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CONSIDERATIONS ON THE REPLACEMENT OF A TYPE SPECIES IN THE CASE OF THE SAUROPOD DINOSAUR *DIPLODOCUS* MARSH, 1878

Emanuel Tschopp, Daniel Brinkman, Jaime Henderson, Mary Ann Turner, and Octávio Mateus

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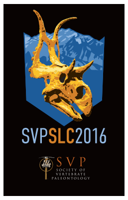

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Caudal vertebral elements of the type specimen of ***Diplodocus longus*** *(YPM VP.001920). The letters indicate the vertebrae shown on figures 1 to 5. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.*

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Considerations on the Replacement of a Type Species in the Case of the Sauropod Dinosaur *Diplodocus* Marsh, 1878

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ABSTRACT

The sauropod dinosaur genus *Diplodocus* Marsh, 1878, is currently typified by a morphologically undiagnosable type species, *D. longus* Marsh, 1878. Only two caudal vertebrae and an associated partial chevron of its holotype (Yale Peabody Museum [YPM] VP.001920) remain reasonably complete, but more, fragmentary caudal vertebrae are available, and provide additional morphological information. YPM VP.001920 can be referred to *Diplodocus* generally, but cannot be distinguished from other *Diplodocus* species based on autapomorphies. Thus, the genus *Diplodocus* would have to be considered a *nomen dubium*. In order to resolve this unsatisfactory taxonomic issue, Tschopp and Mateus (2016) proposed to designate a new type species for the genus *Diplodocus*: namely, the well-known *D. carnegii* Hatcher, 1901.

Herein, we expand upon historical and taxonomic issues concerning the holotype of *D. longus*, in order to: (1) provide additional imagery and information on the specimen and (2) to address comments against the replacement of *D. longus* by *D. carnegii* as the type species of *Diplodocus* as proposed by Tschopp and Mateus (2016).

INTRODUCTION

The sauropod *Diplodocus* Marsh, 1878, is one of the most famous dinosaurs from the Upper Jurassic Morrison Formation, and probably the most viewed dinosaur skeleton worldwide thanks, in part, to the widely-distributed sets of casts of the holotype of *D. carnegii* provided to museums around the globe by American steel magnate Andrew Carnegie (Rea, 2004; Otero and Gasparini, 2014). However, its taxonomic history is problematic, being based on a very fragmentary and incomplete specimen (YPM VP.001920) from a multi-taxa bonebed near Garden Park, Colorado (the Marsh-Felch Quarry), which cannot be reasonably distinguished from any other specimen referred to the genus *Diplodocus* (Gilmore, 1932; Tschopp and others, 2015; Tschopp and Mateus, 2016). Other sauropod genera and species reported from the type locality include the diplodocids *Apatosaurus* and *Galeamopus pabsti*, the putative diplodocoids "*Morosaurus agilis*" and *Haplocanthosau-*

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rus priscus, and the macronarians *Camarasaurus* and *Brachiosaurus* (Evanoff and Carpenter, 1998; McIntosh and Carpenter, 1998; Foster, 2003; Tschopp and Mateus, 2017). YPM VP.001920, the holotype of the type species of *Diplodocus*, *D. longus* Marsh, 1878, was briefly described by Marsh (1878) and reassessed by McIntosh and Carpenter (1998). Doubts about its validity have previously been put forward by Gilmore (1932) and Tschopp and others (2015). Based on these studies, Tschopp and Mateus (2016) formally proposed a case to the International Commission on Zoological Nomenclature (ICZN) to replace the type species *D. longus* with the much more complete and better known *D. carnegii*. To date, published comments on this case, ICZN Case 3700, have been mixed, with the case receiving three positive (Lucas, 2017; Taylor, 2017; Woodruff, 2017), and three negative comments (Carpenter, 2017; Demirjian, 2017; Mortimer, 2017).

Herein, we provide additional information and photographs of the most complete caudal vertebrae (figures 1 to 8) and of the associated partial chevron (figure 9) of the holotype specimen YPM VP.001920. These photographs were not published in the original case (Tschopp and Mateus, 2016) due to limited space and restrictions on the use of color. They show that the chevron has the anterior and posterior projections for which the genus was named (figure 9; *Diplodocus* means "double beam"), whereas the fragmentary caudal vertebrae have strongly excavated ventral hollows (figures 1 and 3) and well-developed pneumatic foramina typical for *Diplodocus* (figure 4). However, the photographs also further illustrate the very fragmentary nature of the specimen (figure 8), and, thus, the need for a new type species in *Diplodocus*. We also expand upon the complicated curatorial history of the cataloged YPM sauropod specimens from Garden Park and we correct an error found in the initial proposal to the ICZN by Tschopp and Mateus (2016).

Over the years, additional material from the type locality, either currently or previously stored in the YPM VP collections, was thought by one person or another to be attributable to *D. longus*, perhaps even to the type specimen itself (see McIntosh and Carpenter, 1998; Carpenter, 2017 for reviews). This additional material consists of two skulls (one of which had an associated atlas), a mid- to posterior cervical vertebra, part of a pelvis, and several fore- and hindlimb elements (McIntosh and Carpenter, 1998; Carpenter, 2017). In many cases, it is unclear who attributed this material to *D. longus* or when, but, in some cases, the attributions go all the way back to Othniel C. Marsh, who appears to have relied heavily on the letters and diagrams of his collectors at Garden Park: Benjamin F. Mudge, Samuel W. Williston, and Marshal P. Felch (see McIntosh and Carpenter, 1998; Carpenter, 2017). However, McIntosh and Carpenter (1998), in their revision of YPM VP.001920, restricted the holotype to the series of caudal vertebrae (figures 1 to 8) and an associated partial chevron (figure 9) because these were the bones on which the species *D. longus* was established by Marsh (1878). In fact, much of the other YPM material attributed to this species (and, perhaps, even to the type specimen itself) has since been attributed to different taxa (see McIntosh and Carpenter, 1998) and given different catalog numbers (i.e., YPM VP.001906, .001921X, .001922X, .004688, .004689, .059136, and .059137). Some of these specimens have since been deaccessioned at the YPM and transferred to the Smithsonian Institution where they now bear United States National Museum (USNM V) catalog numbers (e.g., the two skulls USNM V 2672 and 2673). However, those cataloged sauropod specimens from Garden Park that remain in the YPM VP collections are still stored, regardless of their current taxonomic identifications, near the restricted type so that the YPM can maintain the historic connections between these specimens. Recently, Carpenter (2017) backed away from his earlier attribution of many of these specimens to different taxa (McIntosh and Carpenter, 1998), but did not provide any information on shared morphological features or otherwise unequivocal evidence to support an attribution to the same species, or even individual, as the type tail. Below, we briefly discuss these additional referred specimens and we address the critiques of ICZN Case 3700 by Carpenter (2017), Demirjian (2017), and Mortimer (2017).

INSTITUTIONAL ABBREVIATIONS

AMNH FARB, fossil amphibian, reptile, and bird collection, American Museum of Natural History, New York City, New York, USA; SMA, Sauriermuseum Aath-

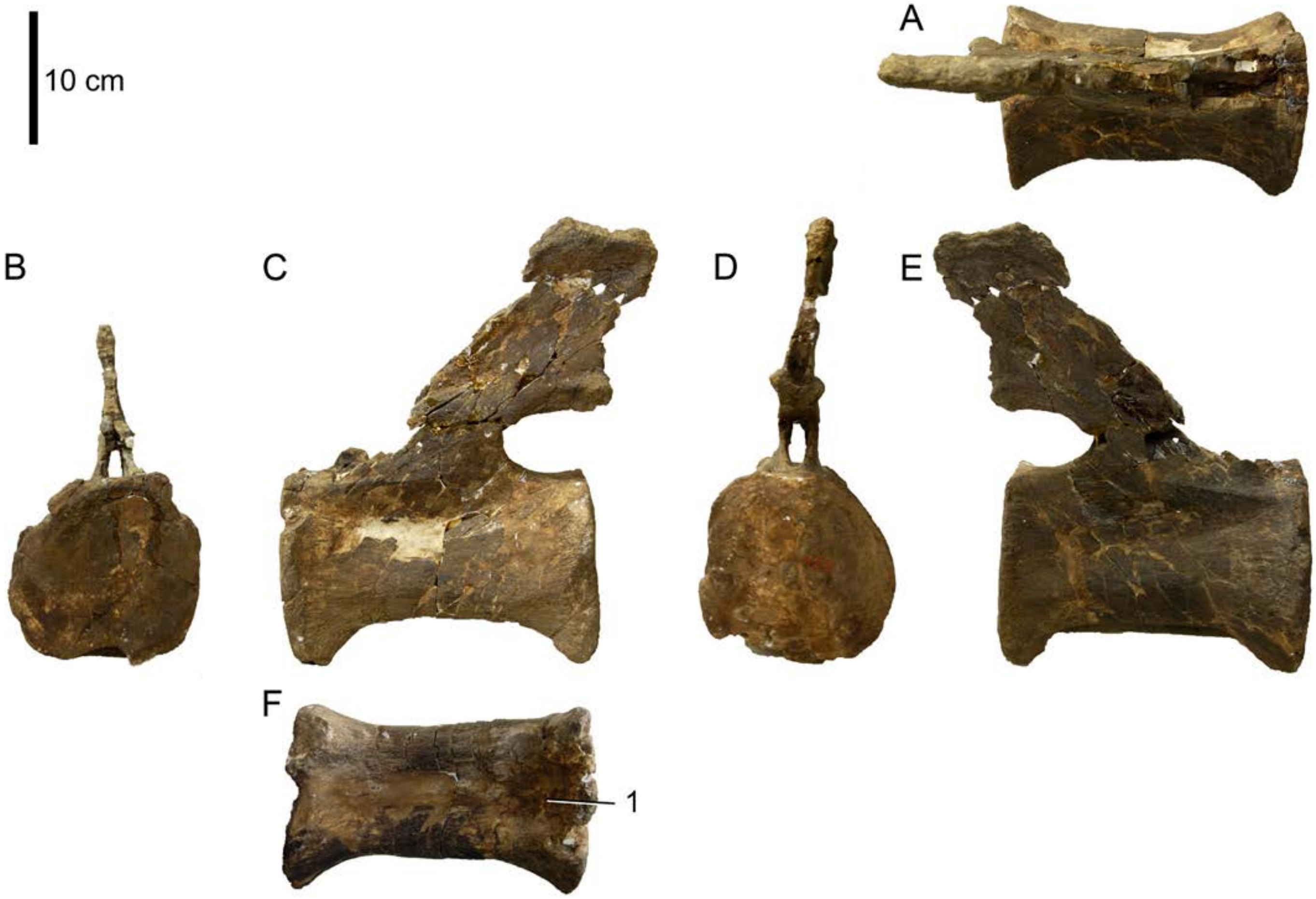

Figure 1. Anterior to mid-caudal vertebra of the holotype specimen of *Diplodocus longus* (YPM VP.001920, vertebra "f" on figure 8), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Note the deep ventral hollow in the centrum (1). This is the most complete preserved element of the holotype. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

al, Switzerland; USNM V, vertebrate paleobiology collection, United States National Museum, Washington D.C., USA; and YPM VP, vertebrate paleontology collection, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

PREVIOUSLY CATALOGED YPM VP MATERIAL ATTRIBUTED TO *DIPLODOCUS LONGUS* FROM THE TYPE LOCALITY

Below is a compilation of previously cataloged YPM material from the type locality that has been attributed to *Diplodocus longus* in the past, and perhaps even to the type specimen itself.

Specimen YPM VP.001906

This specimen was mentioned by Tschopp and Mateus (2016), who erroneously stated that it includes a pes. As demonstrated by McIntosh and Carpenter (1998), and correctly cited in Tschopp and others (2015), YPM VP.001906 consists of a left ulna, radius, metacarpals I-V, and a single atrophied phalanx that is attached to metacarpal V. The metacarpals were figured as *D. longus* by Marsh (1896) and all of the elements were illustrated by McIntosh and Carpenter (1998, figure 3). The elements making up YPM VP.001906 were initially referred to "*Morosaurus,*" but later assigned to *D. longus* by Marsh himself (Marsh, 1896; McIntosh

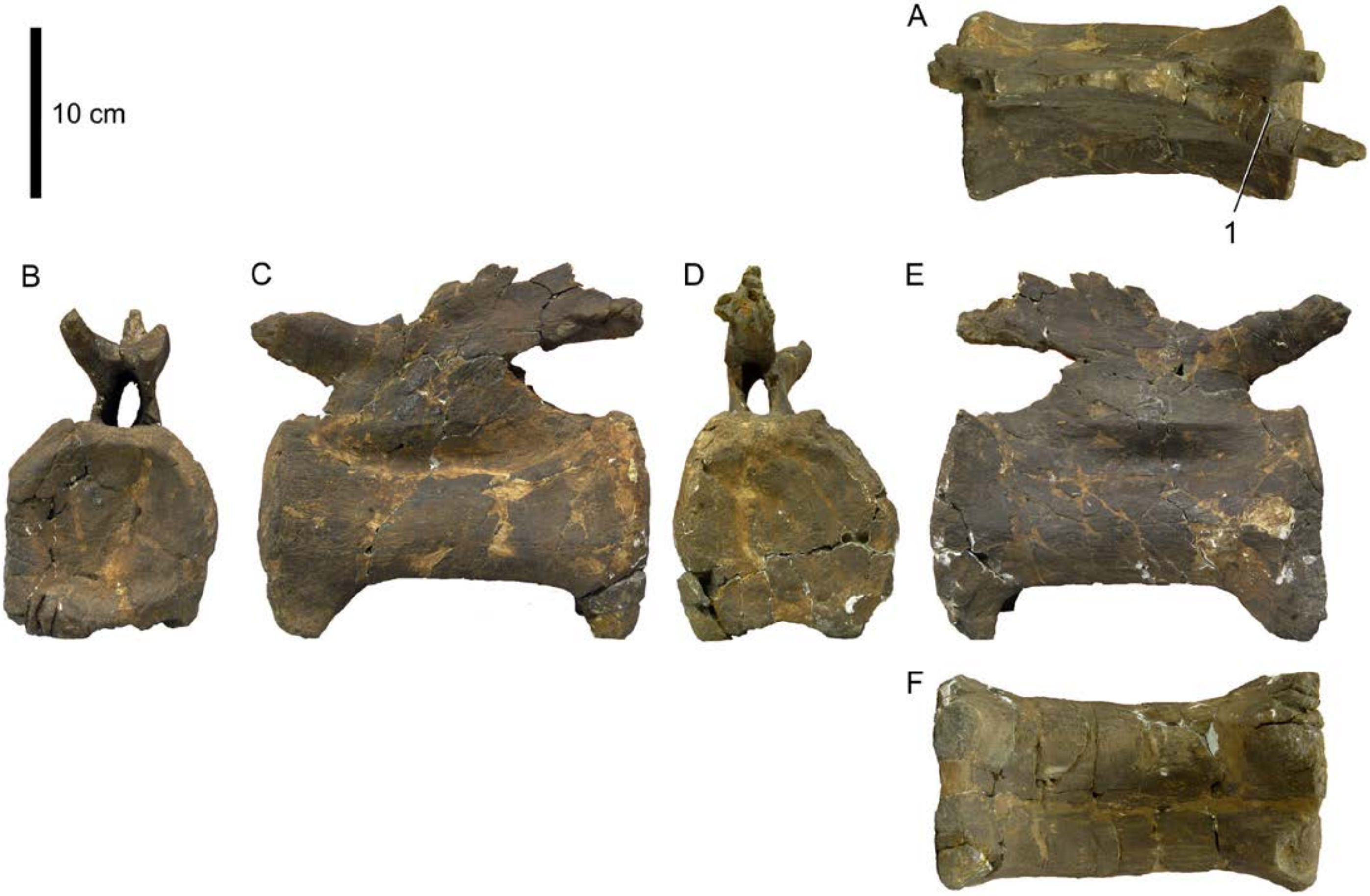

Figure 2. Anterior to mid-caudal vertebra of the holotype specimen of *Diplodocus longus* (YPM VP.001920, vertebra "b1" on figure 8), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Note the transverse lamina connecting the two prezygapophyses (1). This is the second most complete preserved element of the holotype. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

and Carpenter, 1998). McIntosh and Carpenter (1998) excluded YPM VP.001906 from the holotype specimen based on its size relative to that of the femur (recently cataloged as part of YPM VP.059136) that was found in association with the type tail, though they did note that the two specimens (YPM VP.001906 and .001920) would have been from a similarly sized, if not the same individual of sauropod. However, sauropod forelimb material is difficult to identify to species, and only a few specimens clearly referable to *Diplodocus* preserve an ulna or a radius, whereas none of them has a manus (Bedell and Trexler, 2005; E. Tschopp, personal observations). Based on morphology alone, it is therefore questionable if these bones can be attributed to *D. longus*, and because of the lack of comparative material in other species, it is unlikely that they would provide reliable autapomorphic features. Although YPM VP.001906 is currently identified as *Diplodocus* sp. in the YPM VP database, it could, according to McIntosh and Carpenter (1998), possibly either belong with the type tail or be the partial forelimb of an immature *Apatosaurus* (which included *Brontosaurus* at the time; see Tschopp and others, 2015) or, even, *Haplocanthosaurus*. YPM VP.001906 differs from most apatosaurine specimens with a manus, which generally have a metacarpal I that is longer than the metacarpal IV (e.g., CM 3018, Tate-001, UW 15556, but see NSMT-PV 20375; Tschopp and others, 2015). On the other hand, it differs from diplodocines in the less developed distal expansion of the ulna. Thus, while we can exclude an attribution to a macronarian sauro-

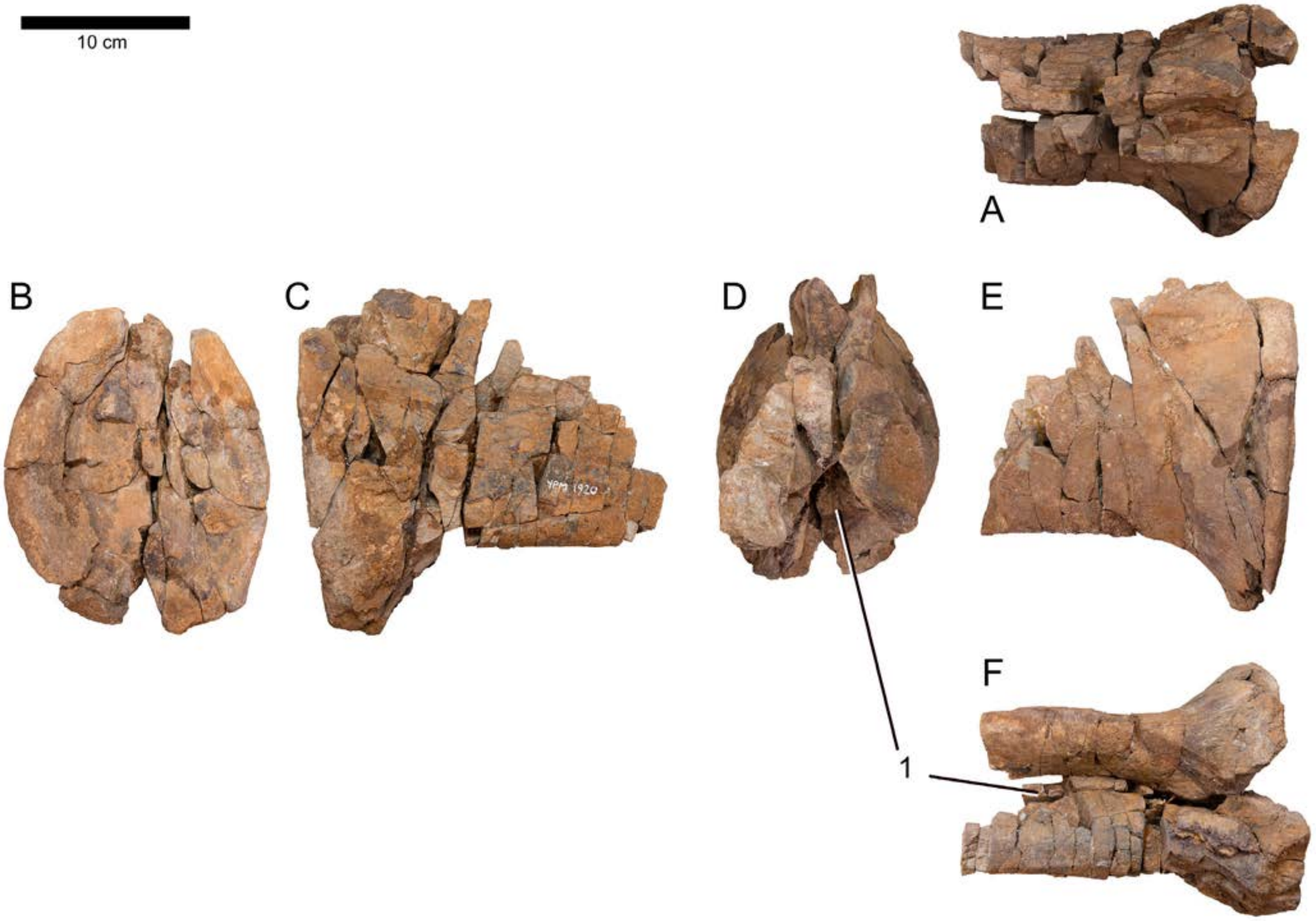

Figure 3. Anterior to mid-caudal vertebra of the holotype specimen of *Diplodocus longus* (YPM VP.001920, vertebra "b2" on figure 8), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Note the deep ventral hollow in the centrum (1). Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

pod based on the relatively short metacarpals compared to the radius, it is currently impossible to provide any more detailed identification within Diplodocoidea.

Specimen YPM VP.001921X (= USNM V 2672 + V 5368)

This specimen consists of a skull with articulated lower jaws, and an associated atlas. These two specimens, together with a second, less well-preserved skull that was collected in 1884 (YPM VP.001922X), and accessioned together with a mid- to posterior cervical vertebra in January 1885 (i.e., a specimen received as part of YPM Accession Number 1738 but never cataloged by the YPM) were eventually transferred to the Smithsonian Institution where they now bear the catalog numbers USNM V 2672, 5368, 2673, and 4712, respectively (McIntosh and Carpenter, 1998). USNM V 2672 was attributed to *D. longus* by Marsh (1884), one year before USNM V 2673 was received at the YPM and referred to the same species without detailed description or illustration (McIntosh and Carpenter, 1998). USNM V 2672, 4712, and 5368 were subsequently figured as *D. longus* by Marsh (1896) and later by McIntosh and Carpenter (1998), though the latter authors attributed USNM V 4712 to *Apatosaurus* sp.

Although USNM V 2672 can most probably be referred to the genus *Diplodocus* (Evanoff and Carpenter, 1998; McIntosh and Carpenter, 1998; Tschopp and others, 2015; Carpenter, 2017), a definitive attribution

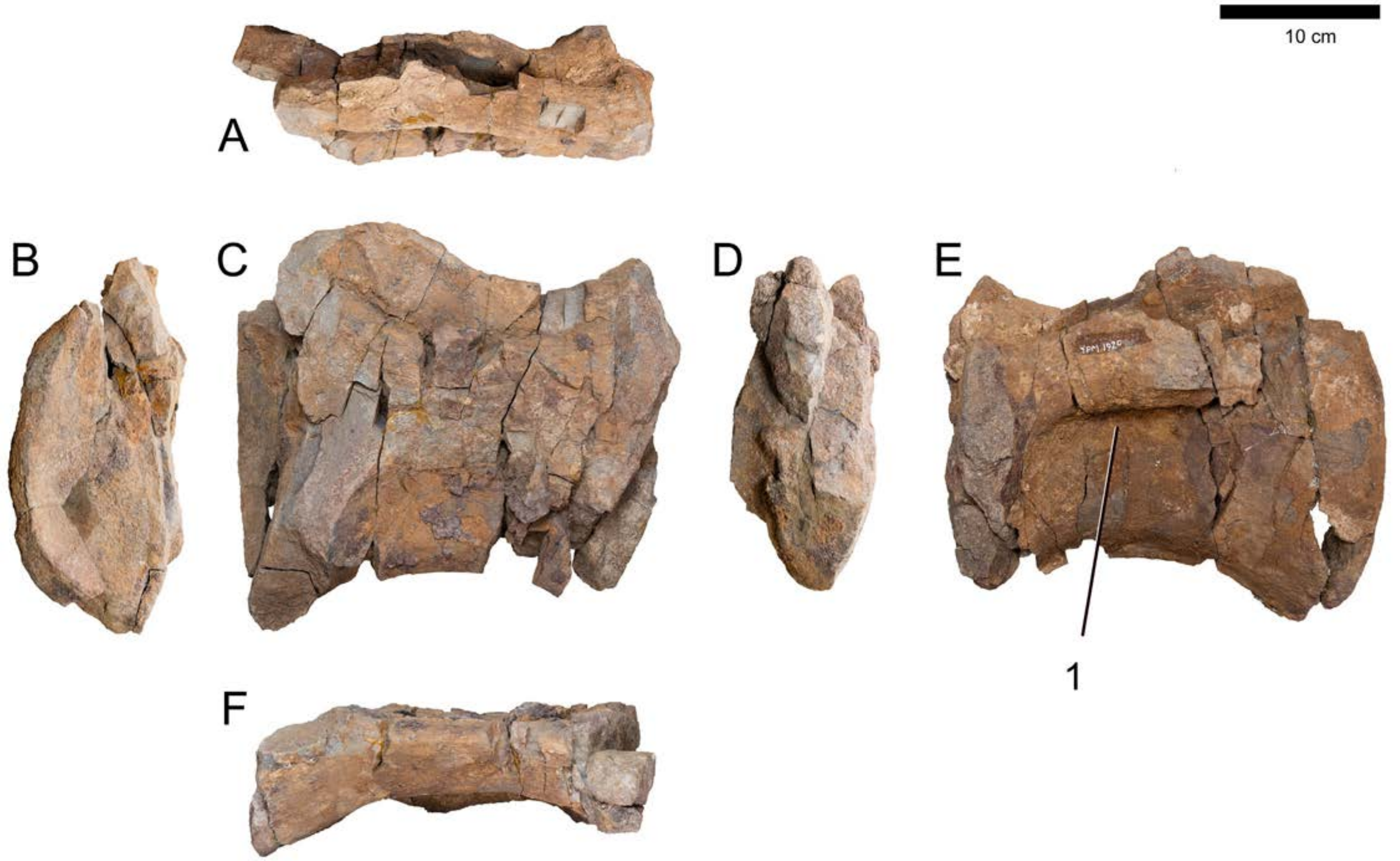

Figure 4. Anterior to mid-caudal vertebra of the holotype specimen of *Diplodocus longus* (YPM VP.001920, vertebra "d" on figure 8), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Note the deep pneumatic foramen on the lateral surface of the centrum, below the transverse process (1). Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

to the holotype specimen of *D. longus,* or even the species, as purported by Carpenter (2017) remains doubtful, and cannot be scientifically justified due to lack of a direct association with the type tail (which was some 15 m away and separated from it by a jumble of bones from multiple individuals; McIntosh and Carpenter, 1998). According to Evanoff and Carpenter (1998), McIntosh and Carpenter (1998), and Carpenter (2017), USNM V 2673 also likely belongs to *D. longus*, whereas Tschopp and Mateus (2017) referred it to *Galeamopus pabsti*, based on shared autapomorphic features with the holotype SMA 0011. Diplodocid skulls are generally very similar and are rarely found in articulation with the postcranial skeleton (Whitlock and others, 2010; Whitlock, 2011b), so that referrals to a species or even genus is very difficult and are tentative at best (Tschopp and others, 2015). The atlas USNM V 5368 cannot be assigned to a specific genus of sauropod, but it clearly does not exhibit the specific features found in the atlases of *G. hayi* and *G. pabsti* (Tschopp and others, 2015; Tschopp and Mateus, 2017), so an attribution to that genus is unlikely. The single, mid- to posterior cervical vertebra USNM V 4712 was assigned to *Brontosaurus* by Hatcher (1903) and to *Apatosaurus* (then including *Brontosaurus*) by McIntosh and Carpenter (1998). Several features including the strongly ventrolaterally projecting cervical ribs with a reduced anterior process, the absence of pneumatic foramina on the ventral surface, and the extended postzygapophyseal centrodiapophyseal fossa onto the posterior surface of the transverse

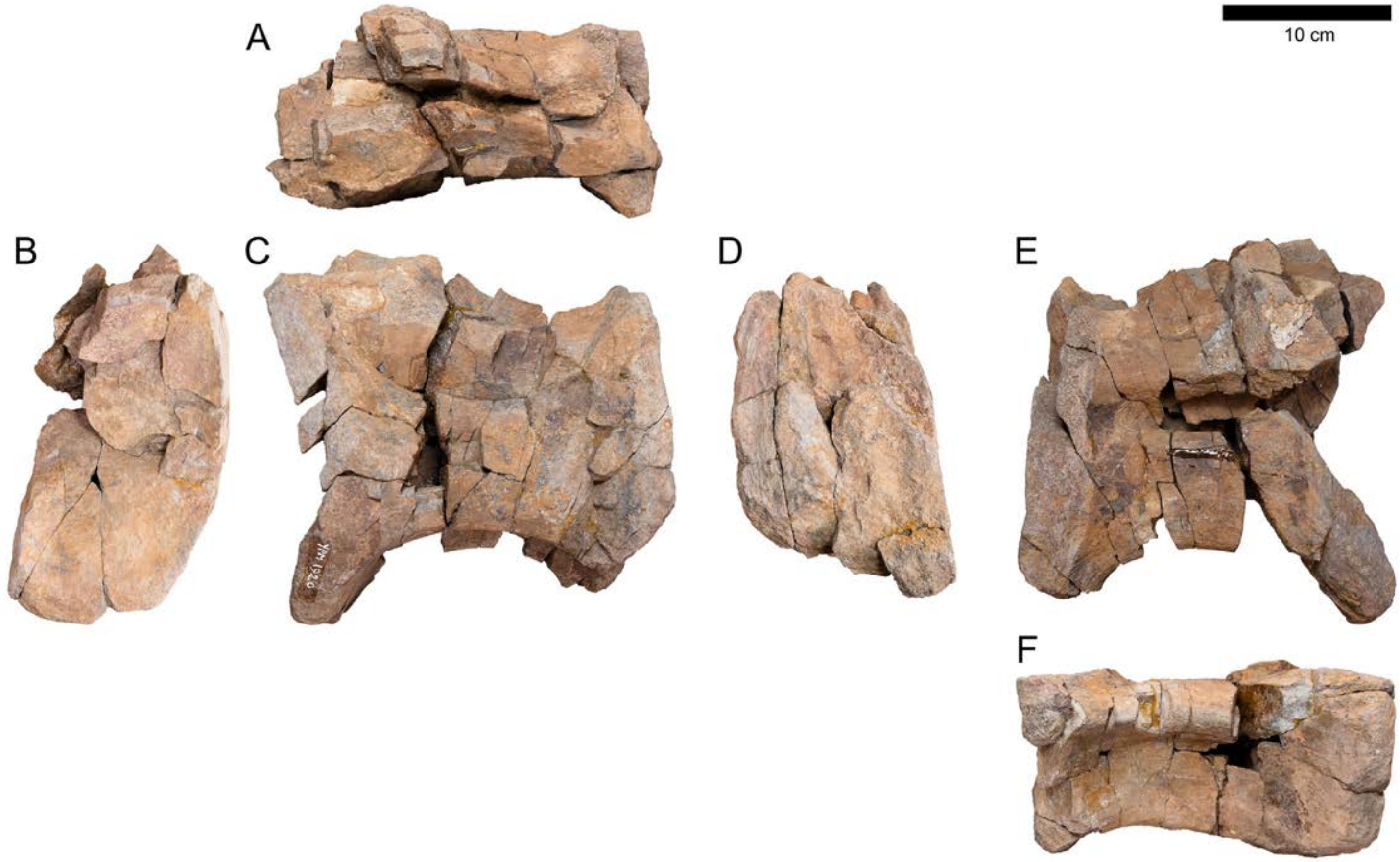

Figure 5. Anterior to mid-caudal vertebra of the type specimen of *Diplodocus longus* (YPM VP.001920, vertebra "e" on figure 8), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

process, support a referral to Apatosaurinae (Tschopp and others, 2015). A referral to either *Apatosaurus* or *Brontosaurus* would require a more detailed study, which is not in the scope of this paper.

Specimen YPM VP.004688

This specimen consists of a right scapula, humerus, ulna, and radius. As with the other appendicular material and the beforementioned skulls, the lack of a direct association with the type tail and chevron precludes any unambiguous referral of the material to the holotype individual of *D. longus*. YPM VP.004688 is currently tentatively cataloged as ?*Haplocanthosaurus* sp. in the YPM VP database. However, according to John ("Jack") S. McIntosh's unpublished notebook (McIntosh, undated), it was thought at some point that an identification as *Haplocanthosaurus* was likely for at least the humerus and radius, but that the scapula and ulna might be ?*Brachiosaurus*. We add to this reassessment that the radius has a distinct medial projection on the proximal articular surface, resembling the condition in the brachiosaurids *Giraffatitan* (Janensch, 1961) and *Lusotitan* (Mannion and others, 2013). It is therefore possible that the entire foreleg belonged to a brachiosaurid.

Specimen YPM VP.004689

This specimen consists of a sacrum and right ilium. It has been figured by both Marsh (1896) and McIntosh

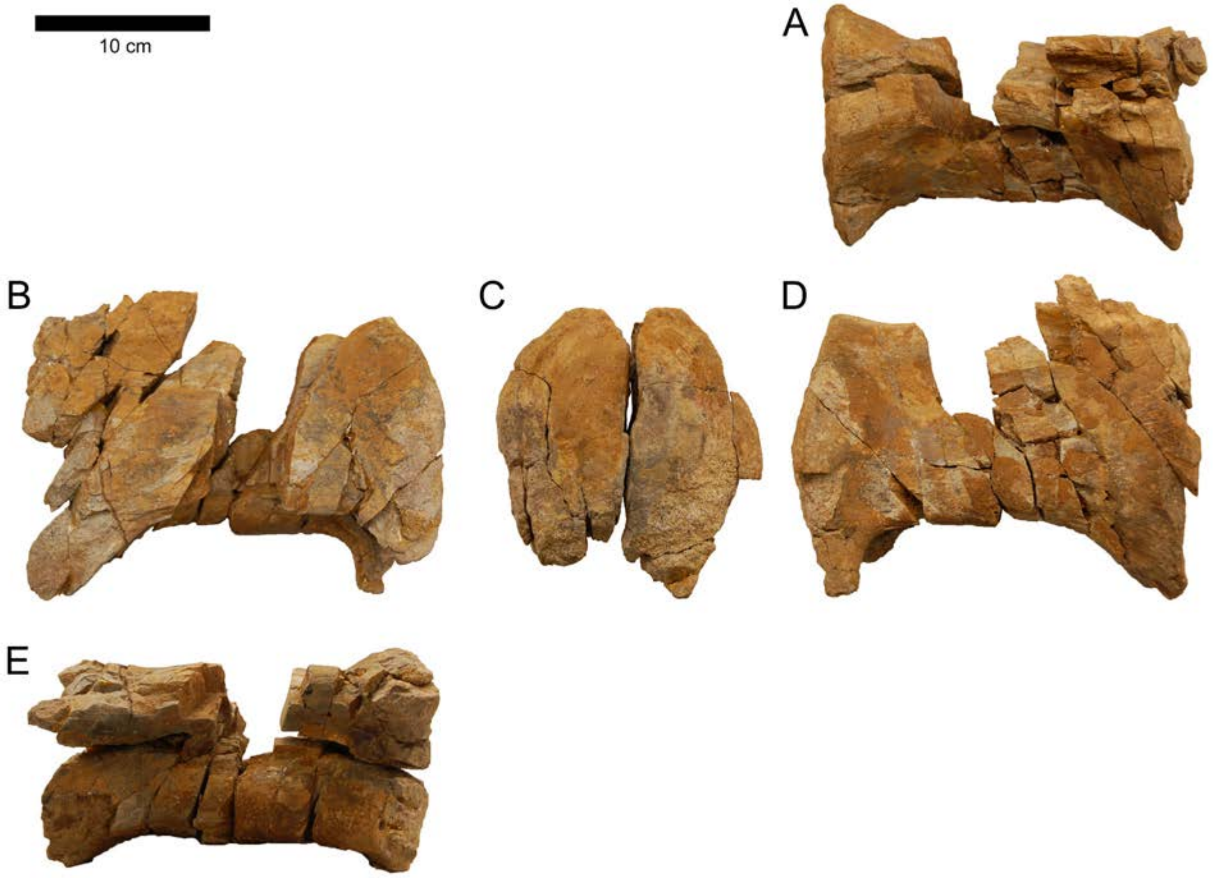

Figure 6. Anterior to mid-caudal vertebra of the type specimen of *Diplodocus longus* (YPM VP.001920), in dorsal (A), left lateral (B), posterior (C), right lateral (D), and ventral view (E). The vertebra lacks the neural arch and parts of the centrum. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Emanuel Tschopp.

and Carpenter (1998). Marsh (1896) referred these pelvic elements to *D. longus*, but they were reidentified by McIntosh and Carpenter (1998) as *Apatosaurus* sp. (or possibly *Brontosaurus*, see above). There is some doubt as to whether or not these pelvic elements belong to the left hindlimb (recently cataloged as YPM VP.059136) that was mentioned by Marsh (1878) in his original description of *D. longus* and by both McIntosh and Carpenter (1998) and Carpenter (2017). Both specimens were thought to be apatosaurine by McIntosh and Carpenter (1998) and, following McIntosh and Carpenter (1998), they are currently identified as *Apatosaurus* sp. in the YPM VP database. However, according to Carpenter (2017) he and the late Jack McIntosh now think that these pelvic and hindlimb elements are part of the holotype of *D. longus* as originally thought by Marsh's collectors at Garden Park: Mudge, Williston, and Felch. Until this new article by Carpenter and McIntosh is published, it remains unclear based on what evidence they changed their opinion, and, consequently, YPM VP will refrain from changing the current taxonomic identifications of these pelvic and hindlimb elements in its database.

RECENTLY CATALOGED YPM VP MATERIAL ATTRIBUTED TO *DIPLODOCUS LONGUS* FROM THE TYPE LOCALITY

Below is a compilation of recently cataloged material from the type locality that has been attributed to *D. longus* in the past, perhaps even to the type specimen itself. As mentioned above, the caudal series (figures

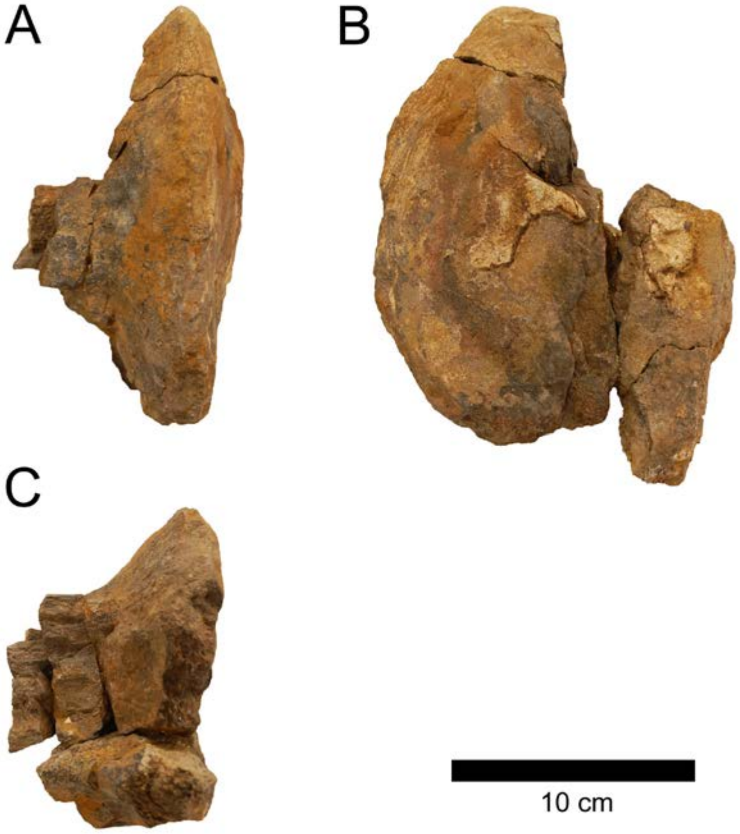

Figure 7. Anterior to mid-caudal vertebra of the type specimen of *Diplodocus longus* (YPM VP.001920), in left lateral (A), posterior (B), and ventral view (C). We interpret this as the posterior end of the centrum, because of the presence of relatively well-developed eminences for the articulation with chevrons. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Emanuel Tschopp.

1 to 8) and associated partial chevron (figure 9) were the elements used by Marsh (1878) to erect the new genus and species *D. longus* (see also McIntosh and Carpenter, 1998). However, the section of the YPM VP collections containing YPM VP.001920 (and the other YPM specimens mentioned above) not only includes the caudal series and chevron of the restricted holotype (McIntosh and Carpenter, 1998), but also includes a partial right pes that was recently cataloged as YPM VP.059137, the partial left hindlimb mentioned above (YPM VP.059136), and a partial right femur recently cataloged as YPM VP.060256.

Specimen YPM VP.059136

This specimen, which consists of a partial left hindlimb, is figured in McIntosh and Carpenter (1998: figure 5). The long bones of YPM VP.059136 are badly crushed and consist of a left femur, fibula, tibia, and an attached astragalus, as well as some associated left pedal elements, including metatarsals that are shorter and more robust than the right metatarsals in YPM VP.059137 (see Hatcher, 1901; McIntosh and Carpenter, 1998; Carpenter, 2017). Unfortunately, the left pes elements, along with two unguals from a right pes and five other phalanges that were mentioned by McIntosh and Carpenter (1998), were not seen during a recent reorganization/conservation project on the Marsh dinosaur collection at the YPM and are presently considered to be missing. The left hindlimb of the specimen now cataloged as YPM VP.059136 was mentioned as being part of the holotype in the initial description by Marsh (1878), but McIntosh and Carpenter (1998) excluded the limb from the holotype, following an earlier suggestion by Hatcher (1901: p. 55). No features diagnostic of the genus *Diplodocus* were recognized in this hindlimb material by these authors or by us, though Carpenter and McIntosh appear to have had second thoughts on this (see Carpenter, 2017). To us, however, the robustness of these hindlimb elements (presumably including the currently unaccounted for left metatarsals mentioned by McIntosh and Carpenter [1998]) indicate a referral to an apatosaurine (see McIntosh and Carpenter, 1998), or possibly *Galeamopus*, a diplodocine genus

Figure 8. Caudal vertebral elements of the type specimen of *Diplodocus longus* (YPM VP.001920). The letters indicate the vertebrae shown on figures 1 to 5. Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

with similarly stout limbs as apatosaurines (Tschopp and others, 2015; Tschopp and Mateus, 2017). Therefore, following McIntosh and Carpenter (1998), YPM VP.059136 is currently identified as *Apatosaurus* sp. in the YPM VP database.

Specimen YPM VP.059137

This specimen, which consists of the right metatarsals I-V, was figured by McIntosh and Carpenter (1998: figure 5) and was identified by them as possibly belonging to either *Haplocanthosaurus* sp. or *Brachiosaurus*, both of which are also known from other elements from the Marsh-Felch Quarry No. 1 (Foster, 2003). Thus, YPM VP.059137 is currently recorded as an indeterminate sauropod in the YPM VP database. The close spatial proximity of these pes elements in the YPM VP collections to both the elements of the restricted holotype and to the elements constituting YPM VP.001906 was the reason for the erroneous statement by Tschopp and Mateus (2016) that specimen YPM VP.001906 included a pes. Brachiosaurid pedes are identifiable, because the distal articular surface of the metatarsal IV is beveled compared to the long axis (D'Emic, 2012; Mannion and others, 2013; Maltese and others, 2018). Such a beveling is present in the metatarsal IV of YPM VP.059137, but no pedal material has ever been found articulated with a specimen clearly referable to *Brachiosaurus* (Maltese and others, in 2018), so that we herein refer YPM VP.059137 to Brachiosauridae indet.

SPECIMEN YPM VP.060256

Three additional fragments present in the YPM col-

Figure 9. Right half of middle chevron of the holotype specimen of *Diplodocus longus* (YPM VP.001920), in dorsal (A), anterior (B), left lateral (C), posterior (D), right lateral (E), and ventral view (F). Courtesy of the Division of Vertebrate Paleontology; YPM VP.001920, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

lections are of a crushed right femur. These have never been mentioned or figured in any publication and have only recently been cataloged as *Apatosaurus* sp. in the YPM VP database. Only the distal portion provides some morphological information, and an indication of its robustness, which appears to be comparable to the robustness of the left femur of YPM VP.059136 mentioned above. We therefore tentatively attribute YPM VP.060256 to Apatosaurinae indet.

DOUBTS RAISED ON THE ICZN CASE

Autapomorphies

Mortimer (2017) correctly pointed out that the case of Tschopp and Mateus (2016) was mainly based on a single phylogenetic analysis (Tschopp and others, 2015), which he argued did not include characters representing "every potential aspect of morphological variability" (Mortimer, 2017: p. 129). Therefore, according to Mortimer (2017), the fact that the analysis of Tschopp and others (2015) was not able to find autapomorphic features could not be taken as evidence for the type specimen YPM VP.001920 being morphologically undiagnosable. Whereas we agree that a phylogenetic analysis based on morphological characters always only captures an incomplete picture of osteological features and their shapes, which is necessarily influenced by the researcher creating the matrix, we also note that the matrix used by Tschopp and others (2015) was based on several previous analyses tailored to diplodocoid sauropods (e.g., Whitlock, 2011a; Carballido and others, 2012; Mannion and others, 2012), and added many more characters based on the personal observations of E. Tschopp in numerous collections, including the YPM's. The final matrix analyzed in Tschopp and others (2015) included 477 characters, of which 67 (14%) coded for features in the tail (i.e., caudal vertebrae and chevrons). Due to the incompleteness of YPM VP.001920, this type specimen could only be scored for 19 of these characters. Such an extensive matrix based on the work of a number of researchers can be expected to cover the most significant morphological variability (especially taxonomically informative variation). Moreover, the fact that YPM VP.001920 could only be scored for 4% of the characters highlights the very fragmentary state of this specimen, and the improbability of finding new, unique features to accurately diagnose the species.

Because the matrix of Tschopp and others (2015) was designed to study the relations between specimens, and to assess intraspecific variation, it was specifically constructed to capture as much morphological variability as could be recognized, and also included potentially autapomorphic features, which is usually not the case in morphological phylogenetic analyses at species level. In fact, the transverse lamina behind the prezygapophyses found in both YPM VP.001920 (figure 2) and AMNH FARB 223 (Tschopp and others, 2015; Tschopp and Mateus, 2016) was added as a character to the phylogenetic analysis after E. Tschopp's personal observations at the YPM. By including potentially autapomorphic features as phylogenetic characters, a specimen level analysis can serve as an objective test if they are found to be homologous (and thus of taxonomic importance; Longrich, 2015; Tschopp and others, 2015; Tschopp and Upchurch, in press), in particular when using a maximum parsimony criterion, which minimizes the amount of homoplasies during the tree search (Farris, 1983). However, as pointed out by Tschopp and Mateus (2016), the analysis of Tschopp and others (2015) could not confirm the lamina to be a phylogenetically informative, and, thus, a potentially diagnostic character for the species *D. longus*. Therefore, we would strongly disagree with Carpenter (2017) that an interpretation of this lamina as an autapomorphy of *D. longus* would be "more conservative" than the result of an extensive phylogenetic analysis (Carpenter 2017: p. 48).

Mortimer (2017) also mentioned two features suggested by McIntosh and Carpenter (1998) to be autapomorphic in YPM VP.001920: relatively short caudal centra, and pneumatic foramina that do not extend as far back in the tail as in other specimens of *Diplodocus*. Contrary to what Mortimer (2017) implies in his comment, characters describing these features were included in the analysis of Tschopp and others (2015; see characters 308, 309, 332). However, even if this would not have been the case, these proposed autapomorphies are questionable. The correct interpretation of both of these features depends on the position of the vertebrae in the caudal column. The elongation of the centrum increases considerably from anterior to mid-caudal centra in diplodocine sauropods, and characters describing this elongation have already been included in earlier phylogenetic analyses of sauropod dinosaurs (e.g., Yu, 1993; Upchurch, 1998). As noted by Tschopp and others (2015: p. 130), the relatively low mean elongation ratio of the caudal vertebrae of YPM VP.001920 compared to other specimens of *Diplodocus* is probably just a result of the fact that the specimen only preserves the less elongate anterior mid-caudal elements. Difficulties in correctly identifying the position of the series of preserved vertebrae of YPM VP.001920 are highlighted by McIntosh and Carpenter (1998), who dedicated more than a page to this issue. They concluded that the caudal series could range from positions 6-23 to 12-29, with the most probable positions being 9-26 (McIntosh and Carpenter, 1998: p. 96). These variable positions obviously also impact the interpretation of how far back in the tail the vertebrae still bear pneumatic foramina, which appears to be individually variable within specimens referred to *Diplodocus hallorum* as well as the non-diplodocine sauropods *Apatosaurus* and *Giraffatitan* (Wedel, 2005; Wedel and Taylor, 2013). Consequently, and given that erroneous positional interpretations have already led to taxonomic confusion in diplodocines (see the case of "*Seismosaurus;*" Gillette, 1991; Lucas and others, 2006; Lovelace and others, 2007; Tschopp and others, 2015), we would argue that the two potentially autapomorphic features proposed by McIntosh and Carpenter (1998) and cited by Mortimer (2017) are not suitable for diagnosing a species of diplodocine sauropod.

Stratigraphic Age

The presumably older stratigraphic age of YPM VP.001920 compared to other specimens and species of *Diplodocus* has been put forward as an argument against a replacement of the type species, *D. longus,* by Demirjian (2017) and Mortimer (2017), because it would indicate that *D. longus* is actually a distinct species and therefore available as the type species of *Diplodocus*. The geologically older age is most probably true (Tschopp and others, 2016), even though long-distance correlation of quarries across the Morrison Formation is still difficult (Trujillo, 2006; Maidment and others, 2017). However, it would be questionable to diagnose a paleontological species solely based on the fact that it occurs in a layer of minimally different geological age than another species. Evolutionary rates have been shown to be variable, with certain species evolving very slowly, while others experience fast radiations (e.g., Adams, 2013; Herrera-Flores and others, 2017), so that time alone is an unreliable feature for a species diagnosis. The use of apomorphy-based species concepts instead of chronospecies in paleontology is therefore crucial and indeed widespread in paleontology (Allmon and Yacobucci, 2016).

The mention of *D. longus* as a potential ancestral species in the abstract of Tschopp and others (2016) that was cited by Demirjian (2017) was not meant to imply that YPM VP.001920 is diagnosable at the species level, but rather to show that the methodology employed by Tschopp and others (2016) might be capable of recognizing ancestral species in a phylogenetic analysis (though we admit that the wording of Tschopp and others [2016] did not properly reflect this). YPM VP.001920 is undiagnosable at the species level, thus making the species *D. longus* a *nomen dubium*. Even in the unlikely case that additional, more complete specimens would be found in strata of an equivalent age as YPM VP.001920, and that these new specimens would also share unique, diagnostic features with YPM VP.001920, a future revalidation of the species *D. longus* would have no effect on the use and validity of the proposed new type species *D. carnegii*. The two species would simply both be considered valid, as YPM VP.001920 will always remain the holotype for *D. longus*, it would just not be considered to be the type species and thus reference for the genus *Diplodocus*, a fact that is effectively already the case now (Taylor, 2017).

Taxonomic Instability

One of the main arguments of Tschopp and Mateus (2016) was the fact that having a species declared to be a *nomen dubium* as the type species would create taxonomic confusion, a fact that Mortimer (2017) challenged. Whereas it is true that Tschopp and others (2015) found YPM VP.001920 to belong to the genus *Diplodocus*, it is also true that highly incomplete specimens like YPM VP.001920 are more prone to phylogenetic instability (Wilkinson, 1995; Wiens, 2006; Butler and Upchurch, 2007). Indeed, YPM VP.001920 was identified by Tschopp and others (2015) as one of the most unstable operational taxonomic units in their analysis (see also Taylor, 2017). It also has already been the cause for some taxonomic confusion in the past because of the incorrect identification of the reasonably complete specimen AMNH FARB 223 as *D. longus* by Osborn (1899), and the subsequent morphological comparisons of newly found specimens with the referred specimen, AMNH FARB 223, instead of the holotype specimen, YPM VP.001920 (see a summary in Tschopp and Mateus, 2016). A similar case was the genus *Titanosaurus*, which also was typified by a type species represented by a highly incomplete holotype specimen (Wilson and Upchurch, 2003). As in *Diplodocus*, the features originally proposed to be diagnostic for the type species *T. indicus* were later found to be more widespread among sauropods, resulting in *T. indicus* being a *nomen dubium*. Therefore, Wilson and Upchurch (2003) suggested to abandon the use of the genus and its co-ordinated higher-ranked taxa, which has since been followed by all sauropod workers. In order to avoid the same fate for *Diplodocus*, Tschopp and Mateus (2016) proposed to substitute the type species.

Although the ICZN Code does not directly have an article discussing the replacement of a type species, and the necessity to have a diagnosable type species for a genus (see Article 70, and Mortimer, 2017), we argue that similar principles should be applied at the level of genera as the ones that apply at the level of species. As article 61.1 of the Code states: “the name-bearing type of a nominal taxon provides the objective standard of reference for the application of the name it bears.” It goes on in Article 61.1.1, stating: “No matter how the boundaries of a taxonomic taxon may vary in the opinion of zoologists the valid name of such a taxon is determined (Article 23.3) from the name-bearing type(s) considered to belong within those boundaries.” Given the instability of YPM VP.001920, and thus the species *D. longus* in phylogenetic analyses, it is not entirely improbable that future discoveries or changes to the matrix or methodology will find YPM VP.001920 in a slightly more basal position, potentially in a polytomy with the well known, and widely accepted genus *Barosaurus* Marsh, 1890, which is often found to be the sister genus of *Diplodocus* (Whitlock, 2011a; Gallina and others, 2014; Tschopp and Mateus, 2017). In case the relatively robust hindlimb (YPM VP.059136) from the type locality would indeed belong to the type tail, as suggested by Carpenter (2017), this might even result in a recovery of YPM VP.001920 within the genus *Galeamopus*, which occurs in the type locality and has more robust limbs than other diplodocine genera (Tschopp and Mateus, 2017). In these cases, retaining *D. longus* as the type species of *Diplodocus*, and a strict application of nomenclatural rules would result in the synonymization of the genera *Diplodocus*, *Barosaurus*, *Galeamopus*, and possibly *Kaatedocus* (depending on the phylogenetic analysis used), consequently resulting in the loss of the latter three genera as valid taxa because of the Principle of Priority. Thus, although the non-diagnostic nature of YPM VP.001920 and the invalidity of *D. longus* might not be an imminent threat to the genus *Diplodocus* (Mortimer, 2017), because it was one of the first named sauropod dinosaurs, it could be a threat to other genera erected after *Diplodocus* and considered to be its sister taxa. Whereas *Kaatedocus* and *Galeamopus* have only been recently named, and still need to be studied in more detail to be considered to be well-established genera, *Barosaurus* has been studied widely since its erection in the late 1800s, and its validity has never really been questioned (see McIntosh, 2005 for the latest review), so that a synonymization with *Diplodocus* because of the instability of a single, incomplete operational taxonomic unit would be unreasonable. Through a replacement of *D. longus* as the type species of *Diplodocus* by the phylogenetically stable, and well-studied *D. carnegii*, potential future problems like the one outlined above could be avoided (see also Taylor, 2017).

At the level of species, the type concept is described in chapter 16 of the Code. The designation of a neotype at species level can be the equivalent to the proposal of replacement of the type species at the genus level. Article 75.5 states the following: “When an author considers that the taxonomic identity of a nominal species-group taxon cannot be determined from its existing name-bearing type (i.e., its name is a *nomen dubium*), and stability or universality are threatened thereby, the author may request the Commission to set aside under its plenary power (Article 81) the existing name-bearing type and designate a neotype.” And further: “When an author discovers that the existing name-bearing type of a nominal species-group taxon is not in taxonomic accord with the prevailing usage of names and stability or universality is threatened thereby, he or she should maintain prevailing usage (Article 82) and request the Commission to set aside under its plenary power (Article 81) the existing name-bearing type and designate a neotype.” (Article 75.6). *D. longus* is both a *nomen dubium*, and its holotype YPM VP.001920 has generally been substituted by AMNH FARB 223 as the reference specimen for comparisons with this species (Tschopp and Mateus, 2016). Therefore, both articles 75.5 and 75.6 apply to this case, but with the peculiar difficulty that the incompleteness of YPM VP.001920 also prevents the identification of another specimen suitable to serve as a neotype (Tschopp and Mateus, 2016). Consequently, Tschopp and Mateus (2016) proposed the replacement of the type species instead of proposing a neotype. There is strong precedent for this among other equally undiagnosable Marsh-named taxa, the most similar recent case being the one concerning the well-known Marsh dinosaur genus, *Stegosaurus* Marsh, 1877, in which the Commission preserved the taxonomic stability by choosing to replace the unidentifiable type species of the genus, i.e., *Stegosaurus armatus* Marsh, 1877 (whose holotype specimen is YPM VP.001850), with the very well represented nominal species *Stegosaurus stenops* Marsh, 1887 (whose holotype specimen is USNM V 4934) (ICZN 2013).

Possible Synonymization

The possibility that future finds might lead to the conclusion that *D. longus* is synonymous to the newly proposed type species *D. carnegii* has already been discussed by Tschopp and Mateus (2016), but was put forward again by Mortimer (2017) as a potential future threat to the validity of *D. carnegii*. However, just as it is highly improbable that future studies would find unique features diagnosing *D. longus* (see above), the same applies for the finding of unique, shared features with *D. carnegii*, but not with the other valid species in the genus *D. hallorum*.

Precedent ICZN Cases

Tschopp and Mateus (2016) mentioned several cases with similar issues of undiagnostic holotypes of the type species, where a replacement of the type species was accepted by the Commission in the past, including the one discussed above (ICZN 2013). Whereas we agree with Carpenter (2017) and Mortimer (2017) that details may differ among these cases, the main issues of the undiagnosability of the holotype, and the unavailability of a neotype remain the same. We acknowledge that there is no "case law" (Principle 8 in the Introduction of the Code), but given that the nomenclatural rules in the Code are intended to serve as "tools that are designed to provide the maximum stability compatible with taxonomic freedom" (Principle 4 in the Introduction of the Code), we should not apply them strictly and equally in all groups of animals with various taxonomic histories. Citing precedents outside of Dinosauria (Mortimer, 2017) is arguable, and the fact that most of the sauropod specialists who expressed an opinion on the case were favorable (Lucas, 2017; Taylor, 2017; Woodruff, 2017) supports the rationale for the Tschopp and Mateus (2016) proposal.

CONCLUSION

The famous dinosaur genus *Diplodocus* is currently typified by *D. longus*, a species with an incomplete and undiagnostic holotype (YPM VP.001920). No bones other than some caudal vertebrae (figures 1 to 8) and an associated partial chevron (figure 9) can be confidently referred to the individual comprising YPM VP.001920 (per McIntosh and Carpenter, 1998; and contra Carpenter, 2017). Even though there is still a lot of sauropod material from the Garden Park area that remains unprepared and uncatalogued, including several robust phalanges at the YPM, it appears improbable that additional diagnostic material from the same individual will be identified in future. A designation of a new type species for *Diplodocus*, as proposed by Tschopp and Mateus (2016) is the most reasonable solution to this taxonomic quagmire and the negative comments from others against the case are debatable, further supporting the proposed replacement of *D. longus* with *D. carnegii* as the type species for the genus *Diplodocus*.

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