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Response to Brownstein (2018) 'Rebuttal of McFeeters, Ryan and Cullen, 2018'

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We agree that the pedal unguals from the Arundel Clay described by Brownstein (2017) more likely belong to ornithomimosaurs than to any other theropod clade, and treated them as such in our original discussion (McFeeters et al. 2018). We thank Brownstein (2018) for providing further elaboration of morphological characters that may be useful for distinguishing ornithomimosaur pedal unguals from those of other theropods. We interpret the character of a triangular cross-section, which we do not dispute occurs in ornithomimosaur pedal unguals, to refer to the overall morphology of the ungual being grossly defined by having relatively distinct ventral, dorsomedial, and dorsolateral surfaces, such that a section taken along an arbitrary point along the length of the ungual can be considered generally triangular. However, this characterization of a generalized section of the ungual is not necessarily an adequate description of the specific outline of the proximal facet, which must articulate with the corresponding penultimate phalanx, and varies according to position within each pes.

While it is possible that two (or more) ornithomimosaur taxa are represented by the pedal unguals currently known from the Arundel Clay, the appropriate null hypothesis in this situation is that no taxonomic variation is present in the sample, and the burden of evidence is on demonstrating that the two morphotypes must belong to different taxa. We concluded that the differences noted by Brownstein (2017) resemble the type of positional ungual variation we observed in related taxa from Alberta, and therefore do not offer a compelling case for rejecting the null hypothesis. The range of expected intraspecific variation in ornithomimosaur pedal unguals has largely not been quantified, and further work is needed if Brownstein's claims on this topic are to be supported. For example, whether or not the degree of dorsoventral curvature is judged to support taxonomic separation of the two morphotypes is at this point little more than a matter of opinion. The objective of our short paper was to document consistent patterns of variation between different pedal ungual positions in ornithomimids, rather than to establish ranges of intraspecific variation for all pedal ungual characters. While we distinguished between characters that can be considered diagnostic of position in the pes and those that are not consistently informative in this regard, observed variation was not limited to the former category. As many of the specimens in our study were only figured in proximal and ventral view, it is not apparent how Brownstein has estimated the range of variation present in our sample in characters more appropriately observed in medial and lateral view, such as the prominence of the grooves for the claw sheath. The form of the proximodorsal process and the claw sheath grooves were mentioned in the summation of the digit III ungual morphology as examples of their symmetry, rather than to assign importance to the relative prominence of these features.

Regarding the other material described by Brownstein, we reiterate our citation of Osmólska et al. (1972: fig. 14) clearly showing a distinct flexor tubercle on all manual unguals of the ornithomimid *Gallimimus*. In a *Struthiomimus* manus figured by Osborn (1917: fig. 3), the flexor tubercles of manual unguals II and III (following Osborn; III and IV of some authors) are hidden by the orientation of these unguals in dorsal view, but are visible in palmar view in the same figure (see also Nicholls and Russell 1985: fig. 8, for *Struthiomimus* unguals in medial view). We view the robustness of the humerus, even if verified, as of dubious phylogenetic significance, since the distribution of this character suggests that a relatively robust humerus is the likely plesiomorphic condition for both *Harpymimus* and ornithomimids (Kobayashi and Lü 2003: appendix 2). The most robust ornithomimid humeri, such

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as that of *Anserimimus*, are comparable to *Harpymimus* (Kobayashi and Barsbold 2006: fig. 6), so the robustness of the Arundel element does not offer strong support for the grade of ornithomimosaur present.

The Aptian–Albian is a critically interesting, yet incompletely understood interval in the history of ornithomimosaurs. It contains the globally youngest occurrences of (non-ornithomimid, non-deinocheirid) 'basal ornithomimosaurs' and oldest occurrences of possible basal deinocheirids (Lee et al. 2014; Sues and Averianov 2016), and immediately precedes the oldest definitive occurrences of ornithomimids in the Cenomanian–Turonian of Asia (Sues and Averianov 2016, and references therein), as well as preceding a possible hiatus in the presence of ornithomimosaurs from the Cenomanian to Santonian of North America (McFeeters et al. 2016). The presence of coexisting basal and derived ornithomimosaurs in the Aptian of North America would indeed have important larger evolutionary and palaeobiogeographic implications, if further work supports this interpretation. However, while we appreciate Brownstein's work for documenting new material of Early Cretaceous North American ornithomimosaurs, we remain cautious of such far-reaching claims given the current state of evidence.

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