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OSTEICHTHYANS FROM THE PALEOCENE CLAYTON LIMESTONE OF THE MIDWAY GROUP, HOT SPRING COUNTY, ARKANSAS, USA: BONY FISH EVOLUTION ACROSS THE CRETACEOUS–PALEOGENE BOUNDARY

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ABSTRACT

The Clayton Limestone of the (Paleocene) Midway Group in southwestern Arkansas preserves one of the oldest osteichthyan Cenozoic assemblages yet reported from the Gulf Coastal Plain of the United States. The fauna consists of pycnodont, albulid and phyllodont taxa including: *Pycnodus* sp.; *Albula oweni* (Owen, 1845); *Paralbula marylandica* Blake, 1940; and cf. *Phyllodus toliapicus* Agassiz, 1843. Also present are osteichthyan vertebral centra and fin spines of indeterminate origin. The Clayton Limestone osteichthyan assemblage is of limited generic diversity and is dominated by genera with shell-crushing dentitions. Exposures of the Clayton Limestone occur geographically near to, and stratigraphically directly above, a site exposing an assemblage of Maastrichtian osteichthyans from the upper Arkadelphia Formation marl. Comparison of the two local assemblages suggests that the end-Cretaceous mass extinction event may have significantly reduced post-impact osteichthyan diversity in Arkansas, particularly those forms with piscivorous dentitions.

INTRODUCTION

Late Cretaceous osteichthyan localities in North America are numerous and are known from every state and province inundated during the Late Cretaceous shallow marine sea level maximum (e.g., Estes, 1964; Bardack, 1968; Case and Schwimmer, 1988; Hartstein et al., 1999; Hoganson and Murphy, 2002; Robb, 2004; Parris et al., 2007). The largest assemblage of Late Cretaceous osteichthyans is known from Kansas where Shimada and Fielitz (2006) reported a total of fifty-four species from the Smoky Hill Chalk. Other Late Cretaceous North American localities preserve many of these same taxa (e.g., Fowler, 1911; Thurmond and Jones, 1981; Gallagher, 1993; Russell, 1993) including pelagic and benthic piscivores and shell-crushers such as *Enchodus*, *Xiphactinus*, *Anomoedus*, and *Palaeobalistum*.

In contrast to the abundant and diverse of shallow-marine osteichthyans found in the Late Cretaceous, only a few localities in North America preserve shallow-marine osteichthyans from the Paleocene. A comparative survey by Weems (1998) documented only ten states out of twenty-five across the Atlantic and Gulf Coastal Plains as well as the Western Interior Seaway that preserved a record of Paleocene and early Eocene osteichthyans. He also noted in this same study, that Paleocene taxa consisted primarily of shallow-marine forms with robust crushing teeth and tooth plates. To date, few Paleocene osteichthyans have been documented from the Gulf Coast Plain of the United States. The oldest Cenozoic osteichthyans reported are from the late Paleocene-Early Eocene Tuscahoma and Bashi Formations of Mississippi (Case, 1986; 1994). This paucity of Paleocene osteichthyans is noteworthy considering: 1) a prominent shallow-marine shoreline extended throughout this region during the Paleocene (Kennedy et al., 1998; Smith et al., 1994); 2) abundant osteichthyans occur throughout the entire Gulf Coastal Plain during the Late Cretaceous (e.g., Thurmond and Jones, 1981; Case and Schwimmer 1988; Manning and Dockery, 1992; Becker et al., 2010a); and 3) prominent Late Cretaceous osteichthyans such as *Enchodus* sp. are known to survive the K-Pg mass extinction (Parris et al. 2007).

In this paper, we describe an assemblage of Paleocene osteichthyans recovered from the Clayton Limestone of the Midway Group in Hot Spring County, Arkansas. The fauna is unique in that it documents the

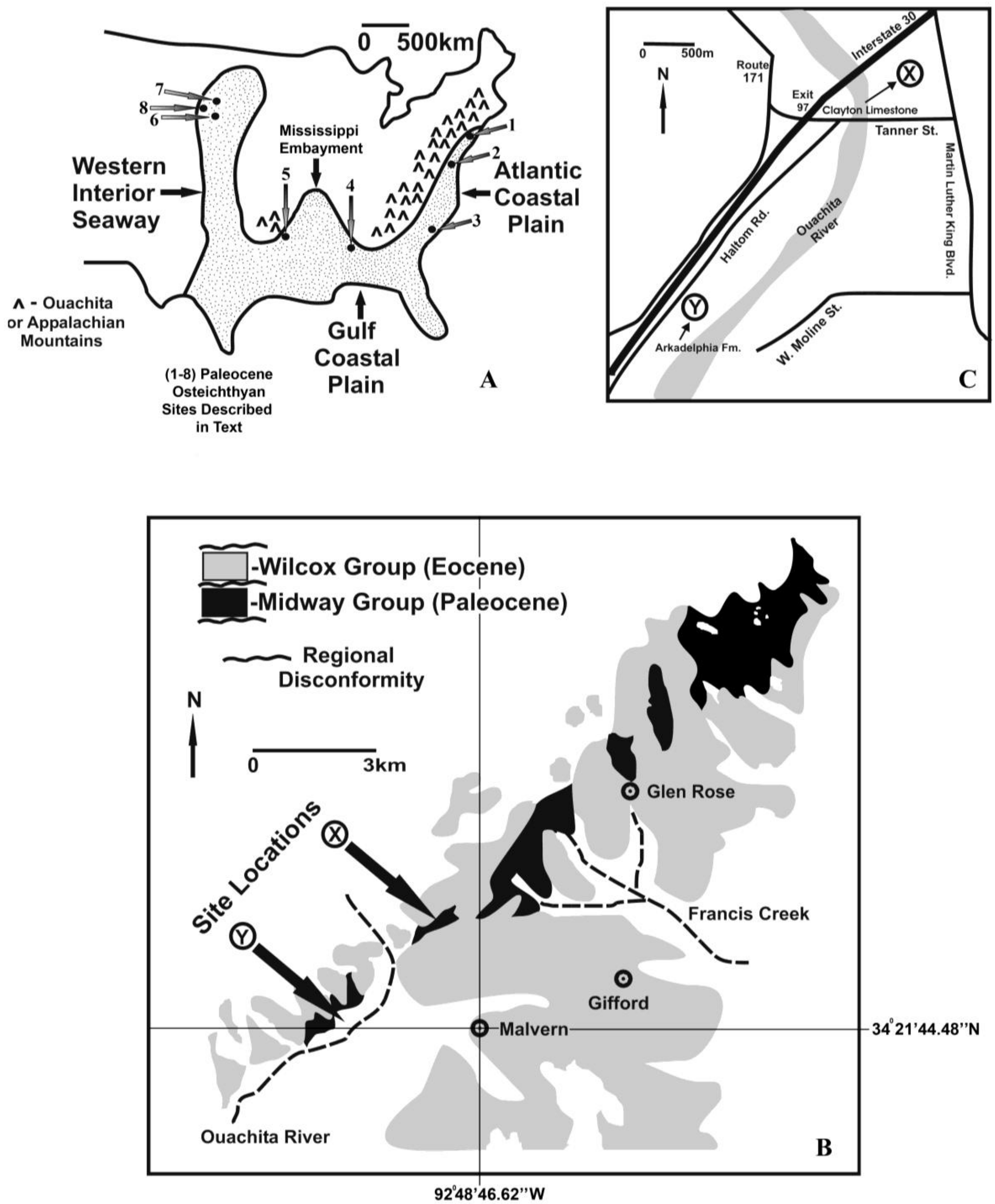

FIGURE 1. Location maps of the Clayton Limestone (Paleocene) of the Midway Group and the Arkadelphia Formation (Maastrichtian), Hot Spring County, Arkansas. A, late Maastrichtian-early Paleocene paleogeographic reconstruction of the Atlantic and Gulf Coastal plains and Western Interior Seaway (redrawn from Kennedy et al., 1998; Smith et al., 1994). Dots indicate the location of Paleocene osteichthyan sites discussed in this study: 1, New Jersey, (Fowler, 1911; Estes, 1969); 2, Maryland and Virginia, (Estes, 1969; Weems, 1999); 3, South Carolina, (Weems, 1998); 4, Mississippi, (Case, 1986); 5, Arkansas, (this study); 6–7, North and South Dakota (Cvancara and Hoganson, 1993), 8–Montana, (Estes, 1969). B, Geologic map of Midway and Wilcox Groups (Paleogene) in the southwestern Arkansas study area (modified from Haley et al., 1993). Location of Clayton Limestone chondrichthyan site (this study) indicated by (X) and Arkadelphia Formation site of Becker et al. (2006; 2010a) indicated by (Y). C, Detailed locator map of Clayton Limestone (X) and Arkadelphia Formation (Y) osteichthyan sites discussed in this study. Global Positioning System coordinates for our two collecting localities can be obtained from the authors and is included in the repository information for each of our specimens now in the collections of the Academy of Natural Sciences of Philadelphia.

oldest Cenozoic osteichthyan assemblages currently reported from the Gulf Coastal Plain of the United States. It also occurs in close proximity to, and stratigraphically directly-above, a rich and diverse assemblage of Maastrichtian osteichthyans found in the Arkadelphia Formation–Midway Group contact originally reported by Becker et al. (2010a). Comparison of the two assemblages provides a unique opportunity to locally assess the effects of the K-Pg mass extinction on osteichthyans within this region. In addition to the overall reduction in osteichthyan diversity, it is striking that all teeth recovered from the Clayton Limestone consist entirely of shell-crushing forms.

GEOLOGIC SETTING

The osteichthyans described in this report were recovered approximately 3 km northwest of Malvern, Hot Spring County, Arkansas (Figure 1). This site was originally reported by Becker et al. (2010b) and found to contain at least ten species of chondrichthyans. The locality lies on the southwestern side of the Mississippi embayment (Figure1) in an area that includes of erosional islands of nearly flat-lying Late Cretaceous and Lower Tertiary marine sediments bordered to the west and also underlain by folded Paleozoic rocks. Our site lies about 3 km northeast of a small, isolated exposure of the Late Cretaceous Arkadelphia Formation; it is exposed in the bed of the Ouachita River, and we extracted from it Late Cretaceous chondrichthyans (Becker et al., 2006), and osteichthyans (Becker et al., 2010a).

The units described in this report are exposed as a narrow, elongate belt defining the western margin of the Mississippi embayment (Figure 1). This band of sediments continues northeastward into Missouri, and Illinois, and then recurves southeastward through western Kentucky, Tennessee, Mississippi, and Alabama to form the eastern edge of the Mississippi Embayment. Our focus in this paper is on the Paleocene Midway Group.

Although the Midway Group in Arkansas has not been formally divided into formations, recent work by McFarland (1998) indicates the presence of two distinct and recognizable Midway Group units: the Clayton Limestone and the overlying Porters Creek Clay. These names are employed here. In Arkansas the Clayton Limestone consists primarily of highly fossiliferous, light-colored limestone separated by thin beds of clay and sand. In Arkansas the Porters Creek Clay consists of highly expansive, dark-colored calcareous clay with few fossils. Near Malvern, the Porters Creek Clay occurs only intermittently (McFarland, 1998); at some localities it is missing altogether. Where the Porters Clay is absent, the light brown sands and limonite-stained quartz gravel beds of the Wilcox Group lie disconformably above the top of the Clayton Limestone and form erosion-resistant bluffs (McFarland, 1998).

The Paleocene fossils described here were collected from outcrops along both sides of an access road to a commercial shopping facility located near Malvern. Figures 1 and 2 show this site. The lower part of the exposure is composed of thin (10-20 cm-thick), beds of hard limestone separated from one another by fine grained sands and clays. We identify this unit as the Clayton Limestone based on the location of our site on the Arkansas geologic map of Haley et al. (1993). This interpretation is reinforced by: 1) the occurrence of chondrichthyan teeth at this locality known only from the Paleocene–Eocene of North America (Becker et al., 2010b, Becker et al. 2011); 2) foraminifera, palynology and ostracod stratigraphy for this locality has been compiled by Cushman (1949), Jones (1962), and Pitakpaivan and Hazel (1994); and, 3) the general limestone and marl lithology found at this site is consistent with that of the Clayton Limestone in this region. We collected our material from both the limestones and the interbedded clastic horizons in this lower unit. Above this limestone unit, and clearly disconformable with it, are sands and gravels of the Wilcox Group (undifferentiated). Additional discussion of the regional lithology, stratigraphy and paleontology can be found in Becker et al. (2011).

Our site lies in an area in which the Porters Creek Clay is missing above the Clayton Limestone and in which the contact of the Clayton Limestone with the overlying Eocene Wilcox Group is obviously erosional. The contact of the Clayton Limestone with the underlying Late Cretaceous Arkadelphia Formation is not visible at the collection site. We thus cannot be certain exactly how much of the Clayton Limestone, and therefore the time that it represents, is missing in our exposure at its top and at its bottom. However, McFarland (1998) indicates that the Clayton Limestone Unit has a thickness of no more than 6 m in Arkansas. Our site has at least 4 m of Clayton Limestone exposed, so that implies that at most we are missing about 2 m of the available record. Thus, our fossils were collected in beds lying within a few meters of the Maastrichtian Arkadelphia Formation and thus within a few meters of the K-Pg boundary in this part of Arkansas. Some of our material could actually be as close as a few decimeters above the K-Pg boundary. This suggests to us that the age of our osteichthyans is most probably lower to middle Danian. This makes them the oldest Cenozoic osteichthyans found to date in the Gulf Coastal Plain, and places them as close to the K-Pg boundary as perhaps several hundred

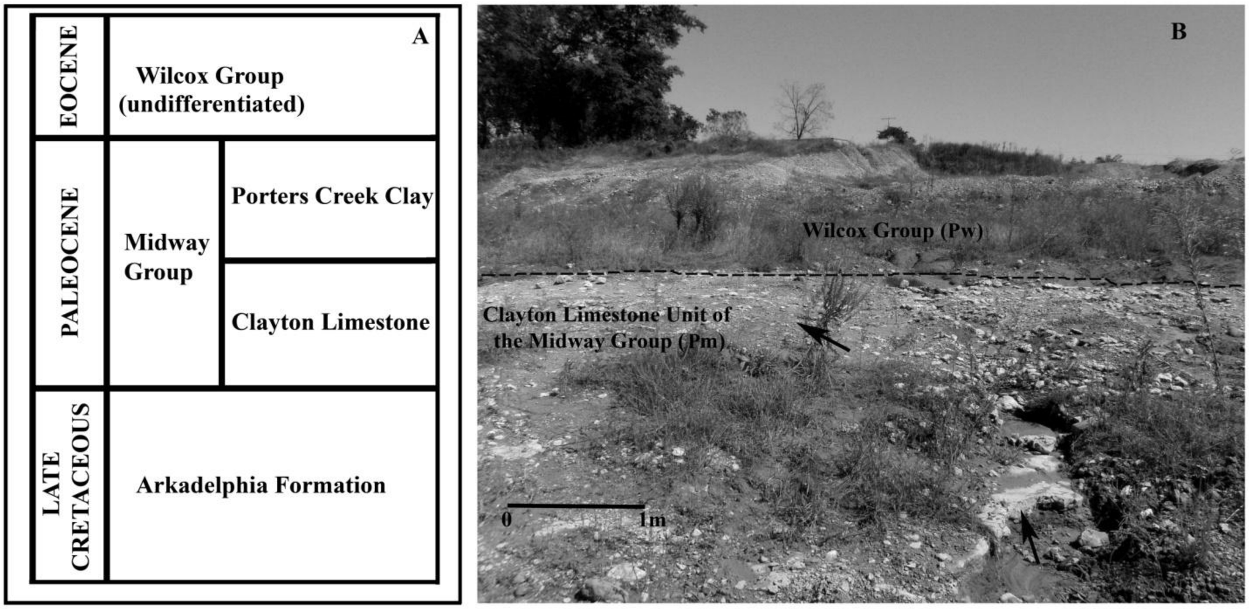

FIGURE 2. Osteichthyan fossil site. **A,** General stratigraphy of the Midway Group at the collection area. **B,** Main osteichthyan collection area. Arrows indicate position of white to light gray, highly fossiliferous limestone beds and thin beds of light gray marl and sandy marl of the Clayton Limestone. The Wilcox Group overlies it disconformably and consists of light brown sands and limonite-stained quartz gravel. Scale bar only applies to the beds in the foreground.

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thousand years but no further than about 1 million years, based on sea level cyclicity considerations (e.g., Busch and Rollins, 1984; Case and Schwimmer, 1988; Brett and Baird, 1993; Kidwell, 1993; Sugarman et al. 1995; Becker et al., 1996; 1998; Shimada et al., 2006).

MATERIALS AND METHODS

Osteichthyan teeth and skeletal elements were collected over four field seasons by sieving and surface-collecting. Mesh sizes for sieving in the field ranged from 5.0 to 1.0 mm. Additionally, approximately 150 kg of sediment were recovered for laboratory sieve analysis. In the lab, sediment was disarticulated by application of three percent hydrogen peroxide, thoroughly washed through progressively finer meshed screens ranging from 5.0 to 0.5mm, and dried under heat lamps. We recovered and analyzed in this study approximately 500 osteichthyan teeth. Teeth were removed using a magnifying glass and imaged directly with an Olympus SZ61 Binocular Microscope attached to an Infinity–2 Digital Camera and an EVEX-3000 Scanning Electron Microscope operating at 20Kv. It is noteworthy to report that all recovered osteichthyan teeth and skeletal elements discovered were smaller than 2.0 cm in total length.

SYSTEMATIC PALEONTOLOGY

Because no new genera or species were identified among the specimens we recovered, abbreviated synonymies are utilized with specific reference to those found in: Agassiz, 1833-1844; Owen, 1840–1845; Blake, 1940 and Weems, 1999. Specimens described here have been deposited in the vertebrate fossil collections of the Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA (abbreviated ANSP).

Class OSTEICHTHYES Huxley, 1880
Order PYCNODONTIFORMES Berg, 1940
Family PYCNODONTIDAE Agassiz, 1833
Genus *PYCNODUS* Agassiz, 1833
PYCNODUS sp.
(Figures 4A–H)

Pycnodus Agassiz, 1833. vol. 1, pl. g, f. (name and figure only).

Referred Material—ANSP 23262–23263, two jaw fragments with tooth caps; ANSP 23264, isolated tooth cap.

Description—In occlusal view, the jaw fragments contain elongated and oval-shaped tooth caps with a thick layer of enamel. The largest tooth on the jaw fragments measures 9.0 mm by 4.0 mm across its

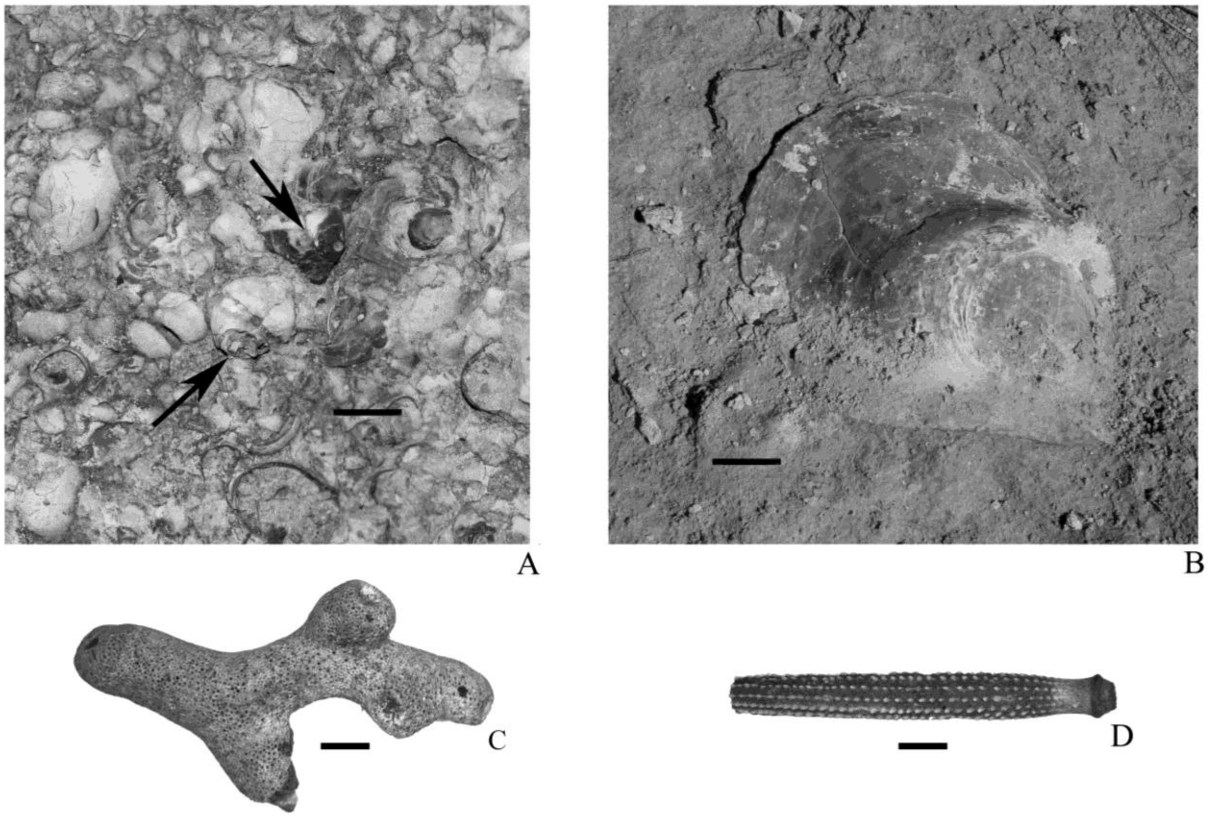

FIGURE 3. Invertebrate fossils common to the Clayton Limestone of the Midway Group, Hot Spring County, Arkansas. **A,** white to light gray, highly fossiliferous limestone bed with multiple steinkerns of gastropods and oyster shells (see arrows); **B,** large oyster within light gray marl and sandy marl; **C,** branching coral fragment; **D,** nearly complete echinoid spine. Scale bars: **A**–**B** = 1.0 cm. **C**–**D** = 1.0 mm.

longest dimensions. In basal view, the jaw fragments are osseous and have oval-shaped concavities that reside directly below the corresponding tooth caps. The isolated tooth cap has thick enameled tooth edges with a deep basal cavity measuring 11.0 mm by 5.0 mm across its longest dimensions.

Discussion—The individual tooth caps attached directly to the jaw fragments and basal view of an isolated tooth cap readily identify these specimens as belonging to pycnodonts. These characteristics distinguish the Clayton Limestone specimens from those belonging to phyllodonts whose teeth tend to be more concentric and are stacked in tooth files for continuous replacement during the animal's lifetime (Estes, 1969; Nursall, 1999a; 1999b). Both families of these osteichthyans are well adapted for shell-crushing lifestytes and are known from shallow-marine environments, particularly those with abundant molluscs and arthropods (e.g., Estes, 1969; Case and Schwimmer, 1988; Nursall, 1996; Poyato-Ariza and Wenz, 2002).

The Clayton Limestone specimens resemble those belonging to the Late Cretaceous North American pycnodont species *Anomoedus phaseolus* (Hay, 1899) and *Phacodus punctatus* Dixon, 1850. However, these specimens are much smaller and oval-shaped relative to those belonging to *Anomoedus phaseolus* (see Figure 6 for comparison) and are also unlike those of *Phacodus punctatus* which are far more concentric as figured and described by Hooks et al. (1999). *Pycnodus* sp. teeth have been previously identified in the Paleocene and Eocene of Mississippi, South Carolina and Virginia (Case, 1986; Weems, 1998; 1999). Multiple species of *Pycnodus* sp. are known globally with generally similar tooth morphology (Agassiz 1833-44; Woodward, 1902; Arambourg, 1952; Casier, 1966; Blot, 1987; Kemp et al., 1990). Until additional specimens from the Clayton Limestone can be recovered, we follow Weems (1999) and refrain from species assignment.

Order ELOPIFORMES Greenwood, Rosen, Weitzman, and Myers, 1966
Family ALBULIDAE Bleeker, 1859
Genus *ALBULA* Scopoli, 1777
ALBULA OWENI (Owen, 1845)

(Figures 4I–K)

Pisodus oweni Agassiz, 1843. vol. 2, pt. 2, p. 247 (name only).
Albula oweni (Owen, 1845), p. 138. Pl. xlvii, fig. 3.

Referred Material—ANSP 23265, isolated tooth cap.

Description— In occlusal view, the isolated tooth cap is roughly circular in outline, approximately 2.0 mm in diameter and contains a thin layer of enamel. The base of the tooth is deeply concave, osseous and has thick edges. Partial deterioration of the enamel layer and osseous tooth edges is visible in lateral view.

Discussion—A single tooth cap belonging to *Albula oweni* (Owen, 1845) was recovered from the Clayton Limestone. The specimen bears striking similarity to those figured from the Eocene of Mississippi, South Carolina and Virginia (Case, 1986; Weems, 1998; 1999). Weems (1999) indicated that *Albula oweni* teeth were also 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. This type of modern marine environment is analogous to the lithology and invertebrate fossil assemblage found in the Clayton Limestone near Malvern, Arkansas. The tooth from *Albula oweni* can be readily distinguished from those belonging to other phyllodonts such as *Paralbula casei* Estes (1969) by its much smaller size, thick tooth edges and higher profile in lateral view. In basal view, the tooth from *Albula oweni* resembles *Fisherichthys folmeri* Weems (1999) known from the Lower Eocene of Mississippi, South Carolina and Virginia (Cicimurri and Knight, 2009). However, in lateral and occlusal views, *Fisherichthys folmeri* is distinctly conical and not cylindrical like *Albula oweni*.

Family PHYLLODONTIDAE Sauvage, 1875
Genus *PARALBULA* Blake, 1940
PARALBULA MARYLANDICA Blake, 1940
(Figures 4L–M)

Paralbula marylandica Blake, 1940, vol. 30, p. 205-209, 2 figs. (original description).

Referred Material—ANSP 23266, isolated tooth cap.

Description—In occlusal view, the isolated tooth cap is circular in outline and 2.0 mm in diameter. Faint granular surface sculpturing occurs across the thin layer of enamel. The tooth base is slightly concave and partially osseous.

Discussion—*Paralbula marylandica* was first identified from the Aquia Formation of Maryland by Blake (1940). This tooth differs from *Paralbula casei* Estes, 1969 (known from the Late Cretaceous of North America) by having a larger diameter, lower vertical profile in lateral view and no thin margin protruding around the base of the crown. Other species of *Paralbula* are known globally, including *P*. *stromeri* (Weiler, 1929) and *P*. *salavai* (Arambourg, 1952), but these have yet to be reported from North America. Another interesting and similar species of phyllodont, *Pseudoegertonia granulosus* (Arambourg, 1952), also is found in North America (Hutchinson, 1985; Estes and Hiatt, 1978; Becker et al., 2010a), but teeth belonging to *Pseudoegertonia granulosus* are not round or uniform in shape and thus differ from those of *Paralbula marylandica*. (see Figure 6 for comparison of *Paralbula marylandica* to *Paralbula casei* and *Pseudoegertonia granulosus*).

Genus *PHYLLODUS* Agassiz, 1843
cf. *PHYLLODUS TOLIAPICUS* Agassiz, 1843
(Figures 4N–P)

Phyllodus toliapicus Agassiz, 1843, vol. 2, pt. 2, p. 239, pl. lxix a, f, 1-3.

Referred Material—ANSP 23267, isolated tooth cap.

Description—In occlusal view, the isolated tooth cap is oval-shaped and very elongated, measuring 9.0 mm by 2.0 mm across its longest dimensions. The base of the tooth is slightly concave and partially osseous. A thin layer of enamel covers the tooth as seen in occlusal and lateral views.

Discussion—*Phyllodus toliapicus* was first figured and described in North America from the Paleocene of Montana by Estes (1969). Our tentative assignment of the single Clayton Limestone specimen to cf. *Phyllodus toliapicus* is based on the facts that: 1) the overall morphology suggests that this tooth is stacked in a file and is similar to that found in median teeth of this species; 2) Estes (1969) and later Weems (1999) indicated that this species showed considerable variation in morphology and many named species are probably synonyms to *P*. *toliapicus*; and 3) this species has been documented from the Paleocene and Eocene of North America including nearby Mississippi (Estes, 1969; Case, 1986, Weems, 1998; 1999).

TELEOSTEI incertae sedis
(Figures 5A–N)

Referred Material—ANSP 23268–23269, two fin spines; ANSP 23270–23271, two tuberculated skull elements, ANSP 23272–23273, two amphicoelous vertebrae.

Description—The two fin spines are 7.0 mm and 8.0 mm in height, slightly curved in the posterior

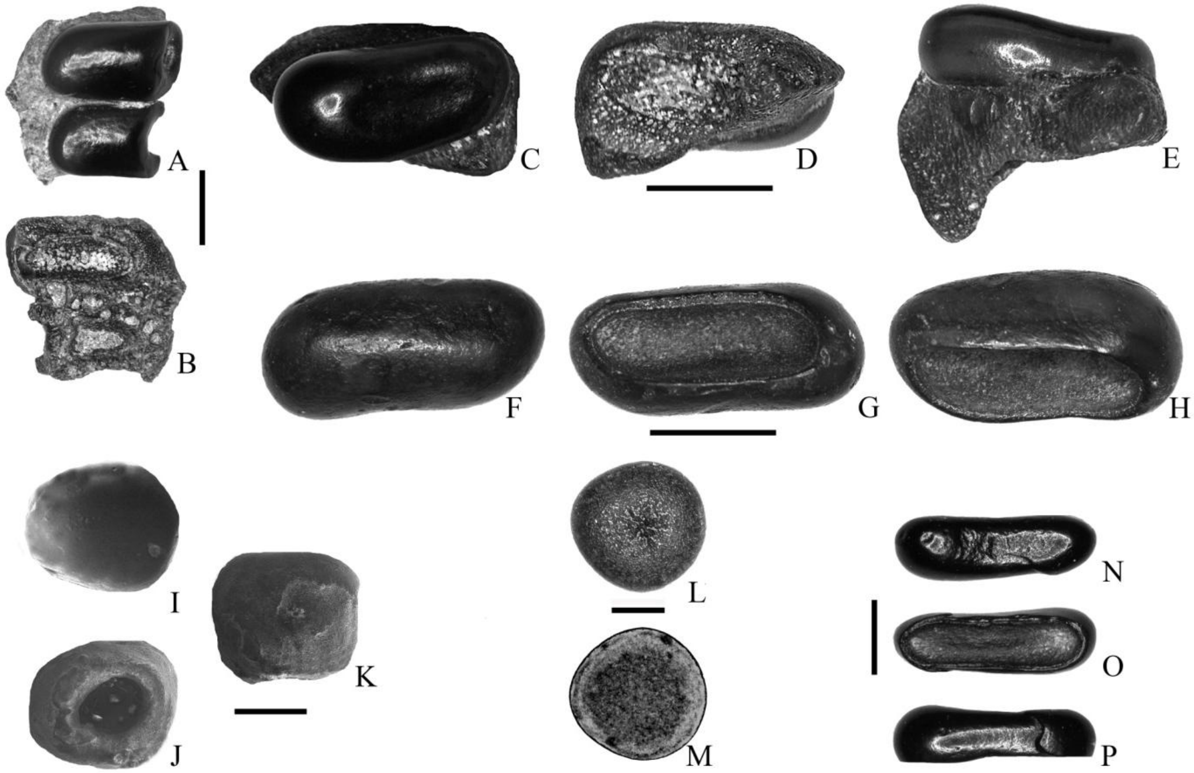

FIGURE 4. Teeth and jaw fragments of Pycnodontidae, Albulidae, and Phyllodontidae from the Clayton Limestone, Hot Spring County, Arkansas. **A–H,** *Pycnodus* sp. (ANSP 23262–23264); **I–K**, *Albula oweni* (Owen, 1845) (ANSP 23265); **L–M,** *Paralbula marylandica* Blake, 1940 (ANSP 23266); **N–P,** cf. *Phyllodus toliapicus* Agassiz, 1843 (ANSP 23267). Scale bars: **A**–**H**; **N**–**P** = 5.0 mm and **I**–**M** = 1.0 mm. Orientations: **A, C, F, I, L, N** = occlusal view; **B, D, G, J, M, O** = basal view; **E, H, K, P** = lateral view.

direction, and missing their distal points. An anterior median ridge spans the length of the spine shaft from the distal apex to the basal lumen. From the posterior view, a medial posterior sulcus extends along the length of the spine shaft. The two incomplete skull elements are approximately 4.0 mm across their longest dimension, irregularly shaped and contain remnants of sutures to adjacent skull elements along some edges. The exterior surface displays glossy tuberculate sculpturing, and the interior surface is partially osseous and relatively smooth. The amphicoelous vertebra are 7.5 mm in length and 6.5 mm in diameter and 5 mm in length and 6.0 mm in diameter respectively. Dorsally and ventrally the centra have remnants of their neural and hemal arches that are broken away from their corresponding spines.

Discussion—The overall asymmetric morphology of these fin spines as seen in lateral and anterior view allows individual spines to rise and collapse in a manner similar to those seen in percomorph osteichthyan dorsal fin spines. Differences in vertical length suggest the vertebral centra are from trunk versus caudal locations. The tuberculated skull elements resemble those seen in both pycnodonts and boxfish (Nursall, 1999a, 1999b; Weems, 1999; Bardet et al., 2000; Poyato-Ariza and Wenz, 2002). Skeletal elements similar to the Clayton Limestone specimens are known from partial and whole skeletons of Late Cretaceous beryciforms (Patterson, 1964; Stewart, 1990a, 1990b, 1996; Becker et al., 2009) and are also found in the nearby Arkadelphia Formation (Becker et al, 2010a). Although the fin spines, tuberculated skull elements and amphicoelous vertebra can be definitively assigned to percomorph osteichthyans, the generic nature of the Clayton Limestone specimens precludes any lower order taxonomic assignment.

DISCUSSION

Paleoecology of the Clayton Limestone Osteichthyan Assemblage—Invertebrate fossils (including molluscs, echinoderms and particularly corals) recovered in matrix with the osteichthyans described in this report indicate that the paleo-

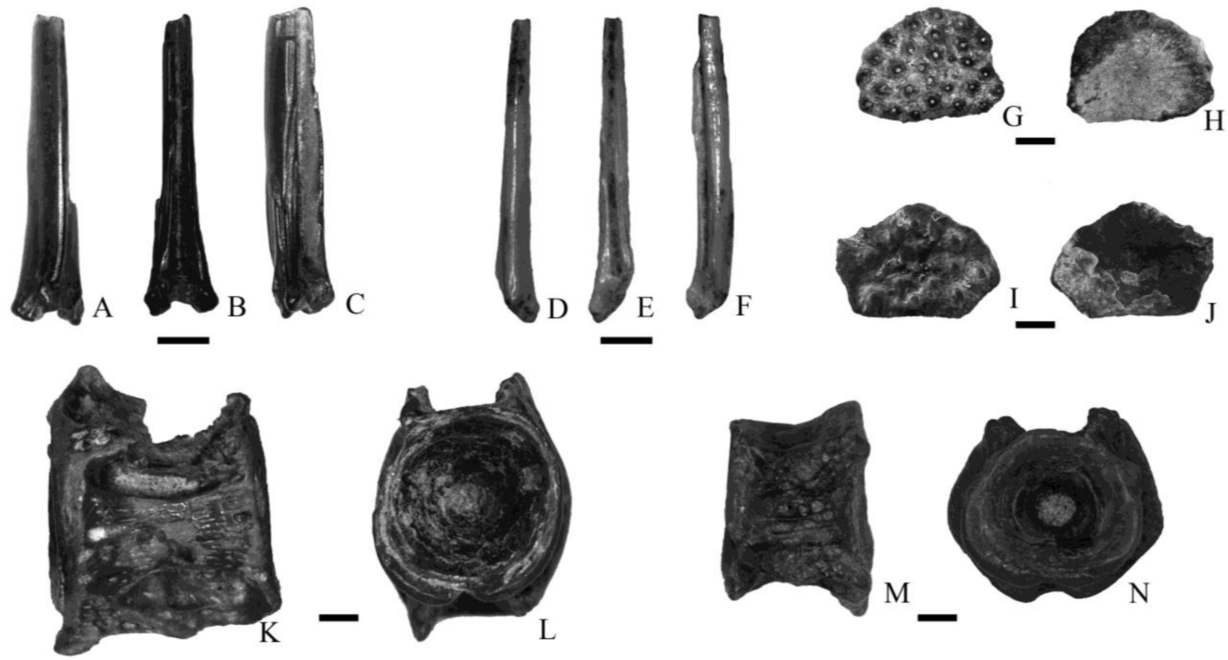

FIGURE 5. Teleostei incertae sedis skull and skeletal elements from the Clayton Limestone, Hot Spring County, Arkansas. **A–F,** dorsal fin spines (ANSP 23268–23269); **G–J,** tuberculate skull fragments (ANSP 23270–23271); **K–N,** amphicoelous vertebrae (ANSP 23272–23273). All scale bars = 1.0 mm. Orientations: **A, D** = anterior view; **B, E** = posterior view; **C, F** = lateral view; **K, M** = dorsolateral view; **L, N** = articular surface; **G, I** = exterior view; **H**, **J** = interior view.

environment of the Clayton Limestone near Malvern is best characterized as a shallow-marine platform or shelf with low biohermal mounds or patch-reefs. This interpretation is reinforced by the limestone and marl lithology occurring in outcrop as well as the occurrence of at least ten species of chondrichthyans known to have inhabited similar shallow, near-shore environments throughout North America during the early Cenozoic (Becker et al., 2010b; 2011). No material belonging to Acipenseridae, Amiidae and Lepisosteidae is present in our assemblage, although these osteichthyans occur in the late Mesozoic and early Cenozoic elsewhere in North America (Wiley and Stewart, 1977; Grande, 1980; Weems, 1998; Becker et al., 2010a). The absence of such fresh to brackish water fish is further evidence supporting the suggestion that our site was fully marine in character.

The osteichthyan material we recovered at the Clayton Limestone site consists of pavements of small, closely spaced, rounded teeth, as well as isolated teeth of the same type. Such teeth are considered characteristic of a shell-crushing, bottom feeding lifestyle. The small size of the teeth and supporting jaw fragments suggest that the populations from which our fossils derive were composed primarily, or perhaps entirely, of small individuals. The dentitions of these fish are well designed for targeting the invertebrate prey present at this site.

Composition of the Clayton Limestone Osteichthyan Assemblage, Faunal Turn-over and the K/Pg Extinction—Table 1 provides a list of osteichthyan species occurring in the Clayton Limestone near Malvern, Arkansas. Also contained in this table is a list of osteichthyan species recovered from the nearby Arkadelphia Formation–Midway Group contact as reported in Becker et al. (2010a). On a local scale and within a relatively narrow geologic time frame, both osteichthyan assemblages provide details of species diversity bracketing the K/Pg boundary in the Gulf Coastal Plain of Arkansas. From Table 1, both osteichthyan assemblages are represented by pavement-style teeth evolved for crushing shells and soft-bodied prey. This is not surprising considering the abundance of hard-shelled invertebrates such as mollusks, echinoderms and corals that occur at both localities. However, noticeably absent from the Clayton Limestone assemblage are osteichthyans with piscivorous dentitions, particularly *Enchodus*, whose teeth are extremely abundant in the Arkadelphia Formation–Midway Group contact (Figure6).

Another notable difference documented in Table 1 is the reduction in total species identified between the

TABLE 1. Osteichthyans from the Arkadelphia Formation–Midway Group contact (AFMG) and Clayton Limestone (CL) near Malvern, Hot Spring County, Arkansas. Data from Becker et al. (2010a) and this study.

(AFMG)	(CL)
Cylindracanthus ornatus Leidy, 1856	
Atractosteus sp.	
Lepisosteus sp.,	cf. *Phyllodus toliapicus* Agassiz, 1843
cf. *Hadrodus priscus* Leidy, 1857	*Pycnodus* sp.
Pseudoegertonia cf. *P. granulosus* (Arambourg, 1952)	*Albula oweni* (Owen, 1845)
Paralbula casei Estes, 1969	*Paralbula marylandica* Blake, 1940
Enchodus gladiolus (Cope, 1872)	
Enchodus ferox Leidy,1855	
Enchodus petrosus (Cope, 1874)	

two assemblages: nine species in the Arkadelphia Formation–Midway Group contact versus four species in the Clayton Limestone. Only a single genus from two different species of *Paralbula* occurs in both assemblages. It is important to note that both localities were extensively collected by the same field and bulk sampling techniques and over multiple field seasons. Based on these sampling techniques and known Paleocene osteichthyans from other North American localities (Figure1), we believe it is unlikely that any additional sampling will appreciably alter the number of identified species in Table 1. Another consideration is the fact that no osteichthyan species previous identified from only the post-Cretaceous Paleocene of North America occurs in the Arkadelphia Formation–Midway Group assemblage. Thus, osteichthyans recovered from both localities represent distinct assemblages living at different geologic times bracketing the K/Pg boundary.

Based on our Clayton Limestone sample, we suggest that two possibilities exist to explain the overall reduction in species between the two assemblages. The first explanation may be related to local effects such as habitat preferences of tropically specialized species in the geographically small areas sampled. This would explain the Clayton Limestone osteichthyan assemblage as being comprised largely of pavement-style, shell-crushing teeth. However, invertebrate fossils at both localities indicate the existence of similar shallow-marine platform or shelves with low biohermal mounds or patch-reefs. This similarity between localities does not account for the overall absence of osteichthyans with pisciverous dentitions from the Clayton Limestone.

An alternative explanation is that the Clayton Limestone osteichthyans provide a local snapshot of the detrimental environmental consequences and faunal-turnover related to the end-K Chicxulub impact in Mexico’s Yucatan Peninsula. The current view regarding the effect of this event on the biosphere is that it produced mass extinction through ecologic collapse by temporary attenuation of photosynthesis, global temperature decline, widespread wildfires and environmental acidification (e.g., Kring, 2007; Belcher et al., 2009; Shulte et al, 2010). Further, evidence suggests that the intensity of the extinction was more severe in North America due its proximity to the impact site and to the northward directionality of the impact debris field (Schultz and D’hondt, 1996; Claeys et al., 2002) than was the case for regions more remote from the impact site.

This alternative explanation supports global studies indicating an evolutionary bottleneck in chondrichthyan diversity occurred during the end-Cretaceous mass extinction (e.g. Kriwet and Benton, 2004). It also supports prior local studies of chondrichthyan assemblages that occur in the same localities as the osteichthyans contained in this report (Becker et al. 2006; 2010a). However, it will be necessary to further sample Paleocene osteichthyans from other Gulf Coastal Plain localities and beyond to obtain additional scaling parameters necessary to compare our local osteichthyan assemblages to the global end-Cretaceous mass extinction. Only then can other factors on local or regional scales that alter species abundance be ruled out. Larger, local data sets such as those by Weems (1999) suggest that recovery of osteichthyans in North America from the global end-Cretaceous mass extinction had taken place by the early Eocene.

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FIGURE 6. Phyllodontidae, Pycnodontidae and Enchodontidae tooth plates and teeth from the Arkadelphia–Midway Group Contact Hot Spring County, Arkansas and lowermost Navesink Formation Monmouth County, New Jersey. All scale bars equal 1.0 cm. **A–B,** basibranchial tooth of *Pseudoegertonia* cf. *granulosus* (Arambourg, 1952); **C–D,** volmer tooth plate of *Paralbula casei* Estes, 1969; **E–F,** buccal tooth plate of *Anomoedus phaseolus* (Hay, 1899); **G,** Abundance example of *Enchodus ferox* Leidy, 1855; *Enchodus gladiolus* (Cope, 1872); and *Enchodus petrosus* (Cope, 1874) palatine teeth. Orientations: **A, C, D** = occlusal view; **B, E, F** = basal view; **G** = anterior, lateral, posterior views. **A–D, G** = Arkadelphia Formation–Midway Group contact, Hot Spring County, Arkansas; **E–F** = Lowermost Navesink Formation, Monmouth County, New Jersey. Specimens in private collection of William Paterson University.

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