The biogeography and ecology of the Cretaceous non-avian dinosaurs of Appalachia

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ABSTRACT

The Cenomanian to Maastrichtian of the Late Cretaceous saw the flooding of the interior of North America by the Western Interior Seaway, which created the eastern landmass of Appalachia and the western landmass of Laramidia. Though Appalachian dinosaur faunas are poorly known, they are nevertheless important for understanding Cretaceous dinosaur paleobiogeography and ecology. In order to better track the vicariance of eastern and western North American dinosaur faunas over the duration of the Cretaceous, the former were compared with the latter from the Aptian to Maastrichtian Stages of the Late Cretaceous using several similarity indices. The data gathered from biogeographic similarity indices suggest that an almost completely homogenous North American dinosaur fauna found in the Early Cretaceous experienced significant vicariance, splitting into a Laramidian fauna differentiated by the presence of ceratopsids, pachycephalosaurids, saurolophids, lambeosaurines, ankylosaurids, therizinosaurids, and troodontids and an Appalachian fauna characterized by the lack of the aforementioned groups and the presence of non-hadrosaurid hadrosauroids, massive hadrosauroids, basal hadrosaurids, leptoceratopsians, "intermediate"-grade tyrannosauroids, and nodosaurids between the Cenomanian and Campanian, with these two faunas later experiencing limited dispersal after the disappearance of the Western Interior Seaway from the American Interior during the Maastrichtian. Dinosaur provincialism and ecology on Appalachia are also investigated and discussed. Though the fossil record of dinosaurs for parts of the Cretaceous is poor throughout North America and in the eastern portion of the continent especially, the analyses herein nevertheless allow for a greater glimpse at dinosaur biogeography and ecology in Appalachia and in North America generally during the time.

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INTRODUCTION

During the Albian to Cenomanian stages of the Late Cretaceous, the interior of North America was flooded by a shallow sea called the Western Interior Seaway (e.g., Russell, 1995; Roberts and Kirschbaum, 1995). The creation of the seaway caused the formation of a long, slender landmass known as Laramidia to the west and the wider, more rectangular Appalachia to the east (e.g., Schwimmer, 2002; Sampson et al., 2010), having appreciable consequences in the evolution of North American dinosaurs. The former of these two landmasses apparently experienced a heightened level of non-avian dinosaur diversification during the Campanian (Sampson et al., 2010; Loewen et al., 2013), when a high level of local dinosaur endemism partnered with regional differences in non-avian dinosaur faunas may have occurred there (Lehman, 1997; Sampson et al., 2010; Loewen et al., 2013). The cause for this rapid diversification of non-avian dinosaurs and other vertebrates on Laramidia has been hypothesized as a consequence of climate variability leading to floral variability, of orogenesis or orogenic activity, and of transgressions and regressions of the Western Interior Seaway (Horner et al., 1992; Lehman, 1997; Sampson et al., 2010; Loewen et al., 2013). There has been some disagreement regarding the existence of faunal provinces on this continent (e.g., Larson and Vavrek, 2010; Lucas et al., 2016).

Unfortunately, the terrestrial fauna of Appalachia is not well-sampled, and only a limited number of dinosaur taxa are known due to lack of Cretaceous-age terrestrial sediments in eastern North America (Baird and Horner, 1977; Baird and Galton, 1981; Baird, 1986; Schwimmer, 1986; King et al., 1988; Gates et al., 2012). Preservation bias thus exists against any articulated specimens of terrestrial animals, including non-avian dinosaurs (e.g., Schwimmer et al., 1993; Schwimmer, 1997). Schwimmer (1997) suggested that, antithetic to the hypotheses of Russell (1995), the known dinosaurs from Appalachia may represent a fair selection of non-avian dinosaur groups endemic to the continent. Schwimmer (2002) also suggested that a lack of theropod diversity or abundance on Appalachia may have also been caused by competition from the massive crocodylian *Deinosuchus rugosus*, a species abundant in eastern North America with bite marks on both theropod and ornithopod bones attributed to it (Schwimmer, 1997; Gallagher, 1993, 1995; Schwimmer 2002).

The recent discoveries of a leptoceratopsian from the Campanian Tar Heel Formation of North Carolina (Longrich, 2016), the description of the dinosaurs *Eotrachodon orientalis* from the Santonian-Campanian Mooreville Chalk Formation (Prieto-Marquez et al., 2016a) and *Appalachiosaurus montgomeriensis* from the Campanian Demopolis Chalk Formation (Carr et al., 2005), and the description of new dinosaur remains from microfossil sites like Ellisdale and Stokes Quarry (e.g., Gallagher, 1993; Denton et al., 2011; Schwimmer, 2015) have largely increased the non-avian dinosaur diversity of Appalachia. The dinosaur fauna of Appalachia itself was apparently dominated by relict forms isolated by the Western Interior Seaway (Schwimmer et al., 1993). However, the development of Appalachian faunas and their eventual mixing with Laramidian ones during the Maastrichtian (Schwimmer et al., 1993; Carr et al., 2005) is poorly understood.

Here, I review and statistically compare faunas known from the Aptian through Maastrichtian of eastern North America with those known from the west to better illustrate the vicariance of Appalachian and Laramidian non-avian dinosaur faunas after the creation of the Western Interior Seaway. This analysis provides a temporal framework for the evolution of non-avian dinosaur faunas on Appalachia. Additionally, non-avian dinosaur provincialism during the Coniacian, Santonian, and Campanian Stages of the Cretaceous was tested using several biogeographic similarity indices and discussed, as were ecological implications regarding competition between predatory dinosaurs and crocodyliforms in Appalachian ecosystems. Because the vast majority of Appalachian dinosaur remains occur in marine deposits and Laramidian dinosaurs are comparatively well-known from terrestrial ones, depositional bias was surely a factor that may have skewed the results of the statistical analyses conducted (e.g., Schwimmer, 1997) and is discussed below. This analysis is important for being the first major one to compare the non-avian dinosaur faunas of Appalachia with Laramidian ones statistically. Specific depositional comparisons between Appalachian and Laramidian faunas analyzed are noted in the results section.

MATERIALS AND METHODS

Permits

No permits were required for the described study, which complied with all relevant regulations. Photographs of specimens from the Arundel Clay

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referred to herein were supplied by Thomas Jorstad of the National Museum of Natural History. Photographs of the specimens figured herein from the Yale Peabody Museum were provided by Jamie Henderson.

Institutional Abbreviations

The following abbreviations for museum collections are used in the manuscript: USNM V/PAL: United States National Museum (Smithsonian), Washington, DC, USA; UAM(1): University of Arkansas at Fayettville, Fayettville, AK, USA; YPM VPPU: vertebrate paleontology collections, Yale Peabody Museum, New Haven, CT, USA; RMM/MCWSC: McWane Science Center, Birmingham, Alabama, USA; AMNH FARB: American Museum of Natural History (fossil amphibian, bird, and reptile collections), New York, NY, USA; ANSP: Academy of Natural Sciences at Drexel University, Philadelphia, PA, USA; AUMP: Auburn University Museum of Paleontology, Auburn, AL, USA; CCK: Columbus State University (Cretaceous research collections), Columbus, GA, USA; FMNH: Field Museum of Natural History, Chicago, IL, USA; MMNS: Mississippi Museum of Natural Science, Jackson, MS, USA; MOG: Mississippi Office of Geology, Jackson, MS, USA; PPM: Memphis Pink Palace Museum, Memphis, TN, USA; UAM: University of Alabama Museum, Tuscaloosa, AL, USA.

Methods

Faunal lists. Occurrences documenting a total of 54 major clades of non-avian dinosaurs were catalogued from the western and eastern portions of North America. Faunal lists were created for all eastern North American dinosaur-bearing units that corresponded to the Aptian, Albian, Cenomanian, Turonian, Coniacian, Santonian, Campanian, and Maastrichtian stages of the Cretaceous. The biogeographic occurrences that fed the compilation of such faunal lists were taken from an extensive review of previously published works, access to unpublished information, and personal observation, representing to the author's knowledge the most rigorous review of Appalachian dinosaur faunas to date. Detailed review and references for the faunal lists included in Appendix 1 may be found below. Aptian Appalachian faunas were compared with those of the western North American (pre-Laramidian) Ruby Ranch Member of the Cedar Mountain Formation and units V through VII of the Cloverly Formation, whereas Albian Appalachian faunas were compared with those of the Blackleaf Formation, Wayan Formation, and Willow Tank Formation. Cenomanian Appalachian faunas were compared with the upper Cedar Mountain Formation (Mussentuchit Member), Chandler Formation, and Dunvegan Formation. Turonian Appalachian faunas and the non-avian dinosaur faunas of the Moreno Hill, Frontier, and Matanuska formations were compared. Santonian Appalachian faunas were compared with those of the Milk River Formation. Campanian Appalachian faunas were compared to those of the Wahweap, Kaiparowits, and Kirtland formations representing southern Campanian Laramidian faunas and with the Oldman, Dinosaur Park, and Judith River formations representing northern Campanian Laramidian faunas, whereas the Maastrichtian Appalachian faunas were compared with those of the Javelina, Hell Creek, Lance, and Horseshoe Canyon formations. The Laramidian (western North American) faunas used for comparisons are among the most well known (e.g., Kirkland et al., 1998; Weishampel et al., 2004, Weishampel, 2006; Gates et al., 2010; Zanno and Makovicky, 2013; Sampson et al., 2013; Farke et al., 2014) and represent a sampling of northern, middle, and southern faunas, both factors being considered to minimize statistical bias and error on the part of such faunas. As such, formations like the Foremost Formation, from which only a few taxa and indeterminate elements are known (e.g., Weishampel et al., 2004), were not included.

Statistical comparisons. For comparisons between Appalachian and Laramidian faunas, Simpson's similarity index, the Jaccard coefficient, and Jaccard distance were employed to quantify the differentiation of the faunas of the aforementioned landmasses over time (Jaccard, 1902; Jaccard, 1912; Simpson, 1943). The former two indices show the statistical similarity of two faunas, with Simpson's similarity index emphasizing similarity and the Jaccard coefficient emphasizing differences, whereas the Jaccard distance measures the dissimilarity between two faunas and is equal to one minus the Jaccard similarity value (e.g., Jaccard, 1902; Jaccard, 1912; Simpson, 1943). These indices were calculated by comparing dinosaurian faunas at the genus and "family" (= the next highest identifiable clade above genus) levels for the purpose of shedding light on what taxa were differentiating in the context of their parent clades as well as to better factor in the many Appalachian occurrences unable to be identified to the genus or species level. Indeterminate specimens assignable to the "family level", even those which were the only representation of the presence of a particular clade in a faunas, were only included in "family

level" calculations. This protocol was used in order to make the analyses herein more comparable to those of Gates et al. (2010), who coded their datasets at the "family", genus, and genus-species levels. The latter level was not used in analyses herein, as so few Appalachian dinosaur fossils are identifiable past the genus level (see Appendix 1 and the Review section).

As some Appalachian dinosaur faunas with biogeographically significant records (e.g., the Owl Creek Formation) have yielded less than four distinct species, they were not included in calculations of the Jaccard coefficient, Jaccard distance or of the Simpson similarity index, and instead were compared analytically with western faunas. This group of geological units includes 14 of the Appalachian faunas examined, three of which have yielded the holotype specimens of Appalachian dinosaur taxa. The results of the calculation of these indices can be found in Appendix 1 (the Jaccard distance and Jaccard coefficient are listed in the same tables, with parentheses around values of the former).

Analysis of dinosaur faunal provincialism on Appalachia. Because it has been noted that Laramidia may have had multiple different dinosaur faunal provinces during the Campanian (e.g., Lehman, 1997; Sampson et al., 2010a; Loewen et al., 2013), dinosaur provincialism on Appalachia was also investigated for during the Coniacian, Santonian, and Campanian Stages of the Late Cretaceous. This was done by first rarefying the assemblages, which represent the most well-known (in terms of number of specimens) faunas of units from the aforementioned Stages of the Late Cretaceous and then by employing the Simpson similarity index and Jaccard coefficient to compare faunal similarities at the genus and family levels for each. Rarefaction, which calculates the expected number of taxa in a given sample A if that sample were reduced to the size of a smaller sample B (e.g., Sanders, 1968), was used to examine sampling differences between Appalachian dinosaur-bearing strata and assess for sampling bias between the corresponding faunas. The relative ages of each of the stratigraphic units was also taken into account during this process, and the ages of the formations included in this analysis of provincialism are given in the results section. The fauna of the coeval Campanian Mooreville Chalk, Blufftown, and Coffee Sand formations and an unnamed clay from Missouri were also rarefied for comparison with the Coniacian/Santonian Eutaw Formation in order to track the development of dinosaur faunas in the southeastern United States during Late Cretaceous. In comparing faunas, the presence of larger phylogenetic groups was considered. In the case of Aptian, Cenomanian, and Maastrichtian Appalachian faunas, the existence of only one comparatively well-sampled fauna in each case did not allow for considerations of provincialism. The Albian Appalachian Formations were also too poorly sampled to allow for rarefaction.

Biases. As previous studies have noted, biases in the collection of fossils, use of previously published literature, taphonomic biases among and within sedimentary units, and temporal differences among sedimentary units studied and within their faunas all play a role in skewing paleobiogeographic analyses (e.g., Nicholls and Russell, 1990; Lehman, 1997; Gates et al., 2010). Because of these factors, the specific paleoenvironments, taphonomy, and age of sediments compared herein were extensively reviewed and compared in the Results section.

Biases in the collection of fossils have been noted as an appreciable hindrance to paleobiological analyses previously (e.g., Alroy et al., 2001; Smith, 2001, 2007; Lloyd et al., 2011). Indeed, such biases among the Campanian Kaiparowits, Judith River, Dinosaur Park, and Kirtland formations were reviewed by Gates et al. (2010), who noted that significant biases exist even between these and the other Campanian faunas they compared. However, because few extensive dinosaur faunas are known from the Aptian to Santonian of North America (e.g., Carpenter et al., 1995; Kirkland et al., 1998; Main, 2013), the ability to perform statistical analysis on known faunas would be severely limited if an attempt was made to rule out certain collection biases for such comparisons. Regarding to the analysis of Appalachian dinosaur provincialism during the Campanian, collection biases are easier to take into account and are discussed below.

As noted, biases in this study reflecting taxonomically or occurrence-wise inaccurate faunal lists relied on herein may also be present (e.g., Lehman, 1997; Lloyd et al., 2011). However, given the extensive literature review undertaken for the review of Appalachian faunas and for their comparison with Laramidian faunas and the large amount of data compiled, any such discrepancies seem not to be a large bias in the analyses undertaken.

REVIEW

Aptian

Arundel Clay. The most well-represented dinosaur fauna from the Early Cretaceous of eastern North America comes from the Arundel Clay of Maryland. The classification of these elongate, discontinuing clays as a formation has been debated, and the deposits have been interpreted by at least one author as those of oxbow swamps (Kranz, 1998). Further support against the existence of the Arundel as a formation comes from the fact that the palynomorphs of the Patuxent and Arundel sediments cannot be distinguished (Brenner, 1963; Doyle and Hickey, 1973; Doyle and Robbins, 1977; Robbins, 1991; Kranz, 1998). Lipka et al. (2006) considered the Arundel Clay to be a facies contained within the Potomac Formation of late-early Aptian age. The Arundel is made up of black lignite and massive dark-grey mudstones containing limonite and siderite and is the second oldest and most fossiliferous of the three Potomac facies (Lipka et al., 2006). Here, the classification of the Arundel Clay by Lipka et al. (2006) is followed.

The non-avian dinosaur fauna present within the Arundel Clay facies consists of a variety of theropods, at least one species of sauropod, and specimens representing at least three ornithischian clades. The theropods of this unit include the dubious *"Allosaurus" medius* described on the basis of a single tooth (Figure 1.1) (Marsh, 1888) and other elements that were later assigned to *"Dryosaurus" grandis* (Lull, 1911), *Coelurus gracilis* described on the basis of a pedal claw (Figure 2.5) (Marsh, 1888; Lipka, 1998), and *Creosaurus potens* based on a caudal vertebra (Lull, 1911). *"Allosaurus" medius* was regarded by Lipka (1998) as a carnosaur and *Coelurus gracilis* a coelurosaur. Lipka (1998) noted that Ostrom (1970) had considered the holotype pedal ungual of the latter as similar to *Deinonychus* and suggested a possible relation. Holtz et al. (2004) listed all three of these theropods as indeterminate.

Several large teeth (Figure 1.2-4) described by Lipka (1998) and reviewed and figured in Weishampel (2006) have been assigned to a large allosauroid similar to or synonymous with *Acrocanthosaurus*. Lipka (1998) was able to assign these large, serrated teeth to *Acrocanthosaurus* based on several features diagnostic to that taxon found on its teeth, discussing the controversy over assigning teeth to a specific taxon of dinosaur. This carcharodontosaur has been regarded as the apex predator of the Arundel ecosystem (Weishampel,

2006). Importantly, two distinct possibilities regarding the presence of two carnosaurs in the Arundel facies have been stated (Lipka, 1998). The first, regarding the Arundel *"Creosaurus" potens* and *Acrocanthosaurus* material, suggested they represented distinct taxa, whereas the second held that the *"C." potens* material belonged to the taxon *Acrocanthosaurus* (Lipka, 1998). This latter hypothesis is more congruent with data on carcharodontosaur ecology from geologically younger Appalachian sites and from other Early Cretaceous localities (e.g., Weishampel et al., 2004; Appendix 1). Though the fairly diverse ornithischian and small theropod fauna and the presence of at least one species of sauropod in the Arundel may have allowed for the coexistence of two large carnosaur species, more complete carcharodontosaurid specimens must be recovered to accurately test this hypothesis (Lipka, 1998). In addition to the teeth, a massive manual ungual from the Arundel (Figure 1.5) may also be assignable to *Acrocanthosaurus*.

Another clade of carnivorous theropod dinosaurs represented in the Arundel are the dromaeosaurids. Lipka (1998) assigned strongly recurved, laterally compressed teeth retrieved from the Arundel facies to *Deinonychus*, and several are figured herein (Figure 2.1-4). Lipka (1998) noted that these teeth and those of *Acrocanthosaurus* from the Arundel extended the range of both taxa during the Aptian across North America.

One of the better records of theropod dinosaurs from the Arundel is of at least two indeterminate taxa of ornithomimosaurs. The bones originally described as *"Dryosaurus" grandis* by Lull (1911) and later as a species of *Ornithomimus (O. affinis)* (Gilmore, 1920) are currently in the collections of the USNM (Figure 3.1-6). More recently, the specimens were assigned to *Archaeornithomimus* (Russell, 1972), to indeterminate theropods (Smith and Galton, 1990), and to Ornithomimosauria indet. (Makovicky et al., 2004; Weishampel, 2006; Brownstein, 2017a). All but one of the original specimens of Arundel ornithomimosaurs were found at the same site near Muirkirk, Maryland (Gilmore, 1920). These original specimens include a dorsal vertebral centrum, two elongated caudal vertebrae, the distal ends of metatarsals II and III, two phalanx II-1s, a partial astragalus from the left hindlimb, a pedal phalanx III-2, a partial phalanx identified as from pedal digit IV, and a single pedal ungual (Figure 3.1-6). Additionally, a partial anteroposteriorly short pedal phalanx IV-? was assigned to *"Ornithomimus affinis"* (Gilmore, 1920). Gilmore
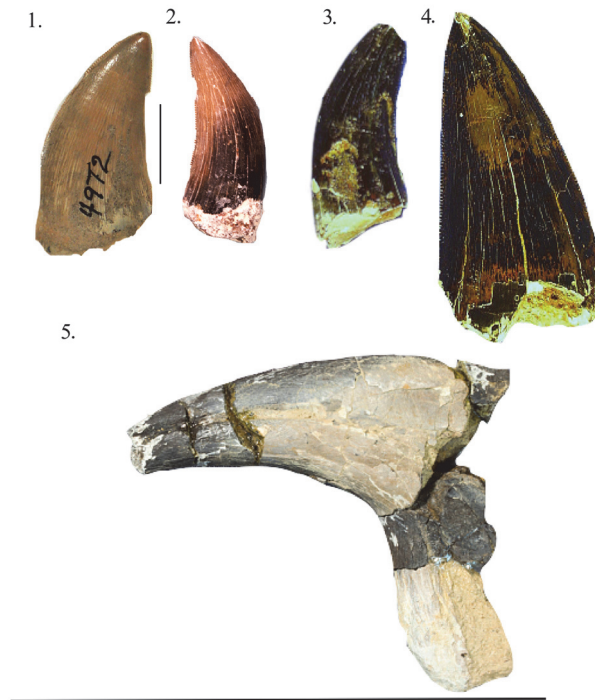
FIGURE 1. Selected carcharodontosaur elements from the Arundel Clay. Holotype tooth of *"Allosaurus" medius* (1), teeth assigned to *Acrocanthosaurus* (2-4), and a manual ungual possibly assignable to the latter allosaur in ?lateral (5) view. Scale bar equals 10 mm (1-4), scale bar equals 254 mm (5). Courtesy of the Smithsonian Institution. Photos by M. Brett-Surman.

(1920) noted that more material from Arundel ornithomimosaurs, including a partial tibia, phalanx and pedal ungual (USNM PAL 466054) had been recovered (Figure 3.1) (Weishampel and Young, 1996), and there are also many other specimens which have not yet been described formally in the literature (pers. obs.). The original fossils found nearby Muirkirk likely come from the Dinosaur Park site, which has yielded the tibia and other pedal elements as well as a variety of other elements including many pedal unguals (Brownstein, 2017a). Notably, two morphotypes of ornithomimosaur pedal unguals (diagnosed as such based on a single flexor fossa on the ventral surfaces of the elements) are found at this site: the shorter and smaller recurved unguals like that described by Gilmore (1920), and elongated, larger unguals with more flattened ventral surfaces in lateral view and less expansive dorsal and ventral faces over their proximal articular facets (Brownstein, 2017a). This latter morphology is more akin to the pedal unguals of more derived ornithomimosaurs, suggesting the possibility of two distinct ornithomimosaurs coexisting within the Arundel facies. Two ornithomimosaur

taxa are known from the Yixian Formation of China, which is of similar age to the Arundel.

The sauropod material from the Arundel facies has been the subject of some taxonomic confusion (Figure 4.1-4). A sauropod tooth was named *Astrodon johnstoni* (Leidy, 1865). Marsh (1888) named two species of his new genus *Pleurocoelus* from sauropod bones discovered near Muirkirk, Maryland. *Pleurocoelus nanus* was named from cranial elements and multitude of other fragmentary and isolated remains of several individuals, whereas *P. altus* was named on the basis of a partial hindlimb (Weishampel, 2006). Later studies have synonymized the three taxa (Hatcher, 1903; Gilmore, 1921; Carpenter and Tidwell, 2005), though some have doubted this taxonomic classification and instead regard all three Arundel sauropod species as dubious (Rose, 2007; D'Emic, 2013). If the Arundel material does indeed belong to one valid species, the correct name would be *Astrodon johnstoni,* which Carpenter and Tidwell (2005) classified as a basal titanosauriform. This placement is consistent with the data on sauropod clades in North America during the Early Cretaceous (e.g., Weishampel et al., 2004; Appen-

FIGURE 2. Selected elements of dromaeosaurs from the Arundel Clay. Teeth of *Deinonychus* sp. (1-4), claw of *Coelurus gracilis* (5). Scale bar equals 10 mm (1-4), scale bar equals 100 mm (5).
Courtesy of the Smithsonian Institution. Photos by M. Brett-Surman.

FIGURE 3. Selected ornithomimosaur remains from the Arundel Clay. Proximal tibia in medial (1) view, distal end of metatarsal III in lateral (2) view, left pedal phalanges II-1 in dorsolateral (3-4) view, pedal phalanx III-2 in dorsal (5) view, pedal ungual USNM6107 in medial (6) view. Scale bar equals 10 mm (1-2), 100 mm (3), 50 mm (4-6), 19.05 mm. Courtesy of the Smithsonian Institution. Photos by M. Brett-Surman.

dix 1). Carpenter and Tidwell (2005) and Weishampel (2006) suggested that the three Arundel sauropod taxa represented different growth stages of the same taxon; Weishampel (2006) estimated juveniles at 5 m and 500 kg in size with adults approaching 20 m and 18000 kg. Juveniles of the Arundel titanosauriform may have been prey items of the carcharodontosaurids, which were present in the region.

A single tooth was referred to the medium-sized ornithopod dinosaur *Tenontosaurus* sp. by Galton and Jenson (1979). This assignment was followed by Weishampel and Young (1996). Norman (2004) later assigned this specimen to Iguanodontia indet. Nevertheless, the tooth provides evidence for a large iguanodont in the Arundel ecosystem, adding to the similarities between the eastern Arundel fauna and the Aptian faunas of western North America (e.g., Ostrom, 1970; Forster, 1984; Forster, 1990; Winkler et al., 1997; Weishampel et al., 2004).

Armored dinosaurs left one of the better records of Early Cretaceous eastern North American ornithischians, and are represented by the genus *Priconodon crassus* in the Arundel Clay (Figure 5.1-5). This animal was first described on the basis of a single tooth (e.g., Carpenter and Kirkland, 1998), and additional teeth, an osteoderm (Weishampel, 2006), and a tibia (Carpenter, 2001; Vickaryous et al., 2004) have since been recovered. A multitude of teeth and the tibia referred to this taxon are in the collections of the United States National Museum. These teeth are all similar in being triangular, short, and having large denticles, and are assigned to nodosaurs based on the presence of a cingulum on the tooth between the base and the entirety of the crown and their narrow morphology (Weishampel, 2006). Notably, *Priconodon crassus* has been regarded as an unusually large nodosaurid based on the huge size of the teeth assigned to it (Carpenter, 2001). Though some have regarded this fragmentary taxon dubious (Vickaryous et al., 2004), the validity of this species has been supported by multiple studies comparing the morphology of the teeth of *Priconodon* with other nodosaurids (Carpenter, 2001; West and Tibert, 2004).

Lastly, the Arundel has surprisingly yielded teeth (Figure 5.6-7) described in detail and found to be most similar to those of neoceratopsians by Chinnery et al. (1998). The Arundel neoceratopsian teeth are especially important as they predate the age of the holotype skeleton of *Aquilops americanus*, which was discovered in Albian deposits

(Farke et al., 2014), teeth from the Cenomanian Mussentuchit Member of the Cedar Mountain Formation (Chinnery et al., 1998), and possible ceratopsian remains from the late Albian of Idaho (Weishampel et al., 2002). This makes the Arundel teeth the oldest occurrence of neoceratopsians in North America, suggesting that the clade arrived in the continent during the middle Early Cretaceous and thus supporting the hypothesis that neoceratopsians had dispersed into North America during the Aptian (Farke et al., 2014). Farke et al. (2014) suggested that at least three interchanges of neoceratopsians, the first being of *Aquilops*-like taxa, occurred between North America and Asia. Therefore, the Aptian age of the Arundel teeth suggests that the Arundel neoceratopsian may have been part of this dispersal and therefore would have been similar to the small *Aquilops* in form.

The Arundel Clay dinosaur fauna therefore consists of *Acrocanthosaurus* sp. and perhaps another large carnosaur, indeterminate coelurosaurs, the dromaeosaurid *Deinonychus* (including *"Coelurus" gracilis*), two unnamed possible species of ornithomimosaurs, the titanosauriform sauropod *Astrodon johnstoni*, iguanodontian dinosaurs similar to or possibly synonymous with *Tenontosaurus*, the large nodosaurid dinosaur *Priconodon crassus,* and a neoceratopsian.

Patuxent facies. Another one of the facies assigned to the Aptian by Lipka et al. (2006) is the Patuxent, the oldest unit exposed in the coastal plain of Maryland and Virginia (Stanford et al., 2004). This facies consists of sandstones mixed with light grey mudstones (Lipka et al., 2006). Though this formation has not preserved an extensive faunal list like the western Cloverly or Cedar Mountain Formations (Weems and Bachman, 1997), a somewhat extensive ichnological record of dinosaurs has been preserved in Patuxent facies. These include the tracks of theropods (*Megalosauropus* sp.), euornithopods (*Amblydactylus* sp.), and an ichnotaxon based on the tracks of a small ornithopod with possible affinities to the western form *Zephyrosaurus (Hypsiloichnus marylandicus)* (Weems and Bachman, 1997; Stanford, 1998; Stanford and Stanford, 1998; Stanford et al., 2004; Weishampel et al., 2004). One study (Lockley and Stanford, 2004) reported from the siliciclastic Patuxent facies the tracks of 14 different morphotypes of ornithopod, theropod, sauropod, and ankylosaur tracks. Lockley and Stanford (2004) also reported the presence of small tracks interpreted as those of hatchling dinosaurs alongside those of juveniles and adults, which they

FIGURE 4. Selected elements of *Astrodon johnstoni*. Teeth (1), mandible with teeth in lateral view (2), femur in dorsal view (3) and humerus in ventral (4) view. All scale bars equal 50 mm. Courtesy of the Smithsonian Institution. Photos by M. Brett-Surman and B. Martin.

regarded as indicating the presence of nests nearby. Weems and Bachman (2015) reviewed and added to the known dinosaur ichnotaxa from the Patuxent facies, which they found to include the theropod ichnotaxon *Megalosauropus* sp., the ornithomimosaur ichnotaxon *Ornithomimipus angustus*, the sauropod ichnotaxon *Brontopodus birdi* (suggested to be the track of a titanosauriform), the ichnontaxon *Tetrapodosaurus borealis* (interpreted as a nodosaurid and compared with *Propanoplosaurus*), the small ornithopod taxon *Hypsiloichnus marylandicus* (suggested to be tracks of a dinosaur of similar grade to *Zephyrosaurus schaffi*), and the medium-sized to large
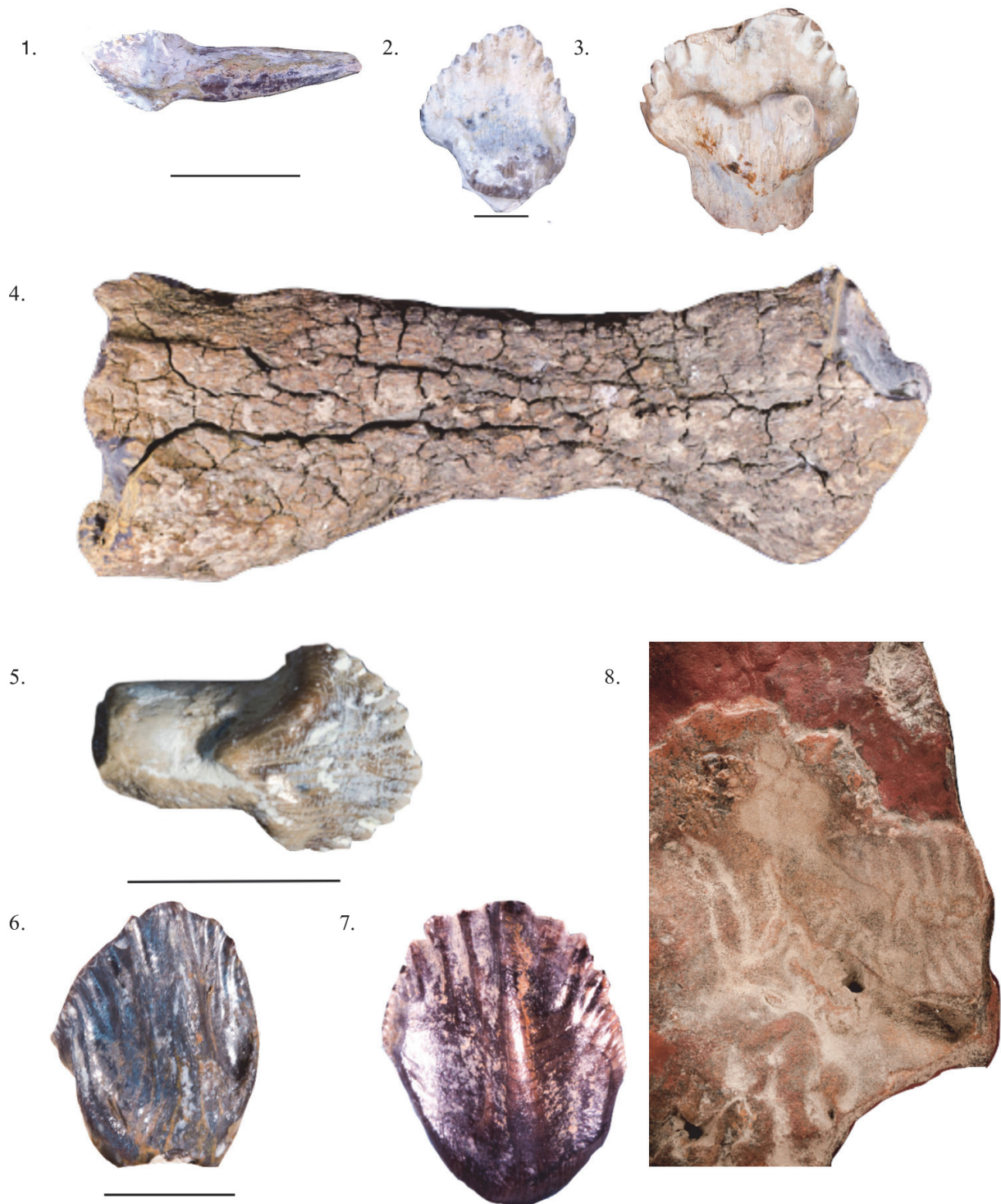
FIGURE 5. Selected elements of Arundel Clay and Patuxent facies ornithischians. Teeth and tibia of *Priconodon crassus* (1-5), teeth of an indeterminate neoceratopsian (6-7), and the holotype of *Propanoplosaurus* (8). Scale bar equals 50 mm (1, 4); equals 5 mm (2-3, 5, 6-7). (H) not to scale. Courtesy of the Smithsonian Institution. Photos by M. Brett-Surman, G. R. King, and C. Clark.

euornithopod tracks *Caririchnium leonardii* (suggested to be tracks of *Tenontosaurus*), *Gypsichnites pacensis* (suggested to be tracks of an iguanodontid of similar size to *Hippodraco scutodens*), and *Amblydactylus gethingi* (suggested to be the tracks of a hadrosauroid similar to *Eolambia*) (Weems and Bachman, 2015).

The nodosaur genus *Propanoplosaurus marylandicus* (Figure 5.8) is known from a specimen constituting of both molds and casts of the skeleton of a neonate individual which was recovered alongside the ichnofossils of dinosaurs (Stanford et al., 2011). The specimen included the posterior cranium, the ribcage vertebrae, the right femur and portions of the pes, and the partial right forelimb. The holotype of *Propanoplosaurus* is important for being the first nodosaur skeleton from the eastern seaboard (Stanford et al., 2011) and along with *Priconodon* is the only valid nodosaur taxon named from the Aptian of the east coast of North America.

Arkansas Trinity Group. The Trinity Group in Arkansas consists of varying layers of fine quartz sand, clay, barite, celestite, gravel, and fossiliferous gypsum and limestone (Dane, 1929; Hunt-Foster, 2003). These sediments, which are deposited in an unconformity with eroded Paleozoic rock, originated in the Ouachita Mountains (Hunt-Foster, 2003). The record of dinosaurs from the Aptian of Arkansas is limited. However, the partial right pes of an ornithomimosaurian dinosaur (Quinn, 1973; Hunt-Foster and Kirkland, 2017) was collected from what is now termed the "Friday Site". This specimen, UAM(1) 74, consists of metatarsals II, III, and IV and four phalanges and portions of the pedal unguals from pedal digits II, III, and IV reported from what is now termed the "Friday site" (due to it being on the property of Joe B. Friday, discoverer of the specimen) in Lockesburg Arkansas (Quinn, 1973; Hunt-Foster, 2003). Both the holotype and casts of the specimens are in the collections of the University of Arkansas.

Albian

Dakota Formation. The Albian Dakota Formation of Kansas and Nebraska has yielded the remains of a variety of dinosaurs whose relatives are also observed from the facies of the Potomac Formation. This formation consists of coastal and marine fluvial deposits in Kansas (e.g., Liggett, 2005) and as fluvial to estuarine deposits characterized by major facies changes and having common hydromorphic paleosols and disticontinous, long lignites and carbonaceous mudstones in Nebraska (e.g., Brenner et al., 2000; Joeckal et al., 2004). The

most complete dinosaur skeleton ever found on the eastern margin of the Dakota Formation is the Kanas taxon *Silvisaurus condrayi*. The holotype specimen of this dinosaur was retrieved from a site pertaining to the Terra Cotta Clay member of the Dakota Formation in Ottawa County, Kansas, a hard, limonite-containing sandstone that was cross-bedded (Eaton, 1960). The environment in which *Silvisaurus condrayi* would have lived is regarded as a warm-temperate forest based on fossil leaves found nearby the *Silvisaurus* site (Eaton, 1960). In addition to a partial skeleton including cervical and dorsal vertebra, a sacrum, and armor including a spike possibly from the shoulder, the holotype of *Silvisaurus condrayi* also includes a skull and a left mandible, all of it corresponding to an individual approximately 3 m long (Eaton, 1960). During the Skull Creek highstand, the site where *Silvisaurus condrayi* was found would have been on the coast of the newly-formed continent of Appalachia (e.g., Eaton, 1960). The natural mold of the possible sacrum of another *Silvisaurus* has been retrieved from Russell County Dakota Formation exposures (Liggett, 2005).

In addition to *Silvisaurus*, the Dakota Formation of Kansas has yielded the tracks of ornithomimosaurs (*Magnoavipes* sp.), of possible ankylosaurids, and of indeterminate dinosaurs (Liggett, 2005). The probable sacrum of an ankylosaur has also been found in Cloud County, Kansas (Liggett, 2005). In Nebraska, both ornithopod footprints and the proximal end of an ornithopod femur have been recovered from Dakota Formation sediments (Joeckel et al., 2004).

Paw Paw Formation. The Paw Paw Formation of Texas is middle Albian in age and has produced the remains of two to three species of nodosaurid dinosaurs along with indeterminate nodosaur remains (e.g., Coombs, 1995; Lee, 1996; Weishampel et al., 2004). The formation is made up of ferruginous clay and sand (Hill, 1894) and was deposited in a nearshore marine setting (Scott et al., 1978). Nodosaurid dinosaurs have left a number of specimens in this formation, including a juvenile nodosaur (Jacobs et al., 1994) and two named taxa.

Pawpawsaurus campbelli is known from a complete skull lacking mandibles from Tarrant County, Texas that is morphologically similar in some ways to *Silvisaurus condrayi* (Lee, 1996 Paulina-Carabajal et al., 2016). *Texasetes pleurohalio* is known from a partial skeleton including a skull fragment, a tooth, elements from the limbs, portions of the pelvis and scapulocoracoid, and

vertebrae (Coombs, 1995) and may be a synonym of *Pawpawsaurus* (Lee, 1996). However, in the phylogenetic analysis of Ankylosauria, the two Paw Paw nodosaur taxa and the Paw Paw nodosaur juvenile were found to be in notably different phylogenetic positions, with *Pawpawsaurus* the sister taxon to *Europelta, Texasetes* a sister taxon to *Edmontonia, Denversaurus,* and an unnamed nodosaur from Argentina, and the Paw Paw juvenile a sister taxon to *Niobrarasaurus* (Arbour et al., 2016).

Paluxy Formation. The Paluxy Formation of Texas, which is also middle Albian in age (e.g., Jacobs and Winkler, 1998; Weishampel et al., 2004; D'Emic, 2013), is a thin unit composed of shale and sandstone (Caughey, 1977). This unit has preserved arguably the most diverse of dinosaur faunas corresponding to Appalachia during the Albian. In addition to the remains of indeterminate theropods, the fossils of indeterminate dromaeosaurids have been recovered (e.g., Langston, 1974; Weishampel et al., 2004). Importantly, remains assigned to *Ornithomimus* sp. have also been recovered from the formation (e.g., Langston, 1974; Weishampel et al., 2004). As noted, both ornithomimosaurs and dromaeosaurs are known from Aptian to Albian deposits in the American west (Ostrom, 1969; Ostrom, 1970; Ostrom 1976; Cifelli, 1997; Cifelli and Gardner, 1997, Weishampel et al., 2004; Signac and Mackovicky, 2010; Oreska and Carrano, 2013; Brownstein, 2017a). Notably, *"Laelaps"* (=*Dryptosaurus* sp.) has also been reported from the Paluxy Formation (Langston, 1974), but these remains are likely those of indeterminate coelurosaurs or simply indeterminate theropods. Remains assigned to titanosauriforms (=*"Pleurocoelus"*) have also been reported from the formation (Langston, 1974; Weishampel et al., 2004). These specimens have more recently been assigned to the taxa *Astrophocaudia* and *Cedarosaurus* by D'Emic (2013). Indeterminate sauropod fossils have also been reported from the Cloverly Formation (e.g., Ostrom, 1970; Oreska and Carrano, 2013), while in Texas the ichnotaxon *Brontopodus birdi* has been reported from multiple localities (e.g., Langston, 1974; Pittman, 1989). Additionally, specimens assigned to nodosaurids and *Tenontosaurus* have been reported from the Paluxy Formation (Langston, 1974; Weishampel et al., 2004).

Glen Rose Formation. The Glen Rose Formation, which consists of alternating hard limestone and marl or marly limestone (Sellards et al., 1932), has preserved both dinosaur body specimens and ich-

nofossils. Trackways include the ichnotaxon *Eubrontes glenrosensis* (=?*Acrocanthosaurus*), which is found alongside the tracks of sauropods (*Brontopodus*) in the Paluxy River Valley (Farlow et al., 2010). There are also additional sites within this valley which have produced tridactyl tracks (Farlow et al., 2010). The Glen Rose has produced the trackways of both theropods and ornithopods (e.g., Wrather, 1922; Gould, 1929; Houston, 1933; Bird, 1939; Bird, 1944; Langston, 1974; Kuban, 1986; Pittman, 1989; Hawthorne and Bonem, 2002; Vance, 2002; Rogers, 2003). The ornithopod *Tenontosaurus* has also been reported from the formation (Weishampel et al., 2013). A partial juvenile titanosauriform skeleton is known from the Glen Rose as well (e.g., Langston, 1974; D'Emic, 2013), though it is not diagnostic to the genus level. In its entirety, the documented Glen Rose fauna consists of large theropods represented by tracks, sauropods, and ornithopods. This fauna is also somewhat similar to the theropod and ornithopod fauna of a track locality from the Chuta Formation of Mexico (Ferrusquía-Villafranca and Applegate, 1978).

Cenomanian

Woodbine Formation. The Woodbine Formation of Texas has preserved the singularly most complete dinosaur fauna of eastern North America during the early Late Cretaceous, representing fluvial, shelf, and deltaic deposits (Oliver, 1971; Trudel, 1994; Main, 2005; Main, 2013), and consisting primarily of sandstones and shales (Johnson, 1974).

The most diverse non-avian theropod dinosaur assemblage from the Woodbine Formation comes from a locality known as the Arlington Archosaur Site, which would have been on the Rudradia Peninsula of Appalachia during the Cenomanian (Main, 2013). This locality has produced the teeth of both dromaeosaurids and adult and juvenile allosauroids as well as the remains of other coelurosaurs (Main, 2013). The proximal portion of a large manual ungual was also recovered and may belong to an animal similar to *Allosaurus, Acrocanthosaurus,* or *Suchomimus* (Main, 2013). The latter possibility is unlikely, as no spinosaurid remains have currently been reported from North America. Main (2013) also discussed the possibility that some of the material recovered at the site could belong to tyrannosauroids. Additionally, teeth assigned to the taxon *Richardoestesia* have also been retrieved from the Arlington Archosaur Site (Main, 2013). Additions to the theropod fauna

known from the Woodbine Formation include cf. *Richardoestesia* teeth and the tracks of theropods, including ornithomimosaurs (*Magnoavipes*) (Lee, 1997a, 1997b; Lockley et al., 2001; Lockley et al., 2011). The Arlington Archosaur Site also has preserved the remains of the hadrosauroid dinosaur *Protohadros byrdi* and *P.* sp. (Main, 2013). This genus of hadrosauroid dinosaur was originally named on the basis of a partial skull and fragmentary skeleton retrieved from Flower Mound in Denton County, Texas, and has been estimated at 7 to 8 m in length (Head, 1996; Head, 1998). This species possessed a robust set of ventrally oriented mandibles suggested as an adaptation for the consumption of low-lying plant matter (Head, 1996; Head, 1998). A set of ornithopod tracks from the Woodbine Formation have been assigned the name *Caririchnium protohadrosaurichnos* based on the hypothesis that they may represent the tracks of this taxon (Lee, 1997b).

Ornithischian remains assigned to indeterminate hadrosaurs and a basal nodosaurid have reported from the Woodbine Formation (Lee, 1997a). The Woodbine nodosaur, which is known from teeth, limb elements, and an osteoderm, may be a distinct species (Lee, 1997a).

Raritan Facies. The Cenomanian Raritan facies of the upper Potomac Formation (e.g., Dalton et al., 1999; Miller et al., 2004; Lipka et al., 2006) preserves a scant but biogeographically significant non-avian dinosaur fossil record. This unit is made up of alternating clay and sand beds (Kimyai, 1966; Dalton et al., 1999; Miller et al., 2004; Lipka et al., 2006) and has produced both the only record of dinosaur tracks from the Cretaceous east of the Mississippi river and several other specimens, including an isolated distal metatarsal II of a tyrannosaur (YPM VPPU 016760) most similar to *Appalachiosaurus montgomeriensis* (Figure 6.1-5) (Baird, 1988, 1989; Gallagher, 1997; pers. obs.).

The trackway described in detail by Baird (1989) consists of the pes prints of a large theropod dinosaur. These tracks have been regarded to have affinities with those of a "megalosaurian type" (Baird, 1989). More recent studies have cast doubt on assigning any Cretaceous tracks to megalosaurs (Lockley et al., 1998). All of these tracks are now lost except for one track on display at the Rutgers University Geology Museum (Baird, 1989; Gallagher, 1997). A trace of the track at Rutgers was figured in Baird (1989) and is nearly identical in form to the *Saurexallopus* tracks from western North America figured by Gierlinski and Lockley (2013) in the slenderness and lengths of digits II

through IV, the morphology for the impression of digit I, the relative size and shape of the digits to each other, and the presence of a noticeable hallux track alongside a somewhat centrally located noticeable metatarsophalangeal pad suggesting the presence of an arctometatarsus in the track maker. The swelled pad behind pedal digit III and the reversed hallux were noted by Gierlinski and Lockley (2013) to be features of avian pedal morphology. Additional tracks figured in Baird (1989) in photographs taken before the tracks were lost are identical to some western *Saurexallopus* tracks listed in Gierlinski and Lockley (2013) (Gierlinski and Lockley, 2013, figures 23.1A, C, 23.3B) and also seem to show the presence of a clearly centralized triangular metatarsophalangeal pad extremely indicative of an arctometatarsalian condition and a hallux toe indicative of an avian pes as noted by Gierlinski and Lockley (2013). Gierlinski and Lockley (2013) suggested that the trackmakers of western *Saurexallopus* were oviraptorosaurians, especially noting *Hagryphus* and *Chirostenotes* as plausible candidates based on the presence of a well-developed hallux toe among members of the Oviraptorosauria. This feature is shared by the larger Woodbridge tracks. Thus, it may be that the Woodbridge tracks represent some large oviraptorosaur. However, here the relationships of the tracks are regarded as equivocal among Theropoda.

In addition to theropod material, euornithopod tracks have also been recovered from the Raritan facies of the Potomac Formation (e.g., Weishampel et al., 2004). These represent an important occurrence as they evince the presence of herbivorous dinosaur taxa in the upper Potomac fauna. The possibility also remains that these tracks belong to hadrosauroids, though any assignment beyond Euornithopoda would be tentative.

The Potomac Formation clearly represents an enticing look into the non-avian dinosaur fauna of the Cenomanian of northern Appalachia. Currently, the sparse record of non-avian dinosaurs has produced at least three different types of dinosaur. Importantly, the Raritan Facies of the Potomac Formation is a terrestrial deposit, suggesting a likelihood that future dinosaur specimens may be discovered from the formation (e.g., Gallagher, 1997).

Coniacian and Santonian

Niobrara Formation (Smoky Hill Chalk). The Niobrara Formation non-avian dinosaur fauna is important for being the only known non-avian dino-

FIGURE 6. Indeterminate tyrannosauroid metatarsal in dorsal (1), ventral (2), lateral (3), medial (4), proximal (5), and distal (6) views. Scale bars equal 100 mm. Courtesy of the Division of Vertebrate Paleontology; YPM VPPU.016760, Peabody Museum of Natural History,Yale University, New Haven, Connecticut, USA; peabody.yale.edu. Photography by Jamie Henderson.

saur fauna from the Coniacian of Appalachia as well as for being one of the only records of Coniacian North American dinosaurs. The two most completely known taxa from this formation are the nodosaurid *Niobrarasaurus coleii* and the derived non-hadrosaurid hadrosauroid *Claosaurus agilis*, both from Coniacian-Santonian sediments (Carpenter et al., 1995; Weishampel et al., 2004; Prieto-Márquez et al., 2016b). Additionally, the nodosaurid *Heirosaurus sternbergi* is known from more fragmentary remains (Carpenter et al., 1995),

though it may be a synonym of *Niobrarasaurus* (Carpenter et al., 1995; Everhart, 2005).

Indeterminate nodosaurid and hadrosauroid specimens have also been recovered (Carpenter et al., 1995; Everhart, 2005; Everhart and Hamm, 2005; Everhart and Ewell, 2006; Everhart, 2014). One set of hadrosaurid caudal vertebrae from an animal somewhat larger than the holotype of *Claosaurus agilis* has been recovered with evidence of consumption by a large shark (Everhart and Ewell, 2006). The preservation of partial specimens in the marine Smoky Hill Chalk is typical of the bloat-and-float model of preservation, which often characterizes Appalachian dinosaur specimens (Schwimmer, 1997). The author follows Carpenter et al. (1995) and Prieto-Márquez et al. (2016b) in considering this fauna to be Appalachian, a hypothesis which is supported by the close position of *Claosaurus* to *Lophorhothon* as a non-hadrosaurid hadrosauroid and of *Niobrarasaurus* as outside the group containing the derived western nodosaurids of the Late Cretaceous (e.g., Arbour et al., 2016; Prieto-Márquez et al., 2016b), being congruent with the current understanding of Appalachian as a refugium (e.g., Schwimmer, 1997). Further discussion on the assignment of the Niobrara fauna to an Appalachian origin may be found in the discussion section.

Claosaurus agilis was a small hadrosauroid and is only known presently from a fragmentary specimen that has been described in detail (Carpenter et al., 1995) and compared with other Appalachian hadrosauroids (Prieto-Márquez et al., 2016b). *Claosaurus* has most recently been resolved as a derived hadrosauroid just outside to Hadrosauridae (Prieto-Márquez et al., 2016a).

Niobrarasaurus coleii is the most completely known of the three ornithischians from the Smoky Hill Chalk, and the holotype of that taxon consists of a partial specimen including portions of the skull, vertebrae, partial limbs, and a variety of osteoderms (Carpenter et al., 1995) originally described as a species of *Hierosaurus* (Mehl, 1936). *Hierosaurus sternbergi*, the original "Niobrara nodosaur", is based on a multitude of osteoderms first described in 1905 by George Wieland (Wieland, 1905). More recently, *Heirosaurus* has been regarded as a nomen dubium (e.g., Carpenter et al., 1995).

McShan Formation. The McShan Formation of the southeastern United States also provides an important glimpse into Coniacian Appalachian faunas, arguably making the Appalachian dinosaur record from the Coniacian more complete than that from Laramidia. Several tyrannosaur fossils have been reported from this unit (Ebersole and King, 2011).

Eutaw Formation. The Santonian strata of southeastern North America produce the first complete non-avian dinosaur faunas from the Late Cretaceous that are distinctly 'Appalachian' in composition. One of the units has preserved a non-avian dinosaur fauna dating from the late Coniacian to the Campanian is the Eutaw Formation of Alabama and Mississippi, which has preserved a diverse fauna of dinosaurs including indeterminate theropods, hadrosaurids, and possibly indeterminate ankylosaurids (Kaye and Russell, 1973; Lamb, 1996; Weishampel et al., 2004). A complete review of Alabama dinosaur material (excluding *Eotrachodon orientalis*) found the Tombigbee Sand Member of the Eutaw Formation to have an even more diverse fauna consisting of dromaeosaurs, indeterminate tyrannosaurs (including possibly *Appalachiosaurus montgomeriensis*), ornithomimosaurs, nodosaurids, *Lophorhothon atopus*, and a multitude of hadrosaur specimens (including one notable partial specimen in the collections of the Mississippi Museum of Natural Science) (Ebersole and King, 2011).

Campanian

Demopolis Chalk Formation. The Demopolis Chalk Formation is a marine layer deposited around 78 million years ago that has yielded the most complete skeleton of an Appalachian tyrannosaur currently known: the holotype of *Appalachiosaurus montgomeriensis* (Carr et al., 2005). The holotype of *Appalachiosaurus montgomeriensis* was found at the Turnipseed Dinosaur Site and consists of the mostly complete skull and partial skeleton of a subadult tyrannosauroid (Carr et al., 2005). Multiple phylogenetic analyses using different character lists and different taxa have consistently recovered *Appalachiosaurus montgomeriensis* as a close outgroup to Tyrannosauridae and slightly more derived than the other currently named Appalachian tyrannosaur *Dryptosaurus aquilunguis* (e.g., Carr et al., 2005; Brusatte et al., 2011; Loewen et al., 2013; Fiorillo and Tykoski, 2014; Brusatte and Carr, 2016; Brusatte et. al., 2016). Two caudal vertebrae of the holotype of *A. mongomeriensis* are fused, possibly due to an injury the young dinosaur sustained to the tail (Carr et al., 2005). The holotype subadult specimen is estimated to have been around 6-7 meters long (Carr et al., 2005).

Additional remains of non-avian dinosaurs from the Demopolis Chalk Formation include vertebrae, hindlimb elements, and a single tooth assignable to indeterminate hadrosaurs (Ebersole and King, 2011). These large herbivores likely constituted as a prey source for *Appalachiosaurus montgomeriensis*.

Mooreville Chalk, Blufftown, Coffee Sand Formations, and unnamed Missouri clay unit

The Mooreville Chalk has yielded a diverse dinosaur fauna from the Santonian and Campanian. This dinosaur fauna included at least two species of hadrosauroid dinosaur (*Lophorhothon atopus* and *Eotrachodon orientalis*), the ornithomimosaur *"Ornithomimus" antiquus,* the dromaeosaurid *Saurornitholestes*, indeterminate hadrosauroids, nodosaurids, indeterminate theropods, and notably two different avian dinosaur taxa (Lull and Wright, 1942; Langston, 1960; Olson, 1975; Dobie, 1978; Lamb et al., 1993; Lamb, 1996, 1997, 1998, 2001; Chiappe et al., 2002; Weishampel et al., 2004; Kiernan and Schwimmer, 2004; Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). Its equivalent to the east, the Blufftown Formation (e.g., Schwimmer, 1993; Kiernan and Schwimmer, 2004; Ebersole and King, 2011), has preserved additional non-avian dinosaur fossils, including those assigned to indeterminate hadrosaurids, ?*Albertosaurus* sp. and indeterminate ornithomimids (e.g., Schwimmer et al., 1993; Ebersole and King, 2011). Schwimmer et al. (1993) noted that one element assigned to *Albertosaurus* was virtually indistinguishable from that of *Appalachiosaurus montgomeriensis*, and more recent studies have considered the Blufftown "*Albertosaurus*" material to be of *A. montgomeriensis* (Ebersole and King, 2011). The holotype of *Appalachiosaurus montgomeriensis* itself was also previously referred to *Albertosaurus* prior to its recognition as a new taxon (Carr et al., 2005).

In addition to the large tyrannosauroid *Appalachiosaurus montgomeriensis,* smaller theropod remains have also been recovered from these Campanian strata. The dromaeosaurid dinosaur *Saurornitholestes* sp. was reported from the Mooreville Chalk Formation on the basis of a tooth (Kiernan and Schwimmer, 2004), and indeterminate dromaeosaurid remains are also known from the Mooreville Chalk and Blufftown Formations (e.g., Ebersole and King, 2011). Ornithomimosaurs are represented by a single element assigned to *"Ornithomimus" antiquus* from the Blufftown Formation (Schwimmer et al., 1993; Ebersole and King, 2011).

Lophorhothon atopus is known from a partial skull and skeleton collected from lower Campanian Mooreville Chalk sediments outcropping in Dallas County, Alabama (Langston, 1960; Prieto-Márquez et al., 2016b). This hadrosauroid dinosaur was around 7.5 m in length (Schwimmer, 2002) and has been resolved as a derived hadrosauroid close to Hadrosauridae in a recent phylogenetic analysis (Prieto-Márquez et al., 2016a). *Eotrachodon orientalis*, the most recently described hadrosauroid from the Mooreville Chalk Formation, was described on the basis of a juvenile specimen estimated between 4 and 5.1 m in length (Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). This specimen represents the most completely known hadrosauroid dinosaur from the landmass of Appalachia and along with other Appalachian hadrosaurid taxa suggests that the landmass was where the hadrosaurid dinosaurs may have first evolved (Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). *Eotrachodon orientalis* may have gotten somewhat larger in size than the holotype juvenile specimen, which is thought to have been several years old at the time of death (Prieto-Márquez et al., 2016b). In addition to the two named taxa from the Mooreville Chalk, indeterminate hadrosaurids (including hadrosaurines) are known from both the Blufftown and Mooreville Chalk Formations, and indeterminate ornithischian remains from the Selma group may also be from these geological units (Langston, 1960; Schwimmer et al., 1993; Ebersole and King, 2011).

In addition to the hadrosauroids of the Mooreville and Blufftown Formations, the armored nodosaurids were also present. These are represented by indeterminate remains and the notable partial specimen of a juvenile nodosaur labeled RMM 1224 from the Mooreville Chalk (Langston, 1960; Lamb, 1996; Ebersole and King, 2011; Ebersole, personal commun., 2016). This specimen is the most complete nodosaur known from east of the Mississippi river (e.g., Ebersole and King, 2011) and probably represents a distinct taxon based on its stratigraphic location in comparison to other nodosaurs.

The Chronister Site of southeastern Missouri (e.g., Fix and Darrough, 2004) represents a unique chance to view the dinosaur fauna found in western Appalachia, bearing a notable assemblage corresponding to an unnamed smectite clay unit of Santonian to Campanian age overlapping in age

with the Coffee Sand Formation (Ebersole, 2009) and thus perhaps with the Mooreville Chalk and Blufftown formations (Ebersole and King, 2011). The non-avian dinosaur fauna known from the Chronister site is somewhat diverse, containing both indeterminate dromaeosaurid and tyrannosauroid material, as well as a species of hadrosauroid (Fix and Darrough, 2004). This latter species, originally named *Neosaurus missouriensis* and incorrectly identified as a sauropod (Gilmore and Stewart, 1945), was later assigned a new genus *Parrosaurus* due to the name *Neosaurus* being occupied (Gilmore, 1945). Later, Baird and Horner (1979) assigned *P. missouriensis* to *Hypsibema* based on the similarity of their caudal vertebrae. More recent discoveries show the site is rich in dinosaur fossils warranting study (Darrough, personal commun., 2016) and in some places the site may even constitute as a bone bed (Fix and Darrough, 2004). Additional remains of *Hypsibema missouriensis*, including skull elements, have also been recovered (Darrough et al., 2005; Darrough, personal commun., 2016). This dinosaur is likely assignable to its own genus, *Parrosaurus*, as it is not only separated from the localities where the material assigned to *H. crassicauda* was found but also is now known from more material, which may allow for detailed description (e.g., Darrough et al., 2005). Therefore, the name *Parrosaurus missouriensis* is preferred herein. This hadrosauroid was of huge size, as its distal caudal vertebrae are similar in dimensions to those of *Hypsibema crassicauda* (Baird and Horner, 1979). As Baird and Horner (1979) suggested, the similarity of the vertebrae of these two taxa indeed suggest a relationship between the two species. The Coffee Sand has been considered equivalent in age to the Mooreville Chalk and Blufftown Formations (Ebersole and King, 2011). Additional remains from the Coffee Sand include those of an indeterminate hadrosauroids and the limb element of a possible *Eotrachodon orientalis* adult (Ebersole and King, 2011; Prieto-Márquez et al., 2016b).

Tar Heel and Coachman formations. The Tar Heel and Coachman formations, which are equivalent in age (Schwimmer et al., 2015), have produced among the most extensive Appalachian dinosaur faunas. This fauna is middle Campanian in age (e.g., Baird and Horner, 1979; Self-Trail et al., 2004; Weishampel et al., 2004; Schwimmer et al., 2015), and is most extensively known from two sites. These are the Phoebus Landing site on the Cape Fear river of southern North Carolina (Bladen County) and the Stokes Quarry Site in northern

South Carolina (Darlington County) (e.g., Miller, 1967; Baird and Horner, 1979; Schwimmer et al., 2015). The former site has produced four or more different species of dinosaur (e.g., Miller, 1967; Baird and Horner, 1979; Weishampel and Young, 1996; Weishampel, 2004), whereas the latter has preserved an extensive theropod dinosaur fauna and indeterminate material from hadrosaurids (Weishampel and Young, 1996; Schwimmer et al., 2015).

The Phoebus Landing fauna includes a multitude of hadrosauroid taxa. The taxon *Lophorhothon* has been reported from the site (Miller, 1967; Baird and Horner, 1979; Weishampel and Young, 1996; Weishampel et al., 2004) alongside material assigned to *Hadrosaurus* sp. and a small unnamed taxon or juvenile hadrosaur (=*"Hadrosaurus" minor*) (Baird and Horner, 1979). Additional remains assignable to indeterminate hadrosaurids have also been recovered from the Phoebus Landing Site and Stokes Quarry (Miller, 1967; Baird and Horner, 1979; Schwimmer et al., 2015). A right metatarsal III recovered from the Phoebus Landing site is comparable to that of *Hadrosaurus foulkii* and provides evidence for the presence of an ~8 m hadrosaur in the Phoebus Landing fauna (Baird and Horner, 1979). Additionally, a partial tooth from Stokes Quarry was noted by Schwimmer et al. (2015) to compare favorably with "hadrosaurines" (Hadrosauroidea indet.). Weishampel and Young (1996) documented the discovery of many hadrosaur teeth, vertebrae, and limb material, including the partial femur of a hadrosauroid.

The behemoth hadrosauroid *Hypsibema crassicauda* is also known from caudal vertebrae from Phoebus Landing (Figure 7.1) and from other sites pertaining to the Tar Heel Formation (e.g., Cope, 1871; Miller, 1967; Baird and Horner, 1979; Weishampel and Young, 1996). A very large partial hadrosaur humerus from the Tar Heel Formation was described by Baird and Horner (1979) and is tentatively referred to as *Hypsibema crassicauda* based on its estimated complete size of 830 mm, massive for a hadrosaur (Baird and Horner, 1979). This dinosaur has been estimated at 12 m or more in length (Baird and Horner, 1979; Weishampel and Young, 1996), and based on comparisons with the vertebrae of the hadrosaurs *Hadrosaurus foulkii* (Cope, 1871) and *Eotrachodon orientalis* (Prieto-Márquez et al., 2016b) in comparison to the estimated size of each of these taxa (Weishampel and Young, 1996; Prieto-Márquez et al., 2016b), the author herein makes a tentative estimate of the size of this hadrosaur as being around 12-17 m in

length. The implications of the large size attained by *H. crassicauda* and other Appalachian hadrosauroids are considered in the Discussion section.

Hypsibema crassicauda has been placed as a hadrosaurid and as dubious taxon within Hadrosauroidea (e.g., Weishampel and Young, 1996; Horner et al., 2004; Weishampel, 2006; Prieto-Márquez et al., 2016b). The author concurs with the sentiment of Baird and Horner (1979) that *H. crassicauda* represents a valid species among Hadrosauroidea based on its caudal vertebrae being laterally uncompressed. In any case, the vertebrae assigned to *H. crassicauda* represent a distinct morphotype of hadrosauroid in the Phoebus Landing fauna. Further discussion of *Hypsibema* as a distinct hadrosauroid may be found in the discussion.

The ceratopsian dinosaurs, though extremely rare on Appalachia, left a single indication of their presence within the Tar Heel non-avian dinosaur fauna. This record includes a derived leptoceratopsid left maxilla from sediments of the Tar Heel Formation of equivalent age to the Phoebus Landing Site (Longrich, 2016). Longrich (2016) noted that Appalachia belonging to a distinct palynofloral province may have implications for the adaptations found on the Tar Heel leptoceratopsian for the consumption of less-resistant plant matter.

The theropod dinosaurs also left behind an extensive record at Phoebus Landing. Hindlimb material comparable to *Dryptosaurus aquilunguis* was noted by Baird and Horner (1979). The femoral material compared to *D. aquilunguis* and figured by Baird and Horner (1979) may show an autapomorphic feature of this taxon. This is the presence of an ovoid fossa on the medial surface of the femur just above the distal condyles (Brusatte et al., 2011). More recently, Weishampel and Young (1996) also regarded *Dryptosaurus aquilunguis* as present at Phoebus Landing. This large tyrannosauroid theropod is known from a holotype specimen from the New Egypt Formation of New Jersey (e.g., Brusatte et al., 2011).

In addition to *Dryptosaurus aquilunguis,* material assigned to the tyrannosauroid dinosaur *Appalachiosaurus montgomeriensis* was reported from Stokes Quarry by Schwimmer et al. (2015). Some of these elements may be from juvenile individuals (Schwimmer et al., 2015). Therefore, two large tyrannosauroid dinosaurs were present in the Tar Heel-Coachman non-avian dinosaur fauna. Adults of both of these species probably measured from 6-9 m in length, comparable in size to the crocodylian *Deinosuchus rugosus* (Schwimmer, 1997;

Schwimmer, 2002). An address on competition between large tyrannosauroids and *D. rugosus* is made in the Discussion section.

Small carnivorous theropod dinosaurs are represented by at least two taxa in the Upper Tar Heel-Coachman non-avian dinosaur fauna. Schwimmer et al. (2015) identified the dromaeosaurid *Saurornitholestes langstoni* from diagnostic teeth and a pedal ungual. These 1.8 m long dromaeosaurids (Currie and Koppelhus, 2005) were small predators in their environment. Additionally, two teeth were noted by Schwimmer et al. (2015) to be distinct from the Coachman *Saurornitholestes* material and similar to those of the western species *Troodon* and *Dromaeosaurus*, though they noted that the teeth are not sufficient to affirm the presence of either of the two taxa in the Coachman Formation. Additional teeth from small theropods have been uncovered in North Carolina (Weishampel and Young, 1996).

Remains assigned to ?*Ornithomimus* sp. and indeterminate ornithomimosaurs have been recovered from Phoebus Landing and Stokes Quarry, respectively (Miller, 1967; Baird and Horner, 1979; Schwimmer et al., 2015). These medium-sized feathered dinosaurs represent an important addition to the theropod diversity of the Tar Heel-Coachman non-avian dinosaur fauna.

Additionally, Schwimmer et al. (2015) mentioned "bird-like" limb elements which they assigned to Maniraptora indet. These remains are indicative of the presence of small maniraptorans within the Tar Heel-Coachman non-avian dinosaur fauna. A small, pathological metatarsal was also assigned to Theropoda indet. by Schwimmer et al. (2015) from Stokes Quarry. Thus, a population of small, maniraptoran theropods likely existed among the Upper Tar Heel-Coachman Formation ecosystem.

Bladen Formation. The Bladen Formation also preserves a record of dinosaurs from the Carolinas, but from the late Campanian. This record includes the remains of indeterminate dromaeosaurids, indeterminate tyrannosaurs, *Ornithomimus* sp. and indeterminate hadrosauroids (Crane, 2011). This fauna, along with that of the Donoho Creek Formation below, indicates that a fairly homogeneous dinosaur fauna persisted in the Carolinas through the Campanian.

Donoho Creek Formation. The Donoho Creek Formation of the Carolinas is slightly younger in age than the Coachman Formation, dating to the late Campanian (e.g., Schwimmer et al., 2015). This formation has not preserved as diverse of a

FIGURE 7. Originally designated holotype of *Hypsibema crassicauda*. Lectotype caudal vertebra of *Hypsibema crassicauda* (1), distal tyrannosauroid femur (=?*Dryptosaurus aquilunguis*) (2), hadrosauroid metatarsal II and limb shaft (3). Scale bar equals 100 mm. Assignments after Baird and Horner (1979). Courtesy of the Smithsonian Institution. Photo by M. Brett-Surman.

dinosaur fauna as earlier Late Cretaceous sediments in the Carolinas. However, Schwimmer et al. (2015) reported a diverse theropod assemblage from the Donoho Creek Formation including the large tyrannosauroid *Appalachiosaurus montgomeriensis*, the dromaeosaurid *Saurornitholestes langstoni*, and indeterminate ornithomimosaurians.

Indeterminate hadrosaurid material has been reported from the Donoho Creek non-avian dinosaur fauna (Weishampel and Young, 1996; Weishampel et al., 2004; Schwimmer et al., 2015), including from skull elements (Schwimmer et al., 2015). The presence of the same two theropod taxa (*A. montgomeriensis* and *S. langstoni*) in the Coachman and Donoho Creek formations suggests that theropod faunas remained somewhat homogeneous throughout the Campanian in the Carolinas.

Merchantville Formation. The Merchantville Formation of the Atlantic Coastal Plain has preserved at least three different species of dinosaurs representing three distinct clades. *Hadrosaurus foulkii* is present in this formation (Gallagher, 1993; Weishampel and Young, 1996; Weishampel et al., 2004). One specimen from this unit, YPM VPPU.021795, represents an indeterminate tyrannosauroid distinct from either *Appalachiosaurus* or *Dryptosaurus* (Brownstein, 2017b). This unit is early to middle Campanian in age (e.g., Miller et al., 2004).

Woodbury Formation. Like the Merchantville Formation, the Woodbury Formation is middle Campanian in age and has preserved the remains of only *Hadrosaurus foulkii* (e.g., Prieto-Márquez et al., 2006; Prieto-Márquez, 2011). This medium-sized basal hadrosaurid dinosaur represents, along with the Alabama taxon *Eotrachodon orientalis*, an important discovery from Appalachia in regards to the evolution of hadrosaurs due to its placement as a basal hadrosaurid outside Saurolophidae (Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). In addition to the holotype of *Hadrosaurus foulkii*, a historically important specimen described by paleontologist Joseph Leidy (Leidy, 1858) and the first somewhat complete skeleton of a dinosaur known from the Americas (Prieto-Márquez et al., 2006), hindlimb material originally assigned as the holotype of the taxon *"Ornithotarsus immanis"* by Cope (1869) has been more recently assigned to *Hadrosaurus foulkii* (Baird and Horner, 1977; Weishampel and Young, 1996). Gallagher (1997) remarked on the huge size of these remains, noting that a truly large hadrosaurid was present in the Upper Cretaceous of New Jersey. Weishampel and

Young (1996) gave a length estimate of *Hadrosaurus foulkii* at 10 m, though the individual to which the holotype of *"Ornithotarsus" immanis* pertains may have approached 12 or more meters in length. Additionally, a large partial femur discussed by Gallagher (1997) from the Matawan Group (which includes the Woodbury Formation) (e.g., Gallagher, 1997) may also belong to a large individual of *H. foulkii*, though the extremely poor condition of this bone (Gallagher, 1997) means that any assignment to a specific taxon is nearly or completely impossible. Another occurrence of large hadrosaur possibly from the Woodbury Formation is based on the single pedal phalanx of a hadrosaur assigned to *"Ornithotarsus" (=Hadrosaurus foulkii)* by Edward Drinker Cope, which is a third larger than the corresponding element in the holotype of *H. foulkii* (Weishampel and Young, 1996).

Marshalltown Formation. The most extensive non-avian dinosaur fauna from the Campanian of New Jersey and also Delaware comes from the early late Campanian Marshalltown Formation (Sugarman et al., 1995; Miller et al., 2004) consisting of fine, quartz-rich glauconite clays (Olsson, 1988; Weishampel and Young, 1996). This dinosaur fauna consists of at least two different hadrosaur taxa, a large tyrannosauroid dinosaur, ornithomimosaurs, dromaeosaurids and nodosaurids (Lauginiger, 1984; Grandstaff et al., 1992; Gallagher, 1993; Weishampel and Young, 1996; Weishampel et al., 2004; Denton et al., 2011; pers. obs.). The Ellisdale fossil site of New Jersey in particular has produced an array of fossils assignable to at least three different species of non-avian dinosaur (e.g., Grandstaff et al., 1992; Gallagher, 1993; Weishampel and Young, 1996).

Hadrosauroid dinosaurs are represented in the Marshalltown Formation by remains assigned to the gigantic hadrosauroid *Hypsibema crassicauda* and the hadrosaurid *Hadrosaurus* sp. from the Ellisdale site (Grandstaff et al., 1992; Weishampel and Young, 1996), *Hadrosaurus* (including *H. foukii*) remains from Marshalltown exposures elsewhere in New Jersey (Gallagher, 1993; Weishampel and Young, 1996, Weishampel, 2006), and indeterminate remains from both New Jersey and Delaware (Gallagher, 1993; Weishampel and Young, 1996; Weishampel et al., 2004). Additionally, indeterminate ornithopods have been reported from the Ellisdale site (Grandstaff et al., 1992).

Nodosaurids are also present in the Marshalltown Formation (Gallagher, 1993; Weishampel and Young, 1996; Weishampel et al., 2004). Though

they are known only by indeterminate remains, they represent the earliest record of nodosaurids from New Jersey and the possibility remains that they correspond to an unnamed taxon or taxa.

Theropods left a diverse fauna within the Marshalltown Formation. *Dryptosaurus* (sometimes assigned to *D. aquilunguis*) was reported from the Marshalltown by Grandstaff et al. (1992), Gallagher (1993), Weishampel and Young (1996), and Weishampel et al. (2004). Ornithomimosaur specimens, including material assigned to *Ornithomimus (="Coelosaurus")* have also been collected from the Marshalltown Formation (Gallagher, 1993; Weishampel and Young, 1996; Weishampel et al., 2004; pers. obs.). Teeth referable to indeterminate dromaeosaurids are also known from the Marshalltown Formation (Kiernan and Schwimmer, 2004; Denton et al., 2011; pers. obs.), increasing the carnivorous theropod diversity of this late Campanian unit. In addition, Grandstaff et al. (1992) reported the remains of indeterminate theropods from the Ellisdale site.

Mount Laurel/Wenonah Formations. The Mount Laurel/Wenonah Formations are latest Campanian-early Maastrichtian units from New Jersey (e.g., Gallagher, 1993) that preserve a variety of dinosaur taxa. *Dryptosaurus* sp. has been reported from the formations, as have indeterminate ornithomimosaurs (Weishampel et al., 2004). Additionally, material assigned to *Hadrosaurus* sp. has been collected from the formations along with bones from indeterminate hadrosaurids (Gallagher et al., 1993). Overall, this fauna is similar in composition to that of the Marshalltown Formation.

Coon Creek and Ripley Formations. The Coon Creek and Ripley Formations represent late Campanian deposits that are equivalent in age (e.g., Ebersole and King, 2011; Ebersole, personal commun., 2016) and have yielded a non-avian dinosaur fauna consistent with faunas from earlier in the Campanian. Ebersole and King (2011) listed hadrosaurid remains as coming from the Ripley and Coon Creek Formations. Of note is a hadrosaurid skull which was recovered from the Coon Creek Formation in Tennessee (Ebersole and King, 2011). Additionally, the partial skeletons of multiple ornithopods were noted to be recovered from the Ripley Formation (Ebersole and King, 2011).

Kanguk Formation. This Campanian/Maastrichtian age deposit lies to the north of Nunavut, Canada, and has preserved a fairly diverse assemblage of dinosaurs (e.g. Gangloff, 2012; Vavrek et al., 2014). This assemblage includes a lambeosaurine and possibly another type of hadrosaurid as well as a tyrannosauroid dinosaur (Gangloff, 2012). The lambeosaurines of the Kanguk are possibly the earliest known from the continent of Appalachia, and this fauna is the only one known from the far north of the landmass.

Maastrichtian

Navesink Formation. The Maastrichtian Navesink Formation is mainly composed of glauconitic clays (e.g., Sugarman et al., 1995; Kennedy et al., 2000; Miller et al., 2004) and has preserved the best known non-avian dinosaur fauna from the Maastrichtian of Appalachia. This extensive fauna includes a diverse assemblage of theropods, including an ornithomimosaur and two possibly distinct species of tyrannosauroid, a nodosaurid, a basal hadrosaurid, and lambeosaurines.

The hadrosaurid species found within the Navesink Formation include the medium-sized *Hadrosaurus "cavatus" (=foulkii),* an unnamed genus of very small hadrosaur *("Hadrosaurus" minor)* currently considered a hadrosaurid of undetermined affinities, remains originally designated as the holotype of *Hadrosaurus minor* with the possibility that they represent juvenile remains, and an indeterminate species of lambeosaurine dinosaur (Colbert, 1948; Gallagher, 1993; Gallagher, 1997; Prieto-Márquez et al., 2006). The original specimen of *Hadrosaurus minor* consisted of dorsal vertebrae, and has been rendered a nomen dubium (Horner et al., 2004). Thus, the Navesink specimen described by Colbert (1948) has been referred to as *"Hadrosaurus" minor* (e.g., Weishampel et al., 2004; Weishampel, 2006). While Baird and Horner (1977) suggested the Navesink *"Hadrosaurus" minor* specimen was closely related to the saurolophine *Edmontosaurus* from the American west, more recent studies have suggested the taxon to be an unresolved taxon within "Hadrosaurinae" (=Saurolophinae) and as a hadrosaurid of uncertain affinities (Horner et al., 2004; Prieto-Márquez et al., 2006). Prieto-Márquez et al. (2006) noted that referral of *"H." minor* to *Edmontosaurus* would be equivocal. Furthermore, the presence of multiple species of basal hadrosaurids and non-hadrosauroids on Appalachia suggests a higher likelihood of *"Hadrosaurus" minor* being of a basal phylogenetic position among the hadrosaurs.

In addition to the hadrosaurids, nodosaurid remains have also been recovered from the Navesink Formation. This clade of armored dinosaurs is represented by a single vertebra (e.g., Gallagher, 1993; Weishampel et al., 2004; Weishampel, 2006). As nodosaurid remains have

been recovered from the somewhat older Campanian Marshalltown Formation in New Jersey, the possibility that the Navesink vertebrae represents a distinct taxon from the Marshalltown animal is certainly possible. Regardless, this vertebrae certainly shows that another distinct group of herbivorous dinosaurs was present alongside the hadrosaurids in the Navesink ecosystem.

Theropods also left a somewhat diverse fauna behind in the Navesink Formation. The tyrannosauroids are represented by remains attributable to *Dryptosaurus aquilunguis* (Weishampel and Young, 1996; Weishampel, 2006), a tibia, AMNH 2550, of an unnamed tyrannosauroid *(="Laelaps" macropus)* (e.g., Holtz, 2004; Weishampel et al., 2004; pers. obs.), and indeterminate material, including a taxon named *Diplotomodon horrificus* known from a single tooth (e.g., Weishampel and Young, 1996; Holtz, 2004; Weishampel et al., 2004; Weishampel, 2006). Additionally, the holotype of *"Ornithomimus" antiquus,* which has most recently been regarded as a distinct taxon of ornithomimid dinosaur, is known from the Navesink (e.g., Leidy, 1865; Weishampel and Young, 1996; Makovicky et al., 2004; Weishampel et al., 2004; Weishampel, 2006; Brusatte et al., 2012).

The Navesink Formation was the only one of the few Maastrichtian Appalachian dinosaur-bearing formations included in statistical analyses herein, being compared to the Hell Creek, Lance, Horseshoe Canyon, and Javelina Formations. The Navesink was found by Miller et al. (2004) to be approximately 69-67 million years old (early to middle Maastrichtian), whereas the dinosaur fauna of the Horseshoe Canyon Formation is early and those of the Hell Creek, Lance, and Javelina Formations are late Maastrichtian in age (e.g., Weishampel et al., 2004). The results of the statistical analyses performed on these faunas may be found in Tables 27-31 of Appendix 1.

Severn Formation. The Maastrichtian (~70.7 Ma) (Hazel et al., 1984; Baird, 1986) Severn Formation of Maryland has also produced an important record of dinosaurs. This record includes the partial femur of an ornithomimosaur assigned by Baird (1986) to *"Ornithomimus" antiquus,* an ornithomimosaur pedal phalanx (Hartstein et al., 1986), and indeterminate hadrosauroid limb portions and partial vertebrae (e.g., Baird, 1986; Hartstein et al., 1986).

New Egypt Formation. The New Egypt Formation preserves the most complete late Maastrichtian dinosaur fauna from the eastern United States. The dinosaur remains retrieved from this formation include the holotype of the large tyrannosauroid dinosaur *Dryptosaurus aquilunguis* (e.g., Brusatte et al., 2011) and are housed in the AMNH FARB and ANSP collections. This partial skeleton is one of the most complete theropod dinosaur skeletons known from the Cretaceous of eastern North America (e.g., Schwimmer, 1997; Brusatte et al., 2011). One of the most intriguing features of *D. aquilunguis* are its large hands and massive manual ungual. The hadrosaurid dinosaurs from the New Egypt Formation include lambeosaurines, the dubious taxon *Hadrosaurus minor*, and indeterminate forms (e.g., Colbert, 1948; Weishampel and Young, 1996; Weishampel et al., 2004; Prieto-Márquez et al., 2006; Weishampel, 2006).

Kingstree Formation Equivalent. This unit is late Maastrichtian in age and has preserved the vertebra of an indeterminate theropod dinosaur (Schwimmer et al., 2015).

Prairie Bluff Formation. The late Maastrichtian Prairie Bluff Formation has preserved the vertebra of an indeterminate hadrosaur (Ebersole and King, 2011; George Phillips, personal commun., 2015).

Owl Creek Formation. The Owl Creek Formation of late Maastrichtian age has preserved an extremely important record of a single type of non-avian dinosaur. This is the single tooth of a possibly chasmosaurine ceratopsid (Farke and Phillips, 2017).

RESULTS

Aptian Dinosaur Faunas. Because the Arundel Clay has been dated to the upper Aptian to Albian (e.g., Kranz, 1998; Lipka et al., 2006), it was compared with two well-known upper Aptian to Albian units of the western United States: the Ruby Ranch Member of the Cedar Mountain Formation (e.g., Kirkland et al., 1999; Mori, 2009) and the Cloverly Formation (e.g., Chen and Lubin, 1997). The age of the Cloverly Formation is not well-constrained, but several studies regarding Ostrom's (1970) units V-VII have found an Aptian-Albian age for those sediments with dates that range from about 113-108 Ma (Burton et al., 2006; Zaleha, 2006; Farke et al., 2014). However, D'Emic and Britt (2012) found a much younger age of about 103 Ma for sediments corresponding to unit VI or VII of Ostrom (1970) (Farke et al., 2014). The age of the Ruby Ranch member is also relatively unconstrained, with some estimates placing the unit from 120-108 Ma and others at around 104 Ma, overall corresponding to the Aptian and Albian (Mori, 2009; Chure et al., 2010). Units V-VII of the Cloverly Formation represent fluvial to overbank and lacustrine environments (e.g., Ostrom, 1970; May, 1992),

whereas the environment represented by the Ruby Ranch Member was a semi-arid one punctuated by low-sinuosity rivers and ephemeral ponds (e.g., Harris, 1980; Kirkland et al., 1999; Kirkland and Madsen, 2006). Though depositional differences between these formations certainly hinder precise statistical analysis by causing possible biases, the author emphasizes that Aptian dinosaur faunas containing several taxa are lacking in North America save for very few units (e.g., Weishampel et al., 2004).

Analytic comparisons of the Arundel Clay fauna and those of these two units (Table 1 of Appendix 1) show the Arundel fauna is somewhat similar in composition to that of the Ruby Ranch in containing *Deinonychus, Tenontosaurus, Acrocanthosaurus,* or a similar taxon, a large nodosaurid, and a large titanosauriform (e.g., Leidy, 1865; Marsh, 1888; Kranz, 1996; Weishampel, 2006; Ostrom, 1970; Weishampel et al., 2004; Mori, 2009; Woodruff, 2012; D'Emic and Foreman, 2012; Mannion et al., 2013; Oreska et al., 2013). Notably, ornithomimosaurs and neoceratopsians are absent from the Ruby Ranch Member, though they are present in both the Arundel and the Cloverly Formation along with a large nodosaurid *(Sauropelta), Deinonychus, Acrocanthosaurus, Tenontosaurus,* ornithomimosaurs, and titanosauriforms (Ostrom, 1969, 1970, 1976; Kranz, 1996; Chinnery et al., 1998; Makovicky and Sues, 1998; Weishampel et al., 2004; Gignac and Makovicky, 2010;Woodruff, 2012; d'Emic et al., 2012; Oreska et al., 2013; Farke et al., 2014; Brownstein, 2017a). Nevertheless, the Arundel ceratopsian material remains problematic (e.g., Farke et al., 2014), and so future work on the Arundel fauna will be needed to better comparisons between these formations. Statistical comparisons of these faunas show medium to medium-high similarity (50-70% Simpson Similarity index values, 0.5-0.6) on the family level between the Arundel and these two units, although the same comparisons yield low genus level similarity when measured with the Simpson similarity index (30-50%) and Jaccard coefficient (0.2-0.3) (Tables 2-5 of Appendix 1). The low genus-level similarity between the faunas is likely augmented because of the lack of specimens from the Arundel assignable to specific genera, as half the genera known from the Arundel *(Deinonychus, Acrocanthosaurus, Tenontosaurus)* are known from the Cloverly and Ruby Ranch faunas (Table 1 of Appendix 1). *Acrocanthosaurus* and *Deinonychus* specimens have also been collected from the Twin Mountain and Antlers formations of Texas and Oklahoma (Stovall

and Langston, 1950; Cifelli, 1997; Harris, 1998; Currie and Carpenter, 2000; D'Emic et al., 2012), and in addition to the common occurrence of *Tenontosaurus* remains (e.g., Ostrom, 1970; Forster, 1984; Forster, 1990; Winkler et al., 1997; Weishampel et al., 2004), the ankylopollexian iguanodontians *Hippodraco* and *Theiophytalia* are present during the Aptian in the American west (Brill and Carpenter, 2006; McDonald et al., 2010). The lack of reported ornithomimosaur material from the Ruby Ranch member of the Cedar Mountain Formation is not regarded as significant, as the possible ornithomimosaur *Nedcolbertia justinhofmanni* is known from the slightly older Yellow Cat Member of the Cedar Mountain Formation (Brownstein, 2017a; Kirkland and Hunt-Foster, 2017).

Nodosaurids and titanosauriforms were also spread across North America during this time, with the latter also known from the Early Cretaceous of Texas *(Sauroposeidon proteles, Astrophocaudia slaughteri, Cedarosaurus* sp., and Titanosauriformes indet.) (e.g., Larkin, 1910; Langston, 1974; Cifelli, 1997; Wedel et al., 2000; Weishampel et al., 2004; D'Emic, 2013), from Utah *(Brontomerus mcintoshi; Cedarosaurus weiskopfae)* (Taylor et al., 2011), and from the Cloverly Formation of Montana and Wyoming (including *Sauroposeidon*) (Tidwell et al., 1999; Ostrom, 1970; Weishampel et al., 2004; Woodruff, 2012; D'Emic and Foreman, 2012; Mannion et al., 2013; Oreska et al., 2013). The nodosaurid taxon *Sauropelta* was present in the Aptian of the Little Sheep Mudstone of the Cloverly Formation in the western United States (e.g., Ostrom, 1970; Kirkland et al., 1997; Weishampel et al., 2004; Oreska et al., 2013). Additional fossils assigned to *Sauropelta* have been recovered from middle Cedar Mountain Formation (Jensen, 1984; Weishampel et al., 2004). Fossils of the nodosaurid taxa *Hoplitosaurus* sp. and *Tatankacephalus cooneyorum* have also been recovered from the middle Cedar Mountain Formation and the Cloverly Formation, respectively (Weishampel et al., 2004; Parsons and Parsons, 2009). Finally, the polacanthine *Gastonia lorriemcwhinneyae* was described in 2016 (Kinneer et al., 2016).

Though the lack of body fossils from the Patuxent facies and the Trinity Group in Arkansas warranted against statistical comparisons between the faunas of these and western units, several analytical similarities can be observed between them. Indeed, the Patuxent facies shares with the Cloverly Formation and other western units nodosaurids, small (=*Zephyrosaurus*-like) and large

euornithopods, ornithomimosaurs (as does the Arkansas Trinity Group) (e.g., Quinn, 1973; Kirkland and Hunt-Foster, 2017), large theropods, and titanosauriforms (e.g., Ostrom, 1970; Weishampel et al., 2004; Kirkland et al., 1999; Mori et al., 2009; D'Emic, 2013) and thus supports the hypothesis that a relatively homogenous dinosaur fauna existed throughout land now within the United States during the Early Cretaceous.

Albian Dinosaur Faunas. The Dakota Formation is late Albian to early Cenomanian in age (e.g., Joeckel et al., 2004; Koch, 2007) and was compared with the similarly-aged Wayan, Blackleaf, and Willow Tank formations of the western United States (Varricchio et al., 2007; Bonde et al., 2012; Ullman et al., 2012; Krumenacker et al., 2017). The Wayan Formation of Idaho was found to be deposited between 101.8 and 95.5 Ma by Krumenacker (2010), who reviewed the formation's stratigraphy. The Willow Tank Formation has been found to be between 98.5 and 98.1 million years old (e.g., Fleck, 1970; Troyer et al., 2006; Bonde et al., 2012), and the Blackleaf Formation has been dated to the late Albian and early Cenomanian (e.g., Dorr, 1985; Varricchio et al., 2007; Ullman et al., 2012). All of these western formations have been considered as overlapping in age (e.g., Bonde et al., 2012; figure 2 in Krumenacker et al., 2017). The Dakota Formation in southeastern Nebraska has been interpreted as representing fluvial to estuarine environments (e.g., Joeckal et al., 2004), whereas the Dakota Formation in Kansas has been interpreted as a coastal plain (e.g., Eaton, 1960), and the Blackleaf, Wayan, and Willow Tank formations all seemingly represent fluvial-deltaic environments (e.g., Kirkland et al., 1999; Bonde et al., 2008; Ullman et al., 2012; Krumenacker et al., 2017). Thus, these formations were compared due to their similar paleoenvironments and ages (Table 6 of Appendix 1). Although these formations are not as well-known as those from the Cenomanian (e.g., Krumenacker et al., 2017), the majority share the presence of iguanodonts and ankylosaurs. Genus level comparisons of these formations' faunas yielded low values for both the Simpson similarity index and Jaccard coefficient, yet family level comparisons yielded a medium-high (50-70%; 0.5-0.7) Simpson similarity index value between the faunas of the Dakota and Wayan formations (Tables 7-10 of Appendix 1) and lower Simpson similarity index values between the Dakota and the other western faunas. The Simpson similarity index and Jaccard coefficient values found for comparisons of the Dakota with the Blackleaf and Willow Tank formations' faunas were also low (Tables 7-10 of Appendix 1). Family-level comparisons between the Dakota and Paluxy formations yielded a 100% Simpson similarity index and a 0.6 Jaccard similarity index value.

Although the Paluxy is middle Albian in age (112.2-106 Ma) (Jacobs and Winkler, 1998; D'Emic, 2013) and the Dakota, Wayan, Blackleaf and Willow Tank formations were deposited in the late Albian to early Cenomanian (e.g., Liggett, 2005; Varricchio et al., 2007; Bonde et al., 2012; Krumenacker et al., 2017), the scarcity of dinosaur-bearing deposits from this time in North America and the relatively well-documented state of the Paluxy Formation fauna warranted statistical comparison between it and the faunas of the other aforementioned sedimentary units. Genus level similarity for both indices used was 0.0 between the Paluxy and all other formations, whereas family-level comparisons resulted in low Simpson similarity index and Jaccard coefficient values between the Paluxy fauna and those of all other formations save for the Dakota (Tables 7-10 of Appendix 1).

Because of the limited number and diversity of dinosaur taxa from the Paw Paw and Glen Rose Formations, statistical comparisons between these and other formations were not conducted. The Paw Paw formation was deposited during the Late Albian (e.g., Lee, 1996), thus being similar in age to the Dakota, Wayan, Blackleaf, and Willow Tank Formations (e.g., Liggett, 2005; Varricchio et al., 2007; Bonde et al., 2012; Ullman et al., 2012; Krumenacker et al., 2017). Like these other formations, the Paw Paw evinces that nodosaurids continued being widespread across North America during the Albian. The Glen Rose fauna further shows that large theropods, titanosauriforms, and *Tenontosaurus* were included in the Aptian-Albian fauna of North America.

Cenomanian Dinosaur Faunas. The non-avian dinosaur fauna of the deltaic plains (e.g., Main, 2005; Main, 2010; Main, 2013) represented by the Woodbine Formation included large carcharodontosaurs, dromaeosaurs, ornithomimosaurs, indeterminate theropods (including possible tyrannosauroids), hadrosauroids, and nodosaurids (e.g., Main, 2005, 2013). Possible allosauroid and carcharodontosaurid dinosaurs are known from the Mussentuchit Member of the Cedar Mountain Formation (*Siats meekorum*) (Zanno and Makovicky, 2013) and from the Turney Ranch Formation (Thayer and Ratkevich, 1995). Dromaeosaurids are also known from the Mussentuchit Member of the Cedar Mountain Formation (Garrison and

Brinkman, 2007) and from the Blackleaf Formation (Ullman et al., 2012). The nodosaurid *Animantarx caroljonesa* is also known from the Mussentuchit Member of the Cedar Mountain Formation (Carpenter et al., 1999). Adding to similarities between the Woodbine Formation and the Mussentuchit Member of the Cedar Mountain Formation is the presence of the hadrosauroid dinosaur *Eolambia* in the latter unit (Kirkland et al., 1998). This taxon has been found as an outgroup to hadrosauridae behind *Protohadros* or as a sister taxon to *P. byrdi* in phylogenetic analyses (Prieto-Marquez and Norell, 2010; Wenhao and Godefroit, 2012), although another study found it to be a sister taxon of *Probactrosaurus* and *Protohadros* to be a more derived hadrosauroid (McDonald et al., 2012).

The Woodbine Formation was statistically compared to the Mussentuchit Member of the Cedar Mountain Formation of Utah and the Dunvegan Formation of western Canada (Tables 11-15). The Mussentuchit Member of the Cedar Mountain Formation is latest Albian to Cenomanian in age (~104-98 Ma) (e.g., Cifelli et al., 1997; Chure et al., 2010) and represents fluvial to deltaic environments (e.g., Kirkland et al., 1998; Carpenter et al., 1999; Kirkland et al., 1999; Garrison and Brinkman, 2007; McDonald et al., 2012; Ullman et al., 2012; Main, 2013; Zanno and Makovicky, 2013; Krumenacker et al., 2017), whereas the Dunvegan Formation represents a middle Cenomanian-age delta complex (e.g., Burns and Vavrek, 2014). The Lewisville Member of the Woodbine Formation, to which the Arlington Archosaur Site corresponds, is middle Cenomanian in age (~96-95 million years old) and preserves a coastal deltaic environment (e.g., Main, 2005; Main, 2013), making it closely comparable to the Dunvegan Formation and somewhat so to the Mussentuchit. The faunas of these units and the results of statistical analysis of the similarity of those faunas are listed in Tables 11-15 of Appendix 1.

Because the record of dinosaurs from the Raritan facies is so scant, no statistical comparisons were made between it and other Cenomanian units' faunas. It is notable that the Raritan shares with the Mussentuchit, Wayan, and Blackleaf formations tyrannosauroid dinosaurs (e.g., Baird, 1989; Kirkland et al., 1998; Varricchio et al., 2007; Ullman et al., 2012; Zanno and Mackovicky, 2013). The size of the Raritan facies tyrannosauroid is relatively large compared to Cenomanian North American tyrannosauroids (pers. obs.). The dinosaur trackways of the Raritan are additionally important for being the only Late Cretaceous dinosaur tracks known east of the Mississippi (e.g., Baird, 1989).

Coniacian/Santonian Dinosaur Faunas. The Niobrara Chalk is late Coniacian to Santonian in age in the general area surrounding Hackleberry Creek (where *Niobrarasaurus, "Heirosaurus",* indeterminate nodosaurids, and the caudal vertebrae of an indeterminate hadrosaurid have been found) and late Santonian in Logan County (where the holotype of *Claosaurus* was uncovered) (e.g., Carpenter et al., 1995; Weishampel et al., 2004; Everhart and Ewell, 2006; Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). Thus, the Niobrara Formation is comparable in age to the Eutaw Formation, which has been dated to the Santonian (87-83 Ma) (e.g., Weishampel et al., 2004; Ebersole and King, 2011; Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). Additionally, the Eutaw represents marginal marine to marine deposits and was formed during a sea transgression (Liu, 2009), somewhat comparable to the marine setting of the Niobrara Formation (e.g., Carpenter et al., 1995; Liggett, 2005; Ebersole and Ewell, 2006). Both of these formations share hadrosaurids, nodosaurids, and non-hadrosaurid hadrosauroids, whereas only hadrosaurids are observed in the latest Santonian (~84.5-83.5 Ma) Milk River Formation (thus overlapping with the Eutaw Formation entirely) (e.g., Payenberg et al., 2002; Weishampel et al., 2004; Ebersole and King, 2011; Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b). Additionally, the fauna of the Milk River Formation differs from those of the Eutaw and Niobrara, other Coniacian-Santonian, and Campanian Appalachian formations (e.g., Tables 17, 22 of Appendix 1; Carpenter et al., 1995; Ebersole and Ewell, 2006; Gallagher, 1993; Weishampel et al., 2004; Denton et al., 2011; Ebersole and King, 2011; Schwimmer et al., 2015) in containing pachycephalosaurids, centrosaurines, troodontids, and tyrannosaurids. Thus, it seems that major differences in the composition of dinosaur faunas emerged between Laramidia and Appalachia sometime during the "mid"-Cretaceous. Statistically, this hypothesis is supported by the low Simpson similarity index value at the family level (40%) found between the Eutaw and Milk River formations, the low Jaccard coefficient (0.2) value found from comparisons of Coniacian-Santonian Appalachian faunas (Eutaw Niobrara faunas) with that of the Milk River Formation, and the 100% Simpson similarity index value found between the Niobrara and Eutaw faunas at the family level (Tables 17-21 of Appendix 1). Unfortunately, the

poor record of dinosaurs during the Turonian-Santonian of North America (e.g., Carpenter et al., 1995) hinders more precise estimates of when such faunas experienced vicariance. Indeed, all comparisons Coniacian-Santonian formations at the genus level yielded values of 0.0 for both metrics.

Though the Santonian McShan Formation preserves a heavily incomplete dinosaur fauna (e.g., Ebersole and King, 2011) and thus was not compared statistically to other Appalachian and Laramidian faunas, the presence of tyrannosauroids and hadrosauroids in its fauna supports the notion that Appalachian and Laramidian faunas had already differentiated appreciably during the Santonian.

Campanian Dinosaur Faunas. Among the several dinosaur-bearing units of the Campanian of Appalachia, the Mooreville Chalk, Blufftown and Coffee Sand formations and unnamed Missouri clay, the Tar Heel and Coachman formations, and the Marshalltown Formation were used in statistical comparisons with several western Campanian-age strata as well as with each other for the investigation herein of dinosaur provincialism on Appalachia. The Mooreville Chalk, Blufftown, and Coffee Sand formations and the unnamed Missouri clay all latest Santonian to middle Campanian in age (e.g., Ebersole, 2009; Ebersole and King, 2011; Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b), with the marine Mooreville Chalk being approximately 80-83 million years old (e.g., Prieto-Márquez et al., 2016b) and equivalent with the Blufftown and Coffee Sand formations (e.g., Schwimmer et al., 1993; Ebersole and King, 2011), and the apparently terrestrial (representative of an oxbow lake) (Fix and Darrough, 2004) Chronister site also apparently Campanian in age (e.g., Fix and Darrough, 2004; Ebersole, 2009). The fauna of these equivalent formations thus correspond in age to the 81-76 million year old Wahweap (Sampson et al., 2013a) and the Oldman (coeval with the Wahweap; e.g., Roberts et al., 2005; Gates et al., 2010) formations.

The dinosaur-bearing sites of the Tar Heel and Coachman formations, as noted previously, are middle Campanian in age, with the upper portion of the Tar Heel (Tar Heel II sequence) dated to be between 78.7-74.5 million years ago. This range overlaps somewhat with that of the Marshalltown Formation, which may be slightly younger at 75.7-71.2 million years of age (e.g., Miller et al., 2004; Self-Trail et al., 2004; Harris and Self-Trail, 2006; Schwimmer et al., 2015). Thus, the Marshall-

town and Tar Heel-Coachman faunas overlap by at least 1.2 million years, the former overlapping with the main fossiliferous zones of the Dinosaur Park, Kaiparowits, upper Judith River, and lower Kirtland formations in age by approximately 1.5 million years and the latter by at least 2 million years (the main fossiliferous zones of these latter four units being between ~76-74 Ma; e.g., Eberth and Hamblin, 1993; Rogers et al., 1993; Horner et al., 2001; Eberth and Deino, 2005; Roberts et al., 2005; Hanson et al., 2006; Lucas et al., 2006; Gates et al., 2010). The Kaiparowits Formation has been dated to 76.6-74.4 Ma (Sampson et al., 2013a), the Dinosaur Park Formation to 76.9 and 75.8 Ma (e.g., Gates et al., 2010; Gates et al., 2012; Sampson et al., 2013a), the Hunter Wash Member (lower Kirtland Formation) to between 74.5-74.1 Ma (e.g., Gates et al., 2010), and the the Judith River Formation to between 80-75 Ma (e.g., Sullivan and Lucas, 2006). The Dinosaur Park, Judith River, Oldman, and Kirtland formations are apparently coastal plain deposits, whereas the Kaiparowits and Wahweap are apparently representative of alluvial plains (e.g., Roberts et al., 2005; Gates et al., 2010). Thus, even though the Kaiparowits Formation and the formation coeval to it correspond well to the Tar Heel, Coachman, and Marshalltown formations and the Wahweap and Oldman correspond partially to the Mooreville Chalk, Blufftown, Coffee Sand, and unnamed Missouri clay unit temporally, depositional bias may indeed be somewhat detrimental to statistical analysis. Nevertheless, the author notes that at least some eastern sites included in the formations analyzed represent coastal or inland environments (e.g., the marginal-marine Phoebus Landing site of the Tar Heel Formation, the storm-surge deposit of an inland biota at the Ellisdale site of the Marshalltown Formation, or the Chronister site of the unnamed Missouri clay unit) (e.g., Fix and Darrough, 2004; Self-Trail et al., 2004; Denton et al., 2011). Key sites such as the three just mentioned are critical for minimizing depositional bias in statistical analyses of biogeography such as those presented herein. Genus-level comparisons yielded low Jaccard coefficient and Simpson similarity index values for all faunas except for comparisons for calculation of the latter among those of the Oldman, Judith River, and Dinosaur Park formations and between the Marshalltown and Tar Heel and Coachman faunas (50-60% values for the former comparisons; 70% value for the latter) (Tables 23, 25 of Appendix 1). On the family level, high Simpson similarity index values were found from comparisons among Appalachian

faunas (80-90%) and from comparisons among Laramidian faunas (80-100%) (Table 24 of Appendix 1). However, comparisons at the family level between Appalachian and Laramidian faunas yielded only low to moderately high (20-70%) values (Table 24 of Appendix 1). Family-level comparisons between these Campanian faunas for calculation of the Jaccard coefficient yielded a stronger version of this pattern of high similarity between faunas of the same landmass and low similarity between faunas of different landmasses. Comparisons between the Marshalltown, Tar Heel and Coachman, and Mooreville Chalk, Blufftown, and Coffee Sand formations and unnamed Missouri unit faunas yielded Jaccard coefficient values of 0.6-0.7, whereas comparisons between Laramidian faunas at the family level yielded Jaccard coefficient values of 0.53-0.86. Comparisons between western and eastern faunas at the family level, however, yielded Jaccard coefficient values of 0.3 or less. Even though the Oldman, Wahweap, and Mooreville Chalk, Blufftown, and Coffee Sand formations and unnamed Missouri clay unit faunas are approximately 7 million years older or less than those of the Tar Heel and Coachman formations, Marshalltown, lower Kirtland, upper Judith River, Kaiparowits, and Dinosaur Park formations, comparisons between them and these younger faunas generally yielded similar Simpson similarity index and Jaccard coefficient values to those found between formations of the same age (Tables 23-26 of Appendix 1). Indeed, both the aforementioned Appalachian faunas used in statistical comparisons and those of the Merchantville, Woodbury, Donoho Creek, Bladen, and Mt. Laurel/Wenonah formations show that Campanian Appalachian dinosaur faunas differed from Laramidian ones in containing hadrosauroids, basal hadrosaurids, and "indetermediate"-grade (Brusatte et al., 2011) tyrannosauroids as well as lacking ceratopsids, tyrannosaurids, saurolophines, lambeosaurines, pachycephalosaurids, therizinosaurs, troodontids, and ankylosaurids (e.g., Baird and Horner, 1979; Gallagher, 1993; Weishampel and Young, 1996; Gallagher, 1997; Schwimmer, 1997, 2002; Fix and Darrough, 2004; Carr et al., 2005; Brusatte et al., 2011; Denton et al., 2011; Ebersole and King, 2011; Schwimmer et al., 2015; Prieto-Márquez et al., 2016a, 2016b).

Maastrichtian Dinosaur Faunas. The Navesink Formation fauna was the only Maastrichtian Appalachian one statistically compared to western faunas of the time. The Maastrichtian-age portion of the Navesink Formation has been dated to between 69 and 67 Ma (e.g., Miller et al. 2004), whereas the Javelina Formation has been dated to 70 to 66.5 Ma (Woodward and Lehman, 2005) and the Lance and Hell Creek formations to the middle-late Maastrichtian (~69-66 Ma) generally (e.g., Johnson et al., 2002; Weishampel et al., 2004). Genus-level comparisons between the Navesink fauna and those of western formations all yielded a value of 0.0 for the Jaccard coefficient and Simpson similarity index, whereas family-level comparisons yielded medium Simpson similarity index values (40-60%) and low Jaccard coefficient values (0.2) for the same comparisons. Analytically, the faunas of both the Navesink and New Egypt formations show that Appalachia still harbored relict forms that included non-tyrannosaurid tyrannosauroids (e.g., *Dryptosaurus*) (e.g., Brusatte et al., 2011). However, the presence of lambeosaurines in the late Maastrichtian New Egypt Formation (which overlies the Navesink Formation) (e.g., Gallagher, 1993; Miller et al., 2004; Brusatte et al., 2011) and ceratopsids in the late Maastrichtian Owl Creek Formation (Farke and Phillips, 2017) show that several clades of dinosaur found only in the western United States during the Campanian and earlier (e.g., Schwimmer, 1997) had dispersed into the eastern United States.

DISCUSSION

Issues Regarding the Biogeographic Analysis of Cretaceous Appalachian Dinosaurs

Though the fossil record from Cretaceous Appalachian non-avian dinosaurs is important, as demonstrated in this paper, several statistical issues are encountered when trying to measure faunal similarity between Appalachian dinosaur faunas and others by means of the Jaccard coefficient and Simpson similarity index. At the genus level, calculations may not truly account for the diversity of dinosaur genera in Appalachian faunas that would be found with categorial examination. For example, the genus level calculation of an Appalachian fauna containing "Dromaeosauridae indet." and no specific dromaeosaurid taxa for both the Simpson similarity index and Jaccard coefficient would not take into account the presence of a genus or of multiple genera of dromaeosaur. Likewise, the understudied nature of Appalachian dinosaur faunas also may bias calculations on the family level, as certain obscure genera may compose unknown families or subfamilies within a level. One example would be the gigantic hadrosauroids with massively constructed tails of Appa-

lachia (*Hypsibema crassicauda, Parrosaurus missouriensis*). In future years, these animals may turn out to form a distinct family within or outside Hadrosauridae, but are simply referred to herein as hadrosauroids of uncertain phylogenetic placement.

Analytic comparison of Appalachian non-avian dinosaur faunas to the western faunas in Appendix 1 and to other Cretaceous faunas listed in Weishampel et al. (2004) also shows that even the most speciose Appalachian non-avian dinosaur faunas from the Coniacian to Maastrichtian are somewhat lacking in the number of represented dinosaur groups and known species compared to faunas of similar environments and times (i.e., when compared to the Nemegt Formation of early Maastrichtian Mongolia) (e.g., Weishampel et al., 2004; Appendix 1). However, there may be both taphonomic and ecological reasons for this disparity, as discussed above and below.

The Turonian of Appalachia is clearly poorly known. During the Aptian to Cenomanian, however, eastern North American faunas have a relatively similar number and composition of represented groups to western ones, and so the results from the aforementioned interval may be considered as more accurate.

One sampling bias among Appalachian faunas themselves also occurs temporally, as certain stages of the Cretaceous are currently known to be recorded by more units in eastern North America than other stages. This is true especially in the cases of the Coniacian to Campanian stages of the Late Cretaceous, when a variety of relatively species-rich faunas are known from all across the landmass of Appalachia (e.g., Baird and Horner, 1979; Gallagher, 1993; Carpenter et al., 1995; Denton et al., 2011; Ebersole and King, 2011; Schwimmer et al., 2015; Schwimmer, 2016). Contrast such a record with that from the Cenomanian, when the Woodbine Formation gives the only record of dinosaurs from the aforementioned eastern landmass (e.g., Main, 2013). As such, it is important to note that the Cenomanian, Turonian, and Maastrichtian faunas catalogued in this paper are lacking in the number and species-richness of stratigraphic units compared to the Coniacian-Campanian ones. In the case of the Cenomanian dinosaur faunas known from Appalachia, the small number of species may be contributed to the lack of vertebrate fossils known from the Potomac Formation (e.g., Baird, 1989; Gallagher, 1997; Main, 2013) and the lack of dinosaur-bearing Turonian strata in the eastern portion of North America.

Finally, though the Maastrichtian faunas hail from across the eastern United States, only the Navesink Formation has produced more than three clades of dinosaur (e.g., Gallagher, 1993). Future work will hopefully reveal the dinosaur faunas of other Maastrichtian localities pertaining to Appalachia.

Importantly, sampling biases clearly exist between the much better sampled western North American (e.g., Kirkland et al., 1998; Roberts et al., 2005; Jinnah et al., 2009; Gates et al., 2010) and poorly sampled Appalachian ones that are mostly representative of marine deposits (e.g., Schwimmer, 1997). Future work will be needed to reduce this bias. Additionally, the comparatively slow rate at which new dinosaur taxa are named from Appalachia means that Appalachian faunas are only somewhat represented in the known fossil record. However, because the author extensively reviewed the fauna of Appalachian dinosaur faunas statistically compared herein through review of the literature and personal observation, the comparisons herein represent currently the most complete glimpse at Appalachian dinosaur faunas. Specific discussion regarding the presence of dinosaur genera in certain provinces may be found below.

As Late Cretaceous dinosaurs have been excavated from sediments in New Jersey and Delaware since the 19th century and dinosaur specimens have only been collected, identified, and described in detail from southeastern North America rather recently (Langston, 1960; Schwimmer, 1993; Weishampel and Young, 1996; Carr et al., 2005; Ebersole and King, 2011), sampling biases certainly exist among Campanian-Maastrichtian Appalachian dinosaur faunas of these areas and needed to be taken into account for analysis of dinosaur provincialism on the landmass. Though it has been critiqued as a method of comparing species richness (e.g., Alroy, 2000, 2010a, 2010b, 2010c; Alroy et al., 2008), the method of rarefaction (Sanders, 1968) was used to assess the comparability of Appalachian Campanian faunas analyzed herein. The results of rarefaction on the most well-known (in terms of numbers of specimens) Appalachian faunas also allows for insight into the different sampling between each formation's fauna. The Conacian-Santonian faunas that were used in rarefaction were those of the Eutaw Formation and Niobrara Formation. The results of rarefaction of these assemblages yielded an estimated number of clades of five for the Eutaw Formation when rarefied using the total number of specimens from the Niobrara. This result shows

the unequal nature of sampling between the two formations, a discrepancy already present when comparing the number of specimens from each. This is relatively unsurprising, as the dinosaur fauna from the Niobrara Formation consists entirely of animals which were washed out into the Western Interior Seaway (e.g., Carpenter et al., 1995). Nevertheless, it may be assumed that the dinosaurs of the Niobrara correspond to the coastal areas of western Appalachia, as the portion of the landmass west of the Appalachians was essentially flat (e.g., Sampson et al., 2010a; Figure 8.1), and thus the rivers and creeks of the area probably could not generate the force needed to wash the remains of the dinosaurs found in the Niobrara Formation out to sea from far inland. Additionally, previous studies have found *Claosaurus* to be closer to Appalachian hadrosauroids and basal hadrosaurids (i.e., *Lophorhothon, Hadrosaurus, Eotrachodon*) than Laramidian forms of similar age (i.e., *Jeyawati rugoculus*) (Prieto-Márquez et al., 2016a). Finally, the localities where the type specimens of *"Heirosaurus"* and *Niobrarasaurus* were collected are in the middle of Kansas (e.g., Carpenter et al., 1995), which would have been much closer to the western shore of Appalachia than the eastern shore of Laramidia during the Santonian (e.g., figure 6 in Schröder-Adams, 2014). As such, the author follows previous studies (e.g., Prieto-Márquez et al., 2016b) in regarding the Niobrara Formation dinosaur fauna as Appalachian in origin.

The results of rarefaction on the most well-known (in terms of specimens) faunas of the Campanian of Appalachia showed that there was little difference between different assemblages in terms of sampling. The number of specimens from the Marshalltown Formation was the smallest out of the number of specimens from each of the Campanian Formations whose faunas were rarefied (these were the fauna of the Mooreville Chalk, Blufftown, and Coffee Sand formations and unnamed Missouri clay unit, that of the Tar Heel and Coachman formations, and the Marshalltown Formation), and thus it was used as the subsample value (n). The resulting estimated number of clades for the Mooreville Chalk, Blufftown, and Coffee Sand formations and unnamed Missouri clay unit was seven, one less than that of the faunal list from the equivalent units. The rarefaction of the Tar Heel and Coachman formations using this value produced an estimated number of nine clades of dinosaur, the same number represented from the formation in the faunal list. Thus, these three

groups of units may be considered significantly comparable.

The Appalachian Dinosaur Fauna

The landmass of Appalachia harbored a diverse dinosaur fauna from the Aptian to the Maastrichtian stages of the Cretaceous. The data compiled in Tables 1-5 of Appendix 1 suggest that North American faunas of the Aptian were differentiated at the genus level to an extent, but a distinct east-west division was not present. A summary of the stage-by-stage results of the biogeographic analyses performed can be found in Table 1. At the family level, the biogeographic data compiled from Aptian North American dinosaur faunas suggest that even though genera were different across regions, the same clades were present across the continent. This Aptian North American fauna would therefore have included basal ornithomimosaurs, the carcharodontosaurid *Acrocanthosaurus akotensis*, dromaeosaurids (especially the taxon *Deinonychus*), nodosaurids, iguanodontians, basal neoceratopsian dinosaurs, possibly the orodromine dinosaur *Zephyrosaurus*, and titanosauriform sauropods. Albian-Cenomanian North American faunas include nodosaurids, dromaeosaurids, macronarian sauropods, carcharodontosaurids, and basal hadrosauroids. The absence of therizinosaurs and oviraptorosaurs from eastern North America during this time is considered ambiguous, as a large portion of the Arundel facies theropod material remains to be formally studied. During the Albian, orodromine dinosaurs are no longer found in Appalachian dinosaur faunas (Table 6 of Appendix 1), though orodromines and other small ornithopod dinosaurs are known from all three western North American dinosaur faunas from the same time (Table 6 of Appendix 1). Nevertheless, western and eastern faunas still share nodosaurids, iguanodontians, and titanosauriformes (Table 6 of Appendix 1). The lack of faunal data from the Dakota Formation and Paluxy Formation may have caused the calculation of inflated values for their Simpson similarity index and Jaccard coefficient. Among the better-known western faunas, these values are all fairly high (Tables 7-10 of Appendix 1), suggesting relative faunal homogeneity in the western portion of North America.

The Cenomanian Woodbine Formation of Appalachia, when compared to the Mussentuchit Member of the Cedar Mountain Formation, is clearly differentiated at the genus level but more similar at the family level to the latter fauna in both the calculated values for the Simpson similarity

FIGURE 8. Approximate locations of non-avian dinosaur provinces of Appalachia superimposed on the landmass after Gallagher (1993), Carpenter et al. (1995), Schwimmer (1997), Schwimmer et al. (2015), and this paper. Atlantic Coastal Plain province indicated in aquamarine, Carolina Abbreviations: Kg., Kanguk Formation; Mt., Marshalltown Formation; Th.-Cm., Tar Heel-Coachman equivalent formations; Mc.-Bt.-Cs.-Gs, Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen" Sand equivalent formations. Red circle indicates the ?Northern Appalachian province; aquamarine circle indicates the Atlantic Coastal Plain province; green circle indicates Carolinian province; orange circle indicates Gulf Coastal Plain province; purple circle indicates Western Appalachian province. Map courtesy Ron Blakey (https://deeptimemaps.com/).

TABLE 1. Summary of biogeographic results included in appendix.

Stage	Simpson Similarity Index (emphasizes similarity between two faunas) Low (≤30%) Low-medium (31-40%) Medium (41-60%) Medium-high (61-80%) High (≥81%)	Jaccard Coefficient/Distance (emphasizes differences between two faunas) Low (≤0.30) Low-medium (0.31-0.40) Medium (0.41-0.60) Medium-high (0.61-0.80) High (≥0.81)
Aptian	Genus: -medium (Arundel and Ruby Ranch) -low (Arundel and Cloverly) Family: -medium-high (Arundel and Cloverly) -medium (Arundel and Ruby Ranch)	Genus: -low (Arundel and Ruby Ranch, Cloverly) (medium-high distance) Family: -medium (Arundel and Ruby Ranch, Cloverly) (medium, low-medium distance)
Albian	Genus: -low (all eastern-western comparisons except w/ Willow Tank) -N/A (Willow Tank) Family: -high (Dakota and Paluxy) -medium-high (Dakota and Wayan) -low-medium (Paluxy and Wayan, Willow Tank) -low (Dakota and Blackleaf, Willow Tank; Paluxy and Blackleaf)	Genus: -low (all eastern-western comparisons except w/ Willow Tank) (high distance) -N/A (Willow Tank) Family: -medium (Dakota and Paluxy) (low-medium distance) -low (Dakota and Blackleaf, Wayan, Willow Tank; Paluxy and Blackleaf, Wayan, Willow Tank) (medium-high, high distance)
Cenomanian	Genus: -low (all eastern-western comparisons) Family: -high (Woodbine and Mussentuchit) -low (Woodbine and Dunvegan)	Genus: -low (all eastern-western comparisons) Family: -medium (Woodbine and Mussentuchit) -low (Woodbine and Dunvegan)
Turonian	N/A	N/A
Coniacian/ Santonian	Genus: -low (all comparisons) Family: -high (Niobrara and Eutaw) -medium high (Niobrara and Milk River) -low-medium (Eutaw and Milk River)	Genus: -low (all comparisons) (high distance) Family: -low-medium (Niobrara and Eutaw) (medium distance) -low (Niobrara, Eutaw and Milk River) (medium-high distance)
Campanian	Genus: --low (all eastern-western comparisons; Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" and Tar Heel-Coachman) -medium-high (Tar Heel-Coachman and Marshalltown) Family: -high (Mooreville Chalk- Blufftown-Coffee Sand-"Glenallen Clay" and Tar Heel-Coachman) -medium-high (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" and Marshalltown; Tar Heel-Coachman and Marshalltown; Marshalltown and Judith River) -medium (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" and Kirtland, Judith River, Oldman, Dinosaur Park; Tar Heel-Coachman and Judith River; Marshalltown and Kirtland, Oldman, Dinosaur Park)	Genus: -low (all eastern-western comparisons, Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" and Marshalltown) -low-medium (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" and Tar Heel-Coachman; Tar Heel-Coachman and Marshalltown) Family: -medium-high (Mooreville Chalk- Blufftown-Coffee Sand-"Glenallen Clay" and Marshalltown) (low distance) -medium (Mooreville Chalk- Blufftown-Coffee Sand-"Glenallen Clay" and Tar Heel-Coachman; Tar Heel-Coachman and Marshalltown) (low-medium distance) -low (all eastern-western comparisons) (medium-high to high distance)
Maastrichtian	Genus: -low (all eastern-western comparisons) Family: -medium (all eastern-western comparisons)	Genus: -low (all eastern-western comparisons) (high distance) Family: -low (all eastern-western comparisons) (medium-high, high distance)
Multiple Stages	Genus: -high (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" Eutaw) Family: -high (Mooreville Chalk-Blufftown-Coffee Sand "Glenallen Clay" Eutaw)	Genus: -low (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay" Eutaw) Family: -medium-high (Mooreville Chalk-Blufftown-Coffee Sand-"Glenallen Clay"-Eutaw)

index and for the Jaccard coefficient (Tables 11-15 of Appendix 1). Both of these two aforementioned faunas are dissimilar to the more incomplete Chandler and Dunvegan formations from the north of the continent.

During the Turonian, though faunal comparisons could not be made, several significant fossils paint a picture of Appalachian non-avian dinosaur ecology. The *Appalachiosaurus*-like tyrannosauroid material from the Potomac Formation (Baird, 1989) suggests that tyrannosaurs were gaining in size on Appalachia during the time and may also suggest that *Appalachiosaurus* and other Appalachian tyrannosaurs were endemic to the landmass. The possible oviraptorosaur tracks from the Raritan Formation would also be the first record of large oviraptorosaurs, let alone oviraptorosaurs, from the eastern portion of North America. However, the lack of information and surviving tracks from this trackway makes any assignment at this time of the footprints to a specific theropod group dubious until more study of the trackway is done. In the west, several groups which prove to be absent from Appalachia for the rest of the Cretaceous appear, including the ceratopsoids (represented by *Zuniceratops*) and the therizinosaurids (represented by *Nothronychus*) (Table 16 of Appendix 1). Thus, it may be that the Turonian marks the beginning of the major differentiation of eastern and western Appalachian faunas.

By the Coniacian and Santonian, the difference between eastern and western North American faunas becomes clear. Notably, the Appalachian faunas of the time are arguably better known than those from Laramidia. In Appalachia, the non-hadrosaurid hadrosauroids and non-tyrannosaurid tyrannosauroids are still present, whereas in the western Milk River fauna, they are not. A distinctly Appalachian fauna of the combination of hadrosauroids, hadrosaurids, nodosaurids, tyrannosauroids, ornithomimosaurs, and dromaeosaurids appears, notably devoid of two major groups of herbivorous dinosaurs found in the west: the pachycephalosaurids and ceratopsoids. The Simpson similarity index and Jaccard coefficient values between the Appalachian faunas are very high (Table 1), whereas those between the Appalachian faunas and Milk River Formation fauna are low. Importantly, the first occurrences of hadrosaurids on Appalachia, their probable place of origin, are from the Coniacian and Santonian (Prieto-Márquez et al., 2016a, Prieto-Márquez et al., 2016b), suggesting that the group first evolved during this time. The hadrosaurids from the Niobrara Formation

would have coexisted with the relatively small hadrosauroid *Claosaurus agilis* (Table 17 of Appendix 1).

The Campanian non-avian dinosaur faunas of Appalachia show best the distinct non-avian dinosaur fauna which appeared on the continent. Ornithopods of uncertain affinities, hadrosauroids, basal hadrosaurids, nodosaurids, and leptoceratopsians constitute the ornithischian fauna, while at least two or more taxa of derived non-tyrannosaurid tyrannosauroids (*Dryptosaurus aquilunguis*, ?*Dryptosaurus* sp., *Appalachiosaurus montgomeriensis*) and indeterminate tyrannosauroid remains, multiple species of dromaeosaurids (*Saurornitholestes langstoni*, *Saurornitholestes* sp., ?*Dromaeosaurus* sp.) as well as indeterminate specimens, ornithomimosaurs *(“Ornithomimus” antiquus, Ornithomimus* sp., indeterminate specimens), indeterminate maniraptorans, indeterminate coelurosaurs, and indeterminate theropods represent the saurischian fauna. At least three different ecomorphs of hadrosauroid dinosaur existed during this time. These were smaller non-hadrosaurid hadrosauroids (represented in the Campanian by *Lophorhothon atopus* and indeterminate remains), medium-sized (~6-10 m long) hadrosaurids (*Eotrachodon orientalis, Hadrosaurus* sp., a possibly unnamed taxon from the Coachman Formation, indeterminate remains from the Donoho Creek, Bladen, Coon Creek/Ripey, and Demopolis Chalk Formations) and large to supermassive (~10-17 m long) hadrosauroid taxa (*Hadrosaurus foulkii* based on the large Woodbury Formation remains, *Hypsibema crassicauda*, and *Parrosaurus missouriensis*) (Table 30 of Appendix 1). The hypothesis that large hadrosaurid taxa represent adults of *Hadrosaurus* is rejected based on the large size of the holotype of the latter taxon and referred specimens of similar size (comparable to adult specimens of western taxa) (e.g., Gallagher, 1993; Prieto-Márquez et al., 2006; pers. obs.). Though the holotype of *Eotrachodon* is a juvenile of only several years of age (e.g., Prieto-Márquez et al., 2016a; Prieto-Márquez et al., 2016b), Prieto-Márquez et al. (2016b) mentioned that several Appalachian specimens referable to hadrosaurids that are 40%+ larger than the same elements in the *Eotrachodon* holotype could be referable to that taxon. However, based on the estimated 4-5.1 m length for the holotype of *Eotrachodon* (e.g., Prieto-Márquez et al., 2016b), such adult animals would be around 5.6-7.4 m in length, much smaller than the estimated length for taxa like *Hypsibema* and *Parrosaurus* (e.g., Weishampel and Young, 1996;

this paper). It should also be noted that, in the case of hadrosaurs for which individuals of varying sizes are known, very large adult individuals comparable to the size of *Hypsibema* are rare (e.g., for *Edmontosaurus*) (e.g., Horner et al., 2011), whereas the Phoebus Landing site has produced many specimens assignable to *Hypsibema* (e.g., Baird and Horner, 1979). Additionally, the author regards the differences between the vertebrae of *Hypsibema crassicauda* and *Hadrosaurus foulkii* as further evidence these taxa are not synonymous.

The possible lack of nodosaurid dinosaurs within the Upper Tar Heel-Coachman fauna is likely due to taphonomic bias, as their remains have occurred both north and south of the Carolinas during the same interval of the Campanian (e.g., Ebersole and King, 2011; Schwimmer et al., 2015). The Coniacian-Santonian taxon *Claosaurus agilis* and the indeterminate hadrosaurids of the same time from Appalachia may be grouped into the first and second of these ecomorphs, respectively.

The presence of these three distinct ecomorphs of hadrosauroids as well and several nodosaurid taxa from the Campanian of Appalachia may be due to the lack or rareness of three herbivorous dinosaur groups on the eastern landmass present on Laramidia. The ceratopsids, lambeosaurines, and ankylosaurids are almost certainly absent from Appalachia proper until the Maastrichtian (Appendix 1). Both Appalachia and Laramidia share a lack of sauropod dinosaurs from the Cenomanian to Maastrichtian, a phenomenon termed the sauropod hiatus on the latter Landmass (e.g., Lucas and Hunt, 1989; Lehman, 2001; D'Emic et al., 2010; D'Emic et al., 2011; Mannion and Upchurch, 2011; D'Emic et al., 2012). Mallon and Anderson (2013) suggested the presence of a niche partitioning system was present among the herbivorous dinosaurs of the Dinosaur Park Formation and also hypothesized particular niches for each of the large herbivorous clades they examined. Ceratopsids and hadrosaurids were regarded by Mallon and Anderson (2013) as consumers of similar foods, though they also suggested that the hadrosaurs were higher browsers than their ceratopsid contemporaries. Nodosaurids and ankylosaurids were recovered as low browsers, though the former group was suggested to have persisted on tougher food than the latter. The lack of ceratopsids may have also been a factor in the evolution of the Black Creek leptoceratopsian to consume less resistant plant material (Longrich, 2016).

Hadrosaurids were likely the most common herbivorous dinosaurs on Appalachia, and make up more than half of the known dinosaur fauna in southern Appalachia (e.g., Ebersole and King, 2011). Two to five or more taxa of hadrosauroids are present in almost all Appalachian ecosystems sampled from the Coniacian to late Campanian (Tables 23, 31 of Appendix 1), while a maximum of only five taxa is reached in southern Laramidian faunas (with most western hadrosauroid faunas containing on average one lambeosaurine and one to two saurolophines per geological unit) (Table 31 of Appendix 1).

Though ankylosaurs only make up 5% of dinosaur faunas in assemblages from southeastern Appalachia and are the rarest of dinosaurs in the Atlantic Coastal Plain during the Late Cretaceous (Weishampel and Young, 1996; Gallagher, 1997; Ebersole and King, 2011), probably around three taxa (e.g., *Niobrarasaurus coeii*, the unnamed Mooreville taxon, and possibly *Hierosaurus sternbergii*) as well as multiple indeterminate remains of nodosaurid dinosaurs, are known from the Coniacian through Campanian of Gulf Coastal and Atlantic Coastal plains. This number is indeed comparable to the three named taxa of nodosaurids known from Laramidia during the same stages of the Late Cretaceous (e.g., Weishampel et al., 2004; Appendix 1), though notably the Appalachian forms only represent those which existed near the coast of about half of Appalachia. Though Butler and Barrett (2008) found a positive correlation between ankylosaurs and marine environments, Arbour et al. (2016) only found significant evidence for association of nodosaurids with the paleoenvironment they died within for those from the Paw Paw Formation. In the case of other nodosaurid-bearing strata from the Cretaceous, there is little statistical evidence for such associations (Arbour et al., 2016). However, the geography of Appalachia, which as noted was almost entirely flat west of the Appalachians, likely could not have produced waterways with forces great enough to carry dinosaur corpses over long distances. Thus, it may be more likely that, in the case of Appalachian nodosaurids, the carrying of specimens out to sea indicate such animals were living near the shore.

Theropod faunas from southern Appalachia are mostly consistent with those from southern Laramidia. Both contain ornithomimosaurs and usually one to two dromaeosaurid taxa. Notably, though large tyrannosauroids are known from Laramidia and Appalachia, the Appalachian forms are derived non-tyrannosaurid tyrannosauroids while all Laramidian forms are nested within Tyrannosauridae (e.g., Weishampel et al., 2004; Carr et al., 2005;

Brusatte et al., 2011; Loewen et al., 2013; Brusatte and Carr, 2016; Brusatte et al., 2016). The only taxon of dromaeosaurid reported with certainty from Appalachia is *Saurornitholestes*, found to be basal eudromaeosaur outside Dromaeosaurinae in at least one analysis (DePalma et al., 2015). Notably, three clades of dinosaurs present on Laramidia (the troodontids, therizinosaurids and oviraptorosaurs) are absent from Appalachia from the Coniacian through the Maastrichtian, though given the small sample size of Appalachian dinosaurs, it is possible that future work will discover the presence of these groups on the eastern landmass. This is especially possible considering the scarcity of these groups on Laramidia (e.g., Weishampel et al., 2004).

Alongside non-tyrannosaurid tyrannosauroids, the presence of at least one taxon of basal eudromaeosaur (*Saurornitholestes*) in addition to hadrosauroids and nodosaurids with a lack of ceratopsids and lambeosaurines until the Maastrichtian is consistent with Schwimmer (1997) in that non-avian dinosaurs from Appalachia represent relict faunas. At least one group of dinosaurs markedly successful in the Late Cretaceous (the hadrosaurids) seems to have evolved on the continent and remains only in the form of basal taxa. Additionally, one clade of dinosaurs (leptoceratopsians) do not occur on Appalachia until the middle Campanian (Table 31 of Appendix 1), suggesting that they had migrated to the landmass during the middle Late Cretaceous. Therefore, it is probably better to refer to Appalachian non-avian dinosaur faunas as consisting of both relict and endemic clades as well as of those which had migrated to the landmass after it became isolated. Lambeosaurines and ceratopsids likely represent nonnative species which only occurred in Appalachia proper during the Maastrichtian (e.g., Farke and Phillips, 2017). This is supported by the fact that the former clade only occurs on Appalachia during the late Campanian/Maastrichtian, whilst the latter does so during the Maastrichtian (e.g., Gangloff, 2012; Farke and Phillips, 2017). Arbour et al. (2016) additionally speculated that the ankylosaurids, which also are not found on Appalachia, were also isolated from the continent by the Western Interior Seaway.

It is notable that some dinosaur taxa are found across a wide geographic range on Appalachia and in formations of slightly different ages. Of the Coniacian-Campanian Appalachian hadrosauroid taxa *(Claosaurus agilis, Lophorhothon atopus, Hadrosaurus foulkii, Hadrosaurus* sp.*, Hypsibema crassicauda, Parrosaurus missouriensis, Eotrachodon orientalis,* unnamed Kanguk lambeosaurine), four are known from multiple formations comprising multiple different provinces *(Lophorhothon atopus; Hadrosaurus foulkii, Hadrosaurus* sp.*, Hypsibema crassicauda)* (see below) and from multiple different intervals of time (Tables 23, 31, 38 of Appendix 1). This is the same for the tyrannosauroid taxa *Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*, the dromaeosaurid taxon *Saurornitholestes langstoni*, and the ornithomimosaur *"Ornithomimus" antiquus,* and may be due to the geography of Appalachia allowing dinosaurs to migrate across the landscape or alternatively be a signal that taxa reported from many wide-ranging and temporally disparate faunas are actually divisible into multiple species. Notably, reports of the three hadrosauroids listed above that have been reported from faunas other than from whence their holotype was recovered are mostly based on one or a few elements (Baird and Horner, 1979; Grandstaff et al., 1992; Prieto-Márquez et al., 2016b). This suggests that an even wider variety of hadrosauroid species may have existed on Appalachia then stated herein. For example, if the multiple occurrences of these three aforementioned taxa are regarded as distinct species, a total of about 10 or more, rather than seven to eight, hadrosauroid taxa are known from the surviving deposits of the landmass of Appalachia. Accounting for the badly-sampled interior, west, and north of Appalachia as well as the lack of localities corresponding to the landmass from the Coniacian and Santonian, the actual number of distinct hadrosauroid species from the Coniacian-Campanian of the landmass may have been twice or thrice as many as currently known. This may also apply to other ornithischian and theropod dinosaurs, though the latter group seems to have been constrained in diversity in some areas for several reasons ecologically (see below).

Dinosaur Provincialism on Appalachia

Very little work has been done on the possibility of non-avian dinosaur provincialism on Appalachia. Schwimmer (2016) suggested the presence of distinct northern and southern non-avian dinosaur faunas on Appalachia, though did not mention the presence of ornithomimosaurians in the Atlantic Coastal Plain and also included Maastrichtian lambeosaurines within the northern dinosaur province, using the presence of these crested hadrosaurs to help differentiate the different provinces. The results herein, however, nevertheless support

the hypothesis of Schwimmer (2016) that dinosaur provincialism did occur on Appalachia. On Laramidia, the presence of non-avian dinosaur provincialism is notably debated (e.g., Lehman, 1997, Sampson et al., 2010; Sampson et al., 2013a; Lucas et al., 2016).

The rarefaction of Coniacian/Santonian dinosaur faunas of Appalachia, as noted previously, showed the discrepancy between the sample bins of the Eutaw and Niobrara Formations. However, a few conclusions may still be reached about the biogeographic relations of the Eutaw and Niobrara Formations. Firstly, their dinosaur faunas may be distinguished from each other by the different genus of hadrosauroid found in each. *Claosaurus agilis* is only known from the Santonian of the Niobrara (e.g., Carpenter et al., 2011), whereas the Eutaw Formation preserves bones assignable to *Lophorhothon* (e.g., Ebersole and King, 2011). Secondly, both share nodosaurids, hadrosauroids, and hadrosaurids, three key components of the general Appalachian fauna discussed later in this manuscript. The calculated Simpson similarity index and Jaccard coefficient values do show support for the differentiation of these two faunas, as though they have values of 0.0 on the genus level, on the family level the Simpson similarity index has a value of 100% and the Jaccard coefficient has a value of 0.4 (as noted, calculation of the Jaccard coefficient emphasizes differences). Thus, it may be that a distinct dinosaur fauna from that of the southeastern portion of of Appalachia existed in the western portion of the landmass during the Santonian, but further discoveries will be needed to better validate this hypothesis.

Because the rarefaction of Campanian Appalachian dinosaur faunas showed relatively small differences between the represented number of clades from each of the three formations analyzed, the hypothesis of dinosaur provincialism can be more confidently tested for this stage of the Late Cretaceous. The Simpson similarity index and Jaccard index values for comparisons between the three formations analyzed are low and the Jaccard distance values are high between the southern Appalachian Mooreville Chalk, Blufftown, and Coffee Sand formations and the unnamed Missouri deposit and the Marshalltown Formation of the Atlantic Coastal Plain (Tables 32-37 of Appendix 1), whereas the former two indices are moderate to high and the latter is low in value between either of the former two formations and the upper Tar Heel and Coachman Formations (Tables 32-37 of Appendix 1). Thus, the presence of distinct north-

ern and southern Appalachian non-avian dinosaur provinces is supported by the calculated values of Simpson similarity index and Jaccard coefficient. The Atlantic Coastal Plain province is the name suggested herein for the northern fauna, and the Gulf Coastal Plain province is the name suggested herein for the southern.

The Campanian Atlantic Coastal Plain province can be characterized by the presence of one or more species of tyrannosauroid (*Dryptosaurus aquilunguis,* ?*Dryptosaurus* sp.), a scarcity of dromaeosaurids compared to their presence in southern deposits (Tables 31, 46 of Appendix 1; Appendix 1), and the presence of the hadrosaurid *Hadrosaurus foulkii* and remains assignable to *Hadrosaurus* sp. A Campanian southeastern Appalachian province can be defined by the inclusion of only one taxon of tyrannosauroid that is unknown in the Atlantic Coastal Plain (*Appalachiosaurus montgomeriensis*), the presence of the dromaeosaurid *Saurornitholestes* and numerous remains from indeterminate dromaeosaurids (Table 46 of Appendix 1; Ebersole and King, 2011), and the presence of the hadrosaurids *Eotrachodon orientalis, Parrosaurus missouriensis,* and hadrosauroid *Lophorhothon atopus* (Table 31 of Appendix 1).

The upper Tar Heel and Coachman Formations, as indicated by the Simpson similarity index, Jaccard coefficient, and Jaccard distance values as well as analytical observations, thus represents an intersection between these two faunas. It also includes several taxa unique to itself among the three Campanian Appalachian faunas analyzed, including a leptoceratopsian and a second morphotype of dromaeosaurid besides *Saurornitholestes* (i.e., ?*Dromaeosaurus* sp.) (Schwimmer et al., 2015). That these taxa are not present in the other Campanian Appalachian formations (Table 31 of Appendix 1) may simply be a product of their rarity. However, the distinct combination of dinosaurs in the Atlantic *(Dryptosaurus, Hadrosaurus)* and Gulf Coastal Plains *(Lophorhothon, Appalachiosaurus)* found in the Tar Heel and Coachman Formations suggest the Atlantic and Gulf Coastal Plain provinces may have graded into each other on a longitudinal axis, similar to the hypothesis Gates et al. (2010) suggested regarding Laramidian provinces. This mixed fauna is referred to herein as the Carolinian province.

Though several of the formations comprising the Gulf Coastal Plain province are of older age than the Tar Heel, Coachman, and Marshalltown formations (e.g., Schwimmer et al., 1993; Miller et al., 2004; Self Trail et al., 2004; Harris and Self-

Trail, 2006; Ebersole and King, 2011; Schwimmer et al., 2015), it should be noted that Atlantic Coastal Plain dinosaur faunas from early Campanian formations of comparable age to southern formations (i.e., the Merchantville Formation) (Miller et al., 2004) contain elements distinct from southern Appalachian faunas, including *Hadrosaurus*, an indeterminate but distinct taxon of tyrannosauroid, and several specimens of ornithomimosaur (only one specimen of ornithomimosaur is documented from the Campanian of the Gulf Coastal Plain) (e.g., Schwimmer et al., 1993; Ebersole and King, 2011). Among the Gulf Coastal Plain units, the Demopolis Chalk, which is of middle-late Campanian age (e.g., Carr et al., 2005; Ebersole and King, 2011) bears the ~78 million year old holotype specimen of *Appalachiosaurus*, which is apparently not found in the Atlantic Coastal Plain (e.g., Schwimmer, 2016; pers. obs.). Further examination of the specimens of these early Campanian formations (the hadrosauroid/hadrosaurid and non-tyrannosauroid coelurosaurian taxa especially) will be needed to corroborate the results of biogeographic comparisons between the earlier Gulf Coastal Plain and later Atlantic Coastal Plain and Carolinian faunas, though the current weight of evidence does seem to suggest that Appalachian dinosaur provincialism occurred during the Campanian Stage.

Additionally, one other stratigraphic unit may suggest the presence of another dinosaur province. Though the small sample size of the Campanian/Maastrichtian Kanguk Formation warrants only analytical comparison with the faunas, the presence of lambeosaurines in this unit (Gangloff, 2012) may suggest the presence of another non-avian dinosaur province in northern Appalachia. However, the hypothesis of the existence of a northern Appalachian province requires further data from the northern reaches of North America to be thoroughly tested.

Loewen et al. (2013) suggested the presence of dinosaur provincialism on Laramidia was due to transgressions and regressions of the Western Interior Seaway isolating local dinosaur faunas from each other along the Sevier orogeny. Indeed, the dinosaur faunas from the eastern seaboard of North America were proximal to the Appalachian mountains (e.g., Schwimmer, 2002), and so transgressions and regressions of the Atlantic Ocean may have resulted in a similar result, creating the northern and southern dinosaur faunas. The rarefaction of the Mooreville Chalk, Blufftown, and Coffee Sand formations and unnamed Missouri

clay fauna with the subsample of the Eutaw Formation (=45) gives an estimated number of seven clades, showing that a small discrepancy exists between bins. However, these two units, when compared, have Simpson similarity index values of 100% on both the genus and family levels, as well as high Jaccard coefficient values and thus low Jaccard distance values (Table 49 of Appendix 1). Thus, they may be grouped together in the Gulf Coastal Plain province. This grouping provides further evidence that the Niobrara Formation represents another fauna, which is referred to herein as the Western Appalachian fauna (Figure 8.1).

Thus, three to five non-avian dinosaur provinces on Appalachia may be apparent from current data. Four of these (the Atlantic Coastal Plain, Gulf Coastal Plain, Carolinian, and Western Appalachian provinces) are quantifiable based on data from the calculation of Jaccard coefficient and Simpson similarity index values. A possible fifth, from northern Appalachia and represented in the Kanguk Formation, may be differentiated by the presence of lambeosaurines, but further data from northern North America is required to support its existence.

Possible Ecological Constraints on Appalachian Dinosaur Diversity and Commonality

Several patterns in Appalachian dinosaur biogeography may relate to Appalachian ecology. One such case involves the tyrannosauroids of Appalachia. Though several tyrannosaurid tyrannosauroids are present in far southern Laramidia during the Campanian, only the species *Appalachiosaurus mongomeriensis* is present in the Gulf Coastal Plain province of Appalachia during the Campanian (e.g., Tables 23, 31 of Appendix 1). Additionally, most remains of this sole taxon are probably juveniles (e.g., Schwimmer, 2002; Carr, Williamson and Schwimmer, 2005; Schwimmer et al., 2015). Schwimmer (1997), Schwimmer (2002), and Schwimmer et al. (2015) suggested that rather than large theropod dinosaurs, the massive crocodylian *Deinosuchus rugosus* constituted the apex predator of southeastern Appalachian ecosystems. Multiple observations from this study and others both indirectly and directly support this hypothesis, and as such previous work on the abundance of *Deinosuchus* is reviewed herein. Firstly, this large, predatory crocodylian was extremely abundant in the Gulf Coastal Plain (Schwimmer and Williams, 1993; Schwimmer and Williams, 1997; Schwimmer, 1997; Schwimmer, 2002) and reached sizes

of up to 10 meters in length (Schwimmer, 1997). Secondly, possible evidence of predation on medium-sized theropods (~400 kg) (including tyrannosauroids) by *Deinosuchus rugosus* is known from bones recovered from the Ellisdale site in New Jersey and from Georgia (Schwimmer, 2002). *Deinosuchus rugosus* remains are also extremely common in the Gulf Coastal plain (e.g., Schwimmer and Williams, 1993; Schwimmer, 1997; Schwimmer and Williams, 1997; Schwimmer, 2002). However, *Deinosuchus rugosus* remains have been noted as less common in sediments from the Coachman and Tar Heel Formations of the Carolinas (Baird and Horner, 1979; Schwimmer et al., 2015). Finally, only one significant *Deinosuchus rugosus* bearing locality is known from the Atlantic Coastal Plain (Schwimmer, 2002). Notably, only one scute possibly assignable to *Deinosuchus* has been recovered from the Missouri Chronister Site (Darrough, personal commun., 2016), which may be due to the separation of the Chronister site from other Gulf Coastal Plain sites by the Mississippi Water Gap causing a change in fauna. However, the western portion of Appalachia is poorly sampled and so any attempt to estimate western Appalachian *Deinosuchus* populations should be considered tentative. Although, as noted herein, there is a temporal difference of several million years between the most dinosaur-speciose southern Appalachian faunas and those from the Carolinas and Atlantic Coastal Plain, it does seem that across this ~10 million year timescale (e.g., Miller et al., 2004; Harris and Self-Trail, 2006; Ebersole and King, 2011) the abundance of *Deinosuchus* in certain formations and rareness in others noted by Schwimmer (2002) correlates with the number of species and abundance of tyrannosauroids as well as with the abundance of dromaeosaurid material as reviewed and compared in this study. This correlation was also noted by Schwimmer (2002). However, the extensive review of Appalachian dinosaur faunas and specimens (for rarefaction) herein importantly adds additional support to this hypothesis. At least two to three different taxa of tyrannosauroid existed in the Atlantic Coastal Plain (*Dryptosaurus*, the Merchantville taxon, and possibly others represented by fragmentary or isolated specimens) (e.g., Gallagher, 1993; Schwimmer, 2016; Table 22 of Appendix 1; pers. obs.), while the south has only *Appalachiosaurus montgomeriensis* during the Campanian (e.g., Carr et al., 2005; Ebersole and King, 2011; this paper). Sampling and depositional biases as causes of this difference in the diversity

of tyrannosauroids between the Atlantic and Gulf Coastal plains is unlikely, as the Merchantville, Marshalltown, Mooreville Chalk, Blufftown, etc., all represent marginal marine to marine deposits (e.g., Gallagher, 1993; Miller et al., 2004; Carr et al., 2005; Ebersole and King, 2011) and the results of rarefaction indicate minimal differences between examined formations (this paper). This latter statement is especially true when the thousands of dinosaur specimens collected from the Ellisdale site but not yet closely evaluated (e.g., Denton et al., 2011; Denton, personal commun., 2017) and thus excluded here is taken into account. However, further collection and description of Merchantville Formation dinosaur specimens will be needed for the use of that unit in rarefaction and statistical analysis.

This apparent north-south (though note Appalachian coastal plains were rotated relatively southward compared to the condition today) (e.g., Schwimmer, 1997; Schwimmer, 2002) correlation between the abundance of *Deinosuchus* and the diversity and numerousness of large and small theropods supports the hypothesis of Schwimmer (2002) that the large crocodylian may have been outcompeting large, predatory theropod dinosaurs in the Gulf Coastal plain and became rarer towards the middle of Appalachia. However, as the vast majority of Appalachian dinosaur occurrences from the Gulf Coastal Plain, Carolinian, and Atlantic Coastal Plain provinces are from marine sediments, it may be that the preservation of *Deinosuchus* and other crocodylians in these sediments was taphonomically favored. Thus, better evidence for large crocodyliforms being the apex predators of their respective ecosystems in Appalachia comes from the Arlington Archosaur Site of the Woodbine Formation, which preserves a deltaic ecosystem. The presence of a large, generalist crocodyliform within southern Appalachian ecosystems is notably not restricted to Campanian faunas. The large crocodyliform *Deltasuchus motherali* is known from the Cenomanian Woodbine Formation where it was apparently very common (e.g., Main et al., 2012; Noto et al., 2012; Main, 2013; Adams et al., 2017). Evidence of feeding on dinosaurs by this large crocodyliform has been documented (Noto et al., 2012) and the possibility that for ~20 million years (Cenomanian to Campanian) crocodyliforms were the apex predators in at least Texas ecosystems has been discussed (Main et al., 2012). Importantly, theropod remains are rare at the Arlington Archosaur Site, the locality of the discovery of *Deltasuchus mother-*

ali (e.g., Main et al., 2012; Main, 2013; Adams et al., 2017). The commonality of this unnamed crocodyliform in an inland ecosystem combined with direct evidence of feeding on dinosaurs further suggests that crocodyliforms were taking on the role of apex predators in Appalachian ecosystems. However, as with many other hypotheses regarding the ecology of the inhabitants of Appalachia, more specimens will be needed to support the hypothesis of crocodyliforms being apex predators in Appalachia.

The possibility of ecological competition helping to create distinct dinosaur provinces may also be applicable to other Mesozoic and especially Campanian southern Laramidian ecosystems, where *Deinosuchus* were also somewhat abundant and where the most diverse Laramidian crocodylomorph assemblage (comparable to that of the Upper Tar Heel and Coachman formations per Baird and Horner, 1979; Schwimmer et al., 2015) occurred (Schwimmer, 2002; Sampson et al., 2013b).

Comparisons of Appalachian and European Coniacian-Campanian Faunas

Though the data from this paper corresponds to Laramidian and Appalachian dinosaurs, a comparison with those from the Cretaceous of Europe is warranted. Both faunas are similar in sharing leptoceratopsians, derived non-hadrosaurid hadrosauroids, nodosaurids, and dromaeosaurids (e.g., Weishampel, 2004; Dalla Vecchia, 2009; Kirkland et al., 2013). Notably, the European hadrosauroid taxon *Tethyshadros insularis* was recovered by Prieto-Márquez et al. (2016a) as the sister taxon of Hadrosauridae and therefore as one closer node to that clade than the Appalachian taxon *Claosaurus agilis* and as two closer nodes than *Lophorhothon atopus*. This phylogenetic data is suggestive that interchanges between European and Appalachian non-avian dinosaur faunas occurred during the middle Late Cretaceous. This evidence for interchange between Europe and Appalachia supports the hypothesis that the immigration of leptoceratopsians to Appalachia was from Europe rather than from Laramidia (e.g., Lindgren et al., 2007; Longrich, 2016).

Appalachian and European faunas can be distinguished from each other in several ways. First, the dominant clade of large (~5+ meter) predatory theropods on Appalachia was the tyrannosauroidea, while in Europe the ceratosaurian abelisaurids seemingly take this role (e.g., Weishampel et al., 2004; Tortosa et al., 2013). Secondly, ornithom-imosaurs are fairly common and widespread on Appalachia during the Late Cretaceous (e.g., Weishampel et al., 2004; Erickson and Ebersole, 2011; Schwimmer et al., 2015), whereas during the same time only one probable occurrence is known from Europe (Mateus et al., 2009). European nodosaurids seem to form a distinct clade, the Struthiosaurinae (Kirkland et al., 2013), while the majority of Appalachian taxa (*Texasetes pleurohalio*, the unnamed Paw Paw juvenile, *Silvisaurus condrayi*, *Niobrarasaurus coleii*) have consistently not been found as close relatives of any 'struthiosaurines' (e.g., Carpenter, 2001; Vickaryous et al., 2004; Arbour et al., 2016). These major differences affirm that Appalachian faunas were distinct from European ones, and suggest along with the data recounted herein on Laramidian and Appalachian non-avian dinosaurs that Appalachia itself was a distinct non-avian dinosaur faunal zone during the majority of the Late Cretaceous.

CONCLUSIONS

Appalachian non-avian dinosaurs represent a distinct fauna, which included both relict (hadrosauroids, *Saurornitholestes*, comparatively abundant nodosaurids, non-tyrannosaurid tyrannosauroids), endemic (non-saurolophid hadrosaurids), and immigrant (leptoceratopsians) forms. This fauna lasted from the Coniacian to the Late Campanian with its possible origins in the Turonian, and changed by the immigration of nonnative clades from the American west by the Maastrichtian. Jaccard coefficient and Simpson similarity index comparisons when combined with the results of rarefaction suggest the presence of three to five different non-avian dinosaur provinces on Appalachia from the Coniacian to Campanian Stages of the Late Cretaceous. Four are named the Gulf Coastal Plain, Atlantic Coastal Plain, Carolinian, and Western Appalachian faunas herein, while a possible fifth is represented by the Kanguk Formation in Nunavut, Canada. Hadrosauroids occurred in at least three different ecomorphs (small hadrosauroids, medium-sized hadrosaurids and hadrosauroids, and supermassive hadrosaurids), nodosaurids were relatively abundant, and tyrannosauroids constituted as the apex predators towards the middle of Appalachia. In the southern portion of the landmass, *Deltasuchus* and *Deinosuchus rugosus* crocodylians may have outcompeted large theropod dinosaurs as apex predators, though more specimens will be needed to quantify this hypothesis. The Appalachian non-avian dinosaur record and the possibility of ecological inter-

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APPENDIX 1.

Faunal lists, biogeographic index and rarefaction data (presented as PDF file at palaeo-electronica.org/content/2018/2123-appalachia-biogeography).