

Dental sexual dimorphism and morphology of *Urotrygon microphthalmum*

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Abstract Dental sexual dimorphism has been described for different species of batoids, and it has been suggested that this differentiation is advantageous to reproduction in most cases. The aim of the present study was to investigate the morphology of the dentition in the ray *Urotrygon microphthalmum* using scanning electron microscopy. The present study brings a detailed description of morphological characteristics in males and females during ontogenetic development. Dental sexual dimorphism was observed both in maturing and mature males, while females maintain the same crushing shape dentition during all development stages. The teeth modification in males corresponds to the onset of maturation, which occurs when the animal reaches approximately 171.7 mm in total length, indicating that this morphological modification is closely related to mating

behavior—grasp females during copulation thus ensuring body attachment and clasper insertion during swimming.

Keywords Elasmobranch · Secondary sexual characteristics · Copulation · Scanning electron microscopy

Introduction

Batoids and sharks feature polyphyodont teeth, inserted on the palatoquadrate and Meckel's cartilage, organized in rows and replaced at regular periods throughout life. In myliobatids, the dentition is presented in a pavement form, replaced regularly and many components arranged in tooth files (Bigelow and Schroeder 1953; Moss 1977; Kemp 1999; Motta 2004; Motta and Huber 2012). Since the dentition is attached in fibrous connective tissue instead of being attached directly in the jaw, tooth replacement is continuous, with teeth being formed on the lingual region moving to labial region, where older teeth (worn or modified) are discarded (Moss 1972; Motta and Wilga 2001).

Elasmobranchs show a large variety in feeding strategies, being molded during the evolutionary process with major modifications in dentition forms and function (Motta and Wilga 2001). In batoids, feeding strategy is strictly associated to suction, with a jaw-skull dissociation that allows protrusion (Wilga et al. 2007). That way in batoids, suction movements seem to be the principal method for prey capture, since even in species with sexual dentition modifications, difference in diet are not observed between males and females or during ontogenetic development (Navia et al. 2011; Gutteridge and Bennett 2014; Belleggia et al. 2016).

Dentition modification related to gender observed in male batoids during mating (sharp teeth) does not always occur in other elasmobranchs (Kajiura and Tricas 1996; Gutteridge

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and Bennett 2014). Despite the adaptive functions of crushing teeth in batoids for feeding purposes, this shape is ineffective for males to grasp onto the pectoral fins of females during mating (Kajiura and Tricas 1996), in order to increase the chances of clasper insertion (Carrier et al. 2004). Male elasmobranchs exhibit a set of morphological, physiological and behavioral changes when reaching sexual maturation, such as clasper calcification, stronger jaws, spines on the fins (in some species), greater activity and an increase in aggressiveness (Dodd 1983).

The smalleye roundray *Urotrygon microphthalmum* (Delsman 1941; reaching approximately 300 mm in total length) occurs in shallow, coastal waters of the tropical West Atlantic at a depth of approximately 50 m (McEachran and Carvalho 2000). This species has been recorded in Venezuela, Suriname, French Guyana and Brazil (states of Amapá, Pará, Maranhão, Ceará, Paraíba and Pernambuco; Delsman 1941; Boeseman 1963; Cervigón and Alcalá 1999; Almeida et al. 2000; Gadig et al. 2000; Rosa 2004; Santander-Neto and Lessa 2013). *U. microphthalmum* perform matrotrophic viviparity (Hamlett et al. 2005), with size an estimated maturation of 187.74 and 198.73 mm in total length for males and females, respectively (Santander-Neto et al. 2016).

Studying the morphology of the dentition in batoids helps to elucidate the biological role that teeth play in feeding as well as the importance in reproductive behavior allowing understanding of the importance of such modifications during the animal's life. Teeth are often the only available structure as fossil records elasmobranchs. Thus, the morphological description of recent groups can provide important clues for identification and future comparisons, helping to determine phylogenetic relations and development during evolution within the group (Underwood et al. 2015).

The aims of the present study were to describe morphological aspects of the dentition in the smalleye roundray, *U. microphthalmum*, using scanning electron microscopy to determine morphological differences in the dentition of sexually mature animals, determine whether dental dimorphism in males is associated with gonad maturation and estimate at which size males begin to exhibit secondary sexual characteristics (such as differentiated dentition).

Materials and methods

All specimens were caught between April and July 2011 as accompanying fauna during shrimp operations in the municipalities of Jaboatão dos Guararapes and Sirinhaém in the state of Pernambuco, Brazil (08°11'43"S/034°54'13"W; 08°38'44"S/035°01'24"W). The fishing gear used by the fleet was a dual bottom drag net with outrigger booms. Each net

was 10 m in length, approximately 6 m at the mouth and mesh widths of 20 mm in the body of the net and 15 mm in the bag.

Total length (TL in mm), disk width (DW in mm), total weight (TW in g) and sex were determined for each specimen. The teeth were examined in six groups separated based on sex and maturation stage (immature, maturing and mature), as proposed for *U. microphthalmum* (Santander-Neto et al. 2016). Voucher specimens are deposited in the private collection of the *Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Brazil*. Eighteen individuals (nine females with TL ranging from 133.6 to 289.4 mm and nine males with TL ranging from 117.6 to 231.15 mm (Table 1) were used for the analysis of dental morphology.

For scanning electron microscopy, dental arch samples were dissected and immersed in a 10 % formaldehyde fixing solution. The arches were then rinsed in water, submitted to dehydration in an ethanol series with an increasing proportion of alcohol (70, 80, 90 and 100 %) and left to dry at room temperature. The samples were positioned and attached with carbon glue to aluminum bases and submitted to gold ion sputtering in the EMI-TECH-K550 device, followed by analysis and photography using LEO 435VP scanning electron microscope. The description of the teeth was based on the nomenclature suggested by Moss (1977) and Cappetta (1987).

Table 1 Specimens of *Urotrygon microphthalmum* analyzed separated into six groups based on sex and stage of gonad maturation

Sex (sexual maturation)	Code	TL (mm)	DW (mm)	TW (g)
Females				
Immature	UR 250	117.1	64.25	4.02
	UR 271	133.6	74.3	9.65
	UR 272	150	82	11.42
Maturing	UR 276	206.85	108.35	48.43
	UR 274	210.65	108.65	34.18
	UR 275	210.85	104.55	38.16
Mature	UR 270	252.7	124.3	77.11
	UR 248	285.25	149	77.37
	UR 269	289.4	140.8	87.33
Males				
Immature	UR 241	117.6	66.55	5.34
	UR 257	142.25	78.35	8.05
	UR 258	147.8	81.1	13.65
Maturing	UR 262	171.7	91.95	23.44
	UR 260	175.75	94.2	26.24
	UR 261	178.85	91.45	23.91
Mature	UR 252	209.25	105.9	36.85
	UR 264	224.65	116	51.85
	UR 238	231.15	123.45	48.83

Results

Females

Slight intraspecies variation was found in the female's dentition, such as crown characteristics and shape varying in individuals with different sizes. Immature individuals (Fig. 1a, b) exhibit gradual monognathic heterodonty with

symphyseal teeth presenting cuspids and laterals presenting molariform shape (Fig. 1a). The occlusal face is flattened with small elevations and a slightly pronounced cusp slanted in the lingual direction (Fig. 1b). The teeth in the central region overlap and are larger than the molariform teeth in the distal region (Fig. 1a).

In maturing females, the dentition is molariform (Fig. 1c, d). The lower jaw has more rows of teeth than the

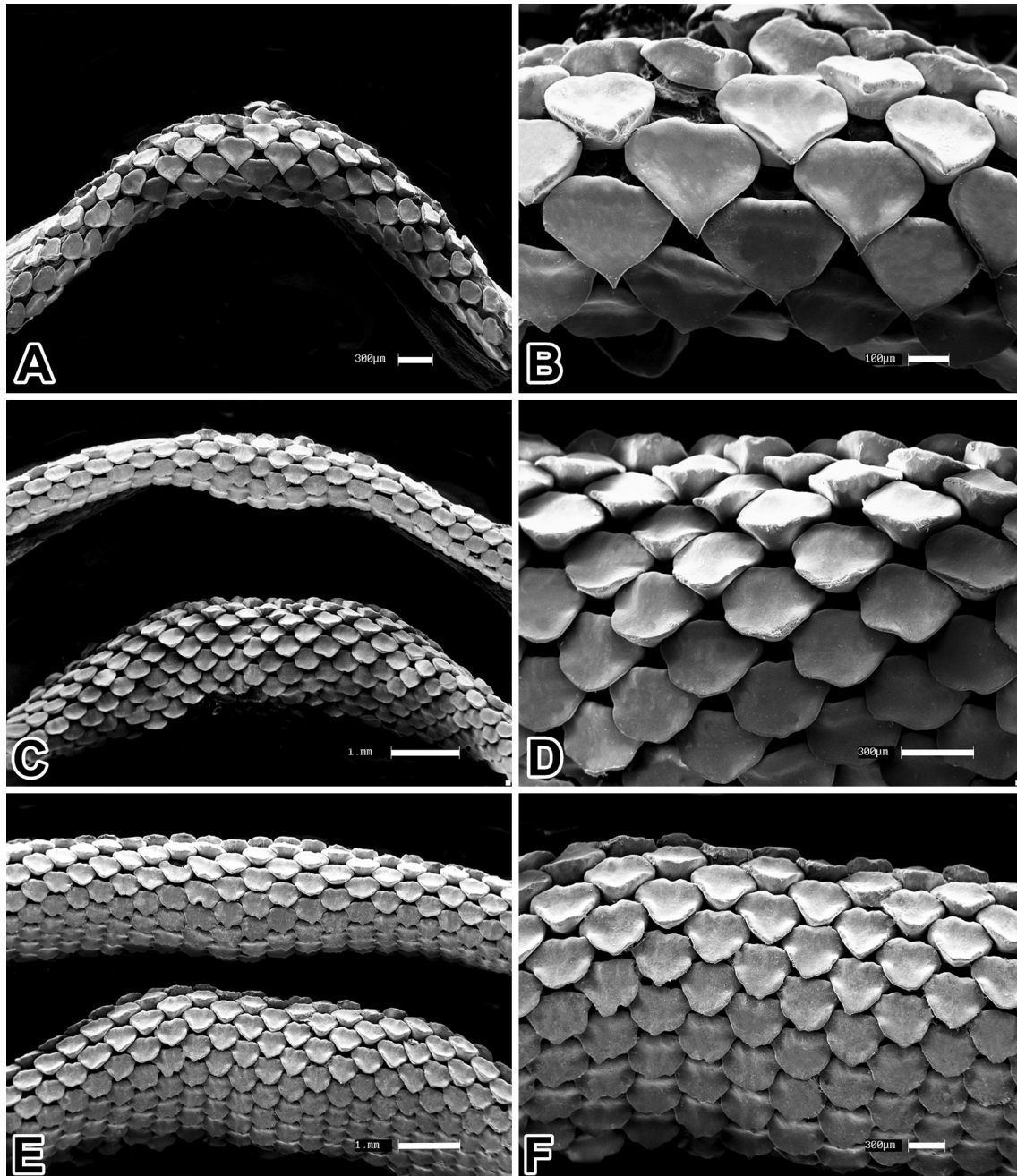


Fig. 1 Dentition of *Urotrygon microphthalmum* females. **a, b** Upper jaw of immature female UR 271, crushing monocuspide teeth; **c, d** upper and lower jaw of maturing female UR 274, teeth exhibiting

small elevations on occlusal surface of crown; **e, f** mature female UR 248, morphology similar to maturing female; *bar scale* **c, e** 1 mm; **a, d, f** 300 μ m; **b** 100 μ m

upper jaw, and a greater number of teeth are found in the symphyseal region (Fig. 1c). The teeth in the distal region are molariform, with a smooth crown and oval occlusal face. The teeth of the central face are overlapped, with the crown in an irregular shape, smooth and flattened with elevations (Fig. 1d).

In mature females (Fig. 1e, f), the teeth morphology is similar to that found in maturing females. However, the teeth are well delineated, with a greater number in the upper jaw (Fig. 1e). The teeth in the central region are overlapped, with an irregular shape (smooth and flattened with elevations; Fig. 1f).

Males

The change in dentition is evident with increase in TL. All males exhibit gradual monognathic heterodonty. Immature males have molariform teeth similar to that found in immature females (Fig. 2a, b). Teeth in the symphyseal region exhibit a slightly pronounced rounded cusp slanted in the lingual direction, with a smooth and flat crown and small elevations on the occlusal face of some teeth (Fig. 2b). Teeth overlap is an important feature in the species, except in the distal region of the lower jaw where dentition shows separated distribution (Fig. 2a).

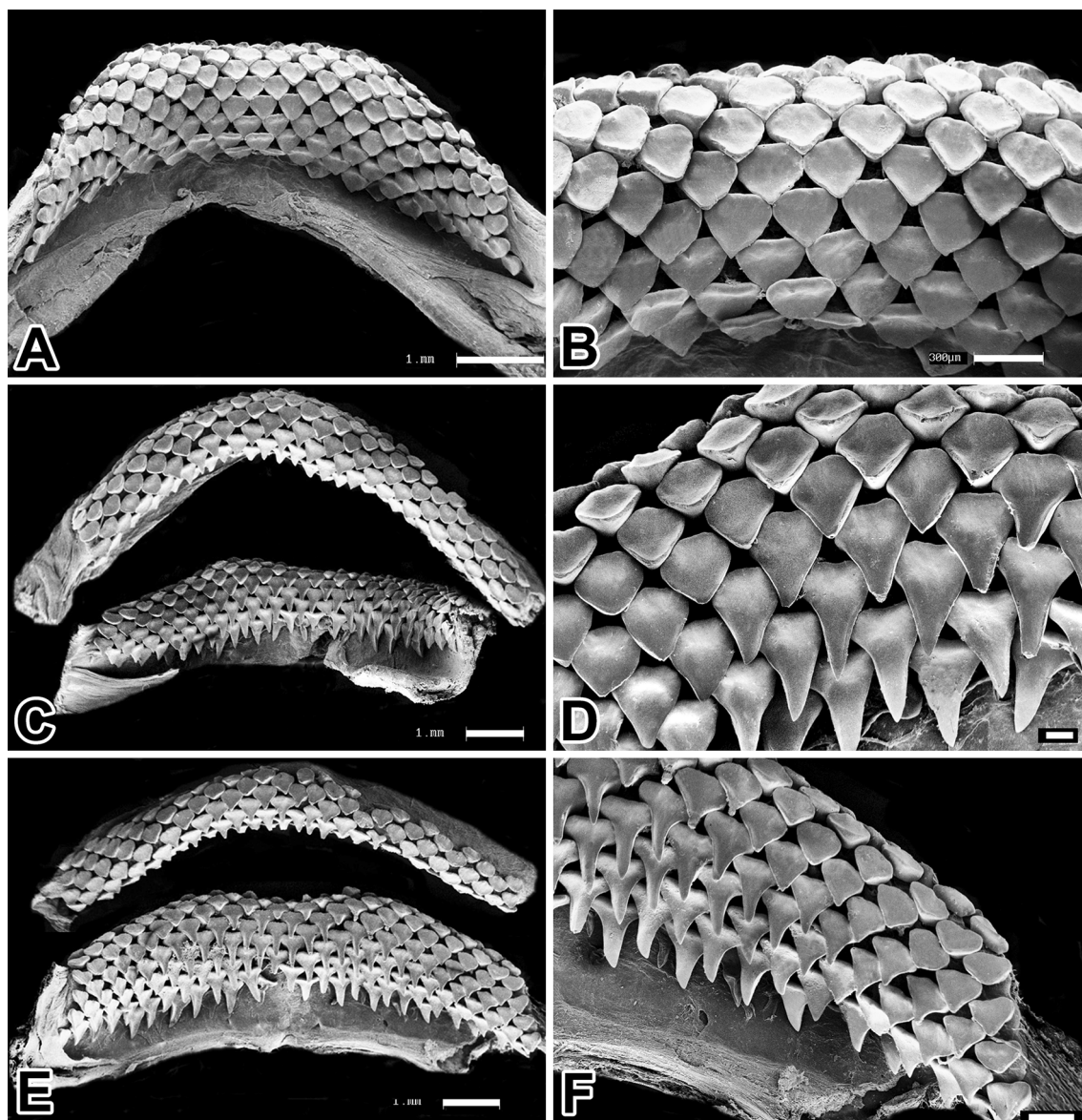


Fig. 2 Dentition of immature and maturing *Urotrygon microphthalmum* males. **a, b** Lower jaw of immature male UR 258, crushing dentition; **c, d** Maturing male UR 261 and **e, f** UR 262, with crushing

teeth in labial region and grasping teeth in lingual region; *bar scale a, c, e* 1 mm; *b, f* 300 μ m; *d* 100 μ m

In maturing males, an gradual differentiated growth in the dentition is observed. The teeth in the labial region are molariform, while in the lingual region, the crown of symphyseal teeth have a relatively elongated shape (Fig. 2c–f). The molariform teeth in the labial region have a similar shape to those found in immature individuals, overlapped with a smooth flat crown (Fig. 2c, d). A slightly pronounced cusp slanted in the lingual direction is found in some (Fig. 2f). The teeth of the distal region of the upper

jaw have an oval crown with small elevations on the surface. The teeth in the labial region vary in cusp size by the growth line. The cusp exhibits a sharp triangular shape and is slanted in the lingual direction. The face of the crown is smooth and flat, like the molariform teeth (Fig. 2d, f).

In sexually mature males, the dentition is completely different, with all teeth in the upper and lower jaws featuring elongated cusps (Fig. 3). The cusp of the symphyseal teeth has a triangular shape (Fig. 3a, d) being more

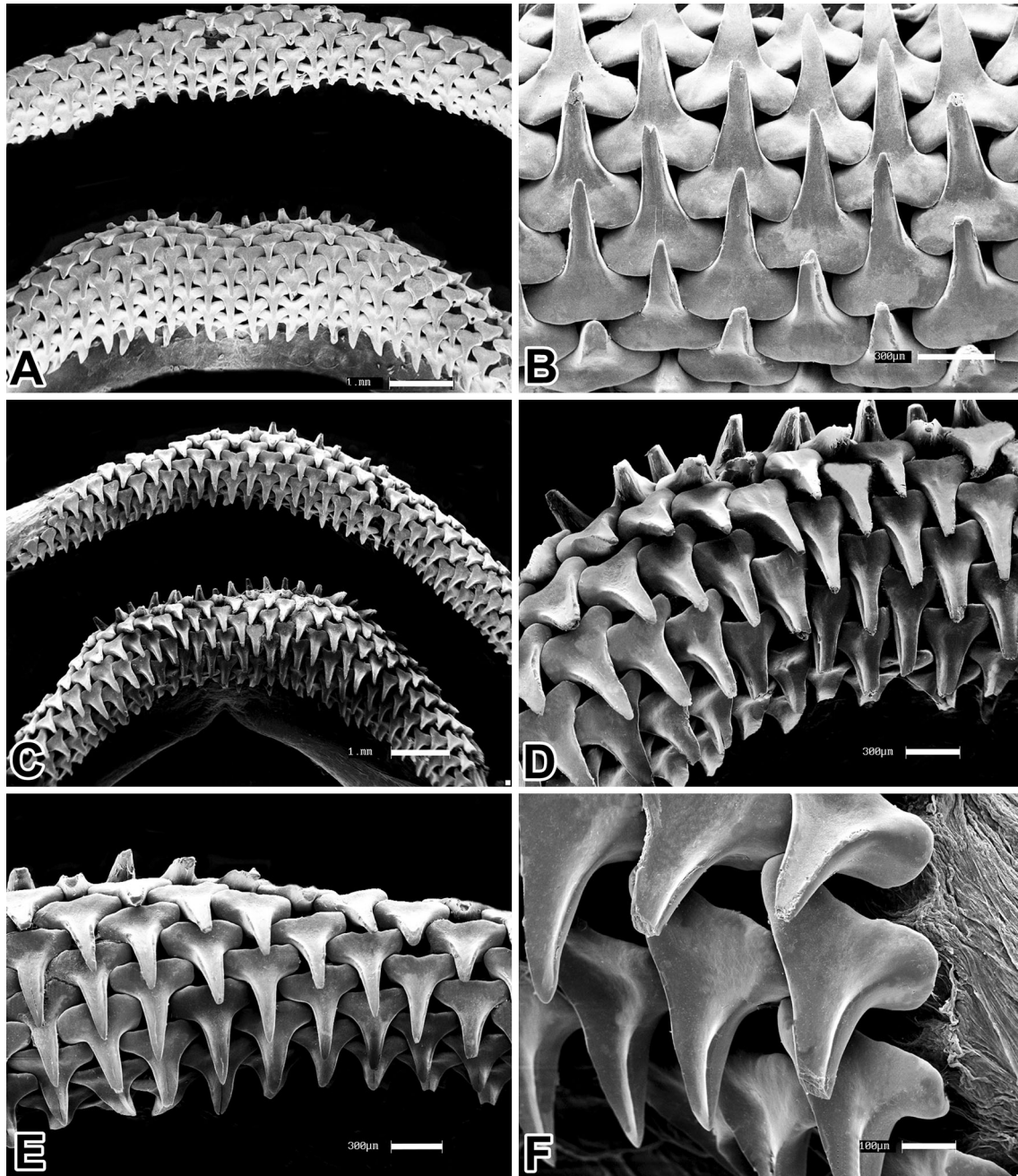


Fig. 3 Dentition of mature *Urotrygon microphthalmum* male. **a, b** Upper and lower jaw of male UR 252 and **c, d** UR 264, grasping dentition with sharper central teeth; **e, f** teeth of upper jaw of male UR 238; bar scale: **a, c** 1 mm; **b, d, e** 300 µm; **f** 100 µm

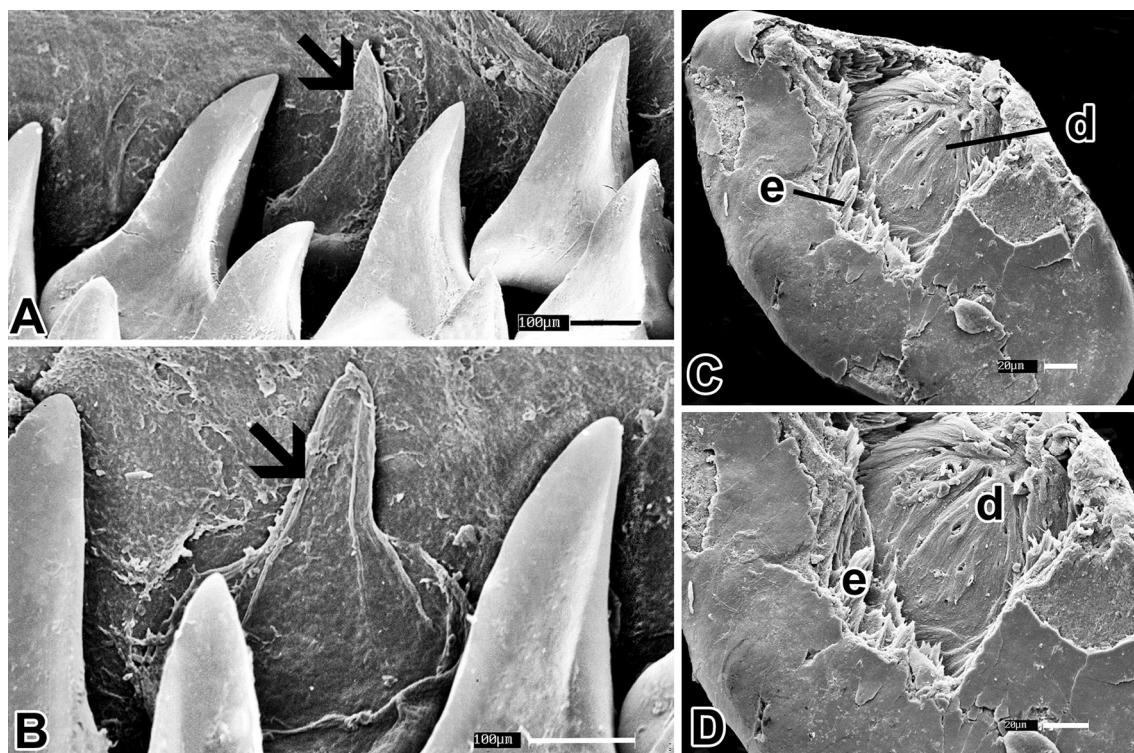


Fig. 4 Teeth of maturing male UR 262. **a, b** Growth of sharp, monocuspide teeth (*arrow*); **c, d** layers of enamel (**e**) and dentin (**d**); *bar scale*: **a, b** 100 μm ; **c, d** 20 μm

elongated and sharper than the cusp of the distal teeth (Fig. 3f). Sharp, monocuspide teeth are found in maturing males (Fig. 4a, b), which are still covered with a tissue layer of Meckel's cartilage, with the structure conferring layers of enamel and dentin (Fig. 4c, d).

Discussion

The present study brings a detailed description of morphological characteristics in males and females of *U. microphthalmum* during ontogenetic development. Besides dental sexual dimorphism, mature males also exhibit monognathic heterodonty related to cusp size, with symphyseal teeth being more elongated and sharper than distal teeth. In other species, lateral teeth remain molariform and anterior teeth exhibit elongated cusps, with a similar shape in the meso-distal direction along the rows for both jaws (Kajiura and Tricas 1996; Taniuchi and Shimizu 1993; Gutteridge and Bennett 2014; Rangel et al. 2014a, b).

Dental sexual dimorphism has been described for different species of batoids (Bigelow and Schroeder 1953). Feduccia and Slaughter (1974) suggested that sexual heterodonty occurs due to differences in feeding preferences and niche use to avoid intraspecific competition. However, this was contested by McEachran (1977) after examining the

stomach contents of more than 1600 rays with dental sexual dimorphism showing no significant differences in food items consumed between sexes for immature and mature specimens. The same is observed in the guitarfish *Aptychotrema rostrata* and skate *Zearaja chilensis* with dental differentiation being more related to mating process than feeding (Gutteridge and Bennett 2014; Belleggia et al. 2016).

Likewise, in *U. microphthalmum*, no significant differences were found between feeding habits of males and females or throughout ontogeny (the species feeds mainly on decapods crustaceans and species of the family Mysidacea; Freitas et al. in prep.), indicating that dentition modification does not alter feeding habits in the species. This seems to be a pattern for the genre, since the same was observed for *U. rogersi* (Navia et al. 2011). However, studies with other species need to be performed. The maintenance of food items regardless of sex or stage of life may be a reflex of feeding preference related to habitat use (niche occupation and lower competition) and/or metabolic gain, essential for gonadal and somatic growth. However, the energy needed during breeding period, not only for gonadal maturation, but also for mating behaviors, and in the case of rays which perform secondary sexual modifications (such as dentition alteration), changes in feeding habits may mean an unnecessary and harmful metabolic expenditure, since the energy spent in chasing a new type

of prey with different escape strategies is high. It is also possible that the species in fact show a different type of prey ingestion, but since *U. microphthalmum* is generalist opportunist (Freitas et al. in prep.), it is possible that a clearer differentiation in stomach content needs a careful and more detailed assessment (at species level).

In the present study, pre-emerging, sharp-cusped teeth were found in maturing males. This change in tooth shape from crushing to grasping corresponds to the length at which males begin the process of gonad maturation (171.7 mm of TL; Santander-Neto et al. 2016) by equating the appearance of other secondary sexual characteristics as observed in other batoids (Taniuchi and Shimizu 1993), suggesting that hormonal signaling occurs, modifying both reproductive apparatus and dentition in males. Seasonal analyses are needed to determine whether the dentition in mature males returns to crushing shape after the reproductive period or remains the sharp throughout life cycle. For the stingray *Dasyatis sabina*, dental dimorphism in males was demonstrated not to be static or permanent. This species shows seasonal variations in which the dentition of mature males modifies to a more pronounced shape in cusps during the reproductive period and returns to crushing shape (more functional for feeding) after this period (Kajiura and Tricas 1996). Yet, Gutteridge and Bennett (2014) suggest that the sexually dimorphic dentition remains throughout the life cycle in males of *Aptychotrema rostrata*. Due to biannual and asynchronous mating period suggested for *U. microphthalmum* (Santander-Neto et al. 2016) we believe that in males, after first sexual modification, teeth format (sharper) remain throughout life cycle.

Thus, sexual dental dimorphism in *U. microphthalmum* is suggested to be advantageous to reproductive events. The same has been reported for *Urolophus concentricus* (McCourt and Kerstitch 1980), *D. akajei* (Taniuchi and Shimizu 1993), *Urolophus halleri* (Nordell 1994), *D. sabina* (Kajiura and Tricas 1996), *A. rostrata* (Gutteridge and Bennett 2014), *Atlantoraja cyclophora*, *A. castalnavi*, *A. platana*, *Zapteryx brevirostris* (Rangel et al. 2014a) and *D. hypostigma* (Rangel et al. 2014b) as well as the shark *Scyliorhinus canicula* (Ellis and Shackley 1995). Due to internal fecundation, pre-copulation activities involve actions that result in the male grasping the female to achieve adequate alignment for the clasper (copulation organ) insertion into the female (Carrier et al. 2004). In many sharks and batoids, males orally secure the fins of females with bites that are less tenacious than those used for feeding and generally do not employ total force or the complete closing of the jaws (Nordell 1994; Tricas 1980; Kajiura et al. 2000; Carrier et al. 2004). According to Springer (1960), this behavior serves as a pre-copulation release mechanism that facilitates female's cooperation during copulation. Gutteridge and Bennett (2014)

demonstrated that the characteristics of sharp-cusped teeth in mature *A. rostrata* males provide significantly stronger adherence than that seen in immature males and females. This is in agreement with data described by Kajiura and Tricas (1996), who found that the dentition in mature *D. sabina* males has nearly twice the adherence of that in mature females. We believe the same occurs in *U. microphthalmum*, due to similarities in their structural conformity.

In elasmobranchs, the teeth and dermal denticles have a similar composition, which consists of three hard tissues, a calcified base and a protruded dentin covered with an outer layer of enamel. The enamel and dentin are very solid, which explains why these structures are commonly preserved as fossils (Gravendeel et al. 2002; Yabumoto et al. 1997). In the present study, broken teeth at the enamel and dentin layers were observed, with the enamel characterized during scanning electron microscopy as organized in a de-fibered tangled mesh and the dentin more porous region (Reif 1982; Gillis and Donoghue 2007). Besides the importance of sexual differentiation in dentition for breeding purposes, this can be a valuable tool for paleontological studies, since it represents an evolutionary adaptation for batoids. It is also extremely important to characterize morphological alterations in dentition in order to avoid misinterpretation during fossil identification, since such changes if not described can lead to gaps in the phylogenetic classification of the group.

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