

Dermal denticles as a tool to reconstruct shark communities

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ABSTRACT: The last 50 yr of fisheries catch statistics and ecological surveys have reported significant decreases in shark populations, which have largely been attributed to human activities. However, sharks are challenging to census, and this decline likely pre-dated even the longest fishery-dependent time series. Here we present the first use of dermal denticles preserved in reef sediments as a novel tool to reconstruct shark communities. We first built a dermal denticle reference collection and conducted a morphometric analysis of denticle characters to relate denticle form to taxonomy, shark ecology, and denticle function. Denticle morphology was highly variable across the body of an individual shark and between taxa, preventing species- or genus-level identification of isolated denticles. However, we found that denticle morphology was strongly correlated with shark ecology, and morphometric analysis corroborated existing functional classifications. In a proof of concept, we extracted 330 denticles from modern and fossil reef sediments in Bocas del Toro, Panama and found them to be morphologically diverse and sufficiently well-preserved to allow classification. We observed a high degree of correspondence between the denticles found in the sediments and the sharks documented in the region. We therefore propose that (1) denticle assemblages in the recent fossil record can help establish quantitative pre-human shark baselines and (2) time-averaged denticle assemblages on modern reefs can supplement traditional surveys, which may prove especially valuable in areas where rigorous surveys of sharks are difficult to perform.

KEY WORDS: Dermal denticle · Functional morphology · Shark · Paleoecology · Baseline

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INTRODUCTION

Understanding the temporal and spatial dynamics of shark communities and how they are affected by human activities is challenging (Ferretti et al. 2010, Nadon et al. 2012, Roff et al. 2016). Both fishery-dependent and independent assessments reveal that shark populations worldwide have suffered significant declines over the past several decades due to overfishing and habitat degradation (Myers & Worm 2003, Ferretti et al. 2010). Pelagic longline surveys and landing statistics from fisheries in the northwest Atlantic reported 49 to 89% declines in catch rates of 18 shark species between 1985 and 2000 (Baum et al. 2003), while even higher losses of up to 99% were

found in the Gulf of Mexico between the 1950s and the late 1990s (Baum & Myers 2004). This decline has likely continued since. Diver and video surveys have examined patterns of reef-associated species across oceanographic, habitat, and anthropogenic gradients as well as in space-for-time analyses (Sandin et al. 2008, Espinoza et al. 2014, Williams et al. 2015). For example, top predator biomass was found to be 5 to 15-fold higher at unfished islands in the Line Islands as compared to populated, fished islands (DeMartini et al. 2008). However, these records are sporadic, limited in detail or taxonomic resolution, and only date back half a century (Odum & Odum 1955, Baum & Myers 2004, Ward & Myers 2005, Ferretti et al. 2008, Ward-Paige et al. 2010b). Cryptic behavior, rarity, and

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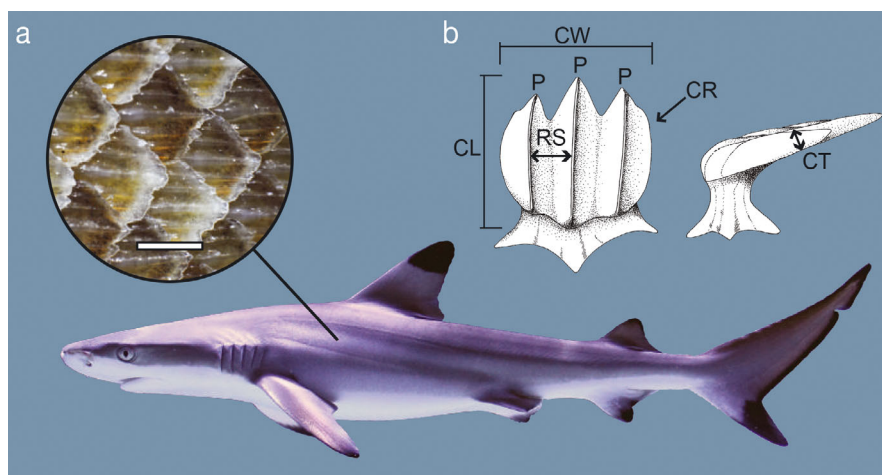


Fig. 1. (a) A blacktip reef shark *Carcharhinus melanopterus* with inset dermal denticles. Scale bar = 200 μ m. Photo adapted from Kakidai/Wikimedia Commons/CC-BY-SA-3.0. (b) Illustration of the dorsal and lateral view of a dermal denticle from the body of a lemon shark *Negaprion brevirostris*, showing the morphological measurements taken with an ocular micrometer and important landmarks. CR: crown; CL: crown length; CT: crown thickness; CW: crown width; P: peak; RS: ridge spacing

diurnal and seasonal movement patterns prevent sharks from being meaningfully censused in many regions (Sale & Douglas 1981, MacNeil et al. 2008, Ward-Paige et al. 2010a, McCauley, et al. 2012a). Time series or replicated surveys have also shown conflicting trends for the same area depending on the survey method used and its associated biases (Burgess et al. 2005, Ward-Paige, et al. 2010a, Nadon et al. 2012), leading to misrepresentations of the status of shark populations and their unfished baseline conditions (Heupel et al. 2009, Rizzari et al. 2014).

To address this problem, we explored whether dermal denticles, the small, tooth-like scales covering the skin of nearly all elasmobranchs (Fig. 1), can be used as a tool to reconstruct shark communities on coral reefs. Denticles are several orders of magnitude more abundant than teeth on a living shark and are continually shed (Reif 1985a, Compagno et al. 2005). Like teeth, denticles preserve well and have a long fossil record (Janvier 1996, Sansom et al. 2012), potentially providing a unique opportunity to retrospectively 'survey' modern and pre-exploitation shark assemblages. In this paper, we (1) review denticle morphology, taxonomy, and function; (2) present a reference collection of shark dermal denticles; (3) introduce a technique to extract and identify denticles from modern and fossil reef sediments; and (4) discuss the limitations and potential applications of the approach.

BACKGROUND: DERMAL DENTICLE MORPHOLOGY, TAXONOMY, AND FUNCTION

Dermal denticles are composed of a dentine and enameloid crown attached to a basal plate, which is anchored to the skin by collagen fibers (Applegate

1967). Denticles display considerable variation in crown shape, size, and thickness (Figs. 1 & 2). Crowns can possess ridges of varying length, height, orientation, and spacing and may or may not terminate in an equal number of peaks (Tway 1979, Reif 1985a, Raschi & Musick 1986, Raschi & Tabit 1992) (Fig. 2).

Individual sharks possess multiple types of denticles arranged systematically along their bodies (Reif 1985a, Raschi & Tabit 1992, Bargar & Thorson 1995, Salini et al. 2007), and denticle morphotypes can be shared across taxa (Reif 1982, 1985a, Muñoz-Chápuli 1985a, Tanaka et al. 2002, Gilligan & Otway 2011). Denticle morphology can also vary with sex (Crooks et al. 2013) and ontogeny (Reif 1985a). Only in a few cases can isolated denticles be identified beyond the family level (Reif 1985a, Mello et al. 2013, Ferrón et al. 2014). Conversely, denticle morphology appears to be more closely linked to the ecological guild of the shark species to which it belongs as well as to the specific function it plays on the shark's body (Reif 1978, 1985b, Raschi & Musick 1986, Raschi & Tabit 1992).

Five major functional groups of dermal denticles have thus far been established: (1) *drag reduction*, (2) *abrasion strength*, (3) *defense*, (4) *luminescence* and (5) *generalized functions* (Reif 1982, 1985a, 1985b, Raschi & Tabit 1992). In general terms, fast, pelagic sharks are covered almost entirely by thin, highly ridged *drag reduction* denticles, while demersal sharks possess thick, smooth *abrasion strength* denticles that provide protection from the substrate (Reif 1985a, Raschi & Tabit 1992). However, *abrasion strength* denticles can also occur in small areas of the head and leading edges of the fins on non-demersal sharks (Reif 1985a, Bargar & Thorson 1995, Motta et al. 2012). Other demersal and schooling species pos-

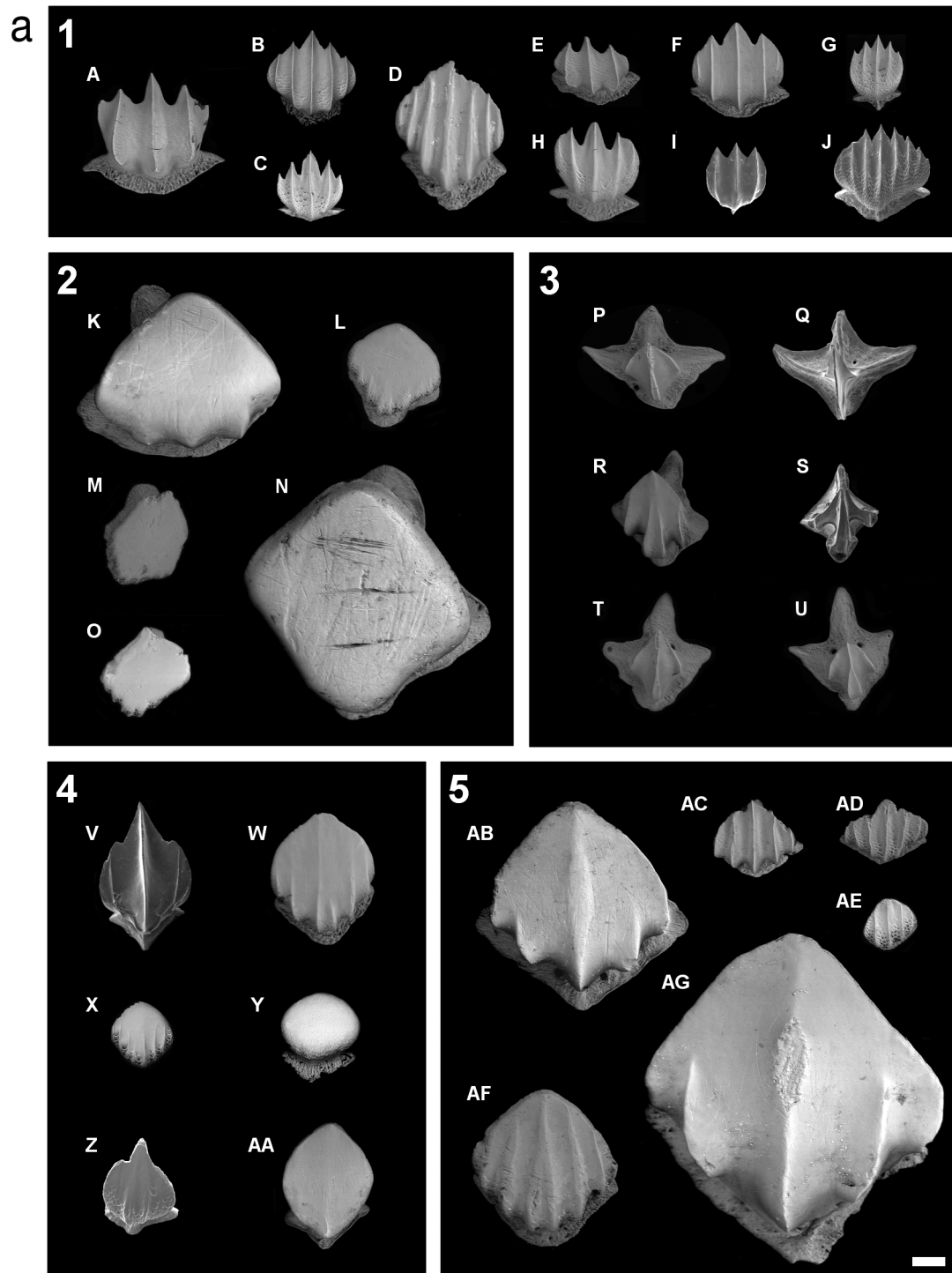


Fig. 2. Scanning electron microscope images of dermal denticles from the reference collection demonstrating morphological variation across functional morphotypes and shark families.

(a) Examples of each functional morphotype: (1) *drag reduction*; (2) *abrasion strength*; (3) *defense*; (4) *generalized functions*; (5) *ridged abrasion strength*. The luminescence morphotype is not shown due to its rarity in the reference collection, which focused on shallow, coastal species.

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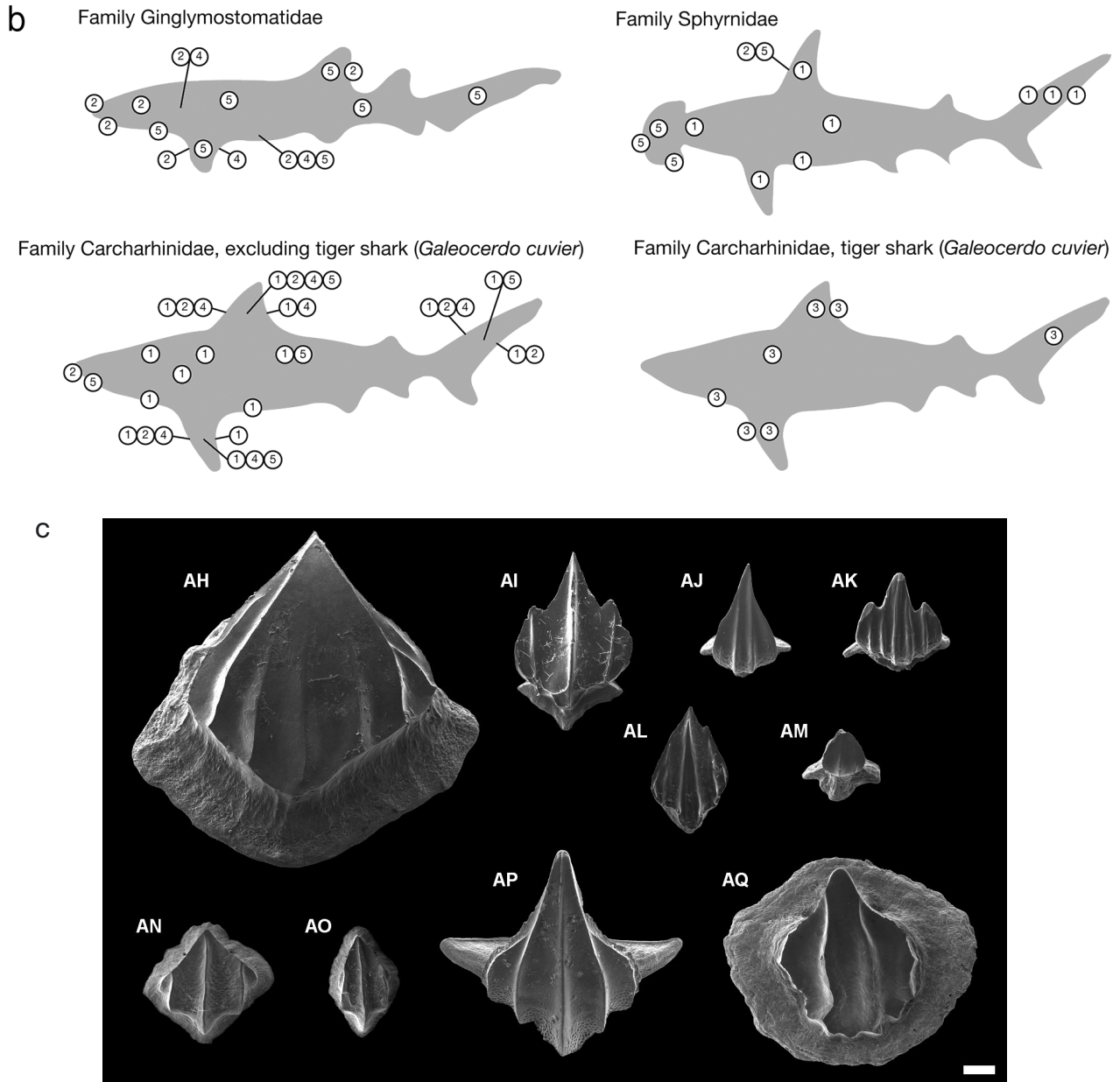


Fig. 2 (continued)

(b) Distribution of functional morphotypes across the bodies of 3 reef-associated shark families. Numbers correspond to boxes in panel (a). Note that the tiger shark *Galeocerdo cuvier* is characterized by *defense* type denticles, unlike the other species sampled in *Carcharhinidae*.

(c) Scanning electron microscope images of denticles from mesopelagic and pelagic families included in the reference collection. Many are visually distinct from the denticles of the reef-associated families sampled. Scale bars = 100 μ m.

Species and anatomical position of each denticle (see Fig. 3 for explanation of sample location codes following the species names): (A) *Carcharhinus leucas*, B2; (B) *Carcharhinus falciformis*, B2; (C) *Sphyrna lewini*, B2; (D) *Carcharhinus acronotus*, C2; (E) *Carcharhinus perezi*, B2; (F) *Negaprion brevirostris*, B3; (G) *Sphyrna mokarran*, P2; (H) *Carcharhinus obscurus*, B2; (I) *Alopias vulpinus*, B3; (J) *Sphyrna zygaena*, H2; (K) *Ginglymostoma cirratum*, B3; (L) *Carcharhinus galapagensis*, H1; (M) *Sphyrna tiburo*, D1; (N) *Ginglymostoma cirratum*, H1; (O) *Carcharhinus obscurus*, D1; (P) *Galeocerdo cuvier*, B2; (Q) *Squalus acanthias*, B2; (R) *Galeocerdo cuvier*, C1; (S) *Squalus cubensis*, B2; (T) *Galeocerdo cuvier*, C2; (U) *Galeocerdo cuvier*, D2; (V) *Heptranchias perlo*, H2; (W) *Negaprion brevirostris*, D2; (X) *Carcharhinus falciformis*, D2; (Y) *Carcharhinus falciformis*, D3; (Z) *Mustelus canis*, D3; (AA) *Ginglymostoma cirratum*, D3; (AB) *Ginglymostoma cirratum*, P2; (AC) *Carcharhinus limbatus*, nostril; (AD) *Sphyrna couardi*, eye; (AE) *Sphyrna lewini*, H1; (AF) *Triaenodon obesus*, C2; (AG) *Ginglymostoma cirratum*, B2; (AH) *Centrophorus granulosus*, B3; (AI) *Heptranchias perlo*, B2; (AJ) *Mustelus canis*, B2; (AK) *Mustelus canis*, B3; (AL) *Squalus cubensis*, C2; (AM) *Pristis perotteti*, B2; (AN) *Pseudocarcharias kamoharai*, B2; (AO) *Pseudocarcharias kamoharai*, C2; (AP) *Scyliorhinus retifer*, B2; (AQ) *Squatina dumeril*, B2

sess spiny *defense* denticles, which are hypothesized to deter the settlement of ectoparasites and epibionts (Applegate 1967, Reif 1985a). Bioluminescent mesopelagic sharks possess *luminescence* denticles that permit light emission from photophores on the skin (Reif 1985b, Raschi & Tabit 1992). *Generalized functions* denticles are widely distributed across taxa (Reif 1985a). Intermediate forms between these groups also exist (Reif 1985a, Raschi & Tabit 1992).

METHODS

Dermal denticle reference collection

Given the diverse spectrum of denticle morphology, our aim was to facilitate the identification of isolated denticles extracted from sediments by (1) morphometrically categorizing denticles and (2) determining the extent to which the occurrences of established denticle morphotypes are constrained with taxonomic and ecological groups of sharks. To do so, we first built a reference collection of modern shark dermal denticles from the ichthyology collection at the Smithsonian National Museum of Natural History and catches by fishermen in Bocas del Toro and Colón, Caribbean Panama. We focused on tropical coastal and reef-associated sharks, with a total of 37 species representing 16 families (Table 1). Given ontogenetic variation in denticle morphology, the largest individuals in the museum's collection were sampled when possible, although many of the specimens were juveniles (Table 1). From each specimen, ~1 cm² pieces of skin were excised from standardized locations along the body (Fig. 3). Excised tissues were immersed in a 1% sodium hypochlorite solution until the denticles detached from the skin. Between 1 and 4 denticles were

selected for morphometric analysis from each of the 191 skin samples collected, for a total of 215 denticles (Table S1 in the Supplement at www.int-res.com/articles/suppl/m566p117_supp.pdf). More than 1 denticle was characterized per skin sample when there were multiple visually distinct morphological forms present. All denticles were imaged via light and scanning electron microscopy.

Morphometric analysis of the dermal denticle reference collection

Each denticle in the reference collection was assigned to one of 6 functional morphotypes following Reif (1985a): *drag reduction*, *abrasion strength*, *ridged abrasion strength*, *defense*, *luminescence*, and *generalized functions* (Fig. 2, Table S1). *Abrasion strength* denticles were divided into 2 sub-categories to account for differences in proposed hydrodynamic function due to the presence of ridges (Raschi & Tabit 1992). To explore the correspondence between denticle morphology and shark taxonomy and ecology, we collected morphometric character data from each denticle in the reference collection. Crown shape, size, and thickness, the number and types of peaks, and the presence, length, orientation, and spacing between ridges were recorded (Fig. 1, Tables 2 & S1). Character selection was based on proposed functional significance (e.g. Reif & Dinkelacker 1982), previous studies (Tway 1979, Raschi & Musick 1986, Salini et al. 2007, Ferrón et al. 2014), and observed variation in denticle morphology. Character data was ordinated using principal component analysis (PCA; R Core Team 2014), and each categorical character was included in the ordination as multiple isolated dichotomous variables. This allowed us to examine

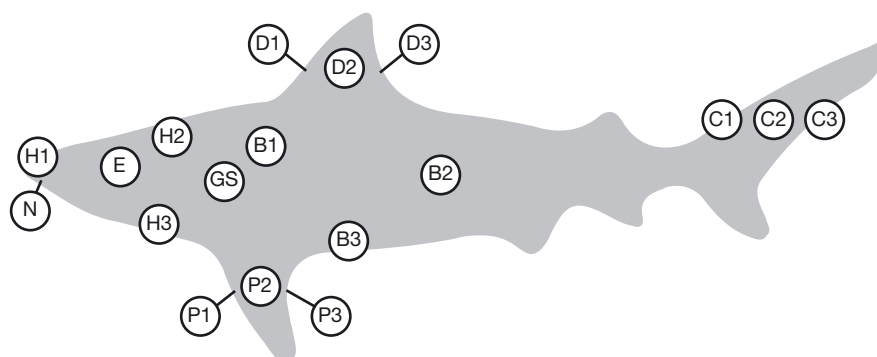


Fig. 3. Locations of skin samples for the dermal denticle reference collection. All anatomical positions are shown, although samples from each were not taken for every family. The B2, C2, D2, and P2 regions were selected as standard sampling positions, and auxiliary positions were haphazardly sampled in each family to better characterize variation in denticle morphology across the body (see Table S2 in the Supplement). All positions correspond to sampling locations from previous studies to allow comparison. B: body; C: caudal fin; D: dorsal fin; E: eye; GS: gill slit; H: head; N: nostril; P: pectoral fin

Table 1. Summary of the shark species included in the dermal denticle reference collection and their ecological attributes. BIC: benthic invertebrate consumption, where benthic invertebrates comprise >15% of diet items recorded

Family	Species	Reef-associated ^a	Life mode ^a	Trophic level ^a	BIC ^a	Specimen length (cm)	Maximum length (cm) ^a	Functional morphotype (body) ^b	No. of samples
Alopiidae	<i>Alopias vulpinus</i>	No	Pelagic	4.5	No	172	760	Drag reduction	5
Carcharhinidae	<i>Carcharhinus acronotus</i>	Yes	Benthopelagic	4.2	No	108	200	Drag reduction	4
	<i>Carcharhinus albimarginatus</i>	Yes	Benthopelagic	4.2	No	86	300	Drag reduction	4
	<i>Carcharhinus falciformis</i>	Yes	Pelagic	4.5	No	96	350	Drag reduction	21
	<i>Carcharhinus galapagensis</i>	Yes	Benthopelagic	4.2	Yes	90	370	Drag reduction	5
	<i>Carcharhinus leucas</i>	Yes	Benthopelagic	4.3	Yes	88	360	Drag reduction	5
	<i>Carcharhinus limbatus</i>	Yes	Benthopelagic	4.2	No	90	275	Drag reduction	7
	<i>Carcharhinus melanopterus</i>	Yes	Benthopelagic	4.2	Yes	104	200	Drag reduction	5
	<i>Carcharhinus obscurus</i>	Yes	Pelagic	4.5	No	111	420	Drag reduction	8
	<i>Carcharhinus perezi</i>	Yes	Benthopelagic	4.5	No	44	300	Drag reduction	4
	<i>Galeocerdo cuvier</i>	No	Benthopelagic	4.5	Yes	100	750	Defense	7
	<i>Negaprion acutidens</i>	Yes	Benthopelagic	4.3	No	72	380	Drag reduction	4
	<i>Negaprion brevirostris</i>	Yes	Benthopelagic	4.4	Yes	73	340	Drag reduction	5
	<i>Prionace glauca</i>	No	Pelagic	4.2	No	118	400	Drag reduction	4
	<i>Rhizoprionodon porosus</i>	Yes	Benthopelagic	3.8	Yes	96	110	Drag reduction	15
	<i>Rhizoprionodon terraenovae</i>	No	Benthopelagic	4.3	No	50	110	Drag reduction	4
<i>Triaenodon obesus</i>	Yes	Demersal	4.2	Yes	92	213	Ridged abrasion strength	6	
Centroproridae	<i>Centroprorus granulosus</i>	No	Demersal	4.1	No	113	170	Ridged abrasion strength	5
Dalatiidae	<i>Isistius brasiliensis</i>	No	Pelagic	4.3	No	46	42	Luminescence	1
Etmopteridae	<i>Etmopterus pusillus</i>	No	Benthopelagic	4.2	No	58	50	Luminescence	1
Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	Yes	Demersal	3.8	Yes	125	430	Abrasion strength, Ridged abrasion strength	11
	<i>Nebrius ferrugineus</i>	Yes	Demersal	4.1	Yes	230	320	Abrasion strength, Ridged abrasion strength	4
Hexanchidae	<i>Hextranchias perlo</i>	No	Demersal	4.2	Yes	110	137	Generalized functions	4
Lamnidae	<i>Isurus oxyrinchus</i>	No	Pelagic	4.5	No	97	400	Drag reduction	4
Pristidae	<i>Pristis perotteti</i>	No	Benthopelagic	4.0	Yes	78	650	Generalized functions	4
Pseudocarchariidae	<i>Pseudocarcharias kamoharui</i>	No	Pelagic	4.2	Yes	106	110	Ridged abrasion strength	4
Rhinobatidae	<i>Rhinobatos lentiginosus</i>	Yes	Demersal	3.6	Yes	56	75	Abrasion strength	2
Scyliorhinidae	<i>Scyliorhinus retifer</i>	No	Demersal	4.4	Yes	47	48	Generalized functions	4
	<i>Sphyrna couardi</i>	No	Benthopelagic	4.2	Yes	242	300	Drag reduction	2
	<i>Sphyrna lewini</i>	No	Benthopelagic	4.1	Yes	97	430	Drag reduction	5
	<i>Sphyrna mokarran</i>	Yes	Benthopelagic	4.3	No	86	610	Drag reduction	6
	<i>Sphyrna tiburo</i>	Yes	Benthopelagic	3.9	Yes	92	150	Drag reduction	5
	<i>Sphyrna zygaena</i>	No	Benthopelagic	4.5	Yes	79	500	Drag reduction	5
Squalidae	<i>Squalus acanthias</i>	No	Benthopelagic	4.3	Yes	30	160	Defense	1
	<i>Squalus cubensis</i>	No	Demersal	4.2	Yes	68	110	Defense	4
Squatimidae	<i>Squatina dumeril</i>	No	Demersal	4.5	Yes	46	152	Defense	1
Triakidae	<i>Mustelus canis</i>	No	Demersal	3.7	Yes	68	150	Generalized functions	5

^aSource: FishBase (Froese & Pauly 2016); ^bCross-referenced with Reif (1985a)

Table 2. Dermal denticle characters measured for the morphometric analysis. See Figs. 1 & 2 for definitions and examples of traits

	Character	Examples from Figs. 1 & 2
Crown shape	1 Circular or elliptical	C, H, Y
	2 Lanceolate or teardrop-shaped	V, AJ, AP
	3 Diamond-shaped, square, or triangular	K, N, AG
	4 Cruciform or arrow-shaped	Q, R, T
	5 Lobed on all sides	-
Crown size	$\sqrt{(\text{length (CL)} \times \text{width (CW)})}$	See Fig. 1
Crown thickness ratio	$\sqrt{(\text{length (CL)} \times \text{width (CW)})} / \text{thickness (CT)}$	See Fig. 1
Crown micro-structures	0 Absent	D, I, AB
	1 Present	H, J, L
Number of peaks	0 Single peak	X, AC, AO
	1 >1 peak	A, E, V
Peak type	1 Rounded peaks or single V-shaped peak	W, AD, AF
	2 Distinct serrated peaks	F, G, H
	3 Scalloped (unpronounced, short) peaks	D, AD
	4 Peak edges curve inward to form single tip (teardrop)	S, V, Z
Presence of ridges	0 No ridges	K, M, N
	1 ≥ 1 ridge	B, AE, AK
Ridge length	1 Incomplete, medially-reduced ridges	W, Z, AG
	2 Complete ridges	A, D, AD
Upward-pointing medial spine	0 Absent	C, AF, AN
	1 Present	P, Q, S
Ridge orientation	1 Parallel ridges	B, F, AC
	2 Sub-parallel ridges	U, AF, AI
Ridge spacing	0 No ridge spacing	O, Y, AA
	1 1 to 100 μm ridge spacing	G, I, AE
	2 >100 μm ridge spacing	AG, AH, AI

the effect of each variable separately in the ordination as opposed to solely the aggregate character categories. Ecological attributes of each species (life mode, reef-association, trophic position, benthic invertebrate consumption, and maximum length; Table 1) were added *a priori* to observe relationships between denticle characters and shark ecology. For each strongly explanatory character in the PCA, regressions or 1-way ANOVAs with Tukey's HSD post-hoc tests were used to evaluate pairwise differences between groups and assess correlations with shark ecology. Character frequency of occurrence was calculated for each shark family and functional morphotype to describe the range of variability within each group.

Proof of concept: extracting dermal denticles from modern and fossil sediments

To explore the application of dermal denticle analysis to reconstruct shark communities, we collected sediments from modern reefs and a mid-Holocene fossil reef in Bocas del Toro, Panama. Sub-recent time-averaged samples were collected from 2 fringing reefs in Almirante Bay (9.3619° N, 82.2799° W; 9.3361° N, 82.2561° W) using SCUBA. At both reefs, 4 replicate 10 kg bulk samples of fine sediments were excavated from the uppermost 10 cm in patches of mud, silt, and sand adjacent to live coral. An *in situ* fossil reef on Isla Colón (9.3603° N, 82.2730° W) dating between 7.2 and 5.7 ka (Fredston-Hermann et al. 2013) was sampled comparably, with 3 replicate 10 kg bulk samples collected from 3 localities characterized by branching *Acropora* or *Porites* coral. In total, 8 modern samples and 9 fossil samples were collected.

Samples were processed following the approach of Sibert et al. (in press) to extract dermal denticles with as little damage as possible. Sediments were dried, weighed, and sieved. The 106 μm to 2 mm size fraction was then digested with 10% glacial acetic acid. After several acid rinses to eliminate the calcitic and aragonitic components, the remaining particles were treated with 100 to 200 ml 5% hydrogen peroxide and heated for no more than 15 min to remove organic material. All denticles were manually picked from the residue with a paintbrush. They were photographed, counted, measured, and identified to functional morphotype and family using the reference collection.

RESULTS AND DISCUSSION

Dermal denticle reference collection

Denticle characters correlate to shark ecology

PCA Axis 1 and 2 explained 34.7 and 19.1% of the variation in denticle morphology, respectively (Fig. 4). The characters that had the highest explanatory power in the PCA were crown shape, the presence of ridges and multiple peaks, the types of peaks, ridge spacing, and whether the ridges were complete (Table 3). The first PC axis largely described the dif-

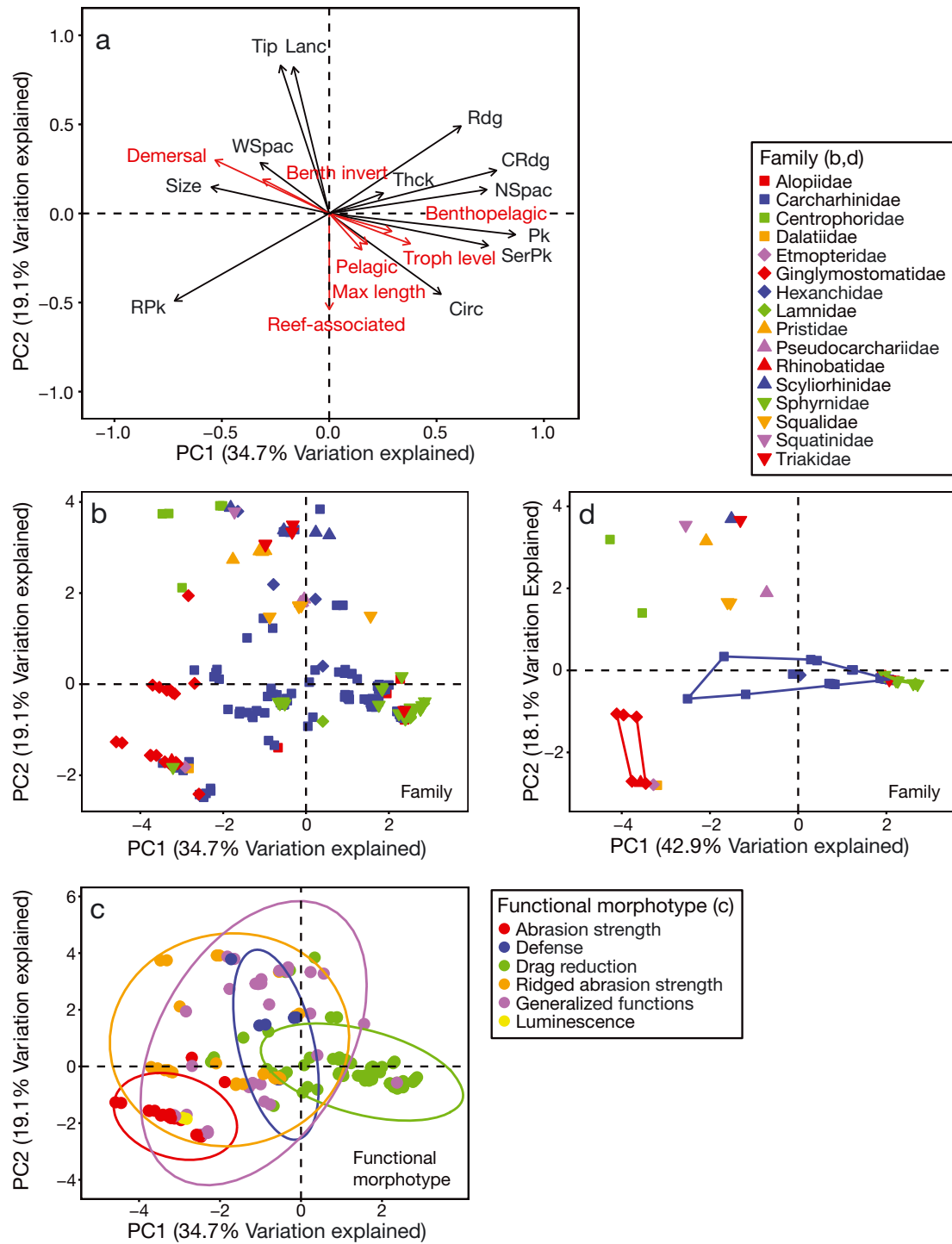


Fig. 4. Principal component analysis (PCA) performed on 12 denticle characters in the reference collection. (a) Correlation circle of characters (black) with ecological attributes overlaid *a priori* (red). Abbreviations of characters are those shown in Table 3; the ecological attributes of each species sampled are reported in Table 1. All denticles in the reference collection (Table S1 in the Supplement) were included in the analysis, and each is represented by a point in the ordination. The colours designating the shark families in panels (b) and (d) do not correspond with those designating the functional morphotypes in panel (c). (b) PCA scores labeled with respect to family. (c) PCA labeled with respect to functional morphotype, with 95% prediction ellipses shown. (d) Results of a separate PCA performed on the same characters using only denticles located on the trunk of the body. The PCA scores are labeled with respect to family, and convex hulls of the reef-associated families Carcharhinidae, Ginglymostomatidae, and Sphyrnidae are shown

Table 3. Dermal denticle characters included in the principal component analysis (PCA). Characters were selected from Table 2 based on their percent contribution to principal components (PC) 1 and 2. The crown thickness ratio, while contributing little to PC1 and PC2, was found to be useful when distinguishing between groups, and was therefore included in the analysis. Abbreviations are used to present the results of the analysis graphically in Fig. 4A

Character	Abbreviation	PC1 % contribution	PC2 % contribution
Circular or elliptical crown shape	Circ	6.52	8.92
Lanceolate or teardrop crown shape	Lanc	0.66	29.48
Crown size	Size	7.24	0.96
Crown thickness ratio	Thck	1.53	0.57
>1 peak present	Pk	18.08	0.62
Rounded peaks or single V-shaped peak	RPk	12.46	10.51
Distinct serrated peaks	SerPk	13.20	1.41
Peak edges curve inward to form single tip	Tip	1.23	30.12
≥1 ridge present	Rdg	9.05	10.49
Complete ridges	CRdg	14.6	2.55
1 to 100 μm ridge spacing	NSpac	12.95	0.78
>100 μm ridge spacing	WSpac	2.47	3.54

ference between highly ridged denticles with narrow ridge spacing and multiple peaks and smooth denticles with a single peak. The second PC axis described differences in crown shape, namely pointed, teardrop-shaped denticles as opposed to rounded denticles.

Morphological variation in PC space had high correspondence with the ecological attributes of the shark species (Fig. 4A). For example, demersal sharks typically possess either large, thick, unridged denticles with a single rounded peak (i.e. *abrasion strength*) or ridged, lanceolate denticles (i.e. *ridged abrasion strength* and *generalized functions*). Pelagic and benthopelagic sharks possess circular denticles with several complete, narrowly-spaced ridges and multiple peaks (i.e. *drag reduction*). These ridges improve hydrodynamic efficiency by disrupting the boundary layer between the skin and surrounding water, reducing turbulence as water flows around the shark's body (Reif & Dinkelacker 1982, Raschi & Musick 1986, Dean & Bhushan 2010, Lang et al. 2012, Díez et al. 2015). PCA of denticle morphology also revealed high co-correlation between trophic level, maximum length, and life mode, strongly supporting the use of morphological characters to broadly predict shark ecology (Fig. 4A).

Shark families share denticle characters

Shark families overlapped extensively in PC space due to the high diversity of denticle forms found

across individuals and species (Figs. 2B & 4B, Table S2). There was minor overlap between the coastal families Carcharhinidae, Ginglymostomatidae, Sphyrnidae, Alopiidae, and Lamnidae, whose denticles could plausibly accumulate in reef sediments. The discrimination between these groups, however, was more pronounced when only the denticles found on the trunk of the body—which cover the greatest surface area of the skin and are the most likely to enter the fossil record—were included in the analysis (Fig. 4D). Carcharhinidae covered a wide area in PC space; this is possibly due to the high diversity of ecological guilds occupied by species within this family, although it could also be an artifact of the large number of species sampled relative

to other families. Sphyrnidae, Lamnidae, and Alopiidae clustered together and overlapped slightly with Carcharhinidae, which is likely due to the functional similarities between these groups (Muñoz-Chápoli 1985a, Reif 1985a, Mello et al. 2013). In contrast, the denticles on the body of Ginglymostomatidae were separate in PC space due to their characteristic thick crowns and V-shaped peaks (Fig. 4D).

Ridge spacing (Fig. 1) was found to be useful in distinguishing between morphologically similar denticles belonging to Carcharhinidae, Ginglymostomatidae, Sphyrnidae, Alopiidae, and Lamnidae. Ridge spacing has previously been correlated with swimming speed, with narrower ridges conferring hydrodynamic advantage at faster speeds (Reif & Dinkelacker 1982, Raschi & Elsom 1986, Raschi & Musick 1986), and has been used to define ecological swimming groups (Reif 1985a). In fast swimming species, ridge spacing has also been found to remain constant despite the positive correlation between denticle and body size (Reif 1985a, Raschi & Musick 1986). We found Sphyrnidae, Lamnidae, and Alopiidae to have narrowly-spaced ridges, in concordance with their fast burst speeds (Raschi & Musick 1986, Froese & Pauly 2016). Their ridge spacing was significantly smaller than Carcharhinidae, which in turn had smaller spacing than Ginglymostomatidae (ANOVA, $F_{4,145} = 33.25$, $p < 0.0001$; Fig. 5, Table S3). Again, this pattern was stronger when only denticles on the trunk of the body were considered, as some denticles on the fins had uniformly narrow spacing

Table 4. Frequency of occurrence of dermal denticle characters measured for each shark family in the reference collection. Character descriptions are provided in Table 2. Crown size, thickness, and the number of ridges are averages, where not noted. **Bold:** mode values

Family	Crown shape					Crown size	Crown thickness	Micro-structures	>1 peak	Peak type				Ridges			Ridge length	Spine Orientation		Ridge spacing					
	1	2	3	4	5					1	2	3	4	≥1	0	1		2	1	2	0	1	2	Avg.	
Alopiidae	0.60	0	0.40	0	0	148	6.3	0.2	0.80	0.20	0.80	0	0	0	3	0.20	0.80	0	1	0	0	0	0	0	43
Carcharhinidae	0.50	0.07	0.37	0.06	0	278	5.5	0.72	0.55	0.38	0.35	0.22	0.06	0.87	4	0.09	0.77	0.06	0.75	0.12	0.13	0.79	0.13	0.80	67
Centrophoridae	0	0.80	0.20	0	0	785	6.3	0	0	0	0	0	1	1	5	0.60	0.40	0	0	1	0	0.20	0.80	144	
Dalatiidae	0	0	1	0	0	131	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
Etmopteridae	0	0	0	0	0	194	5.2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
Ginglymostomatidae	0.05	0.05	0.84	0	0	636	4.5	0	0	0.95	0	0	0.05	0.42	1	0.42	0	0	0.32	0.11	0.53	0	0.42	199	
Hexanchidae	0	0.75	0.25	0	0	404	6.1	0	0.75	0.25	0.75	0.25	0.25	1	3	0	1	0	0.50	0.50	0	0	1	116	
Lamnidae	1	0	0	0	0	163	10.2	0	0.75	0.25	0.75	0	0	1	3	0	1	0	0.75	0.25	0	1	0	38	
Pristidae	0	1	0	0	0	151	4.5	0	0	0	0	0	1	1	2	1	0	0	0.80	0	0.20	0.80	0	56	
Pseudocarchariidae	0	0	1	0	0	245	4.9	1	0	0	0	0	1	1	3	0	0	0	1	0	0	1	0	77	
Rhinobatidae	0	0	0	0	1	418	5.6	0	0.50	0	0	0	1	1	4	0	0	0.25	0.75	0	0	1	0	85	
Scyliorhinidae	0	1	0	0	0	407	6.6	1	0.79	0.21	0.75	0.04	0	0.96	4	0	0.96	0	0.96	0	0.04	0.96	0	49	
Sphyrnidae	0.63	0	0.38	0	0	212	8.1	0.96	0.20	0	0.20	0	0.80	1	3	0	1	1	0	0.80	0.60	0.40	0	65	
Squalidae	0	0.20	0	0.80	0	390	6.2	0	0	0	0	0	1	1	2	0	1	1	1	0	0	0	0	113	
Squatinae	0	1	0	0	0	275	8.2	1	0.20	0	0.20	0	0.80	1	3	0.40	0.60	0	1	0	0	0	0	50	
Triakidae	0.20	0.80	0	0	0	275	8.2	1	0.20	0	0.20	0	0.80	1	3	0.40	0.60	0	1	0	0	0	0	50	

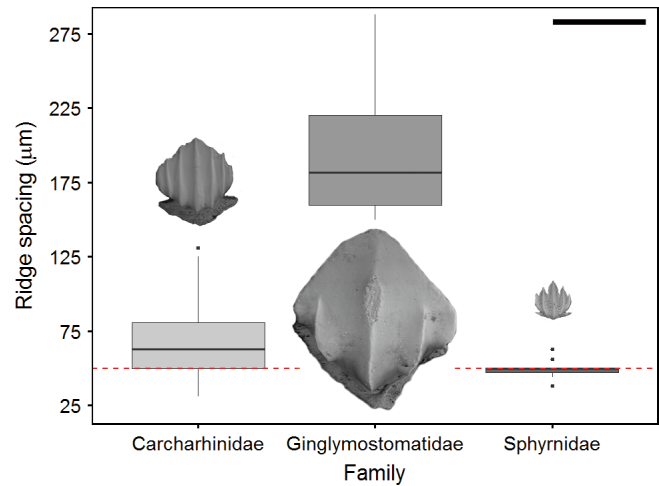


Fig. 5. Boxplots of ridge spacing for the reef-associated families in the reference collection. Distances were measured between the central ridge and adjacent medial ridge on the crown (Fig. 1). Only denticles possessing ridges were included in the analysis. Ginglymostomatidae (n = 8) possessed much wider ridge spacing than Carcharhinidae (n = 110) and Sphyrnidae (n = 23) (p < 0.0001). Ridge spacing in Carcharhinidae was also significantly wider than in Sphyrnidae (p = 0.005). Denticles with ridge spacing <50 µm (dotted line) were only found on the fins in Carcharhinidae and Sphyrnidae. Scale bar = 500 µm

across families (Fig. 5). We conclude that ridge spacing, with some degree of confidence, can aid the taxonomic identification at the family level of isolated denticles possessing ridges that are indistinguishable by other characters.

In addition to ridge spacing, crown size and microstructures can be used to help differentiate between Carcharhinidae, Sphyrnidae, Alopiidae, and Lamnidae (Table 4). The crown size of Carcharhinidae was significantly larger than Sphyrnidae, Alopiidae, and Lamnidae (ANOVA, $F_{3,156} = 12.65$, $p < 0.0001$; Tukey's HSD, $p < 0.05$; Table S3). Furthermore, a higher proportion of denticles in Sphyrnidae (96%) and Carcharhinidae (72%) had prominent microstructures—which are thought to play a fine-scale hydrodynamic role (Muñoz-Chápuli 1985b, Mello et al. 2013)—on their crowns than denticles in Alopiidae (20%) and Lamnidae (0%) (Table 4).

Characters quantitatively define boundaries between functional morphotypes

The PCA corroborated the existing qualitative descriptions of functional morphotypes established by Reif (1985a) and reviewed in Raschi & Tabit (1992) while quantitatively refining the boundaries between them and identifying areas of overlap (Fig. 4C). The 95% prediction ellipses for drag reduction and abrasion strength denticles

Table 5. Frequency of occurrence of dermal denticle characters measured for each functional morphotype (numbers in parentheses correspond to panels in Fig. 2a). Character descriptions are provided in Table 2. Crown size, thickness, and the number of ridges are averages, where not noted. **Bold**: mode values

Functional morphotype	Families	Crown shape				Crown size	Crown thickness	Micro-structures	>1 peak	Peak type				Ridges		Ridge length		Spine		Orientation		Ridge spacing—Avg.			
		1	2	3	4					5	1	2	3	4	≥1	0	1	2	1	2	1	2	1	2	1
Abrasion strength (2)	Carcharhinidae,	0.32	0	0.55	0	0.05	446	3.5	0.28	0	0.95	0	0	0.05	0	0.05	0	0	0	0.05	0	1	0	0	0
	Ginglymostomatidae, Rhinobatidae, Sphyrnidae																								
Defense (3)	Carcharhinidae, Squalidae, Squatinidae	0	0.08	0	0.92	0	210	2.4	0.08	0	0.50	0	0	0.50	1	3	0.08	0.92	1	0.08	0.83	0.25	0.67	0.08	71
	Alopiidae, Carcharhinidae, Lamnidae, Sphyrnidae																								
Drag reduction (1)	Carcharhinidae, Lamnidae, Sphyrnidae	0.63	0.06	0.31	0	0	261	6.7	0.77	0.83	0.12	0.60	0.25	0.03	1	4	0.01	0.99	0	0.96	0.04	0	0.92	0.08	62
	Carcharhinidae, Hexanchidae, Pristidae, Squalidae, Triakidae																								
Generalized functions (4)	Carcharhinidae, Ginglymostomatidae, Hexanchidae, Pristidae, Squalidae, Triakidae	0.22	0.50	0.28	0	0	279	6.9	0.50	0.19	0.44	0.11	0.03	0.42	0.75	3	0.42	0.33	0.03	0.50	0.22	0.28	0.58	0.14	68
	Scyllorhinidae, Squalidae, Dalatiidae, Etmopteridae, Carcharhinidae, Centrophoridae, Ginglymostomatidae, Pseudocarchariidae, Sphyrnidae																								
Luminescence (-) Ridged abrasion strength (5)	Carcharhinidae, Centrophoridae, Ginglymostomatidae, Pseudocarchariidae, Sphyrnidae	0	0	0.50	0	0	163	5.2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Carcharhinidae, Centrophoridae, Ginglymostomatidae, Pseudocarchariidae, Sphyrnidae	0	0.21	0.79	0	0	487	4.2	0.50	0	0.61	0	0	0.39	1	4	0.46	0.54	0	0.68	0.32	0	0.57	0.43	120

were completely separate, and the 95% prediction ellipse for *ridged abrasion strength* denticles overlapped with both constituent groups. *Generalized functions* denticles covered a broad area in the center of PC space, given their range of characters and functions. However, crown thickness can be used to distinguish between thinner *generalized functions* or *drag reduction* denticles and thicker *abrasion strength* or *ridged abrasion strength* denticles (ANOVA, $F_{5,209} = 25.83$, $p < 0.0001$; Tukey's HSD, $p < 0.0001$; Table S3). Furthermore, *drag reduction* denticles can be differentiated from *generalized functions* denticles, as the former typically possess a larger number of complete, parallel ridges ending in peaks of equal height (Table 5). The 95% prediction ellipse for *defense* denticles overlapped almost entirely with *ridged abrasion strength* denticles in PC space, although they can be distinguished by the upward-pointing, spine-shaped crowns (Fig. 2A, Table 5).

Proof of concept: reef sediments contain well-preserved denticles

A total of 330 denticles (240 modern, 90 fossil) were extracted from the bulk samples of reef sediments. On average, 50.4 denticles (± 24.5 SD) were recovered per 10 kg of the 63 μm to 2 mm size fraction. Denticles ranged from approximately 100 μm to 1 mm in size, and were predominantly collected in the 250 μm to 2 mm size fraction, with only 8% of the denticle assemblage found in the 106 to 250 μm size fraction. The vast majority of denticles (86.0%) were intact and well-preserved (Fig. 6). We found that just 13.3% of modern and 2.2% of fossil denticles were too poorly preserved to allow clear classification or measurement. The *drag reduction*, *abrasion strength*, and *ridged abrasion strength* morphotypes comprised 84.5% of the overall denticle assemblage. These functional morphotypes corresponded with the reef-associated families Carcharhinidae, Ginglymostomatidae, and Sphyrnidae (Fig. 2B, Tables 5 & S2), which are reported in the Bocas del Toro Archipelago (Robertson & Van Tassell 2015). While *drag reduction* denticles are also possessed by the pelagic



Fig. 6. Examples of dermal denticles extracted from (a) modern and (b) fossil reefs in Bocas del Toro, Panama. Functional morphotypes and predicted families: (1) drag reduction, Carcharhinidae; (2) ridged abrasion strength, Ginglymostomatidae; (3) defense, Squalidae?; (4) generalized functions, Ginglymostomatidae; (5) abrasion strength, family unknown; (6) drag reduction, Carcharhinidae; (7) ridged abrasion strength, Carcharhinidae; (8) generalized functions, family unknown; (9) generalized functions, Carcharhinidae?; (10) abrasion strength, Ginglymostomatidae. Denticles with unknown family classifications did not match up to examples in the reference collection. Scale bar = 100 μ m

families Alopiidae and Lamnidae (Tables 1, 5 & S2), these taxa have not been observed inshore in Caribbean Panama (Robertson & Van Tassell 2015), so we consider them unlikely contributors to these reef assemblages.

Generalized functions denticles were present in small numbers in both modern and fossil sediments, composing 10.4% and 18.9% of their respective denticle assemblages. In the reference collection, this morphotype was uncommon in reef-associated families (Table 5). It was found only on small sections of the fins in Carcharhinidae and very sparsely on the body, fins, and gill slits in Ginglymostomatidae (Fig. 2B, Table S2).

Three *defense* denticles were found in the modern reef sediments. In the reference collection, this morphotype was found on the bodies of mesopelagic sharks (Fig. 2C, Tables 5 & S2), which have not been observed on the lagoonal reefs of the Bocas del Toro Archipelago. However, the tiger shark *Galeocerdo cuvier* also possesses distinctive *defense* type denticles (Fig. 2B), and its presence in Almirante Bay was corroborated by a tooth discovered at the fossil reef. Two of the 3 denticles extracted from the modern

reefs were morphologically similar to denticles belonging to *G. cuvier* in the reference collection and were thus likely to have been shed by this species.

Predictably, *luminescence* denticles were not observed in the modern nor fossil reef sediments, as they were possessed only by mesopelagic species in the reference collection (Table 5). Less than 15% of the denticles found in the sediments could not be attributed to examples in our reference collection, suggesting the infrequent presence of pelagic or undocumented species. Alternatively, they may have originated from obscure anatomical positions that were not included in our reference collection, such as the nictitating membrane, oral cavity, or pit organs (Reif 1985a).

Potential applications

Morphometric analysis as a denticle classification tool

The measurement and categorization of denticle characters constitute a quantitative and consistent

Table 6. A comparative summary of shark survey methods. 'Taxonomic resolution' describes the commonly reported taxonomic levels, which often correspond to the highest possible taxonomic resolution for each survey method. CPUE: catch per unit effort

Technique	Common measurement metrics	Time frame	Taxonomic resolution	Selected citations
Diver surveys (e.g. belt transects, timed surveys, point counts)	Abundance, density, biomass	Hours	Species	Sandin et al. (2008), McCauley et al. (2012a)
Citizen science diver observations (e.g. REEF)	Sighting frequency, density, individual observations	Hours	Species, family	Ward-Paige et al. (2010b)
Baited remote underwater videos (BRUVs)	maxN (max number of sharks in one video frame)	Hours	Species	Brooks et al. (2011), White et al. (2013), Espinoza et al. (2014)
Aerial surveys (e.g. drones)	Abundance, density, sighting frequency (per unit effort)	Hours	Species (restricted to shallow, clear waters or surface swimmers)	Rowat et al. (2009)
Environmental DNA (eDNA)	Presence/absence, abundance (DNA/amount water)	Days – weeks	Species	Miya et al. (2015)
Longline surveys	Abundance (catch rate per unit effort [soak time, number and type of hooks, hook depth]), biomass	Months – years	Species	Baum & Myers (2004), Myers et al. (2007)
Landings statistics (e.g. Food and Agriculture Organization of the United Nations, FAO), fisheries observer programs	Tonnes caught, tonnes caught km ⁻² , CPUE	Months – years	Species (~15%), family, 'sharks and rays'	Bonfil (1997), Dulvy & Reynolds (2002), Clarke et al. (2006)
Mark and recapture studies (e.g. tagging)	Survival and recapture probability, population size	Years	Species	Bradshaw et al. (2007), MacNeil et al. (2008)
Genetics (e.g. microsatellites, mtDNA)	Population size and dynamics	Generations, years	Species	Vignaud et al. (2014)
Logbooks and artifacts	Qualitative or anecdotal abundance, presence/absence, sighting frequency, biomass	Years – centuries; historical periods	Species (occasionally), genus/family, 'sharks and rays'	Ferretti et al. (2008), McClenachan (2009), Drew et al. (2013)
Dermal denticle assemblages	Abundance (denticles/amount sediment/time)	Years – centuries	Family, ecological guild	This study

framework with which to group isolated denticles extracted from reef sediments. Specifically, these measurements could serve as a powerful, objective denticle classification tool in conjunction with a discriminant analysis or machine learning program. While taxonomic identification, particularly beyond the family level, is generally constrained due to shared morphological characters and large variation across individuals and species, this method may distinguish between functional groups of denticles. Functional morphotypes reflect ecological guilds of sharks as opposed to the species-level data reported in existing census methods (Table 6). While seemingly limited in scope, such data can be very powerful in exploring community change at a mechanistic level (McGill et al. 2006).

Setting quantitative shark baselines

While considerable anecdotal, historical, and ecological evidence suggests that sharks were previously present in numbers unheard of today, it is likely that population assessments began after the initial degradation of marine ecosystems (Colón 1959, Pauly 1995, Jackson et al. 2001, Pandolfi et al. 2003, Knowlton & Jackson 2008, Ferretti et al. 2008, Lotze & Worm 2009). Over the last 20 to 60 yr, longline surveys, commercial fishery observer programs, and fishery landings statistics (Table 6) have documented declines of > 50% in many shark species (Baum et al. 2003, Myers et al. 2007, Ferretti et al. 2010). However, issues with misreporting (especially of by-catch), misidentification, gear biases, and data resolu-

tion undermine these estimates of population status (Burgess et al. 2005, Clarke et al. 2006, Dulvy et al. 2008). Written accounts, ship logbooks, and artifacts, although often qualitative or isolated in time and space, provide the only indication of shark abundance before this period (Holden 1977, Ferretti et al. 2008, Drew et al. 2013; Table 6). More empirical data is therefore needed to characterize unfished shark communities. We propose that denticle assemblages extracted from fossil reefs can help characterize missing region-specific pre-human shark baselines. They can also be used to explore how dynamic these baselines are. Moreover, shifts in the relative abundance of different denticle morphotypes over time may reveal changes in shark communities and, consequently, alterations in community function through sharks' trophic and behaviorally mediated impacts on prey (Bascompte & Melia 2005, Heithaus et al. 2008, McCauley et al. 2012b, Heupel et al. 2014, Frisch et al. 2016).

Surveying modern shark communities

On coral reefs, traditional fish surveys using diver transects or videos represent 'snapshots' of the standing population and, as such, can overlook rare, cryptic, nocturnal, or seasonally-ephemeral species (Sale & Douglas 1981, Edgar et al. 2004, MacNeil et al. 2008, McCauley et al. 2012a; Table 6). They also lack the temporal resolution of some fishery-dependent records, and fail to capture natural fluctuations in populations over time (Connell et al. 1998, MacNeil et al. 2008). Consequently, estimates of top predator biomass at the same study sites often differ substantially (DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011, Nadon et al. 2012). In contrast, time-averaged assemblages of denticles in bulk sediment samples are a product of the accumulation of denticles shed from the long-term shark community (c.f. Vermeij & Herbert 2004, Kidwell 2008, 2013, Kosnik & Kowalewski 2016; Table 6). This has clear benefits in regions such as Bocas del Toro, where sharks are rarely or never reported (e.g. Dominici-Arosemena & Wolff 2005; see also the website of the Reef Environmental Education Foundation, www.reef.org) yet leave a significant record of their presence in the form of denticles preserved in reef sediments. Based on predictions of shark species distributions in the Bocas del Toro Archipelago (Robertson & Van Tassell 2015), our findings suggest that the denticle record has a basic level of fidelity with the living shark community, supporting the use of denti-

cles as a register of relative shark abundance and community composition. We therefore propose that denticle assemblages offer a new approach to measuring relative shark abundance on modern reefs, and can supplement existing surveys if the limitations of the approach are respected.

Limitations and considerations

If denticle assemblages in sediments are to be used to reconstruct shark communities, we must explore the taphonomic processes involved in the accumulation of denticles in sediments and the limitations of the approach.

Mechanism of denticle accumulation on reefs

Denticles are continually shed over a shark's lifetime by either rubbing off or through resorption of the anchoring fibers attached to the base (Reif 1985a). After being shed, we propose that denticles are transported by currents or turbulence as they sink to the seabed. In calm conditions, shed denticles would quickly be incorporated into the accumulating sediment. Denticles could also reach the sediment post-mortem, although a carcass would be expected to produce dense patches of morphologically similar denticles, a pattern which was not observed in any of our bulk samples. Predation, ingestion, and defecation may be another route by which denticles could arrive at the sediment. If this occurs, denticles could potentially be transported long distances. However, we consider this a relatively rare process given that most sharks are meso- or apex-predators.

The density of denticles incorporated into a unit of sediment is controlled by (1) the number of sharks in the area, (2) the rate of denticle shedding on each shark, and (3) the rate of sediment accumulation. To assess the fidelity and resolution of the denticle record, comparisons between visual shark surveys and their corresponding denticle assemblages in bulk samples could enlighten our understanding of how denticles accumulate in sediments from living shark communities. Sharks are presently so rare on the reefs we studied, however, that a fidelity study would be meaningless. We recommend conducting such a study on reefs with large numbers of sharks and sufficient survey data, such as Palmyra Atoll (Sandin et al. 2008). Finally, denticle shedding rates are likely to vary between taxa and species' life habits. For example, demersal species frequently associated with abrasive

coral may shed more denticles by mechanical abrasion than pelagic species.

Temporal and spatial considerations of denticle accumulation

The temporal scale of time averaging is influenced by the rate of sediment accumulation as well as bioturbation or other mixing (Kidwell & Bosence 1991, Kidwell & Flessa 1995). Deep sea, lagoonal, reef matrix, and anoxic sediments have low levels of bioturbation, making them most likely to preserve short timescales of ecological communities, whereas more heavily mixed sediments best represent long-term estimates of communities (Kosnik & Kowalewski 2016). However, assuming quick burial and no post-burial transportation of sediments, which can often be easily detected in the fossil record, denticle assemblages are likely to have an equally wide spatial scale as living shark communities.

Sediment reworking and sorting

Water energy may transport, sort, and rework denticles after they accumulate in the substrate. The specific density of dentine and enamel (~2.1 and 3.0 g ml⁻¹, respectively) is similar to that of calcite and aragonite (2.7 and 2.8 g ml⁻¹, respectively), so we would expect denticles to be affected by these erosional and depositional processes to the same degree as other microfossils in the same size range, such as foraminifera. Careful selection of low energy, sheltered sites that show no evidence of large storms and currents reduces the likelihood that the assemblages have been sorted or reworked. For example, we limited our preliminary study to sediments deposited in a semi-enclosed lagoon where currents and wave action are minimal.

Selective preservation of denticles

Environmental factors, such as wave action and water chemistry, can affect microfossil preservation (Kidwell & Flessa 1995), although ichthyoliths tend to be resistant to preservation biases (Helms & Riedel 1971, Sibert & Norris 2015). We observed that *drag reduction* denticles tended to fragment more easily than other denticle morphotypes, although this did not affect our ability to identify them. There was also no obvious superficial difference in the state of preservation between fossil and modern denticles. In

fact, the proportion of fragmented denticles was higher in modern (18.3%) than fossil (3.3%) sediments, which may be because modern denticles are likely to be exposed for a longer period of time prior to burial due to the slow-down of coral reef accretion. Alternatively, if present, fossilized shark teeth may provide supplemental insight into the presence of pelagic sharks in the case that their *drag reduction* denticles are not well-preserved (Ferrón et al. 2014).

SUMMARY

The durable composition, high abundance on sharks' bodies, distinctive characteristics, and degree of preservation of dermal denticles support their use as a tool for reconstructing shark communities. We have shown that bulk sediment samples from modern and fossil reefs can yield sufficient numbers of well-preserved denticles to permit analysis. Denticle morphology can be used to taxonomically classify denticles, although the resolution is limited (typically family-level) except in a few groups (e.g. the tiger shark *Galeocerdo cuvier* and nurse shark *Ginglymostoma cirratum*). Conversely, denticle morphology is highly correlated with function and shark life mode. As such, the relative abundance of different denticle functional groups can yield powerful ecological information about the shark communities that contribute to the denticle record. We recommend further study of the processes of denticle shedding and accumulation, with particular focus on the fidelity of the denticle record to living shark communities. This new source of data may offer valuable insight into past and present shark communities, facilitating important assessments of the magnitude and ecological impacts of global shark declines and producing more meaningful conservation targets.

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