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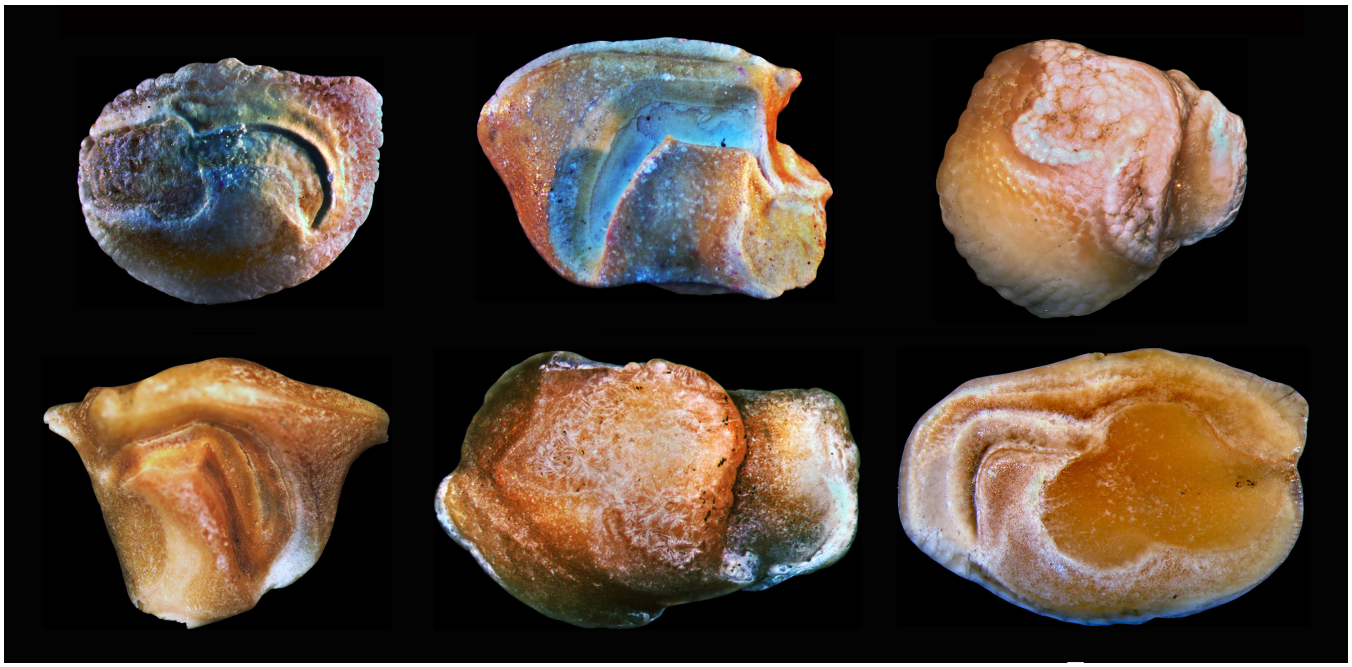

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TELEOSTEAN OTOLITHS REVEAL DIVERSE PLIO-PLEISTOCENE FISH ASSEMBLAGES IN COASTAL GEORGIA (GLYNN COUNTY)

Gary L. Stringer[1] and Dennis Bell[1]

ABSTRACT

Extensive bulk sampling at seven Plio-Pleistocene sites spanning approximately 4.5 Ma to 120,000 years ago in age near Brunswick, Glynn County, Georgia, produced 1,803 teleostean otoliths. The otolith assemblage was relatively diverse with 50 taxa (representing 18 families) of Plio-Pleistocene teleosts. The otoliths represented mainly shallow-marine fishes, which were all extant except for four species. The assemblage was dominated by 16 sciaenid taxa that represented 65.8% of the total number of otoliths. The Plio-Pleistocene otoliths indicated fishes that are almost identical to the marine fishes from present-day coastal Georgia. The teleostean otoliths are considered especially important for several reasons. This study represents the first description of fish otoliths from the Plio-Pleistocene of coastal Georgia and describes the bony fishes present from approximately 4.5 Ma (Raysor Marl equivalent) to 120,000 years ago (late Pleistocene). This time interval includes the late Neogene climatic changes as well as the glacial-interglacial climatic cycles in North America. Also, the preservation of aragonitic otoliths is rare in coastal Georgia given the very high water table and the intense and rapid weathering. Furthermore, there is a paucity of Plio-Pleistocene fossils, especially bony fishes, in coastal Georgia related to various geological constraints such as highly erosive transgressive sequences. The Plio-Pleistocene otolith assemblage from coastal Georgia contains 13 families representing 28 taxa not recognized by skeletal fossils in Georgia. Although the Ariidae and Sciaenidae were previously recognized based on skeletal fossil material in Georgia, there are 14 newly reported taxa based on otoliths in these families (1 and 13 respectively) including ***Protosciaena kirbyorum*** **n. sp.**, the first fossil species of this genus in the U.S. Otolith data also verified fishes previously indicated by skeletal remains and provided greater specificity in several cases.

Key words: otoliths; teleosts; Pliocene; Pleistocene; Georgia; Glynn County; Sciaenidae.

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INTRODUCTION

Decades of comprehensive and exhaustive collecting by several individuals in the Plio-Pleistocene sediments of the coastal region of Glynn County, Georgia, have resulted in the recovery of hundreds of thousands of invertebrate and vertebrate fossils. Included in this tremendous quantity of fossils has been a notable number of teleostean ear stones or otoliths. Seven sites, all in the proximity of Brunswick, Georgia (Fig. 1), have produced 1,803 otoliths. While this is not an overly large number of otoliths compared to some studies (e.g., Fitch and Lavenberg, 1983; Müller, 1999; Nolf and Stringer, 2003), it is sufficient to provide valuable information regarding the occurrence of bony fishes during the Plio-Pleistocene in coastal Georgia, where Plio-Pleistocene bony fishes had previously been known only from skeletal remains. The geologic age of the otoliths (all less than approximately 4.5 Ma) results in fish taxa that are represented primarily by extant taxa. In most cases, identification to species would be possible, but the preservation of the otoliths prohibited species determination in some specimens. It appears that the extensive rainfall, a high water table, and sediment composition (i.e., porous sands and silts) in the area adversely affected the preservation of the otoliths. Even with this limitation, the majority of the otoliths could be assigned to at least genus level.

Studies of Plio-Pleistocene otoliths worldwide have been quite numerous for many years (Gaemers and Schwarzhans, 1973; Nolf, 1978, 1985; Nolf and Marques da Silva, 1997; Aguilera and Aguilera, 1999; Girone et al., 2006; Fulgosi et al., 2009; Nolf, 2013, Schwarzhans and Aguilera (2013), Aguilera et al. (2016), and Schwarzhans and Aguilera (2016), but in the United States, investigations have been limited, especially in the Gulf Coast region. Published research on Plio-Pleistocene otolith assemblages for the entire United States probably numbers less than 20. Fitch, one of the leading researchers on fish otoliths, investigated numerous Plio-Pleistocene otolith assemblages in California (Fitch, 1964, 1966, 1967, 1968, 1970; Fitch and Reimer, 1967). Fitch also completed works on fossil lanternfishes (Myctophidae) of North America (Fitch, 1969a), fossil schooling fishes of the California Current System (Fitch, 1969b), and modern and fossil morids that included Plio-Pleistocene otoliths from the U.S. (Fitch and Barker, 1970). Casteel (1974) reported on Plio-Pleistocene salmonids from the Pacific coast. Firestine et al. (2012) published a catalog of all published accounts of Neogene fishes in California, which included otoliths. The Plio-Pleistocene otoliths of the western U.S. involve taxa that are found primarily in the Pacific realm and are of minimal value in the investigation of the otoliths of coastal Georgia.

Pertinent to the Plio-Pleistocene otolith assemblages of Georgia was the research conducted on teleost otoliths from the Yorktown Formation (Pliocene) from the Lee Creek Mine in North Carolina (Fitch and Lavenberg, 1983). The researchers obtained 8,808 otoliths from the Yorktown Formation from which they identified at least 45 taxa representing 17 families. These taxa would be slightly older than any of the otoliths from coastal Georgia. A large number of the taxa recognized in the Yorktown Formation are also present in the coastal Georgia Plio-Pleistocene otolith assemblages. Chandler (2015) illustrated 32 of the otoliths from the Yorktown Formation previously described by Fitch and Lavenberg (1983) in his extensive review of fossil fish of North Carolina. Müller (1999) investigated the elasmobranchs and teleosts of the Paleogene and Neogene of the U.S. Atlantic Coastal Plain, examining approximately 12,000 otoliths ranging in age from the middle Eocene to the early Pliocene as far south as South Carolina.

Another relevant investigation is the late Pleistocene-early Holocene teleostean otoliths from the Mississippi River in Louisiana by Stringer (1992). This study, based on 446 otoliths from a mudlump island in the South Pass area, revealed 40 species of marine fishes representing 25 families. The taxa recognized show many similarities to the Plio-Pleistocene otoliths of coastal Georgia. Haman (1981) in an investigation of the nanoflora of the mudlump islands listed otoliths as present but gave no further information. Hulbert and Pratt (1998) detailed Pleistocene (Rancholabrean) vertebrate faunas from eight sites in coastal Geor-

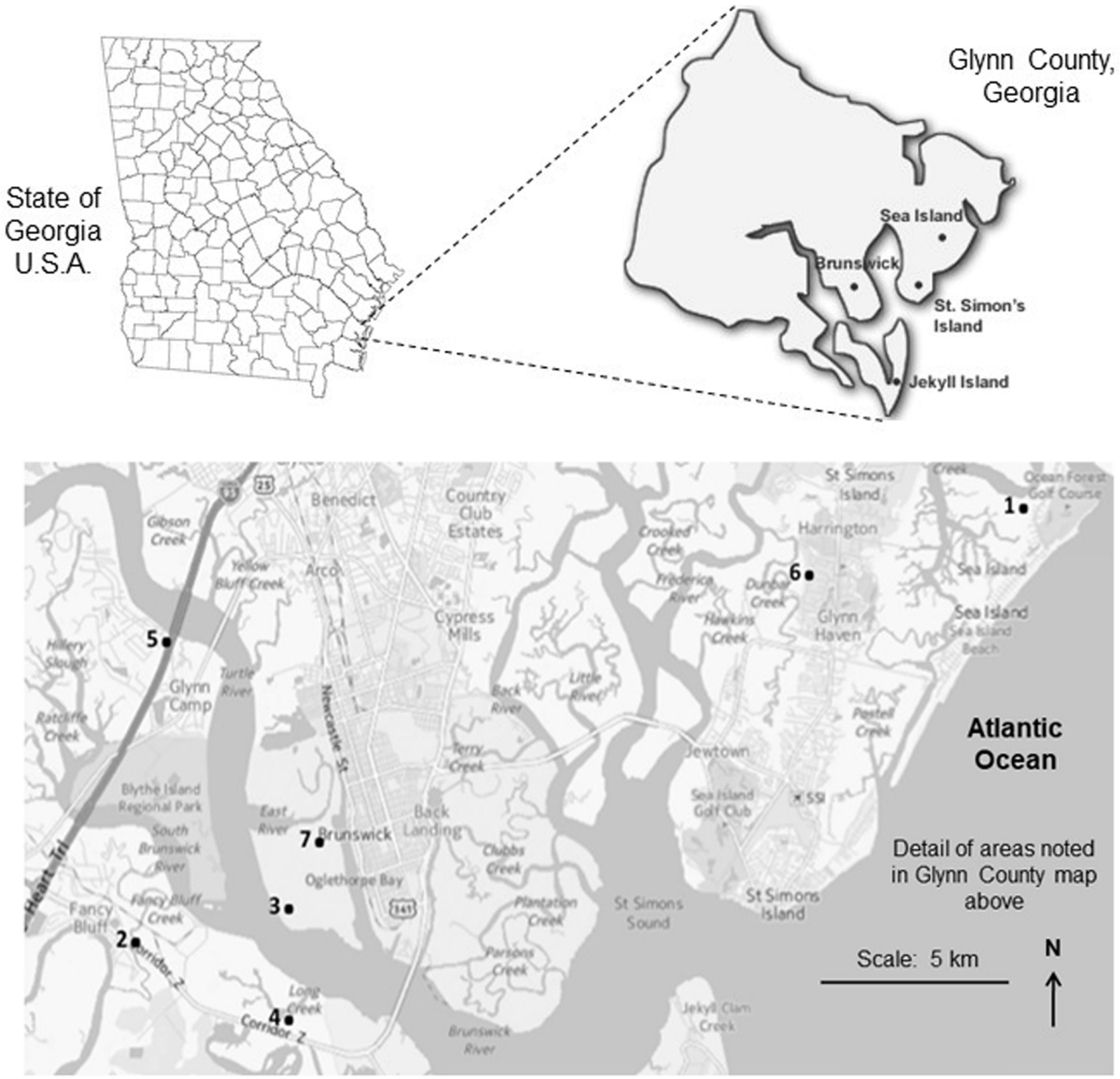


Figure 1. Plio-Pleistocene localities in the vicinity of Brunswick, Glynn County, Georgia. Site 1 = Sea Island; Site 2 = Fancy Bluff; Site 3 = South Brunswick River; Site 4 = Joiner Creek; Site 5 = Turtle River; Site 6 = Dunbar Creek; Site 7 = East River.

gia that included both marine and terrestrial taxa. They listed 25 actinopterygians based on skeletal remains from the Isle of Hope and Mayfair sites in Chatham County. The authors reported unidentified otoliths as present at the Isle of Hope and Jones Girls sites. Most recently, Stringer et al. (2017) described a matched pair of otoliths and associated skeletal remains from *Apogon townsendi* from the Caloosahatchee Formation (early Pleistocene) of Florida.

Several relevant studies have been completed on Pliocene otoliths from the eastern Caribbean. Nolf (1976) described Neogene otoliths from Trinidad including Pliocene forms. Nolf and Stringer (1992) reported on a highly diversified Mio-Pliocene otolith assemblage (84 species) from the

Dominican Republic. Stringer (1998) detailed late Pliocene otoliths (68 species) from the Bowden shell beds of the Bowden Member of the Layton Formation, previously known as the Bowden Formation (James-Williamson and Mitchell, 2012) of Jamaica. Neogene otoliths, including Pliocene, have also been described from the western Caribbean and tropical America by Schwarzhans and Aguilera (2013), Aguilera, Schwarzhans, and Bearéz (2016), and Schwarzhans and Aguilera (2016). These studies detailed otoliths of the Myctophidae, Sciaenidae, and Ophidiidiformes, respectively.

LOCALITY DATA AND STRATIGRAPHY

We studied Plio-Pleistocene teleostean otoliths from seven sites in coastal Georgia, USA. Each collection site was in the proximity of Brunswick in Glynn County, in the southeastern portion of Georgia along the Atlantic coast (Fig. 1). The seven collecting sites have local names based primarily on geographic features, as follows (with latitude/longitude coordinates): Site 1 = Sea Island (31.214, -81.328); Site 2 = Fancy Bluff (31.127, -81.552); Site 3 = South Brunswick River (31.135, -81.511); Site 4 = Joiner Creek (31.113, -81.512); Site 5 = Turtle River (31.187, -81.542); Site 6 = Dunbar Creek (31.120, -81.384); Site 7 = East River (31.143, -81.506).

The difficulty and complexity of geologic mapping in the Georgia Coastal Plain have long been recognized (Veatch and Stephenson, 1911; Cooke and Munyan, 1938; Cooke, 1943; Henry and Hoyt, 1965; Hoyt and Hails, 1974; Huddleston, 1988). Markewich et al. (1992) reported that each late Pliocene and Pleistocene transgression in southeast Georgia was highly erosive and removed almost all underlying Plio-Pleistocene strata. The result was thin, carbonate poor, and largely unfossiliferous or "fossil-poor" Plio-Pleistocene sediments. Campbell and Campbell (1995) emphasized similar problems with the Pliocene in adjacent South Carolina and noted that stratigraphic relationships among Pliocene beds have not been clearly demonstrated in spite of 150+ years of study. The Plio-Pleistocene stratigraphy in Glynn County is equally complex. In some cases, it was possible to determine the geologic age, but not the specific formation. This is especially true for the Pleistocene strata (Markewich et al., 1992; Hulbert and Pratt, 1998). In addition to the references above, the stratigraphy for the sites relied heavily upon the extensive work of L. Campbell (University of South Carolina Upstate).

Site 1 (Sea Island) is late Pleistocene in age, probably around 120,000 years old, and the formation is uncertain. Site 2 (Fancy Bluff) is early Pliocene in age (~3.8–4.5 Ma) and a Raysor Marl equivalent (Willoughby et al., 1999). Site 3 (South Brunswick River) is early Pliocene in age and appears to be either the Duplin Formation (~3.2 Ma) or a Raysor Marl equivalent (~3.8–4.5 Ma). The stratigraphy of Site 4 (Joiner Creek) is the most complex, with both late Pleistocene sediments and a Raysor Marl equivalent (~3.8–4.5 Ma). There are even possible indications of middle Miocene Marks Head Formation based on mollusk remains. Site 5 (Turtle River) is early Pliocene and a Raysor Marl equivalent (~3.8–4.5 Ma). Site 6 (Dunbar Creek) is late Pleistocene in age, but the formation is not known. Site 7 (East River) is early Pliocene and a Raysor Marl equivalent (~3.8–4.5 Ma). Ca. 96% of the otoliths originate in sediments known to be either Pliocene or Pleistocene.

METHODS AND MATERIAL

The fish otoliths for this study were obtained from bulk sampling of the seven sites. Unfortunately, precise data are not known on the weight of the bulk samples. All of the bulk samples were wet-screened using plain water with no additives to prevent damaging the aragonitic otoliths, which is normal procedure in otolith research. During the wet-screening, all residue that was retained on a 30-mesh sieve (U.S. Standard Sieve) was kept for otolith study. Following the wet sieving, the residue was labeled and air-dried. Microscopic examination was employed to extract the otoliths from the residue of each bulk sample. Otoliths that were at least one-half complete were extracted from the residue. All figured otolith specimens are reposited in the Georgia Southern Museum (GSM), Statesboro, Georgia. The remaining otoliths are retained by the individuals who collected the specimens.

The taxa represented by otoliths from the seven localities are presented in Table 1, shown in Figures 2–4, and are briefly described below. Unless noted otherwise, classification follows that of Nelson et al. (2016), which was greatly influenced by the work of Betancur-R. et al. (2013). Ordinal names follow Wiley and Johnson (2010), while the family-group names and authors of modern fishes follow van der Laan et al. (2014). Otolith classification used an open generic nomenclature for many years (Nolf, 1985). Nolf (2013) proposed an alternative method that employs collective group names as a genus group name. This methodology has been questioned by numerous paleontologists such as Janssen (2012), Schwarzhans (2012:87–88), and Tracey (2014). These concerns have led the authors to use modern and fossil genera for this study.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Order ANGUILLIFORMES GOODRICH, 1909
Family HETERENCHELYIDAE REGAN, 1912

Material.–1 sagitta from Fancy Bluff.

Description.–Although the one sagitta is not preserved well, it has sufficient features to assign it to this family, but not to the genus level. Key characters of the otoliths of this family include the discoid outline of the sagitta and the shape and orientation of the sulcus (Nolf, 2013:pl. 17). The family consists of only two genera, which are found in the Atlantic, Mediterranean, and Pacific (Nelson et al., 2016). Several species are known from the eastern Atlantic, but only one species, *Pythonichthys sanguineus*, is known from the western Atlantic (Smith et al., 2012). Preservation of the specimen prohibits more precise identification.

Family CONGRIDAE KAUP, 1856
RHYNCHOCONGER FLAVUS (GOODE AND BEAN, 1896)
Figure 2A

Material.–2 sagittae; Fancy Bluff (1) and Dunbar Creek (1).

Description.–The two sagittae have diagnostic features of the Congridae, specifically an undivided sulcus and a distinctive ostial channel that opens onto the anterodorsal margin. Characteristics that place the otoliths in this species include the shape and outline, the medially located sulcus, and the prominent rectangular area located above the caudal area. An otolith of a modern *Rhynchoconger flavus* is illustrated in Nolf (2013:pl. 21).

GNATHOPHIS AFF. *G. BRACHEATOPOS* (SMITH AND KANAZAWA, 1977)
Figure 2B

Material.–14 sagittae; Fancy Bluff (5), Joiner Creek (2), Turtle River (1), and East River (6).

Description.–These 14 sagittae also have diagnostic features of the family Congridae, specifically an undivided sulcus and a distinctive ostial channel that opens onto the anterodorsal margin, but they differ from *Rhynchoconger flavus* in several key features. The sulcus of *Gnathophis* tends to slant slightly in an anterior to posterior direction, especially with larger, more mature specimens. Also, the outline of the sagitta of *Gnathophis* is less angular, and the ostial channel is not nearly as prominent and well defined. Lastly, but importantly, there is no depressed area above the sulcus. These specimens seem to best match *Gnathophis bracheatopos*, but this cannot be attributed unequivocally. Otoliths of modern *Gnathophis* were illustrated in Smale et al. (1995:pl. 4), and several fossil species of *Gnathophis* are shown in Nolf (2013:pls. 22–23).

ARIOSOMA CF. *A. BALEARICUM* (DELAROCHE, 1809)
Figure 2C

Material.–1 sagitta from East River.

Description.–The sulcus in *Ariosoma balearicum* is quite prominent and is not divided into a distinct ostium and cauda. The sulcus is located medially and extends across most of the inner face. There is a conspicuous ostial channel at the anterior of the sulcus. The ostial channel extends upward into a pronounced dorsal dome that is somewhat flattened and characterizes the dorsal margin. The anterior outline is broadly rounded, while the posterior outline is tapered and more pointed. The

Table 1. Summary of fossil fish otoliths from coastal Plio-Pleistocene sites, Glynn County, Georgia USA (Fig. 1).

Family Genus and species	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**
Family Heterenchelyidae							
Heterenchelyidae indeterminate	—	1	—	—	—	—	—
Family Congridae							
Rhynchoconger flavus	—	1	—	—	—	1	—
Gnathophis aff. *G. bracheatopos*	—	5	—	2	1	—	6
Ariosoma cf. *A. balearicum*	—	–	—	—	—	—	1
Family Engraulidae							
Anchoa hepsetus	2	—	—	—	1	—	—
Anchoa mitchilli	1	—	—	—	—	—	—
Family Clupeidae							
Clupeidae indeterminate	—	—	—	—	1	—	—
Family Ariidae							
Bagre marinus	—	8	2	7	—	—	2
Ariopsis felis	—	10	1	5	—	—	2
Family Merlucciidae							
Merluccius albidus	—	3	—	2	—	–	1
Merluccius bilinearis	—	3	—	—	—	–	—
Family Gadidae							
Urophycis cf. *U. floridana*	—	—	—	—	1	–	—
Family Ophidiidae							
Lepophidium profundorum	—	101	—	30	1	—	29
Lepophidium elongatum	—	—	—	1	—	—	—
Lepophidium marmoratum	—	4	1	—	—	—	—
Otophidium lacinius	—	12	1	4	3	—	—
Otophidium omostigma	—	156	4	37	1	—	44
Otophidium cf. *O. robinsi*	—	—	—	—	—	—	1
Otophidium sp.	—	1	—	1	—	—	4
Ophidion cf. *O. marginatum*	4	9	—	3	2	—	1
Ophidion cf. *O. grayi*	—	—	—	—	—	1	—
Ophidiidae indeterminate	—	—	—	3	—	—	3
Family Opistognathidae							
Lonchopisthus micrognathus	—	3	—	—	—	—	—
Family Paralichthyidae							
Citharichthys macrops	—	1	—	—	1	—	—
Family Cynoglossidae							
Symphurus diomedeanus	—	2	—	—	—	—	—
Family Ammodytidae							
Ammodytes cf. *A. hexapterus*	—	—	—	—	1	—	—
Family Serranidae							
Centropristis philadelphica	—	3	—	3	—	—	1
Serranidae indeterminate	—	1	—	–	—	—	—

Table 1. Continued.

Family Genus and species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Family Haemulidae							
Orthopristis chrysoptera	1	1	—	1	—	—	—
Haemulon? sp.	—	1	1	—	—	—	—
Family Triglidae							
Prionotus cf. *P. carolinus*	—	3	—	1	—	—	—
Family Scorpaenidae							
Scorpaenidae indeterminate	—	1	—	—	—	—	—
Family Sciaenidae							
Micropogonias undulatus	85	101	49	22	—	3	128
Pogonias cromis	1	—	—	—	—	—	1
Stellifer lanceolatus	204	30	—	2	—	3	20
Bairdiella chrysoura	10	2	—	—	—	—	6
Larimus fasciatus	20	9	1	1	—	—	3
Cynoscion regalis	10	26	8	5	—	—	18
Cynoscion nebulosus	2	14	2	2	—	—	15
Cynoscion nothus	—	10	—	—	—	—	4
Cynoscion sp.	—	—	—	—	—	1	—
Pachyurus? *jeanae*	—	191	10	28	4	—	85
Leiostomus aff. *L. xanthurus*	6	12	1	2	—	—	8
Menticirrhus americanus	4	2	—	1	—	—	—
Menticirrhus? sp.	—	—	—	—	1	—	—
Protosciaena kirbyorum n. sp.	—	9	—	—	—	—	—
Umbrina cf. *U. coroides*	—	—	4	—	—	—	—
Sciaenidae indeterminate	—	—	—	1	—	—	1
Family Sparidae							
Sparidae indeterminate	—	—	—	1	—	—	—
Family (Unknown)							
Utricular otolith	—	8	2	—	—	—	3
Indeterminate	6	14	6	9	—	—	9
Total number of specimens	356	758	93	173	18	9	396

Explanation: Site 1 = Sea Island; Site 2 = Fancy Bluff; Site 3 = South Brunswick River; Site 4 = Joiner Creek; Site 5 = Turtle River; Site 6 = Dunbar Creek; Site 7 = East River.

ventral outline is broadly v-shaped. The differences in the margin outlines produce a rather rhomboidal shape (Smale et al., 1995). Nolf and Stringer (1992) reported this species from the late Miocene of the Dominican Republic (as *A. balearica*).

Order CLUPEIFORMES GOODRICH, 1909
Family ENGRAULIDAE GILL, 1861

ANCHOA HEPSETUS (LINNAEUS, 1758)
Figure 2D

Material.–3 sagittae; Sea Island (2) and Turtle River (1).

Description.–These three otoliths have representative engraulid characteristics, specifically the diagnostic sulcus, prominent rostrum, well-defined antirostrum, and oval shape, that allow them to be

assigned to *Anchoa hepsetus*.

ANCHOA MITCHILLI (VALENCIENNES, 1848)
Figure 2E

Material.–1 sagitta from Sea Island.

Description.–This otolith has typical features of an engraulid. It is distinguished by its oval shape with a prominent rostrum that is slightly rounded on the anterior. The antirostrum is well defined. The ostium is located almost entirely on the rostrum. The cauda is larger, more expanded, and noticeably depressed. A conspicuous crista superior is located above the cauda. The anterior margin is slightly pointed. The ventral margin has pronounced serrations. Although engraulid otoliths are often found in Neogene strata (Nolf and Stringer, 1992; Stringer, 1998; Müller, 1999), they are rarely abundant and tend to be small, juvenile specimens. This is also the case for the coastal Georgia Plio-Pleistocene otoliths.

Family CLUPEIDAE RAFINESQUE, 1810

Material.–1 sagitta from Turtle River.

Description.–This single sagitta has characteristics of the family Clupeidae (oval outline, medially located sulcus, prominent rostrum, and an antirostum). Poor preservation does not allow identification beyond the family level.

Order SILURIFORMES HAY, 1929
Family ARIIDAE GUNTHER, 1864
BAGRE MARINUS (MITCHILL, 1815)
Figure 2F

Material.–19 lapilli; Fancy Bluff (8), South Brunswick River (2), Joiner Creek (7), and East River (2).

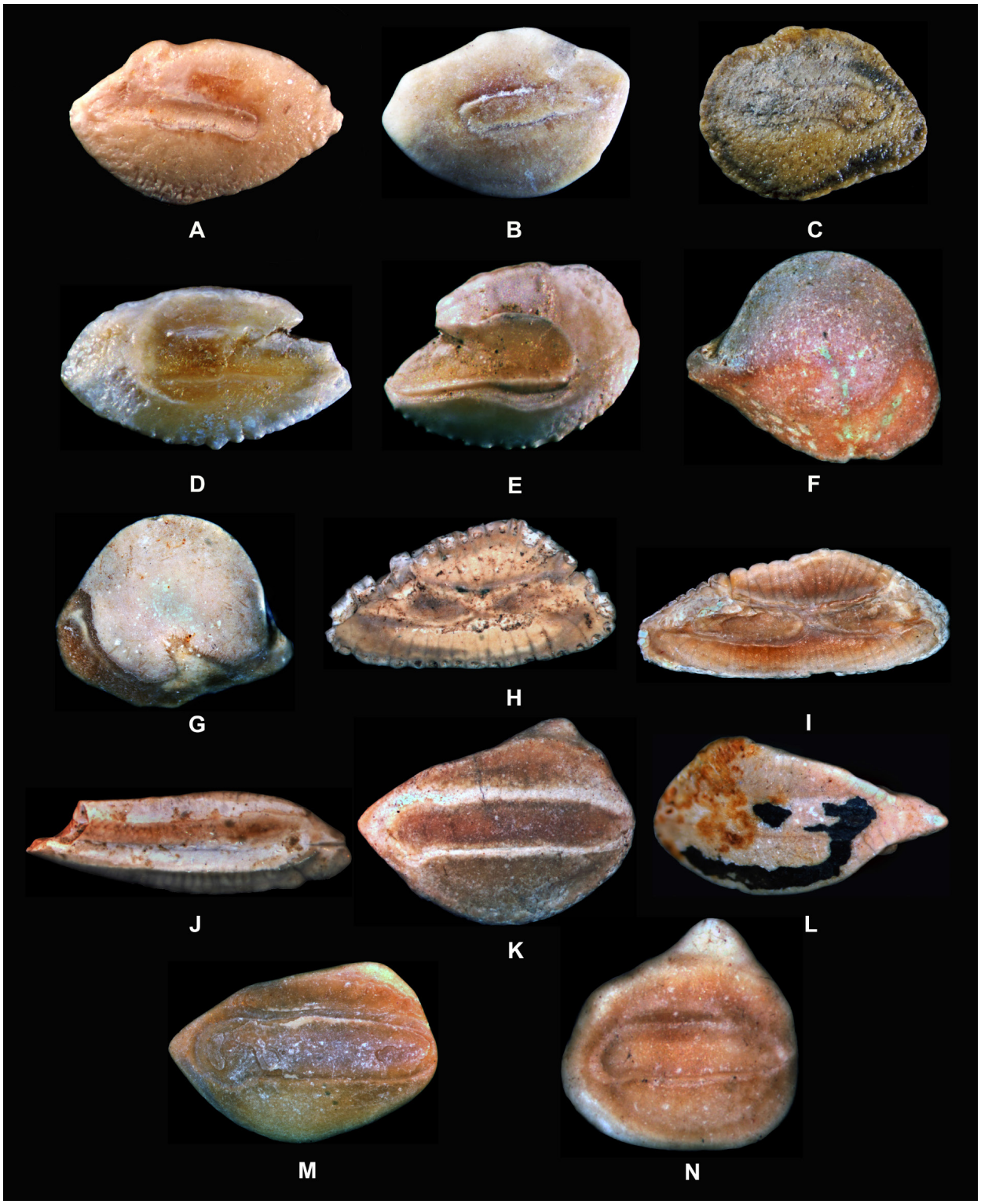
Description.–These lapilli (otoliths from the utriculus rather than the sacculus) have typical features associated with the ariids including a circular shape and a sulcus-like feature along the margin (not a true sulcus as on the sagitta). The inner face is convex and quite smooth. The lapilli of *Bagre marinus* can be distinguished from those of *Ariopsis felis* by several key features. The dorsal outline of the inner face of *B. marinus* tends to more oval with a central axis that is slanted, whereas the dorsal outline of the inner face of *A. felis* is more circular, and the central axis is almost perpendicular. Although slightly older than the coastal Georgia ariids, several species of *Arius* (now classified as *Ariopsis*) have been described from the Cercado Formation of the Dominican Republic (Nolf and Stringer, 1992) and the Cantaure Formation of Venezuela (Nolf and Aguilera, 1998). Aguilera et al. (2013) detailed ariid catfishes from the late Miocene in Brazil, Columbia, and Venezuela.

ARIOPSIS FELIS (LINNAEUS, 1766)
Figure 2G

Material.–18 lapilli; Fancy Bluff (10), South Brunswick River (1), Joiner Creek (5), and East River (2).

Description.–The lapilli of *Ariopsis felis* have typical ariid characteristics, but are distinguished by a more circular dorsal outline of the inner face with the central axis of the lapillus almost perpendicular. Approximately 100 lapilli of modern *A. marinus* and *B. marinus* were available for comparison from the Gulf Coast Research Laboratory in Ocean Springs, Mississippi. Neogene catfish lapilli have been reported in the Caribbean area by Nolf and Stringer (1992), Nolf and Aguilera (1998), and Aguilera et al. (2013).

Figure 2. The taxonomic identification of each otolith (all inner views), location of the otolith in the labyrinth (right or left side), and type of otolith (sagitta or lapillus) are given. Length of otolith is given in mm, and specific collection site is noted. All specimens shown in the figures are reposited in the Georgia Southern Museum (GSM), Statesboro, Georgia 30458, and catalog numbers are provided. **A.** *Rhynchoconger flavus*, right sagitta, 3.16 mm, Dunbar Creek, GSM-1404. **B.** *Gnathophis* aff. *G. bracheatopos*, left sagitta, 4.50 mm, Fancy Bluff, GSM-1405. **C.** *Ariosoma* cf. *A. balearicum*, right sagitta, 6.05 mm, East River, GSM-1406. **D.** *Anchoa hepsetus,* left sagitta, 3.67 mm, Sea Island, GSM-1407. **E.** *Anchoa mitchilli*, right sagitta, 2.36 mm, Sea Island, GSM-1408. **F.** *Bagre marinus*, lapillus, 5.10 mm, Joiner Creek, GSM-1409.



G. *Ariopsis felis*, lapillus, 10.67 mm, Fancy Bluff, GSM-1410. **H.** *Merluccius albidus*, left sagitta, 6.51 mm, Fancy Bluff, GSM-1411. **I.** *Merluccius bilinearis*, left sagitta, 9.71 mm, Fancy Bluff, GSM-1412. **J.** *Urophycis* cf. *U. floridana*., left sagitta, 5.89 mm, Turtle River, GSM-1413. **K.** *Lepophidium profundorum*, left sagitta, 6.39 mm, Fancy Bluff, GSM-1414. **L.** *Lepophidium elongatum,* right sagitta, 6.58 mm, Joiner Creek, GSM-1415. **M.** *Lepophidium marmoratum*, left sagitta, 6.22 mm, Fancy Bluff, GSM-1416. **N.** *Otophidium lacinius*, left sagitta, 2.87 mm, Fancy Bluff, GSM-1417.

Order GADIFORMES GOODRICH, 1909
Family MERLUCCIIDAE RAFINESQUE, 1815
MERLUCCIUS ALBIDUS (MITCHILL, 1818)
Figure 2H

Material.–6 sagittae; Fancy Bluff (3), Joiner Creek (2), and East River (1).

Description.–*Merluccius albidus* is one of two merluccid hakes found in the Plio-Pleistocene otoliths from coastal Georgia. The fossils have typical merluccid features, such as the homosulcoid type sulcus and being quite thin, and matches sagittae of extant *M. albidus*, the offshore silver hake, almost perfectly (Campana, 2004:68). *M. albidus* is widespread and is found along the western Atlantic U. S. coast and throughout the Gulf of Mexico and Caribbean (Cohen et al., 1990). Its sagitta differs from that of the similar *M. bilinearis* by a higher height to length ratio and a less expanded ostium and cauda. Fitch and Lavenberg (1983) reported 85 *M. albidus* otoliths from the Pliocene Yorktown Formation at the Lee Creek Mine, North Carolina.

MERLUCCIUS BILINEARIS (MITCHILL, 1814)
Figure 2I

Material.–3 sagittae from Fancy Bluff.

Description.–These specimens represent a second merluccid hake recovered from the Plio-Pleistocene sites. They have a lower height/length ratio, and the ostium and cauda are slightly more expanded. They are a nearly perfect match to *M. bilinearis,* the silver hake (Campana, 2004:69). Fitch and Lavenberg (1983) identified 493 *M. bilinearis* otoliths from the Pliocene Yorktown Formation at the Lee Creek Mine in North Carolina.

Family GADIDAE RAFINESQUE 1810
UROPHYCIS CF. *U. FLORIDANA* (BEAN AND DRESEL, 1884)
Figure 2J

Material.–1 sagitta from Turtle River.

Description.–Sagittae of *Urophycis* are characterized by a very narrow, oblong shape where the length is at least five times greater than the height. The greatest otolith height is near the anterior, and the otolith tapers toward the posterior. The sulcus is undivided and is almost as long as the otolith. Müller (1999) described *Urophycis* aff. *regius* from the Pliocene of Virginia (Yorktown Formation). and Fitch and Lavenberg (1983) reported *Urophycis tenuis* from the Pliocene of North Carolina (Yorktown Formation), however the sulcus of the Georgia specimen indicates that it is more closely related to *Urophycis floridana.*

Order OPHIDIIFORMES BERG, 1937
Family OPHIDIIDAE RAFINESQUE, 1810
LEPOPHIDIUM PROFUNDORUM (GILL, 1863)
Figure 2K

Material.–162 sagittae; Fancy Bluff (101), Joiner Creek (30), Turtle River (1), and East River (29).

Description.–The undivided sulcus of the sagitta from this common ophidiid is almost the same width for its entire length except for a very slight enlargement at the posterior end. The sulcus is mainly medially located and almost reaches the anterior and posterior margins. The posterior is pointed and quite aculeate in most specimens, while the anterior is rounded. Another distinguishing feature is the prominent anterodorsal dome. Although not wide, the dome is high and variable in shape. Some margins along the dome can be lobate. The L/H ratios tend to decrease with increased size. It has been reported from the Pliocene of North Carolina (Fitch and Lavenberg, 1983) and Jamaica (Stringer, 1998), and the late Pleistocene-early Holocene of Louisiana (Stringer, 1992), all as *Lepophidium cervinum*. According to Robins et al. (2012), with very few exceptions, previously published identifications of *L. cervinum* refer to *Lepophidium profundorum.*

LEPOPHIDIUM ELONGATUM MÜLLER, 1999
Figure 2L

Material.–1 sagittae from Joiner Creek.

Description.–The undivided sulcus of this rare ophidiid is fairly constant in width except that it constricts slightly at the anterior and has a slight enlargement on the ventral margin of the posterior. The sulcus is mainly medially located and almost reaches the anterior margin. The posterior of the otolith is the most prominent feature and is quite aculeate. The posterior projection accounts for almost 20% of the total length of the otolith. An

anterodorsal dome is present although not nearly as high or pronounced as in *Lepophidium profundorum*. The specimen matches that in Müller (1999:fig. 25, 17a), who first described this species from the Miocene of Maryland.

LEPOPHIDIUM MARMORATUM (GOODE AND BEAN, 1885)
Figure 2M

Material.–5 sagittae; Fancy Bluff (4), and South Brunswick River (1).

Description.–The sagitta of this uncommon species is oval in outline and characterized by a wide, undivided sulcus that is located slightly more dorsally. The sulcus is extremely close to the anterior margin and close to the posterior margin. The dorsal margin of the sulcus is arched, while the ventral margin of the sulcus is almost horizontal except for a distinct posterior expansion. The ventral margin of the otolith is broadly rounded (widest at the midpoint), while the dorsal margin has a small anterodorsal dome. Except for the anterodorsal dome, the dorsal margin tends to be fairly straight with a distinct angle toward the posterior. The posterior end is tapered but not distinctly pointed. Schwarzhans and Aguilera (2016) reported this species from the late early Pliocene of Panama.

OTOPHIDIUM LACINIUS MÜLLER, 1999
Figure 2N

Material.–20 sagittae; Fancy Bluff (12), South Brunswick River (1), Joiner Creek 4), and Turtle River (3).

Description.–These otoliths tend to be small, with most less than 3 mm. The smaller specimens are more elongated, while the larger ones become more oval and rounded. The sulcus is obvious and centrally located. The sulcus is essentially undivided although ostial and caudal regions can be ascertained on the larger specimens. There is a prominent anterodorsal dome on the smaller specimens. The conspicuous dorsal dome becomes more centrally located on the larger specimens. This species is known from the Pliocene Yorktown Formation of North Carolina (Lee Creek Mine). Fitch and Lavenberg (1983:fig 2f) referred to this species as Ophidiidae sp. A, and Müller (1999:fig. 27, 17–24) described this species as "aff. *Otophidium*" *lacinius*, both from the Pliocene of North Carolina. Schwarzhans and Aguilera (2016) identified the form from the late Pliocene of Jamaica and the middle Pleistocene of Panama. This ophidiid is one of only four extinct species recognized in the Plio-Pleistocene in coastal Georgia.

OTOPHIDIUM OMOSTIGMA (JORDAN AND GILBERT, 1882)
Figure 3A

Material.–242 sagittae; Fancy Bluff (156), South Brunswick (4), Joiner Creek (37), Turtle River (1), and East River (44).

Description.–This taxon is the most abundant ophidiid recovered and is characterized by a medially located, longitudinally divided sulcus. In larger specimens, the dorsal margin of the sulcus is conspicuously arched. One of the most distinguishing features is the high, wide anterodorsal dome, which significantly skews the shape toward the anterodorsal margin. The posterior end tapers but is not sharply pointed. The shape is oval to more rounded with increased size.

OTOPHIDIUM CF. *O. ROBINSI* NOLF AND STRINGER, 1992
Figure 3B

Material.–1 sagitta from East River.

Description.–Although worn, the specimen shows several characteristics of the sagitta of *Otophidium robinsi*. The sagitta is round except for a small posterior projection. The medially located sulcus is undivided and extends from the anterior margin almost to the posterior margin. One of only four extinct species in the assemblage, *O. robinsi* was originally described from the upper Miocene of the Dominican Republic (Nolf and Stringer, 1992:pl. 11, 16–19b). The species was subsequently reported from Jamaica (Stringer, 1998) and Ecuador to Panama, the Caribbean, and Venezuela (Schwarzhans and Aguilera, 2016).

OTOPHIDIUM SP.

Material.–six sagittae; Fancy Bluff (1), Joiner Creek (1), and East River (4).

Description.–These specimens have characteristics of the ophidiid genus *Otophidium*,

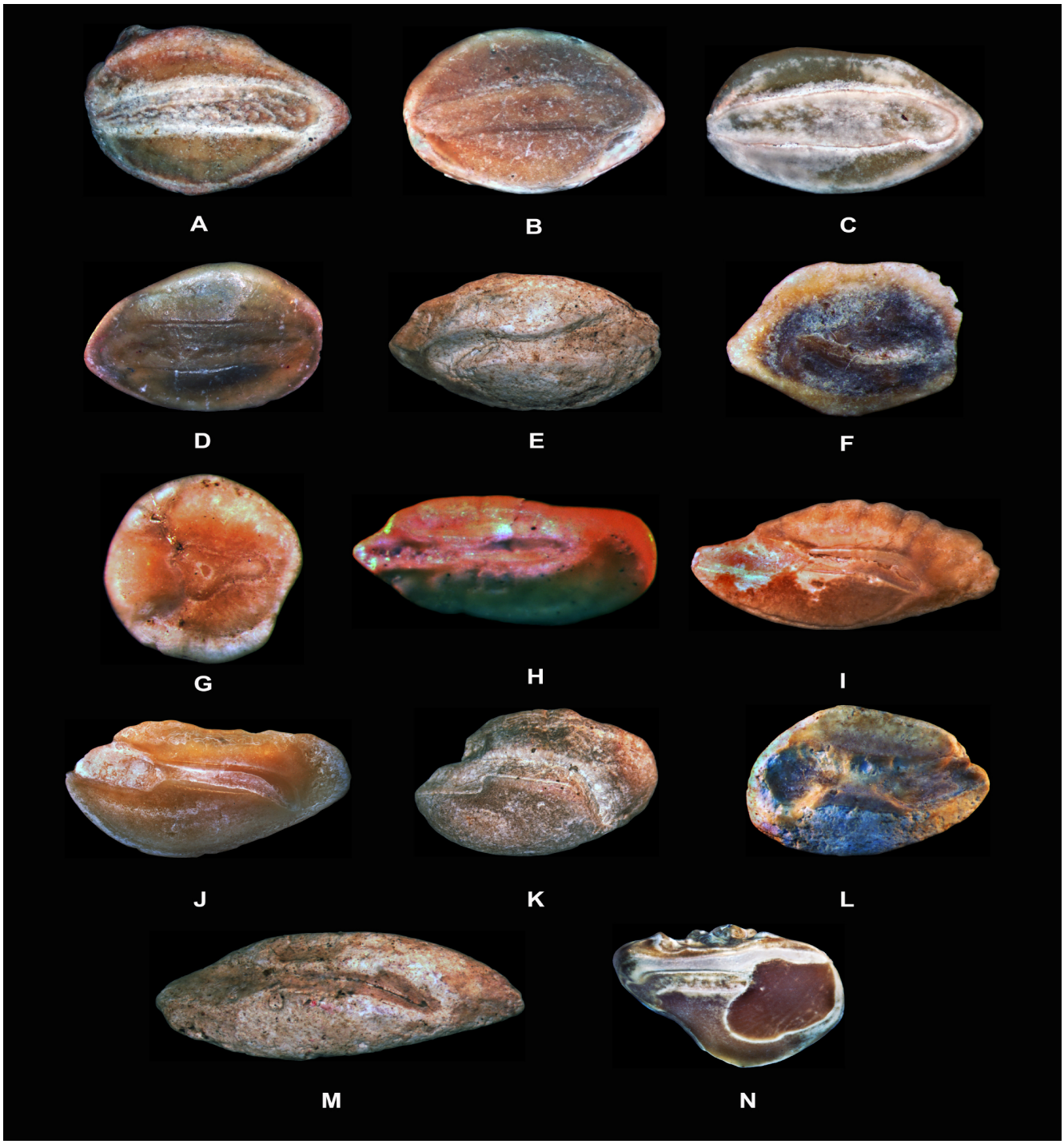


Figure 3. See Figure 2 for explanation. **A.** *Otophidium omostigma*, right sagitta, 5.56 mm, Fancy Bluff, GSM-1418. **B.** *Otophidium* cf. *O. robinsi*, left sagitta, 4.43 mm, East River, GSM-1419. **C.** *Ophidion* cf. *O. marginatum*, right sagitta, 4.49 mm, Sea Island, GSM-1420. **D.** *Ophidion* cf. *O. grayi*, left sagitta, 4.98 mm, Dunbar Creek, GSM-1421. **E.** *Lonchopisthus micrognathus*, left sagitta, 7.18 mm, Fancy Bluff, GSM-1422. **F.** *Citharichthys macrops*., right sagitta, 3.12 mm, Fancy Bluff, GSM-1423. **G.** *Symphurus diomedeanus*, right sagitta, 1.88 mm, Fancy Bluff, GSM-1424. **H.** *Ammodytes* cf. *A. hexapterus*, right sagitta, 1.53 mm, Turtle Creek, GSM-1425. **I.** *Centropristis philadelphica*, right sagitta, 5.57 mm, Fancy Bluff, GSM-1426. **J.** *Orthopristis chrysoptera*, right sagitta, 8.26 mm, Sea Island, GSM-1427.

although more specific identification was not possible because of their preservation.

OPHIDION CF. *O. MARGINATUM* DEKAY, 1842
Figure 3C

Material.–19 sagittae; Sea Island (4), Fancy Bluff (9), Joiner Creek (3), Turtle River (2), and East River (1).

Description.–The shape is primarily oval with a small dorsal dome. The dorsal dome is anterior to medial in location. The sulcus is fairly wide and reaches the anterior margin. The dorsal margin of the sulcus arches slightly from anterior to posterior and is widest in the middle. The ventral margin of the sulcus is primarily straight except for an expansion at the posterior. There is conspicuous tapering of the sulcus toward the anterior. The sulcus width is smallest just before the anterior margin. The sulcus tends to be located slightly more ventrally (Nolf, 1980:pl. 5, fig. 12).

OPHIDION CF. *O. GRAYI* (FOWLER, 1948)
Figure 3D

Material.–One sagitta from Dunbar Creek.

Description.–This ophidiid specimen has several characteristics of *Ophidion grayi*. The outline is mainly oval with a conspicuous sulcus, which is divided longitudinally. A dorsal dome is present but is more rounded and not pronounced. The dome is located between the anterior and medial on the dorsal margin. A ventral furrow is present near the ventral margin. Müller (1999:fig 27, 4–9) reported this species from the Pliocene of North Carolina.

OPHIDIIDAE INDETERMINATE

Material.–6 sagittae; Joiner Creek (3), and East River (3).

Description.–These six eroded specimens have morphological features of the family Ophidiidae, but more specific identification is not possible given the preservation.

Order GOBIIFORMES GÜNTHER, 1880
Family OPISTOGNATHIDAE BONAPARTE, 1835
LONCHOPISTHUS MICROGNATHUS (POEY, 1860)
Figure 3E

Material.–3 sagittae from Fancy Bluff**.**

Description.–The shape of this otolith is oval, and the sulcus is primarily homosulcoid (as defined by Smale et al., 1995). The dorsal margin of the sulcus tends to undulate. The ostium opens onto the anterior and is somewhat larger than the cauda. Anterior and posterior collicula are present. There is a prominent ventral furrow, and an oval-shaped depression above the center of the sulcus. Nolf and Stringer (1992) noted this species from the Dominican Republic Pliocene, and Stringer (1998) reported it from the Pliocene of Jamaica.

Order PLEURONECTIFORMES BLEEKER, 1859
Family PARALICHTHYIDAE REGAN, 1910
CITHARICHTHYS MACROPS DRESEL, 1885
Figure 3F

Material.–2 sagittae; Fancy Bluff (1) and Turtle River (1)

Description.–The otolith shape is pentagonal in outline with distinct predorsal, postdorsal, and midventral angles as well as an anterior tip (broken) and a prominent posterior tip that is rounded. It is characterized by a unique sulcus in which the anterior and posterior portions are narrower, but the middle portion is widened (termed fusiform by Schwarzhans, 1999). Ostial and caudal colliculi are fused. The fusiform sulcus and the fused colliculi are key morphological features of *Syacium*, to which the specimens were originally attributed, and *Citharichthys*. However, further examination indicated that the specimens closely matched *Citharichthys macrops*, which is known from the U.S. Atlantic coast and Gulf of Mexico (Schwarzhans, 1999:figs. 274–275; Page et al., 2013). Stringer

K. *Haemulon*? sp., right sagitta, 12.53 mm, Fancy Bluff, GSM-1428. **L.** *Prionotus* cf. *P. carolinus*, left sagitta, 4.19 mm, Fancy Bluff, GSM-1429. **M.** Scorpaenidae indeterminate, right sagitta, 7.61 mm, Fancy Bluff, GSM-1430. **N.** *Micropogonias undulatus*, left sagitta, 8.25 mm, Sea Island, GSM-1431.

(1992) noted the presence of *Citharichthys* from the late Pleistocene-early Holocene of Louisiana. Nolf (1976) reported *Citharichthys* from the Pliocene of Trinidad, while Fitch and Lavenberg (1983) and Müller (1999) described several species of *Citharichthys* from the Pliocene of North Carolina.

Family CYNOGLOSSIDAE JORDAN AND GOSS, 1889
SYMPHURUS DIOMEDEANUS (GOODE AND BEAN, 1885)
Figure 3G

Material.–2 sagittae from Fancy Bluff.

Description.–These sagittae exhibit characteristics that point to the cynoglossid *Symphurus*. The small otoliths (< 3 mm) are discoid to almost perfectly round in shape with a very unique hammer-shaped sulcus with fused colliculi. The ostial portion of the sulcus is reduced while the cauda is bilobate in shape. The sulcus tends to be shallow with a well-developed circumsulcal depression. The sulcus characteristics indicate *S. diomedeanus*. The posterior of the dorsal rim tends to be higher. Although rare in the fossil record, they have been reported by Nolf (1976) in the Miocene of Trinidad, by Nolf and Stringer (1992) in the Miocene of the Dominican Republic, and Stringer (1992) in the late Pleistocene-early Holocene of Louisiana.

Order TRACHINIFORMES sensu BETANCUR-R. et al., 2013
Family AMMODYTIDAE BONAPARTE, 1835
AMMODYTES CF. *A. HEXAPTERUS* PALLAS, 1814
Figure 3H

Material.–1 sagitta from Turtle River.

Description.–The morphological features of this specimen indicate an affinity with *Ammodytes.* The otolith is oblong in shape with a lightly impressed sulcus (heterosulcoid type). The sulcus extends about 70% of the length of the inner face. The ostium and cauda are about the same width and length. The single specimen is small (length 1.53 mm). Fitch and Lavenberg (1983) found a small number of this species in the Pliocene Yorktown Formation from Lee Creek in North Carolina. Müller (1999:pl. 17, figs. 1–6) reported *Ammodytes* aff. *A. hexapterus* (526 specimens) from the Mio-Pliocene of Maryland, Virginia, and North Carolina.

Order PERCIFORMES BLEEKER, 1859
Family SERRANIDAE SWAINSON, 1839
CENTROPRISTIS PHILADELPHICA (LINNAEUS, 1758)
Figure 3I

Material.–7 sagittae; Fancy Bluff (3), Joiner Creek (3), and East River (1).

Description.–This otolith has a conspicuous sulcus (heterosulcoid), an ostium that is a little wider but shorter than the cauda, a cauda that is slightly downturned at the posterior, and a prominent, pointed rostrum. The ostium is about 75% of the length of the cauda. The dorsal margin may have some small lobes but the ventral margin is primarily smooth. The shape is somewhat elliptic and oblong per Smale et al. (1995). *Centropristis* was reported by Nolf and Stringer (1992) from the Dominican Republic Pliocene and by Stringer (1992) from the Pleistocene of Louisiana.

SERRANIDAE INDETERMINATE

Material.–1 sagitta from Fancy Bluff.

Description.–This otolith has several features of the Serranidae, but poor preservation prohibits any further identification.

Family HAEMULIDAE GILL, 1885
ORTHOPRISTIS CHRYSOPTERA (LINNAEUS, 1766)
Figure 3J

Material.–3 sagittae; Sea Island (1), Fancy Bluff (1), and Joiner Creek (1).

Description.–The sagitta of this species has an oval outline. The sulcus has a well-defined ostium and cauda. The ostium is wider than the cauda but only about one-half the cauda's length. The cauda is narrow and consistent in width. The cauda is horizontal except for the posterior, which is prominently downturned. A ventral furrow is present and primarily centrally located.

HAEMULON? SP.
Figure 3K

Material.–2 sagittae; Fancy Bluff (1) and South Brunswick River (1).

Description.–These sagittae have characteristics of *Haemulon*, especially the ostial and caudal juncture of the heterosulcoid-type sulcus. Preservation prevented specific identifications.

Order **SCORPAENIFORMES sensu IMAMURA AND YABE, 2002**

Family TRIGLIDAE RAFINESQUE, 1810

***PRIONOTUS* CF. *P. CAROLINUS* (LINNAEUS, 1771)**

Figure 3L

Material.–4 sagittae; Fancy Bluff (3) and Joiner Creek (1).

Description.–The sagitta of this species is characterized by a distinctive, homosulcoid-type sulcus. The ostium is slightly larger than the cauda. Anterior and posterior colliculi are present. There is a slightly depressed area above the anterior and central portion of the sulcus. The shape of the otolith is basically oval, but the anterior and posterior are somewhat pointed. *Prionotus* has been reported from the Pliocene of the Dominican Republic (Nolf and Stringer, 1992), the Pliocene of Jamaica (Stringer, 1998), the Pliocene of North Carolina (Fitch and Lavenberg, 1983), and the late Pleistocene-early Holocene of Louisiana (Stringer, 1992).

Family SCORPAENIDAE RISSO, 1827

Figure 3M

Material.–1 sagitta from Fancy Bluff.

Description.–The single specimen has an outline and sulcus that are indicative of the family Scorpaenidae. However, the poor preservation of the specimen limits any further identification. Scorpaenidae indeterminate are also reported from the Dominican Republic and Jamaica (Nolf and Stringer, 1992; Stringer, 1998).

Order ACANTHURIFORMES JORDAN, 1923

Family SCIAENIDAE CUVIER, 1828

***MICROPOGONIAS UNDULATUS* (LINNAEUS, 1766)**

Figure 3N

Material.–388 sagittae; Sea Island (85), Fancy Bluff (101), South Brunswick River (49), Joiner Creek (22), Dunbar Creek (3), and East River (128).

Description.–The unique otolith is shield-like in shape with the thickened dorsal rim relatively flat, but the sharp ventral rim is deeply curved anteriorly with a distinct concavity posteriorly. The heterosulcoid sulcus is large and encompasses much of the inner face. The ostium is compressed but very deep and extends from almost the dorsal rim to near the ventral rim. The width of the cauda is only about one-quarter of the height of the ostium and has a characteristic enlarged caudal tip (Schwarzhans, 1993). The outer face commonly has a prominent, raised umbo. A growth series of the sagittae of *Micropogonias undulatus* is illustrated in Nolf and Kerckhof (2007:pl. 3). It is known from the Pliocene of North Carolina (Fitch and Lavenberg, 1983) as *Micropogonias* sp., from the late Pleistocene-early Holocene of Louisiana, and from the subsurface Miocene of Mississippi (Stringer, unpublished data).

***POGONIAS CROMIS* (LINNAEUS, 1766)**

Figure 4A

Material.–2 sagittae; Sea Island (1) and East River (1).

Description.–The sagittae attributed to *Pogonias cromis* have a typical sciaenid sulcus with a strongly enlarged ostium and a short, narrow cauda with a prominently downturned posterior portion (Schwarzhans, 1993). The inner face is moderately convex. The dorsal rim is primarily horizontal with slight crenulations and has a highly characteristic mediodorsal angle (dome) and postdorsal projection, while the ventral rim is deeply rounded (Campana, 2004). Significant ontogenetic changes have been noted in *P. cromis*. Fitch and Lavenberg (1983) described one specimen as *Pogonias* cf. *P. cromis* from the Pliocene of North Carolina.

***STELLIFER LANCEOLATUS* (HOLBROOK, 1855)**

Figure 4B–C

Material.–259 sagittae and lapilli; Sea Island (204), Fancy Bluff (30), Joiner Creek (2), Dunbar Creek (3), and East River (20).

Description.–The sagitta of *Stellifer lanceolatus* is easily distinguished by its almost vertical anterior margin and nearly horizontal, almost straight dorsal and ventral margins that produce an


A
B
C
D
E
F
G
H
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N

essentially rectangular anterior shape. The predorsal spine is sharp but greatly reduced in size. The postdorsal projection is massive and lacks a postventral notch (Chao, 1978:fig. 27B). The ostium is short and nearly vertical (80–90°) according to Schwarzhans (1993). The ostium appears to be below the anterior tip of the cauda. The cauda is long, deep, and regularly and strongly curved. The sciaenids are one of the few families in which utricular (lapillus) otoliths can be used for identification. The lapilli of *S. lanceolatus* are suboval in outline (terminology of Chao, 1978). The groove ("sulcus" in some references) at the anteroventral end is deeper but thinner than in *Bairdiella chrysoura*. The end opposite the groove is rounded and has a small, rounded projection visible on well-preserved specimens. The inner face of *S. lanceolatus* lapilli is more convex than *B. chrysoura*.

BAIRDIELLA CHRYSOURA (LACEPÈDE, 1802)
Figure 4D–E

Material.–18 sagittae and lapilli; Sea Island (10), Fancy Bluff (2), and East River (6).

Description.–The otoliths of *Bairdiella* are some of the most curious in all of the Sciaenidae and show a close relationship with *Stellifer* (Schwarzhans 1993). The sagittae of *Bairdiella* from three of the sites match those of *B. chrysoura* almost exactly. The most prominent features are the long and sharp predorsal and postdorsal spines, the short ostium that is steeply inclined and bent downwardly, and the deep, wide, steeply curving cauda that terminates almost on the posteroventral rim. There is a well-defined postventral notch, and the ventral margin is short and broadly rounded on the posterior (Schwarzhans, 1993:figs. 393–395). The lapilli of *B. chrysoura* are elongate and rectangular in outline although Chao (1978) noted them as irregular in shape. The groove along the anteroventral end is broader and thicker than in *S. lanceolatus.* The groove opens to the ventral surface.

LARIMUS FASCIATUS HOLBROOK, 1855
Figure 4F

Material.–34 sagittae; Sea Island (20), Fancy Bluff (9), South Brunswick River (1), Joiner Creek (1), and East River (3).

Description.–The only similar sagitta to *Larimus fasciatus* in the western Atlantic, Gulf of Mexico, and eastern Caribbean is *Larimus breviceps*, which is typically found south of Cuba in the Caribbean. The anterodorsal edge of the ostium of *L. fasciatus* is slanted in an anteroventral direction (Schwarzhans, 1993:figs. 326–327) as opposed to the almost horizontal, anterodorsal edge of the ostium in *L. breviceps.* The downturned portion of the cauda of *L. fasciatus* tends to be closer to the posteroventral rim than in *L. breviceps.* The downturned portion of the cauda of *L. fasciatus* also tends to be narrower. The dorsal rim tends to be more horizontal, and the anterodorsal domes are not as pronounced in *L. fasciatus*. The fossil specimens were compared to otoliths of modern *L. fasciatus* of almost identical size obtained from the National Marine Fisheries Service, Southeast Fisheries Science Center in Pascagoula, Mississippi, and the specimens were essentially identical.

Figure 4. See Figure 2 for explanation. **A.** *Pogonias cromis*, right sagitta, 3.84 mm, East River, GSM-1432. **B.** *Stellifer lanceolatus*, left sagitta, 5.08 mm, Fancy Bluff, GSM-1433. **C.** *Stellifer lanceolatus*, lapillus, 3.64 mm, Sea Island, GSM-1434. **D.** *Bairdiella chrysoura*, right sagitta, 6.03 mm, Sea Island, GSM-1435. **E.** *Bairdiella chrysoura*, lapillus, 4.63 mm, Sea Island, GSM-1436. **F.** *Larimus fasciatus*, left sagitta, 6.67 mm, Sea Island, GSM-1437. **G.** *Cynoscion regalis*, right sagitta, 9.91 mm, South Brunswick, GSM-1438. **H.** *Cynoscion nebulosus*, left sagitta, 13.85 mm, Fancy Bluff, GSM-1439. **I.** *Cynoscion nothus*, right sagitta, 10.72 mm, Fancy Bluff, GSM-1440. **J.** *Pachyurus*? *jeanae*, right sagitta, 8.21 mm, Fancy Bluff, GSM-1441. **K.** *Leiostomus* aff. *L. xanthurus* , right sagitta, 4.52 mm, Sea Island, GSM-1442. **L.** *Menticirrhus americanus,* right sagitta, 6.92 mm, Fancy Bluff, GSM-1443. **M.** *Protosciaena kirbyorum* n. sp., right sagitta, 7.24 mm, Fancy Bluff, GSM-1444. **N.** *Umbrina* cf. *U. coroides*, left sagitta, 10.40 mm, South Brunswick, GSM-1445.

CYNOSCION REGALIS (BLOCH AND SCHNEIDER, 1801)
Figure 4G

Material.–67 sagittae; Sea Island (10), Fancy Bluff (26), South Brunswick River (8), Joiner Creek (5), and East River (18).

Description.–Sagittae representing several species of *Cynoscion* are present in the Plio-Pleistocene deposits in coastal Georgia. *Cynoscion regalis* is the most common of these closely related species. The ostium of this species tends to be narrower, the cauda longer, and the inframedian posterior projection is not as pronounced as in the similar *Cynoscion nebulosus*. Schwarzhans (1993) reported that *Cynoscion* otolith specimens smaller than 10 mm do not exhibit enough diagnostic characters to warrant specific determinations.

CYNOSCION NEBULOSUS (CUVIER, 1830)
Figure 4H

Material.–35 sagittae; Sea Island (2), Fancy Bluff (14), South Brunswick River (2), Joiner Creek (2), and East River (15).

Description.–Sagittae of *Cynoscion nebulosus* are the second most common species present of this genus. As noted earlier, the proportions of the sulcus are different from those in *C. regalis*, and the inframedian posterior projection is much more pronounced. In numerous specimens of this species from the Gulf of Mexico, the posterior tip tends to be more acute. This species is reported from the Yorktown Formation by Fitch and Lavenberg (1983) and Müller (1999).

CYNOSCION NOTHUS (HOLBROOK, 1848)
Figure 4I

Material.–14 sagittae; Fancy Bluff (10) and East River (4).

Description.–Found only at the Fancy Bluff and East River sites, the sagittae of *Cynoscion nothus* are not as elongate as in *C. regalis* and *C. nebulosus*, and the L/H ratio of *C. nothus* is smaller than in *C. nebulosus* and *C. regalis*. The ostium of *C. nothus* is more compressed, and the posterior tip is more centrally located. Stringer (1992) noted this species from late Pleistocene-early Holocene mudlump islands of Louisiana.

CYNOSCION SP.

Material.–One sagittae from the Dunbar Site.

Description.–This sagitta may represent one of the species of *Cynoscion* previously reported (*C. regalis, C. nebulosus*, or *C. nothus*), or it could be a different species. Preservation unfortunately does not allow this determination.

PACHYURUS? *JEANAE* MÜLLER, 1999
Figure 4J

Material.–318 sagittae; Fancy Bluff (191), South Brunswick River (10), Joiner Creek (28), Turtle River (4), and East River (85).

Description.–This very abundant species is characterized by a very conspicuous, heterosulcoid sulcus. The prominent ostium reaches the anterior margin and is approximately three times wider than the cauda. The cauda has a distinct horizontal and downturned portion, which are approximately equal in length. The downturned portion of the cauda is strongly curved and almost reaches the ventral rim. Larger specimens develop a very unique and characteristic j-shaped spur on the median portion of the ventral rim. This taxon was first recognized by Fitch and Lavenberg (1983:fig. 3h–i) from the Yorktown Formation (Lee Creek Mine) as Sciaenidae sp. A and represented the most abundant sciaenid in their study. Müller (1999) first described the species from North Carolina (Rushmere Member, Yorktown Formation) as "genus aff. *Pachyurus" jeanae*. A growth series of this species is illustrated in Nolf (2013:pl. 282) as "*Sciaenida*" *jeanae*. It is one of only four extinct species from the seven Plio-Pleistocene sites in coastal Georgia.

LEIOSTOMUS AFF. *L. XANTHURUS* LACEPÈDE, 1802
Figure 4K

Material.–29 sagittae; Sea Island (6), Fancy Bluff (12), South Brunswick River (1), Joiner Creek (2), and East River (8).

Description.–All otoliths from *Leiostomus* aff. *xanthurus* were relatively small (~5 mm) and had a plesiomorphic sciaenid sulcus. The ostium is moderately large and spoon-shaped, while the cauda is narrow, moderately deep with a downturned posterior portion. The dorsal rim is primar-

ily flat, while the ventral rim is gently and regularly curving. Sagittae of *L. xanthurus* are very similar to those in juveniles of other sciaenids. Müller (1999) reported this species from the Pliocene Yorktown Formation.

MENTICIRRHUS AMERICANUS (LINNAEUS, 1758)
Figure 4L

Material.–7 sagittae; Sea Island (4), Fancy Bluff (2), and Joiner Creek (1).

Description.–The sagittae of *Menticirrhus americanus* have several highly characteristic features including a sulcus that covers almost the entire inner face, a prominent postdorsal spine at the posterior tip that is directed upward diagonally (more developed in larger specimens), and the greatest height is toward the posterior. The anterior is somewhat narrowed and rounded and contributes to the peculiar, elongated shape.

MENTICIRRHUS? SP.

Material.–1 sagitta from Turtle River.

Description.–One sagitta had characteristics that indicated *Menticirrhus*, but being small and eroded, further identification was not possible.

PROTOSCIAENA SASAKI, 1989
PROTOSCIAENA KIRBYORUM n. sp.
Figure 4M

Zoobank Nomenclatural Act.—02AC256C-2F69-4BA8-9CF4-C5E7EBAF0E32.

Holotype.–GSM-1444, a right sagitta measuring 7.24 mm in length (Fig. 4M).

Additional Material.–8 sagittae from Fancy Bluff.

Type locality.–The Fancy Bluff site is located near Fancy Bluff on Fancy Bluff Creek, approximately 2.2 km southeast of Interstate 95 and just north of U. S. Highway 17 (Corridor Z) in the proximity of Brunswick, Glynn County, Georgia, USA (31.128° N, -81.551° W). The specimen is from an early Pliocene (approximately 3.8 – 4.5 Ma) equivalent to the Raysor Marl.

Etymology.–The species name is in honor of Chet Kirby, Chet Lee Kirby, Jr., and Chester Lee Kirby of Waynesville, Georgia. They collected the bulk samples from which the otoliths of the new species were found. They have also collected tens of thousands of Plio-Pleistocene vertebrates and invertebrates from Glynn County, Georgia, and have graciously shared the fossils with researchers and institutions.

Diagnosis.–The morphological characteristics of the sagittae place them clearly in the genus *Protosciaena* as illustrated by Chao and Miller (1975), Schwarzhans (1993), Chao (2003), and Aguilera et al. (2016). However, the early Pliocene specimens from Georgia differ significantly in the orientation and length of the downturned portion of the cauda from *Protosciaena trewavasae* (Chao and Miller, 1975) and *Protosciaena bathytatos* (Chao and Miller, 1975), the only known modern species. There are no known fossil species of *Protosciaena* from the U.S, and the early Pliocene Georgia specimens differ from the fossil species *Protosciaena brasiliensis* and *Protosciaena neritica* reported by Aguilera et al. (2016:pl. 1, figs. 1-10) from tropical America.

Description.–The sagittae of *Protosciaena kirbyorum* are oval in shape (sensu Smale et al., 1995). The inner face is smooth and moderately convex. Height/length ratios are approximately 75%. The height is greatly affected by the depth of the central portion of the ventral margin. Margins are smooth in all specimens with several prominent angles, especially on the dorsal. The anterior margin is broadly rounded, while the anterodorsal margin is inclined and primarily straight. The dorsal margin is longer than the anterodorsal margin and almost horizontal to slightly inclined toward the posterior. The anterodorsal margin forms an obtuse angle with the dorsal margin. The posterodorsal margin is longer than the anterodorsal margin and slightly arched. It forms an obtuse angle with the dorsal margin. The posterior margin is somewhat tapered but rounded. The posteroventral margin is steeply inclined toward the ventral margin. The ventral margin is short and forms a broad v-shape. The anteroventral margin is slightly arched. A prominent and distinct sulcus (heterosulcoid type) is present on the inner face. The ostium is approximately 60% of the length of the cauda. The anterior end of ostium reaches the anterior margin. The ostium is moderately large and extends dorsally

and ventrally. The cauda is much narrower than the ostium (only about 30% of the greatest width of the ostium) and shallow in depth. The cauda has distinct horizontal and downturned portions. The sides of the horizontal portion of the cauda are roughly parallel. The downturned portion of the cauda is not as long as the horizontal portion (about 50% of the length of the horizontal portion). The angle of the downturned portion of the cauda is around 80–90°. The posterior end of the cauda is rounded and obviously expanded. A shallow, elongated, narrow depressed area is located above the sulcus. Crista superior and crista inferior are present. A ventral furrow is present but not pronounced. The outer face is concave with a slight centrally located umbo.

Remarks.–Although the holotype was the best preserved specimen of *Protosciaena kirbyorum*, eight other specimens of the new species were available for examination. These referred specimens were helpful in ascertaining the morphological features and characteristics of the species and were used in the writing the description. The holotype was reposited along with all of the figured specimens in the Georgia State Museum in Statesboro, Georgia. Unfortunately, the other specimens of *Protosciaena kirbyorum* are retained in private collections.

Initially, worn specimens of this taxon were attributed to *Ctenosciaena*, but additional specimens showed salient characteristics that indicated *Protosciaena.* As noted by Schwarzhans (1993) and Nolf and Aguilera (1998), well-preserved specimens are required to distinguish the two. The horizontal portion of the cauda of *Protosciaena* is almost twice as long as the more vertical portion of the cauda. Even more conspicuous is the widened caudal end or tip of *Protosciaena.* According to Schwarzhans (1993), *Protosciaena trewavasae* is found off Columbia and Venezuela in the Atlantic Ocean, but others also noted it from the western central Atlantic (Dennis et al., 2004). *Protosciaena trewavasae* has been reported from the early Miocene of Brazil (Aguilera et al., 2014), the Miocene of Venezuela (Nolf and Aguilera, 1998), from the Mio-Pliocene of the Dominican Republic (Nolf and Stringer, 1992; Aguilera et al., 2016), the late Pliocene of Panama (Aguilera et al., 2016) and from the Pliocene of Jamaica (Stringer, 1998). *Protosciaena bathytatos* is known from the late Pliocene of Venezuela (Aguilera et al., 2016). Fossil evidence indicates that the modern *Protosciaena trewavasae* has been widespread since the early Miocene in the Caribbean and western central Atlantic. However, it also appears that *Protosciaena kirbyorum* was an allopatric species that lived off the coast of present-day Georgia during the early Pliocene.

UMBRINA CF. *U. COROIDES* CUVIER, 1830
Figure 4N

Material.–4 sagittae from South Brunswick River.

Description.–Four large and massive otoliths were assigned to *Umbrina* cf. *U. coroides*. These otoliths have a typical sciaenid sulcus with a greatly enlarged ostium and a narrow, steeply curving cauda. The ostium encompasses essentially the entire front half of the otolith, and the ventral margin of the ostium is almost straight. The posterior portion tends to narrow slightly (Schwarzhans, 1993:fig. 118). Fitch (1964) reported *Umbrina* from the Pleistocene of California, and Müller (1999) identified numerous species of *Umbrina* from the Paleogene and Neogene of the Atlantic Coastal Plain.

SCIAENIDAE INDETERMINATE

Material.–Two sagittae; one from Joiner Creek, and one from East River.

Description.– These specimens, which were juveniles and eroded, have features that indicated they were sciaenids. However, further identification was not possible.

Order SPARIFORMES sensu BETANCUR-R. et al., 2013
Family SPARIDAE RAFINESQUE 1818

Material.–1 sagitta from Joiner Creek.

Description.–The shape and sulcus of this sagitta indicate the family Sparidae, although its condition does not allow more specific identification.

TELEOSTEI incertae sedis

Material.–13 lapilli; Fancy Bluff (8), South Brunswick River (2), and East River (3).

Description.–The lapilli, utricular otoliths, are nearly identical and appear to be from the same taxon, possibly *Stellifer*, but their preservation prohibits definitive identification.

SUMMARY

A total of 1,803 teleostean otoliths, including sagittae and lapilli, was obtained from seven Plio-Pleistocene coastal Georgia sites. The identification and number of otoliths for each taxon are shown in Table 1. The otoliths represented 50 taxa from 18 families. The late Pleistocene Sea Island site produced 356 otoliths representing 13 taxa, and sciaenids accounted for 9 of the 13 taxa (69.2%) and 342 specimens (96.1%). The early Pliocene Fancy Bluff site yielded the most otoliths (758 specimens or 42.0% of the total number for all sites) and the most taxa (35). The early Pliocene South Brunswick River site produced 93 otoliths representing 14 taxa, while the early Pliocene to late Pleistocene Joiner Creek site supplied 173 otoliths and 22 taxa. The early Pliocene Turtle River site and the late Pleistocene Dunbar Creek site provided the smallest number of otoliths at 18 and 9, and the smallest number of taxa at 12 and 5 respectively. The early Pliocene East River site supplied the second largest number of otoliths at 396, with sciaenids making up 11 of the 24 taxa (45.8%) and 289 specimens (73.0%). Furthermore, sciaenids (n = 16) represented important components at each of the 7 sites and accounted for 1,187 of the 1,803 total specimens (65.8%). The ophidiids or cusk-eels were the second most abundant taxa with 10 taxa and 432 specimens (24% of the total specimens). Taxa from the other families were obviously not as abundant since the otoliths from sciaenids and ophidiids (1,619 specimens) represented 89.8% of the total number of specimens and over half of the taxa from the sites.

DISCUSSION

What impact does the discovery of otoliths representing 50 taxa have on the understanding of actinopterygians from the "fossil-poor" Plio-Pleistocene of Georgia? First, it describes the bony fishes as represented by otoliths that were present during the Pliocene and Pleistocene (approximately 4.5 Ma to 120,000 years ago) in coastal Georgia. This time span would include late Neogene climatic changes as well as glacial and interglacial climatic cycles in North America (Cerling et al., 1997; Marlow et al., 2000; Ravelo et al., 2004; Bintanja and van de Wal, 2008). The otoliths afford an opportunity to ascertain changes to actinopterygians during this time span. The vast majority of the Plio-Pleistocene otoliths from coastal Georgia represent extant bony fishes with only a few extinct forms. Except for these extinct forms, the Plio-Pleistocene otoliths indicate fishes that are quite similar to the marine fishes from present-day coastal Georgia (Dahlberg, 1975; Georgia Department of Natural Resources, 2018).

The Plio-Pleistocene otolith assemblage includes 13 families not recognized by skeletal remains in Georgia (Heterenchelyidae, Congridae, Engraulidae, Merlucciidae, Gadidae, Ophidiidae, Opistognathidae, Paralichthyidae, Cynoglossidae, Ammodytidae, Serranidae, Haemulidae, Triglidae, and Scorpaenidae). These families represent 28 new Plio-Pleistocene taxa for Georgia. In addition, there are 14 newly reported taxa in families previously recognized on skeletal material. These were primarily sciaenid species except for one ariid. Hulbert and Pratt (1988) recognized three sciaenids based on skeletal material in coastal Georgia. The otoliths indicate the presence of 13 additional sciaenids including *Micropogonias undulatus, Cynoscion nothus, Cynoscion nebulosus, Cynoscion regalis*, *Larimus fasciatus, Leiostomus* aff. *L. xanthurus, Menticirrhus americanus, Protosciaena kirbyorum, Stellifer lanceolatus, Pachyurus*? *jeanae*, and *Umbrina* cf. *U. coroides*. Equally impressive to the additional sciaenid taxa is the abundance of specimens of several species (e.g., 388 *Micropogonias undulatus*, 318 *Pachyurus*? *jeanae*, and 259 *Stellifer lanceolatus*,). The additional sciaenids noted above represent the first fossil occurrence of these species in the Plio-Pleistocene of coastal Georgia.

Second, the otolith taxa verify bony fishes previously known only by skeletal remains, and in some cases, provide greater detail on certain species. For example, Hulbert and Pratt (1998) found

evidence of *Ariopsis felis* (as *Arius felis*), which was also found as otoliths. Additionally, the otoliths indicate the presence of another marine catfish, *Bagre marinus.* Likewise, the otoliths identify the *Prionotus* sp. reported by Hulbert and Pratt (1998) as most likely being *Prionotus carolinus.* The otoliths also confirm two of three sciaenids reported by Hulbert and Pratt (1998) and verify the *Bairdiella* sp. as most likely *Bairdiella chrysoura.* While *Sciaenops ocellatus* (as *Sciaenops ocellata*) was reported by Hulbert and Pratt (1998), we found no otoliths of this species.

Only four of the taxa (*Otophidium lacinius*, *Otophidium* cf. *O. robinsi*, *Pachyurus*? *jeanae*, and *Protosciaena kirbyorum*) represent extinct forms. All of the extinct taxa are found in Raysor Marl equivalent sediments (~3.8–4.5 Ma) but are absent in the two sites known to be late Pleistocene. *Otophidium lacinius*, *Otophidium* cf. *O. robinsi*, and *Protosciaena kirbyorum*.are represented by a limited number of specimens (20, 1, and 9 respectively). However, *Pachyurus*? *jeanae* specimens are quite abundant (n = 318 or 17.6% of the total specimens) and found at all of the sites except at the two late Pleistocene-age sites. It appears that *Pachyurus*? *jeanae*, although widespread and abundant in the Pliocene, may have become extinct before the late Pleistocene. *Protosciaena kirbyorum* represents the first fossil species of this genus recognized in the U.S. Although the modern species, *Protosciaena trewavasae*, is known from the early Miocene in the Caribbean (Aguilera et al., 2016), an allopatric form, *Protosciaena kirbyorum*, was present in the early Pliocene in the coastal waters of Georgia. Present data indicate that *Protosciaena kirbyorum* became extinct before the late Pleistocene.

CONCLUSIONS

The otolith assemblage (1,803 specimens) from the seven Plio-Pleistocene sites in coastal Georgia represents 50 taxa (18 families) of teleosts. The primarily shallow-marine fishes are from extant species except for four (*Otophidium lacinius*, *Otophidium* cf. *O. robinsi*, *Pachyurus*? *jeanae*, and *Protosciaena kirbyorum* n. sp.). Sciaenids (16 taxa) make up 65.8% of the total number of otoliths. The Plio-Pleistocene otolith assemblage features 13 families representing 28 taxa not recognized by skeletal remains in Georgia. There are also 14 newly reported taxa (all sciaenids except for one ariid) in families previously recognized on skeletal material. One of these taxa is *Protosciaena kirbyorum* n. sp., the first U.S. fossil species of this sciaenid genus. Otolith data verify taxa of fishes previously indicated by skeletal remains and provide more refined identifications in several cases. This teleostean assemblage appears to have been quite stable in spite of late Neogene and Pleistocene climatic changes with all but four of the fossil taxa representing extant forms that are very similar to the present-day marine fishes of coastal Georgia.

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