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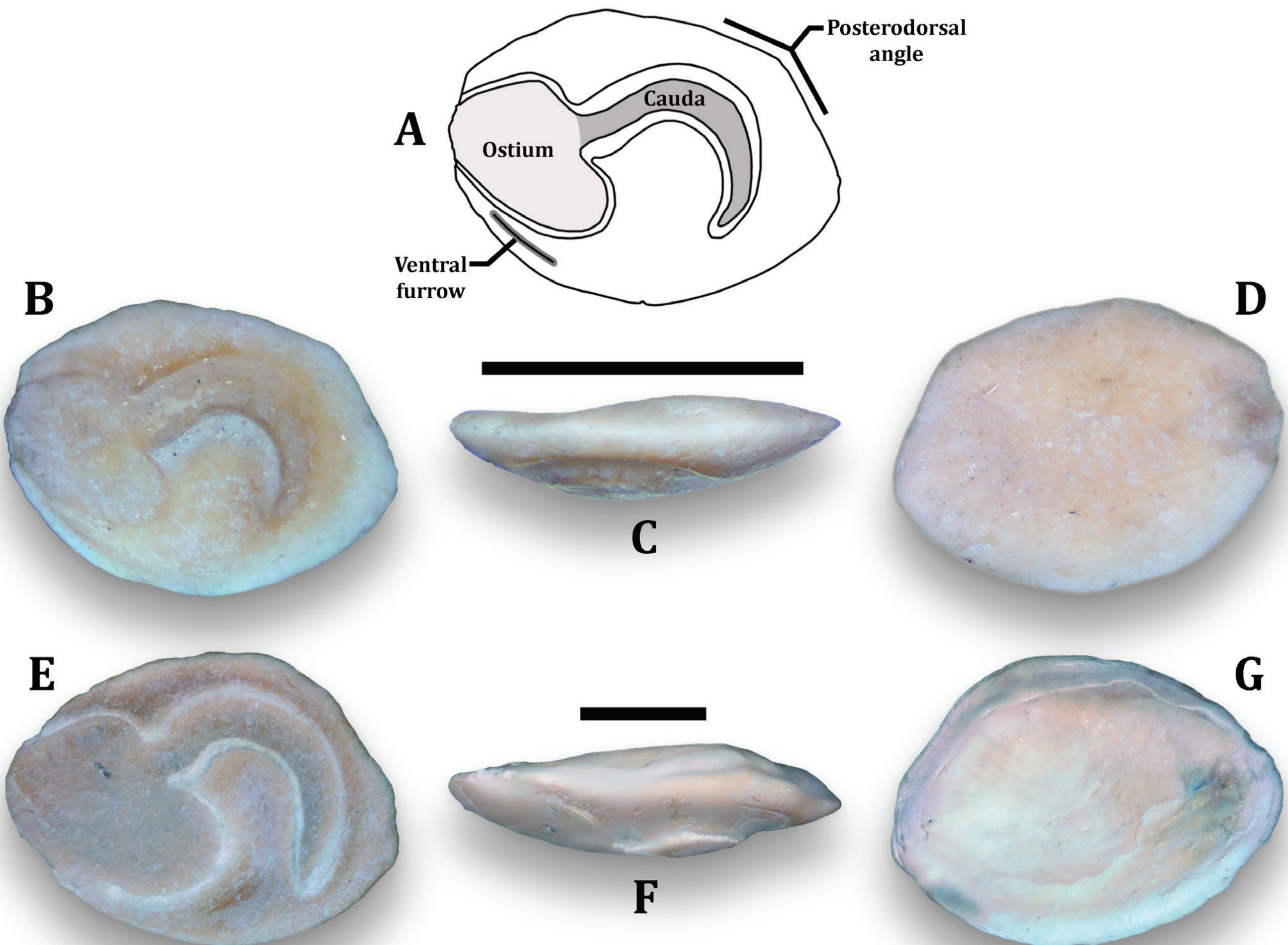

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Cover: Teleostean fish otoliths of a juvenile *Equetulus silverdalensis* n. comb. from Alabama (Paynes Hammock Sand, late Oligocene, top two rows) and an adult from North Carolina (Belgrade Formation, late Oligocene to early Miocene). Scale bars=2mm

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First description of the fossil otolith-based sciaenid, *Equetulus silverdalensis* n. comb., in the Gulf Coastal Plain, USA, with comments on the enigmatic distribution of the species

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The fossil otolith-based sciaenid genus *Equetulus* is known almost exclusively from South America, the Caribbean, and Central America, with the various species ranging in age from the late Oligocene to late Miocene. The only exception to this geographical distribution is the isolated occurrence of *Equetulus silverdalensis* n. comb. in the Belgrade Formation (latest Oligocene–early Miocene) in the Atlantic Coastal Plain of the USA (North Carolina) and a mention of its occurrence in the Chickasawhay Limestone (late Oligocene) in the Gulf Coastal Plain of the USA (Mississippi). However, sampling of the Paynes Hammock Sand (late Oligocene, Chattian) near Millry, Alabama, USA, resulted in the discovery of an otolith representing the first occurrence of *E. silverdalensis* in Alabama and the first systematic description of the species from the Gulf Coastal Plain of the USA. These occurrences suggest a potential distribution of this fossil species from Atlantic Coastal Plain of North Carolina to the central Gulf Coastal Plain of Alabama and possibly Mississippi.

Keywords: otoliths, Alabama, Oligocene, Paynes Hammock Sand, fossil sciaenids, teleostean fish

INTRODUCTION

Equetulus Aguilera and Schwarzhans (in Aguilera et al. 2014) is a fossil otolith-based sciaenid genus that has been reported from South America, the Caribbean, Central America, and the Atlantic Coast of the United States. This genus has a known late Oligocene to late Miocene range, with occurrences being limited to the late Oligocene to early Miocene in North America. The genus currently contains the four species *E. amazonensis* Aguilera and Schwarzhans (in Aguilera et al. 2014), *E. davidandrewi* (Nolf and Aguilera, 1998), *E. fitchi* (Schwarzhans, 1993), and the new combination, *Equetulus silverdalensis* (=”*Pachypops” silveraldensis* of Müller 1999).

Equetulus amazonensis, *E. davidandrewi*, and *E. fitchi* are known from South America, the Caribbean, and Central America. *Equetulus amazonensis* is the type species for the genus and is known from the Pirabas Formation (early Miocene, Aquitanian) in Brazil (Aguilera et al. 2014, Aquilera et al. 2016). *Equetulus davidandrewi* was first named as *Equetus davidandrewi* (Nolf and Aguilera 1998) (pl. 10, figs. 1–5). It is known from several formations ranging from the early to late Miocene. Formations include the Castilletes in Columbia, the Cantaure and Urumaco in Venezuela, the Gatunin Panama, and the Angostura in Ecuador (Aguilera et al. 2016). *Equetulus fitchi* was first recognized by Schwarzhans (1993, figs. 15–18) but by the name *Pachypops fitchi*. It was subsequently assigned to *Equetulus* by Aguilera et al. (2016). *Equetulus fitchi* is coeval with *E. amazonensis* in the Pirabas Formation (early Miocene, Aquitanian) of Brazil, but *E. fitchi* also occurs in the Manzanilla and Brasso formations in Trinidad (Nolf 1976). According to Aguilera et al. (2016), *E. fitchi* appears to have replaced *E. davidandrewi* eastward of Venezuela in Trinidad and Brazil during the early to late Miocene (Fig. 1).

Equetulus silverdalensis n. comb. was first named by Müller (1999) as “genus aff. *Pachypops*” *silverdalensis* based on specimens from the Belgrade Formation (Haywood Landing Member) from localities on the

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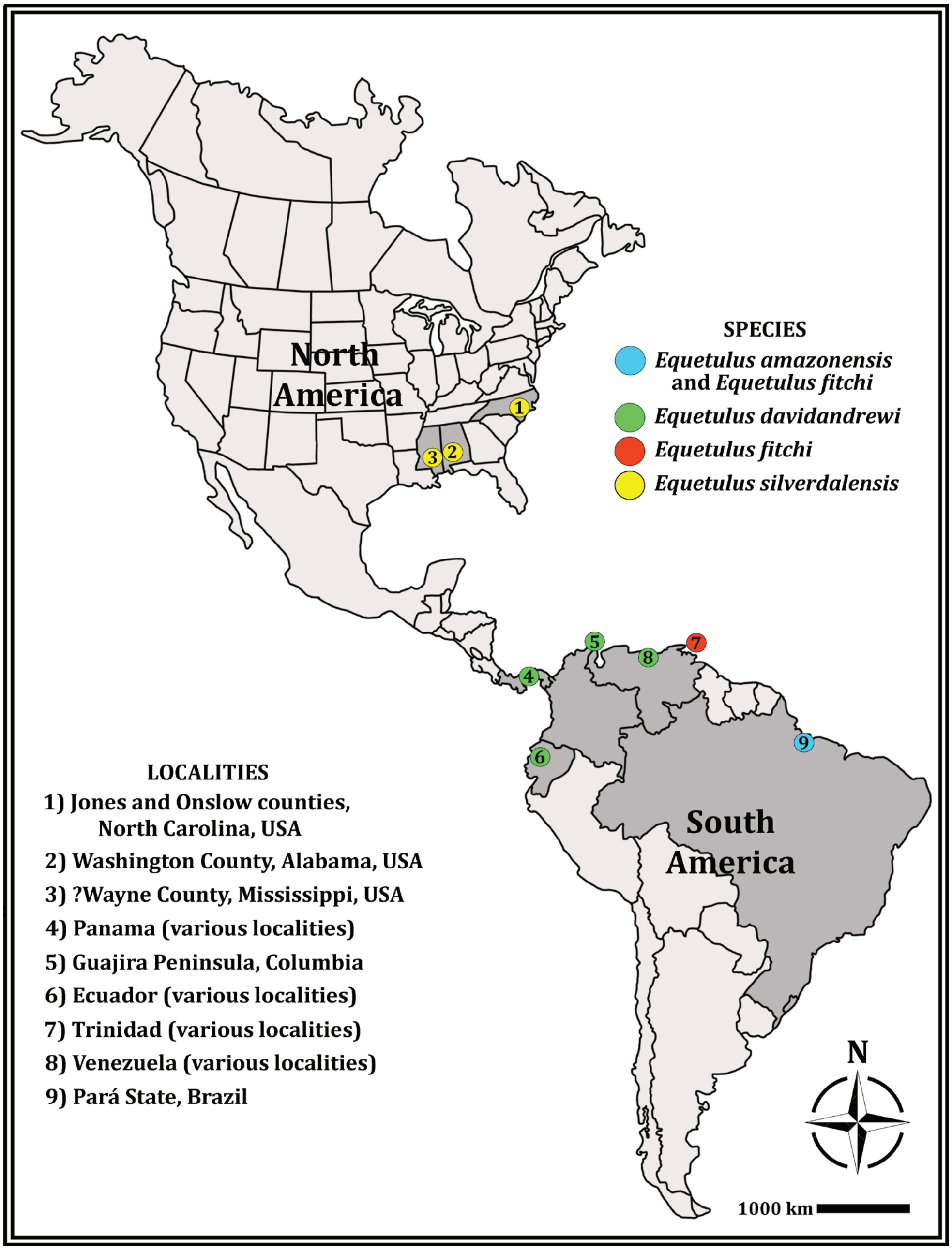

Figure 1. Map showing the paleobiogeographic distribution of the species of *Equetulus* in North America, the Caribbean, and South America.

White Oak River in Onslow and Jones counties in North Carolina, USA. The assignment to "genus aff. *Pachypops*" was done in open generic nomenclature, which has been questioned in regard to validity and compliance with the *International Code of Zoological Nomenclature* (Janssen 2012, Schwarzhans 2012, Tracey 2014, Ebersole et al. 2019). Therefore, based on the investigations by Schwarzhans (1993), Aguilera et al. (2014), and Aguilera et al. (2016) as well as Schwarzhans (2019, personal communication), "genus aff. *Pachypops*" *silverdalensis* is assigned in this study to the valid fossil genus *Equetulus* Aguilera et al. (2014). Müller (1999) reported that a total of 120 specimens of "genus aff. *Pachypops*" *silverdalensis* were obtained from three bulk samples taken in the Belgrade Formation (Haywood Landing Member). The specimens appear to be fairly common as 25 otoliths of "genus aff. *Pachypops*" *silverdalensis* were obtained from a single 50-kg bulk sample. Müller (1999) illustrated juvenile and adult specimens (fig. 38/19–21, fig. 39/1–5), which included the holotype and paratypes.

Equetulus silverdalensis is currently the only member of the genus known in North America, with the otoliths reported by Müller (1999) being the only verified occurrences. The species has not been reported from any sites in the Gulf Coastal Plain of the U.S. with the exception of a curious figure with two specimens in Nolf (2013, pl. 283) that stated "*Sciaenida*" *silverdalensis* (Müller, 1999) as occurring in the lower Miocene Belgrade Formation in North Carolina. However, the text stated that the lower specimen was from the Chickasawhay Formation at Taylor's Creek in Mississippi (Fig. 1). Unfortunately, no additional information or description was provided. It appears that the figure label was not correct, but that the text was accurate. No additional occurrences of *E. silverdalensis* have since been reported.

During a survey of potential formations in southwest Alabama for the recovery of bony fish otoliths by a McWane Science Center (MSC) crew, a bulk sample was collected by the senior author (GLS) from a well-known Paynes Hammock Sand locality (late Oligocene, Chattian) near Millry in Washington County, Alabama (MSC site AWa-11). Analysis of the sample produced only a small number of otoliths. However, one of the otoliths differed from any commonly described taxa from the Gulf Coastal Plain showing affinities with *Equetulus*, specifically *E. silverdalensis*, from the middle Atlantic Coastal Plain. This study details the investigation of this specimen and includes a morphological description, taxonomic assignment, stratigraphic range, and biogeographic implications.

MATERIALS AND METHODS

Geologic setting

The fossil otolith, MSC 42698, examined in this study was collected by the senior author (GLS) from a historical locality along Alabama State Route (SR) 17 approximately 2.25 km) (1.4 miles) north of the town of Millry in Washington County, Alabama, USA (Fig. 2), and has been given the MSC locality designation AWa-11. The locality consists of two small Paynes Hammock Sand (PHS) exposures in a road cut along SR 17 and another outcrop nearby in a Tennessee and Northern Railway railroad cut that once paralleled the highway (Cushman

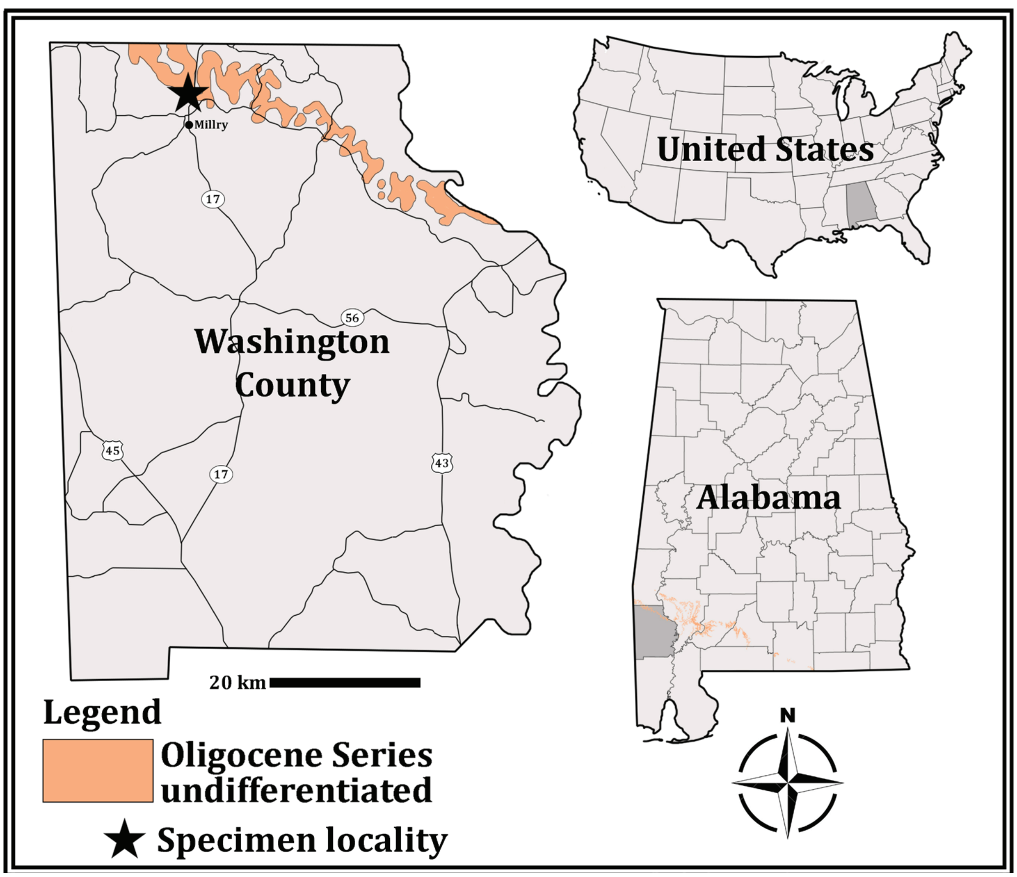

Figure 2. Map showing location of collection site near Millry, Washington County, Alabama, USA.

and McGlammery 1942). The Millry locality was first reported by Cooke (1926) who interpreted the exposures as belonging to the Oligocene Byram Marl. Howe and Alexander (1934) reported the exposures as being part of the lower Miocene Chickasawhay Member of the Catahoula Sandstone. Cooke (1935) and Cushman and McGlamery (1942) assigned the exposures to the upper Oligocene Chickasawhay Marl. Today, based on its lithology and location, the exposures at site AWa-11 are known to belong to the Oligocene (Chattian) PHS (Tew 1992) (Fig. 3).

In Alabama, this lithostratigraphic unit is called the PHS as originally named by MacNeil (1944). However, in Mississippi, the unit is called the PHS (Poag 1975, Dockery and Thompson 2016). The PHS is overlain by the Miocene Catahoula Formation in Mississippi and Miocene undifferentiated units in Alabama and underlain by the Oligocene Chickasawhay Limestone in both Alabama and Mississippi (Raymond et al. 1988, Dockery and Thompson 2016). The PHS type section is exposed along Fisher Creek, at Paynes Hammock in Clarke County, Alabama (Tew 1992).

In Alabama, the PHS stretches eastward into Clarke County, where it truncates at the Jackson fault. No PHS exposures are recognized east of this location (Tew 1992). The unit has gradational, conformable, and disconformable boundaries with its upper and lower lithologic units (Tew 1992, Dockery and Thompson 2016). The lithology of the PHS varies across strike and includes grayish, greenish, and bluish fossiliferous glauconitic marl, clay, claystone, and sand, and grayish and cream color fossiliferous limestone (MacNeil 1944, Toulmin 1962, Jones 1967, Raymond et al. 1988, Tew 1992, Dockery and Thompson 2016). At the type section specifically, the lithology is described as grayish blue-green, calcareous, fossiliferous sand and clay (Toulmin 1962, Tew 1992).

At site AWa-11, a 2.44 m-thick section of PHS is exposed that is overlain with 3.04 m of Miocene red sandy clay (Cushman and McGlamery 1942). From the base upward, the Oligocene lithology is described as 0.30 m of cream-colored limestone with some glauconite and *Eulepidina* c.f. *Eu. undosa* (Cushman, 1919); 0.61 m of

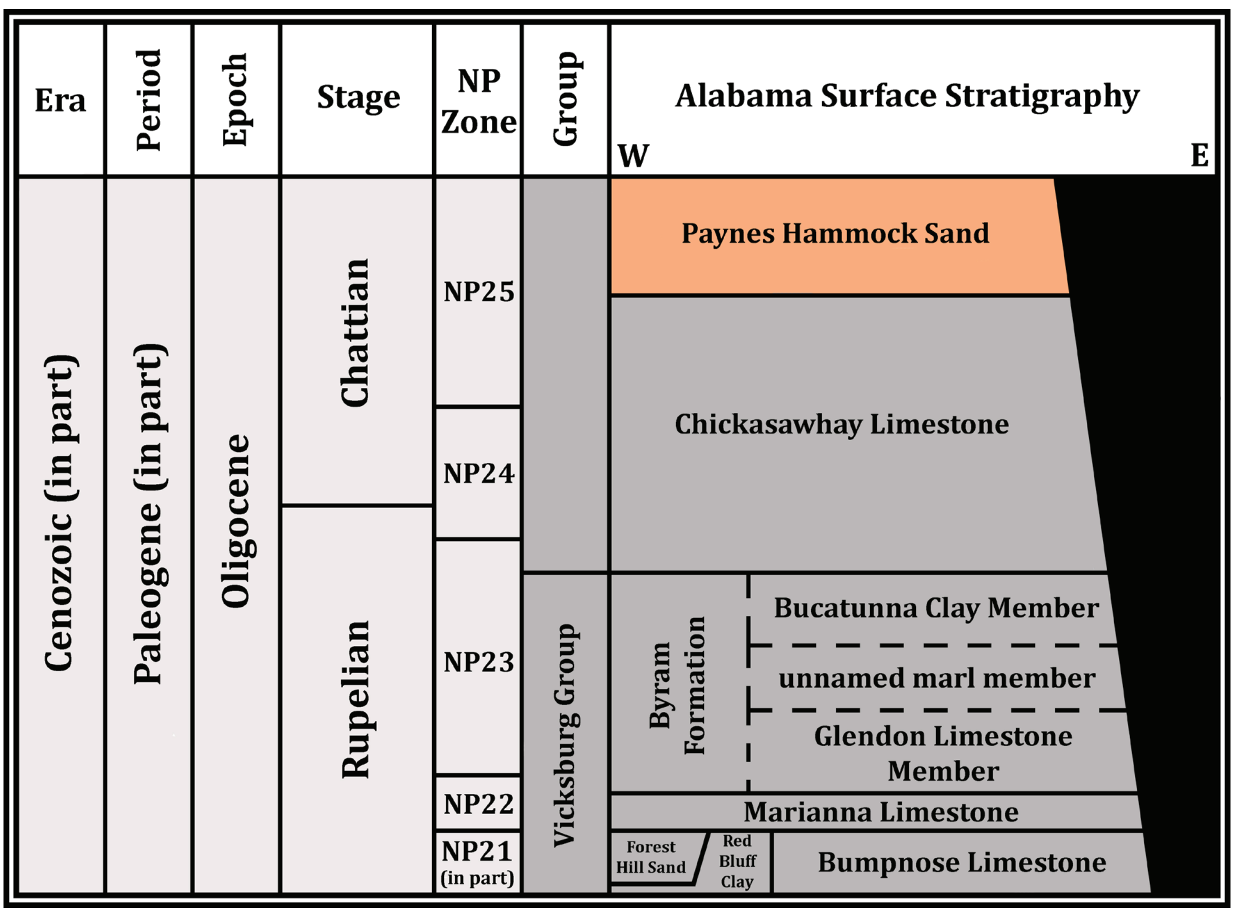

Figure 3. Stratigraphy of the Paynes Hammock Sand (late Oligocene, Chattian) in western Alabama, USA. NP Zone=Calcareous nannoplankton zone. Stratigraphy modified from Szabo et al. (1988).

greenish-gray, fossiliferous sandy clay with bryozoa, *Lepidocyclina* Gümbel (1868), and barnacles; 0.15 m of cream-colored highly fossiliferous sandy limestone with bryozoa, *Lepidocyclina*, and *Pecten* Müller (1776); 0.91 m of greenish gray fossiliferous clay with lime nodules; 0.15 m of cream-colored sandy limestone; and 0.30 m of greenish-gray fossiliferous sandy clay (Cushman and McGlamery 1942).

Based on macro- and microfossil taxa, the PHS is diachronous and spans from the late Oligocene to early Miocene. Butler (1960) correlated ostracode zonations to the *Cibicides hazzardi* Ellis (1939) zone (lower Miocene) of the Tampa Formation in Florida. Later, Marlin and Schramm (1991) correlated the upper and lower contacts of the unit with the middle/late Oligocene Frio Formation in Louisiana. Poag (1972, 1975) assigned the unit to the late Oligocene based on a planktonic foraminiferan assemblage that included *Globigerina angulisuturalis* Bolli (1957) and *G. ciperoensis* Bolli (1957). Based on ostracods collected in part from AWa-11, Poag's (1974, 1975) age assignment was later reaffirmed by Siesser (1983) and Siesser et al. (1985) who used calcareous nannoplankton to provide a late Oligocene age for the unit (Tew 1992).

Methodology

The specimen described in this study, MSC 42698, was collected from MSC site AWa-11, a PHS exposure (late Oligocene, Chattian) near the town of Millry in Washington County, Alabama, USA. A small bulk sample (~4.0 kg) was collected, air dried, then wet screened using water following standard protocol, but with no additives since many additives can adversely affect the aragonitic otoliths. Screening was done using a U.S. Standard Sieve #30, and all reside was kept for study. Following the wet sieving, the residue was labeled and air-dried. U.S. Standard sieves (#5 to #30) were employed to separate the residue into similar-sized material for microscopic examination. An Olympus binocular microscope model, SZ4045TR, 0.8x to 40x, was used to extract the otoliths from the residue. For comparison purposes, specimens of *Equetulus silverdalensis* n. comb. were collected for the senior author (GLS) by colleagues from the type horizon of the Belgrade Formation, Haywood Landing Member in Jones County, North Carolina, one of which was donated by the senior author (GLS) to MSC for use in this study.

The classification scheme, unless otherwise noted, follows that of Nelson et al. (2016), which was greatly influenced by the molecular work of Betancur-R. et al. (2013). 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, 2017, 2018). 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. The specimens described in this study are housed in the scientific collections at the MSC, Birmingham, AL, USA.

RESULTS

The small bulk sample from the Paynes Hammock Sand produced invertebrate and a limited number of vertebrate remains, including otoliths. Microfossils such as foraminifera and ostracods were abundant. Macrofossils included bivalves and abundant barnacles. Skeletal vertebrate remains included teleostean vertebrae and phyllodont teeth (from a tooth plate) of which none were identifiable. All of the retrieved otoliths were representatives of the family Sciaenidae, chiefly of *Sciaena pseudoradians* Dante and Frizzell in Frizzell and Dante (1965), with the exception of a single specimen which is described below.

SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII *sensu* Goodrich, 1930
TELEOSTEOMORPHA Arratia, 2001
TELEOSTEI Müller, 1846
ACANTHURIFORMES *sensu* Nelson, Grande, & Wilson, 2016
SCIAENIDAE Cuvier, 1829
EQUETULUS Aguilera & Schwarzhans in Aguilera et al., 2014
EQUETULUS SILVERDALENSIS (Müller, 1999) n. comb.
Fig. 4A–G

Synonyms—"genus aff. *Pachypops*" *silverdalensis* (Müller, 1999), "*Sciaenida*" *silverdalensis* (Nolf, 2013).

Holotype—"genus aff. *Pachypops*" *silverdalensis* Müller (1999), Nr. 355(P49), Miocene (Aquitanian), Belgrade Formation, Haywood Landing Member ("Silverdale Beds"), Silverdale on the White Oak River, Onslow County, North Carolina, USA.

Paratypes—"genus aff. *Pachypops*" *silverdalensis* Müller (1999), Nr. 352(P49), Nr. 353(P49), Nr. 354(P49), Nr. 357(P49), Nr. 358(P49), Nr. 359(P49), Nr. 360(P49), type locality and stratum as above.

Referred specimens and localities—MSC 42698: right sagitta (Fig. 4, A–D), Paynes Hammock Sand, locality MSC AWa-11; MSC 42699: right sagitta (Fig. 4, E–G), Belgrade Quarry, NC; Nr. 352(P49): right sagitta; Nr.

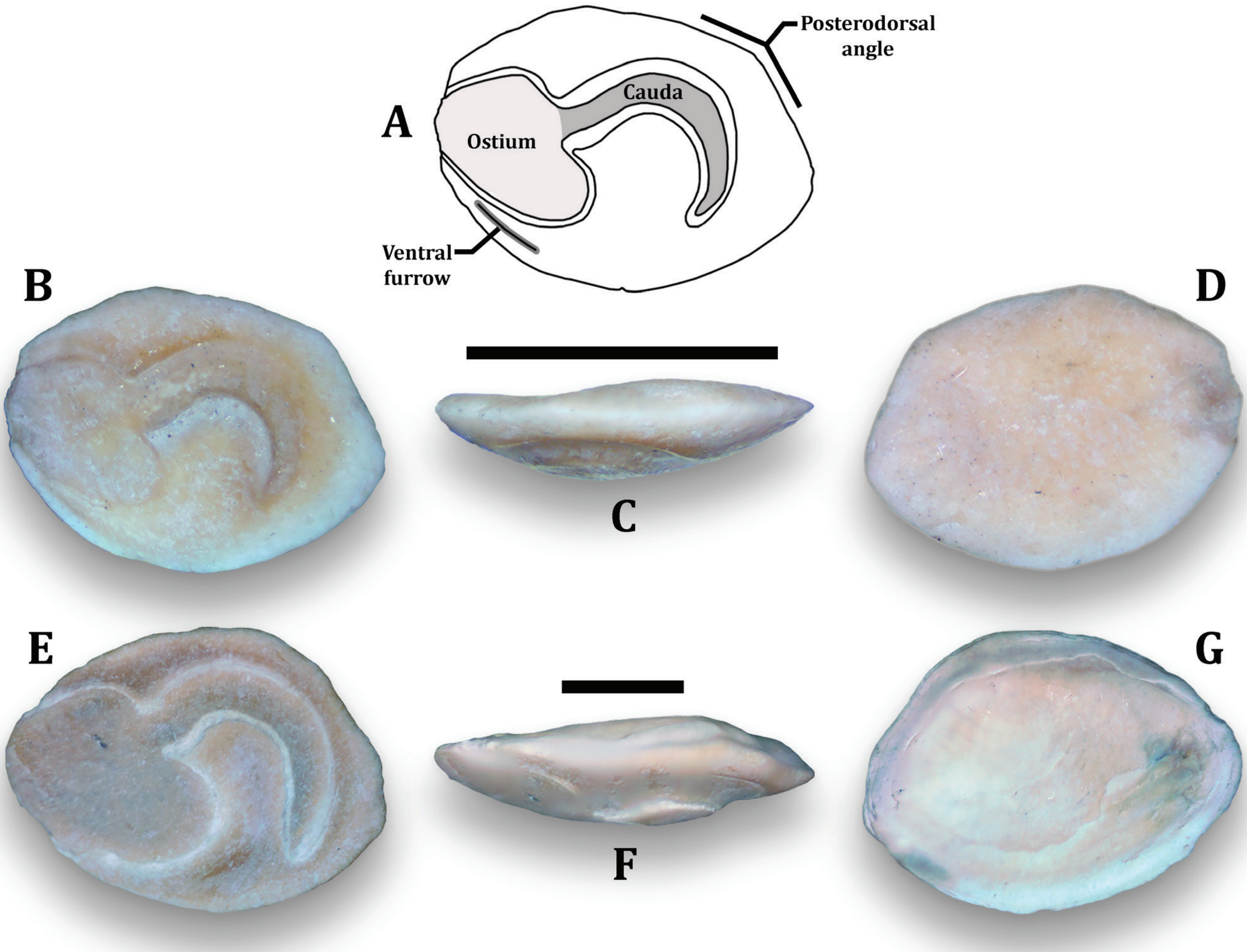

Figure 4. A–G. Otoliths of a presumed juvenile *Equetulus silverdalensis* n. comb. from Alabama and an adult from North Carolina. **A–D.** Right sagitta of juvenile MSC 42698 from the Paynes Hammock Sand (late Oligocene, Chattian), Millry locality, Washington County, Alabama, USA. Illustrative drawing of the inner face (**A**) of MSC 42698 (**B**). **C.** Dorsal view. **D.** Outer face. **E–G.** Right sagitta of adult MSC 42699 from the Belgrade Formation (late Oligocene to early Miocene), Silverdale, North Carolina, USA. **E.** Inner face. **F.** Dorsal view. **G.** Outer face. Scale bars=2mm.

353(P49): right sagitta; Nr. 354(P49), left sagitta; Nr. 355(P49), left sagitta; Nr. 357(P49), right sagitta; Nr. 358(P49), right sagitta; Nr. 359(P49), left sagitta; Nr. 360(P49), right sagitta, all from the Belgrade Formation type locality at Silverdale, Onslow Co., NC.

Occurrences —Paynes Hammock Sand, late Oligocene (Chattian), MSC site AWa-11, Washington County, AL, USA (this report); the type locality Belgrade Formation, Haywood Landing Member ("Silverdale Beds"), late Oligocene (Chattian) to early Miocene (Aquitanian), Silverdale on the White Oak River, Onslow County, North Carolina, USA, and the Martin Marietta Belgrade Quarry in Maysville, Jones County, North Carolina, USA (Müller 1999).

Diagnosis—Outline of sagitta is oval; L/H ratio of 1.30 (juveniles) to 1.44 (adults); inner face smooth and slightly convex; prominent heterosulcoid-type sulcus that extends 85% of length; ostium shorter than cauda but two times higher; cauda evenly curved and extends above dorsal margin of ostium; cauda tapers near posterior and is pointed.

Description—The shape of the sagitta of MSC 42698 is primarily oval (*sensu* Smale et al. 1995). The sagitta is fairly small with a length of 2.40 mm and a height of 1.84 mm (length/height ratio of 1.30) and appears to represent a juvenile since the smallest specimen illustrated by Müller (1999; fig. 38/19a–19b) was approximately 5.0 mm. The margins and inner face of MSC 42698 are smooth (Fig. 4B) and the inner face is slightly convex (Fig. 4C). The anterior margin is evenly rounded and nearly vertical. The anterodorsal margin is nearly straight and leans toward the dorsal margin at approximately 45°.

The dorsal margin is typically horizontal with a slight rounding at the center. The posterodorsal margin is nearly straight and forms a distinct posterodorsal angle of approximately 45° from the horizontal (Fig. 4A). Based on specimens from the Belgrade Formation in North Carolina (Müller 1999; fig. 38), this posterodorsal angle is present in juveniles and adults. The posterior margin is tapered and slightly pointed. The posteroventral margin, ventral margin, and anteroventral margins are fairly evenly and broadly rounded. The inner face has a large and prominent heterosulcoid-type sulcus that extends from the anterior margin for about 85% of the length of the sagitta (Fig. 4B). Although not large, there is a noticeable space between the sulcus and the posterior margin. The ostium, which is not excavated or deeply impressed, extends from the anterior margin for approximately 30% of the length of the inner face. The oval-shaped ostium has a nearly horizontal to slightly arched dorsal margin, but the ventral portion of the ostium is noticeably expanded and rounded. It extends under the anterior portion of the cauda and is about two times greater than the height of the cauda. The cauda is slightly excavated, characterized by a unique semi-circular shape (no horizontal portion), evenly curved, and extends above the dorsal margin of the ostium (Fig. 4B). The posterior portion of the cauda tapers slightly near the tip, which is pointed. There is no discernible dorsal depression above the sulcus (Fig. 4A). The ventral furrow is most prominent under the ostium and very faint elsewhere (Fig. 4A). The outer face is smooth and slightly more concave towards the center (Fig. 4D).

For comparison purposes, a specimen of *E. silverdalensis* (MSC 42699) from the type horizon at the Martin Marietta Belgrade Quarry locality in Jones County, NC, is also illustrated (Figs. 4E–G). This specimen is considered an adult and has a length of 6.40 mm and a height of 5.05 mm (length/height ratio of 1.27).

Remarks—*Equetulus silverdalensis* was first named as “genus aff. *Pachypops*” *silverdalensis* by Müller (1999) based on specimens from the Belgrade Formation (Haywood Landing Member) in North Carolina. Müller (1999) noted the age of the Belgrade Formation as early Miocene based on work by Ward et al. (1978). However, the more recent studies of Zullo et al. (1992) and Denison et al. (1993a, 1993b) show that the Belgrade Formation is late Oligocene (Chattian) to early Miocene (Aquitanian), corresponding primarily to calcareous nannofossil zones NP24 and NP25. This nannofossil zonation corresponds with the Alabama *E. silverdalensis* specimen, which was derived from the Paynes Hammock Sand within Zone NP25 (late Oligocene, Chattian) (Fig. 2).

The *E. silverdalensis* specimen from Alabama has several distinct and unique features. Although the sagitta is fairly small (2.40 mm length and 1.84 mm height) and presumed to be from a juvenile, the inner face displays the morphological features of essentially an adult specimen. This is unusual as most small juvenile sciaenids have very generalized, plesiomorphic features and are often difficult, if not impossible, to identify to species (Schwarzhans 1993, Müller 1999, Aguilera et al. 2014, Aguilera et al. 2016). However, this is not the case with the juvenile Alabama specimen as the morphological features are very comparable to adult specimens. For example, the posteroventral portion of the ostium extends beneath the cauda in the juvenile specimen, just as it does in the adult specimen (Fig. 4). In addition, the near evenly smooth surface and semicircular-shape of the cauda is very distinct in *E. silverdalensis*, and the cauda has no horizonal portions as is the case with many sciaenids (Schwarzhans 1993, Nolf 2013, Aguilera et al. 2016, Stringer and Bell 2018). Finally, the cauda extends above the dorsal margin of the ostium, which is also an uncommon and peculiar feature for sciaenid otoliths (Chao 1978, Schwarzhans 1993, Nolf 2013). Although the juvenile Alabama specimen is very similar to the adult specimen from North Carolina, there are two minor differences that appear to be ontogenetically related. The highest point of the dorsal rim is slightly more anterior in the Alabama juvenile specimen, and there is a little more space between the cauda and the posterior margin in the juvenile (Fig. 4B, E). These small variances are considered ontogenetic in nature.

DISCUSSION

Taxonomic assignment

The assignment of MSC 43698 to *Equetulus silverdalensis* n. comb. is based on several major morphological considerations. When the salient characteristics of *E. silverdalensis* are compared to other sciaenid species of the genera *Pachypops* Gill (1861), *Equetus* Rafinesque (1815), *Pareques* Gill in Goode (1876), and *Plagioscion* Gill (1861), it becomes evident that none of them fully match the features of *E. silverdalensis.* For example, the figure of *Plagioscion* aff. *P. ternetzi* Boulenger (1895) in Schwarzhans (1993, fig. 23) shows some similarities such as a larger ostium and a curved cauda. However, closer examination shows that the ostium has only a slight dorsal expansion and does not extend beneath the cauda. Also, the cauda has a section that is near horizontal in orientation, but *E. silverdalensis* has ascending and descending portions but no horizontal portion. Also, the outline of the otolith is quite different from *E. silverdalensis*, especially the posterodorsal margin, posterodorsal angle, posterior margin, and posteroventral margin.

Aguilera et al. (2014) proposed the otolith-based fossil genus *Equetulus.* The type species for *Equetulus* is an early Miocene sciaenid from South America with features very close to the Alabama sciaenid specimen given the variation often seen in the ostia of fossil and recent sciaenids such as *Aplodinotus distortus* Nolf (2003: pl. 4). Similarities include the shape of the sagitta, the length/height ratio (approximately 1.3 for juveniles of *E. silverdalensis* and the Alabama specimen is 1.3), and the configuration of the sulcus, especially the cauda. However, there are some differences, including the size of the ostium (*Equetulus* tends to have a smaller ostium that does not extend under the cauda) and the lack of a ventral furrow. Close examination of the specimens figured by Aguilera et al. (2016) indicates there is a degree of variation in the size and shape of the ostium in *E. davidandrewi* (Aguilera et al. 2016; pl. 6, figs. 5–10), and even more so in *E. fitchi* (Aguilera et al. 2016, pl. 6, figs 11–15). In fact in the specimen of fig. 13, the ostium is more expanded and extends underneath the cauda.

The ventral furrow, the other varying feature in the Alabama specimen, is prominent only underneath part of the ostium, suggesting these two variations are not as pronounced as first believed. The variations may be intraspecific and/or ontogenetic, but they may also be related to plesiomorphic features retained in the juvenile *E. silverdalensis* specimen from Alabama. Since only one *E. silverdalensis* was found, the discovery of additional specimens would provide further clarification into the taxonomy of this genus and species. In summary, it is believed that the morphological features of MSC 42699 are within the variability evident in *Equetulus* and that the specimen should be placed provisionally in this genus. The specimen also matches the characteristics of the species proposed by Müller (1999) in open generic nomenclature as "genus aff. *Pachypops*" *silverdalensis*.

Stratigraphic range and paleogeographic distribution

For many years, *Equetulus silverdalensis* was known only from the late Oligocene–early Miocene Belgrade Formation in North Carolina. The only exception is the figure of a specimen in Nolf (2013) from the Chickasawhay Limestone at Taylor's Creek in Mississippi that included no description or other information. Including the occurrence of MSC 42699, it appears that *E. silverdalensis* is limited to the late Oligocene–early Miocene in the Atlantic and Gulf coastal plains.

The paleogeographic distribution of *E. silverdalensis* in the late Oligocene is certainly enigmatic. Based on existing data (especially abundance), the center for the evolution of *E. silverdalensis* would appear to be in the Atlantic Coastal Plain, i.e., North Carolina. From this center of development, it is possible that the range of the species subsequently expanded south and west. However, the age of the Belgrade Formation in North Carolina and the Paynes Hammock Sand in Alabama appear to be essentially the same (late Oligocene; approximately NP24 and NP25). It is feasible that *E. silverdalensis* was present in the Atlantic Coastal Plain earlier than the Belgrade Formation since Oligocene otoliths are very poorly known from that area. Even more confusing is the possible occurrence of *E. silverdalensis* in the Chickasawhay Limestone in Mississippi as shown in Nolf (2013). The Chickasawhay Limestone (late NP23) is stratigraphically older than the Belgrade Formation (Dockery and Thompson 2016).

Examination of the late Oligocene paleogeography provides pertinent data regarding a potential range from North Carolina to Alabama or Mississippi for *E. silverdalensis*. The present-day Floridian peninsula would present a formidable barrier with a length of approximately 720 km. However, numerous sources indicate that during the Oligocene the Floridian peninsula was essentially nonexistent, and at most, was only a fraction of the length of today. Smith et al. (1994: figs 4–5) shows the Florida peninsula completely submerged during the Oligocene (30 Ma) and only a small central portion emerged in the early Miocene (Burdigalian–Aquitanian; 20 Ma). Markwick (2007) used fossil climate proxies (crocodilians, amphibians, and turtles) in conjunction with lithological proxies (peats, coals, reefs, and evaporites) in the interpretation and construction of their paleogeographic maps. The map (Markwick 2007, fig. 43) for the late Oligocene (Chattian; approximately 27.8–23.0 Ma), which approximates the age of the Paynes Hammock Sand (Dockery and Thompson 2016), indicated that none of the Floridian peninsula was emergent suggesting absence of a land barrier. Likewise, the late Oligocene (Chattian; approximately 25.7 Ma) paleogeographic map shown by Scotese (2014) showed no emergent land mass in Florida. The map was reflective of a transgressive systems tract with sea level approximately 40 m greater than the present level. Even in the early Miocene (approximately 20 Ma), Blakey (2014) only denotes a small portion of the Floridian peninsula

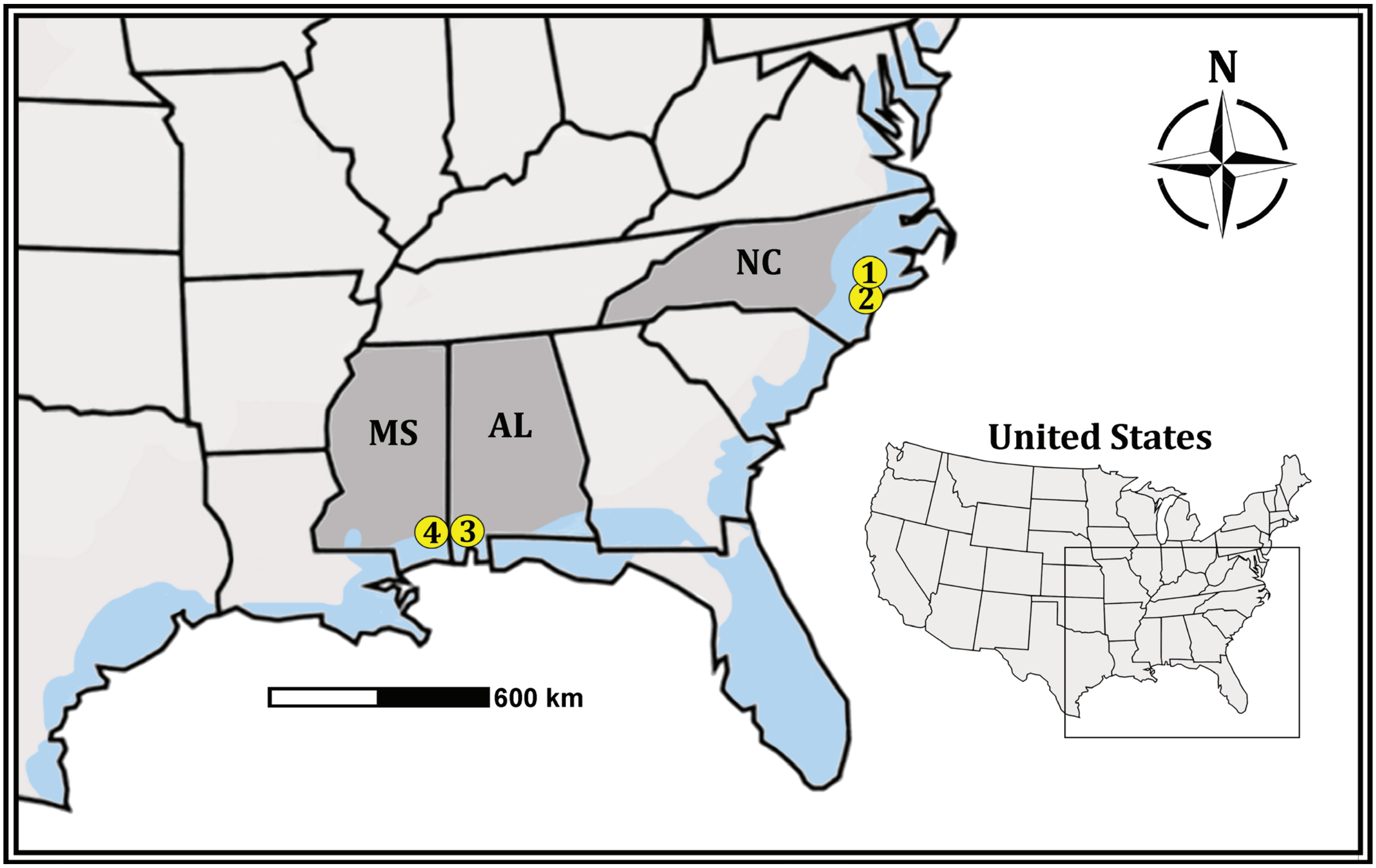

Figure 5. Paleogeographic map of the southeastern USA during the late Oligocene (23 million years ago). Numbers refer to the following counties and states with occurrences of *Equetulus silverdalensis* n. comb.: **1.** Jones County, North Carolina, USA. **2.** Onslow County, North Carolina, USA. **3.** Washington County, Alabama, USA **4.** ?Wayne County, Mississippi, USA. The blue areas represent the Oligocene seaway ~23 mya after Blakey (2014).

as emergent (less than 10% of the present-day length and about 20% of the present-day width). Therefore, the evidence is convincing that the Floridian peninsula would not have been a barrier or impediment to the distribution of marine fishes during the late Oligocene or even the earliest Miocene (Fig. 5). The distribution of Recent sciaenids from North Carolina to the north-central Gulf of Mexico are known even with an emergent Floridian peninsula (Robins and Ray 1986, Hoese and Moore 1998, Froese and Pauly 2019). For example, the distribution of a potential sciaenid analogue, the Recent *Micropogonias undulatus* (Linnaeus, 1766), extends from Massachusetts to the northern Gulf of Mexico and even to northern Mexico, although it is missing from the Atlantic side of Florida (Frosese and Pauly 2019).

While a range of *E. silverdalensis* from North Carolina to southwestern Alabama and southeastern Mississippi during the late Oligocene and early Miocene seems possible and even likely, there are still remaining questions. The rarity of *E. silverdalensis* in the Gulf Coastal Plain may be related to the paleogeographic factors discussed above, or it could reflect the abundance of, or lack thereof, the species due to paleoenvironmental parameters. There are significant differences in the late Oligocene–early Miocene paleoenvironments of the *E. silverdalensis* in North Carolina compared with southernmost Alabama with a latitudinal difference of approximately 5° and the contrast between the impacts of the Atlantic Ocean versus the Gulf of Mexico. An overarching paleoenvironmental consideration is the climate of the Oligocene and early Miocene. According to Pälike et al. (2006), the Oligocene climate system response to intricate orbital variations suggested a fundamental interaction of the carbon cycle, solar forcing, and glacial events. Detailed and extensive studies from St. Stephens Quarry, Alabama (located near the Millry site) by Miller et al. (2006) indicated global increases in ice volume, a 55 m decrease in sea level, and an overall temperature depression when compared to the Eocene. Paleoenvironmental differences, especially temperature, nutrient supply, and salinity, between North Carolina and southern Alabama could have also been exacerbated by the continued closing of the Tethys Seaway, changes in oceanic circulation, and reversals of ocean transport (Ricou 1987, Von der Heydt and Dijkstra 2005, Allen and Armstrong 2008, Bialik et al. 2019 and references therein). Therefore, the scarcity of *E. silverdalensis* in the Gulf Coastal Plain compared to the Atlantic Coastal Plain may be associated with paleoenvironmental differences between the two coastal plains.

CONCLUSIONS

A recently discovered otolith from the Paynes Hammock Sand (late Oligocene, Chattian) of Alabama has been assigned to *Equetulus silverdalensis* n. comb., an otolith-based, fossil sciaenid. This study represents the first description of *E. silverdalensis* from the USA Gulf Coastal Plain. The Alabama specimen and the possible second occurrence in Mississippi from the Chickasawhay Limestone (late Oligocene, latest Rupelian) indicate a potential distribution range from the Atlantic Coastal Plain to the central Gulf Coastal Plain. This extensive range would have been promoted by the essentially submerged Floridian peninsula during the late Oligocene and early Miocene. The scarcity of *E. silverdalensis* in the southern Atlantic Coastal Plain and its rarity in the Gulf Coastal Plain remain enigmatic, but it may be a consequence of inadequate sampling, a lack or absence of suitable late Oligocene–early Miocene strata, or a reflection of actual abundance related to paleoenvironmental factors.

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