

A new species of *Hypolophites* (Chondrichthyes, Myliobatiformes) from the Lower Clayton Limestone Unit of the Midway Group (Paleocene), near Malvern, Arkansas, USA

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Abstract.—A new species of *Hypolophites* (Chondrichthyes, Myliobatiformes) is described from an assemblage of isolated pavement teeth recovered from the Lower Clayton Limestone Unit of the Midway Group (Paleocene) near Malvern, Arkansas. These teeth were collected from several localized lag deposits containing an abundance of chondrichthyan and osteichthyan teeth, invertebrate remains, and trace fossils indicative of a marginal-shallow marine depositional environment. To date, only four additional species of *Hypolophites* have been reported from Paleocene deposits that occur along the west coast of central-northern Africa and in central New Jersey, USA. The identification of *Hypolophites beckeri* n. sp. in southwestern Arkansas extends the distribution of this biostratigraphically significant genus ~1,750 km westward into the Mississippi Embayment and Gulf Coastal Plain of the USA. The distribution of *Hypolophites* species during the Paleocene attests to the uniformity of shallow marine shelves between western Africa and the Atlantic and Gulf Coastal Plains of the USA, as well as myliobatiform diversification following the K/Pg mass extinction event.

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Introduction

In this report, a new species of myliobatiform ray, *Hypolophites beckeri* n. sp., is described from isolated pavement teeth recovered from the Lower Clayton Limestone Unit (LCLU) of the Midway Group near Malvern, Arkansas (AR), USA. This particular *Hypolophites* species is the fifth known globally and represents the westernmost occurrence and first report of the genus in the Mississippi Embayment and Gulf Coastal Plain (GCP) of the USA. *Hypolophites* species are biostratigraphically significant in regional and global stratigraphic analyses because they have only been reported from the Paleocene. The occurrence of an additional *Hypolophites* species in AR extends the known paleogeographic distribution of *Hypolophites* ~1,750 km westward and suggests that the genus is more diverse and widespread than originally recognized. Moreover, the distribution of *Hypolophites* during the Paleocene attests to the migratory abilities and diversification of myliobatiforms following the K/Pg mass extinction event.

Geologic setting

In southwestern Arkansas, Upper Cretaceous and Paleocene formations are infrequently exposed due to dense vegetation overgrowth (Haley et al., 1993, 2009; McFarland, 1998, 2004). Near the town of Malvern, Arkansas, highway stabilization, commercial development, and erosion in the Ouachita River has discontinuously exposed the: (1) Maastrichtian Arkadelphia

Formation that consists of dark, micaceous clays interbedded with fossiliferous sandy coquina lenses; (2) Arkadelphia Formation–Midway Group Contact (K/Pg boundary) that occurs as a coquina lag deposit that includes phosphate pebbles and distinctly Cretaceous macrofossils, including chondrichthyans, osteichthyans, plesiosaurs, turtles, and ammonites (see Becker et al., 2006, 2010, 2013, 2016; Maisch et al., *in press*); (3) lower Midway Group (Paleocene) that is composed of gray clays and sandy limestones; and (4) upper Midway Group (Paleocene) that occurs mainly as orange/tan clays and limestones.

Currently, the Paleocene Midway Group in Arkansas has been informally subdivided into the Clayton Limestone (or Clayton Formation) and Porters Creek Clay (McFarland, 1998, 2004; Becker et al., 2011; Becker and Chamberlain, 2012). The Clayton Limestone can be further divided into the Lower and Upper Clayton Limestone Units (LCLU and UCLU), as observed in recent excavations along Interstate-30 (I-30) directly adjacent to the Ouachita River, ~4 km northwest of Malvern, Arkansas (Fig. 1; Maisch et al., *in press*). The LCLU exposed in this outcrop is the source of the *Hypolophites* teeth featured in this study and consists of >20 m of massive, dark gray clays containing invertebrate casts and molds, thin interbedded sandy limestone units, and three locally phosphatic, sand and pebble lag deposits containing chondrichthyan and osteichthyan remains (Fig. 1; Maisch et al., *in press*). Higher in this section, tan and yellow clays with thin limestone beds of the UCLU are exposed and appear identical to those occurring ~2.7 km to the northeast, as described by Becker et al. (2011) and Becker

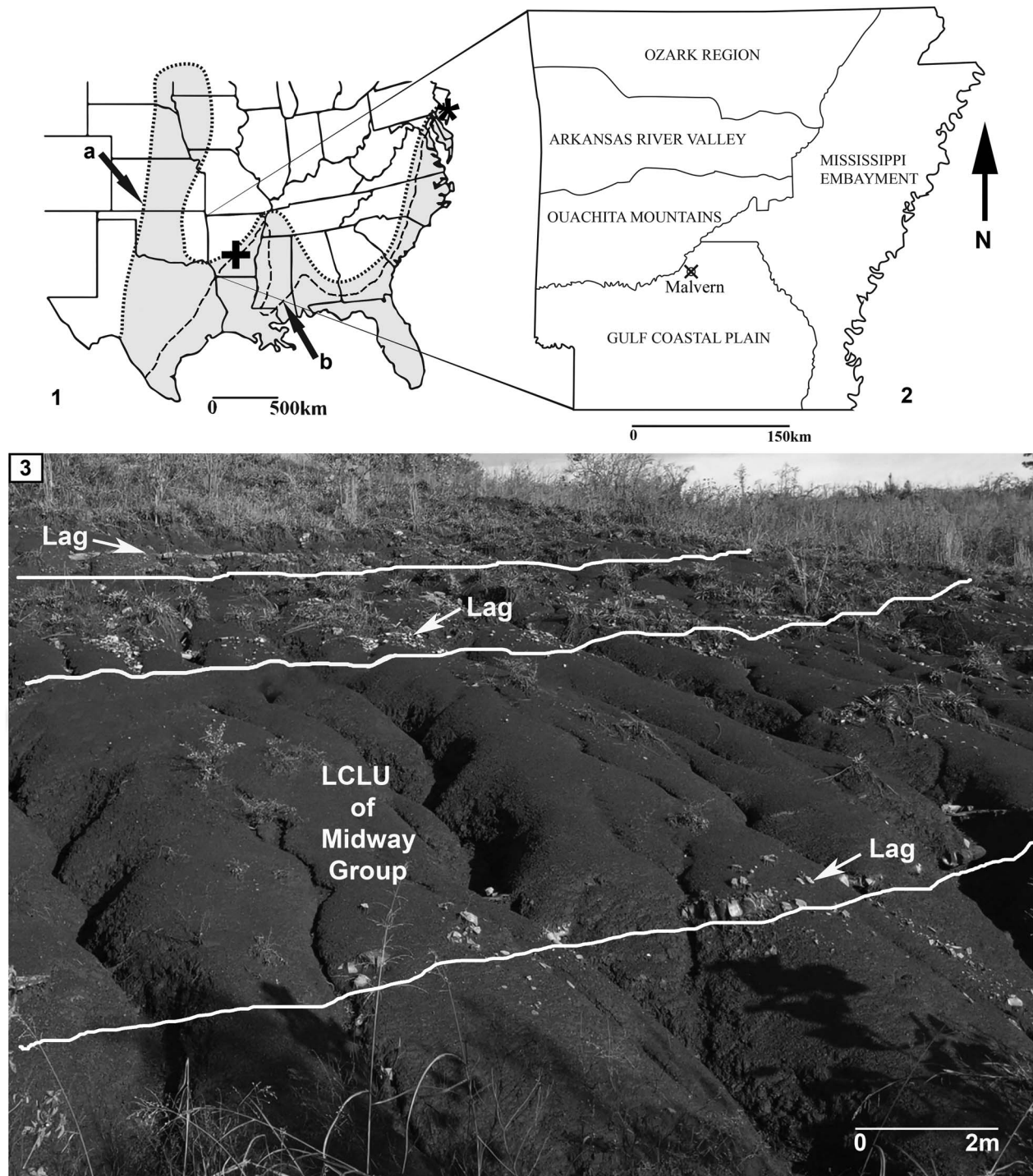


Figure 1. Location of the Lower Clayton Limestone Unit of the Paleocene Midway Group near Malvern, Arkansas, USA. (1) Reconstructed Late Cretaceous–Maastriichtian (a) and Paleocene–Danian (b) shorelines across the Atlantic and Gulf Coastal Plains and Western Interior Seaway indicated by arrows (modified from Scotese, 2014; Becker et al., 2016). The location of *Hypolophites beckeri* n. sp. described in this study near Malvern, AR, is indicated by + and the location of *Hypolophites hutchinsi* Case, 1996, in NJ, is indicated by *. (2) Physiographic provinces in Arkansas, with Malvern indicated by X. (3) Outcrop exposure of the Lower Clayton Limestone Unit (LCLU) of the Midway Group adjacent to I-30 near Malvern, Arkansas.

and Chamberlain (2012). Myliobatiforms occur in the UCLU; however, *Hypolophites* teeth have not been recovered (Becker et al., 2011; Maisch et al., in press).

Although the Midway Group in Arkansas has not been formally sub-divided into formations or correlated to specific Paleocene stage boundaries as recognized in the eastern

Mississippi Embayment, preliminary data from dinoflagellates and otoliths indicate that the lower Midway Group in this section is Danian in age (Mancini et al., 1989; McFarland, 2004; Mancini and Puckett, 2005; Dastas et al., 2010; Stringer and Sloan, 2018). Additionally, many chondrichthyans reported from the LCLU have also been found in contemporaneous Paleocene

deposits in the Atlantic Coastal Plain (ACP) of the USA, western Europe, and northern Africa (e.g., Ward and Wiest, 1990; Case, 1996; Cappetta, 2012; Adolfssen and Ward, 2015).

Materials and methods

Over 500 kg of sediment was bulk sampled from the LCLU for laboratory analysis. Sediment was thoroughly rinsed through 5.0–0.5 mm sieves and dried under heat lamps. Fossils, including the holotype and paratypes featured in this report, were recovered from dried sediment using forceps and imaged using an Olympus SZ61 binocular microscope attached to an Infinity 2 Digital Camera. An Evex Mini SEM SX-3000 operating in the range of 20kv was also utilized to image several specimens with diagnostic morphological features.

Repositories and institutional abbreviations.—For comparative purposes, the holotype and paratypes of *Hypolophites hutchinsi* Case, 1996, were examined at the American Museum of Natural History (AMNH), New York, USA (holotype: AMNH: FF14585; paratypes: AMNH: FF13875–13877; 14583, 14584). Specimens of *Hypolophites beckeri* n. sp. included in this study have been deposited in the Academy of Natural Science (ANSP) of Drexel University, Philadelphia, Pennsylvania, USA, under the catalog numbers ANSP: VP25128–25132; 25148–25152.

Systematic paleontology

- Class Chondrichthyes Huxley, 1880
- Subclass Elasmobranchii Bonaparte, 1838
- Cohort Euselachii Hay, 1902
- Subcohort Neoselachii Compagno, 1977
- Order Myliobatiformes Compagno, 1973
- Superfamily Myliobatoidea Compagno, 1973
- Family Myliobatoidea insertae familiae
- Genus †*Hypolophites* Stromer, 1910

Type species.—*Hypolophites myliobatoides* Stromer, 1910.

†*Hypolophites beckeri* new species
 Figures 2, 3

Holotype.—ANSP: VP25131; paratypes: ANSP: VP25128–25130; 25132; 25148–25152.

Diagnosis.—A *Hypolophites* species with median and lateral pavement teeth that have hexagonal and rhombus-shaped, trilobate, and finely pitted occlusal surfaces, heavily wrinkled crown edges, a “U- or V-shaped” labial uvula, and small lingual shelf. Occlusal surface pitting forms a vermiculate pattern and is more frequently preserved on lateral teeth. The occlusal surfaces of median and lateral teeth have a mesial-distal width that may exceed 5.0 mm. In general, the length between the lingual and labial surfaces is half the mesial-distal occlusal surface width. As seen in profile view, crown and root thicknesses of median and lateral teeth are nearly equivalent and teeth may exceed 4.0 mm in total height. The lingual

tooth surfaces are concave and extensively wrinkled, while the labial tooth surfaces are flat to slightly convex with dorso-ventrally oriented furrows. Roots of median and lateral teeth are generally bilobate, terminate with rounded bases, and may contain several foramina within the nutritive groove and on the edges of the root lobes. The roots of some median teeth may contain two nutritive grooves that asymmetrically divide the root.

Occurrence.—Lower Clayton Limestone Unit of the Midway Group (Paleocene), adjacent to Highway 84, Interstate-30, and the Ouachita River ~4 km NW of Malvern, Arkansas, USA.

Description.—Median and lateral teeth have crowns that overhang the labial root surface and hexagonal-like, vermiculated surface-pitting on the occlusal surfaces when unworn. 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 with nearly straight, smooth edges. Median teeth are mesio-distally elongated, while lateral teeth are more equidimensional. Lateralmost teeth are labio-lingually elongated and increasingly compressed in dorsal-ventral and mesial-distal dimensions. Teeth in all jaw positions have lingual crown surfaces that are concave in profile view, labial tooth surfaces that are straight to slightly convex in profile view, and contain well-defined, vertical wrinkles or furrows that extend from the occlusal surface to the crown-root interface on all tooth edges. Median and lateral teeth have an enameloid crown that overhangs the root on the labial surface in profile view. The lingual surfaces of median and lateral teeth form a small but distinct “L”-shaped ledge and contain a “U- or V-shaped” uvula that is directed at the separation between the underlying root lobes. The roots of median and lateral teeth are generally bilobate, peg-like to pentagonal in shape, and have slightly convex, basal surfaces. Median teeth may contain roots with symmetric or asymmetric lobes. Lateral tooth roots become progressively more offset with increasing distance from the symphysis, such that the root lobes extend to different lengths beyond the lingual crown surface. A well-defined nutritive groove occurs between the root lobes in all teeth and frequently contains 1–3, centrally located foramina. Several small foramina may also be present on the edge of the root lobes. Although infrequent, median teeth may have a second, less-developed nutritive groove.

Etymology.—Named in honor of Dr. Martin Becker for his pioneering and ongoing field endeavors focusing on the paleontology of Late Cretaceous–Paleocene marine vertebrates in the Malvern, Arkansas, region.

Remarks.—Pavement teeth of *Hypolophites beckeri* n. sp. can be distinguished from similar teeth of *Hypolophus sylvestris* White, 1931, *Rhombodus binkhorsti* Dames, 1881, *Myliobatis* sp., and *Rhinoptera* sp. previously reported from the Malvern, Arkansas, region based on the presence of hexagonal to trilobate occlusal surfaces, well-developed, vertical wrinkles on all tooth edges in profile view, labial enameloid

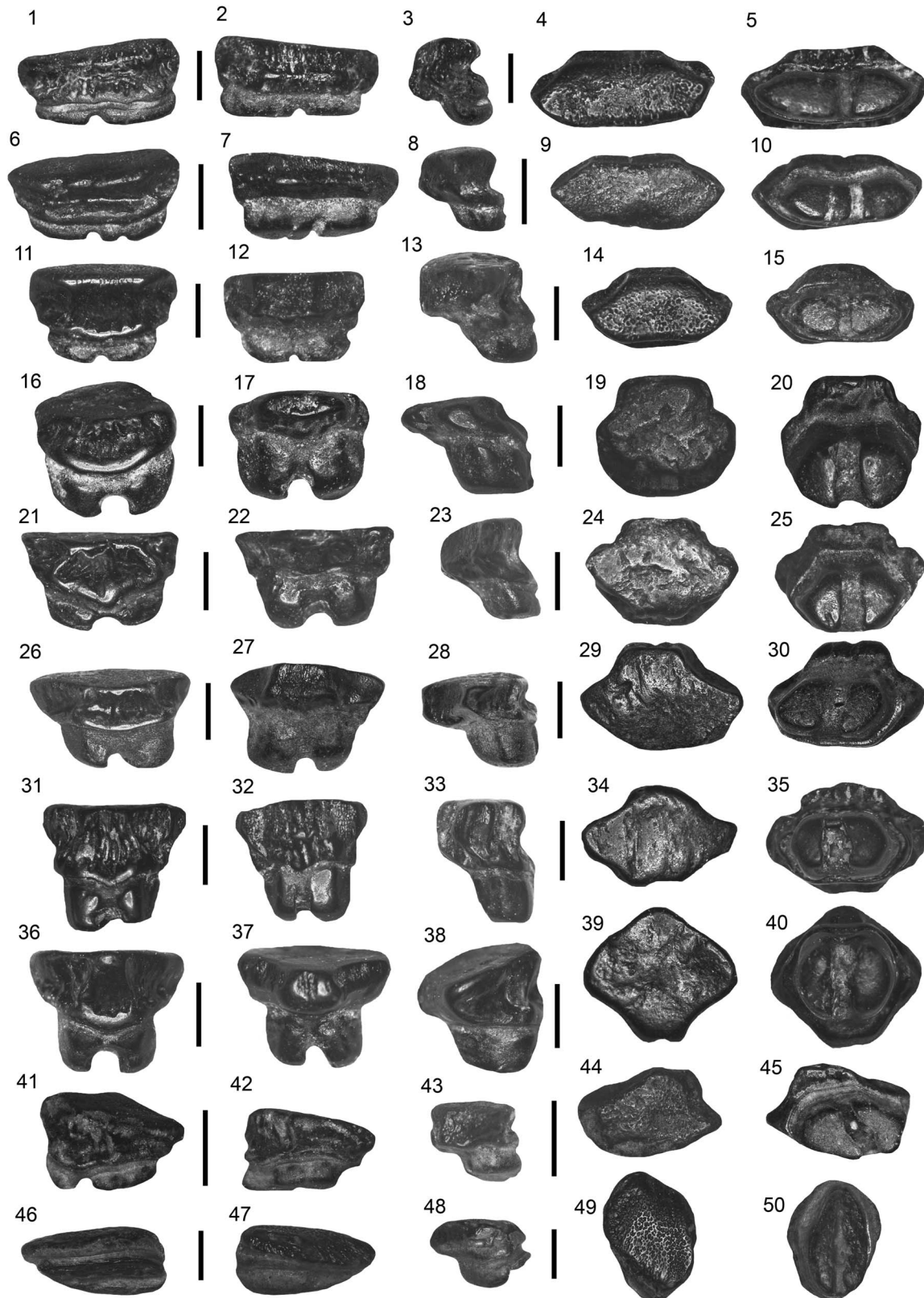


Figure 2. *Hypolophites beckeri* n. sp. teeth from the Lower Clayton Limestone Unit of the Paleocene Midway Group near Malvern, Arkansas, USA. (1–5) Median tooth (ANSP: VP25128), (6–10) median tooth (ANSP: VP25148), (11–15) median tooth (ANSP: VP25129), (16–20) lateral tooth (ANSP: VP25149), (21–25) holotype: lateral tooth (ANSP: VP25131), (26–30) lateral tooth (ANSP: VP25150), (31–35) lateral tooth (ANSP: VP25130), (36–40) lateral tooth (ANSP: VP25132), (41–45) lateral-most tooth (ANSP: VP25151), (46–50) lateral-most tooth (ANSP: VP25152). Orientations: (1, 6, 11, 16, 21, 26, 31, 36, 41) = lingual; (2, 7, 12, 17, 22, 27, 32, 37, 42) = labial; (46, 47) = lateral; (3, 8, 13, 18, 23, 28, 33, 38, 43, 48) = profile; (4, 9, 14, 19, 24, 29, 34, 39, 44, 49) = occlusal; (5, 10, 15, 20, 25, 30, 35, 40, 45, 50) = basal. Note: Extensively wrinkled lingual and labial surfaces, occlusal surface ornamentation (4, 14, 44, 49), and wear facets (19, 24, 29), hexagonal to trilobed occlusal surfaces (14, 19, 24, 29), root with two nutritive grooves (10), and well-defined foramina (30, 45). All scale bars = 2 mm.

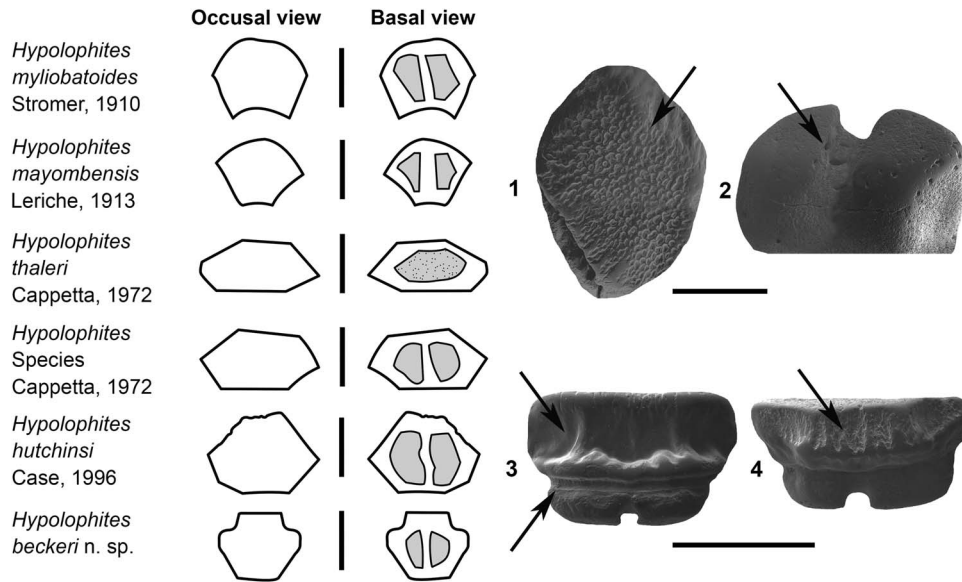


Figure 3. Comparison of lateral teeth from all presently known *Hypolophites* species showing diagnostic occlusal and basal tooth surfaces and scanning electron microscope images of unique features observed on *Hypolophites beckeri* n. sp. teeth from the Lower Clayton Limestone Unit of the Paleocene Midway Group near Malvern, Arkansas, USA. For line drawings, the shaded areas seen in basal view correspond to root lobes and the stippled pattern on the root of *Hypolophites thaleri* indicates that the root lobes are worn and obscured. (1) Pitted and vermiculate pattern on the occlusal surface of *Hypolophites beckeri* n. sp. lateralmost tooth (ANSP: VP25151) indicated by arrow; (2) basal surface view of *Hypolophites beckeri* n. sp. lateral tooth (ANSP: VP25131) with numerous foramina between and around the edges of the root lobes indicated by arrow; (3) labial view of *Hypolophites beckeri* n. sp. median tooth (ANSP: VP25129) with concave and wrinkled surface and distinct separation of the crown from the root as indicated by arrows; (4) lingual view of *Hypolophites beckeri* n. sp. median tooth (ANSP: VP25129) with flattened, slightly furrowed surface indicated by arrow. All scale bars = 2 mm.

overhanging the root base, a lingual uvula, and a bilobate root generally separated by a single nutritive groove containing at least one central foramen (Becker et al., 2006, 2011; Maisch et al., in press). *Hypolophites beckeri* n. sp. teeth are also distinct from those of *Hypsobatis weileri* Cappetta, 1992, *Pseudohypolophus mcultyi* (Cappetta and Case, 1975), and *Myledaphus* species because they do not have a two-tiered occlusal surface, a transverse ridge and faint labio-lingual folds on the occlusal and lateral surfaces, smooth crown surfaces in occlusal and profile view, well-developed foramina near the crown-root interface, or occur in the Late Cretaceous (e.g., Cappetta, 2012). Teeth of *Apocopodon sericeus* Cope, 1886, appear similar to those of *Hypolophites*; however, they have thick crowns with anastomosing ridges on the occlusal surface, are polyaulachorhizous, and have only been reported from the Paleocene of Brazil and South Carolina (Ribiero de Santana et al., 2011; Cappetta, 2012). *Potobatis semperei* Cappetta and Gayet, 2013, teeth also appear similar to those of *Hypolophites*; although, they have a smaller overall size, noticeable round-conical projections on the occlusal surface, thin roots that are nearly as wide as the crown, and are only known from the Paleocene of Bolivia.

Hypolophites beckeri n. sp. teeth have only been found as isolated specimens; however, they are distinct from those of previously reported taxa including: (1) *Hypolophites myliobatoides* Stromer, 1910; (2) *Hypolophites mayombensis* Leriche, 1913; (3) *Hypolophites thaleri* Cappetta, 1972; (4) *Hypolophites* sp. Cappetta, 1972; and (5) *Hypolophites hutchinsi* Case, 1996. *Hypolophites beckeri* n. sp. teeth are distinct due to the presence of mesio-distally elongated, labio-lingually compressed median teeth that may contain more than one nutritive groove, lateral

teeth with hexagonal to tri-lobed occlusal surfaces, lateral-most teeth that are dorsoventrally flattened and ovular to rhombus-shaped. Additionally, all teeth lack crowns that are noticeably thicker than the roots are tall (Fig. 3).

The genus *Hypolophites* was erected for a fragmentary lower tooth plate of *Hypolophites myliobatoides* Stromer, 1910 from the Paleocene of Adabion, Togo, Africa. A second species, *Hypolophites mayombensis* Leriche, 1913, was also identified based on a fragmentary tooth plate from the Paleocene of the Enclave of Cabinda, Landana, Africa, and was interpreted to be a partial upper tooth plate due to the presence of median and lateral teeth with convex, hexagonal, vermiculated occlusal surfaces. An additional, larger, and more complete partial tooth plate and isolated teeth of *Hypolophites myliobatoides* were reported by White (1934) from Nigeria, Africa. White (1934) included line drawings of the occlusal and basal surfaces of the tooth plate and images of isolated teeth and a portion of the tooth plate's occlusal surface. This same specimen has been figured as line drawings in Cappetta (1987, 2012) and photographed and figured by Claeson et al. (2010). As seen in these studies, the *H. myliobatoides* tooth plate contains: (1) median and lateral teeth that have a hexagonal occlusal surface with a rounded labial edge; (2) median and lateral teeth with wrinkled lateral edges; (3) lateral teeth with thinner crowns than median teeth; and (4) wide, bilobate roots with as many as five distinct edges and nearly flat basal surfaces in all teeth. White (1934) interpreted the upper tooth plate of *H. mayombensis* described by Leriche (1913) to correspond with the lower teeth of *H. myliobatoides* and represent a composite dentition of a single species (i.e., *H. myliobatoides*). However, Cappetta (1972) indicated that the specimens identified by White

(1934) as *H. myliobatoides* should in fact be identified as *H. mayombensis* because the tooth crowns lack a well-developed separation from the root on the labial surface.

A third species, *Hypolophites thaleri* Cappetta, 1972, was identified based on a partial tooth plate from the Paleocene of Sessao, Niger, Africa. The teeth of *H. thaleri* can be distinguished from those of *H. myliobatoides* and *H. mayombensis* because they have a distinct separation between the crown and root on the labial surface, thick, hexagonal-shaped crowns, and nearly straight, wrinkled lateral edges. Isolated teeth of *Hypolophites* sp. were also identified in Niger (Cappetta, 1972) and Mali, Africa (Cappetta, 1987). These teeth were distinguished from those of *H. thaleri* because the tooth crown rests directly above the root without any noticeable separation, the lateral tooth edges contain fewer wrinkles, and the lingual uvula is less developed. Currently, these isolated *Hypolophites* sp. teeth are thought to belong to *H. myliobatoides* or *H. mayombensis* (Cappetta, 1972, 2012).

A fourth species, *Hypolophites hutchinsi* Case, 1996, was identified from the Paleocene of Monmouth County, New Jersey, USA, and was the first known outside of Africa. All median and lateral teeth of *H. hutchinsi* have smooth occlusal surfaces that may contain irregular grooves or notches along the edge, thinner crowns, shorter overall heights, thick, wedge-shaped lateral teeth, and labial and lingual indentations near the crown-root interface that readily distinguishes them from the teeth of *H. myliobatoides*, *H. mayombensis*, and *H. thaleri*. Among teeth from the known *Hypolophites* species described above, those of *H. hutchinsi* are the most similar to those of *Hypolophites beckeri* n. sp. from the LCLU near Malvern, Arkansas. However, *Hypolophites beckeri* n. sp. teeth can be distinguished from those of *H. hutchinsi* because they have: (1) vermiculated or pitted, hexagonal to trilobate occlusal surfaces with smooth edges; (2) thin, rhombus to ovular-shaped lateral teeth; (3) noticeably wrinkled lingual and labial tooth surfaces; and (4) roots that are generally shorter and more rounded, rather than pentagonal, in shape.

Despite having teeth with an intermediate evolutionary grade between the Dasyatidae and Myliobatidae, Cappetta (1987, 2012) indicated that *Hypolophites* should not be considered a direct ancestor to Myliobatidae and placed the genus within the Dasyatidae. Conversely, the phylogenetic analysis of Myliobatidae completed by Claeson et al. (2010), indicated that *Hypolophites* is not closely related to other members of the Dasyatidae and is instead the immediate sister taxon to a monophyletic Myliobatidae with uncertain family-level placement.

Discussion

Paleoecology.—All reported *Hypolophites* species have teeth that form pavement plates and are diagnostic of crushing/grinding dentitions ideal for feeding upon a variety of small invertebrates (Fig. 3; Cappetta, 2012). This interpretation is supported by the abundance of bivalves and crustaceans (e.g., oysters, nut clams, and crustacean elements) that co-occur with teeth belonging to *Hypolophites beckeri* n. sp. in the LCLU as well as wear facets on the occlusal surfaces of some

teeth (Fig. 2.19, 2.24, 2.29). Additionally, many co-occurring chondrichthyan taxa in the LCLU are durophagous and represented by small teeth (~0.5–25 mm) that also form crushing/grinding dentitions ideal for feeding upon these same types of prey (Maisch et al., *in press*). Furthermore, these chondrichthyans have benthic-epibenthic lifestyles, marginal to shallow marine affinities, and occur in Paleocene exposures in New Jersey, northern Africa, and Denmark (Arambourg, 1952; Case, 1996; Noubhani and Cappetta, 1997; Cappetta, 2012; Adolfsson and Ward, 2015).

In the LCLU, locally abundant, isolated chondrichthyan, osteichthyan, and crocodylian teeth co-occur with invertebrate remains and trace fossils, including *Thalassinoides* isp., *Gastrochaenolites* isp., and *Entobia* isp., within three sand-pebble, phosphatic lag deposits (Fig. 1; Maisch et al., *in press*). These assemblages are known to be time-averaged and form in response to regressive-transgressive sea-level fluctuations across shallow marine shelves over thousands to millions of years (e.g., Becker et al., 1998, 2008; Shimada et al., 2006). Prior studies indicate that a minimum of five, 3rd order, eustatic sea-level cycles have occurred during the early Paleocene, which suggests that sea-level cyclicity is responsible for the formation of fossiliferous lag deposits within the LCLU (Haq et al., 1988; Briskin and Fluegeman, 1990; Mancini and Puckett, 2005; Haq, 2014). These transgressive pulses contributed to variations in: (1) shallow marine habitat; (2) sea water temperature; and (3) the dispersal and diversification of marine vertebrates, including myliobatiforms (e.g., Brett, 1998; Frisk, 2010; Holland, 2012). In this regard, extant myliobatiforms with tooth morphologies similar to *Hypolophites* are known to migrate large distances across shallow marine shelves for feeding and reproductive purposes (Frisk, 2010; Last et al., 2016; Martins et al., 2018; Rangel et al., 2018).

Biostratigraphic implications.—All *Hypolophites* species have been reported from Paleocene stratigraphic sections containing associated vertebrate and invertebrate remains indicative of shallow marine environments within the Northern Atlantic Ocean Basin (Stromer, 1910; Leriche, 1913; White, 1934; Cappetta, 1972, 1987; Case, 1996; Maisch et al., *in press*). However, the exact chronostratigraphic ages of some of these Paleocene sections remain uncertain or have been re-evaluated (Cappetta, 1987, 2012; Solé et al., 2018). In particular, Solé et al. (2018) reassessed the age of Paleocene outcrops, including the Landana section where Leriche (1913) identified *H. mayombensis* in the Congo Basin of west-central Africa. Their study demonstrated that although many of these outcrops were originally identified as early Paleocene (Danian): (1) Danian sediments are almost entirely absent, (2) the uppermost Danian is only represented in Landana, and (3) the majority of these exposures are Selandian–Thanetian in age. In this regard, *H. mayombensis* and *H. myliobatoides* are more likely late Danian/early Selandian–Thanetian in age while *H. thaleri* has been reported from the late Paleocene (Thanetian) of Niger (Cappetta, 1972, 2012).

The *H. hutchinsi* specimens originally identified as early Paleocene, Montian (i.e., upper Danian), from NJ by Case (1996), have also been reinterpreted as being late Paleocene

(Thanetian) in age (Cappetta, 2012). However, *H. hutchinsi* was reported from the basal Hornerstown Formation, which has been identified as early Paleocene (upper Danian–Selandian) and occurs directly above a disconformable contact with the Late Cretaceous (Maastrichtian) New Egypt (Tinton) Formation (Sugarman et al., 1995; Case, 1996; Miller et al., 2004, 2010). The *H. hutchinsi* specimens, in addition to other chondrichthyan remains from the Hornerstown Formation repositated at AMNH by Case (1996), lack evidence for extensive reworking (e.g., fragmentary, rounded crown and root elements, polishing, or phosphatization), and reinforce the upper Danian–Selandian age of *H. hutchinsi* and the basal Hornerstown Formation.

Preliminary studies on the Midway Group near Malvern, Arkansas, have identified Danian sediments in the lowermost LCLU (Dastas et al., 2010; Stringer and Sloan, 2018). However, temporal gaps are represented by the disconformity and lag deposit at the contact between the Arkadelphia Formation and Midway Group (i.e., K/Pg boundary) and the three additional lag deposits stratigraphically higher within the LCLU (e.g., Becker et al., 2010, 2013, 2016; Maisch et al., in press). Although, the precise age of the LCLU and *Hypolophites beckeri* n. sp. requires further investigation, the regional K/Pg stratigraphy and taphonomy of LCLU chondrichthyan remains support an upper Danian–Selandian age assignment (McFarland, 2004; Becker et al., 2011, 2016; Maisch et al., in press).

Diversification and paleobiogeographic distribution.—Several global studies on chondrichthyan faunal turnover across the K/Pg boundary indicate batoids were disproportionately affected, where shallow-water, demersal taxa were more susceptible to extinction, in contrast to those with benthopelagic and deep-water affinities (Kriwet and Benton, 2004; Guinot et al., 2012; Aschliman et al., 2012). Despite relatively high rates of extinction among shallow-water taxa, ancestral myliobatiforms existed in the Late Cretaceous, survived the K/Pg mass extinction event, and radiated throughout the Paleocene (Kriwet and Benton, 2004; Claeson et al., 2010; Aschliman et al., 2012; Aschliman, 2014; Bertozzi et al., 2016). Many extinct myliobatiforms have wide geographic distributions while others appear to be endemic to specific regions and habitats (refer to taxa mentioned in the systematic paleontology section above, as well as in Noubhani and Cappetta, 1997; Cappetta, 2012, and references therein). Although the isolated occurrences of these extinct taxa may be the result of preservation and collecting biases, numerous extant myliobatiforms are also known to exhibit endemism (Frisk, 2010; Last et al., 2016).

The first reported *Hypolophites* species in the USA, *H. hutchinsi*, extended the known paleobiogeographic range of the genus ~7,200 km westward from Mali, northern Africa to Monmouth County, New Jersey (Cappetta, 1987; Case, 1996). *Hypolophites beckeri* n. sp. described in this study, is the second North American species of *Hypolophites* identified and further extends the range of this genus ~1,750 km westward into the Mississippi Embayment and Gulf Coastal Plain (GCP) of the USA. Neither *Hypolophites beckeri* n. sp. nor *H. hutchinsi* has been reported in any other Paleocene–early Eocene

chondrichthyan assemblages across the ACP and GCP of the USA (e.g., Ward and Wiest, 1990; Case, 1994; Purdy, 1998; Kent, 1999; Becker et al., 2011; Phillips and Case, 2019), suggesting both of these taxa are endemic and the result of myliobatiform diversification after the K/Pg mass extinction event.

Hypolophites beckeri n. sp. and *H. hutchinsi* are more similar to each other than any of the African species, which suggests they may have stemmed from a common ancestor. According to Claeson et al. (2010) and Bertozzi et al. (2016), myliobatiforms originated in the Late Cretaceous and rapidly diversified across the K/Pg boundary. Many of these Late Cretaceous and early Paleocene myliobatiforms are known from only northern or central Africa, while others have dispersed globally (Noubhani and Cappetta, 1997; Cappetta, 2012). As a result of the extensive myliobatiform diversification across the K/Pg boundary in Africa, it is likely that *Hypolophites* originated in Africa and dispersed through post-Tethyan connections to the Gulf and Atlantic coastal plains of the USA.

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