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1 **The first reported ceratopsid dinosaur from eastern North America (Owl Creek Formation,**
2 **Upper Cretaceous, Mississippi, USA)**

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15 **ABSTRACT**

16 Ceratopsids (“horned dinosaurs”) are known from western North America and Asia, a
17 distribution reflecting an inferred subaerial link between the two landmasses during the Late
18 Cretaceous. However, this clade was previously unknown from eastern North America,
19 presumably due to limited outcrop of the appropriate age and depositional environment as well
20 as the separation of eastern and western North America by the Western Interior Seaway during
21 much of the Late Cretaceous. A dentary tooth from the Owl Creek Formation (late Maastrichtian)
22 of Union County, Mississippi, represents the first reported occurrence of Ceratopsidae from
23 eastern North America. This tooth shows a combination of features typical of Ceratopsidae,
24 including a double root and a prominent, blade-like carina. Based on the age of the fossil, we
25 hypothesize that it is consistent with a dispersal of ceratopsids into eastern North America during
26 the very latest Cretaceous, presumably after the two halves of North America were reunited
27 following the retreat of the Western Interior Seaway.

28

29 **INTRODUCTION**

30 The Western Interior Seaway split North America during much of the Late Cretaceous,
31 which in turn may have driven terrestrial faunal differences between eastern and western North
32 America (Appalachia and Laramidia, respectively). Non-avian dinosaur fossils from the Late
33 Cretaceous of Appalachia are, with a few notable exceptions, largely fragmentary and indicative
34 of a fauna including theropods (ornithomimosaurids and tyrannosauroids), nodosaurids,
35 hadrosauroids, and potentially leptoceratopsids (Schwimmer, 1997; Weishampel et al., 2004;
36 Longrich, 2016; Prieto-Márquez, Erickson & Ebersole, 2016a). The hadrosauroids and
37 tyrannosauroids in particular have been suggested as representing clades distinct from their
38 relatives in western North America (Longrich, 2016). This is further supported by the notable
39 absence of ceratopsid dinosaurs, which are abundant in Laramidia, from the published fossil
40 record of Appalachia. Faunal differences between Laramidia and Appalachia presumably were
41 reduced when the two land masses rejoined following the retreat of the interior seaway during
42 the late Maastrichtian (if they were indeed rejoined; see Slattery et al., 2015 for a discussion of
43 this issue). Yet, late Maastrichtian fossils of terrestrial origin are virtually unknown from eastern
44 North America, so there is little evidence to test this hypothesis.

45 Here, we report the first definitive ceratopsid specimen from eastern North America, a
46 tooth recovered from the Maastrichtian Owl Creek Formation of Union County, Mississippi. The

47 fossil, collected by the second writer (G. E. Phillips) in July 2016, suggests a dispersal of
48 ceratopsids into eastern North America following the regression of the Western Interior Seaway.

49

50 **GEOLOGIC SETTING**

51 **Occurrence**

52 The tooth described here (MMNS VP-7969) was collected in loose association with the
53 Upper Cretaceous marine Owl Creek Formation (and other units) in northeast Mississippi (Fig.
54 1). More precisely, it was found out of context in the active fluvial lag of a modern stream,
55 albeit probably in close proximity to its presumed stratigraphic origins. The pebbly, fossiliferous
56 stream lag contains Pleistocene terrestrial-alluvial, Paleocene marine, and Cretaceous marine
57 fossil float originating from the channel floor and (to a limited extent) the walls. The Paleocene
58 is represented in the area by the Clayton Formation (Fig. 2), the nearest outcrop (preserving the
59 base of the formation) of which is ~4.3 km upstream (and up-section) from the tooth collection
60 point. Fossil float originating from the Clayton Formation has been limited to fragments of the
61 Paleocene index gastropod *Kapalmerella mortoni* (Conrad, 1830). Based on the extent of
62 channel length explored thus far, Quaternary alluvium, slumping, vegetation, and water level
63 conceal the underlying Owl Creek Formation (Upper Cretaceous) rather thoroughly, making
64 direct access to the Owl Creek beds very difficult. Although rarely exposed in the stream, these
65 beds crop out intermittently along the channel length between the base of the Clayton and the
66 tooth recovery point. The tooth was retrieved from the stream float within a few meters of the
67 contact between the Owl Creek Formation and the subjacent Chiwapa Sandstone Member of the
68 Ripley Formation at MMNS locality MS.73.001b (Fig. 1).

69 Both the Cretaceous and Paleocene units cropping out in the channel contain marine
70 vertebrate fossils, although vertebrate fossils are considerably more common in the former than
71 in the latter. Cretaceous deposits in the area have previously produced dinosaur fossils, and the
72 Paleocene occasionally contains reworked Upper Cretaceous fossils. Based on observations of
73 several short-lived, partial exposures in the greater vicinity (e.g., MMNS locality MS.73.030), a
74 persistent phosphatic fossil assemblage occurs in the uppermost part of the Owl Creek
75 Formation. This assemblage consists largely of a shell bed of locally common, dark, well-
76 lithified phosphatic mollusk and decapod steinkerns along with less frequently occurring
77 fragments of marine vertebrates—most of which are characteristically Maastrichtian (Fig. 3,
78 Table 1; Baird, 1986; Phillips, Nyborg & Vega, 2014; Martínez-Díaz et al., 2016). The upper
79 Owl Creek steinkern assemblage is conspicuously populated by baculitid and scaphitid
80 ammonites not seen elsewhere in the local Maastrichtian section. These same ammonites are
81 common in the stream float that yielded the ceratopsian tooth. The Chiwapa Sandstone is very
82 fossiliferous, as is the basal Owl Creek Formation. However, the suite of Cretaceous fossils in
83 the float is generally inconsistent with the assemblage contained in either of these intervals. The
84 Chiwapa contains crystalline calcite pseudomorphs of mollusk shells, none of which are scaphitid
85 or baculitid ammonites. Also, the highly lithified Chiwapa Sandstone does not surrender fossils
86 to the stream bed in one piece—shark teeth, bones, and even shells shatter as soon as they begin
87 weathering from the surface of the rocky exposure. Where the ceratopsian tooth was recovered,
88 the basal Owl Creek is exposed and deeply weathered and contains mollusk steinkerns; however,
89 it also lacks the kinds of ammonites consistent with the stream float. Of all the sourceable
90 constituents of the modern stream lag, the ceratopsian tooth is most consistent with the average
91 size, specific gravity, and color of the phosphatic fossils and pebbles that populate the upper part
92 of the Owl Creek Formation.

93

94 The Owl Creek Formation

95 The Owl Creek Formation crops out in portions of several states within the former
96 Mississippi Embayment—Missouri, Illinois, Tennessee, and Mississippi (Fig. 1). Local thickness
97 of the Owl Creek Formation is about 12 m, and it is rich in Maastrichtian neritic marine fossils
98 (Stephenson, 1955; Sohl, 1960; Sohl & Koch, 1983, 1986). The Owl Creek Formation in
99 northeast Mississippi is composed of glauconitic, variably micaceous, fine-grained beds ranging
100 from sandy clay to clayey sand that become increasingly calcareous to the south where the
101 mostly siliciclastic facies of Tippah and Union counties (including MMNS locality MS.73.001b)
102 grade into the bedded marls and ‘dirty chalk’ of the Prairie Bluff Formation (Stephenson &
103 Monroe, 1940; Sohl, 1960). Thus, terrigenous input in this part of the outcrop belt decreases
104 towards the more pelagic waters of the gulfward shelf. The Owl Creek sediments on the opposite
105 side of the embayment in Missouri and at the head of the embayment in Illinois are texturally
106 and compositionally similar. Likewise, the formation becomes decreasingly calcareous, and then
107 entirely terrigenous, moving northward into the head of the embayment and nearer to the
108 McNairy delta system.

109 In the first grand interpretation of Upper Cretaceous sedimentation in the Mississippi
110 Embayment, the depositional sequence in the embayment proper was revealed to consist of
111 sediments mineralogically derived from the Appalachian Plateaus and Blue Ridge Mountains
112 (Pryor, 1960). In that study, the Owl Creek Formation was described as an inner prodelta facies
113 of the McNairy Delta complex, although deposited on top of, and partially reworked from, the
114 lower Maastrichtian McNairy Formation during the very last Cretaceous marine transgression
115 into the embayment. In a sequence stratigraphic model, the lower contact of the Owl Creek with
116 the McNairy Sand or Chiwapa Member of the Ripley Formation represents a transgressive
117 surface. Subsequent beds in the Owl Creek would thus represent sediments associated with a
118 transgressive systems tract followed by progradational beds of a highstand systems tract
119 (Mancini et al., 1995).

120 A palynomorph assemblage from the Owl Creek Formation across the embayment in
121 Missouri suggests an inner neritic marine environment with high terrestrial input (Eifert, 2010).
122 Angiosperms (Betulaceae, Juglandaceae, Oleaceae, Fagaceae, and Nyssaceae) dominate the
123 assemblage, followed by palm (Areaceae) and cycads (Cycadaceae). A foraminiferal suite from
124 the same samples indicates a hypersaline marsh, and a low-diversity/low-abundance
125 dinoflagellate assemblage is inconsistent with a highstand systems tract (Mancini et al., 1995;
126 Eifert, 2009).

127

128 Taphonomy

129 The discovery of dinosaur remains in marine environments occurs infrequently and
130 typically consists of isolated elements or, more rarely, larger skeletal portions (e.g. partial limb or
131 vertebral associations) shed from a bloat-and-float carcass (Schäfer, 1972; Schwimmer, 1997). In
132 this scenario, the buoyant carcasses of coastal dinosaurs, particularly those originating in riparian
133 habitats of tide-dominated estuaries and deltas, are carried to sea by seasonal or episodic freshets
134 and tides. Dinosaur remains from more distal shelf deposits, particularly the more complete
135 skeletal associations, may result from transport enhanced by maritime storms, such as tropical
136 cyclones. Dinosaur fossils in marine sediments seem to be more commonly encountered, and
137 possess greater taxonomic diversity, as fragmentary yet identifiable bones and teeth from
138 nearshore lag deposits (Schwimmer, 1997).

139 In addition to being the first dinosaur tooth documented from the Owl Creek Formation,
140 the ceratopsian tooth is the first terrestrial macrofossil ever reported from this unit—much-
141 studied previously for its marine macroinvertebrate content. Although characteristically rich in
142 neritic fossils, the aforementioned terrigenous microfossils suggest a not too distant shoreline
143 (Eifert, 2009). Thus, the occurrence in the Owl Creek of a dinosaur fossil, although rare, is not
144 entirely unexpected.

145 Still, the Mississippi tooth is, literally, one of only a handful of North American ceratopsian
146 fossils from a marine context. Compared to other types of dinosaurs, hadrosaur bones and teeth
147 are the most common dinosaur fossils from Campanian and Maastrichtian marine sediments
148 (Schwimmer, 1997). A possible explanation for the scarcity of ceratopsian remains versus that of
149 other dinosaur taxa recovered from marine deposits may lie in habitat preferences. A summary of
150 generalized ceratopsian lithofacies associations suggests an affinity for “lacustrine, alluvial, and
151 coastal plain” habitats, at least among Ceratopsidae (Eberth, 2010). Alluvial wetland ecosystems
152 can be separated into riparian (channel margin) and more distal floodplain habitats—clast size
153 decreasing with increasing distance from the channel. A study of alluvial wetland lithofacies in
154 the upper Maastrichtian Hell Creek Formation documents a greater proportional contribution of
155 *Triceratops* remains (out of seven dinosaur families) to floodplain (muddy) over fluvial
156 (sandy) deposits. The hadrosaur *Edmontosaurus* is found with greater frequency in the latter
157 (Lyson & Longrich, 2011). If rivers are the principal conveyor of bloat-and-float dinosaur
158 carcasses to the marine realm, then a possible preference among coastal plain ceratopsids for
159 habitats outside of riparian zones may explain their paucity in marine sediments.

160 The tooth described here exhibits mechanical abrasion (see Description) ostensibly due to
161 fluvial transport since its exhumation. Thus, a relatively uneroded condition is presumed for
162 the specimen prior to burial. Not knowing the exact stratigraphic origin of the specimen, or
163 whether it fell loose from an as yet undiscovered partial dentary or was buried in isolation,
164 precludes any further speculation as to its postmortem journey and exactly when it entered the
165 Owl Creek depositional system. Nonetheless, based on the locality’s close proximity to the
166 eastern side of the Mississippi Embayment at the time as well as its near-shore sedimentological
167 context (Figs. 1, 5), we consider it most parsimonious that the tooth originated from an animal in
168 that region, rather than a carcass that had floated from the direction of Laramidia.

169 170 **Age**

171 The Owl Creek Formation lies entirely within the upper Maastrichtian (Fig. 2), according
172 to published ammonite stratigraphy (Larina et al., 2016) and non-cephalopod mollusk
173 assemblage zonation (Sohl & Koch, 1986). Planktonic foraminiferan zonation is consistent with
174 the deposits being at least *partly* (or mostly) within the upper Maastrichtian (e.g., Puckett, 2005),
175 although these are likely less reliable than ammonites or dinoflagellates for identifying that
176 lithostratigraphic interval (Larina et al., 2016). Owl Creek dinocyst composition immediately
177 below the K-Pg boundary on the opposite side of the Mississippi Embayment in Missouri
178 supports a latest Maastrichtian age for the uppermost part of the formation (Oboh-Ikuenobe et
179 al., 2012). Finally, at the head of the embayment in southern Illinois, $^{40}\text{K}/^{40}\text{Ar}$ dating of pelletal
180 glauconite in the uppermost Owl Creek Formation yielded an age of 65.7 ± 1.4 Ma (Reed et al.,
181 1977). As indicated above, the exact placement of the tooth within the Owl Creek is uncertain,
182 but associated fossils suggest that it is from considerably closer to the K-Pg boundary (top) than
183 it is to the base of the unit. According to Matt Garb of Brooklyn College (pers. comm., 2016),
184 scaphitid ammonite steinkerns in the fossil float accompanying the ceratopsian tooth are almost

185 entirely dominated by *Discoscaphites iris* (Conrad, 1858; Fig. 3C,E), which equates to the
186 uppermost portion of calcareous nannofossil zone CC 26 of Perch-Nielsen (1985) within the
187 latest Maastrichtian (Fig. 2). Thus, we posit that the ceratopsian tooth described here dates to the
188 late Maastrichtian.

189 Reworking is always a consideration with condensed, phosphatic pebble beds. To date,
190 suspected anachronistic fossils have not been detected at any interval within the Owl Creek
191 Formation. Considering the exceptional condition of the tooth, and that it was collected from
192 modern stream lag below a small waterfall produced by a resistant calcareous sandstone ledge
193 (Ripley Formation, Chiwapa Member), prior to which it had traveled at least several meters
194 across the irregular surface of the exposed sandstone, reworking from a notably older Cretaceous
195 interval prior to entombment in the Owl Creek sediments is highly unlikely.

196

197 **METHODS**

198 In order to illustrate the details of MMNS VP-7969 at high resolution, stacked images
199 were produced with a Visionary Digital Passport system (Dun, Inc., Virginia, USA). The stacking
200 device was interfaced with a Canon EOS 6D camera (Canon, Inc., Tokyo, Japan) with attached
201 50 mm macro lens and a 1.4× Tamron extension, at a magnification setting of 1:2. Images were
202 processed within Helicon Focus 5.3 (Helicon Soft Ltd., Kharkiv, Ukraine).

203 To produce a three-dimensional digital model for archival and illustration purposes,
204 MMNS VP-7969 was digitized using a NextEngine 3D Scanner Ultra 3D with MultiDrive
205 (NextEngine, Inc., Santa Monica, California, USA). The initial scans were acquired and
206 processed in ScanStudio PRO 2.0.2 (ShapeTools LLC and NextEngine, Inc., Santa Monica,
207 California, USA). Data were collected in several passes, with all set for the maximum resolution
208 on the scanner (6,300 points per square millimeter), using macro mode, and assuming a dark
209 target object. The first pass included six scans taken around the long (apico-basal) axis of the
210 tooth. The second pass included three scans bracketing the apical view of the tooth, and the third
211 pass included three scans bracketing the basal view of the tooth. A final scan captured a portion
212 of the tooth in distal view. The scans were aligned using both manual and automatic alignment,
213 and then fused into a single watertight mesh using the “mesh reconstruction” fuse method (high
214 resolution mesh fitting, and relax fitting selected as an option). This mesh was downsampled to
215 reduce file size, creating a final mesh of 83,312 vertices and 166,620 faces. The file was
216 exported in stereolithography (STL) format and is archived at MorphoSource
217 (<http://www.morphosource.org>), under project P275.

218 Measurements were taken from the original specimen using digital calipers, to the nearest
219 0.1 mm. Comparison with measurements taken from the digital model showed the latter to be
220 consistent with the physical specimen to between 0.5–2.5%.

221 All fossils figured and described here are accessioned at the Mississippi Museum of
222 Natural Science (MMNS). The tooth was molded in silicone rubber, and a limited number of
223 plastic resin casts are available to research institutions by placing requests with the MMNS.

224

225 **Institutional abbreviations**

226 AZMNH, Arizona Museum of Natural History, Mesa, Arizona, USA; MMNS,
227 Mississippi Museum of Natural Science, Mississippi Department of Wildlife, Fisheries and
228 Parks, Jackson, Mississippi, USA.

229

230 **SYSTEMATIC PALEONTOLOGY**

231 Dinosauria Owen, 1842
232 Ornithischia Seeley, 1887
233 Ceratopsia Marsh, 1890
234 Ceratopsoidea Hay, 1902
235 Ceratopsidae Marsh, 1888
236 Ceratopsidae indet.
237

238 **Referred material.** MMNS VP-7969, an isolated right dentary tooth, Fig. 4.

239 **Locality and horizon.** MMNS locality MS.73.001b, Union County, Mississippi, United
240 States of America (Fig. 1); Owl Creek Formation (late Maastrichtian). Precise locality data are
241 on file at MMNS and are available to qualified investigators upon request.

242 **Description.** For simplicity, the following description presumes that the tooth is from the
243 right dentary. This is based on the sharply protruding primary ridge, characteristic of dentary
244 teeth in ceratopsids and contrasting with the relatively subdued primary ridge in maxillary teeth.
245 Once oriented as a dentary tooth, the offset of the primary ridge must be in the mesial direction,
246 and the tooth is thus from the right side (Mallon & Anderson, 2014). Terminology follows that
247 illustrated by Tanoue et al. (2009:fig. 2).

248 MMNS VP-7969 preserves both the crown and the root of the tooth (Fig. 4). Portions of
249 the crown were slightly chipped and the extreme ends of the roots were broken off prior to
250 discovery. Due to dark and consistent coloration across the surface of the tooth, it is not possible
251 to describe enamel distribution with any confidence.

252 The crown as preserved is taller (18.9 mm) than wide (15.8 mm) in lingual view (Fig.
253 4C,D). A slight peak at the mesial and distal edges, where the root intersects with the carinae,
254 produces a rhomboid profile. A prominent primary ridge divides the tooth crown into a smaller
255 mesial lobe and a larger distal lobe (Fig. 4G). Towards the base of the crown, the ridge has a
256 slight mesial curvature (Fig. 4C,D). In mesial and distal views, the primary ridge is strongly
257 arched, and a slight inflection marks the point where the ridge and the cingulum/root connect
258 (Fig. 4A,B,E,F). The primary ridge is fin-like and strongly compressed mesio-distally. The
259 lingual edge of the ridge bears very fine and imbricating crenulations. A single, very poorly
260 defined secondary ridge occurs at the mesial edge of the mesial lobe (Fig. 4C); otherwise,
261 secondary ridges are completely absent. No unambiguous denticles appear on the tooth, either. A
262 distinct cingulum separates the crown from the root on the tooth's lingual surface (Fig. 4E,G). As
263 preserved, the maximum apico-basal length of the entire tooth in lingual view is 26.8 mm.

264 In labial view, the crown and root are not distinctly separated (Fig. 4I,J). The labial
265 surface is gently arched from mesio-distally, with at least seven faint plications along the surface
266 of the tooth oriented apico-basally. A flat, approximately quadrangular wear surface marks the
267 apical end of the tooth in this view. A handful of minor scratches mark this area, although the
268 lack of consistent orientation suggests that they are taphonomic in origin rather than representing
269 microwear. Assuming a standard tooth orientation for a ceratopsid, the wear facet was at least
270 subvertical. As preserved, the maximum apico-basal length of the entire tooth in labial view is
271 28.4 and the maximum width is 16.8 mm.

272 The root is bipartite, with the two halves having a maximum span of 22.2 mm. The labial
273 root is more robust and longer than the lingual root (Fig. 4E). A v-shaped resorption groove
274 marks the basal surface of the root (Fig. 4K,L).

275
276 **DISCUSSION**

277 **Referral to Ceratopsidae.** The prominent primary ridge and split root of MMNS VP-
278 7969 definitively distinguish it from teeth belonging to other ornithischian dinosaurs present in
279 North America during the Late Cretaceous, such as hadrosaurs, ankylosaurs, pachycephalosaurs,
280 and basal ornithopods, all of which lack these features. This gross morphology, thus, is most
281 consistent with referral to Ceratopsidae. However, to avoid the hazards of “overidentification,”
282 we here examine the phylogenetic distribution of notable apomorphies in MMNS VP-7969 to
283 arrive at the most conservative identification possible. This is particularly important in light of
284 teeth described for *Turanoceratops*, a non-ceratopsid ceratopsoid from Uzbekistan that also
285 displays some apomorphies historically recognized only in ceratopsids (Sues & Averianov, 2009;
286 Farke et al., 2009). The subject is further complicated by variation across the tooth row in
287 ceratopsids; teeth at the very mesial or distal end differ from those in the middle in the
288 development of some features (Hatcher, Marsh & Lull, 1907).

289 *Split tooth root.* This feature is noted in *Turanoceratops tardabilis* (Nessov, Kaznyshkina
290 & Cherepanov, 1989; Sues & Averianov, 2009) and all ceratopsids for which the relevant tooth
291 anatomy is preserved, but does not occur in other ceratopsians, nor in other ornithischians as a
292 whole.

293 *Absence of secondary ridges on tooth crown.* Secondary ridges paralleling the median
294 carina (primary ridge) are common in teeth of non-ceratopsid neoceratopsians (Tanoue, You &
295 Dodson, 2009), and also occur variably in *Turanoceratops* (Sues & Averianov, 2009) as well as
296 in *Zuniceratops christopheri* (personal observation, A. Farke; AZMNH P2224, AZMNH P3600).
297 Due to their variable occurrence in *T. tardabilis*, the near absence of these ridges in MMNS VP-
298 7969 can only restrict a tooth to Ceratopsoidea.

299 *Projecting, blade-like primary ridge on dentary teeth.* The primary ridge projects strongly
300 from the body of the tooth in MMNS VP-7969 and all ceratopsids, but is far more subdued in
301 dentary teeth of *T. tardabilis* (Sues & Averianov, 2009:fig. 2e,f) and *Z. christopheri* (personal
302 observation, A. Farke; AZMNH P3600). Most notably, in the known *Turanoceratops* specimens
303 (as well as non-ceratopsoid neoceratopsians such as *Protoceratops*), the carina is smoothly
304 continuous with the root in mesial and distal views. By contrast, the carina is arched away from
305 the main body of the tooth in MMNS VP-7969 and many ceratopsid dentary teeth (but not all,
306 particularly from those at the extreme ends of the rows). Our observations suggest that the
307 morphology is only found in Ceratopsidae.

308 In total, the anatomy of MMNS VP-7969 identifies it as a tooth from a ceratopsid
309 dinosaur. At present, a more constrained identification is not possible due to the general
310 similarities in teeth across ceratopsid clades (Mallon & Anderson, 2014). However, only
311 chasmosaurines are known in North America during the late Maastrichtian, so the silhouettes in
312 Fig. 5 are illustrated as such.

313 **Biogeographic and paleogeographic implications.** The tooth described here (MMNS
314 VP-7969) represents the first reported occurrence of Ceratopsidae from eastern North America
315 (Appalachia). Previous reports of ceratopsians from Appalachia have been from non-ceratopsid
316 neoceratopsians, including isolated teeth from the Aptian-aged Arundel Formation of Maryland
317 and a potential leptoceratopsid from the Campanian-aged Tar Heel Formation of North Carolina
318 (Chinnery et al., 1998; Chinnery-Allgeier & Kirkland, 2010; Longrich, 2016). The dispersal
319 route of these earlier ceratopsians into Appalachia is uncertain, and the overall evidence supports
320 a lengthy geographic separation of Appalachia from Laramidia during the Late Cretaceous (late
321 Cenomanian to latest Maastrichtian, ~95–66 Ma, Slattery et al., 2015). Although there is some
322 limited biogeographical evidence for occasional connections between Europe and Appalachia

323 during the Late Cretaceous (summarized in Csiki-Sava et al., 2015), no ceratopsids are known
324 from Europe. So, a European origin for the animal associated with the Mississippi tooth is highly
325 unlikely.

326 We thus hypothesize that the occurrence of a ceratopsid in Mississippi represents a
327 dispersal event from western North America into eastern North America. Significantly, this is the
328 first time that a representative of this previously Laramidian dinosaur clade has been identified
329 from eastern North America. This provides strong biogeographic evidence for a physical
330 connection between eastern and western North America during the late Maastrichtian (Fig. 5).

331 Because many regions of the former Western Interior Seaway do not have the relevant
332 strata preserved or accessible, the seaway's extent during the terminal Maastrichtian has been
333 debated (summarized in Berry, in press; Boyd & Lillegraven, 2011; Slattery et al., 2015 and
334 references therein). For instance, ammonite distribution suggests a marine connection from the
335 Gulf of Mexico northward to South Dakota (but not continuous with marine environments
336 around present-day Greenland) up until the *Hoploscaphites nebrascensis* biozone during part of
337 the late Maastrichtian (Kennedy et al., 1998). In turn, the shared occurrence of the plant
338 "*Cissites*" *panduratus* between Laramidia and Appalachia during the late Maastrichtian supports
339 a subaerial connection between the two land masses during this time, too (Berry, in press). The
340 ceratopsid tooth in Mississippi provides additional evidence consistent with this scenario.

341 **Eastern dinosaurs.** Non-avian dinosaurs from Cretaceous deposits in the eastern U. S.
342 have been well publicized (e.g., Weishampel & Young, 1996; Schwimmer, 1997)(e.g.,
343 Weishampel & Young, 1996; Schwimmer, 1997). Although few discoveries are complete enough
344 for comprehensive description and precise taxonomic assignment, recent notable exceptions
345 include a tyrannosauroid and hadrosaurid from Alabama (Carr, Williamson & Schwimmer, 2005;
346 Prieto-Márquez, Erickson & Ebersole, 2016a,b). Cretaceous dinosaur finds from eastern North
347 America are not rare, but they are infrequent. Since Cretaceous dinosaur remains were first
348 reported on the east coast in the 1850s, numerous specimens representing several groups, both
349 ornithischian and theropod, have been reported from Mississippi to New Jersey. Most of this
350 material consists of isolated and often fragmentary elements, like the ceratopsian tooth reported
351 herein. Collectively, however, the scattered discoveries across the Gulf and Atlantic Coastal Plain
352 reveal an eastern North American Cretaceous dinosaur bestiary that included six major dinosaur
353 clades. To date, these include hadrosauroids (e.g., Langston, Jr., 1960; Prieto-Márquez,
354 Weishampel & Horner, 2006; Prieto-Márquez, Erickson & Ebersole, 2016a), ankylosaurians
355 (Langston, Jr., 1960; Weishampel & Young, 1996; Stanford, Weishampel & DeLeon, 2011),
356 tyrannosauroids (Baird & Horner, 1979; Schwimmer et al., 1993; Carpenter et al., 1997; Carr,
357 Williamson & Schwimmer, 2005), dromaeosaurids (Kiernan & Schwimmer, 2004),
358 ornithomimids (Baird & Horner, 1979; Carpenter, 1982; Schwimmer et al., 1993), and
359 ceratopsians (Chinnery et al., 1998; Longrich, 2016; this paper).

360 Mississippi's published fragmentary dinosaur remains currently encompass only
361 hadrosaurs (e.g., Horner, 1979) and indeterminate theropods (Carpenter, 1982), although one
362 association of over two dozen elements of a single juvenile hadrosaur has been described (Kaye
363 & Russell, 1973). One of the unassigned theropod pedal phalanges (Carpenter, 1982) was later
364 identified as Mississippi's first known ornithomimid (Baird, 1986). In addition to previously
365 described Mississippi material (Carpenter, 1982), MMNS possesses unpublished, largely isolated
366 elements of hadrosaurs (the most commonly encountered), nodosaurs (teeth and fragmentary
367 bones), dromaeosaurids (teeth), and ornithomimids (the second most common dinosaur). Except
368 for the ceratopsian tooth, all MMNS Mississippi dinosaur holdings (most of it unpublished) are

369 derived from upper Santonian through lower Maastrichtian deposits. Dinosaurs have been
370 reported (Ebersole & King, 2011) but are otherwise undescribed from the upper Maastrichtian of
371 the Gulf Coastal Plain. Many more dinosaur discoveries have been encountered and
372 substantiated in the Maastrichtian of the Atlantic Coastal Plain, namely from the Navesink
373 Formation in New Jersey (see reviews by Weishampel & Young, 1996; Gallagher, 1997).

374

375 **CONCLUSIONS**

376 The ceratopsid tooth from the Owl Creek Formation of Mississippi represents the first
377 unequivocal occurrence of this clade in Appalachia (eastern North America). The fossil is
378 consistent with the hypothesis that clades from Laramidia (western North America) dispersed
379 eastward during the retreat of the Western Interior Seaway sometime during the Maastrichtian.
380 We predict that future work will uncover additional evidence of “western” vertebrate clades in
381 Appalachia; in particular, careful placement within a geological context will help to establish the
382 exact timing and tempo of the seaway retreat.

383

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397

398

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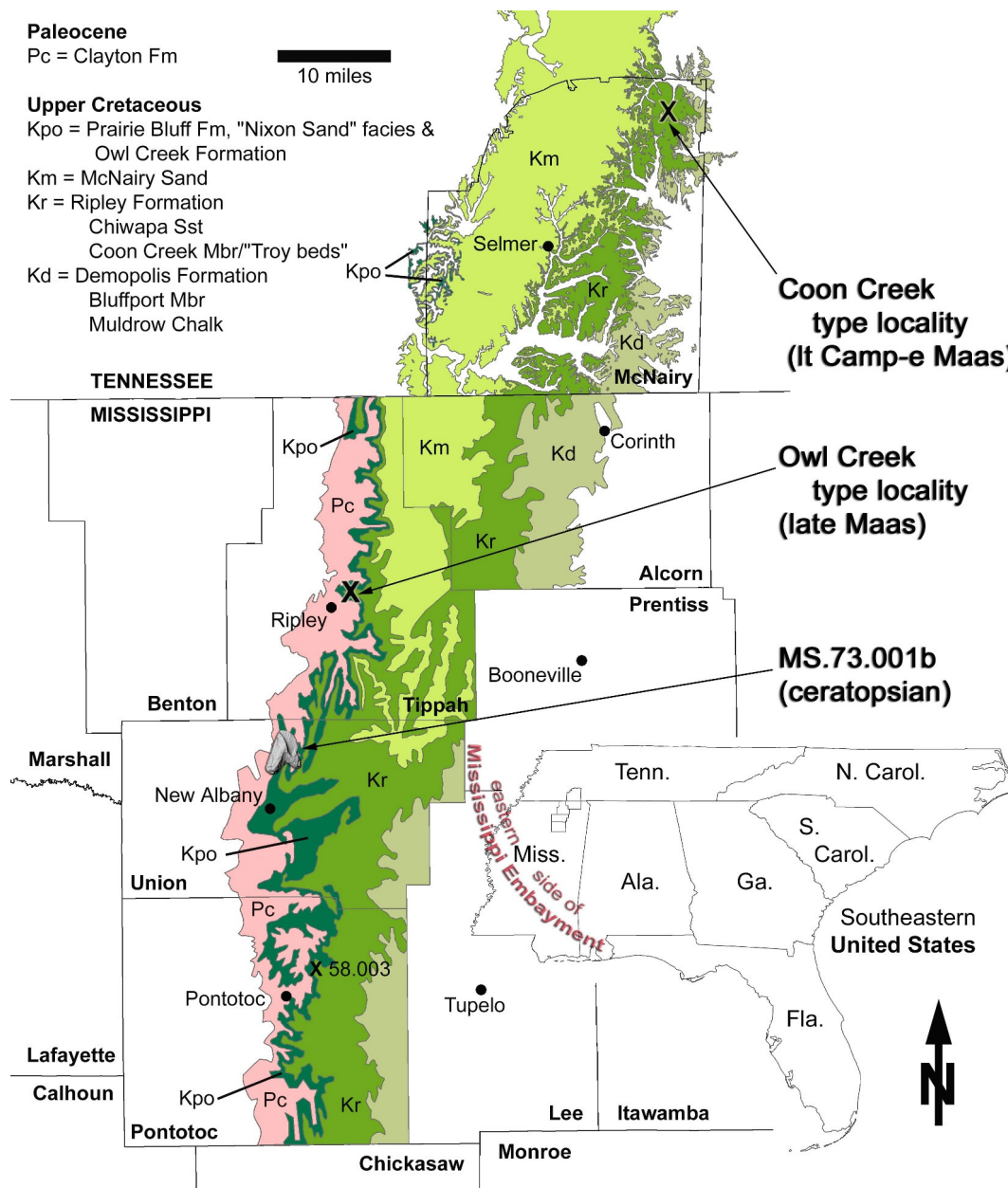
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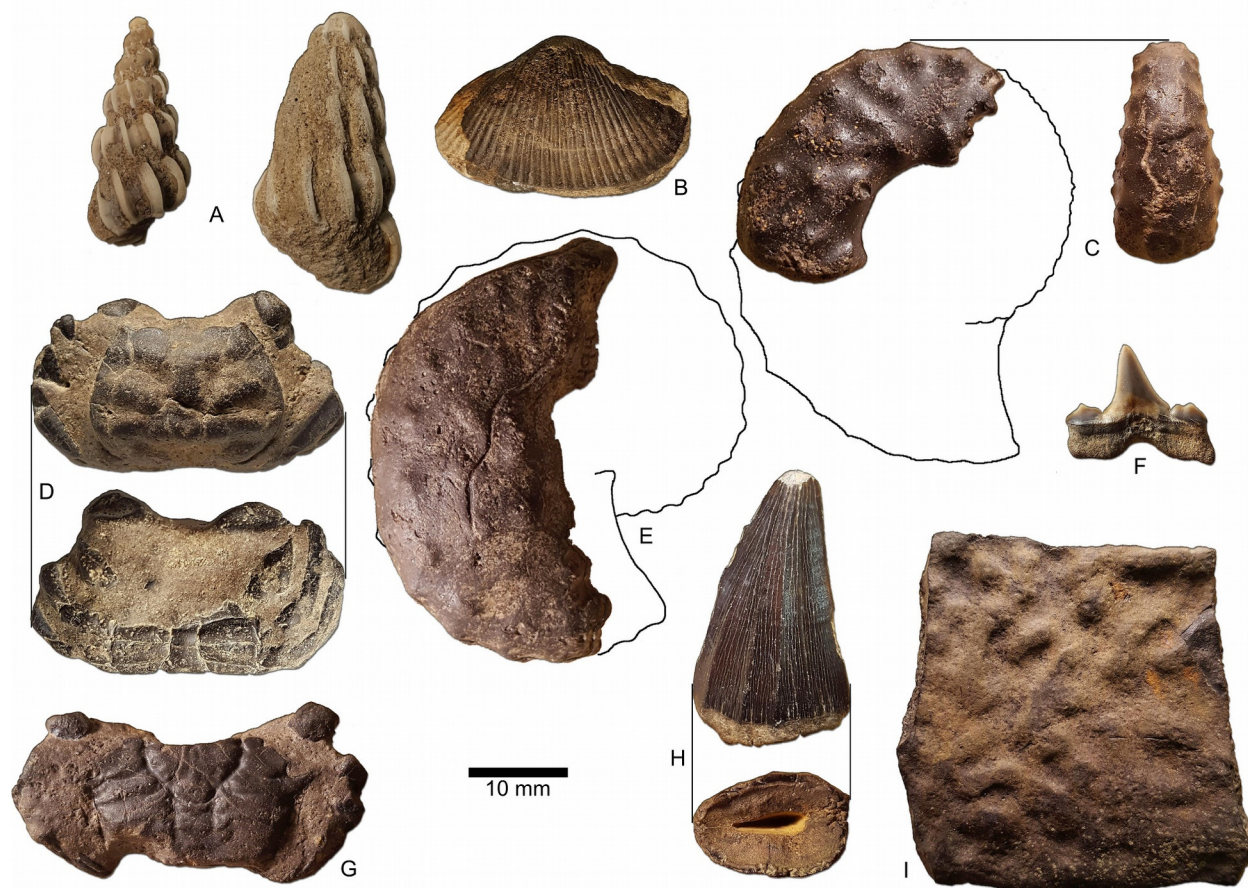
666 **Figure 1.** Geologic map of Maastrichtian deposits in northeast Mississippi. The area of interest
 667 includes the noteworthy type localities of the Coon Creek Formation (latest Campanian–early
 668 Maastrichtian) and Owl Creek Formation (late Maastrichtian). Base map composed by the
 669 Mississippi Office of Geology in 2010, from data in Bicker (1969).
 670
 671



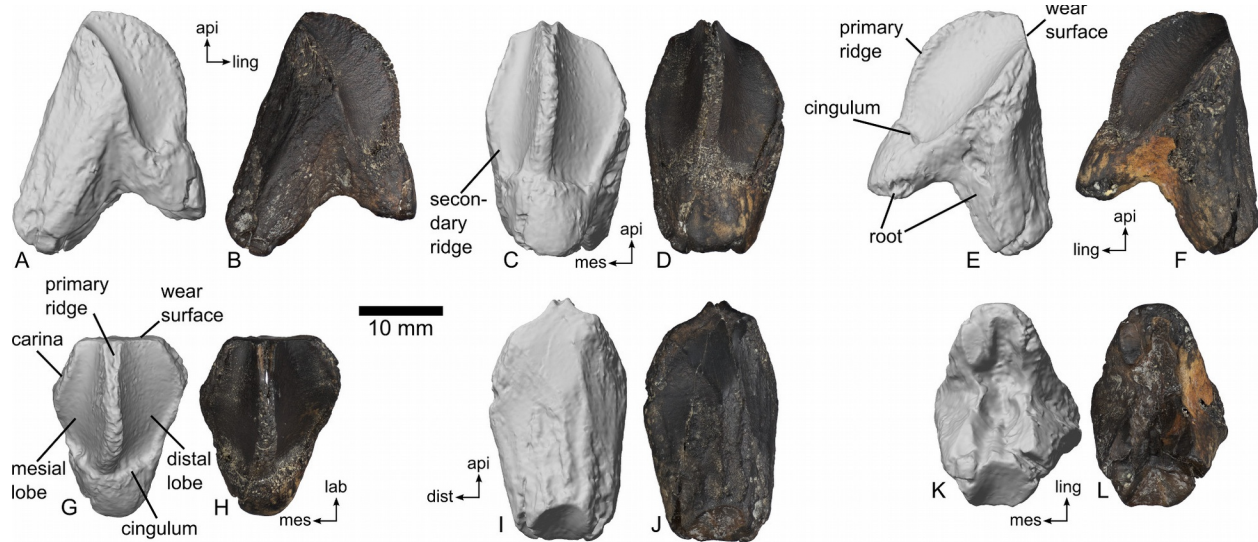
672 **Figure 2.** Stratigraphic chart of Maastrichtian deposits in northeast Mississippi. Basic chart
 673 chronostratigraphy and most of the biostratigraphic columns were produced using TS
 674 (TimeScale) Creator (© 2005-2010, A. Lugowski and J. Ogg). All ages are standardized to the
 675 Geologic Time Scale 2016 and the Concise Geologic Time Scale compilation of the International
 676 Commission on Stratigraphy and its Subcommittee on Stratigraphic Information. The
 677 stratigraphic data used in TS Creator is based on numerous events borrowed from many global
 678 and regional reference sections and integrated time scales. The Gulf Coastal Plain (GCP)
 679 ammonite zones and their correlative ages are based primarily on Cobban (1974), Cobban and
 680 Kennedy (1991a,b, 1995; 1993), Landman et al. (2004), and Larina et al. (2016). The
 681 relationship of GCP to WIS ammonite zones as presented here should be considered provisional.
 682 The position of the stage and substage boundaries is based, in part, on the work of Sohl and Koch
 683 (1986). The informal units “Nixon beds,” “Troy beds,” and “transitional clay” were introduced
 684 by Phillips (2010), Swann and Dew (2008, 2009), and Sohl (1960), respectively. The Coon Creek
 685 and correlative beds are time transgressive, the Campanian-Maastrichtian boundary being
 686 located higher in the section in the northern part of the outcrop belt (Tennessee). A major
 687 unconformity is recognized at the base of the Chiwapa Sandstone, separating it from the
 688 remainder of the subjacent Ripley Formation. Contrary to the age of the sub-Chiwapa Ripley
 689 given here (early Maastrichtian), foraminiferal zonation established for the Gulf Coast by
 690 Mancini et al. (1995) and Puckett (2005) defines the Campanian-Maastrichtian boundary as
 691 coincident with the transgressive surface marking the base of the Chiwapa Sandstone, thus
 692 making the lower Ripley beds Campanian. The dashed vertical arrow represents the uncertainty
 693 of the exact stratigraphic position for the ceratopsid tooth within the Owl Creek Formation.
 694

Age	Euro. Stratotypes		MISSISSIPPI-TENNESSEE		Planktonic Forams	Calcareous Nannos	Gulf Coast Ammonite Zones	North American West. Interior Ammo. Zones
	Stage	Substage	SOUTH Pontotoc Co. Formation	NORTH McNairy Co.				
66	Danian		Clayton Fm		P1 Pa P0	NP2 NP1	Discoscaphites iris Discoscaphites minardi	[Few usable ammonites]
	Maas-trichtian	Late	Owl Creek Fm "Nixon beds"		Abathom-phalus mayaroensis	CC26b		
70		Early	Prairie Bluff Fm "transitional base"	Chiwapa Sst	Racemi-guembelina fructifera	CC25	Discoscaphites conradi	Jeletzkytes nebrascensis Hoploscaphites nicolleti Hopl. birkelundi
	Ripley Fm "Troy beds"		Coon Creek Member	McNairy Sand	Gansserina gansseri	CC24	Nostoceras alternatum	Baculites clinolobatus Bac. grandis Bac. baculus
72	Camp-anian	Late	Demopolis Fm		Globo-truncana aegyptica	CC23	Nostoceras rugosum Nostoceras hyatti	Bac. eliasi Bac. jenseni Bac. reesidei Bac. cuneatus Bac. compressus

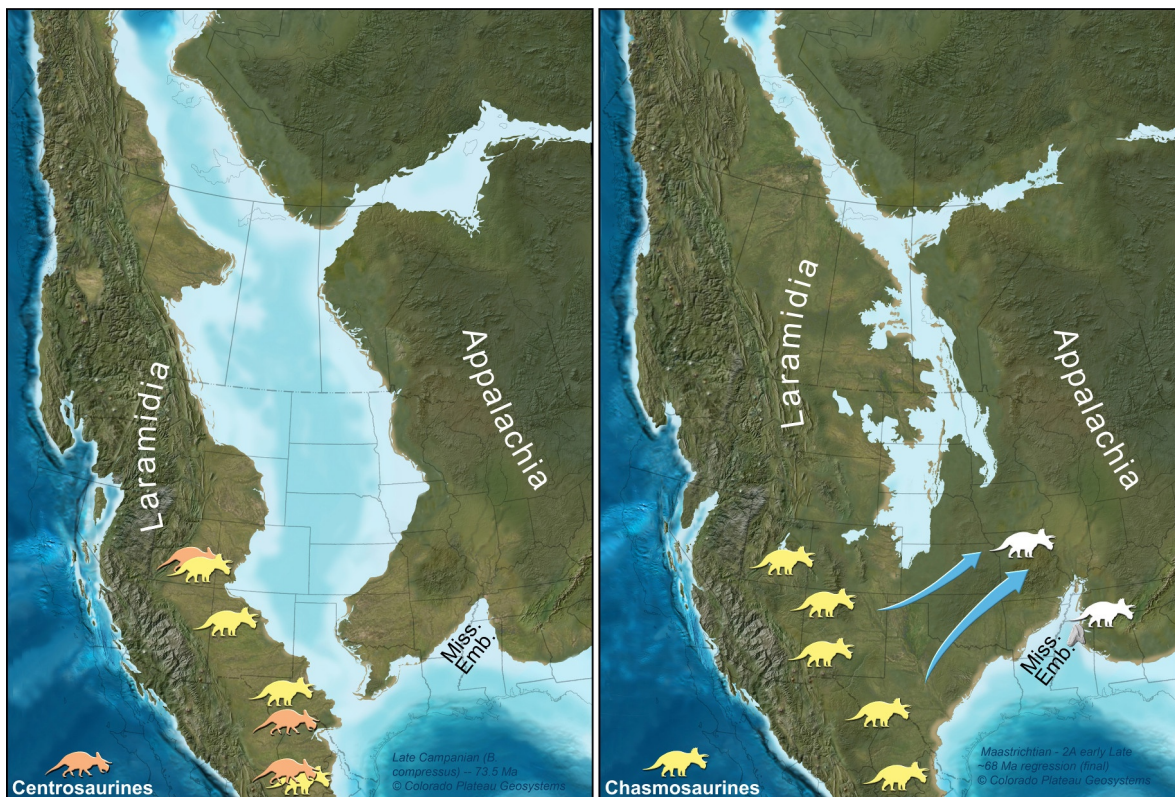
696 **Figure 3.** Marine macrofossils collected in loose association with ceratopsian tooth (from Table
697 1), most consistent with a Maastrichtian age. A) *Striaticostatum* cf. *S. sparsum* Sohl, MMNS IP-
698 8648; B) *Liopistha protexta* (Conrad), MMNS IP-6116; C) *Discoscaphites iris* (Conrad),
699 microconch, MMNS IP-8646; D) *Costacopluma grayi* Feldmann & Portell, larger Maastrichtian
700 variety (Martínez-Díaz et al., 2016), MMNS IP-8647 (distinct from the smaller Danian variety);
701 E) *Discoscaphites iris* (Conrad), macroconch, MMNS IP-494; F) *Cretalamna appendiculata*
702 (Agassiz), variant of a lower posterior tooth, MMNS VP-8041; G) *Branchiocarcinus flectus*
703 (Rathbun), MMNS IP-6115.3; H) *Mosasaurus hoffmani* Mantell, MMNS VP-6803; I) *Peritresius*
704 *ornatus* (Leidy), costal carapace fragment, MMNS VP-4407.
705



707 **Figure 4.** Right dentary tooth of ceratopsid dinosaur, MMNS VP-7969. Digital renderings and
 708 photographs in A, B) mesial (posterior); C, D) lingual (medial); E, F) distal (anterior); G, H)
 709 apical (dorsal); I, J) labial (lateral); K, L) root (ventral) views. Scale bar equals 10 mm.
 710 Directional abbreviations: api, apical; dist, distal; mes, mesial; lab, labial; ling, lingual.
 711



713 **Figure 5.** Paleogeographic maps of two key geochronologic intervals in the uppermost
714 Cretaceous of North America. Late Campanian (left) and late Maastrichtian (right) time slices are
715 depicted with southern Laramidia ceratopsid localities on the appropriate time interval map.
716 Ceratopsid occurrences and their associated ages are taken from numerous references (Lehman,
717 1996; Sullivan, Boere & Lucas, 2005; Loewen et al., 2010; Sampson et al., 2010, 2013; Sullivan
718 & Lucas, 2010; Porras-Múzquiz & Lehman, 2011; Wick & Lehman, 2013; Rivera-Sylva,
719 Hedrick & Dodson, 2016; Lehman, Wick & Barnes, 2016). Arrows designate late Maastrichtian
720 dispersal of ceratopsians, in this interpretation, along an emerging southern route formed by a
721 northerly retreating seaway. We note, however, that the exact placement of any subaerial
722 connection is uncertain (Berry, in press; Boyd & Lillegraven, 2011; Slattery et al., 2015).
723 Although the exact identity of the Mississippi tooth is unknown, we have illustrated only
724 chasmosaurine silhouettes on this part of the figure because no centrosaurines are known from
725 North America during the late Maastrichtian. This Mississippi Embayment is labeled as “Miss.
726 Emb.”. Maps are part of the Key Time Slices of North America series, © 2013 Colorado Plateau
727 Geosystems, Inc., and used with their kind permission by licensed agreement. Silhouettes are by
728 Raven Amos (chasmosaurine) and Lukas Panzarin (centrosaurine, from Sampson et al., 2013),
729 via www.phylopic.org.
730



732 **Table 1.** Partial faunal list produced from Upper Cretaceous marine fossils collected in loose
 733 association with MMNS VP-7969. The mollusks were previously established as characteristic of
 734 the late Maastrichtian Owl Creek Formation at the type locality, Tippah County, as well as
 735 historic outcrops in the vicinity of the ceratopsian locality, Union County (Sohl & Koch, 1983).
 736 Many of the other listed species have also been previously reported as distinguishing
 737 Maastrichtian marine deposits of the eastern United States (e.g., Baird, 1986; Phillips, Nyborg &
 738 Vega, 2014; Martínez-Díaz et al., 2016). Selected specimens are illustrated in Figure 3.
 739 *Mollusks represented by original calcitic shell. Remaining macroinvertebrates are largely
 740 internal molds.

741

742 Mollusca

743 Bivalvia

744 *Cucullaea capax* Conrad, 1858745 *Tenuipteria argentea* (Conrad, 1858)746 *Pinna* cf. *P. laquata* Conrad, 1858747 *Exogyra costata* Say, 1820*748 *Pycnodonte vesicularis* Lamarck, 1806*749 *Pterotrigonia* cf. *P. eufalensis* (Gabb, 1860)750 *Pterotrigonia* sp.751 *Crassatella* sp.752 *Linearia* cf. *L. metastriata* Conrad, 1860753 *Eufistulana ripleyana* (Stephenson, 1941)754 *Liopistha protexta* (Conrad, 1853)

755 Gastropoda

756 *Turritella* sp(p).757 *Striaticostatum* cf. *S. sparsum* Sohl, 1964*

758 Cephalopoda

759 *Discoscaphites iris* (Conrad, 1858)760 *Trachyscaphites* sp.761 *Eubaculites carinatus* (Morton, 1834)

762

763 Crustacea

764 Decapoda

765 *Branchiocarcinus flectus* (Rathbun, 1926)766 *Costacopluma grayi* Feldmann & Portell, 2007767 *Palaeoxanthopsis libertiensis* (Bishop, 1986)

768

769 Vertebrata

770 Chimaeriformes

771 *Ischyodus* sp.

772 Selachii

773 *Cretalamna appendiculata* (Agassiz, 1843)774 *Squalicorax pristodontus* (Agassiz, 1843)

775 Testudines

776 *Peritresius ornatus* (Leidy, 1856)

777 Squamata

778

Mosasaurus hoffmani Mantell, 1829