



Another Look at the Dinosaurs of the East Coast of North America

Otro vistazo a los dinosaurios de la Costa Este de Norte América

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Abstract

The dinosaurs of the East Coast of North America are rich in terms of their historical significance, but they have also been the source of considerable research over the past quarter century. Known from the Late Triassic, Early Jurassic, Early Cretaceous, and Late Cretaceous from South Carolina to Massachusetts in the United States, and from Nova Scotia, Canada, this fossil record consists of both skeletal remains and tracks. The theropods, prosauropods, sauropods, primitive ornithischians ankylosaurs, ornithopods, and ceratopsians from the eastern seaboard are reviewed and their importance for paleobiological, phylogenetic, and biogeographic interpretations are discussed.

Key words: Dinosauria, Triassic, Jurassic, Cretaceous, eastern North America, faunistics

Resumen

Los dinosaurios de la Costa Este de Norte América son ricos en cuanto a su significado histórico aunque también han sido fuente de considerable investigación durante el pasado cuarto de siglo. Conocidos a partir del Triásico Superior, Jurásico Inferior, Cretácico Inferior y Cretácico Superior de Carolina del Sur hasta Massachusetts en Estados Unidos y desde Nueva Escocia, Canadá, su registro fósil está constituido tanto por restos esqueléticos como por huellas. Se revisan los terópodos, prosaurópodos, saurópodos, anquilosaurios ornitisquios primitivos, ornitópodos y ceratópsidos de la costa este y se discute su importancia para interpretaciones paleobiológicas, filogenéticas y biogeográficas.

Palabras clave: Dinosauria, Triásico, Jurásico, Cretácico, Este de Norte América, faunístico

Introduction

It has been nearly two centuries since the first dinosaur was discovered along the eastern seaboard of North America (an indeterminate prosauropod discovered in 1818, first recognized as dinosaurian by Galton 1976) and eight years since the publication of the most recent treatment of all the East Coast dinosaurs (Weishampel and Young 1996). Despite its historical significance, research on these dinosaurs was eclipsed by the great dinosaur rush in the Western Interior of the United States in the late 19th century and later, in the 1910s and 1920s, in western Canada. After that, there was no looking back as amazing discoveries were made elsewhere, such that now dinosaurs are well known from spectacular occurrences across the globe (Weishampel and White 2003, Weishampel *et al.* 2004).

The dinosaurs of the East Coast of North America, despite their rarity and relatively poor preservation, have had an important influence on our understanding of dinosaurian faunistics, paleobiology, phylogeny, and biogeography. In what follows, I will summarize what is known about the dinosaurs along the eastern seaboard and how they fit into contemporary issues in dinosaur research.

Distribution

Dinosaurs are known from a discontinuous 100-km wide swath of the Atlantic Coastal Plain extending from Nova Scotia in the north to South Carolina to the south (Fig. 1; Weishampel and Young 1996). Stratigraphically, the best record (though consisting nearly entirely of ichnofossils) comes from the geographically disjunct rift valleys that formed during the Late Triassic and Early Jurassic, preserved in what is now a belt from North Carolina to Nova Scotia. The East Coast record of dinosaurs is absent thereafter until the Early Cretaceous. This 160 million year long Jurassic hiatus is followed by a modest, but important fauna from the mid-Atlantic region. Finally, there are several well-known, but patchy dinosaur faunas distributed throughout the Late Cretaceous from New Jersey, Delaware, and Maryland. These faunas provide the best body fossil record of all the East Coast dinosaurs.

The rarity of discoveries of dinosaurs along the eastern seaboard of North America is certainly unfortunate when attempts are made to compare what has been uncovered with the faunas known from elsewhere in the world. The biases against their preservation are obvious. First and foremost, much of the Mesozoic record is absent in the Appalachian region and along the Atlantic Coastal Plain (Weishampel *et al.* 2004), so the possibilities for having access to the appropriate strata are limited. Second, human activity along the East Coast has further reduced access to whatever outcrops may be available. For example, much of the eastern seaboard has been either paved over (the roads, office buildings, homes, malls, etc.

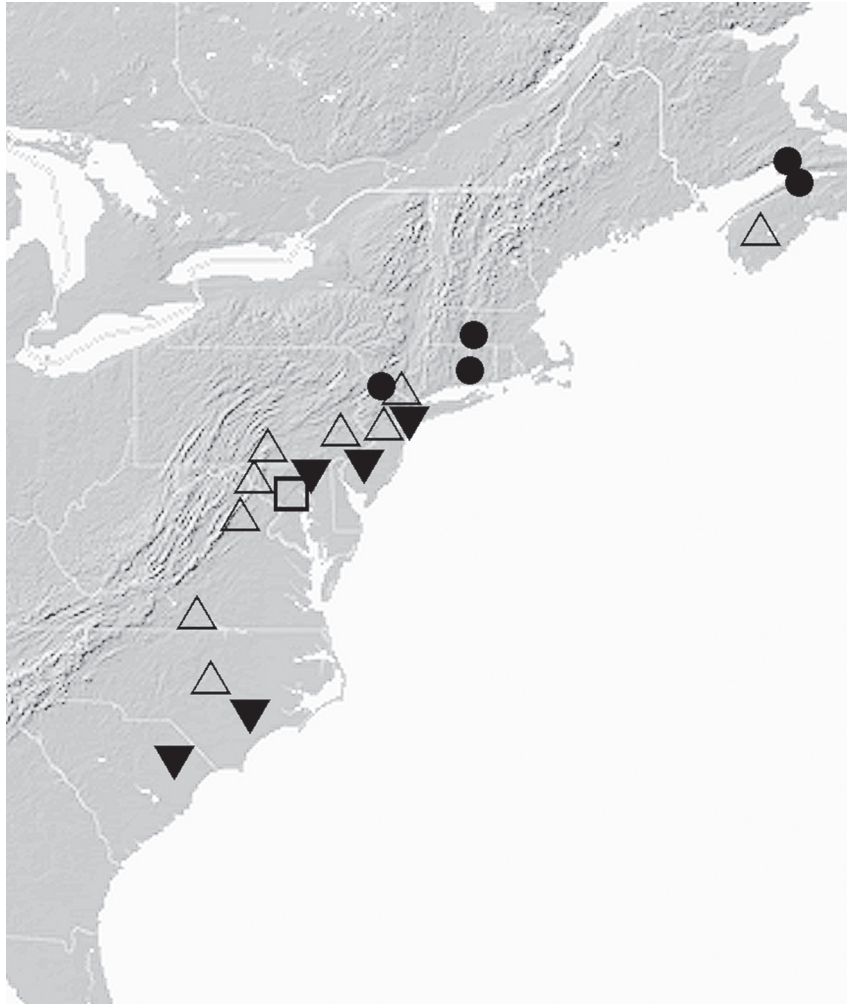


Figure 1. General geographic distribution of the dinosaurs of the East Coast of North America. Symbols: Δ : Late Triassic; \bullet : Early Jurassic; \square : Early Cretaceous; \blacktriangledown : Late Cretaceous.

that constitute the Atlanta-Boston “megapolis”) or dedicated to agriculture. If it had not been for the creation of outcrop through commercial mining during the 1800s (i.e., surface mining for brownstone building material in New England, bog iron in Maryland and glauconite in New Jersey; Guinness 2003, Singewald 1911, Gallagher 1997), much of the historically significant fossil discoveries would never have been made. Today we rely mostly on the occasional new road cuts, construction sites, and along river banks for the opening-up of pockets of sediment and, with luck, their included fossils.

From a paleogeographic and paleoecological perspective, the dinosaurs of the Late Triassic-Early Jurassic interval (Carnian-Toarcian) are found in cyclically deposited sandstones, shales, and black argillites, indicating the presence of alluvial fans, rivers and floodplains, lakes, and eolian conditions (LeTourneau 2003, Tanner 2003). The cyclicity of these beds corresponds to repetitive climatic shifts between semiarid and wet seasons (Tanner 2003).

During the Early Cretaceous, what was to become an extensive epicontinental seaway (Western Interior Seaway) that isolated western North America (Laramidia) from its eastern counterpart (Appalachia) in the mid-Cretaceous, developed in the north of this continental landmass (Archibald 1996). The sole Early Cretaceous dinosaur fauna from the East Coast (the Arundel Clay fauna; Aptian) has been recovered from dark gray and maroon lignitic clays that also include abundant iron carbonate concretions. Thought to be the remnants of successive oxbow lakes and fluviodeltaic back-swamps developed along the eastern piedmont of the Appalachian Mountains (Glaser 1969). The iron nodules formed the basis for the iron manufacturing industry of eastern Maryland and Virginia, which had been in its heyday in the 18th and early 19th centuries, but was in decline when fossils were initially found here thereafter (Singewald 1911, Kranz 1998).

The Late Cretaceous dinosaur faunas are known from sequences of marine rocks exposed along the eastern margin of the Cretaceous outcrop belt that extends from New Jersey to South Carolina (Gallagher 1984, 1993, Weishampel and Young 1996). These strata, mostly glauconitic sands and brown clays, record a series of transgressive-regressive shallow marine cycles during the latest Cretaceous (Campanian-Maastrichtian) and into the Tertiary.

East Coast Dinosaurs

Late Triassic

As has been well documented, the Late Triassic faunas of the East Coast are dominated by ichnotaxa, while body fossils are rare (Olsen 1980a, b, 1997, Olsen and Flynn 1989, Weishampel and Young 1996). From their first discovery in 1886 (Eyerman 1886) until the present, only theropods and primitive ornithischians are at all well known. The Late Triassic record of prosauropods is both enigmatic and controversial, consisting of a few teeth from Nova Scotia and an ichnotaxon from Virginia.

Late Triassic theropods from the East Coast are presently known only from tracks and trackways (Olsen 1980a, b, Olsen *et al.* 2002, Weishampel and Young 1996). Their footprints – all from the pes, indicating the track maker was bipedal – have been given a wide variety of generic and specific designations depending on their size. Ranging from 5-15 cm in length, all *Grallator* footprints (among them *G. cursorius* and *G. tenuis*) have a digital formula of ?-3-4-5-?, terminal claw marks, the impression of a heel, and the trace of digit I to the rear of the track (Fig. 2; see Gatesy *et al.* 1999 for functional interpretations of this track pattern). The impression of digit III is always the longest, while those of digits II and IV are subequal in length. With all these features in common, it is often the size of the prints that determines the names applied to them. First described by Hitchcock in 1858, *Grallator* prints are abundant and widely distributed from Virginia to Nova Scotia along the eastern seaboard during the Late Triassic.

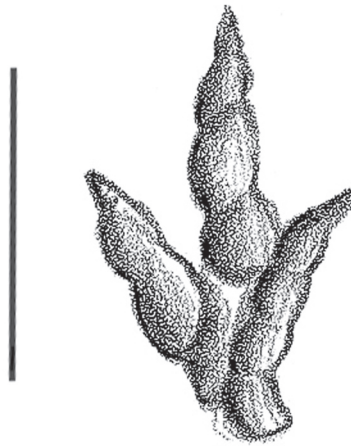


Figure 2. Pedal track of *Grallator*, thought to have been made by a ceratosaurian theropod, Late Triassic and Early Jurassic. Scale = 5 cm (after Lull 1953).

Often found with *Grallator* are 5-25 cm long pedal prints that have been named *Anchisauripus*, first described by Lull (1904) as the probable track of the prosauropod dinosaur *Anchisaurus*. Olsen (1980b) suggested that *Anchisauripus* tracks were made not by a prosauropod but instead are the footprints of large individuals of the *Grallator* track maker.

The third of these Late Triassic footprints is *Kayentapus* (Weems 1987), which appear to come from a different theropod track maker than *Grallator*. The East Coast *Kayentapus* tracks are large – 30 cm long – with a much longer, claw-tipped digit III and subequal, diverging digits II and IV. The digital formula of *Kayentapus* is the same as for *Grallator*.

Judging from the size of the prints, the animal responsible for these *Grallator* tracks was 2-6 m long, whereas the *Kayentapus* trackmaker was probably 3-4 m long. Based on their form and size, the maker of *Kayentapus* tracks has been likened to *Dilophosaurus*, a 6 m long theropod known from the Early Jurassic of Arizona, whereas a *Coelophysis*-like theropod (i.e., 1-2 m long, also known from the desert Southwestern United States, but from beds roughly contemporary with those in the east (i.e., Late Triassic), is thought to have made the *Grallator* tracks.

Prosauropoda

Although known elsewhere as the first large browsers of the Mesozoic, the Late Triassic prosauropods are poorly represented on the East Coast. Only a few badly preserved bony and dental specimens are known from Nova Scotia (Olsen *et al.* 1982) and Pennsylvania, and some indistinct pedal prints from Culpeper that may have been made by a prosauropod known as *Agrestipus ho-*

ttoni (Weems 1987). The taxonomy of the body fossils cannot be ascertained with any certainty and may in fact not be prosauropod (or even dinosaurian) in affinity. The duck-like pes prints of *Agrestipus* reveal three, and sometimes four, blunt digits. Originally thought to have been made by a sauropod dinosaur (Weems 1987), they are probably prosauropod prints because of their bipedal occurrence.

Ornithischians

The record of ornithischian dinosaurs presently consists of a few teeth and a single ichnotaxon. Of the dental material, *Galtonia gibbidens* is represented by several teeth collected in the mid-1800s from near Emigsville, Pennsylvania (Cope 1878, Hunt and Lucas 1994). The teeth were originally described by Cope (1878) as the prosauropod dinosaur *Thecodontosaurus gibbidens*, based on similarities with *Thecodontosaurus antiquus* from England (Riley and Stutchbury 1836, 1840; see also Benton *et al.* 2000) and were first attributed to Ornithischia by Galton (1983). Hunt and Lucas (1994) named these teeth *Galtonia gibbidens*. The other tooth taxon from the Late Triassic of the Atlantic Coastal Plain is *Pekinosaurus olseni*, also named by Hunt and Lucas (1994) based on several ornithischian teeth collected in Paul Olsen near the town of Pekin, North Carolina. No more than 5-6 mm high and broadly triangular, these features are found in other primitive ornithischians as well. Thus *Galtonia* and *Pekinosaurus* appear to represent primitive, but indeterminate ornithischians (Fig. 3; Norman *et al.* 2004). Other indeterminate ornithischian dental material consists of a fragmentary and very small maxilla with teeth (Galton 1983).

In contrast to this rarity of these skeletal remains on the East Coast, ornithischian footprints and trackways are abundant, particularly the print known as *Atreipus* (Fig. 4). There are several kinds of the quadrupedal *Atreipus*, among them *Atreipus milfordensis* and *A. acadianus*. Among the oldest dinosaur footprints on the East Coast are *Atreipus* tracks discovered at Leaksville Junction on the border of Virginia and North Carolina, currently under study by Olsen and Fraser. *Atreipus* is so common and sufficiently restricted in time – known only from about a 10 million year period – that it is often used as an index fossil for part of the Late Triassic (Olsen and Baird 1986). The three digit pedal prints of *Atreipus* have a long digit III and digits II and IV that are shorter than digit III but equal in length to each other. Its digital formula is ?-3-4-5-? (digits I and V, if present, were not preserved as prints). On the basis of the pedal and manual footprints, the maker of *Atreipus* tracks was an animal similar to *Lesothosaurus*, a basal ornithischian from southern Africa (Olsen and Baird 1986).

Gregaripus bairdi is a less common ornithischian track maker from this interval of time. Named by Weems (1987), these tracks have been found in only one location: the upper of two footprint horizons at the stone and gravel quarry near Culpeper, Virginia. *Gregaripus* tracks are blunt, tridactyl, and small, less than 10 cm long.

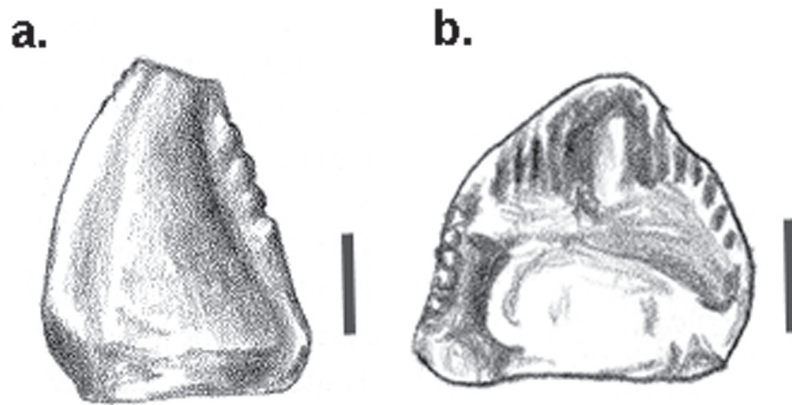


Figure 3. a. Premaxillary tooth of *Galtonia gibbidens*. b. *Pekinosaurus olseni*, both indeterminate primitive ornithischians, Late Triassic. Scale = 2 mm (after Hunt and Lucas 1994).



Figure 4. Manual and pedal tracks of *Atreipus*, thought to have been made by a primitive ornithischian, Late Triassic. Scale = 1 cm (after Olsen and Baird 1986).

Early Jurassic

The last part of the Triassic was marked by at least one mass extinction. Among vertebrates, procolophonids, phytosaurs, rhynchosaurs, dicynodonts, cynodonts, and many archosaur taxa are lost (many compendia of the “winners and losers” across the Triassic-Jurassic boundary are available; here I cite Benton 1983, 1994, Fraser and Sues 1994, Padian 1994, Olsen *et al.* 2002, but there are many others). This extirpation has been linked to competition among archosaurian and non-mammalian therapsids (Charig 1984), rapid climate change (Benton 1983, 1994; see

also this volume), and bolide impact (Olsen *et al.* 2002). Whatever the cause, it is clear that new major taxa have their origin during earliest Jurassic times, and that pterosaurs, turtles, and dinosaurs survived the extinction event (Benton 1994, Olsen *et al.* 2002).

Theropoda

The fossil record for Early Jurassic theropod dinosaurs fits the same pattern as for the ornithischians: many footprints and trackways but few skeletal remains, with localities primarily in the Connecticut Valley, Newark Basin, and Fundy Basin.

The first adequate skeletal material of East Coast dinosaurs is known from the Early Jurassic – a theropod (*Podokesaurus*) and two prosauropods (*Anchisaurus*, *Ammosaurus*). Unfortunately, the type and only specimen of *Podokesaurus* was destroyed in the fire of 1916 that consumed Williston Hall on the campus of Mt. Holyoke College, where the specimen was kept. However, casts of *Podokesaurus* now reside at the Yale Peabody Museum and the American Museum of Natural History. No additional material has been referred unambiguously to *Podokesaurus*, so the significance of this dinosaur came to depend on the original, poorly preserved skeleton.

When first discovered in 1910 in Massachusetts, this 1 m long theropod was known from part of the vertebral column (including some of the tail), a fragmentary humerus, some ribs, a pubis and ischium, a partial left femur, and much of the right leg (Fig. 5). Although the bones were poorly preserved, Mignon Talbot described and named *Podokesaurus holyokensis* in 1911. Three years later, von Huene (1914) used *Podokesaurus* as the founding member of a new group of small theropods, Podokesauridae, under the umbrella of the taxon he called Coelurosauria. At the same time, Lull (1915) reviewed Talbot's earlier description and recognized additional features of the material.

Thereafter, except for the discovery in Connecticut of a natural cast of a pubis, tibia, and ribs very tentatively referred to this taxon (Colbert and Baird 1858), *Podokesaurus* was to receive little attention other than mere mention in taxonomic and faunistic studies. However, with the discovery of important new, well preserved, and abundant material of the small theropod *Coelophysis* in Upper Triassic rocks at Ghost Ranch, New Mexico (Colbert 1961, 1989), the anatomy of small theropods came into much better focus. Colbert (1964) compared the surviving casts of *Podokesaurus* with this new *Coelophysis* material, concluding that *Podokesaurus* and *Coelophysis* were synonymous, with *Coelophysis* having priority. Consequently, he called the Massachusetts species *Coelophysis holyokensis*.

As more theropod material came to light and the research issues shifted to theropod phylo-

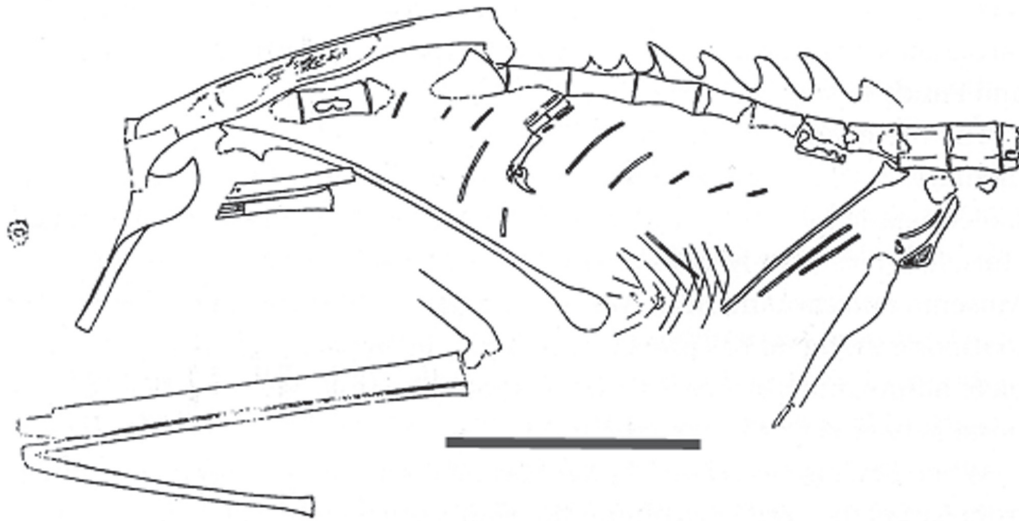


Figure 5. Skeleton of the ceratosaurian *Podokesaurus holyokensis*, Early Jurassic. Scale = 5 cm (after Talbot 1911).

geny and avian origins over the past quarter century, the Mt. Holyoke specimen has receded from view. Since Colbert's (1964) paper, it is discussed by Olsen (1980a), who rejected Colbert's synonymy of *Podokesaurus* and *Coelophysis*, designating *P. holyokensis* as *Theropoda incertae sedis*. Norman (1990) regarded it a theropod *nomen dubium*, while Weishampel and Young (1996) provided evidence that it may have ceratosaurian affinities. This is the position, specifically in Coelophysoidea, that Tykoski and Rowe (2004) have placed *Podokesaurus*. As a coelophysoid, it is likely that this theropod was built much like *Coelophysis* or *Dilophosaurus*: a slender, long-necked, fleet-footed predator with powerful forelimbs and grasping hands and jaws lined with sharp recurved teeth.

With the exception of a single tooth (Galton 1976), all other records of theropods from the Early Jurassic along the East Coast come from the footprint record. Since the early discoveries and analysis by Edward Hitchcock (1858; see also Weishampel and White 2003; Bakker 2003) and as in the Late Triassic, small and large *Grallator* prints are well known from many sites from Virginia to Nova Scotia. In addition to *Grallator*, *Eubrontes* is a much larger theropod track maker. These tracks – given such names as *Eubrontes approximatus* and *E. giganteus* – are typically 50 cm long, have a ?-3-4-5-? digital formula, and may display impressions of the heel and manus (Fig. 6; Farlow and Galton 2003, Galton and Farlow 2003). Based on the size of these tracks, the *Eubrontes* track maker must have been over 1 m high at the hip and 5 to 6 m long, smaller but otherwise consistent with *Dilophosaurus* from the desert Southwest of the United States. *Eubrontes* is not known from the Late Triassic, giving it a special place in arguments about the Triassic-Jurassic extinction (Olsen *et al.* 2002).



Figure 6. Pedal track of *Eubrontes*, thought to have been made by a large ceratosaurian theropod, Early Jurassic. Scale = 20 cm (after Lull 1923).

Prosauropoda

The first good record of prosauropod body fossils along the Atlantic Coastal Plain comes from the Early Jurassic – *Anchisaurus* and *Ammosaurus*. The best known of these – now recognized as *Anchisaurus polyzelus* – is a nearly complete skeleton discovered in a brownstone quarry at Manchester, Connecticut, in 1855 and several bones from East Windsor, Connecticut collected in 1818. It was first described as *Megadactylus polyzelus* and later as *Amphisaurus polyzelus* (Hitchcock 1865 and 1882, respectively), but both names were preoccupied. Consequently Marsh renamed the animal *Anchisaurus polyzelus* and described additional remains as *Anchisaurus colurus* (Marsh 1885 and 1891, respectively). Not satisfied with this assessment, von Huene (1932) renamed this latter species *Yaleosaurus colurus*. Most recently, Galton (1976) synonymized *Yaleosaurus colurus* with *Anchisaurus polyzelus*, with the name *Anchisaurus polyzelus* having priority.

Anchisaurus was a 2.5 m long, lightly-built prosauropod, known from a nearly complete skull and skeleton missing only the tail and part of the neck (Fig. 7a; Galton 1976, Galton and Upchurch 2004). Its skull is small in proportion to the rest of the body. Even so, the snout is relatively long and slender, and the jaws are lined with teeth that bear coarse serrations on their front and back edges. Like all prosauropods, *Anchisaurus* had a long and flexible neck, a somewhat rotund trunk, and a long, flexible tail. The shoulders and forelegs were robust in form. Digits IV and V are small, slender, and probably bore no claws. By contrast, digits II and III, and especially I are strongly built, the latter tipped by a greatly enlarged, sharply curved claw. The hind legs were strong, and the narrow, four-toed pes is sturdy (digit V is rudimentary).

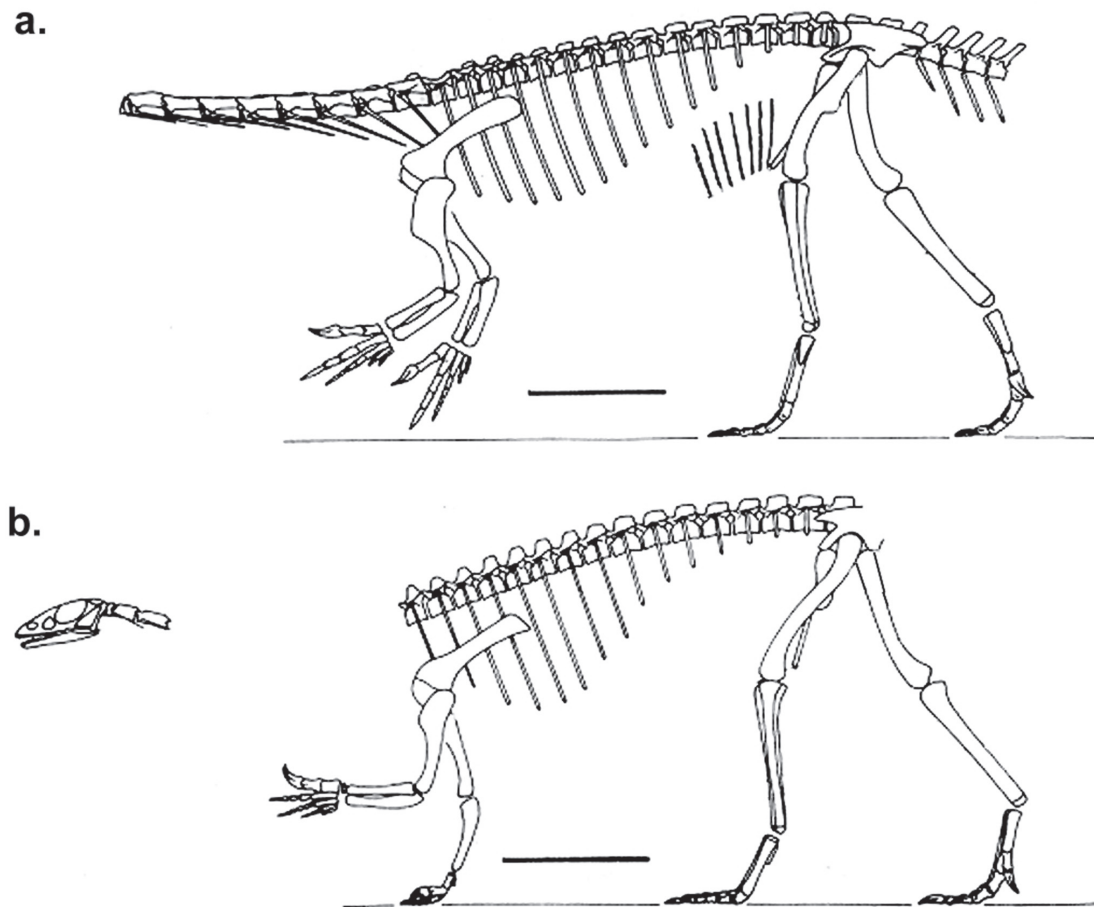


Figure 7. a. Skeletons of the prosauropods *Anchisaurus polyzelus* and b. *Ammosaurus major*, Early Jurassic. Scale = 10 cm (after Galton 1976).

The other prosauropod from the Early Jurassic of the East Coast is *Ammosaurus major* (Fig. 7b; Galton 1976, Galton and Upchurch 2004; considered by Yates 2004 as synonymous with *Anchisaurus polyzelus*), whose skeletal remains were found in the same Manchester quarry as *Anchisaurus*. Originally known as *Anchisaurus major* (Marsh 1889), it was renamed *Ammosaurus major* by Marsh (1895). Also included within *Ammosaurus major* is a smaller, perhaps juvenile form (*Anchisaurus solus*), another prosauropod skeleton found at the Manchester Quarry. Known principally from the Connecticut Valley, *Ammosaurus* has also been reported from the Early Jurassic of Arizona and Nova Scotia (Galton 1976; Shubin *et al.* 1994) and Nova Scotia (Shubin *et al.* 1994), but more recent studies (pers. comm. T. J. Fedak to P. M. Galton) suggest that it may be a new prosauropod taxon. *Ammosaurus* itself grew to a length of approximately 4 m.



Figure 8. Pedal track of *Otozoum*, thought to have been made by a prosauropod, Early Jurassic.
Scale = 5 cm (after Rainforth 2003).

In addition to these body fossils, prosauropod tracks are also known from the Early Jurassic. Hitchcock (1847) named these pentadactyl, but functionally tetradactyl pedal prints *Otozoum* (Fig. 8). Hitchcock originally regarded them as being made by a large amphibian, but it was Lull (1904, 1915), using available skeletal comparisons, who provided a more realistic inference by suggesting that *Otozoum* tracks were made by an ornithischian dinosaur (see also Thulborn 1990, Gierliński 1995). In contrast, Baird (1957, 1980) and Olsen (1980a) argued for a sphenosuchid crocodilian as the maker of the trackway. Finally, thanks to a comprehensive study by Rainforth (2003), the most likely attribution of *Otozoum* is to Prosauropoda (originally suggested by Nopcsa in 1923).

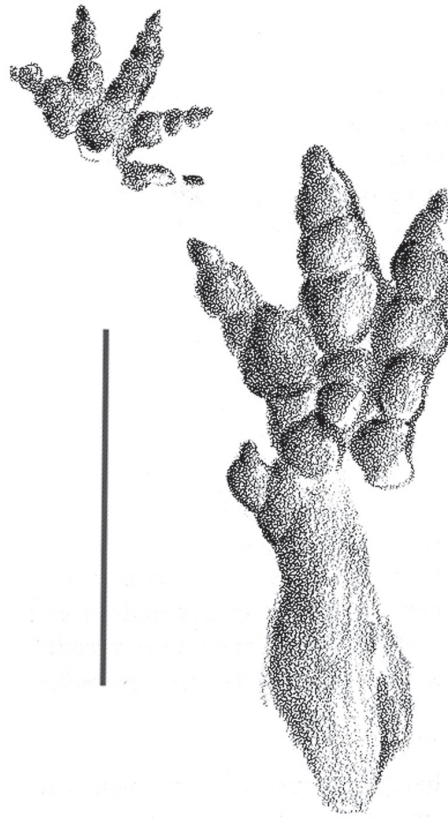


Figure 9. Manual and pedal tracks of *Anomoepus*, thought to have been made by a primitive ornithischian, Early Jurassic. Scale = 10 cm (after Olsen and Baird 1986).

The *Otozoum* pedal track, ranging in length from 13-21 cm, indicate a digitigrade foot posture, with a digital formula of 2-3-4-5-?0. Claw marks are often found on digits II, III, and I. The commonness of pedal prints indicates that the track maker was preferentially bipedal, but a few manual prints indicate that quadrupedality was part of the locomotor repertoire. The tetradactyl manual prints range in length from 12-13 cm and have a digital formula of 2-3-3-3-?0.

Ornithischia

From Nova Scotia in the north to New Jersey in the south, we find rare body fossils and abundant and widely distributed footprints of a new kind of primitive ornithischian. Called *Anomoepus* (Hitchcock 1848; see also Olsen and Rainforth 2003 and references therein), this track was made by a 1 to 2 cm pes with three narrow and highly divergent digits and an occasional digit IV (Fig. 9). It often includes a five-digit manus print. Most *Anomoepus* tracks were made by animals walking or running, although some were apparently produced by a crouching or sitting trackmaker, for there is the distinct impression of the rest of the pes from the heel to the ankle. These same prints provide the impression of the first digit and give enough room for

the fifth metatarsal, which apparently bore no phalanges. From this evidence we can reconstruct the digital formula of the pes of *Anomoepus*: 2-3-4-5-0. That of the smaller manus is 2-3-4-3-2. These proportions and formulas compare well with the Late Triassic *Atreipus* and with a primitive ornithischian track maker (Olsen and Rainforth 2003).

In contrast to the footprints, the rare ornithischian skeletal remains are tantalizing at best and frustrating at worst. So far, all that has been discovered are yet to be described teeth, jaws, and other skeletal material, all from Nova Scotia (Shubin et al. 1994). As with the Late Triassic ornithischians *Galtonia* and *Pekinosaurus*, comparisons with better-known relatives from elsewhere help us understand these Early Jurassic remains.

The teeth from Nova Scotia look similar to the cheek teeth of all primitive ornithischians: small, broad-based, triangular, and coarse along the front and back margins. These same features can be found in *Lesothosaurus* from southern Africa and in *Scutellosaurus*, a basal thyreophoran from the American Southwest. Both of these ornithischians were relatively small plant eaters, 1 to 1.5 m long. They were also long-legged, bipedal runners, though *Scutellosaurus* may also have rested and walked on all fours.

The Great Jurassic Hiatus – 160 million years of silence

For the eastern seaboard of North America, the fossil record of Middle and Late Jurassic dinosaurs is absent. If any sediments were laid down during these 160 million years, a time of uplift along the Appalachian chain to the west, they were subsequently eroded away. Or their absence may be due to non-deposition during this interval. In any event, the East Coast is silent about the origin and diversification of many dinosaurian clades – Sauropoda, Ornithopoda, Stegosauria, Ankylosauria, and possibly Aves.

Early Cretaceous

When the stratigraphic curtain along the Atlantic Coastal Plain opens again, it does so in a restrictive sense. For only in the mid-Atlantic region (Maryland, Washington, D.C., and Virginia) is there a dinosaur fossil record. The Arundel Clay, a lignitic facies in the upper part of the Patuxent Formation (Brenner, 1963; Robbins, 1991), has long yielded a skeletal fauna, first as a bi-product of the open quarrying of bog iron in the second half of the 19th century and more recently through the efforts of local paleontologists. This dinosaur fauna includes theropods, sauropods, ankylosaurs, ornithopods, and neoceratopsians.

Theropoda

The Arundel theropods are represented by a number of poorly preserved teeth, vertebrae, and limb bones that have been named and renamed over the years. *Allosaurus medius*, named by

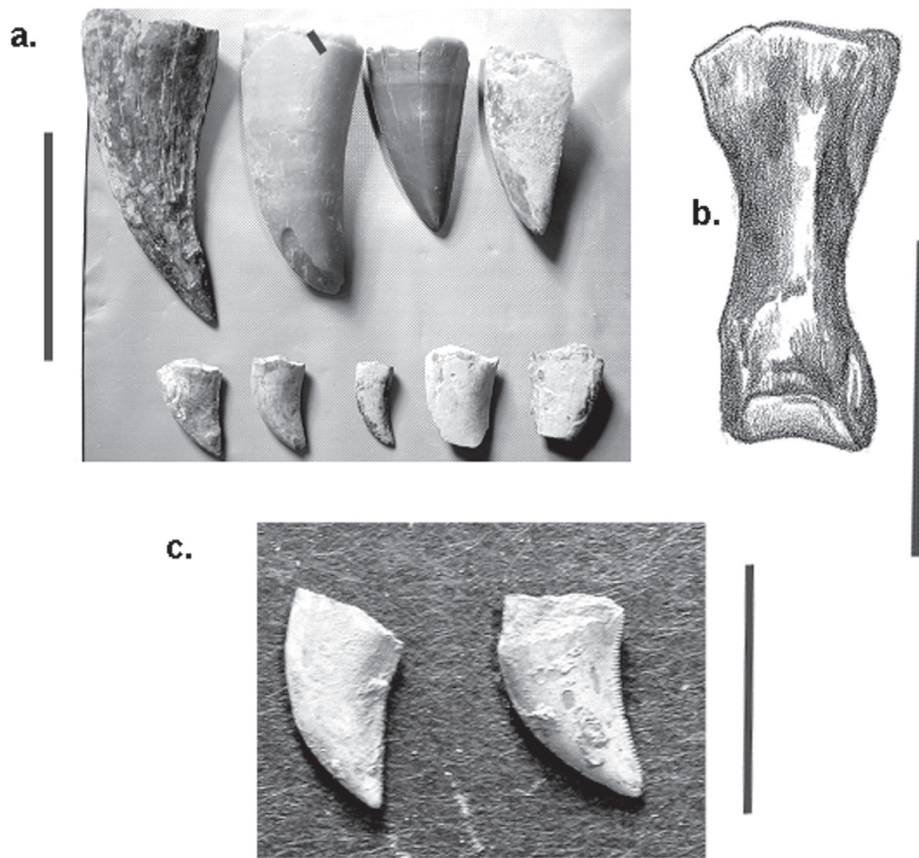


Figure 10. a. Teeth of the *Acrocanthosaurus*-like theropod. Scale = 2 cm (photograph courtesy of T. R. Lipka). b. Pedal phalanx of *Coelosaurus affinis*, an indeterminate ornithomimosaur, Early Cretaceous. Scale = 5 cm (after Gilmore 1921). c. Teeth of *Deinonychus* sp. (photograph courtesy of T. R. Lipka). Scale = 1 cm. All from the Arundel fauna, Early Cretaceous.

Marsh (1888), is based on a single tooth. At the same time, Marsh described a new theropod, *Coelurus gracilis*, from a manual claw. *Creosaurus potens* is based on a single caudal vertebra (Lull 1911).

In 1920, Gilmore referred all this material to *Dryptosaurus*, otherwise known from the Late Cretaceous of New Jersey. Gilmore (1920) also described a new theropod, *Ornithomimus affinis*, from a recurved pedal claw, two small caudal vertebrae, another partial vertebra, an astragalus, and two incomplete metatarsals. These remains had been mistakenly referred by Lull (1911) to an ornithopod that he named *Dryosaurus grandis*. Russell (1972) reassigned *Ornithomimus affinis* to his new genus *Archaeornithomimus*, making it *Archaeornithomimus affinis*, but Smith and Galton (1990) argued that *A. affinis* may not share important features with ornithomimids, describing it instead as a poorly preserved small theropod.

Today, the Arundel theropods (Fig. 10) include an *Acrocanthosaurus*-like allosauroid (Lipka 1998), an indeterminate ornithomimosaurian (*Coelosaurus affinis*), and an undetermined species

of *Deinonychus* (Lipka 1998). As for *Creosaurus potens*, *Allosaurus medius*, and *Coelurus gracilis*, these Arundel theropods are now considered indeterminate (Holtz *et al.* 2004).

The *Acrocanthosaurus*-like allosauroid is known only from seven large teeth (Lipka 1998), which compare well with those of *Acrocanthosaurus atokensis* from the Early Cretaceous of Oklahoma and Texas (Stovall and Langston 1950, Harris 1998, Currie and Carpenter 2001; Holtz *et al.* 2004). At 12 m long and 4 m tall, *A. atokensis* was probably the dominant predator of the times and the same was probably true of the Arundel allosauroid. Its teeth – tall and narrow, with fine-grained denticulations on the carina – were well suited for slashing flesh from bone and generally eating the softer parts of prey. Whether the Arundel allosauroid had extremely elongate neural spines, as in *A. atokensis*, is unknown.

Ornithomimosaur, on the other hand, are known principally from the Late Cretaceous of western North America and central Asia. Virtually all are toothless, likely filter-feeding on soft aquatic vegetation (Norell *et al.* 2001). All are slender, 3-5 m long, and clearly built for fast running, resembling in these respects many modern ground-dwelling birds (Makovicky *et al.* 2004). Although *Coelosaurus affinis*, based on isolated limb elements, is regarded as an indeterminate ornithomimosaur (Makovicky *et al.* 2004), it may also have had some or all of these features.

Finally, Lipka (1998) has identified four teeth as belonging to an unnamed species of *Deinonychus*. The carinae of these strongly recurved, laterally compressed teeth bear numerous denticles; those on the mesial edge being much smaller than those on the distal edge. These compare very well with the tooth morphology of *Deinonychus antirrhopus*, one of the best known dromaeosaurid dinosaurs from the Early Cretaceous of the western United States. *D. antirrhopus*, 3 m long, 1.2 m high, and weighing approximately 80 kg, was a lightly built, fast running theropod, with a curved, flexible neck, a large head, and powerful jaws (Ostrom 1969, Norell and Makovicky 2004). Each of its three manual digits bore large, sharp, curved claws, while on its four-digit pes, digit II had a 13 cm long sickle-like claw, and the other toes bore smaller claws. Its long tail was rigid, flexible only at the proximal end; it has been speculated that this rigidity provided balance and fast turning ability for the animal. It has also been inferred that *Deinonychus* hunted in packs (Maxwell and Ostrom 1995). To the degree that such inferences can be made on the basis of phylogenetic relationships and tooth taxa, it is likely that the Arundel *Deinonychus* looked and acted similarly.

Sauropoda

The first dinosaur discovered from the Maryland/Washington, D.C. area was the tooth of a sauropod from Bladensburg, Maryland (Fig. 11a). Johnston (1859) described this tooth and named it *Astrodon*. Leidy (1865) provided the species epithet *A. johnstoni*. Additional sauropod

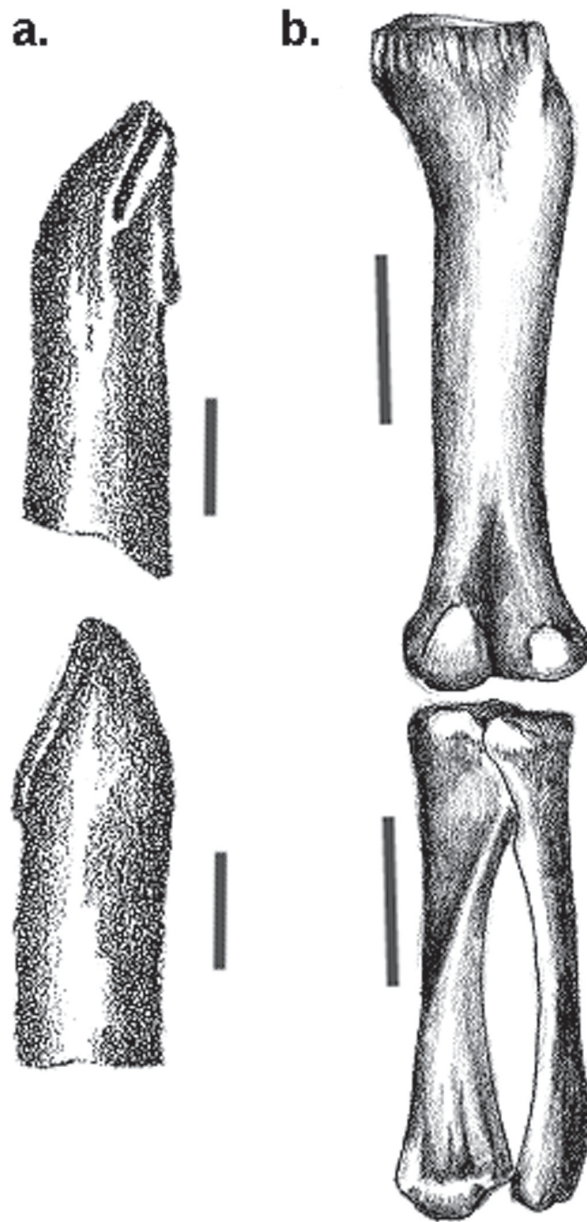


Figure 11. a. Tooth of *Astrodon johnstoni*, an indeterminate titanosauriform sauropod. (after Leidy 1865). Scale = 1 cm. b. Femur, tibia, and fibula of the titanosauriform *Pleurocoelus nanus* (after Lull 1911b). Scale = 10 cm. All from the Arundel fauna, Early Cretaceous.

remains were recovered from the Arundel Clay throughout the remainder of the 19th century. In 1888 Marsh recognized *Pleurocoelus nanus* from skull material and isolated remains of more than six individuals and also described another species, *P. altus*, on the basis of a tibia and fibula (Fig. 11b).

Although three sauropod taxa have been identified in the Arundel fauna, it is more likely that they represent different growth stages of a single species. The young individuals weighing no more than 500 kg and measuring less than 5 m in length, while adults weight up to 18,000 kg and were 20 m in length. What this species should be called is problematic. Upchurch *et al.* (2004) regarded *Astrodon johnstoni* a *nomen dubium*, lacking features that uniquely separate it from other sauropod species; therefore this name is not available. *Pleurocoelus* is considered a problematic taxon; the original Arundel material has yet to be properly diagnosed, while much better material referred to *Pleurocoelus* from the Early Cretaceous of Texas (Langston 1974, Gomani *et al.* 1999) indicates a relationship of at least the Texan form within Titanosauriformes (i.e., Brachiosauridae + Titanosauria; Upchurch *et al.* 2004).

Ankylosauria

The Arundel ankylosaur *Priconodon crassus* (Fig. 12a) is known from isolated teeth first named and described by Marsh (1888) and an isolated scute (Lipka pers. comm.). It is presently regarded as an indeterminate nodosaurid (Vickaryous *et al.* 2004); nodosaurid affinities for *Priconodon* are based on the large size of the teeth, the narrowness of the tooth crown, and the presence of a cingulum between the base and crown. Such a paucity of material makes it difficult to assess the anatomy, phylogenetic position, and biology of *P. crassus*. Whether it had a long parascapular spine, a prominent acromial process on the scapula, and skull ornamentation – general features of members of Nodosauridae (Vickaryous *et al.* 2004) – is not yet known.

Ornithopoda

The Arundel Clay has yielded only a single record of ornithopod dinosaurs: a large, broken crown and part of the root of a tooth from the left dentary (Fig. 12b). Originally referred by Galton and Jensen (1979) to *Tenontosaurus* sp., a euornithopod otherwise well known elsewhere from the Early Cretaceous of Montana, Wyoming, Idaho, and Oklahoma (Ostrom 1970, Forster 1990, Winkler *et al.* 1997), this tooth displays features characteristic of basal iguanodontians (Norman 2004), but little else. If the referral of this tooth to *Tenontosaurus* is correct, then the Arundel fauna will have included a 6 m long bipedal herbivore that weighed in excess of 1.8 tonnes.

Ceratopsia

The most startling discovery from the Arundel Clay is the recent recognition of ceratopsian teeth (Fig. 12c; Chinnery *et al.* 1998). Otherwise extremely abundant from the Early and Late Cretaceous of Asia and western North America but unknown from the East Coast, these two teeth (all that is presently known) have a bulbous convex shape of the non-enameled or less-enameled side of the crown (it is not known whether these teeth are from the maxilla or dentary), the presence of indentations that are deepest closest to the root, a well-developed cingulum enclosing the

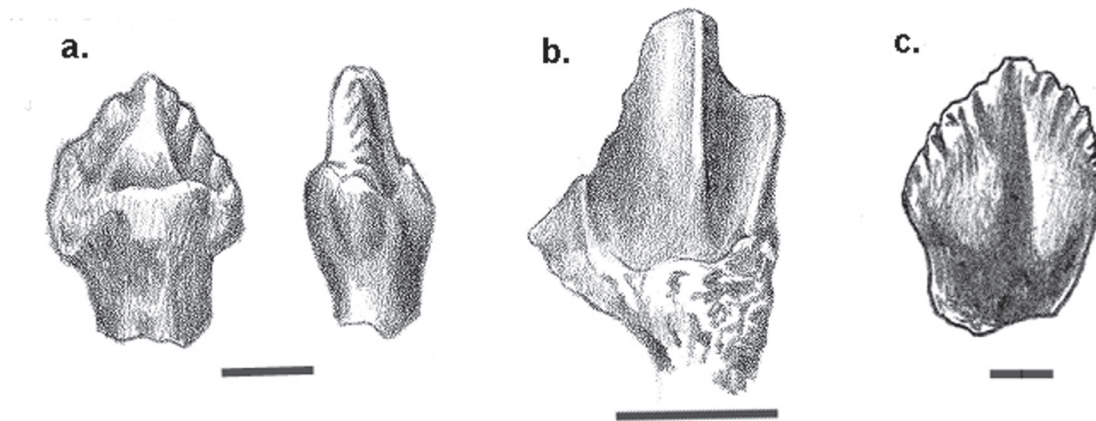


Figure 12. a. Tooth in buccal/lingual and mesial/distal views of *Priconodon crassus*, an indeterminate nodosaurid (after Lull 1911b). Scale = 1 cm. b. Dentary tooth of cf. *Tenontosaurus* sp., an iguanodontian ornithopod in lingual view (after Galton and Jensen 1979). Scale = 1 cm. c. neoceratopsian indet. (after Chinnery et al. 1998). Scale = 1 mm. All from the Arundel fauna, Early Cretaceous.

indentations, an offset primary ridge (distally if these are maxillary teeth and mesially if they are mandibular teeth), secondary ridges that terminate within the indentations, and vertical wear facets. Based on these features, the teeth are considered to be *Neoceratopsia* indet. (Chinnery et al. 1998).

Finally and most recently, a rich dinosaur ichnofauna has been discovered and is under study by Ray and Sheila Stanford. To date (Stanford 1998, Stanford and Stanford 1998, Stanford et al. 2004, Stanford pers. comm.), these mostly isolated footprints can be referred to a wide array of dinosaurs: large and small theropods, including dromaeosaurids, both subadult and adult sauropods, ankylosaurs, several kinds of ornithopods, and ceratopsians. In addition, the ichnofauna includes pterosaur and mammal tracks (Stanford pers. comm.). These spectacular footprints, when fully investigated, will provide a new perspective on the dinosaurs of the Early Cretaceous along the eastern seaboard that has not been recorded through skeletal remains.

Late Cretaceous

By the Late Cretaceous, North America had been completely divided by the Western Interior Seaway, producing Laramidia in the west and Appalachia in the east. Although Appalachia apparently comprised the greater terrestrial area for its time, it is Laramidia that, because of its preservation of huge wedges of terrestrial sediment, produced the rich dinosaur faunas of the Late Cretaceous. In contrast, all of the East Coast Late Cretaceous dinosaur record comes from marine rocks. These allochthonous occurrences suggest that their taphonomic overprint should be relatively great: a high occurrence of transported isolated, fragmentary material or, much more rarely, as relatively complete individuals (the so-called “bloat and float” specimens; Gallagher 1993, Fiorillo and Eberth 2004). It has never been seriously argued that these dinosaurs were marine-dwelling organisms, but that they lived along the extensive coastal lowlands near the sea.

Given the obvious bias attendant to the depositional environment, theropods, ankylosaurs, and hadrosaurids are reasonably well represented from the Cenomanian to the end of the Maastrichtian from New Jersey down to South Carolina.

Theropoda

The theropods from the Late Cretaceous of the East Coast are better known skeletally than from earlier in the Mesozoic (only one theropod track site in the Raritan Formation of New Jersey; Baird 1989, Gallagher 1997). Specimens of *Coelosaurus antiquus* from central New Jersey, northern Delaware, central Maryland, and eastern North Carolina, the much larger *Dryptosaurus aquilunguis* also from central New Jersey, and an unusually broad and straight tooth from New Jersey named *Diplotomodon horrificus* constitute the named Late Cretaceous theropods from the East Coast (Leidy 1865, Weishampel and Young 1996, Gallagher 1997). In addition, seven species of avian theropods are known from the Navesink and Hornerstown formations of New Jersey (Olson and Parris 1987).

Coelosaurus antiquus (Fig. 13a), the first named species of this genus (Leidy 1865; *C. affinis* from the Arundel Clay was the second named species – see above), appears to be an indeterminate ornithomimosaur from the Navesink Formation (late Campanian-early Maastrichtian) of New Jersey and elsewhere along the eastern seaboard (Makovicky *et al.* 2004, Weishampel *et al.* 2004). Although based on only a tibia, it likely would have shared features common to all ornithomimosaurs: an elongate, bird-like skull within which are an assortment of air sinuses, a slender body and long tail, and long hindlimbs. [Even though it is a *nomen dubium*, a word needs to be said about the taxonomic history of *Coelosaurus*. Baird and Horner (1979) rediscovered Owen's (1854; author anonymous but known to be Owen) use of the name *Coelosaurus* for a mutilated centrum of an unknown taxon of indeterminate age from New Jersey and suggested as a solution for its compromised usage that all East Coast ornithomimosaur material from the Late Cretaceous be called *Ornithomimus*. Unfortunately, no case was made that the East Coast *Coelosaurus* was synonymous with *Ornithomimus*, otherwise known only from roughly contemporaneous beds of the Western Interior of North America. For this reason and because few if any subsequent paleontologists have used Owen's name *Coelosaurus*, I have chosen not to refer to this Late Cretaceous ornithomimosaur as *Ornithomimus antiquus*, instead maintaining Leidy's original name *Coelosaurus antiquus*.]

Diplotomodon horridus (originally *Tomodon*, preoccupied by a genus of modern colubrid snakes) was thought to be a plesiosaur when first described by Leidy (1865). He later thought it was a fish (Leidy 1868). Based solely on a broad tooth that is symmetrical rather than recurved in lateral view, from the Navesink or Hornerstown Formation (Maastrichtian) of New Jersey (Fig. 13b), it was much later attributed to a mosasaur (Miller 1955), a group of large swimming lizards

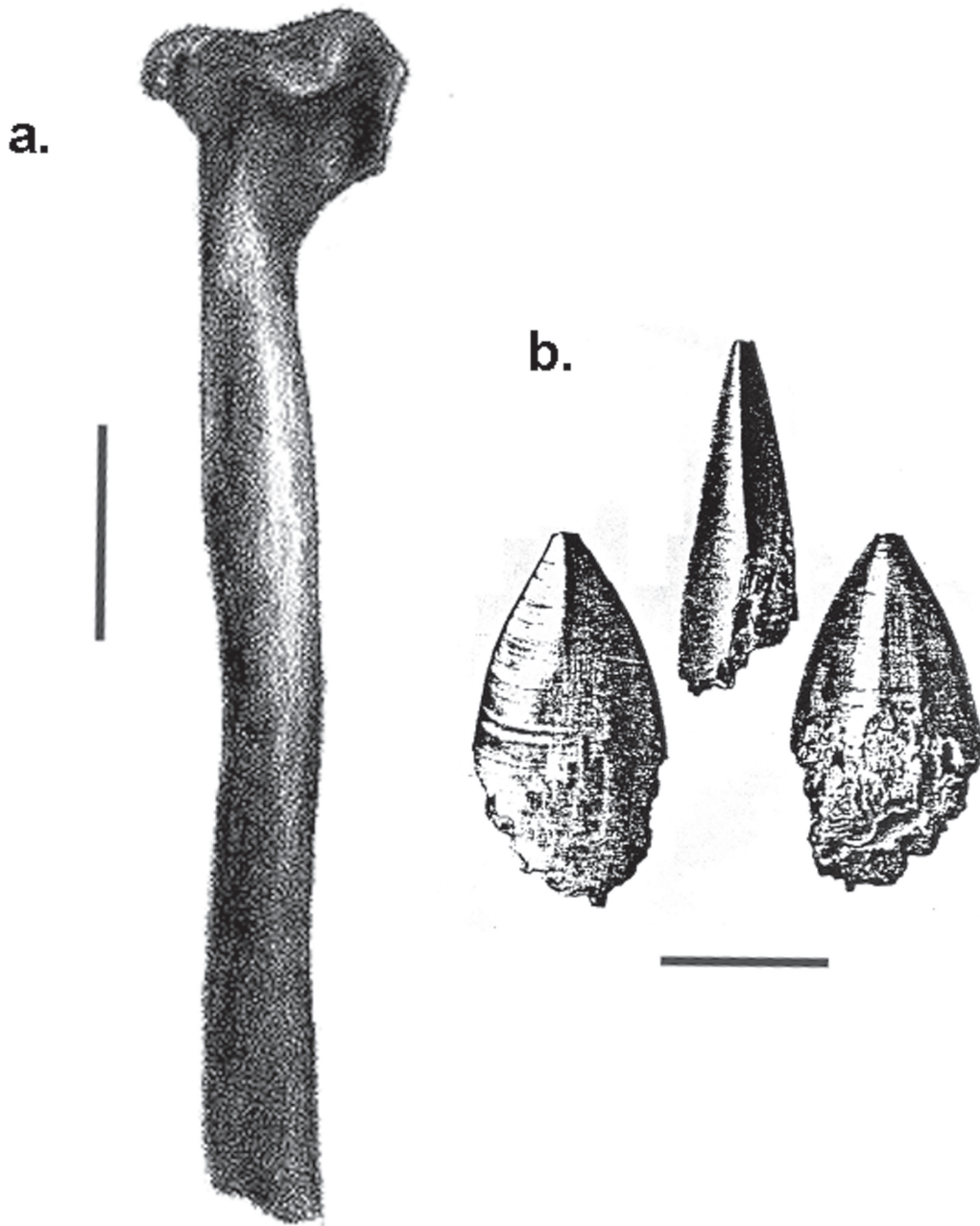


Figure 13. a. Tibia of *Coelosaurus antiquus*, an indeterminate ornithomimosaur. Scale = 10 cm. b. Tooth, in labial?, mesial?, and lingual? views, of *Diplotomodon horridus*, an indeterminate tetanuran theropod (after Leidy 1865). Scale = 3 cm. Both from the Late Cretaceous.

common in the Upper Cretaceous marine beds of the region (Russell 1967, Mulder 1999, Holmes and Sues 2000). However, Welles (1952) interpreted *Diplotomodon* as a theropod dinosaur. Most recently, it is considered a tyrannosauroid *nomen dubium* (Holtz 2004).

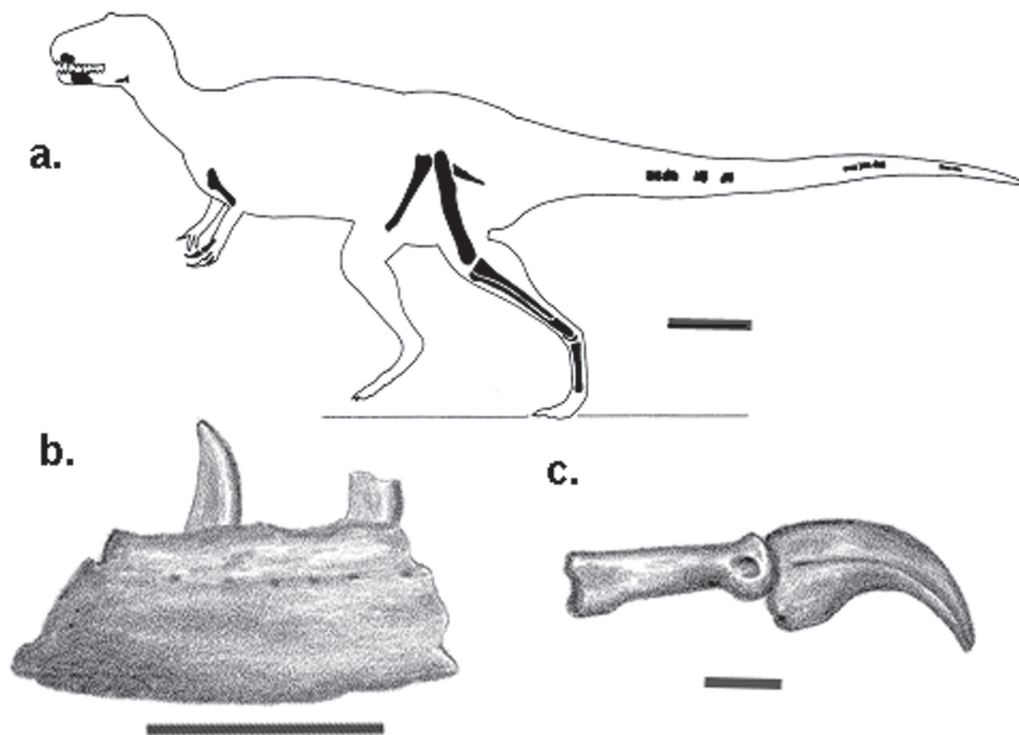


Figure 14. *Dryptosaurus aquilunguis*, a tyrannosauroid theropod. a. Skeleton, known material silhouetted in black. Scale = 1 m (after Carpenter et al. 1997). b. Partial dentary with in situ teeth. Scale = 5 cm. c. manual phalanx and claw. Scale = 5 cm. All from the Late Cretaceous.

Turning finally to *Dryptosaurus aquilunguis*, this theropod is based on a partial skeleton and numerous referred teeth and pedal elements from the Navesink, Mt. Laurel, and Marshalltown formations (late Campanian-early Maastrichtian) of New Jersey (Fig. 14). It was originally named *Laelaps aquilunguis* by Cope (1866). However, because this name was preoccupied by a spider, Marsh (1877) replaced it with the name *Dryptosaurus*. Once thought to be a carnosaur (*sensu* Huene 1932), *Dryptosaurus* has been considered a coelurosaur (Denton 1990; Carpenter et al. 1997), but is now regarded as a basal tyrannosauroid (Currie 2000, Holtz 2004). The teeth of this predator are laterally compressed, with serrated mesial and distal carinae. Of particular interest, the manus bore a large trenchant claw (46 cm long). The long and gracile hindlimb indicates that *Dryptosaurus* was an agile carnivore.

In addition to these “conventional” theropods, a number of important, though poorly preserved avian species are known from the latest Cretaceous (Navesink Formation and lower part of the Hornerstown Formation; late Campanian-late Maastrichtian) of New Jersey. They include such charadriiforms (shorebirds, gulls, and terns) as *Telmatornis affinis*, *T. priscus*, *Anatolavis rex*, *Graculavus velox*, *Laornis edvardianus*, *Palaeotringa littoralis*, and *P. vagans*, and a single procellariiform (albatrosses, petrels, and shearwaters) *Tithostonyx glauconiticus*. Most have been known since Marsh’s (1870) *Odontornithes* monograph and were most recently reviewed by Olson and Parris (1987).

Ankylosauria

The armored ankylosaurs are the rarest dinosaur fossils from the Late Cretaceous of the East Coast (Horner 1979, Gallagher 1993). So far, all that is known, both from New Jersey, is a caudal vertebra (Navesink Formation; late Campanian-early Maastrichtian) collected from central New Jersey and a keeled scute (?Marshalltown Formation; late Campanian) that is lost. Fortunately, a cast of it is still available for study (Horner 1979, Gallagher 1993). These specimens indicate that a nodosaurid was present in the Late Cretaceous of the eastern seaboard.

Ornithopoda

Hadrosaurus foulkii (Fig. 15) is certainly a cause célèbre in the history of dinosaur research in North America. For its time, *H. foulkii* was the most complete dinosaur skeleton from anywhere in the world and the first mounted dinosaur skeleton in a museum exhibition (Weishampel and Young 1996, Gallagher 1997, and references therein). The discovery and historical significance of *H. foulkii* has been well described elsewhere (Colbert 1968, Weishampel and White 2003). Based on a fragmentary maxilla, two cervical, seven dorsal, and eighteen caudal vertebrae, humerus, ilium, ischium, femur, tibia, astragalus, and pedal phalanges, *H. foulkii* became the type genus of Hadrosauridae and Hadrosaurinae (Cope 1869, Lambe 1918). The past 134 years has seen Hadrosauridae become one of the most diverse dinosaurian clade, known principally from western North America and central and eastern Asia, but also Europe and South America. Obviously herbivorous, hadrosaurids are especially well known among dinosaurs in terms of their skeletal anatomy, aspects of soft tissue anatomy (especially cranial neurovasculature, cranial and postcranial myology, and integument), growth series from embryos to old adults, sophisticated jaw mechanics, locomotion (from tracks and skeletons), intraspecific social behavior and herding, and parental care (Horner *et al.* 2004 and references therein).

H. foulkii has been identified from the Woodbury Formation (early Campanian), Merchantville Formation (early Campanian) and Marshalltown Formation (late Campanian) of New Jersey. In addition, two other New Jersey taxa (*Hadrosaurus cavatus*, *Ornithotarsus immanis*) have been referred to *H. foulkii* (Baird and Horner 1977, Prieto-Marquez *et al.* 2005).

The remaining hadrosaurids from the East Coast are much less understood than *H. foulkii*. The best of these is a partial skeleton referred to as “*Hadrosaurus*” *minor* (Baird and Horner 1977, Horner 1979, Horner *et al.* 2004, Prieto-Marquez *et al.* 2005). Originally collected from the Navesink Formation (late Campanian-early Maastrichtian) and described by Colbert (1948), this material consists of ribs, vertebrae, and right pelvis and hindlimb (right pubis, partial right ischium, right and left femora, left fibula) that are approximately 75% the size of *H. foulkii*. Colbert (1948) referred this skeleton to *Hadrosaurus minor*; also known from the Navesink or Hornerstown Formation (Marsh 1879). The original material of *H. minor* (dorsal vertebrae),

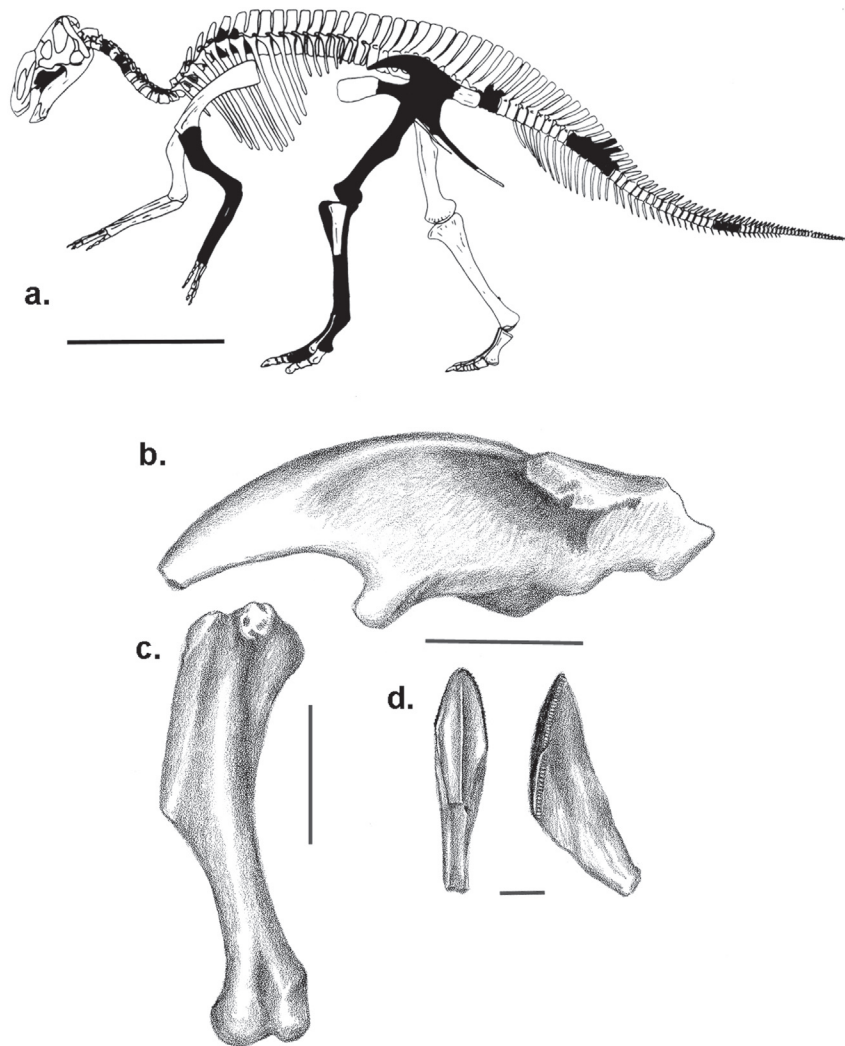


Figure 15. The hadrosaurid *Hadrosaurus foulkii*, from the Late Cretaceous. a. Skeleton; known material silhouetted in black. Scale = 1 m (after Gallagher 1990). b. Left ilium. Scale = 10 cm. c. Left humerus. Scale = 10 cm. d. Dentary tooth, in lingual and mesial views. Scale = 1 cm (b, c, d). (after Lull and Wright 1942).

however, is not sufficient to diagnose this species; *H. minor* is thus rendered Hadrosauridae *nomen dubium* (Horner *et al.* 2004). To make this distinction, quotes are provided around the generic designation of the skeleton. Baird and Horner (1977) suggested that “*H.*” *minor* may be a close relative of or congeneric with *Edmontosaurus*, otherwise known from the Late Cretaceous of the northern Western Interior of North America (Horner *et al.* 2004).

Baird and Horner (1979) and Horner (1979) reported a *Lophorhothon*-like hadrosaurine from the Phoebe Landing fauna of North Carolina. Here the Black Creek Formation (Campanian) has yielded only isolated and fragmentary jaws and teeth.

The other major clade of Hadrosauridae – Lambeosaurinae – was thought to be absent from the Appalachian landmass in the Late Cretaceous. Recently, however, Gallagher (1993, 1997) identified possible lambeosaurine specimens from the Navesink Formation (early Maastrichtian) of New Jersey. Thus far, this material consists of a well-preserved left humerus with a prominent deltopectoral crest and two separate occurrences of paired radii and ulnae.

Finally, many hadrosaurid species have not survived the test of time and taxonomic clarifications. Thus, *Hypsibema crassicauda*, *Hadrosaurus minor* (mentioned previously), and *H. tripos*, all of which are distributed in Upper Cretaceous rocks across the eastern seaboard, are presently considered indeterminate hadrosaurids (Horner *et al.* 2004, Prieto-Marquez *et al.* 2005).

Dinosaurian Demise on the East Coast

The ultimate demise of so many dinosaurs precisely at the Cretaceous-Tertiary boundary is not recorded along the East Coast. Nevertheless, it is clear from many sites around the globe that there was a bolide impact approximately 65 million years ago that would have had cataclysmic effects on all global ecosystems (Alvarez *et al.* 1980, Silver and Schultz 1990, Hildebrand *et al.* 1991, Archibald and Fastovsky 2004) and may have been the forcing factor for dinosaurian extinction. As pertains to the Atlantic Coastal Plain, the interval of time directly before and after this mass extinction is well known in New Jersey. (Gallagher 1990, 1992, 1993). Even without an iridium concentration, microtektites, shocked quartz, or a dense record of dinosaurs, the marine invertebrates across the KT boundary within the region indicate that, although the extinction was relatively rapid, it also appears to have been somewhat selective. The oysters and other mollusks, all of which had planktotrophic larvae, dominated the ocean-bottom communities at the end of the Cretaceous. By the earliest Tertiary (early Paleocene), however, these marine mollusks no longer dominated, having been replaced by non-planktotrophic brachiopods. This pattern of selective extinction also applies to ammonites, the most common and diverse of marine invertebrate predators at that time. Ammonites also had planktotrophic larvae, whereas their nautiloid relatives laid large, self-sustaining eggs. It is the ammonites that go extinct at the KT boundary, while nautiloids survived.

Gallagher attributed this pattern of rapid, though selective, extinction to a global population crash of planktonic organisms – the food source for the planktotrophs during the Cretaceous – at the K-T boundary, with its cascading effect on all marine and terrestrial ecosystems. This plankton collapse may have been triggered by the bolide impact, most likely through changes in the chemistry of the oceans.

Discussion

Based on the foregoing, the present census of East Coast dinosaurs is 29 different taxa recognized from the East Coast record of Mesozoic Dinosauria (from a total of a possible 19 body and 10 footprint taxa). Of these, only 16 can be diagnosed to species (or genera, because all genera under consideration here are monospecific; generic designations are used here for tracks), eight of which are body taxa and another eight are ichnotaxa. Among these species, seven are known elsewhere in the world (three body and four footprint taxa) and nine appear to be endemic (five body and four footprint taxa). The occurrences of endemism are greater for the end of the Mesozoic than they are in the Late Triassic and Early Jurassic.

Over the past 24 years, the number of dinosaur localities worldwide has increased by 55% compared to those known from all of the previous 121 years, but is this increase restricted to more regional phenomenon or is it generally global? In order to assess the degree to which the fossil record of the eastern seaboard has enjoyed this tremendous upswing in dinosaurian discoveries everywhere in recent years, I have compared the number of localities discovered along the East Coast of North America from 1858 (the announcement of *Hadrosaurus*) to 1980, to the number of new localities established from 1981 to the present (December 2004). Data come from Weishampel and Young (1996), Weishampel (1990), and Weishampel *et al.* (2004). No comparative statistics were performed on these data because of the volatility of such a small sample size. Nevertheless, as can be seen from Figure 16, the rate of locality discovery prior to 1980 at its best is 0.107/year (or 1 locality per 9.3 years). At its poorest, foregoing the Middle and Late Jurassic when no localities have been discovered, the pre-1981 rate is 0.016/year (or 1 locality every 62.5 years). As for the rate of locality discovery since 1980, the relative pattern is the same but in all cases the numbers have increased, in a few cases considerably (Late Triassic, Late Cretaceous). When the pre-1980 and post-1980 records are averaged, there is more than a four-fold increase in the rate of increase in the discovery of dinosaur localities for the Atlantic Coastal Plain over the past 24 years.

In order to see how this pattern compares with other regions of the world, I have compared these data with those of Britain, a region of the world with a similar modern climate and industrialization. In addition, it has a roughly equivalent range of history of dinosaur discoveries. The British record parallels that of the eastern seaboard of North America, with the exception of the Middle and Late Jurassic record (Fig. 17). Both show a large increase in new localities discovered since 1980. Especially impressive is the six-fold increase in the British Early Cretaceous. As is no surprise, the East Coast record is the better during the Late Triassic-Early Jurassic and in the Late Cretaceous, while Britain dominates during the Middle-Late Jurassic (when there is no record on the East Coast) and especially in the Early Cretaceous. Although dinosaur fossils may be poorly preserved and distributed patchily along the Atlantic Coastal Plain, but they are as available as consistently as those from Britain.

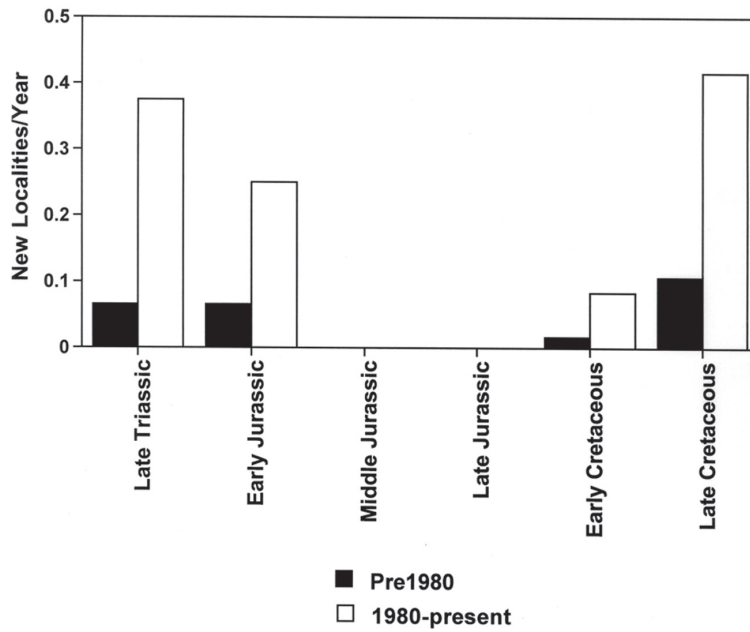


Figure 16. Comparison of the rate of locality discovery (new localities/year) for the Late Triassic through the Late Cretaceous along the East Coast of North America for the pre1980s and for 1980 to the present.

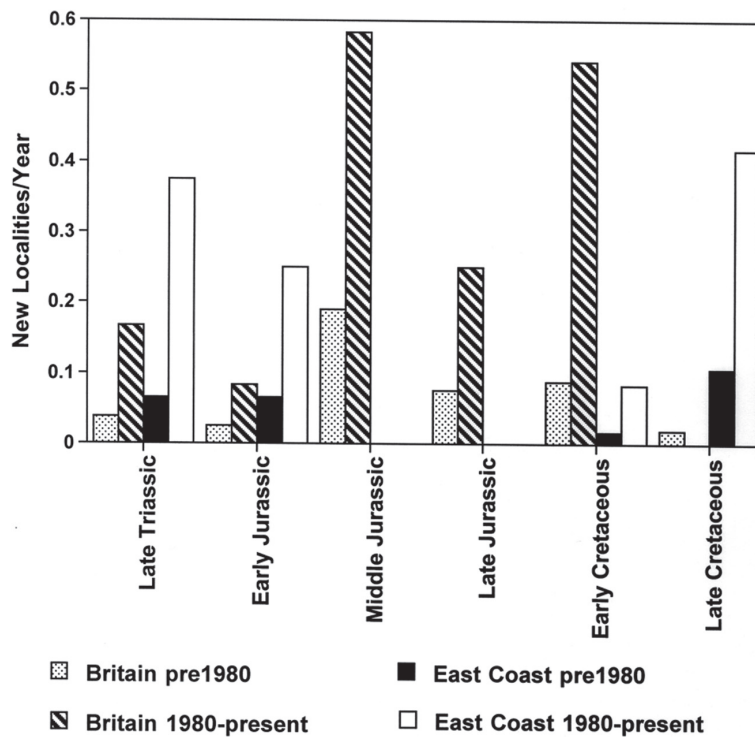


Figure 17. Comparison of the rate of locality discovery (new localities/year) for the Late Triassic through the Late Cretaceous along the East Coast of North America and from Britain for the pre1980s and for 1980 to the present.

Despite its relative scarcity, the discovery of dinosaurs from the eastern seaboard of North America has gone beyond the compilation of taxonomic and faunistic data. In several cases, they have been instrumental in changing our ideas about dinosaurian paleobiology; I will recount two here, one that arose early in the history of discovery of East Coast and the other from more recent times.

With his involvement in the construction of the Crystal Palace exhibition of dinosaurs, finished in 1854, Owen iconized those few taxa that had been discovered in England up until that time (McCarthy and Gilbert 1994). These outdoor reconstructions were of large, quadrupedal, thick-skinned, and generally reptile-like animals. But by the end of the 1850s, with the arrival of *Hadrosaurus foulkii*, dinosaur posture was about to change. Specifically, Leidy (1858) observed the disparity in limb length: the forelimbs are much shorter than hindlimbs; on this basis Leidy inferred that *H. foulkii* was bipedal. This difference in limb length is obvious, but for its time it broke with conventional wisdom and was influential in the reconstructions of a number of dinosaurs as bipeds. Among modern tetrapods, the body posture of these bipedal dinosaurs was fashioned after kangaroos (and later ratites; see Dollo 1883). Leidy (1858) further suggested that, with its kangaroo-like posture, *H. foulkii* would have browsed on foliage using its hindlimbs and tail as a tripodal support. This “mobilizing” of dinosaurs to get up on their hindlimbs held sway in both scientific investigations and museum exhibits for the remainder of the 19th century and most of the 20th century. Reconstructions since then did not refute the dinosaurian bipedal stance, but instead altered the orientation of the dorsal, sacral, and caudal regions to near-horizontal (Galton 1970).

Going from the 19th to the late 20 century, from bones to tracks, and from body posture to social behavior, Ostrom (1972) analyzed the distribution of abundant theropod trackways from two Early Jurassic sites in New England. At Mt. Tom in central Massachusetts, 134 prints were arranged in 28 trackways along a single bedding plane. Approximately 70% of these tracks, mostly *Grallator*, are oriented in nearly parallel courses. In order to explain this pattern, Ostrom suggested that these theropods were traveling as a large group, all at the same time, across a broad mudflat. In contrast, at Dinosaur State Park in Rocky Hill, Connecticut, 86 trackways, most of which are *Eubrontes*, show only a modest preferred orientation, either to the northeast or southwest, but the pattern is not as striking as at Mt. Tom. To Ostrom, Rocky Hill trackways suggest that large theropods ambled across the mudflat over a much longer period of time than at Mt. Tom. In this way, Rocky Hill may represent several comings and goings of a few theropod herds. These two sites, especially Mt. Tom, provide rare, but unambiguous evidence of gregarious behavior in theropod dinosaurs, which had only been guessed at before.

The *Eubrontes* footprints at Rocky Hill have also been used to evaluate theropod swimming

abilities (Coombs 1980). Most of these prints show the usual three-toed impressions complete with digital pads and claw and heel marks. However, occasional prints and short trackways show exceptionally clear claw marks, with little phalangeal impression and no heel whatever. Coombs suggested that the unusual tracks were made by an animal swimming in shallow water, kicking the bottom with the tips of its toes. For track sequences that end abruptly, the theropod may have been buoyed up while swimming so it temporarily lost contact with the bottom. Interesting though this scenario is, it has recently been investigated and found to be unlikely. In a reexamination of same tracks used in Coombs's work, Farlow and Galton (2003; see also Galton and Farlow 2003) provided not only track descriptions, but also experimental evidence from among living bipeds (in this case, the tracks of an emu walking and running at different velocities to test the swimming hypothesis). They determined that the transition of walking to swimming identified by Coombs could equally have been made by the *Eubrontes* track maker going from a walking to a fast-running theropod.

Turning finally to the evolutionary significance of the dinosaurs of the East Coast, these animals have rarely been featured in many phylogenetic analyses, most likely because of their relatively poor preservation and consequent abundance of missing data. However, as computers are becoming faster and more powerful, and as new software is being developed to handle missing data, some of the East Coast dinosaurs are now being analyzed for their phylogenetic (and biogeographic) context. The latter is particularly important in view of the breakup of Pangea and the development of a mid-North American seaway. As a geographic intermediate between Laramidia in the west and the increasingly more insular Europe to the east, the dinosaurs of Appalachia should provide important biogeographic information, especially relating to the dynamics between Europe and western North America. In particular, the bisection of North America by the Western Interior Seaway and the establishment of the North Atlantic Ocean throughout the Mesozoic should be reflected in the phylogenies of the dinosaurian taxa considered in this paper.

In their comprehensive treatment of Prosauropoda, Galton and Upchurch (2004) identified two major clades of these early dinosaurian herbivores: Anchisauria and Plateosauria (Fig. 18a). Within the former, *Anchisaurus* and *Ammosaurus* form a monophyletic clade (Anchisauridae) that is the sister taxon to Melanorosauridae (*Riojasaurus*, *Camelotia*, and *Melanorosaurus*). On the basis of optimizing the geographic distribution of all the terminal taxa onto this cladogram, anchisaurids likely reached what is now the eastern seaboard of North America via a single migration. *Anchisaurus* and *Ammosaurus* represent the known diversification products from this invading ancestor. Where they dispersed from is not yet known because there is no geographic resolution for the more inclusive clades beyond Anchisauridae.

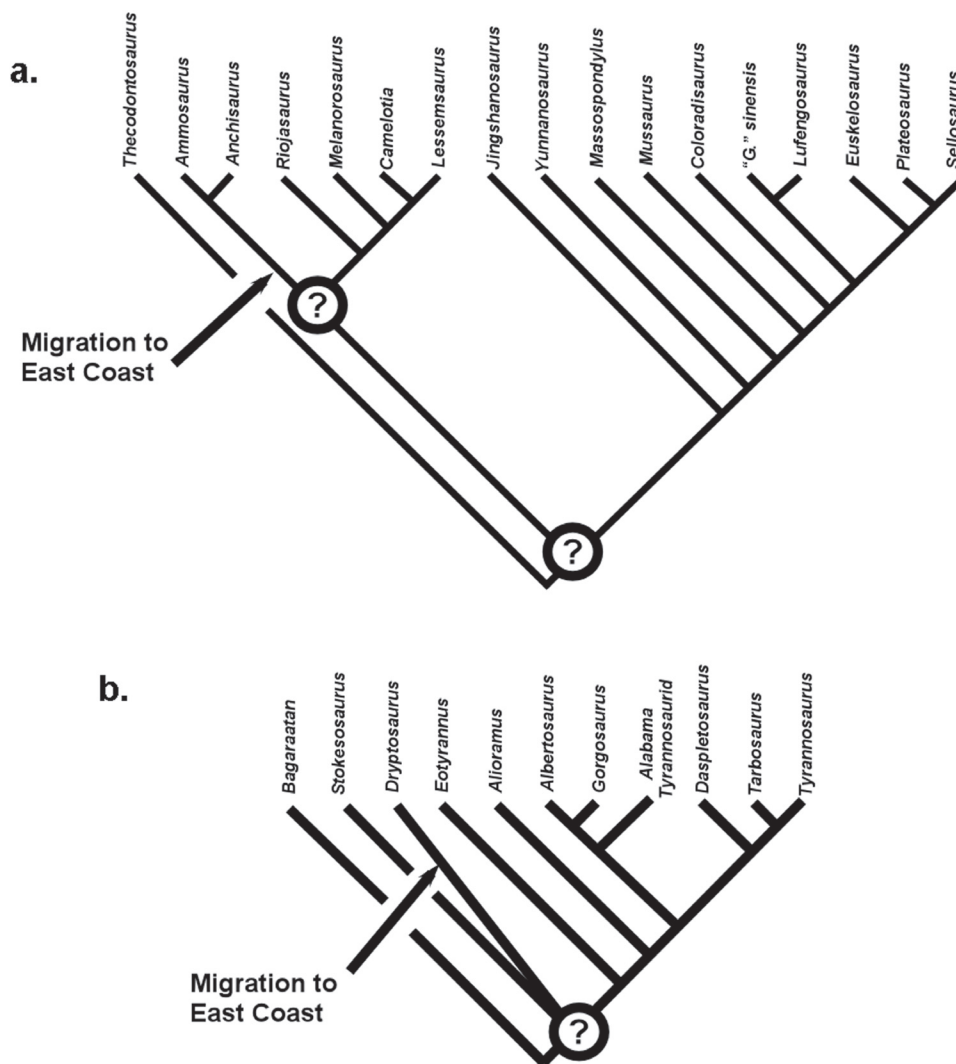


Figure 18. a. Cladogram of Prosauropoda (after Galton and Upchurch 2004). b. Cladogram of Tyrannosauroidae (after Holtz, 2004).

Obviously, this biogeographic interpretation is fully dependent on the robustness of its phylogeny. Should another, different cladogram be used as the backbone of the biogeographic investigation, then conclusions about biogeography will also likely differ, sometimes to the extreme. Only recently has such a phylogenetic analysis become available (Yates 2003, 2004). This cladistic study identifies Prosauropoda as a monophyletic clade, but a more restricted one than other authors. Most unusual is the position of *Anchisaurus* (Yates regarded *Ammosaurus* as a synonym of *Anchisaurus*), shifted from having a well-nested position in Prosauropoda to a new place as the sister-group of all remaining sauropods. If true, then the East Coast of North America may have been inhabited by among the first of the truly gigantic of all dinosaurs.

Prior to last decade of the 20th century, *Dryptosaurus aquilunguis* had been considered a member of several theropod groups, among them Deinodontidae (Cope 1866, Matthew and Brown 1922), Megalosauridae (Lydekker 1888, Osborn 1902, Gilmore 1920, Huene 1926), and Tyrannosauridae (Russell 1970, Baird and Horner 1979). However, Denton (1990) showed that *Dryptosaurus* had no relationships with any of these groups (most of which have vanished from current use because they turn out not to be monophyletic) but instead may have been an exceptionally large basal member of the monophyletic Coelurosauria. Most recently, Holtz's (2004) extensive cladistic analysis positioned *Dryptosaurus* in an unresolved polytomy with *Stokesosaurus* and tyrannosauroids near the base of Tyrannosauroidea. As before, the geographic distribution of all tyrannosauroids was mapped onto their cladogram, *Dryptosaurus* appears to stand alone in its East Coast location (the other tyrannosauroid from this region – *Appalachisaurus montgomeriensis*, recently described by Carr *et al.* [2005]) – is nested higher in the cladogram than is *Dryptosaurus*). However, its unresolved phylogenetic relationship near the base of Tyrannosauroidea and the lack of geographic resolution that comes from the remaining members of the clade make it presently impossible to determine whether *Dryptosaurus* itself dispersed to what is now New Jersey and environs, or whether it and *Stokesosaurus* (Utah) represent endemic diversification in North America from a single dispersal event.

These are promising times for dinosaur research nearly everywhere in the world, including the Atlantic Coastal Plain of North America. The value of the latter comes not just from its historical and archival perspective; this region has experienced the expansion of dinosaurian research from 1980 onward that is most manifest in places like China, Argentina, and western North America. Despite the obvious problem of paving over, building upon, and growing grains and produce over, available and future outcrop make it likely that we will continue to learn more about the dinosaurs of the East Coast.

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Nota

1. Parker *et al.* (2005) have demonstrated that some, if not all, of the Late Triassic teeth ascribed to ornithischians for North America, but rather are likely it belong to pseudosuchian archosaurs. This would render *Pekinosaurus olseni* and *Galtonia gibbidens* irrelevant to this volume.