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Biogeographic, stratigraphic, and environmental distribution of *Basilosaurus* (Mammalia, Cetacea) in North America with a review of the late Eocene shoreline in the southeastern coastal plain

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Abstract.—A new specimen of *Basilosaurus cetoides* was discovered on the banks of the Flint River in Albany, Georgia, USA, in 2010. This fossil, which was the most complete specimen of the species from Georgia to date, consisted of five nearly complete and two partial post-thoracic vertebrae, tentatively identified as S4 through Ca6. During excavation, however, the site was looted and most of the specimen was lost to science. Nonetheless, we use this discovery as an opportunity to update the current state of knowledge on the stratigraphic, biogeographic, and environmental distribution of *Basilosaurus* in North America, as well as the position of the late Eocene shoreline in the southeastern United States. The results show that *Basilosaurus* was most abundant across the southeastern coastal plain during the early to middle Priabonian, coincident with the late Eocene maximum marine transgression. The decline in *Basilosaurus* localities is associated with the retreating shoreline of the terminal Eocene. The majority of *Basilosaurus* localities fall well south of the position of the late Eocene shoreline hypothesized in this study, suggesting the genus favored middle to outer neritic zones of the epicontinental sea. The comparatively low number of Priabonian specimens in the Atlantic Coastal Plain versus the Gulf Coastal Plain, then, suggests the presence of shallow zones in the Atlantic Coastal Plain that may have limited the distribution of *Basilosaurus* across the region. The hypothesized shoreline of this study ultimately differs from earlier reconstructions by extending the Mississippi embayment at the Bartonian/Priabonian boundary farther north than previously noted.

Introduction

Basilosaurus cetoides (Owen, 1839) is an extinct cetacean common to the southeastern coastal plain of the United States. The most complete *B. cetoides* skeleton from Georgia, USA, to date was discovered by employees of the Georgia Department of Natural Resources during a routine fish survey of the Flint River in downtown Albany (Dougherty County) in the fall of 2010. Five post-thoracic vertebrae, portions of at least two additional post-thoracic vertebrae, and possible rib fragments were observed at the site. Excavation of this specimen began in August 2012, but by October 2012 the site was looted, and most of the skeleton was lost to science. All that remains of this *Basilosaurus* are portions of a single vertebra, additional bone fragments, photographs, field notes, and sketches. Despite the loss of the majority of this specimen, its discovery increases the number of reported *Basilosaurus* localities in Georgia to five and provides potential for further understanding the late Eocene landscape of the southeastern United States. Here we explore the temporal, environmental, and geographic distribution of *Basilosaurus* in the Atlantic and Gulf coastal plains to re-evaluate the position of the late Eocene shoreline and investigate possible limits to the distribution of this taxon.

Background

Basilosauridae are fully aquatic archaeocete cetaceans that occupied marine environments around the world during the Bartonian and Priabonian (late middle Eocene to late Eocene). They are known from deposits in Antarctica (e.g., Buono et al., 2016), Austria (Uhen and Tichy, 2000), Egypt (see Gingerich, 1992, and the references therein), Germany (Uhen and Berndt, 2008), Italy (Pilleri and Cigala Fulgosi, 1989), Jordan (Zalmout et al., 2000), Libya (Wight, 1980), Morocco (e.g., Gingerich and Zouhri, 2015), New Zealand (Köhler and Fordyce, 1997), Pakistan (Gingerich et al., 1997), Peru (Martínez-Cáceres and de Muizon, 2011), Russia (Kalmykov, 2012), Senegal (Elouard, 1966), Tunisia (Batik and Fejfar, 1990), Ukraine (Gol'din and Zvonok, 2013), the United Kingdom (Halstead and Middleton, 1972), and the United States (see Uhen, 2013, and the references therein, as well as Uhen and Taylor, 2020). Basilosauridae includes 19–24 species, depending on the equivocal interpretations of certain specimens (e.g., Uhen, 2013, 2018; Gingerich and Zouhri, 2015; van Vliet et al., 2020). They are characterized by: a lack of upper third molars; the presence of multiple, well-

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developed accessory denticles on cheek teeth; modification of forelimbs into flippers; greatly reduced hind limbs with no articulation between the pelvic girdle and sacrum; and an elevated number of posterior thoracic and/or lumbar vertebrae (Uhen, 2013). Basilosauridae has often been divided into the subfamilies Dorudontinae and Basilosaurinae, with the latter exhibiting a larger body size and elongated posterior thoracic, lumbar, and anterior caudal vertebrae (e.g., Uhen, 1998). However, this distinction has not often been followed in recent years due to the uncertainty of phylogenetic relationships among basilosaurids and the possibility that one of these subfamilies may be paraphyletic (Uhen, 2013).

The first known archaeocete specimens were an elongated vertebral centrum and partial dentary discovered in Louisiana in the early nineteenth century. Harlan (1834) coined the genus *Basilosaurus* (meaning "king lizard") for this specimen based on the interpretation that these elements belonged to a marine reptile, but he failed to give the taxon a specific epithet. Owen (1839) recognized the mammalian nature of the material and coined the name *Zeuglodon cetoides*, with the specific epithet signifying the taxon's cetacean affinities. Gibbes (1847) recognized the priority of Harlan's genus and proposed the new combination *Basilosaurus cetoides* for this taxon. The genus has come to include a well-known Egyptian species, *B. isis* (Andrews, 1904), and *B. drazindai* (Gingerich et al., 1997), a proposed species from Pakistan that was based on a single, well-preserved lumbar vertebra.

Basilosaurus is so abundant along the Gulf Coast of the United States that it has been adopted as an official state fossil of both Mississippi and Alabama. Reel (1972) speculated that a large number of fossil whales were preserved in this region because its warm climate, ample food sources, and openness to the Atlantic Ocean made it an ideal mating area during the late Eocene. Regardless of the reason for their abundance, documenting the distribution of *Basilosaurus* through space and time has implications for understanding the paleogeography of the southeastern coastal plain of the United States during the late Eocene.

Materials and methods

The primary specimen in this study is GSM 1465, which is the most complete *Basilosaurus* discovered in Georgia to date. The fossil was embedded in the late Priabonian Ocala Limestone Formation along the banks of the Flint River in Albany, Georgia, USA (Paleobiology Database collection 138667). It was oriented in an approximately east-west position, perpendicular to the direction of river flow, with the anterior to the east. Fossils found in association with the *Basilosaurus* were an isolated carcharhiniform shark vertebra, the bivalve *Amusium ocalanum* Dall, and an unidentified, microscopic gastropod, all of which were collected prior to looting. The *Basilosaurus* fossil is described based on measurements, field notes, and photographs (Fig. 1). Measurements of length, width, and height were collected from each vertebra, when preservation allowed, and compared to data from Buchholtz (2001) to determine the position of each along the vertebral column.

Locations of *Basilosaurus* fossils in North America were sourced from the Paleobiology Database (PBDB) (paleobiodb.org; as downloaded on June 30, 2020) and the literature. GSM 1465 was already included in the PBDB based on an abstract (Smith et al., 2013). The following data, when available, were recorded for each locality (Supplemental Data 1): (1) county and state, (2) geologic age, (3) site stratigraphy, (4) environment of deposition, (5) latitude and longitude, (6) literature reference, and (7) PBDB collection number. All data from the PBDB were crosschecked against the original references. The geologic age of a *Basilosaurus* locality lacking explicit age data was interpreted from site stratigraphy.

All *Basilosaurus* localities (N = 61) were mapped using ArcMap 10.6. *Basilosaurus* localities with stratigraphic data (N = 53) were added to a schematic of late Eocene stratigraphy to illustrate the temporal distribution of the genus. *Basilosaurus* localities with more specific stratigraphic information (N = 36) were sorted into four time bins: early Bartonian, Bartonian/Priabonian boundary, early to middle Priabonian (in which the upper boundary of the Pachuta Marl Member of the Yazoo Clay Formation marks the end of the "middle Priabonian" for this study), and late Priabonian. These 36 sites were coded by time bin and plotted on a second map. The time bins were chosen with the intention of including as many specimens as possible, given the limited stratigraphic data for some specimens. Different time bins were considered, but these differences would not have affected the overall picture of *Basilosaurus* dispersal during the late Eocene. For example, substituting the late Priabonian category with a middle to late Priabonian category would change the designation for two Georgia specimens, including GSM 1465, but the map would still show that dispersal was generally later in the eastern states than in the western states.

Previously published paleogeographic features of the late Eocene in the southeastern United States were added to the map of *Basilosaurus* localities produced in this study. Schuchert (1929, fig. 6) posited the location of a late Eocene shoreline based on Jackson (late Eocene) and Claiborne (middle Eocene) deposits, broadly defining a shoreline for, presumably, the period stretching from the end of the Bartonian to the late Priabonian. Rainwater (1964, fig. 7) posited a shoreline based on marine deposits at the base of the upper Eocene Moody's Branch Formation (late Bartonian). Reel (1972, fig. 5) based a late Eocene shoreline on the presence of Jackson Group sediments, as interpreted from Rainwater (1964), with the caveat that the true shoreline lies farther landward due to the erosion of original coastal sediments. Huddlestun (1993, figs. 51, 54) postulated an approximate location of the shoreline in Georgia during the latest Priabonian based on lithology, a tentative position for the terminal Eocene low sea stand in the state, and an approximate location and the direction of the Suwannee Current, which flowed through the relatively deep Gulf Trough during the middle to late Eocene. Tew and Mancini (1995, fig. 9D) presented a latest Eocene shoreline in Mississippi and Alabama based on the northernmost extent of deposition for the Shubuta Member of the Yazoo Clay. Scott (2011, fig. 2.3) illustrated the axis of the Ocala Platform, a topographically high feature in Florida that arose in the post-early Cenozoic.

A new late Eocene shoreline was developed as a composite of the maximum landward portions of each previously interpreted shoreline and the maximum landward portions of a new

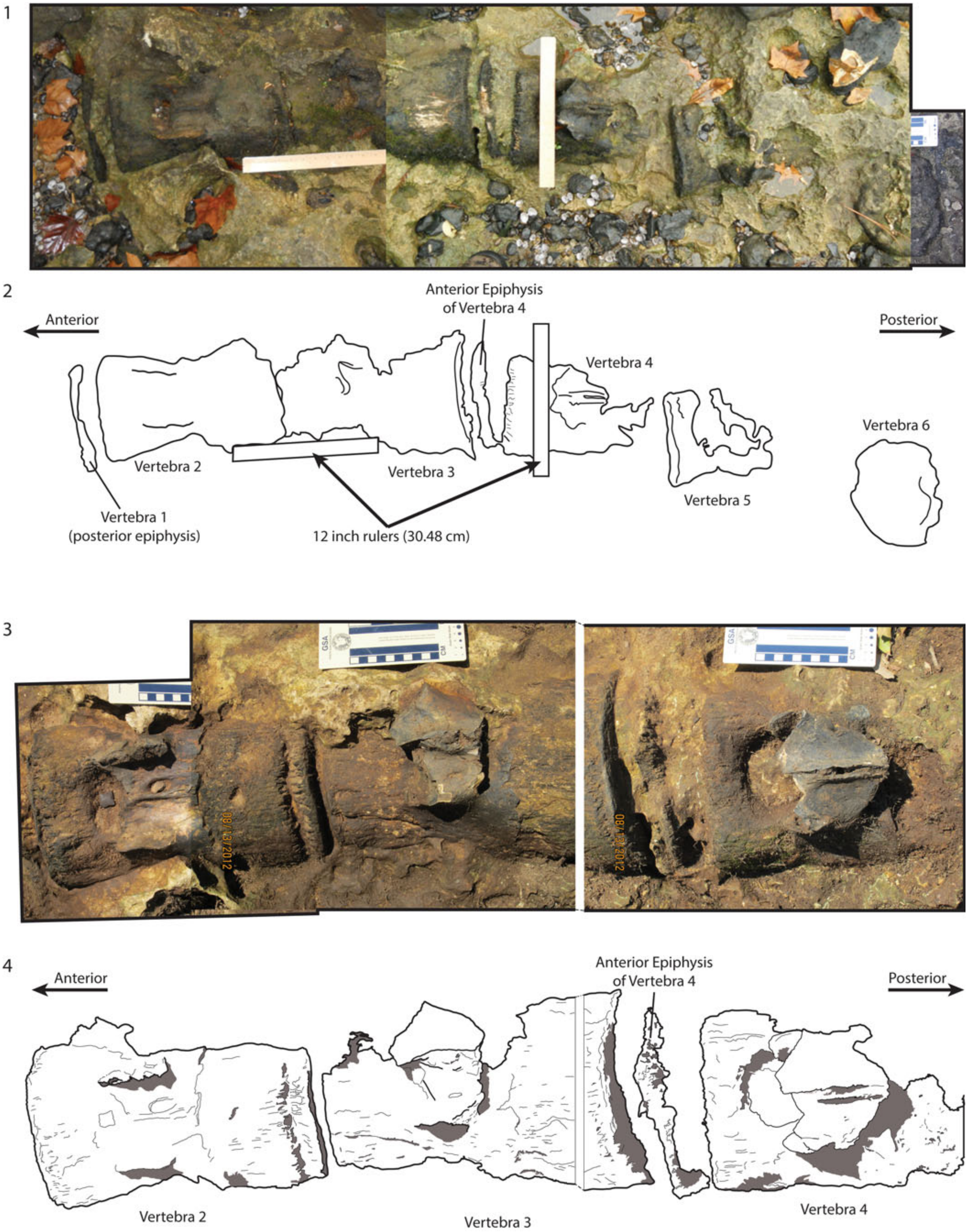

Figure 1. (**1**) View of GSM 1465 in situ, upon discovery; 12-inch ruler for scale. (**2**) Illustration of vertebrae visible in (**1**). (**3**) Close up of the three most complete vertebrae. (**4**) Illustration of vertebrae visible in (**3**). Photography by Rob Weller (**1**) and Arthur Berger (**3**).

shoreline developed using the location of *Basilosaurus* fossils. Because shorelines are constantly shifting features, each shoreline used in this study most likely accurately depicts the location of the shoreline for some time slice, however large or small, for the late Eocene. Our goal is to combine paleogeographic evidence from multiple sources to produce one shoreline that best represents the maximum transgression of the epicontinental sea across the Atlantic and Gulf coastal plains from the early Bartonian to the late Priabonian, which is the time when *Basilosaurus* inhabited North America.

Abbreviations.—Ca, caudal vertebra; L, lumbar vertebra; PBDB, Paleobiology Database; S, sacral vertebra; V, vertebra.

Repositories and institutional abbreviations.—Specimens examined in this study are deposited in the Georgia Southern University Museum Paleontology Collections (GSM), Statesboro, GA, USA. Additional discussed specimens are deposited in the National Museum of Natural History (USNM), Washington, DC, USA; the Academy of Natural Sciences (ANSP), Philadelphia, PA, USA; and the Florida Museum of Natural History, University of Florida (UF), Gainesville, FL, USA.

Systematic paleontology

Cetacea Brisson, 1762
Pelagiceti Uhen, 2008
Basilosauridae Cope, 1868
Basilosaurus Harlan, 1834

Type species.—*Basilosaurus cetoides* (=*Zeuglodon cetoides* Owen, 1839).

Other species.—*Basilosaurus isis* (=*Zeuglodon isis* Andrews, 1904).

Diagnosis.—*Basilosaurus* is unique among basilosaurids for its long body (length >15 m) and post-thoracic vertebrae that are approximately twice as long as they are wide or tall (Uhen, 2013). *Basilosaurus cetoides* has been differentiated from *B. isis* based primarily on the former's larger size (Gingerich et al., 1990), but additional work is needed to assess the validity of this distinction and whether there are any diagnostic morphological characters (Uhen, 2013).

Basilosaurus cetoides Owen, 1839
Figures 1, 2

1839	*Zeuglodon cetoides* Owen, p. 69.
1842	*Zeuglodon harlani* DeKay, p. 123.
1845a	*Hydrargos sillimanii* Koch, p. 1.
1845b	*Hydrarchos sillimanii* Koch, p. 1.
1845a	*Hydrarchos harlani*; Koch, p. 1.
1845	*Zeuglodon ceti* Wyman, p. 65.
1847	*Basilosaurus cetoides* Geinitz in Carus, p. 1.
1847	*Basilosaurus cetoides* Reichenbach in Carus, p. 13.
1848	*Basilosaurus harlani* Hammerschmidt, p. 323.
1849	*Zeuglodon macrospondylus* Müller, p. 3.
1906	*Alabamornis gigantea* Abel, p. 450.
1936	*Basilosaurus cetoides*; Kellogg, p. 15.

Holotype.—Elongated vertebral centrum (ANSP 12944A) from the undifferentiated Jackson Group, Caldwell Parish, Louisiana, USA (Harlan, 1834, plate XX, figs. 1, 2).

Diagnosis.—*Basilosaurus cetoides* is the only species in the genus known from the United States to date. Because GSM 1465 possesses the characteristic elongate vertebrae of a *Basilosaurus* and was found in the United States, the specimen is referred to *B. cetoides*.

Occurrence.—GSM 1465 was discovered on the eastern bank of the Flint River in downtown Albany, Dougherty County, GA, USA (31.58°N, 84.15°W). GSM 1465 was encased in the late Eocene Ocala Limestone Formation of the Jackson Group. In Dougherty County, Georgia, this formation is exposed as a "white to very light pink pure to sandy aphanitic oolitic and crystalline limestone [that contains] bones of zeuglodonts … abundant foraminifera, macroshells, and bryozoan" (Wait, 1963, p. 18). In Florida, where the formation was originally identified (Dall and Harris, 1892), it is exposed as fine-grained, white- to cream-colored fossiliferous limestone (both packstone and grainstone) that is sometimes dolomitized and rarely contains the macroscopically visible foraminifera *Lepidocyclina* sp. in the lower member (Scott, 2001). *Lepidocyclina* is not observed at the Flint River site, but because the Flint River tends to expose only the upper section of the Ocala (Wait, 1963) and *Lepidocyclina* has been identified at outcrops in Dougherty County, the site is likely an exposed portion of the upper Ocala (middle to late Priabonian).

Fossils found at the same stratum as GSM 1465 are a single vertebra of a small, carcharhiniform shark (Dana Ehret, personal communication, 2019; Fig. 3.1), multiple specimens of the pectinid bivalve *Amusium ocalanum* (Dall) (David Campbell, personal communication, 2014; Fig. 3.2), as well as unidentified gastropod and bivalve shell fragments. The sedimentary provenance and associated fauna indicate a shallow marine environment of deposition.

Description.—GSM 1465 originally consisted of seven partial to nearly complete post-thoracic vertebrae (heretofore referred to as V0–V6) and additional bone fragments. Five post-thoracic vertebrae were partially articulated (V1–V5 in Fig. 1): V1 is represented only by an epiphysis; V2 lacks a neural arch, neural spine, and transverse processes; V3 and V4 lack neural spines and transverse processes; V5 has a broken neural arch and lacks a neural spine; V2 and V4 have unfused epiphyses (Fig. 1), indicating that this specimen may not be fully mature. The size of the vertebrae, comparable to measurements reported in the literature (e.g., Uhen, 1998; Buchholtz, 2001), suggests the specimen is an adult. No juvenile specimens of *Basilosaurus* have been found to date, however, so no comparison between GSM 1465 and a juvenile can be done. V0 and V6, not in articulation, are represented by epiphyses (V6 in Fig. 1; V0 in Fig. 2); V6 was oriented epiphysis up, suggesting more of the bone may be encased in the rock.

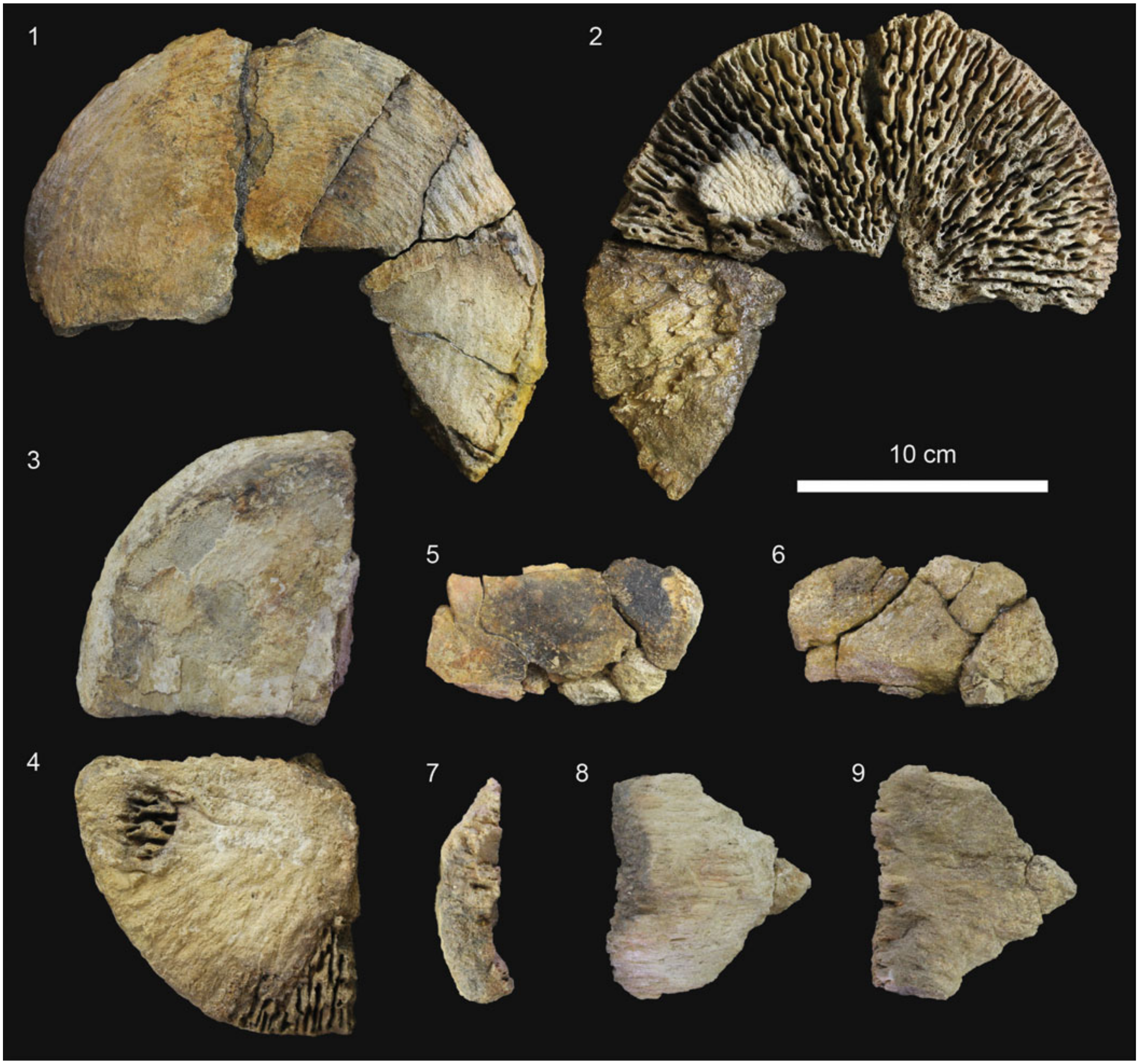

Figure 2. Recovered portions of GSM 1465. All were found anterior to V1, but none was in articulation with V1. Partial vertebral epiphysis (referred to as V0 in the text) in (**1**) exterior and (**2**) interior view. Fragment of vertebral epiphysis in (**3**) exterior and (**4**) interior view. Isolated bone fragment in (**5**) exterior and (**6**) interior view. Vertebral centrum fragment in (**7**) anterior or posterior, (**8**) lateral, and (**9**) interior view.

V1, V2, V3, and V4 were lost to science when the site was looted. V0 was collected prior to looting and is currently held in the Vertebrate Paleontology Collections of the Georgia Southern Museum. The original excavations were conducted in drought conditions; since 2012, V5 and V6 have been inundated by the Flint River and presumably remain in place. The full amount of the skeleton preserved remains unknown.

Materials.—GSM 1465 (Figs. 1, 2). All other specimens are listed in Supplemental Data 1.

Remarks.—Many of the vertebral features that would allow for interpretation of position along the vertebral column either were not preserved or were lost when the fossils were stolen, so the proposed position of each vertebra is tentative. The possible positions of these vertebrae were interpreted using measurements of epiphyseal width and height (as measured on the anterior), anteroposterior centrum length, and qualitative morphological characteristics, as compared to a composite skeleton of *Basilosaurus cetoides* (USNM 4675 and USNM 12261) from Kellogg (1936), graphically represented in Buchholtz (2001), and modified here in Figure 4. Vertebral length was obtained for V2, V3, and V5. Centrum length decreases from V2 to V3, then increases to V5. Vertebral width was obtained for V0 and V6. Width slightly increases from V0 to V6. Height was obtained for V6. There is a substantial

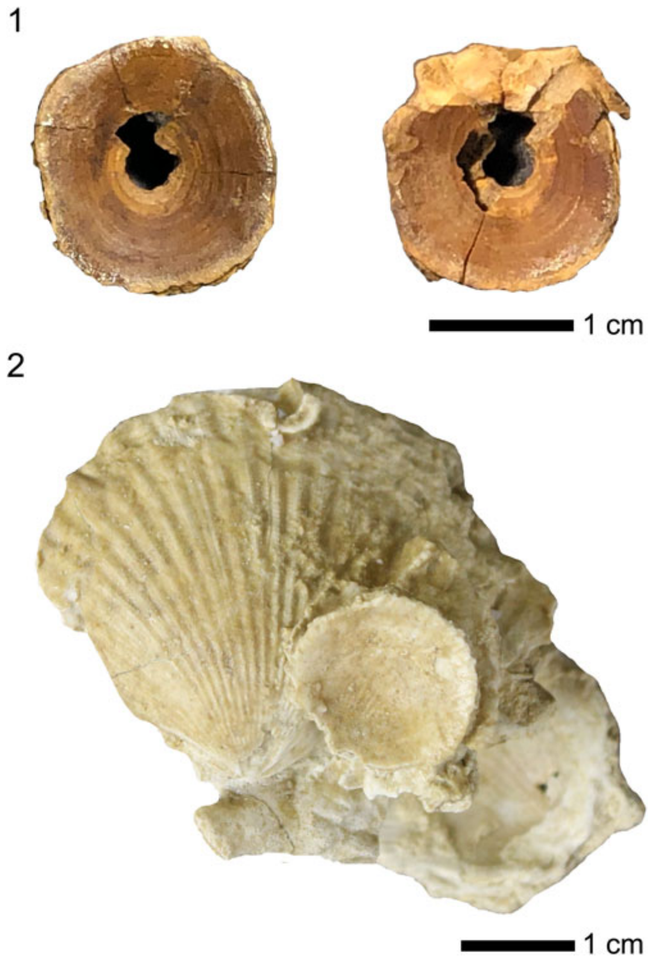

Figure 3. Fossils found in association with GSM 1465. (**1**) A single vertebral centrum from an unknown carcharhiniform shark (GSM 1466) in anterior (left) and posterior (right) view. (**2**) Disarticulated valves of the pectinid bivalve *Amusium ocalanum* (GSM 4724).

difference between width and height for V6. Based on these dimensions, and following the identifications of Kellogg (1936), this sequence of vertebrae falls between vertebrae 34 and 43 (inclusive), either L12 through Ca3 or S2 through Ca6. The remnants of neural arches on V3 and V4 are positioned slightly towards the anterior, and the metapophyses, although broken, are positioned in such a way that suggests they were directed more anteriorly than dorsally. Based on comparison with images in Kellogg (1936, pl. 6), this morphology is most pronounced on Ca3 through Ca5. The combination of quantitative and qualitative morphological data suggests that this vertebral sequence more likely represents S2 through Ca6.

However, Kellogg's (1936) vertebral designations require updating. The composite specimen of *Basilosaurus cetoides* was reconstructed from two non-overlapping vertebral series. The anterior end of the vertebral column (USNM 4675) included a consecutive series of seven cervical, 15 thoracic, and one lumbar vertebrae, while the posterior end of the vertebral column (USNM 12261) included a consecutive series of what Kellogg identified as 12 lumbar, two sacral, and 21 caudal vertebrae. This gives an estimated vertebral formula of C7:T15:L13:S2:Ca21. Gidley (1913) justified the non-overlapping nature of these series based on anatomical differences between the lone lumbar of USNM 4675 and the anteriormost lumbar of USNM 12261, but noted that the overall lumbar count may be an underestimate. Buchholtz (1998) noted that the sacral vertebrae identified by Kellogg lack intervertebral fusion and bear no articulations with the ilia, referring to them as 'sacral lumbars' and including them in the lumbar count (C7:T15:L15:Ca21). However, in recent years, it has been recognized that earlier archaeocetes with definitive vertebral counts possessed four fused sacral vertebrae, and vertebral counts for fully aquatic archaeocetes have typically identified the last four 'lumbars' anterior to the caudal region as sacral vertebrae (Bebej et al., 2012; Uhen, 2014; Buchholtz and Gee, 2017). Following this convention, Kellogg's formula for *B. cetoides* should be revised to C7:T15:L11:S4:Ca21. *Basilosaurus isis* from Egypt possesses a vertebral formula of C7:T16:L19:S4:Ca20 (Bebej et al., 2012), suggesting that the lumbar series of *B. cetoides* may indeed be missing multiple vertebrae. Regardless, the vertebral series described here overlaps with the terminal sacral vertebra and first six caudal vertebrae in Kellogg's composite specimen, and is tentatively identified as S4 through Ca6 (V0/S4, V1/Ca1, V2/Ca2, V3/Ca3, V4/Ca4, V5/Ca5, V6/Ca6).

Chondrichthyes Huxley, 1880
Carcharhiniformes Compagno, 1973
Carcharhiniformes indet.
Figure 3.1

Occurrence.—Same as GSM 1465.

Description.—GSM 1466, isolated vertebral centrum (Fig. 3.1). The centrum is disk shaped with concave anterior and posterior surfaces. Two foramina for attachment of the neural and hemal arches are present dorsally and ventrally, respectively. The vertebra has an anteroposterior length of 9.1 mm, a dorsoventral height of 16.6 mm, and a width of 17.9 mm.

Remarks.—Carcharhiniformes are the most abundant sharks in late Eocene sediments of Georgia (Parmley and Cicimurri, 2003). Carcharhiniform shark vertebrae lack identifying features, so taxonomic resolution remains coarse for this specimen. However, *Negaprion* (lemon shark), the most abundant shark in the Priabonian Hardie Mine Local Fauna of central Georgia (Parmley and Cicimurri, 2003), has vertebrae of similar size to GSM 1466, so it is a likely candidate for the taxon represented here.

Pterioida Newell, 1965
Pectinidae Wilkes, 1810
Amusium Röding, 1798

Type species.—*Amusium pleuronectes* (=*Ostrea pleuronectes* Linnaeus, 1758).

Amusium ocalanum Dall, 1898
Figure 3.2

Holotype.—From Levy County, Florida (Dall, 1898, pl. 29).

Occurrence.—Same as GSM 1465. *Amusium ocalanum* is restricted to the southeastern United States; it is common in

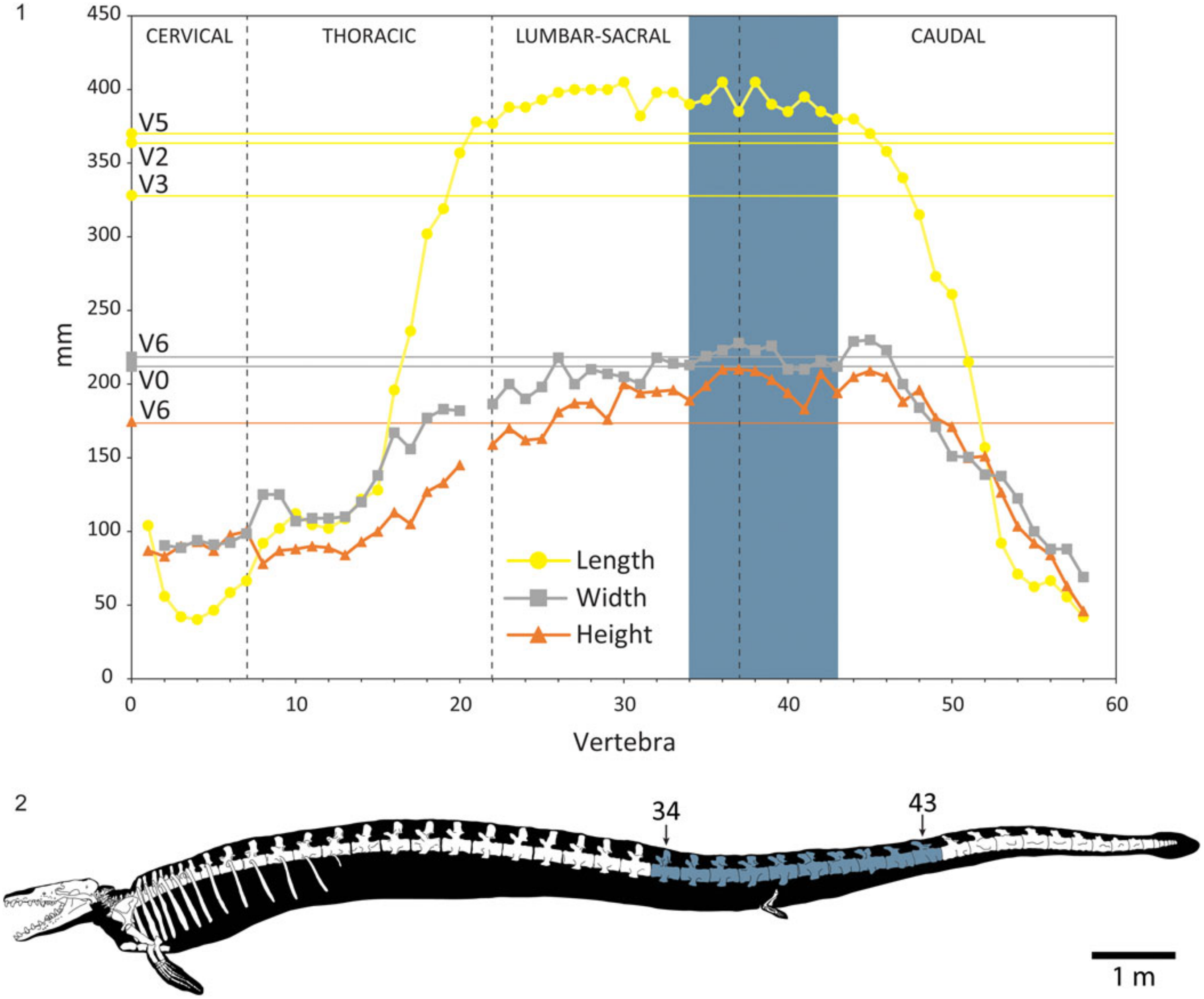

Figure 4. (**1**) Measurements of length, width, and height for GSM 1465 vertebrae (this study) compared to the same measurements from a composite skeleton of *Basilosaurus cetoides* (Buchholtz, 2001). (**2**) Schematic of a *Basilosaurus* skeleton, with possible positions of the GSM 1465 vertebrae highlighted.

the Ocala Limestone of Georgia and Florida and less common in similarly aged clastic units (Glawe, 1974).

Description.—GSM 4724, internal mold of one valve and multiple disarticulated valves (Fig. 3.2). Valves are convex and not quite bilaterally symmetrical, apical angle is acute, and internal ribbing is present. Specimens recovered at this location range in size from ∼10 mm to >30 mm at their greatest width.

Remarks.—Valves may exhibit well-defined, obvious ribbing, or may be nearly smooth (Dall, 1898).

Results

Stratigraphic and biogeographic distribution of Basilosaurus *in North America.*—Fossil occurrences of *Basilosaurus* in North America are restricted to the Bartonian and Priabonian of the Atlantic and Gulf coastal plains (Figs. 5, 6). The oldest and most southern *Basilosaurus* fossil is from the early Bartonian portion of the Avon Park Formation in Florida. No other *Basilosaurus* fossils of early or middle Bartonian age have been reported on the continent to date. *Basilosaurus* next occurs at the Bartonian/Priabonian boundary in several locations, including western Tennessee, extending the geographic range of the taxon to the west and north. *Basilosaurus* exhibits its largest geographic range and greatest abundance in the early to middle Priabonian, with localities as far west as Arkansas, as far east as South Carolina, and at every state in between (except Florida). By the late Priabonian, the abundance of the taxon declined, and its distribution was limited to southeastern Mississippi, southwestern Alabama, and southwestern Georgia.

Paleogeography of the late Eocene shoreline in North America.—A hypothetical position of the late Eocene shoreline, based on 61 *Basilosaurus* localities, is illustrated in Figure 6.1. Because this shoreline is defined by specimens

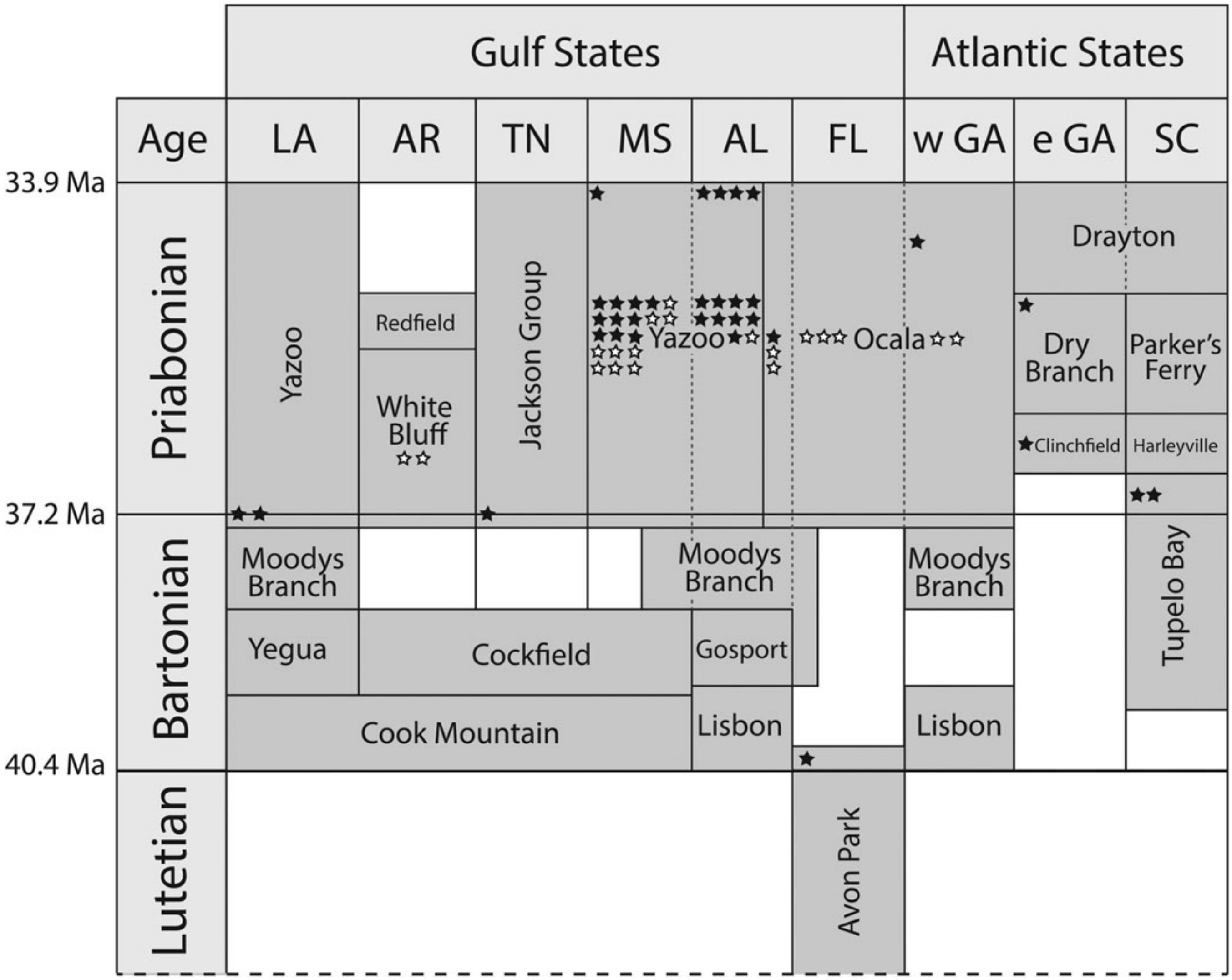

Figure 5. Stratigraphy of the Gulf and Atlantic coastal plains from the middle Lutetian to the end-Priabonian, modified from Uhen (2013, fig. 7). Data from the PBDB and additional sources (Supplemental Data 1). Closed stars indicate that there is some information regarding where in the stratigraphic column the specimen was found; open stars indicate that the position within the stratigraphic column is unknown.

found in a range of shallow marine environments, from nearshore to outer neritic, the true maximum extent of the late Eocene marine transgression was likely north of this hypothetical shoreline. Late Eocene shorelines from the literature are shown in Figure 6.2.

Basilosaurus localities can be roughly associated with paleogeographic features reported in the literature. The oldest reported *Basilosaurus* in North America (early Bartonian) lies just west of the axis of the Ocala Platform in Florida. *Basilosaurus* fossils of the Bartonian/Priabonian boundary broadly track the late Bartonian Rainwater (1964) shoreline. The early-middle Priabonian *Basilosaurus* fossils of Arkansas, Mississippi, and Alabama fall on or around the Rainwater (1964) shoreline; Arkansas specimens also align with the overlapping middle to late Eocene Schuchert (1929) and late Eocene Reel (1972) shorelines. In Georgia, one early–middle Priabonian locality falls on the intersection of the Schuchert (1929) and Reel (1972) shorelines, and another is just north of the Rainwater (1964) shoreline; early–middle Priabonian specimens of South Carolina are just south of the Reel (1972) shoreline. No *Basilosaurus* specimens from the late Priabonian are located north of any shorelines from the literature. In the west, these specimens fall on or south of the Rainwater (1964) shoreline that extends the farthest seaward. The solitary late Priabonian locality in the east is located on the terminal Eocene low sea stand (Tew and Mancini, 1995). Only two *Basilosaurus* localities are farther north than any of the shorelines in the literature: the early–middle Priabonian site in St. Francis County, Arkansas (Palmer, 1939), and the Bartonian/Priabonian boundary site in Lauderdale County, Tennessee (Moore and Brown, 1969). These localities extend the composite late Eocene shoreline to the middle of Tennessee's western boundary, farther inland than previously noted (Fig. 6.1).

Environmental distribution of Basilosaurus *in North America.*—The majority of *Basilosaurus* depositional environments in this study (N = 39) are described as "coastal indeterminate," "carbonate indeterminate," or "marine indeterminate," and the remainder are associated with some

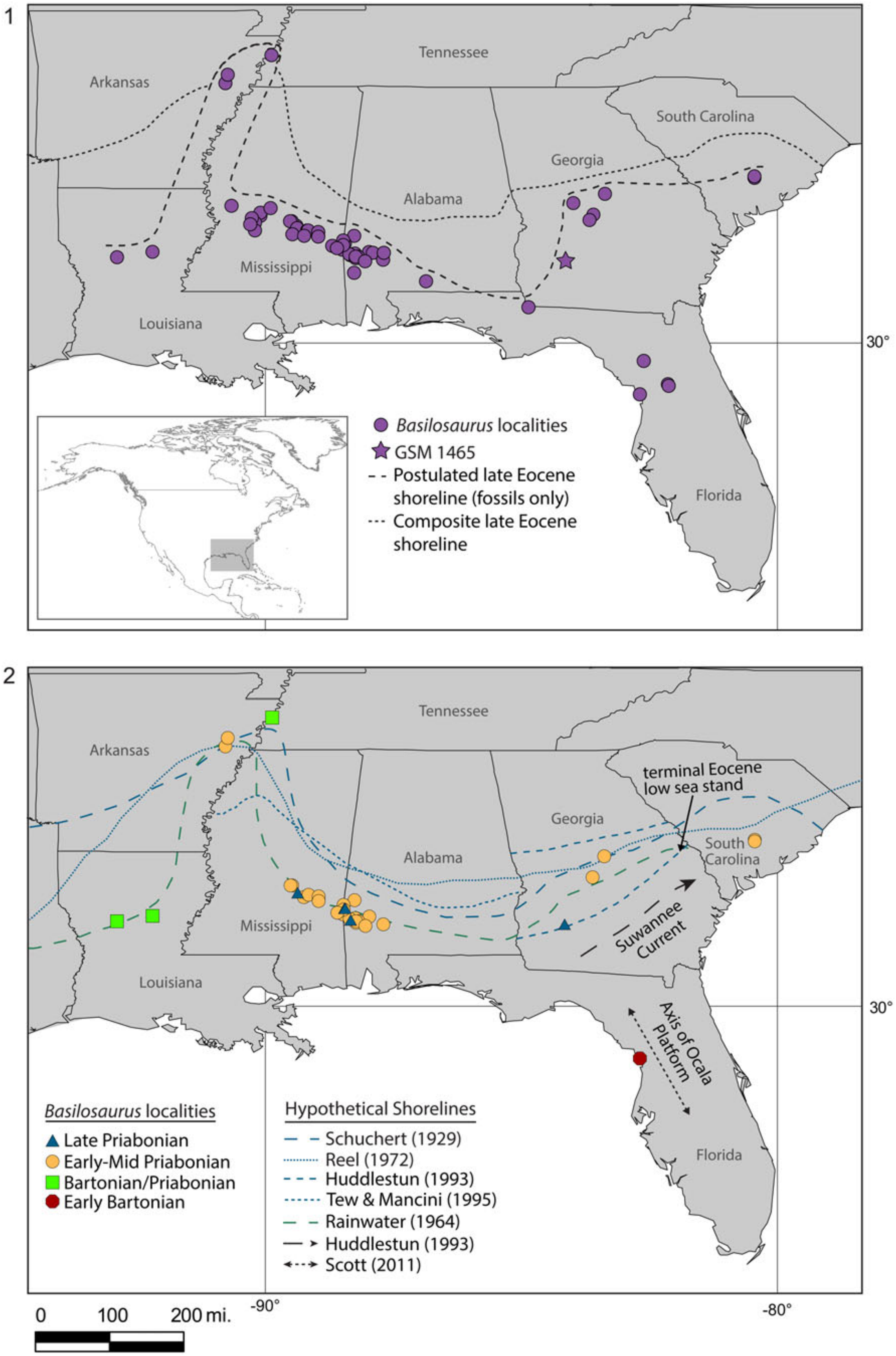
1
Tennessee
Arkansas
South Carolina
Georgia
Alabama
Mississippi
Louisiana
Florida
30°
● *Basilosaurus* localities
★ GSM 1465
- - Postulated late Eocene shoreline (fossils only)
··· Composite late Eocene shoreline
2
Tennessee
Arkansas
terminal Eocene low sea stand
Georgia
South Carolina
Alabama
Mississippi
Suwannee Current
Louisiana
30°
Axis of Ocala Platform
Florida
Basilosaurus localities
▲ Late Priabonian
● Early-Mid Priabonian
■ Bartonian/Priabonian
● Early Bartonian
Hypothetical Shorelines
Schuchert (1929)
Reel (1972)
Huddlestun (1993)
Tew & Mancini (1995)
Rainwater (1964)
Huddlestun (1993)
Scott (2011)
0
100
200 mi.
-90°
-80°

Figure 6. (**1**) Location of all *Basilosaurus* fossils listed in Supplemental Data 1, a postulated shoreline based only on these fossil occurrences, and a composite of the shorelines from Schuchert (1929), Rainwater (1964), Reel (1972), Huddlestun (1993), Tew and Mancini (1995), and this study. (**2**) Location of *Basilosaurus* fossils that could be sorted into one of four time bins and shorelines from the literature used to draw the composite in (**1**). Shoreline colors roughly correspond with the color key for stratigraphic age. The axis the of Ocala Platform is redrawn from Scott (2011) and the track of the Suwannee Current through the Gulf Trough is redrawn from Huddlestun (1993).

subset of the shallow marine environment (Supplemental Data 1). Four sites are associated with deeper zones of the epeiric sea. The Ouachita and Grant County, Louisiana, sites (Harlan, 1834; Lancaster, 1986), both in the Bartonian/Priabonian boundary time bin, are both described as offshore shelf, likely middle neritic environments. Two sites in Jasper County, Mississippi (Reel, 1972; early–middle Priabonian), are described as offshore, likely outer neritic environments. All four localities are positioned well south of the composite shoreline of this study. Multiple sites are in closer proximity to the paleocoastline, and are described as foreshore (N = 6), estuary (N = 2), and nearshore marine (N = 1). Specimens specifically associated with a coastal environment are found in Arkansas, Georgia, and Mississippi, and, with the exception of the Arkansas locality, are not notably closer to the composite shoreline than are deeper-water specimens.

Discussion

In the late Eocene, most of the southeastern coastal plain of the United States was covered by a relatively deep epicontinental sea, which resulted from a marine transgression that began in the late Bartonian (Frederiksen, 1980). This sea was the environment in which *Basilosaurus* expanded its range across the region. Sea level in Mississippi reached a high in the eastern part of the state by the middle to late Priabonian (Huff, 1970), corresponding in time and geography with the majority of *Basilosaurus* occurrences in the region.

Basilosaurus was present across a spectrum of shallow marine environments, from nearshore to outer neritic, indicating that it, like *Basilosaurus isis* at Wadi Al-Hitan in Egypt (Peters et al., 2009), was a generalist of the epicontinental seas. Because fossils of the genus were most abundant when and where the sea level was the highest, *Basilosaurus* in North America may have had a slight preference for a deeper, middle- to outer neritic environments, also like *B. isis* at Wadi Al-Hitan (Peters et al., 2009). Of all specimens with specific information on the environment of deposition, those associated with the deepest waters are present in Louisiana at the Bartonian/Priabonian boundary, when there was rapid, but slight, deepening of the epicontinental sea to a midsublittoral environment (Huff, 1970), and the middle Priabonian of Mississippi, when the environment ranged from midsublittoral to shallow, outer sublittoral (Huff, 1970; Supplemental Data 1). Nearly all *Basilosaurus* occurrences are well south of the late Eocene composite shoreline (Fig. 6.1), again suggesting an environmental preference for deeper zones of the shallow sea. In this way, the relative paucity of the taxon in the Atlantic Coastal Plain as compared to the Gulf Coastal Plain may be related to environmental differences, in which *Basilosaurus* preferred the presumably deeper waters over the Gulf.

The proximity of two Bartonian/Priabonian boundary *Basilosaurus* localities to the Rainwater (1964) shoreline of approximately the same age at first appears to counter the hypothesis that *Basilosaurus* preferred middle to outer neritic environments. These two specimens, however, are associated with offshore shelf and middle neritic environments, suggesting that the shoreline was actually farther inland at this time than shown by Rainwater (1964). Another possible counterargument involves a *Basilosaurus* (UF 115000) found in a nearshore, shallow subtidal environment, adjacent to the long axis of the Ocala Platform. This topographically high point in the Cenozoic of Florida (Scott, 2011) would have created a shallow zone around the possibly inundated platform, making it a potential death trap for the *Basilosaurus*. The three occurrences located at the landward edge of the Mississippi embayment, also a shallow area, may have suffered a similar fate.

Basilosaurus has not been found near the Suwannee Current in Georgia, which is somewhat surprising because the current flowed through the relatively deep Gulf Trough of the late Eocene (Huddlestun, 1993), making it a seemingly favorable environment for the taxon. The area surrounding the Gulf Trough, however, may have been topographically high, creating a shallow-water barrier that prevented *Basilosaurus* dispersal to the deeper waters over the trough itself. The lack of *Basilosaurus* occurrences in the Priabonian of Florida likewise could be related to water depth, in which the topographically high Ocala Platform of central Florida (Fig. 6.2; Scott, 2011) created a zone of water too shallow for *Basilosaurus* to inhabit throughout much of the late Eocene.

Changes to the temporal distribution of *Basilosaurus* fossils in the Gulf Coastal Plain can be associated with regional marine transgressions and regressions. The first appearance of *Basilosaurus* in the North American fossil record is equivalent in time to the early Bartonian Cook Mountain transgression, which is associated with intertidal to inner neritic environments (Rainwater, 1964). The middle Bartonian Yegua regression, which followed the Cook Mountain transgression, is dominated by continental and intertidal environments (Rainwater, 1964) and coincides with an absence of *Basilosaurus* occurrences across the entire southeastern United States. *Basilosaurus* reappears in the fossil record at the Bartonian/Priabonian boundary, in conjunction with a slight deepening of the epicontinental sea (Huff, 1970). The northernmost *Basilosaurus* lived at this time, when an inner to middle neritic environment spread across much of the Gulf Coastal Plain (Rainwater, 1964; Huff, 1970). *Basilosaurus* was most abundant during the middle Priabonian, in the middle to outer neritic zones of the deepening Jackson Sea (Huff, 1970). The last appearance of *Basilosaurus* occurs near the end of the Jackson depositional episode/Jackson transgression (Rainwater, 1964; Galloway, 2008), when portions of the Gulf Coastal Plain were well within the outer neritic zone (Huff, 1970).

The limited number of *Basilosaurus* localities in the fossil record of the Atlantic Coastal Plain prevents a detailed assessment of any connection between *Basilosaurus* abundance and sea level in this region. In general, all *Basilosaurus* localities of the Atlantic Coastal Plain can be chronologically associated with the Jackson transgression of the Gulf Coastal Plain. The maximum landward extent of the Jackson sea was north of the Fall Line (Huddlestun, 1993), and all *Basilosaurus* occurrences are located south of this Jackson shoreline. GSM 1465 lies on the terminal Eocene shoreline, a low sea stand, but because this specimen can only be broadly dated as middle to late Priabonian it is equally possible that it lived in the deeper sea of the middle Priabonian.

Basilosaurus fossils provide evidence that a Mississippi embayment extended as far north as central Tennessee at the Bartonian/Priabonian Boundary (PBDB Collection 32902; Moore and Brown, 1969). The presence of this embayment has been noted in the early Eocene, corresponding to the Upper Wilcox depositional episode (Galloway, 2008), in a middle (Bartonian/Lutetian boundary) and late (Priabonian) Eocene worldwide paleocoastline map (Smith et al., 1994), in the broadly defined "Jackson Time" of the late Eocene (Schuchert, 1929), and in the Jackson Group outcrops reflecting the late Eocene seas (Reel, 1972). To the best of our knowledge, this feature has not previously been shown extending as far north as in our interpretation. The depositional environments of the two northernmost specimens used to extend this feature are nearshore (estuary/bay and coastal indeterminate), so this embayment likely did not extend much farther north than depicted by our composite shoreline.

Summary and conclusions

The temporal range and geographic distribution of *Basilosaurus* in North America suggest that the maximum landward extent of the late Eocene epicontinental sea occurred between the late Bartonian and middle Priabonian. The decline in *Basilosaurus* localities in the late Priabonian suggests that a regional marine regression was occurring by this time. The most notable change to the late Eocene shoreline, based on *Basilosaurus* fossil occurrences, is the northward shift of the Mississippi embayment at the Bartonian/Priabonian boundary.

The environmental distribution of *Basilosaurus* across the southeastern coastal plain provides support for a previously proposed preference of the taxon for middle to outer neritic environments of the epicontinental seas. The absence of *Basilosaurus* fossils in the middle Bartonian, then, is likely related to a marine regression that resulted in a temporary lack of favorable environments for the taxon in the region. Likewise, the relatively few *Basilosaurus* occurrences in the Atlantic Coastal Plain suggests the environment there was less favorable for the taxon than it was over the Gulf Coastal Plain. The difference between regions is likely due to the presence of topographic highs, such as the Ocala Platform in Florida and, potentially, the area surrounding the Gulf Trough in Georgia, that resulted in a shallower epicontinental sea and barriers to dispersal in the east.

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Data availability statement

Data available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.5167386

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