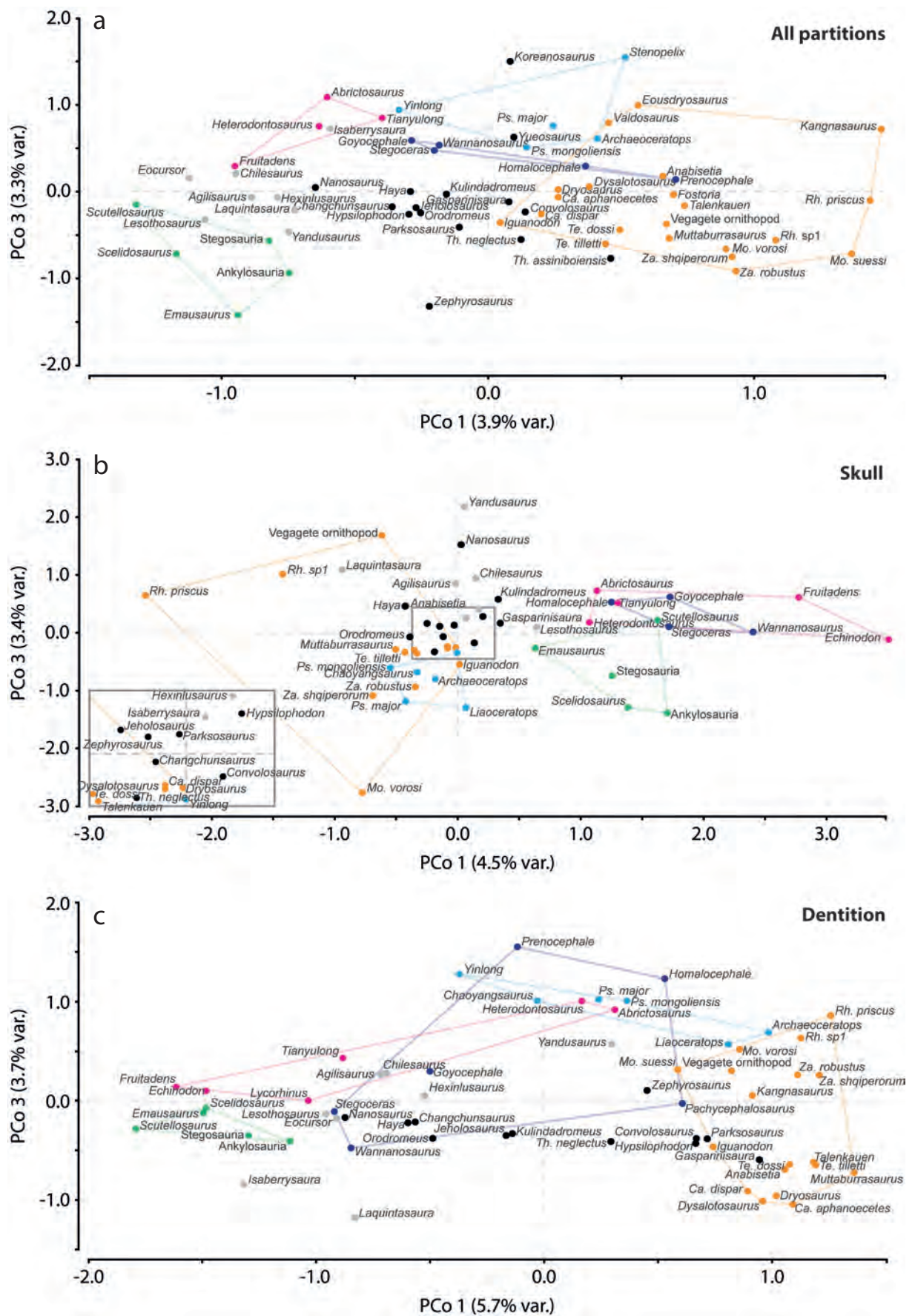
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0289	0.0044	0.0178	0.0045	0.0966	0.0071	e) pectoral girdle & forelimb
EDO/EDN		0.0019	0.1389	0.0529	0.1647	0.0802	
THY			0.0001	0.0001	0.0042	0.0003	
T/EDO				0.0044	0.0044	0.0303	
CER					0.0088	0.0069	
PAC						0.0464	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0032	0.0019	0.0014	0.002	0.0091	0.0013	e) pelvic girdle & hind limb
EDO/EDN		0.0022	0.0001	0.0007	0.0015	0.0003	
THY			0.0001	0.0001	0.0006	0.0004	
T/EDO				0.0003	0.0003	0.0001	
CER					0.0006	0.0003	
PAC						0.0014	



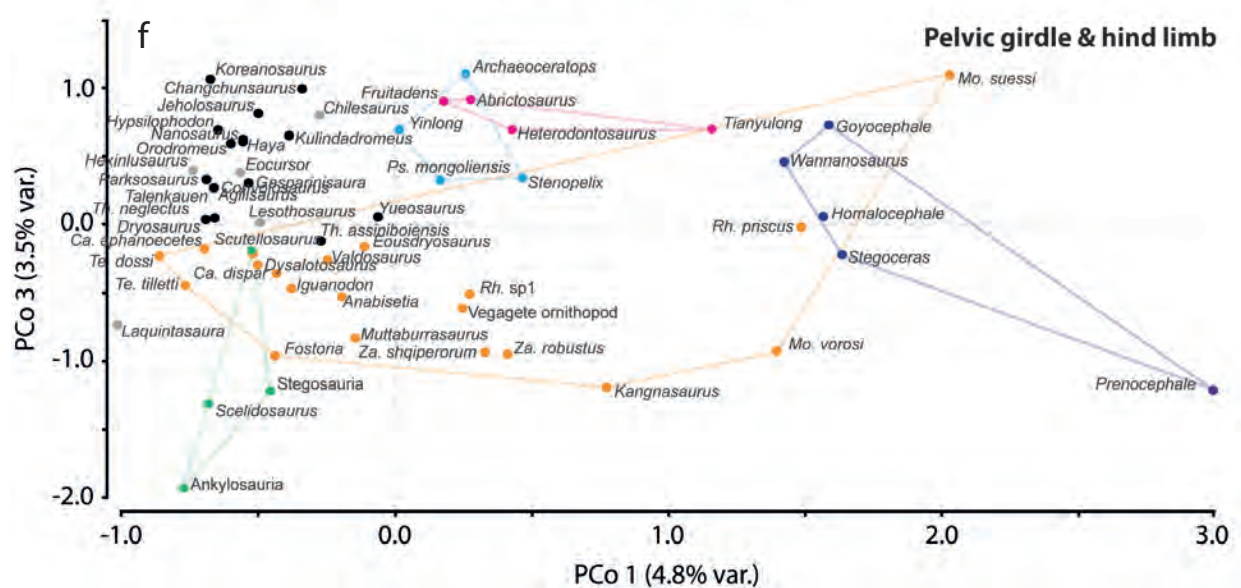
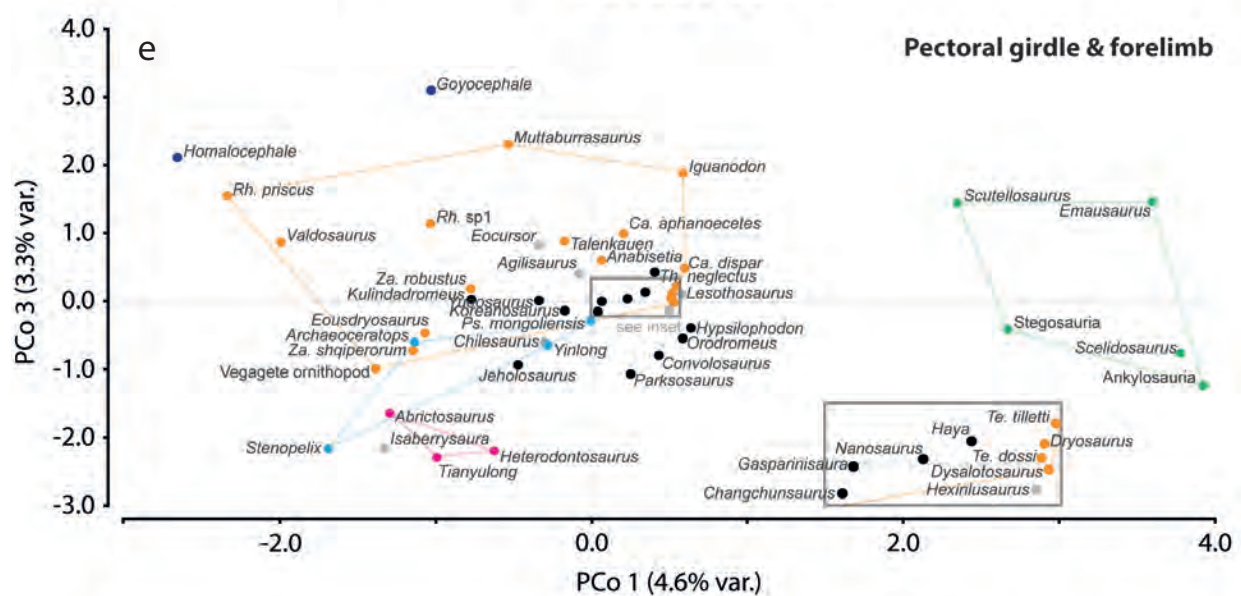
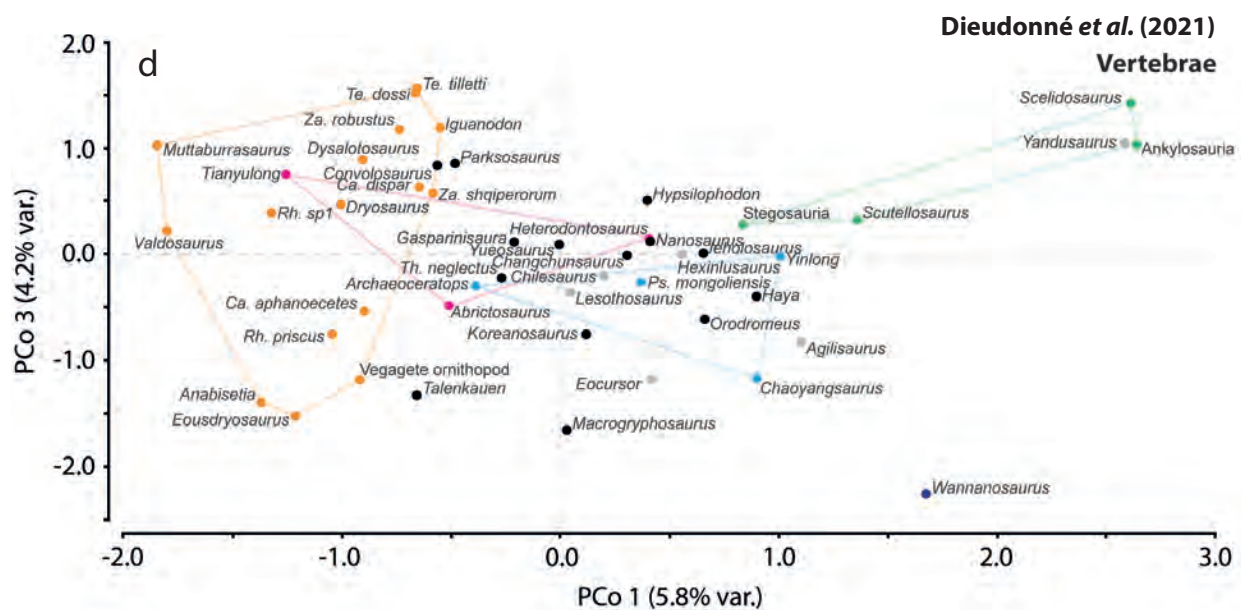


A3.9 (caption on following page)

A3.9. Morphospace plot (PCo 1 vs. PCo 2) showing the results of principal coordinate analyses derived from the morphological matrix by Dieudonné *et al.* (2021), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Ca.*, *Camptosaurus*; *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Mo.*, *Mochlodon*; *Ps.*, *Psittacosaurus*; *Rh.*, *Rhabdodon*; *Za.*, *Zalmoxes*.



A3.10 (cont. on following page)



A3.10 (caption on following page)

A3.10. Morphospace plot (PCo 1 vs. PCo 3) showing the results of principal coordinate analyses derived from the morphological matrix by Dieudonné *et al.* (2021), using: **a**, all characters; **b**, skull characters; **c**, dental characters; **d**, vertebrae characters; **e**, pectoral girdle and forelimb characters; **f**, pelvic girdle and hind limb characters. Colour key: ceratopsian (blue); EDO/EDN, early-diverging ornithischian/neornithischian (grey); iguanodontian (orange); heterodontosaurid (pink); pachycephalosaurian (dark blue); T/EDO, thescelosaurid/early-diverging ornithopod (black); thyreophoran (green). Abbreviations: *Ca.*, *Camptosaurus*; *Te.*, *Tenontosaurus*; *Th.*, *Thescelosaurus*; *Mo.*, *Mochlodon*; *Ps.*, *Psittacosaurus*; *Rh.*, *Rhabdodon*; *Za.*, *Zalmoxes*.

A3.11. Results of one-way PERMANOVA test on distance scores derived from partitioned versions of the Dieudonné *et al.* (2021) matrix between phylogenetic groupings using all axes. Partitions: **a**, all partitions; **b**, skull; **c**, dentition; **d**, vertebrae; **e**, pectoral girdle & forelimb; **f**, pelvic girdle & hind limb. Abbreviations: EDO/EDN, early-diverging ornithischian/neornithischian; THY, thyreophoran; T/EDO, thescelosaurid/early-diverging ornithopod; CER, ceratopsian; PAC, pachycephalosaurian; IGU, iguanodontian. Results in bold italics show statistical significance at $p = 0.05$.

	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.002	0.0079	0.0003	0.0083	0.0089	0.0004	a) all partitions
EDO/EDN		0.0028	0.0001	0.0005	0.0009	0.0001	
THY			0.0001	0.0081	0.0078	0.0002	
T/EDO				0.0006	0.0001	0.0001	
CER					0.0076	0.0001	
PAC						0.0001	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0015	0.0097	0.0002	0.0022	0.0578	0.0002	b) skull
EDO/EDN		0.0177	0.0383	0.0009	0.0026	0.0008	
THY			0.0002	0.0023	0.0071	0.0001	
T/EDO				0.0002	0.0002	0.0003	
CER					0.0038	0.0002	
PAC						0.0003	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0461	0.0063	0.0001	0.0049	0.0096	0.0001	c) dentition
EDO/EDN		0.0034	0.0055	0.0005	0.0011	0.0001	
THY			0.0003	0.0025	0.0049	0.0001	
T/EDO				0.0001	0.0001	0.0011	
CER					0.0022	0.0002	
PAC						0.002	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.3691	0.0289	0.3801	0.2509	0.507	0.5867	d) vertebrae
EDO/EDN		0.0031	0.0071	0.0059	0.3859	0.0001	
THY			0.0003	0.0315	0.1977	0.0005	
T/EDO				0.028	0.3365	0.0004	
CER					1	0.0046	
PAC						0.0611	

A3.11 (cont. on following page)

A3.11. cont.

	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.0125	0.0176	0.0014	0.0283	0.0961	0.0018	e) pectoral girdle & forelimb
EDO/EDN		0.0016	0.6655	0.0783	0.0359	0.059	
THY			0.0001	0.0086	0.0495	0.0002	
T/EDO				0.0957	0.0065	0.289	
CER					0.0663	0.0179	
PAC						0.0434	
	EDO/EDN	THY	T/EDO	CER	PAC	IGU	
HET	0.115	0.3217	0.5062	0.1743	0.3433	0.0165	e) pelvic girdle & hind limb
EDO/EDN		0.7216	0.1962	0.0502	0.0412	0.0008	
THY			0.3043	0.1728	0.2945	0.0239	
T/EDO				0.3291	0.0396	0.2567	
CER					0.0456	0.0941	
PAC						0.0047	

A4.1. Limb bone measurements of *Hypsilophodon foxii* used for the linear regression in Chapter 4 (section 4.2.4): limb bone length; proximal end width; distal end width; and the length from the proximal tip to the distal base of the fourth trochanter. Dashes indicate unobservable or inapplicable measurements.

Specimen no.	Element	Limb bone Length (mm)	Proximal end width (mm)	Distal end width (mm)	Length to fourth trochanter (mm)
NHMUK PV R5830m	Femur	100.79	28.58	24.9	31.13
NHMUK PV R39460	Femur	142.43	42.69	34.5	68.77
NHMUK PV R5829	Femur	190	53	50	93
IWCMS 5191	Femur	178	40.42	38.94	-
NHMUK PV R192a	Femur	179	35.79	39.77	77.99
NHMUK PV R196	Femur	164	-	30.16	-
NHMUK PV R752	Tibia	168	30.58	33.93	-
NHMUK PV R199	Tibia	227.34	52.17	-	-
NHMUK PV R5830m	Tibia	114.04	25.59	25.51	-
IWCMS 6526	Tibia	79.97	11.6	14.67	-

A5.1. Parameters used when μ CT scanning the partial braincase and left dentary of NHMUK PV R 36760. Specimens were scanned at the Natural History Museum (London; NHMUK) using a Nikon Metrology XT H 225 ST.

Specimen	Voltage (kV)	Current (μ A)	Power (W)	Source filter	Number of projections	Frame per images	Exposure time (sec)
left partial braincase	155	129	19.995	1.0 mm Cop- per	3723	4	354
left dentary	160	180	28.8	1.0 mm Cop- per	3172	4	500