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ARTICLE

THE TRANSITION BETWEEN *CARCHAROCLES CHUBUTENSIS* AND *CARCHAROCLES MEGALODON* (OTODONTIDAE, CHONDRICHTHYES): LATERAL CUSPLET LOSS THROUGH TIME

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ABSTRACT—The teeth of two megatooth macro-predatory shark species (*Carcharocles chubutensis* and *Carcharocles megalodon*; Otodontidae, Chondrichthyes) occur within the Miocene Chesapeake Group of Maryland, U.S.A. Definitive separation between all the teeth of *Carcharocles chubutensis* and *Carcharocles megalodon* is impossible because a complex mosaic evolutionary continuum characterizes this transformation, particularly in the loss of lateral cusplets. The cuspleted and uncuspleted teeth of *Carcharocles* spp. are designated as chronomorphs because there is wide overlap between them both morphologically and chronologically. In the lower Miocene Beds (Shattuck Zones) 2–9 of the Calvert Formation (representing approximately 3.2 million years, 20.2–17 Ma, Burdigalian) both cuspleted and uncuspleted teeth are present, but cuspleted teeth predominate, constituting approximately 87% of the *Carcharocles* spp. teeth represented in our sample. However, in the middle Miocene Beds 10–16A of the Calvert Formation (representing approximately 2.4 million years, 16.4–14 Ma, Langhian), there is a steady increase in the proportion of uncuspleted *Carcharocles* teeth. In the upper Miocene Beds 21–24 of the St. Marys Formation (representing approximately 2.8 million years, 10.4–7.6 Ma, Tortonian), lateral cusplets are nearly absent in *Carcharocles* teeth from our study area, with only a single specimen bearing lateral cusplets. The dental transition between *Carcharocles chubutensis* and *Carcharocles megalodon* occurs within the Miocene Chesapeake Group. Although this study helps to elucidate the timing of lateral cusplet loss in *Carcharocles* locally, the rationale for this prolonged evolutionary transition remains unclear.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The Neogene megatooth shark *Carcharocles megalodon* (Agassiz, 1843) has received much attention from both the media as well as amateur and professional paleontologists (Jordan and Hannibal, 1923; Kent, 1994; Gottfried et al., 1996; Renz, 2002; Yabe et al., 2004; Aguilera et al., 2008; Pimiento et al., 2010; Diedrich, 2013; Pimiento and Clements, 2014; Pimiento and Balk, 2015). The large, serrated teeth of this species, some up to 184 mm (over 7 inches) in vertical height (Renz, 2002), drive this ongoing fascination. Currently, there are several competing models for the evolution and systematic placement of the megatooth sharks within the order Lamniformes (Jordan and Hannibal, 1923; Casier, 1960; Glickman, 1964; Kent, 1994; Applegate and Espinosa-Arrubarrena, 1996; Gottfried et al., 1996; Purdy, 1996; Zhelezko and Kozlov, 1999; Gottfried and Fordyce, 2001; Nyberg et al., 2006; Ehret et al., 2009; Pimiento et al., 2010; Siversson et al., 2015; Shimada et al., 2017; Kent, 2018). Here, we follow Kent (2018) in adopting the '*Carcharocles* model' in which the megatooth sharks represent a separate lineage (†Otodontidae) from that leading to the extant *Carcharodon carcharias* (Lamnidae), thus necessitating their placement in a separate genus (i.e., *Carcharocles*). This model depicts otodontids as a chronospecific lineage from the Paleocene (*Otodus obliquus*) to the Mio-Pliocene (*C. megalodon*; Ehret, 2010; Pimiento and Clements, 2014; Pimiento and Balk, 2015). However, it is worth noting that the otodontid lineage extends into the Cretaceous, with *Cretalamna* as the immediate ancestor of *Otodus* (Siverson, 1992; Zhelezko and Kozlov, 1999; Zhelezko, 2000; Ehret and Ebersole, 2014; Siversson et al., 2015; Ebersole and Ehret, 2018).

Cappetta (2012) argued that the presence of serrations is not a sufficient character to warrant a separate generic assignment, in

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reference to the transition from *Otodus obliquus* to *Carcharocles auriculatus*. Consequently, Cappetta (2012) proposed the use of three subgenera within *Otodus* to define this lineage. The subgenera are *Otodus* (*Otodus*), *Otodus* (*Carcharocles*), and *Otodus* (*Megaselachus*). The first subgenus comprises the non-serrated morphology: *Otodus* (*Otodus*) *obliquus* Agassiz, 1838. The second refers to irregularly serrated teeth with lateral cusplets: *Otodus* (*Carcharocles*) *auriculatus* (Blainville, 1818) and *Otodus* (*Carcharocles*) *angustidens* (Agassiz, 1835). The third refers to regularly serrated teeth with lateral cusplets reduced or absent and a basal root margin that is parallel to the crown-root margin on the labial face: *Otodus* (*Megaselachus*) *chubutensis* (Ameghino, 1901) and *Otodus* (*Megaselachus*) *megalodon*. This scheme is in essence a compromise between Jordan and Hannibal (1923) and Glickman (1964), who originally described the genera *Carcharocles* and *Megaselachus*, respectively. Jordan and Hannibal (1923) erected the genus *Carcharocles* with *C. auriculatus* as the type species, whereas Glickman (1964) proposed that the species *chubutensis* and *megalodon* be placed within the genus *Megaselachus*. However, we do not feel that the transition from *angustidens* to *chubutensis* is as marked as suggested by Cappetta (2012), given that the lineage represents a chronospecies with very gradual morphological change through time. As such, we choose to maintain a single genus for all serrated forms, given that they are easily distinguished from *Otodus obliquus*, and use the genus *Carcharocles* for subsequent taxa (*C. auriculatus* through *C. megalodon*) because the description of *Carcharocles* by Jordan and Hannibal (1923) precedes that of *Megaselachus* by Glickman (1964).

The continually eroding sea cliffs along the western shore of Chesapeake Bay (Calvert Cliffs, Maryland, U.S.A.), and also the intermittent bluffs along some of its tributaries, provide the best exposures of Miocene marine siliciclastic sediments in the Atlantic Coastal Plain of eastern North America (Kidwell, 1984, 1989, 1997; Ward, 1992; Ward and Andrews, 2008; Visaggi and Godfrey, 2010). These sediments of the Chesapeake Group preserve (except for a few hiatal intervals; Fig. 1) a nearly complete record of paleoenvironmental conditions and many of the biotic constituents that inhabited the Salisbury Embayment during parts of the Miocene epoch (approximately 20–8 Ma). The teeth of two otodontid species, *Carcharocles chubutensis* and *Carcharocles megalodon*, are found within the Miocene Chesapeake Group of Maryland, U.S.A. We agree with Kent (2018) that *C. chubutensis*, derived from *C. angustidens*, is the immediate ancestor of *C. megalodon*. Adult *C. chubutensis* teeth retain lateral cusplets (also referred to as lateral denticles or secondary cusps), whereas those of *C. megalodon* do not (Kent, 1994). However, this transition is confounded by the morphological variation associated with the ontogeny of *C. megalodon*, in which juveniles may or may not retain lateral cusplets (Applegate and Espinosa-Arrubarrena, 1996; Pimiento et al., 2010). Further, adult *C. megalodon* may retain lateral cusplets as a vestigial character (Perez et al., 2017). Thus, although the presence of lateral cusplets is regarded as a definitive character for *C. chubutensis*, this trait alone is not sufficient for distinguishing *C. chubutensis* from *C. megalodon* (Kent, 1994).

Experienced collectors know (and a cursory examination of museum collections substantiate the observation) that the cuspleted teeth of *C. chubutensis* become less common as one ascends stratigraphically through these deposits, ultimately becoming replaced by the uncuspleted teeth of *C. megalodon*. However, definitive separation between the teeth of *C. chubutensis* and *C. megalodon* is impossible because a complex mosaic evolutionary continuum appears to characterize the transformation from cuspleted to uncuspleted teeth. Consequently, the cuspleted and uncuspleted teeth of these *Carcharocles* spp. are designated as chronomorphs because they show wide overlap both morphologically and chronologically within the Chesapeake Group in Maryland. These Miocene sediments appear to capture the time interval during which uncuspleted chronomorph *C. megalodon* teeth replaced the cuspleted teeth of *C. chubutensis*.

Hitherto, no attempt has been made to describe in any quantitative way this morphological/evolutionary transformation by providing a census of teeth found in the Chesapeake Group (Kent, 2018). In spite of variations in abundance and distribution (e.g., in situ *Carcharocles* teeth are not known from the Eastover Formation in the collections of either the Calvert Marine Museum or the United States National Museum of Natural History, the Smithsonian Institution), this study seeks to document the transition from a *C. chubutensis* chronomorph-dominated population to one dominated by *C. megalodon*. The analysis is somewhat complicated by the fact that lateral cusps do not occur as an all-or-none character state. Rather, cusplets are variable in their morphology, and truly vestigial cusplets are common (Kimmel and Purdy, 1984; Kent, 1994). Thus, it seems impossible to draw a sharp line between *C. chubutensis* and *C. megalodon*. For this reason, the focus of this study is not on attempting to create a consistent definitional differentiation between these two species, but rather on documenting the changes in the presence or absence of lateral cusplets on *Carcharocles* spp. teeth within the Calvert, Choptank, and St. Marys formations and the duration of this transformation.

GEOLOGICAL SETTING

The Miocene stratigraphy of Calvert Cliffs and southern Maryland has been described in detail by Harris (1893), Shattuck (1904), Gernant (1971), Gibson (1983), Kidwell (1984), Ward and Andrews (2008), Kidwell et al. (2015), Powars et al. (2015), and Vogt et al. (2018) (Fig. 1). The Miocene exposures within our study area (Fig. 2) comprise three formations, in ascending order: the Calvert, Choptank, and St. Marys (Fig. 1). There is consensus that these siliciclastic sediments record an overall shallowing pattern that occurred within the Salisbury Embayment during the Miocene (Gernant et al., 1971; Blackwelder and Ward, 1976; Kidwell, 1984, 1989, 1997; Ward and Strickland, 1985; Ward, 1992; Ward and Andrews, 2008; Visaggi and Godfrey, 2010). Multiple small-scale transgressive-regressive cycles occurred within the aforementioned overall shallowing. Paleoenvironmental complexity, as well as erosional and hiatal surfaces, has been utilized to establish intraformational units. Shattuck (1904) termed these intraformational units 'zones,' which Ward and Andrews (2008) revised and formalized as 'beds.' The Calvert Formation is composed of the Fairhaven Member (which includes Beds 1, 2–3A, Popes Creek Sand, and 3B) and the Plum Point Member (Beds 4–9, 10–11, 12–13, and 14–16A). The Choptank Formation consists of the Drumcliff Member (Beds 16B and 17), the St. Leonard Member (Bed 18), and the Boston Cliffs Member (Bed 19). According to Ward and Andrews (2008), the St. Marys Formation is composed of the Conoy Member (Bed 20), the Little Cove Point Member (Beds 21, 22, and 23), and the Windmill Point Member (Bed 24). Weems advocates keeping the Conoy Member (Bed 20) in the Choptank Formation as originally proposed and defined by Shattuck (1904). Either way, the choice of stratigraphic hierarchy does not affect the results of this study. The inferred ages for each of these beds can be seen in Table 1. The age of Bed 1 remains poorly constrained within the early Miocene, but no teeth of *Carcharocles* have been found there, so the precise age of this bed is not relevant to this study.

MATERIALS AND METHODS

The study area in southern Maryland encompasses an area of approximately 4,000 km^2 (Fig. 2). The fossil shark teeth used in this study were found along Calvert Cliffs (Chesapeake Bay,

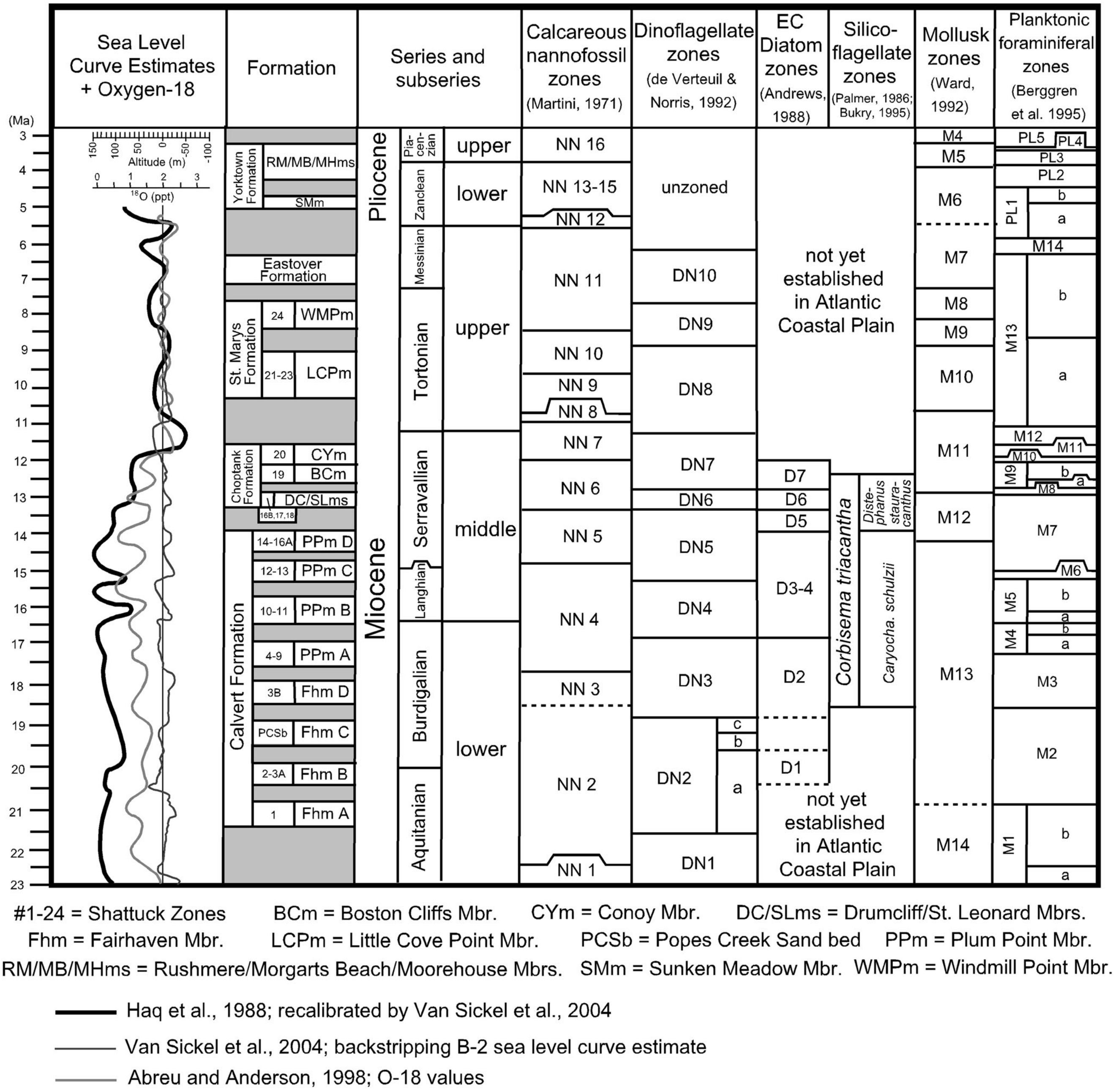

FIGURE 1. Stratigraphic column of the Calvert Cliffs. Age estimates established on the basis of various biostratigraphic indices and the likelihood that the ~405 ka orbital eccentricity cycle controlled depositional cyclicity.

Maryland), as well as along bluffs near Popes Creek (Potomac River, Maryland), Langley Bluff (Chesapeake Bay, Maryland), and Chancellors Point (St. Mary's River, Maryland; Fig. 2). Including the Popes Creek, Langley Bluff, and Chancellors Point localities extends the spatial range of our sample, but more importantly it extends the temporal range of this study. The age of each bed was inferred from Figure 1 and is approximate given the uncertainties that still accompany these stratigraphic subdivisions.

The oldest Maryland Miocene sediments crop out along Lyons Creek and nearby portions of the Patuxent River (Zones 1, 2, and 3A of Shattuck, 1904). The Eocene Nanjemoy Formation underlies the Miocene Calvert Formation at both Lyons Creek and Popes Creek and provides a lower boundary and convenient starting point for the morphological differences documented here. There is both a depositional and a major temporal hiatus between the Eocene Nanjemoy Formation and the Miocene Calvert Formation at both localities. A decline in eustatic sea level during the Oligocene accounts for the absence of sediments from that time (Edwards and Powars, 2003; Browning et al., 2009; Edwards et al., 2009). *Carcharocles chubutensis* and *C. megalodon* teeth are not found in the Nanjemoy Formation. However, teeth from the otodontid species *Carcharocles auriculatus* (Fig. 3A), a predecessor in the *C. chubutensis* and *C. megalodon* lineage (Cappetta, 1987; Kent, 1994), are present and provide an outgroup to anchor the polarity of the morphological change seen during the Miocene.

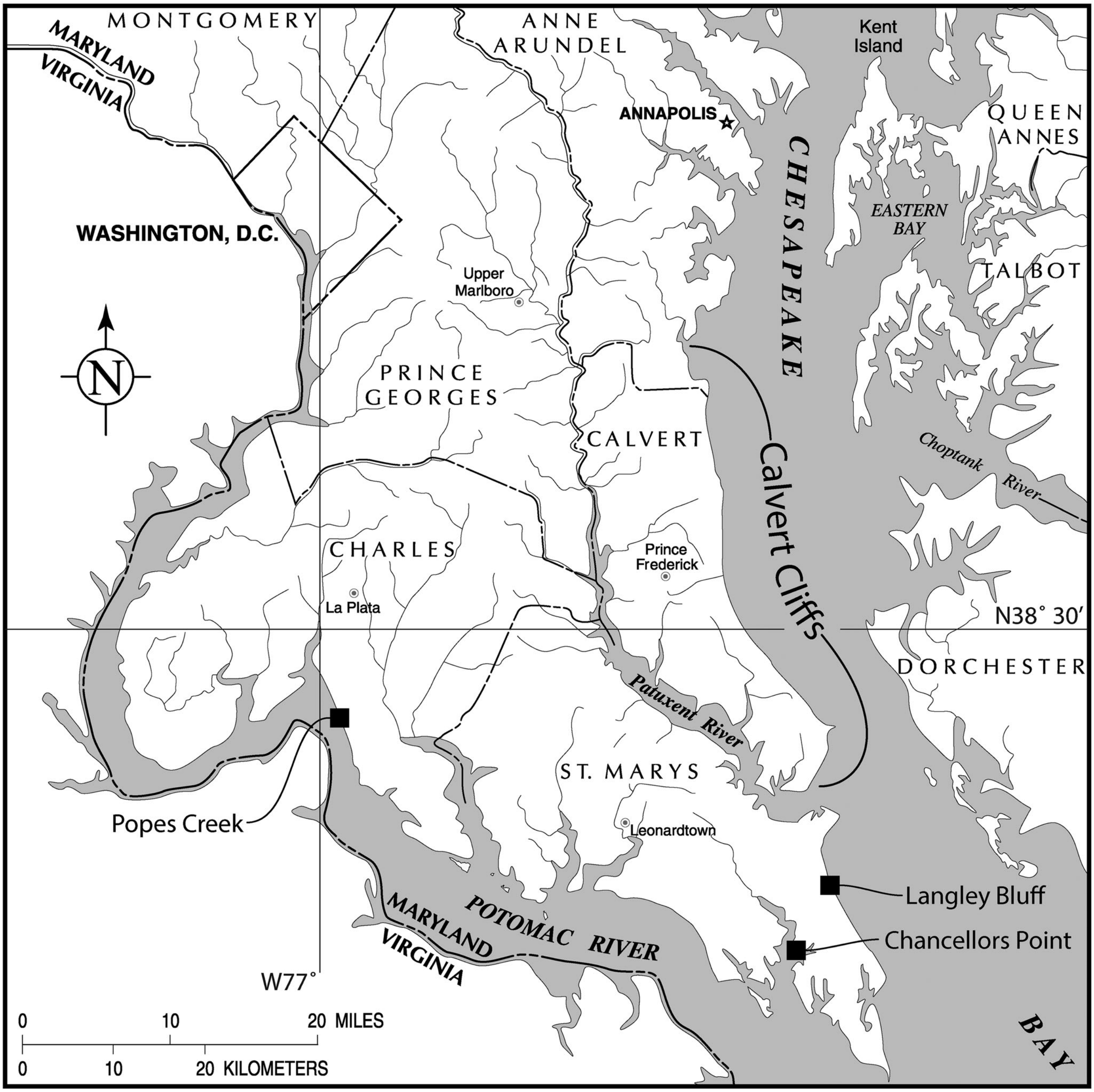

FIGURE 2. Map of the northern Chesapeake Bay region of Maryland and Virginia showing the localities incorporated in this study: Calvert Cliffs, Popes Creek, Langley Bluff, and Chancellors Point. Modified from Visaggi and Godfrey (2010).

All the teeth used in this study were found either in situ or on beaches with inferable stratigraphic context. In other words, the teeth were sourced directly from the cliffs, in fallen blocks from the cliffs for which bed origins were unequivocal, or as beach float from localities that have limited exposures of only specific beds. Beaches that have inferable stratigraphic context include Popes Creek (Woodstock Member of the Nanjemoy Formation and Popes Creek Sand plus Bed 3B of the Calvert Formation), Fairhaven (Bed 3B, Calvert Formation), Driftwood Beach (Beds 21–23, St. Marys Formation), and Chancellors Point (Bed 24, St. Marys Formation). The limited stratigraphic exposures at these sites reasonably constrain the source of the teeth found therein. Time bins for cusplet presence versus absence (P/A) over time were established based on these specimens, which have unequivocal or reasonably inferable Miocene origins in specific intraformational units (beds) as established by Shattuck (1904) and updated by Ward and Andrews (2008).

The teeth used in this study are reposited physically at the Calvert Marine Museum (CMM) and the National Museum of Natural History of the Smithsonian Institution (USNM), or digitally through the myFOSSIL online database (www.myfossil.org) (list of specimens used in this study is provided in Table S1). The data set was limited to well-preserved teeth for which stratigraphic context is known. In order to assess cusplet P/A and

TABLE 1. The beds as they were grouped for this study, with the inferred time duration for each.

Formation	Bed(s)	Estimated age (Ma)	Total	TUC	Cusplet P/A	TCH	TLM
Nanjemoy (upper Woodstock Member)		50.5–48	9	8	8 (100%)	6	3
Calvert	2–3B	20.2–19.1 18.4–17.6	48	38	33 (86.8%)	17	22
Calvert	4–9	17.5–17	7	5	4 (80%)	2	4
Calvert	10–11	16.4–15.6	43	35	18 (51.4%)	22	21
Calvert	12–13	15.5–14.6	178	130	48 (36.9%)	81	95
Calvert	14–16A	14.5–14	34	24	8 (33.3%)	11	10
Choptank	19	12.6–12.2	2	2	0 (0%)	1	1
St. Marys	21–23	10.4–9	36	28	1 (3.6%)	24	25
St. Marys	24	8.5–7.6	2	1	0 (0%)	1	1
Total			359	271 (75%)	120 (44%)	165 (61%)	179 (50%)

Total refers to the total number of in situ teeth available. TUC refers to the total number of teeth that can be assessed on the basis of lateral cusplet presence versus absence. TCH refers to the total number of teeth that are well enough preserved to measure crown height (only teeth that could be assessed for cusplet presence versus absence were included in TCH). Cusplet P/A refers to the total number of teeth with lateral cusplets. TLM refers to the number of in situ teeth that potentially could be used in a landmarks study. Detailed specimen data is available in Table S1.

size, the junction between the enameloid serrated cutting edge and the tooth root had to be intact, at least on one side. Within the study area, *C. chubutensis* and *C. megalodon* cusplet P/A forms a morphological continuum. Consequently, determining cusplet P/A was somewhat subjective when it came to transitional teeth that may not have been truly cuspleted, because these teeth still vestigially retain this character (Fig. 3). In an attempt to approach objectivity, the mathematical definition of a cusp was used (i.e., a point where two curves intersect). Thus, if there was no pronounced ‘point’ at the cutting edge/root junction, then the tooth was deemed to be uncuspleted. Also, if the ‘cusplet’ was reduced to a few pronounced serrations, then the tooth was recorded as uncuspleted, reflecting the vestigial nature of that character. In spite of our efforts to objectively assess cusplet P/A, scoring teeth thus posed a challenge because of the gradational expression of this feature.

All teeth that met the requirements are recorded in Table 1. Among the 359 teeth with sufficient stratigraphic information, only 271 (75%) are preserved well enough to determine cusplet P/A. The percentage of cuspleted versus uncuspleted teeth through time is shown in Figure 4.

In addition to cusplet P/A, whether a tooth would be suitable for a two-dimensional (2D) landmark analysis in the future was also recorded. Of the 359 teeth initially recorded, only 179 (50%) are preserved well enough to reliably place landmarks (Table 1).

A traditional morphometric approach was used to assess whether or not the P/A of cusplets is related to crown height (CH) or the crown height to crown width ratio (CH:CW). Measurements of every tooth that could be assessed on the basis of cusplet P/A were taken (Table S1). However, if the crown was broken in a way that would require inferring the CH or CW, then the tooth was not included for this portion of the study. These stipulations further limited the data set available for this portion to 165 teeth for CH alone and 156 teeth for both CH and CW. Because there is currently no standard (or metric) for determining tooth position (which would be necessary to identify position in the jaw or estimate the age of the shark), this analysis only sought to find a relationship between cusplet P/A and CH as well as cusplet P/A and CH:CW, rather than a relationship between cusplet P/A and ontogenetic development (age) or cusplet P/A and tooth position within the jaw.

Abbreviations

Institutional Abbreviations—**CMM**, Calvert Marine Museum, Solomons, Maryland, U.S.A.; **USNM**, National Museum of Natural History of the Smithsonian Institution, Washington, D.C., U.S.A.

Anatomical Abbreviations—**CH**, crown height; **CW**, crown width; **CH:CW**, crown height to crown width ratio; **P/A**, presence versus absence; **SHH**, sonic hedgehog pathway; **TL**, total body length.

RESULTS

Figure 4 shows the results of the cusplet P/A analysis. The highly variable numbers of teeth from the various bed bins is attributed to varying paleoenvironments and preservational and/or collecting bias (Visaggi and Godfrey, 2010).

All *C. auriculatus* teeth from the lower Eocene Woodstock Member of the Nanjemoy Formation are cuspleted (Fig. 4, left-most column). In the lower Miocene Beds 2–9 of the Calvert Formation (Shattuck Zones 2–9, an interval of approximately 3.2 million years, 20.2–17 Ma, Aquitanian and Burdigalian), both cuspleted and uncuspleted teeth are present but cuspleted teeth predominate, constituting approximately 86% of the *Carcharocles* spp. teeth represented in our sample. However, in the middle Miocene Beds 10–16A (Shattuck Zones 10–16, an interval of approximately 2.4 million years, 16.4–14 Ma, Langhian), there was a steady increase in the proportion of uncuspleted *C. megalodon* teeth (Fig. 4). If the tooth sample accurately reflects the time of morphological transition, then most of the change from a cuspleted *C. chubutensis* chronomorph population to an uncuspleted-dominated *C. megalodon* chronomorph population took place over a period of about 2.4 million years (from approximately 16.4–14 Ma; Fig. 4). *Carcharocles megalodon* teeth lacking cusplets are known from the lowermost beds of the Calvert Formation, whereas only a single tooth with cusplets was known in our sample from the St. Marys Formation (Fig. 4, right-most columns). The paucity of *Carcharocles* spp. teeth among our samples from the Choptank Formation precludes assessing cusplet P/A in this formation, given that only two teeth have been recovered. Beginning at approximately 10.4 Ma, lateral cusplets are nearly absent in *C. megalodon* teeth from the Tortonian St. Marys Formation in our study area. It is worth noting that the only tooth bearing a lateral cusplet from the St. Marys Formation is a posterior tooth (CMM-V-6007).

DISCUSSION

From a macroevolutionary perspective, the gradual progression in tooth morphology from the Paleocene *Otodus obliquus* to the Mio-Pliocene *Carcharocles megalodon* could be linked to a shift in diet and feeding style. Over this roughly 50-million-year interval, teeth of this lineage shift from, arguably, a tearing-grasping type to a cutting-dominant dentition. Teeth of *Otodus obliquus* have a complete cutting edge lacking serrations,

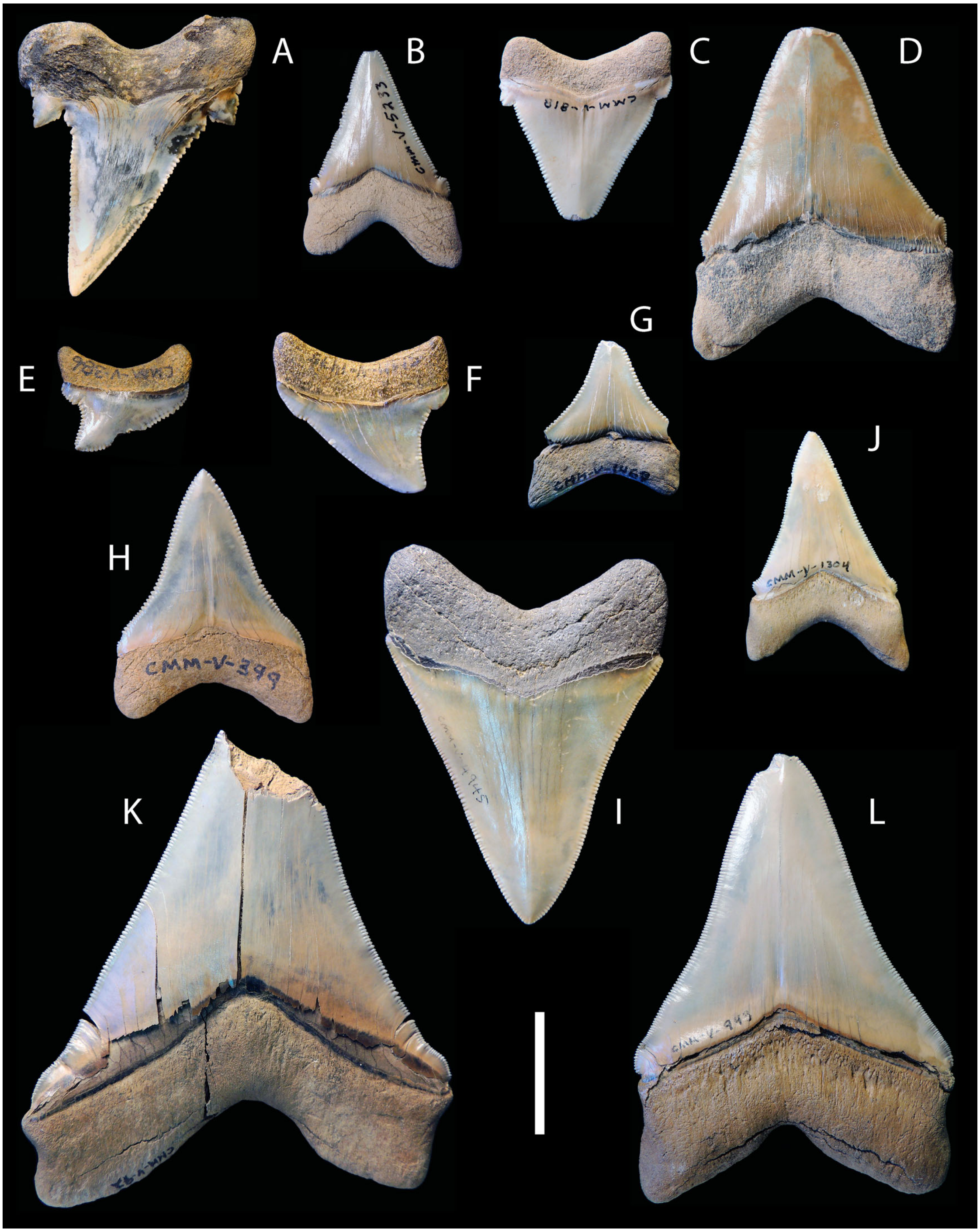

FIGURE 3. *Carcharocles* spp. teeth, all in labial view. **A**, CMM-V-4933, *C. auriculatus*, Eocene, Nanjemoy Formation, Popes Creek, Charles County, Maryland, U.S.A. Collected by W. Counterman. **B**, CMM-V-5233, *C. chubutensis*, Miocene, Calvert Formation, Popes Creek, Charles County, Maryland, U.S.A. Collected by J. Osborne. **C**, CMM-V-818, *C. chubutensis*, Miocene, Calvert Formation, Popes Creek, Charles County, Maryland, U.S.A. Collected by S. Bentley. **D**, CMM-V-86, *C. chubutensis*, Miocene, Calvert Formation, Popes Creek, Charles County, Maryland, U.S.A. Collected by D. Bohaska and N. Riker. **E**, CMM-V-386, *Carcharocles* sp., distal lateral cusplet present, mesial one not. Miocene, Calvert Formation, Bed 12, Calvert County, Maryland, U.S.A. Collected by W. Ashby. **F**, CMM-V-1475, *Carcharocles* sp., distal lateral cusplet present, mesial one reduced. Miocene, Calvert Cliffs, Calvert County, Maryland, U.S.A. Collected by W. Holliman. **G**, CMM-V-1469, *Carcharocles* sp., lateral cusplet presence uncertain. Miocene, Scientists Cliffs, Calvert County, Maryland, U.S.A. Collected by W. Holliman. **H**, CMM-V-399, *C. megalodon*, Miocene, Calvert Formation, Bed 12, South of Parkers Creek, Calvert County, Maryland, U.S.A. Collected by W. Ashby. **I**, CMM-V-4945, *C. megalodon*, Miocene, Calvert Formation, North of Parkers Creek, Calvert County, Maryland, U.S.A. Collected by J. Nance. **J**, CMM-V-1304, *C. chubutensis*, Miocene, Calvert Formation, Popes Creek, Charles County, Maryland, U.S.A. Collected by D. Bohaska. **K**, CMM-V-92, *C. megalodon*, Miocene, Calvert Formation, Bed 12, South of Parkers Creek, Calvert County, Maryland, U.S.A. Collected by W. Ashby. **L**, CMM-V-943, *C. megalodon*, Miocene, Calvert Formation, Bed 14, Governor Run, Calvert County, Maryland, U.S.A. Collected by M. Gottfried. Scale bar equals 2 cm.

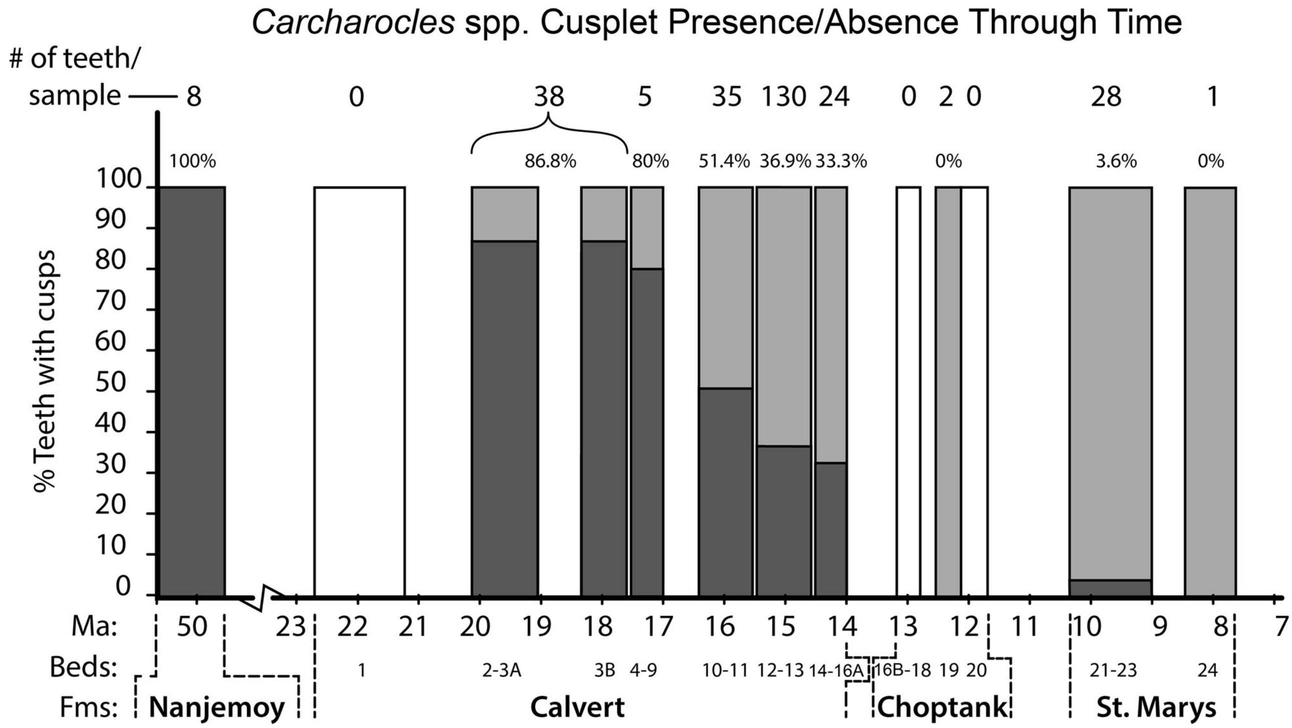

FIGURE 4. Histogram depicting the percentage of cuspleted *Carcharocles* spp. teeth through time. The width of each bar reflects the time elapsed. The light gray represents percent uncuspleted, and the dark gray represents percent cuspleted. The percent number above each bar (time bin) is the percentage of cuspleted teeth in that sample. The larger number above the percent number is the total tooth sample size available that could be assessed in terms of cusplet presence versus absence (TUC) for each particular group of beds (time bins).

a robust root and crown, and broad, triangular lateral cusplets. In stark contrast, teeth of *Carcharocles megalodon* have fully serrated cutting edges, a less robust root, and lack lateral cusplets.

The Eocene species, *Carcharocles auriculatus*, represents the first of this lineage to have a fully serrated cutting edge (Fig. 3A), which is coincident with the origin of cetaceans in the early Eocene (Uhen, 2010). Although, locally, serrated *C. auriculatus* teeth precede the appearance of cetaceans, given that archaeocetes first occur in the Chesapeake Bay region in the middle Eocene Piney Point Formation (Weems et al., 2011; Godfrey et al., 2013). Thus, at this early evolutionary stage, it seems more plausible that *C. auriculatus* was feeding primarily on large teleosts and/or other chondrichthyans. No specimens of *Carcharocles angustidens* are included in this study, but it is worth noting that in this Oligocene species, serrations become more uniform and the root begins to flatten (Kent, 1994, 2018); this is coincident with the origin of mysticetes in the early Oligocene (Fordyce, 1980; Uhen, 2010). Further, over the course of this evolutionary progression from *O. obliquus* to *C. megalodon*, there is an apparent increase in maximum overall tooth size, although no formal study has been conducted to document this. Cetaceans also exhibit an increase in body size beginning in the Oligocene (Pyenson and Sponberg, 2011; Slater et al., 2011), coincident with the apparent increase in *Carcharocles* tooth size. A number of studies have documented evidence of predation on cetaceans by *Carcharocles megalodon* (Deméré and Cerutti, 1982; Purdy et al., 2001; Renz, 2002; Godfrey and Altman, 2005; Aguilera et al., 2008; Kallal et al., 2010; Collareta et al., 2017; Godfrey et al., 2018; Kent, 2018), which leaves little doubt that the development of tooth morphology in the *Carcharocles* lineage is closely tied to the evolution of cetaceans, but this does not fully explain the role of lateral cusplets.

The fundamental paper on shark tooth biomechanics by Frazzetta (1988) outlined two functions for lateral cusplets. One function would be enhancing grasping ability, which Frazzetta (1988) noted is more typical of slender, lingually recurved cusplets (e.g., *Odontaspis*). The other possible function is to fill the tooth gap between the widely spaced teeth, a character observed in many lamniform sharks, which is more typical of a broad, triangular morphology (e.g., *O. obliquus* and *C. auriculatus*). The tooth gap in chondrichthyan dentitions occurs as a result of the tooth formation process in lamniform sharks known as single file addition (Smith et al., 2012). Filling this tooth gap would prevent small food items from getting trapped between the teeth, which could help to retain food and potentially reduce the likelihood of gum or tooth pathology. If this were indeed the function, the loss of lateral cusplets could actually be viewed as being counterproductive.

Given that lateral cusplets are characteristically reduced and rounded in *C. chubutensis* (Fig. 3), it could be argued that lateral cusplets had already been rendered non-functional by the early Miocene. If this is the case, it is difficult to rationalize a selective pressure that would have driven this final stage in the morphological development of the *Carcharocles megalodon* dentition. However, it would help to explain why this transition from cuspleted to uncuspleted teeth was drawn out over roughly 12.6 million years (20.2–7.6 Ma). A similar trend was observed in the transition from *Cretoxyrhina vraconensis* (Zhelezko, 2000) to *Cretoxyrhina mantelli* (Agassiz, 1843), in which anterior teeth devoid of cusplets appear at the Albian–Cenomanian boundary, yet teeth bearing cusplets can still be observed into the beginning of the Coniacian (Siverson et al., 2013). However, no explanation has been suggested as to what drove the loss of lateral cusplets.

The greatest rate of change in terms of lateral cusplet P/A was in Shattuck Zones 10–16, an interval of approximately 2.4 million years, 16.4–14 Ma. This interval of time is coincident with the Middle Miocene Climatic Optimum (MMCO; Zachos et al., 2001, 2008; Vogt and Parrish, 2012), and a peak not only in *C. megalodon* abundance (Fig. 4) but in chondrichthyan taxa in general (Visaggi and Godfrey, 2010), as well as in cetaceans (Uhen and Pyenson, 2007; Uhen, 2010). This increase in *Carcharocles* tooth abundance may imply an increase in the local population of *C. megalodon*, which would have required increased rates of reproduction and, subsequently, increased genetic diversity. Although this peak in abundance is coeval with the MMCO, the variations in abundance could be attributed to a sampling bias, given that there has been greater collecting effort in localities that expose Shattuck Zones 10–16.

Yet another consideration for the loss of lateral cusplets is the gene expression involved in odontogenesis. There is significant research indicating that tooth development in all vertebrates over the past 450 million years is linked to the sonic hedgehog (SHH) pathway (Smith et al., 2009; Maisey et al., 2013; Rasch et al., 2016). During the embryonic development of the catshark (*Scyliorhinus*), a superficial layer of epithelial cells makes up an odontogenic band from which teeth form (Smith et al., 2009; Rasch et al., 2016; Seppala et al., 2017). The SHH pathway and enamel knot dictate the position and shape of a tooth within this odontogenic band. Rasch et al. (2016) found that teeth in *Scyliorhinus* are simple in shape and progressively become more complex as the individual approaches adulthood. Further, tooth formation is initiated in the anterior of the jaw and progresses posterolaterally, with greater complexity (i.e., more lateral cusplets) in lateral positions. Perhaps the gradual loss of lateral cusplets in *Carcharocles* documented herein is not related to function, but rather due to this feature being lost earlier during ontogeny as a result of changes in the SHH pathway. The presence of both tooth morphologies within an individual can be seen in Figure 5, which supports the hypothesis that lateral cusplet presence is linked to ontogeny.

In *Carcharodon carcharias*, lateral cusplets first develop on the distal edge of the principal cusp in the mid-term embryo and then on both sides of the principal cusp in the full-term embryo (Tomita et al., 2017). Lateral cusplets are retained after birth, but eventually lost during ontogeny (Hubbell, 1996). Bemis et al. (2015) have argued that lateral cusplets in *C. carcharias* should be termed ‘serrational cusplets’ because they form as part of a series of serrations associated with the principal cusp. However, in other lamniforms, lateral cusplets form independent of the principal cusp. Thus, the loss of lateral cusplets/serrational cusplets in *C. carcharias* may not be analogous to that of *Carcharocles megalodon*; however, in both instances, there is a clear link to ontogeny.

Taking into account the overall shift in tooth morphology from *O. obliquus* to *C. megalodon*, it is apparent that there is a long-term transition in tooth functional morphology. Evidence of predation on cetaceans by *Carcharocles* spp. (Purdy et al., 2001; Aguilera et al., 2008; Collareta et al., 2017; Godfrey et al., 2018; Kent, 2018) and the conspicuous increase of body size in cetaceans since the Oligocene (Pyenson and Sponberg, 2011; Slater et al., 2011, 2017) supports the idea of an evolutionary driver for the overall shift in tooth functional morphology from *Otodus obliquus* to *Carcharocles megalodon*. However, the reduced and rounded lateral cusplets of *C. chubutensis* would likely not have functioned for either grasping or filling of a tooth gap, which makes it difficult to evoke an evolutionary driver for the loss of lateral cusplets from *C. chubutensis* to *C. megalodon*. Rather, the gradual loss of lateral cusplets may be more closely tied to changes in the SHH pathway, resulting in the more derived morphology lacking lateral cusplets occurring earlier during ontogeny. Regardless, the explanations for why lateral cusplets were gradually reduced, and eventually lost entirely, remain speculative.

Is the Observed Trend Real?

There are three possible explanations for why the results (Fig. 4) indicate that there is a gradual loss of lateral cusplets in this lineage. The first would be that our sampling has captured the actual rate of this morphological transition in the *Carcharocles* lineage. The other two explanations would be results of sampling bias: the first of which would be an uneven sampling of teeth by age of individual sharks and the second would be an uneven sampling of teeth by position in the jaw. Applegate and Espinosa-Arrubarrena (1996) and Pimiento et al. (2010) have proposed that juvenile *C. megalodon* retained lateral cusplets but then lost them during ontogenetic development. It is also possible that *Carcharocles* spp. lost lateral cusplets at different rates in different parts of its dental sequence (Figs. 3 and 5). If the various beds have a predominance of either juveniles versus adults or anterior versus posterior teeth, then the results could potentially not reflect the evolutionary transition that is herein proposed.

The reflection of phylogeny in the ontogeny of an organism is the basis of evolutionary developmental biology (Hall, 2012). Thus, the loss of lateral cusplets during individual development (i.e., ontogeny) may reflect the evolutionary history (i.e., phylogeny) of a species. During the development of modern mysticetes, fetal whales develop tooth buds in utero, then transition to teeth and baleen, and finally only baleen, all before birth (Ishikawa and Amasaki, 1995; Ishikawa et al., 1999; Deméré et al., 2008). This developmental progression is thought to reflect the evolutionary transformation that occurred in the mysticete whale lineage (Deméré et al., 2008). Similarly, the loss of lateral cusplets throughout the ontogeny of *C. megalodon* may also be an atavistic character that illustrates the evolutionary progression within the *Carcharocles* lineage.

Alternatively, a tooth position bias could have obscured our data set, given that the P/A of lateral cusplets is more complicated in posterior positions. In posterolateral tooth positions, as teeth become increasingly more asymmetric, lateral cusplets on the mesial and distal edges become disproportionate. Specifically, the cusplet on the distal edge becomes more pronounced than that of the mesial edge (Fig. 3E, F). This could be attributed to a number of things: tooth size, tooth shape, or replacement rate. Personal observations of modern dentitions of *Carcharodon carcharias* in the private collection of Gordon Hubbell revealed that posterior tooth positions are more crowded and retain juvenile characteristics longer relative to anterior teeth. This may explain why the posterior tooth found in the upper Miocene St. Marys Formation still retained a lateral cusplet.

Purdy et al. (2001) also noted the disproportionate presence of lateral cusplets in an associated dentition of *Carcharocles chubutensis* (USNM 411881, referred to as *Carcharodon subauriculatus* by Purdy et al., 2001). This specimen lacks lateral cusplets in anterior tooth positions but retains well-developed cusplets in posterolateral tooth positions. Purdy et al. (2001:figs. 35, 36) provided a partial reconstruction of this dentition, but it is unclear why they chose to omit the majority of the dentition. Further, the reconstruction is made under the assumption that this dentition belonged to an ancestral species of the living great white; however, many researchers now consider *Carcharocles* and *Carcharodon* to belong to separate families: Otodontidae and Lamnidae, respectively. As such, a novel reconstruction of the first tooth rows is provided in Figure 5 to better illustrate the variation in lateral cusplet presence relative to tooth position.

The difficulty in determining if a bias related to either ontogeny or tooth position exists can be attributed to the necessity of identifying isolated teeth to their original tooth position. Based on the

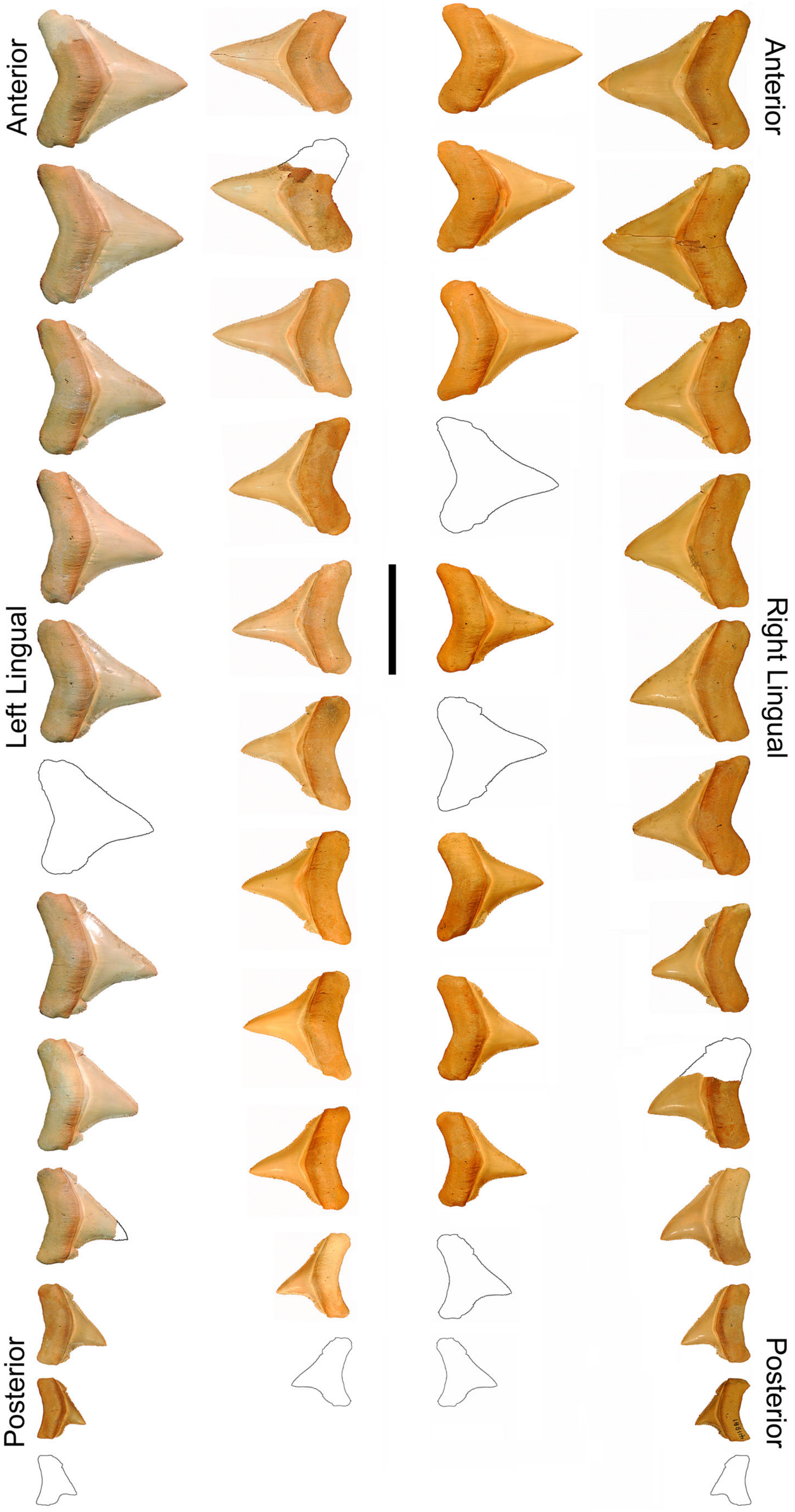

FIGURE 5. *Carcharocles chubutensis*, USNM 411881, dentition in lingual view from the Pungo River Formation of the Lee Creek Mine in Aurora, North Carolina. Outlines are used to denote missing or broken teeth. Scale bar equals 5 cm.

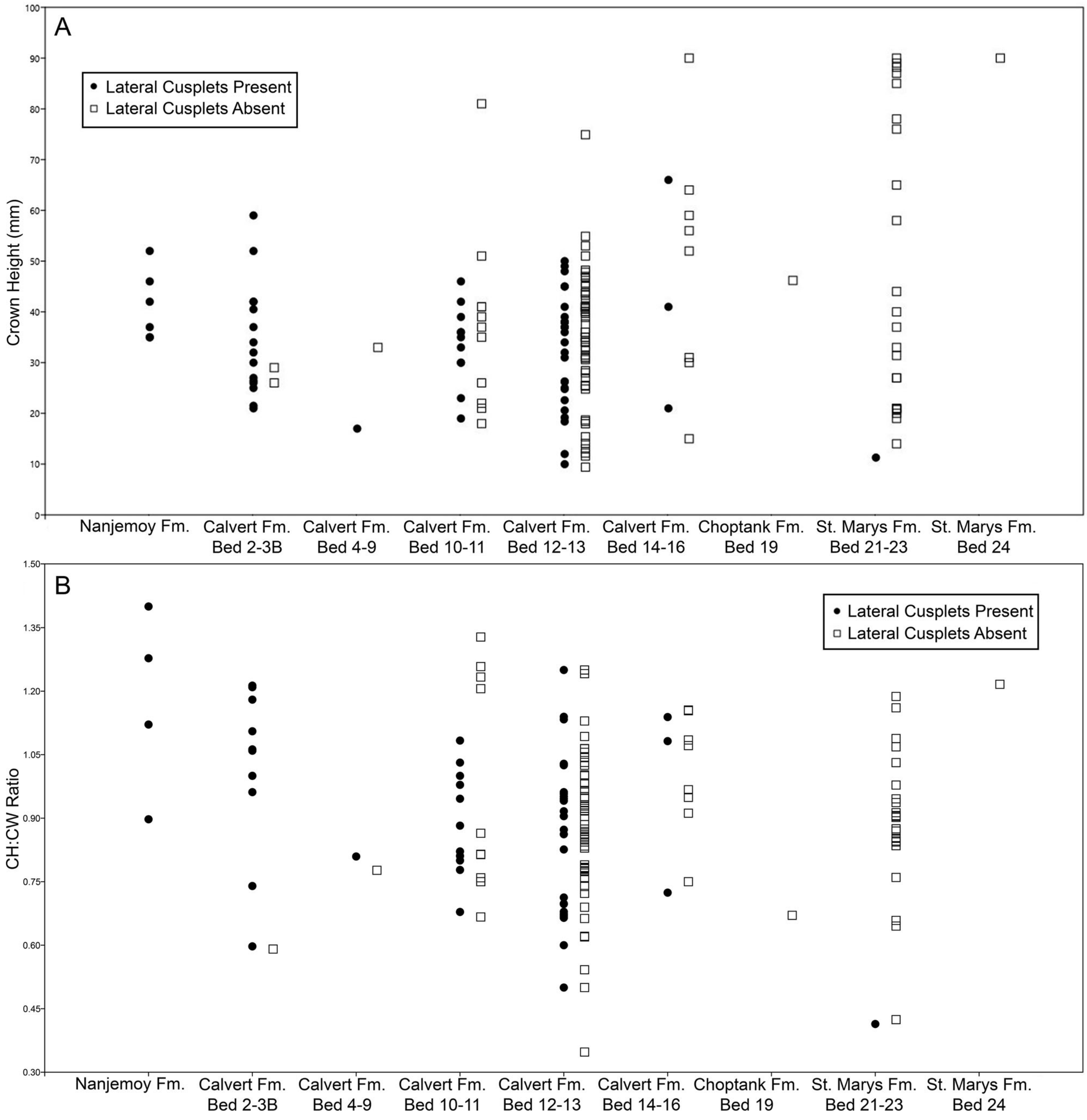

FIGURE 6. **A**, crown height (CH) in mm plotted against stratigraphic origin. **B**, crown height to crown width ratio (CH:CW) plotted against stratigraphic origin. Black circles (left) mark teeth that have lateral cusplets, and open squares (right) indicate teeth without lateral cusplets.

few known partially associated *C. megalodon* dentitions and the use of the *C. carcharias* dentition as a rough analogue, it is possible to estimate the relative tooth position within a dentition (Gottfried et al., 1996; Shimada, 2003; Pimiento et al., 2010). Shimada (2003) developed a series of linear equations for every tooth position that relate crown height (CH) to total body length (TL) based on measurements of modern dentitions of *C. carcharias*. Gottfried et al. (1996) proposed that life stages of *C. megalodon* would correspond to specific body length ranges: neonates (<4 m TL), juveniles (4–10.5 m TL), and adults (>10.5 m TL). However, without an established metric for determining tooth position of isolated teeth, any effort to determine body length or life stage will be highly subjective and likely result in varying interpretations between researchers. Thus, rather than attempt to determine tooth position or life stages, we first treat CH as a proxy for both (Fig. 6A).

Figure 6A shows the CH distribution observed in teeth bearing and lacking lateral cusplets, respectively, from each of our stratigraphic bins. At first glance, it appears that the maximum crown height is larger for teeth lacking lateral cusplets. However, it should be noted that there are two teeth, one tooth from Bed 12 (CMM-V-92; Fig. 3K) and one from Bed 14 (USNM 392158; Fig. 3L), that would have a CH exceeding 90 mm. Both have lateral cusplets but are not included in Figure 6 due to their

TABLE 2. Crown height to crown width ratios (CH:CW) derived from teeth in this study and three associated dentitions.

Category	Sample size	Min	Max	Mean
Cuspleted (this study)	57	0.41	1.40	0.92
Uncuspleted (this study)	99	0.35	1.33	0.90
Anterior (associated sets)	29	0.73	1.17	0.99
Lateral (associated sets)	43	0.71	1.08	0.87
Posterior (associated sets)	23	0.36	0.80	0.61

Teeth utilized in this study were separated into two categories: those with lateral cusplets and those lacking lateral cusplets. Teeth from the three associated dentitions were separated into three categories: anterior (A1–A3 and a1–a3), lateral (L1–L5 and l1–l5), and posterior (L6–L9 and l6–l8). For each category, the number of teeth available (sample size), minimum, maximum, and mean CH:CW are reported.

partially broken crown and slightly pathological cutting edge. As such, the overlapping CH ranges for teeth with and without lateral cusplets suggests that sampling bias by individual age or tooth position is unlikely.

Given that CH is strongly linked to ontogeny and tooth position, to remove, or at least reduce, the influence of ontogeny we use the ratio of CH to CW as a more direct proxy for tooth position (Fig. 6B), although it should be noted that CH:CW may also vary during ontogeny. Pimiento et al. (2010) reported measurements for two associated dentitions of *C. megalodon*, a juvenile from the Bone Valley region in Florida and an adult from the Lee Creek Mine in Aurora, North Carolina. The presumed status as a juvenile and adult, respectively, are based upon the life stages proposed by Gottfried et al. (1996). Both specimens are from the private collection of Dr. Gordon Hubbell in Gainesville, Florida. The adult from Aurora has since been donated to the Florida Museum of Natural History (UF 311000), and 3D scans are freely available on morphosource.org. The juvenile from Bone Valley is technically still in the possession of Dr. Hubbell; however, the specimen is available for study by researchers and reproductions of this dentition can be purchased from Bone Clones, Inc. (CH-31-46P). Measurements from these two dentitions, as well as USNM 411881 shown in Figure 5, were used to determine CH:CW ranges from anterior, lateral, and posterior tooth positions (Table 2). The overlapping ranges between anterior and lateral positions and lateral and posterior positions indicate that CH:CW does not directly correspond to tooth position but can serve as an approximation.

Figure 6B shows the distribution of CH:CW observed in teeth bearing and lacking lateral cusplets, respectively, from each of our stratigraphic bins. One hypothesis for the loss of lateral cusplets in *Carcharocles* is that they were first lost in the anterior tooth positions, which is supported by the associated dentition in Figure 5. Therefore, a sampling bias related to tooth position could obscure our results in Figure 4. However, the range and distribution of CH:CW in cuspleted and uncuspleted teeth are nearly identical (Figs. 6B and S1), which indicates that our sample is not biased by tooth position.

Finally, the observed trend of a gradual loss of lateral cusplets in *Carcharocles* from 20.2 to 7.6 Ma represents a local phenomenon and cannot be considered representative of global rates of change. *Carcharocles megalodon* teeth bearing lateral cusplets and/or vestigial characters possibly have been observed in localities exposing younger strata outside the study area addressed herein, if the ages given for these localities are accurate. Pimiento et al. (2010, 2013) noted lateral cusplets in *C. megalodon* teeth from the middle to upper Miocene Gatun Formation of Panama and used this character as supporting evidence for the claim that the site represents a nursery habitat for *C. megalodon*. Perez et al. (2017) reported a single *C. megalodon* tooth from the upper Miocene Chucunaque Formation (~10–9.5 Ma) of Panama that exhibited a vestigial cusplet. These observations of lateral cusplets in younger deposits makes it imperative that we consider the results of this study in a local context.

CONCLUSION

The primary goal of this study is to document an evolutionary transition over geological time by determining the timing and rate at which lateral cusplets were lost in the *Carcharocles chubutensis/megalodon* chronospecies complex. Lateral cusplets appear to have been lost during deposition of the Burdigalian–Langhian portion of the Calvert Formation, although this transition may have continued somewhat longer into the Serravallian Choptank Formation and/or Tortonian St. Marys Formation. This shift in tooth morphology appears to represent the culmination of a long-term evolutionary trend that resulted in an uncuspleted, broad-bladed, serrated tooth ideal for preying upon marine mammals. It is important to keep in mind that the timing of this transition should be considered in a regional context. A larger local sample size and studying the same phenomenon elsewhere in the world would likely shed additional light on this remarkable lineage of macro-predatory sharks. Further, more intensive exploration of the modern ecological analogue, *Carcharodon carcharias*, will be necessary in order to procure a more detailed narrative of *Carcharocles*'s bionomics.

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