OSTEICHTHYANS FROM THE TALLAHATTA–LISBON FORMATION CONTACT (MIDDLE EOCENE–LUTETIAN) PIGEON CREEK, CONECUH-COVINGTON COUNTIES, ALABAMA WITH COMMENTS ON TRANSATLANTIC OCCURRENCES IN THE NORTHERN ATLANTIC OCEAN BASIN

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Harry M. Maisch, IV, Martin A. Becker, Ben H. Raines & John A. Chamberlain, Jr. 2016. Osteichthyans from the Tallahatta–Lisbon Formation Contact (middle Eocene–Lutetian) Pigeon Creek, Conecuh-Covington Counties, Alabama with Comments on Transatlantic Occurrences in the Northern Atlantic Ocean Basin. - PalArch's Journal of Vertebrate Palaeontology 13, 3 (2016), 1-22. ISSN 1567-2158. 22 pages + 4 figures.

Keywords: Eocene, Osteichthyans, Alabama, Transatlantic occurrences, Northern Atlantic Ocean Basin, Taphonomy

ABSTRACT

A disconformity and lag deposit that separates the Tallahatta and Lisbon Formations along Pigeon Creek near Red Level, Conecuh-Covington Counties, Alabama contains osteichthyan remains belonging to: *Pycnodus* sp.; *Lepisosteus* sp.; *Albula* sp.; *Egertonia isodonta* Cocchi, 1864; *Cylindracanthus rectus* Agassiz, 1843; *Sphyraena* sp.; *Triciurides* cf. *T. sagittidens* Winkler, 1874; *Scomberomorus* sp.; Ariidae gen. indet.; *Ostraciidae* gen. indet., and cf. Beryciformes. This fossil osteichthyan assemblage is similar to other contemporaneous nearshore faunas found throughout Alabama, the Atlantic and Gulf Coastal Plains, and elsewhere throughout the Northern Ocean Basin. The accumulation and concentration of osteichthyans between the Tallahatta and Lisbon Formations is the result of third order eustatic sea level fluctuation and reflects a complex taphonomic history of exhumation, transport, and reburial across a shallow, middle Eocene shelf. Wide spread distribution of osteichthyan genera found in the Pigeon Creek assemblage demonstrates the continuity of shallow marine shelf environments of the Northern Atlantic Ocean Basin during the middle Eocene and the utility of osteichthyans in regional and transatlantic stratigraphic studies.

Introduction

For well over one hundred and fifty years, the occurrence of fossil fish from the Eocene of Alabama has been known (White, 1956). Historically, these fossil fish specimens derive from bluffs and cliffsides along the Alabama and Tombigee Rivers and their associated tributaries that are centered near Clarke and Monroe Counties (*e.g.*, Leidy, 1856, Woodward, 1891; White, 1956). Outcrops are abundant in this region of southwestern Alabama and are the products of water erosion, downcutting, and the regional drainage network into Mobile Bay. The stratigraphy and paleontology of this area was originally figured and described by Charles Lyell in (1846) while studying the continuity of Eocene formations between Georgia and Alabama.

The correlative properties of fish fauna in tracing contemporaneous strata between Alabama and other states across the Atlantic and Gulf Coastal Plains was first recognized by Leidy (1856) in describing the occurrence of the genus *Cylindracanthus*. Subsequent studies by Woodward (1891); Fowler (1911); Leriche (1942) and Thurmond & Jones (1981) built upon Leidy's earlier interpretations and documented the occurrence of additional genera including: *Sphyraena*, *Arius*, and *Albula* during the Paleocene and Eocene in multiple Atlantic and Gulf coastal plain states. More recent studies extended this distribution even further and many Early and Middle Cenozoic fish from North American have a broad Northern Atlantic Ocean distribution across Greenland, Western Europe and North Africa (*e.g.*, De Beaufort, 1926; White, 1926; Bendix-Almgreen, 1969; Kemp *et al.*, 1990; Murray, 2000; Van den Eeckhaut, pers comm.). This distribution is thought to reflect closer proximity of landmasses, greater uniformity of sea surface temperatures, and continuity of shallow marine shorelines throughout the ancestral Northern Atlantic Ocean Basin (Smith *et al.*, 1994; Scotese *et al.*, 1998; Hooks *et al.*, 1999; Weems, 1999).

In this paper, we describe an unreported middle Eocene (Lutetian) osteichthyan assemblage from a shallow marine lag deposit that separates the Tallahatta and Lisbon Formations along Pigeon Creek, Conecuh-Covington Counties, Alabama (Figure 1). The Pigeon Creek lag assemblage is the product of third order sea level cyclicity and resembles other osteichthyan assemblages reported in contemporaneous strata throughout the Atlantic and Gulf Coastal Plains and elsewhere in the Northern Atlantic Ocean Basin. Accordingly, the Pigeon Creek osteichthyans and associated lag have important implications for biostratigraphic and sequence stratigraphic correlative studies throughout the Northern Atlantic Ocean Basin during the middle Eocene.

Geology of Pigeon Creek, Conecuh-Covington Counties, South-central Alabama

Alabama's Cenozoic formations crop out in a belt running east-west and northwest-southeast through the south central portion of the state (Figure 1). This outcrop belt reflects marine inundation of topographically low-lying areas in the Gulf Coastal Plain during the Late Cretaceous and Cenozoic (Toulmin & La Moreaux, 1963; Ivany, 1998; Manning, 2003; Savrda *et al.*, 2005; 2010). Eocene sediments in Alabama are represented by the upper Wilcox, Claiborne, and Jackson Groups. These groups are divided from oldest to youngest into the Hatchetigbee, Tallahatta and Lisbon, Yazoo Clay, Crystal River and Moody's Branch Formations as well as numerous members, units, and beds (Szabo *et al.*, 1988; Mancini & Tew, 1991; 1994; Ivany, 1998).

Pigeon Creek is a tributary to the Sepulga River that flows southward through Butler, Conecuh, and Covington Counties and between Routes 55 and 84. Water erosion along Pigeon Creek has exposed numerous sections of the upper Tallahatta formation, lower Lisbon Formation, and the contact horizon. In an outcrop along Pigeon Creek, the upper Tallahatta Formation consists primarily of greenish-gray, siliceous, sandy claystone while the lower part of the Lisbon Formation consists of coarse, glauconitic sands with interbedded, silty and glauconitic claystone and abundant *Thalassinoides* burrows (Figure 1). The *Thalassinoides* burrows form an erosion-resistant hardpan that crops out in multiple locations along Pigeon Creek and can be subaerially exposed during times of lower water flow. The Tallahatta and Lisbon Formations are separated by a disconformity and basal lag deposit that varies between 15 and 25 cm thick. The macrofossil lag is a quartz, glauconite sand containing original shell material and steinkerns belonging

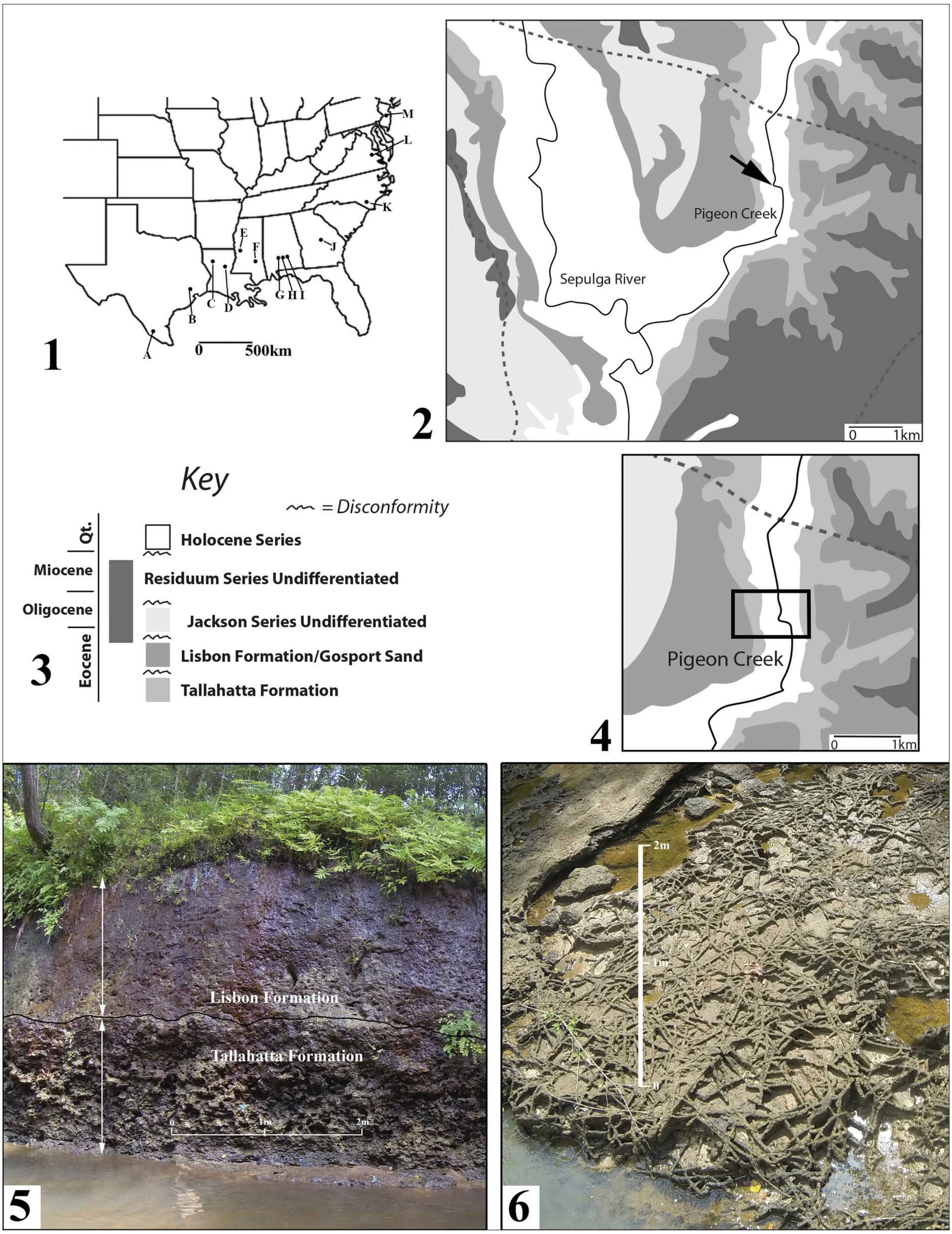

Figure 1. Location maps of the Pigeon Creek field locality and Tallahatta-Lisbon Formation Contact (middle Eocene), Conecuh-Covington Counties, Red Level, Alabama. 1) Distribution of Eocene Gulf and Atlantic Coastal Plain osteichthyan localities discussed in this study: A, eastern Texas (Breard & Stringer, 1999); B, western Texas (Westgate, 1989); C, west central Louisiana (Stringer, 2002); D, east central Louisiana (Breard & Stringer, 1995); E, west central Mississippi (Breard, 1991); F, east central Mississippi (Case, 1994); G, H, I, central Alabama (White, 1956; Clayton *et al.*, 2013; This study); J, central Georgia (Case & Borodin, 2000b); K, Southeastern North Carolina (Case & Borodin, 2000a); L, Virginia, (Weems, 1999); M, New Jersey, (Fowler, 1911); 2 and 3) Stratigraphic column and geologic map of Covington County (southwestern Alabama) study area (modified from Osborne *et al.*, 1989); 4) Detailed geologic map of the Tallahatta-Lisbon Formation contact along Pigeon Creek as seen in Figure 1.5 and discussed in text; 5) Outcrop exposure of the upper Tallahatta and lower Lisbon Formations along Pigeon Creek, Conecuh-Covington Counties, Red Level, Alabama. Note prominent disconformity directly above creek level and 1 meter shovel. Location of the Tallahatta-Lisbon Formation contact; 6) Large scale *Thalassinoides* burrows in exposure of the lower Lisbon Formation along Pigeon Creek.

to oysters, bivalves, gastropods, and invertebrate ichnofossil casts, in addition to bones and teeth from chondrichthyans, osteichthyans, reptiles, and marine mammals.

Multiple sources including: Bandy (1949; planktonic foraminifera); Toulmin (1977; mollusks); Siesser (1983; calcareous nannofossil zonation); Bybell & Gibson (1985; core hole data); Szabo *et al.* (1988; geologic mapping), and Mancini & Tew (1994) and Ivany (1998; sequence stratigraphy) indicated that the age of the upper Tallahatta and lower part of the Lisbon Formations belongs to the lower part of the middle Eocene and Lutetian Stage Boundary.

This is also consistent with the known ages and stratigraphic occurrences of chondrichthyans and osteichthyans recovered from the Pigeon Creek locality and described in this report (Maisch *et al.*, 2015).

Several other localities across western and central Alabama provide additional outcrop exposures of these formations, the contact horizon and vertebrate fossils concentrated within a lag deposit (White, 1956; Holman & Case, 1988; Breard & Stringer, 1999; Westgate, 1989; 2001; Clayton *et al.*, 2013; Maisch *et al.*, 2014). These outcrop exposures extend across 200 kilometers between Silas in Choctaw County along Turkey Creek and Andalusia in Covington County just below the Point A Dam. Currently, little or no evidence of this lag exists in southeastern Alabama where the Tallahatta and Lisbon Formations are thinner, more extensively eroded, and reflect more distal deposition relative to the ancestral shoreline.

Field and Laboratory Methods

Osteichthyan fossils described in this report were recovered over three field seasons directly from the lag separating the upper Tallahatta and lower part of the Lisbon Formations along Pigeon Creek. Areas in Pigeon Creek, immediately adjacent to the Tallahatta–Lisbon Formation contact, were also collected and represent accumulations of fossil fish remains eroded directly out of the lag and hydrodynamically concentrated nearby in deeper pools. These deeper pools were also collected via scuba diving and required float bags to retrieve accumulations of locally eroded lag sediments. Outcrop sediment and creek accumulations were sieved on site with screens ranging from 10.0-5.0 mm.

Approximately 200 kg of sediment was recovered for laboratory sieve analysis. In the lab, sediment was thoroughly washed through progressively finer meshed screens ranging from 5.0 to 0.5 mm and dried under heat lamps. Teeth were removed using a magnifying glass and imaged directly with an Olympus SZ61 Binocular Microscope attached to an Infinity–2 Digital Camera. Osteichthyan remains were identified by comparison with well-known regional and international literature including: Thurmond & Jones, 1981, Weems, 1998; 1999; Westgate, 2001. Reposited osteichthyan remains described in this report were selected from an assemblage of over 500 specimens and are included in the collections of the New Jersey State Museum with the catalogue numbers: NJSMGP 24036-24046.

Systematic Paleontology

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Klein, 1885
Order Pycnodontiformes Berg, 1940
Family Pycnodontidae Agassiz, 1833
Genus *Pycnodus* Agassiz, 1833
Pycnodus sp.

Figure 2: 1-2

Referred Material – One molariform tooth: NJSMGP: 24037

Description – In occlusal view, the tooth is irregularly oval-shaped and displays a large wear facet. In basal view, the tooth exposes a concave pulp cavity and thick enamel.

Discussion – The teeth of *Pycnodus* can be readily distinguished from those of phyllodonts that have more concentric teeth that are stacked in tooth files for continuous replacement during the animal's lifetime (Estes, 1969; Nursall, 1999a; 1999b). The *Albula* teeth in the Pigeon Creek assemblage are more circular, have thinner enameloid, and a shallower pulp cavity than those of *Pycnodus*. Pycnodonts are well adapted for shell-crushing lifestytes and are known from shallow-marine, patch-reef environments, particularly those with abundant molluscs and arthropods (*e.g.*, Estes, 1969; Case & Schwimmer, 1988; Nursall, 1996; Poyato-Ariza & Wenz, 2002).

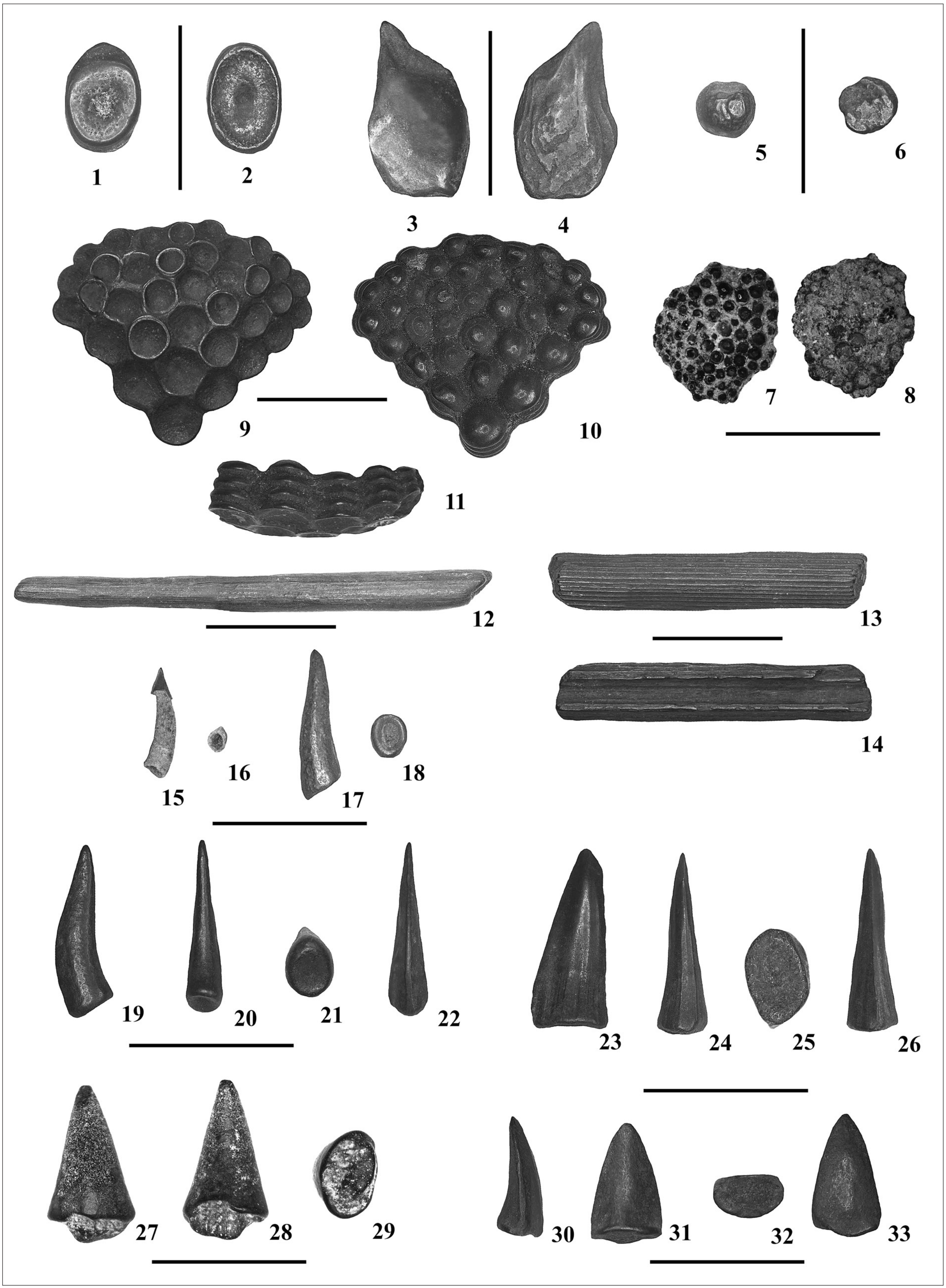

Figure 2. Teeth of osteichthyans from the Tallahatta–Lisbon Formation contact, Pigeon Creek, near Red Level, Conecuh-Covington Counties, Alabama; 1-2) *Pycnodus* sp. (NJSMGP: 24037); 3-4) *Lepisosteus* sp. (NJSMGP: 24038); 5-8) *Albula* sp. (NJSMGP: 24039); 9-11) *Egertonia isodonta* Cocchi, 1864 (NJSMGP: 24040); 12-14) *Cylindracanthus rectus* Agassiz, 1843 (NJSMGP: 24041); 15-18) *Triciurides* cf. *T. sagittidens* Winkler, 1874 (NJSMGP: 24043); 19-26) *Sphyraena* sp. (NJSMGP: 24042); 27-33) *Scomberomorus* sp. (NJSMGP: 24044). Scale bars: 1-2; 5-6; 21-24= 0.5 cm; 3-4; 7-20; 24-32= 1 cm. Orientations: 1, 5, 7, 10 = occlusal view; 2, 6, 8, 9, 16, 18, 21, 25, 29, 32 = basal view; 3, 11, 12, 13, 15, 17, 19, 23, 30 = lateral view; 20; 24, 28; 31 = lingual view; 22, 26, 27; 33 = labial view; 4, 14 = interior view.

Order Lepisosteiformes Hay, 1929
Family Lepisosteidae Cuvier, 1825
Genus *Lepisosteus* Lacépède, 1803
Lepisosteus sp.

Figure 2: 3-4

Referred Material – One ganoid scale: NJSMGP: 24038.

Description – The ganoid scale is complete and smooth on all surfaces. The exterior scale enameloid is thicker near the center and thinner near the edges. These thinned edges facilitate imbrication with adjacent scales. The interior surface is more osseous, has an anterior depression, and lacks thickened enameloid.

Discussion – *Lepisosteus* scales, although infrequently recovered, are a distinct and readily identifiable component of Pigeon Creek osteichthyans assemblage. Ganoid scales, teeth and skeletal elements from the Lepisosteidae are classified as either *Atractosteus* or *Lepisosteus* (*e.g.*, Wiley, 1976; Wiley & Stewart, 1977; Gottfried & Krause, 1998; Weems, 1999; Gayet *et al.*, 2002; Barton, 2007). Scales assigned to *Atractosteus* display distinct enameloid sculpturing on their exterior surfaces, whereas *Lepisosteus* scales are characteristically smooth and unsculptured. Fossils of individual teeth and skeletal elements from the Lepisosteidae are infrequently assigned to higher taxonomic levels (*e.g.*, Case & Schwimmer, 1988; Manning & Dockery, 1992; Rana *et al.*, 2005; Manning, 2006). *Lepisosteus* is predominantly a freshwater and estuarine, piscivorous fish although has been known to occasionally occur in shallow marine environments (Gilbert & Williams, 2002).

Order Elopiformes Sauvage, 1875
Family Albulidae Bleeker, 1859
Genus *Albula* Scopoli, 1777
Albula sp.

Figure 2: 5-8

Referred Material – One isolated tooth cap and fragmentary tooth plate: NJSMGP: 24039

Description – In occlusal view, the isolated tooth cap is roughly circular in outline and contains a thin layer of smooth enamel. The base of the tooth exposes the pulp cavity that is deeply concave, osseous, and has thick edges. The tooth plate has 2-3 stacked tooth caps that are nearly flat on the edges and highly convex in the center when viewed in occlusal view. Some of the tooth caps bear wear facets. The base of the tooth plate exposes the deeply concave pulp cavities of individual tooth caps.

Discussion – This isolated tooth cap and fragmentary tooth plate resembles those belonging to *Albula* sp. from the Eocene of Alabama, Mississippi, South Carolina, and Virginia (Case, 1986; Weems, 1998; 1999; Clayton *et al.*, 2013). The tooth plate from *Albula* sp. from the Pigeon Creek osteichthyan assemblage can be readily distinguished from those belonging to other phyllodonts such as *Paralbula*, *Egertonia*, and *Pycnodus* by its thick tooth edges, higher profile in lateral view, and strongly concave pulp cavity. Teeth of *Albula* sp. may resemble *Fisherichthys folmeri* Weems (1999) from the lower Eocene of the Atlantic and Gulf Coastal Plains however, in lateral and occlusal views, *F. folmeri* teeth are distinctly conical and not cylindrical like *Albula*. Most Eocene *Albula* teeth have been assigned to *Albula owenii* (Casier, 1966). The tooth and tooth plate figured here appear similar to and may in fact belong to *A. owenii*. However, We refrain from species level classification based on two isolated specimens. Weems (1999) indicated that *Albula* teeth are similar to the modern bonefish, *Albula vulpes* (Linnaeus, 1758) known to prey upon marine invertebrates along the sea floor in the tropical shallow marine environments.

Family Phyllodontidae Dartevelle & Casier, 1943
Genus *Egertonia* Cocchi, 1864
Egertonia isodonta Cocchi, 1864

Figure 2: 9-11

Referred Material – One fragmentary tooth plate: NJSMGP: 24040

Description – In occlusal view, the tooth plate contains equidimensional, circular tooth caps that are approximately 1.5 mm in diameter. Some tooth caps display a granular surface while others are smooth. In lateral view, the tooth plate is slightly convex and exposes 3-4 stacked tooth caps on all edges. The base of the tooth plate is slightly concave and partially osseous.

Discussion – The Pigeon Creek *Egertonia isodonta* teeth are associated on a partial tooth plate and appear as thin, regularly stacked circular caps with convex occlusal surfaces and shallow, concave basal surfaces. *Egertonia* appears similar to the phyllodont *Paralbula,* known from the Cretaceous, due to the presence of small, thin, stacked, circular tooth caps. However, the teeth of *Egertonia* can be differentiated from *Paralbula* by the presence of vertically stacked tooth caps containing shallow, concave pulp cavities on the basal tooth surfaces. The teeth of *Pseudoegertonia granulosus* (Arambourg, 1952) are distinct from those of *Egertonia* sp. because they are irregular in shape. Since there are no extant *Egertonia* species, it is inferred based on the dentition that *Egertonia* preyed upon hard shelled invertebrates (Estes, 1969; Weems, 1999).

Order Aulopiformes Rosen, 1973
Family Dercetidae Pictet, 1850
Genus *Cylindracanthus* Leidy, 1856
Cylindracanthus rectus (Agassiz, 1844)

Figure 2: 12-14

Referred Material – Two rostral fragments: NJSMGP: 24041

Description – The rostral fragment is cylindrical and contains equally-spaced longitudinal ridges. In cross section, the rostral fragment is symmetrical and has a cogwheel-like appearance.

Discussion – The Pigeon Creek *Cylindracanthus rectus* remains consist entirely of rostral fragments. Although fragmentary, these remains have a cylindrical shape with a cogwheel-like appearance in cross-section, making them highly diagnostic. Despite an enigmatic taxonomic past, *Cylindracanthus* currently resides within *Acipenser*iformes (Parris *et al.*, 2001; 2007). This assignment is based on the presence of tooth remains associated with rostral fragments and the interpretation that *Cylindracanthus* had a cartilaginous skeleton similar to modern *Acipenser* and *Polyodon* (Parris *et al.*, 2001; 2007). Currently, three species are assigned to *Cylindracanthus* and they include: *C. acus* Cope, 1870 which is an Eocene species displaying more ossification and smaller tooth remains than *C. ornatus* (Kemp *et al.*, 1990); and *C. rectus* which is another Eocene species that lacks the bilateral symmetry seen in *C. ornatus* (Arambourg, 1952; Kemp *et al.*, 1990). *Cylindracanthus rectus* likely had a durophagous to piscivorous feeding behavior (Fallaw, 1964; Weems, 1999; Parris *et al.*, 2001; 2007)

Order Perciformes Günther, 1880
Family Sphyraenidae Bonaparte, 1831
Genus *Sphyraena* Bloch & Schneider, 1801
Sphyraena sp.

Figure 2: 19-26

Referred Material – Two teeth: NJSMGP: 24042.

Description – The teeth are laterally compressed with a slightly recurved tip that may contain a small post-apical barb. The anterior tooth edge is convex while the posterior edge is nearly vertical to slightly concave. Lateral tooth surfaces may contain faint longitudinal ridges. The teeth broaden near the base which is ovular in cross-section.

Discussion – Teeth of *Sphyraena* sp. bear some resemblance to the teeth of Scomberomorus and *Trichiurides* sp. which also occur in the Pigeon Creek osteichthyan assemblage. However, the teeth of *Sphyraena* sp. are unique and are laterally compressed with an ovular tooth base. These features are markedly different from those of *Scomberomorus* sp. which has shorter, recurved, and broad teeth and *Trichiurides* sp. which has teeth that are more slender, recurved, and circular near the tooth base in comparison to *Sphyraena* sp. (Weems, 1999). Although longitudinal ridges or striations present on the lateral tooth edges of *Sphyraena* sp. have been utilized to distinguish between species (*i.e. Sphyraena striata* Casier, 1946), the Pigeon Creek teeth display the same overall tooth morphology regardless of the presence of longitudinal grooves. Due to the variable dental morphology exhibited in modern *Sphyraena* sp., we refrain from species level classification of the isolated Pigeon Creek *Sphyraena* teeth (Nishimoto & Ohe, 1982; Santini *et al.*, 2015). Species of extant *Sphyraena* are known to be piscivorous and commonly occur in schools in coral reef and shallow marine environments (Weems, 1999; Purdy *et al.*, 2001; Gilbert & Williams, 2002).

Family Trichiuridae Rafinesque, 1810
Genus Trichiurides Winkler, 1874
Trichiurides cf. *T. sagittidens* Winkler, 1874

Figure 2: 15-18

Referred Material – Two teeth: NJSMGP: 24043.

Description – The teeth are gracile, elongated, and recurved posteriorly. A small barb may be present on the lingual tooth edge at the tooth apex. The teeth are laterally compressed although become broader near the base and are teardrop to circular in cross-section.

Discussion – The teeth of *Trichiurides* cf. *T. sagittidens* from the Pigeon Creek osteichthyan assemblage may appear similar to those belonging to *Sphyraena* sp.. Although both species exhibit a laterally compressed tooth morphology, those belonging to *Trichiurides* cf. *T. sagittidens* are much more gracile, bear a needlelike-barbed tooth apex, and have a slightly concave, teardrop-circular tooth base (Weems, 1999). As indicated by Weems (1999), there are no conclusive grounds to assign teeth identified as *Trichiurides* cf. *T. sagittidens* to variation in tooth position of other similar species including *Eutrichiurides winkleri* Casier, 1946 or *Trichiurus gulincki* Casier, 1967. Teeth assigned to *Trichiurides* were originally described from the Eocene of Belgium by Winkler (1874); Leriche (1905) and Casier (1946) and compare favorably to those from the Eocene of Pigeon Creek, AL. It is inferred that *Trichiurides* cf. *T. sagittidens* resembled modern cutlassfish such as *Trichiurus lepturus* (Linnaeus, 1758) which are piscivorous and inhabit estuarine to shallow and deep marine regions with mud-rich sediment (Weems, 1999; Gilbert & Williams, 2002).

Family Scombridae
Genus *Scomberomorus* Lacepède, 1801
Scomberomorus sp.

Figure 2: 27-33

Referred Material – Two teeth: NJSMGP: 24044.

Description – The teeth are short in height, recurved posteriorly, and increase in thickness towards the tooth base that is ovular in shape. The lingual surfaces are more convex than the labial surfaces.

Discussion – Teeth of *Scomberomorus* sp. are similar to those of the Pigeon Creek *Sphyraena* sp. and *Trichiurides* cf. *T. sagittidens* described above. However, *Scomberomorus* teeth are broader, shorter, and more convex on the lingual tooth surface than teeth from *Sphyraena* and *Trichiurides* sp.. Eocene teeth of *Acanthocybium proosti* Storms, 1897 are shorter and more triangular in shape and teeth of *Scomberomorus bleekeri* Storms, 1892 are more erect and display less lingual curvature that those of the Pigeon Creek *Scomberomorus* sp.. As with the the *Sphyraena* sp. found in Pigeon Creek, we refrain from species level classification due to the variable dental morphology exhibited in modern *Scomberomorus* sp., and lack of articulated fossil specimens from Pigeon Creek. Extant *Scomberomorus* sp. such as the Spanish mackerel, *Scomberomorus maculatus* (Mitchell, 1815), is known to school in shallow marine and open ocean areas and are piscivorous; feeding on schooling bait fish (Gilbert & Williams, 2002).

Order Siluriformes Cuvier, 1817
Family Ariidae Günther, 1864
Ariidae gen. indet.

Figure 3: 1-4

Referred Material – Two fragmentary fin spines: NJSMGP: 24045.

Description – The side of the fin spines contain irregular, longitudinal grooves. The anterior spine edges are smooth, and the posterior spine edges contain numerous triangular barbs.

Discussion – The occurrence of Ariidae in the Pigeon Creek osteichthyan assemblage is known only from fragmentary fin spines. However, the Pigeon Creek Ariidae fin spines can be distinguished from those of *Bagre* due to the lack of triangular barbs or serrations on the anterior spine edges (Weems, 1999). Extant Ariidae including the Hardhead Catfish, Ariopsis felis (Linnaeus, 1766) and the Gaftopsail Catfish, *Bagre marinus* (Mitchell, 1815), are known to inhabit shallow coastal waters and have durophagous to piscivorous feeding behaviors (Wheeler, 1975; Weems, 1999; Gilbert & Williams, 2002).

Family *Ostraciidae* (Tyler, 1980)
Ostraciidae gen. indet.

Figure 3: 5-6

Referred Material – One dermal ossicle: NJSMGP: 24046.

Description – The dermal ossicle has a polygonal shape, is smooth on the internal surface and is ornamented with round, scattered papillae on the external surface. Papillae are slightly larger near the center and decrease in size towards the edge of the ossicle.

Discussion – Dermal ossicles resembling the Pigeon Creek specimen have been attributed to various species of boxfish (Weems, 1999). Boxfish have been divided into two families that are the Aracanidae (Hollard, 1860) and *Ostraciidae* (Tyler, 1980). These families have distinct dermal ossicle morphology; the Aracanidae have a large, central papilla with six radiating rows of large papillae with smaller papillae in between, whereas the *Ostraciidae* lack radiating rows and papillae are not organized into distinct patterns (Weems, 1999). We assign the Pigeon Creek specimens to the *Ostraciidae* due to the presence of a large, centrally located papilla and lack of distinct, radiating rows of papillae. Although, due to the variation in dermal ossicle patterns within the *Ostraciidae* depending on location on the body and with age, we refrain from higher level classification (Winterbottom & Tyler, 1983; Tyler & Gregorova, 1991; Weems, 1999). Extant *Ostraciidae* such as the Honeycomb Cowfish, *Acanthostracion polygonius* (Poey, 1876), are known to inhabit shallow marine environments and exhibit a durophagous feeding behavior (Weems, 1999; Gilbert & Williams, 2002).

Order Beryciformes Regan, 1909
Cf. Beryciformes

Figure 3: 7-10

Referred Material – One fin spine: NJSMGP: 24036

Description – The fin spine is posteriorly curved, saber-like in shape, and tapers to a distal sharp tip. Along the length of the spine shaft, there is a prominent and deep posterior sulcus extending nearly the entire length of the spine. The spine has smooth anterior, posterior, and lateral edges, but it also has a well-defined non-dentate ridge extending along the anterior midplane of the spine shaft. Towards the base, the spine shaft thickens and forms a complex box-like structure for moveable articulation of the spine with the underlying pterygiophores. The attachment structure consists of a pair of lateral processes, oriented antero-posteriorly and surrounding a tubular lumen. Flooring the lumen is a solid basal bar that is centrally thickened.

Discussion – The spine shaft and articulation structure at the base of the spine, especially the solid basal bar, resembles those found in modern beryciform fish, particularly of the Holocentridae (*e.g.*, Johnson & Patterson, 1993; Becker *et al.*, 2009). The spine is also nearly bilaterally symmetrical, but is modified by a distinct heterocanthy, as is typical among beryciform fin spines. However, due to the variation in beryciform fin spine morphology and lack of articulated specimens from the Pigeon Creek locality, we tentatively assign this spine to Beryciformes and refrain from lower level classification.

Discussion

Composition and Paleoecology of the Pigeon Creek Fish Assemblage

Osteichthyans found within the Pigeon Creek assemblage include species with piscivorous, and durophagous, shell crushing and nibbling tooth morphologies such as *Sphyraena*, *Egertonia*, and *Ostraciidae* gen. indet. Both fossil and modern osteichthyans from these species are known to inhabit shallow marine, coastal environments and nearshore or beach facies communities (Gilbert &Williams, 2002; Helfman *et al.*, 2009). This interpretation is also consistent with the abundant *Thalassinoides* burrows and shell horizons comprised of oysters, gastropods, and pelecypods found throughout the upper Tallahatta and Lower Lisbon Formations (Ivany, 1998; Savrda *et al.*, 2010).

Some additional shoreline and shallow marine environments identified throughout the Gulf Coastal Plain during the middle Eocene that would have provided habitat for the Pigeon Creek osteichthyans included mangrove palm swamps, bays, and lagoons separated by offshore marine sandbar complexes, patch reefs, and tidal channels (Westgate, 1984; 1989; Breard, 1991; Gunnell, 2001). It is noteworthy

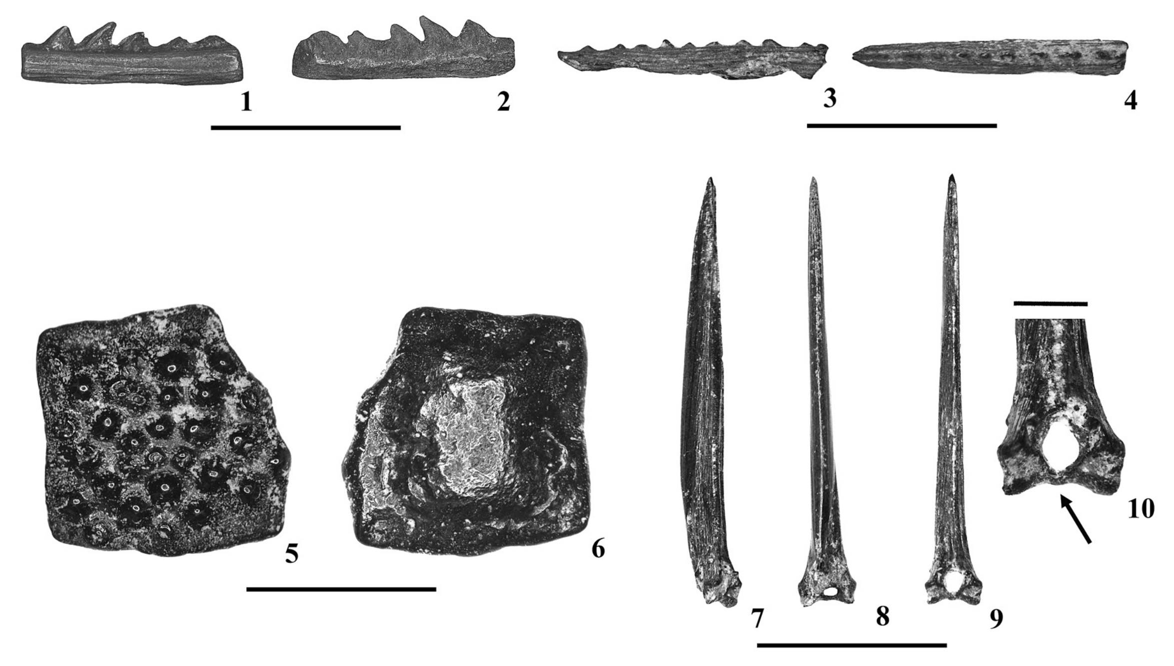

Figure 3. Indeterminate osteichthyan remains from the Tallahatta–Lisbon Formation contact, Pigeon Creek, near Red Level, Conecuh-Covington Counties, Alabama; 1-4) Ariidae gen. indet. (NJSMGP: 24045); 5-6) *Ostraciidae* gen. indet. Dermal ossicle (NJSMGP: 24046); 7-10) Cf. Beryciformes fin spine (NJSMGP: 24036). Scale bars for 1-9 = 1 cm; 10 = 1 mm. Orientations: 1, 2, 3, 5, 7 = lateral view; 4 = dorsal view; 8 = anterior view; 9-10 = posterior view. Arrow denotes the lumen and solid basal bar on the fin spine.

that most of the osteichthyan genera identified in these studies also occur in the Pigeon Creek osteichthyan assemblage. The Pigeon Creek osteichthyans inhabited an environment largely devoid of coral reefs, which are known to diversify throughout the late Eocene and Oligocene in the southeastern United States and Caribbean (Budd, 2000). Development of coral reefs on a global scale across this boundary is thought to account for the great radiation and diversification of reef fishes during the middle Cenozoic (Budd, 2000; Goatley *et al.*, 2010; Cowman & Bellwood, 2011).

The presence of certain osteichthyan and chondrichthyan species found in Alabama and Mississippi during the middle and late Eocene has been used to indicate the nearby proximity of a deeper marine, open ocean environment (Manning, 2003; Fierstine & Starnes, 2005; Maisch *et al.*, 2014). Two of the species identified in these studies, *Cylindracanthus rectus* (Agassiz, 1844) and *Carcharocles auriculatus* (Blainville, 1818), are known from the contact horizon of the upper Tallahatta and Lower Lisbon Formations along Pigeon Creek and throughout south-central and southwestern Alabama (Clayton *et al.*, 2013; Ehrert & Ebersole, 2014; Maisch *et al.*, 2014; 2015). The occurrence of teeth from ancestral mackerels and barracudas, *Scomberomorus* and *Sphyraena*, respectively, in the Pigeon Creek osteichthyan assemblage also supports the nearby proximity of a deeper marine, open ocean environment. Both modern and fossil *Scomberomorus* and *Sphyraena* are known to have streamlined-bodied, piscivorous dentitions, partial pelagic life mode, and global distribution (Weems, 1999; Gilbert & Williams, 2002; Daly-Engel *et al.*, 2012).

Taphonomy of the Pigeon Creek Assemblage

Along Pigeon Creek, the osteichthyan lag deposit occurs between the upper Tallahatta and lower Lisbon Formations at various meander bends between the towns of Red Level and Brooklyn, Alabama, and the confluence of Pigeon Creek with the Sepulga River. While both formations have distinct lithological characteristics, the contact horizon between these two formations along Pigeon Creek can be best recognized in outcrop by the prominent *Thalassinoides* burrow horizon that forms an erosion-resistant hardpan of the lower Lisbon Formation. This hardpan channelizes water along straight sections of the creek and creates many of the deeper pools and waterfalls along meander bends.

Numerous studies throughout the Gulf Coastal Plain indicate that the observed differences between lithologies such as the upper Tallahatta and lower Lisbon Formations are bathymetrically controlled and indicative of climatically driven, eustatic sea level fluctuation (Van Wagoner *et al.*, 1988; Cattaneo & Steel, 2003; Manning, 2006; Rogers *et al.*, 2007). In Alabama and Mississippi, Mancini and Tew (1994) placed the contact between the Tallahatta and Lisbon Formations at the sequence boundary within second-order supercycle TA3 and between third-order cycle 3.1 and 3.2 of Haq *et al.* (1988). Because the Pigeon Creek osteichthyan lag deposit resides directly above a disconformity between upper Tallahatta and lower Lisbon Formations, we interpret this lag deposit to represents a transgressive surface of locally eroded and redeposited fossils during these third order sea level events. Other studies have identified this same lag deposit near the Point A Dam along the Coneuch River in Andalusia and Turkey Creek in Silas, Alabama (Clayton *et al.*, 2013; Maisch *et al.*, 2014). The regional occurrence of the Pigeon Creek lag across 200 kilometers of the Alabama Coastal Plain reinforces the role of sea level cyclicity in lag deposit formation.

The fossil osteichthyans from Pigeon Creek are in various states of preservation and also lend support to the role of sea level cyclicity in lag deposit formation. Many of the osteichthyan teeth collected directly from the lag deposit display abraded cusps and roots along with cutting edges that are reduced and rounded. However, some teeth display delicate tooth structures and sharp cutting edges on main cusps. We interpret these differences to reflect varying degrees of reworking where some remains have been exposed to physical erosion for prolonged periods (Rogers *et al.*, 2007; Becker & Chamberlain, 2012; Boessenecker *et al.*, 2014). Teeth eroded from the lag and recovered immediately adjacent to the Tallahatta–Lisbon Formation contact and within Quaternary gravels of Pigeon Creek typically display an even greater degree of physical erosion. Chondrichthyan teeth co-occurring with osteichthyan teeth in the Pigeon Creek lag as well as those eroded and deposited directly adjacent to the lag in creek gravels exhibit similar taphonomic wear patterns.

Correlative Properties and Transatlantic Occurrence of Fossil Fish Lags

Over the past half a century, multiple invertebrate fossils have been utilized to correlate shallow marine formations across the Atlantic and Gulf Coastal Plains. Some examples of these include: oysters, planktonic foraminifera, calcareous nannofossils, mega-invertebrates, and trace fossils (Stephenson *et al.*, 1942; Loeblich & Tappan, 1957; Hosman, 1960; Powell & Baum, 1982; Siesser, 1984; Worsley & Werle 1984; Bybell & Gibson 1985; Jiang, 1997; Harris *et al.*, 1984; Ivany, 1998; Savrda *et al.*, 2010). Studies of these invertebrate fossils also include trans-Atlantic correlations of taxa and from equivalent aged formations (Loeblich & Tappan, 1957; Palmer, 1979; Dockery, 1984; Dockery & Lozouet, 2003). Recently, this list of fossils has also identified the correlative potential of vertebrates and in particular, osteichthyans and chondrichthyans (Bendix-Almgreen, 1969; Weems, 1999; Cappetta, 2012). Both osteichthyans and chondrichthyans have well-documented fossil records from all states within the Atlantic and Gulf Coastal Plains since the Late Cretaceous (Westgate, 1989; Breard, 1991; Kent, 1994; Weems, 1999; Cappetta, 2012; Maisch *et al.*, 2014). Fossil teeth, in particular, from both osteichthyans and chondrichthyans are abundant in shallow marine sediments and have biostratigraphic ranges that can provide stage boundary resolution (Cappetta, 2012).

The middle Eocene (Lutetian) Pigeon Creek osteichthyan genera are all found across the Atlantic and Gulf Coastal Plains, Greenland, Western Europe, and Western Africa (Figures 1; 4). With the exception of Greenland that has *Arius* sp. fin spines, genera in the Pigeon Creek assemblage occur across the shallow marine shelves that fringe each of these continents (Figure 4; White, 1926; 1956; Kemp *et al.*, 1990; Weems, 1999; Case & Borodin, 2000; Van den Eeckhaut (pers comm.); Murray, 2000; Gonzalez-Rodriguez *et al.*, 2013). Such broad scale correlation of osteichthyan genera at regional, continental, and intercontinental scales attests to an ancestral Northern Atlantic Ocean Basin with greater uniformity of sea surface temperatures and continuity of shallow marine shoreline habitat relative to the modern Northern Atlantic Ocean (Haq *et al.*, 1988; Lear *et al.*, 2004; Miller *et al.*, 2008; Liu *et al.*, 2009; Norris *et al.*, 2013). These

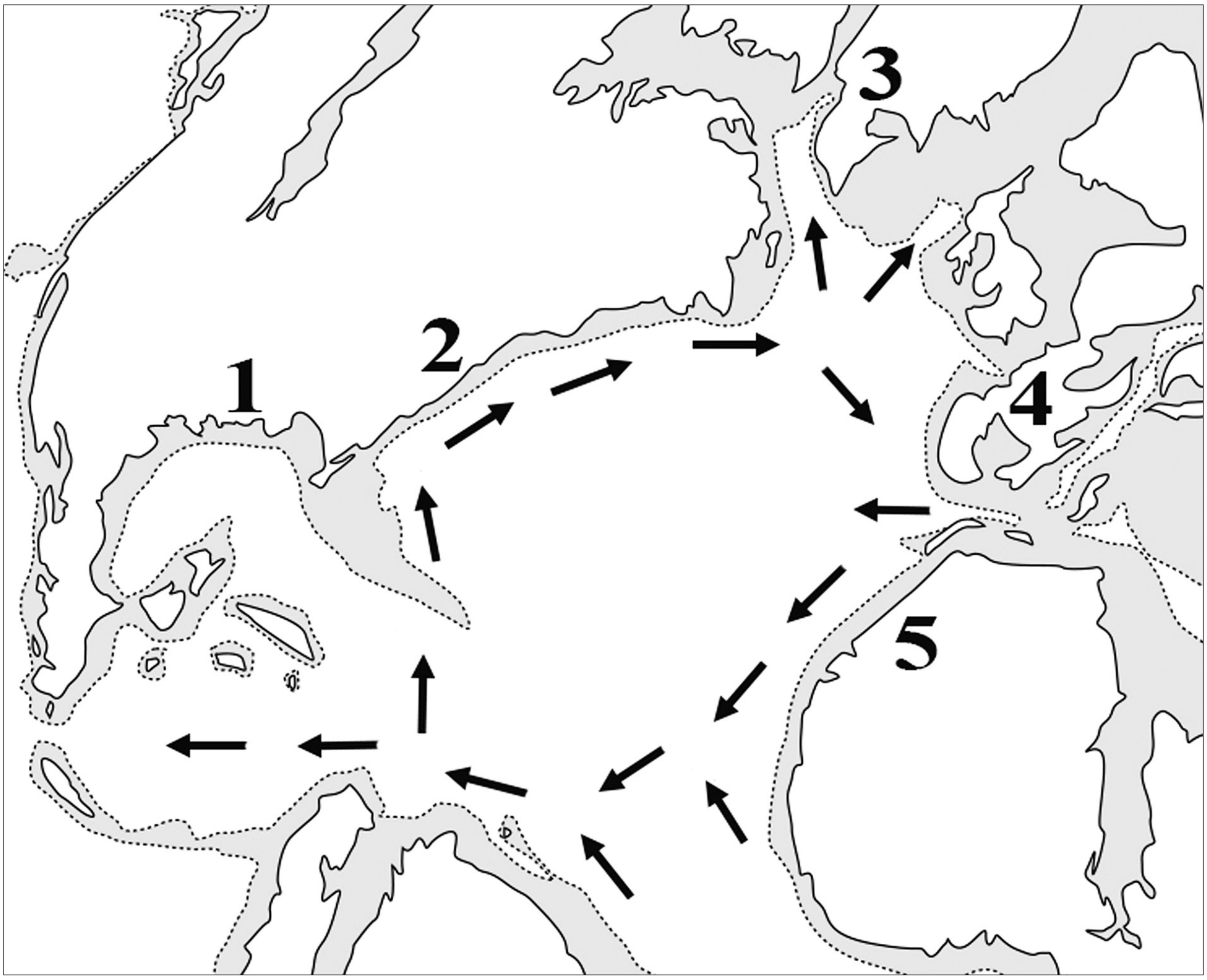

Figure 4. Paleogeography of the middle Eocene Northern Atlantic Ocean Basin documenting ocean circulation and continuity of shallow marine shorelines between the Gulf and Atlantic Coastal Plains (1-2); Greenland (3); Western Europe (4); and, Western Africa (5). For osteichthyan occurrence data referring to: GCP: White, 1956; Case, 1984; 1986; Westgate, 1984; 1989; Breard, 1991; Breard & Stringer, 1995; 1999; Clayton *et al.*, 2013; Pigeon Creek (this study); ACP: Fowler, 1911; Rapp, 1946; Weems, 1998; 1999; Case & Borodin, 2000a,b; Greenland: Bendix-Almgreen, 1969; Western Europe: Kemp *et al.*, 1990; Van den Eeckhaut, pers. comm.; Western Africa: White, 1926; 1935; Arambourg, 1952; Longbottom, 1984; Murray, 2000; Adnet *et al.*, 2010; and Mexico: González-Rodriguez *et al.*, 2013). Paleogeography and paleocurrent maps redrawn from: Berggren & Hollister, 1974; Barron & Peterson, 1991; Scotese *et al.* 1998; Blakey, 2011; and Scotese, 2014.

observations also suggest that the Pigeon Creek osteichthyans were highly mobile, nektonic predators and scavengers that had broad geographic ranges where migration and dispersal reflects ancestral ocean circulation (Figure 4). In the modern Northern Atlantic Ocean, physical barriers known to restrict migration and distribution of osteichthyans include sea surface temperatures, major ocean currents, and bathymetry (*e.g.*, Hooks *et al.*, 1999; Weems, 1999; Murray, 2000).

We hypothesize, based on modern analogy, that genera found in the Pigeon Creek osteichthyan assemblage would have been dispersed based on ocean circulation traveling clockwise within the Northern Atlantic Ocean Basin along the shallow shelf and between major landmasses (*e.g.*, Moyer, 1984; Gilbert and Williams, 2002; Thurman and Trujillo, 2004; Leis *et al.*, 2013; Simpson *et al.*, 2013). This pathway would have provided limited open ocean exposure during eastward travel between North America, Greenland, western Europe and northwestern Africa. Tethyan currents from the eastern side of the Northern Atlantic would have provided a westward pathway towards North America and the Caribbean Sea.

To date, few reports document the occurrence of Paleocene and Eocene osteichthyans reported from the Caribbean, eastern South America, and eastern Mexico (*e.g.*, Iturralde-Vinent *et al.*, 1996; Ferrusquia-Villafranca *et al.*, 1999; 2000; Gonzalez-Rodriguez *et al.*, 2013). However, there have been numerous reports on

Oligocene, Miocene, Pliocene, and Pleistocene osteichthyans and chondrichthyans and from these same regions (*e.g.*, Applegate, 1978; 1986; Gillette, 1984; Longbottom, 1979; Purdy *et al.*, 1996; Sanchez-Villagra *et al.*, 2000; Aguilera & De Aguilera, 2001; 2004; Nieves-Rivera *et al.*, 2003; Underwood & Mitchell, 2004; Fernandes dos Reis, 2005; Ferreira-Costa *et al.*, 2009; Pimiento *et al.*, 2010; 2013a; 2013b; Carnevale *et al.*, 2011; Underwood & Gunter, 2012; Gonzalez-Rodriguez *et al.*, 2013; Laurito *et al.*, 2014; Carrillo-Briceño *et al.*, 2015). While the occurrence of Paleogene osteichthyans throughout the Americas in shallow marine sediments represents opportunity for future study, the general absence of shallow marine shelf between western Africa and Eastern South America as well as counter currents in the southern portion of the ancestral Northern Atlantic Ocean gyre may have represented a substantial barrier to migration and dispersal of some osteichthyans during the Paleogene. Additional opportunity exists to document Paleogene osteichthyans from these regions and interpret the dispersal patterns of these fish throughout the ancestral Northern Atlantic Ocean. Future reports on Paleogene osteichthyans will not only continue to improve their taxonomy, but also the utility of osteichthyans remains in chronostratigraphic analyses.

Acknowledgments

The authors would like to thank E. Lowe, D. Pagano, and R. Scimeca for their assistance with field work and fossil collection. We thank R. Pellegrini and D. Parris, New Jersey State Museum (NJSM), for providing assistance with specimen repository. We thank B. Beatty and two anonymous reviewers that improved an earlier version of this manuscript. This research was supported in part by Assigned Release Time and Center for Research grants from William Paterson University to MAB.

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Submitted: 26 December 2015
Published: 9 May 2016

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