Chondrichthyans from the Lower Clayton Limestone Unit of the Midway Group (Paleocene) near Malvern, Arkansas, USA, with comments on the K/Pg boundary

Harry M. Maisch, Martin A. Becker & Michael L. Griffiths

ONLINE FIRST

PalZ
Paläontologische Zeitschrift

Springer

www.palaeontologische-gesellschaft.de

Springer

Springer

RESEARCH PAPER

Chondrichthyans from the Lower Clayton Limestone Unit of the Midway Group (Paleocene) near Malvern, Arkansas, USA, with comments on the K/Pg boundary

Harry M. Maisch IV[1] · Martin A. Becker[1] · Michael L. Griffiths[1]

Abstract

The Lower Clayton Limestone Unit (LCLU) of the Midway Group (Paleocene) near Malvern, Arkansas, USA contains an assemblage of chondrichthyans recently exposed by excavation for highway stabilization. Chondrichthyan teeth in this assemblage belong to at least 12 taxa including: *Ginglymostoma subafricanum*, *Carcharias* cf. *whitei*, *Carcharias* sp., *Odontaspis winkleri*, *Palaeohypotodus rutori*, *Palaeogaleus vincenti*, *Dasyatis* cf. *hexagonalis*, *Dasyatis* sp., *Hypolophites* sp., *Myliobatis* sp., *Rhinoptera* sp., and an indeterminate chimaerid. Locally, these chondrichthyans occur within a stratigraphic section directly above the Cretaceous–Paleogene (K/Pg) boundary that also contains chondrichthyans. This occurrence is uncommon in the global fossil record and provides an opportunity to (1) assess chondrichthyan diversity across the K/Pg boundary in the Malvern region and Gulf Coastal Plain of southwestern Arkansas and (2) evaluate the timing of marginal to shallow marine chondrichthyan faunal turnover and extinction at a proximal location $\approx$ 1500 km from the Chicxulub, Mexico, K/Pg impact site. Observed patterns within this K/Pg stratigraphic section indicate that changes in chondrichthyan assemblages are primarily the result of sea-level cyclicity and habitat losses that occurred across several million years.

Keywords Paleocene · Chondrichthyans · K/Pg boundary · Arkansas

Introduction

In the global fossil record, outcrop exposures that preserve chondrichthyan assemblages across both intervals of the K/Pg mass extinction boundary remain uncommon. Examples of this occurrence include (1) the New Egypt and Hornerstown Formations of Monmouth County, New Jersey (Case 1996; Case et al. 2001); (2) several phosphate basins in Morocco (Noubhani and Cappetta 1997; Noubhani 2010; Belben et al. 2017); (3) the Stevns Klint section in Denmark (Adolfssen and Ward 2014, 2015); and (4) the El Kef section in Tunisia (MacLeod et al. 2018). At these localities, major changes in chondrichthyan diversity are observed, although the exact magnitude and rate of recovery seen in these chondrichthyan assemblages differ below and above the K/Pg boundary.

For more than a decade, similar details have begun to emerge in a K/Pg boundary outcrop section near Malvern, Arkansas (Becker et al. 2006, 2011; Becker and Chamberlain 2012). Exposures of this section are related to ongoing river erosion as well as excavations for residential and industrial buildings. Near Malvern, chondrichthyan species found in the Maastrichtian Arkadelphia Formation are different from those in the overlying Paleocene Upper Clayton Limestone Unit (UCLU) of the Midway Group, and there is a noticeable reduction in species abundance and diversity between these formations (Becker et al. 2011). Over the last several years, an excavation for highway stabilization along Interstate-30 (I-30) has exposed a previously covered and unreported section of the Paleocene Lower Clayton Limestone Unit (LCLU) of the Midway Group directly adjacent to the Arkadelphia Formation and the Ouachita River. Recent fieldwork along the I-30 excavation led to the discovery and collection of fossil chondrichthyans concentrated into lag deposits from this LCLU section. These LCLU chondrichthyans completely differ from any species previously

---

Handling Editor: Jürgen Kriwet.

✉ Harry M. Maisch IV
maischh@wpunj.edu

1 Department of Environmental Science, William Paterson University of New Jersey, 300 Pompton Road, Wayne, NJ 07470, USA

reported from the Arkadelphia Formation, and only several species are found higher in the section and UCLU within the I-30 field site.

In this study, we describe a new Paleocene chondrichthyan assemblage from an outcrop of the LCLU of the Midway Group near Malvern, Arkansas. This assemblage is composed primarily of small teeth (≈ 0.5 to 25 mm) from chondrichthyans with marginal to shallow marine affinities found in contemporaneous strata of the Atlantic Coastal Plain of the United States, Western Europe, and northern Africa (e.g., Cappetta 2012; Bazzi et al. 2018). The unique stratigraphic occurrence of the LCLU chondrichthyans offers the opportunity to further access the effects of the K/Pg boundary mass extinction in the Gulf Coastal Plain of Arkansas. Chondrichthyan assemblages found in this K/Pg boundary section demonstrate extensive taxonomic turnover and the destructive effects of this global mass extinction on these highly mobile marine predators. Available evidence based on stratigraphy, chronological ranges, and sea-level cyclicity indicates that changes in these chondrichthyan assemblages are related to habitat losses that occurred across several million years.

Materials and methods

Regional geology, study location, and geologic age interpretation

In southwestern Arkansas, the coastal plain physiographic province is separated by the Ouachita Mountains to the north and a prominent border fault related to the formation of the Mississippi Embayment (Fig. 1; Haley et al. 1993, 2009; McFarland 2004). This coastal plain consists predominantly of Upper Cretaceous and Paleocene formations and is dissected by the Red, Little, Cossatot, Saline, Little Missouri, Ouachita, and Caddo rivers and their tributaries. Outcrops of these formations are limited due to dense vegetation overgrowth, and the best exposures occur along the banks and beds of these rivers and their tributaries.

Near the town of Malvern, Arkansas, the Arkadelphia Formation and Midway Group are discontinuously exposed and bisected by the Ouachita River. In this region, the uppermost Arkadelphia Formation is dark gray, thinly bedded micaceous marl with occasional lenses of glauconitic sands, bivalve shells, and chondrichthyan and osteichthyan teeth. A lithology change represented by a sharp and undulatory contact between the dark-colored micaceous marl of the uppermost Arkadelphia Formation and a light-colored, thick-bedded coquina lag with interbedded micrite and occasional lenses of fine-grained, cross-bedded quartz sand and rip-up clasts of Arkadelphia composition comprises the lowermost Midway Group (Figs. 2, 3, 4).

The Arkadelphia Formation and Midway Group (K/Pg boundary) contact is best exposed within the Ouachita River during times of low water flow (Figs. 3, 4). Stratigraphically, the coquina lag at this contact occurs within the lowermost Midway Group and is laterally discontinuous, varies in thickness from a few centimeters to over 30 cm thick in outcrops, and contains an upper surface exposing well-rounded quartz and phosphate pebbles and Late Cretaceous (Maastrichtian) vertebrate fossil assemblages. Large blocks of this coquina lag also occur scattered in deeper pools of the Ouachita River and have broken off from steeply dipping, submerged outcrops (e.g., Becker et al. 2016). This lag deposit has been previously interpreted to be part of a K/Pg boundary section and is supported by various lines of field evidence including (1) foraminifera (Cushman 1949); (2) palynology (Jones 1962); (3) magnetostratigraphy (Liddicoat et al. 1981); (4) geologic mapping (Haley et al. 1993, 2009; McFarland 2004); (5) ostracods (Pitakpaivan and Hazel 1994); (6) vertebrates (Becker et al. 2006, 2010a, 2013, 2016); and (7) dinoflagellates (Dastas et al. 2010).

Approximately 2.7 km to the NE of the K/Pg boundary lag deposit within Ouachita River, exposures of the Midway Group and upper Clayton Limestone Unit (UCLU) containing chondrichthyan and osteichthyan assemblages were originally reported by Becker et al. (2011) and Becker and Chamberlain (2012). This outcrop consists of nearly horizontal beds of light gray-white fossiliferous limestone as much as 0.5 m thick that are separated by thin sand and clay units. An unconformity between the light-colored Clayton Limestone Unit and red-brown sands and gravels of the overlaying Wilcox Group is also exposed near the top of this stratigraphic section.

More recently, excavations along I-30 have yielded an exposure of the Midway Group and both the Lower and Upper Clayton Limestone Units (LCLU–UCLU) directly adjacent to the K/Pg boundary in the Ouachita River as described above (Figs. 2, 3, 4). This outcrop is the source of the LCLU chondrichthyan assemblage documented in this study and consists of over 20 m of massive, dark gray clays containing invertebrate casts and molds, thin interbedded limestone units, and locally phosphatic, sand and pebble lag deposits. Examples of non-chondrichthyan fossils from the LCLU include shelled invertebrates, trace fossils, and osteichthyan and crocodilian remains (Fig. 5). The 12 chondrichthyan taxa described below can be found throughout this entire LCLU section and are concentrated within three lags deposits identified in Fig. 3c. Near the top of this section, the contact between the LCLU and UCLU of the Midway Group occurs, and approximately 5 m of light gray-white fossiliferous limestone beds with thin sand and clay units belonging to the UCLU are exposed (Figs. 3, 4). Chondrichthyan species occurring in this exposure of the

Fig. 1 Location maps for the Arkadelphia Formation–Midway Group K/Pg boundary section near Malvern, Hot Spring County, Arkansas, USA. **a** Reconstructed Late Cretaceous–Maastrichtian (1) and Paleocene–Danian; (2) shorelines across the Atlantic and Gulf Coastal Plains and Western Interior Seaway indicated by arrows (modified from Kennedy et al. 1998; Scotese 2014; Becker et al. 2016). **b** Physiographic provinces in Arkansas with field sites discussed in this study indicated by (X). **c** Geologic map of Upper Cretaceous and Paleocene formations within the Gulf Coastal Plain of southwestern Arkansas and the study area. Arrows and numbers 3–5 identify the Late Maastrichtian Arkadelphia Formation documented by Becker et al. (2006); the Upper Clayton Limestone Unit of the Midway Group (UCLU) documented by Becker et al. (2011), and the Lower Clayton Limestone Unit (LCLU) of the Midway Group documented in this study, respectively
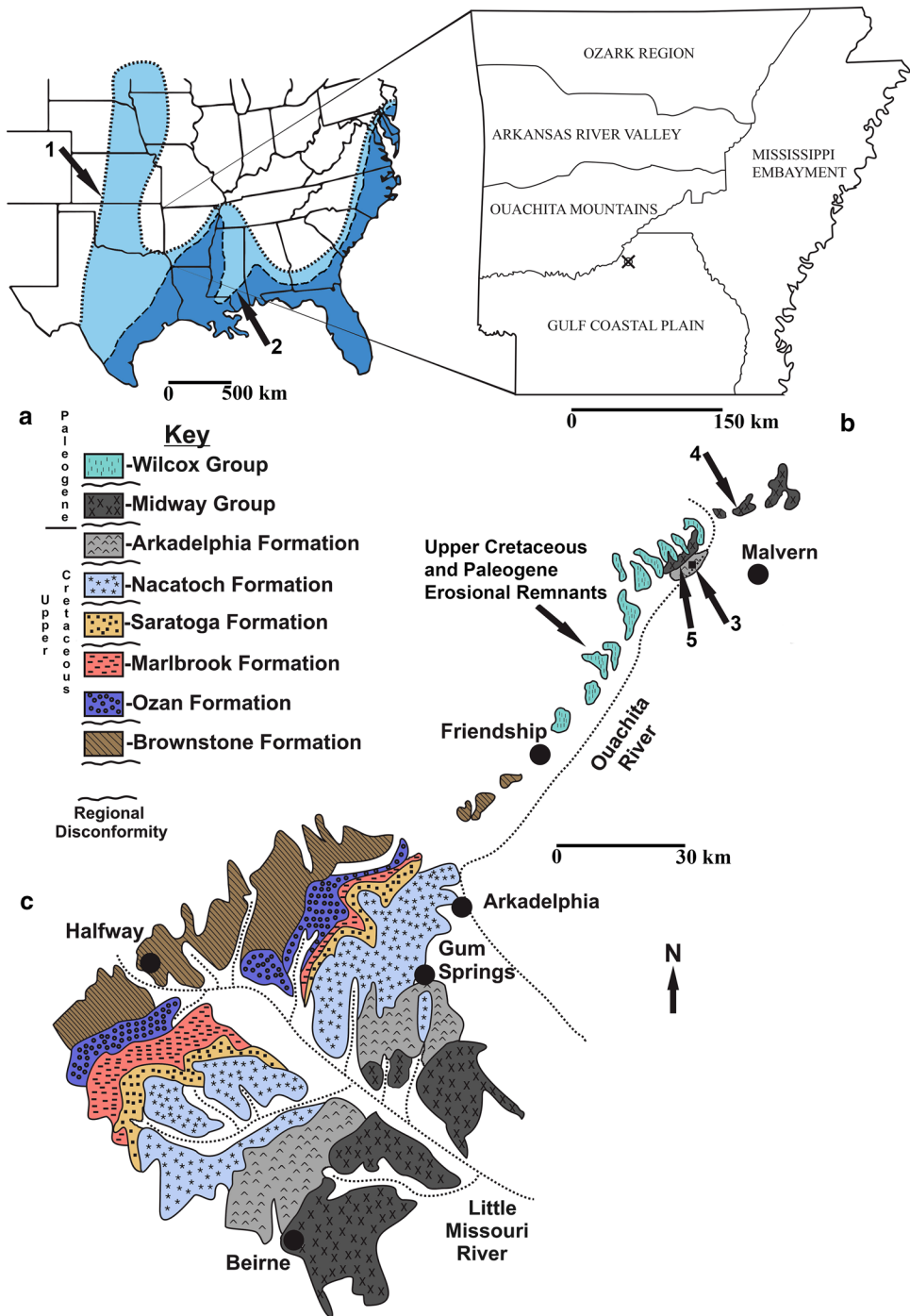

UCLU are the same as those previously reported ≈ 2.7 km to the NE by Becker et al. (2011).

The LCLU–UCLU in this localized stratigraphic section represents part of a large, rotational slide that occurs on both sides of I-30 (Fig. 2; also see Phillips et al. 2015; Hart 2017; Stringer and Sloan 2018). Beds of the LCLU on the northern side of the highway strike N 10°E and dip ≈ 25° to 30° to the NW. At the top of this section and within the UCLU, a fissure occurs as part of rotational sliding and loss of original horizontality (Fig. 3). On the southern side of the highway, beds of the LCLU as well as the K/Pg boundary contact and uppermost Arkadelphia Formation are exposed in the Ouachita River, strike N 5°–10°E as seen in Fig. 3 and dip between 50° and 75° to the NW.

Currently, the Midway Group in Arkansas has not been formally divided into formations or assigned specific stage boundaries within the Paleocene as recognized

Fig. 2 Geologic map (**a**) and corresponding cross-section (**b**) of the I-30 rotational slide and K/Pg boundary section near Malvern, Hot Spring County, Arkansas, USA. Numbers 1–9 in **a** correspond to specific locations identified in outcrop photos below. Note steeply dipping beds of the Arkadelphia Formation, coquina lag containing the K/Pg boundary, and Arkadelphia Formation–Midway Group contact in (1–3) of the cross-section. Chondrichthyans identified in the systematic paleontology of this report were collected from the Lower Clayton Limestone Unit (LCLU) of the Midway Group in (4–6) of the geologic map. A fissure related to rotational sliding occurs within (6) of the LCLU; the contact between the LCLU and Upper Clayton Limestone Unit (UCLU) occurs in (7); and small outcrop exposures of the UCLU and vegetative cover occur in (8–9)
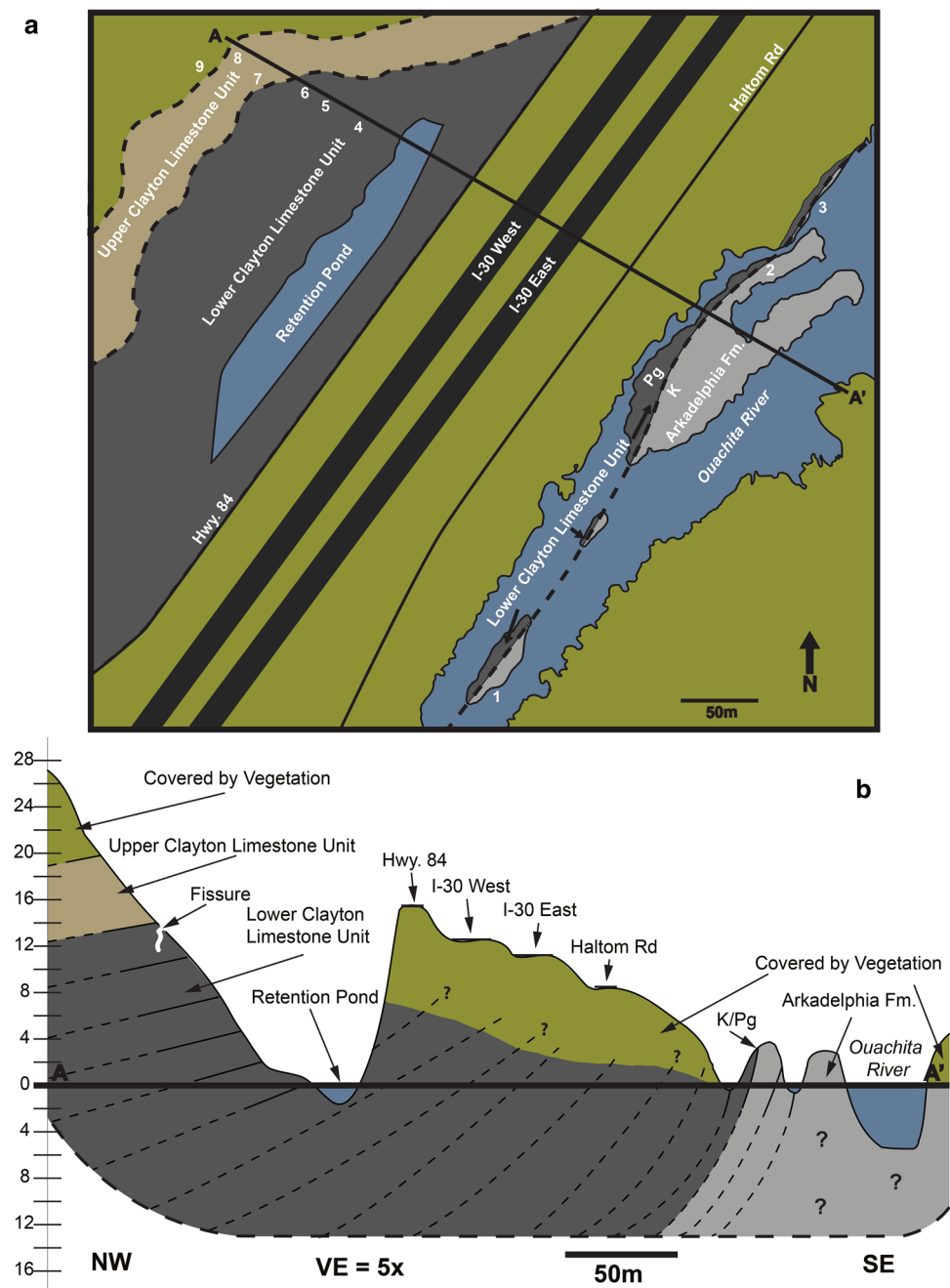
in the eastern Mississippi Embayment (e.g., McFarland 2004; Mancini and Puckett 2005). Preliminary data from dinoflagellates and otoliths indicate that the Midway Group exposed in this K/Pg boundary section near Malvern, Arkansas, is Paleocene (Danian) in age (Dastas et al. 2010; Stringer and Sloan 2018). Chondrichthyans found in the LCLU in this K/Pg boundary section discussed below have also been reported from the Danian of New Jersey, Denmark, and Morocco and support this age assignment.

Field and laboratory methods

LCLU chondrichthyans identified and described in this study consist primarily of teeth recovered through a combination of sieving sediment through 10.0–5.0-mm mesh in the field and bulk sampling of over 500 kg of sediment for laboratory processing. In the laboratory, sediment was thoroughly rinsed through 5.0–0.5 mm sieves, dried, and fossils were recovered with forceps using both a magnifying glass and an Olympus SZ61 binocular microscope attached to an

Infinity-2 digital camera. Primary literature sources utilized in taxonomic analysis of the LCLU chondrichthyans include Noubhani and Cappetta (1997), Cappetta (2012), and Adolfssen and Ward (2014, 2015). Vertebrate and invertebrate specimens identified and described in this study (Figs. 5, 6, 7, 8, 9, 10, 11, 12) have been reposited in the Academy of Natural Science (ANSP) of Drexel University, Philadelphia, Pennsylvania, USA under the catalog numbers ANSP: VP25069–25147 and ANSP: IP81670–81677. Matrix specimens included in Figs. 4, 5, and 13 from the coquina lag at the Arkadelphia Formation–Midway Group Contact in the Ouachita River and from the LCLU exposed adjacent to I-30 are included in the collections of the Department of Environmental Science at William Paterson University, Wayne, New Jersey, USA, under the catalog numbers WPU:AR:LCLU-1–3 and WPU:AR:MOR-1–4.

Systematic paleontology

Class **Chondrichthyes** Huxley, 1880
Subclass **Elasmobranchii** Bonaparte, 1838
Cohort **Euselachii** Hay, 1902
Subcohort **Neoselachii** Compagno, 1977
Order **Orectolobiformes** Applegate, 1972
Family **Ginglymostomatidae** Gill, 1862

Genus *Ginglymostoma* Müller and Henle, 1837

Ginglymostoma subafricanum Arambourg, 1952
Figures 6a–h, 12n

Studied material. Four anterior teeth and four lateral teeth. ANSP: VP25069–25077.

Description. Anterior teeth are symmetrical with an erect, central main cusp that is flanked by one to three pairs of lateral cusplets. Lateral teeth have narrower main cusps and lateral cusplets that are distally inclined and angled in the posterior direction. The primary cusplet in anterior and lateral teeth is larger and more erect than secondary cusplets. Anterior and lateral teeth generally have smooth lingual and labial surfaces, although faint grooves emanating from the intersection of the main cusp and lateral cusplets may occur on the labial surface. The basal labial tooth surface contains a rounded apron that extends below the crown–root interface. In lateral view, the labial surface is nearly flat while the lingual tooth surface appears concave. The roots of anterior and lateral teeth are hemiaulacorhizous and contain a well-developed lingual protuberance. The lingual protuberance contains a well-defined, central foramen and foramina on the mesial and distal margins. The basal root surface is slightly concave, contains a channel-like furrow, and central foramen.

Remarks. Teeth of *G. subafricanum* are distinct from those of *Palaeogaleus vincenti* (Daimeries, 1888) that also occur in the LCLU and *Ginglymostoma lehneri* (Leriche, 1938) and *Plicatoscyllium* cf. *derameei* Case and Cappetta, 1997, previously reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006). Teeth of *G. subafricanum* are labiolingually thickened, have broader cusps with erect cusplets, hemiaulacorhizous roots that contain several well-developed foramina, and labial aprons that overhang the crown–root interface which distinguishes them from teeth belonging to similar K/Pg chondrichthyans in the Malvern region. Teeth of *Ginglymostoma* species including *G. botmaense* (Noubhani and Cappetta, 1997); *G. chenanei* (Noubhani and Cappetta, 1997); *G. erramii* (Noubhani and Cappetta, 1997); *G. khouribgaense* (Noubhani and Cappetta, 1997); and *G. moroccanum* (Noubhani and Cappetta, 1997) are also similar to those of *G. subafricanum.* However, teeth from these species contain one or more of the following characteristics, which include greater numbers of lateral cusplets, reduced lateral cusplet height, slender main cusps, labial tooth surface furrows or ridges, well-developed bifid aprons at the base of the labial enamel, and broader tooth roots, making them distinct from those of *G. subafricanum* (Noubhani and Cappetta, 1997; Cappetta 2012). Additionally, teeth from genera including *Pseudoginglymostoma*, *Chiloscyllium*, *Hemiscyllium*, *Delpitoscyllium*, and *Plicatoscyllium* may appear similar to those of *G. subafricanum.* However, in comparison, teeth from (1) *Pseudoginglymostoma* sp. have fewer lateral cusplets that are reduced in height, contain labial tooth surface furrows or ridges, and are primarily known from the Maastrichtian of Africa; (2) *Chiloscyllium* sp. have lateral cusplets that are reduced in size or are entirely absent, are mesiodistally elongate, lack a distinct apron but contain enameloid that overhangs the root on the labial surface; (3) *Hemiscyllium* sp. have a single pair of well-developed lateral cusplets that either diverge from the main cusp or are rounded and form broad mesial and distal heels; (4) *Delpitoscyllium* sp. are dorsoventrally compressed, contain main cusps and primary cusplets that are nearly the same height and steeply inclined in the posterior direction, do not have more than two pairs of lateral cusplets, contain furrows or ridges on the labial tooth surface, and have heart-shaped roots; and (5) *Plicatoscyllium* sp. have well-developed labial surface furrows and ridges and broad, bifid labial aprons (for additional discussion see Noubhani and Cappetta 1997; Cappetta 2012; Adolfssen and Ward 2015). *Ginglymostoma* and many of the similar genera included in this summary are known from the Late Cretaceous-present day and as a result have a diverse fossil record (Cappetta 2012). However, differences in tooth morphology in *Ginglymostoma* and similar genera are often subtle, and as a result it is possible that earlier identifications may have been based on ontogenetic and intraspecific
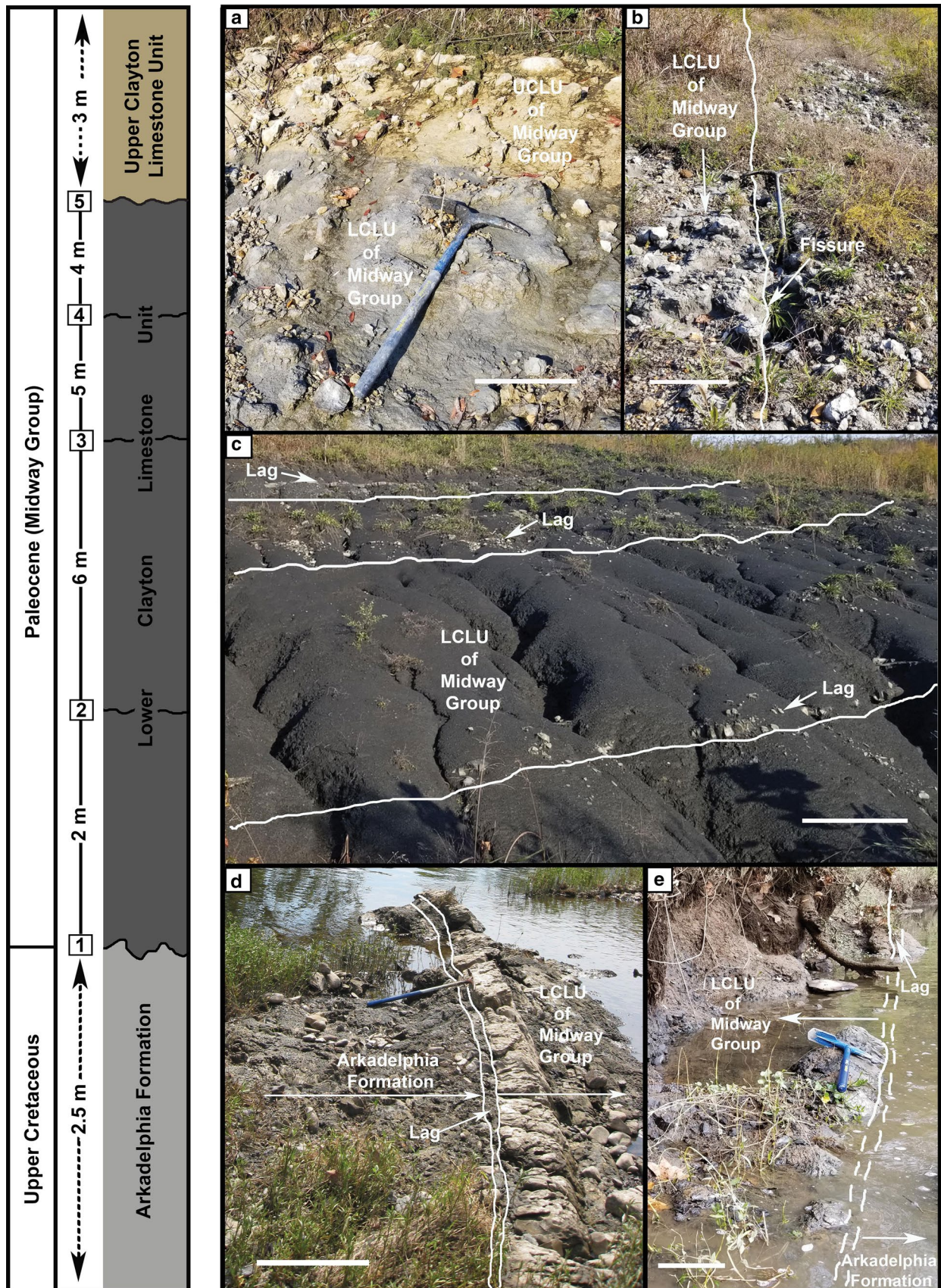
◄**Fig. 3** Stratigraphic column and outcrop photos of the K/Pg boundary section near Malvern, Hot Spring County, Arkansas, USA. **a** Lithology change across the contact between the Lower Clayton Limestone Unit (LCLU) and Upper Clayton Limestone Unit (UCLU) of the Midway Group. **b** Fissure within the LCLU. **c** Exposure of the LCLU containing three lag deposits indicated by arrows. **d, e** Outcrop exposures of the Arkadelphia Formation, coquina lag containing the K/Pg boundary, and Arkadelphia Formation–Midway Group contact within the Ouachita River. Note steeply dipping beds as the result of rotational sliding, coquina lag containing the K/Pg indicated by arrows, and lithology change between Arkadelphia Formation marl and Midway Group limestone. Numbers 1–4 on the stratigraphic column identify lag deposits in this K/Pg boundary section, and number 5 identifies the contact between the LCLU and UCLU. Scale bars in **a, b, e** 30 cm, and **c, d** 1 m

variations, biostratigraphic occurrence, and geographic location (Noubhani and Cappetta 1997; Cappetta 2012). Nonetheless, we identify these Malvern teeth as *G. subafricanum* since they are identical to those reported in prior taxonomic studies on K/Pg chondrichthyans in North America, Africa, and Europe (e.g., Ward and Wiest 1990; Case 1994; Kent 1994; Noubhani and Cappetta 1997; Cappetta 2012; Adolfssen and Ward 2015). *Ginglymostoma subafricanum* has previously been reported from the Paleocene of the Atlantic Coastal Plain of the USA and Morocco (Arambourg 1952; Ward and Wiest 1990; Noubhani and Cappetta 1997; Cappetta 2012); however, this study is the first to document this taxon in the Gulf Coastal Plain of the USA.

Order **Lamniformes** Berg, 1958
Family **Odontaspididae** Müller and Henle, 1839

Genus *Carcharias* Rafinesque, 1810

***Carcharias* cf. *whitei* (Arambourg, 1952)**
Figure 7a–f

Studied material. Two anterior teeth and four lateral teeth. ANSP: VP2578–25083.

Description. Anterior and lateral teeth have slender main cusps with apices that are distally curved and a single pair of small, triangular lateral cusplets. The lingual anterior tooth surfaces are convex and may contain faint ridges near the base of the cusp. Labial tooth surfaces are nearly flat and smooth. The main cusps of lateral teeth are broader and more triangular than those of anterior teeth, while lateral tooth cusplets are rectangular and flattened. As seen on the labial surface of anterior and lateral teeth, cusplets are connected with the enameloid of the main cusp. Anterior and lateral tooth roots are holaulacorhizous and those of anterior teeth are rounded and slender, while those of lateral teeth are labiolingually compressed. A lingual protuberance with a nutritive groove is present on all teeth with fully developed roots.

Remarks. Teeth of *Carcharias* cf. *whitei* are (1) identical to those previously reported from the UCLU near Malvern, Arkansas, by Becker et al. (2011); (2) distinct from those of *Carcharias* sp., *Odontaspis winkleri*, and *Palaeohypotodus rutori* that occur in the LCLU; (3) distinct from those of *Anomotodon novus* (Winkler, 1876) previously reported from the UCLU near Malvern, Arkansas, by Becker et al. (2011); and (4) distinct from those of *Odontaspis aculeatus* Case and Cappetta, 1997, and *Carcharias* cf. *holmdelensis* Cappetta and Case, 1975, previously reported from the Maastrichtian of Malvern, Arkansas, by Becker et al. (2006) based on the presence of slender main cusps, single, reduced, triangular lateral cusplets, and nearly smooth tooth crowns. Over the last several decades, numerous taxonomic revisions have occurred within the Odontaspididae to address newly described species, the paleobiogeographical distributions and biostratigraphic implications of certain species, and prior identification issues resulting from dignathic heterodonty and ontogenetic and intraspecific variation (e.g., Compagno 1977; Ward 1988; Siverson 1995; Purdy 1998; Cappetta and Nolf 2005; Cappetta 1987, 2012 and references therein). In regional and global K/Pg boundary chondrichthyan assemblages, species with teeth that may appear similar to those of *Carcharias* cf. *whitei* include *Scapanorhynchus texanus* (Roemer, 1849); *Scapanorhynchus raphiodon* (Agassiz, 1843); *Carcharias gracilis* (Davis, 1890); *Odontaspis speyeri* Dartville and Casier, 1943; *Striatolamia cederstroemi* Siverson, 1995; *Striatolamia striata* (Winkler, 1876); *Brachycarcharias lerichei* (Casier, 1946); and *Sylvestrilamia teretidens* (Cappetta and Nolf, 2005). Teeth from these species frequently have one or more characteristics that include well-defined lingual furrows or striations, well-developed needle-like and broad lateral cusplets in all tooth positions, and larger overall sizes that distinguish them from *Carcharias* cf. *whitei* (Moreau and Mathis 2000; Cappetta 2012; Adolfssen and Ward 2015). Some of these species are known to go extinct at the end of the Cretaceous (*S. texanus*, *S. raphiodon*), while others are known from the late Paleocene–Eocene (*S. striata*, *S. teretidens*, *B. lerichei*) or appear to be endemic to certain regions during the Paleocene (*S. cederstroemi*, *O. speyeri*). Although teeth of *C. gracilis* are known from the Paleocene and have been poorly defined in prior studies, they can be distinguished from teeth of *Carcharias* cf. *whitei* teeth from the LCLU since they have larger lateral cusplets and completely lack lingual tooth surface ornamentation (Siverson 1995; Adolfssen and Ward 2015). Due to discrepancies in the taxonomic placement of certain species (including *Carcharias* cf. *whitei*), dignathic and

Fig. 4 Chondrichthyan teeth from the K/Pg boundary outcrop exposures near Malvern, Hot Spring County, Arkansas, USA. **a** *Carcharias* sp. tooth in lingual view from the Upper Clayton Limestone Unit (UCLU) of the Midway Group. **b** *Thalassinoides* isp. burrows from the marginal to shallow marine shelf of the UCLU. **c** *Carcharias* sp. chondrichthyan tooth in labial view from the Lower Clayton Limestone Unit (LCLU) of the Midway Group. **d** Coquina lag containing phosphatic sand and pebbles within the LCLU indicated by arrow. **e** Coquina lag matrix sample containing *Squalicorax kaupi* and *Serratolamna serrata* chondrichthyan teeth indicated by arrows (WPU:AR:MOR:1) from the K/Pg boundary (Arkadelphia Formation–Midway Group Contact) within the Ouachita River. **f** Exposure of the Arkadelphia Formation, coquina lag containing the K/Pg boundary and Arkadelphia Formation–Midway Group contact indicated by arrow, and LCLU within the Ouachita River. Note steeply dipping beds as the result of rotational sliding. Scale bars in **a**, **c**, **e** 2 cm and **b**, **d**, **f** 30 cm

intraspecific variability of *Carcharias* sp. teeth, and the global abundance of *Carcharias* species documented at or near the K/Pg boundary, we follow Becker et al. (2011) for consistency and tentatively identify these LCLU teeth as *Carcharias* cf. *whitei* (Cappetta and Nolf 2005; Cappetta 1987, 2012; Adolfssen and Ward 2015). However, we acknowledge that some researchers assign Paleocene *Carcharias* sp. teeth, including *Carcharias* cf. *whitei*, to *Striatolamia* and that the taxonomy of Paleocene *Carcharias*-like taxa may be further revised in future studies. *Carcharias* (*Striatolamia*) *whitei* has been previously reported from the Atlantic and Gulf Coastal Plains of the USA and northern Africa (Arambourg 1952; Ward and Wiest 1990; Becker et al. 2011; Cappetta 2012).

***Carcharias* sp.**
Figures 7g–l, 12k–l

Studied material. Two anterior teeth and four lateral teeth. ANSP: VP25084–25091.

Description. Anterior and lateral teeth have main cusps with apices that are nearly straight and a single pair of well-developed, triangular lateral cusplets. The lingual tooth surfaces are convex, labial tooth surfaces are nearly flat, and both are smooth. The main cusps of anterior teeth are narrower and more erect than those of lateral teeth that are broader, more elongate, and triangular in shape. As seen on the lingual and labial surfaces of anterior and lateral teeth, cusplets are connected to the enameloid of the main cusp. Anterior and lateral tooth roots are holaulacorhizous, rounded, thicker in lateral teeth, and contain a lingual protuberance with a nutritive groove.

Remarks. Teeth of *Carcharias* sp. are (1) identical to those previously reported from the UCLU near Malvern, Arkansas, by Becker et al. (2011); (2) distinct from those of *Carcharias* cf. *C. whitei*, *O. winkleri*, and *P. rutori* that occur in the LCLU; (3) distinct from those of *Anomotodon novus* (Winkler, 1876) previously reported from the UCLU near Malvern, Arkansas, by Becker et al. (2011); and (4) distinct from those of *Odontaspis aculeatus* Case and Cappetta, 1997, and *Carcharias* cf. *holmdelensis* Cappetta and Case, 1975, previously reported from the Maastrichtian of Malvern, Arkansas, by Becker et al. (2006) based on the presence of smooth and erect main cusps and well-defined and triangular lateral cusplets. Teeth of *Carcharias* sp. from the LCLU appear similar to those of *Carcharias samhammeri* (Cappetta and Case, 1975); *Carcharias gracilis* (Davis, 1890); and *Odontaspis speyeri* Dartville and Casier, 1943. However, teeth from these species frequently have larger, more robust main cusps and lateral cusplets in all tooth positions, anterior teeth that are recurved and

sigmoidal, and restricted chronological ranges and geographic distributions that distinguish them from *Carcharias* sp. from the LCLU near Malvern, Arkansas (Becker et al. 2011; Cappetta 2012; Adolfssen and Ward 2015). We follow Becker et al. (2011) and identify these teeth as *Carcharias* sp. due to discrepancies in the taxonomic placement of certain species, dignathic and intraspecific variability of *Carcharias* teeth, and the global abundance of *Carcharias* species documented at or near the K/Pg boundary (Siverson 1995; Cappetta and Nolf 2005; Cappetta 1987, 2012; Adolfssen and Ward 2015; Belben et al. 2017).

Genus ***Odontaspis* Agassiz, 1838**

***Odontaspis winkleri* Leriche, 1905**
Figure 8a–e

Studied material. Two anterior teeth and three lateral teeth. ANSP: VP25092–25096.

Description. Anterior and lateral teeth have a slender main cusp with two or more well-separated and pronounced lateral cusplets that progressively decrease in size on both tooth heels. The lingual surface of the main cusp and cusplets is convex and may contain well-defined striations, whereas the labial surface is smooth and nearly flat. In labial view, enameloid from the main cusp is connected to the lateral cusplets and may contain irregular furrows near the crown–root interface. Anterior and lateral tooth roots are holaulacorhizous with slender root lobes and contain a nutritive groove on the lingual surface.

Remarks. Teeth of *O. winkleri* are identical to those previously reported from the UCLU near Malvern, Arkansas, by Becker et al. (2011) and can be distinguished from those of *Carcharias* cf. *whitei*, *Carcharias* sp., and *P. rutori* that also occur in the LCLU by the presence of slender main cusps, two or more well-defined, needle-like and progressively smaller cusplets, striated lingual tooth surfaces, and irregular furrows at the base of the enameloid on the labial tooth surface. The similarity between teeth of *Odontaspis* and *Carcharias* led many early researchers to group these types of teeth in the genus *Odontaspis* (e.g., Agassiz 1837; Winkler 1876; Welton 1974; Case 1981). However, more recent taxonomic studies place teeth of *Carcharias* and *Odontaspis* into separate genera and distinguish between the two primarily on tooth size, lingual and labial tooth surface ornamentation, cusplet development, and cusplet number (Compagno 1977; Kent 1994; Cappetta 2012; Adolfssen and Ward 2014). Additional species occurring at or near the K/Pg boundary that have teeth similar to *O. winkleri* include *Odontaspis aculeatus*, *Odontaspis speyeri*, and *Striatolamia*
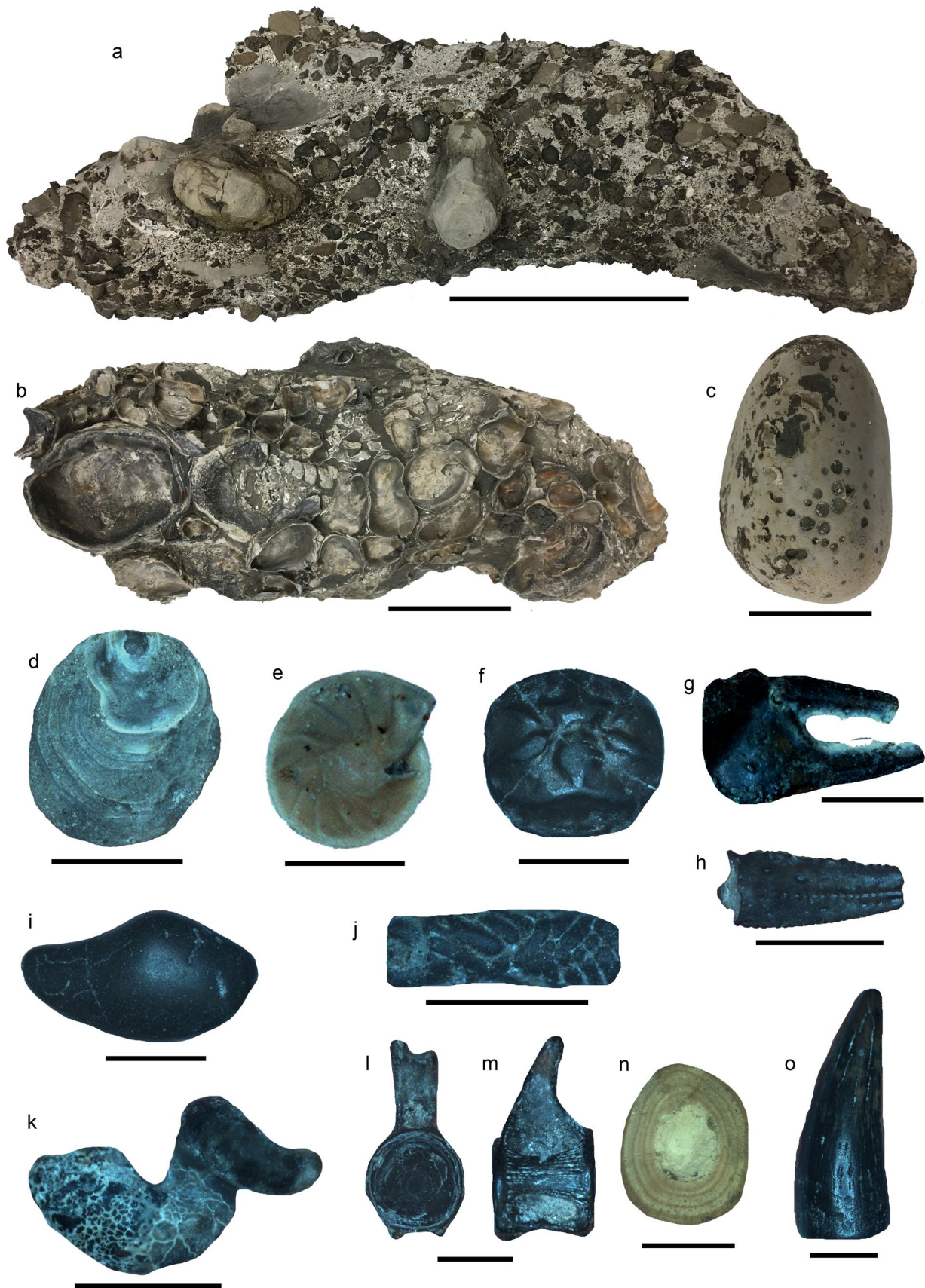
◄**Fig. 5** Sedimentary features, invertebrate and vertebrate fossils representing marginal to shallow marine depositional conditions co-occurring with Lower Clayton Limestone Unit (LCLU) chondrichthyans adjacent to I-30 near Malvern, Hot Spring County, Arkansas, USA. **a** Lithified gutter cast containing phosphatic pebbles, bivalve casts, crab carapace and claw elements, chondrichthyan teeth, osteichthyan bones and otoliths, and oyster shells (WPU:AR:LCLU-1). **b** Concretion containing gastropods and oyster growth (WPU:AR:LCLU-2). **c** Rounded cobble with *Gastrochaenolites* isp. borings (WPU:AR:LCLU-3). **d** Juvenile oyster valve (ANSP: IP81670). **e** *Lenticulina* sp. Foraminifera (ANSP: IP81671). **f** Crab carapace (ANSP: IP81672). **g**, **h** Crab claw elements (ANSP: IP81673–81674). **i** *Nuculana* sp. nut clam cast with *Entobia* isp. borings (ANSP: IP81675). **j** *Ophiomorpha* isp. burrow cast infilled with callianasid crustacean microcoprolites (ANSP: IP81676). **k** *Turritella* sp. gastropod cast with *Entobia* isp. borings and microcoprolitic sedimentary infill (ANSP: IP81677). **l**, **m** Articular and lateral views of indeterminate osteichthyan vertebrae (ANSP: VP25145). **n** Osteichthyan otolith (ANSP: VP25146). **o** Crocodilian tooth (ANSP: VP25147). Scale bars in **a** 10 cm; **b**, **c** 5 cm; **d**, **f**, **g**, **i**, **n** 5 mm; **e** 1 mm; **h**, **j**–**m**, **o** 2 mm

striata; however, these species have larger main cusps, fewer cusplets, and lack irregular furrows at the base of the enameloid on the labial tooth surface (Cappetta and Case 1975; Ward and Wiest 1990; Becker et al. 2006; Cappetta 2012). *Odontaspis winkleri* has previously been reported from the Paleocene in the Atlantic and Gulf Coastal Plains of the USA, Greenland, northern Africa, Europe, and New Zealand (Arambourg 1952; Bendix-Almgreen 1969; Ward and Wiest 1990; Baut and Genault 1995; Mannering and Hiller 2008; Becker et al. 2011; Cappetta 2012).

Genus *Palaeohypotodus* Glickman, 1964

Palaeohypotodus rutori (Winkler, 1876)
Figures 8f–n, 12m

Studied material. Three anterior teeth, three lateral teeth, and three posterior teeth. ANSP: VP25097–25106.

Description. Anterior teeth are robust, contain erect main cusps, and 1–2 conical lateral cusplets on both tooth heels that progressively decrease in size and are inclined towards the main cusp. Lateral teeth have wider main cusps that are angled distally and have smaller cusplets than anterior teeth. Posterior teeth have a greater distal inclination than lateral teeth, frequently have either a single pair of reduced lateral cusplets or only a single lateral cusplet on either the mesial or distal tooth heel. Posteriormost teeth have a weakly developed, shovel-shaped crown and do not contain lateral cusplets. The lingual tooth surfaces of anterior, lateral, and posterior teeth are smooth and convex, while the labial surface is nearly flat and may contain distinct, longitudinal furrows in the enameloid near the crown–root interface. Enameloid on the labial surface of anterior and lateral teeth frequently overhangs the root. Tooth roots of anterior, lateral, and posterior teeth are robust, holaulacorhizous, and U-shaped. A lingual protuberance containing a distinct nutritive groove is present in all but posteriormost teeth.

Remarks. Teeth of *P. rutori* are distinct from those of (1) *Odontaspis winkleri, Carcharias* cf. *whitei,* and *Carcharias* sp. that also occur in the LCLU, (2) *Cretalamna* sp. and *Otodus obliquus* Agassiz, 1843, that have previously been reported from the UCLU by Becker et al. (2011), and (3) *Odontaspis aculeatus* and *Serratolamna serrata* (Agassiz, 1843) previously reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006), based on the presence of robust teeth containing 1–2 pairs of conical cusplets, well-defined longitudinal furrows in the enameloid near the crown–root interface and enameloid that overhangs the root on the labial surface, and thick, U-shaped roots. In regional and global K/Pg boundary chondrichthyan assemblages, additional species with teeth similar to those of *P. rutori* include *Palaeohypotodus bronni* (Agassiz, 1843), *Odontaspis speyeri, Brachycarcharias lerichei, Glueckmanotodus heinzelini* (Casier, 1967), and *Jaekelotodus trigonalis* (Jaekel, 1895). These teeth can be distinguished from those of *P. rutori* by the presence of one or more of the following characteristics: noticeably larger main cusps, sigmoidal main cusps, lingual tooth surface ornamentation, lateral cusplets that are reduced in size and frequency, labially–lingually thinner teeth, and the occurrence of a concave, triangular sulcus at the base of the main cusp on the labial surface (e.g., Purdy 1998; Cappetta 2012; Adolfssen and Ward 2014). *Palaeohypotodus rutori* has been previously reported from the Paleocene in the Atlantic Coastal Plain of the USA, northern Africa, Greenland, Europe, and Asia (Glickman 1964; Bendix-Almgreen 1969; Herman 1973; Ward and Wiest 1990; Baut and Genault 1995; Case 1996; Cappetta 2012); however, this study is the first to document this taxon in the Gulf Coastal Plain of the USA.

Order **Carcharhiniformes** Compagno, 1973
Family **Triakidae** Gray, 1851

Genus *Palaeogaleus* Gurr, 1962

Palaeogaleus vincenti (Daimeries, 1888)
Figure 9a–n

Studied material. Three anterior teeth and eleven lateral teeth. ANSP: VP25107–25120.

Description. Anterior teeth have erect main cusps that are labiolingually thickened in contrast to lateral teeth that are labiolingually compressed and have distally inclined main cusps. Anterior and lateral teeth contain two or more lateral
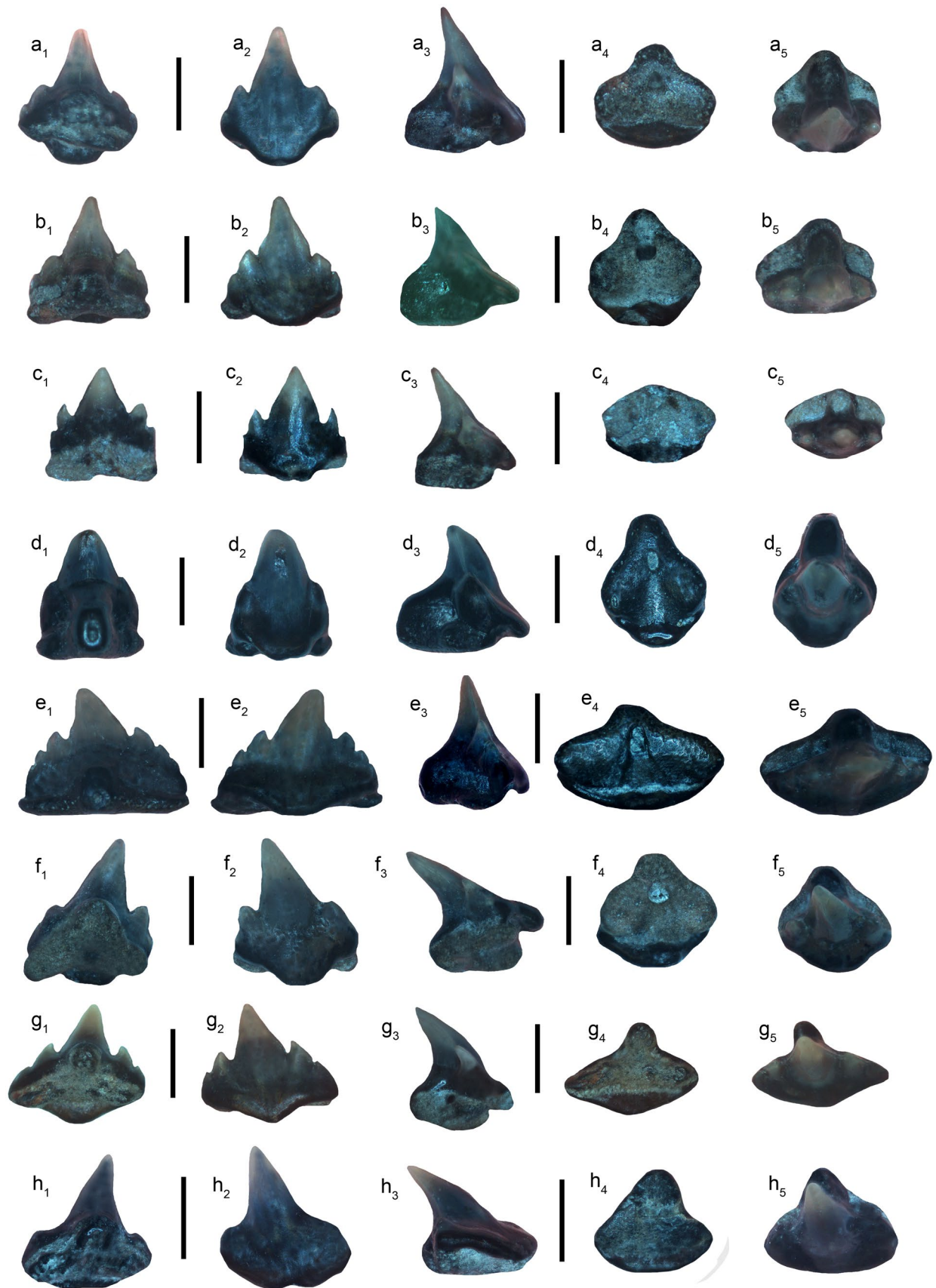
◄**Fig. 6** *Ginglymostoma subafricanum* teeth (ANSP: VP25069–25076) from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Variations in anterior teeth = a_1–d_5 and variations in lateral teeth = e_1–h_5. Orientations: Lingual = a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1. Labial = a_2, b_2, c_2, d_2, e_2, f_2, g_2, h_2. Lateral = a_3, b_3, c_3, d_3, e_3, f_3, g_3, h_3. Basal = a_4, b_4, c_4, d_4, e_4, f_4, g_4, h_4. Occlusal = a_5, b_5, c_5, d_5, e_5, f_5, g_5, h_5. Scale bars in **a**, **b**, **d**–**h** 2 mm; **c** 1 mm

cusplets on the mesial and distal heels that become progressively reduced and smooth in more posterior tooth positions. In lateral and posterior teeth, the distal heel is frequently shorter than the mesial heel, and the number of lateral cusplets on each side of the main cusp is frequently asymmetrical. Some anterior and lateral teeth have smooth margins and entirely lack cusplets. Anterior, lateral, and posterior teeth have smooth, convex lingual surfaces and slightly convex labial surfaces that overhang the root and contain longitudinal furrows near the crown–root interface. The roots of anterior, lateral, and posterior teeth are holaulacorhizous with a flat basal surface and contain a lingual protuberance with a nutritive groove and infrequent, small foramina.

Remarks. Teeth of *P. vincenti* can be distinguished from those of (1) *G. africanum* and posterior teeth of *P. rutori* that also occur in the LCLU and (2) *Galeorhinus girardoti* Herman, 1977, that have previously been reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of small teeth with slender main cusps, lateral cusplets that become progressively reduced or absent in posterior teeth, furrows at the base of the enameloid on the labial tooth surface, a protuberance containing a nutritive groove and foramina on the lingual root surface, and flat basal root surfaces. Although numerous *Palaeogaleus* species have been described in Late Cretaceous–Eocene chondrichthyan assemblages, those with teeth that are most similar to *P. vincenti* include the Late Cretaceous and Paleocene species *Palaeogaleus navarroensis* Case and Cappetta, 1997; *Palaeogaleus brivesi* (Arambourg, 1952); *Palaeogaleus larachei* Noubhani and Cappetta, 1997; *Palaeogaleus faujasi* (Geyn, 1937); *Palaeogaleus dahmanii* Noubhani and Cappetta, 1997; and *Palaeogaleus prior* (Arambourg, 1952). In addition to these species, those within the genera *Foumtizia*, *Danogaleus*, *Tingaleus*, *Galeorhinus*, and *Abdounia* may also contain teeth similar to those of *P. vincenti*. However, the morphological similarities in teeth among these species differ by containing one or more of the following characteristics: (1) teeth that are nearly symmetrical in all tooth positions, (2) the retention of lateral cusplets in all tooth positions, (3) well-defined, triangular cusplets, (4) wider main cusps, (5) serrated mesial or distal tooth heels, (6) longitudinal ridges on both lingual and labial tooth surfaces, and (7) restricted paleogeographic distributions (Noubhani and Cappetta 1997; Cappetta 2012;

Adolfssen and Ward 2014). We identify these LCLU teeth as *P. vincenti* since they are distinct from those of similar species and compare favorably with those previously reported in North America (e.g., Noubhani and Cappetta 1997; Case et al. 2001; Cappetta 2012; Adolfssen and Ward 2014). Due to the variable degrees of sexual, ontogenetic, and dignathic heterodonty that are known to occur in Triakid teeth, we also identify *Palaeogaleus* teeth that have smooth margins and lack lateral cusplets from the LCLU as *P. vincenti*. *Palaeogaleus vincenti* has been previously reported from the Paleocene in the Atlantic Coastal Plain of the USA, Greenland, and Europe (Gurr 1962; Bendix-Almgreen 1969; Ward and Wiest 1990; Baut and Genault 1995; Case 1996; Cappetta 2012); however, this study is the first to document this taxon in the Gulf Coastal Plain of the USA.

Order **Myliobatiformes** Compagno, 1973
Family **Dasyatidae** Jordan, 1888

Genus *Dasyatis* Rafinesque, 1810

Dasyatis cf. *hexagonalis* Arambourg, 1952
Figure 10a–d

Studied material. Five teeth. ANSP: VP25121–25125.

Description. Teeth of dasyatid species are known to exhibit a marked degree of sexual dimorphism. In general, the tooth crowns of females are globular-hexagonal in shape, and the tooth crowns of males are smooth, elongated, and hook-like. Using these general characteristics, we identify median and lateral teeth from both female and male *Dasyatis* cf. *hexagonalis* in the LCLU. Female median teeth have slightly convex occlusal surfaces that contain an abundance of fine surface pits and a large U-shaped lingual visor that is subdivided into two marginal faces by a dorsoventral ridge. Female lateral teeth also have a pitted occlusal surface that is roughly hexagonal in shape, contain a lingual visor that is not subdivided into two marginal faces, and a labial visor that is reduced in size and contains a shallow, U-shaped concavity rather than a uvula. The bilobate roots of female median and lateral teeth extend slightly beyond the lingual visor and have round, peg-like basal surfaces that are gently inclined in the posterior direction. Male median teeth have elongated, spine or hook-like crowns that are smooth, taper to a rounded apex, and curve in the posterior direction. When viewed laterally, the crowns of male teeth are noticeably thicker in the anterior–posterior dimension in comparison to the mesiodistal dimension. The crown–root interface of male median teeth is generally ovular in shape and forms a smooth apron. The labial surface of this apron is smooth, convex, and is the origination point for the upper, hook-like crown. The lingual surface of the apron is smooth, nearly flat, and
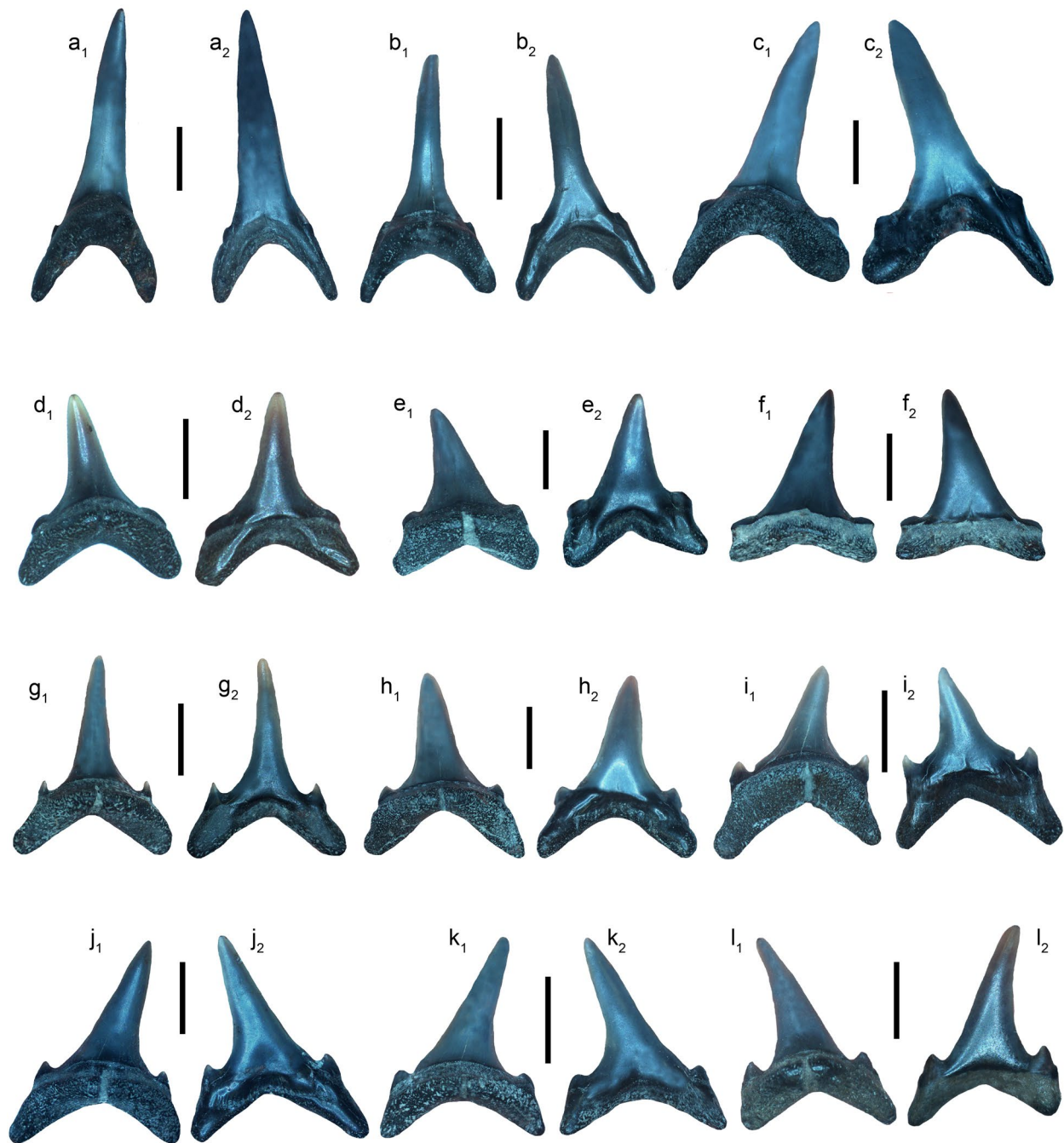
Fig. 7 *Carcharias* cf. *whitei* (a_1–f_2) (ANSP: VP25078–25083) and *Carcharias* sp. (g_1–l_2) (ANSP: VP25084–25089) teeth from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Note the difference in lateral cusplet size and shape between both species. Anterior teeth = a_1–b_2; g_1–h_2 and lateral teeth = c_1–f_2; i_1–l_2. Orientations: Lingual = a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1, j_1, k_1, l_1. Labial = a_2, b_2, c_2, d_2, e_2, f_2, g_2, h_2, i_2, j_2, k_2, l_2. All scale bars 5 mm

angled posteriorly. The roots of male median teeth begin on the lingual-half of the crown base, are short and peg-like, angled in the posterior direction, and protrude slightly beyond the lingual apron. Male lateral teeth are similar to male median teeth; however, the hook-like crown becomes distally inclined and slightly reduced in height.

Remarks. Teeth of *Dasyatis* cf. *hexagonalis* can be distinguished from those of (1) *Dasyatis* sp. that also occur in the LCLU and (2) *Dasyatis* sp. that has previously been reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of teeth with rounded-hexagonal, pitted occlusal surfaces and large lingual visors

Fig. 8 *Odontaspis winkleri* (a_1–e_2) (ANSP: VP25092–25096) and *Palaeohypotodus rutori* (f_1–n_2) (ANSP: VP25097–25105) teeth from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Note the multiple pairs of narrow lateral cusplets in *O. winkerli* teeth and the progressive loss of lateral cus-plets in posterior *P. rutori* teeth. Anterior teeth = a_1–b_2; f_1–h_2 and lateral teeth = c_1–e_2; i_1–k_2; posterior teeth = l_1–n_2. Orientations: Lingual = a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1, j_1, k_1, l_1, m_1, n_1. Labial = a_2, b_2, c_2, d_2, e_2, f_2, g_2, h_2, i_2, j_2, k_2, l_2, m_2, n_2. Scale bars in **a**, **g**, **h** = 5 mm; **b–f**, **i–l** = 2 mm; **m**, **n** = 1 mm

and teeth that are smooth, elongated, and hook-like in shape. Prior studies indicate that male *Dasyatis* sp. have hook-like teeth that are similar to those of *Raja* sp.; however, they are more elongated and posteriorly curved and contain peg-like, rounded root lobes that are angled posteriorly in contrast to the more conical crowns and divergent, flattened roots of *Raja* sp. The lack of triangular-conical teeth of female *Raja* sp. in the LCLU, and the occurrence of rounded teeth of *Dasyatis* sp. in the LCLU, further supports our identification. However, distinguishing between fossil species
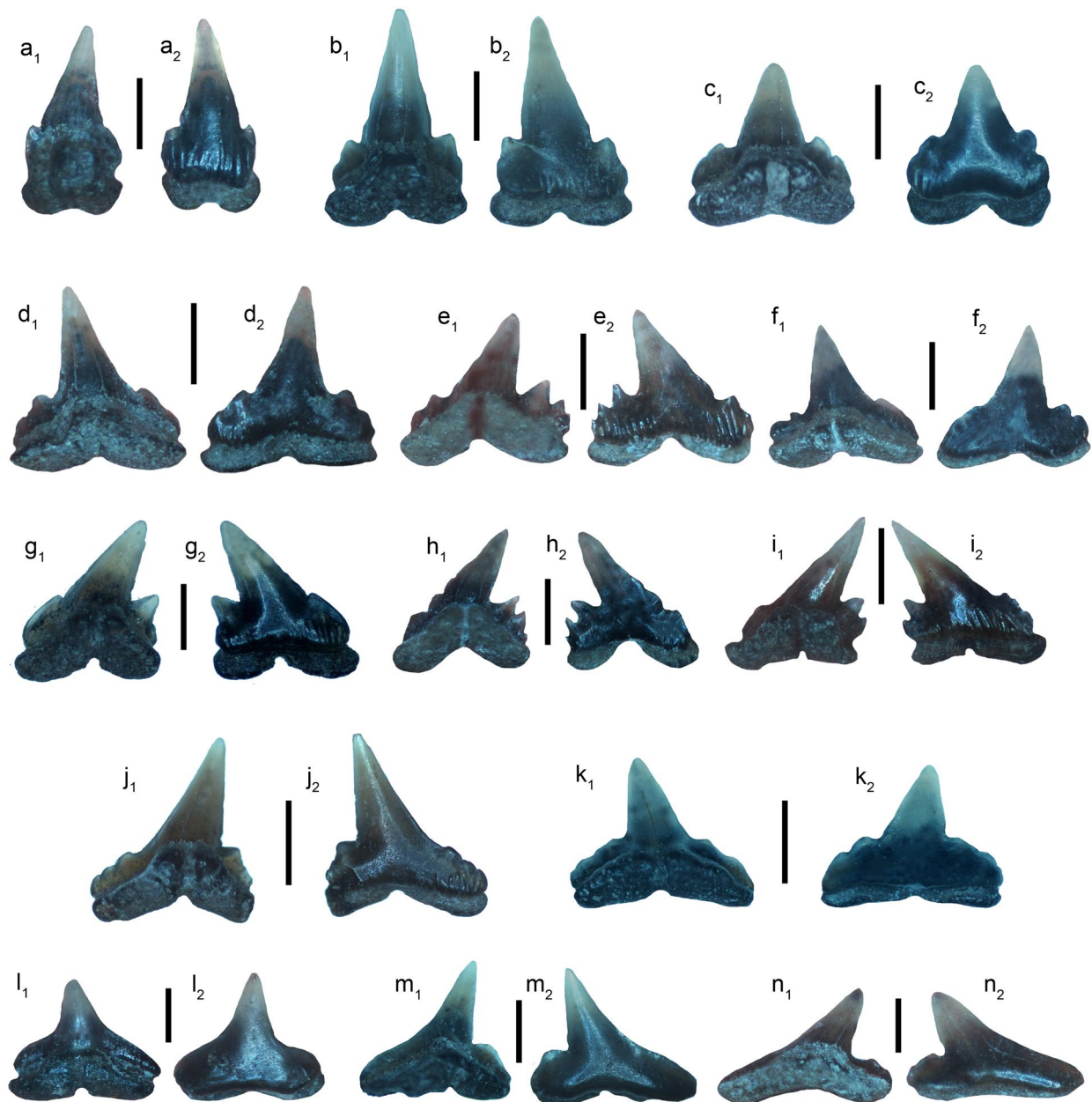
Fig. 9 *Palaeogaleus vincenti* teeth (a_1–n_2) (ANSP: VP25107–25120) from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Note longitudinal furrows in the lower labial enameloid surface and varying amount of lateral cusplets. Anterior teeth = a_1–c_2 and lateral teeth = d_1–n_2. Orientations: Lingual = a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1, j_1, k_1, l_1, m_1, n_1. Labial = a_2, b_2, c_2, d_2, e_2, f_2, g_2, h_2, i_2, j_2, k_2, l_2, m_2, n_2. All scale bars 1 mm

of *Dasyatis* based on isolated teeth can be difficult due to dignathic, ontogenetic, and sexual heterodonty, seasonal variations in tooth morphology, high degrees of intraspecific variation, the lack of articulated fossil dentitions, and poorly known dentitions of extant species (e.g., Kajiura and Tricas 1996; Kajiura et al. 2000; Herman et al. 1998, 1999, 2000; Rangel et al. 2014; Cappetta 1987, 2012; Underwood et al. 2015). As indicated by Cappetta (2012), the generic placement of many fossil species with dasyatid-like teeth is suspect, and dozens of species have been identified since the early Cretaceous from highly variable, isolated teeth and assigned to *Dasyatis*.

Several species that have teeth similar to those of *Dasyatis* cf. *hexagonalis* include *Dasyatis jaekeli* (Leriche, 1905); *Dasyatis tricuspidatus* Casier, 1946; *Dasyatis newegyptensis* Case et al. 2001, and *Palaeodasyatis hermani* Halter, 1989. However, teeth from these species differ from those of *Dasyatis* cf. *hexagonalis* since they may contain (1)

rounded-ovular occlusal surfaces with concave centers, (2) elongated labial visors with distinct anteroposterior furrows, (3) broad lingual visors that lack distinct uvulas, (4) roots with flattened basal surfaces, (5) restricted chronological and geographic ranges, and (6) the degree of intraspecific and sexual variation in teeth from these species is uncertain (for additional information see Halter 1989; Case 1994; Noubhani and Cappetta 1997; Case et al. 2001; Cappetta 1987, 2012; and references therein). We fully acknowledge these complications in identifying isolated fossil teeth of *Dasyatis* sp., and as a result tentatively identify these LCLU teeth as *Dasyatis* cf. *hexagonalis* based on similarities in tooth structure and chronological age with those originally reported from Morocco (Arambourg 1952; Noubhani and Cappetta 1997). Future studies on the taxonomy and distribution of dasyatid species and the variation of their teeth are needed to confirm the presence of *D. hexagonalis* in the LCLU or designate these teeth as a separate, distinct species. *Dasyatis hexagonalis* has been previously reported from the Paleocene in northern Africa (Arambourg 1952; Cappetta 2012). However, if these LCLU teeth do in fact belong to *D. hexagonalis*, then they would represent the westernmost occurrence of this species and first report of *D. hexagonalis* in North America.

***Dasyatis* sp.**
Figure 10f–g

Studied material. Two teeth. ANSP: VP25126–25127.

Description. As seen in labial, lingual, and lateral view, these dasyatid-type teeth have a triangular-globular shape. The labial surfaces have a roughly triangular cross-section, and the lingual surfaces contain a large, wide, and smooth visor, a conical posterior edge that forms two marginal faces, and a globular and irregularly pitted occlusal surface. In lateral view, the teeth have a triangular shape and a bilobate root that does not protrude beyond the labial crown surface and is located beneath the labial-most portion of the tooth. In basal view, the exposed dentine surface containing the root lobes is noticeably smaller than the overlying crown base.

Remarks. Teeth of *Dasyatis* sp. can be distinguished from those of (1) *Dasyatis* cf. *hexagonalis* that also occur in the LCLU and (2) *Dasyatis* sp. that have previously been reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of a triangular-globular, irregularly pitted occlusal surface, triangular cross-section, large lingual visor, and reduced, bilobate roots. As indicated in the *Dasyatis* cf. *hexagonalis* remarks above, many complications exist when identifying isolated fossil dasyatid-like teeth, and these LCLU specimens are no exception. Although *Dasyatis* sp. from the LCLU shares

some similarities, including a triangular profile and cross-section, and irregularly pitted occlusal surface, with *Dasyatis tetraedra* Arambourg, 1952, *Dasyatis datasi* Noubhani and Cappetta, 1997, *Viperecucullus kuehnei* Case, 1996, and other dasyatid species, we acknowledge that a high degree of intraspecific and ontogenetic variation is present in dasyatid teeth. As a result, we refrain from lower-level classification of these two, isolated specimens.

Genus ***Hypolophites*** Stromer, 1910

***Hypolophites* sp.**
Figure 11a–e

Studied material. One median pavement tooth and four lateral pavement teeth. ANSP: VP25128–25132.

Description. Median and lateral teeth have hexagonal-like occlusal surfaces containing minute enameloid pitting and thick crowns that overhang the labial root surface. Edges of the occlusal surface in median and lateral teeth may be (1) rounded and form a trilobate shape on the labial crown edge or (2) hexagonal and jagged. Median teeth are dorsoventrally thickened and mesiodistally elongated, whereas lateral teeth become progressively more compressed in the dorsoventral and mesiodistal dimensions. As seen in lateral view, the sides of median and lateral teeth contain well-defined, vertical wrinkles or furrows that extend from the occlusal surface to the crown–root interface. Median and lateral teeth also contain an enameloid apron on the lingual surface that slightly overhangs the crown–root interface. The roots of median and lateral teeth are bilobate, pentagonal to peg-like in shape, and have slightly convex, rounded basal surfaces.

Remarks. Pavement teeth of *Hypolophites* sp. from the LCLU can be distinguished from those of (1) *Dasyatis* cf. *hexagonalis*, *Dasyatis* sp., *Myliobatis* sp., and *Rhinoptera* sp. that also occur in the LCLU, (2) *Hypolophus sylvestris* White, 1931, and *Myliobatis dixoni* Agassiz, 1843, previously reported from the UCLU by Becker et al. (2011), and (3) *Rhombodus binkhorsti* Dames, 1881, previously reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of hexagonal to trilobate occlusal surfaces, well-developed, vertical wrinkles on the lateral tooth surfaces, and a bilobate root with rounded, basal surfaces. *Hypolophites* sp. teeth from the LCLU are also distinct from those of *Hypsobatis weileri* Cappetta, 1992 and *Myledaphus* sp. since they do not have a two-tiered occlusal surface, a transverse ridge and faint labiolingual folds on the occlusal and lateral surfaces, smooth lateral crown surfaces, and well-developed foramina near the crown–root interface, and are not known from the Late Cretaceous (e.g., Cappetta 2012).
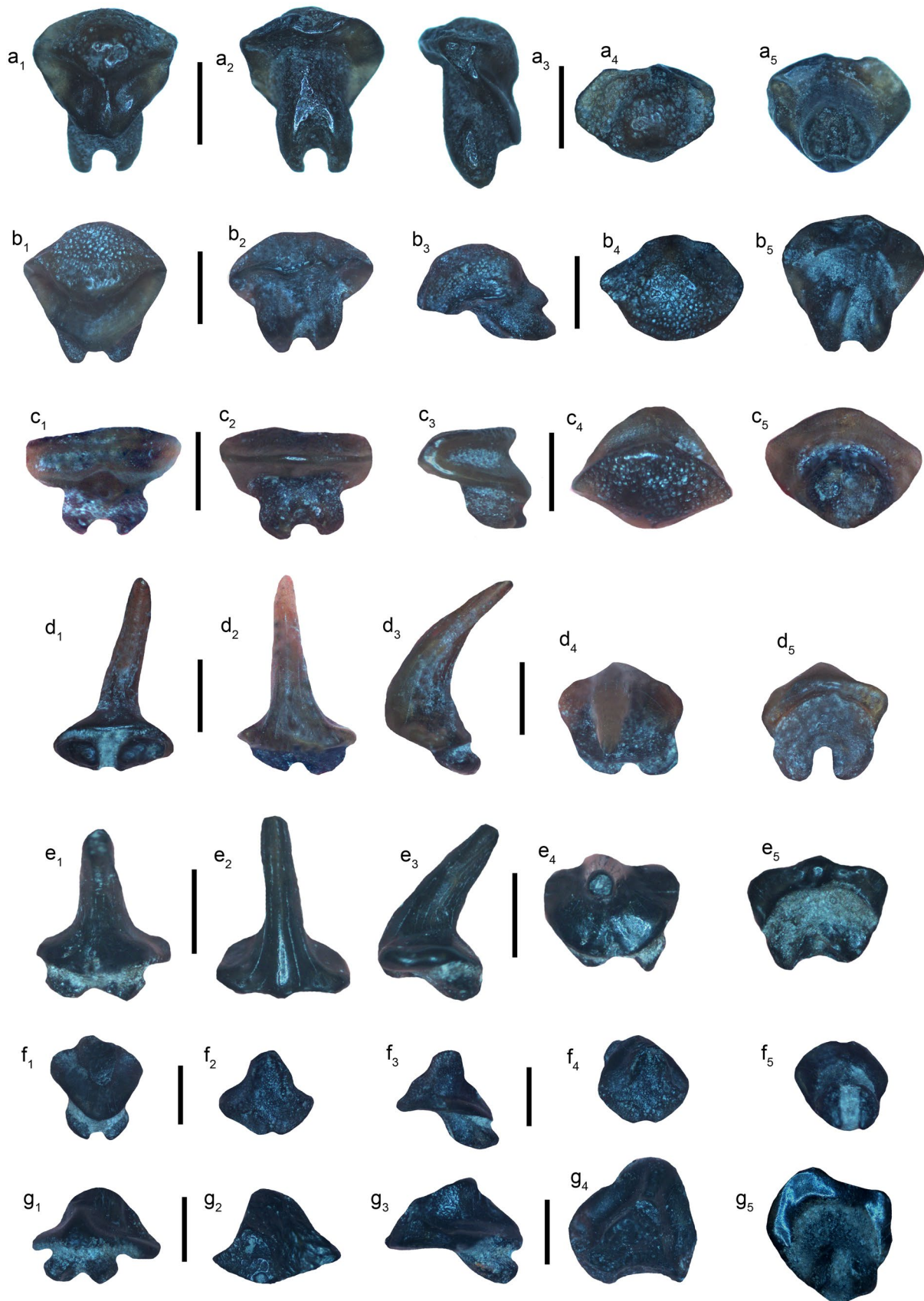
◄**Fig. 10** *Dasyatis* cf. *hexagonalis* (a_1–e_5) (ANSP: VP25121–25125) and *Dasyatis* sp. (f_1–g_5) (ANSP: VP25126–25127) teeth from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Note hook-like *Dasyatis* cf. *hexagonalis* male teeth in d_1–e_5 (ANSP: VP25124–25125). Orientations: Lingual = a_1, b_1, c_1, d_1, e_1, f_1, g_1. Labial = a_2, b_2, c_2, d_2, e_2, f_2, g_2. Lateral = a_3, b_3, c_3, d_3, e_3, f_3, g_3. Occlusal = a_4, b_4, c_4, d_4, e_4, f_4, g_4. Basal = a_5, b_5, c_5, d_5, e_5, f_5, g_5. All scale bars 1 mm

To date, only five species of *Hypolophites* are known globally. Four of these species have been reported from the Paleocene of western Africa (i.e., *Hypolophites myliobatoides* Stromer, 1910, *Hypolophites mayumbensis* Leriche, 1913, *Hypolophites thaleri* Cappetta, 1972, and *Hypolophites* sp.; Cappetta 1972), while the remaining species, *Hypolophites hutchinsi* Case, 1996, was reported from the Paleocene of New Jersey. Teeth of *H. hutchinsi* can be distinguished from those of *H. myliobatoides*, *H. mayumbensis*, *H. thaleri*, and *Hypolophites* sp. since they have a shorter overall height and have distinct labial and lingual surface shelves. The isolated *Hypolophites* teeth from the LCLU near Malvern, Arkansas, are most similar to those of *H. hutchinsi*; however, *H. hutchinsi* teeth appear distinct since they have a rhombohedral–hexagonal occlusal surface that frequently contains irregular grooves along the edges, wedge-shaped lateral teeth, and roots that are longer and wider. Morphological differences between these species may represent ontogenetic, sexual, or dignathic variability, or the LCLU teeth may in fact derive from a distinct species. As a result, we tentatively identify these LCLU teeth as *Hypolophites* sp. until further study is conducted on these isolated teeth (Maisch, in prep.). However, the identification of *Hypolophites* sp. from the Paleocene of southwestern Arkansas in this study extends the known distribution of *Hypolophites* and indicates that this genus may be more diverse and widespread than originally recognized. All previously identified *Hypolophites* species have been reported from Paleocene stratigraphic sections in the Atlantic Coastal Plain of the USA and Africa that are indicative of shallow marine environments much like the LCLU near Malvern, Arkansas (Stromer 1910; Leriche 1913; Cappetta 1972; Case 1996).

Family **Myliobatidae** Bonaparte, 1838

Genus *Myliobatis* Cuvier, 1816

Myliobatis sp.
Figure 11f

Studied material. One lateral pavement tooth. ANSP: VP25133.

Description. The crown of the lateral tooth is mesiodistally elongated, smooth, weakly convex, and roughly hexagonal in occlusal view. The lateral edges of the crown are wrinkled, and the crown is extremely thin relative to the root. The crown overhangs all but the lingual surface that contains a shallow shelf. The lateral tooth root is polyaulacorhizous and contains seven narrow nutritive grooves.

Remarks. The lateral tooth of *Myliobatis* sp. from the LCLU (1) can be distinguished from the lateral tooth of *Rhinoptera* sp. that was also recovered from the LCLU, (2) bears some resemblance to the teeth of *Myliobatis dixoni* Agassiz, 1843, that have previously been reported from the UCLU by Becker et al. (2011), and (3) can be distinguished from *Rhombodus binkhorsti* Dames, 1881, that has previously been reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of a mesiodistally elongated, hexagonally shaped crown that is smooth and thinner than the root (e.g., Herman et al. 2000; Cappetta 1987, 2012; Hovestadt and Hovestadt-Euler 2013). The tooth of *Myliobatis* sp. from the LCLU is also distinct from those of the Late Cretaceous species *Brachyrhizodus witchitaensis* Romer, 1942, which contains far fewer nutritive grooves and has not been reported from the Maastrichtian Arkadelphia Formation near Malvern, Arkansas (Becker et al. 2006; Cappetta 2012). As indicated in prior studies, the highly variable dental morphology of pavement teeth belonging to extant genera including *Myliobatis*, *Rhinoptera*, *Aetomylaeus*, and *Pteromylaeus* makes the identification of isolated median and lateral pavement teeth extremely difficult (Nishida 1990; Herman et al. 2000; Cappetta 2012). As such, we refrain from lower-level taxonomic classification of the single, isolated *Myliobatis* sp. lateral tooth from the LCLU until further studies are conducted on fossil and extant specimens.

Family **Rhinopteridae** Jordan and Evermann, 1896

Genus *Rhinoptera* Cuvier, 1829

Rhinoptera **sp.**
Figure 11g

Studied material. One lateral pavement tooth. ANSP: VP25134.

Description. The crown of the lateral pavement tooth has a flat, regularly and deeply pitted enameloid, roughly hexagonal occlusal surface, and is uniform in thickness. In lateral view, all crown edges are heavily wrinkled forming dorsoventral furrows. The base of the crown overhangs the labial root surface. The root is polyaulacorhizous and contains six nutritive grooves.
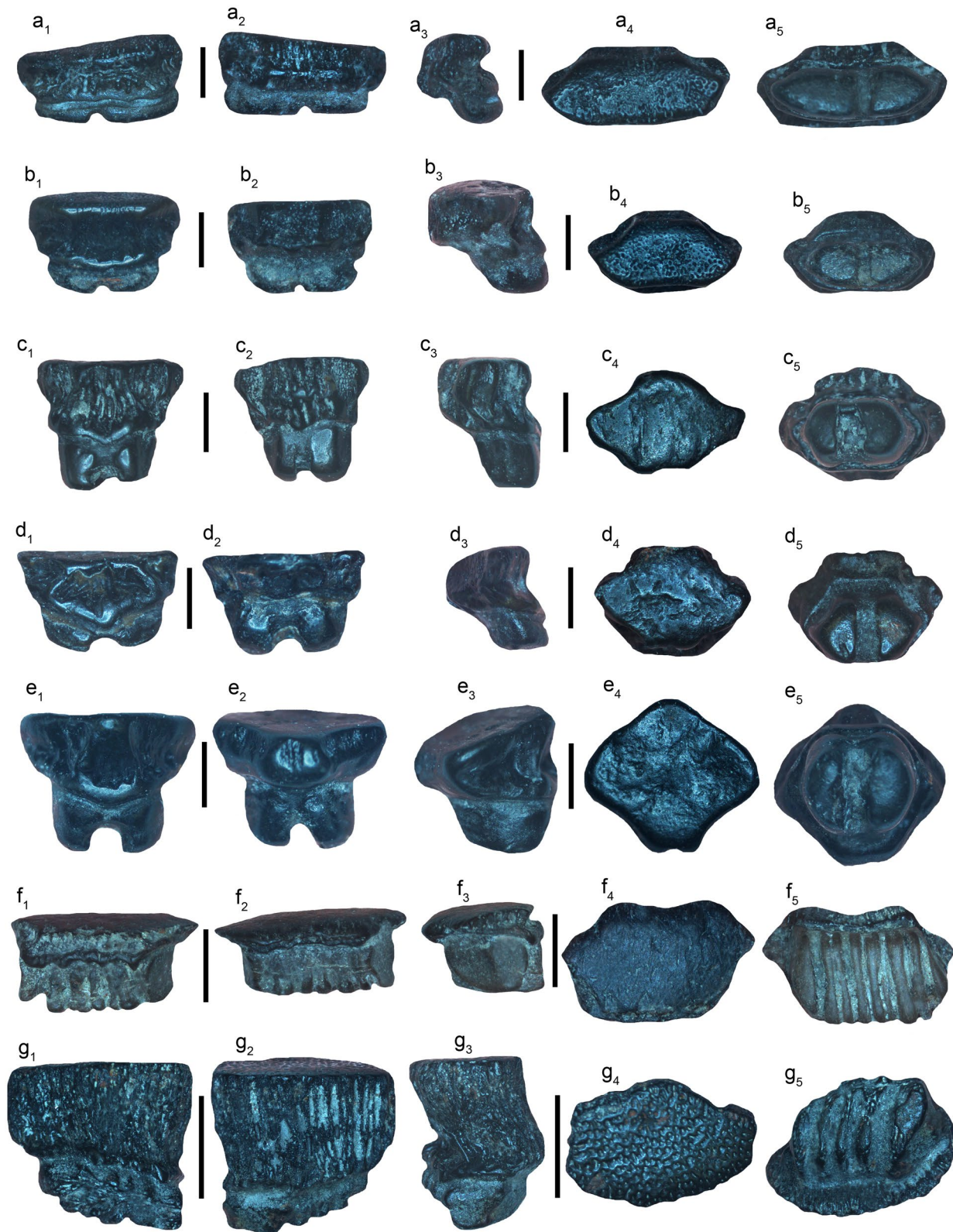
Fig. 11 *Hypolophites* sp. (**a₁–e₅**) (ANSP: VP25128–25132), *Myliobatis* sp. (**f₁–f₅**) (ANSP: VP25133), and *Rhinoptera* sp. (**g₁–g₅**) (ANSP: VP25134) teeth from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Median teeth = **a₁–a₅** and lateral teeth = **b₁–g₅**. Orientations: Lingual = **a₁**, **b₁**, **c₁**, **d₁**, **e₁**, **f₁**, **g₁**. Labial = **a₂**, **b₂**, **c₂**, **d₂**, **e₂**, **f₂**, **g₂**. Lateral = **a₃**, **b₃**, **c₃**, **d₃**, **e₃**, **f₃**, **g₃**. Occlusal = **a₃**, **b₄**, **c₄**, **d₄**, **e₄**, **f₄**, **g₄**. Basal = **a₅**, **b₅**, **c₅**, **d₅**, **e₅**, **f₅**, **g₅**. Scale bars in **a–e** 2 mm; **f**, **g** 5 mm

Remarks. The lateral tooth of *Rhinoptera* sp. from the LCLU (1) can be distinguished from the lateral tooth of *Myliobatis* sp. that was also recovered from the LCLU, (2) bears some resemblance to the teeth of *Myliobatis dixoni* Agassiz, 1843, that have previously been reported from the UCLU by Becker et al. (2011), and (3) can also be distinguished from *Rhombodus binkhorsti* Dames, 1881, that has previously been reported from the Maastrichtian near Malvern, Arkansas, by Becker et al. (2006) based on the presence of a mesiodistally elongated and hexagonally shaped crown, flat occlusal surface with regularly pitted enameloid on the occlusal surface, and a crown that is noticeably thicker than the root (e.g., Herman et al. 2000; Cappetta 1987, 2012; Hovestadt and Hovestadt-Euler 2013). This *Rhinoptera* sp. lateral tooth may also resemble those of *Rhinoptera prisca* Woodward, 1907, *Apocopodon sericeus* Cope, 1886, *Garabatis atlasi* Cappetta, 1993, and *Igdabatis sigmodon* Cappetta, 1972; however, teeth from these species have one or more of the following characteristics: (1) more regular, hexagonal shapes, (2) smoother occlusal and lateral surfaces, (3) fewer nutritive grooves and wider roots, (4) a greater number of nutritive grooves, (5) sigmoidal shapes, and (6) restricted chronological and geographic ranges (e.g., Silva 1994; Ribeiro de Santana et al. 2011; Cappetta 1987, 2012; Hovestadt and Hovestadt-Euler 2013). As noted in the *Myliobatis* sp. remarks above, the highly variable dental morphology of pavement teeth belonging to extant genera including *Myliobatis*, *Rhinoptera*, *Aetomylaeus*, and *Pteromylaeus* makes the identification of isolated median and lateral pavement teeth extremely difficult (Nishida 1990; Herman et al. 2000; Cappetta 2012). As such, we refrain from lower-level taxonomic classification of the single, isolated lateral *Rhinoptera* sp. tooth from the LCLU until further studies are conducted on fossil and extant specimens.

Myliobatiformes indet.
Figure 12a

Studied material. One fragmentary caudal spine. ANSP: VP25135.

Description. The caudal spine is fragmentary and roughly rectangular in shape. The ventral surface is smooth and convex, while the dorsal surface contains faint, anteroposterior furrows and slightly curved, triangular barbs on the lateral edges.

Remarks. Prior research indicates that a high degree of intraspecific variation occurs in the myliobatiform caudal spines making identification at the genus and family level difficult (Marmi et al. 2010; Bor et al. 2012; Cappetta 2012; Hovestadt and Hovestadt-Euler 2013). In the LCLU, myliobatiform caudal spines are uncommon, and to date,

no complete caudal spines have been recovered. Until further studies are conducted on myliobatiform caudal spines, we refrain from higher-order classification of the LCLU caudal spine fragments.

Chondrichthyes indet. 1
Figure 12c–e

Studied material. Three vertebral centra. ANSP: VP25136–25138.

Description. The vertebral centra have circular–ovular shapes with concave, circular–ovular articulation surfaces that contain concentric lamella and a centrally located birthmark. The edges of centra may contain radial lamella or large foramina for basal cartilage attachment.

Remarks. Isolated vertebral centra were previously reported from the UCLU by Becker et al. (2011) and also occur with chondrichthyan teeth in the LCLU near Malvern, Arkansas. In general, chondrichthyan vertebral centra can be identified as (1) lamnoid-type centra with many septa and large, paired basidorsal and basiventral foramina; (2) carcharhinoid-type centra that lack abundant septa and paired foramina; and (3) orectolobiform and batoid-type centra that have ovular or dorsoventrally compressed articulation surfaces with basidorsal and basiventral foramina (Shimada 1997; Blanco Piñón et al. 2005; Becker et al. 2007). The abundance of teeth belonging to lamniforms including *Carcharias*, *Odontaspis*, and *Palaeohypotodus* in the LCLU suggests the lamnoid-type vertebral centra may belong to these species. In contrast, carcharhinoid-type vertebral centra in the LCLU may belong to *Palaeogaleus*, while batoid-type centra likely belong to *Dasyatis*, *Hypolophites*, *Myliobatis*, or *Rhinoptera*. Additionally, *Ginglymostoma* teeth are also abundant in the LCLU, and their vertebrae may by dorsoventrally compressed and resemble either carcharhinoid- or batoid-type centra. We acknowledge that associating isolated chondrichthyan vertebra with a particular genus or species is problematic since some species (e.g., *Squalicorax* sp.) may contain teeth and associated tooth tissues that are indicative of a lamniform but vertebral centra that are more similar to those of a carcharhiniform (e.g., Shimada and Cicimurri 2005; Becker et al. 2007). In this regard, we refrain from a more detailed analysis of the LCLU vertebral centra until more is known about the skeletal anatomy of Paleocene chondrichthyans.

Chondrichthyes indet. 2
Figure 12b

Studied material. One dermal denticle. ANSP: VP25139.
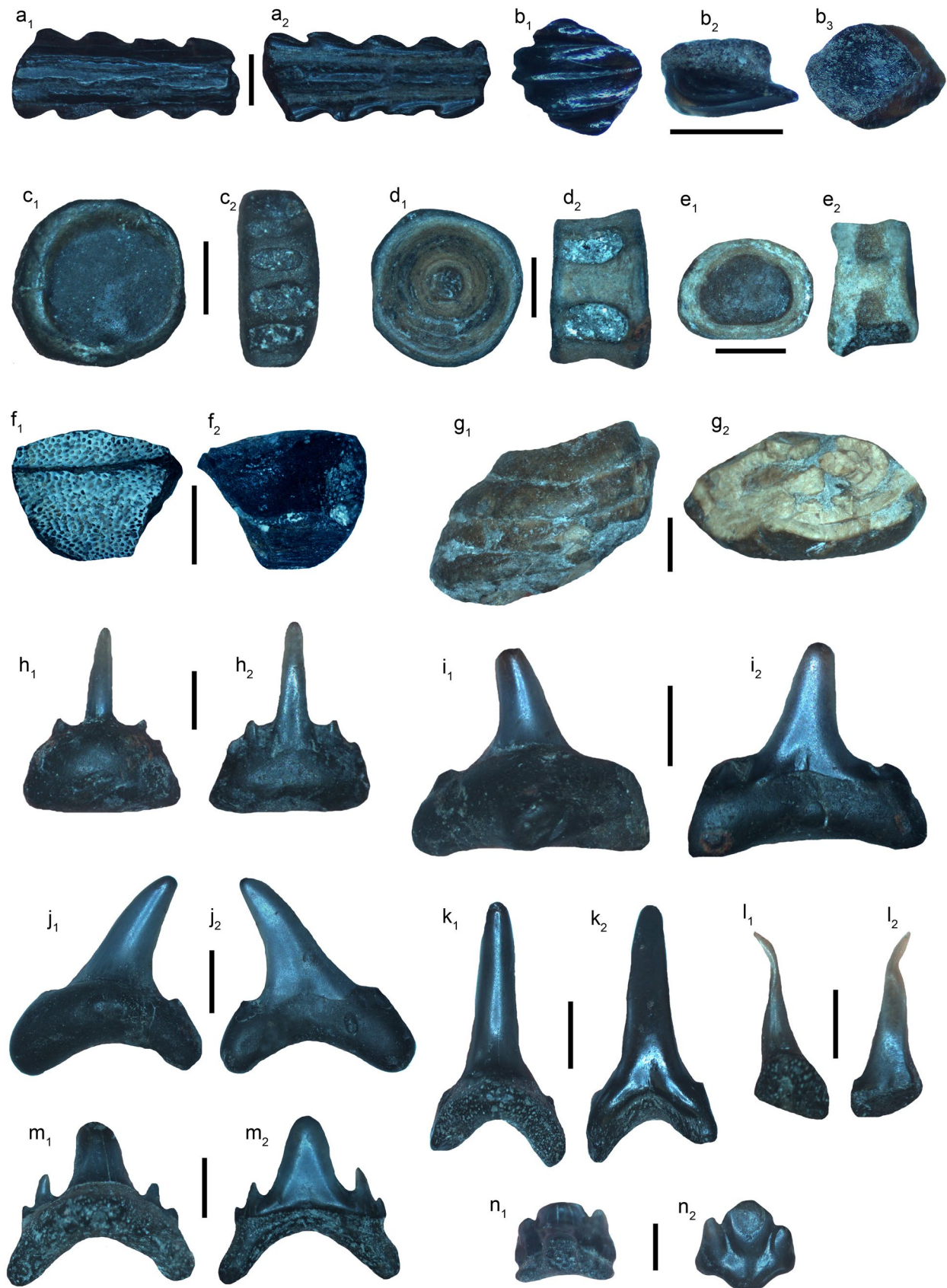
◄**Fig. 12** Additional chondrichthyan remains from the Lower Clayton Limestone Unit (Paleocene: Midway Group) near Malvern, Arkansas, USA. Myliobatiformes indet. caudal spine (a_1–a_2) (ANSP: VP25135), Chondrichthyes indet. 2, dermal denticle (b_1–b_3) (ANSP: VP25136), Chondrichthyes indet. 1, lamniform-type vertebral centrum (c_1–c_2) (ANSP: VP25137), Chondrichthyes indet. 1, carcharhiniform-type vertebral centrum (d_1–d_2) (ANSP: VP25138), Chondrichthyes indet. 1, batoid-type vertebral centrum (e_1–e_2) (ANSP: VP25139), indeterminate chimaerid jaw fragment (f_1–f_2) (ANSP: VP25140), spiral chondrichthyan coprolite (g_1–g_2) (ANSP: VP25141), phosphatic nodule development around LCLU chondrichthyan teeth (h_1–j_2) (ANSP: VP25142–25144), *Carcharias* sp. tooth displaying extensive rounding and polishing (k_1–k_2) (ANSP: VP25090), pathological *Carcharias* sp. tooth (l_1–l_2) (ANSP: VP25091), and *Palaeohypotodus rutori* (m_1–m_2) (ANSP: VP25106) and *Ginglymostoma subafricanum* (n_1–n_2) (ANSP: VP25077) teeth with feeding damage to the main cusp. Orientations: Dorsal = a_1. Ventral = a_2. Exterior = b_1, f_1, g_1. Interior = f_2. Lateral = b_2, g_2. Basal = b_3, c_2, d_2, e_2. Lingual = h_1, i_1, j_1, k_1, l_1, m_1, n_1. Labial = h_2, i_2, j_2, k_2, l_2, m_2, n_2. Scale bars in **a**, **e** 1 mm; **b** 0.5 mm; **c**, **d**, **h**, **l**, **m**, **n** 2 mm; **f**, **g**, **i**–**k** 5 mm

Description. The dermal denticle is complete and roughly hexagonal in shape with a scallop-like edge. An enameloid surface is present and contains four well-developed grooves, while the opposing surface exposes a flat dentine base.

Remarks. This is the first report of a chondrichthyan dermal denticle from the Malvern, Arkansas, region. Do to their small size, dermal denticles are frequently winnowed away or destroyed in (1) high-energy, shallow marine depositional environments and (2) during lag deposit formation, (3) are not recovered as a result of collecting biases, or (4) are collected but not included in studies focusing on chondrichthyan teeth. Additionally, prior studies on dermal denticles from deep-sea cores and extant chondrichthyans indicate that denticle morphology is highly variable across the body and within a single species, therefore eluding genus- and species-level identification (e.g., Cappetta 2012; Sibert et al. 2016; Dillon et al. 2017; Ankhelyi et al. 2018).

Order **Chimaeriformes** Obruchev, 1953

gen. et sp. indet.
Figure 12f

Studied material. One jaw fragment. ANSP: VP25140.

Description. The jaw fragment has dark, osseous surfaces and includes a portion of a tritor that is lighter in color and regularly ornamented with small, rounded nodes.

Remarks. The fragmentary, indeterminate chimaerid jaw fragment from the LCLU is generally similar to that reported by Becker et al. (2011) from the UCLU near Malvern, Arkansas. While the morphology of this jaw fragment is characteristic of similar species including *Ischyodus* and

Edaphon, its small size and highly fragmentary condition precludes lower-level taxonomic classification. Although chimaerid remains have not been reported from the Maastrichtian Arkadelphia Formation near Malvern, Arkansas, they are known to occur in other Late Cretaceous and Paleogene chondrichthyan assemblages throughout North America (e.g., Case 1978; Case and Schwimmer 1992; Manning and Dockery 1992; Stahl and Parris 2004; Parmley and Cicimurri 2005; Cicimurri et al. 2008; Becker et al. 2011; Johnson-Ransom et al. 2018).

Discussion

Faunal turnover and extinction of chondrichthyans at the K/Pg boundary near Malvern, Arkansas

As a framework for interpreting faunal turnover and extinction, our analysis utilizes prior studies of chondrichthyans preserved across both intervals of the K/Pg mass extinction boundary in the Atlantic Coastal Plain of the United States, Western Europe, and northern Africa (Case 1996; Noubhani and Cappetta 1997; Case et al. 2001; Becker et al. 2006, 2011; Adolfssen and Ward 2014, 2015). Principal features identified in these studies to interpret the magnitude of this global mass extinction event on chondrichthyans include (1) taxonomic composition; (2) depositional environment and bathymetry; (3), erosional hiatuses, reworking, and sea-level cyclicity; and (4) the Chicxulub bolide impact.

Taxonomic composition of the LCLU and K/Pg boundary section

The chondrichthyan assemblage described in this study consists of species with grasping, clutching, and crushing teeth utilized for consuming small chondrichthyans, osteichthyans, and shelled invertebrates that are also found in the LCLU (Applegate 1965; Welton and Farish 1993; Cappetta 1987, 2012). More than half of all the teeth comprising these dentitions recovered from the LCLU belong to lamniforms including *Carcharias* cf. *whitei*, *Carcharias* sp., *Odontaspis winkleri*, and *Palaeohypotodus rutori*, described above. In the LCLU chondrichthyan assemblage, large teeth (> 25 mm), serrated teeth that represent cutting or tearing dentitions, and teeth from species with deep-water affinities were not recovered (e.g., Mannering and Hiller 2008; Cappetta 2012; Adolfssen and Ward 2014, 2015; Bazzi et al. 2018).

Table 1 compares the chondrichthyan species occurring in the K/Pg boundary section near Malvern, Arkansas. This section consists of chondrichthyans found in the (1) Arkadelphia Formation and coquina lag containing the K/Pg boundary and Midway Group contact (Becker et al.

Fig. 13 Ammonites from the coquina lag containing the K/Pg boundary (Arkadelphia Formation–Midway Group Contact) near Malvern, Hot Spring County, Arkansas, USA. **a** *Placenticeras* sp. cast with broken and infilled body chamber, rounded phosphate pebbles and fragmentary osteichthyan remains indicated by arrows (WPU:AR:MOR-2). **b** Lateral view of **a** showing ammonites in cross-section indicated by arrows. **c** *Baculites* sp. exposed in transverse section indicated by arrows (WPU:AR:MOR-3). **d** Partial *Discoscaphites iris* with shell material (WPU:AR:MOR-4). Scale bars in **a** and **c** 5 cm, and **b** and **d** 2 cm
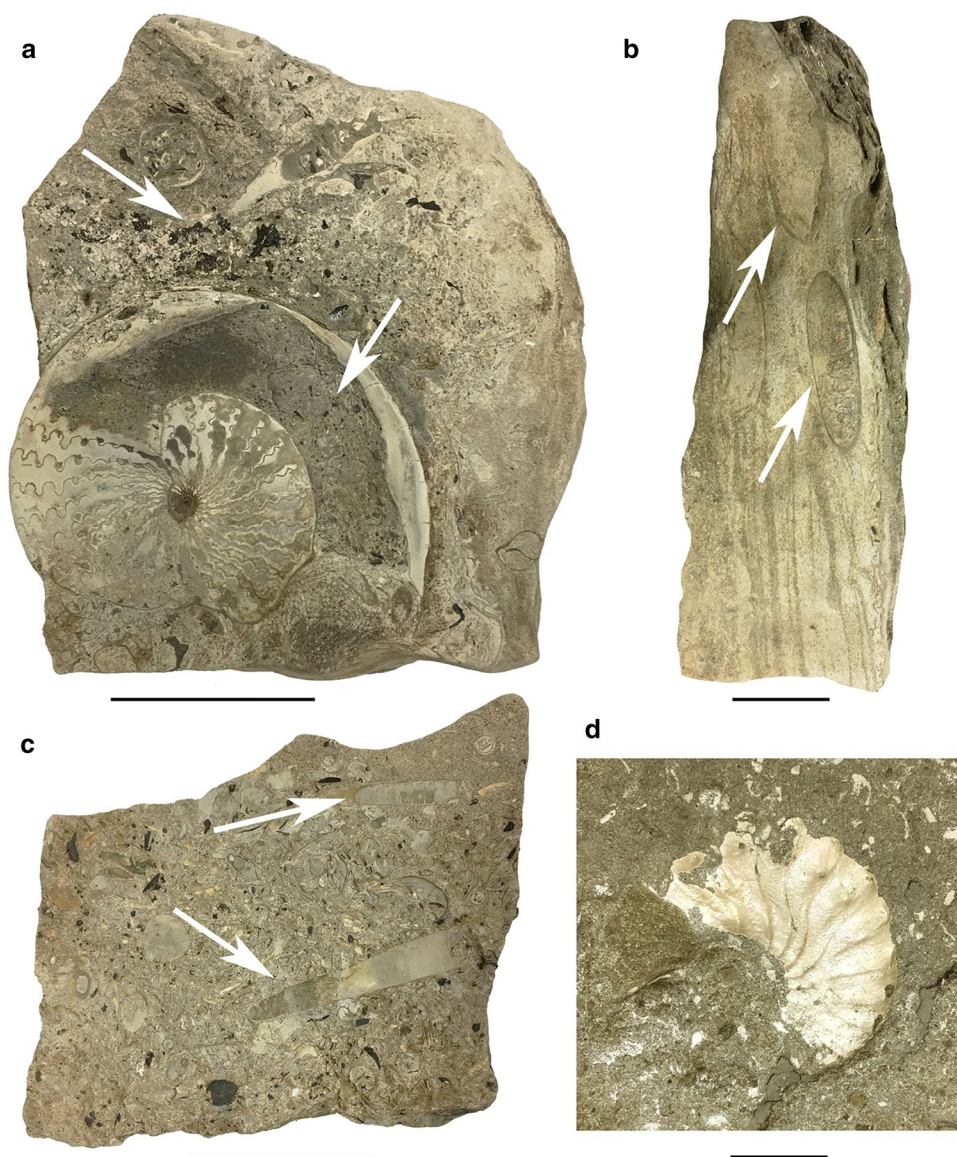
2006), (2) LCLU described in this study, and (3) UCLU occurring ≈ 2.75 km to the NE (Becker et al. 2011) that is also exposed directly above the LCLU at the I-30 site. In the LCLU chondrichthyan assemblage, (1) no teeth belonging to pelagic species (e.g., *Anomotodon*, *Otodus*) have been identified, (2) only three species identified and described in this study are identical to those found in the UCLU, (3) large myliobatiform pavement crushers are scarce (e.g., *Myliobatis dixoni*, *Myliobatis* sp., *Rhinoptera* sp.), and (4) pristiodontiform, rhinobatiform, and rajiform teeth found in other parts of this K/Pg section have not been identified.

The data in Table 1 also indicate that the most taxonomically diverse chondrichthyan assemblage consists of 18 species and occurs in the Arkadelphia Formation and coquina lag containing the K/Pg boundary and Midway Group contact. In this study, we report 12 chondrichthyan species from the LCLU, whereas eight chondrichthyan taxa have been previously reported from the UCLU by Becker et al. (2011). All three chondrichthyan assemblages in this the K/Pg boundary section contain the nektobenthic genera *Carcharias* and *Odontaspis*. No distinctly Cretaceous genera common in the global stratigraphic record including *Squalicorax* and *Ischyrhiza* are found in either the LCLU or UCLU (e.g., Kriwet and Benton 2004; Cappetta 2012). Other large, apex predators found in the Arkadelphia Formation and coquina lag containing the K/Pg boundary including plesiosaurs and turtles parallel global K/Pg trends and are either eliminated or reduced in number (Becker et al. 2013, 2016).

Table 1 Chondrichthyan assemblages from the K/Pg boundary section near Malvern, Hot Spring County, Arkansas, USA, discussed in this study

Arkadelphia Formation–Midway Group		Lower Clayton Limestone Unit		Upper Clayton Limestone Unit	
Contact (K/Pg):		(LCLU: Paleocene Midway Group):		(UCLU: Paleocene Midway Group):	
Becker et al. (2006)		Maisch et al. (this study)		Becker et al. (2011)	
Genus	Species	Genus	Species	Genus	Species
Sharks		**Sharks**		**Sharks**	
Squatina	*hassei*	*Ginglymostoma*	*subafricanum*	*Odontaspis*	*winkleri*
Ginglymostoma	*lehneri*	*Odontaspis*	*winkleri*	*Carcharias*	cf. *whitei*
Plicatoscyllium	*derameei*	*Carcharias*	cf. *whitei*	*Carcharias*	sp.
Odontaspis	*oculeatus*	*Carcharias*	sp.	*Cretalamna*	sp.
Carcharias	cf. *holmdelensis*	*Palaeohypotodus*	*rutori*	*Otodus*	*obliquus*
Serratolamna	*serrata*	*Palaeogaleus*	*vincenti*	*Anomotodon*	*novas*
Cretalamna	*appendiculata*	**Rays**		**Rays**	
Squalicorax	*kaupi*	*Dasyatis* cf.	*hexagonalis*	*Hypolophodon*	*sylvestris*
Galeorhinus	*girardoti*	*Dasyatis*	sp.	*Myliobatis*	*dixoni*
Guitarfish/Sawfish/Skates/Rays		*Hypolophites*	sp.	**Ratfish**	
Rhinobatos	*casieri*	*Myliobatis*	sp.	Chimaerid	indet.
Ptychotrygon	cf. *vermiculata*	*Rhinoptera*	sp.		
Ischyrhiza	*avonicola*	**Ratfish**			
Ischyrhiza	*mira*	Chimaerid	indet.		
Sclerorhynchus	sp.				
Schizorhiza	cf. *stromeri*				
Raja	*farishi*				
Rhombodus	*binkhorsti*				
Dasyatis	sp.				

Depositional environment and bathymetry

Prior studies, geologic mapping, and paleogeographic reconstructions of the Malvern, Arkansas, region indicate that the K/Pg boundary section identified in this study represents a marginal to shallow marine depositional environment adjacent to a rocky coastline consisting of the Paleozoic Ouachita Mountains and Mesozoic igneous deposits of Magnet Cove (Haley et al. 1993, 2009; Kennedy et al. 1998; McFarland 2004; Becker et al. 2010a; Scotese 2014). In the LCLU, this interpretation is further reinforced by the occurrence of sedimentary structures, trace fossils (i.e., *Thalassinoides* isp., *Gastrochaenolites* isp., and *Entobia* isp.), oysters, nut clams (i.e., *Nuculana* sp.), and crocodilian teeth (Figs. 4, 5). Within this K/Pg boundary section, localized differences in bathymetry are indicated by deposition of light to dark gray, organic-rich clay beds interspersed with limestone beds and concretions (Figs. 3, 4). Nearby fluvial influences are also recorded throughout this section as fragments of wood and plants occur with osteichthyans and turtles that have brackish to freshwater affinities (Becker et al. 2010a, 2016).

Erosional hiatuses, reworking of fossils, and sea-level cyclicity

In the Gulf Coastal Plain of the United States, recent studies indicate that some of the shallow marine sections representing the K/Pg boundary are relatively complete and free from structural complexities (Larina et al. 2016; Witts et al. 2018). A key feature identified in both these studies is the occurrence of the latest Maastrichtian *Discoscaphites iris* ammonite zone in Alabama, Mississippi, Missouri, and Arkansas (also see Landman et al. 2004, 2012). In this regard, reworked ammonites including *Discoscaphites iris* are common in the coquina lag containing the K/Pg boundary near Malvern, Arkansas, and occur on bedding surfaces with shell material, in multiple orientations, and with broken body chambers (Fig. 13).

The chondrichthyan assemblages found in the Arkadelphia Formation and coquina lag containing the K/Pg boundary, and lags of the LCLU identified in his report, do not occur within horizontal or slightly dipping beds like those reported from contemporaneous strata on the eastern side of the Mississippi Embayment (e.g., Larina et al. 2016; Witts et al. 2018; Phillips and Case 2019) or further to the west in the Brazos River region of Texas (e.g., Gale 2006; Hart

et al. 2012). This structural complexity and localized rotational sliding discussed above has distorted bed orientation and thickness, particularly on the southern side of the outcrop exposure and within the Ouachita River (Figs. 2, 3). Moreover, concentrations of vertebrate fossils in lag deposits documented throughout this section indicate that (1) teeth and bones as well as co-occurring shelled invertebrates and sediments have experienced a degree of reworking, and (2) these lag deposits represent erosional hiatuses and missing time that are the products of sea-level changes (Figs. 3, 4, 14; Case and Schwimmer 1988; Becker et al. 1996, 1998, 2010b; Shimada et al. 2006; Otero et al. 2013; Boessenecker et al. 2014; Maisch et al. 2014, 2015, 2018a, b). In fact, all chondrichthyan teeth recovered from these lags show variable stages of reworking and taphonomic wear including phosphatization, abrasion, and polishing of cusp, cusplet, and root elements and range from pristine condition to highly fragmented (Fig. 12). These taphonomic conditions as seen in chondrichthyan teeth, and the duration of missing time represented by these lag deposits, have important implications to interpreting the nature of the end-Cretaceous extinction event in the Malvern, Arkansas region.

The transition across the K/Pg boundary and Arkadelphia Formation–Midway Group contact near Malvern, Arkansas, occurs during multiple third-order eustatic sea-level cycles of Haq (2014) including KMa5–PaDa3. The bounding unconformities for these events represent several million years and have relative sea-level fluctuations of approximately 25–100 m, with cycle (KMa5) occurring just below the K/Pg boundary (Haq 2014). In the Gulf Coastal Plain, similar sea-level events across the K/Pg boundary are recognized and include three depositional sequences also bounded by unconformities (Mancini et al. 1989, 1995; Mancini and Puckett 2005). The first of these Gulf Coastal Plain depositional sequences occurs during the Maastrichtian below the K/Pg boundary, while the other two depositional sequences occur in the Danian. Both of these Gulf Coastal Plain studies acknowledged the fact that the K/Pg boundary is disconformable and does not record a continuous record of time.

Based on these global and regional studies, we interpret the changes observed in the Maastrichtian–Paleocene chondrichthyan assemblages identified in Table 1, including the coquina lag containing the K/Pg boundary and Midway Group contact, to have occurred across several million years as constrained by the global third-order eustatic sea-level and regional sea-level cycles identified above. The coquina lag containing the K/Pg boundary and Midway Group contact seen in Figs. 3 and 4 is a prominent disconformity and strengthens the fact that this marginal to shallow marine stratigraphic section is also incomplete. In this regard, both sediments and fossils have been exhumed and reworked across this K/Pg boundary and within the overlying Midway Group multiple times during these globally and regionally recognized sea-level cycles.

The Chicxulub impact site, Yucatan, Mexico

The chondrichthyan assemblage contained in the K/Pg section near Malvern, Arkansas, resides ≈ 1500 km north of the Chicxulub, Mexico, bolide impact site. This bolide impact represents the leading cause for the most intensely studied global mass extinction event in Earth history (Alvarez et al. 1980; Hildebrand et al. 1991; D'Hondt 2005; Kring 2007; Miller et al. 2010; Keller et al. 2013; Witts et al. 2016). However, conflicting viewpoints exist as to whether or not this single event accounts for observed patterns of extinction and survival in both land-based and marine organisms and may actually represent multiple causes including impact, marine regression, volcanic activity, and climatic changes (e.g., Schulte et al. 2010; Archibald et al. 2010; Schoene et al. 2019; Sprain et al. 2019).

In the Gulf Coastal Plain, an increasing body of evidence identifies the occurrence of impact spherules as the result of K/Pg bolide impact (e.g., Gale 2006; Campbell and Landman 2010; Adatte et al. 2011; Keller et al. 2013; Witts et al. 2018). In fact, Rovelli et al. (2014) and Larina et al. (2016) have also reported impact spherules in the K/Pg section near Malvern, Arkansas, discussed in this study. These studies and others (e.g., Albertão et al. 1994; Stinnesbeck and Keller 1995) in the Gulf Coastal Plain offer opposing data as to whether these impact spherules represent a single event horizon, at or above the K/Pg boundary, or multiple horizons that have been subsequently eroded and redeposited by sea-level cyclicity. Additional complications are also thought to exist due to post-impact tsunamis, although these effects are not recorded in all K/Pg stratigraphic sections of the Gulf Coastal Plain (e.g., Savrda 1993; Smit et al. 1996; Campbell et al. 2008; Oboh-Ikuenobe et al. 2012; Dastas et al. 2014; Larina et al. 2016). Regardless of these different scenarios, the proximity of the Malvern, Arkansas, region to the Chicxulub, Mexico, impact site indicates that chondrichthyans and other organisms living in this marginal to shallow marine environment would have been exposed to the aftermath of K/Pg bolide impact.

The chondrichthyans found in Table 1 are also known from the shallow marine global record (see "Systematic paleontology"), and in particular the Tethys Seaway of Western Europe and northern Africa, where current evidence for impact spherules and post-depositional tsunamis are few (e.g., Korbar et al. 2015). Similar trends in faunal turnover and extinction to those seen in chondrichthyans found in Arkansas also occur throughout the Tethys Seaway and in particular Morocco (Noubhani 2010; Adolfssen and Ward 2014, 2015; Belben et al. 2017; Bazzi et al. 2018). According to Adolfssen and Ward (2014), sea-level regression

and losses of shallow marine habitat represents the most plausible explanation for faunal turnover and extinction of chondrichthyans in this region. In contrast, chondrichthyans found in deeper water of the Tethys and the Pacific Ocean were not subjected to these same habitat losses at the K/Pg boundary and do not follow similar trends of faunal turnover and extinction as observed in shallow marine assemblages (Hallam and Wignall 1999; Mannering and Hiller 2008; Adolfssen and Ward 2014; Sibert et al. 2014; Sibert and Norris 2015; Belben et al. 2017).

Conclusions

What patterns can be observed in chondrichthyans found across the K/Pg boundary section near Malvern, Arkansas?

The chondrichthyans preserved across both intervals of a K/Pg boundary section near Malvern, Arkansas, are globally distributed with several species known to occur as far south as Antarctica and in more remote locations to the north in Greenland and to the west in New Zealand (Bendix-Almgreen 1969; Zinsmeister 1998; Mannering and Hiller 2008; Cappetta 2012; Otero et al. 2013). As highly mobile apex predators, this distribution of chondrichthyans as well as other marine vertebrates points to more uniform seawater temperatures and the interconnected nature of the shallow marine Tethys Seaway to the Mississippian Embayment, Gulf of Mexico, South America, and elsewhere globally (Moody and Sutcliffe 1993; Chumakov et al. 1995; Hooks et al. 1999; Zakharov et al. 2006; Ribeiro de Santana et al. 2011; Cappetta 2012; Otero et al. 2013; Scotese 2014). Chronological ranges of the three chondrichthyan assemblages identified in this study also confirm those found in the global stratigraphic record where patterns of faunal turnover and extinction occur within a relative narrow time interval that traverses the K/Pg boundary (Gallo et al. 2001; Cappetta 2012). During this time interval, large expanses of shallow marine seaway including the Western Interior Seaway, Atlantic and Gulf Coastal Plains, and the Tethys Seaway continued to rapidly diminish as global regression occurred throughout the Late Cretaceous and the beginning of the Cenozoic (Haq et al. 1988; Savrda 1993; Li et al. 2000; Archibald et al. 2010; Boulila et al. 2011; Haq 2014; Scotese 2014).

These conditions represent broad-scale shallow marine habitat losses that we interpret as the primary cause responsible for the differences found in the chondrichthyan assemblages identified in this study. This interpretation is further reinforced by the chondrichthyan assemblages found in the LCLU and UCLU that occur stratigraphically well above the K/Pg boundary and into the Paleocene. In this regard, rapid faunal turnover and extinction by K/Pg boundary bolide impact is unlikely to account for the observed differences in these Paleocene chondrichthyan assemblages. Moreover, in the marginal to shallow marine environment near Malvern, Arkansas, patterns of change in sedimentology and the lag deposits containing chondrichthyans and shelly invertebrates found throughout this entire K/Pg section are not derived from any single erosional or depositional event and are the products of sea-level cyclicity. The range of reworking and taphonomic wear seen in chondrichthyan teeth and co-occurring fossils found in these lags is additional evidence of multiple stages of erosion and deposition as well as missing time.

While this does not rule out the combined effects of K/Pg bolide impact and sea-level cyclicity acting in combination on chondrichthyans across the Arkadelphia Formation–Midway Group contact, these conditions require further investigation throughout this entire stratigraphic section. In our view, the chondrichthyan lag deposits identified in this study are analogous to those found throughout the Late Mesozoic and Cenozoic of North America in the aforementioned studies that occur at contacts between formations, members, or units. These lag deposits are the result of sea-level cyclicity and represent several million years of mixing of chondrichthyan teeth at stage and substage boundary levels. Consequently, current evidence presented in this study favors a more conventional view seen in the global stratigraphic record at distant proximity to the Chicxulub Impact site where the primary cause of faunal turnover and extinction of K/Pg chondrichthyans is the result of sea-level cyclicity and shallow marine habitat losses.

References

Adatte, T., G. Keller, and G. Baum. 2011. Age and origin of the Chicxulub impact and sandstone complex, Brazos River, Texas: evidence from lithostratigraphy, sedimentology and sequence stratigraphy. In *The End-Cretaceous Mass Extinction and the Chicxulub Impact in Texas. Society for Sedimentary Geology (SEPM), Special Publication* 100: 43–80.

Adolfssen, J., and D. Ward. 2014. Crossing the boundary: an elasmobranch fauna from Stevns Klint, Denmark. *Palaeontology* 57: 591–629.

Adolfssen, J., and D. Ward. 2015. Neoselachians from the Danian (early Paleocene) of Denmark. *Acta Palaeontologica Polonica* 60: 313–339.

Agassiz, L. 1833–1844. *Recherches sur les Poissons fossiles Vol. 1–5*. Neuchâtel and Soleure: Imprimerie de Petitpierre.

Albertão, G., E. Koutsoukos, M. Regali, M. Attrep, and P. Martins. 1994. The Cretaceous–Tertiary boundary in southern low-latitude regions: preliminary study in Pernambuco, northeastern Brazil. *Terra Nova* 6: 366–375.

Alvarez, L., W. Alvarez, F. Asaro, and H. Michel. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* 208: 1095–1108.

Ankhelyi, M.V., D.K. Wainwright, and G. Lauder. 2018. Diversity of dermal denticle structure in sharks: skin surface roughness and three-dimensional morphology. *Journal of Morphology* 279: 1132–1154.

Applegate, S. 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. *Los Angeles County Museum Contributions in Science* 86: 1–18.

Applegate, S. 1972. A revision of the higher species of orectoloboids. *Journal of the Marine Biological Association of India* 14: 743–751.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc* 92: 1–372.

Archibald, J., W. Clemens, K. Padian, T. Rowe, N. Macleod, P.M. Barrett, A. Gale, et al. 2010. Cretaceous extinctions: multiple causes. *Science* 328(5981): 973.

Baut, J., and B. Genault. 1995. Contribution à l'étude des élasmobranches du Thanétien (Paléocène) du Bassin de Paris. 1. Découverte d'une faune d'Elasmobranches dans la partie supérieure des Sables de Bracheux (Thanétien, Paléocène du Bassin de Paris) des régions de Compiègne (Oise) et de Montdidier (Somme). *Belgian Geological Survey Professional Paper* 278: 185–259.

Bazzi, M., B. Kear, H. Blom, P. Ahlberg, and N. Campione. 2018. Static Dental Disparity and Morphological Turnover in Sharks across the End-Cretaceous Mass Extinction. *Current Biology* 28: 2607–2615.

Becker, M., W. Slattery, and J. Chamberlain Jr. 1996. Reworked Campanian and Maastrichtian macrofossils in a sequence bounding transgressive lag deposit, Monmouth County, New Jersey. *Northeastern Geology and Environmental Science* 18: 234–252.

Becker, M., W. Slattery, and J. Chamberlain Jr. 1998. Mixing of Santonian and Campanian chondrichthyan and ammonite macrofossils along a transgressive lag deposit, Greene County, western Alabama. *Southeastern Geology* 37: 205–216.

Becker, M., J. Chamberlain Jr., and G. Wolf. 2006. Chondrichthyans from the Arkadelphia Formation (Upper Cretaceous: late Maastrichtian) of Hot Spring County, Arkansas. *Journal of Paleontology* 80: 700–716.

Becker, M., R. Chamberlain, and J. Chamberlain Jr. 2007. The paradox of large carcharhinoid-type shark vertebrae in the Upper Cretaceous of New Jersey. In *Contributions to the Paleontology of New Jersey (II) Field Guide and Proceedings, Geological Association of New Jersey Annual Meeting XXIV*, ed. E. Rainforth, 69–84. East Stroudsburg: East Stroudsburg University.

Becker, M., C. Mallery, and J. Chamberlain Jr. 2010a. Osteichthyans from the Arkadelphia Formation (Late Maastrichtian) of Hot Spring County, Arkansas, USA. *Journal of Vertebrate Paleontology* 30: 1019–1036.

Becker, M., R. Wellner, C. Mallery, and J. Chamberlain Jr. 2010b. Chondrichthyans from the Lower Ferron Sandstone Member of the Mancos Shale (Upper Cretaceous: Middle Turonian) of Emery and Carbon Counties Utah, USA. *Journal of Paleontology* 84: 248–266.

Becker, M., L. Smith, and J. Chamberlain Jr. 2011. Chondrichthyans from the Clayton Limestone Unit of the Midway Group (Paleogene: Paleocene) of Hot Spring County, Arkansas, USA. *Cainozoic Research* 8: 13–28.

Becker, M., and J. Chamberlain Jr. 2012. Osteichthyans from the Paleocene Clayton Limestone of the Midway Group, Hot Spring County, Arkansas, USA: Bony fish evolution across the Cretaceous-Paleogene Boundary. *Paludicola* 4: 194–207.

Becker, M., H. Maisch IV, and J. Chamberlain Jr. 2013. Plesiosaurian Remains from the Arkadelphia Formation-Midway Group Contact (Maastrichtian-Paleocene) Hot Spring County, Near Malvern, Arkansas, USA. *Paludicola* 9: 131–143.

Becker, M., H. Maisch IV, and J. Chamberlain Jr. 2016. Turtles from an Arkadelphia Formation–Midway Group Lag Deposit (Maastrichtian–Paleocene) Hot Spring, County, Arkansas, USA. *Geosciences* 6: 1–14.

Belben, R., C. Underwood, Z. Johanson, and R. Twitchett. 2017. Ecological impact of the end-Cretaceous extinction on lamniform sharks. *PLoS One* 12: e0178294.

Bendix-Almgreen, S. 1969. Notes on the Upper Cretaceous and Lower Tertiary fish faunas of northern West Greenland. *Meddelelser fra Dansk Geologisk Forening* 19: 204–217.

Berg, L. 1958. System der rezenten und fossilen Fischartigen und Fische. *Hochschulbücher für Biologie*, *vol. 4*, 1–310. Berlin: Deutscher Verlag der Wissenschaften.

Blanco Piñón, A., K. Shimada, and G. González Barba. 2005. Lamnoid vertebrae from the Agua Nueva Formation (Upper Cretaceous: Lower Turonian), northeastern Mexico. *Revista Mexicana de Ciencias Geológicas* 22: 19–23.

Boessenecker, R., F. Perry, and J. Schmitt. 2014. Comparative Taphonomy, Taphofacies, and Bonebeds of the Mio-Pliocene Purisima Formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. *PLoS One* 9: e91419.

Bonaparte, C. 1832–1841. *Iconografia della fauna Italica per le quattro classi degli animali vertebrati 3*. Rome: Tipographia Salviucci.

Bor, T., T. Reinecke, and S. Verschueren. 2012. Miocene Chondrichthyes from Winterswijk-Miste, the Netherlands. *Palaeontos* 21: 1–136.

Boulila, S., B. Galbrun, K. Miller, S. Pekar, J. Browning, J. Laskar, and J. Wright. 2011. On the origin of Cenozoic and Mesozoic "third-order" eustatic sequences. *Earth-Science Reviews* 109: 94–112.

Campbell, C., F. Oboh-Ikuenobe, T. Eifert, K. Evans, J. Horton, D. King, and J. Morrow. 2008. Megatsunami deposit in Cretaceous-Paleogene boundary interval of southeastern Missouri. In *The Sedimentary Record of Meteorite Impacts. Geological Society of America, Special Paper* 437: 189–198.

Campbell, C., and N. Landman. 2010. Microtektite morphology and affinities at the Cretaceous-Paleogene boundary interval in southeast Missouri. *Geological Society of America Abstracts with Programs* 42: 91.

Cappetta, H. 1972. Les poissons crétacés et tertiaires du bassin des Iullemmeden (République du Niger). *Palaeovertebrata* 5: 179–251.

Cappetta, H. 1987. *Handbook of paleoichthyology. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii*, 1–193. New York: Gustav Fischer.

Cappetta, H. 1992. Nouveaux Rhinobatoidei (Neoselachii, Rajiformes) à denture spécialisée du Maastrichtien du Maroc. Remarques sur l'évolution dentaire des Rajiformes et des Myliobatiformes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 187: 31–52.

Cappetta, H. 1993. Sélaciens nouveaux (Chondrichthyes, Neoselachii) du Paléocène supérieur de la région d'Ouarzazate, Maroc. *Paläontologische Zeitschrift* 67: 109–122.

Cappetta, H. 2012. Chondrichthyes (Mesozoic and Cenozoic Elasmobranchii: Teeth). In *Handbook of Paleoichthyology, vol. 3E*, ed. H. Schultze, 1–512. München: F. Pfeil.

Cappetta, H., and G. Case. 1975. Contribution à l'étude des Sélaciens du groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica (A: Paläozoologie–Stratigraphie)* 151: 1–46.

Cappetta, H., and D. Nolf. 2005. Révision de quelques Odontaspidae (Neoselachii: Lamniformes) du Paleocene et de l'Eocene du Bassin de la mer du Nord. *Bulletin de l'institut Royal des Sciences Naturelles de Belgique Sciences de la Terre* 75: 237–266.

Case, G. 1978. *Ischyodus bifurcatus*, a new species of chimaeroid fish from the upper cretaceous of New Jersey. *Géobios* 11: 21–29.

Case, G. 1981. Late Eocene selachians from South-central Georgia. *Palaeontographica (A: Paläozoologie–Stratigraphie)* 176: 52–79.

Case, G. 1994. Fossil fish remains from the Late Paleocene Tuscahoma and Early Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. *Palaeontographica (A: Paläozoologie–Stratigraphie)* 230: 97–138.

Case, G. 1996. A new selachian fauna from the Lower Hornerstown formation (Early Paleocene/Montian) of Monmouth County, New Jersey. *Palaeontographica (A: Paläozoologie–Stratigraphie)* 242: 1–14.

Case, G., and D. Schwimmer. 1988. Late Cretaceous fish from the Blufftown Formation (Campanian) in western Georgia. *Journal of Paleontology* 62: 290–301.

Case, G., and D. Schwimmer. 1992. Occurrence of the chimaeroid Ischyodus bifurcatus Case in the Cusseta Formation (Upper Cretaceous, Campanian) of western Georgia and its distribution. *Journal of Paleontology* 66: 347–350.

Case, G., and H. Cappetta. 1997. A new selachian fauna from the late Maastrichtian of Texas (Upper Cretaceous/Navarroan; Kemp formation). *Münchner Geowissenschaftliche Abhandlungen* 34: 131–189.

Case, G., P. Borodin, and J. Leggett. 2001. Fossil selachians from the New Egypt Formation (Upper Cretaceous, Late Maastrichtian) of Arneytown, Monmouth County, New Jersey. *Palaeontographica (A: Paläozoologie–Stratigraphie)* 261: 113–124.

Casier, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique. *Mémoire du Musée royale d'histoire naturelle de Belgique* 104: 1–267.

Casier, E. 1967. Le Landénien de Dormaal (Brabant) et sa faune ichthyologique. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique* 156: 1–66.

Chumakov, N., M. Zharkov, A. German, M. Doludenko, N. Kalandadze, Y. Lebedev, A. Ponomarenko, and A. Rautian. 1995. Climatic zones in the middle of the Cretaceous Period. *Stratigraphy and Geologic Correlation* 3: 3–14.

Cicimurri, D., D. Parris, and M. Everhart. 2008. Partial dentition of a chimaeroid fish (Chondrichthyes, Holocephali) from the Upper Cretaceous Niobrara Chalk of Kansas, USA. *Journal of Vertebrate Paleontology* 28: 34–40.

Compagno, L. 1973. Interrelationships of living elasmobranchs. *Journal of the Linnaean Society (Zoology)* 53: 63–98.

Compagno, L. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17: 303–322.

Cope, E. 1886. A contribution to the vertebrate paleontology of Brazil. *Proceedings of the American Philosophical Society* 23: 1–21.

Cushman, J. 1949. The foraminiferal fauna of the Upper Cretaceous Arkadelphia Marl of Arkansas. *U.S. Geological Survey Professional Paper* 221: 1–19.

Cuvier, G. 1816. *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides*, 1–532. Paris: Deterville.

Cuvier, G. 1829. Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. *Règne Animal* 2: 1–406.

Daimeries, A. 1888. Notes ichthyologiques (Système Landénien). I. *Annales de la Société royale malacologique de Belgique, Bulletin des des Séances* 23: 42–43.

Dames, W. 1881. Über Fischzähne aus der obersenonen Tuffkreide von Maastricht für welcher den Gattungsnamen Rhombodus vorschlug. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1881: 1–3.

Dartville, E., and E. Casier. 1943. Les poissons fossiles du Bas-Congo et des régions voisines. *Annales du Musée du Congo Belge (Sér. A: Minéralogie Géologie, Paléontologie)* 3(2): 1–200.

Dastas, N., J. Chamberlain Jr., and M. Becker. 2010. Palynomorphs of the Arkadelphia Formation and Midway Group transition (Maastrichtian–Danian), Hot Spring County, Arkansas. *Geological Society of America, Abstracts with Programs* 42: 185.

Dastas, N., J. Chamberlain Jr., and M. Garb. 2014. Cretaceous-Paleogene Dinoflagellate Biostratigraphy and the Age of the Clayton Formation, Southeastern Missouri, USA. *Geosciences* 4: 1–29.

Davis, J. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society* 2: 363–434.

D'Hondt, S. 2005. Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems. *Annual Review of Ecology Evolution and Systematics* 36: 295–317.

Dillon, E., R. Norris, and A. Dea. 2017. Dermal denticles as a tool to reconstruct shark communities. *Marine Ecology Progress Series* 566: 117–134.

Gale, A. 2006. The Cretaceous-Palaeogene Boundary on the Brazos River, Falls County, Texas: Is there evidence for Impact Induced Tsunami Sedimentation? *Proceeding of the Geologists Association* 117: 173–185.

Gallo, V., F. Figueiredo, L. de Carvalho, and S. de Azevedo. 2001. Vertebrate assemblage from the Maria Farinha Formation after the K-T boundary. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 219(3): 261–284.

Geyn, W. 1937. Les élasmobranches du Crétacé marin du Limbourg Hollandais. *Natuurhistorisch Maandblad Maestricht* 26: 16–69.

Gill, T. 1862. Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera. *Annals of the Lyceum of Natural History of New York* 7: 367–408.

Glickman, L. 1964. *Sharks of Paleogene and their stratigraphic significance*, 1–229. Moskva: Nauka Press.

Gray, J. 1851. *List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii*, 1–160. London: British Museum (Natural History).

Gurr, P. 1962. A new fish fauna from the Woolwich Bottom Beds (Sparnacian) of Herne Bay, Kent. *Proceedings of the Geologists' Association* 73: 419–447.

Haley, B., E. Glick, W. Bush, B. Clardy, C. Stone, M. Woodward, and D. Zachry. 1993. *Geologic map of Arkansas. 1:500,000 scale*. *Arkansas Geologic Commission* 1.

Haley, B., C. Stone, B. Clardy, and W. Hanson. 2009. *Geologic Map of the Arkadelphia, Quadrangle, Clark, Garland, Hempstead, Hot Spring, Howard, Montgomery, Pike, and Polk Counties, Arkansas 1:100,000 Scale*. Little Rock: DGM-AR-01100; Arkansas Geologic Commission.

Hallam, A., and P. Wignall. 1999. Mass extinctions and sea-level changes. *Earth-Science Reviews* 48: 217–250.

Halter, M. 1989. Additions to the fish fauna of N.W. Europe. A new dasyatid genus from the Early Palaeocene (Danian) of the Limburg area, Belgium. *Tertiary Research* 10: 179–191.

Haq, B. 2014. Cretaceous eustasy revisited. *Global and Planetary Change* 113: 44–58.

Haq, B., J. Hardenbol, and P. Vail. 1988, Mesozoic and Cenozoic chronostratigraphy and eustatic cycles. In *Sea Level Changes: An Integrated Approach*, eds. C. Wilgus, H. Posamentier, C. Ross, and C. Kendall. *SEPM Special Publication* 42: 71–104.

Hart, B. 2017. *Paleoecological Analysis of the Clayton Formation (Paleocene) near Malvern, Arkansas.* University of Southern Mississippi Honors Thesis, 1–26.

Hart, M., T. Yancey, A. Leighton, B. Miller, C. Liu, C. Smart, and R. Twitchett. 2012. The Cretaceous-Paleogene boundary on the Brazos River, Texas: New stratigraphic sections and revised interpretations. *Gulf Coast Association of Geological Societies Journal* 1: 69–80.

Hay, O. 1902. On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bulletin of the American Museum of Natural History* 19: 395–452.

Herman, J. 1973. Contribution à la connaissance de la faune ichthyologique des phosphates du Maroc. *Annales de la Société Géologique de Belgique* 95: 271–284.

Herman, J. 1977. Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique* 15: 1–401.

Herman, J., M. Hovestadt-Euler, D. Hovestadt, and M. Stehmann. 1998. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific species of Chondrichthyan fishes. Part B: Batomorphii No. 4a: Order Rajiformes-Suborder Myliobatoidei-Superfamily Dasyatoidea-Family Dasyatidae-Subfamily Dasyatinae-Genera: *Amphotistius, Dasyatis, Himantura, Pastinachus, Pteroplatytrygon, Taeniura, Urogymnus* and *Urolophoides* (incl. Supraspecific species of uncertain status and validity), Superfamily Myliobatoidea-Family Gymnuridae-Genera: *Aetoplatea* and *Gymnura*, Superfamily Plesiobatoidea-Family Hexatrygonidae-Genus: *Hexatrygon*. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 68: 145–197.

Herman, J., M. Hovestadt-Euler, D. Hovestadt, and M. Stehmann. 1999. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific species of chondrichthyan fishes. Part B: Batomorphii. No.4b: Order Rajiformes-Suborder Myliobatoidei-Superfamily Dasyatoidea-Family Dasyatididae-Subfamily Dasyatinae-Genus: *Taeniura, Urogymnus, Urolophoides*-Subfamily Potamotrygoninae-Genera: *Disceus, Pleisiotrygon*, and *Potamotrygon* (incl. Supraspecific species of uncertain status and validity), Family Urolophidae-Trygonoptera, Urolophus and Urotrygon-Superfamily Myliobatidea-Family: Gymnuridae-Genus: *Aetoplatea*. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*. *Biologie* 69: 161–200.

Herman, J., M. Hovestadt-Euler, D. Hovestadt, and M. Stehmann. 2000. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superaspecific species of Chondrichthyan fishes. Part B: Batomorphii 4c: Order: Rajiformes-Suborder Myliobatoidei-Superfamily Dasyatoidea-Family Dasyatididae-Subfamily Dasyatinae-Genus: *Urobatis*, Subfamily Potamotrygoninae-Genus: *Pomatotrygon*, Superfamily Plesiobatoidea-Family

Plesiobatidae-Genus: *Plesiobatis*, Superfamily Myliobatoidea-Family Myliobatidae Subfamily Myliobatinae-Genera: *Aetobatus, Aetomylaeus, Myliobatis*, and *Pteromylaeus*, Subfamily Rhinopterinae-Genus: *Rhinoptera* and Subfamily Mobulinae-Genera: *Manta* and *Mobula*. Addendum 1 to 4a: erratum to Genus *Pteroplatytrygon*. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*. *Biologie* 70: 5–67.

Hildebrand, A., G. Penfield, D. Kring, M. Pilkington, A.Z. Camargo, S. Jacobsen, and W. Boynton. 1991. Chicxulub crater: a possible Cretaceous/Tertiary boundary impact crater on the Yucatan Peninsula, Mexico. *Geology* 19: 867–871.

Hooks, G., D. Schwimmer, and G. Williams. 1999. Synonymy of the pycnodont *Phacodus punctatus* Dixon, 1850, and its occurrence in the Late Cretaceous of the southeastern United States. *Journal of Vertebrate Paleontology* 19: 588–590.

Hovestadt, D., and M. Hovestadt-Euler. 2013. Generic Assessment and Reallocation of Cenozoic Myliobatinae based on new information of tooth, tooth plate and caudal spine morphology of extant species. *Palaeontos* 24: 1–66.

Huxley, T. 1880. On the application on the laws of evolution to the arrangement of the vertebrata and more particularly of the Mammalia. *Zoological Society of London Scientific Memoirs* 4: 457–472.

Jaekel, O. 1895. Unter-Tertiäre Selachier aus Südrussland. *Mémoirs du Comité Geologique de St Petersburg* 9: 1–35. (in Russian and German).

Johnson-Ransom, E., E. Popov, T. Deméré, and K. Shimada. 2018. The Late Cretaceous chimaeroid fish, *Ischyodus bifurcatus* Case (Chondrichthyes: Holocephali), from California, USA, and its Paleobiogeographical Significance. *Paleontological Research* 22: 364–373.

Jones, E. 1962. Palynology of the Midway-Wilcox boundary in south-central Arkansas. *Gulf Coast Association of Geological Societies Transactions* 12: 285–294.

Jordan, D. 1888. *A manual of the vertebrate animals of the northern United States, including the district north and east of the Ozark mountains, south of the Laurentian hills, north of the southern boundary of Virginia, and east of the Missouri river, inclusive of marine species*. New York: World Book Co.

Jordan, D., and B. Evermann. 1896. The fishes of North and middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. *Bulletin of U.S. National Museum* 5: 1–1240.

Kajiura, S., and T. Tricas. 1996. Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray *Dasyatis sabina*. *Journal of Experimental Biology* 199: 2297–2306.

Kajiura, S., A. Sebastian, and T. Tricas. 2000. Dermal bite wounds as indicators of reproductive seasonality and behaviour in the Atlantic stingray, *Dasyatis sabina*. *Environmental Biology of Fishes* 58: 23–31.

Keller, G., H. Khozyem, T. Adatte, N. Malarkodi, J. Spangenberg, and W. Stinnesbeck. 2013. Chicxulub impact spherules in the North Atlantic and Caribbean: age constraints and Cretaceous-Tertiary boundary hiatus. *Geological Magazine* 150: 885–907.

Kennedy, W., N. Landman, W. Christensen, W. Cobban, and J. Hancock. 1998. Marine connections in North America during the late Maastrichtian: palaeogeographic and palaeobiologic significance of *Jeletzkytes Nebrascensis Zone Cephalopod Fauna* from the Butte Member of the Pierre Shale, southeastern South Dakota and northeastern Nebraska. *Cretaceous Research* 19: 745–775.

Kent, B. 1994. *Fossil Sharks of the Chesapeake Bay Region*, 1–146. Baltimore: Egan Rees and Boyer Publishers.

Korbar, T., A. Montanari, V.P. Fućek, L. Fuček, R. Coccioni, I. McDonald, P. Claeys, T. Schulz, and Christian Koeberl. 2015. Potential Cretaceous-Paleogene boundary Tsunami Deposit

in the Intra-Tethyan Adriatic carbonate platform section of Hvar (Croatia). *Geological Society of America Bulletin* 127: 1666–1680.

Kring, D. 2007. The Chicxulub impact event and its environmental consequences at the Cretaceous-Tertiary Boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255: 4–21.

Kriwet, J., and M. Benton. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) Diversity Across the Cretaceous-Tertiary Boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214: 181–194.

Landman, N., R. Johnson, and L. Edwards. 2004. Cephalopods from the Cretaceous/Tertiary boundary interval on the Atlantic Coastal Plain, with a description of the highest ammonite zones in North America. Part 2. Northeastern Monmouth County, New Jersey. *Bulletin of the American Museum of Natural History* 33: 1–107.

Landman, N., M. Garb, R. Rovelli, D. Ebel, and L. Edwards. 2012. Short-term survival of ammonites in New Jersey after the end-Cretaceous bolide impact. *Acta Palaeontologica Polonica* 57: 703–715.

Larina, E., M. Garb, N. Landman, N. Dastas, N. Thibault, L. Edwards, G. Phillips, R. Rovelli, C. Myers, and J. Naujokaityte. 2016. Upper Maastrichtian Ammonite biostratigraphy of the Gulf Coastal Plain (Mississippi Embayment, southern USA). *Cretaceous Research* 60: 128–151.

Leriche, M. 1905. Les poisons tértiaires de la Belgique. II. Les poissons eocénes. *Mémoires du Musee Royal d'Histoire Naturelle Beligique* 11: 49–228.

Leriche, M. 1913. Les poissons paléocènes de Landana (Congo). Les gisements de poissons paléocènes et éocènes de la côte occidentale d'Afrique. *Annales du Musée du Congo Belge* 1: 67–91.

Leriche, M. 1938. Contribution à l'étude des poissons fossiles des pays riverains de la Méditerranée américaine (Venezuela, Trinité, Antilles, Mexique). *Mémoires de la Société Paléontologique Suisse* 61: 1–42.

Li, L., G. Keller, T. Adatte, and W. Stinnesbeck. 2000. Late Cretaceous Sea Level Changes in Tunisia: A Multi-Disciplinary approach. *Journal of the Geological Society* 157: 447–458.

Liddicoat, J., J. Hazel, and E. Brouwers. 1981. Magnetostratigraphy of Upper Cretaceous deposits in southwestern Arkansas and northeastern Texas. *American Association of Petroleum Geologists* 65: 764–765.

MacLeod, K., P. Quinton, J. Sepúlveda, and M. Negra. 2018. Postimpact earliest Paleogene warming shown by fish debris oxygen isotopes (El Kef, Tunisia). *Science* 360: 1467–1469.

Maisch IV, H., M. Becker, B. Raines, and J. Chamberlain Jr. 2014. Chondrichthyans from the Tallahatta-Lisbon Formation Contact (Middle Eocene) Silas, Choctaw County, Alabama. *Paludicola* 9: 183–209.

Maisch IV, H., M. Becker, and J. Chamberlain Jr. 2015. Chondrichthyans from a lag deposit between the Shark River Formation (Middle Eocene) and Kirkwood Formation (Early Miocene), Monmouth County, New Jersey. *Paludicola* 10: 149–183.

Maisch IV, H., M. Becker, and J. Chamberlain Jr. 2018a. Lamniform and Carcharhiniform Sharks from the Pungo River and Yorktown Formations (Miocene–Pliocene) of the Submerged Continental Shelf, Onslow Bay, North Carolina, USA. *Copeia* 106: 353–374.

Maisch, H., IV, M. Becker, and J. Chamberlain Jr. 2018b. Bioerosion of megatoothed shark teeth: Implications for timing vertebrate fossil lag deposits (Onslow Bay, North Carolina, USA). *Society of Vertebrate Paleontology Annual Conference*. B-82.

Mancini, E., B. Tew, and C. Smith. 1989. Cretaceous-Tertiary contact, Mississippi and Alabama. *The Journal of Foraminiferal Research* 19: 93–104.

Mancini, E., T. Puckett, B. Tew, and C. Smith. 1995. Upper Cretaceous sequence stratigraphy of the Mississippi—Alabama Area. *Gulf Coast Association of Geological Societies, Transactions*. 45: 377–384.

Mancini, E., and T. Puckett. 2005. Jurassic and Cretaceous transgressive-regressive (TR) cycles Northern Gulf of Mexico, USA. *Stratigraphy* 2: 31–48.

Mannering, A., and N. Hiller. 2008. An Early Cenozoic Neoselachian Shark Fauna from the Southwest Pacific. *Palaeontology* 51: 1341–1365.

Manning, E., and D. Dockery. 1992. A guide to the Frankstown vertebrate fossil locality (Upper Cretaceous), Prentiss County, Mississippi. *Mississippi Department of Environmental Quality, Office of Geology Circular* 4: 1–43.

Marmi, J., B. Vila, O. Oms, A. Galobart, and H. Cappetta. 2010. Oldest records of stingray spines (Chondrichthyes, Myliobatiformes). *Journal of Vertebrate Paleontology* 30: 970–974.

McFarland, J. 2004. Stratigraphic Summary of Arkansas; Information Circular. *Arkansas Geological Commission: Little Rock, Arkansas, USA* 36: 1–44.

Miller, K., R. Sherrell, J. Browning, M. Field, W. Gallagher, Richard K. Olsson, P. Sugarman, S. Tuorto, and H. Wahyudi. 2010. Relationship Between Mass Extinction and Iridium Across the Cretaceous-Paleogene Boundary in New Jersey. *Geology* 38: 867–870.

Moody, R., and P. Sutcliffe. 1993. The sedimentology and palaeontology of the Upper Cretaceous-Tertiary deposits of central West Africa. *Modern Geology* 18: 539–554.

Moreau, F., and S. Mathis. 2000. Les élasmobranches du Thanétien (Paléocène) du Nord de la France, des carrières de Templeuve et de Leforest. *Cossmanniana* 7: 1–4.

Müller, J., and J. Henle. 1837. On the generic characters of cartilaginous fishes with descriptions of new genera. *Magazine of Natural History* 2: 1–91.

Müller, J. and J. Henle. 1838–1841 [1838]. *Systematische Beschreibung der Plagiostomen*, xxii + 1–200. Berlin: Veit.

Nishida, K. 1990. Phylogeny of the suborder Myliobatoidei. *Memoirs of the Faculty of Fisheries Hokkaido University* 37: 1–108.

Noubhani, A. 2010. The Selachian Faunas of the Moroccan phosphate deposits and the KT mass extinctions. *Historical Biology* 22: 71–77.

Noubhani, A., and H. Cappetta. 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. *Palaeo Ichthyologica* 8: 1–327.

Oboh-Ikuenobe, F., M. Spencer, C. Campbell, and R. Haselwander. 2012. A Portrait of Late Maastrichtian and Paleocene palynoflora and paleoenvironment in the northern Mississippi Embayment, southeastern Missouri. *Palynology* 36: 63–79.

Obruchev, D. 1953. Izuchenie edestid y raboty A. P. Karpinskogo. *Trudy Paleontologičeskogo Instituta Akademija Nauk SSSR* 45: 1–85.

Otero, R., J. Oyarzún, S. Soto-Acuña, R. Yury-Yáñez, N. Gutierrez, J. Le Roux, T. Torres, and F. Hervé. 2013. Neoselachians and Chimaeriformes (Chondrichthyes) from the latest Cretaceous–Paleogene of Sierra Baguales, southernmost Chile. Chronostratigraphic, Paleobiogeographic and Paleoenvironmental Implications. *Journal of South American Earth Sciences* 48: 13–30.

Parmley, D., and D. Cicimurri. 2005. First Record of a Chimaeroid Fish from the Eocene of the Southeastern United States. *Journal of Paleontology* 79: 1219–1221.

Phillips, G., C. Sloan, and D. Linck. 2015. Early Paleocene beds at the I-30 slide locality near Rockport. *Southeastern Association of Vertebrate Paleontology eighth Annual Research Conference*. (n.v., n.p.).

Phillips, G. and G. Case. 2019. An elasmobranch assemblage from the Danian (Early Paleocene) of Mississippi. *Geologic Society of America Abstracts with Programs* 33-3.

Pitakpaivan, P., and J. Hazel. 1994. Ostracods and Chronostratigraphic Position of the Upper Cretaceous Arkadelphia Formation of Arkansas. *Paleontology* 68: 111–122.

Purdy, R. 1998. Chondrichthyan Fishes from the Paleocene of South Carolina. *Transactions of the American Philosophical Society, New Series* 88: 122–146.

Rafinesque, C. 1810. *Caraterri di alcuni nuovi generi e nuove specie di animali piante Della Sicilia*, 1–105. Palermo: Sanfilippo.

Rangel, B., S. Rodrigues, P. Favaron, A. Amorim, and R. Rici. 2014. Structure and dental sexual dimorphism in *Dasyatis hypostigma* (Santos & Carvalho, 2004) (Myliobatiformes, Dasyadae). In *Microscopy: advances in scientific research and education*, ed. A. Méndez-Vilas, 89–94.

Ribeiro de Santana, F., D. Cicimurri, and J. Barbosa. 2011. New material of *Apocopodon sericeus* Cope 1886 (Myliobatiformes, Myliobatidae) from the Paraíba basin (northeastern Brazil), and South Carolina (USA) with a reanalysis of the species. *PalArch's Journal of Vertebrate Paleontology* 8: 1–20.

Roemer, C. 1849. Mit besonderer Rücksicht auf deutsche Auswanderung und die physische Verhältnisse des Landes. Mit einem naturwissenschaftlichen Anhange und einer topographisch-geognostischen Karte von Texas. *Index Specierum et generum* 1: 1–464.

Romer, A. 1942. Notes on certain American Paleozoic fishes. *American Journal of Science* 240: 216–228.

Rovelli, R., M. Garb, E. Larina, J. Sloan, N. Landman, J. Naujokaityte, and G. Phillips. 2014. Evidence of Chicxulub Impact Record for the First Time in Arkansas. *Geologic Society of America Abstracts with Programs* 320-6.

Savrda, C. 1993. Ichnosedimentologic evidence for a noncatastrophic origin of Cretaceous Tertiary boundary sands in Alabama. *Geology* 21: 1075–1078.

Schoene, B., M. Eddy, K. Samperton, C. Keller, G. Keller, T. Adatte, and S. Khadri. 2019. U-Pb constraints on pulsed eruption of the Deccan Traps across the end-Cretaceous mass extinction. *Science* 363: 862–866.

Schulte, P., L. Alegret, I. Arenillas, J. Arz, P. Barton, P. Bown, T. Bralower, et al. 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science* 327: 1214–1218.

Scotese, C. 2014. *Atlas of Late Cretaceous Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 16–22, Mollweide Projection*. Evanston, Ill.: PALEOMAP Project.

Shimada, K. 1997. Skeletal anatomy of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* from the Niobrara Chalk in Kansas. *Journal of Vertebrate Paleontology* 17: 642–652.

Shimada, K., and D. Cicimurri. 2005. Skeletal anatomy of the Late Cretaceous shark, *Squalicorax* (Neoselachii: Anacoracidae). *Paläontologische Zeitschrift* 79: 241–261.

Shimada, K., B. Schumacher, J. Parkin, and J. Palermo. 2006. Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. *Journal of Paleontology* 63: 1–45.

Sibert, E., P. Hull, and R. Norris. 2014. Resilience of Pacific pelagic fish across the Cretaceous/Palaeogene mass extinction. *Nature Geoscience* 7: 667–670.

Sibert, E., and R. Norris. 2015. New Age of Fishes initiated by the Cretaceous–Paleogene mass extinction. *Proceedings of the National Academy of Sciences* 112: 8537–8542.

Sibert, E., R. Norris, J. Cuevas, and L. Graves. 2016. Eighty-five million years of Pacific Ocean gyre ecosystem structure: long-term stability marked by punctuated change. *Proceedings of the Royal Society B: Biological Sciences* 283: 20160189. https://doi.org/10.1098/rspb.2016.0189.

Silva, V. 1994. Chondrichthyes das formações Gramame e Maria Farinha: aspectos evolutivos e paleoecológicos. I. Superordem Batomorphii. *Acta Geologica Leopoldensia* 17: 315–328.

Siverson, M. 1995. Revision of the Danian cow sharks, sand tiger sharks, and goblin sharks (Hexanchidae, Odontaspididae, and Mitsukurinidae) from southern Sweden. *Journal of Vertebrate Paleontology* 15: 1–12.

Smit, J., T. Roep, W. Alvarez, A. Montanari, P. Claeys, J. Grajales-Nishimura, and J. Bermudez. 1996. Coarse-grained clastic sandstone complex at the K/T boundary around the Gulf of Mexico: deposition by tsunami waves induced by the Chicxulub impact. *Geological Society of America Special Paper* 307: 151–182.

Sprain, C., P. Renne, L. Vanderkluysen, K. Pande, S. Self, and M. Tushar. 2019. The Eruptive tempo of Deccan volcanism in Relation to the Cretaceous-Paleogene boundary. *Science* 363: 866–870.

Stahl, B., and D. Parris. 2004. The complete dentition of *Edaphodon mirificus* (Chondrichthyes: Holocephali) from a single individual. *Journal of Paleontology* 78: 388–392.

Stinnesbeck, W., and G. Keller. 1995. The Cretaceous-Tertiary boundary in southern low-latitude regions: preliminary study in Pernambuco, northeastern Brazil—Comments and Reply. *Terra Nova* 7: 375–378.

Stringer, G. and J. Sloan. 2018. Significance of Early Paleocene Fish Otoliths from two Clayton Formation (Danian) Sites in Central Arkansas. *Geologic Society of America Abstracts with Programs*, P. 2-11.

Stromer, E. 1910. Reptilien und Fischreste aus dem marinen Alttertiär von Südtogo (Westafrika). *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 52: 478–505.

Underwood, C., Z. Johanson, M. Welten, B. Metscher, L. Rasch, G. Fraser, and M. Smith. 2015. Development and evolution of dentition pattern and tooth order in the skates and rays (Batoidea; Chondrichthyes). *PLoS One* 10: e0122553.

Ward, D. 1988. *Hypotodus verticalis* (Agassiz 1843), *Hypotodus robustus* (Leriche 1921) and *Hypodus heinzelini* (Casier 1967), Chondrichthyes, Lamniformes, junior synonyms of *Carcharias hopei* (Agassiz 1843). *Tertiary Research* 10: 1–12.

Ward, D., and R. Wiest. 1990. A checklist of Paleocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. *Tertiary Research* 12: 81–88.

Welton, B. 1974. Preliminary note on the Paleocene elasmobranchs of the Lodo Formation, Fresno County, California. In *Pacific Section, S.E.P.M., Fall Guidebook for the Paleogene of the Panoche Creek–Cantua Creek area, Central California*, 91–97.

Welton, B., and R. Farish. 1993. *The Collector's Guide to Fossil sharks and rays from the Cretaceous of Texas*, 1–204. Lewisville: Before Time Publishers.

White, E. 1931. *The vertebrate faunas of the English Eocene. I. From the Thanet Sands to the Basement Bed of the London Clay*, 1–121. London: British Museum (Natural History).

Winkler, T. 1876. Deuxième Mémoire sur des dents de poisons du terrain Bruxellien. *Archives du Musée Teyler* 4: 16–48.

Witts, J., R. Whittle, P. Wignall, J. Crame, J. Francis, R. Newton, and V. Bowman. 2016. Macrofossil evidence for a rapid and severe Cretaceous-Paleogene mass extinction in Antarctica. *Nature communications* 7: 11738.

Witts, J., N. Landman, M. Garb, C. Boas, E. Larina, R. Rovelli, L. Edwards, R. Sherrell, and J. Kirk Cochran. 2018. A fossiliferous spherule-rich bed at the Cretaceous-Paleogene (K–Pg) boundary in Mississippi, USA: Implications for the K-Pg mass extinction event in the Mississippi Embayment and Eastern Gulf Coastal Plain. *Cretaceous Research* 91: 147–167.

Woodward, A. 1907. Notes on some Upper Cretaceous fish-remains from the Provinces of Sergipe and Pernambuco, Brazil. *Geological Magazine* 4: 193–197.

Zakharov, Y., A. Popov, Y. Shigeta, O. Smyshlyaeva, E. Sokolova, R. Nagendra, T. Velivetskaya, and T. Afanasyeva. 2006. New Maastrichtian oxygen and carbon isotope record: Additional evidence for warm low latitudes. *Geosciences Journal* 10: 347.

Zinsmeister, W. 1998. Discovery of fish mortality horizon at the K/T boundary on Seymour Island: re-evaluation of events at the end of the Cretaceous. *Journal of Paleontology* 72: 556–571.

Springer