

LATE CRETACEOUS DINOSAURS IN EASTERN USA: A TAPHONOMIC AND BIOGEOGRAPHIC MODEL OF OCCURRENCES

DAVID R. SCHWIMMER

Department of Chemistry and Geology, Columbus State University,
Columbus, Georgia, USA 31907-5645

ABSTRACT—The eastern Coastal Plains of the USA contain a Late Cretaceous dinosaur assemblage of limited taxic diversity, but with wide distribution and reasonably good abundance. The ages of specimens range from Santonian through late Maastrichtian. All Late Cretaceous eastern dinosaur specimens occur in pericontinental or marine strata, and therefore all such fossils are likely to be allochthonous. New materials and insights bear on the taphonomy of these marine occurrences, suggesting that fluvially-transported, floating carcasses, many scavenged by sharks, make up most of the eastern marine dinosaur record.

There is little evidence of faunal provinciality across the entire eastern outcrop: fossil collections everywhere are dominated by hadrosaurines and immature theropods, mostly tyrannosaurids (cf. *Albertosaurus*) and *Dryptosaurus aquilunguis*. Remains of all other taxa are rare and several are known from single occurrences. Eastern hadrosaurines and tyrannosaurids appear generically similar to western taxa, implying migration by their ancestors during extreme regressions of the Interior seaway. The timing of such migrations is constrained by the presence of characteristically western clades in eastern USA by Santonian time, and by the complete absence of ceratopsians in the East. Migration must have begun or occurred during the Santonian, and must not have been possible after the middle Campanian.

INTRODUCTION

DINOSAUR FOSSILS are found in nearly all Late Cretaceous deposits in the eastern USA featuring reasonably good preservation of fossil bone. These eastern strata with dinosaur fossils are of marine or paralic origin, consisting of silty, phosphatic sandstones along the Atlantic Coastal Plain from New Jersey to South Carolina, chalks and chalky shales in the central Gulf of Mexico Coastal Plain from Tennessee to western Alabama, and sediments with a variety of lithologies transitional between sands and chalks in the eastern Gulf Coastal Plain in eastern Alabama and Georgia. Because they formed in marine paleoenvironments, and because dinosaurs have never been assumed marine inhabitants, all the dinosaurs found in these deposits must have been transported to the sea, if only from the proximal shoreline area.

Approximately twenty localities have yielded the described or identifiable eastern USA dinosaur remains (Figure 1). A primary observation is that a fairly long outcrop is sampled in these occurrences (extending well over 2400 km [1500 mi] from New Jersey to southeastern Missouri), and, yet, the dinosaur fauna shows limited specific diversity with between six and ten known species represented across the outcrop (discussed subsequently). One may be sure, at minimum, that this limited diversity of dinosaurs is not due to a lack of preserved bone in these same deposits, because well over 100 species of fishes, mosasaurs, plesiosaurs, turtles, crocodiles, pterosaurs and others of the Cretaceous bestiary are represented in the same rocks (see, e.g. Applegate, 1970; Baird, 1986; Cappetta and Case, 1975; Manning and Dockery, 1992; Gallagher, et al, 1986; Gallagher, 1993; Lauginiger, 1984; Miller, 1967, 1968; Robb, 1989; Russell, 1970, 1988; Schwimmer, 1986; Zangerl, 1948, 1953). Therefore, either some mechanism must be limiting representation of dinosaur diversity in these deposits, or else dinosaurs must not have been very diverse in the Eastern USA.

An additional, and integral consideration of Late Cretaceous eastern dinosaur paleobiology concerns the nature of their origins: specifically, from where did they all come, and, assuming most had relationships with taxa in western USA, when and how did they migrate across the midcontinental sea? For most of Late Cretaceous time, eastern North America is presumed to have been an Appalachian subcontinent, isolated from western North America by the Western Interior seaway (Kauffman, 1984; Erickson and Slingerland, 1990; Kauffman and Caldwell, 1993).

Certain observations demonstrate that cross-continental dinosaur migration must have occurred, indicating that the Interior seaway barrier must have been imperfect at times. Additional data to be presented also constrain the migrations to the interval of the early Santonian to the middle Campanian.

TAPHONOMY OF EASTERN MARINE DINOSAUR FOSSILS

Prior Views

It has been assumed traditionally that all USA marine dinosaur occurrences contain the admixed remains of both shore-dwelling animals and fluvially-transported carcasses (Morris, 1973; Horner, 1979); in the latter case, coming to the seas from indeterminable inland sources. The shore-dwelling component of a Late Cretaceous marine dinosaur fauna might be analogized with the feral horses of the modern Atlantic coastal barrier islands (descendants from escaped colonial Spanish imports). The assumption of such shore-dwelling dinosaur fauna is reinforced by knowledge that the majority of marine Late Cretaceous dinosaur fossils from all regions in the USA come from hadrosaurine hadrosaurs, which are assumed to have favored deltaic and marine coastal habitats (Fiorello, 1990).

Langston (1960) discussed the preservation of a presumably shore-dwelling young hadrosaurine (the holotype of *Lophorhynchon atopus*) in a marine shelf chalk deposit in western Alabama. Langston proposed that the carcass lay on the beach, desiccating on the upper surface, and decomposing on the bottom against the sediment. Subsequently, it was floated on the tide into the open marine environment, reaching the subtidal shelf, and eventually sinking. Langston (1960) invoked this taphonomic scenario to explain the curious assemblage of preserved bones he found, hypothesizing that many were lost from the decomposed (hence, unbound by integument) bottom of the specimen during the floating stage.

Few marine dinosaur occurrences have been attributed formally to fluvial transport, but dinosaur faunas in western USA are very commonly associated with riverine environments. Some amount of fluvial transport is implicit where any non-marine taxa are reported to occur in estuarine paleoenvironments (e.g. Miller, 1967; Baird and Horner, 1979; Schwimmer, 1986; Gallagher, 1993; Schultze, 1995). Similarly, Horner (1979) suggested that marine dinosaur remains in western USA were likely to be found concentrated in deltaic deposits: in hypothesizing both estuarine and deltaic final paleoenvironments of deposition

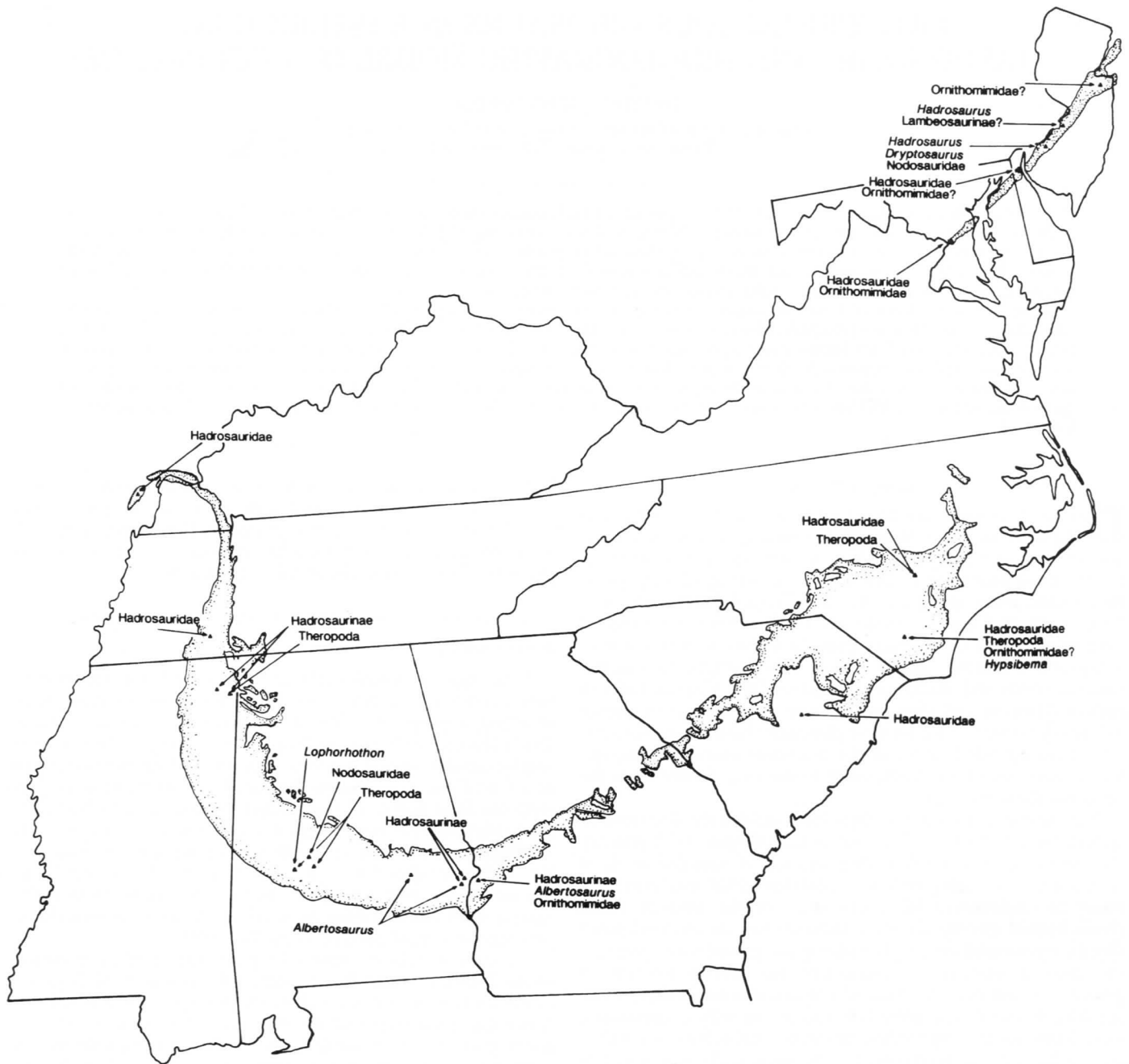


FIGURE 1—Localities of eastern USA Late Cretaceous dinosaur occurrences, with taxa as identified in this paper.

for a fossil assemblage, there is the assumption that riverine fauna were transported to the fluvial-marine interface. As a modern analogy, Weigelt (1927, p. 60–61) quoted Charles Darwin’s graphic description of the fluvial transport of literal herds of dead cattle down South America’s Paraná River, to be deposited in the Río del la Plata estuary.

Revised Model

A synoptic view of all eastern Upper Cretaceous Coastal Plain dinosaur fossils shows that three different modes of occurrence are consistently represented:

Mode 1—Single teeth, bones or bone fragments, usually ablated and water worn, commonly occurring in lag-type accumulations.

The bones are almost exclusively from lower jaws, limbs, and tails, and from within these structures, most are distal caudal vertebrae and terminal limb bones (i.e. phalanges, metapodials). These lag-type accumulations contain bones and teeth of other vertebrates and invertebrate shells, and are by far the most common occurrences of eastern Late Cretaceous dinosaur fossils.

Mode 2—Associated sets of bones representing a single (usually partial) limb or tail. These are often relatively well-preserved and show little or no evidence of marine transportation. Associated bones rarely or never occur in lag accumulations. Specimens in this category I have examined in field context in Southeastern USA usually show evidence of shark scavenging (Schwimmer, et al. 1997), which will be a focal point of dis-

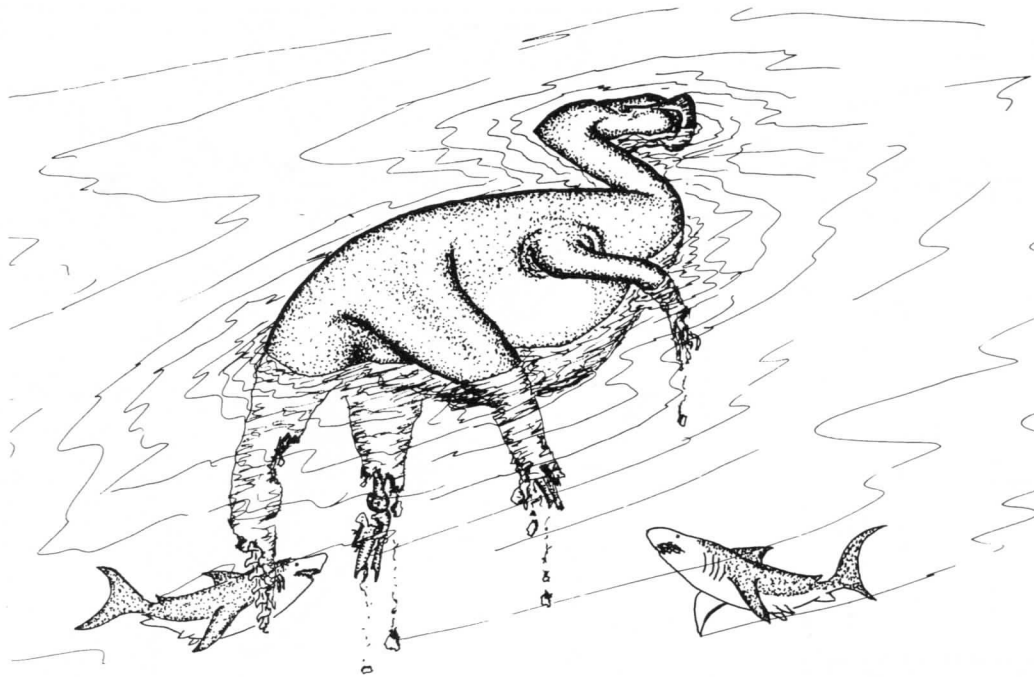


FIGURE 2—Illustration of the bloat-and-float-with-scavenging-model, explaining preferential deposition of distal dinosaur bones while limiting occurrences of skull, trunk, and many proximal limb bones. The sharks represent reconstructions of *Squalicorax kaupi*. Drawing by William J. Frazier, Columbus State University.

cussion to follow. Several such specimens are also observed encrusted with bivalve (usually oyster) spat, implying they lay on the marine bottom for some time before burial.

Mode 3—Remains of dinosaurs with areas of most body regions present, although usually missing many bones. This mode of preservation is the only situation where skull material may likely be found. Three eastern holotype specimens (*Lophorhothon atopus* and *Hadrosaurus foulkii*, both hadrosaurines, and *Dryptosaurus aquilunguis*, a large theropod) are good examples of this preservation mode. Scavenging signs have not been reported in any such case; but, then, neither have they apparently been searched for when the dinosaur remains were recovered. It is especially significant that among the many dinosaur remains reported and otherwise known from the Late Cretaceous of eastern USA, only three, incomplete, skulls are known: the *Lophorhothon atopus* holotype, a juvenile hadrosaur from western Alabama; a young tyrannosaurid, possibly an *Albertosaurus*, from central Alabama (which has not yet been prepared or published, but see Baird, 1989 for discussion); and the holotype of *Dryptosaurus aquilunguis*, from New Jersey. In all three cases, bones from the trunk and limbs were also preserved, indicating that these were typical of this third preservational mode.

Although these three forms of dinosaur preservation might appear to represent substantially different taphonomic events, on examination, all may result from the basic process of fluvial transport of floating dinosaur carcasses, with the additional important contribution of marine shark scavenging. The “bloat-and-float-with-scavenging” model proposed here initiates with carcasses of riverine dinosaurs floating downstream with significant decay-gas bloating of the abdomen (with or without some degree of desiccation before becoming buoyant and water-borne, as described in Langston, 1960). Such bloated carcasses could float downstream to river-mouth estuaries, and, occasionally, into offshore marine settings, bypassing high-energy surf zones.

These would become the basis of the eastern Late Cretaceous dinosaur fossils. Dead dinosaurs not experiencing these post-mortem events would simply not be preserved.

Essential to this hypothetical model is the buoyancy of carcasses in the marine realm for times sufficient for scavengers to reach and sever body parts hanging down into the water column (Figure 2). The dinosaur’s skin, tendons and zygapophyses likely kept pelvis, dorsal vertebrae, ribs, gastralia, neck and the skull in association with the inflated abdomen and largely above or at the water surface. The events during and following marine floating episodes determined the nature of the fossilized remains.

The commonplace eastern marine dinosaur remains, isolated distal limb and tail bones, represent the parts simply dropped from the extremities of the floating carcasses during scavenging, or by initial marine decay events (Figure 2). During marine transgressions, very low rates of terrigenous-sediment deposition (i.e. sediment starvation) on the marine shelf resulted in concentration of these bones at the sediment-water interface, where they were eroded, current-tumbled, and admixed with mollusk shells, and bones and teeth of many other Late Cretaceous vertebrates. This set of events created the common, lag-type bone beds of the Atlantic and eastern Gulf Coastal Plain.

The associated, single-organ remains of dinosaurs are whole or partial legs, forelimbs and tails, which were severed by sharks or dropped by advanced decay from the floating carcass. Since such structures (while intact) are relatively large, they remained physically stable on the marine shelf bottom by size alone, for sufficient time to be fossilized in place. Such preservations are much less common than the isolated bone occurrences, but a good example is the hadrosaur lower leg figured in Schwimmer, et al. 1993 (which also had numerous shark teeth in direct association, as discussed below).

The whole-body preservations of eastern dinosaurs are readily explained by this general model. These resulted when floating carcasses finally sank to the marine shelf bottom, after the ab-

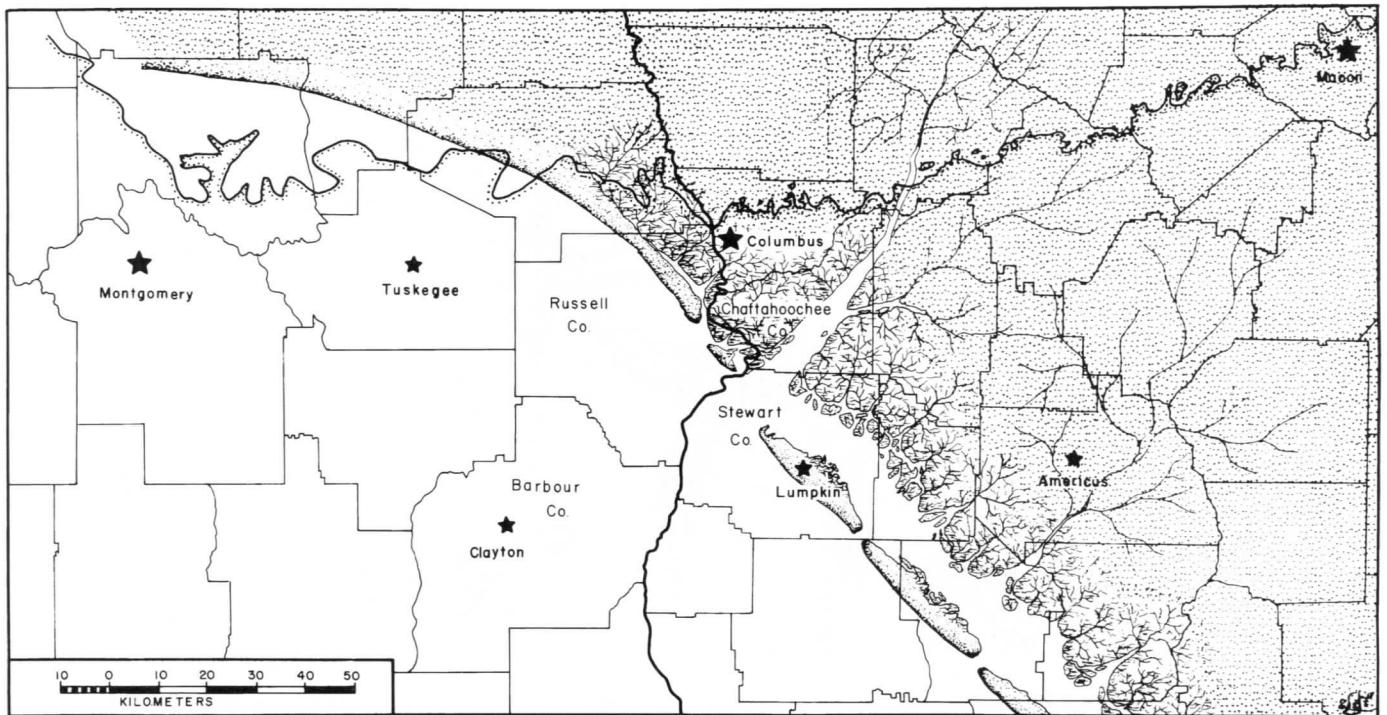


FIGURE 3—Reconstruction of the middle Campanian coastal paleogeography of Western Georgia and eastern Alabama, in the vicinity of the dinosaur localities discussed in Schwimmer, et al., 1993. The primary regional dinosaur locality, Hannahatchee Creek, is in the estuarine region astride the state border. Drawing and sedimentological data for the reconstruction provided by William J. Frazier.

domen was breached by scavenging or decay. As in the previous case, the associated body, with much skin still in place, would be much less likely transported by marine currents than would be isolated bones, and thus would be preserved as an associated fossil skeleton in a marine shelf deposit. However, during the entire taphonomic process, it is inevitable that many bones and often sizeable body portions would be lost to scavengers, decay and marine currents. This is the precise impression received from even the most complete eastern Cretaceous specimens.

Evidence For The “Bloat-and-Float-With-Scavenging” Model

Three independent lines of evidence were used to develop the taphonomic model:

Bias toward preservation of distal body parts—The body regions most commonly represented among all eastern marine dinosaur fossils are those most likely to hang below the trunk of a floating carcass, and thus, be most vulnerable to scavenging by sharks. These pendant body parts would also be the first dropped from a carcass by decay dissociation. It is assumed for the model here that bones from limbs and tails would be deposited on the sea bottom, following soft-tissue scavenging by sharks.

The rarity of eastern late Cretaceous dinosaur skull, neck, and trunk bones cannot be happenstance, because the same strata contain common skull bones, dorsal and cervical vertebrae, pelvises, and ribs, of crocodiles, mosasaurs, turtles and marine fishes. These marine vertebrates were not necessarily transported and fossilized from bloated carcasses as were the dinosaurs, and therefore the taphonomic events assumed for the latter would not apply. The lack of preservation of dinosaur skulls and necks from floating carcasses is explained by observations on both Recent and fossil tetrapod preservations. Typically, a dead tetrapod's neck arches sharply dorsally and caudally due to shrinkage of dorsal muscles and ligaments (Weigelt, 1927). In a float-

ing dinosaur carcass, such flexure would likely pull the skull and neck on or above the water surface, shielding them from marine scavenging (Figure 2). Weigelt (1927) also observed that lower jaws easily dissociate from skulls during decay and, indeed, we do find many hadrosaur dentaries as fossils in the eastern Cretaceous among the lag-type bone beds.

Dinosaur localities in estuarine environments—The most consistently productive eastern Cretaceous dinosaur localities (but never those yielding near-complete specimens or skulls) are assumed to represent estuarine paleoenvironments. These localities include the Ellisdale site in New Jersey (Parris, et al., 1987; Denton and Gallagher, 1989; Gallagher, 1993), Phoebus Landing and adjacent sites along the Cape Fear River in North Carolina (Miller, 1967; Baird and Horner, 1979), and the Hannahatchee Creek locality (Figure 3) in Western Georgia (Schwimmer, 1986; Schwimmer and Best, 1989; Schwimmer, et al., 1993). It is significant that these localities are assumed to represent ancient estuaries because of multiple evidences (e.g. sedimentary structures and textures, presence of sizeable non-marine vertebrate fauna, fossil wood, and admixed marine and brackish-water vertebrate and invertebrate species). The assumption of dinosaur abundances in estuarine deposits is therefore not logically circular (i.e. based solely on dinosaur occurrences), and the proximity of these dinosaur localities to Cretaceous river mouths is too frequent to be coincidental.

Shark scavenging evidence—There is abundant evidence of scavenging by sharks on dinosaurs and a variety of other Late Cretaceous marine vertebrates. The common Cretaceous neoselachian genus *Squalicorax* includes at least two Late Cretaceous species (*S. falcatus* and *S. kaupi*) whose serrate teeth are found frequently in association with the remains of larger vertebrate fossils (see citations and tables in Schwimmer, et al., 1997).

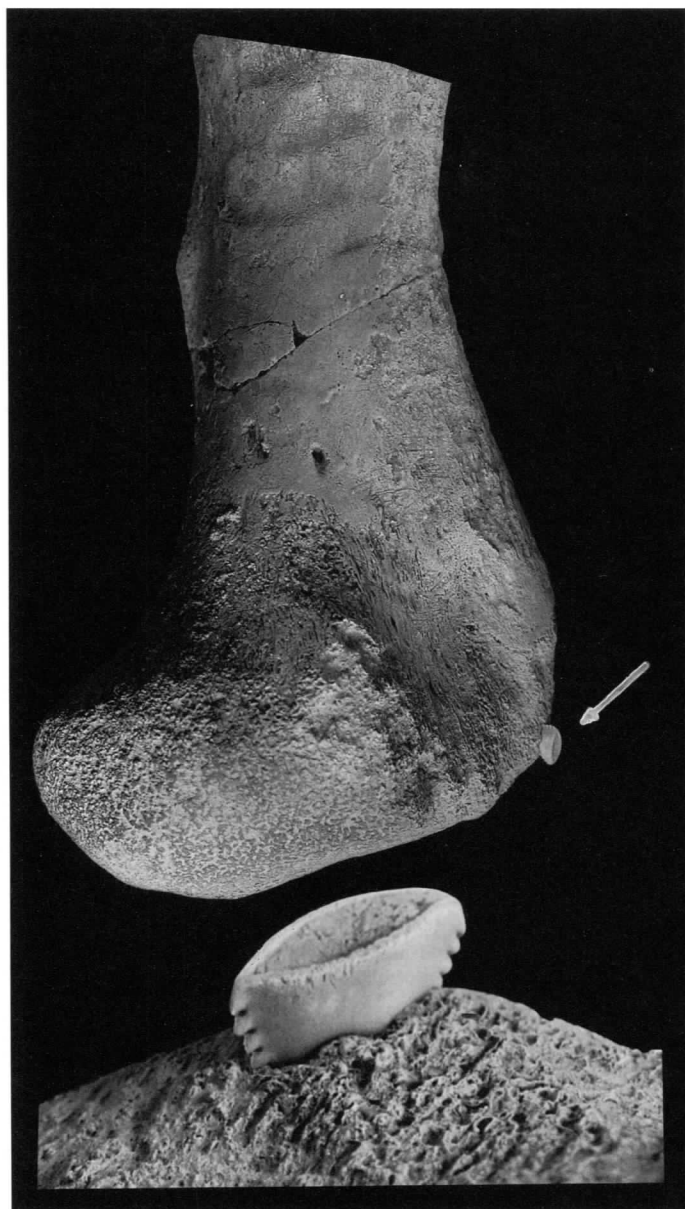


FIGURE 4—Two views of a right metatarsal II from a young hadrosaur, gen. et sp. indet., Alabama Museum of Paleontology (ALAMP) V993.1.2.2. Above: overall view ($\times 1.0$) with arrow indicating position of an embedded tooth tip from the shark *Squalicorax kaupi*. Below: closeup of the shark tooth (inverted for clarity), $\times 6.0$. Note that the tooth is implanted in the distal end of the metatarsal. This specimen came from essentially the same locality and stratum as the holotype of *Lophorhothon atopus* Langston, 1960. It is noteworthy that the bone shows no evidence of ablation, other than the embedded shark tooth and some minor bite marks (not evident in the photographs).

Since *Squalicorax* species were the only Late Cretaceous sharks with serrate teeth, these associations are easily recognized: serrate bite marks and statistically significant associations of *Squalicorax* teeth with marine vertebrate remains occur commonly in Coastal Plain deposits. Figure 4 explicitly demonstrates shark-dinosaur relationship. These same shark-dinosaur associations also occur well outside eastern USA: a nodosaur femur from the Moreno Formation in California, a Campanian marine deposit contemporary with much of the eastern material in discussion,

TABLE 1—Dinosaur taxa recognized as distinct entities in the eastern USA Late Cretaceous. Recognition of taxic distinction here does not signify that current nomenclature is valid, or that relationships with dinosaurs outside eastern USA are properly construed. Taxa correctly synonymized in prior literature are not tabulated. Authorships of all listed taxa are cited in Horner, 1979, Schwimmer, et al. 1993, or Gallagher, 1995.

ACCEPTED, DISTINCT TAXA

- Ornithischia*
 Hadrosauridae
Hadrosaurus (= *Gryposaurus*? = *Kritosaurus*?) *foulkii*
Lophorhothon atopus
 Nodosauridae, gen. and sp. indet.
- Saurischia*
 Tyrannosauridae
 cf. *Albertosaurus* sp.
 Theropoda, family indet.
Dryptosaurus aquilunguis (= *Ornithomimus antiquus*?)
 Ornithomimidae indet. (non *O. antiquus*)

DUBIOUS, OR POORLY-CONSTRAINED TAXA

- Ornithischia*
 Lambeosauridae indet.
 Ornithopoda, family indet.
Hypsibema crassicaudata (non *Parrosaurus missouriensis*)
 Ankylosauridae indet.
- Saurischia*
 Ornithomimidae
Ornithomimus antiquus (? = *Dryptosaurus aquilunguis*, fide Gallagher, 1995)
-

was associated with several *Squalicorax kaupi* teeth (B. Riney, 1993, written communication).

TAXONOMIC DIVERSITY AND ORIGINS OF EASTERN
 LATE CRETACEOUS DINOSAURS

Apparent Low Taxonomic Diversity: Why?

Examination of the eastern Late Cretaceous dinosaur assemblage from a systematically-conservative perspective, shows six clearly discrete taxa among the many names, and four additional named taxa that may prove valid when better material or new study supports their distinction (Table 1). It is not the purpose of this paper to reassess taxonomy of the eastern assemblage (see Horner, 1979; Weishampel and Horner, 1990; Schwimmer, et al., 1993); but, it is significant that even if all ten, plausible eastern Late Cretaceous taxa in Table 1 are valid, this is a dinosaur assemblage of relatively low diversity for the area sampled. [See Russell, 1995, for an opposite opinion on Eastern dinosaur diversity]. Further, among the known occurrences, hadrosaurines and immature theropods, attributable to either *Albertosaurus* or *Dryptosaurus*, make up all but a small percentage of the fossils. It has been assumed generally that this low faunal diversity is an artifact of the limitations imposed on preservation of non-marine animals along a pericontinental, rather than epicontinental, marine setting. However, the fluvial-transport model described in this paper as the basic source for eastern dinosaur fossils implies that a river-based, thus inland, assemblage is sampled, and, therefore, the eastern marine dinosaur record should preserve a fair representation of the whole dinosaur assemblage of at least the eastern half of the Appalachian subcontinent. Given these assumptions, the eastern Cretaceous dinosaur assemblage contrasts with much more diverse contemporary dinosaurs along the western side of the Western Interior seaway. Hypotheses for low diversity of the eastern dinosaur assemblage follow.

Climatic and physiographic homogeneity—During Late Cretaceous time, North America would appear rotated relatively clockwise with respect to its present position (Andrews, 1985; Scotese, et al., 1988), orienting the northern Atlantic Coastal

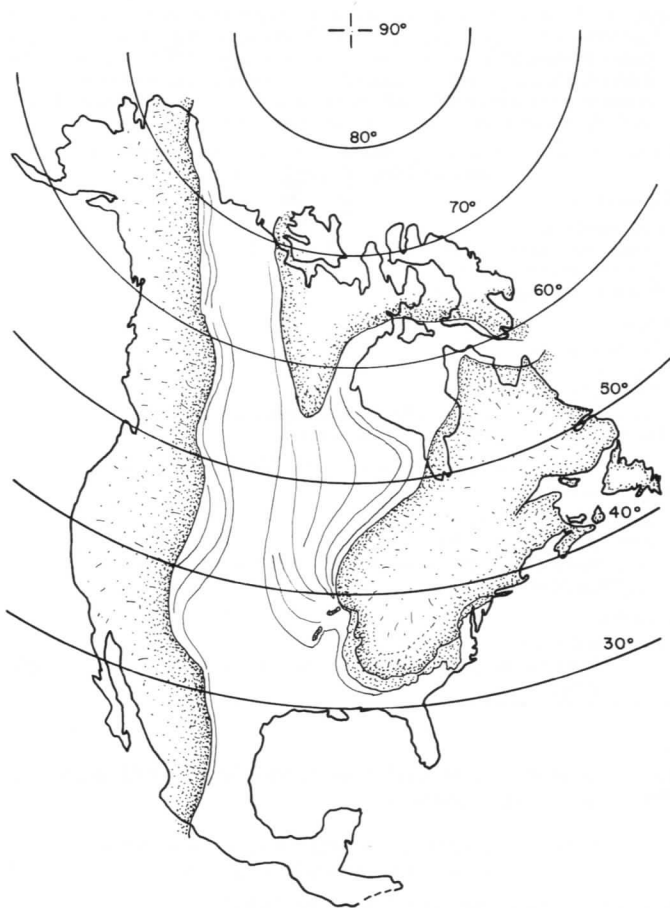


FIGURE 5—Reconstructed continental position during the Late Cretaceous (approximately Santonian Age), showing the relative position of the eastern USA Late Cretaceous outcrop as presently exposed. Continental position based on Scotese, et al., 1988.

Plain considerably farther south than today (Figure 5). The eastern Coastal Plain, overall, lay in a nearly east-west configuration close to sub-tropical latitudes from Tennessee to New Jersey. This Coastal Plain, and the adjacent eroding Appalachian Piedmont, would have significantly less latitudinal range than at present, and likely had limited physiographic heterogeneity. As in today's Gulf Coast, there were warm, humid, heavily forested, estuary- and tidal-swamp dominated coastal environments across the entire range of known dinosaur habitats, probably extending far inland (since sea levels were then not drawn down by Antarctic and Greenland glaciation).

Conditions of uniform, warm climate, and limited physiographic variation tend to limit specific diversity among modern large vertebrates, and probably did the same to the eastern USA dinosaur fauna during the Late Cretaceous. The contrasting higher diversity of dinosaurs in contemporary Western USA may also have been affected by paleogeography. The marine shoreline adjoining the Interior sea would actually have overall latitudinal ranges slightly increased relative to the present by the same continental paleoposition (Figure 5). The western USA interior shoreline was also proximal to active tectonics in the Cordillera. Both effects, latitude and tectonics, would tend to enhance environmental heterogeneity in marine vicinities of Western USA, and hence, would enhance opportunities for specific diversity, at least relative to the East.

There is little evidence of dinosaur endemism within the entire

eastern outcrop, and this too was probably the result of limited environmental heterogeneity. Although some taxa are known only from portions of the eastern outcrop (which might appear to be evidence of endemic species), one must factor in the disjunct ages of the better-known dinosaur beds. For example, along the Atlantic Coastal Plain, especially in well-studied sites in New Jersey, dinosaurs are mostly known from late Campanian through middle Maastrichtian strata, whereas in the central and eastern Gulf region, dinosaurs are best known from the Santonian through middle Campanian. Therefore, for example, one cannot know whether the large, unusual theropod *Dryptosaurus aquilunguis* (known with certainty only as the Maastrichtian type specimen from New Jersey) ever lived on the eastern Gulf Coastal Plain, because no Maastrichtian dinosaur beds are known from there.

Insertion of few dinosaur clades—It is assumed that eastern hadrosaurs and coelurosaurs (*sensu* Gauthier, 1986; Holtz, 1996) had common ancestry with morphologically similar taxa in western USA. Assuming western hadrosaurs and coelurosaurs in turn derived from Asian ancestors, then the origin of eastern clades must be from the west and there must have been cross-continental migration opportunities. However, during most of Late Cretaceous time, the interior of the continent was blocked by seawater (Kauffman, 1984; Kauffman and Caldwell, 1993), suggesting that times of insertion of Late Cretaceous ancestral dinosaur stocks must have been episodes of extreme marine draw-down within eustatic marine cycles. Based on the sea-level curves in Haq, et al., 1987, and the maximum-minimum timing constraints discussed in the next section, the marine regressions which may have allowed cross-continental dinosaur migrations may have occurred at 85, 83, 80, and 79 or 77.5 Ma. Evidence that the sea water over the Gulf Coastal Plain may have been quite shallow at times in the Late Cretaceous (Puckett, 1991), can be extended to suggest that extreme sea-level low stands of the Santonian and Campanian could lower the Interior sea level sufficiently to expose midcontinental land bridges.

Not all eastern dinosaur taxa in Late Cretaceous deposits necessarily or even likely migrated in from the western USA, since there are substantial remains of earlier fauna which may have persisted into the Late Cretaceous. Dinosaur tracks are abundantly represented in eastern USA rift basins of Triassic to early Jurassic age (Olsen and Baird, 1986), representing prosauropods, basal theropods, and perhaps basal ornithischians and more advanced saurischians. A mid-Cretaceous (Cenomanian) large theropod trackway, and a single theropod metatarsal fragment, were described by Baird (1989) from New Jersey (1989). Nodosaurid ankylosaurs, which are rare but widely distributed in the East, are known from limited remains including isolated teeth from the Lower Cretaceous of Maryland (Weishampel and Young, 1996). Nodosaurs likely migrated to North America from Europe during the Early Cretaceous. Pereda-Suberbiola (1991) observed that similar, perhaps congeneric nodosaurs are found in the Lower Cretaceous of England and South Dakota. Subsequent dinosaur migrations from Europe were precluded by the widening Atlantic and the chronically higher sea-levels of the mid- and Late Cretaceous.

It is therefore plausible that part of the older eastern dinosaur fauna survived into the Late Cretaceous and that some of the known fossils represent such clades. This descent-in-place hypothesis is a parsimonious explanation for the occurrence of *Dryptosaurus aquilunguis* in the Maastrichtian of New Jersey (see Gallagher, this volume). *Dryptosaurus* does not reveal evident relationships with other North American Late Cretaceous taxa in several aspects, notably its lack of the "arctometatarsalian" condition (Holtz, 1994) which appears to be synapomor-

TABLE 2—Dinosaur presence and absence data constraining timing of Late Cretaceous dinosaur migrations into eastern North America.

PRESENCE DATA	
→ Hadrosaurines:	Present in eastern USA by late Santonian, pencontemporaneously in western USA
→ Tyrannosaurids	Present in eastern USA by early Campanian, possibly earlier (non-diagnostic bones). <i>Albertosaurus</i> appears in western USA middle Campanian
ABSENCE DATA	
→ Absence of ceratopsians	Absent in eastern USA, earliest appearance in western USA Middle Campanian, abundant by late Campanian

Conclusion: West to east migration in USA likely from Santonian to early Campanian during sea-level low stands. Migration in or out of eastern USA unlikely after middle Campanian.

phous for all other Late Cretaceous theropods in North America (including the tyrannosaurid remains with preserved metatarsals found in the Southeastern USA: see Baird, 1989; Schwimmer, et al. 1993; Holtz, 1994).

Competition by crocodiles—Recent collecting and study (Schwimmer and Williams, 1993; 1997) reveal that giant eusuchian crocodiles of the species *Deinosuchus rugosus*, reaching 10 m length, were locally abundant in estuarine sediments in the southeastern USA Late Cretaceous. The same species is known from New Jersey to Mississippi (Miller, 1967; Meyer, 1984; Manning and Dockery, 1992; Gallagher, 1993; W. Langston, D. Baird, written communications), but population densities outside the eastern Gulf Coastal Plain have not been addressed. Nevertheless, in dinosaur-bearing beds in western Georgia and eastern Alabama, at least, teeth from this species are among the most common large tetrapod fossils.

It is clearly speculative to assume predator-prey relationships from fossils, but given the abundance of smaller theropods and hadrosaurs in a region featuring abundant giant crocodiles, a predator-prey relationship seems self-evident in the eastern USA. Gallagher (1993) has reported theropod teeth apparently dissolved in gastric juices, presumably crocodylian, in the Late Cretaceous of New Jersey. It is plausible that large crocodiles predated directly upon immature tyrannosaurs, other smaller theropods, and hadrosaurs, and that their presence and predatory dominance in coastal habitats may have preempted regional success of larger theropods. Several of these giant crocodiles have been found in marine shelf deposits, implying they were sea-going, in the manner of modern Australian *Crocodylus porosus*. However, the same shelfal strata contain dinosaurs, and it would be helpful in support or falsification of this crocodile-dominance model to determine how far upstream and away from shorelines the crocodiles ranged. If crocodiles were bound to estuaries and shores, theropods could still dominate upstream riverine habitats, contradicting the impression received from the eastern fossil record.

Timing of West-East Dinosaur Migrations

The presence and absence of several Late Cretaceous dinosaur clades in the Eastern Late Cretaceous implicitly constrains the timing of migrations into the region. The argument here is based on the presence of hadrosaurines and tyrannosaurids at about the same time on both sides of the Western Interior seaway (Table 2), and by the absence of ceratopsian fossils anywhere in eastern USA.

The early dates for migrations are constrained by the oldest hadrosaur fossils in the East, which are associated bones from a juvenile hadrosaurine in the lower Eutaw Formation of Mis-

issippi (Kaye and Russell, 1973). These are of late Santonian age, and are similar in proportions to slightly younger gryposaur hadrosaurine remains attributed to *Lophorhothon atopus*, which was described from early Campanian strata in nearby western Alabama. Since it is highly unlikely that hadrosaurines evolved independently on both sides of the Western Interior seaway, hadrosaurine presence shows that cross-continental migration must have been occurring by the late Santonian. The oldest eastern theropod remains attributable on good evidence to tyrannosaurids are of middle Campanian age from Georgia (Schwimmer, et al. 1993), but non-diagnostic, Santonian-age theropod material is also known from the McShan or Eutaw Formations in Mississippi (Carpenter, 1982), and could represent the oldest eastern tyrannosaurids. Recent work in the Gulf of Mexico Coastal Plain shows that the marine eustatic drawdown at 83 Ma was more significant than others during the Santonian (Frazier, 1996; Russell, 1996), and is among the most likely Late Cretaceous events exposing an interior land bridge.

The last plausible date for cross-continental dinosaur migration is constrained by the absence of ceratopsian fossils in the East. Ceratopsians first appeared in Southwestern USA in the middle Campanian (Lehman, 1996) and became common during the late Campanian and early Maastrichtian in most western USA dinosaur localities. However, despite their general western USA abundance and diversity, ceratopsian fossils have never been reliably reported in the East. Two spurious reports of eastern ceratopsian occurrences (King, 1995a, 1995b) were based on misunderstanding of published data and have been recanted (D. T. King, 1995, written communication). The noteworthy absence of ceratopsians in the eastern USA fauna is a valuable datum for the close of immigration possibilities, which would be the middle Campanian. Given that West Texas had a significant population of *Chasmosaurus* and other ceratopsians by the mid-Cretaceous (Lehman, 1996), it seems reasonable to assume they would have spread across the eastern continent, enjoying much the same climate and habitat as West Texas, if only they could have gotten across the seaway.

CONCLUSION

Studies and collections of eastern Late Cretaceous dinosaurs date back to the mid-Nineteenth Century (e.g. Leidy, 1864; Cope, 1866, 1870), and have been relatively extensive; yet, the overall assemblage has remained enigmatic in many aspects, as should be apparent from the preceding discussion. The rarity of complete specimens and skulls certainly accounts for part of the cryptic nature of the fauna, and it would seem convenient to blame marine depositional conditions for the paucity and ambiguity of the overall eastern Late Cretaceous dinosaur record. However, one should reflect that contemporary marine strata in western USA produce relatively abundant and more diverse dinosaur assemblages. The taphonomic and paleogeographic models presented here provide explanations for the general appearance of the eastern fauna, and can also explain why it appears significantly different from that of the contemporary West. The taphonomic differences between East and West key on the variances between marginal oceanic sedimentary settings of the eastern USA and epicontinental-marine settings in the Interior sea fronting western USA dinosaur habitats. In the eastern settings, a mechanism was necessary to carry dinosaur remains over the high-energy shoreface before burial and preservation was likely to occur: this is the essential rationale behind the bloat-and-float-with-scavenging model. For western USA, conditions do not force the same taphonomic model because the eastern shore of the Interior seaway probably did not have high-energy nearshore conditions, and likely could preserve a variety of drowned or transported carcasses close to the shoreline, with-

out the necessity of the carcass floating across the intertidal region. These taphonomic requirements alone could account for many of the differences in appearance between the preserved dinosaur faunas. The apparent disparity in dinosaur diversity between West and East probably result from other factors (enumerated in preceding pages) which are complementary to the differences in preservational styles.

The hypotheses presented are potentially falsified if new collection data shows patterns of occurrences at variance with past results. For example, new eastern Late Cretaceous sites containing abundant, isolated dinosaur skull material, or dorsal vertebrae, would tend to falsify part of the "bloat-and-float-with-scavenging" model. Similarly, the absence of shark scavenging evidence, where it was actively pursued, would weaken the taphonomic model. Discovery of data supporting a large, truly endemic dinosaur fauna would weaken both the paleobiogeographic ideas presented and cross-continental migration hypotheses; and, discovery of eastern ceratopsian fossils would remove some constraints on the timing of migrations. At present, the hypotheses proposed form an integrated, logical set of assumptions which fit all observations made and reported to date.

ACKNOWLEDGMENTS

Ideas and collections leading to this paper were contributed by many individuals over many years. Chief among those contributing dinosaur collections on which this report is based are G. Dent Williams, Patsy Dudley, and James L. Dobie. Others contributing specimens and data are Rodican Reed, Tom D. Scheiwe, Michael Smith, and Bobby Ratliff. The shark-dinosaur specimen in Figure 4 was loaned from the Alabama State Museum collections by W. Brown Hawkins Jr. Valuable discussions, critiques, and general assistance on dinosaur matters were provided by Donald Baird, William B. Gallagher, John R. Horner and Dale Russell. William J. Frazier drew Figure 2 expressly for this paper, and Figure 3 based on his field stratigraphic data and my paleoecology data. I also thank Dale Russell for a helpful review of the manuscript. Support for field research leading to this report came from The National Geographic Society, Grant No. 3787-88, and through Columbus State University Foundation Faculty Development Grants.

REFERENCES

- APPLEGATE, S. P. 1970. The fishes, Part VIII. The vertebrate fauna of the Selma Formation in Alabama. *Fieldiana Geology Memoirs*, 3(8): 385-433.
- BAIRD, D. 1986. Upper Cretaceous reptiles from the Severn Formation of Maryland. *The Mosasaur*, 3:63-85.
- . 1989. Medial Cretaceous carnivorous dinosaur and footprints from New Jersey. *The Mosasaur*, 4:53-64.
- , AND G. R. CASE. 1966. Rare marine reptiles from the Cretaceous of New Jersey. *Journal of Paleontology*, 40:1211-1215.
- , AND J. R. HORNER. 1979. Cretaceous dinosaurs of North Carolina. *Brimleyana*, 2:1-28.
- BRYAN, J. R., D. L. FREDERICK, D. R. SCHWIMMER, AND W. G. SIESSER. 1991. First dinosaur remains from Tennessee: a Campanian hadrosaur. *Journal of Paleontology*, 65:696-697.
- CARPENTER, K. D. 1982. The oldest Late Cretaceous dinosaurs in North America? *Mississippi Geology*, 3(2):11-17.
- , DILKES, AND D. B. WEISHAMPEL. 1995. The dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas). *Journal of Vertebrate Paleontology*, 15:275-297.
- CAPPETTA, H. AND G. R. CASE. 1975. Contribution à l'étude des sélaciens du Groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica*, 151:1-46.
- COPE, E. D. 1866. [Remarks on *Hypsibema crassicaudata*]. *Proceedings of the Academy of Natural Sciences*, Philadelphia, 21:192.
- . 1870. [Description of *Dryptosaurus (Laelaps) aquilunguis*] Synopsis of the Extinct Batrachia, Reptilia and Aves of North America. *American Philosophical Society Transactions*, New Series, 14: 100-119, plates 8-10.
- DENTON, R. K. AND W. B. GALLAGHER. 1989. Dinosaurs of the Ellisdale Site, Late Cretaceous (Campanian) of New Jersey. *Journal of Vertebrate Paleontology*, 9(Supplement to 3):18A.
- ERICKSEN M. C. AND R. SLINGERLAND. 1990. Numerical simulations of tidal and wind-driven circulation in the Cretaceous Interior Seaway of North America. *Geological Society of America Bulletin*, 102: 1499-1516.
- FIORIELLO, A. R. 1990. First occurrence of hadrosaur (Dinosauria) remains from the marine Claggett Formation, Late Cretaceous of south-central Montana. *Journal of Vertebrate Paleontology*, 10:515-517.
- FRAZIER, W. J. 1996. Estuarine deposits in the Eutaw and Blufftown Formations (Santonian and Campanian) of southwestern Georgia and adjacent Alabama and their sequence stratigraphic significance. *Abstracts With Programs*, Southeastern Section Geological Society of America, 28(2):12.
- GALLAGHER, W. B. 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coastal Plain. *The Mosasaur*, 5:75-154.
- . 1995. Evidence for juvenile dinosaurs and dinosaurian growth stages in the Late Cretaceous deposits of the Atlantic Coastal Plain. *Bulletin of the New Jersey Academy of Science*, 40:5-8.
- , D. C. PARRIS AND E. E. SPAMER. 1986. Paleontology, biostratigraphy and depositional environments of the Cretaceous-Tertiary transition in the New Jersey Coastal Plain. *The Mosasaur*, 3:1-36.
- GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds, p. 1-55. *In* K. Padian (ed.), *The origin of Birds and the Evolution of Flight*. *Memoirs of the California Academy of Science*, 8.
- HAQ, B. U., J. HARDENBOL, P. R. VAIL. 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, 235:1156-1166.
- HOLTZ, T. R. JR. 1994. The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. *Journal of Paleontology*, 68:1100-1117.
- . 1996. Phylogenetic taxonomy of the Coelurosauria (Dinosauria: Theropoda). *Journal of Paleontology*, 70:536-538.
- HORNER, J. R. 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-central Montana with a checklist of Upper Cretaceous dinosaur remains from marine sediments in North America. *Journal of Paleontology*, 53:566-577.
- KAYE, J. M. AND D. A. RUSSELL. 1973. The oldest record of hadrosaurian dinosaurs in North America. *Journal of Paleontology*, 47:91-93.
- KAUFFMAN, E. G. 1984. Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America, p. 273-306. *In* G.E.G. Westermann (ed.), *Jurassic-Cretaceous biochronology and paleogeography of North America*, Geological Association of Canada Special Paper, 27.
- , AND W. G. E. CALDWELL. 1993. The Western Interior Basin in space and time, p. 1-30. *In* W. G. E. Caldwell and E. G. Kauffman (eds.), *Evolution of the Western Interior basin*. Geological Association of Canada Special Paper, 39.
- KING, D. T. 1995a. Dinosaurian stratigraphy and modes of occurrence in the Alabama- Georgia Gulf Coastal Plain. *Gulf Coast Association of Geological Societies Transactions*, XLV:327-332.
- . 1995b. Dinosaurian stratigraphy and modes of occurrence in the Alabama- Georgia Gulf Coastal Plain. *Abstracts With Programs*, Geological Society of America National Meeting, 27(6):A-387.
- LANGSTON, W. JR. 1960. The Dinosaurs. The vertebrate fauna of the Selma Formation of Alabama. *Fieldiana: Geology Memoirs*, 3(5): 315-359.
- LAUGINIGER, E. M. 1984. An upper Campanian vertebrate fauna from the Chesapeake and Delaware Canal, Delaware. *The Mosasaur*, 2: 141-150.
- LEHMAN, T. M. 1996. A horned dinosaur from the El Picacho Formation of west Texas, and review of ceratopsian dinosaurs from the American southwest. *Journal of Paleontology*, 70: 494-508.
- LEIDY, J. 1864. Cretaceous reptiles of the United States. *Smithsonian Contributions to Knowledge*, 192:1-135, 20 plates.
- MANNING, E. M. AND DOCKERY, D. T. 1992. A guide to the Frankstown vertebrate fossil locality (Upper Cretaceous), Prentiss County, Mississippi. Mississippi Department of Environmental Quality Office of Geology Circular, 4, 43p.
- MEYER, E. R. 1984. Crocodilians as living fossils, p. 105-131. *In* Eld-

- ledge, N. and S. M. Stanley (eds.), Living Fossils. Springer-Verlag, New York.
- MILLER, H. W. 1967. Cretaceous vertebrates from Phoebus Landing, North Carolina. Proceedings National Academy of Sciences, Philadelphia, 119:219-235.
- . 1968. Additions to the Upper Cretaceous vertebrate fauna of Phoebus Landing, North Carolina. Journal of the Elisha Mitchell Scientific Society, 84:467-471.
- MORRIS, W. J. 1973. A review of Pacific Coast hadrosaurs. Journal of Paleontology, 47:551-561.
- OLSON, P. E. AND D. BAIRD. 1986. The ichnogenus *Atreipus* and its significance for Triassic biostratigraphy, p. 81-88. In K. Padian (ed.), The Beginning of the Age of Dinosaurs. Cambridge University Press, London.
- PARRIS, D. C., B. S. GRANDSTAFF, R. K. DENTON, W. B. GALLAGHER, C. DETAMPLE, S. S. ALBRIGHT, E. E. SPAMER, AND D. BAIRD. 1987. Taphonomy of the Ellisdale dinosaur site, Cretaceous of New Jersey. Final Report, National Geographic Society Grant 3299-86, 92+p.
- PEREDA-SUBERBIOLA, J. 1991. New evidence for an Early Cretaceous land connection between Europe and North America: *Hoplitosaurus*, a junior synonym of *Polacanthus* (Ornithischia: Ankylosauria). Comptes Rendus Académie des Sciences, Paris, 313(II):971-976.
- PUCKETT, T. M. 1991. Absolute paleobathymetry of Upper Cretaceous chalks based on ostracodes—evidence from the Demopolis Chalk (Campanian and Maastrichtian) of the northern Gulf Coastal Plain. Geology, 19:449-452.
- ROBB, A. J. 1989. The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen County, North Carolina. The Mosasaur, 4:75-92.
- RUSSELL, D. A. 1970. The mosasaurs, Part VII. The vertebrate fauna of the Selma Formation of Alabama. Fieldiana Geology Memoirs, 3(4):367-380.
- . 1988. A check list of North American Cretaceous vertebrates, including fresh water fishes. Tyrrell Museum of Palaeontology Occasional Papers, 4: 68p.
- . 1995. China and the lost worlds of the dinosaurian era. Historical Biology, 10:3-12.
- RUSSELL, E. E. 1996. Late Santonian to late Maestrichtian lithofacies and sea-level peaks in northeast Mississippi and western Tennessee. Abstracts with Programs, Southeastern Section Geological Society of America, 28(2):42.
- SCHULTZE, H.-P. 1995. Terrestrial biota in coastal marine deposits: fossil-Lagerstätten in the Pennsylvanian of Kansas, USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 119:255-273.
- SCHWIMMER, D. R. 1986. Late Cretaceous fossils from the Blufftown Formation (Campanian) in Georgia. The Mosasaur, 3:109-123.
- . 1995. East-West Late Cretaceous marine vertebrate provincialism: an artifact of parasynchrony? Abstracts With Programs, Geological Society of America National Meeting, 27(6): A387.
- , AND R. H. BEST. 1989. First dinosaur fossils from Georgia, with notes on additional Cretaceous vertebrates from the state. Georgia Journal of Science, 47:147-157.
- , AND G. D. WILLIAMS. 1993. A giant crocodile from Alabama and observations on the paleobiology of southeastern crocodylians. Journal of Vertebrate Paleontology, 13 (supplement to 3):56A.
- , AND ———. 1997. New Specimens of *Deinosuchus rugosus*, and further insights into chelonivory by Late Cretaceous eusuchian crocodylians. Journal of Vertebrate Paleontology, 16 (supplement to 3): 64a.
- SCHWIMMER, D. R., J. D. STEWART AND G. D. WILLIAMS. 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. Palaios, 47:71-83.
- , G. D. WILLIAMS, J. L. DOBIE AND W. G. SIESSER. 1993. Upper Cretaceous dinosaurs from the Blufftown Formation, western Georgia and eastern Alabama. Journal of Paleontology, 67: 288-296.
- SCOTESE, C. R., L. M. GAHAGAN AND R. L. LARSON. 1988. Plate reconstructions of the Cretaceous and Cenozoic ocean basins. Tectonophysics, 155:27-48.
- WEIGELT, J. 1927 (Translated by J. Schaefer, 1989). Recent vertebrate carcasses and their paleobiological implications. University of Chicago Press, 188p.
- WEISHAMPEL, D. B. AND J. R. HORNER. 1990. Hadrosauridae, p. 534-561. In D. B. Weishampel, P. Dodson and H. Osmolska (eds.), The Dinosauria. University of California Press, Berkeley.
- , AND L. YOUNG. 1996. Dinosaurs of the East Coast. Johns Hopkins University Press, Baltimore, 275 p.
- ZANGERL, R. 1948. The pleurodiran turtles Part II. The vertebrate fauna of the Selma Formation of Alabama. Fieldiana Geology Memoirs, 3(2):23-54.
- . 1953. The turtles of the Family Protostegidae, Part III. The turtles of the Family Toxochelyidae, Part IV. The vertebrate fauna of the Selma Formation of Alabama. Fieldiana Geology Memoirs, 3(4,5):59-276.