Description of Arundel Clay Ornithomimosaur material and a reinterpretation of *Nedcolbertia justinhofmanni* as an “Ostrich Dinosaur”: Biogeographic implications

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The fossil record of dinosaurs from the Early Cretaceous of eastern North America is scant, especially since few stratigraphic units from the east are fossiliferous. Among those that are is the Arundel Clay of the eastern seaboard, which has produced among the best characterized dinosaur faunas known from the Early Cretaceous of eastern North America. The diverse dinosaur fauna of this formation has been thoroughly discussed previously, but few of the dinosaur species originally described from the Arundel Clay are still regarded as valid genera. Much of the Arundel material is in need of review and redescription. Among the fossils of dinosaurs from this formation are those referred to ornithomimosaurians. Here, I describe ornithomimosaur remains from the Arundel Clay of Prince George’s County, Maryland which may be from two distinct ornithomimosaur taxa. These remains provide key information on the theropods of the Early Cretaceous of Eastern North America. Recent discoveries of small theropod material from the Arundel Clay are also reviewed and described for the first time. The description of the Arundel material herein along with recent discoveries of basal ornithomimosaurians in the past 15 years has allowed for comparisons with the coelurosaur *Nedcolbertia justinhofmanni*, suggesting the latter animal was a basal ornithomimosaur rather than a “generalized” coelurosaur as which it was originally described. Comparisons between the Arundel ornithomimosaur material and similar Asian and European specimens suggest that both extremely basal ornithomimosaurians and more intermediate or derived forms may have coexisted throughout the northern hemisphere during the Early Cretaceous.
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Abstract.

The fossil record of dinosaurs from the Early Cretaceous of eastern North America is scant, especially since few stratigraphic units from the east are fossiliferous. Among those that are is the Arundel Clay of the eastern seaboard, which has produced among the best characterized dinosaur faunas known from the Early Cretaceous of eastern North America. The diverse dinosaur fauna of this formation has been thoroughly discussed previously, but few of the dinosaur species originally described from the Arundel Clay are still regarded as valid genera. Much of the Arundel material is in need of review and redescription. Among the fossils of dinosaurs from this formation are those referred to ornithomimosaurids. Here, I describe ornithomimosaur remains from the Arundel Clay of Prince George’s County, Maryland which may be from two distinct ornithomimosaur taxa. These remains provide key information on the theropods of the Early Cretaceous of Eastern North America. Recent discoveries of small theropod material from the Arundel Clay are also reviewed and described for the first time. The description of the Arundel material herein along with recent discoveries of basal ornithomimosaurids in the past 15 years has allowed for comparisons with the coelurosaur *Nedcolbertia justinhofmanni*, suggesting the latter animal was a basal ornithomimosaur rather than a “generalized” coelurosaur as which it was originally described. Comparisons between the Arundel ornithomimosaur material and similar Asian and European specimens suggest that both
extremely basal ornithomimosaurs and more intermediate or derived forms may have coexisted throughout the northern hemisphere during the Early Cretaceous.

Introduction.

The fossil record of dinosaurs from eastern North America during the Cretaceous is sparse compared that of the west of the continent, and the most well-known dinosaur fauna known from eastern North America (on the basis of number of taxa and specimens) comes from the Arundel Clay of the Potomac Group of Maryland. This unit, which is Aptian in age (Kranz, 1998), has yielded specimens of the sauropod dinosaur *Astrodon johnstoni*, the ornithopod *Tenontosaurus* sp., the nodosaur *Priconodon crassus*, ceratopsian material, and a number of theropods including *Deinonychus* sp. and the dubious taxa *Allosaurus medius*, *Creosaurus potens*, and *Coelurus gracilis* (Kranz, 1998; Weishampel et al., 2004: Weishampel, 2006).

Some of the first ornithomimosaur material to come from the Arundel Clay has been the subject of some taxonomic confusion (Weishampel, 2006). Originally found by Lull (1911) to be the bones of an ornithopod he named *Dryosaurus grandis*, the ornithomimosaur specimens from the Arundel have been described as a species of *Ornithomimus* ("O." *affinis*), referred to the genus *Archaeornithomimus*, regarded as a small theropod of indeterminate affinities, and finally regarded as an ornithomimosaur of indeterminate affinities (Gilmore, 1920; Russell, 1972; Smith & Galton, 1990; Makovicky, Kobayashi & Currie, 2004; Weishampel, 2006). The metatarsal III and pedal ungual described by Gilmore (1920) were also referred to as *Ornithomimus sp.* or *Ornithomimus affinis* by Serrano-Brañas et al. (2016). However, if any of the material were to be determined a distinct and valid species in the future, the original species name (*grandis*) given by Lull (1911) would take priority. Given the rather unlikely inclusion of the Arundel material into
the Late Cretaceous western taxon *Ornithomimus* as a distinct species, the proper name would indeed be *O. affinis* due to the preoccupation of *Ornithomimus grandis* by “*O.*” grandis Marsh (1890).

Gilmore (1920) originally described the Arundel material as then a new species of ornithomimosaur based on some pedal elements and caudal vertebrae. Additionally, Weishampel and Young (1996) noted that pedal elements and the proximal portion of a tibia were retrieved in 1992. These are in the collections of the United States National Museum of Natural History.

Most recently, an astralagus was recovered from Prince George’s County, Maryland in 2010 (USNM PAL 540727). Additional material has also been recovered recently from the Arundel but never has been formally described until now.

Early Cretaceous ornithomimosaur remains have been retrieved from from Western North America (Ostrom, 1970; Galton & Jensen, 1975), Europe (Sanz & Wenz, 1988; Perez-Moreno et al., 1994; Naish, 2011; Neraudeau & Allain, 2012; Allain et al., 2014), Asia (Maleev, 1954; Dmitiriev, 1960; Kalandadze & Kurzanov, 1974; Hasegawa & Manabe, 1986; Xu & Wang, 1999; Boonchai & Grote, 2009; Ji et al., 2003; Molnar & Obata, 2009; Buffetaut, Suteethorn & Tong, 2009; Makovicky et al., 2009; Jin, Chen & Godefroit, 2012), and Africa (Choiniere, Forster & de Klerk, 2012). The rich fossil record of Early Cretaceous ornithomimosaur remains which has developed in the past decade has allowed for comparisons of the Arundel specimens with a multitude of new taxa.

Here, I describe new specimens of Arundel ornithomimosaur in the collections of the Dinosaur Park office at Mount Calvert Historical Park in Upper Marlboro, Maryland. These specimens, which were discovered isolated at the Dinosaur Park site, include two different morphotypes of pedal ungual that indicate the presence of two different ornithomimosaur genera.
within the Arundel Clay. The new Arundel ornithomimosaur material has implications for the
evolution of more derived members of the Ornithomimosauria, suggesting that they were present
across North America during the Early Cretaceous. However, the lack of specimens able to be
assigned to a single animal means that any naming of a new Arundel taxon or new taxa must
wait until a skeleton is recovered which can be confidently thought of as formed by associated
material. Additionally, a reinterpretation of *Nedcolbertia justinhofmanni* from the Early
Cretaceous of Utah as an ornithomimosaur is provided. The biogeographic and ecological
implications of more basal and more derived ornithomimosaur genera coexisting in North America are
discussed, though the paucity of material from these North American forms during the Early
Cretaceous makes any conclusions limited. The basal and derived features found in the Arundel
ornithomimosaur material may be indicative that both basal and more derived ornithomimosaur
essisted in the Arundel. The coexistence of two Early Cretaceous ornithomimosaur genera is also
seen in the Early Cretaceous Yixian Formation of China (Ji et al., 2003; Jin, Chen & Godefroit,
2012).

Methods.

Permits.

No permits were required for the described study, which complied with all relevant regulations.
Access to the collections of the Dinosaur Park office, Upper Marlboro, Maryland was given by
Mr. Benjamin Miller.

Institutional Abbreviations.
I use the term NHRD-AP to refer to the National and Historical Resources Division Archaeology Program collections of fossils from Dinosaur Park, Maryland. I use the term USNM PAL and USNM V to refer to the paleontology collections of the United States National Museum of Natural History, Washington DC.

The specimens described herein were photographed using a Canon Powershot G-12 digital camera and cropped for figures using Apple Preview.

Results.

Geological Setting.

The Arundel Clay is made up of black lignite and limonite and siderite massive dark-grey mudstones, appearing as discontinuing elongate sediments probably formed as deposits from oxbow swamps (Kranz, 1998; Lipka et al., 2006). It has been debated whether the sediments attributed to the Arundel comprise a distinct formation, a member of the Patuxent Formation, or a member of the Potomac Group alongside a Patuxent member (e.g., Kranz, 1998; Lipka et al., 2006; Stanford et al., 2010). Here, the classification of Lipka et al. (2006) referring to the Arundel Clay as a member of the Potomac Formation is followed. The sediments referred to as the Arundel are Aptian in age and have produced a diverse vertebrate fauna, including saurischian & ornithischian dinosaurs, testudines, anurans, the shark *Hybodus*, and the lungfish *Ceratodus* (e.g., Kranz, 1998; Weishampel et al., 2004; Weishampel, 2006). Each of the fossils which are for the first time described herein (NHRD-AP. 2015.v.103.9, NHRD-AP 2014.s.196, NHRD-AP 2016.5.503, NHRD-AP 2014.s.195, NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, USNM PAL...
529423 (cast), NHRD-AP 2016.v.1104) were found isolated at the Dinosaur Park site in Maryland. Kranz (2004) established this site as the locality where the holotype of the sauropod Astrodon johnstoni was found, remarking on the fact that the discovery of the holotype Astrodon teeth had originally been said to have been made near Bladensburg. Kranz (2004) explains that, in actually, the site of discovery of these teeth is near Muirkirk. Importantly, Gilmore (1920) remarked that the majority of the ornithomimosaur remains he described as “Ornithomimus affinis” were collected near Muirkirk. However, Gilmore (1920) does not state the precise site of collection. Thus, it may be that some of the originally described ornithomimosaur material came from nearby sites to the Dinosaur Park site from which the material described herein was collected.

Systematic Paleontology.

Dinosauria Owen 1852
Theropoda Marsh 1881
Ornithomimosauria Barsbold 1976
Ornithomimosauria indet.

Material: NHRD-AP 2015.v.103.9, proximal and distal ends of a humerus; NHRD-AP 2014.s.196, manual ungual; NHRD-AP 2016.5.503, caudal vertebra; NHRD-AP 2014.s.195, NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, USNM PAL 529423 (cast), NHRD-AP 2016.v.1104, pedal unguals.

Description: The eroded proximal and distal portions of a small left humerus, NHRD-AP 2015.v.103.9, were preserved (figure 1A-F). The humerus is hollow, and along with the size of the specimen, this feature suggests the humerus came from a small to medium-sized theropod.
dinosaur. The proximal end measures 101 mm long proximodistally, while the distal end is 70 mm in proximodistal length (Table 1). The humeral head is well-preserved. The deltopectoral crest is eroded, but does not seem to have been very prominent as there is no indication of any significant raised portion of bone on the portion of the shaft to which the deltopectoral crest corresponds. As in ornithomimosaurs, the preserved portion of the shaft is relatively straight (Makovicky, Kobayashi & Currie, 2004). The distal portion of the humerus is badly eroded, and the distal condyles are almost completely worn way. The humerus is most similar to that of *Harpymimus okladnikovi* in its relatively robust nature and size of its distal condyles relative to the proximal end (figure 6.4E in Makovicky, Kobayashi & Currie, 2004). Because dromaeosaurids (e.g. *Deinonychus*), troodontids (e.g. *Geminiraptor*), oviraptorosaurs (=*Microvenator*), and therizinosaurs (e.g. *Falcarius*) are also known from the Arundel Clay and other North American units of similar Early Cretaceous age (e.g. Weishampel & Young, 1996; Lipka, 1998; Weishampel, 2004; Kirkland et al., 2005; Weishampel, 2006; Senter et al., 2010; Senter et al., 2012), comparisons with these forms are warranted before assignment of the humerus to a basal ornithomimosaur like *Harpymimus*. NHRD-AP 2015.v.103.9 differs from all of these in lacking a moderately developed to well-developed and large deltopectoral crest (e.g. Clark, Maryańska & Barsbold, 2004; Mackovicky & Norell, 2004; Norell & Makovicky, 2004; Osmólska, Currie & Barsbold, 2004). NHRD-AP 2015.v.103.9 additionally differs from the humeri of tyrannosauroids (Holtz, 2004) in having a slight cleft separate the humeral head from the lateral tubercle. Thus, NHRD-AP 2015.v.103.9 can be assigned to a basal ornithomimosaur. Measurements of the both the proximal and distal portions of the humerus can be found in table 1.
NHRD-AP 2014.s.196 (figure 2A-D) represents the complete manual ungual of an ornithomimosaur. The manual ungual is elongate and flattened, and there is no flexor tubercle present. A small raised area on the ventral surface of this element is asymmetrically positioned and made up of leftover sediment, rather than being a flexor tubercle. The lack of a flexor tubercle and the flattened state of the manual ungual distinguishes this manual ungual from the previously listed clades of theropod dinosaur (Clark, Maryańska & Barsbold, 2004; Holtz, 2004; Mackovicky & Norell, 2004; Norell & Makovicky, 2004; Osmólska, Currie & Barsbold, 2004).

Instead, these morphologies ally the specimen with the manual unguals of ornithomimosaurs (Makovicky, Kobayashi & Currie, 2004). The grooves for the claw sheath are poorly defined, and in proximal view the ungual is ovoid in form. This manual ungual is most similar among basal and intermediate ornithomimosaurs to manual unguals II-3 and III-4 of the African species *Nqwebasaurus thwazi* (Choiniere, Forster & de Klerk, 2012). However, this manual ungual is much less recurved or elongate than those of *N. thwazi* and lacks any flexor tubercle. Instead, NHRD-AP 2014.s.196 best resembles ornithomimid manal unguals, such as those of *Gallimimus* (e.g. Makovicky, Kobayashi & Currie, 2004). This element is not an ornithomimosaur pedal ungual because it lacks a flexor fossa on its ventral surface. Thus, because of the lack of a flexor tubercle and its relatively elongate form, NHRD-AP 2014.s.196 is tentatively placed within Ornithomimosauria indet. Measurements of this element can be found in table 1.

A caudal vertebra NHRD-AP 2016.s.503 (Figure 2E-F) is mentioned here due to its similarities with the vertebrae described by Gilmore (1920) and its possible assignment to Ornithomimosauria indet. This elongate caudal vertebral centrum is somewhat similar to the caudal vertebrae described by Gilmore (1920), and as in the caudal vertebrae of ornithomimosurs, the vertebrae is hollow (e.g. Buffetaut, Suteethorn & Tong, 2009). The
centrum is ovoid in proximal view, and a portion of matrix obscures one end of the element. In some areas, the centrum is eroded. The dimensions of this vertebra are catalogued in table 1.

Five pedal unguals of two different morphotypes were examined and provide the best evidence for the presence of two distinct species of ornithomimosaur in the Arundel Clay ecosystem. These pedal unguals (figure 3A-J, figure 4A-O) share the presence of a flexor fossa on the ventral surface of each pedal ungual, the presence of relatively straight ventromedial edges on each of the unguals, and the presence of ventrolateral and ventromedial edges developed into keels, all diagnostic of ornithomimosaur (Barsbold & Osmólska, 1990; Longrich, 2008; Makovicky et al., 2009; Xu et al., 2011; Choiniere, Forster & de Klerk, 2012).

Though Choiniere, Forster & de Klerk (2012) noted that flattened pedal unguals and the presence of a flexor fossa on the ventral face of each pedal ungual were not exclusive traits to ornithomimosaur, the two traits are mutually exclusive of other taxa. This is because flattened pedal unguals are only known in parvicursorine alvarezsauroidea and *Avimimus portentosus* outside of Ornithomimosauria, whilst the presence of a flexor fossa on the ventral surface of each pedal ungual is only known in *Majungasaurus crenatissimus*. The ventrolateral and ventromedial edges have have been worn down in NHRD-AP 2014.s.197 and NHRD-AP 2016.v.1104. In NHRD-AP 2014.s.197, the flexor fossa on the ventral surface has been obscured by matrix.

However, additional support for the placement of specimens NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, and NHRD-AP 2016.v.1104 within Ornithomimosauria comes from their triangular shape of in proximal view (figure 4E, J, O), a trait considered a synapomorphy of Ornithomimidae by Barsbold & Osmólska (1990) and noted as a morphology found in Ornithomimosauria generally by Makovicky, Kobayashi & Currie (2004) . Table 1 includes the measurements of these elements.
NHRD-AP 2014.s.195 is a slightly recurved and relatively elongate pedal ungual (figure 3A-E)(Table 1) with a proximal surface that is isosceles trapezoid-shaped and thins dorsally towards a proximodorsal process prominent in lateral and medial views. As in Nqwebasaurus thwazi, NHRD-AP 2014.s.195 bears a well-defined flexor fossa with striations on its ventral surface (Choiniere, Forster & de Klerk, 2012). The center of the NHRD-AP 2014.s.195 bears well-defined and deepened grooves for the claw sheath, a feature found in other ornithomimosaur pedal unguals (Makovicky, Kobayashi & Currie, 2004). The tip of NHRD-AP 2014.s.195 is blunt, likely due to erosion. The ventrolateral and ventromedial edges are developed into keels. In lateral and medial view, a depression sits directly proximal to the proximal end of each side’s groove for the claw sheath. In dorsal view, this feature creates a heightened ridge of bone that ends proximally in the proximodorsal process.

A cast of USNM PAL 529423 was also available for study (figure 3F-J). USNM PAL 529423 is very similar to NHRD-AP 2014.s.195 in being relatively elongate (Table 1), having well-defined and deepened grooves for the claw sheath, and having a similar shape in proximal view. USNM PAL 529423 has an eroded ventral surface, but a weakly-defined flexor fossa is still present. The flexor fossa seems to contain striations and is of a similar shape to that of NHRD-AP 2014.s.195 in being relatively circular. The ungual is very slightly recurved and has a blunt tip. The dimensions of USNM PAL 529423 compare closely with NHRD-AP 2014.s.195, though USNM PAL 529423 is 2 mm shorter than NHRD-AP 2014.s.195 (table 1). This difference in height, however, seems less of a morphological difference than a taphonomic one. This is because the dorsal lip of the proximal face has been shortened by erosion (figure 3F-J). Thus, the two millimeter difference is regarded here as a product of taphonomy. As in NHRD-AP 2014.s.195, a depression sits directly proximal to each of the grooves for the claw sheath in
lateral and medial view. These depressions help to define a heightened ridge of bone in dorsal view that develops into the proximodorsal process.

NHRD-AP 2016.v.1104 is the proximal end of a pedal ungual (figure 4A-E). This element has a somewhat flattened ventral surface in lateral and medial views and deviates from the morphology of NHRD-AP 2014.s.195 and USNM PAL 529423 in being triangular in proximal view. The grooves for the claw sheath are weakly defined. There is no indication of mediolateral curvature in ventral view. The ventrolateral and ventromedial edges of the specimen do not take the form of keels, though this may be due to erosion. NHRD-AP 2016.v.1104 also lacks depressions directly proximal to its grooves for the claw sheath.

NHRD-AP 2014.s.198 is a well-preserved recurved pedal ungual (figure 4F-J). NHRD-AP 2014.s.198 is not as long proximodistally or nearly as wide mediolaterally as NHRD-AP 2014.s.195 or USNM PAL 529423. However, NHRD-AP 2014.s.198 is as tall or taller dorsoventrally than NHRD-AP 2014.s.195 or USNM PAL 529423. This gives NHRD-AP 2014.s.198 a blunt appearance in comparison to NHRD AP 2014.s.195 and USNM PAL 529423 in lateral and medial view. The grooves for the claw sheath are poorly defined, dorsoventrally widened, and shallower than those of NHRD-AP 2014.s.195 and USNM PAL 529423. In proximal view, the pedal ungual is triangular in shape as in NHRD-AP 2016.v.1104. The tip is slightly worn, and a portion of the ungual is obscured by matrix. The ventrolateral edge is broken off, and the ventromedial edge is slightly worn. However, the ventromedial edge is still complete enough to show it had been developed into a keel. A flexor fossa is still present on the ventral surface of this specimen. In ventral view the morphology of the claw indicates it was the pedal ungual of either pedal digit II or IV as it is curved mediolaterally. There are no depressions proximal to the grooves for the claw sheath in NHRD-AP 2014.s.198. In NHRD-AP 2014.s.198,
the proximodorsal process is also rather weakly defined. Additionally, the flexor fossa of
NHRD-AP 2014.s.198 lacks striations. NHRD-AP 2014.s.197 (figure 4K-O) is among the best-preserved of the pedal unguals
described herein. This pedal ungual is relatively blunt with poorly-defined grooves for the claw
sheath. Like NHRD-AP 2014.s.198, this pedal ungual curves mediolaterally in ventral view. The
dimensions of NHRD-AP 2014.s.197 are very similar to those of NHRD-AP 2014.s.198 (table
1), and therefore dissimilar to those of NHRD-AP 2014.s.195 and USNM PAL 529423. NHRD-
AP 2014.s.197 is also slightly recurved to a similar degree as NHRD-AP 2014.s.198. As in
NHRD-AP 2016.v.1104 and NHRD-AP 2014.s.198, NHRD-AP 2014.s.197 is semi-triangular in
proximal view. As in NHRD-AP 2014.s.198, NHRD-AP 2014.s.197 has dorsoventrally
widened grooves for the claw sheath. A portion of matrix obscures a portion of the claw towards
its distal end and the flexor fossa. The flexor fossa is obscured by matrix, and the proximodorsal
process is weakly defined in NHRD-AP 2014.s.197. The ventromedial edge is worn, and the
ventrolateral edge is obscured by matrix but present.

Discussion.

Presence of two morphotypes of ornithomimosaur in the Arundel Clay.

The Arundel ornithomimosaur material represents a significant record of one dinosaur
group from the Early Cretaceous of eastern North America. The described axial and appendicular
material herein suggests that two different species of ornithomimosaur may have coexisted
within the Arundel fauna. This is because of the presence of two different morphotypes of pedal
unguals found at the Dinosaur Park site and because other ornithomimosaur specimens from the
same site have affinities with more derived or more basal ornithomimosaur taxa. NHRD-AP
2014.s.195 and USNM PAL 529423 both have well-defined, deepened grooves for the claw sheath, a proximal face that is isosceles trapezoid-shaped and thins dorsally to a prominent proximodorsal process, depressions proximal to their grooves for the claw sheath which contribute to the prominence of a raised portion of bone in dorsal view, and a flexor fossa with striations running through it on their ventral surfaces. NHRD-AP 2014.s.197 and NHRD-AP 2014.s.198, are triangular in proximal view, shorter and less widened mediolaterally than NHRD-AP 2014.s.195 and NHRD-AP 2014.s.197, have shallow grooves for the claw sheath, lack striations running through the flexor fossa on their ventral faces, and are more recurved than NHRD-AP 2014.s.195 and USNM PAL 529423. NHRD-AP 2016.v.1104 is also triangular in proximal view and lacks deepened grooves for the claw sheath. The questions of whether all the pedal unguals represent different ontogenetic stages of ornithomimosaurus or that the unguals are from different digits of the pes of an ornithomimosaur are also addressed here. Intraspecific and ontogenetic variation can be regarded as unlikely due to the disparate morphologies of the pedal unguals in proximal view and the lack of intermediate morphological traits between the morphotype represented by NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, and NHRD-AP 2016.v.1104 and the morphotype represented by NHRD-AP 2014.s.195 and USNM PAL 529423. Further evidence against ontogenetic or intraspecific variation among these unguals comes from previously described unguals from the Arundel Clay assigned to Ornithomimosauria. Gilmore (1920) described a single pedal ungual which he assigned to “Ornithomimus” affinis. The morphology of this ungual (USNM V 6107), which was more recently figured in Serrano-Brañas et al. (2016), closely corresponds to the pedal unguals NHRD-AP 2015.s.197 and NHRD-AP 2015.s.198 in being shortened, recurved, lacking striations in its flexor fossa, and lacking grooves for the claw sheath as well-defined and deep as
those of NHRD-AP 2015.s.195 or USNM PAL 529423. Evidence against the claws being from
different digits of the pes of a single species of ornithomimosaur stems from the significant
differences in morphology between the unguals. In the ornithomimosours where the proximal
faces of more than one pedal ungual is exposed and documented (e. g. Beishanlong grandis,
Rativites evadens, Struthiomimus altus, Ornithomimus edmonticus, Gallimimus bullatus), all
pedal unguals are flattened or slightly recurved to a similar degree and share a distinct triangular
shape in cross-section (e. g. Makovicky, Kobayashi & Currie, 2004; Makovicky et al., 2009;
McFeeters et al., 2016). Thus, it is very unlikely that the pedal unguals described herein belong
to different digits of the pes of one ornithomimosaur, as they significantly vary in their shape in
proximal view and display different degrees of curvature. USNM V 6107 is also straightened in
ventral view (figure 8B in Serrano-Brañas et al., 2016), suggesting that it came from pedal digit
III. Thus, the blunt morphotype of pedal ungual represented by NHRD-AP 2014.s.197, NHRD-
AP 2014.s.198, NHRD-AP 2016.v.1104 and USNM V 6107 is both represented by
mediolaterally curved and straightened forms, suggesting that they not only represent the pedal
unguals of digits II and IV but also of digit III.

Additional support for the two different morphs of ungual described herein representing
two different species stems from their morphological similarities to the unguals of
ornithomimosours of different phylogenetic positions. NHRD-AP 2014.s.195 and USNM PAL
529423 are more similar to the unguals of derived ornithomimosours and ornithomimids in being
flattened, having a prominent ridge of bone oriented proximodistally in dorsal view, having
depressions directly proximal to the proximal end of their grooves for the claw sheath, and being
elongate (e. g. Barsbold & Osmólska, 1990.; Makovicky, Kobayashi & Currie, 2004; Serrano-
Brañas et al., 2016). NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, and USNM V 6107 share
similarities with basal ornithomimosaurs in being recurved and blunt (e. g. Makovicky, Kobayashi & Currie, 2004; Jin, Chen & Godefroit, 2012). These features also provide evidence against the notion of sexual variation among ornithomimosaurs contributing to the presence of two morphotypes of pedal unguals.

Furthermore, evidence for the presence of two different ornithomimosaur species in the Arundel Clay stems from the non-pedal ungual material of ornithomimosaurs known from the Arundel. The humerus described herein is similar to the humerus of Harpyimus in being thickened compared to those of most other ornithomimosaurs (Makovicky, Kobayashi & Currie, 2004), suggesting the humerus is from an ornithomimosaur similar to H. okladnikovi. However, the manual ungual described herein is allied with ornithomimids in completely lacking a flexor tubercle (e. g. Makovicky, Kobayashi & Currie, 2004).

Other remains assigned to ornithomimosaurs from the Arundel Clay follow this pattern of sharing features with derived or basal ornithomimosaurs. The partial metatarsal III USNM V 5684 described by Gilmore (1920) resembles the metatarsal III of ornithomimids like Struthiomimus and Gallimimus much more than it does to Harpyimus in thinning only to abruptly expand near its diaphysis (e. g. figure 6.5 in Makovicky, Kobayashi & Currie, 2004; Serrano-Brañas et al., 2016). The metatarsal III is not as robust as those of arctometatarsalian tyrannosaurs (e. g. Holtz, 2004), and the lack of known tyrannosaur material from North America during the Aptian-Albian (only known from possible teeth)(e. g. Zanno & Makovicky, 2011) is suggestive that this element came from a subarctometatarsalian or artcometatarsalian ornithomimosaur. This coexistence of more derived and more basal ornithomimosaur species also occurs within the Yixian Formation of China (Ji et al., 2003; Jin, Chen & Godefroit, 2012).
Review of previously described Arundel Clay ornithomimosaur material.

With the presence of two different species of indeterminate ornithomimosours within the Arundel Clay, a taxonomic reevaluation for the ornithomimosaur material of the Arundel is warranted. The material originally described by Lull (1911) as “Dryosaurus” grandis was placed within the ornithomimosaur genus Ornithomimus as “O.” affinis by Gilmore (1920). This material included dorsal and caudal vertebrae, a metatarsal II and metatarsal III, an astragalus, pedal phalanges, and a pedal ungual (Lull, 1911; Gilmore, 1920). Russell (1972) later placed the Arundel remains within Archaeornithomimus due to the curvature of the pedal ungual described by Lull (1911) and Gilmore (1920), while Smith and Galton (1990) regarded the material as indeterminate theropod remains. Serrano-Brañas et. al. (2016) regarded the material as ornithomimosaur remains, using the pedal ungual USNM V 6107 and the metatarsal III USNM V 5684 in comparisons with other ornithomimosaur genera. Weishampel & Young (1996) and Weishampel (2006) listed other ornithomimosaur remains, including a tibia, as coming from the Arundel Clay. Indeed, multiple new specimens possibly belonging to ornithomimosours are currently in the collections of the National Museum of Natural History. However, as Gilmore (1920) does not specify the exact location of the pedal ungual and the metatarsal III relative to each other at the site near Muirkirk, Maryland which he gives as the location of their discovery and as the two different morphotypes of pedal unguals described herein come from the same site, it is best to conclude that all of the ornithomimosaur material previously described from the Arundel Clay may represent two different species and thus cannot be confidently assigned to one taxon.

Reassignment of Nedcolbertia justinhofmanni to Ornithomimosauria.
Description of the new Arundel ornithomimosaur material and the naming of new basal
ornithomimosaur taxa in recent years has allowed for the reinterpretation of the “generalized”
North American coelurosaur *Nedcolbertia justinhofmanni* as an ornithomimosaur. This taxon,
originally described as a coelurosaur of uncertain affinities, is known from three specimens from
the Barremian Yellow Cat Member of the Cedar Mountain Formation (Kirkland et al., 1998).
*Nedcolbertia* shares several synapomorphies with ornithomimosauras and ornithomimids in
having anteroposteriorly shortened phalanges from pedal digit IV, the ventral surfaces of the
pedal ungual flattened in lateral view, being triangular in proximal view, having ventrolateral
and ventromedial edges developed into keels, and having a flexor fossa on the proximal end of
the ventral surface of its pedal unguals (Barsbold & Osmólska, 1990; figure 8 & figure 9 in
Kirkland et al., 1998; Choinere, Forster & de Klerk, 2012). The proximal end of metatarsal III is
restricted mediolaterally in a very similar fashion to *Harpymimus*, and in proximal view the
metatarsals are similar in shape to those of *Kinnareeemimus* and *Nqwebasaurus* (figure 8 in
Buffetaut, Suteethorn & Tong, 2009; Choiniere, Forster & de Klerk, 2012). Additional features
shared between *Nedcolbertia* and Ornithomimosauria include elongated caudal vertebra, an
elongated femur with the femoral head directed straight medially and not separated from the
greater trochanter by a sulcus, a large cnemial crest on the tibia which curves laterally towards
the crest’s tip, elongated pedal unguals with deep grooves for the claw sheath, a tall ascending
process on the astragalus, a complex space on the lateral side of the astragalus into which the
calcaneum fits, a sulcus separating the astragalar condyles, and no sulcus separating the femoral
head from the greater trochanter (figure 8D-N, figure 9B, figure 6C-E in Kirkland et al., 1998;
Makovicky, Kobayashi & Currie, 2004).
The subarctometatarsus of *Nedcolbertia* can be differentiated from that of tyrannosauroids by the proximally pinched metatarsal III not being limited to the plantar half of the foot (Holtz, 2004). Additionally, the metatarsal III of *Nedcolbertia* is not restricted to the extent seen in troodontids (Makovicky & Norell, 2004). *Nedcolbertia* can be differentiated from dromaeosaurids, troodontids, oviraptorosaurs, and therizinosaurs in lacking a moderately to well-developed deltopectoral crest (Clark, Maryańska & Barsbold, 2004; Makovicky & Norell, 2004; Norell & Makovicky, 2004; Osmólska, Currie & Barsbold, 2004). Unlike in tyrannosauroids, the greater trochanter of the femur of *Nedcolbertia* is not cleft from the femoral head.

Relationships of *Nedcolbertia justinhofmanni* and the Arundel Clay material.

*Nedcolbertia* notably shares similarities in the morphology of its pes with a partial theropod pes from Arkansas that has been regarded as an ornithomimosaur (Quinn, 1973; Kirkland et al., 1998). Kirkland et al. (1998) also related the *Nedcolbertia* material to the Arundel ornithomimosaur material, suggesting that alongside the Arkansas pes they may represent a distinct radiation. Unlike some ornithomimosaurus, the flexor tubercle of the first manual ungual in is extremely pronounced, the manual unguals are likely differentiated, and the dorsal vertebrae are pneumatic with simplistic air sacs in *Nedcolbertia* (Kirkland et al., 1998).

However, the morphology of the manual unguals of *Nedcolbertia* is indeed similar to the basal ornithomimosaurus *Nqwebasaurus* and *Harpymimus* in having large flexor tubercles. Additionally, *Nedcolbertia* and *Nqwebasaurus* can be linked by having slender pedal unguals, though this is less pronounced in the former taxon. The astragali are also morphologically similar in *Nedcolbertia justinhofmanni* and *Nqwebasaurus thwazi* in the relative height of their ascending processes. Additionally, *Nedcolbertia justinhofmanni* can be distinguished from the derived Arundel ornithomimosaur morphotype in the morphology of their metatarsus. The
known portion of the metatarsal III described by Lull (1911) and Gilmore (1920) suggests that at least one ornithomimosaur taxon found at the Arundel had a subarctometatarsalian condition similar to that of *Kinnareemimus*, while in *Nedcolbertia* the dorsal face of metatarsal III is still completely visible along the entire portion of the metatarsus. Additional differences between the derived Arundel ornithomimosaur material and *Nedcolbertia* include the presence of noticeable flexor tubercles on the manal unguals of the latter taxon and the slightly more recurved nature of the derived Arundel ornithomimosaur’s pedal unguals in comparison with those of *Nedcolbertia*. *Nedcolbertia* can be distinguished from the derived morphotype of pedal ungual described herein by the presence of a ridge of bone separating the flexor fossa in two in the former taxon. *Nedcolbertia* can be distinguished from the more basal Arundel form in the elongate nature of the unguals of the former species (figure 8M-N in Kirkland et al., 1998). *Nedcolbertia* is therefore considered as a basal ornithomimosaur due to its non-arctometatarsalian pedal condition where the shaft of metatarsal III is at least partially visible along its entire run in dorsal view.

Biogeographic Implications.

Along with the basal Arundel ornithomimosaur material and the unnamed pes from the Trinity Group of Arkansas, the presence of *Nedcolbertia* in the Cedar Mountain Formation shows that ornithomimosaurs were present across the continent of North America during the Early Cretaceous. The presence of a derived ornithomimosaur in the Arundel Clay also suggests that more derived ornithomimosaur coexisted with these more basal forms. Ornithomimosaurs with derived traits, such as the loss of teeth in the dentary, already occur in Europe by the Haueterivian to Barremian (Allain et al., 2014). The presence of a species of basal
ornithomimosaur in North America during the Barremian (Yellow Cat Member of Cedar Mountain Formation) (Kirkland et al., 1998) evinces that the clade had already spread to North America in addition to Africa, Europe and Asia during the earliest stages of the Cretaceous (e. g. Allain et al., 2014). Allain et al. (2014) noted that the close relationships between the African taxon *Nqwebasaurus* and other basal ornithomimosaur suggested that the group was widespread before the breakup of Pangaea. The North American ornithomimosaur record (*Nedcolbertia*, Arundel taxa, Arkansas pes) may also indicate this. However, it is also a possibility that, as Allain et al. (2014) discussed, a European-Asian interchange resulting from low sea levels could have also allowed the immigration of ornithomimosaur to North America.

The presence of a large number of species of basal ornithomimosaur (e. g. *Nedcolbertia*, *Nqwebasaurus*, *Hexing*, *Pelecanimimus*) (e. g. Choiniere, Forster & de Klerk, 2012; Jin, Chen & Godefroit, 2012) in North America, Asia, Africa, and Europe during the Barremian and earlier stages of the Cretaceous with little overlap of forms with more derived affinities (represented by an unnamed form from Angeac, France and possibly the British taxon *Valdoraptor*) suggests that basal ornithomimosaur were the most common and widespread of ornithomimosaur during the earliest Cretaceous. However, it is notable that towards the end of the Early Cretaceous (Aptian-Albian), these basal forms start to disappear as more derived taxa (including ornithomimids and deinocichoids) (e. g. *Harpymimus*, *Beishanlong*, an unnamed ornithomimid pes from China, the derived Arundel taxon) occur more often (e. g. Shapiro et al., 2003; Jin, Chen & Godefroit, 2012; Allain et al., 2014). Ornithomimosaur taxa are also known from only North America and Asia at this time and into the Late Cretaceous (e. g. Allain et al., 2014). Thus, it may be that a decrease in basal taxa coincided with the regression of the range enjoyed by ornithomimosaur in the
earliest Cretaceous. However, further discoveries of ornithomimosaurs from the Early
Cretaceous are needed before this hypothesis can be thoroughly tested.

Conclusions.

The Arundel ornithomimosaurs are some of the best-characterized theropods from the
Early Cretaceous of eastern North America. Furthermore, the Arundel material along with
recently described ornithomimosaurs have provided evidence for the placement of *Nedcolbertia
justinhofmanni* as an ornithomimosaur. Both these taxa and an unnamed ornithomimosaur pes
from the Early Cretaceous of Arkansas affirm that ornithomimosaurs were present across North
America during the Early Cretaceous.

Previous studies on ornithomimosaur remains have affirmed that individual postcranial
elements assignable to Dinosauria can be assigned to family level and genus level (e. g. Currie,
1987; Longrich, 2008). Notably, Longrich (2008) and Shapiro et al. (2003) demonstrated that
manal pedal material can be diagnostic for Ornithomimosauria. The species *Tototlmimus
packardensis* was recently named on the basis of solely manual and pedal elements (Serrano-
Brañas et al., 2016). Thus, because *Nedcolbertia* and the Arundel material share a significant
number of diagnostic traits with Ornithomimosauria in their manus and pes, both *N.
justinhofmanni* and the ornithomimosaur material from the Arundel Clay can be assigned to
Ornithomimosauria.

As Longrich (2008) stated, the importance of dissociated elements within an assemblage
should not be understated. This is especially true for dinosaur specimens from the eastern United
States, which are often found dissociated and incomplete (e. g. Weishampel & Young, 1996).

Here, inspection of the pedal unguals described and the hypothesis that they represent different
basal and derived taxa is also consistent with the morphologies of other ornithomimosaur specimens from the Arundel Clay.

Both the Arundel material and *Nedcolbertia* have implications for the biogeography of Early Cretaceous ornithomimosaur lineages, suggesting that basal and more derived ornithomimosaurid had a wide biogeographic range during the Early Cretaceous and may have coexisted in at least Asia and North America. Additionally, the interpretation of the Arundel Clay material representing two different taxa suggests similarities between the dinosaur fauna of the eastern United States and the Yixian Formation of China (Ji et al., 2003; Jin, Chen & Godefroit, 2012). Continued study of the often dissociated dinosaur specimens of the Arundel Clay is likely to aid in the understanding of the biodiversity of dinosaurs in the eastern United States during the Early Cretaceous and provide further data on the evolution of ornithomimosaurid and other smaller theropod groups during the Cretaceous as a whole.

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**Figure 1** (on next page)

Humerus of an Arundel Ornithomimosaur

Left humerus of an indeterminate ornithomimosaur NHRD-AP 2015.v.103.9 in dorsal (A), ventral (B), lateral (C), medial (D), proximal (E), and distal (F) views. Black arrows indicate cleft separating humeral head from lateral tubercle. Blue arrow indicates edge of deltopectoral crest. Scale bars = 10 mm.
**Figure 2** (on next page)

Selected elements of Arundel Ornithomimosaurus

Manual ungual NHRD-AP 2014.s.196 in lateral (A), proximal (B), dorsal (C), and ventral (D) views. Caudal vertebra NHRD-AP 2016.s.503 in lateral (E) and medial (F) views. Scale bars = 10 mm.
Figure 3 (on next page)

Pedal Unguals of Arundel Ornithomimosaur

Pedal ungual NHRD-AP 2014.s.195 in lateral (A), medial (B), dorsal (C), ventral (D), and proximal (E) views. Pedal ungual USNM PAL 529423 in lateral (F), medial (G), dorsal (H), ventral (I), and proximal (J) views. Black arrows indicate flexor fossa. Blue arrows indicate depression proximal to groove for claw sheath. Green arrows indicate ventrolateral and ventromedial keels. Scale bars = 10mm.
Figure 4 (on next page)

Pedal Unguals of Arundel Ornithomimosaurus

Pedal ungual NHRD-AP 2014.s.198 in lateral (A), medial (B), dorsal (C), ventral (D), and proximal (E) views. Pedal ungual NHRD-AP 2014.s.197 in lateral (F), medial (G), dorsal (H), ventral (I), and proximal (J) views. Pedal ungual NHRD-AP 2016.v.1104 in lateral (K), medial (L), dorsal (M), ventral (N), and proximal (O) views. Scale bars = 10 mm.
Table 1 (on next page)

Measurements of Arundel Ornithomimosaur Elements
| Specimen               | Proximodistal Length (measured on lateral (L) or dorsal (D) side) | Dorsoventral Height (measured on proximal side) | Mediolateral Width (measured on proximal side) | Dorsoventral Width (measured on distal side) | Mediolateral Width (measured distal side) |
|------------------------|------------------------------------------------------------------|--------------------------------------------------|------------------------------------------------|---------------------------------------------|------------------------------------------|
| NHRD-AP 2015.v.103.9 (proximal end) | 101 mm (D)                                                      | 51 mm                                            | 30 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2015.v.103.9 (distal end)    | 70 mm (D)                                                      | N/A                                              | N/A                                            | 25 mm                                       | 58 mm                                    |
| NHRD-AP 2014.5.196       | 47 mm (L)                                                      | 20 mm                                            | 18 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2016.s.503       | 77 mm (L)                                                      | 30 mm                                            | 25 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2014.s.195       | 53 mm (L)                                                      | 25 mm                                            | 22 mm                                          | N/A                                         | N/A                                      |
| USNM PAL 529423 (cast)   | 55 mm (L)                                                      | 23 mm                                            | 22 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2014.s.198       | 48 mm (L)                                                      | 25 mm                                            | 19 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2014.s.197       | 50 mm (L)                                                      | 25 mm                                            | 20 mm                                          | N/A                                         | N/A                                      |
| NHRD-AP 2016.v.1104      | 30 mm (L)                                                      | 23 mm                                            | 13 mm                                          | N/A                                         | N/A                                      |