Case 3700

Diplodocus Marsh, 1878 (Dinosauria, Sauropoda): proposed designation of *D. carnegii* Hatcher, 1901 as the type species

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Abstract. The purpose of this application, under Articles 78.1 and 81.1 of the Code, is to replace Diplodocus longus Marsh, 1878 as the type species of the sauropod dinosaur genus Diplodocus by the much better represented D. carnegii Hatcher, 1901, due to the undiagnosable state of the holotype of D. longus (YPM 1920, a partial tail and a chevron). The holotype of D. carnegii, CM 84, is a well-preserved and mostly articulated specimen. Casts of it are on display in various museums around the world, and the species has generally been used as the main reference for studies of comparative anatomy or phylogeny of the genus. Both species are known from the Upper Jurassic Morrison Formation of the western United States. The genus Diplodocus is the basis for the family-level taxa diplodocinae Marsh, 1884, diplodocidae Marsh, 1884, dip-LODOCIMORPHA Marsh, 1884 (Calvo & Salgado, 1995) and DIPLODOCOIDEA Marsh, 1884 (Upchurch, 1995). It is also a specifier of at least 10 phylogenetic clades. With the replacement of D. longus by D. carnegii as type species, Diplodocus could be preserved as a taxonomic name with generally accepted content. Taxonomic stability of the entire clade DIPLODOCOIDEA, and the proposed definitions of several clades within Sauropoda, could be maintained.

Keywords. Nomenclature; taxonomy; Dinosauria; Sauropoda; DIPLODOCIDAE; *Diplodocus*; *Diplodocus*;

1. The genus *Diplodocus* Marsh, 1878 was named by Marsh (1878, p. 412) based on remains from Marsh-Felch Quarry 1, near Garden Park, Colorado, U.S.A. The type and first described species is *D. longus* Marsh, 1878 (p. 414) with the type specimen being YPM 1920 in the Yale Peabody Museum, New Haven, U.S.A. (Marsh, 1878, p. 414, misprinted as p. 514). The specimen was not the only find from the quarry, and various bones were initially referred to the holotype: a skull, a string of anterior to mid-caudal vertebrae, one chevron (on whose morphology with two horizontally oriented rods the

generic name, meaning 'double beam', is based), a femur, and a pes now cataloged as YPM 1906 (Marsh, 1878; McIntosh & Carpenter, 1998). However, only the caudal vertebrae and the chevron can be confidently interpreted to be from the same individual (McIntosh & Carpenter, 1998). Given that Marsh (1878) based his diagnosis of the new genus on characters from the chevron and the caudal vertebrae, only these can be considered to constitute the holotype. Of the 17 caudal vertebrae initially found, only two remain reasonably complete (Figs 1, 2; McIntosh & Carpenter, 1998; Tschopp et al., 2015). These can be confidently identified as belonging to the genus *Diplodocus*, because of the presence of well-developed caudal pneumatopores until at least caudal vertebra 16, a feature that was recovered as an unambiguous synapomorphy for the genus Diplodocus by Tschopp et al. (2015). Although the exact position of the string of caudal elements of YPM 1920 is difficult to establish (McIntosh & Carpenter, 1998), comparisons with AMNH 223 in the American Museum of Natural History, New York City, U.S.A., CM 94 in the Carnegie Museum of Natural History, Pittsburgh, U.S.A., DMNS 1494 in the Denver Museum of Nature and Science, Denver, U.S.A., and USNM 10865 indicate that this diagnostic feature also occurs in YPM 1920 in the Smithsonian Institution, Washington DC, U.S.A. (McIntosh & Carpenter, 1998; Tschopp et al., 2015). However, whereas the attribution of YPM 1920 and the remaining specimens in the same genuslevel clade (as recovered by Tschopp et al., 2015) to a single genus is well supported, the study found no species-level autapomorphies in YPM 1920, so D. longus must be treated as a nomen dubium (Tschopp et al., 2015).

2. A second species, *Diplodocus lacustris* Marsh, 1884 (p. 166) was named based on teeth from Lakes Quarry 5 at Morrison, Colorado, and a supposedly associated

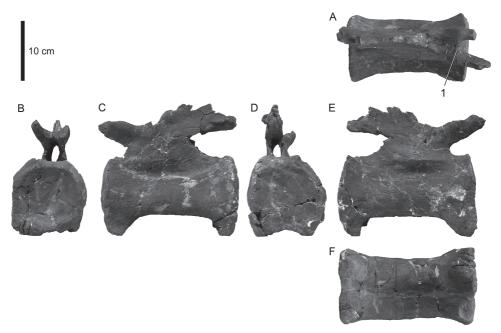


Fig. 1. More anterior of the only two reasonably complete caudal vertebrae of the type specimen of *Diplodocus longus* (YPM 1920) in dorsal (A), anterior (B), left (C), posterior (D), right (E), and ventral (F) views. The neural spine is lost. The estimated position within the caudal column is caudal vertebra 17–24. Note the transverse ridge between the prezygapophyses shared with AMNH 223 (1).

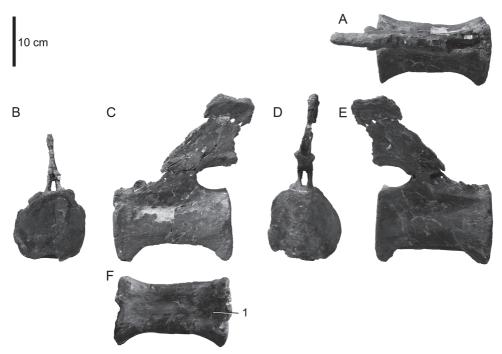


Fig. 2. More posterior of the only two reasonably complete caudal vertebrae of the type specimen of *Diplodocus longus* (YPM 1920) in dorsal (A), anterior (B), left (C), posterior (D), right (E), and ventral (F) views. The prezygapophyses are lost. The estimated position within the caudal column is caudal vertebra 18–25. Note the deep ventral hollow often considered diagnostic for *Diplodocus* (1).

premaxilla and maxilla (Marsh, 1884; type specimen YPM 1922). In the same paper, Marsh (1884, p. 167) coined the name of the higher-level taxon DIPLODOCIDAE, with which the still widely used names DIPLODOCINAE and DIPLODOCOIDEA are coordinate (Upchurch, 1995). A recent study mentions camarasaurid affinities for the premaxilla and maxilla of YPM 1922 (Tschopp et al., 2015), leaving just the teeth to belong definitively to a single individual. YPM 1922 was the most unstable operational taxonomic unit in the specimen-level cladistic analysis of Tschopp et al. (2015), and could not be confidently referred to any clade below Flagellicaudata. '*D.*' *lacustris* should therefore be treated as a nomen dubium and may not even be to a diplodocine (Tschopp et al., 2015).

3. Osborn (1899) described a reasonably complete specimen from Como Bluff, Wyoming (AMNH 223), and referred it to *Diplodocus longus* based on the deep ventral longitudinal hollow in the caudal vertebrae, which is often mentioned as diagnostic feature of the genus *Diplodocus* (Fig. 2F; Osborn, 1899; Curtice, 1996; McIntosh, 2005). However, it has recently been shown that all species of *Diplodocus* bear this hollow, so its presence can be used as an autapomorphy for the genus, but not for a particular species (Tschopp et al., 2015). Even though Tschopp et al. (2015) recognized a feature shared by YPM 1920 and AMNH 223 (a horizontal transverse ridge posterior to the prezygapophyseal facets of the mid-caudal vertebrae; Fig. 1A), their phylogenetic analysis did not recover the two as a clade separate from the other *Diplodocus* specimens. This shared feature is thus considered individually variable and not taxonomically significant. AMNH 223 was referred to *Diplodocus hallorum* (Gillette, 1991) by Tschopp et al. (2015), so a reassignment of AMNH 223 as neotype of *D. longus* cannot be justified.

4. Two years after Osborn's description, Hatcher (1901, p. 57) described a new species, Diplodocus carnegii, based on an articulated specimen with cervical, dorsal, sacral and anterior caudal vertebrae, ribs, and appendicular elements (CM 84). The specimen was found with a second specimen, CM 94 (the paratype specimen of *D. carnegii*), at Quarry D (3) at Sheep Creek, Wyoming, U.S.A. (Hatcher, 1901; McIntosh, 1981). Given the incompleteness of the holotype specimen of D. longus, Hatcher (1901) established the new species based on comparisons with the much better preserved and more complete specimen AMNH 223, which had been referred to D. longus by Osborn (1899; see above). Recent comparisons of CM 84 and CM 94 with the holotype of D. longus, did not reveal unique shared features (Tschopp et al., 2015), so that synonymy of the two species can be ruled out. CM 84 still represents one of the most complete Diplodocus specimen known (Tschopp et al., 2015), and it was complemented with material from CM 94 and other, less complete specimens in order to create a mount for the Carnegie Museum of Natural History in Pittsburgh (Holland, 1906; McIntosh, 1981; Curtice, 1996; Nieuwland, 2010). Casts of this composite skeleton were sent to numerous museums in Europe, Asia and Central and South America, which made this Diplodocus species one of the most famous dinosaurs worldwide (Holland, 1906; McIntosh, 1981; Rea, 2004; Nieuwland, 2010). Thanks to the worldwide distribution and the high quality of its casts, CM 84, with its complementary components, still remains one of the most easily accessible dinosaur specimens to study, and is indeed the most visited dinosaur skeleton of all time (Rea, 2004). Consequently, most studies of comparative anatomy, phylogeny or functional morphology that include Diplodocus are mainly based on D. carnegii (e.g. Stevens & Parrish, 1999; Bedell & Trexler, 2005; McIntosh, 2005; Carrano, 2006; Harris, 2006; Taylor et al., 2009; Whitlock, 2011; Woodruff & Fowler, 2012; Tschopp & Mateus, 2013; Wedel & Taylor, 2013).

5. A fourth nominal species, *Diplodocus hayi*, was added to the genus by Holland (1924, p. 399), based on remains found at Quarry A at Red Fork of the Powder River in Wyoming. The holotype specimen HMNS 175 in the Houston Museum of Nature and Science, Houston, U.S.A. (at the time accessioned at the Carnegie Museum under the number CM 662; McIntosh, 1981) is even more complete than CM 84, and includes a partial skull and cervical, dorsal and anterior and mid-caudal vertebrae, as well as elements from both girdles and fore- and hindlimbs, including a nearly complete manus and a partial pes (McIntosh, 1981; Tschopp et al., 2015). However, the initial description of Holland (1924) solely concerned the braincase. The erection of the new species was based on differences with another skull referred to Diplodocus by the same author (CM 11161 from Dinosaur National Monument, Utah, U.S.A.). The braincase of HMNS 175 remains the only described element of the entire holotypic skeleton. When erecting D. havi as new species of Diplodocus, Holland (1924) noted that differences in braincase morphology between the type specimen HMNS 175 and CM 11161 might prove numerous enough to justify generic distinction of the two (Holland, 1924). Recently, this proposal was corroborated by a phylogenetic study, and the species *hayi* was established as type species of the new genus Galeamopus Tschopp, Mateus & Benson, 2015.

6. A reasonably complete specimen from Dinosaur National Monument (USNM 10865) was preliminarily described by Gilmore (1932). Gilmore (1932) referred USNM 10865 to *Diplodocus longus*, but only due to similarities with AMNH 223. He further noted that specific separation of *D. carnegii* from *D. longus* might not be warranted (Gilmore, 1932), given that USNM 10865 appears to show varying inclinations of the caudal neural

spines (the main character used by Hatcher [1901] to distinguish *D. carnegii* from '*D. longus*' AMNH 223). Tschopp et al. (2015) confirmed the referral of USNM 10865 to the same species as AMNH 223, but to *D. hallorum* instead of *D. longus*.

7. Gillette (1991, p. 418) erected a new genus and species, *Seismosaurus hallorum*, nominating partly articulated material from the vicinity of San Ysidro, New Mexico, as its holotype (NMMNH [New Mexico Museum of Natural History, Albuquerque, U.S.A.] 3690). The generic distinction from *Diplodocus* was mainly based on differences in caudal vertebral ratios (Gillette, 1991), which were later shown to be due to a wrong assignment of anterior elements to a more posterior position (Curtice, 1996; Lucas et al., 2006). *Seismosaurus hallorum* was thus referred to *Diplodocus* (Lucas et al., 2006), possibly even representing a junior synonym of *D. longus* (Lovelace et al., 2007). As in most other cases outlined above, Lovelace et al.'s (2007) referral of NMMNH 3690 to *D. longus* was based on comparisons with the specimen AMNH 223 instead of the holotype specimen YPM 1920. Tschopp et al. (2015) rejected the synonymy of *S. hallorum* as first proposed by Lucas et al. (2006). Tschopp et al. (2015) also referred the specimens AMNH 223, DMNS 1494 and USNM 10865 to this species, and thus confirmed the previous studies in the fact that they all belong to a single species.

8. Although the holotype specimen of the type species *Diplodocus longus* (YPM 1920) can be clearly referred to the genus *Diplodocus* as generally perceived, the lack of specific autapomorphies results in *D. longus* being a nomen dubium. Because *D. longus* is the type species of the genus *Diplodocus*, but is itself not diagnosable, a retention of *D. longus* as type species would create insecurities and confusion concerning the use of *Diplodocus* as a genus. A way to avoid this would be the designation of a neotype, but this is inappropriate, because no other, diagnostic material currently can be referred to the same species based on shared morphology. Due to the frequency of citationand popularity of the name *Diplodocus*, and because of the fact that well-preserved specimens are known from other species confidently referred to the same genus as YPM 1920 (Tschopp et al., 2015), the replacement of *D. longus* as type species is advisable.

9. Since 'Diplodocus' lacustris is also not diagnosable, and may not even be a diplodocine, the most suitable available species to replace D. longus as type species of Diplodocus would be D. carnegii, with the type specimen being CM 84 (Hatcher, 1901). D. carnegii is the best known and documented species of Diplodocus. Its type specimen, CM 84, preserves elements of nearly all portions of the skeleton, including a complete vertebral column from cervical vertebra 2 to caudal vertebra 12, cervical and dorsal ribs, pectoral and pelvic girdle elements, and a femur (Hatcher, 1901; McIntosh, 1981). The designed paratype specimen CM 94 (Hatcher, 1901) complements the knowledge about the species' anatomy by preserving mid-caudal vertebrae, forelimb elements a tibia, fibula and partial pes (Hatcher, 1901; McIntosh, 1981). As mentioned above, D. carnegii has become famous around the world and is the informal reference species for the genus Diplodocus thanks to the wide availability of casts, nearly complete knowledge of its skeletal anatomy, and the high quality of the initial description with a large number of adequate figures (Hatcher, 1901). This informal use of D. carnegii as the reference for the genus Diplodocus could be made official by replacing D. longus as type species by D. carnegii. Also, comparisons of new specimens with AMNH 223 as the wrong reference for the type species could be avoided. In the improbable case that new studies show that D. longus and D. carnegii are in fact the same species, replacing D. longus as type

species by *D. carnegii* could result in the new type species becoming a junior synonym of the old one. However, the incompleteness of YPM 1920 makes the identification of diagnostic features shared with *D. carnegii* highly improbable. In fact, the only currently recognized unique shared morphological feature of the type specimen of *D. longus* with any other *Diplodocus* specimen (AMNH 223, see above) rather indicates synonymy with *D. hallorum*. An alternative to replacing of the type species could be to designate CM 84 (the type specimen of *D. carnegii*) as neotype of *D. longus*. However, there are no morphological grounds for such a proposal, which would furthermore result in the loss of the popular species name *D. carnegii*. Considering the low probability of synonymy of *D. longus* and *D. carnegii*, the proposed replacement of the type species is thus preferable over a designation of CM 84 as neotype of *D. longus*.

10. In addition to giving the names to four higher-level clades within the family group (DIPLODOCINAE, DIPLODOCIDAE, DIPLODOCIMORPHA and DIPLODOCOIDEA), the genus *Diplodocus* is widely used as a specifier in phylogenetic nomenclature (e.g. for APATOSAURINAE Janensch, 1929, DICRAEOSAURIDAE Janensch, 1929, Macronari and Neosauropoda; Taylor & Naish, 2005). Therefore, its retention and stability within the sauropod family tree is important, and it should not be typified by an undiagnosable type species. Taylor & Naish (2005, table 1) alone listed 12 clades for which *Diplodocus* is an internal or external specifier.

11. Similar cases as the one proposed herein were submitted for the dinosaurs *Cetiosauriscus* (Charig, 1993), *Cetiosaurus* (Upchurch et al., 2009) and *Stegosaurus* (Galton, 2011). All of these cases were proposed due to non-diagnostic original type specimens and thus invalid original type species, and were accepted by the Commission (Opinions 1801, 2320 and 2331). Despite Article 80.5 and the Principle 8 of the Code's Introduction, both of which emphasize that a ruling on a case concerns that case only, a different treatment of *Diplodocus* would be unreasonable given the similarity of these cases. Taxonomic uncertainty within the genus *Diplodocus* would be retained and identification of future finds to species level would be considerably hampered.

- 12. The International Commission on Zoological Nomenclature is accordingly asked:
- (1) to use its plenary power to set aside all previous type species fixations for the genus *Diplodocus* Marsh, 1878 and to designate *D. carnegii* Hatcher, 1901 as its type species;
- (2) to place on the Official List of Generic Names in Zoology the name *Diplodocus* Marsh, 1878 (gender: masculine), type species *D. carnegii* Hatcher, 1901, as ruled in (1) above;
- (3) to place on the Official List of Specific Names in Zoology the name *carnegii* Hatcher, 1901 as published in the binomen *Diplodocus carnegii* (specific name of the type species of *Diplodocus* Marsh, 1878), as ruled in (1) above.

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