

# Dental morphology and microstructure of the Prickly Dogfish *Oxynotus bruniensis* (Squaliformes: Oxynotidae)

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## Abstract

This study describes and illustrates the jaws, teeth, and tooth microstructure of the Prickly Dogfish *Oxynotus bruniensis*. Detailed accounts of the dental morphology of *O. bruniensis* are rare and have not addressed the tissue arrangement or microstructure of the teeth. These features are documented and discussed in the contexts of interspecific comparisons with other elasmobranchs and the dietary specialization of *O. bruniensis*. The overall tooth morphology of *O. bruniensis* is similar to those of other closely related members in the order Squaliformes, as is the tissue arrangement, or histotype. *Oxynotus bruniensis* exhibits a simplified enameloid microstructure, which we compare with previously documented enameloid microstructures of other elasmobranchs. Though subtle interspecific differences in dental characters are documented, neither overall tooth morphology nor histotype and microstructure are unique to *O. bruniensis*. We conclude that in the case of *O. bruniensis*, dietary specialization is facilitated by behavioral rather than morphological specialization.

## KEYWORDS

elasmobranch, enameloid, histotype, specialization, teeth

## 1 | INTRODUCTION

The prey-capture abilities of predators reflect interactions between morphological phenotypes, the environment, and behavior (Phillips, 2000; Ferry-Graham *et al.*, 2002; Hulsey and García de León, 2005; Mori and Vincent, 2008). Predators that feed on a narrow range of prey species are often described as dietary specialists, but applications of the terms 'specialist' and 'specialization' are frequently open to debate and assigned relative to other taxa within a clade or community (Futuyama and Moreno, 1988; Ferry-Graham *et al.*, 2002; Irschick *et al.*, 2005). So varied are the interpretations of the term 'specialist' that Ferry-Graham *et al.* (2002: table 1) identified five types of specialists distinguished by the ecological, mechanistic, and evolutionary implications of their specializations. Based on Ferry-Graham *et al.*'s (2002) scheme, functional and behavioral specialists are organisms whose morphology and behavior constrain them to a subset of resources. Despite previous attempts to demarcate specialists and to establish formalized definitions

of 'specialization', much of the usage remains context-dependent (Munroe *et al.*, 2014).

The frequency with which specialization is invoked without a standardized definition to explain interspecific morphological variation complicates the exploration of correlations between form and function, which are not always clearcut (Lauder, 1995; Lauder, 1996). For example, across 14 species of Recent and extinct sharks (Chondrichthyes: Elasmobranchii), Whitenack and Motta (2010) found little difference in the puncture and draw performance of the species' isolated teeth. This does not support the widely accepted scheme of classifying shark tooth morphotypes by presumed function (e.g. cutting type teeth in sharks that prey on large, fleshy marine mammals or piercing type teeth in predominantly piscivorous species of sharks). Furthermore, stomach contents of sharks with a tooth morphotype indicative of specialization on one type of prey may reveal a much broader diet than tooth morphology alone would indicate. For example, the Tiger Shark *Galeocerdo cuvier* (Péron and Lesueur, 1822) typifies the cutting tooth morphotype (Cappetta,

2012; Klimley, 2013). Authors have not shied from labeling this a case of specialization (Witzell, 1987; Hammerschlag *et al.*, 2015). However, stomach contents suggest that *G. cuvier* is an opportunistic generalist. Castro (2011: p. 469) described the Tiger Shark as both specialized for preying on large sea turtles and the species with the most extensive diet known among sharks. Additionally, recent findings that some sharks may be regarded as generalists at the species level but exhibit specialist behaviors at the individual level complicate the distinction of specialist species. Matich *et al.* (2011) report that individual Bull Sharks *Carcharhinus leucas* (Müller and Henle, 1839) sampled off Florida exhibited steady stable isotope values over the course of their study and concluded that although the population may have the niche breadth of a generalist species, that breadth was explained by variation among individual specialist sharks.

Given the ambiguity surrounding the term 'specialist' and its differential application across organizational levels (i.e. individual, population, and species levels), exploring the evolutionary implications of dietary specialization on morphology in sharks is a complicated undertaking. However, it may be aided by a comparative approach in which a putative morphological or behavioral specialization is evaluated against the morphology and behaviors of related taxa. If, as Munroe *et al.* (2014) suggest, specialization is best thought of as a continuum, then by comparing the morphologies and behaviors of elasmobranchs in the middle or generalist end of the spectrum with those of a sister taxon on the highly specialized end, we may better understand whether selected morphological traits indicate dietary specialization. Here, we model this approach using morphological and microstructural characters of the teeth of a dietary specialist, the Prickly Dogfish *Oxynotus bruniensis* (Ogilby, 1893) and compare our findings to the teeth of other elasmobranchs.

The Prickly Dogfish *Oxynotus bruniensis* is a small (adults reach approximately 72 cm total length) squaliform shark found on outer continental and insular shelves and upper slopes of southern Australia and New Zealand and is most common at depths between 350 and 650 m (Compagno, 1984; Ebert *et al.*, 2013). *Oxynotus bruniensis* is one of five extant species in the family Oxynotidae, all of which are readily identified by their triangular body shape, sail-like dorsal fins, and enlarged dermal denticles (Ebert *et al.*, 2013; Finucci *et al.*, 2016). The diet of *O. bruniensis* was only recently described by Finucci *et al.* (2016), who used genetic analysis of the stomach contents of 53 specimens to determine that the Prickly Dogfish feeds exclusively on the egg capsules of holocephalans. The degree to which this dietary specialization is found among oxynotid sharks remains to be seen. However, a captive specimen of the Angular Roughshark *Oxynotus centrina* (Linnaeus, 1758), whose natural diet includes polychaete worms, crustaceans, and small teleosts (Capapé, 2008), was observed feeding on elasmobranch egg cases after caretakers initially offered live invertebrates that the shark did not consume (Guallart *et al.*, 2015).

Detailed descriptions of tooth morphology and microstructure of *O. bruniensis* are sparse despite the utility of tooth morphology. Welton (1981) describes an extinct species of *Oxynotus*, †*O. crochardi*, based on two Meckelian teeth and proposes it as the sister

taxon to *O. bruniensis*. Welton's (1981) description does not describe the teeth of *O. bruniensis* in great detail or with respect to their functional significance, but it proved sufficient for some researchers to postulate, on the basis of shared dental characters with *O. bruniensis*, that dietary specialization in Oxynotidae may have evolved more than 20 million years ago (Welton, 1981; Flammensbeck *et al.*, 2018). Cappetta (2012) offers an overview of oxynotid tooth morphology and arrangement remarking on the extreme heterodonty exhibited by oxynotids, but he does not address *O. bruniensis* explicitly. Bigelow and Schroeder (1957) offer an illustration of the palatoquadrate and Meckelian dentitions of *O. centrina* and note that there are interspecific differences in dental morphology within the genus, but their description of teeth of *O. bruniensis* is limited to a general overview of tooth shape and count. Following Bigelow and Schroeder (1957), Herman *et al.* (1989) provide an account of the arrangement of teeth in *O. centrina* but do not provide odontological details explicitly relating to *O. bruniensis*. Perhaps the most extensively illustrated descriptions of oxynotid dentitions to date are those of Herman *et al.* (2005) in which they compare the external morphologies of teeth of *O. bruniensis*, *O. centrina*, and the Sailfin Roughshark *Oxynotus paradoxus* Frade, 1929 but do not comment on functionality, comparisons with other squaliform taxa or microstructure. Much of what is known about squaliform tooth development, replacement, and microstructure comes from studies of the Spiny Dogfish *Squalus acanthias* Linnaeus, 1758 (Kerr, 1956; Grady, 1970; Nanci *et al.*, 1983; Samuel *et al.*, 1983; Slavkin *et al.*, 1983). Only lately has the taxonomic scope of squaliform tooth development and microstructural studies been increased (e.g. Moyer and Bemis, 2016; Underwood *et al.*, 2016). This is surprising given the use of external morphological characters of teeth in phylogenetic studies of Squaliformes and other clades of elasmobranchs (Casier, 1961; Adnet and Cappetta, 2001; Guinot *et al.*, 2018).

In addition to descriptions of external tooth morphology, histological differences among shark teeth are reported in the literature, but not with respect to *O. bruniensis*. Differences in the arrangement of dental tissues in sharks have been documented since the mid-19th century and continue to be an active field of study (Agassiz, 1833-1843; Owen, 1840-1845; Moyer *et al.*, 2015; Schnetz *et al.*, 2016; Moyer and Bemis, 2017; Jambura *et al.*, 2020). The arrangement of orthodontine around a hollow pulp cavity and a root of osteodontine in orthodont teeth and a pulp cavity filled by osteodontine like that of the root, and the absence of orthodontine in osteodont teeth represent the two principal histotypes of elasmobranch teeth (see Moyer *et al.*, 2015 and references therein for a more detailed account of histotype differentiation). Peyer (1968) noted that elasmobranch teeth may be arranged by histological complexity, and the orthodont and osteodont histotypes represent the extremes. Recently, the term pseudoosteodont has been reintroduced to the literature referring to a histotype in which osteodontine secondarily fills the majority of a pulp cavity surrounded by orthodontine (Jambura *et al.*, 2018). In selachian fishes, crowns of teeth of all histotypes are covered by triple-layered enameloid. Each layer is distinguished by the orientation of fluorapatite crystallite bundles (Reif, 1973; Cuny *et al.*, 2017).

The enameloid layers are the outermost, or shiny layer enameloid (SLE); the middle, or parallel fibered enameloid (PFE); and the innermost, or tangled fibered enameloid (TFE) (Cuny *et al.*, 2017; Gillis and Donoghue, 2007).

We conducted the current study to document the arrangement, morphology, and microstructure of teeth of the Prickly Dogfish *O. bruniensis*, a dietary specialist for which no detailed record of dental morphology and histology exists beyond general tooth shape and tooth counts. By providing detailed morphological and histological documentation of the dentition of *O. bruniensis*, we are able to address two related issues concerning the comparative odontology of elasmobranchs and aspects of morphological specialization: (a) How do the morphology and arrangement of teeth in *O. bruniensis* compare with those of other selachians? (b) Does the dentition of *O. bruniensis* reflect either in gross morphology or microstructure the specialized diet of the species? Here, we not only provide the first in-depth account of tooth morphology and microstructure in relation to the diet of *O. bruniensis* but also model an investigatory framework to document, identify, and analyze morphological traits of a specialist species.

## 2 | METHODS

### 2.1 | Specimen collection

We examined the jaws and teeth of six specimens of *O. bruniensis*, three males and three females ranging from 57.8 to 67.9 cm in total length (TL). Specimens were obtained during fisheries independent research trawl surveys conducted by the National Institute of Water and Atmospheric Research (NIWA; New Zealand) on board RV *Tangaroa* on Chatham Rise of New Zealand during January 2018. Specimens were frozen whole at sea and transported to the mainland for analysis. All but one specimen, a 64.4-cm total length (TL) male (UMA F20812), had empty stomachs. The single specimen that did not, had the partially digested remains of a chondrichthyan egg case in its stomach. The head of each specimen was removed anterior to the pectoral girdle but posterior to the hyoid arch, fixed in 10% formalin, and then transferred to 70% ethanol. Specimens were shipped to the University of Massachusetts Amherst (UMA; Amherst, MA, USA) where they were accessioned into the university's Natural History Collections. The jaws of a 57.8-cm TL male (UMA F20813), 62.6-cm TL female (UMA F20814), and a 67.9-cm TL female (UMA F20815) were excised and prepared as skeletal specimens using a method modified from Enault *et al.* (2016). The jaws, chondrocranium, and hyoid arch of the 64.4-cm male (UMA F20812) were skeletonized using methods described by Bemis *et al.* (2004). The heads of a 59.1-cm TL male and a 52.6-cm TL female (UMA F20810 and UMA F20811, respectively) were retained as whole heads with soft tissue intact and preserved in ethanol as fluid specimens.

To identify specific teeth with respect to position across the rami of the jaws and within tooth files, we used the tooth identification

scheme employed by Moyer *et al.* (2015) and Bemis *et al.* (2015). In this identification scheme, the letter S denotes symphyseal teeth overlaying the palatoquadrate symphysis of the upper jaw or the Meckelian symphysis of the lower jaw. The letters R and L indicate the right or left side of the jaw, the letters P or M indicate whether the tooth is of the palatoquadrate or Meckelian cartilages, and a number indicates the position of the tooth relative to the symphysis of the jaw. For example, the fourth tooth from the Meckelian symphysis on the right side of the Meckelian cartilage would be identified as R (right) M (Meckel's cartilage) 4 (fourth tooth from the center). If a tooth is fully erupted and in a functional position or if it is a replacement tooth, we append the letters F or R, respectively. In the case of replacement teeth or multiple functional teeth in a single tooth file, a number indicating the tooth's position from the labial side of the jaw follows the letters R or F.

After soaking skeletonized jaws in a dilute solution of household ammonia, we excised the following individual teeth from UMA F20813: SMF1, SMR1, RM1F1, RM2F1, LM2F1, LM2R1, SP1F1, SP1F2, RP3F1, RP3F2, and LP3F2. We selected these teeth on the basis of condition and ease of extraction. Teeth were cleaned first in warm water and then in acetone before air-drying. We used the same tooth extraction procedure to isolate teeth of the Shortfin Mako *Isurus oxyrinchus* Rafinesque, 1810 and the Cownose Ray *Rhinoptera bonasus* (Mitchill, 1815) from specimens UMA 00046 and UMA F20809, respectively. We use the same tooth numbering scheme to refer to the isolated teeth of *I. oxyrinchus*. As previously described by Sasko *et al.* (2006) and Berkovitz and Shellis (2016), teeth of *R. bonasus* are arranged in an imbricated, pavement-like dentition with seven files of flattened teeth in the palatoquadrate and Meckelian cartilage. Consequently, the tooth numbering scheme we use for shark teeth is not applicable to *R. bonasus*. We refer to specific teeth of *R. bonasus* by their exact location within the jaw.

### 2.2 | Histological preparation and specimen imaging

SMF1, RM1F1, and LM2R1 teeth of *O. bruniensis* specimen UMA F20813 were flat-lapped using first 1,200 and then 2,000 grit carborundum paper to remove the lingual and labial surfaces of each tooth. Once tooth sections were approximately 70  $\mu$ m thick they were washed again in acetone and allowed to air-dry before being mounted using Permount<sup>TM</sup> mounting medium (Fisher Scientific) on glass slides for light microscopy. We applied the same specimen preparation procedure to the isolated LM4F1 tooth of *I. oxyrinchus* (UMA 00046) and the tooth plate sixth from the front of the central upper jaw tooth file in *R. bonasus* (UMA F20809). Micrographs of tooth sections were taken using a Leica M165 FC light microscope equipped with a Leica DFC450 C digital camera. Following Schmidt and Keil (1971) and Ripa *et al.* (1972), we imaged tooth sections under polarized light to enhance differentiation of dental tissues. We compared the microstructure of teeth in *O. bruniensis* with those of *I. oxyrinchus* and *R. bonasus* as well as previously published descriptions of tooth microstructure in other extant and extinct taxa (e.g. Enault

et al., 2013; Moyer et al., 2015; Moyer and Bemis, 2016; Cuny et al., 2017). In our comparison, *I. oxyrinchus* serves as a representative of modern selachians and *R. bonasus* as a representative of batoids.

To obtain micro-computed tomography (CT) datasets, we used a ZEISS Xradia 520 Versa 3D X-Ray microscope operating at 110 kV source voltage, 10 W power, and using the LE3 propriety high pass ZEISS filter provided with the instrument (Carl Zeiss Microcopy Inc.). The LM2F1 and RP3F2 teeth of UMA F20813 were scanned at 2.7  $\mu\text{m}$  resolution. The jaws of UMA F20810 were scanned in situ at 25.3  $\mu\text{m}$  resolution. We used the open source biomedical image viewer Horos (based on OsiriX™ DICOM imaging software; Rosset et al., 2004) on an Apple Macintosh computer running OSX 10.13.6 to generate two- and three-dimensional reconstructions of scanned specimens. In three-dimensional reconstructions, tissue densities are represented by customized color-lookup tables (CLUTs) with denser tissues appearing lighter shades of yellow or white and less dense tissues appearing darker shades of red or orange.

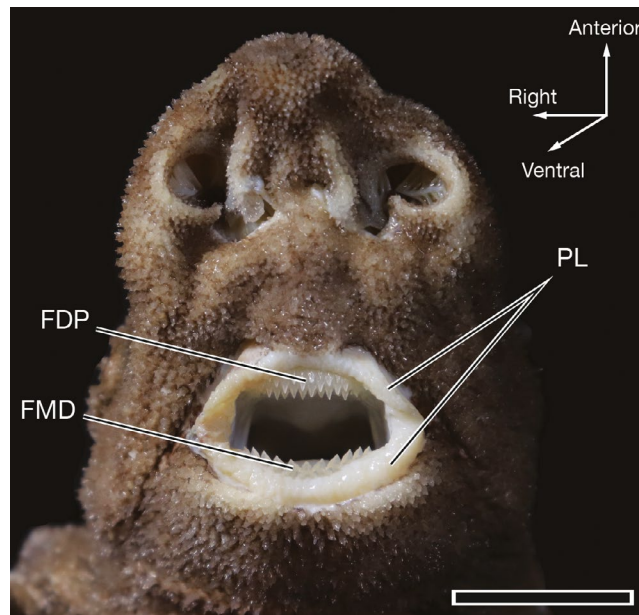
Excised jaws were photographed using a Canon EOS Rebel T7i digital camera. We corrected images for contrast and merged them using through-focus stacking in Adobe Photoshop CS5 (version 15.0.2) to make a single high-resolution image with greater depth of field.

### 3 | RESULTS

#### 3.1 | Jaw morphology and tooth arrangement

In situ, the jaws of *Oxynotus bruniensis* are surrounded by fleshy, papillose lips, and the functional dentition of the palatoquadrate and Meckelian cartilages are visible (Figure 1). The jaws are positioned sub-terminally under the chondrocranium in an orbitostylic mode. Visible in excised and skeletonized jaw specimens, the quadrate process of the palatoquadrate is greatly enlarged (Figure 2a,b). When viewed from a posterior position, two separate quadratomandibular joints are visible behind the wing-like quadrate processes (Figure 2c). These two joints form the points of articulation between the palatoquadrate and Meckelian cartilages. Though present, the orbital processes of the palatoquadrate are very small, and in dried skeletal specimens the orbital process tends to fold under a crest formed on the dorsal ridge of the palatoquadrate (Figure 2b,c). In manually manipulated specimens, the jaws open vertically to create an oral opening approximately twice as high as it is wide. Note that manual manipulation of postmortem material can only serve as a rough approximation of in vivo performance. However, the maximum dimensions allowed by the jaws, the relatively small and inflexible symphyses of the palatoquadrate and Meckelian cartilages (Figure 2c), and the short range of the suspensory ligaments suggest that jaw protrusion and gape expansion do not factor heavily in the predatory mode of *O. bruniensis*.

The functional dentition of *O. bruniensis* displays monognathic and dignathic heterodonty in which tooth shape and size differs within and between the palatoquadrate and Meckelian dentitions

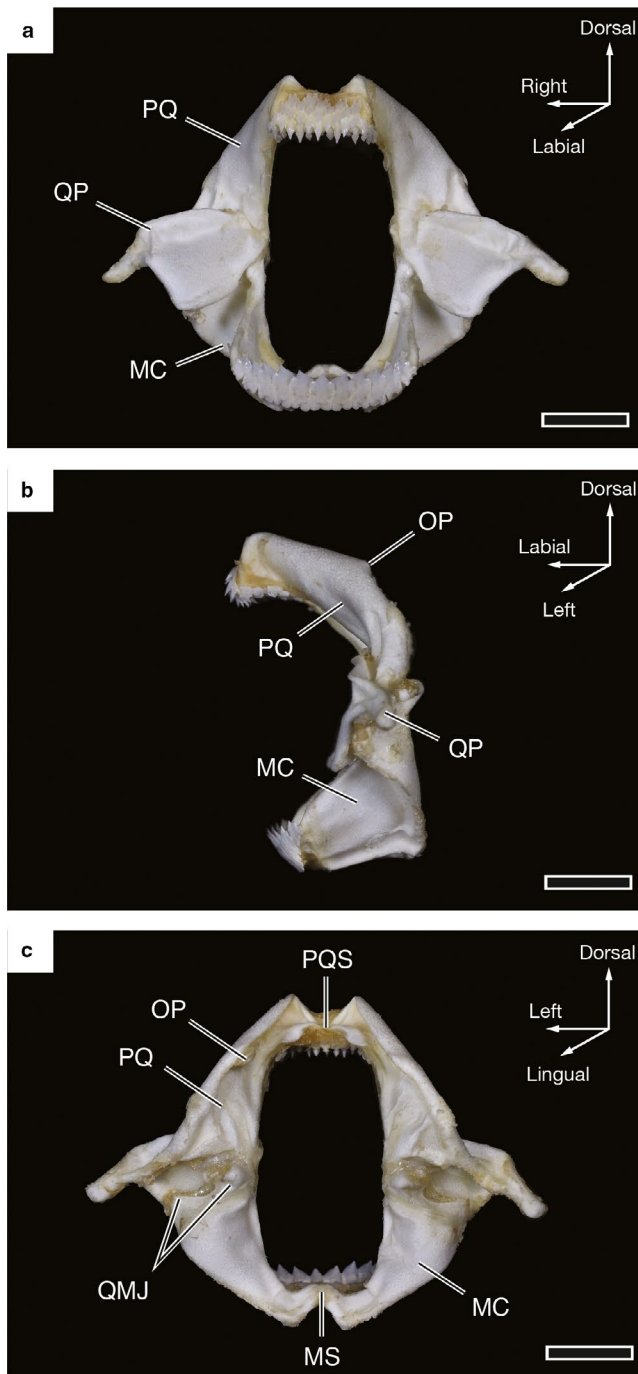


**FIGURE 1** Ventral view of the mouth, functional dentition, and lips of 62.6-cm TL female *Oxynotus bruniensis* (UMA F20811). FDP, functional dentition of the palatoquadrate; FMD, functional Meckelian dentition; PL, papillose lips. Scale bar: 2 cm

(Figures 3a and S1). In anterior tooth files of the palatoquadrate, such as RP1 – 6, SP1, and LP1 – 6 of UMA F20810, the teeth are very similar morphologically and are positioned in an arrangement consistent with alternate file tooth replacement (see Underwood et al. 2016 for an in-depth account of tooth replacement patterns in squaliform sharks). Teeth are offset across developmental rows, and this pattern extends across the anterior region of the palatoquadrate until reaching the lateral region of the rami of the palatoquadrate.

Teeth at the 6th or 7th through 10th loci on the left and right sides of the palatoquadrate are markedly smaller and more asymmetrical than teeth of the anterior region. The crowns of teeth in these lateral loci are less pointed, not as tall, and the structures of the tooth roots are poorly defined. When viewed from a lateral or oblique angle, it is apparent that teeth of the lateral region of the palatoquadrate are not closely associated with the jaw cartilage. Rather, they are held in connective tissue not visible in CT reconstructions when settings are optimized for hard tissue visualization and are not as close to the tessellated cartilage of the palatoquadrate as the more anterior teeth (Figure 3b). The restricted range of the dentition of the palatoquadrate in *O. bruniensis* is noteworthy as the functional dentition is confined to the anterior-most regions of the jaw and does not extend distally across the rami of the palatoquadrate cartilages.

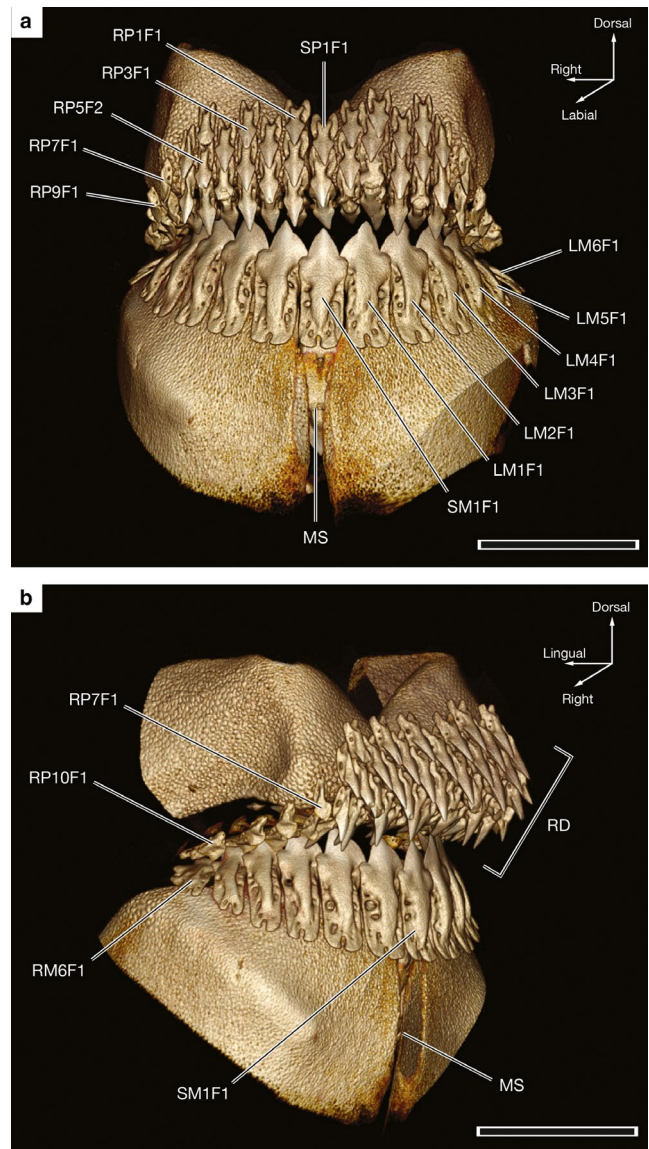
All specimens examined displayed retention of functional teeth in the following tooth files: RP1 – 5 or 6, SP1, and LP 1 – 5 or 6. As a result, each of these tooth files contained up to four functional teeth starting at the margin of the jaw and around to its labial surface. Collectively, these cuspidate teeth make a rasping dentition on the anterior of the palatoquadrate (Figure 3b). This arrangement would likely be suitable for gripping and scratching through food



**FIGURE 2** Photographs of the jaws of a 67.9-cm TL female *Oxynotus bruniensis* (UMA F20815). (a) Labial view of the jaws. (b) Lateral view of the jaws shown in (a). (c) Lingual view of the jaws shown in (a). MC, Meckel's cartilage; MS, Meckelian symphysis; OP, orbital process; PQ, palatoquadrate; PQS, palatoquadrate symphysis; QMJ, quadratomandibular joints; QP, quadrate process. Scale bars: 1 cm

items similar to the anterior Meckelian dentition of *Heterodontus* spp., based on previously published descriptions of the latter (e.g. Garman, 1913; Reif, 1976; Huber *et al.*, 2005).

The Meckelian teeth of *O. bruniensis* are asymmetrical with the exception of the single symphyseal tooth (SM1), which is symmetrical

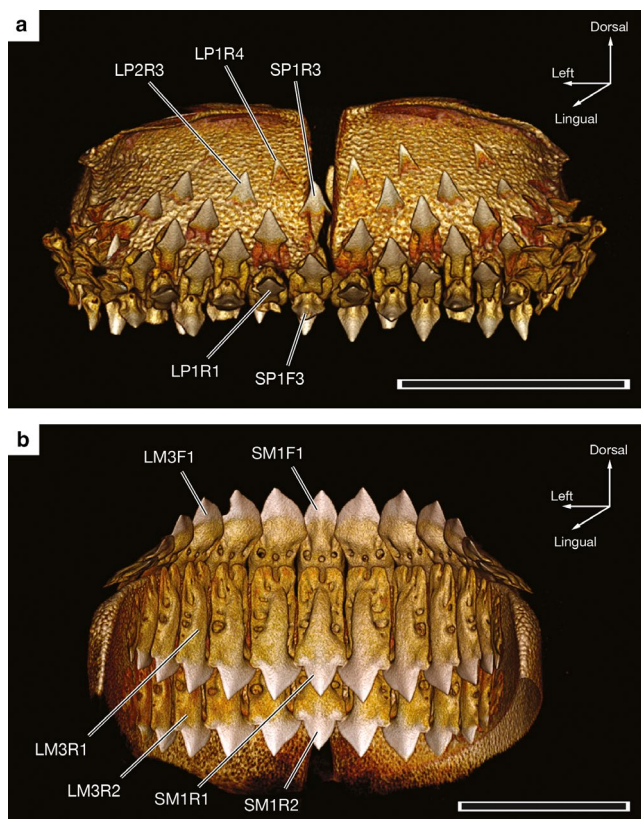


**FIGURE 3** Three-dimensional reconstructions of the dentition of a 59.1-cm TL male *Oxynotus bruniensis* (UMA F20810) generated from CT data. (a) Labial view of upper and lower jaw dentitions with landmark tooth loci labeled. (b) Oblique view from the right side of the same specimen shown in (a) with rasping dentition in the anterior region of the upper jaw identified. MS, Meckelian symphysis; RD, rasping dentition. See the text for tooth numbering scheme. Scale bars: 1 cm

(Figure 3a). Unlike the dentition of the palatoquadrate, only a single functional tooth is present at each tooth locus in all specimens examined. In specimen UMA F20814, the LM2F1 and LM3F1 tooth crowns were broken, leaving a gap in the functional dentition; however, the tooth roots were retained. Presence of the roots indicates that the gap in the dentition was likely due to mechanical breakage of tooth crowns and not variable rates of replacement between tooth files. From mesial to distal Meckelian tooth loci, teeth become shorter, and their angulation relative to the jaw margin changes such that more distal teeth are reclined lingually and point backwards into the mouth (e.g. tooth RM6F1 in Figure 3b). More anterior teeth retain an upright position.

Three-dimensional reconstructions of CT data illustrating the functional and replacement teeth of *O. bruniensis* show dignathic differences in tooth development and replacement (Figure 4). In these reconstructions, tissue density serves as an indicator of mineralization. When the lingual side of the palatoquadrate is viewed, teeth in early stages of development are visible as partial crowns and lack any mineralized root (e.g. SP1R3, LP1R4, and LP2R3 in Figure 4a). Root mineralization appears to take place as the tooth progresses from the R2 to R1 positions in the tooth files of the palatoquadrate. Sequentially added teeth (*sensu* Underwood *et al.*, 2016) progress from replacement to functional positions, giving rise to the alternate tooth replacement pattern observed in the functional teeth. Replacement teeth become functional as their angle relative to the margin of the jaw changes. For example, the SP1F3 tooth depicted in Figure 4a is deemed functional as it is angled downward into the oral cavity, whereas the neighboring LP1R1 tooth remains approximately perpendicular to the margin of the jaw. Tooth files of the palatoquadrate each have three or four replacement teeth.

In contrast to the tooth files of the palatoquadrate, Meckelian tooth files bear a single functional tooth and two replacement teeth per file (Figure 4b). Replacement teeth lay flush with the lingual side of the jaw (e.g. SM1R1, SM1R2, LM3R1, and LM3R2 in Figure 4b).



**FIGURE 4** Three-dimensional reconstructions generated from CT data depicting replacement teeth of a 59.1-cm TL male *Oxynotus bruniensis* (UMA F20810). (a) Lingual view of the tooth-bearing region of the palatoquadrate with landmark tooth loci labeled to illustrate alternate tooth replacement. (b) Lingual view of the tooth-bearing region of Meckel's cartilage with landmark tooth loci labeled. Scale bars: 1 cm

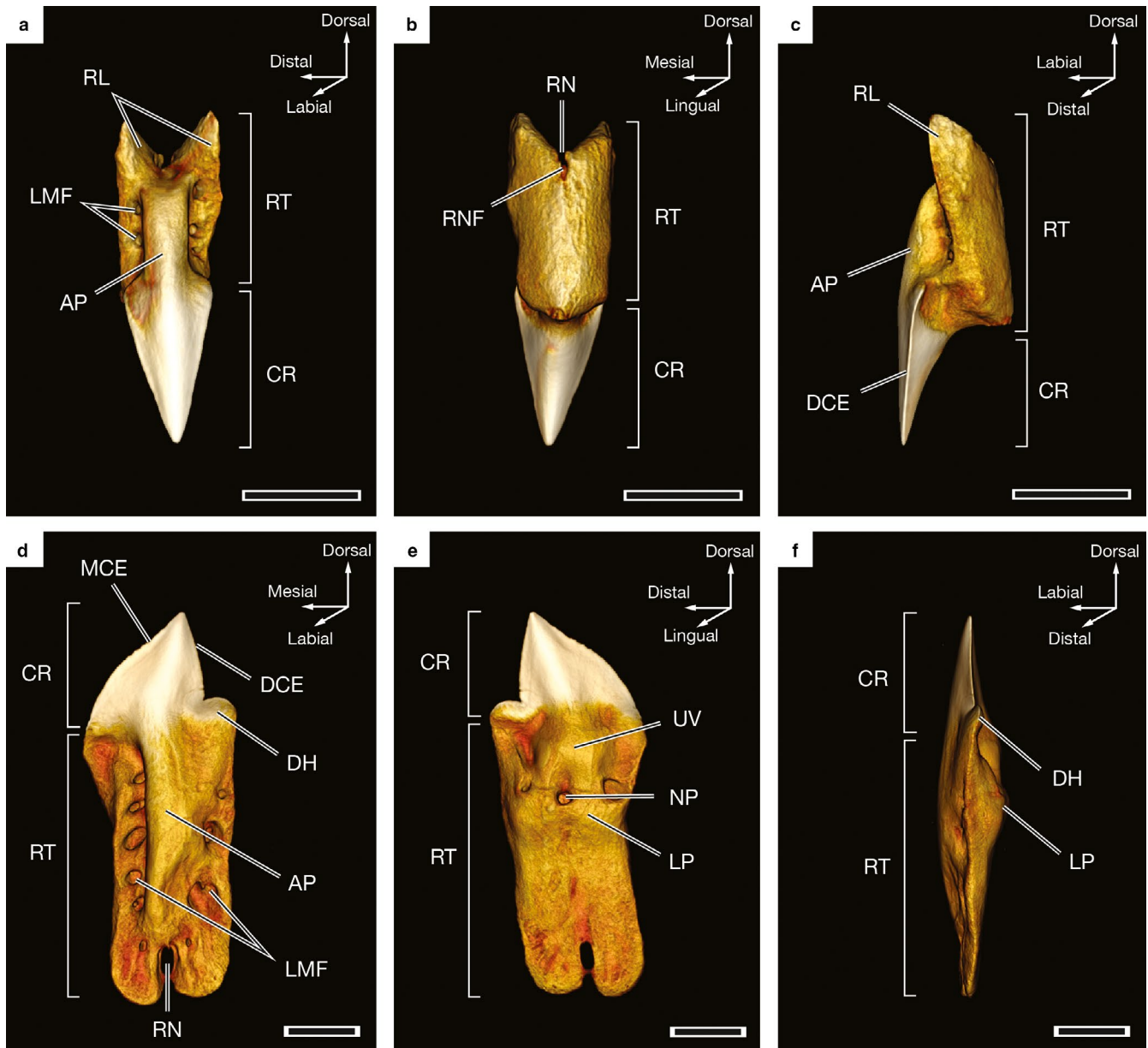
Like the functional Meckelian teeth, replacement teeth remain in close contact and form a single serrated dentition. This indicates a 'single file' pattern of tooth replacement (*sensu* Underwood *et al.*, 2016). Crowns of the earliest replacement Meckelian teeth, designated R2, are complete and connected to roots that are almost completely mineralized. The exceptions to this trend are replacement teeth of the most distal loci, which do not complete mineralization of the root until they transition to a functional position.

Including the small lateral teeth of the palatoquadrate, the dental formula of *O. bruniensis* is U: 9 or 10 - 1 - 9 or 10, L: 6 or 7 - 1 - 6 or 7. Whether there is an ontogenetic difference in tooth number in *O. bruniensis* remains to be determined and would require larger sample sizes spanning multiple ontogenetic stages. However, based on the six specimens observed in the current study, variability in tooth number does not appear to be correlated with sex.

### 3.2 | Tooth morphology

In *O. bruniensis* the symphyseal teeth of the palatoquadrate (SP1) and teeth of the first six or seven tooth files on either side of the symphysis (LP1 through LP6 or 7 and RP1 through RP6 or 7) are small and, in the specimens examined, do not exceed 3.5 mm in height when measured from the tip of the longest root lobe to the apex of the enameloid-covered crown. The crowns of these teeth appear lanceolate, or spear-shaped, and widen before tapering into narrow aprons (*sensu* Cappetta, 2012) of enameloid at the base of the crown (Figure 5a). LP1 and RP1 through LP7 and RP7 teeth are nearly symmetrical. Only in more distal loci are the root lobes uneven in length. Labial marginal foramina are present on both sides of the apron. In CT-scanned teeth, a single marginal foramen is visible at the base of the apron inside the root notch and is referred to as the root notch foramen (Figure 5b). Labial marginal foramina and root notch foramina are small and are difficult to observe without the use of repeated cleanings and micro-CT reconstructions, as the foramina of individually excised teeth are frequently covered by connective tissue or filled with what is presumably vascular tissue. LP1 and RP1 through LP7 and RP7 teeth are linguo-labially robust, such that the distance from the lingual to labial-most points on the teeth equals almost a third of the overall tooth height (Figure 5c). When viewed laterally, the extent of the overlap between the enameloid-covered portions of the tooth and the root becomes more apparent. This arrangement results in the crown of the tooth being situated not under the root when the tooth is in a functional position but overhanging the root (Figure 5c). In contrast, the distal-most teeth of the palatoquadrate are less well defined and are more linguo-labially compressed. None of the teeth of the palatoquadrate exhibit appreciable serrations, although multiple teeth examined during this study bear chipped cutting edges.

The Meckelian teeth of *O. bruniensis* are larger than the teeth of the palatoquadrate. Among the specimens examined, the largest Meckelian teeth are LM and RM2F1 and measure 5 mm from crown apex to root lobe. Tooth height decreases to approximately



**FIGURE 5** Three-dimensional reconstructions of individual teeth of a 57.8-cm TL male *Oxynotus bruniensis* (UMA F20813) generated from CT data. (a) Labial view of RP3F2 tooth. (b) Lingual view of the tooth shown in (a). (c) Lateral view from the distal side of the tooth shown in (a). (d) Labial view of LM2F1 tooth. (e) Lingual view of the tooth shown in (d). (f) Lateral view from the distal side of the tooth shown in (d). AP, apron; CR, crown; DCE, distal cutting edge; DH, distal heel; LMF, labial marginal foramina; LP, lingual protuberance; MCE, mesial cutting edge; NP, nutritive pore; RL, root lobe; RN, root notch; RNF, root notch foramen; RT, root; UV, uvula. Scale bars: 1 mm

3 mm in the distal-most loci. With the exception of the symphyseal tooth (SM1), Meckelian teeth are asymmetrical with a single distal heel at the base of a distal cutting edge on one side of the crown and a curved mesial cutting edge on the opposite side of the crown, (Figure 5d). The SM1 tooth of the Meckelian dentition is symmetrical, with an erect crown and a distal heel on either side (Figures 3 and 4b). Serrations on Meckelian teeth, particularly on the mesial cutting edge, are very light. At 2.7  $\mu\text{m}$  resolution, they are barely visible in CT reconstructions. The apices of functional Meckelian teeth point distally. The exception to this trend is the SM1 tooth, which bears a distal heel on both sides and points dorsally rather than distally.

Meckelian teeth therefore have a discernible distal inclination of the crown apex that indicates the side of the jaw from which they originate. We follow Moyer and Bemis (2016) in referring to this directionality as handedness. The handedness of teeth at a given locus remains consistent within the tooth file. On the labial surfaces of Meckelian teeth, labial marginal foramina penetrate the root down the lengths of each root lobe on either side of the apron, a central ridge covered by a very thin layer of enameloid that extends from the base of the crown to the root notch (Figure 5d). Marginal foramina are not visible on the lingual side of Meckelian teeth. Rather, there is a large nutritive pore beneath a lingual extension of the crown

termed the uvula (*sensu* Cappetta, 2012) and above a lingual protuberance of the root (Figure 5e). Meckelian teeth are linguo-labially compressed. Even with the lingual protuberance, LM and RM1 and 2 teeth are more than five times taller than they are linguo-labially wide (Figure 5f).

### 3.3 | Histotype and microstructure

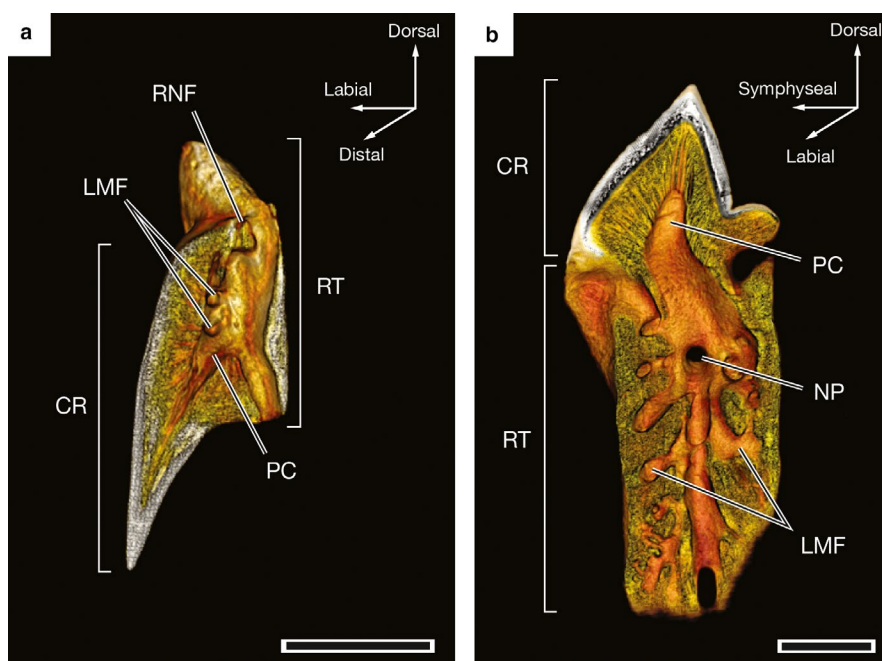
Sectioned reconstructions generated from CT data allow visualization of the pulp cavities of palatoquadrate and Meckelian teeth. The pulp cavities of teeth of the palatoquadrate in tooth files LP1 through LP6 or 7, SP1 and RP1 through RP6 or 7 are best visualized when reconstructions of teeth are sectioned medially (Figure 6a). The extent of pulp cavities in the more linguo-labially compressed Meckelian teeth is more apparent when the labial surfaces of tooth reconstructions are virtually removed (Figure 6b). Figure 6 shows sectioned reconstructions of the RP3F2 and LM2F1 teeth of UMA F20813. In both teeth, the pulp cavities extend into the root, beyond the base of the crown. Labial marginal foramina connect to the pulp cavity, as do the root notch foramen of RP3F2 (Figure 6a) and the nutritive pore of LM2F1 (Figure 6b). The presence of a hollow pulp cavity is indicative of the orthodont histotype, an identification confirmed by light microscopy (Figure 7).

Light microscopy of the fully formed flat-lapped LM2R1 tooth of UMA F20813 reveals three tissue types (Figure 7a). Osteodentine, discernible by the presence of vascular canals, or denteones (*sensu* Smith and Sanson, 2000; formally osteons), forms the root. Orthodentine surrounds much of the pulp cavity in the crown and is distinguished from osteodentine by dentine tubules radiating from the pulp cavity and the absence of denteones. Enameloid covers the outer surface of the crown. Due to differing birefringence indices of the dental tissues, polarized light microscopy makes the junctions

between these tissues, especially the dentine-enameloid junction, more apparent (Figure 7b). Based on the uniform dentine-enameloid junction, serrations of the Meckelian teeth of *O. bruniensis* are superficial secondary serrations (*sensu* Moyer and Bemis, 2017). The underlying orthodentine does not show signs of a serrated dentine-enameloid junction that would mirror the serrated enameloid.

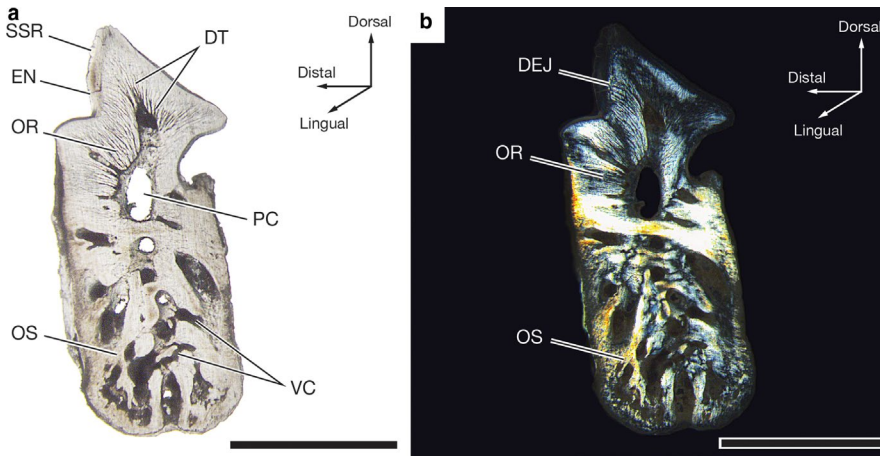
Higher magnification of the region of the dentine-enameloid junction in the same LM2R1 tooth reveals a simplified enameloid microstructure (Figure 8a,b). The outermost layer of enameloid is the shiny layer enameloid (SLE). Beneath the shiny layer enameloid, crystallites appear bundled in an inner enameloid layer (IEL; Figure 8a). In some regions of the crown, the crystallites are oriented more or less perpendicular to the underlying orthodentine. Elsewhere within the same enameloid layer, crystallites are oriented more obliquely. None of the teeth examined showed an enameloid layer in which crystallites were arranged with a shared and consistent orientation (e.g. parallel or perpendicular to the central axis of the tooth). The homology of these enameloid layers to those in other taxa is currently unknown. Therefore, we follow Enault *et al.* (2013) and identify enameloid layers based on location relative to each other. Consequently, *O. bruniensis* does not exhibit the triple-layer enameloid found in other neoselachians, represented in this study by the Shortfin Mako *Isurus oxyrinchus* in concert with the findings of previous documentation of enameloid microstructure in other neoselachians (e.g. the Gulper Shark *Centrophorus granulosus* (Bloch and Schneider, 1801) studied by Moyer and Bemis, 2016; *Heterodontus* spp. studied by Reif, 1973; the Blue Shark *Prionace glauca* (Linnaeus, 1758) studied by Moyer *et al.*, 2015; †*Squalicorax* spp. studied by Andreev, 2010).

*Isurus oxyrinchus* exhibits three layers of enameloid: the outermost SLE, the parallel fibered enameloid discernible by the parallel orientation of its crystallite bundles (PFE), and the tangled fibered enameloid (TFE), which appears as a meshwork of fibers adjacent to

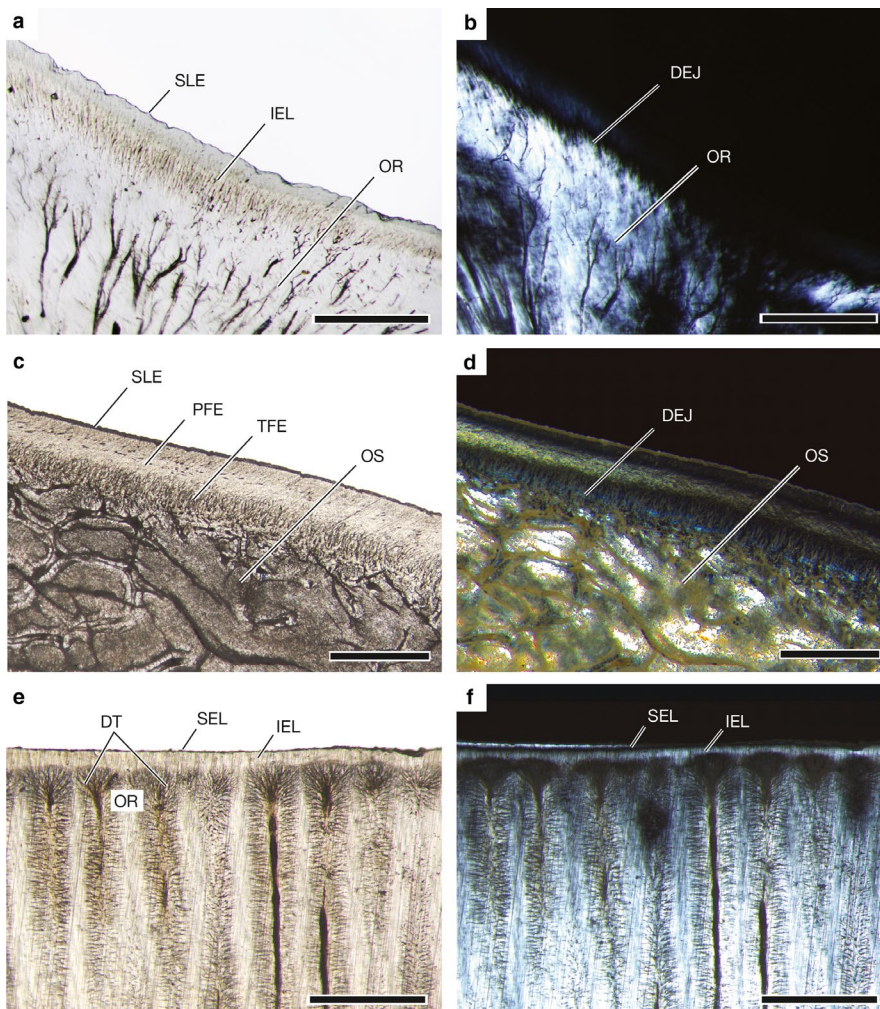


**FIGURE 6** Virtually sectioned three-dimensional reconstructions of individual teeth of a 57.8-cm TL male *Oxynotus bruniensis* (UMA F20813) generated from CT data to illustrate internal anatomy of the teeth. (a) RP3F2 tooth sectioned by virtually removing the distal half of the tooth reconstruction. (b) LM2F1 sectioned by virtually removing the labial surface of the tooth reconstruction. CR, crown; LMF, labial marginal foramina; NP, nutritive pore; PC, pulp cavity; RNF, root notch foramen; RT, root. Scale bars: 1 mm





**FIGURE 7** Light micrographs of the flat-lapped LM2R1 tooth of a 57.8-cm TL male *Oxynotus bruniensis* (UMA F20813). (a) Entire tooth section under unpolarized white light illustrating tissue arrangement and internal structures of the tooth. (b) Same tooth section shown in (a) viewed under polarized light. EN, enameloid; DEJ, dentine-enameloid junction; DT, dentine tubules; OR, orthodentine; OS, osteodentine; PC, pulp cavity; SSR, secondary serration; VC, vascular canal. Scale bars: 2 mm



**FIGURE 8** Enameloid microstructure in teeth of *Oxynotus bruniensis* (UMA F20813), *Isurus oxyrinchus* (UMA 00046), and *Rhinoptera bonasus* (UMA F20809). (a) Simplified enameloid microstructure of LM2R1 tooth of *O. bruniensis* with underlying orthodentine. (b) Same tooth and region shown in (a) viewed under polarized light to distinguish dentine-enameloid junction. (c) Triple-layer enameloid of LM4F1 tooth of *I. oxyrinchus* (UMA 00046). (d) Same tooth and region shown in (c) viewed under polarized light. (e) Tissue arrangement and simplified enameloid of the sixth central tooth plate of the upper jaw of *R. bonasus* (UMA F20809). (f) Same tooth and region shown in (e) viewed under polarized light. DEJ, dentine-enameloid junction; DT, dentine tubules; IEL, inner enameloid layer; OS, osteodentine; OR, orthodentine; PFE, parallel fibered enameloid; SEL, superficial enameloid layer; TFE, tangled fibered enameloid. Scale bars: (a,b) 200  $\mu\text{m}$ ; (c-f) 500  $\mu\text{m}$

the dentine-enameloid junction (Figure 8c,d). Osteodentine fills the crown beneath the dentine-enameloid junction. The arrangement of three enameloid layers in the teeth of *I. oxyrinchus* exemplifies the triple-layer enameloid that is common but not ubiquitous among neoselachians. Thus, it is a useful point of comparison when evaluating the simplified enameloid microstructure of *O. bruniensis*. Another

neoselachian, the Cownose Ray *Rhinoptera bonasus*, exhibits a modified tooth microstructure and simplified enameloid (Figure 8e,f). In *R. bonasus* a thin outer layer of enameloid, here termed the superficial enameloid layer, and an inner enameloid layer covers orthodentine, which is discernible by the rhizoid-like arrangement of dentine tubules. This region of densely packed dentine tubules

appears as a dark band beneath the enameloid under unpolarized light (Figure 8e). The orthodentine-enameloid junction is marked by the termination of the rhizoid-like dentine tubules where they abut an inner layer of enameloid. The inner layer of enameloid is discernible as a faint glow under polarized light as the positively birefringent orthodentine and enameloid form a progressive rather than abrupt dentine-enameloid junction. The superficial enameloid layer is negatively birefringent and therefore not as visible under polarized light (Figure 8f). As is the case with the enameloid of *O. bruniensis*, the homology (or lack thereof) of enameloid layers in *R. bonasus* with those of the triple-layer enameloid exemplified by *I. oxyrinchus* has yet to be determined. We again follow Enault *et al.* (2013) in identifying the layers by their positions relative to each other and not the orientation of their crystallite bundles. The overall tissue arrangement we observe in *R. bonasus* agrees with previous descriptions of tooth histology in myliobatiform rays (note Radinsky, 1961 who identified orthodentine consisting of pallial dentine and circumpulpar dentine noted the presence of both in *Myliobatis* sp.; Berkovitz and Shellis, 2016). Collectively, these results indicate that although simplification of enameloid microstructure is not unique to *O. bruniensis*, the Prickly Dogfish does represent a variant of microstructural modification of enameloid not typically associated with extant selachian fishes or, more broadly, modern neoselachians.

## 4 | DISCUSSION

Our study presents a detailed treatment of the jaws, dentition, tooth morphology, and microstructure of the teeth of the Prickly Dogfish *Oxynotus bruniensis*. Consequently, we are afforded the opportunity to revisit the utility of morphological descriptions of the macro- and microscopic dental morphologies of squaliform sharks and to assess their novelty in *O. bruniensis*. We present illustrated qualitative data on the microstructure of enameloid and histotype in *O. bruniensis*, which is germane to the recent revivals of comparative microstructural studies of chondrichthyan enameloid (e.g. Gillis and Donoghue, 2007; Enault *et al.*, 2015; Cuny *et al.*, 2017) and tissue arrangement (e.g. Moyer *et al.*, 2015; Moyer and Bemis, 2016; Schnetz *et al.*, 2016; Jambura *et al.*, 2020). By evaluating our results in a comparative framework, taking into account phylogenetic relationships and the ubiquity of odontological characteristics exhibited by *O. bruniensis* among neoselachians, we may revisit the topics of specialization and the challenge of evaluating morphological 'specializations' in ecological and evolutionary contexts.

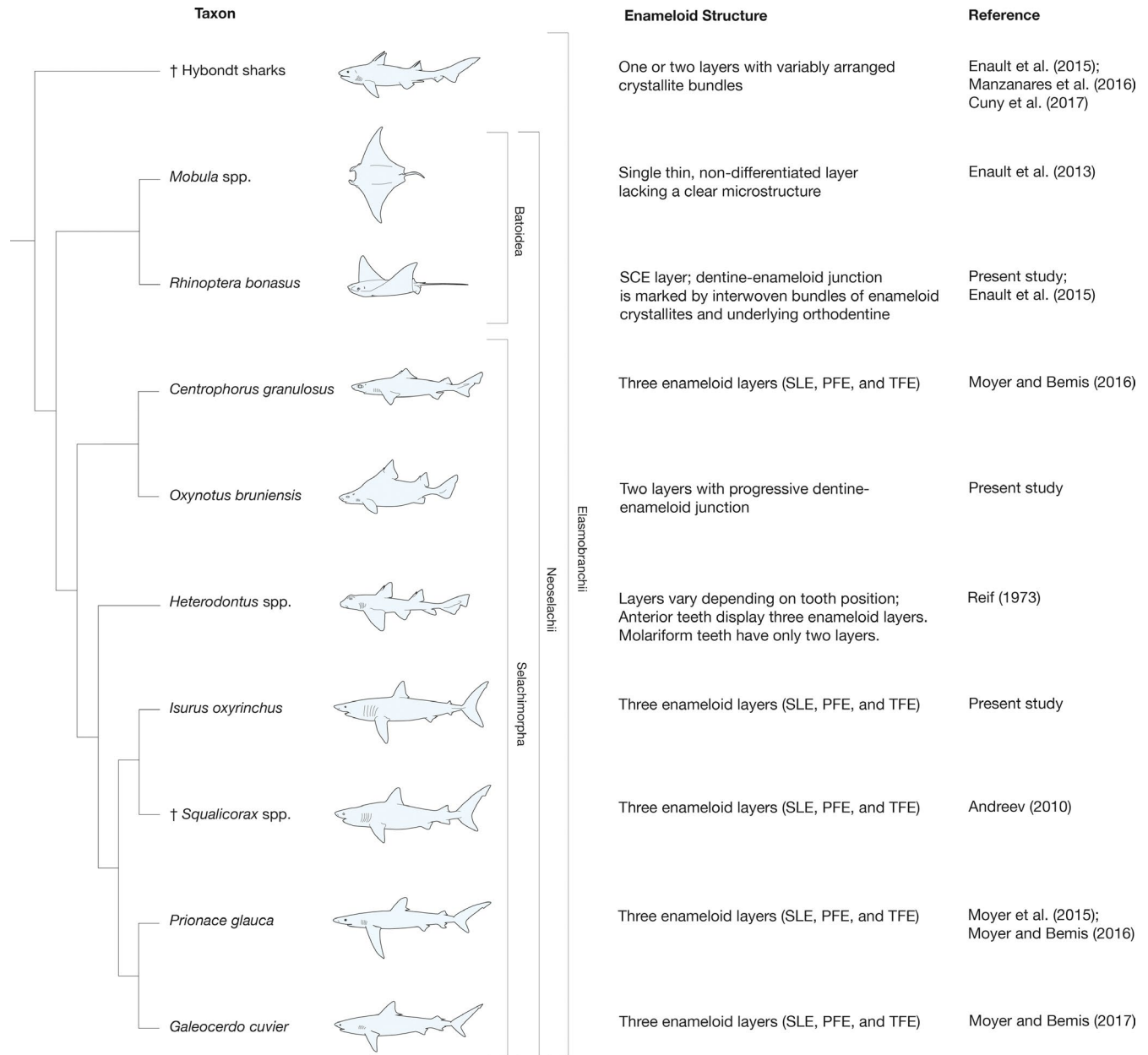
### 4.1 | Comparison of tooth morphology and microstructure

Squaliform teeth are well represented in the fossil record (Ledoux, 1970; 1972; Welton, 1981; Suzuki, 2008; Cappetta, 2012). Accordingly, several authors present phylogenies of the order Squaliformes based heavily or, in some cases, exclusively

on dental characters of extinct and Recent species (Adnet and Cappetta, 2001; Kriwet and Klug, 2009; Klug and Kriwet, 2010; Flammensbeck *et al.*, 2018). Adnet and Cappetta (2001) place the genus *Oxynotus* within the Somniosinae at the base of the clade [[[*Centroscymnus* + *Scymnodon*] + *Scymnodalatias*] + *Oxynotus*]. The authors reason that in the absence of any apomorphic odontological characters to support this clade, the placement of *Oxynotus* could be the result of morphological convergence. Klug and Kriwet (2010) present a supertree combining odontological, morphological, and molecular data from extant and extinct squaliform taxa with slightly different results, notably the recovery of four monophyletic clades within Squaliformes. Nevertheless, inclusion of Oxynotidae on the basis of molecular or morphological data often renders whichever clade it is nested within paraphyletic (e.g. Somniosidae as reported by Flammensbeck *et al.*, 2018). Another trend in phylogenetic analysis of Squaliformes is that *Oxynotus* is consistently recovered in close phylogenetic proximity to the genera *Somniosus*, *Centroscymnus*, and *Scymnodon* in multiple studies but with exact relationships differing slightly (Shirai, 1996; Klug and Kriwet, 2010; Da Silva *et al.*, 2018). The molecular (mtDNA) study conducted by Naylor *et al.* (2012) recovered *Oxynotus* as the sister taxon to two of three species of a paraphyletic *Centroscymnus*.

Though a complete review and revision of these genera and 'Sommiosinae' (as used by Adnet and Cappetta, 2011) is beyond the scope of our study, tooth morphology in *O. bruniensis* does bear a striking similarity to the tooth morphologies of *Centroscymnus* spp. (Suzuki, 2008: table 1; Cappetta, 2012: fig. 111; Underwood *et al.*, 2016: fig. 2d). In particular, the lanceolate morphology of teeth in the anterior region of the palatoquadrate of *O. bruniensis* resembles that of teeth in the palatoquadrate of the Portuguese Dogfish *Centroscymnus coelolepis* Barboza du Bocage and de Brito Capello, 1864 and Roughskin Dogfish *Centroscymnus owstonii* Garman 1906. Cappetta (2012: p. 124) notes in *Centroscymnus* the presence of long, prominent aprons and numerous labial marginal foramina on teeth of the palatoquadrate. This description also matches the teeth of the palatoquadrate in *O. bruniensis* (Figure 5a). Suzuki (2008) notes that in Meckelian teeth of *C. coelolepis* and *C. owstonii*, labial marginal foramina are horizontally expanded and sit alongside a long apron. Our study demonstrates that the same is true in Meckelian teeth of *O. bruniensis* (Figure 5d). Additional morphological similarities between the teeth of *C. coelolepis* and *C. owstonii* and the teeth of *O. bruniensis* include distal inclination of the Meckelian teeth (with the exception of symphyseal teeth of *O. bruniensis*) with elongated root lobes. Although overall tooth morphology and the arrangement of foramina are not themselves sufficient diagnostic characters to resolve the phylogenetic placement of *Oxynotus*, in this case they are consistent with the phylogenetic proximity of *Oxynotus* and *Centroscymnus* hypothesized by Naylor *et al.* (2012).

There is interspecific variation in tooth morphology within the genus *Oxynotus*. Bigelow and Schroeder (1957: fig. 2f), Compagno (1984: p. 127), Cappetta (2012: fig. 118A), and Ebert *et al.* (2013: p. 163) offer line diagrams of either individual symphyseal teeth or the anterior-most regions of the Meckelian dentition of *O. centrina*.



**FIGURE 9** Phylogenetic relationships of elasmobranch taxa for which enameloid microstructure has been documented. Description of enameloid microstructure and the documenting reference(s) are provided next to each taxon. Placement of †hybondt sharks follows Maisey *et al.* (2004). †*Squalicorax* placement within Lamniformes follows Andreev (2010) and Cappetta (2012). Interrelationships of extant species follow Naylor *et al.* (2012)

When compared with previous illustrations, our results indicate that the distal heels on the Meckelian symphyseal teeth of *O. bruniensis* are more pronounced than in *O. centrina*. Furthermore, the very weak secondary serrations of Meckelian teeth of *O. bruniensis* are far less prominent than the serrations of *O. centrina* as described and illustrated by Herman *et al.* (2005). Whether the serrations of *O. centrina* are primary serrations that include the underlying orthodentine or secondary serrations, such as those of *O. bruniensis*, remains to be seen. It is noteworthy, however, that both *O. bruniensis* and *O. centrina* bear teeth with a pulp cavity that extends well into the root (Herman *et al.*, 1989; 2003), displaying a similar gross arrangement of dental tissues. We call on future researchers to quantify

microstructural differences, such as vascular canals and serration composition, between the two species.

The enameloid microstructure that we report in *O. bruniensis* represents a variant of simplified enameloid among elasmobranchs (used here to refer to neoselachians *sensu* Compagno, 1977, along with sister taxa as described by Grogan *et al.*, 2012; for an alternate taxonomic conclusion see Maisey, 2012). Other neoselachian elasmobranchs (*sensu* Grogan *et al.*, 2012) with fewer than three enameloid layers include †*Hybodus* spp. (Enault *et al.*, 2015; Cuny *et al.*, 2017), rays of the order Myliobatiformes and other batoids such as *Rhynchobatus* (Cappetta, 2012; Enault *et al.*, 2015) and, in the lateral teeth, *Heterodontus* spp. (Reif, 1973). Figure 9 summarizes the

phylogenetic relationships of representative elasmobranch taxa and their enameloid microstructure. Enameloid simplifications among neoselachians are attributed to dietary specialization. For example, in durophagous *Heterodontus* spp., lateral teeth lack a PFE layer and have SLE covering TFE, the latter being more resistant to compressive forces than PFE (Preuschoft *et al.*, 1974; Cuny *et al.*, 2017). In batoids, a simplified double-layer enameloid has also been attributed to durophagy and, in the case of filter-feeding taxa, a single enameloid layer likely represents the loss of mechanical constraints (Enault *et al.*, 2013). It is noteworthy that teeth with simplified enameloid may not necessarily represent the same character state variation. That is to say, the homology of the enameloid layers that are present should not be taken for granted.

In *O. bruniensis*, enameloid fibers under the SLE form a single layer, with bundled fibers exhibiting oblique and perpendicular orientation to the underlying orthodentine (Figure 8a). This may be homologous to the TFE of the more common selachian triple-layer enameloid; however, the identification should be confirmed using electron microscopy. If the second enameloid layer of *O. bruniensis* were a modified TFE, then the most parsimonious explanation for the distribution of this variant of simplified enameloid would be its convergent evolution in *Heterodontus* spp. and *O. bruniensis*. As this is, to our knowledge, the first examination of enameloid microstructure in an extant oxynotid, we cannot comment on the commonality of this enameloid microstructure among the other members of the family. We therefore suggest a systematic study of tooth histology and microstructure in the five extant species of *Oxynotus*.

## 4.2 | Histotypes as descriptors and indicators of performance

*Oxynotus bruniensis* represents a variant of the orthodont histotype similar to previously studied squaliform sharks (Moyer and Bemis, 2016; Jambura *et al.*, 2020). The classification of *O. bruniensis* as an orthodont species necessitates a brief overview of the terminology associated with histotypes of shark teeth and comparison with other squaliform species, the histotype classifications of which are matters of debate. The term pseudoosteodontology, coined by Herman *et al.* (1991) to reference a histotype wherein osteodentine completely fills the pulp cavity and is surrounded by orthodentine in fully developed teeth, applies to modern and extinct species of the genus *Hemipristis* as well as multiple extinct taxa, such as †*Notorynchus kempii*, †*Synechodus* sp., and †*Stethacanthus* sp. (Lund, 1985; Compagno, 1988; Herman *et al.*, 1991; Jambura *et al.*, 2020). However, the descriptor 'pseudoosteodont' has also been applied to the histotypes of many other species including modern and extinct representatives of the orders Squaliformes and Orectolobiformes (Jambura *et al.*, 2020). In some cases, species that retain a hollow, albeit reduced pulp cavity surrounded by orthodentine and a portion of root osteodentine within the crown, such as *Centrophorus granulosus*, are also labeled as pseudoosteodonts (Jambura *et al.*, 2020). In many species of the aforementioned orders, the interpretation differs from

the species' previous designations as orthodonts (Compagno, 2002; Moyer and Bemis, 2016). At the center of the debate appears to be the size and location of the pulp cavity.

Herman *et al.*'s (1991) definition of pseudoosteodontology was introduced with respect to *Hemipristis*, in which osteodentine completely, not partially, fills the pulp cavity. In 2003, the same team of researchers noted that in many squaliform taxa (e.g. *Centrophorus* and *Somniosus*) the pulp cavity is reduced to a few denteones in the apical region of the crown (Herman *et al.*, 2003). Reduced pulp cavities are not limited to squalid sharks. In orthodont teeth of some carcharhiniforms, the pulp cavity may be so reduced that Compagno (1988) acknowledged it might be referred to as a central pulp 'canal'. Herman *et al.* (2003: p. 19) refer to pulp cavities made of large denteones (osteons in the original reference) in taxa such as *Etmopterus*, *Centroscyllium*, and *Oxynotus*. In other taxa, they reference the absence of a 'true' pulp cavity but do not define it (Herman *et al.* 2003: p. 19). This raises the question of what a 'true' pulp cavity is.

Based on previous studies and the results observed in *O. bruniensis*, we propose that a true pulp cavity is defined not by size but by the role it plays in the development of the tooth. A true orthodont pulp cavity receives retreating odontoblasts that are responsible for the development of orthodentine, a tissue that can be distinguished visually from osteodentine by the arrangement and size of dentine tubules and often by the presence of lines of Owen, which are the result of periodic changes in dentine deposition (Peyer, 1968; Moyer *et al.*, 2015; Nanci, 2017). With a developmental criterion separating orthodont pulp cavities or 'canals' (*sensu* Compagno, 1988) from vascular canals or osteons such as those found in osteodentine, we offer an amendment to the definition of the orthodont histotype shared by *O. bruniensis* and other squaliformes: Orthodont teeth retain a true pulp cavity or canal into which orthodentine-depositing odontoblasts retreat that renders the junction between orthodentine in the crown and osteodentine of the root discontinuous.

In contrast, pseudoosteodont teeth in which osteodentine fills the pulp cavity have continuous osteodentine-orthodentine junctions that are not interrupted by a true pulp cavity or canal (see Compagno, 1988; fig 3.6D; Jambura *et al.*, 2018). This indicates that pseudoosteodont teeth during development have a true pulp cavity, but that it is filled completely by osteodentine as development progresses. By extension, the crowns of osteodont teeth display a modified and likely derived developmental pattern in keeping with the findings of Jambura *et al.* (2020). Our distinctions are consistent with the taxon Herman *et al.* (1991) used to introduce the term pseudoosteodontology. Additionally, they support histological accounts offered by authors describing fossil and Recent orthodont teeth, including those of the well-studied species *Squalus acanthias*, which resembles in histotype the teeth of *O. bruniensis* (e.g. Kemp and Park, 1974; Moyer *et al.*, 2015; Shimada *et al.*, 2016; Moyer and Bemis, 2017; Jambura *et al.*, 2020).

Distinguishing between histotypes is not simply a matter of semantics. The functional and evolutionary implications of tissue arrangement in shark teeth are active areas of research and have yet to be fully resolved. Therefore, an accurate and standardized

nomenclature is essential when articulating tooth mineralization patterns and their significance. Jambura *et al.* (2020) assert that orthodont, osteodont, and pseudoosteodont are overused descriptors applied to a continuum of tissue arrangements first noted by Peyer (1968) and echoed by Moyer and Bemis (2016). We agree that within each histotype there is a gamut of relative structure (e.g. vascular canals, pulp cavities, etc.) and tissue arrangements. Nevertheless, if the traditional histotype terminology is to be used, even as references to histological extremes, consistent definitions that include the presence or absence of observable features, such as a continuous orthodontine-osteodontine junction or direct contact of orthodontine with a true pulp cavity, should be observed. Given the importance of distinguishing between true pulp cavities, especially those that are greatly reduced, and vascular canals, we call for enhanced study of tooth histology and development with particular focus on odontoblast activity in taxa for which histotype differentiation is a matter of debate.

Despite the restricted diet of *O. bruniensis*, it exhibits a histotype shared by many species including dietary generalists (Compagno, 2002). Consequently, we conclude that histotype alone is not a sufficient indicator of dietary specialization. Thus we are left with an as yet unanswered question: what is the functional significance of different histotypes? Regarding the material properties of the dentinous tissues specifically, osteodontine is significantly harder than orthodontine (Whitenack *et al.*, 2010), and the orthodont histotype is shared by species with a relatively low theoretical bite forces, such as the Bonnethead Shark *Sphyrna tiburo* (Linnaeus, 1758) and the Spiny Dogfish *Squalus acanthias* (Huber and Motta, 2004; Mara *et al.*, 2010). However, perhaps counterintuitively, orthodonty is not restricted to low-force biters. The theoretical maximum bite force of the Blacktip Shark *Carcharhinus limbatus* (Müller and Henle, 1839) and Bull Shark *Carcharhinus leucas* exceeds 1,000 N, and both species share the orthodont histotype (Huber *et al.*, 2006; Habegger *et al.*, 2012). Despite the differences in hardness between osteodontine and orthodontine, review of the literature indicates that there is no singular link between histotype and bite force. Likely, enameloid thickness, tooth crown morphology, and histotype-related variations in a tooth's second moment of area all contribute to how that tooth reacts mechanically to loading. Therefore, estimations of the relative bite force of *O. bruniensis* in the absence of functional data should not be disproportionately influenced by tooth histotype.

### 4.3 | The prickly dogfish as a specialist

*Oxynotus bruniensis* has a very narrow dietary breadth, exclusively reliant upon the eggs of other chondrichthyans for food (Finucci *et al.*, 2016). However, based solely on the macroscopic morphology of its jaws and dentition as reported here, the extreme dietary specialization of the Prickly Dogfish is not self-evident. The mode of feeding is more easily deduced. A Meckelian dentition that forms a serrated blade-like cutting edge, the offset jaw joints, and papillose lips in *O. bruniensis* resemble features found in other squaliform

species such as the Cookiecutter Shark *Isistius brasiliensis* (Quoy and Gaimard, 1824) and *Squalus acanthias* (Strasburg, 1963; Wilga and Motta, 1998). Suction feeding or, in the case of *I. brasiliensis*, a 'strong oral vacuum' (Shirai and Nakaya, 1992) factor prominently in these species' prey acquisition (Wilga and Motta, 1998). Another squaliform and sister taxon to *O. bruniensis*, the Angular Roughshark *O. centrina*, feeds on chondrichthyan eggs but not exclusively. *Oxynotus centrina* leaves a distinct semicircular bite mark, and although there are interspecific variations in tooth morphology (e.g. the size of distal heels on symphyseal teeth), the overall dentition and oral anatomy appears very similar to that of *O. bruniensis* (Guallart *et al.*, 2015). As illustrated by Guallart *et al.* (2015), teeth of the upper jaw in *O. centrina* scratch the surface of egg cases and, if they puncture the egg case, leave small holes. Based on morphological similarities in dentition and jaw position, we posit that *O. bruniensis* displays a similar feeding performance.

Assessment of the simplified enameloid microstructure of *O. bruniensis* in the context of specialization is complicated by several factors. Comparison of simplified enameloid within Neoselachii is limited to a few disparate taxa (Figure 9). Therefore, we may say with certainty that the enameloid microstructure of *O. bruniensis* is uncommon among studied taxa, but that is not sufficient to label it a functional specialization or, by extension, claim that it reflects the species' ecological specialization following the definitions of specialization presented by Ferry-Graham *et al.* (2002). Herein lies another complicating factor of evaluating the enameloid of *O. bruniensis*. A review of the chondrichthyan taxa known to exhibit simplified enameloid in some or all of their teeth reveals durophagous (e.g. *Rhinoptera bonasus*, Mitchell, 1815, and *Heterodontus* spp.) and filter feeding (e.g. *Mobula* spp.) species, as well as species with varied diets and teeth putatively suited for clutching (e.g. †*Hybodus* spp. of the late Jurassic; Cappetta, 2012; Cuny *et al.*, 2017). Thus, a clear functional signal is not apparent. To support or refute functional advantages of simplified enameloid, we call for further research into the mechanical properties of enameloid crystallite orientation in a broader range of neoselachian species, including the four other species of extant oxynotids.

In the absence of a clear interspecific pattern of functional benefit related to diet, the simplified enameloid of *O. bruniensis* may represent not an evolved adaptation to the mechanical stresses of a specialized diet but the lack of a mechanical stress as seen in planktivorous rays (Cuny *et al.*, 2017). Egg cases are non-motile, and the yolk and embryonic tissues within them likely do not provide the same mechanical resistance to teeth as do fully developed prey, which may attempt to escape from the teeth. Therefore, preying exclusively on chondrichthyan eggs may have led to a secondary loss of the triple-layer enameloid typically found in neoselachian fishes. In this scenario, the secondary loss of putatively neoselachian triple-layered enameloid in the absence of a selective pressure may resemble a reversion to a plesiomorphic state. However, given recent findings that two species within the batoid family †Archaeobatidae exhibit complex triple-layered enameloid, the ancestral state of neoselachian tooth enameloid is most likely triple-layered (Manzanares

*et al.*, 2018). Clearly, the evolution of enameloid microstructure is a field in which continued research is required, and a more thorough survey of the enameloid microstructures of planktivorous and durophagous species, both extinct and extant, is a prerequisite to confirm the evolutionary origins of single- or double-layered enameloid in elasmobranchs.

Given the previously reported dietary specificity of *O. brunien-sis*, we conclude that the Prickly Dogfish is an ecological specialist, specifically a behavioral specialist. In other words, the behaviors associated with an ecologically relevant task, such as prey selection and acquisition, in *O. brunien-sis* fall within a narrow range (Ferry-Graham *et al.*, 2002). Irschick *et al.* (2005: p. 405) emphasize that this definition of behavioral specialization assumes that 'morphological adaptations are necessarily linked to behavior'. Indeed, they likely are as form and function are interconnected with behavior (Irschick and Higham, 2016). However, as our findings suggest, a behavior may be specialized, but it is not a foregone conclusion that the morphologies enabling that behavior represent physical specializations as well.

## 5 | CONCLUSION

Two related questions in the field of ecological morphology are whether ecological specialists can be recognized from their morphology and whether ecological specialization allows predictions of morphological specialization (Ricklefs and Miles, 1994). The morphology of teeth and their microstructure in *O. brunien-sis*, when compared with those of other elasmobranchs, demonstrate that there is no universally applicable answer to either question. In reality, the answer likely depends on the scale of inquiry (i.e. specialization at the individual, population, species or higher level) and necessitates a relatively complete library of relevant points of comparison. For example, in the study of neoselachian dentitions, much work remains to be done concerning odontological microstructure and tissue arrangement. Only after a suitably broad frame of reference including numerous taxa is established, can researchers determine whether behavioral or morphological changes precipitated specialization and to what extent. In this way, the search for specializations, both morphological and behavioral, is confirmation of the utility of comparative and descriptive studies of anatomy and performance.

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## AUTHOR CONTRIBUTIONS

J.K.M. and B.F. conceived the study, and B.F. supplied specimens of *Oxynotus brunien-sis*. Computed tomography (CT) datasets were generated by M.L.R. Specimen dissection and preparation, CT dataset reconstruction, and tooth histology were performed by J.K.M. Manuscript and figures were drafted by J.K.M. and reviewed by B.F., M.L.R., and D.J.I. Funding was procured by J.K.M.

## DATA AVAILABILITY STATEMENT

The CT datasets that support the findings of this study are available upon request to the corresponding author. Anatomical specimens used in this study are housed in the University of Massachusetts Amherst Natural History Collection.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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