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Sphyrna gilberti sp. nov., a new hammerhead shark (Carcharhiniformes, Sphyrnidae) from the western Atlantic Ocean

JOSEPH M. QUATTRO[1], WILLIAM B. DRIGGERS III[2], JAMES M. GRADY[3], GLENN F. ULRICH[4] & MARK A. ROBERTS[1]

[1]*Department of Biological Sciences, Marine Science Program, University of South Carolina, Columbia, SC 29208. E-mail JosephQ@mailbox.sc.edu*
[2]*National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, P.O. Drawer 1207, Pascagoula, MS 39567.*
[3]*Department of Biological Sciences, University of New Orleans, New Orleans, LA 70148*
[4]*South Carolina Department of Natural Resources, Marine Resources Division, 217 Fort Johnson Road, Post Office Box 12559, Charleston, SC 29412*

Abstract

Sphyrna gilberti **sp. nov.** is described based on 54 specimens collected in the coastal waters of South Carolina, U.S.A. Morphologically, *S. gilberti* **sp. nov.** is separable from *S. lewini* (Griffith & Smith 1834) only in the number of precaudal vertebrae. Due to rarity of specimens and the highly migratory behavior of most sphyrnids, the range of *S. gilberti* **sp. nov.** is unknown.

Key words: Carolina hammerhead, cartilaginous fishes, Chondrichthyes, cryptic species, Elasmobranchii

Introduction

Cryptic speciation is an increasingly common interpretation of genetic variation and gene tree reconstructions for broadly distributed but morphologically conservative taxa (Quattro *et al.* 2006). Among fishes, a striking example of genetic divergence in the face of morphological conservatism was the discovery that the bonefish, *Albula vulpes* (Linnaeus 1758), was actually a complex of eight sibling species (Colborn *et al.* 2001). Although less dramatic, five independent studies of genetic variation (Abercrombie *et al.* 2005; Quattro *et al.* 2006; Zemlak *et al.* 2009; Naylor *et al.* 2012; Pinhal *et al.* 2012) confirmed a deep evolutionary partition among samples morphologically assignable to the scalloped hammerhead, *Sphyrna lewini* (Griffith & Smith 1834), which is globally distributed in tropical, subtropical, and temperate marine waters. Specifically, a subset of samples from the western Atlantic Ocean was genetically divergent, e.g., 3-7% in mitochondrial control region haplotypes, and constituted an independent evolutionary lineage in gene trees. Speciation would account for these observations and could be confirmed with concordant variation in evolutionarily independent characters (Avise & Ball 1990; Grady & Quattro 1999). Gilbert's (1967) comprehensive revision of hammerhead sharks provided the first suggestion of divergence within *S. lewini* and offered a potential test of the genetic hypothesis of cryptic speciation. The total number of vertebrae reported for a broad geographic sample of nine specimens of *S. lewini* included a conspicuously low count for one individual collected near Charleston, South Carolina (Gilbert 1967). Quattro *et al.* (2006) evaluated a similarly small sample of whole specimens and found that vertebral counts and genetic variation were concordant and distinguished two groups within putative *S. lewini*. With the caveat that the morphological subdivision in *S. lewini* was predicated on very small sample sizes, both of specimens and morphological attributes, Quattro *et al.* (2006) attributed the concordant partitions to cryptic speciation.This study examines meristic and morphometric characters to test for concordant morphological and genetic variation and presents a description of the cryptic species proposed by Quattro *et al.* (2006).

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Material and methods

Eighty juvenile hammerheads diagnosable as *S. lewini* were collected in the coastal waters of South Carolina from 2001–2003 using longline and gillnet gear (Figure 1). After capture, tissue was removed from the right pectoral fin and stored in 95% ethanol. Specimens were then euthanized, stored on ice, transported to the University of South Carolina, and frozen at -20ºC.

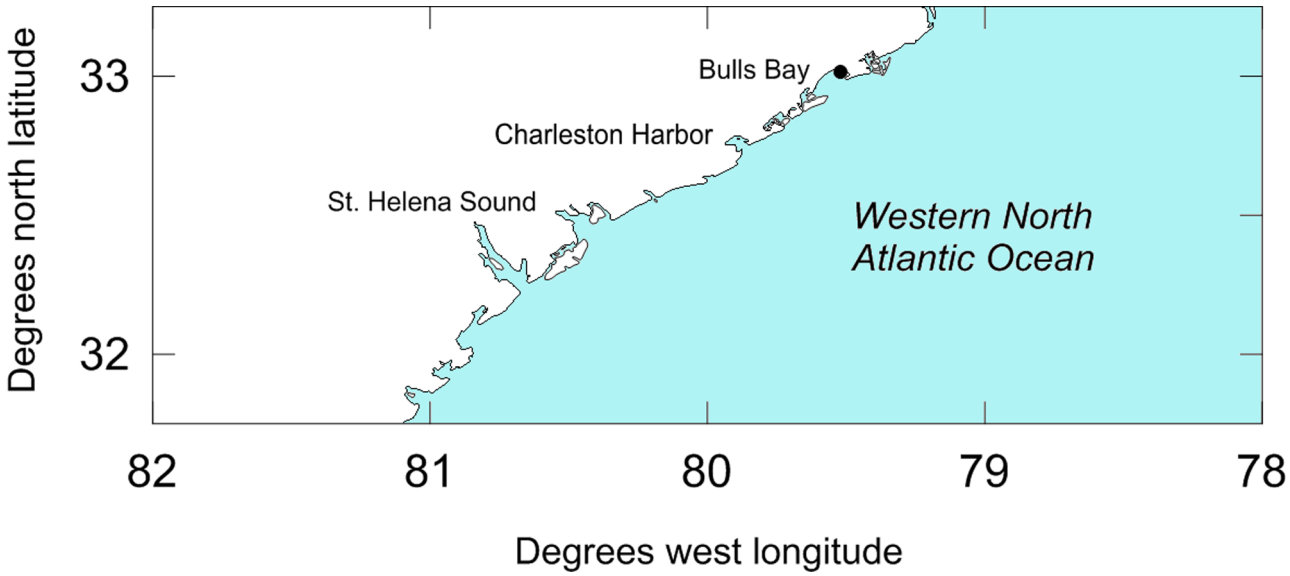

FIGURE 1. Collection locations of *Sphyrna gilberti* **sp. nov.** off the coast of South Carolina, U.S.A.. Black circle indicates sampling location for the holotype (UF 183577)..

Genetic data. Specimens were typed for the nuclear-encoded LDHA6 locus and the mitochondrial DNA control region (CR), and resultant alleles/haplotypes were incorporated into gene trees, following methods outlined in Quattro *et al.* (2006). Alignment files are available upon request to the senior author.

Morphometric data. Using thawed specimens, measurements of precaudal, fork, total and stretch total (STL) lengths were taken on a straight line along the axis of the body, and 67 additional morphometric features were evaluated (Table 1). Compagno's (1984, 1988) terminology and methods were used to identify and evaluate morphometric features.

Meristic data. Aspects of dentition and the vertebral column were evaluated for meristic variation. Teeth in the functional row of the upper and lower jaws were enumerated. Vertebrae were counted by first inserting a dissection pin into the anterior margin of the precaudal pit and perpendicular to the body axis. Radiographs were then taken of each specimen's vertebral column at 90–110 kvp and 2.4 mA using a Toshiba, AV Choice, Universal Linear MC150-C x-ray machine operated by the South Carolina Veterinary Internal Medicine Clinic. Vertebral counts were obtained from the resulting digital radiographs. Posterior to the pin, vertebrae were difficult to distinguish, as described by Springer & Garrick (1964). Therefore, only precaudal vertebrae were counted.

Data Analysis. Prior to assessing the nature, extent, and implication of morphological variation in *S. lewini*, the approach described in Elliott *et al.* (1995) was used to estimate and remove the effect of body size, i.e., allometry, on meristic and morphometric variables. Based on Francis' (2006) recommendation, STL was used as the measure of body length. Original attributes were log transformed and used to calculate a size-adjusted measure (M_{adj}) as follows:

$$M_{adj} = M_o(L_s/L_o)^b$$

where M_o = original morphometric measurement, L_o = STL of fish, and L_s = mean STL of fish from all samples for each variable, and b was estimated for each character from the observed data as the slope of the regression of log M_o on log L_o, using all specimens. Correlation coefficients for regressions of variable-specific M_{adj} on STL were estimated to test for residual effects of body size.

Variation in morphometric and meristic characters was first examined with Principal Components Analysis (PCA). Discontinuous (meristic) and continuous (morphometric) variables were analyzed independently. The

potential for morphological variation to define partitions or groups among nominal *S. lewini* was assessed by examining principal components with eigenvalues greater than one and assessing the proportion of variation explained by those components, character weightings on components, and plots of component scores.

The efficacy of meristic and adjusted morphometric characters in differentiating morphological and genetic groups was evaluated with Discriminant Functions Analysis (DFA), using a backwards selection procedure to remove variables with $F < 4$ from the final model. Finally, the original data (M_o) were standardized as percent of STL and used to test for interspecific differences between means of individual morphometrics using ANOVA. When data were not normally distributed and homoscedastic, the Kruskall-Wallis test was used to test for differences between median values. All statistical tests were considered significant at $\alpha = 0.05$.

Results

Genetic analysis

Control region haplotypes recovered from the 80 nominal *S. lewini* including those reported by Quattro *et al.* (2006) and two new haplotypes, SlCR7 (GenBank accession KC107827) and SlCR8 (GenBank accession KC107826). Control region gene tree reconstructions placed haplotype SlCR7 and others recorded for 56 specimens within the lineage Quattro *et al.* (2006) considered a cryptic species (Figure 2). Haplotypes for the remaining 26 specimens, including haplotype SlCR8, clustered with those from *S. lewini* as indicated in Quattro *et al.* (2006). The distribution of LDHA6 alleles and gene tree reconstructions were consistent with CR results and Quattro *et al.* (2006).

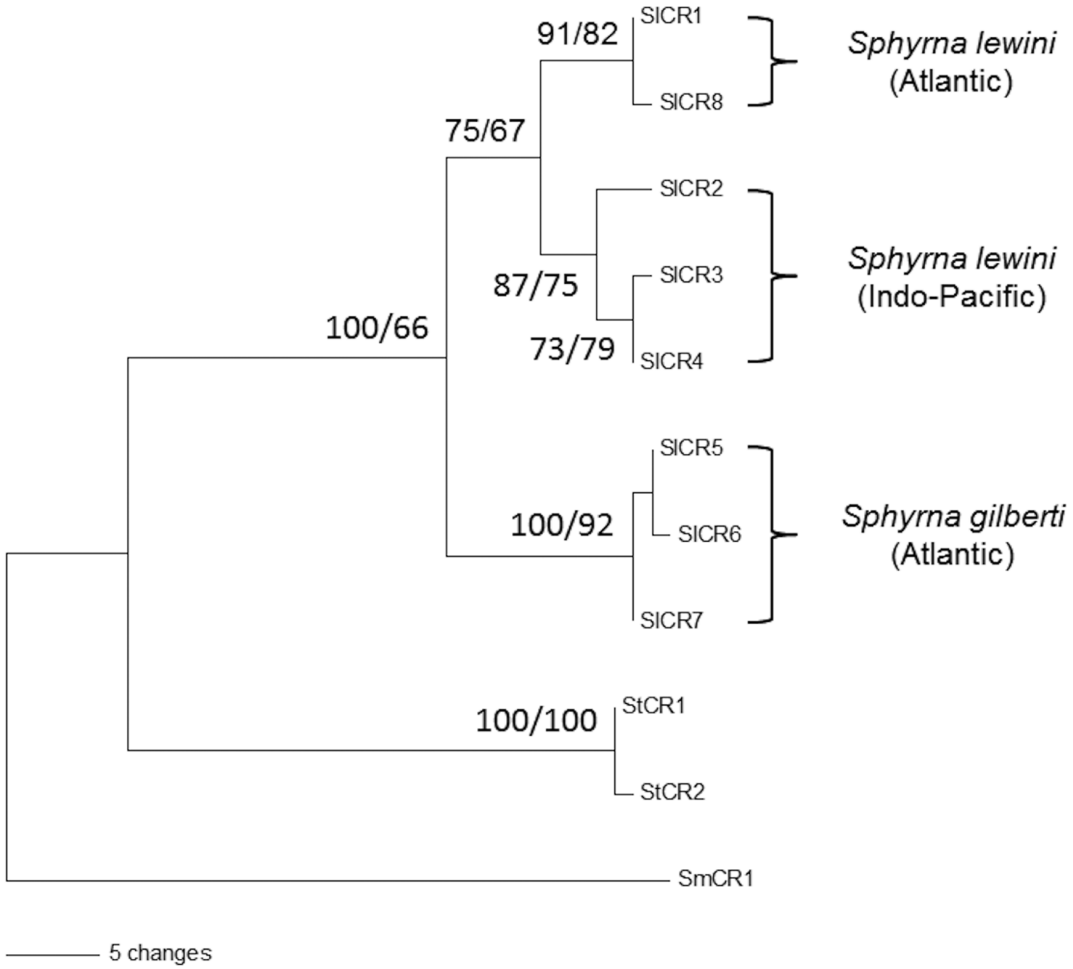

FIGURE 2. Phylogenetic relationships among mtDNA control region haplotypes. Parsimony reconstructions are depicted. Numbers near nodes are maximum parsimony/maximum likelihood bootstrap values. Haplotype descriptions, codes and collection locations can be found in Quattro *et al.* (2006).

Morphometric analysis

Based on correlation coefficients, transformation eliminated the effects of size on all morphometric variables. PCA extracted 19 components with eigenvalues greater than 1.0, although these components only accounted for 78.51% of the total variation. The proportion of variation attributed to each component and across all components indicated that continuous morphological characters could not reliably resolve groups of any type among specimens of putative *S. lewini* (Figure 3).

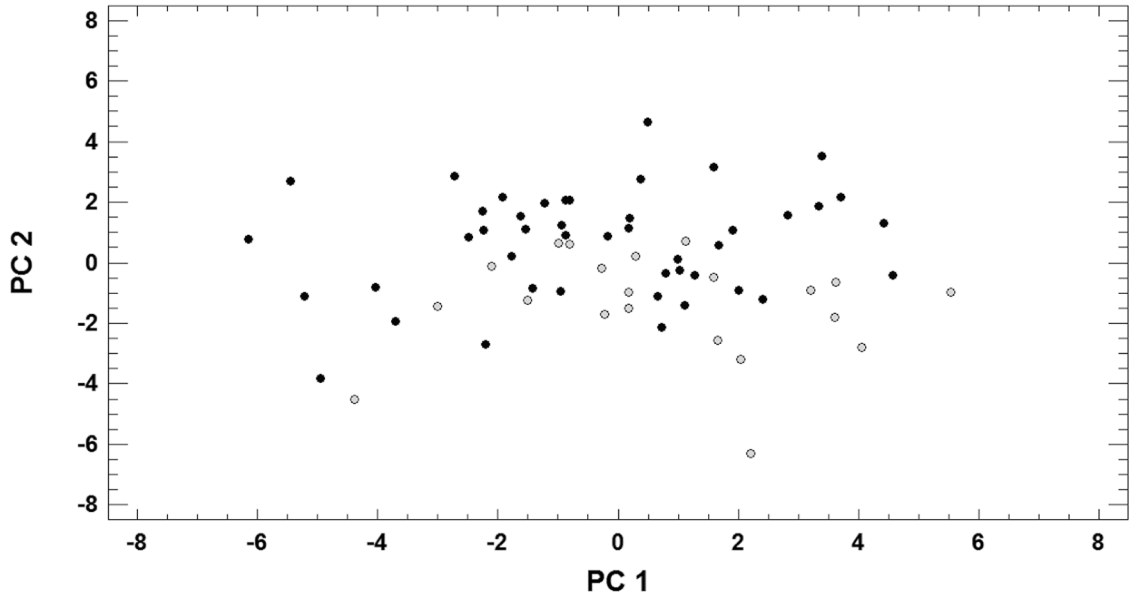

FIGURE 3. Plot of the first two principal components for 67 size-adjusted morphometric variables for putative *Sphryna lewini* specimens collected in the coastal waters of South Carolina. Gray circles indicate specimens with genotypes corresponding to *S. lewini* while black circles indicate specimens with genotypes identified as a cryptic species by Quattro *et al.* 2006.

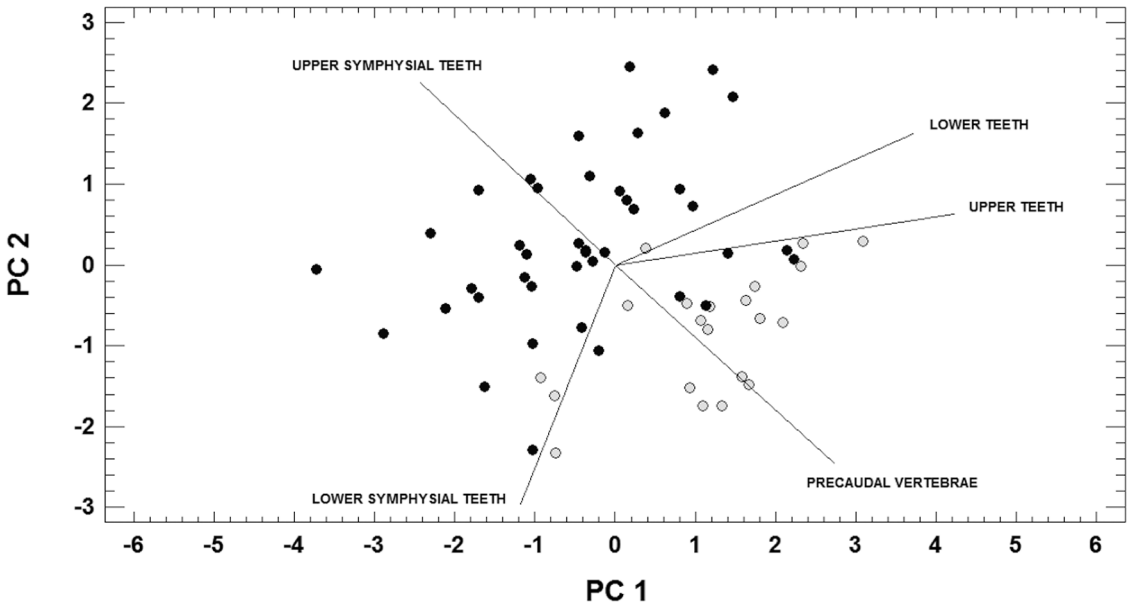

FIGURE 4. Plot of the first two principal components for five meristic variables for putative *Sphryna lewini* specimens collected in the coastal waters of South Carolina. Gray circles indicate specimens with genotypes corresponding to *S. lewini* while black circles indicate specimens with genotypes identified as a cryptic species by Quattro *et al.* 2006.

TABLE 1. Proportional dimensions, expressed as percentage of stretch total length, for *Sphyrna gilberti* **sp. nov.** and *S. lewini*. F-values for all ANOVAs are followed by associated p-values in parentheses. Values not reported when data did not meet the assumption of normality or homoscedasticity. In those cases, a Kruskall-Wallis test was performed and test statistics are reported followed by associated p-value in parentheses. Regression F, p and r^2 values are listed, respectively.

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Head length							
	S. gilberti	54	23.71 (1.11)	20.89 – 25.76	28.34(<0.01)	---	144.83 (<0.01, 0.64)
	S. lewini	26	22.34 (1.02)	20.77 – 24.78			
Pre-first dorsal length							
	S. gilberti	54	28.09 (1.16)	25.18 – 30.10	25.41 (<0.01)	---	129.59 (<0.01, 0.63)
	S. lewini	25	26.66 (1.17)	24.97 – 28.83			
Pre-second dorsal length							
	S. gilberti	54	60.09 (1.20)	56.56 – 63.20	0.78 (0.38)	---	0.57 (0.45, 0.02)
	S. lewini	26	59.85 (0.89)	57.57 – 61.46			
Prepectoral length							
	S. gilberti	54	22.71 (1.28)	19.08 – 24.88	18.01 (<0.01)	---	56.57 (<0.01, 0.47)
	S. lewini	26	21.36 (2.01)	19.13 – 24.11			
Prepelvic length							
	S. gilberti	53	46.20 (1.21)	42.37 – 48.70	27.93 (<0.01)	---	44.73 (<0.01, 0.36)
	S. lewini	25	44.67 (1.15)	43.04 – 47.12			
Preanal length							
	S. gilberti	54	57.84 (1.06)	55.02 – 60.30	11.51 (<0.01)	---	6.45 (0.01, 0.06)
	S. lewini	26	57.02 (0.98)	55.53 – 59.40			
Snout-vent length							
	S. gilberti	54	47.78 (1.17)	44.44 – 50.00	---	19.06 (<0.01)	65.58 (<0.01, 0.46)
	S. lewini	26	46.28 (1.26)	44.47 – 48.89			
Interdorsal space							
	S. gilberti	54	22.39 (0.96)	20.69 – 25.37	6.49 (0.01)	---	45.95 (<0.01, 0.37)
	S. lewini	24	23.03 (1.17)	20.89 – 25.47			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Second dorsal-caudal space							
	S. gilberti	54	6.13 (0.60)	4.46 – 7.56	---	1.46 (0.22)	2.28 (0.13, 0.02)
	S. lewini	26	6.27 (0.45)	5.03 – 6.90			
Pectoral-pelvic space							
	S. gilberti	54	19.18 (1.06)	16.75 – 21.86	5.48 (0.02)	---	0.36 (0.55, <0.01)
	S. lewini	26	18.56 (1.20)	15.62 – 20.97			
Pelvic-anal space							
	S. gilberti	54	7.50 (0.67)	5.95 – 9.53	2.26 (0.14)	---	3.00 (0.09, 0.02)
	S. lewini	26	7.75 (0.73)	6.29 – 9.05			
Anal-caudal space							
	S. gilberti	54	6.35 (0.64)	4.70 – 7.92	0.63 (0.43)	---	4.38 (0.04, 0.04)
	S. lewini	26	6.46 (0.57)	5.32 – 7.32			
Pelvic-caudal space							
	S. gilberti	53	17.80 (0.92)	15.45 – 19.85	15.06 (<0.01)	---	35.40 (<0.01, 0.31)
	S. lewini	26	18.65 (0.91)	17.43 – 20.81			
Vent-caudal length							
	S. gilberti	54	20.80 (0.91)	18.97 – 22.87	12.98 (<0.01)	---	52.36 (<0.01, 0.39)
	S. lewini	26	21.65 (1.09)	19.27 – 23.68			
Head width							
	S. gilberti	54	28.68 (1.38)	25.78 – 31.66	4.35 (0.04)	---	9.34 (<0.01, 0.10)
	S. lewini	26	28.01 (1.25)	25.09 – 30.06			
Median-lateral indentation space							
	S. gilberti	54	7.07 (0.45)	5.99 – 8.28	9.88 (<0.01)	---	15.58 (<0.01, 0.15)
	S. lewini	26	6.74 (0.37)	5.87 – 7.46			
Lateral indentation-nacelle space							
	S. gilberti	54	6.94 (0.43)	6.05 – 8.07	---	5.80 (0.02)	11.96 (<0.01, 0.12)
	S. lewini	26	6.72 (0.42)	5.99 – 8.10			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Head posterior margin							
	S. gilberti	54	7.50 (0.95)	5.58 – 9.30	2.94 (0.09)	---	3.33 (0.07, 0.03)
	S. lewini	26	7.88 (0.85)	6.64 – 9.63			
Snout length							
	S. gilberti	54	7.61 (0.41)	6.34 – 8.48	---	25.65 (<0.01)	259.95 (<0.01, 0.77)
	S. lewini	26	6.79 (0.66)	5.77 – 8.09			
Nacelle length							
	S. gilberti	54	9.83 (0.76)	8.09 – 11.66	36.52 (<0.01)	---	187.31 (<0.01, 0.70)
	S. lewini	26	8.66 (0.89)	6.64 – 10.32			
Nacelle height							
	S. gilberti	53	2.82 (0.46)	1.96 – 4.05	---	2.38 (0.12)	10.35 (<0.01, 0.11)
	S. lewini	26	2.65 (0.32)	2.09 – 4.48			
Eye length							
	S. gilberti	51	2.48 (0.31)	1.96 – 3.40	---	13.22 (<0.01)	89.71 (<0.01, 0.54)
	S. lewini	26	2.16 (0.45)	1.33 – 3.44			
Eye height							
	S. gilberti	48	1.99 (0.24)	1.43 – 2.43	---	1.36 (0.24)	40.58 (<0.01, 0.36)
	S. lewini	26	1.93 (0.34)	1.27 – 2.75			
Internarial space							
	S. gilberti	54	13.19 (0.70)	11.43 – 15.03	0.39 (0.53)	---	2.07 (0.15, 0.01)
	S. lewini	26	13.30 (0.86)	11.67 – 14.92			
Inner narial groove length							
	S. gilberti	54	6.24 (0.52)	4.82 – 7.62	44.23 (<0.01)	---	15.80 (<0.01, 0.16)
	S. lewini	26	5.45 (0.44)	4.62 – 6.19			
Nostril length							
	S. gilberti	54	2.51 (0.19)	2.09 – 2.89	---	4.30 (0.04)	18.52 (<0.01, 0.18)
	S. lewini	26	2.44 (0.15)	2.22 – 2.94			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Mouth width							
	S. gilberti	54	7.26 (0.61)	5.62 – 8.77	---	6.02 (0.01)	0.84 (0.36, <0.01)
	S. lewini	26	6.92 (0.73)	5.33 – 9.03			
Mouth length							
	S. gilberti	54	4.04 (0.36)	3.32 – 4.96	27.98 (<0.01)	---	53.26 (<0.01, 0.40)
	S. lewini	26	3.55 (0.44)	2.83 – 4.20			
Intergill length							
	S. gilberti	54	5.88 (0.54)	4.82 – 7.21	4.73 (0.03)	---	0.68 (0.41, <0.01)
	S. lewini	26	5.58 (0.66)	4.27 – 6.72			
First gill slit height							
	S. gilberti	54	2.81 (0.31)	2.02 – 3.42	---	<0.01 (0.98)	0.07 (0.80, <0.01)
	S. lewini	26	2.79 (0.39)	1.56 – 3.44			
Second gill slit height							
	S. gilberti	54	3.11 (0.32)	2.38 – 3.97	0.47 (0.49)	---	0.17 (0.68, <0.01)
	S. lewini	26	3.05 (0.41)	1.99 – 3.75			
Third gill slit height							
	S. gilberti	54	3.44 (0.29)	2.77 – 4.00	0.05 (0.83)	---	1.62 (0.21, <0.01)
	S. lewini	26	3.42 (0.33)	2.93 – 3.96			
Fourth gill slit height							
	S. gilberti	54	3.18 (0.38)	2.58 – 4.30	0.00 (0.98)	---	7.95 (<0.01, 0.08)
	S. lewini	26	3.18 (0.41)	2.58 – 3.99			
Fifith gill slit height							
	S. gilberti	54	2.43 (0.31)	1.84 – 3.04	2.16 (0.15)	---	2.15 (0.15, 0.01)
	S. lewini	26	2.54 (0.32)	1.86 – 3.13			
Pectoral anterior margin							
	S. gilberti	53	12.19 (0.64)	10.93 – 14.84	---	8.11 (<0.01)	7.90 (0.01, 0.08)
	S. lewini	26	12.50 (0.79)	9.86 – 13.86			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Pectoral base							
	S. gilberti	54	5.36 (0.44)	4.68 – 6.80	---	0.58 (0.45)	4.59 (0.04, 0.04)
	S. lewini	26	5.38 (0.44)	4.19 – 6.17			
Pectoral inner margin							
	S. gilberti	54	4.59 (0.42)	3.71 – 5.70	31.50 (<0.01)	---	14.18 (<0.01, 0.14)
	S. lewini	26	4.03 (0.42)	3.24 – 5.21			
Pectoral posterior margin							
	S. gilberti	52	9.84 (0.65)	8.13 – 11.62	8.33 (<0.01)	---	36.67 (<0.01, 0.32)
	S. lewini	26	10.33 (0.79)	9.07 – 11.52			
Pectoral height							
	S. gilberti	53	10.37 (0.73)	8.80 – 11.84	0.75 (0.39)	---	7.53 (<0.01, 0.08)
	S. lewini	26	10.53 (0.81)	8.39 – 11.98			
First dorsal anterior margin							
	S. gilberti	52	16.08 (0.79)	13.85 – 17.84	3.30 (0.07)	---	6.53 (0.01, 0.07)
	S. lewini	25	16.43 (0.85)	14.61 – 18.05			
First dorsal base							
	S. gilberti	54	9.33 (0.70)	7.93 – 10.78	11.22 (<0.01)	---	59.04 (<0.01, 0.43)
	S. lewini	25	9.91 (0.72)	8.47 – 11.33			
First dorsal inner margin							
	S. gilberti	54	3.64 (0.36)	2.67 – 4.35	7.29 (<0.01)	---	1.11 (0.30, <0.01)
	S. lewini	25	3.87 (0.30)	3.23 – 4.37			
First dorsal posterior margin							
	S. gilberti	53	12.36 (1.53)	8.44 – 14.26	1.53 (0.22)	---	20.83 (<0.01, 0.20)
	S. lewini	25	12.80 (0.15)	10.43 – 14.55			
First dorsal height							
	S. gilberti	53	12.61 (0.93)	10.71 – 14.44	2.60 (0.11)	---	27.18 (<0.01, 0.26)
	S. lewini	25	13.01 (1.21)	10.77 – 15.43			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Second dorsal anterior margin							
	S. gilberti	54	3.77 (0.43)	2.38 – 4.85	---	0.01 (0.90)	0.61 (0.44, <0.01)
	S. lewini	26	3.78 (0.34)	3.22 – 4.36			
Second dorsal base							
	S. gilberti	54	3.01 (0.48)	1.81 – 3.97	0.24 (0.63)	---	3.13 (0.08, 0.03)
	S. lewini	26	2.96 (0.35)	2.25 – 3.90			
Second dorsal inner margin							
	S. gilberti	54	4.84 (0.34)	4.10 – 5.70	16.44 (<0.01)	---	18.93 (<0.01, 0.19)
	S. lewini	26	5.17 (0.33)	4.58 – 5.71			
Second dorsal posterior margin							
	S. gilberti	54	5.33 (0.38)	4.74 – 6.48	14.07 (<0.01)	---	30.78 (<0.01, 0.28)
	S. lewini	26	5.70 (0.24)	4.95 – 6.62			
Second dorsal height							
	S. gilberti	53	2.04 (0.32)	1.24 – 2.79	---	7.41 (<0.01)	24.60 (<0.01, 0.26)
	S. lewini	26	2.29 (0.47)	1.05 – 3.19			
Pelvic anterior margin							
	S. gilberti	54	5.26 (0.66)	4.09 – 6.67	---	0.12 (0.73)	0.94 (0.34, <0.01)
	S. lewini	26	5.27 (0.51)	4.64 – 6.72			
Pelvic base							
	S. gilberti	54	4.84 (0.55)	3.72 – 5.86	7.91 (0.01)	---	12.16 (<0.01, 0.12)
	S. lewini	26	5.18 (0.41)	4.00 – 5.88			
Pelvic inner margin							
	S. gilberti	54	3.29 (0.40)	2.55 – 4.29	---	1.54 (0.21)	5.16 (0.03, 0.05)
	S. lewini	26	3.16 (0.25)	2.73 – 3.60			
Pelvic posterior margin							
	S. gilberti	54	6.11 (0.45)	4.57 – 6.81	---	13.90 (<0.01)	40.29 (<0.01, 0.33)
	S. lewini	26	6.60 (0.59)	5.36 – 8.05			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Pelvic height							
	S. gilberti	54	4.09 (0.48)	3.15 – 5.21	0.60 (0.44)	---	0.69 (0.41, <0.01)
	S. lewini	26	4.18 (0.54)	3.20 – 5.32			
Anal anterior margin							
	S. gilberti	54	4.48 (0.42)	3.50 – 5.42	---	8.94 (<0.01)	19.72 (<0.01, 0.19)
	S. lewini	26	4.87 (0.65)	3.57 – 6.33			
Anal base							
	S. gilberti	54	4.51 (0.41)	3.69 – 5.48	12.27 (<0.01)	---	26.17 (<0.01, 0.24)
	S. lewini	26	4.90 (0.55)	3.66 – 6.33			
Anal inner margin							
	S. gilberti	54	3.83 (0.31)	2.81 – 4.44	7.68 (<0.01)	---	5.33 (0.02, 0.05)
	S. lewini	26	4.04 (0.36)	3.30 – 4.50			
Anal posterior margin							
	S. gilberti	54	5.23 (0.52)	4.00 – 6.58	7.05 (<0.01)	---	11.07 (<0.01, 0.11)
	S. lewini	25	5.56 (0.48)	4.41 – 6.58			
Anal height							
	S. gilberti	54	3.39 (0.49)	2.71 – 4.60	---	0.66 (0.42)	3.15 (0.08, 0.03)
	S. lewini	26	3.27 (0.33)	2.72 – 3.99			
Dorsal caudal margin							
	S. gilberti	54	30.67 (1.11)	28.12 – 34.69	---	5.97 (0.01)	7.98 (<0.01, 0.08)
	S. lewini	26	31.09 (0.80)	29.21 – 32.16			
Preventral caudal margin							
	S. gilberti	54	10.75 (0.83)	8.20 – 12.44	1.25 (0.27)	---	0.57 (0.45, <0.01)
	S. lewini	26	10.51 (0.97)	7.78 – 12.17			
Upper postventral caudal margin							
	S. gilberti	53	25.57 (1.15)	21.52 – 27.86	---	1.81 (0.18)	9.26 (<0.01, 0.10)
	S. lewini	26	26.03 (1.31)	23.34 – 28.39			

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TABLE 1. (Continued)

		n	Mean (S.D.)	Range	ANOVA	K-W test	Regression
Lower postventral caudal margin							
	S. gilberti	53	6.06 (0.70)	4.91 – 7.94	---	0.37 (0.54)	11.98 (<0.01, 0.12)
	S. lewini	26	5.78 (1.03)	3.57 – 7.39			
Caudal fork length							
	S. gilberti	53	7.11 (0.64)	5.36 – 8.28	2.49 (0.12)	---	0.09 (0.80, <0.01)
	S. lewini	26	6.87 (0.57)	5.86 – 7.73			
Caudal fork width							
	S. gilberti	53	8.01 (0.41)	7.20 – 9.26	2.33 (0.13)	---	0.16 (0.69, <0.01)
	S. lewini	26	7.88 (0.32)	6.98 – 8.49			
Subterminal caudal margin							
	S. gilberti	53	2.56 (0.26)	1.98 – 3.17	4.35 (0.04)	---	9.89 (<0.01, 0.10)
	S. lewini	26	2.42 (0.29)	1.94 – 3.15			
Terminal caudal margin							
	S. gilberti	53	6.06 (0.51)	4.51 – 7.37	---	13.64 (<0.01)	1.26 (0.26, <0.01)
	S. lewini	26	5.61 (0.54)	4.17 – 6.38			

When genetic identity was used *a priori* as a classification factor, the DFA identified five variables, including pre-second dorsal length, pre-pectoral length, internarial space, inner narial groove length and lower postventral caudal margin that discriminate lineages. The resulting function correctly classified 81.43% of cases to genetic lineage. Results of the ANOVA and Kruskall-Wallis tests indicated significant differences between species in the mean or median lengths for pre-pectoral length and inner narial groove length. However, the range of all standardized morphometric variables overlap for genetic lineages, limiting the utility of morphometric attributes as distinguishing features (Table 1).

Meristic analysis

PCA of five meristic characters extracted two components with eigenvalues greater than 1 and that explained 59.40% of the total variation. Despite the proportion of total variation attributed to these components, meristic variables identified two putative groups of scalloped hammerheads with marginal overlap (Figure 4). These groups correspond to the two genetic lineages recovered among the 80 specimens. DFA identified only the number of precaudal vertebrae as a significant discriminator of the genetic groups, with 98.70% of specimens classified correctly. One specimen was incorrectly classified and with 91 precaudal vertebrae fell between the ranges for other specimens assigned to the genetic lineages, 92–99 (*S. lewini*) and 83–87 (cryptic species).

***Sphyrna gilberti* sp. nov.**
(Figures 5–6, Table 1)

Proposed common name. Carolina hammerhead

This name was selected based on the type locality of *S. gilberti* **sp. nov.**.

Materials examined. Type specimens were collected in the coastal waters of South Carolina (Figure 1) and placed in the collection of the Florida Museum of Natural History. In parentheses following each specimen's identification code is the CR haplotype and the LDHA6 genotype.

Holotype. UF 183577 (5, 6/6), 467 mm STL, female, Bulls Bay, South Carolina, U.S.A. July 2002, collected by W.B. Driggers III, D. Oakley and G.F. Ulrich.

Paratypes. All from Bulls Bay, South Carolina, U.S.A. and collected by W.B. Driggers III, D. Oakley and G.F. Ulrich. UF 183579 (both 5, 6/6), two males, 468–471 mm STL, July 2001; UF 183578 (both 5, 6/6), two females, 471–506 mm STL, July 2002.

Comparative material. All specimens listed below housed at the University of South Carolina, Department of Biological Sciences, Conservation Genetics Laboratory and collected by W.B. Driggers III, J. M. Grady, D. Oakley and/or G.F. Ulrich in the nearshore waters of South Carolina, U.S.A.

S. gilberti: JQNSP2 (5, 6/6), 441 mm STL, male, Bulls Bay, July 2001; JQNSP3 (5, 6/6), 466 mm STL, female, Bulls Bay, July 2001; JQNSP4 (5, 6/6), 456 mm STL, female, Bulls Bay, July 2001; JQNSP9 (5, 6/6), 481 mm STL, male, Bulls Bay, July 2001; JQNSP10 (5, 6/6), 481 mm STL, Bulls Bay, July 2001; JQNSP11 (5, 6/6), 430 mm STL, male, Bulls Bay, July 2001; JQNSP16 (5, 6/6), 447 mm STL, female, Bulls Bay, June 2002; JQNSP17 (5, 6/6), 430 mm STL, male, Bulls Bay, June 2002; JQNSP19 (5, 6/6), 538 mm STL, male, Bulls Bay, August 2001; JQNSP20 (7, 6/6), 421 mm STL, female, Bulls Bay, August 2001; JQNSP24 (5, 6/6), 420 mm STL, female, Bulls Bay, May 2002; JQNSP25 (5, 6/6), 406 mm STL, female, Bulls Bay, May 2002; JQNSP26 (7, 6/6), 392 mm STL, female, Bulls Bay, May 2002; JQNSP27 (5, 6/6), 675 mm STL, male, Charleston Harbor, June 2002; JQNSP28 (5, 6/6), 462 mm STL, male, Bulls Bay, June 2002; JQNSP29 (5, 6/6), 438 mm STL, female, Bulls Bay, June 2002; JQNSP30 (5, 6/6), 495 mm STL, female, Bulls Bay, July 2002; JQNSP31 (5, 6/6), 488 mm STL, male, Bulls Bay, July 2002; JQNSP32 (5, 6/6), 484 mm STL, female, Bulls Bay, July 2002; JQNSP33 (5, 6/6), 495 mm STL, male, Bulls Bay, July 2002; JQNSP37 (5, 6/6), 541 mm STL, male, Bulls Bay, August 2002; JQNSP38 (5, 6/6), 458 mm STL, female. Bulls Bay, August 2002; JQNSP40 (5, 6/6), 603 mm STL, female, St. Helena Sound, September 2002; JQNSP41 (5, 6/6), 529 mm STL, male, St. Helena Sound, September 2002; JQNSP42 (5, 6/6), 572 mm STL, female, St. Helena Sound, September 2002; JQNSP43 (5, 6/6), 540 mm STL, female, St. Helena Sound, September 2002; JQNSP44 (5, 6/6), 538 mm STL, female, St. Helena Sound, September 2002; JQNSP46 (5, 6/6), 529 mm STL, male, St. Helena Sound, August 2002; JQNSP50 (5, 6/6), 587 mm STL, male, St. Helena

Sound, August 2002; JQNSP60 (5, 6/6), 694 mm STL, female, Charleston Harbor, October 2002; JQNSP78 (5, 6/6), 391 mm STL, male, coastal South Carolina, 2003; JQNSP79 (5, 6/6), 370 mm STL, male, coastal South Carolina, 2003; JQNSP81 (5, 6/6), 406 mm STL, female, coastal South Carolina, 2003; JQNSP82 (5, 6/6), 404 mm STL, female, coastal South Carolina, 2003;JQNSP84 (5, 6/6), 387 mm STL, male, coastal South Carolina, 2003; JQNSP85 (5, 6/6), 375 mm STL, male, coastal South Carolina, 2003; JQNSP86 (5, 6/6), 326 mm STL, male, coastal South Carolina, 2003; JQNSP87 (5, 6/6), 370 mm STL, female, coastal South Carolina, 2003; JQNSP88 (5, 6/6), 420 mm STL, male, coastal South Carolina, 2003; JQNSP89 (5, 6/6), 443 mm STL, male, coastal South Carolina, 2003; JQNSP90 (5, 6/6), 415 mm STL, female, coastal South Carolina, 2003; JQNSP91 (5, 6/6), 409 mm STL, male, coastal South Carolina, 2003; JQNSP93 (5, 6/6), 389 mm STL, female, Bulls Bay, May 2003; JQNSP94 (5, 6/6), 377 mm STL, female, Bulls Bay, May 2003; JQNSP95 (5, 6/6), 400 mm STL, female, Bulls Bay, May 2003; JQNSP96 (5, 6/6), 406 mm STL, male, Bulls Bay, May 2003; JQNSP98 (5, 6/6), 390 mm STL, female, Bulls Bay, May 2003; JQNSP105 (5, 6/6),412 mm STL, male, Bulls Bay, May 2003.

S. lewini: JQNSP12 (1, 2/2), 445 mm STL, male, Bulls Bay, June 2002; JQNSP18 (1, 1/2), 525 mm STL, male, Bulls Bay, June 2002; JQNSP21 (1, 1/1), 436 mm STL, female, Bulls Bay, May 2002; JQNSP22 (1, 1/2), 437 mm STL, female, Bulls Bay, May 2002; JQNSP23 (1, 1/2), 476 mm STL, female, Bulls Bay, May 2002; JQNSP34 (1, 2/2), 906 mm STL, female, Charleston Harbor, July 2002; JQNSP35 (1, 2/2), 883 mm STL, female, Charleston Harbor, July 2002; JQNSP36 (1, 1/2), 918 mm STL, female, Charleston Harbor, July 2002; JQNSP39 (1, 2/2), 469 mm STL, female, Bulls Bay, August 2002; JQNSP45 (1, 1/2), 690 mm STL, male, St. Helena Sound, August 2002; JQNSP48 (1, 1/2), 676 mm STL, male, St. Helena Sound, August 2002; JQNSP49 (1, 1/1), 648 mm STL, female, St. Helena Sound, August 2002; JQNSP51 (1, 1/1), 632 mm STL, female, St. Helena Sound, August 2002; JQNSP52 (8, 2/2), 653 mm STL, male, St. Helena Sound, August 2002; JQNSP53 (8, 2/2), 690 mm STL, male, St. Helena Sound, August 2002; JQNSP54 (1, 2/2), 733 mm STL, female, Charleston Harbor, September 2002; JQNSP58 (1, 2/2), 775 mm STL, female, Charleston Harbor, September 2002; JQNSP59 (1, 2/2), 739 mm STL, female, Charleston Harbor, September 2002; JQNSP61 (1, 1/1), 729 mm STL, male, Charleston Harbor, September 2002; JQNSP100 (1, 1/2), 527 mm STL, female, Bulls Bay, May 2003; JQNSP101 (1, 2/2), 485 mm STL, male, Bulls Bay, May 2003; JQNSP103 (1, 2/2), 452 mm STL, male, Bulls Bay, May 2003; JQNSP104 (1, 1/1), 444 mm STL, male, Bulls Bay, May 2003; JQNSP-C (1, 1/2), 877 mm STL, male, North Edisto, June 2003; JQNSP-D, 526 mm STL, female, North Edisto, June 2003; JQNSP-E (1, 1/2), 801 mm STL, female, Charleston, November 2002.

Diagnosis. *Sphyrna gilberti* **sp. nov.** can be distinguished from congeners by having a head length greater than 20% of STL, cephalofoil with median indentation, inner narial groove present, pelvic fins with straight rear margins, and 91 or fewer precaudal vertebrae.

Description. Direct measures and counts for the holotype of *S. gilberti* **sp. nov.** (UF 183577) are listed below and reported in mm. Values in parentheses represent proportion of each measure as a percentage of STL. Proportions, expressed as percent of STL, of all collected specimens of *S. gilberti* **sp. nov.** are presented in Table 1.

Female; precaudal length 309 (66); fork length 358 (77); natural total length 454 (97); STL 467; head length 113 (24); pre-first dorsal length 130 (28); pre-second dorsal length 281 (60); prepectoral length 106 (23); prepelvic length 217 (46); preanal length 270 (58); snout-vent length 225 (48); interdorsal space 102 (22); second dorsal-caudal space 26 (6); pectoral-pelvic space 89 (19); pelvic-anal space 33 (7); anal-caudal space 34 (7); pelvic-caudal space 86 (18); vent-caudal length 97 (21); head width 138 (30); median-lateral indentation space 34 (7); lateral indentation-nacelle space 33 (7); head posterior margin 35 (7); snout length 36 (8); nacelle length 47 (10); nacelle height 13 (3); eye length 12 (2); eye height 10 (2); internarial space 65 (14); inner narial groove length 30 (6); nostril length 12 (3); mouth width 34 (7); mouth length 19 (4); dental formula U 13–1–13, L 13-1–13; intergill length 28 (6); first gill slit height 15 (3); second gill slit height 16 (3); third gill slit height 18 (4); fourth gill slit height 18 (4); fifth gill slit height 14 (3); pectoral anterior margin 53 (11); pectoral base 25 (5); pectoral inner margin 21 (4)pectoral posterior margin 44 (9); pectoral height 48 (10); first dorsal anterior margin 75 (16); first dorsal base 43 (9); first dorsal inner margin 15 (3); first dorsal posterior margin 60 (13); first dorsal height 60 (13); second dorsal anterior margin 19 (4); second dorsal base 15 (3); second dorsal inner margin 21 (4); second dorsal posterior margin 25 (5); second dorsal height 9 (2); pelvic anterior margin 21 (4); pelvic base 21 (4); pelvic inner margin 16 (3); pelvic posterior margin 27 (6); pelvic height 22 (5); anal anterior margin 20 (4); anal base 21 (4); anal inner margin 18 (4); anal posterior margin 27 (6); anal height 15 (3); dorsal caudal margin 144 (31); preventral caudal margin 49 (10); upper postventral margin 188 (25); lower postventral caudal margin 29 (6); caudal fork length 32 (7); caudal fork width 35 (7); subterminal caudal margin 11 (2); terminal caudal margin 29 (6); 87 precaudal vertebrae.

Body round to oval in cross section becoming rectangular at the caudal peduncle. Head laterally expanded with median indentation. Head width 25–32% of STL. Lateral indentation present on each side of head approximately equidistant between median indentation and anterior margin of nacelle. Inner narial groove extends from nostril to lateral indentation. Nacelle well defined and eye height usually greater than 50% nacelle height. Nictitating eyelid present. Posterior orbit on perpendicular with symphysis of upper jaw. Snout length approximately equal to mouth width. Corners of mouth even with posterior margin of head. Labial furrows small and inconspicuous. Head length approximately equal to interdorsal space. Third gill slit height approximately equal to anal fin height. Fourth gill slit near pectoral fin origin. Fifth gill slit height shorter than other gill slits and posterior to pectoral fin origin.

FIGURE 5. Holotype of *Sphyrna gilberti* **sp. nov.** collected in Bulls Bay, South Carolina, U.U.S.A. UF 183577, 467 mm STL.

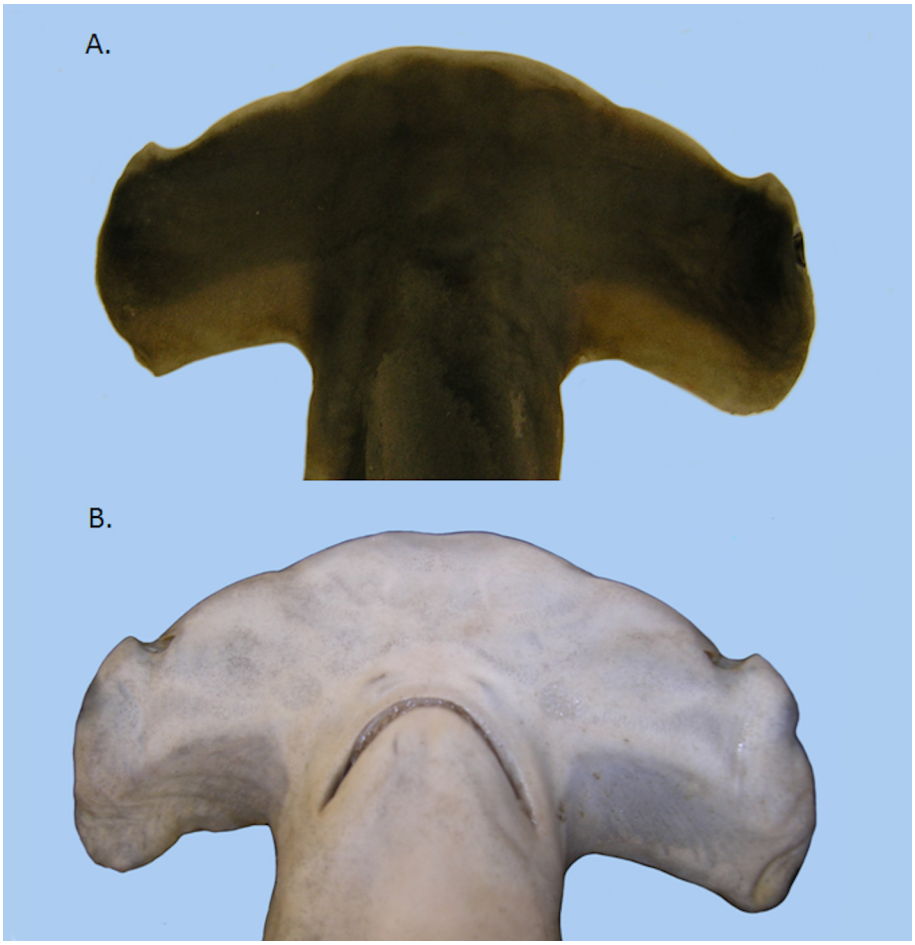

FIGURE 6. Dorsal (A) and ventral (B) views of the cephalofoil from the holotype of *Sphyrna gilberti* **sp. nov.** collected in Bulls Bay, South Carolina, U.S.A. UF 183577, 467 mm STL. Note that indention in ventral view of the left nacelle is an artifact of preservation.

Pectoral fin relatively small and its height approximately equal to the pectoral fin posterior margin. Pectoral fin anterior margin. Pectoral fin anterior margin less than 50% of head width. Apex of pectoral fin rounded and posterior margin relatively straight with rounded free rear tip. First dorsal fin origin ranges from above pectoral fin insertion to above pectoral fin inner margin. First dorsal fin anterior margin straight with apex slightly rounded. First dorsal fin posterior margin straight to slightly concave and its height approximately equal to pectoral anterior margin. Length of first dorsal fin inner margin and pelvic fin inner margin approximately equal. Interdorsal ridge absent in life but can appear present in preserved specimens. Second dorsal fin origin posterior to anal fin origin. Second dorsal fin small and its height equal to or less than 20% of first dorsal fin height. Second dorsal fin inner margin length at least twice as long as second dorsal fin height. Origin of pelvic fin posterior to first dorsal fin free rear tip. Pelvic fin posterior margin straight. Anal fin base broad and equal to or less than anal fin height. Upper and lower precaudal pits present. Caudal fin deeply forked and greater than 25% of STL. Subterminal notch present.

Dental formula U 11 to 15–0 to 2–11 to 15, L 11 to 14–0 to 2–11 to 14 (dental formula should be considered preliminary as jaws were not removed from specimens and small posterior teeth could have gone unnoticed resulting in lower counts than actual number of teeth present). All teeth unicuspidate. Symphysial teeth smaller than adjacent anterior teeth, crown well differentiated from base, smooth edged to weakly serrated, and symmetrical. Upper anterior, lateral and posterior teeth with cusp at an oblique angle that becomes progressively greater moving from the symphysis toward the rear of the palatoquadrate. Mesial edge of upper anterior, lateral and posterior teeth smooth to weakly serrated. Distal edge of upper anterior, lateral and posterior teeth with a central notch and ranging from smooth to serrated from the tip of the cusp toward the base. Lower anterior teeth adjacent to the symphysis erect, symmetrical, smooth to weakly serrated and differentiated from base. Lower lateral and posterior teeth similar in shape to upper anterior, lateral and posterior teeth.

Number of precaudal vertebrae range from 83 to 91. One individual had greater than 87 precaudal vertebrae.

Color. Live specimens with grey to brown dorsal coloration fading to white ventrally. Ventral pectoral fin apex variably white to dusky (60% of specimens with dusky-tipped pectoral fins). Lower lobe of caudal fin with dusky to black tip. Frozen specimens retain similar, yet not as distinct, colorations to live individuals.

Size. Maximum size is unknown; however, the mean size of *S. gilberti* **sp. nov.** and *S. lewini* neonates with an open umbilicus collected during this study was 397 mm and 451 mm STL, respectively. Therefore, assuming equal brood size, lower size at birth for *S. gilberti* **sp. nov.** could indicate that it reaches a smaller maximum size than *S. lewini*.

Etymology. Named in honor of ichthyologist Carter R. Gilbert, who first reported (Gilbert 1967) an anomalous specimen of *S. lewini* collected off Charleston, SC (USNM 25180). Based on vertebral count and collection location, the anomalous specimen is likely the first recorded individual of *S. gilberti* **sp. nov.**.

Distribution. All specimens reported herein and those examined by Quattro *et al.* (2006) were captured in the western North Atlantic Ocean. However, data presented by Pinhal *et al*. (2012) indicate a presence in the western South Atlantic Ocean. Based on the rarity of samples of *S. gilberti* **sp. nov**. relative to *S. lewini* and the absence of morphological attributes for field identification, no definitive information is available on geographic distribution and more data will be required to determine its precise range.

Remarks. Concordant partitions among independent character sets are reliable indicators of both evolutionary divergence and speciation (Avise & Ball 1990; Grady & Quattro 1999). Based on extensive geographic sampling, mitochondrial gene trees recovered a deep divergence within *S. lewini* that was repeated in independent nuclear genes (Abercrombie *et al.* 2005; Quattro *et al.* 2006; Zemlak *et al.* 2009; Naylor *et al.* 2012; Pinhal *et al.* 2012). Although morphometric attributes did not delineate groups among nominal *S. lewini*, meristic characters defined two morphological groups that are consistent with the genetic lineages.

Analyses of the 67 measurements taken on 54 *S. gilberti* **sp. nov.** and 26 *S. lewini* specimens failed to reveal any external character useful in differentiating the two species. While significant differences were found in mean or median values for specific characters between species, the range of each measure overlapped. Gilbert (1967) suggested that chondrocranium structure and the distribution of ampullae on the ventral side of the head are taxonomically valuable for sphyrnids. Comparisons of radiographs of the heads of *S. gilberti* **sp. nov.** and *S. lewini* failed to reveal any structural differences (Figure 7). Visual comparisons of the distribution of ampullae also failed to reveal differences between the two species (Figure 6).

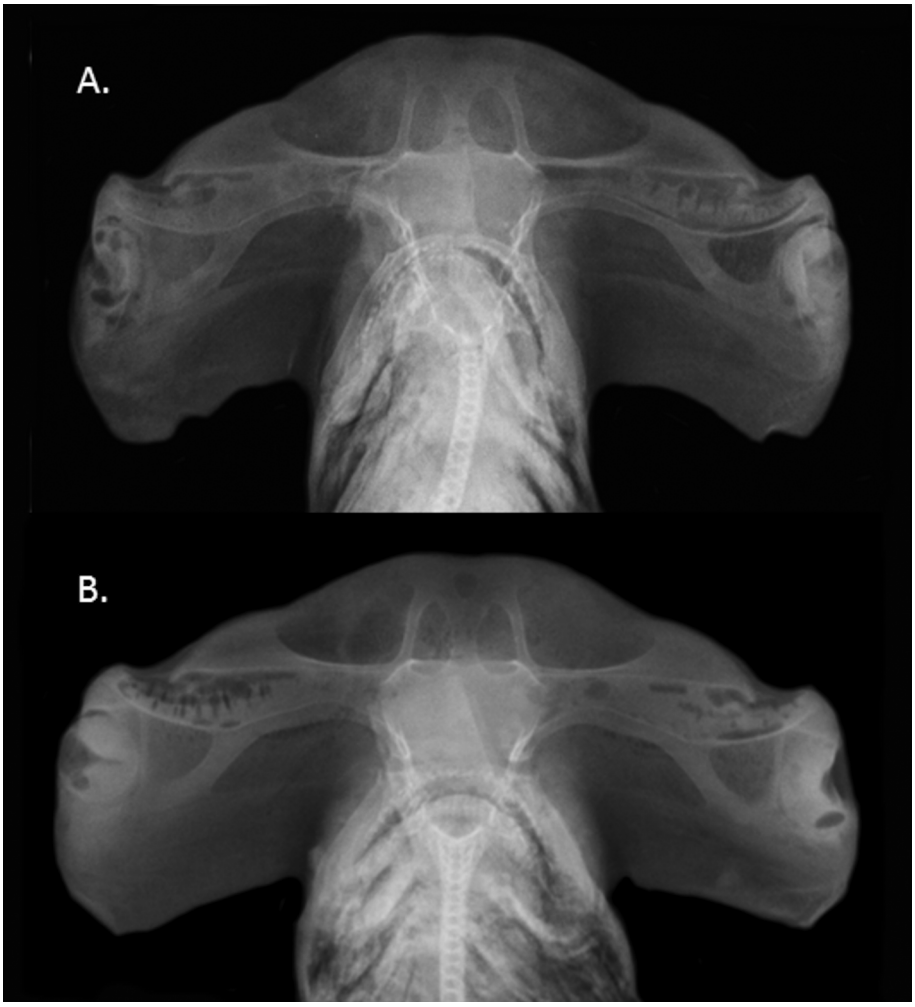

FIGURE 7. Radiograph of chondrocranium from A. *Sphyrna gilberti* **sp. nov.** collected from Bulls Bay, South Carolina, U.S.A. UF 183578, 471 mm STL female and B. *S. lewini* collected in Bulls Bay, South Carolina, U.S.A. JQNSP 23, 476 mm STL female.

Consistency across characters would otherwise support Quattro *et al.*'s (2006) suggestion of cryptic speciation in *S. lewini* but for the reliance on meristic attributes for morphological separation of the genetic groups. Among meristic attributes, only the number of precaudal vertebrae separates *S. gilberti* **sp. nov.** from *S. lewini* (Figure 8). While meristic characteristics, in particular vertebral counts, are subject to environmental influence in fishes, a phenomenon discussed as early as Jordan (1891), the taxonomic efficacy of vertebral counts in differentiating shark species was noted by Springer & Garrick (1964), who stated "of the genera containing two or more species, almost half include at least one species distinguishable on vertebral counts." For example, *Rhizoprionodon terraenovae* (Richardson 1836) and *R. porosus* (Poey 1861) are two species of small sharks in the western North Atlantic Ocean recognized as distinct based on overlapping number of precaudal vertebrae (Springer 1964). Other examples of subspecies or species whose proper identification rely on vertebral counts include *Mustelus canis canis* (Mitchell 1815) vs. *M. canis insularis* Heemstra 1997 (Heemstra 1997), *Carcharhinus galapagensis* (Snodgrass & Heller 1905) vs. *C. obscurus* (Lesueur 1818) (Garrick 1982) and *C. limbatus* (Valenciennes 1839) vs. *C. tilstoni* (Whitley 1950) (Last & Stevens 1994).

The paucity of diagnostic features for *S. gilberti* **sp. nov.** could be related to the use of neonates and young juveniles in morphological comparisons. Adult *S. gilberti* **sp. nov.** and *S. lewini* specimens might reveal additional diagnostic morphological characters, assuming that the effect of allometry on characters is removed. Gilbert (1967) reported significant ontogenetic changes in head morphology, fin shape and fin coloration, but noted that other characters, such as chondrocranium structure and ampullae pore patterns, are reliably stable. Among the 67 morphometric attributes examined in this study, 22 were correlated with body length when standardizing each

measure by STL. Therefore, morphological characters intended as taxonomic keys for *S. gilberti* **sp. nov.** should be carefully evaluated for developmental effects.

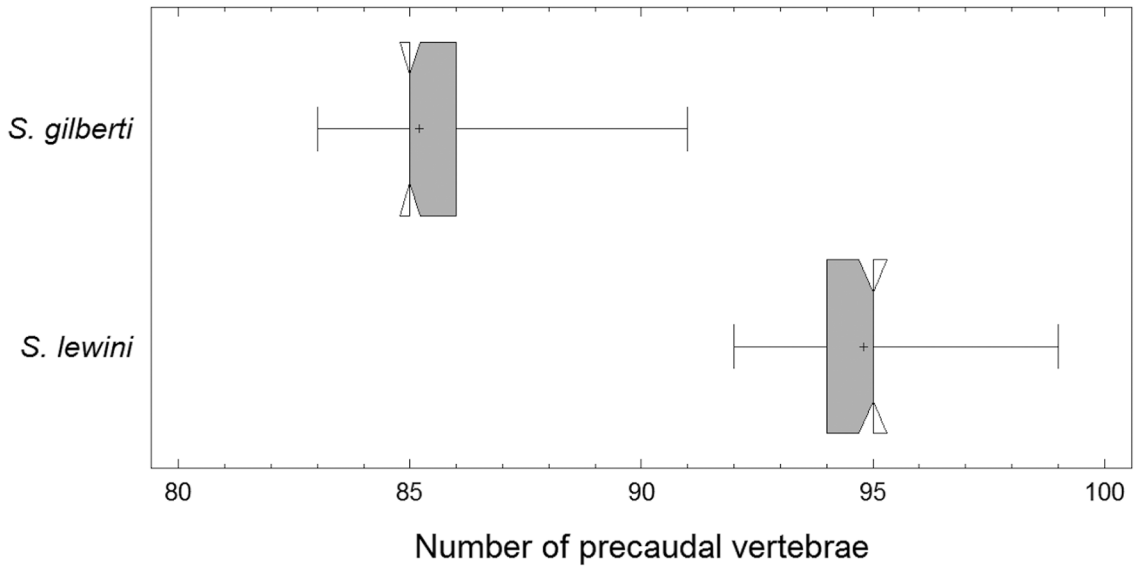

FIGURE 8. Box and whisker plot for number of precaudal vertebrae for *Sphyrna gilberti* **sp. nov.** (n = 54) and *S. lewini* (n = 26) specimens examined in this study. Bars represent minimum and maximum observed values, grey box represents lower and upper quantiles, + indicates the mean, center line represents the median and the notch indicates the 95% confidence interval around the median.

Recently, Castro (2011) suggested that the cryptic species proposed by Quattro *et al.* (2006) could be *S. couardi* Cadenat 1950, a species described from within *S. diplana* Springer 1941 (= *S. lewini*). Cadenat (1950) briefly described what he considered a shark closely resembling *S. diplana*, except the unknown species had a "longer and narrower" head and the ventral sides of the pectoral fins were entirely white. Subsequent addition of diagnostic characters separating *S. couardi* from *S. lewini*, including ampullae pore patterns (Cadenat 1960), chondrocranium structure (Gilbert 1967) and position of first dorsal fin origin relative to the pectoral fin insertion (Compagno 1984), were thoroughly discussed by McEachran & Seret (1987). Based on examination of two heads placed in the Museum National d'Histoire Naturelle and Cadenat's personal collections of jaws, a single skin sample, notes and photographs, McEachran & Seret (1987) concluded that none of the proposed diagnostic characters were valid and could be attributed to intraspecific variability with *S. lewini*. For example, after examining Cadenat's personal photographs, McEachran & Seret (1987) discovered that several *S. couardi* specimens had pectoral apices with dusky coloration. The above factors, in addition to the lack of type specimens upon which to base comparisons, led McEachran & Seret (1987) to designate *S. couardi* as a junior synonym for *S. lewini*; a status it tentatively retains in Compagno (2005). Our data indicate that the head shape and variability in ventral pectoral fin coloration are highly variable among *S. gilberti* **sp. nov.** and *S. lewini*. For example, head width ranged from 25.78–31.66 % STL for *S. gilberti* **sp. nov.** and 25.09–30.06 for *S. lewini* and coloration of the pectoral fins was variable with some individuals of both species having entirely white ventral pectoral apices and others having dusky apices. Based on our data and the conclusions of McEachran & Seret (1987), there is no reason to consider *S. gilberti* **sp. nov.** and *S. couardi* synonymous.

In his description of a new species of hammerhead shark, *S. diplana*, Springer (1941) noted specimens of this taxon collected off the coast of the Carolinas, Florida, Mississippi, Louisiana and Texas, thus a comparison between *S. diplana* and the species described herein is warranted. In the first major work examining chondrichthyan fauna in the western North Atlantic Ocean, Bigelow & Schroeder (1948) documented four species of sphyrnids, including *S. diplana*, that occurred in the region. However, Bigelow & Schroeder (1948) noted that *S. diplana* is "represented in the tropical-subtropical waters of the eastern and western Indo-Pacific by a form (*S. lewini* Griffith, 1834) closely resembling *diplana.*". Nonetheless, the authors regarded *S. lewini* and *S. diplana* as distinct taxa due to possible differences in dentition. The validity of *S. diplana* was subsequently questioned by Tortonese (1950) and Fraser-Brunner (1950), with the latter considering *S. diplana* a junior synonym of *S. lewini*.

Fraser-Brunner (1950) reasoned that Springer (1941) had not considered a circumtropical distribution for *S. lewini* and based comparisons of *S. diplana* to *S. lewini* on a single specimen that was most likely incorrectly identified. Subsequently, others (e.g. Gilbert 1967, Compagno 1984, Castro 2011, Ebert & Stehmann 2013) continue to relegate *S. diplana* to a junior synonym for *S. lewini*. Despite the current taxonomic status of *S. diplana*, it could be suggested that *S. gilberti* **sp. nov.** and *S. diplana* are, in fact, synonymous. Unfortunately, extensive morphological comparisons between *S. diplana* and other members of the genus are hampered by a lack of comparative material as the type series of *S. diplana* consists of a male holotype (USNM 108451) and paratypes comprising a single head (USMN 108452) and two dry jaws (USNM 110296 and USNM 110297) (Howe & Springer 1993). Fortunately, Springer (1941) reports vertebral counts for seven *S. diplana* (without comment on specific location); however, it is not clear if counts were obtained from any of the type specimens. The number of total vertebrae for *S. diplana* reported by Springer (1941) range from 196–204 and he stated that roughly half of the total vertebrae occur after the precaudal pit. Given this, we suggest that precaudual vertebrae counts of 98–102 are consistent with Springer's data. Clearly, Springer's precaudal vertebrae counts for *S. diplana* (98–102) are most similar to *S. lewini* (92–99) and greater than those we report for *S. gilberti* **sp. nov.** (83–91). Furthermore, we obtained radiographs of the holotype from the Smithsonian Museum of Natural History, and counted 94 precadual vertebral for *S. diplana*. The precaudal vertebrae count for *S. diplana* (94) is within the range of *S. lewini* (92–99) and greater than those we report for *S. gilberti* **sp. nov.** (83–91), suggesting a clear distinction of *S. gilberti* **sp. nov.** from *S. diplana* but consistent with no distinction between *S. diplana* and *S. lewini*. Of note, Gilbert (1967) reported total vertebrae counts for eight *S. lewini* to range from 192–204, consistent with Springer's counts for *S. diplana*. One animal studied by Gilbert (1967) had an 'unusually low' total vertebrae count of 174; we suggest that this aberrant animal represents the first report of *S. gilberti* **sp. nov.**.

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