

Additions to the Pliocene fish otolith assemblage from site AMb-2 on Dauphin Island, Alabama, USA, and their taxonomic and paleoecologic implications

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Abstract

The specimens for this investigation were recovered from the only Pliocene locality in the Gulf Coastal Plain known to contain otoliths. A previous study of otoliths from this site was based on a meager 250 specimens and 22 bony fish taxa were identified. The present investigation, which was based on an additional 3,840 otoliths, revealed 12 more taxa and allowed two previously documented taxa to be definitively assigned to species. The additional taxa resulted in an otolith assemblage of 34 taxa and provided further, more detailed information on the paleoenvironmental setting. Within species diversity, the number of otolith-based taxa (34) indicates a moderately high richness. However, the relative abundance of each species present (evenness) is very low with one species (*Micropogonias undulatus*) representing 82.98% of the total number of specimens. Sciaenidae represent an astounding 96.45% of the total number of specimens. The abundance of the sciaenid *M. undulatus* (3,394 specimens) was especially significant for paleoecological determinations and indicated that 99.18% of the otoliths represented fish less than one-year-old (i.e., juveniles). This preponderance of *M. undulatus* sagittae pointed to shallow, soft-bottom estuarine creeks and bays and possibly upstream oligohaline creeks and strongly suggests a primary nursery area for the species. The analysis of the other taxa indicates a more open estuary near a shallow marine environment also existed.

keywords: fish otoliths, Pliocene, Graham Ferry Formation, paleoecology, *Micropogonias undulatus*

Introduction

Site AMb-2, located on Dauphin Island, Alabama, USA, was first reported by Ebersole et al. (2017) who confirmed 12 chondrichthyan and osteichthyan tooth-based taxa derived from deposits at the site. Ebersole et al. (2017) originally reported the dredged deposits at Site AMb-2 to be Early Pleistocene in age, but a subsequent investigation by Stringer et al. (2020) confirmed the deposit to be Early Pliocene and likely part of the Lower Pliocene Graham Ferry Formation or an equivalent unmapped offshore deposit. Stringer et al. (2020) examined 250 otolith specimens from the site, which was a fairly small assemblage compared to many other otolith investigations that often entail thousands, or even tens of thousands, of specimens (Nolf & Stringer 1992, Nolf & Stringer 2003, Schwarzhans 2019, Schwarzhans & Stringer 2020, Lin & Chien 2021). Although not a large sample in terms of the number of specimens, Stringer et al. (2020) identified 22 taxa from the site. This moderate richness of taxa indicated the potential for additional species with further collecting at site AMb-2 on Dauphin Island (Leonhard & Agiadi 2023). A major objective of this investigation was to determine if new taxa could be recovered with extensive, additional sampling at the site. Furthermore, if new taxa were retrieved, could they be utilized to better analyze and understand the paleoenvironment of the dredged deposits? The otoliths recovered from site AMb-2 are highly significant because they represent the only-known Pliocene otolith assemblage in the Gulf Coastal Plain of the USA

and provide unique insights into the paleoenvironment of the northern Gulf of Mexico in this region during the Early Pliocene.

Geographical & geological settings

Site AMb-2 is located on the eastern end of Dauphin Island in Mobile County, Alabama, USA. The site is located in the sandy areas west of the entrance to the Dauphin Island East End Public Beach (Fig. 1).

A detailed discussion of the geologic setting of site AMb-2 is presented in Stringer et al. (2020). The reader is directed to this reference and references therein for a full discussion. The otoliths appear to be derived directly or indirectly from erosional lag deposits of the Graham Ferry Formation or an equivalent unmapped offshore unit. The Graham Ferry Formation is the only marine Pliocene unit presently recognized in nearby Mississippi, USA. Stringer et al. (2020) could not eliminate the possibility that a time-equivalent offshore unit may have contain the Dauphin Island otoliths, and thus, the designation Graham Ferry Formation equivalent was used in the publication. The beach deposits were dredged from two borrow areas located approximately 8 km southeast of Dauphin Island in the Gulf of Mexico and pumped onto the site as part of a 2016 beach restoration project. At site AMb-2, the deposits are composed primarily of a sandy shell hash with abundant bryozoans, bivalves, gastropods, echinoids, and arthropods. The Graham Ferry Formation has commonly been designated as Pliocene (Zanclean) (Dockery 1996). It should be noted that the age of this formation has been called into question (Dockery & Thompson 2016). However, detailed analysis of pollen and dinocysts by Otvos (1998) clearly indicated that the Graham Ferry Formation is Pliocene in age (Fig. 2). Investigations by Stewart and Starnes (2017; updated 2019) in Mississippi indicated that the upper surface of the Graham Ferry Formation is unconformable with the overlying terrace deposits. It is unclear if the upper part of the Graham Ferry Formation extends into the Piacenzian. Therefore, the age of the Pliocene formation could be Zanclean and Piacenzian. Because it is believed that the deposits at site AMb-2 were dredged directly from an offshore lag deposit of the Graham Ferry Formation or an age-equivalent deposit, the age of the deposits could range from a maximum of approximately 5.33 Ma to a minimum of 2.58 Ma B.P. based on Cohen et al. (2018).

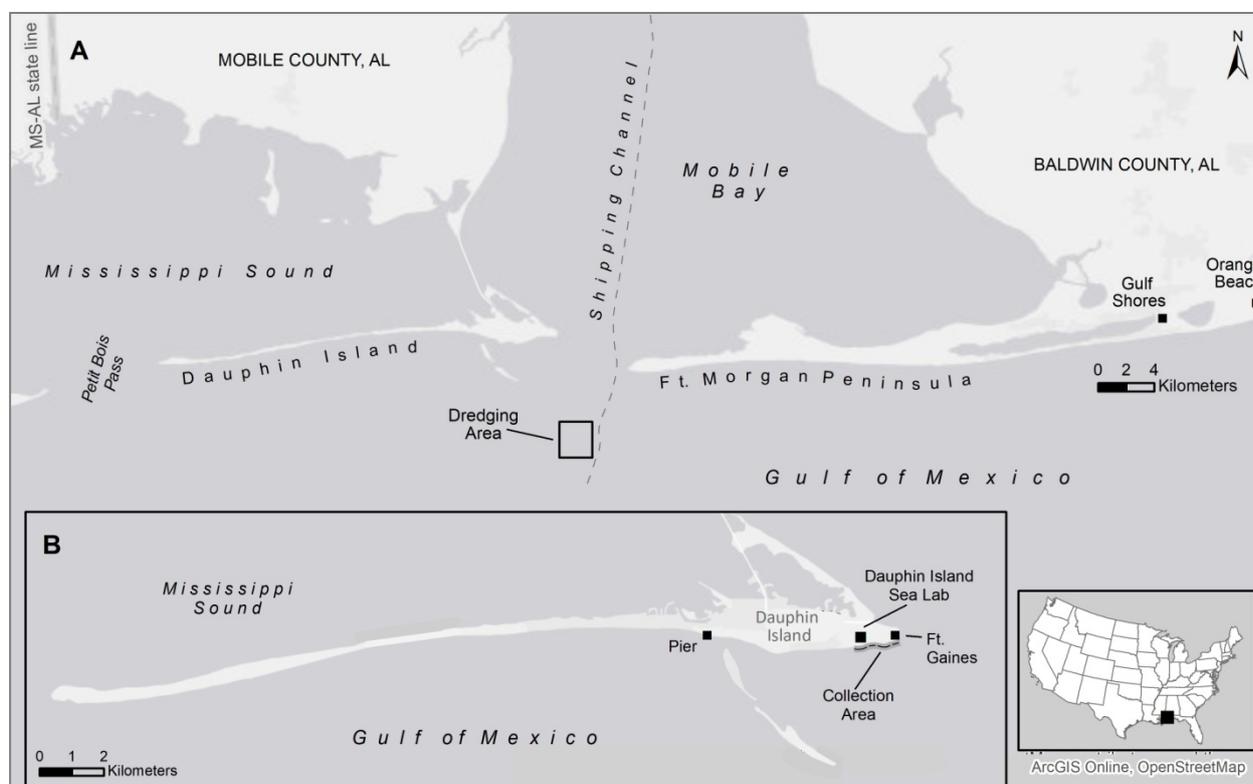


fig. 1. Location of site AMb-2 on Dauphin Island, Mobile County, Alabama, USA.

Era	Period	Epoch	Stage	Alabama Onshore Surface Stratigraphy		
				SE MS	SW AL	
Cenozoic (in part)	Neogene (in part)	Pliocene	Piacenzian			
			Zanclean			Graham Ferry Formation
		Miocene (in part)	Messinian	Pascagoula Formation	Miocene series undifferentiated	
			Tortonian	Hattiesburg Formation		

fig. 2.

Upper Miocene and Pliocene stratigraphy in southeast Mississippi and southwest Alabama, USA.

Material & methods

The first otoliths discovered at site AMb-2 on Dauphin Island were surface collected (Stringer et al. 2020). However, extensive microscopic examination of nearly 45 kg of sandy shell hash has been employed, primarily with a binocular microscope (6.7–40 x magnification). Standard mesh sieves (#5, #10, #20, #35, and pan) were employed to facilitate examination, which was difficult with the extremely abundant invertebrate fossils. Some of the mesh sizes yielded very few or no otoliths. Otoliths were rare in the 5-mesh. Likewise, the 35-mesh and pan contained primarily quartz grains and fossil fragments and produced no or few identifiable otoliths. By far, the most productive sieve size for otoliths was the 10-mesh followed by the 20-mesh. All otoliths that were one-half complete or greater were retained for examination and identification. The taxonomic identification of the otoliths was done by one of the authors (GLS). The otoliths are repositied in the scientific collections at McWane Science Center in Birmingham, Alabama, USA.

Only the taxa not found in Stringer et al. (2020) are described in the systematics of the present study, and readers are directed to Stringer et al. (2020) for descriptions of previously identified taxa. An exception to this is the previously identified taxa where definitive assignment to species was not initially possible. The classification scheme of the fishes follows that of Nelson et al. (2016), which was impacted by the molecular work of Betancur-R. et al. (2013). Any deviation from this classification scheme is duly noted. Ordinal names typically follow Wiley & Johnson (2010), whereas the family-group names and authors of modern fishes follow Van der Laan et al. (2014, 2017, 2018). Authors for genera and species are based primarily on Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al. 2019).

All specimens were photographed with a Nikon D-80 camera with Tamron macro-lens. All photographs were rendered in Adobe Photoshop v. 22.5.9. Figure 1 was produced in ERSI ArcGIS software. The stratigraphic chart (Fig. 2) is based on the Mississippi Geological Survey Open-File Report 285: Surface Geology of Jackson County, Mississippi (Stewart & Starnes 2017; updated 2019).

Institutional abbreviations

MSC McWayne Science Center, Birmingham, Alabama, USA
 USNM National Museum of Natural History, Washington, District of Columbia, USA

Results

A total of 12 additional fish taxa were identified from otoliths that were not represented in Stringer et al. (2020). These taxa are described below. Furthermore, two taxa identified by Stringer et al. (2020) are also described as the additional specimens allowed these taxa to be identified to species.

***Ariosoma balearicum* (Delaroche, 1809)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Elopomorpha	Greenwood et al., 1966
order	Anguilliformes	Berg, 1943
suborder	Congroidei	Regan, 1909
family	Congridae	Kaup, 1856
subfamily	Bathymyrinae	Böhlke, 1949
genus	<i>Ariosoma</i>	Swainson, 1838
species	<i>Ariosoma balearicum</i>	(Delaroche, 1809) figs. 3, 6 A-B

material examined

N = 5: MSC 43230, MSC 43240, MSC 43251, MSC 46679.1-2

description

Ariosoma balearicum sagittae are fairly massive and have a somewhat rhomboidal outline (*sensu* Smale et al. 1995). The height is nearly equal to the length with height/length ratios of approximately 0.8. All of the margins are generally smooth. The anterior margin is generally short and rounded, whereas the anterodorsal margin is slightly concave. The dorsal margin is rounded and often slightly irregular. A concavity frequently occurs along the posterodorsal margin. The posterior margin is tapered but not pointed. The ventral margin is broadly rounded with a distinctive central angularity. The inner face is primarily smooth and convex except for some irregular depressions in the upper dorsal area. The sulcus is wide and lightly incised. It extends from near the anterior margin to the posterior margin (about 85% of the length of the sagitta). The sulcus is filled almost entirely with colliculum except for the dorsal extremity of the ostial channel. The ostial and caudal portions of the sulcus are not clearly defined. The posterior end of the sulcus is broadly tapered. There are no indications of a ventral furrow. The outer face is smooth and convex except for a shallow dorsoventrally oriented depression in the posterior.

remarks

Ariosoma balearicum is the only species of this genus known from site AMb-2. The species is rare with only five specimens recovered. The species is extant and found in the Gulf of Mexico as well as on both sides of the Atlantic as fossil and extant (Hoese & Moore 1998, McEachran & Fehhelm 2005, Agiadi & Albano 2020, Froese & Pauly 2022). *Ariosoma balearicum* is known from the Mio-Pliocene of the northern Dominican Republic (Nolf & Stringer 1992) and the Pliocene Bowden shell bed in southeast Jamaica (Stringer 1998).

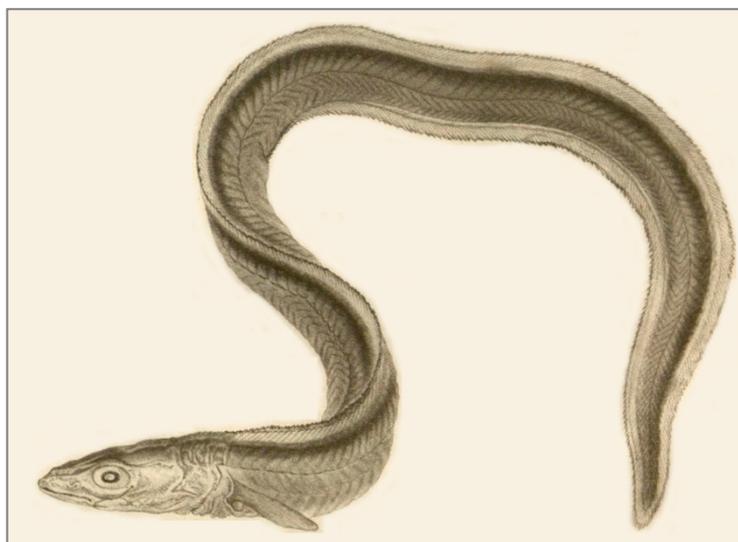


fig. 3.

Muraena balearica from plate 20 of Delaroche's original description.

***Rhynchoconger* sp.**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Elopomorpha	Greenwood et al., 1966
order	Anguilliformes	Berg, 1943
suborder	Congroidei	Regan, 1909
family	Congridae	Kaup, 1856
subfamily	Congrinae	Kaup, 1856
genus	<i>Rhynchoconger</i>	Jordan & Hubbs, 1925
species	<i>Rhynchoconger</i> sp.	figs. 4, 6 C-D

material examined

N = 1: MSC 43233

description

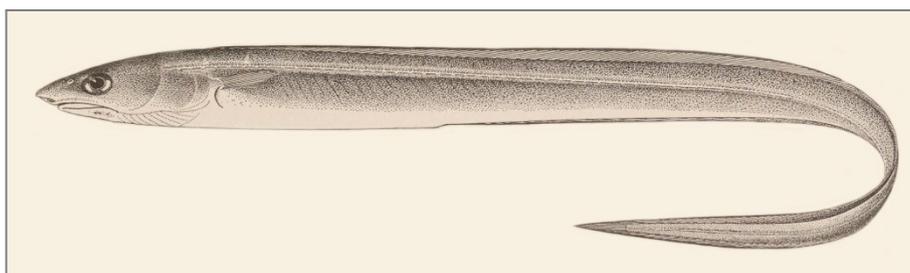
The sagitta of *Rhynchoconger* is primarily elliptical in outline but also somewhat oblong (*sensu* Smale et al. 1995). The height/length ratio is approximately 0.55. The greatest height on the sagitta is located slightly anterior to the mid-point on the dorsal margin. All of the margins tend to be smooth. The anterior margin is tapered but rounded on the tip. The dorsal margin is low and broadly rounded with some slight undulations. The posterior margin is also tapered, but more pointed than the anterior margin. The ventral margin is deeper than the dorsal margin. There is a distinctive angle along the ventral margin just anterior to the mid-point. The inner face is only slightly convex. The sulcus is distinct, undivided, and not very deeply impressed. The sulcus covers about 45% of the inner face and slants slightly in a posteroventral direction. The width of the sulcus is rather consistent throughout its length. There appears to be a small ostial channel that connects the ostial portion of the sulcus to the anterodorsal margin. The ostial channel is situated back from the anterior margin of the sulcus. A well-defined rectangular depression is located above the sulcus, and there is no ventral furrow present. The outer face is slightly convex and usually unsculptured.

remarks

Rhynchoconger sp. has been previously reported from the Gulf Coastal Plain in the USA by Frizzell & Lamber (1962), Nolf & Dockery (1993), Nolf (2013), and Ebersole et al. (2019). However, these forms range back to the Paleocene. This long stratigraphic range of *Rhynchoconger* sp. in Alabama strongly suggests that several different species are present. Only one specimen of *Rhynchoconger* sp. was recovered from site AMb-2, and unfortunately, preservation prohibits its identification to species. However, the specimen most likely represents one of the extant species of the genus found presently in the Gulf of Mexico. Many *Rhynchoconger* species were previously assigned to the genus *Hildebrandia*, but Smith (1989) determined that the latter was a junior synonym of the former.

fig. 4.

Leptocephalus ectenurus Jordan & Richardson, 1909, the type species of *Rhynchoconger* Jordan & Hubbs 1925. Drawing from plate 66 of the original description.



***Bagre marinus* (Mitchill, 1815)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Ostariophysi	Lord, 1922
order	Siluriformes	Cuvier, 1816
suborder	Siluroidei	Frizzell & Dante, 1965
family	Ariidae	Bleeker, 1858
subfamily	Bagreinae	Schultz, 1944
genus	<i>Bagre</i>	Cloquet, 1816
species	<i>Bagre marinus</i>	(Mitchill, 1815) figs. 5, 6 E-F

material examined

N = 4: MSC 46656, MSC 46666, MSC 46675, MSC 46699

description

The otoliths of *Bagre* are represented by the lapillus or utriculith, which is the otolith from the utriculus of the labyrinth as opposed to the sagitta in the sacculus. There are some instances where the lapillus is utilized in taxonomy, especially in the marine catfishes. The lapillus of *Bagre* is basically circular to somewhat oval in shape (*sensu* Smale et al. 1995), with a small projection on the margin. The central axis of the macular side (inner face; *sensu* Schwarzahns et al. 2018) is slanted and not perpendicular to the margin with the confluentia gibbuis maculae. The macular side has a few notable features, while the anti-macular side (outer face) is essentially smooth and featureless. The macular side is convex as is the anti-macular side. The macular side is characterized by the gibbus maculae, which is bi-lobed (linea basalis) and is located very near the margin. The gibbus maculae appears to cover most of the macular side and forms a faint, somewhat undulating feature known as the confluentia gibbuis maculae (Assis 2005) near the margin. The outer face is characterized by lightly impressed radial furrows that extend primarily from the center to the margins. The characteristics of the macular and anti-macular sides are lightly impressed and can be easily obliterated by leaching and other erosional processes since they are lightly impressed.

remarks

There are two lapilli-based marine catfish taxa present at site AMb-2, *Ariopsis felis* and *Bagre marinus*, as well as several species of sciaenid lapilli. However, these latter lapilli are very different from ariid (marine catfish) lapilli. The ariid gibbus maculae, which is bi-lobed (linea basalis), is located very near the margin and appears to extend across the macular side, forming a faint, undulating feature known as the confluentia gibbuis maculae. The lapillus of *Bagre marinus* is very similar to that of *A. felis*. *Bagre marinus* can be distinguished by several key characteristics. The outline of the macular face of *B. marinus* is more oval and broadly rounded as opposed to the higher and more rounded macular face of *A. felis*. *Bagre marinus* has a prominent projection on the margin adjacent to the gibbus maculae as does *A. felis*. The most distinguishing characteristic of *B. marinus* is the central axis of the macular face is slanted and not perpendicular as in *A. felis*. *Bagre marinus* lapilli have also been reported from the Plio-Pleistocene of coastal Georgia (Stringer & Bell, 2018).

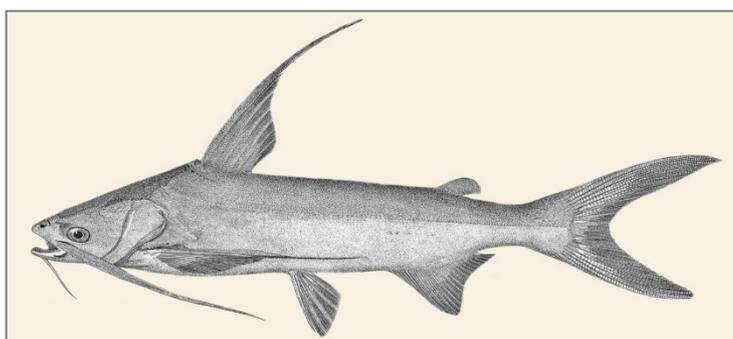


fig. 5.

Aelurichthys marinus. Drawing from plate 235 in Goode (1884): Fisheries and Fishery Industries of the United States.

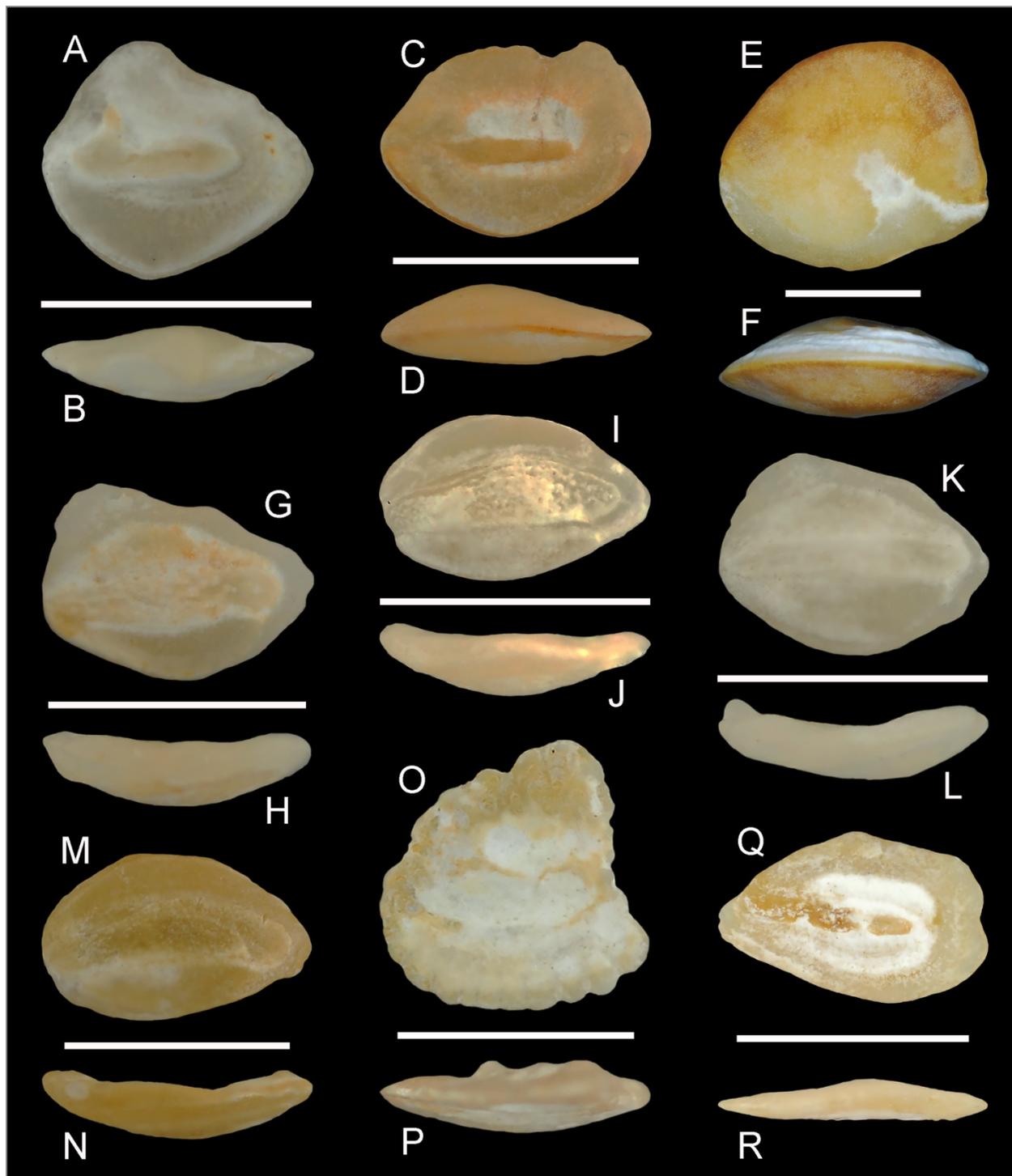


fig. 6. Pliocene otoliths from site AMb-2, Dauphin Island, Alabama, USA. All specimens are right otoliths or photographed as such. A-B) *Ariosoma balearicum* sagitta in A) inner and B) dorsal views. C-D) *Rhynchoconger* sp. sagitta in C) inner and D) dorsal views. E-F) *Bagre marinus* lapillus in C) macular and D) dorsal views. G-H) *Ophidion grayi* sagitta in G) inner and H) dorsal views. I-J) *Ophidion josephi* sagitta in I) inner and J) dorsal views. K-L) *Lepophidium jeannae* sagitta in K) inner and L) dorsal views. M-N) *Ophidion josephi* sagitta in M) inner and N) dorsal views. O-P) *Porichthys plectrodon* sagitta in O) inner and P) dorsal views. Q-R) *Paralichthys albigutta* sagitta in Q) inner and R) dorsal views. Scale bars for A-F, I-J, Q-R = 5 mm. Scale bars for G-H, K-P = 4 mm.

***Ophidion grayi* (Fowler, 1948)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Paracanthopterygii	Grennwood et al., 1966
order	Ophidiiformes	Berg, 1937
suborder	Ophidioidei	Garman, 1899
family	Ophidiidae	Rafinesque, 1810
subfamily	Ophidiinae	Rafinesque, 1810
genus	<i>Ophidion</i>	Linnaeus, 1758
species	<i>Ophidion grayi</i>	(Fowler, 1948) fig. 6 G-H

material examined

N = 1: MSC 43232.1-2.

description

The sagitta of *Ophidion grayi* is oval in outline (*sensu* Smale et al. 1995), but the shape can be affected by the development and extent of an anterodorsal dome. The height/length ratio is approximately 0.75 based on the two specimens recovered. The margins are primarily smooth except for the upper part of the anterior margin and anterodorsal margin, which can have characteristic small irregularities. The anterior margin may be almost vertical and slightly rounded. The anterodorsal margin is rounded and convex and may have conspicuous, small irregularities followed by a prominent and distinctive dome. The dorsal margin is rounded with some irregularities. The extent of the anterodorsal dome determines the slant toward the posterior margin. The posterodorsal margin is slightly rounded and slants downward toward the posterior margin. The posterior margin is slightly tapered and broadly pointed. The posteroventral margin is very slightly rounded outward and slants toward the middle of the ventral margin. The ventral margin is slightly but broadly rounded and forms a somewhat obtuse angle near the center. The anteroventral margin is almost straight and slants upward toward the anterior margin. A fairly large, lightly impressed sulcus occurs on the inner face that is primarily positioned medially. The inner face is generally smooth and evenly convex. The sulcus is long and extends across approximately 95% of the length of the inner face. The sulcus extends nearly to the anterior margin and almost to the posterior margin. The height of the sulcus is about 35% of the height of the inner face. There is no crista superior or crista inferior discernable above or below the sulcus, respectively. There is no clear distinction between the ostial and caudal areas, except for a small expansion near the posterior of the lower sulcus margin. The anterior of the sulcus tapers, and the posterior of the sulcus is slightly, and unevenly, tapered. There is no discernible ventral furrow on the specimen. The outer face is slightly, and unevenly, concave with some small irregularities in the form of rugosities.

remarks

The deposits at site AMb-2 have produced three species of fossil *Ophidion* – *O. grayi* (Fowler, 1948), *O. josephi* Girard, 1858, and *Ophidion cf. marginatum* DeKay, 1842. Prior to the present study, only *Ophidion cf. marginatum* had been documented from the site. Although three species are known, they are very rare at the locality with a total of only seven specimens recovered. *Ophidion grayi* can be easily differentiated from the other three species by having a prominent anterodorsal dome. *Ophidion josephi* is characterized by an evenly broad dorsal margin with no domes, as well as by differences in the margins of the sulcus (inflated upper margin and straight horizontal lower margin). *Ophidion cf. marginatum sagittae* differ by lacking the prominent anterodorsal dome seen on *O. grayi* and also have a more irregular anterodorsal margin than on *O. josephi*. Sagittae of *O. grayi* indicate a significant amount of variation with the development of the anterodorsal dome, which may be ontogenetic.

Fossil *O. grayi* specimens have been reported from the Plio-Pleistocene of Georgia (Stringer & Bell 2018) and the Late Pliocene of North Carolina (Stringer et al. 2022). In addition, Fitch & Lavenberg (1983) and Müller (1999) both reported this taxon from various localities in the Atlantic Coastal Plain.

***Ophidion josephi* Girard, 1858**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Paracanthopterygii	Grennwood et al., 1966
order	Ophidiiformes	Berg, 1937
suborder	Ophidioidei	Garman, 1899
family	Ophidiidae	Rafinesque, 1810
subfamily	Ophidiinae	Rafinesque, 1810
genus	<i>Ophidion</i>	Linnaeus, 1758
species	<i>Ophidion josephi</i>	Girard, 1858 fig. 6 I-J, M-N

material examined

N = 5; MSC 43241, MSC 43254, MSC 43258, MSC 46681, MSC 46700

description

The sagitta of *Ophidion josephi* is essentially oval in outline as illustrated by Smale et al. (1995). The height/length ratio is approximately 0.65. The margins are primarily smooth. The anterior margin is slightly rounded and may be almost vertical. The anterodorsal margin is outwardly and broadly rounded. The dorsal margin is nearly straight and slants toward the posterior. A small dome may be present at the anterior portion of the dorsal margin. The posterodorsal margin is nearly straight and slants downward toward the posterior margin. The posterior margin is tapered and broadly pointed. The posteroventral margin is very slightly rounded outward and slants toward the ventral margin. The ventral margin is slightly but broadly rounded. The anteroventral margin is rounded upward toward the anterior margin. A large, lightly impressed sulcus occurs on the inner face that is usually positioned medially. The inner face is generally smooth and evenly convex. The sulcus is long and extends across about 95% of the length of the inner face. The sulcus extends almost to the anterior margin and near the posterior margin. The height of the sulcus is about 45% of the height of the inner face. There is no crista superior or crista inferior discernible above or below the sulcus, respectively. There is no clear distinction between the ostial and caudal areas. The lower margin of the sulcus is characteristically horizontal and nearly straight except for a small expansion near the posterior tip of the sulcus. The upper margin of the sulcus is characteristically and conspicuously inflated, especially at its mid-point. The anterior tip of the sulcus tapers, whereas the posterior tip of the sulcus is also tapered but not as much as the anterior one. There is a discernible ventral furrow on several of the specimens of *Ophidion josephi* located very near the ventral margin. The outer face is slightly, and unevenly, concave with some small irregularities in the form of rugosities.

remarks

Ophidion josephi sagittae are similar to those of *Ophidion grayi* but differ by not having a prominent anterodorsal dome. The almost horizontal and straight lower margin of the sulcus and the inflated upper margin are highly characteristic of *O. josephi* sagittae. See the *Remarks* under *O. grayi* for further information on the differentiating characteristics of the *Ophidion* species found at site AMb-2. *Ophidion josephi* is the most abundant (four specimens) of any of the ophidiids obtained from Pliocene deposits at the site, and extant representatives are common in the shallow Gulf of Mexico (Hoese & Moore, 1998; McEachran & Feckhelm 1998, Froese & Pauly, 2022). *Ophidion josephi* was previously classified as *Ophidion welschi* as noted in Müller (1999). *Ophidion josephi* was reported from the Late Pliocene in North Carolina by Stringer et al. (2022).

***Lepophidium jeannae* Fowler, 1941**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Paracanthopterygii	Grennwood et al., 1966
order	Ophidiiformes	Berg, 1937
suborder	Ophidioidei	Garman, 1899
family	Ophidiidae	Rafinesque, 1810
subfamily	Ophidiinae	Rafinesque, 1810
genus	<i>Lepophidium</i>	Gill, 1895
species 1	<i>Lepophidium jeannae</i>	Fowler, 1941 fig. 6 K-L
species 2	<i>Lepophidium cf. jeannae</i>	Fowler, 1941 not figured

material examined

N = 3: MSC 43234, MSC 43255, MSC 43257

description

The sagitta of *Lepophidium jeannae* is primarily oval in outline as defined in Smale et al. (1995). However, the anterodorsal dome affects the outline. The height/length ratio of the four recovered specimens was approximately 0.78, which was affected by the anterodorsal dome. The margins were basically smooth. The anterior margin is short, slightly rounded, and almost vertical. The anterodorsal margin is very slightly rounded and also very steep. The dorsal margin appears to be slightly incurved to almost straight and slants toward the posterior from the anterodorsal dome. The posterodorsal margin is almost straight and slopes steeply toward the posterior margin. The posterior margin is tapered into a posterior tip (which is often affected by erosion). The posteroventral margin is straight and slants toward the obtuse angle at the center of the ventral margin. The ventral margin is characterized by an obtuse angle (a feature that is primarily eroded on the specimens examined but was likely broadly V-shaped). The anteroventral margin is for the most part straight and slants at 45° toward the anterior margin. The inner face is smooth and convex. The sulcus is quite long, filled with colliculum, and extends a significant portion of the length of the inner face (95%). Although difficult to discern, the sulcus appears divided. The sulcus is medially located with the upper and lower margins that are roughly parallel except for a slight tapering in the interior and a slight expansion in the posterior. No crista superior is evident, and there is no depressed area visible above the ostium. A ventral furrow appears to be present almost immediately adjacent to the central portion of the ventral margin. The outer face is slightly convex with undulations.

One sagitta from site AMb-2 appeared to be an ophidiid in the genus *Lepophidium*. Unfortunately, the inner face was eroded, but the sulcus was fairly evident. The shape and configuration of the sulcus are very similar to *L. jeannae*. The anterodorsal margin is rounded and very steep leading to an anterodorsal dome. The posterodorsal margin is almost straight like *L. jeannae*. The posterior tapers evenly to a point that is slightly rounded. With these similarities and given the eroded nature of the specimen, it is assigned tentatively to *Lepophidium cf. jeannae*.

remarks

None of the *L. jeannae* specimens were well-preserved due to erosion. Specifically, the posterior margin and the middle of the ventral margin appear to be most affected by erosion. However, enough salient features were present to tentatively identify the specimens to species.

Fossil specimens of *L. jeannae* were reported from the Late Pleistocene of Louisiana (Stringer 1992). However, the extensive study of approximately 12,000 Eocene to Pliocene otoliths from the southern Atlantic Coastal Plain by Müller (1999) produced no *L. jeannae* specimens. The extant range of *L. jeannae* extends along the Atlantic Coast of the USA from North Carolina to Florida and also within the Gulf of Mexico (Hoese & Moore 1998; McEachran & Fechhelm 1998; Froese & Pauly 2022).

***Porichthys plectrodon* Jordan & Gilbert, 1882**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Paracanthopterygii	Grennwood et al., 1966
order	Batrachoidiformes	Berg, 1937
family	Batrachoididae	Jordan, 1896
subfamily	Porichthyinae	Miranda Ribeiro, 1915
genus	<i>Porichthys</i>	Girard, 1854
species	<i>Porichthys plectrodon</i>	Jordan & Gilbert, 1882 fig. 6 O-P

material examined

N = 8: MSC43225.1-3, MSC 43246.1-2, MSC 46046, MASC 46694, MSC 46701

description

Porichthys plectrodon sagittae are distinctive in having a somewhat rectangular outline (*sensu* Smale et al. 1995). The margins can vary from almost smooth to irregular to lobed. The lobed margins occur most frequently on the dorsal margins (i.e., anterodorsal, dorsal, and posterodorsal) and, to a much lesser extent, on the posterior margin. The anterior margin is typically short and rounded, whereas the anterodorsal and dorsal margins slant upward toward a fairly high and prominent posterodorsal projection. The posterodorsal margin forms a prominent obtuse angle. The posterior margin is steep and almost vertical. The ventral margin is nearly horizontal and may be irregular or very small lobes or undulations. The inner face is slightly convex and is characterized by a medially located, enclosed, and oblong-shaped sulcus. The sulcus is excavated but not deeply. The upper and lower margins of the sulcus may be constricted in the middle, but it is difficult to recognize the ostium and cauda on many of the fossil specimens due to erosion. Likewise, the subcaudal iugum appears to be present on several of the better-preserved specimens, but it is affected by erosion. There is a distinct depressed area located above and near the center of the sulcus. This depressed area is usually oval in shape. If a ventral furrow is present, it is indistinct. The outer face ranges from almost flat to slightly convex and may be somewhat sculptured.

remarks

Porichthys taxa are typically distinct by having a prominent projection on the posterodorsal margin as seen in fossil taxa such as *Porichthys* sp. 1 from Trinidad (Nolf, 1976) and modern species like *P. myriaster* Hubbs and Schultz, 1939 from the Pacific Coast of the U.S. (Nolf, 1979, fig. 3c). According to Froese & Pauly (2022), two extant *Porichthys* species are found in the Gulf of Mexico, *P. plectrodon* Jordan & Gilbert, 1882 and *P. porosissimus* (Cuvier, 1829). Two of the *Porichthys* specimens from site AMb-2 (MSC 46694, MSC 46701) compare extremely well to *P. plectrodon*, and comparisons to an extant specimen collected from off the coast of Louisiana (specimen USNM 395252) reveals that the fossil specimens are nearly identical. In contrast, the sagittae of *P. porosissimus* has a very narrow, elongated projection or dome on the dorsal margin (Nolf 2013, pl. 143; Lombarte et al. 2006, Fish ID 11668). Six additional specimens from site AMb-2 (MSC 43225.1-3, MSC 43246.1-2, MSC 46046) are similar to those assigned to *P. plectrodon* but differ slightly by having a posterodorsal projection that represents one-half of the total height of the sagitta, and the projection tapers distally and has a rounded tip. Although these specimens are conservatively assigned to *Porichthys* sp., the morphological differences observed may reflect variation in *P. plectrodon* sagittae. Additional and better-preserved specimens would address this issue.

Fossil *Porichthys* otoliths have been documented from several geologic formations in the Gulf Coast Plain of the USA and Caribbean, although they are never found in large numbers. Stringer & Mixon (2005) reported *Porichthys* sp. from the Byram Formation (Oligocene) in central Mississippi. The taxon has been reported from the Cercado Formation (Upper Miocene) in the Dominican Republic (Nolf & Stringer 1992), from the Late Pleistocene in Louisiana (Stringer 1992), and from the Bowden shell bed (Pliocene) of Jamaica (Stringer 1998).

***Paralichthys albigutta* Jordan & Gilbert, 1882**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Carangiformes	Jordan, 1923
suborder	Pleuronectoidei	Bleeker, 1859
family	Paralichthyidae	Regan, 1910
genus	<i>Paralichthys</i>	Girard, 1858
species	<i>Paralichthys albigutta</i>	Jordan & Gilbert, 1882 figs. 6 Q-R, 7

material examined

N = 2: MSC 43231, MSC 46702

description

Stringer et al. (2020) identified a single otolith specimen from site AMb-2 (MSC 46043) as *Paralichthys* sp. In this study, two additional, better-preserved sagittae were recovered that allowed identification of all three specimens to the species level. A detailed description of the sagitta of these sagittae can be found in Stringer et al. (2020).

remarks

The present-day distribution of *Paralichthys albigutta* extends from North Carolina to southern Florida along the Atlantic Coast of the USA, the northern Bahamas, Gulf of Mexico, western Caribbean to Columbia in South America (Hoese & Moore 1998, Schwarzhans 1999, McEachran & Fechhelm 2005, Froese & Pauly, 2022). Fitch (1964, 1966, 1967, 1970) reported numerous fossil sagittae of the extant *Paralichthys californicus* from several localities in California. However, the Alabama Pliocene specimens reported herein and by Stringer et al. (2020) are believed to represent the first fossil *Paralichthys albigutta* otoliths from the Gulf or Atlantic coastal plains of the USA. Neither Fitch & Lavenberg (1983) nor Müller (1999) identified any fossil *Paralichthys* otoliths from the Atlantic Coast, despite examining over 20,000 specimens collectively. This rarity could be related to the limited studies of Plio-Pleistocene otoliths in the Gulf Coastal Plain, preservational factors (i.e., the susceptibility of the thin sagittae to breakage or erosion), or paleoenvironmental settings. The latter is considered likely since the depth range for *Paralichthys albigutta* is around 20 m to 130 m according to Smith (1997), and the paleodepth of the deposits at sit AMb-2 was probably less (see Stringer et al., 2020 and Discussion herein).



fig. 7. Syntype USNM 30818 of *Paralichthys albigutta*, hosted at the Smithsonian.

***Symphurus cf. plagiusa* (Linnaeus, 1766)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Carangiformes	Jordan, 1923
suborder	Pleuronectoidei	Bleeker, 1859
family	Cynoglossidae	Jordan, 1888
subfamily	Symphurinae	Ochiai, 1963
genus	<i>Symphurus</i>	Rafinesque, 1810
species	<i>Symphurus cf. plagiusa</i>	(Linnaeus, 1766) figs. 8, 12 A-B

material examined

N = 2: MSC 43250.1-2

description

The sagitta of *Symphurus cf. S. plagiusa* has a discoid outline (*sensu* Smale et al. (1995). The height/length ratio is approximately 1.09 (i.e., the height is greater than the length). The margins are generally smooth although there may be some very slight undulations present. The anterior margin is generally rounded, short, and slightly tapered. The anterodorsal margin is almost straight and may be slightly incurved. The dorsal margin is very slightly rounded and is almost horizontal. The posterodorsal and posterior margins are slightly rounded and almost vertical. The posteroventral margin varies from rounded to fairly straight. The ventral margin is slightly rounded and smooth. The middle of the ventral margin is the greatest height of the sagitta. The anteroventral margin is slightly rounded. One of the most unique features of the sagitta is the fairly small and uniquely “hammer-shaped” sulcus, which is located at the center of the inner face. The sulcus does not reach any margins and has no openings. The ostial portion of the sulcus is reduced, whereas the cauda is larger and primarily bilobate. The sulcus can almost become triangular in shape. The sulcus is usually very lightly impressed with a well-developed circumsulcal depression. There is no evidence of a crista superior or crista inferior. No dorsal depression is present, nor is a ventral furrow discernible. Both the inner and outer faces are relatively smooth and convex.

remarks

Extant *Symphurus plagiusa* has a range that extends from New York south along the US Atlantic coast and across the Florida Keys of the USA, to the northern Gulf of Mexico, as well as Mexico, the Bahamas, and Cuba (Hoese & Moore 1998, Froese & Pauly 2022). Fossil sagittae of *Symphurus* are rare in occurrence and abundance in the Plio-Pleistocene of the Atlantic and Gulf coastal plains. Fitch & Lavenberg (1983) reported 11 sagittae of *Symphurus* from the Pliocene Yorktown Formation at the Lee Creek site from an assemblage of almost 8,700 specimens (well less than 1% of the total). *Symphurus* was also reported from the Late Pleistocene of Louisiana (Stringer 1992), Early Pliocene of Georgia (Stringer & Bell, 2018), the Pliocene of North Carolina (Stringer & Shannon 2019), and Late Pliocene of North Carolina (Stringer et al. 2022).

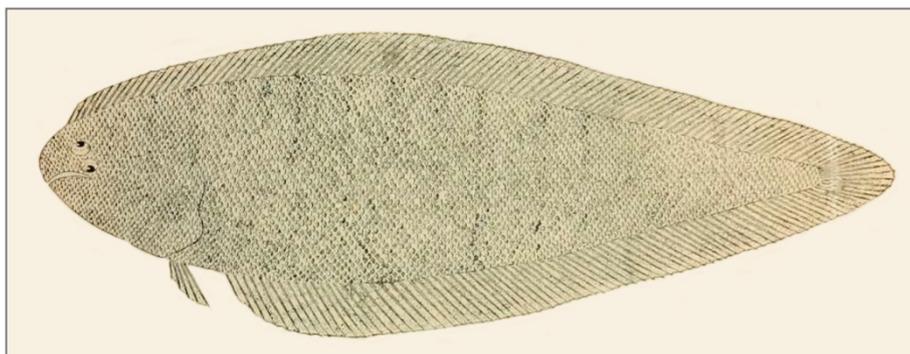


fig. 8.

Symphurus plagiusa. Drawing from plate 388 of Jordan & Evermann (1900): The fishes of North and Middle America. Vol. 4.

***Astroscopus* cf. *ygraecum* (Cuvier, 1829)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Perciformes	Bleeker, 1859
suborder	Trachinoidei	Bertin & Arambourg, 1958
family	Uranoscopidae	Bonaparte, 1831
genus	<i>Astroscopus</i>	Brevoort, 1860
species	<i>Astroscopus ygraecum</i>	(Cuvier, 1829) figs. 9, 12 C-D

material examined

N = 2: MSC 43261, MSC 46680

description

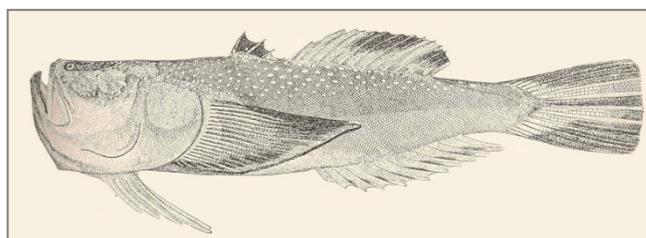
The sagitta of *Astroscopus* has an oval outline (*sensu* Smale et al. 1995). The height/length ratio is approximately 0.6 based on the two available specimens. The margins are primarily smooth, but there are small irregular undulations present on various margins. The anterior margin is tapered and irregularly rounded. There is a hint of a very small rostrum, although this could be the result of erosion. The anterodorsal margin is rounded with conspicuous small irregularities. The dorsal margin is broadly and evenly rounded, with the highest point being located medially. The posterodorsal margin is slightly rounded with some irregularities. The posterior margin is slightly tapered and fairly evenly rounded. The posteroventral margin is evenly rounded, whereas the ventral and anteroventral margins are slightly rounded and smooth. A long and narrow sulcus is located slightly dorsal on the inner face. The sulcus is approximately horizontal, except for the anterior portion which is slightly upturned. The sulcus extends across approximately 90% of the length of the inner face and extends from the anterior margin to near the posterior margin. The height of the narrow sulcus is only about 10% of the height of the inner face. There is a small, faint crista superior located above the sulcus. There is no clear distinction between the ostial and caudal areas. The anterior of the sulcus opens onto the upper part of the anterior margin. The posterior of the sulcus appears to be slightly and unevenly tapered. There is a narrow and oval depression located above the sulcus (slightly more toward the anterior). There is no visible ventral furrow. The inner face is generally smooth and evenly convex, whereas the outer face is unevenly concave and irregular.

remarks

The range of extant *Astroscopus ygraecum* includes off the North Carolina coast, the northern Gulf of Mexico, the Yucatan (Mexico), and the northern coast of South America (Robins & Ray 1986, Hoese & Moore 1998, and Froese & Pauly 2022). Fossil sagittae of *Astroscopus* in the US Atlantic and Gulf coastal plains of the U.S. are extremely rare. Fitch & Lavenberg (1983) reported the first fossil *Astroscopus* otoliths from North America, which were recovered from the Pliocene Yorktown Formation at the Nutrien phosphate mine (formerly known as the Lee Creek Mine) in North Carolina. However, these specimens were identified only to the generic level. Müller (1999) later reported a total of five *Astroscopus* specimens from the Miocene St. Marys Formation in Maryland, the Miocene Eastover Formation in Virginia, and the Pliocene Yorktown Formation in North Carolina. Nolf (2013) noted the occurrence of *Astroscopus* in the middle Eocene Piney Point Formation in Virginia. The specimens reported herein from site AMb-2 represent the first occurrences of *Astroscopus* in the Pliocene of the Gulf Coastal Plain in the USA.

fig. 9.

Upsilonphorus y-Graecum, star-gazer.
Drawing from plate 46 of Evermann & Kendall (1894): Fishes of Texas and the Rio Grande basin.



***Larimus fasciatus* Holbrook, 1855**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Acanthuriformes	Jordan, 1923
suborder	Sciaenoidei	Gill, 1872
family	Sciaenidae	Cuvier, 1829
genus	<i>Larimus</i>	Cuvier, 1830
species	<i>Larimus fasciatus</i>	Holbrook, 1855 figs. 10, 12 E-F

material examined

N = 40: MSC 43239, MSC 43245.1-4, MSC 44450, MSC 46024.1-7, MSC 46035.1-4, MSC 46653.1-3, MSC 46661, MSC 46665.1-2, MSC 46676.1-12, MSC 46687.1-3, MSC 46697.1-2

description

Stringer et al. (2020) tentatively identified four sagittae from site AMb-2 as *Larimus* sp. However, an additional, 36 well-preserved specimens were collected and examined in the present study that allowed identification to the species level. A detailed description of these sagittae can be found in Stringer et al. (2020).

remarks

The subsequent collecting conducted in this study allowed all the *Larimus* sagittae, including those tentatively referred by Stringer et al. (2020), to be definitively assigned to *Larimus fasciatus*. Extant *Larimus fasciatus* is known from Massachusetts to Texas in the USA with the exception of the most southern part of Florida (Robins & Ray 1986, Smith 1997, Hoese & Moore 1998, McEachran & Fechhelm 2005).

Sagittae of fossil *Larimus* appear to be relatively uncommon in the very limited investigations of Plio-Pleistocene otoliths from the Gulf Coast Plain of the USA (Stringer 1992; Stringer et al. 2020b). This observation may also be applied to Atlantic Coastal Plain of the USA. Müller (1999) identified a single *Larimus* aff. *L. fasciatus* specimen from over 12,000 Paleogene and Neogene otoliths from the central Atlantic Coastal Plain in the USA. The one specimen was derived from the Yorktown Formation (Rushmere Member, Pliocene) at the Nutrien phosphate pit (formerly the Lee Creek Mine) in North Carolina. Fitch & Lavenberg (1983) did not report any *Larimus* specimens in the 8,808 otoliths studied from the Yorktown Formation at the same site. Stringer & Bell (2018) reported 34 *L. fasciatus* sagittae from five different Plio-Pleistocene sites in coastal Georgia, while Stringer & Hulbert (2022) recovered 35 *L. fasciatus* from the Late Pleistocene on Skidaway Island in coastal Georgia.

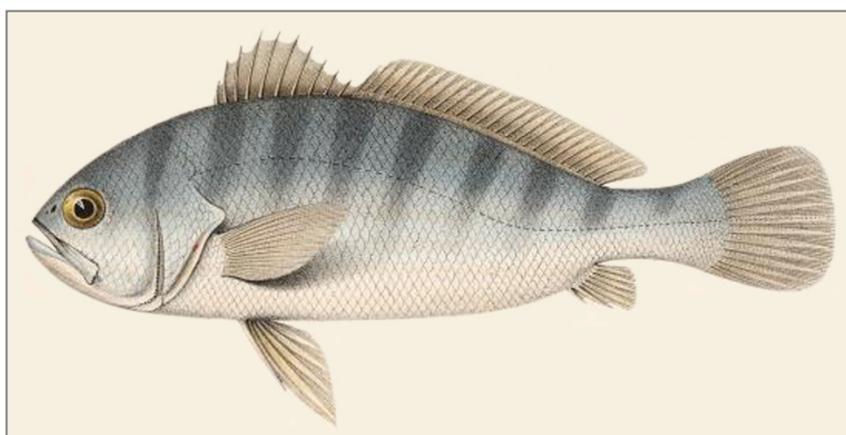


fig. 10.

Larimus fasciatus as shown on plate 22 in the 2nd edition of Holbrook's 'Ichthyology of South Carolina' (1860).

***Cynoscion regalis* (Bloch & Schneider, 1801)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Acanthuriformes	Jordan, 1923
suborder	Sciaenoidei	Gill, 1872
family	Sciaenidae	Cuvier, 1829
genus	<i>Cynoscion</i>	Gill, 1861
species	<i>Cynoscion regalis</i>	(Bloch & Schneider, 1801) figs.11, 12 G-H

material examined

N = 6: MSC 46033, MSC 46658, MSC 46663, MSC 46668, MSC 46671, MSC 46698

description

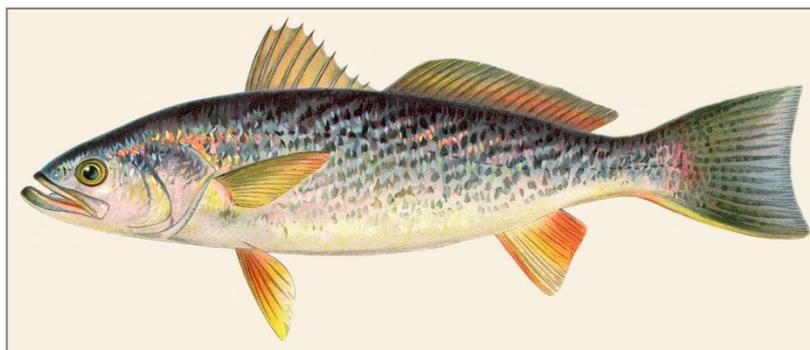
The sagittae of *Cynoscion regalis* have an outline that is essentially oblong (*sensu* Smale et al. 1995) and have morphological features very similar to those of *Cynoscion nebulosus* (Cuvier, 1830) (see description below). Therefore, only the salient features that differentiate the species are presented. Growth series of otoliths from modern fishes of both species (*C. nebulosus* and *C. regalis*) illustrate the similarities, especially at juvenile stages. However, there are features that distinguish the two. The dorsal margin of *C. regalis* sagittae tends to be more evenly rounded and lower. The most prominent differences occur on the inner face. Although both taxa have prominent heterosulcoid-type sulci, the ostium of *C. regalis* is not as expanded and voluminous as *C. nebulosus*. Also, the sulcus of *C. regalis* is more oblong in shape. The distance between the posterior of the ostium and the downturned portion of the cauda is considerably longer on *C. regalis*, and the height of the cauda is about 30% of the height of the ostium. In both of the species, the lower posteroventral portion of the ostium extends slightly beneath the anteroventral portion of the cauda and differentiates them from other *Cynoscion* at site AMb-2. The expansion of the posterior margin behind the caudal tip on *C. regalis* is not as long or pronounced as in *C. nebulosus*.

remarks

The sagitta of *C. regalis* resembles the sagitta of *C. arenarius* Ginsburg, 1930. However, the ostium of the latter is more rounded in shape. Another diagnostic and delineating feature is that the posteroventral portion of the ostium of *C. arenarius* does not extend beneath the anteroventral portion of the cauda. McEachran & Fechhelm (2005) noted the occurrence of extant *C. regalis* from the southwestern coast of Florida in the Gulf of Mexico, and Froese & Pauly (2022) showed unverified occurrences from the northeastern Gulf of Mexico. To further complicate the modern distribution of *Cynoscion* in the Gulf of Mexico, Snyder & Burgess (2016) reported hybridization among several of the species in the Western Atlantic and the Gulf of Mexico. Paleogeographic interpretations indicate a non-emergent or only partly emergent northern Florida during the Late Miocene and Early Pliocene. This connection between the Atlantic and the Gulf of Mexico could serve as a means of migration and explain the presence of *C. regalis* in this region during the Pliocene.

fig. 11.

'Weak-Fish or Squeteague (*Cynoscion regale*)' from 'Annual report of the Commissioners of Fisheries, Game and Forests of the State of New York for 1898'. Made available by Wikimedia Commons.



***Cynoscion nebulosus* (Cuvier, 1830)**systematic relationships

superclass	Osteichthyes	Huxley, 1880
class	Actinopterygii	Klein, 1885
subclass	Neopterygii	Regan, 1923
infraclass	Teleostei	Müller, 1846
superorder	Acanthopterygii	Johnson & Patterson, 1993
order	Acanthuriformes	Jordan, 1923
suborder	Sciaenoidei	Gill, 1872
family	Sciaenidae	Cuvier, 1829
genus	<i>Cynoscion</i>	Gill, 1861
species	<i>Cynoscion nebulosus</i>	(Cuvier, 1830) fig. 12 I-J

material examined

N = 1: MSC 46686

description

The sagittae of *C. nebulosus* have an outline that is primarily oblong (*sensu* Smale et al. 1995). The inner face is generally smooth and broadly convex. The height/length ratios are around 0.42, which indicates that the sagitta is elongated. The margins are primarily smooth but gentle undulations are present on some well-preserved specimens. The anterior margin is fairly short and rounded. The anterodorsal margin tends to be straight and slightly slanted upward toward the dorsal margin. The dorsal margin varies from somewhat straight to slightly convex, while the posterodorsal margin is very slightly incurved and slants fairly steeply toward the posterior margin. The posterior margin is noticeably tapered but not pointed. The posteroventral margin is slightly incurved, whereas the ventral margin is slightly curved outward. The anteroventral margin slants upward toward the anterior margin and is slightly curved outward. A very prominent heterosulcoid-type sulcus covers much of the inner face. It extends from the anterior margin to close to the posteroventral margin. The sulcus is not deeply excavated, but the cauda is more excavated than the ostium. The distance between the ostium and downturned portion of the cauda is shorter than other species of *Cynoscion*. The ostium is voluminous, elongated, and high, extending from close to the dorsal margin to the anteroventral margin. The posteroventral portion of the ostium extends slightly beneath the anteroventral portion of the cauda. The height of the cauda is only about 20% of the height of the ostium. The posterior 25% of the cauda is downturned at close to 90°. The caudal tip is inflated and almost always enlarged to some extent (Schwarzahns 1993). There is an expansion of the posterior margin behind the caudal tip that is often pronounced in larger specimens (see fig. 24 of Schwarzahns 1993). There is a very slight linear depressed area above the sulcus, but no ventral furrow is discernible. The outer face is convex and often has a prominent raised umbo. The outer face thins considerably in the anterior portion.

remarks

Four *Cynoscion* species (*C. arenarius*, *C. nothus*, *C. regalis*, and *C. nebulosus*) have been reported from the present Gulf of Mexico (Hoese & Moore 1998, McEachran & Fechhelm 2005, Page et al. 2013, Froese & Pauly 2022). Hoese & Moore (1998) noted that *C. arenarius* is confined to the Gulf of Mexico. However, Froese & Pauly (2022) showed it as occurring in the Western Atlantic off the east coast of Florida. Hoese & Moore (1998) also noted that biochemical analysis suggested that *C. arenarius* may be an unspotted version of *C. regalis*.

Regarding their sagittae, those of *C. arenarius* sagittae are more elongated (i.e., lower height/length ratio) and have a caudal tip that is more inflated (bulb-like) than the other species. The ostium is more elongated and horizontal. *C. nothus* is not as elongated in outline (higher height/length ratio), and the ostium is oriented from the anterodorsal to posteroventral. The posterior margins of the ostia of both *C. arenarius* and *C. nothus* do not extend under the cauda. *C. regalis* has a relatively small ostium and a long distance between the ostium and the downturned portion of the cauda. Furthermore, there is only a short distance from the caudal tip to the margin. In lateral view, the sagitta of *Cynoscion regalis* is relatively thin with little curvature. Relatively well-preserved specimens are needed for identification of the fossil species of *Cynoscion*, and most small juvenile *Cynoscion* specimens tend to be plesiomorphic and more difficult to differentiate.

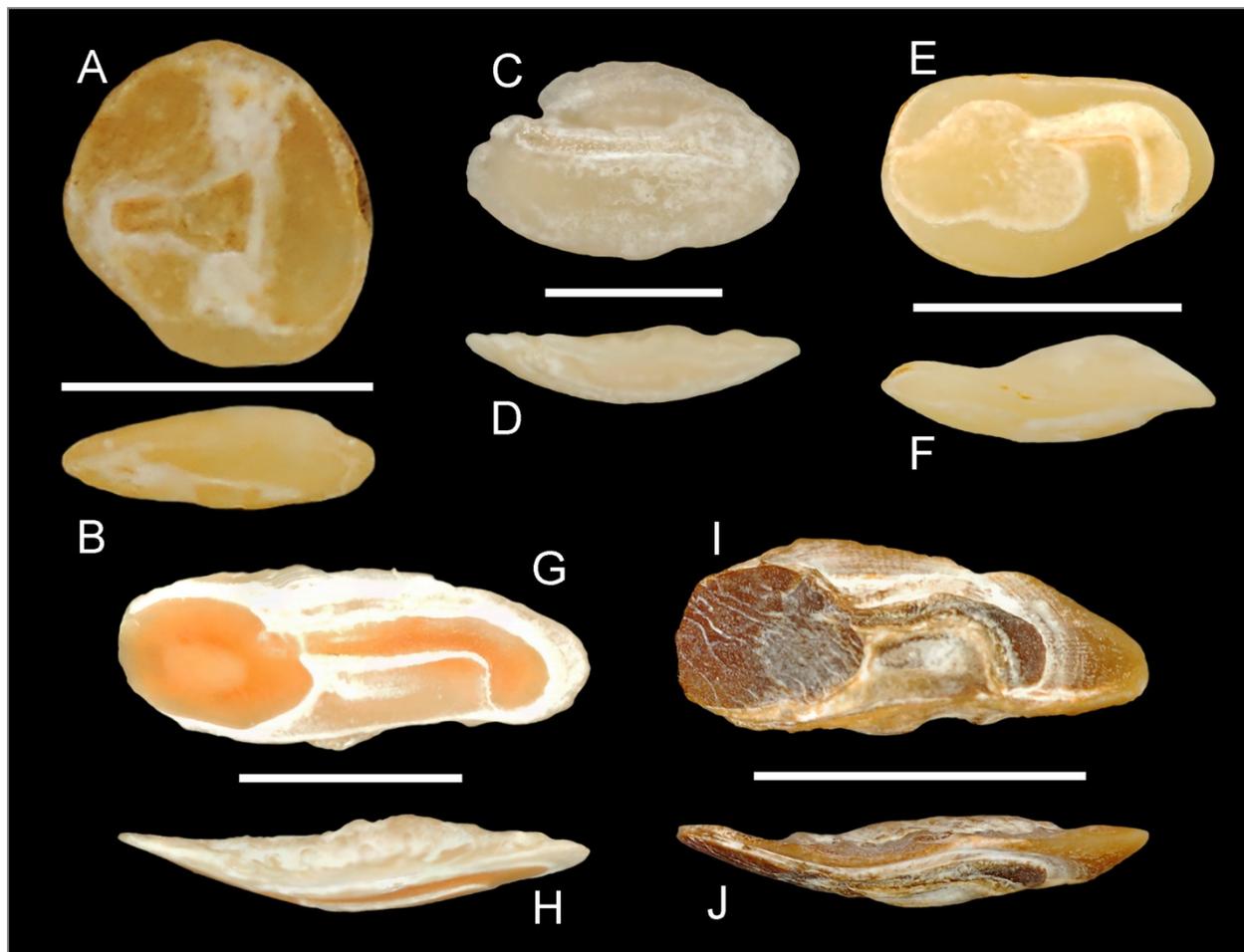


fig. 12. Pliocene otoliths from site AMb-2, Dauphin Island, Alabama, USA. All specimens are right otoliths or photographed as such. A-B) *Symphurus* cf. *S. plagiosa* sagitta in A) inner and B) dorsal views, scale bar = 2 mm. C-D) *Astroscopus* cf. *A. ygraecum* sagitta in C) inner and D) dorsal views, scale bar = 4 mm. E-F) *Larimus fasciatus* sagitta in E) inner and F) dorsal views, scale bar = 5 mm. G-H) *Cynoscion regalis* sagitta in G) inner and H) dorsal views, scale bar = 1 cm. I-J) *Cynoscion nebulosus* sagitta in I) inner and J) dorsal views, scale bar = 1 cm.

Discussion

The Pliocene otolith assemblage at site AMb-2 on Dauphin Island, Alabama, USA

Because the dredged exposures at site AMb-2 are Pliocene in age, the otolith assemblage has a maximum age of approximately 5.33 Ma. This relatively young geologic age would indicate that most of the otoliths represent extant species found in the present-day Gulf of Mexico. An examination of Table 1 demonstrates that this is certainly the case. All of the otoliths identified to species ($n = 4,041$ specimens or 98.80% of the total number) represent extant species found in the Gulf of Mexico with many from the northeastern region of the Gulf. Stringer et al. (2020) found the site AMb-2 otolith assemblage to be relatively diverse with 22 taxa representing 11 families, which is impressive given the initial study was based on 250 specimens. This study examined an additional 3,840 otoliths bringing the total number of specimens for study to 4,090. The subsequent collecting and analysis yielded 12 new taxa representing three additional families and allowed two previously identified taxa to be definitively assigned to species. Therefore, the otolith assemblage increased to 34 taxa (an increase of 35.30%) within 14 families of teleostean fishes (an increase of 21.43%). Because the fossil specimens from site AMb-2 represent the only Pliocene otolith assemblage described in the Gulf Coastal Plain of the USA, it unfortunately precludes their comparison to other Pliocene assemblages in the region. Therefore, a better understanding of the taxa present is significant, and the results of this study point to the importance of large sample sizes in otolith analyses.

Further examination of the taxa present at site AMb-2 revealed that 10 of the 34 taxa are in the family Sciaenidae (29.41% of the total taxa). However, sciaenid otoliths represent an astounding 96.45% of the total number of specimens. This means that all of the remaining taxa ($n = 24$) constitute less than 4% of the total specimens. Moreover, the abundance of the sciaenid *M. undulatus* (Linnaeus, 1766) (3,394 specimens; 82.98% of the total specimens) was especially significant for paleoenvironmental interpretations and will be discussed in detail below.

The otoliths recovered from site AMb-2 consisted predominantly of sagittae (otoliths found in the sacculus of the labyrinth and also referred to as sacculiths) and account for 99.32% of the total specimens. The other 0.68% consisted of lapilli (the otoliths located in the utriculus and also referred to as utriculiths). Lapilli are not used often in otolith studies, whereas sagittae are the most important otoliths for taxonomic study (Chao 1978, Fitch & Lavenberg 1983, Nolf 1985, Nolf 2013, Schwarzhans et al. 2018). However, there are a few groups in which lapilli have been found to be suitable for taxonomic use, such as the family Ariidae (sea catfishes), which have been utilized in many studies such as Nolf & Stringer (1992), Nolf & Aguilera (1998), Schwarzhans (2003), Schwarzhans (2012), Aguilera et al. (2013), Stringer & Bell (2018), and Stringer et al. (2020). Lapilli in the family Sciaenidae have also been found to be diagnostic and useful in several genera such as *Bairdiella* and *Stellifer* (Chao 1978; Stringer & Bell 2018). Lapilli recovered from two ariids (*Ariopsis felis* and *Bagre marinus*) and from two sciaenids (*Bairdiella chrysoura* and *Stellifer lanceolatus*) at site AMb-2, and in total 18 ariid lapilli and 28 sciaenid lapilli were recovered.

table 1.

Fish taxa (based on otoliths), number of otolith specimens, and percentages based on otoliths from the Graham Ferry Formation (Pliocene) from Dauphin Island Site AMb-2, Mobile County, Alabama, USA. Numbers in parentheses by family names are the number of specimens in that family. Note: **Paralichthys albigutta* was present as *Paralichthys* sp., and ***Larimus fasciatus* was present as *Larimus?* sp. in Stringer et al. (2020). Key to superscripts: 1. McEachran & Feckhelm (2005) noted *Cynoscion regalis* from the southwestern coast of Florida. Froese & Pauly (2022) show unverified occurrences from the northeastern Gulf of Mexico. Paleogeographic interpretations indicate a non-emergent or partly emergent northern Florida during the Late Miocene and Early Pliocene. This seaway could have functioned as a connection between the Atlantic and the Gulf of Mexico and explain the presence of *Cynoscion regalis* during the Pliocene in the northeastern Gulf of Mexico.

Family (bold and shaded) Genus and species	count	% of total	present in Stringer et al. (2020)	species in modern Gulf of Mexico
Family Congridae (6)				
<i>Ariosoma balearicum</i>	5	0,12	no	present
<i>Rhynchoconger</i> sp.	1	0,02	no	n/a
Family Engraulidae (13)				
<i>Anchoa hepsetus</i>	12	0,29	yes	present
<i>Anchoa mitchilli</i>	1	0,02	yes	present
Family Ariidae (18)				
<i>Ariopsis felis</i>	14	0,34	yes	present
<i>Bagre marinus</i>	4	0,1	no	present
Family Gadidae (5)				
<i>Urophycis regia</i>	5	0,12	yes	present
Family Ophidiidae (15)				
<i>Ophidion</i> cf. <i>marginatum</i>	1	0,02	yes	n/a
<i>Ophidion grayi</i>	1	0,02	no	present
<i>Ophidion josephi</i>	6	0,15	no	present
<i>Lepophidium jeannae</i>	2	0,05	no	present
<i>Lepophidium</i> cf. <i>jeannae</i>	1	0,02	no	present
<i>Otophidium</i> sp.	2	0,05	yes	n/a
Ophidiidae indeterminate	2	0,05	yes	n/a
Family Batrachoididae (8)				
<i>Porichthys</i> sp.	1	0,02	yes	n/a
<i>Porichthys plectrodon</i>	7	0,17	no	present
Family Paralichthyidae (8)				
<i>Syacium</i> sp.	2	0,05	yes	n/a
<i>Citharichthys macrops</i>	3	0,07	yes	present
<i>Paralichthys albigutta</i>	3	0,07	no*	present
Family Cynoglossidae (2)				
<i>Symphurus</i> cf. <i>plagiatus</i>	2	0,05	no	present
Family Stromateidae (3)				
<i>Peprilus</i> sp.	3	0,07	yes	n/a
Family Uranoscopidae (3)				
<i>Astroscopus</i> cf. <i>ygraeum</i>	3	0,07	no	present
Family Malacanthidae (4)				
<i>Lopholatilus chamaeleonticeps</i>	4	0,1	yes	present
Family Haemulidae (19)				
<i>Orthopristis chrysoptera</i>	19	0,46	yes	present
Family Triglidae (8)				
<i>Prionotus</i> aff. <i>carolinus</i>	8	0,2	yes	present
Family Sciaenidae (3945)				
<i>Micropogonias undulatus</i>	3394	82,98	yes	present
<i>Stellifer lanceolatus</i>	6	0,15	yes	present
<i>Bairdiella chrysoura</i>	28	0,68	yes	present
<i>Larimus fasciatus</i>	36	0,88	no**	present
<i>Cynoscion arenarius</i>	248	6,06	yes	present
<i>Cynoscion nothus</i>	95	2,32	yes	present
<i>Cynoscion regalis</i>	28	0,68	no	present ¹
<i>Cynoscion nebulosus</i>	3	0,07	no	present
<i>Leiostomus xanthurus</i>	79	1,93	yes	present
<i>Menticirrhus</i> cf. <i>americanus</i>	23	0,56	yes	present
Sciaenidae indeterminate	5	0,12	yes	n/a
Indeterminate	33	0,81		
Total number of specimens	4090	~100		

Paleoenvironmental conditions indicated by the Dauphin Island site otolith assemblage

Stringer et al. (2020) postulated the paleoenvironmental conditions present during the deposition of the Pliocene Graham Ferry Formation or equivalent deposits at site AMb-2 based on the recovered otoliths. The paleoenvironmental analysis was based on the ecological requirements and parameters of the extant fishes represented by the otoliths (Robins & Ray 1986, Cohen et al. 1990, Hoese & Moore 1998, McEachran & Fechhelm 1998, 2005, Nelson et al. 2016). Stringer et al. (2020) reconstructed the paleoenvironment based on an array of parameters including the four most abundant species at site AMb-2 as well as other supporting data such as the size and percentage of recovered sagittae of *M. undulatus* and *Leiostomus xanthurus* Lacepède, 1802. Shallow, soft-bottom estuarine creeks and bays and possibly upstream oligohaline creeks (i.e., salinity of 0.5 to 5.0 parts per thousand or ppt) in the estuarine environment were strongly suggested. The preponderance of small (juvenile) sagittae of *M. undulatus* pointed to a primary nursery area for this taxon, and the percentage of marine-only species may indicate more interaction of the open estuary with the accompanying shallow coastal area.

table 2.

Taxa from the Dauphin Island site AMb-2 (Pliocene) including number of specimens, percentage of total, ecological distribution, general bathymetric range, and climate. Numbers in parentheses by family names is number of otolith specimens in the family. Taxa shown in red were not reported by Stringer et al. (2020). Symbols for ecological distribution are **F** = freshwater, **B** = brackish, and **M** = marine. Symbols in bathymetric range are E. = estuarine and Sh. = shallow. All ecological, bathymetric, and climate data from Froese & Pauly (2022) unless noted otherwise. Explanation of superscripts: 1. Based on *Rhynchoconger flavus* (only species in present Gulf of Mexico) from McEachran & Fechhelm (1998), 2. depth range from Cohen et al. (1990) and Snyder & Burgess (2016), 3. average depth for *Otophidium chickcharney*, *O. dormitator*, and *O. omostigma*, 4. depth range for *Porichthys plectrodon* (most common species in the northern Gulf of Mexico), 5. average depth but common in bays, lagoons and shallow coastal waters (Robins & Ray 1986), 6. average depth for three common Gulf of Mexico species (*Peprilus paru*, *P. burti*, and *P. triacanthus*), 7. depth range from Grammer et al. (2009) and noted as primarily estuarine, 8. noted as rarely in estuaries and bays (Kells & Carpenter 2011, Froese & Pauly 2022), 9. depth from Louisiana Sea Grant (2019), but more common nearshore, 10. based on distribution of *Otophidium chickcharney*, *O. dormitator*, and *O. omostigma*, 11. based on two species in the Gulf of Mexico, 12. based on two species reported from Gulf of Mexico.

Family (bold and shaded) Genus and species	count	% of total	ecology	bathymetry range (m)	climate
Family Congridae (6)					
<i>Ariosoma balearicum</i>	5	0,12	M	1–732	subtropical
<i>Rhynchoconger</i> sp.	1	0,02	M	26–183 ¹	tropical
Family Engraulidae (13)					
<i>Anchoa hepsetus</i>	12	0,29	B, M	1–70	subtropical
<i>Anchoa mitchilli</i>	1	0,02	F, B, M	1–70	subtropical
Family Ariidae (18)					
<i>Ariopsis felis</i>	14	0,34	B, M	E.; sh.	subtropical
<i>Bagre marinus</i>	4	0,1	B, M	0–50	subtropical
Family Gadidae (5)					
<i>Urophycis regia</i>	5	0,12	M	1–420 ²	subtropical
Family Ophidiidae (15)					
<i>Ophidion</i> cf. <i>marginatum</i>	1	0,02	M	Sh. coastal	subtropical
<i>Ophidion grayi</i>	1	0,02	M	10–60	subtropical
<i>Ophidion josephi</i>	6	0,15	M	1–55	tropical
<i>Lepophidium jeannae</i>	2	0,05	M	25–280	tropical
<i>Lepophidium</i> cf. <i>jeannae</i>	1	0,02	M	25–280	tropical
<i>Otophidium</i> sp.	2	0,05	M	5–32 ³	sub.-trop. ¹⁰
Ophidiidae indeterminate	2	0,05	M	Marine	—
Family Batrachoididae (8)					
<i>Porichthys</i> sp.	1	0,02	M	0–494 ⁴	subtropical ¹¹
<i>Porichthys plectrodon</i>	7	0,17	M	1–100	tropical
Family Paralichthyidae (8)					
<i>Syacium</i> sp.	2	0,05	M	10–90	tropical
<i>Citharichthys macrops</i>	3	0,07	M	0–100	subtropical
<i>Paralichthys albigutta</i>	3	0,07	M	19–130 ⁵	subtropical
Family Cynoglossidae (2)					
<i>Symphurus</i> cf. <i>plagiusa</i>	2	0,05	B, M	0–183	subtropical
Family Stromateidae (3)					
<i>Peprilus</i> sp.	3	0,07	M	10–277 ⁶	subtropical ¹²
Family Uranoscopidae (3)					
<i>Astroscopus</i> cf. <i>ygraeum</i>	3	0,07	M	2–100	subtropical
Family Malacanthidae (4)					
<i>Lopholatilus chamaeleonticeps</i>	4	0,1	M	80–540	subtropical
Family Haemulidae (19)					
<i>Orthopristis chrysoptera</i>	19	0,46	B, M	10–?	temperate
Family Triglidae (8)					
<i>Prionotus</i> aff. <i>carolinus</i>	8	0,2	B, M	15–170	temperate
Family Sciaenidae (3945)					
<i>Micropogonias undulatus</i>	3394	82,98	B, M	0–100	subtropical
<i>Stellifer lanceolatus</i>	6	0,15	B, M	0–20	subtropical
<i>Bairdiella chrysoura</i>	28	0,68	F, B, M	E.. coastal ⁷	subtropical
<i>Larimus fasciatus</i>	36	0,88	B, M	1–60 ⁸	subtropical
<i>Cynoscion arenarius</i>	248	6,06	B, M	0–90 ⁹	subtropical
<i>Cynoscion nothus</i>	95	2,32	B, M	2–18	subtropical
<i>Cynoscion regalis</i>	28	0,68	B, M	10–26	subtropical
<i>Cynoscion nebulosus</i>	3	0,07	B, M	10–?	subtropical
<i>Leiostomus xanthurus</i>	79	1,93	B, M	0–60	subtropical
<i>Menticirrhus</i> cf. <i>americanus</i>	23	0,56	B, M	0–40	subtropical
Sciaenidae indeterminate	5	0,12	F, B, M	F, B, M	—
Indeterminate	33	0,81			
Total number of specimens	4090	~100			

The newly recovered 3840 otolith specimens proved extremely valuable in refining the paleoenvironmental interpretations of Stringer et al. (2020) for the AMb-2 assemblage. The additional 12 identified taxa and the two taxa now identifiable to species provided more specificity to the ecological setting (e.g., freshwater, brackish, and marine) and furnished further bathymetric ranges for determining paleowater depths. The new taxa also assisted in confirming climatic settings for the deposition of the Graham Ferry Formation or equivalent deposit at site AMb-2 during the Pliocene. A comparison of the fishes represented by otoliths at the site (i.e., those identified to the species level) indicated that all of the fossil otoliths represented fishes that are still extant in the present Gulf of Mexico. An analysis of the represented taxa indicated that none are exclusive to freshwater only, freshwater and brackish, or brackish only settings. Rather, all of the fish taxa pointed to 1) freshwater, brackish, and marine settings, 2) brackish and marine settings, and 3) marine only setting (Table 2). However, only three of the taxa are found in freshwater, brackish, and marine settings, whereas the remainder of the taxa are found in the brackish and marine setting (15 taxa) and marine only (18 taxa) settings. This distribution includes two groups identified only to the family level, and thus, the number shown in Table 2 is 36 rather than the 34 identified to at least the genus level. Therefore, there are no exclusively freshwater or brackish taxa in the assemblage, and all of the fishes may occur in the marine environment. Fig. 13a illustrates the distribution of the number of fish taxa based on otoliths that occur in specific environmental settings at Site AMb-2.

Although Fig. 13a indicates that three taxa may be found in freshwater, brackish, and marine settings (Froese & Pauly, 2022), they are represented by only 34 specimens that accounted for a very meager 0.83% of the total specimens (Fig. 13b). Therefore, they were certainly not abundant in the assemblage. Although 18 taxa are restricted to marine waters as shown in Fig. 13a, this can be misleading when the number of specimens represented by these taxa is examined. The 18 taxa restricted to marine waters comprised only 1.27% of the total 4090 specimens. Fishes found in both brackish and marine environments accounted for 15 taxa, less than in the marine waters only, but these 15 taxa comprised an extremely large percentage of the total specimens (97.1% of the total). This indicated that the fishes found in both brackish and marine settings were very successful and abundant in the paleoenvironment of the Graham Ferry Formation or equivalent deposit. Therefore, it is important to consider not only the taxa that are found in specific environments but also the number of otolith specimens from site AMb-2 in specific paleoecological settings as shown in Fig. 13b. None of the otoliths from site AMb-2 represented fish taxa that are indicative of deep-water marine forms, i.e., those greater than 200 m as a minimum depth. Nolf & Brzobohaty (1992) stated that marine assemblages that were free or almost free of myctophids indicate a neritic environment with little open oceanic influence. The fishes represented by otoliths and their relative abundances at site AMb-2 suggested a brackish and shallow neritic environment with little deep-water influence. This would also agree with the bathymetric ranges (Table 2) that indicate, with one notable exception, that all of the taxa could potentially be found in waters of approximately 20 m or less. A more detailed analysis of the most abundant taxa provides greater specificity of a paleoenvironment of deposits exposed at site AMb-2.

Ten taxa from the family Sciaenidae were recovered in this study from site AMb-2. Although the Ophidiidae had eight taxa represented, this family only accounted for 0.32% of the total specimens. In stark contrast, the sciaenids accounted for an incredible 96.45% of the total specimens. These taxa and their abundances vary significantly from those reported in Stringer et al. (2020) from the same site (albeit from a much smaller size, $n = 250$). This extraordinary number and percentage of sciaenid otoliths are a strong indicator that the paleoenvironmental parameters at the site must have been optimum for the survival, reproduction, and proliferation of the drums and croakers, and the paleoenvironment of the Graham Ferry Formation (or equivalent) was optimal to sciaenid physiological requirements. Studies such as Myers (1960), Darnell et al. (1983), and Nelson et al. (2016) have noted the strict confinement of the Sciaenidae to continental coasts or shallow waters near continental regions. According to Hoese & Moore (1998), sciaenids in the present Gulf of Mexico generally prefer tropical, shallow-marine waters, estuarine, and coastal areas. Nolf (2013) characterized sciaenids as neritic fishes living in warm shallow seas and estuaries, especially the estuaries of large rivers. Schwarzhans (1993) summarized the habits of the sciaenids in a similar manner. Stringer et al. (2020) noted *M. undulatus*, *C. arenarius*, *L. xanthurus*, and *Bairdiella chrysoura* as the most common taxa (approximately 70% of the total specimens) at site AMb-2, and all are in the family Sciaenidae. However, this study found different results with *M. undulatus*, *C. arenarius*, *C. nothus*, and *Leiostomus xanthurus* as the most abundant species in the assemblage, respectively, and all these taxa are sciaenids also. Furthermore, these latter four taxa comprised an exceedingly large percentage of the total specimens at 93.29%. Given the relatively young geological age of the studied otoliths, the modern ecological requirements of these four taxa should mimic the paleoenvironment of the Graham Ferry Formation (or equivalent) exposures at site AMb-2.

In Stringer et al.'s (2020) study of 250 otoliths from site AMb-2, *M. undulatus* (Atlantic croaker) specimens were the most abundant in the otolith assemblage at 53.20% of the total. Likewise in this investigation, this species is the most abundant but accounts for an exceedingly large percentage of the total specimens

recovered at 82.98%. Certainly their dominance must reflect an extraordinarily suitable habitat for this croaker. Snyder & Burgess (2016) characterized *M. undulatus* as primarily an estuarine fish preferring either mud bottoms or open sand. Numerous investigations have found that the juvenile *M. undulatus* utilized different parts of estuarine habitats on a size-specific basis and resided for several months in shallow, soft-bottom estuarine creeks and bays (Parker 1971; Ross 1988, 2003, Hales & Reitz 1992, Pattillo et al. 1997, Whitaker 2005). These subdivisions of the estuarine setting serve as primary nursery areas (PNAs) (Stringer & Shannon 2019; Stringer et al. 2020, and references therein). Many of the studies referenced above also indicated a clear differentiation of the various parts of the estuarine environment according to the age and size of the fish. The distribution of juvenile *M. undulatus* was skewed toward upstream oligohaline creeks (i.e., where salinity is 0.5 to 5.0 parts per thousand or ppt), while the adult croakers are most abundant in mesohaline (salinity of 5.1 to 18 ppt) and polyhaline (salinity of 18 to 30 ppt) salinities and are very rarely found in environments where the salinity is below 10 ppt.

A more in-depth and comprehensive paleoecological analysis of the deposits at site AMb-2 is made possible by the huge number of *M. undulatus* specimens available in the current investigation. The previous study by Stringer et al. (2020) recovered 133 specimens of *M. undulatus*, whereas the current study had 3,394 specimens. Previous, comprehensive studies of the life history of extant *M. undulatus* by Barbieri (1993) and Barbieri et al. (1994) determined the mean length (in mm) for various ages (1-8) of this species. In addition, the authors developed a linear equation based on the length of the sagitta that enables one to ascertain the total length of the fish ($OL = 1.91 + 0.04 TL$, where OL is the otolith length and TL is the total length of the fish). Therefore, it was possible to determine the total length of the *M. undulatus* represented by otoliths at site AMb-2. Furthermore, knowledge of the total length of the fish made it possible to determine the approximate age of the fish.

Based on the investigations of Barbieri (1993) and Barbieri et al. (1994) and comparisons to extant fish from the Gulf of Mexico, it was determined that a sagitta of approximately 10 mm or less in length represented a 1-year-old or less individual, which is a fish approximately 201 mm in TL. A total of 3,394 *M. undulatus* specimens were recovered from site AMb-2, and the length of each specimen was determined. The results of these measurements revealed that 99.18% of the specimens of *M. undulatus* represented juveniles that were 1-year-old or less. This certainly represents a definitive size distribution in the assemblage that is directly related to the paleoenvironmental setting. This size distribution can best be explained based on the distribution of extant *M. undulatus* as this size class would be most often found in shallow, soft-bottom estuarine creeks and bays. The size of the specimens would also strongly indicate the possible presence of upstream oligohaline creeks with salinities of 0.5 to 5.0 parts per thousand or ppt. The especially small number (26) and exceptionally small percentage (0.82%) of *M. undulatus* otoliths that are greater than 10 mm point to the dominance of the 1-year-old or less individuals. Even the uncommon otoliths greater than 10 mm tend to be in the 10.1–12.0 mm range, which would signify 2-year-old individuals. Only five otoliths were larger than 12.0 mm in length with the largest being 17.04 mm, which would indicate a fish over 8-years-old. It should be noted that the paleoenvironmental interpretation is based on fisheries data of present-day *M. undulatus* and denotes the most likely habitat of croakers of this size. As noted in Stringer et al. (2020), the determination of the paleoenvironmental parameters and conditions would be subject to the effects of taphonomic processes. Of course, all paleoecological interpretations can be affected by this process. However, based on several factors including the preservation of the otoliths and sedimentary analysis, the otoliths are believed to demonstrate an accurate approximation of the biocoenosis during the Pliocene and the time of the deposition of the AMb-2 sediments

The second most abundant species recovered from site AMb-2 was *Cynoscion arenarius*, which represented 6.06% of the total specimens. This species also represented the second most abundant species in Stringer et al. (2020) with a similar percentage. The bathymetric distribution of *C. arenarius* was indicated as bays, lagoons, and the shallow open waters of the Gulf of Mexico (Gunter, 1945; Guest & Gunter, 1958). Pattillo et al. (1997) characterized *C. arenarius* as an estuarine-dependent sciaenid that spent the majority of its life in the estuaries and nearshore waters of the Gulf of Mexico. However, it has been noted that *C. arenarius* can be found in depths up to approximately 90 m, but it is not common (Louisiana Sea Grant Program, 2019). Froese & Pauly (2022) reported that *C. arenarius* migrate during the summer months to its nursery and feeding grounds in river estuaries.

There is disagreement on the location of the spawning of the *C. arenarius*. Darnell et al. (1983) and Hoese & Moore (1998) noted spawning in estuaries and the shallow Gulf of Mexico around the mouth of passes. In contrast, Pattillo et al. (1997) stated that spawning appears to take place initially in the middle shelf (20–100 m) and moves shoreward as the season progresses. There is agreement, however, that the eggs are pelagic and buoyant, and the larvae are carried inshore. After the larvae are brought inshore, their preferred habitats for this fish are small bayous, shallow marshes, and channels in the upper estuary (Ditty

et al. 1991). It has been reported that the larvae and juveniles prefer grass beds and marsh areas with soft organic bottoms (Pattillo et al. 1997, and references therein). It appears that after its early development, *C. arenarius* moves into the main estuary. This migration to the main estuary by juveniles has been suggested by numerous studies including Günter (1945), Shlossman & Chittenden (1981), Ditty & Shaw (1994) and Pattillo et al. (1997). The juvenile *C. arenarius* remain in the bays and estuaries until they reach 50-60 mm in length and move into the shallow shelf. Therefore, the larvae of *C. arenarius* are typically in the upper estuary (bayous, shallow marshes, and channels), while the juveniles would be in the bays and main estuaries. The adults would be expected to be more abundant in shallow marine waters, but adults can also be in the estuaries at various times of the year (Pattillo et al. 1997).

Cynoscion nothus was the third most abundant fish represented by otoliths at site AMb-2 (2.32% of the total specimens). Only four *C. nothus* otoliths were recovered in Stringer et al. (2020), but 95 specimens were retrieved in the present study. *Cynoscion nothus* is one of the four *Cynoscion* species known from the Gulf of Mexico, and all four species are present in the AMb-2 assemblage. Two of these species of *Cynoscion*, *C. arenarius* and *C. nothus*, are among the most abundant taxa from the site. Froese & Pauly (2022) reported *C. nothus* as occurring in brackish and marine waters with a depth range 2–18 m. Bowling (2012) also reported its occurrence as shallow marine in the Gulf of Mexico. This species is demersal in its habits and commonly occurs throughout the Gulf of Mexico. It is often found over sandy bottoms in inshore waters along beaches and near the mouths of rivers (McEachran & Fechhelm, 2005). It is subtropical in its distribution and occurs as far north as Maryland along the USA Atlantic Coast (Robins & Ray 1986, Hoese & Moore 1998, McEachran & Fechhelm 2005). The species appears to have a very short life span as DeVries & Chittenden (1982) reported a maximum age of 1.2 years, while other species of *Cynoscion* are known to live 5 years. Snow (2020) stated that *C. nothus* is not well studied and limited information is available about its lifestyle and behavioral patterns including specific details on age, growth, longevity, movement patterns, diet, habitat use, and reproduction.

The fourth most abundant species from site AMb-2 is another sciaenid *Leiostomus xanthurus*, which represents 1.93% of the total specimens. This species and the three aforementioned species account for 93.29% of the total otoliths in the assemblage in the present study. Stringer et al. (2020) reported only 15 specimens of this species, but the present investigation produced 79 specimens. *Leiostomus xanthurus* was the third most abundant taxon in the Stringer et al. (2020) (based on a small number of otoliths), but its relative abundance placed it as fourth in the present investigation. Pattillo et al. (1997) noted that the younger juveniles of *L. xanthurus* commonly occur in the shallow headwaters of tidal creeks with mud and detritus bottoms, and Hales & Van Den Avyle (1989) and Pattillo et al. (1997) reported that adults migrate seasonally between estuarine and coastal waters. If an otolith assemblage has only or predominantly adult *L. xanthurus*, then shallow coastal waters would be the most likely paleoenvironment. However, if an otolith assemblage has a mixture of juveniles, subadults, and adults of *L. xanthurus*, then it would most likely represent estuarine waters. If an otolith assemblage consisted of primarily very young juveniles of *L. xanthurus*, then it could represent a paleoenvironment of an estuarine nursery and the presence of shallow headwaters of tidal creeks. The 79 *L. xanthurus* otoliths from site AMb-2 range from approximately 3.0 mm to 6.5 mm in length and appear to represent fish of different ages. Lombarte et al. (2006) illustrated a *L. xanthurus* otolith that measured 6.7 mm in length and was extracted from a 16.4 cm TL fish. Pattillo et al. (1997) reported that adult *L. xanthurus* are approximately 12.5 cm or larger, while juveniles range from approximately 12.5 cm to 1.5 cm. Therefore, it is likely that the fossil *L. xanthurus* otoliths from site AMb-2 represent a mixture of juveniles, subadults, and adults, which would be most commonly found in an estuarine paleoenvironment.

In addition to ecological settings (e.g., freshwater, brackish, and marine) and bathymetric ranges, the otolith assemblage from site AMb-2 provides information regarding possible climatic conditions for the dredged deposits during the Pliocene. Climatic information was obtained from a variety of sources including Cohen et al. (1990), Snyder & Burgess (2016), Louisiana Sea Grant (2019), and Froese & Pauly (2022). Examination of the data indicates only two taxa that are temperate in distribution, and they account for less than 0.75% of the total specimens. Seven taxa are exclusively tropical but represent less than 0.50% of the total specimens. One species is designated as subtropical to tropical, but is rare at 0.05% of the total specimens. However, there are 25 taxa of fishes represented by otoliths that are specified as subtropical, and these taxa comprise 98.7% of the total specimens recovered from the site. Therefore, the large number of taxa of fishes found in subtropical conditions ($n = 25$) as well as the percentage of those fishes in the total number of otolith specimens (98.7%) certainly seems to signify subtropical conditions for site AMb-2 during the Early Pliocene. The percentage of otolith specimens from taxa found in subtropical climates in this investigation is much larger than that reported by Stringer et al. (2020), which reported only 77.27% as subtropical. The present study strongly confirms subtropical conditions for the Graham Ferry Formation or equivalent deposits at site AMb-2.

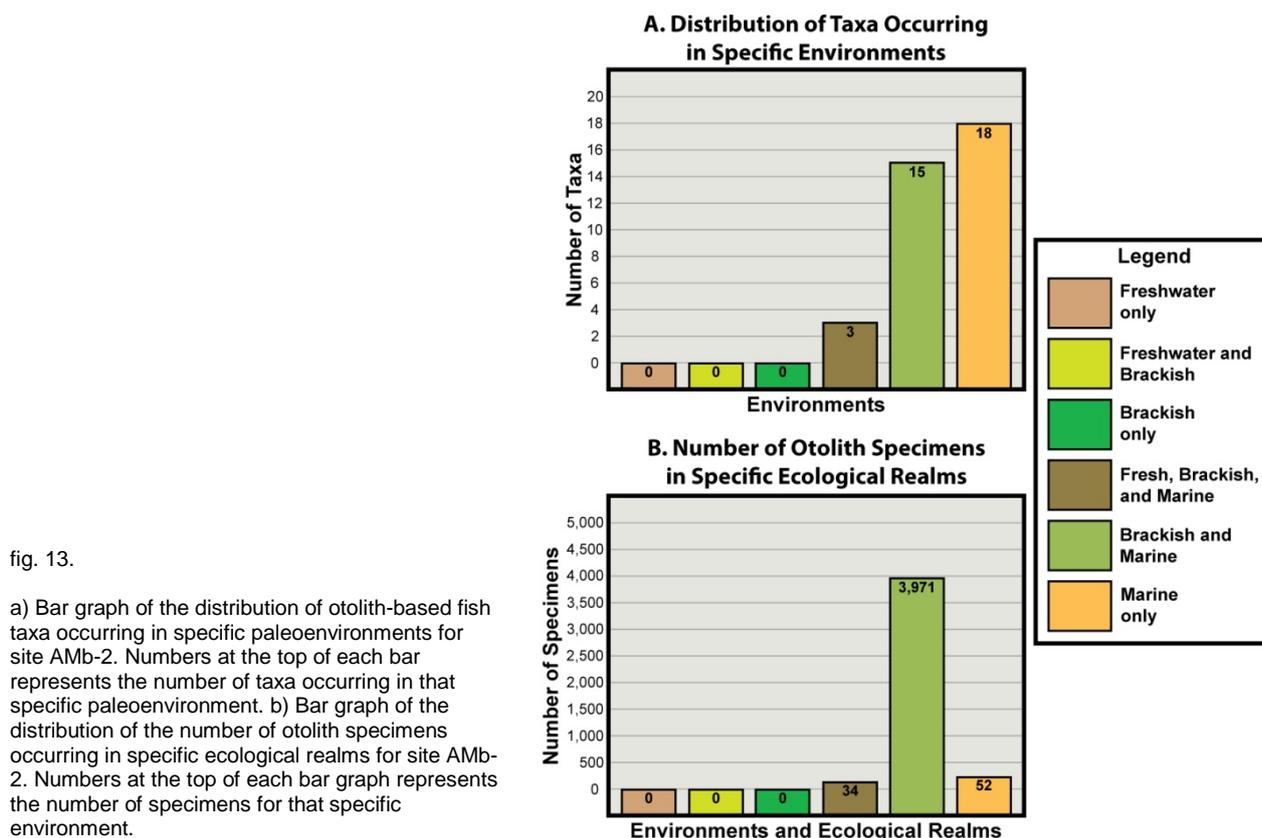


fig. 13.

a) Bar graph of the distribution of otolith-based fish taxa occurring in specific paleoenvironments for site AMb-2. Numbers at the top of each bar represents the number of taxa occurring in that specific paleoenvironment. b) Bar graph of the distribution of the number of otolith specimens occurring in specific ecological realms for site AMb-2. Numbers at the top of each bar graph represents the number of specimens for that specific environment.

There is little evidence of marine invertebrate settlement, such as encrustings or boreholes, on the Graham Ferry Formation or equivalent deposits otoliths recovered from site AMb-2, although 4090 specimens were examined from the site. The paucity of invertebrate settlement and actions on a very large sample size could be an indication of limited surface residence-time (Stringer 2016). This could be a result of a large amount of sediment influx frequently in the environment, which would cover the otoliths and protect them from the actions of invertebrates and settlement. It should also be noted that a large number of the fish species represented by otoliths in the assemblage preferred mud and soft bottoms as well as open sand bottoms (Snyder & Burgess 2016). There are also indications of high organic content in the bottom sediment indicated by some of the fishes (Pattillo et al. 1997).

In summary, there are some strong and salient indicators of the possible paleoenvironmental setting of the dredged deposits at site AMb-2 on Dauphin Island. There appear to be several interacting paleoenvironments and include the following: A) shallow, soft bottom estuarine creeks and bays and possibly upstream oligohaline creeks (i.e., salinity of 0.5 to 5.0 parts per thousand or ppt) representing a primary nursery area, B) an adjacent, more open estuary (perhaps somewhat narrow), and C) a shallow marine coastal area in close proximity. A synopsis of the evidence for these paleoenvironments is provided. First, the preponderance of *M. undulatus* in the assemblage is overwhelming with 3394 specimens (82.98% of the total specimens). Even more discriminating is the percentage of specimens that were 1-year-old or less (99.18%). This size distribution in an otolith assemblage would almost certainly be found in shallow, soft-bottom estuarine creeks and bays that would indicate a primary nursery area. Secondly, the presence of taxa such as *L. xanthurus* and *C. arenarius* (second and fourth most abundant species in number of specimens) are compelling indicators of estuaries and bays as well as shallow marine. Fifteen taxa represent 97.1% of the total assemblage and are found in brackish and marine waters, which is convincing evidence for the brackish estuarine conditions as well as the shallow marine. Furthermore, although not abundant in the number of specimens (1.27% of total number), there are 19 taxa (including Ophidiidae indeterminate) that are restricted to marine environments. This percentage of marine-only species is very similar to the Pliocene Elizabethtown site in North Carolina, which was interpreted by Stringer & Shannon (2019) to represent shallow, soft-bottom estuarine creeks and bays that served as a primary nursery area. The proximity to and the effect of the shallow marine coastal area is evident since all of the site AMb-2 species may be found in marine waters (Table 2). Taken collectively, these factors supply plausible data for the paleoenvironmental interpretations of the site during the Early Pliocene.

Conclusions

The present study examined an additional 3,840 teleostean otoliths from site AMb-2 on Dauphin Island, Mobile County, Alabama, USA. The otolith assemblage, which is believed by the authors to be derived from the Graham Ferry Formation (Pliocene) or equivalent deposits, consisted mainly of sagittae, although lapilli of four taxa were represented. When combined with the limited specimens from Stringer et al. (2020), the total number of specimens available for examination rose to 4,090. The extensive subsequent collecting and analysis yielded 12 new taxa representing three additional families and allowed two previously identified taxa to be definitively assigned to species. The site AMb-2 otolith assemblage increased to 34 taxa (an increase of 35.30%) and to 14 families of teleostean fishes (an increase of 21.43%) in the present study. The additional taxa not only enlarged the bony fishes known from the Pliocene in the Gulf Coastal Plain, but the fossil otoliths also made it possible to delineate paleoenvironmental conditions of site AMb-2 in greater detail. The extremely large number of sagittae of *M. undulatus* ($n = 3,394$ specimens or 82.98% of the total specimens in the assemblage) was especially consequential. Length measurements of the *M. undulatus* sagittae indicated that 99.18% of the specimens represented juveniles that were 1-year-old or less. The remarkable size distribution in the assemblage pointed to the presence of a particular paleoenvironment. When all facets of the otolith assemblage were examined, several interacting paleoenvironments appeared present at site AMb-2 during the Early Pliocene. There is very strong evidence for shallow, soft bottom estuarine creeks and bays and possibly upstream oligohaline creeks (i.e., salinity of 0.5 to 5.0 parts per thousand or ppt) that represented a primary nursery area for *M. undulatus*. Furthermore, an adjacent, more open estuary (perhaps somewhat narrow) existed with a shallow marine coastal area in close proximity. The shallow neritic environment was likely not deeper than 20 m and had little deep-water influence. Many of the fishes preferred mud and soft bottoms as well as open sand bottoms, and climatic conditions were most likely subtropical. The results of this investigation demonstrate once again the value of fish otoliths in ascertaining paleoenvironments and the importance of large sample size in otolith analysis. Comparisons to other Pliocene otolith assemblages in the Gulf Coastal Plain were not possible as the site is the only one known at the present.

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