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Cover Photograph: Tidal creek cut-bank northeast of collecting site on Skidaway Island, Chatham County, Georgia. Photograph © Dr. Clark Alexander. Director and Professor of Skidaway Institute of Oceanography (University of Georgia), Savannah, GA.

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Fish Otoliths Provide Further Taxonomic and Paleoecologic Data for the Late Pleistocene (Rancholabrean) Jones Girls Site, Georgia

Gary L. Stringer[1*] and Richard C. Hulbert Jr.[2]

Abstract - Investigation of teleostean otoliths (n = 418) recovered from the late Pleistocene (Rancholabrean) Jones Girls Site, Chatham County, Georgia, represents just the second study of Pleistocene otoliths in Georgia and only the fifth study of Pleistocene otoliths for the Atlantic and Gulf coastal plains. Geochronologic analysis suggests an age from 80 Ka to 130 Ka for the site. Otoliths indicate 18 extant taxa (10 families) with sciaenids dominant. Otoliths provide seven additional fish taxa (six families) for the Georgia late Pleistocene. Otoliths point to a neritic coastal environment (< 20 m) with strong evidence for soft bottom, estuarine creeks, and bays with no large freshwater input. The fish represented by otoliths indicate temperatures and conditions similar to present-day coastal Georgia.

Introduction

The published record of Pleistocene fishes based on skeletal remains from the Savannah region in Chatham County, Georgia, is extremely scanty according to Hulbert and Pratt (1998). Actually, this appraisal could be applied to the entire state. Descriptions of Pleistocene otoliths for the state and the Gulf and Atlantic coastal plains number less than five. However, Pleistocene otoliths are present, but have experienced almost a total lack of study and analysis. One of the purposes of this study is to increase the knowledge of Pleistocene fishes for both Georgia and the Atlantic Coastal Plain through an analysis of otoliths from the Jones Girls Site. Another purpose is to utilize the otoliths to better understand Pleistocene paleoenvironments and paleogeography. Although Pleistocene vertebrates from the Savannah, Georgia, vicinity have been known for almost 200 years (Lipps et al. 1988), detailed studies on the Pleistocene vertebrate fauna were rarely pursued until the work of Hulbert and Pratt (1998). They described 103 vertebrate taxa, including 25 bony fishes, from four late Pleistocene (Rancholabrean) sites, including the Jones Girls Site, near Savannah. The otoliths from the Jones Girls Site were recovered in 1997–1999 as screen-washed sediment was processed for microinvertebrates being studied as part of an undergraduate student thesis and have never been studied until the present investigation. The otoliths will augment the results of Hulbert and Pratt (1998) by 1) increasing the number of actinopterygian taxa known, including some reported for the first time as fossils from Georgia, 2) verifying bony fishes indicated by skeletal remains, 3) providing greater detail on fish taxa previously described only to family or generic level, and 4) contributing to a better understanding of the Late Pleistocene paleoenvironment of the Jones Girls Site. In addition, the otoliths provide a basis for ascertaining the effect of Pleistocene glacial and interglacial cycles on the actinopterygians in this region.

Investigations of Pleistocene otoliths in the US are extremely limited, especially in the Gulf and Atlantic coasts regions. Published research on Pleistocene otolith assemblages for the entire US number around 10, and the focus of many of these publications was the western US and emphasized Pacific taxa (Firestine et al. 2012; Fitch 1964, 1966, 1967, 1968, 1970). These studies are of minimal value for the investigation of Pleistocene otoliths of coastal Georgia. The only Pleistocene otolith studies for the entire Gulf and Atlantic coastal plains are Stringer (1992); Stringer et al. (2017); Stringer and Bell (2018), which is the only published study of Georgia Pleistocene otolith assemblages; and Stringer and Shannon (2019).

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Geological Setting of the Jones Girls Site

The Jones Girls Site is located in the northern coastal area of Georgia in Chatham County in the vicinity of Savannah (Fig. 1). More specifically, the site is on the southwestern end of Skidaway Island (31°55′ N, 81°4′ W) and designated as Georgia Southern Museum Locality GA017. Two shallow ponds were excavated by the land owners in 1995–1996, which with pumping exposed a 3 to 4 m section that allowed detailed stratigraphic analysis. The main shell bed at the Jones Girls Site approached 1 m in thickness and consisted of a mixture of fine- to medium-sized, subangular to rounded quartz sand grains, invertebrate remains (especially mollusk fragments), and minor amounts of muscovite, feldspar, phosphate, and clay. Enormous variation existed in the preservation of the shells of various mollusk species, which was attributed to the complex taphonomic history of the site by Hulbert and Pratt (1998). For example, complete valves of species with thin, fragile shells, such as penshells (*Atrina* sp.), Campeche angelwing (*Pholas campechiensis*), and angelwing (*Cyrtopleura costata*) were recovered in the shell bed with water-worn fragments of bivalves with much thicker shells. The Jones Girls shell bed was deposited above beds of clay and peat that represent tidal flats, salt marsh, and freshwater swamp environments, based on palynology (Booth 1998).

Investigations of the stratigraphic relationships of Pleistocene sediments in the Savannah area, as in all of coastal Georgia, are generally difficult and complicated for a variety of reasons. Stringer and Bell (2018 and references therein) addressed many of the complexities of the stratigraphy in coastal Georgia. Hulbert and Pratt (1998) noted rapid lateral facies changes, limited sites with exposed in situ strata, extensive erosion during sea-level lowstands, and the common occurrence of bioturbation and physical reworking of both sediments and fossils. The specific formation is not known for the sediments at the Jones Girls Site, but it was possible to obtain an age based on geochronologic analysis (radiocarbon dating, amino acid racemization, and uranium-series dating). The results indicated an age of at least 80 Ka and possibly as old as 110 to 130 Ka (Hulbert and Pratt 1998, Wehmiller et al. 1997). These dates are supported by a radiocarbon date of about 36

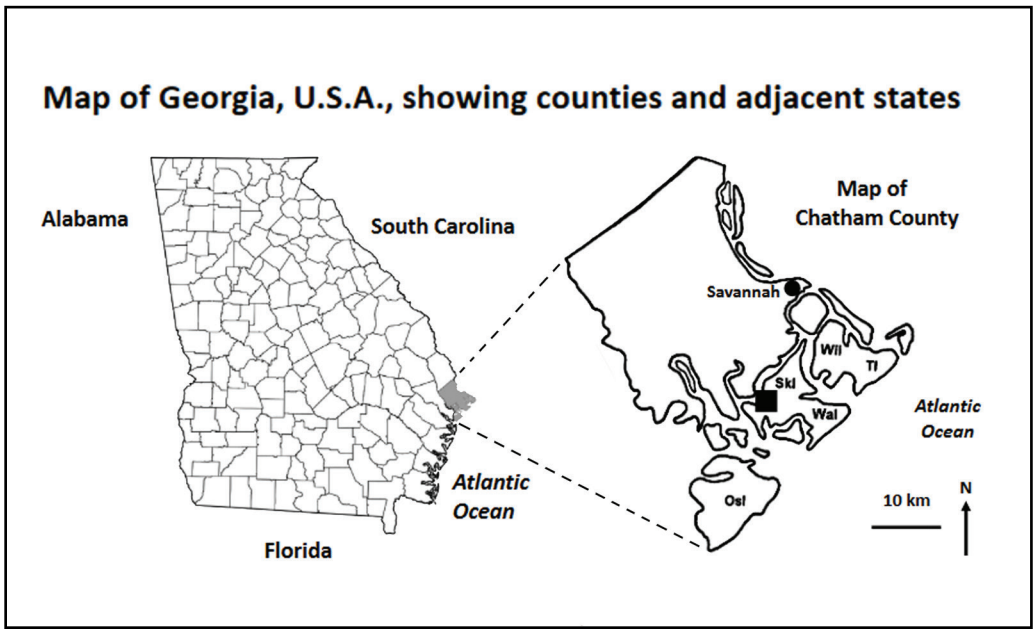

Figure 1. Location of the Jones Girls Site on the southwestern end of Skidaway Island in the vicinity of Savannah, Chatham County, Georgia (indicated by solid square). Geographic abbreviations: OsI, Ossabaw Island; SkI, Skidaway Island; TI, Tybee Island; WaI, Wassaw Island; WiI, Wilmington Island.

Ka for a peat clast found in a channel cut deposit in the sand bed overlying the shell bed (Booth 1998). These dates would place the site in the middle to late Pleistocene. The shell bed at the Jones Girls Site was probably deposited during a sea-level highstand at approximately modern conditions and shows similarity to modern shell accumulations off the Georgia coast in tidal inlet channels (Henderson and Frey 1986).

Table 1. Taxonomic identification of the otoliths from the Jones Girls Site (Chatham County, Georgia) with number of specimens, percentage of total, plate and figure numbers, and GSM catalogue numbers.

Family Genus and species	**Number of specimens**	**% of total**	**Plate and figure numbers**	**GSM catalogue numbers**
Family Engraulidae				
Anchoa hepsetus	5	1.2	Not figured	GSM-1454
Anchoa mitchilli	37	8.9	Pl. 1, Fig. 1	GSM-1446
Family Gadidae				
Urophycis cf. *U. floridana*	9	2.2	Not figured	GSM-1455
Family Ophidiidae				
Ophidion marginatum	10	2.4	Not figured	GSM-1456
Otophidium? sp.	4	1.0	Pl. 1, Fig. 3	GSM-1448
Family Opistognathidae				
Lonchopistus micrognathus	2	0.5	Not figured	GSM-1457
Family Atherinopsidae				
Atherinopsidae indeterminate	1	0.2	Pl. 1, Fig. 2	GSM-1447
Family Uranoscopidae				
Astroscopus? sp.	1	0.2	Pl. 1, Fig. 4	GSM-1449
Family Malacanthidae				
Lopholatilus chamaeleonticeps	4	1.0	Pl. 1, Fig. 5	GSM-1450
Family Haemulidae				
Haemulidae indeterminate	1	0.2	Not figured	GSM-1458
Family Sciaenidae				
Micropogonias undulatus	65	15.6	Pl. 1, Figs. 6–7	GSM-1451
Stellifer lanceolatus	165	39.5	Pl. 1, Figs. 8–9	GSM-1452,1453
Larimus fasciatus	35	8.4	Not figured	GSM-1459
Cynoscion regalis	6	1.4	Not figured	GSM-1460
Leiostomus xanthurus	32	7.7	Not figured	GSM-1461
Menticirrhus americanus	18	4.3	Not figured	GSM-1462
Sciaenidae indeterminate	10	2.4	Not figured	GSM-1463
Family Sparidae				
Sparidae indeterminate	4	1.0	Not figured	GSM-1464
Indeterminate	9	2.2	—	—
Total number of specimens	418	—	—	—

Materials and Methods

Large samples (100s of kilograms) of fossiliferous matrix were collected from the Jones Girls Site for the purpose of studying megascopic and microscopic vertebrates and invertebrates (primarily mollusks). This collecting effort focused on the main shell bed, but relatively small amounts of sediment from the overlying sand unit or the underlying clay bed was likely present in some samples. The bulk samples from the Jones Girls Site were water-screened using nestled sieves with openings of 39 mm^2, 2 mm^2, and 1.1 mm^2. The residue was air dried and examined for vertebrate and complete invertebrate remains using low-power binocular microscopes for the two smaller fractions. All fossils, including otoliths extracted from the residue, were placed in the Georgia Southern Museum (GSM) in Statesboro, Georgia, for further study.

Results

The late Pleistocene Jones Girls Site produced 418 otoliths, which are predominantly sagittae although sciaenid lapilli (utriculiths) are also present. The identification, number of specimens, percentage, plate and figure numbers (if applicable), and GSM catalogue numbers of otoliths for each taxon are shown in Table 1. Identification of the otoliths reveals 18 taxa from 10 families, and all taxa represent extant forms. The family Sciaenidae dominates the assemblage in number of taxa and specimens (7 and 331, respectively). The sciaenids represent 38.9% of the taxa present and 79.2% of the total specimens. Two sciaenids, *Stellifer lanceolatus* and *Micropogonias undulatus*, are the most abundant taxa comprising 55.1% of the total specimens. Quite unexpectedly, the Engraulidae is the second most abundant family with 42 specimens representing 10.1% of the total specimens (see discussion below). One engraulid, *Anchoa mitchilli*, is the third most abundant taxon and comprises 8.9% of the total specimens.

All of the taxa identified from the Jones Girls Site, with the exception of a few, were recently described in Stringer and Bell (2018). Therefore, only those not described by Stringer and Bell (2018) or those requiring further comment are discussed below. Taxa present in the Jones Girls Site that are not reported in Stringer and Bell (2018) are Atherinopsidae indeterminate (Atherinopsidae), *Lopholatilus L. chamaeleonticeps* (Malacanthidae), and *Astroscopus*? sp. (Uranoscopidae). *Anchoa mitchilli, Otophidium*? sp., M. *undulatus* and *S. lanceolatus* are included as requiring further comment (Pl. 1). Classification follows primarily that of Nelson et al. (2016), which contained many taxonomic classification changes, especially regarding orders based on extensive molecular studies by Betancur-R. et al. (2013). Ordinal names follow Wiley and Johnson (2010), while the family-group names and authors of Recent fishes follow van der Laan et al. (2014). Authors for genera and species depend greatly upon Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al. 2019).

Class Osteichthyes
Subclass Actinopterygii
Order Clupeiformes Goodrich
Family Engraulidae Gill
Anchoa mitchilli (Valenciennes) (Bay Anchovy) (Pl. 1, Fig. 1)

Material–37 sagittae
Description–This otolith has features of a typical engraulid. It is distinguished from other species 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

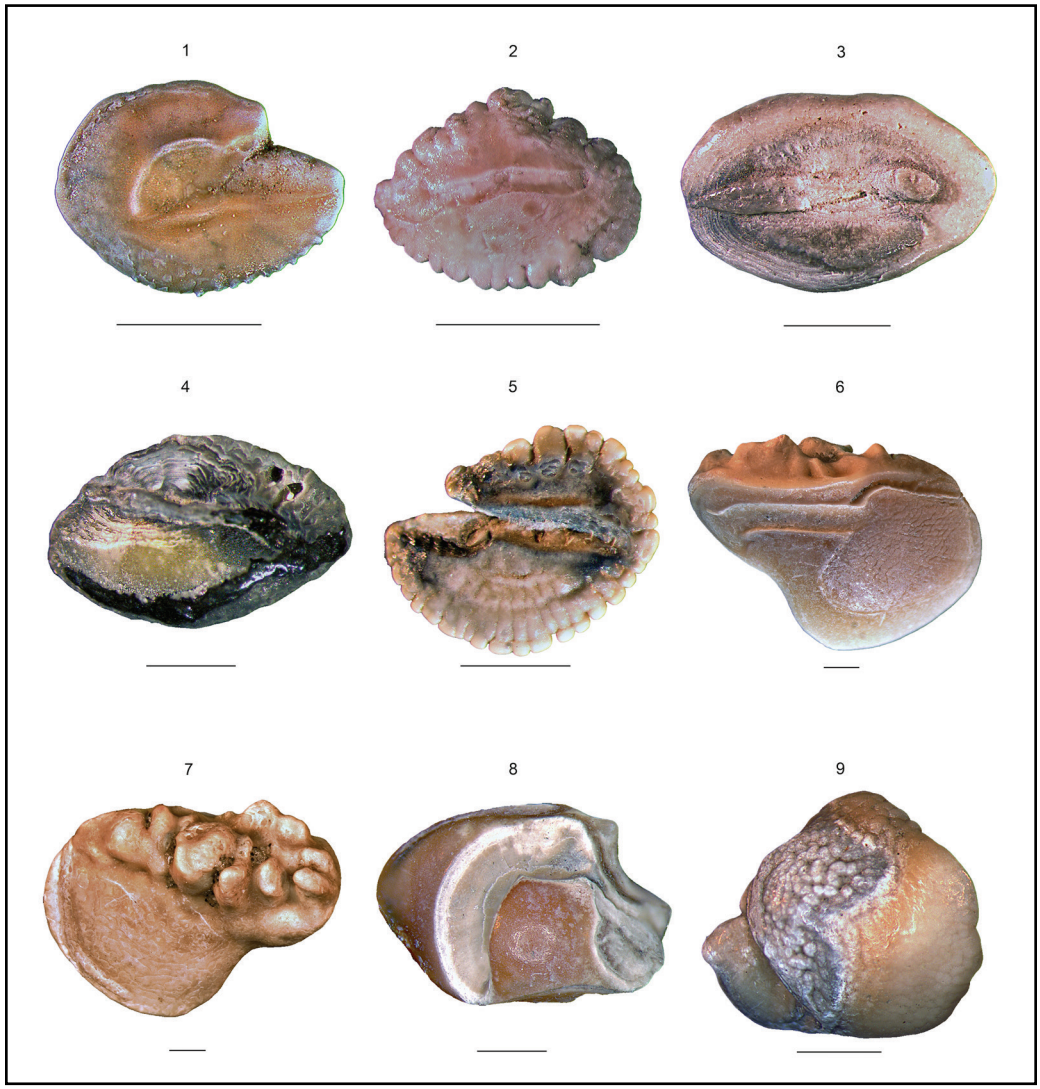

Plate 1. Late Pleistocene otolith specimens from the Jones Girls Site near Savannah, Chatham County, Georgia The taxonomic identification of each otolith, the location of the otolith in the labyrinth (right or left side), type of otolith (sagitta or lapillus), and view (inner or outer) are given. Length of otolith is given in mm (scale is 1 mm). All figured specimens are reposited in the Georgia Southern Museum (GSM), Statesboro, Georgia 30458 (catalogue numbers provided).

Figure 1. *Anchoa mitchilli*, left sagitta, inner view, 2.00 mm, GSM-1146.
Figure 2. Atherinopsidae indeterminate, right sagitta, inner view, 1.64 mm, GSM-1447.
Figure 3. *Otophidium*? sp., right sagitta, inner view, 2.92 mm, GSM-1448.
Figure 4. *Astroscopus*? sp., right sagitta, inner view, 3.43 mm, GSM-1449.
Figure 5. *Lopholatilus chamaeleonticeps*, right sagitta (juvenile), inner view, 2.50 mm, GSM-1450.
Figure 6. *Micropogonias undulatus*, left sagitta, inner view, 8.27 mm, GSM-1451.
Figure 7. *Micropogonias undulatus*, left sagitta, outer view, 8.27 mm, GSM-1451.
Figure 8. *Stellifer lanceolatus*, left sagitta, inner view, 4.27 mm, GSM-1452.
Figure 9. *Stellifer lanceolatus*, lapillus, 3.38 mm, GSM-145.

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 on well-preserved specimens. This species was reported, as *Anchoa* cf. *A. mitchilli*, from the late Pleistocene-early Holocene from a Mississippi River mudlump island by Stringer (1992). One specimen was recovered from the Sea Island Site (Glynn County, Georgia) by Stringer and Bell (2018), and three specimens were reported from the Elizabethtown Locality (Bladen County, North Carolina) by Stringer and Shannon (2019).

Order Ophidiiformes Berg
Family Ophidiidae Rafinesque
Otophidium? sp. (Pl. 1, Fig. 3)

Material–4 sagittae
Description–Although all of the sagittae are worn, there is sufficient evidence to tentatively assign them to *Otophidium*? sp. The outline is mainly oval with the dorsal margin ranging from slightly outcurved to almost horizontal with a slight indentation at the center to straight and steeply slanted toward the posterior margin. The ventral margin is broadly rounded and fairly evenly rounded. The sulcus extends to the anterior margin but is well separated from the posterior margin. The ostium is 1.5 times longer than the cauda. The ostium is narrow at the anterior margin but enlarges noticeably before constricting at the junction with the cauda. The cauda is also constricted at the junction with the ostium but enlarges toward the posterior. The posterior end of the cauda is rounded. Thick colliculum in the ostium and cauda. Specimens compare favorably with several *Otophidium* in Nolf (2013:pl. 126), but preservation does not permit a species determination. Stringer and Bell (2018) reported 4 species of *Otophidium* from the Plio-Pleistocene of coastal Georgia in Glynn County, but preservation does not allow a meaningful comparison.

Order Atheriniformes Rosen
Family Atherinopsidae Fitzinger
Atherinopsidae indeterminate (Pl. 1, Fig. 2)

Material–1 sagitta
Description–This specimen is well preserved with delicate lobate margins, but it represents a juvenile specimen (1.9 mm in length). The specimen has an oval outline with a slight, medial dorsal dome. The anterior and posterior are slightly tapered. The sulcus is medially located at the anterior and slightly above the median near the center of the otolith. The sulcus is depressed anteriorly. The ostium, which is oval and small, is ventrally widened only. The ostium is approximately twice as wide as the cauda. The cauda is very narrow and three times longer than the ostium. There is a distinct crista superior. Salient characteristics, especially the sulcus, indicate a member of the family Atherinopsidae. The small size (immature specimen) limits further identification.

Order Trachiniformes (sensu Nelson et al.)
Family Uranoscopidae Bonaparte
Astroscopus? sp. (Pl. 1, Fig. 4)

Material–1 sagitta
Description–The sagitta of *Astroscopus*? sp. is characterized by an oval shape with relatively smooth margins except for some small undulations on the anterodorsal rim. The sulcus is medially located and long but very narrow. The sulcus extends from the anterior to almost the posterior

margin. The narrow sulcus is fairly horizontal except for slight undulation and downturn in the posterior one-third. There is no clear differentiation of the sulcus into an ostium and cauda. There is a slight depression above the sulcus and possibly a ventral furrow. Although extensively eroded, this specimen has characteristics that agree with the *Astroscopus* sp. from the Lee Creek Mine identified by Fitch and Lavenberg (1983). The 23 *Astroscopus* sp. reported by them from Lee Creek Mine represented the first fossil record for the genus according to the authors. Müller (1999:fig. 41, 16a–16b) reported five otoliths of *Astroscopus* sp. from several different Mio-Pliocene formations in Maryland, Virginia, and North Carolina.

Order Perciformes (sensu Nelson et al.)
Family Malacanthidae Poey
Lopholatilus chamaeleonticeps Goode and Bean (Great Northern Tilefish) (Pl. 1, Fig. 5)

Material–4 sagittae
Description–Although the specimens are small (1.8–2.5 mm) and represent juveniles, there are numerous characteristics that indicate *L. chamaeleonticeps*. The outline of the sagitta is primarily elliptic (sensu Smale et al. 1995). The dorsal margin (except for the anterior portion) has characteristic, pronounced lobes. The sulcus is heterosulcoid and extends from the anterior for approximately 80% of the otolith length. The ostium opens onto the anterior margin with a distinct rostrum and antirostrum. A broad excisura is present. The junction of the ostium and cauda is distinctively v-shaped. The cauda is essentially horizontal and slightly longer than the ostium, but not as wide. The posterior of the cauda appears open. There is a very distinct crista superior that terminates abruptly. Fitch and Lavenberg (1983:fig. 3A) reported this species from the Yorktown Formation (Pliocene; ~3.6–5.0 Ma) at Lee Creek Mine, North Carolina, which represented the first fossil record of the family according to the authors. However, the genus was reported from the middle Miocene of Germany prior to Fitch and Lavenberg (1983), according to Nolf (2013), but it was as "genus aff. *Lepidotrigla*." Müller (1999:fig. 32, 4–5), also noted *L. chamaeleonticeps* from the Yorktown Formation at Lee Creek.

Order Acanthuriformes (sensu Nelson et al.)
Family Sciaenidae Cuvier
Micropogonias undulatus (Linnaeus) (Atlantic Croaker) (Pl. 1, Figs. 6–7)

Material–65 sagittae
Description–The sagitta of *M. undulatus* is unique with its unusual shape and very conspicuous sulcus. The sagitta is shield-like in shape with a relatively flat, thickened dorsal rim and a sharp ventral rim that is deeply curved anteriorly with a distinct concavity posteriorly. The heterosulcoid sulcus is very large and encompasses much of the inner face. The ostium is compressed but very deep and extends from almost the dorsal rim to very near the ventral rim. The width of the cauda is only about 25% of the height of the ostium and has a highly characteristic enlarged caudal tip (Schwarzhans 1993:fig. 347). The outer face commonly has a prominent, raised umbo (unless removed by erosion). The posterodorsal area of the outer face usually has prominent, projecting bosses that often appear to fuse into one another. This genus is known from the subsurface late Miocene of Mississippi (Stringer and Starnes 2018), the Pliocene of North Carolina (Fitch and Lavenberg 1983, as *Micropogonias* sp.; Müller 1999 as *Micropogonias* aff. *undulatus*; Stringer and Shannon 2019), and the late Pleistocene-early Holocene of Louisiana (Stringer 1992).

Table 2. Comparison of the otolith assemblages of the Jones Girls Site (Chatham County, Georgia) and Sea Island Site (Glynn County, Georgia), both late Pleistocene.

Family Genus and species	**Jones Girls**	**% of site total**	**Sea Island**	**% of site total**
Family Engraulidae				
Anchoa hepsetus	5	1.2	2	0.6
Anchoa mitchilli	37	8.9	1	0.3
Family Gadidae				
Urophycis cf. *U. floridana*	9	2.2	–	0.0
Family Ophidiidae				
Ophidion marginatum	10	2.4	4	1.1
Otophidium? sp.	4	1.0	–	0.0
Family Opistognathidae				
Lonchopistus micrognathus	2	0.5	–	0.0
Family Atherinopsidae				
Atherinopsidae indeterminate	1	0.2	–	0.0
Family Uranoscopidae				
Astroscopus? sp.	1	0.2	–	0.0
Family Malacanthidae				
Lopholatilus chamaeleonticeps	4	1.0	–	0.0
Family Haemulidae				
Haemulidae indeterminate	1	0.2	–	0.0
Family Sciaenidae				
Micropogonias undulatus	65	15.6	85	23.9
Pogonias cromis	–	0.0	1	0.3
Stellifer lanceolatus	165	39.5	204	57.3
Bairdiella chrysoura	–	0.0	10	2.8
Larimus fasciatus	35	8.4	20	5.6
Cynoscion regalis	6	1.4	10	2.8
Cynoscion nebulosus	–	0.0	2	0.6
Leiostomus xanthurus	32	7.7	6	1.7
Menticirrhus americanus	18	4.3	4	1.1
Sciaenidae indeterminate	10	2.4	–	0.0
Family Sparidae				
Sparidae indeterminate	4	1.0	–	0.0
Indeterminate	9	2.2	6	1.7
Total number of specimens	418		356	

Stellifer lanceolatus (Holbrook) (American Stardrum) (Pl. 1, Figs. 8–9)

Material–165 sagittae and lapilli
Description–The sagitta of *S. lanceolatus* is identified by its almost vertical anterior margin and nearly horizontal, almost straight dorsal and ventral margins that produce an essentially rectangular anterior shape (Chao 1978:fig. 27B). The predorsal spine is sharp but greatly reduced in size. The postdorsal projection is massive and lacks a postventral notch. 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 lapillus of *S. lanceolatus* is approximately suboval in outline and is large, often as large as the sagitta (Chao 1978). There is a deep, thin groove at the anteroventral end of the inner surface. The posterior end has a rounded margin and may have a small projection on well-preserved specimens. The species was reported from the Plio-Pleistocene of Georgia by Stringer and Bell (2018).

Discussion

The Jones Girls Site otolith assemblage

No skeletal fossils of actinopterygians were found in the shell bed from the Jones Girls Site, but Hulbert and Pratt (1998) did provide a list of fishes from the nearby Isle of Hope and Mayfair sites. Twenty-five fish taxa based primarily on teeth, vertebrae, and various skull elements were identified collectively from these sites, which are about 10 km from the Jones Girls Site. Families represented by otoliths from the Jones Girls Site that are not reported as skeletal remains are the Engraulidae, Gadidae, Ophidiidae, Opistognathidae, Atherinopsidae, Uranoscopidae, Malacanthidae, and Haemulidae. The otoliths indicate six species of the family Sciaenidae not shown by skeletal remains (*M. undulatus*, *S. lanceolatus*, *Larimus fasciatus*, *Cynoscion regalis*, *Leiostomus xanthurus*, and *Menticirrhus americanus*). Three sciaenids (*Bairdiella* cf. *Bairdiella chrysoura*, *Pogonias cromis*, and *Sciaenops ocellatus*, originally reported as *S. ocellata*) were reported from the Isle of Hope and Mayfair sites based on skeletal remains. However, these sciaenids were not represented as otoliths at the Jones Girls Site. Although the reason for their absence is not known for certain, the number of identified skeletal specimens of these sciaenids were not large (e.g., *Pogonias cromis* was represented by only five skeletal elements). Also, the paleoenvironment of the Isle of Hope and Mayfair sites may have varied somewhat from the Jones Girls Site. Furthermore, otoliths often represent small, prey species that may not be well represented by skeletal remains (Breard and Stringer 1995).

The preservation of the otoliths in the Jones Girls Site is interesting and noteworthy. There is a substantial difference in the condition of the otoliths that is not seen normally in fossil otolith assemblages. For example, there are specimens that exhibit excellent preservation, such as *A. mitchilli* (Pl. 1, Fig. 1) and *M. undulatus* (Pl.1, Figs. 6–7). Several delicate serrations are preserved on the ventral margin of *A. mitchilli*, while the figured specimen of *M. undulatus* displays many fine morphological features that are often obliterated. This is in stark contrast to other specimens that show varying degrees of erosion and damage such as *Otophidium*? sp. (Pl. 1, Fig. 3) and *Astroscopus*? sp. (Pl. 1, Fig. 4). It is not certain why there is such a dichotomy in the preservation. Hulbert and Pratt (1998) noted the vast variation in the preservation of mollusk shells at the site and attributed the variances to the site's complex taphonomic history. This could also be the reason for the huge differences in the preservation of the otoliths. Whatever the cause, it created greatly contrasting states of preservation in the otolith assemblage.

Comparison of the Jones Girls Site to the Sea Island Site

The Jones Girls Site was compared to the Pleistocene sites reported by Stringer and Bell (2018) in Glynn County, 130 km south-southwest of the Jones Girls Site, to provide information on variation in late Pleistocene fish assemblages, paleoenvironment, and paleogeography. Stringer and Bell (2018) studied otoliths from seven sites, but only two of the sites were exclusively late Pleistocene in age, the Sea Island Site and the Dunbar Creek Site. The Dunbar Creek Site had a small number of otoliths and was not deemed statistical significant for comparison. Therefore, the only site considered suitable for comparative purposes was the Sea Island Site, which was close in age (possibly overlapping) and contained a similar number of otoliths specimens (n = 356).

Several methods were utilized to compare the Jones Girls Site and the Sea Island Site. The species diversity of each site was examined, and within species diversity, the number of species (richness) and the percentage abundance of each species (evenness) at each site were compared (Table 2). The Jones Girls Site had 18 taxa, which were unevenly distributed (two taxa comprised over 55% of the total number). The Sea Island Site had 13 taxa, and these taxa were distributed even more unevenly with two taxa comprising over 81% of the total. The species diversity of the two localities is fairly similar in richness and unevenly distributed taxa. Another useful tool for comparing the Jones Girls Site and Sea Island Site is the percentage similarity measurement (Reitz and Wing 1999, Stringer et al. 2018, Stringer and Shannon 2019). Percentage similarity measurements were calculated between the two sites using the data in Table 2. The result was a percentage similarity of 68.6%, which indicated definite similarities but also significant differences.

A closer analysis of Table 2 indicates similarities of the site. The two most abundant species at both sites are *S. lanceolatus* and *M. undulatus*, and both of these comprised very large percentages at both sites. However, there is a notable difference in one species, *A. mitchilli*. This species comprised 8.9% of the Jones Girls assemblage, while it represented only 0.3% of the Sea Island fauna. Moreover, the high percentage of this engraulid is extremely unusual. The paucity of fossil engraulid otoliths, specifically *Anchoa*, is well documented for the Gulf and Atlantic coastal plains and the Caribbean. Stringer (1992) analyzed 446 otoliths from the late Pleistocene/early Holocene of Louisiana and reported 2 *Anchoa* cf. *A. mitchilli* (0.4% of total). Müller (1999) studied approximately 12,000 otoliths from the US Atlantic Coastal Plain (Paleogene and Neogene) and did not list a single engraulid. Likewise, Fitch and Lavenberg (1983) reported no engraulids from 8,808 otoliths from the Pliocene of North Carolina. Aguilera and Aguilera (1999) described 7,770 specimens of Miocene to Pleistocene otoliths from 93 collections from the Caribbean coast of Panama and Costa Rica, and yet in this immense collection of otoliths, they noted only 29 specimens of *Anchoa* (0.4% of total). Stringer and Bell (2018) detailed 1,803 otoliths from 7 Plio-Pleistocene coastal Georgia sites and reported 4 *Anchoa* specimens (0.2% of the total). The question would be what factor caused this unexpected and atypical occurrence of *Anchoa* at the Jones Girls Site.

Paleoecology of the Jones Girls Site as indicated by otoliths

The relatively recent geologic age of the Jones Girls Site (approximately 80 Ka–130 Ka) makes the otoliths ideal for interpreting paleoecological conditions. A comparison of the ecological ranges of Recent families of fishes represented at the site by otoliths can be used to ascertain general paleoenvironmental parameters (Nelson et al. 2016). Only a few of the families are restricted to marine waters (Ophidiidae, Opistognathidae, and Uranoscopidae), and these families comprise only about 4% of the total specimens. One other family, Malacanthidae, which represents only 1% of the total specimens, is shown as brackish and marine. All of the other families, which comprise approximately 95% of the specimens, may be found in freshwater, brackish, and marine. However, there are no exclusively freshwater or brackish families found at the site, and all families have marine representatives.

Further general interpretation is possible by comparing the Jones Girls Site fishes to Page et al. (2013), which listed all modern marine fish species inhabiting (as adults) contiguous shore waters, on or above the continental shelf, from shore to the shelf-slope break at 200 m from the United States. All of the Jones Girls Site fish families are shown, and none of the fishes represent deepwater forms, i.e., greater than 200 m. Additionally, there are no representatives of the Myctophidae or Macrouridae. Nolf and Brzobohaty (1992) stated that marine assemblages free or almost free of myctophids indicate a neritic environment with little open oceanic influence. So, the fishes at the Jones Girls Site indicated by otoliths suggest a neritic environment with little deepwater influence and strong indications of possible brackish or freshwater conditions. This is consistent with paleoecologic interpretations based on invertebrate fossils and palynological samples from the shell bed (Booth 1998, Hulbert and Pratt 1998).

A more specific paleoecological analysis can be obtained by examining the most abundant taxa at the site. The family Sciaenidae (drums and croakers) accounts for the most taxa (7, or 38.9% of the total) and the most specimens (331 specimens, or 79.2% of the total). The environment at the site must have been very conducive for sciaenids based on their extremely high percentages. Modern sciaenids generally prefer tropical, shallow-marine waters, estuarine, and coastal areas (Hoese and Moore 1998, Schwarzhans 1993). Some studies (Darnell et al. 1983, Nelson et al. 2016) have noted the strict confinement of the Sciaenidae to continental coasts or shallow waters near continental regions. Nolf (2013) characterized the sciaenids as neritic fishes living in warm shallow seas and estuaries, especially the estuaries of large rivers.

Almost 40% of the total specimens is represented by the sciaenid *S. lanceolatus*. This species usually occurs over hard sandy mud bottoms in coastal waters to about 20 m in depth and is common in river estuaries (Kells and Carpenter 2011). Ayala-Perez et al. (2012) also reported that *S. lanceolatus* prefers high salinity, calcareous sediments, low turbidity, and estuarine-influenced areas. Juveniles utilize the upper estuary as nursery grounds, while adults can be found throughout the basin (Chao and Espinsoa-Perez 2015).

Another sciaenid, *M. undulatus* accounts for 15.6% of the total specimens (second most abundant species). Hales and Reitz (1992) and references therein noted that juvenile *M. undulatus* utilize different estuarine habitats on a size-specific basis. Ross (2003) detailed that juvenile Atlantic croaker resided for several months in shallow, soft bottom estuarine creeks and bays (referred to as primary nursery areas or PNAs). His findings clearly indicated that the distribution of Atlantic croaker juveniles was skewed toward upstream oligohaline creeks (salinity of 0.5 to 5.0 parts per thousand or ppt). Pattillo et al. (1997) stated that adult Atlantic croaker appear to be most abundant in mesohaline (salinity of 5.1 to 18 ppt) and polyhaline (salinity of 18 to 30 ppt) salinities and are rare below 10 ppt. Whitaker (2005) confirmed this distribution and noted the optimal habitat for young Atlantic croaker to be lower-salinity upper reaches of South Carolina estuaries. He also stated that Atlantic croaker move seaward toward higher salinities as they become larger. Since the *M. undulatus* from the Jones Girls Site represent juveniles, this is a strong indication of shallow, soft bottom estuarine creeks and bays.

The third most abundant species at the Jones Girls Site was the engraulid *A. mitchilli,* which comprised 8.9% of total assemblage. Pattillo et al. (1997) and Snyder and Burgess (2016) described *A. mitchilli* as primarily a shallow estuarine and inshore coastal water species that is able to exploit a wide variety of habitats (coastal rivers, bays, sounds, lagoons, estuaries, and high salinity nearshore marine waters). This exploitation is related to its ability to live in a wide range of salinities (virtually fresh to fully saline or hypersaline). It is more commonly found in shallow tidal areas with muddy bottoms and brackish waters and is usually found in depths of less than 20 m. (Whitehead et al. 1988). Unlike *M. undulatus*, salinity appears to have little relationship with age distribution and abundance (Cornelius 1984, Pattillo et al. 1997). The Bay Anchovy is a schooling species, and the schools tend to be located near the surface. However, changes in depth distribution occur seasonally and diurnally (NatureServe 2013).

Numerous references (NatureServe 2013, Newberger and Houde 1995, Pattillo et al. 1997, Snyder and Burgess 2016) have noted that Bay Anchovies are possibly the most abundant fish in the coastal, western North Atlantic and probably constitute the greatest biomass of any fish in the estuarine waters of the southeastern US and the US Gulf of Mexico. Yet, as detailed earlier, there is a lack of fossil engraulid otoliths, such as *Anchoa*, in the Gulf and Atlantic coastal plains and the Caribbean. With its adaptability and tremendous abundance, it would be expected more often in the fossil record. However, it is rarely ever abundant. Perhaps the small, fairly delicate, and thin otoliths are less likely to be preserved and more susceptible to bioerosion in the case of predation. However, this makes the abundance of *A. mitchilli* in the Jones Girls Site even more perplexing. What factor or factors at the Jones Girls Site would account for the difference in the abundance of *A. mitchilli* when compared to the Sea Island Site, which is separated by less than 130 km and shows many similarities in fishes? The abundance of other species at the Jones Girls Site appears to eliminate factors such as temperature, salinity, dissolved oxygen, and turbidity. Perhaps *A. mitchilli*, which was probably abundant but typically not preserved as fossils, were preferentially preserved at the Jones Girls Site. This preferential preservation could be the same mechanism that protected delicate, thin-shelled mollusk valves, while water-worn, thick-shelled mollusk valves were also present. This selective preservation was attributed to the complex taphonomic history of the site by Hulbert and Pratt (1998). The complicated taphonomy of the site could also explain the biased preservation of the otoliths, but details are not known at this time.

Most of the fish families indicated by otoliths at the Jones Girls Site point to tropical to subtropical. Hulbert and Pratt (1998) indicated that the Jones Girls Site was probably deposited during a sea-level highstand during an interglacial period when sea level was close to modern conditions. All of the otoliths at Jones Girls represent fish that are found along the present Georgia coastline (Dahlberg 1975, Georgia Department of Natural Resources 2018), and temperatures would be expected to be similar to the present. Any subsequent climatic events (glacial episodes to the north) do not appear to have permanently altered the fishes present in the area.

Only a few of the fossil otoliths represent fish families restricted to normal marine salinity, and many of the fish families represented could tolerate reduced salinities. Most of the fishes represented by otoliths prefer soft muddy or sandy bottoms. There is almost no evidence of marine invertebrate settlement (e.g., boreholes and encrustings) on the otoliths, which could be an indication of surface residence-time (Stringer 2016). Otolith lengths indicate many juvenile fishes (< than 5 cm and many even smaller), and in the case of *M. undulatus*, probably denote primary nursery areas (Stringer and Shannon 2019). Many of the fishes represented by otoliths were prey for larger piscivorous organisms. The paleoecology indicated by the fishes represented by otoliths agrees well with the findings of Hulbert and Pratt (1998).

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