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EASTERN PALEONTOLOGIST

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Late Pliocene (Yorktown Formation) Teleostean Otoliths from New Localities in North Carolina, USA, and their Relationship to Other North American Assemblages

Gary L. Stringer[1]*, Eric Sadorf[2], and Kevin Shannon[3]

Abstract - Two new outcrops from the Late Pliocene Yorktown Formation in North Carolina, USA, at the Bell Bridge and Dixon localities produced 29 and 13 species, respectively, based on 672 teleostean otoliths. Otoliths are closely related to extant species along the present-day eastern U.S. coast with ophidiids, paralichthyids, and haemulids most abundant. Percentage similarity analysis indicates that the localities are markedly different. Based on the fossil fish assemblage, the paleoenvironment is interpreted as marine, deep inner–middle shelf, normal salinity, and tropical–temperate. The new Pliocene fish otolith assemblages were analyzed to understand the relationship to the coeval Yorktown Formation fish assemblage from the Lee Creek Mine. The new assemblages are significant, considering the limited number of North American Pliocene otolith studies and provide insight into northwestern Atlantic Coast Pliocene paleoenvironments. The relationship of the new Pliocene fish otoliths to known Pliocene otolith assemblages from North America is established.

Introduction

The fish otolith assemblages from the Yorktown Formation (upper Pliocene in North Carolina) at the Bells Bridge and the Dixon localities present an important opportunity to analyze and describe Pliocene otoliths. Previous research on Pliocene otoliths from the Yorktown Formation in North Carolina, USA, was conducted by Fitch and Lavenberg (1983), Müller (1999), and Stringer and Shannon (2019). Studies are not only very limited, but also the focus of these contributions was primarily on Rushmere Member sites in the central coastal area of North Carolina (Fig. 1). The two localities on the Tar River are located significantly further inland and to the northwest, and these factors have paleogeographic implications (such as paleoshorelines, paleowater depths, and latitudinal variations) for the Pliocene of North Carolina, the Atlantic Coastal Plain, and North America.

As indicated by numerous studies (Nolf 2013, Nolf and Stringer 2003, Schwarzhans et al. 2018, Stringer and Bell 2018, and references therein), otoliths often provide data on taxa that are not represented by skeletal remains. This is due primarily to different diagenetic processes related to the contrasting composition of bone (fluorapatite) and otoliths (aragonite), as indicated by studies, such as Aguilera et al. (2020) and references therein. Therefore, the otolith assemblages contribute to a more comprehensive understanding of the bony fishes from the Yorktown Formation, as well as the North American Pliocene. The otoliths from the two new sites will be compared to the abundant otoliths from the Yorktown Formation at the well-known Lee Creek Mine (currently known as the Nutrien phosphate mine) in Aurora, North Carolina. In addition to their taxonomic value, the otolith assemblages provide valuable data in assessing paleoecological parameters during the Pliocene. The relationship of the new North American Pliocene otolith taxa

from the Bells Bridge and Dixon localities reinforces the record of an exceptional fossil assemblage in the northwest Atlantic and allow comparisons to the known Pliocene otoliths from North America.

Geological Setting

The otoliths for this investigation were obtained primarily from bulk samples collected from two different localities on the Tar River in Edgecomb County, North Carolina (Fig. 1). The Bells Bridge locality is located northwest of Tarboro, just beyond the town on
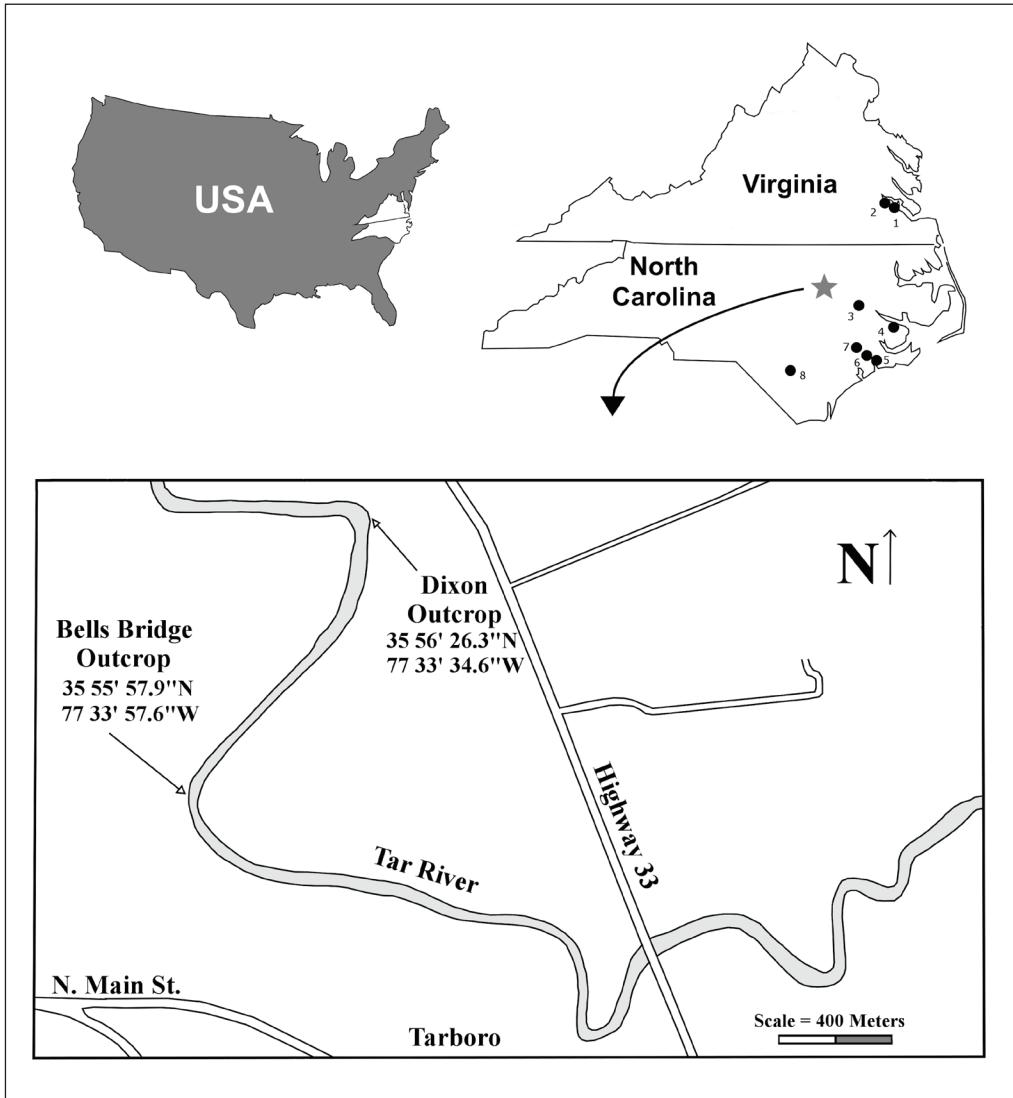
Figure 1. Location map of the Bells Bridge and Dixon localities on the Tar River in Edgecomb County, North Carolina. Other sites relevant to this study include the following: 1-2. James River and Piankatank sites (Müller 1999), 3. Greenville site (Müller 1999), 4. Lee Creek Mine (Fitch and Lavenberg 1983, Müller 1999), 5. Silverdale site (Müller 1999), 6. Hayward Landing (Müller 1999), 7. Belgrade site (Müller 1999), 8. Elizabethtown site (Stringer and Shannon 2019).

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rthe western bank of the Tar River (35 55' 57.9" N, 77 33' 57.6" W). Shell beds with well-preserved mollusks were present at the site (Fig. 2). Bulk samples were collected from two different levels at the site. The lower collecting area (referred to as the "green layer") was located at the water level of the Tar River. The upper collecting area (referred to as the "shell layer") was four m above the lower collecting area. The Dixon locality is situated approximately 800 m upstream (north) of the Bells Bridge locality on the opposite bank of the Tar River (35 56' 26.3" N, 77 33' 34.6" W). Bulk sampling at the Dixon locality was limited to one shell-bearing layer.

Difficulties and problems in understanding the Neogene stratigraphy of the Atlantic Coastal Plain have been enumerated for over 100 years (Campbell 1995, Clark et al. 1912, Cooke 1943, Cooke and Munyan 1938, Dowsett et al. 2019, Henry and Hoyt 1965, Hoyt and Hails 1974, Huddleston 1988, Krantz 1991, Veatch and Stephenson 1911, Ward and Blackwelder 1980). Campbell and Campbell (1995) pointed out that the stratigraphic relationships among Pliocene beds have not been clearly demonstrated in spite of decades of extensive investigations. Albright et al. (2019), in an extensive investigation of the Cenozoic vertebrate biostratigraphy of South Carolina, noted that a clear understanding of the stratigraphy is hindered by the paucity of well-exposed fossil-bearing stratigraphic sections. Furthermore, they pointed out that lateral continuity is often difficult to ascertain, and this is true for much of the Atlantic Coastal Plain. However, in spite of these complications, available stratigraphic and paleontologic evidence, such as lithologic characteristics, stratigraphic correlation, and diagnostic fossil invertebrates, indicates that the bulk samples from both localities were collected from the upper Pliocene Rushmere Member of the Yorktown Formation. This would place the age of the otoliths at no older than 3.3 Ma and most likely 3.2 Ma according to Dowsett et al. (2019) or in the Piacenzian, which is shown as extending from 2.58–3.60 Ma according to Cohen et al. (2018).

Studies of the Atlantic Coastal Plain Pliocene otoliths consist of only four studies: Fitch and Lavenberg (1983), Müller (1999), Stringer and Bell (2018), and Stringer and Shannon

Figure 2. Shell beds with well-preserved mollusks at the Dixon locality, Edgecomb County, North Carolina, USA. There are disarticulated bivalves including shallow-water Pectinidae as well as small gastropods present in the shelly layers.

(2019). There is only one published study of Pliocene otoliths from the Gulf Coastal Plain (Stringer et al. 2020a). Stringer and Bell (2018) reported on the Plio-Pleistocene otoliths (n = 1803; 50 taxa) from coastal Georgia. Five of the sites were primarily early Pliocene in age. Stringer and Shannon (2019) described a Pliocene (Piacenzian) otolith assemblage from southeastern North Carolina (n = 745 specimens; 17 taxa). Fitch and Lavenberg (1983) conducted research on otoliths (n = 8808; 45 taxa) from the Yorktown Formation (upper lower Pliocene) from the Nutrien phosphate mine in North Carolina (formerly known as the Lee Creek Mine). Müller (1999) also described the otoliths from Lee Creek Mine and conducted an extensive investigation of the elasmobranchs and teleosts (including otoliths) of the middle Eocene to the early Pliocene of Maryland, Virginia, and North Carolina. In North Carolina, Müller's research concentrated on the central coastal area, primarily around Aurora and just south of New Bern (Müller 1999, fig. 10). However, Müller did collect at one site on the Tar River near Greenville in Pitt County. The 2 localities of this study are much further inland than the previously studied sites, i.e., the Bells Bridge locality is approximately 96 km north-northwest of Aurora (Fig. 1).

It should be duly noted that the ages of the localities from which Pliocene otoliths have been studied are based on those provided by the authors in the original publications. There is the possibility that these ages have been revised according to more recent and detailed stratigraphic studies and comparisons to more contemporary time scales such as that of Ogg, Ogg, and Gradstein (2016). However, a review and revision of the ages of these localities and contained formations are well beyond the scope of this study.

Materials and Methods

The fish otoliths for this study were obtained from bulk sampling at the two localities by one of the authors (ES). A small number of large otoliths were collected on the surface, but these are not included in the statistical analysis. Surface collecting has been shown to be valuable for developing growth series of taxa (Stringer et al. 2020b). Unless otherwise noted, all specimens are from the residue of bulk samples. Approximately 342 kg of sediment was screened onsite (approximately 1.3 x 1.6 mm openings) from the Bells Bridge locality producing 431 otoliths, while 159 kg was screened from the Dixon locality producing 241 otoliths. Three small bulk samples were processed offsite by thoroughly drying the samples before wet screening with water. Residue from an 18-mesh sieve (US Sieve with 1.00-mm openings) was retained for microscopic examination. After wet screening, the residue was dried, and otoliths were extracted using a stereomicroscope. All figured material is reposited in the North Carolina Museum of Natural Sciences, Raleigh, North Carolina.

The taxa represented by otoliths from the Bells Bridge and Dixon localities are briefly described below. Some of the taxa identified from the two sites are described and illustrated in Fitch and Lavenberg (1983), Müller (1999), Stringer and Bell (2018), and Stringer and Shannon (2019). However, there are some taxa that have not been previously described; some require taxonomic revisions, and some need additional comments. 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 and Johnson (2010), while the family-group names and authors of extant fishes follow Van der Laan et al. (2014, 2017, 2018). Authors of modern genera and species depend greatly upon Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al. 2019). Common names were obtained from Froese and Pauly (2020).

Results

Taxonomy of the Otoliths

The taxonomical composition of the two investigated localities includes at least 672 fish otoliths that represent 31 taxa distributed over 15 families (Table 1). The taxa represented by otoliths from the Bells Bridge and Dixon localities are briefly described below.

Class Osteichthyes
Subclass Actinopterygii sensu Goodrich
Order Anguilliformes Goodrich
Family Congridae Kaup
Gnathophis Kaup
Gnathophis sp.

One sagitta from the Dixon locality is assigned to *Gnathophis* based on several attributes. The shape of the otolith is primarily oval (sensu Smale et al. 1995). The margins are mainly smooth, although the dorsal margin has some small undulations. There is a prominent congrid-type sulcus (i.e., undivided) with an ostial channel that opens onto the anterodorsal margin. The anterior margin of the sulcus (ostial region) is rounded and is located near the anterior margin of the otolith. The posterior portion of the sulcus (caudal region) is also rounded and is well separated from the posterior margin. There is no evidence of a depressed area above the sulcus (a key characteristic of this congrid genus). There appears to be a faint ventral furrow located very close to the ventral margin. Müller (1999) attributed four otoliths to *Gnathophis* sp. from the Rushmere Member of the Yorktown Formation at Lee Creek in North Carolina. Müller also noted that Congridae sp. B (seven specimens from bulk sampling) of Fitch and Lavenberg (1983, fig. 1c) from the same member at Lee Creek belongs to *Gnathophis.*

Order Clupeiformes Bleeker
Family Engraulidae Gill
Anchoa Jordan and Evermann
Anchoa hepsetus (Linnaeus) (Broad-striped Anchovy)
(Fig. 3A)

A single, well-preserved sagitta from Bells Bridge has distinctive engraulid characteristics that allow assignment to *Anchoa hepsetus*. The outline of the sagitta is oval in shape (sensu Smale et al. 1995). The anterior margin is pointed (i.e., the shape of the rostrum), while the posterior margin is fairly equally rounded. The dorsal margin is essentially horizontal, except for a slight slant toward the posterior. The ventral margin is smoothly rounded with the greatest depth at approximately 60% of the length of the sagitta. This species and other engraulids tend to be very rare in Plio-Pleistocene otolith assemblages in the Atlantic and Gulf Coast plains. Fitch and Lavenberg (1983) examined over 8,800 otoliths from the Pliocene Rushmere Member at the Lee Creek Mine in North Carolina and reported no engraulids. Likewise, Müller (1999) found no engraulids in his extensive study of over 12,000 otoliths (Eocene to Pliocene) along the Atlantic Coastal Plain, including numerous sites in North Carolina. Stringer and Bell (2018) reported *A. hepsetus* from the Plio-Pleistocene of coastal Georgia, but it accounted for only 0.2% of the total specimens. Although slightly more abundant at the Jones Girls site (Pleistocene, Georgia), *A. hepsetus* accounted for just

over 1% of the total (Stringer and Hulbert 2020). Stringer and Shannon (2019) reported similar results in the Pliocene of southeastern North Carolina where *A. hepsetus* represented only 0.4% of the total. The largest percentage of this species was 3.20% from the Dauphin Island site (Pliocene) in Alabama (Stringer et al. 2020a).

Family Clupeidae Cuvier
Brevoortia Gill
Brevoortia sp.
(Fig. 3B)

A single clupeid otolith is tentatively assigned to *Brevoortia* sp. because of its preservation. The shape is ovate (sensu Smale et al. 1995) with a very prominent rostrum and antirostrum. The dorsal margin is mainly smooth with some small lobes, while the ventral margin is coarsely serrate. The sulcus is relatively long and wide and comprises much of the inner face. The ostial portion comprises the rostrum and antirostrum, while the caudal portion is located more medially. The specimen has characteristics similar to *Brevoortia tyrannus* known from the US Atlantic coast (Campana 2004:46), but its preservation does not allow a definitive identification.

Order Myctophiformes Regan
Family Myctophidae Gill
Diaphus Eigenmann & Eigenmann
Diaphus sp.
(Fig. 3D)

One eroded myctophid sagitta from Bells Bridge was found to best match *Diaphus.* The outline of the sagitta is oval to elliptic (sensu Smale et al. 1995). The margins are slightly lobed. The sulcus extends across approximately 75% of the length of the otolith but is slightly impressed. The ostium is at least two times longer than the cauda but is about the same width. The cauda tends to be almost oval in shape. A faint ventral furrow appears to be present. Since the specimen is worn, identification of the species is not possible. Müller (1999) identified *Diaphus* sp. 2 from the upper Pliocene Yorktown Formation (Rushmere Member) at the Lee Creek Mine according to the text, but plate 21/figures 29–31 indicate that *Diaphus* sp. 1 is from the Yorktown Formation, while plate 22, figure 1 shows that Diaphus sp. 2 is actually from the Calvert Formation of Maryland. The figures of *Diaphus* sp. 1 and 2 of Müller (1999) are considered correct in their assignment of the taxa, but the text is switched (W. Schwarzhans, Natural History Museum of Denmark, Copenhagen, Denmark, pers. comm.). Stringer and Bell (2018) reported no myctophids from the seven Plio-Pleistocene sites in coastal Georgia.

Order Gadiformes Goodrich
Family Merlucciidae Rafinesque
Merluccius Rafinesque
Merluccius albidus (Mitchill) (Offshore Silver Hake)
(Fig. 3E)

Nine sagittae from Bells Bridge (6) and Dixon (3) were assigned to *Merluccius albidus*, which is one of two merlucciids that are identifiable to species from the Rushmere sites. The specimen has typical merlucciid features, such as the homosulcoid type sulcus and

Table 1. Otolith-based diversity from the Bells Bridge and Dixon localities in Edgecombe County, North Carolina, USA (numbers and percentages).

Taxa present in the Bells Bridge and Dixon sites	Bells Bridge Locality		Dixon Locality	
Family (bold) Genus and species	No. of otoliths	% of total	No. of otoliths	% of total
Congridae (conger eels)				
Gnathophis sp.	0	0	1	0.42
Engraulidae (anchovies)				
Anchoa hepsetus	1	0.23	0	0
Clupeidae (herrings)				
Brevoortia sp.	1	0.23	0	0
Myctophidae (lanternfishes)				
Diaphus sp.	1	0.23	0	0
Merlucciidae (merlucciid hakes)				
Merluccius albidus	6	1.39	3	1.24
Merluccius bilinearis	11	2.55	5	2.07
Merluccius sp.	0	0	6	2.49
Gadidae (cods and haddocks)				
Melanogrammus sp.	7	1.62	1	0.42
Pollachius cf. *P. virens*	1	0.23	0	0
Urophycis chuss	15	3.48	5	2.07
Urophycis regia	2	0.46	0	0
Micromesistius sp.	5	1.16	0	0
Ophidiidae (cusk-eels)				
Otophidium omostigma	12	2.78	0	0
Ophidion aff. *O. josephi*	13	3.02	0	0
Lepophidium profundorum	123	28.54	156	64.73
Lepophidium sp.	7	1.62	0	0
Ophidion aff. *O. grayi*	23	5.34	0	0
Paralichthyidae (sand flounders)				
Citharichthys macrops	83	19.26	43	17.84
Syacium cf. *S. gunteri*	1	0.23	0	0
Cynoglossidae (tonguefishes)				
Symphurus sp.	2	0.46	0	0
Stromateidae (butterfishes)				
Peprilus sp.	2	0.46	1	0.42

Table 1. Continued.

Family (bold) Genus and species	No. of otoliths	% of total	No. of otoliths	% of total
Uranoscopidae (stargazers)				
Kathetostoma albigutta	1	0.23	0	0
Serranidae (sea basses)				
Diplectrum cf. *D. formosum*	22	5.10	5	2.07
Haemulidae (grunts)				
Orthopristis chrysoptera	57	13.23	10	4.15
Triglidae (searobins)				
Prionotus cf. *P. carolinus*	8	1.86	1	0.42
Sciaenidae (drums and croakers)				
Micropogonias undulatus	1	0.23	0	0
Pogonias cromis	2	0.46	0	0
Cynoscion arenarius	12	2.78	0	0
Cynoscion sp.	1	0.23	0	0
Leiostomus aff. *L. xanthurus*	10	2.32	4	1.66
Menticirrhus americanus	1	0.23	0	0
Totals	**431**	—	**241**	—

quite thin in thickness, and matches *Merluccius albidus*, the Offshore Silver Hake, almost perfectly (Campana 2004:68). *Merluccius albidus* is widespread along the western Atlantic US coast and throughout the Gulf of Mexico and Caribbean according to Cohen et al. (1990). It differs from the similar *M. bilinearis* by a lower length/height (L/H) ratio and a less expanded ostium and cauda. Fitch and Lavenberg (1983) reported 85 *M. albidus* from the Pliocene Yorktown Formation at Lee Creek Mine in North Carolina, but most of these were larger specimens from surface collections. Stringer and Bell (2018) noted only 6 specimens from 7 Plio-Pleistocene sites in coastal Georgia.

<div align="center">

Merluccius bilinearis (Mitchill) (Silver Hake)
(Fig. 3F)

</div>

    Merluccius bilinearis, the second merlucciid hake recovered from the Rushmere sites, is represented by 16 sagittae from Bells Bridge (11) and Dixon (5). The specimens have a high length/height ratio, and the ostium and cauda are slightly more expanded than in *Merluccius albidus*. Specimens are nearly a perfect match for *Merluccius bilinearis* (Campana 2004:69). Fitch and Lavenberg (1983) identified 493 *M. bilinearis* from the Pliocene Yorktown Formation at the Lee Creek Mine, primarily from surface collections. Stringer and Bell (2018) reported only 3 specimens of *Merluccius bilinearis* from seven Plio-Pleistocene localities in coastal Georgia.

Merluccius sp.

Six sagittae from Dixon show definite characteristics of *Merluccius*. Unfortunately, the specimens do not show significant morphological features to determine the species. The specimens may be one of the two species of *Merluccius* previously described from the Rushmere sites, but they may represent a different species. Better preservation would answer this question.

Family Gadidae Rafinesque
Melanogrammus Gill
Melanogrammus sp.
(Fig. 3G)

Eight sagittae from Bells Bridge (7) and Dixon (1) show characteristics that compare favorably with *Melanogrammus*. The shape of the sagitta tends to be oblong (sensu Smale et al. 1995). On well-preserved specimens, the margins are fairly regularly lobed with the ventral margin more strongly lobed. The anterior margin is tapered slightly and slightly rounded, while the posterior margin is more tapered and pointed. The inner face is convex. There is a prominent, fairly lighted impressed sulcus (homosulcoid type) that extends essentially across the inner face. The ostium and cauda are about the same heights, but the cauda is longer (about 1.5 times) in length. There is a conspicuous division between the ostium and cauda. Fitch and Lavenberg (1983) reported one specimen of *Melanogrammus* cf. *M. aeglefinus* from the Lee Creek Yorktown Formation, and Müller (1999) assigned one specimen from there to *Melanogrammus* sp.

Pollachius Nilsson
Pollachius cf. *P. virens* Linnaeus (Saithe)
(Fig. 3H)

One sagitta from Bells Bridge compared favorably with *Pollachius virens*. The sagitta is primarily oblong in outline (sensu Smale et al. 1995). The margins tend to be irregularly lobed, but it is not pronounced, especially on the dorsal margin. The anterior is very broadly rounded, while the posterior is tapered to a rounded point. There is a conspicuous sulcus (homosulcoid type) that extends almost across the very slightly convex, inner face. The ostium, which has a tapered anterior, almost reaches the anterior margin. The ostium posterior is noticeably constricted on the ventral just before the cauda. Except for this constriction, the ostium is about the same width as the cauda. The cauda is 1.5 times longer than the ostium. The dorsal and ventral margins of the cauda are almost parallel to one another. This is the first known fossil occurrence of *Pollachius* cf. *P. virens* in the U.S. Pliocene.

Urophycis Gill
Urophycis chuss Walbaum (Red Hake)
(Fig. 3I)

Twenty sagittae from Bells Bridge (15) and Dixon (5) are classified as *Urophycis chuss*, which is characterized by an elongated, undivided sulcus that extends at least 95% of the length of the inner face. The sulcus constricts noticeably in the anterior and opens near the anterodorsal margin. The species is characterized by a high L/H ratio (approximately 4.0). The anterior tip of *Urophycis chuss*, which is elongated and pointed, tends to

be located slightly more ventrally than in *Urophycis tenuis*. The dorsal margin is almost horizontal and only slightly sculptured. The posterior margin is tapered almost to a point but not sharply. The ventral margin tends to be only slightly sculptured, primarily near the center. The posteroventral margin is almost straight and slants toward the ventral, while the anteroventral margin slants very slightly toward the anterior margin. Several species of *Urophycis* have been described in Fitch and Lavenberg (1983), Müller (1999), Stringer and Bell (2018), and Stringer and Shannon (2019), but this is believed to be the first fossil record of *Urophycis chuss* in the U.S.

Urophycis cf. *U. regia* Walbaum (Spotted Codling)

Like other species of *Urophycis*, the 2 sagittae from Bells Bridge are characterized by a very narrow, oblong shape where the length is at least four times greater than the height (very high L/H ratios around 4.0). Greatest height is anterior to the center. Otolith tapers towards posterior but is not acutely pointed. Sulcus is undivided, almost as long as the otolith. Dorsal margin is not as horizontal as in *Urophycis chuss*. Ventral margin of *Urophycis* cf. *U. regia* is more sculptured (pronounced lobes), and the anterior is not as pointed as in *Urophycis chuss*. Otoliths of *Urophycis regia* are shown in Campana (2004:80), and *Urophycis* aff. *U. regia* is figured in pl. 23 (fig. 5a–b) of Müller (1999). *Urophycis regia* was very rare (less than 1%) in the Pliocene Dauphin Island site in Alabama (Stringer et al. 2020a).

Micromesistius Gill
Micromesistius sp.
(Fig. 3J)

Five gadid sagittae from Bells Bridge appear to best match *Micromesistius*. None of the specimens are preserved well enough to assign them to species. The shape of the otolith is oblong (sensu Smale et al. 1995). However, the anterior is rounded, while the posterior is tapered to a point but not sharply. The dorsal margin is smooth to very slightly lobed, while the ventral margin is more noticeably lobed. The sulcus is very long, almost horizontal, and extends almost the entire length of the inner face, which is slightly convex. The well-defined ostium is much smaller in length than the cauda but about the same height, perhaps slightly less. The cauda is approximately 2.5 times longer than the ostium and almost touches the posterior margin. Fitch and Lavenberg (1983) and Müller (1999) did not report any specimens of *Micromesistius* from Lee Creek Mine, but Müller (1999) did identify two broken specimens as *Micromesistius* aff. *M. potassou* from the Yorktown Formation in Virginia.

Order Ophidiiformes Berg
Family Ophidiidae Rafinesque
Otophidium Gill
Otophidium omostigma Jordan and Gilbert (Polka-dot Cusk-eel)
(Fig. 3K)

This taxon is based on 12 sagittae from Bells Bridge and is 1 of 6 ophidiids recovered from the sites. *Otophidium omostigma* is characterized by a medially located, narrow, straight, longitudinally divided sulcus. In larger specimens, the dorsal margin of the sulcus is conspicuously arched. One of the most distinguishing features is the wide middorsal dome, which can significantly skew the shape towards the anterodorsal margin. This

feature is more obvious in the larger specimens. The posterior end tapers but not sharply pointed. The shape is oval to more rounded with increased size. This species was the most abundant ophidiid reported from the Plio-Pleistocene of coastal Glynn County, Georgia (242 specimens) by Stringer and Bell (2018), while Müller (1999) does not report this species the U.S. Atlantic Coastal Plain.

Ophidion Linnaeus
Ophidion aff. *O. josephi* Girard (Crested Cusk-eel)
(Fig. 3L)

This species identification was based on 13 sagittae from Bells Bridge. The sagittae are primarily oval in outline (sensu Smale et al. 1995). The anterior margin is rounded, while the dorsal margin is characterized by a broad, middorsal dome, often more developed in larger specimens. The posterodorsal margin can be almost straight to slightly rounded and slants strongly toward the posterior. The posterior end is tapered but not distinctly pointed. The ventral margin of the otolith is broadly rounded. The slightly convex inner face is characterized by a moderately wide, undivided sulcus. Sulcus is extremely close to the anterior margin but not as close to the posterior margin. Dorsal margin of sulcus may be arched, while sulcus ventral margin is almost horizontal except for a pronounced posterior expansion. Sulcus tapers near the anterior. Müller (1999) reported *Ophidion* aff. *O. josephi* (as *Ophidion* aff. *O. welshi,* a synonym of *O. josephi*) from the Yorktown Formation (Rushmere Member) at Lee Creek.

Ophidion cf. *O. grayi* Fowler (Blotched Cusk-eel)
(Fig. 4B)

These 23 sagittae from Bells Bridge appear to match *Ophidion grayi*, but this cannot be stated unequivocally. Margins are smooth to slightly irregular. Anterior is rounded and can be very close to vertical. The anterodorsal is characterized by a dome, which can become fairly prominent. The dorsal and posterodorsal tend to slant downward toward the posterior. The posterior is tapered but not greatly. Ventral margin tends to be broadly rounded. The very slightly convex inner face is characterized by a fairly large, undivided sulcus that extends from almost the anterior margin to near the posterior margin. Sulcus is somewhat tapered at the anterior and enlarged at the rounded posterior. There is no discernible depressed area above the sulcus. There are indications of a possible faint ventral furrow. Fitch and Lavenberg (1983) and Müller (1999) reported *Ophidion grayi* and *Ophidion* aff. *O. grayi,* respectively, from the Yorktown Formation at the Lee Creek Mine.

Lepophidium Gill
Lepophidium profundorum Gill (Blackrim Cusk-eel)
(Fig. 4A)

This common ophidiid accounts for 279 sagittae from Bells Bridge (123) and Dixon (156). The undivided sulcus is almost the same width for its entire length except for a slight enlargement at the posterior end. The narrow sulcus is mainly medially located and almost reaches the anterior and posterior margins. The sulcus' upper and lower margins are almost horizontal and parallel to one another. The posterior is pointed and quite aculeate in many specimens, while the anterior is rounded. The prominent anterodorsal dome is high and

Figure 3. All illustrated specimens were collected from the Bells Bridge Locality and Dixon Locality in Edgecomb County, North Carolina. The taxonomic identification of each otolith specimen (all inner views of sagittae) and the location of the otolith in the labyrinth (right or left side) are given. Length of otolith is given in mm. Scale for each otolith = 1mm. The specimens figured are reposited in the North Carolina Museum of Natural Sciences, and catalog numbers are provided.

A. *Anchoa hepsetus*, left, 2.55 mm, NCSM 33777
B. *Brevoortia* sp., left, 3.07 mm, NCSM 33778
C. *Peprilus* sp., left, 3.65 mm, NCSM 33779
D. *Diaphus* sp.*,* left, 3.21 mm, NCSM 33780
E. *Merluccius albidus,* right, 6.62 mm, NCSM 33781
F. *Merluccius bilinearis*, right, 13.39 mm, NCSM 33782
G., *Melanogrammus* sp., right, 17.99 mm, NCSM 33783
H. *Pollachius* cf. *P. virens*, left, 18.23 mm, NCSM 33784
I. *Urophycis chuss*, left, 10.57 mm, NCSM 33785
J. *Micromesistius* sp., left, 5.88 mm, NCSM 33786
K. *Otophidium omostigma*, left, 3.46 mm, NCSM 33787
L. *Ophidion* aff. *O. josephi*, left, 4.31 mm, NCSM 33788

variable in shape. Some margins along the dome can be somewhat lobate. The L/H ratios tend to decrease with increased size. It has been reported from the North Carolina Pliocene (Fitch and Lavenberg 1983), from the Louisiana late Pleistocene (Stringer 1992), and from the Jamaica Pliocene (Stringer 1998), all as *L. cervinum.* Müller (1999) also described *Lepophidium* aff. *L. profundorum* (as *Lepophidium* aff. *L. cervinum*) from the Yorktown Formation at Lee Creek. All references to *L. cervinum* (except for 1863 and 1895) refer to *L. profundorum* (Robins et al. 2012.)

Lepophidium sp.

Seven specimens from Bells Bridge have morphological features that point to *Lepophidium*. Unfortunately, the specimens are not preserved well enough to make a species determination.

Order Pleuronectiformes Bleeker
Family Paralichthyidae Regan
Citharichthys Bleeker
Citharichthys macrops Dresel (Spotted Whiff)
(Fig. 4C)

This species was identified on 126 sagittae from Bells Bridge (83) and Dixon (43). The sagitta's shape in well-preserved specimens is pentagonal in outline with distinct predorsal, postdorsal, and midventral angles as well as an anterior tip and a prominent posterior tip that is somewhat rounded. It is characterized by a unique sulcus in which the anterior and posterior portions are much narrower, but the middle portion is widened (termed fusiform by Schwarzhans 1999). Ostial and caudal colliculi are fused. Comparisons to extant forms from the U.S. Atlantic and Gulf coasts indicated *Citharichthys macrops* (Page et al. 2013, Schwarzhans 1999). Stringer (1992) noted the presence of *Citharichthys* from the late Pleistocene of Louisiana. Stringer and Bell (2018) reported only 2 specimens from 7 Georgia Plio-Pleistocene sites.

Syacium sp. Ranzani
Syacium cf. *S. gunteri* Ginsburg (Shoal Flounder)
(Fig. 4D)

The one specimen from Bells Bridge assigned to *Syacium* cf. *S. gunteri* resembles *Citharichthys macrops.* *Syacium* and *Citharichthys* are believed to be closely related phylogenetically (Schwarzhans 1999), which is a likely reason for their similarity. Like *Citharichthys,* the sulcus of *Syacium gunteri* is fusiform (i.e., the anterior and posterior portions are much narrower, but the middle portion is widened). One key difference in *Syacium gunteri* is that the posterior tip is located more toward the dorsal (Schwarzhans 1999, figs 253–254). Stringer (1992) described *Syacium gunteri* from the late Pleistocene mudlump islands in Louisiana.

Family Cynoglossidae Jordan and Goss
Symphurus Rafinesque
Symphurus sp.
(Fig. 4E)

One sagitta from Bells Bridge exhibits characteristics that point to the cynoglossid *Symphurus*. The small otoliths (< 3 mm) are discoid in shape with a very unique hammer-

shaped sulcus with fused colliculi. The ostial portion of the sulcus is reduced while the cauda is bilobate in shape. The shallow sulcus has a well-developed circumsulcal depression. Page et al. (2013) listed 13 species of *Symphurus* from the Atlantic of the United States and Mexico, and specimens or figures of the sagittae of the species are not available. The outline and sulcus of the specimens are similar to *Symphurus plagiusa*, but this cannot be determined unequivocally. Although not abundant in the fossil record, *Symphurus* otoliths have been reported by Nolf (1976) in the Trinidad Miocene, Fitch and Lavenberg (1983) in the North Carolina Pliocene, Nolf and Stringer (1992) in the Dominican Republic Miocene, Stringer (1992) in the Louisiana late Pleistocene, Stringer and Bell (2018) in the Georgia Pliocene, and Stringer and Shannon (2019) in the North Carolina Pliocene. The *Symphurus* sp. from Bells Bridge may be the same as the *Symphurus*, illustrated in Fitch and Lavenberg (1983, fig. 4G) from the Lee Creek Mine.

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Order Scombriformes Betancur-R. et al.
Family Stromateidae Rafinesque
Peprilus Cuvier
Peprilus sp.
(Fig. 3C)

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Three small specimens (slightly larger than 2 mm) from Bells Bridge (2) and Dixon (1) were attributed to *Peprilus*. The outline is primarily ovate (sensu Smale et al. 1995) but with the greatest height in the posterior one-third of the sagittae. Dorsal margin is irregularly lobed along its entirety, while the ventral margin is more uniformly lobed in the best-preserved specimen. The inner face is almost flat and has a long, narrow sulcus (extends almost 95% of the length). The ostium portion is somewhat excavated. The caudal section is shallower and not as wide as the ostium. Cauda has slightly tapered posterior. There is a very conspicuous rostrum and antirostrum. This taxon has not been reported in any of the Pliocene studies in the Atlantic Coastal Plain (Fitch and Lavenberg 1983, Müller 1999, Stringer and Bell 2018, Stringer and Shannon 2019).

<div align="center">

Order Trachiniformes (sensu Nelson et al.)
Family Uranoscopidae Bonaparte
Kathetostoma Günther
Kathetostoma albigutta Bean (Lancer Stargazer)
(Fig. 4F)

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The one sagitta from Bell Bridge matches *Kathetostoma albigutta* extremely well. The shape is oval (sensu Smale et al. 1995), and small lobes characterize most of the margins. The dorsal margin is slightly arched, while the posterior is mainly rounded. The ventral margin is evenly, but only slightly, rounded. Anterior margin is characterized by the sulcus opening, rostrum, and antirostrum. A narrow, distinct sulcus characterizes the convex inner face and extends about 60% of the length slanting slightly from near the anterodorsal towards the middle. There is no discernible ostium and cauda, but this may be related to erosion. A linear depressed area is located above the middle to posterior portion of the sulcus. A slight crista superior and crista inferior appear to be present. A ventral furrow may be present, but the ventral margin is eroded somewhat. Fitch and Lavenberg (1983, fig. 4b) reported 12 surface-collected specimens of *Kathetostoma* from the Rushmere Member at the Lee Creek Mine. The illustrated specimen in Fitch

and Lavenberg (1983) appears to be eroded and possibly broken. This is the first fossil record of *Kathetostoma albigutta*.

Order Perciformes (sensu Nelson et al.)
Family Serranidae Swainson
Diplectrum Holbrook
Diplectrum cf. *D. formosum* Linnaeus (Sand Perch)
(Fig. 4G)

The 27 sagittae from Bells Bridge (22) and Dixon (5) compare favorably with *Diplectrum formosum*. The shape is primarily elliptic, and the margins tend to be smooth to irregular (sensu Smale et al. 1995). The dorsal margin is arched, while the ventral margin is only slightly arched Anterior margin is acutely pointed, while posterior margin is tapered to a more rounded point. The prominent sulcus (heterosulcoid type) extends across approximately 75% of the inner face. The sulcus is excavated with obvious colliculum. Ostium is slightly wider than cauda but about the same length. Ostium extends the length of the prominent and pointed rostrum. The cauda is narrow and horizontal except for the posterior, which downturns at a 45^0 angle. There is a depressed area above the sulcus (more pronounced over the cauda). Ridge-like crista superior is primarily above the cauda. Ventral furrow present and exaggerated by erosion. Fitch and Lavenberg (1983) described 16 specimens of *Diplectrum* cf. *D. formosum* from the Lee Creek Mine, which was the first fossil record of the genus. Müller (1999) reported 2 specimens of *Diplectrum* sp. from the same site.

Family Haemulidae Gill
Orthopristis Girard
Orthopristis chrysoptera Linnaeus (Pigfish)
(Fig. 4H)

This species is identified on 67 sagittae from Bells Bridge (57) and Dixon (10). It has an oval outline with smooth margins. There is a prominent sulcus with a well-defined ostium and cauda (heterosulcoid type). Ostium is wider than the cauda but only about one-half the cauda's length. The cauda is narrow and consistent in width. The cauda is horizontal except for the posterior, which is prominently downturned. A centrally located ventral furrow is present. Stringer and Bell (2018) reported this species from the Plio-Pleistocene of coastal Georgia, but it was rare with only 3 specimens. The species was also rare in the Pliocene Dauphin Island site in coastal Alabama (Stringer et al. 2020a).

Order Scorpaeniformes Garman
Family Triglidae Rafinesque
Prionotus Lacepède
Prionotus cf. *P. carolinus* Linnaeus (Northern Searobin)
(Fig. 4I)

The outline of the 9 sagittae from Bells Bridge (8) and Dixon (1) of *Prionotus carolinus* is basically oval, but the anterior and posterior are somewhat pointed. Ostium is only slightly larger than the cauda. Anterior and posterior colliculum is present. A slightly depressed area is located above the anterior and central portion of the sulcus. Although not abundant, *Prionotus* has been reported from the North Carolina Pliocene (Fitch and Lavenberg 1983),

the Dominican Republic Pliocene (Nolf and Stringer 1992), the Louisiana late Pleistocene (Stringer 1992), and the Jamaica Pliocene (Stringer 1998), and the Plio-Pleistocene of coastal Georgia (Stringer and Bell 2018).

Order Acanthuriformes (sensu Nelson et al.)
Family Sciaenidae Cuvier
Micropogonias Bonaparte
Micropogonias undulatus Linnaeus (Atlantic Croaker)

Micropogonias undulatus, identified on one sagitta from Bells Bridge, is shield-like in outline with the thickened dorsal rim relatively flat, but the sharp ventral rim is deeply curved anteriorly with a distinct concavity posteriorly. Heterosulcoid sulcus is very large and encompasses much of the inner face. Ostium is compressed but very deep and extends from almost the dorsal margin to near the ventral margin. Height of the cauda is only about 1/4 of the ostium's height and has a characteristic enlarged caudal tip (Schwarzhans 1993). The outer face commonly has a prominent, raised umbo. It is reported and figured from the North Carolina Pliocene (Rushmere Member, Yorktown Formation) by Fitch and Lavenberg (1983) and by Müller (1999) (as *Micropogonias* aff. *M. undulatus*), the Louisiana late Pleistocene (Stringer 1992), the Georgia Plio-Pleistocene (Stringer and Bell 2018), the Pliocene of coastal Alabama (Stringer et al. 2020a), the Pleistocene of coastal Georgia (Stringer and Hulbert 2020), the North Carolina Pliocene (Stringer and Shannon 2019), and the Mississippi subsurface Miocene (Stringer and Starnes 2018, 2020).

Pogonias Lacepède
Pogonias cromis Linnaeus (Black Drum)

The 2 specimens from Bells Bridge assigned to *Pogonias cromis* are primarily rectangular in shape (sensu Smale et al. 1995). The compressed sagitta has a dorsal rim that is primarily horizontal with slight crenulations. There is a highly characteristic, small mediodorsal angle (dome) and postdorsal projection. Ventral margin is deeply rounded and smooth. Specimens have a typical sciaenid sulcus with an enlarged ostium and a short, narrow cauda with a prominently downturned posterior section (Schwarzhans 1993). Inner face tends to be moderately convex, whereas outer face is almost flat to slightly concave. A postcentral umbo is absent. Significant ontogenetic changes have been noted in modern specimens of *P. cromis* from the Gulf of Mexico. Fitch and Lavenberg (1983) described one specimen as *Pogonias* cf. *P. cromis* from the North Carolina Pliocene, while Stringer and Bell (2018) reported and figured one specimen (fig. 4A) of the species from the Georgia Plio-Pleistocene. The species is not abundant in any of the known Pliocene localities in the US.

Cynoscion Gill
Cynoscion arenarius Ginsburg (Sand Weakfish)
(Fig. 4J)

The 12 sagittae from Bells Bridge of *Cynoscion arenarius* are more oval in juveniles and oblong in non-juveniles (sensu Smale et al. 1995). Inner face is smooth and broadly, gently convex. Length/height ratios range from approximately 1.60 in juveniles to 2.25 in adults and bespeak how the sagittae become more elongated with maturity. Margins are mainly smooth with some very gentle undulations. Anterior margin is short, slightly

rounded but can be almost vertical. Dorsal margin is primarily straight and horizontal. Posterior margin is slightly tapered but not pointed. Ventral margin is very slightly curved outward. A very prominent sulcus (heterosulcoid type) extends from the anterior margin to almost the posteroventral margin. The oval ostium does not reach the anterodorsal margin and extends for approximately 40% of the length of the inner face. The lower posterior portion of the ostium does not extend beneath the cauda, which is a key characteristic of the species. Cauda is about 45% of the height of the ostium and more excavated. Posterior 20% of the cauda's lower margin is downturned at approximately 90^0 from the horizontal. Caudal tip is typically enlarged both anteriorly and posteriorly. There is a slight, linear, depressed area above the sulcus and no discernible ventral furrow. Outer face is convex, commonly has a prominent, raised umbo, and is noticeably thinner in the anterior portion (often broken). This is the first report of this species as a fossil from North Carolina and only the second fossil occurrence in the USA (Stringer et al. 2020a). It has also been reported from the late Miocene of Trinidad (Aguilera et al. 2016).

Cynoscion sp.

One specimen from Bells Bridge showed characteristics of *Cynoscion*, i.e., the outline of the otolith, sulcus configuration, inframedian posterior projection, and large, distinctive ostium. However, the preservation of the specimen did not allow identification to species.

Leiostomus Lacepède
Leiostomus aff. *L. xanthurus* Lacepède (Spot Croaker)
(Fig. 4K)

The 14 sagittae from Bells Bridge (10) and Dixon (4) assigned to *Leiostomus* aff. *L. xanthurus* are relatively small (approximately 5 mm) and have a plesiomorphic sciaenid sulcus. Ostium is moderately large and spoon-shaped, while the cauda is narrow and moderately deep with a downturned posterior portion. Dorsal rim is mainly flat, while the ventral rim is gently and regularly curving. The sagittae of *L. xanthurus* are very similar to the juveniles of other sciaenids. Some of the small specimens attributed to *Leiostomus* aff. *L. xanthurus* could be juveniles of some of the other sciaenids represented at the two sites, and thus, the *affinis* designation. Müller (1999) reported this species from the Pliocene Yorktown Formation, and Stringer and Bell (2018) described it from the Georgia Plio-Pleistocene. Although not common at Bells Bridge and Dixon, the species was extremely abundant in the Pliocene of southeastern North Carolina representing 40% of the total specimens in Stringer and Shannon (2019). *Leiostomus xanthurus* was reported by Stringer et al. (2020a) in the Pliocene assemblage at Dauphin Island in Alabama, although not nearly as plentiful (6.0% of the total).

Menticirrhus Gill
Menticirrhus americanus Linnaeus (Southern Kingcroaker)
(Fig. 4L)

The one sagitta of *Menticirrhus americanus* from Bells Bridge is characterized by several highly-characteristic features that include a sulcus that covers almost the entire inner face, a prominent postdorsal spine at the posterior tip that is directed upwards diagonally, and the greatest height is towards the posterior. The anterior is somewhat narrowed and rounded, and this contributes to the peculiar, elongated outline. Stringer and Bell (2018) re-

Figure 4: All illustrated specimens were collected from the Bells Bridge Locality and Dixon Locality in Edgecomb County, North Carolina. The taxonomic identification of each otolith specimen (all inner views of sagittae) and the location of the otolith in the labyrinth (right or left side) are given. Length of otolith is given in mm. Scale for each otolith = 1mm. The figured specimens are reposited in the North Carolina Museum of Natural Sciences, and catalog numbers are provided.

A. *Lepophidium profundorum*, right, 5.92 mm, NCSM 33789
B. *Ophidion* aff. *O. grayi*, right, 6.38 mm, NCSM 33790
C. *Citharichthys macrops*, right, 3.46 mm, NCSM 33791
D. *Syacium* cf. *S. gunteri*, right, 2.98 mm, NCSM 33792
E. *Symphurus* sp., left, 1.98 mm, NCSM 33793
F. *Kathetostoma albigutta*, right, 6.04 mm, NCSM 33794
G. *Diplectrum* cf. *D. formosum*, right, 7.23 mm, NCSM 33795
H. *Orthopristis chrysoptera*, right, 5.33 mm, NCSM 33796
I. *Prionotus* cf. *P. carolinus*, right, 4.58 mm, NCSM 33797
J. *Cynoscion arenarius*, left, 11.91 mm, NCSM 33798
K. *Leiostomus* aff. *L. xanthurus*, right, 6.85 mm, NCSM 33799
L. *Menticirrhus americanus*, left, 6.98 mm, NCSM 33800

ported this species from the Georgia Plio-Pleistocene sites, and Stringer and Hulbert (2020) noted it from the Jones Girls site (late Pleistocene) in coastal Georgia.

Bells Bridge and Dixon Localities Otolith Assemblages

Taxa of the families Ophidiidae, Paralichthyidae, and Haemulidae represent the most specimens at Bells Bridge and Dixon (approximately 74% and 87% respectively). The highest species diversity is found in the Sciaenidae, Gadidae, and Ophidiidae (6, 5, and 5 species respectively). All of the otoliths identified in this study represent extant fishes that inhabit the northwestern Atlantic Ocean coast of the U.S.A. (Froese and Pauly 2020, Page et al. 2013). Otoliths from the sites indicate congrids, engraulids, clupeids, myctophids, merlucciids, gadids, ophidiids, paralichthyids, cynoglossids, stromateids, uranoscopids, serranids, haemulids, triglids, and sciaenids (See Table 1, which includes common names of the families).

Comparison of the Bells Bridge and Dixon Otolith Assemblages to the Lee Creek Mine

One of the objectives of this study was to compare the otoliths from the Bells Bridge and Dixon localities to the Lee Creek Mine otolith assemblage, which is the most extensively studied otoliths from a Pliocene site in the Atlantic and Gulf coastal plains. The Lee Creek Mine is approximately 96 km south-southeast of the Bells Bridge and Dixon localities. Fitch and Lavenberg (1983) examined over 8808 Lee Creek Mine otoliths, of which most were collected macroscopically in the field. This technique has value (obtaining larger specimens for taxonomic descriptions and growth series) but is greatly biased for statistics. Therefore, comparisons were made only to those specimens obtained through bulk sampling and microscopic examination by Fitch and Lavenberg (1983). Since the weight of their bulk sample was not specified, the Bells Bridge and Dixon assemblages were also compared to otoliths obtained from a bulk sample collected from Unit 3 (sensu Ward and Blackwelder 1980) of the Yorktown Formation (Snyder et al. 1983) at the Lee Creek Mine, which is the Rushmere Member according to Ward and Blackwelder (1980). P. Harmatuck guided one of the authors (GS) to this otolith-rich unit. Although the sample was only 15 kg, it produced 300 otoliths, which is comparable to the number of Fitch and Lavenberg (n = 352).

Several methods were employed to compare the otolith assemblages of the Bells Bridge, Dixon, and Lee Creek Mine sites. The species diversity of each site was examined, and within species diversity, the number of species (richness) and the percentage abundance of each species (evenness) at each site were compared (Table 2). The Bells Bridge locality is fairly diverse with 29 taxa, which are evenly distributed with no species representing more than 28.54% of the total assemblage. The Dixon locality has 13 taxa, less than half the number of Bells Bridge taxa. The Dixon locality is much less evenly distributed with one species, *Lepophidium profundorum*, representing 64.73% of the assemblage. The Lee Creek Mine otolith assemblage (Fitch and Lavenberg bulk sample) had 27 taxa, which were evenly distributed primarily among the ophidiids, paralichthyids, merlucciids, and myctophids. The Lee Creek Mine otoliths (Stringer sample) had 24 taxa, which were also evenly distributed (no taxon more than 21% of total). The Bells Bridge otolith assemblage was more diverse (29 taxa) than either of the Lee Creek Mine bulk samples (27 and 24).

Another useful tool for comparing the otolith assemblages at Bells Bridge, Dixon, and Lee Creek (two samples) is the percentage similarity measurement (Reitz and Wing 1999, Schwarzhans and Stringer 2020, Stringer et al. 2018, Stringer and Hulbert

2020, Stringer and Shannon 2019). The percentage similarity measurement allows a comparison of assemblages from different localities. The measurement, also known as percent similarity or proportional similarity, is calculated using the following equation:

$P = \sum$ 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

The percentage similarity of the otolith assemblages is calculated between a) Bells Bridge and Dixon localities, b) Bells Bridge and Lee Creek Mine (Fitch and Lavenberg sample) localities, c) Dixon and Lee Creek Mine (Fitch and Lavenberg sample) localities, d) Bells Bridge and Lee Creek Mine (Stringer sample) localities, e) Dixon and Lee Creek Mine (Stringer sample), and f) Lee Creek Mine (Fitch and Lavenberg sample) and Lee Creek Mine (Stringer sample) localities. Data for the percentage similarity calculations are obtained from Table 1 for the Bells Bridge and Dixon localities and from Table 2 for the Lee Creek Mine. The percentage similarity results are presented in Table 3.

The percentage similarity for the Bells Bridge and Dixon localities is 60.9%. This indicates that the otolith assemblages of the two localities are fairly similar. One may have expected a higher similarity since both localities are from the Rushmere Member of the Yorktown Formation and are separated by only 0.8 km on the Tar River. The percentage similarity for the Bells Bridge and Lee Creek Mine (Fitch sample) localities is 54.87%, which is less than the similarity of the Bells Bridge to Dixon. However, the Bells Bridge otolith assemblage is not that different in similarity to the one at Dixon (60.90%) as it is to the Lee Creek Mine (Fitch sample) assemblage (56.96%), although the Lee Creek Mine is 96 km away. The percentage similarity for Bells Bridge and Lee Creek Mine (Stringer sample) is only 46.82%. The percentage similarity for the Dixon and Lee Creek Mine (Fitch sample) localities is 64.83%, which is more similar than it was to the nearby Bells Bridge Locality. Furthermore, Dixon and Lee Creek Mine (Fitch sample) show the most similarity even though they are separated by 96 km. The Dixon and Lee Creek (Stringer sample) percentage similarity is 43.32%, which is the lowest similarity. These 2 assemblages also have the most geographical separation, but Dixon and Lee Creek (Fitch sample) have the same separation and are the most similar.

The 2 Lee Creek localities were also compared (Fitch and Stringer samples), and their percent similarity is 56.20%. Again, one would have expected more similarity coming from the same member at the same locality. However, the 2 samples at Lee Creek were from slightly different stratigraphic levels in the Rushmere Member. The percentage similarity analysis, which ranges from 43.32% to 64.83%, indicates that the sites were moderately alike to fairly alike. However, none of them were greatly similar or dissimilar. There appear to be factors causing variability among the composition of the otolith assemblages even within the Rushmere Member at the same sites. It is not known presently if the variability is related to paleoenvironmental or taphonomical factors.

The species diversity of the 4 samples varies significantly. The richness of the 4 samples ranges from a low of 13 taxa (Dixon) to a high of 29 taxa (Bells Bridge). While the percentage abundance is evenly distributed at Bells Bridge and the 2 Lee Creek Mine sites (Fitch sample and Stringer sample), the Dixon locality has one species that accounts for 64.73% of the total assemblage. In spite of these differences in species diversity, the

Table 2. Otolith-based species diversity from the Lee Creek Mine Locality (Beaufort County, North Carolina) with number and percentage of specimens. Lee Creek data (Fitch) are based on the bulk sample of Fitch and Lavenberg (1983). Lee Creek data (Stringer) are based on bulk sample of this study. Percentages are given in parentheses next to the number of specimens. Explanation of superscripts in table: 1 = Reported as Congrid sp. B in Fitch and Lavenberg (1983); see Müller (1999) for explanation of taxonomic assignment. 2 = Reported as *Lepophidium* cf. *cervinum* in Fitch and Lavenberg (1983); see Robins et al. (2012) for taxonomic change. 3 = Reported as family Brachiostegidae in Fitch and Lavenberg (1983). 4 = Includes *Leiostomus* aff. *xanthurus* (this study) and *Leiostomus* sp. (Fitch and Lavenberg, 1983). 5 = Reported as Sciaenid sp. A in Fitch and Lavenberg (1983).

Taxa and abundance in Lee Creek sites (bulk samples—microscopic examination)	Lee Creek site (Fitch sample)	Lee Creek site (Stringer sample)
Family (bold) Genus and species	Number specimens (% site total)	Number specimens (% site total)
Family Congridae		
Gnathophis sp.[1]	7 (1.99%)	0 (0%)
Rhynchoconger aff. *R. flava*	0 (0%)	4 (1.33%)
Congrid sp. A	1 (0.28%)	0 (0%)
Congrid sp. C	2 (0.57%)	1 (0.33%)
Congrid sp. E	1 (0.28%)	0 (0%)
Family Myctophidae		
Ceratoscopelus cf. *C. maderensis*	31 (8.81%)	3 (1.00%)
Diaphus sp.	0 (0%)	1 (0.33%)
Family Merlucciidae		
Merluccius albidus	5 (1.42%)	9 (3.00%)
Merluccius cf. *bilinearis*	12 (3.41%)	5 (1.67%)
Merluccius sp.	11 (3.13%)	7 (2.33%)
Unidentified *Merluccius*	21 (5.97%)	22 (7.33%)
Family Gadidae		
Microgadus cf. *M. tomcod*	0 (0%)	1 (0.33%)
Pollachius cf. *P. virens*	0 (0%)	0 (0%)
Urophycis tenuis	7 (1.99%)	5 (1.67%)
Merlangiogadus cognatus	3 (0.85%)	0 (0%)
Gadidae indeterminate	0 (0%)	1 (0.33%)
Family Ophidiidae		
Lepophidium sp.	0 (0%)	1 (0.33%)
Lepophidium profundorum[2]	130 (36.93%)	54 (18.00%)
Otophidium lacinus	0 (0%)	3 (1.00%)
Ophidion grayi	4 (1.14%)	0 (0%)
Brotulid sp. B	1 (0.28%)	0 (0%)

Table 2. Continued.

Family (bold) Genus and species	Number specimens (% site total)	Number specimens (% site total)
Ophidiid sp. A	2 (0.57%)	0 (0%)
Ophidiid sp. B	2 (0.57%)	0 (0%)
Family Pleuronectidae		
Pleuronectid sp.	1 (0.28%)	0 (0%)
Family Paralichthyidae		
Citharichthys macrops	62 (17.61%)	46 (15.33%)
Family Cynoglossidae		
Symphurus sp.	10 (2.84%)	14 (4.67%)
Family Ammodytidae		
Ammodytes hexapterus	6 (1.70%)	12 (4.00%)
Family Serranidae		
Diplectrum cf. *D. formosum*	0 (0%)	3 (1.00%)
Family Malacanthidae[3]		
Lopholatilus chamaeleonticeps	1 (0.28%)	0 (0%)
Family Triglidae		
Prionotus cf. *P. carolinus*	12 (3.42%)	6 (2.00%)
Family Sciaenidae		
Micropogonias undulatus	0 (0%)	25 (8.33%)
Micropogonias sp.?	2 (0.57%)	0 (0%)
Cynoscion regalis	0 (0%)	2 (0.67%)
Cynoscion nebulosus	11 (3.13%)	0 (0%)
Leiostomus xanthurus[4]	5 (1.42%)	8 (2.67%)
Pachyurus? *jeanae*[5]	1 (0.28%)	63 (21.00%)
Sciaenidae indeterminate	0 (0%)	1 (0.33%)
Indeterminate	1 (0.28%)	3 (1.00%)
Total number of specimens	352	300

percentage similarity indicates that all of the sites are not greatly alike or greatly dissimilar based on the percentage abundance of shared taxa.

Paleoecological Implications of the Bells Bridge and Dixon Otolith Assemblages

The late Pliocene Bells Bridge and Dixon otoliths make them ideal for interpreting paleoecological conditions at the sites. A comparison of the ecological ranges of modern families of fishes represented at the site by otoliths can be used to ascertain the general paleoenvironmental parameters (Cohen et al. 1990, Froese and Pauly 2020, Nelson et al.

2016, Robins and Ray 1986, Snyder and Burgess 2016). It must be noted that paleoecological interpretations are limited to the 2 beds collected at the Bells Bridge locality in which otoliths were recovered and the collected interval at the Dixon locality. The paleoecological interpretations based on otoliths may not apply to the surrounding strata at the localities since the lithology is different and could represent changes in paleoenvironment.

The ecological distributions of the 15 fish families represented by otoliths at Bells Bridge and Dixon sites provide important data regarding the paleoenvironment. None of the 15 families are restricted to fresh water, and none are brackish only. There is 1 family restricted to brackish and marine waters (Triglidae). There are 8 families that may be found in fresh water, brackish, and marine (Engraulidae, Clupeidae, Gadidae, Paralichthyidae, Cynoglossidae, Serranidae, Haemulidae, and Sciaenidae). Six of the families inhabit exclusively marine environments (Congridae, Myctophidae, Merlucciidae, Ophidiidae, Stromateidae, and Uranoscopidae). It is important to note that all of the families have marine representatives and that the marine environment is the only common setting to account for all of the families (Froese and Pauly 2020, Nelson et al. 2016, Snyder and Burgess 2016). Furthermore, none of the Bells Bridge and Dixon otoliths represent species that are indicative of deepwater marine forms (greater than 200 m) according to Froese and Pauly 2020, Page et al. 2013). Nolf and Brzobohaty (1992) stated that marine assemblages that were free or almost free of myctophids (there was one myctophid specimen from Bells Bridge) indicate a neritic environment with little open oceanic influence. So the fishes represented by otoliths at the 2 Rushmere Member sites on the Tar River suggest a marine (neritic) environment with normal salinity and with little deepwater (greater than 200 m) or freshwater influence. A deep inner shelf and middle shelf is likely.

The fish families represented by otoliths also supply a general indication of climatic conditions. The majority of the families (10 of the 15) are distributed from tropical to temperate environments. There are several families that are mostly tropical or subtropical (Haemulidae, Cynoglossidae, and Clupeidae) but only the Haemulidae represent a substantial portion of the two assemblages. There are several families that have representatives that extend into polar conditions. The Gadidae, which is represented by six taxa but are not greatly abundant, are found from temperate to Arctic environments. The most predominant family, the Ophidiidae, is represented by five taxa that represent approximately 41% and 65% of the total specimens of Bells Bridge and Dixon localities is included in the fishes found in tropical to temperate waters. As a general observation, most of the taxa represented by otoliths prefer soft bottom sediments such as sand, silt, and mud. No evidence of marine

Table 3. Percentage similarity of the otolith assemblages from Bells Bridge, Dixon, and Lee Creek Mine localities. Note that Lee Creek has two bulk samples that were examined microscopically: Fitch and Lavenberg (1983) and Stringer (this study).

Localities compared	Percent similarity
Bells Bridge – Dixon	60.90%
Bells Bridge – Lee Creek (Fitch bulk sample)	56.96%
Bells Bridge – Lee Creek (Stringer bulk sample)	46.82%
Dixon – Lee Creek (Fitch bulk sample)	64.83%
Dixon – Lee Creek (Stringer bulk sample)	43.32%
Lee Creek (Fitch bulk sample) – Lee Creek (Stringer bulk sample)	56.20%

invertebrate settlement (e.g., boreholes and encrustings) was found on the 672 otoliths from Bells Bridge and Dixon. This lack of invertebrate settlement could be an indication of the surface residence-time of the otoliths during the late Pliocene (Stringer 2016).

Discussion

In order to more fully understand the significance of the newly described Pliocene otoliths from the Atlantic Coastal Plain and to place them in the context of other described faunas, they are compared to all known Pliocene otolith assemblages in North America. The comparison of North American Pliocene otolith assemblages is accomplished by geographic areas, primarily the United States (Atlantic Coastal Plain, Gulf Coastal Plain, and Pacific coast), the Caribbean, and Central America. No Pliocene otolith assemblages are known currently from Canada or Mexico.

United States Pliocene Otolith Assemblages

North Carolina (Elizabethtown locality). Stringer and Shannon (2019) investigated the aragonitic-rich shell beds (early late Pliocene, 2.5–3.1 Ma in age) at the Elizabethtown locality in Bladen County, North Carolina (Fig. 1). Bulk sampling resulted in 745 teleostean otoliths, which represented 17 taxa that inhabit the Atlantic Ocean off the eastern U.S. coast. The number of species (richness) was relatively low and the percentage abundance indicated a very large unevenness with *Micropogonias undulatus* and *Leiostomus* aff. *L. xanthurus* representing 91.4% of the total specimens. The modern distributions of these two species are very strong indicators of shallow, soft bottom estuarine creeks and bays. The preponderance of juvenile *M. undulatus* (99.5% of the specimens represent 1-year-old or less in age fish) was a strong indicator for a primary nursery area. A primary nursery area would explain the dominance of juvenile forms of the Atlantic croaker and spot, the high percentage of fishes (96% of the specimens) that may be found in freshwater, brackish, and marine environments, and the small percentage (3.5% of the total specimens) of marine-only species. There were no indications of a primary nursery area at Bells Bridge or Dixon. Although the localities are not separated greatly geographically, the Elizabethtown assemblage differed enormously from the Bells Bridge and Dixon otoliths in the percentage of *Micropogonias undulatus* (51% versus 0.23%) and *Leiostomus* aff. *L. xanthurus* (40% versus 3.98%). This highly significant difference is attributed to very different paleoenvironmental settings at the sites during the Pliocene.

North Carolina (Lee Creek Mine). As previously noted, the Lee Creek Mine otoliths (upper Pliocene Yorktown Formation, Rushmere Member) are the most extensively studied otoliths from a single Pliocene site in the Atlantic and Gulf coastal plains (Fig. 1). Nearly 10,000 otoliths have been examined from the site and reported in 2 studies. The similarity of the Bells Bridge and Dixon otolith assemblages with the Lee Creek Mine otoliths has been analyzed (utilizing percentage similarity measurement) and discussed in detail in the text and Table 3.

North Carolina and Virginia (sites of Müller 1999). In addition to investigating the Pliocene otoliths of the Lee Creek Mine, Müller (1999) also sampled several other sites that produced Pliocene otoliths. Three sites, which consisted primarily of the Yorktown Formation Rushmere Member and the Sunken Meadow Member, which are separated by an unconformity of at least 1 my (Dowsett et al. 2019), were collected along the Piankatank River and James River in Virginia and the Tar River in North Carolina (Fig. 1). Three other Pliocene sites, which were located approximately 50–80 km south of the Lee Creek Mine near the Atlantic coast in North Carolina, were also collected (Fig. 1). Müller (1999) noted 2 of the sites as Duplin Formation and 1 as Croatan Formation. Müller (1999) reported

a wide range in the size of samples collected from the various Pliocene formations from as small as 20 kg to as much as 60 kg. He characterized the Rushmere Member otolith as dominated by Gadidae, Ophidiidae, and Sciaenidae, while he noted Sciaenidae as dominant in the Croatan Formation. In table 4, he listed 46 otolith-based teleostean taxa from the Yorktown Formation (Sunken Meadows and Rushmere members) and the Duplin Formation. The most speciose were the Congridae (5 taxa), Gadidae (5 taxa), Ophidiidae (9 taxa), and Sciaenidae (8 taxa). Müller's findings from the Yorktown and Duplin were more similar to the Bells Bridge assemblage than to the Dixon. He reported a significantly greater number of taxa (46 versus 31), but his table included the Duplin Formation, which could account for the differences with the Bells Bridge assemblage.

Georgia. Stringer and Bell (2018) examined 1803 teleostean otoliths obtained from extensive bulk sampling at seven Plio-Pleistocene sites in Glynn County, Georgia. The teleostean otoliths were considered especially important since it was the first description of fish otoliths from the Plio-Pleistocene of Georgia and described the bony fishes present during a time interval that included the climatic changes in the late Neogene as well as the glacial and interglacial climatic cycles in North America. Furthermore, the preservation of aragonitic otoliths is rare in coastal Georgia because of the very high water table and the intense and rapid weathering as well as various geological constraints, such as highly-erosive transgressive sequences.

Four of the 7 sites investigated by Stringer and Bell (2018) in coastal Georgia were early Pliocene in age (primarily Raysor Marl equivalents; 3.8–4.5 Ma) and relevant to this study. One other site had Pliocene otoliths, but it also had Pleistocene and possibly Miocene. Since it was not possible to distinguish the age of the otolith specimens, it was not included. Table 1 of Stringer and Bell (2018) indicated that 1265 otoliths were obtained from four Pliocene sites, which accounted for 70.16% of the total specimens of the study. Otoliths from the 4 Pliocene sites produced 47 taxa of bony fishes, which represented mainly extant bony fishes with only a few extinct forms. The Pliocene otoliths indicated fishes that are very similar to the marine fishes from present-day coastal Georgia (Georgia Department of Natural Resources 2018). The fishes were dominated by taxa from the Sciaenidae (15 taxa) and the Ophidiidae (8 taxa). These 2 families also represented the most specimens. The coastal Georgia Pliocene sites produced a significantly larger number of taxa (47) than Bells Bridge and Dixon (31). Different paleoenvironments at the four sites could account for additional fish species. The Georgia Pliocene otolith assemblages shared 11 taxa with the Bells Bridge and Dixon sites with the greatest number from the sciaenids (4). Given that all of the sites are in the Atlantic Coastal Plain, a greater number of shared taxa were expected. However, temperature differences related to latitude probably played a role in delineating the distribution of the fish species.

Gulf Coastal Plain. Only 1 Pliocene otolith assemblage is known from the USA Gulf Coast (Stringer et al. 2020a). The assemblage, a Graham Ferry Formation equivalent (Zanclean-Piacenzian) on Dauphin Island, Alabama, consisted of 22 species (from 250 specimens) and was dominated by sciaenids (79.6% of total). The otoliths indicated a shallow (0–20 m) neritic environment with some brackish and rare deep-water influence. There is evidence that the paleoenvironment served as a primary nursery area during its deposition in subtropical waters. The Dauphin Island locality was not nearly as diverse in the number of taxa with only 22 versus 31 from Bells Bridge and Dixon. However, Dauphin Island shared ten taxa with the otolith assemblages of Bells Bridge and Dixon with the greatest similarity with the sciaenids (four species). It differs most in the lack of any representatives of the Merlucciidae or Gadidae, which is not surprising considering the southern location of Dauphin Island.

Pacific coast. Pliocene otoliths are well represented in California as shown in several studies (Firestine et al. 2012; Fitch 1969a, b; Fitch and Barker 1972; Fitch and Reimer 1967). The 2 Pliocene formations in California that have produced the largest number of otoliths are the Pico Formation (two different exposures) and the San Diego Formation (Fitch 1969b). Approximately 21,000 Pliocene otoliths were investigated by Fitch and associates from the aforementioned formations. Originally, Fitch included the Lomita Marl, which produced over 24,000 otoliths (82 species), as Pliocene, but subsequent studies have shown the Lomita Marl to be Pleistocene (Firestine et al. 2012, Powell and Stevens 2000).

Pliocene otoliths were recovered from the Pico Formation in southern California (Fitch 1969a, b; Fitch and Barker 1972). Fitch (1969a) reported on 2 exposures of the deepwater Pico Formation in southern California. The Newport Bay (or Mesa) locality produced 5100 otoliths (55 species), while the Downtown Los Angeles locality produced 4285 otoliths (48 species). The otolith assemblage of the Newport locality of the Pico Formation was dominated by the morid *Physiculus rastrelliger* (1387 specimens), a deepwater, demersal member of the Moridae. *Merluccius productus* was the second most abundant with 427 specimens. The Newport locality of the Pico Formation was characterized by many myctophids (such as *Benthosema* sp., *Diaphus theta*, and *Stenabrachius leucopsarus*) and other mesopelagics, several bathypelagics, and a few extinct northern fishes. The Downtown Los Angeles locality of the Pico Formation was markedly different in the abundance of various species. *Merluccius productus* accounted for 13% of the specimens, while *Physiculus rastrelliger*, which was so abundant in the Newport Bay locality, was represented by only 33 otoliths. Both of the localities of the Pico Formation had *Engraulis mordax*, *Clupea pallasi*, *Scomber japonicus*, and *Trachurus symmetricus* present in their otolith assemblages (Fitch 1969b). Squires (2012), who studied the Pico Formation megafossils in southern California (primarily invertebrate remains), reported that the Pico Formation was late Pliocene in age.

Like the Pico Formation, the San Diego Formation produced a large number of Pliocene otoliths (11,600 specimens, 50 species). However, the composition of the San Diego Formation otolith assemblage is dramatically different from the other assemblages of southern California Pliocene otoliths. The vast majority of the taxa of the San Diego Formation otolith assemblage is shallow-water fishes. There are some mesopelagic and bathypelagic fishes present, but they are not nearly as abundant as in the Pico Formation. All of the taxa in the San Diego Formation represent extant species except for one extinct sciaenid (Fitch 1969a). Kennedy and Tan (2008) placed the San Diego Formation as late Pliocene in age and contained a rich molluscan fauna.

Firestine et al. (2012) published an exhaustive and systemic inventory of all published accounts of Neogene teleostean fishes in California. The inventory included otoliths, primarily from Fitch, individually and with co-authors. In their "Summary Catalog" on pages 183–191, Firestine et al. (2012) listed 33 taxa as occurring in the Pliocene. However, there were other species noted as questionably occurring in the Pliocene, and some species were shown as being found in the Plio-Pleistocene. Of the taxa shown exclusively in the Pliocene, the Myctophidae was the largest with ten taxa followed by the Cottidae with 5 taxa. The Bells Bridge and Dixon otolith assemblages show little to no relationship to any of the California taxa for obvious geographical differences in taxa as well as paleoenvironmental dissimilarities, especially noted by the large number of myctophid taxa.

Caribbean Pliocene Otolith Assemblages

Trinidad. One of the earliest studies of Pliocene otoliths in the Caribbean was the investigation of Trinidad Neogene otoliths by Nolf (1976). Otoliths from Miocene and Pliocene

formations were examined in Nolf's study, and it appears that the Pliocene specimens were obtained from Gros Morne (Pliocene, Zanclean) and the Springvale (Pliocene, Piacenzian) formations (Nolf 1976, fig. 1). Examination of the ranges of the various species indicated that 20 taxa were found in the Pliocene formations (table 1). The Sciaenidae and Ariidae contained the greatest number of Pliocene species (6 and 3 respectively). All of the sciaenids were identified only to the genus, but 2 of the ariids were identified to species. Otoliths from the family Gobiidae, which were found in the Springvale and Gros Morne formations, were some of the most abundant specimens. The myctophid *Diaphus dumerili*, present in the Springvale Formation, was also very abundant.

Aguilera et al. (2016) in their study of the otoliths of the Neogene Sciaenidae of tropical America investigated the Gros Morne Formation (uppermost Miocene to lower Pliocene), the Manzanilla Formation (upper Miocene to lower Pliocene), and the Springvale Formation (lower to upper Pliocene) in Trinidad. Although the Gros Morne and Manzanilla formations were Miocene and Pliocene, it was possible to identify the taxa from the Pliocene in most cases (the sciaenids *Plagioscion ultimus* and *Xenolithus sineostialis*). The studies of Nolf (1976) and Aguilera et al. (2016) revealed little similarity of the Trinidad taxa to those of the Bells Bridge and Dixon. Some of the differences appear to be related to much deeper and more open oceanic paleoenvironments in the Trinidad otolith assemblages (as noted by the abundant myctophids). The Trinidad assemblages had groups (such as the gobiids) that were completely absent from Bells Bridge and Dixon.

Jamaica. The well-known Bowden shell bed (3.5 Ma) in Jamaica is one of the most productive fossil units in the Caribbean and includes abundant otolith specimens (Stringer 1998). The Bowden shell bed was previously placed in the Bowden Formation. However, the Bowden Formation is now designated as a member and is placed in the Layton Formation (James-Williamson and Mitchell 2012). Several studies mention the occurrence of otoliths in the Bowden shell bed (Clarke and Fitch 1979, Fitch 1969a, and Fitch and Barker 1972). Fitch (1969a) first noted examining a small 11.3 kg sample from the Bowden, but it contained 993 sagittae from more than 50 species of teleosts, including several kinds of mesopelagics. Subsequently, Clarke and Fitch (1979) reported processing approximately 225 kg of Bowden matrix that produced around 25,000 otoliths. Fitch indicated that the otoliths represented more than 110 taxa of fishes (50–60 families), which is almost 4 times the number of taxa in the Bells Bridge and Dixon assemblages. Some of the Bowden taxa mentioned included Albulidae (Bonefish), Clupeidae (Herrings), Engraulidae (Anchovies), Ariidae (Sea Catfishes), Holocentridae (Soldierfish), Apogonidae (Cardinalfishes), Opistognathidae (Jawfishes), Carapidae (Pearlfishes), Ophidiidae (Cusk-eels), Gobiidae (Gobies), Mullidae (Goatfishes), Triglidae (Searobins), Bregmacerotidae (Codlets), Sciaenidae (Drums and Croakers), and several deeper-water forms, such as Myctophidae (Lanternfishes), Moridae (Deepsea Cods or Morids), Bythitidae (Brotulids), and Macrouridae (Grenadiers). Family names (taxonomic and common) are based on Nelson et al. (2016) and Froese and Pauly (2020). Stringer (1998) reported 1650 otoliths from the Bowden shell bed representing 68 teleostean taxa (38 families), which is more than twice the taxa of the Bells Bridge and Dixon. The assemblage had shallow-water marine forms (including euryhaline species), neritic species, and middle to outer shelf forms with some upper slope and pelagic elements as well as taxa commonly associated with reef environments. The otolith assemblage was very similar to the modern Atlantic and Caribbean ichthyological fauna, but there were 3 forms that are now Pacific in distribution. These forms were interpreted by Stringer (1998) as relicts of the ancient western Tethys fauna.

Schwarzhans and Aguilera (2013) also examined Pliocene otoliths from the Bowden shell bed in Jamaica in their study of the Neogene myctophids of tropical America and

reported eight species from the Layton Formation. Aguilera et al. (2016) reported no sci-aenids from Jamaica. Schwarzhans and Aguilera (2016) examined the Ophidiiformes from the Layton Formation in Jamaica and reported nine ophidiiform taxa. Two of the 9 taxa were new species; 2 were identified only to genus, and 4 were taxa referred to in Nolf and Stringer (1992). *Otophidium lacinum* was also identified from the Pliocene of Jamaica. This form was first reported by Fitch and Lavenberg (1983) as Ophidiidae sp. A from the Lee Creek Mine (Yorktown Formation) in North Carolina, and then as "genus aff. *Otophidium*" *lacinius* as a new species from the same locality (Müller, 1999). Stringer and Bell (2018) noted *Otophidium lacinius* from 4 Plio-Pleistocene sites in coastal Georgia. If all of these are truly the same species, then the enigmatic and extinct ophidiid had a considerable geo-graphic range during the Pliocene. Equally intriguing is that it is not present in the Bells Bridge and Dixon assemblages but is found in Lee Creek in North Carolina, four sites in Georgia, and Jamaica. Other significant differences exist between the Jamaican otoliths and those of Bells Bridge and Dixon. For example, of the 9 ophidiiform species reported by Schwarzhans and Aguilera (2016), none of them are found in Bells Bridge and Dixon. Likewise, myctophids, which were very abundant in Jamaica with 8 taxa (Schwarzhans and Aguilera 2013), is represented by one specimen in the Bells Bridge and Dixon. Aguilera et al. (2016) reported no sciaenids from Jamaica, but there are 6 taxa in the Bells Bridge. The differences between the Bells Bridge and Dixon assemblages to Jamaica is certainly related to paleoenvironmental and paleobiogeographic differences.

Dominican Republic. Highly diversified Mio-Pliocene otolith assemblages were described from the northern Dominican Republic (Nolf and Stringer 1992). However, the Mao Forma-tion is entirely Pliocene, while the Gurabo is Pliocene except for the lowermost portion, which is Miocene. Examination of Table 2 in Nolf and Stringer (1992) reveals that 42 Pliocene taxa were present in the 2 formations. Collectively, in the 2 formations, congrids (4 taxa), ophidiids (5 taxa), and apogonids (4 taxa) were the most abundant species. There were 27 taxa in the Gurabo Formation, and 33 taxa in the Mao Formation. Some species were found in both formations, while some species were unique to one of the two formations. Much like the Bowden shell bed in Jamaica, the Pliocene formations in the Dominican Republic had otolith assemblages that had shallow-water marine taxa, neritic species, and middle to outer shelf forms with some upper slope and pelagic elements. However, the Mao Formation had many more bathyal and mesopelagic forms such as myctophids and macrourids, much fewer neritic species, and no euryhaline taxa. The Gurabo Formation had euryhaline taxa, such as the *Plotosus* (Catfish), many more neritic species, and no macrourids.

Schwarzhans and Aguilera (2013), in their study of the Myctophidae of the Neogene of the tropical America, examined Pliocene otoliths from the Mao Formation in the Domini-can Republic and reported 2 myctophid species (neither is known from the Bells Bridge or Dixon). Aguilera et al. (2016) investigated sciaenid otoliths from the Mao Formation and reported only 2 sciaenids (again, neither present in the Bells Bridge or Dixon). Five ophi-diiform otoliths were reported from the Mao Formation and the Pliocene of the Gurabo Formation (Schwarzhans and Aguilera (2016), and 1 of them occur in the Bells Bridge and Dixon assemblage.

The 3 studies involving Dominican Republic Pliocene otoliths indicate very little relation-ship to the Bells Bridge and Dixon otolith assemblages. Shared taxa are probably only 3, count-ing the Cynoglossidae ind. of Nolf and Stringer (1992) as *Symphurus* sp. Even shared families, such as the Ophidiidae and Sciaenidae, show little or no relationship between the Dominican Republic otoliths and the Bells Bridge and Dixon assemblages. The dissimilarity appears to be related primarily to paleoenvironmental differences and to paleobiogeography.

Central America Pliocene Otolith Assemblages

Costa Rica. Aguilera and Aguilera (1999) analyzed otoliths from Costa Rica and presented lists for the Rio Banano Formation (upper lower Pliocene to upper Pliocene). They reported 7 collections but only 77 otoliths. However, the small number of specimens produced 19 taxa, including sciaenids, such as *Stellifer* and *Umbrina*, congrids, such as *Ariosoma* and *Rhynchoconger*, and ophidiids, such as *Lepophidium*. They reported only 1 oceanic form, *Diaphus*, and 95% of the taxa lived in waters less than 50 m. The paleoenvironment is more comparable to that of Bells Bridge and Dixon, and there are few of the same taxa, such as *Lepophidium* and *Cynoscion*. However, as expected, the Rio Banano lacks the Gadiformes (8 taxa) found in the Bells Bridge and Dixon, as well as representatives of the Paralichthyidae and Cynoglossidae. Paleobiogeography appear to be the primary reason for differences. The Moin Formation (upper lower Pliocene to upper Pliocene) is not included since the stratigraphy could not be conclusively determined.

Aguilera et al. (2016) investigated sciaenid otoliths from the Pliocene Rio Banano Formation and revealed 9 taxa. Two of the sciaenid otoliths represented extant fishes (*Bairdiella ronchus* and *Cynoscion nothus*). Two of the otoliths were identified only to genus (lapillus from *Stellifer* sp. and sagitta from *Nebris* sp.). All of the other sciaenid otoliths were deemed as new species (*Isopisthus acer*, *Stellifer abbreviatus*, *Stellifer bicornutus*, *Umbrina bananensis*, and *Larimus angosturae*). The Bells Bridge and Dixon assemblages have no species in common and is, again, believed to be related to paleobiogeographic parameters.

Panama. Aguilera and Aguilera (1999) provided lists of otoliths with accompanying paleobathymetric data from the Shark Hole Point Formation (lower Pliocene), the Cayo Agua Formation (lower to middle Pliocene), and the Escudo de Veraguas Formation (upper Pliocene) from the Caribbean side of Panama. The Shark Hole Point Formation (51 otoliths, 9 taxa) produced taxa of mixed environmental affinities including *Diaphus, Bregmaceros*, *Genidens*, *Lactarius*, and *Ariosoma*. None of these taxa are represented in the Bells Bridge and Dixon assemblages with the possible exception of the one *Diaphus* specimen. The Cayo Agua Formation yielded 634 otoliths representing 37 taxa. The 37 taxa comprised the most diverse assemblage obtained from the survey of Panama and Costa Rica in their study. The assemblage contained estuarine taxa, such as *Albula*, *Centropomus*, and *Larimus*, and 84% of the assemblage indicated paleowater depths of less than 50 m, while other bathyal taxa suggested as deep as 100 m. There are some similar genera to the Bells Bridge and Dixon, but Aguilera and Aguilera (1999) only identified the taxa to the genus level, which does not allow detailed comparisons. The Escudo de Veraguas Formation assemblage (920 otoliths, 27 taxa) included neritic and mesopelagic fishes with depths anywhere from 0–300 m. Again, taxa were only identified to genus prohibiting detailed comparisons with the Bells Bridge and Dixon assemblages.

Subsequently, Schwarzhans and Aguilera (2013) studied otoliths from the Panama Pacific and Caribbean including the Burica Formation (middle to upper Pliocene) on the Pacific side. They noted the occurrence of myctophids (*Benthosema panamense*, *Nannobrachium* sp., and *Triphoturus mexicanus*), which represent extant species from the eastern Pacific. They also investigated myctophid otoliths from 4 Pliocene formations on the Caribbean (Bastimentos Formation, Cayo Agua Formation, Shark Hole Point Formation, and the Escudo de Veraguas Formation), which range from latest Miocene to late Pliocene. Myctophids included *Benthosema*, *Hygophum*, *Myctophum*, *Ceratoscopelus*, *Lobiancia*, *Lampadena,* and *Diaphus*. Fourteen species of *Diaphus* were reported collectively from the 4 formations. The preponderance of myctophids is greatly different from the Bells Bridge and Dixon otoliths and is related to both paleoenvironment and paleobiogeography.

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Aguilera et al. (2016) investigated sciaenid otoliths from the Burica Formation from the Pacific coast but reported no specimens. The Bastimentos Formation, the Cayo Agua Formation, and the Escudo de Veraguas Formation were investigated on the Caribbean side, but only a limited number of sciaenid otoliths were recovered. Collectively, the 3 formations yielded 5 sciaenid taxa (*Protosciaena trewavasae*, *Umbrina bananensis*, *Umbrina* aff. *U. sublima*, *Larimus* sp., and *Cynoscion* sp.). None of these species are present in the Bells Bridge and Dixon, and their absence appears to be related to paleobiogeography. Ophidiiformes from the Caribbean side of Panama (Cayo Agua Formation and Shark Hole Point Formation) were studied by Schwarzhans and Aguilera (2016) and revealed *Lepophidium marmoratum*, *Otophidium robinsi*, *Calamopteryx* sp. 2, *Neobythites marginatus,* and *N. multiocellatus*. None of these ophidiids are found in the Bells Bridge and Dixon otolith assemblages.

Summary of relationship of Bells Bridge and Dixon otolith assemblages to North American Pliocene otoliths. A comparison of the newly-described Pliocene otoliths from the Bells Bridge and Dixon localities in North Carolina (U.S. Atlantic Coastal Plain) indicated that North American Pliocene otolith assemblages are found primarily in the US (Atlantic and Gulf coastal plains and Pacific coast), the Caribbean, and Central America. In the US Atlantic Coastal Plain, the otolith assemblages of the Bells Bridge and Dixon were most similar to those from the Lee Creek Mine North Carolina, and these assemblages represent mainly extant teleosts known from the present-day Atlantic Ocean. The Bells Bridge and Dixon otolith assemblage showed similar taxa to the Elizabethtown otolith assemblage in southern North Carolina but differed greatly in abundance due to dramatically contrasting paleoenvironments. The Bells Bridge and Dixon showed less relationship to the Pliocene otoliths from Georgia and is believed to be related to differences in paleoecological conditions. The 1 recently described Pliocene otolith assemblage from the Graham Ferry Formation equivalent in Alabama indicated some relationship between the Atlantic and Gulf coastal plains, which would not be unexpected given the continuity and interchange between the Gulf of Mexico and the Atlantic.

Although Pliocene otoliths were abundant in California, there is little relationship to the Pliocene fishes from the Bells Bridge and Dixon assemblages, or for that matter, to the Atlantic and Gulf coastal plains. The Pliocene otoliths from California largely represent extant Pacific forms, while the Atlantic Coastal Plain otolith assemblages are almost exclusively extant Atlantic taxa. While the Atlantic Coastal Plain and California Pliocene fishes are very distinct, there are some similarities in the Pliocene otolith assemblages from the Bells Bridge and Dixon localities and the Caribbean as seen in the otoliths from Trinidad, Jamaica, and the Dominican Republic. However, the similarities are not as great as one might expect. One notable difference is the presence of some Pacific forms, such as *Lactarius*, *Phthanophaneron*, *Brotula clarkae*, and *Plotosus*, in the Caribbean otolith assemblages. These forms, which are found exclusively in the Pacific today, have been interpreted as relicts of the ancient Tethys seaway fauna in studies by Nolf and Stringer (1992), Schwarzhans and Aguilera (2016), and Stringer (1998). Furthermore, the Pacific forms are evidence of exchange through the Central American Seaway. Based on the evolution of ophidiiform otoliths in tropical America, Schwarzhans and Aguilera (2016) noted that the taxonomic turn-over of the fauna occurred after the late Miocene, accelerated during the Pliocene, and extinctions become the exception during the Pleistocene. These authors relate this process to the emergence of the Isthmus of Panama at approximately 3.4 Ma (late Pliocene). This seems to be congruent with the occurrence of the aforementioned Pacific-only forms in the Pliocene of the Caribbean.

Otoliths of Pacific forms are absent from the Bells Bridge and Dixon assemblages. The Pliocene otolith assemblages from Central America, specifically eastern Costa Rica and eastern Panama, show similarity to the Caribbean Pliocene otolith assemblages, which is logical given the lack of any type of barriers to interchange. Most of the otoliths represent extant species. The Pliocene otolith assemblages from western Panama differ significantly from those on the Caribbean side except for the shared Pacific forms described above. The western Panama Pliocene otoliths are characterized by extant Pacific forms and show significant relationship to the Pliocene assemblages of California but are inherently different from the Bells Bridge and Dixon otolith assemblages due to paleoenvironment and paleobiogeograhy.

Acknowledgments

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