

CHONDRICHTHYANS FROM A LAG DEPOSIT BETWEEN THE SHARK RIVER FORMATION (MIDDLE EOCENE) AND KIRKWOOD FORMATION (EARLY MIOCENE), MONMOUTH COUNTY, NEW JERSEY

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ABSTRACT

A lag deposit that separates the middle Eocene Squankum Member of the Shark River Formation from the early Miocene Asbury Park Member of the Kirkwood Formation near Farmingdale, Monmouth County, New Jersey, preserves an unreported chondrichthyan assemblage dominated by carcharhiniforms and lamniforms. Locally, sea level regression resulted in the exhumation of middle Eocene chondrichthyans from the Squankum Member of Shark River Formation and erosion of Oligocene sediments. Subsequent transgression mixed these middle Eocene chondrichthyan remains with early Miocene chondrichthyan material within a basal lag deposit belonging to the Asbury Park Member of Kirkwood Formation. The chondrichthyan assemblage from the Farmingdale region of New Jersey is similar to other contemporaneous middle Eocene and early Miocene faunas found across the Atlantic and Gulf Coastal Plains in the United States and in shallow marine shelf deposits globally. The global distribution of taxa within the Farmingdale assemblage demonstrates the uniformity of post-Tethyan Ocean conditions and utility of chondrichthyan teeth in stratigraphic correlation. The Farmingdale assemblage supports prior studies that document evolutionary trends throughout the Cenozoic in which carcharhiniforms become the dominant chondrichthyan order in the modern oceans.

INTRODUCTION

Fossil chondrichthyans have been reported from Coastal Plain sediments of New Jersey for over 150 years. The first American shark teeth were figured by S.G. Morton in 1834 from regional greensands in the southern portion of the state and since that time, multiple researchers have documented Mesozoic and Cenozoic chondrichthyan assemblages from the New Jersey Coastal Plain (e.g., Fowler, 1911; Cappetta and Case, 1975; Gallagher et al., 1995; Case, 1996; Case et al., 2001). These chondrichthyan assemblages are typically concentrated into localized lag deposits that represent reworking events associated with third order sea level fluctuation (e.g., Gallagher et al., 1995; Becker, Slattery, and Chamberlain, 1996; Maisch, Becker, and Chamberlain, 2013).

In the New Jersey Coastal Plain, Late Cretaceous chondrichthyan fossils are abundant in the Wenonah–Mt. Laurel and Navesink Formations, primarily in Monmouth, Burlington and Gloucester Counties, where they occur in stream bed exposures and occasionally in greensand marl quarries (e.g., Fowler, 1911; Mansfield, 1923; Gallagher, 1993; 2003).

In contrast to Late Cretaceous assemblages, few reports exist on Paleogene and Neogene

chondrichthyans from the New Jersey Coastal Plain (e.g., Cope, 1875; Leidy, 1877; Fowler, 1911; Gallagher et al., 1995; Case, 1996). Cenozoic assemblages reported from the state typically consist of lamniforms and carcharhiniforms that are distinctly different from those seen in the Late Cretaceous. Late Cretaceous and Cenozoic chondrichthyan assemblages in New Jersey parallel global trends in faunal turnover and extinction across the Cretaceous–Paleogene and Eocene–Oligocene boundaries. Across these boundaries, carcharhiniforms systematically replace the lamniforms as the dominant chondrichthyan order on Earth (Kriwet and Benton, 2004; Underwood and Gunter, 2012; Cappetta, 2012; Sorenson et al., 2014).

This report describes a new chondrichthyan assemblage recovered from a lag deposit between the middle Eocene Shark River Formation and the early Miocene Kirkwood Formation near Farmingdale, Monmouth County, New Jersey and is the northernmost occurrence of Cenozoic chondrichthyans on the Atlantic Coastal Plain. This assemblage provides new insights on the evolution, distribution, and paleoecology of chondrichthyans during the middle Eocene and early Miocene of the Atlantic and Gulf Coastal Plains of North America. The Farmingdale assemblage also demonstrates the utility

of chondrichthyan teeth as chronostratigraphic markers and may aid in regional and global stratigraphic correlation.

GEOLOGIC SETTING AND AGE

During the middle Eocene, sea level transgression inundated large areas of the Atlantic and Gulf Coastal Plains of the United States and the southern portion of New Jersey (e.g., Enright, 1969; Gallagher et al., 1996; Browning, Miller, Van Fossen, and others, 1997; Miller, Rufolo, and others 1997a; Miller, Browning and others, 1997b; Lear et al., 2004; Sugarman and Stanford, 2006; Miller, Mountain, and others, 2011). The Farmingdale locality discussed here occurs within the inner coastal plain of Monmouth County, New Jersey, and occurs on the border of Allaire State Park. Regional geology consists of unconsolidated Eocene, Miocene, and Quaternary sediments dissected by the Shark and Manasquan Rivers, Mingamahone Brook and their associated tributaries (Figure 1). The chondrichthyan fossils described in this report were derived from an area of approximately 0.25 km² along Mingamahone Brook, directly east of the town of Farmingdale, New Jersey.

Along Mingamahone Brook, erosion has exposed the uppermost Squankum Member of the Shark River Formation and the Asbury Park and Grenloch Sand Members of the Kirkwood Formation (Figure 1). At the Farmingdale locality, the uppermost Squankum Member is approximately 1.0 m thick and is composed of coarse, sand-sized glauconite grains in a tan to gray-brown marl. The upper contact is erosional and is characterized by a hardened layer of glauconitic marl that locally preserves molds and casts of molluscs and gastropods. The basal Asbury Park Member of the Kirkwood Formation is comprised of a lag deposit that varies in thickness between 10–0 cm. This lag deposit consists of quartz and glauconite sand composed of angular to sub-rounded particles of quartz and glauconite ranging from 1.5–0.5 mm in diameter. Chondrichthyan fossils are extremely abundant within this lag and co-occur with the remains of osteichthyans, marine and terrestrial mammals, and chelonians. From the basal lag, the Asbury Park Member grades upwards into a dark brown to gray, organic-rich, finely-laminated clayey-silt with casts and molds of bivalves. The basal contact of the Grenloch Sand is gradational and the lithology shifts from gray clay-silt to yellow orange sand. The Grenloch Sand exposed along Mingamahone Brook is approximately 1.0 m thick and consists of cross-bedded, yellow-orange quartz sand with minor amounts of glauconite and localized pebble lenses. Along Mingamahone Brook, erosion, topsoil, and vegetation obscure the upper Grenloch Sand.

Additional details regarding the sedimentology and stratigraphy of the inner coastal plain of New Jersey including the Farmingdale locality described here are available in Ries et al. (1904); Enright (1969); Isphording and Lodding (1969); Isphording (1970a); Sugarman, Owens, and Bybell (1991); and Sugarman and Stanford (2006).

Multiple proxies provide a detailed chronology for the Cenozoic of New Jersey Coastal Plain. Earlier outcrop and borehole analyses utilized biostratigraphy of molluscs, diatoms, foraminifera, and calcareous nannofossils for chronologic interpretation (Richards, 1935; Richards and Harbison, 1942; Olsson, 1978; Andrews, 1988; 1995; Poore and Bybell, 1988; Miller and Sugarman, 1995; Miller, Rufolo, and others, 1997a; Miller, Browning, and others, 1997b). More recently, strontium isotopic age dating, magnetobiostratigraphy, terrestrial and marine mammal analyses, geologic mapping, and additional borehole data have been used to refine previous age interpretations (Sugarman, Owens, and Bybell, 1991; Sugarman, Miller, and others, 1993; Owens, Miller and Sugarman, 1997; Benson, 1998; Emry and Eschelman, 1998; Jones et al., 1998; Gradstein et al., 2004; Sugarman and Stanford, 2006; Browning, Miller, Sugarman, and others, 2008; Uhen, 2014). The Squankum Member of the Shark River Formation is of middle Eocene (Bartonian) age, whereas the Asbury Park and Grenloch Sand members of the Kirkwood Formation are of early Miocene (Aquitania–Burdigalian) age in Monmouth County and the Farmingdale region. Oligocene sediments in New Jersey have only been identified in subsurface boreholes, mainly in the southern portion of the state. The nearest Oligocene sediments to the Farmingdale locality are located 40 km southeast in Island Beach State Park. No fossils with definitive Oligocene ages have been reported from Monmouth County or the Farmingdale locality.

PALEOBATHYMETRY AND TAPHONOMY OF THE FARMINGDALE CHONDRICHTHYAN ASSEMBLAGE

Facies analyses of the middle Eocene Squankum Member of the Shark River Formation in Monmouth County, New Jersey, indicate open ocean shelf deposition with water depths ranging between 30 and 150 m (Enright, 1969; Sugarman and Stanford, 2006). This shelf environment was substantially reduced by the late Eocene and shallow marine deposition was restricted to the southernmost portion of the state throughout the Oligocene. By the early to middle

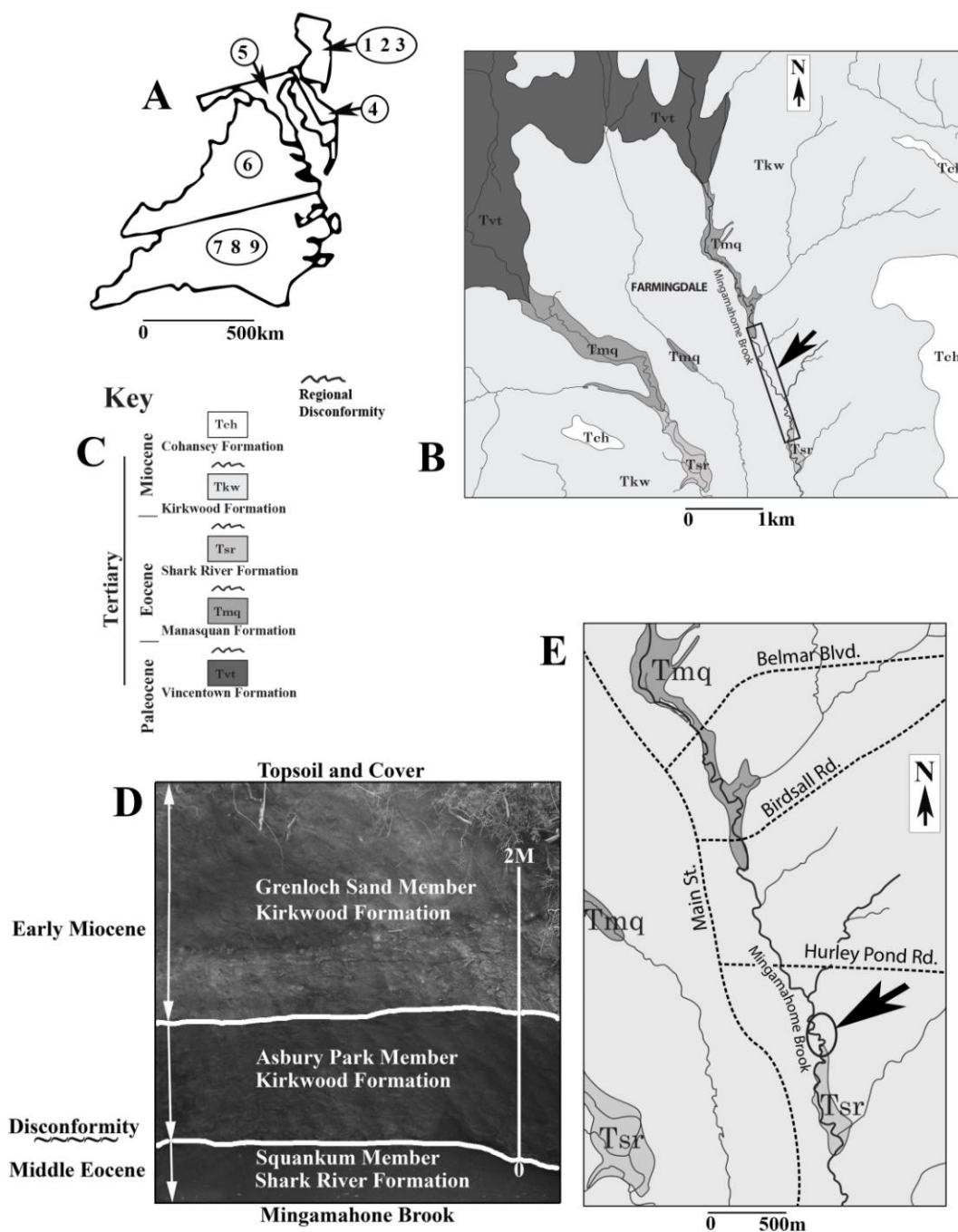


FIGURE 1. Location maps of the Farmingdale field locality and Shark River–Kirkwood Formation Contact (middle Eocene and early Miocene), Monmouth County, New Jersey. A—Late Cretaceous, middle Eocene, and early Miocene Atlantic Coastal Plain chondrichthyan localities discussed in this study: 1, 2, 3, New Jersey, (Case, 1995; Chamberlain et al., 2005; this report); 4, Delaware (Purdy, 1998); 5, Maryland (Hartstein et al., 1999); 6, Virginia (Ward and Wiest, 1990); 7, 8, 9, North Carolina, (Case, 1979; 1980; Case and Borodin, 2000a); B and C—Geologic map and stratigraphic column of the Farmingdale region (modified from Sugarman and Stanford, 2006). Rectangle denotes sampled area. D—Shark River–Kirkwood Formation contact along Mingamahone Brook discussed in text. Note prominent disconformity between the Squankum Member of the Shark River Formation and Asbury Park Member of the Kirkwood Formation. E—Detailed geologic map of the Farmingdale region displaying the middle Eocene Shark River and early Miocene Kirkwood Formations along Mingamahone Brook, Monmouth County, New Jersey, denoted by bold arrow and circle.

Miocene, water depths up to 30 m again submerged Monmouth County and the Farmingdale region. Facies analyses interpret the Asbury Park and Grenloch Sand members of the Kirkwood Formation as nearshore marine to estuarine environments with deltaic influences (Isphording and Lodding, 1969; Isphording, 1970a,b; Goldstein, 1974; Owens, Bybell, and others, 1988; Sugarman, Miller, and others, 1993; Sugarman, Brenner, and others, 1995; Gallagher et al., 1995; Benson, 1998; Sugarman and Stanford, 2006).

Bathymetric changes throughout the middle Eocene and early Miocene in the New Jersey Coastal Plain also resulted in the formation of a regional disconformity. This disconformity occurs in outcrop and the subsurface between the Shark River and Kirkwood Formations (Gibson, 1971; Poag, 1985; Benson, 1998). Miller, Mountain, and others (2011) correlated this disconformity with global third order sea level cycles TA4.5 and TB1.1 of Haq et al. (1987) and suggested sea level may have regressed as much as 75 meters or more (Kominz et al., 1998; Miller, Wright, and others, 2009). It is also noteworthy that this regression can be seen in other Atlantic and Gulf Coastal Plain deposits and has been previously mapped as a disconformity between carbonaceous and siliciclastic deposition (Miller, Rufolo, and others, 1997; Benson, 1998). The leading cause for this global regression has been correlated to the onset of glaciation in Antarctica during the late Eocene and early Oligocene (Olsson, 1978; Browning, Miller, Van Fossen, and others, 1997; Lear et al., 2004; Liu et al., 2009; Miller, Browning, and others, 1997b; Miller, Wright, and others, 2009; Pagani et al., 2011; Norris et al., 2013).

Miller, Rufolo, and others (1997a) indicated that during the early and middle Miocene, a shallow marine seaway again submerged Monmouth County and the Farmingdale region between third order sea level cycles TB1.4 and TB1.5. This would be the last time the Farmingdale region in Monmouth County, New Jersey would experience marine conditions (e.g., Olsson, 1978; Sugarman, Owens, and Bybell, 1991; Miller, Rufolo, and others, 1997a; Miller, Browning, and others, 1997b).

We interpret the disconformity and chondrichthyan lag along Mingamahone Brook between the Squankum Member of the Shark River Formation and the Asbury Park of the Kirkwood Formation to represent an outcrop expression of these third order sea level cycles. The diversity and abundance of chondrichthyans in this lag is also a direct product of these sea level cycles and represents: 1) eroded and reworked fossils from the middle Eocene Squankum Member of the Shark River Formation

during sea level regression; and, 2) mixing of early Miocene fossils into a basal lag when the sea re-inundated the Farmingdale region. No chondrichthyan teeth with distinct and solely Oligocene affinities were recovered from the Farmingdale locality. Chondrichthyan teeth from the Oligocene are poorly known from the Atlantic and Gulf Coastal Plains due to sea level regression and shallow marine shelf habitat loss across the Eocene–Oligocene boundary (e.g., Olsson et al., 1978; Poag, 1985; Benson, 1998; Cicimurri and Knight, 2009).

FIELD AND LABORATORY METHODS

Chondrichthyan fossils described in this report were recovered directly from the lag deposit that occurs in the basal Asbury Park Member of the Kirkwood Formation at the Farmingdale locality. Areas in Mingamahone Brook, immediately adjacent to the contact between the Squankum Member of the Shark River Formation and Asbury Park Member of the Kirkwood Formation, were also collected and represent accumulations of chondrichthyan fossils eroded directly out of the lag and hydrodynamically concentrated nearby in deeper pools. Lag sediments were sieved through 1.0 cm and 0.5 cm grade mesh. Bulk sampling and laboratory analysis of approximately 100 kg of lag sediment, with sieve size ranging down to 1.0 mm, resulted in the recovery of only a few microteeth (teeth less than 5.0 mm) with poor taxonomic certainty. The chondrichthyan assemblage utilized for this study consists of over 5000 teeth recovered from stream gravel and lag sediment over a period of ten years.

In the laboratory, specimens were analyzed and photographed using an Olympus SZ61 binocular microscope attached to an Infinity 2 Digital Camera. Chondrichthyan teeth were identified by comparison with regional and international literature with specific focus on: Purdy (1998); Purdy et al. (2001); Cappetta (2012); and Bor et al. (2012). Tooth terminology follows that of Applegate (1965) and Cappetta (1987; 2012). Chondrichthyan teeth described in this report were recovered from the Farmingdale locality along Mingamahone Brook and have been repositied in the collections of the New Jersey State Museum with the catalogue numbers: NJSM23478–23502.

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Superorder Squalomorphii Compagno, 1973

Order Hexanchiformes de Buen, 1926
 Family Hexanchidae Gray, 1851
 Genus *Hexanchus* Rafinesque, 1810
Hexanchus agassizi Cappetta, 1976
 (Figure 2: A–B, Table 1)

Hexanchus agassizi Cappetta, 1976, Pl. 1, figs. 5, 7, and 8, non fig. 7.

Material Examined—One lower right lateral tooth: NJSM 23478.

Description—The crown contains a complete cutting edge and is labio-lingually compressed and mesio-distally elongated. The acrocone on the lateral tooth is serrated on the mesial edge. The lower lateral tooth also possesses multiple cusplets, resembling a saw-tooth pattern, that are angled distally and decrease in size toward the distal end of the tooth. The root is anaulacorhizous, contains pores near the top of the lingual face, and has a flattened labial face and basal edge.

Remarks—The lower right lateral tooth of *H. agassizi* has a cusp with numerous cusplets that are similar in size. This size uniformity allows *H. agassizi* to be distinguished from *Notorynchus primigenius* Agassiz, 1843 which also occurs in the Farmingdale assemblage. Additionally, teeth of *N. primigenius* are larger than *H. agassizi* and contain fewer secondary cusplets and cusps with a greater distal inclination. Similar Eocene species not found from the Farmingdale assemblage include: *Heptranchias howelli* (Reed, 1946), *Hexanchus hookeri* (Ward, 1979), *Hexanchus collinsonae* (Ward, 1979), *Notidanodon* (Cappetta, 1975), and *Weltonia* (Ward, 1979). These species and genera can be distinguished from *H. agassizi* by having irregular cusplet size and height variation in the distal direction, coarser mesial serrations and a primary distal cusplet that is larger and more erect than the secondary distal cusplets, and a more reduced root lacking deep lingual, longitudinal protuberances in addition to distal cusplets that do not have noticeable apical curvature (Cione and Reguero, 1995; Compagno et al., 2005; Cappetta, 2012).

Genus *Notorynchus* Ayres, 1855
Notorynchus primigenius Agassiz, 1843
 (Figure 2: C–H; Table 1)

Notidanus primigenius Agassiz, 1843, p. 218. Pl. 27, figs. 6–8, 13–17, non 4–5.

Material Examined—One upper anterior tooth and two lower lateral teeth: NJSM 23479.

Description—The upper anterior tooth has an erect crown with a complete cutting edge and a single

cusplet is present on each side of the main cusp. Lower lateral teeth are labio-lingually compressed and mesio-distally extended, have an erect acrocone with up to six secondary distal cusplets that decrease in size and are angled in the distal direction. The roots of the upper anterior and lower lateral teeth are anaulacorhizous, however the root of the upper anterior tooth is more robust and has mesial and apical edges that form a right angle and the lingual surface is steeply inclined towards the root base. The roots of lower lateral teeth are labio-lingually flattened with flat basal edges and irregularly spaced pores are present near the crown base.

Remarks—Teeth from *N. primigenius* resemble those belonging to *N. serratissimus* (Agassiz, 1844) and *N. kemp* (Ward, 1979). However, *N. serratissimus* teeth are smaller, have fewer numbers of distal cusplets, and a less noticeable size difference between the primary and secondary distal cusplets. *Notorynchus kemp* has coarser mesial cusplets and more erect distal cusplets. The extant species, *N. cepedianus* (Péron, 1807) is similar to *N. primigenius* and may be present in some Neogene deposits (Cappetta, 2012). Kemp (1978) and Ávila et al. (2012) indicated that *N. cepedianus* can be distinguished from *N. primigenius*, based on a larger overall tooth size and the presence of less erect primary cusps and cusplets, whereas Purdy et al. (2001) assert that *N. primigenius* is synonymous with *N. cepedianus*. We follow the recent detailed study by Bor et al. (2012) and assign the teeth documented here to *N. primigenius* based on a smaller overall tooth size and the presence of more erect cusps and cusplets.

Order Lamniformes Berg, 1958
 Family Odontaspidae Müller and Henle, 1838
 Genus *Carcharias* Rafinesque, 1810
Carcharias cf. *C. acutissima* (Agassiz, 1843)
 (Figure 2: I–P; Table 1)

Lamna acutissima Agassiz, 1843 p.294. Pl. 37a, figs. 33 and 34

Material Examined—Three anterior teeth and one lateral tooth: NJSM 23480.

Description—The main cusps of the anterior teeth are narrow and contain smooth labial and lingual surfaces, and have noticeable lingual curvature. The anterior teeth contain a single, elongated, needle-like primary cusplet on the mesial and distal sides of the main cusp. The main cusp of the lateral tooth is narrow, thinner than the anterior teeth in labio-lingual thickness, and is angled distally. The lateral tooth contains a

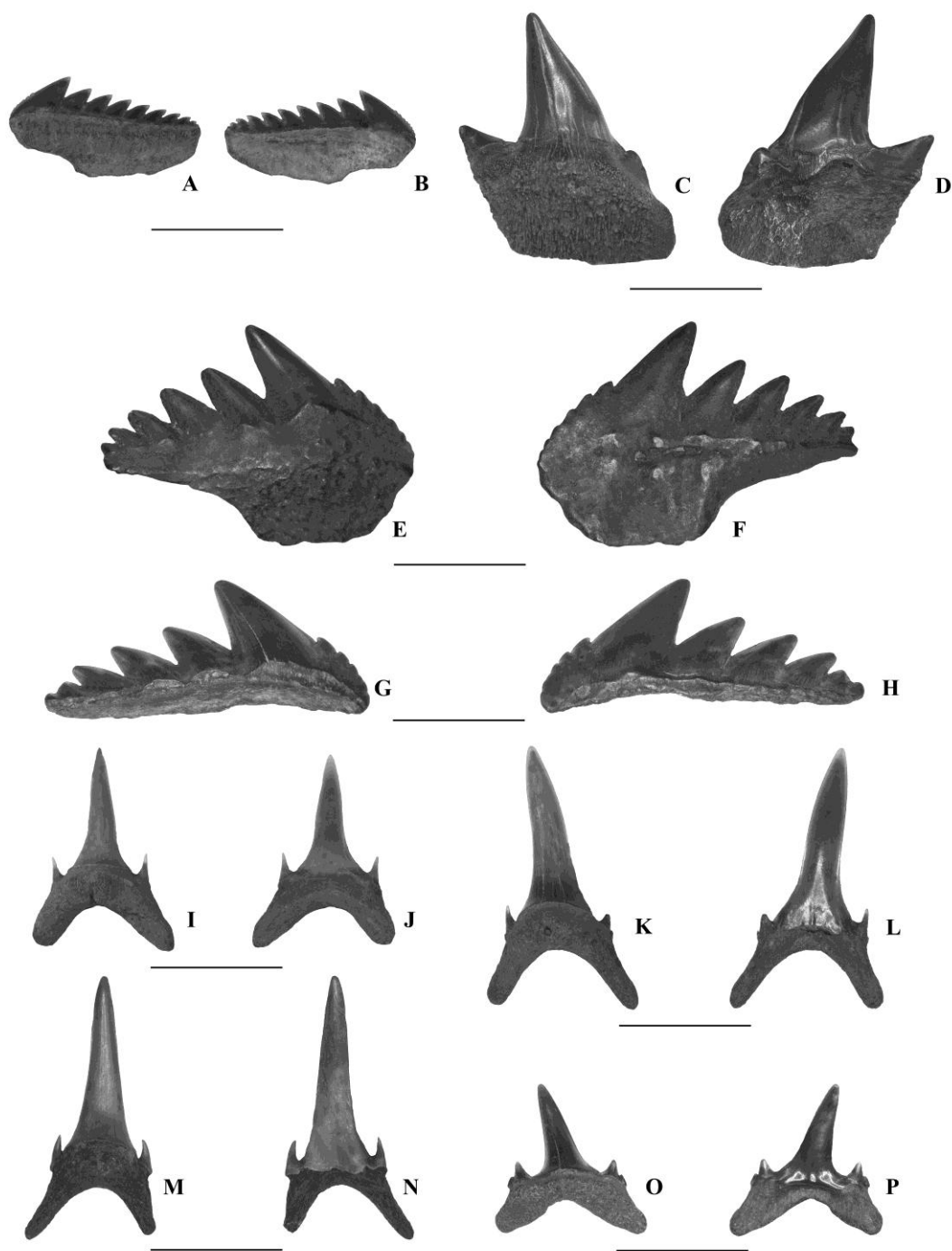


FIGURE 2. Hexanchiform and Lamniform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–B, *Hexanchus agassizi* Cappetta, 1976 (NJSM 23478); C–H, *Notorynchus primigenius* Agassiz, 1843 (NJSM 23479); I–P, *Carcharias* cf. *C. acutissima* (Agassiz, 1843) (NJSM 23480). Orientations: A, C, E, G, I, K, M, P equal lingual view. B, D, F, H, J, L, N, O equal labial view. Tooth positions: C–D, I–N equal anterior; A–B, E–H, O–P equal lateral. All scale bars equal 1 cm.

TABLE 1. Global occurrence of chondrichthyans found in the Farmingdale Assemblage based on region, subcontinent, and continent data (Solid circle equals Eocene and Hollow circle equals Miocene). Relative abundance of chondrichthyan teeth found in the Farmingdale Assemblage included in column 3 (Very Common (VC) >500 teeth; Common (C) between 100 and 500 teeth; Uncommon (UC) <100 teeth; and Rare (R) <20 teeth). References pertaining to location are as follows: Atlantic and Gulf Coastal Plain (Leidy, 1877; Eastman, 1904; Fowler, 1911; Chaffee, 1939; White, 1956; Case, 1967;1980;1981; Thurmond and Jones, 1981; Domning et al., 1982; Westgate, 1984; Dockery and Manning, 1986; Manning and Standhardt, 1986; Holman and Case, 1988; Westgate, 1989; Manning, 1990; Ward and Wiest, 1990; Breard, 1991; Gottfried, 1993; Case, 1994; Kent, 1994; Breard and Stringer, 1995; Gallagher et al., 1996; Chandler and Timmerman, 1995;1997; Hulbert et al., 1998; Purdy, 1998; Breard and Stringer, 1999; Case and Borodin, 2000a,b; Cunningham, 2000; Freile et al., 2001; Hulbert, 2001; Purdy et al., 2001; Parmley and Cicimurri, 2003; Chandler et al., 2006; Feldmann and Portell, 2007; Stidham and Janus, 2008; Cicimurri and Knight, 2009; Visaggi and Godfrey, 2010); Western North America (Minch et al., 1970; Applegate, 1986; Boessenecker et al., 2014); Caribbean (Itturalde-Vinent et al., 1996; Portell et al., 2008); Central and South America (Woodward, 1889; White, 1955; Longbottom, 1979; Gillette, 1984; Long, 1993; Cione and Reguero, 1995; Monsch, 1998; Sánchez-Villagra et al., 2000; Aguilera and Rodrigues de Aguilera, 2004; Fernandes dos Reis, 2005; Suarez et al., 2006; Cione et al., 2011; Otero et al., 2012; Pimiento, Gonzalez-Barba, Hendy, and others, 2013a; Pimiento, Gonzalez-Barba, Ehret, and others, 2013b); Europe (Radwanski, 1965; Cappetta, 1970;1973; Schultz, 1977; Bor, 1985; Kemp et al., 1990; Holec et al., 1995; Baut and Genault, 1999; Ward and Bonavia, 2001; Antunes and Balbino, 2003; Cappetta and Nolf, 2005; Adnet, 2006; Kocsis, 2007; Marsili et al., 2007; Adnet and Cappetta, 2008; Haye et al., 2008; Van den Eeckhaut and De Schutter, 2009; Reinecke and Wienrich, 2009; Gille et al., 2010; Hovestadt et al., 2010; Reinecke et al., 2011; Vialle et al., 2011; Ávila et al., 2012; Bor et al., 2012); Asia (Glikman, 1964; Sahni and Mehrotra, 1981; Case and West, 1991; Case, Udovichenko, and others, 1996; Tanaka et al., 2006; Adnet, Antoine, and others, 2007; Ralte et al., 2011); Africa (Cook et al., 2010; Underwood et al., 2011; Zalmout et al., 2012); Australia and Antarctica (Pledge, 1967; Kemp, 1978; 1991; Long, 1992; Kriwet, 2005).

Genus	Species	Relative Abundance	Continent/Subcontinent/Region							
			Atlantic & Gulf Coastal Plain	Western North America	Caribbean	Central & South America	Europe	Asia	Africa	Australia & Antarctica
<i>Hexanchus</i>	<i>agassizi</i>	R	●○			●	●	●○	●	●
<i>Notorynchus</i>	<i>primigenius</i>	UC	○				○			○
<i>Carcharias</i>	cf. <i>C. acutissima</i>	C	○			○	○			○
<i>Carcharias</i>	<i>cuspidata</i>	VC	○			○	○	○	○	○
<i>Striatolamia</i>	<i>macrota</i>	C	●	●		●	●			●
<i>Jaekelotodus</i>	<i>trigonalis</i>	UC	●				●	●		
<i>Cretolamna</i>	sp.	R	●						●	●
<i>Carcharoides</i>	<i>catticus</i>	R	○			○	○			○
<i>Isurus</i>	<i>oxyrinchus</i>	C	○	○	○	○	○			○
<i>Xiphodolamia</i>	<i>ensis</i>	R	●				●	●		
<i>Carcharocles</i>	<i>auriculatus</i>	UC	●	●			●	●	●	●
<i>Carcharocles</i>	<i>chubutensis</i>	UC	○		○	○	○		○	
<i>Hemipristis</i>	<i>serra</i>	UC	○		○	○	○	○	○	○
<i>Carcharhinus</i>	<i>priscus</i>	VC	○			○	○			
<i>Negaprion</i>	cf. <i>N. eurybathrodon</i>	C	○	○		○	○	○		
<i>Abdounia</i>	<i>recticonia</i>	UC	●				●	●		
<i>Galeocerdo</i>	<i>latidens</i>	UC	●				●	●	●	
<i>Galeocerdo</i>	<i>aduncus</i>	C	○	○		○	○	○		○
<i>Physogaleus</i>	<i>contortus</i>	C	○	○	○	○	○			
<i>Physogaleus</i>	<i>secundus</i>	UC	●				●	●	●	
<i>Sphyrna</i>	<i>zygaena</i>	UC	○	○	○	○	○		○	○
<i>Pristis</i>	sp.	R	●				●	●	●	●
<i>Myliobatis</i>	sp.	VC	●○	○		○	●○	●	●○	●○
<i>Rhinoptera</i>	sp.	C	●○			○	●○	●	●	

broad, more triangular primary cusplet and a stunted, secondary cusplet on both the mesial and distal tooth margin. The roots of anterior and lateral teeth are holaulacorhizous, with well-defined root lobes.

Remarks—The presence of elongated, needle-like primary cusplets and a smaller, more gracile morphology distinguishes teeth of *Carcharias* cf. *C. acutissima* from those of *Carcharias cuspidata* Agassiz, 1843 and *Striatolamia macrota* Agassiz, 1843 which also occur in the Farmingdale assemblage. With respect to *Carcharias* cf. *C. acutissima*, teeth of *C. cuspidata* and *S. macrota* are more robust and have reduced cusplets in anterior teeth and flattened cusplets in lateral teeth. Additionally, *S. macrota* teeth contain well-defined lingual striations and highly reduced cusplets in anterior teeth. Similar species not found in the Farmingdale assemblage include: *C. gustrowensis* (Winkler, 1875), *Odontaspis ferox* Risso, 1826, and *C. taurus* (Rafinesque, 1810). Teeth of *Carcharias* cf. *C. acutissima* can be distinguished from these species based on the lack of crown thickening near the crown base, the lack of two or more elongated, needle-like cusplets, and have a smaller overall size and root lobes that are not as divergent. Additionally, some researchers discuss the possibility that *C. acutissima* is synonymous with *C. taurus* (e.g., Antunes and Jonet, 1970; Kemp, 1991; Ward and Bonavia, 2001; Purdy et al., 2001; Antunes and Balbino, 2003; Reinecke et al., 2011; Cappetta, 2012; and Bor et al., 2012).

Carcharias cuspidata Agassiz, 1843
(Figure 3: A–L; Table 1)

Lamna cuspidata Agassiz, 1843 p.290 Pl. 37a, Figs. 43–50.

Material examined—Three anterior teeth and three lateral teeth: NJSM 23481.

Description—The crowns of anterior teeth are robust, erect, and contain smooth labial and lingual surfaces. Anterior teeth contain a short, reduced cusplet on both the mesial and distal sides of the main cusp. The crowns of lateral teeth are broad and labio-lingually compressed when compared to those of anterior teeth. The cusplets on lateral teeth are reduced and triangular to pectinate in shape. The roots of anterior and lateral teeth are holaulacorhizous with well-defined root lobes. The angle of root lobe divergence increases distally. Anterior tooth roots may display rounded protuberances near the midsection of the root lobes.

Lingual protuberances are present on the roots of anterior and lateral teeth.

Remarks—The presence of reduced primary cusplets on anterior teeth and triangular to rectangular cusplets on lateral teeth, lack of lingual striations, and a robust morphology in teeth of *C. cuspidata*, enable these teeth to be distinguished from *Carcharias* cf. *C. acutissima*, *Striatolamia macrota*, and *Jaekelotodus trigonalis* Jaekel, 1895 which also occur in the Farmingdale assemblage. Teeth of *C. cuspidata* are similar to those of extant *C. taurus* (Rafinesque, 1810) however, *C. cuspidata* anterior teeth have wider crowns and a more robust root morphology (e.g., Purdy et al., 2001). Additionally, teeth of *Hypotodus verticalis* (Agassiz, 1843) can be distinguished from *C. cuspidata* due to the presence of incomplete cutting edges and small, triangular side cusplets on anterior and lateral teeth (Cappetta, 2012). We follow Kent (1994) and Purdy et al. (2001) and assign the Farmingdale teeth to *C. cuspidata* based on the presence of erect and non-striated cusps, reduced and broad cusplets in lateral teeth, and robust roots that become more divergent in the distal direction. For additional discussion on the classification of *C. cuspidata* see: Kent (1994); Purdy et al. (2001); Suarez et al. (2006); Reinecke et al. (2011); and Cappetta (2012).

Genus *Striatolamia* Glickman, 1964
Striatolamia macrota Agassiz, 1843
(Figure 4: A–D; Table 1)

Lamna elegans Agassiz, 1843, p. 289. Pl. 35, figs. 1–7; Pl. 37a, figs. 58–59.

Material examined—One anterior tooth and one lateral tooth: NJSM 23482.

Description—The crown of the anterior tooth is elongated and narrow with a strongly striated lingual face and smooth labial face. Cutting edges are complete and the cusp is sigmoidal in profile. The anterior tooth has a single reduced cusplet on each shoulder. The root of the anterior tooth is holaulacorhizous and the mesial root lobe is commonly elongated. On the dorsal edge of the distal root lobe, a rounded protrusion is present. The crown of the lateral tooth is broad and triangular with a striated lingual face. The lateral tooth possesses wide, triangular to shovel-shaped cusplets. The root of the lateral tooth is holaulacorhizous. Lateral cusplets are highly reduced. A lingual protuberance containing a nutritive groove is present on all teeth.

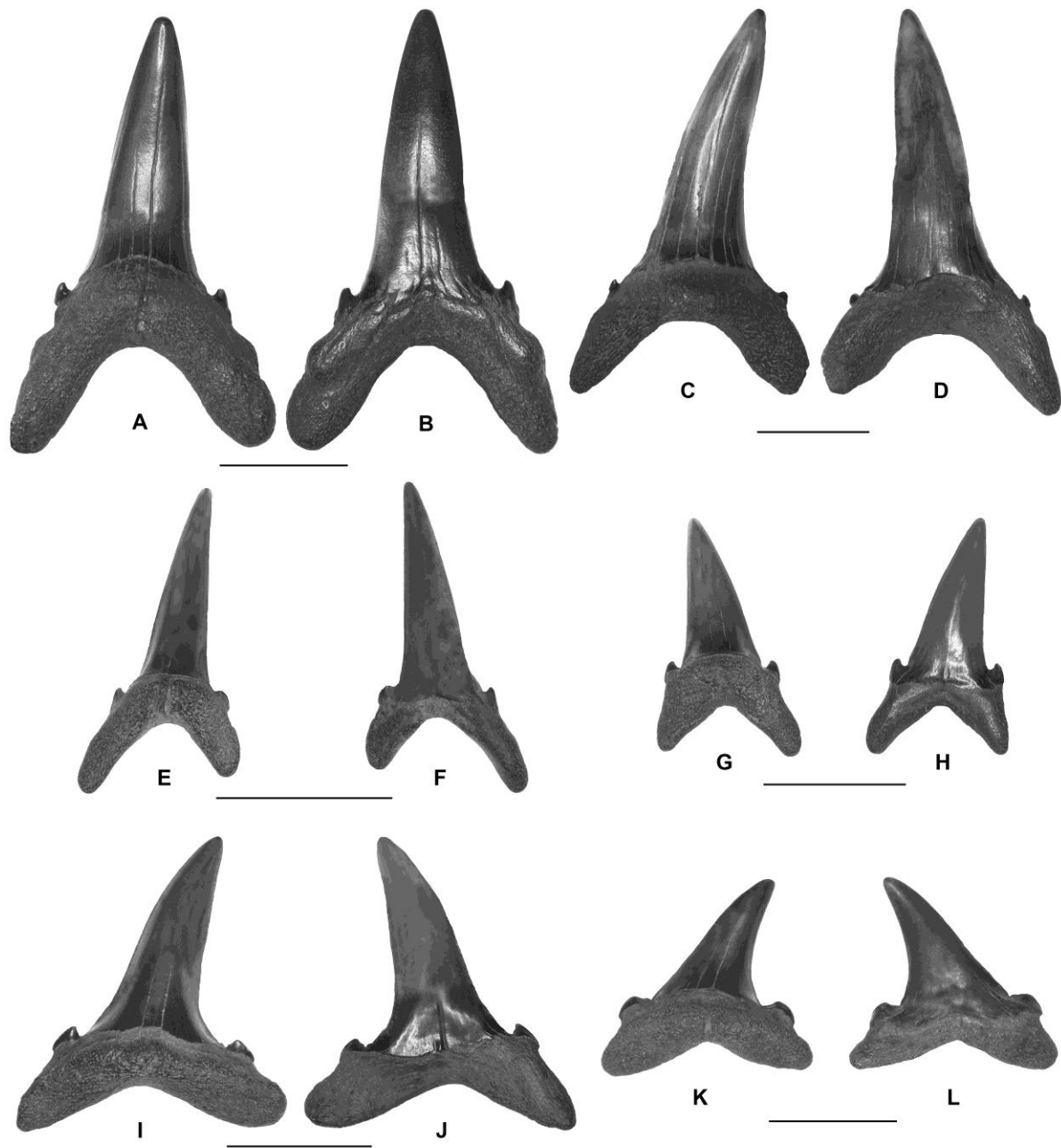


FIGURE 3. Lamniform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–L, *Carcharias cuspidata* Agassiz, 1843 (NJSM 23481); Orientations: A, C, E, G, I, K equal lingual view. B, D, F, H, J, L equal labial view. Tooth positions: A–F equal anterior, I–L equal lateral. All scale bars equal 1cm.

Remarks—Teeth of *S. macrota* from the Farmingdale assemblage have erect cusps that contain characteristic lingual striations that do not span the entire length of the crown, small, triangular cusplets on anterior teeth and shovel-shaped cusplets on lateral teeth. With respect to *S. macrota*, teeth of *S. striata* (Winkler, 1874) differ due to smaller overall tooth size

and lingual striations that span nearly the entire length of the crown. Morphologically, teeth of *S. macrota* are similar to those of *Scapanorhynchus* and *Carcharias* species. However, research by Cunningham (2000) suggested the tooth variation and morphology of *S. macrota* is comparable to that seen in *C. taurus* (Rafinesque, 1810). Due to the variability seen in teeth

of *C. taurus*, and their similarity to teeth of *S. macrotia*, we follow Ward and Wiest (1990), who synonymized *S. striata* with *S. macrotia* based on minor morphological differences and known complications related to ontogenetic variation (Nolf, 1988).

Genus *Jaekelotodus* Menner, 1928
Jaekelotodus trigonalis Jaekel, 1895
 (Figure 4: E–L; Table 1)

Jaekelotodus trigonalis Jaekel, 1895, p. 16–35. Pl. 2.

Material Examined—Three anterior teeth and one lateral tooth: NJSM 23483.

Description—The main cusp of the lateral and anterior teeth is broad, erect, smooth on the lingual and labial surface, and has a concave, V-shaped cavity on the labial tooth surface extending from the root to the tooth midsection. The lateral and anterior teeth have complete cutting edges that progress into broad, erect, triangular primary cusplets. Secondary cusplets may be present, but are smaller in size. The lateral tooth displays minor, irregular serrations near the base of the main cusp. The roots of anterior and lateral teeth are holaulacorhizous, labio-lingually thickened, and the angle of root-lobe divergence increases in the posterior direction. The labial root surface is convex and contains a nutritive groove with central foramina while the lingual root surface is concave.

Remarks—Teeth of *J. trigonalis* are much more robust and broad at the crown base and have a distinct V-shaped concavity on the labial root surface with respect to those of *S. macrotia* and *C. cuspidata* which also occur in the Farmingdale assemblage. *Brachycarcharias lerichei* (Casier, 1946) is a similar Eocene species that has teeth with triangular cusps and cusplets, faint lingual striations, and a more compressed form than those of *J. trigonalis* (Cappetta, 2012).

Family *Lamnidae* Müller and Henle, 1838
 Genus *Cretolamna* Glikman, 1958
Cretolamna sp.
 (Figure 4: M–P; Table 1)

Material Examined—One upper lateral tooth and one lower lateral tooth: NJSM 23484.

Description—The crown of the upper lateral tooth is triangular in shape, angled distally, and also has smooth lingual and labial surfaces. The crown of the lower lateral tooth is erect, triangular in shape, and has smooth lingual and labial surfaces. The cutting edges on both the anterior and lateral teeth are complete and lack serrations. Singular, broad,

triangular lateral cusplets are present on the mesial and distal tooth shoulders of both upper and lower lateral teeth. The root of the upper lateral tooth is holaulacorhizous, labio-lingually compressed, and forms a shallow and wide U-shaped concavity between the mesial and distal root lobes.

Remarks—Teeth of *Cretolamna* species from the Farmingdale assemblage are similar to the teeth of *C. appendiculata* (Agassiz, 1843) known from the Late Cretaceous. Cappetta (2012) noted the occurrence of *C. appendiculata* in the lower Eocene, however questioned the validity of this species having such a long stratigraphical range. For this reason, researchers have erected new species or refrained from species assignment of *Cretolamna* in the early and middle Cenozoic (e.g., Case, 1981; Case and Cappetta, 1990; Case, 1994; Cappetta, 2012). *Cretolamna* species teeth from the Farmingdale assemblage are also similar to those of another early and middle Cenozoic lamniform, *Otodus obliquus*. However, *O. obliquus* teeth contain roots that are more robust, have well-defined and rounded root lobes, and nutritive foramina that are not seen in *Cretolamna* species (Kent, 1994; Cappetta, 2012). For more discussion regarding the classification of *Cretolamna*, see Kent (1994); Shimada (2007); Cappetta (2012); and Siverson et al. (2013).

Genus *Carcharoides* Ameghino, 1901
Carcharoides catticus (Philippi, 1846)
 (Figure 5: A–D; Table 1)

Otodus catticus Philippi, 1846, p. 24. Pl. 2, figs 5–7.

Material Examined—One anterior tooth and one lateral tooth: NJSM 23485.

Description—The crown of the anterior tooth is narrow, straight, and has smooth lingual and labial surfaces. The cutting edge on the anterior tooth terminates before the base of the cusp. A broad, triangular cusplet is present on each shoulder and is bent lingually. The lateral tooth has a flat, triangular crown that is angled distally and contains a complete cutting edge. Cusplets on the lateral tooth are triangular and are separated from the main cusp by a distinct notch. The root is holaulacorhizous and the root lobes of the anterior tooth are short.

Remarks—Teeth of *C. catticus* from the Farmingdale assemblage are similar to those of *Brachycarcharias lerichei* (Casier, 1946), *C. totuserratus* (Ameghino, 1901), and *Triaenodon obesus*

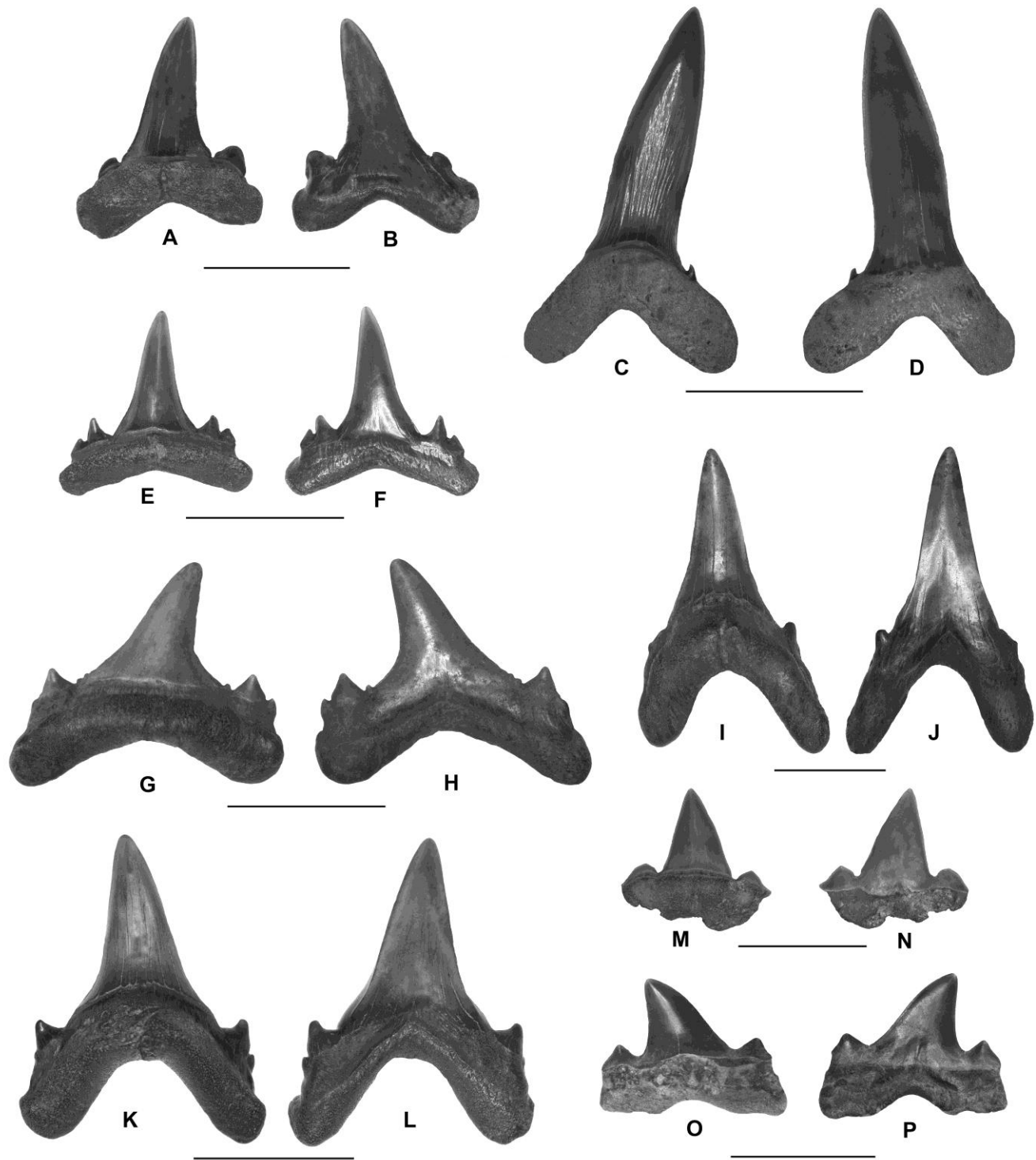


FIGURE 4. Lamniform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–D, *Striatolamia macrota* Agassiz, 1843 (NJSM 23482); E–L, *Jaekelotodus trigonalis* Jaekel, 1895 (NJSM 23483); M–P, *Cretolamna* sp. (NJSM 23484). Orientations: A, C, E, F, I, K, M, O equal lingual view. B, D, F, H, J, L, N, P equal labial view. Tooth positions: C–F, I–L equal anterior; A–B, G–H, M–P equal lateral. All scale bars equal 1 cm.

(Rüppell, 1837). *Carcharoides catticus* teeth described here have more erect cusps with single cusplets and less robust roots without nutritive grooves relative to *B. lerichei*. *Carcharoides totuserratus* teeth bear serrated cutting edges not seen in *C. catticus*. According to Cappetta (2012) teeth of *T. obsesus* may be confused with those of *C. totuserratus* due to similarities in size, cusp inclination, and cusplet morphology. Research recently conducted by Reinecke et al. (2011) and Bor et al. (2012) figure *C. catticus* teeth identical to those found in the Farmingdale assemblage.

Genus *Isurus* Rafinesque, 1810
Isurus oxyrinchus Rafinesque, 1810
 (Figure 5: E–O; Table 1)

Isurus oxyrinchus Rafinesque, 1810, p. 12. Pl. 13, fig. 1.

Material Examined—Two anterior teeth, two lateral teeth, and one posterior tooth: NJSM 23486.

Description—The crowns of the anterior teeth are elongated, robust, angled distally, and have smooth labial and lingual surfaces. The crowns on the lateral teeth are broad, labio-lingually compressed, and have a more erect and triangular shape. The crown of the posterior tooth is broad and displays a more acute distal inclination than the crowns of the lateral teeth. The cutting edges are complete and no lateral cusplets or serrations are present. The roots of anterior, lateral, and posterior teeth are holaulacorhizous and lack nutritive grooves. However, the roots of anterior teeth are more lobate and robust than the roots of lateral and posterior teeth which are labio-lingually compressed and may have flat, angled basal surfaces.

Remarks—Teeth of *I. oxyrinchus* from the Farmingdale assemblage are distinct despite mild heterodonty. These teeth can be distinguished from those belonging to *Cosmopolitodus hastalis* (Agassiz, 1838) by the lack of broad, triangular, blade-like anterior teeth and more robust lower anterior teeth (Purdy et al., 2001). *Macrorhizodus praecursor* (Leriche, 1905) teeth differ from those of *I. oxyrinchus* because anterior teeth are strongly arched lingually with weakly separated root lobes and juvenile teeth frequently contain cusplets (Cappetta, 2012). According to Kent (1994) and Cione and Reguero (1995) lateral teeth of *M. praecursor* are not ideal for differentiating among species as they are essentially indistinguishable from those of similar isurids.

Additionally, *I. oxyrinchus* from the Farmingdale assemblage is similar to *I. retroflexus*

(Agassiz, 1838) and identical to teeth previously identified as *I. desori* Agassiz, 1843. *Isurus desori* Agassiz, 1843, has been synonymized with *I. oxyrinchus* after analyses utilizing composite dentitions and modern tooth sets proved the fossil and modern teeth to be identical (e.g., Purdy et al., 2001; Bor et al., 2012). *Isurus oxyrinchus* differs from *I. retroflexus* by lacking callosities near the medial and distal crown base that extend to the apical part of the root lobes and labio-lingually thickened crowns in all tooth positions (Bor et al., 2012). We follow Purdy et al. (2001) and Bor et al. (2012) and assign the Farmingdale *Isurus* teeth to *I. oxyrinchus* based on their comparative analyses with tooth sets from extinct and extant isurids.

Genus *Xiphodolamia* Leidy, 1877
Xiphodolamia ensis Leidy, 1877
 (Figure 5: P–U; Table 1)

Xiphodolamia ensis Leidy, 1877, p. 252. Pl. 34, figs. 25–30.

Material examined—One anterior tooth and one lateral tooth: NJSM 23487.

Description—The crown of the anterior tooth is elongated, mesio-distally compressed and has a sigmoidal profile. The labial cutting edge is complete and the lingual cutting edge is restricted to the apical portion of the cusp. The crown of the lateral tooth is labio-lingually compressed, triangular, and angled distally. A short distal heel is present and cutting edges are complete. The root of the lateral tooth is flat and aulacorhizous. The root is thickest near the base of the cusp. Small furrows and foramina are aligned perpendicular to the root base.

Remarks—Teeth of *X. ensis* from the Farmingdale assemblage are very distinct and display a high degree of heterodonty. The presence of a distal cutting edge only on the upper part of the cusp and a complete mesial cutting edge enables the teeth of *X. ensis* to be differentiated from symphyseal teeth of *Carcharias* species. Additionally, rotation of the labial cutting edge on *X. ensis* anterior teeth enables proper tooth orientation to be determined (Cappetta, 2012). Anterior and lateral teeth of *X. ensis* described here are also similar to *X. eocaena* (Woodward, 1889) and *X. serrata* Adnet, Hosseinzadeh, and others, 2009. Cappetta (2012) suggests that *X. eocaena* may be a junior synonym of *X. ensis* and that *X. serrata* is clearly a distinct species based on the presence of serrated cutting edges.

Genus *Carcharocles* Jordan and Hannibal, 1923

Carcharocles auriculatus Blainville, 1818

(Figure 6: A–D; Table 1)

Squalus auriculatus Blainville, 1818, p. 384.

Material Examined—One anterior tooth and one lateral tooth: NJSM 23488.

Description—The main cusps of the anterior and lateral teeth are robust with convex lingual surfaces, nearly flat labial surfaces, and have coarsely serrated tooth margins. Lateral teeth are angled distally and have a claw-like appearance. Lateral cusplets are present in all tooth positions and are triangular in shape, coarsely serrated, and separated from the main cusp by a distinct notch in the tooth enamel. The root is not preserved on the anterior tooth however the lateral tooth contains an incomplete root; indicating that the root is robust and holaulacorhizous.

Remarks—The presence of coarse serrations, triangular lateral cusplets, and a larger overall tooth size distinguishes *C. auriculatus* from *C. chubutensis* teeth which also occur in the Farmingdale assemblage. *Carcharocles auriculatus* teeth are similar to *C. sokolovi* (Jaekel, 1895) and *C. angustidens* (Agassiz, 1843) which have also been described from the Eocene and Oligocene. *Carcharocles sokolovi* is distinct from *C. auriculatus* based on the presence of fine, regular serrations on the main cusp, coarse serrations on cusplets, and an overall larger tooth size (e.g., Case and Cappetta, 1990; Adnet, Cappetta, and Tabuce, 2010; Cappetta, 2012). *Carcharocles angustidens* serrations are smaller and lateral cusplets are more reduced relative to those seen in *C. auriculatus*. *Carcharocles chubutensis* Ameghino, 1906 differs from both *C. auriculatus* and *C. angustidens* due to the presence of smaller, regularly spaced serrations and reduced lateral cusplets (Kent, 1994; Purdy et al., 2001; Renz, 2002; Parmley and Cicimurri, 2003). Additional discussions regarding the classification of *C. auriculatus* and similar related taxa can be found in Purdy et al. (2001); Nyberg et al. (2006); Underwood et al. (2011); Ehret et al. (2012); and Cappetta (2012).

Carcharocles chubutensis Ameghino, 1906

(Figure 6: E–H; Table 1)

Carcharodon chubutensis Ameghino, 1906, p. 183. Fig. 49.

Material Examined—One anterior tooth and one lateral tooth: NJSM 23489.

Description—The main cusps of the anterior and lateral teeth are broad, have convex lingual surfaces and nearly flat labial surfaces, and have regularly

serrated tooth margins. The apices of the anterior and lateral teeth are curved labially. Lateral teeth are angled distally and have a shorter total height than anterior teeth. Lateral cusplets are present in all tooth positions and are triangular in shape, finely serrated, and separated from the main cusp serrations by a notch. The lateral tooth root is holaulacorhizous with a slightly convex lingual surface and slightly concave on the labial surface. No nutritive groove is present.

Remarks—The presence of regular serrations and faint, triangular to sub-rounded lateral cusplets distinguishes *C. chubutensis* from *C. auriculatus* teeth which also occur in the Farmingdale assemblage. *Carcharocles chubutensis* teeth are similar to *C. angustidens* and *C. megalodon* (Agassiz, 1843) which have also been described from the Oligocene and Miocene. *Carcharocles angustidens* teeth are distinct and have a narrower morphology with more well-developed lateral cusplets than those of *C. chubutensis* (e.g., Case and Cappetta, 1990; Kent, 1994; Applegate and Espinosa-Arrubarrena, 1996; Gottfried and Fordyce, 2001; Hulbert, 2001; Purdy et al., 2001; Pimiento, Gonzalez-Barba, Hendy, and others, 2013a; Pimiento, Gonzalez-Barba, Ehret, and others, 2013b). Additionally, the retention of lateral cusplets and a more labio-lingually compressed tooth morphology distinguishes *C. chubutensis* from *C. megalodon* (Kent, 1994). Additional discussions regarding the classification of *C. chubutensis* and similar related taxa can be found in Kent (1994); Hulbert (2001); Purdy et al. (2001); Nyberg et al. (2006); Underwood et al. (2011); Ehret et al. (2012); Cappetta (2012); Pimiento, Gonzalez-Barba, Hendy, and others (2013a); and Pimiento, Gonzalez-Barba, Ehret, and others (2013b).

Order Carcharhiniformes Compagno, 1977

Family Carcharhinidae Jordan and Evermann, 1896

Genus *Hemipristis* Agassiz, 1843

Hemipristis serra Agassiz, 1843

(Figure 7: A–H; Table 1)

Hemipristis serra Agassiz, 1843, p. 237. Pl. 27, figs 18–30.

Material Examined—One upper anterior tooth, two lateral teeth, and one lower anterior tooth: NJSM 23490.

Description—The crowns of upper anterior and lateral teeth are triangular, coarsely-serrated and angled distally. The mesial cutting edges are convex near the cusp apex. Serrations increase in size toward the cusp apex but terminate slightly below the apex. Serrations on the concave, distal margin are larger than those on the mesial margin. The roots of upper anterior and

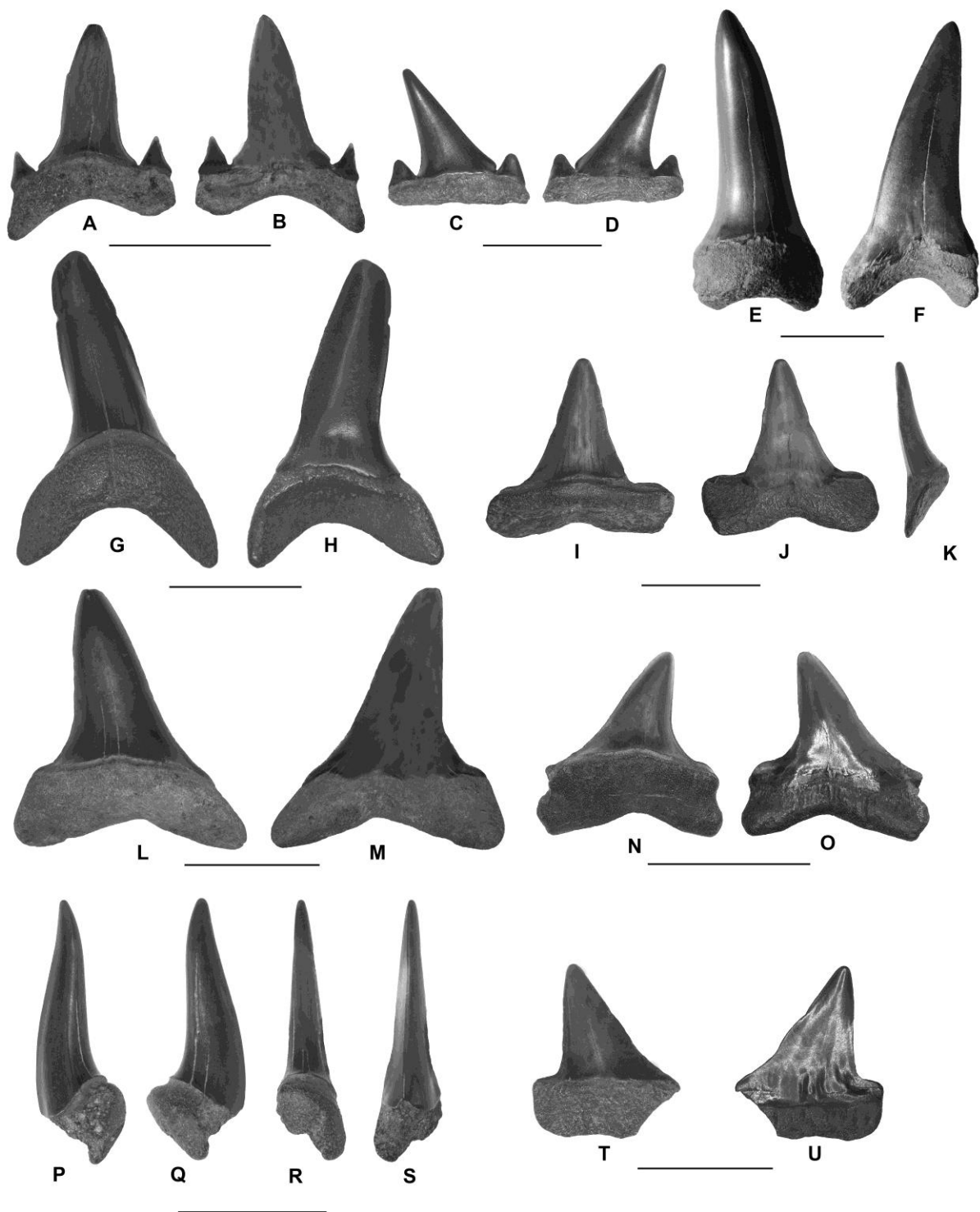


FIGURE 5. Lamniform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–D, *Carcharoides catticus* (Phillips, 1846) (NJSN 23485); E–O, *Isurus oxyrinchus* Rafinesque, 1810 (NJSN 23486); P–U, *Xiphodolamia ensis* Leidy, 1877 (NJSN 23487). Orientations: A, C, E, G, I, L, N, R, T equal lingual view. B, D, F, H, J, M, O, S, U equal labial view. K, P, Q equal lateral. Tooth positions: A–B, E–F; I–K, P–S equal anterior; C–D, G–H; L–M, T–U equal lateral; N–O equal posterior. All scale bars equal 1cm.

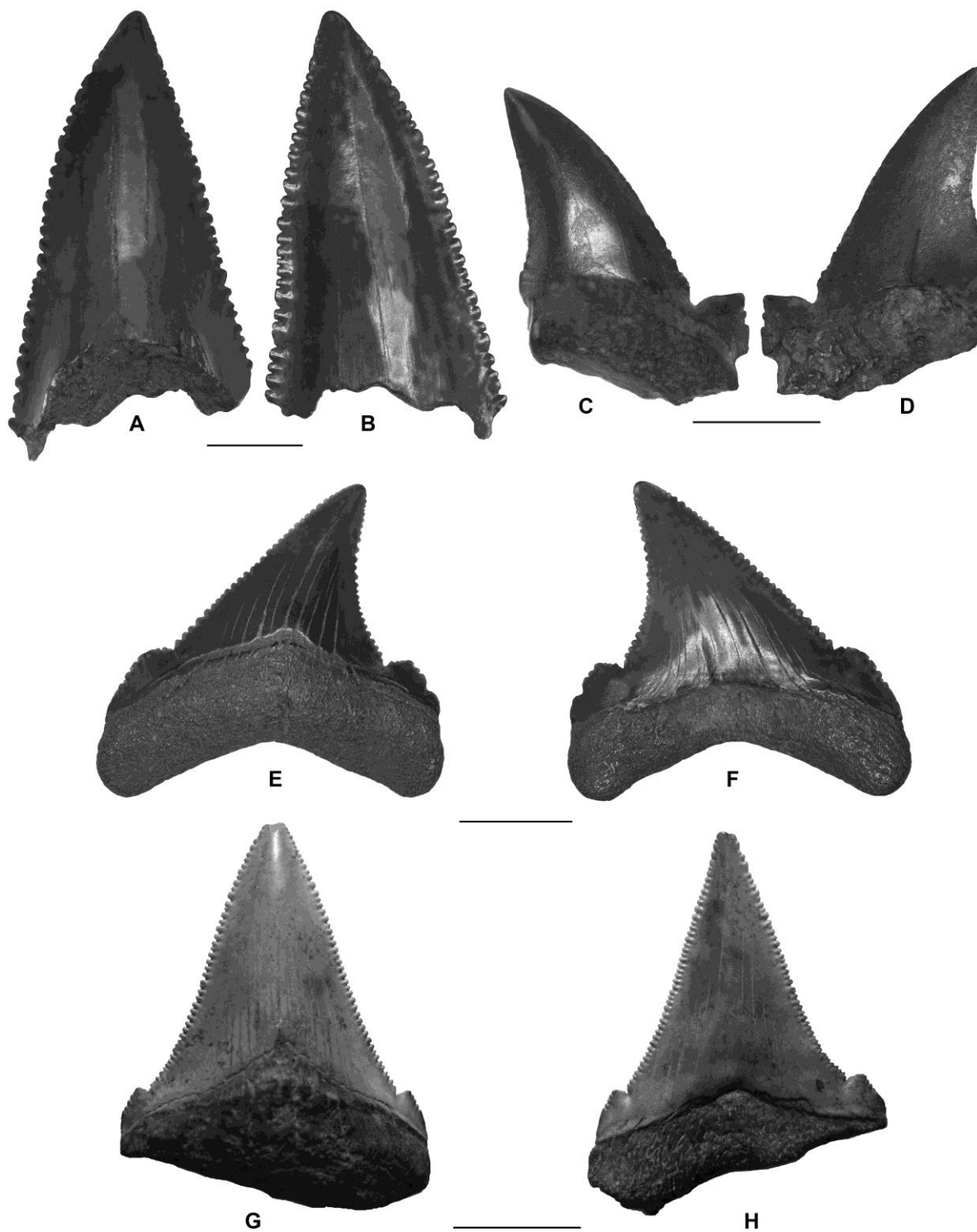


FIGURE 6. Lamniform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–D, *Carcharocles auriculatus* Blainville, 1818 (NJSM 23488); E–H, *Carcharocles chubutensis* Ameghino, 1906 (NJSM 23489). Orientations: A, C, E, G equal lingual view. B, D, F, H equal labial view. Tooth positions: A–B, G–H equal anterior; C–F equal lateral. All scale bars equal 1cm.

lateral teeth are holaulacorhizous, tall, and have well-developed lingual protuberances containing nutritive grooves. The mesial root branches are flatter and taper to a point whereas the distal branches have rounded lobes. The crown of the lower anterior tooth is long, robust, and lingually angled with a sigmoidal profile. The cutting edge on the lower tooth is limited to the apical portion of the cusp. A short, triangular lateral cusplet is present on the distal and mesial tooth shoulder. The root of the lower anterior tooth is holaulacorhizous, mesio-distally compressed, and contains a robust lingual protuberance.

Remarks—Teeth of *H. serra* from the Farmingdale assemblage can be distinguished from the Eocene species, *H. curvatus* Dames, 1883 due to the presence of serrations, that increase in size towards the cusp apex, on both the mesial and distal tooth margins on upper teeth. Teeth of *H. serra* display strong dignathic heterodonty allowing distinction between upper and lower jaw positions. In general, upper teeth of *H. serra* are broad, coarsely serrated, and distally inclined, whereas lower teeth are narrow and erect, incompletely serrated, and have a large lingual protuberance on the root.

Genus *Carcharhinus* Blainville, 1816
Carcharhinus priscus (Agassiz, 1843)
 (Figure 7: I–R; Table 1)

Sphyrna prisca Agassiz, 1843, p. 234. Pl. 26a, figs. 44, 47, ?35–43, ?45, ?48–50.

Material Examined—Two anterior teeth, three lateral teeth, and ten additional teeth: NJSM 23491.

Description—The crowns of anterior teeth are erect, cutting edges may be complete or incomplete, and tooth shoulders are weakly serrated. The labial tooth surfaces are nearly flat while those of lingual surface are convex. Both the labial and lingual tooth surfaces are smooth. The crowns of lateral teeth are angled distally, are wider, and more triangular in shape than those of anterior teeth. The crowns of some anterior teeth may only have serrations on the tooth shoulders. Serrations on the main cusp, decrease in size towards the tooth apex. The labial tooth surfaces are nearly flat, lingual tooth surfaces are convex, although both are smooth. A greater amount of tooth enamel is exposed on the lingual face of anterior and lateral teeth. The roots of anterior and lateral teeth are holaulacorhizous and contain a shallow nutritive groove on the lingual surface. The roots of anterior teeth have nearly flat basal surfaces while those of lateral teeth are wider, thinner, and have a more concave separation between root lobes.

Remarks—The presence of serrations on the main cusps that progress onto the tooth shoulders without being separated by a distinct notch distinguishes *C. priscus* from *Negaprion* cf. *N. eurybathrodon* which also occur in the Farmingdale assemblage. Multiple Cenozoic *Carcharhinus* species (e.g., *C. gibbesi* (Woodward, 1889); *C. obscurus* (Le Sueur, 1818); *C. brachyurus* (Günther, 1870); *C. egertoni* (Agassiz, 1843)) are similar to *C. priscus* described here. Our assignment of the Farmingdale teeth to *C. priscus* is based on the recovery of numerous specimens from multiple positions within the upper and lower jaws. Some distinct features seen in the Farmingdale species include: partially serrated tooth crowns that are continuous with the tooth heels, weakly serrated tooth heels, thin roots with widely spaced root lobes, and the presence of a small nutritive groove on the lingual root surface. Additional comparison between *C. priscus* and similar, related Cenozoic carcharhinids can be found in Garrick (1982); Compagno (1988); Naylor and Marcus (1994); Grace (2001); Purdy et al. (2001); Kocsis (2007); Marsili (2007); Cicimurri and Knight (2009); Cappetta (2012); Bor et al. (2012).

Genus *Negaprion* Whitley, 1940
Negaprion cf. *N. eurybathrodon* (Blake, 1862)
 (Figure 7: S–T and 7: W–X; Table 1)

Lamna eurybathrodon (Blake, 1862) p. 316.

Material Examined—One anterior tooth and one lateral tooth: NJSM 23492.

Description—The crown of the anterior tooth is erect, has complete, smooth cutting edges, and the tooth heels are not serrated and have very little enamel present. The crown of the lateral tooth is erect, has a complete cutting edge, and weakly serrated tooth heels that are separated from the main cusp by notches. The roots of anterior and lateral teeth are holaulacorhizous and contain a small lingual protuberance with a moderately incised nutritive groove. Additionally, the roots of the anterior teeth are straight to slightly arched.

Remarks—The presence of partially serrated tooth shoulders and smooth main cusps distinguishes *Negaprion* cf. *N. eurybathrodon* from *C. priscus* teeth which also occur in the Farmingdale assemblage. *N. eurybathrodon* teeth differ also from those of *N. brevirostris* (Poey, 1868) because anterior teeth display shorter crowns and do not have well-developed, partially serrated tooth shoulders. The teeth described here are assigned to *Negaprion* cf. *N. eurybathrodon* as described by Parmley and Cicimurri (2003) and Cappetta (2012). Additional discussions regarding the

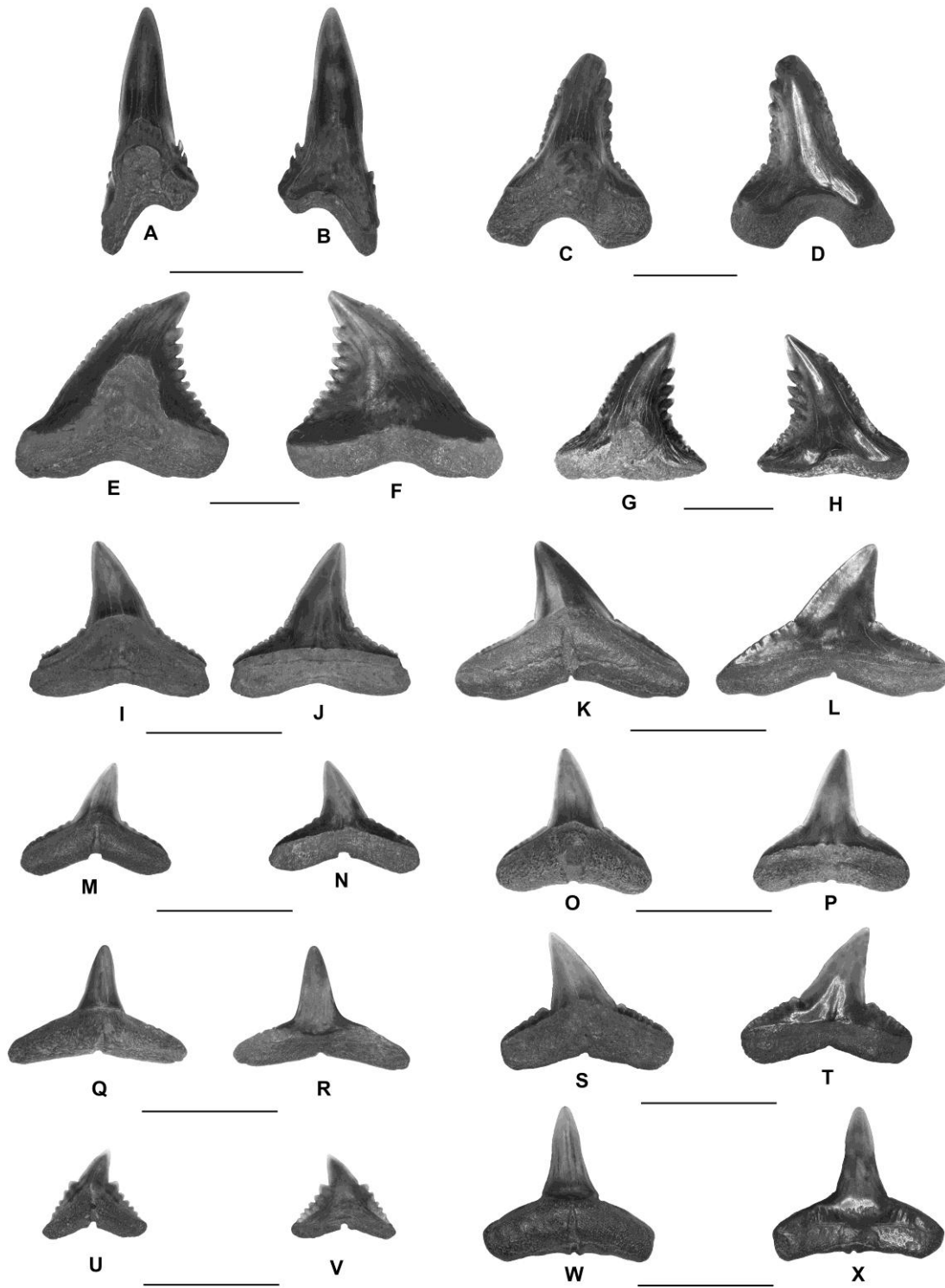


FIGURE 7. Carcharhiniiform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–H, *Hemipristis serra* Agassiz, 1843 (NJSM 23490); I–R, *Carcharhinus priscus* (Agassiz, 1843) (NJSM 23491); S–T; W–X, *Negaprion* cf. *N. eurybathrodon* (Blake, 1862) (NJSM 23492); U–V, *Abdounia recticonia* (Winkler, 1874) (NJSM 23493). Orientations: A, C, E, G, I, K, M, O, Q, S, U, W equal lingual view. B, D, F, H, J, L, N, P, R, T, V, X equal labial view. Tooth positions: A–D, O–R, W–X equal anterior; E–N, S–V equal lateral. Scale bar in U–V equal 0.5cm. All remaining scale bars equal 1cm.

classification of *N. eurybathrodon* can be found in White, 1955; Antunes and Jonet (1970); Longbottom, 1979; Holec et al. (1995); Purdy et al. (2001); Ward and Bonavia (2001); Kocsis (2007); Bor et al. (2012).

Genus *Abdounia* Cappetta, 1980
Abdounia recticon (Winkler, 1874)
 (Figure 7: U–V; Table 1)

Abdounia recticonus Winkler, 1874, p. 295–304. Pl. 7.

Material Examined—One lateral tooth: NJSM 23493.

Description—The crowns of anterior and lateral teeth are smooth with nearly flat labial faces and slightly convex lingual faces. A complete cutting edge is present and up to three coarse, triangular cusplets can be seen on the mesial and distal shoulders of anterior teeth and up to two cusplets can be seen on the lateral tooth. The cusplets are continuous with the main cusp and are not separated by distinct distal and mesial notches on the tooth shoulder. The crown of the lateral tooth is angled distally whereas the crown of the anterior tooth is relatively straight. The root of the anterior tooth is thin, holaulacorhizous, transversely extended, and contains a deep nutritive groove while the root base of lateral teeth is similar but slightly thicker. On both anterior and lateral teeth, the basal edge of the labial and lingual root surface is slightly concave.

Remarks—The presence of erect main cusps, paired, triangular cusplets and the small overall tooth size of *A. recticon*, enable these teeth to be distinguished from all other Farmingdale chondrichthyans. The anterior teeth of *A. beaugei* (Arambourg, 1935), are similar to those of *A. recticon* however, have two or fewer cusplets (Kent, 1994; Cappetta, 2012).

Genus *Galeocerdo* Müller and Henle, 1837
Galeocerdo latidens Agassiz, 1843
 (Figure 8: A–B; Table 1)

Galeocerdo latidens Agassiz, 1843, p. 231. Pl. 26, figs. 22–23.

Material Examined—One lateral tooth: NJSM 23494.

Description—The crown of the lateral tooth is smooth with a flat labial surface, slightly convex lingual surface, and has coarse serrations on the distal heel. Compound serrations are not present. The cusp is angled distally and the distal tooth margin contains a

well-developed, serrated shoulder. Serrations on the distal margin are coarsest near the tooth shoulder and do not extend to the cusp apex. The mesial tooth margin contains approximately equal-sized serrations that are present from the base of the enamel to the middle of the tooth. The root of the lateral tooth is holaulacorhizous, contains a well-defined nutritive groove on the lingual surface, and the basal, lingual root surface is slightly concave. The root is more exposed on the lingual surface.

Remarks—The presence of coarse serrations on the distal heel, equally-sized serrations on the lower mesial tooth margin, and a thin root with a well-defined nutritive groove on the lingual root surface distinguishes teeth of *G. latidens* from those of *G. aduncus* Agassiz, 1843 and *P. contortus* Gibbes, 1849 which also occur in the Farmingdale assemblage. *Galeocerdo latidens* is similar to *G. eaglesomei* (White, 1955) and *G. alabamensis* Leriche, 1942 also known from the Eocene. However, teeth of *G. eaglesomei* differ from those of *G. latidens* due to the presence of finer serrations on the distal margin, a distinct distal notch, and a greater overall tooth height and thickness. Teeth of *G. latidens* also differ from those of *G. alabamensis* because they have a lesser overall tooth height and do not contain compound serrations on the distal heel (e.g., Parmley and Cicimurri 2003). *Physogaleus latus* (Storms, 1894) teeth as documented from the early Miocene of Europe are also similar to those of *G. latidens* but differ due to more robust roots with main cusps that are more erect, sigmoidal, and only smooth or weakly serrated near the base (Bor et al., 2012).

Galeocerdo aduncus Agassiz, 1843
 (Figure 8: C–D; Table 1)

Galeus aduncus Agassiz, 1843, p. 231. Pl. 26, figs. 24, 25–28.

Material Examined—One lateral tooth and three additional teeth: NJSM 23495.

Description—The crown of the lateral tooth is smooth with a flat labial surface and slightly convex lingual surface. The cusp is angled distally and a distinct distal notch separates the main cusp from the distal heel. The distal heel contains well-developed, coarse serrations which decrease in size towards the cusp apex however, compound serrations are not present. The mesial tooth margin contains fine serrations that are present from the base of the enamel to the cusp apex. The root of the lateral tooth is holaulacorhizous, thin, and contains a short, shallow nutritive groove on the lingual surface. The basal, lingual root surface is

slightly concave and the root is more exposed on the lingual surface.

Remarks—Teeth of *G. aduncus* can be distinguished from other chondrichthyan teeth in the Farmingdale assemblage including *G. latidens*, *P. contortus*, and *P. secundus* due to the presence of coarsely serrated distal heels, finely serrated mesial and apical tooth margins, lack of sigmoidal crown profiles, and thin roots lacking lingual protuberances with small, shallow nutritive grooves (Cappetta, 2012; Bor et al., 2012). Teeth of *G. aduncus* also differ from those of the Eocene species *G. eaglesomei* and *G. alabamensis* in their lack of robust roots, tall cusps, coarse serrations on the mesial tooth edge, and compound serrations.

Genus *Physogaleus* Cappetta, 1980
Physogaleus contortus Gibbes, 1849
 (Figure 8: E–H; Table 1)

Galeocерdo contortus Gibbes, 1849, p. 193. Pl. 25, figs. 71–74.

Material Examined—One anterior tooth, one lateral tooth, and two additional teeth: NJSM 23496.

Description—The crown of the lateral tooth is smooth with a flat labial surface and convex lingual surface. The cusp is angled distally and becomes more acute further from the symphysis, is dorso-ventrally elongated, and has a sigmoidal profile. The distal tooth margins contain a weakly developed distal notch and serrated shoulder. Serrations on the distal tooth shoulder are coarse while those on the apical and mesial tooth margins are fine however, compound serrations are not present. The roots of the anterior and lateral teeth are holaulacorhizous and contain nutritive grooves in a robust lingual protuberance. The angle of root lobe divergence is more acute in the anterior tooth root although, the roots are more exposed on the lingual surface in both tooth positions.

Remarks—Teeth of *P. contortus* can be distinguished from other chondrichthyan teeth in the Farmingdale assemblage including *G. latidens*, *G. aduncus*, and *P. secundus* due to the presence of elongated cusps with sigmoidal profiles, finely serrated tooth margins except on the distal heels, and robust roots bearing lingual protuberances with nutritive grooves. Recent analyses of these teeth suggest that this species should be placed in the genus *Physogaleus* rather than *Galeocерdo* based on shared characteristics including robust roots, narrow, erect, and sigmoidal cusps, and finely serrated tooth margins (e.g., Ward and Bonavia, 2001; Reinecke et al., 2011; Cappetta, 2012; Bor et al., 2012). We follow the revised taxonomy of Cappetta (2012) and assign the Farmingdale teeth to *P. contortus*

(Gibbes, 1849) due to similarities between these teeth and those of species assigned to the genus *Physogaleus*.

Physogaleus secundus (Winkler, 1876)
 (Figure 8: I–J; Table 1)

Trigonodus secundus Winkler, 1876, p. 16–48. Pl. 2, figs. A–F.

Material examined—One lower lateral tooth: NJSM 23497.

Description—The crown of the lower lateral tooth is thick, mesio-distally compressed, angled distally, and sigmoidal in profile. The mesial and distal edges of the main cusp are smooth. The base of the mesial cutting edge may contain small serrations and the base of the distal cutting edge that extends onto the tooth shoulder, contains two or more coarse, triangular serrations. The lingual and labial tooth surfaces are convex and the labial surface slightly overhangs the root. The root is holaulacorhizous, thick, and contains a large lingual protuberance with a deep nutritive groove. The basal root surface is nearly flat and has a rectilinear appearance.

Remarks—The presence of a large lingual protuberance, partially serrated crown and distal shoulder, and convex and sigmoidal main cusps distinguishes the teeth of *P. secundus* from those of *G. latidens*, *G. aduncus*, and *P. contortus* which also occur in the Farmingdale assemblage. Teeth of *P. latus* (Storms, 1894) are distinct from those of *P. secundus* and have cusps with a greater distal inclination, weakly serrated or smooth mesial tooth edges, and thinner roots. *Physogaleus secundus* teeth also differ from *P. hemmooriensis* Reinecke and Hodemakers, 2006, due to their less erect main cusp and more robust roots. Additional discussions regarding the classification of *P. secundus* can be found in Purdy et al. (2001) and Cappetta (1980; 2012).

Genus *Sphyrna* Rafinesque, 1810
Sphyrna Zygaena (Linnaeus, 1758)
 (Figure 8: K–L; Table 1)

Squalus zygaena Linnaeus, 1758 Ed. X., 1: 824 p.

Material Examined—One lateral tooth and one additional tooth: NJSM 23498.

Description—The crown of the lateral tooth is smooth, labio-lingually flattened, and contains a complete cutting edge. The labial surface is nearly flat and the lingual surface is slightly convex. The cusp is angled distally and is separated from the distal heel by a notch. The root is holaulacorhizous, thin, and contains a deep nutritive groove.

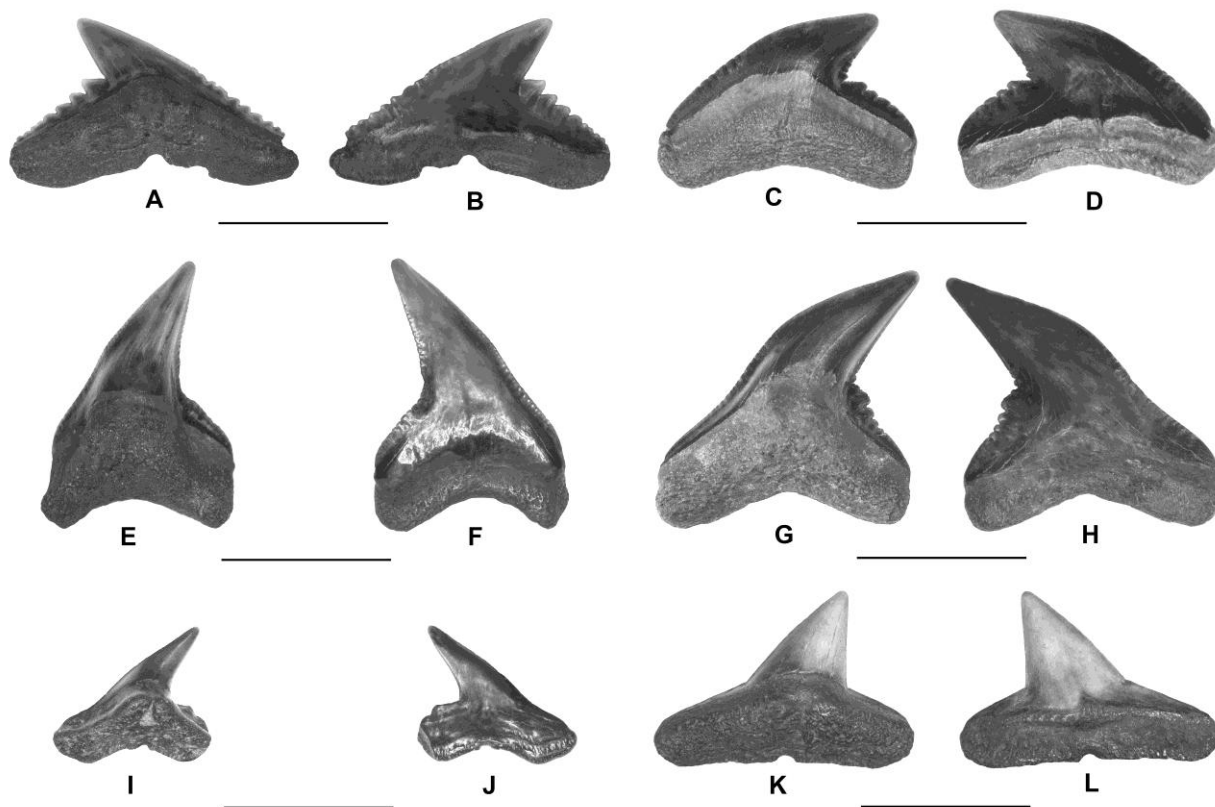


FIGURE 8. Carcharhiniiform teeth from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–B, *Galeocerdo latidens* Agassiz, 1843 (NJSM 23494); C–D, *Galeocerdo aduncus* Agassiz, 1843 (NJSM 23495); E–H, *Physogaleus contortus* Gibbs, 1849 (NJSM 23496); I–J, *Physogaleus secundus* (Winkler, 1876) (NJSM 23497); K–L, *Sphyrna zygaena* (Linnaeus, 1758) (NJSM 23498). Orientations: A, C, E, G, I, K equal lingual view. B, D, F, H, J, L equal labial view. Tooth positions: E–F equal anterior; A–D, G–L equal lateral. All scale bars equal 1cm.

Remarks—The presence of smooth and erect cusps with distinct distal heels distinguishes teeth of *S. zygaena* from those of *C. priscus* and *Negaprion* cf. *N. eurymathrodon* which also occur in the Farmingdale assemblage. Studies on sphyrids document little to no ontogenetic heterodonty which allows for differentiating between species such as *S. media* (Springer, 1940) which has smaller teeth with gracile cusps, *S. integra* (Probst, 1878) which has teeth with low distal heels, *S. lewinii* (Griffith and Smith, 1834) which has teeth with gracile cusps and thin roots, *S. arambourgi* Cappetta, 1970, that has teeth with a concave mesial margin and slender cusp, and *S. mokarran* (Rüppell, 1837) which has serrated teeth (e.g., Kent, 1994; Purdy et al., 2001; Parmley and Cicimurri, 2003; Cappetta, 2012; Bor et al., 2012). *Sphyrna zygaena* teeth are also similar to those of

Rhizoprionodon species but have more erect and blunt cusps, less concave mesial cutting edges, and thicker roots. We follow Purdy et al. (2001) and Cappetta (2012) and assign the Farmingdale specimens to *S. zygaena* based on the presence of non-serrated cusps, distinct distal heels, and a labio-lingually compressed structure.

Suborder Pristioidei Cappetta, 1980
Family Pristidae Bonaparte, 1838
Genus *Pristis* Linck, 1790
Pristis sp.
(Figure 9: A–C; Table 1)

Material examined—One rostral tooth: NJSM 23499.

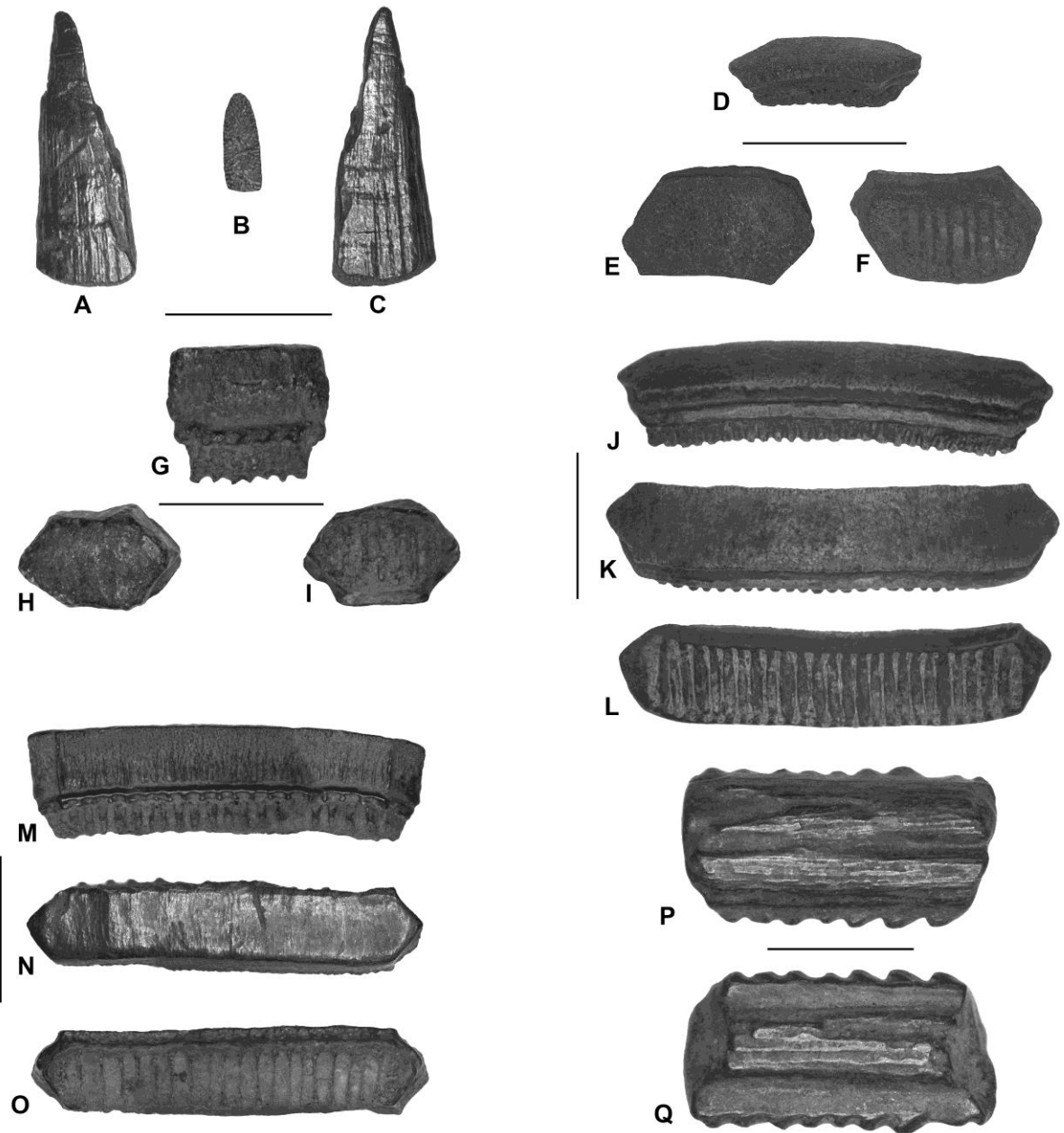


FIGURE 9. Pristiform and Myliobatiform teeth and caudal spine from the Shark River and Kirkwood Formation lag deposit, Farmingdale, Monmouth County, New Jersey. A–C, *Pristis* sp. (NJSN 23499); D–F, and J–L, *Myliobatis* sp. (NJSN 23500); G–I and M–O, *Rhinoptera* sp. (NJSN 23501); P–Q, Myliobatiformes indeterminate caudal spine (NJSN 23502). Orientations: D, G, J, M equal labial view. E, H, K, N equal occlusal view. B, F, I, L, O equal basal view. A, P equal dorsal view. C, Q equals ventral view. Tooth positions: A–C equal Rostral; D–F and G–I equal lateral pavement teeth; J–L and M–O equal median pavement teeth. All scale bars equal 1cm.

Description—The rostral tooth is incomplete however, it displays a rounded anterior tooth edge, nearly flat posterior tooth edge, and an overall dorso-ventrally compressed form. The dorsal and basal tooth surfaces contain longitudinal furrows that extend from the tooth base to the tooth apex. The tooth base has a spongy, texture.

Remarks—According to Cappetta (2012), many pristid species have been named from isolated rostral teeth, leaving their validity in question until further studies are conducted. Some rostral teeth, thought to belong to juvenile sawfish, may lack a groove along the posterior edge; indicating that ontogenetic heterodonty may be present in *Pristis* species (Purdy et al., 2001). Due to the fragmentary nature and rare occurrence of the Farmingdale specimens, we refrain from species assignment.

Superorder Batomorphii Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Family Myliobatidae Bonaparte, 1838
Genus *Myliobatis* Cuvier, 1817
Myliobatis sp.

(Figure 9: D–F and 9: J–L; Table 1)

Material Examined—One median tooth and one lateral tooth and eight additional teeth: NJSM 23500.

Description—The crowns of the median and lateral teeth are mesodistally elongated, smooth, slightly arcuate, weakly convex, and roughly hexagonal in occlusal view. The lateral tooth has a rounded distal edge and distorted rhombic outline. Faint longitudinal ridges and nutritive foramina are present on the transverse edges of the crown. The base of the crown overhangs the root which is polyaulacorhizous and contains numerous, roughly equidimensional, nutritive grooves.

Remarks—The presence of a mesodistally elongated form, multiple nutritive grooves, and flat to slightly convex occlusal surfaces distinguishes *Myliobatis* species teeth from *Rhinoptera* species which also occurs in the Farmingdale assemblage. Additionally, median teeth of *Myliobatis* species may be useful in distinguishing among batoids because they possess angular edges that correspond with the articular surfaces of adjoining lateral teeth (e.g., Herman et al., 2000; Cappetta, 2012). Kent (1999) indicated that *M. dixonii* has a narrow labio-lingual dimension and a width four times that of its length. The Farmingdale *Myliobatis* species teeth compare favorably to these dimensions and may in fact belong to *M. dixonii*. However, due to the highly variable morphology of *Myliobatis* teeth, we refrain from higher level

taxonomic classification until further studies are conducted on fossil and extant specimens.

Family Rhinopteridae Jordan and Evermann, 1896
Genus *Rhinoptera* Cuvier, 1829
Rhinoptera sp.

(Figure 9: G–I and 9: M–O; Table 1)

Material Examined—One median tooth and one lateral tooth: NJSM 23501.

Description—The crowns of the median and lateral teeth have nearly flat and smooth hexagonal occlusal surfaces, non-uniform thicknesses, and are mesodistally elongated. The base of the tooth crown overhangs the root on all but the lingual side and contains numerous longitudinal ridges in both median and lateral teeth. The root is polyaulacorhizous and contains equidimensional nutritive grooves.

Remarks—The presence of nearly flat, hexagonal occlusal surfaces, thickened crowns, a mesodistally elongated form, and similarly sized median and lateral teeth distinguishes the teeth of *Rhinoptera* species from *Myliobatis* species which also occurs in the Farmingdale assemblage. Additionally, median teeth of *Rhinoptera* species may be useful in distinguishing among batoids because they have angular edges that contain irregular, vertical ridges that correspond with the articular surfaces of adjoining, similarly sized and shaped lateral teeth (e.g., Nishida, 1990; Hulbert, 2001; Purdy et al., 2001; Cappetta, 2012).

Order Myliobatiformes Compagno, 1973
Myliobatiformes indet.
(Figure 9: P–Q)

Material Examined—One fragmentary caudal spine: NJSM 23502.

Description—The caudal spine is fragmentary and roughly rectangular in shape. Barbs are present on the lateral edges, the dorsal surface contains antero-posterior furrows, and the ventral surface is smooth and convex.

DISCUSSION

Composition and Paleocology of the Farmingdale Chondrichthyan Assemblage—A list of chondrichthyan species as well as abundance trends and global distribution data for the Farmingdale assemblage is compiled in Table 1. Data from Table 1 indicate that the most common and globally, widespread shallow water species found in the Farmingdale assemblage include: *Carcharias cuspidata*,

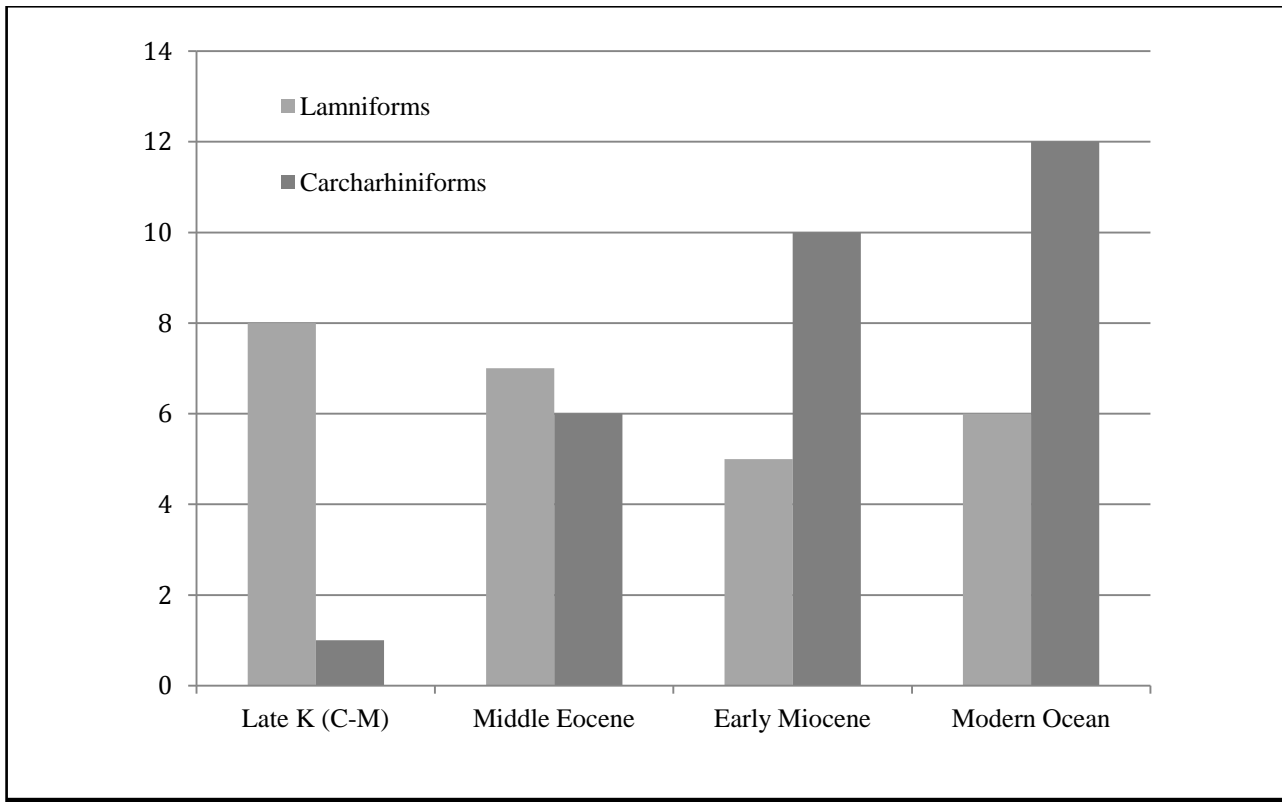


FIGURE 10. Lamniform and carcharhiniform genera known from the Late Cretaceous (Campanian–Maastrichtian), middle Eocene, early Miocene, and modern Atlantic Coastal Plain of the United States. Note overall trend throughout the Cenozoic in carcharhiniforms relative to lamniforms. Sources utilized: Case, 1979; 1980; Compagno, 1988; Ward and Wiest, 1990; Case, 1995; Purdy, 1998; Hartstein et al., 1999; Case and Borodin, 2000a; Chamberlain et al., 2005; and Compagno et al., 2005.

Striatolamia macrora, *Galeocерdo aduncus*, *Carcharhinus priscus*, and *Myliobatis* species. In general, the majority of the Farmingdale chondrichthyans are indicative of shallow, nearshore marine environments (e.g., Purdy, 1998; Underwood et al., 2011; Bor et al., 2012). However, rare occurrences of deeper water chondrichthyans with global occurrence including *Hexanchus agassizi*, and *Xiphodolamia ensis* can also be found in the Farmingdale assemblage (Hulbert, 2001; Compagno et al., 2005; Adnet, 2006; Cappetta, 2012). The availability of shallow, nutrient-rich water in the New Jersey Coastal Plain region and deeper ocean water to the east is supported by the occurrence of *Carcharocles auriculatus*, *Carcharocles chubutensis*, and *Isurus oxyrinchus* (Table 1). Prior research indicates that *Isurus oxyrinchus* is predominantly pelagic although occasionally frequents nearshore waters whereas

species belonging to *Carcharocles* frequent coastal waters but also travel great distances through open water (Breard and Stringer, 1999; Manning, 2003; Aguilera and Rodrigues de Aguilera, 2004; Compagno et al., 2005).

Data from Table 1 also document the occurrence of the Farmingdale chondrichthyans on every continent with the majority of the species occurring between 55° north and south latitude. This occurrence supports the uniformity of post-Tethyan Ocean conditions and the fact that middle Cenozoic chondrichthyans were capable of transoceanic migrations. Such migrations, have been well-documented in many modern chondrichthyans as evidenced by *Isurus oxyrinchus*, *Carcharodon carcharias*, and *Cetorhinus maximus* (Gunnerus, 1765) (e.g., Kohler et al., 1998; Bonfil et al., 2005; Compagno et al., 2005; Gore et al., 2008; Bessudo et al., 2011).

Chondrichthyan Faunal Turnover and Extinction in the Atlantic Coastal Plain: Evidence from the Farmingdale Assemblage—Occurrence data from New Jersey and the Atlantic Coastal Plain during the Late Cretaceous document local chondrichthyan assemblages dominated by lamniform genera such as: *Squalicorax*, *Cretolamna*, and *Scapanorhynchus* (Robb, 1989; Case, 1995; Hartstein et al., 1999). Conversely, only several genera of carcharhiniforms have been reported from these same localities and many well-known Late Cretaceous localities report none (e.g., Manning and Dockery, 1992; Gallagher, 1993; Welton and Farish, 1993; Case and Cappetta, 1997; Hartstein et al., 1999; Chamberlain et al., 2005; Shimada et al., 2006).

By the middle Eocene, local Atlantic Coastal Plain chondrichthyan assemblages like those reported by Case (1980), Ward and Wiest (1990), and Case and Borodin (2000a), document lamniform diversity loss and contain an almost equal number of lamniform and carcharhiniform genera (e.g., Breard and Stringer, 1999; Case and Borodin, 2000a,b; Maisch, Becker, Raines, and Chamberlain, 2014). Across the Atlantic and Gulf Coastal Plains, the replacement of lamniforms by carcharhiniforms as the dominant order of chondrichthyans continued through to the early Miocene and into the present (Figure 10; Case, 1980; Compagno, 1988; Purdy, 1998; Compagno et al., 2005). Today, only 15 species of lamniforms are present in contrast to the carcharhiniforms that comprise approximately 55 % of all 350 + living shark species (Compagno, 1988). Global occurrences of local chondrichthyan assemblages identified in this report from the Late Cretaceous to the present also parallel trends identified in the Farmingdale assemblage and the New Jersey Coastal Plain (See Table 1).

We interpret the changes seen in local chondrichthyan assemblages including that of Farmingdale, New Jersey, to represent snapshots of regional and continental patterns such as those reported by Kriwet and Benton (2004); Guinot et al. (2012); and Underwood and Gunter (2012). These patterns reflect faunal turnover and extinction in chondrichthyan evolution associated with global events such as the Chicxulub Impact, loss of shallow marine habitat associated with continental glaciation of Antarctica, and reconfiguration of ocean circulation associated with changes in landmass paleogeography (Becker, Chamberlain, and Wolf, 2006; Berger, 2007; Norris et al., 2013; Maisch, Becker, Raines, and Chamberlain, 2014). Accordingly, local chondrichthyan assemblages provide excellent proxies to correlate global stratigraphic sections with epoch, stage, and even substage boundary resolution. Chondrichthyan genera and species from the Farmingdale assemblage can be

recovered in both the northern and southern hemispheres and from contemporaneous middle Eocene and early Miocene strata on every continent. Future investigations are necessary to advance the utility of chondrichthyan teeth in stratigraphic studies and how a rapidly warming modern world may again determine the direction of chondrichthyan evolution in local, regional, and global populations.

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