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Submitted for examination for the degree of Doctor of Philosophy

I, Omar Rafael Regalado Fernandez, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis
Reassessment of the evolutionary history of the Late Triassic and Early Jurassic sauropodomorph dinosaurs through comparative cladistics and the supermatrix approach

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Abstract

Non-sauropod sauropodomorphs, also known as 'basal sauropodomorphs' or 'prosauropods', have been thoroughly studied in recent years. Several hypotheses on the interrelationships within this group have been proposed, ranging from a complete paraphyly, where the group represents a grade from basal saurischians to Sauropoda, to a group on its own. The grade-like hypothesis is the most accepted; however, the relationships between the different taxa are not consistent amongst the proposed scenarios. These inconsistencies have been attributed to missing data and unstable (i.e., poorly preserved) taxa, nevertheless, an extensive comparative cladistic analysis has found that these inconsistencies instead come from the character coding and character selection, plus the strategies on merging data sets.

Furthermore, a detailed character analysis using information theory and mathematical topology as an approach for character delineation is explored here to operationalise characters and reduce the potential impact of missing data. This analysis also produced the largest and most comprehensive matrix after the reassessment and operationalisation of every character applied to this group far. Additionally, partition analyses performed on this data set have found consistencies in the interrelationships within non-sauropod Sauropodomorpha and has found strong support for smaller clades such as Plateosauridae, Riojasauridae, Anchisauridae, Massospondylinae and Lufengosarinae. The results of these analyses also highlight a different scenario on how quadrupedality evolved, independently originating twice within the group, and provide a better framework to understand the palaeobiogeography and diversification rate of the first herbivore radiation of dinosaurs.
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This research focused on visiting as many museums and reassessing as many fossils as possible during three years of study. This project was possible thanks to the existence of Natural History Collections. In 2017, during the writing of this thesis, the holotype skeleton of one species relevant for the analysis herein, Gongxianosaurus, was destroyed because the exhibition hall where it was displayed in China collapsed. This dinosaur was deleted from this dataset, and an essential piece of information got lost. Rather than being an isolated case, the safety of our natural heritage cannot be taken for granted. On 26 April 2016 the National Museum of Natural History (NMNH) in New Delhi, India, got ravaged by a fire and the building along with its collection got destroyed. Two years later, 3 September 2018, the National Museum of Brazil, Rio de Janeiro, was also destroyed by a fire that consumed most of its collection. On 4 December 2017, the Society of Vertebrate Paleontology sued the Government of the United States when it was announced that the Grand Staircase-Escalante and Bears Ears National Monuments in Utah would be reduced in area. These two monuments are valuable palaeontological resources, even two dinosaurs analysed in this thesis came from these monuments: Ammosaurus and Seitaad, and there are potentially many more yet to be discovered or reclassified.

This thesis shows that as palaeontology tackles more complex problems, we rely on more countries to acknowledge the societal and cultural value of their natural heritage and the importance of its preservation. The supermatrix approach and character analysis have been useful to give in giving insight into the enigmatic evolutionary history of sauropodomorphs, and this will encourage other researchers to apply them to other fossil groups. The dinosaurs analysed in this thesis were discovered as early as 1837, and as this work has shown showed, nearly 200 years later there is still a lot of new information that can be extracted from these fossils. As new methods evolve, such as the ones implemented and developed herein, they need to be revisited. Our societies need to take natural heritage more seriously to ensure future researchers can also observe them.
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Outline

1. The study of the origin of quadrupedalism in basal sauropodomorphs has produced a large body of literature. These studies are taxon-based, and they are connected by hypothetical scenarios on the evolution of basal sauropodomorphs. Comparative anatomy studies have also involved to a lesser degree the adaptations that led to herbivorous diets, gigantism, and pneumaticity.

2. The hypothetical scenarios have produced conflicting evidence on the characters that support the clades, definitions and interrelationships within Sauropodomorpha.

3. This work constitutes a revision of the literature on basal sauropodomorphs and presents the most complete and near-comprehensive dataset ever published.

4. The new phylogenetic scenario obtained from the analysis of this revised dataset is contrasted with the previous knowledge of basal sauropodomorph anatomy, mainly locomotion, but also gigantism, feeding, and biogeography.
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Acknowledgements

“My grandmother had a fascinating theory. She said that every one of us was born with a matchbox inside that we’re unable to lit up by ourselves; we need the help of oxygen and a candle. The oxygen, for instance, would come from the breath of the person we love. The candle could be any type of food, music, caress, word or sound that generates the explosion to lit one of the matches up. For a moment, it will dazzle us with intense emotion. A pleasant warmness grows inside us, dwindling as the time goes by until a new explosion rekindles the fire. Everyone needs to discover what will create explosions to be alive, as the combustion of each match is what nourishes our souls. That fire, in summary, is sustenance. If one does not find in time what generates the explosions inside us, the matchbox gets damp, and not even one of the matches will ever lit.”

Laura Esquivel (1950-), Like Water for Chocolate. Mexican novelist.

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Through my time in London, I met several people from outside the academic circle who helped me to become a better human being. For that, I will always be very grateful: Miguel, Jacopo, Miles, Pablo, Antonio, and, especially Robin. The last year of my PhD was in course to be the roughest one, and Robin made it the smoothest ride of all.
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I would like to thank my family: my parents, Anabell and Rafael, and to my brothers, Daniel and Andrés, for supporting all this time, for pushing me to come here and without whom I would not have gotten to where I am now.

It would be delusional to think that a PhD can be considered only as an individual achievement. This section is purposefully long to acknowledge the collaborative nature of a PhD project. No one should do this alone. Lastly, I am deeply grateful to the PhD itself. In the darkest and weakest of my moments, getting to this moment, a completed thesis, kept me going through when I did not find strength, meaning or joy in anything else. The PhD did not put a mental strain on me as my life did. I was raised in a society that made me hide; that pushed me to exist as myself only within the four walls of my room. The PhD forced the door open. In that note, UCL Psychological Services are to be thanked, because for the first time this struggle was not dismissed.
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O World, why do you wish to persecute me?

How do I offend you, when I intend only to fix beauty in my intellect, and never my intellect fix on beauty?

Sor Juana Inés de la Cruz (1651-1695)

Sonnet 146, as translated by Edith Grossman in Sor Juana Inés de la Cruz: Selected Works (2014)

To my heroes that were dressed up in gold

Only hoping one day, I could be so bold

Where have all the gay guys gone?

If we are all in the gutter, it doesn't change who we are

'Ccause some of us in the gutter are looking up at the stars

Michael Holbrook Penniman and Skyler Stonestreet

Fragment of Good Guys, 2015
1 Evolutionary history and Palaeobiology of Basal Sauropodomorpha

1.1 Definition of Sauropodomorpha

Sauropodomorpha is one of the three major clades of non-avian Mesozoic dinosaurs that originated in the early Carnian (237-227 Mya), the other two being Theropoda and Ornithischia (Sereno, 1999a; Martínez et al., 2011; Baron et al., 2017a). Whereas the first sauropodomorphs were gracile, bipedal animals weighing less than 10 kg (Benson et al., 2014), by the Middle Jurassic there was an established trend towards gigantic, quadrupedal dinosaurs (Sander et al., 2011; Figure 1.1). Fossils of this group have been found on all continents, and by the Middle Jurassic, sauropodomorphs had reached a worldwide distribution (Upchurch, 1995; Upchurch et al., 2004a).

The branch-based definition used here for Sauropodomorpha is the most inclusive clade that contains all taxa more closely related to Diplodocus than to Herrerasaurus, Passer or Triceratops (Baron et al., 2017a). This definition is the most appropriate for this study since the composition of the stem part of the clade is of interest for this work. The earliest sauropodomorphs have been identified from the Carnian aged strata of South America, including Saturnalia (Langer, 2003), Buriolestes (Cabreira et al., 2016) and Bagualosaurus (Pretto et al., 2018) from Brazil, as well as the Argentinean taxon Panphagia (Martínez and Alcober, 2009), and Nyasasaurus from the Middle Triassic of Tanzania (Baron et al., 2017a). Furthermore, there is Eoraptor, for which there is some debate on whether or not it is a sauropodomorph (Sereno et al., 2012).
Figure 1.1. Time-calibrated phylogram showing the traditional relationship model between the three main dinosaur lineages (Ornithischia, Sauropodomorpha, and Theropoda). The red bars represent single genera, and the blue bars represent suprageneric taxa. In the traditional model, Sauropodomorpha and Theropoda share a common ancestor and form the clade Saurischia. Sauropodomorpha is comprised of two main groupings: basal Sauropodomorpha and Sauropoda. This phylogram ambiguously represents Basal Sauropodomorpha as the sister taxon of Sauropoda, but basal sauropodomorphs are paraphyletic with respect to sauropods. The silhouettes show the derived characteristic bauplan of Sauropoda, and the similar bauplans of non-sauropod sauropodomorphs, non-genosaurian ornithischians, and non-neotheropod theropods (modified from Sereno, 1999a).

The synapomorphies that are used to diagnose Sauropodomorpha as a clade vary from study to study (Gauthier, 1986; Sereno, 1999a; Langer and Benton, 2006; Baron et al., 2017a). Four major character sets that have been compiled to date, i.e. Upchurch et al., (2007), Yates, (2007), Pol et al., (2011), and Sekiya et al., (2013). The apomorphy-based definition of Sauropodomorpha has been in constant flux as these datasets produce different results and have been used as the basis for many further analyses (e.g. Sertich and Loewen, 2010; Otero and Pol, 2013; McPhee et al., 2014, 2015a, 2015b; Wang et al., 2017).
According to Upchurch et al. (2007), the apomorphy-based definition of Sauropodomorpha is\(^1\) (Figure 1.2):

1) a reduced number (five to six) of neurovascular foramina (C15.1),

2) a first dentary tooth inset a short distance from the anterior-most part of the dentary (C87.1),

3) a strong constriction between the sacral rib and the transverse process of the first primordial sacral vertebra (C143.1),

4) a fibular facet facing laterally and vertically oriented (C263.1),

5) a concave lateral margin of the proximal end of metatarsal II (C272.1), and

6) a proximal width to length ratio of metatarsal V greater than 0.25 (C279.1).

\(^1\) The notation for character statements and character states is as follows: C154 denotes character number (C) 154 in a list, C154.1 refers to character state 1 of character 154.
Synapomorphies for Sauropodomorpha
Upchurch et al., (2007)

Figure 1.2. Illustration of the characters that are considered as synapomorphies of Sauropodomorpha according to Upchurch et al. (2007). The code number indicates the character number statement and the character states in the character list by Upchurch et al. (2007).
The analysis performed by Yates, (2007b) proposed the following synapomorphies for Sauropodomorpha (Figure 1.3):

1) a skull to femur ratio less than 0.6 (C1.1),
2) a height to length ratio of the dentary greater than 0.2 (C98.1),
3) a straight long axis of the tooth crowns (C116.1),
4) a loss of the postzygodiapophyseal lamina in the fourth to eighth cervical neural arches (C142.1),
5) weakly developed laminae in the fourth to eighth cervical vertebrae (C143.1),
6) a loss of the prezygodiapophyseal lamina and the associated triangular fossa in the middle dorsal vertebrae (C158.1),
7) a humerus length to femur length ratio between 0.65 and 0.7 (C205.1),
8) a transverse distal humeral width to humeral length ratio greater than 0.33 (C211.1),
9) an iliac pubic peduncle longer than the anteroposterior width of its distal end (C251.1), and
10) a posterior end of the fibular condyle on the proximal articular surface of the tibia placed anteriorly relative to the posterior margin of the proximal articular surface (C304.0).
Figure 1.3 Illustration of the characters that are considered as synapomorphies of Sauropodomorpha according to Yates (2007b). The code number indicates the character number statement and the character states in the character list by Yates (2007b).
By contrast, the analysis of Pol et al., (2011) indicates the following synapomorphies (Figure 1.4):

1) a skull to femur ratio less than 0.666 (C1.1),

2) cervical vertebrae longer than the anterior dorsal vertebrae (C128.1),

3) a deltopectoral crest slanting perpendicular to the transverse axis of the distal condyles (C173.1),

4) a humeral distal width accounting for more than three times the humeral length (C175.1),

5) a radius 80% shorter than the humerus (C180.0),

6) a triangular and pointed preacetabular process (C207.1),

7) an iliac pubic peduncle twice the length of the anteroposterior width of its distal width (C217.1),

8) an expanded distal ischial end with respect to the rest of the shaft (C225.1),

9) an *asymmetrical* fourth trochanter with a steeper distal slop than the proximal slope (C247.1).
Figure 1.4 Illustration of the characters that are considered as synapomorphies of Sauropodomorpha according to Pol et al. (2011). The code number indicates the character number statement and the character states in the character list by Pol et al. (2011).
Finally, the list compiled by Sekiya et al., 2013 includes the character lists published by Upchurch (2007) and Yates (2007b), and proposes a new set of synapomorphies for Sauropodomorpha:

1) a skull that is 50% of the length of the femur (C1.1),
2) an infratemporal fenestra bordered for more than 50% of its length by the squamosal (C87.0),
3) a quadrate foramen completely encircled by the quadrate (C102.1),
4) a dentary ventrally curved towards its tip (C132.1),
5) a hindlimb to trunk length ratio less than 1 (C237.0),
6) a ratio of the transverse width of the distal end of the humerus to the humeral length greater than 0.333 (C292.1),
7) a ratio of the length of the penultimate phalanx of manual digit II to the second metacarpal less than 1 (C331.9).
8) a strongly laterally curved iliac blade in dorsal view (C355.1),
9) an iliac pubic peduncle with an anteroposterior width twice as large relative to its distal width (C356.1),
10) a transverse width of the distal articular surface of metatarsal V in distal view less than its anteroposterior depth (C480.1), and
11) an ungual of pedal digit II longer than pedal phalanx II.2 (C499.1).

A more detailed comparison of these four analyses is presented in Chapter 2. These synapomorphy lists show that the proposed sets of synapomorphies partly conflict with each other. Although non-sauropod sauropodomorphs have been considered to form a grade from basal saurischians to sauropods, there is only partial consensus on the character states supporting the monophyly of Sauropodomorpha.
1.2 Importance of understanding Basal Sauropodomorpha interrelationships

Sauropods have a very distinctive bauplan, possessing small heads, long necks and tails, complex vertebral lamination, a columnar gait, and a quadrupedal stance (Wilson, 2002; Upchurch et al., 2004a; Sander et al., 2011). It has long been established that sauropods are a monophyletic group (Gauthier, 1986; Upchurch, 1995; Wilson, 2002; Galton and Upchurch, 2004; Sander et al., 2011). The most recent common ancestor of Sauropoda was likely already quadrupedal (Sander et al., 2011), meaning that the acquisition of quadrupedality must have occurred before their radiation. To understand how these morphological adaptations led to this change, but also the origins of herbivory, or the trend of gigantism, we need to comprehend the phylogenetic history of no-sauropodan sauropodomorphs.

Conversely, the taxa traditionally referred to as ‘prosauropods’ had more diverse bauplans than sauropods, ranging from gracile, bipedal and cursorial forms, such as *Saturnalia*, and *Thecodontosaurus* (Langer et al., 1999, 2007; Benton et al., 2000; Langer, 2003), to large-sized, bipedal animals such as *Ruehleia*, and *Plateosaurus* (Galton, 1999a, 2001a; Bonnan and Senter, 2007), and large quadrupedal taxa such as *Melanorosaurus* and *Lessemosaurus* (Galton, 1985a; Pol and Powell, 2007; Peyre de Fabrègues and Allain, 2016; Figure 1.5). This diversity of body plans has posed a challenge to our understanding of the interrelationships at the base of Sauropodomorpha. Two main scenarios have been proposed to describe this diversity: either ‘prosauropods’ form a sister clade to Sauropoda (Colbert, 1964; Galton, 1990; Sereno, 1999a; Galton and Upchurch, 2004), or they represent members of the same lineage of Sauropoda that gradually acquired adaptations to a quadrupedal stance and specialisations for a herbivorous diet (Langer et al., 2010b; McPhee et al., 2014, 2015b; Foth et al., 2015).
Figure 1.5 The diversity of basal sauropodomorphs during the Late Triassic mapped on to a reconstruction of Pangaea (based on Langer et al., 2010). The colour scheme in the key box represents the consensus on the position that taxa have been found in iterations of the matrices analysed in this work. The map shows the high diversity of species with the different body plans adapted: from the gracile bipedal forms in Europe and Brazil to the large-sized quadrupedal animals of South Africa. This map also makes clear the lack of shared taxa between sauropodomorph-bearing formations during the Late Triassic and highlights the diversity of the different assemblages. The colour of the silhouettes corresponds to the most common placement of the taxa. Silhouettes to scale.
1.2.1 Origins of quadrupedality

Previous analyses suggest that these adaptations originated in a step-wise fashion. This scenario necessitates a gradual appearance of these features from non-theropod, non-sauropodomorph saurischians or non-saurischian dinosaurs to more derived sauropods. Although it has been widely accepted that this is the case (Yates and Kitching, 2003; Remes, 2007; Fechner, 2009; Yates et al., 2010), there are several problems related to the high degree of homoplasy that this scenario assumes (See 1.4). These homoplasies are mostly reversals, and their distribution varies greatly between different phylogenetic analyses (e.g. Upchurch et al., 2007; Yates, 2007; Pol et al., 2011; Sekiya et al., 2013).

Sauropods, a deeply nested clade within Sauropodomorpha, share a bauplan. All of the non-sauropodan dinosaurs have been referred to traditionally as ‘prosauropods’ (e.g. Galton, 1990; Galton and Upchurch, 2004) or more recently as ‘basal sauropodomorphs’ (e.g. Barrett and Upchurch, 2007; Upchurch et al., 2007; Yates, 2007a).

The earliest sauropodomorphs are from the early Carnian of Brazil and Argentina (see above). An early peak in sauropodomorph diversity occurred in the Norian (Late Triassic, 227-208.5 Mya) but was followed by a drop in the Rhaetian (Late Triassic, 208.5-201.3 Mya; Barrett and Upchurch, 2005). The group survived the Triassic-Jurassic mass extinction with no effect on their diversity, but non-eusauropod sauropodomorphs became extinct before the Middle Jurassic (Barrett and Upchurch, 2005; Upchurch and Barrett, 2005). This decline on the diversity of basal sauropodomorphs coincides with the onset of a the eusauropod radiation (Barrett and Upchurch, 2005; Upchurch and Barrett, 2005; Mannion et al., 2011; McPhee et al., 2016; Figure 1.6).

The lack of consensus on the phylogenetic history of Sauropodomorpha from its basal-most members to the origin of sauropods obscures many aspects of the biology of this group. The most frequently aspects are classification, diversity, and locomotion, but understanding biogeography and evolution of both feeding mechanism and body size rely on having a well-resolved phylogeny for this part of the tree.

Moreover, a reconstruction of the ontogenetic series of various sauropodomorph genera is also needed to better understand the diversity of this clade, since the
taxonomic units included in previous phylogenetic analyses have included an assortment of specimens of all ages, from juveniles such as *Ignavusaurus* (Knoll, 2010), *Massospondylus* (Chinsamy, 1993; Reisz et al., 2013), *Mussaurus* (Cerda et al., 2014) and *Yunnanosaurus* (Sekiya et al., 2013), to sub-adults, e. g. *Aardonyx*, (Yates et al., 2010) and adults.

### 1.2.2 Origins of herbivory

‘Prosauropods’ were initially regarded as carnivorous due to the morphology of their teeth and claws (Von Huene, 1932; Swinton, 1934; Lull, 1953). *Plateosaurus* was considered as a large-sized carnivorous predator (Swinton, 1934), whereas *Anchisaurus* (Lull, 1953) and *Ammosaurus* (Von Huene, 1932) were thought of as small active carnivores. The morphology of the teeth and manus supported the idea of large prosauropods being carnivorous, as originally hypothesised for *Melanorosaurus* (Charig et al., 1965) and *Massospondylus* (Cooper, 1981). A scavenging habit was proposed for the latter taxon, even though they were starting to be recognised as members of the same group that included sauropods by this time (Cooper, 1981).

Several studies based on comparisons of ‘prosauropod’ dentitions with those of iguanid lizards led to the suggestion that all ‘prosauropods’ were largely herbivorous as with the more derived sauropods (Galton, 1973, 1976, 1984, 1985b, 1986a; Fairman, 1999; Barrett, 2000). Over time, this suggestion became the consensus on prosauropod diet, and ideas of a carnivorous diet were side-lined. Some studies continued to suggest that carnivorous or omnivorous diets were still plausible based on tooth morphology. For example, it was observed that in ‘prosauropods’, the maxillary and dentary teeth are mesiodistally expanded, are taller than they are wide, are labiolingually compressed, lack cingula, are not recurved, and have serrated margins (Barrett, 2000). This contrasts with ornithischian teeth, which are presumed to be associated with herbivory, which have a triangular shape and are *asymmetrical* in both distal and mesial views.

In the case of iguanids, it was initially thought that *Iguana* and *Ctenosaura* were exclusively herbivorous, but further studies have shown that iguanid herbivory is present only in more advanced taxa, whereas more primitive iguanids such as *Brachylopus* and *Diprosaurus* have carnivorous or omnivorous diets (Barrett, 2000). Moreover, *Iguana* has been shown to have facultative herbivory, with evidence of
scavenger and predatory habits. Phylogenetic studies indicate that the adaptations to herbivory were acquired in the context of a primitively carnivorous diet (Barrett, 2000; Cabreira et al., 2016).

As ‘prosauropods’ were considered sauropodomorph dinosaurs, a hypothesis of phenotypic plasticity in the group was proposed, so that animals like Plateosaurus were herbivorous, but Anchisaurus was omnivorous (Charig et al., 1965). The cranial anatomy of ‘prosauropods' also indicated that adaptations to an exclusively herbivorous diet were not present in all members of the group, based on the absence of a ventrally displaced craniomandibular joint, a reduced coronoid eminence and the absence of a precise occlusion (Kermack, 1984). Kermack (1984) proposed the idea of omnivorous diets in ‘prosauropods’, conciliating previous analyses that also showed that in many genera there were apical and mesial wear facets that suggested some degree of herbivory.

The high diversity of species in sauropodomorph-bearing formations has led to the suggestion that phenotypic plasticity and niche partitioning also implied that an omnivorous diet was needed to complement the nutrients from scarce xerophytic plants and to avoid competition (Charig et al., 1965; Cooper, 1981; Barrett, 2000; Sander and Klein, 2005; Button et al., 2014; McPhee et al., 2015b). Several species come from formations whose lithology indicates arid, semi-arid, or dry season environments. The small gracile dinosaurs from Argentina (Panphagia, Chromogisaurus and Eodromaeus, also putatively Eoraptor) have been found in sediments that correspond to volcanically active floodplains with heavy rain seasons (Carnian, 235-221.5 Mya; Martínez et al., 2011), whereas large bodied sauropodomorphs such as Coloradisaurus, Leyesaurus and Riojasaurus, have been found in sediments from lacustrine, equatorial and humid environments (Norian, 221.5-205.6 Mya; Bonaparte, 1972).
The diversity of basal sauropodomorph faunas during the Early Jurassic mapped on a reconstruction of Pangaea (based on the map on the PaleoMap Project). The colour scheme in the key box represents the consensus on the position that taxa have been found in iterations of the matrices analysed in this work. In this map the replacement of the basal sauropodomorph fauna by basal sauropod faunas occurs in many sauropodomorph-bearing formations. The highly diverse Lower Lufeng Formation is similar to the Upper Elliot Formation in taxonomic diversity. Silhouettes to approximate scale.
The sauropodomorphs from the Late Triassic of Germany (i.e. *Sellosaurus, Plateosaurus Ruehleia* and *Efraasia*) and England (i.e. *Asylosaurus, Camelotia*, and *Thecodontosaurus*, also *Agnosphytis*, potentially a silesaurid) include a range of gracile and large-sized animals, and come from sediments of lacustrine, fluvial, and deltaic environments deposited in semi-arid conditions (Sander, 1992; Hungerbühler, 1998a; Galton, 2001a, 2007). These palaeoenvironmental reconstructions might indicate that omnivorous diets could allow these dinosaurs to increase their nutrient intake by having scavenger or predatory habits during the dry seasons (Cooper, 1981; Gow et al., 1990; Barrett, 2000).

The palaeoenvironmental reconstructions and the high diversity of genera make the omnivorous diet scenario the most likely (Barrett et al., 2010), and thus a clear and concise phylogenetic scenario is needed to understand the origins of the specialisations of the feeding mechanisms seen in sauropods since tooth morphology alone is not necessarily a reliable predictor for diet. The first sauropods come from formations that correspond to fluvial and lacustrine environments deposited under semi-arid conditions (Smith et al., 1993; Racey and Goodall, 2009).

A caveat on this hypothesis is the fact that taxonomic revisions of several genera are long overdue (Sun et al., 1985; Moser, 2003; Yates and Barrett, 2010). An interesting fact that contrasts with the high diversity of basal sauropodomorphs is the high level of endemism seen in the sauropodomorph-bearing formations. The South American and African faunas, for example, share no species between them, regardless of the palaeogeographic disposition of Pangaea, as can be seen in Figures 1.5 and 1.6. A consensual phylogeny can shed light into the similarities between the faunas and the biogeographic history of the group.

1.3 **Prosaurophoda: basal sauropodomorphs in the precladistic era**

The first attempts to classify dinosaurs involved the selection of certain features that were considered important to understand the group’s evolutionary history (Owen, 1854; Cope, 1866; Huxley, 1870; Seeley, 1887, 1888; Marsh, 1895; Von Huene, 1914a, 1914b; Matthew, 1915; Abel, 1919). Pre-cladistic methods aimed to produce a hierarchical classification in which there are lower classes nested in higher classes. This arrangement was based on seeking overall comprehensive similarities, which were used to create genera that were then grouped into families, which were then
grouped into orders, and so on. This paradigm has been referred to as a Haeckelian classification (Mayr and Bock, 2002). Under this scheme, earlier discoveries of prosauropod material were classified either as theropods (Table 1.1), or as dinosaurs that were related to theropods and sauropods (Table 1.2). For Prosauropoda, roughly half of all of the named taxa were discovered and described before the cladistic era, producing a large body of work that is still relevant as a source of characters and taxa, but that does little to shed light on relationships. Earlier Haeckelian classification did not produce testable phylogenetic hypotheses, since, in the end, all of the hypotheses rely on the level of agreement on the position that each taxon has on the evolutionary history (Mayr and Bock, 2002).

The first classifications considered ‘prosauropods’ as a type of theropod, until Huene (1932) established their similarity with sauropods and erected the group Sauropodomorpha, comprising two divisions: Prosauropoda and Sauropoda. The relationship between these two groups was obscured by the poor fossil record and the poorly understood stratigraphy of the Triassic at the time (Lucas, 2010). On one hand, there was the idea that prosauropods were an independent lineage that originated before Sauropoda, but which shared a common ancestor with Sauropoda (Von Huene, 1932; Young, 1942; Colbert, 1964; Charig et al., 1965; Steel, 1970; Galton, 1971). Alternatively, Prosauropoda was also considered as the lineage that gave rise to sauropods (Van Heerden, 1979; Cooper, 1981, 1984; Galton, 1985a; Galton and Van Heerden, 1985). The different degrees of similarity defined several families, and the taxonomic composition of these was largely debated on the characters that were considered important. Although several groupings were proposed, and an assortment of families erected, their taxonomic content varied greatly through time depending on the characters chosen to define them.
Table 1.1 Comparative table of the different classification systems proposed in the late 19th century. The blue shading indicates the place where ‘prosauropods’ were placed in each classification system.

<table>
<thead>
<tr>
<th></th>
<th>Cope (1866)</th>
<th>Huxley (1870)</th>
<th>Seeley (1874)</th>
<th>Marsh (1878-84)</th>
<th>Cope (1883)</th>
<th>Seeley (1887)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthopoda</td>
<td>Sclerosauridae</td>
<td>Sclerosauridae</td>
<td>Stegosauria</td>
<td>Orthopoda</td>
<td>Ornithischia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Iguanodonidae</td>
<td>Iguanodonidae</td>
<td>Ornithopoda</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Goniopoda</td>
<td>Megalosauridae</td>
<td>Megalosauridae</td>
<td>Theropoda</td>
<td>Goniopoda</td>
<td>Saurischia</td>
<td></td>
</tr>
<tr>
<td>Symphopoda</td>
<td>Compsognathus</td>
<td>Compsognathus</td>
<td></td>
<td>Hallopora</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1.2 Comparative table of the composition of the order Saurischia as defined by Marsh (1895) and subsequent classifications derived from it in the early 20th century that considered ‘prosauropods’ as an independent saurischian lineage (Pachypodosauria). The light blue shade indicates the groups were the families of ‘prosauropods’ were classified. In Marsh (1895), ‘prosauropods’ were classified as carnivorous dinosaurs, whereas in Huene (1914a, b) the order Pachypodosauria was erected to include carnivorous dinosaurs and sauropods. Subsequent classification models were amendments to restrict the definition of Pachypodosauria to include anything that was not a coelurosaurian, a theropod, or a sauropod.

<table>
<thead>
<tr>
<th></th>
<th>Marsh, 1895</th>
<th>von Huene, 1914a, b</th>
<th>Matthew, 1915</th>
<th>Abel, 1919</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>THEROPODA</strong></td>
<td>Coeluridae</td>
<td>Podeosauridae</td>
<td>Podeosauridae</td>
<td>Podeosauridae</td>
</tr>
<tr>
<td></td>
<td>Compsognathidae</td>
<td>Hallopodidae</td>
<td>Coeluridae</td>
<td>Coeluridae</td>
</tr>
<tr>
<td></td>
<td>Hallopora</td>
<td>Compsognathidae</td>
<td></td>
<td>Compsognathidae</td>
</tr>
<tr>
<td><strong>PACHYPODOSAURIA</strong></td>
<td>Megalosauridae</td>
<td>Anchiuridae</td>
<td>Anchiuridae</td>
<td>Anchiuridae</td>
</tr>
<tr>
<td></td>
<td>Dryptosauridae</td>
<td>Plateosauridae</td>
<td>Zancledontidae</td>
<td>Zancledontidae</td>
</tr>
<tr>
<td></td>
<td>Labrosauridae</td>
<td>Sellosauridae</td>
<td>Plateosauridae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plateosaurus (Zancledontidae)</td>
<td>Anchiuridae</td>
<td>Plateosauridae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Anchiuridae</td>
<td>Massospondylidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ceratosauroidea</td>
<td>Ceratosauroidea</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SAUROPODA</strong></td>
<td>Cetiosauridae</td>
<td>Mosasauridae</td>
<td>Megalosauridae</td>
<td>Megalosauridae</td>
</tr>
<tr>
<td></td>
<td>Atlantosauroidea</td>
<td>Ornithosauroida</td>
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</tr>
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</table>
During the pre-cladistic era, the origin of dinosaurs was widely disputed, and many studies aimed to understand the origins of large body size. Some of the earliest scenarios of the evolution of quadrupedalism, for example, in sauropods were based on the assumption that saurischians and ornithischians did not share a common ancestor (Seeley, 1887, 1888; Baur, 1891; Huene, 1914a; Colbert, 1964; Romer, 1971). This model proposed that the families of prosauropods, Thecodontosauridae, Plateosauridae, Plateosauravidae, Anchisauridae, and Melanorosauridae, were part of a transformational sequence that gradually lost their bipedality because of an increase in body size. Under this model, quadrupedalism in sauropods was a reversal, with melanorosaurids as a transitional group.

The main challenge to this scenario came from stratigraphy. The beds that contained plateosaurids and thecodontosaurids in Europe were younger than the beds in South Africa that yielded melanorosaurid material (Charig et al., 1965). Moreover, anatomical considerations of the reduction of the manual and pedal digits in prosauropods and sauropods led to the proposal that quadrupedality was the default condition from a pseudosuchian to sauropod gait, making prosauropods offshoots from this main quadrupedal lineage (Charig et al., 1965). The key character that linked Thecodontosauridae and Plateosauridae to the sauropodomorph lineage was their spatulate dentition. This stratigraphic incongruence led to the proposition that prosauropods were so-called “dead-ends”, a term that at that time alluded to the extinction of side-shoot branches, or that prosauropods and sauropods had different origins (Charig et al., 1965).

The monophyly of Prosauropoda started to be widely accepted based on several characters but most significantly the highly reduced digit V in the pes (Cruickshank, 1975; Van Heerden, 1978, 1997). Although weakly supported, it became the more plausible option when the adaptations that dinosaurs acquired for an erect gait were considered to be too complex to evolve independently several times from ‘thecodontian’ reptiles (Colbert, 1964; Cruickshank, 1975).

Overall, the frameworks to test the many arrangements proposed by Haeckelian classifications were not strong enough to provide falsifiable explanations for the origin of quadrupedality (Figure 1.7). Moreover, much of the taxonomic work done during this period was not contested for a long time, due to the small number of dinosaur
specialists that worked on these animals. The taxonomies of *Plateosaurus* (Moser, 2003), *Eucnemesaurus*, *Euskelosaurus* (both discussed in Heerden, 1979; Yates, 2007b; McPhee et al., 2015), *Melanorosaurus* (Peyre de Fabrègues and Allain, 2016) and *Yunnanosaurus* (Barrett et al., 2007; Lü et al., 2007; Sekiya et al., 2013) have been recently addressed, but there is still no complete revision of all of the materials referred to these taxa.

### 1.4 Basal Sauropodomorpha: the cladistic era

The advent of cladistics came in the first half of the 20th century when method started to be developed to study the classification of birds (Mitchell, 1901), on insects with the first proposed character list (Tillyard, 1921), and to understand evolutionary patterns in plants (Zimmerman, 1943). The cladistic approach considers each character transformation as evidence of grouping (Schuch and Brower, 2009) This transformed from an ordering system based solely on hierarchical arrangement to a proper ordering system based on patterns of descent (Mayr and Bock, 2002). Instead of trying to put emphasis on the place that each individual taxon would have in the hierarchy, there is an emphasis on the character distribution and character history (Bryant and Wagner, 2001; Mayr and Bock, 2002; Sereno, 2007a). This approach is known overall as a Henningian cladification, where the groups that are produced are clades: hypothetical scenarios were all the taxa contained in a clade have a shared ancestry (Mayr and Bock, 2002).
Figure 1.7 Timeline showing the different groups (orders or families) erected during the pre-cladistic era. The content of each group is inside the blue boxes to the right. Whilst some of these names are still in use, they do not relate to the initial definitions proposed here.
Cladistics provides testable frameworks since there are two sets of hypotheses: a hypothesis of primary homology, which are hypotheses of homology based on similarity of structure, position or function, and a hypothesis of secondary homology, which is supported by its distribution in a tree, i.e. there is evidence from topology that it is not homoplasy (Patterson, 1988). The first phylogenetic analysis to apply a cladistic rationale to sauropodomorphs was performed by Paul (1984), who proposed that a group called Segnosauria was related to ornithischians and that prosauropods, as a monophyletic group, were linked with ornithischians, in a ‘Phytodinosauria’ hypothesis similar to the one suggested by Bakker and Galton (1974). Gauthier (1986) performed the first true cladistic analysis to test the monophyly of dinosaurs and birds and he also provided several comments on Sauropodomorpha. He suggested that Sauropodomorpha was a lineage of saurischian dinosaurs, the sister-group of theropods, and not related to ornithischians. He also presented limited evidence that prosauropods were a paraphyletic group, with some taxa closer to sauropod origins than others (Gauthier, 1986). Segnosauria were shown to be a group of theropod dinosaurs (Perle, 1979; Barsbold and Perle, 1980; Barsbold, 1983), now referred to as therizinosauroids (Russell and Dong, 1993), and have been excluded from further consideration of sauropodomorph phylogeny (Figure 1.8).

The term ‘sauropodomorph’ is applied here as coined by von Huene (1932), comprising ‘prosauropods’ and ‘sauropods.’ The cladistic term ‘basal sauropodomorph’ is loosely applied here to refer to any non-sauropod that is in the sauropodomorph lineage, including the most primitive sauropodomorphs, an evolutionary grade rather than a clade.

Galton (1990) did not perform a numerical cladistic analysis but he was the first to look at a large number of the relevant taxa, and recovered prosauropods as a monophyletic group, which he regarded as the sister-taxon to Sauropoda (Figure 1.9). Two families were proposed: Plateosauridae and Melanorosauridae. The other families formed a grade leading towards plateosaurids and melanorosaurids. The same arrangement was later obtained by a more formal numerical cladistic analysis (including 18 ingroup sauropodomorphs) that retrieved a monophyletic group with two clades: Plateosauridae and Melanorosauridae, but with different definitions (Gauffre, 1996).

Monophyly of Prosauropoda was supported by the first cladistic analyses, but these were applied to only small datasets where sauropods were assumed to represent an outgroup. In Sereno (1999) ‘Prosauropoda’ is the sister-taxon to Sauropoda. In this new view, the
prosauropods are unified by a large claw pointing inwards with a twisted thumb, proportionally long cervical vertebrae, such as those found in *Plateosaurus* and *Massospondylus*, and a highly conserved skeletal design (Sereno, 1999). In contrast, an alternative analysis placed *Coloradisaurus* in a basal position, even more basal than *Thecodontosaurus*, and the existence of Plateosauridae and Melanorosauridae was supported (Benton et al., 2000). Subsequent cladistic analyses continued assuming prosauropod monophyly (Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Galton and Upchurch, 2004; Figure 1.10).

In one of the earliest works that included a comprehensive assessment of 212 osteological features and 20 taxa (Yates and Kitching, 2003) some of the ‘prosauropods’ were recovered as basal sauropods for the first time, whereas the rest of them were clustered in a ‘core Prosauropoda’ clade that was the sister clade of Sauropoda. After Yates and Kitching (2003), the name ‘Prosauropoda’ became less inclusive since the most robust forms, such as *Melanorosaurus readi* or *Blikanasaurus cromptoni*, were placed within Sauropoda. The position of *Anchisaurus* was challenged based on the findings in Yates and Kitching (2003), and a re-description of the material led to the conclusion that *Anchisaurus polyzelus* and *Melanorosaurus readi* were the most basal members of the clade Sauropoda, rather than prosauropods, this being the first time that Anchisauridae was considered a derived family within Sauropodomorpha rather than a primitive one. Prosauropoda contained *Lufengosaurus, Massospondylus, Riojasaurus, Plateosaurus* and possibly *Efraasia* (Yates and Kitching, 2003; Yates, 2004; Figure 1.11).
Figure 1.8 Early phylogenetic models for the relationship of monophyletic prosauropods with other dinosaurs. A) evolution of herbivorous dinosaurs and ‘segnosaurids’ from thecodonts (based on Paul, 1984); B) the monophyletic evolution of herbivorous dinosaurs and ‘segnosaurids’ from basal dinosaurs (based on Paul, 1984); C) derivation of ‘segnosaurids’ dinosaurs independently of herbivorous dinosaurs (based on Paul, 1984), and D) the monophyletic saurischians showing the transitional position of the prosauropods towards Sauropoda, considering ‘segnosaurids’ as prosauropods (Gauthier, 1986).
Figure 1.9 First cladistic scenarios of monophyletic ‘prosauropods’ as sauripodomorphs. Above. Cladogram representing the relationships of prosauropods as the sister taxa of Sauropoda, obtained by Galton, 1990. Below. Cladogram showing a division of prosauropods in two families with a different composition from that in Galton, 1990. Analysis performed by Gauffre, 1996.
Figure 1.10 Summary of results from several studies that supported the relationships of Prosauropoda as a monophyletic group: A) Sereno (1999), B) Benton et al. (2000), C) Galton and Upchurch (2004).
Figure 1.11 Cladogram showing a partial paraphyly of prosauropods, having a ‘core Prosauropoda’ (=Plateosauridae), as a paraphyletic series of melanorosaurid sauropodomorphs, according to Yates and Kitching (2003).
Another analysis published by Yates (2003b) produced a phylogeny that included 164 osteological features, compiled from the ones used in previous analyses (Galton, 1985c; Gauthier, 1986; Sereno, 1993; Sereno and Novas, 1993; Novas, 1994; Wilson and Sereno, 1998; Benton et al., 2000; Rauhut, 2003a). This thorough reassessment confirmed that amongst 14 ‘traditional prosauropods’ there was no evidence of subgroupings. This led to the proposition that ‘Prosauropoda’ was completely paraphyletic with respect to Sauropoda (Yates, 2004a). After the removal of Coloradisaurus, a reduced cladistic consensus of the five most parsimonious trees showed that there were only two potential groupings within the paraphyletic ‘Prosauropoda’ (Figure 1.12).

A thorough discussion of the cladistic analyses that were performed between 2004 and 2018 is presented in Chapter 2.
1.4.1 Phylogenetic definitions proposed to describe relationships inside Sauropodomorpha

New analyses performed on larger collections of taxa and characters led to either partial or near-complete paraphyly of Prosauropoda (Galton and Upchurch, 2004; Smith and Pol, 2007; Upchurch et al., 2007a; Kutty et al., 2007; Ezcurra, 2010; Sekiya, 2010; Yates et al., 2010; Novas et al., 2010; Pol et al., 2011; Sekiya et al., 2013; Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Otero et al., 2015; Peyre de Fabrègues et al., 2015; Wang et al., 2017; Chapelle and Choiniere, 2018; Zhang et al., 2019). Several phylogenetic clades have now been erected to capture these alternative groupings and are listed chronologically below. Table 1.3 summarises this information in a hierarchical order for context.

Guaibasauridae Bonaparte et al., 1999 was originally named to include only Guaibasaurus at the base of ‘Prosauropoda’, but after the discovery of a second, more complete specimen, this clade was expanded to include Saturnalia, as the earliest diverging lineage within Sauropodomorpha, although this was suggested without a phylogenetic analysis (Bonaparte et al., 2007). Subsequently, Ezcurra (2010) extended this definition to include Agnosphitys, Panphagia, and Chromogisaurus forming the basal-most clade Sauropodomorpha (Ezcurra, 2010; Novas et al., 2010; Sekiya et al., 2013; Figures 1.19 and 1.21). Yates et al. (2010) recovered Guaibasauridae as the sister clade of Sauropodomorpha rather than its most basal lineage (Knoll, 2010; Yates et al., 2010; Pol et al., 2011; Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Peyre de Fabrègues and Allain, 2016; Figures 1.17, 1.22 and 1.23).

Plateosauria Tornier, 1913 was defined as a node-based taxon containing the most recent common ancestor of Plateosauridae and Massospondylidae (Sereno, 1998, 1999b). The same definition was employed by Galton and Upchurch (2004) but Massospondylidae was replaced by Jingshanosaurus. Upchurch et al. (2007) proposed Jingshanosaurus as a basal sauropod, redefining Plateosauria as the clade containing Plateosauridae and Massospondylidae, and possibly Lufengosaurus (Figure 1.14 and Figure 1.18). Few studies applied this definition for Plateosauria (Kutty et al., 2007; Sekiya, 2010; Figure 1.15 and Figure 1.17). The results derived from the dataset of Yates (2007) have defined Plateosauria as including all sauropodomorphs except for the most basal forms (Ezcurra, 2010; Knoll, 2010; Novas et al., 2010; Yates et al., 2010; McPhee et al., 2015b; Figure 1.17).

Plateosauridae Marsh, 1895 has been proposed as a stem-based taxon that includes all taxa more closely related to Plateosaurus than to Massospondylidae (Sereno, 1999) or
Yunnanosaurus and Massospondylus (Galton and Upchurch, 2004). In Upchurch, et al. (2007), this clade is defined as including Plateosaurus Riojasaurus, and Coloradisaurus, whereas the inclusion of Lufengosaurus is equivocal (Figure 1.14). In Yates (2007), Plateosauridae is restricted to Unaysaurus and Plateosaurus and it was retrieved as such in several subsequent analyses (Smith and Pol, 2007; Ezcurra, 2010; Sertich and Loewen, 2010; Figure 1.17). In Yates, et al. (2010), Plateosauridae includes also Ruehleia, a conclusion that was also followed by Knoll (2010) (who made it more inclusive by grouping therein Riojasauridae, Massospondylidae, and Anchisauria), and Chapelle and Choiniere (2018). Sekiya (2010) used the dataset from Upchurch et al. (2007) and defined Plateosauridae as a core group of prosauropods placed as the sister taxon of Sauropoda. Novas et al. (2010), included in this family the Indian prosauropod Jaklapallisaurus. Plateosauridae contained Unaysaurus and Plateosaurus in subsequent studies (Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Wang et al., 2017) but is retrieved unresolved in Peyre de Fabregues and Allain (2016) (Figure 1.23).

**Massopoda Yates, 2007** is a stem-based clade containing all those taxa more closely related to Saltasaurus loricatus than to Plateosaurus engelhardti, effectively containing Anchisauria, Massospondylidae and Riojasauridae (Yates, 2007a; Ezcurra, 2010; Knoll, 2010; Novas et al., 2010; Yates et al., 2010; Pol et al., 2011; McPhee et al., 2015b, 2015a; Figures 1.17, 1.19 and 1.22). The content of Massopoda is different in Peyre de Fabregues (2016) since Riojasauridae is placed in a more basal position than Plateosauridae (Figure 1.23).

**Massospondylidae Huene, 1914b** has been defined as a stem-based taxon that includes all taxa more closely related to Massospondylus than to Plateosaurus thus including Massospondylus and Yunnanosaurus (Sereno, 1999b) or Massospondylus, Coloradisaurus, and Lufengosaurus (Yates and Kitching, 2003; Yates, 2007a; Figure 1.18). Subsequent analyses applied the same definition as Yates and Kitching (2003), but it has also included Glacialisaurus (Ezcurra, 2010, Knoll, 2010), Jingshanosaurus (Yates et al., 2010), Pradhania (Novas et al., 2011), Adeopapposaurus and Leyesaurus (Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Otero et al., 2015), Ignavusaurus (Chapelle and Choiniere, 2018) and Sarahsaurus (Chapelle and Choiniere, 2018). Several analyses concluded, however, that this clade contained only Massospondylus (Yates, 2003a; Galton and Upchurch, 2004; Kutty et al., 2007; Pol and Powell, 2007a; Upchurch et al., 2007a). In the topology produced in Sekiya (2010), the clade is synonymous with Plateosauria. Pol et al. (2011), retrieved a clade Massospondylidae containing Massospondylus, Yunnanosaurus, Gyposaurus, and
Lufengosaurus (Figure 1.20). Finally, this clade was restricted to Massospondylus, Adeopapposaurus, and Leyesaurus, whereas Jingshanosaurus is placed as the sister taxon of Anchisauria, and Lufengosaurus and Glacialisaurus are placed within their own family as the sister taxon of Anchisauria + Jingshanosaurus in Peyre de Fabregues et al. (2016) (Figure 1.23).

Anchisauria Galton and Upchurch, 2004 was defined as the most inclusive node-based taxon that includes the most recent common ancestor of Anchisaurus and Melanorosaurus (Figure 1.13). The term was originally defined to comprise Anchisaurus, Ammosaurus, and Melanorosauridae (Galton and Upchurch, 2004). More recent analyses changed the topology so that this clade contained all sauropodomorphs except for the most basal forms (Kutty et al., 2007; Upchurch et al., 2007a; Figures 1.14 and 1.16). In the topology obtained by Yates (2007), Anchisauria was restricted to exclude basal sauropodomorphs, plateosaurids, massospondylids and riojasaurids (Smith and Pol, 2007; Yates, 2007a; Ezcurra, 2010; Knoll, 2010; Novas et al., 2010; Yates et al., 2010; Pol et al., 2011; Otero and Pol, 2013; McPhee et al., 2015b; Peyre de Fabrègues and Allain, 2016; Figues 1.17, 1.19, 1.20, 1.22 and 1.23). With this definition, some topologies include massospondylids within Anchisauria (McPhee et al., 2015b), or include all sauropodomorphs, except the basal-most forms, such as Thecodontosaurus or Efraasia (Sekiya, 2010; Sekiya et al., 2013; 1.18 and 1.20)

Anchisauridae Marsh, 1885 was originally defined as comprising only Anchisaurus and Ammosaurus but later recovered only in Galton and Upchurch (2004); Upchurch et al. (2007), Kutty et al. (2007) and Sekiya (2010). In Upchurch et al. (2007), this clade is weakly supported. Subsequent studies have not included Ammosaurus as a separate OTU.

Sauropodiformes Sereno, 2007b was originally defined as the least inclusive clade containing Mussaurus patagonicus and Saltasaurus loricatus (Figure 1.22). This definition is not applicable to several phylogenies because of the exclusion of Mussaurus from the dataset (e.g. Kutty et al., 2007; Yates, 2007a; Ezcurra, 2010; Knoll, 2010; Pol et al., 2011; Yates et al., 2011; Sekiya et al., 2013; Peyre de Fabrègues and Allain, 2016). In analyses where Mussaurus is included, Sauropodiformes is retrieved as all the sauropodomorph dinosaurs that are at the base of the melanosaurid grade, excluding Anchisaurus and the massospondylids, which altogether form Massopoda (McPhee et al., 2015a, b; Otero and Pol, 2013). In earlier analyses that used Mussaurus, Sauropodiformes becomes a synonym of either Plateosauria (Galton and
Upchurch, 2004), an unranked clade between Sauropodomorpha and Anchisauria (Upchurch et al., 2007; Kutty et al., 2007), or Plateosauridae (Sekiya, 2010).

**Riojasauridae Yates, 2007** was defined as a stem-based clade containing *Riojasaurus incertus*, but not *Plateosaurus engelhardti, Massospondylus carinatus*, or *Anchisaurus polyzelus*. In previous works, this clade was synonymised with Melanorosauridae (Galton and Upchurch, 2004; Kutty et al., 2007) or Plateosauridae (Kutty et al., 2007; Upchurch et al., 2007a; Sekiya, 2010) with different contents. However, this clade consistently contains *Eucnemesaurus* in subsequent works (Ezcurra, 2010; Knoll, 2010; Novas et al., 2010; Yates, 2010; Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Peyre de Fabrègues and Allain, 2016; Figures 1.19 and 1.22).

**Melanorosauridae Huene, 1929** was first conceived as containing *Melanorosaurus, Camelotia*, and *Lessemsaurus* (Galton and Upchurch, 2004, Upchurch et al., 2007, Figure 1.14, Kutty et al., 2007, Figure 1.16). However, in the analyses based on the dataset of Yates (2007), this definition is extended to include sauropod-like ‘prosauropods’ and sauropods, which almost overlaps the definition of Anchisauria, with the exclusion of some basal forms, such as *Yunnanosaurus* and *Anchisaurus* (Yates, 2007a; Ezcurra, 2010; Knoll, 2010; Novas et al., 2010; Yates et al., 2010; Pol et al., 2011; Otero and Pol, 2013; McPhee et al., 2015b, 2015a; Peyre de Fabrègues and Allain, 2016; Figures 1.17, 1.19, 1.20, 1.22, and 1.23). Discussions on which basal ‘anchisaurids’ are excluded from the ‘melanorosaurid’ grade are still controversial, to the point where the basal part of Anchisauria has been resolved as a polytomy of all the basal members (Peyre de Fabregues and Allain, 2016; Figure 1.23).

**Sauropoda, Marsh 1878.** As a cladistic definition, this term has been applied to several dinosaurs. In a thorough revision of the group, Sauropoda was defined as the least inclusive clade containing all the taxa that are more closely related to *Saltasaurus* than to *Melanorosaurus* (Yates, 2007a). The definition used here to distinguish between sauropods and basal sauropodomorphs is as the clade containing the most recent common ancestor of *Vulcanodon karibaensis* and Eusauropoda (Salgado et al., 1997). This definition is preferred because ‘prosauropods’ and sauropods were recognised as part of the same lineage based on a detailed description of *Vulcandon* (Cooper, 1984; Figures 1.13 and 1.14).

**Eusauropoda Upchurch, 2004** was defined as a node-based taxon that includes the most recent common ancestor of *Shunosaurus* and *Saltasaurus*, and all the descendants of that
ancestor. Nonetheless, Wilson and Sereno (1998) re-defined Eusaupoda as a stem-based including all taxa more closely related to *Saltasaurus* than to *Vulcanodon*.

Figure 1.13. Cladogram depicting the monophyly of Prosaupoda, showing two families: Plateosauridae and Anchisauridae=Melanorosauridae, after Galton and Upchurch (2004).
Figure 1.14. Cladogram published in Upchurch et al. (2007) showing a ‘core Prosauropoda’ (=Plateosauridae).
Figure 1.15. Cladogram depicting a partial paraphyly of prosauropods based on the two different datasets including the Indian prosauropods, Pradhania and Lamplughsaurs, based on the dataset by Yates and Kitching (2003) retrieving a ‘core Prosauropoda’ as the sister taxon of Sauropoda in Kutty et al. (2007).
Figure 1.16. Cladogram depicting a partial paraphyly of prosauropods based on the two different datasets including the Indian prosauropods based on the dataset by Galton and Upchurch (2004) showing Prosauropoda as the sister taxon to Sauropoda in Kutty et al. (2007).
Figure 1.17. Topology produced in Yates et al. (2010) with the modifications done by Smith and Pol (2007).
Figure 1.18. Topology produced by Sekiya (2010) based on the dataset by Upchurch et al. (2007).
Figure 1.9. Topology produced by Novas et al. (2011), including Indian prosauropods, based on the dataset published by Ezcurra (2010), which is in turn an amended version of the dataset published by Smith and Pol (2007). This topology recovers Guaibasauridae as the basal-most part of the tree.

(this diagram shows a phylogenetic tree with various nodes labeled including Sauropodomorpha, Guaibasauridae, Saturnaliinae, etc.)
Figure 1.20. Topology produced in Pol et al. (2011) based on an original dataset. This recovers guaibasaurid dinosaurs as basal theropods and a complete paraphyly for "Prosauropoda".
Figure 1.21. Topology produced in Sekiya et al. (2013). This is the only topology to have been produced after merging two datasets: Upchurch et al. (2007) and Apaldetti et al. (2011), which is an amended and extended version of Yates et al. (2010). It includes guaibasaurid dinosaurs as sauropodomorphs, but still recovers a ‘core Prosauropoda’.
Figure 1.22. Topology produced in McPhee et al. (2015b), including the revision of Eucemесesaurus. This recovers a complete paraphyly, but resolves three families of ‘prosauropods’: Plateosauridae, Riojasauridae and Massospondylidae. Noteworthy, Guaiabasauridae is considered a basal theropod, whereas Eoraptor is moved to the basal-most part of Sauropodomorpha, agreeing on the position of Eoraptor as a sauropodomorph as posited by Martinez et al. (2011), and as redescribed later by Sereno et al. (2013).
Figure 1.23. Topology obtained in Peyre de Fabregues and Allain (2016) after the revision of Melanorosaurus. Only Massospondylidae is retrieved as a cluster, although with a more reduced definition, and does not resolve the basal part of Anchisauria.
Table 1.3. Definitions of clades pertaining Sauropodomorpha in hierarchical order from more primitive to more derived.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Definition</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sauropodomorpha</td>
<td>The clade including all the taxa more closely related to Diplodocus than to Herrerasaurus, Passer or Triceratops</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Guaibasauridae</td>
<td>The clade containing all taxa more closely related to Saturnalia than to Plateosaurus.</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Plateosauria</td>
<td>The clade containing the most recent common ancestor of Plateosauridae and Massospondylidae</td>
<td>Node-based</td>
</tr>
<tr>
<td>Plateosauridae</td>
<td>The clade including all the taxa more closely related to Plateosaurus than to Massospondylidae</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Massopoda</td>
<td>The clade including all the taxa more closely related to Saltasaurus than to Plateosaurus</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Riojasauridae</td>
<td>The least inclusive clade of taxa more closely related to Riojasaurus than to Plateosaurus Massospondylus, or Anchisaurus</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Massospondylidae</td>
<td>The clade including all the taxa more closely related to Massospondylus than to Plateosaurus</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Anchisauria</td>
<td>The clade including the most recent common ancestor of Anchisaurus and Melanorosaurus</td>
<td>Node-based</td>
</tr>
<tr>
<td>Anchisauridae</td>
<td>The clade containing Anchisaurus and Ammosaurus but not Plateosaurus or Massospondylus</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Sauropodiformes</td>
<td>The least inclusive clade containing Mussaurus and Saltasaurus.</td>
<td>Node-based</td>
</tr>
<tr>
<td>Melanorosauridae</td>
<td>The clade containing Melanorosaurus and Sauropoda, but not Yunnanosaurus nor Anchisaurus</td>
<td>Stem-based</td>
</tr>
<tr>
<td>Sauropoda</td>
<td>The least inclusive clade containing the most recent common ancestor of Melanorosaurus and Saltasaurus</td>
<td>Node-based</td>
</tr>
<tr>
<td>Eusauroidea</td>
<td>The least inclusive clade containing the most recent common ancestor of Shunosaurus and Saltasaurus</td>
<td>Node-based</td>
</tr>
</tbody>
</table>
1.4.2 Inconsistencies between the different topologies

All the terms above have been given to different topologies through the literature. Overall, disagreements on whether there is a core-prosauropod clade, an arrangement of several smaller monophyletic groups, or whether the tree is essentially pectinate.

In an analysis performed by Peyre de Fabregues et al. (2015), it was proposed that the source of discrepancies might lie in the choice of characters in each analysis. The three major datasets most often used to explore early sauropodomorph relationships (i.e., Upchurch et al., 2007, Yates, 2007 and Pol et al., 2011) were independent compilations of characters in the literature plus additions from personal observations. This study by Peyre de Fabregues et al. (2015) noted that character choice and character scoring are at the root of the inconsistencies found, however, character scorings are based mostly on the way in which the character states are defined. Therefore, essentially the same character can be linked to a different set of character states if these are defined incompatibly.

For example, the characterisation of the complexity of character statements (number of character states) showed that while Upchurch et al. (2007) had only 2% of its characters worded as multistate characters, this number increases to 14% and 15% in Yates et al. (2010) and Pol et al. (2011), respectively. Upchurch et al. (2007) employed additive binary coding in all of the characters, whereas Yates et al. (2010) and Pol et al. (2011) used transformational characters more often. The three matrices have the same proportion of neomorphic characters (Peyre de Fabrègues et al., 2015).

Nevertheless, there are two significant differences: the taxonomic scope and the character coding that affects the final topology through the character scores. This might be more important for the treatment of continuous characters since they can be coded through binary coding strategies or as multistate characters. Exploring these differences forms part of the scope of this thesis, where the information coded in each character statement is analysed and compared through the different matrices (see Chapter 3 and Chapter 4).

1.5 Current hypotheses of the origin of quadrupedalism and giantism in Sauropoda

There is an extensive literature regarding the locomotion and the stances of basal sauropodomorphs that dates from as far back as the beginning of the 20th century. Because of this, it makes sense to use this information to contrast the differences between versions of the
data sets that deal directly with the evolution of basal sauropodomorphs. An extensive summary of studies on locomotion in basal sauropodomorphs can be consulted in Appendix 1.

Questions about the ancestral state of dinosaur locomotion have now been addressed via the application of cladistic methodology following the recognition of dinosaur monophyly (Remes, 2007). It was initially proposed that ornithodirans acquired an erect gait first, then bipedalism and finally the independent acquisition of flight in pterosaurs and birds (Sereno, 1997, 1999a). This model implies that ornithodirans are plesiomorphically bipedal and evolved quadrupedalism independently in several lineages, i.e. Sauropodomorpha (Sander et al., 2011), Ornithopoda, Thyreophora and Ceratopsia (Maidment and Barrett, 2012). During the evolutionary history of tetrapods, the reversion to quadrupedality from an ancestral bipedal stance has occurred only amongst ornithodiran archosaurs, where it has happened several times (Maidment and Barrett, 2011; Nesbitt, 2011).

This model has several problems. First, the rise of Dinosauria is obscured by an incomplete fossil record, a small number of well-preserved specimens, and constantly contested phylogenetic relationships. The first dinosaurs are from late Carnian sediments in Argentina (Reig, 1963; Casamiquela, 1967; Sereno, 1993) and Brazil (Colbert, 1970; Bonaparte et al., 1999; Langer et al., 1999), but by this time, dinosaurs had already differentiated into Ornithischia, Sauropodomorpha and Theropoda (Novas, 1996; Sereno, 1997; Langer and Benton, 2006; Baron et al., 2017a). Secondly, recent morphological studies suggest that the fully erect hind limb was not present in basal dinosauromorphs, such as Lagerpeton (Fechner, 2009), and that there is no conclusive evidence on the locomotion of basal dinosauromiforms, such as Lewisuchus, or silesaurids (Remes, 2007; Fechner, 2009).

Small-sized sauropodomorphs are often considered to be bipedal or facultatively bipedal, whilst large-bodied size animals were probably quadrupedal (Barrett and Upchurch, 2007). Several approaches have been applied to infer the stance of sauropodomorphs and dinosaurs in general. One of these approaches involves the trunk to femoral length ratio, where ratios of 1:0.69 to 1:0.9 indicate undoubtedly quadrupedal dinosaurs (Galton, 1970). Accordingly, Thecodontosaurus was fully bipedal since the forelimbs are proportionally longer, with a ratio of 1:1.6, whilst other obligate bipedal dinosaurs have a range between 1:1.22 to 1:1.9 (Galton and Upchurch, 2004). As for the rest of the basal sauropodomorphs traditionally grouped as “prosauropods”, the range from 1:0.95 to 1:1.15 suggest a facultative bipedalism. Anchisauria,
sauropodomorphs, and *Riojasaurus* had a trunk: forelimb ratio of 1:0.71, proposing an obligate quadrupedalism (Galton and Upchurch, 2004).

The sauropodomorph bauplan remained relatively consistent throughout its evolutionary history. Their general morphology comprises a long neck, long tail, a small skull in proportion to the body size, and a large barrel-shaped body (Wilson, 2002; Galton and Upchurch, 2004). The columnar limbs first developed in the Anchisauria, in taxa like *Anchisaurus* and *Aardonyx*, with an accompanying increase in relative and absolute forelimb length (Barrett and Upchurch, 2007). Neck elongation was established in eusauropods (Upchurch, 1995; Wilson and Sereno, 1998) and it seems that this trend of neck elongation occurred at least twice independently (Wilson and Upchurch, 2009). In relation to diet, it is thought that basal sauropodomorphs were facultative herbivorous (Barrett, 2000), but more derived taxa exhibit trends towards an increased body size and dental occlusion, implying a shift towards an obligate herbivory. The increase in size is apparently correlated with the shift to obligate quadrupedality and herbivory, related to the need for larger trunk regions and the processing of large quantities of vegetation (Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a, 2007b; Yates et al., 2010).

A *Melanorosaurus* + Sauropoda clade is recovered by many analyses, and three features in this clade are consistent with the evolution of obligate quadrupedality: 1) the increase of the humeral length relative to femoral length in juveniles and adults; 2) the development of a large anterolateral process at the proximal end of the ulna; and 3) the straightening of the femoral shaft (Yates et al., 2010).

Sauropodomorpha has also been suggested to be the sister taxa of Herrerasauridae (Baron et al., 2017a). A fully carnivorous feeding strategy is not recovered as a plesiomorphic condition for dinosaurs, as theropods and ornithischians share a common ancestor in this hypothetical scenario. Under this hypothesis, some of the anatomical similarities between herrerasaurids and theropods must be interpreted as convergences (Baron et al., 2017a).

Now that more is known about the osteology of basal saurischians such as *Eoraptor* (Remes, 2007; Fechner, 2009; Sereno et al., 2012) and *Herrerasaurus* (Remes, 2007; Sereno, 2007b; Fechner, 2009), it is possible to start making comparisons between sauropodomorphs, basal theropods and ornithischians. Reconstruction of the forelimb musculature of basal sauropodomorphs was performed by Remes (2007), based primarily on *Efraasia minor*.
Thecodontosaurus, Pantydraco and Saturnalia. This study concluded that basal sauropodomorphs lacked adaptations for an efficient mode of quadrupedal locomotion in the forelimb and that if quadrupedal locomotion was displayed, it would be through a semi-sprawling gait. The skeletomuscular system of the shoulder shows an increase in the optimization for mobility of the forelimb, and indirect evidence for a grasping hand, but not for agility and velocity. This confirmed an ability to manipulate branches with the hands that was suggested previously (Galton and Upchurch, 2004), but the forelimbs were still generalized enough as to allow some level of quadrupedal locomotion (Remes, 2007). This trend seems to be observed in the forelimbs of most non-sauropod sauropodomorphs, which exhibit only minor modifications in the forelimb compared to basal sauropodomorphs. The anatomy of Antetonitrus ingenipes and Pulanesaura eocollum show the starting point for major modifications of the forelimb skeletomuscular system as seen in derived sauropods (Yates and Kitching, 2003; Remes, 2007; Upchurch et al., 2007a; McPhee et al., 2014, 2015b; McPhee and Choiniere, 2017).

Mussaurus has not been included in the matrices derived from the dataset of Yates (2007b), but this taxon has specimens of all the ontogenetic stages, from hatchlings to adults (Bonaparte and Vince, 1979; Pol and Powell, 2007b; Otero and Pol, 2013). A recent joint range of motion analysis showed that the glenohumeral protraction was greatly constrained, and that a small amount of active pronation of the manus could have been possible in Mussaurus via long-axis rotation at the elbow to achieve semi-pronation of the entire antebrachium (Otero, 2018). The position of Mussaurus is therefore crucial to understand the origins of quadrupedalism in Sauropodomorpha.

One of the most studied prosauropods is Plateosaurus which was originally suggested as a digitigrade biped (Von Huene, 1910). Further studies considered it to be quadrupedal, as were many other archosaurs, with a sprawling stance and plantigrade feet (Jaekel, 1910; Fraas, 1912; Tornier, 1912; Müller-Stoll, 1935). More recent mechanical analysis of the vertebrae started to test the locomotion suggested for Plateosaurus and many other ornithischians. One approach involved the calculation of the bending moment of the vertebrae along the vertebral column (Christian and Preuschoft, 1996). This study employed assessments of extant birds and mammals to establish a mechanical difference between bipedal and quadrupedal stances. This study showed that in bipedal animals there is a maximum bending moment in the hips, whilst in quadrupedal animals, there is an additional local maximum in the shoulders. By comparing
the results from extant animals with those for non-avian dinosaurs, there was some evidence that *Plateosaurus* may have been a habitual quadruped, with the possibility to use a bipedal stance infrequently, probably restricted to standing or fast movements (Christian and Preuschoft, 1996). By contrast, the ornithischian *Iguanodon* showed a maximum bending moment in the hip region and in bending moments in the shoulder girdle, concordant with a frequent bipedal posture with but less with a frequent quadrupedal stance (Christian and Preuschoft, 1996). However, these conclusions proved that vertebrae can convey information about body posture, and the correlation between the pattern of bending moments and mass distribution and body posture, but it is limited to the assumption that the vertebral column serves only for locomotion and that the epaxial muscles do not extend beyond the neural spines of the vertebrae (Christian and Preuschoft, 1996). Moreover, recent reassessments of the hand of *Plateosaurus* concluded that the animal was not able to sustain a quadrupedal stance since the pronation of the manus was not possible (Bonnan and Senter, 2007; Mallison, 2009; Mallison et al., 2009).

The increase of the forearm: hindlimb ratio is beneficial for a quadrupedal stance, and the basal members of Sauropodomorpha (*Euskelosaurus*, *Lufengosaurus*, *Plateosaurus* *Efraasia*, and *Anchisaurus*) have a humerus: femur ratio less than 0.8 (Cooper, 1981). This proportion is not preserved in hatchling individuals, and this coincides with other indications of obligate quadrupedality, as shown in early stages of *Massospondylus*, characterised by a proportionately enormous skull, horizontal neck, the small caudal vertebrae with weakly developed transverse processes and chevrons (Reisz et al., 2005). This hypothesis has been recently revisited, and a modification of this method in addition with detailed studies of the inner ear show that *Massospondylus* possessed bipedal skeletal proportions from embryo to adult (Chapelle, 2018; Neenan et al., 2018).

The anterolateral process of the ulna defines a radial fossa that holds the radius into a medially shifted position, maintaining the radius laying anteromedially to the ulna. This allows the pronation of the hand, making the flexion-extension of the wrist parallel to the direction of travel (Bonnan, 2003). The evolution of a flat dinosaurian hand into a digitigrade and semi-tubular structure relied on the shift in the position of the radius relative to the ulna, altering the digital arch. In this context, as proposed by Bonnan (2003) the sauropod manus originated as an exaptation, tied more to achieving pronation than to the redistribution of weight.
In basal sauropodomorphs, the proximal lateral margin in anterior view is markedly convex, whereas in *Melanorosaurus* is straightened, a feature observed in basal sauropods. The columnar femur is associated with the reduction of limb excursions during locomotion, a clear trend towards graviportal gaits (Yates et al., 2010). Graviportal animals have limbs more adapted to support heavy weight, which requires that the distance from the joint to the insertion of the muscle that moves the limb, i.e., the input lever, is longer with a proportionally short limb. Also, graviportal stance requires that the proximal sections of the limb are longer in comparison to the distal portions. Other dinosaurian clades that developed graviportal stances are Stegosauria, Ceratopsia and Ankylosauria (Maidment and Barrett, 2012).

*Melanorosaurus*, *Antetonitrus*, and *Aardonyx* have a manus that still retain the offset and mobile pollex (Yates and Kitching, 2003; Bonnan and Senter, 2007). This is on its own no indication of grasping functionality since it could be a retention of a plesiomorphic state. Moreover, the grasping ability is not a constraint for bipedalism, since the animal could easily do this when in a stationary stance (Yates et al., 2010). Sauropoda has a set of diagnostic features that lead to the establishment of quadrupedality, such as the increase in the number of sacral vertebrae and the development of an eccentric femoral shaft to counter increased mediolateral forces. These features are not adaptations to quadrupedalism, but they could be coupled with the support of an increase in the gut volume and mass. Finally, there is an indication of a remodelling in the pelvic-femoral musculature, and this is suggested in the lateral shifting of the anterior trochanter relative to the femoral head, making it visible in posterior view (Yates et al., 2010).

This approach was performed by Remes (2007) on the revision of osteological and myological features on more than 100 individuals of about 50 fossil taxa of basal archosaurs, basal dinosauriforms, basal saurischians, basal theropods, and basal sauropodomorphs. From this, several conclusions were obtained regarding the locomotion of basal sauropodomorphs: 1) it is not possible to conclude that *Eoraptor* was an obligate biped, since it retains a plesiomorphic anatomy in the forelimb that would allow a quadrupedal stance with semi-erect humeri, 2) the bipedality of *Herrerasaurus* shows functional parallelism to theropods, but the osteological and myological adaptations for this are not the same as the ones seen in theropods, 3) the pronation of the hand in basal saurischians may have evolved as a result of the specialization of the *M. biceps brachii*/*M. brachialis* system, possibly correlated with the development of a unique tubercle anteriorly on the radius, 4) there is evidence that basal sauropodomorphs improved manoeuvrability of the humerus, the ulna, the radius, and the manus, enabling them
to develop a more effective grasping, 5) there is no evidence of secondary quadrupedalism in sauropods, 6) most basal sauropodomorphs retained quadrupedal locomotion, with semi-erect, partially abducted forelimbs, and several basal sauropodomorphs evolved unique modifications to effectively pronate the manus for locomotion.

To test these new hypotheses, a better-resolved phylogeny of non-sauropodomorphs is required to corroborate or validate the direction of the evolutionary trends between basal saurischians and sauropods and to establish how many times quadrupedality was achieved. The optimization of forelimbs towards a fully erect, parasagittal-swinging columnar gait required a long evolutionary process that was not coupled with the trend to gigantic sizes (Remes, 2007). This would mean that gigantism evolved as an exaptation to quadrupedality, and not that quadrupedality evolved parallel to gigantism (contra Sander et al., 2011).

Recent work on ornithischians using the approach of the Extant Phylogenetic Bracket (EPB) have shown that quadrupedality evolved independently several times and with different constraints (Maidment and Barrett, 2011, 2012). Archosaurs seem to possess a remarkably conservative myology, which allows the reconstruction of many muscles associated with the locomotor modules of dinosaurs. Applying these concepts to ornithischians showed that it was possible to conclude that the morphology of the pectoral girdle and forelimb indicates that the musculature was more analogous to that of crocodilians than birds (Maidment and Barrett, 2012).

The quadrupedal ornithischian lineages were studied to identify osteological correlates for quadrupedality (Maidment and Barrett, 2012). Stegosauria, Ankylosauria and Ceratopsia are uncontrovertially quadrupedal, whereas basal ornithischians and some ornithopods are unequivocally bipedal. By identifying the features that define quadrupedality in these different lineages, it was possible to draw conclusions about two controversial groups: iguanodontian ornithopods and non-ceratopsid ceratopsians (Maidment and Barrett, 2012). The identification of osteological correlates in basal sauropodomorphs has not been performed in basal sauropodomorphs, and an initial attempt based on Maidment and Barrett (2012) is presented in this thesis using a revised phylogeny.

1.6 Conclusions

The large amount of contradiction and confusion in the various studies has led to the lack of consensus regarding the evolution of the group. There is a need to review all of the character lists and operational taxonomic units published throughout the years to generate a consensus
that can be used for further research. Therefore, a supermatrix approach has been chosen to tackle this problem. The supermatrix approach requires gathering all the information contained in the phylogenetic matrices that have been published so far, and the compatibility of these matrices between them needs to be assessed also (see Chapter 2). Character delineation and operationalisation has been identified as the root of incongruence between the phylogenies since the four main character sets published so far have the same explanatory power and choosing one over the other is an arbitrary decision (a detailed account of the evidence to support this claim is outlined in Chapter 3, and a new phylogenetic analysis is provided in Chapter 5). Finally, since there is a large body of work concerning the quadrupedality of dinosaurs, both in sauropodomorphs and ornithischians, in comparison with the discussions of other aspects of the palaeobiology of basal sauropodomorphs, the evidence collected over the years on the origins of quadrupedality can be used a starting point to assess the explanatory power of the modified supermatrix obtained in this work (this analysis is described in detail in Chapter 5).
2 Comparative Cladistics

Cladistic analyses can be divided into two logically distinct phases: character discovery and phylogenetic analysis (Winther, 2009). The first phase refers to the identification of primary homology (sensu de Pinna, 1991; Rieppel, 1994, 2004). The second phase refers to the identification of secondary homologies through the inference of the most parsimonious cladogram, which is itself based on the data collected in the first phase. Initial cladistic analyses were constrained by computer power, so that the authors would limit the number of characters. This meant that characters were recursively tested against one another to limit the number of characters to be analysed (Kitching et al., 1998). The advent of more efficient computer hardware and parsimony software (e.g. Farris et al., 1970) reduced the restrictions on the size of the matrices (Mounce, 2013). Based on a survey of cladistic analyses of fish, Mooi and Gill (2010) argued that the more relaxed constraints along with the desire to increase the ratio of characters to taxa might have encouraged practitioners to incorporate as many characters as possible, with less stringent quality control. A similar issue has been suggested for all vertebrates in general (Mounce, 2013; Mounce et al., 2016). Given that the phylogenetic analysis phase will identify the ‘noisy’ characters, there has not been an imperative for practitioners to analyse characters a priori (Mooi and Gill, 2010; Mounce, 2013). Here, an extensive literature review did not find any previous attempts to analyse characters a priori in the case of basal sauropodomorph phylogenies, although the problem has been diagnosed by Peyre de Fabrègues et al. (2015).

Many researchers have approached the problem of the early evolutionary history of the sauropodomorph dinosaurs, as outlined in Chapter 1. For this reason, there are many matrices to choose from when doing phylogenetic analyses. Some researchers have leant towards more complete geographic representation of the taxonomic scope to discriminate the best matrix, for example Upchurch et al. (2007) sampled all of the then published sauropodomorphs from Argentina (Martínez, 2009). On the other hand, the recursively modified versions of the dataset of Yates (2007) were built and expanded on the basis that these sample the largest number of characters and taxa (e.g. Apaldetti et al., 2011, 2013, 2014, McPhee et al., 2014, 2015b, 2015a).
In this chapter, the phylogenetic phase of cladistic analysis is explored in comparative terms. The matrices were taken from the original publications, and the most recently amended versions of each matrix were assessed (see Chapter 3 for a detailed account of the modifications carried out on each matrix).

First, taxonomic scope was investigated to assess the claim that one matrix or another has the most comprehensive or largest sample. Then, using standardised searching techniques, the stratigraphic fit was assessed to find if one topology is more congruent with the ages of the specimens than any of the others. Subsequently, the phylogenetic signals derived independently from the three main body regions, i.e. the cranial, axial and appendicular skeletons, were assessed under the same searching techniques for all the matrices to assess whether one part of the skeleton contains more phylogenetic information than others (partition analysis). Using the partition analysis approach, the character delineation is also tested here to assess if there is any difference between the information conveyed by characters that describe qualitative traits (discrete) and the characters that convey continuous information via an incongruence length difference (ILD) test, to assert the homogeneity of these two partitions. Finally, the character composition of each of the matrices was compared to see if any of the identified phylogenetic signals in the partition analysis may be biasing the final topologies.
Currently, there are three competing hypotheses on the early evolution of Sauropodomorpha (Figure 2.1). All three hypotheses agree in considering ‘Prosauropoda’ to be paraphyletic. The first hypothesis, proposed by Upchurch et al. (2007), identifies a clade that can be referred to as ‘core Prosauropoda’, a less inclusive paraphyletic group including the most basal forms, such as *Thecodontosaurus*, *Efraasia* and *Pantydraco*, and a more derived clade that includes Anchisauridae (Marsh, 1885), Melanorosauridae (Von Huene, 1929) and Sauropoda (Marsh, 1878). The second hypothesis was proposed by Yates (2007b) and considers all ‘prosaupods’ to be in a pectinate paraphyletic arrangement. Finally, the third hypothesis, produced by Pol et al. (2011), proposed that some groups are paraphyletic at the base of the tree, i.e. Thecodontosauridae (Haughton, 1924), Plateosauridae (Marsh, 1895) and Riojasauridae (Yates, 2007a), but that a small, derived group of ‘traditional
prosauropods’ [Massospondylidae (Von Huene, 1914a) + Yunnanosauridae (Young, 1942)] is the sister taxon of Anchisauria (Galton and Upchurch, 2004).

These three hypotheses are based on different phylogenetic matrices that have undergone modification over time. Two of the three character lists have been reworked by later authors who added more specimens, more taxa and/or new characters, as well as changing some character wording and definitions (Figure 2.1). The most widely used matrix is Yates et al. (2010), a modified version of the dataset in Yates (2007). A modified form of the Yates et al. (2010) matrix, compiled by Apaldetti et al. (2011), has been used in more recent cladistic analyses as it was considered the most extensive and complete dataset (Otero and Pol, 2013; McPhee et al., 2014, 2015a, b; Otero et al., 2015; Peyre de Fabrègues and Allain, 2016). A similar evaluation was carried out by Martínez (2009) to justify the use of the Upchurch et al. (2007) matrix over that of Yates (2007b). One recent work (Sekiya et al., 2013) attempted to merge the two most comprehensive character lists available at that time (Upchurch et al., 2007a; Apaldetti et al., 2011) and to reassess some characters. However, the number of taxa included was limited to those that were in common between the matrices, and in most of the cases revision of the characters was based solely on the literature rather than first-hand observation of specimens (Sekiya et al., 2013). The matrix of Pol et al. (2011) has largely been ignored and has no modifications. Peyre de Fabrègues et al. (2015) compared the three phylogenies and found a consensus on the general topologies. All three competing hypotheses agree on the existence of Anchisauria as a paraphyletic array of taxa close to the origin of Sauropoda. The clade definitions used here correspond to the phylogenetic definitions stated in Chapter 1 (1.4.1).

2.2 Taxonomic scope

The comparative analysis performed by Peyre de Fabrègues et al. (2015) found that an even reduction of the taxonomic scope in the three matrices supported the original topologies that were derived therefrom. Here, I test the hypothesis that taxon choice plays a role in the topological inconsistencies seen between analyses: this is explored for the first time by including all the operational taxonomic units (OTU) in each matrix. The first step towards this was to search several online databases, i.e. PaleoBiology Database (paleobiodb.org), and Biodiversity Heritage Library (biodiversitylibrary.org), and a comprehensive literature search, for all the taxa that
have been referred historically to either ‘Prosauropoda’ or ‘basal Sauropodomorpha.’ This list guided the sampling of taxa to be included in the analyses presented herein.

The new database was compiled to reflect the year of naming/publication of each taxon, meaning that assuming a representative sampling, species would be added progressively into the new datasets. Although three primary datasets have been regarded as addressing the specific problem of basal sauropodomorph evolution (see above), there are 31 publications dealing with the evolution of saurischians and sauropodomorphs that include basal sauropodomorph taxa as OTUs, the first of these being the phylogenetic analyses published by Upchurch (1995). Taxonomic scope is a two-fold issue: one of taxonomic inclusion, where newly named taxa are thoroughly included in updated versions of the matrices, and geographic inclusion, where there is a trend to include more specimens from specific regions.

2.2.1 Taxonomic inclusion

The first basal sauropodomorph to be described was *Thecodontosaurus antiquus* (Riley and Stutchbury, 1836). From 1836 until 1995, when the first numerical phylogenetic analysis was published, there were 34 named, valid taxa that were available for inclusion (Table 2.1).

The only taxon that has been used in all phylogenetic analyses is *Plateosaurus engelhardtii*. Moreover, only eight of the 34 taxa have been included in >75% of the earlier analyses (see Table 2.1): *Eoraptor lunensis*, *Lufengosaurus huenei*, *Plateosaurus engelhardtii*, *Massospondylus carinatus*, *Anchisaurus polyzelus*, *Vulcanodon karibaensis*, *Barapasaurus tagorei* and *Shunosaurus lii*, the latter three being unambiguous sauropods. Several of the taxa listed in Table 2.1 are taxonomically unstable and we are excluded from half of the analyses for several reasons: (1) there was a taxonomic opinion on the recognition of them as synonyms, e.g. *Ammosaurus* (Marsh, 1889, 1891; Galton, 1971, 2012; Galton and Cluver, 1976; Sereno, 2007c; Tweet and Santucci, 2011), ‘*Gyposaurus’ sinensis* (Young, 1941a; Galton and Cluver, 1976; Haughton, 1924; Van Heerden, 1979; Galton and Upchurch, 2004), *Euskelosaurus* (Seeley, 1894; Haughton, 1924; Van Heerden, 1979; Galton and Upchurch, 2004), *Euchenesaurous* (van Hoepen, 1920; Haughton, 1924; Van Heerden, 1979), *Plateosaurus ingens* (Rütimeyer, 1857; Von Huene, 1932; Galton, 1986b, 2001a), and *Sellosaurus* (Galton, 1985c, 1999b, 2001b; Galton and Bakker, 1985; Moser, 2003; Yates, 2003a; Galton
and Upchurch, 2004); (2) they were excluded because the taxon was known only from juvenile material, e.g. *Mussaurus* (Bonaparte and Vince, 1979; Galton and Upchurch, 2004; Reisz et al., 2013), (3) the validity of the species was doubtful, e.g. the case for *Kotasaurus* being a chimera (Yates, 2007a). Others were considered too incomplete for inclusion in these earlier works, such as *Ohmdenosaurus*.

The availability of specimens for phylogenetic analysis has varied over time because of differences in the history of discovery. To avoid biasing the analysis due to these differences, a calibrated frequency (fi) was calculated to reflect more precisely ‘availability.’ This metric takes into account the year of naming/publication to avoid low percentages when the species have been recently discovered. To calibrate for this frequency, the ‘availability’ of the specimen is considered to be the year when a name-bearing publication with a description of the specimen was produced, because there is a source of information available to assess characters. This year of publication is counted as “year 0 of availability”, and only the years after this are considered in the calculation of the frequency. Therefore, the analyses published before that year of availability are counted as “unavailable” (“u = Unavailability”). This frequency is calculated as in equation 2.1.

$$f_i = \frac{n_i}{\sum_j n_j - U}$$  \hspace{1cm} (2.1)

In Table 2.2 we can see that even the most recently named taxa do not have a high relative frequency of inclusion, meaning that the information that new specimens can contribute to analyses is often still not being captured. For instance, *Meroktenos* would have been available for inclusion in five analyses but has only been used in one. *Meroktenos* then has the same calibrated relative frequency of usage as *Pampadromaeus*, a specimen named five years earlier than *Meroktenos*. Several taxa are consistently used in phylogenetic analyses, but there are several other taxa that have been side-lined without justification as well as for the reasons listed above. This indicates that taxonomic inclusion has not been carried out thoroughly when building or amending a matrix, creating palimpsests.

### 2.2.2 Geographic inclusion

This new, comprehensive dataset allows geographic inclusion to be explored also. Although most of the taxa discovered before 1955 come from Laurasia (North
America, Europe, and Asia) since 1955 there has been an increase in the basal sauropodomorph material collected from Gondwana (South America, Africa, India and Antarctica). Today, there is an almost one-to-one ratio of sauropodomorph species collected from Laurasia and Gondwana (the ratio is 0.91, with few more species recorded from Gondwana; see Table 2.3).

In Figure 2.2 the taxonomic composition of each dataset is plotted against the logarithm of the ratio of species between Laurasia and Gondwana demonstrating that most analyses have been biased towards Laurasian taxa, despite the fact that Gondwanan and Laurasian taxa have been discovered in approximately equal proportions since 1990 (Figure 2.3).” Although every new discovery has not been incorporated systematically into these datasets, analyses since 2015 have had a Gondwanan, rather than Laurasian bias, perhaps because of recent analyses being conducted largely by southern hemisphere researchers.

These two analyses of the taxonomic scope show that matrices are not capturing the same information and that choosing one or another based on data completeness is not an adequate approach.
Table 2.1 Species recognised as unequivocal ‘prosauropods’ or basal sauropods that were discovered between 1836 and 1994. These specimens can be considered as available for the time of study to be considered in the analyses. In total, 32 matrices are being compared, and the frequency of the analyses where they appear is also shown.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Year of discovery</th>
<th>Frequency</th>
<th>Total analyses = 32</th>
</tr>
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<tbody>
<tr>
<td>Plateosaurus</td>
<td>engelhardti</td>
<td>1837</td>
<td>32</td>
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<tr>
<td>Massospondylus</td>
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<td>1854</td>
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<td>Vulcanodon</td>
<td>karibaensis</td>
<td>1972</td>
<td>27</td>
<td>84.38</td>
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<tr>
<td>Barapasaurus</td>
<td>tagorei</td>
<td>1975</td>
<td>27</td>
<td>84.38</td>
</tr>
<tr>
<td>Shunosaurus</td>
<td>lii</td>
<td>1983</td>
<td>27</td>
<td>84.38</td>
</tr>
<tr>
<td>Lafengosaurus</td>
<td>huenei</td>
<td>1940</td>
<td>26</td>
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<td>huangi</td>
<td>1940</td>
<td>23</td>
<td>71.88</td>
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<td>incertus</td>
<td>1969</td>
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<td>fortis</td>
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<td>1978</td>
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Table 2.2 Relative frequency of newly discovered specimens available for research.

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<th>Unavailability</th>
<th>Frequency</th>
<th>Relative frequency</th>
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<td>2007</td>
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<td>nigerensis</td>
<td>2009</td>
<td>11</td>
<td>4</td>
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<tr>
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<td>mognai</td>
<td>2009</td>
<td>12</td>
<td>12</td>
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<td>2009</td>
<td>12</td>
<td>2</td>
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<td>Panphagia</td>
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<td>2009</td>
<td>12</td>
<td>9</td>
<td>45.00</td>
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<td>2009</td>
<td>12</td>
<td>5</td>
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<td>Aardonyx</td>
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<td>2010</td>
<td>12</td>
<td>13</td>
<td>65.00</td>
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<tr>
<td>Seitaad</td>
<td>ruessi</td>
<td>2010</td>
<td>12</td>
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<td>Chromogisaurus</td>
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<td>2010</td>
<td>14</td>
<td>4</td>
<td>22.22</td>
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<tr>
<td>Jaklapallisaurus</td>
<td>asymmetrca</td>
<td>2011</td>
<td>16</td>
<td>1</td>
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<td>Nambalia</td>
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<td>16</td>
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<td>Sarahsaurus</td>
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<td>2011</td>
<td>18</td>
<td>8</td>
<td>57.14</td>
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<td>barberenai</td>
<td>2011</td>
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<td>2015</td>
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<td>Eucnemosauras</td>
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<td>27</td>
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<td>schultzi</td>
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<td>28</td>
<td>2</td>
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</tr>
<tr>
<td>Xingxiulong</td>
<td>chengi</td>
<td>2017</td>
<td>29</td>
<td>1</td>
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Table 2.3 Summary of the analyses compared in this work with the proportion of Laurasian and Gondwanan basal sauropodomorphs used in the analysis. This includes only specimens referred to either ‘prosauropods,’ ‘basal sauropodomorphs’ or ‘basal sauropods.’

<table>
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<th>REFERENCE</th>
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<th>GONDWANAN TAXA</th>
<th>RATIO</th>
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<td>35</td>
<td>0.914286</td>
</tr>
<tr>
<td>2</td>
<td>Upchurch (1995)</td>
<td>6</td>
<td>5</td>
<td>1.2</td>
</tr>
<tr>
<td>3</td>
<td>Wilson and Sereno (1998)</td>
<td>4</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>4</td>
<td>Wilson (2002)</td>
<td>5</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>Yates (2003)</td>
<td>3</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>6</td>
<td>Yates and Kitching (2003)</td>
<td>9</td>
<td>7</td>
<td>1.285714</td>
</tr>
<tr>
<td>7</td>
<td>Galton and Upchurch (2004)</td>
<td>12</td>
<td>9</td>
<td>1.333333</td>
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<tr>
<td>8</td>
<td>Kutty et al. (2007)</td>
<td>12</td>
<td>10</td>
<td>1.2</td>
</tr>
<tr>
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<td>Upchurch et al. (2007)</td>
<td>14</td>
<td>10</td>
<td>1.4</td>
</tr>
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<td>20</td>
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<tr>
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</tr>
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<td>12</td>
<td>Smith and Pol (2007)</td>
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<td>13</td>
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</tr>
<tr>
<td>13</td>
<td>Remes et al. (2009)</td>
<td>5</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>14</td>
<td>Sertich and Loewen (2010)</td>
<td>21</td>
<td>15</td>
<td>1.4</td>
</tr>
<tr>
<td>15</td>
<td>Ezcurra (2010)</td>
<td>20</td>
<td>14</td>
<td>1.428571</td>
</tr>
<tr>
<td>16</td>
<td>Knoll et al. (2010)</td>
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<td>14</td>
<td>1.428571</td>
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<td>17</td>
<td>Nesbitt et al. (2011)</td>
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<td>2</td>
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<td>18</td>
<td>Novas et al. (2011)</td>
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<td>Pol et al. (2011)</td>
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<td>Apaldetti et al. (2011)</td>
<td>21</td>
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<td>1.235294</td>
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<tr>
<td>21</td>
<td>Cabreira et al. (2011)</td>
<td>2</td>
<td>5</td>
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<td>24</td>
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<td>18</td>
<td>1.111111</td>
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<td>16</td>
<td>1.3125</td>
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<td>Otero et al. (2015)</td>
<td>21</td>
<td>18</td>
<td>1.166667</td>
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<tr>
<td>27</td>
<td>McPhee et al. (2015a)</td>
<td>16</td>
<td>21</td>
<td>0.761905</td>
</tr>
<tr>
<td>28</td>
<td>McPhee et al. (2015b)</td>
<td>17</td>
<td>20</td>
<td>0.85</td>
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<tr>
<td>29</td>
<td>Peyre de Fabregues et Allain (2016)</td>
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<td>19</td>
<td>1.105263</td>
</tr>
<tr>
<td>30</td>
<td>Cabreira et al. (2016)</td>
<td>3</td>
<td>5</td>
<td>0.6</td>
</tr>
<tr>
<td>31</td>
<td>Wang et al. (2017)</td>
<td>18</td>
<td>20</td>
<td>0.9</td>
</tr>
<tr>
<td>32</td>
<td>Chapelle et al. (2018)</td>
<td>18</td>
<td>19</td>
<td>0.947368</td>
</tr>
<tr>
<td>33</td>
<td>Muller et al. (2018)</td>
<td>3</td>
<td>5</td>
<td>0.6</td>
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</table>
Figure 2.2 Graph showing the proportion of Laurasian/Gondwanan taxa used in the different analyses considered in this work. The red dashed line represents the proportion of taxa that have been found in this work from studying the online databases mentioned in section 2.2. The solid dots indicate that there are more Laurasian taxa than there are Gondwanan taxa, and the inverse proportion is represented by crosses. Most analyses oscillate around the currently known proportion (red dashed line). For reference, the analysis number is the same as the one given in Table 2.3.

Figure 2.3 Graph showing the increase of taxa described from Laurasia (blue) and Gondwana (red) from 1836 until today.
2.3 Standardised searching techniques

All analyses differ in the search engine and parameters that produce the resulting topologies (Table 2.4). The number of most parsimonious trees (MPTs) and the length of these trees differ between all of the analyses, but the consistency and retention indexes are similar for all of the phylogenies when reported.

When the Consistency Index (CI) = 1 the characters have evolved perfectly parsimoniously. However, as the number of taxa increases, the CI tends to increase as well (Archie, 1989). Therefore, this metric is not a reliable way to compare matrices when the number of OTUs changes. As seen in Table 4, the CI value ranges from 0.23 to 0.4.

Another metric reported in the literature is the Retention Index (RI) that overcomes the problem of the number of OTUs sampled. When RI = 1, the characters are consistent with the phylogeny showing no homoplasy. This metric measures both the amount of homoplasy and how much the synapomorphies support the tree. This metric is more consistent throughout the sauropodomorph literature, with reported values ranging between 0.6 and 0.7.

To explore the impact of different search parameters on the datasets, all of them were analysed using the same search techniques in TNT 1.5 beta (Goloboff et al., 2008). The matrices were all analysed with the new technology search function (ratchet and drift set to their default values of 10 iterations and 10 cycles respectively) with 1000 random additional sequences.

The matrices analysed were the most recent versions of each of the major published matrices, as of January 2018. These matrices were Apaldetti et al. (2013), based on Upchurch et al. (2007) and Wang et al. (2017), based on Yates et al. (2010). Sekiya et al. (2013) and Pol et al. (2011) have not been modified subsequently. To simplify the following section, the code mU2007 stands for the amendments to Upchurch et al. (2007), including the characters and taxa modified by Sekiya (2010), Sertich and Loewen (2010), Rowe et al. (2011) and Apaldetti et al. (2013). The code mY2010 stands for the latest modifications done to Yates et al. (2010) and the recursive modifications that were applied to the dataset in Apaldetti et al. (2011), McPhee et al. (2015) and Wang et al. (2017).
The evolution of quadrupedalism has occupied much of the literature in sauropodomorphs (Appendix 1), and this large amount of independently discussed information provides a framework of evidence to compare the different topologies and the different phylogenetic scenarios they imply.

The analysis of mU2007 generated 22 MPTs with tree lengths of 883 steps. The strict consensus has a CI = 0.350 and a RI = 0.621. Compared to previous analyses of this dataset, mU2007 has a very low number of MPTs, the lowest number of steps, and the CI and RI fall within the previously reported range. The strict consensus shows a topology where most of the non-sauropod sauropodomorphs form a monophyletic group that is the sister clade to a monophyletic Sauropoda (Figure 2.4). *Jingshanosaurus*, *Antetonitrus*, *Blikanasaurus*, and *Melanorosaurus* are placed at the base of Sauropoda. This scenario is consistent with other matrices derived from Upchurch et al. (2007).

The analysis of mY2010 generated 12 MPTs with tree lengths of 1313 steps. The strict consensus shows a comb-like arrangement from basal saurischians to sauropod dinosaurs with a CI = 0.326 and a RI = 0.674. The analysis of mY2010 produced a similar number of MPTs to earlier analyses (i.e. Sertich and Loewen, 2010; Apaldetti et al., 2011; Otero and Pol, 2013; McPhee et al., 2014) that have similar lengths to those in some other publications (Apaldetti et al., 2011; Otero and Pol, 2013; Otero et al., 2015). The CI and RI fall within the ranges published previously.

Several smaller clusters are recovered: Plateosauridae (*Unaysaurus*, *Plateosaurus engelhardti*, *Plateosaurus gracilis*), Riojasauridae (*Eucnemesaurus*, *Riojasaurus*), Massospondylidae (including ‘Lufengosaurinae’, i.e. *Lufengosaurus*, *Coloradisaurus*, *Glacialisaurus* and ‘Massospondylinae’, i.e., *Massospondylus*, *Adeopapposaurus*, *Leyesaurus*) and Yunnanosauridae (*Yunnanosaurus*, *Seitaad*, *Jingshanosaurus*). Plateosauridae has taxa with evidence of obligate bipedality (e.g. *Plateosaurus* in Bonnan and Senter, 2007), whereas ‘Lufengosaurinae’ has taxa considered to be bipedal but with weak evidence. Yunnanosauridae also contains taxa that have been considered to be bipedal, although this has been suggested merely based on the body proportions rather than biomechanical analysis, as has been carried out for Plateosauridae (Bonnan and Senter, 2007; Mallison, 2009; Mallison et al., 2009; Figure 2.5).
Table 2.4 Summary of the various search parameters employed in the different analyses outlined in Chapter 1.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>IG</th>
<th>OG</th>
<th>Ord. chrs.</th>
<th>Polymorphisms</th>
<th>A posteriori deleted OTU</th>
<th>MPTs (L)</th>
<th>Searching algorithm</th>
<th>RI</th>
<th>CI</th>
<th>Searching engine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upchurch et al. (2007)</td>
<td>27</td>
<td>7</td>
<td>1</td>
<td>Uncertainty</td>
<td>Blikanasaurus</td>
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<tr>
<td>Martinez (2009)</td>
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<td>7</td>
<td>1</td>
<td>Uncertainty</td>
<td>Blikanasaurus</td>
<td>1 (739)</td>
<td>Heuristic search, random addition sequence, TBR branch-swapping algorithm</td>
<td>NP</td>
<td>NP</td>
<td>TNT v 1.0</td>
</tr>
<tr>
<td>Yates et al. (2010) (Analysis 1)</td>
<td>29</td>
<td>7</td>
<td>1</td>
<td>Uncertainty</td>
<td>None</td>
<td>82 (744)</td>
<td>Heuristic search, TBR branch swapping, 100 random addition sequence replicates</td>
<td>NP</td>
<td>NP</td>
<td>PAUP 4.0b10</td>
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<tr>
<td>Yates et al. (2010) (Analysis 2)</td>
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<td>7</td>
<td>1</td>
<td>Uncertainty</td>
<td>Blikanasaurus, Lessemsaurus, Plateosauravus</td>
<td>1 (737)</td>
<td>Heuristic search, TBR branch swapping, 100 random addition sequence replicates</td>
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<td>NP</td>
<td>PAUP 4.0b10</td>
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<tr>
<td>Sertich and Loewen (2010)</td>
<td>27</td>
<td>7</td>
<td>1</td>
<td>Uncertainty</td>
<td>Blikanasaurus</td>
<td>18 (767)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates (holding 10 trees per replicate)</td>
<td>0.659</td>
<td>0.387</td>
<td>TNT v 1.1</td>
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</table>
Table 2.4 (cont.)

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<th>A posteriori deleted OTU</th>
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<th>RI</th>
<th>CI</th>
<th>Searching engine</th>
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<td>Yates (2007b)</td>
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<td>Polymorphisms</td>
<td>NA</td>
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<td>NP</td>
<td>PAUP 4.0b10</td>
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<td>Smith and Pol (2007)</td>
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<td>36</td>
<td>Polymorphisms</td>
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<td>PAUP 4.0b10</td>
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<td>Ord. chrs.</td>
<td>Polymorphisms</td>
<td>A posteriori deleted OTU</td>
<td>MPTs (L)</td>
<td>Searching algorithm</td>
<td>RI</td>
<td>CI</td>
<td>Searching engine</td>
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<td>-----</td>
<td>------</td>
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</tr>
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<td>9</td>
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<td>Polymorphisms</td>
<td><em>Plateosaurus ingens</em></td>
<td>208 (1135)</td>
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<td>NP</td>
<td>NP</td>
<td>PAUP 4.0b10</td>
</tr>
<tr>
<td>Yates et al. (2010) (Analysis 4)</td>
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<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td><em>Plateosaurus ingens</em>, <em>Blikanasaurus</em>, <em>Camelotia</em>, <em>Isanosaurus</em></td>
<td>28 (1119)</td>
<td>Heuristic search, TBR branch swapping, 100 random addition sequence replicates</td>
<td>NP</td>
<td>NP</td>
<td>PAUP 4.0b10</td>
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<tr>
<td>Sertich and Loewen (2010)</td>
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<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>16 (1173)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates (holding 10 trees per replicate)</td>
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<td>0.387</td>
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</tr>
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<td>Ezcurra et al. (2010)</td>
<td>43</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>100 (1186)</td>
<td>Heuristic search, 50 replications (holding 10 trees per replicate)</td>
<td>0.697</td>
<td>0.372</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Analysis</td>
<td>IG</td>
<td>OG</td>
<td>Ordered characters</td>
<td>Polymorphisms</td>
<td>(A_{\text{posteriori}}) deleted OTU</td>
<td>MPTs (L)</td>
<td>Searching algorithm</td>
<td>RI</td>
<td>CI</td>
<td>Searching engine</td>
</tr>
<tr>
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</tr>
<tr>
<td>Knoll et al. (2010)</td>
<td>36</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>60 (1128)</td>
<td>Heuristic search, stepwise addition</td>
<td>0.693</td>
<td>0.370</td>
<td>PAUP 4.0b10</td>
</tr>
<tr>
<td>Novas et al. (2010)</td>
<td>45</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>540 (1210)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates (holding 10 trees per replicate)</td>
<td>0.677</td>
<td>0.368</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Apaldetti et al. (2011)</td>
<td>47</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>18 (1301)</td>
<td>Heuristic search, 1000 replicates, TBR branch swapping</td>
<td>0.667</td>
<td>0.325</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Cabreira et al. (2011)</td>
<td>44</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>4 (1171)</td>
<td>Heuristic search, TBR branch swapping, 10,000 random addition sequence replicates</td>
<td>0.679</td>
<td>0.376</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Rowe et al. (2011) (Analysis 1)</td>
<td>43</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>130 (1234)</td>
<td>Not specified</td>
<td>0.657</td>
<td>0.341</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Analysis</td>
<td>IG</td>
<td>OG</td>
<td>Ordered characters</td>
<td>Polymorphisms</td>
<td>A \textit{posteriori} deleted OUT</td>
<td>MPTs (L)</td>
<td>Searching algorithm</td>
<td>RI</td>
<td>CI</td>
<td>Searching engine</td>
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</tr>
<tr>
<td>Martinez et al. (2012)</td>
<td>42</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>60 (1192)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates</td>
<td>0.69</td>
<td>0.37</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Apaldetti et al. (2013) (Analysis 1)</td>
<td>45</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>36 (1277)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates</td>
<td>0.670</td>
<td>0.330</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Otero et al. (2013)</td>
<td>49</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>10 (1332)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates (holding 10 trees per replicate)</td>
<td>0.66</td>
<td>0.32</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>McPhee et al. (2014)</td>
<td>42</td>
<td>9</td>
<td>36</td>
<td>Polymorphisms, Character 184 deleted</td>
<td>NA</td>
<td>16 (1194)</td>
<td>Not specified</td>
<td>NR</td>
<td>NR</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Analysis</td>
<td>IG</td>
<td>OG</td>
<td>Ordered characters</td>
<td>Polymorphisms</td>
<td>A posteriori deleted OUT</td>
<td>MPTs (L)</td>
<td>Searching algorithm</td>
<td>RI</td>
<td>CI</td>
<td>Searching engine</td>
</tr>
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</tr>
<tr>
<td>McPhee et al. (2015a)</td>
<td>44</td>
<td>9</td>
<td>40</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>69 (1264)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates holding 10 trees per replicate</td>
<td>NR</td>
<td>NR</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>McPhee et al. (2015b)</td>
<td>46</td>
<td>9</td>
<td>43</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>8 (1244)</td>
<td>Not specified</td>
<td>0.7</td>
<td>0.34</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Otero et al. (2015)</td>
<td>47</td>
<td>9</td>
<td>37</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>48 (1355)</td>
<td>Heuristic search, TBR branch swapping, 1000 random addition sequence replicates holding 10 trees per replicate</td>
<td>0.66</td>
<td>0.32</td>
<td>TNT v 1.1</td>
</tr>
<tr>
<td>Pol et al. (2011)</td>
<td>15</td>
<td>35</td>
<td>32</td>
<td>Polymorphisms</td>
<td>NA</td>
<td>7452 (619)</td>
<td>Heuristic tree search (1000 replicates), TBR (holding 10 trees per replicate)</td>
<td>0.795</td>
<td>0.519</td>
<td>TNT v. 1.0</td>
</tr>
<tr>
<td>Sekiya et al. (2013)</td>
<td>29</td>
<td>4</td>
<td>30</td>
<td>Polymorphism</td>
<td>10 (1513)</td>
<td></td>
<td>Heuristic search</td>
<td>0.498</td>
<td>0.357</td>
<td>PAUP 4.0b10</td>
</tr>
</tbody>
</table>
Figure 2.4 Strict consensus obtained from the matrix of Upchurch et al. (2007) with the inclusion of the taxa (Lessemsaurus, Coloradisaurus, Glacialisaurus, Adeopapposaurus, Leyesaurus, Sarahsaurus) and characters in Apaldetti et al. (2013) and Xixiposaurus from Sekiya et al. (2010). The tree is plotted against the geological scale using the R package strap. For this, the minimum branch length option was set at 2 million years, estimating the root age for 253.5 Mya, and estimating a synchronous diversification of Sauropoda and Prosauropoda.

Anchisaurus is placed at the base of the clade that leads towards obligate quadrupedality. Based on its morphology it seems that this dinosaur was facultatively bipedal (Galton, 1971; Galton and Cluver, 1976). Anchisauria also contains Mussaurus, which has recently been argued to have been facultatively quadrupedal based on biomechanical analyses (Otero et al., 2017), and Aardonyx, which lacks the specialisations found in other quadrupedal sauropodomorphs (Yates et al., 2010). A polytomy of Blikanasaurus, Melanorosaurus, and Antetonitrus, which have all been proposed to be quadrupedal animals (Charig et al., 1965; Heerden and Galton, 1997; Galton and Heerden, 1998), is at the base of the clade Sauropoda. This topology implies that quadrupedality was acquired gradually from Anchisaurus onwards, becoming established quickly during the Norian. This is consistent with what was reported from several matrices, more recently Wang et al. (2017), but differs from other results, such as those reported by Chapelle and Choiniere (2018), where bipedal ‘massospondylids’ are nested within Anchisauria. In the latter
scenario, quadrupedality arose in Anchisaurus and Aardonyx. Although in Yates et al. (2010) Eoraptor is found as a sauropodomorph, the other topologies place Eoraptor as a basal theropod instead, reducing the role that Eoraptor has in understanding the transition from bipedal locomotion to obligate quadrupedality, and the similarities that Eoraptor has with Buriolestes and Bagualosauras are a case of convergence or plesiomorphic retention of a basal saurischian bauplan.

Reanalyses of the Sekiya et al. (2013) dataset suggest that the reported analyses did not find all of the MPTs, and therefore the scenarios found herein are different. The new analysis herein produced eight MPTs with lengths of 1498 steps, with values of CI = 0.353 and a RI = 0.490. In contrast, the original analysis produced 10 MPTs with a length of 1513 steps. However, the homoplasy metrics are similar (CI = 0.357, RI = 0.498).

Whereas in Sekiya et al. (2013) the clade “Prosauropoda” was found to contain Anchisaurus, Gyposaurus, Sarahsaurus, Massospondylus, Adeopapposaurus, Plateosauras Riojasaurus, Coloradisaurus, and Lufengosaurus, the results of the re-analysis presented here are more similar to the topologies reported from the versions derived from the dataset of Yates et al., 2010 (Figure 2.5). It still supports Guaibasaurus as a basal sauropodomorph, but this merely reflects the small number of non-sauropodomorph taxa in the dataset. Sekiya et al. (2013) produced a matrix that is derived from the matrices of Yates et al. (2010) and Upchurch et al. (2007). Although the character list was compiled through revising and joining the characters that referred to the same feature in both matrices, this dataset displays a preference for additive binary coding. Instead of many multistate characters (as in the matrix by Yates et al., 2010), there are sets of binary characters (as they were worded by Upchurch et al., 2007). This means that some multistate characters in Yates et al. (2010) were split according to the binary characters coded by Upchurch et al. (2007). It was expected that, as with the previous re-analyses, the matrix of Sekiya et al. (2013) would have produced the same results as the ones published. And that because the coding strategies in Upchurch et al. (2007) were implemented when merging the character lists of mU2007 and mY2007, the resulting topologies would resemble the ones in mU2007.

Finally, the reanalysis of the matrix of Pol et al. (2011) produced the largest number of MPTs (318), with the shortest tree lengths (618 steps). The MPTs have homoplasy values of CI = 0.444 and a RI = 0.715. In Pol et al. (2011), the strict consensus exhibits a topology
similar to the topologies obtained from the modified versions of Yates et al (2010). The topology reported by Pol et al. (2011) was modified by those authors *A posteriori* by the removal of *Jingshanosaurus*, *Blikanasaurus*, *Camelotia*, and *Isanosaurus*. For comparative purposes, these taxa were not excluded from the reanalysis here because they were consistently included in the previous three analyses (except for *Isanosaurus*). Two main clades are identifiable: Massospondylidae and Sauropoda (Figure 2.7).

Although the relationships between basal sauropodomorphs are almost completely unresolved in the re-analysis of the Pol et al. (2011) dataset, there is high resolution towards the base of the tree, and it includes more theropods and silesaurids than the other analyses.

Summary. Given that using a standardised set of search techniques and the same number of replicates still results in topologies that differ from one another, we can discount the methodological parameters as the cause of inconsistencies between competing for data matrices. They do result in changes to the originally published topologies, but they do not differ radically from what was published previously.
Figure 2.5 Strict consensus obtained from the matrix by Yates (2007) with the inclusion of the subsequent modifications done by Yates et al. (2010), Apaldetti et al. (2011), McPhee et al. (2015), Wang et al. (2017). The tree is plotted against the geological scale using the R package strap. For this, the minimum branch length option was set at 0.5 million years setting the root age to 251 Mya. This scaled model suggests that the diversification rate of Sauropodomorpha corresponds to an explosive radiation in very short time.
Figure 2.6 Strict consensus obtained from the matrix by Sekiya et al. (2013). The tree is plotted against the geological scale using the R package strap. For this, the minimum branch length option was set at 1.5 million years, setting the root age to 254.7 Mya.
Figure 2.7 Strict consensus tree obtained from the matrix by Pol et al. (2011). The tree is plotted against the geological scale using the R package strap. For this, the minimum branch length option was set at 2 million years, setting the root age to 248 Mya.
2.4 Stratigraphic fit

Data completeness is often used as a discriminator when choosing between different matrices, e.g. Apaldetti et al. (2014). Temporal information can also be explored as an independent test to see if any of the phylogenetic scenarios are stratigraphically more congruent than the others. Stratigraphic congruence of the MPTs derived from the above-mentioned analyses was assessed using the R package strap (Bell and Lloyd, 2015). A clade is stratigraphically congruent if its oldest (first) occurrence is equal to or younger than the oldest first occurrence of the sister taxon of the clade. Stratigraphic congruence tests the topologies against the stratigraphic order of appearance of the taxa included according to the minimum ages of nodes (based on the maximum age of any other sister group above each node; Benton and Hitchin, 1996; Pol et al., 2004; Figure 2.8).

The strap package allows comparison of the MPTs through several measures of congruence. Huelsenbeck (1994) proposed the Stratigraphic Consistency Index (SCI) to identify the topologies whose hierarchical structure was more congruent with temporal information. This index is defined as follows:

\[ SCI = \frac{C}{N} \]  

(2.2)

where N is the number of internal nodes, and C is the number of stratigraphically consistent nodes.

Wills (1999) proposed another measure that considers the number of ghost lineages. This index is called the Gap Excess Ratio (GER), and was formulated as follows:

\[ GER = 1 - \frac{MIG - G_{\text{min}}}{G_{\text{max}} - G_{\text{min}}} \]  

(2.3)
Figure 2.8 Diagrammatic representation of the algorithm to determine the stratigraphic fit. A) The cladistic rank is obtained by counting the sequence of primary nodes in a topology. B) Taxa that meet the main axis at the same point are treated as a single unit to produce a pectinate topology. C) The node number represents the stratigraphic sequence, assessed from the First Appearance Datum (FAD) of sister groups. D) The clade rank and the stratigraphic number (rank) are then compared to obtain a proportion of minimum implied gap (MIG). MIG is the difference between the age of the FAD of a lineage and that of its sister. E) Stratigraphic consistency is assessed as a comparison of the ratio of nodes that are younger than, or of equal age to, the node immediately below (stratigraphically consistent), against the apparently older (stratigraphically inconsistent). The Stratigraphic Consistency Index (SCI) is assessed on the full cladogram (modified from Benton and Hitchin, 1996).

The term Gmin refers to the minimum possible sum of ghost ranges for any given distribution of origination dates, Gmax is the maximum possible sum of ghost ranges, and MIG is the sum of ghost ranges implied by a phylogeny. The strap package uses a modification of this measure that considers the magnitude of ghost lineages via an optimisation for age through Sankoff parsimony. This reformulation gives:

\[
GER = \frac{L_m - L_0}{L_M - L_m}
\] (2.4)

where \(L_M\) is the maximum length for the age character on a completely unresolved topology, \(L_m\) is the minimum length for the age character on any topology, and \(L_0\) is the actual length obtained optimising the age character on the independently derived phylogenetic tree (Pol et al., 2004). Strap then allows the production of randomly generated
trees and compares the stratigraphic conflict that can be generated at random against the one in the input topologies.

In the strap package, the statistical significance of SCI and GER can be established by comparing the stratigraphic fit of the input MPTs against the stratigraphic congruence of random permutations. This means that randomly generated hierarchical structures will fail to have a stratigraphic fit more often than they will produce congruent topologies. The default setting of 1000 random permutations was used here.

When considering the MPTs obtained from mU2007, which includes the outgroup Marasuchus and the ornithischians *Heterodontosaurus* and *Lesothosaurus*, the temporal information is more congruent with the 22 MPTs (according to the SCI and GER indices) than most of 1000 randomly generated trees (Figures 2.9 and 2.10).

![Histograms of the SCI values](image)

**Figure 2.9** Histograms of the SCI values for the most parsimonious trees (top) from the reanalysis of the matrix by Upchurch et al. (2007) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical line.
The same conclusion is found for mY2010, where all of the MPTs have a better fit than almost all the randomly generated trees under both indices, SCI and GER (Figures 2.11 and 2.12). The outgroup chosen here is Euparkeria a basal archosauromorph and includes Crurotarsi, Marasuchus, Silesaurus, and Ornithischia.

The MPTs generated from the reanalysis of the matrix by Pol et al. (2011) also have a better stratigraphic fit under SCI and GRE than randomly generated trees. In contrast to the previous matrices, this matrix has a larger number of non-sauropodomorph dinosaurs, i.e. Marasuchus, Lagerpeton, Pseudolagosuchus, Pisanosaurus, Heterodontosaurus, Lesothosaurus, Silesaurus, Elaphrosaurus, Coelophysis and Liliensternus; Figures 2.13 and 2.14).
Figure 2.11 Histograms of the SCI values for the most parsimonious trees (top) from the reanalysis of the matrix by Yates (2007) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.

Figure 2.12 Histograms of the GER values for the most parsimonious trees (top) from the reanalysis of the matrix by Yates (2007) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.
Figure 2.13 Histograms of the SCI values for the most parsimonious trees (top) from the reanalysis of the matrix by Pol et al. (2011) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.

Figure 2.14 Histograms of the GER values for the most parsimonious trees (top) from the reanalysis of the matrix by Pol et al. (2011) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.

The matrix includes the non-sauropodomorphs *Marasuchus* and *Herrerasaurus*, with Marasuchus set as the outgroup. Although the SCI indicates that most of the trees fit
stratigraphy better than 1000 randomly generated trees, meaning that they are not better supported than randomly generated trees. This could be due to the small number of taxa sampled from similar time intervals (Figures 2.15 and 2.16).

Summary. Stratigraphic congruence tests can indicate whether one data set produces better trees than others. The GER values from the topologies produced from the different datasets fall within similar ranges, and the average GER is similar between the three sets of MPTs. This indicates that the three datasets produce topologies with a similar stratigraphic fit, showing that the potentially different ghost lineages and additional internal nodes are not affecting the stratigraphic congruence.

Table 2.5. Non-sauropodomorphs used in all the analyses.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>MPTs</th>
<th>SCI and GER ranges</th>
<th>Non-sauropodomorphs</th>
</tr>
</thead>
<tbody>
<tr>
<td>mU2007</td>
<td>22</td>
<td>SCI: 0.55-0.75 GER: 0.7-0.75</td>
<td><em>Marasuchus</em>, <em>Eoraptor</em>, <em>Herrerasaurus</em>, <em>Guaibasaurus</em>, <em>Coelophysis</em>, <em>Heterodontosaurus</em>, <em>Lesothosaurus</em></td>
</tr>
<tr>
<td>mY2010</td>
<td>12</td>
<td>SCI: 0.52-0.55 GER: 0.74-0.78</td>
<td><em>Euparkeria</em>, <em>Crurotarsi</em>, <em>Marasuchus</em>, <em>Silesaurus</em>, <em>Ornithischia</em>, <em>Herrerasaurus</em>, <em>Chindesaurus</em>, <em>Staurikosaurus</em>, <em>Guaibasaurus</em>, <em>Neotheropoda</em></td>
</tr>
<tr>
<td>S2013</td>
<td>8</td>
<td>SCI: 0.55-0.6 GER: 0.5-1.0</td>
<td><em>Marasuchus</em>, <em>Herrerasaurus</em>, <em>Eoraptor</em>, <em>Guaibasaurus</em></td>
</tr>
<tr>
<td>P2011</td>
<td>318</td>
<td>SCI: 0.5-0.7 GER: 0.64-0.74</td>
<td><em>Marasuchus</em>, <em>Lagerpeton</em>, <em>Pseudolagosuchus</em>, <em>Pisanosaurus</em>, <em>Heterodontosaurus</em>, <em>Lesothosaurus</em>, <em>Silesaurus</em>, <em>Eoraptor</em>, <em>Herrerasaurus</em>, <em>Guaibasaurus</em>, <em>Elaphrosaurus</em>, <em>Coelophysis</em>, <em>Liliensternus</em></td>
</tr>
</tbody>
</table>
Figure 2.15 Histograms of the SCI values for the most parsimonious trees (top) from the reanalysis of the matrix by Sekiya et al. (2013) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.

Figure 2.16 Histograms of the GER values for the most parsimonious trees (top) from the reanalysis of the matrix by Sekiya et al. (2013) (top) and randomly generated topologies (bottom) with the critical value (at an alpha of 0.05) for the one-tailed test drawn as a vertical dashed line.
2.5 Partition analysis

Total evidence matrices are based on taxonomic congruence, a tenet of phylogenetic analyses that is compatible with the hypothesis of non-specificity of phenetics: an analysis of various large character samples will produce relationship patterns that are positively correlated but not identical (Farris, 1971). This principle states that different sets of characters will be subject to the same evolutionary histories and will show similar topologies. In the context of parsimony-based morphological analyses, this is often assumed to be true (Mounce, 2013). This assumption is largely based on studies that indicate that non-specificity was the rule after this issue was addressed in the context of vertebrate systematics and morphology (Sokal and Sneath, 1963). However, Farris (1971) emphasised that the similarity between cladistic dendrograms from partitions was not necessarily the case in empirical cases, although in theoretical terms there are grounds for assuming congruence of characters.

Cranial and postcranial partitions have often been found to be incongruent in vertebrates, supporting the idea of differential selective pressure through body modularity (Mounce, 2013). Modularity can produce more homoplases in certain regions, whilst others can have morphological constraints that make them conservative.

If character selection is playing an important role in the incongruences seen in the topologies proposed for Sauropodomorpha, partition analyses could show different phylogenetic signals when compared with similar partitions in other datasets. This would indicate that the different characters sampled are capturing variation or various levels of homoplasy.

In the case of basal sauropodomorph dinosaurs, homoplasy seems to play a significant role in the phylogenies, as indicated by the different indices summarised in Table 4. Three partitions are considered here: cranial, axial, and appendicular skeleton. The axial and appendicular skeletons are usually considered together in partition analyses as the postcranial partition (e.g. Apaldetti et al., 2013). However, sauropodomorphs display a lot of variation in vertebral morphology due to the development of pneumaticity (Wedel, 1997, 2003, 2006; Wilson, 1999; Allain and Aquesbi, 2008; Wilson et al., 2011; Butler et al., 2012a; Yates et al., 2012). A partition analysis of the datasets of Upchurch et al. (2007) and Yates et al. (2010) has shown that at least one sauropodomorph taxon, Coloradisaurus,
displays mosaicism by having plateosaurid characters in the skull and massospondylid characters in the postcranial skeleton (Apaldetti et al., 2013).

As discussed above, it is expected that the three partitions, i.e. cranial, axial and appendicular, from the datasets employed to reconstruct the phylogeny of basal sauropodomorph dinosaurs will have different evolutionary histories. Notwithstanding, if the same partitions from different datasets show a certain level of congruence, then character selection is not playing a substantial role in the inconsistencies between datasets. This could point to character definition and character state delineation being at the root of the incongruent topologies obtained in the literature to date. Character analysis is often the least studied aspect of phylogenetic analyses (Pogue and Micke, 1990).

For each set of partitions, an iterative positional congruence (reduced) (iterative PCR) analysis was performed to identify the taxa that are collapsing the trees due to their instability (Pol and Escapa, 2009). Identifying unstable taxa does not provide evidence to remove them from the dataset, because they can have phylogenetic information relevant for understanding the relationships within the rest of the tree, but they provide a framework to more closely study those unstable taxa.

2.5.1 Cranial partition

The cranial partition in the matrix mU2007 has 99 characters and 31 taxa (there is no cranial material referred to the species Guaiabasaurus, Antetonitrus, Blikanasaurus, Camelotia, Lessemsaurus, Plateosauravus, Vulcanodon, Seitaad, and Glacialisaurus). Using the same parameters defined in Section 2.3, this partition produced seven MPTs with a length of 261 steps. A breakdown of some relationship patterns in these seven MPTs is summarised in Tables 2.6 and 2.7. As for the strict consensus, the cranial signal does not support Sauropodomorpha since it collapses into a polytomy with Lesothosaurus and Heterodontosaurus. Two groups are supported: Massospondylidae, containing Massospondylus, Adeopapposaurus, and Leyesaurus, and Sauropoda (Figure 2.17).
Figure 2.17 Strict consensus based on the cranial partition of the dataset mU2007.
Table 2.6 Clades that are obtained in over 50% of the 7 MPTs for the cranial partition of the mU2007 matrix. A core ‘Prosauropoda’ is recovered in five out of the seven MPTs, named here as Anchisauria, although the relationship inside them vary in all the trees. Sauropodiformes and Anchisauria are retrieved as sister taxa in four out of the seven MPTs. An iterative PCR analysis (described in Pol and Escapa, 2009) identifies *Gyposaurus* as an unstable taxon. Brackets inside the clade have the indicated for that row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>(Massospondylus + (Leyesaurus + Adeopapposaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda:</td>
</tr>
<tr>
<td></td>
<td><em>(Shunosaurus + Barapasaurus + Kotasaurus + Omeisaurus + Camarasaurus)</em></td>
</tr>
<tr>
<td>71</td>
<td><em>(Chinshakiangosaurus + Sauropoda)</em></td>
</tr>
<tr>
<td>71</td>
<td><em>(Gyposaurus + Lesothosaurus)</em></td>
</tr>
<tr>
<td>71</td>
<td>Anchisauria</td>
</tr>
<tr>
<td></td>
<td><em>(Anchisaurus + (Yunnanosaurus + Melanorosauridae + Lufengosaurus + Sarahsaurus + Massospondylidae + Riojasaurus + Plateosaurus + Coloradisaurus + Ammosaurus))</em></td>
</tr>
<tr>
<td>57</td>
<td>Saturnalidae <em>(Saturnalia + Efraasia)</em></td>
</tr>
<tr>
<td>57</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Mussaurus + Xixiposaurus + Melanorosaurus)</em></td>
</tr>
<tr>
<td>57</td>
<td><em>(Omeisaurus + Camarasaurus)</em></td>
</tr>
<tr>
<td>57</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td>Jinghsanosaurus + <em>(Chinshakiangosaurus + Sauropoda)</em></td>
</tr>
<tr>
<td>57</td>
<td>Anchisauria + Sauropodiformes</td>
</tr>
</tbody>
</table>
Table 2.7 Clades that are obtained in over 50% of the 6 MPTs for the cranial partition of the mU2007 matrix after removing *Gyposaurus*. The removal of *Gyposaurus* makes *Barapasaurus* unstable and recovers Sauropoda as a polytomy. Moreover, the more primitive sauropodomorphs, theropods and ornithischians are clustered in a modified version of Ornithoscelida (*sensu* Baron et al., 2017) in five out of the six MPTs. Brackets inside the clade have the indicated for that row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>(Massospondylus + (Leyesaurus + Adeopapposaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Anchisauria</td>
</tr>
<tr>
<td></td>
<td><em>(Anchisaurus + Yunnanosauridae)</em></td>
</tr>
<tr>
<td>100</td>
<td>Theropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Coelophysis + Herrerasaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td>*(Anchisauria + Sauropodiformes + “Ornithoscelida”)</td>
</tr>
<tr>
<td>83</td>
<td>Plateosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Riojasaurus + Mussaurus + Coloradisaurus + Plateosaurus + Ammosaurus)</em></td>
</tr>
<tr>
<td>83</td>
<td>Massospondylidae + Plateosaurida</td>
</tr>
<tr>
<td>83</td>
<td>Yunnanosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Yunnanosaurus + Melanorosauridae)</em></td>
</tr>
<tr>
<td>83</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td>*(Melanorosaurus + Xixiposaurus + (Lufengosaurus + (Sarahsaurus + (Massospondylidae + Plateosauridae))))</td>
</tr>
<tr>
<td>83</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Shunosaurus + Kotasaurus + Camarasaurus + Omeisaurus + Barapasaurus)</em></td>
</tr>
<tr>
<td>83</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td><em>(Jingshanosaurus + (Chinshakiangosaurus + Sauropoda))</em></td>
</tr>
<tr>
<td>83</td>
<td>“Ornithoscelida”</td>
</tr>
<tr>
<td></td>
<td><em>(Efraasia + (Thecodontosaurus + (Lesothosaurus + Theropoda) + Eoraptor + Saturnalia + Heterodontosaurus))</em></td>
</tr>
</tbody>
</table>
The cranial partition of the dataset mY2010 includes 120 characters scored for 41 taxa. The taxa excluded lacking cranial scores are Blikanasaurus, Chindesaurus, Chromogisaurus, Eucnemesaurus, Glacialisaurus, Guaibasaurus, Isanosaurus, Seitaad, Vulcanodon, Mussaurus, Plateosauravus, Ruehleia, Antetonitrus, and Lessemsaurus. Although Mussaurus possesses cranial remains (Pol and Powell, 2007), it was excluded due to the early ontogenetic stage of the material.

This partition produces four MPTs with lengths of 350 steps. An exploration of the MPTs shows that there is support for the groupings previously published in the literature with unresolved interrelationships, with Pulanesaura changing its position throughout the trees, an unstable taxon (Tables 2.8 and 2.9). The strict consensus shows there is support for Sauropodomorpha, including Eoraptor as the most basal member of the clade (Figure 2.18). However, most of the tree collapses in a polytomy, finding support for only two other groups: Plateosauridae, containing Coloradisaurus, Plateosaurus engelhardti, Unaysaurus and Plateosaurus gracilis, and a clade containing Adeopapposaurus and Leyesaurus.
Figure 2.18 Strict consensus based on the cranial partition of the dataset mY2010.
Table 2.8. Clades that are obtained in all of the 4 MPTs for the cranial partition of the mY2007. The cranial partition supports the groups Yunnanosaurida, equivalent to a ‘core Prosauropoda’ clade, and two clades: Massospondylidae and Plateosauridae. The cranial partition finds support for *Eoraptor* as a sauropodomorph. An iterative PCR analyses identify *Pulanesaura* as an unstable taxon. Brackets inside the clade have the indicated for that row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Yunnanosauridae (“core Prosauropoda”)</td>
</tr>
<tr>
<td></td>
<td><em>(Yunnanosaurus + (Leonerasaurus + (Massospondylidae + (Lufengosaurus + (Aardonyx + Plateosauridae))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>(Massospondylus + (Adeopapposaurus + Leyesaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Coloradisaurus + (Plateosaurus engelhardti + (Plateosaurus gracilis + Unaysaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Tazoudasaurus + Cetiosaurus + Gongxianosaurus + Spinophorosaurus + Patagosaurus + Shunosaurus + Neosauropoda + Barapasaurus + Omeisaurus + Mamenchisaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Anchisauria</td>
</tr>
<tr>
<td></td>
<td><em>(Anchisaurus + Pulanesaura + Jingshanosaurus + Yunnanosauridae + Xingxiulong + Melanorosaurus + Sauropoda)</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td><em>(Eoraptor + (Saturnalia + (Pantydraco + (Thecodontosaurus + (Efraasia + (Panphagia + (Riojasaurus + (Anchisauria)))))))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Saurischia</td>
</tr>
<tr>
<td></td>
<td><em>(Herrerasaurus + Staurikosaurus) + (Neotheropoda + Sauropodomorpha))</em></td>
</tr>
<tr>
<td>100</td>
<td>(Ornithischia + Silesaurus)</td>
</tr>
</tbody>
</table>
Table 2.9 Clades that are obtained in all of the 4 MPTs for the cranial partition of the mY2007 after removing *Pulanesaura*. The removal of *Pulanesaura* increases the resolution within Sauropoda; iterative PCR finds that *Cetiosaurus* is unstable within Sauropoda. Brackets inside the clade have the indicated for that row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Yunnanosauridae (“core Prosauropoda”)</td>
</tr>
<tr>
<td></td>
<td><em>(Yunnanosaurus + (Leonerasaurus + (Massospondylidae + (Lufengosaurus + (Aardonyx + Plateosauridae)))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>(Massospondylus + (Adeopapposaurus + Leyesaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Coloradisaurus + (Plateosaurus engelhardti + (Plateosaurus gracilis + Unaysaurus)))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Xingxiulong + (Melanorosaurus + (Tazoudasaurus + Cetiosaurus + (Gongxianosaurus + (Spinophorosaurus + Patagosaurus)) + Shunosaurus + Neosauropoda + Barapasaurus + Omeisaurus + Mamenchisaurus)))</em></td>
</tr>
<tr>
<td>100</td>
<td>Anchisauria</td>
</tr>
<tr>
<td></td>
<td><em>(Anchisaurus + (Jingshanosaurus + (Yunnanosauridae + Sauropoda)))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td><em>(Eoraptor + (Saturnalia + (Pantydraco + (Thecodontosaurus + (Efraasia + (Panphagia + (Riojasaurus + (Anchisauria)))))))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Saurischia</td>
</tr>
<tr>
<td></td>
<td><em>(Herrerasaurus + Staurikosaurus) + (Neotheropoda + Sauropodomorpha)</em></td>
</tr>
<tr>
<td>100</td>
<td>(Ornithischia + Silesaurus)*</td>
</tr>
</tbody>
</table>
The cranial partition of the matrix of Sekiya et al. (2013) comprises 163 characters scored for 25 taxa. Again, specimens without cranial material are excluded. This analysis produces only two MPTs with lengths of 411 steps (Table 2 10). The topology supports Sauropodomorpha, with two internal clades: a core Prosauropoda, comprising two smaller clades, Plateosauridae, and Massospondylidae, and Sauropoda, including *Melanorosaurus*, and *Yunnanosaurus*, but not *Anchisaurus* (Figure 2.19).

![Figure 2.19 Strict consensus based on the cranial partition of the dataset by Sekiya et al. (2013).](image)
Table 2.10 Clades that are obtained in all of the 2 MPTs for the cranial partition of the matrix of Sekiya et al. (2013). The cranial partition supports Melanorosauridae, containing Sauropoda, as the sister taxon to Anchisauridae, which has the same composition of a ‘core Prosauropoda’. *Yunnanosaurus huangi* is placed as a primitive sauropodomorph instead of as a ‘prosauropod’. This taxon was first-hand assessed in this matrix. An iterative PCR analyses identify *Gyposaurus* as an unstable taxon. Brackets inside the clade have the indicated for that row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Melanorosaurida</td>
</tr>
<tr>
<td></td>
<td>(<em>Melanorosaurus</em> + (<em>Yunnanosaurus robustus</em> + <em>Jingshanosaurus</em>) + (<em>Shunosaurus</em> + (<em>Omeisaurus</em> + <em>Barapasaurus</em>)))</td>
</tr>
<tr>
<td>100</td>
<td>Anchisauridae (‘core Prosauropoda’)</td>
</tr>
<tr>
<td></td>
<td>(<em>Anchisaurus</em> + (<em>Adeopapposaurus</em> + <em>Massospondylus</em>) + (<em>Lufengosaurus</em> + (<em>Lamplughsaurs</em> + (<em>Aardonyx</em> + <em>Gyposaurus</em> + (<em>Plateosaurus</em> + <em>Coloradisaurus</em>))))</td>
</tr>
<tr>
<td>100</td>
<td>Lessemsauridae</td>
</tr>
<tr>
<td></td>
<td>(<em>Melanorosauridae</em> + <em>Anchisauridae</em>)</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td>(<em>Eoraptor</em> + (<em>Saturnalia</em> + (<em>Efraasia</em> + (<em>Yunnanosaurus huangi</em> + (<em>Sarahsaurus</em> + (<em>Riojasaurus</em> + (<em>Thecodontosaurus</em> + <em>Lessemsauridae</em>)))))))</td>
</tr>
</tbody>
</table>

Finally, the cranial partition of the matrix of Pol et al. (2011) has 107 characters scored for 31 taxa, excluding the same specimens as the previous datasets, but also *Barapasaurus, Lapparentosaurus, Volkheimeria, Lagerpeton, Elaphrosaurus, Pseudolagosuchus, Liliensternus*, and *Patagosaurus* (despite there is cranial material reported in the literature, is not considered in the matrix). This partition produces six MPTs with 200 steps. In the case of *Barapasaurus* and *Lapparentosaurus*, teeth are the only preserved cranial material (Bandyopadhyay et al., 2010), and were excluded here even though they were included in other datasets. All the topologies support the group Phytodinosauria (Table 2.11). The strict consensus supports Sauropodomorpha, Plateosauridae, and Sauropoda (Figure 2.20).
Figure 2.20 Strict consensus based on the cranial partition of the dataset by Pol et al. (2011).
Table 2.11. Clades that are obtained in over 50% of the 6 MPTs for the cranial partition of the matrix of Pol et al. (2011). The trees found in this partition seem to suggest that most of the characters represent adaptations to herbivorous feeding habits as seems to be suggested by the support to Phytodinosauria, a group defined in the literature before to include herbivore dinosaurs sauropodomorphs and ornithischians (*sensu* Bakker, 1986; Parry et al., 2017). An iterative PCR analysis identifies *Gyposaurus* as an unstable taxon. Its removal, however, does not improve any node. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td>(Jingshanosaurus + (Melanorosaurus + (Leonerasaurus + (Shunosaurus +</td>
</tr>
<tr>
<td></td>
<td>Diplodocus + Omeisaurus + Camarasaurus + Brachiosaurus +</td>
</tr>
<tr>
<td></td>
<td>Kotasaurus)))</td>
</tr>
<tr>
<td>100</td>
<td>Riojasauridae</td>
</tr>
<tr>
<td></td>
<td>(Riojasaurus + Sauropodiformes)</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td>(Efraasia + (Plateosaurus engelhardti + Plateosaurus gracilis) +</td>
</tr>
<tr>
<td></td>
<td>Sauropodiformes)</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td>(Saturnalia + (Thecodontosaurus + Pantydraco + Plateosauria))</td>
</tr>
<tr>
<td>100</td>
<td>Phytodinosauria</td>
</tr>
<tr>
<td></td>
<td>(Herrerasaurus + (Pisanosaurus + Lesothosaurus + Heterodontosaurus) +</td>
</tr>
<tr>
<td></td>
<td>(Silesaurus + Sauropodomorpha))</td>
</tr>
<tr>
<td>66</td>
<td>Euauropoda</td>
</tr>
<tr>
<td></td>
<td>(Diplodocus + Omeisaurus + Camarasaurus + Brachiosaurus +</td>
</tr>
<tr>
<td></td>
<td>Kotasaurus)</td>
</tr>
<tr>
<td>50</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td>((Lufengosaurus + Coloradisaurus) + (Massospondylus + Yunnanosaurus</td>
</tr>
</tbody>
</table>
|       | + Aardonyx + Anchisaurus + Gyposaurus + Sauropoda))
These analyses of the four matrices indicate that the cranial partition carries a phylogenetic signal to support Sauropoda and, to a lesser degree, Massospondylidae. However, cranial characters do not capture the variation throughout all sauropodomorphs, and the high resolution at the level of Sauropoda seems to indicate that the characters are based mostly on comparisons between sauropods and basal sauropodomorphs (Table 2.12).

**Table 2.12 Summary of the cranial partition analyses performed on the four main matrices.**

<table>
<thead>
<tr>
<th>Cranial partitions</th>
<th>Characters</th>
<th>Taxa</th>
<th>MPTs (length)</th>
<th>MPTs CI and RI</th>
<th>Unstable taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>mU2007</td>
<td>99</td>
<td>31</td>
<td>7 (261)</td>
<td>0.398, 0.645</td>
<td>Gyposaurus</td>
</tr>
<tr>
<td>mY2010</td>
<td>120</td>
<td>41</td>
<td>4 (350)</td>
<td>0.91, 0.709</td>
<td>Pulanesaura</td>
</tr>
<tr>
<td>Sekiya et al.</td>
<td>163</td>
<td>25</td>
<td>2 (411)</td>
<td>0.423, 0.527</td>
<td>Yunnanosaurus huangi</td>
</tr>
<tr>
<td>(2013)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pol et al.</td>
<td>107</td>
<td>31</td>
<td>6 (200)</td>
<td>0.585, 0.803</td>
<td>Gyposaurus</td>
</tr>
<tr>
<td>(2011)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**2.5.2 Axial partition**

The axial partition of the dataset mU2007 includes 54 characters scored for 37 taxa. The only taxa that were removed from this dataset are Blikanasaurus, Chinshakiangosaurus, and Glacialisaurus, for which there is no vertebral material. The analysis of this partition produced seven MPTs with lengths of 133 steps. The recursive analysis of the MPTs from this partition shows support for a ‘core Prosauropoda’ clade (Tables 2.13 and 2.14). The strict consensus supporting only Sauropodomorpha, with Eoraptor at the basal-most part of this clade. Two of the most basal sauropodomorphs are grouped together, Thecodontosaurus and Saturnalia. Interestingly, there is a group that includes Xixiposaurus and Coelophysis, a sauropodomorph and a theropod (Figure 2.21).
Figure 2.21 Strict consensus from the axial partition of the dataset mU2007.
Table 2.13 Clades that are obtained on more than 50% of the 7 MPTs for the axial partition of the matrix of mU2007. The trees from this partition support Melanorosauridae and a ‘core Prosauropoda’. Based on the axial characters, *Eoraptor* is found to be similar to the vertebrae of more derived sauropodomorphs. An iterative PCR identifies *Lessemosaurus* as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
</table>
| 100   | Melanorosauridae  
       | *(Eoraptor + (Melanorosaurus + (Antetonitrus + (Kotasaurus + (Vulcanodon + Shunosaurus + Barapasaurus + (Omeisaurus + Camarasaurus))))))** |
| 100   | Guaiabasauridae: *(Ammosaurus + Guaiabasaurus)*                                                                                       |
| 100   | Anchisauridae: *(Massospondylus + Anchisaurus)*                                                                                      |
| 100   | *(Xixiposaurus + Coelophysis)*                                                                                                       |
| 100   | Saturnalinae: *(Thecodontosaurus + Saturnalia)*                                                                                       |
| 100   | Ornithischia: *(Lesothosaurus + Heterodontosaurus)*                                                                                   |
| 71    | Plateosauridae: *(Sarahsaurus + Plateosaurus + Guaiabasauridae)*                                                                       |
| 71    | *(Lufengosaurus + Camelotia)*                                                                                                        |
| 71    | Lessemosauridae: *(Lessemosaurus + Anchisauridae)*                                                                                   |
| 71    | ‘core Prosauropoda’  
       | *(Adeopapposaurus + Leyesaurus + Lufengosauridae + Jingshanosaurus + Coloradisaurus + Lessemosauridae + Yunnanosaurus + Seitaad + Plateosauravus + Plateosauridae)* |
| 71    | Gyposauridae  
       | *(Gyposaurus + Efraasia + Riojasauridae)*                                                                                           |
| 57    | Massospondylidae  
       | *(Lufengosauridae + Jingshanosaurus + (Coloradisaurus + Lessemosauridae))*                                                         |
| 57    | Riojasauridae  
       | *(Riojasaurus + ‘core Prosauropoda’)                                                                                               |
| 57    | *(Saturnalinae + Herrerasaurus + Ornithischia)*                                                                                      |
Table 2.14. Clades that are obtained on more than 50% of the 3 MPTs for the axial partition of the matrix of mU2007 after the removal of Lessemsaurus. The clades become more defined and the topologies are more consistent, but it is still very similar to the topologies than before the removal of Lessemsaurus. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Yunnanosauridae</td>
</tr>
<tr>
<td></td>
<td>(Yunnanosaurus + (Leyesaurus + (Adeopapposaurus + (Massospondylidae</td>
</tr>
<tr>
<td></td>
<td>+ ((Lufengosauridae + Jingshanosauridae)))</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae</td>
</tr>
<tr>
<td></td>
<td>(Plateosauravus + (Ammosaurus + Guaibasaurus))</td>
</tr>
<tr>
<td>100</td>
<td>‘core Prosauropoda’</td>
</tr>
<tr>
<td></td>
<td>(Gyposaurus + Efraasia + (Riojasaurus + (Plateosauridae + Yunnanosauridae)))</td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td>(Sarahsaurus + (Coloradisaurus + (Massospondylus + Anchiisaurus)))</td>
</tr>
<tr>
<td>100</td>
<td>(Lufengosaurus + Camelotia)</td>
</tr>
<tr>
<td>100</td>
<td>Jingshanosaurus: (Seitaad + Jingshanosaurida)</td>
</tr>
<tr>
<td>100</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td>(Eoraptor + (Melanorosaurus + (Antetonitrus + (Kotasaurus + (Barapasaurus + Vulcanodon + Shunosaurus + (Omeisaurus + Camarasaurus)))))</td>
</tr>
<tr>
<td>100</td>
<td>(Xixiposaurus + Coelophysis)</td>
</tr>
<tr>
<td>100</td>
<td>Saturnalinae: (Thecodontosaurus + Saturnalia)</td>
</tr>
<tr>
<td>100</td>
<td>Ornithischia: (Lesothosaurus + Heterodontosaurus)</td>
</tr>
<tr>
<td>66</td>
<td>Sauropoda: (Vulcanodon + Shunosaurus + Eusauropoda)</td>
</tr>
</tbody>
</table>

The axial partition of the dataset mY2010 comprises 79 characters scored for 53 taxa. The only taxa lacking scores due to the absence of vertebrae are Blikanasaurus and Glacialisaurus. This analysis produces six MPTs with a length of 254, and there is support for the grade-like scenario (Tables 2.15 and 2.16). The strict consensus supports four clades: Pantydraco + Thecodontosaurus, Plateosauravus + Ruehleia, Massospondylus + Adeopapposaurus, and a fully resolved Sauropoda (Figure 2.22).
Figure 2.22 Strict consensus from the axial partition of the dataset mY2010.
Table 2.15. Clades that are obtained on more than 60% of the 6 MPTs for the axial partition of the matrix of mY2007. Based on vertebral characters, this partition supports a ‘core Prosauropoda’ (here Plateosauria) as the sister taxon of ‘Yunnanosauria’, that includes a grade that leads to Sauropoda. An iterative PCR analysis identified *Seitaad* as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Lessemsauridae</td>
</tr>
<tr>
<td></td>
<td>*(Antetonitrus + (Pulanesaura + (Isanosaurus + (Shunosaurus +</td>
</tr>
<tr>
<td></td>
<td>(Tazoudasaurus + Sauropoda))))*</td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae: <em>(Massospondylus + Adeopapposaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauravidae: <em>(Xingxiulong + (Ruehleia + Plateosauravus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae: <em>(Plateosaurus gracilis + Plateosaurus engelhardti)</em></td>
</tr>
<tr>
<td>100</td>
<td><em>(Saturnalia + Chromogisauridae)</em></td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosauridae: <em>(Thecodontosaurus + Pantydraco)</em></td>
</tr>
<tr>
<td>100</td>
<td>Theropoda: <em>(Neotheropoda + (Herrerasaurus + Staurikosaurus))</em></td>
</tr>
<tr>
<td>83</td>
<td>*(Yunnanosaurus + (Melanorosaurus + (Lessemsaurus + (Eucnemesaurus +</td>
</tr>
<tr>
<td></td>
<td>Aardonyx + Lessemsauridae)))*</td>
</tr>
<tr>
<td>83</td>
<td><em>(Chromogisaurus + Mussaurus + Coloradisaurus + Leonerasaurus)</em></td>
</tr>
<tr>
<td>83</td>
<td>Sauropodomorpha: *(Eoraptor + (Panphagia + Gongxianosaurus +</td>
</tr>
<tr>
<td></td>
<td>(‘Chromogisauria’ + Anisauria)))*</td>
</tr>
<tr>
<td>83</td>
<td><em>(Jingshanosaurus + (Plateosaurus + Yunnanosauridae))</em></td>
</tr>
<tr>
<td>66</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td>*(Efraasia + (Riojasaurus + (Plateosauridae + Unaysaurus +</td>
</tr>
<tr>
<td></td>
<td>Plateosauravidae + Massospondylidae)))*</td>
</tr>
<tr>
<td>66</td>
<td>Anchisauria: <em>(Anchisaurus + Jingshanosauridae)</em></td>
</tr>
<tr>
<td>66</td>
<td>Sauropodiformes: <em>(‘Chromogisauria’ + Anchisauria)</em></td>
</tr>
<tr>
<td>66</td>
<td><em>(Thecodontosauridae + Chindesaurus + Sauropodomorpha)</em></td>
</tr>
<tr>
<td>66</td>
<td><em>(Guaibasaurus + Theropoda)</em></td>
</tr>
</tbody>
</table>
Table 2.16. Clades that are obtained on more than 60% of the 6 MPTs for the axial partition of the matrix of mY2007 after the removal of *Seitaad*. The topologies become more consistent, and an iterative PCR analysis identifies *Chindesaurus* as an unstable taxon in these new topologies.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>‘Yunnanosauria’&lt;br&gt;((Yunnanosaurus + (Melanorosaurus + (Lessemsaurus + (Eucnemesaurus + Aardonyx + Lessemsauridae)))))</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauria&lt;br&gt;((Efraasia + (Riojasaurus + (Plateosauridae + Unaysaurus + Plateosauravidae + Massospondylidae))))</td>
</tr>
<tr>
<td>100</td>
<td>‘Unaysauria’&lt;br&gt;((Unaysaurus + Jingshanosaurus + (‘Yunnanosauria’ + Plateosauria)))</td>
</tr>
<tr>
<td>100</td>
<td>Theropoda: (Neotheropoda + (Herrerasaurus + Staurikosaurus))</td>
</tr>
<tr>
<td>100</td>
<td>Saurischia: ((Guaibasaurus + Theropoda + Sauropodomorpha))</td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosauridae: ((Thecodontosaurus + Pantydraco))</td>
</tr>
<tr>
<td>83</td>
<td>Anchisauria: ((Anchisaurus + ‘Unaysauria’))</td>
</tr>
<tr>
<td>83</td>
<td>‘Chromogisauridae’&lt;br&gt;((Chromogisaurus + Mussaurus + Coloradisaurus + Leonerasaurus))</td>
</tr>
<tr>
<td>83</td>
<td>Sauropodiformes: (‘Chromogisauria’ + Anchisauria)</td>
</tr>
<tr>
<td>83</td>
<td>‘Neosauropodomorpha’&lt;br&gt;((Eoraptor + (Panphagia + Gongxianosaurus + (Saturnalidae + Anchisauria))))</td>
</tr>
<tr>
<td>66</td>
<td>Sauropodomorpha:&lt;br&gt;((Chindesaurus + (Thecodontosauridae + ‘Neosauropodomorpha’)))</td>
</tr>
</tbody>
</table>

The partition by Sekiya et al. (2013) comprises 114 characters scored for 31 taxa, indicating that this is the region where fewer duplicates were identified. Excluded here is *Blikanasaurus*. This analysis produces four MPTs with a length of 316 steps (2.17 and Table 2.18). The Nelsen consensus supports the classic Melanorosauridae, Massospondylidae, and Sauropoda (Figure 2.23).
Figure 2.23 Strict consensus from the axial partition of the dataset by Sekiya et al. (2013).
Table 2.17. Clades that are obtained on more than 50% of the 4 MPTs for the axial partition of the matrix of Sekiya et al. (2013). The vertebral characters of the partition support several smaller clades within Sauropodomorpha, but the grade-like arrangement is mostly supported. An iterative PCR analysis identified *Yunnanosaurus huangi* as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Sauropoda (<em>Sarahsaurus + (Yunnanosaurus robustus + (Shunosaurus + (Barapasaurus + (Vulcanodon + Omeisaurus))))</em>)</td>
</tr>
<tr>
<td>100</td>
<td>Melanorosauridae (<em>((Melanorosaurus + Camelotia) + (Lessmesaurus + Antetonitrus</em>))*)</td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae: (<em>Lufengosaurus + (Adeopapposaurus + Massospondylus</em>))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha (*Eoraptor + Gyposaurus + ‘Neosauropodomorpha’) *</td>
</tr>
<tr>
<td>75</td>
<td>‘Jingshanosauria’: (<em>Jingshanosaurus + Massospondylidae</em>)</td>
</tr>
<tr>
<td>75</td>
<td>Plateosauria (<em>Efraasia + Plateosaurus + Riojasauridae</em>)</td>
</tr>
<tr>
<td>75</td>
<td>Anchisauria (<em>Coloradisaurus + (Anchisaurus + (‘Jingshanosauria’ + Plateosaurus + Plateosauravus + Melanosauridae + Sauropodiformes))</em>)</td>
</tr>
<tr>
<td>75</td>
<td>Herrerasauridae: (<em>Herrerasaurus + (Yunnanosaurus huangi + Lamplughsaursa))</em>)</td>
</tr>
<tr>
<td>50</td>
<td>‘Thecodontosauria’ (*Thecodontosaurus + (Guaiabasauridae+ Herrerasauridae))</td>
</tr>
<tr>
<td>50</td>
<td>Riojasauridae: (<em>Seitaad + Riojasaurus</em>)</td>
</tr>
<tr>
<td>50</td>
<td>Guaiabasauridae: (<em>Saturnalia + Guaiabasaurus</em>)</td>
</tr>
<tr>
<td>50</td>
<td>(‘Thecodontosauria’ + Anchisauria)</td>
</tr>
</tbody>
</table>
Table 2.18. Clades that are obtained on more than 50% of the 2 MPTs for the axial partition of the matrix of Sekiya et al. (2013) after the removal of *Yunnanosaurus huangi*. The topologies become more consistent and support three clades of ‘prosauropods’ and a grade starting with *Seitaad* and *Aardonyx*. *Seitaad* is found to be an unstable taxon after an iterative PCR analysis. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Sarahsaurus + (Yunnanosaurus robustus + (Shunosaurus + (Barapasaurus + (Vulcanodon + Omeisaurus)))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td><em>((Melanorosaurus + Camelotia) + (Lessmesaurus + Antetonitrus))</em></td>
</tr>
<tr>
<td>100</td>
<td>‘Jingshanosauria’: <em>(Jingshanosaurus + Massospondylidae)</em></td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td><em>(Plateosauridae + Sauropodiformes)</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td><em>(Thecodontosaurus + (Saturnalia + (Gyposaurus + (Coloradisaurus + (Anchisaurus + Plateosaurus)))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Guaibasauridae: <em>(Guaibasaurus + (Lamplughsauro + Herrerasaurus))</em></td>
</tr>
<tr>
<td>50</td>
<td>‘Aardonichidae’: <em>(Seitaad + Aardonyx) + Sauropoda</em></td>
</tr>
<tr>
<td>50</td>
<td>‘Melanorosauria’: <em>(Plateosaurus + (Melanorosauridae + ‘Aardonichidae’))</em></td>
</tr>
<tr>
<td>50</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td><em>(‘Jingshanosauria’ + ‘Melanorosauria’))</em></td>
</tr>
<tr>
<td>50</td>
<td>Plateosauridae: <em>(Efraasia + (Riojasaurus + Plateosaurus))</em></td>
</tr>
</tbody>
</table>
The axial partition of Pol et al. (2011) comprises 56 characters scored for 46 taxa, excluding only Blikanasaurus. The five topologies of the five MPTs find support for nested groupings similar to the total evidence matrices of mY2010 (Tables 2.19 and 2.2). The strict consensus shows support only for a fully resolved Sauropoda, whilst the rest of the tree collapses into a polytomy (Figure 2.24).

**Figure 2.24** Strict consensus from the axial partition of the dataset by Pol et al. (2011).
Table 2.19. Clades that are obtained on more than 60% of the 5 MPTs for the axial partition of the matrix of Pol et al. (2011). The vertebral characters of the partition do not support as many clades—An iterative PCR analysis identified several taxa: Guaibasaurus, Silesaurus, Lesothosaurus. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Lessemsauridae</td>
</tr>
<tr>
<td></td>
<td>(Antetonitrus + (Lessemsaurus + (Vulcanodon + Sauropoda))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td>(Isanosaurus + (Shunosaurus + Kotasaurus + (Volkheimeria + (Lapparentosaurus + (Barapasaurus + (Patagosaurus + Omeisaurus + (Neosauropoda)))))))</td>
</tr>
<tr>
<td>100</td>
<td>Neosauropoda: (Diplodocus + (Brachiosaurus + Camarasaurus))</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae: (Plateosaurus gracilis + Plateosaurus engelhardti)</td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosauridae: (Thecodontosaurus + Pantydraco)</td>
</tr>
<tr>
<td>60</td>
<td>Melanorosauridae: (Leonerasaurus + (Melanorosaurus + Lessemsauridae))</td>
</tr>
<tr>
<td>60</td>
<td>Jingshanosauridae: (Eoraptor + Jingshanosaurus)</td>
</tr>
</tbody>
</table>

Table 2.20. Clades that are obtained on more than 50% of the 5 MPTs for the axial partition of the matrix of Pol et al. (2011) after the removal of Guaibasaurus, Silesaurus, Lesothosaurus. The topologies do not change considerably after the removal of the unstable taxa. An iterative PCR analysis identifies three other unstable taxa: Jinghsanosaurus, Pisanosaurus and Camelotia. This indicates that the axial partition in Pol et al. (2011) does not have strong phylogenetic signals in the basal parts of the tree. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Lessemsauridae</td>
</tr>
<tr>
<td></td>
<td>(Antetonitrus + (Lessemsaurus + (Vulcanodon + Sauropoda))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td>(Isanosaurus + (Shunosaurus + Kotasaurus + (Volkheimeria + (Lapparentosaurus + (Barapasaurus + (Patagosaurus + Omeisaurus + (Neosauropoda)))))))</td>
</tr>
<tr>
<td>100</td>
<td>Neosauropoda: (Diplodocus + (Brachiosaurus + Camarasaurus))</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae: (Plateosaurus gracilis + Plateosaurus engelhardti)</td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosauridae: (Thecodontosaurus + Pantydraco)</td>
</tr>
<tr>
<td>83</td>
<td>Jingshanosauridae: (Eoraptor + Jingshanosaurus)</td>
</tr>
<tr>
<td>50</td>
<td>Melanorosauridae: (Leonerasaurus + (Melanorosaurus + Lessemsauridae))</td>
</tr>
</tbody>
</table>

Table 2.21 Summary of the axial partition analyses performed on the four main matrices.

<table>
<thead>
<tr>
<th>Axial partitions</th>
<th>Characters</th>
<th>Taxa</th>
<th>MPTs (length)</th>
<th>MPTs CI and RI</th>
<th>Unstable taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>---------</td>
<td>------------------</td>
</tr>
<tr>
<td>mU2007</td>
<td>54</td>
<td>37</td>
<td>7 (133)</td>
<td>0.414, 0.702</td>
<td>Lessemsaurus</td>
</tr>
<tr>
<td>mY2010</td>
<td>79</td>
<td>53</td>
<td>6 (254)</td>
<td>0.354, 0.720</td>
<td>Seitaad</td>
</tr>
<tr>
<td>Sekiya et al. (2013)</td>
<td>114</td>
<td>31</td>
<td>4 (316)</td>
<td>0.380, 0.550</td>
<td>Yunnanosaurus huangi</td>
</tr>
<tr>
<td>Pol et al. (2011)</td>
<td>56</td>
<td>46</td>
<td>5 (129)</td>
<td>0.589, 0.835</td>
<td>Guaibasaurus, Silesaurus, Lesothosaurus</td>
</tr>
</tbody>
</table>

Summary. The axial partitions show similar topologies to those of the cranial partitions, with a well-resolved Sauropoda clade recovered by each. As with the cranial partition, the partial joining of the information from the datasets increases the resolution of the final topologies (Table 2.21).
2.5.3 Appendicular partition

The appendicular partition of mU2007 does not exclude any taxon, including 40 taxa, and scores for 149 characters. The analysis of this dataset produces five MPTs with lengths of 433 steps. The topologies of the MPTs shift from supported arrangements similar to the ones produced by the mY2010 matrices, to supporting the arrangements of the topology by mU2007 after removing unstable taxa (Tables 2.22 and 2.23). The strict consensus supports several groups. It supports Guaibasauridae containing *Saturnalia* and *Guaibasaurus*, a clade containing *Anchisaurus* and *Ammosaurus*, and Sauropoda, placing *Sarahsaurus* as the basalmost member of the latter clade (Figure 2.25).

Figure 2.25 Strict consensus based on the appendicular partition of the dataset mU2007.
Table 2.22. Clades that are obtained on more than 60% of the 5 MPTs for the appendicular partition of mU2007. This partition supports several sauropodomorph clades, including Phytodinosauria. An iterative PCR analysis identified *Seitaad* and *Gyposaurus* as unstable taxa. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Riojasaurus + (Melanorosaurus + (Camelotia + (Mussaurus + (Blikanasaurus + Antetonitrus)))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Anchisauridae: <em>(Anchisaurus + Ammosaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Chinshakiangosaurus + Xixiposaurus + (Sarahsaurus + (Kotasaurus + Vulcanodon + (Barapasaurus + (Camarasaurus + (Shunosaurus + Omeisaurus))))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td><em>(Leyesaurus + Seitaad + (Massospondylidae + Anchisauria))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td><em>((Saturnalia + Guiabasaurus) + (Thecodontosaurus + (Efraasia + (Plateosaurus + (Sauropodiformes)))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Phytodinosauria</td>
</tr>
<tr>
<td></td>
<td><em>(Lesothosaurus + (Heterodontosaurus + (Sauropodomorpha)))</em></td>
</tr>
<tr>
<td>100</td>
<td><em>(Herrerasaurus + (Eoraptor + (Coelophysis + (Phytodinosauria))))</em></td>
</tr>
<tr>
<td>60</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>((Adeopapposaurus + Massospondylus) + (Lufengosaurus + Plateosaurus + Lessemsaurus + Yunnanosaurus + Jingshanosaurus + Coloradisaurus + Glacialisaurus))</em></td>
</tr>
<tr>
<td>60</td>
<td>Anchisauria: <em>(Sauropoda + Melanorosauridae)</em></td>
</tr>
</tbody>
</table>
Table 2.23. Clades that are obtained on more than 60% of the 5 MPTs for the appendicular partition of mU2007 after the removal of Seitaad and Gyposaurus. The appendicular characters in this partition support the ‘core Prosauropoda’ scenario as the sister taxon of Sauropoda. An iterative PCR analysis identifies Mussaurus as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td>(Efraasia + (Riojasaurus + (Anchisauria)))</td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td>((Lufengosaurus + Camelotia) + Jingshanosaurus + (Coloradisaurus +</td>
</tr>
<tr>
<td></td>
<td>(Lessemsaurus + (Massospondylus + Anchisauria)))</td>
</tr>
<tr>
<td>100</td>
<td>Anchisauria</td>
</tr>
<tr>
<td></td>
<td>(Plateosauridae + Yunnanosaurus + Adeopapposaurus + Massospondylidae)</td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda: (Eoraptor + (Melanorosauridae))</td>
</tr>
<tr>
<td>100</td>
<td>Melanorosaurida</td>
</tr>
<tr>
<td></td>
<td>(Melanorosaurus + (Antetonitrus + (Kotasaurus + (Barapasaurus +</td>
</tr>
<tr>
<td></td>
<td>(Shunosaurus + Vulcanodon + (Omeisaurus + Camarasaurus))))))</td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosaurida: (Thecodontosaurus + Saturnalia)</td>
</tr>
<tr>
<td>100</td>
<td>Ornithischia: (Lesothosaurus + Heterodontosaurus)</td>
</tr>
<tr>
<td>100</td>
<td>Theropoda: (Xixiposaurus + Coelophysis)</td>
</tr>
<tr>
<td>60</td>
<td>Plateosauridae</td>
</tr>
<tr>
<td></td>
<td>(Plateosauravus + (Sarahsaurus + Plateosauravus) + Guiabasaurus +</td>
</tr>
<tr>
<td></td>
<td>Leyesaurus + Ammosaurus)</td>
</tr>
<tr>
<td>60</td>
<td>‘core Prosauropoda’: (Mussaurus + Plateosauria)</td>
</tr>
<tr>
<td>60</td>
<td>Sauropodomorpha: (Sauropoda + ‘core Prosauropoda’)</td>
</tr>
<tr>
<td>60</td>
<td>(Herrerasaurus + Ornithischia)</td>
</tr>
<tr>
<td>60</td>
<td>Saurischia: (Theropoda + Sauropodomorpha)</td>
</tr>
</tbody>
</table>
The appendicular partition of mY2010 is slightly larger than the appendicular partition of mU2007, with 166 characters. No taxa are excluded. The strict consensus of eight MPTs with lengths of 639 steps supports only two groups within Sauropodomorpha: Plateosauridae (Coloradisaurus, Plateosaurus gracilis, Plateosaurus engelhardti, and Unaysaurus), and a clade containing Adeopapposaurus and Leyesaurus. Interestingly, appendicular characters do not provide phylogenetic support for Sauropoda, in contrast to the results from the cranial and axial partitions. Eoraptor is placed as the most basal member of Sauropodomorpha (Interrelationships between the MPTs outlined in Tables 2.24 and 2.25; the strict consensus in Figure 2.26).
Figure 2.26 Strict consensus based on the appendicular partition of the dataset mY2010.
Table 2.24. Clades that are obtained on more than 50% of the 8 MPTs for the appendicular partition of mY2010. The appendicular characters in this partition support the ‘core Prosauropoda’ scenario as the sister taxon of Sauropoda. It is noteworthy to mention Ornithoscelida as a well-supported clade. An iterative PCR analysis identifies *Leonerasaurus* as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td>*(Aardonyx + (Melanorosaurus + (Blikanasaurus + ((Lessemsaurus + Antetonitrus) + (Isanosaurus + (Gongxianosaurus + (Pulanesaura + ((Tazoudasaurus + Vulcanodon) + (Patagosaurus + (Barapasaurus + Sauropoda))))))))))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda: <em>(Shunosaurus + Eusauropoda)</em></td>
</tr>
<tr>
<td>100</td>
<td>Riojasauridae: <em>(Eucnemesaurus + Riojasaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td><em>Plateosaurus</em></td>
</tr>
<tr>
<td>100</td>
<td>Lufengosauridae: <em>(Lufengosaurus + Jingshanosaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodiformes: *(Xingxiulong + (Anchisauridae + Massopoda))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha: <em>(Thecodontosaurus + Plateosaurus)</em></td>
</tr>
<tr>
<td>100</td>
<td><em>(Eoraptor + Panphagia)</em></td>
</tr>
<tr>
<td>100</td>
<td>Saturnalidae: <em>(Saturnalia + Chromogisaurus)</em></td>
</tr>
<tr>
<td>87</td>
<td>Ornithoscelida: <em>(Ornithischia + Neotheropoda)</em></td>
</tr>
<tr>
<td>87</td>
<td>Eusauropoda: *(Mamenchisaurus + Neosauropoda) + (Omeisaurus + Spinophorosaurus))</td>
</tr>
<tr>
<td>62</td>
<td>Massopoda: *(Massospondylus + Leyesaurus + Adeopapposaurus + Coloradisaurus + Yunnanosaurus + Lufengosauridae + Riojasauridae + Ruehleia + Glacialisaurus + (Seitaad + (Mussaurus + Melanorosauridae))))</td>
</tr>
<tr>
<td>62</td>
<td><em>(Guiabsaurus + Ornithoscelida)</em></td>
</tr>
<tr>
<td>62</td>
<td>Dinosauria</td>
</tr>
<tr>
<td></td>
<td>(((Eoraptor + Panphagia) + (Guaibasaurus + Ornithoscelida)) + Sauropodomorpha)</td>
</tr>
<tr>
<td>50</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td>*(Pantydraco + (Plateosauravus + Efraasia + Plateosaurus + Sauropodiformes))</td>
</tr>
<tr>
<td>50</td>
<td>*(Eoraptor + Panphagia) + (Guaibasaurus + Ornithoscelida))</td>
</tr>
</tbody>
</table>
Table 2.25 Clades that are obtained on more than 50% of the 8 MPTs for the appendicular partition of mY2010 after the removal of *Leonerasaurus*. The support for Ornithoscelida disappears and the arrangement is more similar to the one originally published. An iterative PCR analysis identifies *Seitaad* as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Lessemusauridae</td>
</tr>
<tr>
<td></td>
<td>*(Antetonitrus + (Pulanesaura + (Isanosaurus + (Shunosaurus +</td>
</tr>
<tr>
<td></td>
<td>(Tazoudasaurus + Sauropoda))))*</td>
</tr>
<tr>
<td>100</td>
<td>Theropoda (Neotheropoda + <em>(Herrerasaurus + Staurikosaurus))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td>*(Spinophorosaurus + (Omeisaurus + Mamenchisaurus)) + (Barapasaurus +</td>
</tr>
<tr>
<td></td>
<td>(Cetiosaurus + Neosauropoda) + (Vulcanodon + Patagosaurus))*</td>
</tr>
<tr>
<td>100</td>
<td>Thecodontosauridae <em>(Thecodontosaurus + Pantydraco)</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauravidae <em>(Ruehleia + Plateosauvuus)</em></td>
</tr>
<tr>
<td>100</td>
<td><em>Plateosaurus</em></td>
</tr>
<tr>
<td>80</td>
<td>Melanorosauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Melanorosaurus + (Lessemusaur + (Seitaad + Lessemusauridae)))</em></td>
</tr>
<tr>
<td>80</td>
<td>Massospondylidae</td>
</tr>
<tr>
<td></td>
<td><em>(Lufengosaurus + Leyesaurus + Massospondyl + Adeopapposaurus)</em></td>
</tr>
<tr>
<td>80</td>
<td>Anchisauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Anchisaurus + (Panphangia + Gongxianosaurus))</em></td>
</tr>
<tr>
<td>80</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td>*(Thecodontosauridae + (Eoraptor + (Saturnalia + (Coloradisaurus +</td>
</tr>
<tr>
<td></td>
<td>Mussaurus + Chromogisaur + Anchisauridae + Efraasia + Riojasaurus +</td>
</tr>
<tr>
<td></td>
<td>Plateosauravidae + Jingshanosaurus + Unaysaurus + Xingxiulong +</td>
</tr>
<tr>
<td></td>
<td>Plateosaurus + Massospondylidae + Yunnanosaurus + Eucnemesaurus +</td>
</tr>
<tr>
<td></td>
<td>Aardonyx + Melanorosauridae*)</td>
</tr>
<tr>
<td>80</td>
<td>Saurischia <em>(Chindesaurus + Guibasaurus + Theropoda + Sauropodomorpha)</em></td>
</tr>
</tbody>
</table>
The appendicular partition of the matrix by Sekiya et al. (2013) has 236 characters scored for 32 taxa, indicating a 75% duplication of characters between mU2007 and mY2010. The strict consensus of these three MPTs (with lengths of 736 steps) supports Sauropodomorpha, with *Eoraptor* placed as the sister taxon to all other members of this clade. It also supports Sauropoda, placing *Lamplughsauroidea* as the most basal sauropod, and Yunnanosauridae (Interrelationships between the MPTs outlined in Table 2.26; the strict consensus in Figure 2.27).

![Figure 2.27 Strict consensus based on the appendicular partition of the dataset by Sekiya et al. (2013).](image)
Table 2.26. Clades that are obtained on more than 50% of the 3 MPTs for the appendicular partition of the matrix of Sekiya et al. (2013). The topologies obtained from this analysis produce clades similar to the ones produced by the appendicular partition of the mY2010. An iterative PCR analysis identifies *Gyposaurus* as an unstable taxon, and its removal produces one topology not different from the arrangements in this table. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
<tr>
<td></td>
<td><em>(Lamplughsauro + (Vulcanodon + (Barapasaurus + (Shunosaurus + Omeisaurus))))</em></td>
</tr>
<tr>
<td>100</td>
<td>Melanorosauridae (<em>Melanorosaurus + Camelotia</em>)</td>
</tr>
<tr>
<td>100</td>
<td>Lessegmsauridae</td>
</tr>
<tr>
<td></td>
<td><em>(Aardonyx + Blikanasaurus + Lessegmsauridae + Antetonitrus + Melanorosauridae + Sauropoda)</em></td>
</tr>
<tr>
<td>100</td>
<td><em>Yunnanosaurus</em></td>
</tr>
<tr>
<td>100</td>
<td>Lufengosauridae (<em>Lufengosaurus + Jingshanosaurus</em>)</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodiformes</td>
</tr>
<tr>
<td></td>
<td><em>(Plateosauravus + Adeopapposaurus + Massospondylus + Coloradisaurus + Sarahsaurus + Lufengosauridae + Gyposaurus + Yunnanosaurus + Anchisaurus + Riojasaurus + Lessegmsauridae)</em></td>
</tr>
<tr>
<td>100</td>
<td>Plateosauria</td>
</tr>
<tr>
<td></td>
<td><em>(Efraasia + (Plateosauravus + (Seitaad + Sauropodiformes)))</em></td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
</tr>
<tr>
<td></td>
<td><em>((Saturnalia + Guaibasaurus) + Thecodontosaurus + Plateosauria)</em></td>
</tr>
</tbody>
</table>
The appendicular partition of Pol et al. (2011) excludes only two taxa, *Lapparentosaurus*, and *Volkheimeria*, which are not scored in the matrix despite having appendicular remains, consisting of 114 characters and 45 taxa. This analysis produces 8 MPTs with 265 steps. Some interesting signals come from this partition: *Eoraptor* and *Herrerasaurus* are placed at the base of Dinosauria; *Saturnalia* is placed immediately before the split between the three lineages of dinosaurs; *Guaiabasaurus* is placed as the sister taxon of an Ornithoscelida clade sensu Baron et al., (2017); and Sauropodomorpha contains three smaller clades, i.e. Plateosauridae, Massospondylidae, and Sauropoda (Interrelationships between the MPTs outlined in Tables 2.27 and 2.28; strict consensus in Figure 2.28).
Figure 2.28 Strict consensus based on the appendicular partition of the dataset by Pol et al. (2011). This topology is obtained from 167 MPTs with a length of 265 steps.
Table 2.27. Clades that are obtained on more than 50% of the 8 MPTs for the appendicular partition of the matrix of Pol et al. (2011). The topology is similar to the grade-like scenario produced by the mY2010. This partition also supports the clade Ornithoscelida. An iterative PCR analysis identifies Pantydraco as an unstable taxon., and its removal produces one topology not different from the arrangements in this table. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
<th>Clade Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Melanorosauridae</td>
<td>(Melanorosaurus + (Blikanasaurus + (Lessemsaurus + Camelotia + Antetonitrus + Camelotia + Sauropoda)))</td>
</tr>
<tr>
<td>100</td>
<td>Sauropoda</td>
<td>(Kotasaurus + (Vulcanodon + (Barapasaurus + (Isanosaurus + Omeiasaurus + Shunosaurus + Patagosaurus + Diplodocus + (Brachiosaurus + Camarasaurus)))))</td>
</tr>
<tr>
<td>100</td>
<td>Riojasauridae</td>
<td>(Riojasaurus + Aardonyx + Melanorosauridae)</td>
</tr>
<tr>
<td>100</td>
<td>Massospondylidae</td>
<td>(Jingshanosaurus + (Massospondylus + (Gyposaurus + Coloradisaurus + Yunnanosaurus + Lufengosaurus)))</td>
</tr>
<tr>
<td>100</td>
<td>Anchisauria</td>
<td>((Anchisaurus + Leonerasaurus) + Massopoda)</td>
</tr>
<tr>
<td>100</td>
<td>Massopoda</td>
<td>(Massospondylidae + Riojasauridae)</td>
</tr>
<tr>
<td>100</td>
<td>Plateosauridae</td>
<td>(Ruehleia + Plateosaurus gracilis + Plateosaurus engelhardti)</td>
</tr>
<tr>
<td>100</td>
<td>Sauropodomorpha</td>
<td>(Pantydraco + Thecodontosaurus + Plateosauria)</td>
</tr>
<tr>
<td>100</td>
<td>Ornithoscelida</td>
<td>(Guaiabasaurus + ((Lesothosaurus + Heterodontosaurus) + (Pisanosaurus + (Elaphrosaurus + Liliensternus + Coelophyisis)) + Sauropodomorpha))</td>
</tr>
<tr>
<td>100</td>
<td>Dinosauria</td>
<td>((Herrerasaurus + Eoraptor) + (Saturnalia + (Ornithoscelida + Sauropodomorpha)))</td>
</tr>
<tr>
<td>87</td>
<td>Plateosauria</td>
<td>(Efraasia + Plateosauridae + Anchisauria)</td>
</tr>
</tbody>
</table>
Table 2.8. Clades that are obtained on more than 50% of the 5 MPTs for the appendicular partition of the matrix of Pol et al. (2011) after the removal of Pantydraco. The topology supports a grade-like arrangement (Riojasauridae) and Massospondylidae as a sister taxon. An iterative PCR analysis identifies Camelotia as an unstable taxon. Brackets inside the clade have the same frequency of the row.

<table>
<thead>
<tr>
<th>Freq.</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Sauropoda</td>
</tr>
</tbody>
</table>
|       | \((Kotasaurus \, + \, (Vulcanodon \, + \, (Barapasaurus \, + \, (Eusauro{
| 100   | Melanorosauridae \, (Melanorosaurus \, + \, Blikanasauridae)         |
| 100   | Massopospondylidae                                                   |
|       | \((Jingshanosaurus \, + \, (Massopospondylus \, + \, (Gyposaurus \, + \, C\color{red}{l}o\color{red}{r}\color{red}{a}d\color{red}{i}\color{red}{s}\color{red}{a}r\color{red}{u}\color{red}{s\, r\, o\, u\, s}) \, + \, Yunnanosaurus \, + \, Lufengosaurus)))\) |
| 100   | Riojasauridae                                                         |
|       | \((Riojasaurus \, + \, Aardonyx \, + \, Melanorosauridae)            |
| 100   | Massopoda                                                             |
|       | \((\text{Massopospondylidae} \, + \, \text{Riojasauridae})\)        |
| 100   | Plateosauridae                                                        |
|       | \((\text{Ruehleia} \, + \, \text{Plateosaurus gracilis} \, + \, \text{Plateosaurus engelhardt})\) |
| 100   | Anchisauria                                                           |
|       | \(((\text{Anchisaurus} \, + \, \text{Leonerasaurus}) \, + \, \text{Massopoda})\) |
| 100   | Sauropodomorpha                                                       |
|       | \((\text{Thecodontosaurus} \, + \, \text{Efraasia} \, + \, (\text{Plateosauridae} \, + \, \text{Anchisauria}))\) |
| 100   | Ornithoscelida                                                        |
|       | \((\text{Guaibasaurus} \, + \, ((\text{Lesothosaurus} \, + \, \text{Heterodontosaurus}) \, + \, \text{Pisanosaurus} \, + \, (\text{Elaphrosaurus} \, + \, \text{Liliensternus} \, + \, \text{Coelophysis}))\) |
| 100   | Dinosauria                                                            |
|       | \((\text{Herrerasaurus} \, + \, \text{Eoraptor}) \, + \, (\text{Saturnalia} \, + \, (\text{Ornithoscelida} \, + \, \text{Sauropodomorpha})))\) |
Summary. Analyses of the appendicular partitions find support for several smaller groups of basal sauropodomorphs, but not always for Sauropoda. This could suggest that there is more specialization in some aspects of early sauropodomorphs that mean there are features that look synapomorphic of smaller clades. Moreover, the characters from this region are more easily scored from photographs and illustrations in the literature, unlike cranial and axial characters that often require closer study from multiple views (Table 2.29).

Overall, analysis of the three different partitions indicates that the phylogenetic signals captured across the matrices are largely similar and consistent. This also supports the idea that the analysis of character consistency performed by Sekiya et al. (2013) contributed to the increase in the resolution of the two previous datasets.

Table 2.29 Summary of the appendicular partition analyses performed on the four main matrices.

<table>
<thead>
<tr>
<th>Appendicular partitions</th>
<th>Characters</th>
<th>Taxa</th>
<th>MPTs (length)</th>
<th>MPTs CI and RI</th>
<th>Unstable taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>mU2007</td>
<td>149</td>
<td>40</td>
<td>5 (433)</td>
<td>0.346, 0.651</td>
<td>Seitaad, Gyposaurus</td>
</tr>
<tr>
<td>mY2010</td>
<td>166</td>
<td>55</td>
<td>8 (639)</td>
<td>0.322, 0.697</td>
<td>Leonerasaurus</td>
</tr>
<tr>
<td>Sekiya et al. (2013)</td>
<td>236</td>
<td>32</td>
<td>3 (736)</td>
<td>0.346, 0.540</td>
<td>Gyposaurus</td>
</tr>
<tr>
<td>Pol et al. (2011)</td>
<td>114</td>
<td>45</td>
<td>8 (265)</td>
<td>0.485, 0.795</td>
<td>Pantydraco</td>
</tr>
</tbody>
</table>

2.5.4 Continuous versus discrete characters

As an exploratory analysis of how different character coding strategies could affect topology, by obscuring or enhancing phylogenetic signals, the matrices were partitioned between characters that conveyed discrete information and characters that conveyed continuous information.

Continuous characters have been treated as discrete characters by setting boundaries that allow division of these into two, or more, character states. These characters differ from discrete characters in that there needs to be a categorisation process. These discretised continuous characters are here called categorised characters to distinguish them from discrete characters and continuous characters. Thus, the partitions proposed here between categorised and discrete data are justified on the grounds of the different methods to assess
them. Whereas discrete characters require a qualitative assessment, the categorised characters require measurements and further processing to delineate character states.

To help visualise the results in this section, the two trees are put next to each other in a tanglegram (Czabarka et al., 2016). The matrix mU2007 has 113 categorised characters, of which 24 form part of sets of characters coded via additive binary coding, and 189 discrete characters. The partition with categorised characters produces 65 MPTs with lengths of 338 steps, whereas the partition with discrete characters produces 115 MPTs with lengths of 510 steps. Although both partitions support Sauropoda, the smaller clades obtained in the discrete partition collapse in the categorised partition (Figure 2.29).

The matrix mY2010 has 117 categorised characters and 248 discrete characters. The categorised partition does not support any smaller clade within a polytomy for Sauropodomorpha (65 MPTs with a length of 338 steps), whereas a higher resolution is observed from the discrete partition (115 MPTs with a length of 510 steps). The number of trees obtained from the categorised partition is almost double the number of trees from the discrete partition. There is a significant amount of noise, which may come from the categorised characters, which seem to be affecting the resolution provided by the discrete ones (Figure 2.30).

Contrasting with the previous results, the matrix by Sekiya et al. (2013) shows two equally resolved topologies. This analysis performed a review of the character delineation and operationalised the information of the categorised characters in a way that was consistently applied to the assessed OTUs. The categorised partition, however, supports a different scenario than the discrete partition. Whereas in the discrete partition the strict consensus separates sauropodomorphs into two distinctive clades, i.e. Prosauroptoda and Sauropoda, the categorised partition seems to have produced clusters that contain similar-sized animals. For example, Massospondylidae is fully resolved in the discretised partition but split into two groups of non-closely related clades in the categorised partition, with one group containing Massospondylus, Adeopapposaurus, and Seitaad, and the other one Lufengosaurus and Coloradisaurus. Another situation can be observed for Yunnanosaurus huangi and Yunnanosaurus robustus. Whereas the discrete partition places these taxa at the base of Sauropoda and Prosauroptoda, respectively, the categorised partition finds them in the same clade. Aardonyx is placed within Prosauroptoda in the discrete partition but collapsed in a polytomy within Sauropodomorpha in the categorised partition (Figure 2.31).
Figure 2.29 Tanglegram showing the congruence between the topologies produced by the categorised partition and the discrete partitions from the matrix mU2010. The continuous partition produced 65 MPTs with a length of 338 steps (CI = 0.343, RI = 0.645), and the strict Nelsen consensus increases the homoplasy metrics (CI = 0.249, RI = 0.442). The discrete partition produced 115 MPTs with a length of 510 steps (CI = 0.378, RI = 0.644), and the strict consensus increases the homoplasy metrics (CI = 0.302, RI = 0.499).
Figure 2.30 Tanglegram showing the congruence between the topologies produced by the categorised partition and the discrete partitions from the matrix mY2010. The continuous partition produced 153 MPTs with a length of 467 steps (CI = 0.323, RI = 0.707), and the strict Nelsen consensus increases the homoplasy metrics (CI = 0.707, RI = 0.173). The discrete partition produced 80 MPTs with a length of 813 steps (CI = 0.341, RI = 0.681), and the Nelsen consensus increases the homoplasy metrics (CI = 0.3, RI = 0.605).
Figure 2.31 Tanglegram showing the congruence between the topologies produced by the categorised partition and the discrete partitions from the matrix by Sekiya et al. (2013). The continuous partition produced 3 MPTs with a length of 518 steps (CI = 0.347, RI = 0.549), and the strict Nelsen consensus increases the homoplasy metrics (CI = 0.335, RI = 0.524). The discrete partition produced 1 MPT with a length of 940 steps (CI = 0.384, RI = 0.515).

Finally, the partition analysis of the matrix of Pol et al. (2011) comprises a discrete partition with 200 characters and a categorised one with 77. The categorised partition produced 440 MPTs with a length of 171 steps, whereas the discrete partition produced 427 MPTs with a length of 434 steps. (Figure 2.32). The categorised partition has a RI = 0, meaning it has the highest level of homoplasy possible. In contrast, the discrete partition identifies the major groups of dinosaurs but does not provide a resolved topology at the level of basal sauropodomorphs. For comparison, the majority rule consensus of the MPTs obtained from
the categorised partition (with a cut-off of 70%) finds a similar topology to the discrete partition.

Figure 2.32 Tanglegram showing the congruence between the topologies produced by the categorised partition and the discrete partitions from the matrix by Pol et al. (2011). The continuous partition produced 440 MPTs with a length of 171 steps (CI = 0.520, RI = 0.806), and the strict Nelsen consensus increases the homoplasy metrics (CI = 0.806, RI = 0). In the left panel, the topology shown is the majority rule consensus with a cut-off of 70%. The discrete partition produced 427 MPTs with a length of 434 steps (CI = 0.535, RI = 0.796), and the strict Nelsen consensus increases the homoplasy metrics (CI = 0.353, RI = 0.569).
2.5.5 Partition Homogeneity tests

To assess the significance of these results, an Incongruence Length Difference test (ILD test), also known as the Partition Homogeneity test, was performed on the four datasets.

The ILD test measures if the signals obtained from different partitions in a matrix are different from randomly generated partitions (Dolphin et al., 2000; Planet, 2006; Mounce, 2013; Mounce et al., 2016; Sansom and Wills, 2017). The ILD value ($\delta_{ILD}$) is calculated as the difference between the combined tree length ($L_C$) and the tree length of each partition ($L_i$) (equation 2.5).

$$\delta_{ILD} = L_C - \sum_{i=1}^{n} L_i$$ (2.5)

The ILD value from this set of trees is then compared against the ILD values of randomly generated partitions. The difference between the combined tree length and the ILD values from the random partitions is then computed iteratively several times. The p-value is then calculated as the proportion of trees with the same ILD number against the ILD values from the random partitions. A p-value of 0.05 or lower indicates statistical significance on the assertion that the partitions from the original dataset have a distinctive signal over the trees from randomly generated partitions (Figure 2.33).

The anatomical partitions of the analyses described above were analysed using PAUP 4.0a164 (Swofford and Sullivan, 2003). The test was performed on 500 iterations with all the other values set to default in PAUP*. The p-values of the matrices indicate that random partitions do not produce different topologies from the ones described above: mU2007, a p-value of 0.144, mY2010, 0.093, Sekiya et al. (2013), 0.23, Pol et al. (2011), 0.75. This test was performed in the partitions based on character types, i.e. continuous and discrete. The p-values for three of the four ILD tests are non-significant, for mU2007, mY2010, and Pol et al. (2011), whereas the Sekiya et al. (2013) matrix just passes the test (p-value = 0.05). This means that the categorised characters are not producing distinctive topologies that are any better than randomly generated trees. The partial character analysis performed in Sekiya et al. (2013) might have increased the signal contained in the categorised characters. This dataset has a reduced number of taxa compared to the other datasets and has 49 parsimony-uninformative characters (9.7% of the total character number). This borderline statistical significance is more likely to be an artefact.
Combined tree length (ILD) = $L_{C}$

- Cranial partition
- Postcranial partition

Figure 2.33 Diagrammatic representation of the algorithm of the incongruence length difference (ILD), or Partition Homogeneity, test. The process starts calculating the length of the MPTs from a dataset and then calculating the ILD values for the length obtained from the partitions (in this case illustrated with a dataset that includes a cranial and a postcranial partition). Then the software generates random partitions of equal size to the user-defined partitions and new topologies are produced. The ILD values are calculated for the new randomly generated partitions. The P-value is calculated after assessing the frequency of ILD values during the iterations. In the example shown here, the P-value is $1 - \left(\frac{160}{2000}\right) = 0.08$, meaning the two topologies from the partitions are not significantly incongruent since random partitions do produce several similar ILD values.

- ILD$_1$ = $L_{C} - (L_{CP} + L_{PP}) = 2$
- ILD$_2$ = $L_{C}' - (L_{p1} + L_{p2}) = 1$
- ILD$_n$ = $L_{C}' - (L_{p1} + L_{p2}) = 3$
The ILD test allows us to examine if the partitions can be combined to increase phylogenetic accuracy, whether there is any process of heterogeneity, such as different evolutionary processes or differential rates of evolution, or if the partitions experience different evolutionary histories due to cases of non-vertical inheritance (Planet, 2006). There is an ongoing debate on the reliability of this test to measure topological congruence (Dolphin et al., 2000; Darlu and Lecointret, 2002; Planet, 2006; Mounce, 2013). However, the values obtained in the analysis performed here permit the conclusion that the data are compatible and that the signals are congruent within the partitions. It also supports the idea that the different homoplasy patterns could be attributed to character analyses and to a character assessment applied uniformly to all the taxa, as implied by the increase in significance obtained in the partitions of the dataset by Sekiya et al. (2013).

2.6 Differences in the character composition of the different phylogenetic matrices

In an analysis performed by Peyre de Fabrègues et al., (2015), it was proposed that the source of discrepancies between different analyses of sauropodomorph relationships might lie in the character choices made in each analysis. The three matrices examined by Peyre de Fabrègues et al. (2015) were independently derived compilations of the characters gathered from personal observations of specimens and information from the literature. The analysis in Peyre de Fabrègues et al. (2015) concluded that character choice and decisions on character scoring are the roots of the observed inconsistencies. Whereas the latter authors provide evidence that this is the case, the possibility that character delineation is the cause of inconsistent topologies is explored further here in this work (Chapter 3).

Skull characters contribute approximately one-third of the total number of characters in each character list. In the datasets focusing on basal sauropodomorph relationships only a few characters concern the axial skeleton, and for this reason, datasets from some other analyses have been examined to increase the number of characters for this region, i.e. Wilson (2002), Nesbitt et al. (2009, 2010), Remes et al. (2009), Cabreira et al. (2011), Martínez et al. (2011), Langer et al. (2013). On average, one-quarter of each dataset is dedicated to the hind limbs, leaving the forelimbs with fewer characters.

An analysis of the character lists has already been published (Peyre de Fabrègues et al., 2015) where there is a discussion on the composition of those lists. Figure 2.34 shows the distribution of characters in the following body regions: cranial (skull, mandible, and dentition), axial (vertebrae and ribs), and appendicular (pectoral girdle, forelimb, pelvic...
girdle, hindlimb). These characters were mapped on a character distribution map (Figure 2.34), a method for visualising character lists in comparative cladistics that was developed by Whitlock and Wilson (2013).

The maps show that differences in the character distributions between the three character lists explored by Peyre de Fabrègues et al. (2015) are not large and that they are rather similar (Figure 2.34). Regarding cranial characters, the braincase and the palate are under-represented in all three datasets. The same is true for characters concerning the pectoral girdle and forelimbs. Additionally, Peyre de Fabrègues et al. (2015) reported that 60% of the characters overlap in the three datasets, 20% of the characters overlap between Upchurch et al. (2007) and Yates et al. (2010), 13% of overlap between Yates et al. (2010) and Pol et al. (2011), and 7% between Upchurch et al. (2007) and Pol et al. (2011).

Characterization of the complexity of character statements (number of character states) showed that whilst Upchurch et al. (2007) coded only 2% of characters as multistate characters, the number increases to 14% and 15% in Yates et al. (2010) and Pol et al. (2011), respectively. Upchurch et al. (2007) employed additive binary coding in all the characters, whereas Yates et al. (2010) and Pol et al. (2011) used transformational characters more often. The three matrices have the same proportion of neomorphic characters (Peyre de Fabrègues et al., 2015).

Since the partitioned analyses showed that different phylogenetic signals are present in different regionalised subsets of characters, a final analysis was performed to compare if the characters chosen in each matrix are significantly different between the character lists. To compare the composition of the character lists an intraclass correlation coefficient (ICC) was performed in PAST v 3.21 via an ANOVA.

The intraclass correlation coefficient (ICC) is calculated from a table of character proportions where each group is considered a sample population. The between groups sum of squares (SSbg) is given by equation 2.6:

\[
ICC = \frac{s_g^2}{(s_g^2 - s^2)}
\]  

(2.6)
Figure 2.34 Character distribution map of the phylogenetic analyses published by Upchurch et al. (2007), Yates et al. (2010) and Pol et al. (2011) obtained from Peyre de Fabrègues (2015). These maps, however, do not consider the subsequent addition of characters.

Where $s_2$ represents the mean squares within groups (MSwg), and $s_2g$ represents the variance of the mean squares between (MSbg) and within the groups. This is achieved by building an analysis of variance table (ANOVA table) based on the proportions of each group of characters in the references were new characters are compiled or added (Figure 2.2) The following algorithm corresponds to the one employed by PAST v. 3.21.

The sum of squares between groups (SSbg) is given by equation 2.7 where $n_g$ is the size of group $g$ and the means correspond to the group ($\bar{x}_g$) and total means ($\bar{x}_\tau$).

$$SS_{bg} = \sum_g n_g (\bar{x}_g - \bar{x}_\tau)^2$$  \hspace{1cm} (2.7)
The sum of squares within groups is obtained by considering the square difference between
the value $x_i$ in each group $g$ as given by equation 2.8.

$$SS_{wg} = \sum_g \sum_i (x_i - \bar{x}_g)^2$$  \hspace{1cm} (2.8)

The mean squares between and within groups are given by equations 2.9 and 2.10
respectively, where the degrees of freedom for $SS_{bg}$ is the number of groups minus one, in
this case, ten, and the degrees of freedom for $SS_{wg}$ is the number of values minus the
number of groups.

$$MS_{bg} = \frac{SS_{bg}}{df_{bg}}$$ \hspace{1cm} (2.9)

$$MS_{wg} = \frac{SS_{wg}}{df_{wg}}$$ \hspace{1cm} (2.10)

The intraclass coefficient relies on a model II ANOVA that considers random effects, and
for this, the mean square within groups is considered as the variance, as given by equation
2.11, and the variance due to the difference between groups as given by equation 2.12, as
this corresponds to a balanced design.

$$s^2 = MS_{wg}$$ \hspace{1cm} (2.11)

$$s_g^2 = \frac{MS_{bg} - MS_{wg}}{n}$$ \hspace{1cm} (2.12)

These two variances ($s^2$ for variance within groups, and $s_g^2$ as the variance due to the
difference between groups) are then inputted into equation 2.6.

The intraclass correlation coefficient is an unbiased estimator that indicates how much the
units inside the same group resemble each other. In this analysis, the groups that were
studied were the proportions of characters that corresponded to the following skeletal
regions: skull, cervical vertebrae, dorsal vertebrae, sacral vertebrae, caudal vertebrae,
pectoral girdle, forelimb, pelvic girdle, and hind limb. The largest proportion in all datasets
corresponds to the cranial characters, whereas the pectoral girdle, sacral vertebrae, and
caudal vertebrae each represent an average of <5% of the composition of the character lists in all the phylogenetic analyses considered in this work (Figures 2.35 and 2.36).

This has two implications: 1) that the proportion of characters from each region in all the matrices remains the same (ICC ≅ 1), indicating that there is not a sampling bias regarding the character composition, and 2) that in all the matrices the cranial and posterior appendicular characters constitute the largest proportions in all datasets.

Figure 2.35 Stacked bar chart of the proportional composition of characters in the phylogenetic matrices studied in this work (the references are listed in the chart). The characters are classified in the following groups: skull, cervical vertebrae, dorsal vertebrae, sacral vertebrae, caudal vertebrae,
pectoral girdle, forelimb, pelvic girdle, and hindlimb. The group “miscellaneous” refers to the characters that include dermal and soft tissue structures. These are the groups that were compared between and within them to assess if these compilation efforts are inherently different amongst these analyses. This chart was used to create the ANOVA table and test the hypothesis of the matrices having biases towards certain regions.

Figure 2.36 Dot chart showing the distribution of residuals (the difference between the SSwg and the SSBg) in every group. The ICC value (0.994) indicates excellent reliability on the character sampling, indicating that any selected matrix will have the same proportion of character from each region than any other matrix. This highlight the importance of studying the impact of character delineation and the different phylogenetic signals provided by each region.
2.7 Conclusions

After re-analysing the matrices, it is clear that the roots of inconsistencies between the various published analyses of basal sauropodomorph relationships do not lie in the analytical stage of the process. The current consensus that accepts ‘basal Sauropodomorpha’ as a complete grade does not have more support than any other paraphyletic arrangement for ‘prosauropods’ or that a ‘core prosauropods’ clade. Although the taxonomic composition differs between matrices, they rely mainly on the same OTUs. The different OTUs have similar geographic representation across competing data matrices, although there is some oversampling of Gondwanan taxa. Moreover, based on stratigraphic information, only the dataset of Sekiya et al. (2013) fails to produce more stratigraphically coherent trees than randomly generated trees. Finally, the character composition is basically identical in all datasets, indicating that there is not an oversampling of characters from any particular body region and the biases found through the partition analyses are affecting the phylogenetic signals in the final topologies in similar ways.
This chapter presents a description of the methods used to compile all previous
phylogenetic datasets into a single supermatrix. The first section deals with why the
supermatrix approach was chosen over the supertree method, to produce a consensus from
the main, competing phylogenies. The following discussion details the process of
compiling conflicting matrices that have been modified recursively over time without a
proofreading system being implemented. This problem has caused some misunderstandings
recently, e.g. the dataset of Baron et al. (2017a) and the recursive analyses performed by
Baron et al. (2017b), Langer et al. (2017) and Padian (2017). This section details some
strategies currently being implemented in data science to combine datasets. There is also a
discussion on the operational taxonomic units (OTUs) that were included in the final
compilation along with a discussion of the specimen content of each taxon. The last part of
this chapter deals with the series of strategies implemented to reassess all of the characters
compiled and how to ensure that the characters are consistently coded. A comparison
between the advantages and disadvantages of each character coding strategy can be found
elsewhere in the literature and this work does not provide any substantial contribution to
this debate. Here I outline some mechanisms to ensure that the variability observed so far
is consistently and non-redundantly compiled into a single dataset so that new information
can be integrated into it. Moreover, this work contributes to the debate on character
delineation. Character delineation is the identification of character states in a character
statement and here I provide a common logical background for neomorphic and
transformational characters (sensu Sereno, 2007a). Finally, here I provide an analytical tool
to identify when a character is best coded as a neomorphic or a transformational character
statement.

3.1 Definitions

This chapter uses the following definitions, listed here for convenience and presented in
order of appearance:

1. Character list. A catalogue of character statements selected or deemed relevant for
   the evaluation of the phylogenetic relationships of the group of interest.
2. Character statement. A sentence that conveys the information of a character and a
   statement of that character (Sereno, 2007a).
3. Morphological character. The combination of a locator and a variable type, or the feature of the locator that is considered changeable (Sereno, 2007a).

4. Statement. The combination of the qualifier of a variable type, the attribute that changes and all of the character states (Sereno, 2007a).

5. Locator. The anatomical structure on which the variable is being assessed.

6. Character states. The various options of a variable, all independent and mutually exclusive.

7. Discrete character. A character whose character statement can be defined as a discrete set, in which each character condition can be considered as an isolated point in a topological space, i.e. a single point that does not contain any other set points. A discrete character can be transformed into a continuous character. For example: jugal, relationship with the lacrimal: lacrimal overlapping lateral surface of jugal or abutting it dorsally (0), jugal overlapping lacrimal laterally (1) (Rauhut, 2003a).

8. Continuous character. A character whose character-statement can be defined as a sequence of ordinals such as every stage can be the inferior and superior limit of all the values in other stages. A continuous character corresponds to values in the set of positive real numbers. For example: skull length in non-juveniles (Hungerbühler, 1998b).

9. Categorised character. A continuous character where the elements of the set have been distributed into groups (character states). For example: post-temporal opening, size, diameter relative to the diameter of the foramen magnum: greater than or equal to 1.0 (0), less than 1.0 (1) (Sereno and Novas, 1993).

10. Phylogenetic matrix. A rectangular array of numbers with dimensions $m \times n$ and items $a_{i,j}$ that are referred to as ‘character-scorings’, where $m = i$ represents the Operational Taxonomic Unit and $n = j$ represents the character statement.

11. Character delineation. The definition of the different elements of a character-statement.

12. Character coding. The definition of the character states.

13. Character scoring. The assignment of a value $a_{i,j}$ in the data matrix.

3.2 The supermatrix approach

Addressing the problem of character compilation into a supermatrix comes with the concomitant problem of choosing character coding strategies. The most substantial difference between the three major independent character lists used as a basis for this work
is the character coding strategy (see Chapter 2). Comparisons between them are problematic because different taxa have been sampled and different characters compiled. It is also difficult to track all the changes and modifications made to subsequent iterations of the matrices, since the changes do not accumulate on a single working dataset, but generate different versions, each adding new taxa and/or new characters. Since topologies do not have the same taxonomic scope, differences may not be comparable to the phylogenetic information of one taxon in the other data sets.

This problem is very common in biological research, where data sets are constantly and independently assembled with different scopes. Two general methods have been proposed to integrate information disparity into workable frameworks: supertree and supermatrix approaches (de Queiroz and Gatesy, 2007).

The supertree method requires that each data set be analysed independently to produce different topologies and then the trees derived from these independent analyses are joined together to estimate an overall phylogeny. Even though several methods have been developed to obtain supertrees from multiple datasets (Sanderson et al. 1998; Bininda-Emonds et al. 2002; Bininda-Emonds, 2004; Cotton and Wilkinson, 2009), this method does not offer a solution to the problem at hand of obtaining a global phylogeny of non-sauropod sauropodomorphs for the following reasons:

1. The different matrices have a lot of overlap. As noted by Peyre de Fabrègues et al. (2015), Upchurch et al. (2007a) shares 224 characters with Yates et al. (2010) and 191 characters with Pol et al. (2011), whereas Yates et al. (2010) shares 192 characters with Pol et al. (2011). Almost half of the characters in each dataset overlap with those in the other datasets.

2. As shown in Figure 3.1, the character lists come from a common pool of sources. This explains the notable similarities between them. Therefore, they do not represent independent character lists, even if the scorings were made independently. This adds an extra layer of difficulty because there could be disagreements over the same assessed characters, creating a palimpsest of contradictory information for the same characters.

3. Although the characters have duplicates in other matrices, this does not mean that we can establish one-to-one relationships between them. Some duplicates come from characters comparing the same landmarks but using different properties for comparison. Other duplicates are simply a product of different strategies of character coding: for example, whereas in Yates (2007b) continuous characters are coded either with multistate
coding or with two-state coding by choosing an arbitrary limit, in Upchurch et al. (2007) the same character is coded via binary coding with another arbitrarily chosen limit. Thus, one character in Yates (2007b) potentially has at least two relational characters in Upchurch et al. (2007). This adds an extra layer of noise that could significantly affect the outcome of the supertree.

4. Although there are three different matrices, each subsequent revision and modification creates a different version. This means that the super tree method requires that all versions be updated to create a single consensus version. Basically, this effort leads to the supermatrix approach.

Figure 3.1 Timetable of the different sources of characters used in this work that are not directly from the independent three matrices outlined in Chapter 1 as the main compilations of characters employed in Sauropodomorpha. The characters are classified based on their taxonomic scope, from more inclusive at the top (Archosauria) to Sauropodomorpha. The squared labels indicate which of the three major compilations used each character list: Y stands for Yates (2007b), U stands for Upchurch et al. (2007) and P stands for Pol et al. (2011).
The supermatrix approach requires the systematic combination of all the characters into a single phylogenetic matrix and then analysing this new larger, near-comprehensive dataset (Figure 3.2).

The super-tree approach has been applied to study dinosaur diversification patterns (Lloyd et al. 2008). The analysis was built discarding trees for which there was not a matrix accessible either as part of the publication itself or upon request from the author. The tree compiled all the existing trees that involved dinosaurs published prior 2006 and the curation of the data generated a strong skew in the data towards more recent analysis. The purpose of this analysis was to study diversity through time and test whether dinosaurs were part of the Cretaceous Terrestrial Revolution (KTR), a rapid diversification of several clades that contributed to shape modern ecosystems, such as flowering plants, herbivorous and social insects, squamates, birds and mammals. The supertree approach seems to produce interesting results that allow experimenting with how sampling biases and ghost lineages affect the interpretation of diversity in the fossil record and apparent diversity peaks in the Norian and the Campanian-Maastrichtian are greatly reduced when those issues are taken into account. Finally, their supertree for Sauropodomorpha did not consider the three main phylogenies of basal sauropodomorphs that are dealt with herein, as the cut-off date was 2006, but it supports a similar scenario to the one published by the subsequent iterations of modifications from the Yates (2007b) matrix. The results had the (Basal Sauropodomorpha + (Prosauropoda + (Basal sauropoda + Neosauropoda))). This result is not comparable with the subsequent analyses since it does not include them and no revision of this has been carried out, however it does include all the character lists reviewed here before 2006 (Figure 3.1).

Supertree methods imply a loss of information because the final topology could consider some characters irrelevant because of the search parameters employed (de Queiroz and Gatesy, 2007) and they could also produce novel results with no foundation from the original source trees, although this may occur rarely (Bininda-Emonds, 2003). The supermatrix method offers the advantage of enhancing a phylogenetic signal over noise, which in individual data sets could be weaker or negligible (Barrett et al. 1991). Because all of the evidence is being considered, even if the final tree topology is similar in both methods, the character support can increase for relationships that are weak in the individual topologies (Olmstead and Sweere, 1994; Gatesy et al. 1999). Hidden support is not an infrequent phenomenon and has been shown to account for a large percentage of the total
character support. This advantage is relevant for basal sauropodomorph phylogenies because the main weakness of all the topologies is that they find low character support for clades (see Chapter 1).

Moreover, the enhancing of hidden support is key to the case at hand, mostly because hidden support might come from two potential sources: either from the same taxa of interest that are being incorporated into all of the relevant datasets, or additional taxa decrease the likelihood of groupings that are artefacts of long-branch attraction (Hills, 1998). These two situations could converge in the supermatrix approach for non-sauropod sauropodomorphs since the taxonomic scope varies greatly between the datasets and within different versions of the same data set (Chapter 2).

For these reasons, the main objective of this work is to generate a supermatrix that includes all of the evidence from the different datasets, as well as additional, novel character data (Figure 3.3). Additionally, the merging of all of the information from different data sets is a decision-based activity. When two characters are potentially similar or redundant, the supermatrix approach requires one of the characters to be deleted from the dataset, since an assumption of the method is that all characters are independent and that a single topology explains the data. This requires an independent method to assess whether a character is
likely to be independent, or that we at least have theoretical evidence of its independence. The independence of characters is a problematic assumption since, in the end, all biological systems are interdependent (Trewavas, 2006): the organisation of the skeleton relies on genetic instructions that could govern other elements of the anatomy and these could also affect the final skeletal organisation. Here, a method based on topological properties is outlined to diagnose when a character is at least theoretically independent.

Finally, one of the suggested problems of the supermatrix approach is the large amount of missing data. Even though missing data can, in fact, generate conflicting topologies (Kearney, 2002; Wiens, 2006), it is better to include very incomplete taxa to prevent the long-branch attraction problem. Overall, if the supermatrix is considered as the set of all of the available information, incomplete taxa increase the information input in certain characters. Although the incorporation of incomplete taxa can greatly reduce resolution, simulations have shown that missing data only plays a significant role when the incomplete OTUs carry uninformative characters (Kearney, 2002; Wiens et al. 2005; Wiens, 2006; de Queiroz and Gatesy, 2007). Therefore, making sure that the characters are informative enough can diminish the negative impact of missing data. Even if a taxon with a lot of missing data has been excluded from previous datasets, its inclusion into the set of all the information is still more informative than the data set that excluded it, because the dataset without the incomplete taxon is a subset of the supermatrix.

![Figure 3.3 Diagrammatic representation of the methodology used here to produce a supermatrix. The highlighted characters are repeated between the matrices, showing that these duplicates are not a one-to-one correspondence so that the purple character in dataset 2 is equivalent to two characters in datasets 1 and 3.](image)
This is relevant here because several OTUs, such as Agnosphytis, Camelotia and Blikanasaurus, have often been excluded a priori due to their incompleteness. However, as shown here, increasing the parameter search and allowing the software to explore much more of the tree space can produce well resolved topologies, as was shown in the four analyses above (See Chapter 1, section 1.3). None of the data sets produces the large polytomous topologies in their respective strict consensus with all the taxa included.

3.3 Phylogenetic matrices as relational databases

A database can be considered as an organised collection of facts. Data in a database has the property of being persistent and an accurate reflection of reality. Although it might seem trivial that matrices are databases, there has not been a proper treatment of them as such. This can be seen in the extensive discussion of how to compare phylogenetic matrices (e.g. Sereno, 2007b, 2009; Mounce, 2013; Whitlock and Wilson, 2013; Peyre de Fabrègues et al. 2015), contrasting with the limited amount of discussion on how to ensure data integrity. Although integrity is a key aspect of any database development and design in modern information systems, designing for integrity is a much-neglected aspect of database development in general (Stapelberg, 2009; Figure 3.4).
The aim of cladistics is to distinguish homologies from homoplasies (Brazeau, 2011). Modern cladistic analyses are computer-based, where a character-taxon matrix is fed into an algorithm to determine which characters are homologous (Schuch and Brower, 2009). Although character lists can be designed thoroughly and be detailed as possible, the information that the algorithm reads is only a series of codes (tokens) from the observations collected in the character lists (Schuch and Brower, 2009; Brazeau, 2011).

The method employed to transform the morphological observations into character statements is called character delineation and will affect the tree search results and the interpretations of homology (for more discussion see Archie, 1985; Pleijel, 1995; Wiens, 2001; Hawkins et al. 2002; Brazeau, 2011; Müller and Dias-da-Silva, 2017).
The problem of character selection has two components:

1. A biological component, which has at its roots in choosing what is a character. Characters are hypotheses of homology and, therefore, are assessed by criteria of similarity (Schuch and Brower, 2009). This component is also related to taxon sampling and the validity of the individuals that constitute a taxon (Müller and Dias-da-Silva, 2017).

2. A mathematical component, because a character-taxon matrix is a mathematical abstraction. Morphology-based character lists are often a combination of different coding methods. Each coding method has its own set of assumptions; however, the matrix is a collection of tokens that the algorithm interprets as uniform. Therefore, these assumptions are lost when the matrix is compiled, because the algorithm will interpret every change from ‘0’ to ‘1’ as one step in every character statement, notwithstanding that they are logically incongruent. Therefore, the second problem to tackle is to assess whether or not a matrix is mathematically uniform and coherent (Brazeau, 2011).

3.4 Assessment of compatibility

The first stage in compiling incompatible datasets is data wrangling. This is the conversion of any kind of data into a form that is more workable (Figure 3.5). There are two main sources of phylogenetic data for basal sauropodomorphs to date: the supplementary information presented in publications and an informal online repository compiled by Graeme T. Lloyd (http://www.graemetlloyd.com/matrdino.html). The latter specifies that there is no proofreading system to check for the accuracies on the data matrices uploaded. Moreover, errors produced by copying and pasting the datasets into a readable format (i. e. Nexus format) are not systematically avoided or reduced in any way.

As part of data wrangling, the matrices downloaded from the online repository were matched with their respective character lists via the software Mesquite. Once the matrix incorporated the character lists, they were checked by randomly selecting character states and assessing whether they matched with the character states reported in the publication. This system allowed the identification of a mismatch between the character lists and the matrix, as reported in Nesbitt et al. (2010). The correct matrix was obtained via personal communication with the author and from an existing uploaded matrix in the online repository MorphoBank (in: https://morphobank.org/). A similar error in the matrix
uploaded by Baron et al. (2017a) was detected with this mechanism and the original dataset was obtained from the lead author.

Integrity is the maintenance of accuracy of data through its life cycle (Boritz, 2005). Matrices are expected to change as is the case with any dynamic database. Integrity is not a matter of concern when the databases are used for reference purposes, where they will not change over time. Data integrity is therefore needed to prevent unintentional changes to the information stored in the database. However, phylogenetic matrices have previously been treated as references, rather than databases and thus data integrity has not been implemented.

A pre-requisite for data integrity is data validation. Data validation is the process of ensuring that the database has data quality, meaning that every entry is correct and useful. This process requires a set of rules to be thoroughly and consistently applied to all the data entering the database (Boritz, 2005). In the case of phylogenetic matrices, data validation

Figure 3.5 Diagrammatic representation of the data wrangling process. The supplementary information published with the paper is checked against the information contained in the paper and against the online repository graemelloyd.com/matrdino.html. It was assumed that the scorings reported represent the original intention of the authors, with the caveat that the creation of this repository does not guarantee any proofreading of the information. Similar matrices and character lists are integrated, when compatible, in the same matrix. When scorings are contradictory, the scoring that was published first has priority, unless the paper with the modification explicitly indicates this change. The compilations of similar and compatible matrices are then contrasted against the partially compatible matrices. This leads to the process of comparing and standardising character statements.
needs to be a constant procedure to ensure the new incoming information is compatible with the previous one.

Databases do not change continuously; instead, they go through distinct stages of change. Some of the stage changes are invalid if they do not follow the requirements outlined during the data validation process. Each valid stage creates an extension of the original database, whilst invalid stage changes are discarded. Data integrity is thus defined as the process to ensure that a database goes through only valid states (Beynon-Davies, 2000; Connolly and Begg, 2015).

In data science, every change to a database is defined as a transaction (Beynon-Davies, 2000; Boritz, 2005; Connolly and Begg, 2015). In the case of phylogenetic matrices, each addition of new taxa or characters constitutes a transaction (Figure 3.6). To ensure that database changes involve only valid transactions, it is important to have integrity constraints. These constraints need to be placed near the source of information from which we collect our data. In the case of phylogenetic matrices, these constraints need to be placed in the character list, which translates the information observed in fossils into the variables that comprise the database.
Figure 3.6 Network diagram showing the different transactions in the databases by Yates (2007b) and Upchurch et al. (2007). The arrows indicate an independent transaction with modifications. The most common modification is the addition of new taxa (dark green boxes with white numbers), but sometimes the transaction involves the addition of characters (light green boxes with black numbers). The matrices that were used in the final compilation are enclosed in red boxes since they represent the final stages of a path of transactions, hence accumulating the maximum amount of changes. The labels are abbreviations of the matrices compiled for this work (from stage 0 to stage 6): Y2007b – Yates (2007b); Upchurch et al. 2007 – Upchurch et al. (2007), Y2010 – Yates et al. (2010), Y2010’ – Yates et al. (2010) second analysis; M2009 – Martinez et al. (2009), A2013 – Apaldetti et al. (2013), SP2007 – Smith and Pol (2007), SL2010’ – Sertich and Loewen (2010) second analysis; A2013’ – Apaldetti et al. (2013) second analysis; O2013 – Otero et al. (2013); E2010 – Ezcurra et al. (2010); A2011 – Apaldetti et al. (2011); K2010 – Knoll et al. (2010); SL2010 – Sertich and Loewen (2010); R2011’ – Rowe et al. (2011) second analysis; C2011 – Cabreira et al. (2011); N2010 – Novas et al. (2010); M2012 – Martinez et al. (2012); MP2014 – McPhee et al. (2014); R2011 – Rowe et al. (2011); MP2015b – McPhee et al. (2015b); O2015 – Otero et al. (2015); S2013 – Sekiya et al. (2013); MP2015a – McPhee et al. (2015a). Changes of colour in the inner square indicate changes in the character scorings.

3.5 Compilation of phylogenetic matrices

A proposal to ensure data integrity in phylogenetic matrices is to implement a complementary, detailed account of all the character statements with illustrations, information about the authors who proposed them first, the authors who modified it, the
character type and character usage (Sereno, 2009). This would be an additional database that constitutes the metadata of any phylogenetic matrix and it has been achieved in some publications, for exa, ſne. Langer and Benton (2006) for basal dinosaurs, Nesbitt (2011) for basal archosaurs and Gauthier et al. (2012) for squamates. The purpose of metadata is record the means and circumstances of data creation, data usage and its quality (Beynon- 
davies, 2000). Although having the metadata of all character statements does help, this does not ensure data integrity in its totality. A criterion to define whether a character can be included in a matrix is to assess if it represents homology. This is a complicated issue since the purpose of the phylogenetic analyses is to identify homologies from homoplasies. The possibility of using mathematical topology as a proxy of homology and therefore as a constraint for data integrity, is explored here.

To define what kind of data validation needs to be implemented to ensure that matrices travel only through valid transitions it is important to understand the type of database a phylogenetic matrix is. The matrix needs to be interpreted through the taxon list and the character list. The software used in this work to interpret these databases was Mesquite (Maddison and Maddison, 2018).

Phylogenetic matrices can be thought of as relational data models. Any relational data model is restricted to the following set of rules (Beynon-Davies, 2000):

1. Every relation in a database must have a distinct name. All of the relations in a phylogenetic matrix are homologies, meaning that the columns represent characters that we have identified to be homologous.
2. Every column must have a distinct name within the relation. This corresponds to the character statement.
3. All entries in a column must be of the same kind. All the entries correspond to the character states that the character statement contains as valid for each taxon.
4. The ordering of columns in a relation is not significant. The order of the columns is arbitrary, and the information is not affected by the ordering of the character statements.
5. Each row in a relation must be distinct. In phylogenetic matrices, two identical rows correspond to a taxon and as they thus represent the same operational taxonomic unit one of the rows would be discarded.
6. The ordering of the rows is not significant. As with the character statements, the ordering of the taxa is not relevant, nor does it affect the output. Traditionally, the first row is the outgroup, the OTU that provides information of the primitive conditions for the analysis. TNT allows selection of this OTU from any row, meaning that order is not needed; however the default setting is to take the first row of the input matrix as the outgroup.

7. Each cell or column/row intersection in a relation should contain only a so-called atomic value. Although this condition is allowed, the presence of two character-states in the same column/row intersection is first assumed to represent a disagreement, rather than a true polymorphism.

Since we consider matrices as relational databases, we can use the same parameters that are used to assess data integrity in any type of relational data model. These parameters are entity integrity and referential integrity (Beynon-Davies, 2000; Connolly and Begg, 2015).

Entity integrity refers to the enforcement that every primary key is unique and not null (Beynon-Davies, 2000; Connolly and Begg, 2015). The primary keys are the names of each relationship and in the phylogenetic matrices, they correspond to the character statements. The entity integrity rule also applies to the rows, where duplicates are equally forbidden.

Referential integrity refers to the interconnection between separate datasets. This means that there is a set of defined rules that specify what to do when a new row or column is added. For a new row or column to be added there must be a reference dataset to which they are also added. This integrity can be ensured by having metadata datasets.

Finally, referential integrity is also conditioned to the restriction of data manipulation that is imposed on relational data models. The input, removal, amendment and retrieval of data from a relation must be done by obeying only the operators of relational algebra (Beynon-Davies, 2000; Connolly and Begg, 2015).

Therefore, entity integrity allows the determination of whether a row or a column can be added into the target matrix and referential integrity constrains the ways in which new data can be included or excluded.

The compilation of all the datasets was performed using the following sequence of steps:

1) By assessing the OTUs as primary keys it is possible to compare the content of the databases. The three main compilations used specifically to assess the evolutionary history
of basal sauropodomorphs were used as a basis to compare the influence of taxonomic composition, namely Upchurch et al. (2007), Yates (2007b) and Pol et al. (2011). Because they have similar scopes and come from similar pools of sources, these are the most compatible datasets and they should follow the criteria of relational integrity (Figure 3.1).

2) Once the taxonomic composition is dissected in terms of compatible and incompatible sets, it becomes easier to identify the different transactions that have occurred in each of the three main databases. It is worth noting that the only dataset that has remained unmodified is Pol et al. (2011).

3) Comparison between datasets via decomposition into compatible sets shows that the database of Upchurch et al. (2007) is the most compatible with the datasets of Yates (2007b) and Pol et al. (2011), meaning that this dataset has the largest number of elements in the taxonomic lists shared with the other two datasets. This allowed Upchurch et al. (2007) to be chosen as the target database to receive all of the modifications. Moreover, this can be used as a starting point to compare disagreements: if two character statements are scored with different states for the same taxon, the scoring in Upchurch et al. (2007) has priority unless the change is justified in the publication in which the change was implemented.

In total, six stages of modifications were identified for Yates (2007b) whereas only three stages were identified for Upchurch et al. (2007). This also highlights the Upchurch et al. (2007) matrix as a good candidate to be the target dataset, since the accumulative error that could occur in any transaction is less than that based on the various iterations of the Yates (2007b) matrix. This criterion also makes Pol et al. (2011) a good candidate but, regarding the taxonomic composition, it is less compatible with the other two datasets.

4) Instead of merging every dataset ever published, only the ones identified at the end of each chain of transactions were used. These ‘tips’ of the branches would have the largest number of changes and revisions contained in the matrices and would reduce the number of possible polymorphisms derived from human errors. The number of tips is 11 (Figure 3.6).

6) The characters were added in a sequential way. The final merged dataset had the following character composition: 292 characters from Upchurch et al. (2007), seven characters from Smith and Pol (2007), two characters from Apaldetti et al. (2013), 353 characters from Yates (2007b), 16 characters from Ezcurra (2010), three characters from Otero et al. (2013), two characters from Novas et al. (2010) and two characters from
McPhee et al. (2015a,b). This set of character was labelled as belonging to “set A,” and the numbering in the character list reflects this. To this dataset, characters from additional matrices, which included sauropodomorphs in their scope, but whose internal relationships were not the centre of attention (Figure 3.1), were also added and this was named “set B”. This set has a diverse origin from different character lists (Martínez and Alcober, 2009; Nesbitt et al. 2010; Martínez et al. 2011; Nesbitt, 2011; Cabreira et al. 2016; Baron et al. 2017a). Finally, characters from descriptions, anatomical reviews and personal observations of specimens, pictures and illustrations were added also.

7) To ensure compatibility between characters, the character statements need to be in the same format, so that the structures described can be comparable to assess data integrity. This stage required all of the characters in the dataset to be formatted under the system described by Sereno (2007b). In total, the starting point was based on 32 datasets with a total count of 10,103 characters. Twenty-eight out of these 32 are part of the transaction series illustrated in Figure 3.6. Each dataset was initially considered different, since some of the characters are slightly modified or are scored differently for the same taxon. Thus, 10,103 character statements were unevenly applied to a total of 75 taxa. To make the task more manageable, the 677 characters from set A were all standardised with this format and then checked for specific changes in wording in each dataset.

8) Entity integrity was applied to the character lists after their compilation. Every character was assessed individually to ensure that they were not duplicated. The duplicate identification process is not straightforward. Due to different character coding strategies, some characters have character statements that are similar or compatible with other independent characters. In Sekiya et al. (2013) this problem was solved by choosing one coding system over the other. As an example of this, C349 (Yates, 2007b) contains the same information as C289 and C290 (Upchurch et al. 2007).

Example

C349 (Yates, 2007b) Length of the ungual pedal digit two: greater than (0), between 90 and 100 percent of (1), or less than 90 percent of (2) the length of the ungual pedal digit one (Ordered).

This character was coded as a multistate character and was in principle treated as ordered.
C289 (Upchurch et al. 2007) Length of ungual of pedal digit II divided by length of ungual on pedal digit II: > 1.0 (0); < 1.0 (1).

C290 (Upchurch et al. 2007) Length of ungual of pedal digit II divided by length of ungual on pedal digit II: > 0.9 (0); < 0.9 (1).

These form a set of binary coded characters.

The criteria that led to the selection of the character coding by Upchurch et al. (2007) over the strategy in Yates (2007b) is not stated, but it seems that in Sekiya et al. (2013), in all of the cases where Yates (2007b) coded characters using multistate coding they were replaced by the binary coding in Upchurch et al. (2007). Since we are treating phylogenetic matrices as relational databases, the rules that define the constraints to determine data integrity must be consistently applied to all the characters. Assessing which character coding is better under which circumstances is beyond the scope of this thesis. To bypass this discussion, mathematical topology is suggested as a proxy of homology for assessing entity integrity in phylogenetic databases and entropy as a comparative measure to assess how informative a character is.

9) The entity integrity criteria allow for selection of characters and identification of problematic characters. In principle, relational databases must follow the rule of having atomic values, meaning that any tuple (row) must have only one value of the domain of the attribute (column) (Beynon-Davies, 2000). In the context of phylogenetic matrices, each taxon must therefore have only one character state. This principle is outlined in the literature, assuming that morphological polymorphism is an explicit reason to discard a character (Poe and Wiens, 1993; Wiens, 1999, 2012). With this starting point, any polymorphism is assumed to be either as a mistake or a disagreement between authors assessing variability, following the recommendations outlined in Poe and Wiens (1993).

3.5.1 Character adjoining

The largest number of basal sauropodomorph taxa previously assessed in a dataset is 40 (Otero and Pol, 2013), scored for 364 characters. The largest character list (535) was applied to one of the lowest number of taxa (25: Sekiya et al. 2013). The present work is a compilation of all the information that has proposed independently, but that is now merged into a single matrix of 950 characters and 75 taxa.
3.5.1.1 Normalisation of characters

Two problems were encountered when the characters were analysed: 1) there was a lack of consistency in the way they were written; and 2) the anatomical terms for specific osteological features were not homogenised or standardised. These two problems obscured comparisons of characters proposed by different authors: the former because of the difficulty in understanding the structure that is referred to in the character and the latter by complicating the assessment of potential duplicate characters.

In this work, all of the character statements were standardised to identify overlaps and duplicates. Three regions of the body turned out to be particularly troublesome due to the lack of consistency in the anatomical terminology: the braincase (up to 2.64% of the characters sampled), vertebrae (19.28%) and the pectoral girdle (2.78%). A total of 10,100 character statements underwent standardisation. Because of this standardisation, some scorings became disagreements and a re-evaluation was needed to determine whether disagreements are true disagreements or a product of conflicting nomenclature. On a comparative level, this process allowed comparisons between two character statements in different publications. However, if the nomenclature employed throughout the literature to describe the locators is not consistent, then the assessment of entity integrity is not straightforward.

3.5.1.2 Formatting of character statements

The first problem was addressed by applying the rationale of a character statement (Sereno, 2007a). In this revision, there is a distinction between a character and a feature. A feature is an observable condition in an organism, whereas a character is an inheritable feature expressed as an independent variable. This independent variable is composed of a locator and occasionally a qualifier. The character states are, therefore, all of the possibilities that have been observed for a group of organisms. The sum of all of the possible states of characters make a statement and a character and its associated statement make a character statement.

With these definitions, all characters used in a phylogenetic analysis must be in the form of a character statement, with an independent variable and its locators and qualifiers. This format was applied in this work to all of the characters drawn from the literature. In Sereno (2007b) there is a symbolic representation of the composition of a character statement: 1) a primary locator, which is a single structural feature cited for specific character location
(L₁); 2) a secondary locator, which is a structural feature cited for general location of the primary locator (L₂); 3) a variable, that is the aspect that is assessed in each taxon (V); 4) a variable qualifier, which is a modifier of the stated variable (q); and 5) the character states, which are mutually exclusive conditions of a character (vₙ). Thus, a character statement can be symbolized as L₂, L₁, Vq: v₀, v₁, ..., vₙ. Due to the nature of a character statement, it can convey either transformational series (multistate coding) or neomorphic conditions (complementary or binary coding). This format also facilitates the identification of possible duplicate or overlapping characters.

This format also allows the identification of vaguely defined characters, which are those characters that apply to regions rather than specific bones. This must only be done when it has been demonstrated that the variation is uniform throughout the whole selected region. This was recognised as a problem for the axial skeleton, where characters would have been applied to entire sub-regions within the vertebral column. This, in turn, translates into an underrepresentation of axial characters in character lists. In archosaurs, the vertebrae display a complex system of laminae and fossae that varies throughout the vertebral column (e.g. Wilson, 1999). In basal sauropodomorphs, these laminae develop to different degrees and appear or disappear at various points within the axial skeleton (Wedel, 1997, 2006, 2007; Allain and Aquesbi, 2008; Lambertz et al. 2018).

The following character from Yates (2007) is an example of this issue: “Postzygadiapophyseal lamina in cervical neural arches 4–8: present (0) or absent (1)” As conceived, this character discards potential information that could be obtained from various specimens, including, for example, that: 1) the possibility that the postzygadiapophyseal lamina (podl) is not present in every middle/posterior cervical, but might be present in some of them; 2) the possibility that a podl might be present on the axis or third cervical is not considered; and 3) if the specimen has more than eight cervical vertebrae, the possible presence of a podl in these vertebrae is also excluded by this character statement.

Sometimes terms such as ‘anterior’, ‘middle’ and ‘posterior’ cervical vertebrae are employed, whereas in other character statements the vertebral position is given to define the character, such as ‘from cervical 3 to cervical 6’. It is not clear how these regions are defined and, through the literature, it seems that its application is rather intuitive when having a complete series, as is the case in Plateosaurus engelhardtii. Nevertheless, when dealing with an incomplete vertebral series, the numbering system becomes inapplicable
and without a framework to define the anterior, middle and posterior vertebrae the scoring of these characters loses its informativity by forcing the systematist to score it as ‘?’.

In the case of sauropods, a framework to define the regions of the caudal series based on anatomical landmarks was provided by Mannion et al. (2013): (1) anterior caudal vertebrae possess ribs, even reduced ones; (2) middle caudal vertebrae lack ribs, but have distinct neural spines and postzygapophyses; (3) posterior caudal vertebrae lack ribs, as well as distinct neural spines and postzygapophyses; and (4) distal caudal vertebrae lack ribs and neural arches.

It was recently suggested that in *Plateosaurus engelhardti* there are morphological landmarks that help to define the different axial regions (Böhmer et al. 2015) and, with this in mind, a system was produced to make these characters more precisely defined. In the cervical vertebrae, the difference between anterior and middle cervicals is somewhat difficult to define anatomically and therefore it will mean that the characters for this region will be defined as the ‘postaxial cervicals that are not the posterior cervicals’, pointing to the need for proper morphometric analyses of the regions within the vertebral column. Some more accurate definitions for ‘anterior, middle and posterior’ dorsal vertebrae are provided elsewhere in this work.

### 3.5.1.3 Standardisation of nomenclature

In several body regions, the anatomical nomenclature changes through time and between authors. Although the anatomical nomenclature is updated in the main publication, these changes are not performed in the character lists. For example, in C171 Yates (2007b) the term ‘suprapostzigapophyseal lamina’ is employed as defined in classic literature (Osborn and Mook, 1921; Janensch, 1935), whereas the term ‘spinopostzygapophyseal lamina’ had already been widely adopted by then (Wilson, 1999). This term remained intact until very recent phylogenies (McPhee et al. 2015a,b; Wang et al. 2017; Chapelle and Choiniere, 2018).

Standardisation of nomenclature in character statements has been done for archosaurs (Nesbitt, 2011), theropods (Rauhut, 2003a) and eusauropods (Tschopp et al. 2015). These were used as a starting point to standardise the anatomical terminology for basal sauropodomorphs. In addition, there have been several reviews on the historical terminology of specific regions and these were applied to the following regions compiled in this character list: braincase (Paulina Carabajal, 2015); vertebral laminae (Wilson, 1999);
vertebral fossae (Wilson et al. 2011); sacra (Wilson, 2011); forelimb orientation in basal sauropodomorphs (Remes, 2007); and the terminology of pelvic features and hind limbs in basal sauropodomorphs (Moser, 2003; Fechner, 2009).

The braincase is often neglected, comprising <4% of the characters in all datasets. Moreover, when all character lists are considered, 2.64% of the characters come from the braincase. In theropod dinosaurs it has been demonstrated that the braincase, or neurocranium, is not as conserved as once thought, but has the potential to produce informative characters (Rauhut, 2007). A thorough review of the braincase of saurischian dinosaurs was published recently as an attempt to homogenise and standardise the nomenclature applied to the neurocranium (Paulina Carabajal, 2015). Because the literature on dinosaur phylogenies comprises specimens of different ontogenetic stages, it is complicated to choose a strictly descriptive nomenclature. The criterion chosen in Paulina Carabajal (2015) is based on the morphology of a structure rather than its osteological components. The justification to use a merely morphological approach lies on a conception of the neurocranium as a morphofunctional unit with different embryological origins: whilst the inner part of the braincase has an endochondral origin, with several ossification centres, the rooftop is formed by dermal elements (Goodrich, 1958; de Beer, 1971; Romer, 1975; Currie, 1997). For these reasons, the nomenclature proposed by Paulina Carabajal (2015) is appropriate and relevant in this work.

A thorough, revised naming system for vertebral laminae has been used widely in the recent literature (Wilson, 1999). As this system employs sauropod vertebrae as exemplars, the recognition in other taxa can be difficult. One of the most important problems is the degree of development that a sheet of bone needs to be for it to be recognised as a lamina. This question is important to establish the polarity of pneumatic characters as it is relevant to understand whether a distinct lamina or ridge is apomorphic or a modification of a pre-existing lamina (Wedel, 2007). Currently, it is not possible to know whether laminae outgrow the centrum to surround the air sac they are in contact with, or whether the growth of air sacs is concomitant to the removal of bone from the centrum (Wedel, 2007). Moreover, the nomenclature provided by Wilson (1999) for vertebral laminae has proved to be useful in describing other archosaurs that can be used for comparison. Laminae similar to those in basal sauropodomorphs have been found in basal archosaurs, pseudosuchians, theropods and ornithischians (Wedel, 2007). Fossae are present in some basal sauropodomorphs, such as Pantydraco and Camelotia and they are also found in basal
sauropods, such as *Tazoudasaurus naimi* (Allain et al. 2004; Wedel, 2007). Fossae are framed by postzygadiapophyseal lamina (podl) in the cervical vertebrae in *T. naimi*, such as the spinodiapophyseal fossa (spdf), on the lateral neural spine and a larger postzygapophyseal centrodiapophyseal fossa (pocdf), ventral to the spdf. The neural arch fossae provide phylogenetic data; thus, a standardised and unambiguous nomenclatural system was needed, independent of the species or to particular fossae on a given species (Wilson et al. 2011). The nomenclatural system provided by Wilson (1999) and Wilson et al. (2011), allows coding the trends in the development of neural arch fossae through clades.

The reconstruction of the pectoral girdle has been controversial, which led to numerous terms regarding the orientation of the scapulacoracoid and humerus. The scapulacoracoid has been postulated to be horizontal (Parrish and Stevens, 2002), to steeply (Schwarz-Wings et al. 2007) oriented, creating a cumbersome list of terms that makes comparison between characters or their scoring difficult. Similarly, the humerus has changed its orientation during archosaur evolution, with a semi-erect position being plesiomorphic compared to the upright orientation in sauropods. This means that the dorsal side of the humerus in basal representatives changes to be the posterolateral side in more derived taxa. A solution for this problem was posed in an account on dromaeosaurid pectoral musculature (Jasinoski et al. 2006) where instead of using functional orientation, the pectoral girdle was described using developmental topographical attributes. This terminology was also applied in the morphofunctional analyses of Remes (2007) although it mentions the caveat that a strict usage of developmental topographical nomenclature hampers the functional interpretation of the muscles since the functional orientation might differ strongly from the embryological orientation. In this work, the scapulacoracoid is oriented vertically, since the terms ‘anterior’ and ‘posterior’ are easier to determine in this way.

### 3.5.2 Mathematical topology as a proxy to assess homology

A character represents a hypothesis of homology. The logical basis of character coding was outlined by Sereno (2007), who recognised two logically different character types: neomorphic characters and transformational characters. According to Sereno (2007), each character type has its own sets of rules.

Character coding is a different activity from character discovery. Character coding is a link between the discovery of characters and the phylogenetic analysis, as a means of transmitting the observations made on a specimen to a language that the software interprets.
(Winther, 2009). According to Sereno (2007), neomorphic characters are restricted to ‘evolutionary novelties’ and the character state ‘absent’ is only applicable in neomorphic characters.

Characters are discarded as a valid hypothesis of homology when they explicitly convey variation that does not depend entirely on genetic forces, such as phenotype plasticity, ontogenetic changes, intraspecific variation, or sexual dimorphism (Poe and Wiens, 1993; Pleijerl, 1995). In addition, character coding should produce character states that are homologous, independent and non-redundant (Pimentel and Riggins, 1987). In palaeontology, these circumstances are hindered by the fossil record, in which we rely only on partial evidence from the individuals considered within an OTU. For these reasons, homology assessment cannot be done easily for fossil-based character statements.

The idea of considering character statements as mathematical abstractions can be traced back to the 1930s when the phenotype was defined in terms of a fitness landscape (Wright, 1932). Under this visualisation, a population moves through time uphill due to the combined effects of mutation and selection (Wright, 1967). This fitness landscape can be said to represent the phenotype as a specific point of an evolutionary trajectory. More precisely, the phenotype is a distribution of values around a local maximum (Wright, 1967).

Although homology in the fossil record is difficult to assess, mathematical topology is proposed here as a proxy for homology. Mathematical topology is the study of the properties of space that are preserved under continuous deformations, or transformations (Gaal, 1964; Steen and Seebach, 1970). We can consider a character statement as a topological space, where every character state is a transformation of the previous character state (Stadler and Stadler, 2004). Defined in this way, a character state cannot be another character state at the same time.

While geometry deals with measurable properties and distinguishes and classifies objects based in metric space, topology is concerned with the inherent properties that better describe the true differences in different spaces (Sato, 1999). To illustrate this, it is possible to use objective criteria to classify the letters of the alphabet and produce self-contained categories (Figure 3.7). To start, in English all the letters sans serif comprise sets of connected paths. In Spanish, for instance, the connectedness criterion produces two main categories: a group with 26 letters all with connected paths and a set with two unconnected paths in letter Ñ. Furthermore, these 26 letters can be classified depending on the number
of possible intersections that can be done to them. Topologically, nine sets can describe the 26 letters of the alphabet, namely set $\mathcal{A} = \{A, R\}$, $\mathcal{B} = \{B\}$, $\mathcal{C} = \{C, I, G, J, L, M, N, S, U, V, W, Z\}$, $\mathcal{D} = \{D, O\}$, $\mathcal{E} = \{E, F, T, Y\}$, $\mathcal{F} = \{H, K\}$, $\mathcal{G} = \{P\}$, $\mathcal{H} = \{X\}$, $\mathcal{I} = \{Q\}$. This means that the change $\varphi = B \rightarrow O$ cannot be described with a continuous function.

If B and O are homeomorphisms, then we could remove one point in B and obtain the same number of segments in O, since we are using path connectedness to assess the categories. For instance, let us assume we define two points \{p\} and \{q\} in B, these being the intersection points in the middle section. We then define two points in O, \{\varphi(p)\} and \{\varphi(q)\}. If we remove these two points in B, the number of segments of $B - \{p, q\}$ should be the same as $O - \{\varphi(p), \varphi(q)\}$. However, the former operation produces three unconnected segments, whilst the latter produces two. Therefore, B and O are not homeomorphisms. Lastly, all the possible typographies sans serif of B will be included in set $\mathcal{B}$. The classes can then be defined in a way that any letter from any alphabet can be classified into them: $\mathcal{A}$, one hole and two tails; $\mathcal{B}$, two holes and no tails; $\mathcal{C}$, no holes; $\mathcal{D}$, no hole and no tail; $\mathcal{E}$, no holes and three tails; $\mathcal{F}$, a path with four tails; $\mathcal{G}$, one hole and one tail; $\mathcal{H}$, no holes and four tails; $\mathcal{I}$, one hole and a tail crossing the hole. Classes are known as topological spaces (Figure 3.7).

Neomorphic characters were defined in Sereno (2007) as characters composed only of locators, distinguishing them from transformational characters. Neomorphic characters were described therein as equivalent to evolutionary novelties: ‘‘A morphological novelty is a structure that is neither homologous to any structure in the ancestral species nor homonymous to any other structure of the same organism,’’ (Müller and Wagner, 1991, p. 243). Müller and Wagner (1991) also set the concept of apomorphy as the opposite of a novelty. An apomorphy is part of a transformational series where there is also a plesiomorphy. These two definitions are also compatible with a topological approach: the only way ‘absent’ and ‘present’ can be considered homeomorphisms is if they are the only two options in the topological space. Sereno (2007) discussed that neomorphic characters and transformational characters differ logically, but here it is posited that they follow the same logical basis. Considering that neomorphic and transformational characters have the same logical basis facilitates making the decision on when a character is truly neomorphic and when it is part of a transformational series. Neomorphic characters, for instance, refer to the acquisition of new structures, such as a new process or a new foramen. These are
character statements whose character states can be only either absent or present. This means that any other type of character that is not neomorphic should be formulated as a coherent set of homeomorphisms (Figure 3.7).

For instance, C63 (Y2007) “squamosal-quadratojugal contact: present (0); absent (1)” is formulated as a neomorphic character. It can be said that the contact between the squamosal and the quadratojugal is an evolutionary novelty, since the contact of the squamosal with another bone would still follow the definition of Müller and Wagner (1991): it is not homologous to any other type of connection and it is not homonomous to any other structure. Nevertheless, the squamosal can contact other bones when it is not in contact with the quadratojugal. Under the topological approach, any connection with another bone is a geometric property of the bone itself and part of the same topological space. Furthermore, the available connections of the squamosal can be restricted to specific processes of the squamosal. This character is therefore equivalent to: ‘squamosal, ventral contact: quadratojugal (0), quadrate (1)’. Although the original formulation is a neomorphic character, the new character statement as a transformational series makes it a self-contained statement and easily modifiable if one OTU has an additional state not considered before.

Topology is also a good candidate to ensure data integrity when assessing discrete characters. When a character is defined as a topological space with character statements defined as homeomorphisms, the discovery of new character states in new taxa will not modify the character statement nor the adjacent characters.
Figure 3.7 Classification of the letters of the alphabet based on a topological approach. Function $f(x)$ is equivalent to a neomorphic character. In the first case, the letters N and Ñ are not homeomorphs, since N is a path connecting points in a space $O_1$, whereas Ñ is made up two paths connecting points in two different spaces $O_1$ and $O_2$. All the letters of the alphabet are therefore similar to the letter N in that they are all restricted to one space $O_1$. A neomorphic character can transform the letter I into the letter Y. In I the maximum amount of edges any point $p$ can connect is two, except for the end points that connect to only one; on the other hand, Y has a point $q$ that connects at three continuous paths, meaning I and Y are not homeomorphisms. However, a function $g(x)$ can transform I into U continuously and U into Z by adding a vertex. Similarly, Y can be transformed into a T and an E so that they follow the same condition of having one point $q$ connected to three edges. The letters C, G, I, J, L, M, N, S, U, V and Z are all topologically the same class, but they differ from the class that contains E, F, T and Y. Another neomorphic character is the one that allows transforming B and O by the addition of a third path. Whereas in B, two points $p$ and $q$ produce three continuous segments, any two points $\varphi(p)$ and $\varphi(q)$ will produce by maximum only two continuous segments. The letters of the alphabet can then be categorised into unambiguous sets based on a basic set of conditions. Analogically, if a transformation requires a continuous function to be represented, then it can be considered a transformational character, but if this function is not continuous, then it is analogous to a neomorphic character.
C29 in Martinez et al. (2011) is “laterosphenoid-frontal contact: present (0), absent (1)”. This character is formulated as a neomorphic one and leads to the creation of a complementary character: “laterosphenoid-postorbital contact: present (0), absent (1)”. This covers the variation of connectivity between the laterosphenoid, the frontal and the postorbital. If the laterosphenoid is connected to another bone, then a new character is needed. The information conveyed by ‘absent’ becomes then redundant between the three characters. Furthermore, these characters would be strongly correlated and thus not independent of each other. A topological approach would be to consider connectivity as an homeomorph, such that the minimum number of combinations is contained in the character. So, a topological operationalisation of this character would be: “laterosphenoid, connection of the head: frontal and postorbital (0), postorbital only (1)’. If a laterosphenoid connects via its head to the parietal, for instance, this combination can be added to this character without affecting adjacent characters, making them redundant and without affecting the formulation of the character.Since mathematical topology is here proposed as a proxy of homology and as a data integrity constraint, composite coding that includes ‘absent’ as a character state is considered invalid. Under this assumption, character statements were coded using reductive coding. This constraint also avoids non-additive binary coding, where every condition is treated as a set of present/absent character statements (Pleijerl, 1995), since the constraint requires the character statement to contain homeomorphisms. This constraint also avoids a problem of spurious clades based on non-independence of characters, for characters that effectively become coded twice and thus are not independent of each other (Strong and Lipscomb, 1999).

Finally, mathematical topology can be used as a proxy of homology since they can be both abstracted in a similar way. An evolutionary trajectory would then be defined as a transformation function that can occur only within the possibilities defined by the genotype space. This means that the transformation function of an evolutionary trajectory is accessible only from a genotype space level. With this restriction, a jugal bone cannot be transformed into a quadratojugal bone since there are no genetic instructions in the genotype space for that to happen in the phenotype space for archosaurs. The genotype space needs then to be constrained to the group in question and would include more time in the phenotypic space.

In topology, two surfaces are homeomorphisms if there is a continuous transformation function between them. Compression, stretching, bending, crumpling and folding are all
acceptable transformation functions, but not tearing or gluing. The classical example to illustrate this is the thought experiment of being able to transform a mug into a doughnut on a continuous way. The mug and the doughnut have the same basic properties, a continuous plane and a hole so that the surface can be deformed in any way using different transformation functions until we get to the doughnut, which also has a surface and a hole.

Whilst a mug and a doughnut are both homeomorphs, neither of them are an homeomorph to a sphere because the sphere does not have a hole (Hubbard and West, 1990). Furthermore, a sphere and a cube are homeomorphs since a transformation function exists to convert a cube into a sphere, both with a continuous surface. The transformation functions in both scenarios have the following two properties:

- The transformation function is a continuous bijection, such as for every value on \( t \) there is one and only one value on \( f(t) \).
- The transformation function has an inverse function.

With this approach, a character statement is the definition of a homeomorphic space where every character state represents a phenotype that can be transformed into the others. Furthermore, the character statement defines a space of possibilities: every character statement would represent an homeomorph of the other character statements so that they can be converted either way. If we consider that evolutionary trajectories can be represented as homeomorphism, so that every character state is an homeomorph of the others, then the transformation needs to be possible in any direction (Stadler and Stadler, 2004).

After analysing all the character statements published to date, several atomic categories were identified as components of the character statements: allometric, absolute, number, location, shape, orientation, connection and neomorphic. Using topology as a proxy for entity integrity, one character statement should deal with only one category, meaning each category represents a topological space. Approaching this problem in this way also avoids trying to resolve a problem that lies outside the scope of this work, which is the advantages and disadvantages of the different strategies for coding characters. Furthermore, a topological approach provides a framework to assess truly neomorphic characters. Since a transformation corresponds to stages of change that can be defined by functions, any category of the transformational series can be expressed as a continuous character. However, categories such as shape, orientation, location and connectivity can be expressed unambiguously as defined discrete entities. On the other hand, number of elements,
allometric characters and absolute measurements do not have intuitive categories and a
different categorisation process is needed to define them as discrete entities. Therefore,
discrete characters are neomorphic, shape, orientation, location and connectivity and
categorised characters are number, allometric characters and absolute measurements.

**Neomorphic character statements.** Under the topological approach, a neomorphic
character statement is one whose topological space is composed only of character states
‘absent or present’. Under the approach of binary coding, any character can be coded as an
‘absence/presence’ character; thus multistate characters can be recoded as neomorphic
characters (Freudenstein, 2005). Neomorphic characters are only those that assess whether
or not a transformational series exists and cannot include absence as part of the
transformational series. Since a transformational series can have an equivalent continuous
representation as a function, a neomorphic character statement is one that can only be
expressed by means of presence or absence.

**Shape.** Character statements that deal with the shape and size of a feature are part of the
same topological space. The categorisation of shape has here a topological basis, as
described in Figure 3.7, so that these characters do not rely on metric space. Allometric
characters are also shape characters, but their assessment is delineated within metric space.

**Orientation.** This type of character statements refers to the three-dimensional position of
an element with respect to a reference point. This reference point can be a specific landmark
or any adjacent element. Orientations can be given an anatomic reference, as in
anteroposterior/dorsoventral orientation, or as an angle with respect to another element. A
function transformation can exist if it transforms the coordinates of certain landmarks.

**Location.** This type of character statement refers to a feature that can change its position
within the surface of the bone. The coordinate system can be defined as a mesh on the
surface of the bone and the transformational function be defined as a change in the
coordinates of the mesh.

**Connectivity.** This type refers to the direct interaction between two elements, being a
suture or an articulation. Connectivity has no other attribute, such as shape, orientation or
location. The simplest way to represent this type of characters is graphically, where one
element represents a vertex on a graph and the interaction with other bones represents an
edge. The connectedness of a feature can also be considered, meaning how much of the
surface is engaged in the connectivity of the elements.
**Number.** These characters refer to the number of entities in features that are meristic, e.g. teeth, phalanges or vertebrae.

**Allometric characters.** These characters are built as a proportion or ratio between to linear magnitudes. Allometric characters are similar to shape characters, but they are not discretised in a qualitative manner, rather they require a categorisation process. In a meta-analysis, these characters are difficult to compile because the measurements are not always specified as landmarks nor have they been measured in the same way.

**Absolute measurements.** These characters are measurements of bones given as an absolute value. The only absolute measurement used in the character lists compiled here is the length of the femur (C353 in mY2007). The character is first described in Yates (2004a), where it is used as a proxy of body size and identifies two distinctive trends, one for a lineage that leads to Neosauropoda and a second one that includes few ‘prosaupods’, including *Massospondylus* and *Plateosaurus* (Figure 3.8). The trends that support this character are based on a scenario where there is a ‘core-Prosaupoda’ and it has never been reformulated or reassessed. Since the femur is used in several other allometric measurements, this one is rejected and no other absolute measurement is used in this analysis.

![Figure 3.8 The evolution of femur length in two sauropodomorph lineages as justification of C353 in mY2007. Femur lengths are based on ancestral values calculated by square change parsimony. The arrow represents the origin of the Sauropodomorpha, immediately after its divergence from Theropoda. The clade ranks come from the topology obtained in Yates and Kitching (2003).](image-url)
**Ontogenetic series.** The validity of every type of character-statement requires that the transformation function be an evolutionary trajectory. For instance, if a shape of surface type includes character statements that refer to transformation function that can be obtained during an individual’s development, then such a character-statement is not valid because it follows an ontogenetic, rather than an evolutionary, trajectory. For it to be an ontogenetic series, the character statement needs to include the path, represented as a non-cyclic directional path. Then to be a valid character-statement classified as an ontogenetic series, there needs to be at least one other path that is different from the one identified. Characters with ontogenetic signals are discarded from this list and further work using the semaphoront approach is needed. Semaphoront coding treats developmental stages as terminals, were each terminal contains the characters that specify species monophyly, species relationships and characters that change through an individual’s life time (Rieppel, 2004; Sharma et al. 2017).

3.5.3 Comparison of character lists

Having these categories identified as descriptors of the overall geometry of morphological characters also proves useful when trying to quantitatively compare character lists. It seems that there is not a method that can allow straightforward comparison of character lists when deciding which matrix to use for an analysis (Pogue and Micke, 1990). Based on analysis of taxonomic composition, the matrix of Upchurch et al. (2007) seems to be the best candidate matrix to choose as starting point. The iterations of Upchurch et al. (2007) are taxonomically more compatible with both, the matrices by Pol et al. (2011) and Yates (2007b) (see 3.5.4). However, assessing the content of the character lists in a comparative way between the three datasets is more complicated.

In this work, I used the previously discussed categories as a starting point. One character statement is concisely defined when it deals with only one category of transformational series. When a character statement has two categories combined, for instance a neomorphic character and a shape character, there is more probability that one taxon may be scored as an uncertainty. For instance, let us say that Character Statement N has the states ‘absent (0)’, ‘present with shape n (1)’, ‘present with shape m (2)’, ‘present with shape o (3)’. If we have evidence that N is present in certain taxon, but the shape is indistinguishable, we have no grounds to score this taxon other than as ‘1,2 and 3’, or as ‘?’ . The former increases the noise, because we are giving this taxon a more unstable position in the topologies, since it can parsimoniously fit a larger number of trees. If this taxon is found to be unstable in an
iter-PCR analysis in TNT, for instance (Pol and Escapa, 2009), removing it reduces the information actually contained in this taxon. If we choose the latter, scoring it as an uncertainty reduces the information of this character, since we are now allowing the software to assess the option of ‘absent’ in the trees generated, removing the constraint of present.

The topological operationalisation of Character Statement N requires splitting this character into its two categories to reduces the possibility of producing wildcard taxa: 1) a neomorphic character, i.e. N-neomorphic element: absent (0), present (1); 2) a shape transformational series, i.e. N-shape element: shape n (0), shape m (1), shape o (2). The loss of information is reduced and the N-shape element becomes inapplicable to a taxon scored as (1) in the N-neomorphic element. These two character statements are more concise because the ambiguity in the problem taxon is reduced.

If the character list is not redundant, then every character statement can be assigned to one and only one category of the ones discussed above, meaning a one character statement: one category ratio. If one character statement can be assigned to more than one category, then there will be a one: n ratio. Here this ratio is called Cleanness Index (CLI). The closer we get to zero, the more redundant the character list is. This index is not dependent on the size of the character list: if a character list has 263 characters, we would expect a total of 263 categories; any larger number of categories included, and the character list gets closer to zero. A character list would only have a Cleanness Index of zero if there is an infinitely large number of categories contained in a finite number of character statements. After studying the characters compiled in this work, multistate characters are often the product of a combination of two categories and the polymorphisms are disagreements on choosing one state over the other.

A lower Cleanness Index implies that the redundancy in the character list is higher and that there is a higher probability of finding that the criteria of mutual exclusivity and independence are not met. This does not mean that in the data matrix in question there are entries $a_{i,j}$ that violate these criteria, but that we could safely assume that an increase in OTUs, increases the chances of this happening. Therefore, adding a new taxon to this matrix could make characters redundant.

This new metric based on the topological operationalisation of characters is applied to the iterations of the character lists assessed in this work. The character lists assessed correspond
to the latest modification of every data matrix: for Yates et al. (2010), the latest series of modifications was done by McPhee et al. (2015b); for Upchurch et al. (2007), the latest modifications are found in Apaldetti et al. (2013); Pol et al. (2011) has not been used again in any further analysis and Sekiya et al. (2013) is a merging of the two subsequent modifications of Yates (2007b) and Upchurch et al. (2007). The character lists were also assessed in different partitions: cranial, axial and appendicular characters.

The metric CLI applied here also showed that this assessment is independent of method of character coding. For instance, Pol et al. (2011) has 15% multistate characters, whereas Apaldetti et al. (2013) has only 2% multistate characters. Table 3.1 shows the Clearness Index of the different partitions in each dataset. In contrast, McPhee et al. (2015b) has 14% multistate characters, similar to Pol et al. (2011), but the conciseness of it is lower than the other two matrices. This makes sense if we consider that binary coding and multistate coding can involve many contingent character categories in their character delineation (Table 3.1).
Table 3.1 Summary of the categories of characters in four character lists, the numbers are expressed as percentages in each partition. The Clearness Index (CLI) is calculated as the total of characters divided by the total of categories contained in the character statements. In bolds, the highest values of composition and CLI.

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3.5.4 Character analysis: information theory

Whereas a discrete morphological character can be defined with clear boundaries (see 3.5.2), continuous characters are more complicated to implement and operationalise in their discrete equivalent. Categorisation is the process by which we can define certain clear boundaries that allows the recovery of groupings from continuous data. This process transforms continuous characters into discrete characters; however, their nature is different. To ease usage, characters that are inherently discrete characters are going to be named **discrete characters**, whereas discrete characters that required a categorisation process are going to be named **categorised characters**.

There are several strategies to categorise continuous characters and there are several studies that allow the identification of whether one strategy is better than another. These characters are troublesome because the only way to ensure they are objectively coded is by conducting standardised measurements on all the specimens first-hand. Since the present work is a meta-analysis, the following is a set of strategies to maximise the information obtained from previous publications and minimise the noise for the present study.

Information theory is a branch of discrete mathematics that deals with the codification of any type (Truss, 1992). It provides a framework to assess how much information is being contained into one code and compares it with another code that refers to the same information. In a mathematical sense, information means surprise, as something that is not expected or not likely to happen according to a set of prior knowledge. For instance, if we have event $E$, the information on this event, $I(E)$, is going to be inversely related to the probability of this event happening, $P(E)$. If an event $E$ is certain to occur, so that its probability is $P(E)=1$, then the information of that event is $I(E)=0$, because there is no surprise in this event. Nothing has changed our previous knowledge. If we want to compare two events, $E_1$ and $E_2$ and they are independent from each other with $P(E_1)$ and $P(E_2)$, then the more informative event will be the one with the lower probability of happening. Thus, if $P(E_1) > P(E_2)$, then $I(E_1) < I(E_2)$ (Truss, 1992).

Character statements contain information on events, which are the changes from one character state into another. Intuitively, this is the reason why characters are excluded from databases when they are not considered informative. If a character $C$ scores the same character statement for all the OTUs in a sample, then the probability $P(C)=1$ and therefore the information contained therein is $I(C)=0$. Moreover, we also need characters to provide
information on change over time. If we have one OTU where character C can score three character states in the same generation, then its probability of happening in one generation is the same. If another character D reflects a change which has a very low probability of occurring in one generation time, then \( I(D) > I(C) \). If we require information to be an entity integrity requirement, then character D is going to be chosen over C.

Four properties can be noted about the information contained in an event (Figure 3.9).

1. If \( P(E) = 1 \), event E is almost certainly to be true and therefore \( I(E) = 0 \).
2. If \( P(E) = 0 \), then the chances of E holding are neglectable and the assertion of E being true after all would cause infinite surprise, so \( I(E) = \infty \).
3. If \( P(E_1) > P(E_2) \), then \( I(E_1) \leq I(E_2) \).
4. If \( E_1 \) and \( E_2 \) are dependent, then \( P(E_1 \land E_2) = P(E_1) \times P(E_2) \) and \( I(E_1 \land E_2) = I(E_1) + I(E_2) \).

If we define information as in (1), then these four conditions can be defined as follows:

\[
I(E) = \log_b \left( \frac{1}{P(E)} \right) \tag{3.1}
\]

If \( P(E) = 1 \), then \( I(E) = \log_b 1 = 0 \) \( \tag{3.2} \)

If \( P(0) = 1 \), then \( I(E) = \log_b \infty := 0 \) \( \tag{3.3} \)

If \( P(E_1) \geq P(E_2) \), then \( I(E_1) = \log_b \left( \frac{1}{P(E_1)} \right) \leq I(E_2) = \log_b \left( \frac{1}{P(E_2)} \right) \) \( \tag{3.4} \)

\[
I(E_1 \land E_2) = \log_b \left( \frac{1}{P(E_1 \land E_2)} \right) = \log_b \left( \frac{1}{P(E_1) \times P(E_2)} \right) \tag{3.5}
\]

Simplifying (3.5):

\[
I(E_1 \land E_2) = \log_b \frac{1}{P(E_1)} + \log_b \frac{1}{P(E_2)} = I(E_1) + I(E_2)
\]

For a character statement, the condition (5) can measure the information contained based on a sample of OTUs. For instance, character J has two character states: 0 and 1. The uncertainty of character J can be defined as the expected value of surprise based on the OTUs. Based on the sample of OTUs, it is calculated that for character J the \( P(0) = p \) and \( P(1) = q \), so that \( p + q = 1 \).

Then, as defined by (1): \( I(0) = \log_2 \frac{1}{p} \) and \( I(1) = \log_2 \frac{1}{q} \).
The uncertainty for character \( J \) is defined as the sum of the probability of each character state multiplied by the information each of them provide. Therefore, the uncertainty is defined as 

\[
P(0)I(0) + P(1)I(1) = p \log_2 \frac{1}{p} + q \log_2 \frac{1}{q}.
\]

The uncertainty of an event is defined as entropy (H) and it has its basis in the concept outlined by the second law of thermodynamics (Truss, 1992). This association between uncertainty of information and the concept of entropy is referred to as the Shannon Index, a measure of the confusion contained in an event based on its probability. The maximum of confusion is reached when both events have the same probability of happening. For character statements, when both character states are equally probable, the confusion reaches its maximum (Archie, 1985; Wiens, 2001; Winther, 2009).

If for character \( J \), either \( p \) or \( q \) is 0 then the outcome of the average surprise is 0, since we are certain of the outcome and there is no information. If \( p = q = \frac{1}{2} \), then the outcome is evenly matched, and the uncertainty is at its greatest.

If we have a character statement \( K \) with \( n \) character statements, so that \( K = \{a_1, a_2, \ldots, a_n\} \), then the entropy is defined as (3.6), where \( p_i = P(a_i) \) and the base of the logarithm is 2 since for each character state we evaluate either ‘yes’ or ‘no’:

\[
H = \sum_{i=1}^{n} p_i \log_2 \frac{1}{p_i} \quad (3.6)
\]

**Figure 3.9** Behaviour of the entropy as the probability of two independent events increases. The peak of uncertainty is when the two events are equally probable.
This could allow us to compare how informative two strategies of character coding when they refer to the same structure.

As an example, five character statements that code the same information are compared based on the entropy of each of them on the same sampled OTUs.

The characters are:

1. Upchurch et al. (2007: C187): Proximal width of metacarpal I divided by metacarpal length (Yates and Kitching 2003): (0) <0.65; (1) >0.65.
2. Upchurch et al. (2007: C188): Proximal width of metacarpal I divided by metacarpal length (Yates and Kitching 2003): (0) <0.8; (1) >0.8.
3. Upchurch et al. (2007: C189): Proximal width of metacarpal I divided by metacarpal length (Galton and Cluver 1976; modified after Benton et al. 2000): (0) <1.0; (1) >1.0.
4. Yates et al. (2007: C227): Shape of the first metacarpal (modified from Sereno 1999) [Ordered]: (0) Proximal width less than 65 per cent of its length; (1) 80% of its length; (2) Greater than 80% of its length; (3) Broader proximally than long.
5. Pol et al. (2011: 187): Proximal width of the first metacarpal with respect to its length (Sereno 1999) [Ordered]: (0) Less than 65% of its length; (1) 65%-80% of its length; (2) Greater than 80% of its length; (3) Broader proximally than long.

Based on the most recent modification done to each OTU, the coding for each OTU is as follows (Table 3.2):
Table 3.2 Character coding of five characters containing the same information for the same OTUs. C187-189 (Upchurch et al. 2007) represent additive binary coding, whereas C227 (Yates et al. 2010) and C187 (Pol et al. 2011) are multistate characters with different categorisations.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Herrerasaurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coelophysis</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Anchisaurus</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Antetonitrus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Camarasaurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Efraasia</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Jingshanosaurus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>?</td>
</tr>
<tr>
<td>Lessemisaurus</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Lufengosaurus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Massospondylus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Melanorosaurus</td>
<td>?</td>
<td>?</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Omeisaurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Plateosaurus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Riojasaurus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Shunosaurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thecodontosaurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Yunnanosaurus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
The frequencies of each character state or cardinality of each character state \( C(a_i) \) are as follows:

<table>
<thead>
<tr>
<th>Cardinality</th>
<th>( C187 ) (U2007)</th>
<th>( C188 ) (U2007)</th>
<th>( C189 ) (U2007)</th>
<th>( C227 ) (Y2010)</th>
<th>( C187 ) (P2011)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C(0)</td>
<td>6</td>
<td>8</td>
<td>8</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>C(1)</td>
<td>9</td>
<td>7</td>
<td>8</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>C(2)</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>C(3)</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>15</td>
<td>16</td>
<td>17</td>
<td>16</td>
</tr>
</tbody>
</table>

From which we obtain the following set of probabilities and the entropy (Table 3.4) of each character, as defined in (3.6).

<table>
<thead>
<tr>
<th>Probability</th>
<th>( C187 ) (U2007)</th>
<th>( C188 ) (U2007)</th>
<th>( C189 ) (U2007)</th>
<th>( C227 ) (Y2010)</th>
<th>( C187 ) (P2011)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P(0)</td>
<td>0.4</td>
<td>0.53333333</td>
<td>0.5</td>
<td>0.35294118</td>
<td>0.375</td>
</tr>
<tr>
<td>P(1)</td>
<td>0.6</td>
<td>0.46666667</td>
<td>0.5</td>
<td>0.23529412</td>
<td>0.3125</td>
</tr>
<tr>
<td>P(2)</td>
<td></td>
<td></td>
<td></td>
<td>0.17647059</td>
<td>0.1875</td>
</tr>
<tr>
<td>P(3)</td>
<td></td>
<td></td>
<td></td>
<td>0.23529412</td>
<td>0.125</td>
</tr>
<tr>
<td>Entropy (P \times I)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P(0)I(0)</td>
<td>0.52877124</td>
<td>0.48367498</td>
<td>0.5</td>
<td>0.26514712</td>
<td>0.26531953</td>
</tr>
<tr>
<td>P(1)I(1)</td>
<td>0.44217936</td>
<td>0.51311665</td>
<td>0.5</td>
<td>0.24558386</td>
<td>0.26219874</td>
</tr>
<tr>
<td>P(2)I(2)</td>
<td></td>
<td></td>
<td></td>
<td>0.22080885</td>
<td>0.22640977</td>
</tr>
<tr>
<td>P(3)I(3)</td>
<td></td>
<td></td>
<td></td>
<td>0.24558386</td>
<td>0.1875</td>
</tr>
<tr>
<td>H</td>
<td>0.97095059</td>
<td>0.99679163</td>
<td>1</td>
<td>0.9771237</td>
<td>0.94142803</td>
</tr>
</tbody>
</table>

For a character statement that has two character states, the maximum entropy is reached when each character has the same probability of occurring. This means:

\[
H = \frac{1}{2} \log_2 \frac{1}{\frac{1}{2}} + \frac{1}{2} \log_2 \frac{1}{\frac{1}{2}} = 0.5 + 0.5 = 1 \tag{3.7}
\]

The maximum entropy of a character statement with four states is reached when all the states are equally possible. Thus:
\[ H = 4 \left( \frac{1}{4} \log_2 \frac{1}{4} \right) = 2 \] (3.8)

Therefore, the three characters in Upchurch et al. (2007) have a higher entropy closer to the maximum possible entropy as defined in (3.7), whereas the multistate versions of the same character have half of the maximum entropy as defined in (3.8). In this case, the multistate categorisation of this continuous character reduces the entropy more than the additive binary coding.

With these metrics in mind, we can then evaluate other alternatives for this character. Elaborating on this example, the previous five character statements will be categorised using two methods: average coding and gap-coding. Nowadays, TNT accepts the use of continuous data as input in the datasets, making categorisation no longer necessary. Although this possibility could make arguments about methods of categorisation somewhat moot, categorised characters are still useful when dealing with other software, or when reconstructing ancestral states and make predictions that can include fragmentary material. Average coding and gap-coding were used here to fit the tests within the time framework of this project, but several categorisation methods for characters are employed in the literature, such as gap-weighting.

Average coding refers simply to setting the limit of a character state in the sample average. Gap-coding is the technique by which the characters are ordered in a logarithmic scale and the limits between states are sign-posted at every gap in the continuum that is larger than two standard deviations of the difference between data (Rae, 1998; Sansom, 2008; Randle and Sansom, 2017).

The continuous character is stated as follows: metacarpal I, proximal width relative to metacarpal length. For several sauropodomorphs, this measurement is summarised with a histogram, showing the distribution of the character and an ordering of the characters on the logarithmic scale:
Table 3.5 Ratios of the proximal width relative to the length of the metacarpal I and the distribution of the measurements (10 bins).

<table>
<thead>
<tr>
<th>OTU</th>
<th>Metacarpal I Proximal width / length</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aardonyx</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>Adeopapposaurus</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td>Anchisaurus</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>Antetonitrus</td>
<td>1.18</td>
<td></td>
</tr>
<tr>
<td>Apatosaurus</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Coelophysis</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td>Eoraptor</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>Herrerasaurus</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Jingshanosaurus</td>
<td>1.30</td>
<td></td>
</tr>
<tr>
<td>Lamplughshaura</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Lessemsaurus</td>
<td>1.18</td>
<td></td>
</tr>
<tr>
<td>Lufengosaurus</td>
<td>1.14</td>
<td></td>
</tr>
<tr>
<td>Massospondylus</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>Melanorosaurus</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>Omeisaurus</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Plateosaurus</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>Sarahsaurus</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>Sefapanosaurus</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Tazoudasaurus</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td>Yunnanosaurus</td>
<td>0.94</td>
<td></td>
</tr>
</tbody>
</table>

When the ratios are ordered in a logarithmic scale, five gaps are identified as following the rule of two standard deviations in the difference between data (Figure 3.10) but these gaps are not evident in the graph in Table 3.5.
Figure 3.10 Logarithmic distribution of the ratios in Table 3.6 showing five distinctive gaps (arrows) in the distribution.

The new set of categorisations are the following, including a rescoring using the limits defined by Yates et al. (2010) described above (Table 3.6):

Table 3.6 Character scorings of three character coding strategies: average (0.84), gap coding y multistate character as defined by Yates et al. 2010.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Ratio</th>
<th>Average coding</th>
<th>Gap coding</th>
<th>C227 (Y2010)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coelophysis</td>
<td>0.39</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Herrerasaurus</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Eoraptor</td>
<td>0.43</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lamplughseura</td>
<td>0.5</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Apatosaurus</td>
<td>0.6</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Tazoudasaurus</td>
<td>0.61</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Plateosaurus</td>
<td>0.71</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Sarahsaurus</td>
<td>0.71</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Omeisaurus</td>
<td>0.8</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Sefapananosaurus</td>
<td>0.8</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Anchisaurus</td>
<td>0.84</td>
<td>1</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Adeopapposaurus</td>
<td>0.86</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Yunnanosaurus</td>
<td>0.94</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Massospondylus</td>
<td>0.96</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Melanorosaurus</td>
<td>0.96</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Aardonyx</td>
<td>1.01</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Lufengosaurus</td>
<td>1.14</td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Antetonitrus</td>
<td>1.18</td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Lessemssaurus</td>
<td>1.18</td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Jingshanosaurus</td>
<td>1.3</td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>
When measuring how informative a character statement is using entropy, it is clear that using the average as a limit between states produces greater confusion because it is a measure of centrality. In this example, the average is splitting the OTUs into two groups of equal size. The entropies for each new categorisation are detailed in Table 3.7.
Table 3.7 Calculation of the entropies of the three character coding strategies outlined above.

<table>
<thead>
<tr>
<th></th>
<th>Average coding</th>
<th>Gap coding</th>
<th>C227 (Y2010)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P(0)I(0)</td>
<td>0.5</td>
<td>0.33219281</td>
<td>0.52108968</td>
</tr>
<tr>
<td>P(1)I(1)</td>
<td>0.5</td>
<td>0.2160964</td>
<td>0.5</td>
</tr>
<tr>
<td>P(2)I(2)</td>
<td></td>
<td>0.33219281</td>
<td>0.5</td>
</tr>
<tr>
<td>P(3)I(3)</td>
<td></td>
<td>0.33219281</td>
<td>0.46438562</td>
</tr>
<tr>
<td>P(4)I(4)</td>
<td></td>
<td>0.52877124</td>
<td></td>
</tr>
<tr>
<td>P(5)I(5)</td>
<td></td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td></td>
<td>2.24144607</td>
<td>1.9854753</td>
</tr>
<tr>
<td>(H/H_{max})*100</td>
<td>100</td>
<td>96.5724287</td>
<td>99.2737649</td>
</tr>
</tbody>
</table>

For a character statement with five states, the maximum entropy is 2.32. Taking the proportion of actual entropy relative to the maximum available for each character coding (H/H_{max}) it is possible to assess which version is more informative. As summarised in Table 3.7 gap coding is the character coding that reduces the entropy more compared to the other three strategies. Since average coding splits the taxa by the middle, a character coded with the average will produce uninformative characters. Gap coding must be carried out again each time a new taxon is added to the data matrix because a new taxon might fill in the gaps identified, or not fall into any of the character states, making gap coding. These character states based on gap coding only work for the exact matrix they were developed.

3.5.5 Operational taxonomic units

A primary key is an attribute used to uniquely identify the tuples (=rows) of the relation. Since all of the columns are unordered, one of the columns needs to be selected as the primary one (Beynon-Davies, 2000). In phylogenetic matrices, the primary keys are always the OTUs. The first stage is to define each primary key so that they do not overlap among the different datasets.

This imposes the first referential integrity constraint, which is a separate dataset that contains the specimen composition of each OTU. For a new taxon to be added, the specimen cannot be part of another taxon. If a specimen is separated from the OTU to which it was initially assigned, then the previous OTU needs to reflect this change.

Thinking of datasets as mathematical entities, we can apply set theory, a branch of discrete mathematics, to describe the sequential changes observed through the literature. This system allows detecting compatibility, by providing a logical framework to understand the
different stages to which the datasets have been subjected. This also facilitates the reading of the compilation of taxa lists and character lists.

A phylogenetic matrix can be represented as a cardinal product of the taxa list (T) and the character list (C).

\[ M = T \times C \]

Where

\[ T = \{\text{taxa}\} = \{t_1, t_2, ..., t_n\} \]

\[ C = \{\text{characters}\} = \{c_1, c_2, ..., c_n\} \]

\[ \therefore M = \{\text{taxa}\} \times \{\text{characters}\} = \{(t_1c_1), (t_1c_2), ..., (t_nc_{n-1}), (t_nc_n)\} \]

3.5.5.1 The three main compilations on basal Sauropodomorpha

If we define each matrix using the notation described above, comparisons become easier and more logical to follow. We can start by defining the three main compilations discussed in Chapter 1 as subsets of taxa and characters. Starting with the compilation of operational taxonomic units (T), we can interpret the three datasets as three sets interconnected as illustrated in Figure 3.11. Set A contains the taxa that are scored in the three datasets; set B contains the taxa scored in Yates (2007b) and Upchurch et al. (2007); set C, taxa shared by Upchurch et al. (2007) and Pol et al. (2011); set D, the taxa shared in Yates (2007b) and Pol et al. (2011); set E contains the taxa only used in Upchurch et al. (2007); set F contains taxa only used in Yates (2007b); and set G contains only the taxa used in Pol et al. (2011).
Figure 3.11 Venn diagram of the similarities of taxa lists. Set A is then the set of OTUs that are shared by the three main compilations. The content of the different sets is detailed in Table 3.8.

The composition of *Thecodontosaurus* is different in all studies. In Upchurch et al. (2007) this contains two species, *T. antiquus* and *T. caducus*, of which the latter has since been referred to a new genus, *Pantydraco caducus* (see below). In Yates (2007b) and Pol et al. (2011) this OTU contains the specimens YPM 2192, 2195, which have been referred to the new genus *Asylosaurus yalensis* (Galton, 2007). For this study, *Thecodontosaurus* includes only one species, *Thecodontosaurus antiquus*, based on the material housed in Bristol (BRSMG-ANSP) and the descriptions of these specimens (Benton et al. 2000).

The composition of *Massospondylus* refers only to *Massospondylus carinatus* and the different analyses have chosen different definitions for this OTU. In Upchurch et al. (2007), this taxon is restricted to the specimens found in South Africa and Zimbabwe and uses the published descriptions of them (Cooper, 1981; Gow, 1990; Gow et al. 1990; Sues et al. 2004). A similar definition is used in Yates (2007b) but includes more information from the literature (van Hoepen, 1920; Cooper, 1981; Gow, 1990; Sues et al. 2004; Barrett and Yates, 2006) and personal observations. As for Pol et al. (2011), this taxon is defined as the specimen BPI/1/4934 only. It has been suggested that *Massospondylus* requires further
taxonomic study (Upchurch et al. 2007a), as this taxon might be a chimera. For the purposes of this study, Massospondylus carinatus is restricted to specimen BP/1/4934.

The taxonomic composition of Plateosaurus is restricted to Plateosaurus engelhardti. In Upchurch et al. (2007) Plateosaurus comprises P. engelhardti and P. longiceps, the latter being synonymised with P. engelhardti (Moser, 2003). The scorings were based on the descriptions of SMNS 13200, SMNS 17928, AMNH 6810, HMN XXIV, BSP 1292 XLVI, GPIT I and GPIT II (Galton, 1984, 1985a, 2000, 2001; Mallison, 2009; Mallison et al. 2009). The holotype of Plateosaurus engelhardti is a collection of fragmentary remains that are not diagnostic (specimen UE 549), based on a revision carried out in this work, the need for a neotype is proposed. The most studied specimen of Plateosaurus engelhardti is SMNS 13200, but GPIT I and GPIT II are equally complete and there are many more fragmentary remains in the Museum of Geological Sciences of the University of Tubingen, Germany. SMNS 13200 was initially described by Huene (1926) and has since been thoroughly studied and documented in the literature (Galton, 1985a, 1999a, 1999b, 2000, 2007; Sereno and Novas, 1993; Wedel, 1997; Moser, 2003; Yates, 2003a, 2007a, 2010; Klein, 2004; Sander and Klein, 2005; Barrett and Yates, 2006; Bonnan and Senter, 2007; Remes, 2007; Mallison, 2009; Fechner, 2009; Nesbitt, 2011; Rauhut et al. 2011; Fechner and Gößling, 2014; Hofmann and Sander, 2014). This study has considered scorings based on the specimens SMNS 13200, GPIT I and GPIT II. The other two valid species considered in this study are P. gracilis and P. ingens (discussed further, below).

The taxon Yunnanosaurus also has a complicated taxonomic history. In Upchurch et al. (2007) the scorings are based on Yunnanosaurus huangi (Young, 1942), based on first hand assessments of the holotype specimen (NGMJ 004546). In Yates (2007b), this OTU is synonymised with Yunnanosaurus robustus and the scorings are based on IVPP V94 and IVPP V505 and their descriptions (Young, 1942, 1951; subsequently Sekiya et al. 2013). Finally, Pol et al. (2011) based their scorings on the holotype of Y. huangi and a re-description of its skull (Barrett et al. 2007). For this study, this OTU is referred as to Yunnanosaurus huangi and two different OTUs are added: Yunnanosaurus robustus (Young, 1951; Simmons, 1965; Sekiya et al. 2013) and Yunnanosaurus youngi (Lu et al. 2007).

The composition of Anchisaurus varies through phylogenetic studies. In mY2007 this taxon includes the specimen YPM 1883, the proposed neotype for this species (Galton, 2012),
and the rest of the material from the Portland Formation (Cope, 1870; Galton, 1976; Tweet and Santucci, 2011), and it is the same definition used in Pol et al. (2011). In mU2007, Anchisaurus is restricted to specimens YPM 1883, AM 41/109, AM 41/118, and considers Ammosaurus as a separate OTU (with specimens YPM 208 and YPM 209). In this thesis, the latter definition of Anchisaurus and Ammosaurus are analysed to test these two specimens are congeneric.

The composition of Omeisaurus is more diverse. In Upchurch et al. (2007), it is based mostly on Omeisaurus tianfuensis and the description of the specimens by He et al. (1988), whereas in Yates (2007b) it is based on more species, comprising O. junghsiensis (Young, 1939), O. changshouensis (Young, 1958), O. fuxiensis (Dong, 1983) and O. maoianus (Tang et al. 2001). Pol et al. (2011) based their scorings only on O. maoianus (Tang et al. 2001). For this work, Omeisaurus is restricted to Omeisaurus tianfuensis and O. maoianus, for which there are better quality photographs and illustrations and because the skull of O. maoianus was assessed in person.

Set B contains the taxa that are shared only by the matrices of Upchurch et al. (2007) and Yates (2007b) and contains only one taxon: Plateosauravus cullingworthi. This OTU consists of SAM 3341–3356, 3602–3603, 3607–3609, referred by van Heerden (1979) to Euskelosaurus, but latter regarded as Plateosauravus (Yates, 2004b), a basal sauropodomorph from South Africa described initially by Haughton (1924). This leaves Euskelosaurus browni defined only by the holotype ((Galton, 2012)NHMUK PV R1626), fragmentary material that lacks any autapomorphies, but that is included in this analysis to explore any potential relationship under the supermatrix approach.

Set C contains all the taxa that are shared by the taxon lists in Upchurch et al. (2007) and Pol et al. (2011), but not Yates (2007b).

C = \{Heterodontosaurus, Coelophysis, Gyposaurus, Lesothosaurus, Kotasaurus, Camarasaurus\}
Table 3.8 Taxonomic similarity of the three main character compilations analysed here.

<table>
<thead>
<tr>
<th>Sets</th>
<th>Total</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>1</td>
<td>Sauropodomorphs: <em>Plateosauravus</em></td>
</tr>
<tr>
<td>C</td>
<td>6</td>
<td>Non-sauropodomorphs: <em>Heterodontosaurus</em>, <em>Coelophysis</em> Sauropodomorphs: <em>Gyposaurus</em>, <em>Lesothosaurus</em>, <em>Kotasaurus</em>, <em>Camarasaurus</em></td>
</tr>
<tr>
<td>D</td>
<td>6</td>
<td>Non-sauropodomorphs: <em>Silesaurus</em> Sauropodomorphs: <em>Pantydraco</em>, <em>Sellosaurus</em>, <em>Ruehleia</em>, <em>Patagosaurus</em>, <em>Isanosaurus</em></td>
</tr>
<tr>
<td>E</td>
<td>3</td>
<td>Sauropodomorphs: <em>Mussaurus</em>, <em>Ammosaurus</em>, <em>Chinshakiangosaurus</em></td>
</tr>
<tr>
<td>F</td>
<td>15</td>
<td>Non-sauropodomorphs: <em>Crurotarsi</em>, <em>Euparkeria</em>, <em>Chindesaurus</em>, <em>Staurikosaurus</em>, <em>Neotheropoda</em>, <em>Ornithischia</em> Sauropodomorphs: <em>Agnosphitys</em>, <em>Euncemesaurus</em>, <em>Gongxianosaurus</em>, <em>Cetiosaurus</em>, <em>Tazoudasaurus</em>, <em>Unaysaurus</em>, <em>Mamenchisaurus</em>, <em>Plateosaurus ingens</em>, <em>Neosauropoda</em></td>
</tr>
</tbody>
</table>

The taxon *Gyposaurus sinensis* is named after a specimen on display at the Nanjing Geological Museum (NGMJ) and it has also been regarded as *Lufengosaurus huenei* (Galton, 1990). The genotype of *Gyposaurus* is the species *Gyposaurus capensis*, a partial skeleton described by Broom (1911), regarded later as a species of *Anchisaurus* (Galton and Cluver, 1976), or as a synonym of *Massospondylus carinatus* (Cooper, 1981). Since the referral to *M. carinatus* is not considered valid for this study, the information regarding *Gyposaurus* capensis and *Gyposaurus sinensis* is included here independently. Upchurch
et al. (2007) and Pol et al. (2011) based their scorings for *G. sinensis* on the holotype (NGMJ V 108), but the two analyses came to different conclusions: in Upchurch et al. (2007) *G. sinensis* is nested with anchisaurids, whereas in Pol et al. (2011) there is support for it to be a massospondylid. Here, the specimen of *G. sinensis* was analyzed based on photographs provided by Toru Sekiya.

The case for the removal of *Kotasaurus* from the dataset of Yates (2007b) was based on a personal communication from Oliver Rauhut who suggested that the holotype was a chimera. It is included here in this analysis based on the description by Yadagiri (2001).

The OTU *Camarasaurus* includes at least three species. In Upchurch et al. (2007), the composition of this taxon relied on first-hand assessments of specimens that are not listed and also on previous descriptions (Gilmore, 1921; Jensen, 1988; Madsen et al. 1995; McIntosh et al. 1996). In Pol et al. (2011), the definition is restricted to the specimen CM 11383 and the scores in Wilson (2002). For this work, the scorings given in the references above are preserved and complemented with the detailed descriptions published recently (Zheng, 1996; Woodruff and Foster, 2017).

Regarding *Heterodontosaurus*, it is used in both analyses as an ornithischian outgroup, but it has been considered a derived ornithischian with too many morphological specializations to represent the basal group (Norman et al. 2011; Sereno, 2012). This taxon has been removed from this study because it has a large number of unique features within heterodontosaurids; other heterodontosaurids are included here instead: *Fruitadens* and *Tianyulong*.

Set D contains all the taxa contained both in Yates (2007b) and Pol et al. (2011), but not in Upchurch et al. (2007). It contains six OTUs.

D = {*Silesaurus*, *Pantydraco*, *Sellosaurus*, *Ruehleia*, *Patagosaurus*, *Isanosaurus*}

The OTU named here as *Sellosaurus* refers to the species *Plateosaurus gracilis*. In Yates (2007b) this OTU is based on GPIT 18318a, YPM 2679 (c) and SMNS 5715 and the descriptions based on this material (Von Huene, 1908, 1915; Galton, 1985c; Yates, 2003a). In Pol et al. (2011) the specimens referred to *P. gracilis* include SMNS 5715, GPIT 18318a, GPIT Aixheim and GPIT 18392, which are based on a study on the taphonomy of these fossils carried out by Hungerbühler (1998). For this study, the scorings are based on the
material stored in Germany alone, i.e. SMNS 5715, GPIT 18318a, GPIT Aixheim and GPIT 18392.

The OTU Pantydraco is also included in the dataset of Upchurch et al. (2007) under Thecodontosaurus. The genus was thought to have two species: T. antiquus and T. caducus (Kermack, 1984; Yates, 2003b), but the second one was later reassigned to a new genus, Pantydraco (Galton et al. 2007; Galton and Kermack, 2010).

Set E contains all the OTUs that are used only in Upchurch et al. (2007).

E = \{Mussaurus, Ammosaurus, Chinshakiangosaurus\}

In Yates (2007b) Mussaurus was excluded due to the lack of knowledge on the adult morphotypes at the time. Pol et al. (2011) used Mussaurus for comparative purposes, but the taxon was not included in the matrix. Upchurch et al. (2007) included the juvenile specimens as described by Bonaparte and Vince (1979). This taxon was later added by Apaldetti et al. (2011) to an amended version of the matrix by Yates (2007b). The information used for this later usage is based on a revision of adult and juvenile materials (Pol and Powell, 2007b) and this is also the content of this OTU in this thesis, including the information recently published by Otero and Pol (2013), Cerda et al. (2014) and Otero et al. (2017).

As for Chinshakiangosaurus, most of the material is missing and was never described; as such, only a detailed account of the mandible and the dentition is available (Upchurch et al. 2007b). The lack of information from descriptions, pictures and the need to rescore this taxon after the modification of character statements justify the deletion of this OUT from the present work.

Set F contains all the taxa that have only been used in Yates (2007b). Three of these taxa are suprageneric OTUs: Neotheropoda, Neosauropoda and Ornithischia and one suprageneric outgroup OTU (Crurortarsi). Except for Crurortarsi, all the other suprageneric groups in Yates (2007b) are removed and replaced by generic OTUs that are unequivocally established to belong to those clades.

F = \{Agnosphitys, Mamenchisaurus, Eucnemesaurus, Chindesaurus, Gongxianosaurus, Cetiosaurus, Ornithischia, Crurortarsi, Euparkeria, Tazoudasaurus, Unaysaurus, Neosauropoda, Neotheropoda, Plateosaurus ingens, Staurikosaurus\}
The suprageneric Crurotarsi includes three genera: *Parasuchus hislopi* (Chatterjee, 1978), *Stagonolepis robertsoni* (Walker, 1961) and *Erpetosuchus granti* (Benton and Walker, 2002). This OTU was taken as such from the scorings in the matrix and when new character assessments were needed, it was limited to the three taxa used by Yates (2007b), without adding any new taxon.

The suprageneric OTU of Ornithischia includes *Lesothosaurus* (Thulborn, 1972; Sereno, 1991; Norman et al. 2004; Butler, 2005), *Heterodontosaurus* (Santa Luca, 1980), *Hypsilophodon* (Galton, 1974), *Abrictosaurus* (Norman et al. 2004), *Agilisaurus* (Norman et al. 2004), *Orodromeus* (Norman et al. 2004), *Parksosaurus* (Norman et al. 2004) and *Gasparinisaura* (Norman et al. 2004). The selection of taxa overlaps only with two taxa with Upchurch et al. (2007) and Pol et al. (2011), i.e. *Lesothosaurus* and *Heterodontosaurus*. For this analysis, ornithischians are included at the genus level and the independent OTUs selected are *Lesothosaurus*, *Hypsilophodon* and *Agilisaurus*.

The suprageneric OTU of Neotheropoda includes *Elaphrosaurus bambergi*, *Liliensternus liliensterni* (Huene, 1934; Rauhut, 2003), *Dilophosaurus wetherelli* (Welles, 1984), *Sinraptor* (Currie and Zhao, 1993), *Allosaurus fragilis* (Madsen, 1993) and *Ceratosaurus* (Madsen and Welles, 2000). This only overlaps in the selection of taxa with Pol et al. (2011), i.e. *Elaphrosaurus* and *Liliensternus*. All these taxa have been included in this work.

The suprageneric OTU of Neosauropoda includes *Haplocanthosaurus* (Hatcher, 1903), *Rebbachisaurus* (Calvo and Salgado, 1995), *Camarasaurus* (Osborn and Mook, 1921; Madsen et al. 1995), *Apatosaurus* (Gilmore, 1936), *Brachiosaurus*, *Barosaurus* and *Dicraeosaurus* (Janensch, 1935). For this group, the OTU is decomposed into the taxa *Camarasaurus*, *Brachiosaurus* and *Diplodocus* (Zheng, 1996; Tschopp et al. 2015).

The OTU *Agnosphytis* is based on the description presented by Fraser et al. (2002), which is based on a maxilla, humerus, ilium and astragalus. After first-hand examination of the specimen (VMNH 1745), only the ilium and astragalus possess sauropodomorph characters. Furthermore, it is doubtful that these remains belong to the same individual. The ilium of VMNH 1745 resembles that of *Guaibasaurus* (specimen UFRGSPV 0725T in Bonaparte et al. [2007]). The astragalus of VMNH 1745 resembles the morphology observed in *Saturnalia* (specimen MCP 3944-PV in Langer [2003]). The humerus of VMNH 1745 is not comparable to the distinct sauropodomorph morphology seen in
Saturnalia (specimen MCP 3844-PV in Langer et al. [2007]). The maxilla (VMNH 1751) has ankylosed teeth, a feature that has been attributed to silesaurids (Baron et al. 2017a). For these reasons, the OTU Agnosphytis is here restricted only to a restricted set of specimens that form part of VMNH 1745.

Mamenchisaurus is a composite of several species, i.e. Mamenchisaurus hochuanensis (Young and Zhao, 1972; Ye et al. 2001), M. sinocanadorum (Russell and Zheng, 1993) and M. youngi (Hui and Ye, 2002). The composition of this OTU has been kept as a supraspecific OTU containing these specimens.

Eucnemesaurus is based on TM 121, BP/1/6107, 6110-6115 and 6220, and the descriptions of them (van Hoepen, 1920; Van Heerden, 1979; Galton and Van Heerden, 1985; Yates, 2007b). These specimens were referred to the genus Euskelosaurus, discussed above. Eucnemesaurus contains two species, Eucnemysaurus fortis and Eucnemesaurus entaxonis (McPhee et al. 2015a). The latter species was assigned to the previous genus based on the phylogenetic analysis therein, so the two species are here kept as separate OTUs.

The OTU Cetiosaurus is based only on Cetiosaurus oxoniensis and the descriptions by Upchurch and Martin (2002, 2003).

The OTU Gongxianosaurus has been used in all of the modifications of Yates (2007b) dataset. This OTU is based on the description by He et al. (1998), but in 2014 the protective structure in the exhibition hall collapsed and likely destroyed the holotype (Xing et al. 2017). Because of this and due to the poor descriptions found in the literature, the OTU was removed entirely from the dataset in the present work.

The OTU Plateosaurus ingens is based on the description of the plateosaurid material discovered in Switzerland (Galton, 1986b).

Set $G = \{ Azendhosaurus laroussi, Azendhosaurus madagascar, Elaphrosaurus, Pseudolagosuchus, Pisanosaurus, Liliensternus Lagerpeton, Leonerasaurus, Aardonyx, Lapparentosaurus, Ferganasaurus, Diplodocus, Volkheimeria, Brachiosaurus \}$

The OTU Azendhosaurus laroussi was initially described as a prosauropod (Gauffre, 1993; Galton and Upchurch, 2004), but after the discovery of another specimen from Madagascar, A. madagascraiensis, it has been identified as belonging to a new group of basal archosauromorphs, Allokotosauria (Nesbitt et al. 2015). In Pol et al. (2011) these two
species were not found to be prosauropods, and therefore these OTUs were removed from the taxon list in this work.

The OTU *Pisanosaurus* has long been considered as a basal ornithischian (Casamiquela, 1967; Irmis et al. 2007; Ezcurra and Martínez, 2016), but recent phylogenetic reassessments have found it to be a silesaurid (Agnolín and Rozadilla, 2017; Baron et al. 2017a). It is included here with the revised scorings.

The OTU *Aardonyx* in Pol et al. (2011) is based on a description published by Yates et al. (2010). Yates et al. (2010) was, in turn, a modification of the dataset by Yates (2007b), but the characters used to score *Aardonyx* in the latter are not the same as the ones listed by Pol et al. (2011) (Figure 3.6).

With this notation introduced, describing the changes done in the subsequent matrices becomes more coherent.

Yates (2007b)  
\[ M_{Y2007} = T_{(Y2007)} \times C_{(Y2007)} \]
\[ T_{(Y2007)} = A \cup B \cup D \cup F \]
\[ C_{(Y2007)} = \{Y1, ..., Y353\} \]

Upchurch et al. (2007)  
\[ M_{U2007} = T_{(U2007)} \times C_{(U2007)} \]
\[ T_{(U2007)} = A \cup B \cup C \cup E \]
\[ C_{(U2007)} = \{U1, ..., U292\} \]

Pol et al. (2011)  
\[ M_{P2011} = T_{(P2011)} \times C_{(P2011)} \]
\[ T_{(P2011)} = A \cup C \cup D \cup G \]
\[ C_{(U2007)} = \{P1, ..., P277\} \]

3.5.5.2 Recursively modified datasets

Smith and Pol (2007) (SP2007) modified the dataset in Yates (2007b) by adding the OTU *Glacialisaurus* and four appendicular characters (SP354-SP361):

\[ M_{SP2007} = T_{(SP2007)} \times C_{(SP2007)} \]
\[ T_{(SP2007)} = A \cup B \cup D \cup F \cup \{Glacialisaurus\} \]
\[ C_{(SP2007)} = \{Y1, ..., Y353\} \cup \{SP354, ..., SP361\} \]

\[ M_{M2009} = T_{(M2009)} \times C_{(U2007)} \]

\[ T_{(M2009)} = A \cup B \cup D \cup E \cup \{Adeopapposaurus\} \]

\[ C_{(U2007)} = \{U1, \ldots, U292\} \]


\[ M_{E2010} = T_{(E2010)} \times C_{(E2010)} \]

\[ T_{(E2010)} = T_{(SP2007)} \cup \{Chromogisaurus, Panphagia\} \]

\[ C_{(E2010)} = C_{(SP2007)} \cup \{E362, \ldots, E378\} \]

Novas et al. (2010) modified the dataset in Ezcurra (2010) to add two Indian taxa: Jaklapallisaurus and Nambalia. These two OTUs have not been used again in subsequent studies. Furthermore, Novas et al. (2010) added two appendicular characters (N379-N380) to the dataset of Ezcurra (2010). None of these modifications, nor the modifications to the scores in the matrix have been used again, until now:

\[ M_{N2010} = T_{(N2010)} \times C_{(N2010)} \]

\[ T_{(N2010)} = T_{(E2010)} \cup \{Jaklapallisaurus, Nambalia\} \]

\[ C_{(N2010)} = C_{(E2010)} \cup \{N379, N380\} \]

Knoll (2010) (K2010) chose the matrix by Smith and Pol (2007), adding the taxon Ignavusaurus. This taxon was later removed from subsequent iterations because it was posited to be a junior synonym of Massospondylus (Apaldetti et al. 2014). However, because the definition of Massospondylus in this work has changed, the inclusion of Ignavusaurus is justified. This matrix was chosen because it is the only one to include the basal sauropodmorphs Thecodontosaurus and Pantydraco. These two taxa are included in the dataset of Upchurch et al. (2007) but they were combined under the OTU Thecodontosaurus.

\[ M_{K2010} = T_{(K2010)} \times C_{(SP2007)} \]

\[ T_{(K2010)} = T_{(SP2007)} \cup \{Ignavusaurus\} \]
\[ C_{(SP2007)} = \{ Y_1, \ldots, Y_{353} \} \cup \{ SP_{354}, \ldots, SP_{361} \} \]

Yates et al. (2010) (Y2010) produced modifications to the datasets by Yates (2007b) and Upchurch et al. (2007) by adding *Aardonyx* and rescoring several characters in the two matrices to compare the final topologies. This matrix was later modified to include *Arcusaurus* in Yates et al. (2011):

\[ M_{Y2010} = T'_{(Y2010)} \times C_{(Y2007)} \]
\[ T'_{(Y2010)} = T_{(Y2007)} \cup \{Aardonyx\} \]
\[ C_{(Y2007)} = \{ Y_1, \ldots, Y_{353} \} \]
\[ M'_{Y2010} = T''_{(Y2010)} \times C_{(U2007)} \]
\[ T''_{(Y2010)} = T_{(U2007)} \cup \{Aardonyx\} \]
\[ C_{(U2007)} = \{ U_1, \ldots, U_{292} \} \]

Upchurch et al. (2007) modified the two datasets used by Sertich and Loewen (2010) to include *Sarahsaurus*.

\[ M_{SL2010} = T_{(SL2010)} \times C_{(SP2007)} \]
\[ T_{(SL2010)} = T_{(SP2007)} \cup \{Seitaad\} \]
\[ C_{(SP2007)} = \{ Y_1, \ldots, Y_{353} \} \cup \{ SP_{354}, \ldots, SP_{361} \} \]

Rowe et al. (2011) (R2011) modified the two datasets used by Sertich and Loewen (2010) to include *Sarahsaurus*.

\[ M_{R2011} = T_{(R2011)} \times C_{(SP2007)} \]
\[ T_{(R2011)} = T_{(SL2010)} \cup \{Sarahsaurus\} \]
\[ C_{(SP2007)} = \{ Y_1, \ldots, Y_{353} \} \cup \{ SP_{354}, \ldots, SP_{361} \} \]

\[ M'_{R2011} = T'_{(R2011)} \times C_{(R2011)} \]
\[ T'_{(R2011)} = T'_{(SL2010)} \cup \{Sarahsaurus\} \]
\[ C_{(R2011)} = \{ U_1, \ldots, U_{292} \} \cup \{ SP_{354}, \ldots, SP_{361} \} \]
Apaldetti et al. (2011) (A2011) started with the modifications of Smith and Pol (2007) and added the following taxa according to the descriptions published on them: *Aardonyx* (Yates et al. 2010), *Glacialisaurus* (Smith and Pol, 2007), *Seitaad* (Sertich and Loewen, 2010), *Adeopapposaurus* (Martínez, 2009), *Chromogisaurus* (Novas et al. 2010), *Ignavusaurus* (Knoll, 2010) and *Sarahsaurus* (Rowe et al. 2011).

\[
M_{A2011} = T_{(A2011)} \times C_{(SP2007)}
\]

\[
T_{(A2011)} = A \cup B \cup D \cup F \cup \{Aardonyx, Glacialisaurus, Seitaad, Adeopapposaurus, Chromogisaurus, Ignavusaurus, Sarahsaurus\}
\]

\[
C_{(SP2007)} = \{Y1, ..., Y353\} \cup \{SP354, ..., SP361\}
\]

Martínez et al. (2012) (M2012) modified the matrix by Ezcurra (2010) and added *Pampadromaeus*. Information from different sources was added and modified in the 378 characters on the taxa *Chromogisaurus, Eoraptor, Panphagia* and *Saturnalia*.

\[
M_{M2012} = T_{(M2012)} \times C_{(E2010)}
\]

\[
T_{(M2012)} = T_{(E2010)} \cup \{Pampadromaeus\}
\]

\[
C_{(E2010)} = C_{(SP2007)} \cup \{E362, ..., E378\}
\]

Apaldetti et al. (2013) (A2013) also performed a comparative study on two datasets: Yates et al. (2010) and Upchurch et al. (2007). This analysis rescored all the characters applicable to *Coloradisaurus* in both datasets and added two new appendicular characters to each (A362-A363). Although Yates et al. (2010) was also a comparative cladistic study, the dataset employed by Apaldetti et al. (2013) includes only the amendments of the dataset made by Yates (2007b).

\[
M_{A2013} = T_{(Y2010)} \times C_{(A2013)}
\]

\[
T_{(Y2010)} = T_{(Y2007)} \cup \{Aardonyx\}
\]

\[
C_{(A2013)} = C_{(Y2010)} \cup \{A362, A363\}
\]

\[
M'_{A2013} = T_{(U2007)} \times C'_{(A2013)}
\]

\[
T_{(U2007)} = A \cup B \cup C \cup E
\]

\[
C'_{(A2013)} = C'_{(U2007)} \cup \{A362, A363\}
\]

\[
M_{OP2013} = T_{(OP2013)} \times C_{(OP2013)}
\]

\[
T_{(OP2013)} = T_{(SP2007)} \cup \{Mussaurus, Leonerasaurus\}
\]

\[
C_{(OP2013)} = C_{(SP2007)} \cup \{OP362, OP363, OP364\}
\]

Sekiya et al. (2013) (S2013) was the first attempt to join two of the three datasets. Sekiya et al. (2013) took the modifications of Rowe et al. (2011) as a starting point and produced an inner join, i.e. the taxon list by the last modified versions of Yates (2007b) and Upchurch et al. (2007). The merging process is not detailed in the supplementary material since it is not clear which one was the target dataset (the one to which the other dataset is migrated), but only the OTUs present in both datasets were considered in the merging.

\[
M_{S2013} = T_{(S2013)} \times C_{(S2013)}
\]

The intersection of the taxa lists used in R2011, \(T_{(R2011)} \cap T'_{(R2011)}\), contains 28 elements:

\[
T_{(R2011)} \cap T'_{(R2011)} = A \cup B \cup \{Aardonyx, Seitaad, Sarahsaurus\}
\]

In addition to this intersection, Sekiya et al. (2013) included four taxa: *Adeopapposaurus* (Martínez, 2009), *Lamplughsaura* (Kutty et al. 2007), *Gyposaurus* (Young, 1941a; Galton and Upchurch, 2004) and *Yunnanosaurus robustus* (Young, 1947, 1951; Sekiya et al. 2013). Therefore, the final taxon list can be described as follows:

\[
T_{(S2013)} = (T_{(R2011)} \cap T'_{(R2011)})
\]

\[
\cup \{\text{Adeopapposaurus, Lamplughsaura, Gyposaurus,} \}
\]

\[
\text{Yunnanosaurus robustus}
\]

As for the character lists used by Sekiya et al. (2013), they represent the union of the character lists as last modified by Rowe et al. (2011) and Apaldetti et al. (2013).

\[
C_{(S2013)} = C_{(SP2007)} \cup C_{(R2011)} \cup \{A362, A363\}
\]

Because these are relational databases, the union operation implies that all the columns (attributes) in set C(SP2007) that are also present in C(R2011) are merged into one attribute. This revision is part of the integrity constraints that any relational database must have.
Apaldetti et al. (2014) performed a partition analysis to test the mosaicism in *Coloradisaurus*. The original description of *Coloradisaurus* was based predominantly on skull anatomy and only brief references were made to the presence of isolated postcranial remains (Bonaparte 1978). The second known skeleton of *Coloradisaurus* is a postcranial skeleton discovered by José Bonaparte in the upper section of the Los Colorados Formation in 1973 (Yates, 2004a, 2007b; Apaldetti et al. 2013). The holotype specimen (PVL 3976) has a skull and postcranial material, whereas the second specimen is a partially articulated postcranial skeleton, both found in the same locality by Bonaparte (Bonaparte, 1972, 1978; Apaldetti et al. 2013). A third specimen (PULR 136) was used in Yates (2004b) but later it was identified as another sauropodomorph with melanorosaurid characters, but no new species was erected because of the fragmentary nature of the material (Ezcurra and Apaldetti, 2011).

McPhee et al. (2014) updated the dataset by Apaldetti et al. (2011) based on a revision of *Antetonitrus ingenipes*. The 17 characters added by Ezcurra (2010) were not considered in McPhee et al. (2014) due to errors in the matrix that did not allow them to reconcile the information with previous datasets, but the amendments of the previous characters were considered. These errors are, however, not described therein.

Otero et al. (2015) added a correction by erecting the genus *Sefapanosaurus zastroensis* separated from the previous OTU *Aardonyx*. This addition was performed on the dataset published by McPhee et al. (2014), which was a modified version of Apaldetti et al. (2011).

McPhee et al. (2015a,b) (MP2015b) are subsequent analyses where new OTUs were added: in McPhee et al. (2015a) the dataset was based on the matrix published in McPhee et al. (2015b). The dataset in McPhee et al. (2015b) is, in turn, a modification from the dataset published by Apaldetti et al. (2011) and Martinez et al. (2012).

\[ M_{MP2015b} = T_{(MP2015b)} \times C_{(MP2015b)} \]

\[ T_{(MP2015b)} = T_{(A2011)} \cup T_{(M2012)} \cup \{Eucnemesaurus entaxonis\} \]

\[ C_{(M2015b)} = \{MP1, ..., MP362\} \]

The addition of the two new characters in the character lists compiled by Apaldetti et al. (2011) and Martinez et al. (2012) was performed alongside a rearrangement of the characters. Because the correspondence between this matrix and the previous ones is no longer one-to-one, this set is defined as a new set of 362 characters.
McPhee et al. (2015a) referenced the previous matrix and added the OTU *Pulanesaura*.

\[
M_{MP2015a} = T_{(MP2015a)} \times C_{(MP2015b)}
\]

\[
T_{(MP2015a)} = T_{(MP2015b)} \cup \{Pulanesaura\}
\]

\[
C_{(M2015b)} = \{MP1, ..., MP362\}
\]

### 3.5.5.3 Other independent phylogenetic matrices

Kutty et al. (2007) published two modified datasets in the same year as the two first major independent compilations. However, the datasets employed in Kutty et al. (2007) were smaller compilations on which Yates (2007b) and Upchurch et al. (2007) based theirs, i.e. Yates and Kitching (2003) and Galton and Upchurch (2004) respectively.

The dataset by Yates and Kitching (2003) (YK2003) has the following composition:

\[
M_{YK2003} = T_{(YK2003)} \times C_{(YK2003)}
\]

\[
T_{(YK2003)} = \left( A \setminus \{\text{Eoraptor}, \text{Yunnanosaurus} \}ight) \cup \{\text{Kotasaurus}, \text{Neotheropoda} \}
\]

\[
C_{(YK2003)} = \{YK1, ..., YK212\}
\]

The taxon list contains all elements in set A except for *Eoraptor*, *Yunnanosaurus*, *Marasuchus*, *Lessesaurus*, *Camelotia*, *Guiabasaurus* and *Jingshanosaurus* and adds *Kotasaurus*, *Isanaurus* and two suprageneric taxa of unknown composition, *Neotheropoda* and *Neosauropoda*.

The dataset in Galton and Upchurch (2004) (GU2004) is described with the following array:

\[
M_{GU2004} = T_{(GU2004)} \times C_{(GU2004)}
\]

\[
T_{(GU2004)} = \{\text{Ammosaurus, Anchisaurus, Barapasaurus, Blikanasaurus, Camelotia, Coloradisaurus, Gyposaurus, Jingshanosaurus, Kotasaurus, Lessemsaurus, Lufengosaurus, Massospondylus, Melanorosaurus, Mussaurus, Plateosaurus, Riojasaurus, Saturnalia, Sellosaurus, Shunosaurus, Thecodontosaurus, Vulcanodon, Yunnanosaurus, Euskelosaurus,} \}
\]

\[
C_{(GU2004)} = \{GU1, ..., GU137\}
\]
The taxonomic composition in Galton and Upchurch (2004) is very incompatible with the sets defined above since it takes some elements of some sets and some of the others, but none of the sets are completely contained. Figure 3.12 and Table 3.9 summarise these comparisons for reference.

Table 3.9 Taxonomic similarity between Galton and Upchurch (2004) and previous datasets.

<table>
<thead>
<tr>
<th>Sets</th>
<th>Total</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Set A</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Set C</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Set E</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.12 Venn diagram showing the compatibility of the dataset of Galton and Upchurch (2004) with the sets A and B defined in Figure 3.7.

The final arrays employed by Kutty et al. (2007) (K2007) are the following:

\[
M_{K2007} = T_{(K2007)} \times C_{(YK2003)}
\]

\[
T_{(K2007)} = T_{(YK2003)} \cup \{Pradhania, Lamplughsaura\}
\]

\[
C_{(YK2003)} = \{YK1, ..., YK212\}
\]

\[
M'_{K2007} = T'_{(K2007)} \times C_{(GU2004)}
\]

\[
T'_{(K2007)} = T_{(GU2004)} \cup \{Pradhania, Lamplughsaura\}
\]

\[
C_{(GU2004)} = \{GU1, ..., GU137\}
\]

Cabreira et al. (2011) described *Pampadromaeus* and tested its phylogenetic position by adding it to four different datasets:

Dataset 1) Langer and Benton (2006) compiled characters to study the early evolution of dinosaurs. The characters were selected from multiple sources based on the relevance in capturing the variation of the specimens assessed. This is an important source of information because the characters are illustrated and several of these characters are also collected in the three main compilations detailed elsewhere in this work. The interpretations
illustrated in Langer and Benton (2006) are used as reference when assessing the character scorings.

Dataset 2) Martínez and Alcober (2009) took the dataset from Langer and Benton (2006) and added Panphagia and a modification of the character states of Eoraptor. The corrections done to Eoraptor in this matrix were implemented accordingly in this work.

Dataset 3) Nesbitt et al. (2010) is a character compilation to study archosaur evolution. These characters are discussed and illustrated thoroughly in Nesbitt (2011) and this dataset has been used recursively in part in several other datasets that deal with early dinosaur evolution, such as Cabreira et al. (2011, 2016) and Baron et al. (2017b).

Dataset 4) Martínez et al. (2011) is an expansion of the dataset by Sereno (1999; matrix 1) that includes character from other sources (i. e. Tykoski, 2005; Langer and Benton, 2006; Ezcurra and Novas, 2007; Nesbitt et al. 2009; Ezcurra, 2010). The scope of this matrix is also the early dinosaur evolution.

\[ M_{LB2006} = T_{LB2006} \times C_{LB2006} \]

\[ T_{LB2006} = \{ \text{Eoraptor, Guaibasaurus, Herrerasaurus,} \]
\[ \text{Lagerpeton, Lewisuchus, Marasuchus, Pisanosaurus, Pseudolagosuchus,} \]
\[ \text{Saturnalia, Silesaurus, Staurikosaurus} \} \]

\[ C_{LB2006} = \{ LB1, ..., LB98 \} \]

Martínez and Alcober (2009) (MA2009)

\[ M_{MA2009} = T_{MA2009} \times C_{LB2006} \]

\[ T_{MA2009} = T_{LB2006} \cup \{ \text{Panphagia} \} \]

Cabreira et al. et al. (2011) (C2011)

\[ M_{C2011} = T_{C2011} \times C_{LB2006} \]

\[ T_{C2011} = T_{MA2009} \cup \{ \text{Pampadromaeus} \} \]


\[ M'_{C2011} = T'_{C2011} \times C_{E2010} \]

\[ T'_{C2011} = T_{E2010} \cup \{ \text{Pampadromaeus} \} \]

\[ C_{E2010} = C_{SP2007} \cup \{ E362, ..., E378 \} \]

Nesbitt et et al. (2010) (N2011)

\[ M''_{C2011} = T''_{N2011} \times C_{N2011} \]
\[ T_{(N2011)} = I \cup \left\{ \text{Herrerasaurus, Eoraptor, Marasuchus, Saturnalia, Silesaurus, Plateosaurus, Efraasia, Lagerpeton, Pisanosaurus, Pseudolagosuchus, Heterodontosaurus, Lesothosaurus, Coelophysis, Euparkeria} \right\} \]

\[ C_{(N2011)} = \{N1, \ldots, N290\} \]

Set I is the list of taxa that do not belong to any previous taxa lists:

\[ I = \{t | t \notin A \cup B \cup C \cup D \cup E \cup F \cup G \cup H\} \]

\[ T'_{(N2011)} = T_{(N2011)} \cup \{\text{Pampadromaeus}\} \]

Martinez et al. (2011) \( M^{'''}_{C2011} = T'_{(M2011)} \times C_{(M2011)} \)

\[ T_{(M2011)} = J \cup \left\{ \text{Silesaurus, Plateosaurus, Lagerpeton, Heterodontosaurus, Lesothosaurus, Coelophysis, Massospondylus, Staurikosaurus, Dilophosaurus, Asilisaurus, Dromomeron, Tawa} \right\} \]

\[ C_{(M2011)} = \{M1, \ldots, M139\} \]

Set J contains all taxa that do not explicitly belong to any previous list:

\[ J = \{\text{Ceratosaurus, Eodromaeus, Syntarsus, Psittacosaurus, Hypsilophodon, Tianyulong, Scutellosaurus, Panphangia}\} \]

\[ T'_{(M2011)} = T_{(M2011)} \cup \{\text{Pampadromaeus}\} \]

New compilations of characters have also been generated recently. Cabreira et al. (2016) described a new basal sauropodomorph, \textit{Buriolestes} and suggested that it was the earliest sauropodomorph after a new compilation based on the dataset of Bittencourt et al. (2015) with the addition of information from other sources, which includes most of the datasets in Figure 3.1. Because this represents a new compilation effort that samples character from previous matrices, the characters were identified and synonymised with characters in the other lists and the information was complemented with the information from a recent anatomical description of \textit{Buriolestes} (Müller et al. 2018).

The dataset of Bittencourt et al. (2015) is a compilation of characters mainly from Nesbitt (2011), a dataset already included in this work, but also from other character lists compiled
in this work as well, i.e. Yates (2004a, 2007b). Moreover, there are characters from character lists (i.e. Tykoski, 2005; Ezcurra, 2006) that are in this compilation via other compilations. This makes the character list in Bittencourt et al. (2015) compatible to be integrated into this work.

The dataset of Cabreira et al. (2016) has already undergone a new transaction, i.e. it has a new stage in database jargon and was used along with three other datasets in Pretto et al. (2018): Ezcurra (2010), Baron et al. (2017b) and Langer et al. (2017). The comparative analysis of these four datasets was used to identify the position of Bagualosaurus as also a basal sauropodomorph at the base of the tree. Baron et al. (2017b) and Langer et al. (2017) are matrices that differ only on the character scorings and they represent the same compilation. Moreover, Ezcurra (2010) does not represent the latest updated version of the matrix and does not take into account almost a decade of changes. For these reasons, the scorings of Bagualosaurus are partially taken into account and are complemented with the description of the specimen in Pretto et al. (2018).

Baron et al. (2017a) is an independent compilation of several sources, notably Nesbitt et al. (2010), Nesbitt (2011) and Butler et al. (2008) with the scope of early dinosaur evolution. Several basal sauropodomorphs are included in this analysis. Moreover, this dataset provides evidence for Ornithischia + Theropoda and Sauropodomorpha + Herrerasauridae. The relationships at this part of the tree were not the main part of the scope of this thesis; however, the disputed position of Eoraptor as either a theropod or a sauropodomorph can only be tested by including theropods in the matrix. If theropods and ornithischians are also related as part of the clade Ornithoscelida, characters that may support Eoraptor as an ornithoscelid dinosaur are also relevant. The idea of Eoraptor nested in a clade with ornithischians and theropods was also obtained in Sekiya (2010), which is an expansion of the dataset by Upchurch et al. (2007) that included the sauropodomorph Xixiposaurus. The inclusion of the dataset by Baron et al. (2017a) is justified on the large amount of characters and taxa that overlapped with the study in this thesis.

3.6 Overview of character analysis and character coding

Standardisation and formatting. Almost all characters pooled here needed a formatting and standardisation. This was done with the characters in their respective character list. Once they were all in the same format, they were pooled and compared against each other
to identify duplicated characters. Sekiya et al. (2013) performed a similar task and their final character list was contrasted with the one obtained here.

**Redistribution.** Several characters covered entire anatomical regions where certain degrees of variation were identified. The axial skeleton experienced most of the cases of redistribution, with characters being applied to general regions such as all of the cervical series, all of the dorsal series, etc. The same process of redistribution was also performed for appendicular characters that referred to distal carpals, metacarpals, manual phalanges, metatarsals and pedal phalanges. To a lesser degree, characters dealing with the dentition were also redistributed to differentiate between premaxillary, maxillary and dentary teeth.

**Topological operationalisation.** Using the categories outlined in section 3.5.2, characters with more than one category were operationalised to reduce redundancy.

**Reduction of polymorphisms.** Polymorphisms were considered here as disagreements to start with, before considering them as true polymorphisms. In most of the cases confusing character statements produced the polymorphisms and the second cause of polymorphisms was a different interpretation of what the character states tried to convey. Moreover, other cases of polymorphisms were caused due to the clustering of several taxa into suprageneric taxa. In the particular case of Upchurch et al. (2007) and subsequent modifications, *Thecodontosaurus* possessed a large number of polymorphisms because it contained two different genera: *Thecodontosaurus antiquus* and *Pantydraco caducus*. Furthermore, in Yates (2007b) and recursive modifications and in Pol et al. (2011), polymorphisms are mostly concentrated in categorised characters.

**Reassessment of uninformative characters.** Finally, using PAUP 4.0a164 (Swofford and Sullivan, 2003), a list of parsimoniously uninformative characters was produced. Parsimoniously uninformative characters are identified in PAUP 4.0a164 if one character state is not applied to any taxon or if it represents an autapomorphy. The matrix with fewest informative characters is Yates (2007b) and subsequent modifications (four uninformative characters), followed by Upchurch et al. (2007) and its recursive modifications (five), with Pol et al. (2011) having the most (eight). In the case of Sekiya et al. (2013), the number of uninformative characters is larger (32), but this is mostly a result of its reduction in taxonomic scope. This large number of uninformative characters in Sekiya et al. (2013) could be the source of contradictions seen in replications of the analyses conducted in this work compared to the topology that was reported in the original publication. Using the
framework of information theory outlined in 3.5.4, only characters where only one character state is being used are discarded, whereas autapomorphies are kept in the analysis, since they are still mathematically informative. The impact of autapomorphies on the final topologies is beyond the scope of this work, because phylogenetic analyses based on only one group will not provide statistical significance.

**Character assessment.** All of the OTUs were rescored after analysing and modifying several characters from the literature with the above-mentioned changes. The published scores were contrasted with information from the literature for each OTU's updated composition. Priority was given to the scores obtained from authors’ personal observations, followed by the scores interpreted from illustrations in the publications. In addition, when first-hand assessments were carried out in this work, the specimens were scored from scratch. In summary, this work does not represent a compilation of all of the character scores published in the literature, but a thorough review and rescoring of all of the character statements for all of the OTUs selected for this work (Table 3.10).

In addition to characters obtained from the literature, comparative anatomical study (either personal handling of the specimens or comparisons between monographs) revealed several new character statements, which were also assessed for all OTUs considered for this work.

Five non-sauropod sauropodomorphs were included in the last iteration of this matrix. Four of them were published after the cut-off date of late 2018: *Ingentia prima* (Apaldetti et al. 2018), *Ledumahadi mafube* (McPhee et al. 2018), *Yizhousaurus sunae* (Zhang et al. 2018) and *Macrocollum itaquii* (Müller et al. 2018). The only excluded non-sauropod in this thesis is the sauropodomorph referred to as the ‘Maphutseng sauropodomorph’, as a description has yet to be formally published (Peyre de Fabregues, pers. comm.). The re-descriptions of *Sarahsaurus* (Marsh and Rowe, 2018), *Pampadromaeus* (Langer et al. 2019) and *Jingshanosaurus* (Zhang et al., 2019) are included here to increase the accuracy of the analysis even though they were published after the cut-off date.

A more detailed account of this comparative anatomical study is presented in this work in Chapter 4 as a fully documented and illustrated character list.
The following Chapter represents the first attempt to analyse characters under a topological approach. The information for this character analysis comes from previous publications and from personal observations. However, this compilation implies two problems: firstly, if the supplementary material is not annotated specifying what changes have been applied to the matrix for each taxon, a disagreement between authors regarding a score can come from errors accumulated from previous iterations or represent different anatomical opinions. Whereas with most characters these disagreements can be resolved from the literature, meristic characters are problematic (teeth, vertebrae, carpals, metacarpals, manual phalanges, tarsals, metatarsals and pedal phalanges). For example, if a character is applied to two fingers but only one finger is present, this character cannot be assessed without amplifying the phylogenetic signal, by means of assuming the other finger is present, or by ignoring it, by scoring everything as missing. Sometimes these bones are also fragmentary, and if this comes from a literature review where the fingers are not appropriately illustrated, choosing between amplifying or ignoring could add extra noise to the supermatrix. One of the problems outlined for the supermatrix is that missing data and noise produce unpredictable outcomes (see Chapter 3; Appendix 2 for the ode and character list).

The second problem is that comparative anatomy between basal sauropodomorphs is not possible now. With so many contradictory phylogenetic scenarios, it is not possible to establish patterns of covariation between groups that allow merging atomised characters into one. To make sure all of the information from the literature is included in this phylogenetic analysis, or that as much information as possible can be reviewed via meta-analysis, this thesis is doing a preliminary character catalogue to identify whether the true topology corresponds to either a completely paraphyletic arrangement, a partial paraphyly or a complete monophyly of ‘Prosauropoda’. To ensure this, a bottom-up approach is taken here: compile all the characters with as much information as possible to see if a general topology appears with a large amount of characters. Then, use this information to revisit the characters as the relationships between taxa become clearer. This means that the final topologies described in Chapter 5 are preliminary, and further work is needed.
The following character list comprises the first fully documented and illustrated character list for non-sauropod sauropodomorphs. The list is organised in anatomical order in three sections: cranial, axial, and appendicular characters.

Each subsection has its own numbering system. Each character statement has also an indexation number, that refers to their precedence from the compiled characters. Characters with an indexation code starting with ‘A’ come from the matrices that deal only with non-sauropod sauropodomorphs (see Figure 3.1); character statements starting with a code ‘B’ correspond with the matrices from other groups, such as archosaurs, basal dinosaurs, ornithischians and theropods. Some characters from pool B have correspondence with characters in pool A, and this is indicated in the character list. Characters identified with code ‘C’ correspond to characters that have been proposed to be indicators of quadrupedality and they have been flagged to map them over the phylogenetic trees (see Chapter 5). Finally, characters identified with code ‘D’ are new characters that were discovered when assessing specimens first-hand.

![Graph showing distribution of proportion of missing characters](image)

**Figure 4.1 Distribution of the proportion of missing characters analysed in this work in the different regions of the body.** The highest proportion of missing characters is located along the axial skeleton, whereas the most complete characters are in the appendicular skeleton. This is due to the combination of the preservation bias and axial characters neglected most of the times in the literature.
4.1 Cranial characters

CR1. A8. Skull, premaxillary-maxillary index (PMI) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Yates, 2007a; Pol et al., 2011; Whitlock, 2011; Sekiya et al., 2013; Figure 4.3).


Figure 4.2. Colour key for the bones the series of the cranial bones. The skull of Melanorosaurus is here colour-coded to identify the different regions in this work. The neurocranium is colour-coded differently (see 1.1.4 Neurocranium).

Comment: The original formulation of this character considered the following character states: ‘U’-shaped and ‘V’-shaped snout. The interpretation of this character is somewhat confusing since the definition of what ‘U’-shaped and ‘V’-shaped depends on the interpretation of this character, whether as parallel or convergent tooth rows or with a rounded snout or a vertex. This character was operationalised as a set of measurements to capture the variation of snout shape in sauropods (Whitlock, 2011): the upper arcade index
(uAI), the premaxillary-maxillary index (PMI) and the angle of divergence on the anterior margin of the premaxilla (PMDA).

Figure 4.3 Metrics used to determine snout shape as defined by Whitlock (2011) using Diplodocus as a reference. The upper arcade index (uAI) measures the ratio between the arcade width to arcade depth; the premaxilla-maxilla index (PMI) is determined by taking the ratio of the area covered by the snout within a square triangle which hypotenuse has a slope of 26 relative to the middle axis of the snout; the premaxillary divergence angle (PMDA) measures the angle formed by a line tangent to the premaxilla-premaxilla articulation, and the line connecting the anteromedial and anterolateral corners of the premaxilla. When the PMI is equal to or larger than 80% the morphology of the snout is considered to be square, whereas any value below that corresponds to round (Whitlock, 2011). Here, the covariation between these characters was tested using Euparkeria, Silesaurus sauropodomorphs, theropods (Herrerasaurus, Ceratosaurus, Allosaurus), and ornithischians (Lesothosaurus, Agilisaurus). The results indicate that the three measurements show a degree of correlation, but mostly uAI against the other two. The values of uAI are then discarded from this list (Figure 4.4).

Figure 4.4. Biplot of the principal component analysis of the three metrics used to determine snout shape across dinosaurs. The data concerning eusauropods was taken from Whitlock (2011). Two clusters can be identified, with eusauropods clustering on the right, and the other dinosaurs cluster on the left side of the plot. Although there is a strong correlation between the three metrics, PMDA and PMI explain most of the variation along PC1 and PC2 respectively. Solid dots represent non-
eusauropod sauropodomorphs, crosses represent eusauropods. Open circles represent ornithischians, plus symbols represent silesaurids and open squares represent theropods.

CR3. A3/B3. Skull, length relative to the femoral length (Gauthier, 1986; Benton et al., 2000; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a, b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.5 and 4.6).

Comment: This character has been used by Upchurch et al. (2007), Yates (2007b) and Pol et al. (2011). A condition needed for this character is to have a skull and a femur in the same specimen to reduce noise (Peyre de Fabregues, 2016). This character assumes that the proportions of the skull and the femur are not affected by heterochrony (Figure 4.5). There is evidence that sauropods grew isometrically (Bonnan, 2004, 2007). Lack of complete developmental series in ‘prosauropods’ does not allow us to test whether this isometric growth was established early in the evolutionary history of the group, or if it is a derived condition. Growth patterns have been studied in Massospondylus (Chinsamy, 1993) and Plateosaurus (Sander, Klein, 2005) and support the isometric growth established earlier in the evolutionary history of this group. Using the condition in sauropods also, we consider this character to be unaffected by ontogeny, but it is worth mentioning that further work is needed to test this hypothesis more thoroughly.

![Graph](image)

<table>
<thead>
<tr>
<th></th>
<th>Original coding</th>
<th>Gap-coding</th>
</tr>
</thead>
<tbody>
<tr>
<td>P(0)</td>
<td>0.46341463</td>
<td>0.26829268</td>
</tr>
<tr>
<td>P(1)</td>
<td>0.53658537</td>
<td>0.73170732</td>
</tr>
<tr>
<td>Entropy</td>
<td>0.99613448</td>
<td>0.83900406</td>
</tr>
</tbody>
</table>

Figure 4.5. The same value is retrieved by gap coding, where the cut-off is identifying the lack of samples in the interval (0.7, 0.85). Log (Cr 1 / Fm 1) stands for the logarithm of the cranial length relative to the femoral length. Under these two methods, character state 0 (i. e. 0: ratio less than 0.7) is assigned only to three sauropodomorphs Adeopapposaurus, Massospondylus and Mussaurus, and the
theropod *Eodromaeus*. The original formulation specified a limit of 0.6: longer than 0.6 (0), shorter than 0.6 (1), which is closer to the average obtained from the sample analysed here.

Figure 4.6 Landmark-based definitions of the measurements employed in CR3, CR4 and CR5. Top, *Massospondylus carinatus* based on the reconstruction in Chapelle and Choiniere (2018), and *Plateosaurus engelhardti* based on AMNH 1680 as illustrated in Prieto-Márquez and Norell (2011). Both in right lateral view.

CR4. A6. Skull, height of the rostrum at the posterior margin of the naris relative to the height of the skull at the middle of the orbit (Langer, 2004; Yates, 2007b; Sekiya et al., 2013; Figures 4.6 and 4.7).
In the original coding the limit is set 0.6, but gap coding shows that sauropodomorphs show more variation than these two states capture. This character has been scored as 1 only for Neotheropoda and Ornithischia in the matrix mY2007. This continuous character can be assessed in several basal sauropodomorphs for which there is enough cranial material. Log (R h / Or Cr h) stands for the logarithm of the rostral height relative to the height of the skull at the middle of the orbit. Gap coding also reduces the entropy way much more than any other alternative coding. The original coding was set to 0.8: more than 0.6 (0), equal to or less than 0.6 (1). From 37 OTUs sampled for the analysis of this character, the following frequencies are reported (table). The gap coding identifies the following categories: < 0.06 (0), [0.06, 0.19) (1), [0.19, 1.23) (2), [1.24, 1.63) (3), ≥1.63 (4). Gap-coding reduces the entropy from 88% to 40.29%.

### 4.1.1 Infratemporal fenestra

CR5. A129. Infratemporal fenestra, proportion of infratemporal fenestra bordered by squamosal relative to the depth of the infratemporal fenestra (Yates, 2007a; Sekiya et al., 2013; Figures 4.6 and 4.8).
Figure 4.8. A reassessment of this character produced three distinctive character states via gap coding. Character state 0 is a proportion \( \leq 0.24 \) is assigned only to *Shunosaurus*, most of the assessed taxa are given to character state 1, \([0.24, 0.85)\) and two basal sauropodomorphs are *Sarahsaurus* and *Adeopapposaurus* are scored as state 2, \([0.85, \infty)\). The original formulation set the limit at a proportion of 0.5, which is not far from the average obtained in this analysis, i.e. 0.65, and that is also the value of the proportion in the specimen SMNS 13200 referred to *Plateosaurus engelhardti*, which depending on the measurement, could be scored as either 0 or 1. The entropy of gap coding for this character is greatly improved when compared with the original formulation.

CR6. A127. Infratemporal fenestra, anterior margin, position relative to the orbit: posterior (0), ventral (1) (Gauthier, 1986; Upchurch, 1995; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013; \( \leftarrow \) Figure 4.9).

**Comment:** The original formulation of this character considered three states: posterior to the orbit (0), partially below the orbit (1) and below the orbit (2). Between states 1 and 2 there is a degree of subjectivity for any intermediate. To operationalise this character, the orbit is divided by two axes: a longitudinal axis that represents the longest distance between the posterior and anterior margins of the orbit, regardless of its shape, and a perpendicular dorsoventral axis that cuts the longitudinal axis at its midlength. Posterior in this character
is defined as behind the posterior half, and ventral defined as below the ventral half. These new boundaries are also used in CR7.

CR7. A128. Infratemporal fenestra, anteroventral corner, extension below the posteroventral margin of the orbit: below the posterior half of the orbit (0), below the anterior half of the orbit (1) (Upchurch, 1995; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.9).

**Comment:** Anteroventral corner refers to a point only, which represents an angle in the circumference of the orbit, and it is in the articulation between the lacrimal and the jugal. The anterior margin refers to the margin that is around the two anterior quarters of the orbit (see Figure 4.7).
Figure 4.9. Cranial characters illustrated in lateral view (left) and a dorsal view of the vault (right) on the skull of basal saurischians. A) Skull of Herrerasaurus based on specimen PVSJ 407 and Sereno and Novas (1993); B) Skull of Eoraptor based on specimen PVSJ 512 according to Sereno et al. (2012); C) Skull of Coelophysis based on the illustration on Colbert (1981). Not drawn to scale.

Figure 4.10. Cranial characters illustrated in lateral view (left) and a dorsal view of the vault (right) on the skull of sauropod-line sauropodomorphs. A) Skull of Melanorosaurus based on specimen NM QR3314 and Yates (2007a), B) Skull of Shunosaurus based on Zheng (1996); C) Skull of Camarasaurus based on Zheng (1996). Not drawn to scale.
4.1.2 Supratemporal fenestra

CR8. A137. Supratemporal fenestra, long axis, orientation: longitudinal (0), transverse (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.8)

CR9. A138. Supratemporal region, anteroposterior length of temporal bar relative to its transverse width (Wilson and Sereno, 1998; Wilson, 2002; Remes et al., 2009; (←)Figure 4.11).

Comment: The original formulation puts as a limit a quadrangular temporal bar, where the anteroposterior length is similar to the transverse width. To measure this character, the anteroposterior length is measured between the two dorsal vertexes of the infratemporal fenestra, and the transverse width is measured at midlength of the anteroposterior length. In the original formulation, it is not clear in which view the transverse width needs to be measured. In *Spinorphorosaurus*, the temporal bar can only be assessed in dorsal view, if the original formulation implied a lateromedial length, opposite to a dorsoventral width. The character statement in Remes et al. (2009) adds a third character state, which is (2) supratemporal fenestra reduced suggesting that this character is assessing the lateromedial width ((←)Figure 4.11).

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CR10. A141. Sagittal crest: absent (0), present (1) (Clark et al., 2000, 2004; Benton and Walker, 2002; Sues et al., 2003; Nesbitt, 2011; Figure 4.10).

Comment: This character was originally defined for crocodylomorphs, but as noted by Nesbitt (2011), there is significant variation of this character within dinosaurs. The original formulation makes a distinction between a broad flat area and a narrow thin strip of flat bone. When comparing crocodylomorphs with dinosaurs this assessment is more difficult, such as in Leyesaurus and Coloradisaurus, where this area is not clearly defined as either broad or flat. A sagittal crest is an unequivocally defined structure for reptiles and mammals as an osteological correlate for the insertion of the m. temporalis and correlated with a more powerful jaw musculature. The sagittal crest is seen in Heterodontosaurus, Hypsilophodon and Agilisaurus, but it is absent in Lesothosaurus and Eocursor. In theropods, this structure is absent. In Herrerasaurus, the sagittal crest is incipient, limited only to the posterior part of the supratemporal fenestrae, gradually expanding to form a flat surface separating the anterior margins of the supratemporal fenestrae. A well-developed sagittal crest on the parietals is seen in Massospondylus carinatus (BP/1/5241) and Yunnanosaurus huangi. The structures in Coloradisaurus and Leyesaurus are narrow supratemporal flat surfaces, but not sagittal crests.

CR11. A142-1. Frontoparietal process: absent (0), present (1) (Leal et al., 2004; Figure 4.12).

Comment: This character was described in Leal et al. (2004) as a feature present only in Unaysaurus and Plateosaurus. The character was formulated as C60 (Yates, 2007b) as a character referring to the shape of the medial margin of the supratemporal fossa, however the original formulation was specific to a process on the site of the frontoparietal suture.
and character C60 of Yates (2007b) included the postorbital suture in the same character state. It is not specified why this inclusion was needed since a process on the postorbital-parietal suture is not seen in any of the OTUs assessed.

Figure 4.12 Disarticulated bones from the roof top of Unaysaurus showing the presence of the fronto-parietal process (fp.p) on the supratemporal fossa. Taken from Leal et al. (2004).

CR11. A119/A142/B83. Supratemporal fossa, location: restricted to the parietals (0), expanded onto the parietals and frontals (1), expanded onto the parietals, frontals and postorbitals (2), expanded onto parietals and postorbitals only (3) (Gauthier, 1986; Novas, 1996; Nesbitt, 2011; Baron et al., 2017; Figure 4.13).

Comment: This character was defined initially by Gauthier (1986) as an expansion of the temporal muscles onto the skull roof and he identified it as a synapomorphy of Dinosauria. Novas (1996) also identified this character, but with much more variation among dinosaurs. This character deals with the expansion of the supratemporal fossa, which is primitively restricted to the parietal bones only, but in other dinosaurs it expands onto the frontals and postorbitals. This character is scored as (1) in Unaysaurus and Plateosaurus where the expansion produces the fronto-parietal process and a depression after it. This character refers to the location of the supratemporal fossa, so here each character state corresponds to the bones where the temporal muscles extend to. In Cabreira et al. (2011) only Coelophysis and Syntarsus are scored as (0) absent, with the supratemporal fossa limited to the parietal, but this feature is also seen in several basal sauropodomorphs:
Coloradisaurus, Lufengosaurus and Massospondylus carinatus (BP/1/4934 and BP/1/5241).

4.1.3 Dermatocranium

4.1.3.1 Facial series

Figure 4.14 Terminology of the osteological features of the bones that compose the facial series of the dermatocranium in non-sauropod sauropodomorphs (Plateosaurus engelhardti, Adeopapposaurus mognai and Melanorosaurs readi) and theropods (Allosaurus fragilis and Tawa hallae). A-E Plateosaurus engelhardti based on AMNH FARB 6810 in the description by Prieto-Márquez and Norell (2011), A-C, left premaxilla in A) medial, B) posterior and C) lateral views; F Tawa hallae, premaxilla in lateral view based on specimen GR 241 as illustrated in Nesbitt et al. (2009), G-H Adeopapposaurus mognai, articulated premaxilla and maxilla in G, lateral, and H, medial view based on the illustration in Martínez (2009); I-J, Allosaurus fragilis, articulated premaxilla, maxilla, and nasal, based on the illustration of the UUVP 1657 in Madsen (1993), K-L Melanorosaurs readi, articulated premaxilla, maxilla, and nasal based on the skull reconstruction in Yates (2007a).
4.1.3.1.1 Premaxilla

The premaxilla in non-sauropod sauropodomorphs is trapezoidal with four margins (premaxillary anterior margin, anterior margin of the external nares, premaxillary posterior margin, and alveolar margin), mediolaterally compressed, where the anterior and posterior margins lead to two rod-like processes that encloses the anterior part of the narial fenestra. The dorsal part of the premaxillary body bears the two processes, and the ventral part is tooth-bearing. The description of Anchisaurus polyzelus in Yates (2004) contains a list of characters that was later used in Yates (2007a) and the ventral-most process is termed as caudolateral in Yates (2004) and posterolateral Yates (2007a). In other exhaustive revisions of cranial anatomy, the processes are named nasal and maxillary processes (Prieto-Márquez and Norell, 2011; Chapelle and Choiniere, 2018). Since connectivity is part of the character lists, in this work the processes are termed anterodorsal and posterolateral, respectively. The two premaxillae articulate along the anterior margin, and the anterodorsal processes of each form the internarial bar. The recessed region along the anterior margin of the external nares has been termed the nasal recess (Prieto-Márquez and Norell, 2011) and possibly the median nasal depression (Yates, 2004, C6), and in some revisions of ornithischian cranial anatomy the same structure is named the subnarial fossa, e.g. Heterodontosaurus tucki (Butler et al., 2008a) and Fruitadens haagarorum (Butler et al., 2012). The latter is used in this revision (Figure 4.14).

PMX1. A4. Premaxilla, lateral side: not surpassing the lingual margin (0), expanded beyond the level of the lingual margin and over the teeth as lateral plates (1) (Upchurch, 1995; Yates and Kitching, 2003; Upchuch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.14 and 4.15).

Comment: This character was originally formulated to assess the premaxilla, the maxilla and the dentary. It has been expanded to be assessed in individual bones to reduce noise in cases where individual tooth-bearing bones are not preserved and to increase detail in order to assess if the lateral plates appeared first on one bone or another.
PMX2. A10. Premaxilla, anterior margin of premaxilla in lateral view, angle relative to buccal margin (Pol et al., 2011; Figures 4.15 and 4.21).

**Comment:** To assess the character, the angle was defined as the one between the alveolar margin and the first anterodorsal inflection of the premaxillary profile in lateral view. The two orientations defined were subvertically and posterodorsally inclined (Figure 4.16).

PMX4. D11. Premaxilla, anterior half of the premaxillary body, multiple premaxillary foramina: absent (0), present (1) (Figure 4.23) NEW.

Comment: This character is new, based on the observation of multiple premaxillary foramina in *Massospondylus carinatus* (Gow et al., 1990; Chapelle and Choiniere, 2018), *Leyesaurus* (Apaldetti et al., 2011), *Adeopapposaurus* (Martínez, 2009), and *Massospondylus kaalae* (Barrett, 2009). All of these specimens have been grouped in the clade Massospondylidae. *Coloradisaurus*, found to be either a massospondylid or a plateosaurid, lacks any foramina in the lateral surface of the premaxilla. It is not possible to assess this character for *Lufengosaurus* nor *Glaciatisaurus*.

PMX5. A12. Premaxilla, anterodorsal margin, profile in lateral view: convex (0), concave with an inflection point at the base of the anterodorsal process (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.220, 4.23 and 4.24).

Comment: This character could be coded as an absent/present character for the ‘inflection at the base of the anterodorsal process’. However, it describes the curvature of the anterodorsal margin in lateral view. The concave shape could be produced by having an inflection at other points of the anterodorsal process. In sauropodomorphs, the inflection point, defined as the point where the concavity of a curve changes, is located at the base of the anterodorsal process, as seen in *Melanorosaurus*, *Shunosaurus* and *Camarasaurus*. In *Hypsilophodon*, the concavity is more pronounced, but the inflection point is still at the base of the anterodorsal process. In *Diplodocus*, the concavity is also present in the anterodorsal margin, but the inflection point is located above the base of the anterodorsal process.

PMX6. A13. Premaxilla, main body, anteroposterior length relative to the dorsoventral length (Pol et al., 2011; Figure 4.21).

Comment: This character was initially discretized as either ‘subrectangular’ or ‘subquadrangular’. Neither of these terms is precisely defined and reflect continuous shape change in the premaxilla. ‘Subrectangular’ implies that one of the dimensions is either larger or shorter than the other one, but in the original formulation this restricts the character to be anteroposteriorly elongated. This formulation leaves ‘sub-quadrangular’ for anything where the premaxilla is deeper than it is longer.
Pol et al. (2011) Average coding Gap coding

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Figure 4.17. Shape of the premaxillary main body. There is a lot of variation in this character, ranging from the shortest premaxilla in *Lesothosaurus*, with a ratio of 0.36, all the way to *Shunosaurus*, with a ratio of 2.31. Under the original coding, any taxa < 1 would be scored as ‘subquadangular’, whereas anything above is going to be ‘subrectangular’. The average ratio for this character is 0.87. Four states are identified through gap coding: \( \leq 0.44 \) (0), (0.44, 1.04] (1), (1.04, 1.52] (2), > 1.52 (3). Most of the OTUs examined here fall within character state 1.

PMX7. A31. Premaxilla, contact with the maxilla: the premaxillary and maxillary tooth row are continuous (0), separated by a subnarial gap or diastema (1) (Ezcurra, 2010; Apaldetti et al., 2011; Martínez et al., 2011; Sekiya et al., 2013; Figures 4.14, 4.220, 4.23 and 4.24).

Comment: The subnarial gap is also known as a diastema. It is consistently defined as a separation in the continuity of the alveolar row, so that there is a space larger than an alveolus between the last premaxillary tooth and the first maxillary tooth.

PMX8. A19. Premaxilla, posterior margin: posterolateral process with a rounded margin (0), posterodorsal corner connected with the posteroventral corner by a
Comment: this is named ‘caudolateral process’ or ‘maxillary process’. This term makes sense in the case of some sauropods, like *Camarasaurus*, where the posterodorsal process, or the process that contacts with the maxilla, is divided into two processes, a lateral and a medial process, due to the wide snout. In basal sauropodomorphs, the premaxilla connects to the maxilla by one process only. It was scored as ‘absent’ for sauropods in C7 of Pol et al. (2011), in *Shunosaurus, Omeisaurus, Camarasaurus, Diplodocus* and *Brachiosaurus*. In *Camarasaurus*, the premaxillary body is lateromedially expanded, so that the posterodorsal process is medially displaced, with the subnarial fossa being expanded and separating the posterodorsal process, placed medially, from the anteroventral margin of the external naris, which is laterally offset (Zheng, 1996; Wilson and Sereno, 1998). An analogous situation seems to be true for *Shunosaurus* (Zheng, 1996; Chatterjee and Zheng, 2002). The posterodorsal process is reported to be absent in *Brachiosaurus* and *Diplodocus* as illustrated in Wilson and Sereno (1998). Upon observation of *Omeisaurus maoianus*, the posterodorsal process is also absent (Feng et al., 2001).

PMX9. A26-1. Premaxilla, posterodorsal process: extends posterior to the ventral border of the external naris (0), restricted to the ventral border of the external naris (1) (Gauthier, 1986; Yates, 2003a; Yates and Kitching, 2003; Upchurch et al., 2007a; Martínez et al., 2011; Pol et al., 2011; Figures 4.220, 4.23 and 4.24).

Comment: This character has been included in different formulations in the character lists of Upchurch et al. (2007), Yates et al. (2010) and Pol et al. (2011). The total of character states is as follows: ‘Relationship between posterodorsal process of the premaxilla and the anteroventral process of the nasal (modified from Gauthier 1986) [Ordered]: (0) broad sutured contact; (1) point contact; (2) separated by maxilla; (3) widely separated, the maxilla forming almost the entire caudal margin of the external naris’.

Topologically, this character has several categories associated to it. It conveys information on the connectivity between the premaxilla and the nasal, more precisely between the premaxillary posterodorsal process and the nasal anteroventral process. It also conveys information on the location of the posterodorsal process relative to the external naris, regardless of its relationship with the nasal. The character states (2) and (3) effectively
reflect the absence of a connection between these two processes from the premaxilla and nasal.

Although this character could be thought of as a multistate character, since the changes in the posterodorsal process and the anteroventral process of the nasal can be considered three-dimensional homeomorphs, this character is hiding information where the two processes are absent. The maxilla can still contribute to the external nares if the two processes are absent. Having this as a separate character within a character would produce redundancy in the information.

To make this character operative it can be split into different characters. One that deals only with whether the processes are connected or not and a second one dealing with the expansion of the premaxillary posterodorsal process along the margin of the external naris. Character state (3) as originally conceived is a maxillary character pertaining to the contribution of the maxilla to the external nares.

PMX10. A26-2. Premaxilla, posterodorsal process, contact: forming a suture with the anteroventral process of the nasal (0), premaxilla-nasal in point contact (1), sutured along the maxilla but not with the anteroventral process of the nasal (2) (Gauthier, 1986; Yates, 2003a, 2007a; Yates and Kitching, 2003; Upchurch et al., 2007a; Martínez et al., 2011; Pol et al., 2011; Figure 4.22).

PMX11. A20. Premaxilla, posteroventral process: absent (0), present (1) (Rauhut, 2003a; Martínez et al., 2011; Figure 4.14).

Comment: This character corresponds to an additional projection from the posterodorsal process, making the maxillary process to be divided into two prongs at their distal end.

PMX12. B8. Premaxilla, posterodorsal process, lateromedial width relative to its anteroposterior length (Gauthier, 1986; Rauhut, 2003a; Langer and Benton, 2006; Smith et al., 2007; Nesbitt, 2011; Baron et al., 2017b; Figure 4.17).

Comment: This character is treated as continuous because the terms ‘plate-like’ and ‘bar-like’ in the original formulation have intermediates that cannot be distinguished.
Plate vs bar
Average coding
Gap coding

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Figure 4.18. Gap coding for character PMX12. \( \log \left( \frac{w}{l_{Pmx pdp}} \right) \) stands for the logarithm of the lateromedial width relative to its anteroposterior length of the posterodorsal process of the premaxilla. The original formulation considers ‘plate-like’ and ‘bar like’, without setting a clear limit between character states. Here, the information in the formulation of more than or equal to 1.0 (plate-like) and less than 1.0 (bar like) is tested against the average coding and the gap-coding. Gap-coding reduces the entropy to 43.6%, and produces the following character states: > 0.5 (0), [0.5, 1.15) (1), [1.15, \( \infty \)).

PMX13. A21. Premaxilla, subnarial foramen: absent (0), present (1) (Benton and Clark, 1988; Parrish, 1993; Juul, 1994; Benton, 1999; Yates, 2007a; Martínez et al., 2011; Nesbitt, 2011; Sekiya et al., 2013; Baron et al., 2017a; Figure 4.14, 4.220 and 4.23).

Comment: There is a lot of discussion on this character, but the term is referred as to a perforation that runs between the premaxilla and the maxilla. When there is a foramen inset into the maxilla close the premaxilla-maxilla suture, this foramen is then called the anterior maxillary foramen. It is certain that the maxillary foramina are homologous in birds and crocodiles, and the same can be said of dinosaurs. The subnarial foramen could be an additional branch from the maxillary nerve and the maxillary artery (Witmer, 1995).

Comment: Although this character could be formulated as a continuous character, the size of the foramina in several specimens makes it very complicated to measure the two diameters and produce a ratio. However, the anatomical difference between a slot-shaped and a circular morphology is usually clear cut and there is not necessarily any ambiguity in this character. The difference in the morphology of this foramen could result from the arrangement and size of the nerves and arteries.

PMX15. A23. Premaxilla, subnarial foramen, internal opening: above the tooth row below the midlength of the premaxillary body height (0), opens into the palate, at or above the midlength of the premaxillary body height (1) (Yates, 2003a; Pol et al., 2011; Figures 4.220, 4.23 and 4.24).

Comment: In its original formulation, the character states were vaguely defined. Here, the midlength of the premaxillary height is set as a limit, the difference being in which half the foramen traverses.

PMX16. A24. Premaxilla, subnarial foramen, position: positioned outside of narial fossa (0), on the rim of, or inside, the narial fossa (1) (Sereno et al., 1993; Figures 4.220, 4.23 and 4.24).

Comment: This character was originally formulated as a more complex multistate character: C13 (Y2007b) Size and position of subnarial foramen: absent (0), small (no larger than adjacent maxillary neurovascular foramina) and positioned outside of narial fossa (1), large and on the rim of, or inside, the narial fossa (2). Ordered. It has been decomposed into a neomorphic character (PMX13), and a character dealing with the morphology of the subnarial foramen (PMX14), since small foramina are circular, and the enlarged ones are so because of this slot-shaped morphology. The location component discussed here was re-examined. For instance, it is scored as (2) in Melanorosaurus, however, the narial fossa is restricted to the premaxillary anterodorsal process so that the subnarial foramen is outside. It is also scored as (2) for Lufengosaurus, but the premaxilla is not preserved in this taxon preventing assessment of this character. However, Adeopapposaurus and Leyesaurus do have a subnarial foramen in the narial fossa, because the narial fossa is well developed and extends on to the maxilla.

PMX18. A25. Premaxilla, subnarial fossa, extension: expands into the internarial bar and main body (0), restricted to internarial bar (1) (Gauthier, 1986; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013; Figures 4.14 and 4.220).

**Comment:** This feature is only present in a few basal sauropodomorphs where the narial fossa expands into the internarial bar. It is prominent in *Plateosaurus engelhardti* and *Melanorosaurus*. This feature was named the ‘nasal depression’, but this feature is extended into the premaxilla and is not restricted to the nasal. The original formulation referred to this as a ‘median nasal depression’.

PMX19. A27. Premaxilla, suture with the nasal: plane (0), limbous (1), schindylesis (2), denticulate (3), serrate (4). Unordered (Sereno, 1999a; Martínez et al., 2011; Figure 4.19).

**Comment:** The original formulation was simply whether the suture was ‘V’-shaped or ‘W’-shaped. This character is treated as unordered because it is not possible to assess temporal arrangement. In *Adeopapposaurus*, the two processes seem to form a mitre joint (limbous articulation), in *Melanorosaurus* it is not really clear from the skull, although the reconstruction shows a somewhat ‘V’-shaped articulation. In *Plateosaurus* the articulation is more of a butt joint (planar articulation). In *Allosaurus*, for instance, the ‘W’-shape is because of a brittle joint (schindylesis) between the two processes. Operationalised as it is, ornithischians have a planar articulation that is not visible in dorsal view. In most sauropodomorphs, the same articulation is planar.
PMX20. A29. Premaxilla, palatal process: present (0), absent (1) (Sampson et al., 1998; Tykoski, 2005; Martínez et al., 2011; Figure 4.20).

Comment: This character is based on Sampson et al. (1998) where they described *Majungatholus*. This character is illustrated therein in Fig. 1 (Figure 4.20), and Tykoski (2005) observed the absence of this character as an ambiguous apomorphy for Ceratosauroida. However, Tykoski (2005) and Martínez et al. (2011) formulated this character in a way that ‘faint ridge’ and ‘absent’ are both scored as (1). The ridge would clearly be defined as faint in *Majungatholus* and is absent in other theropods, such as *Coelophysis* and *Tawa*. The character was here reassessed since Martinez et al. (2011) considered this a sauropodomorph character shared with *Eoraptor*. The feature was not identified in the monograph, and *Eoraptor* is now scored as missing. These palatal processes are also identified in *Melanorosaurus*, *Plateosaurus engelhardti*, *Massospondylus carinatus* and *Yunnanosaurus huangi*, according to Yates (2007a). In the
monograph on *Plateosaurus engelhardti* (Prieto-Márquez and Norell, 2011), these processes are termed ‘articular surface for the maxillae’.

PMX21.  A80. Premaxilla, narial fossa, anteroventral corner, position relative to the mid-length of the premaxillary body: anterior to or at (0), posterior to (1) (Yates, 2007b; Sekiya et al., 2013; Figures 4.220, 4.23 and 4.24).
Figure 4.21. Measurements are taken from the premaxilla illustrated on the snouts of sauropod dinosaurs, and premaxillary characters that need a dorsal view to be assessed. Not drawn to scale. Left side, lateral views, right side, dorsal views.
Figure 4.22. Premaxillary characters illustrated in lateral view on the skull of basal saurischians. A) Skull of *Herrerasaurus* based on PVSJ 407 and Sereno and Novas (1993); B) Skull of *Eoraptor* based on PVSJ 512 according to Sereno et al. (2012); C) Skull of *Coelophysis* based on the illustration on Colbert (1981). Not drawn to scale.
Figure 4.23. Premaxillary characters illustrated in lateral view on the skull of non-sauropod sauropodomorphs. A) Skull of Massospondylus carinatus based on the reconstruction in Chapelle and Choniere (2018) to illustrate a massospondyloid skull; B) Skull of Plateosaurus engelhardti based on SMNS 13200 to illustrate a plateosaurid skull. Not drawn to scale.
Figure 4.24. Premaxillary characters illustrated in lateral view on the skull of sauropod-line sauropodomorphs. A) Skull of *Melanorosaurus* based on NM QR3314 and Yates (2007); B) Skull of *Shunosaurus* based on Zheng (1996); C) Skull of *Camarasaurus* based on Zheng (1996). Not drawn to scale.
4.1.3.1.2 External naris

EN1. A74. External nares, maximum diameter relative to the orbital maximum anteroposterior axis length (Wilson and Sereno, 1998; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.25, 4.27, 4.28 and 4.29).

Figure 4.25 Gap-coding for character EN1. MD_{EN}, the maximum diameter of external naris, APo, the maximum anteroposterior length of the orbit. Gap-coding using ornithischian samples identifies two states: (0,0.24) (1) scoring only Agilisaurus; [0.24, ∞). When removing Agilisaurus, the saurischian samples distribute along with four states.

EN2. A77. External naris, narial fossa, rims: absent (0), present (1) (Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.27, 4.28 and 4.29).

Comment: This character comes from the formulation of C10 Pol et al. (2011) and C11 Y2007 dealing with the depth of the narial fossa. These two characters capture the variation of the snout simply as neomorphic characters, to avoid confusion with a ‘poorly defined’ or ‘shallow’ fossa in contrast with a ‘well-defined’ or ‘deep fossa’.

EN3. A81. External naris, narial fossa, posterior margin, position relative to the anterior internal antorbital fenestra: lies anterior to (0), lies posterior (1) (Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013; Figures 4.27, 4.28 and 4.29).

EN4. A82-1. External naris, narial fossa, level of the posterior margin of external naris relative to the premaxilla-maxilla suture: anterior to or at the same level as
Comment: In its original formulation, this was scored as a polymorphism in *Pantydraco*. This polymorphism included the states: ‘posterior to the first maxillary alveolus (1)’, and ‘posterior to the midlength of the maxillary tooth row and the anterior margin of the antorbital fenestra (2).’ This captures the fact that the posterior margin of the external naris is not preserved. However, the arrangement of the other bones of the specimen allows some assumptions. This character can be operationalized to avoid this polymorphism by dividing into two character statements. One establishing whether the posterior margin is at the level of the premaxilla-maxilla suture, and another dealing with the position along the length of the maxillary.

EN5. A82-2. External naris, narial fossa, extension of the posterior margin: not extending beyond the midlength of the maxilla (0), extending beyond the midlength of the maxillary tooth row (1) (Wilson and Sereno, 1998; Yates, 2007b; Sekiya et al., 2013; Figures 4.27, 4.28 and 4.29).

4.1.3.1.3 Antorbital fenestra

According to Witmer (1995), the antorbital fenestra can be though as part of a cone, where there is an external antorbital fenestra and an internal antorbital fenestra. When the margins are offset, they produce an antorbital fossa. Here, the antorbital fenestra is defined only as what Witmer (1995) defined as the internal antorbital fenestra since a fenestra is a hole. There may be an antorbital fossa associated with it. Since the antorbital fenestra occupies potentially the maxilla, the nasal, and the lacrimal, the antorbital fossa can be present in any of these three bones, either in one or all of them.

AOF1. A57. Antorbital fossa: present (0), absent (1) (Yates, 2003a; Upchurch et al., 2007a; Figures 4.27, 4.28 and 4.29).

A56. Antorbital fenestra, length between the posterior margin of the maxillary dorsal process to the posterior margin of the antorbital fenestra or fossa relative to the maximum anteroposterior length of the orbit (McIntosh, 1990; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013; Figures 4.26, 4.27, 4.28 and 4.29).
Figure 4.26. Gap-coding of character AOF2. APaof, the anteroposterior length of the antorbital fenestra, APO, the anteroposterior length of the orbit. Two character states have been identified and this formulation singles out *Zupaysaurus*. The original formulation used as a limit the boundary of a ratio 1.0. The average of the sample is a ratio of 0.75.

AOF2. A58. Antorbital fenestra, shape: the anterior margin of the external antorbital fenestra and the anterior margin of the internal antorbital fenestra are both concave (0), the anterior margin of the external antorbital fenestra is concave, whilst the anterior margin of the internal antorbital fenestra is convex (1) (Yates and Kitching, 2003; Figures 4.27, 4.28 and 4.29).

**Comment:** This character originally formulated by Yates and Kitching (2003) requires a distinction between the internal and the external fenestra. The formulation of described the character states as follows: “Shape of the rostral margin of the antorbital fenestra: strongly concave, roughly parallel to the rostral margin of the antorbital fossa, creating a narrow antorbital fossa (0) or straight to gently concave creating a broad, subtriangular antorbital fossa (1).” The wording is confusing, but it is establishing a relationship of distance between the external and internal antorbital fenestrae, here defined on terms of the margins of the antorbital fossa. This character considers as antorbital fenestra only the inner antorbital fenestra, in agreement with the definition employed here.
Figure 4.27 External naris and antorbital fenestra characters illustrated in lateral view on the skull of basal saurischians. A) Skull of *Herrerasaurus* based on PVSJ 407 and Sereno and Novas (1993); B) Skull of *Eoraptor* based on PVSJ 512 according to Sereno et al. (2012); C) Skull of *Coelophysis* based on the illustration in Colbert (1981). Not to scale. Measurements: a) maximum diameter of the external naris, b) maximum anteroposterior length of the antorbital fenestra, c) maximum diameter of the orbit.
Figure 4.28 External naris and antorbital fenestra characters illustrated in lateral view on the skull of non-sauropod sauropodomorphs. A) Skull of *Massospondylus carinatus* based on the reconstruction in Chapelle and Choiniere (2018) to illustrate a massospondylid skull; B) Skull of *Plateosaurus engelhardti* based on SMNS 13200 to illustrate a plateosaurid skull. Not to scale. Measurements: a) maximum diameter of the external naris, b) maximum anteroposterior length of the antorbital fenestra, c) maximum diameter of the orbit.
Figure 4.29 External naris and antorbital fenestra characters illustrated in lateral view on the skull of non-sauropod sauropodomorphs. A) Skull of *Melanorosaurus* based on NM QR3314 and Yates (2007); B) Skull of *Shunosaurus* based on Zheng (1996); C) Skull of *Camarasaurus* based on Zheng (1996). Not drawn to scale. Measurements: a) maximum diameter of the external naris, b) maximum anteroposterior length of the antorbital fenestra, c) maximum diameter of the orbit.
4.1.3.1.4 Maxilla

The maxilla in non-sauropod sauropodomorphs has a similar lateral profile with a triradiate shape: an anterior process, a dorsal process, and a posterior process. In some cases, the anterior margin of the maxilla has a pronounced concavity that makes the dorsal and the ventral margins parallel to each other along the anterior process; in others, the anterior process has convergent dorsal and ventral margins. The dorsal process is often posterodorsally curved, and it has received several names through the literature. The process has been termed: ascending process (Yates, 2004, 2007a), dorsal process (Prieto-Márquez and Norell, 2011), and lacrimal ramus (Chapelle and Choiniere, 2018). Here the term ‘dorsal process’ is adopted. The anterior process can also have an anteromedial process that articulates with the premaxilla. The posterior process in non-sauropod sauropodomorphs has two morphologies, one continuously tapering, as in Adeopapposaurus, and a second where the dorsal and ventral margins are parallel throughout most of its length, as it is the case of Melanorosaurus. The antorbital fossa primarily excavates the dorsal process and the anterodorsal margin of the posterior process but can also extend further posteriorly.

MX1. A4. Maxilla, lateral plates appressed to the labial side: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.15).

MX2. A33. Maxilla, anterior profile: slopes continuously towards the anterior tip (0), inflection at the base of the dorsal process, creating an anterior process (1) (Sereno et al., 1996; Langer, 2004; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.33 and 4.34).

Comment: The concept of inflection here is similar to that outlined for PMX5, but considering it as a change of slope. C18 and C20 in Pol et al. (2011) are conveying the same information, but based on the anterior process, adding the possibility of a convex margin. A ‘strong inflection’, as stated in C20-1 is correlated with a ‘markedly offset anterior margin from the anterodorsal margin of the dorsal process’ described in C18-1. In Herrerasaurus is an inflection that changes the outline of the anterior process of the maxilla, but this process still tapers to a point. Although Pol et al. (2011) scored the anterior process as concave, there is no anatomical difference between these two states. It is
considered herein that these two characters are clearer if considered as one character dealing with the morphology of the anterior process, as either having two margins (character state 0) or three (character state 1).

**MX3. A40/A63.** Maxilla, main body, shape: alveolar margin and margin of internal antorbital fenestra converging posteriorly (0), alveolar margin and margin of internal antorbital fenestra diverge (1) (Yates, 2007b; Sekiya et al., 2013; Figures 4.33 and 4.34).

**Comment:** Character state (0) refers to the ventral and dorsal never being parallel. In the case of *Lufengosaurus*, it tapers posteriorly, but the margins are parallel at some point along the maxillary body. In its original formulation, the margins needed to be parallel for most of the length of the maxillary body. As a result, *Lufengosaurus* could be scored as either 0 or 1, because although the margins are parallel along some of the lengths of the maxillary body after the dorsal process, there is a posterior tapering that constitutes the maxillary jugal articulation.

**MX4. A41/B31.** Maxilla, promaxillary fenestra and antrum: absent (0), present (1) (Carpenter, 1992; Witmer, 1997a; Sereno, 1999b; Rauhut, 2003a; Smith et al., 2007; Butler et al., 2008b; Martínez et al., 2011; Nesbitt, 2011; Figure 4.19).

**MX5. A43/A67.** Maxilla, external antorbital fenestra, ventral margin: present (0), absent (1) (Rowe, 1989; Martínez et al., 2011; Xing et al., 2015; Figures 4.33 and 4.34).

**MX6. A66-2.** Maxilla, antorbital fenestra, the margin on the dorsal process: absent (0), present (1) (Yates and Kitching, 2003; Figures 4.33 and 4.34).

**Comment:** The characters pertaining to the antorbital fenestra and the antorbital fossa include a cumbersome amount of terms. Here, the anatomical review done of Witmer (1997) is used as a guide to standardize terms. The internal antorbital fenestra always has well-defined margins. The external antorbital fenestra can share all or some of the internal fenestra’s margins. The ventral and anterodorsal margins are within the maxilla, and the posterodorsal and posterior margins are within the lacrimal.

Terms given to the ventral margin of the antorbital margin are the ‘alveolar ridge’ (Rowe, 1989; Arcucci and Coria, 2003; Tykoski, 2005; Ezcurra, 2006), ‘alveolar border’ (Nesbitt,
2011) and ‘longitudinal (alveolar) ridge’ (Yates, 2003b; Nesbitt et al., 2010; Apaldetti et al., 2011; Martínez et al., 2011; Baron et al., 2017a).

This new formulation allows distinguishing from the maxillary ridge (see MX7) described in *Lufengosaurus* (Barrett et al., 2005) and that according to Yates (2007a) is also present in *Melanorosaurus*. However, this feature is not illustrated therein and is therefore still regarded as an autapomorphy of *Lufengosaurus*.

**MX7.** A43-1. Maxilla, maxillary ridge: absent (0), present (1) (Barrett et al., 2005; Yates, 2007b).

**MX8.** A44. Maxilla, anterior maxillary foramen: present (0), absent (1) (Wilson and Sereno, 1998; Wilson, 2002; Remes et al., 2009).

**Comment:** This foramen is the only foramen that runs through the maxillary part of the nasal fossa. This character is illustrated in Wilson and Sereno (1998) and it is independent of the neurovascular foramina on the lateral surface of the maxilla.

**MX9.** A48. Maxilla, neurovascular bundle, opening: entering the maxilla through a foramen on the medial or dorsal margin of the maxilla (0), after passing through a dorsally open canal on the posterior floor of the antorbital fossa (1) (Yates and Kitching, 2003; Pol et al., 2011; Figure 4.30).

**Comment:** This character is outlined in Yates (2003a), based on a description of the anatomical features of the antorbital fossa by Witmer (1997b). This is a thin groove found in the maxillary part of the antorbital fossa, which is the dorsal surface of the maxilla. This canal is illustrated for *Pantydraco* in NHMUK PV P24.

**MX10.** A49. Maxilla, lateral maxillary neurovascular foramina, arrangement: linear (0), irregular (1) (Sereno et al., 1996; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figure 4.30).

**MX11.** A51. Maxilla, external antorbital fenestra, the shape of the ventral margin: sharp, compressed ridge (0), rounded-bulbous (1) (Galton, 1990; Witmer, 1997b; Figure 4.31).

**MX12.** A51-2. Maxilla, external antorbital fenestra, the orientation of the ventral margin: laterally (0), dorsolaterally (1) (Rowe, 1989; Sereno, 1999b; Martínez et al., 2011; Figure 4.31).
MX13. A55. Maxilla, anterior-most part of the maxilla, alveolar margin: straight (0), gradually upturned from an extension of more than three teeth along the alveolar margin and orienting the first maxillary alveolus anteroventrally (1), mediadorsally upturned in the anterior-most tip of the maxilla and orienting the first maxillary alveolus anteroventrally (2) (Unordered) (Rowe, 1989; Tykoski, 2005; Ezcurra and Novas, 2007; Ezcurra, 2010; Novas et al., 2010; Martínez et al., 2011; Sekiya et al., 2013; Figures 4.33 and 4.34).

**Comment:** Ezcurra (2010) assigned character state 2 to Ornithischia, applicable to *Pisanosaurus* and *Sacisaurus*. Further evidence has suggested that *Sacisaurus* and *Pisanosaurus* are silesaurids (Kammerer et al., 2012; Agnolín and Rozadilla, 2017), and this character state is also seen in *Silesaurus*.

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**Figure 4.30** Maxilla of *Pantydraco caducus* (specimen NHMUK PV P24) showing the neurovascular canal (MX9) through which the maxillary nerve is hypothesised to pass. Image taken from Yates (2003a).
MX14. A34. Maxilla, length of the maxilla relative to its maximum dorsoventral depth at the anterior margin of the dorsal process (Sereno et al., 1996; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figure 4.32).

**Comment:** This character is reformulation to make it applicable to the cases where the specimens score (0) in MX2.
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<th>Average coding</th>
<th>Gap-coding</th>
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</table>

Figure 4.32. (→) Gap-coding of character MX14. L_{\text{MX}}, length of the maxilla, DV_{\text{APMX}}, maximum dorsoventral depth at the anterior margin of the dorsal process. Gap-coding produces two gaps: ratio less than or equal to 0.14 (0), more than 0.14 (1). The original coding set a boundary of 1.0, whereas the average obtained for this sample is 2.05. The entropy is the lowest with gap-coding for character MX14.

MX15. A54-1/A39. Maxilla, narial fossa: absent (0), present (1) (Upchurch, 1995; Sereno, 1999a; Galton and Upchurch, 2004; Yates, 2007a; Sekiya et al., 2013).

**Comment:** This character refers to the depression that surrounds to some extent the external nares. It is the same feature formulated in C11 Galton and Upchurch (2004).

MX16. A54-2. Maxilla, narial fossa, orientation of the surface: laterally (0), dorsally (1) (Upchurch, 1995; Sereno, 1999a; Galton and Upchurch, 2004; Yates, 2007a; Sekiya et al., 2013).

**Comment:** This character is assessed in lateral view and is equivalent to assess whether the narial fossa was visible in lateral view or not.

MX17. A54-3. Maxilla, narial fossa, development: flat surface (0), concave surface (1) (Upchurch, 1995; Yates, 2007a; Sekiya et al., 2013).

**Comment:** The original formulation considered ‘shallow’ and ‘well-developed’.

MX18. A53. Maxilla, lacrimal contact above the antorbital fenestra: visible in lateral view (0), obscured by an overhanging portion of the nasal (1) (Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013; Figure 4.32).

**Comment:** The distribution of this character was reviewed for potential correlation with character N1. The postero lateral process of the nasal can overlap the lacrimal, but not necessarily overlap the maxilla-lacrimal contact. The postero lateral process is folded over the maxilla-lacrimal process in *Lamplughsauroidea* (Kutty et al., 2007), in the skull of BP/1/5241 (referred to *M. carinatus*), but not in BP/1/4934, and in *Plateosaurus engelhardti* in SMNS 13200, GPIT 1 and AMNH FARB 6810 (Prieto-Márquez and Norell,
2011). Although identified in *Sarahsaurus*, the extension of the nasal does not seem to cover the maxilla-lacrimal contact. The nasal overlaps only the lacrimal failing to reach the maxilla-lacrimal contact in *Eoraptor, Melanorosaurus* and *Adeopapposaurus*. A piece of bone is covering the lacrimal in *Leyesaurus*, but it is not clear what bone this corresponds to; Apaldetti et al. (2013) scored this character as ‘unknown’ for character state (0) given by Upchurch et al. (2007).

**MX19.** B53. Maxilla, medial interdental plates: separated (0), fused (1) (Nesbitt, 2011; Figure 4.14).

**MX20.** D54. Maxilla, medial interdental plates, alignment with the lateral plates: below, displaced ventrally (0), at the same level (1), above, displaced dorsally (2) (Figure 4.31). NEW.
Figure 4.33. Maxillary characters illustrated in lateral view on the skull of non-sauropod sauropodomorphs. A) Skull of *Massospondylus carinatus* based on the reconstruction in Chapelle and Choiniere (2018) to illustrate a massospondylid; B) Skull of *Plateosaurus engelhardtii* based on specimen SMNS 13200 to illustrate a plateosaurid. Not to scale.
Figure 4.34 Maxillary characters illustrated in lateral view on the skull of sauropod-line sauropodomorphs. A) Skull of *Melanorosaurus* based on NM QR3314 and Yates (2007a); B) Skull of *Shunosaurus* based on Zheng (1996); C) Skull of *Camarasaurus* based on Zheng (1996). Not to scale.
4.1.3.1.5 Nasal

In overall shape, the nasal has a rectangular dorsal lamina and two anteroventrally directed processes, which form the dorsal, posterior, and posterodorsal margins of the narial fenestra. Anteriorly it contacts the premaxilla. The ventral margin of the nasal forms articulates with the dorsal process of the maxilla. Posteriorly, the nasal may have one or two processes: a posterolateral process, that articulates with the frontal bone along its lateral margin and a posterodorsal process that articulates with its antimere. The presence of this second process produces a limboous nasofrontal suture.

N1.A71. Nasal, posterolateral process, overlapping of the lacrimal: absent (0), present (1) (Gauthier, 1986; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Martínez et al., 2011; Sekiya et al., 2013; Figure 4.35).

Comment: See comment in MX18.

N2.D72-1. Nasal, posterodorsal process: present (0), absent (1) NEW (Figure 4.35).

N3.A72. Nasal, posterodorsal process, conjoined nasals in dorsal view: divergent posterodorsal processes (0), convergent posterodorsal process (1) (Yates and Kitching, 2003; Pol et al., 2011; Figure 4.35)

Comment: The original formulation made the distinction between two states: concave or W-shaped (0), and convex (1).

The posterodorsal processes are divergent from each other in Lesothosaurus (Porro et al., 2015), Coelophysis (Tykoski, 2005; Rinehart et al., 2009), Diplodocus (Wilson and Sereno, 1998) and Camarasaurus. The posterodorsal processes converge towards the midline in Plateosaurus. The character can be inferred by the morphology of the anterior margin of the frontals, as is the case in Aardonyx (Yates et al., 2010), with posterodorsal processes convergent, or Anchisaurus, with divergent ones.

There are cases where the original formulation scored OTUs as having a flat articulation, with posterodorsal processes of the nasals absent (such as in Brachiosaurus). Therefore, this character is dealing with two topological categories and is split accordingly.

The original formulation was not applicable in some specimens, such as Adeopapposaurus, where the posterior margin forms a denticulate suture, rather than having just a pair of posterodorsal processes. Thus, character N3 is only applied when the posterodorsal
processes are present (N2), and when the overall morphology of the articulation follows the standardised arthrological nomenclature for fibrous joints (N5). Moreover, the suture nasal-frontal suture can be denticulate and have two distinct posterodorsal processes, as in *Emausaurus* (Haubold, 1990), and *Herrerasaurus*, where the medial portion of the articulation is denticulate, whilst the posterodorsal processes diverge (Sereno and Novas, 1992, 1993); on the other hand, denticulate and converging posterodorsal processes are present in *Lamplughsaura* (Kutty et al., 2007). In *Lufengosaurus*, this area is damaged, and the morphology of the articulation is unclear, but the right posterodorsal process is discernible. Having these three characters allows unambiguous scorings and the characters are independent.

N4.A61-1. Nasal, antorbital fossa: absent (0), present (1) (Sereno, 1999a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.35).

**Comment:** The nasal forms a small portion of the dorsal margin of the external antorbital fenestra in a few taxa: *Lufengosaurus, Melanorosaurus*, and *Xingxiulong*. When the nasal folds over the maxilla-lacrimal contact, a part of the nasal forms the posterior margin of the external antorbital fenestra.

N5.D72-2. Nasal, articulation with the frontal: planar suture (0), denticulate suture (1) NEW (Figure 4.35).
Figure 4.35 Nasal, jugal and lacrimal characters illustrated in lateral view (A, B, C) and dorsal (D, E, F) on the skull of non-sauropod sauropodomorphs. A) Skull of *Massospondylus carinatus* based on the reconstruction in Chapelle and Choiniere (2018) to illustrate a massospondylid; B) Skull of *Plateosaurus engelhardti* based on SMNS 13200 to illustrate a plateosaurid; D) Snout in dorsal view of *Adeopapposaurus*, based on the reconstruction in Martínez (2009); E) Snout in dorsal view of *Plateosaurus engelhardti*; F) Snout in dorsal view of *Coloradisaurus*, based on the reconstruction in Apaldetti et al. (2014). Not to scale.
4.1.3.2 Orbital series

4.1.3.2.1 Lacrimal

The lacrimal is often described as having the outline of an inverted ‘L’ or ‘J’, where there is a dorsoventrally oriented process and an anterior dorsomedial process. This morphology is typically seen in non-sauropod sauropodomorphs, such as *Plateosaurus* and *Massospondylus carinatus*, but in *Melanorosaurus* and *Lufengosaurus* the anterior process is reduced compared to the proportions in *Plateosaurus* or *Massospondylus* and it is absent in *Massospondylus kaalae*, *Shunosaurus* and *Camarasaurus*. The rod-like morphology or the absence of the anterior process of the lacrimal are associated with a triangular outline of the antorbital fenestra. A distinctive feature in several non-sauropod sauropodomorphs is the presence of a lacrimal antorbital fossa, which is present in *Pantydraco*, *Coloradisaurus*, *Massospondylus*, *Plateosaurus Riojasaurus*, *Melanorosaurus*, *Lufengosaurus* and *Efraasia*. This medial lamina that forms the lacrimal antorbital fossa is absent in other sauropodomorphs such as *Anchisaurus*, *Yunnanosaurus huangi*, *Mussaurus* and *Jingshanosaurus*.

The anterior dorsomedial process bifurcates into a ventromedial process in *Plateosaurus* (Figure 4.36), whereas in *Massospondylus carinatus* this process diverges at the base of the dorsomedial process (Figure 4.37). In *M. carinatus*, there is an additional anterolateral process. The details of the anterior dorsal components of the lacrimal are poorly known in other sauropodomorphs due to its articulations with the nasal and prefrontal.

The ventral process also termed the shaft, can be anteroposteriorly expanded at its ventral-most end. The ventral process can articulate with the jugal alone, as in *Herrerasaurus*, *Massospondylus carinatus*, *Melanorosaurus* and *Shunosaurus*, or articulate with the maxilla also, as is in *Eoraptor*, *Plateosaurus* and *Camarasaurus*. 
Figure 4.36 Anatomy of the lacrimal in *Plateosaurus engelhardti* (AMNH FARB 6810). Modified from Prieto-Márquez and Norell (2011) in A) lateral, B) posterior, C) medial, D) dorsal and E) ventral views. The lateral lamina is a continuous extension of the external antorbital margin. In the case of *Plateosaurus* the external antorbital margin is not continuously raised, producing two laminae, the lateral lamina that starts from the ventromedial process, and a ventral lamina, that covers the posteroverentral corner of the antorbital fenestra.

L1. A84. Lacrimal, dorsoventral length relative to the width at its mid-height (Rauhut, 2003a; Yates and Kitching, 2003; Yates, 2007b; Sekiya et al., 2013; Figures 4.35 and 4.38).


L3. A68/B47. Lacrimal, lateral lamina extending over the internal antorbital fenestra: absent (0), present (1) (Sereno, 1999a; Nesbitt, 2011; Pol et al., 2011; Baron et al., 2017a; Figures 4.35, 4.36, 4.37 and 4.39).

**Comment:** Several characters have been defined to refer to this structure. Here the character is formulated as a neomorphic character. This feature is potentially an osteological correlate of the attachment site of the *m. pterygoideus* or a pneumatic fossa (contra Sereno, 2012, where it is reconstructed as the attachment site of the *m. adductor mandibulae externus superficialis*).
Figure 4.37 Anatomy of the lacrimal in *Massospondylus carinatus* (BP/1/5241). Modified from Chapelle and Choiniere (2018) in lateral, anterior and medial views.

Figure 4.38. Gap-coding of character L1. $DV_{Lac}$, dorsoventral length of the lacrimal, $W_{MDV_{Lac}}$, width at the midlength of the dorsoventral length of the lacrimal. The original formulation of this character considered two character states, block-shaped and dorsoventrally elongated. After analyzing this character, the scores in the matrices where this character is used coincides with block-shaped with a ratio less than or equal to 3.
Figure 4.39. Lacrimal, maxilla and jugal in lateral view showing three morphologies of the lacrimal lateral lamina. A) Eoraptor, B) Coelophysis, C) Allosaurus (based on Ezcurra and Novas, 2007; Sereno et al., 2012).

L4. A93. Lacrimal, lateral lamina, extension: posterior corner of the antorbital fenestra and body of the lacrimal (0), restricted to the posterior corner of the antorbital fenestra (1), restricted to the body of the lacrimal (2) (Ezcurra and Novas, 2007; Ezcurra, 2010; Novas et al., 2010; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013; Figures 4.37 and 4.39).

L5. A85. Lacrimal, anterior dorsomedial process: present (0), absent (1) (Wilson and Sereno, 1998; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Otero et al., 2015; Figure 4.39).

L6. D85-1. Lacrimal, anterior dorsolateral process: absent (0), present (1) NEW (Figure 4.36).

L7. D85-2. Lacrimal, anterior ventromedial process, origin: along the anterior dorsomedial process (0), at the base of the anterior dorsomedial process (1) NEW (Figure 4.37).

Comment: Characters L5, L6 and L7 are part of a reassessment of the character statement describing the lateral outline of the lacrimal with two character states: inverted ‘L’-shaped or strut-like morphologies. As discussed above, the anterodorsal portion of the lacrimal is more complex than previously described. An anterior ventromedial process can be seen in Plateosaurus Massospondylus carinatus and Adeopapposaurus. Anchisaurus has been described as possessing a block-shaped lacrimal (Yates, 2004), but the anterodorsal portion
of the lacrimal is damaged (YPM 1883). An anterior dorsolateral process seems to be present but broken off. The lacrimal of \textit{Leyesaurus} has a very similar morphology to that of \textit{Adeopapposaurus} in lateral view, but the presence of an anterior ventromedial process is not clearly discernible in \textit{Leyesaurus}.

L8. A86. Lacrimal, length of the anterior dorsomedial projection of the lacrimal relative to the length of the ventral projection (Galton, 1990; Yates and Kitching, 2003; Tykoski, 2005; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

![Graph](image)

**Figure 4.40.** Gap-coding of character L8, AP$_{\text{APRLac}}$, the anteroposterior length of the anterior process of the lacrimal, DV$_{\text{LVPR}}$, dorsoventral length of the ventral process. The original formulation set the limit between states to a ratio of 0.5. The average for the sample taken here is 0.98. Gap-coding identifies four character states: < 0.18 (0), [0.18,0.32) (1), [0.32,1.33) (2), [1.33,\(\infty\)) (3). Gap-coding reduces the entropy to 67%.

L9. A94. Lacrimal, ventral process, orientation relative to the anterior dorsomedial process: strongly sloping posteriorly (0), perpendicular (1), slopping anteriorly (2) (Yates, 2007b; Sekiya et al., 2013; Figure 4.35).
**Comment:** This character is a categorisation of the angle between the anterior process and the ventral process. When the two processes are on the same quadrant, they are oriented anteriorly.

4.1.3.2.2 Jugal

The jugal has a conserved morphology among non-sauropod sauropodomorphs. It consists of three processes that delimit the ventral margin of the orbit and the anteroventral corner of the infratemporal fenestra. However, the interactions with other bones, such as the maxilla or the lacrimal, vary across taxa. The interaction of the jugal and the quadratojugal is quite distinctive for saurischian dinosaurs, where the posteroventral process is forked and articulates with the quadratojugal by two or three tines (Currie and Zhao, 1993). This morphology is greatly modified in neosauropods because of the displacements of the nostrils towards the rooftop of the skull, with the anterior and posteroventral processes merging into the main body.

J1. A101. Jugal, relationship with the lacrimal: lacrimal overlapping lateral surface of the jugal (0), jugal overlapping lacrimal laterally (1) (Sereno et al., 1993; Yates, 2007b; Sekiya et al., 2013; Figures 4.35 and 4.41).

**Comment:** This character seems to be scored as (0) only in Crurotarsi and *Marasuchus*, and it is scored as (1) for all dinosaurs.

J2. D101-1. Jugal, relationship with the maxilla: maxilla articulates ventrolaterally (0), maxilla articulates ventrally (1). NEW (Figure 4.41).

**Comment:** The maxillary articular surface is located laterally along the ventral half of the anterior process in *Plateosaurus* but it is ventrally located in *Massospondylus* so that the articular maxillary surface is visible in both medial and lateral sides of the jugal. In contrast, in the massospondylid *Adeopapposaurus* the maxilla articulates on the ventrolateral side of the jugal, as it is the case in *Anchisaurus*; in *Leyesaurus*, however, the jugomaxillary contact is not preserved. In *Lufengosaurus* and *Jingshanosauru*, the articulation seems to be restricted to the ventral side as in *Massospondylus*. In *Yunnanosaurus huangi* the jugal is displaced from the maxilla and the articular surfaces are not preserved.
Figure 4.1 Anatomy of the jugal in *Plateosaurus engelhardti* (AMNH FAR 6810), above, and *Massospondylus carinatus* (BP/1/5241) below. Above: lateral and medial, below: lateral and medial. The red margin represents the dorsal margin, which contains the orbital margin at its middle part; the blue margin represents the ventral margin. Modified from Prieto-Márquez and Norell (2011) and Chapelle and Choiniere (2018).

J3. A102/B67. Jugal, ratio of the minimum depth of the jugal below the orbit to the distance between the anterior end of the jugal and the rostroventral corner of the infratemporal fenestra (Galton, 1985a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figure 4.42).
J4. B58-1. Jugal, ridge dividing the lateral surface into two planes: absent (0), present (1) (Butler et al., 2008b; Nesbitt, 2011; Baron et al., 2017a; Figure 4.35).

J5. B58-2. Jugal, ridge dividing the lateral surface two planes: sharp (0), round (1), bulbous (2) (Butler et al., 2008b; Nesbitt, 2011; Baron et al., 2017a).

Comment: This character has been recently reassessed for non-sauropodomorph sauropods in Baron et al. (2017). The change from a smooth surface to two surfaces by a ridge is a neomorphic character, whereas the morphology of the ridge is considered a separate character.

J6. A103. Jugal, anterior process, extension: contacting only the lacrimal-maxilla articulation (0), separating the lacrimal from the maxilla (1) (Holtz, 1994; Yates
and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figure 4.35).

J7. A104/A105. Jugal, anterior process, accessory dorsal process: present (0), absent (1) (Rauhut, 2003b; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figure 4.41).

**Comment:** The original formulation was open to interpretation, but the feature was clearly illustrated in Rauhut (2003). From the anterior process, there is a dorsally oriented prong that articulates with the lacrimal on its lateral side. The feature is seen in several theropods, such as *Dilophosaurus,* and *Ceratosaurus.* In mY2007, the suprageneric clade Neotheropoda is scored as ‘1’: absent. The accessory dorsal process is also present in *Herrerasaurus.* In *Eoraptor* this character is scored as ‘?’ because although in Sereno et al. (2012) it is speculated to be present, the location of the feature is missing. An accessory process seems to be absent in all of the sauropodomorphs assessed here. This character overlaps with C40 Pol et al. (2011), defined as an ‘expansion onto the anterior margin of the orbit’.

J8. A106. Jugal, anterior process, shape: dorsal margin meets the ventral margin in the proximal-most tip (0), distinct anterior margin separating the dorsal and ventral margin of the jugal (1) (Holtz, 1994; Yates and Kitching, 2003; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.35 and 4.41).

**Comment:** A jugal with an anterior process ending in a vertex will be defined as ‘sharply tapered’, and when the anterior process does not end in a vertex then the feature would be defined as ‘blunt’. This original formulation is ambiguous when the anterior process does taper but not to a point.

J9. B61. Jugal, anterior extent of the slot for the quadratojugal: well posterior to the posterior edge of the posterodorsal process of the jugal (0), level with or anterior to the posterior edge of the posterodorsal process of the jugal (1) (Nesbitt, 2011; Baron et al., 2017a; Figure 4.35).

J10. A111. Jugal, posterior termination, position relative to the posteroventral corner of the infratemporal fenestra: anterior (0), posterior (1) (Nesbitt, 2011; Baron et al., 2017a; Figure 4.35).
J11. A112-2. Jugal, posterodorsal process, orientation relative to the anterior process: on opposite directions (0), parallel, on the same direction (1) (based on (Yates, 2007b; Figure 4.41).

Comment: This character is an operationalisation of C46 in mY2007, dealing with the shape of the orbit. Character state (2) in C46 mY2007 is a character on its own dealing with the morphology of the jugal that in turn modifies the morphology of the orbit.

4.1.3.2.3 Prefrontal

There are two distinctive morphologies for prefrontals: a ‘T’-shape, with three processes, as in Plateosaurus or an inverted ‘L’-shape as in Massospondylus. These different outlines are due to the presence or absence of an anterior process that articulates with the lacrimal. Most of the variation within the prefrontal is allometric (Figure 4.43).

Figure 4.43 Anatomy of the prefrontal of Plateosaurus engelhardti (AMNH FARB 6810) and Massospondylus carinatus (BP/1/5241). Above: lateral, medial, dorsal, and anterior. Below: lateral, posterior, dorsal. Modified from Prieto-Márquez and Norell (2011) and Chapelle and Choiniere (2018).

PF1. A97. Prefrontal, dorsal anteroposterior length relative to the dorsal anteroposterior length of frontal (Galton, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013; Figure 4.44).
Figure 4.44 Gap-coding of character PF1. Using 22 skulls where the prefrontal and frontal are both preserved, the following gaps are identified: (0, 0.39) (0), Buriolestes only; [0.39, 0.74) (1), most of the samples, including Lesothosaurus, Shunosaurus and Camarasaurus; [0.74, 0.95) (2), only Sarahsaurus and Xixiposaurus; [0.95, ∞), containing only Diplodocus, Plateosaurus Pampadromaeus and Melanorosaurus (3). The limit between character states in the original coding (0.75) almost coincides with the average of the proportion between the anteroposterior length of the prefrontal and the anteroposterior length of the frontal (0.74).

PF2. A97-1. Prefrontal, anterior process: present (0), absent (1) NEW (Figure 4.43).

PF3. A98. Prefrontal, the maximum transverse width of the prefrontal relative to the skull transverse width at that level (Galton, 1990; Yates, 2007b; Sekiya et al., 2013; Figure 4.45).
Figure 4.45. Gap-coding of character PF3. Gap-coding defines two sets of morphologies: (0, 0.61] (1); (0.61, 1], scored to only two non-sauropod sauropodomorphs, Panphagia and Leyesaurus. The original coding used as limit 0.25, which coincides with the average obtained from the sample (0.27). Gap-coding identified a limit between the two characters at 0.35, and this version has the lowest entropy.

PF4. A99. Prefrontal, ventral process, height relative to the lacrimal height (Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figure 4.46).

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Figure 4.46. Gap-coding of character PF4. Gap-coding identifies four character states: (0, 0.11) (0), that scored for *Lufengosaurus* and *Coloradisaurus*; [0.11,0.19) (1), that scored to *Efraasia* and *Adeopapposaurus*; [0.19, 0.53) (2), that scores most of the sample; [0.53, ∞) (3) that singles out *Melanorosaurus*. This character was originally defined with a limit of 0.25 when the average is 0.33. Although the original character has a lower entropy than the average, the gap-coding has even lower entropy.

4.1.3.2.4 Postfrontal

POF1. A120. Postfrontal, as a separate ossification: present (0), absent (1) (Sereno et al., 1993; Yates, 2007a; Sekiya et al., 2013).
4.1.3.2.5 Postorbital

The postorbital has a conserved morphology in non-sauropod sauropodomorphs, as a triradiate bone with an anterodorsal process, a posterodorsal process and a ventral process. The posterodorsal process varies the most within sauropodomorphs, being relatively gracile in *Plateosaurus* and *Massospondylus* (Figure 4.47), but stouter and shorter in *Riojasaurus*, *Lufengosaurus* (Figure 4.49) and *Yunnanosaurus huangi*. The relative position of the posterodorsal process compared to the supratemporal fenestra also varies, exposing the supratemporal fenestra in lateral view in *Massospondylus* and *Yunnanosaurus huangi*. However, based on the morphologies illustrated in Gow et al., (1990), and Sues et al. (2004) and the ontogenetic sequence proposed in Neenan et al. (2018), the change in the position of the temporal bar (the structure comprised of the postorbital posterodorsal process and the squamosal anterodorsal process) may represent ontogenetic variation.

![Diagram of postorbital bones](image)

*Plateosaurus engelhardti*

*Massospondylus carinatus*

PO1. A114. Postorbital, the height of the postorbital part of the posterior orbital margin relative to the height of the posterior lateral process (Yates, 2007b; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

PO2. D114-1. Postorbital, anterodorsal process, orientation relative to the main body: the distal end of the anterodorsal process is anteromedially deflected (0), the distal end of the anterodorsal process is medially deflected (1) NEW (Figures 4.48, 4.49 and 4.5).

PO3. A116. Postorbital, posterodorsal process, extension: extensive, reaching the posterodorsal corner of the external infratemporal fenestra (0), not reaching the posterodorsal corner of the external infratemporal fenestra (1) (Pol et al., 2011; Figures 4.48, 4.49 and 4.5).

Comment: In the original scoring, this character was only scored as (1) for Coloradisaurus. Nonetheless, the feature is also seen in Aardonyx, where the posterodorsal corner of the infratemporal fenestra is restricted to the squamosal. For character state (1), the postorbital may articulate the squamosal laterally, even dividing the anterior process of the squamosal into two portions, but the margins of the infratemporal fenestra remain restricted only to the squamosal. Considering these landmarks, the character state (0) is widely distributed in sauropodomorphs since it is seen in Anchisaurus, Arcusaurus, Buriolestes, Camarasaurus, Diplodocus, Eoraptor, Pantydraco, Plateosaurus engelhardti, Riojasaurus, Sarahsaurus, Unaysaurus, Xinxulong, Yimenosaurus (based on the schematic drawing), and Yunnanosaurus huangi. It was scored as (0) extensive in Lufengosaurus, but this portion of the skull is reconstructed, and here is rescored as ‘?’.

In several outgroups, character state (1) is given to Euparkeria, Herrerasaurus, Heterodontosaurus, Lesothosaurus, Scelidosaurus, and Tawa. In the case of Coelophysis, for example, the infratemporal fenestra expands into the postorbital (0), but the articulation with the squamosal is the same as described in Aardonyx above.

PO4. A117. Postorbital, posterodorsal process, orientation relative to the main body in dorsal view: the distal tip of the posterodorsal process is medially bowed (0), the distal tip of the posterodorsal process is aligned posteriorly and at 90° from the transverse process of the postorbital main body (1), the distal tip of
posterodorsal process is laterally bowed (2) (Pol et al., 2011; Figures 4.48, 4.49 and 4.5).

**Comment:** The original formulation defined character state (0) as ‘straight’, but this is an ambiguous as a straight margin in this region is rare. Three character states were identified dealing with the orientation of the postorbital and the posterodorsal process. In *Aardonyx*, the posterodorsal process is medially bowed relative to the main axis of the postorbital main body. In *Adeopapposaurus*, the posterodorsal process is set perpendicular to the transverse axis of the postorbital main body. In *Coloradisaurus*, the posterodorsal process is laterally bowed. The terms ‘lateral’ and ‘medial’ are then relative to the sagittal axis perpendicular to the transverse axis of the main body.

PO5. A113. Postorbital, ventral process, transverse width relative to its anteroposterior width at midshaft (Galton, 1985a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

PO6. A118. Postorbital, ventral process, ventral tip: ventrally directed (0), anteriorly deflected (1) (Pol et al., 2011; Figures 4.48, 4.49 and 4.5).
Figure 4.48 Quadratojugal, quadrate, postorbital and squamosal characters illustrated in lateral view on the skull of basal saurischians. A) Skull of *Herrerasaurus* based on PVSJ 407 and Sereno and Novas (1993); B) Skull of *Eoraptor* based on PVSJ 512 according to Sereno et al. (2012); C) Skull of *Coelophysis* based on the illustration in Colbert (1981). Not to scale.
Figure 4.49 Quadratojugal, quadrate, postorbital and squamosal characters illustrated in lateral view on the skull of non-sauropod sauropodomorphs. A) Skull of *Massospondylus carinatus* based on the reconstruction in Chapelle and Choiniere (2018) to illustrate a massospondylid; B) Skull of *Plateosaurus engelhardti* based on SMNS 13200 to illustrate a plateosaurid. C) Skull of *Lufengosaurus* based on IVPP V15. Not to scale.
Figure 4.50 Quadratojugal, quadrate, postorbital and squamosal characters illustrated in lateral view on the skull of sauropod-line sauropodomorphs. A) Skull of *Melanorosaurus* based on NM QR3314 and Yates (2007a); B) Skull of *Shunosaurus* based on Zheng (1996); C) Skull of *Camarasaurus* based on Zheng (1996). Not to scale.
4.1.3.3 Temporal series

4.1.3.3.1 Squamosal

The squamosal is a tetraradiate bone that forms the posterodorsal-most corner of the skull and constitutes the posterodorsal corner of the infratemporal fenestra, and the posterolateral corner of the fenestra (Figures 4.51 and 4.52). In *Massospondylus* the posterior region has two processes that are separated by a thin lamina of bone so that an articular surface that splits the posterodorsal process into two tines. This auxiliary process is illustrated and described in Chapelle and Choiniere (2018), but is not named; here the term ‘auxiliary posteroventral process’ is employed.

Figure 4.51. Anatomy of the squamosal in *Plateosaurus engelhardti* (AMNH FARB 6810). Modified from Prieto-Márquez and Norell (2011). Top, dorsal view, middle left, right lateral view, middle right, medial view, bottom, ventral view.
Figure 4.52 Anatomy of the squamosal in *Massospondylus carinatus* (BP/1/5241). Modified from Chapelle and Choiniere (2018). From left to right and top to bottom: lateral view, medial view, posterior view, ventral view, dorsal view, and anterior view.

SQ1. A150. Squamosal, ventral process, length relative to the width at its base (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013).

**Comment:** In the matrix of Yates (2007a) and its derivatives, C61 and C63 refer to the same process. In C61 the process is termed the ‘quadratojugal process’, which would be misleading in the cases where the squamosal fails to reach the quadratojugal.

SQ2. A151-1. Squamosal, ventral process, connection: quadratojugal and quadratojugal (0), quadratojugal only (1) (Gauthier, 1986; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Baron et al., 2017a; Figure 4.51).

SQ3. D151-2. Squamosal, ventral contact with the quadratojugal: point contact (0), suture (1) NEW (Figure 4.51).

SQ4. D151-3. Squamosal, postorbital articular surface, auxiliary posteroventral process: absent (0), present (1) NEW (Figure 4.51).
4.1.3.3.2 Quadrate

The quadrate is a columnar bone that forms the posterolateral margin of the skull. Two laminar processes project anteromedially and anterolaterally from the shaft. The interactions of this bone with neighbouring elements are conserved in non-sauropod sauropodomorphs. The quadrate head articulates with the squamosal, the anteromedial process articulates with the pterygoid, the anterolateral process articulates with the quadratojugal, and the distal portion has two condyles, laterally and medially, that articulate with the mandible. In Massospondylus carinatus the outline of the medial surface is concave because the anteromedial process is orientated laterally, in the same direction that the anterolateral process. In Plateosaurus and Lufengosaurus, the medial outline is sinusoidal since the anteromedial process is oriented medially, creating a wide anterior groove (Figure 4.53). In Plateosaurus the lateral condyle is larger and slightly more ventrally offset than the medial condyle. In contrast, in Massospondylus carinatus the medial condyle is larger and more ventrally offset than the lateral condyle, a condition also reported in Riojasaurus and Yunnanosaurus huangi (Figure 4.54). Another feature with considerable variation amongst non-sauropod sauropodomorphs is the position of the quadrate foramen. The foramen can be entirely inside the quadrate or displaced towards the articulations with either the squamosal or the quadratojugal.

Q1.A152. Quadrate head, relationship with the squamosal: partially exposed laterally (0), completely covered by the squamosal (1) (Sereno et al., 1993; Yates, 2007b; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

Q2.A153. Quadrate, orientation in lateral view: posteroventral (0), ventral (1), anteroventral (2) (Nesbitt, 2007, 2011; Baron et al., 2017a; Figures 4.48, 4.49 and 4.5).

Q3.A156-1. Quadrate, quadrate foramen: absent (0), present (1) (Wilson, 2002; Yates, 2007b; Remes et al., 2009; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).
Figure 4.53 Anatomy of the right quadrate in *Plateosaurus elenghardtii* (AMNH FARB 6810). Modified from Prieto-Márquez and Norell (2011). Views from top to bottom and left to right: proximal, medial, lateral, distal, anterior and posterior.
Figure 4.54 Anatomy of the squamosal in *Massospondylus carinatus* (BP/1/5241). Modified from Chapelle and Choiniere (2018). Views from top to bottom and left to right: lateral, medial, distal, proximal, anterior, posterior.

Q4.A156-2. Quadrate, quadrato foramen, location on the posterior surface: inset into the quadrate (0), on the quadrato-quadratojugal suture (1), on the quadrato-squamosal suture (2) (Yates, 2007b; Figures 4.48, 4.49 and 4.5).
Comment: Characters Q3 and Q4 are based on C68 Y2007. The character refers to the location of the quadrate foramen in posterior view. This was scored as polymorphic in Tazoudasaurus, but the illustrations in Allain and Aquesbi (2008) show that the foramen is likely absent. The original formulation of the character statement left the character states ambiguously written, since character state (1) was ‘deeply incised into and partly encircled by the quadrate’, meaning that a foramen on either suture could be scored as 0-2 or 1 depending on the definition of ‘deeply’ and ‘partly’. Here the states define absolute terms, and even if the quadrate foramen is deeply incised on one of the sutures, it is assessed as being on the margins and along the sutures. For C54 U2007, the polymorphism is scored in Thecodontosaurus, but the presence of the quadrate foramen can only be discussed for on the specimens assigned to Pantydraco, and it seems the foramen was absent (Yates, 2003a; Galton et al., 2007). Sarahsaurus has been described having the quadrate foramen on the quadrate-quadratojugal foramen, but it was recently determined it is inset into the bone (Marsh and Rowe, 2018)

Q5.A157. Quadrate, posterolateral margin, orientation: sloping anterolaterally from the posteromedial margin (0), slopes posteriorly (1) (Wilson, 2002; Yates, 2007b; Sekiya et al., 2013; Figures 4.53 and 4.54).

Q6.D157-1. Quadrate, distal portion, position of the lateral condyle: ventrally offset relative to the medial condyle (0), dorsally offset relative to the medial condyle (1) NEW (Figures 4.53 and 4.54).

Q7.A158. Quadrate, the proportion of the length of the quadrate that corresponds to the articulation with the pterygoid wing (Rauhut, 2003a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

4.1.3.3.3 Quadratojugal

The quadratojugal forms the posteroventral-most corner of the skull and comprises of the main body and two processes. In general, this bone is described by assessing the divergence angle between these processes. However, in Plateosaurus and Coloradisaurus, the two processes emerge from the same side and are somewhat parallel, opposite to the situation in most non-sauropod sauropodomorphs where the two processes diverge, in which this angle is easy to measure (Figure 4.55). A better description of these two morphologies is by
thinking of an imaginary point of intersection between the long axes. In the morphology of
Plateosaurus the intersection of the long axes of the two processes can be identified outside
of the main body, whereas in Massospondylus (Figure 4.55), this same point is located inside
the main body. The dorsal process articulates with the quadrate or the squamosal, and the
anterior process articulates with the jugal. Posterolaterally there is an articular surface
where the quadrate fits into.

QJ1. A121. Quadratojugal, articulation with the jugal: jugal articulates
dorsolaterally to the quadratojugal (0), jugal articulates ventrolaterally to the
quadratojugal (1), jugal articulates with the quadratojugal via two posterior
processes (2) (Yates, 2007b; Nesbitt, 2011; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

Comment: This character was scored as polymorphic in Leyesaurus by Apaldetti et al.,
(2011), where the jugal can either overlap the quadratojugal on the lateral surface or suture
along the anterodorsal margin of the quadratojugal. This character has also been defined in
C71 Nesbitt (2011) under different terms. According to Nesbitt (2011), in all the dinosaurs
he assessed, the jugal is split into a posterodorsal and posteroventral process by the
quadratojugal. In the formulation of C67 Yates (2007b), Euparkeria is scored as the state
(0): jugal overlaps the lateral surface of the quadratojugal. As it is, this formulation is
confused with what can be seen in Euparkeria: the jugal is lying dorsally to the anterior
process of the quadratojugal (Ewer, 1965; Nesbitt, 2011; Sookias, 2016). In some basal
dinosaurs the quadratojugal splits the jugal into two posterior processes, as in
Herrerasaurus (pers. obs., Sereno and Novas, 1993), Lesothosaurus, Coelophysis (pers.
ob., Nesbitt, 2011), and Plateosaurus engelhardti (pers. obs., Galton, 1985; Nesbitt,
2011). However, in Melanorosaurus, the quadratojugal possesses an anterior fossa where
the jugal articulated, so that in lateral view the quadratojugal sutures along the jugal on its
ventrolateral margin (Yates, 2007a), a condition also seen in Euparkeria. The new
formulation proposed here assesses the articulation of the two bones as an unordered
multistate character. The quadratojugal articulates to the jugal via two anterior processes
only in Revueltosaurus and Aetosaurus (Nesbitt, 2011). In Leyesaurus, the jugal-
quadratojugal articulation is not preserved and this character is scored as ‘?’.
QJ2. A123-1/A122. Quadratojugal, anterior process, long axis relative position to the long axis of the dorsal process: the intersection point of the two long axes is inside the main body of the quadratojugal (0), the intersection point of the two long axes is outside the main body of the quadratojugal (1) (Galton, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007b; Sekiya et al., 2013; Figure 4.55).

Comment: This character was initially formulated as a continuous character measuring the angle between the two processes. Several complications arose from this measurement. First, the processes can curve, as it is the case of Lufengosaurus, so that the angle can be defined in several ways. Conversely, in Herrerasaurus, the processes are not curved at all. Measuring the angle can be difficult, since it is in the corner of the skull, and any shearing will affect the angle. The angle of divergence can also be affected by ontogeny, as it seems to be the case in Massospondylus carinatus (Gow et al., 1990). However, there is an anatomical difference between the skulls of Coloradisaurus, Lufengosaurus and in Plateosaurus engelhardti. The long axes of the quadratojugal intersect outside of the skull. In the case of Massospondylus carinatus, the skulls that are probably conspecific and
represent an ontogenetic series (according to Neenan et al., 2018) have different angles, but the long axes intersect inside the main body of the quadratojugal.

QJ3. A124. Quadratojugal, length of the dorsal projection of the quadratojugal relative to the anterior projection (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

QJ4. A125. Quadratojugal, anterior process, shape of the anterior end: tapered, one vertex along the anterior end (0), three vertexes along the anterior end (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

Comment: In C57 P2011, Camarasaurus is scored as polymorphic. In the specimens from different species of Camarasaurus, the quadratojugals are dorsoventrally expanded (i.e. C. grandis YPM 1905, C. lentus DNM 28, DNM 975, as illustrated in Madsen et al. [1995]). Following the topological criterion, the quadratojugal in sauropods articulates with the jugal in a planar way and does not taper to a point. The ‘dorsoventral expansion’ of the original formulation can be interpreted also as a thickening on the quadratojugal process, so this delimitation is needed. The skull of Diplodocus shows a quadratojugal with two vertexes and a dorsoventral expansion (Wilson and Sereno, 1998).

QJ5. A126. Quadratojugal, posteroventral process: present (0), absent (1) (Wilson and Sereno, 1998; Upchurch et al., 2007a; Sekiya et al., 2013; Figures 4.48, 4.49 and 4.5).

QJ6. D126-1. Quadratojugal, posteroventral process, shape: spike-like process (0), club-like process (1), knob-like process (2) NEW (Figures 4.48, 4.49 and 4.5).

Comment: The original formulation specified character state (1) as a ‘rounded heel-like posteroventral process absent’. This is ambiguous, since it is not clear whether the entire process is absent and if it is always ‘heel-like’, or if only the ‘heel-like’ morphology is assessed. The OTUs that scored (1) in this character were Yunnanosaurus huangi, Omeisaurus, Shunosaurus, and Camarasaurus (Upchurch et al., 2007a; Sekiya et al., 2013). In these specimens, the posteroventral process is absent, the articulation with the quadrate and the retroarticular process is done by the main body of the quadratojugal. In Lufengosaurus, the process is spike-like, but in Melanorosaurus this process is rounded, and square-shaped in Cryolophosaurus.
4.1.3.4 Vault series

4.1.3.4.1 Frontal

The frontal is a sheet-like bone that contributes to the skull roof, above the anterior part of the braincase. It is composed of three processes: the posterolateral process that articulates with the postorbital, an anterolateral process that articulates with the prefrontal, and an anteromedial process that articulates with the nasal. In *Plateosaurus* the anteromedial processes meet at the midline, whereas in *Massospondylus* the anteromedial processes diverge (Figure 4.56). This massospondylid morphology is also present in *Adeopapposaurus* and *Leyesaurus*, although there is a considerable damage in the anterior region of the frontals. By contrast, the morphology of *Plateosaurus* is not identifiable in other plateosaurid dinosaurs, such as *Unaysaurus* (Leal et al., 2004), where the anterior margin is not clearly preserved, but it is similar to the morphology of *Massospondylus kaalae* (Barrett, 2009). The frontal crest extends along half of the main body in *M. carinatus* but runs along most of the bone in *Plateosaurus*.

FR1. A131. Frontal, anterior portion, articulation, orientation: planar suture (0), limbous suture (1), denticulate suture (2) (based on Nesbitt, 2011; Figures 4.19 and 4.56).

FR2. A132. Frontal, anterior process, orientation: anteriorly directed (0), anterolaterally directed (1) (Sereno, 1999a; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figure 4.56).

**Comment:** FR1 and FR2 overlapped in their original formulations. The presence or absence of an anterior process modifies the morphology of the articulations. *Herrerasaurus* and *Camarasaurus* both have planar sutures, but in *Camarasaurus* this suture is product of the absence of the anterior process, but in *Herrerasaurus* the suture outline is medially convergent to the sagittal plane. The outline in *Efraasia* is, on the other hand, denticulate, with two anterior processes directed anteriorly, a similar condition to the one seen in *Allosaurus*. Moreover, when the anterior process is directed laterally, it always insets between the frontal and the nasal. These are true anatomical differences, and these new formulations capture this variation unambiguously. According to Apaldetti et al. (2013), these features are not assessable in *Coloradisaurus*. 
FR3. A133-1. Frontal, extension: contributes to the dorsal margin of the orbit (0), restricted to the interior of the skull roof (1) (Galton, 1985a, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

FR4. A133-2. Frontal, length of the frontal visible in lateral view relative to the maximum diameter of the orbit (Galton, 1985a, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

Comment: Characters FR3 and FR4 are operationalisations of C45 Upchurch et al. (2007). This multistate character was a combination of a location character (FR3) and a continuous character (FR4).

FR5. A134. Frontal, contribution to supratemporal fossa: present (0), absent (1) (Upchurch, 1995; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).
Comment: As noted by Sekiya et al. (2013), the character has been formulated without a clear distinction between fossa and fenestra. For C49 Pol et al. (2011), Anchisaurus has been scored as a polymorphism. In specimen YPM 1883, the frontal does not contribute to the supratemporal fenestra, but it is not clear if the supratemporal fossa extended onto the frontal.

FR6. A135. Frontal contribution to the internal margin of the supratemporal fenestra: present (0), absent (1) (excluded by a parietal-postorbital contact) (Galton, 1990; Yates, 2007b; Figure 4.13).

Comment: The modification of this character distinguishes between the external and internal margins of the supratemporal fenestra, whose offset produces the supratemporal fossa. The scoring of this character has probably confusing information since it confuses supratemporal fenestra with fossae. This character was scored as polymorphism in C91 Sekiya et al. (2013). The two specimens where this feature is illustrated are BP/I/4779 and BP/I/5241 (Sues et al., 2004; Chapelle and Choiniere, 2018). In both specimens, the frontal reaches the supratemporal fossa but does not form part of the supratemporal fenestra, excluded by the parietal-postorbital contact. There is some level of evidence BP/I/4779 is not referable to M. carinatus, and the feature is scored as missing data in BP/I/4934. However, in Sarahsaurus the frontal does not reach the supratemporal fenestra either, although it does contribute to the supratemporal fossa as illustrated in Rowe et al. (2011) and is then rescored as absent (this observation is corroborated in Marsh and Rowe, 2018). The frontal is completely excluded from the internal margin of the supratemporal fenestra in Adeopapposaurus, Leyesaurus, and Lufengosaurus.

FR7. A136. Frontal, frontal-parietal suture: planar (0), limbous (1), denticulate (2) (Pol et al., 2011; Figure 4.19).

4.1.3.4.2 Parietal

The parietal is a sheet-like bone posterior to the frontal. It has two processes, an anterior process that articulates with the frontal, and a posterior process that articulates with the squamosal. The paired bones form the medial margins of the supratemporal fenestrae, and the space between the external supratemporal fenestrae sometimes bears a sagittal crest. The latter feature is not present in all non-sauropod saurpodomorphs: it is present in *Massospondylus* (Figure 4.57) but not in *Plateosaurus* (Figure 4.58).

![Diagram of Massospondylus carinatus parietals](image)

**Massospondylus carinatus**

Figure 4.57 Anatomy of the parietals in *Massospondylus carinatus*. Modified from Chapelle and Choiniere (2018). Views from left to right and top to bottom: dorsal, ventral, anterior, posterior.
Figure 4.58 Anatomy of the parietals in *Plateosaurus engelhardti*. Modified from Prieto-Márquez and Norell (2011). Views from top to bottom and from left to right: ventral, dorsal and posterior.

**PA1.** A144. Parietals, fusion: absent (0), present (1) (Figures 4.58 and 4.57).

**Comment:** In C50 U2007, *Massospondylus* and *Plateosaurus* are scored as polymorphic. Considering the morphometric analysis of the labyrinth of *M. carinatus* in Neenan et al. (2018), the only specimen where the parietals can be assessed in the literature is SAM/PK/1314 where the parietals are paired and sutured, but this is at the moment not considered part of *M. carinatus*. The skull of BP/1/5241 referred to *M. carinatus* has fused parietals. In the case of *Plateosaurus engelhardti*, SMNS 13200, GPIT I and AMNH 6810 all show fused parietals.

**PA2.** A145. Parietal, depth of the occipital wing of the parietal compared to the maximum dorsoventral length of the foramen magnum.

### 4.1.3.5 Palatal series

The palatal complex displays a considerable degree of variation among non-sauropod sauropodomorphs. The sample is very limited, and it is very difficult to discern whether some characters are autapomorphies. Moreover, the preservation state of the palatal complex is not always optimal for comparative studies.
4.1.3.5.1 Vomer

V1.D198. Vomer, anterior-most articulation: maxilla (0), reaches the premaxilla (1) (Wilson, 2002; Remes et al., 2009; Figure 4.59).

**Comment:** The vomer articulates with the maxilla in *Plateosaurus Lufengosaurus, Melanorosaurus, Shunosaurus* and *Diplodocus*, but reaches the premaxilla in *Massospondylus carinatus* (BP/1/5241), *Mamenchisaurus, Omeisaurus* and *Camarasaurus*. The scorings based on the skull diagram in Wilson and Sereno (1998, p. 9) indicate that the vomer articulates with the premaxilla, but in Wilson (2002) and Remes et al. (2009) the dataset indicates that it articulates with the maxilla, which is consistent with
the description in Prieto-Márquez and Norell (2011). To reduce the ambiguity of this character, it is restricted to the anterior-most portion of the vomer, which does not alter the scorings given to other taxa.

4.1.3.5.2 Pterygoid

The pterygoid bone consists of two main laminae, an anterior process that meets its antimere medially (medial process sensu Yates, 2007a), and a posterior lamina that articulates with the quadrate, referred to as quadrate ramus sensu Prieto-Márquez and Norell (2011).

PT1. A190. Pterygoid, relationship with ectopterygoid: ectopterygoid ventral to pterygoid (0), ectopterygoid dorsal to pterygoid (1) (Sereno et al., 1993; Yates, 2007b; Sekiya et al., 2013; Figure 4.59).

Comment: Among non-sauropod sauropodomorphs, the ectopterygoid is only placed ventrally in Jingshanosaurus and Leyesaurus.

PT2. D190-1. Pterygoid, quadrate lamina: divided into three processes (0), divided into two processes (1); one process (2) NEW (Figures 4.6 and 4.61).

Comment: It was reported that in Massospondylus carinatus the quadrate lamina or ramus divides into three processes (Chapelle and Choiniere, 2018, therein referred to as processes 1, 2, and 3), unlike Plateosaurus engelhardti, where the quadrate ramus is divided into two processes. After examining the plates published in the description by Prieto-Márquez and Norell (2011), it is clear that at the base of the ventral process there is a conical projection directed ventrally in the same location as the process 1 in Chapelle and Choiniere (2018). This topological similarity leads to conclude that in both ‘prosauropods’ the quadrate ramus is divided into three processes, referred to as posterodorsal process (process 3 in Chapelle and Choiniere, 2018), posteroverentral process (process 2), and accessory posteroverentral process (process 1). In Chapelle and Choiniere (2018) it is posited that process 1 may correspond to a fused epipterygoid in Massospondylus carinatus, however, the epipterygoid is also fused in Plateosaurus engelhardti, and this conical process at the base of the posteroverental process is present as well, meaning that in the former the epipterygoid is not preserved, because no suture was found in this process. According to Martínez (2009), the quadrate ramus is divided only into two processes, and the
examination of specimen PVSJ610 along with the diagrams illustrated therein support the idea of the absence of an accessory posteroventral ramus, a condition recently reported also in *Pampadromaeus* (Langer et al., 2019). The pterygoids of *Sarahsaurus* and *Pantydraco* are damaged in this section, making further comparisons impossible, and in *Buriolestes* and *Lufengosaurus* the quadrate ramus is covered by matrix. In sauropods the quadrate process is not divided (McIntosh and Berman, 1975; Tschopp et al., 2015).

Figure 4.60 Anatomy of the pterygoid and epipterygoid in *Plateosaurus engelhardtii*. Modified from Prieto-Márquez and Norell (2011). From left to right and from top to bottom: right pterygoid in ventral, dorsal, lateral, medial, laterodorsal, and medioventral; left pterygoid and epipterygoid in lateral, anterior, medial and posterior views.
Figure 4.61 Anatomy of the left and right pterygoids in articulation in *Massospondylus carinatus*. Modified from Chapelle and Choiniere (2018). Views from left to right and top to bottom: ventral, dorsal, anterior, posterior.

PT3. A191. Pterygoid, basisphenoid process: absent (0), present (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.6 and 4.61).

PT4. A192. Pterygoid, anterior process, shape: horizontal (0), dorsally directed (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.6 and 4.61).
4.1.3.5.3 Palatine

Figure 4.62. Anatomy of the palatine in Plateosaurus engelhardti (four to the left) and Massospondylus carinatus (three to the right). Left hand side: dorsal, lateral, ventral, medial; right hand side: dorsal, lateral, medial. Left modified from Prieto-Márquez and Norell (2011) and right from Chapelle and Choiniere (2018).

PL1. A194. Palatine, anterior process, shape: tapered, one vertex (0), no vertex, the anterior process is lobe-shaped (1) (Sereno, 1999a; Martínez et al., 2011; Figure 4.62).

PL2. A193. Palatine, connection: pterygoid only (0), pterygoid and ectopterygoid (1) (Pol et al., 2011; Figure 4.59).

Comment: This character is reformulated to convey only connectivity between elements.

PL3. A195. Palatine shaft, anteroposterior length relative to the maximum transverse width (Pol et al., 2011).

PL4. A196. Palatine, maxillary articular surface of the palatine, position: along the lateral margin of the bone (0), restricted to the lateral process (1) (Sereno et al., 1996; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figure 4.62).
Comment: According to C91 mY2007, there is a centrally located tubercle in *Adeopapposaurus, Massospondylus, Lufengosaurus* and *Plateosaurus*. The ventral surfaces of the palatine in *Adeopapposaurus* and *Lufengosaurus* show a flat ventral surface. *Plateosaurus* has a ventral peg-like process that according to Martínez (2009) is also present in some individuals referred to *Massospondylus, contra* Sues et al. (2004) who describes the absence of this process after assessing the skulls that compose the ontogenetic series of *Massospondylus carinatus*. Evidence of a ventral process in *Massospondylus* comes from a circular rugosity in the ventral surface of SAM PK K1314 (Barrett and Yates, 2006; Galton and Kermack, 2010). Since it is not clear what the ‘centrally located tubercle’ refers to in mY2007, it is considered that this character statement describes the ventral process discussed in the literature as the peg-like process of *Plateosaurus*. Since there is some evidence that this structure could be present in SAM PK K1314 and as *Plateosaurus* needs a taxonomic review with a phylogenetic approach, this character is not currently considered an autapomorphy of *Plateosaurus*.

4.1.3.5.4 Ectopterygoid

Ec1. A186/A187. Ectopterygoid, body, pneumatic fossa on the ventral surface: present (0), absent (1) (Gauthier, 1986; Sereno et al., 1993; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a, 2007b; Sekiya et al., 2013).

Comment: This feature has also been termed as the ‘ventral recess’ (Gauthier, 1986; Pol et al., 2011).

Ec2. A188. Ectopterygoid, articulation of the lateral process: to the jugal (0), to the maxilla (1) (Wilson, 2002; Remes et al., 2009; Pol et al., 2011; Figure 4.59).

Comment: The ectopterygoid connects to the jugal via the lateral process in basal sauropodomorphs, such as *Massospondylus carinatus* (Chapelle and Choiniere, 2018) and Plateosaurus (Prieto-Márquez and Norell, 2011), and where it received the name ‘jugal process’. In sauropods, such as in *Camarasaurus* and *Brachiosaurus*, the lateral process articulates with the maxilla (Wilson and Sereno, 1998).
Ec3. A189/B112. Ectopterygoid, lateral process, shape: curved (0), hooked-like (1) (Yates, 2003b; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Nesbitt, 2011; Pol et al., 2011; Sekiya et al., 2013; Baron et al., 2017a; Figure 4.59).

**Comment:** A curve is defined here as a function where the slopes are always in the same direction, outwards from the ectopterygoid to the lateral plane of the skull. A hook is defined as a curvature where the tip points towards the ectopterygoid process.


**Comment:** When the lateral process has a curvature opening posteriorly, the process arcs anteriorly.

### 4.1.3.6 Neurocranium

There is a large body of literature that deals extensively with the terminology of the structures in the otoccipital. This bone has been also identified as the opisthotic-exoccipital complex (Yates, 2003a; Upchurch et al., 2004a, 2007a; Galton and Knoll, 2006; Butler, 2010; Galton and Kermack, 2010; Bittencourt et al., 2015; Chapelle and Choiniere, 2018), or referred to by its individual components, i.e. the opisthotic and exoccipital (Yates, 2007a, 2007b). In adult archosaurs, the exoccipital and the opisthotic are fused into a single element termed the otoccipital (Benton and Clark, 1988; Nesbitt, 2011; Bittencourt et al., 2015; Piechowski et al., 2018), and this has been followed in recent revisions of dinosaur neuroanatomy (e.g. Sampson and Witmer, 2007; Bronzati, 2017; Bronzati et al., 2017). The term otoccipital is used here reflecting its nature as an individual element (Figure 4.63).

The otoccipital contains the structures of the inner and middle ear. The *fenestra ovalis* is the anterior-most opening in this element. This lateral opening receives the stapes and leads into the vestibular apparatus. This duct contains the *scala vestibuli*, the *scala media* and the tectorial membrane. The tectorial membrane extends along the ventral ramus of the otoccipital, which receives several names. The name adopted here is that of *crista interfenestralis*, consistently used to refer to this process. The *crista interfenestralis* separates the *fenestra ovalis* from the metotic foramen. The metotic foramen corresponds to the embryonic metotic fissure that separates the otic placodes from the parachondral bars (Pradel et al., 2013). Cranial nerves IX–XI exit the embryonic neurocranium through the metotic fissure. The metotic foramen also provides a duct to dissipate excess energy
from the otic system and is connected medially with the fenestra ovalis (Figure 4.63). These terms can be consistently applied to sauropodomorphs across the tree. In Saturnalia, the fenestra ovalis is also connected to the metotic foramen ventrally through an unossified gap. The crista interfenestralis is identified due to the presence of a stapedial groove, where the stapes rests and fits into the fenestra ovalis. The fenestra ovalis is dorsally delimited by the otoccipital, and ventrally defined by the basioccipital (Figure 4.64). In Adeopapposaurus, the crista interfenestralis is hook-shaped and contacts the parabasisphenoid and the basioccipital. The anterior foramen is the fenestra ovalis, and posteriorly the metotic foramen (Figure 4.64).

Figure 4.63. Schematic diagram of the organisation of the inner ear in archosaurs showing its interaction between the braincase, dermocranium, and mandible. This schematic representation modified from Kardong (2012) was used as a guide for the terminology applied to sauropodomorphs along with the revision and comparative study in Paulina Carabajal (2015).
Figure 4.64 Osteology of the braincase in three sauropodomorphs. Top, the basal sauropodomorph *Saturnalia tupiniquim*, based on MCP 3845 PV, middle, the massospondylid *Adeopapposaurus mognai*, based on PVSJ568, and the bottom, the basal sauropod *Shunosaurus lii*, based on ZG65430. For the following characters, the braincase orientation is standardised by placing the basioccipital and the parabasisphenoid rostrum on horizontal planes. Abbreviations: atr – anterior tympanic recess, cif – crista interfenestralis, ea – ethmoidal artery, fo – fenestra ovalis, mf – metotic foramen, ns – nuchal crest, tr – posterior tympanic recess, III - foramen for oculomotor nerve, IV - foramen for trochlear nerve, V – foramen for trigeminal nerve, V1 – foramen for ophthalmic branch of the trigeminal nerve, vcm – vena capitis medium. Not to scale.
In some basal sauropodomorphs, the metotic foramen is divided into two foramina, and anterior one through which the *scala tympani* dissipates the excess energy and where the paralymphatic duct communicates with the Eustachian tube, and the posterior foramina, through which cranial nerves IX—XI exit the endocranial cavity. The anterior foramen is consistently described as the *fenestra pseudorotunda* in archosaurs. The posterior foramen through which the blood vessels pierce the lateral surface of the otoccipital and is consistently referred to as the vagal foramen. These two foramina are separated by the crista metotica. In *Efraasia* and *Plateosaurus engelhardtii*, the metotic foramen is divided into a fenestra pseudorotunda and a vagal foramen. In the former, the crista metotica and the *crista interfenestralis* are orientated perpendicularly, whereas in the latter the two processes are parallel. In *Asylosaurus yalensis*, a braincase previously referred to *Thecodontosaurus* but later reassigned to its own genus (Galton, 2007), the metotic foramen is large and anteroposteriorly narrow, but there is no metotic foramen dividing it. In *Massospondylus carinatus*, the metotic foramen is also undivided, a condition consistently identified in *Adeopapposaurus* and *Saturnalia*. In *Melanorosaurus*, a crista metotica is absent but two foramina can be seen in the bottom of the metotic foramen. The dorsal foramen has been hypothesised to correspond to the exit of the CN IX–XI and a ventral foramen that corresponds to the exit of the jugular artery. The term *foramen jugularis* has also been assigned to the vagal foramen, but here these two terms are describing distinctive conditions. The vagal foramen is delimited by a *crista metotica*, whereas the *foramen jugularis* is present inside the metotic foramen, and thus represents the absence of a *crista metotica*. 
Figure 4.65 Comparative anatomy of the braincases of five non-sauropod sauropodomorphs. This plate emphasises the changes in the morphology of the foramina. The first four are traditionally referred as ‘prosauropods’, shown here in lateral view: that at the bottom is Melanorosaurus readi in occipital view. Efraasia based on the CT-scans in Bronzati (2017); Asylosaurus based on diagrams in Fedak and Galton (2007) and pictures in Bronzati (2017); Massospondylus based on Chapelle and Choiniere (2018), Plateosaurus based on Prieto-Márquez and Norell (2011), in lateral view; Melanorosaurus based on Yates (2007a) in posterolateral view. Not to scale.
4.1.3.6.1 Occiput-otic region

BC 1. A185-1. Braincase, basal tuberae, position relative to the base of the basiptyerygoid process in lateral view: above the level of the base of the basiptyerygoid process(0), below the level of the base of the basiptyerygoid process (1) (Galton, 1985a; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

BC 2. A185-2. Braincase, basal tuberae, position relative to the anteriormost point of the parabasisphenoid in lateral view: below the level of the the anteriormost point of the parabasisphenoid (0), above the level of the anteriormost point of the
parabasisphenoid (1). (Galton, 1985a; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

**Comment:** C81 Y2007 was originally formulated as a multistate character describing the shape of the braincase floor. First this character required a braincase to be complete, and in the case of *Spinophorosaurus* this character leads to a polymorphism to exclude character state (0). Therefore, the character has been reformulated as two independent character statements, assessing the position of the basipterygoid processes relative to the basioccipital and the parabasisphenoid process. This also removes the uncertainty when the three of them are ‘roughly aligned’. In the case of *Spinophorosaurus*, the basipterygoid processes are posterovertrally displaced relative to the basioccipital, scored for character BC 1 as (1), whilst the absence of the parabasisphenoid would not let us know the level of the parabasisphenoid was similar to the level of the basioccipital, but clearly the basipterygoid process are below the parabasisphenoid level, scoring character BC2 as (1). A recent CT scan analysis of *Sarahsaurus* also describes a ‘roughly aligned’ braincase floor, instead of the original score that indicated a basioccipital condyle more dorsally displaced relative to the basipterygoid processes and the parabasisphenoid process (Marsh and Rowe, 2018).


**Comment:** In *Herrerasaurus* this feature is present between the paraoccipital process and the parietal. The terms post-temporal fenestra and post-temporal foramen have been used for the same opening depending on the size, but the distinction of when a foramen becomes a fenestra is not assessed. Here the term post-temporal foramen is chosen.
4.1.3.6.2 Supraoccipital

SO1.  A161. Supraoccipital, shape in occipital view: diamond-shaped (0), semilunate (1) (Yates, 2003b, 2007b, 2007a; Yates and Kitching, 2003; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

A162. Supraoccipital, proportions transversal width relative to its height (Baron et al., 2017a; Figures 4.64, 4.65 and 4.66).

SO2.  A164. Supraoccipital, orientation: its anterior tip lies posterior to the posterior margin of the basiptyerygoid processes (0), its anterior tip lies anterior to the posterior margin basiptyerygoid processes (1) (Galton, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

SO3.  B94. Supraoccipital, extension onto the foramen magnum: excluded from dorsal border of foramen magnum by mediodorsal midline contact between opposite exoccipitals (0), contributes to border of foramen magnum (1) (Gower and Walker, 2002; Nesbitt, 2011; Baron et al., 2017a; Figures 4.64, 4.65 and 4.66).

SO4.  B95. Supraoccipital, rugose ridge on the anterolateral edges: absent (0), present (1) (Nesbitt, 2011; Baron et al., 2017a; Figures 4.64, 4.65 and 4.66).

4.1.3.6.3 Otoccipital

OTO1.  A165. Otoccipital: meeting along the midline on the floor of the endocranial cavity (0), separated by basioccipital (1) (Gower and Sennikov, 1996; Nesbitt, 2011; Figures 4.64, 4.65 and 4.66).

OTO2.  A167-A170. Paroccipital processes in occipital view, the orientation of long axis relative to the horizontal: directed laterally (0), dorsolaterally (1), ventrolaterally (2) (Rauhut, 2003a; Yates, 2007b; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

OTO3.  B87. Paraoccipital process: expanded distally (0), distal end pendent (1) (modified from Rauhut, 2003a; Ezcurra, 2010; Nesbitt, 2011; Baron et al., 2017 Figures 4.64, 4.65 and 4.66).
OTO4. A168. Otoccipital, posteroventral process forming lateral margin of basal tubera: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).

OTO5. D92-1. Otoccipital, crista interfenestralis dividing the metotic foramen: absent (0), present (1) NEW (Figures 4.64, 4.65 and 4.66).

OTO6. D89-2. Otoccipital, crista interfenestralis, extension: expansion from the basal tuber to the ventral surface of the paraoccipital process (0), unossified gap between the crista interfenestralis and the parabasisphenoid (1) (Gower, 2002; Nesbitt, 2011; Baron et al., 2017a; Figures 4.64, 4.65 and 4.66).

OTO7. A166. Otoccipital, exits of the hypoglossal nerve (XII), relative positions: aligned in an anteroposterior plane (0), aligned in a dorsoventral plane (1) (Nesbitt, 2011; Figures 4.64, 4.65 and 4.66).

OTO8. D93. Otoccipital, crista metotica: absent (0), present (1) NEW (Figures 4.64, 4.65 and 4.66).

OTO9. A159. Otoccipital, post-temporal foramen on occiput, position: between the parietal, the supraoccipital and the otoccipital (0), fully enclosed by the supraoccipital (1), totally enclosed within the paraoccipital process (2) (Benton et al., 2000; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

4.1.3.6.4 Prootic

POT1. A172-1. Prootic: single foramen for trigeminal nerve (0), separate maxillomandibular (V2-3) and ophthalmic foramina (V1) (1).

**Comment:** The exit of the trigeminal nerve (V) through the prootic has two morphologies in specimens referred to *Massospondylus*: BP/1/5276 has two foramina, whereas BP/1/5231 and BP/1/5241 have only one. BP/1/4934 is disarticulated and incomplete and this character is not unequivocally assessed, and BP/1/5276 was not included as part of the ontogenetic sequence in Neenan et al. (2018), but BP/1/5231 is. For this character, *M. carinatus* is scored based on the specimens described in Neenan et al. (2018), and BP/1/5231 is considered as a separate OTU.

4.1.3.6.5 Basioccipital

BO1. A183/A184. Basioccipital, basal tubera, ossification of the extremities: complete so that the basioccipital and the parabasisphenoid form a single rugose
tuber (0), unossified with the basioccipital forming a transverse ridge (1) (Yates, 2003b; Yates and Kitching, 2003; Upchurch et al., 2007a; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.66).

**Comment:** This character had an alternative formulation that specified character state (0) as ‘knob-like’, and character state (1) as ‘a transverse ridge’. These morphologies seem to be a product of the degree of ossification since there is a correlation in the scores for the two characters.

**BO2.** D183-1. Basioccipital, basal tubera: visible in anterior view of the braincase (0), not visible in anterior view of the braincase (1) NEW (Figures 4.64, 4.65 and 4.66).

**BO3.** D183-2. Basioccipital, basal tubera, morphology in posterior view: club-shaped (0), knob-shaped, so that there are a spherical and a stalk component (1) NEW (Figures 4.64, 4.65 and 4.66).

**BO4.** D183-3. Basioccipital, basal tubera, divergence of the columnar basal tubera: parallel (0), divergent (1) NEW (Figures 4.64, 4.65 and 4.66).

**Comment:** Characters BO2, BO3 and BO4 are derivations from character 82 in mY2007 to capture all the variable aspects of the basal tubera. The different morphologies of the basal tubera correlates with variation at the level of neck musculature, such as the *m. rectus capitis ventralis*, which attaches to these processes in birds (Snively and Russell, 2007).

### 4.1.3.7 Sphenoid region

#### 4.1.3.7.1 Parabasisphenoid

**PB1.** A175. Parabasisphenoid, anterior part, depth relative to its transverse width (Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013; Figures 4.64, 4.65 and 4.68).

**PB2.** D175. Parabasisphenoid, anteroposterior length relative to the anteroposterior length of the basioccipital (Bronzati and Rauhut, 2017).

**Comment:** This character reflects variation in the relative size of the parabasisphenoid, and captures the difference between neosauropods and *Spinophorosaurus*, and non-sauropod sauropodomorphs. PB2 reflects a trend in the reduction of the cultriform process, with the concomitant reduction of the palate.

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PB3. B105. Parabasisphenoid, space between basal tubera and basipterygoid processes, transverse length relative to its width (Rauhut, 2003a; Nesbitt, 2007, 2011; Baron et al., 2017a; Figures 4.64, 4.65 and 4.68).

PB4. A178. Parabasisphenoid, contact with the basioccipital: straight line contact (0), concave, opening posteriorly (Rauhut, 2003a; Nesbitt, 2011; Baron et al., 2017a; Figures 4.64, 4.65, 4.68 and 4.67).

Comment: This character refers to the morphology at the ‘junction of the parabasisphenoid and basioccipital’, distinguishing between the morphologies ‘ridge with a smooth anterior face’, and ‘ridge a median fossa on the anterior face’. The junction of these bones occurs in the parabasisphenoid recess and it is confused whether this character statement refers to the articulation or to the recess. In sauropods, the two bones meet at a straight line, while in Plateosaurus and Efraasia, they intersect in curved line with a posterior concavity. Character PB4 thus replaces C84 in mY2007. This operationalisation is similar to the one performed by Bronzati and Rauhut (2017), but character state (1) is therein defined as ‘U/V-shaped’.

Figure 4.67. Braincase characters in Yates (2004). The character list in Yates (2004) is an immediate precursor to the character list in Yates (2007a,b). This is the only source of illustrated characters from the author. C44 Y2004 and C45 Y2004 are the only illustrated braincase characters. The delineation uses ‘sauropods’ and Anchisaurus as limits for primitive and derived characters. Here they are reassessed for Anchisaurus (my photograph) and correspond to characters BO1 (=C45 Y2004) and PB4 (=C44 Y2004).
PB1. A174/A176/A177. Parabasisphenoid, basisphenoid recess in ventral view: divided by a ridge through the midline (0), undivided (1) (Forster, 1999; Sereno, 1999a; Martínez et al., 2011) (Forster, 1999, Sereno, 1999,C30 M2011; Figures 4.64, 4.65 and 4.68).

Comment: Other names for this structure are median pharyngeal, hemispherical sulcus and hemispherical fontanelle.

PB2. D181.2 Parabasisphenoid, subsellar recess: absent (0), present (1) NEW (Figures 4.64, 4.65 and 4.68)

PB3. A181/B100. Parabasisphenoid, basisphenoid recess, development: the recess does not reach the posterior margin of the subsellar recess and creates a wide space between both recesses (0), the recess reaches the posterior wall of the subsellar recess (1) (Galton, 1985a, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a, 2007b; Pol et al., 2011; Sekiya et al., 2013; Baron et al., 2017a; Figures 4.64, 4.65 and 4.68).

Comment: These two characters come from C85 mY2007, defined based on the presence of a deep septum between the interbasipterygoid space. As discussed in Bronzati and Rauhut (2017), this character refers to the relative positions of the subsellar recess and the basisphenoid recess. The interbasipterygoid septum is produced when the posterior wall of the subsellar recess is the same strut that delineates the anterior wall of the basisphenoid recess. The septum will be deep or shallow depending on the concavities of both recesses. The interbasipterygoid septum is, therefore, conditioned to deep recesses and close to each other sharing the same wall. In Bronzati and Rauhut (2017), this character was reformulated as a categorised character, as a ration between the maximum width of the subsellar recess and the maximum dorsoventral height. The limit between the two states is arbitrary, and to categorise this character via gap-coding the metrics of these distances need to be taken. These measurements were not provided in the original publication and based on first hand-assessments, the size of these structures is on the limits of the instrument error. Instead, two new characters are proposed here: PB2 and PB3. PB2 assesses the presence of the subsellar recess, and PB3 assesses whether the two recesses share the same strut of bone as their posterior and anterior walls respectively. This is closer to the original
formulation of an interbasipterygoid septum, but also reduces the conflict on how big a strut needs to be.

PB4. D181. Parabasisphenoid, subsellar recess: closed anteriorly, so that the lateral laminae converge in the ventral face of the cultriform process forming an anterior margin (0), open anteriorly, so that the lateral laminae reduce in size until they intersect the ventral face of the cultriform process (1) (modified from Bronzati and Rauhut, 2017; Figures 4.64, 4.65 and 4.68).

PB5. B101. Parabasisphenoid, foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the surface: ventral (0), lateral (1) (modified from Parrish, 1993; Gower and Sennikov, 1996; Gower, 2002; Nesbitt et al., 2009; Nesbitt, 2011; Baron et al., 2017; Figures 4.64, 4.65 and 4.68).

PB6. B102. Parabasisphenoid, laterally positioned foramina for entrance of cerebral branches of internal carotid artery into the braincase: located anteriorly (0), located posteriorly (1) (modified from Parrish, 1993; Gower and Sennikov, 1996; Gower, 2002; Nesbitt et al., 2009; Nesbitt, 2011; Baron et al., 2017; Figures 4.64, 4.65 and 4.68).

PB7. B104. Parabasisphenoid, anterior tympanic recess on the lateral side of the braincase: absent (0), present (1) (Rauhut, 2003a; Nesbitt, 2011; Baron et al., 2017a; Figures 4.64, 4.65 and 4.68).

4.1.3.7.2 Laterosphenoid

LA1. A173. Laterosphenoid, connection: frontal and postorbital (0), postorbital only (1) NEW (Figures 4.64 and 4.68).

LA2. D172. Laterosphenoid, foramen for the maxillomandibular branches of the trigeminal nerves (V2,3): absent (0), present (1) NEW.

LA3. D174. Laterosphenoid, contribution to the trigeminal nerve foramen (V): present (0), absent (1) NEW (Figures 4.64 and 4.68).

LA4. D173. Laterosphenoid, exit foramen of trigeminal nerve (V), forming anterodorsal margin (0), forming only the dorsal margin of the foramen (1) NEW (Figures 4.64 and 4.68).
Figure 4.68. More detailed anatomy of the braincase of two sauropodomorphs at the base of the tree. Top and middle, braincase of *Efraasia* in left lateral and ventral view, based on Bronzati and Rauhut (2017), and bottom, braincase of *Asylosaurus*, previously referred to *Thecodontosaurus*, based on Fedak and Galton (2007).
4.1.4 Mandibular series

Several terms for the mandible correspond to morpho-functional concepts that do not have a one-to-one correspondence with its individual bones. The retroarticular process projects behind the craniomandibular articulation and can be composed of any combination of the articular, angular and surangular. The coronoid eminence is a dorsal process of the mandible that may be formed by a separate coronoid bone or as a process of the dentary and surangular. The Meckelian groove is a canal that runs through the ventromedial side of the mandible and extends through the splenial and the dentary (Figure 4.69).

Figure 4.69. Anatomical regions of the mandible that do not have a one-to-one correspondence with individual bones. Right mandible of *Plateosaurus engelhardti* in lateral (top) and medial (bottom) views, based on (Prieto-Márquez and Norell, 2011).

Several continuous characters have been proposed as phylogenetically important. Within sauropodomorphs, a PCA of the six continuous characters showed that the variation spans through all the quadrants, and three characters are responsible for nearly 90% of the variance in the sample. A correlation analysis indicates that within the mandible, these six characters do not show a lot of correlation between them, with only one character positively or negatively correlating with three of them (Figure 4.70). This result is consistent with the PCA, where character MA5 possesses the second loading in all the principal components (Figure 4.71). These results highlight the important role of mandibular continuous characters in capturing variation within sauropodomorph dinosaurs. Some sauropodomorphs show mandibular morphometrics similar to theropod morphology (e.g. *Eoraptor, Buriolestes, Sarahsaurus, Arcusaurus, Anchisaurus, Coloradisaurus* and *Plateosaurus*), and a few others seem to be similar to ornithischian morphologies (e.g.
Adeopapposaurus and Lamplughsauroidea. Tazoudasaurus and Jingshanosaurus have morphometrics similar to Shunosaurus and Camarasaurus, respectively. The rest of the sauropodomorphs in the sample occupy their own space, but this is likely an artefact from the limited sampling of theropods and ornithischians. There are three outliers, Leyesaurus, Pampadromaeus and Efraasia, which are separated from the rest of the dinosaurs sampled herein.

Figure 4.70. Correlation map between the assessed continuous mandibular characters. The only character that shows statistical significance in the covariation with other characters is character ‘A202. Mandible, mandibular fenestra, anteroposterior diameter relative to the maximum depth of dentary ramus (Sereno, 1999a; Martínez et al., 2011)’.
Figure 4.71. Biplot of the principal component analysis of the mandibular continuous characters. The largest load of variance is on character A202 and character A225 (MA9). Closed circles represent sauropodomorphs, open circles represent basal ornithischians, open squares represent basal theropods, crosses represent silesaurids, and the rhomboid represents Euparkeria. Although limited samples for non-sauropodomorphs, other groups seem to be confined to morphospaces, whereas sauropodomorphs have a morphospace overlapping with all of the others. This provides evidence that sauropodomorphs were experiencing with different feeding habits that converge with strategies of theropods and ornithischians. These results coincide with those published recently in Muller and Garcia (2019).

MA1. A199. Mandible, outline in dorsal view: the mandibular projections meet each other at an acute angle (0), the anterior ends of the dentaries curve towards each other (1) (Upchurch, 1998; Upchurch et al., 2007a; Sekiya et al., 2013).

MA2. B133. Mandible, maximum depth relative to the dorsoventral height beneath the posteriormost part of the dentary tooth row (modified from Sereno, 1999a; Butler, 2005; Irmis et al., 2007; Butler et al., 2008a; Nesbitt, 2011; Baron et al., 2017; Figure 4.72).
Figure 4.72. Gap-coding of character MA2. Gap-coding identifies three character states: <0.064) (0), [0.64,2.12) (1); [2.12, ∞) (2). The original coding set a limit of less than or equal to 1.5 (character state 0) and more than 1.5 (1), which corresponds with the average in this sample.

MA3. A200. Mandible, mandibular fenestra: present (0), absent (1) (Upchurch, 1998; Upchurch et al., 2007a; Sekiya et al., 2013).

MA4. A201. Mandible, mandibular fenestra, anteroposterior length relative to the length of the mandible (Upchurch, 1995; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Sekiya et al., 2013).
Figure 4.73. Gap-coding of character MA4. Gap-coding identifies three character states: \(<0.009\) (0), \([0.009, 0.3]\) (1); \([0.3, \infty]\) (2). The original coding set a limit of less than or equal to 0.05 (character state 0) and more than 0.05 (1), and the average for this sample is 0.145. The original coding and gap-coding improve entropy in a similar way.

MA5. A203. Mandible, intramandibular joint: absent (0), present (1) (Sereno and Novas, 1992; Sereno, 1999a; Yates, 2007a; Sekiya et al., 2013).

**Comment:** This character is explained in Sereno and Novas (1992) as a sliding joint between the splenial and the concave portion of the dentary. It has been identified for theropods and *Herrerasaurus* as prominent ventral projections of the dentary. This joint allows the anterior tooth-bearing part of the mandible to rotate approximately 15° against the posterior tooth-less part.

MA6. A204. Mandible, splenial-angular contact, polarity of articulation: (0) splenial convex, angular concave (0), splenial concave, angular convex (1) (Sereno and Novas, 1992; Sereno, 1999a; Yates, 2007a; Sekiya et al., 2013).

MA7. A205. Mandible, craniomandibular joint, position: with the level of the dorsal margin of the dentary (0), below the level of the dorsal margin of the dentary
(1) (Galton, 1976, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figure 4.74).

Comment: This has been scored as a polymorphism in *Mussaurus*, but the description of the skull in Pol and Powell (2007) shows that this craniomandibular joint is well below the dorsal margin of the dentary.

MA8. D225-2. Mandible, retroarticular process, composition: surangular with an angular portion (0), surangular with an articular portion (1), comprised entirely by the surangular (2) NEW (Figure 4.74).

MA9. A225. Surangular-articular, retroarticular process, length relative the depth of the mandible below the glenoid (Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Figure 4.74).

Figure 4.74. Mandibular characters of *Plateosaurus engelhardti*. Right mandible of *Plateosaurus engelhardti* in lateral (top) and medial (bottom) views, based on (Prieto-Márquez and Norell, 2011).
4.1.4.1 Dentary

D1.A5. Dentary, lateral plates appressed to the labial side: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b; Pol et al., 2011; Sekiya et al., 2013; Figure 4.15).

D2.A207. Dentary, maximum height in the posterior half, relative to the maximum anteroposterior length of the dentary (Sereno, 1999a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a, 2007b; Pol et al., 2011; Sekiya et al., 2013).

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Figure 4.75. Gap-coding of character D2. Gap-coding identifies three character states: <0.04) (0), [0.04,1) (1); [1, ∞) (2). The original coding set a limit of less than or equal to 0.05 (character state 0) and more than 0.05(1), and the average for this sample is 0.145. The original coding was established as “more (0) or subequal to (1)” and was interpreted here as a ratio of 1.0. This corresponds to the average for the sample assessed here. Gap-coding captures the variation for D2 in a more efficient way.
D3.B129. Dentary, tooth row (and edentulous anterior portion) in lateral view: straight (0), anterior end downturned (1), anterior end upturned (dentary ventrally bowed) (2) (Butler et al., 2008b; Nesbitt, 2011; Baron et al., 2017a; Figures 4.76 and 4.77).

D4.B127. Dentary, anterior half, position of the Meckelian groove: dorsoventral centre of the dentary (0), restricted to the ventral border (1) (Nesbitt, 2011; Baron et al., 2017a; Figure 4.74).

D5.A208. Dentary, symphysis: restricted to the anterior margin of the dentary (0), expanded along the ventral border of the bone (1) (Sereno, 1999a; Pol et al., 2011).

D6.A209. Dentary, symphysis, form: dentary bodies are convergent to a point (0), dentary bodies are parallel to each other (1) (Sereno, 1999a; Martínez et al., 2011).

D7.A210. Dentary, symphysial end, orientation of ventral margin in lateral view: in line with the long axis of the dentary (0), displaced ventrally (1) (Sereno, 1999a; Yates and Kitching, 2003; Yates, 2007a; Sekiya et al., 2013).

Comment: This character refers to the endpoint of the dentaries, but it is not clear where this point is. Here it is defined as the point at the middle dorsoventral height of the symphysial end. In Plateosaurus engelhardti, Adeopapposaurus, Aardonyx, Unaysaurus and Coloradisaurus the anterior-most end is ventrally displaced creating a downturned mandible. This character is partly correlated with D3 in that a ventrally displaced end point relative to the long dentary axis produces a downturned dentary tooth row. However, when the endpoint is ventrally displaced, the dentary tooth row can remain straight if the symphysial end is ventrally expanded, as it is the case in Riojasaurus, and Omeisaurus.

D8.A213/A218. Dentary, posterior end, buccal emargination on the lateral surface (tooth row medially inset with a thick lateral ridge on the dentary, possibly associated with a fleshy cheek in life): absent (0), present (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Yates, 2007a; Sekiya et al., 2013).

Comment: There is a polymorphism in Thecodontosaurus reported for C74 Upchurch et al. (2007) and C133 Sekiya et al. (2013), but this refers to Pantydraco.

D9.A216. Dentary, coronoid eminence: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).

D10. A217. Dentary, coronoid eminence, length relative to depth of the dentary at mid-length (Sereno, 1999a; Martínez et al., 2011).
B128. Dentary, Meckelian groove: ends before the dentary symphysis (0), opens through the dentary symphysis (1) (Nesbitt, 2011; Baron et al., 2017a).

Figure 4.76. Mandibular characters illustrated in lateral view on the skull of basal saurischians. A) Skull of *Herrerasaurus* based on PVSJ 407 and Sereno and Novas (1993); B) Skull of *Eoraptor* based on PVSJ 512 according to Sereno et al. (2012); C) Skull of *Coelophysis* based on the illustration on Colbert (1981). Not to scale.
Figure 4.77. Mandibular characters illustrated in lateral view on the skull of sauropod-line sauropodomorphs. A) Skull of *Melanorosaurus* based on NM QR3314 and Yates (2007); B) Skull of *Shunosaurus* based on Zheng (1996); C) Skull of *Camarasaurus* based on Zheng (1996). Not to scale.
4.1.4.2 **Splenial**

SP1. A219(A220). Splenial, ventral margin, mylohyoid foramen: absent (0), present (1) (Rauhut, 2003a; Yates, 2007b; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013; Figures 4.77 and 4.78).

**Comment:** In Pol et al. (2011) character state 0 is applied only to *Heterodontosaurus*.

SP2. A221. Splenial, mylohyoid foramen: enclosed (0), open anteriorly (1) (Rauhut, 2003a; Yates, 2007b; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013; Figures 4.77 and 4.78).

![Figure 4.78. Mylohyoid foramen in the left splenial of two theropods. A) Majungatholus, scale bar 50 mm. B) Saurornitholestes, scale bar 100mm.](image)

4.1.4.3 **Surangular**

SA1. A225. Surangular-articular, retroarticular process, length relative the depth of the mandible below the glenoid fossa (Gauffre, 1996; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

SA2. A226. Surangular-articular, retroarticular process, shape: terminates blunt in lateral and dorsal views (0), terminates in a vertex, with a posterior tapering in lateral and dorsal views (1) (Yates, 2003a; Pol et al., 2011)

SA3. A227. Surangular-articular, retroarticular process, orientation: forms nearly a right angle with the rest of the mandible (0), retroarticular is upturned at its distal end (1), retroarticular extends straight out from the caudal part of the mandible (2) (Baron et al., 2017a).
SA4. A223-1. Surangular, anterior surangular foramen: present (0), absent (1) (Baron et al., 2017a).
SA5. A223-2. Surangular, posterior surangular foramen: present (0), absent (1) (Baron et al., 2017a).

Comment: The anterior and the posterior foramina of the surangular are not always both present. The anterior foramen is positioned on the dorsal surface of the surangular, anterior to the maximum mandibular depth. The posterior foramen is on the lateral surface, posterior to the maximum mandibular depth.

4.1.4.4 Articular

AR1. A224. Articular, stout, triangular, medial process of the articular, behind the glenoid: present (0), absent (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).
AR2. A228. Articular, strong medial embayment behind glenoid of the articular in dorsal view: absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

4.1.5 Dentition

Dental characters often describe variation in the dentition as homogenous, so that the character statements are applied to all the teeth. This variation was explored further, and a certain degree of heterodonty was found in some dinosaurs. This trend is also seen in basal sauropodomorphs, who experienced a change from an ancestrally carnivorous diet, to a non-specialised omnivorous diet, to a derived specialised herbivore diet, to a more reduced masticatory system.

According to McPhee et al. (2014), all the mandibular and dental characters proposed by Yates et al. (2010) given to Aardonyx were rescored as unknown as the referral of the material is based on stratigraphy and not on overlapping of diagnostic features. This is the case for many more sauropodomorphs, such as Pulanesaura (McPhee and Choiniere, 2017) and Barapasaurus (Bandyopadhyay et al., 2010). The atomisation of dental characters here comes to ensure that the information of teeth morphology is captured in detail and determine patterns of covariation. For instance, several characters were split in mesial and distal views in the cases where the information is only specified for one view, or when it is
not clear if the teeth are symmetrical or not. Thus, this section on dental characters is preliminary.

DEN1. A237. Teeth, tooth crowns in the anterior quarter of the tooth bearing areas of the upper and lower jaws relative to the heights of the crowns in the more posterior teeth (Wilson, 2002; Remes et al., 2009; Pol et al., 2011).

DEN2. A247. Teeth, occlusal wear facets: absent (0), present (1) (Gauthier, 1986; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

DEN3. A244. Teeth, lingual concavities: absent (0), present (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

DEN4. A248. Teeth, enamel surface, texture (at naked eye): smooth (0), coarsely wrinkled (1) (Benton et al., 2000; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011).

Comment: Anchisaurus was scored as polymorphic in C117 Y2007, because the enamel texture is reported to have wrinkles when observed to the microscope compared to Thecodontosaurus (Yates, 2004). The teeth of Anchisaurus do not look wrinkled with the naked eye, in contrast to what has been reported in, for instance, Pulanesaura (McPhee et al., 2015b). This character has been reformulated to be assessed without a microscope, as a well-developed wrinkling of the enamel. This character is scored (1) in the basal sauropodomorphs Pulanesaura, Chinshakiangosaurus, and Tazoudasaurus.

DEN5. A264/B181. Pterygoid teeth: present (0), absent (1) (Juul, 1994; Gower and Sennikov, 1996; Sereno, 1999a; Nesbitt et al., 2009; Martínez et al., 2011; Nesbitt, 2011; Baron et al., 2017a)

Comment: Pterygoid teeth develop on the palatal process of the pterygoid.

4.1.5.1 Premaxillary teeth

PMXT1. A249. Premaxillary teeth, number (Galton, 1985b; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).
Comment: Yates et al. (2010) scored this character for *Coloradisaurus* as ‘(0) four premaxillary teeth’, but then rescored by Apaldetti et al. (2013) as ‘unknown’. The last one is updated here.

PMXT2. A250. Premaxillary tooth 1, position: adjacent to midline (0), inset posteriorly the width of one or more crowns (1) (Sereno, 1999a; Martínez et al., 2011).

PMXT3. A251. Premaxillary teeth, position of posteriormost tooth relative to external naris: ventral (0), anterior (1) (Sereno, 1999a; Martínez et al., 2011).

4.1.5.2 Maxillary teeth

MXT1. A259. Maxillary teeth, position of largest tooth in tooth row: anterior half (0), posterior half (1) (Sereno, 1999a; Martínez et al., 2011).

A230. Maxillary teeth, crown, alignment: linearly placed so they do not overlap in lateral view (0), angled relative to the long-axis of the jaw so tooth crowns appear to overlap in lateral view (imbricated, each tooth has its mesial margin lying lingual to the distal margin of the crown immediately in front) (1) (Galton, 1985b, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: Yates et al. (2010) scored this character as ‘imbricated’ for *Coloradisaurus* but rescored as ‘linearly placed’ by Apaldetti et al. (2013). The same condition is applied in the original formulation of the character to the dentary teeth.

MXT2. A232/B176. Maxillary teeth, tooth crowns, contact with adjacent teeth: absent (0), present (1) (Wilson and Sereno, 1998; Upchurch et al., 2007a; Sekiya et al., 2013).

MXT3. A241-1. Maxillary teeth, tooth crowns, serrations in mesial margin: absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Pol et al., 2011).

Comment: Apaldetti et al. (2013) describes a level of variation along the teeth in the maxilla and the dentary. One of the posterior maxillary teeth has broad, rounded denticles restricted to the apical third of the mesial and distal margins.

MXT5. A258/B169. Maxillary teeth, tooth crowns, marginal ornamentation, form: serrations (0), denticles (1) (Juul, 1994; Sereno, 1999a; Irmis et al., 2007; Butler et al., 2008b; Martínez et al., 2011; Nesbitt, 2011; Baron et al., 2017a).

MXT6. A233/A241. Maxillary teeth, tooth crowns, mesial serrations: project perpendicular to the long axis of the crown (0), project at 45 degrees to the crown long axis (1) (Galton, 1984, 1985b, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MXT7. A234/A241. Maxillary teeth, tooth crowns, distal serrations: project perpendicular to the long axis of the crown (0), project at 45° to the crown long axis (1) (Galton, 1984, 1985b, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MXT8. A235. Maxillary teeth, tooth crown, curvature of lingual surfaces: convex mesiodistally (0), concave mesiodistally (1) (Upchurch, 1995; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

MXT9. A238. Maxillary teeth, tooth crowns, maximum width of lanceolate tooth, position: located at the base of the crown, above the tooth-crown constriction (0), at the midpoint of crown’s height (1) (Pol et al., 2011).

MXT10. A239/B177. Maxillary teeth, tooth crowns, basal constriction: absent (0), present (1) (Gauthier, 1986; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: Dental characters can produce more polymorphisms than other character when there is any degree of heterodonty. In C112 U2007, Eoraptor has been scored as polymorphic. However, the maxillary teeth show basal constrictions along the maxilla. As for the dentary teeth, they are not visible.

MXT11. A253. Maxillary teeth, maxillary crowns, shape of conical teeth: posteriorly curved (0), not curved (1) (Yates, 2007a; Sekiya et al., 2013).

MXT12. A255. Maxillary teeth, tooth crowns, labial surface: evenly convex (0), bearing low eminence (1) (Langer, 2004; Pol et al., 2011).

MXT13. A256. Maxillary teeth, tooth crowns, lingual surface: evenly convex (0), bearing low eminence (1) (Langer, 2004; Pol et al., 2011).

MXT14. A257/A231. Maxillary teeth, tooth crowns, shape: recurved (0), subtriangular (1), lanceolate (2) (Sereno, 1999a; Martínez et al., 2011).
Comment: There are several characters referring to the morphology of the teeth. C116 Y2007 indicated a polymorphism for *Leyesaurus* and *Adeopapposaurus*. C116 included all teeth in the assessment. *Leyesaurus* exhibits a certain level of heterodony: the premaxillary teeth are recurved, the maxillary teeth and the dentary teeth are triangular (Apaldetti et al., 2011). The same is truth in *Adeopapposaurus*, with an heterodony in the following pattern: lanceolate premaxillary teeth, triangular maxillary and dentary teeth, and the first two dentary crowns being recurved. This is reflected as a polymorphism in C155 Sekiya et al. (2013). Apaldetti et al. (2013) rescored *Coloradisaurus* as “lanceolate in at least the middle and posterior part of the tooth row,” however the maxillary teeth are preserved along the entire length of the maxilla and show a lanceolate morphology.

MXT15. B166. Maxillary teeth, cingulum: absent (0), present (1) (Butler et al., 2008b; Nesbitt, 2011; Baron et al., 2017a).

MXT16. A242-1. Maxillary teeth, serrations, distribution along the mesial carina of the tooth: extend along most of the length of the crown (0), restricted to the upper half of the crown (1) (Upchurch, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

Comment: Characters MXT17, MXT18, DT19 and DT20 were originally formulated as only one character. Apaldetti et al. (2013) rescored this character to (1) from the score given by Yates et al. (2010).

MXT17. A242-1. Maxillary teeth, serrations, distribution along the distal carina of the tooth: extend along most of the length of the crown (0), restricted to the upper half of the crown (1) (Upchurch, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MXT18. A245. Maxillary teeth, longitudinal distal labial grooves: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MXT19. A246. Maxillary teeth, longitudinal mesial labial grooves: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).
MXT20. A254/B175. Maxillary teeth, posterior maxillary teeth, posterior edge: concave (0), straight (1), convex (2) (Sues et al., 2003; Nesbitt, 2011; Baron et al., 2017a).

Figure 4.79 Morphometric data defined for teeth in four sauropodomorphs. (a), Adeopapposaurus PVSJ 568 (b), SAM-PK-K1314, referred to M. carinatus but excluded from this dataset (c), and Riojasaurus PVSJ 849 (d). Red lines represent the maximum mesiodistal length and labiolingual width at mid-height of the tooth. Taken from Apaldetti et al. (2011, fig. 5b).

4.1.5.3 Dentary teeth

DT1. A259. Dentary teeth, position of largest tooth in tooth row: anterior half (0), posterior half (1) (Sereno, 1999a; Martínez et al., 2011).

DT2. A260. Dentary teeth, number (Wilson and Sereno, 1998; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

DT3. A263/A215. Dentary teeth, dentary tooth 1, position: terminal (0), inset (1) (Sereno, 1989, 1999a; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

DT4. B147. Dentary teeth, distribution in the dentary: present in the entire length (0), present in the posterior half only (1) (Parrish, 1993; Irmis et al., 2007; Nesbitt, 2011; Baron et al., 2017a).

DT5. A230/262. Dentary teeth, crown, alignment: linearly placed so they do not overlap in lateral view (0), angled relative to the long-axis of the jaw so tooth
crowns appear to overlap in lateral view (imbricated, each tooth has its mesial margin lying lingual to the distal margin of the crown immediately in front) (1) (Galton, 1985b, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: Massospondylus is the only taxon scored as polymorphic. This work has restricted the definition of Massospondylus to specimen BP/1/46934, where all dentary teeth have an erect orientation.

DT6. A257/A231. Dentary teeth, tooth crowns, shape: recurved (0), subtriangular (1), lanceolate (2) (Sereno, 1999a; Martínez et al., 2011).

DT7. A232/B176. Dentary teeth, tooth crowns, contact with adjacent teeth: absent (0), present (1) (Wilson and Sereno, 1998; Upchurch et al., 2007a; Sekiya et al., 2013).

DT8. A233/A241. Dentary teeth, tooth crowns, mesial serrations: project perpendicular to the long axis of the crown (0), project at 45° to the crown long axis (1) (Galton, 1984, 1985b, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

DT9. A234/A241. Dentary teeth, tooth crowns, distal serrations: project perpendicular to the long axis of the crown (0), project at 45° to the crown long axis (1) (Galton, 1984, 1985b, 1990; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

DT10. A235. Dentary teeth, tooth crown, curvature of lingual surfaces: convex mesiodistally (0), concave mesiodistally (1) (Upchurch, 1995; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

DT11. A238. Dentary teeth, tooth crowns, maximum width of lanceolate tooth, position: located at the base of the crown, above the tooth-crown constriction (0), at the midpoint of crown’s height (1) (Pol et al., 2011).

DT12. A240/A236. Dentary teeth, tooth crowns, basal constriction: absent (0), present (1) (Gauthier, 1986; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

DT14. B166. Dentary teeth, cingulum: absent (0), present (1) (Butler et al., 2008b; Nesbitt, 2011; Baron et al., 2017a).

DT15. A258/B169. Dentary teeth, tooth crowns, marginal ornamentation, form: serrations (0), denticles (1) (Juul, 1994; Sereno, 1999a; Irmis et al., 2007; Butler et al., 2008b; Martínez et al., 2011; Nesbitt, 2011; Baron et al., 2017a).

DT16. B177. Dentary teeth, tooth crowns, basal constriction: absent (0), present (1) (Gauthier, 1986; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).


DT19. A243-1. Dentary teeth, serrations, distribution along the mesial carina of the tooth: extend along most of the length of the crown (0), restricted to the upper half of the crown (1) (Upchurch, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

DT20. A243-2. Dentary teeth, serrations, distribution along the distal carina of the tooth: extend along most of the length of the crown (0), restricted to the upper half of the crown (1) (Upchurch, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

DT21. A245. Dentary teeth, longitudinal distal labial grooves: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

DT22. A246. Dentary teeth, longitudinal distal labial grooves: absent (0), present (1) (Upchurch, 1995; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

DT23. A255. Dentary teeth, tooth crowns, labial surface: evenly convex (0), bearing low eminence (1) (Langer, 2004; Pol et al., 2011).


DT25. A258/B169. Dentary teeth, tooth crowns, marginal ornamentation, form: serrations (0), denticles (1) (Juul, 1994; Sereno, 1999a; Irmis et al., 2007; Butler et al., 2008b; Martínez et al., 2011; Nesbitt, 2011; Baron et al., 2017a).
4.2 Axial characters

The axial characters compiled in this work accumulate most of the changes and amendments done to the character list. Because most of the changes are the same throughout the characters, the characters are discussed here as an overview to avoid repetition. Continuous characters applied to several elements of the vertebral column pose a cumbersome problem for character coding, mostly because there are no clear landmark definitions that allow differentiating between the different regions in the vertebral column. Consider the following character: ‘C127 (Y2007) Anterior cervical vertebrae (CE3-5), centrum, length relative to that of the axis: less than or equal to 1.0 (0), more than 1.0 (1)’.

Several interpretations can be made for this character. One could be to consider the average length of three of the anterior vertebrae relative to the length of the axis. Under this scenario, three vertebrae with a length larger than the length of the axis can be scored as (1). Another possibility is to consider each relation individually and assess the length of every vertebra against the length of the axis and consider the possibility of having polymorphic conditions. By taking the average, there is a risk of hiding a phylogenetic signal where it could be the case of differential enlargement of the cervical vertebrae. Taking all the individual circumstances could bring noise to the analysis of the variation responds to ontogenetic factors or is strongly correlated between them.

4.2.1 Vertebral column

Ve1. A273. Cervical vertebrae, number: 9 (0), 10 (1), 11 (2), >12 (3) Ordered (Wilson and Sereno, 1998; Upchurch et al., 2007; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Table 4.1).

**Comment:** The cervical vertebrae are defined here as the vertebrae in which the ribs are oriented along the anteroposterior plane. The parapophyses remain in the centrum, restricted to the anteroventral corner. The number of cervicals in sauropodomorphs is variable, but the actual number is obscured for most taxa by different preservation status across the vertebral column. It seems that the minimum number of cervical vertebrae is nine in *Ammosaurus, Buriolestes* and *Lamplughsaurs*, whereas the maximum number for non-sauropod sauropodomorphs is found in *Adeopapposaurus*, with eleven.

Ve2. B273-2. Dorsal vertebrae, number: 15 (0), 14 (1), 13 (2), 12 (3), 11 (4) Ordered (McIntosh, 1990; Russell and Zheng, 1993; Table 4.2).
Comment: As discussed above for cervical vertebrae, the same is true along the rest of the vertebral column. It is commonly assumed that non-sauropod sauropodomorphs possess 15 dorsal vertebrae (Von Huene, 1926; Galton, 1973; Sereno et al., 2012), and in several taxa, such as in Buriolestes, the position of isolated vertebrae is based on this assumption. The dorsal vertebrae can be differentiated from the cervical vertebrae by the position of the parapophyses. In cervical vertebrae, the diapophysis is connected to the centrum via the anterior centrodiapophyseal lamina (acdl). As the parapophyses migrate towards the neurocentral junction, they contact the acdl, which then becomes the anterior paradiapophyseal lamina (apdl). Therefore, presence of an apdl is a diagnostic feature of dorsal vertebrae, a pattern also seen in early non-dinosaur dinosauromorphs such as Silesaurus and Marasuchus (Langer et al., 2013). The minimum number of dorsal vertebrae is found in Camarasaurus (11), with two dorsosacrals.

Ve3. DA417. Sacral vertebrae, number: 2 (0), 3 (1), 4 (2), 5 (3), 6 (4) Ordered (Salgado et al., 1997; Table 4.3).

Comment: The number of sacral vertebrae varies a lot across sauropodomorphs. Saturnalia, Efraasia and Pampadromaeus have the fewest number of sacrals (two primordial sacrals), whereas the largest number is found in Camarasaurus (six: three primordial sacrals, three dorsosacrals). Most of the basal sauropodomorphs have three, e.g. Adeopapposaurus, Euchennesaurus and Massospondylus, but several others have four, such as Leonerasaurus or Mussaurus. It has been suggested that the increase in the number of sacral vertebrae may have an ontogenetic effect, adding dorsosacrals with age, as in Camarasaurus (Tidwell et al., 2005) and Apatosaurus (Tschopp et al., 2015). There is not enough evidence to suggest this is the case in basal sauropodomorphs and the character is kept.


Comment: The anterior caudal vertebrae are defined as the caudal vertebrae that possess ribs; the middle caudals do not have ribs; the posterior caudal series lacks ribs, zygapophyses and neural spine; the distal caudals are those elements that lack any rib or neural arch. V4 correlates then with the character dealing with the disappearance of the transverse processes before or after caudal vertebra 16 (Wilson, 2002).
Ve5. D273-5. Middle caudal vertebrae, number: >16 (0), 14 (1), 13 (2), 12 (3), 11 (4), <10 (5).

Table 4.1. Completeness of the cervical series in sauropodomorphs. Symbology: A indicates that there was a complete articulated vertebral sequence, A' indicates that the series is articulated but the position is inferred, S indicates that the vertebra is disarticulated but the position can be confidently diagnosed, S' stands for a vertebra that is isolated and its position is inferred, S* stands for isolated vertebral fragments that can be assigned or inferred to a position, P refers to partial elements which position can be diagnosed, R refers to a vertebra whose morphology is inferred based on the ribs, I stands for vertebrae inferred by the scars on the ilium, NA indicates that there is evidence to conclude that the vertebrae in the row were not present, and ? stand for missing data.

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<tr>
<th>Taxa</th>
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### Table 4.1. Completeness of the cervical series in sauropodomorphs (cont’d).

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Table 4.2. Completeness of the dorsal series in sauropodomorphs. Symbology: A indicates that there was a complete articulated vertebral sequence, A’ indicates that the series is articulated but the position is inferred, S indicates that the vertebra is disarticulated but the position can be confidently diagnosed, S’ stands for a vertebra that is isolated and its position is inferred, S* stands for isolated vertebral fragments that can be assigned or inferred to a position, P refers to partial elements which position can be diagnosed, R refers to a vertebra whose morphology is inferred based on the ribs, ? is given when it is not clear that the diagnosis was made, NA indicates that there is evidence to conclude that the vertebrae in the row were not present, and ? stand for missing data.

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Symbology: A indicates that there was a complete articulated vertebral sequence, A’ indicates that the series is articulated but the position is inferred, S indicates that the vertebra is disarticulated but the position can be confidently diagnosed, S’ stands for a vertebra that is isolated and its position is inferred, S* stands for isolated vertebral fragments that can be assigned or inferred to a position, P refers to partial elements which position can be diagnosed, R refers to a vertebra whose morphology is inferred based on the ribs, I stands for vertebrae inferred by the scars on the ilium, ! is given when it is not clear that the diagnosis was made, NA indicates that there is evidence to conclude that the vertebrae in the row were not present, and ? stand for missing data. Abbreviations: DS – dorsosacral, S – primordial sacral, SC – Sacrocaudal.
Table 4.3. Completeness of the sacral series in archosaurs (cont’d).

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Symbology: See previous page.
Table 4.3. Completeness of the sacral series in archosaurs (cont’d)

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Symbology: See previous page.
Table 4.4. Completeness of the caudal series in sauropodomorphs (first 25). Symbology: A indicates that there was a complete articulated vertebral sequence, A’ indicates that the series is articulated but the position is inferred, S indicates that the vertebra is disarticulated but the position can be confidently diagnosed, S’ stands for a vertebra that is isolated and its position is inferred, S* stands for isolated vertebral fragments that can be assigned or inferred to a position, P refers to partial elements which position can be diagnosed, R refers to a vertebra whose morphology is inferred based on the ribs, ! is given when it is not clear that the diagnosis was made, NA indicates that there is evidence to conclude that the vertebrae in the row were not present, and ? stand for missing data.

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Table 4.4. Completeness of the caudal series in sauropodomorphs (first 25).

| Taxa             | Ca1 | Ca2 | Ca3 | Ca4 | Ca5 | Ca6 | Ca7 | Ca8 | Ca9 | Ca10 | Ca11 | Ca12 | Ca13 | Ca14 | Ca15 | Ca16 | Ca17 | Ca18 | Ca19 | Ca20 | Ca21 | Ca22 | Ca23 | Ca24 | Ca25 |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| G. sinensis      | S   | S   | S   | S   | S   | S   | S   | S   | S   | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    | S    |
| Ingavusaurus     | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Jinghsanosaurus  | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Lufengosaurus    | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| M. carinatus     | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Melanorosaurus   | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Mussaurus        | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Panphagaia       | ?   | S'  | S'  | ?   | ?   | S'  | S'  | S'  | S'  | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   | S'   |
| P. engelhardtii  | A   | A   | A   | A   | A   | A   | A   | A   | A   | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
Table 4.4. Completeness of the caudal series in sauropodomorphs (first 25) (cont’d).

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Table 4.4. Completeness of the caudal series in archosaurs (first 25) (cont’d).

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Table 4.5. Completeness of the caudal series in sauropodomorphs (last 25). Symbology: A indicates that there was a complete articulated vertebral sequence, A’ indicates that the series is articulated but the position is inferred, S indicates that the vertebra is disarticulated but the position can be confidently diagnosed, S’ stands for a vertebra that is isolated and its position is inferred.

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S’ stands for a vertebra that is isolated and its position is inferred.
Table 4.5. Completeness of the caudal series in sauropodomorphs (last 25).

| Taxa                | Ca26 | Ca27 | Ca28 | Ca29 | Ca30 | Ca31 | Ca32 | Ca33 | Ca34 | Ca35 | Ca36 | Ca37 | Ca38 | Ca39 | Ca40 | Ca41 | Ca42 | Ca43 | Ca44 | Ca45 | Ca46 | Ca47 | Ca48 | Ca49 | Ca50 |
|---------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Jing Shan Nomosaurus| A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Lufengosaurus       | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| M. carinatus        | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| Mussaurus           | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |
| P. engelhardti      | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    | A    |

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Table 4.5. Completeness of the caudal series in sauropodomorphs (last 25).

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4.2.2 Cervical vertebrae

4.2.2.1 Atlas

AT1. A311. Atlas, atlantal neurapophysis, shallow, dorsally facing fossa bordered by a dorsally everted lateral margin in dorsal view: absent (0), present (1) (Yates, 2003a, 2007a; Yates and Kitching, 2003; Upchurch et al., 2007; Pol et al., 2011; Figure 4.78).

Comment: Whereas Pantydraco does have this dorsally facing fossa (Yates, 2003a; Galton, 2007), it is absent in Thecodontosaurus.

AT2. A312. Atlas, atlantal intercentrum, length compared to that of the axial intercentrum (Yates, 2003b; Pol et al., 2011; Otero and Pol, 2013; Otero et al., 2015; Peyre de Fabrègues and Allain, 2016).

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Figure 4.78. Atlas-axis complex of Adeopapposaurus (top) based on Martínez (2009) and Herrerasaurus (bottom) based on Sereno and Novas (1993). Not to scale.
4.2.2.2 Axis

AX1. A313. Axial intercentrum, atlantal articulation facet, shape: saddle-shaped (0), concave with upturned lateral borders (1) (Yates, 2003b; Pol et al., 2011; Otero and Pol, 2013; Otero et al., 2015; Peyre de Fabrègues and Allain, 2016; Figure 4.78).

AX2. A319. Axis, maximum mediolateral width of axial intercentrum relative to that of the axial centrum: <1.0 (0), ≥ 1.0 (1) (Sereno, 1999a; Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013).

Comment: The sample size for this character is very low, and the limit set at 1.0 is kept here instead.

AX3. A320. Axis, centrum, dorsoventral height relative to its anteroposterior length: <1.0 (0), ≥ 1.0 (1) (Upchurch, 1995; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

AX4. A321. Axis, neural canal, maximum diameter relative to the maximum centrum diameter: <1.0 (0), ≥ 1.0 (1) (Sereno, 1999a; Martínez et al., 2011).
**Comment:** The original formulation compared the neural canal to a quarter of the centrum diameter, here the limit is set 1.0 because the sample size does not produce a significant gap-coding.

![Diagram](image)

**Figure 4.80.** Axis of several sauropodomorphs. Top, *Ruehleia*, based on MB RvL1 in anterior, left lateral and posterior views. Middle, *Yunnanosaurus youngi*, based on Lu et al. (2007) in anterior, left lateral, and posterior views. Bottom, *Tazoudasaurus*, based on Allain and Aquesbi (2008).

**AX5.** B187. Axis, dorsal margin of the neural spine: the anterior margin is at a lower level than the posterior margin (0), anterior and posterior margins are at the same level, or posterior margin is lower (1) (Nesbitt, 2011; Baron et al., 2017a).

**Comment:** The original formulation of this character was a multistate character: “Axis, dorsal margin of the neural spine: 0, expanded posterodorsally; 1, arcs dorsally, where the anterior portion height is equivalent to the posterior height” from Nesbitt (2009). The variation this character is trying to capture is that the neural spine of the axis can either slope dorsally or be stepped. This formulation is a bit clearer and does not involve any morphology on the dorsal margin.
AX6.  A316. Axis, distance of the distalmost tips of the prezygapophyses from the midline sagittal plane of the axis relative to that of the postzygapophyses: equidistant (0), postzygapophyses laterally expanded (1) (Gauthier, 1986; Yates, 2003a; Pol et al., 2011).

AX7.  A317. Axis, anteriorly projected pedicels bearing axial prezygapophyses: (0) absent, (1) present (Sereno, 1999a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

AX8.  A318. Axis, axial postzygapophyses, posterior margin: extends beyond the posterior face of the axial centrum (0), flushes with the posterior face of the axial...
centrum or is anterior to it (1) (Sereno, 1999a; Galton and Upchurch, 2004; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

AX9. A287-1. Axis, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Galton, 1990; Upchurch et al., 2007a; Sekiya et al., 2013).

Comment: Here and throughout, a lamina is here defined as any ridge that clearly connects the landmarks defined in Wilson (1999), and leaves the development of these laminae as a matter of further study.

AX10. A288-1. Axis, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Galton, 1990; Upchurch et al., 2007a; Sekiya et al., 2013).


AX16. A298-1. Axis, centropostzygapophyseal lamina (cpol): absent (0), present (1) (Bonaparte, 1999).


AX19. A315-1. Axis, centrum, posterior articular surface: flat (0), concave (1), convex (2) (Sereno, 1999a; Martínez et al., 2011).

AX20. A314-1. Axis, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).
Comment: The original formulation of characters AX19 and AX20 referred to “postlantal vertebrae”. Here the character is distributed to all the vertebrae and synonymised with characters that already dealt with pneumatic features.

4.2.2.3 Anterior cervical vertebrae

The main problem pertaining to these characters is the lack of consensus on the definitions of the subregions in the cervical, dorsal, and caudal vertebrae. In Upchurch et al. (2007), there are no definitions for anterior, middle, and posterior cervical vertebrae. In Yates (2007), C127 defined anterior cervical vertebrae as being cervicals 3-5, but there is not a clear delimitation for the middle and posterior regions. Middle and posterior were used loosely, and only C143 seems to define middle as cervicals 4-8. In contrast, Pol et al. (2011) defined middle cervicals in C127 as cervicals 3-5, and posterior cervicals are defined in C128 as cervicals 6-8. However, a contradiction is found in C126, where anterior cervicals are also defined as cervicals 3-5. These confused definitions make it difficult to assess whether the authors refer to the same characters and encumber the elucidation of conflicts.

Figure 4.82. Cervical series in Efraasia. There is an abrupt contrast in the laminae system between the posterior and the anterior to middle part of the cervicals. The ventral keel is present in all the series, but its development changes the morphology of the ventral margin of the centra. In posterior cervicals, the diapophyses migrate from the middle part of the centra in the anterior to middle cervicals, to above the neural junction. The epipophyses are not restricted to the posterior cervicals alone, and Efraasia has developed epipophyses from Ce6 to Ce7, where the diapophyses is in the middle part of the centrum. This justifies having a character dealing with the presence or absence of the epipophyses in the anterior to middle cervicals, but it may amplify the signal in the anterior cervicals. The conjunction of diapophyses in the centra and epipophyses could indicate the presence of ‘middle cervicals’ in some sauropodomorphs.

Böhmer et al. (2015) performed a morphometric analysis on the cervical vertebrae of Plateosaurus engelhardti (specimen GPIT I). A Principal Component Analysis (PCA) of 17 landmarks in archosaurs (birds, crocodiles, and Plateosaurus) suggests that the anterior
region comprises CE3-5, the middle region comprises CE6-8, and the posterior region consists of CE9 and 10. In the case of *Plateosaurus engelhardti*, cervicals 3-5 are longer than they are high, the parapophyses and diapophyses are reduced, and the neural spines are also longer than high. Cervicals 6-8 bear more developed diapophyses, the parapophyses are higher on the centrum, and both the diapophyses and parapophyses migrate towards the neurocentral junction. In cervicals 9-10, the diapophyses are past the neurocentral joint, they are as long as they are high, and the neural spines extend along the posterior half of the neural arch. Using this study as a baseline, here the anterior to middle cervicals are included in the same group. Future work should use comparative morphometric analyses to evaluate these issues across a wide range of taxa.

Figure 4.83. Cervical series of *Mamenchisaurus*, from Ce5-10. *Mamenchisaurus youngi* has 18 vertebrae. In the case of *Mamenchisaurus*, the epipophyses are present very anteriorly in the series (from Ce6), and the conjunction with the diapophysis restricted to the centrum persists until Ce9.

ACE1. A314-2. Anterior to middle cervicals, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).
ACE2. A307-1. Anterior to middle cervical vertebrae, lateral pneumatic fossa, divided by an oblique ridge: absent (0), present (1) (Wilson and Sereno, 1998; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

ACE3. A332. Anterior to middle cervical vertebrae, centrum, ventral midline keel: present (0), absent (1) (Upchurch, 1998; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

**Comment:** The ventral keels are structures with high variability along the neck. The ventral keel is defined here as a midline ventral ridge that interrupts the continuity of the surface in the centrum, effectively creating two lateral surfaces. The ventral keel can then be a prominent flange, a distinct pinched ridge, or a low rounded ridge bordered by two ventral recesses.

ACE4. D332-2. Anterior to middle cervical vertebrae, centrum, extension of the ventral midline keels: anterior half only (0), along the whole centrum (1). NEW.

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**Figure 4.84. Ventral views of the cervicals of Panphagia and Spinophorosaurus.** Top, posterior cervical vertebra (presumptive C8) of Panphagia (PVSJ 874) in ventral view (Martínez et al., 2012b), displaying the autapomorphy of lateral keels (lk), bottom, Spinophorosaurus, ‘middle cervical’ of the paratype (NMB-1698-R) in ventral view (Remes et al., 2009), showing a ventral keel restricted to the anterior half only.

ACE5. A265-A266-1. Anterior to middle cervical vertebrae, neural spines in anterior or posterior view: lateral walls parallel through the neural spine (0), laterally expanded tables at the dorsal end of the neural spine (1) (Yates, 2003a; Yates and Kitching, 2003).
Comment: This character was originally defined as “laterally expanded tables at the midlength of the distal surface of the neural spine”. As it is, this character is confusing, and it is not clear on the location of the expanded tables in the neural spine. The character states referred to its distribution throughout the vertebral column (absent -0-, present in the pectoral vertebrae -1-, present in cervical and pectoral vertebrae -2-). There is no imaging of this character, but the scorings specify that this feature is present in the anterior dorsals of Riojasaurus, and in the cervicals and anterior dorsals of Plateosaurus and Massospondylus. Here, this character is reformulated to refer to the spine tables illustrated for the dorsal vertebrae of Herrerasaurus in Novas (1994). Moreover, here the character has been split into independent neomorphic characters for each sub region of the vertebral column (Figure 4.85).

Figure 4.85. Illustration of the expanded tables as identified in the dorsal 3 of Ruehleia (MB.R.4718.43) in anterior view and compared with the illustration of this character in the dorsal 13 of Herrerasaurus (Novas, 1994).

ACE6. A334. Anterior to middle cervical vertebrae, neural spine, anterior spur-like projections at the dorsal margin: absent (0), present (1) (Yates, 2007a; Sekiya et al., 2013; Figure 4.86).

Comment: This character was not described in the original publication in which it was listed: C138 Yates (2007b), but was scored as present in Panphagia, Lufengosaurus, Anchisaurus, Leyesaurus, Massospondylus, and Adeopapposaurus. The mid-cervical of Panphagia displays an anterior margin of the neural spine with a spike-shaped morphology,
where the margin projects anteriorly at the dorsal margin, and dorsally at the base of the neural spine. This character is not assessable in the vertebrae of *Lufengosaurus*, since the neural spines are not preserved in any vertebrae of the cervical series. In the case of *Anchisaurus* (YPM 1883), it is not possible to assess this character either. In *Leyesaurus*, this spur-like process is identified in CE6, but in the illustrations of the other vertebrae provided in Martínez and Alcober (2009) this portion of the neural arch is not preserved. In the neotype of *Massospondylus*, this anterior spur is seen in CE6, CE8, and CE9. In *Adeopapposaurus*, the structure is distributed in CE7-9, and disappears by CE10.

![ACE6-1](image)

**Figure 4.86.** Putative ‘middle’ cervical of *Panphagia* showing character state ACE6-1.


**Comment:** Lamination along the cervicals correlates in some sauropodomorphs with the lamination in the axials, but it is not always the case. In *Ruehleia* the lamination in the axis is very simple but becomes more complex by the ‘middle’ cervicals. Moreover, having the axis independent from the rest of the cervicals allows capturing variation when there is only an axis preserved, or on the contrary, when is absent, without amplifying the signal. Identifying patterns of variation within sauropodomorph groups is not possible now without having groups defined. Here and throughout, this reasoning justifies the atomisation of the laminar characters and outlines the basis for further research.

ACE8. A325/A339/B189. Anterior to middle cervical vertebrae, epipophyses, on the dorsal surface of the postzygapophyses: absent (0), present (1) (Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).
ACE9.  A324/A338/A322. Anterior to middle cervical vertebrae, epipophyses: restricted to the postzygapophyses (0), overhang the posterior margin of the postzygapophyses (1) (Upchurch et al., 2007a; Yates et al., 2010; Nesbitt, 2011; Pol et al., 2011).

**Comment:** In the original formulation C137 Yates (2007a), *Plateosaurus engelhardti* is scored as a polymorphism. The epipophyses overhang the postzygapophyses only in the posterior cervicals in the specimens SMNS 13200 and GPIT I. A similar condition seems to be the case in the pictures of the juvenile specimen referred to *Plateosaurus engelhardti* (Hofmann and Sander, 2014). The epipophyses extend along the whole length of the postzygapophyses in most basal sauropodomorphs, except for *Leyesaurus* and *Massospondylus*, where they only occupy the posterior third. The epipophyses are present in the anterior to middle portion of the cervicals in *Leonerasaurus* and *Leyesaurus*.


ACE11.  A276-1. Anterior to middle cervical vertebrae, anterior surface of pedicels of cervical neural arches, centroprezygapophyseal fossa (cprf): absent (0), present (1) (Nesbitt, 2011; Pol et al., 2011; Baron et al., 2017a).

ACE12.  A288-2. Anterior to middle cervical vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Upchurch et al., 2007a; Apaldetti et al., 2013).


**Comment:** The prdl appears on the last cervical of *Adeopapposaurus*. In *Plateosaurus* and *Ruehleia* it appears first on the 6th cervical, in *Mussaurus* it starts on the 8th, and on *Massospondylus* in the 9th.

ACE14.  A293-2. Anterior to middle cervicals, centroprezygapophyseal lamina (cprl): absent (0), present (1) (Wilson, 2002; Remes et al., 2009).


ACE17. A298-2/B196/A281. Anterior to middle cervicals, centropostzygapophyseal lamina (cpol): absent (0), present (1) (Bonaparte, 1999).

**Comment:** This character is the same as the “infrapostzygapophyseal constriction”. In Bonaparte (1999), this structure is defined as a consequence of elevated postzygapophyses and a deep spinopostzygapophyseal fossa (spof). The illustrations of this character in Bonaparte (1999, fig. 40) refer to the strut of bone between the centropostzygapophyseal fossae *sensu* Wilson et al. (2011), which in turns corresponds to the centropostzygapophyseal lamina *sensu* Wilson (1999).


ACE20. D198. Anterior to middle cervical vertebrae, anterior centroparapophyseal lamina (acpl): absent (0), present (1) NEW

ACE21. D199. Anterior to middle cervical vertebrae, posterior centroparapophyseal lamina (pcpl): absent (0), present (1) NEW

ACE22. A287-2. Anterior to middle cervicals, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Upchurch et al., 2007a; Apaldetti et al., 2011; Sekiya et al., 2013).

ACE23. A286/A280-1/A315. Anterior to middle cervical vertebrae, centrum, articulations: amphicoelous-amphiplatyan (0), opisthocoelous (i.e. a cranial hemispherical convexity articulates with a corresponding concavity on the caudal surface of the preceding cervical) (1) (Gauthier, 1986; Sereno, 1999a; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

ACE24. A278-1. Anterior to middle cervical vertebrae, parapophyses: smooth dorsal surface (0), dorsal excavation (1) (Sereno, 1999a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013)

ACE25. B195. Anterior to middle cervical vertebrae, bases of the diapophysis and parapophysis: well separated (0), touching (1) (Nesbitt, 2011; Baron et al., 2017a).
**Comment:** this character is difficult to assess as the expression “nearly touching” is not clear. In here, this character is operationalised by assessing whether the bases of the diapophyses and parapophyses contact each other or not.

ACE26. A279-2. Anterior to middle cervical vertebrae, cervical ribs, shape of the shaft: posterovertrally directed (0), parallel to cervical column (1) (Sereno, 1999a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

ACE27. A306-1. Anterior to middle cervical vertebrae, ribs, position of the base of the cervical rib shaft: level with, or higher than the ventral margin of the cervical centrum (0), located below the ventral margin due to a ventrally extended parapophysis (1) (Wilson and Sereno, 1998; Yates, 2007a; Sekiya et al., 2013).

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**Figure 4.87.** Mid-cervical vertebra of *Panphagia* in ventral view.
Figure 4.88. Neural arch of 6th cervical in a juvenile ‘prosauropod’ referred to P. engelhardti. Although the laminae were consistent with the observed in Plateosaurus the referral to this species was done on the basis of geographical proximity and it has been largely assumed that Plateosaurus showed dimorphism and phenotypic plasticity (Galton, 1999; Sander and Klein, 2005; Hofmann and Sander, 2014). Here, P. engelhardti is restricted to SMNS 13200, GPIT I and GPIT II.
4.2.2.4 Posterior cervical vertebrae

Figure 4.89. Anatomical differences between the posterior cervicals in Plateosaurus (AMNH 6810, picture by Matt Wedel) and Ruehleia (MB RvL2).

PCE1. A314-3. Posterior cervicals, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).


PCE4. D332-4. Posterior cervical vertebrae, centrum, extension of the ventral keels: anterior half (0), along the whole centrum (1). NEW.

PCE5. A278-2. Posterior cervical vertebrae, parapophyses, dorsal excavation: absent (0), present (1) (Sereno, 1999a; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

PCE6. A265/A266-2. Posterior cervicals, neural spines, neural spines in anterior or posterior view: lateral walls parallel through the neural spine (0), laterally expanded tables at the dorsal end of the neural spine (1) (Yates, 2003a, 2007a; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).
PCE7. A351. Posterior cervical vertebrae, diapophyses, shape of rib articulation surface: elongated transversely (0), circular (1). (Sereno, 1999a; Martínez et al., 2011).


PCE9. A287-3. Posterior cervicals, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Galton, 1990; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

PCE10. A288-3. Posterior cervical vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Galton, 1990; Upchurch et al., 2007a; Sekiya et al., 2013).

PCE11. A289-3. Posterior cervicals, prezygodiapophyseal lamina (prdl): absent (0), present (1) NEW.


Comment: The podl appears on the 9th cervical in Plateosaurus and Ruehleia.

PCE13. A293-3. Posterior cervicals, centroprezygapophyseal lamina (cprl): absent (0), present (1) (Wilson, 2002; Remes et al., 2009).


PCE19. D291. Posterior cervicals, spinodiapophyseal lamina (spdl): absent (0), present (1) NEW.
PCE20. D293. Posterior cervicals, anterior centroparapophyseal lamina (acpl): absent (0), present (1) NEW.
PCE21. D294. Posterior cervicals, posterior centroparapophyseal lamina (pcpl): absent (0), present (1) NEW.
PCE22. D295. Posterior cervicals, prezygoparapophyseal lamina (prpl): absent (0), present (1) NEW.
PCE23. D296. Posterior cervicals, prespinal lamina (prsl): absent (0), present (1) NEW.
PCE24. D297. Posterior cervicals, prespinal lamina (posl): absent (0), present (1) NEW.
PCE25. A286/A280-2/A315. Posterior cervical vertebrae, centrum, articulations: amphicoelous-amphiplatyan (0), opisthocoelous (i.e. a cranial hemispherical convexity articulates with a corresponding concavity on the caudal surface of the preceding cervical) (1) (Gauthier, 1986; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).
PCE26. A279-2. Posterior cervical vertebrae, cervical ribs, shape of the shaft: short and posteroventrally directed (0), longer than the length of their centra and extending parallel to cervical column (1) (Sereno, 1999a; Yates, 2007a; Apaldetti et al., 2011; Sekiya et al., 2013).
PCE27. A306-2. Posterior cervical vertebrae, ribs, position of the base of the cervical rib shaft: level with, or higher than the ventral margin of the cervical centrum (0), located below the ventral margin due to a ventrally extended parapophysis (1) (Wilson and Sereno, 1998; Yates, 2007a; Sekiya et al., 2013).

4.2.3 Dorsal vertebrae

4.2.3.1 Anterior dorsal vertebrae

ADO1. A315-4. Anterior dorsal cervical vertebrae, centra, posterior articular surface: flat (0), concave (1), convex (2) (Sereno, 1999a; Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013).

Comment: The original formulation was assessed through all dorsal vertebrae. The only polymorphism, as reported in Yates (2007a), is Seitaad, scored as “entirely amphicoelous” (0) and “first two dorsals are opisthocoelous.” (1). This polymorphism attempts to capture
the uncertainty around the first two anterior dorsals, since the first four dorsals are fragmentary and still embedded in the matrix. From D6 to D11 the vertebrae are amphicoelous, and this corresponds to the middle and posterior dorsals, but scored as ‘?’ for the anterior dorsals.

ADO2. A314-4. Anterior dorsal vertebrae, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).

ADO3. A406. Anterior dorsal vertebrae, neural arches, separation of lateral surfaces beneath transverse processes: spaced (0), only separated by a thin midline septum (1) (Upchurch et al., 2004b; Yates, 2007a; Sekiya et al., 2013).

ADO4. A407. Shape in anterior/posterior view: lateral margins parallel (0), diverging, expanding transversely towards dorsal end (1) (Yates, 2007a; Sekiya et al., 2013).

ADO5. A364. Anterior dorsal vertebrae, parapophyses, location: centrum (0), neurocentral junction (1), neural arch (2) Ordered (Langer, 2004; Yates, 2007a; Sekiya et al., 2013).

Comment: In Eoraptor, Saturnalia and Lamplughysaura, the parapophyses move onto the neurocentral junction in the first dorsals, and character state (1) was added to incorporate this state.

ADO6. A353-1. Anterior dorsal vertebrae, hyposphenes: absent (0), present (1) (Gauthier, 1986; Sereno, 1999a; Upchurch et al., 2007a; Yates, 2007a; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

Comment: The original formulation in C157 Yates (2007a) assessed the hyposphene-hypantrum in all the dorsal vertebrae and compared the processes with the neural canal. Lessensaurus is scored as present, but in the illustrations of the neural arches in Bonaparte (1999) the articulation is not shown. Here it is assumed that this character was observed first-hand and not recorded in the publication. It is also scored as present in Vulcanodon, but there is no record of dorsal vertebrae referred to Vulcanodon (Raath, 1972; Cooper, 1984), and it is here rescored as “?” Spinophorosaurus has a hyposphene-hypantrum throughout all dorsals, but the articulation increases its size through the dorsals relative to the neural canal of the vertebra (Remes et al., 2009). Pulanesaurus has a hyposphene in all dorsal vertebrae, and the size of the hyposphene increases in middle and posterior dorsals
(McPhee and Choiniere, 2017). For Antetonitrus, the hyposphene is present in middle and posterior dorsals, but there is no anterior dorsal preserved, and the new scorings reflect this uncertainty (McPhee et al., 2014). Finally, in Melanorosaurus, the hyposphene-hypantrum is present throughout all dorsals (Galton et al., 2005). The second qualifier of the original character statement has been considered as a distinctive feature to separate ‘prosauropods’ from ‘sauropods.’ A dorsoventral height that equals that of the neural canal has been considered a sauropod trait, whereas a smaller dorsoventral height has been attributed to ‘prosauropods’ (Yates, 2003a; Galton et al., 2005). This is coded accordingly in Sekiya et al. (2013), with only Vulcanodon being scored as polymorphic. The variability of this character in the dorsals of taxa placed in the basal part of the sauropod lineage indicates a complexity that is not being appropriately assessed in the current characters. Measuring this character without having clear morphometric diagnoses of each vertebral region will not reduce the noise from this character, thus this second element has been separated from the character statement.

ADO7. A405/A270-3. Anterior dorsal vertebrae, transverse processes, orientation: laterally (0), dorsolaterally (1) (Upchurch, 1998; Bonaparte, 1999; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

ADO8. A387-1. Anterior dorsal vertebrae, centropostzygapophyseal lamina (cpol): absent (0), present (1) (Wilson, 2002; Upchurch et al., 2007a; Remes et al., 2009; Sekiya et al., 2013).

ADO9. A389-1. Anterior dorsal vertebrae, spinopostzygapophyseal lamina (spol): absent (0), present (1) (Wilson, 2002; Yates, 2007a; Remes et al., 2009).

ADO10. A390-1. Anterior dorsal vertebrae, spinopostzygapophyseal lamina (spol), shape at its distal end: singular (0), bifurcated (1) (Wilson, 2002; Upchurch et al., 2007a; Remes et al., 2009; Sekiya et al., 2013).

Comment: There are no spol in the dorsal vertebrae of Coloradisaurus, Eoraptor, or Melanorosaurus.

ADO11. A391-1. Anterior dorsal vertebrae, spinopostzygapophyseal lamina (spol), shape: rounded ridge (0), sheet-like (1) (Bonaparte, 1986a; Upchurch et al., 2007a; Yates, 2007a; Remes et al., 2009; Sekiya et al., 2013).
ADO12. A392-1. Anterior dorsal vertebrae, spinopostzygapophyseal laminae (spol): weakly developed, terminating below the summit of the spine (0), extending to the top of the spine (1) (Bonaparte, 1986a; Galton and Upchurch, 2004).

ADO13. A395-1. Anterior dorsal vertebrae, interpostzygapophyseal lamina (tpol): absent (0), present (1).

Figure 4.90. Anterior dorsals of Ruehleia, ‘Plateosaurus’ and middle dorsal of Efraasia. A1-A3 – 3rd dorsal vertebra of Ruehleia (MB.R.4718.43) in anterior (A1), right lateral (A2) and posterior (A3) views. B. anterior dorsal vertebrae of ‘Plateosaurus’ (SMNS 81914) in left lateral view. C) mid-dorsal vertebra of Efraasia (SMNS 12354b) in right anterolateral view.
Figure 4.91. Anterior dorsal of *Antetonitrus* (taken from McPhee et al., 2014) showing a laminar system similar to *Ruehleia*. A, anterior, B, posterior, C, D, lateral views. Scale bar = 5 cm.


**Comment:** In the case of *Herrerasaurus*, there is a polymorphism in the original formulation, with this character being applied to all the dorsals. The acpl is present in dorsals from D9 to D15 in specimen PVL 2566 (Novas, 1994). The anterior dorsals are not preserved.

ADO15. A399-1. Anterior dorsal vertebrae, prezygaparapophyseal lamina (prpl): absent (0), present (1) (Wilson and Sereno, 1998; Yates, 2007b)

ADO16. A400-1. Anterior dorsal vertebrae, prespinal lamina (prsl): absent (0), present (1) NEW.

ADO17. A379-1. Anterior dorsal vertebrae, spinodiapophyseal lamina (spdl): separated from spinopostzygapophyseal lamina (spol) (0), joining spol to form a


**Comment:** The podl is present in all the dorsals of *Massospondylus* and *Plateosaurus* but it is reported absent in all the vertebrae in *Riojasaurus* (Bonaparte, 1999).


**Comment:** The sprl are absent in the dorsals of *Aardonyx*, *Lufengosaurus* and *Massospondylus*.


**Comment:** ADO 25 and ADO26 characters are not the same than having a bifid spinopostzygodiapophyseal lamina (spol), where the medial spol tends to present this condition.


ADO28. A372-1. Anterior dorsal vertebrae, centrum: acamerate (0), procamerate (1), camerate (2) Ordered (Bonaparte et al., 1999; Pol et al., 2011).
Figure 4 92. Different degrees of pneumaticity in the centra of three neosauropods.

ADO29. A265-A266. Anterior dorsal vertebrae, vertebrae, neural spines in anterior or posterior view: lateral walls parallel through the neural spine (0), laterally expanded tables at the dorsal end of the neural spine (1) (Yates, 2003a, 2007a; Yates and Kitching, 2003; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: The original formulation of this character assessed the expanded tables on the “pectoral vertebrae” (0), and “pectoral and cervical vertebrae” (1). The only polymorphism for this character as reported by Yates (2007a) is for Plateosauravus. The plates can be seen in an anterior dorsal vertebra (specimen SAM 3345a), but the cervical neural spines are broken in their distal parts and the feature is not assessable in the figures in Heerden (1979). The polymorphism captures the uncertainty of the presence of this character in the cervicals by asserting its presence in the anterior dorsal vertebrae (pectorals). Redistributing the characters increases the information from this OTU.

ADO30. A373-1/A367. Anterior dorsal vertebrae, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Bonaparte, 1999; Pol et al., 2011).

ADO31. A374-1. Anterior dorsal vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Bonaparte, 1999; Upchurch et al., 2007a; Sekiya et al., 2013).

ADO32. A375-376-1. Anterior dorsal vertebrae, prezygodiapophyseal lamina (prdl) and associated prezygapophyseal centrodiapophyseal fossa (prcdf): absent (0), present (1) (Bonaparte, 1986b; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: The taxon Pulanesaura is scored as a polymorphism in the original formulation, with the character states “present on all dorsals” (0), and “absent in mid-
dorsals” (1). In the pictures contained in McPhee et al. (2015), the prdl is present in the anterior and middle dorsals. There are prezygapophyses in the posterior dorsals.


ADO34. A383-1. Anterior dorsal vertebrae, spinoprezygapophyseal lamina (sprl): absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Sekiya et al., 2013).

ADO35. A362-1. Anterior dorsals, centrum, articulation: posterior articular surface: flat (0), concave (1), convex (2) (Bonaparte, 1999; Yates and Kitching, 2003; Pol et al., 2011).

ADO36. D363. Anterior dorsals, centrum, ventral midline keel: absent (0), present (1). NEW.

Comment: A ventral keel is present only on anterior dorsals in *Massospondylus*, *Plateosaurus* and *Ruehleia*, where it disappears beyond the fourth dorsal. In *Adeopapposaurus*, the ventral keel is present only on the first dorsal.

4.2.3.2 Middle dorsal vertebrae

MDO1. A409-1. Middle dorsal vertebrae, lateral pneumatic fenestra in centrodiapophyseal fossa, opening into neural cavity: absent (0), present (1) (Wilson and Sereno, 1998; Yates, 2007a; Sekiya et al., 2013).

MDO2. A372-2. Middle dorsal vertebrae, centrum: acamerate (0), procamerate (1), camerate (2) Ordered (Bonaparte, 1999; Pol et al., 2011).

MDO3. A314-5. Middle dorsal vertebrae, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Sereno, 1999a; Martínez et al., 2011).

MDO4. A353-2. Middle dorsal vertebrae, hyopsphene-hypantrum articulation: absent (0), present (1) (Gauthier, 1986; Upchurch et al., 2007a; Yates, 2007a; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

MDO5. A410. Mid-dorsal vertebrae, neural spine, shape of posterior margin in lateral view: approximately straight (0), concave with a projecting posterodorsal corner (1) (Yates, 2003a, 2007a; Sekiya et al., 2013).
MDO6. A270-4. Middle dorsal vertebrae, transverse processes of the vertebrae, orientation respect to their sagittal plane: perpendicular (0), dorsally deflected (1) (Bonaparte, 1999; Pol et al., 2011; Apaldetti et al., 2013).

MDO7. A369-2. Middle dorsal vertebrae, spinoprezygapophyseal lamina (sprl): absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Sekiya et al., 2013).

MDO8. A373-2/A367. Middle dorsal vertebrae, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Bonaparte, 1999; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

MDO9. A373-2. Middle dorsal vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Bonaparte, 1999; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

MDO10. A374-2. Middle dorsal vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Bonaparte, 1999; Upchurch et al., 2007a; Sekiya et al., 2013).

MDO11. A375-376-2. Middle dorsal vertebrae, prezygodiapophyseal lamina (prdl) and associated prezygapophyseal centrodiapophyseal fossa (prcdf): absent (0), present (1) (Bonaparte, 1986b; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013)

MDO12. A378-2. Middle dorsal vertebrae, spinodiapophyseal lamina (spdl): absent (0), present (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Yates, 2007a; Remes et al., 2009; Sekiya et al., 2013)


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MDO17. A383-1. Middle dorsal vertebrae, spinoprezygapophyseal lamina (sprl): absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Sekiya et al., 2013).


MDO20. A387-2. Middle dorsal vertebrae, centropostzygapophyseal lamina (cpol): absent (0), present (1) (Wilson, 2002; Upchurch et al., 2007a; Remes et al., 2009; Sekiya et al., 2013).

MDO21. A389-2. Middle dorsal vertebrae, spinopostzygapophyseal lamina (spol): absent (0), present (1) (Wilson, 2002; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MDO22. A390-2. Middle dorsal vertebrae, spinopostzygapophyseal lamina (spol), shape at its distal end: singular (0), bifurcated (1) (Wilson, 2002; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MDO23. A391-2. Middle dorsal vertebrae, spinopostzygapophyseal lamina (spol), well developed, sheet-like: absent (0), present (1) (Bonaparte, 1986a; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MDO24. A392-2. Middle dorsal vertebrae, spinopostzygapophyseal laminae (spol), weakly developed, terminating below the summit of the spine (0), extending to the top of the spine (1) (Bonaparte, 1986b; Galton and Upchurch, 2004)

MDO25. A393-2. Middle dorsal vertebrae, medial spinopostzygapophyseal lamina (m spol): absent (0), present (1) (based on Allain and Aquesbi, 2008).


MDO28. A396-2. Middle dorsal vertebrae, anterior centroparapophyseal lamina (acpl): absent (0), present (1) (Wilson, 2002; Yates, 2007b; Remes et al., 2009)

MDO29. A398-2. Middle dorsal vertebrae, posterior centroparapophyseal lamina (pcpl): absent (0), present (1) (Wilson, 2002; Remes et al., 2009).

MDO31. A400-2. Middle dorsal vertebrae, prespiNAL lamina (prsl): absent (0), present (1) NEW.


MDO33. A408. Mid-dorsal vertebrae, contribution of the paradiapophyseal (ppdl) lamina to the margin of the prezygapophyseal centrodiapophyseal fossa (prcdf): present (0), prevented by high placement of parapophysis (1) (Upchurch, 1998; Upchurch et al., 2007a; Yates, 2007a; Sekiya et al., 2013).

MDO34. A362-1. Middle dorsals, centrum, articulation: posterior articular surface: flat (0), concave (1), convex (2) (Bonaparte, 1999; Yates and Kitching, 2003; Pol et al., 2011).

MDO35. A315-4. Anterior dorsal cervical vertebrae, centra, posterior articular surface: flat (0), concave (1), convex (2) (Sereno, 1999a; Martínez et al., 2011).

4.2.3.3 Posterior dorsal vertebrae

PDO1. A412. Posterior dorsal vertebrae, neural canal, shape: subcircular (0), slit-shaped along the dorsoventral axis (1) (Yates, 2007a; Sekiya et al., 2013).


PDO3. A373-3/A367. Posterior dorsal vertebrae, anterior centrodiapophyseal lamina (acdl): absent (0), present (1) (Upchurch et al., 2007a; Sekiya et al., 2013).

PDO4. A373-4. Posterior dorsal vertebrae, posterior centrodiapophyseal lamina (pcdl): absent (0), present (1) (Upchurch et al., 2007a; Sekiya et al., 2013).

PDO5. A375-376-3. Posterior dorsal vertebrae, prezygodiapophyseal lamina (prdl) and associated prezygapophyseal centrodiapophyseal fossa (prcdf): absent (0), present (1) (Yates, 2007a; Sekiya et al., 2013).
Several characters have assessed the presence of fossae in the vertebrae for the cases where the laminae or the landmarks are not clearly defined. However, these fossae have constant anatomical positions but not necessarily a constant laminar composition. Here, the posterior centrodiapophyseal fossa (pocdf) is formed by a posterior centrodiapophyseal fossa (pcdl) and the postzygodiapophyseal fossa, whereas the centrodiapophyseal fossa (cdf) is formed by the pcdl and the paradiapophyseal lamina (ppdl). The cdf could be in turn be formed by the anterior centroparapophyseal lamina (acpl), but in *Eucnemosaurus fortis* the latter is not developed since the parapophyses are quite large.


PDO10. A383-1. Middle dorsal vertebrae, spinoprezygapophyseal lamina (sprl): absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Sekiya et al., 2013).


Figure 4.94. Posterior dorsal of Ruehleia in anterior, lateral and posterior view (from left to right) (MB.R.4718.67). The morphology of the D10 in Ruehleia is quite similar to the morphology of Eucnemesaurus in that the hyposphene (ho) is prominent and the ppdl is composed only by the posterior centrodiapophyseal lamina (pcdl) and the parapodiapophyseal lamina (ppdl) with a very prominent parapophysis (pa).
Figure 4. 95. Posterior dorsal vertebra (14th dorsal) of Ruehleia. From left to right and top to bottom: right lateral, posterior, dorsal, and anterior views. The hyposphene is very reduced by the last posterior dorsal, whereas in the anterior and middle dorsals it has been a prominent feature. It is not clear if this is last dorsal or if the diapophyses contacted with the ilium, making it a dorsosacral. The reduced preacetabular process in Ruehleia suggests this is a very modified dorsal vertebra, but not a dorsosacral.


PDO17.  A392-3. Posterior dorsal vertebrae, spinopostzygapophyseal laminae (spol): weakly developed, terminating below the summit of the spine (0), extending to the top of the spine (1) (Bonaparte, 1986b; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).


PDO23. A399-3. Posterior vertebrae, prezygaparaphyseal lamina (prpl): absent (0), present (1) (Yates, 2007a)


PDO26. A270-5. Posterior dorsal vertebrae, transverse processes of the vertebrae, orientation with respect to their sagittal plane: perpendicular (0), dorsally deflected (1) (Apaldetti et al., 2013; Sekiya et al., 2013).

PDO27. B314-6. Posterior dorsal vertebrae, lateral pneumatic fossa, rimmed so that bony ridges extend from the centrum and define a clear fossa: absent (0), present (1) (Martínez et al., 2011).

PDO28. B315-6. Posterior dorsal vertebrae, centra, cervical centra, posterior articular surface: flat (0), concave (1), convex (2) (Martínez et al., 2011).


PDO30. A362-1. Posterior dorsals, centrum, articulation: posterior articular surface: flat (0), concave (1), convex (2).


PDO34. A414-3. Posterior dorsal vertebrae, parapophyses, location: centrum (0), neurocentral junction (1), neural arch (2) Ordered (Langer, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

PDO35. A415. Posterior dorsal vertebrae, last presacral rib, ossification: free (0), fused to vertebra (1) (Upchurch et al., 2007a; Yates et al., 2010; Pol et al., 2011; Sekiya et al., 2013).

PDO36. D389-1. Posterior dorsal vertebrae, centropostzygapophyseal fossa (cpol-f, accessory lamina dividing the postzygocentrodiaphyseal fossa): absent (0), present (1) NEW.
4.2.4 Sacral vertebrae

![Diagram of sacral vertebrae for various species]

Figure 4.96. Diagrammatic reconstruction of the sacra of several basal saurischians and non-sauropod sauropodomorphs. Code: purple, dorsosacrals, blue, first primordial sacral, green, second primordial sacral, orange, sacrocaudal.

4.2.4.1 Dorsosacral vertebrae

DS1. A402. Dorsosacral vertebrae: absent (0), present (1) (Yates, 2007a; Sekiya et al., 2013; Baron et al., 2017a).

DS2. A403. Dorsosacral vertebrae: one (0), two (1) (Yates, 2007a; Sekiya et al., 2013; Baron et al., 2017a).
DS3. A404. Dorsosacral vertebrae, transverse process, anteroposterior extension of medial region relative to the central length (Yates, 2010; Pol et al., 2011)

DS4. A416. Dorsosacral vertebra 1, transverse processes, contact with preacetabular process: absent (0), present (1) (Martínez et al., 2011).

4.2.4.2 Primordial vertebrae

SAC1. A417. Sacral vertebrae, width of the sacral rib relative to the width of the transverse process (and dorsosacral if present) in dorsal view (Yates, 2007a; Sekiya et al., 2013).

SAC2. A419. Sacral vertebrae, primordial sacral vertebrae, length of the ribs of the two primordial sacrals relative to the medial surface of the iliac alae (Langer, 2004; Pol et al., 2011)

SAC3. A420. Sacral vertebrae, primordial sacral vertebrae, number: two (0), three (1), four (2), five (3) (Wilson, 2002; Remes et al., 2009).

SAC4. A421. Sacral ribs, sacricostal yoke (distal ends of sacral ribs fuse together): absent (0), present (1) (Wilson and Sereno, 1998; Galton and Upchurch, 2004; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

SAC5. A422. Sacral vertebrae, sacricostal yoke, contribution to the dorsal rim of the acetabulum: absent (0), present (1) (Wilson and Sereno, 1998; Galton and Upchurch, 2004; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

SAC6. D422. Sacral vertebrae, sacricostal yoke, shape: flat horizontally (0), bevelled ventromedially (1) NEW.

SAC7. A423. Sacral vertebrae, primordial sacral vertebrae, depth of the iliac articular surface relative to the depth of the ilium (Novas, 1992; Yates, 2007a; Sekiya et al., 2013).

SAC8. D423. Sacral vertebrae, parapophyses, position: located on a single centrum (0), shared between two centra (1) NEW.

SAC9. A424. Sacral vertebrae, first primordial sacral vertebrae, strong constriction between the sacral rib and the transverse process of the first primordial sacral rib (and dorsosacral if present) in dorsal view: absent (0), present (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).

SAC10. D426. Sacral vertebrae, sacral rib 1, shape: undivided distally (0), divided distally into alar and acetabular rami (1) (Wilson, 2011)
SAC11.  B217. Sacral vertebrae, centra: separate (0), at least partially co-ossified (1) (Nesbitt, 2011; Baron et al., 2017a).


SAC13.  B223. Sacral ribs: almost entirely restricted to a single sacral vertebra (0), shared between two sacral vertebrae (2) (Nesbitt, 2011; Baron et al., 2017a).

SAC14.  D428. Sacral vertebrae, timing of fusion: neurocentral fusion before interneural fusion (0), interneural fusion before neurocentral fusion (1) (Wilson, 2011).

SAC15.  D428. Sacral vertebrae, neural spines, contact: fused (0), connected via fused prespinal and postspinal laminae (1) (Wilson, 2011).

SAC16.  B224. First primordial sacral, articular surface of sacral rib: circular (0), C-shaped in lateral view (1), rectangular (2) (Nesbitt, 2011; Baron et al., 2017a).

SAC17.  A427. First and second primordial sacral vertebrae, posterior and anterior expansion of the transverse processes of the first and second primordial sacral vertebrae, respectively, partly roofing the intercostal space: absent (0), present (1) (Langer, 2004; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013)

SAC18.  A426. First primordial sacral vertebrae, iliac articular facets, shape: singular (0), divided into dorsal and ventral facets separated by a non-articulating gap (1) (Yates, 2007a; Sekiya et al., 2013).

4.2.4.3 Sacrocaudal vertebrae

CAS1.  A430. Sacrocaudal vertebra: absent (0), present (1) (Yates, 2010; Pol et al., 2011).

CAS2.  A428. Sacrocaudal 1, transverse process, contact with the postacetabular process of the ilium: absent (0), present (1) (Martínez et al., 2011).

CAS3.  429. Caudosacral 2, transverse process, contact with the postacetabular process of the ilium: absent (0), present (1) (Martínez et al., 2011).
4.2.5 Caudal vertebrae

![Diagram of caudal vertebrae]

Figure 4.97. Regionalisation of the caudal series in *Plateosaurus engelhardti* (GPIT I).

4.2.5.1 Anterior caudal vertebrae

ACa1. A431. Anterior caudal vertebrae, caudal I, length of the centrum relative to its height (Yates, 2007a; Sekiya et al., 2013; Baron et al., 2017a).

ACa2. A433-1. Anterior caudal vertebrae, hyposphenal ridge: absent (0), present (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

ACa3. A434-A439. Anterior caudal vertebrae, neural spines, length of base of the spines relative to the length of the neural arch (Yates and Kitching, 2003; Pol et al., 2011; Baron et al., 2017a).

ACa4. A440. Anterior caudal vertebrae, anteriormost caudals, centrum, length relative to the central height (Cooper, 1981; Upchurch et al., 2007a; Pol et al., 2011).

ACa5. A441. Anterior caudal vertebrae, diapophyses, bases, depth: restricted to the neural arches (0), extending from the centrum to the neural arch (1) (Upchurch, 1998; Yates, 2007a; Sekiya et al., 2013).


ACa7. A443. Anterior caudal vertebrae, postzygapophyses, position: protruding with an interpostzygapophyseal notch visible in dorsal view (0), placed on either side of the posterior end of the base of the neural spine without any interpostzygapophyseal notch (1) (Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).
ACa8. A432-1. Anterior caudal vertebrae, centrum, longitudinal ventral sulcus: absent (0), present (1) (Upchurch and Martin, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: In the original formulation, *Lufengosaurus* was scored as a polymorphism, with the character states “longitudinal ventral sulcus in anterior and middle caudals: present (0), absent (1)”. In *Lufengosaurus*, the sulcus is present on caudals V and VI, but from caudal VII to caudal XXI the ventral sulcus is present but restricted to the posterior part of the centrum, and fainter than the sulcus in the caudals V and VI.

4.2.5.2 Middle caudal vertebrae

MCa1. A433-2. Middle caudal vertebrae, hyposphenal ridge: absent (0), present (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MCa2. A444. Middle caudal vertebrae, length relative to height of the anterior articular surface (Yates, 2003a, 2007a; Upchurch et al., 2007a; Sekiya et al., 2013)

MCa3. A432-2. Middle caudal vertebrae, centrum, longitudinal ventral sulcus: absent (0), present (1) (Upchurch and Martin, 2003; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

4.2.5.3 Posterior caudal vertebrae

PCa1. A433-3. Posterior caudal vertebrae, hyposphenal ridge: absent (0), present (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

PCa2. A448/B231. Posterior caudal vertebrae, length of posterior caudal prezygapophyses relative to the length of the preceding the centrum (Gauthier, 1986; Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013)

PCa3. B230. Posterior caudal vertebrae, prezygapophyses: not extending beyond the anterior face of the centrum (0), elongated beyond the anterior face of the centrum (1) (Gauthier, 1986; Nesbitt, 2011; Baron et al., 2017a).

Comment: PCa3 has been defined in the literature as a ‘distal caudal’ character. Under the regionalisation implemented here, this is a character of the posterior caudal vertebrae.

4.2.5.4 Distal caudal vertebrae

DCa1. A447. Distal caudal vertebrae, centra, cross-sectional shape: oval with rounded lateral and ventral sides (0), square-shaped with flattened lateral and ventral sides (1) (Yates, 2007a; Sekiya et al., 2013)
DCa2. A449. Distal caudal vertebrae, distalmost biconvex caudal centra, length relative to it is height (Wilson, 2002; Remes et al., 2009).

DCa3. A450. Distal caudal vertebrae, distalmost biconvex caudal centra, number: less than 5 (0), more than 5 (1) (Wilson, 2002; Remes et al., 2009).

DCa4. A451. Distal caudal vertebrae, shape of terminal distals: unfused (0), fused (1) (Yates, 2007a; Sekiya et al., 2013).

4.2.5.5 Chevrons

Chv1. D445. Chevrons, shape: dorsally closed (0), dorsally open with two prongs projecting dorsolaterally (1) NEW.

Chv2. A445. Middle caudal vertebrae, chevrons, ventral slit: absent (0), present (1) (Yates, 2007a; Sekiya et al., 2013)

Chv3. A436. Posterior caudal vertebrae, forked chevrons, anterior and posterior projections: absent (0), present (1) (Galton and Upchurch, 2004)

Chv4. A437. Chevrons, distribution forked chevrons: posterior caudal vertebrae (0), throughout middle and posterior caudal vertebrae (1) (Upchurch et al., 2007a; Sekiya et al., 2013)

Chv5. A438. Caudal vertebrae, length of the longest chevron relative to length of the preceding centrum: less than or equal to 1.0 (0), more than 1.0 but less than or equal to 2.0 (1), or greater than 2.0 (2) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: Gap coding is not possible with this character, but the change in size of the chevron relative to the vertebrae might represent a phylogenetic signal. There is a trend on more derived animals to have a lower ratio than more primitive ones.
Figure 4.98. Temporal analysis of Chv5. This character is very continuous in the sample as to establish a gap-coding, and the original formulation was kept instead. A distinctive pattern emerges from the logarithmic distribution where there is a trend that more modern dinosaurs have smaller ratios than the primitive ones. Log Lm Cvn / L Ca(n-1) stands for length of the longest chevron relative to length of the preceding centrum.
4.3 Appendicular characters

4.3.1 Pectoral girdle

4.3.1.1 Sternum

ST1. A456. Sternal plate, dorsal surface, longitudinal ridge: absent (0), present (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: This character is present in the three matrices (C198 Y2007, C154 U2007, C164 P2011). The longitudinal ridge is reported in Massospondylus (Cooper, 1981), Lufengosaurus (Young, 1941), and Jingshanosaurus (Zhang and Yang, 1994), contrary to the previous scorings that restricted this character to sauropods.

4.3.1.2 Clavicle

CL1. A478. Clavicles: unfused into a furcula (0), fused into a furcula (1) (Gauthier, 1986; Nesbitt, 2011)

Comment: Clavicles have been identified in relatively few dinosaurs. In basal sauropodomorph dinosaurs, there are clavicles in Plateosaurus Massospondylus (Yates and Vasconcelos, 2005), Seitaad, Adeopapposaurus (Martínez, 2009) and Spinophorosaurus (Remes et al., 2009). The clavicles are not fused in any of them, although in Massospondylus the clavicles have a furcula-like arrangement. The homology of the character states has been subject to scrutiny in the literature (more details in Bryant and Russell, 1993; Yates and Vasconcelos, 2005). Here they are treated as homologous structures, so that the furcula is treated as a product of co-ossification of two clavicles.

4.3.1.3 Coracoid

CO1. D472. Coracoid, lateral side, number of faces divided by anteroposterior edge: one (0), dorsal and ventral (1), three (2) NEW (Figure 4.99).

Comment: This character was discussed first in Remes (2007) as the presence of an anteroposterior ridge dividing the lateral side into two facets, a dorsal and a ventral facet. In the specimen GPIT I of Plateosaurus engelhardtii mounted in Tubingen, this character is diagnosed in ventral view as a change in the slope of the surfaces. The dorsal facet is the largest, and the ventral facet is making the coracoids point medially on their anterior-most margin. These two facets are also seen in Lufengosaurus (specimen IVPP V15), and is reported for Eoraptor, and Barapasaurus (Remes, 2007). The coracoid has a continuous surface in Herrerasaurus, Saturnalia, Dilophosaurus, Efraasia, Unaysaurus,
Patagosaurus, Cetiosaurus, Shunosaurus, and Cetiosaurus (Remes, 2007). In ‘massospondylids,’ the coracoid also has only one continuous surface, as is reported in Massospondylus carinatus and Adeopapposaurus. The coracoid of Ruehleia attached to the scapula has lost the ventral half, but there is no evidence of the anteroposterior edge in anterior view, meaning the coracoid had only one facet. In Buriolestes, a very basal sauropodomorph, the coracoid is twisted medially, producing these distinct dorsal and ventral sides. Only in the case of Barapasaurus, there is an additional facet, a central one (Remes, 2007). This structure is not the same as the biceps ridge, discussed below. The biceps ridge is a protuberance from the lateral surface, and this structure is the product of a kinked coracoid. The medial orientation of the coracoids has been thought to be a plesiomorphy, shared with more basal dinosauromorphs too, and this edge may correlate with the trend of a more erect shoulder girdle (Remes, 2007).

CO2. A477. Coracoid, coracoid tubercle: present (0), absent (1) (Upchurch et al., 2007; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.99).

CO3. D473. Coracoid, posteroventral portion, biceps ridge: absent (0), present (1) (Figure 4.99).

Comment: There are two main osteological correlates present in the coracoids of archosaurs. The structure referred here as coracoid tubercle has been termed as ‘biceps tubercle’ through the literature. The biceps tubercle has been thought to be the correlate of the M. biceps brachii, a muscle that is widely distributed in basal archosauromorphs. Recent revisions have suggested that this rounded process in posteroventral position corresponds to the attachment site of the M. coracobrachialis (Meers, 2003; Remes, 2007; Otero, 2018). In Otero (2018), it is posited that the osteological correlate for the M. biceps brachii is a longitudinal ridge perpendicular to the margin of the coracoid. The pattern for these two muscles has also been proposed in muscular reconstructions on Mussaurus (Otero et al., 2017). In theropods, this same tubercle has been considered as the origin site of the M. biceps brachii (Madsen, 1993; Brochu, 2003; Burch and Carrano, 2012; Burch, 2014), but it has also been proposed that in the basal theropod Tawa, the origin of the M. biceps brachii and M. coracobrachialis is reconstructed as originating from the same area (Burch, 2014), and in Coelophysis the lateral surface is smooth (Rinehart et al., 2009). As for ornithischians, there are no osteological correlates for the M. biceps brachii, although there are some striations in the same area in Scutellosaurus (Maidment and Barrett, 2011). To
avoid confusion, the structure is named here as coracoid tubercle (CO2), and the ridge seen in sauropodomorphs is known as biceps ridge (CO3). Moreover, the biceps ridge is present in *Antetonitrus*, *Sefapanosaurus* and sauropods, and absent in more primitive sauropodomorphs such as *Efraasia*, *Lufengosaurus* and *Plateosaurus*. The biceps ridge could be an indicator of quadrupedalism, since the more derived sauropods have a more developed ridge.

**CO4.** A472. Coracoid, posterior process: absent (0), present (1) (Nesbitt, 2011).

**Comment:** Alternative terms: post-glenoid process, notch ventral to the glenoid.

**CO5.** A476. Coracoid, posterior process: not expanded beyond glenoid fossa (0), expanded beyond margin of glenoid fossa (1) (Tykoski, 1998; Clark et al., 2004; Nesbitt, 2011; Figure 4.99).

**Comment:** This character was redefined for theropods in Tykoski (1998) and scores all the sauropodomorphs with character state (0) at the same level than the glenoid fossa. However, the posterior process is expanded beyond the glenoid fossa in *Saturnalia*, *Adeopapposaurus*, *Lufengosaurus*, *Sarathsaurus*, *Sefapanosaurus*, *Antetonitrus*, and sauropods. It does not expand beyond the glenoid fossa in *Euparkeria*, and the theropods *Syntarsus*, *Ceratosaurus*, and *Allosaurus*. 
Characters related to the orientation of the scapula are discarded since there is not a consensus on the position of this bone in vivo. The orientation used here for all the other characters considers the scapulocoracoid articulation as the ventral side. After assessing all the continuous characters that have been proposed in the literature, only two characters were found to be neither positive nor negatively correlated. Interestingly, this is the bone with the most character correlation identified thus far, and several of them have appeared in the same character lists.
Correlation map between scapular characters. Most of the characters identified thus far in the literature turned out to be significantly correlated.

SC1. D246-1. Scapula, articulation with coracoid: straight margin (0), stepped (1), inflection (2). NEW.

SC2. A457. Scapula, minimum anteroposterior length relative to its dorsoventral length: less than 0.2 (0), equal to or greater than 0.2 (1) (Yates and Kitching, 2003; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013; Figure 4.101).


Comment: This character is retained as a neomorphic character. The continuous version correlates positively and negatively with other characters dealing with the size of the scapular blade. However, this distal expansion is suggested to be an osteological correlate of the *M. teres major* (Remes, 2007). This muscle has been hypothesised to be a specialised part of *M. latissimus dorsi* that attaches to the dorsal part of the scapula. This muscle seems to have originated at least four times in mammals, agamids, archosaurs, and chelonians (Remes, 2007). The distal expansion, which is more posteriorly expanded than it is anteriorly, supporting the idea of it being an extension of the *M. latissimus dorsi* that extends along the neural spines, is present in *Eoraptor, Dilophosaurus.* and absent in *Herrerasaurus.* Within sauropodomorphs: in *Saturnalia* there is a posterodistal process that...
also expands distally the scapular blade; in *Efraasia*, where the structure is less pronounced; in *Massospondylus carinatus* (specimen BP/1/5241) the expansion is also similar to a process, as in *Saturnalia*; prominent posterior expansions are also present in *Ruehleia, Unaysaurus, Plateosaurus* and *Antetonitrus*; finally, in *Lufengosaurus*, the structure is present, but not as prominent. The size of this expansion could also be related to the size of the suprascapular cartilage.

Figure 4.101. Orientation and measurement defined in this thesis. The codes correspond to the measurements reported in the correlation map above (Figure 4.100). Right and left scapula of *Efraasia* based on SMNS 12997 in anterior view.

SC4. D464. Scapula, scapular blade, distal expansion on the anterior margin: absent (0), present (1). NEW

This second character treats the anterior expansion as the osteological correlate of the *M. levator scapulae* (Remes, 2007) and an increase of size in the *M. deltoideous scapulari* (Otero, 2018). In *Ruehleia*, there is evidence of a posterior distal expansion, but the anterior margin is not expanded as much as the posterior margin. In *Unaysaurus*, the anterior margin is as expanded as the posterior one, condition also present in *Lufengosaurus*,

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Massospondylus carinatus, and Plateosaurus. In the case of basal sauropods, such as Patagosaurus, only the anterior expansion is present, and has the scar of a *M. levator scapulae*, whereas the posterior margin is slightly expanded but without a scar. This reduction on the distal expansion can be attributed to several phenomena: an increase of the area occupied for the suprascapular cartilage, so that the attachment site for the *M. teres major* is still present in the posterior margin of the suprascapular cartilage or reflect a true loss of the *M. teres major*. The presence of the anterior expansion within the scapula correlates with the speculated development of the neck muscles. The *M. levator scapulae* also has osteological correlates along the cervical vertebrae (Otero, 2018). The size of the distal expansion is related to the size of the scapula, as discussed above, so this character is also treated as a neomorphic character only.

SC5. A467. Scapula, scapular blade, minimal anteroposterior breadth relative to its dorsal margin (Wilson, 2002; Remes et al., 2009).

![Figure 4.102. Gap-coding for character SC5. The original formulation considered the limit in 0.5, which is close to the average identified in the sample analysed here. Gap-coding identified four character states: < 0.36 (0), [0.49, 0.68) (1), [0.68, 0.77) (2), [0.77, ∞).](Image)
SC6. A468. Scapula, base, cross section: flat or rectangular (0), D-shaped (1) (Wilson, 2002; Remes et al., 2009).


Comment: This ridge was named as the ventromedial ridge in Otero and Pol (2013) and it is probably the insertion site of the M. scapulohumeralis posterior (Otero, 2018). The term “posteromedial ridge” follows the convention of the myological terms. After assessing this character in several outgroups (i.e. Lesothosaurus, Scelidosaurus, Scutellosaurus, Coelophysis) this ridge is present on dinosaurs that have unequivocally been referred as bipedal, being absent in Scelidosaurus and sauropods.

SC9. D470-1. Scapula, posteromedial ridge, extension: before the ventral most third of the scapular blade (0), extending beyond the most ventral third of the scapular blade (1) NEW.

SC10. D460-1. Scapula, acromial ridge: absent (0), present (1) NEW.

Comment: The term acromion in Sereno (1993) refers to the anterior portion of the scapula, however the most consistent term is to restrict the acromion to the process or facet to articulate with the clavicle (sensu Romer, 1956). In this sense, the acromial ridge has a component in the acromial region of the scapula, and coincides with the character illustrated in Otero (2018).

SC11. D460-2. Scapula, acromial ridge, extending posteriorly beyond the acromial length: present (0), absent (1) NEW.

SC12. D460-3. Scapula, scapular fossa, area that the fossa occupies in the scapular head: less than or equal to 50% (0), more than 50% (1) NEW.

SC13. A460-4. Scapula, surface posterior to acromial ridge and distal blade: is excavated (0); is flat or slightly convex (1) (Upchurch et al., 2004a, 2004b; Tschopp et al., 2015)
Figure 4.103. Scapulocoracoid from several sauropodomorphs.
4.3.2 Forelimb

4.3.2.1 Humerus

H1. A480. Humerus, length relative to the length of the femur.

Figure 4.104. Anatomy of the articulated forelimb of Seitaad, based on UMNH VP 18040.

Figure 4.105. Gap-coding of character H1. The ratio was measured only in the taxa whose individual had the two bones. Three character states are identified: <0.38 (0), [0.38,0.42) (1), [0.42,0.58) (2), [0.58, 1]. The original formulation set limits between less than 0.6, between 0.6 and 0.8, and more than 0.8.
H2.A497. Humerus, maximum humeral distal width relative to the length of the humerus (Yates and Kitching, 2003; Langer, 2004; Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

**Comment.** The distal width is defined here as the maximum distance between the furthest points of the epicondyles, whereas the humeral length is defined as the maximum distance between the proximalmost point of the humeral head and distalmost point of the distal end.

![Graph showing the variation of character H2](image)

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<th>Gap-coding</th>
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<td>45.76613</td>
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</table>

Figure 4.106. Gap-coding of character H2. Gap-coding identified three states that describe the variation with less entropy than the original coding, setting the limit to 0.3. The three states identified by gap-coding are: <0.6 (0), [0.16,0.42) (1), [0.42, 0.6) (2).
H3.B257. Humerus, proximal end, relationship between the surfaces of the humeral head and the median tuberosity: continuous surface (0), separated by a groove (1) (Han et al., 2012; Baron et al., 2017; Figure 4.108).

**Comment:** When orientated in proximal view, if there are two distinct surfaces separated, then that space of separation is defined as a groove. This character has been modified from Baron et al., 2017, where the medial tuberosity is conditioned to being “prominent”. It also specifies that this separation needs to be a groove, but to reduce confusion it is better to simply state that proximally there is one continuous surface or two distinct ones. The proximal surface is delimited by a margin that separates the body of the bone, that is concave in two directions, whereas the proximal surface is convex in two directions.
Figure 4.108. The arrow points at two distinct types of grooves. The one in *Eoraptor* is a deformation of the proximal surface, which stays convex in two directions. The one in *Herrerasaurus* effectively produces two condyles.

H4.A483/A483-1. Humerus, proximal articular surface, continuity with the deltopectoral crest: continuous convexity (0), humeral head separated by an indentation from the deltopectoral crest (1)

H5.A483-2. Humerus, proximal articular surface, separation between the humeral head and the deltopectoral crest: ridge (0), edge (1), hinge (2) Unordered (modified from Nesbitt, 2011; Baron et al., 2017; Figure 4.109).

**Comment:** This character refers to the relationship between the surfaces of the anterolateral margin of the deltopectoral crest (=dorsal margin in Nesbitt, 2010). In Nesbitt, 2010 the character state 0 is scored for *Euparkeria* and *Silesaurus*, and for *Nyasaurus* in Baron et al., 2017. The rest of the dinosaurs are scored 1. The term “gap” is not clearly defined, since in Nesbitt, 2010 there is a reference to a connection between the anterolateral surface of the deltopectoral crest and the proximal articular surface by a thin ridge. Redefining the ridge of bone as a topography with only two identifiable faces, then this means that for character state 1 to be scored, the two surfaces need to be separated somehow. In the case of *Lufengosaurus* and *Ruehleia*, the proximal articular surface forms
a continuous surface with the anterolateral margin of the deltopectoral crest, but it is clearly separated by an inflection point, or a hinge line. To operationalise this character, the surface is considered here as a Euclidean plane, so that all the points of a surface are connected within its edges. This means that there are three ways in which the deltopectoral can be spatially separated from the proximal articular surface: a) by a ridge of bone, b) with an edge that effectively produces two distinct surfaces, c) or by a hinge line creating two limbs of the same surface plane.

Figure 4.109. Interpretation of character H5.

H6.A482-1. Humerus, humeral head, shape of the dorsal margin in lateral-medial view: flat (0), convex (1) (modified from McPhee et al., 2015).

**Comment:** This character is operationalised by only specifying the general form of the dorsal margin of the humeral head. The humeral head and the medial tuberosity, named “internal tuberosity” in other archosaurs (Nesbitt, 2011), are usually separated by an indentation in their continuous surface in sauropodomorphs, as in *Mussaurus*. The morphologies of the deltopectoral crest and the medial tuberosity are excluded from this character.

H8.B253. Humerus, deltopectoral crest, location of the apex along the humeral length. (modified from Bakker and Galton, 1974; Juul, 1994; Novas, 1996; Benton, 1999; Nesbitt, 2011; Baron et al., 2017)

H9.A490/A487. Humerus, deltopectoral crest, orientation: laterally orientated (0), anterolaterally orientated (1), anteriorly orientated (2) (Ordered) (Gauffre, 1996; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

**Comment:** This character is here redefined as a multistate character to include the degrees of variation on the orientation of the deltopectoral crest. Originally, it was a presence/absence character regarding the visibility of this feature in posterior view. The visibility of a structure depends on their relative orientation and is not a neomorphic character.

H10. A487. Humerus, deltopectoral crest, orientation of the longitudinal axis relative to the transverse axis of the distal condyles: slants at 45°-60° (0), perpendicular to the transverse axis or greater than 90° of the distal condyles (1) (Sereno, 1999a; Galton and Upchurch, 2004; Upchurch et al., 2007a; Pol et al., 2011; Sekiya et al., 2013).
Figure 4.110. Comparison of the orientations of the deltopectoral crest in the humerus in the sauropodomorph *Ruehleia* (anterior view), in the theropod *Tawa* (anterior view) and the dinosauromorph *Nyasasaurus*. In Baron et al. (2017), *Nyasasaurus* was found nested within Massospondylidae. After a reassessment of the morphology of the humerus of *Nyasasaurus*, the orientation of the deltopectoral crest and the morphology of the proximal part of the humerus displays an array of sauropodomorph features similar to *Ruehleia*, *Plateosaurus* *Efraasia* and *Asylosaurus*.

H11. A486. Humerus, deltopectoral crest: flange (0), ridge (1) (Wilson and Sereno, 1998; Yates and Kitching, 2003; Remes et al., 2009; Pol et al., 2011).

H12. A495. Humerus, deltopectoral crest, rugose pit centrally located on the lateral surface: absent (0), present (1) (Upchurch et al., 2007a; Yates, 2007a).

H13. A494. Humerus, deltopectoral crest, shape: triangular (0), polygonal with four or more vertices (1) (Gauthier, 1986; Upchurch et al., 2007a; Yates, 2007a)

**Comment:** To operationalise this character the shape is assessed by counting the corners instead of the subtriangular/sub-rectangular shapes. Three vertices are found in *Silesaurus*, *Euparkeria*, and *Nyasasaurus*. 

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H14. A485. Humerus, deltopectoral crest, extension relative to the humeral length from its proximal end: less than 0.3 (0), equal to or more than 0.3 but less than 0.5 (1), more than 0.5 (2) (Galton, 1990; Sereno et al., 1993; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

H15. A496. Humerus, distal end, shape of the ulnar condyle: rounded process (0), with a flat distal-medially facing surface bounded by a sharp proximal margin (1) (Yates, 2007a; Sekiya et al., 2013).

H16. A498. Humerus, distal condyles, articular surface: restricted to distal portion of humerus (0), exposed on anterior portion of humeral shaft (1) (Wilson, 2002; Remes et al., 2009).

H17. D499. Humerus, distal flexor surface, well-defined fossa: present (0), absent (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

H18. A499-1. Humerus, distal end, groove separating radial and ulnar condyles: absent (0), present (1) NEW.

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**Figure 4.** Variation in the humeral morphology displayed by three sauropodomorphs spread through the tree (all in anterior view, not to scale). *Coloradisaurus* has been considered as member of Massospondylidae, with a developed cuboid fossa that suggests a reduced level of manoeuvrability. *Antetonitrus* displays a more columnar humerus, with the median tuberosity more aligned with the ulnar condyle, signs of an obligate quadruped. *Lufengosaurus*, traditionally found in the same group than *Coloradisaurus*, shows a more developed cuboid fossa and more prominent distal condyles, indicating a developed grasping ability and a more biped stance.
4.3.2.2 Radius

R1. A505. Radius, length relative to the length of the humerus (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

R2. A510. Radius, distal condyle, shape: subcircular or oval in outline (0), subrectangular with a flattened posterior margin for articulation with the ulna radius (1) (Upchurch et al., 2007a; Pol et al., 2011).

R3. A509. Radius, distal breadth relative to midshaft breadth: less than 1.0 (0), equal to or more than 1.0 (1) (Wilson, 2002; Remes et al., 2009).

R4. A506. Radius, radial tuber for the *M. brachialis*: absent (0), present (1) (Otero et al., 2015).

R5. D507. Radius, radial ulnar process: triangular projection (0), rectangular lamina (1) NEW.

![Graph](image)

Figure 4.112. Gap-coding of character R1. The original formulation established the limit in 0.8. Here, four gaps are identified: <0.32 (0), [0.32, 0.66) (1), [0.66, 0.75) (2), [0.75, 0.8) (3), >0.8 (4).

4.3.2.3 Ulna

U1. C1/A500-1. Ulna, proximal end, shape: circular or quadrangular (0), subtriangular (1), triradiate (2) Unordered (Wilson and Sereno, 1998; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).

U2. C2/A500-2. Ulna, proximal end, anterolateral process: absent (0), present (1).

U3. C3/A500-3. Ulna, proximal end: anterolateral process closer to the olecranon (0), anterolateral process equidistant or closer to the anterior process (1) (Wilson and Sereno, 1998; Galton and Upchurch, 2004; Upchurch et al., 2007a; Sekiya et al., 2013).
Figure 4.113. Outlines of the proximal end of the ulnae of some sauropodomorphs. The proximal end of the ulna experiences a large variation within sauropodomorphs, and the disparity in the morphology observed in *Melanorosaurus* may indicate that the material needs further reassessment to test its referral. R stands for the radial fossa.

U4.A501. Ulna, proximal end, curvature of the medial surface that contacts the radius: flat or gently concave (0), deep radial fossa (1) (Yates, 2007a; Sekiya et al., 2013).

U5.A503. Ulna, olecranon process, greatly enlarged with a separate ossification forming a strongly striated proximo-anterior portion: present (0), absent (1).

U6.A504. Ulna, proximal end, anterior condylar process, length relative to the lateral condylar process: equal to 1.0 (0), greater than 1.0 (1).


U8.C2/A500-2. Ulna, proximal end, anterolateral process: absent (0), present (1).

U10. C3/A500-3. Ulna, proximal end: anterolateral process closer to the olecranon (0), anterolateral process equidistant or closer to the anterior process (1) (Yates, 2007a; Sekiya et al., 2013).

4.3.2.4 Carpals

Figure 4.114. Interpretation of the carpals in *Adeopapposaurus* and *Plateosaurus*. The distal carpal I is very reduced in *Plateosaurus* whereas in *Adeopapposaurus* the distal carpal I extends for most of the distal carpal I. This interpretation, as outlined in Peyre de Fabrègues (2016), considers the intermedium absent in *Plateosaurus* and reduced in *Adeopapposaurus*.

CAR1. A516. Distal carpal I, transverse width relative to the transverse width of the distal carpal II (Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

CAR2. A513. Distal carpal I, medial end, sulcus: absent (0), present (1) (Yates, 2007a; Sekiya et al., 2013).

CAR3. A515. Distal carpal I, lateral end onto distal carpal II: abuts (0), overlaps (1) (Yates, 2007a; Sekiya et al., 2013).

CAR4. A514. Distal carpal I, size relative to other carpals: equal to other distal carpals (0), significantly larger than other distal carpals (1) (Nesbitt, 2011).

CAR5. A517. Distal carpal I, transverse width relative to metacarpal I: less than 1.0 (0), equal to or greater than 1.0 (1).

CAR6. A518. Distal carpal II, relationship with the proximal end of metacarpal II: covering (0), not covering (1) (Yates, 2007a; Sekiya et al., 2013).

CAR7. A519. Distal carpal V, ossified: present (0), absent (1) (Ezcurra, 2010; Pol et al., 2011).

**Comment:** In Pol et al. (2011) character state 1 is only applied to *Heterodontosaurus*. In Ezcurra et al. (2010) character state 0 is “absent”, and it is applied to Crurotarsi and
Neornithischia. In Sekiya et al. (2013) this character is uninformative since all the scores are (1) “present, larger than other distal carpals”.

**Figure 4.115.** Manus of *Lufengosaurus* with the interpretation of the preserved carpals.

### 4.3.2.5 Metacarpals

**MC1.** A520. Manus, digits and metacarpals, longest: digit III, metacarpal 3 (0), digit II, metacarpal 2 (1) (Martínez et al., 2011).

**MC2.** A521. Manus, length of the manus relative to the whole length of the humerus and the radius (Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013).

**Figure 4.116.** Gap-coding for character MC2. The sample includes 21 specimens where the forelimb was preserved in the same individual. The original character states were: less than 0.3 (0), equal to 0.3 but less than 0.45 (1), equal to or greater than 0.45 (2). The new formulation considers the following states: \(<0.32\) (0), \([0.32,0.35)\) (1), \([0.38,0.44)\) (2), \([0.44,0.51)\) (3), \(>0.51\) (4).
MC3. A522. Metacarpus, shape: flattened to gently curved and spreading (0), a colonnade of subparallel metacarpals tightly curved into a U-shape (1) (Yates, 2007a; Sekiya et al., 2013).

MC4. A537. Metacarpals I-III, proximodorsal portion, extensor pits: symmetrical (0), asymmetrical (1) (Yates, 2007a; Nesbitt, 2011; Pol et al., 2011; Sekiya et al., 2013)

MC5. A525. Metacarpal I, proximal width relative to the proximal width of the second metacarpal: less than or equal to 1.0 (0), or greater than 1.0 (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MC6. A531. Metacarpal I, minimum transverse shaft width relative to the minimum transverse shaft width of second metacarpal: less than 2.0 (0), greater than 2.0 (1) (Yates, 2007a; Sekiya et al., 2013).

MC7. A524. Metacarpal I, proximal end: flush with other metacarpals (0), inset into the carpus (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MC8. A526. Metacarpal I, proximal width of the first metacarpal relative to its length: less than 0.65 (0), equal to or more than 0.65 but less than 0.8 (1), more than 0.8 but less than or equal to 1.0 (2), more than 1.0 (3) (Yates, 2007a; Sekiya et al., 2013).

MC9. A537-1. Metacarpal I, proximodorsal portion, extensor pits: symmetric depression (0), asymmetric concavity (1).

MC10. A533. Metacarpal I, distal condyle, transverse axis orientation relative to the axis of shaft: bevelled approximately 20° proximodistally (0), perpendicular (1) (Wilson, 2002; Remes et al., 2009).

MC11. A530. Metacarpal I, ventromedial margin of first metacarpal: poorly concave (0) or deeply concave (1) (Otero et al., 2015).


MC13. A534. Metacarpal I, distal condyles, alignment relative to medial condyle: approximately aligned or slightly offset (0), lateral condyle strongly distally expanded relative to medial condyle (1) (Yates, 2003a; Nesbitt, 2011; Pol et al., 2011).
MC14. A529. Metacarpal I, width at the middle of the shaft relative to the length of the bone: less than or equal to 0.35 (0), more than 0.35 (1) (Nesbitt, 2011).
MC15. A528. Metacarpal I, medial distal condyle: of the same size (0) or dorsoventrally smaller (1) than the lateral distal condyle.
MC17. A537-2. Metacarpal II, proximodorsal portion, extensor pits: symmetric depression (0), asymmetric concavity (1)
MC18. A541-1. Metacarpal II, distal end, shape in distal view: rectangular (0), trapezoidal with flexor rims of distal collateral ligament pits flaring beyond extensor rims (1)
MC19. A539. Metacarpal II, length relative to that of metacarpal III: less than 1.0 (0), equal or greater than 1.0 (1) (Nesbitt, 2011; Pol et al., 2011)
MC21. A537-3. Metacarpal III, proximodorsal portion, extensor pits: symmetric depression (0), asymmetric concavity (1)
MC23. A542. Metacarpals IV-V, proximal portions, position relative to metacarpals III and IV respectively: lateral (0), set at the palmar surfaces (1).
MC24. A543. Metacarpal IV-V, shaft width relative to that of metacarpals I-III: more than or equal to 1.0 (0), less than 1.0 (1) (Nesbitt, 2011; Pol et al., 2011)
MC25. A545. Metacarpal IV, length respect to that of metacarpals I-III: more than or equal to 1.0 (0), less the 1.0 but more than 0.5 (1), equal to or less than 0.5 (Wilson, 2002 Nesbitt, 2011)
MC26. A544. Metacarpals IV-V, ventral to metacarpals I-III: absent (0), present (1).
MC27. A547. Metacarpal V, proximal end, articulation surface curvature: flat (0), convex (1) (Upchurch et al., 2007a; Yates, 2010; Pol et al., 2011).
MC28. A546. Metacarpal V, length relative to its width at the proximal end: more than 1.0 (0), equal to or less than 1.0 (1) (Upchurch et al., 2007a; Yates, 2007a; Pol et al., 2011; Sekiya et al., 2013).

MC29. A550. Metacarpal V, length relative to the length of the metacarpal III: less than 0.75 (0), or greater than 0.75 (1) (Yates, 2007a; Sekiya et al., 2013).

MC30. A549. Metacarpal V, length relative to the length of the longest metacarpal: more than 0.9 (0), equal to or less than 0.9 (1).

MC31. A548. Metacarpal V: absent (0), present, although reduced (1)

MC32. A523. Metacarpals, proximal ends: overlap (0), abut one another without overlapping (1) (Nesbitt, 2011)

4.3.2.6 Manual digits

Figure 4. 117. Outlines of the manus of Anchisaurus, Asylosaurus and Ammosaurus, showing the differences in the morphologies in the metacarpals and phalanges and the clear distinction in robustness between Anchisaurus and Ammosaurus.

MD1. A556. Manual digit I, length relative to the length of manual digit II: less than 1.0 (0), equal to or greater than 1.0 (1) (Yates, 2007a; Sekiya et al., 2013).

MD2. A552. Manual digit I, angle of ventrolateral twisting of the transverse axis of the distal end of the first phalanx relative to its proximal end (Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013).

MD3. A553. Manual digit I, ventrolateral twisting of the transverse axis of the distal end of the first phalanx of manual digit one relative to its proximal end: absent (0), present proximodorsal lip aligned with dorsal margin of medial distal condyle (1), present proximodorsal lip aligned with central region of medial ligament pit of the distal condyle (2)

MD4. A554. Manual digit I, phalanx I.1, length relative to that of metacarpal I: more than 1.0 (0), equal to or less than 1.0 (1) (Yates, 2007a; Martínez et al., 2011; Sekiya et al., 2013).
MD5. A557. Manual digit I, phalanx I.1, shape of the proximal articular surface: rounded (0), with an embayment on the medial side (1) (Yates, 2007a; Sekiya et al., 2013).

MD6. A561. Manual digit I, phalanx I.1, shape: subcylindrical (0), wedge-shaped (1) (Wilson, 2002; Yates, 2007a; Remes et al., 2009; Sekiya et al., 2013).

MD7. A564. Manual digit II, length of the penultimate phalanx of manual digit I relative to the length of the metacarpal II: less than 1.0 (0), equal to or greater than 1.0 (1) (Yates, 2007a; Sekiya et al., 2013).

MD8. A565. Manual digit III, length of the penultimate phalanx relative to the length of metacarpal III: less than 1.0 (0), equal to or greater than 1.0 (1) (Yates, 2007a; Sekiya et al., 2013).


MD10. A570. Manual digits II and III, shape of the unguals: straight (0), strongly curved with tips projecting well below flexor margin of proximal articular surface (1) (Yates, 2010; Pol et al., 2011).

MD11. A566. Manual digit II, length of the ungual of manual digit II relative to the ungual of digit I: more than 1.0 (0), equal to or less than 1.0 but more than 0.75 (1), equal to or less than 0.75 (2) (Yates, 2007a; Sekiya et al., 2013).


MD13. A571. Manual digits II and III, phalangeal formula: 3 4 (0), with at least one phalanx missing from each digit (1) (Yates, 2007a; Sekiya et al., 2013).

MD14. A573. Manual digits IV and V, phalangeal formula: greater than 2-0 respectively (0), less than 2-0 respectively (1) (Yates, 2007a; Sekiya et al., 2013).

MD15. A562. Manual digit I, phalanx I.1, proximal heel: absent (0), present (1) (Upchurch et al., 2007a; Pol et al., 2011).

MD16. A568. Manual digit II, phalanx II.2, length respect to that of phalanx II.1, indicating the elongation of the penultimate phalanges in the manus: less than 1.0 (0), equal to or more than 1.0 (1).

MD17. A574. Manual digit V, phalanges: present (0), absent (1) (Martínez et al., 2011; Nesbitt, 2011; Pol et al., 2011).
MD17. A572. Manual digits II-IV, length of phalanx II.1 and IV.1 relative to the length of the rest non-ungual phalanges in their respective digits: less than 1.0 (0), equal to or more than (1) (Yates, 2003b)

MD18. A551. Manual digits, non-ungual phalanges, proximodistal length relative to its transverse breadth: less than 1.0 (0), more than 1.0 (1) (Yates and Kitching, 2003).

MD19. A563. Manual digit I, phalanx I.1, proximodistal length relative to its width: more than 1.0 (0), equal to or less than 1.0 (Wilson, 2002).


MD21. A559. Manual digit I, phalanx I.1, length relative to its mediolateral width at proximal end: much greater than (0), subequal or equal to (1), or much less than (2) (Yates, 2007; Otero et al., 2015).

MD22. A555. Manual digit I, length of the digit I plus the length of the metacarpal relative to that of the ungual: more than 1.0 (0), equal to or less than the 1.0 (1) (Nesbitt, 2011).


MD24. A558. Manual digit I, phalanx I.1 relative to all the non-ungual phalanx of the manus: is not the longest (0), is the longest (1) (Nesbitt, 2011).

4.3.3 Pelvic girdle

PG1. A575. Pelvic girdle, acetabular fossa proportions, length relative to height: more than or equal to 1.0 (0), less than 1.0 (1) (Yates, 2003; Pol et al., 2011).
Figure 4. 118. Operationalisation of the pelvic characters using the orientation of the elements. Illustrated above the combinations that are observable in archosaurs.

Figure 4. 119. Operationalisation of the pelvic characters using connectivity. Illustrated above the combinations that are observable in archosaurs.
4.3.3.1 Ilium

I1. A602. Ilium, iliac blade in dorsal view: straight (0), sigmoidal (1), laterally curved (2) (Ezcurra, 2010).

I2. A599. Ilium, dorsal margin, curvature of the outline in lateral view: describes a periodic or sinusoidal curve (0), describes a polynomial curve (1).

I3. A599-2. Ilium, dorsal margin, polynomial outline in lateral view: straight (0), concave parabolic (1), convex parabolic (2), sigmoidal (3) (modified from Gauffre, 1996; Heerden and Galton, 1997; Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007b; Yates, 2007b, 2007a; Pol et al., 2011; Sekiya et al., 2013).

Comment: There is a lot of variation in the formulation of this character. The original formulation of this character had two character states: strongly convex (0), straight (1). In C245 Y2007, this character was formulated as a neomorphic character regarding to the presence of a strongly convex dorsal margin. In C204 P2011, the character alludes to a step in the dorsal margin that can be observed in *Melanorosaurus* and *Riojasaurus*, as illustrated in Heerden and Galton (1997). Ezcurra (2010) modified this character adding three states: straight (0), concave (1), and convex (2). The state concave (1) is therein assigned to *Marasuchus* and *Eoraptor*. The dorsal margin in *Eoraptor* cannot be considered concave,
but the feature is clear in *Marasuchus*, and resembles the condition in *Agnosphitys*, and could also be argued that the step-like feature in *Melanorosaurus* and *Riojasaurus* can be also considered concave. There is a lot of variation on the morphology of the dorsal margin of the ilium, and it could be more descriptive to think of the number of crest and valleys in the curved outlines. The dorsal outline of the iliac blade of *Plateosaurus* looks parabolic, as so it is the outline of *Herrerasaurus* because the outlines have one crest. In the case of *Lesothosaurus* the iliac blade has an anterior crest and a posterior valley, whereas *Agnosphitys* has an anterior valley and a posterior crest; these outlines describe periodic or sinusoidal curves. In the case of *Melanorosaurus* and *Riojasaurus*, the stepped outline describes a sigmoid curve, which is also a polynomial curve.

Figure 4. 121. Anatomy of the ilium of *Ruehleia*. Top, dorsal view, middle, posterolateral view, bottom, anterolateral view.
I4. A608. Ilium, iliac blade, orientation of the long-axis: horizontal (0), slopes anterodorsally in lateral view (1) (Salgado et al., 1997; Upchurch et al., 2007a; Nesbitt, 2011; Sekiya et al., 2013).

I5. D608. Ilium, iliac blade, position relative to the acetabulum: projected posteriorly (the length posterior to the acetabulum is larger than the anterior length) (0); projected anteroposteriorly (1); projected anteriorly (2) (based on Rasskin-Gutman and Buscalioni, 2001).

I6. A578. Ilium, preacetabular process, scar corresponding to the attachment of the *M. iliofemoralis cranialis*: absent (0), present (1) (Sereno, 1999a; Galton and Upchurch, 2004; Upchurch et al., 2007a; Martínez et al., 2011; Sekiya et al., 2013).

I7. A579. Ilium, preacetabular process, extension relative to the anterior-most extension of the pubic peduncle: not extending anteriorly to the pubic peduncle (0), extending anteriorly to the pubic peduncle (1) (Galton, 1971, 1990; Galton and Cluver, 1976; Gauffre, 1996; Yates and Kitching, 2003; Galton and Upchurch, 2004; Yates, 2007a; Upchurch et al., 2007a; Yates, 2007b; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

**Comment:** In C206 Pol et al. (2011) *Melanorosaurus* has been scored as a polymorphism. In all the illustrations from specimens referred to *Melanorosaurus readi*, namely NM QR 1551 and NM QR 3532, the preacetabular process does not expand beyond the level of the pubic process. The ilium referred to *Meroktenos thabanensis*, considered *Melanorosaurus*, does not have a preserved preacetabular process (Peyre de Fabrègues and Allain, 2016). In the modified versions from Yates (2007b), *Anchisaurus* is scored as a polymorphism; the specimen YPM 1883 has a damaged ilium, and it is not possible to assess the level of the two processes, although they seem to have surpassed the pubic peduncle, which is the case on specimen YPM 208. Specimen YPM 209, here referred to *Ammosaurus*, is also broken on this part of the ilium.

I8. A580. Ilium, preacetabular process, offset of the vertical curve of the anterior margin (Sereno, 1999a; Yates and Kitching, 2003; Martínez et al., 2011; Pol et al., 2011; Sekiya et al., 2013).

**Comment:** This character was conceived originally as a multistate character covering the different morphologies, being either triangular, blunt, hatchet-shaped or subcircular. The character was defined in the three matrices using different parameters: C205 U2007 defines
it on terms of its length and the outline, C247 Y2007 uses the angle of the ventral margin of the preacetabular process, and C207 P2011 that combines the number of vertices, the outline, and the linear measurements of the preacetabular process. Martinez et al. (2011) defined this character as well and the same taxa that are scored as “subcircular” are the same that Pol et al. (2011) scored as hatchet-shaped. Although the two definitions are contradictory, they have been assigned to the same taxa. This conflicts in the definition of this character use the measurement of the offset of the two slopes that generate the curve of the anterior margin. This measurement is described in detail in the scapular characters.

I9. A581. Ilium, preacetabular process, depth relative to the depth of the ilium above the acetabulum (Wilson, 1999; Yates and Kitching, 2003; Upchurch et al., 2007a; Yates, 2007b, 2007a; Apaldetti et al., 2011; Sekiya et al., 2013)

![Figure 4.122. Gap-coding of character I9. This character is correlated with C296 in Nesbitt, 2011 and only this one is kept in this work because it was obtained for basal sauropodomorphs. This character finds four distinct categories through gap coding: (0, 0.37] (0), (0.37, 0.71] (1), (0.71, 0.85] (2), (0.85, ∞) (3). Moreover, this character is positively correlated with character C296 in Nesbitt (2011), which measures the anteroposterior length of the preacetabular and postacetabular processes. This correlation is based on 57 dinosaur ilia.](image)

I10. A582. Ilium, preacetabular process, length relative to its depth (Yates and Kitching, 2003; Galton and Upchurch, 2004; Upchurch et al., 2007a; Yates, 2007b, 2007a; Pol et al., 2011; Sekiya et al., 2013).
Figure 4.123. Gap-coding of character I10. This character finds four distinct categories through gap coding: < 0.6 (0), (0.6, 1.65] (1), (1.65, 1.96] (2), > 1.96 (3). Moreover, this character is positively correlated with character C296 in Nesbitt (2011), which measures the anteroposterior length of the preacetabular and postacetabular processes. This correlation is based on 57 dinosaur ilia.

I11. A584. Ilium, preacetabular process, iliac preacetabular ridge: absent (0), present (1) (Yates, 2010; Pol et al., 2011).

Comment: This ridge could have provided additional attachment to the *M. iliofemoralis cranialis* that extends from the preacetabular process to the anterior face of the femur. This extra attachment is present in *Chromogisaurus, Panphagia, Agnosphytys, Staurikosaurus, Marasuchus, Herrerasaurus, Silesaurus, Guaibasaurus, Saturnalia, Bagualosaurus* and *Eoraptor*. Except for *Agnosphytys*, there is evidence that all these forms were of morphotype 1 and were cursorial. The distribution of the character states seems to be a good predictor of obligate bipedality in dinosaurs. It is also present in the theropods *Coelophysis* (Rinehart et al., 2009), *Liliesternus, Elaphrosaurus* (Langer and Benton, 2006), and *Allosaurus*, in the latter the ridge does not extend onto the supraacetabular crest (Madsen, 1993); and the bipedal basal ornithischians *Lesothosaurus* (Sereno, 1991) and *Hypsilophodon* (Galton, 1974), although absent in the quadrupedal basal ornithischians *Scelidosaurus* and *Scutellosaurus*.

In the case of *Yunnanosaurus robustus*, an iliac preacetabular ridge is observed in the referred specimen CUP 2102, considered to be a hatchling (Simmons, 1965). The possibility that this character is ontogenetically affected is briefly discussed here. In the embryos referred to *Massospondylus* (Reisz et al., 2005, 2010) and *Lufengosaurus* (Reisz et al., 2013) the lateral surface of the iliac blade does not have any feature, and the ridge is
also absent in the adults of *Massospondylus* and *Lufengosaurus*. In the early post hatchling of *Yunnanosaurus robustus*, the ridge is also absent (Sekiya et al., 2013). Despite scarce evidence, it seems to be that the most likely explanation is that CUP 2102 is more similar to the ilia of the basal most sauropodomorphs, remarkably similar to *Chromogisaurus*, *Saturnalia* and *Buriolestes*.

**Figure 4.124. Anatomy of ilium of *Yunnanosaurus* sp (CUP61). This ilium corresponds to a possibly 'prosaupod' embryo, referred to the genus *Yunnanosaurus*.**

I12. A616. Ilium, postacetabular process, posterodorsal margin: meets at a point with the posteroventral margin (0), is separated from the posteroventral margin by a posterior margin (1) (Upchurch et al. 2007, Yates, 2010 Pol et al., 2011) (Y258).

**Comment:** The formulation in C258 Y2007 and C218 U2007 include the morphology of the posterodorsal margin, which is covered in I2 and I3. To make this character independent from the morphology of the dorsal margin, the character state for “square ended postacetabular process” is replaced by the presence of a posterior margin separating the posterodorsal margin of the ilium from the posteroventral margin.

I13. A620. Ilium, postacetabular process, muscle origin areas (*Mm. flexor tibialis* and *iliotibialis*) on the posterior portion: smooth (0), strong trapezoidal rugosity extended along the whole height of the posterior third of the process (1) (Ezcurra, 2010).

I14. A594/A597/A596. Ilium, acetabulum, medial wall (=ventral acetabular flange): fully closing acetabulum (0), partially open acetabulum (1), open
acetabulum, with the medial wall at the same level of the lateral iliac margin of the acetabulum (2) (modified from Butler et al., 2008).

**Comment:** Several versions of this character have been proposed dealing with the concavity or convexity of the ventral margin of the ilium. The ventral margin has a lateral and a medial component, and the topology of the acetabulum is widely understood and discussed as being fully closing, partially opened, or opened. To make this character precise, the terms “open” and “closed” as strictly assessed, so that if there is a bone sheet in front of the femoral head, the acetabulum is not open. This bone sheet has been named as either medial wall or as the ventral acetabular flange (Sereno and Arcucci, 1994; Novas, 1996; Benton, 1999; Fraser et al., 2002; Irmis et al., 2007; Martínez et al., 2011; Nesbitt, 2011; Baron et al., 2017a). *Guaibasaurus* was scored as polymorphism in C251 mY2007, but the wall seems to be consistent with a partially open acetabulum, although the rest of the acetabulum is not preserved (Bonaparte et al., 2007; Langer et al., 2010; Agnolín and Martinelli, 2012).

I15. A586/A587. Ilium, supraacetabular margin: ridge (0), well-developed crest (1) (Ezcurra et al., 2010; Pol et al., 2011).

I16. A591. Ilium, supra-acetabular crest, widest point: located halfway between the pubic and ischial contacts (0), on the pubic peduncle (1) (Yates, 2003b; Pol et al., 2011).

I17. A593. Ilium, supraacetabular crest, extension along the pubic peduncle: partially along the pubic peduncle (0), along the entire pubic peduncle (1) (Ezcurra et al., 2010).

**Comment:** In C348 in Sekiya et al. (2013) there is a polymorphism for *Plateosaurus*. In GPIT 1, the ilia have a supraacetabular crest along the pubic peduncle all the way to the distal end, and the highest point of the supraacetabular crest is located at the base of the pubic peduncle, and the rest of the crest is a narrow ridge.

I18. A590/A588. Ilium, supra-acetabular crest, orientation: projects laterally (0), ventrolaterally (1), projects ventrally (2) (C264 Nesbitt, 2011)

I19. A603. Ilium, pubic peduncle, length of the pubic peduncle relative to the anteroposterior width of its distal end (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).
**Comment:** It was found that C254 Y2007 is inversely correlated to C252 Y2007. To assess the relation on a closer detail, six outliers were excluded from the regression: ilia belonging to *Shunosaurus*, *Pantydraco* and *Thecodontosaurus*, outliers for C254 Y2007, and ilia belonging to *Barapasaurus*, *Coelophysis* and *Meroktenos* for C252 Y2007. Regarding *Shunosaurus*, *Barapasaurus* and *Coelophysis*, the regression model may fail to predict them due to the small sample of sauropods and theropods included in the analysis. The ilium of *Meroktenos* has its distal ends worn off, and therefore the measurements taken from the picture might not be correct. The ilia in *Pantydraco* and one ilium from *Thecodontosaurus* that were removed from the analysis are well preserved but skewed the correlation. A lot of the taxa show intraspecific variation, such as *Plateosaurus engelhardti*, *Efraasia* and *Thecodontosaurus*, and there are cases where there is intraindividual variation (left from right), such as in *Lufengosaurus*, ‘*Sellosaurus*’ *Gyposaurus*, *Jaklapallisaurus* and *P. engelhardti*. This could suggest that as the anteroposterior length of the pubic peduncle reduces, the ischiadic peduncle is more developed.

![Figure 4.125. Regression model between the ratio of the length of the pubic peduncle relative to the anteroposterior width of its distal end against length relative of the ischium and that of the pubic peduncle.](image-url)
Figure 4.126. Gap coding of I19 produces the following character states: (0, 0.89] (0), (0.89, 1.3] (1), (1.3, 1.71] (2), (1.71, 3] (3), (3, 4.1] (4), (4.1,∞) (5).

I20. A604. Ilium, ischial peduncle: present (0), not borne on a protruding peduncle (so that the chord connecting the distal end of the pubic peduncle with the ischial articular surface contacts the postacetabular process) (1) (Yates, 2010).

I21. A606. Ilium, ischial peduncle, posteriorly projecting 'heel' at the distal end: absent (0), present (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

Comment: Saturnalia has been scored as polymorphic for this character in C253 mY2007, and C359 in Sekiya et al. (2013), but in the illustrations in Langer (2003), the ischiadic peduncle is very reduced, to simply the articular facet of the antitrochanter. It is therefore scored as I20-1, and not applicable for I21.

I22. A605. Ilium, ischial peduncle, axis of process: ventrally directed (0), posterovertrally directed (1) (Martinez et al., 2011; Nesbitt et al., 2011).

I23. A612. Ilium, brevis fossa (attachment of the m. caudifemoralis brevis), well-developed with clear margins on the ventral surface of the postacetabular process: absent (0), present (1) Ordered (Yates, 2007; Nesbitt, 2011; Pol et al., 2011).

Comment: The brevis fossa is here considered only when there is a depression on the posterovertral margin that is delimited by clear margins on the ventral surface of the
postacetabular process. If the margins are not delimited, then the fossa becomes indistinct of the rest of the iliac surface. Pol et al. (2011) scored *Eoraptor* as a ventral slope or as a *brevis* fossa, but the illustrations in Sereno et al. (2012) indicate the presence of a *brevis* fossa.

I24. D619-1. Ilium, posteroverentral margin: J-shaped (0), M-shaped (1) (based on Lu et al., 2007).

**Comment:** This character was proposed by Lu et al. (2007) as a distinctive feature between *Yunnanosaurus youngi* and *Y. huangi*. The posteroverentral margin has a M-shape outline when there is an embankment where the *m. cadufemoralis brevis* attaches, and when there is a *brevis* fossa. The J-outline can be present regardless of the *brevis* fossa.


4.3.3.2 Pubis

![Pubis](image)

Figure 4.127. Anatomy of the pubis of *Coloradisaurus*, based on Apaldetti et al. (2013).
Comment: The original description of this character used the terms “anteroventral” and “opisthopubic” as character states. A review of the morphospace of the pelvic girdle of archosaurs proposed a categorisation of the angles relative to the vertebral column: propubic [0 to 68), mesopubic [68, 108], and opisthopubic (108, 180) (Rasskin-Gutman and Buscalioni, 2001). However, in the same review they proposed a defined set of categories to describe the orientation of the elements in the pelvic girdle. Those terms have been adopted in this work. An anteroverted pubis is found in Crurotarsi, basal dinosauromorphs such as Marasuchus, and basal sauropodomorphs, like in Riojasaurus. The pubis is vertical also in Crurotarsi, Herrerasaurus, and sauropods. Finally, the retroverted orientation is found in ornithischians and some theropods. The original formulation that includes the terms “propubic” and “opisthopubic” generates polymorphisms as the one reported for Herrerasaurus in Pol et al. (2011) scored as both propubic and opisthopubic.

PU2. A623. Pubis, length relative to the femoral length: less than 0.7 (0), equal to or more than 0.7 (1).

PU3. A622. Pubis, the width of the conjoined pubes relative to their length: less than 0.75 (0), equal to or more than 0.75 (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

PU4. A628. Pubis, proximal pubis, pubic tubercle on the lateral surface: present (0), absent (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

PU5. A638. Pubis, pubic tubercle, shape: rounded (0), semilunate plate (1) (Yates and Kitching, 2003; Pol et al., 2011)

PU6. A629. Pubis, proximal anterior profile of pubis: anterior margin of pubic apron smoothly confluent with anterior margin of the iliac pedicel (0), iliac pedicel set anterior to the pubic apron creating a prominent inflexion in the proximal anterior profile of the pubis (1) (Yates, 2010).

PU7. Pubis, ambiens process: present (0), absent (1). NEW

PU8. A627-1. Pubis, pubic obturator foramen: absent (0), present (1)

PU9. A627-2. Pubis, pubic obturator foramen, diameter relative to the acetabulum diameter
Comment: This character was originally a mixture of a continuous character and a neomorphic one. The acetabulum diameter is here measured as the distance between the pubic and ischiadic peduncle of the ilium.

PU10. A626. Pubis, obturator foramen, position in anterior view: iliac pedicel right anterior to the obturator foramen (0), iliac pedicel and obturator foramen lateromedially displaced (1). (Y263).

Comment: The original formulation of this character had an overlap between state 0 “partially occluded” and state 1 “completely visible”. Tectonic deformation could affect these states. The reformulation here requires an assessment of the proximal end and see how likely the two structures have shifted along a mediolateral plane.

PU11. B335. Pubis, pubic plate, length: 0, less than 40% of the pubic shaft length, 1, more than 40% of the pubic shaft length (Pol and Powell, 2007).

PU12. A636/B347. Pubis, pubic apron: present (0), absent (1). NEW

Comment: The pubic apron is a structure defined as the pubic shafts twisted lateromedially with respect to the proximal end. The pubic shafts are placed on the same anteroposterior plane as the proximal end in Genasauria.


Comment: This reformulation reduces the variable “distally tapering” from the state (0). The shape of the distal end is dealt with in other character statements.

PU15. B348. Pubis, median gap below the pubic apron: present (0), absent (1). NEW

PU16. A630. Pubis, transverse pubic blades: absent (0), present (1).

PU17. A642. Pubis, the orientation of distal third of the blades of the pubic apron: confluent with the proximal part of the pubic apron (0), twisted posterolaterally relative to the proximal section so that the anterior surface turns to face laterally (1) (Yates, 2010)
PU18. A639. Pubis, pubic apron, minimum transverse width relative to the width across the iliac peduncles of the ilium: more than 0.4 (0), less than 0.4 (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).


PU20. B349. Pubis, anteroposterior expansion of the distal portion: 0, present, 1, absent.

PU21. A641/A635/B350/A644. Pubis, anteroposterior expansion of the distal pubis relative to the length of the pubis: less than 0.15 (0), equal to or more than 0.15 (1) (Yates, 2010; Baron et al., 2017).


PU24. B346-1. Pubis, pubic symphysis: present (0), absent (1).

PU25. B346-2. Pubis, pubic symphysis, extension: elongated (0), restricted to the distal ends (1).

PU26. A645. Pubis, puboischial symphysis: absent (0), present (1) (Martinez et al., 2011).

4.3.3.3 Ischium

IS1. A648/A624. Ischium, length of the ischial blade relative to that of the pubis: less than or equal to 1.0 (0), greater than 1.0 (1) (Yates and Kitching, 2003; Yates, 2010; Pol et al., 2011).

IS2. A624. Pubis, length relative to that of the ischium: less than 0.9 (0), less than or equal to 1.0 but more than or equal to 0.9 (1), more than 1.0 (2).

IS3. B326. Ischium length: 0, about the same length or shorter than the dorsal margin of the iliac blade, 1, longer than the dorsal margin of the iliac blade (Juul, 1994, Nesbitt et al., 2009c, Nesbitt, 2011).

IS4. A647. Ischium, the orientation of the long axes of the transverse section of the distal ischia: meet at an angle (0), coplanar (1) (Yates, 2007; Upchurch et al. 2007, Pol et al., 2011).

IS5. A668. Ischium, ischiadic plate, extension: more than half the length (0), restricted to its proximal third (1) (Yates, 2003b; Pol et al., 2011).
IS6. A660. Ischium, medial contact with antimere: restricted to the medial edge (0), extensive contact but the dorsal margins are separated (1), extensive contact and the dorsal margins contact each other (2) Ordered (Nesbitt, 2011).

IS7. A649. Ischium, proximal ischium, longitudinal dorsolateral sulcus: absent (0), present (1) (Yates, 2010).

IS8. A650. Ischium, proximal articular surfaces: articular surfaces with the ilium and the pubis continuous (0), articular surfaces with the ilium and the pubis continuous but separated by a fossa (1), articular surfaces with the ilium and the pubis separated by a large concave surface (2) Ordered (Nesbitt, 2011)

IS9. A655. Ischial, midshaft, medial margin at midshaft: edge suture (0), dorsoventral expansion (1).

**Comment:** The original formulation of this character considered character states such as “ovoid to rectangular” and “triangular.” There are several disagreements on how to assess this character when there is a tear-drop cross-sectional outline, as it is the case of *Leonerasaurus*, scored as a polymorphism in Pol et al. (2011). *Eoraptor* is scored as “ovoid to subrectangular,” but the illustration in Sereno et al. (2012) shows a triangular outline. What this character is conveying is that in the medial margin there is a dorsoventral expansion articulating the ischium to its antimere. The character state “ovoid to subrectangular,” captures this variation, since what is being assessed is not the shape of the margin, but the morphology of the articulation. Likewise, the triangular cross-section is always with a dorsoventral expansion on the medial margin, and a dorsoventrally expanded margin has not been identified in any of the specimens included in this work.

IS10. A654. Ischium, ischial shaft, depth of the transverse section relative to the transverse width of the section: less than 1.0 (0), equal to or more than 1.0 (1) (Yates, 2010)

IS11. A657. Ischium, antitrochanter, nonarticular acetabular margin: concave (0), notch that undercuts antitrochanter (1). (Sereno, 1999; Martinez et al., 2011)

IS12. A658. Ischium, antitrochanter, anteroposterior length relative to the adjacent length of the articular surface for the ilium: greater (0), less (1) (Sereno, 1999; Martinez et al., 2011).
IS13. A664. Ischium, ischial obturator plate, the distal end of the proximal: abrupt and proximal to the midpoint of the ischium (0), elongate, gradually tapering distal end that reaches the midpoint of the ischium (1) (Y2003)


IS15. A656. Ischium, ventral plate-like flange: extending along the full length of the ischium (0), restricted to the proximal end where it forms an obturator plate (1) (Yates, 2003b).

IS16. A667. Ischia, the transverse width of the conjoined distal ischial expansions relative to their sagittal depth: greater than 1.0 (0), equal to or less than 1.0 (1) (Yates, 2010).

IS17. A651. Ischium, notch separating the posteroventral end of the ischial obturator plate from the ischial shaft: present (0), absent (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

IS18. A652. Ischium, elongate interischial fenestra: absent (0), present (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

IS19. A663. Ischium, distal end: without an expansion (0), expanded, knob-like termination (1) (Upchurch et al. 2007; Pol et al., 2011).

IS20. A661. Ischium, distal ischial expansion: absent (0), present (1) (Yates, 2007; Martinez et al., 2011).

IS21. A665. Ischium, distal end, maximum thickness relative to the minimum thickness: less than or equal to 3.0 (0), more than 3.0 (1) (Upchurch et al. 2007, Pol et al., 2011).

IS22. A653. Ischium, shape of distal ischium: broad and plate-like, not distinct from the obturator region (0), with a discrete rod-like distal shaft (1) (Yates, 2007).

IS23. A659/B324. Ischium, ventral margin: continuous ventral margin (0), notch present (1), abrupt change in angle between the proximal end and the shaft (2) (Nesbitt, 2011).

IS24. A666/A662. Ischium, distal outline of ischium in distal view: plate-like (0), roughly semicircular (1), sub-triangular (2) (Upchurch et al. 2007; Ezcurra et al., 2010).
IS25. A646. Ischium, pubis contact: present and extended ventrally (0), present and reduced to a thin proximal contact (1) (Nesbitt, 2011).

4.3.4 Hindlimb

4.3.4.1 Femur

Fe1. A670/A671/A722/B360/A675/A717. Femur, shape in lateral view: gently sigmoid in with the proximal end bowed posteriorly and the distal end bowed anteriorly (0), columnar and straight (1) (Upchurch et al. 2007, Pol et al., 2011; Baron et al., 2017)

Comment: There are several characters in the literature dealing with the shape of the femur and its curvature. These characters need to be treated with care, since femora are often deformed. As seen in Ruehleia, for instance, the variability on the femora is a product of differential deformation rather intraspecific variation. Fechner (2009) used the longitudinal bone curvature to capture the shape of the femur in lateral view. The femoral curvature (ζ) represents the moment arm of the axial component force on the femur, and although it is considered to be a function of body size (Fechner, 2009), there is some phylogenetic signal to it, since in several basal sauropods, e. g. Vulcanodon, Shunosaurus, and Cetiosaurus, ζ = 0, whereas the curvature is low in Antetonitrus (ζ = 4.9) and Anchisaurus (ζ = 5.6).

Fe2. A672/A685. Femur, angle between the long axis of the femoral head and the transverse axis of the distal femur in distal view (Y282).

Fe3. A681. Femur, proximal surface, transverse groove: absent (0), present (1) (C314-Nesbitt, 2011) B375
Figure 4.128. Anatomy of two femora of *Ruehleia* showing deformation. On the left, right femur of *Ruehleia* in dorsolateral, posteromedial, posterolateral and distal views; on the right, femur deformed in proximal, anterior, posteromedial and distal views. The scores in the proximal and distal regions are very different and have been given as polymorphisms. This highlights the importance of scoring characters in non-deformed specimens or retro-deformed interpretations of them.
Fe4. A684. Femur, femoral head, orientation of the long axis of the femoral head compared to the shaft in anterior view and with the distal condyles aligned on a horizontal plane: projects ventromedially (0), projects medially (1), projects dorsomedially (2).

Comment: The original formulation of this character put in the same character state the directions ‘medially’ and ‘ventromedially,’ opposite to the state ‘dorsomedially’ seen in sauropods. Topological operationalisation of this character needs that ‘medially’ and
‘ventromedially’ be placed in separate character states. The character becomes more informative in this way and captures better the morphology seen in ‘prosauropods.’ Some degree of polymorphism is seen in Plateosaurus but this could be related to the needed revision of the taxonomy of this genus. The holotype and paratype of Sarahsaurus also differ in their orientations. The holotype, which is more mature, has a medially oriented femoral head, whereas the less mature specimen has a ventromedially oriented femoral head, as illustrated in Marsh and Rowe (2018). The change of orientation from ventromedial to medial could be of ontogenetic effect.

The ventromedial orientation is found in fewer specimens compared to the other two orientations. It has been found in this work to be (0) in the ‘prosauropods’ Saturnalia, Pampadromaeus, Ruehleia, Adeopapposaurus, Lufengosaurus, Yunnanosaurus huangi, Melanorosaurus, Antetonitrus, and Jingshanosaurus, in the ornithischians Lesothosaurus and Eodromaeus, and in the theropods Tawa and Herrerasaurus. It was possible to assess this character in 75 taxa, and the optimisation shows a reduction of the entropy by half compared to the original one.

Fe5. A689. Femur, lateromedial length of the posterior tuberosity measured from the lowest points of the sulcus for ligamentum captis femoris and the facies antitrochanterica relative to the maximum lateromedial length of the proximal end of the femur in proximal view.

Comment: The original formulation in Pol et al. (2011) is based on the description of the femoral head in Novas (1996), where it is referred simply as “tuberosity.” In Langer and Benton (2006) the same structure is referred as “lateral tuberosity”, whereas in Müller et al. (2016) it is referred to as “posteromedial tuberosity”. The comparative study of archosaurs performed in Nesbitt (2011) also uses the term “posteromedial tuberosity”. The term “lateral tuberosity” orientates the femur so that the femoral head is pointing anteriorly, and that the side with the condyles is the lateral side. The structures then define the anterior surface and the posterior surface even if there is some degree of torsion with respect to the femoral head. The posterior surface holds the medial and lateral condyles in the distal end, and the lateral margin connects the greater trochanter with the fibular condyle. According to Nesbitt (2011), nearly all archosaurs have three tubera in the proximal end of the femur. An anterolateral tuber on one side, an anteromedial, and a posteromedial tubera on the opposite side. Matching these terms with the orientation of the anterior and posterior
surfaces, the two medial tubera are on the posterior surface, and the anterolateral tuber is on the anterior surface. The lateral tuberosity sensu Novas (1996) and Pol et al. (2011) is then the same as the posteromedial tuberosity sensu Nesbitt (2011) and Müller et al. (2016). In this work, this would then be the posterior tuberosity. Standardising the orientations regardless of the torsion and orientation in vivo of the femur allows describing partial femora when only the distal or proximal portions are preserved, and the torsion is unknown.

Considering the femoral head, the medial side is more consistent with previous literature in dinosaurs and makes sense anatomically, since the femoral head is articulating closer to the main body axis. The posterior tuberosity is separated from the posteromedial tuberosity by a sulcus where the ligamentum captis femoris inserts into, and from the greater trochanter by the facies articularis antitrochanterica. In the original formulation, all dinosaurs are scored with a reduced posterior tuberosity, but a similar outline to the one in Marasuchus can be seen in Lufengosaurus too. This character has then been reformulated as a continuous character.

Figure 4.130. Standardisation of the femoral nomenclature with a phylogenetic background for archosaurs. Abbreviations: at, anterior trochanter, faa, facies articularis antitrochanterica, fh, femoral head, gt, greater trochanter, sl, sulcus for ligamentum capitis femoris.
Fe6. A709. Femur, posteromedial tuber: absent (0), present (1) (modified from Gauthier, 1986; Benton, 1999; Benton and Walker, 2002; Clark et al., 2004; Nesbitt, 2011).

**Comment:** In Nesbitt (2011), this structure is named “anteromedial tuber”. *Euparkeria* and phytosaurs are the only to lack this tuber (Nesbitt, 2011).

Fe7. A710. Femur, posterior tuberosity, lateromedial length, measured from the medial-most point to the lowest point of the sulcus for *ligamentum captis femoris*, relative to the maximum lateromedial length of the proximal end of the femur in proximal view (modified from Gauthier, 1986; Benton, 1999; Benton and Walker, 2002; Clark et al., 2004; Nesbitt, 2011).

**Comment:** This character, along with F3 and F4, was part of a multistate character C300 in Nesbitt (2011) that captured the variation in size. Originally, this variation was only quantified as “small” and “large.”

Fe8. A711. Femur, posteromedial tuber, position: offset posteriorly relative to the posterior tuber (0), aligned with the posterior tuber (1) (modified from Gauthier, 1986; Benton, 1999; Benton and Walker, 2002; Clark et al., 2004; Nesbitt, 2011).

**Comment:** Characters Fe6-Fe5 sed to be part of an unordered multistate character in Nesbitt (2011). Here the character is modified to capture presence/absence of the posteromedial tuber, the size of the posteromedial tuber relative to the proximal end, and relative position with the posterior tuber.
Figure 4.131. Comparative diagram of the disparity in femoral anatomy in four Late Triassic sauropodomorphs. First row shows the femora in anterior view; middle row shows femora in lateral and medial view; bottom row, in posterior view. Pampadromaeus, Thecodontosaurus and Efraasia have been reconstructed as biped animals. The complexion of the femur in Pampadromaeus suggests a more gracile and cursorial lifestyle Müller et al. (2016); Thecodontosaurus and Efraasia also have somewhat gracile femora, but they are more robust and with less muscle attachments. The femur of Riojasaurus is columnar and more robust in comparison with the other three. It is a clear indicator that Riojasaurus was more of an obligate quadruped or at least a facultative biped.


Comment: The femoral neck is a flattened pyramidal process of bone, connecting the femoral head with the femoral shaft, and forming with the latter a wide angle opening medial-ward.
Fe10. A700. Femur, lesser trochanter: present (0), absent (1) (Y285-2).

Comment: The anterior trochanter is named also as lesser trochanter. It corresponds to the attachment of the muscle *iliofemoralis cranialis*. The absence or presence of anterior trochanter has been included in all the dinosaur-centred matrices collated for this work as part of multistate characters. Character 287 in mY2007 is considered equivalent to this character, since a scar is topologically different from a process, and anatomically describes the morphology of the muscle attachment of the *iliofemoralis cranialis*. When the anterior trochanter is absent, the osteological correlate of this muscle would be a scar, but this might not be present. In their current state, the characters 285 and 287 in mY2007 are redundant, and the operationalisation done in this work captures this variation better.

Fe11. A701. Femur, lesser trochanter, shape: rounded tubercle (0), conical (spike-like) (1) rod-shaped (elongate ridge, finger-like) (2), blade shape (3) Unordered (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011; Baron et al., 2017).

Comment: The topological operationalisation of this character distinguishes four morphologies: a hemispherical-ellipsoid shape, where there is a spherical section and a basal surface; a cone, where there is a curved circular plane and a basal surface; a cylinder, where there is a basal surface, an apical surface, and a circular plane connecting both surfaces; and a sheet-like or blade-like structure, where there is a basal surface, an apical surface, lateral and medial surfaces, and two parallel planes. This characterisation is more objective since descriptions such as “finger-like” or “spike-like” fit properly into these categories unambiguously. A finger-like process has a basal surface and an elongated continuous surface, whereas a spike-like process has a basal surface connected to a point via a plane folded onto itself. If the process seems to have a finger-like shape, but there is clearly a flattened apical surface, then this fits the description of a deformed cylinder.

Fe12. A697-B373. Femur, lesser trochanter, level of the most proximal point of the anterior trochanter relative to the level of proximal femoral head: on the femoral shaft (0), on the proximal end (1).

Fe13. A699. Femur, lesser trochanter, position: near the centre of the anterior face (0), or close to the lateral margin (1), of the femoral shaft in anterior view (Yates, 2007).
Comment: Character 291 (Yates, 2007a, b) requires the assessment on whether the anterior trochanter can be seen from posterior view. This character is confused in the cases where there is torsion of the proximal end with respect to the distal end. Under the landmark-based definition adopted here, there is an anterior surface and a posterior surface of the femur. The anterior trochanter is always contained within the anterior surface. Since the visibility on conventional posterior view will depend on how lateral the anterior trochanter is on the anterior surface, C291 Y2007 is deleted since is considered redundant with C290. The torsion of the femur is also dealt with in other character.


Comment: This character is assumed to be the same as C288 mY2007, described there as “transverse ridge extending laterally from the lesser trochanter.” In C238 mY2007, *Saturnalia* is scored as polymorphic, but the trochanteric shelf is illustrated in Langer (2003). The trochanteric shelf corresponds to the muscle attachment of the ilium femoralis muscle between the anterior and the greater trochanter.

Fe15. A714. Femur, *facies antitrochanterica articularis*: level with the greater trochanter (0), distally descended (1). (Nesbitt, 2011; Pol et al., 2011)

Fe16. B366. Femur, greater trochanter: present (0), absent (1).

Comment: The dorsolateral trochanter and the greater trochanter refer to the same structure. The term “dorsolateral trochanter” is used in several studies (e. g. Bonaparte et al., 1999; Langer, 2004; Butler, 2010; Kammerer et al., 2012; Griffin and Nesbitt, 2016; Müller et al., 2016), and matches consistently with the descriptions of the greater trochanter in other classic papers on dinosaur anatomy (e. g. Sereno, 1991; Novas, 1994). The term greater trochanter is used here instead of dorsolateral trochanter to avoid confusion when the torsion in the femur alters the orientation of the lateral and medial surfaces.

Fe17. A690/A691. Femur, fourth trochanter, shape: mound-like (0), flange (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

Comment: the fourth trochanter is the osteological correlate of the *m. caudofemoralis* placed on the anterior surface.

Fe18. A692. Femur, fourth trochanter, position of the maximum height of the fourth trochanter along the femoral length: closer to the proximal half (0), closer to
the midpoint (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011; Baron et al., 2017).

**Comment:** The original formulation of this character specified that character state (0) occurred when the fourth trochanter is on the proximal half, and character state (1) is when the projection is “straddling” on the midpoint. To make this clearer, the highest point of the fourth trochanter needs to be defined as the point that is the furthest from the shaft, and the distance between this point and the proximal-most point of the femur and the mid-point of the femur are compared. This leads to a potential intermediate state of “equidistant between the proximal-most point of the femur, and the mid-shaft,” but this state is not met in any of the taxa under study.

**Fe19.** Femur, fourth trochanter, distal margin, angle to the shaft.

**Comment:** this character is present in the three matrices, but it is difficult to assess. Both character states overlap: a low angle in the proximal margin can be steeper than the angle forming the distal margin; there is no comparative framework to state how similar two angles are in order to consider them symmetrical. To operationalise this character, only the angle of the distal margin is taken into account. In the original formulation, it has been scored as a polymorphism. Specimen YPM 1883 does not have sharp corners in the fourth trochanter and its morphology is that of round crest, but it is also not symmetrical, making ambiguous the distinction between character state (0) “subsymmetrical” and (1) “symmetrical.”

**Fe20.** A693. Femur, fourth trochanter, angle of distal corner.

**Comment:** the original formulation required the assessment on the absence/presence of a “sharp distal corner”. This does not correspond to a truly neomorphic character.

**Fe21.** A696. Femur, fourth trochanter, orientation: anteriorly orientated (0), mediolaterally orientated (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

**Fe22.** B381. Femur, fourth trochanter, lateral deflection in distal section: absent (0), present (1) (Baron et al., 2017).

**Fe23.** A718/A719. Femur, mid-shaft, mediolateral length relative to the anteroposterior length (Yates, 2007b).

**Fe24.** A712. Femur, basal width of the medial condyle relative to the sum of the basal widths of the tibiofibular and lateral condyles (Yates, 2007b).
Comment: This character excludes the popliteal fossa from consideration and is similar to C382 Baron et al. (2017).

Fe25. A724. Femur, distal surface of tibiofibular condyle, anteroposterior depth relative to the mediolateral depth.

Fe26. B386. Femur, lateral condyle, orientation in distal view: laterally (0), medially (1) (modified from Butler et al., 2008)

4.3.4.2 Tibia

Ti1. A727. Tibia, proximal half, fibular flange: absent (0), present (1).

Comment: The formulation of this character in Yates (2007b) “Proximal end of tibia with a flange of bone that contacts the fibula” did not include the location referred by Gauthier (1986). This refers to an additional projection on the lateral side. In the matrix by Yates (2007b) and amendments, this character is restricted to *Silesaurus* and Neotheropoda. In *Silesaurus*, this fibular flange is not located in the proximal end, rather on the proximal half on the lateral side of the tibial shaft at the same height that the cnemial crest. This structure becomes a process in *Allosaurus* but remains as an elongated flange in *Ceratosaurus*. Throughout the literature in theropods, this structure is named as the fibular flange or fibular ridge, and the term fibular flange is chosen to define this character.

According to Rauhut (2003), the fibular flange is absent in ornithischians and sauropodomorphs, as well as in *Eoraptor, Herrerasaurus* and *Staurikosaurus*. Several taxa point out to the relevance of this character for all the groups of dinosaurs.

*Tawa* has been found to be a theropod in several analyses (e. g. Nesbitt et al., 2009; Sues et al., 2011; Martill et al., 2016; Baron et al., 2017) and lacks a fibular flange (Nesbitt et al., 2009). *Chilesaurus* also lacks a fibular flange, and although it has been considered to be a theropod (Novas et al., 2015), it has also been suggested to be an ornithischian (Baron et al., 2017a). In the case of *Pisanosaurus*, a recent revision found it to be a silesaurid, which is consistent with the presence of a fibular flange in this taxon (Agnolín and Rozadilla, 2017).

There is also evidence of fibular flanges in sauropodomorphs. The fibular flange is defined as the fibular articular facet in *Saturnalia* (Langer, 2003), and was interpreted as a fibular crest in Nesbitt (2010). In the images and text for *Lamphughsaura*, a prominent fibular flange can be identified (Kutty et al., 2007). In *Chromogisaurus*, there is a description of a
“lateral tuberosity” (Ezcurra, 2010) in the same position than the fibular flange in theropods and silesaurids. In larger sauropodomorphs. Furthermore, the fibular articular facet is also recognised in Coloradisaurus (Apaldetti et al., 2013), Bagualosaurus (Pretto et al., 2018), and Buriolestes (Müller et al., 2018), whereas the illustrations of Adeopapposaurus in Martinez (2009) resemble the “lateral tuberosity” described for Chromogisaurus. In contrast, these features are absent in plateosaurid-type sauropodomorphs, such as Jaklapallisaurus and Plateosaurus and in robust basal sauropodomorphs and basal sauropods. In the former, there is evidence of an oval scar, whilst in the latter there is a rugose or smooth concavity.

The only ornithischians where a fibular crest has been identified so far are Heterodontosaurus (Nesbitt et al., 2010; Nesbitt, 2011) and Fruitadens (Butler et al., 2012). The entropy for this character in its original formulation is larger (C303, McPhee et al., 2015, H=0.876) than this one (Ti1, H=0.716), mostly because character state (1) in McPhee et al., (2007b) was scored to Silesaurus and Neotheropoda (comprising at least 12 taxa).

**Ti2.** A728/A733. Tibia, cnemial crest: absent (0), present (1).

**Comment:** The cnemial crest was defined by Novas (1996), and it is the one employed here. This feature is present in all dinosauromorphs, but absent in all non-dinosauromorph archosaurs (Crurotarsi, Euparkeria).

**Ti3.** A729/A730. Tibia, cnemial crest, curvature: anteriorly (0), arcs anterolaterally (1), laterally (2). Ordered. (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011; Nesbitt, 2011).

**Comment:** This character has been used in character lists for basal sauropodomorphs (Upchuch et al., 2007a; Yates, 2007a; Pol et al., 2011) and archosaurs (Nesbitt et al., 2010; Nesbitt, 2011). In the former, the formulation assigns character state (0) to anterior to anterolaterally, and state (1) to laterally. In the latter, this is a multistate character: “(0) absent; (1) present and anteriorly strait; (2) present and curved anterolaterally”. The neomorphic character is considered in Ti2. The information of character states (1) and (2) in Nesbitt et al. (2010) is contained in the codification of character states (0) and (1) found in the three compilations mentioned above.
The anterior and lateral orientation are clearly defined in space, whereas anterolaterally can be anything in between these two orientations. The degree of the curvature in between can also be produced as a continuous character, with the value 0 to being closer to the anterior axis, and 1.0 closer to the lateral axis. This value has never been measured in the literature, where the terms “slightly”, and “greatly” are used as quantifiers. Nevertheless, quantifying these measurements would require a thorough analysis of retro deformation to correct for tectonic deformation.

Therefore, the new formulation considers simply three easily identifiable states: anteriorly, anterolaterally, and laterally. In *Camarasaurus*, the cnemial crest is orientated laterally, whereas in *Spinophorosaurus* is orientated anteriorly.

**Ti4.** A732. Tibia, cnemial crest, position of the tallest point: close to the proximal end of the crest (0), about half-way along the length of the crest, creating an anterodorsally sloping proximal margin of the crest (1) (Y302).

**Ti5.** A734. Tibia, proximal portion, alignment of the lateral (fibular) condyle relative to the medial condyle in proximal view: offset anteriorly from the medial condyle (0), level with the medial condyle at its posterior border (1), displaced posteriorly (2) (Nesbitt, 2011).

**Comment:** Under topological criteria, this multistate character is justified.

**Ti6.** A736. Tibia, proximal surface, curvature in lateral or medial view: flat or convex (0), concave, the posterior condyles are separated from the cnemial crest by a concave surface (1) (Nesbitt, 2011).

**Comment:** The initial formulation of this character put together the conditions flat and convex in character state (0). Since this corresponds to the deformation of a surface,

**Ti7.** A737. Tibia, proximal articular surface, shape: ovoid (0), subcircular (1) (Y305)

**Ti8.** A740. Tibia, proximal end, lateral condyle: set on the center of its lateroproximal corner (0), level with the medial condyle at the posterior border of the bone (1)

**Ti9.** A741. Tibia, distal portion, posterolateral flange: absent (0), present (1) (Nesbitt, 2011)
Ti10. A744. Tibia, distal end, shape of the posterior face: rounded surface (0), distinct proximodistally oriented ridge present (1) (Nesbitt, 2011)

Ti11. A745. Tibia, distal end, relationship of the posterolateral process with the fibula: not flaring laterally and not making significant contact with the fibula (0), flaring laterally and backing the fibula (1) (Y308)

Ti12. A746. Tibia, distal end, distal posterolateral process: exceeds laterally the anterolateral corner of the distal tibia (0), protrudes laterally as far as the anterolateral corner of the distal tibia (1), set well back from the anterolateral corner of the distal tibia (2) (Y311) (Pol et al., 2011).

Comment: C257 Pol et al. (2011) scored Anchisaurus polyzelus as a polymorphism. The specimen YPM 1883 has a posterolateral process set well back from the anterolateral corner of the distal view from distal view. In the specimen referred as to Ammosaurus, YPM 209, the tibia is broken in its distal part and tectonically deformed, so this character is scored uncertain for this taxon.

Ti13. A747. Tibia, distal end, curvature of the posterolateral corner: convex (0), concave (1).

Ti14. A748. Tibia, distal end, shape: anteroposteriorly elongated (0), quadrangular (1), transversely elongated (2)

Ti15. A749. Tibia, distal end medial condyle of the tibia, relationship with the astragalus: extends posterovertrally to cover the astragalus in posterior view (0), is reduced, exposing the posterior fossa of the astragalus in posterior view (1) (Upchurch et al. 2007, Wilson, 2002)

Ti16. A751. Tibia, distal tibia, posteromedial notch in with respective bump in the proximal astragalus: absent (0), present (1).

Ti17. A753. Tibia, distal portion, lateral surface: smooth (0), longitudinal groove (1).

Ti18. A754. Tibia, distal anteromedial corner, form: rounded obtuse (0), right angle (1), acute angle (2) (Yates, 2010 Pol et al., 2011) (Y310)

Comment: This character has been scored as a polymorphism in C310 mY2007 for Melanorosaurus. The tibiae are not illustrated in distal view, and the character is not described (Van Heerden and Galton, 1997; Galton et al., 2005)
Ti19. A755-1. Tibia, distal articular surface, forms an oblique angle with the long axis of the tibia in anterior and posterior views: absent (0), present (1) (C403 B2017).

Ti20. A755-1. Tibia, distal articular surface, inner and outer malleoli are roughly at the same level, forming a right angle between the articular surface the inner condyles form and the long axis: absent (0), present (1) (C403 B2017).

Ti21. A755-2. Tibia, distal articular surface, forms an oblique angle with the long axis of the tibia in anterior and posterior views: outer malleolus extends further distally than the inner malleolus creating an oblique between the articular surface and the long axis (0), inner malleolus extends further distally (1) (C403 B2017).

Ti22. A756. Tibia, distal articular end, shape in distal view: ovoid (0), subrectangular (1) (Y309)

4.3.4.3 Fibula

Fi1. A762. Fibula, fibular condyle, position of the posterior end on the proximal articular surface tibia relative to the posterior margin of proximal articular surface: anterior to (0) or level with (1) (Y304)

Fi2. A758. Fibula, proximal end, trigonal striated articular crest on medial surface: absent (0), present (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

Fi3. A763. Fibula, transverse width of the midshaft of the fibula relative of the transverse width of the midshaft of the tibia: greater than 0.75 (0), less than or equal to 0.75 but more than or equal to 0.5 (1), or less than 0.5 (2) (Yates, 2007b).

Fi4. A764. Fibula, fibular trochanter, position: on anterior surface of fibula (0), laterally facing (1), anteriorly facing but with strong lateral bulge (2) Unordered (Yates, 2007b).

Fi5. A765. Fibula, lateral surface, muscle scar trochanter (at mid-length): absent (0), present (1) (Wilson, 2002 Upchurch et al. 2007, Pol et al., 2011).

Fi6. A768. Fibula, distal condyle, breadth relative to mid-shaft breadth: less than or equal to 1.0 (0), more than 1.0 but less than or equal to 2.0 (1), more than 2.0 (2) (Wilson, 2002)

Fi7. B408. Fibula, distal end is strongly reduced and splint-like: 0, absent, 1, present (Han et al., 2012).

Fi8. A761. Fibula, proximal portion, symmetricity in lateral view: symmetrical or nearly symmetrical (0), posterior part expanded posteriorly (1) (Nesbitt, 2011)
Fi9. A767. Fibula, distal end, symmetricity in lateral view: angled anterodorsally (asymmetrical) (0), rounded or flat (symmetrical) (1) (Nesbitt, 2011)
Fi10. A760. Fibula, proximal portion, shape of anterior edge: rounded (0), tapers to a point and arched anteromedially (1) (Nesbitt, 2011)
Fi11. A759. Fibula, proximal tibial scar, development: not well-marked (0), well-marked and deepening anteriorly (1) (Wilson, 2002)
Fi12. A766. Fibula, lateral surface, lateral trochanter: absent (0), present (1).

4.3.4.4 Astragalus
The astragalus and the calcaneum are the proximal-most components of the ankle. In dinosaurs, the astragalus articulates mainly with the tibia and with the medial side of the fibula, whereas the calcaneum articulates laterally with the astragalus and proximally with the fibula. In some theropods, these two bones are fused together and are then termed astragalocalcaneum. From the posterior margin of the astragalus there is projection that points proximally and fits into the tibia; this process is called the ascending process and provides extra articulation surface for the tibia. In some theropods, such as *Coelophysis* (Colbert, 1989) and *Dilophosaurus* (Welles, 1984), the ascending process is not completely fused to the astragalus (or astragalocalcaneum, accordingly), and a suture can be seen at the base of this process. In Sauropodomorphs, the astragalus and the calcaneum are always ossified separately, and the ascending process is always fused to the astragalus.

In the taxa revised in this work, the proximal view of the astragalus may have three distinctive fossae: a fibular facet on the lateral side, a facet for the tibia on most of the body, and a non-articular posterior fossa on the base of the astragalus that is not always present.

In the same taxa, the calcaneum may articulate only with the fibula or may also have a facet for the tibia. The former is found in Sauropodomorphs, *Herrerasaurus ischigualastensis*, and basal theropods such as *Coelophysis bauri*, *Syntarsus*, *Dilophosaurus wetherilli* and *Liliensternus liliensterni*, whereas the latter is found in all the other theropods and ornithischians.

The terms referred to identify locations within the astragalus vary between basal sauropodomorphs and sauropods. This is because the astragalus rotates longitudinally through the sauropodomorph lineage: whereas in basal saurischians and basal sauropodomorphs the astragalus is placed vertically, and the proximal surface is parallel to the longitudinal plane of the astragalus, in sauropods the proximal surface is tilted relative
to the astragalar longitudinal plane (Cooper, 1980). For this reason, the terms of dorsal and ventral refer to different things depending of the position of the astragalus. Whereas the dorsal surface in the astragalus of *Massospondylus carinatus* corresponds entirely with the proximal surface, the dorsal surface of the astragalus of *Vulcanodon karibaensis* corresponds with what would be the anterior margin of *M. carinatus*. To ease the interpretation of character scoring across sauropodomorphs, the terms that will be used to describe the astragali will be: proximal (the articulation with tibia and fibula), distal (the articulation surface with the rest of the tarsals), anterior margin, posterior margin, medial, and lateral.


AS2. A786. Astragalus, posteromedial margin, shape in dorsal view: forming a moderately sharp corner of a subrectangular astragalus (0), evenly rounded without formation of a posteromedial corner (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

AS3. A787. Astragalus, dorsally facing horizontal shelf forming part of the fibular facet: present (0), absent with a largely vertical fibular facet (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

AS4. A779. Astragalus, ascending process, posterior extent relative to the posterior margin: well anterior to (0), close to (1) (Yates, 2007b).

AS5. A783. Astragalus, sharp medial margin around the depression posterior to the ascending process: absent (0), present (1) (Yates, 2007b).


AS7. A774. Astragalus, ascending process, depression and vascular foramina in front of the base: present (0), absent (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

**Comment:** In C323 mY2007, this is scored as a polymorphism for *Glacialisaurus*, but the vascular foramen is present.

AS8. A789. Astragalus, posterior groove: present (0), absent (1).

**Comment:** In C261 Pol et al. (2011), *Silesaurus* is scored as polymorphism, but in Dzik (2003), the ascending process is illustrated pyramid-shaped. This formulation is preferred over the formulation in C318 mY2007, that simply assess whether there is an pyramid-shaped ascending process.


AS11. A780. Astragalus, shape of the ascending process of the astragalus, anteroposterior depth relative to its transverse depth: anteroposteriorly deeper than transversely wide (0), transversely wider than anteroposteriorly deep (1) (Yates, 2007b).

AS12. A769. Astragalus, fibular facet on the lateral margin of the proximal surface: large (0), reduced to small articulation (1) (Butler et al., 2008; Baron et al., 2017).

AS13. B419. Astragalus, symmetry in distal view: 0, astragalar body is fairly symmetric, medial and lateral margins are about equal in depth, 1, astragalar body is strongly asymmetric, medial margin is at least 1.4 times as deep as lateral margin. (Baron et al., 2017).

AS14. A778. Astragalus, proximal articular facet for fibula, relative occupation of the transverse width: more than 0.3 (0), less than or equal to 0.3 (1) (Nesbitt, 2011)

AS15. A782. Astragalus, medial condyle anteroposterior depth relative to the depth of the lateral condyle: less than 1.6 (0), equal or more than 1.6 (1)

AS16. A776. Astragalus, anterior ascending flange (anterior process), height relative to the dorsoventral height of the posterior side of the astragalus: less than 1.0 (0), greater than 1.0 (1) Ordered (Nesbitt, 2011)

AS17. A770. Astragalus, proximal surface: lacks a marked rimmed and elliptical fossa posterior to the anterior ascending process (0), possesses a marked rimmed and elliptical fossa posterior to the anterior ascending process (1) (Nesbitt, 2011)

AS18. A790. Astragalus, posterior margin, curvature: straight, or almost so, in proximal view (0), strongly convex in dorsal view (1) (Y2003) (Otero et al., 2013) (Y362)
AS19. A781. Astragalus, mediolateral surface of distal portion: straight (0), concave (1), convex (2) (Yates, 2007b; Otero et al., 2013).


AS21. A772. Astragalus, ascending process, arising in anterior view: from the medial end of the bone and slopes continuously upwards to its peak at the lateral end of the process (0), abruptly from the centre of the bone and forms a plateau or rounded summit, medial to its lateral edge (1) (Yates, 2007b).

4.3.4.5 Calcaneum

Cal1. A794. Calcaneum, transverse width of the calcaneum relative to transverse width of the astragalus: greater than (0), or less than 0.3 (1) (Yates, 2007b).


Cal3. A796. Calcaneum, medial peg fitting into astragalus: present, even if rudimentary (0), absent (1) (Yates, 2007b).

Cal4. A797. Calcaneum, calcaneal tuber: present (0), absent (1) (Y327)

Cal5. A793. Calcaneum, shape: proximodistally compressed with a short posterior projection and medial process (0), transversely compressed, with the reduction of these projections (1) (Nesbitt, 2011; Baron et al., 2017).

Cal6. A792. Calcaneum, articular surfaces for fibula and Distal tarsal 4, continuity: separated by a nonarticular surface (0), continuous (1) (Nesbitt, 2011)

Cal7. A791. Calcaneum, articular surface for the fibula: convex (0), concave (1) (Nesbitt, 2011)

4.3.4.6 Metatarsals

MT1. A810. Metatarsal I, proximal width of the first metatarsal: less than (0), or at least as great as (1), the proximal width of the second metatarsal (Yates, 2007b).


MT4. A819. Metatarsal II, medial margin of the proximal end, shape: straight or convex (0), concave (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).
MT5. A820. Metatarsal II, lateral margin of the proximal end, shape: straight or convex (0), concave (1) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

MT6. A827. Metatarsal III, length relative to the length of the tibia: more than or equal to 0.4 (0), less than 0.4 but more than 0.3 (1), less than or equal to 0.3 (2) (Wilson, 2002; Remes, 2009; Upchurch et al. 2007; Yates, 2010; Pol et al., 2011)

MT7. A829. Metatarsals III and IV, minimum transverse shaft diameters relative to the minimum transverse shaft diameter of the metatarsal II: greater than 0.6 (0), or less than 0.6 (1). (Yates, 2007b).

MT8. A832. Metatarsal IV, transverse width relative to the anteroposterior depth of the proximal end: less than or equal to 2.0 (0), more than or equal to 2.0 but less than 3.0 (1), equal to or more than 3.0 (2) (Upchurch et al. 2007; Yates, 2010; Pol et al., 2011).

MT9. A839. Metatarsal V, transverse width of the proximal end of the metatarsal V relative to its length: less than 0.25 (0), equal to or more than 0.30 but less than 0.5 (1), greater than or equal to 0.50 (2) (Yates, 2007b).

MT10. A833. Metatarsal IV, transverse width of distal articular surface of in distal view relative to the anteroposterior depth: greater than 1.0 (0), equal to or less than 1 (1) (Yates, 2007b; Nesbitt, 2011)

MT11. A816. Metatarsal I, length relative to its width: more than or equal to 1.5 (0), less than 1.5 (1) (Yates, 2007b).

MT12. A809. Metatarsals, area of proximal ends of metatarsals I and V relative to the areas of metatarsals II and IV: smaller (0), longer (1)

MT13. A821. Metatarsal II, length relative to its proximal width: less than or equal to 0.25 (0), more than 0.25 (1)

MT14. A825. Metatarsal III, length relative to its proximal width: less than or equal to 0.25 (0), more than 0.25 (1)

MT15. A838/B444. Metatarsal V, length relative to metatarsal III length: less than or equal to 0.50 (0), more than 0.50 (1) (modified from Butler et al., 2008; Upchurch et al. 2007; Pol et al., 2011)

MT16. A813. Metatarsal I, width of the midshaft relative to the width of the midshaft of the metatarsals II-IV: less than or equal to 1.0 (0), more than 1.0 (1) (Wilson, 2002, Yates, 2003b).
MT17. A814. Metatarsal I, transverse width relative to that of metatarsal II: less than 1.0 (0), equal to or more than 1.0 (1) (Yates, 2003b; Pol et al., 2011)

MT18. A823. Metatarsal II, proximal end: subtriangular or subquadrangular in shape (0), hourglass-shaped (1) (Sereno, 1999a; Galton and Upchurch, 2004).

MT19. A843. Metatarsal V, shape: proximal and distal ends subequal in breadth (0), triangular shaped, with wide proximal surface and pointed distal end (1)

MT20. A842. Metatarsal V, length relative to metatarsal IV: less than 0.7 (0), equal or more than 0.7 (1) (Wilson, 2002; Remes, 2009).

MT21. B433. Longest metatarsal: 0, metatarsal III is the longest, 1, metatarsal IV is the longest (Baron et al., 2017).

MT22. B436. Metatarsal I: 0, subequal or greater in length than metatarsal II, 1, significantly shorter in length than metatarsal II (Baron et al., 2017).

MT23. A811. Metatarsal I, maximum proximal breadth relative to its proximal breadth: less than 0.4 (0), equal to or more than 0.4 but less than 0.7 (1), more than 0.7 (2). Ordered (Yates, 2010; McPhee et al., 2015b).

MT24. A830. Metatarsal IV, length: longer than metatarsal II (0), subequal or shorter than to metatarsal II (1) (Nesbitt, 2011)

MT25. A808. Metatarsals, midshaft diameters: I and V subequal or greater than II-IV (0), I and V less than II-IV (1) (Nesbitt, 2011)

MT26. A831. Metatarsal IV, proximal portion, elongated lateral expansion that overlaps the anterior surface of metatarsal V: absent (0), present (1) (Nesbitt, 2011)

MT27. A841. Metatarsal V, phalange V.1, development: fully developed (0), poorly developed (1) Ordered (Nesbitt, 2011)

MT28. B441. Metatarsal V: 0, present, 1, absent.

MT29. B445. Metatarsals fused or partly fused into tarsometatarsus: 0, absent, 1, present.

MT30. A806. Metatarsus, configuration: metatarsals diverging from ankle (0), compact metatarsus, with metatarsals II-IV tightly bunched (at least half of the length) (1) (Nesbitt, 2011)

MT31. A840. Metatarsal V, phalanges: absent and tapers to a point (0), present (1) (Nesbitt, 2011)
MT32. A815. Metatarsal I, extension: reaches the proximal surface of metatarsal II (0), does not reach the proximal surface of metatarsal II and attaches onto the medial side of metatarsal II (1) (Nesbitt, 2011; Baron et al., 2017).

MT33. A807. Metatarsus, longest metatarsal: shorter than 50% of tibial length (0), longer than 50% of tibial length (1) (Nesbitt, 2011)

MT34. A817. Metatarsal I, shaft: closely appressed to metatarsal II throughout its length (0), only closely appressed proximally, with a space between metatarsals I and II distally (1) (Smith and Pol, 2007).

MT35. A822. Metatarsal II, lateral extent of ventrolateral flange on plantar surface proximal aspect: neither corner appreciably more developed than the other (0), laterally flaring (1), medially flaring (2) (Smith and Pol, 2007; Yates, 2010; McPhee et al., 2015).


MT37. A828. Metatarsal III, proximal outline: subtriangular with acute or rounded posterior border (0), subtrapezoidal, with posterior border broadly exposed in plantar view (1) (Smith and Pol, 2007).

MT38. A834. Metatarsal IV, angle formed by the anterior and anteromedial borders of metatarsal IV: obtuse (0), right angle, or acute (1) (Smith and Pol, 2007).

4.3.4.7 Pedal digits


PD2. A845. Pedal phalanges, non-terminal pedal phalanges, length relative to width: all longer than wide (0), proximal-most phalanges longer than wide, more distal phalanges are as wide as long (1), all non-terminal phalanges as wide, if not wider, than long (2). (Wilson and Sereno 1998; Yates 2007b).

PD3. A849. Pedal digit I, length of the first phalanx of pedal digit one relative to the length of the ungual of pedal digit one: greater than 1.0 (0), less than 1.0 (1) (Yates 2007b).

PD4. A851. Pedal digit I, ungual, length relative to all non-terminal phalanges: less than at least some non-terminal phalanges (0), longer than the mt I (1) (McPhee et al., 2015).
PD5. A850. Pedal digit I, ungual, shape: shallow, pointed, with convex sides and a broad ventral surface (0), deep, abruptly tapering, with flattened sides and a narrow ventral surface (1) (Yates 2007b).

PD6. A848. Pedal unguals, proximal articular, shape: proximally facing, visible on medial and lateral sides (0), proximomedially facing and visible only in medial view, causing medial deflection of pedal unguals in articulation (1) (Yates 2007b).

PD7. A856. Pedal digits II-III, penultimate phalanges, development: well developed (0), reduced disc-shaped elements if they are ossified at all (1) (Yates 2007b).

PD8. A857. Pedal digits II-III, unguals, shape: dorsoventrally deep with a proximal articulating surface that is at least as deep as it is wide (0), dorsoventrally flattened with a proximal articulating surface that is wider than deep (1) (Yates 2007b).

PD9. A859. Pedal digit II, ungual, length relative to the length of the ungual of pedal digit I: greater than 1.0 (0), less than or equal to 1.0, but more than 0.90 (1), equal to or less than 0.90 (2) (Yates 2007b).

PD10. A861. Pedal digit III, ungual, size relative to the ungual pedal digit II in all linear dimensions: greater than 0.85 (0), equal to or less than 0.85 (1) (Yates 2007b).

PD11. A862. Pedal digit IV, phalanges, number: four (0), fewer than four (1), more than four (2) (Yates 2007b).


PD13. A844. Pedal phalanges, non-terminal pedal phalanges, apart from unguals: are longer proximodistally than their transverse widths (0), are wider transversely than their proximodistal lengths (1) (Wilson and Sereno 1998; Upchurch et al., 2007).

PD14. A852. Pedal digit I, ungual, length relative to the other pedal unguals: shorter than other pedal unguals (0), subequal than other pedal unguals (1), longer than other pedal unguals (2) (Yates et al., 2010; Pol et al., 2011).

PD15. A855. Pedal digit I, ungual, length relative to that of metatarsal I: less than or equal to 1.0 (0), more than 1.0 (1).

PD16. A860. Pedal digit III, ungual, length relative to the length of ungual on pedal digit II: larger than 1.0 (0), equal to or less than 1.0 but more than 0.9 (1), equal to
or less than 0.9 but more than 0.85 (1), equal to or less than 0.85 (2) (Upchurch et al. 2007, McPhee et al., 2015b).

PD17. A846. Pedal phalanges, at least some pedal phalanges apart from unguals, proximodistal length compared to their transverse width: greater than 1.0 (0), equal to or less than (1).

PD18. A853. Pedal digit I, ungual, length relative to the length of the phalanx I.1 and metatarsal I: less than phI.1 and mtI (0), greater than phI.1 but less than mtI (1), greater than both (2) (Yates and Kitching, 2003)

PD19. A858. Pedal digit II, ungual, length relative to the length of pedal phalanx II-2: less than or equal to 1.0 (0), longer than 1.0 (1).

PD20. A854. Pedal digit I, ungual relative to the pedal ungual II: less than 1.0 (0), equal to or more than (1) (Yates, 2003b).

PD21. A863. Pedal digit IV, ungual, development: subequal in size to unguals of pedal digits II and III (0), rudimentary (Wilson, 2002; Remes, 2009).

PD22. B451. Unguals of digits II-IV: 0, deeper than broad, with curved ventral surfaces, 1, broader than deep, with flat plantar surfaces (Baron et al., 2017).

PD23. B446. Digit 1: 0, metatarsal I robust and well-developed, distal end of phalanx 1-1 projects beyond the distal end of metatarsal II, 1, metatarsal I reduced, end of phalanx 1-1 does not extend much beyond the end of metatarsal II if at all, 2, metatarsal I reduced to a vestigial splint or absent, does not bear digits Ordered (Butler et al., 2008; Baron et al., 2017).

PD24. B449. Majority of pedal unguals, shape: 0, claw-like, 1, hoof-like (modified from Butler et al., 2008; Baron et al., 2017).


4.4 Final remarks

This chapter represents the first attempt to produce a systematic review of the anatomy of non-sauropod sauropodomorphs and the first detailed character analysis for this group. This chapter does not represent a finished product nor presents all the character analyses performed during this project, due to space constrains for this thesis. In turn, this character analysis has produced a large amount of data, mostly morphometric data. All of these characters will be revised in future iterations of this data set, and the indexation performed
in this chapter to understand where the matrices are coming from has helped in making the incorporation of new datasets quicker and less error prone.
5 Phylogenetic analyses

5.1 Results

The total evidence matrix, with the 870 characters outlined in Chapter 4 (i.e. discrete and categorised) and containing the three partitions (i.e. cranial, axial and appendicular) was analysed using three different approaches: equally weighted characters, extended implied weighting and a probabilistic search using Lewis’s model (Lewis, 2001).

5.1.1 Methods

Equally-weighted parsimony analyses are the standard in all previously published studies (see Chapter 3). Here, the total evidence matrix was analysed using the New Technology Search in TNT, with default settings and 1000 random addition sequences. An iterative positional congruence (reduced) analysis was performed to identify unstable taxa (Pol and Escapa, 2009).

Reanalysis of previous phylogenies indicated that homoplasies were frequent (see Chapter 2) and extended implied weighting was implemented for comparison with unweighted phylogenies (Goloboff et al., 2017). Extended implied weighting is applied in TNT by setting several concavity values (k=2, k=5, k=10, k=12, k=15, k=20, k=30, and k=50) to see the changes in the topologies and the nodes (Goloboff, 2014).

Probabilistic phylogenetic methods (e.g. Bayesian inference) have been suggested to outperform parsimony (O’Reilly et al., 2016; Puttick et al., 2019), but they have not been applied to non-sauropod sauropodomorph datasets. Nonetheless, there is also evidence that probabilistic methods do not produce the most stratigraphically congruent phylogenetic trees, and are outperformed by parsimony-based analyses in this respect (Sansom et al., 2018). Here, a Bayesian analysis using Lewis’ Mk model (Lewis, 2001) was run in MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The topology was a tip-dated analysis using the assumption that Nyasasaurus and Asilisaurus are of Carnian age. The outgroup was constrained to Euparkeria, although the models do not always consider this as the most likely outgroup, and the clock model was set to ‘independent gamma rates’ (igr) so that the
evolutionary rates are drawn from an underlying gamma distribution. The prior on the variance of the gamma distribution refers to the rate variation between branches, set to the default 10. The clock rate set here is a diffuse prior assuming that the number of substitutions per site per millions of years has a normal distribution with a mean of 0.0025 and a standard deviation of 0.01. This default setting allows an initial exploration of the probabilistic model. The search was set with the Fossilised Birth-Death (FBD) model and setting the option of ‘random’ so that fossil taxa are sampled randomly and can be ancestral to other taxa; this is the default setting in MrBayes. The FBD parameters, i.e. speciation rate, extinction rate and fossilisation rate, are set to their defaults, with the speciation rate being the uniform prior from zero to ten species/species/million years. The age of the root was set to 253 Mya, a period corresponding to one of the first archosauromorphs for which we have fossil evidence, *Aenigmastropheus* (Ezcurra et al., 2014). Finally, a set of characters was added to the matrix to account for autapomorphies, an assumption needed when using tip-dating with clock-like data (Matzke and Irmis, 2018). Because these characters were not considered in the parsimony-based analyses, they are listed in Appendix 3. The study was run for 200,000 generations, with ten runs and ten chains, sampling every 500 generations, and a burn-in fraction of 25%.
Figure 5. 1. Strict consensus from 4 MPTs of 4785 steps with equally weighted characters. The dotted lines labelled with A, B, C and D represent the ages when Pangaea started to break up based on paleomagnetic and phylogenetic data as determined by McIntyre et al. (2017). A) beginning of the divergence between Gondwana and Laurasia, B) Gondwana and Laurasia finally separate, C) beginning of divergence between East (India, Madagascar, Australia, Antarctica, Oceania) and West Gondwana (South America).
5.1.2 Description of the topologies

5.1.2.1 Equal weights

This work put much more emphasis on sampling characters to increase the resolution of Sauropodomorpha than to test the relationships of Sauropodomorpha within Dinosauria. When selecting Crurotarsi as the outgroup, all the ornithischians are nested within Sauropodomorpha, where the MPTs have a length of 4785 steps. In this scenario, Phytodinosauria *sensu* Bakker and Galton (1974), placing Ornithischia as the sister taxon to *Thecodontosaurus, Arcusaurus* and *Pantydraco*. Selecting *Euparkeria* as the outgroup does not find support for Phytodinosauria, but moves some sauropodomorphs outside of Saurischia, namely *Ammosaurus, Euskelosaurus, Plateosaurus ingens* and *Agnosphytis*. *Ammosaurus* needs more preparation or CT-scanning, as the specimen is very embedded into the matrix; *Euskelosaurus* is too incomplete and is by many considered as a *nomen dubium* since must of the remains assigned to it have been renamed as *Plateosauravus*; *Agnosphytis* is represented only by an ilium and an astragalus; *Plateosaurus ingens* is both incomplete and poorly described, and must of the characters need to be rescored first-hand. When removing these taxa, 4 MPTs are found placing silesaurids and ornithischians as a monophyletic group, *Saltopus* as the most basal dinosaur, and Saurischia divided into two clades: Theropoda and Sauropodomorpha. More characters to differentiate between silesaurids and ornithischians are needed. The following nodes are found in the strict consensus of these 4 MPTs, with a length of 4768 steps, a CI = 0.179 and a RI = 0.418.
Figure 5.2. Section of the cladogram zooming in to the base of the tree showing the general body plans as summarised in Appendix 1 and the ages of the group. Silhouettes not to scale. The node numbers are the ones described in this Chapter for more detail see text. The trend towards gigantism started very early in the evolution of Sauropodomorpha, and several smaller clades developed independent patterns towards more substantial sizes.

Weight ranges in terms of comparisons to extant animals

- *Meleagris pavo*: 2-9Kg
- *Castor canadensis*: 9-23Kg
- *Canis lupus*: 22-43Kg
- *Panthera pardus*: 45-91Kg
- *Panthera leo*: 91-227Kg
- *Ursus arctos horribilis*: 227-454Kg
- *Repus ferox caballus*: 454-907Kg
- *Diceros bicornis*: 0.9-3.6t
- *Loxodonta africana*: 3.6-7.2t

Node 155
5.1.2.1.1 Node 138 Sauropodomorpha

Bremer support: 4

Sauropodomorpha is currently defined as the most inclusive clade containing *Saltasaurus loricatus* but not *Passer domesticus* or *Triceratops horridus* (Sereno, 2005, Nesbitt, 2011). This definition is supported in this topology, with the node-based definition of the most inclusive clade containing the most common ancestor of *Saltasaurus* and *Eoraptor*. The following unambiguous synapomorphies support this clade: MX15, maxillary narial fossa (1), DT3, first dentary tooth inset (1), CO1, the coracoid is divided into two faces, a dorsal and a ventral (1), U1, the proximal end of the ulna has a quadrangular outline (1), MC4, metacarpal I with a broader proximal end compared to that of the metacarpal II (1), MC12, lateral condyle distally expanded relative to the medial condyle of the metacarpal I (1), PU19, anteroposterior expansion of the pubic distal end (1), FI10, rounded anterior edge of the proximal portion of the fibula (0), and AS12, asymmetric astragalar body in distal view (1). Most of these synapomorphies are in the appendicular skeleton, suggesting that the changes in the locomotory apparatus in sauropodomorphs started early in their evolutionary history.

5.1.2.1.2 Nodes 152, Bagualosauria, and Node 151

*Bagualosaurus* is at the base of this node, supported only by two unambiguous synapomorphies, B25, the anterior premaxillary foramen is placed outside the narial fossa (0), and EN4, the external naris is posterior to the premaxilla-maxilla suture (1). These two features differentiate most members of Node 152 from *Eoraptor* and relate to the blood supply of the nostrils; whereas *Bagualosaurus* sees a reversal of character B25 compared to *Eoraptor*, *Eoraptor* retains the plesiomorphic condition for the narial fossa, suggesting that the modifications of the nostril morphology distinctive in sauropods (Witmer, 2001) also started early in the Sauropodomorph lineage. Node 151 leads to *Pampadromaeus*, showing the following unambiguous synapomorphies: PMX9, posterodorsal process of the maxilla restricted to the ventral border of the external naris (1), PMX21, anteroventral corner of the narial fossa posterior to the mid-length of the premaxillary body (1), MX2, inflexion at the base of the dorsal process (1), DT10 (1) concave mesiodistally lingual surfaces in the dentary teeth crowns (1), DT20, serrations restricted to the upper half of the mesial carina of the dentary teeth (1), CAR3, lateral end of the distal carpal I overlap onto distal carpal II (1), and PU4,
absence of the ambiens process in the pubis (1). This set of synapomorphies are related
to changes in both the buccal and locomotory apparatus. These features in
Bagualosaurus are not preserved in the skull. Recent analyses have shown that the first
sauropodomorphs, i.e. Pampadromaeus and Bagualosaurus, changed from the
faunivorous diet, as seen in Saturnalia, to a more omnivorous diet. The ambiens
process is lost in Sauropodomorpha and appears independently later in Plateosaurus,
Efraasia, and Sauropoda.

5.1.2.1.3 Node 160

This node contains Buriolestes and Chromogisaurus, the latter previously placed
within Guaibasauridae, as the sister taxon to Saturnalia (Ezcurra, 2010, Pretto et al.,
2018). In this topology, the members of this clade are distributed along the saurischian
lineage, with Saturnalia at the base of Saurischia, Guaibasaurus at the base of
Theropoda, and Panphagia nested within Sauropodomorpha, more derived than Node
160. The unambiguous synapomorphies supporting this node are I13, strong
trapezoidal rugosity in the postacetabular process (1), I14, partially open acetabulum
(1), FE11, a spike-like lesser trochanter (1), FE12, lesser trochanter on the proximal
end of the femur (1), and FE13, and a lesser trochanter on the lateral margin of the
femoral shaft (1). The modifications in the locomotory apparatus may also relate to a
change to a more faunivore diet and a more active lifestyle, a reversal from the rest of
the sauropodomorph condition but convergent with theropods, namely Chindesaurus,
Tawa, Diloophosaurus and Liliensternus. The lack of cranial material in
Chromogisaurus obscures this trend.

5.1.2.1.4 Nodes 150, 149, 148, 147: unequivocal sauropodomorphs

These nodes include all the unequivocally considered as sauropodomorphs, starting
with Panphagia (node 150), Pantydraco (node 149) and Thecodontosaurus (node
148). Four unambiguous synapomorphies support node 150: D3, anterior end of the
dentary downturned (1), and SA5, loss of the posterior surangular foramen (1), SC1,
inflexion in the articulation of the scapula with the coracoid (1), and I17,
supraacetabular crest extended partially along the pubic peduncle (0); node 149 is
supported by also four unambiguous synapomorphies: I11, loss of the iliac
preacetabular ridge (0), I14, completely open acetabulum (2), I18, laterally oriented
supraacetabular crest (0), and AS3, slopped fibular facet in the astragalus (1). Finally,
node 148 is supported by six unambiguous synapomorphies: PT3, basisphenoid process (1), D8, buccal emargination on the lateral surface of the dentary (1), DT7, dentary tooth crowns contact adjacent teeth (1), DT10, concave mesiodistally crowns in the dentary teeth (1), DT13, dentary teeth are not curved (1), and AT1, a dorsally facing fossa in the atlantal neurapophysis (1). All these synapomorphies reflect a trend towards a more specialised herbivory diet and changes in the morphology of the appendicular skeleton, for instance, the inflexion of the scapulocoracoid articulation increases the surface contact between the scapula and the coracoid and interlocks them and could reflect an initial trend towards facultative quadrupedality. Pantydraco and Thecodontosaurus come from deposits of the same age (Rhaetian, Late Triassic), and based on the lithology, the remains of Pantydraco seemed to have deposited in the Rhaetian fissure fills of naturally formed caves in the Carboniferous limestones in what was an emergent archipelago in Bristol and South Wales (Benton, 2000, Galton 2010). The high levels of diversity in the sauropodomorph fauna is a constant throughout their history, and the differences between Thecodontosaurus and Pantydraco suggest that niche partitioning and the concomitant phenotypic plasticity is also a trend that started early in sauropodomorph evolution (see also McPhee et al., 2014). The clade Thecodontosauridae includes then the most common ancestor of Saltasaurus and Thecodontosaurus.

5.1.2.1.5 Node 146, Plateosauria

Bremer support: 3

Plateosauria is a less inclusive clade in this topology, including the most common ancestor of Plateosaurus and Efraasia, but not Massospondylus. This group includes several specimens traditionally placed at the base of the Sauropodomorpha tree: Plateosaurus, Plateosaurus (=Sellosaurus) gracilis, Unaysaurus, Ruehleia, and Efraasia. It also includes Asylosaurus, always included as part of the OUT Thecodontosaurus, Pradhania, a sauropodomorph recovered as a massospondylid (Novas, 2011), Arcusaurus, an Early Jurassic sauropodomorph placed as the sister taxon to Efraasia (Yates et al., 2011), and Nyasasaurus, recently recovered as a massospondylid (Baron et al., 2017). 13 unambiguous synapomorphies support node 146: AOF3, antorbital fossa has a concave anterior margin and a convex posterior margin (1), MX8, loss of the anterior maxillary foramen (1), N1, posterolateral process
of the nasal overlapping the lacrimal (1), BC3, loss of the post-temporal foramen in
the occiput (1), SA2, retroarticular process tapering in lateral and dorsal views (1),
PCE14, spinoprezygapophyseal lamina (sprl) in the posterior cervicals (1), CO4,
posterior process in the coracoid (1), SC1, stepped articulation in the scapulocoracoid
(1), that changes to an inflexion in *Macrocollum* and *Unaysaurus* (2), H8,
anterolaterally oriented deltopectoral crest (1), MC20, proximal portions of the
metacarpal IV lateral to metacarpal III (0), I11, iliac preacetabular ridge (1), FI10,
proximal portion of the fibula tapers to a point and is arched anteromedially (1), and
AS19, concave mediolateral surface of the astragalar distal portion (0), this changes to
straight in *Macrocollum* and *Unaysaurus*.

Inside Plateosauria, two clades are distinguished: Node 145, that includes *Efraasia,*
Arcusaurus, *Asylosaurus, Nyasasaurus* and *Pradhania*; and Node 195, which
coincides with the definition of Plateosauridae that contains *Unaysaurus* and
Plateosaurus but not *Efraasia* and *Massospondylus.*

Eight unambiguous synapomorphies support node 145: OTO3, paraoccipital process
with distal end pendent (1), PB3, elongated space between the basal tubera and the
basipterygoid process (1), MXT19, longitudinal distal and mesial (MXT20) labial
grooves in the maxillary teeth (1), DT21, longitudinal distal and mesial (DT22)
grooves in the dentary teeth, SC15, slightly convex surface posterior to the acromial
ridge and distal blade (1) convergent with *Plateosaurus*, H12, triangular deltopectoral
crest (0), a reversal respective to the rest of Sauropodomorpha and convergent with
*Pantydraco*, and MC8, symmetric depression on the proximodorsal portion of the
metacarpal I (0). The braincase of *Asylosaurus* has been considered as part of
*Thecodontosaurus*, suggesting that this lumping may have obscured this clade. Cranial
material is fragmentary in *Asylosaurus, Arcusaurus* and *Efraasia*, and lacks in
*Nyasasaurus* and *Pradhania*. This topology also confirms the consideration of
Arcusaurus as a relictual taxon into the Early Jurassic and puts *Pradhania* in the same
position. With *Nyasasaurus* likely to be of Late Triassic age, yet the oldest
sauropodomorph, Node 145 represents the only plateosaurian lineage to pass the
Triassic-Jurassic extinction.

Node 195, Plateosauridae, is supported by nine unambiguous synapomorphies: the
development of three laminae in the axis, AX13, centroprezygapophyseal lamina
(cprl) (1), AX14, spinoprezygapophyseal lamina (sprl) (1), and AX17, spinopostzygapophyseal lamina (spol) (1), ACE13, prezygodiapophyseal lamina (prdl) absent in the anterior cervicals (0), PCE12, postzygodiapophyseal lamina (podl) present in the posterior cervicals (1) (which independently reappears several times in the tree, e.g. Riojasaurus, Lamplughsaura and Neosauropoda), PCE15, intraprezygapophyseal lamina present in posterior cervicals (1) (which regardless originates in Node 155), CO3, biceps ridge in the posteroventral portion of the coracoid (1), H6, flat dorsal margin in anteroposterior view (1), and PU15, median gap below the pubic apron (1). The morphology of the axis of Plateosaurus and Ruehleia is very similar and distinctive, as it is the morphology of the cervicals in both specimens. The taxonomic status of Plateosaurus may have obscured this clade making Plateosauria a paraphyletic arrangement, and some of the material referred to Plateosaurus may belong to any of the other groups.

Node 196 corresponds to Unaysauridae, a recently published node (Muller et al., 2019) that includes Macrocollum and Unaysaurus, and is supported by five unambiguous synapomorphies: MX11, rounded-bulbous ventral margin of the antorbital fenestra (0), Q4, reversal of the quadrate foramen to be inset into the quadrate (0), Fr2, anterolaterally directed anterior process of the frontal (1), SC1, articulation of the scapulocoracoid as an inflexion (2), and AS19, straight mediolateral surface of the astragalar body (1).
Figure 5.3: Section of the cladogram zooming in to the base of the tree showing the general body plans as summarised in Appendix 1 and the ages of the group. Silhouettes not to scale. This section of the cladogram shows the first appearance of quadrupedality, with outlined profiles indicating species for which there is strong anatomical evidence to suggest obligate quadrupedality. Most of this part of the tree has specimens from the Early Jurassic, but all the groups also have representatives in the Late Triassic.
5.1.2.1.6 Node 155

This clade contains all the taxa that are not traditionally placed in Plateosauridae, except for Pradhania and Nyasasaurus, considered as a grade-like arrangement towards Sauropoda. However, seven clades are recovered along the way. Twelve unambiguous synapomorphies support Massospondylidae: EN2, loss of narial fossa (0), L7, lacrimal anterior ventromedial process originates at the base of the lacrimal anterior dorsomedial process (1), OTO6, unossified gap between the crista interfenestralis and the parabasisphenoid (1), PB1, anterior part of the parabasisphenoid process has a depth: width ratio equal to or less than 1.0 (1), MXT22, more than 14 but less than 20 maxillary teeth (5), ACa3, length of the centrum of anterior caudal vertebrae relative to their height is less than or equal to 1.0 (1); ACa6, length of the base of the neural spines relative to the length of the neural arch of the anterior caudal vertebrae have a ratio equal to or more than 1.0 (1), MC1, digit II is the most extended (1), MC23, metacarpal V with a convex proximal articulation surface (1), MD8, manual digit I with curved tips projecting well below flexor margin of proximal articular surface (1), PD10, pedal ungual III is 85% smaller in all linear dimensions than pedal ungual II (1).

5.1.2.1.7 Node 175, Mussauridae, Node 183, Node 173, Node 179

Bremer support: 2

Mussauridae (Bonaparte and Vince, 1976) is defined here as the clade that contains the most common ancestor of Mussaurus, but not Plateosaurus nor Massospondylus carinatus. In this group are included Yimenosaurus, Lufengosaurus, Sarahsaurus, Gryponyx, Ignavusaurus, Xixiposaurus, Massospondylus kaalae, Mussaurus, Pulanesaura, Leyesaurus, Ngwevu, Sefapanosaurus, Leonerasaurus and Yizhouosaurus. Eleven unambiguous synapomorphies are supporting this clade: MX16, narial fossa orients dorsally on the maxilla (1), MX17, the narial fossa is developed into a concave surface (1), ACE1, lateral pneumatic fossa rimmed in the anterior to middle cervicals (1), ACE19, intrapostzygapophyseal lamina (tpol) present in the anterior to middle cervicals (1), MDO18, and tpol in the middle dorsals (1), PDO7, postzygodiapophyseal lamina (podl) in the posterior dorsal vertebrae (1), PDO26, diapophyses dorsally deflected from the sagittal plane (1), ST2, loss of the longitudinal ridge on the dorsal surface of the sternal plate (1), H6, rounded humeral head in
anteroposterior view (0), PU14, straight-sided pubic apron in anterior view (0), later reverted to concave in Adeopapposaurus and Anchisauria (0), and PU22, mediolaterally unexpanded distal margin compared to the lateral margins (1).

Within Mussauridae, several groups are also identified, a clade containing Yimenosaurus and Lufengosaurus (Node 183), a clade containing Sarahsaurus, Gryponyx and Ignavusaurus (Node 173), and a clade containing Xixiposaurus, Massospondylus kaalae, Mussaurus, Pulanesaura, Leyesaurus, Ngwevu, Sefapanosaurus, Leonerasaurus and Yizhousaurus (Node 179). This group includes several specimens that are seldom analysed with all the other sauropodomorphs, i.e. Yimenosaurus, never used before, Gryponyx, last used in Galton and Upchurch (2004), and Ignavusaurus, considered as a juvenile of Massospondylus.

Three unambiguous synapomorphies support node 183: I1, iliac blade straight in dorsal view (0), I17, supraacetabular crest extended along the entire pubic peduncle (1), and Fe9, femoral neck present (1). Both Yimenosaurus and Lufengosaurus come from sediments deposited during the Early Jurassic (Hettangian-Sinemurian) in the Yunnan Province. Five unambiguous synapomorphies define node 173: PDO14, loss of the spinopostzygapophyseal lamina (spol) in the posterior dorsal vertebrae (0), H5, edge dividing the proximal articular surface of the humeral head from the deltopectoral crest (1), MC1, reversal to digit III being the longest, MC22, metacarpal IV-V placed dorsal to metacarpals I-III (0), and T14, quadrangular tibial distal end (1). Ignavusaurus and Sarahsaurus being sister taxa were recently proposed in the iteration performed by Chapelle and Choiniere (2018).

Node 179 is the largest clade within Mussauridae and is supported by three synapomorphies: N5, planar frontonasal suture (0), I15, reversal to a ridge supraacetabular margin (0), and PD12, loss of pedal digit V. Further up the tree and skipping Xixiposaurus, Node 178 (Pulanesaura, Leyesaurus, Ngweu, Sefapanosaurus, Leonerasaurus and Yizhousaurus) is supported by four unambiguous synapomorphies, PrF2, loss of anterior prefrontal process (1), H3, the articular surface of the humeral head is separated by a groove from the median tuberosity (1), I1, ilium is sigmoidal in dorsal view (1), and Fe9, loss of the femoral neck (0), and one ambiguous synapomorphy, H8 deltopectoral crest oriented anterolaterally (1). Node 177 contains all the other mussaurids, except for M. kaalae and Mussaurus, and is supported by nine
unambiguous synapomorphies: PMX3, presence of anterior premaxillary foramen (1), MXT2, maxillary teeth angled relative to the long axis of the jaw (0), MXT3, and contacting adjacent teeth (1), MXT11, loss of the basal constriction of the maxillary tooth crowns (0), DT5, dentary teeth angled relative to the long axis of the jaw (1), DT10, dentary tooth with curvature of lingual surfaces concave mesiodistally (1), PCE9, loss of the anterior centrodiapophyseal lamina (acdl) (0), and PCE10, loss of the posterior centrodiapophyseal lamina (pcdl) (0).

The monophyly of *M. kaalae* and *Mussaurus* (node 199) is in turn supported by six unambiguous cranial synapomorphies: PMX13, loss of the subnarial foramen (0), MX15, loss of the narial fossa on the maxilla (0), MA8, retroarticular process composed of portions of the surangular and angular (0), SA4, anterior (1) and SA5, posterior surangular foramen (1), and MXT6, serrated maxillary teeth.

### 5.1.2.1.8 Nodes 154

Node 154 is supported by 12 unambiguous synapomorphies and includes two groupings, Anchisauria (Node 159) and a clade containing *Aardonyx*, *Xingxiulong*, *Seitaad*, *Glacialisaurus* and *Adeopapposaurus* (Node 153). The unambiguous synapomorphies are MX20, medial interdental plates displaced dorsally relative to the lateral plates (2), L4, lateral lamina of the lacrimal restricted to the lacrimal body (2), J2, maxilla articulating the jugal ventrally (1), PO2, anterodorsal process of the postorbital medially deflected relative to the prefrontal main body (1), BO3, knob-shaped basal tubera (1), LA6, postorbital process of the laterosphenoid laterally oriented (0), SA5, posterior surangular foramen present (0), DEN4, dental enamel extensively wrinkled (2), PCE26, cervical rib of the posterior cervicals placed parallel to the cervical column (1), MC14, metacarpal II with trapezoidal shape in distal view (1), I15, supraacetabular margin as a ridge (0), and IS5, the ischium contacts its antimere only in the medial edge (0).

Seven unambiguous synapomorphies support node 153 that contains *Aardonyx*, *Xingxiulong*, *Seitaad*, *Glacialisaurus* and *Adeopapposaurus*: B13, second anterior premaxillary foramen (also present in *Massospondylus carinatus*), D7, symphyseal end displaced ventrally in lateral view (1) (even current in *M. carinatus* and *Coloradisaurus*), PCE16, centropostzygapophyseal (cpol) in the posterior cervicals, SC12, acromial ridge absent in the scapula (0), but present in *Adeopapposaurus*, U4,
radial fossa in the proximal end of the ulna (1), which also appears in Node 164, PU16, opening in the proximal portion of the pubic apron (1), also present in Coloradisaurus, and PU19, anteroposterior expansion of the distal pubis (1), which appears later on in Node 168, Node 182, and Sauropoda. All these sauropodomorphs have been assigned to the Early Jurassic; Aardonyx has been considered to be one of the first Sauropodiformes, positions similarly attributed to Xingxiulong and Seitaad, which are also in this clade. Glacialisaurus was placed next to Lufengosaurus, but here is recovered next to Adeopapposaurus. Several sauropod-like features in these animals seem to be convergence.

5.1.2.1.9 Node 159, Anchisauria

Node 159 includes Node 158 (=Anchisauridae: Anchisaurus, Blikanasaurus and Gyposaurus sinensis), Node 185 (=Yunnanosauridae: Yunnanosaurus huangi, Yunnanosaurus robustus, Eucnemesaurus fortis) and Massopoda (Node 167).

Ten unambiguous synapomorphies support node 159: CR12, supratemporal fossa present in the parietals (0), Fr5, but absent in the frontal (1), ACE6, spur-like projections on the anterior margin of the neural spine (1), present as well in Adeopapposaurus and Leyesaurus, ADO17, prespinal lamina (prsl) in the anterior dorsal vertebrae (1), MDO11, prezygodiapophyseal lamina (prdl) in the middle dorsal vertebrae (1), CO1, coracoid with only one face (0), also present in Adeopapposaurus, SC1, straight articulation of the scapulocoracoid (0), Fe11, spike-like lesser trochanter (1), T10, distal end with a rounded surface in the posterior face (0), and AS8, posterior groove in the astragalus (0). Several features of Anchisauria are also found in Leyesaurus and Adeopapposaurus, and these similarities also appear in M. carinatus and Coloradisaurus, which means that further observation of these specimens would, in turn, place Massospondylus outside Anchisauria, or Adeopapposaurus and Leyesaurus inside Anchisauria. The matrix surrounds the postcranial material restricted here to M. carinatus, and some features observed clearly in Adeopapposaurus and Leyesaurus are not easily discernible in M. carinatus. The position of these four specimens is therefore subject to revision.

Node 158 includes Anchisaurus, Blikanasaurus and Gyposaurus sinensis. The first two have been considered as part of the gradient towards sauropodan quadrupedality, but here they form a more reduced clade (Anchisauridae). Seven unambiguous
synapomorphies support this clade, four of them applicable to the three members since there is only hindlimb material referred to *Blikanasaurus*: PCE10, posterior centrodiapophyseal lamina (pcdl) is absent in the posterior cervicals (0), MDO5, straight mid-dorsal vertebrae (0), U7, olecranon process (1), Fe13, lesser trochanter on the lateral margin of the femoral shaft (1), T15, reduced distal end, exposing the posterior fossa of the astragalus in posterior view (1), Fi9, fibular distal end angled anterodorsally producing an asymmetrical lateral view (1), and PD10, pedal ungual III is more than or equal to 85% of the size of pedal ungual II in all linear dimensions (0).

Eight unambiguous synapomorphies support node 185 (=Yunnanosauridae), containing Yunnanosaurus huangi, Yunnanosaurus robustus and Eucnemesaurus fortis: MXT19, longitudinal distal labial grooves in the maxillary teeth (1), not applicable to *E. fortis*, ACE17, centropostzygapophyseal lamina (cpol) in the anterior to middle cervicals (1), not relevant to *E. fortis*, present also in *Adeopapposaurus*, SACa1, Sacrocaudal vertebrae (1), and present in *Xingxiulong* too, Chv5, most extended chevron relative longer than twice the length of the preceding centrum (2), H8, deltopectoral crest anteriorly oriented (2), CAR1, transverse width of the distal carpal I, less than or equal to 1.2 times that of the distal carpal II, PU19, anteroposterior expansion of the pubis (1), and Fe8, and posteromedial tuber aligned with the posterior tuber (1). The position of *Eucnemesaurus fortis* in this clade is not definite since only one of these synapomorphies, CAR1, applies to it; the fragmentary nature of the material and the lack of an updated monograph are highlighted for this taxon.

5.1.2.1.10 Node 167, Sauropodiformes, and Node 166, Riojasauridae

Sauropodiformes defined as the most inclusive clade containing *Saltasaurus* but not *Massospondylus* is supported by nine synapomorphies: N5, frontonasal articulation as a planar suture (0), PA1, parietals fused on the midline (1), DT18, tooth crown serrations absent in the distal margin (0), ACE12, posterior centrodiapophyseal lamina (pcdl) in the anterior to middle cervical vertebrae, ADO5, parapophyses of the anterior dorsal vertebrae located in the neurocentral junction (1), also present in *Adeopapposaurus*, ST2, longitudinal ridge in the dorsal surface of the sternal plate (1), CO3, biceps ridge in the coracoid (1), H6, domed hemispherical humeral head (2), also present in *Adeopapposaurus*, Fe11, rounded lesser trochanter (0), CA3, loss of the
medial peg of the calcaneum fitting into the astragalus (1), and V2, 13 dorsal vertebrae (4).

Node 166 contains two clades, Riojasauridae and Node 165 (which includes the most common ancestor of Lessemysaurus and Saltasaurus). The following unambiguous synapomorphies support this node: MX17, anterodorsal process of the premaxilla tapers to a point (0), SA5, loss of the posterior surangular foramen (1), ACE6, loss of the intraprezygapophyseal lamina (tprl) in the anterior to middle cervicals (1), SC10, posteromedial ridge of the scapula absent (0), and U3, anterolateral process equidistant to the olecranon and the anterior process of the ulna (1).

Node 189 contains two Late Triassic sauropodomorphs from Argentina, Coloradisaurus and Riojasaurus. It was proposed that Coloradisaurus exhibited a degree of mosaicism by having massospondylid and plateosaurid features, and in this topology is recovered as more derived than both Massospondylus and Plateosaurus, suggesting that these features are all plesiomorphic. Although there are several anatomical differences between Coloradisaurus and Riojasaurus, such as the number of dorsal vertebrae (13 in the former, 16 in the latter), in this topology the clade is supported by nine synapomorphies: MX16, narial fossa oriented dorsally in the maxilla (1), BC1, basal tubera above the level of the base of the basipterygoid process (0), PB7, basisphenoid recess reaches the subsellar recess creating an interbasipterygoid lamina (1), MA8, retroarticular process composed by the surangular and the angular (0), MXT22, more than 20 maxillary teeth (6), DT4, dentary teeth distributed only in the anterior and middle thirds of the dentary (2), ACE9, epipophyses restricted to the postzygapophyses (0), CO1, coracoid with two faces (1), and I17, supraacetabular ridge partially along the entire pubic peduncle (0). Riojasauridae is thus a Late Triassic clade bracketed by clades containing mostly Early Jurassic specimens. Nevertheless, Late Triassic specimens are peppered along with several clades in Anchisauria, i.e. Blikanasaurus, Eucnemesaurus entaxonis, Eucnemesaurus fortis, Lessemysaurus, Plateosauravus, Jaklapallisaurus, Camelotia, Melanorosaurus, Meroktenous, Ingentia and allegedly Isanosaurus. Consequently, the diversification of Sauropodomorpha occurred entirely in the Late Triassic, with all the groups diverging at this point. Furthermore implying that quadrupedality in Sauropoda originated during the Late Triassic and via accumulation of exaptations, whereas the quadrupedality in Mussauridae was likely acquired via paedomorphosis.
Figure 5. Section of the cladogram zooming in to the base of the tree showing the general body plans (as summarised in Appendix 1) and the ages of the group. Silhouettes not to scale. This section shows Sauropoda, which collapses into a polytomy, and the non-sauropodan sauropodomorphs that belong to Node 165. Most of the members of this clade are quadruped and of larger sizes, but the most primitive members are bipeds and of more gracile bauplan. Outlined silhouettes represent specimens for which there is anatomic evidence of obligate quadrupedality.
5.1.2.1.11 Node 165: Lessemsauridae and Node 182

Node 165 includes sauropodomorphs that are more closely related to sauropods. The following unambiguous synapomorphies support this node: ACE17, cpol in the anterior to middle cervicals reappears (1), ADO25, medial spinopostzygapophyseal (1) and ADO26, lateral spinopostzygapophyseal lamina appear in the anterior dorsal vertebrae (1), MDO5, straight posterior margin of the neural spines in the mid-dorsal vertebrae (0), SACa1, sacrocaudal vertebrae present (1), ACa7, length of the caudal centrum is less than the height of the centrum (0), Fe18, the maximum height of the fourth trochanter is placed closer to the midpoint of the femoral length (1), MT25, the midshafts of metatarsals I and V are similar in size, or larger than, the metatarsals II and III (0), MT35, the ventrolateral flange on the plantar surface of metatarsal II is medially flaring (2), and MT33, the longest metatarsal is between 40% and 25% the tibial length (1).

Node 182 includes Lessemsaurus, Ohmdenosaurus, Eucnemesaurus entaxonis, Antetonitrus and Ledumahadi. This clade has been named as Lessemsauridae elsewhere, and here is recovered as the sister taxon to the clade from where Sauropoda originates. Thus, quadrupedality developed in this clade may differ biomechanically than that established in sauropods. Eight unambiguous synapomorphies support Lessemsauridae: ADO4, transversely expanded neural spines in the dorsal in anterior dorsal vertebrae (1), SC13, acromial ridge extending beyond the acromial length (1), U4, development of a radial fossa (1), MC11, ligament pits on the extensor surface of the distal ends in metacarpal I (1), MC16 and metacarpal II (1), PU22, distal margin of the pubis not expanded mediolaterally (1), ISI9, plate-like distal ischium, not distinct from the obturator region (0), Fe9, loss of femoral neck (0), and T12, posterolateral process protruding laterally as far as the anterolateral corner of the distal tibia (1); pertaining carpal anatomy, MC10, hemispherical concavity in the ventromedial margin of metacarpal I (1) is found as an ambiguous synapomorphy.

5.1.2.1.12 Node 164

Bremer support: 2

Node 164 includes the most common ancestor of Jingshanosaurus and Saltasaurus. It is supported by 11 unambiguous synapomorphies distributed along the entire body:
AX17, spinopostzygapophyseal lamina (spol) in the axis (1), ACE7, centropostzygapophyseal lamina (cpol) in the anterior to middle cervicals (1), MC8, symmetric depression of the proximodorsal portion extensor pits of metacarpal I (0), transformed again to asymmetric in Sauropoda, MC14, rectangular outline of the distal end of metacarpal II (0), CAR1, lateral end of distal carpal 1 abuts distal carpal 2 (0), MD5, rounded proximal articular surface of the manual phalanx I.1 (0), MD6, subcylindrical body of the manual phalanx I.1 (0), PU6, iliac pedicel set anterior to the pubic apron creating a prominent inflexion in the proximal anterior profile of the pubis (1), IS5, ischium contacts the antimere along its length until the dorsal margins (2), IS8, dorsoventral expansion of the ischiadic medial margin at midshaft (1), and T13, concave posterolateral corner of the distal end of the tibia (1), convergent in Blikanasaurus and Coloradisaurus.

5.1.2.1.13 Node 187, Plateosauravidae

Node 187 is considered here synonym to Plateosauravidae to refer to the most inclusive clade that contains the common ancestor of Plateosauravus but not Melanorosaurus. Four synapomorphies support the clade: I3, straight outline in lateral view of the iliac dorsal margin (0), Fe21, fourth trochanter centrally located along the mediolateral axis (0), T14, quadrangular distal end of the tibia (1), and evenly rounded posteromedial margin of the astragalar body in dorsal view (0). Plateosauravus has been traditionally placed at the base of Sauropodomorpha, but it has been noted that some characters are incongruent with this phylogenetic position (McPhee et al., 2017). The results discussed here suggests that, except for Blikanasaurus, all the sauropodomorphs from the Lower Elliot Formation (Eucnemesaurus entaxonis, Eucnemesaurus fortis, Plateosauravus and Melanorosaurus) are part of the same diversification event of massopodan sauropodomorphs.

5.1.2.1.14 Node 163, Melanorosauridae and Node 162

The node 163, Melanorosauridae, is the most inclusive clade that contains the most common ancestor of Melanorosaurus and Saltasaurus. This clade includes an assortment of Late Triassic and Early Jurassic taxa that lead towards the sauropod-type locomotion and diet. The older taxa are Camelotia, Melanorosaurus, Meroktenos, Ingentia and putatively Isanosaurus. Chuxiongosaurus, here recovered in this node, was recently described as a juvenile specimen of Jingshanosaurus, but several cranial
characters support a sauropodan cranial morphology. Fourteen unambiguous synapomorphies support this node: Q5, posterolateral margin of the quadrate slopes posteriorly relative to the posteromedial margin (1), Ec1, pneumatic fossa on the ventral surface of the ectopterygoid (0), AR2, loss of the strong medial embayment behind the glenoid (0), longitudinal mesial (DT21) and medial (DT22) grooves in the dentary teeth (1), H4, humeral head separated by an indentation from the deltopectoral crest (1), MD8, straight manual ungual I (0), PD2, proximal-most phalanges longer than wide, more distal phalanges as wide as long (1), and V3, four sacral vertebrae (2).

5.1.2.1.15 Node 169, Sauropoda

Bremer support: 4

Sauropoda is defined as the most inclusive clade that contains the most common ancestor of Saltasaurus and Ingentia. Nine unambiguous synapomorphies support the sauropodan node: D8, loss of the buccal emargination on the lateral surface of the dentary (0), SA2, retroarticular process terminates blunt in lateral and dorsal views (0), PMT3, posteriormost premaxillary tooth anterior to the external naris (1), MXT6, maxillary crowns with denticles (1), U5, loss of a greatly enlarged olecranon process in the ulna (1), R2, distal condyle of the radius with a flattened posterior margin for articulation with the ulna (1), R3, flat distal portion of the posterior margin (1), MC3, intermetacarpal articular facets (1), MC8, proximodorsal part of the extensor pits in metacarpal I with asymmetric concavity (1).

5.1.2.2 Extended implied weighting

The analysis of the dataset under equal weighting has four taxa removed, i.e. Plateosaurus ingens, Ammosaurus, Euskelosaurus and Agnosphytis, but of these four specimens, the last three were first-hand assessed in this work. When included under equal weight, they produced the spurious clade of Phytodinosauria (Ornithischia nested inside Sauropodomorpha at the base with Ammosaurus as the most primitive ornithischian). All the synapomorphies that supported the clade applied only to the ornithischians, and after running an iter-PCR analysis, the four taxa mentioned above were found to move around the tree. When pruned a priori, Phytodinosauria disappears, and the topology discussed above is obtained. Here, the four taxa are reincorporated into the analyses to see the impact under extended implied weighting.
The sensitivity analysis performed here assessed how much the nodes described above change when different concavity values are considered in the extended implied weighting. The weighted homoplasy ($w$) is calculated as a ratio between the homoplasy values for a character ($h$) and the homoplasy value plus a concavity constant ($k$), as in equation 5.1:

$$w = \frac{h}{(h + k)} \quad (5.1)$$

Different concavity values penalise the weighted homoplasy differently, with smaller values of $k$ producing weighted values closer to 1, and more significant numbers penalising homoplasy the least, closer to 0. If some of the synapomorphies listed above behave as homoplasies, e.g. convergences or losses, they are penalised strongly under smaller concavities, and analysing the stability of each node under different concavities can highlight potentially more stable nodes. For instance, the clade Silesauridae containing *Pisanosaurus*, *Silesaurus* and *Asilisaurus* is recovered in all the topologies in its totality regardless of the concavity value. However, under extended implied weighting, theropods and ornithischians move around the tree producing spurious clades, such as Theropoda originating from the base of Sauropodomorpha (with $k = 12$), or Ornithischia originating from the base of Sauropodomorpha (with $k = 2$ and $k = 5$). In the latter, a substantial penalisation of homoplasies produces Phytodinosauria, as the more likely explanation for the similarities in the cranial characters specialised for herbivory. The position of Ornithischia in the Sauropodomorpha tree is just at the transition from faunivory to herbivory. Several theropods and ornithischians are clustered together outside of Sauropodomorpha matching some of the contents of Ornithoscelida, however, as the $k$ value increases, this clade is not supported and the traditional arrangement Saurischia + Ornithischia emerges instead.

Bagualosauria appears partially in all the topologies except when the $k = 2$, with some members alternating position between more primitive or more derived than Bagualosaurus, such as *Saturnalia*, *Pantydraco* and *Pampadromaeus*. *Buriolestes* and *Chromogisaurus* in the same clade (node 160) is supported under all concavity values. The position of *Pantydraco* and *Thecodontosaurus* as paraphyletic alternates with a monophyletic Thecodontosauridae under specific values of $k$, i.e. 2, 10 and 20. Clade
145, which includes *Efraasia*, coincides totally in content to the node described above and is supported under all the concavities, with only *Nyasasaurus* changing position through the tree. All the topologies support *Nyasasaurus* as a sauropod, but its position changes from very derived (*k* = 2, 5 and 10), to more primitive (*k* = 12, 15, 20 and 30). Clade 195, Plateosauridae, is supported under all the concavities, and the arrangement of Unaysauridae (*Unaysaurus* and *Macrocollum*) is supported under most of the concavities. The content of Node 145, Plateosaurus becomes more restricted as the concavity values increase. However, *Agnosphytis* is placed within Unaysauridae as the concavities increase, going from the most basal part of Silesauridae when *k* = 2, to Ornithoscelida when *k* = 5, 10, 12.

Clade 175, defined here as the most inclusive clade that contains *Mussaurus* and *Lufengosaurus*, but not *Massospondylus* nor *Plateosaurus*, is not supported with low concavities but appears partially as values increase. Interestingly, the topology from equal weighting supports that the origin of quadrupedality occurred twice, whereas topologies with low *k* values show a more traditional grade-like arrangement. As the *k* value increases and homoplasies are penalised less, this clade appears more consistently through the topologies.

In all the topologies, *Massospondylus carinatus* is placed with other members traditionally regarded as massospondylids, such as *Adeopapposaurus* and *Ngwevu*. However, *Leyesaurus* is placed within massospondylids with lower *k* values, and it moves to other groups as the values increase. Interestingly, *Aardonyx* is always placed within Massospondylidae. This grouping is consistent with the one found in the topology under equal weighting, except for the exclusion of *M. carinatus*. It is worth noting that as the *k* values increase, some taxa represented by very fragmentary material, *Ohmdenosaurus* and *Euskelosaurus*, are also placed inside Massospondylidae. The position of *Ohmdenosaurus* changes from inside Sauropoda with *k* = 2, to the outside of Sauropodomorpha (in Theropoda, with *k* = 10, 15 and 20).

On the other hand, *Euskelosaurus* moves from outside Dinosauria (*k* = 2, Silesauridae with *k* = 10 and 30), to Massospondylidae (*k* = 12 and 15). Therefore, caution is needed when very fragmentary material is included in the supermatrix, as they seem to become erratic depending on the weighting, or completely unstable under equal weighting. Similar behaviour is seen with *Nambalia*, which under equal weight is found as a basal
theropod, but under different concavities it is consistently placed within Plateosauria, moving from outside to inside the tree. *Nambalia* has always been placed at either the base of Sauropodomorpha or inside Plateosauridae.

Massospondylidae, a clade that includes *Massospondylus* and *Mussaurus* but not *Plateosaurus* and *Jingshanosaurus*, is supported by several unambiguous synapomorphies, most of them from the skull: L6, anterior dorsolateral process of the lacrimal is present (1), J2, maxilla articulates ventrally to the jugal (1), SQ4, auxiliary anteroventral process on the postorbital articular surface of the squamosal (1), SA5, posterior surangular foramen (1), DEN4, enamel surface wrinkled in patches (1), MXT2, maxillary teeth angled relative to the long axis of the jaw (1), DT5, dentary teeth angled relative to the long axis of the jaw (1), ACE6, anterior spur-like projections on the anterior margin (1), ADO14, loss of the intrapostzygapophyseal lamina (tpol) (0), ACa3, first anterior caudal vertebrae shorter in length relative to its height (1), and PU6, iliac pedicel set anterior to the pubic apron (1).

Massospondylidae includes all the traditional massospondylids, i.e. *Massospondylus*, *Adeopapposaurus* and *Leyesaurus*. However, this clade also includes *Aardonyx*, *Mussaurus*, *Yizhouaurus*, *Seitaad*, *Anchisaurus* and *Pulanesaura*, more closely related to each other than to Sauropoda. This clade supports the idea of two types of quadrupedality originating in Sauropodomorpha, with a gradient of successively more quadrupedal sauropodomorphs arising from bipedal ones. In this clade, *Massospondylus* is the most primitive member, an obligate bipedal, then along Massospondylidae forms with a facultative quadrupedality appear, such as *Anchisaurus* and *Aardonyx*, and the taxa with the more derived characters with an obligate quadrupedality, such as *Pulanesaura*, but also *Mussaurus*, with evidence of an ontogenetic locomotory shift. The scenarios that support Massospondylidae also show that obligate quadrupedality must have originated twice in Sauropodomorpha, but place *Massospondylus* as either at the base of Massospondylidae or at the base of Massopoda, a clade that contains Sauropoda. Under equal weight, cranial characters and characters related to locomotion show homoplastic behaviour, but under extended implied weighting (*k* = 15, 20 and 30), the homoplastic behaviour is reduced in both. Cranial characters are mostly defining Massospondylidae.
Massopoda, a grouping that contains most of Sauropodomorpha except for *Lufengosaurus*, *Meroktenos*, *Sarahsaurus*, *Riojasaurus* and Plateosauria, is also defined mostly by unambiguous cranial synapomorphies. The exclusion of *Riojasaurus* from Massopoda would suggest that either the locomotion in *Riojasaurus* has been wrongly reconstructed as quadrupedal, or that quadrupedality evolved once in primitive sauropodomorphs and twice in Massopoda. Under both equal weighting and extended implied weighting, the adaptations to herbivory appear before the adaptations to quadrupedality. The synapomorphies that support Massopoda under extended implied weighting ($k = 15$, 20 and 30) are: PMX1, lateral side of the premaxilla not expanded beyond the level of the lingual margin (0), PMX5, concave anterodorsal margin of the premaxilla (1), PMX14, slot-shaped subnarial foramen of the premaxilla (1), L4, lateral lamina of the lacrimal restricted to the body of the lacrimal (2), BO3, basal tubera knob-shaped in posterior view (1), LA6, postorbital process of the laterosphenoid oriented laterally (0), LA7, frontal process of the laterosphenoid oriented anterodorsally (1), DT18, tooth crowns lacking serrations in the distal margin (0), ACE9, epipophyses restricted to the postzygapophyses (1), PCE26, cervical ribs of the posterior cervicals parallel to the long axis of the cervical column (1), DSA1, dorsosacral vertebrae present (1), IS5, the medial contact of the ischium with its antimere is restricted to the medial edge (0), and FI10, anterior margin of the proximal portion of the fibula is rounded (0).

Five very fragmentary taxa are clustered together with a $k = 30$, i.e. *Blikanasaurus*, *Plateosauravus*, *Jaklapallisaurus*, *Eucnemesaurus fortis* and *Gryponyx*, but with lower concavities, the taxa distribute along the tree. Four unambiguous synapomorphies support this clade: ACa11, loss of the longitudinal ventral sulcus of the vertebrae (0), scored only for *Plateosauravus* and *E. fortis* only, U4, flat radial surface of the ulna (0), scored only for *Plateosauravus*, CA3, medial peg fitting into astragalus (0), scored only for *E. fortis*, changes to absent (1) in *Jaklapallisaurus*, and scored as ‘?’ in the others, and CA4, loss of the calcaneal tuber (0), scored present for *Eucnemesaurus* fortis. These taxa may cluster together due to incompleteness and may be an artefact.

Two other taxa are also widely unstable under equal weights. *Plateosaurus ingens* is consistently found in Theropoda in all but one of the concavity values, suggesting that
the material needs to be reviewed as no monograph exists of this material. *Ammosaurus* generates Phytodinosauria under equal weights, placed outside of Sauropodomorpha in a clade with a composition similar to Ornithoscelida, and stays in this position until the concavity is set to $k = 30$ when it is placed as the sister taxon of *Anchisaurus*. The material also needs to be reviewed and see if more information can be obtained from it.
Table 5. I. Summary results of the sensitivity analysis performed to the supermatrix. The k values indicate different concavities. Numerical nodes refer to the content described for the nodes mentioned above, and alphabetic nodes refer to nodes discussed in Chapter 1 not found in the topology under equal weights. The letters above represent if, for each concavity (k) value, the node is found with all its members in the topologies (t, total coincidence), some of its members (p, partial coincidence), or none of them (n, no coincidence). When a node number is put under one of the columns, this represents that the two nodes are considered synonyms in the topology (contain the same taxa).

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5.1.2.3 Bayesian analysis

Bayesian analyses ran over 200,000 generations were insufficient for the model to reach stationarity, and two of the ten runs converged into lower logarithmic likelihood values (Figure 5.5). After letting the phylogenies run for up to 400,000 generations, the trend was still observed, and there was no way to estimate if the two scenarios were going to converge. If, for example, they converge after 600,000 generations, the analysis would still have had to run 2,400,000 simulations to allow the first 600,000 generations to be discarded as part of the ‘burn-in fraction of 25%’. Instead, this thesis focused on analysing the two more likely topologies in both trends. In one direction Nyasasaurus is a saurischian, nested either in Sauropodomorpha or Theropoda (Figure 5.6) and in the other Nyasasaurus is nested as either a sauropodomorph or an ornithischian, recovering Phytodinosauria (Bakker, 1986; Figure 5.7). Phytodinosauria might be an artefact caused by the atomisation of dental characters, which are specialised for a herbivorous diet. However, this problem may be avoided by increasing the number of generations of trees and the number of runs. Most of the runs reached stationarity and converged. In Run 10, Phytodinosauria collapsed, and the new topologies recovered favoured the traditional Saurischia model, with higher likelihoods. The likelihood of the ‘Phytodinosauria’ model is significantly lower than the likelihood for the Saurischian model, providing support for the idea that this might be an artefact caused by character oversampling and a more prolonged Bayesian analysis would prevent it, although how long is not possible to say.

Because of these disparities, majority rule collapses Dinosauria and most of the sauropodomorphs at the base of the tree. However, several groupings are well supported in all the runs. Sauropoda, comprising Vulcanodon, Tazoudasaurus, Nebulasaurus, Katasaurus, Isanosaurus, Spinophorosaurus and Neosauropoda has an estimated age of divergence of 212.21–199.08 Ma extending to the Norian–Rhaetian (95% confidence interval). Ornithischia is also proposed to have diverged between 217.5–203.32 Ma, during the Norian. Theropoda has an estimated divergence age of 232.6–223.77 Ma, in the Carnian. Eoraptor is not placed in Theropoda. Pisanosaurus is clustered with silesaurids in all of the runs and has an estimated divergence age of 245.53–234.9 Ma (Anisian). Another consistent clade found in over 50% of the trees is Guaibasauridae (Guibasaurus, (Buriolestes, Bagualosaurus)), diverging 241.4–201.73 Ma (Anisian–Rhaetian), and Saturnalidae (Saturnalia, Panphagia), diverging
243.74–236.03 Ma (Anisian-Carnian). Well supported sauropodomorph groups are Thecodontosauridae (Pantydraco, (Arcusaurus, Thecodontosaurus)), diverging 224.02–210.12 Ma (Carnian–Norian), a clade containing Eucnemesaurus entaxonis, Leonerasaurus and Selapanosaurus (not found in the parsimony-based analysis) diverging 214.4–201.73 Ma (Norian–Rhaetian), Massospondylidae, containing only M. carinatus and Leyesaurus, diverging 211.14–198.33 Ma (Norian–Hettangian), Melanorosauridae (Melanorosaurus and Camelotia) diverging 219.28–206.69 Ma (Carnian–Norian), Plateosauridae (Plateosaurus and Unaysaurus) diverging 227.89–217.1 Ma (Carnian–Norian), and Riojasauridae (Riojasaurus, Xixiposaurus) diverging 224.25–212.23 Ma (Carnian–Norian). In all the runs, Saltopus is recovered within Dinosauria.

The most likely scenarios from run 4 (generation 159000) and run 10 (generation 198000) produce similar results to the parsimony-based analysis but are half as likely compared to the other runs. The odd position of several taxa explains this low likelihood values and allows building a framework of where specific taxa are not likely to be. The most likely scenario in run 4 (lnL=-12695) retrieves Massospondylidae in the arrangement of Massospondylinae and Lufengosaurinae (surprisingly placing the highly incomplete taxon Ohmdenosaurus in the latter), the clade Plateosauravidae, Anchisauridae (restricted only to Seitaad, Anchisaurus and Ammosaurus), Riojasauridae (Riojasaurus and Xixiposaurus only). This topology also supports Sauropoda as the sister taxon to Melanorosauridae. The most likely scenario in run 10 is also the most likely scenario of all situations in all the runs (lnL=-12510). As in run 4, this also places Guiabasauridae at the base of Sauropodomorpha, finds a less likely more inclusive Massospondylidae, that contains Riojasaurus, Pradhania, Sarahsaurus, and Adeopapposaurus, an Anchisauridae clade that includes Ammosaurus, Anchisaurus and Seitaad, Plateosauravidae with Ruehleia and Plateosauravus, and Thecodontosauridae (Arcusaurus, Thecodontosaurus, Saltopus, and Pantydraco). Like in the other topology, Sauropoda is the sister taxon to Melanorosauridae.
Figure 5.5. Logarithmic likelihoods of the models simulated in MrBayes showing the two stationarities that ten different runs reached. Two runs (3 and 4) converge in models where Phytodinosauria is recovered in the topologies. Run 10 starts to reach a plateau in the same scenarios than runs 3 and 4 but then changes to the Saurischian scenario.
Figure 5.6. The most likely scenario of all the runs produced by the Bayesian analysis showing similar groupings to the topology described under equal-weighted parsimony approach.
Figure 5.7. Most likely scenario obtained during run 4, showing the arrangement of Phytodinosauria and Nyasasaurus as the first ornithischian.
Figure 5.8. Majority rule from the Bayesian simulations showing the estimated divergence ages for the nodes found.
6 Conclusions

6.1 Discussion

The early evolution of Sauropodomorpha has been subjected to constant debate in the literature. Phylogenetic analyses conducted in recent years have led to the conclusion that the specialisations that led to a herbivorous diet, gigantic size and quadrupedal locomotion were acquired in a step-wise fashion as part of a rapid correlated progression (Yates, 2004a): An increase in specialisations for herbivory led to an increase in size to process more significant amounts of plant material and to reduce the vulnerability towards predation, and eventually, graviportal locomotion was established as a consequence.

However, as discussed in Chapter 1, there is a lot of conflicting evidence about the interrelationships between the different non-sauropod sauropodomorphs. Moreover, the sequence adaptations were acquired to reach the sauropod bauplan are obscured by unresolved topologies at the base of Sauropodomorpha, and a lack of fossils from the Triassic-Jurassic transition. Furthermore, non-sauropod sauropodomorphs have complicated taxonomic histories with specimens having been classified as theropods or ornithischians, and with silesaurids having been classified as ‘prosauropods.’ This complicated taxonomic history is at the root of the incongruences between phylogenies, with different authors using different taxonomic definitions, even if when they used the same operational taxonomic units (OTUs). Chimaeras are everyday OTUs in the most studied ‘prosauropods’ in the literature, e.g. *Thecodontosaurus*, *Plateosaurus Massospondylus*, *Anchisaurus* and *Yunnanosaurus*. Several specimens are referred to these taxa, and the taxonomic opinions range from these OTUs being monospecific to containing as many as fifty species (for *Plateosaurus*).

The pattern of explosive radiation that can be identified in topology recovered herein is that of a disparification, in which both species richness and morphological disparity increase (Ackerly, 2009; Simões et al., 2016). Disparification, for example, is seen as a product of ecomorphological differentiation via niche partitioning (Glor, 2010; Mahler et al., 2010; McPhee et al., 2015b, 2015a). It is necessary to quantify rates of speciation rates and character evolution to test the hypothesis of niche partitioning. More accurate stratigraphic data is needed to improve the speciation rate estimation.
Many of these species’ ranges are currently based on the regional age of the outcrops and not necessarily on the age of the strata where the fossils were found (Smith et al., 2007; McPhee et al., 2017; Viglietti et al., 2018), and further detailed dating is required if we are to thoroughly test the hypothesis proposed here that sauropodomorphs increased in species richness and disparity concurrently. The rapid, explosive diversification of Sauropoda could be interpreted as the product of an exaptive radiation, where specific key innovations are acquired gradually, contributing to the diversification in that clade (Simões et al., 2016). It could also be the case that after the disparification of particular clades, exaptive radiations occurred after the establishment of one or another trait being particularly advantageous for a specific niche. This new evolutionary framework presented herein allows palaeoecological methods to be used to examine whether trends correspond to actual disparification events or exaptive radiations, or whether they are apparent radiations (pseudoradiation event) due to a decline in extinction rates, with the accompanying result in the accumulation of species richness. Patterns of disparification may also be the result of sampling bias, because the sauropodomorph-bearing localities from the Late Triassic and Early Jurassic may not necessarily capture the trends occurring worldwide (Figures 6.1 and 6.2). Finally, having this new topology as a starting point encourages a focus on biomechanical adaptations that each clade of non-sauropod sauropodomorphs developed through time. It will allow examination of the trends to herbivory, gigantism and quadrupedalism, and whether they are convergent with strategies seen

6.1.1 Herbivory

During the Late Triassic, sauropodomorphs expanded over Pangaea and became the more representative herbivorous fauna by the end of the Rhaetian (Figure 6.1). This diversification of herbivore dinosaurs coincides with the complex vegetation that evolved as a result of the peak amalgamation of Pangea and the hothouse conditions produced by the low equator-to-pole temperature gradient (Kustatscher et al., 2018). Overall, the fossil record shows two distinct plant biogeographic provinces: one in the Southern Hemisphere of Gondwanan origin, and another one in the Northern Hemisphere of Laurasian descent (Kustatscher et al., 2018). The two provinces were primarily separated by the Tethys Ocean and an arid palaeotropical belt. The dinosaur bearing formations of the Late Triassic do not capture the faunal composition of the
Northern part of Gondwana (i.e. northern part of South America, Mexico, north and central parts of Africa, and Australia) nor most of the Northern and Southern parts of Laurasia (i.e., China and North America).

The faunivore morphotype of the Carnian corresponds to biped animals of small size, with an anatomy similar to other saurischians, such as *Guaiabasaurus* and *Herrerasaurus*. The sauropodomorphs of Carnian age from Brazil (*Bagualosaurus* and *Pampadromaeus*) and Argentina (*Panphagia, Eoraptor* and *Chromogisaurus*) display a similar faunivore morphotype. On the other hand, *Nyasasaurus*, putatively Carnian in this work (see discussion above), is recovered here as a more derived sauropodomorph, closely related to the Norian sauropodomorph *Efraasia*. Consequently, the first event of diversification of sauropodomorphs occurred during the Anisian (Middle Triassic), where the nodes 138 (Sauropodomorpha), 152 (Bagualosauria), node 147 originate, and a second diversification event during the Ladinian, the origins of node 151 (Chromogisauridae), node 146 (Plateosauria), and by the end of the Ladinian, node 145 (which includes *Nyasasaurus* and *Efraasia*). During the Middle Triassic, there is also an increase of diversity of ferns (Pteridophyta), cycads (Cycadophyta), and conifers (Coniferophyta) (Nowak et al., 2019), and a decline on the synapsid diversity, which includes the fall of the large dicynodonts that for most of the Permian and Early Triassic were the dominant herbivore fauna (Tanner et al., 2004; Irmis and Whiteside, 2012; Whiteside et al., 2015). This plant diversification and decline of herbivore tetrapods are suitable conditions for dinosaurs to occupy new niches and develop specialised herbivore diet.
Figure 6.1 Diversity of the sauropodomorph fauna in the Late Triassic showing the associated flora for each age and locality. The locality, written inside the boxes, indicates the stratigraphic name from which the associated flora was obtained from using the Paleobiology Database (paleobiol.org). The vegetation in Gondwana was more homogeneous than the flora in Laurasia. The number correlates to the nodes described in Chapter 5: 1) Theropoda, 2) ‘faunivore’ Sauropodomorpha, 3) stem sauropodomorphs, 4) ‘Efraasian’ type, 5) plateosaurid type, 6) mussaurid type, 7) anchisaurid type, 8) yunnanosaurid type, 9) Massospondylus, 10) riojasaurid type, 11) lessemsaurid type, 12) plateosauravid type, 13) non-sauropodan melanorosaurids, 14) sauropods.
Figure 6.2. Diversity of the sauropodomorph fauna in the Early Jurassic showing the associated flora for each age and locality. The locality, written inside the boxes, indicates the stratigraphic name from which the associated flora was obtained from using the Paleobiology Database (paleobiodb.org). The vegetation in Gondwana was more homogeneous than the flora in Laurasia. The number correlates to the nodes described in Chapter 5: 1) Theropoda, 2) ‘faunivore’ Sauropodomorpha, 3) stem sauropodomorphs, 4) ‘Efraasia’ type, 5) plateosaurid type, 6) mussaurid type, 7) anchisaurid type, 8) yunnanosaurid type, 9) Massospondylus, 10) riojasaurid type, 11) lessepsosaurid type, 12) plateosauravids, 13) non-sauropodan melanorosaurids, 14) sauropods. By the Carnian, all the morphotypes of
sauropodomorph have developed in Pangaea: the omnivore type (node 151, Bagualosauria), the small gracile herbivores (such as Panphagia), the Efraasian-type, the plateosaurian type, and the different massopodan types (nodes 154, 159, 168, 167 and 166). Thus, the dinosaur diversification event (DDE) is pushed to the Middle Triassic along with the herbivore revolution in Sauropodomorpha as they displaced the other herbivore tetrapods. The second pulse of diversification is observed during the Carnian, probably coinciding with the Carnian Pluvial Event (CPE). A more thorough stratigraphy is needed at this point to discern whether the phylogenies are capturing true diversification or anagenesis. Anagenesis is a potential explanation here since the CPE consisted of at least three pulses of dry-humid-dry conditions as a consequence of the Wrangellian basaltic deposits extruded for 5 million years about 230 Mya (Harris et al., 2017). With the vegetation changing from xerophytic to hygrophytic, sauropodomorphs may have adapted accordingly.

The Carnian Gondwanan floras are divided into two main subprovinces: the Ipswich Microflora represents the southern polar vegetation from eastern Australia, New Zealand and Antarctica, and the Onslow Microflora, describing the warm temperate floras that spanned across northern Australia and along the western Tethys coasts, to westernmost Gondwana (Kustatscher et al., 2018). The Molteno Formation of the Karoo Basin of South Africa bears a high diversity of seed ferns (Pteridospermatophyta), with seven species of *Dicrodium* in the locality, constituting 90% of the leaf-dominated assemblages. In co-dominance with seed ferns, the Molteno Formation also displays an abundance of Peltaspermales, Ginkgoales, pinalean conifers, and Matatiellales. The understorey vegetation comprises mostly ferns, dominantly members of Osmundaceae and Dipteridaceae), with a high diversity ranging from rare to moderately common (16 genera and 37 species) (Kustatscher et al., 2018). Elsewhere in the Onslow Microflora subprovince, plant assemblages display strong similarities to the Molteno Formation flora in terms of taxonomic and relative group abundance (Kustatscher et al., 2018).

Sauropodomorphs become the dominant herbivores throughout the continent during the Norian. Although there is no record of Norian sauropodomorphs from the North-western part of Pangaea, i.e. North America, this may be a preservation bias, since the Jurassic sauropodomorphs from North America are related to groups that originated during the Carnian, e.g. *Anchisaurus* and *Seitaad* are closely associated with *Blikanasaurus*, of Norian age, and *Sarahsaurus* is closely related to *Mussaurus*, also of Norian age.

In Europe, the plateosaurid type constitutes the dominant herbivore fauna, and many of the fossil remains were excluded from this analysis pending a taxonomic revision of the sauropodomorph fauna from Europe. Plateosaurus shows a trend towards giantism: node 145 includes both gracile morphotypes, like *Nyasasaurus*, and medium-sized animals like *Efraasia*, whereas Plateosauridae contains medium-sized animals in Gondwana and large-sized animals in Europe. The very distinctive dental morphology in *Efraasia* suggests a
different diet compared to Plateosauridae. *Efraasia* was found in sandstones, indicating that it lived in an arid environment with occasional floods (Barth et al., 2014), a similar climate to that where *Asylosaurus* was found (Galton, 2007). The Norian floras from Europe are dominated by conifers, with cycads, lycophytes, sphenophytes and seed ferns becoming rare. The Norian of Central Europe has been interpreted to be subject of cyclic changes from playa lakes to arid conditions, strongly influenced by the Pangaeane monsoon circulation system (Barth et al., 2014). Plateosaurian dentition shows more dependence on herbivory, but the heterodonty between the premaxillary and dentary teeth coincides with a retained level of faunivory. This faunivory could be advantageous during the long dry periods recorded in the German Norian deposits (Button et al., 2014). Moreover, the lack of evident specialisations in the skull can be explained by reliability on gut processing and generalist herbivory.

The Gondwanan sauropodomorph faunas from the Norian are restricted to Argentina, where two morphotypes appear: Lessemsauridae (*Lessemsaurus*), Riojasauridae (*Riojasaurus* and *Coloradisaurus*) and tentatively Sauropoda. The Norian floras from Gondwana, like the ones from Laurasia, are also dominated by gymnosperms (Gingkoales and Voltziales), and accessory ferns and sphenophytes. Unlike the plateosaurians, the skull of *Riojasaurus* displays characters consistent with more specialised herbivory, including evidence of a specialised rhamphotheca, and the robustness is related to relying more on gut processing. On the other hand, the skull of *Coloradisaurus* has a similar morphology to the plateosaurian head, suggesting less specialised herbivory than *Riojasaurus*. The herbivory in *Lessemsaurus* cannot be discussed due to the lack of cranial material from any of the members of Lessemsauridae (*Antetonitrus*, *Ledumahadi*, *Eucnemesaurus* *entaxonis* and *Ohmdenosaurus*). Whereas in the Norian of Europe is dominated by a conservative bauplan (the high phenotypic plasticity attributed to *Plateosaurus* could be due to anagenesis due to the cyclic dry-humid changes, and more detailed stratigraphy of all the plateosaurian bone-beds is needed to address this), the high diversity of morphotypes in Gondwana during the Norian suggest events of niche-partitioning of more derived sauropodomorphs.

Plateosaurus and other plateosaurids still dominate the Rhaetian communities of Central Europe. However, the Fissure Fills from England and Wales provide insight into a more diverse community: *Thecodontosaurus* and *Pantydraco*, very primitive sauropodomorphs with a gracile and omnivore morphotypes, *Asylosaurus*, a plateosaurian, and *Camelotia*, a
melanorosaurid. The Rhaetian vegetation is more diverse than the Norian, with a rich and varied representation of lycophytes, sphenophytes, ferns, seed ferns, cycads, and gingkophytes along with conifers (Kustatscher et al., 2018). This increase in diversity of the flora may have supported a more diverse sauropodomorph community allowing different feeding habits to coexist.

Unfortunately, only a skull referred to *Melanorosaurus* exists to represent this group, and not much about trends on herbivory can be said at this point. The head of *Melanorosaurus* retains a constitution similar to the plateosaurian skull and suggest an increase in the masticatory apparatus. In the case of melanorosaurids, it seems that the adaptations towards quadrupedal stance happened before the onset of the cranial transformation to a more specialised form of browsing. Furthermore, the Rhaetian floras from Gondwana are poorly studied. Based on deposits from Australia and New Zealand, there is a decline on ginkgophytes as they become replaced by conifers as the dominant arborescent components, and a change of the understorey components from ferns to lycophytes (Kustatscher et al., 2018).

Considerable sedimentary evidence suggests that during the Late Triassic there was a gradual aridification of Pangaea, from the humid but seasonal climate from the Late Carnian to the strongly seasonal sub-humid climate of the Late Carnian to middle Norian, to an arid environment with abundant playas and aeolian settings in the Rhaetian (Tanner et al., 2004; Harris et al., 2017). Towards the end of the Rhaetian, the Central Atlantic Magmatic Province (CAMP) originated leading to the subsequent breaking up of Pangaea, around 201 Mya. This volcanic activity may have been a succession of four pulses and led to a climate change in the continent. Several lines of evidence support disruption of the carbon cycle during the Triassic Jurassic Boundary (TJB) (Tanner et al., 2004; Lucas and Tanner, 2007; Harris et al., 2017).

Although the fossil record is ambiguous regarding a mass extinction in the terrestrial communities of the Rhaetian, the fossil record of marine communities shows evidence of mass extinction (Harris et al., 2017). The CAMP led an increase in the atmospheric CO₂, producing both a greenhouse effect, ocean acidification, and a decrease of the level of CaCO₃ saturation in the ocean. While the last two phenomena explain a marine extinction, the greenhouse effect on land is supported in the fossil record by the biotic turnover product of a change in the regional climates. The megaflora experienced a turnover as plants with
large entire leaves, such as the Ginkgoales, were replaced by species with dissected leaves, such as ferns, or narrow leaves, such as Equisetaceae, because of the increased temperatures of a CAMP-induced super greenhouse between the Rhaetian and the Early Hettangian (Mccown et al., 1999). This increase in temperature is followed by a transition towards colder and drier environments in the Late Hettangian.

The plateosaurians, a mostly Laurasian group, suffered the most substantial loss of diversity through the TJB, with only two Jurassic taxa (Arcusaurus and Pradhania). The Laurasian floras show a high degree of provincialism, whereas the Gondwanan floras were rather homogenous, and the loss of diversity as the product of the climate change linked to the CAMP likely affected more the Laurasian floras than the Gondwanan communities. The floral fossil record shows a turnover as seed ferns families disappeared (Glossopteridaceae, Peltaspermaceae and Corytospermaceae) and were replaced by ferns. In Greenland, for instance, the abundant seed fern Lepidopteris is replaced by the fern Thaumatopteris (Tanner et al., 2004). This replacement coinciding with the decline of plateosaurians in Europe could suggest that the plateosaurian skull was somewhat specialised to a diet relying on the abundant plant families of the Late Triassic. A similar situation explains the decline of Riojasauridae in Gondwana, which also shows more specialised herbivory compared to the other saurpodomorphs.

The floral turnover of the TJB may be reflected in a turnover in the sauropodomorph fauna. Whereas plateosaurian dinosaurs declined, Mussauridae diversified during the Lower Jurassic, with most of the taxa in this family found in the Hettangian-Sinemurian beds. Node 153 is of Jurassic age and Sauropods expanded after the Toarcian. All but one member of Mussauridae are from the Early Jurassic and of the synapomorphies that support this group only two out of 11 are in the skull and refer to the distinctive morphology of the narial fossa. On the other hand, anchisaurians (Node 154) are supported for eight cranial synapomorphies, out of the 12. The clade containing Xingxiulong, Aardonyx, Seitaad, Glacialisaurus and Adeopapposaurus is only supported by one cranial character (out of 7 synapomorphies), whereas Anchisauridae is supported by only two cranial synapomorphies, out of 10. Finally, Yunnanosauridae is only supported by one cranial synapomorphy out of 10. Consequently, during the Late Triassic, the anchisaurian cranial anatomy was more conservative, contrary to the more disparate morphologies in the mussaurid skulls.
The mussaurid-type sauropodomorphs have a good sample of cranial material. *Yimenosaurus* is described as having a long and gracile skull morphology with a somewhat heterodont dentition and teeth with developed denticles. In this analysis, it is placed as the sister taxon to *Lufengosaurus*, from the same locality and time. Unlike *Yimenosaurus*, *Lufengosaurus* displays several features that suggest a particular type of herbivory: maxillary, jugal and parietal bosses, and maxillary and dentary ridges, implying a more complex masticatory apparatus than the observed in plateosaurians. Nevertheless, the postcranial morphology of *Lufengosaurus* conserves features of the plateosaurian bauplan, which is reflected as placed in a very primitive position within Mussauridae. Just as in *Yimenosaurus*, and unlike *Lufengosaurus*, *Sarahsaurus* displays moderate heterodoncy and a cranial morphology similar to the massospondylid-type. The cranial morphology of *Ngewu* resembles the morphology of *Lufengosaurus* and *Sarahsaurus* in the nasal, lacrimal, postorbital, squamosal and quadrate. The mandibular morphology of *Ngewu* also resembles that of *Massospondylus kaalae*, and the dental labial fluting is very similar to that in *Pulanesaurus* and *M. kaalae* too. *Yizhousaurus* possesses a parietal boss and a postorbital morphology similar to that of *Leyesaurus*.

Non-sauropodan sauropodomorphs became extinct by the end of the Toarcian. Only five pre-Toarcian Jurassic sauropods have been found, i.e. *Tazoudasaurus*, *Barapasaurus*, *Kotasaurus*, *Vulcanodon* and likely *Isanosaurus*. The lack of sauropodan fossils of this age may explain the lack of resolution at this part of the topology. The Toarcian was marked by a perturbation of the carbon cycle that led to a shift towards an extreme greenhouse climate, an episode known as the Toarcian Oceanic Anoxic Event (T-OAE). The Pliensbachian-Toarcian in Gondwana is marked by a gradual change towards more arid conditions, favouring the less specialised skull morphology of the anchisaurian over the mussaurid skull types.

### 6.1.2 Quadrupedality and gigantism

Sauropodomorphs rapidly evolved from gracile bipedal small-sized animals in the Carnian to medium to large animals with either bipedal or quadrupedal locomotion. Regarding size, Plateosauridae (Node 146) clearly shows a trend towards gigantism, with *Plateosaurus* and *Sellosaurus* having estimated weights between 600 and 1000Kg, and *Ruehleia*, *Unaysaurus* and *Macrocollum*, with weights ranging between the 100 and 750Kg. The other plateosaurian clade, Node 145, has medium-sized sauropodomorphs ranging from 10 to
600Kg. As summarised in Appendix 1, *Plateosaurus* and *Efraasia* have been considered as bipeds or facultative quadrupeds.

In Gondwana, the Rhaetian is dominated by robust and large-sized animals. As discussed above, except for *Blikansaurus*, the Rhaetian communities from South Africa have very conserved morphologies. *Blikansaurus* is closely related to *Anchisaurus*, suggesting a different type of quadrupedality to the one observed in *Melanorosaurus, Plateosaurus, Eucnemesaurus fortis, Eucnemesaurus entaxonis* and *Meroktenos*. *Plateosauravus* is closely related to other melanosaurids in this topology, and *Jaklapallisaurus*, from the Norian-early Rhaetian beds of India. Interestingly, these two sauropodomorphs have been found consistently as very primitive sauropodomorphs.

The consensus for the members of Mussauridae is that they were bipeds during their adult life. Nonetheless, a recent study on *Mussaurus* has shown that, during their first year of life, the juveniles of *Mussaurus* were quadrupeds, and as they grew the centre of mass moved towards the pelvic girdle, producing a shift to a bipedal stance. Embryos recovered from the Lufeng Formation referred to *Lufengosaurus* show similar proportions to the ones in *Mussaurus*, and a quadrupedal stand for the neonates is also supported by the histological evidence (Reisz et al., 2013). Furthermore, this transition from early ontogenetic quadrupedality to bipedality has been suggested for *Mussaurus* but not for *Massospondylus carinatus* using quantitative methods to compare embryos referred to these two taxa (Chapelle et al., 2019). Interestingly, the Late Triassic *Sefapanosaurus* and the Early Jurassic *Pulanesaurus* and *Leonerasaurus* have always been recovered at the base of the transition to quadrupedality towards Sauropoda. *Pulanesaurus* displays an axial and forelimb morphology concordant with the loss of the grasping ability of the hand and a more parasagittal and erect posture of the hands for to a more specialised mid-browsing diet acquired independently from sauropods. On the same line, the sauropod-type sacrum of *Leonerasaurus* may be a convergence with a more quadrupedal stance, as shown by *Pulanesaurus*. Thus, the ontogenetic quadrupedality evidenced in *Mussaurus* indicate that quadrupedality in this clade likely originated via paedomorphosis. The origins of this transition are observed in the manual and pedal morphology in *Sefapanosaurus* (Otero et al., 2015), and the retention of the ‘prosauropod’-type robust antebrachium to provide motility to the forelimb of *Yizhousaurus*. 
Furthermore, the cranial morphology of Yizhousaurus, very similar to that of Anchisaurus and Melanorosaurus, indicates a convergent acquisition of sauropod diets and the concomitant quadrupedal stance for efficient browsing, which are not seen in Mussaurus nor Lufengosaurus. The cranial morphology of Ngewwu is similar to that of Lufengosaurus, but in the same analyses, Leyesaurus is closely related to Massospondylus. In this topology, a restricted Massospondylidae is not recovered, and the massospondylid-type skull is also found in Node 153 (where Adeopapposaurus is), and at the base of Node 167 (which includes Massospondylus).

The morphology of the limbs of the sauropodomorphs in Node 185 suggests facultative bipedality, with very robust limbs. Gyposaurus sinensis was initially referred to Anchisaurus (Galton and Cluver, 1976, Dong, 1992), and a reassessment of this specimen from photographs provided by Toru Sekiya show an anchisaurid-type morphology. Blikanasaurus is only known from a partial hindlimb, but the proportions of the animal suggest a robust complexion. The other four sauropodomorphs of the Lower Elliot Formation, i.e. Plateosauravus, Eucnemesaurus fortis, Eucnemesaurus entaxonis and Melanorosaurus, are found as more derived and closely related to sauropods than to Blikanasaurus, all of them with a more similar complexion and morphology.

The set of synapomorphies in Node 154 suggests that both herbivory and locomotion evolve in conjunction with each other. The reorganisation of the cervicals and the occipital region may be related to an increase in the mobility of the neck, facilitating browsing. The face is reorganised from the primitive pleistosaurid and mussaurid arrangement, with bones actively associated with rumination (lacrimal, maxilla and jugal) also changing their morphology to more specialised herbivory. The changes in pelvic girdle are consistent with a reduced attachment for muscles to the hindlimb as the forelimb develops as a weight-bearing unit.

Following the sequence of changes described above, the sauropodan bauplan can be understood in two phases: first the modifications of the gait (sacral configuration, posture of forelimbs and hindlimbs, configuration of the pelvic girdle), in Melanorosauridae, and then the rearrangement of the forelimb into a weight-bearing unit and the reduction of the masticatory apparatus happened as a continued specialisation towards mid- and high-browsing. Jinghsanosaurus and Plateosauravus, closest non-sauropodan relatives to sauropods, seemed to have a facultative quadrupedality, see Appendix 1, whereas
Lessemosauridae, *Lessemaurus* and *Antetonirus*, show evidence of habitual quadrupedality, with the distribution of the weight across the metatarsus biasing towards the medial side. These two non-sauropodan clades suggest that the trend towards obligate quadrupedality was an exaptation and not a consequence of larger sizes. The morphological features that originated the posture change seem to have started with *Riojasaurus*. The synapomorphies defining the subsequent clades from Lessemosauridae upwards in the tree are mostly located in the postcranial anatomy and are related to changes in locomotion, suggesting this is the point where the obligate quadrupedalism may have originated.

Finally, this topology suggests that quadrupedality originated independently three times: first in Mussauridae, likely via paedomorphosis, and twice in Anchisauridae. The first quadrupedal gait is observed in *Anchisaurus* and *Blikanasaurus*, then the phylogenetic position of *Yunnanosaurus*, which has been reported to have the shortest forelimb to hindlimb ratio in sauropodomorphs, suggests either a reversal to obligate bipedality or that Anchisauridae evolved quadrupedality on its own; the last transition occurs with *Riojasaurus*, where reversal to bipedality happened twice, obligate in *Massospondylus* and facultative in *Jingshanosaurus*. *Ingentia* is unequivocal of Late Triassic age, whereas the stratigraphic position of *Isanosaurus* is dubious. Thus, the origin of Sauropoda occurred in the Late Triassic, with the rest of the sauropodomorph groups discussed above. The lack of resolution at this level of the tree reflects the lack of fossils showing this transition. The sauropodan specialisations to an obligate quadrupedality, longer necks, and a herbivore diet occurred as exaptations product of a diversification event of Sauropodomorpha before the separation of Pangaea. The disparification displayed by Sauropodomorpha in the Late Triassic is best explained because of niche partitioning. After the Triassic-Jurassic extinction, the sauropodan bauplan outcompeted the other sauropodomorphs, which became extinct by the Middle Jurassic.

### 6.2 Synthesis

The comparative cladistic analyses, described in Chapter 2, showed that inconsistencies in topology between phylogenetic analyses do not come from the taxa selected or from the character list chosen to perform the phylogenetic analysis. All the data sets have a similar taxonomic scope, a same geographic representation, and the anatomic regions are similarly represented in the character lists. The only differences come from the taxonomic definitions they used (which specimens belong to which OTUs) and the character delineation.
strategies. This problem was tackled using the supermatrix approach: including all the taxa referred to ‘Prosauropoda’ or ‘Basal Sauropodomorpha’ and then performing a detailed character analysis to compile all the information available. This required first-hand assessments of as many specimens as possible. Specimens from Argentina, South Africa, and some material from China, were not examined first-hand, however, due to time and funding constraints, and thus results of this analysis are limited to the information published on these specimens. However, this work represents a reasonable basis on which future studies that aim to update anatomical information and describe new species can build. Furthermore, the comparative cladistics performed here shows the importance of constant revising of the matrices and its components (characters and taxa) to understand the underlying causes of the contradictory information. In the case of Sauropodomorpha, character coding, character delineation and scoring consistency are the most likely explanation for the different scenarios.

The structure of the meta-analyses performed here was based on obtaining as much information as possible from publications and observations of the specimens, detailed in Chapter 3. A standardisation of taxonomic definitions was required, restricting several OTUs to holotypes or neotypes and separating taxonomic definitions based on previous phylogenetic analyses (for example, Plateosaurus engelhardti is limited to specimens SMNS 13200, GPIT 1 and GPIT 2, and Massospondylus carinatus was restricted to the neotype). One of the most challenging problems of integrating all the previously used characters into a coherent list was to assess whether they were referring to the same structures or if the traits were correlated. As noted in Chapter 3, phylogenetic analyses have two phases, the identification of primary homology based on comparative anatomy, and the identification of secondary homology, when it is established these similarities have an ancestor-descendant relationship. Discovering characters is difficult when much of the information can come from distorted or incomplete specimens, and there has been a tendency to include poorly defined continuous characters that capture changes in size or shape that is easier to represent as measurements. As discussed in Chapter 3, continuous characters have been treated as categorised characters instead, where a limit is established to separate character states. Analysing continuous characters as such is possible in TNT, but it is not possible to include them in other phylogenetic software. Regardless of the method chosen to categorise characters, here the unweighted gap-coding method was employed, it was found that information theory can be used to compare the
‘informativeness’ of the character states and provide a more objective framework to categorise continuous characters. Moreover, to avoid the production of a large number of continuous characters, mathematical topology is suggested here as a potential proxy to discover characters without having to rely on the metric space.

After comparing the character lists produced in the literature, a limited set of changes are always used as transformation series (neomorphic characters, shape, orientation, location, connectivity, meristic and allometric characters). The final dataset comprised 870 characters, plus 75 characters in the waiting list needing more information, and 113 taxa, making it the largest and most taxonomically comprehensive ever carried out to examine basal sauropodomorph relationships.

In Chapter 4, a thorough anatomical review was performed and represented the first attempt to catalogue and illustrate all the characters employed in this phylogenetic analysis. Further work is needed to understand patterns of intraspecific variation, and this should be a focus for future work. Furthermore, because this was mostly a meta-analysis aiming to obtain as much information as possible, there is still work needed to produce a final character list. Using this new framework and comparative anatomy from other dinosaur and archosaur groups, consistent patterns of serial variation can be identified in the teeth and vertebral column, where a lot of characters were atomised or treated as independent herein. Chapter 4 deals with the first stage of establishing primary homology, and identifying secondary homology, patterns of variation, is part of the further work needed to produce better resolved phylogenetic analyses. This second stage should also be complemented with incorporating characters that have been identified as affected by ontogeny, and for this several phylogenetic methods have been proposed, e.g. the semaphoront approach (Rieppel, 2004; Sharma et al., 2017).

To conclude, the supermatrix approach did provide an insight into the phylogenetic relationships between the Late Triassic and Early Jurassic sauropodomorphs. Whereas at the base of the tree some unique clades are obtained under extended implied weighting, such as Phytodinosauria and Ornithoscelida, the scope of this work did not aim to assess these relationships and the taxonomic range needs to be taken into account as the character selection plays a significant role. Dinosauria started with a very similar bauplan: faunivore, bipedal and gracile animals. Dinosaurs originated during the Middle Triassic and rapidly spread through Pangaea by the early Late Triassic, from which time we have a more
complete fossil record. The poor fossil record and the scarce dinosaurian material from this age are obscuring the relationships between the three main dinosaurian lineages: Ornithischia, Theropoda and Sauropodomorpha.

Regarding Sauropodomorpha, the clades outlined in this work show a reasonable degree of stratigraphic consistency and geographic coherence, particularly for the Hettangian from South Africa, with most of the sauropodomorph fauna classified within Mussauridae. This new scenario suggests that two types of quadrupedality evolved in Sauropodomorpha: one via paedomorphosis, in Mussauridae, and one via gradual accumulation of changes in Sauropoda. Niche partitioning is proposed here as the main driver of the evolution of the first herbivore dinosaurs, whose diversification occurred during two biotic turnovers as the aftermath of two climate changes that occurred during the Late Triassic and the Late Triassic-Early Jurassic respectively. Finally, the approach taken here to revise all the literature and produce a near-comprehensive dataset allows extracting as much information from every taxon and provide a scenario that explains several lacunae in our knowledge, such as the changes from a quadrupedal to a bipedal stance in *Mussaurus*, the different degrees of manual locomotion seen in *Anchisaurus, Aardonyx* and *Riojasaurus*, the obligate bipedality of *Massospondylus*, the phenotypic plasticity of *Plateosaurus* and the apparent mixed fauna of primitive and derived sauropodomorphs seen in South Africa, with a more homogenous composition in this topology.

This supermatrix represents a good starting point to close the gaps in our knowledge regarding the evolution of Sauropodomorpha, as this can be used to produce detailed biogeographic analyses to understand the dispersion, vicariance and speciation rate of the group, and provides a new framework to assess how much convergent evolution played a role in the first herbivore revolution within Dinosauria. For future iterations of this dataset, more detailed stratigraphic information is needed to differentiate speciation events from anagenesis; the fossil faunas of sauropodomorphs are found in formations that capture changes through millions of years, and they could reflect events of species changing along with their environment and food sources. Indeed, more information regarding fossil floras is also needed to start correlating feeding habits with craniomandibular biomechanics and morphology.
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CHAPTER 3

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**Figure 3.9** Behaviour of the entropy as the probability of two independent events increases. The peak of uncertainty is when the two events are equally probable.

**Figure 3.10** Logarithmic distribution of the ratios in Table 3.6 showing five distinctive gaps (arrows) in the distribution.

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**Figure 3.12** Venn diagram showing the compatibility of the dataset of Galton and Upchurch (2004) with the sets A and B defined in Figure 3.7.

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**Table 3.1** Summary of the categories of characters in four character lists, the numbers are expressed as percentages in each partition. The Clearness Index (CLI) is calculated as the total of characters divided by the total of categories contained in the character statements. In bolds, the highest values of composition and CLI.

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**Table 3.7** Calculation of the entropies of the three character coding strategies outlined above.

**Table 3.8** Taxonomic similarity of the three main character compilations analysed here.

**Table 3.9** Taxonomic similarity between Galton and Upchurch (2004) and previous datasets.

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**Chapter 4**

**Figure 4.1** Distribution of the proportion of missing characters analysed in this work in the different regions of the body. The highest proportion of missing characters is located along the axial skeleton, whereas the most complete characters are in the appendicular skeleton. This is due to the combination of the preservation bias and axial characters neglected most of the times in the literature.
FIGURE 4.2. Colour key for the bones the series of the cranial bones. The skull of Melanorosaurus is here colour-coded to identify the different regions in this work. The neurocranium is colour-coded differently (see 1.1.4 Neurocranium).

FIGURE 4.3 Metrics used to determine snout shape as defined by Whitlock (2011) using Diplodocus as a reference. The upper arcade index (UAI) measures the ratio between the arcade width to arcade depth; the premaxilla-maxilla index (PMI) is determined by taking the ratio of the area covered by the snout within a square triangle which hypotenuse has a slope of 26 relative to the middle axis of the snout; the premaxillary divergence angle (PMDA) measures the angle formed by a line tangent to the premaxilla-premaxilla articulation, and the line connecting the anteromedial and anterolateral corners of the premaxilla. When the PMI is equal to or larger than 80% the morphology of the snout is considered to be square, whereas any value below that corresponds to round (Whitlock, 2011). Here, the covariation between these characters was tested using Euparkeria, Silesaurus sauropodomorphs, theropods (Herrerasaurus, Ceratosaurus, Allosaurus), and ornithischians (Lesothosaurus, Agilisaurus). The results indicate that the three measurements show a degree of correlation, but mostly UAI against the other two. The values of UAI are then discarded from this list (Figure 4.4).

FIGURE 4.4. Biplot of the principal component analysis of the three metrics used to determine snout shape across dinosaurs. The data concerning eusauropods was taken from Whitlock (2011). Two clusters can be identified, with eusauropods clustering on the right, and the other dinosaurs cluster on the left side of the plot. Although there is strong correlation between the three metrics, PMDA and PMI explain most of the variation along PC1 and PC2 respectively. Solid dots represent non-eusauropod sauropodomorphs, crosses represent eusauropods. Open circles represent ornithischians, plus symbols represent silesaurids and open squares represent theropods.

FIGURE 4.5. The same value is retrieved by gap coding, where the cut-off is identifying the lack of samples in the interval (0.7, 0.85). Log (Cr l / Fm l) stands for the logarithm of the cranial length relative to the femoral length. Under these two methods, character state 0 (i.e., 0: ratio less than 0.7) is assigned only to three sauropodomorphs Adeopapposaurus, Massospondylus and Mussaurus, and the theropod Eodromaeus. The original formulation specified a limit of 0.6: longer than 0.6 (0), shorter than 0.6 (1), which is closer to the average obtained from the sample analysed here.

FIGURE 4.6 Landmark-based definitions of the measurements employed in CR3, CR4 and CR5. Top, Massospondylus carinatus based on the reconstruction in Chapelle and Choiniere (2018), and Plateosaurus engelhardti based on AMNH 1680 as illustrated in Prieto-Márquez and Norell (2011). Both in right lateral view.

FIGURE 4.7 In the original coding the limit is set 0.6, but gap coding shows that sauropodomorphs show more variation than these two states capture. This character has been scored as 1 only for Neotheropoda and Ornithischia in the matrix MY2007. This continuous character can be assessed in several basal sauropodomorphs for which there is enough cranial material. Log (R h / Or Cr h) stands for the logarithm of the rostral height relative to the height of the skull at the middle of the orbit. Gap coding also reduces the entropy way much more than any other alternative coding. The original coding was set.
to 0.8: more than 0.6 (0), equal to or less than 0.6 (1). From 37 OTUs sampled for the analysis of this character, the following frequencies are reported (table). The gap coding identifies the following categories: < 0.06 (0), [0.06, 0.19] (1), [0.19, 1.23] (2), [1.24, 1.63] (3), ≥1.63 (4). Gap-coding reduces the entropy from 88% to 40.29%. 

Figure 4.8. A reassessment of this character produced three distinctive character states via gap coding.

Character state 0 is a proportion ≤ 0.24 is assigned only to Shunosaurus, most of the assessed taxa are given to character state 1, [0.24, 0.85] and two basal sauropodopomorphs are Sarahsaurus and Adeopapposaurus are scored as state 2, [0.85, ∞]. The original formulation set the limit at a proportion of 0.5, which is not far from the average obtained in this analysis, i. e. 0.65, and that is also the value of the proportion in the specimen SMNS 13200 referred to Plateosaurus engelhardti, which depending on the measurement, could be scored as either 0 or 1. The entropy of gap coding for this character is greatly improved when compared with the original formulation. 

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Chapter 5

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CHAPTER 6

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