LATE EOCENE SHARKS OF THE HARDIE MINE LOCAL FAUNA OF WILKINSON COUNTY, GEORGIA

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ABSTRACT

A shark fauna from the Late Eocene Hardie Mine of Wilkinson County, Georgia is described on the basis of thousands of teeth collected at the site. Included in the fauna are at least 16 species of which *Heterodontus, Palaeorhincodon, Scyliorhinus,* and *Mustelus* are reported from the Hardie Mine site for the first time. On the basis of numbers of teeth recovered, the Hardie Mine shark fauna was dominated by carcharhinids with *Negaprion* being the most common taxon. The generic composition of the fauna is remarkable modern with 10 (71%) of the 14 genera being extant. Most of the Hardie Mine sharks were nearshore inhabitants, but offshore forms such as *Isurus, Carcharocles*, and *Palaeorhincodon* were also present. Warm-water sharks also dominated the fauna.

Key words: Sharks, Late Eocene, Hardie Mine l.f., Georgia, warm water nearshore fauna.

INTRODUCTION

Although fossil shark remains, mainly teeth, are common in Eocene marine Gulf Coast deposits of the southeast United States, published analyses are lacking in general (see 1 and references therein). In Georgia, fossil shark teeth often are the most abundant vertebrate fossils in middle-to-late Eocene sediments exposed in open-pit kaolin mines. While kaolin mines are numerous along the Fall Line of central Georgia, the vertebrate Eocene fossils they may yield usually offer little information in terms of provenance or paleoecology due to poor stratigraphic controls. Here we report a moderately diverse shark fauna collected from a kaolin mine in central Georgia known as the Hardie Mine. Some of the fossils were taken from *in situ* Clinchfield Formation sediments exposed in the mine, but most were taken off of spoil piles deposited near the *in situ* formation.

Location, Geologic Setting, Age, and Previous Paleontological Works

The Hardie Mine is a small, inactive open-pit kaolin mine located 3.9 km NNW of Gordon, Wilkinson County, central Georgia (32° 54.335'N, 83° 21.543'W latitude and longitude; Fig. 1). Late Eocene (36.0-34.2 Ma; 2) fossiliferous sediments of the Clinchfield Formation (basal unit of the Barnwell Group, see Huddlestun and Hetrick, 3) are exposed in the mine in two ways. First, a 1-1.5 m thick section of *in situ* Clinchfield Formation sediments is exposed in the north-facing wall of the mine. The sediments overlay kaolin clays and underlie local Twiggs Clay sediments (Fig. 2, A-C; also see Westgate, 1). Second, past mining operations in the pit have resulted in tons of fossiliferous Clinchfield sediments being removed and deposited as surface spoil piles near the *in situ* sediments (Fig. 2, D). These spoil piles are especially rich in shark, ray, and, to a lesser degree, bony fish, reptile, and mammal fossils. It is important to note that the origin of the spoil pile sediments clearly are referable to Clinchfield Formation sediments of the mine, and there is no evidence to suggest that there has been mixing of intrusive (reworked) fossils from older or younger fossiliferous horizons (also see Parmley and Holman, 2). Consequently, the spoil piles exposed in the Hardie Mine are part of a locally discrete fossiliferous unit of Clinchfield Formation sediments.

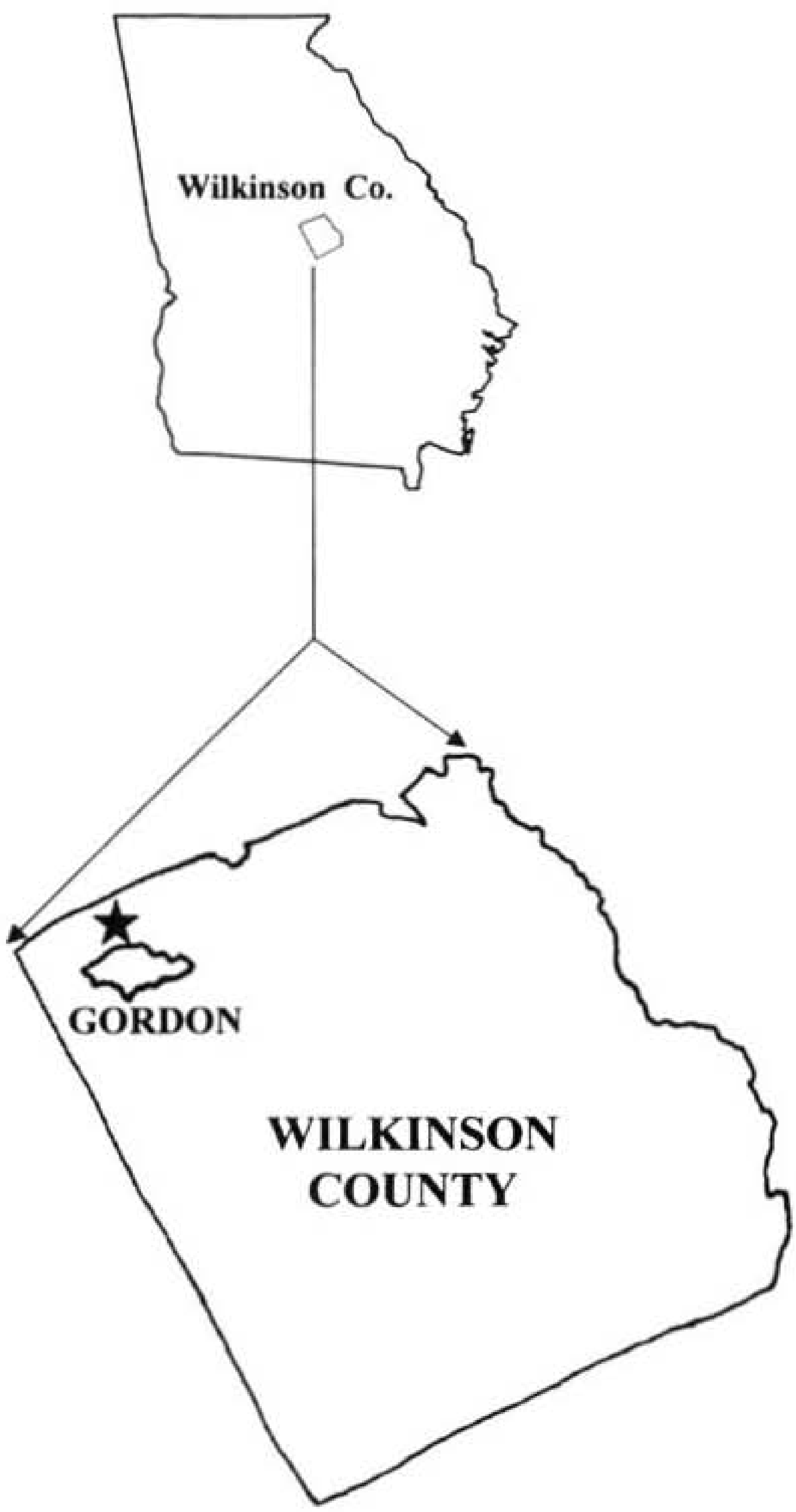


Figure 1. General location of the Hardie Mine fossil site, Wilkinson County, GA

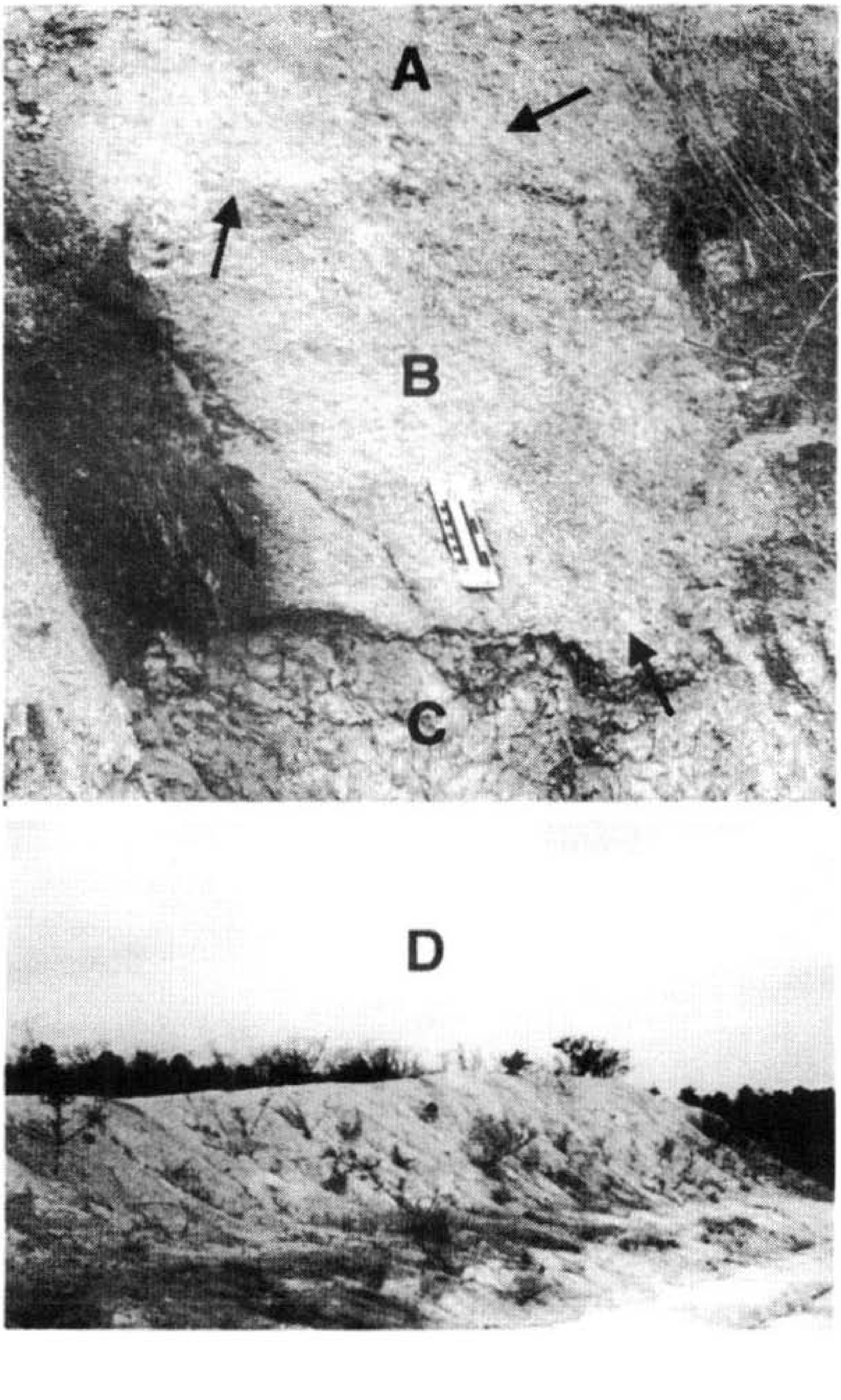


Figure 2. Fossiliferous sediments of the Hardie Mine: close up of *in situ* Clinchfield Formation sediments in the north wall of the mine, A = nonfossiliferous Twiggs Clay sediments, B = Clinchfield sediments, C = nonfissiliferous kaolin sediments, arrows indicate unconformities; D = typical spoil pile of Clinchfield sediments in the mine.

Although fossils have been collected from the Hardie Mine for several years, only recently have vertebrates from the site been reported in the literature (4, 5). Most recently, Westgate (1) listed 26 different vertebrate taxa in the Hardie Mine local fauna (hereafter l.f.), including eleven shark species. Beginning in the summer of 1998, parties from Georgia College and State University, and, later, Clemson University have systematically collected in the Hardie Mine. Intensive surface collecting of spoil piles and sorting screen-washed *in situ* sediments have yielded a moderately diverse shark fauna based on thousands of fossil teeth. This report details the shark fossils collected from the site, and it supplements Westgate's (1) report by adding new taxa to the Hardie Mine l.f. In addition, descriptive species accounts of all taxa are provided for the first time. Unless a taxon was represented by only a few teeth, the fossils that form the basis of this report (n=4809 teeth) were selected for identification because they retained clear diagnostic characters or structures.

SYSTEMATIC PALEONTOLOGY

The Hardie Mine fossils reported here are mainly deposited in the vertebrate paleontological collections of Georgia College & State University (GCVP), but a few specimens are cataloged in the collections of the Bob Campbell Geology Museum, Clemson University (BCGM). Shark taxonomy and tooth terminology generally follow Compagno (6, 7), Cappetta (8), and Kent (9).

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Squantiniformes Goodrich, 1909
Family Squantinidae Bonaparte, 1838
Genus *Squantina* Dumeril, 1906
Squantina prima (Winkler, 1874)
(Fig. 3A)

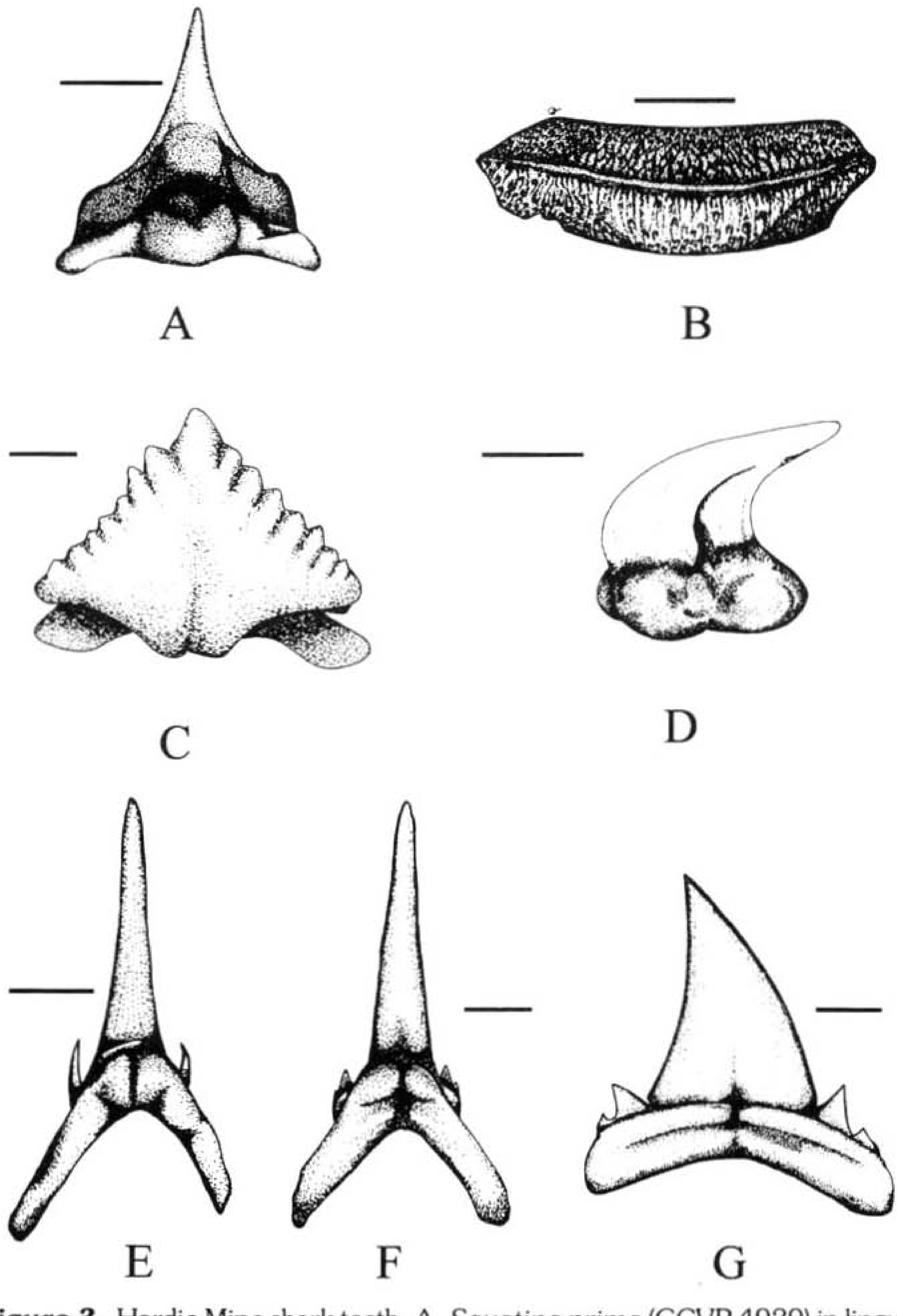


Figure 3. Hardie Mine shark teeth: A, *Squatina prima* (GCVP 4929) in lingual view, line = 2 mm; B, *Heterodontus* sp. (GCVP 6099) in occlusal view, line = 2 mm; C, *Nebrius theilensis* (GCVP 4934) in labial view, line = 2 mm; D, *Palaeorhincodon* sp. (GCVP 6090) in lateral view, line = 1 mm; E, *Carcharias accutissima* (GCVP 4936) in lingual view, line = 6 mm; F, *Carcharias hopei* (GCVP 4937) in lingual view, line = 6 mm; and G, *Carcharias* sp. aff. *C. koerti* (GCVP 5583) in lingual view, line = 5 mm.

Referred Material

6 isolated teeth, GCVP 4929, 4930.

Description

Teeth are mesio-distally elongate and rather small, measuring up to 7 mm in this dimension. Anterior teeth have a tall, narrow, lingually curving cusp that is flanked by a pair of long, oblique enameloid shoulders. The labial face is weakly convex and a short, narrow, rounded protuberance extends basally past the root. The lingual face is strongly convex and there is a distinct lingual protuberance located at the base of the cusp. This protuberance is covered with enameloid on its dorsal surface. The cutting edge is smooth and continuous across the cusp and shoulders. The root is dorso-ventrally flattened, perpendicular to and extending lingually past the crown. The basal attachment surface is convex and perforated by a large foramen.

Lateral and posterior teeth are lower crowned with a distally inclined cusp. The enameloid shoulders are more perpendicular to the cusp, and the basal attachment surface becomes flatter.

Remarks

Angel sharks are warm-water, nearshore, benthic animals that feed on bottom-dwelling fish and invertebrates (7, 10). The dentition of *Squatina* has remained remarkable stable since the Jurassic and is highly suited to grasping prey (8). *Squatina prima* has been reported from Eocene sediments of England (11), Belgium (12), Morocco (13), and in North America from Virginia (14, 15), North Carolina (16), and Maryland (9).

Order Heterodontiformes Berg, 1937
Family Heterodontidae Gray, 1851
Genus *Heterodontus* Blainville, 1816
Heterodontus sp. indet.
(Fig. 3B)

Referred Material

1 tooth, GCVP 6099

Description

The specimen represents a lateral tooth from an adult individual. The crown is arched and domed, mesiodistally elongated (9 mm), but labio-lingually thin (3 mm). Crown height measures 2.1 mm. A distinct carina divides the crown into nearly equal labial and lingual parts. The labial face is convex and ornamented with strong, closely spaced longitudinal ridges that extend from the carina. These ridges bifurcate and anastomose distally toward the crown foot. The lingual face exhibits medial convexity, but is concave mesially and distally. Ornamentation consists of discontinuous irregular ridges, and the enameloid appears pitted along the crown foot and at the mesial and distal ends. The root is not preserved.

Remarks

In addition to monognathic and dignathic heterodonty, Port Jackson sharks exhibit ontogenetic heterodonty. As individuals mature, the number of lateral cusplets is reduced in anterior teeth, and lateral and posterior teeth develop into crushing batteries (see Cappetta, 8). This reflects a dietary change to incorporate hard-shelled invertebrates. Living heterodontid sharks are small benthic feeders (17) that inhabit temperate and tropical waters of the Pacific and Indian Oceans (7).

The conservative morphology of *Heterodontus* teeth makes them difficult to identify at the specific level (9). Various fossil species of *Heterodontus* are based on crown ornamentation and size of lateral and posterior teeth. Several Eocene species have been reported from sites in Europe and North America (e.g., *H. woodwardi* Casier, 11; *H. vencenti* [Leriche], 11, 2; *H. pineti* Case, 18, 19; and *H. lerichei* Casier, 15), but a larger sample size is needed to determine a specific identification of the Hardie Mine species.

Order Orectolobiformes Applegate, 1972
Family Ginglymostomidae Gill, 1862
Genus *Nebrius* Ruppel, 1837
Nebrius thielensis (Winkler, 1873)
(Fig. 3C)

Referred Material

79 isolated teeth, GCVP 4934, 5576.

Description

Teeth consist of a rather low, thick crown measuring up to 12 mm in mesio-distal dimension. In labial view, anterior teeth are symmetrical or nearly so. There is a tall, broad, lingually inclined cusp. Mesial and distal cutting edges possess seven to nine serrations that decrease in size towards the root. The labial face is slightly convex, may be weakly crenulated, and forms a 45° angle with the root. A large, thick, rounded labial protuberance (apron of Kent, 15) extends basally past the root. The lingual face is rather convex with a large protuberance at the base of the cusp that forms nearly a 90° angle with the crown. The root is very short, triangular in basal view, with a flat or slightly convex attachment surface that is perforated by a large foramen.

Teeth of lateral and posterior row groups are asymmetrical, lower crowned, and with a smaller, distally inclined cusp. The mesial cutting edge is long with up to 14 fine serrations, whereas the distal edge is much shorter with only approximately five serrations. The labial basal protuberance is thinner than in anterior teeth, and the lingual protuberance remains under the cusp, being offset distally.

Remarks

Recent nurse sharks inhabit nearshore subtropical to tropical marine waters (7). They are bottom dwellers that feed on a variety of small fish and invertebrates (7, 10). The teeth of *Nebrius* can be distinguished from the similar taxon *Ginglymostoma* in having a mesio-distally wider crown, more serrations on the cutting edges, and a longer labial protuberance (8, 15). Ward and Weist (14) reported *N. thielensis* and *N. blanckenhorni* (Stromer) from Eocene sediments of the Chesapeake Bay region. The *N. blanckenhorni* teeth, however, may represent lateral and posterior teeth of *N. thielensis* (also see discussion in Kent, 9). *Nebrius thielensis* appears to have been a Northern hemisphere species, occurring in Eocene sediments of Belgium (12), England (11), and the United States: Mississippi (20); Georgia (8); North Carolina (16); and Virginia (21).

Family Rhincodontidae Garmen, 1913
Genus *Palaeorhincodon* Herman, 1974
Palaeorhincodon sp. indet.
(Fig. 3D)

Referred Material

One tooth, GCVP 6090

Description

The tooth is small, measuring 2.7 mm in total height and 2.04 mm in greatest root length. The crown has a high, narrow cusp that is weakly sigmoidal and strongly inclined lingually. The cusp appears conical, but conspicuous mesial and distal cutting edges are present. The cutting edges are weak apically, but are sharp basally and extend onto short lateral shoulders. Both the labial and lingual faces are unornamented and convex, with the lingual face being more convex. In labial view, the crown foot is wide and does not reach the basal level of the root. The root is bulbous with a large lingual protuberance. A narrow, deep nutritive groove bisects the root and extends from just below the lingual crown foot to just below the labial crown foot. There is a large foramen within the nutritive groove that is located near the posterior end of the root. Margino-lingual foramina are located on each side of the nutritive groove.

Remarks

This tooth does not possess some characteristics that have been attributed to *Palaeorhincodon*, including lateral cusplets, a labially expanded nutritive groove, and enameloid covering the dorso-lingual surface of the root (8, 15). However, we believe the overall morphology and size of GCVP 6090 compares favorably with *Palaeorhincodon*, and the differences cited simple reflect morphological and positional variation. This specimen appears to represent a lateral tooth, which lack lateral cusplets (D. Ward Pers. comm., 2002). The rarity of the taxon in the Hardie Mine l.f. is likely related both to the small size of its teeth and the offshore, pelagic habits of whale sharks (7). *Palaeorhincodon* has been reported from Eocene sediments of Belgium (22), Togo (8), Morocco (8), and the United States (Virginia, 15).

Order Lamniformes Berg, 1958
Family Odontaspididae Muller and Henle, 1839
Genus *Carcharias* Rafinesque, 1810
Carcharias acutissima (Agassiz, 1844)
(Fig. 3E)

Referred Material

446 isolated teeth, GCVP 4936, 5588, 7013, 7014.

Description

Maximum tooth height measures 32 mm. Anterior teeth have a tall, narrow, sigmoidal cusp. The labial face is nearly flat and without ornamentation. The lingual face is convex with fine longitudinal striations extending one-half to three-fourths of the crown height. The cutting edges are smooth but do not reach the crown foot. There is a single pair of tall, sharply pointed, lingually curving lateral cusplets. Some teeth exhibit a second pair of short cusplets. The root is bilobate with long, narrow, diverging lobes. There is a large lingual boss that is bisected by a deep nutritive groove.

Lateral teeth are lower crowned, broad-based, and distally recurving. The labial face is flat and unornamented, whereas the lingual face is convex with very fine longitudinal striations extending to one half the crown height. Generally, there is only a single pair of low, pointed, broadly triangular lateral cusplets. The cutting edge is smooth, sharp, and continuous across the lateral cusplets and central cusp. Root lobes are shorter and highly diverging. The lingual boss is reduced and the nutritive groove is narrow and deep.

Remarks

The lingual striations on these teeth are so fine that they were often seen only under magnification. Abraded teeth were excluded from this study because it was not clear if striations had been worn away. The striated odontaspid teeth from the Hardie Mine differ from other types such as *Carcharias teretidens* White and *Striatolamia macrota* (Agassiz) in having much finer striations (11, 15). Though somewhat smaller in size than teeth of *C. acutissima* reported by Kent (9), the striations on the teeth in our sample compare closely with this taxon. Three large anterior teeth measuring 35 to 36 mm are referred to *C. acutissima* rather than *S. macrota* because of their larger lateral cusplets and finer lingual ornamentation. The teeth of *Carcharias* are well adapted for a piscivorous diet (7). *Carcharias acutissima* has been reported from the early Oligocene of North America (9) and Middle Eocene of England (11).

Carcharias hopei (Agassiz, 1843)
(Fig. 3F)

Referred Material

296 isolated teeth, GCVP 4937, 5587, 7012, 7016.

Description

Maximum tooth height measures 41 mm. Anterior teeth have a tall, rather narrow, slightly sigmoidal cusp. The labial face is flat to weakly convex and unornamented. The lingual face is convex, generally smooth but sometimes with very fine, faint longitudinal striations. The cutting edges are smooth, usually straight, and may not reach the crown foot. There is a single pair of sharply pointed lateral cusplets that curves toward the central cusp. A second vestigial pair was observed on some teeth. The root is bilobate with long diverging lobes. A prominent lingual boss is bisected by a deep nutritive groove. A few large anterior teeth have a wide crown and cutting edges that are slightly convex rather than straight.

Lateral teeth have a lower, labio-lingually thinner, distally curving cusp. The cusp is also much broader basally and is nearly flat (i.e., not sigmoidal). There is a single pair of low, broadly triangular lateral cusplets. The cutting edge is continuous across the cusplets and central cusp. It is smooth and sharp, but a few serrations between the cusplets and central cusp were observed on some teeth. The root lobes are short, sub-rectangular, and widely diverging. A weak lingual boss is bisected by a short nutritive groove.

Remarks

It could be argued that the rather large anterior teeth described above represent *Carcharias robusta* (Leriche; 23, 24), but we agree with Ward (25) that these are morphological variants of *C. hopei*. We also believe Eocene teeth previously identified as *C. cuspidata* (Agassiz) from Georgia and Louisiana (18, 26) are referable to *C. hopei*. Though Kent (9) considered *C. cuspidata* a valid taxon, Ward (25) placed it in synonymy with *C. hopei*. *Carcharias hopei* has previously been reported from other North American Eocene sites in Alabama (27), Arkansas (28), Virginia (15), and Maryland (9).

Carcharias sp. aff. *C. koerti* (Stromer 1910)
(Fig. 3G)

Referred Material

123 isolated teeth, GCVP 5575, 5583, 6095, 7008.

Description

The largest anterior teeth measure 28 mm in height. These have a tall, broadly triangular, labio-lingually thin crown. The crown may be flat or weakly sigmoidal in profile. There is one pair of large, triangular, diverging lateral cusplets, but a second pair of smaller cusplets occur on most teeth. The cutting edge is smooth, sharp, and continuous. The root is bilobate with rather short, rounded and widely diverging lobes. An inconspicuous lingual boss usually possesses a single foramen. A weak, long nutritive groove is present on most teeth.

Lateral teeth are lower crowned with a weakly to highly distally recurved crown (recurvature appears to increase posteriorly). Crowns are labio-lingually thin with sharp, smooth, continuous cutting edges. The primary pair of lateral cusplets are broadly triangular and diverging, and the second pair are very small or absent. Root lobes are short, sub-rectangular, and highly diverging. The nutritive groove, if present, is long and shallow.

Posterior teeth are much smaller with a high distally recurved cusp. The primary pair of lateral cusplets is large, broadly triangular, and diverging, whereas the second pair is much reduced. A third vestigial pair was observed on some teeth. The root lobes are very short, rounded, and diverging, and the nutritive groove may be absent.

Remarks

Eocene teeth of the type described above have variously been referred to *Lamna* (18), *Cretolamna* (20) and *Serratolamna* (9). Though the crown morphology is similar, the Hardie Mine l.f. teeth can be distinguished from *Cretolamna* by the consistent presence of a weak nutritive groove, which is usually absent in Cretoxyrhinidae (8). A lingual nutritive groove is found on teeth of *Serratolamna* (29), which can also have up to three pairs of lateral cusplets (30). The teeth in our sample generally have one large pair of lateral cusplets and, if present, a second smaller pair. For these reasons we exclude this tooth type from *Cretolamna* and *Serratolamna*, and place it within *Carcharias*, retaining the species epithet *koerti*, which is a taxon originally described by Stromer (31) from the Eocene of Africa.

Genus *Striatolamia* Gluckman, 1964
cf. *Striatolamia macrota* (Agassiz, 1843)

Referred Material

1 tooth, GCVP 5592.

Description

The tooth measures 33 mm in height and has a tall, broad cusp. The labial face is flat and unornamented. The lingual face is convex with striations extending to one half the cusp height. The cusp curves slightly distally. Cutting edges are smooth and continuous across the cusp, reaching the crown foot. The root lobes are short, labio-lingually thin and diverging. The lingual boss is shelf-like with a wide nutritive groove.

Remarks

This tooth differs from *C. hopei* in that it is more gracile and there is well-developed lingual crown ornamentation. The specimen also differs from typical *C. acutissima* in that it is broader and the lingual ornamentation is more robust. Though this tooth could represent an aberrant *C. acutissima*, we believe it compares favorably to *S. macrota*. The taxon had a worldwide distribution during the Eocene (8, 11, 13, 15, 32, 33).

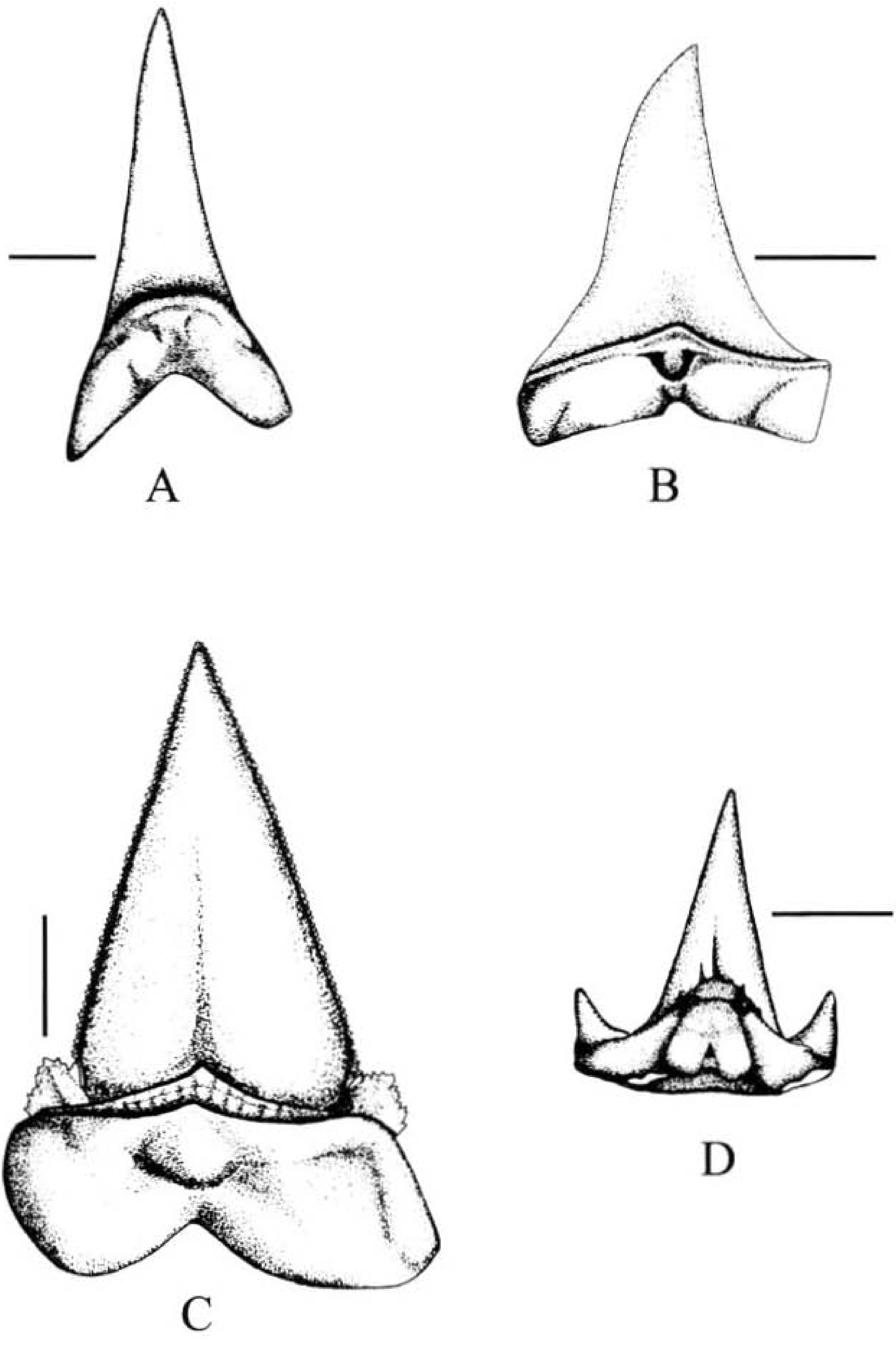


Figure 4. Hardie Mine shark teeth: A, *Isurus praecursor* (GCVP 5585) lower anterior in lingual view, line = 10 mm, and B, upper anterior (GCVP 5584) in lingual view, line = 10 mm; C, *Carcharocles angustidens* (GCVP 6092) in lingual view, line = 10 mm; and D, *Scyliorhinus gilberti* (GCVP 4930) in lingual view, line = 1 mm.

Family Lamnidae Muller and Henle, 1838
Genus *Isurus* Rafinesque, 1810
Isurus praecursor (Leriche, 1905)
(Fig. 4A, B)

Referred Material

27 isolated teeth, GCVP 5577, 5584, 5585, 5590, 7009, 7010.

Description

Upper anterior teeth measure up to 30 mm in total height, and are broadly triangular and labio-lingually thin. They are symmetrical with short enameloid shoulders extending onto the root lobes. The cutting edge is smooth and continuous across the entire crown. The root is rectangular with a weak lingual bulge.

Lower anterior teeth have a tall, rather narrow, lingually curving, slightly sigmoidal crown. The labial face is flat, whereas the lingual face is convex; both faces are smooth. The apex is sharply pointed and the cutting edge is smooth, sharp, and continuous across the entire crown. The root is bilobate with long, thin lobes (mesial lobe longer than distal lobe). There is a large lingual boss that is perforated by small foramina. The largest teeth measure 45 mm in total height.

Lateral teeth are very similar to upper anterior teeth except that they are lower crowned and distally inclined.

Remarks

Isurus praecursor is an uncommon element in the Hardie Mine l.f. The taxon is also known from Eocene rocks of Belgium (34), Syria (8), Africa (31, 35, 36), England (11, 37), and the Chesapeake Bay area, U.S.A. (9).

The large teeth of *Isurus* indicate it was a top predator able to ingest a wide variety of prey. Teeth form a tearing dentition, tending toward a cutting function (i.e., the teeth pierce the prey and the smooth, sharp cutting edges allow the shark to tear away large pieces of flesh). Recent mako sharks are large, mainly offshore predators that feed on fish and squid (7, 17).

Family Otodontidae Gluckman, 1964
Genus *Carcharocles* Jordan and Hannibal, 1923
Carcharocles angustidens (Blainville, 1818)
(Fig. 4C)

Referred Material

Two teeth: GCVP 6091, upper right lateral tooth; GCVP 6092, lower left anterior tooth of young individual.

Description

GCVP 6091 is a large tooth, measuring 7.2 cm in total height. The crown is broadly triangular with a flat labial face and very convex lingual face. There is also slight distal recurvature of the crown. The cutting edge is coarsely and evenly serrated, and it is continuous along the crown. Only the distal lateral cusplet is preserved, which is low and broadly triangular, separated from the main cusp by a notch in the enameloid. The distal edge of the cusplet is coarsely serrated, whereas serrations on the mesial edge are much finer. The lingual dental band is low and broadly triangular. The root is massive and bilobate, with very short, rounded, highly diverging lobes. The lingual boss possesses several foramina.

GCVP 6092 is a smaller tooth, measuring 4.4 cm in total height. The crown is labio-lingually thin with a flat labial face and convex lingual face. The crown is erect and triangular, with a pointed apex that curves slightly labially. The cutting edge is continuous along the crown, and it is evenly and coarsely serrated. There is a single pair of lateral cusplets that is separated from the main cusp by a deep notch in the enameloid. The cusplets are large, triangular, and coarsely serrated. The lingual dental band is low and broadly triangular. The root is robust and bilobate, with very short, rounded, asymmetrical lobes.

Remarks

These teeth are referred to *C. angustidens* based on their coarsely, evenly serrated cutting edges. This characteristic separates them from *C. auriculatus* (Blainville), in which the teeth (especially juveniles) are partially or irregularly serrated (9, 38). The lateral cusplets of the teeth in our sample are larger than those of *C. chubutensis* (Ameghino; see Kent, 9).

This species was undoubtedly a top predator in the Hardie Mine seas. The species probably inhabited the offshore, deeper waters of the Late Eocene Georgia coastline, which would account for its apparent rarity in the nearshore sediments of the site.

Order Carcharhiniformes Compagno, 1977
Family Scyliorhinidae Gill, 1862
Genus *Scyliorhinus* Blainville, 1816
Scyliorhinus gilberti Casier, 1946
(Fig. 4D)

Referred Material

53 isolated teeth, GCVP 4931, 4932, 5580, 6094.

Description

Anterior teeth measure up to 4 mm in total height and have a tall, straight, slightly distally inclined cusp. The labial face is weakly convex with coarse longitudinal striations restricted to the crown foot. The lingual face is more convex and appears to be smooth. There is a single pair of tall, conical cusplets that is closely connected to the central cusp. The cutting edge is smooth and nearly continuous across the cusp and cusplets (except for blunt apices). The root is bilobate with rather short, labio-lingually thin lobes. The lingual attachment surface is flat, and a thick boss is bisected by a deep nutritive groove. There is a large foramen located within the nutritive groove.

Lateral teeth are lower crowned (2.5 mm total height) and more distally and lingually inclined. The labial face is moderately convex with coarse longitudinal ridges extending from the crown foot to one half the crown height. The lingual face is more convex with finer longitudinal striations. There is a single pair of diverging, bi-convex lateral cusplets, also with labial and lingual striations. Apices of the cusp and cusplets are blunt. The cutting edge is smooth, rather sharp, and continuous. The root is bilobate with short, rounded diverging lobes. The attachment surface is convex and bisected by a long, deep nutritive groove.

Remarks

Scyliorhinus gilberti was a widespread taxon during the Eocene, being reported from England (15), Uzbekistan (15), Belgium (39), France (40), England (11), and the United States (9, 15, 20).

We believe the reason this shark is uncommon in the Hardie Mine l.f. is not the result of a collecting bias, as we have recovered many microfossils of dasyatid and gymnurid ray teeth. If recent deep-water scyliorhinid sharks (10) can be used as an analogue, this rarity is related to the shallow-water environment represented by the Clinchfield sediments in Hardie Mine. Catsharks are a diverse group of small carcharhiniform sharks that range from tropical to polar marine waters. They use their clutching dentition to seize small fishes and invertebrates (7, 17).

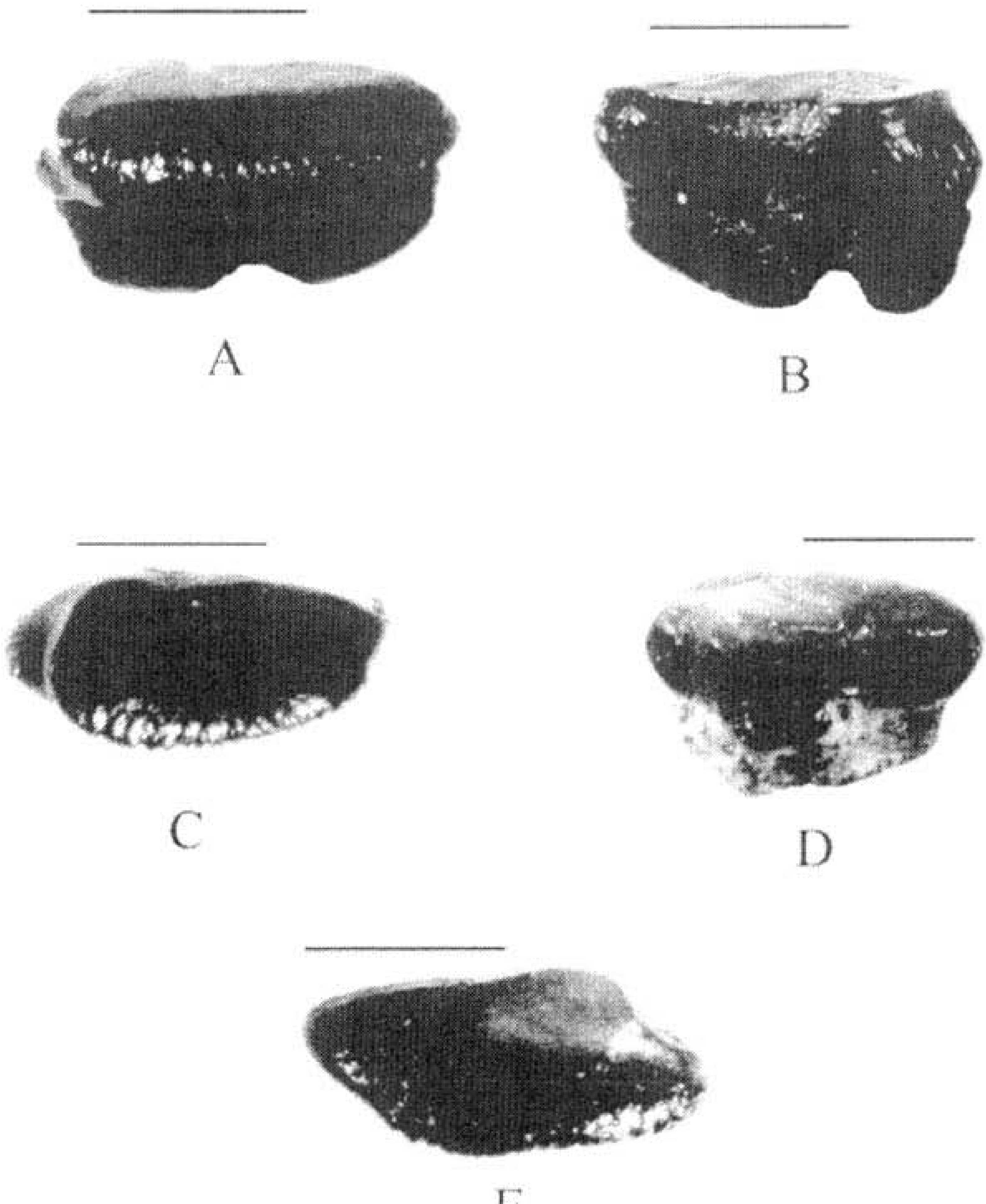


Figure 5. Hardie Mine *Mustelus* cf. *M. vanderhoefti* lateral teeth, all GCVP specimens: A=C, 5573, A in labial view, B in occlusolingual view, and C in occlusal view; D-E, 5589, D in occlusolingual view, E in occlusol view. Line = 1 mm in all views.

Family Triakidae Gray, 1851
Genus *Mustelus* Linck, 1730
Mustelus cf. *M. vanderhoefti* Herman, 1982
(Fig. 5)

Referred Material

3 isolated teeth, GCVP 5573, 5589, 6093

Description

GCVP 5573 is the most complete tooth. It is a lateral tooth measuring just over 2 mm in greatest dimension. The crown is low with a blunt, distally offset, distally inclined cusp. The labial face is a flat crushing surface. The crown foot is thick, greatly overhangs the root, and is ornamented with fine longitudinal striations. The lingual face is high with a sinuous profile and distinct bulge located below the cusp. There are fine longitudinal striations and some enameloid ripples extending from the crown foot to the sinuous, transverse cutting edge. The root is thick, with a weakly convex basal attachment surface that is bisected by a deep nutritive groove. This groove is located directly under the cusp, and there is a large central foramen. There is also one pair of margino-lingual foramina.

GCVP 5589 and 6093 are also lateral teeth, each measuring about 2.5 mm in greatest dimension. They are like GCVP 5573 in all discernable features.

Remarks

This is the first reported occurrence of *Mustelus* from the Eocene of North America, and only the second from the early Paleogene (late Paleocene of Mississippi; see Case, 20). Two species of *Mustelus* commonly occur in Eocene sediments of Europe, *M. whitei* Cappetta and *M. vanderhoefti*. *Mustelus whitei* is smaller in overall size and has finer crown ornamentation (41) than the teeth in our sample. Herman (42) described *M. vanderhoefti* based on its relatively large size and coarse ornamentation. The teeth from our sample compare closely with this taxon, but due to their worn condition only a tentative species placement is suggested here.

As noted by Cappetta (8), the durophagous teeth of *Mustelus* are remarkable convergent with certain batoids. The flat worn surfaces indicate a high degree of specialization for crushing hard-shelled invertebrates, although *Mustelus* is known to also feed on small fish (7). Recent *Mustelus* inhabit a wide variety of environments including brackish water, nearshore marine, and continental shelf at depths of up to 340 meters (7, 10).

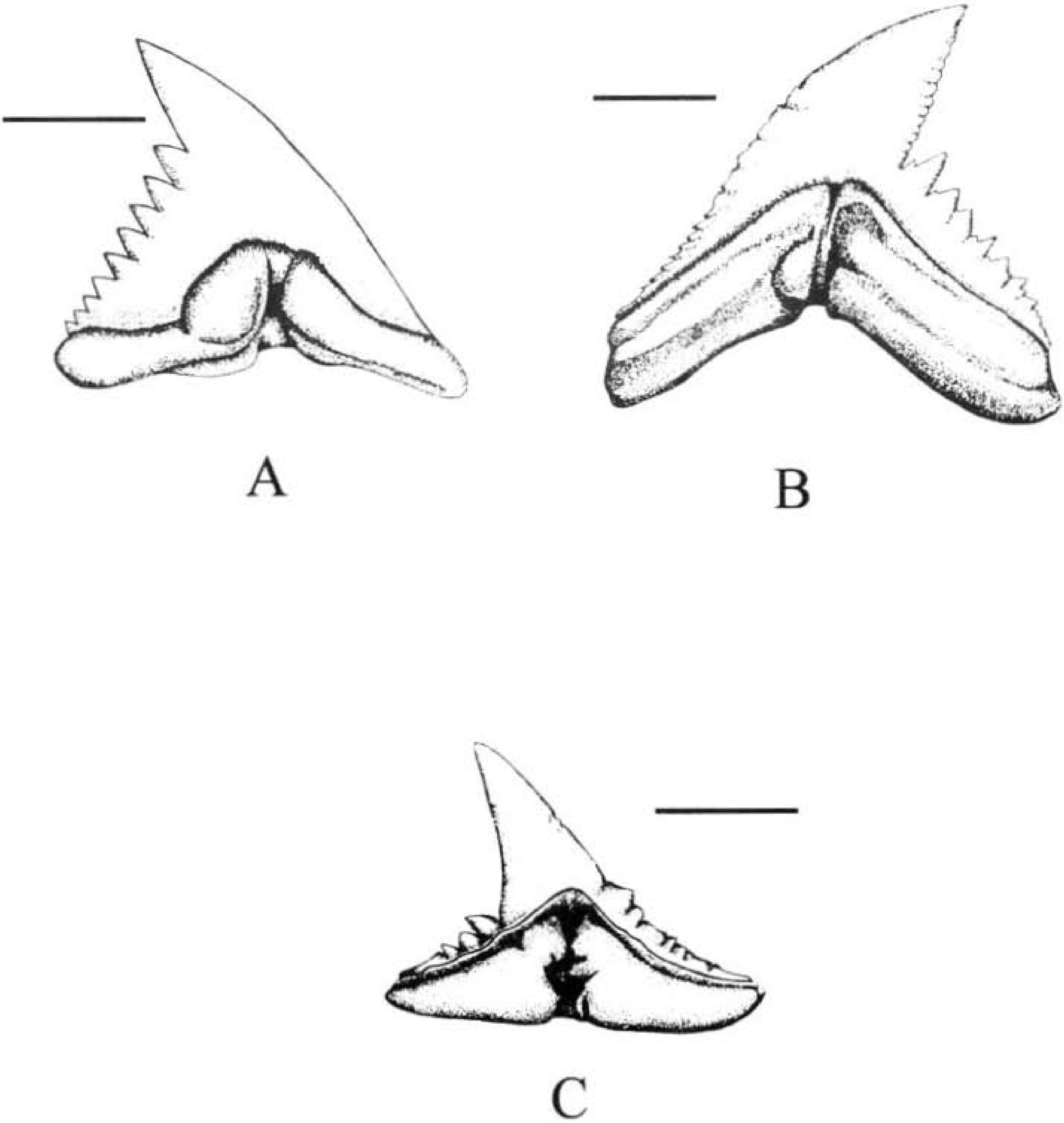


Figure 6. Hardie Mine shark teeth: A, *Hemipristis curvatus* (GCVP 4933) in lingual view, line = 5 mm; B, *Galeocerdo alabamensis* (GCVP 4938) in lingual view, line = 6 mm; C, *Physogaleus secundus* (GCVP 5586) in lingual view, line = 5 mm.

Family Hemigaleidae Hasse, 1879
Genus *Hemipristis* Agassiz, 1843
Hemipristis curvatus Dames, 1883
(Fig. 6A)

Referred Material

635 isolated teeth, GCVP 4933, 5578, 7006, 7015.

Description

The largest upper anterior teeth in our sample measure up to 13 mm in total height. They have a broad, labio-lingually compressed, distally inclined crown. The mesial cutting edge is long and nearly straight, and smooth except for fine irregular serrations at the basal portion. The apical half of the distal edge is smooth, with the lower half bearing four to five large, apically directed serrations. The labial face of the crown extends basally over the root. The root is bilobate with short, widely diverging sub-rectangular lobes. There is a large lingual boss that is bisected by a short nutritive groove.

Upper lateral teeth are very broad and more distally recurved than anterior teeth, with distinct lingual flexure of the crown. The mesial cutting edge is very long and generally convex, but may be sinuous. It is smooth except for irregular serrae developed on the medial or basal portion. Only a few teeth in our sample have a mesial edge that is almost entirely serrated. The upper one third of the distal edge is smooth, whereas the basal two thirds bears five to six large serrations (becoming finer distally). The root is broad with very short lobes. A long nutritive groove bisects a weak lingual boss.

Lower anterior teeth measure up to 14 mm in total height and have a tall, narrow, distally inclined and lingually flexed crown. Both the labial and lingual faces are convex. Enameloid shoulders extend basally onto the root lobes, with one or two pairs of needle-like serrations. The cutting edge is smooth but does not reach the serrations. The root is bilobate with short, rounded lobes. A massive lingual boss is bisected by a long nutritive groove.

Lower lateral teeth are similar to upper anteriors, except that the mesial edge is convex, nearly smooth, and generally with only three distal serrations.

Remarks

This tooth type has been referred to *Hemipristis wyattdurhami* White in older literature (18, 26, 28, 43), but Cappetta (8) has synonymized it with *H. curvatus*. *Hemipristis curvatus* appears to have been about the same size as Recent *Hemipristis elongatus* (approximately 2 m; see Compagno, 7). During the Miocene and Pliocene, however, *Hemipristis* attained a very large size (*H. serra* Agassiz), and the mesial cutting edge of the upper teeth are much more extensively serrated (see Kent, 9).

Hemipristis curvatus is common in the Hardie Mine l.f. and Cappetta (8) noted that the taxon commonly occurs in sediments deposited in warm-water environments, but it is much scarcer in more northern, cooler water deposits. The only living snaggletooth shark, *H. elongatus*, is a nearshore piscivorous species of Indo-West Pacific oceans (7, 9).

Family Carcharhinidae Jordan and Evermann, 1896
Genus *Galeocerdo* Muller and Henle, 1838
Galeocerdo alabamensis Leriche, 1942
(Fig. 6B)

Referred Material

351 isolated teeth, GCVP 4938, 5574, 7011.

Description

Teeth are mesio-distally elongate, measuring up to 25 mm in this dimension. The crown is broadly triangular with a distally inclined cusp. Anterior teeth are higher crowned with a more erect cusp, but teeth become lower crowned and more distally inclined toward the posterior end of the jaw. The mesial cutting edge is very long with serrations almost to the cusp apex. The serrations on the basal half of the crown are large, but become finer apically. The distal edge is only one third as long as the mesial edge, and it is convex and finely serrated. The distal blade is long, with numerous coarse, weakly compound serrations that become finer distally. A distinct lingual flexure was observed on most teeth. The labial face extends basally to overhang the root, and the lingual face is convex. The root is thick in anterior teeth, becoming thinner in lateral and posterior teeth. It is highly bilobate with a thin attachment surface and a wide, shallow nutritive groove. There is a distinct interlobe area that is either U or V-shaped. The labial face of the root of all teeth is distinctly concave.

Symphyseal teeth are nearly symmetrical with sinuous cutting edges. The mesial edge is evenly serrated, whereas the distal edge bears coarse serrations that become finer apically.

Remarks

Several species of *Galeocerdo* have been described from Eocene deposits worldwide, including *G. alabamensis, G. clarkensis* White, *G. eaglesomei* (White), and *G. latidens* (Agassiz; see 11, 19, 26, 28, 36). Manning and Standhardt (26) synonymized *G. clarkensis* with *G. alabamensis*, suggesting that the former represented the upper teeth of the latter. Regardless of the morphology of the mesial cutting edge, the teeth described in this report are referred to *G. alabamensis* because the distal heel possesses compound serrations, which in the Eocene are apparently unique to this taxon (D. Ward pers. comm., 2001). These compound serrations are not nearly as well developed as in Recent *G. cuvier* (8).

Genus *Physogaleus* Cappetta, 1980
Physogaleus secundus (Winkler, 1874)
(Fig. 6C)

Referred Material

70 isolated teeth, GCVP 5586, 5591, 7007.

Description

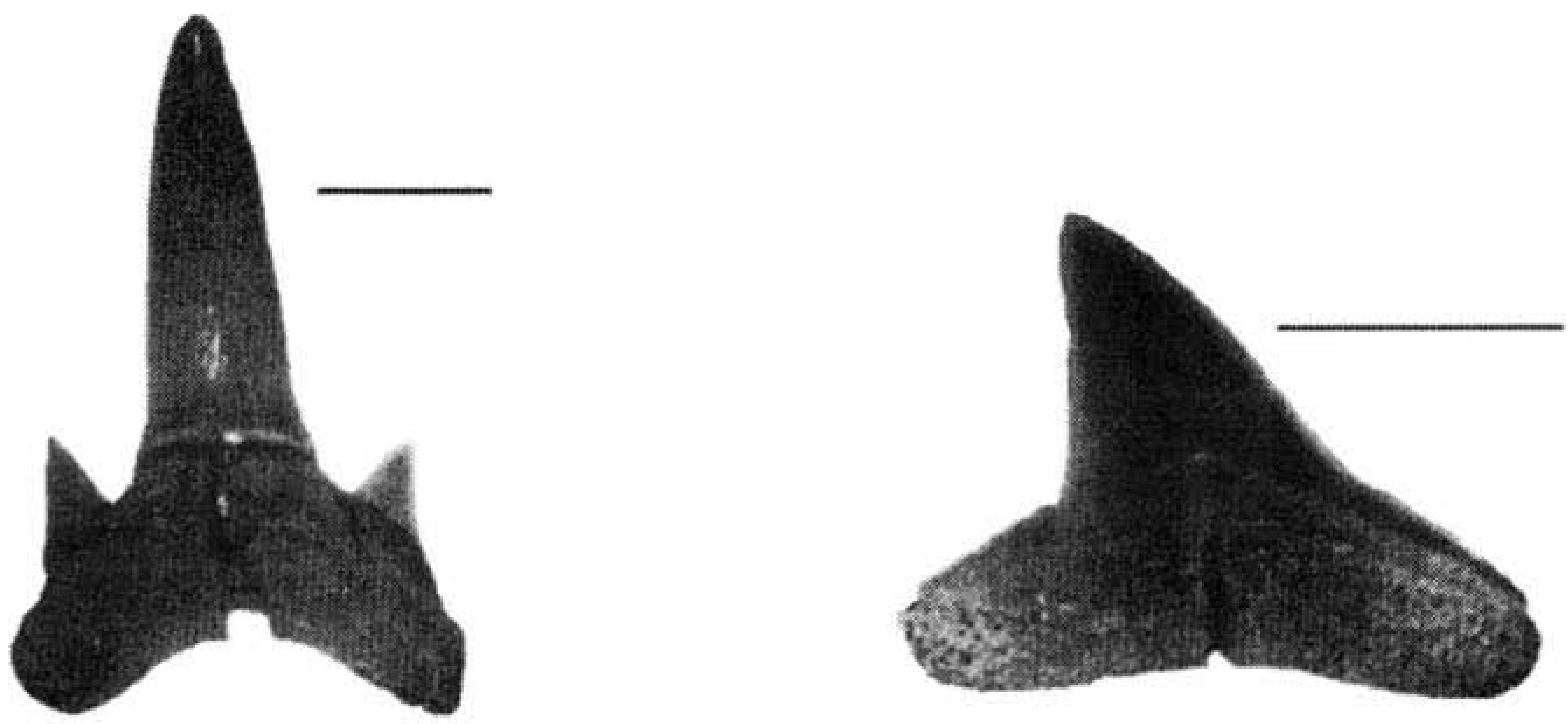
Large teeth measure 12 mm in height and 13 mm mesio-distally. Upper teeth have a crown with a broad cusp. The labial face is flat or nearly so, and extends basally over the root, whereas the lingual face is highly convex. The mesial cutting edge is straight or convex, smooth except for weak to coarse serrations that may occur at the basal portion. The distal edge is short and smooth. The distal blade is rather long with up to four large serrations, becoming finer distally. The root is bulky with a flat attachment surface and long lingual nutritive groove. Posteriorly, teeth become lower crowned and the cusp is more distally inclined.

Lower teeth have a rather narrow, sharply distally inclined, sigmoidal cusp. The labial face is nearly flat and overhangs the root, whereas the lingual face is highly convex. The mesial cutting edge is long, sharp, and may bear weak serrations at the basal portion. The distal edge is only one half the length of the mesial edge and is smooth. Up to three large serrations occur on the short distal blade. The root lobes are short and highly diverging. Lateral and posterior teeth have lower crowns with a more distally inclined cusp.

Remarks

Physogaleus is common in the Eocene and Oligocene of North America, Europe, and Africa (8). In addition to dignathic heterodonty seen in male teeth, sexual heterodonty is evident in that male lower teeth are more gracile than female lower teeth. This taxon can be distinguished from *Galeocerdo alabamensis* in several respects: overall tooth size is much smaller; the mesial cutting edge is smooth except for weak basal serrations; the distal heel bears fewer serrations (only 1 to 4); root lobes are more robust and straighter, nearly forming a horizontal line; and the nutritive groove is narrower and deeper.

Genus *Abdounia* Cappetta, 1980
Abdounia enniskilleni (White, 1956)
(Fig. 7A)



A B

Figure 7. Hardie Mine shark teeth: A, *Abdounia enniskilleni* (GCGM 2743a) in lingual view, liine = 3 mm; B, *Negaprior eurybathrodon* (BCGM 5303a) in lingual view, line = 5 mm.

Referred Material

589 isolated teeth, GCVP 5579, 5582, 7017; BCGM 2743a.

Description

Anterior teeth measure up to 15 mm in total height. The crown consists of a tall, rather narrow, slightly sigmoidal cusp. The labial face is nearly flat and smooth, whereas the lingual face is highly convex with very fine longitudinal striations extending nearly to the cusp apex. There is a single pair of tall, narrow, slightly diverging lateral cusplets that is closely connected to the central cusp. These also bear fine lingual striations. The cutting edge is smooth and continuous across the cusplets and main cusp. The root is bilobate with short, rounded lobes (the mesial lobe may be slightly longer). The attachment surface is broad and generally flat, but may be weakly concave. A large lingual boss is bisected by a long, narrow nutritive groove.

Lateral teeth have a thinner, broader, more distally recurved central cusp. The lingual striations are much finer and the lateral cusplets are broader. The root is also more gracile with narrow, rounded lobes, a reduced lingual boss, and deep nutritive groove.

Remarks

Abdounia is an Eocene genus of carcharhiniform shark. In older literature, this tooth type has been identified as *Scyliorhinus enniskilleni* White (18, 26, 28, 43), but Cappetta (44) placed the taxon within his new genus *Abdounia*. The teeth are well adapted for clutching and holding prey and superficially resemble teeth of the reef whitetip shark, *Triaenodon obesus* (Ruppell). Lingual ornamentation and only one pair of lateral cusplets distinguish *A. enniskilleni* from other Eocene species of the genus such as *A. beaugei* (Arambourg) and *A. recticona* (Winkler). The teeth also are much larger and the ornamentation better developed than in *A. minutissima* (Winkler).

Genus *Negaprion* Whitley, 1940
Negaprion eurybathrodon (Blake, 1862)
(Fig. 7B)

Referred Material

2127 isolated teeth, GCVP 4935, 5581, 6090, 7005; BCGM 5303a.

Description

Larger anterior teeth measure just over 10 mm in height and 13 mm mesio-distally. Upper teeth have a broad, triangular, distally inclined cusp. The labial face is nearly flat, whereas the lingual face is more convex. Long mesial and distal shoulders are weakly serrated. The edge of the cusp is smooth and sharp, and the cutting edge is continuous with the cusp and lateral shoulders. The root is widely expanded with a thin attachment surface and a long, deep nutritive groove. Anterior teeth are symmetrical and not as wide mesio-distally as lateral teeth.

Lower anterior teeth have a tall, narrow, erect cusp that is nearly perpendicular to the long lateral shoulders. The labial face is nearly flat and the lingual face is convex. The cutting edge is smooth and continuous across the entire crown. Root lobes are thin, nearly horizontal, with a deep lingual nutritive groove. The cusps of lateral teeth are more distally inclined.

Remarks

The lemon shark is the most common shark taxon in the Hardie Mine l.f. White (43) assigned several tooth types to the taxon *Negaprion gibbesi* Woodward, but these have since been split into two taxa, *N. eurybathrodon* and *Cacharhinus gibbesi* (see Kent, 9). The lateral shoulders of *C. gibbesi* teeth are coarsely serrated, whereas those of *N. eurybathrodon* and the Hardie Mine teeth are, in general, weakly serrated to smooth (9). Recent lemon sharks are mainly piscivorous and inhabit tropical and temperate marine waters. It is a nearshore species that will also inhabit estuaries (7, 17). *Negaprion eurybathrodon* has previously been reported from other North American Eocene sites in Virginia (15), North Carolina (16), South Carolina (pers. obs.), and Alabama (43).

RESULTS AND DISCUSSION

Westgate (1) listed 11 species of sharks in the Hardie Mine l.f. Here we describe teeth of at least 16 species, excluding a tentative identification (cf. *Striatolamia macrota*). Some of these differences reflect differing opinions of identification and taxonomic placement. For example, Westgate (1) reported one species of *Carcharias, C. hopei*, while we believe three species of sand tiger sharks are present in the fauna, *C. acutissima, c. hopei*, and *C.* cf. *koerti*. Nonetheless, noteworthy additions to the Hardie Mine shark fauna include representatives of *Heterodontus, Palaeorhincodon, Scyliorhinus*, and *Mustelus*. These are sharks with small teeth that were discovered in the Hardie Mine sediments only after sorting screen-washed matrix. On the basis of numbers of teeth recovered from the Hardie Mine sediments (n=4809), Carcharhiniformes are by far the dominant group, comprising 80% of the assemblage. Of the carcharhinids, *Negaprion* is the most common taxon (56%). In fact, teeth of *Negaprion* is followed by *Hemipristis, Abdounia*, and *Galeocerdo* (13, 12, and 7%, respectively). Lamniforms sharks constitute about 19% of the selachian assemblage, with odontaspidids being the dominant forms. This group represents 97% of the Hardie Mine lamnid assemblage (*Carcharias acutissima* and *C. hopei* in descending order of abundance).

The Late Eocene Hardie Mine shark fauna is remarkably modern at the generic level, with 10 (71%) of the 14 identified genera being extant (Table I). Based on known habitat preferences of living genera and speculated habitat requirements of the extinct genera, the Hardie Mine shark fauna is an admixture of mainly nearshore sharks but offshore taxa are represented in the fauna as well (Table I). This would include benthic or pelagic forms that today inhabit relatively shallow waters of nearshore coastal habitat. Five (36%) of the 14 genera are mainly offshore, oceanic forms: *Palaeorhincodon, Isurus, Carcharocles, Scyliorhinus*, and *Galeocerdo* (Table I). Of these, the habitat requirements of *Scyliorhinus* and *Galeocerdo* are difficult to interpret. For example, species of catsharks (*Scyliorhinus*) and tiger sharks (*Galeocerdo*) inhabit a wide variety of environments - offshore deep-water (10) to nearshore habitat, including intertidal zones (15) and river estuaries (7). Excluding these two genera, 75% of the fauna is made up of taxa that typically would have inhabited the relatively shallow nearshore coastline of the Late Eocene Hardie Mine, while 25% were offshore taxa that would have inhabited deeper water.

Table I. General habitat preferences of the Hardie Mine sharks. Known habitat preferences of extant taxa are indicated by an X, whereas O indicates inferred habitat preferences of extinct (*) genera. The chart is based on material presented in this report, as well as material gathered from Bigelow and Schroeder (45), Compagno (7), Tricas et al. (10), Kent (15), Cappetta (8), Kemp et al. (11), Westgate (1, 28), and Manning and Standhardt (26).

Genus	*Nearshore*	*Oceanic*
Squatina	X	
Heterodontus	X	
Nebrius	X	
**Palaeorhincodon*		O
Carcharias	X	
Isurus		X
**Carcharocles*		O
Scyliorhinus	X	X
Mustelus	X	
Hemipristis	X	
Galeocerdo	X	X
**Physogaleus*	O	
**Abdounia*	O	
Negaprion	X	

The Hardie Mine shark paleofauna is also characterized by a high number of genera that today live in warm-temperate and tropical waters. If Late Eocene sharks had the same temperature requirements as their living counterparts, then of the 10 extant genera in the paleofauna, at least six (60%) had warm-temperate or tropical temperature preferences (*Heterodontus, Nebrius, Hemipristis, Negaprion*, and probably *Isurus* and *Galeocerdo*; see discussions in Kent, 15, and references therein). The same is likely true for *Palaeorhincodon*, as its living counterpart, *Rhincodon*, occurs mainly in relatively warm waters (70-77°F). Some of the other Hardie Mine taxa, such as *Squatina, Scyliorhinus*, and *Isurus*, do occur in cool temperature waters today, but also they range into at least warm temperate waters. This suggests that the Late Eocene nearshore coastal waters of Georgia were probably at least subtropical, perhaps much like the nearshore coastal waters of southern Florida today. It is not clear, however, if warm water conditions persisted year round. Westgage (1) argues that the co-occurrence in the paleofauna of cold water sharks, such as *Lamna* (*Carcharias* here) and *Carcharodon* (= *Carcharocles* here), and warm water sharks, such as *Galeocerdo* and *Ginglymostoma* (= *Nebrius* here), suggests that the Late Eocene nearshore waters of the Hardie Mine coastline "fluctuated from cold to warm," perhaps in a seasonal manner. Nonetheless, the occurrence of predominantly nearshore warm-water sharks and non-shark taxa (unreported fossils in the GCVP collections), such as sawfishes (*Pristis* sp.), barracudas (*Sphyraena* sp.), boxfishes (Ostraciidae), crocodiles, trionichid turtles, emydid-like turtles, sea turtles, palaeopheid snakes, and a moderately large brontotherid, all suggest that warm climatic conditions persisted year round.

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