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Zachary Boles
Rowan University

Paul V. Ullmann

Ian Putnam
Rowan University

Mariele Ford
Rowan University

Joseph T. Deckhut

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New vertebrate microfossils expand the diversity of the chondrichthyan and actinopterygian fauna of the Maastrichtian–Danian Hornerstown Formation in New Jersey

ZACHARY M. BOLES, PAUL V. ULLMANN, IAN PUTNAM, MARIELE FORD, and JOSEPH T. DECKHUT

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The abundance of shark and actinopterygian fossils in the Cretaceous and Paleogene strata of the Atlantic Coastal Plain is well documented; but much remains unknown about the survivorship patterns of these major components of shallow marine faunas in the western Atlantic through the K/Pg mass extinction. To shed light on this subject, we describe an assemblage of new actinopterygian, chondrichthyan, and reptilian microfossils recently recovered from the Maastrichtian Navesink and Maastrichtian–Danian Hornerstown formations at the Jean and Ric Edelman Fossil Park at Rowan University in Mantua Township, New Jersey. The new microfossils clarify extinction patterns across the K/Pg, create temporal and geographic range extensions for several taxa, and expand the known fauna of this regionally-rare and important K/Pg-boundary locality. We report 11 new additions to the vertebrate fauna of Edelman Fossil Park, the first Paleocene record of *Saurocephalus lanciformis*, the first Cretaceous records of *Paralbula marylandica* and *Palaeogaleus vincenti*, and the first recovery of gar and dercetid fish remains from the Paleocene in New Jersey (the last indicating that these fish survived the K/Pg extinction in the western Atlantic). Geographic range extensions include: *Notidanodon brotzeni* into the Western Hemisphere, *Saurocephalus* into northeastern North America and *Phyllodus paulkatoi* to the eastern coast of North America. A dentary of a juvenile alligatorid, *Bottosaurus harlani*, indicate that the mandible exhibited isometric growth through ontogeny. Our findings generally agree with other studies that these groups were significantly impacted by the extinction event, that extinctions were selective, and recovery was slow. This wealth of novel insights garnered from microfossils in this study highlights their critical importance for elaborating past faunas and illuminating the character of ancient ecosystems. We therefore recommend microsieving as a fruitful method for future faunal studies of shallow-marine strata and predict that such efforts will frequently yield similar important insights.

Key words: Actinopterygii, Chondrichthyes, microfossils, K/Pg, Hornerstown Formation, Edelman Fossil Park, New Jersey, USA.

Zachary M. Boles [bolesz@rowan.edu; ORCID: https: //orcid.org/0009-0007-4086-6860], Department of Geology, Rowan University, Glassboro, New Jersey 08028, USA; Jean and Ric Edelman Fossil Park at Rowan University, Mantua Township, New Jersey 08080, USA.
Paul V. Ullmann [paul.ullmann@und.edu; ORCID: https: //orcid.org/0000-0003-1457-6580], Harold Hamm School of Geology and Geological Engineering, University of North Dakota, Grand Forks, North Dakota 58202, USA.
Ian Putnam [ianputnamdvc@yahoo.com], Jean and Ric Edelman Fossil Park and Museum of Rowan University, Mantua Township, New Jersey 08080, USA.
Mariele Ford [marieleford3@gmail.com], Biomedical Arts and Visualization, Rowan University, Glassboro, New Jersey 08028, USA.
Joseph T. Deckhut [jdeckhut@ewu.edu; ORCID: https: //orcid.org/0000-0001-5034-6788], Department of Biology, Eastern Washington University, Cheney, Washington 99004, USA.

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Introduction

The remains of sharks and actinopterygian fish represent the most common vertebrate fossils in Cretaceous and Paleogene shallow-marine deposits across the Gulf and Atlantic Coastal Plain Provinces of North America (Case and Schwimmer 1988). Like today, these groups accounted for the majority of marine vertebrate diversity during these time periods, yet they tend to receive less attention than larger inhabitants of Cretaceous and Paleogene seas (i.e., turtles, crocodilians, extinct marine reptiles, and birds; Gallagher 1993). This unintentional bias continues to result in numerous uncertainties regarding the taxonomic identities (i.e., potential synonymies), phylogenetic relationships, and geographic and temporal ranges of chondrichthyan and actinopterygian taxa that inhabited coastal waters along the eastern margin of Appalachia (Case and Schwimmer 1988; Case 1996; Callahan et al. 2014; Andrews et al. 2023). In many cases, it also remains unclear which taxa survived the K/Pg mass extinction and which did not (Adolfssen and Ward 2014; Schwarzhans and Stringer 2020).

The collective dearth of knowledge of Cretaceous and Paleogene fish arises in-part from their fossil record consisting primarily of shed teeth and disarticulated, isolated specimens, the vast majority of which are "microfossils" <10 mm in size (e.g., Bazzi et al. 2015; Ebersole et al. 2019). This problem is compounded for sharks due to the cartilaginous composition of the majority of their skeleton (Heinicke et al. 2009), leaving only their teeth and vertebrae as mineralized remains (e.g., Adolfssen and Ward 2014, 2015); as well as by their routine shedding and replacement of teeth (e.g., Cappetta 1987). Teeth of select, larger sharks and fish are sizable enough that they may be found by surface collecting at several prolific fossil sites across the Gulf and Atlantic Coastal Plain Provinces (e.g., Jean and Ric Edelman Fossil Park at Rowan University, Gallagher 1993; Holmdel Park, New Jersey, Callahan et al. 2014; Dinosaur Park, Maryland, Frederickson et al. 2018; Ten Bits Microsite, Texas, Schubert et al. 2017); but the teeth and bones of many selachians and fish are so small that they can only be found by sieving/screen-washing (Peterson et al. 2011). For this reason, screen-washing has become a standard method to explore the diversity of microvertebrates in unconsolidated sediments around the world (e.g., Case and Schwimmer 1988; Purdy et al. 2001; Kirkland et al. 2013; Adolfssen and Ward 2014, 2015; Callahan et al. 2014; Schubert et al. 2017; Frederickson et al. 2018).

In this study, we describe a microvertebrate assemblage recovered from the Jean and Ric Edelman Fossil Park Quarry (EFPQ) at Rowan University (formerly an Inversand Company marl quarry) in Mantua Township, New Jersey (Fig. 1). The EFPQ preserves one of the best exposures of Cretaceous–Paleogene strata along the eastern coast of the United States (Gallagher 2003), and fossils from this famous locality provide a nearly-unrivaled snapshot into the diversity of west-Atlantic, shallow-marine faunas across the K/Pg boundary (Gallagher 1993). Strata in the EFPQ not only host evidence of the K/Pg impact event, but also of its subsequent effects on shallow-marine invertebrate and vertebrate faunas and ecosystems (e.g., Koch and Olsson 1977; Obasi et al. 2011; Esmeray-Senlet et al. 2017; Wiest et al. 2016). Our study of vertebrate microfossils recovered from the EFPQ expands the known fauna from this K/Pg locality, reveals patterns of survivorship and extinction across this mass extinction, and yields temporal and geographic range extensions for several chondrichthyan and actinopterygian taxa.

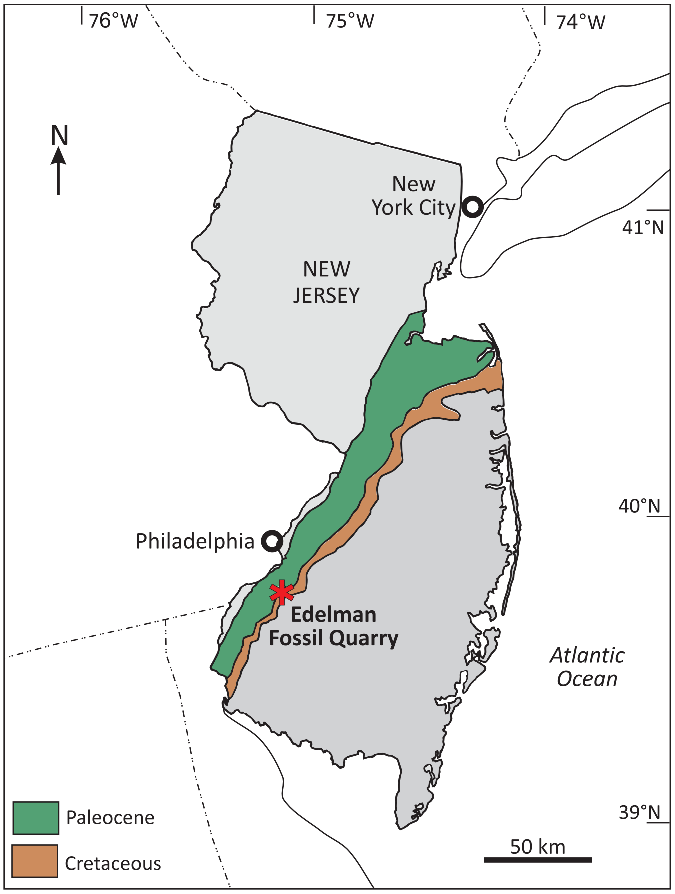

Fig. 1. Map showing the location of the outcrops of Cretaceous and Paleocene strata and Jean and Ric Edelman Fossil Park Quarry in Mantua Township, New Jersey, USA. Reproduced, with permission, from Ullmann et al. (2018).

Institutional abbreviations.—ANSP, Academy of Natural Science of Drexel University, Philadelphia, USA; RU-EFP, Jean and Ric Edelman Fossil Park, Rowan University, Mantua Township, USA; NJSM, New Jersey State Museum, Trenton, USA.

Other abbreviations.—EFPQ, Jean and Ric Edelman Fossil Park Quarry; MFL, main fossiliferous layer.

Geological setting

The majority of the fossils described herein were recovered from the Main Fossiliferous Layer (MFL) of the Maastrichtian–Danian Hornerstown Formation. Within the EFPQ, the Hornerstown Formation is underlain by the Maastrichtian Navesink Formation and overlain by the Thanetian Vincentown Formation (see Gallagher 1993 for a graphic representation of the full stratigraphic sequence exposed at the EFPQ). All three of these formations consist of glauconitic greensands deposited in organic-rich, siliciclastic, shallow-marine environments (Gallagher 1993). More specifically, in the EFPQ only the uppermost ~1.5 m of the underlying Navesink Formation is exposed in the bottom of the quarry; it is composed of olive-gray to dusky brown, clayey-glauconitic sand that was deposited on the inner shelf (Wiest et al. 2016). The overlying Hornerstown Formation is 6.2 m thick and consists of fine- to medium-grained, grayish-olive-green glauconitic sand that was deposited on the mid-to-outer shelf (Wiest et al. 2016). The overlying Vincentown Formation, which is above the interval examined herein, represents the end of the conformable sequence of strata in the lower portion of the EFPQ; it is 1.6 m thick and composed of very fine- to medium-grained, grayish-olive-green to grayish-yellow, clayey-glauconitic sand that was deposited on the inner shelf (Gallagher 1993).

Within the lower Hornerstown Formation, the MFL is a prolific, ~10 cm-thick, regionally-vast bonebed located approximately ~20–30 cm above the Navesink-Hornerstown formational contact (Voegele et al. 2021). Remains of numerous shallow-marine invertebrates and paralic turtles, birds, crocodilians, fish, sharks, and rays are preserved within the MFL (Gallagher 1993, 2003); as well as occasional remains of mosasaurs and "bloat-and-float" dinosaur carcasses (e.g., Schein and Poole et al. 2011).

The taphonomic origin of the MFL has been debated for decades, with explanations ranging from attritional accumulation (i.e., a condensed assemblage; Gallagher 2003, 2012; Schein et al. 2008), reworking of Cretaceous remains into an early Danian storm/tsunami lag deposit (Minard et al. 1969; Gallagher 2002; Olsson et al. 2002; Horner et al. 2016), or relatively-rapid accumulation of remains via mass-death following the Chicxulub impact (Gallagher 1993; Obasi et al. 2011; Boles 2016; Wiest et al. 2016). We continue to conduct excavations in the EFPQ to resolve this question; but recent discoveries of shocked quartz grains within a burrow immediately below the MFL (Obasi et al. 2011) and a spike in iridium concentrations within the MFL in the EFPQ (Esmeray-Senlet et al. 2017) indicate that the MFL may represent a thanatocoenosis recording ecosystem collapse during the K/Pg mass extinction. Based on the inclusion of impact indicators and the definition of the K/Pg boundary as the moment of impact (Molina et al. 2006), we regard the MFL as Danian in age.

Material and methods

The majority of the fossils described herein were recovered by traditional screen-washing of sediments from the uppermost Navesink Formation and the lower Hornerstown Formation. A few (primarily-larger) fossil specimens were recovered either by surface collecting from outcrops of the Hornerstown Formation within the current quarry or during field excavations through the MFL in the EFPQ. Many specimens we describe were recovered during a recent, detailed microstratigraphic study of the MFL (Voegele et al. 2021). A 1.4 mm mesh sieve was used, at times in the field and at other times with collected sediment samples in a lab setting, to produce concentrates which were dried and hand-picked under a dissecting microscope, following traditional methods (e.g., Cifelli et al. 1996). Screen-washing of the 61 sediment samples collected as part of that project yielded abundant microvertebrate fossils (e.g., teeth, vertebrae, scales) whose positions relative to the Navesink-Hornerstown formational contact are constrained with centimeter resolution. A number of additional specimens were recovered by earlier screen-washing of excavated sediments sourced from our ongoing field excavations through this same, roughly half-meter, stratigraphic interval spanning the MFL; the precise origin of these sediments, and thus the microfossils within them, were only constrained to "above MFL", "within MFL", or "(within the basal Hornerstown Fm.) below the MFL" (this last category equates with the lowest ~20 cm of the Hornerstown Formation; cf. Voegele et al. 2021). All but the largest few specimens were imaged using a Zeiss Stemi 508 dissecting microscope with an integrated AxioCam 506 camera, occasionally using the Manual Extended Depth of Focus (Z-stack) module (where needed for clarity).

Systematic palaeontology

Chondrichthyes Huxley, 1880

Carcharhiniformes Compagno, 1973

Triakidae Gray, 1851

Genus *Palaeogaleus* Gurr, 1962

Type species: *Galeocerdo vincenti* Daimeries, 1888; Thanetian, Orple-Grand, Belgium.

Palaeogaleus vincenti (Daimeries, 1888)

Fig. 2A.

Material.—Seventeen teeth: one lateral tooth (RU-EFP-00284-1) from the upper Navesink Formation; one anterior tooth (RU-EFP-00268-1) from the lower Hornerstown Formation below the MFL; two anterior teeth (RU-EFP-00248-1 and 00254-1) from the MFL; one anterior tooth (RU-EFP-04143) and four lateral teeth (RU-EFP-00158-1, 00225-1, 00233-1, and 00238-1) from the lower Hornerstown Formation above the MFL. The remainder (RU-EFP-04144, 04145, and 00157-1–00157-6) were collected as float. All from the Maastrichtian Navesink and Maastrichtian–Danian Hornerstown formations, Jean and Ric Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The principal cusp is broad, strongly convex lingually, labiolingually thick, and angled slightly apicodistally in anterior teeth; in lateral teeth, it is more strongly apicodistally directed. The mesial and distal cutting edges are smooth. Distal cusplets vary in distinction and range from one to four in number. The first distal cusplet is generally around one-third the height of the principal cusp, and succeeding distal cusplets (when present) are shorter. Mesial cusplets range from one to four in number on anterior teeth, and are generally absent in lateral teeth (cf. Cappetta 1987: fig. 100D). Only one of the lateral teeth possesses a subtle, undulating peak along the mesial heel. In lateral teeth, the distal heel is shorter than the mesial heel. The labial base of the crown strongly overhangs the root in all specimens preserving roots, and appears to curl lingually in the same manner in specimens lacking the root. Coarse vertical costules cover the entire labial crown base on most specimens, as well as basal portions of each heel on the lingual face; however, a single lateral and anterior tooth each exhibit nearly smooth labial heels. The basal border of the crown ranges from flat to slightly concave. The root is labiolingually thick and holaulacorhizid in structure, with a deep central groove vertically traversing the lingual protuberance. A small, circular pit occupies the center of this groove on the lingual face in six of the specimens. Where preserved, lateral branches of the root are broad and have flat, wide basal faces.

Remarks.—These teeth can be assigned to *Palaeogaleus* owing to strong overhang of the labial crown base over the root, the strongly convex lingual face of the principal cusp, relative shortness of the principal cusp, and having a thick, holaulacorhizid root (Cappetta 1987; Hovestadt and Hovestadt-Euler 2002). Among the eight species of *Palaeogaleus* currently recognized, the combination of coarse, vertical costules on the labial crown base and overall weak development of mesial and distal cusplets in the Edelman Fossil Park teeth compares best with *Palaeogaleus vincenti*. Cusplets are generally more well developed in *Palaeogaleus havreensis* Herman, 1977, *Palaeogaleus dahmanii* Noubhani & Cappetta, 1999, and *Palaeogaleus larachei* Noubhani & Cappetta, 1999, and labial crown base ornamentation is absent or poorly developed in *Palaeogaleus brivesi* Arambourg, 1952, *Palaeogaleus faujasi* Geyn, 1937, and *Palaeogaleus prior* Arambourg, 1952 (Hovestadt and Hovestadt-Euler 2002). Also, in contrast to *Palaeogaleus prior*, *Palaeogaleus sublaevis* Noubhani & Cappetta, 1999, and *Palaeogaleus larachei* (Hovestadt and Hovestadt-Euler 2002), the principal cusp is not serrated in any of the RU-EFP specimens. A pit within the midline groove was also described in *Palaeogaleus vincenti* teeth by Cvancara and Hoganson (1993).

Palaeogaleus vincenti represents a new addition to the fauna of the EFPQ. Case (1996) briefly described 12 specimens of *Palaeogaleus vincenti* from the lower Hornerstown Formation of Monmouth County, New Jersey, which, at the time, represented the first occurrence of the species in eastern North America. However, the stratigraphic occurrences of *Palaeogaleus vincenti* teeth from the EFPQ are more precisely constrained and demonstrate that it is present throughout all portions of the lower Hornerstown Formation (specifically above, within, and below the MFL) as well as in the upper Navesink Formation. All previous occurrences, including that described by Case (1996), were from the Paleogene (Cappetta 2012; Maisch et al. 2020); thus, the two specimens of *Palaeogaleus vincenti* recovered the Navesink Formation and beneath the MFL in the Hornerstown Formation represent the first Cretaceous occurrences of this species, indicating that *Palaeogaleus vincenti* evolved before the K/Pg extinction.

Stratigraphic and geographic range.—Upper Cretaceous, Maastrichtian to Paleocene of New Jersey in the USA, Belgium, England, France, and Morocco

Chondrichthyes Huxley, 1880
Chimaeriformes Obruchev, 1953
Callorhynchidae Garman, 1901
Genus *Ischyodus* Egerton, 1843

Type species: *Ischyodus townsendi* Buckland, 1835; Jurassic, Stonesfield, England.

Ischyodus bifurcatus (Case, 1978)

Fig. 2B.

Material.—Seventeen tooth plates: four left mandibulars, six right mandibulars, five left palatines, and two right palatines from the MFL of the Maastrichtian–Danian Hornerstown Formation, Jean and Ric Edelman Fossil Park, Mantua Township, New Jersey, USA. (SOM 1: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app69-Boles_etal_SOM.pdf).

Description.—Mandibular tooth plates are robust, labiolingually narrow, and possess a short mesial ramus and "stepped" labial margin (cf. Cicimurri and Ebersole 2014). They possess four tritors in occlusal view: anterior inner tritor, "median" tritor (fused middle and posterior inner tritors; Case 1978), anterior external tritor, and posterior external tritor. The "median" tritor is expansive with an embayment into its mesial margin that creates bifurcations that are unequal in length: the outer bifurcation extends further mesially than the inner bifurcation. The mandibular symphysis is thin and curves longitudinally. The anterior external tritor is positioned slightly ventrally compared to the surface of the "median" tritor and is commonly angled slightly anterolaterally relative to the sagittal axis. Axes of the other tritors are nearly parallel and parasagittal. Where preserved, the labial face is smooth and slightly concave.

Palatine tooth plates are roughly triangular in occlusal view and narrower than the mandibular tooth plates. Four tritors are present: anterior inner tritor, posterior inner tritor, median tritor, and outer tritor. Each of these tritors are long and narrow labiolingually. The anterior inner tritor is positioned on an elevated, roughly flat platform compared to the rest of the lingual face and is commonly angled slightly anterolaterally relative to the sagittal axis. The posterior inner and median tritors are approximately equal in length, though the median tritor occasionally extends slightly further mesially in some specimens. The medial face is flat and straight. The aboral surface is roughly flat in most specimens, except those in which surficial bone and internal tissue of the anterior inner tritor have been lost; in these specimens, erosion

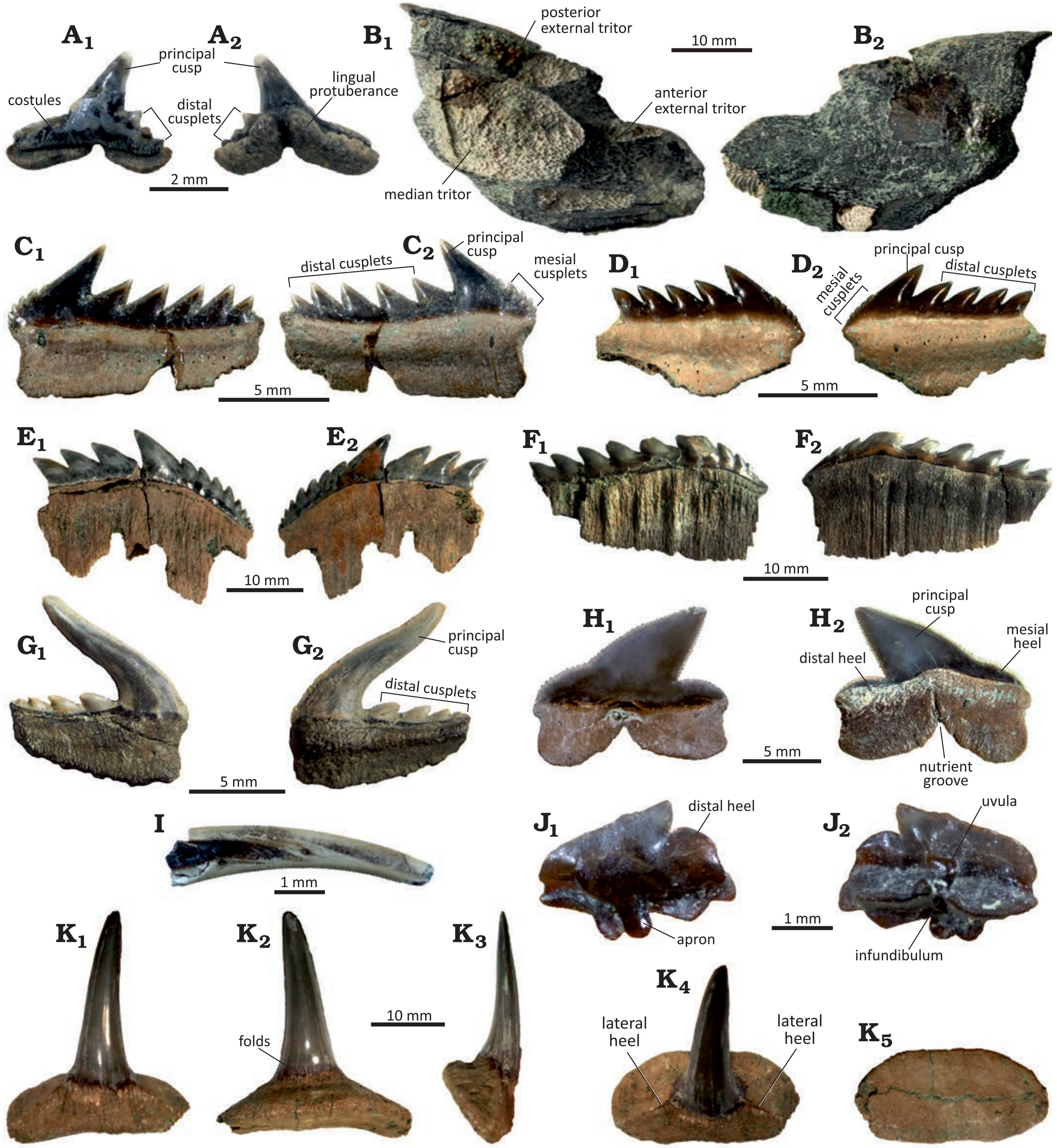

Fig. 2. Chondrichthyan ichthyoliths from the Cretaceous–Paleogene lower Hornerstown Formation at the Jean and Ric Edelman Fossil Park in Mantua Township, New Jersey, USA. Anterolateral (A, I, K) and lateral (C–H) teeth, mandibular toothplate (B), and spine (J). **A**. Triakid carchariniform *Palaeogaleus vincenti* (Daimeries, 1888) (RU-EFP-04145) in labial (A$_1$) and lingual (A$_2$) views. **B**. Callorhynchid chimaeriform *Ischyodus bifurcatus* (Case, 1978) (RU-EFP-03717) in oral (B$_1$) and labial (B$_2$) views. **C**. Hexanchid *Heptranchias howellii* (Reed, 1946) (RU-EFP-04139) in labial (C$_1$) and lingual (C$_2$) views. **D**. Hexanchid *Hexanchus* sp. (RU-EFP-02633) in labial (D$_1$) and lingual (D$_2$) views. **E**, **F**. Hexanchid *Notidanodon brotzeni* (Siverson, 1995), RU-EFP-04141 (**E**) and RU-EFP-03586 (**F**) in labial (E$_1$, F$_1$) and lingual (E$_2$, F$_2$) views. **G**. Hexanchid *Weltonia ancistrodon* (Arambourg, 1952) (RU-EFP-04142) in labial (G$_1$) and lingual (G$_2$) views. **H**. Pseudocoracid lamniform *Pseudocorax affinis* (Münster in Agassiz, 1843) (RU-EFP-02832) in labial (H$_1$) and lingual (H$_2$) views. **I**, **J**. Squalid *Squalus* sp. **I**. RU-EFP-02582 in lateral view. **J**. RU-EFP-00157-7 in labial (J$_1$) and lingual (J$_2$) views. **K**. Orthacodontid synechodontiform *Sphenodus lundgreni* (Davis, 1890) (RU-EFP-02913) in labial (K$_1$), lingual (K$_2$), mesial or distal (K$_3$), occlusal (K$_4$), and basal (K$_5$) views.

has created a deep, rounded longitudinal groove representing the lingual border of the anterior inner tritor tissue. The labial face is flat with a sigmoidal lateral margin.

Remarks.—Gallagher (1993, 2003) listed five chimaeroid fish among the fauna recovered from the EFPQ, including *Ischyodus bifurcatus*, *Ischyodus thurmanni* Pictet & Campiche, 1858, and three species of *Edaphodon* Buckland, 1838. The specimens described here most notably differ from *Edaphodon* in their possession of four tritors (rather than three) in both mandibular and palatine tooth plates (Cicimurri and Ebersole 2014; Ward and Grande 1991; Duffin and Reynders 1995; Stahl 1999). Additionally, the mandibular symphysis is thin and curved in mandibular tooth plates described herein, whereas in *Edaphodon* it is thick and nearly straight/flat (Cicimurri and Ebersole 2014; Ward and Grande 1991). Finally, the aboral surface of the palatine tooth plates are generally flat, as in *Ischyodus*, whereas those of *Edaphodon* usually exhibit a deep longitudinal sulcus (Cicimurri 2010, and references therein). Among the two species of *Ischyodus* listed by Gallagher (1993, 2003), the specimens described here can be assigned to *I. bifurcatus* based on attributes of the tritors: mandibulars exhibit an embayment into the anterior margin of the "median" tritor characteristic of this species, and the median and posterior inner tritors of the palatines extend approximately the same length anteriorly (whereas in *I. thurmanni* the posterior inner tritor commonly extends further anteriorly; Case 1978). Also as in *I. bifurcatus* (Case 1978), the outer tritor of the palatine is longer and narrower than in *I. thurmanni*. Mandibular tooth plates of *I. rayhaasi* Hoganson & Erickson, 2005, also exhibit an embayment into the "median" tritor, but it is the inner bifurcation that extends further anteriorly as opposed to the outer as in our specimens and *I. bifurcatus* (Hoganson and Erickson 2005; Hoganson et al. 2015).

Gallagher (1993, 2003) listed *I. thurmanni* as the only species of the genus present in the MFL, with *I. bifurcatus* being recovered from the underlying Navesink Formation. Elsewhere, *I. bifurcatus* has been described from Santonian to Maastrichtian deposits in Belgium and across the United States (Case and Schwimmer 1992). Our identification of numerous specimens of *I. bifurcatus* in the MFL extends its range across the K/Pg boundary into (presumably) the initial few years of the Danian (cf. Esmeray-Senlet et al. 2017).

Stratigraphic and geographic range.—Upper Cretaceous (Santonian) to lower Paleocene (Danian) of California, Delaware, Montana, New Jersey, and North Carolina in the USA, Belgium, and Russia.

Hexanchiformes Buen, 1926

Hexanchidae Gray, 1851

Genus *Heptranchias* Rafinesque, 1810

Type species: *Squalus perlo* Bonnaterre, 1788; Recent, in temperate waters worldwide.

Heptranchias howellii (Reed, 1946)

Fig. 2C.

Material.—Four teeth: three (RU-EFP-03582, 4137, and 4138) from the MFL and one (RU-EFP-04139) collected as float. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The principal cusp is fairly slender, apicodistally directed, and approximately twice as tall as the first few distal cusplets. The labial face of the principal cusp is nearly flat, whereas the lingual face is distinctly convex. The mesial and distal cutting edges of the principal cusp are nearly straight. Six mesial cusplets are present on each tooth. In the two nearly complete teeth, the first mesial cusplet is small and appears almost confluent with the mesial edge of the principal cusp, and it is followed by a larger, more distinct, second mesial cusplet. In the incomplete MFL specimen, the first mesial cusplet is large and distinct. Additional mesial cusplets steadily decrease in size. The mesial-most cusplet is directed mesially whereas succeeding cusplets turn to point apically then apicodistally as one follows their sequence up to the base of the principal cusp. The first three to four distal cusplets are roughly equal in breadth and height, while the final, distal-most cusplet is considerably smaller. Distal cusplets are directed apicodistally and exhibit roughly straight mesial and distal edges. The crown of RU-EFP-04138 has five distal cusplets, and RU-EFP-04139 has six. The basal border of the crown in these two specimens is slightly concave. The root is roughly rectangular in shape, with a pronounced mesial depression. In each tooth, the root is nearly as tall as the principal cusp, with a flat labial face and a rounded, mesio-distally directed ridge near the top of the lingual face. The basal border of RU-EFP-04139 (the only specimen with this edge complete) is flat.

Remarks.—The irregular decrease in size of the distal cusplets identify these teeth as belonging to *Heptranchias* (Cappetta 1987). Among described species, only *Heptranchias howellii* is known to commonly have more than three mesial cusplets (Welton 1974; Cappetta 1981; Adolfssen and Ward 2015); we therefore assign these teeth to that species. The Oligocene taxon *Heptranchias ezoensis* Applegate & Uyeno, 1968, is known to possess three or fewer mesial cusplets (Cappetta 1981; Carlsen and Cuny 2014), and *Heptranchias tenuidens* Leriche, 1938, is now considered a likely synonym of *H. howellii* (Cappetta 1987; Carrillo-Briceño et al. 2016).

Case (1973, 1980) mentioned the potential discovery of *Heptranchias howellii* from the Hornerstown Formation in Cream Ridge, New Jersey, which was viewed as suspect by Siverson (1995) based on similarity to teeth he described as *Heptranchias* sp. from the Danian of Sweden. We do not agree that the three features listed by Siverson (1995), namely slenderness of the principal cusp and sizes of the first distal and first mesial cusplets, readily distinguish any of these specimens from *H. howellii*. Rather, we find that the very subtle variations noted by Siverson (1995) to fit within the spectrum of morphologies in teeth attributed to *H. howellii* (e.g., Welton 1974; Cappetta 1987; Adolfssen and Ward 2015; Carrillo-Briceño et al. 2016). Thus, the specimens described here constitute a second recovery of *H. howellii* from the lower Hornerstown Formation of New Jersey and a new addition to the fauna of the EFPQ. Occurrence of two specimens in the MFL also indicates that *H. howellii* already existed in the earliest Danian, slightly older than other reports of Danian specimens from New Jersey (Case 1980) and elsewhere (Mannering and Hiller 2008).

Stratigraphic and geographic range.—Lower Paleocene (Danian) to lower Oligocene of Oregon and New Jersey in USA, Poland, and New Zealand.

Genus *Hexanchus* Rafinesque, 1810

Type species: *Squalus griseus* Bonnaterre, 1788; Recent, worldwide.

Hexanchus sp.

Fig. 2D.

Material.—Four lower lateral teeth: one (RU-EFP-02633) from the lower Hornerstown Formation above the MFL, three (RU-EFP-04140-1–04140-3) collected as float. All from the Maastrichtian-Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The teeth are labiolingually narrow and, in lingual view, are low and mesiodistally elongate with up to nine distal cusplets (in the sole complete specimen). In all specimens where it is preserved, the principal cusp is modestly larger than the first distal cusplet, termed “grisiform” by Ward (1979), with a nearly straight and unserrated distal cutting edge. Fine serrations are present along the lower half of the mesial edge of the principal cusp. The tip of the principal cusp is broadly triangular and apicodistally directed. Distal cusplets decrease slowly and regularly in size and their tips are all directed apicodistally; their mesial edges are strongly convex, and their distal edges are weakly convex. The basal border of the crown is nearly straight, with only a very slight convexity developed beneath the principal cusp. The root is nearly twice as tall as the principal cusp and exhibits a distinct mesial depression. A longitudinal ridge traverses mesiodistally across the lingual face near the top of the root. The labial face of the root is flat, and its basal border is nearly straight and slightly angled to the basal border of the crown such that the root height decreases distally.

Remarks.—These teeth are assigned to *Hexanchus* based on their low, mesiodistally elongate form, fine serrations on the mesial cutting edge of the principal cusp, and distally-reducing distal cusplets (Ward 1979). Serrations along the mesial cutting edge are larger in *Notorynchus* Ayres, 1855 (Ward 1979) than in the specimens described here. Among the many species names ascribed to fossil *Hexanchus* teeth over the last 150 years, only two are generally still considered valid: *H. microdon* Agassiz, 1843, and *H. agassizi* Cappetta, 1976 (Adolfssen and Ward 2014, 2015). Adolfssen and Ward (2014) note that there are no appreciable anatomical differences among teeth of these two species and that they are normally used for *Hexanchus* material of different ages: *H. microdon* occurs in the Maastrichtian through the Danian whereas *H. agassizi* is restricted to the Eocene. Although the Danian age of the four specimens described here is hence more consistent with *H. microdon*, we refrain from assigning them to a particular species at this time because multiple authors note that tooth morphology in modern *Hexanchus* is known to vary ontogenetically, by gender, among individuals, and within the jaw (= monognathic heterodonty), and that, because of this, fossil species within the genus are in need of revision (Adnet 2006; Adolfssen and Ward 2014, 2015).

Hexanchus sp. has previously been reported from the Paleocene–Eocene Vincentown, Manasquan, and Shark River formations in New Jersey (Gallagher 1993) and from the MFL at the EFPQ by Gallagher (Gallagher et al. 1986; Gallagher 1993); though his more recent faunal lists for the MFL have not included this taxon (perhaps by accidental omission in Gallagher 2002 and 2003?). Case (1996) also described several teeth he assigned to *Hexanchus* sp. and *H. microdon* from the lower Hornerstown Formation in “Deep Run” in Monmouth County, NJ. Recovery of at least one specimen from above the MFL extends Gallagher’s (1993) stratigraphic range for *Hexanchus* sp. in the EFPQ beyond the MFL into the upper Hornerstown Formation.

Genus *Notidanodon* Cappetta, 1975

Type species: *Notidanus pectinatus* Agassiz, 1843; Late Cretaceous, Sussex, England.

Notidanodon brotzeni (Siverson, 1995)

Fig. 2E, F.

Material.—Three lower lateral teeth: two (RU-EFP-00244-1, 03586) from the MFL and one (RU-EFP-04141) collected as float. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The principal cusp and distal cusplets are weakly convex both labially and lingually. In RU-EFP-04141 and 00244-1, the preserved principal cusp is broad, only slightly taller than the first distal cusplet, and apicodistally directed. It has a convex mesial edge and slightly concave distal edge. Mesial cusplets vary in number, with three present in the RU-EFP-03586, seven in RU-EFP-00244-1, and eight in the RU-EFP-04141. They are usually apicodistally directed, though the mesial-most mesial cusplets of the RU-EFP-00244-1 and 04141 are directed apically. The distal edges of both the mesial and distal cusplets are concave. Distal cusplets decrease slowly and regularly in size, and the basal border of the crown is distinctly convex beneath the principal cusp. The nearly complete root of RU-EFP-03586 is mesiodistally wide, decreases in height distally, and would have been roughly two to three times as tall as the principal cusp if it were complete. A pronounced horizontal ridge traverses the lingual face of the root of both RU-EFP-03586 and 04141, roughly one-third of the way down from the basal border of the crown. Apicobasally oriented ridges are present on the labial face of the root and are roughly positioned such that they descend beneath the notches between each cusp of the crown. A mesial depression is present in the root of both as well.

Remarks.—The combination of distal cusplets that regularly decrease in size from a modestly large acrocone that exhibits multiple, distinct, large cusplets along its mesial edge identify these specimens as belonging to the genus *Notidanodon* (Cappetta 1987; Siverson 1995). As in all known species except *N. loozi* Vincent, 1876, the mesial cusplets are apicodistally directed (Ward 1979; Ward and Thies 1987; Siverson 1995). The distal cutting edges of the principal cusp and mesial cusplets are slightly concave, similar to those of *N. brotzeni*, *N. pectinatus* Agassiz, 1843, and *N. dentatus* Woodward, 1886, but in contrast to those of *N. loozi* and *N. lanceolatus* Woodward, 1886, which are convex (Ward 1979; Cione and Medina 1987; Siverson 1995). Also as in *N. brotzeni*, the basal border of the crown in these specimens is distinctly convex beneath the principal cusp; this differs from *N. dentatus* and *N. pectinatus* which exhibit a flatter border (Ward and Thies 1987; Siverson 1995). *N. dentatus* and *N. loozi* also generally tend to exhibit fewer and larger distal cusplets (Ward 1979; Cione and Medina 1987) than in the specimens described here. Similar to *N. brotzeni* and *N. loozi*, the mesial margins of the principal cusp and distal cusplets are convex, whereas in *N. lanceolatus* they are nearly straight (Ward and Thies 1987; Siverson 1995). The proportionately tall root seen in our specimens compares best with the tall roots of *N. brotzeni* and *N. loozi* (Siverson 1995; Cappetta 1987; Ward and Thies 1987).

To summarize, among known species of *Notidanodon*, the EFPQ specimens share the most similarities with *N. brotzeni*. These features include apicodistally directed mesial cusplets, slightly concave distal edges of the principal cusp and mesial cusplets, a convex basal borderline of the crown, and convex mesial margins of the principal cusp and distal cusplets (Siverson 1995). We therefore assign the specimens to *N. brotzeni*, and further note that *N. brotzeni* is also the only one of the five known species reported from the Danian, the same age as the majority of the Hornerstown Formation at the EFPQ.

Notidanodon brotzeni was previously only known from the middle Danian of Sweden and Denmark (Siverson 1995), with a second possible occurrence later in the Paleocene of New Zealand (Mannering and Hiller 2008). The three specimens described here represent the first occurrence of *N. brotzeni* in the Western Hemisphere. Further, occurrence of two of the new specimens in the MFL demonstrates that *N. brotzeni* existed in the very beginning of the Danian and most likely evolved in the Maastrichtian, if not earlier.

Stratigraphic and geographic range.—Lower Paleocene (Danian) of New Jersey in USA, Denmark, Sweden, and Morocco.

Genus *Weltonia* Ward, 1979

Type species: *Notidanus* (*Heptranchias*) *ancistrodon* Arambourg, 1952, Thanetian, Ouled Abdoun basin, Morocco.

Weltonia ancistrodon (Arambourg, 1952)

Fig. 2G.

Material.—One lower lateral tooth (RU-EFP-04142) from either the upper Danian portion of the Hornerstown Formation or the Thanetian Vincentown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The principal cusp is elongate, slender, distally directed, and sigmoidal. It is over four times taller than the first distal cusplet. The lingual face of the principal cusp is strongly convex whereas its labial face is slightly convex. A single, subtle protuberance ("serration") occurs near the base of the mesial edge of the principal cusp. Four distal cusplets are present, which are distally directed, slightly labially inclined, and decrease regularly in size. The root is trapezoidal, lessening in height distally, with a distinct mesial depression. Its labial face is flat whereas a distinct mesiodistal ridge runs along the upper portion of the lingual face, creating a slightly concave region below it.

Remarks.—Possession of an extremely tall principal cusp (≥50% taller than the first distal cusplet) that is slender and sigmoidally curved identifies this specimen as *Weltonia* (Ward 1979; Cappetta 1987). The extremely elongate nature of the principal cusp (over four times as tall as the first distal cusplet) is consistent with the condition in *W. ancistrodon*, whereas in the only other known species, *W. burnhamensis* Ward, 1979, the principal cusp is only about 50% taller than the first distal cusplet (Ward 1979).

Case (1996) reported eight specimens of *Weltonia ancistrodon* recovered from an exposure of the lower Hornerstown Formation in "Deep Run", a tributary of Crosswicks Creek in Monmouth County, New Jersey. This was the first report of *W. ancistrodon* from North America. The new specimen described here also likely derives from the Danian portion of the upper Hornerstown Formation and represents a new addition to the fauna of the EFPQ.

Stratigraphic and geographic range.—Lower Paleocene (Danian) to lower Eocene (Ypresian) of New Jersey in USA, England, and Morocco.

Lamniformes Berg, 1958

Pseudocoracidae Cappetta, 2012

Genus *Pseudocorax* Priem, 1897

Type species: *Corax affinis* Münster in Agassiz, 1843, Maastrichtian, Netherlands.

Pseudocorax affinis (Münster in Agassiz, 1843)

Fig. 2H.

Material.—Six isolated teeth (SOM: table 1): five (RU-EFP-02463, 2832, 4158, 4166, 4167) from the MFL and one (RU-

EFP-04168) collected as float. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—All of the teeth are small, measuring less than 13 mm in mesiodistal length at the base of the crown. The crown is labiolingually thin and moderately inclined posteriorly with a flat labial face and weakly-convex lingual face. The base of the crown extends into distinct, obliquely-oriented mesial and distal heels, with the rounded distal heel being nearly detached from the central cusp whereas the mesial heel forms a comparatively-weaker convex berm. The mesial heel possesses a weakly-pointed apex in specimens RU-EFP-04167 and 4168. Fine serrations are present along the entire mesial and distal margins of the central cusp and both heels. The root is tall, generally of approximately the same height as the central cusp, with large mesial and distal lobes that are divided by a broadly-triangular basal notch. A shallow nutrient groove bisects a weak, yet distinct, lingual protuberance. Subtle, rounded ridges extend just beneath the crown-root boundary from this protuberance to the mesial and distal margins of the root. These margins each exhibit a concavity just below the crown-root boundary.

Remarks.—The specimens can be differentiated from *Squalicorax* Whitley, 1939, by their gracile morphology and presence of a nutrient groove (Hamm and Cicimurri 2011). The specimens can be assigned to the genus *Pseudocorax* based on their possession of a weakly-inclined and triangular central cusp that is flanked mesially and distally by oblique heels, and a large root with weakly-separated lobes that have slightly-concave mesial and distal edges (Jambura et al. 2021). Among the six currently-recognized species of *Pseudocorax*, only *Pseudocorax affinis* possesses serrations (Hamm and Shimada 2007). The presence of a nutrient groove on the lingual side of the root is characteristic of *Pseudocorax affinis* (Case et al. 2017).

The specimens described here represent the first recovery of *Pseudocorax* from the MFL. Case and Cappetta (2004) reported two teeth of *Pseudocorax affinis* from the lower Maastrichtian Navesink Formation at Big Brook in Marlboro, NJ. "*Pseudocorax affinis*" has also been reported from the Campanian of Georgia (Case and Schwimmer 1988) and Alabama (Applegate 1970), though due to their lack of serrations, those specimens should be assigned to *Pseudocorax laevis* Leriche, 1906 (Shimada 2009). Teeth of the species *Pseudocorax laevis* (possibly including *Pseudocorax granti* Cappetta & Case, 1975, Hamm and Shimada 2007) have also been described from the Campanian Marshalltown and Mount Laurel formations near the Chesapeake and Delaware Canal area in Delaware (Lauginger and Hartstein 1983). *Pseudocorax* teeth have been reported from the Paleocene only once before: Eaton et al. (1989) described several specimens from the Shotgun Member of the Fort Union Formation of Wyoming, although they were interpreted as being reworked from Cretaceous deposits.

Stratigraphic and geographic range.—Upper Cretaceous (Maastrichtian) to lower Paleocene (Danian) of New Jersey in USA, Denmark, Netherlands, and Africa.

Squaliformes Goodrich, 1909

Squalidae Bonaparte, 1834

Genus *Squalus* Linnaeus, 1758

Type species: *Squalus acanthias* Linnaeus, 1758, Recent, temperate waters, worldwide.

Squalus sp.

Fig. 2I, J.

Material.—One lateral tooth (RU-EFP-00157-7) from the MFL; eight partial squalid fin spines including one (RU-EFP-00267-1) from the lower Hornerstown Formation below the MFL, two (RU-EFP-02582 and 3942) from the MFL, one (RU-EFP-03567) from the lower Hornerstown Formation above the MFL, and four (RU-EFP-00157-8, 0157-9, 0267, and 4146) collected as float. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA. Because the tooth can be assigned to *Squalus*, we tentatively assign the fin spines to this genus as well.

Description.—The single cusp is broad, low, labiolingually narrow, and strongly turned distally. Weak serrations are present along its mesial cutting edge. The distal heel is proportionately short, with a tall, rounded profile, and is separated from the cusp by an acute notch. A distinct, tongue-shaped apron of the crown extends below the basal border of the root from the center of the labial face. The sides of the apron are parallel, and its distal tip is circular. The mediolingual uvula of the crown is large and forms a rounded, linguodistally directed apex. The root is short and approximately the same breadth as the crown, with a well-developed basal lobe descending from its midpoint nearly to the apex of the apron. A pronounced horizontal shelf traverses the lingual face of the root. It is perforated beneath the uvula by a subcircular, moderately-broad infundibulum. The basal face of the root is shallowly concave and only slightly turned lingually.

Remarks.—Among Squalinae, the tooth can best be assigned to *Squalus* based on the basal face being only slightly lingually turned, presence of a modestly broad infundibulum, and a long mediolabial apron on the crown with parallel sides (Cappetta 1987; Adolfssen and Ward 2014). Although teeth of *Centrophoroides* Davis, 1887, and *Centrosqualus* Signeux, 1950, are very similar in form (Adolfssen and Ward 2014), the basal face is more strongly turned lingually in *Centrophoroides* and the apron in *Centrosqualus* is more bulbous in form owing to narrowing of its base (Müller and Schöllmann 1989). The apron is comparatively broader and more triangular in *Protosqualus* Cappetta, 1977, and *Megasqualus* Herman, 1982 (Cappetta 1987). Teeth of *Deania* Jordan & Snyder, 1902, and *Centrophorus* Müller & Henle, 1837, lack the projection of the apron beneath the basal plane of the root (Cappetta 1987). While absence of well-developed serrations suggests the specimen is not *S. serriculus* Jordan & Hannibal, 1923, or *S. crenatidens* Arambourg, 1952 (Cappetta 1987), other features used to diagnose species within the genus are known to vary in form ontogenetically (Adolfssen and Ward 2014), individually (Cappetta et al. 2016), and by gender (Siverson 1993). Thus, we refrain from assigning the specimen to any particular species at this time.

To our knowledge, among *Squalus* species only *S. minor* Daimeries, 1888, has been reported in Paleocene deposits in northeastern North America. This species is reported from the Danian Brightseat Formation in Maryland (Ward and Wiest 1990) and from the lower (Danian) portion of the Hornerstown Formation in Monmouth County, New Jersey (Case 1996). The teeth described by Case (1996) thus derive from the same stratigraphic range as our tooth. However, Case (1996) did not provide a differential diagnosis among *Squalus* species; therefore, we view his species assignment as inconclusive and do not follow it; instead assigning RU-EFP-00157-7 to *Squalus* sp. This specimen derives from the MFL, placing it in the very earliest Danian, and the fin spines tentatively inferred to also pertain to *Squalus* include a specimen from beneath the MFL in the Hornerstown Formation, indicating squalid sharks crossed the K/Pg at this site.

Synechodontiformes Duffin & Ward, 1993

Orthacodontidae Glikman, 1957

Genus *Sphenodus* Agassiz, 1843

Type species: *Lamna longidens* Agassiz, 1843, Late Jurassic, Switzerland.

Sphenodus lundgreni (Davis, 1890)

Fig. 2K.

Material.—Two teeth: one (RU-EFP-02913) from the MFL and another (RU-EFP-04159) collected as float. All from Fossil Park, Mantua Township, New Jersey, USA.

Description.—RU-EFP-02913 is essentially complete, measuring 30.2 mm in maximum height, with a root that is 25.5 mm in width and 12.3 mm in length. The crown is nearly vertically oriented and weakly sigmoidal in mesial and distal views. The crown is smooth, with the lingual surface being more convex than the labial surface. Two sharp carinae extend from the crown to form lateral heels on the root. The carinae thin towards the tooth tip and at the base of the crown. Numerous folds are present along the crown-root junction, with enamel ridges extending onto the root. Folds are more tightly spaced and shorter on the lingual side of the tooth. The root is short with a nearly flat basal surface. Abundant nutrient foramina are present, especially on the lingual surface, as well as distinct labiolingually-oriented grooves on its basal surface.

Remarks.—The teeth can be confidently assigned to *Sphenodus* due to their possession of a straight, sharp central cusp, lateral heels of each carina extending onto the lingual surface of the root, a more lingually convex crown (in cross section), and shallow, basally-flat root with labiolingually-oriented vascularization (Cusumano et al. 2021). Among the currently-recognized species of *Sphenodus*, *S. lundgreni* is the only species known from the Maastrichtian (Adolfssen and Ward 2014) and Danian (Cappetta 2012). The presence of numerous folds across the crown-root junction further supports assignment to this species (Kanno et al. 2017).

Callahan et al. (2012) reported the first known occurrence of the synechodontiform shark *S. lundgreni*, a single lateral tooth (NJSM 23223), from the EFPQ, which was also the first report of this taxon from North America. However, NJSM 23223 was not found in situ, thus its exact stratigraphic provenance within the Hornerstown Formation remains uncertain. Recovery of RU-EFP-02913 constrains the occurrence of this taxon at least to the MFL. We also report the second and third known occurrences of this taxon from the EFPQ, and thus from North America.

Stratigraphic and geographic range.—Upper Cretaceous (Maastrichtian) to Paleocene (Thanetian) of New Jersey in USA, Denmark, Sweden, UK, and Kazakhstan.

Osteichthyes Huxley, 1880

Actinopterygii Klein, 1885

Teleostei Müller, 1845

Aulopiformes Rosen, 1973

Dercetidae Pictet, 1850

Dercetidae gen. et sp. indet.

Fig. 3A, B.

Material.—Twenty-eight dercetid flank scutes (SOM 1: table 1): one (RU-EFP-00282-1) from the upper Navesink Formation, two (RU-EFP-00269-1 and 0277-1) from the Hornerstown Formation below the MFL, ten (including RU-EFP-00228-1, 02490, and 03667) from the MFL, and seven from the Hornerstown Formation above the MFL; the precise stratigraphic origin of the remaining eight within the Hornerstown Formation is uncertain. All from the Maastrichtian Navesink and Maastrichtian–Danian Hornerstown formations, Edelman Fossil Park, Mantua Township, New Jersey, USA. Please see SOM 1: table 1 for the remaining specimen numbers.

Description.—Scutes vary from tripartite to cordiform in shape with a pronounced, elevated median crest along the central axis. Where preserved, the anterior extension is always longer than the two posterior extensions. The largest specimen (RU-EFP-02490) collected from the MFL, is cordiform in shape with large, distinct, randomly arranged tubercles ornamenting its external surface. The second largest specimen (RU-EFP-03667), also from the MFL, exhibits similar ornamentation but is tripartite in shape with a less pronounced median crest. Surface ornamentation is variably developed among the smaller specimens, with some scutes exhibiting well-developed, minute tubercles (occasionally oriented in radial rows) whereas others are essentially smooth. The median

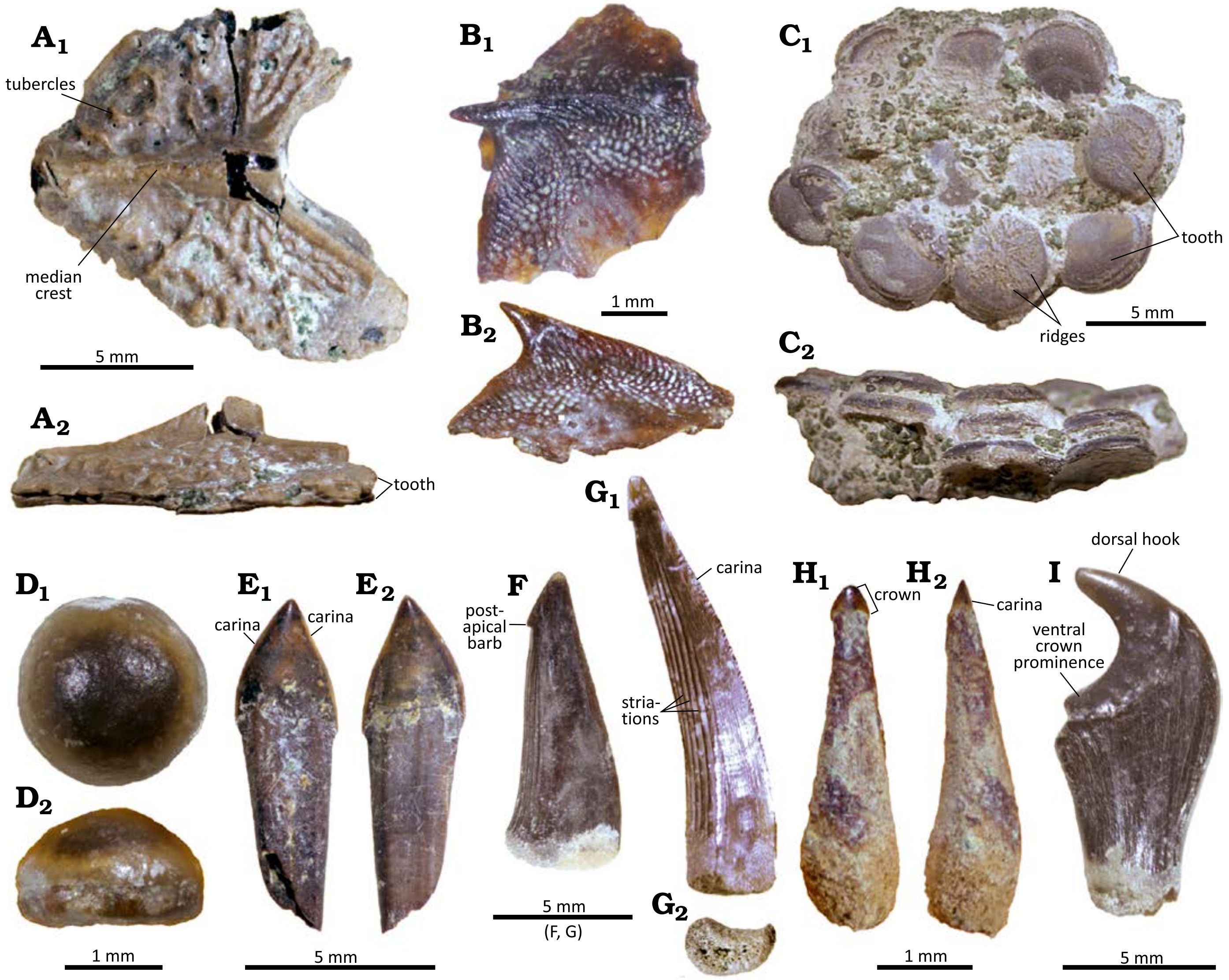

Fig. 3. Exemplar actinopterygian scutes (A, B) and teeth (C–I) recovered from the Cretaceous–Paleogene lower Hornerstown Formation at the Jean and Ric Edelman Fossil Park in Mantua Township, New Jersey, USA. **A**, **B**. Aulopiform teleost Dercetidae gen. et sp. indet., RU-EFP-02490 (**A**) and RU-EFP-00228-1 (**B**), in dorsal (A_1, B_1) and lateral (A_2, B_2) views. **C**. Phyllodontid elopiform *Phyllodus paulkatoi* Estes & Hiatt, 1978 (RU-EFP-04165-1) in occlusal (C_1) and lateral (C_2) views. **D**. Phyllodontid elopiform *Paralbula marylandica* Blake, 1940 (RU-EFP-00228-2) in occlusal (D_1) and lateral (D_2) views. **E**. Saurodontid ichthyodectiform *Saurocephalus lanciformis* Harlan, 1824 (RU-EFP-04151) in labial (E_1) and lingual (E_2) views. **F**, **G**. Enchodontid aulopiform *Enchodus gladiolus* (Cope, 1872). **F**. RU-EFP-04157-1 in lateral view. **G**. RU-EFP-02188 in lateral (G_1) and basal (G_1) views. **H**. Lepisosteid lepisosteiform *Atractosteus* sp. (RU-EFP-02939) in labial (H_1) and mesial or distal (H_2) views. **I**. Pycnodontid pycnodontiform *Anomoeodus phaseolus* (Hay, 1899) (RU-EFP-02858) in lateral view.

crest terminates in a posterolaterally-directed spine in many of the scutes, and its keel ranges from sharp to rounded in profile; this variation does not appear to correlate with scute size. The posterior extensions diverge from near the posterior end of the median crest and each possess a distinct ridge along the posterior margin. In lateral view, these two ridges range from straight to posteriorly concave in orientation. These ridges rotate to become parallel behind the median keel in one scute, but in most specimens the posterior extensions diverge to form an acute or right angle. The inner surface is smooth and occasionally exhibits a shallow, triangular hollow beneath the posterior half of the median crest.

Remarks.—The tripartite and cordiform shapes of these scutes with a distinct median crest identify them as belonging to a dercetid fish (Chalifa 1989; Figueiredo and Gallo 2006; Friedman 2012; Taverne and Goolaerts 2015). Ornamentation on many of the scutes with large or minute tubercles occasionally aligned in radial rows is similar to some dercetids (e.g., *Brazilodercetis longirostris* Figueiredo & Gallo, 2006) but differs from others in the family which are smooth (e.g., *Apuliadercetis indeherbergei* Taverne & Goolaerts, 2015; *Rhynchodercetis gracilis* Chalifa, 1989; *Dercetoides venator* Chalifa, 1989).

Members of the family Dercetidae are known from the

Late Cretaceous and early Paleocene around the world (Silva and Gallo 2011), though it appears only a few species survived the K/Pg mass extinction (Adolfssen et al. 2017). The only previous report of dercetid material from the northeastern United States was by Oman et al. (2016) who described similarly-sized, small, tripartite and cordiform scutes of an indeterminate dercetid from the Campanian Woodbury Formation in Cherry Hill, New Jersey. Recovery of dercetid scutes from the Navesink and Hornerstown formations in the EFPQ extends the known temporal range of these fish in New Jersey through the end of the Cretaceous and into the early Danian. The indeterminate dercetid represented by these fossils also represents a new addition to the fauna.

Enchodontidae Lydekker, 1889

Genus *Enchodus* Agassiz, 1835

Type species: *Esox lewesiensis* Mantell, 1822, Turonian, Sussex, England.

Enchodus gladiolus (Cope, 1872)

Fig. 3F, G.

Material.—Eight specimens: two (RU-EFP-00277-2 and 4156) from the lower Hornerstown Formation below the MFL, four (RU-EFP-01916, 2188, 2956, 3698) from the MFL, and two (RU-EFP-04157-1, 4157-2) collected as float. All from the Maastrichtian-Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The teeth are sigmoidal and range in apicobasal height 6–14 mm. Longitudinal striations are present on the rounded posterior face of the crown which extend from the base of the crown to just beneath a pronounced post-apical barb. A longitudinal carina is present along the mesial margin and extends the entire height of the crown. There is subtle variation in overall morphology among the specimens, with some being narrow and elongate whereas others are comparatively shorter and mesiodistally wider. Teeth of the latter morphology have an ovoid-shaped basal cross section, whereas those of the former possess a shallow depression on one side of the basal portion of the crown, making their basal cross section crescentic. This variation may reflect differing tooth positions (i.e., palatine versus mandibular crowns).

Remarks.—The sigmoidal, fang-like character of the teeth is characteristic of aulopiform actinopterygians, especially of the genus *Enchodus* (Kriwet 2003; Kriwet et al. 2006). *Enchodus* is a diverse genus of fish known from the early Cretaceous through the Paleocene. Approximately 30 taxa have been recognized, with five currently-valid species known from North America (Goody 1976; Fielitz 1997; Holloway et al. 2017). The specimens described here are best assignable to the species *E. gladiolus* due to their possession of a post-apical barb, full-length mesial carina, and striations on the basal portion of the distal face (Goody 1976; Parris et al. 2007; Becker et al. 2010; Alvarado-Ortega et al. 2020; Gouric-Cavalli et al. 2021).

The only species of *Enchodus* previously reported from the MFL was *E. ferox* Leidy, 1855 (Miller 1955; Gallagher 1993, 2003), although elsewhere in New Jersey *E. gladiolus* has been reported from the basal lag of the Navesink Formation at Holmdel Park and in cut bank exposures along Ramanessin Brook (Callahan et al. 2014). Here, we report the first occurrence of *E. gladiolus* from the MFL, indicating it survived in the western Atlantic until the K/Pg mass extinction.

Stratigraphic and geographic range.—Upper Cretaceous (Coniacian to Maastrichtian) of Arkansas, Colorado, Iowa, Kansas, Nebraska, New Jersey, New Mexico, and South Dakota in USA, Argentina, Canada, Mexico, and Russia.

Elopiformes Sauvage, 1875

Phyllodontidae Sauvage, 1875

Paralbulinae Estes, 1969

Genus *Paralbula* Blake, 1940

Type species: *Paralbula marylandica* Blake, 1940, Eocene, Maryland, USA.

Paralbula marylandica Blake, 1940

Fig. 3D.

Material.—Twenty-eight teeth (for repository numbers see SOM 1: table 1): five from the lower Hornerstown Formation below the MFL, seven from the MFL, six from the lower Hornerstown Formation above the MFL, and ten collected as float. All from the Maastrichtian-Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The teeth are roughly circular in occlusal view and hemispherical in form. The enamel of each tooth is smooth, and many exhibit fairly thin enamel structure when viewed in profile. A basilar foramen is present in several complete specimens. A few specimens consist of only the enamel cap, with the underlying dentine broken away/not preserved. One specimen consists solely of a dentine core. All specimens range ~0.5–2 mm in diameter.

Remarks.—The hemispherical shape of the teeth, in combination with possession of a basilar foramen (in some specimens), identify them as pertaining to a paralbuline fish (Estes 1969). Their round shape in occlusal view is more consistent with *Paralbula* than *Pseudoegertonia*, the only other genus within Paralbulinae Estes, 1969. Further, the smooth, unornamented enamel of these teeth is consistent with *Paralbula marylandica* Blake, 1940, but differs from the condition in the only other known *Paralbula* species from North America, *Paralbula casei* Estes, 1969, which exhibits intricate and often radiating sculpturing of the enamel surface (Estes 1969).

As all other previously-described specimens of this taxon derive from the Paleocene and Eocene (Blake 1940; Estes 1969; Ebersole et al. 2019; Schein et al. 2011), our recovery of teeth in Hornerstown sediments beneath the MFL constitutes a range extension for *Paralbula marylandica* back into the latest Maastrichtian, indicating it survived the K/Pg mass extinction.

Stratigraphic and geographic range.—Upper Cretaceous (Maastrichtian) to lower Eocene (Lutetian) of Alabama, Arkansas, Maryland, New Jersey, Texas, and Virginia in USA.

Phyllodontinae Darteville & Casier, 1943

Genus *Phyllodus* Agassiz, 1843

Type species: *Phyllodus toliapicus* Agassiz, 1844, Ypresian, England.

Phyllodus paulkatoi Estes & Hiatt, 1978

Fig. 3C.

Material.—One incomplete tooth plate (RU-EFP-04165-1), partially encased in concretion, found as float, and an isolated tooth (RU-EFP-04165-2) from the Hornerstown Formation. The presence of mature, bright green glauconite within the concretion matrix suggests that the tooth plate almost certainly derives from the Hornerstown Formation. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—All teeth within the partial tooth plate are circular in occlusal view, tightly packed, and phyllodont. The teeth are superimposed in directly successional stacks, being up to three deep (as preserved). Each tooth is ~3 mm in diameter, very flat, and thin when viewed in profile. Two of the "highest" exposed crowns exhibit a finely punctate occlusal surface texture, whereas four of the other crowns exposed slightly deeper within the tooth plate exhibit intricate, radially-oriented ridges which anastomose with one another, indicating they were each covered by another tooth which is not preserved. RU-EFP-04165-2 exhibits the same round outline in occlusal view and flat shape in profile as those in the partial tooth plate; its occlusal surface is covered by similarly faint, radially-oriented, anastomosing ridges, indicating that it is an unerupted replacement tooth.

Remarks.—Stacking of teeth in direct succession identifies RU-EFP-04165-1 as pertaining to a phyllodontine fish, differentiating it from paralbulines (Estes 1969). The very flat, thin shape of the teeth in profile is more consistent with the genus *Phyllodus* than *Egertonia* (the only two genera within Phylodontinae; Halliday et al. 2016), the latter of which tends to exhibit more domed teeth with thicker enamel (Estes 1969). Among the two currently-recognized species of *Phyllodus*, the consistently-round shape of all tooth stacks and degree of punctate sculpturing on the occlusal surface in the tooth plate are both consistent with *Phyllodus paulkatoi*. In contrast, the teeth of *Phyllodus toliapicus* Agassiz, 1839, are slightly smoother and both the basibranchial and parasphenoid tooth plates possess transversely-elongate teeth in their central rows (Estes and Hiatt 1978).

Phyllodus paulkatoi was previously only known from the Maastrichtian and Danian of Montana (Estes and Hiatt 1978) and the Maastrichtian of Wyoming (Brinkman et al. 2021). Recovery of two specimens from the Hornerstown Formation at Edelman Fossil Park extends its geographic range to the eastern coast of North America at this time (Maastrichtian–Danian).

Stratigraphic and geographic range.—Upper Cretaceous (Maastrichtian) to Paleocene (Danian) of Montana, New Jersey, and Wyoming in USA.

Ichthyodectiformes Bardack & Sprinkle, 1969

Saurodontidae Cope, 1871

Genus *Saurocephalus* Harlan, 1824

Type species: *Saurocephalus lanciformis* Harlan, 1824, Campanian, Kansas, USA.

Saurocephalus lanciformis Harlan, 1824

Fig. 3E.

Material.—One tooth (RU-EFP-04151) from the lower Hornerstown Formation above the MFL, Danian, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The crown is triangular and strongly laterally compressed, giving it a flat, spatulate form. Its tip is directed apically and forms a roughly 55° angle in labial view. A sharp, unserrated carina is present on both cutting edges of the crown. The base of the crown, which is slightly wider than the root, curves smoothly and evenly to join it. The root is straight, hollow, ~2.5 times as tall as wide, gradually tapers toward its base, and exhibits a faint, longitudinal groove on both flat sides; these grooves give the root an hourglass cross section when viewed basally.

Remarks.—The broad, laterally-compressed shape of the crown and length of the root identify this tooth as belonging to a saurodontid fish (Bardack and Sprinkle 1969; Stewart 1999). Among the three genera of saurodontids, the flat, broad character of the crown is most similar to that of *Saurocephalus* (Hays 1830). In *Saurodon* and *Prosaurodon*, the teeth are more acutely lanciform (Hays 1830; Stewart 1999). Additionally, the teeth of *Prosaurodon* are inclined anteriorly and exhibit a more ovoid shape in cross section (Stewart 1999; Everhart 2005), and the crown in *Saurodon leanus* Hays, 1830, appears more cuspate/curved (cf. Hays 1830: pl. 16: 7, 8). Of the two known species of *Saurocephalus*, only *S. lanciformis* has been described from North America (Friedman 2012). The only other species, *S. woodwardii* Davies, 1878, known exclusively from Europe (Netherlands and Belgium), is based on disparate geographic occurrences compared to known specimens of *S. lanciformis* rather than an anatomical diagnosis. For this reason, Friedman (2012) noted that *S. woodwardii* may be a synonym of *S. lanciformis* and that detailed taxonomic review of specimens assigned to the genus is needed.

Fossils of *Saurocephalus lanciformis* have been recovered from Campanian strata in the Western Interior and Gulf Coast of the United States (Friedman 2012; Irwin and

Fielitz 2013). The only previous report of a saurodontid from New Jersey was the description of a partial skull of *Saurodon leanus* collected from the Navesink Formation in Pensauken Creek near Moorestown (Hays 1830; Fowler 1911). The tooth described here constitutes the first record of *Saurocephalus* from northeastern North America and the first record of the genus in the Danian, thus extending the geographic range of *S. lanciformis* (from the Campanian) and demonstrating that it survived briefly into the early Paleocene.

Stratigraphic and geographic range.—Upper Cretaceous (Campanian) to lower Paleocene (Danian) of Arkansas, Kansas, and New Jersey in USA, and Russia.

Lepisosteiformes Hay, 1926

Lepisosteidae Cuvier, 1825

Genus *Atractosteus* Rafinesque, 1820

Type species: *Atractosteus spatula* Lacépède, 1803, Recent, southern USA.

Atractosteus sp.

Fig. 3H.

Material.—Eleven teeth (SOM 1: table 1): two (RU-EFP-00265-2, 268-2) from the lower Hornerstown Formation below the MFL; five (RU-EFP-00159-3, 2761, 2939, 2970, 4068) from the MFL; one (RU-EFP-00234-1) from the lower Hornerstown Formation above the MFL; and three (RU-EFP-00157-23, 3374, 4152) collected as float. All from the Maastrichtian–Danian Hornerstown Formation, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The teeth are apicobasally tall and exhibit the plicidentine structure unique to lepisosteids (Grande 2010): a circular cross section with longitudinal striae/grooves present along the lower half of the dentine tooth base. The enameled crown is restricted to the tip of the tooth and comprises 10% or less of the apicobasal height; its ventral border is broadly concave in labial and lingual views. The crown is lanceolate in form, being labiolingually flattened with distinct, unserrated carinae along the mesial and distal edges that gently curve inward to meet the dentine at their bases. This morphology gives the impression of a slight constriction beneath the crown, but it is actually due to broadening of the basal crown rather than narrowing of the subjacent dentine. The tip of the crown forms a rounded, obtuse angle in most specimens, but one exhibits a semicircular profile without an angled apex.

Remarks.—Plicidentine tooth structure and enamel restricted to the tip of the crown identify these teeth as belonging to a lepisosteid gar (Grande 2010). Among lepisosteids, only *Lepisosteus* Lacépède, 1803, and *Atractosteus* possess tall, fang-like teeth (Grande 2010). Though teeth of these genera are morphologically similar in most respects, *Atractosteus* possesses more lanceolate, blade-like crowns with a slight constriction beneath the enamel tip (Sigé et al. 1997; Szabó et al. 2016); whereas the enamel tip in *Lepisosteus* is rounder and lacks such constriction (Grande 2010). We therefore refer the teeth described here to *Atractosteus*. At present, no features of the teeth are known to be diagnostic at the species level, so we refer the specimens to *Atractosteus* sp.

Fossils of gars have previously been described from the Cretaceous of New Jersey, including remains of *Lepisosteus* collected from the Campanian Marshalltown, Wenonah, and Mount Laurel formations (Gallagher 1993) and *Atractosteus* material from the Marshalltown Formation at Ellisdale (Denton et al. 1996). Scales of an indeterminate lepisosteid have also been recovered from the basal portion of the Maastrichtian Navesink Formation at Holmdel Park in Monmouth County (Callahan et al. 2014). The six teeth described here thus constitute the first gar fossils from the Hornerstown Formation and include the first records of *Atractosteus* in the Paleocene (Danian) in New Jersey and a new addition to the fauna of Edelman Fossil Park.

Pycnodontiformes Berg, 1940

Pycnodontidae Agassiz, 1833

Genus *Anomoeodus* Forir, 1887

Type species: *Anomoeodus subclavatus* Agassiz, 1834, Maastrichtian, Netherlands.

Anomoeodus phaseolus (Hay, 1899)

Fig. 3I.

Material.—Eight teeth: four branchial teeth (RU-EFP-00159-4, 2474, 2858, 4153), one prearticular/vomerine tooth (RU-EFP-03620) from the MFL, one branchial tooth (RU-EFP-04154) from the lower Hornerstown Formation above the MFL. One branchial tooth (RU-EFP-04155-2) and one prearticular/vomerine tooth (RU-EFP-04155-1) were collected as float. All from Danian, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The prearticular/vomerine teeth are low crowned with a smooth occlusal surface. They are reniform in shape and have a concave base. The larger prearticular/vomerine tooth (RU-EFP-03620) is considerably more elongate that the smaller specimen and measures 7.3 mm in length by 3.3 mm in maximum width. In occlusal view, one end of this tooth is more acute whereas the other is more rounded.

The six branchial teeth are mediolaterally compressed with an apically or apicodistally-directed dorsal hook on the crown. These teeth vary considerably in size, development of a ventral crown prominence (sensu Kriwet 1999), and degree of curvature of the dorsal hook. The largest specimen, recovered from the MFL, has the largest ventral prominence and its dorsal hook forms the most acute angle with the base of the crown (approximately 40°). In contrast, the smallest teeth have a poorly developed ventral prominence and a short, nearly apically-directed dorsal hook. It therefore appears that the ventral prominence may grow in size and the dorsal hook may lengthen and rotate to curve more acutely through ontogeny. In the two specimens retaining their root, the root gradually tapers toward the jaw in the large specimen but exhibits nearly parallel mesial and distal margins in the smaller specimen. The crown-root border is rounded; in lateral view, it appears as a quarter-circle that is horizontally oriented near the distal margin and curves dorsally toward the mesial margin.

Remarks.—Identification of isolated, laterally compressed, hooked teeth has been a subject of debate and confusion for over a century, with teeth of this form previously being assigned to Pycnodontidae, Sclerodontidae, Semionotidae, Amiidae, and Trigonodontidae (Case and Schwimmer 1988; Kriwet 1999, and references therein). Traditionally, many such specimens were assigned to a tetraodontiform, *Stephanodus* (for a historical review see Kriwet 1999). However, studies of fish skulls in the last few decades have resolved the identity of such teeth as branchial (or "pharyngeal") teeth of pycnodont fish (Thurmond and Jones 1981; Kriwet 1999). Given concurrent reports of "*Stephanodus*" (pycnodont branchial teeth) and *Anomoeodus* (palatine/vomerine teeth) from multiple formations in New Jersey (see below) and Gallagher's (2003) listing of only *Anomoeodus phaseolus* at Edelman Fossil Park, we provisionally assign the branchial teeth as belonging to this species.

The smooth, reniform shape of the palatine/vomerine teeth is consistent with the genus *Anomoeodus* (cf. Case and Schwimmer 1988; Bazzi et al. 2015). Possession of a concave base identifies these teeth as pertaining to the species *Anomoeodus phaseolus* (Case and Schwimmer 1988), and this assignment is circumstantially supported by their occurrence in North America where this species was known to have been widespread (see below).

Gallagher (2003) previously reported *Anomoeodus phaseolus* from the Navesink Formation at EFPQ, and Gallagher (1993) reported recovery of branchial teeth of this taxon from multiple other Cretaceous formations across New Jersey, including the Marshalltown, Wenonah, and Mount Laurel formations (as *Stephanodus* sp.). Fowler (1911) also described a partial jaw from an indeterminate Cretaceous formation from Crosswicks Creek in Burlington County (as *Pycnodus phaseolus*), and Baird and Case (1966) reported recovery of branchial and prearticular/vomerine teeth of *Anomoeodus* from the Navesink Formation in Burlington County (with the branchial teeth again listed as *Stephanodus*). Thus, the new specimens described here include the first report of *Anomoeodus phaseolus* from the Hornerstown Formation and the Danian; all previous reports of this taxon across North America derive from Campanian and Maastrichtian deposits (references above, and Bazzi et al. 2015).

As only a single, small, worn specimen has been found above the MFL, it may be that this specimen was reworked up section by bioturbation and that the more abundant occurrences of *Anomoeodus* teeth in the MFL represent the actual latest occurrence of the species (i.e., *A. phaseolus* only briefly survived into the very earliest Danian, as recorded by the MFL death assemblage).

Stratigraphic and geographic range.—Upper Cretaceous (Coniacian) to lower Paleocene (Danian) of Delaware, Georgia, Maryland, Mississippi, New Jersey, North Carolina, and South Carolina in USA.

Sarcopterygii Romer, 1955

Reptilia Laurenti, 1768

Crocodilia Owen, 1842

Alligatoridae Cuvier, 1807

Genus *Bottosaurus* Agassiz, 1849

Type species: *Crocodilus harlani* von Meyer, 1832, Maastrichtian and Danian, Fieldsboro, New Jersey, USA.

Bottosaurus harlani (von Meyer, 1832)

Fig. 4A–C.

Material.—A relatively large, isolated posterior tooth (RU-EFP-02450), a left juvenile dentary (RU-EFP-03820), and two small partial crowns (RU-EFP-03876, 4169) from the MFL. All from Danian, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—RU-EFP-02450 is large, measuring 56.8 mm in height and 24.0 mm in mesiodistal width. The crown itself is short and blunt, measuring only 12.7 mm in height. The tooth is strongly labiolingually compressed, making the crown subrectangular in cross section. The enamel is strongly folded and exhibits abundant apical striations, giving the crown a wrinkled appearance. A modest, smooth carina is present on the mesial and distal edges of the crown. This keel extends to the base of the crown and would likely have extended over the tip of the tooth, which is worn. Enamel extends slightly further down the root on the lingual side than the labial side.

The left dentary (RU-EFP-03820) is significantly smaller than any previously described specimen of the genus, measuring approximately 58.2 mm (Fig. 4C). Its mandibular symphysis is intact, but its rostral and posterior regions are damaged, making the exact number of alveoli difficult to determine. The specimen possesses either 11 or 12 alveoli with the largest being the most-posteriorly positioned. Based on the morphology of the articulation facet for the splenial, the splenial possessed an anterior tip that passed dorsal to the Meckelian groove, but did not contribute to the mandibular symphysis. The mandibular symphysis extends posteriorly to about the fourth or fifth alveolus, and the tooth row forms a gentle, medially-concave curve between the ?fourth and ?tenth alveolus.

Two small isolated teeth (RU-EFP-03876, 4169) were also recovered within relatively close proximity (~4 m) to the dentary. Each is incomplete, consisting of most of the crown and a small portion of the root (e.g., Fig. 4B). They are similar to RU-EFP-02450 in being labiolingually compressed, possessing wrinkled enamel with apicobasally-aligned striations, and development of distinct mesial and distal carinae. Their morphology suggests that they are pos-

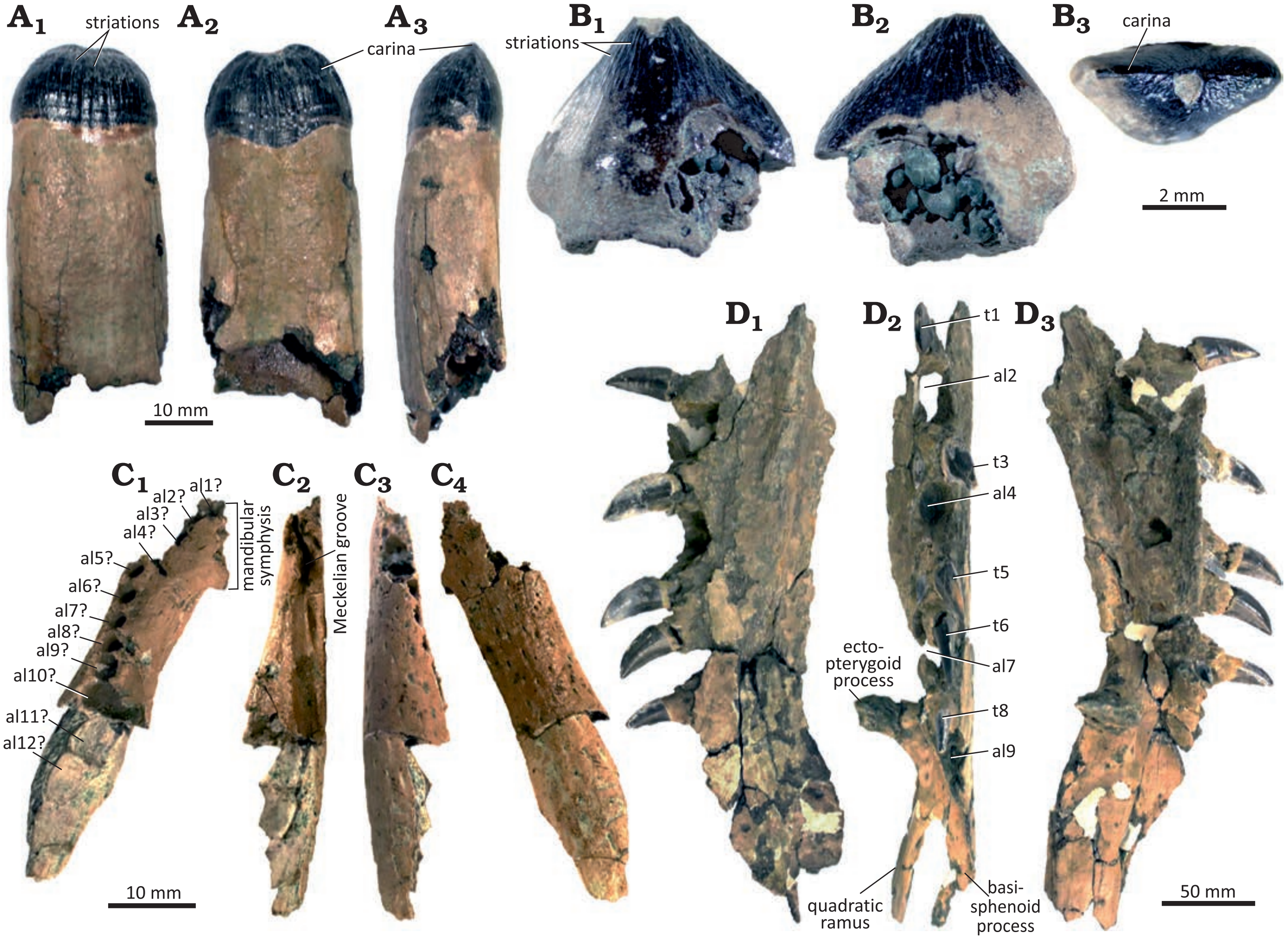

Fig. 4. Remains of the alligatorid crocodilian *Bottosaurus harlani* (von Meyer, 1832) (**A**–**C**) and mosasaurid cf. *Mosasaurus hoffmannii* Mantell, 1829 (**D**) recovered from the Cretaceous–Paleogene lower Hornerstown Formation at the Jean and Ric Edelman Fossil Park in Mantua Township, New Jersey, USA. **A**. Posterior tooth (RU-EFP-02450) in labial (A_1), lingual (A_2), and mesial or distal (A_3) views. **B**. ?Posterior tooth (RU-EFP-03876) in labial (B_1), lingual (B_2), and occlusal (B_3) views. **C**. Left dentary (RU-EFP-03820) in dorsal (C_1), medial (C_2), lateral (C_3), and ventral (C_4) views. **D**. Right pterygoid (RU-EFP-03592) in medial (D_1), ventral (D_2), and lateral (D_3) views. Abbreviations: av, alveolus; t, tooth.

terior teeth and are of the appropriate size to have derived from the dentary.

Remarks.—RU-EFP-02450 differs from durophagous mosasaurs in that the base of the crown is not inflated and by its lack of multiple cusps, as seen in the mosasaur *Carinodens* (e.g., Schulp et al. 2004). Of the five crocodilians known from the Hornerstown Formation, namely *Hyposaurus* Owen, 1849, cf. *Procaimanoidea* Gilmore, 1946, *Bottosaurus*, *Thoracosaurus* Leidy, 1852, and *Borealosuchus* Brochu, 1997 (Gallagher 2003; Brochu et al. 2012), only *Bottosaurus* possesses similar blunt, crushing-style teeth. In particular, RU-EFP-02450 is assigned to *Bottosaurus harlani* based on its large size, short and blunt crown, and wrinkled enamel, each of which are characteristic of this taxon (Cossette and Brochu 2018). This specimen is nearly identical to the paralectotype (ANSP 9174) and to the teeth described from a new, partially-articulated specimen of *Bottosaurus harlani* from the MFL in the EFPQ (Cossette and Brochu 2018).

Although the dentary (RU-EFP-03820) is incomplete, its morphology is inconsistent with that of *Borealosuchus* because the mandibular symphysis extends posterior to the fourth alveolus and the ninth alveolus is distinctly larger than the eighth. In *Borealosuchus*, alveoli diameter doesn't increase until the tenth alveolus. The majority of the complete alveoli in our specimen are slightly labiolingually compressed (~20%), implying that the teeth within them would also have been compressed, consistent with the genus *Bottosaurus* (Cossette 2021).

Bottosaurus harlani is a rare and enigmatic caimanine known only from the Maastrichtian to early Danian of the Atlantic Coastal Plain (Erickson 1998; Schwimmer et al. 2015; Cossette and Brochu 2018). *Bottosaurus harlani* has previously been described from the MFL by Gallagher (1993) and Cossette and Brochu (2018), yet the small dentary described here represents the first juvenile remains for this taxon. The morphology of RU-EFP-03820 is strikingly consistent with that of adult specimen NJSM 11265 (Cossette and Brochu 2018: fig. 5), indicating that this alligatorid acquired its mandibular morphology early in life.

Stratigraphic and geographic range.—Upper Cretaceous (Maastrichtian) to lower Paleocene (Danian) of New Jersey, USA.

Squamata Oppel, 1811

Mosasauridae Gervais, 1853

Genus *Mosasaurus* Coneybeare, 1822

Type species: *Mosasaurus hoffmannii* Mantell, 1829, Maastrichtian, Maastricht, Netherlands.

cf. *Mosasaurus hoffmannii* Mantell, 1829

Fig. 4D.

Material.—A nearly-complete right pterygoid (RU-EFP-03592) from the MFL, nine isolated teeth (RU-EFP-00109, 01826, 01901, 02703, 02916, and 00120-1–00120-4) and seven isolated vertebral centra (RU-EFP-00033, 02645, 03640, and 00043-1–00043-4) of mosasaurids have also been recovered from the MFL; many, if not all, of these specimens likely pertain to this same taxon, but they are too incomplete or lack enough diagnostic features for confident referral. All from Danian, Edelman Fossil Park, Mantua Township, New Jersey, USA.

Description.—The pterygoid is well preserved and represents one of the rarer skeletal elements of a mosasaurid recovered from the EFPQ in the last half century. Its preserved anteroposterior length is ~33 cm. Five erupted and three replacement teeth are present, although the specimen possesses a total of nine alveoli. The enamel of the preserved teeth is generally smooth or faintly faceted. Where these facets are present, they are much less well pronounced than in the marginal teeth of *Mosasaurus hoffmannii*. Faintly-serrated carinae are present on both the anterior and posterior margins of each tooth. As in other *Mosasaurus* species, the middle teeth are larger (crown height = 28 mm) than the posteriormost ones (~18 mm). As described for the holotype of *M. hoffmannii* by Street and Caldwell (2017), the tooth row is spindle shaped in ventral view with a rather flat parapet on the medial side and a bowed outwards parapet laterally. The basisphenoid and quadratic rami are each thin, with the quadratic ramus also being dorsomedially concave.

Remarks.—Several mosasaurs are known from Cretaceous strata in New Jersey, including the large-bodied taxa *Mosasaurus conodon* Cope, 1881, *M. hoffmannii*, and *Prognathodon rapax* Hay, 1902 (see Gallagher 2005, 2015; Gallagher et al. 2012, for full taxa lists). Of these, *M.* cf. *hoffmannii* is known from the MFL whereas *M. conodon* and *Prognathodon rapax* are known from the underlying Navesink and Mount Laurel formations (Gallagher 2005; Gallagher et al. 2012). RU-EFP-03592 differs from *Prognathodon* in having teeth with distinct facets (Dortangs et al. 2002) and both anterior and posterior carinae (Konishi et al. 2011). It also differs from *M. conodon* in having serrated carinae (Ikejiri and Lucas 2015). The overall size and morphology of the pterygoid is consistent with that of *M. hoffmannii*; although the only diagnostic feature reported for this species is the presence of eight teeth in the pterygoid (Street and Caldwell 2017). However, other mosasaur genera have eight pterygoid teeth as well (e.g., *M. conodon*), and tooth count can vary within mosasaurid genera or species (Ikejiri and Lucas 2015). Given this uncertainty, we conservatively identify RU-EFP-03592 as belonging to cf. *M. hoffmannii*.

Mosasaur material is relatively rare in the MFL, being more common and more complete in the underlying formations (Gallagher 2005, 2015; Gallagher et al. 2012). Within the MFL, typical finds include isolated teeth and worn centra. Thus, the recovery of a relatively complete and well-preserved pterygoid with teeth represents an exceptional discovery. These better-preserved specimens (RU-EFP-03592 and 00033, a large anterior ?caudal retaining portions of the transverse processes and neural spine) also suggest that mosasaur material in the MFL is not reworked (contra Gallagher 1993, 2005).

Stratigraphic and geographic range.—Upper Cretaceous (Campanian to Maastricthtian) of Maryland, Missouri, New Jersey, South Dakota, Tennessee, and Texas in USA, Angola, Belgium, Brazil, Bulgaria, Canada, Denmark, Germany, Italy, Japan, Jordan, Morocco, Netherlands, New Zealand, Niger, Poland, Russia, South Africa, Spain, Syria, and Turkey.

Discussion

Faunal insights.—Ichthyofaunal assemblages spanning the K/Pg boundary are rare (Cavin 2001; Becker and Chamberlain 2012; Argyriou and Davesne 2021), as are surface outcrops of the K/Pg boundary along the Atlantic and Gulf Coastal Plains. This is especially true along the northeastern seaboard where the boundary has often become deeply buried by sediments derived from ongoing erosion of the Appalachian Mountains since the Mesozoic (e.g., Olsson et al. 1997; Miller et al. 1999). Former excavations by the Inversand Company in Mantua Township, New Jersey, allowed geologists and paleontologists to circumvent this challenge for nearly a century. This property, now the Jean and Ric Edelman Fossil Park and Museum, continues to afford a regionally-unrivaled window into the Maastrichtian–Thanetian strata and fossil faunas of the western Atlantic, making it one of the most informative K/Pg boundary sites along the Atlantic Coastal Plain (Gallagher 1993).

Prior studies of the fossilized faunas preserved in the EFPQ (e.g., Gallagher 1993, 2003) identified a diverse suite of 67 taxa within the MFL of the lower Hornerstown Formation, as well as 42 taxa within the underlying Navesink Formation and 19 taxa within overlying sediments of the Hornerstown Formation above the MFL (Table 1). Our study of vertebrate microfossils recovered from the EFPQ adds 11 taxa to the known faunal list for this K/Pg locality (Table 1):

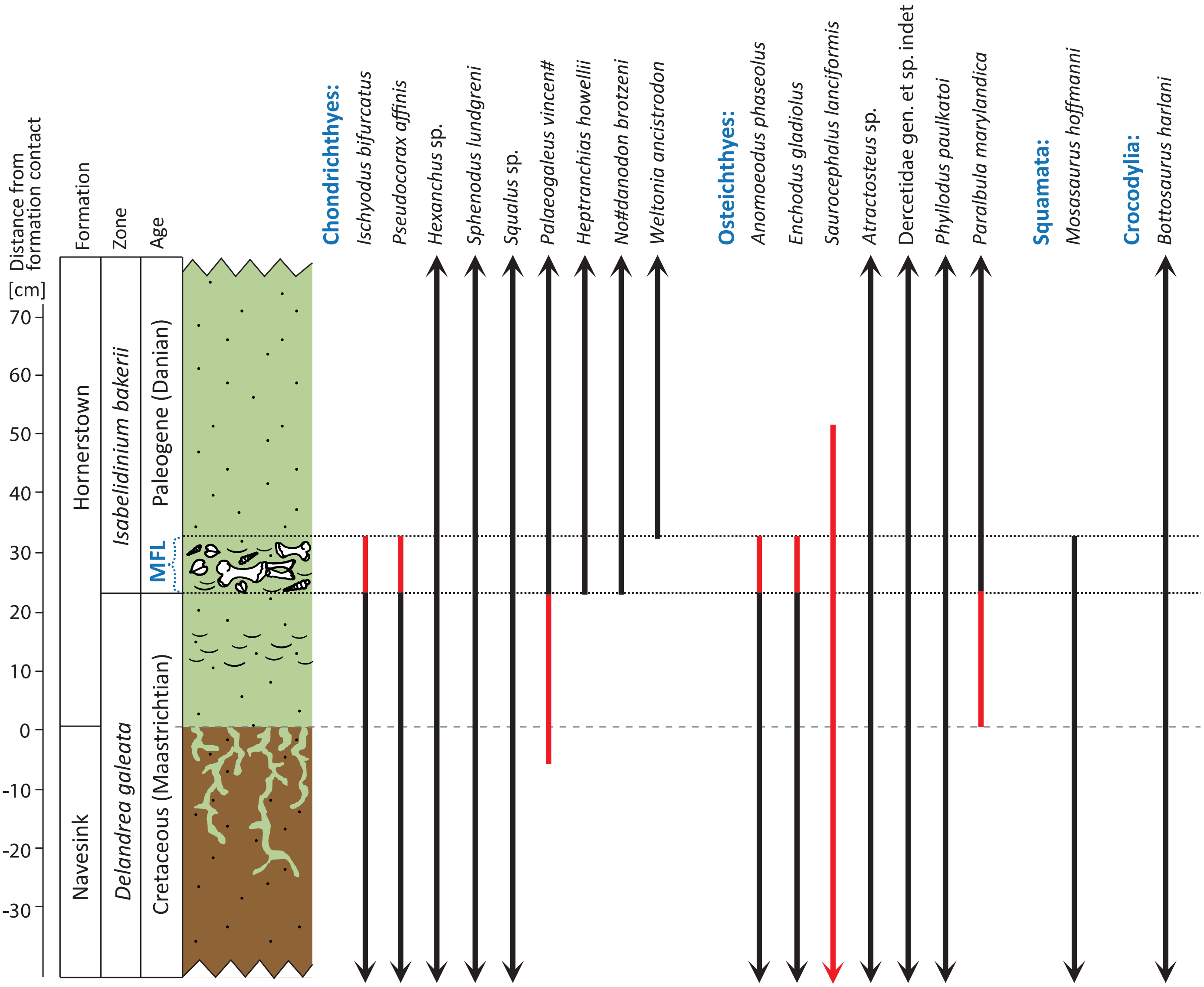

Fig. 5. Stratigraphic occurrences of each taxon discussed in this study, with new range extensions noted in red. The range extensions shown are based on the global record of each taxon, and thus represent global temporal range extensions (i.e., they are not merely extensions in the record solely at Edelman Fossil Park). Placement and thickness of the Main Fossiliferous Layer (MFL) and "oyster layer" beneath it within the lower Hornerstown Formation are based on the findings of Voegele et al. (2021), and assignment of the dinoflagellate zones is based on Koch and Olsson (1977) and Aurisano (1989).

Palaeogaleus vincenti, *Heptranchias howellii*, *Notidanodon brotzeni*, *Weltonia ancistrodon*, *Pseudocorax affinis*, *Squalus* sp., Dercetidae indet., *Enchodus gladiolus*, *Phyllodus paulkatoi*, *Saurocephalus lanciformis*, and *Atractosteus* sp. The remains of the majority of these new taxa were recovered from the MFL but as shown in Table 1, several new species occurrences were also identified in the Navesink Formation and Hornerstown Formation above the MFL. Each of the newly-identified taxa are generally compatible with prior paleoecological interpretations by Gallagher (1993), Wiest et al. (2016), and Vellekoop et al. (2016) that the Hornerstown Formation records deposition on the mid-to-outer shelf under warm/subtropical conditions.

Geographic and temporal range extensions.—Taken as a whole, identification of these new microfossils reveals important new insights into patterns of vertebrate survivorship and extinction across the K/Pg boundary, as well as temporal and geographic range extensions for several chondrichthyan and actinopterygian taxa (Fig. 5). Of primary significance, we have identified the first Paleocene (Danian) record of *Saurocephalus* and first Cretaceous (Maastrichtian) records of *Paralbula marylandica* and *Palaeogaleus vincenti*, demonstrating for the first time that these taxa survived the K/Pg mass extinction. Our recovery of dercetid scutes from both the Navesink and Hornerstown formations (including above the MFL) reveals that these predatory needlefish also survived the mass extinction in the western Atlantic (contra Cavin 2001). Further, we have identified the first record of gars in the Hornerstown Formation, including the first Paleocene (Danian) occurrences of *Atractosteus* in New Jersey, as well as the first records of *Enchodus gladiolus*, *Ischyodus bifurcatus*, *Anomoeodus phaseolus*, and *Pseudocorax affinis* from the MFL (which represent the youngest occurrences of these taxa in the region). These latter discoveries indicate that those four taxa survived all the way through the Maastrichtian in the western Atlantic, ultimately perishing during the collapse of the local ecosystem in the earliest Danian following the Chicxulub impact (cf. Obasi et al. 2011; Esmeray-Senlet et al. 2017). Three geographic range extensions were also identified in this study, namely the first records of *Notidanodon brotzeni* from the Western Hemisphere, *Saurocephalus* from northeastern North America, and *Phyllodus paulkatoi* along the eastern coast of North America. Finally, the dentary of *Bottosaurus* we describe from the MFL indicates that the mandible of this poorly-known alligatorid likely grew isometrically through ontogeny (cf. Cossette and Brochu 2018).

These novel insights highlight the importance of microfossils for expounding knowledge of past faunas and illuminating the character of ancient ecosystems (Sankey and Baszio 2008). Moreover, given the wealth of microfossil specimens recovered in our recent projects in the EFPQ (e.g., Boles 2016; Voegele et al. 2021), it is almost certain that further microsieving of sediments of each of the formations examined herein, as well as from other unconsolidated Cretaceous and Paleocene formations across the Atlantic and Gulf Coastal Plains, would yield a wealth of microfossil specimens stemming from as-yet unrecognized taxa (and potentially taxa new to science). For instance, despite over a century of study of the Cretaceous–Paleocene faunas of New Jersey (e.g., Cope 1869), to this day new vertebrate taxa continue to be named based on newly-discovered macrofossils from these deposits (e.g., *Borealosuchus threeensis* Brochu et al., 2012, *Iridopristis parrisi* Andrews et al., 2023). We therefore infer that this study likely only elucidates a portion of the "hidden" microfauna of the EFPQ and predict that further microsieving studies here and elsewhere across the region will continue to yield similar insights.

Comparisons.—The late Maastrichtian–early Danian ichthyofauna of the EFPQ is broadly similar to those of many other K/Pg boundary localities across the Atlantic and Gulf Coastal Plains, and from deposits of the Western Interior Seaway (e.g., Becker et al. 2010, and references therein). Further, as at Stevns Klint in Denmark, hexanchids were common at EFPQ and chondrichthyan macrofossils are more abundant than those of osteichthyans (Adolfssen and Ward 2015; Adolfssen et al. 2017). Aulopiforms (e.g., *Enchodus*) were especially abundant during the Cretaceous at EFPQ, as in the Pindos Unit in Greece (Argyriou and Davesne 2021); and as in the vertebrate record of the López de Bertodano Formation of Seymour Island, Antarctica (Cione et al. 2018), there is no apparent decline in fish diversity leading up to the K/Pg at EFPQ.

Our findings also generally agree with the growing consensus (Noubhani and Cappetta 1997; Becker et al. 2011; Adolfssen and Ward 2014; Poyato-Ariza and Martín-Abad 2016; Guinot and Condamine 2023) that both osteichthyans and chondrichthyans were significantly impacted by the K/Pg extinction. For instance, at the EFPQ 50% of actinopterygian (4 of 8) and 71% of chondrichthyan genera (10 of 14) disappear at the top of the MFL (Table 1). These extinctions were selective, with our results from the EFPQ showing strong correspondence with those of other studies that crocodilians (Jouve and Jalil 2020), teleosts (Poyato-Ariza and Martín-Abad 2016), durophagous actinopterygians (e.g., *Paralbula*, *Anomoeodus*), gars (e.g., *Atractosteus*), hexanchids (e.g., *Hexanchus*), and squalids (e.g., *Squalus*) weathered the extinction well while durophagous chondrichthyans (e.g., edaphodontids), rhombodontids (e.g., *Rhombodus*), and large, fast, open-water predators (e.g., enchodontids and anacoracids, such as *Enchodus* and *Squalicorax*) went extinct (Cavin 2001; Kriwet and Benton 2004; Friedman 2009; Friedman and Sallan 2012; Adolfssen et al. 2017; Schwarzhans and Stringer 2020; Guinot and Condamine 2023). Perhaps due to the decimation of invertebrates, rays also seem to disappear above the MFL at the EFPQ; this finding matches global trends of severe declines for myliobatiforms in the immediate aftermath of the Chicxulub impact (Kriwet and Benton 2004; Guinot and Condamine 2023).

The comparative rarity of fish fossils in the Hornerstown Formation above the MFL implies that recovery of elasmobranchs and fish after the extinction was slow. The recovery of chondrichthyans, especially sharks, in New Jersey appears to have occurred more slowly than in Denmark (cf. Adolfssen and Ward 2014) but faster than along the Gulf Coastal Plain in Arkansas (cf. Maisch et al. 2020), perhaps reflecting its intermediate distance from the Chicxulub impact site compared to these other localities. Collectively, these trends align well with slow recovery patterns inferred from ichthyoliths in the southern Atlantic Ocean (Sibert et al. 2014) and based on studies of the global fossil record of Cretaceous–Paleogene fish (Friedman 2009; Guinot and Condamine 2023).

Macro- and microfossils collected from above the MFL at the EFPQ in this study, and by Gallagher (1993), indicate that the local ichthyofauna during the initial phase of recovery after the Chicxulub impact was dominated by durophagous fish and hexanchid and lamniform sharks. This is evident by sediments of the Hornerstown Formation above the MFL yielding a relative abundance of teeth of *Odontaspis*, *Otodus* (personal observations by ZMB and PVU), and *Paralbula* (this study), as well as by hexanchids and lamniforms representing five of the eight (63%) known chondrichthyans in the upper Hornerstown Formation (Table 1). Such abundance of odontaspid and otodontid teeth differs from the early Danian ichthyofaunas of Antarctica, where these sharks appear to have been rare (Cione et al. 2018). However, similar recovery patterns have been noted in the Paleocene Clayton Limestone of Arkansas, where scarce food may have favored the survival of durophagous taxa

Table 1. Comprehensive list of the invertebrate and vertebrate fauna recovered from Jean and Ric Edelman Fossil Park, sorted by geologic Formation and fossil-rich horizons. Revised from prior lists by Gallagher (2002, 2003) to include more recent additions from previous studies (e.g., Schein et al. 2011; Brochu et al. 2012; Callahan et al. 2012), taxonomic revisions and/or recombinations, and synonymizations over the last 20 years. New additions to the vertebrate fauna identified herein are denoted by an asterisk (*) after their name. Based on recent discoveries, a few additions to the invertebrate and ichnotaxa lists are also included (denoted by a superscript diamond after their name, $^{\lozenge}$); these are being formally described in a separate manuscript currently in preparation. Abbreviation: MFL, Main Fossiliferous Layer.

Taxon	Navesink Formation	Main Fossiliferous Layer (MFL)	Hornerstown Formation (above MFL)	Vincentown Formation
Porifera	*Cliona cretacea*	*Cliona cretacea*	*Peronidella dichotoma*	
Cnidaria		*Flabellum mortoni*	*Flabellum mortoni*	
Brachiopoda	*Choristothyris plicata*	*Terebratulina atlantica*	*Oleneothyris harlani* *Oleneothyris* cf. *manasquani* *Terebratulina atlantica*$^{\lozenge}$	*Oleneothyris harlani*
Bryozoa	Indet. encrusting bryozoans			Indet. encrusting bryozoans
Bivalvia	*Agerostrea nasuta* *Crassatellites vadosus* *Cucullaea antrosa* *Cucullaea neglecta* *Cucullaea vulgaris* *Exogyra costata* *Glycymeris mortoni* *Gryphaeostrea vomer* *Liopistha protexta* *Lithophaga ripleyana* *Pachycardium spillmani* *Pycnodonte convexa* *Solyma* cf. *lineolatus* *Spondylus echinata* *Trigonia mortoni*	*Cardium tenuistriatum* *Crassatellites vadosus* *Cucullaea vulgaris* *Cuspidaria* sp.$^{\lozenge}$ *Etea delawarensis* *Gervilliopsis ensiformis* *Glycymeris mortoni* *Gryphaeostrea vomer* *Linearia* sp.$^{\lozenge}$ *Lithophaga ripleyana* *Nuculana stephensoni* *Panopea decisa* *Pycnodonte dissimilaris* *Veniella conradi*	*Caryatis veta* *Clavipholas* sp.$^{\lozenge}$ *Crassatellites* cf. *littoralis* *Cucullaea macrodonta* *Ostrea glandiformis* *Veniella conradi*	*Cyprimeria densata* *Polorthus tibialis* *Pycnodonte* sp. *Venericardia antiqua*
Gastropoda	*Anchura* cf. *abrupt* *Anchura pennata* *Euspira halli* *Gyrodes petrosus* *Pleurotomaria* sp.$^{\lozenge}$ *Pyrifusus macfarlandi* *Turbinopsis curta* *Turritella* cf. *vertebroides* *Volutomorpha ponderosa*	*Acteon cretacea* *Anchura abrupt* *Avellana* sp.$^{\lozenge}$ *Cylichna* sp.$^{\lozenge}$ *Euspira halli* *Gyrodes abyssinus* *Pleurotomaria* sp.$^{\lozenge}$ *Pyropsis trochiformis* *Turbinella parva* *Turbinella subconical* *Turritella vertebroides* *Volutoderma ovata*	cf. *Volutocorbis* sp.	
Nautiloidea	*Eutrephoceras dekayi*	*Eutrephoceras dekayi* *Hercoglossa* sp.$^{\lozenge}$	cf. *Aturia* sp.	
Ammonoidea	*Baculites ovatus* *Discoscaphites conradi*	*Baculites* sp. *Discoscaphites iris* *Pachydiscus mokotibensis* *Sphenodiscus lobatus*		
Echinodermata	*Hemiaster* sp.			
Crustacea		*Hoploparia* sp.		
Chondrichthyes	*Heptranchias howellii** *Odontaspis* sp. *Palaeogaleus vincenti** *Squalicorax pristodontus*	*Cretolamna appendiculata* *Edaphodon mirificus* *Edaphodon stenobyrus* *Heptranchias howellii** *Hexanchus* sp. *Ischyodus bifurcatus** *Ischyodus thurmanni* *Myliobatis* cf. *leidyi* *Notidanodon brotzeni** *Odontaspis cuspidata* *Palaeogaleus vincenti** *Pseudocorax affinis**	*Edaphodon agassizi* *Hexanchus* sp.* *Odontaspis* sp. *Otodus obliquus* *Palaeocarcharodon* sp. *Palaeogaleus vincenti** *Squalus* sp.* *Weltonia ancistrodon**	Lamnidae gen. et sp. indet.

Taxon	Navesink Formation	Main Fossiliferous Layer (MFL)	Hornerstown Formation (above MFL)	Vincentown Formation
Chondrichthyes		*Rhinoptera* sp. *Rhombodus laevis* *Sphenodus lundgreni* *Squalicorax pristodontus* *Squalus* sp.* *Squatina* sp. Batomorpha gen. et sp. indet.		
Osteichthyes	*Paralbula marylandica** *Anomoeodus phaseolus* *Enchodus ferox* Dercetidae gen. et sp. indet.* Osteichthyes gen. et sp. indet.	*Acipenser* cf. *albertensis* *Anomoeodus phaseolus** *Atractosteus* sp.* cf. *Bananogmius* sp. *Enchodus ferox* *Enchodus gladiolus** *Paralbula marylandica* *Phyllodus paulkatoi** Dercetidae gen. et sp. indet.* Teleostei gen. et sp. indet.	*Anomoeodus phaseolus** *Atractosteus* sp.* *Paralbula marylandica** *Saurocephalus lanciformis** Dercetidae gen. et sp. indet.*	
Testudines	Cheloniidae gen. et sp. indet. *Peritresius ornatus*	*Adocus beatus* *Agomphus turgidus* *Bothremys* sp. *Euclastes wielandi* *Peritresius ornatus* *Taphrosphys sulcatus*	*Euclastes wielandi* Testudines gen. et sp. indet.	
Crocodylia		*Borealosuchus threeensis* *Bottosaurus harlani* cf. *Procaimanoidea* sp. *Hyposaurus rogersii* *Thoracosaurus neocesariensis*	*Hyposaurus rogersii* *Thoracosaurus neocesariensis*	
Mosasauridae	*Halisaurus platyspondylus* *Mosasaurus hoffmanni* *Prognathodon rapax*	*Mosasaurus hoffmanni** *Plioplatecarpus* sp.		
Dinosauria	*Hadrosaurus minor* Hadrosauridae gen. et sp. indet.	Hadrosauridae gen. et sp. indet.		
Aves		*Graculavis velox* *Novacaesareala hungerfordi* *Palaeotringa littoralis* *Telmatornis priscus* *Tithostonyx glauconiticus*		
Plantae		Plantae gen. et sp. indet. (wood, seeds)		
Ichnotaxa	*Thalassinoides* isp.	*Gnathichnus*◊ *Radulichnus*◊ *Rhizocorallium* isp.◊ *Thalassinoides* isp. *Xylophagella irregularis*	*Thalassinoides* isp.	

(Becker and Chamberlain 2012), and in Danian strata across Denmark, where cooler waters stemming from the impact winter may have provided suitable conditions for sharks adapted to cool, deep settings (Adolfssen and Ward 2015; Adolfssen et al. 2017).

Finally, in agreement with global trends inferred by Bazzi et al. (2018) and Guinot and Condamine (2023), there is no significant shift in shark tooth shape disparity across the K/Pg at the EFPQ. Wide-ranging Cretaceous chondrichthyan genera (4 of the 11, or 36%) present at EFPQ survived the K/Pg slightly better than endemic taxa (1 of the 5, or 20%), and lamniforms diversified in its aftermath (i.e., two new genera, *Otodus* and *Palaeocarcharodon*, are first observed in the Hornerstown Formation above the MFL; Table 1). However, unlike these studies, at the EFPQ there are no signs of carcharhiniform sharks rising to dominance following the K/Pg (cf. Bazzi et al. 2018) nor of differential survivorship by short-lived (37%) versus long-lived (33%) shark genera (Table 1; cf. Guinot and Condamine 2023). These contrasts highlight the value of detailed studies of individual sites, like this one, toward characterizing how regional geography, climate, and ecological relationships interact to control survivorship and recovery patterns through mass extinction events.

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