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Chondrichthyans from the Clayton Limestone Unit of the Midway Group (Paleogene: Paleocene) of Hot Spring County, Arkansas, USA

Martin A. Becker[1], Lauren C. Smith[1] & John A. Chamberlain Jr.[2]

[1]*Department of Environmental Science, William Paterson University, Wayne, New Jersey 07470; e-mail: beckerm2@wpunj.edu*
[2]*Department of Geology, Brooklyn College and Doctoral Program in Earth and Environmental Sciences, City University of New York Graduate Center, New York 10016; email: johnc@brooklyn.cuny.edu*

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The Clayton Limestone Unit of the Midway Group (Paleocene) in southwestern Arkansas preserves one of the oldest chondrichthyan Cenozoic assemblages yet reported from the Gulf Coastal Plain of the United States. Present are at least eight taxa, including: *Odontaspis winkleri* Leriche, 1905; *Carcharias* cf. *whitei* (Arambourg, 1952); *Carcharias* sp.; *Anomotodon novus* (Winkler, 1874); *Cretalamna* sp.; *Otodus obliquus* Agassiz, 1843; *Hypolophodon sylvestris* (White, 1931); *Myliobatis dixoni* Agassiz, 1843; and a chimaerid of indeterminate affiliation. Also present are lamnoid-type and carcharhinoid-type chondrichthyan vertebral centra. The Clayton chondrichthyan assemblage derives from an outcrop located only a few kilometers from a site exposing an assemblage of Maastrichtian chondrichthyans from the upper Arkadelphia Marl. Because these assemblages are closely spaced stratigraphically and geographically, they provide data on chondrichthyan taxonomic turnover across the Cretaceous/Paleocene boundary in this region of the Gulf Coastal Plain. The evolutionary bottleneck in chondrichthyan diversity associated with the end-Cretaceous mass extinction event that has been documented from other parts of the world also appears to be strongly expressed in the Arkansas region of the Gulf Coastal Plain.

KEY WORDS: Clayton Limestone Unit, southwest Arkansas, chondrichthyans, Paleocene, K/P boundary.

Introduction

For over one and a quarter centuries, the occurrence of Cenozoic chondrichthyan fossils has been well-documented in North America. Earliest reports are those of famous vertebrate paleontologists such as Edward Cope, Othniel Marsh and Joseph Leidy who published numerous descriptions and identifications of Cenozoic chondrichthyans from the Atlantic Coastal Plain (*e.g.* Marsh, 1869; Cope, 1875a; Leidy, 1877). To date, most states inundated by sea level rise during the Cenozoic contain some record of chondrichthyan fossils (*e.g.* Fowler, 1911; Thurmond & Jones, 1981; Wroblewski, 2004); and in some instances their occurrence in consecutive formations (*e.g.* Ward & Weist, 1990). Such occurrences in consecutive formations have provided an important basis for classifying the appearance of new species as well as documenting faunal turnover and extinction of other species. This is particularly evident throughout the Chesapeake Bay Region where subtle changes in tooth morphology are stratigraphically chronicled in major chondrichthyan orders such as Lamniformes (Kent, 1994; 1999a).

To date, only a few reports of fossil chondrichthyans have been documented from Arkansas, none of which occur in consecutive formations. These reports include: 1) two Mississippian teeth from the Pitkin Formation and a single Paleocene tooth from the Midway Group (Freeman, 1966); 2) sixteen species from the uppermost Santonian–lowermost Campanian, including one new genus and two new species from the Brownstown Marl (Meyer, 1974); and, 3) at least seventeen species from the Maastrichtian Arkadelphia Formation (Becker *et al.*, 2006). This is surprising considering that the stratigraphic record in the southwestern part of the state consists largely of marginal and shallow marine limestone, sand, marl and chalk. It is also interesting to note that the shoreline of the western Gulf Coastal Plain ran through this region during much of the late Cretaceous and early Cenozoic (Kennedy *et al.*, 1998). This shoreline reconstruction indicates that entrance to the Western Interior Seaway from the east would have taken place across southwestern Arkansas and near the base the Ouachita Mountains.

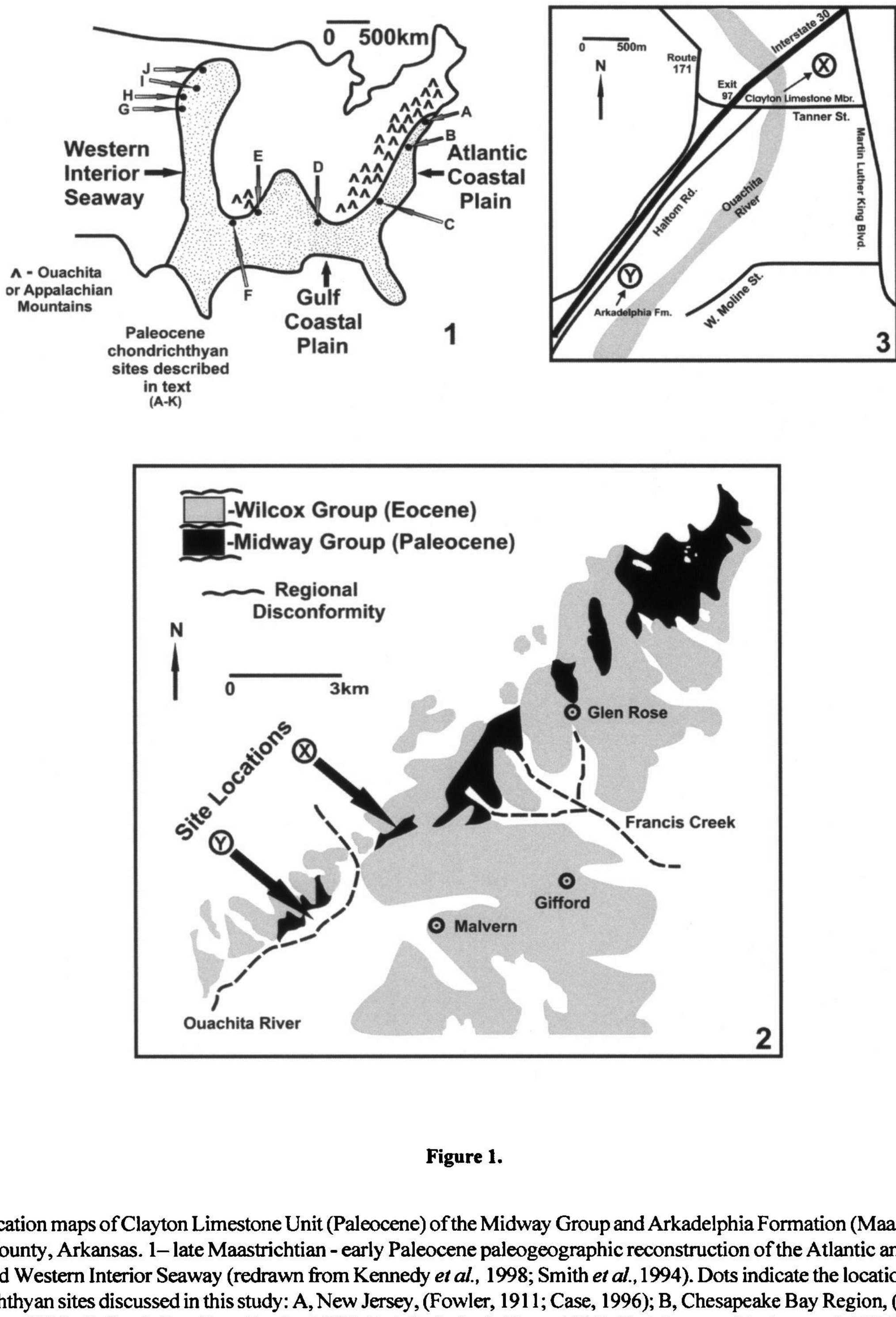

Figure 1.

Figure 1. Location maps of Clayton Limestone Unit (Paleocene) of the Midway Group and Arkadelphia Formation (Maastrichtian), Hot Spring County, Arkansas. 1– 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 chondrichthyan sites discussed in this study: A, New Jersey, (Fowler, 1911; Case, 1996); B, Chesapeake Bay Region, (Ward & Weist, 1990; Kent, 1994); C, South Carolina, (Purdy, 1998); D, Mississippi, (Case, 1994); E, Arkansas, (Becker *et al.*, 2006; this study); F, Texas, (Stidham & Janus, 2008); G–H, South and North Dakota, (Cvancara & Hoganson, 1993); I, Wyoming, (Wroblewski, 2004); J, Montana, (Bryant, 1989). 2– Geologic map of Midway and Wilcox Groups (Paleogene) in the southwestern Arkansas study area (modified from Haley *et al.*, 1993). Location of Clayton Limestone Unit chondrichthyan site (this study) indicated by (X) and Arkadelphia Formation site of Becker *et al.* (2006) indicated by (Y). 3– Detailed locator map of Clayton Limestone Unit (X) and Arkadelphia Formation (Y) chondrichthyan sites discussed in this study.

Figure 2. Fossil site. 1– Main chondrichthyan 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 Unit. The Wilcox Group is disconformable with the upper contact of the Clayton Limestone Unit and consists of light brown sands and limonite-stained quartz gravel. 2– Closeup of *Cretalamna* sp. tooth eroding directly out of Clayton Limestone Unit. 3– Closeup of *Carcharias* cf. *whitei* (Arambourg, 1952) tooth eroding directly out of Clayton Limestone Unit.

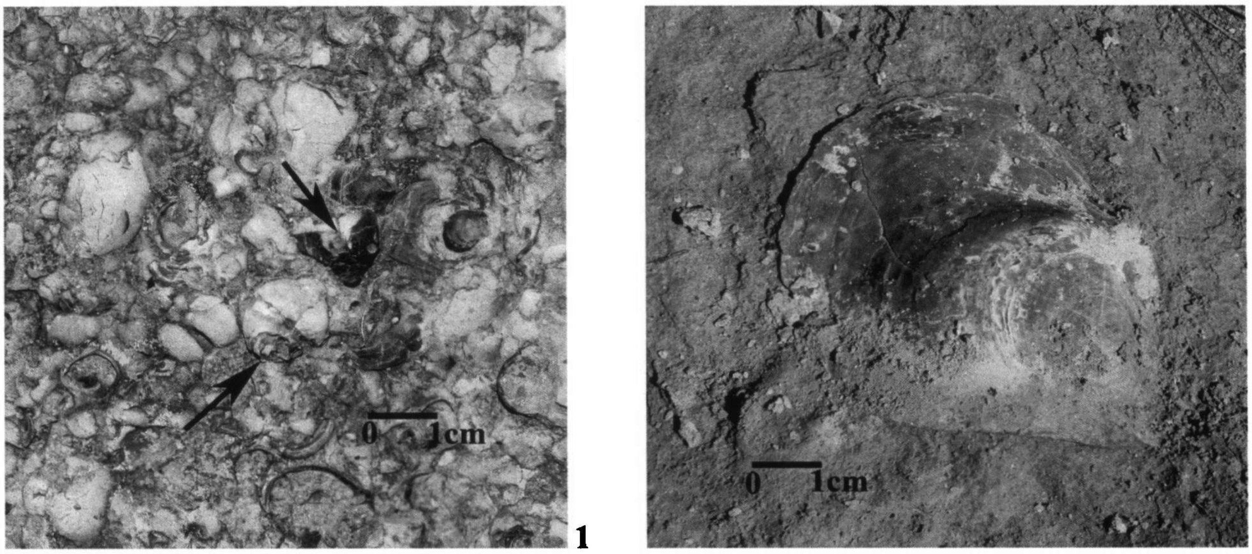

Figure 3. Closeup of the Clayton Limestone Unit of the Midway Group, Hot Spring County, Arkansas. 1– White to light gray, highly fossiliferous limestone bed with multiple steinkerns of gastropods and oyster shells; 2– Valve of typical large oyster seen in light gray marl and sandy marl.

Such broad distribution of contemporaneous shoreline and shallow seaway across the Atlantic and Gulf Coastal Plains as well as the Western Interior Seaway may account for the overall similarities in genera and species seen in North America chondrichthyan assemblages.

In this paper, we describe a new chondrichthyan assemblage recovered from the Paleocene Clayton Limestone Unit of the Midway Group in Hot Spring County, Arkansas (Fig. 1). Although no new genera or species are reported here, the Paleocene chondrichthyan fauna is significant because it occurs stratigraphically directly above, and within a few kilometers, of an outcrop exposing an assemblage of Maastrichtian chondrichthyans from the upper Arkadelphia Marl (Becker *et al.*, 2006). The Arkadelphia and Clayton Limestone assemblages provide a unique opportunity to study chondrichthyan taxonomic turnover across the Cretaceous/Paleogene boundary and within close geographic proximity. Large scale, global studies of Kriwet & Benton (2004) have previously demonstrated the devastating effects of the K/P mass extinction event on these highly mobile marine predators.

Materials & Methods

Regional Geology, Location and Age

The Midway Group is a fossiliferous marginal marine deposit of Paleocene age that can be found throughout the Gulf Coastal Plain and several states of the Mississippi Embayment. In Arkansas, the Midway Group occurs in the southwestern part of the state along a northeastern trend that runs from Texarkana to Little Rock. Intermittent outcrop exposures occur along the banks of creeks and rivers throughout this region where erosion has removed the dense vegetative overgrowth. Regional disconformities separate the Midway Group from the underlying marine Arkadelphia Formation (Maastrichtian) and overlying non-marine Wilcox Group (Eocene) (Haley *et al.*, 1993). Historically, the Midway Group which is over 180 metres has not been divided into distinct geologic units. However, recent studies by the Arkansas Geologic Commission have identified expansive clays within the Midway Group to be an area of concern to construction practices (McFarland, 1998). Such concerns have resulted in localized division of the Midway Group into the Clayton Limestone Unit that resides directly below the Porters Creek Clay Unit (McFarland, 1998). The Clayton Limestone Unit consists primarily of highly fossiliferous, light-colored limestone separated by thin beds of clay and sandy intervals while the Porters Creek Clay Unit consists of highly expansive, dark-colored calcareous clay with minimal fossil evidence.

Our Clayton Limestone Unit site is approximately 3 kilometers northwest of Malvern and outcrops along both sides of an access road to a commercial shopping facility (Figs. 1–2). Outcrop exposures consist of white to light gray, highly fossiliferous limestone beds up to 0.5 meters thick that contain multiple steinkerns of mollusks, particularly gastropods and oyster shells (Fig. 3). Interbedded with the limestone are thin beds of light gray marl and sandy marl typically less than 10 centimeters with occasional disarticulated oyster shells. Small invertebrate fossils, typically less than 2 centimeters, are abundant throughout the site and include shells, spines and skeletal structures of mollusks, brachiopods, arthropods, echinoids, bryozoans and corals. Teeth and vertebral centra from chondrichthyans up to 3.5 centimeters are also abundant and our collecting efforts recovered a few teeth belonging to indeterminate species of pycnodonts and gharials. Light brown sands and limonite-stained quartz gravel of the Wilcox Group are disconformable with the upper contact of the Clayton Limestone Unit and form erosion resistant buffs (Fig. 2). The lower contact is obscured by dense vegetation overgrowth and Quaternary alluvium and terrace deposits near the banks of the Ouachita River and its tributaries. No dark colored, highly expansive, calcareous clay with minimal fossil evidence typical of the Porters Creek Clay Unit of the Midway Group were identified at this site. Multiple lines of evidence including magnetostratigraphy, ostracods, ammonites, chondrichthyans and osteichthyans have been utilized to establish a late Maastrichtian age for the Arkadelphia Formation and Paleocene age for the overlying Midway Group (Cushman, 1949; Jones, 1962; Liddicoat *et al.*, 1981; Haley *et al.*, 1993; Pitakpaivan & Hazel, 1994; Becker *et al.*, 2006; 2010b). Additional description of the Arkadelphia Formation and Midway Group biostratigraphy as well as their lithology are given in Becker *et al.*, (2006; 2010b).

Field and Laboratory Techniques

The Clayton Limestone Unit chondrichthyan assemblage is comprised of approximately 2000 total teeth and vertebrae recovered across three seasons of fieldwork. In the field, fossils were collected through both sieving and surface-collecting. Most productive collecting occurred after rainfall events and during the colder months which reduced seasonal plant cover. The *in situ* specimens in the matrix of the fossiliferous limestone beds were removed by pry bars, sledge hammers and chisels. Mesh sizes for sieving in the field ranged from 1.0 to 5.0 mm. Approximately 250 kg of sediment was recovered for laboratory sieve analysis. In the lab, sediment was thoroughly washed through progressively finer meshed screens ranging from 0.5 to 5.0 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. Because no new genera or species were identified among the specimens we recovered, abbreviated synonymies are utilized. Specimens described here have been deposited in the fossil fish collections of the Academy of Natural Sciences Philadelphia, Pennsylvania (ANSP).

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Lamniformes Berg, 1958
Family Odontaspididae Muller & Henle, 1838
Genus *Odontaspis* Agassiz, 1838

Odontaspis winkleri Leriche, 1905
Figure 4.1a–2b

1905 *Odontaspis winkleri* Leriche, p. 117, pl. 6, figs. 1-12.

Material examined — ANSP 23243, one anterior tooth; ANSP 23244, one lateral tooth.

Description — Two teeth from 7–11 mm in total height; central cusp erect and slender in anterior tooth; distally curved and broader near the central cusp base in lateral tooth; pair of narrow cusplets on mesial and distal root lobes progressively smaller toward edge of root lobe; lingual face moderately convex and labial face relatively flat; both the central cusp and cusplets with multiple longitudinal ridges in anterior tooth on lingual face; labial face smooth in anterior tooth; lingual face in lateral tooth with short longitudinal ridges near crown foot; lingual face smooth in lateral tooth; root lobes elongated and slender with rounded tips; holaucorhizous root with well-defined nutritive groove.

Discussion — *Odontaspis winkleri* teeth can be distinguished from other teeth in the Clayton Limestone Unit by their smaller total height, narrow central cusp, pair of progressively smaller cusplets on the mesial and distal root lobes, and presence of longitudinal ridges on tooth crowns. Currently, there are at least seven species of *Odontaspis* that have been identified from the Cretaceous-Paleogene of North America (*e.g.* Eastman, 1901; Leriche, 1905; Cappetta & Case, 1975; Case, 1981, Case & Borodin, 2000). Some of these taxa are based on a few individual teeth from single locations and detailed study may synonymize a number of these species.
Two of the more established taxa are *O. aculeatus* (Cappetta & Case, 1975) from the Campanian-Maastrichtian and *O. winkleri* Leriche, 1905 from the Paleocene-Eocene (*e.g.* Ward & Wiest, 1990; Hoganson & Murphy, 2002; Becker *et al.*, 2006). Kent (1994) indicated that these two species can be distinguished by the larger overall size of *O. winkleri* and the fact that this species has reduced secondary cusplets that are less divergent and more erect. It is also important to note that many earlier taxonomic assignments presently associated with the genus *Carcharias* were originally placed with *Odontaspis* (*e.g.* Cappetta & Case, 1975; Thurmond & Jones 1981). In general, distinctions between the two contemporaneous genera assigned from fossil teeth are based primarily on the smaller tooth size and multiple, narrow cusplets that occur on both root lobes of *Odontaspis*.

Genus *Carcharias* Rafinesque, 1810

Carcharias* cf. *whitei (Arambourg, 1952)
Figure 4.3a–4b

1931 *Odontaspis teretidens* White, p. 53, figs. 16-27; p. 54, figs. 32-44; p. 57.

Material examined — ANSP 23245, one anterior tooth; ANSP 23246, one lateral tooth.

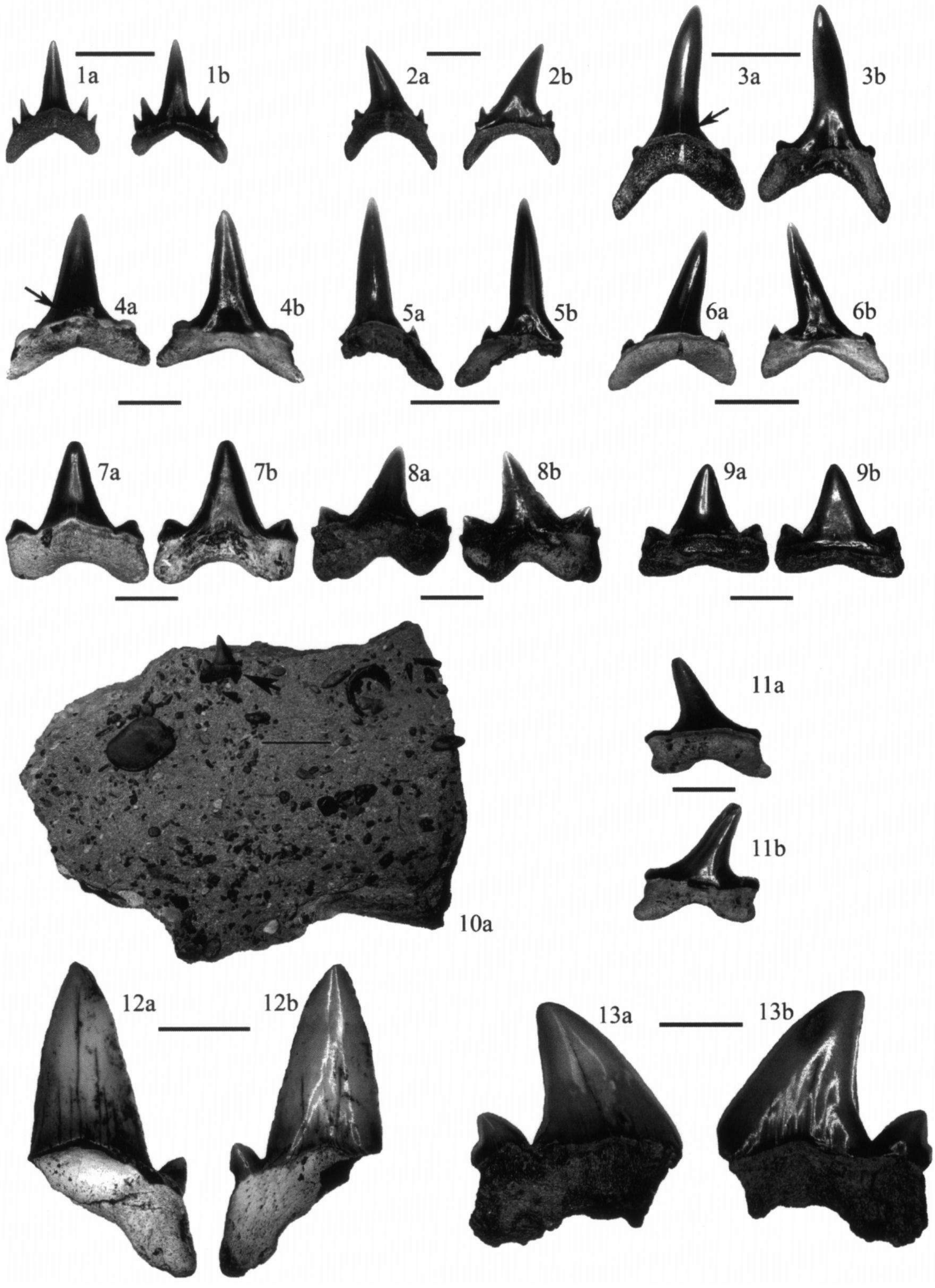

Figure 4.

Figure 4. Teeth of Odontaspididae, Cretoxyrhinidae, Mitsukurinidae and Otodontidae from the Clayton Limestone Unit, Hot Spring County, Arkansas. 1–2– *Odontaspis winkleri* (ANSP 23243–23244); 3–4– *Carcharias* cf. *whitei* (ANSP 23245–23246); 5–6– *Carcharias* sp. (ANSP 23247–23248); 7–9– *Cretalamna* sp. (ANSP 23249–23250); 10– Matrix specimen of *Cretalamna appendiculata* (AMNH FF 20357); 11– *Anomotodon novus* (ANSP 23252); 12– 13– *Otodus obliquus* (ANSP 23253–23254). Orientations: 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, 9a, 10a, 11a, 12a, 13a = lingual view; 1b, 2b, 3b, 4b, 5b, 6b, 7b, 8b, 9b, 11b, 12b, 13b = labial view. Scale bars: 1–2, 4, 7–9 = 0.5 cm; 3, 5, 6, 10 = 1.0 cm; 12–13 = 2.0 cm. 1–9, 11–13 = Clayton Limestone Unit. 10 = Arkadelphia Formation.

Description — Two teeth from 13–23 mm in total height; central cusp erect, slender and sigmoidal with slight distal curve near apex in anterior tooth; lingual face moderately convex and labial face relatively flat in anterior tooth; central cusp more triangular, broad-based and labiolingually compressed in lateral tooth; single, triangular cusplet on mesial and distal root lobes attached to central cusp as seen in labial view; multiple longitudinal ridges near the central cusp base directly above a well-defined dental band on lingual face (see arrows in Figs. 4.5, 4.7); well-defined lingual root protuberance on anterior tooth; root lobes rounded in anterior tooth, spatulate in lateral tooth; holaucorhizous root with well-defined, nutritive groove.

Discussion — *Carcharias* cf. *whitei* teeth can be distinguished from other teeth in the Clayton Limestone Unit by their multiple longitudinal ridges that occur near the central cusp base on the lingual crown face, sigmoidal central cusp in anterior tooth, more triangular central cusp in lateral tooth and single cusplet on the mesial and distal root lobes. In North America, teeth belonging to this species are most similar to those of the *Carcharias holmdelensis* (Cappetta & Case, 1975) from the Campanian-Maastrichtian and *Sylvestrilamia teretidens* (White, 1931) from the Paleocene and Eocene. Distinctions between *C. whitei* and *C. holmdelensis* are based on the larger overall tooth size and more robust cusp elements of *C. whitei*. *C. holmdelensis* was previously reported from the nearby Arkadelphia Formation by Becker *et al.* (2006). Our tentative assignment of the Clayton Limestone Unit teeth to *C.* cf. *whitei* is based on similarities between this species and *Carcharias teretidens*, recently reassigned to *Sylvestrilamia* by Cappetta & Nolf (2005). Both *C. whitei* and *S. teretidens* have been identified from multiple locations in North America (*e.g.* Ward & Wiest, 1990; Case, 1994; 1996; Kent, 1999a). A survey of tooth descriptions from various authors demonstrates that both these species are very similar and differences may be more chronostratigraphic than morphological in nature. Kent (1994) indicated that *C. whitei* appears before *S. teretidens* in the Brightseat Formation of the Chesapeake Bay Region. This formation is roughly equivalent in age to the Midway Group (Powars & Bruce, 1999) and furthers our taxonomic association of the Clayton Limestone Unit teeth with *C.* cf. *whitei*.

Carcharias **sp.**
Figures 4.5a–6b

Material examined — ANSP 23247, one anterior tooth; ANSP 23248, one lateral tooth.

Description — Two teeth from 18–20 mm in total height; central cusp smooth, slender, and erect in anterior tooth; lingual face moderately convex and labial face relatively flat in anterior tooth; central cusp smooth, more triangular, broad-based, distally-inclined and labiolingually compressed in lateral tooth; well-defined cutting edges along the central cusp with single, short, triangular and recurved cusplet on mesial and distal root lobes attached to central cusp in labial view; weak lingual root protuberance on anterior tooth with one root lobe incomplete and one root lobe elongated with rounded tip and poorly defined dental band in lingual view; root spatulate in lateral tooth above a well-defined dental band; holaucorhizous root with well-defined nutritive groove.

Discussion — The most frequently encountered teeth in the Clayton Limestone Unit belong to *C.* cf. *whitei* and this *Carcharias* sp. Overall tooth morphology in both these Clayton Limestone Unit species is very similar and taxonomic distinctions are based on the presence or absence of multiple longitudinal ridges on the lingual crown face. *Carcharias* sp. teeth from the Clayton Limestone Unit can be distinguished from other taxa of the Clayton Limestone Unit based on the absence of longitudinal ridges on the lingual crown face and similar criteria utilized for *Carcharias* cf. *whitei* In general, *Carcharias* sp. teeth are most similar to *Carcharias samhammeri* (Cappetta & Case, 1975) from the Campanian-Maastrichtian of North America (*e.g.* Gallagher, 1993; Hartstein *et al.*, 1999; Becker, 2004). *C. samhammeri* has not been reported from the Arkadelphia Formation. Distinctions between these two species are subtle and based primarily on the overall much larger tooth size of *Carcharias* sp. from the Clayton Limestone Unit along with the narrower crown base of the central cusp as seen in anterior teeth.
Teeth belonging to the genus *Carcharias* are common in the Paleogene of the Atlantic and Gulf Coastal Plains of North America (Table 1). Our assignment of these Clayton Limestone Unit teeth to *Carcharias* is based on the overall similarities of many Paleogene species from this genus reported in sources such as Kent (1994). Review of both historical and current North American literature demonstrates these similarities and the problems associated with taxonomic classification based on isolated teeth. Although outside the scope of this paper, further study and taxonomic revision is needed for many Cenozoic North American sand tiger sharks to resolve these classification issues.

Family Cretoxyrhinidae Glickman, 1958
Genus *Cretalamna* Glickman, 1958

Cretalamna **sp.**
Figures 4.7a–10a

Material examined — ANSP 23249, one anterior tooth; ANSP 23250, one lateral tooth; ANSP 23251, one additional lateral tooth.

Description — Three teeth from 13–14 mm in total height; central cusp smooth, triangular and erect in anterior tooth, distally inclined in lateral tooth; lingual face convex and labial face flat with smooth cutting edges; single, broad,

Arkansas Species	NJ	CBR	VA	NC	SC	GA	AL	MS	LA	TX	SD	ND
Odontaspis winkleri		X	X					X				
Carcharias* Cf. *C. whitei	X[1]	X	X[1]	X[2]				X[1]				
***Carcharias* sp.**		X[3]	X[3]	X[3]	X[3]	X[3]	X[3]	X[3]	X[3]			
***Cretalamna* sp.**	X[3]	X[3]	X[3]		X[2]		X[2]			X[2]		
Anomotodon novus		X	X					X[2]				
Otodus obliquus		X	X	X	X						X	X
Hypolophodon sylvestris	X	X	X								X	X
Myliobatis dixoni		X	X	X[2]	X[2]	X[2]	X[2]	X	X[2]	X[2]	X[2]	X[2]

Table 1. Geographic distribution in North America of Clayton Limestone Unit sharks and rays discussed in this report.

NOTES:
Acronyms: NJ - New Jersey; CBR - Chesapeake Bay Region; VA - Virginia; NC - North Carolina; SC - South Carolina; GA - Georgia; AL - Alabama; MS - Mississippi; LA - Louisiana; TX - Texas; SD - South Dakota; ND - North Dakota. References: NJ - Case, 1996; CBR - Kent, 1994; Ward & Wiest, 1990; VA - Kent, 1999, Part 2; Kent, 1999, Part 3; NC - Case & Borodin, 2000; SC - Purdy, 1998; GA - Parmley *et al.*, 2003; Case, 1981; AL - Thurmond & Jones, 1981; MS - Case, 1994; LA - Manning & Standhardt, 1986; TX - Stidham *et al.*, 2008; SD - Cvancara & Hoganson, 1993; ND - Cvancara & Hoganson, 1993. Superscripts: 1 – listed as *Carcharias teretidens*; 2 – *Carcharias*, *Cretalamna*, *Anomotodon* and *Myliobatis* genera occur in these states and are similar to the Clayton Limestone Unit specimens. However, no species names were assigned; 3 – Species similar to the Clayton Limestone Unit specimens occur in these states.

triangular cusplets on mesial and distal root lobes in anterior tooth; pair of triangular and divergent cusplets on lateral teeth with secondary cusplets near edge of root lobe substantially smaller; outer edges of root lobes relatively straight and directly below tooth crown; shallow U-shaped interlobe area; lingual root protuberance; no nutritive groove; holaucorhizous root.

Discussion — *Cretalamna* sp. teeth can be distinguished from most other teeth in the Clayton Limestone Unit by the presence of a smooth faced, broad triangular cusp and triangular cusplets that are continuous with the cusp. These teeth are substantially smaller in total height than *Otodus obliquus* Agassiz, 1843 from the Clayton Limestone Unit whose lingual central cusp and cusplets are more convex and robust. Another Maastrichtian species found in the Arkadelphia Formation that shares some similar characteristic to Clayton Limestone Unit *Cretalamna* sp. is *Serratolamna serrata* (Agassiz, 1843); (Becker *et al.*, 2006). Teeth belonging to *S. serrata* display tooth asymmetry, multiple diverging cusplets, smooth crown faces, and a short nutritive groove (Landemaine, 1991; Welton & Farish, 1993; Kent, 1994). None of these features is noted to occur in members belonging to Clayton Limestone Unit *Cretalamna* sp. Subsequent study in the Arkadelphia Formation of Hot Spring County, Arkansas since Becker *et al.*, (2006) indicates the occurrence of *Cretalamna appendiculata* (Fig. 4.9–10). *Cretalamna* sp. teeth from the Clayton Limestone Unit can be distinguished from those belonging to *C. appendiculata* by their overall larger size, narrower cusp base and well-defined bilobate roots.
These teeth differ in their morphology from those traditionally assigned to *C. appendiculata* and other *Cretalamna* species and subspecies infrequently reported from the Cretaceous and Paleogene in North America such as *C. biauriculata maroccana* (Arambourg, 1935) (see Kent, 1994). *C. appendiculata* is a well-reported species with a long chronological range (Albian – Ypresian) and a worldwide geographic distribution (Cappetta, 1987; Shimada, 2007). Such a long chronological range is atypical of any Cretaceous – Paleogene chondrichthyan species and supports the need for a revision of species assigned to this genus, particularly those surviving the K/P mass extinction.

Family Mitsukurinidae Jordan, 1898
Genus *Anomotodon* Arambourg, 1952

Anomotodon novus (Winkler, 1874)
Figure 4.11a–b

1874 *Oxyrhina nova* Winkler, p. 7, pl. 2, fig. 8.

Material examined — ANSP 23252, one lateral tooth.

Description — Single lateral tooth 13 mm in total height; central cusp smooth, distally inclined with complete cutting edges that extend across root lobes and incipient cusplets; edge of mesial root lobe rounded and projects outward beyond edge of tooth crown; distal root lobe directly below tooth crown; moderate lingual protuberance with weak nutritive groove; well-defined dental band on lingual face; holaucorhizous root.

Discussion — The *Anomotodon novus* tooth can be distinguished from other teeth in the Clayton Limestone Unit by its smooth central cusp and complete cutting edges that extend across root lobes and incipient cusplets. The incipient cusplets and complete cutting edges readily distinguish *A. novus* from those of *Scapanorhynchus* whose teeth are well represented throughout the late Cretaceous by multiple species. Teeth from another late Cretaceous species, *Paranomotodon angustidens* (Reuss, 1845) superficially resemble those of *A. novus*. However, the overall tooth size of *P. angustidens* is much smaller and the central cusp is more narrow, particularly near its base. Neither *Scapanorhynchus* sp. nor *P. angustidens* have been identified from the Arkadelphia Formation (Becker *et al.*, 2006). Only a few teeth of *A. novus* were recovered at the Clayton Limestone Unit site. *A. novus* is also known to occur in the Atlantic Coastal Plain (Table 1) and apparently is less frequently encountered. Additional species belonging to the genus *Anomotodon* that do not resemble *A. novus* may also be present in the late Cretaceous of North America (*e.g.* Case & Cappetta, 1997).

Family Otodontidae Glickman, 1964
Genus *Otodus* Agassiz, 1843

Otodus obliquus Agassiz, 1843
Figures 4.12a–13b

1843 *Otodus obliquus* Agassiz, p. 267-269, pl. 31, 36, figs. 22-27.

Material examined — ANSP 23253, one anterior tooth; ANSP 23254, one lateral tooth.

Description — Two teeth from 27–33 mm in total height; central cusp robust and smooth; anterior tooth triangular and erect; lateral tooth with distal hook; lingual face convex and labial face flat with smooth cutting edges; enameloid with broad wrinkles near central cusp base on labial face; single, well-defined triangular and divergent cusplet in anterior tooth; broad, triangular and divergent cusplet with distinct notch on distal root lobe; root lobes incomplete; root lobe elongated and rounded in anterior tooth; root lobe straight and compressed in lateral tooth; majority of root lobe directly below tooth crown; well-defined dental band on lingual face of anterior tooth; multiple foramina throughout root lobes; no nutritive groove; holaucorhizous root.

Discussion — *Otodus obliquus* teeth are substantially larger and more robust than any other species recovered from the Clayton Limestone Unit. Additionally, the presence of multiple foramina throughout the root lobes, more narrow and divergent cusplets in the anterior tooth and distal hook on the lateral tooth readily distinguish this species from *C. appendiculata*. Other late Cretaceous species bear some resemblance to *O. obliquus* such as *Cretoxyrhina mantelli* although this species became extinct in North America well before the Maastrichtian (Shimada, 1997a).

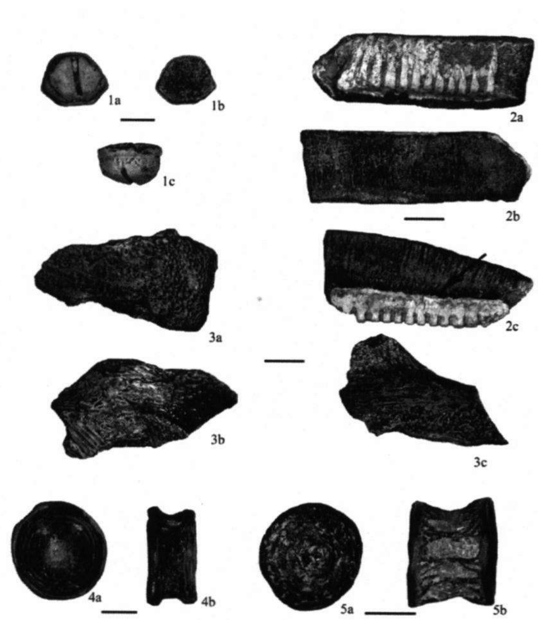

Figure 5. Teeth of Myliobatidae, chimaerid jaw fragment and vertebral centra from the Clayton Limestone Unit, Hot Spring County, Arkansas. 1– *Hypolophodon sylvestris* (ANSP 23255); 2– *Myliobatis dixoni* (ANSP 23256); 3– Chimaerid jaw fragment (ANSP 23259); 4–5– Vertebral centra (ANSP 23260–23261). Orientations: 1a, 2a, 3a = basal view; 1b, 2b, 3b = occlusal view; 1c, 2c, 3c = lateral; 4a, 5a = articular surface view; 4b,5b = dorsolateral view; All scale bars = 2.0 mm.

According to Cappetta (1987) and followed later by Kent (1994), *Otodus* may have arisen from *Cretalamna* and possibly represents the ancestor of some of the larger and later Cenozoic lamniforms. *O. obliquus* teeth are much larger than any encountered in the nearby Arkadelphia Formation (Becker *et al.*, 2006), and may represent a global trend toward lamniforms with greater total body lengths such as those deduced from teeth traditionally assigned to *Carcharodon megalodon* Agassiz, 1843; (*e.g.* Gotfried, 1996; Renz, 2002).

Superorder Batomorphii Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Family Dasyatidae Jordan, 1888
Genus *Hypolophodon* Cappetta, 1980

Hypolophodon sylvestris White, 1931
Figures 5.1a–c

1931 *Hypolophodon sylvestris* White, p. 70-73, figs. 94-115.

Material examined — ANSP 23255, one pavement crusher.

Description — Single tooth 4mm in greatest dimension (mesodistal width); crown relatively smooth, flat and hexagonal in occlusal view; basal ledge overhangs bilobate root; well-defined and centrally located nutritive groove; holaucorhizous root.

Discussion — The *Hypolophodon sylvestris* tooth can be distinguished from other batoid teeth in the Clayton Limestone Unit by its wide hexagonal outline, single and deep nutritive groove and flat crown surface. The species bears some resemblance to *Pseudohypolophus mcnultyi* (Thurmond, 1971) which is well-known from the late Cretaceous of North America (*e.g.* Cappetta & Case, 1975; Case & Schwimmer, 1988; Hartstein *et al.*, 1999; Becker *et al.*, 2004), although it has not been documented from the Arkadelphia Formation. *H. sylvestris* lacks the more numerous and larger foramina on the lingual and labial root faces just below the crown foot, and has a flatter and wider crown and shallower nutritive groove than *P. mcnultyi*. According to Kent (1999b), *H. sylvestris* is known from the early Paleocene through early Eocene of the New Jersey and the Chesapeake Bay Region. A survey of all available regional literature suggests this is the first noted occurrence of the species in the Gulf Coastal Plain.

Family Myliobatidae Bonaparte, 1838
Genus *Myliobatis* Cuvier, 1817

Myliobatis dixoni Agassiz, 1843
Figures 5.2a–c

1843 *Myliobatis dixoni* Agassiz, p. 319.

Material examined — ANSP 23256, one pavement crusher. ANSP 23257 and ANSP 23258, two additional pavement crushers.

Description — Largest tooth 17 mm in greatest dimension (mesodistal width); crown mesodistally elongated, smooth, slightly arcuate, weakly convex and hexagonal; numerous longitudinal ridges on vertical crown faces; basal ledge overhangs root with numerous, roughly equally-dimensional, deep nutritive grooves; root polyaulacorhizous.

Discussion — The *Myliobatis dixoni* teeth can be distinguished from other batoid teeth in the Clayton Limestone Unit by their mesodistally elongated form, multiple nutritive grooves and roughly uniform thickness as seen in lingual view. Similar Paleogene species from North America include: *Myliobatis striatus* Buckland, 1837 and *Myliobatis latidens* Woodward, 1889. Kent (1999b) indicated that *M. dixoni* is the narrowest of these three species and has a width four times that of its length. The Clayton Limestone tooth compares favorably to these dimensions and is the most commonly occurring batoid at this site. Two additional genera of dasyatids, *Aetobatus* sp. Blainville, 1816 and *Rhinoptera* sp. Cuvier, 1829 bear some resemblance to *M. dixoni* from the Clayton Limestone Unit. However, these genera are noted to appear in the early Eocene (*e.g.* Cappetta, 1987; Weems, 1999). Similar teeth from the late Cretaceous to *M. dixoni* are those from *Brachyrhizodus wichitaensis* Romer, 1942. This species is not represented in the Arkadelphia Formation although it is common in Campanian chondrichthyan faunas in North America (*e.g.* Case & Schwimmer, 1988; Robb, 1989; Welton & Farish, 1993). Teeth from *B. wichitaensis* are wider and possess far fewer nutritive grooves than those of *M. dixoni*.

Order Chimaeriformes

Chimaerid sp. indet.
Figures 5.5a–c

Material examined — ANSP 23259 one incomplete (right mandibular?) jaw fragment.

Description — One incomplete (right mandibular?) jaw fragment with longest dimension 6mm; osseous surfaces in occlusal, lateral and basal views; fragmentary tritors present.

Discussion — The occurrence of chimaerids from the late Cretaceous and Paleogene of North America has been well-documented from multiple locations by a number of species belonging to the genera *Ischyodus* and *Edaphon* (*e.g.* Case, 1978; Case & Schwimmer, 1992; Hoganson & Murphy, 2002; Stahl & Parris, 2004; Parmley & Cicimurri, 2005; Cicimurri *et al.*, 2008). While the osseous jaw fragment with tritors from the Clayton Limestone Unit is characteristic of members of this order, its fragmentary nature precludes any higher order taxonomic classification. To date, chimaerids have been unreported in the fossil literature of Arkansas but are known from the bordering states of Texas and Mississippi (Manning & Dockery, 1992; McKinzie *et al.*, 2001).

Various species indet. - vertebral centra
Figures 5.6a–7b

Description — Two vertebral centra with articular surface 6 mm in diameter; articular surface circular with multiple concentric lamella and centrally-located birthmark; vertebral rim well-defined; large foramina for basal cartilage in dorsolateral view (see arrows); radial lamella in lamnoid-type vertebra in dorsolateral view; carcharhinoid-type vertebra dorso-laterally compressed; lamnoid-type vertebra dorso-laterally elongated.

Material examined — ANSP 23260, one lamnoid-type vertebral centra; ANSP 23261, one carcharhinoid-type vertebral centra.

Discussion — In addition to the chondrichthyan teeth, a number of lamnoid-type and carcharhinoid-type vertebral centra were also recovered from the Clayton Limestone Unit. Lamnoid-type vertebral centra have many septa and large, paired basidorsal and basiventral foramina while carcharhinoid-type vertebral centra lack paired foramina, are more solid, and lack distinctive septa (Shimada, 1997b; Blanco-Piñón *et al.*, 2005; Becker *et al.*, 2008). Association of isolated chondrichthyan vertebrae with any particular species is problematic as demonstrated by the well-known late Cretaceous lamniform, *Squalicorax* sp. In this species, teeth and associated teeth tissues are those of a lamniform but vertebral centra are more similar to those of a carcharhiniform (Shimada & Cicimurri, 2005; Becker *et al.*, 2008). In this regard, the Clayton Limestone Unit vertebrae are no exception and little is known about the skeletal anatomy of Paleogene chondrichthyans from North America. The presence of carcharhinoid-type vertebral centra may also suggest that Paleogene sharks belonging to carcharhiniforms occur in the Clayton Limestone Unit, although none were recovered during this research project. This interpretation is supported by the appearance of multiple genera of carcharhiniforms in North America and globally during the Paleocene (*e.g.* Gurr, 1963; Arambourg, 1952; Cappetta, 1987; Kent, 1994).

Discussion

Composition of the Clayton Limestone chondrichthyan assemblage

As indicated in the discussions above, the chondrichthyans recovered from the Clayton Limestone site represent species widely-known from North America (Table 1). Absent from the Clayton Limestone site are chondrichthyan species belonging to orders including: Hexanchiformes, Squaliformes, Squatiniformes, Heterodontiformes, Orectolobiformes and Carchariniformes. In North America, species belonging to these orders have been documented elsewhere during the Paleocene but are few in number (*e.g.* Ward & Weist, 1990; Case, 1994). Kent (1994) indicated that such species may be infrequently encountered due to small size, species rarity, and offshore pelagic life modes. It is important to note that teeth from most North American Paleocene species belonging to the above mentioned orders are less than 1.0 cm in total height. Thus, the apparent rarity of these chondrichthyan species at some localities may be in part the result of sampling techniques. Our bulk sampling techniques both on site and in the laboratory utilized sieves with mesh sizes capable of recovering chondrichthyan teeth well within this size range. Additionally, sediment samples throughout the entire site were collected and sieved. Similar techniques were employed at our nearby Arkadelphia site where multiple examples of small teeth belonging to Squatiniforms, Orectolobiforms, and Carchariniforms were recovered (Becker *et al.*, 2006). No lag deposits indicative of taphonomic effects were encountered at the Clayton Limestone site. Individual teeth were eroding directly out of the light-colored limestone, marl and sandy marl intervals and are sporadically distributed. Such lags are known to concentrate chondrichthyan teeth from all sizes, including those less than 1.0 cm, and may bias age, abundance and palecological interpretations (*e.g.* Case & Schwimmer, 1988; Eaton *et al.*, 1989; Ward & Weist, 1990; Manning & Dockery, 1992; Rogers & Kidwell, 2000; Burris, 2001; Becker *et al.*, 2010a). Additional bulk sampling may result in the recovery of a few more chondrichthyan species with small teeth belonging to the above mentioned orders. However, it is evident by comparison to other contemporaneous formations from single locations, that the Paleocene chondrichthyan record in North America is limited in species diversity when compared to the late Cretaceous and Eocene.

In the Gulf Coastal Plain, few reports exist on the occurrence of Paleocene chondrichthyans. To date, these include a late Paleocene–early Eocene assemblage from Mississippi and Alabama (Thurmond & Jones, 1981; Case, 1994), and a preliminary report of a late Paleocene fauna from the Calvert Bluff Formation of Texas (Stidham & Janus, 2008). Additional chondrichthyan reports from the Gulf Coastal Plain states are from the Eocene or younger (*e.g.* Manning & Standhardt, 1986; Case & Borodin, 2000; Hulbert, 2001; Parmley *et al.*, 2003). In this regard, the Clayton Limestone chondrichthyans provide another important snapshot of species diversity directly above the K/P boundary and during the Paleocene of the Gulf Coastal Plain.

Paleoecology, faunal turnover and extinction

The limestone, marl and sandy marl of the Clayton Limestone site along with the co-occurring invertebrate fossils are typical of a shallow tropical seaway that would have covered southwestern Arkansas during the Late Cretaceous and Paleogene. The Clayton Limestone chondrichthyans are represented by pelagic apex predators, shallow water pisciverous forms and durophagous shell-crushers, as evidenced by tooth morphology (Figs. 4–5). Such a diverse range of feeding modes are typical of other contemporaneous chondrichthyan assemblages throughout North America and reflect analogous shallow marine and near-shore ecosystems.

No Cretaceous–Paleogene chondrichthyans indicative of brackish or transitional marine conditions such as *Myledaphus bipartitus* Cope, 1875b (*e.g.* Bryant, 1989; Wroblewski, 2004) were recovered at the Clayton Limestone site. However, evidence also indicates that Arkadelphia Formation-Midway Group shoreline had nearby fluvial connections as documented by the presence of fragments of wood and plants and osteichthyans belonging to the Acipenseridae and Lepisosteidae (Becker *et al.*, 2010b). Osteichthyans from these two families have both fossil and modern representatives known to inhabit a broad range of salinities.

Squatina hassei	
Ginglymostoma lehneri	
Plicatoscyllium derameei	
Ondontaspis aculeatus	*Odontaspis winkleri*
Carcharias cf. *holmdelensis*	*Carcharias* cf. *whitei*
Serratolamna serrata	*Carcharias* sp.
Cretalamna appendiculata	*Cretalamna* sp.
Squalicorax kaupi	*Anomotodon novus*
Galeorhinus giradoti	*Otodus obliquus*
Rhinobatos casieri	*Hypolophodon sylvestris*
Ischyrhiza avonicola	*Myliobatis dixoni*
Ischyrhiza mira	
Sclerorhynchus sp.	
Schizorhiza cf. *stromeri*	
Ptychotrygon cf. *vermiculata*	
Raja farishi	
Rhombodus binkhorsti	
Dasyatis sp.	

Table 2. Chondrichthyans reported from the Arkadelphia Formation (left) and Clayton Limestone Unit of the Midway Group, (right) Hot Springs County, Arkansas. Occurrence data for the Arkadelphia Formation is from Becker *et al.* (2006).

A comparison between chondrichthyans recovered from the Arkadelphia Formation and Clayton Linestone Unit in Hot Spring County is given in Table 2. Only three genera, *Odontaspis*, *Carcharias*, and *Cretalamna*, represented by different Maastrichtian and Paleocene species, occur in both assemblages. The most striking differences between the two assemblages occur in the Rajiforms, particularly those belonging to the Sclerorhynchidae. All species belonging to the genus *Rhombodus* and family Sclerorhynchidae are known to go extinct at the K/P boundary (Kriwet & Benton, 2004). In their analysis of chondrichthyan diversity across the K/P boundary, Kriwet & Benton (2004) also indicated that six other chondrichthyan families go extinct along with genera *Scapanorhynchus*, *Paranomotodon*, *Archaeolamna* and *Squalicorax* at this boundary. These families and genera are well-known throughout the Campanian–Maastrichtian of North America with *Squalicorax kaupi* occurring in the Arkadelphia Formation.

Based on tooth morphology comparison between similar Arkadelphia Formation and Clayton Limestone Unit species included in the discussions above, many of these extinctions at the genus and species levels were replaced by groups with similar adaptations. Pavement crushers belonging to Myliobatiforms below and above the K/P boundary share similar morphological characteristics, although teeth from *M. dixoni* are generally larger. Such similarities ideally evolved to exploit the abundance of benthic mollusks and invertebrates found throughout the shallow marine environments during the Maastrichtian–Paleocene and found throughout North America and elsewhere. Teeth from the genera *Odontaspis* and *Carcharias* are also morphologically very similar with grasping dentitions evolved for pisciverous life modes (Applegate, 1965; Welton & Farish, 1993). The appearance of *O. obliquus* in the Paleocene also demonstrates replacement of pelagic apex predators across the K/P boundary. As indicated in the discussions above, tooth morphology in this species is similar to that of *C. mantelli* although this species became extinct in the early Campanian (Shimada, 1997a; 2007).

The geographic proximity of the Arkadelphia Formation–Clayton Limestone Unit sites offers a unique opportunity to sample extinction, replacement and survivorship in consecutive formations that cross the most well-studied mass extinction event in earth history. These sites support global studies (*e.g.* Kriwet & Benton, 2004) that indicate an evolutionary bottleneck in chondrichthyan diversity occurred during the end–Cretaceous mass extinction. Comparison of both assemblages also suggests that chondrichthyan diversity remained low in the Paleocene until radiation of fishes and marine mammals in the middle Cenozoic provided a resource base necessary for their diversification. Further investigation is necessary to document the exact timing and age of both chondrichthyan assemblages relative to the K/P boundary. However, the catastrophic effects of the of the K/P boundary mass extinction in southwestern Arkansas seem apparent.

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