FOSSIL CHONDRICHTHYANS AND OTHER NEW PALEONTOLOGICAL RESOURCES AT GULF ISLANDS NATIONAL SEASHORE

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Abstract—Gulf Islands National Seashore (GUIS), established in 1971, encompasses parts of coastal Florida and Mississippi, including seven offshore barrier islands. Historically, paleontological resources documented within and near GUIS were limited to mollusks and microfossils identified from drill cores. As a result of a National Park Service paleontological resources inventory at GUIS conducted during 2021 and 2022, abundant marine fossils were documented at the park from multiple localities. These new finds consist of 711 specimens primarily represented by shark teeth and other chondrichthyan or bony fish remains that were found as float on beaches. Specimens recovered at GUIS are significant as very few chondrichthyan fossils are known from along the northern Gulf of Mexico in these states. Preliminary analysis and contextual insights suggest that the GUIS collection represents Plio-Pleistocene assemblages. Six genera and at least 11 species of fossil shark as well as two ray taxa are now reported from this coastline at GUIS, as well as a variety of bony fish mostly represented by teeth, spines, and otoliths. These paleontological resources represent the first fossilized marine vertebrates described from the Mississippi barrier islands and the largest single assemblage of chondrichthyan fossils across this region from the Florida panhandle through Mississippi.

INTRODUCTION

Gulf Islands National Seashore (GUIS) was authorized by the United States Congress on January 8, 1971 (Schupp, 2019). The park's purpose is to preserve and interpret an interconnected system of barrier islands, wilderness, and coastal and marine ecosystems and coastal defense fortifications in Mississippi and northwest Florida, while providing for public use and enjoyment (NPS, 2016a). GUIS has administrative units in both Florida and Mississippi (Fig. 1). The Florida units of the park include the Naval Live Oaks, Santa Rosa, Okaloosa, and Perdido Key areas, Fort Barrancas (at the Pensacola Naval Air Station) and Fort Pickens, in Escambia, Okaloosa, and Santa Rosa counties. Apart from the Naval Live Oaks and Fort Barrancas areas, all land-based Florida units are on Santa Rosa Island or Perdido Key. The Mississippi units of the park consist of five barrier islands (Petit Bois, Sand [also known as "West Petit Bois"], Horn, and Ship, as well as part of Cat Island) in Harrison and Jackson counties. The Davis Bayou area is on the mainland of Mississippi. The park preserves both natural and cultural resources along the Gulf of Mexico, a large marine sedimentary basin that extends roughly 1,600 km from the western coast of Florida to the US–Mexico border (Williams et al., 2012). The park is more than 160 km long and encompasses 56,322 ha (139,175 ac), although ~80% of the park's area is submerged or intertidal (Schupp, 2019). GUIS has a wide variety of geomorphological features unique to coastal units, including but not limited to: beaches, active and stabilized dune complexes, and active and inactive overwash zones (Schupp, 2019).

METHODS

The first paleontological resources inventory at GUIS was conducted during 2021 and 2022. A research and collecting permit (GUIS-2021-SCI-0037) was approved by the NPS in early November 2021 in response to a Technical Assistance Request submitted by the park. Staff at GUIS had been made aware of visitors finding fossil shark teeth on the beaches within park boundaries (D. Fairchild and B. Pitts, personal commun., 2021). Additionally, prior discussions with the GUIS law enforcement rangers raised concerns of rumored unauthorized collection of fossils (presumed to be shark teeth) on Ship Island associated with the ferry concessionaire. As a result of these concerns, our goals were to confirm and document the presence and distribution of paleontological resources in GUIS coastal areas, explore the origin or source of any fossils found, and attempt to collect representative specimens for identification, scientific interest, and to serve as reference voucher specimens for the park.

A paleontological resource inventory team, led by researchers from Georgia State University, participated in seven days of fieldwork during November 2021 to survey the Florida portion of GUIS and gather baseline information on paleontological resources. Members of the main investigative team who participated in field surveys include John Michael Clinton and Christy Visaggi. Additionally, numerous other individuals associated with GUIS participated in field surveys and collection efforts throughout this inventory. The Florida areas surveyed within GUIS included Santa Rosa (Opal Beach), Fort Pickens, and Perdido Key (Johnson Beach). Two shorter field surveys were additionally completed in Florida during December 2021 and August 2022. Field investigation was also conducted at the Mississippi units of GUIS including West Petit Bois, Horn and Ship Islands in March 2022 by co-authors Clinton, Visaggi, and others. Multiple park staff stationed in Florida and Mississippi, as well as several local visitors, provided insight on fossil resources and where they might be found during site visits from 2021–2022.

No previous park-specific paleontological resource inventories had been conducted at GUIS prior to this effort, although a review of geological formations and fossil resources was addressed in the 2007 Gulf Coast Inventory & Monitoring Network (GULN) paleontological resource summary report (Kenworthy et al., 2007). Information in that report relied primarily on articles and correspondence regarding the geology of the seashore and offshore units encompassing the park and known fossil specimens within museum collections. Kenworthy et al. (2007) noted a lack of documented paleontological resources at GUIS, especially compared to several other NPS units within the GULN. This same report also highlighted the

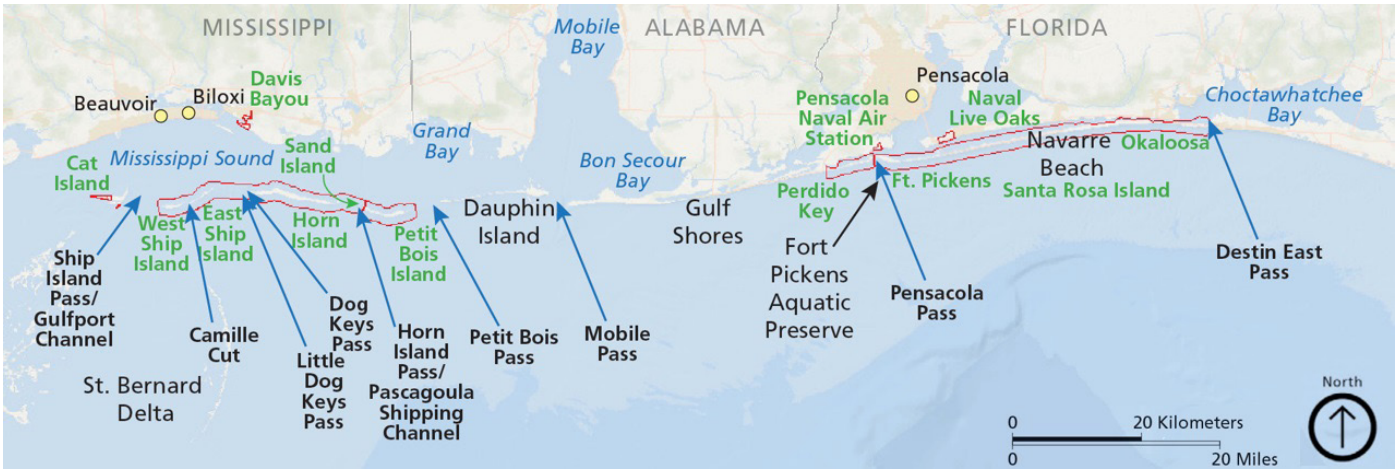


FIGURE 1. Map of significant features and landmarks in and near GUIS. This figure identifies the locations of towns (yellow dots); islands and park areas (labeled in green); natural and artificial inlets, referred to as channels, cuts, and passes (labeled in black); bathymetric features (also labeled in black), and water bodies (labeled in blue). The park boundary is delineated in red. Bathymetry is from ESRI oceans base map. Reproduced from Schupp (2019, fig. 1). Graphic by Trista Thornberry-Ehrlich (Colorado State University).

geologically young age of the barrier islands in GUIS given that Holocene surficial sediments cover large portions of the national seashore. Further literature review of paleontological resources in the vicinity of GUIS was conducted as part of this research effort, but only specimens uncovered from field collections in the park are herein reported.

Each collected specimen (including associated fragments that could belong to the same individual) was assigned a unique number as recovered in the field. A more comprehensive labeling system was then adopted once the collections were analyzed upon being moved to Georgia State University for study. Since GUIS land area spans the coasts of both Florida and Mississippi, the research team elected early on to differentiate specimen labels based upon the state where they were collected. The numbering system for specimens collected in Florida versus Mississippi are separate, so specimens from either state may possess the same number. However, additional signifiers were given to specimen labels to differentiate Florida and Mississippi specimens, as well as if chondrichthyan versus other non-chondrichthyan taxa. All labels begin with "GUIS", followed by the state abbreviation ("FL" or "MS"), and then also "NC" if non-chondrichthyan, and finally the number. For example, a chondrichthyan fossil from Florida would be GUIS-FL_00[X], while a non-chondrichthyan specimen from Mississippi would be GUIS-MSNC_00[X]. Numbers were generally assigned in the order in which specimens were collected. For a complete review of specimen details, see Clinton et al. (2023). As of the publication of this report, planning is underway for the final repository of specimens to be at the Florida Museum of Natural History in Gainesville, FL.

GEOLOGICAL SETTING

The geologic framework of GUIS influences where potentially fossiliferous formations are located relative to the land surface, and how they formed. As sea level fluctuated over millions of years, the geologic units described below have influenced the geospatial distribution and sediment types deposited along what is now the northern Gulf Coast. Not every formation is present beneath the land areas managed by GUIS; information as to the presumed location of each formation at the park is listed in Table 1. All geologic formations included within this section are known to contain some form of fossil material. However, no fossil specimens collected at GUIS thus far can be definitively attributed to a specific geologic formation. This is, in large part, due to seafloor dredging and subsequent beach renourishment activities resulting in the mixing of older, pre-Holocene sediments with modern sands.

Table 1 includes a summary of stratigraphic units and corresponding depositional environments present beneath and around GUIS. The description and information provided for each formation in this section represents a broad overview of formation characteristics. However, no consensus yet exists regarding the presence, categorization, and correlation of all such formations along the northern Gulf Coast as these units are still being actively researched by others. Descriptions included in Table 1 are based upon prior literature and in particular the NPS geologic resources inventory report for GUIS by Schupp (2019). However, recent developments in understanding the geological framework along this coastline indicate that widespread revisions of formation terminology and correlation of deposits across state lines is needed (J. Starnes, personal commun., 2023). A cohort of experts from Alabama, Florida, Louisiana, and Mississippi are working on an updated geologic framework of the region. Because this work is not yet complete, all previously described formations for GUIS from the existing literature are represented in Table 1. Further discussion on the potential for fossils from different units in and around GUIS as well as any formations presently under evaluation for revision are described further in Clinton et al. (2023).

All fossils at GUIS described in this report represent specimens recovered loose as transported and redistributed float on beaches. Considering the Holocene age of all surficial sandy beach units within GUIS, fossils discovered as float are presumed to have originated from pre-Holocene geologic formations either underlying or offshore from these areas or otherwise in the vicinity of GUIS. After evaluation of dredging and renourishment activities at the park and naturally occurring geologic formations and sediments in the area as reviewed in Clinton et al. (2023), it is presumed that the origin of transported and redistributed float specimens is predominantly due to pre-Holocene sediments that were dredged from the ocean floor and placed on or near adjacent beaches. There is precedent for the discovery of fossils from dredged sediments; a similar scenario was hypothesized and later confirmed to explain occurrences of fossil shark teeth and fish otoliths among other specimens collected nearby at Dauphin Island in Alabama (Ebersole et al., 2017; Stringer et al., 2020, 2023). Dredged sediment may contain a high abundance of shell material and may include

TABLE 1. Summary of GUIS stratigraphy and depositional settings in descending order of age, from youngest to oldest. Details and references can be found in McNair et al. (2019), Schupp (2019), Stewart and Starnes (2019), Stringer et al. (2020), and Clinton et al. (2023). The ages and descriptions of certain formations are also referenced from the National Geologic Map Database (ngmdb.usgs.gov). Note: Correlation issues may exist among listed formations. As previously mentioned (J. Starnes, personal commun., 2023), a cohort of experts from Florida, Alabama, Mississippi, and Louisiana are working to form an updated geologic framework for the region which may eventually combine or invalidate certain formations listed.

Formation	Age	Depositional Environment	Purported Locations Within GUIS
Holocene sediments	Less than 11,000 before present (B.P.)	N/A	FL & MS: Naturally occurring surficial beach sands on all barrier island units of GUIS.
Prairie Formation	Pleistocene (130,000–80,000 B.P.)	Floodplain alluvial	FL: Deposited seaward of Sangamonian estuarine and marine unit. Light yellowish-gray, yellowish-brown, silty-sandy and sandy deposits. May be present under Santa Rosa Island as unfossiliferous silty-muddy sands. MS: On mainland coast, bounded by Mississippi Sound and estuarine embayments. Thickness of 4.5–12 m. Wedge narrows landward. Interfingers with the Biloxi Formation.
Biloxi Formation	Pleistocene (132,000–112,000 B.P.)	Open nearshore marine and estuarine-lagoonal brackish	FL: Deposited in open nearshore marine and estuarine-lagoonal brackish environments. Clay and mud units are primarily sandy in FL. Present in the Pleistocene core below Santa Rosa Island. MS: Not present beneath Horn Island. Much muddier in MS and AL than in FL, which is sandier.
Gulfport Formation	Pleistocene (132,000–112,000 B.P.)	Barrier complex. Shallow nearshore marine	FL: Forms continuous zone north of Santa Rosa Sound. Present in the Pleistocene core below Santa Rosa Island where it is 3–10 m thick, well sorted sand. Forms eastern portion of Dauphin Island, AL. MS: Forms discontinuous mainland zone north of Mississippi Sound. Not present beneath MS barrier islands.
Montgomery Terrace	Pleistocene (216,000–176,000 B.P)	Penultimate interglacial fluvial	MS: Present in AL, LA, and MS. Presumed to comprise much of the Pleistocene-aged coastal terrace deposits along and near GUIS MS coastline.
Citronelle Terrace	Plio–Pleistocene (3.6–1.8 Ma)	Terrestrial, fluvial	No longer presumed to be present in the vicinity of GUIS. The "Citronelle Formation", now thought to be invalid, had been attributed before to various Plio-Pleistocene sediments described on GUIS barrier island units via core samples.
Graham Ferry Formation	Pliocene (5.3–2.6 Ma)	Deltaic to nearshore marine	FL: Correlates with the Perdido Key Formation and may correlate to the former Citronelle Formation. Current research points to the Graham Ferry Formation being the sole Pliocene-aged formation near the GUIS barrier island units.
Perdido Key Formation	Pliocene (5.3–3.6 Ma)	Nearshore marine	Nearshore fossil-rich marine lens 15–30 m beneath Perdido Key in northwest FL at AL border. Overlain by a 5–15 m thick fossil-free, fine siliciclastic sandy Neogene deposit. Correlative with the Graham Ferry Formation.
Pensacola Clay	late Miocene–early Pliocene (8.9–3.6 Ma)	Fluvial, estuarine, and nearshore marine (undifferentiated)	FL: Present beneath Santa Rosa Island (Pensacola Beach east of Fort Pickens area). May be divided into Pliocene Graham Ferry Formation and Miocene Pascagoula Formation.
Pascagoula Formation	late Miocene (8.9–5.3 Ma)	Fluvial, estuarine, and nearshore marine (undifferentiated)	MS: Present 300–900 m below Horn Island.
Hattiesburg Formation	Miocene (23.8–8.9 Ma)	Fluvial, deltaic, estuarine, and nearshore marine (undifferentiated)	MS: Present 300–900 m below Horn Island.
Arcadia Formation (Tampa Member)	late Oligocene–early Miocene (~23–16 Ma)	Marine	FL: Present beneath Santa Rosa Island (Pensacola Beach east of the park).

TABLE 1 (continued)

Formation	Age	Depositional Environment	Purported Locations Within GUIS
Catahoula Formation	late Oligocene–early Miocene (28.5–14.8 Ma)	Lower portion is marine. Upper is deltaic, fluvial-paralic sequences	MS: fluvial-paralic sequences. Top of formation on sound side of islands is about 1300 m thick at Ship Island or 760 m thick at Horn Island.
Chickasawhay Limestone (Catahoula Formation)	late Oligocene	Marine	FL: Present beneath Santa Rosa Island (Pensacola Beach east of the park).

fossil specimens (Reilly and Bellis, 1983).

Upon reviewing historical core samples, dredge source locations, lithologic formation characteristics, and species represented in these assemblages, the presumed age of the fossil material recovered at GUIS is Pliocene–Pleistocene. Depending upon the exact dredge locations and formation depths (which vary throughout GUIS), deposits classified presently as the Pliocene Graham Ferry or Perdido Key formations and the Pleistocene Gulfport, Biloxi, or Prairie formations may be sources of the fossiliferous sediments. This determination was made with the limited depth utilized by dredging equipment in mind. Pliocene–Pleistocene sediments will naturally occur at shallower depths (usually within 30 m of the seafloor), which may be reached and exposed by dredging equipment.

Measures are normally taken to ensure that the sediment being dredged is compatible compositionally and visually to the existing beach sediment being renourished (Schupp, 2019). This is the case with most renourished beaches where fossils have been collected at GUIS. However, there are several localities with very distinctive renourished sediments that may indicate lithologic formations of origin. One such locality features unique reddish-orange quartz sands that are fossiliferous on part of West Petit Bois Island (also known as "Spoils Island" or "Sand Island" as it is made up entirely of spoils as a designated disposal area for nearby dredging operations of the Pascagoula Shipping Channel). Several different formations containing iron-rich/limonitic sediments, such as the upper Miocene Pascagoula Formation and the Pliocene Graham Ferry Formation, may exhibit this color (Stewart and Starnes, 2019). Further investigation is needed at this locality and others identified to see if any sourcing connections can be made to specific geologic units for the fossils found. It is likely that different fossiliferous formations have been used as source sediments for beach renourishment in different areas of GUIS, depending upon the exact dredge locations and formation depths.

INVENTORY

A total of 711 specimens were collected during the 2021–2022 surveys. Shark teeth dominated the collections with 632 specimens. Other confirmed fossil specimens recovered include stingray teeth and caudal spines (known also as "caudal barbs") and actinopterygian teeth, spines, and otoliths. Additional specimens collected (i.e., turtle shell fragments, decapod remains, and mollusks) are only briefly reviewed as they are not yet confirmed as fossils but are under investigation. Details for different taxonomic groups are provided below for the 686 confirmed paleontological specimens from GUIS, and a summary of the distribution of all specimens collected for both Florida and Mississippi at GUIS follows in the discussion.

Class CHONDRICHTHYES

Second-hand accounts of fossil shark teeth being found within GUIS extend back to at least 2012 (J. Higgs, personal commun., 2022). However, it was not until fieldwork in 2021 that the presence of fossil shark teeth at GUIS was confirmed and the process of formal documentation began. Multiple surveys at five of the seven barrier island units (Santa Rosa, Perdido Key, West Petit Bois, Horn, and Ship Islands) managed by GUIS during 2021 and 2022 have yielded a collection of 632 fossil shark teeth. Presence of fossilized chondrichthyan (shark and ray) teeth was confirmed in all six major GUIS localities surveyed: Santa Rosa (Opal Beach), Fort Pickens, Perdido Key (Johnson Beach), West Petit Bois Island, Horn Island, and Ship Island. Two orders, Lamniformes and Carcharhiniformes, are represented among the shark tooth specimens. Additionally, 29 stingray (order Myliobatiformes) teeth and caudal spines were collected on Perdido Key (Johnson Beach), West Petit Bois Island, and Ship Island. All specimens identified appear to be attributable to extant taxa.

Infraclass SELACHII
Order LAMNIFORMES

Members of the order Lamniformes differ from other orders in that they possess eyes without nictitating membranes (protective inner eyelids), and a mouth extending behind the eyes. The 15 extant species within Lamniformes are separated into seven families (Compagno et al., 2005). However, only the family Odontaspididae is represented among the collections from GUIS.

Family ODONTASPIDIDAE

Within Odontaspididae, only *Carcharias taurus* (Fig. 2A), also known as the sand tiger shark, has been recovered. *Carcharias taurus* possess teeth with a slender, smooth crown lacking serrations and a very curved root with elongate root lobes and a deep basal root margin. Additionally, the teeth of *Carcharias taurus* feature lateral cusplets on either side of the crown. However, these gracile lateral cusplets are often broken in the fossil record. One *Carcharias taurus* tooth was collected from Perdido Key in Florida. Ten teeth of *Carcharias taurus* were collected from West Petit Bois and Ship Island in Mississippi (Fig. 2A).

Infraclass SELACHII
Order CARCHARHINIFORMES

Carcharhiniformes is the most diverse extant order of sharks, with more than 250 species around the world represented by eight families (Compagno et al., 2005). Unlike Lamniformes, members of the order Carcharhiniformes possess a nictitating membrane over the eye. Three families of Carcharhiniformes are represented among the collections thus far at GUIS: Carcharhinidae, Galeocerdidae, and Sphyrnidae.

Family CARCHARHINIDAE

Carcharhinidae, also known as the requiem sharks, are a family of sharks that tend to live in warm environments in both salt and freshwater (Compagno et al., 2005). Many carcharhinid species are found in the northern Gulf of Mexico, including

Carcharhinus leucas (Bull Shark), *Carcharhinus obscurus* (Dusky Shark), *Negaprion brevirostris* (Lemon Shark), and *Rhizoprionodon terraenovae* (Atlantic Sharpnose Shark). Among the collections at GUIS, three genera belonging to Carcharhinidae are represented: *Carcharhinus*, *Negaprion*, and *Rhizoprionodon* (Fig. 2). Preliminary analysis has yielded the following species belonging to *Carcharhinus* from GUIS collections: *Carcharhinus* cf. *C. brachyurus* (Fig. 2E), *Carcharhinus* cf. *C. brevipinna* (Fig. 2D), *Carcharhinus* cf. *C. limbatus* (Fig. 2F), *Carcharhinus* cf. *C. obscurus* (Fig. 2B), and *Carcharhinus* cf. *C. plumbeus* (Fig. 2C). Both *Negaprion* and *Rhizoprionodon* are also represented and by one species each: *N. brevirostris* (Fig. 2H) and *Rhizoprionodon* cf. *R. terraenovae* (Fig. 2I–J), respectively.

Among the three main coastal areas managed by GUIS in Florida (Santa Rosa [Opal Beach], Fort Pickens, and Perdido



FIGURE 2. Chondrichthyan fossils identified from Florida and Mississippi. **A,** *Carcharias taurus*, anterior tooth, lingual view (GUIS-MS_269). **B,** *Carcharhinus* cf. *obscurus*, upper lateral tooth, lingual view (GUIS-FL_002). **C,** *Carcharhinus* cf. *plumbeus*, upper lateral tooth, lingual view (GUIS-FL_067). **D,** *Carcharhinus* cf. *brevipinna*, upper lateral tooth, lingual view (GUIS-FL_049). **E,** *Carcharhinus* cf. *brachyurus*, upper lateral tooth, lingual view (GUIS-FL_028). **F,** *Carcharhinus* cf. *limbatus*, lower anterior tooth, lingual view (GUIS-FL_059). **G,** *Carcharhinus* sp., lower tooth, lingual view (GUIS-FL_056). **H,** *Negaprion brevirostris*, upper lateral tooth, lingual view (GUIS-FL_070). **I, J,** *Rhizoprionodon* cf. *terraenovae*, upper lateral tooth, lingual and labial views (GUIS-FL_080). **K,** *Galeocerdo cuvier*, upper lateral tooth, lingual view (GUIS-FL_145). **L,** *Sphyrna zygaena,* upper lateral tooth, lingual view (GUIS-MS_236). **M, N,** *Sphyrna mokarran*, lower? tooth, lingual and labial views (GUIS-FL_012). **O,** *Aetobatus* cf. *narinari*, partial tooth, oblique occlusal view (GUIS-FL_296). **P, Q,** *Myliobatis* or *Rhinoptera* tooth, occlusal and basal views (GUIS-FL_305). **R,** Myliobatiformes caudal spine (GUIS-FL_306). All scale bars = 1 cm.

Key [Johnson Beach]), carcharhinid teeth were collected from Fort Pickens and Perdido Key. *Carcharhinus* and *Negaprion* are represented among collections from Fort Pickens and Perdido Key, whereas *Rhizoprionodon* is only represented from collections at Perdido Key. In Mississippi, Carcharhinidae is represented at all three GUIS units surveyed for paleontological resources in 2022: West Petit Bois Island, Horn Island, and Ship Island. *Carcharhinus, Negaprion*, and *Rhizoprionodon* are represented among collections on West Petit Bois Island. Of the five shark teeth collected on Horn Island, three belong to *Carcharhinus* and two are too worn to enable specific identification. *Carcharhinus, Negaprion,* and *Rhizoprionodon* are all represented among the collections from beaches on Ship Island.

Family GALEOCERDIDAE

Galeocerdidae, also known as the tiger sharks, are a family within Carcharhiniformes. There is one extant species represented by this family, *Galeocerdo cuvier*. *G. cuvier* and other species within family Galeocerdidae exhibit distinctive serrated teeth with a distally inclined cusp, a tight notch where the distal edge meets the distal heel, and a convex mesial edge (Ebersole et al., 2019). After preliminary analysis, all Galeocerdidae specimens within the GUIS paleontological collections are presumed to represent *G. cuvier* (Fig. 2K). One tooth of *G. cuvier*, GUIS-FL_145, was recovered near Fort Pickens. Twelve additional teeth were recovered from Perdido Key during several field visits. In Mississippi, one tooth from *G. cuvier*, GUIS-MS_265, was collected on West Petit Bois Island. Four more teeth of *G. cuvier* were recovered on Ship Island over two field visits.

Family SPHYRNIDAE

Sphyrnidae, also known as the hammerhead sharks, are a family within Carcharhiniformes that possess laterally elongated and dorsoventrally flattened heads (cephalofoils). Among the 10 extant species of Sphyrnidae, *Sphyrna* cf. *S. zygaena* (Fig. 2L) and *Sphyrna* cf. *S. mokarran* (Fig. 2M–N) have been identified from GUIS. Of the three main survey areas of GUIS in Florida, *Sphyrna* teeth were only collected on Perdido Key. Of the three barrier islands surveyed in Mississippi, *Sphyrna* teeth were only recovered from Ship Island.

Infraclass BATOIDEA
Order MYLIOBATIFORMES

Myliobatiformes is the order of flat-bodied, cartilaginous fish that includes most stingrays. Myliobatiformes is a very diverse order, with more than 200 species represented around the world (Nelson, 2006).

Superfamily MYLIOBATOIDEA

Myliobatoidea is an informal superfamily of Batoidea, which includes among others the families Aetobatidae, Dasyatidae, Myliobatidae, and Rhinopteridae. All ray teeth and caudal spines collected at GUIS are presumed to belong to members of Myliobatoidea. Among the three main coastal areas managed by GUIS in Florida (Santa Rosa [Opal Beach], Fort Pickens, and Perdido Key [Johnson Beach]), multiple teeth as well as caudal spines belonging to Myliobatoidea were recovered from Perdido Key. Among the three GUIS barrier island units in Mississippi surveyed for fossils in 2022, specimens belonging to Myliobatoidea were collected on West Petit Bois Island and Ship Island. On West Petit Bois Island, a single tooth specimen, GUIS-MS_346, was collected. On Ship Island, six myliobatoid specimens consisting of teeth and caudal spines were collected. Myliobatoidea specimens were not recovered from Horn Island. Specimens featured in Figure 2 include GUIS-FL_305 representing *Myliobatis* or *Rhinoptera* (Fig. 2P–Q), and also GUIS-FL_306, representing Myliobatiformes (Fig. 2R).

Family AETOBATIDAE

Aetobatidae includes the eagle rays, some of the largest species of ray. There is only one extant species present in the Gulf of Mexico, *Aetobatus narinari* (Spotted Eagle Ray). Specimen GUIS-FL_296, a tooth from *Aetobatus* cf. *A. narinari* was collected on Perdido Key (Fig. 2O).

Class OSTEICHTHYES
Subclass ACTINOPTERYGII

Actinopterygii, also known as the ray-finned fishes, is an extremely diverse and widespread group of bony fish with many thousands of species living today. Virtually all bony fish fossils found in the Gulf of Mexico, from both extant and extinct taxa, belong to this subclass. Fossilized remains of actinopterygians have been identified in the GUIS collections (Fig. 3). A majority of the remains consist of disarticulated and often fragmental fin spines from bony fishes. Initially, Clinton et al. (2022a, 2022b) identified several of these specimens as ratfish dorsal spines, but they are curved and not straight, and are instead representative of bony fishes. Due to the fragmented nature of these spines and the vast amount of possible actinopterygian taxa, none of the fin spines from the GUIS collections can be currently identified beyond subclass.

Among the three main coastal areas managed by GUIS in Florida (Santa Rosa [Opal Beach], Fort Pickens, and Perdido Key [Johnson Beach]), fin spines belonging to actinopterygians were collected on Perdido Key (Fig. 3V–Y). In addition to the actinopterygian fin spines, a variety of other bony fish remains were recovered in Florida. Specimen GUIS-FLNC_020, also collected at Perdido Key, has tentatively been identified as an element from a bony fish, such as part of the pre-operculum. Among the three GUIS barrier island units in Mississippi surveyed in 2022 (West Petit Bois Island, Horn Island, and Ship Island), two fin spines belonging to actinopterygians (GUIS-MSNC_002, GUIS-MSNC_023) were collected on Ship Island. One probable bony fish tooth (GUIS-MSNC_028) was additionally collected at Ship Island (Fig. 3R–U). All other bony fish specimens that could be identified beyond subclass are described further herein at the family level.

Order ACANTHURIFORMES
Family SCIAENIDAE

Three sciaenid tooth specimens were collected and identified in Florida, all of them from Perdido Key. Two presumed crushing teeth belonging to a black or red drumfish, GUIS-FLNC_015 (Fig. 3P) and GUIS-FLNC_016, were recovered. Specimen GUIS-FLNC_014 is another tooth from this family (Fig. 3N–O), presumedly *Pogonias cromis*. This specimen is larger and has a more rectangular shape than the other two specimens. Three additional small sciaenid teeth were collected from Mississippi from both West Petit Bois and Ship Islands.

Four sciaenid otoliths were collected from Florida. Specimen GUIS-FLNC_008 (Fig. 3C–D), recovered at Perdido Key, is a sagittae from *Cynoscion arenarius.* Specimen GUIS-FLNC_019 (Fig. 3E–F), also collected on Perdido Key, is a heavily weathered sagittae from *Cynoscion nebulosus.* Specimens GUIS-FLNC_018 (Fig. 3G–H) collected from Perdido Key as well as GUIS-FLNC_019 (Fig. 3I–J) collected near Fort Pickens are both sagittae of *Micropogonias undulatus*. The sagittae, which is found in the sacculus, is typically larger and much more diagnostic than the generally smaller lapillus (G. Stringer, personal commun., 2023). Sagittae specimens are more commonly utilized in taxonomic studies of large otolith assemblages (e.g., Stringer et al., 2020, 2023).

Order PERCIFORMES
Family SPARIDAE

Specimen GUIS-FLNC_001 is a tooth from *Archosargus*

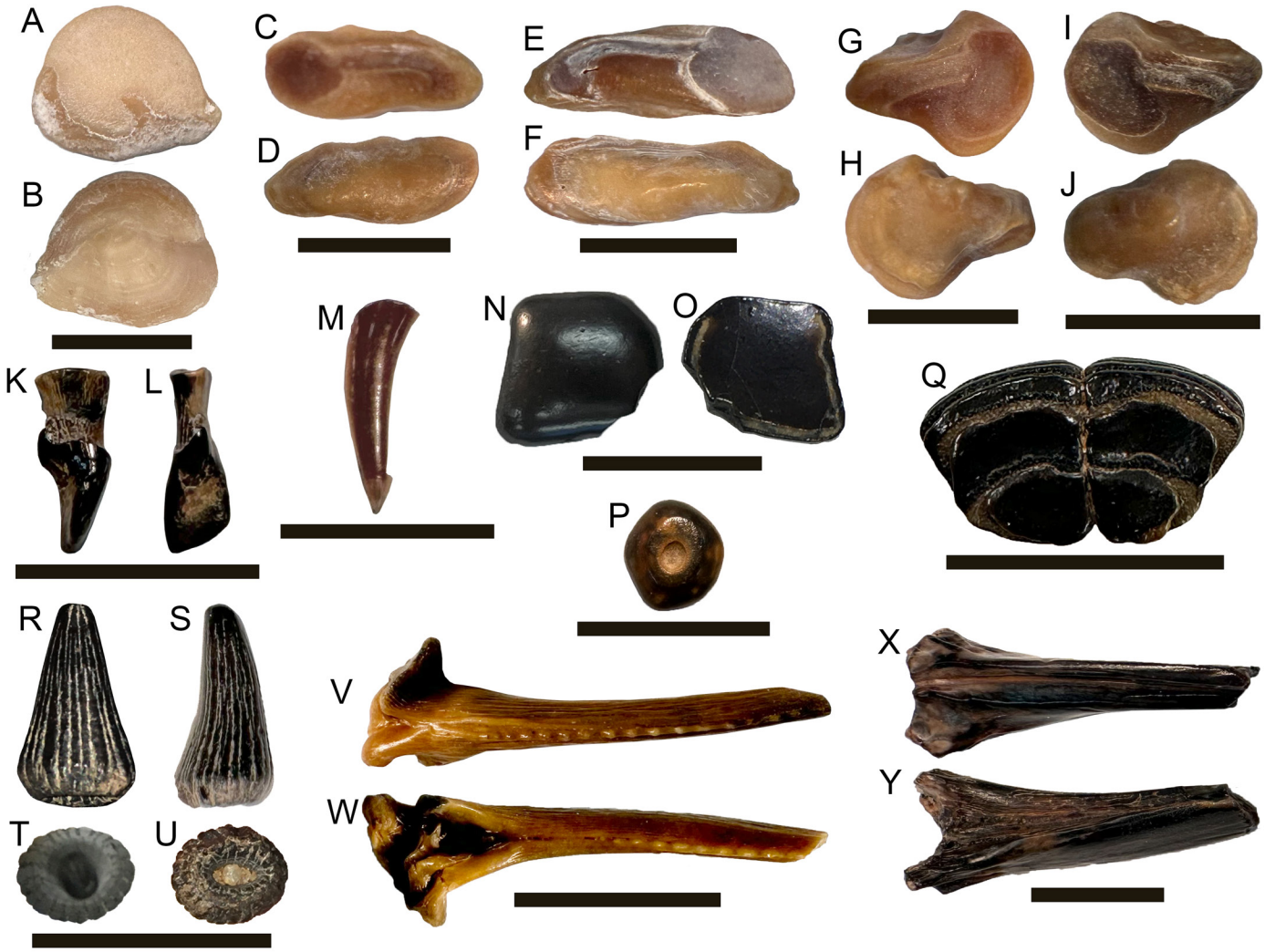


FIGURE 3. Osteichthyan fossils identified from Florida and Mississippi. **A, B,** *Ariopsis felis* otolith, right lapillus, macular and anti-macular views (GUIS-FLNC_007). **C, D,** *Cynoscion arenarius* otolith, right sagittae, inner and outer views (GUIS-FLNC_008). **E, F,** *Cynoscion nebulosus* otolith, left sagittae, inner and outer views (GUIS-FLNC_019). **G, H,** *Micropogonias undulates* otolith, left sagittae, inner and outer views (GUIS-FLNC_018). **I, J,** *Micropogonias undulates* otolith, right sagittae, inner and outer views (GUIS-FLNC_013). **K, L,** *Archosargus* sp. tooth, lateral and labial views (GUIS-FLNC_001). **M,** *Trichiurus* cf. *lepturus* tooth, lateral view (GUIS-FLNC_011). **N, O,** *Pogonias cromis* tooth, occlusal and basal views (GUIS-FLNC_014). **P,** Sciaenidae tooth, occlusal view (GUIS-FLNC_015). **Q,** Diodontidae mouth plate, occlusal view (GUIS-FLNC_004). **R, U,** Osteichthyes indet. tooth, lateral, apical, and basal views (GUIS-MSNC_028). **V, W,** Osteichthyes indet. left pectoral spine, dorsal and ventral views (GUIS-FLNC_009). **X, Y,** Osteichthyes indet. dorsal spine, dorsal and ventral views (GUIS-FLNC_012). All scale bars = 1 cm.

(Fig. 3K–L). This specimen was collected on Perdido Key in Florida and it is the only specimen representing this taxon from the GUIS collections.

Order SCOMBRIFORMES
Family TRICHIURIDAE

Specimen GUIS-FLNC_011, collected from Perdido Key, is a fang belonging to *Trichiurus lepturus,* a species of cutlassfish (Bemis et al., 2019; J. Ebersole, personal commun., 2023). It is the only representative specimen from this taxon (Fig. 3M).

Order SILURIFORMES
Family ARIIDAE

Specimen GUIS-FLNC_007 is an otolith from *Ariopsis felis* (Fig. 3A–B), the hardhead catfish. Specifically, this specimen is a lapillus, which is the otolith found in the utriculus of the labyrinth of bony fish (G. Stringer, personal commun., 2023). This specimen, collected on Perdido Key, is the only lapillus collected during the 2021–2022 surveys.

Order TETRAODONTIFORMES
Family DIODONTIDAE

Diodontidae, also known as the porcupinefish, is a family of bony fishes belonging to Actinopterygii. Porcupinefish are often confused with the closely related pufferfish of the family Tetraodontidae. Diodontids possess unique fused platy teeth that aid them in crushing prey (Leis, 2007). Among the three main coastal areas managed by GUIS in Florida, only one fossilized dental plate from a diodontid, GUIS-FLNC_004, was collected on Perdido Key (Fig. 3Q). No diodontid remains were collected from the three GUIS barrier island units in Mississippi surveyed in 2022.

Other Specimens

While pre-Holocene chondrichthyan and osteichthyan fossils made up the vast majority of those recovered during the inventory, other specimens were collected from the same sediments and localities at GUIS, and as such may be fossilized. Fossilized shells and other specimens can have a

similar appearance to modern ones however, especially when weathered and exposed in coastal areas. Thus, it is often difficult to distinguish a fossil from a modern specimen, particularly if the species is extant as many are in this region. All specimens reviewed in this section have yet to be confirmed as fossil but are thought to be probable paleontological resources. Twenty-two of the 25 specimens in this 'other' category comprise decapods from localities in both Florida and Mississippi. Some of these specimens include multiple fragments that were grouped together in collection as potentially coming from the same individual. While most of the decapod specimens exhibit weathering and discoloration consistent with fossilization, not all specimens appear to be fully mineralized. Nonetheless, an attempt was made to feature the taxonomic variety represented by several of the decapod specimens presumed to be fossil or subfossil (Fig. 4B–F). Tentatively, specimens include pincers from both *Menippe* (stone crab) and a portunid (swimming crab), merus (walking leg segments) from *Persephona*, as well as the propodus of a callianassid shrimp (R. Portell, personal commun., 2023). Phylum Mollusca is only represented in the collections presently by a scaphopod (tusk shell) that may be fossil in origin but is not fully confirmed (Fig. 4G). Shells of gastropods and bivalves found alongside fossil shark teeth on GUIS beaches may include other potential paleontological specimens, but none are recorded as such at this time. In addition, other mollusks to note at GUIS include shells embedded in parts of the construction at Fort Pickens; it is not known if these shells are modern, subfossil, or paleontological resources. Two specimens that resemble weathered sections of peripheral carapace from the order Testudines may also be fossils or subfossils. The two specimens, GUIS-MSNC_030 (Fig. 4A) and GUIS-MSNC_031, are not thought to be marine but may belong instead to the family Emydidae (pond turtles). These fragments were recovered by park staff on Petit Bois Island in Mississippi; further analysis of these specimens is needed. In summary, because preservation of modern and fossil specimens can be quite variable and many (but not all) species represented by fossils in Neogene and younger deposits in the area still live along this coastline, geochemical analysis may be needed to confirm whether the specimens described in this section are indeed paleontological resources.

DISCUSSION

All fossils documented during GUIS surveys were collected as transported float material on beaches, likely originating out of sediments that have been dredged from nearby sources and redeposited on and near beaches as part of nourishment projects. A review of geologic units purported to be in and around the park, and consideration of the identified species, suggest a probable Pliocene-Pleistocene source for these fossils. In total, 711 specimens were collected at GUIS, of which 686 are documented here as paleontological resources. Further work is needed to determine if the other 25 specimens noted above can be more fully confirmed as fossils as well. The vast majority of specimens collected from the GUIS inventory (661 or ~93%) are from class Chondrichthyes. Table 2 shows the total counts for all major taxa collected.

Of the 661 chondrichthyan fossils recovered, 632 (~96%) of the specimens belong to sharks. The remaining 29 (~4%) specimens belong to rays. All shark fossils consist of teeth with a total of 292 specimens recovered from Florida and 340 specimens recovered from Mississippi. In an effort to protect and preserve the localities of these paleontological resources at GUIS, no further information on spatial occurrences of specimens is provided. Of the 632 shark teeth, ~54% could be identified at least to genus level (and many more could be attributed at least to the family Carcharhinidae). Thus far, six selachian genera have been identified among the specimens collected: *Carcharias*, *Carcharhinus*, *Galeocerdo*, *Negaprion*, *Rhizoprionodon*, and *Sphyrna*. Overall, ~73% of the shark teeth from Florida and ~37% of the shark teeth from Mississippi were identifiable to genus level. Distribution of genera by state for GUIS is listed in Table 3.

While ~54% of the shark teeth were identified at least to genus level, many shark teeth from different genera are difficult to distinguish due to convergence in their functional morphology. For example, *Negaprion* teeth from the lower jaw and *Carcharhinus* teeth from the lower jaw look extremely similar and serve a similar function to aid in grasping prey (Perez, 2022). Of the 495 shark teeth identified to at least the family level, ~93% belonged to the family Carcharhinidae. Carcharhinidae became the dominant selachian family in nearshore marine environments, in terms of overall abundance and taxonomic diversity, following the Eocene–Oligocene transition (Maisch et al., 2014; Condamine et al., 2019; Perez, 2022). Based on the samples recovered so far from GUIS, this trend is apparent in our current collections. While additional taxa are likely to be recovered with continued sampling, it is clear that carcharhinid teeth dominate these assemblages.

In both Florida and Mississippi, *Carcharhinus* spp. were the most abundant taxa recovered. *Carcharhinus* is the most diverse genus in the family Carcharhinidae, with 34 extant species known (Nelson et al., 2016). Today, there are 16 species belonging to the family Carcharhinidae that occur within the Gulf of Mexico, of which 13 belong to the genus *Carcharhinus* (Compagno et al., 2005). In Florida, the genus with the second



FIGURE 4. Other possible fossil specimens. **A,** Emydidae carapace peripheral, dorsal view (GUIS-MSNC_030). **B,** Callianassidae propodus, lateral view (GUIS-MSNC_022). **C,** *Menippe* sp. pincer, lateral view (GUIS-MSNC_016). **D,** Portunidae pincer, lateral view (GUIS-MSNC_029). **E,** *Persephona* sp. merus, lateral view (GUIS-MSNC_011). **F,** *Persephona* sp. merus, lateral view (GUIS-MSNC_012). **G,** Scaphopoda shell, lateral view (GUIS-MSNC_007). All scale bars = 1 cm.

TABLE 2. Total specimens of all major taxa from 2021–2022 surveys for GUIS collections. Taxa are listed in rank order based on abundances of specimens found for all confirmed paleontological resources. Taxonomic groups marked by an asterisk are not yet fully confirmed as fossils and are still under investigation. Note: Shells of gastropods and bivalves found alongside these specimens may also include pre-Holocene fossils; however, only a single scaphopod is retained for now as part of GUIS collections.

Taxa	# of Specimens
Chondrichthyes (Sharks)	632
Chondrichthyes (Rays)	29
Actinopterygii (Bony Fishes)	25
Decapoda* (Crabs)	22
Testudines* (Turtles)	2
Mollusca* (Scaphopod)	1
Total	711

TABLE 3. Distribution of all 339 fossil shark teeth identifiable to genus level collected during the 2021 and 2022 surveys at GUIS for Florida and Mississippi.

Genus	Florida GUIS Specimens	Mississippi GUIS Specimens
Carcharias	1	10
Carcharhinus	109	52
Galeocerdo	13	5
Negaprion	39	45
Rhizoprionodon	47	10
Sphyrna	5	3
Total teeth (identifiable to genus)	214	125

largest proportion of specimens recovered was *Rhizoprionodon*. There were markedly fewer teeth belonging to *Rhizoprionodon* recovered in Mississippi. While there are 10 extant species of *Rhizoprionodon*, only *R. terraenovae* occurs in the Gulf of Mexico (Compagno et al., 2005). *Negaprion* was the third most abundant genus represented among Florida collections and the second most abundant genus represented among Mississippi collections. *Negaprion brevirostris* is the only extant species within the genus that occurs in the Gulf of Mexico. The remaining three selachian genera (*Carcharias*, *Galeocerdo* and *Sphyrna*) comprised the fewest teeth represented among collections from both Florida and Mississippi. All three of these genera also have modern counterparts that inhabit the Gulf of Mexico (e.g., Castro, 2011; Ebert et al., 2021). The association of the fossil chondrichthyan material with extant species that inhabit the Gulf of Mexico additionally supports the relatively young Plio-Pleistocene presumed geologic age for the collection at GUIS.

Fossils collected during site visits at GUIS were all recovered as float and are presumed to have been transported to beaches primarily via renourishment activities. There is a documented history of beach renourishment at GUIS, with most of the sediment being sourced from nearby shipping channels in the passes between barrier islands (Kenworthy et al., 2007; Byrnes et al., 2012; NPS, 2016b; Schupp, 2019). Pre-Holocene fossiliferous sediment is presumed to have been excavated from the shipping channels and ocean floor during these dredging operations, and then placed on or near beaches at GUIS. The Fort Pickens and Perdido Key (Johnson Beach) areas in Florida, as well as West Petit Bois, Ship, and Cat Islands in Mississippi, have been subjected to beach renourishment in recent years, and as a result new fossils may continually be exposed and/or washed up onto beaches. The occurrences of dredging and beach renourishment with presumed fossiliferous sediments, as well as confirmed presence of fossilized marine vertebrate remains at multiple localities in GUIS, provide a unique opportunity for the scientific community to examine under-studied specimens which would otherwise be inaccessible in the region due to no exposures of these fossiliferous formations.

SIGNIFICANCE OF GUIS COLLECTIONS

The paleontological resources inventory by Clinton et al. (2023) included extensive background literature review to examine existing knowledge of chondrichthyan fossil assemblages along the northern Gulf Coast. Apart from limited studies in adjacent coastal areas, few reports of fossil shark teeth are noted in the peer-reviewed literature from this stretch of coastline. One of the only publications to include any significant mention of fossil shark teeth is that of Ebersole et al. (2017) from nearby Dauphin Island in Alabama. This barrier island is situated between the Florida and Mississippi portions of GUIS and is the only Alabama unit of this barrier island system. While Dauphin Island is outside of park boundaries, it used to be connected to Petit Bois Island, but in the early 18th century was breached by a large storm (Otvos, 1979; Otvos and Giardino, 2004). The 91 fossil chondrichthyan and bony fish specimens from Dauphin Island were also collected as float material similar to the specimens at GUIS. The Dauphin Island fossils were originally suspected to be late Pliocene or early Pleistocene in age originating from either the Citronelle or Biloxi formations (Ebersole et al., 2017). However, the Citronelle Formation is no longer recognized as a valid unit along the Gulf Coast of Alabama (Stringer et al., 2020). Ebersole and co-authors have since proposed that the plausible source of the fossils collected on Dauphin Island is most likely the Pliocene Graham Ferry Formation (Stringer et al., 2020, 2023). These specimens, similar to GUIS fossils found on beaches, are presumed to be largely the result of nearby dredging activities.

Twelve taxa were identified in Ebersole et al. (2017): *Carcharias taurus*, *Carcharodon carcharias*, *Cosmopolitodus hastalis* (now usually assigned to *Carcharodon* instead), *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharhinus obscurus*, *Carcharhinus* sp. cf. *C. plumbeus*, *Negaprion brevirostris*, *Galeocerdo cuvier*, *Hemipristis serra*, *Aetobatus* sp., and Diodontidae. Many of the same taxa are also noted from this study; however, *Carcharhinus leucas*, *Carcharhinus* sp. cf. *C. longimanus*, *Carcharodon carcharias*, *Hemipristis serra*, and *Cosmopolitodus hastalis* were not recovered from GUIS. The following taxa were previously unreported from the Plio-Pleistocene fossil record of the northern Gulf of Mexico prior to this paleontological resource inventory: *Carcharhinus* cf. *C. brachyurus*, *Carcharhinus* cf. *C. brevipinna*, *Carcharhinus* cf. *C. limbatus*, *Rhizoprionodon* cf. *R. terraenovae*, *Sphyrna* cf. S. *mokarran*, and *Sphyrna* cf. *S. zygaena*. Certain genera reported only from GUIS (e.g., *Rhizoprionodon*) are represented by very small teeth, including many at <1cm in length. Thus, it is likely that they could be found elsewhere but have not yet due to a lack of intense study of shark teeth from this region. The study at Dauphin Island represented 91 specimens collected intermittently over 25 years, whereas the inventory by Clinton et al. (2023) had a dedicated focus on understanding and expanding knowledge of fossil resources for the park through intense field surveys that were

conducted over a series of short multi-day visits in the course of a single year. Yet, additional taxa are likely to be recovered with continued survey efforts including perhaps if screenwashing or other focused sampling strategies were applied to recover smaller fossils.

The publications regarding the 91 fossils from Dauphin Island and now the 661 shark and ray specimens from GUIS are the only major peer-reviewed reports detailing presumed Plio-Pleistocene chondrichthyan fossils from the barrier islands and coastline of the northern Gulf. The only other report of shark teeth from nearby in the Florida panhandle that may overlap in age are 13 poorly preserved limonitic specimens presumed to Miocene-Pliocene (Means, 2009). These fossils were recovered from a pit near the Alabama state line much farther inland in Okaloosa County. Otherwise, knowledge of shark teeth is more commonly limited to social media posts by the public along this stretch of coastline (Clinton et al., 2023), and as such, it is important to have collections like the specimens from GUIS for scientific research since chondrichthyan remains of this age are not well-documented in the literature from this region. Furthermore, additional studies of fish otoliths and some shark and bony fish fossils from a renourished beach on Dauphin Island helped to reveal that dredging was likely responsible for the presence of at least some fossils recovered in that location (Stringer et al., 2020). Similar processes are proposed as influential at GUIS, in that, nearly all specimens recovered from the park are presumed to have originated from dredged sediments that were redistributed on or near GUIS beaches. Along with the publications by Ebersole et al. (2017) and Stringer et al. (2020, 2023), Perez (2022) reviewed the chondrichthyan fossil record of the Florida platform based on specimens in the vertebrate paleontology collection at the Florida Museum of Natural History. The museum did not have any records of fossil occurrences from GUIS and very few from nearby in Florida. Fossil assemblages recovered as part of the inventory by Clinton et al. (2023) have now expanded an understanding of chondrichthyan remains from the Plio-Pleistocene of the northern Gulf Coast for both Florida and Mississippi. The lack of previous reports of such fossils from this coastline and the proposed source material as otherwise inaccessible dredged sediments elevates the importance of the fossils uncovered at GUIS and any future finds that might be documented at the park. These non-renewable resources are not otherwise available to study in situ and are not well-represented in the literature. Other studies have shown the importance of fossil shark teeth found as float specimens on beaches and that they can serve as a proxy for understanding certain aspects of chondrichthyan assemblages when specimens are not easily accessed in situ (e.g., Visaggi and Godfrey, 2010). The collections from GUIS fill a gap in the known fossil record of this region, particularly for documenting fossil chondrichthyans as well as in contributing new knowledge on a variety of fossil bony fish now also reported from the park.

Management considerations to aid in protecting these newly discovered paleontological resources at GUIS are described further in Clinton et al. (2023). Protection of these fossils from both anthropogenic activities and natural processes should be considered to help ensure that such resources are available for future study. Expanding our knowledge of these faunas from this understudied coastline is still needed. Existing regulations prohibit unauthorized collection of natural resources on National Park Service lands, and more recently the Paleontological Resources Preservation Act signed into law in 2009 as part of the Omnibus Public Land Management Act provides additional support for the protection of fossils. The lack of existing knowledge of similar fossils along the northern Gulf Coast and the potential for new finds emphasizes the significance of paleontological resources at GUIS. This study has amplified our overall knowledge of fossil occurrences across the northern Gulf of Mexico and serves as a foundation for continued efforts to expand our understanding of the paleontological diversity of sharks as well as other marine vertebrate fossils from this coastal region.

CONCLUSIONS

The 711 fossils collected at GUIS upon several field visits during 2021 and 2022, predominantly represented by chondrichthyan remains, hold special significance in contributing new reports of paleontological specimens from the northern Gulf Coast. Examination of the existing literature revealed a noted gap in scholarly knowledge relating to chondrichthyan fossil assemblages from areas in and near the coastal units managed by GUIS. Apart from an ancillary study of fossils that were collected intermittently over 25 years at Dauphin Island, there is a lack of information in the literature on Pliocene-Pleistocene chondrichthyan specimens from the western panhandle of Florida or the Mississippi–Alabama barrier islands. The source sediments, while unknown, are likely Pliocene-Pleistocene in age given an examination of species represented and the proximity of potentially fossiliferous units underlying and/or near the park. Most, if not all, of the fossil chondrichthyan specimens at GUIS are presumed to have been inadvertently placed on or near beaches as a result of anthropogenic activities. The localities with the greatest fossil abundance at GUIS are beaches that have been subject to renourishment using dredged sediment from the area which is likely pre-Holocene and fossiliferous. Proper management of these newly discovered fossils is critical as is fostering opportunities for expanded research by preserving and sharing the significance of these finds with the scientific community. The fossils recently collected at GUIS are important specimens that add extensive data to building our understanding of shark and ray fossil assemblages from the northern Gulf Coast as well as an array of other vertebrate faunas that were uncovered as a result of this inventory. Monitoring plans should be developed not only to preserve these non-renewable resources at GUIS but to support the potential discovery of new paleontological finds of significance along this coastline in the future.

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