

Eocene teleostean otoliths, including a new taxon, from the Clinchfield Formation (Bartonian) in Georgia, USA, with biostratigraphic, biogeographic, and paleoecologic implications

GARY L. STRINGER^{a*}, DENNIS PARMLEY^b, ASHLEY QUINN^c

^aUniversity of Louisiana at Monroe, Geosciences/Museum of Natural History, Monroe, LA 71209 USA

^bGeorgia College, Department of Biological and Environmental Science, Milledgeville, GA 31061 USA

^cGeorgia College, William P. Wall Museum of Natural History, Milledgeville, GA 31061 USA

*corresponding author: stringer@ulm.edu

Abstract: Investigations of the Clinchfield Formation (middle Eocene, upper Bartonian) exposed at the Hardie Mine (Wilkinson County, Georgia, USA), produced 4,768 actinopterygian otoliths representing 14 taxa and increased the number of bony fishes threefold from the site. The Clinchfield otolith assemblage had limited richness with a relatively even distribution of the most common families: Ophidiidae (cusk-eels), Congridae (conger eels), and Sciaenidae (drums). Included in the otolith taxa was a new sciaenid genus and species, *Eosciaena ebersolei*, with unknown relationships to other Sciaenidae. The Clinchfield otoliths were compared to other middle and late Eocene otolith assemblages in Alabama, Mississippi, and Louisiana utilizing percentage similarity analysis, which indicated that the Clinchfield shared taxa with the Moodys Branch and Yazoo Clay otolith assemblages but the relative abundance of species was markedly different. However, the Clinchfield assemblage showed little relationship to the slightly older Lisbon Formation in adjacent Alabama, which had at least ten unique fish species. This difference is postulated to be related to global climatic (Antarctica glacial initiation) and plate tectonic (early closure of Tethys Seaway and continued separation of Australia and Antarctica) events. Given the similarity in paleowater depth, significant differences of abundance of Clinchfield species may indicate a sub-bioprovince in the eastern Gulf Coastal Plain. The Clinchfield otoliths indicate a tropical to perhaps subtropical, soft substrate, mainly normal marine to slightly reduced salinities, inner shelf (0-20 m) paleoenvironment with indications of proximal continental coastlines. This investigation represents an initial step in addressing immensely understudied Paleogene otolith assemblages in Georgia.

Keywords: Ophidiidae, Congridae, Sciaenidae, climate, tectonics

Submitted 07 July 2021, Accepted 20 October 2021

Published Online 03 January 2022, doi: [10.18563/pv.45.1.e1](https://doi.org/10.18563/pv.45.1.e1)

© Copyright Gary L. Stringer January 2022

INTRODUCTION

Although the Eocene vertebrate fauna of the Hardie Mine site near Gordon, Georgia, USA, has been scientifically investigated and reported for over 25 years (Westgate *et al.*, 1994), a detailed description of the teleostean otolith assemblage has never been achieved. This is unusual since abundant otoliths (242 specimens) were noted by Westgate (2001) and preliminary investigations of the otoliths were conducted by Stringer *et al.* (2007a, 2007b). Yet, these were the only studies of the prolific otolith specimens present at the site. It is also unfortunate since otoliths often provide insight into the actinopterygian fauna often not discernible by skeletal remains (Schwarzshans *et al.*, 2018; Stringer & Bell, 2018; Ebersole *et al.*, 2019; Stringer & Hulbert, 2020). Other marine vertebrate groups such as sharks, rays, bony fishes (skeletal remains), reptiles (marine snakes and turtles), marine mammals (whales) (Riley & Westgate, 1999; Westgate, 2001; Parmley & Cicimurri, 2003; Parmley & Holman, 2003; Parmley & Cicimurri, 2005; Parmley & DeVore, 2005; Parmley *et al.*, 2006; Cicimurri *et al.*, 2020) and even terrestrial remains of reptiles (freshwater turtles and colubrid snakes), birds (auk), and mammals (five taxa) (Westgate, 2001; Parmley & Holman, 2003; Chandler & Parmley, 2003; Parmley & Cicimurri, 2005; Parmley *et al.*, 2006) have been described from the locality. A detailed examination of

an extensive number of otoliths (bulk samples and surface collections) identifies taxa of bony fishes not available based solely on the skeletal remains (only four taxa known from the site) and produces a more complete understanding of the diverse and important Eocene marginal marine assemblage at the Hardie Mine site. This investigation substantially increases the bony fishes fauna by over threefold and provides data to augment and supplement the paleoecological interpretation of this significant site, which has produced several oldest and first records of various vertebrate fossil taxa. Added to the impressive records from the Hardie Mine site is a new Eocene sciaenid genus and species of unknown affinities.

Geological and stratigraphical settings

The otoliths in this investigation were obtained from an open-pit kaolin mine, locally known as the Hardie Mine. The site is 3.2 km northwest of the post office in Gordon, Wilkinson County, Georgia, USA (34.5071, -84.8785) (Fig. 1). Westgate (2001) reported the Clinchfield Formation (basal lithostratigraphic unit of the Eocene Barnwell Group) was exposed as a one-meter thick, fossiliferous, coarse sand at the site. The Clinchfield Formation is upper middle Eocene (Bartonian; see discussion below) in age. At the Hardie Mine site, the Clinchfield Formation sands unconformably overlay non-fossiliferous, middle Eocene kaolin clay and underlie the Priabonian Dry



Figure 1. Generalized location (country, state, and county) of the Hardie Mine site in Wilkinson County, Georgia, USA (34.5071, -84.8785) (modified from Cicimurri *et al.*, 2020).

Branch Formation, which is locally non-fossiliferous (Fig. 2). Cicimurri *et al.* (2020) reported that the Riggins Mill Member of the Clinchfield Formation was exposed at the locality.

While there appears to be a consensus that the Hardie Mine Clinchfield sediments were deposited during the Eocene sometime between the middle to late Bartonian and the Priabonian, their exact age within the Eocene has received extensive investigations with differing opinions. An overview of some of the inquiries are discussed briefly. Herrick (1972) identified over 50 foraminifera species from the Clinchfield Formation in Georgia. He compared the Clinchfield foraminiferal assemblage with Claibornian and Jacksonian sites in South Carolina, Alabama, and Mississippi. He concluded that the Clinchfield Formation was Jacksonian in the calcareous nannofossil zone NP19–20 based on the foraminifera. Glawe (1974), while investigating the Eocene and Oligocene pectens of Georgia, indicated that the Clinchfield was equivalent to the lower Moodys Branch Formation, which would be NP17 according to Dockery & Thompson (2016). Toulmin (1977) in his classic study of Paleocene and Eocene fossils in the eastern Gulf Coast region stated that the Moodys Branch Formation continued into Georgia from Alabama as a sandy limestone and calcareous sand known as the Clinchfield. He further noted that it could be traced into eastern Georgia on the basis of the presence of abundant specimens of *Periarchus lyelli*. Huddleston & Hetrick (1986) in their stratigraphic study of the upper Eocene of central and eastern Georgia correlated the Clinchfield Formation with the Moodys Branch Formation of the Gulf Coastal Plain. The two formations were placed at the base of planktonic foraminifera zone P16.

Westgate (2001) suggested that the Clinchfield sediments were deposited either during the upper middle Eocene

(Dockery, 1996) or early in the upper Eocene (Huddleston & Hetrick, 1986; Huddleston, 1993). However, based on South Carolina vertebrates (skeletal remains), Albright *et al.* (2019) contended that the Clinchfield Formation should be in zone P14 and the lower half of zone P15 (late Bartonian and earliest Priabonian) or NP17. This is similar to Dockery (1996) and Dockery & Thompson (2016) as they placed the Moodys Branch Formation in Mississippi in the upper portion of zone P14, although they did not extend it into P15 (i.e., they indicated the upper portion of the Moodys Branch Formation as slightly older remaining in the zone P14). However, Nystrom *et al.* (1992) contend that most of the Clinchfield Formation of Georgia is Claibornian rather than Jacksonian. Cicimurri *et al.* (2020) in their study of selachians identified the Clinchfield Formation as middle Eocene (Bartonian) in calcareous nannofossil zone NP 17.

There have been some studies that point to a late (but not latest) Eocene age for the fossil-bearing Clinchfield sediments at the Hardie Mine. The shark fauna of the Hardie Mine site is generally typical of other late Eocene nearshore shark faunas of the Gulf Coastal region of North America (Parnley & Cicimurri, 2003). Additionally, ten brontothere teeth from the Hardie Mine fauna have been assigned to *Megacerops* by Rhinehart *et al.* (2019). This rules out an early Oligocene age, as brontotherids were extinct by the end of the Eocene (Mader, 1998). Other evidence cited for a late Eocene age of the sediments comes from invertebrate evidence. The pectinid species *Chlamys clinchfieldensis* is relatively common in the Hardie Mine molluscan fauna. Glawe (1974) interpreted *C. clinchfieldensis* as being an excellent stratigraphic marker due to its widespread geographic distribution (central Georgia to western Alabama) and short age range (late Eocene only). Analysis of the Barnwell Group dinocysts by Edwards (2001) indicated that the higher samples were correlative with the upper Eocene Yazoo Clay in Alabama as well as a form that is found in the Gosport and Moodys Branch Formation (upper middle Eocene). However, several studies, including Dockery (1996), Manning & Standhardt (1986), and Dockery & Thompson (2016), indicate that the lower Yazoo Clay is uppermost Bartonian (NP17). Finally, the National Geologic Map Database reported the age of the Clinchfield as middle Eocene (Claibornian) and upper Eocene (Jacksonian) (USGS, 2020).

Despite the somewhat differing results on the precise delineation of the age of the Clinchfield Formation at the Hardie Mine, a generalization is possible that encompasses the majority of the biostratigraphic investigations. The Clinchfield

Era	Period	Epoch	Stage	NP Zone	Group	Hardie Mine Stratigraphy Wilkinson County, Georgia	Lithology of units at the Hardie Mine
Cenozoic (in part)	Paleogene (in part)	Eocene (in part)	Priabonian	NP 19/20	Barnwell Group	Dry Branch Formation	Orange-red, cross-bedded, non-fossiliferous sand
				NP18		Unconformity	
			Bartonian	NP17		Clinchfield Formation	Orange, massive, well-sorted sand
						Unconformity	
					Kaolinite	White, soft, non-plastic, non-fossiliferous kaolinite	

Figure 2. Stratigraphic chart of the Hardie Mine site illustrating the middle to upper Eocene lithostratigraphic units exposed at the mine. The shaded areas on the chart represent unconformities (modified from Cicimurri *et al.*, 2020).

Formation is primarily middle Eocene and upper Bartonian (a very small portion of the uppermost Clinchfield may be lower Priabonian). This would place the Clinchfield Formation at approximately 37.1–40.2 Myr (Albright *et al.*, 2019). This would entail the uppermost Claibornian and lowermost Jacksonian within the calcareous nannofossil zone NP17. Furthermore, the Clinchfield Formation is likely temporally and laterally equivalent to the Gosport Sand and the Moodys Branch Formation in the Gulf Coast Plain.

MATERIAL AND METHODS

The otoliths for this investigation were obtained from both bulk samples and surface collections of the middle Eocene Clinchfield Formation at the Hardie Mine, Georgia, USA (34.5071, -84.8785). The majority of the specimens were surface collected from the spoil banks that were produced by the kaolin mining operations. Since there are no other fossiliferous units at the Hardie Mine, Cicimurri (2020) noted that all of the material originated in the highly fossiliferous Clinchfield Formation. Bulk samples of in situ Clinchfield Formation sediments were also obtained from the mine wall. Furthermore, the vertical extent of the Clinchfield Formation (approximately 1 m) greatly limits the spatial interval represented. Many of the specimens were collected by one of the authors (DP), and several others contributed otoliths for study (see Acknowledgments).

Bulk samples of the Clinchfield Formation were wet screened using plain water with no additives to avoid any adverse effect on the aragonitic otoliths. During the wet screening, all residue that was retained on a U.S. Standard Sieve #30 (0.595 mm) was kept for study. Following the wet sieving, the residue was air-dried. U.S. Standard sieves (#5 to #30; 4.00 mm–0.595 mm) were employed to separate the residue into similar-sized material for more efficient microscopic examination. An Olympus binocular microscope (0.8x to 40x) was employed to extract the otoliths from the bulk sample residue.

The Clinchfield Formation otoliths were photographed using the imaging system in the Department of Biological and Environmental Sciences, Georgia College, Milledgeville, Georgia. The imaging system uses a Canon EOS 5DS R on a vertically mounted carriage with multiple lenses (Canon MP-E 65 mm and Canon Macro 100 mm) and Mitutoyo oculars (5X and 10X) mounted with the Canon 200 mm. Raw image file processing is accomplished through CaptureOne, Visionary, and Zerene stacking software. All figured specimens are repositied in the Georgia College and State University Vertebrate Paleontology Collections (GCVP) in the William P. Wall Museum of Natural History in Milledgeville, Georgia.

Fossil and Holocene comparative otolith collections and references were utilized for the identification of the Clinchfield Formation specimens. The classification scheme follows that of Nelson *et al.* (2016), which was greatly influenced by the molecular work of Betancur-R. *et al.* (2013). Any deviation from this classification is noted. Ordinal names follow Wiley & Johnson (2010), while the family-group names and authors of modern fishes follow Van der Laan *et al.* (2014, 2017, 2018). Authors of Holocene genera and species depend greatly upon Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke *et al.*, 2019). Common names were obtained from Froese & Pauly (2020). When the generic designation for an otolith specimen was not evident, the recommendations of Janssen (2012) were employed. This is accomplished by

placing the unknown genus in the type genus of the family followed by a question mark indicating that the taxon might belong to any other of the known (or as yet unknown) genera in that family.

Abbreviations commonly utilized in otolith descriptions include the following: OL = otolith length, OH = otolith height, OT = otolith thickness, SuL = sulcus length, CaL = cauda length, CCL = length of caudal colliculum, CCH = height of caudal colliculum, OsL = ostium length, OsH = ostium height, OCL = length of ostial colliculum, and OCH = height of ostial colliculum. Details on how these measurements are made may be found in Schwarzahns & Stringer (2020).

In order to compare the otolith assemblage of the Clinchfield Formation of Georgia to other middle and late Eocene otolith assemblages in Alabama, Mississippi, and Louisiana formations, the percentage similarity measurement was utilized. This analysis allows a comparison of assemblages from different localities (Reitz & Wing, 1999; Stringer *et al.*, 2016; Stringer *et al.*, 2018; Schwarzahns & Stringer, 2020). The percentage similarity measurement (also known as percent similarity or proportional similarity), is calculated using the equation:

$$P = \sum \text{minimum}(p_{1i}, p_{2i})$$

where:

P = percentage similarity between assemblages 1 and 2

p_{1i} = percentage of species *i* in assemblage 1

p_{2i} = percentage of species *i* in assemblage 2

Institutional abbreviations:

BCGM = Bob Campbell Geology Museum (Clemson University, Clemson, South Carolina, USA),

GCVP = Georgia College Vertebrate Paleontology Collections (Georgia College and State University, Milledgeville, Georgia, USA),

IRSNB = Royal Belgian Institute of Natural Sciences (Brussels, Belgium),

MSC = McWane Science Center (Birmingham, Alabama, USA),

SC = South Carolina State Museum (Columbia, South Carolina, USA).

RESULTS

Surface collecting and bulk sampling of the Clinchfield Formation at the Hardie Mine site resulted in the procurement of 4,768 otoliths, which represent 14 taxa distributed in 9 families (Table 1). The bony fish otoliths from the Clinchfield Formation at the Hardie Mine are shown in Figures 3 and 4. The Clinchfield Formation taxa are described and discussed in the Systematic Paleontology.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass ACTINOPTERYGII sensu Goodrich, 1930

Order ALBULIFORMES Jordan, 1923

Family ALBULIDAE Bleeker, 1859

Genus *Albula* Scopoli, 1777

Albula sp.

Fig. 3A (GCVP 19904)

Description

Twenty specimens (19 surface; 1 bulk) were assigned to *Albula* sp. The outline is somewhat oblong to elliptic (sensu Smale *et al.*, 1995) and can obtain lengths near 20 mm. The margins are mainly smooth, and the inner face is conspicuously convex and twisted. The prominent, long sulcus is primarily developed in the dorsal and posterior regions. The sulcus is commonly indistinctly divided with a wide, anterodorsally opening ostium that is filled with colliculum. The caudal area has an anterior sub-horizontal portion and a posterior downturned portion that is deeply excavated. A caudal keel is present but usually broken. Outer face is concave, twisted (especially in adults), thins toward the anterior, thickest in posterodorsal, and annual growth rings are often visible.

Discussion

Albulid otoliths are commonly present in Paleogene formations in the Gulf Coastal Plain, but they are usually not abundant elements in the assemblages (Breard & Stringer, 1995; Stringer & Breard, 1997; Breard & Stringer, 1999; Stringer & Miller, 2001; Schweitzer *et al.*, 2014). For example, only 5 specimens of *Albula* sp. were found in the 5559 otoliths examined from the upper Eocene (Priabonian) Yazoo Clay by Nolf & Stringer (2003). This scarcity of albulid otoliths is also present in the

Clinchfield Formation as *Albula* sp. only represented 1.33% of the total specimens in the bulk sample. The abundance of *Albula* sp. is not unexpected giving their distribution in the present-day Gulf of Mexico (Hoese & Moore, 1998; Froese & Pauly, 2020).

Oder ANGUILLIFORMES Goodrich, 1909

Family HETERENCHELYIDAE Regan, 1912

Genus *Pythonichthys* Poey, 1868

Pythonichthys colei (Müller, 1999)

Fig. 3B (GCVP 19905)

Description

Sixteen specimens (11 surface; 5 bulk) were attributed to *Pythonichthys colei*. This species is characterized almost exclusively by small sagittae, usually less than 3 mm in length. The outline is almost circular to sometimes slightly oval (sensu Smale *et al.*, 1995) with smooth margins. The inner face is convex and smooth with an obvious, not deeply impressed sulcus that extends mainly medially across 75% of the length. There is no clear distinction of the ostium and cauda. The ventral margin of the sulcus may undulate, especially in the posterior portion, while the posterior end of the sulcus is rounded. The outer face is slightly concave and fairly featureless.

Discussion

Pythonichthys colei is widely distributed in many of the

Table 1. Taxa represented by otoliths at the Hardie Mine site (middle Eocene, Bartonian), near Gordon, Wilkinson County, Georgia, USA. Numbers include surface collections and bulk samples. For specifics on bulk sample results, see Table 2.

Orders (upper case, shaded) Family (sentence case, bold)	Total otoliths	Surface collected	Bulk sample	Figure numbers
ALBULIFORMES				
Family Albulidae				
<i>Albula</i> sp.	20	19	1	Fig. 3A
ANGUILLIFORMES				
Family Heterenchelyidae				
<i>Pythonichthys colei</i>	16	11	5	Fig. 3B
Family Congridae				
<i>Ariosoma nonsector</i>	30	20	10	Fig. 3C
<i>Paraconger sector</i>	35	27	8	Fig. 3D
SILURIFORMES				
Family Ariidae				
<i>Arius?</i> sp.	1	0	1	Fig. 3E
OPHIDIIFORMES				
Family Ophidiidae				
<i>Preophidion meyeri</i>	1	0	1	Fig. 3F
<i>Sirembo? granus</i>	153	131	22	Fig. 3G
PERCIFORMES				
Family Centropomidae				
<i>Centropomus?</i> sp.	1	1	0	Fig. 3H
Family Haemulidae				
<i>Orthopristis americana</i>	16	8	8	Fig. 3I
ACANTHURIFORMES				
Family Sciaenidae				
<i>Jefitchia claybornensis</i>	1959	1948	11	Figs. 3J–3K
<i>Eosciaena ebersolei</i>	10	9	1	Figs. 3L–3N; 4A
<i>Sciaena intermedia</i>	272	272	0	Figs. 4B–4E
<i>Sciaena</i> aff. <i>S. pseudoradians</i>	2253	2247	6	Figs. 4F–4K
SPARIFORMES				
Family Sparidae				
<i>Sparus?</i> sp.	1	1	0	Fig. 4L
Non-identifiable specimens	1	0	1	–
Total specimens for site	4768	4693	75	–

Paleogene formations of the Gulf and Atlantic coastal plains, but it rarely ever represents a significant portion of the assemblage (Breard & Stringer, 1995; Nolf & Stringer, 2003; Ebersole *et al.*, 2019). The rare occurrence of the species is well illustrated by the findings of Müller (1999) in his examination of approximately 12,000 Paleogene and Neogene otoliths of the US Atlantic Coastal Plain that indicated only 11 specimens. The abundance of *Pythonichthys colei* in the Clinchfield Formation is significantly higher at 6.67% of the assemblage and may be related to paleoenvironmental conditions. An extremely atypical abundance of *Pythonichthys colei* (over 20%) was

reported in the Clayton Formation (Paleocene, Danian) otolith assemblage in Arkansas by Schwarzhans & Stringer (2020). Heterenchelyids or mud eels are presently rare in the Atlantic and Gulf of Mexico and not well studied according to Smith *et al.* (2012).

Family CONGRIDAE Kaup, 1856

Genus *Ariosoma* Swainson, 1838

Ariosoma nonsector Nolf & Stringer, 2003

Fig. 3C (GCVP 19909)

Description

A total of 30 specimens (20 surface; 10 bulk) were assigned to the congrid *Ariosoma nonsector* (sensu Nolf & Stringer, 2003). The outline of the species is primarily oval (sensu Smale *et al.*, 1995), which is result of the presence of prominent dorsal domes (i.e., height of otolith approaches that of the length because of the middorsal expansion). There is often some concavity at the posterodorsal margin. The inner face is mainly smooth and convex with a wide, only slightly incised, undivided sulcus. The sulcus is long (about 85% of the inner face length) and filled with colliculum (except for backward curving ostial channel). The outer face is mainly smooth and convex.

Discussion

Ariosoma nonsector (as defined by Nolf & Stringer, 2003) is widely distributed across the Gulf Coastal Plain in Paleogene sediments (Stringer & Breard, 1995; Ebersole *et al.*, 2019). It was one of the most abundant species in the lower sample of the upper Eocene (Priabonian) Yazoo Clay in Louisiana with 577 specimens or 10.9% of the total (Nolf & Stringer, 2003). The specimens of *Ariosoma nonsector* from the Clinchfield Formation have several characteristics in common with *Ariosoma* as defined by Schwarzhans (2019b). These include an backward curving ostial channel and the middorsal expansion. The Eocene specimens are believed to be a precursor to the Oligocene specimens of *Ariosoma nonsector* (Ebersole *et al.*, 2021), but all of the Paleogene congrids require review based on the work of Schwarzhans (2019b) on extant representatives of the Congridae.

Genus *Paraconger* Kanazawa, 1961

Paraconger sector (Koken, 1888)

Fig. 3D (GCVP 19908)

Description

Thirty-five specimens (27 surface; 8 bulk) were identified as *Paraconger sector*. The outline of *Paraconger sector* is somewhat oblong but greatly affected by the anterodorsal dome. The margins tend to smooth with a tapered posterior margin. The inner face is usually smooth and convex with a fairly wide, slightly incised, colliculum-filled sulcus with a distinct ostial channel. There is no clear division of the ostium and cauda, which is typical of congrid otoliths. The outer face is smooth and convex, except for a shallow dorsoventrally oriented depression.

Discussion

The distribution of *Paraconger sector* in the Gulf Coastal Plain is very similar to that of *Ariosoma nonsector* described above. The abundance of *Paraconger sector* is typically much less than the coeval *Ariosoma nonsector* (Breard & Stringer, 1995; Nolf & Stringer, 2003; Ebersole *et al.*, 2019). However, in the Clinchfield Formation bulk sample, the two species were almost

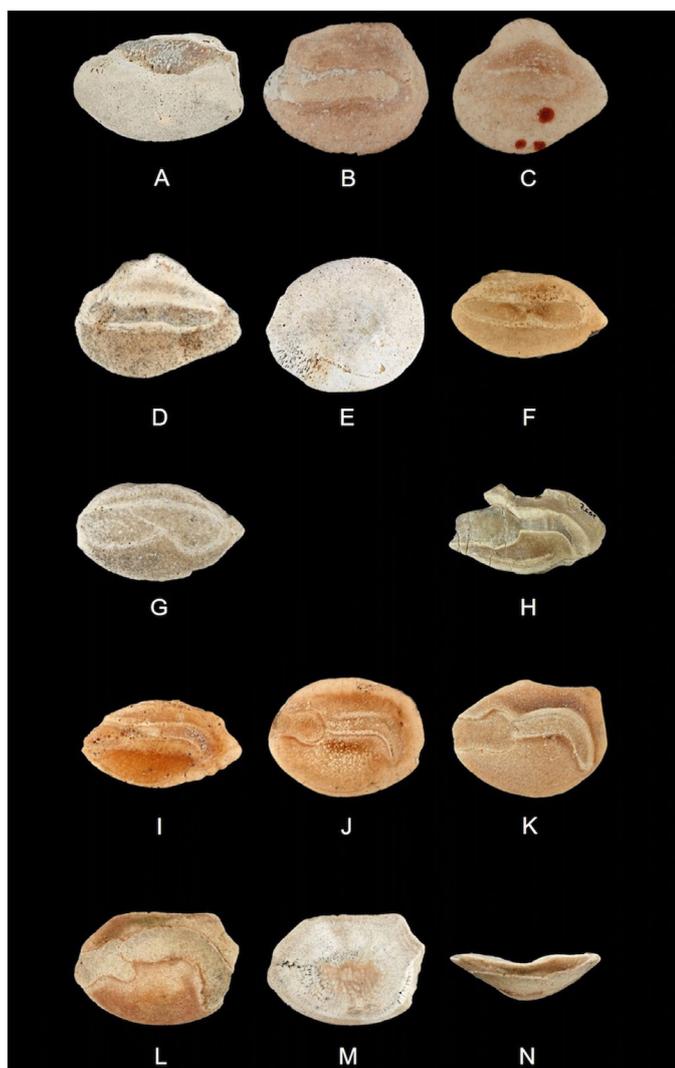


Figure 3. Taxa of bony fishes from the Hardie Mine site, Clinchfield Formation (Eocene, Bartonian). All views are of the right inner face except for E, which is the anti-macular side, and M and N, which are outer face and dorsal views, respectively. Length of each specimen is given in mm. F, G, H, and L have been reversed in order to have right views of the sagittae. **A.** *Albula* sp., 21.48 mm (GCVP 19904), **B.** *Pythonichthys colei*, 3.39 mm (GCVP 19905), **C.** *Ariosoma nonsector*, 3.15 mm (GCVP 19909), **D.** *Paraconger sector*, 3.11 mm (GCVP 19908), **E.** *Arius?* sp., 6.61 mm (GCVP 19907), **F.** *Preophidion meyeri*, 3.16 mm (GCVP 19912), **G.** *Sirembo? granus*, 4.72 mm (GCVP 19906), **H.** *Centropomus* sp., 34.82 mm (BCGM 7025), **I.** *Orthopristis americana*, 4.84 mm (GCVP 19910), **J.** *Jefitchia claybornensis*, 3.91 mm (GCVP 19902), **K.** *Jefitchia claybornensis*, 7.30 mm (GCVP 19903), **L.** *Eosciaena ebersolei* sp. nov. (**holotype**), 13.18 mm (GCVP 19914), **M.** *Eosciaena ebersolei* sp. nov. (**holotype**), 13.18 mm (outer face) (GCVP 19914), **N.** *Eosciaena ebersolei* sp. nov. (**holotype**), 13.18 mm (dorsal view) (GCVP 19914).

the same. *Paraconger sector* and *Ariosoma nonsector* were originally described as one species by Koken (1888) as the type material of Koken's *Otolithus (Platessae) sector* was a mixture of the two (pl. 17, fig. 14 is *Paraconger sector*, whereas figs. 15 and 16 belong to *Ariosoma nonsector*). *Ariosoma nonsector* was separated by Nolf & Stringer (2003) in their study of the otoliths from the upper Eocene (primarily Priabonian) Yazoo Clay in Louisiana.

Order SILURIFORMES Cuvier, 1817

Family ARIIDAE Bleeker, 1858

Genus *Arius* Valenciennes in Cuvier & Valenciennes, 1840

Arius? sp.

Fig. 3E (GCVP 19907)

Description

A single specimen from a bulk sample was identified as *Arius?* sp. The Clinchfield Formation *Arius?* sp. lapillus is primarily circular in shape (sensu Smale *et al.*, 1995) with a projection on the margin that gives it more of an elongated shape. Normally, the convex macular side has several morphological features, while the anti-macular side is essentially smooth and featureless. Unfortunately, the one Clinchfield Formation specimen is too leached to show the subtle features on the macular side. Typically, the anti-macular has few features, but sometimes due to erosion, lightly impressed radial furrows that extend primarily from the center to the margins may be present. Some of these radial furrows are visible on the Clinchfield Formation specimen.

Discussion

The specimen is the lapillus or utriculith (the otolith in the utriculus of the fish's labyrinth) rather than the typically utilized sagitta. The order Siluriformes is one of the exceptions in which the lapillus is large, especially in the family Ariidae or sea catfishes (Nolf, 2013). Ariid lapilli tend to be uncommon in many of the Paleogene and Neogene formations in the Gulf and Atlantic coastal plains (Nolf & Dockery, 1993; Stringer & Bell, 2018; Ebersole *et al.*, 2019; Stringer *et al.*, 2020a). Ariids were very rare in the upper Eocene Yazoo Clay in Louisiana with only two lapilli from the 5599 otoliths recovered (Nolf & Stringer, 2003). This is also the case in the Clinchfield Formation with only one specimen from all of the collections. However, there are Paleogene formations in the Gulf Coastal Plain where ariids are very abundant such as in the early Paleocene (Danian) Clayton Formation in Arkansas (Schwarzahns & Stringer, 2020). In this formation, two ariid species account for 36.89% of the otolith assemblage. In the Cretaceous, siluriform distribution often varies greatly in different formations and appears to be in an inverse relationship with the number of beryciforms (Stringer & Schwarzahns, 2021)

Order OPHIDIIFORMES (sensu Nelson *et al.*, 2016)

Family OPHIDIIDAE Rafinesque, 1810

Genus *Preophidion* Frizzell & Dante, 1965

Preophidion meyeri (Koken, 1888)

Fig. 3F (GCVP 19912)

Description

A single otolith recovered from a bulk sample was classified as *Preophidion meyeri*. This ophidiid or cusk-eel, one of two found in the Clinchfield Formation, is oblong to elliptic in outline (sensu Smale *et al.*, 1995) with primarily smooth

margins. The sagitta is characteristically biconvex with a distinct, lightly impressed sulcus on the inner face. The sulcus is fairly narrow and extends most of the length of the inner face. The dorsal and ventral margins of the sulcus are almost parallel. The completely enclosed sulcus is divided into an ostium and cauda and is marked by incised lines. Both the ostium and cauda are filled with colliculum. The convex outer face can be sculptured to undulating.

Discussion

Preophidion meyeri is one of the most widely distributed and common species in the Gulf Coastal Plain Paleogene (Frizzell & Dante, 1965; Breard & Stringer, 1995; Breard & Stringer, 1999; Nolf, 2013; Schwitzer *et al.*, 2014; Ebersole *et al.*, 2019). In some of the Alabama Lisbon Formation (middle Eocene) otolith assemblages, *Preophidion meyeri* accounts for nearly 50% of the total specimens (Ebersole *et al.*, 2019). In the upper Eocene (Priabonian) Yazoo Clay in Louisiana, 3120 specimens of the species were collected in the lower sample, which accounted for 58.9% of the total (Nolf & Stringer, 2003). Therefore, the one specimen from the Clinchfield Formation is highly unusual in the Gulf Coast Eocene, especially since it is commonly found with the taxa present in the Clinchfield otolith assemblage. This occurrence is examined in detail later in the paleoecology discussion.

Genus *Sirembo* Bleeker, 1857

Sirembo? granus Müller, 1999

Fig. 3G (GCVP 19906)

Description

A total of 153 specimens (131 surface; 22 bulk) were assigned to *Sirembo? granus*, the second and most abundant ophidiid from the Clinchfield Formation. The species is very similar to the coeval *Preophidion meyeri*. The species has an oblong to suboval shape and is biconvex with smooth margins. The sagitta is at least twice as long as it is wide with a strongly convex, very smooth inner face. The inner face is characterized by an obvious, distinct, lightly impressed, divided sulcus. *Sirembo? granus* is distinguished from *Preophidion meyeri* by the strong constriction of the lower margin of the sulcus near its center. Furthermore, in larger specimens, the ostium and cauda become greatly enlarged, which exaggerates the lower margin constriction. However, very small, as well as eroded, ophidiid sagittae can be very difficult to delineate to species. The outer face is convex and typically strongly sculptured. The dorsal and medial portions tend to be much more strongly convex. The outer face thins noticeably on the ventral margin.

Discussion

Sirembo? granus was first described as “*genus Sirembinorum*” *granus* by Müller (1999) from the Piney Point Formation (middle Eocene, Claibornian) in Virginia. Nolf (2013) noted *Sirembo? granus* (as “*Sirembinus*” *granus*) from the middle and upper Eocene formations of Louisiana and Virginia. Nolf & Stringer (2003) also reported *Sirembo? granus* (as “*genus Sirembinorum*” *granus*) from the lower sample of the Yazoo Clay Formation (upper Eocene, Priabonian) in northeastern Louisiana. It represented 1.44% of the total number, while *Preophidion meyeri* accounted for 58.94% in the same sample. This is more typical of the expected abundance of the two species. Yet, in the Clinchfield Formation bulk sample, *Sirembo? granus* is much more abundant (29.33% versus 1.33%). This unusual trend will be addressed later.

Order PERCIFORMES

Family CENTROPOMIDAE Poey, 1867

Genus *Centropomus* Lacepède, 1802*Centropomus* sp.

Fig. 3H (BCGM 7025)

Description

Two specimens from the Clinchfield Formation were assigned to *Centropomus*. One of the specimens is approximately 18 mm in length although it is broken. It appears to be about 65% complete. The anterior portion is broken, but the posterior margin appears to be slightly tapered but still rounded. The inner face is convex. Only a small portion of the ostium is present, but the entire cauda is preserved. The cauda has a sub-horizontal portion and a more downturned portion (at approximately 45°). The specimen shows some similarity to the present-day *Centropomus undecimalis* known from the Gulf of Mexico. However, the sub-horizontal portion of the Clinchfield Formation specimen is not as long, and the posterior is more downturned. The specimen is extensively eroded and leached and affects the morphological features. A second specimen from the Hardie Mine was recovered by D. Cicimurri (Curator of the Natural History Museum of the South Carolina State Museum). The *Centropomus sagitta* (Fig. 3H) was an enormous specimen that measured 34.82 mm in length, and although broken, essentially all of the pieces were present (except for slight damage to the anterodorsal and dorsal margins). The sulcus was completely preserved and allowed its assignment to *Centropomus*. The specimen also demonstrated that convexity of the inner face increased dramatically with greater length.

Discussion

An otolith specimen of a modern *Centropomus undecimalis* that was 30.17 mm in length (supplied by R. Taylor with the Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute at that time) was removed from a fish that was 103.4 cm in length and weighed 11.7 kg. This gives an estimate of the size of the large Hardie Mine centropomid specimen, but the length of the Clinchfield Formation otolith was almost 14% greater.

Representatives of the Centropomidae are not well known in the fossil record. Nolf (2013) lists only four centropomids known as fossils worldwide. The examination of 5559 otoliths from the upper Eocene (primarily Priabonian) Yazoo Clay at Copenhagen, Louisiana by Nolf & Stringer (2003) yielded no centropomids. However, since that investigation, *Centropomus* sp. has been reported from the upper Eocene (primarily Priabonian) Yazoo Clay from Louisiana by Stringer & King (2010). The otolith, while not as large as the Clinchfield Formation *Centropomus*, was still very large at 30.58 mm.

Family HAEMULIDAE

Genus *Orthopristis* Girard 1858*Orthopristis americana* (Koken, 1888)

Fig. 3I (GCVP 19910)

Description

Sixteen specimens (8 surface; 8 bulk) were recovered and assigned to the haemulid *Orthopristis americana*. The sagitta of this species is oval to elliptic in outline (sensu Smale *et al.*, 1995) with a fairly prominent, somewhat blunt rostrum with excisura. The strongly convex inner face has a conspicuous sulcus (heterosulcoid type) that extends for at least 75% of the

length of the otolith. The fairly narrow, subquadrate-shaped ostium is significantly shorter than the cauda. The very narrow cauda is approximately 2.5 times longer than the ostium. The posterior portion of the cauda is bent sharply downward. A ridge-like crista superior is conspicuous above the horizontal portion of the cauda, and a depressed area is found above the crista superior. The somewhat concave outer face tends to be slightly irregular.

Discussion

Orthopristis americana was first reported as *Otolithus (Carangidarum) americana* by Koken (1888) from the Eocene (Jackson Group) in the Gulf Coast. The species appears to be much more common in the Gulf Coastal Plain than in the Atlantic Coastal Plain. Müller (1999) only reported three specimens assigned to *Orthopristis* in his analysis of over 12,000 fossil otoliths from the Atlantic Coastal Plain. However, the species was a significant component of the upper Eocene (primarily Priabonian) Yazoo Clay Formation otolith assemblage from Copenhagen, Louisiana, with 230 specimens in the lower sample (Nolf & Stringer, 2003). Likewise, Green (2002) reported that *Orthopristis americana* accounted for 18.17% of the total number of otoliths in the middle Eocene (Bartonian) Moodys Branch Formation at the Heison Landing locality along the Ouachita River in Caldwell Parish, Louisiana.

Order ACANTHURIFORMES (sensu Nelson *et al.*, 2016)

Family SCIAENIDAE Cuvier, 1829

Genus *Jefitchia* Frizzell & Dante, 1965*Jefitchia claybornensis* Frizzell & Dante, 1965

Figs. 3J–K (GCVP 19902–19903)

Description

A total of 1959 specimens (1948 surface; 11 bulk) were assigned to the sciaenid *Jefitchia claybornensis*. The species is mainly oval in outline, and the margins may be somewhat crenulate to lobed in small specimens (< 3 mm) to smooth in larger specimens. The convex and smooth inner face has a very prominent sulcus (heterosulcoid type) that extends for approximately 90% of the length of the otolith. The moderately narrow ostium is filled with colliculum and extends for about 30% of the inner face length. The long and narrow cauda has horizontal and downturned portions. The downturned portion forms an angle of around 120° with the horizontal portion. There is a slight depression above the horizontal portion of the cauda. The outer face is almost flat or slightly concave and often sculptured.

Discussion

Jefitchia claybornensis is common in many of the upper middle to upper Eocene formations of the Gulf Coastal Plain (Stringer, 1979; Stringer, 1986; Breard & Stringer, 1995). In the lower bulk sample (450 kg) of the upper Eocene (primarily Priabonian) Yazoo Clay collected by Nolf & Stringer (2003), 631 specimens of the 5293 otoliths were *Jefitchia claybornensis* (11.92% of the total). In the bulk sample of the Clinchfield Formation from the Hardie Mine, *Jefitchia claybornensis* was the second most abundant species (14.67% of the otolith assemblage). Only the ophidiid, *Siremba? granus* was more abundant (29.33%). Although a small number of putative juveniles of *Jefitchia claybornensis* were present in the Clinchfield Formation otolith assemblage (approximately 3.5 mm), the vast majority of the specimens represent adults.

Genus *Eosciaena* gen. nov.

urn:lsid:zoobank.org:act:848514B9-8326-4E07-A213-4BBECFC1DE22

Type species: *Eosciaena ebersolei* sp. nov.

Etymology: Referring to the Eocene in which the species is found and *Sciaena* in reference to its relationship to the sciaenids.

Diagnosis: A massive, large, but prone to breakage, otolith which is placed in the order Acanthuriformes and the family Sciaenidae (sensu Nelson *et al.*, 2016), and defined by the following combination of characters. The otolith outline is approximately oval with a short, rounded anterior margin, prominent and distinct antero- and posterodorsal angles, a tapered posterior tip, and a broadly rounded ventral margin. The otolith is strongly convex along a medial, horizontal axis. The sulcus is long (90% of inner face), lightly impressed, and filled with colliculum. The ostium opens onto the anterior margin. The greatest height of the ostium is just before the intersection with the cauda. At this point, the ostium height is approximately 1.5 times greater than the maximum height of the cauda. The cauda has a sub-horizontal section and a downward turned section. The sub-horizontal section is slightly longer than the downturned section. The caudal tip is expanded. There is no depressed area above the sulcus or a ventral furrow.

Discussion: The obvious and strongly heterosulcoid-type sulcus with the expanded ventral portion of the ostium and the prominently downturned cauda is highly characteristic of the family Sciaenidae. Furthermore, the massive size of the sagitta is common in the Sciaenidae, both modern and fossil. These enigmatic sciaenid otoliths do not match any of the sciaenids known from the USA Holocene as noted by Nolf & Stringer (2003). Furthermore, the highly distinct and unusual sagitta does not match any sciaenids known from any other bioprovinces (Schwarzhan, 1993; pers. comm., 2021). The one broken, but complete, somewhat worn specimen recovered by Nolf & Stringer (2003) from the upper Eocene Yazoo Clay from Copenhagen, Louisiana, USA, was tentatively classified as “genus aff. *Nibea*” sp. and was not formally described awaiting the recovery of further specimens (13 additional specimens have now been obtained).

Species: The type species *Eosciaena ebersolei* has been recovered from the upper middle Eocene (Bartonian) Riggins Mill Member of the Clinchfield Formation of Georgia. The species is also known from the upper middle Eocene to upper Eocene (upper Bartonian to upper Priabonian) Tullos Member of the Yazoo Clay of Louisiana, USA, and is the only species allocated to the genus *Eosciaena* at this time.

Eosciaena ebersolei sp. nov.

Figs. 3L–N (GCVP 19914); Fig. 4A (SC2013.44.86)

urn:lsid:zoobank.org:act:B8D3577F-DAED-40EC-933D-52F0D26BB907

Holotype. GCVP 19914 (Figs. 3L–N).

Paratype. SC2013.44.86 (Fig. 4A) (same locality as holotype).

Type locality. Hardie Mine, 3.2 km northwest of the post office in Gordon, Wilkinson County, Georgia, USA (34.5071, -84.8785).

Age. Clinchfield Formation, middle Eocene and upper Bartonian (a very small portion of the uppermost Clinchfield may be lower Priabonian; see discussion in Geological and Stratigraphical section).

Etymology. Named in honor of Jun Ebersole (Collections Manager, McWane Science Center, Birmingham, Alabama, USA) for his extensive contributions to the study of cartilaginous and bony fishes, especially in Alabama and the Gulf Coast Province.

Other specimens. Nine other specimens were examined (3 complete and 6 partial) from the Hardie Mine (Clinchfield Formation). GCVP 19915, MSC 43418, and IRSNB P7027, which are all from the upper Eocene (primarily Priabonian) Yazoo Clay from Copenhagen, Caldwell Parish, Louisiana, USA (32.1025, -92.0779), were also examined and assigned to *Eosciaena ebersolei*.

Diagnosis. Fairly massive, approximately oval otoliths with well-defined anterodorsal and posterodorsal angles and a ratio OL:OH of 1.29–1.77. Ventral margin of otolith fairly deep, deepest just posterior to center. Upper and lower ostium margins greatest at posterior just prior to intersection with cauda. Cauda is wide with sub-horizontal and downturned portions. Caudal tip is widened and almost on posteroventral margin.

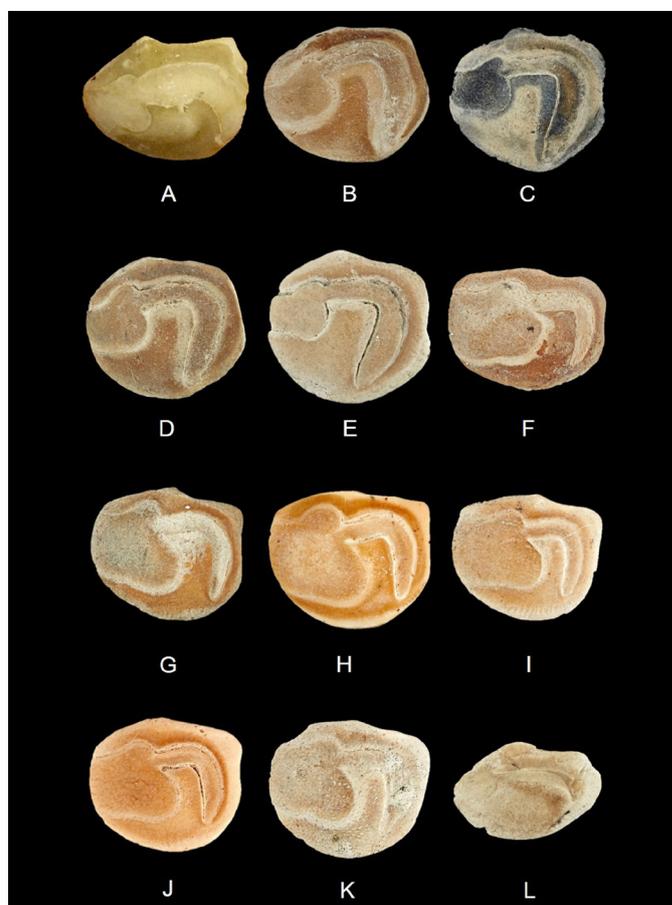


Figure 4. Taxa of bony fishes from the Hardie Mine site, Clinchfield Formation (Eocene, Bartonian). All views are of the right inner face. Length of each specimen is given in mm. A, C, and E have been reversed in order to have right views of the sagittae. **A.** *Eosciaena ebersolei* sp. nov. (paratype), 17.25 mm (SC2013.44.86), **B.** *Sciaena intermedia*, 11.99 mm (GCVP 19891), **C.** *Sciaena intermedia*, 10.07 mm (GCVP 19892), **D.** *Sciaena intermedia*, 7.14 mm (GCVP 19893), **E.** *Sciaena intermedia*, 6.15 mm (GCVP 19894), **F.** *Sciaena* aff. *S. pseduoradians*, 13.02 mm (GCVP 19896), **G.** *Sciaena* aff. *S. pseduoradians*, 10.68 mm (GCVP 19897), **H.** *Sciaena* aff. *S. pseduoradians*, 8.21 mm (GCVP 19898), **I.** *Sciaena* aff. *S. pseduoradians*, 7.16 mm (GCVP 19899), **J.** *Sciaena* aff. *S. pseduoradians*, 4.76 mm (GCVP 19900), **K.** *Sciaena* aff. *S. pseduoradians*, 6.39 mm (GCVP 19901), **L.** *Sparus?* sp., 6.53 mm (GCVP 19911).

Description

These are fairly massive, long otoliths that reach a size of at least 17.25 mm in length (broken specimens could have been larger) (the holotype is 13.18 mm long). The OL:OH ratio is variable ranging from 1.29–1.77 with most around 1.40–1.50 (based on 8 complete specimens). The ratio OH:OT is from 1.60–2.17. The greatest thickness is near the center of the otolith just below the anterior portion of the cauda. Otolith outline is mainly oval (sensu Smale *et al.*, 1995), and the margins are smooth. The anterior margin is short and rounded. The anterodorsal margin is long and straight, slanted at approximately 45° toward the posterior, and forms a distinct angle with the dorsal margin. The dorsal margin is mainly straight, slanted very slightly toward the posterior, and forms a prominent angle with the posterodorsal margin. The posterodorsal angle is concave, while the posterior margin is short with a tapered tip. The ventral margin is broadly rounded with its greatest depth just posterior to the center of the margin. The otolith is strongly convex along a medial horizontal axis. The sulcus is long (90% of inner face), not deeply impressed, and filled with colliculum. The ostium appears to open on the anterior margin. The greatest height of the ostium is just before the intersection with the cauda. At this point, the ostium height is approximately 1.5 times greater than the maximum height of the cauda. The cauda is longer (approximately 1.5 times longer than the ostium). The cauda has a sub-horizontal section and a downward-turned section. The sub-horizontal section is slightly longer than the downturned section. The caudal tip is expanded, which almost touches the posteroventral margin. There is no depressed area above the sulcus or a ventral furrow. The outer face is strongly and obviously concave with the greatest concavity in the center. The outer face is somewhat irregular with three ridges that extend from the margin toward the center. These ridges are located at the intersection of the anterodorsal and dorsal margins, the dorsal and posterodorsal margins, and the posterior margin.

Comparisons

Eosciaena ebersolei sp. nov. has a heterosulcoid-type sulcus that is typical of many sciaenids with its expanded ventral portion of the ostium and prominently downturned cauda. The massive size of the sagitta is also characteristic of many representatives in the family Sciaenidae. However, there are no known sciaenids, modern or fossil, that have the shape and orientation of the sulcus of *Eosciaena ebersolei*. Nolf and Stringer (2003) postulated that it may have affinities with *Nibea*, but additional specimens indicated that the resemblance was superficial and that the ostium and cauda have significant and salient differences. Therefore, *Eosciaena ebersolei* has no meaningful comparisons.

Discussion

Although these otoliths are fairly massive, they have a tendency to break because of their convexity and corresponding concavity (6 of the 14 specimens are broken in a similar manner and location). Most of the specimens appear to be adults with no small specimens recovered (the shortest length of a complete specimen was 11.75 mm). The holotype (GCVF 19914, Fig. 3L–N) and paratype (SC2013.44.86, Fig. 4A), as well as GCVF 19915, MSC 43418; and IRSNB P7027, are essentially complete. At this time, no other species are assigned to this genus. Additionally, the stratigraphic and geographic distributions of the species are not well understood at this point. The species has been rare in known assemblages with only eight complete and six partial sagittae from the Clinchfield Formation (Georgia) and the Yazoo Clay (Louisiana).

Genus *Sciaena* Linnaeus, 1758

Sciaena intermedia (Koken, 1888)

Figs. 4B–E (GCVF 19891–19894)

Description

A total of 272 specimens, all from surface collections, were identified as *Sciaena intermedia*. The outline of the species can be described as almost subrectangular. The margins tend to be smooth although very small, well-preserved specimens may be sinuate. The height of the otolith is about 85% of the length. The inner face is convex with a prominent sulcus (heterosulcoid type), which extends for almost 90% of the length of the otolith. The ostium covers about 35% of the length of the inner face is not greatly expanded ventrally. The height of the cauda is less than 50% of the height of the ostium. The cauda has a horizontal portion and a downturned portion. The length of these portions are usually about the same. The outer face is can be almost flat or slightly concave.

Discussion

This species was first identified by Koken (1888) as *Otolithus (Sciaenidarum) intermedius* in the Eocene of the US Gulf Coast. It was reported by Frizzell & Dante (1965) in several middle Eocene formations in Texas and Alabama (under the genus *Corvina*). The species has been placed in a number of different genera (Ebersole *et al.*, 2019), but it appears to best fit in *Sciaena*. Nolf (2013) noted it as occurring in the middle Eocene, and it is noted as one of the most abundant taxa in the Claiborne Group (Lisbon Formation and Gosport Sand) of Alabama (Ebersole *et al.*, 2019).

Sciaena aff. *S. pseudoradians* (Dante & Frizzell in Frizzell & Dante, 1965)

Fig. 4F–K (GCVF 19896–19901)

Description

A total of 2253 specimens (2247 surface; 6 bulk) were assigned to *Sciaena* aff. *S. pseudoradians*. The outline of this species is subrectangular and resembles the shape of *Sciaena intermedia*. The margins are typically smooth, and the inner face is convex. The inner face is characterized by a very large, prominent sulcus of the heterosulcoid type. The ostium is extremely large, especially compared to the cauda. The ostium extends from near the anterodorsal margin well down into the ventral field and is largest at the posterior. The posteroventral portion of the ostium extends underneath the cauda. The cauda is approximately 20% of the height of the ostium (i.e., narrow in comparison). The cauda has a horizontal and downturned component. The horizontal portion appears to shorten in length compared to the downturned portion during ontogenetic development. The irregular outer face is convex but not nearly as much as the inner face.

Discussion

Sciaena pseudoradians was first named by Dante & Frizzell in Frizzell & Dante (1965) as *Covina pseudoradians* from specimens from the Byram Formation (Oligocene, Rupelian) in Mississippi. It is known from numerous Oligocene formations in Mississippi, Louisiana, and Alabama (Stringer & Worley, 2003; Worley, 2004; Stringer & Starnes, 2020). Nolf & Stringer (2003) designated a sciaenid from the upper Eocene Yazoo Clay as *Sciaena* aff. *S. pseudoradians*. It was not nearly as abundant as the coeval *Jefitichia claybornensis*. However, in the lower sample at the Copenhagen site, it did account for 78 specimens (1.47%) of the 5293 otoliths. The large sagittae of

this species account for more surface-collected specimens than any other species in the Clinchfield Formation. However, this is related to a size-collecting bias, because in the bulk samples, there are several other taxa that are more abundant. However, it still represents 8% of the total number of specimens in the bulk sample and is important component of the faunal assemblage at the Hardie Mine.

Order SPARIFORMES (sensu Nelson *et al.*, 2016)

Family SPARIDAE Rafinesque, 1818

Genus *Sparus* Linnaeus, 1758

Sparus? sp.

Fig. 4L (GCVP 19911)

Description

This genus is represented by a single surface-collected specimen. The outline of the specimen is oval (sensu Smale *et al.*, 1995), and the margins are mainly irregular with some small lobes. The slightly convex inner face is characterized by a conspicuous sulcus (heterosulcoid type) that extends across about 85% of the length of the otolith. The ostium, which opens on the anterior margin, is almost rectangular in shape and larger in height than the cauda but not by much. The cauda is mainly horizontal with a short downwardly turned posterior (about 45° from the horizontal). There is a depressed area above the sulcus that is somewhat irregular in shape, and there is a faint indication of a ventral furrow. The outer face is concave.

Discussion

The Clinchfield Formation specimen shows similarity to *Sparus? elegantulus*, which was first named by Koken (1888). *Sparus? elegantulus* was reported by Nolf & Stringer (2003) from the upper Eocene (primarily Priabonian) Yazoo Clay in Louisiana, where it was a minor component in the lower sample accounting for 129 specimens (2.44%) of the 5293 otoliths. Unfortunately, the Clinchfield Formation specimen is not preserved well enough to make a species designation.

DISCUSSION

Characteristics of the Clinchfield Formation otolith assemblage

The species diversity of the Clinchfield Formation was examined to obtain a characterization of the otolith assemblage (Table 2). Only data from bulk samples are utilized to eliminate bias due to size differences. Within species diversity, the number of species (richness) found and the relative abundance of each species present (evenness) was determined. The number of species or richness for the Clinchfield Formation is 13 taxa identified to at least the genus level (1 of the 14 taxa was found only in the surface collection). All of the taxa are identified on the basis of sagittae except for one (*Arius?* sp.) that is recognized by the lapillus or utricular otolith. This is not a very rich otolith assemblage compared to other Eocene assemblages in the Gulf Coast. For example, the upper Eocene Yazoo Clay from Caldwell Parish in Louisiana had 44 actinopterygian taxa recognized on the basis of otoliths (Nolf & Stringer, 2003; Stringer & King, 2010). Table 2 was utilized to determine the relative abundance (evenness) of each species in the Clinchfield Formation otolith assemblage since it was based on a bulk sample rather than surface collections, which

have value but not for statistical analysis. Table 2 indicates that the assemblage exhibits evenness although one species, *Sirembo? granus*, represents 29.33% of the total specimens. However, no other species represents more than 14.67% of the total, and 6 of the 13 taxa range from 6.67%–14.67%. So, there is a relative evenness to the distribution.

Taxa from three orders of fishes, the Anguilliformes, Ophidiiformes, and the Acanthuriformes, are the most common and collectively account for 85.34% of the total specimens (Table 2). However, it must be considered that there are only six orders represented in the bulk sample. The order Anguilliformes consists of representatives from the Heterenchelyidae and Congridae and comprise 30.67% of the specimens. The order Ophidiiformes has taxa from the family Ophidiidae and constitute 30.67% of the total specimens. The order Acanthuriformes consists of four taxa from the family Sciaenidae that constitute 24.00% of the total assemblage. Not surprisingly, the most abundant specimens come from taxa within these orders (Table 2). The most abundant species are the ophidiid *Sirembo? granus*, (29.33% of the total specimens), the sciaenid *Jefitchia claybornensis* (14.67%), and the congrid *Ariosoma nonsector* (13.33%).

If the Clinchfield Formation otolith assemblage is compared to extant fishes, then it would consist of bonefishes (Albulidae), mud eels (Heterenchelyidae), conger eels (Congridae), sea catfishes (Ariidae), cusk-eels (Ophidiidae), grunts (Haemulidae), drums and croakers (Sciaenidae), and porgies (Sparidae). The actinopterygian otolith assemblage of the Clinchfield Formation in Georgia consists of only 14 taxa (13 in bulk sample), which are fairly evenly distributed. Although not a large number of taxa (14 taxa), it is much greater than what was previously known based on osteological remains by Westgate (2001), which was only 4 species.

Comparison of Clinchfield Formation assemblage to other assemblages

As previously noted, there has been considerable discourse on the exact age of the Clinchfield Formation and its stratigraphic relationships to other upper Claibornian and lower Jacksonian formations. In order to gain further insight into these possible correlations, the otolith assemblage of the Clinchfield Formation is compared to otolith assemblages of other middle Eocene and upper Eocene formations in Alabama, Mississippi, and Louisiana using the percentage similarity measurement. The percentage similarity measurement was calculated using data from Table 2 for the Clinchfield Formation (bulk sample) and Table 3 for the three Moodys Branch Formation sites in Louisiana and Mississippi, the Yazoo Clay site in Louisiana, and the “upper” Lisbon Formation (sensu Szabo *et al.*, 1988) in Alabama (all bulk samples).

The results of the percentage similarity measurements are shown in Table 4. The percentage similarity measurements are related to factors such as temporal parameters (formations with very similar geologic age), geographical distribution of sites (Georgia, Alabama, Mississippi, and Louisiana), paleogeography (especially proximity of coastlines and related features such as estuaries and deltas), and paleoecology (including factors that may affect or change paleoenvironmental parameters including temperature, substratum, water clarity, salinity, dissolved oxygen, and nutrients).

Examination of Table 4 reveals some very interesting, if not perplexing, results. The percentage similarity of the Clinchfield

Formation otolith assemblages to those of the Moodys Branch Formation (sites 1–3) are 30.36%, 39.85%, and 40.96% (respectively) and the Yazoo Clay (33.25%). The Clinchfield otolith assemblage is most similar to the assemblage from the Mississippi location but not greatly. Overall, the Clinchfield otoliths are not greatly similar to or greatly unlike those of the Moodys Branch and Yazoo Clay. What is unusual is that the two sites in closest proximity (sites 1 and 2 in Louisiana, which are both in Caldwell Parish) only indicate a similarity of 48.06% even though they share 15 taxa. Even more intriguing is that the Moodys Branch from site 1 (Bunker Hill) in Louisiana has a percentage similarity of only 28.55% with the Moodys Branch site 3 (Techeva Creek) in Mississippi with 11 shared taxa, although the paleoenvironments appear to be similar. This similarity percentage is less than the Clinchfield Formation assemblage with the sites in Mississippi and Louisiana. However, the Moodys Branch site 2 (Heison Landing) in Louisiana has a significant percentage similarity of 71.83% with the Moodys Branch site 3 (Techeva Creek) in Mississippi with 12 shared taxa (only 1 taxon more than between sites 1 and 3). Examination of the taxa in the percent similarity of sites 1 and 3 indicate that the high value is primarily related to the shared abundance of the sciaenid *Jefitchia claybornensis* (42.39%) and the haemulid *Orthopristis americana* (18.17%). This could be related to subtle, but significant, differences in paleoecological parameters. There are also ten other shared taxa, but they are all less than 3% each.

The percent similarity analysis of the Clinchfield Formation otoliths compared to that of the “upper” Lisbon Formation is certainly the most enigmatic. Although the “upper” Lisbon

Formation locality is closer geographically to the Hardie Mine than any of the other sites, the percent similarity between the two is only 6.61% with only four shared taxa. This indicates that there is very little similarity between the otolith assemblages of the Clinchfield and Lisbon formations and that great differences exist. However, the Lisbon Formation has fairly significant similarity with the Moodys Branch assemblages in Louisiana (sites 1 and 2) and the Yazoo Clay assemblage in Louisiana (site 4) with 52.36%, 54.74%, and 55.41% respectively. Yet, the Lisbon Formation otoliths have only a 9.00% similarity (6 taxa in common) with the Moodys Branch assemblage in Mississippi (site 3). There is very little temporal differences between the Moodys Branch sites 1, 2, and 3. So, this should not be a factor. Likewise, the “upper” Lisbon Formation locality is actually closer geographically to the Moodys Branch site in Mississippi than to sites 1 and 2 in Louisiana. It appears that the profound differences in similarity are not geographical either. This would imply that there are other parameters accounting for the differences.

Biostratigraphic and biogeographic implications

The only taxon found in both the Clinchfield Formation in Georgia and the upper Lisbon Formation in Alabama that is not represented in the Moodys Branch Formation and the Yazoo Clay in Mississippi and Louisiana is the sciaenid *Sciaena intermedia*. In one bulk sample from the Lisbon Formation in Choctaw County, *Sciaena intermedia* represented 19.70% of the total assemblage. Although not found in the Clinchfield

Table 2. Taxa of otoliths, percentage of total otoliths, and percentage of otoliths in each order in the bulk sample from the Hardie Mine site (middle Eocene, Bartonian), near Gordon, Georgia.

Orders (upper case, shaded) Family (lower case)	Total specimens	Percentage of total	Percent of taxa in order
ALBULIFORMES			1.33
Family Albulidae			
<i>Albula</i> sp.	1	1.33	
ANGUILLIFORMES			30.67
Family Heterenchelyidae			
<i>Pythonichthys colei</i>	5	6.67	
Family Congridae			
<i>Ariosoma nonsector</i>	10	13.33	
<i>Paraconger sector</i>	8	10.67	
SILURIFORMES			1.33
Family Ariidae			
<i>Arius?</i> sp.	1	1.33	
OPHIDIIFORMES			30.67
Family Ophidiidae			
<i>Preophidion meyeri</i>	1	1.33	
<i>Sirembo?</i> <i>granus</i>	22	29.33	
PERCIFORMES			10.67
Family Haemulidae			
<i>Orthopristis americana</i>	8	10.67	
ACANTHURIFORMES			24.00
Family Sciaenidae			
<i>Jefitchia claybornensis</i>	11	14.67	
<i>Eosciaena ebersolei</i>	1	1.33	
<i>Sciaena</i> aff. <i>S. pseudoradians</i>	6	8.00	
Unidentified specimen	1	1.33	
Total specimens - bulk sample	75	~100	~100

Formation bulk sample (Table 2), *Sciaena intermedia* was fairly abundant in surface-collected specimens (n = 272). Although the number is biased because of the size of the otolith, it still provides clear evidence of the presence of *Sciaena intermedia* in the Clinchfield Formation. Another sciaenid of notable interest in the Clinchfield Formation otolith assemblage is *Sciaena* aff. *S. pseudoradians*. It is the sixth most common species in the Clinchfield Formation representing 8.00% of the total assemblage (Table 2). It is by far the most common surface-collected otolith with 2,247 specimens. Despite its abundance in the Clinchfield Formation, it has not been reported from the Lisbon Formation in Alabama (Ebersole *et al.*, 2019).

As noted previously, the percent similarity of the Clinchfield

Formation and the Lisbon Formation was extremely low at 6.61% with only four shared taxa in the bulk samples. Additionally, there is a stark contrast in the number of species found in the Lisbon Formation in Alabama that are not known from the Clinchfield Formation (Georgia), the Moodys Branch Formation (Mississippi and Louisiana) and the Yazoo Clay (Louisiana). These include the ophidiids (*Signata stenzeli*, *Signata nicoli*, *Lepophidium? mucronatus*, *Hoplobrotula melrosensis*, *Lepophidium? lamberi*), lactariids (*Lactarius kokeni*, *Lactarius amplus*), diretmid (*Diretmus serratus*), haemulid (*Orthoprists burlesonensis*), and sciaenids (*Jefitchia copelandi*, *Ekokenia eporrecta*). It is unlikely that paleoenvironmental parameters in the Lisbon Formation and the Clinchfield Formation would account for these faunal

Table 3. Taxa and percentage of total otoliths from the Moodys Branch Formation (Louisiana and Mississippi localities), the Yazoo Clay (Louisiana locality), and the “upper” Lisbon Formation (Alabama locality). Explanation: Site 1 = Bunker Hill, Louisiana (Moodys Branch Formation); Site 2 = Heison Landing, Louisiana (Moodys Branch Formation); Site 3 = Techeva Creek, Mississippi (Moodys Branch Formation); Site 4 = Copenhagen, Louisiana (Yazoo Clay); Site 5 = Souwilpa Creek, Alabama (“upper” Lisbon Formation). *Only taxa in common with the bulk samples of the Moodys Branch or Clinchfield are shown for the Yazoo Clay. For a complete list of the Yazoo Clay taxa (n = 43), see table 1 in Nolf & Stringer (2003). **Only taxa in common with the bulk samples of the Moodys Branch, Yazoo Clay, or Clinchfield are shown for the Lisbon Formation. The entire otolith assemblage of the Lisbon Formation is described in Ebersole *et al.* (2019).

Orders (upper case, bold, shaded) Family (lower case, bold) Genus sp.	Site 1 No. of otoliths (% of total)	Site 2 No. of otoliths (% of total)	Site 3 No. of otoliths (% of total)	Site 4 No. of otoliths (% of total)	Site 5 No. of otoliths (% of total)
ANGUILLIFORMES					
Family Hetenenchelyidae					
<i>Pythonichthys coleii</i>	2 (1.12%)	3 (0.46%)	1 (0.75%)	81 (1.50%)	1 (0.51%)
Family Congridae					
<i>Ariosoma nonsector</i>	8 (4.76%)	46 (7.14%)	3 (2.26%)	577 (10.90%)	1 (0.51%)
<i>Paraconger sector</i>	5 (2.98%)	3 (0.46%)	8 (6.02%)	17 (0.32%)	1 (0.51%)
<i>Paraconger yazooensis</i>	—	1 (0.15%)	—	23 (0.43%)	—
<i>Pseudophichthys glaber</i>	2 (1.12%)	3 (0.46%)	—	50 (0.94%)	—
<i>Rhynchoconger</i> sp.	—	4 (0.62%)	—	1 (0.02%)	—
CLUPEIFORMES					
Family Clupeidae					
<i>Opisthonema</i> sp.	—	—	2 (1.50%)	—	—
SILURIFORMES					
Family Ariidae					
<i>Arius?</i> sp.	1 (0.60%)	2 (0.31%)	—	1 (0.02%)	—
GADIFORMES					
Family Bregmacerotidae					
<i>Bregmaceros</i> sp.	2 (1.12%)	—	1 (0.75%)	15 (0.28%)	—
HOLOCENTRIFORMES					
Family Holocentridae					
<i>Myripristis</i> sp.	6 (3.57%)	6 (0.93%)	1 (0.75%)	2 (0.04%)	—
BERYCIFORMES					
Family Berycidae					
<i>Centroberyx</i> sp.	—	2 (0.31%)	—	1 (0.02%)	—
OPHIDIIFORMES					
Family Carapidae					
Carapidae indeterminate	1 (0.60%)	—	—	1 (0.02%)	—
Family Ophidiidae					
<i>Brotula aquitanica</i>	1 (0.60%)	—	—	1 (0.02%)	—
<i>Preophidion petropolis</i>	2 (1.12%)	—	—	—	1 (0.51%)
<i>Preophidion meyeri</i>	69 (41.07%)	128 (19.88%)	2 (1.50%)	3120 (58.9%)	94 (47.72%)
<i>Sirembo? granus</i>	3 (1.79%)	12 (1.86%)	2 (1.50%)	76 (1.44%)	—

dissimilarities as both formations are not believed to be significantly different in depositional environments, i.e., shelf environments (Westgate *et al.*, 1994; Westgate, 2001; Parmley & DeVore, 2005; Ebersole *et al.*, 2019). Therefore, the pronounced differences in the faunal composition of the Clinchfield Formation and the Lisbon Formation appear to be related to other factors.

Biogeography is one consideration for the differences in the vast percentage similarity measurements of the otolith assemblages of the Clinchfield Formation and the Lisbon Formation. Perhaps, the two formations were deposited in different faunal provinces or subprovinces, which is possible since the Hardie Mine is approximately 570 km northeast of Lisbon Formation site. Furthermore, paleogeographical interpretations indicate either an absence of the Florida Peninsula or only a partial development (Smith *et al.*, 1994; Blakey, 2013; Scotese, 2014). In either scenario, the Hardie

Mine site would be open to the influences of the North Atlantic such as the effects of present-day Labrador Current in winter (Westgate, 2001). This could create a sub-bioprovince in the eastern portion of the Gulf Coastal Plain during the middle Eocene and account for the marked differences in the otoliths of the Clinchfield Formation and the Lisbon Formation. However, there are no cooler-water fishes, such as gadids, represented in the Clinchfield otoliths, and gadids have been known from the Late Cretaceous in the US Gulf Coast (Schwarzhan & Stringer, 2020).

If the bony fishes of the Clinchfield Formation were in a different sub-bioprovince, then differences in the otolith assemblages of the Clinchfield versus those of the Moodys Branch and Yazoo Clay would be expected. As reported previously, the Clinchfield otolith assemblage was neither greatly similar or greatly unlike the Moodys Branch and Yazoo Clay otoliths. However, there are some conspicuous

Table 3 (continued).

Orders (upper case, bold, shaded) Family (lower case, bold) Genus sp.	Site 1 No. of otoliths (% of total)	Site 2 No. of otoliths (% of total)	Site 3 No. of otoliths (% of total)	Site 4 No. of otoliths (% of total)	Site 5 No. of otoliths (% of total)
GOBIIFORMES					
Family GOBIIDAE					
<i>Gobius? vetustus</i>	8 (4.76%)	—	—	55 (1.04%)	—
BLENNIIFORMES					
Family Blenniidae					
<i>Blennius? cor</i>	1 (0.60%)	—	—	14 (0.26%)	—
ATHERINIFORMES					
Family Atherinidae					
<i>Atherina? debilis</i>	1 (0.60%)	2 (0.31%)	—	16 (0.30%)	—
PLEURONECTIFORMES					
Family Citharidae					
<i>Citharus? hoffmani</i>	—	3 (0.46%)	—	4 (0.08)	—
Family Paralichthyidae					
<i>Citharichthys altissimus</i>	2 (1.12%)	1 (0.15%)	—	6 (0.11%)	—
TRACHINIFORMES					
Family Trachinidae					
<i>Trachinus? laevigatus</i>	—	2 (0.31%)	—	4 (0.08%)	—
PERCIFORMES					
Family Priacanthidae					
<i>Pristigenys obliquus</i>	1 (0.60%)	—	—	44 (0.83%)	—
Family Serranidae					
<i>Centropristis priaboniana</i>	—	4 (0.62%)	1 (0.89)	28 (0.53%)	—
Family Malacanthidae					
<i>Malacanthus? sulcatus</i>	7 4.17%)	3 (0.46%)	1 (0.89)	57 (1.08%)	15 (7.62%)
Family Haemulidae					
<i>Orthopristis americana</i>	14 (8.33%)	117 (18.17%)	29 (21.80%)	230 (4.35%)	—
ACANTHURIFORMES					
Family Sciaenidae					
<i>Jeftichia claybornensis</i>	14 (8.33%)	273 (42.39%)	71 (53.38%)	631 (11.92%)	10 (5.08%)
<i>Sciaena aff. S. pseudoradians</i>	2 (1.12%)	19 (2.95%)	5 (3.76)	78 (1.47%)	—
SPARIFORMES					
Family Sparidae					
<i>Sparus? elegantulus</i>	7 (4.17%)	2 (0.31%)	1 (0.89)	129 (2.44%)	—
Non-identifiable specimens	9 (5.36%)	8 (1.24%)	6 (4.51%)	—	—
Total specimens for site	168	644	133	*	**

Table 4. Percentage similarity measurements between the Clinchfield Formation (Hardie Mine site, Georgia), Moodys Branch Formation site 1 (Bunker Hill, Louisiana), Moodys Branch Formation site 2 (Heison Landing, Louisiana), Moodys Branch Formation site 3 (Techeva Creek, Mississippi), Yazoo Clay site 4 (Copenhagen, Louisiana), and Lisbon Formation site 5 (Souwilpa Creek, Alabama). Comparisons made between bulk sample results based on Tables 2–3. The percentage similarity between any site can be determined at the intersection of the appropriate row and column. N/A = not applicable.

Localities	Clinchfield Formation (Hardie)	Moodys Branch (site 1)	Moodys Branch (site 2)	Moodys Branch (site 3)	Yazoo Clay (site 4)	Lisbon Formation (site 5)
Clinchfield Fm. (Hardie Mine, Georgia)	N/A	30.36%	39.85%	40.96%	33.25%	6.61%
Moodys Branch (site 1, Louisiana)	30.36%	N/A	48.06%	28.55%	70.46%	52.36%
Moodys Branch (site 2, Louisiana)	39.85%	48.06%	N/A	71.83%	49.56%	54.74%
Moodys Branch (site 3, Mississippi)	40.96%	28.55%	71.83%	N/A	27.11%	9.00%
Yazoo Clay (site 4, Louisiana)	33.25%	70.46%	49.56%	27.11%	N/A	55.41%
Lisbon Fm. (site 5, Alabama)	6.61%	52.36%	54.74%	9.00%	55.41%	N/A

and unmissable differences in abundance, especially regarding the ophiidiids. In the Moodys Branch (Bunker Hill site), *Preophidion meyeri* accounts for 41.07% of the total otoliths, while in the Clinchfield, the species accounts for 1.33%. However, at the Bunker Hills site, another ophiidiid, *Sirembo? granus*, represents only 1.79% of the specimens, but in the Clinchfield, the ophiidiid comprises 29.32% of the assemblage. These differences are even greater in the Yazoo Clay otoliths with 58.94% *Preophidion meyeri* and 1.44% *Sirembo? granus*. Furthermore, Müller (1999) did not report any *Preophidion meyeri* from his study of over 12,000 otoliths (middle Eocene–Pliocene) in the USA Atlantic Coastal Plain. Could these profound contrasts be related to distributional differences in a sub-bioprovinces? It is certainly possible and plausible, although it cannot be stated with absolute confidence.

While the presence of a possible sub-bioprovince in the eastern Gulf Coast Plain may explain differences in the abundance of taxa between the Clinchfield versus the Jacksonian formations (Moodys Branch Formation and Yazoo Clay), it still does not address the profound and fundamental dissimilarity of the Clinchfield and Lisbon otolith assemblages. The “upper” Lisbon Formation otolith fauna, which differs significantly from the Clinchfield Formation and Jacksonian otolith assemblages, are well documented from the Claibornian strata of Alabama, Mississippi, Louisiana, and Texas (Stringer & Breard, 1997; Breard & Stringer, 1999; Ebersole *et al.*, 2019). This widespread occurrence across the Gulf Coast seems to exclude the presence of sub-bioprovinces to account for the enormous variation in otolith species between the Clinchfield and the Lisbon formations. Evolutionary changes of the bony fishes seem unlikely as a cause since the temporal differences between the Clinchfield Formation and Lisbon Formation do not seem sufficient to account for such extensive and far-reaching modifications in the bony fish fauna (Szabo *et al.*, 1988; Dockery & Thompson, 2016; Waterman *et al.*, 2017; Albright *et al.*, 2019). Taking into account the above observations, a more consequential and encompassing reason for the lack of similarity between the Clinchfield and Lisbon otoliths may be related to a combination of global influences.

The Claibornian seas began regressing in the late middle Eocene (Hall, 1976; Westgate, 2001). This regression appears

to coincide with the initiation of glaciation in Antarctica, which probably had moved into higher latitudes in the late Mesozoic (Helfert, 1974; Kennett, 1977; Barrett, 1989). Other major climatic conditions began to occur, which resulted in dramatic changes. The middle Eocene surface waters at 35° latitude were approximately 20° C in the marine subtropical climatic zone (Devereaux, 1967; Hall, 1976). By the late Eocene, the surface waters were 24° C but would drop by 10° C by the end of the Eocene. However, Miller *et al.* (2009) noted that the cooling began in the middle Eocene. Other significant global events began in the late middle Eocene and early late Eocene such as changes to the extent and effect of the Tethys Seaway, which is known to have affected otolith distribution (Nolf & Stringer, 1992; Stringer, 1998; Nolf & Stringer, 2003; Schwarzahans, 2019a). Manning (2003) noted changes, primarily in the sharks and rays, at the Claiborne/Jackson groups boundary (near the end of the Bartonian) in the Gulf Coastal Plain. Furthermore, the drifting apart of Australia and Antarctica in the early Eocene and the early development of a connection between the Indian and Pacific oceans began to have worldwide consequences (Kennett, 1977). It is postulated that a combination of factors such as initiation of climatic changes and plate tectonic activity in the late middle Eocene accounted for the dramatic and extraordinary changes (disappearances and appearances) in the faunal composition between the Claibornian and the Jacksonian otolith assemblages in the Gulf Coastal Plain. These events could account in part for the fundamental and dramatic alteration of the Lisbon Formation otolith assemblage when compared to the overlying Clinchfield Formation otoliths.

Paleoecology indicated by the otoliths

Although the age of the Clinchfield Formation otolith assemblages is middle Eocene (primarily late Bartonian), Stringer *et al.* (2020b) argued that it was still possible to ascertain generalized paleoecological parameters with otoliths in the geological past. However, these interpretations must be made within limitations, and the interpretations should be carefully scrutinized and compared to other paleoecological indicators (such as foraminifera, ostracodes, and various types of invertebrates) as well as paleogeographical and

sedimentological data. This type of protocol was utilized in Stringer *et al.* (2016), Stringer *et al.* (2018), Stringer *et al.* (2020b), Stringer & Starnes (2020), and Stringer & Schwarzahns (2021).

An examination of Table 1 reveals the presence of nine identifiable families from the Clinchfield Formation otoliths. This provides a general overview of the types of bony fishes present in the paleoenvironment. The Clinchfield Formation families represent bonefishes (rare), mud eels (common), conger eels (very common), sea catfishes (very rare), cusk-eels (abundant), snooks (very rare), grunts (common), drums (very common), and porgies (very rare). All of these families are shown as presently occurring in fresh water or in shore waters of the continental USA, Canada, and Mexico on or above the continental shelf (less than 200 m) according to Page *et al.* (2013). Thus, the otolith assemblage of the Clinchfield Formation shows an absence of representatives that are indicative of deep waters only (greater than outer shelf or 200 m) and show similarity to present-day families in the Atlantic and Gulf Coast.

An analysis of the families present based on the Clinchfield Formation otoliths can also provide general data on likely paleoenvironments (freshwater, brackish, or marine) based on the distribution and ecological preferences of extant fish families as well as climatic data and bottom sediments. There are most certainly limitations and considerations when applying modern fisheries data to Eocene fishes, but it is believed that the comparisons provide broad and approximate environmental parameters for the middle Eocene Clinchfield Formation. Analyses based on fossil otoliths and Holocene fishes data are compared to other criteria utilized for paleoecological determinations such as other fossil groups (invertebrates and vertebrates), paleogeography, and sedimentological data. As shown in Table 5, all nine of the Clinchfield Formation actinopterygian families represented by otoliths are presently found in marine waters, and three of them restricted to marine waters. Six of the families may also be found in brackish waters and fresh water, but four of the six are characterized as chiefly marine. Also, none of the fishes that may be encountered in freshwater are exclusively freshwater. Therefore, the families of bony fishes identified by otoliths are highly indicative of marine conditions with all of the families with marine representatives, three families confined to marine waters, and four of the families with brackish and freshwater forms are chiefly marine (Froese & Pauly, 2020; Nelson *et al.*, 2016). Nolf & Brzobohaty (1992) stated that otolith assemblages that were free or almost free of myctophids or macrourids indicate a neritic environment with little oceanic influence. There are no myctophids or other deepwater fishes indicated in the Clinchfield Formation otoliths assemblage. Therefore, a general paleoenvironment for the Clinchfield Formation based on the otolith assemblage is a shallow marine, shelf setting with little oceanic influence.

It is possible to determine more specific paleoecological conditions by examining the most common taxa in the Clinchfield Formation. The most abundant species at the site was an ophidiid or cusk-eel *Sirembo? granus*. Extant ophidiids are marine fishes that are mainly bathybenthic with a few neritic and pelagic forms (Nelson *et al.*, 2016). However, it is well documented that during the Paleogene that the ophidiids were characterized by a very rich neritic fauna that lived primarily on muddy and soft substrates (Schwarzahns, 1981; Breard & Stringer, 1995; Nolf & Stringer, 2003; Nolf, 2013; Schweitzer *et al.*, 2014). In the early Paleogene, ophidiids were some of the

most common and speciose fishes in shallow-marine deposits (Nolf, 1985).

The sciaenids or drums account for the most taxa in a family (3), and along with the congrids, are the second most abundant (24.00% of the Clinchfield Formation otolith assemblage). Sciaenids are neritic fishes living in warm, shallow seas and estuaries, especially of large rivers (Nolf, 2013). Extant sciaenids generally prefer tropical, shallow-marine waters, estuarine, and coastal areas (Schwarzahns, 1993; Hoese & Moore, 1998). Studies have noted the strict confinement of the present-day Sciaenidae to continental coasts or shallow waters near continental regions (Myers, 1960; Darnell *et al.*, 1983; Nelson *et al.*, 2016). Stringer & Shannon (2019) detailed the use of sciaenids to make detailed paleoenvironmental interpretations. An important aspect of the analysis is the age of the sciaenids (determined by the length of the sagittae). The preponderance of juvenile sciaenids (representing 1-year-old or less) was interpreted as a strong indicator of shallow, soft bottom estuarine creeks and bays, especially upstream oligohaline creeks (i.e., a primary nursery area). This specialized habitat explained the dominance of juvenile sciaenids, the extremely high percentage of fishes that may be found in freshwater, brackish, and marine environments, and the paucity of marine-only species. The lengths of the sciaenid sagittae in the Clinchfield Formation otolith assemblage indicate predominantly adults, and there is no indication of an estuarine nursery.

The family Congridae, which also represents 24% of the otolith assemblage at the Hardie Mine, has two taxa. Members of this family are commonly referred to as conger and garden eels, and extant congrids are reported as marine only in mainly tropical and temperate waters (Nelson *et al.*, 2016; Froese & Pauly, 2020). Juveniles tend to be found mainly in shallow, marine, coastal waters, while the adults occur in deeper waters (Hoese & Moore, 1998; Nelson *et al.*, 2016). In the Paleogene, congrid otoliths are very common and abundant in many sediments of neritic environments with soft, muddy bottoms (Nolf, 1985; Nolf & Stringer, 2003; Nolf, 2013). In summary, the most common taxa of the Clinchfield Formation otolith assemblage indicate shallow marine waters (probably inner shelf) close to a continental coast but not estuarine.

The Clinchfield Formation otolith assemblage can also provide general climatic data. Table 5 indicates that all nine of the families have tropical representatives with three families restricted to the tropics. There are six families that extend into the subtropical, and three into the temperate. The percentages of abundance of the various families and other factors (such as primary distributions) are taken into account, then tropical to perhaps subtropical conditions seem most likely. These interpretations agree in general with the middle and late Eocene climate indicated by Markwick (2007) for Georgia. Markwick utilized five different climatic zones (tropical, arid, warm temperate, cool temperate, and cold) based on fossil climate proxies (such as crocodilians, amphibians, and turtles) in conjunction with lithological proxies (such as bauxites, coals, laterites, kaolinites, calcretes, tillites, and evaporites). Many of the extant bony fish families indicated by otoliths in the Clinchfield Formation have representatives that are found exclusively in soft or muddy bottoms (e.g., sand, silt, clay), and there are no indications of taxa expected in rocky environments. Most of the fossil otoliths from the Clinchfield Formation represent fish expected in normal marine salinity although a few of the forms tolerated reduced salinities, which could be an indication of the influence of nearby shorelines.

Table 5. Generalizations of the environmental distributions and climatic ranges of Holocene families represented in the Clinchfield Formation. Explanations of superscripts: Albulidae¹ = Rarely in freshwater and brackish. Ariidae² = Chiefly marine; shown as tropical to subtropical as well as tropical to warm temperate (Foese & Pauly, 2020; Nelson *et al.*, 2016). Haemulidae³ = Chiefly marine (Foese & Pauly, 2020). Sparidae⁴ = Chiefly marine; very rare in fresh or brackish water (Foese & Pauly, 2020).

Fish family	Distribution of family			General climatic ranges		
	Freshwater	Brackish	Marine	Tropical	Subtropical	Temperate
Albulidae ¹						
Heterenchelyidae						
Congridae						
Ariidae ²						
Ophidiidae						
Centropomidae						
Haemulidae ³						
Sciaenidae						
Sparidae ⁴						

The Clinchfield Formation paleoenvironment does not appear to have been conducive to extensive invertebrate settlement such as boring and encrusting on the otoliths. There are some examples in the Clinchfield otoliths, but they are not numerous. Of the limited specimens with invertebrate settlement, the most common is cheilostome bryozoans on the larger sagittae (Fig. 4K, especially evident in the posteroventral of the ostium and immediately below the ostium). The paucity of otoliths with evidence of invertebrate settlement is likely related to limited surface residence-time in the paleoenvironment (Stringer, 2016). The otoliths were covered by sedimentation before being exposed for long periods on the sea bottom and increasing the chances for invertebrate settlement. It should be noted that the leaching on the Clinchfield Formation otoliths, especially the larger specimens, could have removed or obliterated evidence of invertebrate settlement.

As noted previously, paleoecological interpretations based on otoliths should be carefully scrutinized and compared to other paleoecological indicators as well as sedimentological and paleogeographical data when available. This type of protocol was utilized in Stringer *et al.* (2016, 2018, and 2020b). Numerous studies based on invertebrates and vertebrates (skeletal remains) of the Clinchfield Formation generally agree with the paleoenvironment denoted by the otolith assemblage. Pickering (1971) described the Clinchfield as a greenish-gray, argillaceous sand with abundant marine bryozoans and pectens. Herrick (1972) noted that the foraminiferal fauna was dominated by benthonic taxa and the planktonic to benthonic ratio was extremely low. This ratio would indicate shallow marine conditions also. Glawe (1974) in his study of Eocene and Oligocene Pectinidae of Georgia refers to the Clinchfield as a high energy marine depositional environment. Garner *et al.* (2000) postulated that the Hardie Mine was a “marginal marine environment composed of low lying and marshy areas.” This was based primarily on molluscan and bryozoan remains from the site.

The paleoenvironment indicated by the otoliths is also in agreement with vertebrate studies on the Clinchfield Formation. Westgate (2001) categorized the Hardie Mine as nearshore marine waters and noted the presence of warm-water and cold-water sharks (due to the absence of the Floridian Peninsula). However, it should be emphasized that the Clinchfield Formation otoliths have no indications of cooler

water fishes such as Gadidae and Merlucciidae. Parmley & Cicimurri (2003) reported that warm-water sharks dominated the fauna. Parmley & Cicimurri (2005) in the description of a chimaeroid fish from the Hardie Mine referred to the site as a nearshore marine environment. Parmley & DeVore (2005) in their indepth study of palaeopheid snakes from the Hardie Mine suggested an open marine, nearshore, shallow-water habitat that was similar to shallow inlet bays found along the present-day Gulf of Mexico coastline.

Sedimentological analyses of the Clinchfield Formation have also indicated a shallow, shelf marine environment. For example, Westgate (2001) noted that the Clinchfield consisted of coarse, well-sorted quartz sands with diverse near-shore marine fossils that were deposited as the Jackson seas transgressed across central Georgia. Early studies described the Clinchfield as a fine to medium-grained sand having little or no interstitial clay (LeGrand, 1962). Pickering (1970) noted the Clinchfield sediments as a medium-grained, well-sorted, poorly consolidated quartz sand with no observable crossbedding. All of these sediment descriptions would match a shallow, shelf marine environment as indicated by the teleostean otoliths.

Therefore, when the various paleoecological parameters suggested by the bony fishes based on otoliths are considered, they compare extremely well with the paleoenvironmental conditions indicated by other fossil groups (invertebrate and vertebrate) and sedimentological evidence. It should also be noted that the otolith-based paleoenvironment compares well with the paleogeography indicated by Smith *et al.* (1994), Markwick (2007), Blakey (2013), and Scotese (2014). In conclusion, the Clinchfield Formation is believed to be deposited in a tropical to perhaps subtropical, soft substrate, mainly normal marine to slightly reduced salinities, inner shelf (0–20 m) environment with indications of nearby continental shorelines as evidenced by several lines of evidence, including various terrestrial vertebrate remains.

CONCLUSIONS

The 4,768 otoliths analyzed from the Clinchfield Formation at the Hardie Mine site represent 14 actinopterygian taxa (9 families and 7 orders) with a relatively evenness of distribution. Although the Clinchfield otolith assemblage is not very rich

(diverse), it presents a more indepth understanding of the bony fishes at this significant Eocene marginal marine locality by increasing the fish taxa by over threefold and describing a new Eocene sciaenid, *Eosciaena ebersolei*. Furthermore, the otolith assemblage provides data to augment and supplement the paleoecological and paleogeographical interpretation of this significant site. The Clinchfield otolith assemblage indicates a tropical to perhaps subtropical, soft substrate, mainly normal marine to slightly reduced salinities, inner shelf (0–20 m) paleoenvironment with indications of proximal continental coastlines. Lastly, this investigation represents an initial development in addressing the understudied Paleogene otolith assemblages in Georgia. The differences in taxa abundance between the Clinchfield and Jacksonian (Moody Branch and Yazoo Clay) otolith assemblages may be related to a sub-bioprovince in the eastern Gulf Coast Plain related to effects of the North Atlantic (i.e., no Floridian peninsula). The profound differences in the otolith assemblages of the Clinchfield Formation and the underlying Lisbon Formation (percentage similarity of only 6.61%) is postulated to be related to late middle Eocene worldwide climatic occurrences (such as initiation of glaciers in Antarctica) and plate tectonic events (such as the initial closures of parts of the Tethys Seaway and continued separation of Australia and Antarctica).

ACKNOWLEDGMENTS

This investigation was greatly facilitated by several people who shared otolith specimens from surface collections or provided bulk samples of the Clinchfield Formation. Sincere appreciation is extended to David Cicimurri (South Carolina State Museum, Columbia, SC, USA), Kelly Irwin (Arkansas Game and Fish Commission, Little Rock, AR, USA), Gary Leonard (Villa Rica, GA, USA), and James Westgate (Professor Emeritus, Lamar University, Beaumont, TX, USA). David Cicimurri also provided information on Clinchfield otolith specimens from the South Carolina State Museum.

K. A. Johnson (National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS, USA), Ron Taylor (formerly of the Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA), and J. Read Hendon (Center for Fisheries Research and Development, Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, MS, USA) generously provided modern fishes and otoliths. Dirk Nolf (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium) also supplied Holocene and fossil otolith specimens. W. Schwarzhans (Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark) made valuable and insightful suggestions on the identity and taxonomy of specimens, especially the newly described sciaenid genus and species. A very special thanks to Jun Ebersole (McWane Science Center, Birmingham, Alabama, USA) for his assistance with figures. The authors especially appreciate the reviewers (Konstantina Agiadi and an anonymous reviewer) and the editor Guillaume Guinot for their thoughtful input in approving this manuscript.

BIBLIOGRAPHY

- Albright, L., Sanders, A., Weems, R., Cicimurri, D., Knight, J., 2019. Cenozoic vertebrate biostratigraphy of South Carolina, U.S.A., and additions to the fauna. *Bulletin of the Florida Museum of Natural History* 57(2), 77-236.
- Barrett, P. J., 1989. Antarctic Cenozoic history from the CIROS-1 drill-hole. *New Zealand Department of Scientific Research Bulletin* 245, 1-245.
- Betancur-R. R., Broughton, R., Wiley, E., Carpenter, K., López, J., Li, C., Holcroft, N., Arcila, D., Sanciangco, M., Cureton, J., II, Zhang, F., Buser, T., Campbell, M., Ballesteros, J., Roa-Varon, A., Willis, S. Borden, W., Rowley, T., Reneau, P.C., Hough, D., Lu, G., Grande, T., Arratia, G., Orti, G., 2013. The Tree of Life and a New Classification of Bony Fishes. *PLOS Currents Tree of Life*. 2013 April 18. Edition 1. <https://doi.org/10.1371/currents.tol.53ba26640df0ccae75bb165c8c26288>
- Blakey, R., 2013. Cenozoic 40 Ma Eocene and 35 Ma Eocene-Oligocene. *Deep Time Maps*. Colorado Plateau Geosystems. <https://deeptimemaps.com>.
- Bleeker, P., 1857. Vierde bijdrage tot de kennis der ichthyologische fauna van Japan. *Acta Societatis Regiae Scientiarum Indo-Neerlandicae* 3, 1-46.
- Bleeker, P., 1858. De heer Bleeker brengt nog ter tafel het eerste deel van eene ichthyologie Archipelagi Indici Prodrum. *Natuurkundig Tijdschrift voor Nederlandsch Indi*. 16, 38-41.
- Bleeker, P., 1859. Enumeration speciorum piscium hujusque in Archipelago Indico observatarum, adjectis habitationibus citationibusque, ubi descriptions earum recentiores reperiuntur, nec non species Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societe Science Indo-Neerland* 6, 1-276.
- Breard, S., Stringer, G., 1995. Paleoenvironment of a diverse marine vertebrate fauna from the Yazoo Clay (Late Eocene) at Copenhagen, Caldwell Parish, Louisiana. *Gulf Coast Association of Geological Societies Transactions* 45, 77-85.
- Breard, S., Stringer, G., 1999. Integrated paleoecology and marine vertebrate fauna of the Stone City Formation (Middle Eocene), Brazos River section, Texas. *Transactions of the Gulf Coast Association of Geological Societies* 49, 132-142.
- Chandler, R., Parmley, D. 2003. The earliest North American record of auk (*Aves: Alcidae*) from the Late Eocene of Central Georgia. *The Oriole* 68, 7-9.
- Cicimurri, D., Ebersole, J., Martin, G., 2020. Two new species of *Mennerotodus zhelezko*, 1994 (Chondrichthyes: Lamniformes: Odontaspidae), from the Paleogene of the southeastern United States. *Fossil Record* 23, 117-140. <https://doi.org/10.5194/fr-23-117-2020>
- Cuvier, G., 1816 (1817*). *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Edition 1. v. 2: i-xviii + 1-532, [Pls. 9-10, in v. 4].* * *Le Règne Animal* was actually published in 1816, but the title page was 1817. Both dates are often seen.
- Cuvier, G., 1829. *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, Tome II, 2nd edition.* Chez Dêterville; Paris.
- Cuvier, G., Valenciennes, A., 1840. *Histoire naturelle des poissons. Tome quinzisième. Suite du livre dix-septième. Siluroïdes* 15, 1-450.
- Darnell, R. M., Defenbaugh, R. E., Moore, D., 1983. *Northwestern Gulf Shelf Bio-Atlas: A study of the distribution of demersal fish and penaeid shrimp of the soft bottoms of the continental shelf from the Rio Grande to the Mississippi River Delta.* Minerals Management Service, United States Department of the Interior Open File Report 82-04, 1-438.
- Devereaux, I., 1967. Oxygen isotope paleotemperature measurements on New Zealand Tertiary fossils. *New Zealand Journal of Science* 10, 988-1011.
- Dockery, D., 1996. Toward a revision of the generalized stratigraphic column of Mississippi. *Mississippi Geology* 17(1), 1-9.
- Dockery, D., Thompson, D., 2016. *The Geology of Mississippi.* University Press of Mississippi, Jackson, Mississippi.
- Ebersole, J. A., Cicimurri, D. J., Stringer, G. L., 2019. Taxonomy

- and biostratigraphy of the elasmobranchs and bony fishes (Chondrichthyes and Osteichthyes) of the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama, USA, including an analysis of otoliths. *European Journal of Taxonomy* 585, 1-274. <https://doi.org/10.5852/ejt.2019.585>
- Ebersole, J. A., Cicimurri, D. J., Stringer, G. L., 2021. Marine fishes (Elasmobranchii, Teleostei) from the Glendon Limestone Member of the Byram Formation (Oligocene, Rupelian) at site Awa-9, Washington County, Alabama, USA, including a new species of gobiid (Gobiiformes: Gobiidae). *Acta Geologica Polonica* 71.
- Edwards, L. E., 2001. Dinocyst biostratigraphy of Tertiary sediments from five cores from Screven and Burke counties, Georgia (part G). In: Edwards, L. E. (Ed.), *Geology and paleontology of five cores, Screven and Burke counties, eastern Georgia*. United States Geological Survey Professional Paper 1603, 1-25. <https://doi.org/10.3133/pp1603>
- Fricke, R., Eschmeyer, W., Van der Laan, R., 2019. Eschmeyer's Catalog of Fishes: Genera, Species, References. <https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>
- Froese, R., Pauly, D., 2020. FishBase. <https://fishbase.se/home.htm>
- Frizzell, D. L., Dante, J. H., 1965. Otoliths of some early Cenozoic fishes of the Gulf Coast. *Journal of Paleontology* 39(4), 687-718.
- Garner, E., Freile, D., DeVore, M., 2000. Depositional environment, lithology, and taphonomy of an Eocene marginal marine section in Central Georgia and its modern analogue. The 49th Annual Meeting of the Southeast Section of the Geological Society of America Abstracts 32, 18.
- Girard, C. F., 1858. Notes upon various new genera and new species of fishes in the museum of the Smithsonian Institution collected in connection with the United States and Mexico boundary survey: Major William Emory, Commissioner. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10, 167-171.
- Glawe, L. N., 1974. Upper Eocene and Oligocene Pectinidae of Georgia and their stratigraphic significance. *Geological Survey of Georgia Information Circular* 46, 1-27.
- Goodrich, E. S., 1909. *Vertebrata craniata*, fasc. 1. Cyclostomes and fishes. In: Lankester, E. R. (Ed.), *A treatise on zoology*, part 9. Adam and Charles Black, London, pp. 1-518.
- Goodrich, E. S., 1930. *Studies on the structure and development of Vertebrates*. Macmillan and Co., London. <https://doi.org/10.5962/bhl.title.82144>
- Green, J. M., 2002. A comparison of paleoecological determinations based on vertebrate and invertebrate faunas from the Moodys Branch Formation (upper Eocene) of Louisiana and Mississippi. Unpublished MS, University of Louisiana at Monroe.
- Hall, J. L., 1976. Paleoecology and age of the upper Eocene *Basilosaurus cetoides* beds of Louisiana, Mississippi, and southwestern Alabama. Unpublished MS, University of Louisiana at Monroe.
- Helfert, M., 1974. The association of geomagnetic field intensity decreases to climatic coolings during the late Cenozoic. Unpublished PhD, The University of Texas.
- Herrick, S. M., 1972. Age and Correlation of the Clinchfield Sand in Georgia. *Contributions to Stratigraphy*. United States Geological Survey Bulletin 1354-E, 1-17.
- Hoese, H., Moore, R., 1998. *Fishes of the Gulf of Mexico*. Texas A&M University Press, College Station, Texas.
- Huddlestun, P., 1993. A revision of the lithostratigraphic units of the coastal plain of Georgia: the Oligocene. *Georgia Geologic Survey Bulletin* 105, 1-152.
- Huddlestun, P., Hetrick, J. H., 1986. Upper Eocene stratigraphy of central and eastern Georgia. *Georgia Geologic Survey Bulletin* 95, 1-78.
- Huxley T. H., 1880. On the application of the laws of evolution to the arrangement of the vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880, 649-662.
- Janssen, A. W., 2012. Validation of holoplanktonic molluscan taxa from the Oligo-Miocene of the Maltese Archipelago, introduced in violation with ICZN. *Cainozoic Research* 9, 189-199.
- Jordan, D. S., 1923. *A classification of fishes including families and genera as far as known*. Stanford University Publications, University Series, *Biological Sciences* 3(2), 77-243. <https://doi.org/10.5962/bhl.title.161386>
- Kanazawa, R. H., 1961. *Paraconger*, a new genus with three new species of eels (family Congridae). *Proceedings of the United States National Museum* 113(3450), 1-14. <https://doi.org/10.5479/si.00963801.113-3450.1>
- Kaup, J., 1856. Uebersicht der Aale. *Archiv für Naturgeschichte* 22(1), 41-77. <https://doi.org/10.5962/bhl.part.11240>
- Kennett, J., 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. *Journal of Geophysical Research* 82(27), 3843-3860. <https://doi.org/10.1029/JC082i027p03843>
- Koken, E., 1888. Neue Untersuchungen an tertiären fisch-otolithen. *Deutsche Geologischen Gesellschaft Zeitschrift* 40, 274-305.
- Lacépède, B. G. E., 1802. *Histoire naturelle des poissons* 4, 1-728.
- LeGrand, H. E., 1962. Geology and ground-water resources of the Macon area, Georgia. *Georgia Geologic Survey Bulletin* 72, 1-69.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 10th edition, vol. 1. Laurentii Salvii; Holmiae. <https://doi.org/10.5962/bhl.title.542>
- Mader, B. J., 1998. Brontotheriidae. In: Janis, C., Scott, K., Jacobs, L. (Eds.), *Evolution of Tertiary Mammals of North America. Volume I: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, New York, New York, pp. 525-536. <https://doi.org/10.1017/CBO9780511529924.038>
- Manning, E., 2003. The Eocene/Oligocene transition in marine vertebrates of the Gulf Coastal Plain (Chapter 21). In: Prothero, D., Ivany, L., Nesbitt, E. (Eds.), *From Greenhouse to Icehouse, the marine Eocene-Oligocene transition*. Columbia University Press, New York, New York, pp. 366-385.
- Manning, E., Standhardt, B., 1986. Late Eocene sharks and rays of Montgomery Landing, Louisiana. In: Schiebout, J., Van Den Bold, W. (Eds.), *Montgomery Landing Site, Marine Eocene (Jackson), Central Louisiana*. *Proceedings of a Symposium, Gulf Coast Association of Geological Societies, Baton Rouge, Louisiana*, pp. 133-162.
- Markwick, P., 2007. The palaeogeographic and palaeoclimatic significance of climate proxies for data-model comparisons. In: Williams, A., Gregory, F., Schmidt, D. (Eds.), *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. The Geological Society, London, pp. 251-312. <https://doi.org/10.1144/TMS002.13>
- Miller, K., Wright, J., Katz, M., Wade, B., Browning, J., Cramer, B., Rosenthal, Y., 2009. Climate threshold at the Eocene-Oligocene transition: Antarctic ice sheet influence on ocean circulation. In: Koeberl, C., Montanari, A. (Eds.), *The Late Eocene Earth—Hothouse, Icehouse, and Impacts*. The Geological Society of America Special Paper 452, 169-178. [https://doi.org/10.1130/2009.2452\(11\)](https://doi.org/10.1130/2009.2452(11))
- Müller, A., 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften* 9/10, 1-360.
- Myers, G. S., 1960. Restriction of the croakers (Sciaenidae) and anchovies (Engraulidae) to continental waters. *Copeia* 1960(1), 67-68. <https://doi.org/10.2307/1439860>
- Nelson, J., Grande, T., Wilson, M., 2016. *Fishes of the World* (5th edition). John Wiley and Sons, Hoboken, New Jersey. <https://doi.org/10.1002/9781119174844>
- Nolf, D., 1985. Otolithi Piscium. In: Schultze, H. (Ed.), *Handbook of Paleoichthyology*, 10, Gustav Fischer Verlag, Stuttgart, Germany and New York, United States, pp. 1-145.
- Nolf, D., 2013. *The Diversity of Fish Otoliths, Past and Present*. Royal

- Belgian Institute of Natural Sciences, Brussels, Belgium.
- Nolf, D., Brzobohaty, R., 1992. Fish otoliths as paleobathymetric indicators. *Paleontologica and Evolutio* 24-25, 225-264.
- Nolf, D., Dockery, D., 1993. Fish otoliths from the Matthews Landing Marl Member (Porters Creek Formation), Paleocene of Alabama. *Mississippi Geology* 14, 24-39.
- Nolf, D., Stringer, G., 1992. Neogene paleontology in the northern Dominican Republic. 14. Otoliths of teleostean fishes. *Bulletins of America Paleontology* 102, 45-81.
- Nolf, D., Stringer, G., 2003. Late Eocene (Priabonian) fish otoliths from the Yazoo Clay at Copenhagen, Louisiana. *Louisiana Geological Survey Geological Pamphlet* 13, 1-23.
- Nystrom, P., Jr., Willoughby, R., Dockery, D., 1992. Claibornian stratigraphy of the Savannah River Site and surrounding area. In: Zullo, V., Harris, W., Price, V. (Eds.), *Savannah River region: transition between the Gulf and Atlantic Coastal Plains. Proceedings of the Second Bald Head Island Conference on Coastal Plains Geology. University of North Carolina-Wilmington Special Publication*, North Carolina, pp. 56-61.
- Page, L., Espinosa-Pérez, H., Findley, T., Gilbert, C., Lea, R., Mandrak, N., Mayden, R., Nelson, J., 2013. Common and scientific names of fishes from the United States, Canada, and Mexico, 7th edition. *American Fisheries Society Special Publication* 34, 1-384.
- Parmley, D., Cicimurri, D., 2003. Late Eocene sharks of the Hardie Mine local fauna of Wilkinson County, Georgia. *Georgia Journal of Science* 61, 153-179.
- Parmley, D., Cicimurri, D., 2005. First record of a chimaeroid fish from the Eocene of the southeastern United States. *Journal of Paleontology* 79, 1219-1221. [https://doi.org/10.1666/0022-3360\(2005\)079\[1219:FROACF\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2005)079[1219:FROACF]2.0.CO;2)
- Parmley, D., DeVore, M., 2005. Palaeopheid snakes from the late Eocene Hardie Mine local fauna of central Georgia. *Southeastern Naturalist* 4, 703-722. [https://doi.org/10.1656/1528-7092\(2005\)004\[0703:PSFTLE\]2.0.CO;2](https://doi.org/10.1656/1528-7092(2005)004[0703:PSFTLE]2.0.CO;2)
- Parmley, D., Holman, A., 2003. *Nebraskophis* Holman from the Late Eocene of Georgia (USA), the oldest known North American colubrid snake. *Acta Zoologica Cracoviensia* 46,1-8.
- Parmley, D., Hutchison, J., Parham, J., 2006. Diverse turtle fauna from the late Eocene of Georgia including the oldest records of aquatic testudinoids in southeastern North America. *Journal of Herpetology* 40, 343-350. [https://doi.org/10.1670/0022-1511\(2006\)40\[343:DTFFTL\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2006)40[343:DTFFTL]2.0.CO;2)
- Pickering, S. M., 1970. Stratigraphy, paleontology, and economic geology of portions of Perry and Cochran quadrangles, Georgia. *Georgia Geologic Survey Bulletin* 81, 1-67.
- Pickering, S. M., 1971. Lithostratigraphy and biostratigraphy of the north-central Georgia Coastal Plain. In: *Georgia Geological Society 6th Annual Field Trip Guidebook. Georgia Geological Survey, Atlanta, Georgia*, pp. 13-25.
- Poey, F., 1867. Cubensium genera piscium. *Repertorio fisico-natural de la isla de Cuba* 2, 205-216.
- Poey, F., 1868. *Monografia de las Morenas cubanas. Repertorio Físico-Natural de la Isla de Cuba* 2, 245-268.
- Rafinesque C., 1810. *Indice d'ittologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvencono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione de alcuni nuovi pesci siciliani. G. del Nobolo, Messina.* <https://doi.org/10.5962/bhl.title.58965>
- Rafinesque, C. S., 1818. Description of three new genera of fluviatile fish, *Pomoxis*, *Sarchirus* and *Exoglossum*. *Journal of the Academy of Natural Sciences of Philadelphia* 1(2), 417-422.
- Regan, C. T., 1912. The osteology and classification of the teleostean fishes of the Order Apodes. *Annals and Magazine of Natural History (Series 8)* 10, 377-387. <https://doi.org/10.1080/00222931208693250>
- Reitz, E., Wing, E., 1999. *Zooarchaeology. Cambridge University Press, Cambridge, England.*
- Rhinehart, P., Mead, A., Parmley, D., 2019. Eocene terrestrial mammals from central Georgia. *Georgia Journal of Science* 77(article 6), 1-9.
- Riley, K. S., Westgate, J., 1999. Community structure of the Jacksonian age (late Eocene) Hardie Mine local fauna, Wilkinson County, Georgia. *Texas Academy of Science Annual Meeting Program with Abstracts*, 74.
- Schwarzahns, W., 1981. Vergleichende morphologische untersuchungen an rezenten und fossilen otolithen der Ordnung Ophidiiformes. *Berliner Geowiss. Abh.* 32, 63-122.
- Schwarzahns, W., 1993. A comparative morphological treatise of Recent and fossil otoliths of the family Sciaenidae (Perciformes). In: Pfeil, F. (Ed.), *Piscium Catalogus, Otolithi Piscium. Verlag Dr. Freidrich Pfeil, Munich, Germany*, pp. 1-245.
- Schwarzahns, W., 2019a. Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano* 46, 3-325.
- Schwarzahns, W., 2019b. A comparative morphological study of Recent otoliths of the Congridae, Muraenesocidae, Nettastomatidae and Colocongridae (Anguilliformes). *Memorie della Società Italiana di Scienze Naturali e del Museo di Storia Naturale di Milano* 46, 327-354.
- Schwarzahns, W., Huddleston, R., Takeucki, G., 2018. A Late Santonian fish-fauna from the Eutaw Formation of Alabama reconstructed from otoliths. *Rivista Italiana di Paleontologia e Stratigrafia* 124, 45-72.
- Schwarzahns, W., Stringer, G., 2020. Fish otoliths from the late Maastrichtian Kemp Clay (Texas, USA) and the early Danian Clayton Formation (Arkansas, USA) and an assessment of extinction and survival of teleost lineages across the K-Pg boundary based on otoliths. *Rivista Italiana di Paleontologia e Stratigrafia* 126, 395-446.
- Schweitzer, C., Feldmann, R., Stringer, G., 2014. *Neozanthopsis americana* (Decapoda, Brachyura, Carpilioidea) from the middle Eocene Cane River Formation of Louisiana, USA, and associated teleost otoliths. *Scripta Geologica* 147, 163-183.
- Scopoli, J. A., 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague.* <https://doi.org/10.5962/bhl.title.10827>
- Scotese, C. R., 2014. The PALEOMAP Project PaleoAtlas for ArcGIS, version 2, Volume 1, Cenozoic Plate Tectonic, Paleogeographic, and Paleoclimatic Reconstructions, Maps 1-15. PALEOMAP Project, Evanston, Illinois.
- Smale, M., Watson, G., Hecht, T., 1995. Otolith atlas of southern African marine fishes. *Ichthyological Monographs of the J. L. B. Smith Institute of Ichthyology* 1, 1-253 (+ 149 plates). <https://doi.org/10.5962/bhl.title.141860>
- Smith, A. G., Smith, D. G., Funnell, B. M., 1994. *Atlas of Mesozoic and Cenozoic coastlines. Cambridge University Press, Cambridge, Great Britain.*
- Smith, D., Irmak, E., Özen, Ö., 2012. A redescription of the eel *Panturichthys fowleri* (Anguilliformes: Heterenchelyidae), with a synopsis of the Heterenchelyidae. *Copeia* 2012(3), 484-493. <https://doi.org/10.1643/CI-11-174>
- Stringer, G., 1979. A study of the Upper Eocene otoliths of the Yazoo Clay in Caldwell Parish, Louisiana. *Tulane Studies in Geology and Paleontology* 15, 95-105.
- Stringer, G., 1986. Teleostean otoliths and their paleoecological implications at the Montgomery Landing Site. In: Schiebout, J. A., Van den Bold, W. A. (Eds.), *Montgomery Landing Site, Marine Eocene (Jackson) of Central Louisiana, Proceedings of a Symposium. Gulf Coast Association of Geological Societies, Baton Rouge, Louisiana*, pp. 209 -222.
- Stringer, G., 1998. Otolith-based fishes from the Bowden shell bed (Pliocene) of Jamaica: systematics and palaeoecology. In: Donovan, S. K. (Ed.), *The Pliocene Bowden Shell Bed, southeast Jamaica. Contributions to Tertiary and Quaternary Geology* 35, 147-160.

- Stringer, G., 2016. Evidence and implications of marine invertebrate settlement on Eocene otoliths from the Moodys Branch Formation of Montgomery Landing (Louisiana, U.S.A.). *Cainozoic Research* 16(1), 3-11.
- Stringer, G., Bell, D., 2018. Teleostean otoliths reveal diverse Pliocene fish assemblages in coastal Georgia (Glynn County). *Bulletin of the Florida Museum of Natural History* 56(3), 83-108.
- Stringer, G., Breard, S., 1997. Comparison of otolith-based paleoecology to other fossil groups: an example from the Cane River Formation (Eocene) of Louisiana. *Transactions of the Gulf Coast Association of Geological Societies* 47, 563-570.
- Stringer, G., Cicimurri, D., Parmley, D., 2007a. Bony fishes based on otoliths from the Eocene Clinchfield Formation, central Georgia: initial findings. *The Proceedings of the Louisiana Academy of Sciences* 70.
- Stringer, G., Cicimurri, D., Parmley, D., 2007b. Fish otoliths from the Eocene Clinchfield Formation of Georgia with note of a haemulid and centropomid of gigantic proportions. *Journal of Vertebrate Paleontology* 27(30), 154A.
- Stringer, G., Clements, D., Sadorf, Shannon, K., 2018. First description and significance of Cretaceous teleostean otoliths (Tar Heel Formation, Campanian) from North Carolina. *Eastern Paleontologist* 1, 1-22.
- Stringer, G., Ebersole, J., Starnes, J., Ebersole, S., 2020a. First Pliocene otolith assemblage from the Gulf Coastal Plain, Dauphin Island, Mobile County, Alabama, USA. *Historical Biology*. <https://doi.org/10.1080/08912963.2020.1773457>
- Stringer, G., Hulbert, R. C., Jr., 2020. Fish otoliths provide further taxonomic and paleoecologic data for the late Pleistocene (Rancholabrean) Jones Girls Site, Georgia. *Eastern Paleontologist* 5, 1-15.
- Stringer, G., King, L., 2010. New fossil centropomid fish (snook) from the late Eocene Yazoo Clay of northeast Louisiana. *The Proceedings of the Louisiana Academy of Sciences* 73.
- Stringer, G., Miller, M., 2001. Paleoenvironmental interpretations based on vertebrate fossil assemblages: an example of their utilization in the Gulf Coast. *Transactions of the Gulf Coast Association of Geological Societies* 51, 329-338.
- Stringer, G., Oman, L., and Badger, B., 2016. Woodbury Formation (Campanian) in New Jersey yields largest known otolith assemblage of teleostean fishes in North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 165, 15-36. <https://doi.org/10.1635/053.165.0101>
- Stringer, G., Schwarzshans, W., Phillips, G., Lambert, R., 2020b. Highly diversified Late Cretaceous fish assemblage revealed by otoliths (Ripley Formation and Owl Creek Formation, northeast Mississippi, USA). *Rivista Italiana di Paleontologia e Stratigrafia* 126(1), 111-155.
- Stringer, G., Schwarzshans, W., 2021. Late Cretaceous osteichthyan otoliths from the Severn Formation (Maastrichtian) of Maryland, USA, with an unusual occurrence of Siluriformes and Beryciformes and the oldest Atlantic Coast Gadiformes. *Cretaceous Research*. <https://doi.org/10.1016/j.cretres.2021.104867>
- Stringer, G. L., Shannon, K., 2019. The Pliocene Elizabethtown otolith assemblage (Bladen County, North Carolina, USA) with indications of a primary fish nursery area. *Historical Biology* 32(8), 1108-1119. <https://doi.org/10.1080/08912963.2019.1566324>
- Stringer, G., Starnes, J., 2020. Significance of late Miocene fish otoliths (*Micropogonias undulatus*) from a *Rangia johnsoni* bed in the Pascagoula Formation in the subsurface of Mississippi. *Southeastern Geology* 54(1), 21-28.
- Stringer, G., Worley, L., 2003. Implications of recently discovered marine Oligocene vertebrates from the Rosefield Formation of Louisiana. *Texas Academy of Sciences Abstracts with Programs* 106, 67.
- Swainson, W., 1838. On the natural history and classification of fishes, amphibians, & reptiles, or monocardian animals, volume 1. A. Spottiswoode, London. <https://doi.org/10.5962/bhl.title.62140>
- Szabo, E. W., Osborne, W. E., Copeland, C. W., Jr., Neathery, T. L., 1988. *Geologic Map of Alabama*. Geological Survey of Alabama Special Map 220.
- Toulmin, L., 1977. Stratigraphic distribution of Paleocene and Eocene fossils in the eastern Gulf Coast region. *Alabama Geological Survey Monograph* 13, 1-602.
- USGS., 2020. National Geologic Map Database, Geolex-Unit Summary. United States Geological Survey. Accessed online 12/2020. http://ngmdb.usgs.gov/Geolex/Units/Clinchfield_1110.html
- Van der Laan, R., Eschmeyer, W., Fricke, R., 2014. Family-group names of Recent fishes. *Zootaxa* 3882 (1), 1-230. <https://doi.org/10.11646/zootaxa.3882.1.1>
- Van der Laan, R., Eschmeyer, W., Fricke, R., 2017. Addenda to Family-group names of Recent fishes. *Zootaxa* 3882(1), 1-230. <https://doi.org/10.11646/zootaxa.3882.1.1>
- Van der Laan, R., Eschmeyer, W., Fricke, R., 2018. Addenda to Family-group names of Recent fishes. *Zootaxa* 3882(1), 1-230. <https://doi.org/10.11646/zootaxa.3882.1.1>
- Waterman, A., Weber, R., Lu, Y., George, R., Reilly, T., Roederer, R., Edmunds, J., Parker, B., Myers, N., Avery, A. J., 2017. *Paleogene Biostratigraphic Chart, Gulf Basin, USA*. PaleoData, Inc.
- Westgate, J., 2001. Paleoecology and biostratigraphy of marginal marine Gulf Coast Eocene vertebrate localities. In: Gunnell, G. F. (Ed.), *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*. Plenum Press, New York, pp. 263-297. https://doi.org/10.1007/978-1-4615-1271-4_11
- Westgate, J., Gillette, M., Rolater, E., 1994. Paleoecology of an Eocene coastal community from Georgia. *Journal of Vertebrate Paleontology* 14(3), 52A. <https://doi.org/10.1080/02724634.1994.10011559>
- Wiley, E. O., Johnson, G. D., 2010. A teleost classification based on monophyletic groups. In: Nelson, J., Schultze, H.-P., Wilson, M. (Eds.), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, München, Germany, pp. 123-182.
- Worley, L. E., 2004. Paleoecologic and evolutionary implications of bony and cartilaginous fishes from Oligocene sites of the Rosefield Formation in northwestern Catahoula Parish, Louisiana. Unpublished MS, University of Louisiana at Monroe.