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Introduction to Diplodocoidea

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ABSTRACT

Diplodocoidea is one of the most iconic clades of the giant sauropod dinosaurs, known for their elongated necks and tails, and distinctive skull morphology. This group, existing from the Middle Jurassic to the early Late Cretaceous, encompasses three main families: Rebbachisauridae, Dicraeosauridae, and Diplodocidae. These sauropods were globally distributed, demonstrating significant diversity in body plans, feeding strategies, and ecological niches. Diplodocoid paleontology has been marked by extensive studies focusing on skeletal morphology, biomechanics, histology, and evolutionary relationships. Significant research has also explored their ontogeny and niche partitioning, suggesting that diplodocoids had specialized adaptations for low- to mid-level browsing. This contribution is the introduction to a special volume that aims to synthesize current research on Diplodocoidea, offering insights into their evolutionary success, with subsequent contributions addressing their phylogenetic relationships, ontogeny, and morphological variation.

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Diplodocoidea (Dinosauria, Sauropoda): Systematics, Phylogeny, Biogeography

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INSTITUTIONAL ABBREVIATIONS

AMNH FARB – American Museum of Natural History, New York, NY, USA. Fossil Amphibian, Reptile, and Bird Collections
ANS – Academy of Natural Sciences, Philadelphia, PA, USA
BYU – Brigham Young University Museum of Paleontology, Provo, UT, USA
CM – Carnegie Museum of Natural History, Pittsburgh, PA, USA
CMC – Cincinnati Museum Center, Cincinnati, OH, USA
CMNH – Cleveland Museum of Natural History, Cleveland, OH, USA
DINO – Dinosaur National Monument, Jensen, UT, USA
HMNS – Houston Museum of Natural Science, Houston, TX, USA
LM – Lingwu Museum, Lingwu, Ningxia, China
MACN – Museo Nacional de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina
MB.R. – Museum für Naturkunde, Berlin, Germany
MDS – Museo de Dinosaurios de Salas de los Infantes, Salas de los Infantes, Burgos, Spain
ML – Museu da Lourinhã, Lourinhã, Portugal
MLL – Museo Municipal de Las Lajas, Las Lajas, Neuquén, Argentina
MMCh-PV – Museo Municipal ‘Ernesto Bachmann,’ Villa El Chocón, Neuquén, Argentina
MHNM – Muséum d’Histoire Naturelle de Marrakech, Marrakech, Morocco
MNN – Museé National du Niger, Niamey, Niger
MOZ – Museo Provincial de Ciencias Naturales “Dr. Prof. Juan A.Olsacher,” Zapala, Argentina
MUC – Museo de Geologia y Paleontologia, Universidad Nacional del Comahue, Neuquén, Argentina
NMMNH – New Mexico Museum of Natural History and Science, Albuquerque, NM, USA
NHMUK – Natural History Museum, London, England, UK
NMZ – Natural History Museum, University of Zurich, Zurich, Switzerland
ONM – Musée de l’Office National des Mines, Minestère de L’Industrie et de la Technologie, La Charguia, Tunis, Tunisia
RWR – Palaeontology Division, Geological Survey of India, Western Region, Jaipur, Rajasthan, India
SMA – Sauriermuseum Aathal, Aathal, Switzerland
SMNS – Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Baden-Württemberg, Germany
TATE– Tate Geological Museum, Casper College, Casper, WY, USA
UFMA – Fossil collection of the Universidade Federal do Maranhão, São Luís, Brazil
UFRJ-DG – Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, Department of Geology
UFRJ-MN – Universidade Federal do Rio de Janeiro, Museu Nacional, Departamento de Geologia e Paleontologia, Paleovertebrate collection, Rio de janeiro, Brazil
UNPSJB-Pv – Universidad Nacional de la Patagonia “San Juan Bosco,” Comodoro Rivadavia, Chubut, Argentina, paleovertebrate collection
USNM – United States National Museum, Smithsonian Institution, Washington, D.C., USA

WN – ‘without number,’ an informal designation for specimens awaiting accession/Museum of Bale, Croatia

YPM – Yale Peabody Museum, New Haven, CT, USA

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INTRODUCTION

Sauropod dinosaurs were the largest terrestrial vertebrates to have ever lived (e.g., Jensen, 1985; Bonaparte and Coria, 1993; Novas et al., 2005; Calvo et al., 2007; Carballido et al., 2017; Carpenter, 2018; Pal and Ayyasami, 2022), and have been intensively studied ever since their initial discovery over 180 years ago (e.g., Owen, 1841b; Gomez et al., 2024a). Well known for their massive body mass and lengths (e.g., Calvo, 2023), graviportal stance (e.g., McPhee et al., 2018), and hyperelongate necks (e.g., Vidal et al., 2020b; Moore et al., 2023) and tails (e.g., Holland, 1915a; Conti et al., 2022), these megaherbivores were among the most successful dinosaur groups during the Mesozoic Era. The earliest members of Sauropoda evolved in the Late Triassic (e.g., Lallensack et al., 2017; Pol et al., 2021; Barrett et al., 2024) or Early Jurassic (e.g., Rauhut et al., 2020; Wang et al., 2024), and were globally one of the dominant clades of terrestrial herbivores until the end of the Maastrichtian in the latest Cretaceous (e.g., Gilmore, 1922; Wilson and Upchurch, 2003).

Within Sauropoda, neosauropods are divided into two clades (Figure 1): 1) Macronaria, containing the largest sauropods, the titanosaurs; and 2) Diplodocoidea (e.g., Salgado et al., 1997; Wilson and Sereno, 1998; Wilson, 2002; Whitlock, 2011a; Tschopp and Mateus, 2013; Tschopp et al., 2015; Bajpai et al., 2023). Diplodocoid sauropods are amongst the most iconic of all sauropods. With a more horizontal body plan compared to their macronarian counterparts (Taylor et al., 2009; Stevens, 2013), elongated tails (e.g., Conti et al., 2022), and specialized skulls with pencil-like teeth (e.g., Sereno and Wilson, 2005; Whitlock et al., 2010; Whitlock, 2011b; Tschopp and Mateus, 2013; Schwarz et al., 2015; Tschopp et al., 2015; Tschopp and Mateus, 2017; Peterson et al., 2022), this clade was globally successful from the Middle Jurassic until the early Late Cretaceous (Bajpai et al., 2023; Lerzo et al., 2024b).

Diplodocoidea (stem-based definition: neosauropod taxa closer to *Diplodocus* than to *Saltasaurus*; Marsh, 1884; Upchurch, 1995; Taylor and Naish, 2005) consists of three main lineages: Rebbachisauridae, Dicraeosauridae, and Diplodocidae, which are united in the clade Diplodocimorpha (node-based definition: *Rebbachisaurus tessonei* + Diplodocidae, and all descendants of their common ancestor; Calvo and Salgado, 1995; Taylor and Naish, 2005) (Figure 1). Rebbachisaurids are primarily, and possibly exclusively, known from the Cretaceous (Lerzo et al., 2024a, 2024b, but see Carpenter, 2018), whereas Dicraeosauridae and Diplodocidae are primarily known from the Jurassic, though Cretaceous forms are known (Gallina et al., 2014; Tschopp et al., 2015; McPhee et al., 2016; Xu et al., 2018; Gallina et al., 2019; Whitlock and Wilson Mantilla, 2020; Bajpai et al., 2023). Non-diplodocimorph diplodocoid genera usually only include *Haplocanthosaurus* (Hatcher, 1903), though *Amphicoelias* (Cope, 1877b), has also been recovered as such (e.g., Mannion et al., 2021).

Previous studies on diplodocoid sauropods have focused on osteological descriptions (e.g., Hatcher, 1901, 1903; Lull, 1919; Janensch, 1929b; Gilmore, 1936; McIntosh and Williams, 1981; Gillette, 1991; Harris and Dodson, 2004; Harris, 2006a, 2006b, 2007; Tschopp and Mateus, 2013; Wilson and Allain, 2015; Tschopp and Mateus, 2017; Xu et al., 2018; Whitlock and Wilson Mantilla, 2020; Mannion et al., 2021; Bajpai et al., 2023; Lerzo et al., 2024a, 2024b), diplodocoid evolution (e.g., Whitlock, 2011a; Mannion et al., 2012; Tschopp et al., 2015; Bates et al., 2016; Bajpai et al., 2023; Lerzo et al., 2024a, 2024b), histology (e.g., Hedrick et al., 2014; Lambertz et al., 2018; Woodruff et al., 2018; Waskow, 2019; Price and Whitlock, 2022; Woodruff et al., 2024), pneumaticity (e.g., Wedel, 2003; Schwarz et al., 2007; Taylor and Wedel, 2021), ontogeny (e.g., Klein and Sander, 2008; Whitlock et al., 2010; Woodruff and Fowler, 2012; Tschopp and Mateus, 2013; Hanik et al., 2017; Woodruff et al., 2018), diseases (e.g., Woodruff et al., 2022), biomechanics (e.g., Wilhite, 2003; Taylor et al., 2009; Stevens, 2013; Taylor and Wedel, 2013a; Klinkhamer et al., 2018; Conti et al., 2022; Jannel et al., 2022), feeding mechanisms (e.g., Whitlock et al., 2010; Whitlock, 2011b; Young et al., 2012; D’Emic et al., 2013; Price and Whitlock, 2022), niche partitioning (e.g., Fiorillo, 1998; Whitlock et al., 2010; D’Emic et al., 2013;

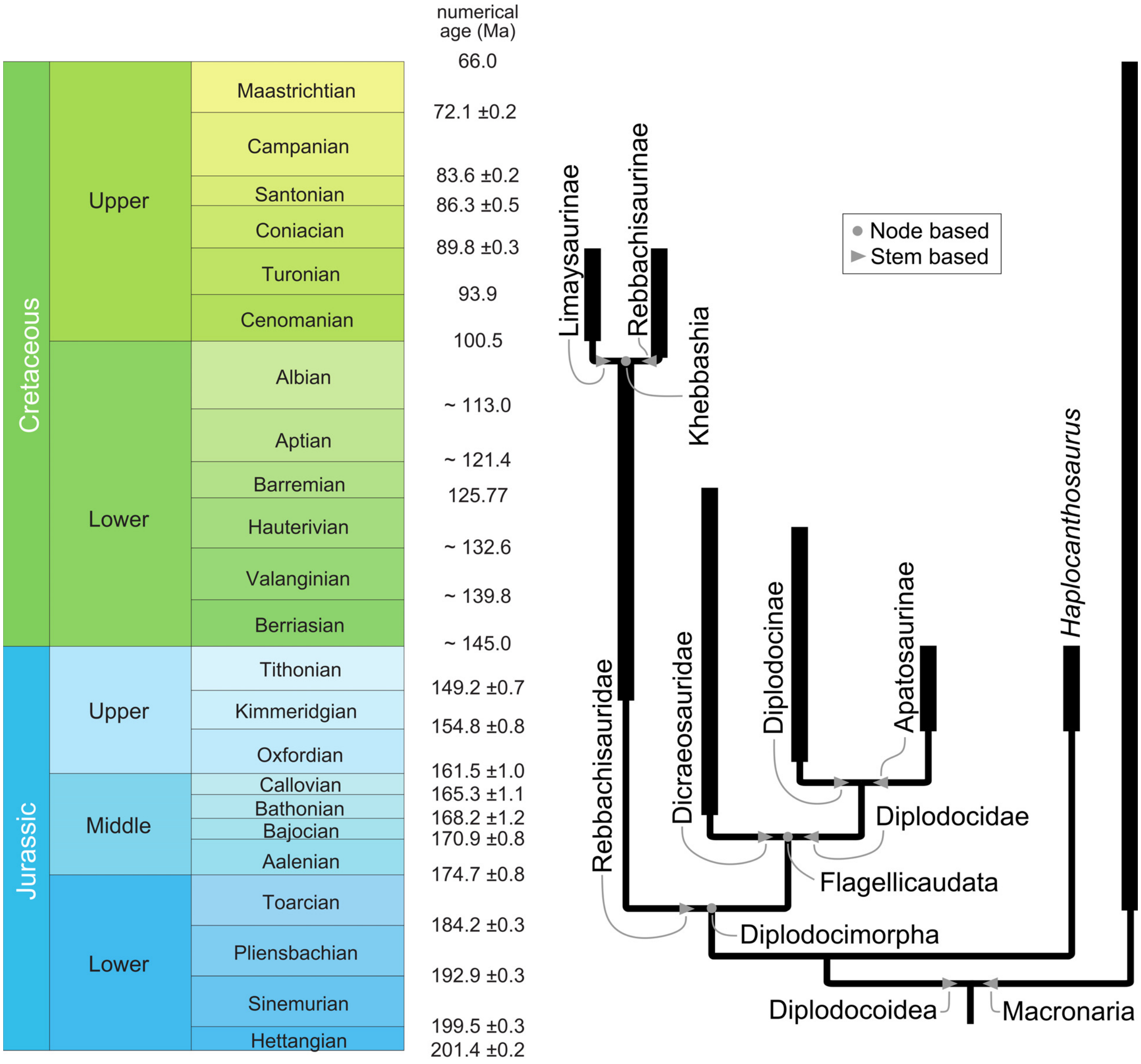


FIGURE 1. Generalized, time-correlated phylogenetic tree of neosauropod sauropods, showing the main clades within Diplodocoidea and their interrelationships. Thick bars indicate from which period a certain clade is represented by fossils. Times of occurrence taken from the Paleobiology Database. Phylogenetic tree follows Harris (2006) and Wilson and Allain (2015). Phylogenetic nomenclature follows Taylor and Naish (2005) and Wilson and Allain (2015). Timeline modified from the International Chronostratigraphic Chart v2023/09 (https://stratigraphy.org/chart).

McHugh, 2018; Woodruff et al., 2018), and soft tissue reconstructions (e.g., Schwarz et al., 2007; Gallagher et al., 2021; Cerda et al., 2022). As such, diplodocoid sauropods represent an invaluable resource of information for sauropod paleobiological research.

In this contribution, we aim to summarize the status of research on diplodocoid sauropods. This introduction to diplodocoid sauropods will lead to a collection of studies describing new specimens, redescribing old specimens, deciphering ontogeny, revealing inter- and intraspecific variation, and describing skull morphology. These studies will inform a novel, extensive study on the phylogenetic relationships of these animals based on several matrices used in previous studies (e.g., Whitlock, 2011a; Tschopp et al., 2015, Xu et al., 2018; Whitlock and Wilson Mantilla, 2020; Mannion et al., 2021; Lerzo et al., 2024a, 2024b).

HISTORY OF DIPLODOCOID PALEONTOLOGY

The first sauropods to be described were *Cardiodon* (Owen, 1841a) and *Cetiosaurus* (Owen, 1841b), but the former was based only on a tooth, and the latter, also represented by only very fragmentary material, was initially interpreted as a gigantic marine predator (see summary in Taylor, 2010). It was only with the description of *Cetiosaurus oxoniensis* (Phillips, 1871) that *Cetiosaurus* was recognized to be a terrestrial, or at most amphibious, animal. Seven years later, the name Sauropoda was coined by Marsh (1878), for a group containing *Atlantosaurus* (Marsh, 1877b), *Apatosaurus* (Marsh, 1877b), *Morosaurus* (Marsh, 1878), and *Diplodocus* (Marsh, 1878), as well as "others … from this country and Europe described by various authors" (p. 412), including *Cetiosaurus*. Of these examples, three – *Apatosaurus, Diplodocus,* and the dubious *Atlantosaurus* – were diplodocids (though that name, and its corresponding superfamily name Diplodocoidea, had not yet been coined), so this group has always loomed large in the perception of sauropods.

Confusingly, the first diplodocoid to be described was *"Titanosaurus" montanus* (Marsh, 1877a), which was named in ignorance of Lydekker's (1877) slightly earlier use of the same genus name for a very different Indian sauropod. Marsh swiftly replaced this homonym with the new name *Atlantosaurus montanus* (Marsh, 1877b), and in the same paper named the second diplodocoid, *Apatosaurus ajax*. These were followed later that same year by *Amphicoelias altus* (Cope, 1877b), then the next year by *Diplodocus longus* (Marsh, 1878), a year later by *Brontosaurus excelsus* (Marsh, 1879), then after 11 further years by *Barosaurus lentus* (Marsh, 1890). All these taxa were diplodocids; the first named non-diplodocid diplodocoid was *Dicraeosaurus hansemanni* (Janensch, 1914), followed by *Rebbachisaurus garasbae* (Lavocat, 1954).

Most of these early descriptions were hopelessly inadequate by modern standards, in many cases illustrated by a single drawing (e.g., *"Amphicoelias" fragillimus;* Cope, 1878) or none (e.g., *Amphicoelias altus),* providing only the most cursory descriptive text, and giving no sense of the overall body-plan of these animals. This changed with Marsh's (1883, plate I) skeletal reconstruction of *Brontosaurus* (Figure 2A). Marsh's reconstruction showed a form readily recognizable today, but was erroneous in several respects: the back is too arched so that the anterior part of the trunk descends at a sharp angle; there are only 11 cervical vertebrae (rather than 15); the skull (then unknown) is based on that of a camarasaurid (YPM VP.001911); the forelimbs are strongly flexed rather than columnar, the forefeet are in the then-ubiquitous near-plantigrade posture, and the tail is much too short. Eight years later, Marsh (1891, plate XVI) published a revised reconstruction (Figure 2B). Although this correctly increased the number of cervical vertebrae – though only to 13, not 15 – it also increased the dorsal vertebral count from the correct 10 to 14 and provided a new but equally incorrect skull – this one based on YPM VP.001986, which is now considered brachiosaurid (Carpenter and Tidwell, 1998; D'Emic and Carrano, 2019). In modern, anatomically rigorous skeletal reconstructions such as that of Scott Hartman (Figure 2C), these errors are corrected, showing a very different animal with a compact torso supporting a longer neck and a much longer tail, with a characteristically diplodocid skull, and with erect forelimb and unguligrade forefeet.

Several years after Marsh's skeletal reconstructions, artists began creating life restorations of diplodocoids. The earliest known artistic life reconstruction of any sauropod is an 1897 drawing by Charles R. Knight, executed under Cope's instruction, of several *Amphicoelias* individuals underwater (at the time, it was believed that sauropods were aquatic due to their great mass [see below]; reproduced by Osborn and Mook, 1921, figure 127). This was followed later that same year by Knight's much better-known painting of a swamp-bound *Brontosaurus* (reproduced by Taylor, 2010, figure 6), which set the template that would dominate the perception of diplodocoid (and, more broadly, sauropod) ecology for 70 years.

The idea that sauropods were amphibious animals goes back to Phillips's (1871) description of *Cetiosaurus oxoniensis*. Phillips noted that "all the articulations [of the limb bones] are such as to be suited for walking" (p. 294), but nevertheless concluded that "we have, therefore, a marsh-loving or river-side animal" (p. 294). Although Marsh (1877a) referred to *Atlantosaurus montanus* as "this largest of land animals," a few years later he wrote of *Brontosaurus* that "the very small head and brain, and slender neural cord, indicate a stupid, slow-moving reptile. [...] In habits, *Brontosaurus* was more or less amphibious, and its food was probably aquatic plants or other succulent vegetation." As noted above, Knight's 1897 painting of an amphibious *Brontosaurus* helped to fix this notion in the minds of scientists and the public alike.

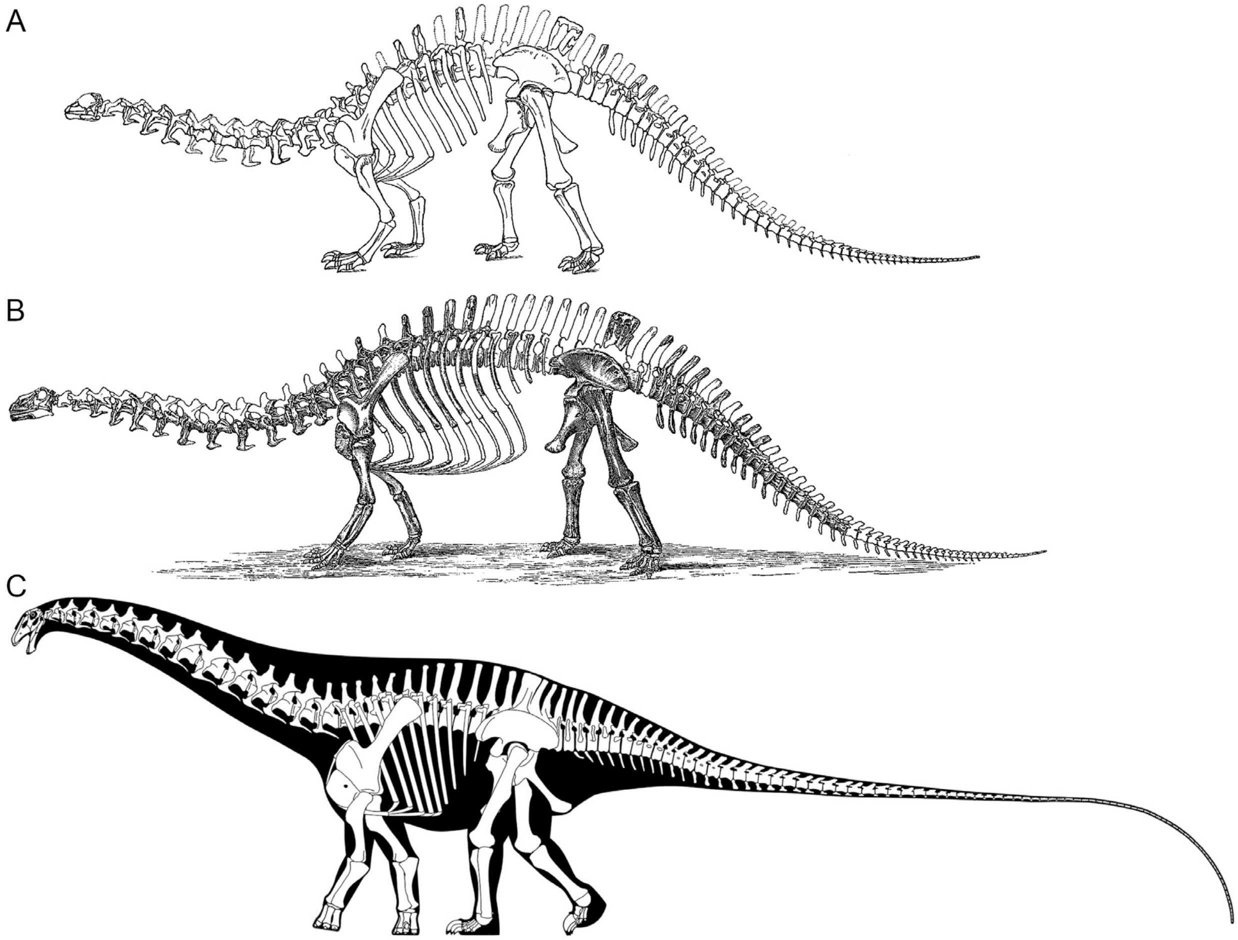


FIGURE 2. Skeletal reconstructions of *Brontosaurus*, including the first two reconstructions of any diplodocoids, scaled to the same femur length and horizontally aligned at the shoulder. **A.** First reconstruction, from Marsh (1883, plate I). **B.** Second reconstruction, from Marsh (1891, plate XVI). **C.** Modern reconstruction by Scott Hartman, 2022, used by kind permission.

The first diplodocoid to receive a comprehensive description meeting today's scientific standards was *Diplodocus carnegii* (Hatcher, 1901). Hatcher's monograph included 13 plates culminating in a beautifully executed skeletal reconstruction. Hatcher (1901, p. 59-61) reaffirmed and expanded on the then-orthodox notion of sauropods in general, and diplodocoids in particular, as sluggish, swamp-bound creatures: "Though living for the most part in the more important rivers and freshwater lakes, it may not infrequently have left the water and taken temporarily to the land, either in quest of food or in migration from one to another of adjacent bodies of water."

When King Edward VII of England visited Andrew Carnegie's Scottish home at Skibo Castle in 1902, he was so taken with a framed print of the skeletal reconstruction from Hatcher's monograph that he asked Carnegie to provide a *Diplodocus* skeleton for the British Museum. This led to the very first casting of a sauropod skeleton, which was donated by Carnegie to the Natural History Museum in London, where it stood until recently as the entry centerpiece of the museum. From these original molds, Carnegie had nine additional replica skeletons made which were donated and mounted in natural history museums in Berlin, Paris, Vienna, Bologna, St. Petersburg, La Plata, Madrid, and Mexico City, with a tenth cast traded to Munich but never mounted (Rea, 2001; Nieuwland, 2019; Taylor et al., 2025).

After the Carnegie Museum had finished with the molds used to make these cast skeletons, they were acquired by the Utah Field House of Natural History State Park Museum in Vernal, Utah, and used one last time to make a concrete *Diplodocus* that was exhibited outdoors from 1957 to 1989 (Taylor et al., 2023). When this cast was taken down, it was used to make second-generation molds which in turn have been used to make yet more copies of the Carnegie *Diplodocus*, which are now mounted in multiple locations in the USA, Canada, and Japan. As a result of this rich history, the Carnegie *Diplodocus* is probably the best-known individual dinosaur in the world, and certainly the sauropod that most formed public impressions of the sauropod form.

Around the same time that the Carnegie Museum was mounting *Diplodocus*, the American Museum of Natural History was creating a mounted skeleton of *"Brontosaurus"* (mainly based on the specimen AMNH FARB 460) – now considered an indeterminate apatosaurine (Tschopp et al., 2015). The question of which was the first mounted sauropod skeleton is a complex one. The Carnegie *Diplodocus* was the first to be erected, on 29 June 1904, but only as a trial mount before the cast was sent to England. This was not available to the public, nor did it include any real bone. The AMNH *"Brontosaurus,"* which largely consisted of real bone (albeit from several individuals), was unveiled to the public on 16 February 1905, three months before the public debut of the Carnegie cast in London on 12 May 1905.

The first diplodocoids recognized from outside North America were those discovered by the German expeditions in the Tendaguru Formation of Tanzania (then Deutsch Ostafrika). Janensch (1914) identified two sauropods that are relevant here. *"Gigantosaurus" africanus* was recognized as related to *Diplodocus*. The taxonomic history of *"Gigantosaurus"* is exceedingly complex, but the outcome is that the species described by Janensch is currently known as *Tornieria africana* (Remes, 2006), identified as a diplodocine. Perhaps more significant, it was in this paper that Janensch (1914) named *Dicraeosaurus hansemanni*, the first representative of the diplodocoid family Dicraeosauridae.

The last major group of diplodocoids to be recognized was Rebbachisauridae, first known from the remains of *Rebbachisaurus garasbae* (Lavocat, 1954), found in Morocco, and subsequently from numerous taxa from South America and elsewhere.

The "Dinosaur Renaissance" of the late 1960s and 1970s is often considered to have been catalyzed by Ostrom's (1969) description of the bird-like, agile, active, and intelligent dromaeosaurid theropod *Deinonychus*. However, this was preceded by Bakker's (1968) article "The Superiority of Dinosaurs," in which he forcefully refuted the long-standing orthodoxy of swamp-bound sauropods. Critical to the impact of his argument was a pencil drawing of two *Barosaurus* individuals striding briskly across a dry Mesozoic landscape with their heads held high. Bakker's arguments for terrestriality were placed on a firmer theoretical footing by Coombs (1975), and this perception of sauropod lifestyles has held sway ever since.

The vision of sauropods in general, and diplodocines such as *Barosaurus* in particular, as active terrestrial animals was sealed in the public imagination by the AMNH's unveiling of a mounted cast skeleton of *Barosaurus* in a rearing posture in 1991, positioned as though to defend a juvenile from an attacking *Allosaurus* (Taylor et al., in prep.). Although this exhibit has provoked some controversy (e.g., Hicks and Badeer, 1992; Choy and Altman, 1992), it remains the iconic image of *Barosaurus* and was likely the inspiration for the briefly rearing *Brachiosaurus* in the 1993 film *Jurassic Park.*

THE MAIN DIPLODOCOID GROUPS

Overview of Diplodocoid Phylogeny

Diplodocoidea had already been recognized as a major clade of neosauropod sauropods in the early years of cladistic analyses of Sauropoda (Calvo and Salgado, 1995; Upchurch 1995, 1998, 1999; Salgado et al., 1997, 1999; Wilson and Sereno, 1998). Its exact position within Sauropoda remained debated, however, with Upchurch (1995) recovering it as a sister clade to Titanosauria, whereas many other analyses (e.g., Calvo and Salgado, 1995; Salgado et al., 1997; Wilson and Sereno, 1998), including a subsequent iteration of Upchurch's (1995) own analysis (Upchurch, 1998), found Diplodocoidea as a sister clade to a clade consisting of *Camarasaurus, Brachiosaurus,* and titanosaurs – a view that has since been confirmed by many other analyses. This sister clade to Diplodocoidea was named Macronaria by Wilson and Sereno (1998). These two major clades form Neosauropoda. As with the phylogenetic position of Diplodocoidea among sauropods, the composition of Diplodocoidea has also been debated.

Upchurch (1995, 1998, 1999) and Upchurch et al. (2004a) proposed that Nemegtosauridae was part of Diplodocoidea. Salgado and Calvo (1997), Curry Rogers and Forster (2001), and Wilson (2002) alternatively recovered Nemegtosauridae within Macronaria as derived titanosaurs. The genus *Haplocanthosaurus* has also regularly meandered between Diplodocoidea (e.g., Wilson, 2002), Macronaria (e.g., Upchurch, 1995; Wilson and Sereno, 1998), and even non-neosauropod Eusauropoda (e.g., Harris, 2006). The general structure and taxonomic contents of Diplodocoidea have converged since then, most importantly thanks to the in-depth analyses of diplodocoid relationships by Rauhut et al. (2005), Salgado et al. (2006), Sereno et al. (2007), Whitlock (2011a), Mannion et al. (2012), and Tschopp et al. (2015). These have mostly confirmed Wilson (2002) in that Diplodocoidea consisted of *Haplocanthosaurus* as its most basal member, and the three main lineages: Rebbachisauridae, Dicraeosauridae, and Diplodocidae (which are united in the clade Diplodocimorpha; originally proposed by Calvo and Salgado, 1995). Several additional clades within Diplodocoidea have been defined phylogenetically (Sereno, 1998; Harris and Dodson, 2004; Taylor and Naish, 2005); all of which were reviewed and summarized by Taylor and Naish (2005, table 1).

Based on their review, Taylor and Naish (2005) proposed a series of recommendations regarding the use and phylogenetic definition of these clades, which have since largely been followed. According to their scheme, Diplodocoidea is the stem-based taxon including all taxa more closely related to *Diplodocus* than to *Saltasaurus*. Diplodocimorpha is a node-based taxon including *Diplodocus* and *Rebbachisaurus*, their most recent common ancestor, and all its descendants (Figure 1). As such, it excludes *Haplocanthosaurus* in most phylogenetic analyses (see below). Included in Diplodocimorpha are the stem-based Rebbachisauridae and node-based Flagellicaudata (Figure 1). Rebbachisauridae is defined as all taxa more closely related to *Rebbachisaurus* than to *Diplodocus*. Flagellicaudata includes *Dicraeosaurus*, *Diplodocus*, their most recent common ancestor, and all its descendants (Figure 1). *Dicraeosaurus* and *Diplodocus* are also used to define the two stem-based taxa Dicraeosauridae and Diplodocidae that make up Flagellicaudata (Harris and Dodson, 2004). Finally, Diplodocidae includes the stem-based clades Apatosaurinae (all taxa more closely related to *Apatosaurus* than to *Diplodocus*) and Diplodocinae (all taxa more closely related to *Diplodocus* than to *Apatosaurus*) (Figure 1). These definitions have turned out to be applicable in a fairly stable way in a number of follow-up studies focusing on Diplodocoidea as a whole (e.g., Whitlock, 2011a; Mannion et al., 2012), or on distinct subgroups (Carballido et al., 2012; Tschopp et al., 2015; Canudo et al., 2018; Xu et al., 2018; Lindoso et al., 2019; Whitlock and Wilson, 2020; Windholz et al., 2022; Lerzo et al., 2024a, 2024b). These subgroups will be discussed below.

Rebbachisauridae (Table 1)

The first rebbachisaurid to be published, *Rebbachisaurus garasbae* (Lavocat, 1954), was based on a scapula, a posterior dorsal vertebra, and some undescribed elements. However, it was not until the nineties when Bonaparte (1997) recognized a new clade formed by *Rebbachisaurus garasbae, "Rebbachisaurus" tessonei* (Calvo and Salgado, 1995), and *Rayososaurus agrioensis* (Bonaparte, 1996), which he called Rebbachisauridae. The first phylogenetic definition of the family was published by Salgado et al. (2004) as all diplodocoids more closely related to *Rebbachisaurus garasbae* than to *Diplodocus* (Salgado et al., 2022). Since Bonaparte (1997), several articles have been published increasing the knowledge of the group (Dalla Vecchia, 1998; Pereda Suberbiola et al., 2003; Salgado et al., 2006, 2022; Carballido et al., 2010, 2012; Torcida Fernandéz-Baldor et al., 2011; Fanti et al., 2013, 2014, 2015; Ibiricu et al., 2013, 2015; Canudo et al., 2018; Lindoso et al., 2019; Bellardini et al., 2022a, 2022b, 2023; Lerzo et al., 2024a, 2024b; Simón and Salgado, 2025).

Whitlock (2011a) was the first to recognize two subclades within Rebbachisauridae: The South American Limaysaurinae *(Limaysaurus* not *Nigersaurus)* and the Euro-African Nigersaurinae *(Nigersaurus* not *Limaysaurus).* Limaysaurinae was an unstable clade supported solely by a character from the scapula (Carballido et al., 2012; Canudo et al., 2018). Recent analyses did not recover Limaysaurinae due to the multiple positions taken by *Cathartesaura* (Bellardini et al., 2022b, Lerzo et al., 2024a) or the different positions taken by *Rebbachisaurus* (Lerzo et al., 2024b). Wilson and Allain (2015) provided a complete description of *Rebbachisaurus garasbae*, recovering it within the Euro-African subclade. Consequently, following the ICZN rules, the clade name Rebbachisaurinae has priority over Nigersaurinae (Wilson and Allain, 2015; Canudo et al., 2018; Salgado et al., 2022). In the same year, Fanti et al. (2015) defined the clade Khebbashia as the least inclusive clade containing *Limaysaurus tessonei, Nigersaurus taqueti,* and *Rebbachisaurus garasbae* (Salgado et al., 2022).

Limaysaurus tessonei is based on an articulated, well-preserved skeleton, including cranial remains. The species was initially described as

TABLE 1. List of all currently valid rebbachisaurid species. *Bellardini et al. (2023) incorrectly state that the holotype of *H. boscarollii* is 'lost'; the vertebra still exist and is available for study (T.T.P. van der Linden, personal obs., 2025; F. Vidaković, personal comm., 2025).

Taxon	Holotype	Comment	Reference
Maraapunisaurus fragillimus (Cope, 1878)	AMNH FARB 5777	Type species	Carpenter, 2018
Rebbachisaurus garasbae Lavocat, 1954	MNHN-MRS 1958	Type species	Lerzo et al., 2024a, 2024b
Limaysaurus tessonei (Calvo and Salgado, 1995)	MUCPv-205	Type species	Lerzo et al., 2024a, 2024b
Rayososaurus agrioensis Bonaparte, 1996	MACN-N 41	Type species	Lerzo et al., 2024a, 2024b
Histriasaurus boscarollii Dalla Vecchia, 1998	WN V-6*	Type species	Lerzo et al., 2024a, 2024b
Agustinia ligabuei Bonaparte, 1999	MCF-PVPH-110	Type species	Bellardini et al., 2022b; Lerzo et al., 2024a, 2024b
Nigersaurus taqueti Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, G.P. Wilson, and J.A. Wilson, 1999	MNN GAD512	Type species	Lerzo et al., 2024a, 2024b
Amazonsaurus maranhensis Carvalho, Santos Avilla, and Salgado, 2003	MN & UFRJ-DG; multiple specimen numbers, see Carvalho et al., 2003	Type species	Lerzo et al., 2024a, 2024b
Cathartesaura anaerobica Gallina and Apesteguía, 2005	MPCA-232	Type species	Lerzo et al., 2024a, 2024b
Zapalasaurus bonapartei Salgado, Carvalho, and Garrido, 2006	Pv-6127-MOZ	Type species	Lerzo et al., 2024a, 2024b
Xenoposeidon proneneukos Taylor and Naish, 2007	NHMUK R2095	Type species	Taylor, 2018; Salgado et al., 2022
Nopcsaspondylus alarconensis Apesteguía, 2007	The holotype is lost and never got an inventory number	Type species	Salgado et al., 2022
Demandasaurus darwini Torcida Fernández-Baldor, Canudo, Huerta, Montero, Suberbiola, and Salgado, 2011	MDS-RII; multiple specimen numbers, see Torcida Fernández-Baldor et al., 2011	Type species	Lerzo et al., 2024a, 2024b
Comahuesaurus windhauseni Carballido, Salgado, Pol, Canudo, and Garrido, 2012	MOZ-Pv 6722	Type species	Lerzo et al., 2024a, 2024b
Tataouinea hannibalis Fanti, Cau, Hassine, and Contessi, 2013	ONM DT; multiple specimen numbers, see Fanti et al., 2013	Type species	Lerzo et al., 2024a, 2024b
Katepensaurus goicoecheai Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, 2013	UNPSJB-PV; multiple specimen numbers, see Casal et al., 2013	Type species	Lerzo et al., 2024a, 2024b
Lavocatisaurus agrioensis Canudo, Carballido, Garrido, and Salgado, 2018	MOZ-Pv1232	Type species	Lerzo et al., 2024a, 2024b
Itapeuasaurus cajapioensis Lindoso, Araújo Medeiros, Souza Carvalho, Araújo Pereira, Dienes Mendes, Vidoi Iori, Pinheiro Sousa, Souza Arcanjo, and Costa Madeira Silva, 2019	UFMA; multiple specimen numbers, see Lindoso et al., 2019	Type species	Lerzo et al., 2024a, 2024b
Sidersaura marae Lerzo, Gallina, Canale, Otero, Carballido, Apesteguía, and Makovicky, 2024	MMCh-PV 70	Type species	Lerzo et al., 2024a, 2024b
Campananeyen fragilissimus Lerzo, Torcida Fernández-Baldor, Canale, Whitlock, Otero, and Gallina, 2024	MMCh-PV 71	Type species	Lerzo et al., 2024b
Cienciargentina sanchezi Simón and Salgado, 2025	MMCh-PV 45	Type species	Simón and Salgado, 2025

"Rebbachisaurus" tessonei and included in Diplodocimorpha (Calvo and Salgado, 1995). Later, Salgado et al. (2004) renamed this species from the Cenomanian Candeleros Formation of Argentina as *Limaysaurus tessonei* and recognized it as part of Rebbachisauridae. In recent years, *L. tessonei* has been a derived member within Rebbachisauridae (e.g., Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b).

Before the referral of *"Rebbachisaurus" tessonei* to its own genus *Limaysaurus*, several new rebbachisaurids were described. *Rayososaurus agrioensis* (Bonaparte, 1996; Carballido et al., 2010) is also from the Cenomanian Candeleros Formation, with the holotype consisting of appendicular elements. Upon description, *R. agrioensis* was not assigned to any family, but later works included this species in Rebbachisauridae (e.g., Salgado et al., 2004; Gallina and Apesteguía, 2005; Carballido et al., 2010). The species is tentatively considered to be a derived member closely related to *Rebbachisaurus* (Lerzo et al., 2024b), although several recent analyses omit this taxon due to its fragmentary nature (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a).

The geologically oldest unambiguous rebbachisaurid taxon is *Histriasaurus boscarollii* (Dalla Vecchia, 1998) from Istria (Croatia). It is solely represented by a partial middle/posterior dorsal vertebrae. *H. boscarollii* is one of the earliest-branching species in Rebbachisauridae (Bellardini et al., 2022; Lerzo et al., 2024a), which – combined with its Hauterivian-Barremian age – highlights its importance for untangling the biogeographic origin of Rebbachisauridae.

Agustinia ligabuei was originally described as a member of "Agustinidae" (Bonaparte, 1999) and later assigned to Titanosauria (Upchurch et al., 2004a; Curry Rogers, 2005). A recent redescription of the holotypic and newly referred materials, consisting of axial and appendicular elements, of *Agustinia* by Bellardini et al. (2022b) recovered rebbachisaurid affinities, and placed *Agustinia* as a basal member of the group. Other recent phylogenetic analyses find *Agustinia* as a problematic taxon, recovering the taxon in different positions within Rebbachisauridae (Lerzo et al., 2024a; Lerzo et al., 2024b).

The discovery and description of *Nigersaurus taqueti* (Sereno et al., 1999) informed the scientific community of the anatomy and ecology of rebbachisaurids. Represented by multiple individuals of different ontogenetic stages, including near complete skulls, *N. taqueti* from the Lower Cretaceous Elrhaz Formation shows feeding adaptations not previously documented in other sauropod skulls (Sereno et al., 2007). *N. taqueti* is nested well within Khebbashia and depending on the analysis included in Rebbachisaurinae (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a) or Nigersaurinae (Lerzo et al., 2024b).

Amazonsaurus maranhensis (Carvalho et al., 2003) was the first named rebbachisaurid from the Aptian-Albian of Brazil. Represented by axial and appendicular material, this species is often recognized as the most basal member of Rebbachisauridae (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b).

Following the redescription of *Limaysaurus* in 2004, several additional rebbachisaurid taxa have been established. Two new Argentinian rebbachisaurids were described shortly after the erection of *Limaysaurus: Cathartesaura anaerobica* (Gallina and Apesteguía, 2005) from the Cenomanian-Turonian Huincul Formation and *Zapalasaurus bonapartei* (Salgado et al., 2006) from the Barremian-Aptian La Amarga Formation. The holotype of *C. anaerobica* consists of several axial and appendicular elements. It represents a more derived rebbachisaurid (Bellardini et al., 2022a; Lerzo et al., 2024b), although some recent analyses (Lerzo et al., 2024a) suggest that this species may lie outside of Khebbashia. *Z. bonapartei* is represented also by axial and appendicular elements and has rather consistently been recovered as one of the earliest-branching members of the family (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b).

Demandasaurus darwini (Torcida Fernández-Baldor et al., 2011) is the most complete European rebbachisaurid, represented by cranial, axial, and appendicular elements. Although recovered as derived member (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b), it is also one the oldest rebbachisaurids, known from the Late Barremian to Early Aptian Castrillo de la Reina Formation (Torcida Fernández-Baldor et al., 2011). Its age and relative completeness aids investigations into the origins of the derived forms in Rebbachisauridae.

In 2013, a novel African and yet another Argentinian rebbachisaurid were described: *Tataouinea hannibalis* (Fanti et al., 2013) and *Katepensaurus goicoecheai* (Ibiricu et al., 2013). Originating from the Albian Ain el Guettar Formation of Tunesia, *T. hannibalis* was initially described based on fragmentary sacral and caudal remains, but in 2015, Fanti et al. described additional remains from the holotype, including a well-preserved articulated caudal vertebral series. *K. goicoecheai* comes from the Cenomanian-Turonian Bajo Barreal Formation, and its holotype consists of cranial, axial, and appendicular elements (Ibiricu et al., 2013, 2015). Both *Tataouinea* and *Katepensaurus* are considered to be derived members of Rebbachisauridae (Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b).

In subsequent years, two new South American taxa were named: *Lavocatisaurus agrioensis* (Canudo et al., 2018) and *Itapeuasaurus cajapioensis* (Lindoso et al., 2019). *L. agrioensis* is represented by significant skull and axial material, as well as appendicular elements, from the Aptian to lower Albian part of the Rayoso Formation in Argentina. *I. cajapioensis* was described from the Cenomanian Alcântara Formation and is represented by two dorsal and three caudal vertebrae. *Lavocatisaurus* was originally, and still is, thought to be a non-khebbashian rebbachisaurid (Canudo et al., 2018; Bellardini et al., 2022a, 2022b; Lerzo et al., 2024a, 2024b). *Itapeuasaurus*, however, was originally recovered as a derived member in Rebbachisauridae (Lindoso et al., 2019), but recent analyses have found it to be a non-khebbashian rebbachisaurid as well (Lerzo et al., 2024a, 2024b).

Most recently, three new rebbachisaurids were described: *Sidersaura marae* (Lerzo et al., 2024a), *Campananeyen fragilissimus* (Lerzo et al., 2024b), and *Cienciargentina sanchezi* (Simón and Salgado, 2025). All three species are represented by axial and appendicular materials, but *Sidersaura* and *Campananeyen* also preserve cranial elements. *Sidersaura* and *Cienciargentina* are both from the Cenomanian-Turonian Huincul Formation (Lerzo et al., 2024a; Simón and Salgado, 2025), whereas *Campananeyen* is from the Cenomanian Candeleros Formation (Lerzo et al., 2024b). *Sidersaura* and *Campananeyen* are recovered in a basal clade closely related to *Zapalasaurus* (Lerzo et al., 2024a; Lerzo et al., 2024b; Simón and Salgado, 2025). *Cienciargentina* possibly represents the earliest diverging member of Rebbachisauridae (Simón and Salgado, 2025). *Sidersaura* represents one of the largest known rebbachisaurid sauropods, with an estimated length of approximately 20 m and a weight of 15 tonnes. In contrast to *Sidersaura, Campananeyen* represents a small rebbachisaurid characterized by a novel sacral structure, resulting from the fusion of the dorsal ends of the sacral transverses processes (Lerzo et al., 2024b). *Cienciargentina* is characterized by a suite of 'basal' and 'derived' features and is important for our understanding of faunal turnovers in the Cretaceous (Simón and Salgado, 2025).

Over the years, several taxa have been part of Rebbachisauridae, but their taxonomic assignment requires further studies. This is the case for *Nopcsaspondylus alarconensis, Maraapunisaurus fragillimus, Xenoposeidon proneneukos,* and *Dzharatitanis kingi* (Apesteguía, 2007; Carpenter, 2018; Taylor, 2018; Averianov and Sues, 2021). In the case of *Nopcsaspondylus alarconensis* and *Maraapunisaurus fragillimu*s, all original material is lost (Carpenter, 2018; Salgado et al., 2022), and their referral to Rebbachisauridae was solely based on published figures (Apesteguía, 2007; Carpenter, 2018). *Nopcsaspondylus alarconensis* (Apesteguía, 2007) was represented by a missing middle or posterior dorsal vertebra and it represents one of the first dinosaur remains collected in Argentina (Canale et al., 2023). Nopcsa (1902) referred that vertebra to *Bothriospondylus* (Owen, 1985) but later, Hatcher (1903) referred to it as *Haplocanthosaurus* (Salgado et al., 2022; Canale et al., 2023). McIntosh (1990b) was the first to relate this vertebra with *Rebbachisaurus garasbae*. More findings are needed to corroborate the position of this species within Diplodocoidea.

Maraapunisaurus fragillimus was originally 'described' within two paragraphs and a single illustration in a popular science periodical in 1878 by Cope. Initially identified as the holotype for a second species of *Amphicoelias* (Cope, 1878), it was officially noted as 'missing' from the AMNH's acquisition of Cope's collection by Osborn and Mook (1921). With the original material being lost, this taxon has often been a synonym of *Amphicoelias altus* (Osborn and Mook, 1921; McIntosh, 1990b; Upchurch et al., 2004a; Woodruff and Foster, 2014) but was recently hypothesized to represent large rebbachisaurid (Carpenter, 2018).

Xenoposeidon proneneukos was originally placed within Neosauropoda (Taylor and Naish, 2007) and later reassigned to Rebbachisauridae based on similarities with *Rebbachisaurus garasbae* (Taylor, 2018). *Xenoposeidon* is represented only by a partial posterior dorsal vertebra. Both *Xenoposeidon* and *Maraapunisaurus* could be the first step in investigating the origin of diplodocoid sauropods because they could represent among the oldest rebbachisaurids. However, both assignments require new material, because one is based solely on a drawing and the other is a fragmentary specimen (Whitlock and Wilson Mantilla, 2020; Salgado et al., 2022).

Dzharatitanis kingi was originally described as a titanosaurian sauropod (Sues et al., 2015) and is only known from a single anterior caudal vertebra. Recently, Averianov and Sues (2021) redescribed this caudal vertebra as a rebbachisaurid sauropod. However, a subsequent phylogenetic analysis recovered *Dzharatitanis* within Titanosauria (Lerzo et al., 2021).

Dicraeosauridae (Table 2)

The clade Dicraeosauridae was first coined by Huene (1927) and is defined as all taxa more closely related to *Dicraeosaurus* than *Diplodocus* (Sereno, 1998). The first described genus was *Dicraeosaurus* (Janensch, 1914) of which there are two recognized species, *D. hansemanni* and *D. sattleri*, both from the Upper Jurassic Tendaguru Formation of Tanzania. Both species were distinguished based on differences in the robustness of their appendicular bones and geological age, with the more robust material from the Middle Dinosaur Member attributed to *D. hansemanni* and the more gracile elements from the Upper Dinosaur Member attributed to *D. sattleri* (Janensch, 1914). *D. hansemanni* is represented by a largely complete specimen, with all areas of the skeleton preserved, excluding the lower forelimbs and parts of the skull. Known *D. sattleri* material consists of more isolated remains, predominantly long bones and caudal vertebrae. *Dicraeosaurus* was the only genus included within Dicraeosauridae for 90 years, until the 1991 description of *Amargasaurus cazaui* (Salgado and Bonaparte, 1991) from the Early Cretaceous of Argentina. Since then, a further 8 species have been recovered as dicraeosaurids.

The holotype of *Dicraeosaurus hansemanni* (Janensch, 1914) is made up largely of a single articulated individual from quarry m within the Tendaguru area. Isolated remains of *D. hansemanni* have been found in numerous quarries across the Middle Dinosaur Member of the Tendaguru Formation, with all skull material having been found in a single quarry (dd). The holotype of *D. sattleri* consists of material from quarry M (note that this is not the same quarry as quarry m) within the Tendaguru area. Isolated elements of *Dicraeosaurus sattleri* (Janensch, 1914) from all regions of the postcranium are represented and have been

TABLE 2. List of all currently valid dicraeosaurid species.

Taxon	Holotype	Comment	Reference
Smitanosaurus agilis (Marsh, 1889)	USNM 5384	Type species	Whitlock and Wilson-Mantilla, 2020
Dicraeosaurus hansemanni Janensch, 1914	MB.R. 4886; skelett "m" from Quarry m	Type species	Bajpai et al., 2023
Dicraeosaurus sattleri Janensch, 1914	Skelett "M" from quarry M; multiple MB.R. specimen numbers		Schwarz-Wings and Böhme, 2014
Amargasaurus cazaui Salgado and Bonaparte, 1991	MACN-N 15	Type species	Gallina et al., 2022
Suuwassea emilieae Harris and Dodson, 2004	ANS 21122	Type species	Harris and Dodson, 2004; Lovelace et al., 2007; Whitlock, 2011a; Tschopp et al., 2015; Whitlock and Wilson-Mantilla, 2020
Brachytrachelopan mesai Rauhut, Remes, Fechner, Cladera and Puerta, 2005	MPEF-PV 1716	Type species	Whitlock and Wilson-Mantilla 2020; Bajpai et al., 2023
Amargatitanis macni Apesteguía, 2007	MACN PV N53	Type species	Gallina et al., 2022
Lingwulong shenqi Xu, Upchurch, Mannion, Barrett, Regalado-Fernandez, Mo, Ma, and Liu, 2018	LM V001a	Type species	Xu et al., 2018; Bajpai et al., 2023
Pilmatueia faundezi Coria, Windholz, Ortega, and Currie, 2019	MLL-Pv-005	Type species	Coria et al., 2019; Whitlock and Wilson-Mantilla 2020
Bajadasaurus pronuspinax Gallina, Apesteguía, Canale, and Haluza, 2019	MMCh-PV 75	Type species	Gallina et al., 2019, 2022
Tharosaurus indicus Bajpai, Datta, Pandey, Ghosh, Kumar, and Bhattacharya, 2023	RWR-241 (A–K)	Type species	Bajpai et al., 2023

discovered across multiple quarries within the Upper Dinosaur Member of the Tendaguru Formation.

Amargasaurus cazaui (Salgado and Bonaparte, 1991) is from the Lower Cretaceous La Amarga Formation of Argentina. It is represented by the basicranial and temporal skull region, and most elements of the postcranium. *Brachytrachelopan mesai* (Rauhut et al., 2005) from the Upper Jurassic Cañadón Calcáreo Formation of Argentina is known from an articulated partial postcranial skeleton consisting of cervical, dorsal, and sacral vertebrae, cervical and dorsal ribs, ilia, and distal elements of the left femur and left tibia (Rauhut et al., 2005). *Dicraeosaurus, Brachytrachelopan,* and *Amargasaurus* have been consistently recovered as forming a derived subclade within Dicraeosauridae across phylogenetic analyses (Whitlock, 2011a; Gallina, 2016; Tschopp and Mateus, 2017; Xu et al., 2018; Gallina et al., 2019; Whitlock and Wilson Mantilla, 2020; Bajpai et al., 2023).

Suuwassea emilieae (Harris and Dodson, 2004) from the Upper Jurassic Morrison Formation of Montana, USA, is represented by the basicranial, temporal, and partial rostral regions of the skull, cervical, dorsal, and caudal vertebrae, scapulocoracoid, humerus, and lower hind limb elements (Harris and Dodson, 2004). The phylogenetic analysis of Harris and Dodson (2004) recovered *Suuwassea* as a Flagellicaudatan, though not recovered in either Dicraeosauridae or Diplodocidae. Later, Lovelace et al. (2007) recovered *Suuwassea* as nested within Apatosaurinae, whereas all recent phylogenies recover it as a dicraeosaurid. The position of *Suuwassea emilieae* in Dicraeosauridae, however, is unstable, with analyses recovering the taxon as one of the most basal (Salgado et al., 2006; Whitlock, 2011a; Mannion et al., 2012; Tschopp and Mateus, 2017; Xu et al., 2018; Gallina et al., 2019; Bajpai et al., 2023) or belonging to a more derived clade as sister taxon to *Amargatitanis* (Whitlock and Wilson Mantilla, 2020).

Amargatitanis macni (Apesteguía, 2007) from the early Cretaceous La Amarga Formation of Argentina is known from a partial hind limb, ischium, and two partial caudal vertebrae. It was initially referred to Titanosauria (Apesteguía, 2007), subsequently considered a nomen dubium by D’Emic (2012) and Mannion et al. (2013); and then, following a redescription by Gallina (2016), was recovered nested within Dicraeosauridae as a sister taxon to *Suuwassea*. Subsequent analyses have recovered it within Dicraeosauridae (Coria et al., 2019; Whitlock and Wilson Mantilla, 2020; Mannion et al., 2021; Windholz et al., 2022; Bajpai et al., 2023; Windholz et al., 2023).

Lingwulong shenqi (Xu et al., 2018) from the Middle Jurassic of Lingwu, China is known from material of multiple individuals and referred material, and includes the basicrania, dentary teeth, and all postcranial regions. It has consistently been recovered as a basal member of Dicraeosauridae (Xu et al., 2018; Gallina et al., 2019; Whitlock and Wilson Mantilla, 2020; Windholz et al., 2022; Bajpai et al., 2023).

Pilmatueia faundezi (Coria et al., 2019) from the Lower Cretaceous Mulichino Formation of Argentina was first described based on a posterior dorsal vertebra and dorsal neural arch, a partial cervical vertebra, and two mid-caudal vertebrae. It was recovered in a derived position within Dicraeosauridae as the sister taxon to *Amargasaurus* (Coria et al., 2019). Subsequent analyses (partially) corroborated this finding, recovering *Pilmatueia* as belonging to a sister group of the clade *Dicraeosaurus, Amargasaurus,* and *Brachytrachelopan* (e.g., Gallina, 2019; Whitlock and Wilson Mantilla, 2020; Bajpai et al., 2023). Windholz et al. (2022) described three articulated cervical vertebrae, seven dorsal vertebrae, a caudal vertebra, and scapula belonging to *Pilmatueia* and scored the taxon in matrices from both Tschopp and Mateus (2017) and Whitlock and Wilson Mantilla (2020). From the Tschopp and Mateus (2017) matrix *Pilmatueia* formed a polytomy with *Amargatitanis* and *Bajadasaurus* with *Amargasaurus, Brachytrachelopan,* and *Dicraeosaurus* as successive steps down the tree. The Whitlock and Wilson Mantilla (2020) matrix resolved *Pilmatueia* in a group with *Suuwassea* and *Amargatitanis* as the sister group to the clade containing *Amargasaurus, Brachytrachelopan,* and *Dicraeosaurus*.

Bajadasaurus pronuspinax (Gallina et al., 2019; Garderes et al., 2023), from the Lower Cretaceous Bajada Colorada Formation of Argentina consists of a nearly complete skull, proatlases, atlantal neurapophyses, axis, and a mid-cervical vertebra from a single individual. Gallina et al. (2019) recovered the species as sister taxon to a group containing *Pilmatueia* and an unresolved grouping of *Dicraeosaurus, Amargasaurus,* and *Brachytrachelopan*. Later analyses have recovered *Bajadasaurus* in various positions basal to the *Amargasaurus, Brachytrachelopan,* and *Dicraeosaurus* group (Whitlock and Wilson Mantilla, 2020; Windholz et al., 2022; Bajpai et al., 2023).

Smitanosaurus agilis (Marsh, 1889; Whitlock and Wilson Mantilla, 2020) from the Morrison Formation of Colorado, USA was originally described as a species of *'Morosaurus'* (Marsh, 1889) and consists of the braincase and parts of the skull roof, proatlases, and cervical vertebrae 1-3. In 2020 the material was redescribed and recovered within Dicraeosauridae as a basal dicraeosaurid (Whitlock and Wilson Mantilla, 2020).

The most recently described dicraeosaurid, *Tharosaurus indicus* (Bajpai et al., 2023) from the Middle Jurassic Fort Member of the Jaisalmer Formation of India is known from partial mid/posterior cervical vertebrae, a partial dorsal neural arch, dorsal neural spines, dorsal rib, and partial caudal vertebrae. It was recovered as a sister taxon of a clade containing *Pilmatueia, Amargatitanis, Brachytrachelopan, Dicraeosaurus,* and *Amargasaurus* (Bajpai et al., 2023). Its inclusion thus far in only a single analysis and the fragmentary nature of the specimen means that more evidence is needed in order to corroborate its position within Dicraeosauridae.

Several taxa have been proposed to represent putative dicraeosaurid sauropods. *Kaatedocus siberi* (Tschopp and Mateus, 2013) from the Upper Jurassic Morrison Formation of Wyoming, USA has traditionally been recovered within Diplodocinae (Tschopp et al., 2015; Tschopp et al., 2017) until Whitlock and Wilson Mantilla (2020) recovered it as the basal-most dicraeosaurid taxon. A supplementary analysis using a matrix derived from Mannion et al. (2019) corroborated the results of the main analysis (Whitlock and Wilson Mantilla, 2020).

Dyslocosaurus polyonychius (McIntosh et al., 1992) is known for fragmentary appendicular elements and was initially described as a diplodocid (McIntosh et al., 1992). The specimen is of particular interest, as its locality data suggests that *Dyslocosaurus* may be from the Maastrichtian Lance Formation. However, knowing the current temporal extent of diplodocoid sauropods, it is most likely that this specimen was excavated from nearby outcrops of the Morrison Formation (McIntosh et al., 1992). It was recovered as the most basal dicraeosaurid by Tschopp et al. (2015) and Coria et al. (2019). Mannion et al. (2021) recovered *Dyslocosaurus* nested within Dicraeosauridae as a polytomous group with *Amargasaurus, Brachytrachelopan,* and *Dicraeosaurus* on its inclusion in the matrix of Xu et al. (2018). Other isolated dicraeosaurid remains have been suggested to be present in the Wadi Milk Formation in Sudan (Rauhut, 1999), Kirkwood Formation in South Africa (McPhee et al., 2016), and Podosinki Formation in European Russia (Averianov and Zverkov, 2020).

Apatosaurinae (Table 3)

Apatosaurines were among the first diplodocoids to be described, with *Apatosaurus* (Marsh, 1877b) named in the same year as the first diplodocoid, the dubious *Atlantosaurus* (Marsh, 1877a), and with *Brontosaurus* (Marsh, 1879) following only two years later. The subfamily name Apatosaurinae was first used by Janensch (1929a, p. 31), without comment, alongside Diplodocinae, Dicraeosaurinae, and "Titanosaurinae" as subfamilies within his proposed family Homalosauropodidae in a ranked taxon list. Bakker (1998) used the term as "an informal category for all the massive limbed, wide necked-wide tailed diplodocids" (p. 74). It was not given a phylogenetic definition until that of Taylor and Naish (2005) as the clade of all individuals more closely related to *Apatosaurus* than to *Diplodocus*.

For many years, *Apatosaurus* and *Brontosaurus* were the only known apatosaurines, and Riggs's (1903) synonymization of the latter with the former left only a single apatosaurine genus, though one containing several species. Although the name *Brontosaurus* continued to be used in informal contexts, scientific writing mostly followed Riggs's scheme until the phylogenetic analysis of Tschopp et al. (2015) argued based on morphological differences for the generic separation of the

TABLE 3. List of all currently valid apatosaurine species.

Taxon	Holotype	Comment	Reference
Apatosaurus ajax Marsh, 1877a	YPM VP.001860	Type species	Tschopp et al., 2015; Mannion et al., 2021
Apatosaurus louisae Holland, 1916	CM 3018		Tschopp et al., 2015; Mannion et al., 2021
Brontosaurus excelsus Marsh, 1879	YPM VP.001980	Type species	Tschopp et al., 2015; Mannion et al., 2021
Brontosaurus parvus (Peterson and Gilmore, 1902)	CM 566		Tschopp et al., 2015; Mannion et al., 2021
Brontosaurus yahnahpin (Filla and Redman, 1994)	TATE-001		Tschopp et al., 2015; Mannion et al., 2021

species *Brontosaurus excelsus* from *Apatosaurus ajax*. The separation has generally been followed (e.g., Vidal et al., 2020a; King et al., 2023; Taylor and Wedel, 2023; Wedel and Taylor, 2023).

Peterson and Gilmore (1902) named *Elosaurus parvus* for a small specimen, CM 566, which they considered to belong to "Morosauridae" (i.e., Camarasauridae). This specimen has been generally considered a juvenile individual of *Apatosaurus (=Brontosaurus) excelsus* (e.g., McIntosh, 1995), or a separate species *Apatosaurus parvus* (e.g., Upchurch et al., 2004b). Tschopp et al. (2015) recovered it as more closely related to *Brontosaurus excelsus*, yielding the new combination *Brontosaurus parvus*. The immature status of the holotype influences character scoring and makes it impossible to be confident about its low-level taxonomic affinities, but all authors since Peterson and Gilmore seem to have agreed that it is an apatosaurine.

Filla and Redman (1994) described the new species *Apatosaurus yahnahpin*, which they considered to be a primitive species of *Apatosaurus* (i.e., a basal apatosaurine, as they were working within Riggs's schema where all apatosaurines were considered species of *Apatosaurus).* Bakker (1998) moved this species to its own new genus as *Eobrontosaurus yahnahpin*, considering it ancestral to *Brontosaurus*, but giving no specific rationale for generic separation. Tschopp et al. (2015) found the species to be closely related to *Brontosaurus excelsus* and referred it to the new combination *Brontosaurus yahnahpin*. As with *B. parvus,* the exact phylogenetic position of *B. yahnahpin* is not certain, but it seems to be unambiguously apatosaurine.

Some other taxa were recovered as apatosaurines in the past, too. In Lovelace et al.'s (2007) description of a second specimen of *Supersaurus*, they found that this taxon, previously considered diplodocine (e.g., Curtice, 1996), was recovered as an apatosaurine in a phylogenetic analysis. However, the result has not been replicated, and Whitlock (2011), Mannion et al. (2012), and Tschopp et al. (2015) found *Supersaurus* to be diplodocine.

In some trees of Tschopp et al. (2015), including those obtained by equal weighting (figure 115), *Amphicoelias altus* was also found to be apatosaurine. This is in contrast to earlier analyses such as that of Whitlock (2011a), in which *Amphicoelias* was found as a very basal diplodocoid, outside Diplodocimorpha. A reassessment of *Amphicoelias altus* (Mannion et al., 2021) also concluded that this taxon is unlikely to be an apatosaurine.

Diplodocinae (Table 4)

For a long time, the term Diplodocidae (Marsh, 1884) – erected based on the type genus *Diplodocus* (Marsh, 1878) – was used for the clade that is now called Diplodocoidea (e.g., McIntosh 1990a, 1990b). Given that, the name Diplodocinae first appeared in Janensch (1929a, p. 31), who proposed it as a name for the sister clade to his "Dicraeosaurinae." In its current use, with Diplodocidae forming the sister clade to Dicraeosauridae, Diplodocinae includes all taxa more closely related to *Diplodocus* than *Apatosaurus* (Taylor and Naish, 2005). Until the 1990s, what we now call Diplodocinae (following Taylor and Naish, 2005) mostly included the genera *Diplodocus* and *Barosaurus*. However, additional genera have been recognized to belong to this clade in more recent years. At least 10 species and seven genera are currently considered valid by most researchers (Table 4).

The first diplodocine genus to be named was *Diplodocus* (Marsh, 1878). Its type species, *Diplodocus longus* (Marsh, 1878) consists of an incomplete tail (YPM VP.001920; McIntosh and Carpenter, 1998; Tschopp and Mateus, 2016; Tschopp et al., 2018), which is often considered undiagnostic, with the result that the species should be treated as a nomen dubium (Tschopp et al., 2015, 2018; Tschopp and Mateus, 2016; Lucas, 2017; Taylor, 2017). Three more species were described later (Marsh, 1884; Hatcher, 1901; Holland, 1924). Of these, *Diplodocus lacustris* (Marsh, 1884) comprises a single articulated tooth row (YPM VP.001922), which also does not bear any diagnostic features (Tschopp et al., 2015; Tschopp and Mateus, 2016). *Diplodocus carnegii* (Hatcher, 1901) is known from at least two partial postcranial skeletons that were complete enough to allow Hatcher (1901) to publish the first full-skeleton reconstruction (CM 84, CM 94). *Diplodocus hayi* (Holland, 1924) consists of a single, nearly complete specimen (HMNS 175), and was later referred to its own diplodocine genus *Galeamopus* (Tschopp et al., 2015) as the type species. Another species, initially described as *Seismosaurus halli* (Gillette, 1991) was later referred to *Diplodocus* with its corrected species epithet as *Diplodocus hallorum* (Lucas et al., 2006). Several specimens initially referred to *Diplodocus longus* were later assigned to *Diplodocus hallorum* (Tschopp et al., 2015), so this species is now known from all parts of the skeleton except for the skull.

Given that the undiagnosability of the type species of *Diplodocus* may in the future lead to an invalidation of all connected higher-level taxa,

TABLE 4. List of all currently valid diplodocine species.

Taxon	Holotype	Comment	Reference (position in clade)
Diplodocus longus Marsh, 1878	YPM VP.001920	Type species	Tschopp et al., 2015
Barosaurus lentus Marsh, 1890	YPM VP.000429	Type species	Mannion et al., 2021
Diplodocus carnegii Hatcher, 1901	CM 84		Tschopp et al., 2015; Mannion et al., 2021
Tornieria africana (Fraas, 1908)	SMNS 12141a	Type species	Tschopp et al., 2015
Galeamopus hayi (Holland, 1924)	HMNS 175	Type species	Tschopp et al., 2015; Mannion et al., 2021
Supersaurus vivianae Jensen, 1985	BYU 12962	Type species	Lovelace et al., 2007; Tschopp et al., 2015; Mannion et al., 2021
Diplodocus hallorum (Gillette, 1991)	NMMNH 3690		Tschopp et al., 2015
Supersaurus lourinhanensis (Bonaparte and Mateus, 1999)	ML 414		Tschopp et al., 2015
Kaatedocus siberi Tschopp and Mateus, 2013	NMZ 1000004 (SMA 0004)	Type species	Whitlock and Wilson Mantilla 2020; Mannion et al., 2021
Leinkupal laticauda Gallina, Apesteguía, Haluza, and Canale, 2014	MMCh-PV 63-1	Type species	Tschopp et al., 2015; Gallina et al., 2022
Galeamopus pabsti Tschopp and Mateus, 2017	NMZ 1000011 (SMA 0011)		Tschopp and Mateus, 2017; Mannion et al., 2021
Ardetosaurus viator van der Linden, Tschopp, Sookias, Wallaard, Holwerda, and Schulp, 2024	MAB011899	Type species	van der Linden et al., 2024

Tschopp and Mateus (2016) proposed an ICZN case to replace the type species with the third described species, *Diplodocus carnegii* (see also Tschopp et al., 2018). That case, however, was declined two years later (ICZN 2018), after having received three comments in support (Lucas, 2017; Taylor, 2017; Woodruff, 2017), and three in opposition (Carpenter, 2017; Demirjian, 2017; Mortimer, 2017). With the status of *Diplodocus longus* being debated, there are currently two *Diplodocus* species that are universally considered valid: *D. carnegii* (Hatcher, 1901) and *D. hallorum* (Gillette, 1991).

The second described diplodocine genus was *Barosaurus*. The only currently accepted species of *Barosaurus* is its type species *Barosaurus lentus* (Marsh, 1890). It is represented by at least two fairly complete specimens (Lull, 1919; McIntosh, 2005; Tschopp et al., 2015). Two other proposed species, *B. affinis* (nomen dubium) and *B. gracilis* (nomen nudum) are no longer considered valid (Tschopp et al., 2015). Specimens that were referred to *B. africanus* (Janensch, 1914), a diplodocine from the Upper Jurassic Tendaguru Formation of Tanzania, are now placed in *Tornieria africana* or are indeterminate diplodocines (Remes, 2006, 2009; Tschopp et al., 2015).

Tornieria africana is the only known species of *Tornieria* and was initially described as *Gigantosaurus africanus* (Fraas, 1908). The genus *Gigantosaurus*, however, was preoccupied, so alternatively, Sternfeld (1911) proposed *Tornieria* as a replacement name. It was the first taxon in this clade from outside North America. Janensch (1922) later referred the species *Tornieria africana* to *Barosaurus*. In 2006, Remes demonstrated generic distinction from *Barosaurus* and reinstated *Tornieria africana* as a valid taxon. This has since been confirmed by several phylogenetic analyses that recovered *Tornieria* distinct from *Barosaurus* (Remes, 2006; Whitlock, 2011a; Mannion et al., 2012; Tschopp et al., 2015). Two specimens can be confidently referred to the species, which preserve cranial and postcranial material (Remes, 2006, 2009; Tschopp et al., 2015).

Diplodocinae also includes the more recently described North American species *Supersaurus vivianae* (Jensen, 1985). In the first phylogenetic analysis including this species, it was recovered as an apatosaurine (Lovelace et al., 2007), but it has since been consistently recovered as a diplodocine (Whitlock, 2011a; Mannion et al., 2012; Tschopp et al., 2015; Mannion et al., 2021). It is represented by at least two partial skeletons, one of which includes the holotypic dorsal vertebra of *Ultrasau-*

ros macintoshi (BYU 725-9044; Curtice et al., 1996) and *Dystylosaurus edwini* (BYU 725-4503; Curtice and Stadtman, 2001). More recently, Tschopp et al. (2015) suggested that the only named European diplodocine, *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999), is alternatively a second species of *Supersaurus*. If corroborated, *Supersaurus* would be the only currently known diplodocine genus present on two continents.

An important taxon belonging to Diplodocinae is *Leinkupal laticauda* (Gallina et al., 2014) from the Lower Cretaceous Bajada Colorado Formation of Argentina. It is so far the only named diplodocid from South America and from the Cretaceous. A single caudal vertebra from the Cretaceous of South Africa has also been referred to Diplodocinae, but the authors refrained from erecting a new species (McPhee et al., 2016). The description of *Leinkupal* contradicted the general understanding at the time that diplodocids went extinct at the Jurassic-Cretaceous boundary (Gallina et al., 2014). The taxon is represented by a proportionally small anterior caudal vertebra and possibly other cranial and postcranial material from the same locality. However, the disarticulated nature of the material and the fact that multiple taxa were recovered from this locality disallows unambiguous attribution of all diplodocid bones to a single species (Gallina et al., 2014, 2022; Garderes et al., 2022).

The new genus *Galeamopus* was proposed by Tschopp et al. (2015) for the species *"Diplodocus" hayi,* for which they confirmed earlier proposals of generic distinction based on their phylogenetic analysis (Holland, 1924). A second species, *Galeamopus pabsti* (Tschopp and Mateus, 2017) was erected shortly thereafter, based on a specimen with a nearly complete skull and a fairly complete postcranial skeleton (NMZ 1000011 – formerly SMA 0011; lacking its tail). Several other individual skeletons have since been tentatively referred to that species, including both cranial and postcranial elements (Tschopp et al., 2019).

The most recent addition to Diplodocinae is *Ardetosaurus viator* (van der Linden et al., 2024). Consisting of cervical, dorsal, sacral, and caudal vertebrae, as well as appendicular elements mainly from the hindlimbs, this taxon likely represents a more basal member of diplodocine sauropod, similar to *Galeamopus* (Tschopp and Mateus, 2017) and possibly *Kaatedocus* (Tschopp and Mateus, 2013).

Other Diplodocoids (Table 5)

Several sauropod species have been, or are currently, included in Diplodocoidea, which have fluctuated in and outside the clade. We focus here on taxa that remain taxonomically valid. Former diplodocoid taxa that are no longer considered to be taxonomically valid (e.g., *Diplodocus lacustris* or *Apatosaurus laticollis*) and their current phylogenetic positions can be found in Tschopp et al. (2015) and references therein.

In 1877 and 1878, several diplodocoid taxa were erected. Two species of *Atlantosaurus* were named: *Atlantosaurus montanus* (Marsh, 1877b) and *Atlantosaurus immanis* (Marsh, 1878). *Atlantosaurus montanus*, from Lakes Quarry 1 in the Morrison Formation, consists solely of an incomplete sacrum (Marsh, 1877b; Ostrom and McIntosh, 1966). This dubious taxon has never been included in any phylogenetic analysis but likely represents an apatosaurine diplodocoid (Foster, 2020). *Atlantosaurus immanis* was included in Tschopp et al. (2015) and possibly constitutes a new genus and species within Apatosaurinae. *Dystrophaeus viaemalae* (Cope, 1877a) has been regarded as a diplodocoid (McIntosh, 1990b), but is most likely a non-neosauropod eusauropod, though its affinities remain dubious due to its fragmentary nature (Tschopp et al., 2015; Foster et al., 2016). The affinities of *Amphicoelias altus* (Cope, 1877b), although generally found inside Diplodocoidea, also remain uncertain, with different analyses grouping this taxon in different clades within Diplodocoidea (e.g., Whitlock, 2011a; Tschopp et al., 2015; Mannion et al., 2021).

One of the more complete non-diplodocimorph diplodocoid taxa is *Haplocanthosaurus*. *Haplocanthosaurus* currently comprises two species, *Haplocanthosaurus priscus* (Hatcher, 1903) and *Haplocanthosaurus delfsi* (McIntosh and Williams, 1981) and has proven to be a problematic taxon throughout most sauropod phylogenetic analyses. Various analyses have recovered *Haplocanthosaurus* as a macronarian (Upchurch, 1995; Wilson and Sereno, 1998; Upchurch et al., 2004a), a non-neosauropod eusauropod (Upchurch, 1998, 1999; Rauhut et al., 2005; Harris, 2006c), and a basal neosauropod (Harris and Dodson, 2004), although most analyses favor a non-diplodocimorph diplodocoid placement (Wilson, 2002; Salgado et al., 2004; Barco et al., 2005, 2006; Salgado et al., 2006; Lovelace et al., 2007; Whitlock, 2011a; Tschopp and Mateus, 2013, 2017; Tschopp et al., 2015; Whitlock and Wilson Mantilla, 2020; Mannion et al., 2021). However, recently,

TABLE 5. List of all currently valid diplodocoid species with uncertain phylogenetic placements.

Taxon	Holotype	Comment	Reference
Dystrophaeus viaemalae Cope, 1877a	USNM 2364	Type species	Tschopp et al., 2015
Amphicoelias altus Cope, 1877b	AMNH FARB 5764	Type species	Mannion et al., 2021
*Haplocanthosaurus priscu*s Hatcher, 1903	CM 572	Type species	Tschopp et al., 2015; Mannion et al., 2021; Boisvert et al., 2024
Haplocanthosaurus delfsi McIntosh and Williams, 1981	CMNH 10380		Mannion et al., 2021
Dyslocosaurus polyonychius McIntosh, Coombs, and Russell, 1992	AC 663	Type species	Tschopp et al., 2015

some analyses have again favored non-diplodocoid positions for *Haplocanthosaurus* (Bajpai et al., 2023; Gomez et al., 2024b).

Several other diplodocoid taxa were erected during the 1900s. Formerly considered to be an apatosaurine, *“Apatosaurus” minimus* (Mook, 1917) consists solely of a sacrum and a pelvic girdle. Currently, this species is thought to represent some form of macronarian sauropod (Upchurch et al., 2004a; Tschopp et al., 2015), though its affinities remain uncertain (Taylor and Wedel, 2012; Mannion et al., 2021). Although diplodocoid affinities have been suggested for the European taxon *Cetiosauriscus stewarti* (e.g., Upchurch et al., 2004a), more recent analyses place it as a non-neosauropod eusauropod (e.g., Tschopp et al., 2015; Schwarz et al., 2020). In earlier analyses investigating (diplodocoid) sauropod interrelationships, the Mongolian taxa *Nemegtosaurus* and *Quaesitosaurus* were placed in Diplodocoidea (Upchurch, 1995, 1998, 1999; Upchurch et al., 2004a); these are currently considered to be lithostrotian titanosaurs (e.g., Wilson, 2002, 2005; Filippi et al., 2024). The Portuguese sauropod *Apatosaurus alenquerensis* was erected by Lapparent and Zbyszewski (1957) and later referred to *Camarasaurus* by McIntosh (1990b). Dantas et al. (1998) erected a new genus for the species, *Lourinhasaurus*, and subsequent analyses have shown basal macronarian affinities for *Lourinhasaurus alenquerensis* (e.g., Mocho et al., 2014; Tschopp et al., 2015). *Dyslocosaurus polyonychius* was originally described as a diplodocid diplodocoid (McIntosh et al., 1992), but reanalysis has shown that it is more likely to be a dicraeosaurid diplodocoid (Tschopp et al., 2015).

In the last 25 years, interrelationships of diplodocoid sauropods have been more thoroughly studied, such that few new taxa have been erected with dubious affinities to the clade. *Losillasaurus giganteus* was a basal diplodocoid (Casanovas et al., 2001), but is currently placed in Turiasauria (e.g., Royo-Torres et al., 2021). *Galvesaurus herreroi* from Spain was placed in Diplodocoidea in its initial description (Barco et al., 2005) but is currently thought to be a brachiosaurid macronarian (Barco et al., 2006; Pérez-Pueyo et al., 2019). Most recently, the Tendaguru sauropod *Australodocus bohetii* (Remes, 2007) was described as a diplodocine diplodocoid but is currently considered to represent a titanosauriform sauropod (Whitlock, 2011a, 2011c; Mannion et al., 2013; Mannion et al., 2019).

OVERVIEW OF DIPLODOCOID MORPHOLOGY

Diplodocoid sauropods can be distinguished from other sauropods based on a series of postcranial features, as well as potentially some cranial traits. The latter, however, hinges on the unknown cranial morphology and still debated phylogenetic position of *Haplocanthosaurus*. Consequently, the following cranial synapomorphies could be either valid for Diplodocoidea or Diplodocimorpha.

The premaxilla of diplodocoid (or diplodocimorph) sauropods is an elongate unit with a straight ascending process in lateral view, which is not separated from the tooth-bearing portion by a step. This ascending process of the premaxilla connects to the dorsal process of the maxilla, which reaches more posteriorly than the posterior process of the same bone. The nasal opening is retracted dorsally, and relatively small, whereas the antorbital fenestra is large relative to the orbit. The entire rear part of the skull is tilted and the snout elongated and rather squared. This results from an oblique orientation of the quadrate and the basipterygoid processes on the parabasisphenoid in relation to the skull roof, as well as an elongation of the basipterygoid processes, the ectopterygoid flanges on the pterygoid, and anterior rami of the quadratojugals. Moreover, the jugal contributes to the antorbital fenestra, and there are multiple generations of pencil-shaped replacement teeth present in the jaws. The teeth do not occlude (possible exception of *Nigersaurus*, see Sereno and Wilson, 2005; Canudo et al., 2018), and their wear produced one or two planar facets on the tooth apex (Berman and McIntosh, 1978; McIntosh, 1990b; Calvo and Salgado, 1995; Upchurch, 1995; Wilson, 2002; Upchurch et al., 2004a; Rauhut et al., 2005; Tschopp et al., 2015). Postcranial synapomorphies include short cervical ribs and an obliquely oriented fibular facet on the astragalus (Berman and McIntosh, 1978; Tschopp et al., 2015).

Gross morphology of cervical vertebrae is among the most distinctive difference among diplodocoids (Figure 3). More basal forms, such as *Haplocanthosaurus* (Figure 3A) and rebbachisaurids show an unsplit neural spine. In Dicraeosauridae, Apatosaurinae, and Diplodocinae, the neural spines are split into two metapophyses. Dicraeosaurid cervical vertebrae are smaller in absolute terms, lack deep invasive pneumatic structures, and show dorsoventral elongation of the hemispinous processes (Figure 3B), with extremes seen in *Amargasaurus* and *Bajadasaurus*. The cervical vertebrae of apatosaurines (Figure 3C) are far more robustly constructed than those of diplodocines and are notable especially for their tall neural arches and very deep and robust cervical ribs. In diplodocines (Figure 3D), the cervical vertebrae are more slender and anteroposteriorly elongated, showing extreme lengths in *Barosaurus* and *Supersaurus*. Both rebbachisaurids, apatosaurines and diplodocines independently evolved more complex laminar structures, whereas the ‘simpler’ morphology was retained in *Haplocanthosaurus* and the dicraeosaurids.

Rebbachisaurid skulls (mostly known from *Limaysaurus, Nigersaurus,* and *Lavocatisaurus*; Calvo and Salgado, 1995; Sereno et al., 2007; Canudo et al., 2018) are characterized by an elongate jugal, which articulates with the squamosal, which is ventrally expanded (Canudo et al., 2018; Salgado et al., 2022). In this way, the postorbital is not delimiting the infratemporal fenestra as it does in Flagellicaudata (Tschopp and Mateus, 2013, 2017; Canudo et al., 2018; Garderes et al., 2023). The skull roof is closed – lacking a frontoparietal foramen – except for *Sidersaura* (Lerzo et al., 2024a). The postcranial skeleton is characterized by racquet-shaped scapular blades and a hook-like acromion process, and tetralaminated and petal-shaped middle to posterior dorsal neural spines (Haluza et al., 2012; Salgado et al., 2022; Lerzo et al., 2024a). Rebbachisaurids present extreme postcranial pneumatization. Within Diplodocoidea, Rebbachisauridae is the only clade that presents a laterodiapophyseal fossa/fenestra and an intradiapophyseal chamber in the dorsal vertebrae (Ibiricu et al., 2013, 2015, 2017; Lerzo et al., 2024b). The pneumatization is extended to anterior to middle caudal vertebrae and invades the pelvic girdle (Fanti et al., 2015; Ibiricu et al., 2017). Indeed, the most recent phylogenetic analyses of the group recovered the camerate pneumatization of the ilium as one of the synapomorphies of Rebbachisauridae (Lerzo et al., 2024a, 2024b).

Skull features that unite all dicraeosaurids as recovered by the analysis of Whitlock and Wilson Mantilla (2020) include the presence of a large foramen posterior to the anterior maxillary foramen, dorsal to preantorbital fossa on the maxilla; a reduced or absent preantorbital fenestra; a prominent, ventrally directed ‘prong’ on the posteroventral margin of the squamosal; distance of the supratemporal fenestrae of the parietal are greater than 1.5 the length of the supratemporal fenestrae; the presence of a postparietal foramen; a nearly flat distal margin of the paroccipital processes; maximum diameter of the supratemporal fenestra is equal to the greatest length of the foramen magnum; the sagittal nuchal crest of the supraoccipital is narrow and distinct; the crista prootica is expanded laterally into a distinct sheet-like process; the basipterygoid processes diverge narrowly; and the basioccipital depression between the foramen magnum and basal tubera is absent. Postcranial characteristics recovered by the same analysis include the presence of an epipophyseal-prezygapophyseal lamina in the anterior cervical vertebrae; a dorsally divided centroprezygapophyseal lamina in the middle and posterior cervical vertebrae, whereby the medial branch connects to the intraprezygapophyseal lamina, and not to the prezygapophysis; and the bifid neural spines in the posterior cervical and anterior dorsal vertebrae are narrow, parallel to converging.

Apatosaurines are immediately distinguishable from other diplodocoids because of their much heavier build (Wilhite, 2005). Their humeri, for example, are far more robust than those of most diplodocines (although *Galeamopus pabsti* is an exception: see Tschopp and Mateus, 2017, figures 60-61). The most distinctive apatosaurine feature is the neck, the vertebrae of which are topologically similar to those of diplodocines – bifid neural spines after the first few cervicals, similar lamination – but constructed more robustly and are far taller dorsoventrally, partly because the cervical ribs are suspended so far below the centra. For example, the cervical vertebrae of *Apatosaurus*

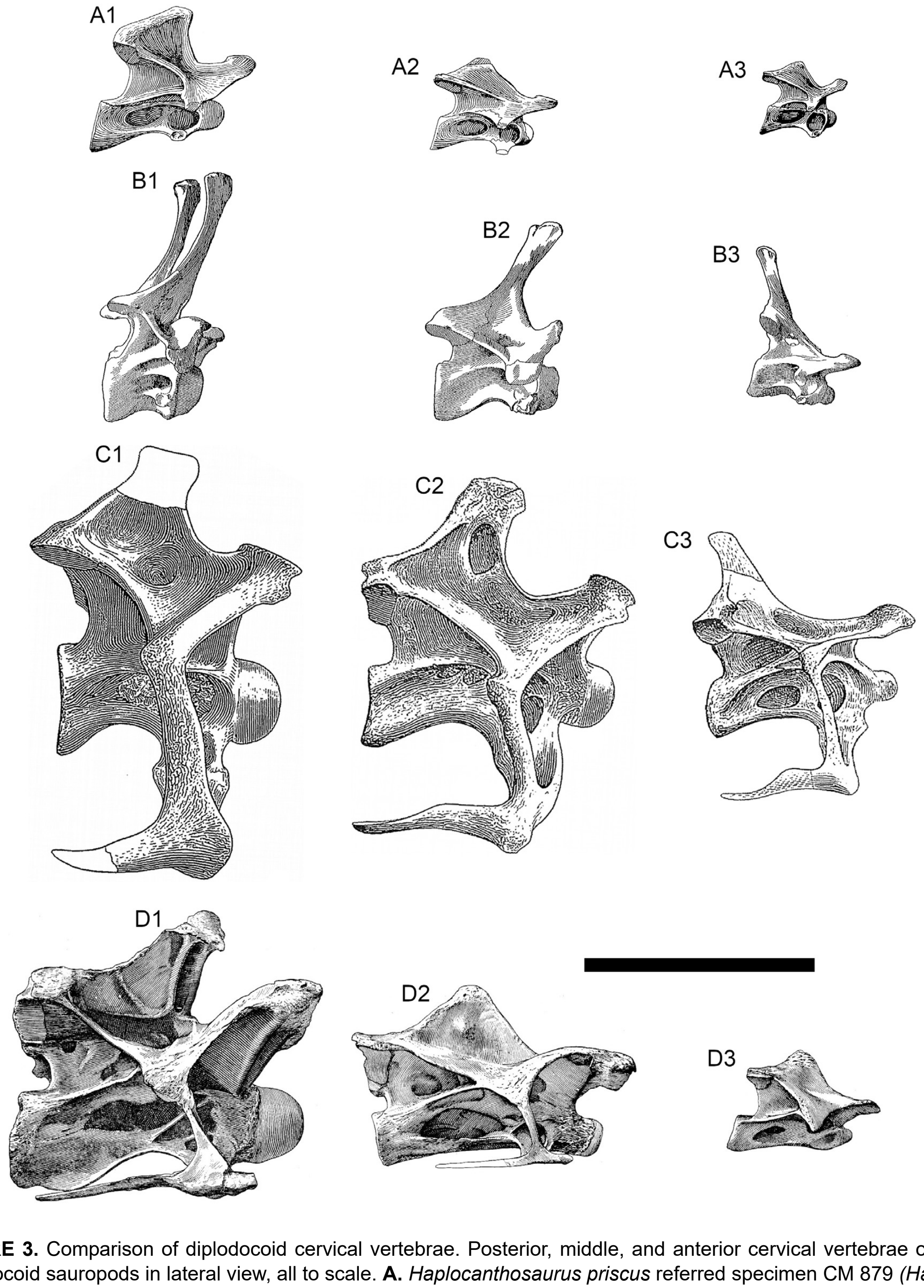


FIGURE 3. Comparison of diplodocoid cervical vertebrae. Posterior, middle, and anterior cervical vertebrae of four diplodocoid sauropods in lateral view, all to scale. **A.** *Haplocanthosaurus priscus* referred specimen CM 879 *(Haplocanthosaurus utterbacki* of Hatcher's usage), right lateral view, modified from Hatcher (1903, plate II): A1 = Cv13, A2 = Cv8, A3 = Cv4. **B.** *Dicraeosaurus hansemanni* holotype MB.R.4886, right lateral view, modified from Janensch (1929b, plate I): D1 = Cv11, D2 = Cv7, D3 = C3. **C.** *Apatosaurus louisae* holotype CM 3018, left lateral view (reversed), modified from Gilmore (1936, plate XXIV): C1 = Cv13, C2 = Cv8, C3 = Cv4. **D.** *Diplodocus carnegii* holotype CM 84, right lateral view, modified from Hatcher (1901, plate III): B1 = Cv14, B2 = Cv8, B3 = Cv4. Scale bar equals 50 cm.

louisae CM 3018 are about 85% as long as those of *Diplodocus carnegii* CM 84, but nearly twice as tall from the tip of the high neural spine to the lowest point of the attachment of the cervical ribs to the capitulum (Figure 3C, D). Similarly, the cervical vertebrae of apatosaurines are much wider than in diplodocines: compare Gilmore (1936, plate XXIV) with Hatcher (1901, plate V).

In the analysis of Tschopp et al. (2015), the clade Apatosaurinae was supported by six synapomorphies, four of them in cervical vertebrae: paired pneumatic fossae absent from ventral surface of anterior cervical vertebrae; postzygapophyseal centrodiapophyseal fossa extends onto posterior face of transverse process in cervical vertebrae; cervical ribs projecting well beneath centrum; anterior process of posterior cervical ribs reduced to a short bump-like process or absent; postspinal lamina or rugosity terminates at or beneath dorsal margin of neural spine in anterior caudals; rectangular anteroventral margin of coracoid. More derived apatosaurines were separated from the most basal, *“Atlantosaurus” immanis,* by 14 additional synapomorphies, so that the group of well-recognized apatosaurs is separated from the sister group Diplodocinae by 20 characters.

Diplodocines can be morphologically distinguished from most other flagellicaudatans by a generally more strongly developed postcranial pneumatization of the vertebral column and often elongate mid-cervical and mid-caudal vertebral centra. Additionally, most diplodocines have rather gracile limbs, except for *Galeamopus* (McIntosh, 1990a, 1990b, 2005; Tschopp et al., 2015, 2019; Tschopp and Mateus, 2017). Synapomorphic features found to represent Diplodocinae by Tschopp et al. (2015) include one cranial and several postcranial traits. The only cranial synapomorphy found by Tschopp et al. (2015) were box-like basal tubera. The proposed postcranial synapomorphies were dorsally elongate coels on posterior cervical neural spines; convex prezygapophyseal facets in mid- and posterior cervical vertebrae (not flat, as erroneously stated in Tschopp et al., 2015, p. 249); relatively weakly developed triangular aliform processes on mid- and posterior dorsal neural spines, which do not project as far laterally as their respective postzygapophyses; parapophyseal centrodiapophyseal fossae that are deeply excavated and triangular in posterior dorsal neural arches; ‘fan’-shaped caudal ribs that transition to ‘normal’ caudal ribs between caudal vertebrae 6 and 7, or more posteriorly; triangular lateral processes on caudal neural spines; a posteriorly displaced scapular acromial process, lying nearly at midpoint of the scapular body; a pubis that contributes equally or more to the acetabular opening compared to the ischium; an elongate muscle scar on the ischial shaft; a subtriangular proximal articular surface of the tibia; and several foramina marking the dorsal/anterior surface of the metatarsal I. The validity of some of these synapomorphies was questioned by Whitlock and Wilson Mantilla (2020), however, in part because their analysis recovered *Kaatedocus siberi* as a dicraeosaurid, whereas Tschopp et al. (2015) recovered this species as a diplodocine.

ECOLOGY AND ONTOGENY OF DIPLODOCOIDS

Ecology

Diplodocoids are generally characterized by an anteroposteriorly elongated skull and teeth with peg-shaped crowns (Upchurch and Barrett, 2000), all of which differ from the non-titanosaurian macronarian cranial conditions (e.g., Wilson and Sereno, 1998; D’Emic et al., 2013; Button et al., 2014; Peterson et al., 2022). The necks of diplodocoids, as in other sauropods, supported energy-efficient feeding as the animal would need to move less to gather food (Stevens and Parrish, 1999; Sander, 2013; Woodruff, 2016).

Diplodocoidea, as herbivorous dinosaurs, co-occurred with other herbivores like macronarian sauropods and ornithischian dinosaurs (Paulina Carabajal et al., 2014; Foster, 2020; Melstrom et al., 2021). Contrary to the general belief that all herbivores found in e.g., the Morrison Formation and the Tendaguru beds are coeval or even coexisting, only a fraction of the found taxa would share the same environment, due to the extensive temporal and spatial distribution of these fossils within these formations (Aberhan et al., 2002; Maidment, 2024). For example, Aberhan et al. (2002) list *Dicraeosaurus hansemanni,* the macronarian *Giraffatitan*, and the stegosaur *Kentrosaurus* as co-occurring in the Middle Saurian bed, whereas *Dicraeosaurus sattleri* and *Tornieria* (referred as *Barosaurus africanus*, prior to the revision of Remes, 2006) appear only in the Upper Saurian Bed, suggesting two ecosystems of different ages and faunal compositions. More prominent, the faunal compositions in the Morrison Formation are not only separated by time but also by different types of segregation (Maidment, 2024). Whereas *Apatosaurus, Diplodocus,* and *Camarasaurus* are abundant and found in several different localities (Foster, 2020), examples like *Kaatedocus*, *Suu-*

wassea, and the stegosaur *Hesperosaurus* seem to be restricted to the northern regions and systems tracts of different age (Maidment, 2024). Regardless, the occurrence of several large herbivores might result in competition for food sources. Niche partitioning, which has been proposed several times for these ecosystems (e.g., Fiorillo, 1998; Upchurch and Barrett, 2000; Hummel and Claus, 2011; Whitlock, 2011b; McHugh, 2018) could explain the sustainability of an ecosystem with several large herbivores of different clades.

Although diplodocoids are generally considered to prefer low- to medium-level browsing (Stevens and Parrish, 1999; Whitlock, 2011b), there are noteworthy specializations on certain feeding strategies in the large groups of Diplodocimorpha. Examples of such adaptations can be seen in the diversity of skull morphologies (Figure 4), the microwear of teeth combined with a rapid tooth replacement rate (D´Emic et al., 2013; Hummel and Claus, 2011; Whitlock, 2011b; Melstrom et al., 2021), and the anatomy of the cervical region, which is connected to the osteological neutral position and the range of motion of the cervical series (Stevens and Parrish, 1999; Christian and Dzemnski, 2011; Taylor, 2014; Peterson et al., 2022).

Rebbachisauridae

Rebbachisaurids are generally considered to be small- to medium-sized (Salgado et al., 2022) with total body length estimates for *Nigersaurus* between 9 m (Sereno et al., 2007) and possibly 15 m (Sereno et al., 1999; Mannion, 2009) and *Rebbachisaurus* similar in size to some dicraeosaurids (Wilson and Allain, 2015). Rebbachisaurid cranial remains are sparse, even compared to the other families in Diplodocoidea. However, based on the known skulls and their size, their diet is more likely connected to low-level browsing. The potentially most drastic adaptation for low-level browsing in any diplodocoid skull is found in *Nigersaurus taqueti* from the Lower Cretaceous Elrhaz Formation of Niger (Sereno et al., 1999). This species had tooth batteries housed in the anterior-most section of the snout. Although often described as a "dental battery" similar to those in ornithischian dinosaurs (Sereno and Wilson, 2005), the ornithischian dental battery is composed of extensive, overlapping tooth rows that work in unison to create a large slicing and grinding surface (Erickson et al., 2012). Conversely, the elongated single upper and lower tooth rows of *N. taqueti* are sensu stricto not a "battery." The reconstructed neutral cranial posture (and subsequent cervical posture), derived from the orientation of the semicircular canals observed in the endocast of the holotype, results in a downward orientation of the muzzle (Sereno et al., 2007). Whitlock (2011b) supports the finding of *N. taqueti* as a low-level browsing animal, which could be compared today with grazing mammals (Sereno et al., 2007).

Another important taxon for inferring feeding strategies within Rebbachisauridae is *Lavocatisaurus agrioensis* (Canudo et al., 2018) from the Lower Cretaceous Rayoso Formation of Argentina. Canudo et al. (2018) recovered *L. agrioensis* in a more stemward phylogenetic position than *N. taqueti*. *L. agrioensis* has a different morphology of the snout and positioning of the teeth compared to *N. taqueti*. The microwear of the teeth differs in *L. agrioensis* from *N. taqueti* resulting in a different method of biting (Canudo et al., 2018), implying a different preferred level of browsing, which is less specialized than more derived rebbachisaurids.

Dicraeosauridae

Several dicraeosaurid species are known from both cranial and postcranial remains. The cranial remains of *Dicraeosaurus hansemanni* (Janensch, 1914), from the Tendaguru beds (Upper Jurassic) of Tanzania and those of *Amargasaurus cazaui* (Salgado and Bonaparte, 1991), from the Lower Cretaceous La Amarga Formation of Argentina, suggest that dicraeosaurids were adapted for low to mid-level browsing (Whitlock 2011b; Paulina Carabajal et al., 2014; Schwarz et al., 2015). This corresponds with their general small to medium body size, as exemplary body size estimates reach between 9 m in *Amargasaurus* (Mazzetta et al., 2004) and 12 m in *Dicraeosaurus* (Schwarz et al., 2015), as well as the comparatively small necks and more robust morphology in contrast to diplodocids (Gallina, 2022). Whitlock (2011b) proposed that dicraeosaurids favored more forested ecosystems, rather than savannah-type ecosystems. A thoroughly studied dicraeosaurid regarding feeding strategies is *D. hansemanni* (Whitlock, 2011b; Schwarz et al., 2015). *D. hansemanni* is considered to be a mid-level browser, which is supported by the results of carbon isotope analysis by Tütken (2011). Schwarz et al. (2015) suggested that *D. hansemanni* fed specifically on lower mid-level foliage and speculated on the possible use of the tongue for feeding.

A bizarre example of the diversity of ecological niches in dicraeosaurids is *Brachytrachelopan mesai* (Rauhut et al., 2005) from the Upper Juras-

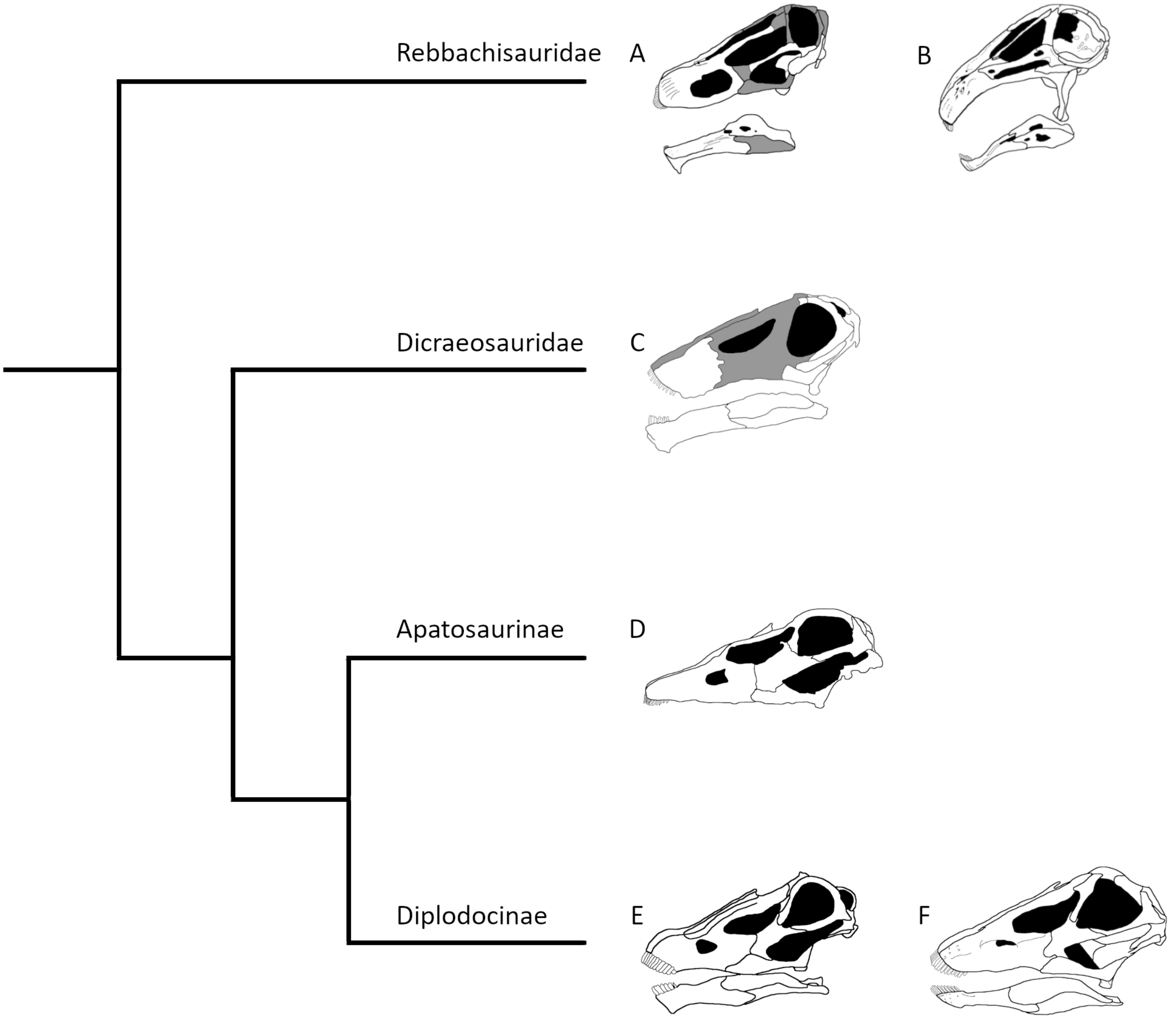


FIGURE 4. Skull morphology in Diplodocimorpha. **A.** *Lavocatisaurus agrioensis* MOZ-Pv1232 (modified from Canudo et al., 2018). **B.** *Nigersaurus taqueti* MNN GAD512 (modified from Sereno et al., 2007). **C.** *Bajadasaurus pronuspinax* MMCh-PV 75 (modified from Garderes et al., 2023). **D.** *Apatosaurus* skull CM 11162 (modified from Carpenter, 2010). **E.** Diplodocine skull CM 11161 (modified from Woodruff et al., 2018). **F.** *Galeamopus pabsti* NMZ 1000011 (modified from Tschopp and Mateus, 2017). Skulls are not to scale. Missing elements in grey.

sic Cañadón Calcáreo Formation of Argentina. *B. mesai* is estimated to be less than 10 m long and has, compared to other diplodocoids, extremely anteroposteriorly shortened cervical vertebrae (Rauhut et al., 2005). Rauhut et al. (2005) suggested that this morphology paired with a restricted dorsiflexion of the cervical series might be an adaptation to the lowermost level of browsing (Rauhut et al., 2005). Based on the phylogenetic position of *B. mesai* and other dicraeosaurids (such as *Lingwulong shenqi*, Xu et al., 2018), this clade in general evolved shortened cervical series.

Diplodocidae

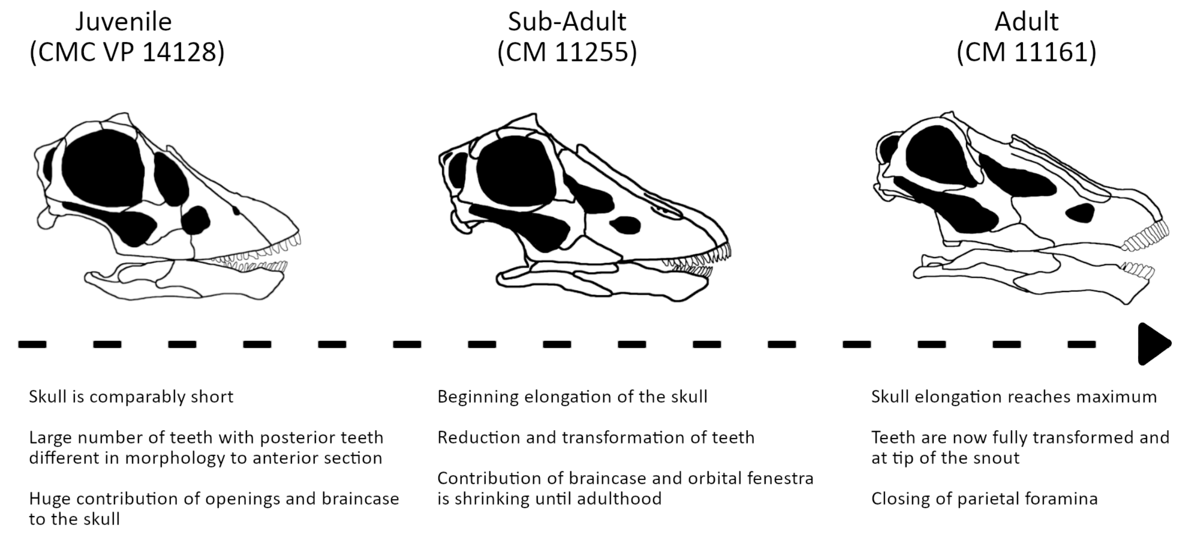
Diplodocids show a large range of total body lengths. Smaller taxa like *Kaatedocus* (assuming diplodocid affinities) are estimated at 14 m in length (Tschopp and Mateus, 2013) whereas larger taxa like *Diplodocus* and *Supersaurus* are found to reach body lengths beyond 25 m (Woodruff et al., 2024). Several diplodocid species are represented by well-preserved cranial and axial remains (see Tschopp et al., 2015), which can be studied to reconstruct their feeding strategies. *Diplodocus* (Marsh, 1878), was studied extensively regarding its ecology and diet (e.g., Fiorillo, 1998; Tütken, 2011; Whitlock 2011b, 2017; Young et al., 2012; Price and Whitlock, 2022) which can be generally summarized as follows: 1) *Diplodocus* seems to have preferred a diet of low-level vegetation based on analysis of $\delta^{13}C$ isotopes (Tütken, 2011), further supported by neck posture and dental microwear (Stevens and Parrish, 1999; Tütken, 2011; Whitlock, 2011b); 2) recent analyses suggest that the bite was orthal and used for cutting/cropping, rather than the historical portrayal of stripping leafy foliage (Price and Whitlock, 2022); and 3) additionally, the elongation of the skull is connected to accumulating more food rather than reducing stress while feeding (Young et al., 2012).

Conversely, *Apatosaurus* appears to differ from *Diplodocus*, which might support the niche partitioning within diplodocids (Peterson et al., 2022). A recently studied *Apatosaurus* skull (TATE-099) by Peterson et al. (2022) underlined that apatosaurines had a larger capacity of replacement teeth than *Diplodocus*. That capacity, noted especially for the premaxillae, is only eclipsed by *Nigersaurus* (Peterson et al., 2022). This variation in replacement teeth was suggested by McHugh (2018) and Peterson et al. (2022) to indicate that *Apatosaurus* fed on tougher vegetation than *Diplodocus*. Tütken (2011) noted a higher value of $\delta^{13}C$ isotopes in *Apatosaurus* than in *Diplodocus* teeth, further supporting different dietary preferences. Tütken (2011) also noted that seasonal and ontogenetic shifts in the diet of sauropods need to be considered when analyzing the diet of the tested taxa. Such shifts seemed to be a crucial factor in the life cycle of diplodocoids (Whitlock et al., 2010; Woodruff et al., 2018).

Ontogeny

Griffin et al. (2021) suggested that when using the concept of ontogenetic stages, a combination of independent proxies is more beneficial in delimiting maturational ranges. At first glance, the seemingly low amount of fossil remains of immature diplodocoids contradicts estimates of their percentage in the total population of their ecosystem (Farlow et al., 2022). However, as exemplified by the ceratopsian *Triceratops*, specimens that were historically thought to represent the ‘adult morphological condition’ have since been osteohistologically demonstrated to have been ‘subadults’ (Scannella and Horner, 2010). Likely the same holds true for most iconic, museum-mounted sauropod taxa (although this needs osteohistological verification), but former maturational assumptions, a rapid growth rate during early ontogeny, and potentially a high predator-driven mortality rate during early ontogeny, are all factors that contribute to our paucity of exceptionally small-statured (i.e., ‘baby’) diplodocoids. Nevertheless, some studies have been able to trace important ontogenetic patterns and developmental pathways in Diplodocoidea, especially diplodocids (e.g., Curry, 1999; Klein and Sander, 2008; Whitlock et al., 2010; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Woodruff et al., 2017, 2018, Waskow, 2019; Wiersma-Weyand et al., 2021).

Although less common, smaller-statured, immature diplodocoids are known from the Morrison Formation and assigned to flagellicaudatans like *Apatosaurus, Barosaurus, Diplodocus, Kaatedocus,* and *Suuwassea* (e.g., Curtice and Wilhite, 1996; Harris and Dodson, 2004; Foster, 2005; Whitlock et al., 2010; Tschopp and Mateus, 2013; Melstrom et al., 2016; Hanik et al., 2017); although relative body size has primarily served as the means for generalizing a specimen’s maturation. Though osteohistological analyses have not yet been conducted, several diplodocoid holotypes (e.g., the apatosaurine *“Elosaurus” parvus* [Peterson and Gilmore, 1902], the diplodocine *Kaatedocus siberi*, and *Smitanosaurus agilis* [Whitlock and Wilson-Mantilla, 2020]) are likely not skeletally mature. However, taxonomic referral of immature specimens is challenging (Woodruff, 2019) and some studies questioned the validity of certain taxa (see Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Tschopp et al., 2015). The lack of skeletal maturity and full osteological development may lead to the potential absence of apomorphies which are needed for a clear taxonomic assignment, leading to a different phylogenetic position categorically (Tschopp et al., 2015). Similar to the increasing skeletal pneumaticity and complexity of vertebrae through ontogenetic stages (Wedel, 2007; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Tschopp and Mateus, 2017; Woodruff et al., 2017), heterochrony seems to be a large factor in the growth of sauropods. For instance, the skull changes in variable dimensions throughout growth (Figure 5); a prime example of allometric, not isometric, development in sauropods (Salgado, 1999; Whitlock et al., 2010; Tschopp and Mateus, 2017; Woodruff et al., 2018; Fabbri et al., 2021). These changes might also be linked to shifts in the ecological niche as their size restricts the potential food sources (Woodruff et al., 2018). But as exemplified by the allometry of the skull, an organism that hatched out of an approximately cantaloupe-sized egg (13-15 cm in diameter; Chiappe et al.,



Skull is comparably short

Large number of teeth with posterior teeth different in morphology to anterior section

Huge contribution of openings and braincase to the skull

Beginning elongation of the skull

Reduction and transformation of teeth

Contribution of braincase and orbital fenestra is shrinking until adulthood

Skull elongation reaches maximum

Teeth are now fully transformed and at tip of the snout

Closing of parietal foramina

FIGURE 5. Transformation of the cranial bones in diplodocids with noted trends from Whitlock et al. (2010) and Woodruff et al. (2018). Skulls are modified after Woodruff et al. (2018).

1998) and grows to more than 25 m in body length in some cases (Woodruff et al., 2024), is expected to show numerous, variable degrees of ontogenetic changes throughout the skeleton towards adulthood.

Taxonomic assignments are difficult when dealing with unique immature diplodocids that have no readily evident adult counterpart. In several documented cases, cranial remains in particular have been challenging to taxonomically identify. CM 11255, which consists of an isolated skull (Holland, 1924; Whitlock et al., 2010), is considered to be either a specimen of *Diplodocus* or *Barosaurus* (Whitlock et al., 2010; Woodruff et al., 2018). Another skull, CMC VP 14128 was found together with some cervical material and is referred to cf. *Diplodocus* (Woodruff et al., 2018). However, several diplodocine taxa are not yet known by cranial remains. For example, there is no unambiguous specimen of *Diplodocus* with a clear association of a skull and a postcranial skeleton (Tschopp et al., 2015; Woodruff et al., 2018); therefore, an unquestionable assignment to *Diplodocus* or *Barosaurus* based strictly on cranial material is not yet possible. However, other juvenile diplodocids, like CM 79038 and DINO 2921, are known from vertebrae and appendicular remains which could be compared and assigned to *Barosaurus* (Melstrom et al., 2016; Hanik et al., 2017).

Subadult diplodocoid specimens, as evident by morphological and osteohistological examinations, are known in *Kaatedocus siberi* (morphological), *Nigersaurus taqueti*, and *Suuwassea emilieae* (osteohistological) which have nevertheless developed enough morphologies to be differentiated from known taxa (Hedrick et al., 2014; Tschopp and Mateus, 2013; Wedel and Taylor, 2013; Tschopp et al., 2015). However, as the holotypes of *Kaatedocus* and *Suuwassea* are incomplete and show features known from both immature diplodocoids and dicraeosaurids, their phylogenetic position remains debated (Harris, 2006c; Whitlock, 2011a; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Tschopp et al., 2015; Whitlock and Wilson-Mantilla, 2020). Until a series of ontogenetic stages of a taxon is known, repositionings of non-adult specimens must be expected, unless ontogenetic morphological characters are outweighed by characters with a connection to diagnostic features and no connection to ontogeny (Tschopp et al., 2015).

BIOGEOGRAPHY OF DIPLODOCOIDS

The earliest unambiguous diplodocoid sauropod remains represent the dicraeosaurid *Lingwulong*, from the Middle Jurassic of China (Xu et al., 2018). *Tharosaurus indicus* from the Middle Jurassic of India (Bajpai et al., 2023) may represent an even earlier diplodocoid, but its fragmentary nature sheds doubt on its dicraeosaurid affinities and thus the origins of Diplodocoidea. Other remains from the Callovian (latest Middle Jurassic) of western Eurasia may also represent indeterminate diplodocoids (Holwerda et al., 2019; Averianov and Zverkov, 2020). Additionally, fragmentary pedal elements from the Bathonian-Callovian of Mexico were assigned to Flagellicaudata (Rivera-Sylva and Espinosa-Arrubarrena, 2020), although the assignation of that material to the group is based on characters that may have a wider distribution and are likely not diagnostic at this level (Mannion and Whitlock, in press). An isolated tooth from the Bathonian of Madagascar has also been suggested as a potential diplodocoid (Bindellini and Dal Sasso, 2021), but identification of isolated teeth can be troublesome.

Late Jurassic sediments, by contrast, are relatively rich with diplodocoids and, in particular, flagellicaudatans. The Upper Jurassic Morrison Formation (Kimmeridgian-Tithonian) of North America is especially dense taxonomically, including the diplodocids *Amphicoelias* (Cope, 1877b), *Apatosaurus* (Marsh, 1877), *Barosaurus* (Marsh, 1890), *Brontosaurus* (Marsh, 1879; Tschopp et al., 2015), *Diplodocus* (Marsh, 1878), *Galeamopus* (Tschopp et al., 2015; Tschopp and Mateus, 2017), and *Supersaurus* (Jensen, 1985), the dicraeosaurids *Dyslocosaurus* (McIntosh et al., 1992; Tschopp et al., 2015), *Smitanosaurus* (Marsh, 1889; Whitlock and Wilson Mantilla, 2020), and *Suuwassea* (Harris and Dodson, 2004; Whitlock, 2011a), the putatively basal diplodocoid *Haplocanthosaurus* (Hatcher, 1903; Wilson, 2002; Whitlock, 2011a), the putative rebbachisaurid *Maraapunisaurus* (Carpenter, 2018, but see Carpenter, 2006 and Woodruff and Foster, 2014), and the flagellicaudatan *Kaatedocus* (Tschopp and Mateus, 2013, 2017; Tschopp et al., 2015; Whitlock and Wilson Mantilla, 2020). The Late Jurassic record of Portugal includes the diplodocid *Dinheirosaurus* (Bonaparte and Mateus, 1999; Mannion et al., 2012, but see Tschopp et al., 2015, Mannion et al., 2019, and Whitlock and Wilson Mantilla, 2020). Additional Late Jurassic diplodocoid material is known from Georgia and Spain (see Mannion et al., 2012 and references therein).

The Gondwanan Late Jurassic is less diverse, probably owing to a less extensive rock record. The Tendaguru Formation of Tanzania includes both the diplodocid *Tornieria* (Janensch, 1922) and the dicraeosaurid *Dicraeosaurus* (Janensch, 1914). The Upper Jurassic outcrops of Argentina have thus far only yielded the dicraeosaurid *Brachytrachelopan* (Rauhut et al., 2005), though more unnamed diplodocoid material is known from Argentina and Chile (Rauhut et al., 2015; Salgado et al., 2015). This situation is reversed in the Cretaceous, however, with limited Laurasian exposures (and accompanying reduction in fossil specimens), and radiation in Gondwanan taxa. There are no known North American Cretaceous diplodocoids. The probable rebbachisaurid *Xenoposeidon* is known from the Early Cretaceous of England (Taylor, 2018). *Histriasaurus* from the Early Cretaceous of Istria (Croatia) is also commonly recovered as a basal rebbachisaurid (Dalla Vecchia, 1998). Finally, the Spanish rebbachisaurid *Demandasaurus* (Pereda Suberbiola et al., 2003; Torcida Fernández-Baldor et al., 2011) is known from the Barremian-Aptian, making it the latest-appearing Laurasian diplodocoid.

The Gondwanan record is dominated by Argentinian fossils, including the latest-appearing members of both Diplodocidae and Dicraeosauridae. *Leinkupal*, from the late Berriasian-Valanginian (Early Cretaceous), is the only named diplodocid to have survived past the Jurassic (Gallina et al., 2014). The dicraeosaurid record is much richer, however, boasting the Early Cretaceous taxa *Amargasaurus* (Salgado and Bonaparte, 1991), *Amargatitanis* (Gallina, 2016; Whitlock and Wilson Mantilla, 2020), *Bajadasaurus* (Gallina et al., 2019) and *Pilmatueia* (Coria et al., 2018), comprising roughly one-third of known dicraeosaurid diversity. Rebbachisaurids primarily flourished in South America during this time, including two taxa from Brazil, the Aptian-Albian aged *Amazonsaurus* (Carvalho et al., 2003) and the Cenomanian *Itapeuasaurus* (Lindoso et al., 2019). The remainder of South American taxa are Argentinean, including *Agustinia* (Bellardini et al., 2022b), *Campananeyen* (Lerzo et al., 2024b), *Cathartesaura* (Gallina and Apesteguía, 2005), *Comahuesaurus* (Carballido et al., 2012), *Katepensaurus* (Ibiricu et al., 2013), *Lavocatisaurus* (Canudo et al., 2018), *Limaysaurus* (Calvo and Salgado, 1995), *Nopcsaspondylus* (Apesteguía, 2007), *Sidersaura* (Lerzo et al., 2024a), and *Zapalasaurus* (Salgado et al., 2006). The African Cretaceous record is less speciose but still contains the rebbachisaurids *Rebbachisaurus* (Lavocat, 1954), *Nigersaurus* (Sereno et al., 1999), and *Tataouinea* (Fanti et al., 2013), which belong to the same radiation (Rebbachisaurinae) as *Demandasaurus* and a handful of South American taxa. Additional unnamed remains belonging to dicraeosaurids and diplodocids have been reported from the Lower Cretaceous Kirkwood Formation of South Africa (McPhee et al., 2016).

Historically, the presence of early-diverging members of both Dicraeosauridae and Diplodocidae (and putatively Rebbachisauridae), as well as putative basal members lying outside of Diplodocimorpha (e.g., *Haplocanthosaurus, Amphicoelias)* has led some researchers to indicate North America as a center of origin for either Flagellicaudata or Diplodocoidea as a whole (i.e., Whitlock, 2011a; but see Remes, 2006 for a contrary opinion). The recent discovery of the derived dicraeosaurid *Lingwulong* from the late Middle Jurassic of China, however, casts some doubt on this hypothesis (Xu et al., 2018; Mannion et al., 2019; Bajpai et al., 2023), although as noted by those authors, a Laurasian origin for Flagellicaudata remains plausible. Under this scenario, Gondwanan appearances of flagellicaudatan sauropods would be the result of multiple excursions out of Laurasia (Whitlock, 2011a; Mannion et al., 2019). Multiple studies have suggested the presence of a distinctly Gondwanan clade within dicraeosaurids (e.g., Rauhut et al., 2005; Coria et al., 2019; Gallina et al., 2019; Whitlock and Wilson Mantilla, 2020), which would suggest geographic isolation of a lineage independent from the putatively more plesiomorphic North American forms. Similarly, a sister relationship between the Argentinean diplodocid *Leinkupal* and the African *Tornieria* has been posited (Mannion et al., 2019), which would be further evidence of expansion out of North America. The fragmentary sauropod *Tharosaurus*, being possibly the oldest flagellicaudatan, presents some challenges to a North American origin, however. Bajpai et al. (2023) argue for an Indian (and thus Gondwanan) origin for the clade through a pan-Pangean dispersal event. However, given the highly fragmentary nature of *Tharosaurus*, the evidence is somewhat thin and requires accepting several caveats to make this the most probable scenario. Nonetheless, it appears that the center of origin for Flagellicaudata is far from a settled question.

The origins of Rebbachisauridae have often been recovered as South American (e.g., Whitlock, 2011a; Carballido et al., 2012; Fanti et al., 2015), although there are several caveats to this. The first and most obvious is that the earliest occurrences of the group are Laurasian *(Histriasaurus, Maraapunisaurus,* and *Xenoposeidon),* as are the putatively most basal members of the more inclusive clade Diplodocoidea *(Amphicoelias, Haplocanthosaurus).* Additionally, the internal relationships of Rebbachisauridae point to a more complicated origin as well. Although limaysaurines (if monophyletic) appear to have been endemic to Patagonia (Whitlock, 2011a; Mannion et al., 2019), the sister clade Rebbachisaurinae was more cosmopolitan, boasting members from South America *(Katepensaurus,* possibly *Itapeuasaurus),* Africa *(Nigersaurus, Rebbachisaurus,* and *Tataouinea)* and Europe *(Demandasaurus).* Lerzo et al. (2024b) recover Nigersaurinae, synonymizing Limaysaurinae and Rebbachisaurinae, thus showing a different distribution of taxa among the rebbachisaurid subclades. However, all taxa outside Khebbashia are South American in Lerzo et al. (2024b), supporting a South American origin regardless of the change within interrelationships in Rebbachisauridae. The distribution of Rebbachisauridae is often thought to be the result of an “Apulian Route” between North Africa and Europe (Pereda Suberbiola et al., 2003; Gheerbrant and Rage, 2006; Canudo et al., 2009; Pereira et al., 2020; Lerzo et al., 2024b), with the European taxa being descendants from North African taxa, themselves being the result of a pre-Aptian dispersal into Africa from South America (Canudo et al., 2018; Lerzo et al., 2024b). This fits with current analyses placing the South American taxa *Amazonsaurus, Agustinia, Comahuesaurus,* and *Lavocatisaurus* as more basal members in Rebbachisauridae. However, given the probable Laurasian origins of the sister clade Flagellicaudata, and the timing of the first occurrence of members of the group, it remains possible (if less well supported by phylogeny at this time) that the known distribution of Rebbachisauridae is the result of dispersal into Gondwana out of Laurasia, as for flagellicaudatans.

LIFE APPEARANCE OF DIPLODOCOIDS

As our scientific knowledge of diplodocoids has expanded, so has our understanding of their life appearance. From their earliest life restorations, diplodocids (and all sauropods) were depicted as *Hippopotamus*-like behemoths that were restricted to aquatic realms given their immense girth (e.g., *Amphicoelias* reconstruction, see Osborn and Mook, 1921, figure 127). Although Phillips (1871) correctly noted anatomy indicative of an active terrestrial quadruped, given the then hypothesized taxonomic relationship between dinosaurs and reptiles, in 1910, O.P. Hay depicted the life restoration of *Diplodocus* with greatly splayed lizard-like limbs and locomotion (echoed by G. Tornier in 1909). Using drawings, anatomical dissections, scaled models, and even life-sized sauropod casts, this sprawling hypothesis was quickly challenged and put to rest by W.J. Holland later that same year. Although capable of some form of aquatic movements, we know now from extensive evidence, such as numerous global occurrences of trackways (e.g., Day et al., 2002; Santos et al., 2009; Calvo et al., 2022), that all sauropods expressed a graviportal, not sprawling stance, and were fully terrestrial (morphologically and ichnologically championed by Coombs, 1975).

Interestingly, the reconstruction of the external nares of diplodocids (and all sauropods) also derives from the historic aquatic hypothesis. Depicted as early as E.D. Cope's 1897 sketch, to C. Knight's 1897 scientific reconstruction, *Amphicoelias altus* was depicted with its long neck vertically outstretched in the water column with the head just above water level as a snorkel. In his later works, such as his 1907 depiction of a tripodally rearing *Diplodocus*, Knight reconstructed the external nares as medial to the orbits, occupying the actual bony nares. Unlike many of his contemporaries, Knight variably reconstructed the external nares in his sauropod reconstructions. In his 1897 *Amphicoelias* and his 1897, 1906, and 1939 *Diplodocus*, the nares are anteriorly positioned on the skull near the snout, whereas his 1897, 1929, and 1946 *Brontosaurus* and 1907 *Diplodocus* have external nares dorsally situated within the bony nares. Whereas many of the sauropod life reconstructions for much of the 20th Century had such dorsally situated external nares, Z. Burian's 1957 *Brachiosaurus* is likely the most iconic, and explicit, functional depiction of the position of the external nares as a snorkel.

In his same 1975 paper championing fully terrestrial sauropods, W.P. Coombs additionally noted the morphology of the bony nares in comparison to mammals. Though cautiously not advocating the idea, Coombs (1975) noted the morphology of the bony nares in sauropods was like that of elephants and tapirs; thus, a sauropod with a proboscis-like soft-tissue structure was not entirely implausible. Inspired by Coombs's (1975) observation between the bony nares of sauropods and elephants, Bakker (1986, p. 141) reconstructed a *Diplodocus* with an elephant-style trunk. The factual implausibilities of *Diplodocus* (and all sauropods) with elephantine trunks were examined and refuted by Knoll et al. (2006).

In a review of the bony nares in Dinosauria with respect to the external nares, Witmer (2001) proposed that the fleshy nostrils were contrarily located anteriorly on the skull near the tip of the 'snout'. Witmer (2001) cited evidence for this alternative positioning from the extant phylogenetic bracket, and importantly from osteological remnants of the nasal vestibular vascular plexus which all advocated for rostroventrally placed nares. Whereas the study of Witmer (2001) is of extreme importance to the life history reconstructions of all Dinosauria, pertinent to this volume is that the Witmer study was selected as the cover article for the Volume 293 Number 5531 issue of *Science*, and the cover art synthesizing these findings was of a rostroventrally fleshy nostriled *Diplodocus*.

Perhaps the most debated aspect of diplodocid reconstructions and function is the neck. Since the days of C. Knight's submersible *Brontosaurus*, diplodocids (and all sauropods) were historically reconstructed with a vertical, swan-like cervical series. Once sauropods were determined to be terrestrial, not aquatic organisms (Riggs, 1904; Bakker, 1971; Coombs, 1975), their bauplan was likened to that of giraffes (a similar comparison was made by Cope, 1877b). From then on, the hyperelongated cervical series was inferred to have evolved for feeding high in trees. This depiction of a vertically necked, canopy-feeding sauropod has become a classic cultural image (e.g., *Jurassic Park).*

Whereas the high-browsing sauropod depiction is an established cultural reference, the legitimacy of such cervical posturing was called into question by the studies of Martin (1987) and Stevens and Parrish (1999). Examining the degrees of cervical pre- and postzygapophyseal overlap of *Apatosaurus louisae* and *Diplodocus carnegii,* Stevens and Parrish (1999) concluded that the cervical series of diplodocids was incapable of being oriented in such a position. Instead, Stevens and Parrish (1999) proposed that in these diplodocids, the neck was habitually held at a more horizontal angle and that the cervical range of movement was primarily in a lateral plane. From such, Stevens and Parrish (1999) suggested that diplodocids like *Apatosaurus* and *Diplodocus* were alternatively low, not high, browsers. The study of Stevens and Parrish (1999) has been received with mixed academic opinions. However, the work of Stevens and Parrish (1999) has generated several analyses exploring numerous avenues of the neck posture debate (Upchurch, 2000; Christian, 2002; Stevens and Parrish, 2005a, 2005b; Christian and Dzemski, 2007; Dzemski and Christian, 2007; Sereno et al., 2007; Taylor et al., 2009; Christian, 2010; Clauss, 2011; Woodruff and Fowler, 2012; Cobley et al., 2013; Preuschoft and Klein, 2013; Stevens, 2013; Taylor and Wedel, 2013a; Taylor, 2014; Woodruff, 2016; Vidal et al., 2020a, 2020b). Whereas the topic of diplodocid (and all sauropods) neck posture is still the subject of investigation, we have at least reached a general agreement that the necks were not habitually held vertically. What might be tentatively deemed as a 'general consensus' is that diplodocids had a more horizontal habitual neck posture than their macronarian counterparts. More recently, both Stevens and Parrish (2005a) and Vidal et al. (2020a) advocated that contra the century-old idea that a long neck allowed sauropods to feed at greater vertical heights, as exemplified by the macronarian *Brachiosaurus*, placement of the shoulder girdle, and most importantly, increasing the length of the forelimbs automatically raises the head height (i.e., it is more effective to stand on a step stool as opposed to straining on your tiptoes with an outstretched arm). But pertinent to diplodocids, the study of Vidal et al. (2020b) recognized a new synapomorphy for Eusauropoda: a 10° anterodorsally oriented sacrum. By anterodorsally inclining the hips, the dorsal series is likewise raised, which is further expressed in the cervical series. Therefore, diplodocids may have exhibited some anterodorsally oriented postures simply from a shallow inclination of the pelvis. However, the low forelimb/hindlimb ratio observed in diplodocoids and vertebral angles in the cervico-dorsal transition (e.g., Tschopp et al., 2015) shows that this newly proposed synapomorphy must be studied further, as these factors may nullify the effect of the wedge-shaped sacrum.

Moving on from the head and neck, perhaps the most unique physical trait first recognized in diplodocids, which has since seemingly been ubiquitously applied to all Sauropoda, are the dermal scales. In 1992, S. Czerkas reported on sauropod integument from excavations at the Howe Quarry in Wyoming, USA. In addition to "pebbly" skin impressions, Czerkas (1992) documented a minimum of 14 conical to spine-like ornaments (then attributed to either *Diplodocus* or *Barosaurus*). Unlike an osteoderm, which has an osseous core with a keratinous sheath, these dermal spines had no osseous core (Czerkas, 1992), and instead appear to have been preserved as a three-dimensional carbonaceous structure infilled with sediment (E. Tschopp, personal obs., 2020) – the very thin carbonaceous layer presumably representing a diagenetically altered remnant of the original keratinous structure (Tschopp et al., 2020).

Although few of the reported 14 dermal spines were complete, Czerkas (1992) estimated the largest ones were approximately 18 cm in dorsoventral height. Regarding their morphology, Czerkas (1992) described them as quite variable; some were more mediolaterally compressed, while others were more conical, and some with straight and pointed apices, others with recurved apices. Czerkas (1992) claimed that while some of these conical dermal scales were found isolated, others were found associated, and others in semi-articulation, with caudal vertebrae. For the few in association/articulation, Czerkas (1992) reported they formed a single, midline row along the distalmost region of the caudal series. Czerkas (1992) reported that these dermal spines were thus far only known from the caudal region but given the distribution of similar structures in hadrosaurs (and in many extant lizards like *Iguana* spp.), he reconstructed a *Diplodocus* skeleton with these midline dermal spines running from the back of the skull continuously to the tip of the tail. Since Czerkas (1992), these midline dermal spines have been near ubiquitously reconstructed on all sauropods (not just diplodocids), with some being more conservative (such as the *Diplodocus* in *Walking with Dinosaurs),* to those with more artistic licensing being depicted nearly buzzsaw or mohawk-like. To date, no other sauropods have been documented with similar dermal spines, nor have any geochemical analyses been conducted on the specimens reported in Czerkas (1992). Whereas such integumentary reconstructions are likely in diplodocids (and any sauropod), much like the documented osteoderms in titanosaurs, patchworks or singular occurrences have been reconstructed more broadly anatomically and phylogenetically.

Unlike the extreme rarity of the dermal spines, both skin and skin impressions from Morrison Formation sauropods are known from several localities. Whereas skin impressions have been reported from the Morrison Formation – from tracks (though likely macronarian; Platt and Hasiotis, 2006) to isolated occurrences (such as one is tentatively referred to as "Sauropoda?"; Foster and Hunt-Foster, 2011) – there are well-documented examples in context with diplodocid remains. Czerkas (1992, 1994) reported on skin impressions and likely diagenetically altered skin from the Howe Quarry in Wyoming, USA. B. Brown noted the abundance of skin remains from the Howe Quarry in popular articles, and in one 1935 article he wrote, "Patches of skin impression, in many cases overlaid by the actual substance of the epidermal covering, were found all over the quarry in such profusion that much of it had to be destroyed in preparing the bones for shipment." Whereas only a few tiny fragments of this Brown-era skin survive, Czerkas (1994) reported on new material from the Howe Quarry collected by the Sauriermuseum Aathal during expeditions in 1990 and 1991. Czerkas (1994) states that the scales are polygonal in shape (pentagonal to heptagonal according to his drawing), do not overlap, and vary in size from less than 1 cm to over 3 cm.

Czerkas (1994) further mentions that some skin fragments from Dinosaur National Monument (DNM; Vernal, Utah, USA), that are presumed, given proximity, to belong to *Barosaurus* bear a resemblance to his reported Howe Quarry (HQ) material. Czerkas (1994) noted the similar large size of the polygonal, non-overlapping scales, and that the scales appeared to be arranged in an ornamental cluster. This ornamental cluster consisted of smaller scales surrounding progressively larger scales at the center (Czerkas, 1994). Additionally, on both the DNM and HQ specimens, Czerkas (1994; figures 2 and 4) shows that the large polygonal scales are each covered in a small, rounded, papilliform-like texture. Only one section of skin from the HQ reported by Czerkas (1994) appeared to be associated with skeletal remains, and Czerkas (1994) reported that it was from the belly region. In this sample, Czerkas (1994) reports that the scales are 2-3 cm in width, non-overlapping, and are not in an ornamental pattern as observed in the other examples.

Our best examples to date of how integument varies across the body of a diplodocid comes from the cf. *Diplodocus* reported by Gallagher et al. (2021). From an in-situ slab preserved potentially in association with dorsal ribs, Gallagher et al. (2021) documented up to six different scale morphologies. Gallagher et al. (2021) describe these scales as non-overlapping, and other than their size (likely an indication of the young maturation of the individuals from this quarry), some of the scale morphotypes are like those reported by Czerkas (1994). From comparisons to crocodilian skin, Gallagher et al. (2021) hypothesized the approximate location on the body. Gallagher et al. (2021) noted: 1) polygonal scales were the most common, with smaller scales (<5 mm) more ventral than the larger (>5 mm) dorsal scales; 2) pebble scales were the smallest observed (1-2 mm), and were located ventrally along the polygonal scales; 3) rectangular scales that varied from 2-10 mm in length, with these rectangular scales “abruptly” intersecting the ventral polygonal scales, creating a demarcated change in scale type; 4) irregular globular scales that had three-dimensional (3D) relief; 5) ovoid scales are the largest (~10 mm), have 3D relief as well, the pointed ends all face the same direction, and they also abruptly intersect the adjacent polygonal scales; and 6) domed scales which are also 3D, located near the ovoid scales, and come in two distinct sizes (5 mm and <5 mm). In a life reconstruction based on these samples, Gallagher et al. (2021) placed the large ovoid scales dorsally along the sacral-caudal transition, with the remaining scale types positioned laterally and ventral – all indicative of changing scale morphology across and along different regions of the body.

Although the research mainly focused on diplodocid diplodocoids, meaningful inferences can be made for Rebbachisauridae and Dicraeosauridae as well. Rebbachisaurids are generally characterized by small to large body sizes, see above, and show specialized skull forms (e.g., *Nigersaurus*). However, the lack of complete specimens has resulted in a poor understanding of their overall appearance. Possible skin impressions of rebbachisaurids have been discovered in trackways from the Candeleros Formation in Argentina, but the lack of associated skeletal material makes the referral ambiguous (Apesteguía et al., 2023). Dicraeosaurids are characterized by their relatively small body size (see ecology and ontogeny of diplodocoids) and their elongated cervical and dorsal neural spines, resulting in a ‘hump’ or ‘sail’ like structure (e.g., Janensch, 1914; Salgado and Bonaparte, 1991; Bailey, 1997; Rauhut et al., 2005; Xu et al., 2018). In at least two dicraeosaurid taxa, namely *Amargasaurus* and *Bajadasaurus*, the cervical region shows hyperelongated hemispinous processes, which have variably been reconstructed as being covered in keratinous sheaths (like a bovid horn), to support a sail of skin thinly stretched between the hemispinous processes, to variable combinations of ‘sail and spikes’. These – then unique – cervical spines of *Amargasaurus* made this taxon the first of what would popularly and generationally be referred to as “bizarre dinosaurs.” However, in 2022, Cerda et al. osteohistologically examined these hyperelongated hemispinous processes and demonstrated that in life, thin sheet muscles would have covered and anteroposteriorly spanned the entire hemispinous processes (though questions regarding the presence of connective tissues transversely between the bifurcated spines remain). Much like the historic reconstructions of external nares, examination and study of these bizarre vertebral structures upends decades-long popular notions and reconstructions; yet, despite the Cerda et al. (2022)

FIGURE 6. Collage of modern life-reconstruction of the main families in Diplodocoidea. From left to right and top to bottom: the rebbachisaurid *Nigersaurus*, the dicraeosaurid *Bajadasaurus*, the diplodocine *Diplodocus*, and the apatosaurine *Brontosaurus*. Artwork kindly provided for *Nigersaurus* by Ole Zant, for *Bajadasaurus* by Jorge González, for *Diplodocus* by Andrey Atuchin, for *Brontosaurus* by Mark P. Witton.

study, the function of these thinly muscled covered hyperelongate cervical processes remains unknown. In summary, notable advances have been made in reconstructing diplodocoids to their life appearance (Figure 6), which in turn reflects, at least partially, their ecological role.

CONCLUDING REMARKS

Diplodocoidea is a thoroughly studied group of highly successful sauropods, but there remain numerous questions that need answers. This summarizing contribution leads into a selection of studies which together form the volume titled: “Diplodocoidea (Dinosauria, Sauropoda): Systematics, Phylogeny, Biogeography.” Through studying inter- and intraspecific variation and ontogeny, and the description of several new taxa, we aim to provide more insight into the origin and relationships of diplodocoid sauropods, as well as their ecology and biogeography.

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