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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)

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ABSTRACT:

Ebersole, J.A., Cicimurri, D.J. and 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** (4), 481–518.

The Oligocene (Rupelian) Byram Formation (Vicksburg Group) in Alabama, USA, is divided into three members, including (in ascending order) the Glendon Limestone, unnamed marl, and the Bucatunna Clay. The Oligocene marine units in Alabama have been historically under-investigated, but bulk samples recently obtained from Glendon Limestone Member exposures at site AWa-9 in Washington County yielded 20 unequivocal elasmobranch and teleost taxa. This surprisingly diverse paleofauna, based on isolated teeth, bones and otoliths, includes the new taxon, *Gobiosoma*? *axsmithi* sp. nov., as well as "*Aetomylaeus*" sp., *Albula* sp., *Aplodinotus gemma* Koken, 1888, *Ariosoma nonsector* Nolf and Stringer, 2003, Balistidae indet., *Citharichthys* sp., Myliobatoidei indet., *Diretmus*? sp., *Hemipristis* sp., *Negaprion* aff. *N. gilmorei* (Leriche, 1942), *Pachyscyllium* sp., *Paralbula* sp., *Physogaleus* sp., *Preophidion meyeri* (Koken, 1888), *Sciaena pseudoradians* (Dante and Frizzell in Frizzell and Dante, 1965), *Sciaenops*? sp., *Sparus*? *elegantulus* Koken, 1888, *Sphyraena* sp., and *Syacium* sp. Additional remains were recovered but could not be identified beyond undetermined Elasmobranchii or Teleostei. All these taxa represent first occurrences within the Glendon Limestone Member in Alabama, and the "*Aetomylaeus*" sp., *Pachyscyllium* sp., *Paralbula* sp., and *Sciaenops*? sp. specimens represent the first occurrences of each in the Oligocene of the Gulf Coastal Plain of the USA. We also report the first record of Oligocene *Paralbula* Blake, 1940 teeth, and the first occurrence of an Oligocene member of the Balistidae in the Western Hemisphere. This marine vertebrate assemblage indicates that the Glendon Limestone Member at site AWa-9 represented a subtropical to temperate, middle shelf paleoenvironment with a paleowater depth interpreted as 30–100 m.

Key words: Chondrichthyes; Teleostei; Otoliths; Paleogene; Gulf Coastal Plain; Vicksburg Group.

INTRODUCTION

Surface exposures in southwest Alabama, USA, preserve a nearly complete Oligocene marine sequence that includes, in ascending order, the Rupelian Bumpnose Limestone, Red Bluff Clay, Forest Hill Sand, Marianna Limestone, and Byram Formation (including Glendon Limestone, unnamed marl, and Bucatunna Clay members), and the Chattian Chickasawhay Limestone and Paynes Hammock Sand (Szabo *et al.* 1988). The Bumpnose Limestone, Red Bluff Clay, Forest Hill Sand, Marianna Limestone, and Byram Formation are all part of the Vicksburg Group, whereas the Chickasawhay Limestone and Paynes Hammock Sand are not assigned to a geologic group (Raymond *et al.* 1988). These Oligocene formations have long been known for their abundance of marine invertebrates (see Cooke 1918; Howe 1942; Glawe 1967, 1969), but very little research has been conducted in Alabama on the vertebrates from these units.

The first scientific study of Oligocene vertebrate remains from the state was by Koken (1888), who described 23 otolith-based taxa from Eocene and Oligocene strata in both Alabama and Mississippi, USA. Cooke (1926) noted the occurrence of fossil otoliths in the Byram Formation of Alabama, but none of these were described or figured. Campbell (1929a) figured many of Koken's (1888) Alabama taxa in a *Journal of Paleontology* article, and later that year he republished the same specimens in his *Bibliography of Otoliths* (Campbell 1929b).

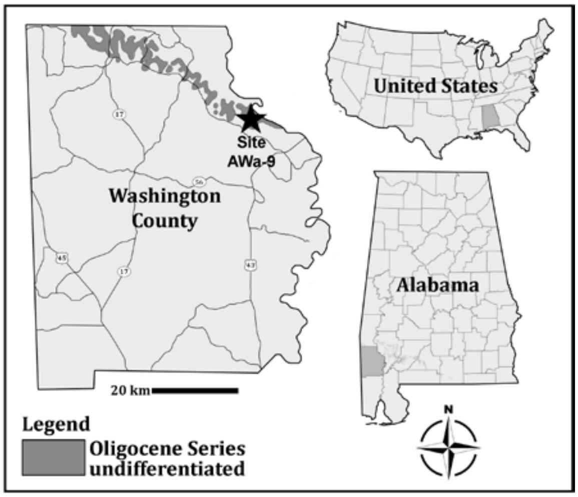
Frizzell and Lamber (1962) described several congrid otoliths from the Oligocene Red Bluff Clay in Alabama. The specimens they reported were collected from the Lone Star Cement Company Quarry at St. Stephens in Washington County, Alabama, the same locality (albeit a different unit) from which the material forming the basis of the current study was obtained. As part of their work on Cenozoic fishes of the Gulf Coast, Frizzell and Dante (1965) listed the St. Stephens quarry, and specifically the Red Bluff Clay, as one of the localities from which their sample of otoliths was derived. A few years later, Salem (1971), a graduate student of Frizzell, studied the Red Bluff Clay otoliths from the St. Stephens quarry, and several of these specimens were later reported by Nolf (1985, 2013).

Whetstone and Martin (1978) described a fossil sirenian from the Bucatunna Clay Member of the Byram Formation at the St. Stephens quarry. This specimen represented the first non-otolith vertebrate to be described from any Oligocene unit in Alabama and was the first vertebrate to be described from any Oligocene unit other than the Red Bluff Clay. Whetstone and Martin (1978) also provided a list of vertebrates that were associated with the sirenian, which included crocodilian osteoderms, spines and dental plates of myliobatid rays, teeth from the shark genera *Odontaspis*, *Galeocerdo*, and *Isurus*, and vertebrae and otoliths of teleost fishes. These specimens were reported to be in the collections of the Geological Survey of Alabama in Tuscaloosa, USA, but they now reside in the collections of the Alabama Museum of Natural History in Tuscaloosa. Thurmond and Jones (1981, p. 6) discussed the lack of studies on Oligocene vertebrates in Alabama but mentioned that the "Oligocene Red Bluff Formation has produced at least one specimen." It is unclear, however, if the specimen in question was one of the otolith taxa described earlier by Frizzell and Lamber (1962), Frizzell and Dante (1965), or Salem (1971), or a different taxon altogether. The fossil fishes of the Bucatunna Clay are in need of further investigation.

A more recent note of chondrichthyan taxa from the Oligocene Vicksburg Group in Alabama was by Manning (2003), who made mention of (but did not describe) several species. Later, Ehret and Ebersole (2014) noted the presence of carcharhinid, ginglymostomatid, and myliobatid teeth from Oligocene deposits in Alabama, but these specimens were also not figured or described. Lastly, Stringer *et al.* (2020a) reported the first occurrence of the enigmatic otolith taxon, *Equetulus silverdalensis* (Müller, 1999), in the state. This specimen was collected from the Chattian Paynes Hammock Sand in Washington County, Alabama.

To date, no vertebrate specimens have been described from the Rupelian Glendon Limestone Member of the Byram Formation in Alabama. Vertebrate fossils have, however, been described from this lithostratigraphic unit in neighboring Mississippi, including fossil otoliths that were reported by Salem (1971), Daly (1992), Phillips and Stringer (2007), and Stringer and Starnes (2020). Daly (1992, p. 10) also listed 'shark' and 'fish' among the vertebrate taxa occurring in the Glendon Limestone, and DeVries (1963, p. 40) noted that "a few fish vertebrae and shark teeth can be found in the Glendon Formation in Jasper County." Two years later, Moore (1965, p. 72) made mention of a "shark-tooth locality in the Lower Oligocene Glendon Formation" located south of Jackson, Mississippi. Dockery and Thompson (2016) reported and figured an articulated skeleton of the fossil squirrelfish, *Holocentrites ovalis* Conrad, 1941, that was collected from the Glendon Limestone in Rankin County, and this taxon has subsequently been confirmed from the same unit in Smith County (James Starnes, pers. comm.). Although Dockery and Manning (1986) reported the occurrence of *Otodus* (*Carcharocles*) *auriculatus* (de Blainville, 1818) from the Vicksburg Group and Byram Formation in Mississippi, this taxon was not confirmed specifically from the Glendon Limestone. Additionally, Manning (1997) reported terrestrial mammals from the Byram Formation in Mississippi. It is important to note that in Mississippi the Byram Formation is considered a distinct lithologic unit that overlies the Glendon Limestone, whereas in Alabama the Glendon Limestone represents the lowest member of the Byram Formation. Furthermore, the Byram Formation in Mississippi is stratigraphically equivalent to the unnamed marl member of the Byram Formation in Alabama (Raymond *et al*. 1988; Dockery and Thompson 2016).

Herein we provide the first account of marine vertebrate taxa occurring in the Oligocene Glendon Limestone Member of the Byram Formation in Alabama, USA. We provide detailed descriptions and figures of the various remains, discuss the taxonomic issues and paleobiogeographic significance of the taxa, and comment on the paleoenvironment in Alabama during this interval in the Rupelian.



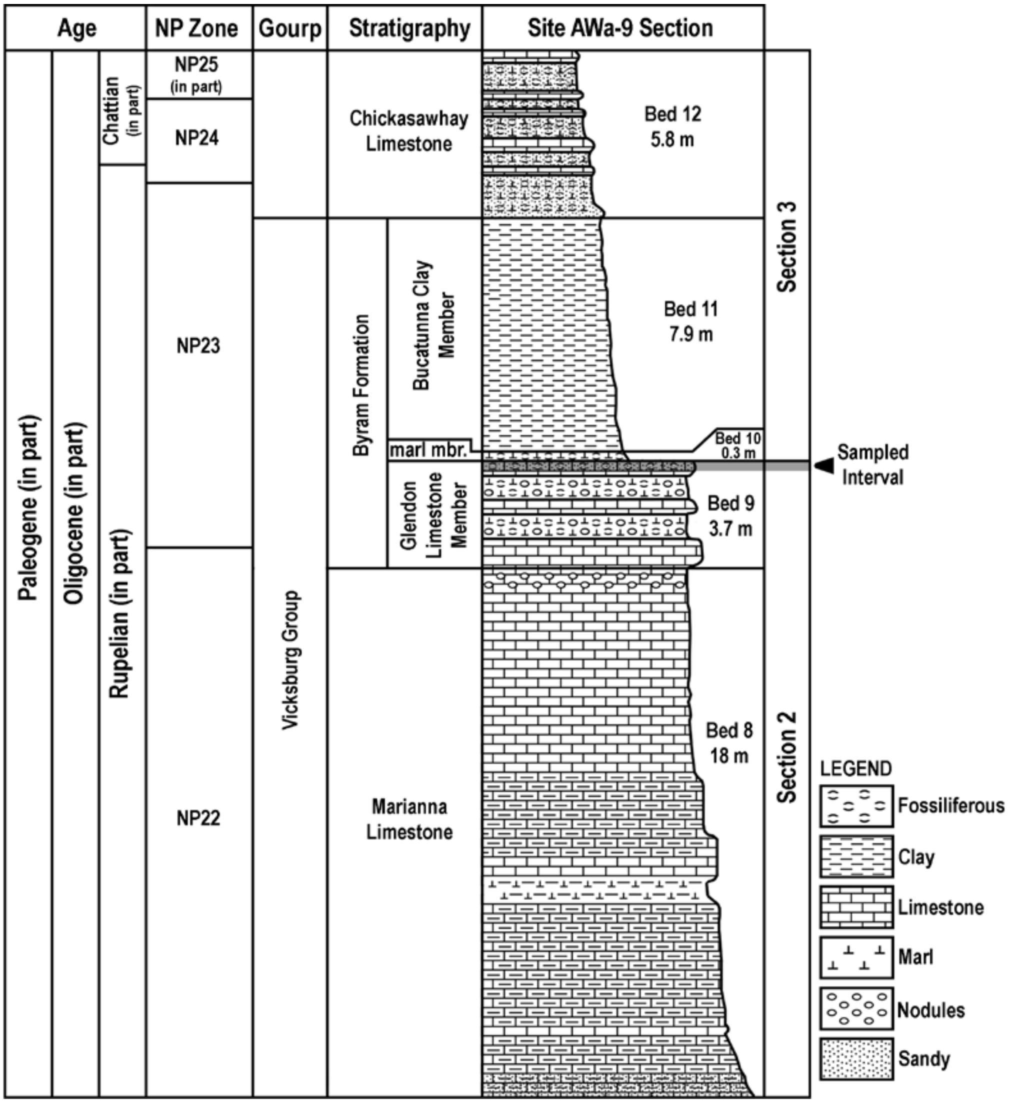
Text-fig. 1. Approximate location of site AWa-9 and Oligocene surface exposures in Washington County, Alabama, USA. Modified from Stringer *et al*. (2020a).

GEOLOGICAL SETTING

The vertebrate specimens described herein were derived from bulk samples collected from the top of the Glendon Limestone Member of the Byram Formation exposed along a hillside at St. Stephens Historical Park in Washington County, Alabama, USA (locality designation AWa-9, Text-fig. 1). This historical locality, once a prominent landmark known as St. Stephens Bluff, was purchased in the early 20th century by the Lone Star Cement Company (LSCC), which started quarrying operations at the site in 1928. Over its many years of operation, LSCC quarrying activity at the locality revealed the most complete and continuously exposed Oligocene marine section in Alabama, down to the Eocene/Oligocene contact (Glawe 1967). Today this locality resides within the boundaries of St. Stephens Historical Park.

In Alabama, the Byram Formation represents the uppermost lithostratigraphic unit of the Oligocene (Rupelian) Vicksburg Group. The formation is divided into three members, including the Glendon Limestone Member at the base, an unnamed marl member, and the Bucatunna Clay Member at the top (Raymond *et al.* 1988). The Byram Formation conformably overlies the Marianna Limestone, also of the Vicksburg Group, and is conformably overlain by the Chickasawhay Limestone. All of these lithologic units are exposed in sequence at site AWa-9 (Glawe 1967, 1969). Hopkins (1917) credited the name Glendon Limestone to Charles Wythe Cooke, who described the unit in an earlier unpublished manuscript. Hopkins (1917) originally designated the Glendon Limestone Member as the top member of the Marianna Limestone, but Cooke (1923) later elevated the unit to formation rank. MacNeil (1944) and Monroe (1954) disagreed with the latter assessment and recognized the Glendon Limestone as the basal member of the Byram Formation. According to Dockery and Thompson (2016), this attribution was logical because both the Glendon Limestone and Byram Formation occur within the *Lepidocyclina supera* large-foraminifera zone of Gravell and Hanna (1938) and the *Pecten perplanus byramensis* pecten zone of Glawe (1969). Following MacNeil (1944) and Monroe (1954), the Geological Survey of Alabama currently recognizes the Glendon Limestone as the lower member of the Byram Formation (Raymond *et al.* 1988), and this interpretation is followed here. In Mississippi, however, the Mississippi Office of Geology has chosen to follow Cooke (1923) in recognizing the Glendon Limestone as a distinct lithological formation (Dockery and Thompson 2016).

In Alabama, exposures of the Glendon Limestone Member crop out in Choctaw, Clarke, and Washington counties in the southwestern part of the state (Szabo *et al*. 1988). The unit extends into eastern Mississippi



Text-fig. 2. Geologic section of site AWa-9 showing the sampled interval. Section modified from Glawe (1967). NP Zones follow Mancini and Tew (1992).

where it thickens and becomes more detrital, with surface exposures occurring in at least seven counties (Dockery and Thompson 2016). Although the Glendon Limestone has also been reported in Georgia and northern Florida (Cooke 1923), further investigation by Huddlestun (1993) showed that this unit is exposed at only a single locality in central Georgia, and the reported occurrences in Florida instead represent other time-equivalent units.

The type section for the Glendon Limestone Member is located at Glendon, a flag station of Southern Railway situated between Jackson and Walker Springs in Clarke County, Alabama (Hopkins 1917; MacNeil 1944). Although the Glendon Limestone type locality is in a different county than site AWa-9, it is located only 15 km to the east and the Glendon Limestone exposures at St. Stephens Historical Park are considered a reference section for the unit (Hopkins 1917). The geologic exposures at site AWa-9 were extensively investigated by Glawe (1967, 1969) and Mancini and Copeland (1986). Glawe (1967) thoroughly mapped and described the hillside outcrops at our specific collecting site, and he recognized five distinct lithologic units within the exposed section that he designated beds 8–12. The samples examined herein were collected from an exposure of the Glendon Limestone Member located at the top of bed 9 of section 2 of Glawe (1967;

Text-fig. 2), and this particular bed is comprised of three irregularly indurated coquinoid and crystalline limestone ledges that weather into indurated rocks containing large tubular cavities (known locally as 'horse bone' weathering). The limestone ledges are interbedded with cream-colored fossiliferous, argillaceous and glauconitic marl that weathers brown and contains a shell hash composed of the macro-foraminiferan *Lepidocyclina* Gümbel, 1870 and bivalves like *Ostrea vicksburgensis* (Conrad, 1848), *Chlamys duncanensis* (Mansfield, 1934), *Chlamys anatipes* (Morton, 1833), *Pecten perplanus poulsoni* Morton, 1834 (in the lower beds), *P. perplanus byramensis* Gardner, 1945 (in the upper beds), and *P. howeri mariannensis* Glawe, 1969 (Glawe 1967; Szabo *et al.* 1988; Mancini and Tew 1992), and occasional vertebrate remains (this report). The specimens we examined were collected *in situ* from the top limestone ledge of this unit. Although the lower ledges are visible at the base of this section, they are exposed as part of sheer 20 m high cliff that cannot be sampled without the aid of rappelling equipment.

The age of the Glendon Limestone Member has been disputed. Siesser (1983a, b) placed the upper part of the Marianna Limestone and the entirety of the Byram Formation (including all three members) within calcareous nannoplankton Zone NP22 of Martini (1971) based on the absence of *Cyclococcolithus formosus* Kamptner, 1963 and the presence of *Lanternithus minutus* Stradner, 1962. Later, Hazel *et al.* (1980) placed the upper part of the Glendon Limestone Member, the unnamed marl member, and the lower part of the Bucatunna Clay Member within zones NP22 and 23 of Martini (1971). Mancini and Tew (1992) placed the entirety of the Marianna Limestone and Byram Formation within zones NP22 and 23, and this latter interpretation is followed here (Text-fig. 2). Mancini and Tew (1992) also placed these units within the *Pseudohastigerina micra* planktonic foraminiferal interval zone and interpreted the fossiliferous limestones of the Glendon Limestone Member to represent a TO1.1 type 2 depositional sequence (*sensu* Mitchum *et al.* 1977; Baum and Vail 1988) and highstand systems tract regressive deposits.

Huddlestun (1993) documented two separate foraminiferal populations within the Glendon Limestone, with those in Alabama generally representing moderately deep-water assemblages, whereas the flanking Georgia and Mississippi populations are characterized by more shallow-water foraminifera. This latter interpretation is corroborated by the recent discovery of sea grasses within the lower Glendon Limestone in Rankin County, Mississippi, which were likely deposited after the Vicksburg highstand (James Starnes, pers. comm.).

METHODS

Four bulk samples weighing approximately 10–15 kg each were collected by two of the authors (JAE and DJC) from site AWa-9, Washington County, AL, USA (Text-fig. 1) during the summer and fall of 2019 and the winter of 2020. The samples were collected from the base of a hillside outcrop at site AWa-9, and specifically from an unconsolidated lens exposed at the top of the Glendon Limestone Member of the Byram Formation at the top of bed 9 of section 2 of Glawe (1967; Text-figs 1 and 2). The bulk field samples were processed in the laboratories at McWane Science Center (MSC) in Birmingham, AL, USA and the South Carolina State Museum (SC) in Columbia, USA, where they were wet screened down to a 0.25 mm mesh (No. 60 USA Standard Testing sieves) to ensure the recovery of both macro- and micro-vertebrate remains. The resulting concentrates were dried, and fossils were hand-picked using magnification. Figured specimens that exceeded 0.5 cm in greatest dimension were photographed with a Nikon D80 camera with Tamron macro lens. Specimens smaller than 0.5 cm were photographed using an AmScope MU1000 camera mounted to an AmScope 3.5x–90x stereo microscope and 10MB TIFF images were captured using AmScope Toupview software version 3.7. All photographs were rendered in Photoshop CC 2017 software as part of the production of the presented figures. Whenever possible, vertebrate remains were compared directly to comparative skeletal remains housed at MSC, SC, and the otolith collection of one of the authors (GLS) in West Monroe, Louisiana, USA. All specimens have been permanently deposited within the scientific collections at either MSC or SC. Unless otherwise specified, higher taxonomic rankings used herein follow that of Nelson *et al.* (2016). In the classification of the otoliths, ordinal names typically follow Wiley and Johnson (2010), while the family-group names and authors of Recent fishes follow Van der Laan *et al.* (2014). Authors for genera and species depend greatly upon *Eschmeyer's Catalog of Fishes: Genera, Species, References* (Fricke *et al.* 2019). Information from Froese and Pauly (2019) was also utilized. Elasmobranch tooth terminology follows that of Shimada (2002) and Cappetta (2012), and tooth group terminology follows that of Siverson

(1999). Teleost tooth terminology follows that of Ebersole *et al*. (2019), and otolith terminology largely follows that of Smale *et al*. (1995) and Nolf (2013).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Cope, 1871
Superorder Galeomorphi (*sensu* Nelson, Grande and Wilson, 2016)
Order Carcharhiniformes Compagno, 1973
Family Scyliorhinidae Gill, 1862
Subfamily Premontreinae Cappetta, 1992
Genus *Pachyscyllium* Reinecke, Moths, Grant and Breitkreuz, 2005

Pachyscyllium sp.
(Text-fig. 3A)

MATERIAL: SC2019.61.30 (anterior tooth).

DESCRIPTION: The specimen is a complete anterior tooth measuring 2 mm in total height and 1.6 mm in crown width. The crown consists of a very tall, narrow main cusp flanked by a single pair of large lateral cusplets. The main cusp is sharply tapered and very slightly distally inclined. The labial face is weakly convex and smooth, whereas the lingual face is very convex but also smooth. The crown foot is thickened and overhangs the root. The lateral cusplets are large, with the mesial cusplet noticeably wider and shorter than the distal one. The cusplet faces are equally convex, and very faint vertical plications occur on the lingual face. The cutting edge is sharp, smooth, and complete from the main cusp apex to the lateral base of the cusplets. The root is low, particularly in labial view, and bilobate. The lobes are very short and diverging, with a sub-triangular attachment surface that is weakly convex. A lingual nutritive groove is long and narrow, with a central foramen. A large margino-lingual foramen occurs on each side of a large lingual protuberance.

REMARKS: Four Oligo-Miocene species of *Pachyscyllium* are currently recognized (see Reinecke *et al*. 2005, 2011; Cappetta 2012; Collareta *et al*. 2020) including *P. albigensis* Reinecke, Moths, Grant and Breitkreuz, 2005, *P. braaschi* Reinecke, Moths, Grant and Breitkreuz, 2005, *P. dachiardii* (Lawley, 1876), and *P. distans* (Probst, 1879). The Glendon Limestone tooth appears to differ from these other taxa by having a labial crown base that overhangs the root to a lesser degree than on *P. albigensis*, *P. braaschi*, or *P. dachiardii*, and it lacks the labial crown ornamentation observed on *P. distans*. Although these characteristics might suggest the Glendon Limestone specimen represents a unique species, this is difficult to ascertain based on a single specimen.

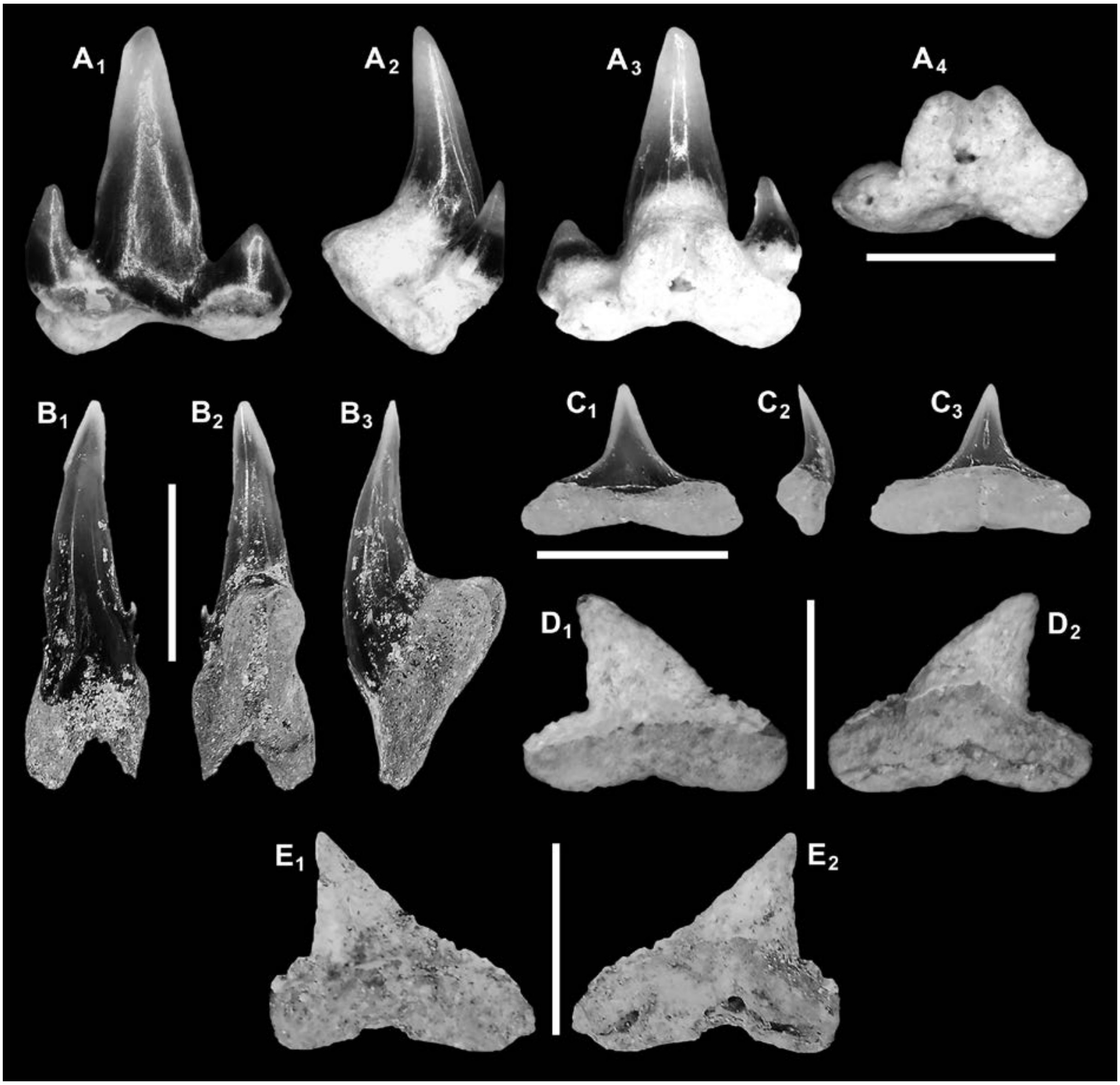
Pachyscyllium has been described from numerous Paleogene and Neogene localities in Europe (see Cappetta 2012), however North American occurrences appear extremely rare. The only such published occurrence appears to be by Case (1980, pl. 5, figs. 1, 2), who described two *P. distans* teeth (as *Scyliorhinus distans*) from the Trent Formation in North Carolina, USA. Although Case (1980) reported these specimens as being derived from the lower Miocene (Aquitanian) Trent Formation, this formational name was previously abandoned (see Ward *et al*. 1978), and the described deposits are part of the River Bend Formation, which is regarded as early Oligocene in age (Rossbach and Carter 1991). Nevertheless, the teeth figured by Case (1980) differ from the Glendon Limestone tooth by having robust enameloid folds at the labial crown foot. With only a single, incompletely preserved tooth available to us, specimen SC2019.61.30 is here not speciated. However, the lack of labial ornamentation on this specimen does suggests the presence of a second species of *Pachyscyllium* in the Oligocene of North America.

Family Hemigaleidae Hasse, 1878
Genus *Hemipristis* Agassiz, 1835

Hemipristis sp.
(Text-fig. 3B)

MATERIAL: MSC 43055 (lower left anterior tooth).

DESCRIPTION: The tooth measures approximately 11.8 mm in total height. The main cusp is tall and curved lingually and has a slight distal curvature. Both labial and lingual faces of the main cusp are strongly convex and smooth. The mesial and distal cutting edges are restricted to the upper 25% of the crown to where, in labial or lingual views, the upper portion of the crown is flared mesio-distally and is spade-shaped. Two conical cusplets are situated near the distal crown base that are medially curved, and the more apical cusplet is twice the height of the more basally situated cusplet. A single small cusplet is preserved on the mesial edge; however, a small ridge-like



Text-fig. 3. Scyliorhinidae, Hemigaleidae, and Carcharhinidae teeth from the Oligocene of site AWa-9, Washington County, Alabama. **A** – *Pachyscyllium* sp.; SC2019.61.30, tooth in (1) labial, (2) distal, (3) lingual and (4) basal views. Scale bar = 1 mm. **B** – *Hemipristis* sp.; MSC 43055, lower tooth in (1) labial, (2) lingual and (3) distal views. Scale bar = 5 mm. **C, D** – *Negaprion* aff. *N. gilmorei* (Leriche, 1942); C – MSC 43057, lower tooth in (1) labial, (2) distal and (3) lingual views. Scale bar = 4 mm; D – SC2019.61.31, upper tooth in (1) labial and (2) lingual views. Scale bar = 5 mm. **E** –*Physogaleus* sp.; MSC 43056, tooth in (1) labial and (2) lingual views. Scale bar = 5 mm.

denticle is present below the mesial cusplet that is likely analogous to a secondary cusplet. The mesial cusplet is comparable in size to the more basal distal cusplet. The root is tall, and lingually is nearly equal in height to the main cusp. The lingual protuberance on the root is robust and is incised by an elongated nutritive groove that extends basally to a U-shaped interlobe area. The root is mesiodistally compressed and the root lobes are short and only slightly divergent.

REMARKS: MSC 43055 was directly compared with the dentition of a Recent *Hemipristis elongata* (Klunzinger, 1871) (MSC 42327), and the specimen compares very favorably to that of a lower left anterior tooth. In Alabama, teeth belonging to *Hemipristis curvatus* Dames, 1883 have been confirmed from the Bartonian Gosport Sand (Ebersole *et al.* 2019), and this species is also present within the Priabonian (upper Eocene) Yazoo Clay and Rupelian Marianna

Limestone (JAE, unpublished data). Additionally, teeth belonging to *Hemipristis serra* Agassiz, 1843 have been confirmed from Pliocene Graham Ferry Formation equivalent deposits in southwest Alabama (Ebersole *et al*. 2017; Stringer *et al*. 2020b). Although these species have morphologically similar teeth, those of *H. curvatus* are smaller in overall size and have fewer mesial denticles. Traditionally, *H. curvatus* teeth have been reported from upper Eocene deposits, whereas *H. serra* has been documented from the late Oligocene through the early Pleistocene (Adnet *et al.* 2007; Cicimurri and Knight 2009; Cappetta 2012).

Unfortunately, we are unable to determine with confidence if the single small specimen available to us represents *H. curvatus*, *H. serra*, or a transitional form between the two (i.e., Adnet *et al*. 2007). Additional teeth, especially those from the upper lateral files, will be needed to ascertain which species of *Hemipristis* is present within the Glendon Limestone Member of Alabama.

Family Carcharhinidae Jordan and Evermann, 1896

Genus *Negaprion* Whitley, 1940

Negaprion aff. *N. gilmorei* (Leriche, 1942)

(Text-fig. 3C, D)

MATERIAL: MSC 43057 (lower right lateral tooth), SC2019.61.31 (upper left lateral tooth).

DESCRIPTION: Specimen MSC 43057 is small, measuring 5 mm in width and 3 mm in total height. The main cusp is short and triangular and has a very slight distal inclination. The main cusp has a slightly convex labial face and is strongly convex lingually. The crown is lingually bent in mesial and distal views, and the enameloid is smooth. The crown base is strongly sloped and extends onto elongated mesial and distal shoulders, but does not extend to the mesial and distal edges of the root. The root lobes are rounded and strongly divergent. In lingual view, the height of the root is slightly shorter than the height of the crown. The root has a rounded lingual protuberance that is bisected by a shallow nutritive groove. The interlobe area is wide and shallow, and a small distal notch is present.

SC2019.61.31 shows the effects of root etching. The specimen measures 6.5 mm in width and 5 mm in total height. The crown consists largely of a wide-based, inclined cusp and low distal heel. The mesial cutting edge is oblique, elongated, slightly sinuous, and appears to be smooth. There is an inconspicuous notch that we believe represents the transition to a mesial heel, which is continuous with the apical part of the mesial edge. The distal cutting edge is much shorter, nearly vertical, and forms a pointed apex with the mesial edge. The low distal heel is elongated and forms a nearly 90º angle with the distal cutting edge. The distal cutting edge is evidently also smooth. The labial crown face is flat, whereas the lingual face is very convex. The root is bilobate, with very thin and widely separated lobes. A nutritive groove is visible on the medial lingual root face.

REMARKS: Although the Glendon Limestone specimens are small, they appear to be conspecific with *Negaprion gilmorei* teeth that have been reported from the Claibornian (late Ypresian to Bartonian) of Alabama (Ebersole *et al*. 2019). This taxon has also been confirmed from the Chattian Chickasawhay Limestone in section 3 of Glawe (1967) at site AWa-9 (JAE and DJC, unpublished data). In contrast, upper teeth of the similar *Carcharhinus elongatus* (Leriche, 1910) from the early (Rupelian) and late (Chattian) Oligocene of Europe (Baut and Génault 1999; Reinecke *et al*. 2001, 2005; Génault 2012) and *C. gibbesii* (Woodward, 1889) from the Chattian of South Carolina (Cicimurri and Knight 2009) have clearly separated mesial and distal heels that are moderately to coarsely serrated. The Glendon Limestone specimens are tentatively assigned to *Negaprion gilmorei* due to their diminutive size, poor preservation, and the small number of teeth in our sample (n=2).

Genus *Physogaleus* Cappetta, 1980a

Physogaleus sp.

(Text-fig. 3E)

MATERIAL: MSC 43056 (lateral tooth).

DESCRIPTION: Specimen MSC 43056 is weathered, but as preserved measures 6.8 mm in width and 5.2 mm in greatest height. The main cusp is short, triangular, and distally inclined. The mesial cutting edge is elongated, slightly concave, and extends almost to the mesial edge of the root. Poorly preserved denticulation occurs on the basal part of the mesial edge, but otherwise the edge is smooth. The distal cutting edge is smooth, slightly concave, and forms an oblique angle with the distal heel. The distal heel is short and separated from the distal cutting edge by a notch. The distal edge of the crown extends to the distal edge of the root. Two pronounced cusplets are present on the distal heel. The root is bilobate with divergent and rounded lobes, and the interlobe area is shallow and U-shaped. An indistinct nutritive groove occurs on a low lingual root protuberance.

REMARKS: Although specimen MSC 43056 is poorly preserved, salient features visible on the specimen include a slightly concave mesial cutting edge, an upturned cusp apex, two distal cusplets, and irregular and poorly defined denticulations on the lower half of the mesial cutting edge. This suggests that MSC 43056 was from a lower jaw tooth file, as upper teeth of *Physogaleus* tend to have a more convex or sigmoidal mesial cutting edge, a distally directed cusp apex, and often have more defined mesial denticulation (see Pharisat 1991; Reinecke *et al.* 2001; Ebersole *et al.* 2019).

Three species of *Physogaleus* have previously been confirmed from Paleogene deposits in the Gulf Coastal Plain of the USA, including the Eocene *P. alabamensis* (Leriche, 1942), *P. americanus* Case, 1994, and *P. secundus* (Winkler, 1874) (see Case 1994; Ebersole *et al.* 2019). When compared to the lower teeth of these taxa, MSC 43056 differs from *P. americanus* by lacking the single, pronounced, mesial denticle as seen on the type specimens (Case 1994, figs 214–218). MSC 43056 also differs from *P. alabamensis*, which can have up to 12 distal cusplets and has well-defined mesial denticulations that often extend to nearly two-thirds the height of the mesial cutting edge (see Ebersole *et al.* 2019). Although MSC 43056 appears to fall within the morphological range of *P. secundus*, assignment to this taxon is problematic because its Rupelian age is well outside the known stratigraphic range for this taxon. *Physogaleus secundus* is generally regarded as a middle Eocene taxon (see Cappetta 2012), a notion that is supported by the Alabama fossil record, where this species is common in the lower to middle Eocene Claiborne Group (Ebersole *et al.* 2019) but appears to be absent from Priabonian deposits in the state (JAE, unpublished data). Although several Oligocene *Physogaleus* species have been named from elsewhere, meaningful comparisons to MSC 43056 are difficult to conduct due to the poor preservation of the tooth. With only a single specimen represented in our sample, MSC 43056 is herein not speciated.

Division Batomorphi Cappetta, 1980b
Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Incertae sedis

Gen. et sp. indet.
(Text-fig. 4A)

MATERIAL: SC2019.61.32 (tooth crown).

DESCRIPTION: The root is not preserved on specimen SC2019.61.32, but the crown measures 1.3 mm in width (mesio-distal) and 1 mm in length (labio-lingual). The crown is roughly diamond-shaped in occlusal view and the labial crown margin is somewhat angular, whereas the lingual margin is uniformly convex. The crown is low, with an oblique labial face that is overall weakly concave. The basal rim is thickened and forms a distinctive rim around the concave surface along with the transverse crest. Of note is a thin transverse ridge located on the lower half of the labial face, which does not connect with the lateral crown margins. The transverse crest is massive, thick and flat-topped (as preserved), and it divides the crown into nearly equal labial and lingual halves. The lingual crown face is convex mesio-distally but concave apico-basally, and the enameloid is smooth. Although the root is not preserved, a profile view shows that it was located near the lingual crown margin.

REMARKS: Herman *et al.* (2000) and Hovestadt and Hovestadt-Euler (2010) noted that several extant Myliobatoidei taxa, within at least two families, the Dasyatidae and Urolophidae, can have teeth bearing a secondary labial transverse crest in addition to the primary transverse crest. Of the extant genera they examined, which included *Himantura* Müller and Henle, 1837a, *Pteroplatytrygon* Fowler, 1910, *Taeniura* Müller and Henle, 1837b, *Urolophus* Müller and Henle, 1837a, *Urolophoides* Lindberg, 1930, and *Urobatis* Garman, 1913, Hovestadt and Hovestadt-Euler (2010) observed that only the teeth of *Himantura* and *Urobatis* lacked strongly developed labial ornamentation. Although the lack of labial ornamentation, combined with an occlusal outline consisting of an angled labial margin and broadly rounded lingual margin, appears to ally SC2019.61.32 with *Urobatis* (see Herman *et al.* 2000; Hovestadt and Hovestadt-Euler 2010), additional specimens are needed to further elucidate the identity and paleobiology (i.e., gynandric heterodonty) of the Glendon Limestone taxon.

Family Myliobatidae Bonaparte, 1835
Subfamily Myliobatinae Bonaparte, 1835
Genus *Aetomylaeus* Garman, 1908

"*Aetomylaeus*" sp.
(Text-fig. 4B, C)

MATERIAL: MSC 43053 (upper symphyseal tooth), MSC 43061 (upper symphyseal tooth).

DESCRIPTION: The two specimens are incomplete. As preserved, MSC 43053 measures 13.9 mm in mesiodistal width and 3.7 mm in labiolingual length, whereas MSC 43061 measures 11.1 mm in mesiodistal width and 3.8 mm in labiolingual length. In oral view the lateral angles are seen to be obtuse and located closer to the labial margin. The occlusal crown surface of both teeth is convex, and in labial view the crown is thickest medially and thins toward the mesial and distal edges. The labial crown face is nearly vertical and straight, and the crown foot slightly overhangs the root. The lingual face is lingually inclined and straight. Both the labial and lingual crown faces are ornamented with a fine network of reticulated ridges basally, transitioning into irregular and bifurcating longitudinal ridges that extend to the occlusal surface. The lingual crown foot is marked by a thin transverse ridge. The root is polyaulocorhize and consists of a series of thin lamellae that are separated by shallow nutritive grooves. The lamellae are ablated, but they extend at least to the lingual crown margin.

REMARKS: We interpret that both specimens were from the upper dentition because their occlusal surfaces are convex, and the crown foot is straight. Teeth from the lower dentition typically have a straight occlusal surface, but a medially convex crown foot. The labial crown face on MSC 43061 is unusually curved, suggesting this tooth was at the very front of the tooth plate.

Historically, fossil myliobatid teeth exhibiting the morphology described above have been identified as *Myliobatis* Cuvier, 1816. The Glendon Limestone teeth can be differentiated from extant *Myliobatis* and fossil specimens attributed to this genus in that the lateral angles are obtuse and located closer to the labial crown margin, the lingual transverse ridge is thin and sharp, and the ornamentation on crown faces consists of reticulated ridges (at least basally, but often on the entire surface). In contrast, the *Myliobatis* and *Myliobatis*-like teeth generally have lateral angles that are about 90º, the lingual transverse ridge is thick and rounded, and the crown faces have longitudinal ridges. The morphology also differs from specimens attributed to *Rhinoptera* Cuvier, 1829 in the same respects. The gross morphology of the Glendon Limestone specimens is most similar to teeth of extant *Aetomylaeus*.

Although Hovestadt and Hovestadt-Euler (2013) referred many fossil specimens previously identified as *Myliobatis* to *Pteromylaeus* Garman, 1913, other analyses have shown *Pteromylaeus* to be a junior synonym of *Aetomylaeus* (Naylor *et al*. 2012; White 2014). The latter assignment was followed by Ebersole *et al*. (2019), who demonstrated that the presence of reticulated crown ornamentation on fossil myliobatid teeth is a generic identifier for *Aetomylaeus*-like taxa. Recent phylogenetic analyses by Villalobos-Segura and Underwood (2020) indicated that the radiation of Recent myliobatid genera occurred much more recently than previously thought, with an estimated divergence during the early to middle Miocene. From a taxonomic perspective, this data suggests that the usage of extant myliobatid generic names in the fossil record should be restricted to Neogene and younger fossils, but morphologically similar Paleogene taxa should be referred to different genera within the myliobatid lineage. Because the number of fossil taxa within this newly established ghost lineage are currently unknown, MSC 43053 and MSC 43061 are herein assigned to "*Aetomylaeus*" sp. with the understanding that they may belong to an undescribed Paleogene representative within the *Aetomylaeus* lineage.

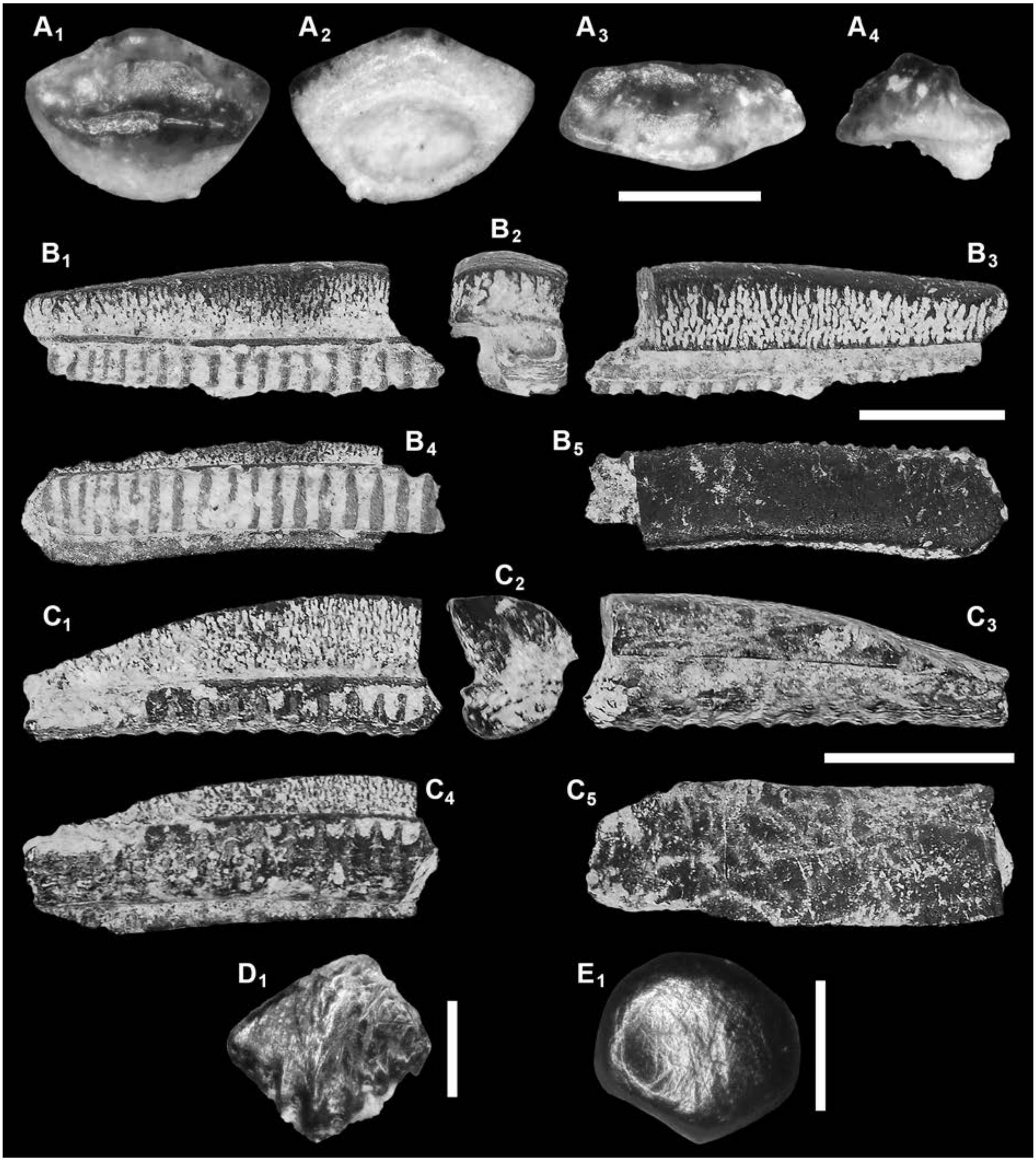
Infraclass Elasmobranchii indet.
(Text-fig. 4D, E)

MATERIAL: SC2019.61.33 (placoid scale), SC2019.61.34 (placoid scale).

DESCRIPTION: Two scale morphotypes have been recovered. The first morphotype (SC2019.61.33) consists of a massive rhomboidal crown measuring 1.2 mm in width and 1.1 mm in length. The anterior margin is thick and bears seven robust ridges on the anterior face. The dorsal surface is smooth and flat. The posterior edge is thin and sharp. The base is not preserved but appears to have been only slightly smaller in area than the crown.

The second morphotype (SC2019.61.34) consists of a very thin, ovate crown measuring 1.1 mm in greatest dimension. The crown has an even thickness, with marginal faces being convex and the upper surface being flat, and the enameloid is smooth. The base is imperfectly preserved, but appears to have been rather narrow and medially located.

REMARKS: SC2019.61.33 is very similar to material



Text-fig. 4. Myliobatiformes teeth and Elasmobranchii indet. placoid scales from the Oligocene of site AWa-9, Washington County, Alabama. **A** – Myliobatoidei indet.; SC2019.61.32, tooth in (1) occlusal, (2) basal, (3) labial and (4) profile views. Scale bar = 0.5 mm. **B**, **C** – "*Aetomylaeus*" sp.; B – MSC 43053, tooth in (1) lingual, (2) profile, (3) labial, (4) basal and (5) occlusal views. Scale bar = 5 mm; C – MSC 43061, tooth in (1) lingual, (2) profile, (3) labial, (4) basal and (5) occlusal views. Scale bar = 5 mm. **D**, **E** – Elasmobranchii indet. placoid scales in (1) outer view. Scale bar = 0.5 mm. D – SC2019.61.33; E – SC2019.61.34.

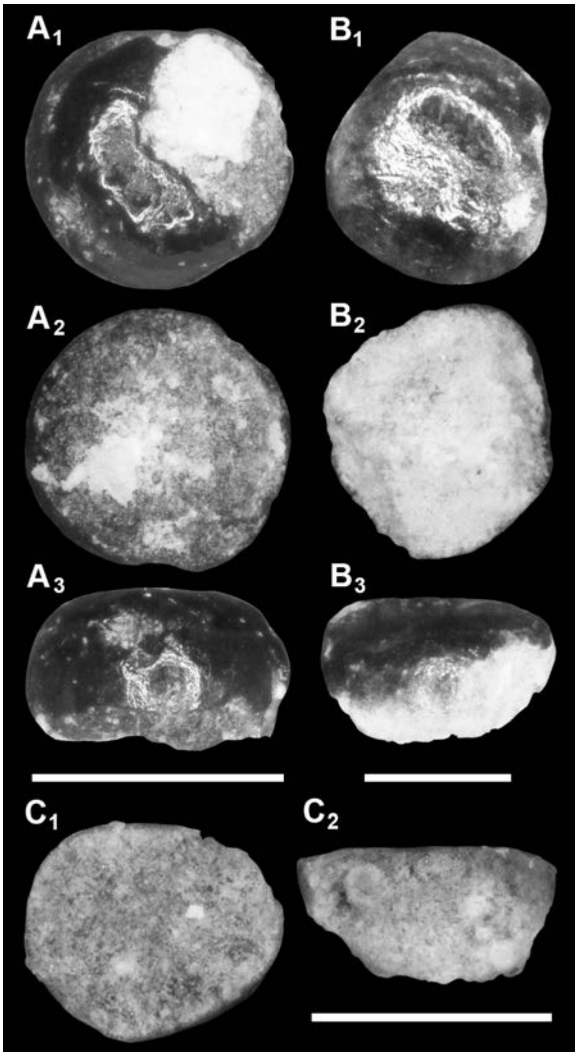
described by Laurito Mora (1999) from the Miocene of Costa Rica that was referred to Galeocerdidae. However, the identification of taxa based on isolated placoid scales is complex, as studies of extant chondrichthyans has shown that scale morphology can vary greatly depending on gender, location on the body, and ontogenetic stage (Reif 1985; Cappetta 2012). As a result, the Glendon Limestone placoid scales are not identified beyond the infraclass level.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii (*sensu* Goodrich, 1930)
Unranked Neopterygii Regan, 1923
Infraclass Holostei Müller, 1845
Division Teleosteomorpha Arratia, Scasso and Kiessling, 2004
Subdivision Teleostei Müller, 1845
Supercohort Teleocephala de Pinna, 1996
Cohort Elopomorpha Greenwood, Rosen, Weitzman and Myers, 1966
Order Elopiformes Sauvage, 1875
Family Phyllodontidae Dartevelle and Casier, 1943
Subfamily Paralbulinae Estes, 1969
Genus *Paralbula* Blake, 1940

Paralbula sp.
(Text-fig. 5A, B)

MATERIAL: SC2019.61.45 (tooth), SC2019.61.46 (tooth).

DESCRIPTION: Specimens SC2019.61.45 and SC2019.61.46 measure less than 1 mm in greatest diameter. The teeth have a circular occlusal outline with smooth enameloid, and have a conspicuous cingulum around the crown margin. In profile view the teeth have a flat-topped occlusal surface and convex lateral edges. The teeth are low-crowned in that the overall tooth height is less than their greatest occlusal diameter. The enameloid does not extend to the tooth base, exposing an irregular basal ring of dentine around both teeth. In basal view the teeth have a small medially located pulp cavity that is framed by a thick wall of dentine.



Text-fig. 5. Phyllodontidae and Albulidae teeth from the Oligocene of site AWa-9, Washington County, Alabama. **A**, **B** – *Paralbula* sp.; A – SC2019.61.45, tooth in (1) occlusal, (2) basal and (3) profile views. Scale bar = 1 mm; B – SC2019.61.46, tooth in (1) occlusal, (2) basal and (3) profile views. Scale bar = 0.5 mm. **C** – *Albula* sp.; SC2019.61.4, tooth in (1) occlusal and (2) profile views. Scale bar = 1 mm.

REMARKS: Specimens SC2019.61.45 and SC2019.61.46 differ from other similar teeth in our sample by having the combination of a low and smooth crown with enameloid cingulum, and small basal pulp cavity. These characteristics suggest that the specimens are referable to *Paralbula*, a phyllodontid taxon that has been reported from various Paleocene and Eocene localities around the world, including Alabama (Weiler 1929; Blake 1940; Arambourg 1952; Estes 1969; Weems 1999; Schein *et al.* 2011; Ebersole *et al.* 2019). Four species of *Paralbula* have been recognized, including *P. casei* Estes, 1969, *P. marylandica* Blake, 1940, *P. salvani* (Arambourg, 1952), and *P. stromeri* (Weiler, 1929). The smooth crown enameloid of the Glendon Limestone teeth is comparable to the condition seen on *P. stromeri* and many *P. marylandica* teeth, whereas *P. casei* and *P. salvani* teeth bear crown ornamentation consisting of granulation and concentric ridges. Although the teeth of *P. marylandica* can also have a granular ornamentation, it is much less apparent than on *P. casei* or *P. salvani*, and many *P. marylandica* teeth can lack ornamentation altogether (Blake 1940; Estes 1969; Ebersole *et al.* 2019).

Paralbula marylandica is the only smooth-crowned species to be reported in North America, but the stratigraphic range of this taxon is thus far only known to extend from the lower Paleocene to middle Eocene (Blake 1940; Estes 1969; Weems 1999; Schein *et al.* 2011; Ebersole *et al.* 2019). *Paralbula stromeri* is the only member of the genus known to have a range that extends into the upper Eocene (Priabonian), but this species has thus far only been confirmed from Egypt and the United Kingdom (Weiler 1929; Estes 1969). Estes (1969) noted the morphological similarities between the teeth of *P. marylandica* and *P. stromeri*, but was able to differentiate the two taxa based on their basibranchial plates (skeletal features). The Glendon Limestone specimens represent the first Oligocene record of *Paralbula*, but with only two incomplete teeth in our sample, we cannot determine if they represent new records of *P. marylandica* or *P. stromeri*, or an undescribed Oligocene species.

Order Albuliformes Greenwood, Rosen, Weitzman and Myers, 1966
Family Albulidae Bleeker, 1849
Subfamily Albulinae Bleeker, 1849
Genus *Albula* Scopoli, 1777

Albula sp.
(Text-fig. 5C)

MATERIAL: SC2019.61.44 (tooth).

DESCRIPTION: The specimen has a sub-circular occlusal outline and measures slightly under 1 mm in greatest diameter. The occlusal surface is flat and lacks enameloid due to *in vivo* usage. In profile view the edges of the tooth taper basally. The crown margins bear a thin layer of smooth enameloid. In basal view, there is a very small, circular, medially located pulp cavity.

REMARKS: The morphology of the specimen is similar to that of *Albula oweni* (Owen, 1845), a taxon that occurs in lower to middle Eocene Claibornian strata of Alabama (Ebersole *et al.* 2019). The morphological similarity to *Albula oweni* is based on the basally tapering sides of the tooth. This characteristic differentiates SC2019.61.44 from all other Paleogene teleost teeth that have been reported from Alabama, including *Albula eppsi* White, 1931, which has teeth with evenly convex lateral edges (Ebersole *et al.* 2019). Due to the poor preservation of the single tooth in our sample, specimen SC2019.61.44 is conservatively referred only to *Albula* sp.

Order Anguilliformes Goodrich, 1909
Suborder Congroidei Kaup, 1856
Family Congridae Kaup, 1856
Subfamily Bathymyrinae Böhlke, 1949
Genus *Ariosoma* Swainson, 1838

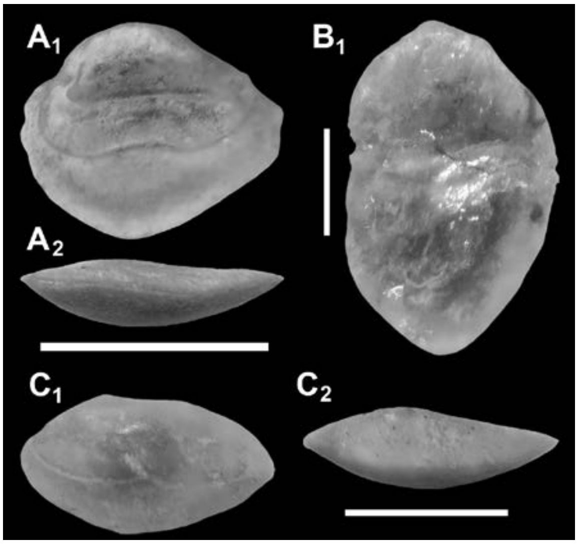
Ariosoma nonsector Nolf and Stringer, 2003
(Text-fig. 6A)

MATERIAL: MSC 43054.2 (sagitta), MSC 43059.9 (sagitta), SC2019.61.3 (sagitta), SC2019.61.4 (sagitta), SC2019.61.28 (incomplete sagitta).

DESCRIPTION: The sagittae are primarily oval in outline (*sensu* Smale *et al.* 1995), but a very prominent dorsal dome results in a more rounded shape. The height/length ratios range from 0.80–0.86. The margins are typically smooth, and the anterior margin is rounded, but not broadly. The anterodorsal margin is convex with a slight concavity occurring just before the prominent dorsal dome. The dorsal margin consists of a high, rounded dome, which is primarily medially located. The posterodorsal margin is generally slightly concave. The posterior margin is typically tapered, often pointed, and the ventral rim is usually broadly rounded and marked by a distinctive, nearly medially located angle. The inner face is smooth and convex, except for some irregular depressions in the upper portion of the dorsal area. The sulcus is wide, only slightly incised, and extends from near the anterior margin to near the posterior margin (about 85% of the length of the sagitta). The anterior portion of the sulcus is lower than the posterior portion. Except for the dorsal extremity of the ostial channel, the sulcus is filled entirely with colliculum, and the ostial channel curves backward. There is no conspicuous division of the ostial and caudal portions of the sulcus, and the posterior end of the sulcus is broadly tapered and somewhat widened ventrally. There are no indications of a ventral furrow. The outer face is smooth and convex except for an area near the posterior end, where a shallow and dorsoventrally oriented depression occurs.

REMARKS: The Oligocene specimens assigned to *Ariosoma nonsector* have several characteristics in common with *Ariosoma* as defined by Schwarzhans (2019). These include an S-shaped sulcus (see Schwarzhans 2019, fig. 2), a middorsal expansion (i.e., dorsal dome), and a backward curving ostial channel.

The Eocene specimens assigned to *Ariosoma nonsector* by Nolf and Stringer (2003) have the backward curving ostial channel and the middorsal expansion. However, the sulcus is not S-shaped as seen in the specimens illustrated by Schwarzhans (2019). The Eocene specimens are believed to be a precursor to the Oligocene specimens of *Ariosoma nonsector*. It should be noted that the Oligocene specimens may represent a new species of *Ariosoma*, but we feel this determination is not warranted based on the preservation and limited number of specimens in our sample. Large adult specimens of *Ariosoma nonsector* and the coeval *Paraconger sector* Koken, 1888 are rather distinctive, but smaller adult and particularly juvenile specimens can be difficult to distinguish. In fact, Koken's (1888) type suite of *Otolithus* (*Platessae*) *sector* is actually a mixture of these two taxa (see his pl. 17, fig. 14 for *P. sector*, and figs 15 and 16 for *A. nonsector*). However, *P. sector* has a greater length compared to its height (i.e., is more elongate) and a has a narrower sulcus than on *A. nonsector*. The latter taxon was separated from *P. sector* by Nolf and Stringer (2003) based on their examination of over 5,500 late Eocene otoliths from the Yazoo Clay in Louisiana, USA.



Text-fig. 6. Congridae, Diretmidae , and Ophidiidae otoliths from the Oligocene of site AWa-9, Washington County, Alabama. **A** – *Ariosoma nonsector* Nolf and Stringer, 2003; SC2019.61.3, right sagitta in (1) inner and (2) dorsal views. Scale bar = 5 mm. **B** – *Diretmus* sp.; MSC 43059.10, right sagitta in (1) inner view. Scale bar = 1 mm. **C** – *Preophidion meyeri* (Koken, 1888); MSC 43054.5, right sagitta in (1) inner and (2) dorsal views. Scale bar = 3 mm.

Unranked Clupeocephala Patterson and Rosen, 1977
Cohort Eutelostei Rosen, 1985
Superorder Acanthopterygii Greenwood, Rosen, Weitzman and Myers, 1966
Series Berycida (*sensu* Nelson, Grande and Wilson, 2016)
Order Trachichthyiformes (*sensu* Nelson, Grande and Wilson, 2016)
Suborder Anoplogastroidei (*sensu* Nelson, Grande and Wilson, 2016)
Family Diretmidae Gill, 1893
Genus *Diretmus* Johnson, 1864

Diretmus? sp.
(Text-fig. 6B)

MATERIAL: MSC 43059.10 (sagitta).

DESCRIPTION: The sagitta is unique by being tall (*sensu* Smale *et al.* 1995). The height is approximately twice its length, and the dorsal and ventral margins are both conspicuously tapered. The margins appear fairly smooth, probably due to erosion, but there is evidence of several lobes on some margins. The anterior margin is short, nearly vertical, and characterized by the sulcus opening. The anterodorsal margin is steep and outwardly curved. The dorsal margin is very short and pointed, and the posterodorsal margin is steep and slightly convex (and possibly incurved). The posterior margin is short, slightly rounded, and nearly vertical. The posteroventral margin is steep, nearly straight, and slants from the posterior to the ventral margin. The ventral margin is represented by a short, rounded point, whereas the anteroventral margin is steep and slightly outwardly curved. There is a prominent sulcus extending across almost 90% of the otolith length. The details of the sulcus are difficult to discern to due to erosion, but the ostium is taller than the cauda and ventrally expanded. The cauda is approximately twice the length of the ostium. There is a distinct circular depressed area above the cauda. The outer face is slightly convex and appears to have been highly sculptured (erosion has obliterated the features).

REMARKS: The shape of the sagitta of *Diretmus*? sp. is unusual and uncommon, especially for otoliths of the Gulf Coastal Plain. This species was originally described by Müller (1999) as "genus *Caproidarum*" *serratus*, but Nolf (2013) described it as "*Diretmida*" *serratus* and placed it in the family Diretmidae. Ebersole *et al.* (2019) described the only other fossil diretmid specimen known from Alabama, a single sagitta of *Diretmus* cf. *D. serratus* (Müller, 1999) recovered from the Eocene (Lutetian and Bartonian)

Lisbon Formation. Unfortunately the poor preservation of the Glendon Limestone specimen inhibits more specific taxonomic identification.

Series Percomorpha (*sensu* Nelson, Grande and Wilson, 2016)
Subseries Ophidiida (*sensu* Nelson, Grande and Wilson, 2016)
Order Ophidiiformes (*sensu* Nelson, Grande and Wilson, 2016)
Suborder Ophidioidei (*sensu* Nelson, Grande and Wilson, 2016)
Family Ophidiidae Rafinesque, 1810
Subfamily Incertae sedis
Genus *Preophidion* Frizzell and Dante, 1965

Preophidion meyeri (Koken, 1888)
(Text-fig. 6C)

MATERIAL: MSC 43054.3 (sagitta), MSC 43054.5 (sagitta), MSC 43054.6 (sagitta), MSC 43059.4 (sagitta), MSC 43067.1 (sagitta), MSC 43067.6 (sagitta), SC2019.61.9 (sagitta), SC2019.61.10 (sagitta), SC2019.61.11 (sagitta), SC2019.61.12 (sagitta), SC2019.61.13 (sagitta), SC2019.61.17 (sagitta).

DESCRIPTION: The sagitta is oblong to elliptic in shape (*sensu* Smale *et al.* 1995) with height/length ratios ranging from approximately 0.44–0.53. Adult specimens measure up to 6 mm in length, and both adult and juvenile specimens tend to have smooth margins. The inner face of the sagitta is smooth and convex. The anterior margin is bluntly pointed, whereas the anterodorsal margin is long and slightly arched. A rounded anterodorsal dome is usually visible, and the dorsal margin is short and almost horizontal. The posterodorsal margin is very slightly arched and longer than the anterodorsal margin. The posterior margin is thinly pointed, and the ventral margin is evenly and broadly rounded. The sulcus is lightly impressed, divided, completely enclosed, and marked by incised lines. The ostium is about equal in length and height to the cauda and has sides that are nearly parallel. The anterior end of ostium is sharply pointed and extends almost to the anterodorsal margin. The ostium is not excavated but is filled with colliculum. With the exception of a slight ventral constriction near the junction with the ostium, the sides of the cauda are nearly parallel. The intersection of the cauda and ostium is marked by a thin, slightly inclined, incised line. The cauda is filled with colliculum and is not excavated. The posterior end of the cauda is bluntly rounded and separated from the posterior margin by a distinct, narrow border. There is a shallow, elongated and irregularly depressed area located medially, above the sulcus. A crista superior is weakly developed, a crista inferior is either lacking or very weakly developed, and a ventral furrow is typically absent. The outer face is convex, with the dorsal portion more strongly so, and is strongly sculptured to undulated.

REMARKS: The otolith-based fossil cusk-eel genus *Preophidion* was established by Frizzell and Dante (1965). *Preophidion* is particularly widely distributed and often abundant in Eocene strata of the Gulf Coastal Plain of the USA (Ebersole *et al*. 2019), but the genus has also been reported from Oligocene strata (Stringer *et al*. 2001; Stringer and Miller 2001). In the Gulf Coastal Plain, *Preophidion* is known to occur in Alabama, Georgia, Louisiana, Mississippi, and Texas (Frizzell and Dante 1965; Breard and Stringer 1995; Stringer and Miller 2001; Green and Stringer 2002; Nolf and Stringer 2003; Stringer 2016; Ebersole *et al*. 2019).

Subseries Gobiida Betancur-R *et al*., 2013
Order Gobiiformes (*sensu* Nelson, Grande and Wilson, 2016)
Family Gobiidae Cuvier, 1816
Subfamily Gobiinae Cuvier, 1816
Genus *Gobiosoma* Girard, 1858

Gobiosoma? *axsmithi* sp. nov
(Text-fig. 7A, B)

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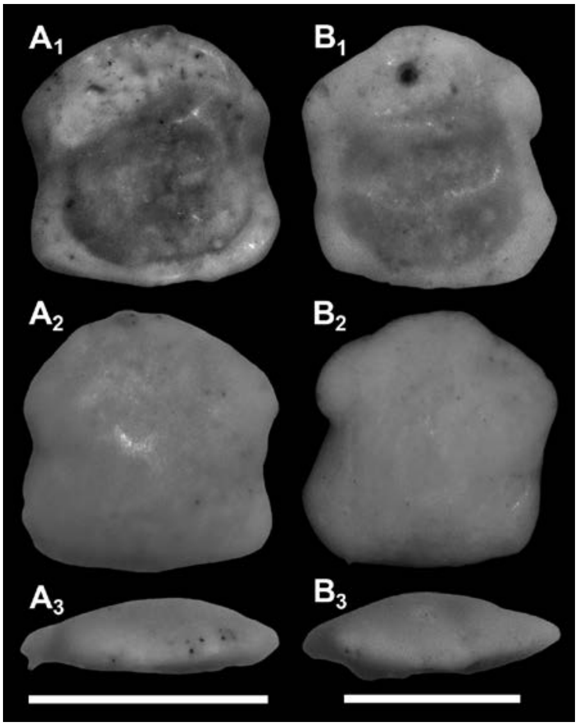
TYPE MATERIAL: Holotype (SC2019.61.18, sagitta) and paratype (SC2019.61.19, sagitta).

OTHER MATERIAL: SC2019.61.171 (broken sagitta), SC2019.61.172 (broken sagitta).

TYPE LOCALITY: Site AWa-9, St. Stephens Historical Park, Washington County, Alabama, USA, base of hillside at the top of section 2 of Glawe (1967).

TYPE STRATUM: Unconsolidated section at the top of bed 9, section 2 of Glawe (1967), Glendon Limestone Member of the Byram Formation, lower Oligocene (Rupelian), zones NP22/23, *Pseudohastigerina micra* planktonic foraminiferal interval zone.



Text-fig. 7. *Gobiosoma*? *axsmithi* sp. nov. from the Oligocene of site AWa-9, Washington County, Alabama, right sagittae in (1) inner, (2) outer and (3) dorsal views. A – SC2019.61.18, holotype. Scale bar = 1 mm. B – SC2019.61.19, paratype. Scale bar = 0.5 mm.

DERIVATION OF NAME: Named in honor and memory of Brian J. Axsmith, an American paleobotanist, paleoecologist, and professor of biology at the University of South Alabama, Mobile, Alabama, USA.

DIAGNOSIS: Sagittae are small (1 mm length), essentially square in outline, with a height/length ratio of 1.04. Specimens are almost plano-convex, with a rounded dorsal margin and a ventral margin that is almost straight and horizontal. The sulcus is small, medially positioned, and inclined at about 15° towards the anteroventral. The ostium is slightly tapered and the cauda slightly shorter in length and rounded posteriorly, with a raised, oblong-shaped subcaudal iugum. The cauda length/ostium length ratio is approximately 0.83 and the ostium height/cauda height ratio 1.67. An oblong subcaudal iugum is present. There is a prominent dorsal depression and ventral furrow. The inner face very slightly convex to almost flat, but the outer face is broadly convex.

DESCRIPTION: The outline of the sagitta is primarily square (*sensu* Smale *et al.* 1995). The inner face is somewhat convex and generally smooth (except for the dorsal depression). The margins are typically smooth and may be somewhat sharp in transversal view. The anterior margin ranges from nearly straight to slightly incurved, and the anterodorsal margin is unevenly rounded and distinguished by a predorsal projection. The dorsal margin is broadly rounded and characterized by a weakly developed obtuse medial angle. The posterodorsal margin is rounded, with a postdorsal projection that is similar to the predorsal projection. The posterior margin is incurved, and the posteroventral margin is characterized by a slight posteroventral projection or angle. The ventral margin is almost straight and horizontal, whereas the anteroventral margin has a slight anteroventral projection or angle. There is a well-defined, somewhat excavated, divided sulcus that slants approximately 15º from the posterodorsal margin to the anteroventral margin. There appears to be a small ridge-like crista superior located above the sulcus, and the ostium is slightly longer and higher than the cauda. The ostium is well separated from the anterior margin, and is tapered and somewhat pointed. There is an indication of a slight ostial lobe. The slightly smaller cauda ends well before the posterior margin and is distinguished by an evenly rounded posterior tip. A diagnostic raised, oblong-shaped subcaudal iugum is present. There is a prominent and rather deep dorsal depression that appears rounded or irregular. The ventral furrow is very distinct and curves from the anterior to the posterior of the sulcus. The outer face is thickest near the center, slightly convex, and has smooth, rounded structures.

REMARKS: Nolf *et al.* (2006) reported a gobioid sagitta from Eocene (Ypresian) strata of India that thus far represents the oldest known member of the order. Gobioid otoliths are very rare in all known teleost assemblages until the late Eocene. Of the few specimens that have been reported, Ebersole *et al.* (2019) described a single sagitta from the Lisbon Formation (Lutetian to Bartonian) of Alabama, and Nolf and Stringer (2003) reported 57 specimens (as “genus *Gobiidarum*” *vetustus*) from the upper Eocene Yazoo Clay of Louisiana. Schwarzhans (pers. comm.) noted that the ostial and caudal colliculi are always fused in the gobies, and the ventral furrow curves around the back of the cauda and coalesces with the dorsal depression (or fades).

As the diversity and abundance of Eocene and Oligocene gobioid otoliths is very low in the Gulf Coastal Plain, younger fossil gobioid otoliths and Recent specimens were compared to the Glendon

Limestone specimens. Critical comparisons were made of the predorsal angle of projection, postdorsal projection, postventral angle, preventral projection, and the presence/absence (and characteristics) of the subcaudal iugum. The most extensive and comprehensive comparative study of fossil gobioids is that of Schwarzhans *et al*. (2020) for the middle Miocene of the Czech Republic, Slovakia, and Poland. Their work included the gobiid groups of *Aphia* Risso, 1827, *Priolepis* Valenciennes in Cuvier and Valenciennes, 1837, *Gobius* Linnæus, 1758, *Thorogobius* Miller, 1969, and *Pomatoschistus* Gill, 1863b, all of which were compared to the Alabama gobiids. The Alabama specimens were also compared to Recent and fossil gobiids reported by Arellano *et al*. (1995), Nolf (2013, pls 316–325), and Gut *et al*. (2020). In a study of early Oligocene otoliths from Japan, Schwarzhans *et al*. (2017) illustrated additional Recent gobiid sagittae from *Chaenogobius* Gill, 1859 and *Gymnogobius* Gill, 1863b. The fossil forms, however, were placed in a separate and new genus and species.

Based on the aforementioned critical characteristics, we believe that the Alabama otoliths compare most favorably to the Recent genus *Gobiosoma*, which has a very similar plesiomorphic sagitta. Comparisons of the Glendon Limestone specimens to sagittae of Recent species of *Gobiosoma*, such as *G. aceras* (Ginsburg, 1939), *G. bosc* (de Lacépède, 1798), *G. chiquita* (Jenkins and Evermann, 1889), *G. robustum* Ginsburg, 1933, *G. schultzi* (Ginsburg, 1944), *G. seminudum* (Günther, 1861), and *G. yucatanum* Dawson, 1971, indicate that the Alabama *Gobiosoma* represents a new fossil species and is herein described as such. The addition of the "?" at the end of the generic name indicates that, although the fossil species compares well to the extant genus, it is possible that the form represents an unknown fossil genus. This can only be determined with certainty through the discovery of skeletal remains that are associated with *in situ* otoliths.

Subseries Ovalentaria Smith and Near in Wainwright *et al*., 2012
Order Istiophoriformes Betancur-R *et al*., 2013
Family Sphyraenidae Rafinesque, 1815
Genus *Sphyraena* Artedi, 1793

Sphyraena sp.
(Text-fig. 8A–C)

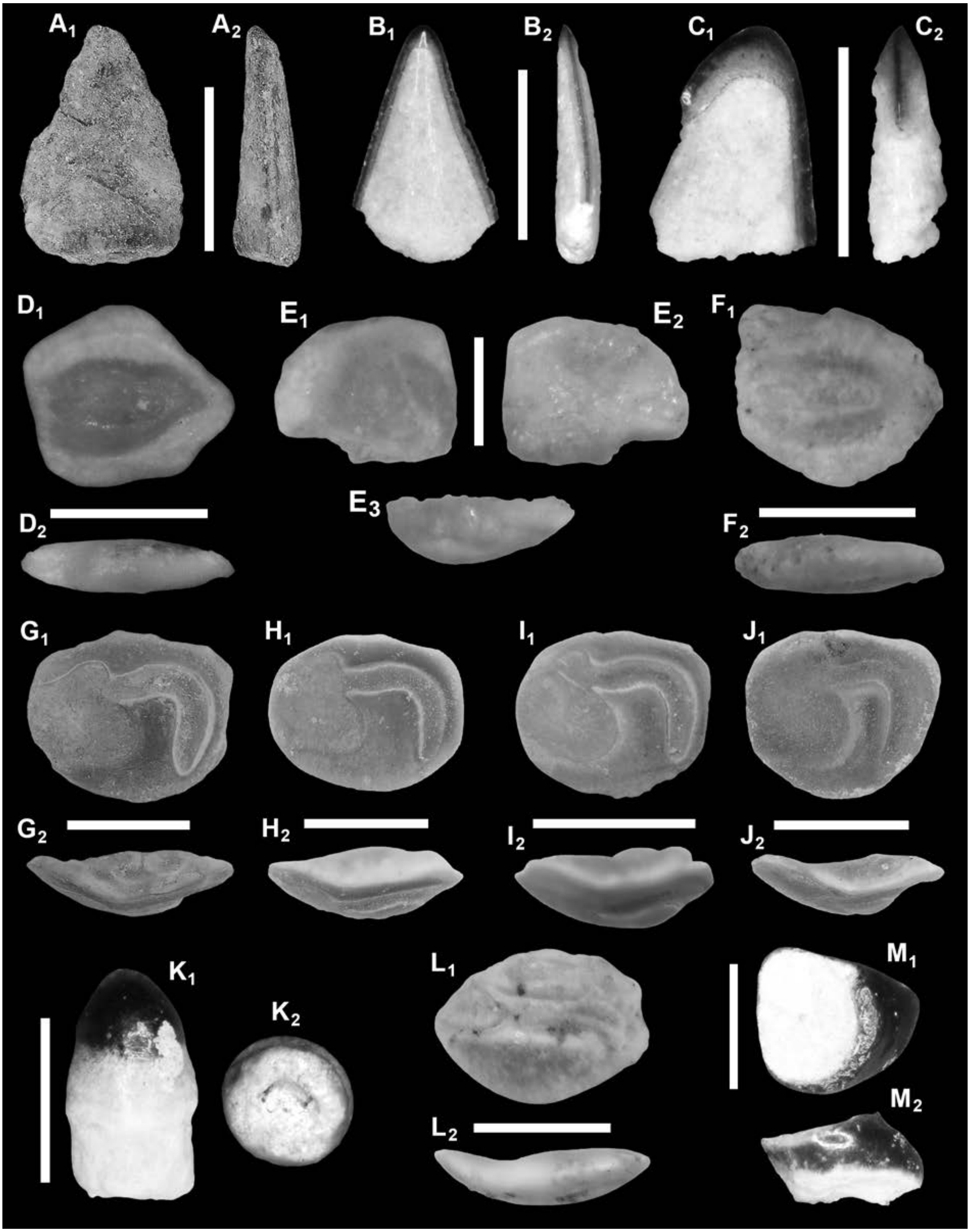
MATERIAL: SC2019.61.35 (tooth), SC2019.61.36 (tooth apex), SC2019.31.37 (laniary tooth apex).

DESCRIPTION: SC2019.61.35 is the most complete specimen, consisting of an ablated crown measuring 8 mm in total height. The crown is lanceolate in labial view, with sharp, smooth, convex anterior and posterior carinae. The labial face is nearly flat, but the lingual face is convex, particularly near the crown base. In anterior/posterior view there is a slight medial curvature. In basal view there is a small medially located pulp cavity. Specimens SC2019.61.36 and SC2019.31.37 are represented by tooth apices that are similar to that described above. SC2019.31.37, however, is not symmetrical in labial or lingual views, indicating it is a laniary tooth.

REMARKS: The Glendon Limestone Member teeth are similar to several fossil taxa previously described from the Paleogene of Alabama, like *Palaeocybium* Monsch, 2005 and *Scomberomorus* de Lacépède, 1801 (Ebersole *et al*. 2019). However, the Glendon Limestone *Sphyraena* teeth differ from *Palaeocybium* by being more labio-lingually compressed and by having less pronounced and pointed carinae in profile view. These teeth also lack the basal thickening seen on Paleogene *Scomberomorus* teeth, and the carinae extend to the base of the tooth (they do not on *Scomberomorus*; see Ebersole *et al*. 2019). Furthermore, both *Palaeocybium* and *Scomberomorus* lack the laniary tooth morphology that occurs in the dentition of *Sphyraena*.

The Glendon Limestone teeth were compared directly to those of the extant *Sphyraena barracuda* (Edwards in Catesby, 1771) (MSC 43215, SC2018.3.1) and *Sphyraena borealis* DeKay, 1842 (MSC 43076). Because the teeth have unserrated carinae, they appear better aligned with the smaller members of the genus, such as *S. borealis*, as opposed to the much larger and serrated-toothed *S. barracuda*. Furthermore, based on the size and shape of the teeth, both SC2019.61.35 and SC2019.61.36 appear to have been derived from the palatine or dentary. SC2019.61.37, on the other hand, has a sharp anterior carina and a posterior barb, features which can occur on *Sphyraena* laniary teeth. Unfortunately, all of the teeth in our sample are incomplete and we cannot provide a more precise taxonomic assignment.

Order Pleuronectiformes Bleeker, 1859
Suborder Pleuronectoidei (*sensu* Nelson, Grande and Wilson, 2016)
Superfamuly Pleuronectoidea Rafinesque, 1815
Family Paralichthyidae Regan, 1910
Genus *Citharichthys* Bleeker, 1862



Text-fig. 8. Sphyraenidae, Paralichthyidae, Sciaenidae, Sparidae, and Balistidae elements from the Oligocene of site AWa-9, Washington County, Alabama, except when stated otherwise. **A–C** – *Sphyraena* sp.; A – SC2019.61.35, tooth in (1) labial and (2) profile views. Scale bar = 5 mm; B – SC2019.61.36, tooth in (1) labial and (2) profile views. Scale bar = 1 mm; C – SC2019.61.37, laniary tooth in (1) labial and (2) profile views. Scale bar = 1 mm. **D** – *Citharichthys* sp.; SC2019.61.22.1, right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 1 mm. **E** – gen. et sp. indet.; SC2019.61.27, lapillus in (1) macular, (2) anti-macular and (3) side views. Scale bar = 0.5 mm. →

Citharichthys sp.
(Text-fig. 8D)

MATERIAL: SC2019.61.22 (14 sagittae), SC2019.61.23 (43 sagittae).

DESCRIPTION: Sagittae of this taxon are typically no larger than 3.0–3.5 mm in length, but the Glendon Limestone Member specimens are much smaller, with many of them only around 1.0 mm. The sagittae tend to be relatively thin, and the outline is primarily a compressed pentagon (*sensu* Schwarzhans 1999). The margins range from smooth to occasionally undulated, and the rims of the margins are usually sharp. The anterior margin has an obtuse median angle with no rostrum. The anterodorsal margin ranges from nearly straight to concave. In contrast, the dorsal margin is almost horizontal and characterized by a predorsal projection and postdorsal angle, which is usually bent slightly outward. The posterodorsal margin is weakly concave and located between the postdorsal angle and the posterior margin. The posterior margin is distinguished by a pointed, outwardly projected posterior tip that occupies a slightly supramedian position. The ventral margin is deeply curved and has an obtuse medioventral angle. The inner face is moderately convex and smooth, and bears a very distinctive fusiform sulcus. The sulcus is medially located, almost horizontal, and widens just behind the centerline, with the anterior and posterior portions being narrower. Distinction of the ostium and cauda cannot be made because the colluculi are completely fused. If present, the ventral furrow is indistinct. There are dorsal and ventral depressions that nearly continuously connect around the sulcus, forming a circumsulcal depression. The outer face is generally flat to slightly concave, with little ornamentation.

REMARKS: *Citharichthys* otoliths appear to be rare in Alabama, as none were reported from the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama (Ebersole *et al.* 2019) and only two *Citharichthys macrops* Dresel, 1885 sagittae were documented from Pliocene (Zanclean to Piacenzian) Graham Ferry Formation equivalent deposits in Alabama (Stringer *et al.* 2020b). The large number of *Citharichthys* sagittae in the Glendon Limestone Member assemblage (nearly 50% of the total number of specimens) is unusual and may be related to unique or unusual paleoenvironmental conditions.

Citharichthys? sp.
(Text-fig. 8E)

MATERIAL: SC2019.61.27 (2 lapilli).

DESCRIPTION: The utricular otoliths (or lapilli) are very small and approximately 0.6 mm in length. Both specimens appear to have an oval outline (*sensu* Smale *et al.* 1995), although one is not as well preserved. The macular side (ventral side *sensu* Assis 2005) is noticeably convex, and it is smooth except for the well-defined gibbus macula and the prominentia marginalis. Although well defined, the gibbus macula is not large relative to the size of the lapillus. The linea basalis appears to be a single lobe. The anti-macular side (dorsal side *sensu* Assis 2005) is essentially flat and featureless.

REMARKS: The two Glendon Limestone Member lapilli appear to be conspecific. Due to their unremarkable morphology, lapilli are generally not utilized in the study of fossil otoliths. However, there are exceptions, including taxa within families like Ariidae (sea catfishes) and Sciaenidae (drums and croakers) (Nolf 2013; Schwarzhans *et al.* 2018; Stringer and Bell 2018; Schwarzhans and Stringer 2020). Although the lapilli for many species of Ariidae and Sciaenidae are known (Chao 1978; Aguilera *et al.* 2020), the Glendon Limestone lapilli do not appear to conform to any of these taxa. Our two specimens are similar to lapilli of Recent *Citharichthys arctifrons* Goode, 1880 (see Campana 2004, p. 204), and it is interesting to note that *Citharichthys* comprises almost 50% of the otoliths within the Glendon assemblage. Therefore, there is a relatively good possibility that the lapilli represent this genus, and we tentatively assign them to *Citharichthys*.

F – *Syacium* sp.; SC2019.61.21, right sagitta in (1) inner and (2) dorsal views. Scale bar = 1 mm. **G**, **H** – *Sciaena pseudoradians* (Dante and Frizzell in Frizzell and Dante, 1965); G – MSC 43059.1, right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 5 mm; H – MSC 43507, from the Glendon Limestone of Mississippi (included for comparison), right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 5 mm. **I**, **J** – *Aplodinotus gemma* Koken, 1888; I – SC2019.61.1, right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 5 mm; J – MSC 43506, from the Glendon Limestone of Mississippi (included for comparison), right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 5 mm. **K** – *Sciaenops*? sp.; SC2019.61.43, tooth in (1) profile and (2) basal views. Scale bar = 1 mm. **L** – *Sparus*? *elegantulus* (Koken, 1888); MSC 43067.5, right sagitta (reversed for comparison) in (1) inner and (2) dorsal views. Scale bar = 2 mm. **M** – Balistidae indet.; SC2019.61.38, tooth in (1) occlusal and (2) profile views. Scale bar = 1 mm.

Genus *Syacium* Ranzani, 1842

Syacium sp.
(Text-fig. 8F)

MATERIAL: SC2019.61.20 (sagitta), SC2019.61.21 (sagitta), SC2019.61.25 (sagitta).

DESCRIPTION: The sagittae are primarily square (*sensu* Smale *et al.* 1995). The inner face is smooth and weakly convex. The margins are generally smooth, but can be variable and irregular. The anterior margin ranges from nearly vertical to slightly outward slanted from the anteroventral margin to the anterodorsal margin. There is no rostrum because the sulcus does not extend to the anterior margin. The anterodorsal margin is distinguished by a slightly acute, prominent angle, and the dorsal margin is irregular and almost horizontal. The posterodorsal margin is distinguished by a posterodorsal projection that is conspicuous, but not very large. The posterior margin is typically straight, but it can be nearly vertical or slightly slanted toward the posteroventral margin. The posteroventral margin is characterized by a distinct, slightly rounded angle that joins with the posterior margin. The fairly smooth ventral margin is nearly straight and horizontal, and the anteroventral margin is slightly rounded and forms a distinct angle with the anterior margin. The inner face bears a highly specialized, fusiform sulcus that slants downward from the posterodorsal margin, almost to the anteroventral margin. Additionally, the fusiform sulcus widens just behind its midline, with the anterior and posterior portions being narrower. Although the sulcus extends across approximately 75% of the inner face, it is narrow and represents only about 20% of the of the height of the inner face. The sulcus is divided into ostial and caudal areas, with the ostium located near the lower portion of the anterior and anteroventral margins, but not reaching the margins. The ostium is narrow and constricted at the anterior and posterior, and the anterior portion is tapered and almost pointed. The cauda is longer and wider than the ostium, and the anterior of the cauda is tapered, whereas the center portion is enlarged. The posterior of the cauda is tapered with a somewhat pointed tip, and the cauda appears to be excavated slightly deeper than the ostium. The ostium and cauda are conspicuously connected or fused, and colliculum occurs within. There is a marked circumsulcal depression extending from above the ostium to around the cauda, ending below the ostium. This extended depression forms an elevated flattened area for the fusiform sulcus. There is no visible ventral furrow. The outer face is relatively flat on the dorsal and ventral areas, but slightly convex in the center.

REMARKS: The fossil record of *Syacium* in Alabama was previously represented by a single sagitta (Stringer *et al.* 2020b), and the genus appears to be rare in all reported assemblages across the Gulf and Atlantic coastal plains of the USA. With the exception of the Alabama specimens and a single *Syacium* otolith reported by Stringer (1992) from the Mississippi River mudlump islands (late Pleistocene−early Holocene), very few other specimens are known (Nolf and Stringer 2003; Nolf 2013; Stringer *et al.* 2017; Stringer and Bell 2018; Ebersole *et al.* 2019; Stringer and Shannon 2019; Stringer and Hulbert 2020).

Family Paralichthyidae indet.

MATERIAL: SC2019.61.26 (eroded sagitta).

REMARKS: The specimen attributed to Paralichthyidae indet. is significantly eroded, but the discernible features align it with this family. The outline and general morphology of the specimen is very similar to taxa like *Citharichthys* or *Syacium*, both of which are present within our Glendon Limestone Member sample. The position and the shape of the fusiform sulcus is also comparable to members of the Paralichthyidae. Unfortunately, the preservation of SC2019.61.26 does not allow for a more refined identification.

Order Acanthuriformes (*sensu* Nelson, Grande and Wilson, 2016)
Suborder Sciaenoidei Betancur-R *et al*., 2013
Family Sciaenidae Cuvier, 1829
Genus *Sciaena* Linnæus, 1758

Sciaena pseudoradians (Dante and Frizzell in Frizzell and Dante, 1965)
(Text-fig. 8G, H)

MATERIAL: MSC 43054.13 (sagitta), MSC 43059.6 (sagitta), MSC 43059.1 (sagitta), MSC 43059.11 (sagitta).

DESCRIPTION: The sagittae are generally oval to subrectangular in outline (*sensu* Smale *et al.* 1995), and have approximate height/length ratios ranging from 0.75–0.82 (however the ratios are affected by the appreciable erosion of the anterior margin). The inner face is convex and smooth. The margins are primarily smooth, with the anterior margin being very broadly and evenly rounded. The anterodorsal margin is slightly convex and the dorsal margin slopes gently downward anteriorly and posteriorly from a subtle obtuse central angle. There is a conspicuous posterodorsal angle on almost all specimens. The posterior margin is almost straight and vertical, whereas the ventral margin is broadly rounded. There is a very prominent sulcus (heterosulcoid type) that extends across almost 95% of the inner face. The ostium extends for almost 50% the length of the sulcus, and the height of the cauda is only about 25% the height of the ostium. The ventral portion of the ostium is much more expanded, and the ostium is filled with colliculum. The anterior of the ostium is even with the anterior margin of the sagitta, and the dorsal and ventral margins of the ostium tend to be constricted anteriorly. The cauda is long and narrow, and it has a horizontal portion and a sharply downturned portion. The horizontal portion of the cauda is slightly shorter than the downturned portion, and the angle between the two is close to 90°. The downturned portion is tapered but still somewhat rounded, and it almost reaches the posteroventral margin. The outer face is generally weakly concave and sculptured.

REMARKS: Unfortunately, all four of the specimens we assigned to *Sciaena pseudoradians* are considerably eroded, and they would have been more elongate if not for abrasion and attrition on the thin edges of the anterior margin. Additionally, the ventral edge of the ostium would be longer and remain essentially horizontal. The posterior margin is usually almost vertical, as is illustrated by Nolf (2013, pl. 277). These features allow one to differentiate *S. pseudoradians* from the very similar and coeval *Aplodinotus gemma* Koken, 1888 (see below). Additionally, although larger specimens of *S. pseudoradians* develop lower height/length ratios (i.e., more elongated), the height/length ratios of larger specimens of *A. gemma* tend to have higher height/length ratios (i.e., are more rounded). These characteristics are well-illustrated in figures of *A. gemma* in Nolf (2013, pl. 269), who also noted the similarity of small *A. gemma* (around 5 mm) sagittae to those of small *S. pseudoradians* specimens (see Nolf 2013, pl. 277). Because it is typical for very small (juvenile) sciaenid otoliths to be plesiomorphic and more difficult to identify, we figure two well-preserved adult specimens from a different locality (but same stratigraphic unit) for comparison with our less adequately preserved specimens from site AWa-9.

Genus *Aplodinotus* Rafinesque, 1819

Aplodinotus gemma (Koken, 1888)

(Text-fig. 8I, J)

MATERIAL: MSC 43059.2 (sagitta), SC2019.61.1 (sagitta), SC2019.61.2 (sagitta).

DESCRIPTION: The sagittae range from somewhat oval to an almost elongated discoid outline (*sensu* Smale *et al.* 1995), and generally have height/length ratios ranging from 0.90–0.95. The inner face is convex and smooth, with the greatest thickness in the area between the ostium and the cauda. The margins are primarily smooth. The anterior margin is broadly and evenly rounded, and the anterodorsal margin is slightly convex. The dorsal margin slopes gently downward anteriorly and posteriorly from a very subtle obtuse central angle. There is a conspicuous posterodorsal angle on almost all specimens. The posterior margin is almost straight and slants slightly inward to varying degrees. The ventral margin is broadly rounded and a very prominent sulcus (heterosulcoid type) extends across almost 95% of the inner face. The ostium extends for over 50% of the length of the inner face, and the height of the cauda is only about 20% of the height of the ostium. The ventral portion of the ostium is greatly expanded toward the ventral margin, especially on large specimens. The ostium is filled with colliculum, and its anterior portion is even with the anterior margin of the sagitta. The dorsal and ventral margins of the ostium generally constrict anteriorly. The cauda is long and narrow and divided into a horizontal portion and a sharply downturned portion. The horizontal portion is slightly shorter than the downturned portion, and the angle between the two is close to 90º. The downturned portion of the cauda is tapered, somewhat rounded, extends almost to the posteroventral margin, and is usually curved toward the posterior of the ostium. The outer face is usually slightly concave and sculptured.

REMARKS: According to Nolf (2003), this species is known from the Oligocene of Mississippi (Mint Spring Formation, Byram Formation, and Chickasawhay Limestone) and Louisiana (Rosefield Formation), USA. Nolf (2003) postulated that present-day freshwater genera (for example, *Aplodinotus grunniens* Rafinesque, 1819 of the Mississippi River drainage system in the USA) are descendants of marine ancestors like *A. gemma* and related species from the USA and Central and South America. Juvenile specimens of this species are more difficult to identify because of their plesiomorphic morphology. The similarity of *A. gemma* sagittae to *Sciaena pseudoradians*, especially among smaller specimens (< 6 mm), is outlined above. The ontogenetic changes observed in *A. gemma* include the curving of the distal portion of the cauda toward the posteroventral margin of the ostium. This feature is highly characteristic and not observed on *S. pseudoradians* (Nolf 2013, pl. 269, top specimen of *A. gemma*) otoliths. The curving of the distal part of the cauda toward the ostium is not seen on the specimen of *A. gemma* from site AWa-9 due to its small size (approximately 5 mm).

Genus *Sciaenops* Gill, 1863a

Sciaenops? sp.

(Text-fig. 8K)

MATERIAL: SC2019.61.43 (tooth).

DESCRIPTION: Specimen SC2019.61.43 is a high-crowned tooth, with an overall height (1.2 mm) that exceeds its occlusal diameter (0.7 mm). The tooth has smooth crown enameloid and a circular occlusal outline. In profile view the edges of the crown are straight and gently tapered apically, and the occlusal surface is evenly convex. The enameloid covers the upper two-thirds of the tooth, whereas the lower third is comprised of exposed dentine. The upper half of the enameloid crown is a darker in color than the lower half. The edges of the dentine base are parallel and straight, and slightly inset from the crown base. The tooth base is cylindrical and has a wide, deep, and medially positioned pulp cavity.

REMARKS: SC2019.61.43 appears to be congeneric with the pharyngeal teeth of a Recent *Sciaenops ocellatus* (Linnæus, 1766) specimen in the MSC collection (MSC 42611). The pharyngeal bones of MSC 42611 exhibit two distinct tooth morphologies, including those that are recurved with a pointed apex and those that are erect with a blunt and evenly convex apex. Specimen SC2019.61.43 compares very favorably to the latter morphology. The specimen differs from other teeth in our Glendon Limestone sample by being high-crowned and having a more convex apex and deeper pulp cavity. Although SC2019.61.43 is similar in size and proportion to teeth of *Albula eppsi* that have been reported from the Eocene of Alabama (see Ebersole *et al*. 2019, fig. 60a–c), teeth of that taxon differ by having evenly convex lateral edges and crown enameloid that extends almost to the base of the tooth.

Near *et al*. (2013) provided molecular evidence indicating that *S. ocellatus* and *Micropogonias undulatus* (Linnæus, 1766) diverged from a sciaenid ancestor sometime during the Oligocene. Lo *et al*. (2015) further postulated that *S. ocellatus* originated in the western Atlantic Ocean during the early Miocene, roughly 15.8 Ma. Specimen SC2019.61.43 is therefore conservatively assigned to *Sciaenops*? sp. because it is unclear if the tooth represents a basal representative of the genus or an altogether different and undescribed Oligocene sciaenid within the *Sciaenops* and *Micropogonias* lineage.

Order Spariformes (*sensu* Nelson, Grande and Wilson, 2016)

Family Sparidae Rafinesque, 1818

Genus *Sparus* Linnæus, 1758

Sparus? *elegantulus* (Koken, 1888)

(Text-fig. 8L)

MATERIAL: MSC 43054.4 (sagitta), MSC 43054.7 (sagitta), MSC 43059.7 (sagitta), MSC 43067.2 (sagitta), MSC 43067.3 (sagitta), MSC 43067.4 (sagitta), MSC 43067.5 (sagitta), SC2019.61.5 (sagitta), SC2019.61.6 (sagitta), SC2019.61.7 (sagitta), SC2019.61.8 (sagitta), SC2019.61.14 (sagitta), SC2019.61.15 (sagitta), SC2019.61.24 (sagitta).

DESCRIPTION: The sagittae are generally small, with most ranging from 3 to 4 mm in length. The sagitta outline is oval (*sensu* Smale *et al*. 1995), and the height/length ratios range from 0.64–0.70. The inner face is slightly convex and smooth, and the margins are variable in shape, with irregular lobes common. The anterior margin is characterized by the rostrum and antirostrum, and the anterodorsal margin is convex and often irregular. The dorsal margin is convex and usually irregular, and the posterodorsal margin is convex and steeper than the anterodorsal margin. The posterior margin is tapered and may be somewhat pointed, and the ventral margin is broadly rounded. A prominent sulcus (heterosulcoid type) extends across 85% of the inner face, and the ostium is about one-half the length of the cauda. The height of the cauda is less than the height of the ostium. A slight ventral expansion of the ostium is filled with colliculum. The anterior portion of the ostium extends onto the rostrum, and the ventral margin of the ostium is essentially horizontal. The cauda is elongated, with a long horizontal portion and a short downturned portion. The angle of the horizontal and downturned portions is approximately 45º, and the downturned portion is slightly tapered and significantly separated from the posteroventral margin. An irregular depressed area occurs above the sulcus, largely above the cauda. A ventral furrow is present, and the outer face is slightly concave.

REMARKS: This species was first reported from the Gulf Coast of the USA by Koken (1888), and it has since been documented from the upper Eocene Yazoo Clay of Louisiana (as "genus Sparidarum" *elegantulus*) where it was reported as common (Nolf and Stringer 2003). The assignment of the taxon to *Sparus*? is based on Janssen (2012), who recommended the use of the type genus for the family followed by a question mark in the event the family and species is known, but the genus is unknown. This convention indicates that the species belongs to a known or possibly undescribed genus in the family.

Order Tetraodontiformes Berg, 1940
Suborder Balistoidei Rafinesque, 1810
Family Balistidae Rafinesque, 1810

Gen. et sp. indet.
(Text-fig. 8M)

MATERIAL: SC2019.61.38 (worn tooth).

DESCRIPTION: This tooth measures just over 1 mm in length and width. The labial two-thirds of the occlusal surface of the tooth is represented by a large and flat wear facet, and the anterior portion of the main cusp is not preserved. The lingual one-third of the crown is lingually projected and strongly convex. The labial portion of the tooth is much wider than the lingual portion, giving the tooth a tear-drop shaped occlusal outline. The mesial, distal, labial, and lingual edges are rounded. The crown enameloid does not extend to the base of the tooth, revealing a basal concentric ring of exposed dentine. The basal edge of the tooth is abraded and irregular.

REMARKS: Specimen SC2019.61.38 appears to be comparable to teeth assigned to the Balistidae that were recovered from middle Eocene deposits in Alabama (see Ebersole *et al*. 2019, fig. 67). The combination of tear-drop shaped occlusal outline and rounded lateral edges is unique among the Glendon Limestone Member teeth described herein, and separates this taxon from other similar Paleogene taxa like *Eotrigonodon* Weiler, 1929 (see Ciobanu 2011, figs 5–10). The morphology is consistent with extant balistid incisiform teeth, but a more refined identification is currently not possible due to the incomplete preservation of the single specimen available. The only described Paleogene balistid is the middle Eocene taxon, *Gornylistes prodigiosus* Bannikov and Tyler, 2008, a species known only from a complete skeleton. However, as the dentition of that species has not been described and no meaningful comparisons can therefore be made with the Glendon Limestone tooth, specimen SC2019.61.38 is assigned only to the Balistidae. Although similar teeth occur in the Bartonian Gosport Sand, and they are relatively common in the Priabonian Yazoo Clay in Alabama (JAE, unpublished data) and the Parkers Ferry Formation of South Carolina (DJC, unpublished data), specimen SC2019.61.38 extends the temporal range of this morphology into the Rupelian.

Teleostei indet.

MATERIAL: MSC 43054.9 (sagitta), MSC 43059.8 (sagitta), SC2019.61.16 (sagitta), SC2019.61.29 (sagitta), SC2019.61.39 (tooth), SC2019.61.40 (tooth), SC2019.61.41 (tooth), SC2019.61.42 (tooth), SC2019.61.47 (worn tooth), SC2019.61.48 (dorsal fin spine), SC2019.61.49 (dorsal fin spine), SC2019.61.50 (dorsal fin spine), SC2019.61.51 (dorsal fin spine), SC2019.61.52 (dorsal fin spine), SC2019.61.53 (dorsal fin spine), SC2019.61.54 (dorsal fin spine), SC2019.61.55 (2 fin spine fragments), SC2019.61.56 (fin spine), SC2019.61.57 (fin spine), SC2019.61.58 (fin spine), SC2019.61.59 (fin spine), SC2019.61.60 (left quadrate), SC2019.61.61 (left quadrate), SC2019.61.62 (right premaxilla), SC2019.61.63 (left dentary), SC2019.61.64 (dentary?), SC2019.61.65 (jaw fragment), SC2019.61.66 (atlas vertebra), SC2019.61.67 (atlas vertebra), SC2019.61.68 (vertebra), SC2019.61.69 (atlas vertebra), SC2019.61.70 (vertebra), SC2019.61.71 (vertebra), SC2019.61.72 (vertebra), SC2019.61.73 (vertebra), SC2019.61.74 (vertebra), SC2019.61.75 (vertebra), SC2019.61.76 (vertebra), SC2019.61.77 (vertebra), SC2019.61.78 (vertebra), SC2019.61.79 (vertebra), SC2019.61.80 (vertebra), SC2019.61.81 (vertebra), SC2019.61.82 (vertebra), SC2019.61.83 (vertebra), SC2019.61.84 (bone fragment), SC2019.61.85 (bone fragment), SC2019.61.86 (bone fragment), SC2019.61.87 (bone fragment), SC2019.61.88 (bone fragment), SC2019.61.89 (bone fragment), SC2019.61.90 (epihyal?), SC2019.61.91 (bone fragment), SC2019.61.92 (epihyal?), SC2019.61.93 (bone fragment), SC2019.61.94 (bone fragment), SC2019.61. 95 (bone fragment) SC2019.61.96 (bone fragment), SC2019.61.97 (preoperculum fragment), SC2019.61.98 (bone fragment), SC2019.61.99 (cranial? element), SC2019.61.100 (bone fragment), SC2019.61.101 (bone fragment), SC2019.61.102 (scale), SC2019.61.103 (scale), SC2019.61.104 (scale), SC2019.61.105 (scale), SC2019.61.107 (bone fragment), SC2019.61.168 (2 scales), SC2019.61.169 (scale), SC2019.61.170 (scale).

REMARKS: Our Glendon Limestone sample contains a plethora of micro-teleost remains that cannot be identified, including ablated sagittae and teeth, dorsal and pectoral fin spines, vertebral centra, scales, miscellaneous cranial and jaw elements, and unidentified bone fragments. The otoliths listed in this section are too poorly preserved to be assigned to any lower taxonomic ranking, but they likely belong to one of the taxa described herein. A majority of the teeth are represented by broken or incomplete tooth caps that are too worn or abraded for further identification. One well preserved tooth, SC2019.61.39, differs by being slightly recurved and cone-shaped. Unfortunately the lack of adequate comparative specimens did not allow us to further identify this specimen.

Three morphologies of dorsal and pectoral fin spines are present in our sample. These include: 1) spines that are ornamented with fine or coarse lateral longitudinal ridges, but with no anterior or posterior denticulation; 2) smooth spines lacking anterior and/or posterior denticulation; and 3) a single spine ornamented with coarse lateral ridges and two rows of posterior denticles, but no denticles occur on the anterior margin. As the denticulation and lateral ornament on this last spine morphology (SC2019.61.56) is reminiscent of spines occurring on members of the Ariidae (sea catfishes), the specimen was directly compared to those of Recent *Ariopsis felis* (Linnæus, 1766) and *Bagre marinus* (Mitchill, 1815) (MSC 43216 and MSC 43217, respectively). Although the ridged ornamentation is similar between all three spine morphologies, SC2019.61.56 lacks anterior denticulation but has two rows of posterior denticles that flank a posterior furrow. This morphology differs from the dorsal and pectoral spines of *A. felis* and *B. marinus*, which exhibit a single row of both anterior and posterior denticles, with those at the posterior residing within a longitudinal furrow. The other ornamented and unornamented spine morphologies in the Glendon Limestone sample share characteristics with a variety of Recent bony fishes, and all are therefore left in open nomenclature.

The remaining elements, including vertebrae, scales, cranial elements, and bone fragments, are also left in open nomenclature. Unfortunately the lack of available comparative material of small marine fishes and the paucity of prior studies on Oligocene micro-teleosts have not allowed us to further identify these specimens.

DISCUSSION

There is evidence that the vertebrate and invertebrate paleofaunas within the Glendon Limestone Member in Alabama and the Glendon Limestone (formation) in Mississippi vary appreciably with regard to paleoecological preferences (Mumma 1965; Fisher and Ward 1984; Huddlestun 1993; Fluegeman *et al.* 2019; Stringer and Starnes 2020), and this probably also occurs at site AWa-9. Only a single lithostratigraphic horizon at the site was investigated, and the paleoecological interpretations provided herein are therefore limited to the sampled interval at the locality from which the vertebrate remains were recovered, and may not apply to the sub- and superjacent strata. The species diversity of the Glendon Limestone Member assemblage was evaluated based on all of the recovered vertebrates (teeth, skeletal remains, otoliths) that could be identified to at least the family level. Regarding species diversity, both the number of species (diversity or richness) and the percentage of each species (relative abundance) were considered. Twenty unequivocal taxa were identified in the assemblage, including six cartilaginous fishes and fourteen bony fishes (nine based on otoliths and five based on osteological remains). The assemblage is strongly skewed in the percentage each taxon comprises, with one bony fish, *Citharichthys*, constituting over 49% of the total number of identifiable otolith specimens. Furthermore, three taxa of bony fishes, *Citharichthys*, *Sparus*? *elegantulus*, and *Preophidion meyeri*, account for over 60% of the identifiable otolith assemblage.

The remains of cartilaginous fishes are very limited within the Glendon Limestone Member, both in number of specimens (n=8) and species (n=6). This greatly influences their contribution to an understanding of the paleoenvironment. Likewise, a large percentage of the osteological remains of the bony fishes were not identifiable beyond anatomical element, which greatly inhibits their application in paleoenvironmental reconstruction. Despite these limitations, we were able to glean paleoenvironmental data based on the otoliths and osteological remains we could identify.

Taxa identified from otoliths	**Quantity**	**% of total**	**Ecology**	**Climate**
ANGUILLIFORMES				
Congridae			M	Trop. – temp.
Ariosoma nonsector	6	5.17		
TRACHICHTHYIFORMES				
Diretmidae			M	Trop. – temp.
Diretmus? sp.	1	0.86		
OPHIDIIFORMES				
Ophidiidae			M	Trop. – temp.
Preophidion meyeri	12	10.34		
GOBIIFORMES				
Gobiidae			F. B. M[1]	Trop. – subtrop.
Gobiasoma? *axsmithi* sp. nov.	4	3.45		
PLEURONECTIFORMES				
Paralichthyidae			F. B. M[2]	Trop. – temp.
Syacium sp.	3	2.58		
Citharichthyes sp.	57	49.13		
Citharichthyes? sp. (lapilli)	2	1.72		
Paralichthyidae indet.	1	0.86		
ACANTHURIFORMES				
Sciaenidae			F. B. M	Trop. – temp.
Sciaena pseudoradians	4	3.45		
Aplodinotus gemma	3	2.58		
Sciaenidae indet.	1	0.86		
SPARIFORMES				
Sparidae			F. B. M[3]	Trop. – temp.
Sparus? *elegantulus*	14	12.06		
ORDER INDET.				
Family indet.				
Teleostei indet.	8	6.89		
Total	116	100		

Table 1. Taxa represented by otoliths from the Glendon Limestone Member of the Byram Formation (Oligocene, Rupelian), site AWa-9, Washington County, Alabama, USA. Ecologic and climatic information based on families is represented. Abbreviations: B – brackish; F – freshwater; M – marine; Temp. – temperate; Subtrop. – subtropical; Trop. – tropical. Ecology data superscripts as follows: 1 – chiefly marine and brackish water; 2 – chiefly marine and rare in fresh water; 3 – chiefly marine and very rare in fresh- and brackish water. Ecologic and climatic data derived from Hoese and Moore (1998), Nelson *et al*. (2016), Froese and Pauly (2019), and World Register of Marine Species Editorial Board (2020).

The families of fishes represented by otoliths were utilized to ascertain the general paleoenvironmental parameters represented by the Glendon Limestone Member assemblage, following methods that have been effectively applied to similar assemblages in both the Gulf and Atlantic coastal plains (Stringer and Bell 2018; Ebersole *et al*. 2019; Stringer and Shannon 2019; Stringer and Hulbert 2020; Stringer *et al*. 2020b). This was accomplished by comparing the ecological ranges of extant families of fishes represented by the fossil otoliths (Cohen *et al*. 1990; Hoese and Moore 1998; Nelson *et al*. 2016; Snyder and Burgess 2016; Froese and Pauly 2019). We include here the caveat that there are limitations and considerations inherent to this application of biological uniformitarianism, which are compounded in temporally much older assemblages, especially in the Mesozoic (Schwarzhans *et al*. 2018; Stringer *et al*. 2018, 2020c; Schwarzhans and Stringer 2020).

As is shown in Table 1, three of the families identified by otoliths are restricted to marine waters (Congridae, Diretmidae, and Ophidiidae), and these comprise about 17% of the total specimens. Additionally, there are four families that are known to inhabit fresh, brackish, and marine waters. However, there are factors to consider regarding these four families, as the Gobiidae are chiefly brackish and marine, whereas the Paralichthyidae and Sparidae are chiefly marine but rare in freshwater, and very rare in fresh and brackish waters (respectively). The only family equally abundant in freshwater, brackish, and marine environments, the Sciaenidae, comprises only approximately 6% of the total otolith sample. There are no families present in the Glendon Limestone

Member otolith assemblage that represent exclusively freshwater or brackish environments. As the otolith assemblage is largely comprised of families that have marine representatives, it is likely that the Glendon Limestone Member represents marine deposition, with little evidence of brackish or freshwater influence (i.e., probably not very close to shore).

The Glendon Limestone Member otoliths also furnish information regarding paleo-water depths. Of the specimens we identified, none represent families that are indicative of deep water (i.e., greater than 200 m). Nolf and Brzobohaty (1994) stated that marine assemblages that lack or contain very few Myctophidae (lanternfish) likely indicate a neritic environment with little open oceanic influence. Although myctophids are known from as early as the Eocene (Nolf 2013), none are present in our Glendon Limestone Member assemblage. The assemblage also does not contain any Macrouridae (grenadiers), a family of typically bathybenthic fishes living below 200 m, thus providing strong evidence for water depths less than 200 m (i.e., outer shelf or less).

An analysis of the most abundant otolith taxa in our sample offers additional information on paleoenvironmental conditions. At a minimum, the data presented above indicates that the Glendon Limestone Member at site AWa-9 represents a marine inner to outer shelf-depth paleoenvironment. *Citharichthys* is by far the most abundant bony fish in our sample, representing nearly 50% of the total number of identified specimens. This high percentage would therefore indicate that the paleoecological conditions at the site must have been optimum for the survival and proliferation of *Citharichthys*. Page *et al.* (2013) reported six species of *Citharichthys* in the present-day Atlantic Ocean and Gulf of Mexico of the USA, and according to Froese and Pauly (2019) many of these species occur at relatively shallow depths, although some occur in much deeper water (i.e., *Citharichthys dinoceros* Goode and Bean, 1886 as deep as 2000 m). Three *Citharichthys* species are not found at depths of less than approximately 35 m, but two species occur in shallow coastal waters (sounds, bays, lagoons). As there is no evidence that the Glendon Limestone Member paleowater depth was 200 m or more, the deep-water *Citharichthys* are not considered. Additionally, the presence of very shallow-water species (Carpenter *et al.* 2015) is not supported by the balance of the Glendon Limestone Member assemblage. Thus, the remaining *Citharichthys* species would support a paleowater depth of no less than 30 m (i.e., shallow middle shelf). Of course, it must be considered that the preceding paleowater depth determination is based on the present distribution of *Citharichthys* species in the modern Gulf of Mexico, and could be affected or altered by various factors. However, when taken in conjunction with other lines of evidence, it appears to be feasible.

Sparus? *elegantulus* is the second most abundant species in the Glendon Limestone Member assemblage, constituting 12.06% of the total identified specimens. Janssen (2012) recommended using the type genus for the family followed by a question mark in the event that the family and species known, but the genus is unknown. This convention indicates that the species could belong to a known or possibly undescribed genus in that family. Therefore, for the specimens identified as *Sparus*? *elegantulus* we only utilize ecological information as it applies to the familial level. Members of the Sparidae can be found in fresh, brackish, and marine waters (Froese and Pauly 2019), although Nelson *et al.* (2016) noted that this group rarely occurs in freshwater or brackish environments. Sparids are demersal inhabitants of the continental shelf and slope, but usually most common along the shore, from shallow to deeper water (Iwatsuki and Heemstra 2015). Therefore, the presence of *Sparus*? *elegantulus* indicates a marine environment, but this taxon is not a useful paleoenvironmental indicator.

The third most abundant species in the otolith assemblage is the ophidiid (cusk-eel) *Preophidion meyeri*, which represents 10.34% of the assemblage. *Preophidion meyeri* is a fossil otolith-based genus and species, and its relationship to modern ophidiid taxa is unclear. However, extant ophidiids only occur in marine waters (Nelson *et al*. 2016; Froese and Pauly 2019), and these fish are therefore a good indication that the Glendon Limestone Member paleoenvironment was not freshwater or brackish. Nolf (2013) assigned *P. meyeri* to the subfamily Neobythitinae, and according to Nelson *et al.* (2016), representatives of this subfamily range from littoral to abyssal (> 2000 m). However, during the Paleogene the ophidiids were represented by a very rich neritic fauna living mainly on soft and muddy substrates, and these are some of the most common and most speciose groups of teleosts recovered from shallow-marine deposits (Nolf 1985, 2013; Stringer 1986; Breard and Stringer 1995; Stringer and Miller 2001; Nolf and Stringer 2003; Schwarzhans and Bratishko 2011).

Two Sciaenidae taxa represent roughly 6% of the total number of otolith specimens in our Glendon Limestone Member sample. Although Recent sciaenids are found in fresh, brackish, and marine waters, it is unlikely that the Glendon Limestone sciaenids represent freshwater forms because, as Nolf (2003) has noted, all Paleogene sciaenids known from the USA Gulf Coast deposits are associated with marine assemblages. Although some taxa may have been derived from strata representing nearshore paleoenvironments, none can be qualified as freshwater or even lagoonal. Although many modern sciaenids utilize estuaries as nurseries (Barbieri 1993; Barbieri *et al*. 1994; Pattillo *et al*. 1997; Snyder and Burgess 2016), the otoliths are usually very small (i.e., larval and juveniles) and abundant (Stringer and Shannon 2019, and references therein). The Glendon Limestone sciaenids do not meet either of these criteria, as the size of these otoliths indicate they all represent adult individuals, and very few specimens were recovered in our sample. Based on these observations, there are no indications that the Glendon Limestone sciaenids were living in freshwater, brackish water, or estuaries.

In addition to *Citharichthys*, a second paralichthyid, *Syacium*, was recovered during our investigation. Although only two specimens were identified, the presence of *Syacium* offers particular insight into the Glendon Limestone Member paleoenvironment. According to Page *et al*. (2013) and Froese and Pauly (2019), only three species of *Syacium* are currently found in the Atlantic Ocean and Gulf of Mexico [*S. gunteri* Ginsburg, 1933, *S. micrurum* Ranzani, 1842, and *S. papillosum* (Linnæus, 1758)], and these taxa usually occur in waters ranging from 27–95 m, 0–100 m, and 27–95 m in depth, respectively. Therefore given the modern distribution of these extant species, the presence of *Syacium* in the Glendon Limestone Member could reflect a paleowater depth of up to 100 m.

The families of fishes represented by otoliths also provide a general indication of climatic conditions. Six of the seven families in our sample are found in tropical to temperate waters, including the Paralichthyidae (which are represented by the largest number of specimens). The genus *Gobiosoma* of the Gobiidae, represented by four specimens (3.45% of the total sample), currently inhabits tropical to subtropical waters of the Americas. Thus, the majority of the otolith taxa we identified are indicative of a climatic setting that was tropical to temperate, based on the modern distribution of fish families (Hoese and Moore 1998; McEachran and Fechhelm 1998, 2005; Nelson *et al*. 2016; Froese and Pauly 2019; World Register of Marine Species Editorial Board 2020). Most of the otolith taxa in our sample represent fishes that preferred soft substrates like sand or mud. Furthermore, only one specimen (*Gobiosoma*) was recovered that exhibited invertebrate settlement indications (a very small boring in the dorsal depression, Text-fig. 7B), which could be an indication of very little surface residence time.

In addition to the otoliths, several of the chondrichthyan fossils in our sample provide clues to the Glendon Limestone Member paleoenvironment (Table 2). For example, *Hemipristis elongata* (Klunzinger, 1871), a modern analogue for *Hemipristis* sp., is a tropical marine taxon that prefers water depths of between 1–130 m (Froese and Pauly 2019). Interestingly, Müller (1999) indicated that *H. serra* was common in warm water during the Neogene, but during the Rupelian in Europe the absence of *Hemipristis* was taken to be related to the colder water conditions that existed during that time (von der Hocht 1978). Furthermore, *Negaprion brevirostris* (Poey, 1868), an extant analogue for the extinct *N. gilmorei*, is a marine/brackish subtropical taxon with depth preferences of between 1–92 m (Froese and Pauly 2019). The depth ranges for both of these genera are well within the 30–100 m Glendon Limestone Member paleowater depth as indicated by the otolith taxa, and they also corroborate the tropical/subtropical to temperate conditions indicated. Another elasmobranch in our sample, *Pachyscyllium* sp., is an extinct genus within Scyliorhinidae (catsharks). According to Collareta *et al*. (2020), extant scyliorhinids inhabit moderately deep waters in tropical to temperature seas worldwide. Yet another taxon, *Physogaleus* sp., is an extinct requiem shark in the Carcharhinidae, one of the largest families of extant sharks that includes both coastal and offshore taxa that inhabit tropical to temperate marine waters (Castro 1983; Villafaña *et al*. 2020). Although these latter two extinct taxa contribute little to our understanding of the paleowater depth, they do indicate tropical/subtropical to temperate climatic conditions. Two teeth assigned to “*Aetomylaeus*” sp. were identified in our Glendon Limestone sample. Froese and Pauly (2019) recognized seven extant members of this genus, with all but one of them preferring tropical waters and depths of 117 m or less. The only exception is *Aetomylaeus bovinus* (Geoffroy St. Hilaire, 1817), a subtropical taxon with water depth preferences of 150 m or less (Froese and Pauly 2019). Thus, the presence of “*Aetomylaeus*” sp. in the Glendon assemblage suggests the maximum paleowater depth likely did not exceed 117 m.

Several of the bony fishes identified from osteological remains provide some paleoecological data on the Glendon Limestone Member (Table 2). For example, a single tooth assigned to *Albula* sp. was identified in our sample. Extant members of the family primarily inhabit marine waters but are extremely

Taxa identifed from osteological remains	**Quantity**	**% of total**	**Ecology**	**Climate**
CARCHARHINIFORMES				
Scyliorhinidae			M	Trop. – temp.
Pachyscyllium sp.	1	1.15		
Hemigaleidae			M	Trop. – temp.
Hemipristis sp.	1	1.15		
Carcharhinidae			F, B, M	Trop. – temp.
Negaprion aff. *N. gilmorei*	2	2.29		
Physogaleus sp.	1	1.15		
MYLIOBATIFORMES				
Myliobatoidei			–	–
Gen. et sp. indet.	1	1.15		
Myliobatidae			F, B	Trop. – temp.
"*Aetomylaeus*" sp.	2	2.29		
ELOPIFORMES				
Phyllodontidae			–	–
Paralbula sp.	2	2.29		
ALBULIFORMES				
Albulidae			F, B, M[1]	Tropical
Albula sp.	1	1.15		
ISTIOPHORIFORMES				
Sphyraenidae			M	Trop. – subtrop.
Sphyraena sp.	3	3.44		
ACANTHURIFORMES				
Sciaenidae			F, B, M	Trop. – temp.
Sciaenops? sp.	1	1.15		
TETRADONTIFORMES				
Balistidae			M	Trop. – subtrop.
Gen. et sp. indet.	1	1.15		
ORDER INDET.				
Family indet.			–	–
Elasmobranchii indet.	2	2.29		
Teleostei indet.	69	79.31		
Total	87	100		

Table 2. Taxa represented by osteological remains from the Glendon Limestone Member of the Byram Formation (Oligocene, Rupelian), site AWa-9, Washington County, Alabama, USA. Ecologic and climatic information based on families is represented. Abbreviations: B – brackish; F – freshwater; M – marine; Temp. – temperate; Subtrop. – subtropical; Trop. – tropical. Ecology data superscripts as follows: 1 – chiefly marine and very rare in fresh- and brackish water. Ecologic and climatic data derived from Hoese and Moore (1998), Nelson *et al*. (2016), Froese and Pauly (2019), Collareta *et al*. (2020), and World Register of Marine Species Editorial Board (2020).

rare in fresh or brackish environments (Froese and Pauly 2019), and they primarily occur in the tropics (Nelson *et al*. 2016). We also identified *Sphyraena* (barracuda) teeth in our sample. Extant representatives of the genus generally inhabit tropical to subtropical marine waters and prefer water depths of between 3–30 m, although some species have been reported as deep as 100 m (Nelson *et al*. 2016; Snyder and Burgess 2016; Froese and Pauly 2019). A single *Sciaenops*? tooth in our sample is comparable to the Recent *Sciaenops ocellatus*, a species in which juveniles are found in bay shores, open waters of estuaries, and secondary bays in depths up to 3 m, but adults can occur in nearshore waters off beaches and at depths as great as 40–70 m (Pattillo *et al*. 1997 and references cited therein). The single Balistidae tooth indicates a marine environment (Froese and Pauly 2019), and representatives of the family are found primarily on the shelf, although there are oceanic species (Snyder and Burgess 2016).

Comparison of the paleoenvironmental parameters based on the osteological remains (cartilaginous and bony fishes) to those indicated by the teleostean otoliths reveal interesting similarities. The paleowater depths indicated by the osteological remains of the sharks and bony fishes corroborates the paleowater depths determined based on the otoliths. There are no taxa based on skeletal remains that are completely outside the range indicated by the taxa identified by otoliths. Furthermore, the taxa represented by osteological remains reflect the same climatic conditions as the taxa indicated by the otoliths, and osteological remains do not contradict any of the paleoecological assertions based on the otoliths. In summary, the skeletal remains of the cartilaginous and bony fishes corroborate in a general sense (i.e., less detailed but still supportive) the paleoenvironment as evidenced by the bony fish otoliths, which agrees with the findings of Miller (2000) and Stringer and Miller (2001).

CONCLUSIONS

Bulk samples collected from the Glendon Limestone Member exposures at site AWa-9 in Washington County, Alabama, USA yielded an unexpectedly large number and diverse assortment of marine vertebrate remains, and 20 unequivocal elasmobranch (n=6) and teleost (n=14) taxa were identified. Each of these taxa represent the first occurrence within the Oligocene (Rupelian) Glendon Limestone Member in Alabama, USA, and one new species, *Gobiosoma*? *axsmithi* sp. nov., is recognized. Several other taxa, including "*Aetomylaeus*" sp., *Pachyscyllium* sp., *Paralbula* sp., and *Sciaenops*? sp., represent the first occurrences of each in the Oligocene of the Gulf Coastal Plain of the USA. Furthermore, the Glendon *Paralbula* teeth represent a slight range extension for this genus from the Priabonian (upper Eocene) into the Rupelian (lower Oligocene). Finally the Balistidae indet. tooth in our sample represents the first Oligocene occurrence of this family in the Western Hemisphere.

The compilation of the environmental data obtained from the vertebrate assemblage in the Glendon Limestone Member at site AWa-9 indicates that paleowater depth was at least 30 m (shallow middle shelf). This is shallower than the minimum depth for the Glendon Limestone of Mississippi postulated by Mumma (1965), which was 75 m (deep middle shelf). However, this minimum depth is very similar to the deep inner shelf (approximately 20 m) depth indicated by foraminifera (Fisher and Ward 1984) from the Glendon Limestone in Warren County, Mississippi. The maximum depth is more difficult to ascertain, but there is evidence that the maximum water depth did not exceed 200 m (outer shelf) based on the presence and absence of diagnostic fish species. Although not a strong indicator, the presence of "*Aetomylaeus*" and *Syacium* could indicate a maximum paleowater depth of 100 m and tropical/subtropical to temperate climatic conditions. The fishes represented by otoliths attest to soft substrate of mud, sand, or a mixture of the two. The lack of invertebrate settlement on the otolith specimens indicates short surface residence-time (fairly rapid burial).

As Oligocene units in Alabama are highly fossiliferous but historically understudied, future examination of these strata will undoubtedly yield additional vertebrate taxa. Thus, the need for further investigations in the Alabama Oligocene is certainly warranted and encouraged.

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