

THE FIRST DOCUMENTED FOSSIL RECORDS OF *ISISTIUS* AND *SQUATINA* (CHONDRICHTHYES) FROM FLORIDA, WITH AN OVERVIEW OF THE ASSOCIATED VERTEBRATE FAUNA

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ABSTRACT

In October 2016, an email inquiring about the geologic age of a creek in Sarasota County led to the serendipitous ‘discovery’ of fossil teeth of the sharks *Isistius triangulus* and *Squatina* sp. in Florida. Up to that point, no fossils of *Isistius* or *Squatina* from Florida were present in the vertebrate paleontology collections at the Florida Museum of Natural History, nor had they been listed in any scientific publication. However, public inquiries revealed that the presence of both genera in the Florida fossil record has been known among the amateur paleontology community for well over a decade. Once co-author Marks was made aware that the *Isistius* teeth represented something novel, more rigorous collecting was conducted to procure more specimens. A total of 94.5 kg of matrix from four gravel deposits within the creek, informally known as Cookiecutter Creek, were screenwashed and picked to produce 186 whole or partial lower teeth of *Isistius triangulus* and four teeth belonging to *Squatina*. In addition, a diverse vertebrate fauna was recovered that ranged from Pliocene to Pleistocene in age. Screenwashing of 7.5 kg of matrix from the *in situ* Pleistocene Caloosahatchee Formation revealed no specimens of *Isistius* or *Squatina*, which implies their actual source is the underlying Pliocene Tamiami Formation. The unprecedented occurrence of *Isistius triangulus*, with such a high density in Cookiecutter Creek relative to other sites in Florida, may indicate that Cookiecutter Creek preserves a unique deep-water facies within the Tamiami Formation. The associated vertebrate fauna includes taxa from marine, brackish, freshwater, and fully terrestrial paleoenvironments; providing evidence of local sea-level fluctuations during the Pliocene to Pleistocene. The temporally mixed accumulation in these gravel deposits inhibits a more accurate reconstruction of these sea-level fluctuations.

Key words: *Isistius*; *Squatina*; Cookiecutter Shark; Tamiami Formation; Pliocene; sharks; paleontology; Florida.

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INTRODUCTION

The opportunity to collect fossils in Florida attracts people from all over the world and, consequently, many new fossil records are recovered. However, these new occurrences are not always made known to the scientific community. The recent acquisition of fossil teeth of the Cookiecutter Shark, *Isistius* (Gill, 1865), and Angel Shark, *Squatina* Duméril, 1806 into the Florida Museum of Natural (FLMNH) is a prime example. The presence of *Isistius* in the fossil record of Florida has been known among private collectors for well over a decade (G. Hubbell, pers. comm., 2017); and yet no records existed in the FLMNH until October 2016. This article documents the first published occurrence of *Isistius triangulus* and *Squatina* sp. from the fossil record of Florida, both of which are the first representatives of their respective orders from the Florida fossil record. Further, an overview of the entire vertebrate fauna is provided to interpret the local paleoenvironmental history.

There are several reasons why a disconnection exists between amateur and professional collectors. Some collectors simply are not aware that they have found something new, while others wish to keep their personal collecting localities private. In the case of *Isistius* and *Squatina* from Florida, the donor of these specimens and co-author of this publication, Ken Marks, was not aware that these genera had never been formally reported from the state of Florida. An email to Richard Hulbert, Collections Manager of Vertebrate Paleontology at FLMNH, inquiring about the geologic age of a site informally known as Cookiecutter Creek led to the serendipitous realization that the teeth themselves represented something novel.

Subsequently, we put out a call to the public, inquiring if others had found *Isistius* teeth in Florida. This public inquiry was disseminated via multiple social media outlets, including Facebook, Twitter, myFOSSIL, and The Fossil Forum (TFF). Responses to this announcement all led to Dr. Gordon Hubbell's personal collection (Gainesville, FL), which represents one of the largest private collections of sharks (modern and fossil) in

the world. Upon visiting his collection, we found that all the fossil *Isistius* teeth from Florida in the Hubbell collection were collected by Debra Powell in 2003 and based on the locality data, they likely originated from the same creek collected by Marks.

In tandem with this effort, a cursory Google search was used to ferret out any additional known occurrences of *Isistius* from Florida. With the exception of a specimen posted on Pinterest (a website that allows users to manage online images), we were able to determine that every online mention of fossil Cookiecutter Shark teeth from Florida had some connection to TFF and all specimens were seemingly collected from the same locality. This led to the hypothesis that fossil *Isistius* teeth are only known from a single locality in Florida, which must represent a unique facies within a Plio-Pleistocene sequence. *Squatina*, on the other hand, was known among collectors from Charlotte, DeSoto, Hardee, Indian River, and Sarasota counties; but was said to be relatively uncommon.

Interestingly, Cōcke (2002:117) figured a tooth from an unspecified locality in Sarasota County, Florida and identified it as *Isistius brasiliensis*. However, no additional information is provided to determine if it was sourced from the same locality as the material described in this study or the whereabouts of the specimen. It is worth noting that based on the equilateral crown, the specimen imaged in Cōcke (2002) likely belongs to *Isistius triangulus* rather than *Isistius brasiliensis*. Further, through a personal communication with Bill Heim, an avid collector of fossil shark teeth, we were able to find evidence of a single *Isistius* tooth recovered from Apollo Beach in Hillsborough County, Florida collected by Montine Heim in April 1999. Unfortunately, the tooth was found on a sand pile near where new homes were being built and the origin of the sediment is unknown. In fact, Apollo Beach has been constructed/replenished with dredged material since at least the 1950s, making it exceedingly difficult to retrace the origin of any of the fossils found there. For that reason, this paper will focus on *Isistius* and the associated vertebrate fauna from Cookiecutter Creek in southern Sarasota County.

GEOLOGIC SETTING

Materials described herein are derived from a tributary of the Myakka River near North Port in Sarasota County, Florida. This tributary is informally referred to as “Cookiecutter Creek” among the amateur paleontology community. The banks of the tributary expose an unconsolidated marl and shell layer that is attributed to the early Pleistocene Caloosahatchee Formation (Fig. 1). The age of the Caloosahatchee Formation has experienced numerous revisions, from the original late Pleistocene assignment (DuBar, 1958) to an older latest Pliocene assignment (Morgan and Hulbert, 1995). These reassignments are primarily based on vertebrate biostratigraphy of material derived

from the Caloosahatchee River, which indicate an Irvingtonian or Rancholabrean North American land mammal age (NALMA). Extensive sampling of vertebrate material from exposures of the Caloosahatchee Formation in the DeSoto Shell Pit in DeSoto County, Florida suggested an earliest Irvingtonian (late Pliocene) land mammal age (Morgan and Hulbert, 1995). Lyons (1991) also reported a late Pliocene age on the basis of molluscan biostratigraphy and He/U dating of corals done by Bender (1972, 1973), which provided an age range of 2.5–1.8 Ma for the Caloosahatchee Formation. Subsequently, the International Commission on Stratigraphy ratified moving the Plio-Pleistocene boundary from 1.8 Ma to 2.6 Ma (Walker et al.,

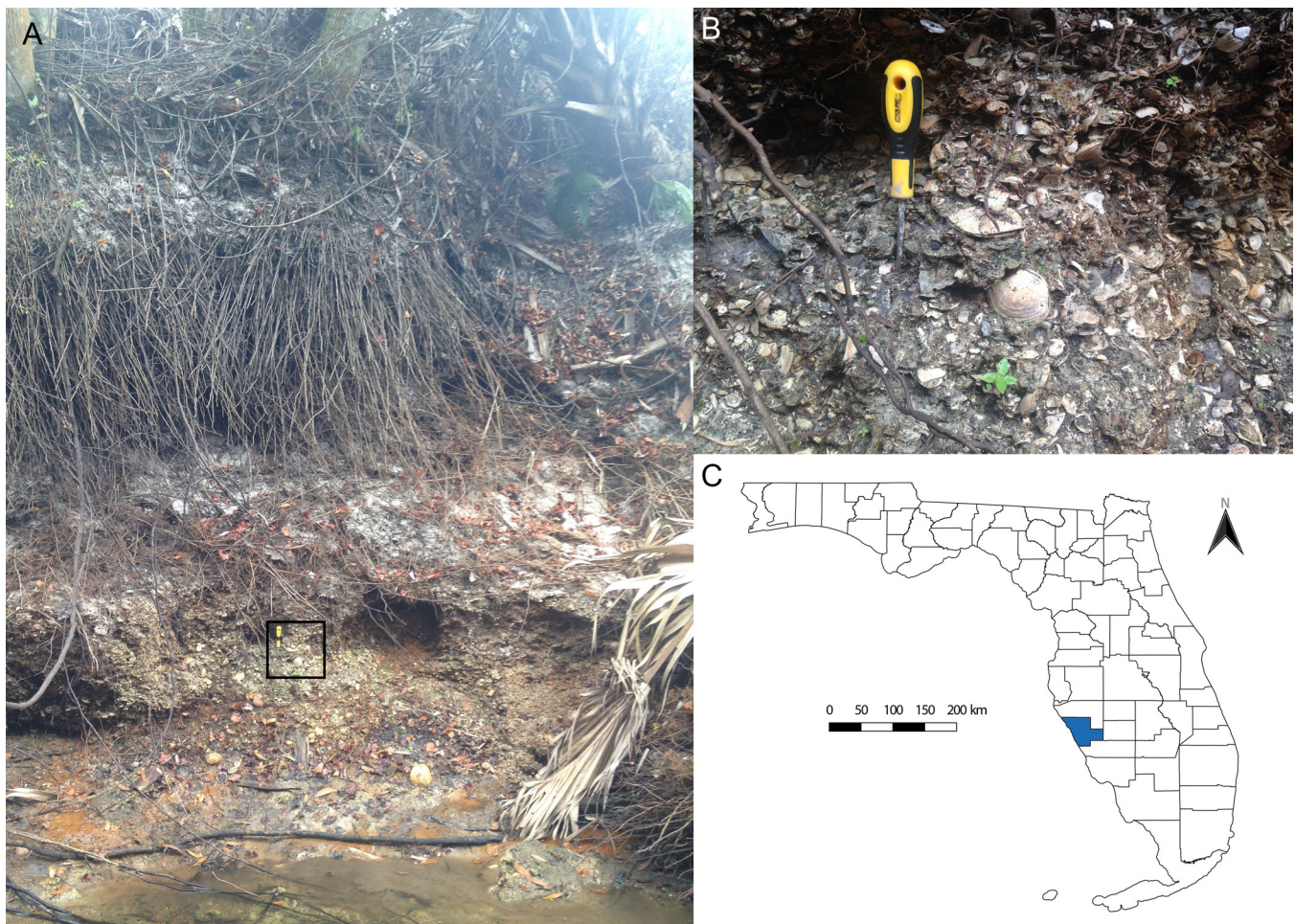


Figure 1. **A.** Image of the bank of Cookiecutter Creek, exposing the shell-rich Caloosahatchee Formation. The pocket to the right of the screwdriver is where *in situ* material was collected. The screwdriver used for scale has a handle length of 11 cm. **B.** Close-up view of the shell-rich Caloosahatchee Formation. **C.** Map of Florida highlighting Sarasota County, where Cookiecutter Creek is found.

2012). As such, the Caloosahatchee Formation is now regarded as early Pleistocene. Our sampling of the *in situ* shell beds of the Caloosahatchee Formation revealed a few chondrichthyan remains, but no specimens of *Isistius* or *Squatina*. Further, these *in situ* chondrichthyan fossils are extremely water-worn and dark in color, indicating that they may be reworked.

The majority of the chondrichthyan remains from Cookiecutter Creek derive from gravel deposits consisting of eroded materials from multiple late Cenozoic stratigraphic units. These deposits are rich in phosphate and fossils. The latter are predominantly marine, but terrestrial taxa are present in small numbers. Given the geologic origin of these gravel deposits, it is difficult to attribute specific specimens to an exact geologic age. In many areas of this part of Florida, the Tamiami Formation directly underlies the Caloosahatchee Formation (Mansfield, 1939). Since then, Hunter (1968) subdivided the Tamiami Formation into five members: the Ochopee Limestone Member, Buckingham Limestone Member, Pinecrest Sand Member, Murdock Station Member, and the Bayshore Clay Member. A sixth member, the Golden Gate Reef Member, was later described by Meeder (1979). This entire sequence of the Tamiami Formation was constrained to an age of 4.95 to 1.95 Ma via strontium isotopic geochronology (Mismir, 1992), which encompasses almost all of the Pliocene as well as the early Pleistocene.

A search of the FLMNH Vertebrate Paleontology database for the class Chondrichthyes from the Tamiami Formation resulted in 1134 specimens spread across four counties in Florida (Lee, Charlotte, Sarasota, and St. Johns). While chondrichthyan remains are prevalent from the Tamiami Formation, they have never been formally described and only appear in a few informal publications (Morgan and Pratt, 1983; Brown, 1988). Further, *Isistius* and *Squatina* have never been reported from any of these localities.

MATERIAL AND METHODS

Five different collecting stations along a short stretch of Cookiecutter Creek were sampled,

with the initial sampling on December 20, 2014 resulting in the first donated specimens. However, most material included in this study was collected by the authors on December 24, 2016 and March 2, 2017. Collecting efforts were heavily focused on screenwashing matrix from gravel deposits, although surface collecting was also conducted while probing the creek bed for coarse gravel. Fifteen specimens of *Isistius* and two specimens of *Squatina* were recovered in 2014, but the amount of matrix picked was not recorded. Between December 2016 and March 2017, a total of 94.5 kg of micro-matrix gravel was picked and an additional 186 whole or partial specimens of *Isistius* lower teeth were recovered, as well as four specimens of *Squatina*. The four gravel deposits collected between December 2016 and March 2017 produced on average two *Isistius* teeth per kg of matrix, with the recovery rate ranging from 0.7 teeth/kg and 3.6 teeth/kg. Apart from the time spent traveling to the collection locality and gathering the micro-matrix, this represents approximately 110 hours of time spent sorting through micro-matrix searching for *Isistius* specimens. We refrain from providing the exact location of this site to prevent poaching; however, locality data will be made available for research purposes upon request and is retained at the Florida Museum of Natural History. Additionally, several other localities were surveyed for the presence of *Isistius*. More than 20 kg of micro-matrix material was collected and picked from a variety of other localities in South Florida (Table 1).

FIELD SAMPLING

Bulk micro-matrix material was collected from the stream by screenwashing gravel deposits from the creek bed. Custom-built sifting screens usually employed while searching for larger fossils in nearby localities like the Peace River were repurposed for the collection of a fine grade of gravel material. Sifting screens were constructed of 1 inch \times 3 inch lumber fastened together with screws to construct a square frame of approximately 15 inch \times 15 inch internal dimensions. Galvanized steel welded wire mesh was stapled to the bottom of these square frames. Two mesh sizes were used,

Table 1. Localities surveyed for the presence of *Isistius* teeth. Note that the amount of matrix picked is based on the sifted dry weight, after fine-grained material had been removed and the material had been desiccated. Further, the number of *Isistius* teeth does not include the 15 teeth collected in 2014 because the amount of matrix picked was not recorded at that time.

Location	Formation(s)	Age	Matrix picked	# of <i>Isistius</i> teeth
Cookiecutter Creek (Gravel Deposits)	Tamiami + Caloosahatchee	Pliocene–Pleistocene	94.5 kg	186
Cookiecutter Creek (<i>In situ</i>)	Caloosahatchee	Pleistocene	7.5 kg	0
Peace River	Peace River	Miocene–Pleistocene	> 20 kg	0
Horse Creek	Peace River	Miocene–Pleistocene	> 20 kg	0
Gap Creek	Arcadia	Miocene	10 kg	0
Little Payne Creek	Peace River	Miocene–Pleistocene	12 kg	0

with the finer mesh consisting of 23-gauge wire spaced with $\frac{1}{4}$ inch \times $\frac{1}{4}$ inch openings and the coarser mesh consisting of 19-gauge wire spaced with $\frac{1}{2}$ inch \times $\frac{1}{2}$ inch openings. The two sifting screens were stacked with the $\frac{1}{4}$ inch sifting screen placed above the $\frac{1}{2}$ inch sifting screen. Before stacking, a loose square (approximately 24 inch \times 24 inch) of fine screen mesh was inserted into the lower $\frac{1}{2}$ inch sifting screen. This loose piece of window screen was constructed of black aluminum wire (0.011 inch diameter) with a mesh size of 18 \times 14 (strands per inch in either dimension) resulting in openings approximately 1.2 mm \times 1.6 mm.

Material was shoveled out of the creek bed and placed into the top sifting screen. The creek level was very low at the time of collection, so a bucket was used to scoop water into the stack of screens to sort the material through the sifters. Larger fossil specimens (mostly chondrichthyan) were removed from the top sifter and bagged. The top sifter was then removed and additional water was poured into the lower sifter to remove as much of the fine sand as possible before the loose screen material was removed from the lower sifter and the retained micro-matrix was dumped into a five-gallon bucket.

POST-PROCESSING

The collected materials were spread out on a tarp to dry in the sun. Then the micro-matrix material was dry sifted to remove more of the loose fine-grained sand by passing it through a sifting screen with 0.05 inch (1.3 mm) mesh. The resultant material was then picked in 1 kg samples, separating out identifiable fossil material from the phosphatic gravel and shell hash. The 1 kg sample batches were passed through a graded set of stackable sieves (0.125 inch, 0.083 inch, 0.050 inch) to organize the material into various size fractions. These subsamples were then picked by spreading small amounts of the sample onto a paper plate. Using a dental probe to move the material on the plate and an LED-lighted high-power (5 \times) large-diameter magnifier to aid in viewing, fossil specimens were picked from the micro-matrix gravel and collected for later examination. Dental measurements were taken from the lingual face, with crown width (CW) being the distance between the crown-root contact on the distal and mesial edges and crown height (CH) being a perpendicular line from the crown-root margin to the crown apex. Taxonomy in the Systematic Paleontology section follows Cappetta (2012).

Abbreviations and Acronyms.—Anatomical: **AW**, anterior width; **CH**, crown height; **CW**, crown width; **MML**, metaconid to metastylid length. Institutional: **FLMNH**, Florida Museum of Natural History; **TFF**, The Fossil Forum; **UF**, University of Florida. Timescale: **NALMA**, North American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Squaliformes Goodrich, 1909

Family Dalatiidae Grey, 1851

Genus *Isistius* Gill, 1865

***Isistius triangulus* (Probst, 1879)**

Figure 2A–F

Description.—Only lower teeth were recovered, which are small with a broadly triangular crown resembling an equilateral triangle and a nearly square root with height approximately equaling the height of the crown. The crown is labiolingually flattened with complete mesial and distal cutting edges. On some specimens, faint serrations are present; however, the majority lack serrations entirely. On the lingual face, the crown-root junction is essentially linear, forming a horizontal margin; whereas on the labial face, the enameloid extends down onto the distal root lobe. On the distal edge, the crown and root meet fluently to form a convex outline. On the mesial edge, the crown extends beyond the root, creating a facet for interlocking with the neighboring tooth. The only exception is the symphyseal tooth (UF 413774; Fig. 2C–D), which is faceted on both edges of the lingual face. On the lingual face, there is a small medial-lingual foramen (i.e., the buttonhole) oriented above an elliptical nutrient groove (i.e., the keyhole) that penetrates through the root. Given the delicate nature of these teeth, often at least one of the root lobes is missing. Most specimens are symmetrical, except for posterior teeth that have mesially deflected crowns (UF 413775; Fig. 2E–F). Teeth from this site have a range in CH=1.6–3.4 mm and CW=1.9–4.6 mm.

Material.—201 lower teeth: UF 405059–405073, 413742–413927.

Occurrence.—FLMNH Vertebrate Paleontology Locality SA072, North Port, Sarasota County, Florida. Most likely originated from the Tamiami Formation.

Remarks.—Extant representatives of the genus *Isistius* have a heterodont dentition, with very small, gracile upper teeth and relatively large, triangular lower teeth. Upper teeth are rarely, if ever, found in the fossil record given their smaller size, more delicate nature, and lack of diagnostic characters. Only a single upper tooth attributed to *Isistius* has been reported from the fossil record, from the Eocene of France (Adnet, 2006). Therefore, the fossil record of *Isistius* is primarily limited to lower teeth. Two extinct species are recognized: the Paleocene to Eocene *Isistius triturator* and the Miocene to Pliocene *Isistius triangulus* (Probst, 1879). No specimens of *Isistius* have been reported from the Oligocene or Pleistocene (Kriwet and Klug, 2008; Cappetta, 2012). *Isistius triturator* has been found in Europe (Germany, France, England, Belgium, and Jordan), Eurasia (Russia), Africa (Morocco), and North America (Virginia) (Kriwet and Klug, 2008 and references therein). *Isistius triangulus* is known from Europe (Germany, France, Belgium, Spain, Portugal, Holland, Austria, and Switzerland), North America (North Carolina and Mexico), Caribbean (Barbados), Central America (Costa Rica and Panama), and South America (Ecuador and Venezuela) (Kriwet and Klug, 2008 and references therein).

Dental characters distinguishing extinct species from extant species are scarce, but extant individuals tend to have a crown that is narrower, resembling an isosceles (rather than equilateral) triangle. Additionally, the root of the extinct species tends to be more square whereas the extant species have remarkably narrower rectangular roots (Probst, 1879, Laurito, 1997; Pino, 2014). A molecular phylogeny of the order Squaliformes found that the genera *Isistius* and *Dalatias* split in the Eocene approximately 50 million years ago (Straube et al., 2015). While Straube et al. (2015:fig. 2) shows a single branch for *Isistius brasiliensis* extending back to the split with *Dalatias*, this branch actually represents the genus *Isistius* as a clade which may

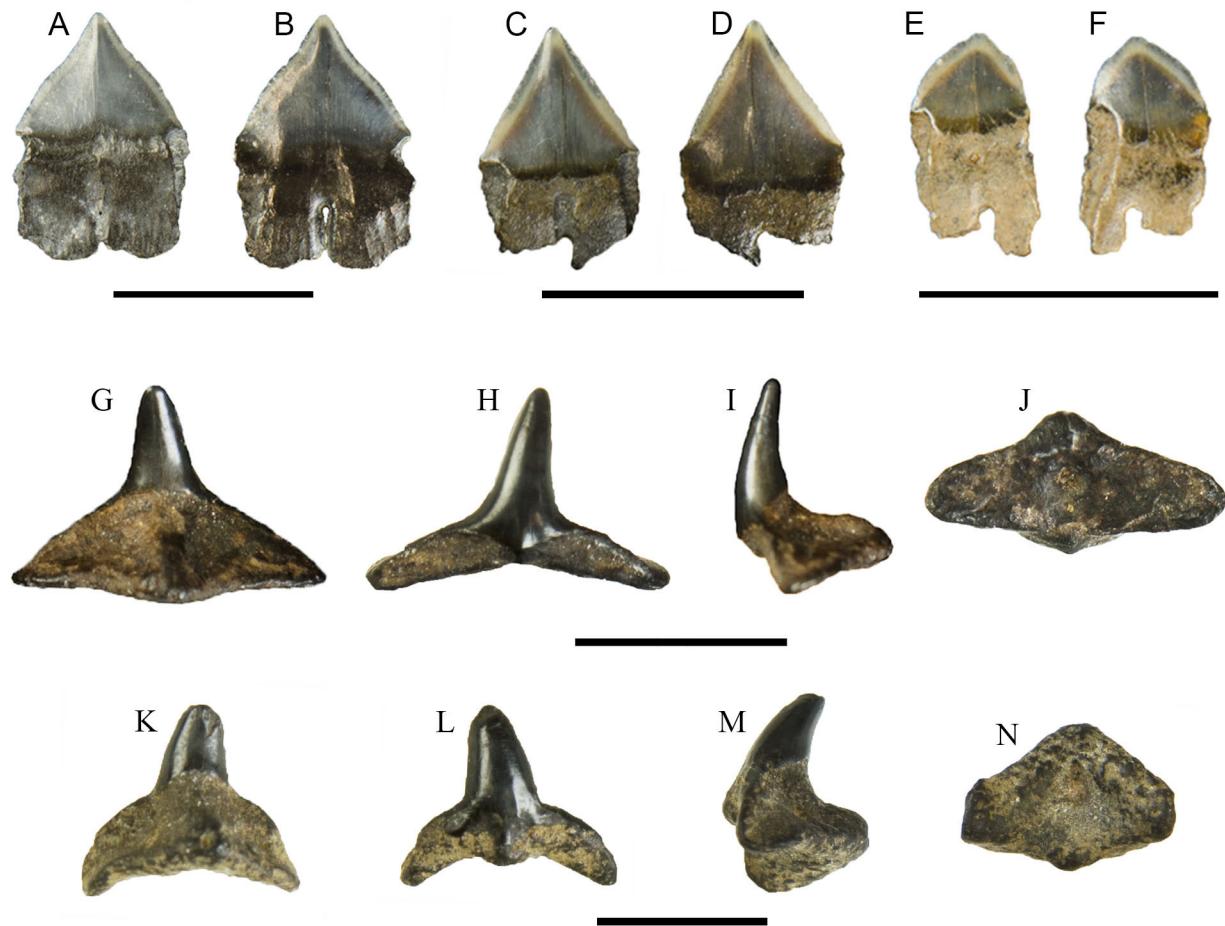


Figure 2. Two new published records for the Florida fossil record: *Isistius triangulus* and *Squatina* sp. A–J from the Cookiecutter Creek Site, Sarasota County; K–N from Peace River 12, Hardee County. A–F. *Isistius triangulus*; A–B: UF 413753, lower tooth, lingual and labial views respectively; C–D: UF 413774, symphyseal lower tooth, lingual and labial views respectively; E–F, UF 413775, posterior lower tooth, labial and lingual views respectively. G–J. *Squatina* sp., UF 415408, indeterminate tooth position, lingual, labial, lateral, and basal views respectively. K–N. *Squatina* sp., UF 333801, indeterminate tooth position, lingual, labial, lateral, and basal views respectively. Scale bars = 5 mm.

include more than one species. Further, the split between these two genera is not calibrated by fossil evidence. Thus, the resolution of the phylogenetic study by Straube et al. (2015) cannot capture the presence or absence of extinct species of *Isistius* or the appearance date of the extant species.

There are two valid extant species of *Isistius*, *I. brasiliensis* and *I. plutodus*. Compagno et al. (2005) recognized a third extant species, *Isistius labialis*; however, this description is based on a single individual that is likely a junior synonym of *I. brasiliensis* (White and Last, 2013; Nelson et al.,

2016). The two valid extant species have a tropical to subtropical range, but have different depth preferences. *Isistius brasiliensis* inhabits water depths from 3700 m to the surface and is known to make daily vertical migrations through the water column, spending time deep in the water column during the day and traveling to the surface at night (Kiraly et al., 2003; Compagno et al., 2005). *Isistius plutodus*, on the other hand, typically occurs in a narrower depth range between 60 and 200 m (Zidowitz et al., 2004; Compagno et al., 2005). Despite this difference in depth preference, both spe-

cies share a unique feeding strategy that has earned them the common name, the Cookiecutter Sharks, and the status as the only parasitic sharks. Both species possess suctorial lips that allow them to attach to prey items. They then employ their large lower teeth to remove a plug of flesh from their prey, which typically includes large fish and marine mammals. However, *Isistius* tends not to discriminate what it feeds on, with reports of attacks on everything from Great White Sharks (Hoyos-Padilla et al., 2013) to rubber sonar devices on nuclear submarines (Compagno et al., 2005), and even one recorded attack on a human (Welsh, 2011). *Isistius plutodus* has a scattered distribution throughout the Atlantic and Pacific, whereas *I. brasiliensis* has a very widespread distribution in the Atlantic, Pacific, and Indian oceans (Compagno et al., 2005).

Order Squatiniformes Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Duméril, 1806

***Squatina* sp.**

Figure 2G–N

Description.—The teeth are broader than they are tall. The crown is vertically erect, but curves lingually and may bear a slight distal deflection. The enameloid extends well onto the shoulders of the root, with complete cutting edges that lack serrations. On the labial face, an enameloid apron extends down over the root, forming a central point. In some cases, the enameloid apron does not extend beyond the root; although, this is likely due to wear. The root is very short relative to the crown, but bears an extremely prominent lingual protuberance. This feature and the mesial-distal width form a broadly triangular base that is perpendicular to the crown. The root base may be flat or concave, bearing a prominent central foramen. Teeth from Cookiecutter Creek range from CH=3.3–6.0 mm and CW=1.9–9.0 mm (note: the smallest specimen is incomplete such that CW cannot be measured; it would have been less than 1.9 mm).

Material.—Seven teeth: UF 333801–333803, 415394–415396, 415408.

Occurrences.—FLMNH Vertebrate Paleontology Locality SA072, North Port, Sarasota County, Florida. FLMNH Vertebrate Paleontology

Locality HR066, Peace River 12, Hardee County, Florida.

Remarks.—The genus *Squatina*, the only representative of the order Squatiniformes, has a long chronologic record, Jurassic to the present. Despite 160 million years of evolution, the tooth morphology of *Squatina* has remained fairly stable, making it difficult to distinguish different species (Kent, 1994; Cappetta, 2012). As such, isolated teeth attributed to extinct species tend to be distinguished by their stratigraphic position more so than by their morphological differences (Kent, 1994). Representatives from the Mio-Pliocene have classically all been assigned to *Squatina subserrata* (Kent, 1994; Cappetta, 2012), despite the fact that the genus is represented by up to 22 different extant species (Compagno et al., 2005; Stelbrink et al., 2010; Nelson et al., 2016). A molecular phylogeny of 17 of the extant species of *Squatina* found that many of these likely originated during the Miocene (Stelbrink et al., 2010), which means that stratigraphic position is not sufficient for delineating different species.

Extant individuals have a flattened skate-like body, with a terminal mouth, and teeth adapted for clutching prey (Compagno et al., 2005; Cappetta, 2012). This body form is ideal for their demersal habit, and allows them to bury themselves in the substrate and ambush prey items. Through a review of the extant species listed in Compagno et al. (2005), Stelbrink et al. (2010), and FishBase.org (Froese and Pauly, 2017), we determined that only *Squatina dumeril* has a range proximal to our collecting site. The BEAST analysis conducted by Stelbrink et al. (2010) estimated the split between *S. dumeril* and *S. californica* occurred at 6.11 ± 2.53 Ma, which they proposed was linked to the rise of the Panamanian Isthmus. Thus, it is plausible that the specimens described herein could belong to the extant species *S. dumeril*; however, unfortunately, a detailed morphometric analysis would likely be necessary to differentiate different species of *Squatina* on the basis of isolated teeth, which is outside the scope of this paper. *Squatina dumeril* is known to range from close inshore to depths up to 1290 m, but most commonly is encountered between 40

and 250 m (Compagno et al., 2005). In the spring and summer, *S. dumeril* can be found inshore off the Atlantic coast of USA, and is thought to migrate to deeper water in the winter (Compagno et al., 2005). Thus, unlike *Isistius*, which makes daily migrations through the water column, *Squatina* makes seasonal migrations.

DISCUSSION

Given the nature of gravel deposits, which often represent accumulations from multiple stratigraphic units, it is difficult to confidently reconstruct the paleoenvironment. While we report the associated chondrichthyan fauna, we understand that these species are not all contemporaneous. Further, our sampling is largely limited to screenwashing, which may bias the sample in favor of smaller taxa. This study did not seek to conduct a detailed statistical analysis of the fauna present, but rather compose a taxonomic list of the vertebrate fauna. Consequently, relative abundance of different chondrichthyan taxa derived from the 94.5 kg of matrix is reported using a qualitative measure of abundance as common, moderate, or uncommon (Table 2), rather than a quantitative metric. Nonetheless, an attempt to interpret the paleoenvironment is made with the chondrichthyan evidence available and other associated vertebrate taxa.

So far, at least seven chondrichthyan orders, represented by at least 18 taxa, are found in the gravel deposits of Cookiecutter Creek: Squaliformes, Carcharhiniformes, Lamniformes, Orectolobiformes, Squatiniformes, Pristiformes, and Myliobatiformes (Table 2; Figs. 2 and 3). The two most prevalent orders are Carcharhiniformes and Myliobatiformes, as is often the case in Mio-Pliocene deposits. Lamniformes may be as or more speciose than Myliobatiformes, but are much less abundant. The other four orders (Squaliformes, Orectolobiformes, Squatiniformes, and Pristiformes) are each represented by a single species. Interestingly, *Isistius triangulus* and *Squatina* sp. are not only the first published record of their respective genera or species, but also the first of their respective orders (Squaliformes and Squatiniformes) for the fossil record of Florida, based on material available in the

Vertebrate Paleontology collection at FLMNH, and a review of the paleontological literature.

Based on the responses received from amateur collectors, the known occurrence of *Isistius triangulus* in Florida is seemingly limited to Cookiecutter Creek. The true origin of the single specimen from Apollo Beach cannot be determined. Several locations on the Peace River lithologically similar to the Cookiecutter Creek site were sampled and no *Isistius* teeth were found among the copious micro-fossil material recovered; however, a single tooth belonging to the genus *Squatina* was recovered, validating its occurrence outside of Cookiecutter Creek. With the presumption that the substantial summer flood-stage flow of a waterway the size of the Peace River might fragment delicate *Isistius* teeth rendering them too pulverized to recover, various smaller creeks were sampled. Horse Creek (DeSoto County), Gap Creek (Manatee County), and Little Payne Creek (Hardee County) all yielded significant chondrichthyan fossil material, but lacked any *Isistius* specimens (Table 1). These sites vary in stratigraphic units and so the hypothesis that *Isistius* specimens might be gleaned from a wide geological range by searching in low-energy waterways where the delicate specimens might be preserved seems disproven. While there are still many other localities in Florida that could potentially contain *Isistius* teeth, our efforts thus far indicate that Cookiecutter Creek is unique in that respect.

Further, the density of these teeth in Cookiecutter Creek is fairly high (on average two *Isistius* teeth per kg of matrix) relative to other sites documenting the occurrence of *Isistius*. The only publication to document a higher density of *Isistius* in the fossil record is from the late Miocene Piña Sandstone facies of the Chagres Formation in Panama (Carrillo-Briceño et al., 2015), from which 272 teeth were recovered from 69.3 kg of matrix (nearly four *Isistius* teeth per kg of matrix on average). However, it is not mentioned if every *Isistius* tooth reported was found via screenwashing, so the density may be inflated. The Piña Sandstone facies of the Chagres Formation has been interpreted to be a bathyal environment, with depth estimates

Table 2. List of all chondrichthyan taxa recovered from Cookiecutter Creek, their relative abundance (rarity), habitat, and known depths. Abundance of chondrichthyan taxa from the 94.5 kg sample is defined as follows: common (>100 specimens), moderate (10–100 specimens), and uncommon (<10 specimens). For extinct taxa (†), depth range is based on extant analogs when possible. Data for habitat and depth is primarily from Compagno et al. (2005) and FishBase.org.

Taxa	Abundance	Habitat	Depth Range (m)	Iconography
Order Squaliformes				
† <i>Isistius triangulus</i>	Common	Epipelagic – Benthopelagic	0 – 3700 (<i>I. brasiliensis</i>) 60 – 200 (<i>I. plutodus</i>)	Fig. 2A–F
Order Carcharhiniformes				
† <i>Hemipristis serra</i>	Uncommon	Benthopelagic	1 – 132 (<i>H. elongata</i>)	Fig. 3A
<i>Galeocerdo cuvier</i>	Uncommon		0 – 800 (usually 0–140)	Fig. 3B–C
† <i>Physogaleus contortus</i>	Uncommon			Fig. 3D–E
<i>Carcharhinus</i> spp.	Common			Fig. 3F–G
<i>Rhizoprionodon</i> spp.	Moderate		1 – 500	Fig. 3H
<i>Negaprion brevirostris</i>	Moderate	Neritic	0 – 92	Fig. 3I
Order Lamniformes				
<i>Carcharias taurus</i>	Moderate	Neritic	0 – 191	Fig. 3J
<i>Alopias</i> cf. <i>A. vulpinus</i>	Uncommon	Pelagic	0 – 650 (usually 0 – 200)	Fig. 3K
<i>Isurus</i> sp.	Uncommon	Pelagic		Fig. 3L
† <i>Carcharocles megalodon</i>	Uncommon			Not imaged
<i>Carcharodon carcharias</i> *	N/A	Pelagic	0 – 1200 (usually 0 – 250)	
† <i>Carcharodon hastalis</i> *	N/A			
Order Orectolobiformes				
<i>Ginglymostoma</i> sp.	Uncommon	Demersal	0 – 130 (usually 1 – 35) (<i>G. cirratum</i>)	Fig. 3M–N
Order Squatiniformes				
<i>Squatina</i> sp.	Uncommon	Demersal	0 – 1290 (usually 40 – 250) (<i>S. dumeril</i>)	Fig. 2G–N
Order Pristiformes				
Pristidae	Uncommon	Demersal – Benthopelagic		Fig. 3O–P
Order Myliobatiformes				
<i>Dasyatis</i> sp.	Common	Demersal		Fig. 3Q–R
<i>Aetobatus</i> sp.	Moderate	Benthopelagic	0 – 80 (<i>A. narinari</i>)	Fig. 3S–T
Myliobatidae	Common	Benthopelagic		Fig. 3U–V

*Species reported anecdotally from Cookiecutter Creek, but their presence has yet to be validated by the authors of this study.

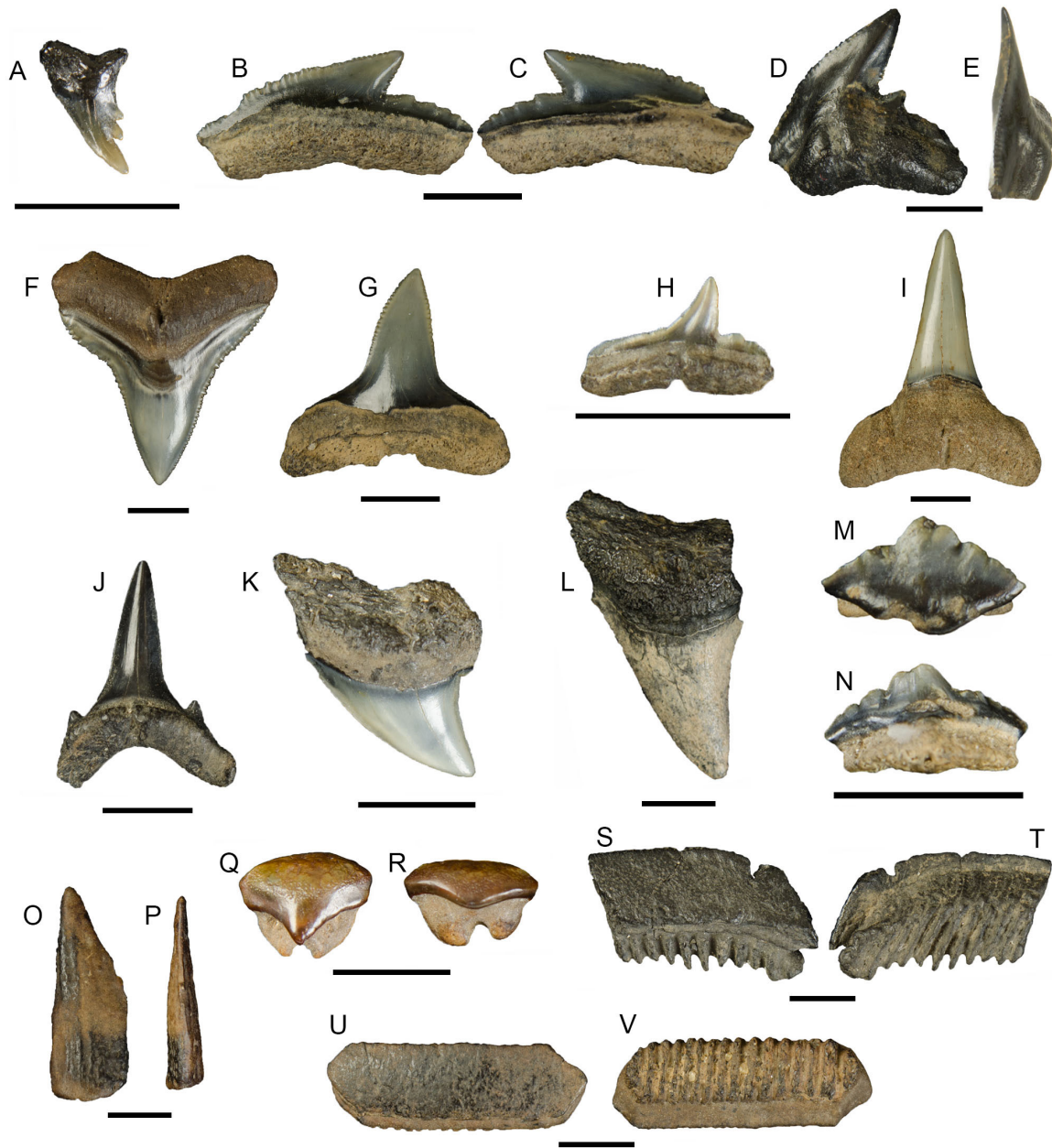


Figure 3. Chondrichthyan taxa represented in Cookiecutter Creek. **A.** *Hemipristis serra*, UF 415397, juvenile upper tooth, lingual view. **B–C.** *Galeocerdo cuvier*, UF 415398, indeterminate tooth position, lingual and labial views respectively;. **D–E.** *Physogaleus contortus*, UF 415410, indeterminate tooth position, lingual and mesial profile views respectively. **F–G.** *Carcharhinus* sp.; **F:** UF 415401, upper anterior tooth, lingual view; **G:** UF 415403, lower tooth, labial view. **H.** *Rhizoprionodon* sp., UF 415412, indeterminate tooth position, lingual view. **I.** *Negaprion brevirostris*, UF 415411, lower tooth, lingual view. **J.** *Carcharias taurus*, UF 415400, lower tooth, lingual view. **K.** *Alopias* cf. *A. vulpinus*, UF 415432, upper tooth, lingual view. **L.** *Isurus* sp., UF 415419, upper lateral tooth, lingual view. **M–N.** *Ginglymostoma* sp., UF 415399, indeterminate tooth position, lingual and labial views respectively. **O–P.** Pristidae, UF 415409, rostral denticle, upper face and anterior views respectively; **Q–R.** *Dasyatis* sp., UF 415420, indeterminate tooth position, lingual and labial views respectively. **S–T.** *Aetobatus* sp., UF 415430, fragmentary medial tooth, occlusal and basal views respectively. **U–V.** Myliobatidae, UF 415423, medial mouth plate, occlusal and basal views respectively. Scale Bars = 5 mm.

ranging from 200–500 m (Carrillo-Briceño et al., 2015; Perez et al., 2017).

Depth preferences of the entire chondrichthyan fauna range from neritic to pelagic (Table 2), which implies that the gravel deposits are capturing a wide swath of paleoenvironmental facies. Osteichthyan taxa also reflect a range of paleoenvironments, with marine and freshwater species occurring together (Table 3; Fig. 4). The two most common bony fish are the genus *Pogonias* (Black Drum) and the family Lepisosteidae (Gar). *Pogonias* is predominantly marine, but may also inhabit brackish environments (Chao et al., 2015). Species within the family Lepisosteidae typically inhabit freshwater and brackish environments, except for one species, *Atractosteus spatula*, which enters marine habitats (Cavin, 2010). Most of the osteichthyan taxa prefer nearshore, marine environments, e.g. *Pogonias*, *Sphyraena*, *Lagodon*, *Archosargus*, and Diodontidae. However, the presence of freshwater taxa, such as Lepisosteidae and Ictaluridae (Catfish), offer the possibility of an aquatic terrestrial facies, or at least close proximity to one, within this Plio-Pleistocene sequence.

Evidence of a freshwater facies is not limited to bony fish. Additional taxonomic groups include amphibians, reptiles, birds, and mammals (Table 4). Class Amphibia (Fig. 5A–C) is represented by a single frog vertebra (indeterminate taxon). Class Reptilia (Fig. 5D–H) is represented by freshwater turtle carapace elements (family Emydidae), tortoise carapace elements (genus *Hesperotestudo*),

three snake vertebrae (indeterminate taxa), and two *Alligator* teeth (Table 4). While the herpetofauna does not offer much chronological context, it does provide insight into the paleoenvironment and again supports the interpretation of a marginal marine or fully terrestrial environment within a predominantly marine sequence.

Class Aves is represented by a single pedal phalanx belonging to the family Procellariidae (Fig. 5I–J), which includes shearwaters and petrels (Table 4). While the distal end of this fossil is not present, the proximal articulation and the elongate nature of the specimen are intact. This specimen is referred to the family Procellariidae because of the well-developed point on the dorsal (acrotarsial) border of the articulation, combined with the moderate concavity of the plantar surface. The specimen represents a large shearwater in the size range of the living *Puffinus gravis* (Great Shearwater) or *Calonectris diomedea* (Scopoli's Shearwater). This level of identification does not offer much chronological context beyond the Cenozoic; however, the preservation is typical of other Pliocene deposits in Florida (D. W. Steadman, pers. comm., 2017). Further, the family Procellariidae has been documented from the Miocene Calvert Formation and the Mio-Pliocene Yorktown Formation (Purdy et al., 2001).

Class Mammalia is represented by two horse teeth, a fragment of a mammoth tooth, a proboscidean tusk fragment, and two rodent teeth (Table 4; Fig. 5K–N). The two horse teeth provide im-

Table 3. Osteichthyan taxa present in Cookiecutter Creek (Fig. 4).

Order	Family	Species	Element(s)	Iconography
Perciformes	Sciaenidae	<i>Pogonias cromis</i>	Dentary; teeth	Fig. 4A–B
	Sphyracidae	<i>Sphyracna barracuda</i>	Teeth	Fig. 4C
	Sparidae	<i>Archosargus</i> sp.	Teeth	Fig. 4D–E
		<i>Lagodon</i> sp.	Teeth	Fig. 4F
Tetraodontiformes	Diodontidae	Indeterminate	Dentary	Fig. 4G–H
Lepisosteiformes	Lepisosteidae	<i>Atractosteus</i> sp.	Scales	Fig. 4I
		Indeterminate	Teeth; scales; vertebrae	Fig. 4J–M
Siluriformes	Ictaluridae	Indeterminate	Pectoral spines	Fig. 4N–O
Indeterminate	Indeterminate	Indeterminate	Vertebrae; hyperostotic spines; teeth	Fig. 4P–T

portant temporal context, as they represent two different species. The first tooth, UF 415434 (Fig. 5K), is small and heavily worn; however, enough is preserved to measure the metaconid to metastyloid length (MML=8.2 mm) and the anterior width (AW=8.3 mm). Based on the overall morphology

and these two quantitative metrics, we determined that the tooth represents *Nannippus aztecus*, which occurs in the Hemphillian from the late Miocene to early Pliocene (~7–4 Ma; Hulbert, 1993). The second tooth, UF 415435, is also fragmentary, but is much higher crowned than the other equid tooth.

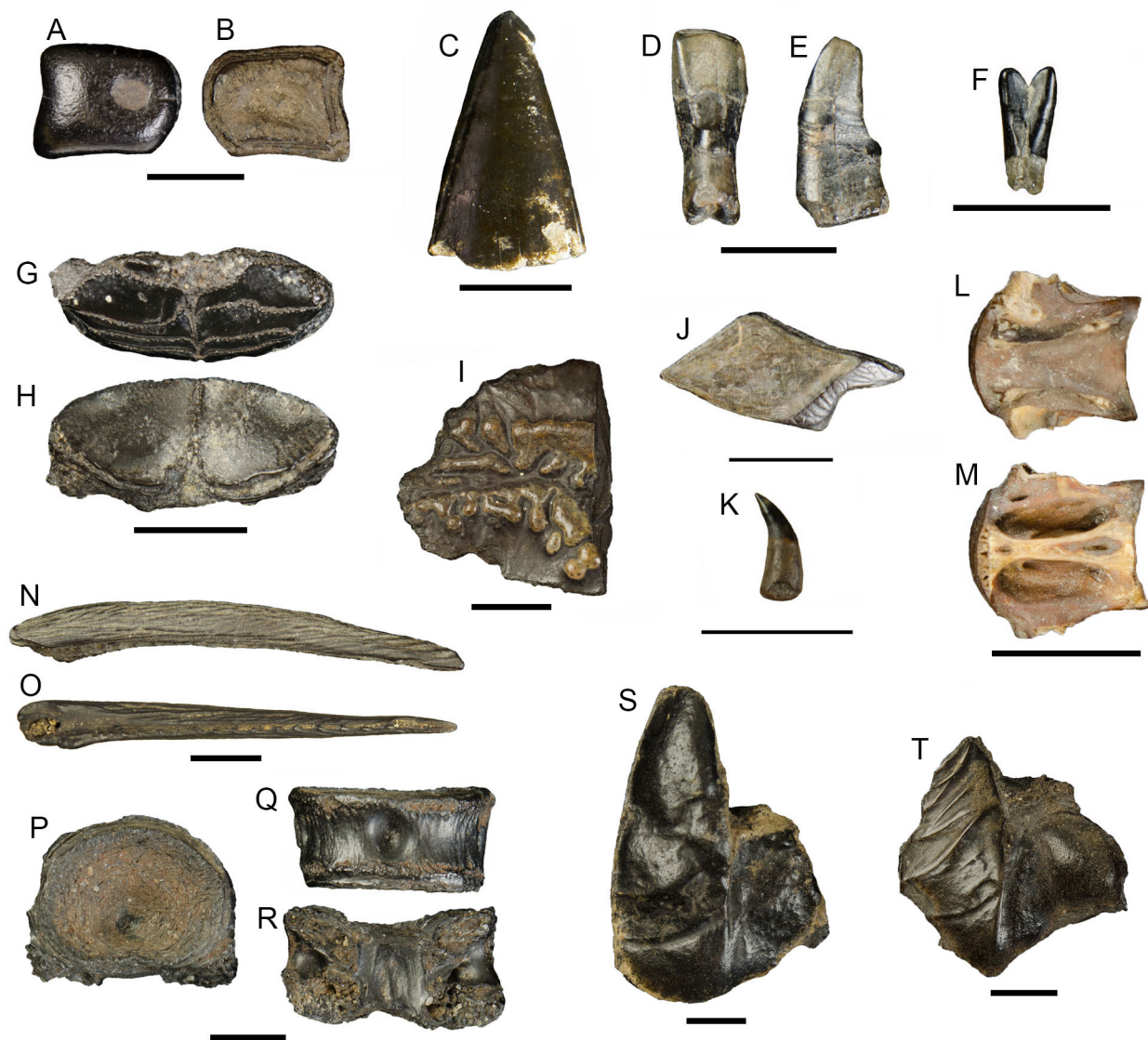


Figure 4. Osteichthyan taxa represented from the Cookiecutter Creek Site, Sarasota County, Florida. **A–B.** *Pogonias cromis*, UF 415457, tooth, occlusal and basal views respectively. **C.** *Sphyræna barracuda*, UF 415458, tooth. **D–E.** *Archosargus* sp., UF 415446, tooth, lingual and lateral views respectively. **F.** *Lagodon* sp., UF 415449, tooth, lingual view. **G–H.** Diodontidae, UF 415443, dentary, occlusal and basal views respectively. **I.** *Atractosteus* sp., UF 415448, scale. **J.** Lepisosteidae, UF 415833, scale. **K.** Lepisosteidae, UF 415465, tooth, lateral view. **L–M.** Lepisosteidae, UF 415464, vertebra, ventral and dorsal views respectively. **N–O.** Ictaluridae, UF 415445, pectoral spine, lateral and basal views respectively. **P–R.** indeterminate taxon, UF 415834, vertebra. **S:** indeterminate taxon, UF 415461, hyperostotic spine, lateral view. **T.** indeterminate taxon, UF 415459, hyperostotic spine, lateral view. Scale bars = 5 mm.

Table 4. All non-fish vertebrates recovered from Cookiecutter Creek (Fig. 5).

Class	Order	Family	Species	Element(s)	Iconography
Amphibia	Anura	Indeterminate	Indeterminate	Vertebra	Fig. 5A–C
Reptilia	Testudines	Emydidae	Deirocheylinae*	Carapace elements	Fig. 5D
		Testudinidae	† <i>Hesperotestudo</i> sp.	Carapace elements	Not imaged
	Squamata	Colubridae?	Indeterminate	Vertebrae	Fig. 5E–G
	Crocodylia	Alligatoridae	<i>Alligator</i> sp.	Teeth	Fig. 5H
Aves	Procellariiformes	Procellariidae	Indeterminate	Pedal phalanx	Fig. 5I–J
Mammalia	Cetacea	Indeterminate	Indeterminate	Vertebral epiphysis	Not imaged
	Perissodactyla	Equidae	† <i>Nannippus aztecus</i>	Right lower premolar	Fig. 5K
			<i>Equus</i> sp.	Lower molar	Not imaged
	Proboscidea	Elephantidae	† <i>Mammuthus</i> sp.	Tooth fragment	Not imaged
		Indeterminate	Indeterminate	Tusk fragment	Not imaged
	Rodentia	Cricetidae	<i>Sigmodon</i> sp.	Molar	Fig. 5L–N
		Indeterminate	Indeterminate	Incisor	Not imaged

*Genus or species level identification is not warranted, but the specimens can be placed in the subfamily Deirochelyinae.

The morphology is distinctive of the genus *Equus*, which is an index fossil used to mark the beginning of the Blancan NALMA (Lundelius et al., 1987; Morgan and Hulbert, 1995). Further, mammoths have a temporal range limited to the Pleistocene, with their first appearance in Florida being 1.5–1.1 Ma from the Leisey Shell Pit (Webb et al., 1989; MacFadden and Hulbert, 2009). The presence of these temporally distinct terrestrial taxa may indicate multiple transgressive–regressive events within this Plio-Pleistocene sequence.

Unraveling a chronological narrative for Cookiecutter Creek is impossible from gravel deposits alone, yet the documentation of this fauna provides insight into this story. The unique occurrence of *Isistius*, along with other pelagic taxa, indicates a fully marine environment; however, the presence of two temporally distinct equids suggests that sea level likely lowered multiple times. This interpretation of a transgressive–regressive sequence is further supported by the range of paleoenvironments inferred from the entire vertebrate fauna, which includes marine, freshwater, and terrestrial

components. While marine taxa dominate, it seems that the gravel deposits in Cookiecutter Creek record paleoenvironments ranging from open-ocean to marginal marine or even fully terrestrial at times.

CONCLUSIONS

The aptly named Cookiecutter Creek in Sarasota County contains an unprecedented occurrence for Florida, the extinct Cookiecutter Shark *Isistius triangulus*. The 201 specimens described herein represent the first published record of the order Squaliformes from the fossil record of Florida. Additionally, seven teeth attributed to *Squatina* sp. represent the first published record of the order Squatiniformes from the Florida fossil record. Based on the local geology and associated fauna, we attribute the *Isistius* and *Squatina* teeth from Cookiecutter Creek to the Pliocene Tamiami Formation. The single *Squatina* tooth from the Peace River is attributed to the Miocene Peace River Formation. Extant *Isistius* species typically inhabit pelagic environments, which may indicate that these teeth are sourced from a unique deep-water

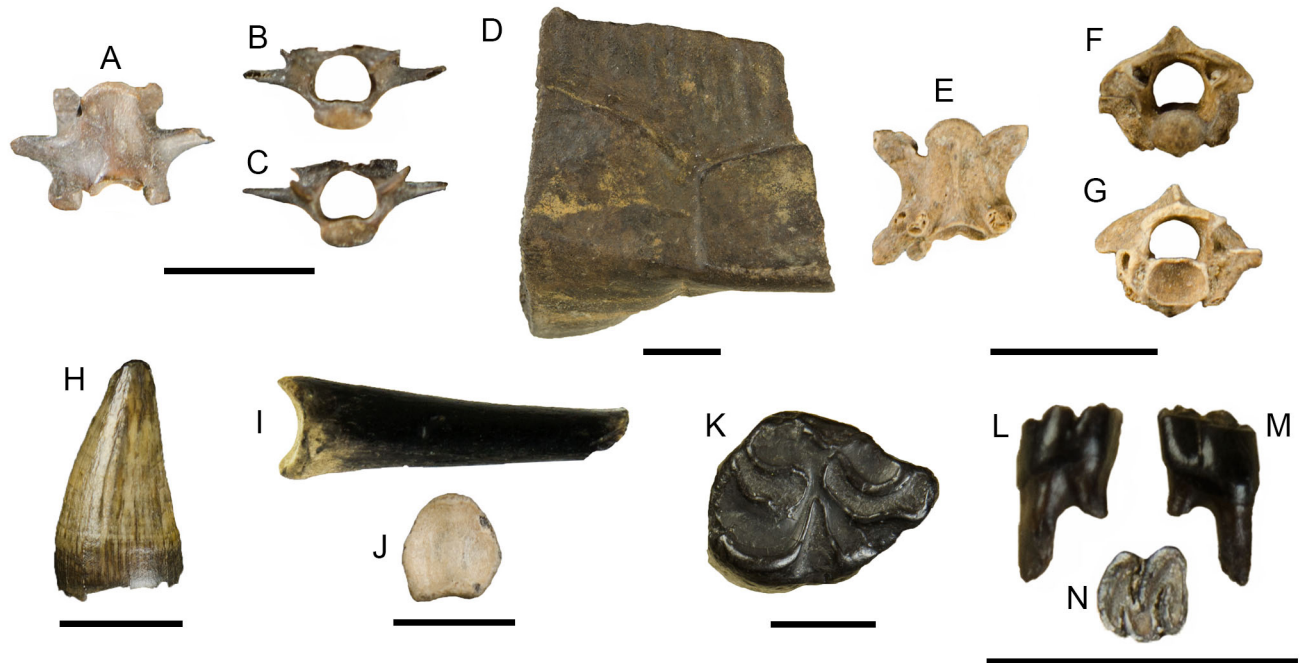


Figure 5. Non-fish vertebrates from the Cookiecutter Creek Site, Sarasota County, Florida. **A–C.** Anura, UF 415438, vertebra, ventral, anterior, and posterior views respectively. **D.** Emydidae, UF 415829, bridge peripheral, dorsal view. **E–G.** Colubridae?, UF 415442, vertebra, ventral, anterior, and posterior views respectively. **H.** *Alligator* sp., UF 415440, tooth, lateral view. **I–J.** Procellariidae, UF 416304, medial phalanx, lateral and proximal views respectively. **K.** *Nannippus aztecus*, UF 415434, right lower premolar, occlusal view. **L–N.** *Sigmodon* sp., UF 416303, second molar, buccal, lingual, and occlusal views respectively. All scale bars = 5 mm, except scale bar = 10 mm for D.

facies within the Tamiami Formation. Despite our tentative Pliocene assignment for these specimens, they were sourced from gravel deposits that inhibit more accurate dating. The associated vertebrate fauna in these gravel deposits represent multiple paleoenvironments including marine, brackish, freshwater, and terrestrial. Further, two temporally distinct equids indicate that the paleoenvironment may have been fully terrestrial more than once, implying local sea-level fluctuations from the Pliocene to Pleistocene. The documentation of these novel taxa and the associated vertebrate fauna was entirely serendipitous. The fact that the presence of *Isistius* and *Squatina* in the fossil record of Florida had been known for more than a decade warrants for better communication between the public and scientific community. There are undoubtedly more discoveries akin to this in private collections waiting to be brought to light.

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