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Rebuttal of McFeeters, Ryan and Cullen, 2018, 'Positional variation in pedal unguals of North American ornithomimids (Dinosauria, Theropoda): A Response to Brownstein (2017)'

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Abstract: The Arundel Clay of Maryland is among the only Early Cretaceous terrestrial units known from eastern North America. Research on some theropod dinosaur bones from this layer has indicated the presence of two ornithomimosaur taxa in the assemblage. However, a recent paper discussed issues with the definite assignment of any of these unguals to Ornithomimosauria and suggested that morphological differences originally interpreted to be indicative of the presence of two ornithomimosaurs could be explained by positional variation. Here, I show that substantial evidence persists for the presence of two ornithomimosaurs in the Arundel Clay assemblage, even considering the recent description of positional variation in ornithomimosaur pedal unguals. Furthermore, the argument against the confident assignment of these unguals to ornithomimosaurs is shown to be based on oversimplified comparisons that do not take into account the combination of features in the Arundel specimens that allow for their assignment to that clade. Although several small points made in the initial paper describing the Arundel specimens are incorrect or unsubstantiated, the differences between the Maryland unguals are outside the spectrum of positional variation and are indicative of the presence of two ornithomimosaurs in the Arundel Clay assemblage.

The Arundel Clay of Maryland is an Aptian unit (e.g., Lipka et al. 2006) that preserves a diverse assemblage of terrestrial vertebrates (e.g., Gilmore 1920; Weishampel and Young 1996; Weishampel et al. 2006). Dinosaur clades represented in the Arundel Clay include the Dromaeosauridae, Titanosauriformes, Carcharodontosauridae, Nodosauridae, Iguanodontia, Ceratopsia, and Ornithomimosauria, together comprising one of the most diverse faunas of this group of archosaurus known from the Early Cretaceous of North America (e.g., Weishampel and Young 1996; Kranz 1998; Weishampel 2006). Because of its extensiveness, the Arundel Clay assemblage has the potential to greatly inform models of Cretaceous vertebrate biogeography (e.g., Weishampel and Young 1996; Kranz 1998; Lipka et al. 2006; Weishampel 2006).

Brownstein (2017) examined new theropod material from the Arundel Clay and concluded the bones reflected the presence of two distinct ornithomimosaurs in the assemblage. However, McFeeters et al. (2018) disagreed with four major acts in that paper: (1) the confident assignment of the Arundel Clay pedal unguals to ornithomimosaurs, (2) the identification of one bone as the manual ungual of an ornithomimosaur, (3) comparisons of the Arundel Clay humerus to the corresponding element in other ornithomimosaur taxa, and (4) the identification of two distinct morphotypes of ornithomimosaur based on comparisons of the pedal unguals. Here, I respond to the arguments made by McFeeters et al. (2018) regarding these and other points of interest.

Institutional abbreviations: NHRD-AP, fossil collections of the National and Historical Resources Division Archaeology Program from Dinosaur Park, Maryland, United States; USNM PAL/USNM V, paleontology collections of the National Museum of Natural History, Washington, DC, United States.

Assignment of the Arundel Clay pedal unguals to ornithomimosaurs

Regarding the assignment of the pedal unguals (NHRD-AP 2014.s.195, NHRD-AP 2014.s.197, NHRDAP 2014.s.198, NHRD-AP 2016.v.1104, USNM PAL 529423, and USNM V6107) to ornithomimosaurs, McFeeters et al. (2018) cautioned that the features used to assign the unguals to this group in

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Brownstein (2017) were either apparently undiagnostic to Ornithomimosauria (i.e., a triangular outline in proximal view) or found in other dinosaur clades (e.g., flattened pedal unguals, presence of a flexor fossa on the ventral surface of each ungual, lack of flexor tubercle on each ungual, straightened ventral edges). However, the validity of this argument relies on oversimplified comparisons of the Arundel Clay unguals with those of spinosaurids, abelisauroids, and *Gualicho shinyae* (e.g., Novas et al. 2005; Ibrahim et al. 2014; Apesteguía et al. 2016; Sereno 2017). In addition to representing theropods much larger than those of the Arundel Clay material, the flattened unguals of spinosaurids are heavily mediolaterally broadened with a larger flexor fossa that extend to the edges of the ungual and includes multiple large ridges (e.g., Novas et al. 2005; Ibrahim et al. 2014; Maganuco and Dal Sasso 2018). This contrasts with the condition in the Arundel Clay unguals, which are mediolaterally compressed and have ventral fossa that are smaller, more localized (i.e., surrounded by bone of the ventral surface) and divided in some specimens by a single ridge (Fig. 1B). The pedal unguals from the Arundel Clay also lack a combination of features found in abelisauroids, namely a triangular portion of raised bone on their ventral surfaces and secondary grooves for the claw sheath that run parallel to the dorsal edge of the ungual along the medial and lateral surfaces (e.g., Sereno 2017). Although the Arundel unguals share with those of noasaurids slight curvature, they differ from that group in possessing localized flexor fossa on their ventral surfaces (e.g., Novas et al. 2005; Sereno 2017). Finally, the Arundel Clay pedal unguals are much smaller than those of *Gualicho*, are not as recurved as in the unguals of that taxon, and lack any flexor tubercles (e.g., Apesteguía et al. 2016). Abelisauroids and spinosaurids are currently unknown from the fossil record of North America, which is extensive for medium-sized (>10 kg) and large dinosaurs during the Jurassic and Cretaceous (e.g., Weishampel et al. 2004). Thus, it is highly improbable that the Arundel Clay unguals are representative of any of the theropod groups discussed by McFeeters et al. (2018). Based on a combination of their size, slightly recurved to flattened nature, straightened ventral edges, lack of flexor tubercles, proximoventral edges developed into keels, and the presence of localized, deepened flexor fossa on their ventral surfaces, the unguals are assignable to Ornithomimosauria (Barsbold and Osmólska 1990; Makovicky et al., 2004; Choiniere et al. 2012). As noted, the assignment of the unguals to ornithomimosaurs among other theropod groups is further supported by the absence in North America of theropods that possess unguals morphologically similar in some ways to those of ornithomimosaurs.

Identification of one bone as the manual ungual of an ornithomimosaur

Concerning the forelimb elements described by Brownstein (2017), McFeeters et al. (2018) disputed the identification of the bone NHRD-AP 2014.s.196 as a manual ungual. Contra McFeeters et al. (2018), a reduced or nearly absent flexor tubercle is found in ornithomimid manual unguals from the third and fourth digits of the manus (e.g., Osborn 1921; Osmólska et al. 1972; Makovicky et al. 2004). Although an interpretation of NHRD-AP 2014.s.196 as an eroded pedal ungual (with the flexor fossa on the ventral surface absent due to erosion) is certainly plausible, the curvature and relative mediolateral compression compared to the ornithomimosaur pedal unguals from the Arundel Clay support the hypothesis that the specimen comes from the manus rather than the pes (e.g., Osmólska et al. 1972; Makovicky et al. 2004). A reduced flexor tubercle in this specimen may have been eroded away, as the bone is clearly somewhat abraded (Brownstein 2017:fig. 2A-D).

The Arundel Clay humerus compared to that of other ornithomimosaur taxa

McFeeters et al. (2018) also disputed the interpretation of the partial humerus described by Brownstein (2017) as of similar robust grade to the corresponding bone in *Harpymimus* based on the incompleteness of the Maryland specimen, suggesting that the robust aspect of basal ornithomimosaur humeri previously described could not be determined in the Arundel Clay specimen. Although McFeeters et al. (2018) are certainly correct that the complete length of the Arundel Clay humerus is unknown, the size of the distal condyles relative to the proximal end and the thickened, robust nature of the bone in medial and lateral views can all be determined from the bone as preserved (Brownstein 2017:fig. 1) and compare favorably to *H. okladnikovi* (Barsbold and Perle 1984; Kobayashi and Barsbold, 2005).

Identification of two distinct morphotypes of ornithomimosaur in the Arundel Clay

The most extensive critique of Brownstein (2017) by McFeeters et al. (2018) concerned the issue of variation in the unguals of ornithomimosaurs due to their position on the foot rather than to their affinities to multiple taxa. Several issues confound the argument of McFeeters et al. (2018) that differences between the unguals of different digits in the pes account for variation in the Arundel Clay specimens. McFeeters et al. (2018) identified five morphological differences among pedal unguals from the same foot in ornithomimids: the outline of the proximal articular facet, the relative sizes of concavities present in this facet, the symmetry of the grooves for the claw sheath, the mediolateral curvature of the unguals, and their shape in ventral view; they suggested that these accounted for the differences noted by Brownstein (2017) for the unguals described from the Arundel Clay. However, only two of the features noted by McFeeters et al. (2018) to vary in ornithomimid unguals known to be from the foot of the same individual correspond to those used to differentiate the unguals from the Arundel Clay by Brownstein (2017): the shape of the grooves for the claw sheath and the proximal articular facet. Furthermore, despite the claims of McFeeters et al. (2018) that the different contributions of the proximodorsal process to the shape of the proximal articular facets in the Arundel Clay unguals are due to the presence of deepened sulci proximally adjacent to the grooves for the claw sheath on both the medial and lateral surfaces of NHRD-AP 2014.s.195 and USNM PAL 529423 and the relative depth of the medial and lateral grooves for the claw sheath are consistent with positional variation, the differences in these features among the Arundel Clay bones as described by Brownstein (2017) either pertain to characteristics that McFeeters et al. (2018:63) considered uninformative for the position of the unguals in the foot (i.e., "the development of the proximodorsal process") or differ from the positional variation described in that study (e.g., the deepness of the grooves for the claw sheath). Regarding the shape of the proximal articular facet, the variation in the Arundel Clay unguals is due to the contribution of the proximodorsal process to the shape of the bone, as noted in Brownstein (2017), and not to any asymmetrical morphology. In NHRD-AP 2014.s.195 and USNM PAL 529423, the unguals of one morphotype, the proximodorsal process is shortened. However, it is distinctly pinched off from the main bone in proximal view. McFeeters et al. (2018) claim that the sulci present in NHRD-AP 2014.s.195 and USNM PAL 529423 among the Arundel Clay unguals contribute to their shape in proximal view and use this interpretation to support their argument that the Arundel Clay unguals represent positional variation in a single ornithomimosaur taxon. However, this is an incorrect interpretation of the anatomy of these specimens. Brownstein (2017) noted that the sulci contribute to the ridge on the dorsal surface of NHRD-AP 2014.s.195 and USNM PAL 529423 that becomes the proximodorsal process proximally. However, these sulci are separated from the proximal articular facets in NHRD-AP 2014.s.195 and USNM PAL 529423 by an area of bone (Fig. 1A; Brownstein, 2017:figs. 3C, H), and thus do not contribute to the proximal shape of these specimens. The condition in NHRD-AP 2014.s.195 and USNM PAL 529423 is unlike that in NHRD-AP 2014.s.197 and NHRD-AP 2014.s.198 (the most well-preserved unguals of the "blunt" morphotype), where enlarged sulci proximal to the grooves for the claw sheath are absent and a more heavily developed proximodorsal process in lateral and medial views does not distinctly diverge from the smooth outline of the ungual in proximal view. Whereas McFeeters et al. (2018) note that asymmetrically deepened grooves for the claw sheath are diagnostic of pedal unguals II and IV in many ornithomimosaurs from western North America and elsewhere (e.g., in *Aepyornithomimus*, Tsogtbaatar et al. 2017) the condition noted by Brownstein (2017) to distinguish the two Arundel Clay ungual morphotypes was that in NHRD-AP 2014.s.198 and possibly NHRD-AP 2014.s.197, both the lateral and medial grooves for the claw sheath are reduced (Brownstein, 2017:figs. 4A–B, F–G). In addition to the greater curvature of the unguals NHRD-AP 2014.s.197 and NHRD-AP 2014.s.198 than in NHRD-AP 2014.s.195 and USNM PAL 529423 (Fig. 1A, D), the different position of the flexor fossa in either morphotype, and the lack of any ridge (= striations of Brownstein, 2017) dividing the flexor fossa of the former two bones, these features of the proximodorsal process, proximal articular facet, and grooves for the claw sheath are outside the range of positional variation documented by McFeeters et al. (2018) and are thus indicative of the presence of two ornithomimosaurs in the Arundel Clay. Although I concur with McFeeters et al. (2018) in their assignment of particular pedal unguals described by Brownstein (2017) to the marginal or central digits of the foot, their argument regarding the assignment of the Arundel Clay unguals to different positions in the foot of a single taxon of ornithomimosaur is lacking in anatomical evidence. A comparison of well-preserved ornithomimosaur pedal unguals from the Arundel Clay assigned to different morphotypes by Brownstein (2017) may be found in Figure 1.

Additional comments

Several other comments by McFeeters et al. (2018) also warrant reply. McFeeters et al. (2018) challenge the nature of pedal unguals with triangular proximal articular facets as a diagnostic feature of Ornithomimosauria. McFeeters et al. (2018) remarked on the sparse information on ornithomimosaur pedal ungual morphology present in Makovicky et al. (2004) and on the shape of the unguals of *Gallimimus*, *Ornithomimus*, and *Struthiomimus* in proximal view. However, in their discussion of the anatomy of these and other ornithomimosaur taxa, Makovicky et al. (2004:146) note that in ornithomimosaurs "the pedal unguals are triangular in cross-section with flat ventral surfaces and without flexor tubercles." Nevertheless, I concur with McFeeters et al. (2018) that this feature may not be entirely diagnostic of unguals of the group, being positionally variable as they describe in western North American ornithomimosaur taxa. This does not affect the assignment of the Arundel Clay specimens to Ornithomimosauria, which is based on a variety of other characteristics. McFeeters et al. (2018:65) claimed that the proximal surfaces of the pedal unguals of *Beishanlong* were not documented by Makovicky et al. (2009) [("Makovicky et al. (2009:fig. 3) figured three pedal unguals of *Beishanlong grandis*, but did not document their shapes in proximal view, and pedal ungual III is not represented"] and regarded this as an issue in the argument of Brownstein (2017) against positional variation as the cause of the differences in the Arundel Clay unguals. However, Makovicky et al. (2009:194–195) explicitly remarked that the "recovered pedal unguals [of *Beishanlong*] are triangular in cross section and bear shallow ventral depressions surrounding the highly reduced flexor tubercle." McFeeters et al. (2018) also noted the incompleteness of the pedal unguals of *Rativates evadens* as a confounding factor in the argument made by Brownstein (2017) against assignment of the Arundel Clay unguals to different pedal digits of the same ornithomimosaur. However, based on the same figures in McFeeters et al. (2016:fig. 11A) suggested by them to show unguals too incomplete for discussion of their similarity in proximal view, enough of the proximal end of pedal ungual IV is preserved to demonstrate it possessed a relatively similar triangular outline to pedal ungual II. McFeeters et al. (2018) also briefly remarked on the interpretation of USNM 6107 as a pedal ungual III by Brownstein (2017), suggesting it to be curved in dorsal and ventral views in published figures (e.g., Gilmore 1920; Serrano-Brañas et al. 2016). However, asymmetry in this specimen may be amplified due to erosion, as the ventromedial edge is clearly somewhat abraded and is seen as so in the photographs they referenced (Serrano-Brañas et al. 2016:fig. 8.2b). Finally, McFeeters et al. (2018) discuss issues with the comparison of the Arundel Clay ornithomimosaur fauna to that of the Yixian Formation of China by Brownstein (2017), noting Jin et al. (2012) recovered both taxa from this formation (*Hexing* and *Shenzhousaurus*) within a polytomy of basal ornithomimosaurs. Although I concur here that phylogenetic disparity between these genera does not seem extensive, the coexistence of these two taxa in the Yixian Formation, even when considered closely related, does resemble the condition in the Arundel Clay in that two genera coexist. This note on the relationships of the Yixian Formation ornithomimosaurs does not greatly affect the biogeographic discussion of Brownstein (2017).

McFeeters et al. (2018) address positional differences in the unguals of ornithomimosaurs, the presence of which have implications for the identification and taxonomic assessment of material from this clade. However, as discussed herein, the arguments made by McFeeters et al. (2018) against the interpretations of a theropod humerus and possible manual ungual from the Arundel Clay, the assignment of ornithomimosaur unguals from that unit to the clade and their assignment to two morphotypes, and discussion of the biogeographic implications of all these bones by Brownstein (2017) is unsupported by the anatomy of the Arundel Clay specimens and the data collected in their paper for western North American ornithomimids or unimportant to the discussions in the earlier study.

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