



Comparative investigation into the morphology of oral papillae and denticles of four species of lamnid and sphyrnid sharks

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Abstract

The microstructures of the oral cavity in sharks have received relatively little study, despite their potential functional importance for gustation, feeding, and ventilation. Accordingly, here we conducted a preliminary comparative investigation into the structure and organization of oral papillae and denticles found on the ventral surface of the oral cavity in four species of shark (bigeye thresher, shortfin mako, scalloped hammerhead, and smooth hammerhead). Despite a limited sample size, differences in complexity and ornamentation of oral papillae and denticles were found across the four species. The scalloped hammerhead shark exhibited the largest oral papillae compared to the bigeye thresher and the shortfin mako. The most complex oral denticles, in terms of number of ridges and microstructures, were found in the scalloped hammerhead, followed by the bigeye thresher, smooth hammerhead and shortfin mako. For smooth hammerheads, in which samples were available from both juveniles and adults, differences in denticle microstructures were found suggesting possible ontogenetic variations. These results suggest that shape, size and arrangement of oral papillae and denticles may be related to ecology and phylogeny of the species studied. Based on these emerging patterns we discuss several plausible hypotheses relating to the function of these structures for consideration in future studies.

Keywords Ecomorphology · Gustation · RAM ventilation · Apex predators · Feeding ecology

Introduction

It is widely known that sharks present highly developed sensory specializations for olfaction, vision, electroreception, lateral line, vestibular control, gustation, and somatosensations (temperature and touch) (Collin 2012; Gardiner et al.

2012). Such sensory systems are especially important for behavioral activities such as feeding, avoiding predators, spatial orientation, social interactions, navigation, among others which play a significant role in their survival and longevity (Collin 2012). Although the sensory biology of sharks is well studied, the gustatory system has received relatively less attention, despite its likely importance in prey selection and capture (Atkinson and Collin 2010; Collin 2012; Rangel et al. 2017).

Taste modality in sharks is mediated by oral papillae (composed of gustatory receptor cells) distributed along the ventral and dorsal epithelium of the oropharyngeal cavity, gill arches, gill rakers, but are more abundant on the jaw (maxillary and mandibular valve). Through direct contact, oral papillae allow sharks to evaluate the suitability of potential prey, leading to ingestion or rejection of the item (Atkinson and Collin 2010; Collin 2012; Kirino et al. 2013; Atkinson et al. 2016). The oral papillae appear to develop early in shark embryos, for example, *Prionace glauca* and *Chiloscyllium punctatum*, and are functional before birth or on emergence from the egg case (Atkinson et al. 2016; Rangel et al. 2017). These papillae increase in size and decrease

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in density as the animal grows (Rangel et al. 2017); however, the total number of papillae is maintained throughout the ontogeny (Atkinson et al. 2016; Rangel et al. 2017). Overall, the oral papillae seem to have the same morphological configuration in all species of elasmobranchs studied (Whitear and Moate 1994; Rangel et al. 2016, 2017) and conserved throughout vertebrate evolution (Atkinson et al. 2016).

Together with the oral papillae, sharks also possess oral denticles in their oropharyngeal cavity, with species-specific patterns of morphology, distribution and density (Atkinson and Collin 2012; Rangel et al. 2017). While the structure and function of dermal denticles in the skin of sharks have been relatively well studied (Raschi and Tabit 1992; Mello et al. 2013; Dillon et al. 2017), the presence and role of denticles in the oropharyngeal cavity of sharks is poorly understood (Imms 1905; Nelson 1970). However, recent morphological studies in a few species have provided insights in their structure and function of oral denticles, which may be to reduce drag of water through the mouth, control hydrodynamic flow in the gills, permit greater ventilatory efficiency, and also protect the oral papillae against abrasion during food processing (Atkinson and Collin 2012; Atkinson et al. 2016; Rangel et al. 2016, 2017). However, understanding the organization and function of these structures remains a nascent field, with investigation to date in only a few species.

To address these gaps, we conducted a preliminary comparative investigation into the morphological structure of oral papillae and denticles from the ventral surface of the oral cavity from four sympatric species of two Galeomorphii sharks lineages: Lamniformes, bigeye thresher (*Alopias superciliosus*) and shortfin mako (*Isurus oxyrinchus*) and Carcharhiniformes, scalloped hammerhead (*Sphyrna lewini*) and smooth hammerhead (*Sphyrna zygaena*). Specifically, we generated species-specific description of the oral papillae and denticles to access what are the differences in shape, size and arrangement of oral papillae and denticles among these four sympatric sharks. Preliminary results are discussed in terms of the potential functional significance of these structures and species-specific differences in ecology.

Materials and methods

Sample collections

Specimens were obtained from a commercial fishing vessel (*Marbella I*, Kowalsky Ind. and Com. de Pescados Ltda company) in South and Southeastern Brazil, except the *S. zygaena* juvenile, which was caught incidentally in trawling in the coastal region, Southeastern Brazil. The animals were donated to the Surgery Department of *Faculdade de Medicina Veterinária da Universidade de São Paulo* (FMVZ-USP). Sample use was approved from the

Brazilian Ministry of Environment and IBAMA through SISBIO license number 48348-7 and Animal Ethics Committee (CEUA) no 9623050214, from FMVZ-USP. Upon capture, samples were removed from anterior ventral region of the oral cavity (Fig. 1; Table 1). All specimens were collected and processed in the same manner, except samples from the *S. zygaena* juvenile, which had been frozen prior to collection.

Scanning electron microscopy (SEM, LEO 435VP) was used to examine the three-dimensional microstructure and distribution of oral papillae, denticles and mucous cells on the oral cavity samples obtained. Prior to scanning, tissue samples were fragmented and fixed in 10% formaldehyde solution and then dehydrated in series of increasing ethanol density (70–100%). After dehydration, the samples were dried in a Balzers CPD 020 critical-point device mounted onto metal stubs with carbon adhesive and sputtered with gold in an Emitech K550 sputter apparatus for scanning.

Identification of oral papillae were based on descriptions of Whitear and Moate (1994), Atkinson and Collin (2010), Atkinson et al. (2016) and Rangel et al. (2017), which are described as projections located on the oral epithelium, where the gustatory receptor cells (microvilli) are situated

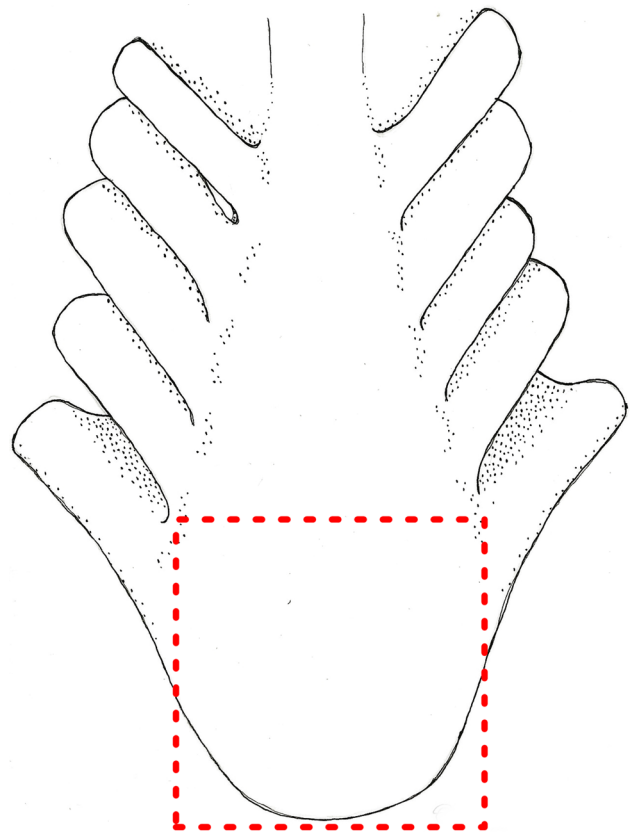


Fig. 1 Schematic of the shark oral cavity and region sampled for papillae and denticles

Table 1 Information on species analyzed in this study (cm)

Order	Species	Common name	# Specimens	Total length	Original description
Lamniformes	<i>Alopias superciliosus</i>	Bigeye thresher	2 adults	~300	Lowe, 1841
	<i>Isurus oxyrinchus</i>	Shortfin mako	5 adults	200–270	Rafinesque, 1810
Carcharhiniformes	<i>Sphyrna lewini</i>	Scalloped hammerhead	2 adults	200–234	Griffith and Smith, 1834
	<i>Sphyrna zygaena</i>	Smooth hammerhead	2 adults 1 juvenile	210–230 70	Linnaeus, 1758

on the apical ends of the papillae. The nomenclature for oral denticle was based on Dillon et al. (2017). We generated qualitative morphological measurements, including diameter of the papillae and size of oral denticles using images obtained by SEM and analyzed with ImageJ software (version 1.48). Size of these structures were determined by measuring diameter of the papillae as well as crown width of the denticles (10–25 denticles per species). For round-shaped papillae (*A. superciliosus* and *I. oxyrinchus*) the diameter of the structure was measured (2–4 papillae per species). For the oval-like papillae (*S. lewini*, $n = 13$ papillae), the measurements were performed considering the smaller and larger diameter of the structures. The diameter of the *S. zygaena* was not measured.

Results

The bigeye thresher shark, *A. superciliosus*

In adult bigeye thresher, the oral papillae were the smallest among the sharks here investigated; they occur between the denticles (Fig. 2a, b; Table 2). These papillae exhibited a rounded and slightly pronounced shape above the surface of the epithelium. Two pores were detected adjacently in the central region of the surface of the oral papillae (Fig. 2c, d). Adjacent to the pore, the presence of microvilli surrounding the pore opening were also observed (Fig. 2d). The concentration of microvilli appeared to be higher in central regions compared to the lateral regions of the papillae (Fig. 2d).

The oral denticles were distributed throughout the anterior ventral surface of the oral cavity (Table 2). The denticles exhibited a single-bladed shape, with three main ridges pronounced on the crown surface, with four to six smaller ridges in between (Fig. 2e, f). The apex of denticles were all oriented posteriorly, with individual denticles spaced apart with minimal overlap (Fig. 2a, e, f). Near the base of the crown, interconnected microstructures of hexagonal-shape were also identified (Fig. 2f).

The shortfin mako shark, *I. oxyrinchus*

The oral papillae of shortfin mako projected out of the epithelium of the oral cavity and had a rounded-shape (Fig. 3a,

b, d, e; Table 2). In the lateral portions of the anterior ventral surface of the oral cavity, was observed regions with isolated papillae, some denticles segregated and some regions with the absence of both (Fig. 3b). On the apical surface of the papillae, depressions with large amounts of microvilli were identified (Fig. 3e–g). Pores were not detected in the surface of the papillae. A large number of mucous cells were observed, filling the gaps between papillae and oral denticles (Fig. 3c–f). Denticles appeared generally distributed throughout the surface of the oral cavity (Fig. 3a–c; Table 2), with the exception of a few regions where the denticles were either absent or found in small clusters (Fig. 3b). Denticles were all single-pointed and had a smooth crown, without ridges or microstructures. Mucosal cells were observed among the denticles (Fig. 3a–c).

The scalloped hammerhead shark, *S. lewini*

The largest oral papillae was found in the scalloped hammerhead shark (Table 2), which showed two different morphologies: circular and oval-shaped (Fig. 4a, b). However, the oval-shaped papillae could be due to the merging of two oral papillae (Fig. 4b). The papillae exhibited one or two pores in the central region of the surface (Fig. 4a–c). The oral denticles were largest and most complex among the sharks here investigated. They were distributed adjacent to each other, overlapped and exhibited one to three triangular cusps, with the central cusp being the most pronounced (Fig. 4a–d; Table 2). The denticles also possessed four to seven ridges that extended almost all over of the crown and hexagonal-shaped microstructures were present on the rostral region of the crown (Fig. 4d). Mucous cells were observed between the denticles (Fig. 4c, d).

The smooth hammerhead shark, *S. zygaena*

In the anterior ventral region of the adult smooth hammerhead samples analyzed, the oral papillae (Table 2) appeared as rounded elevations from the epithelium found between the oral denticles (Fig. 5a), and exhibited a pore (Fig. 5b). The diameter was not measurements in smooth hammerhead, due to low sample size. Denticles in the juvenile were smaller than in the adult, but both were distributed adjacent to each other (Fig. 5c, d). The

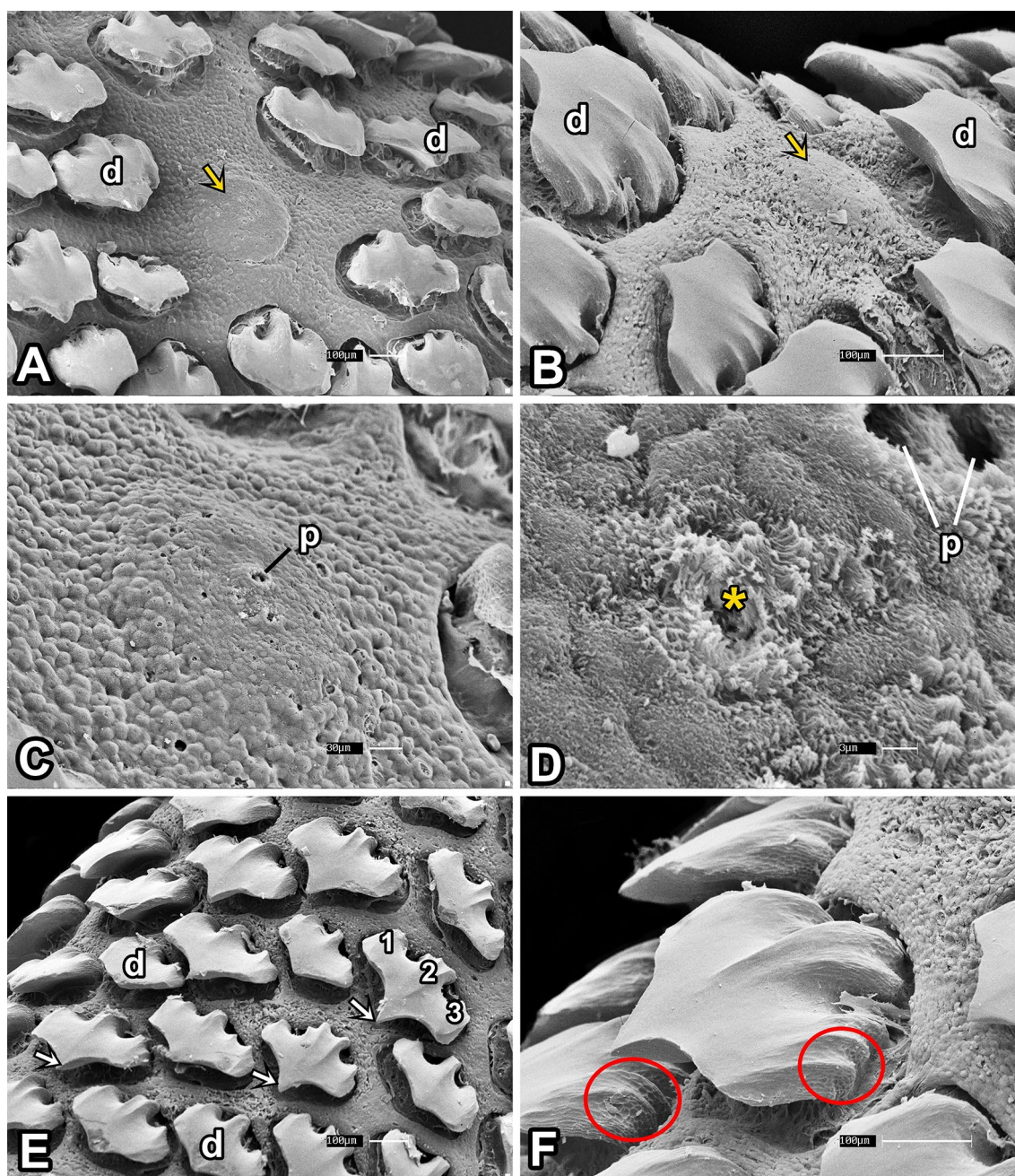


Fig. 2 Oral papillae and denticles of the bigeye thresher shark, *Alopias superciliosus*. In scanning electron microscopy, **a, b** oral papillae (yellow and black arrow) and oral denticles (d); **c, d** epithelial pore (p) and microvilli (yellow *), **e** oral denticles (d) composed of a single-bladed shape (black and white arrow), with three main ridges

pronounced on the crown surface (1–3) and four to six smaller ridges in between. **f** Interconnected microstructures of hexagonal-shape (red circle) on the near the base of the crown. Scale bars: **a, b, e, f** 100 μm ; **c** 30 μm ; **d** 3 μm

denticles exhibited rounded-shape crowns, composed by a small central cusp and up to three ridges, with the central cusp being the most prominent (Fig. 5c; Table 2). On the surface of the crown, interconnected hexagonal-shaped microstructures were found (Fig. 5d). The structures exhibited one to three triangular cusps, with small side cusps (Fig. 5e, f) and three to six ridges that extended

from the base to half of the crown. At the base of the crown, hexagonal-shaped microstructures were also observed in the samples (Fig. 5e).

Table 2 Summary for the shape and size of oral papillae and denticles in the shark species examined

Species	Oral papillae			Denticles		
	Diameter (μm)	Papillae shape	Association with pore or depression	Denticle shape	Number of ridges	Crown surface width of denticles (μm)
<i>A. superciliosus</i>	199.8 \pm 25.3	Round	Central	Single blade	3 main, 4–6 smaller ones	271.6 \pm 37.2
<i>I. oxyrinchus</i>	239.8 \pm 18.5	Round	Central	Single blade	0	205.3 \pm 36.1
<i>S. lewini</i>	341.2 \pm 48.7 (\emptyset smaller)	Oval	Central	1–3 triangular cusps	4–7 ridges	262.2 \pm 18.5
	497.8 \pm 27.6 (\emptyset larger)					
	321.8 \pm 41.9 (round)	Round				
<i>S. zygaena</i>	–	–	–	A: 3 cusps J: Single blade	A: 3–6 J: 1–3	A: 210.5 \pm 17.3 J: 141.3 \pm 26.2

Diameter and crown surface width of denticles (μm) mean \pm SD. The diameter were not measurements in *S. zygaena*
A adults, J juveniles

Discussion

Here we provide a preliminary structural description of oral papillae, denticles and mucosal cells present in the oral cavity samples of bigeye thresher, shortfin mako, scalloped hammerhead and smooth hammerhead sharks. Our findings demonstrate that shape, size and arrangement of oral papillae and denticles may be related to ecology and phylogeny of the species studied. In the discussion that follows, we summarize the patterns found and consider several plausible hypotheses relating to the function of these structures.

Oral papillae

We found that oral papillae present in the oral cavity of the four species were slightly pronounced above the surface of the epithelium as has been found in *Scyliorhinus canicula* (Whitear and Moate 1994), *P. glauca* (Rangel et al. 2017), and *C. punctatum* (Atkinson et al. 2016). The structure of these oral papillae is comparable to Type II of teleost fishes, mainly found in the oropharyngeal cavity, including the ventral region and gill rakers (Reutter et al. 1974). In this study, only samples from the ventral region of the oral cavity were examined; however, recent studies have described the presence of oral papillae on the dorsal epithelium of the oropharyngeal cavity, gill arches, gill rakers, and the maxillary and mandibular valve.

The microvilli, described as protrusions of gustatory receptor cells (Whitear and Moate; Atkinson et al. 2016), were only observed in bigeye thresher and shortfin mako samples. They were projected into several clusters, some more centralized, and others scattered over almost the entire surface of the papillae, as has been found previously in *S. canicula* (Whitear and Moate 1994) and *C. punctatum*

(Atkinson et al. 2016). These microvilli are usually observed within a pore and are associated with clusters in the apical papillar surface, covering $\sim 0.5\%$ this area (Atkinson et al. 2016). Unlike the other three sharks, depressions were observed on the apical surface of the papillae in the shortfin mako. This may have functional significance, for example increasing the area to the microvilli. A pore was found in hammerhead sharks, but microvilli were not observed, which could have functional significance or could be attributed to tissue preparation, damage, or aged microvilli that are degenerating as suggested by Atkinson et al. (2016). Additional sampling is needed to determine if this is the case.

Studies have shown that there is a positive correlation between body size and papillae diameter across ontogeny, however, a decrease in density as the animal grows (Atkinson et al. 2016; Rangel et al. 2017). Despite this, the papillae size did not correlate with the total length of shark (Atkinson et al. 2016). In the present study, the pelagic sharks showed similar total length, however, the papillae diameter varied considerably among some species, which is consistent with observations in *C. punctatum* (Atkinson et al. 2016). This indicates that larger sharks do not necessarily have larger papillae, for example, the bigeye thresher and shortfin mako sharks of the present study, which have a larger total length, but small papillae.

For sharks, it has previously been suggested that papillae size and density may be related to taste sensitivity, with larger diameters and increased density providing increased gustatory capacity (Atkinson et al. 2016). We found that the scalloped hammerhead exhibited the largest oral papillae when compared to the bigeye thresher and shortfin mako. From an evolutionary perspective, hammerhead sharks present greater cognitive capacity, more complex sensorial-motor integration, and greater behavioral complexity

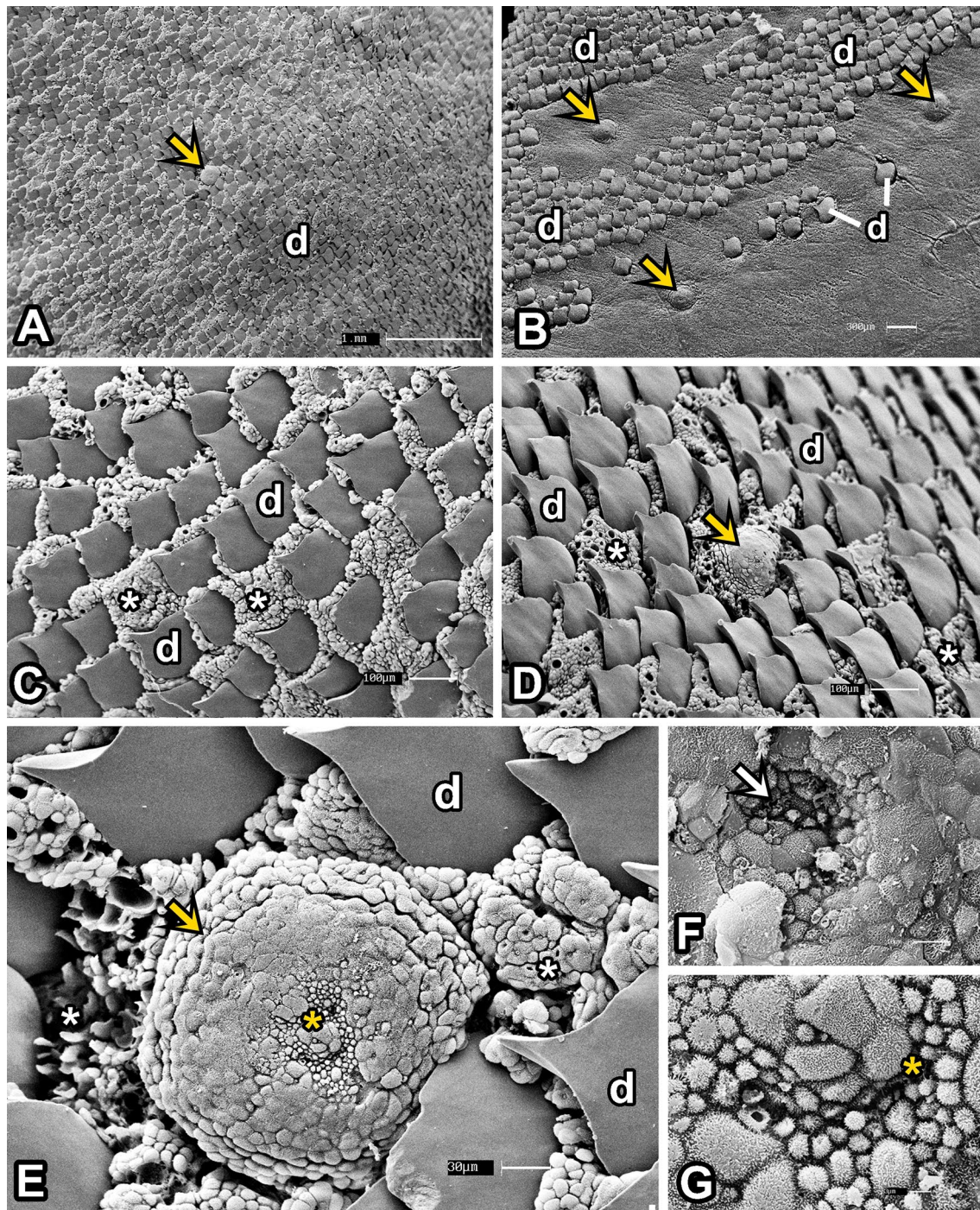


Fig. 3 Oral papillae and denticles of the shortfin mako shark, *Isurus paucus*. In scanning electron microscopy, **a–d** distribution of the oral papillae (yellow and black arrow), oral denticles (d) and mucous cells (*)

and white arrow) with large amounts of microvilli (yellow *) was observed in oral papillae (yellow and black arrow). Scale bars: **a** 1 mm; **b** 300 μm; **c, d** 100 μm; **e** 30 μm; **f** 10 μm; **g** 3 μm

compared to other sharks (Gallagher et al. 2014). In addition, they present specialization/optimization of sensory systems, such as the electrosensory (Kajiura and Holland 2002) and the olfactory systems (Abel et al. 2010). These results indicate, as observed in other sensorial systems and

brain size, the possible complexity found in the gustatory system of hammerhead sharks may be due, in part, to phylogeny (Collin 2012; Yopak et al. 2007); however, experimental comparative studies are needed to investigate this hypothesis.

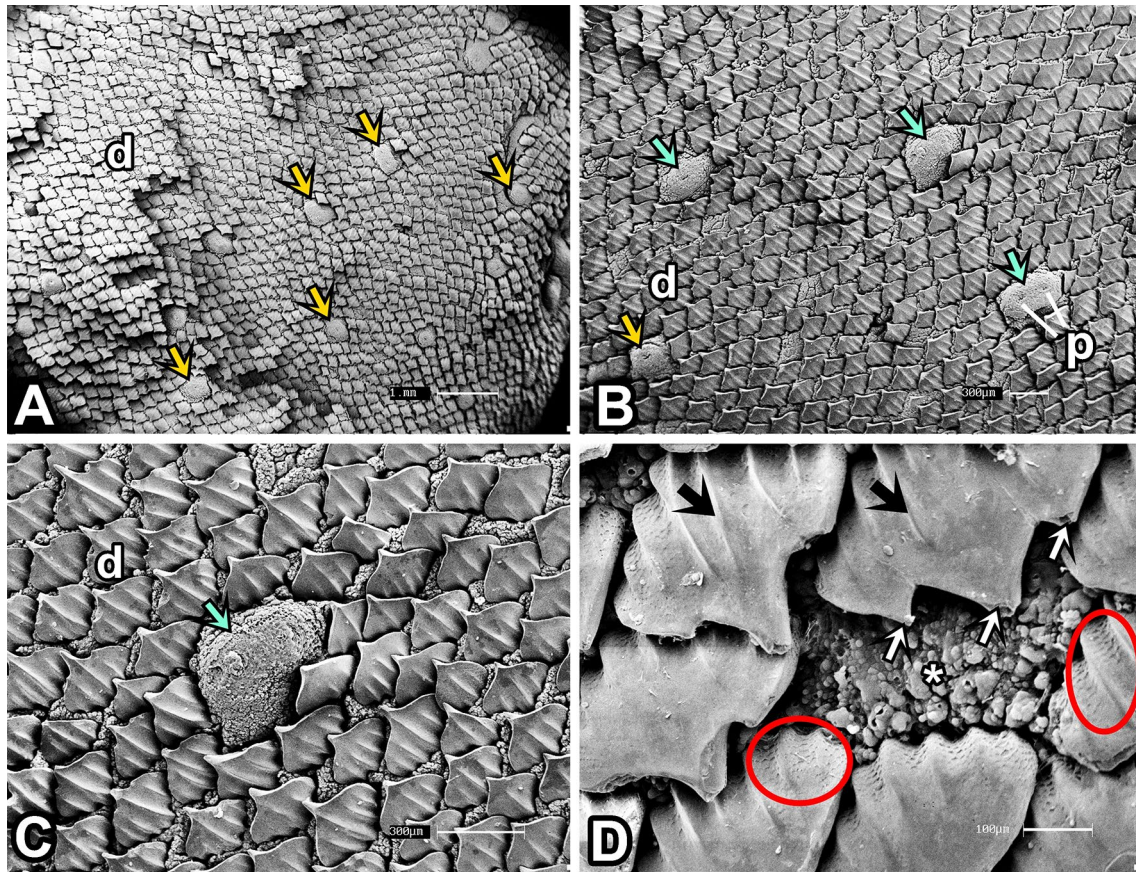


Fig. 4 Oral papillae and denticles of the scalloped hammerhead, *Sphyrna lewini*. In scanning electron microscopy, **a** distribution of the oral papillae (yellow and black arrow) distributed among the oral denticles (d). **b** Highlighting the two different morphologies observed in the papillae: circular (yellow and black arrow) and oval-

shaped (blue arrow), with the pore (p). **c, d** oral denticles (d) with one to three triangular cusps (black and white arrow) and four to seven ridges (black arrow); hexagonal-shaped microstructures on the rostral region of the crown (red circle) and mucous cells (*) between the denticles. Scale bars: **a** 1 mm; **b, c** 300 μm ; **d** 100 μm

The reduced size of papillae found in the bigeye thresher and shortfin mako sharks suggest that these two species may rely less on gustation during feeding than the scalloped hammerhead, perhaps since they are recognized to be highly visual predators (Yopak 2012; Yopak and Lisney 2012), thereby relying more on visual versus gustatory discrimination. For example, bigeye thresher sharks use tail-eye coordination to visual select schools of prey fishes and stun prey with their caudal fins (Preti et al. 2008; Aalbers et al. 2010; Yopak and Lisney 2012). However, it is also possible that other regions of the oropharyngeal cavity, not sampled here, exhibit greater concentrations of papillae. Accordingly, we recommend future studies of this kind to analyze samples throughout the oral cavity. Interestingly, the samples examined from shortfin mako sharks appeared to harbor a relatively larger number of mucous cells in the epithelium of the oral cavity compared to the other four species examined. The associated potential for greater mucus production may aid in feeding (Shephard 1994), lubricating the epithelium and thus

facilitating swallowing while protecting the epithelium from possible mechanical injury (Yashpal et al. 2009).

The observed morphological differences in oral papillae, and associated gustatory discrimination, may also affect prey selectivity and vulnerability to consuming indigestible human debris. Blue shark, for example, are among the sharks that are usually reported with ingested plastic debris (e.g., 25.3% of sharks sampled, Bernardini et al. 2018). This shark have a similar size of oral papillae ($295 \pm 81.2 \mu\text{m}$, Rangel et al. 2017) when compared to bigeye thresher and shortfin mako sharks of the present study. It is plausible that prey selectivity due to gustatory preferences may make some species or size classes of sharks more or less likely to bite and/or consume novel objects, which has implications for human safety and also vulnerability to being captured in fisheries. In this sense, for example, changing metal hook or bait type may reduce capture rates of scalloped hammerhead, which are more specialists (Gallagher et al. 2014), and also others, which have significant conservation concern, resulting in a decrease of incidental capture.

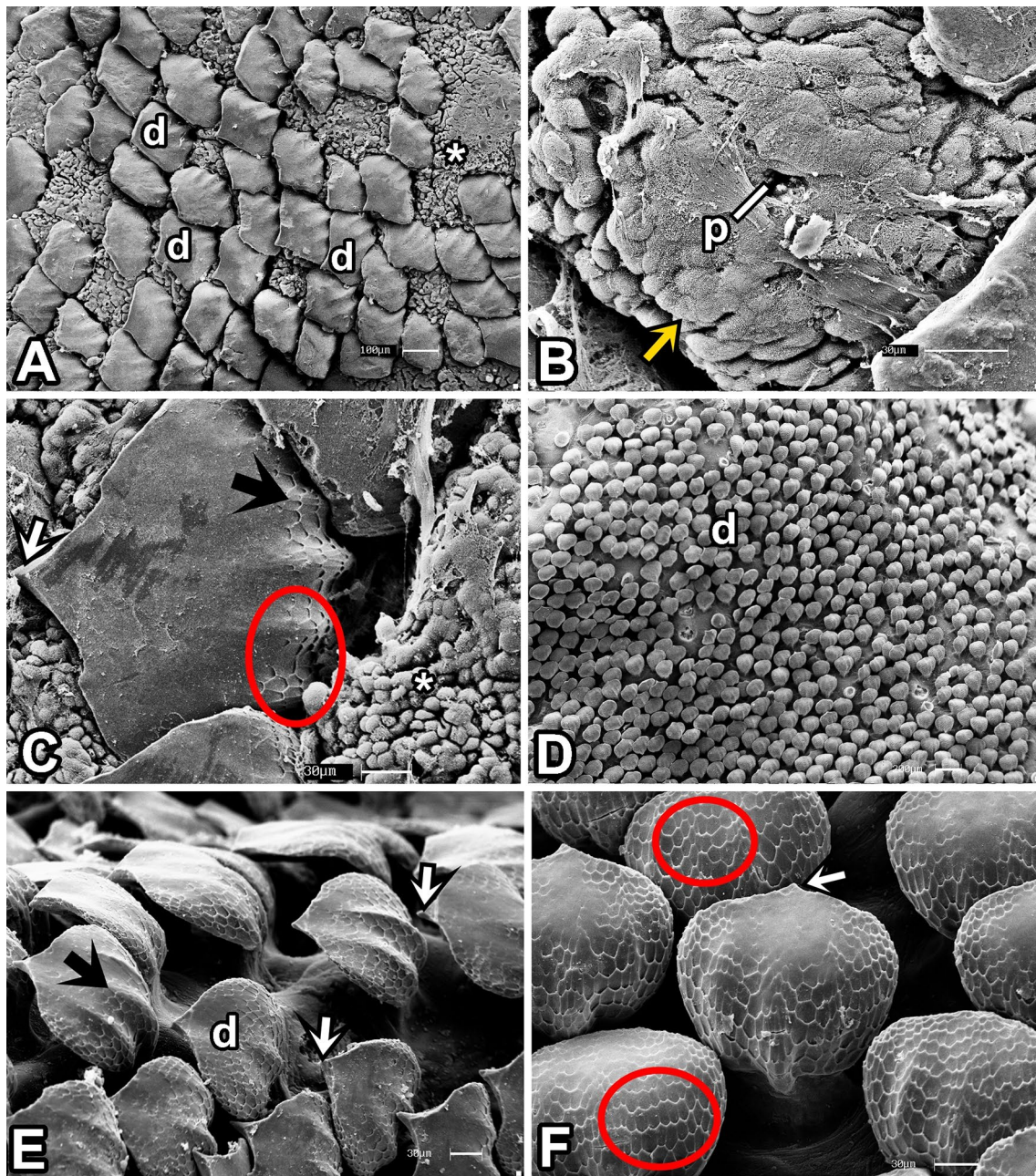


Fig. 5 Oral papillae and denticles of the smooth hammerhead, *Sphyrna zygaena*. In the adult, scanning electron microscopy of **a–c** oral denticles (d), papillae (yellow and black arrow) with a pore (p), and mucous cells (*) between denticles. The denticles exhibited rounded-shaped crowns, composed of a small central cusp (black and white

arrow) and up to three ridges (black arrow). **d–f** oral denticles in the juvenile composed of a small central cusp (black and white arrow) and up to three ridges (black arrow), with hexagonal-shaped microstructures (red circle). Scale Bars: **d** 200 µm; **a** 100 µm; **b, c, e, f** 30 µm

It is worth considering that it has previously been suggested that the density and distribution of oral denticles in the oropharyngeal cavity may limit the distribution of papillae (Atkinson and Collin 2012). This, however, was not the case in the shortfin mako sharks, whereby these two structures were spatially separated in some regions,

demonstrating that the relationship between papillae and denticles need to be further studied. A comparison of oral papillae density in other groups with and without oral denticles, such as some skates and stingrays, would help to test this hypothesis.

Oral denticles

Denticle morphology has been described to be closely linked to phylogeny, ecology, including trophic level, maximum length, and life mode (Raschi and Musick 1986; Mello et al. 2013; Dillon et al. 2017). In terms of function, oral denticles in sharks have been suggested to (1) help aid in RAM ventilation by reduce the drag of water flow through the oral cavity and over the gills, (2) help to protect the oral papillae from injury of items ingested during feeding, and (3) facilitate food retention due to abrasion of the cusps, thereby improving feed efficiency (Atkinson and Collin 2012; Rangel et al. 2016). The functional morphotype for drag reduction found on the oral denticles, are similar to those reported for dermal denticles in lamnid and carcharhinid sharks. This morphotype is characterized by a crown exhibiting a prominent primary keel and a variable number of smaller keels (Raschi and Musick 1986; Dillon et al. 2017). However, the oral denticles exhibited higher morphological variability among the four species examined in the present study, being more similar between hammerhead sharks.

While denticle sizes (crown surface width) were similar among the sharks analyzed, samples from the shortfin mako exhibited absence of denticle ridges or microstructures on the denticles which were found on those of the other sharks. This pattern may reflect greater hydrodynamic drag reduction efficacy, once that the shortfin mako shark present specializations to increase gas exchange (e.g., a larger gill surface area) and withstand the forceful branchial flow induced by RAM ventilation (Bernal et al. 2001; Wegner et al. 2010). In contrast to the shortfin mako, denticles observed in samples from the others three sharks exhibited both ridges and microstructures on the crown surface. The spacing, size and quantity of ridge differed among sharks, as well as observed in dermal denticles of Sphyrnidae, Alopiidae and Lamnidae (Dillon et al. 2017).

Here we found that the most complex oral denticle structures in the scalloped hammerhead and the intermediately complex in the bigeye thresher and smooth hammerhead sharks. This is consistent with the ornamental patterns found in the dermal denticles for this species (Mello et al. 2013; Dillon et al. 2017). Furthermore, ridges and microstructures found in hammerhead sharks may improve more RAM ventilation efficiency, since they have a decreased mouth size (Gallagher et al. 2014), and this functional morphotype may be beneficial to reduce hydrodynamic drag (Dillon et al. 2017). Elaborate ornate microstructures of dermal denticles has been considered a derived condition in sharks, suggesting a plesiomorphic condition of reduced ornaments (Mello et al. 2013). However, the complexity of microstructures is homoplastic, with different selective pressures triggering the emergence or reemergence of such traits (Mello et al. 2013);

with recent studies showing a strong correlation with function and shark ecology (Dillon et al. 2017).

The oral denticle found in the juvenile had hexagonal-shaped microstructures throughout the surface of the crown. This is similar to that described in the *Rhizoprionodon lalandii*, which is a small-sized benthopelagic shark that inhabits shallow waters (Ciena et al. 2016). However, this pattern differs in adults, with a reduction in the portion occupied by microstructures, and an increase in the number of ridges. Such features may be related to ontogeny, once juveniles of this species using coastal regions as nursery area (Speed et al. 2010), and may have some functional relevance related to habitat.

The present study revealed differences in the complexity and ornamentation of oral papillae and denticles across the four species. Based on our results, it is possible that gustation may play a more important role in elasmobranch feeding than currently appreciated, permitting elasmobranchs to discriminate between potential prey (Hart and Collin 2015). The morphology and distribution of oral denticles varied among sharks, which could have both phylogenetic and functional significance, possibly linked to the processes of RAM ventilation and secondarily to protection of the papillae. Future descriptive and experimental studies are needed to better understand the functional role of the oral structures investigated here. Such studies should include other elasmobranchs using a combination of morphological, physiological, and phylogenetic variables as a comparative approach.

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