A megatoothed shark (*Carcharocles angustidens*) nursery in the Oligocene Charleston Embayment, South Carolina, USA

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ABSTRACT

Many extant sharks are cosmopolitan as adults but inhabit nursery areas as youngsters - often shallow, dynamic ecosystems with abundant prey for neonates and juveniles. Megatoothed sharks (Otodontidae) were the largest sharks of all time, and nursery areas have been demonstrated for *Carcharocles megalodon* in the Miocene of Panama, Spain, Florida, and Maryland. An earlier study hypothesized a nursery area for *Carcharocles angustidens* in the upper Oligocene (23-25 Ma) Chandler Bridge Formation of Charleston, South Carolina. We tested this by reporting and analyzing two collections (n=127) dominated by small teeth of *C. angustidens* from the Chandler Bridge Formation and some teeth from the underlying lower Oligocene (29-26.57 Ma) Ashley Formation (n=9). Correcting for tooth position, published body length estimation equations yielded body length estimates of 1.5-6.5 m for most individuals. Size-based assignment to age classes (neonates, juveniles, adults) is modified from the larger *C. megalodon* and scaled based on the largest available specimens of *C. angustidens*, reported herein. These assemblages are dominated by small individuals (juveniles and neonates) and include few adults. The Oligocene Charleston embayment therefore represents the first documented paleo-nursery area for *C. angustidens*.

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INTRODUCTION

Otodontid sharks are giant extinct predatory sharks found worldwide from the Cretaceous through the Pliocene, including the prominent *Carcharocles* lineage terminating with the extinction of *Carcharocles megalodon* 3.5 Ma (Gottfried et al., 1996; Purdy, 1996; Purdy et al., 2001; Kent, 2018). *Carcharocles* evolved from *Otodus obliquus* during the Eocene through the development of serrations, an adaptation for feeding upon newly evolved marine mammals with thick blubber (Frazzetta, 1988; Abler, 1992), which first became globally widespread during the middle Eocene. A megatoothed shark chronospecies from the Oligocene, *Carcharocles angustidens*, is found worldwide (Atlantic Coastal Plain, USA; Belgium; France; Japan; Ecuador; Australia; New Zealand). Adult size of 8-9 m body length was estimated for *C. angustidens*, based on a partial skeleton from New Zealand (Gottfried and Fordyce, 2001). Teeth of *C. angustidens* are triangular, serrated, bear serrated lateral cusplets, and a robust U-shaped root with triangular lobes (Gottfried and Fordyce, 2001). Bite marks on fossil marine mammal bones are frequently attributed to *Carcharocles* (Purdy, 1996; Aguilera et al., 2008; Kallal et al., 2010; Collareta et al., 2017; Godfrey et al., 2018).

Many species of modern sharks return to particular locations to pup that are favorable for the growth of juveniles (Castro, 1993; Heithaus, 2007). Shark nurseries are often found in protected shallow marine embayments lacking larger sharks, therefore offering protection, whereas others are on the open coast (Heithaus, 2007; Heupel et al., 2007). In addition to offering protection from potential predators, nurseries are typically rich in small prey items (Castro, 1993; Heithaus, 2007). Multiple species may use the same nursery area (Castro, 1993). Many ancient examples of shark nurseries have been interpreted from the Cenozoic fossil record, based on a preponderance of juvenile or neonate teeth, evidence of protected shallow marine settings, and abundant potential prey or high primary productivity (Pimiento et al., 2010; Landini et al., 2017; Herraiz et al., 2020; Villafaña et al., 2020). Nurseries for the megatoothed shark *C. megalodon* have been reported from Miocene and Pliocene assemblages in Panama, Spain, and the Atlantic coast of the USA (Maryland and Florida; Pimiento et al., 2010; Herraiz et al., 2020).

Carcharocles angustidens teeth are frequently collected in Oligocene deposits of the Charleston embayment in South Carolina (Figure 1), which has yielded a diverse assemblage of marine vertebrates including sharks, bony fish, sea turtles, an estuarine crocodile, sea birds, sea cows, and early whales and dolphins (Boessenecker and Geisler, 2018, and references therein). Sea turtles, early dolphins (Odontoceti), and baleen whales made for ample prey (Purdy, 1996; Sanders et al., 1982). Excavation of a bonebed in the Chandler Bridge Formation with a large sample ("about 100") of *C. angustidens* dominated by small teeth interpreted as juveniles and rare large teeth representing adults led Purdy (1996) to propose that the Charleston embayment hosted a megatoothed shark nursery during the Oligocene. We evaluate the shark nursery hypothesis through formal study of this bonebed sample and also report a newly discovered second sample of megatoothed sharks from the same strata.

Institutional Abbreviations

CCNHM, Mace Brown Museum of Natural History, College of Charleston, Charleston, South Carolina, USA; ChM, Charleston Museum, Charleston, South Carolina, USA; OU, University of Otago Geology Museum, Dunedin, New Zealand.

GEOLOGIC BACKGROUND

The specimens in this study were collected from two localities in the vicinity of Ladson and Summerville, South Carolina, from the Oligocene Chandler Bridge and Ashley formations (Figure 1). The Ashley Formation is 10-25 m thick, made up of olive-tan sandy limestone, and has been dated to 28-29 Ma using $^{87}Sr/^{86}Sr$ ratios (Rupelian equivalent; Weems et al., 2016; Boessenecker and Fordyce, 2017). The Ashley Formation is mainly calcareous, besides the basal phosphatic bed. The Ashley Formation is made up of three members: the Gettysville Member, the Runnymede Marl Member, and the Givhan's Ferry Member. The Gettysville Member has only been recorded in a single core, but the Runnymede Marl and Givhan's Ferry Members are commonly exposed in excavations around the Charleston area. The Runnymede Marl Member is a pale green-gray calcarenite with abundant burrows, shells, vertebrate skeletal fragments, and phosphate nodules. The Givhan's Ferry Member consists of olive brown glauconitic calcarenite (R.W. Boessenecker, personal obs.) that is more fossiliferous than the Runnymede Marl Member. The basal contact of the Givhan's Ferry Member is a diffuse, bioturbated boundary with pods of mollusk and barnacle shell fragments, phosphate pebbles, and vertebrate elements forming burrow infill.
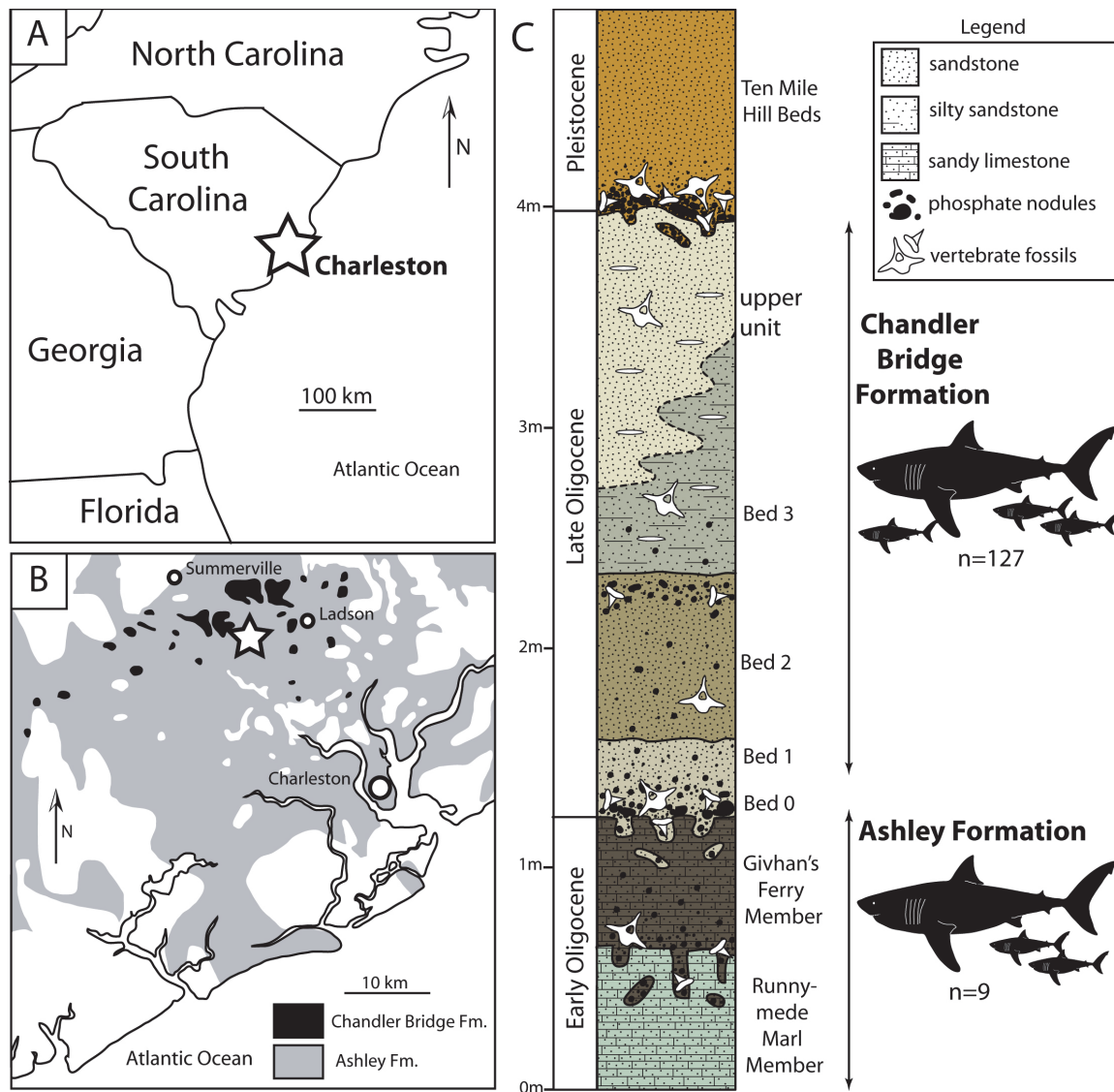
FIGURE 1. Generalized geology and stratigraphy of Oligocene marine strata in the vicinity of Ladson and Summerville, South Carolina, USA. A) Map of South Carolina showing Charleston. B) Map of Charleston showing the extent of Oligocene marine rocks; star denotes the location of the McKewn subdivision and Chandler Bridge excavation localities. C) Stratigraphic column of Oligocene marine rocks and overlying deposits as exposed in stormwater pond excavations at the McKewn Subdivision locality near Ladson, South Carolina. Modified from Fallon and Boessenecker (2020).

Most specimens in this study were collected from the Chandler Bridge Formation, which overlies the Ashley Formation. The Chandler Bridge Formation is typically thin (30-100 cm at most localities) but is 2.5 m thick at the McKewn subdivision locality. The Chandler Bridge is upper Chattian and is dated to 24.7-23.5 Ma based upon dinoflagellates and strontium isotopes (Weems et al., 2016; Boessenecker and Fordyce, 2017, and references therein). This large range in thickness and patchiness is most likely caused by later Neogene erosion (Katuna et al., 1997). The Chandler

Bridge Formation consists of several beds composed chiefly of tan, brown, and olive, richly fossiliferous, unlithified, massively bedded, fine-very fine sandstone and siltstone. A phosphatic bonebed typically mantles the lower contact, though vertebrates are common throughout the unit. At the McKewn subdivision locality, the basal bonebed is rich in large, brown, irregularly-shaped nodules, and there is a second bonebed 70 cm higher that is less richly fossiliferous but dominated by tan to light gray phosphate nodules 1-3 cm in diameter. A more detailed description of the stratigraphy at this

locality is provided by McCuen et al. (2020). All specimens collected from the McKewn subdivision locality originated from beds 1 and 2 (and possibly bed 0) of the Chandler Bridge Formation, whereas at the Chandler Bridge excavation, most were derived from bed 3 (Sanders, 1980).

A well-established vertebrate assemblage from the Chandler Bridge Formation includes bony fish, marine birds, marine mammals, crocodiles, and most important for this study, sharks (Sanders et al. 1982, Boessenecker and Geisler 2018, and references therein). Fossil bony fish and sharks suggest that the Chandler Bridge Formation was deposited under constant open marine conditions (Cicimurri and Knight, 2009), in contrast to earlier estuarine interpretations (Katuna et al., 1997). The shark assemblage in particular suggests inner to middle shelf environments (Cicimurri and Knight, 2009).

MATERIALS AND METHODS

Teeth were identified to tooth position based on the reconstructed dentition of *Carcharocles angustidens* reported by Gottfried and Fordyce (2001). Crown height and width (after Pimiento et al., 2010: figure S2) was measured to the nearest tenth of a millimeter using digital calipers. Based on tooth position, body length was estimated using regression equations derived from tooth size to body length data for extant *Carcharodon carcharias* analyzed by Shimada (2002). In the absence of complete skeletons permitting measurement of body length, *Carcharodon carcharias* is a reasonable modern analog for reconstructing body length from otodontid tooth dimensions (Pimiento et al., 2010). Note, however, that a recent study suggests that these estimates might underestimate the maximum body length, and that posterior teeth overestimate body length versus anterior teeth (Perez et al., 2021). Because the goal of this study is to evaluate the relative size, and not evaluate different methods, we follow Pimiento et al. (2010) and Shimada et al. (2020) in using the equations from Shimada (2002). Photographs were taken with a Canon Rebel T5 and a Tokina f/2.8 100 mm macro lens.

Pimiento et al. (2010) and Gottfried et al. (1996) demarcated growth stage bins for three age classes in *Carcharocles megalodon*: neonates, juveniles, and adults. Pimiento et al. (2010) and Gottfried et al. (1996) identified neonates as individuals less than 4 m reconstructed body length, juveniles between 4 m and 10.5 m, and adults over 10.5 m. However, *Carcharocles angustidens* is smaller than *C. megalodon*, and these size bins need adjustment. Gottfried and Fordyce (2001) identified the maximum length of OU 22261 *C. angustidens* to be 9.3 m. However, we recalculated this using Shimada's (2002) regression-derived equations using the largest tooth of OU 22261 (Gottfried and Fordyce, 2001:fig. 3a), and found a slightly smaller body length of 8.46-8.81 m (depending upon the A1 or A2 tooth position, A1 being upper first anterior).

Because Purdy (1996) referred to teeth of even larger *Carcharocles angustidens* specimens rivaling teeth of *Carcharocles megalodon* in size, we searched collections at CCNHM and ChM for large specimens from other localities in South Carolina to reconstruct the maximum size of *C. angustidens*. We located several specimens exceeding 75 mm crown height (n=6; Figure 2, Table 1). The largest single specimen we could locate is ChM PV 7281, an isolated A1 lacking locality data but from the Charleston area. Using Shimada's (2002) equation for the A1 tooth position, we calculated the body length of ChM PV 7281 (Figure 2; Table 1) as 11.22 m. Using a maximum length of 17 m for *C. megalodon* (after Pimiento et al., 2010), and 11.2 m for *C. angustidens* based on the specimen ChM PV 7267, we estimated that *C. angustidens* had a maximum length 65% of the length of *C. megalodon* and applied a 65% correction to these growth stage bins (Pimiento et al., 2010; Gottfried et al., 1996) and consider *C. angustidens* neonates to be less than 2.6 m, juveniles between 2.6 m and 6.8 m, and adults more than 6.8 m. Isometric scaling of these growth stage bin boundaries is defensible on the grounds that lamniform and carcharhiniform sharks do not exhibit allometric growth (Irschick and Hammerschlag, 2014; Irschick et al., 2017; Cooper et al., 2020).

'Ex situ' teeth (discovered after they had been eroded from Oligocene strata, typically found on beaches, dredge spoils, streambeds, and river bottoms) from other localities were only used to estimate the maximum size of *C. angustidens* and were not included in the body size distribution analysis.

Specimens studied here (n=136) originate from three collections made at two localities: the Chandler Bridge Formation at the Chandler Bridge excavation site (n=95), and the Ashley (n=9; not included in analyses of the Chandler Bridge samples) and Chandler Bridge formations (n=32) at the McKewn subdivision in the vicinity of Ladson and Summerville, South Carolina. Rather than reporting all specimens of *Carcharocles angustidens* in
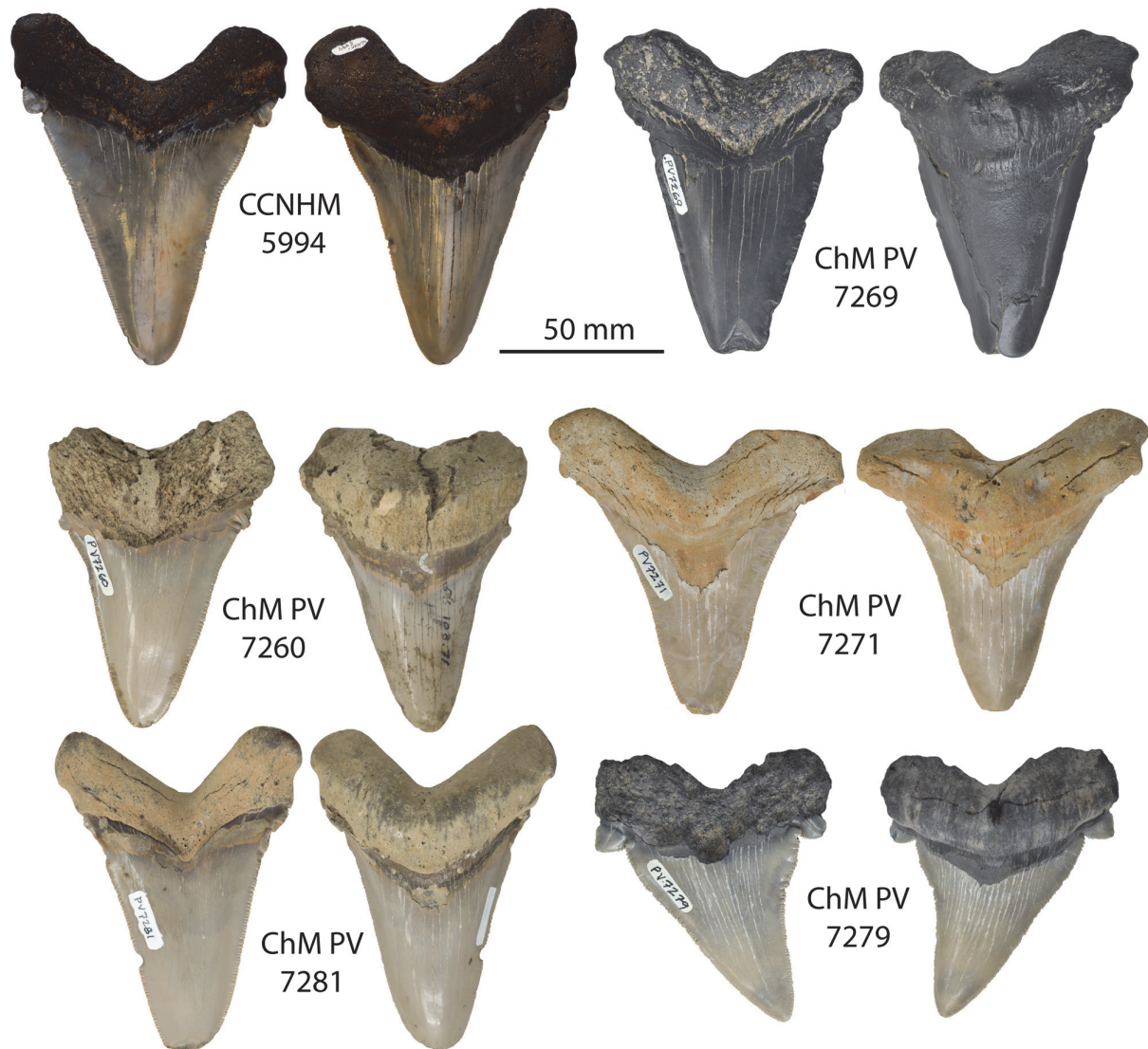
FIGURE 2. The largest available specimens (crown height >75 mm) of *Carcharocles angustidens*, in labial view (left) and lingual view (right).

museum collections from the area, we restricted the studied sample to these collections to limit collection bias. Collection bias affects fossils at Oligocene exposures near Charleston in a number of ways. Shark tooth diving in the Wando, Cooper, and Ashley rivers is popular, but is obviously biased towards collection of large trophy specimens: 1) murky water with poor visibility limits the ability of divers to find small teeth and biases collection towards larger specimens; 2) larger teeth are more likely to be exposed and recognized on the river bottom, and 3) there is intense desire and competition for collecting large trophy specimens. Further compounding this is the lack of geological context for most river-collected specimens. Collect-

ing ex situ specimens from local beaches and spoils along waterways is a popular activity for local collectors and paleontological tourists, who may retrieve the biggest, most complete teeth while leaving the small, incomplete teeth behind. These ex situ collections also lack stratigraphic context. Lastly, private collectors are unlikely to donate an entire collection - even if made in an unbiased fashion from in situ exposures - owing to the commercial and prestige value placed on these coveted teeth by the collecting community.

We instead focused on unbiased samples collected 'in situ' (specimens discovered while still embedded in the rock or by screenwashing, so stratigraphic origin is certain) by field paleontolo-

TABLE 1. Measurements, identifications, and estimated total lengths of specimens used in this study. "~" denotes estimated measurement. Tooth position after Shimada et al. (2003); A=anterior; L=lateral; upper case denotes upper tooth, lower case denotes lower tooth. AF = Ashley Formation; CB = Chandler Bridge Formation.

Specimen	CW(mm)	CH(mm)	Tooth Position	TL(m)	Age class	Formation
CCNHM 5173	43	~40	L2-L3	5.62	juvenile	AF, McKewn
CCNHM 5175	31	?	?	?	juvenile?	AF, McKewn
CCNHM 5187	35	43	A1-A3, a1-a3	6.10	juvenile	AF, McKewn
CCNHM 6081	70	70-80	?	?	adult?	AF, McKewn
CCNHM 6082	27	~22	l1	3.93	juvenile	AF, McKewn
CCNHM 6083	25.4	?	?	?	juvenile?	AF, McKewn
CCNHM 6084	~36	?	?	?	juvenile?	AF, McKewn
CCNHM 6085	28	~34	A1-A3, a1-a3	4.83	juvenile	AF, McKewn
CCNHM 6087	18	~23	L1-L3, l1-l3	4.07	juvenile	AF, McKewn
CCNHM 6086	33	29	L1	4.24	juvenile	CB, McKewn
CCNHM 5151	~42	45	a2	6.04	juvenile	CB, McKewn
CCNHM 5152	35	41	a1	6.62	juvenile	CB, McKewn
CCNHM 5153	~41	~40	A2-A3,a2-a3	5.9	juvenile	CB, McKewn
CCNHM 5154	35	~29	A3	4.76	juvenile	CB, McKewn
CCNHM 5155	~44	~34	L1	4.88	juvenile	CB, McKewn
CCNHM 5156	~26	38	A2-A3,a2-a3	5.61	juvenile	CB, McKewn
CCNHM 5157	39	26	L4-L5	5.72	juvenile	CB, McKewn
CCNHM 5158	40	38	L2	5.15	juvenile	CB, McKewn
CCNHM 5159	~32	~20	a2-l2	3.37	juvenile	CB, McKewn
CCNHM 1560	23	15	L5	3.9	juvenile	CB, McKewn
CCNHM 1563	29	~29	A1-A3, a1-a3	4.12	juvenile	CB, McKewn
CCNHM 1564	~40	~38	L2-L4	5.82	juvenile	CB, McKewn
CCNHM 1566	~42	39	L2	5.29	juvenile	CB, McKewn
CCNHM 1567	40	47	A1	5.47	juvenile	CB, McKewn
CCNHM 5168	~30	~33	A1-A3, a1-a3	4.69	juvenile	CB, McKewn
CCNHM 5169	~15	~25	a1-l1	3.93	juvenile	CB, McKewn
CCNHM 5170	~40	~39	A1-A3, a1-a3	5.55	juvenile	CB, McKewn
CCNHM 5171	~34	~31	a1-l1	4.88	juvenile	CB, McKewn
CCNHM 1572	~22	~34	A1-A3, a1-a3	4.84	juvenile	CB, McKewn
CCNHM 5174	~18	10	L4	1.82	neonate	CB, McKewn
CCNHM 1576	35	30	L4	5.35	juvenile	CB, McKewn
CCNHM 5177	35	33	A2	3.97	juvenile	CB, McKewn
CCNHM 5178	~38	~40	a1-a2	5.62	juvenile	CB, McKewn
CCNHM 5179	33	29	L1	4.17	juvenile	CB, McKewn
CCNHM 5180	~40	34	a1	4.98	juvenile	CB, McKewn
CCNHM 5181	38	22	L2	3	juvenile	CB, McKewn
CCNHM 5182	~28	23	L1	3.32	juvenile	CB, McKewn
CCNHM 5183	25	26	l1-l2	4.82	juvenile	CB, McKewn
CCNHM 5184	~30	~25	L1	3.61	juvenile	CB, McKewn
CCNHM 5185	~28	~19	L5	4.96	juvenile	CB, McKewn
CCNHM 5186	~30	~29	a1	4.24	juvenile	CB, McKewn
CHM PV 541	47	48	A1-a1	6.33	juvenile	CB, excavation
CHM PV 21	46	~41	L1-l1	6.56	juvenile	CB, excavation

TABLE 1 (continued).

Specimen	CW(mm)	CH(mm)	Tooth Position	TL(m)	Age class	Formation
CHM PV 22	~33	~35	A2-a2	4.45	juvenile	CB, excavation
CHM PV 23	34	30	L1	4.32	juvenile	CB, excavation
CHM PV 24	42	~35	L1-L3	4.96	juvenile	CB, excavation
CHM PV 25	31	24	I1-I2	4.45	juvenile	CB, excavation
CHM PV 26	37	~30	L1	4.32	juvenile	CB, excavation
CHM PV 27	33	28	a1-a3	4.22	juvenile	CB, excavation
CHM PV 28	39	15	A1-a1	1.97	neonate	CB, excavation
CHM PV 281	46	40	L1-L3, I1-I3	7.02	adult	CB, excavation
CHM PV 29	41.2	31.1	L3-I3	6.02	juvenile	CB, excavation
CHM PV 297	26.4	22.2	L1-L3, I1-I3	3.94	juvenile	CB, excavation
CHM PV 298	~32	~41	A1-a1	5.4	juvenile	CB, excavation
CHM PV 30	35	41	A1-a1	5.4	juvenile	CB, excavation
CHM PV 31	33	~42	A1-a1	5.53	juvenile	CB, excavation
CHM PV 32	28	26	A1-A3, a1-a3	3.7	juvenile	CB, excavation
CHM PV 33	~35	~36	A1-A3, a1-a3	5.12	juvenile	CB, excavation
CHM PV 34	36	34	a1	4.98	juvenile	CB, excavation
CHM PV 35	40	~37	L1	5.31	juvenile	CB, excavation
CHM PV 36	32	~38	a1	5.58	juvenile	CB, excavation
CHM PV 37	34	~40	a1	5.88	juvenile	CB, excavation
CHM PV 38	33	27	L1-L3, I1-I3	4.77	juvenile	CB, excavation
CHM PV 39	42	~26	L3-I3	5.01	juvenile	CB, excavation
CHM PV 40	~27	24	I1-I2	4.45	juvenile	CB, excavation
CHM PV 41	~30	~32	A1-a1	4.21	juvenile	CB, excavation
CHM PV 42	36	~37	A1-A3, a1-a3	5.26	juvenile	CB, excavation
CHM PV 43	37	~33	L1-L2, I1-I2	5.36	juvenile	CB, excavation
CHM PV 44	36	~40	A1-A3, a1-a3	5.69	juvenile	CB, excavation
CHM PV 45	44	35	L3	5.1	juvenile	CB, excavation
CHM PV 46	29	~27	L1-I1	4.35	juvenile	CB, excavation
CHM PV 47	31	~24	L1-L2, I1-I2	3.91	juvenile	CB, excavation
CHM PV 48	~34	27.8	L2-L4	4.27	juvenile	CB, excavation
CHM PV 49	45	~33	L1-L2	4.61	juvenile	CB, excavation
CHM PV 50	34.9	~29	L1-L3, I1-I3	5.11	juvenile	CB, excavation
CHM PV 51	34	32	L1	4.6	juvenile	CB, excavation
CHM PV 52	34	~31	L1-L3	4.4	juvenile	CB, excavation
CHM PV 53	~34	~30	L2-L3	4.22	juvenile	CB, excavation
CHM PV 54	~33	~31	A3-a3	5.21	juvenile	CB, excavation
CHM PV 540	83.6	74.5	A2-A3,a2-a3	10.88	adult	CB, excavation
CHM PV 55	44	~32	L1-L2	4.47	juvenile	CB, excavation
CHM PV 56	~44	~32	a3	5.53	juvenile	CB, excavation
CHM PV 564	38.2	32.3	L1-L3	4.58	juvenile	CB, excavation
CHM PV 57	~27	~20	L4-I4	5.06	juvenile	CB, excavation
CHM PV 58	~35	32	L1-L2, I1-I2	5.2	juvenile	CB, excavation
CHM PV 59	35	~30	L3	4.37	juvenile	CB, excavation
CHM PV 60	30	29	A1-a1	3.82	juvenile	CB, excavation

TABLE 1 (continued).

Specimen	CW(mm)	CH(mm)	Tooth Position	TL(m)	Age class	Formation
CHM PV 61	~30	29	a1	4.24	juvenile	CB, excavation
CHM PV 62	~32	24	L1-L3	3.41	juvenile	CB, excavation
CHM PV 63	36	~40	a1-a3	6.06	juvenile	CB, excavation
CHM PV 64	~48	33	I1	5.89	juvenile	CB, excavation
CHM PV 65	~34	41	a1	6.03	juvenile	CB, excavation
CHM PV 66	~42	~34	I2	6.54	juvenile	CB, excavation
CHM PV 67	25	21	I4	6.88	adult	CB, excavation
CHM PV 68	38	~30	L1-L3	4.25	juvenile	CB, excavation
CHM PV 69	~48	34.4	a1	5.04	juvenile	CB, excavation
CHM PV 70	25.1	26.8	A3	4.41	juvenile	CB, excavation
CHM PV 71	~27	~25	L1-I1	4.03	juvenile	CB, excavation
CHM PV 72	~27	~31	L4-L5	6.83	adult	CB, excavation
CHM PV 73	~33	~30	a1-a2	4.2	juvenile	CB, excavation
CHM PV 75	30.6	31.3	L2-L4	4.8	juvenile	CB, excavation
CHM PV 76	29.8	~25	L1-I1	4.03	juvenile	CB, excavation
CHM PV 77	29	20	L4-L5	4.4	juvenile	CB, excavation
CHM PV 78	~35	35	A1-a1	4.61	juvenile	CB, excavation
CHM PV 79	~34	26	L1-L2	3.64	juvenile	CB, excavation
CHM PV 80	39	35.5	L1-L3, I1-I3	6.24	juvenile	CB, excavation
CHM PV 81	24.2	~23	L1-L3, I1-I3	4.07	juvenile	CB, excavation
CHM PV 82	~26	22.3	L1-L3, I1-I3	3.95	juvenile	CB, excavation
CHM PV 83	~27	15	L1-L3	2.15	neonate	CB, excavation
CHM PV 84	~20	18.1	L1-L2, I1-I2	2.96	juvenile	CB, excavation
CHM PV 86	27	~24	A1-A3, a1-a3	3.41	juvenile	CB, excavation
CHM PV 87	30	~30	A2-A3, a2-a3	4.42	juvenile	CB, excavation
CHM PV 88	~16	~13	I2	2.51	neonate	CB, excavation
CHM PV 89	~25	~17	L1-L3, I1-I3	3.03	juvenile	CB, excavation
CHM PV 90	26.2	~20	L1-L3, I1-I3	3.55	juvenile	CB, excavation
CHM PV 91	~37	~28	L1-L2	3.92	juvenile	CB, excavation
CHM PV 9835	31.8	28.2	L1-I1	4.54	juvenile	CB, excavation
CHM PV 9836	24.9	21.6	L1-L3	3.07	juvenile	CB, excavation
CHM PV 9837	34.7	~31	L1-L3, I1-I3	5.46	juvenile	CB, excavation
CHM PV 9838	~32	~26	a1-I1	4.09	juvenile	CB, excavation
CHM PV 9839	~78	~74	a1	10.94	adult	CB, excavation
CHM PV 9840	~27	~22	L5	5.75	juvenile	CB, excavation
CHM PV 9842	28.6	29.3	L4	5.23	juvenile	CB, excavation
CHM PV 9843	28.7	~27	A1-A3, a1-a3	3.84	juvenile	CB, excavation
CHM PV 9844	28.6	~22	I2	4.24	juvenile	CB, excavation
CHM PV 9845	29.5	~23	L1	3.32	juvenile	CB, excavation
CHM PV 9846	~32	~25	L4	4.47	juvenile	CB, excavation
CHM PV 9847	30.9	34.3	A1-a1	4.52	juvenile	CB, excavation
CHM PV 9848	-	40.7	L2	5.52	juvenile	CB, excavation
CHM PV 9849	31.8	~37	A1-a1	4.87	juvenile	CB, excavation
CHM PV 9850	25.2	~23	A1	2.7	juvenile	CB, excavation

TABLE 1 (continued).

Specimen	CW(mm)	CH(mm)	Tooth Position	TL(m)	Age class	Formation
CHM PV 9851	24	~22	A2	2.64	juvenile	CB, excavation
CHM PV 9852	33.8	33.5	A2	4.03	juvenile	CB, excavation
CHM PV 9853	41.5	35	I2	6.73	juvenile	CB, excavation
CHM PV 9855	~37	~34	A2	4.1	juvenile	CB, excavation
CHM PV 9856	~34	29.1	I3	7	adult	CB, excavation
CCNHM 5994	76.3	81.4	A1	9.44	adult	Ex situ
PV-7271	87.01	~76.90	A3-L2	7.75	adult	Ex situ
PV-7281	74.99	~97	A1	11.22	adult	Ex situ
PV-7269	~83.20	~84.93	L1-L3	9.83	adult	Ex situ
PV-7279	~75.90	~92	A1-A2	10.88	adult	Ex situ
PV-7260	~83.26	~78.34	A1	9.07	adult	Ex situ

gists who collected all vertebrate fossils as a 'census assemblage' at two different localities, decades apart. At the Chandler Bridge excavation site, a controlled excavation of an unusually densely fossiliferous bonebed (550 m^2; Sanders, 1980) within bed 3 of the Chandler Bridge Formation was performed over six weeks in 1970, seven weeks in 1971, and seven weeks in summer 1972 (Sanders, 1980). Because all specimens of *Carcharocles angustidens* from this excavation site were sampled, collection bias is not a factor. At the McKewn Subdivision locality, teeth were collected by one of us (R.W. Boessenecker, S.J. Boessenecker, and A. Gale) over three months while the locality was inaccessible to hobby collectors. Rather than being collected under controlled quarrying operations like the Chandler Bridge excavation site, these specimens were naturally weathered out prior to collection from a somewhat larger area of outcrop (907 m^2; measured in ImageJ based upon photogrammetric models of the locality) – similarly not biased by hobby collecting, but collected intermittently and aided by natural weathering rather than systematic quarrying. Because all vertebrate fossils from the McKewn locality were collected, collection bias can be excluded as a factor in interpreting the size distribution of these teeth. We also evaluated the taphonomic condition of specimens, examining them for evidence of reworking that could potentially bias the results, including evidence of abrasion, fragmentation, bioerosion, and phosphatization.

Tooth shape and size vary within *Carcharocles angustidens* as in other sharks. If the tooth position is incorrect, body length estimates might be overestimated. In order to exclude tooth posi-

tion as a variable, each tooth was identified to approximate position based on comparison with the only known dentition of *C. angustidens* (OU 22261, Gottfried and Fordyce, 2001), but use A3 over I1 (intermediate) and include the posteriors as a continuation of the laterals after Shimada (2002) and Perez et al. (2021). Anterior teeth are the largest, and generally have the longest (relative to root width) and most symmetrical crowns; lateral teeth are relatively smaller than anteriors and have proportionally shorter and more distally inclined crowns, and increasingly have proportionally smaller crowns in further distal tooth positions closer to the commissure (=posteriors of some authors, e.g., Gottfried and Fordyce, 2001). Because individual specimens could not always be confidently placed to a single position, equations for multiple adjacent (and plausible) positions were calculated, and an average of these was used and entered into Table 1.

Taxonomic Note

In recent years the taxonomy of Paleogene megatoothed sharks has grown considerably. The transition from *Otodus obliquus* to serrated *Carcharocles angustidens* has now been subdivided into a number of different chronospecies of uncertain utility, largely by Zhelezko and Kozlov (1999), either by the introduction of newly named taxa or resurrection of disused taxa, including (but not limited to) the Eocene species *Otodus aksuaticus, Otodus minor, Otodus naidini, Otodus poseidoni, Otodus sokolovi,* and several subspecies of these. Some of these have been subdivided or included into subgenera (Cappetta, 2012), which are generally not advised in vertebrate paleontol-

ogy (Ehret and Ebersole, 2014). Most of these species in the transition from non-serrated *O. obliquus* to fully serrated *C. angustidens* are differentiated entirely on the basis of slight variations in cusplet shape and crown proportions (broad, narrow). Because large sample sizes reveal considerable variation in cusplet morphology (see below), we consider the late Eocene *C. sokolovi* to be a junior synonym of *Carcharocles auriculatus* as the cusplet morphology of these broadly overlaps in the context of variation within single individuals documented by Gottfried and Fordyce (2001). Most of these species and subspecies are subjectively diagnosed (Ehret and Ebersole, 2014), and variation within these species is not addressed or quantified (Kent, 2018). Despite careful stratigraphic work by Zhelezko and Kozlov (1999), morphometric studies within a stratigraphic context have not been attempted to evaluate the diagnoseability of these taxa (but see King et al., 2013; Perez et al., 2019), and we note that King et al. (2013) identified only a single transitional species – *Carcharocles aksuaticus* –- between nonserrated *Otodus obliquus* and fully serrated *Carcharocles auriculatus*. We follow Kent (2018) and Perez et al. (2019) in using *C. chubutensis* over *C. subauriculatus* owing to the lack of cusplets in and locality provenience for the *C. subauriculatus* type specimen (but see Purdy et al., 2001). Further evaluation will require morphometric study of statistically large samples within a detailed stratigraphic context (e.g., Perez et al., 2019).

The genus-level taxonomy of megatoothed sharks has recently changed somewhat, but generally stabilized around either the use of *Carcharocles* or *Otodus* (Shimada et al., 2017, and references therein). Shimada et al. (2017) proposed placing all species of otodontids with serrated teeth *(Carcharocles auriculatus, Carcharocles angustidens, Carcharocles chubutensis, Carcharocles megalodon)* into the genus *Otodus* in order to prevent the genus *Otodus* from being para- or polyphyletic, and because *Otodus* has priority over *Carcharocles*. The cladograms presented in Shimada et al. (2017) are hypothetical (Shimada et al., 2017: figs. 3-4) and do not represent trees derived from cladistic analyses of morphological data. Though subsequent studies have followed this taxonomic decision (e.g., Boessenecker et al., 2019; Cooper et al., 2020; Herraiz et al., 2020; Perez et al., 2021), not all have (e.g., Godfrey et al., 2018; Kent, 2018; Perez et al., 2019). An exhaustive review of this subject is provided by Kent (2018: 80-85). Because

ancestor-descendant relationships in this group have not been demonstrated (or evaluated) quantitatively (e.g., cladistics, stratophenetics), and because taxonomic revision of *Otodus* and Eocene *Carcharocles* spp. is still needed (Ehret and Ebersole, 2014; Kent, 2018), we agree with Kent (2018) and conservatively suggest that use of *Carcharocles* is still acceptable for the time being; we further echo Kent's (2018) call for further research on early megatoothed sharks and emphasize the need for application of quantitative and/or cladistic methods.

RESULTS

New specimens (n=136) from Ashley and Chandler Bridge Formation exposures at the McKewn subdivision and Chandler Bridge excavation site (Figures 3-5) are assignable to *Carcharocles angustidens* because they possess regular serrations (rather than the more irregular serrations of Eocene *Carcharocles auriculatus*), triangular lateral cusplets with regular fine serrations separated from the main cusp by a distinct notch, U-shaped roots, rectangular to triangular root lobe apices, and relatively narrow crowns in comparison to geochronologically younger members of this lineage (e.g., *Carcharocles chubutensis, Carcharocles megalodon*). Just over half (n=73) represent lateral tooth positions, and just under half (n=54) represent anterior tooth positions.

Maximum estimated body length of *Carcharocles angustidens* appears to be in the range of 10-11 m (Figure 2, Table 1). Many of these large specimens were collected ex-situ, and some are damaged with estimated crown lengths. The largest individual specimen was ChM PV 7281, which is incomplete, but with an estimated body length of 11.2 meters. The largest specimen with a completely preserved crown is CCNHM 5994, a slightly smaller A1 with an estimated body length of 9.44 m. Other specimens slightly smaller than this represented estimated body lengths of 7.75-10.88 m (Figure 2, Table 1), suggestive of a maximum body length between 11 and 12 m, broadly in accordance with Shimada et al. (2020).

Crown height measurements of *Carcharocles angustidens* teeth from the Chandler Bridge Formation exposed in the McKewn Subdivision (CCNHM collections), and Chandler Bridge excavation site (ChM collections) range from 10 mm to 74.5 mm (Table 1). The McKewn Subdivision sample consists of rare neonates (3.12%, n=1) and completely lacks adults (0%, n=0), and is dominated by juveniles (96.87%, n=31; Figure 6A; Table
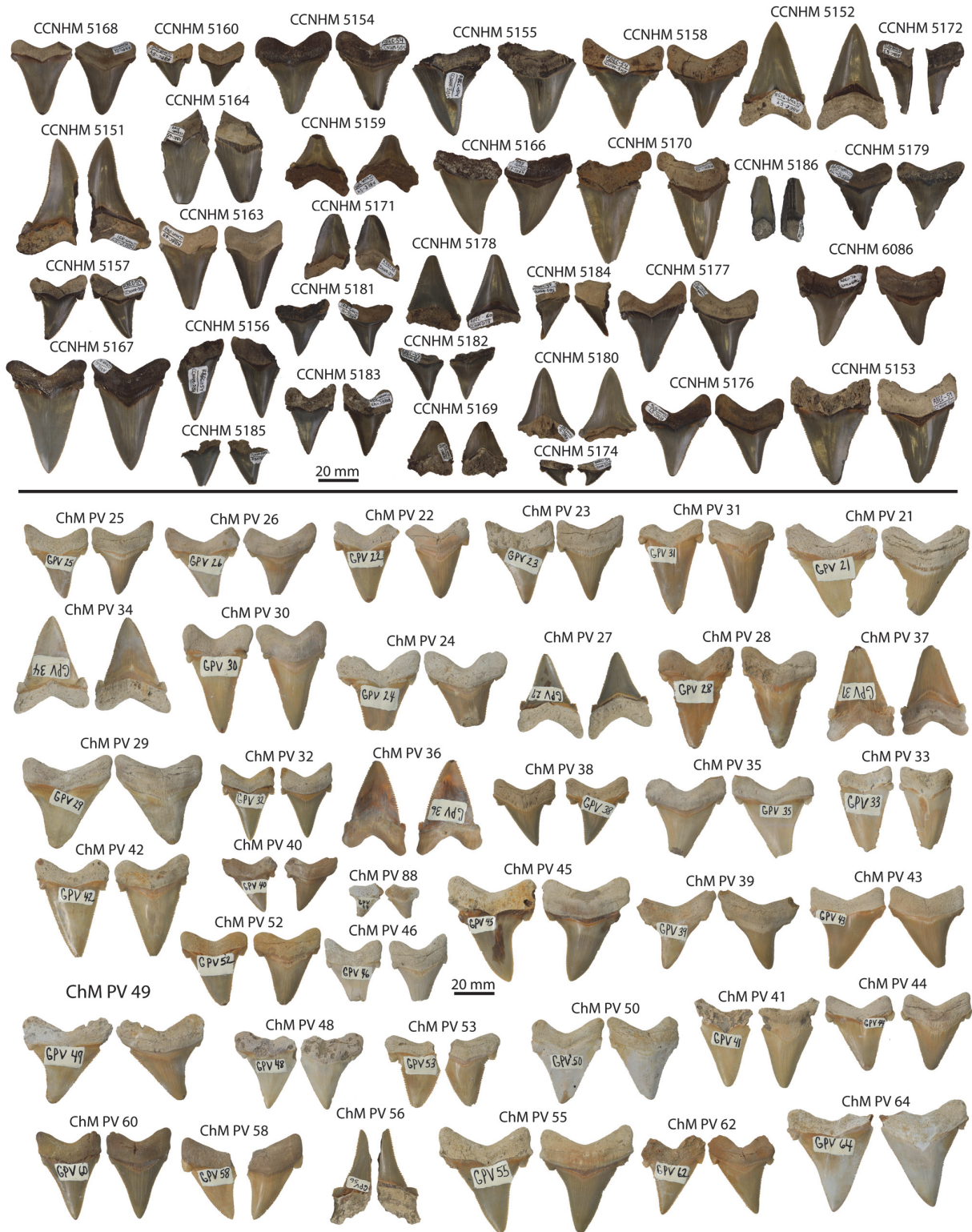
FIGURE 3. Teeth of *Carcharocles angustidens* from the Chandler Bridge Formation (late Oligocene), from the McKewn subdivision sample (top, CCNHM specimens) and part of the Chandler Bridge excavation sample (bottom, ChM specimens). Teeth shown in anatomical orientation (e.g., crown downwards for upper teeth); labial on left, lingual on right in all cases. All specimens shown to scale.
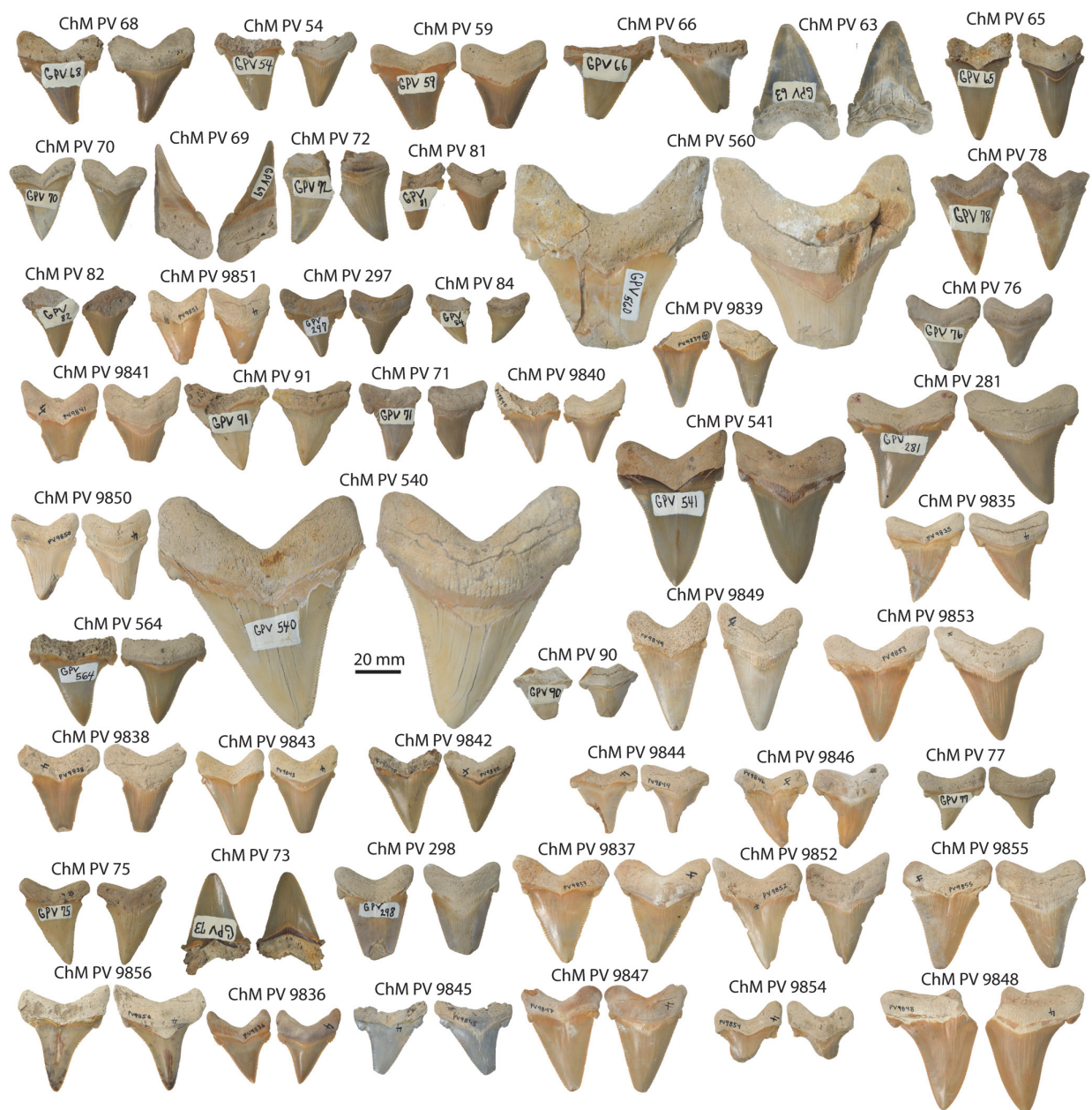
FIGURE 4. Teeth of *Carcharocles angustidens* from the Chandler Bridge Formation (late Oligocene), from the Chandler Bridge excavation sample, in anatomical orientation (e.g., crown downwards for upper teeth); labial on left, lingual on right in all cases. All specimens shown to scale.

1). The Chandler Bridge excavation sample is similarly dominated by juveniles (90.52%, n=86), with rare neonates (3.15%, n=3) and adults (6.31%, n=6; Figure 6B; Table 1). The combined assemblage is therefore also dominated by juveniles (92.1%, n=117), with few neonates (3.14%, n=4) and adults (4.72%, n=6; Figure 6C; Table 1).

The majority of teeth from these samples have a crown height around 30mm (median crown height: 30 mm; mean crown height: 30.7 mm; Table

1). Using published formulae for calculating body length of lamniform sharks (Shimada, 2002), the majority of *Carcharocles angustidens* from the combined sample were reconstructed between 4-6 m long (n=83; 65.35%; Figure 6C; Table 1). The McKewn subdivision and Chandler Bridge excavation collections do not seriously differ from one another.

The estimated body length of the largest specimens from the McKewn sample ranges to 7
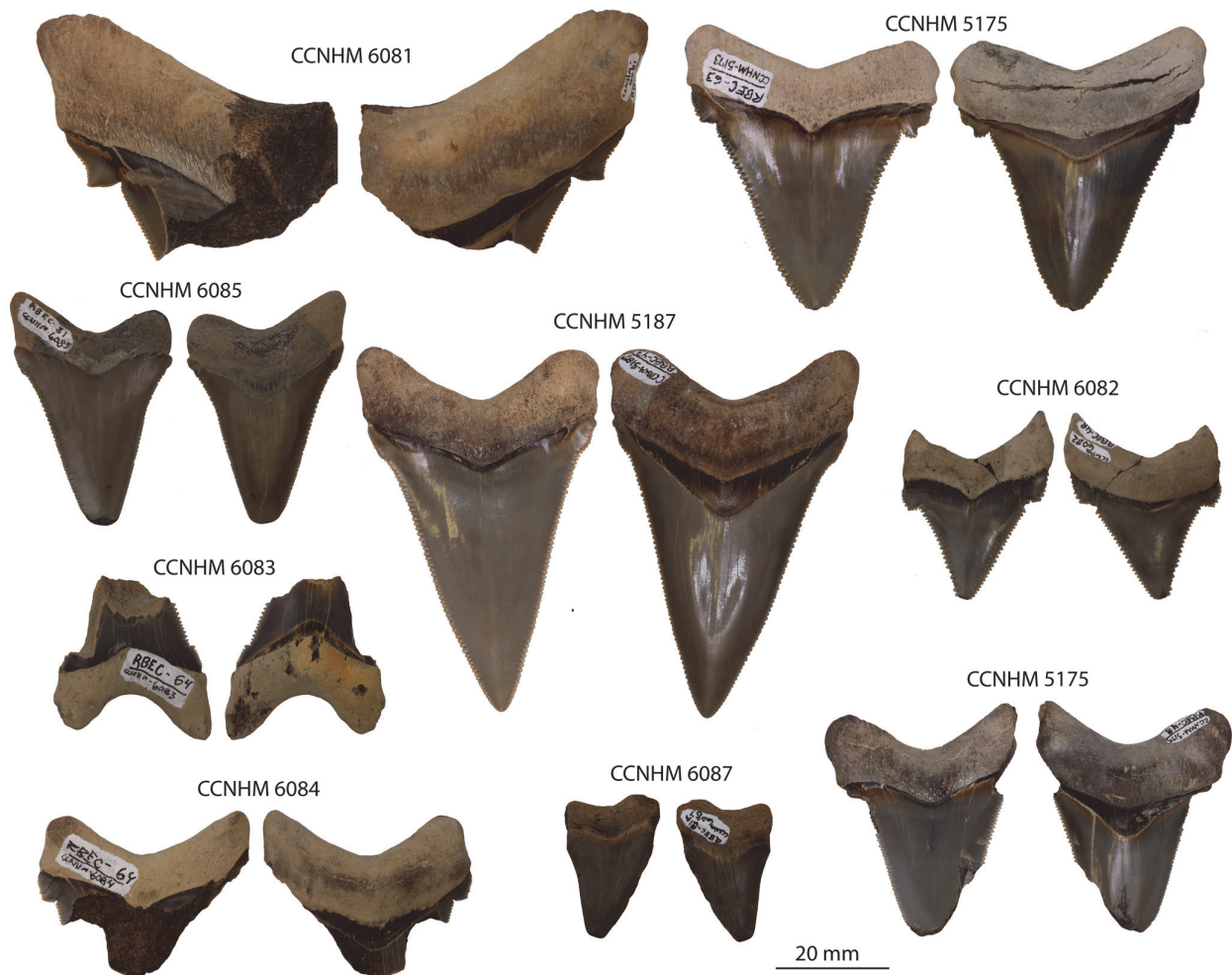
FIGURE 5. Teeth of *Carcharocles angustidens* from the Ashley Formation (early Oligocene), from the McKewn subdivision sample, in anatomical orientation (e.g., crown downwards for upper teeth); labial on left, lingual on right in all cases. All specimens shown to scale.

m, whereas two outlier specimens occur within the Chandler Bridge excavation sample (Figures 4, 5B, Table 1): ChM PV 540 and 9839, each with estimated body lengths of 10.88 and 10.94 m (respectively), and similar in size to the largest known specimens of *Carcharocles angustidens* (Figures 2, 5B, Table 1).

A small sample of *Carcharocles angustidens* teeth from the Ashley Formation (n=9; Figure 5) mostly represent juvenile specimens (CCNHM 5173, 5187, 6082, 6085, 6087, and probably 5175, 6083, 6084). A single fragment of a large tooth (CCNHM 6081; Figure 5) must have had about a 70 mm crown width and rivals the two largest teeth from the Chandler Bridge excavation, ChM PV 540 and 9839, likely representing a +10 m long shark.

Some teeth are incomplete (e.g., CCNHM 5151, 5153, 5159, 5171, 5186, ChM PV 24, 46, 56,

69, 90, 298, 9854), some bear bioeroded roots (e.g., CCNHM 5153, 5156, 5159, ChM PV 41, 54, 73, 91, 9840), and some are lightly abraded (e.g., CCNHM 5179, 5180, 5186, ChM PV 29, 48, 63, 69, 75, 76); most are not phosphatized and are remarkably uniform in coloration.

DISCUSSION

Identification

Otodontid teeth have been reported ex situ from various Oligocene-Pliocene strata in South Carolina, but few specimens have been reported from in situ Oligocene rocks. Purdy (1996) figured three teeth of "*Carcharodon* sp." from the Chandler Bridge Formation (USNM 476833, figure 3c of Purdy, 1996; ChM PV 540, and probably ChM PV 9849, figure 8b and 8a, respectively, of Purdy,
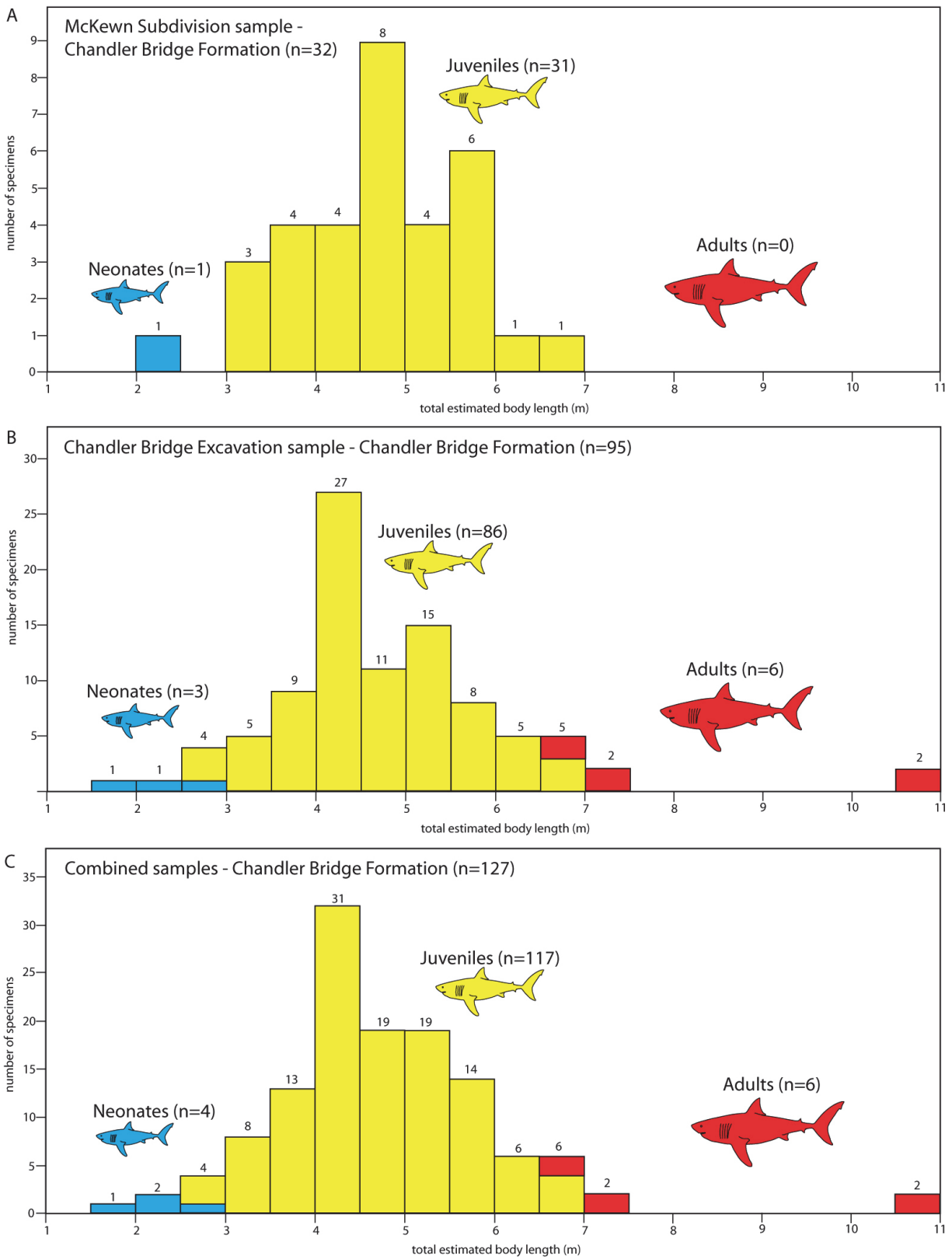
13

FIGURE 6. Histogram showing range of body length estimates from A) the McKewn subdivision sample (n=32), B) the Chandler Bridge excavation sample (n=95), and C) combined samples from the Chandler Bridge Formation (McKewn subdivision and Chandler Bridge excavation; n=127).

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1996). Purdy (1996) cautiously refrained from identifying these to the species level. A single small tooth described by Cicimurri and Knight (2009) from the Chandler Bridge Formation was cautiously identified as *Carcharocles* sp. owing to incomplete separation of the cusplets from the crown. Several teeth from each sample similarly have an incomplete notch between the crown and the cusplet, more closely resembling *Carcharocles chubutensis* than *Carcharocles angustidens*. However, we consider this a case of morphological variation within a sample, and owing to 1) more specimens possessing notches than not (66.6% of the McKewn subdivision sample, and 87% of the Chandler Bridge excavation sample; Figures 3 and 4), 2) other features distinguishing these teeth from *C. chubutensis* (e.g., narrower crowns), and 3) Oligocene age (since *C. chubutensis* is an early Miocene chronospecies; Perez et al., 2019), we refer all serrated otodontid teeth from the Ashley and Chandler Bridge formations to *C. angustidens*. We further highlight morphological variation even within a single dentition of *C. angustidens*, represented by OU 22261 from the Oligocene of New Zealand, which preserves teeth with triangular cusplets separated by a distinct notch, triangular cusplets lacking a notch, and low, ridge-like cusplets (Gottfried and Fordyce, 2001: figures 3-4). Assemblage-level and dentition-level polymorphisms argue for caution when interpreting individual otodontid specimens and highlight the utility of large sample sizes with stratigraphic control. These results further cast doubt on supposedly diagnostic but in actuality subtle and variable features (Gottfried and Fordyce, 2001; Kent, 2018; this study) used to erect the overly-parsed taxonomy of Eocene otodontids.

Nursery Area for *Carcharocles angustidens*

Two newly reported census assemblages of *Carcharocles angustidens* from the Chandler Bridge Formation are dominated by teeth of juveniles and neonates   (Figures 3-5). Taphonomic bias in the form of size-sorting is unlikely to be a controlling factor because the bonebeds within the Chandler Bridge Formation at the McKewn subdivision locality include relatively small, delicate shark teeth (<0.5 cm diameter) and fish bones along with larger teeth, bones, and phosphate nodules (10-40 cm). At the McKewn Subdivision locality, most vertebrates originated from one of two matrix supported bonebeds with a wide variety of bioclast sizes (teeth and fish bones under   1 cm, and bones over 15 cm in length) and phosphate nod-

ules in excess of 20 cm diameter. Owing to gradational lower and upper contacts, these are likely hiatal bonebeds rather than completely erosional in origin (Boessenecker et al., 2014). This evidence does not support size-sorting to have occurred during deposition. Collection bias also cannot be considered owing to controlled collecting methods and an absence of interference by hobby collectors (see above). Controlled excavation at the Chandler Bridge excavation further eliminates collection bias as a possibility. Despite lack of a formal taphonomic analysis, this assemblage has been prematurely interpreted as a stranding owing to the number of cetacean skeletons, variety of species, and apparent parallel development of skeletal material in rows aligned northwest/southeast (Erickson, 1990). However, it is also possible that this assemblage is a hiatal concentration like the majority of shallow marine bonebeds (e.g., Boessenecker et al., 2014). Tooth fracturing in this sample is consistent with feeding damage (Becker and Chamberlain, 2012); in some cases, some damage in the McKewn sample was possibly caused by machinery or modern weathering (CCNHM 5151, 5164, 5172) and other fracturing happened during collection (CCNHM 5157, 5158) or was likely exacerbated by bioerosion of the root (CCNHM 5155, 5170, 5182, 5185) . Light abrasion is typical in parautochthonous shallow marine assemblages (Boessenecker et al., 2014), perhaps suggestive of a hiatal origin rather than a stranding as envisioned by Erickson (1990). Similarity in density and coloration suggests a lack of phosphatization, which, in concert with absence of strong abrasion (e.g., stage 2 of Boessenecker et al., 2014: fig. 5), point towards these teeth being autochthonous or at most parautochthonous, rather than allochthonous (reworked) in taphonomic origin. Lastly, *Osedax* bioerosion is unusually common in Oligocene shallow marine vertebrate assemblages worldwide relative to younger Neogene assemblages (see Boessenecker and Fordyce, 2015), but reported from shark teeth herein for the first time. A similar incidence of occasional light abrasion, somewhat more frequent *Osedax* bioerosion, and typical tooth fracturing is present in the McKewn Subdivision sample. Altogether, taphonomic aspects of the Chandler Bridge Formation samples of *C. angustidens* suggest autochthonous or, at worst, parautochthonous concentrations of fossils - without evidence of size-sorting or reworking. Because collection bias and taphonomic bias cannot reliably explain this size distribution, we interpret this

assemblage as being genuinely dominated by neo-natal and juvenile teeth.

Three criteria have been proposed to identify paleo-nursery areas for extinct sharks: nursery areas must consist of 1) relatively shallow water environments with 2) high primary productivity with abundant prey species, and 3) a preponderance of young individuals (Castro, 1993; Heithaus, 2007; Heupel et al., 2007; Pimiento et al., 2010; Landini et al., 2017; Villafaña et al., 2020; Herraiz et al., 2020). The Chandler Bridge Formation is clearly a shallow shelf deposit, and some evidence from this unit suggests the Charleston Embayment was somewhat protected (Katuna et al., 1997). Primary productivity was evidently high, with a rich marine vertebrate fossil assemblage (Sanders et al., 1982; Cicimurri and Knight, 2009; Boessenecker and Geisler, 2018, and references therein) and wide-spread phosphogenesis (Katuna et al., 1997) indic-ative of high primary productivity (Föllmi, 1996). Lastly, our combined collections are dominated by juveniles (92.1% of the sample), and, with the exception of two outlier specimens from the Chan-dler Bridge excavation (ChM PV 540 and 9839), most of the largest teeth represent relatively large juveniles or small or adults in both samples. All three criteria are satisfied by the Chandler Bridge Formation. This study therefore confirms the hypothesis of Purdy (1996) that the Chandler Bridge Formation records a nursery area for *Carcharocles angustidens* in the Charleston Embayment.

A small sample of *Carcharocles angustidens* teeth is available from the Ashley Formation (n=9; Figure 5), and most (except for CCNHM 6081) are also within the juvenile size range (Table 1). The Ashley Formation represents somewhat deeper deposition but 1) has yielded a diverse marine ver-tebrate fauna similar to the Chandler Bridge For-mation, 2) is also rich in phosphate indicating high primary productivity, and 3) was deposited within the same protected Charleston Embayment. At present, the limited sample suggests that the Charleston Embayment was a *C. angustidens* nursery area during deposition of the Ashley For-mation. We hypothesize that this embayment was a nursery area for several million years, and predict that a larger sample from the Ashley Formation will bear this out. Most other specimens of *C. angus-tidens* collected in situ from other Ashley Formation localities are also from juveniles (e.g., CCNHM 1901). Critically, these are the first records of *Carcharocles angustidens* to be reported from the Ashley Formation (Figure 5), and indeed among the very first sharks ever reported from the unit. The Ashley Formation is not as richly fossiliferous as the overlying Chandler Bridge Formation, and discoveries from it have been more haphazard and biased towards cetaceans, sirenians, and sea tur-tles. Future studies of the McKewn subdivision assemblage will greatly expand knowledge of the marine vertebrate record from this unit.

Furthermore, it is noteworthy that nearly iden-tical collections from the same strata were made in duplicate at two different (but nearby – 2.4 km sep-aration) localities by different field paleontologists and decades apart from one another. These data demonstrate the power of careful technical field-work, and reciprocally enhance the juvenile-weighted body size signal documented herein. We predict that future 'census' collections from the Ashley and Chandler Bridge formations will be sim-ilarly dominated by juvenile teeth. We further high-light the fact that similar modern embayments along the South Carolina coast are nursery areas for multiple shark species (Castro, 1993) and pro-pose future similar studies of other commonly pre-served sharks in the Oligocene of South Carolina, including *Physogaleus*, *Galeocerdo*, and *Hempris-tis*, as juvenile teeth of these taxa are abundant in both Oligocene formations and may have also used the embayment as a nursery ground.

CONCLUSIONS

New assemblages of teeth of the extinct megatoothed shark *Carcharocles angustidens* from the Oligocene Chandler Bridge Formation of South Carolina are dominated by small teeth repre-senting juveniles, and to a lesser extent, neonates. Owing to the shallow, warm, and somewhat pro-tected geography of the Charleston Embayment, high primary productivity and abundant prey spe-cies, and a preponderance of small individuals, the Charleston Embayment is supported as a nursery area for extinct megatoothed sharks. The largest known teeth of *C. angustidens* indicate a maximum length of around 10-11 m. Fossil teeth representing the first known specimens of *C. angustidens* from the underlying Ashley Formation are also mostly small, perhaps indicating a nursery area through-out the Oligocene epoch. Modern species of *Carcharhinus, Rhizoprionodon, Mustelus,* and *Sphyrna* use nearby Bulls' Bay, South Carolina, as a nursery area today (Castro, 1993). Shark faunas have changed over time and the Charleston embayment may have filled with sediment, but new nurseries have been established in favorable habi-tats nearby, highlighting the suitability of the South

Carolina coast for sharks over the recent geologic past.

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