

Teeth morphology and dental sexual dimorphism of three species of the sandskate genus *Psammobatis* Günther, 1870 from the Brazilian coast (Rajiformes, Arhynchobatidae)

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Resumo

Morfologia e dimorfismo sexual de dentes de três espécies de raias do gênero *Psammobatis* Günther, 1870 da costa brasileira (Rajiformes, Arhynchobatidae). Conjuntos de mandíbulas das raias *Psammobatis extenta* (n = 10), *P. lentiginosa* (apenas indivíduos adultos, n = 8) e *P. rutrum* (apenas indivíduos adultos, n = 10) foram examinados utilizando microscopia eletrônica de varredura. Os dentes das fêmeas das três espécies e os dos imaturos de *P. extenta* não apresentaram diferenças, todos com dentes esmagadores monocuspidados, com uma cúspide pequena ou ausente. A heterodontia monognática foi observada em espécimes adultos de ambos os sexos das três espécies analisadas. Espécimes imaturos de *P. extenta* e fêmeas das três espécies diferiram dos machos adultos por terem dentes esmagadores ao invés dos dentes agarradores dos machos, indicando heterodontia sexual. Os dentes dos machos de *P. extenta* são pontiagudos e bem pronunciados, com as cúspides arredondadas, enquanto os machos de *P. rutrum* e *P. lentiginosa* possuem cúspides elípticas e similares entre si. Espécimes imaturos de *P. extenta* possuem cúspides pequenas. Os dentes de *P. lentiginosa* apresentam um sulco longitudinal em sua face labial, um caráter aqui hipotetizado como uma condição derivada.

Palavras-chave: Atlântico Sul; Batoidea; Elasmobrânquios; Microscópio Eletrônico de Varredura; Raias

Abstract

Sets of jaws of the sandskates *Psammobatis extenta* (n = 10), *P. lentiginosa* (only adult specimens, n = 8) and *P. rutrum* (only adult specimens, n = 10) were examined by scanning electron microscopy. Female teeth of the three species and those of the immature *P. extenta* did not show differences, all having monocuspid crushing teeth, with a small, unpronounced or absent cusp. Monognathic heterodonty was observed in adult specimens in both sexes of the three species analyzed. Immature *P. extenta* and females of the three species differed from the adult males in having a crushing as opposed to a clutching dentition, implying gynandric heterodonty. Teeth of males of *P. extenta* have pointed, well-pronounced, rounded cusps, whereas males of *P. rutrum* and *P. lentiginosa* have elliptical and similar cusps. Immature specimens of *P. extenta* have small cusps. Teeth of *P. lentiginosa* have a longitudinal sulcus on their labial face, a character herein hypothesized as a derived condition.

Key words: Batoids; Elasmobranchs; Rays; Scanning Electron Microscopy; South Atlantic



Introduction

Species of *Psammobatis* Günther, 1870 are endemic to the eastern South Pacific and western South Atlantic coasts of South America, occurring from Rio de Janeiro, Brazil to Chile (EBERT; COMPAGNO, 2007). Eight species are recognized: *Psammobatis rudis* Günther, 1870 (type species), from the coasts of Argentina and Chile; *P. bergi* Marini, 1932, *P. extenta* (Garman, 1913), *P. lentiginosa* McEachran, 1983, and *P. rutrum* Jordan, 1891 from Rio de Janeiro to Rio Grande do Sul, Brazil, Uruguay and Argentina; *P. normani* McEachran, 1983 from Uruguay to Chile; *P. parvacauda* McEachran, 1983 Argentina; and *P. scobina* (Philippi, 1857) from Uruguay to Argentina (GOMES, 2002; GOMES et al., 2010; LAST et al., 2016). Species of *Psammobatis* feed on small invertebrates such as crustaceans, polychaetes, mollusks, and more rarely on small fishes; they are demersal and inhabit the continental shelves and slopes (MUTO et al., 2001; LAST et al., 2016).

Studies of species of *Psammobatis* are mostly limited to reproductive biology (e.g., BRACCINI; CHIARAMONTE, 2002; MARTINS; ODDONE, 2017), feeding habits (e.g., MUTO et al., 2001; MABRAGAÑA; COUSSEAU, 2004; BRACCINI; PEREZ, 2005) and geographical distribution (e.g., MENNI; STEHMANN, 2000; GOMES et al., 2010). Concerning sexual dimorphism, the unpublished study of Paragó (2001) analyzed *P. extenta* and *P. rutrum* and sex-related shape of the anterior margin of the disc; Barbini and Lucifora (2012) recorded the gynandric heterodonty in *Psammobatis bergi* and *P. extenta*, and Braccini and Chiaramonte (2002) sex-related differences in measurement variables and in tooth morphology in both sexes of *P. extenta* to the reproductive habit of the species. Herman et al. (1995), in their extensive batoid study, observed the dentition of *P. rudis* as a gradient monognathic heterodonty and pointed out its sexual heterodonty as seen in adults only. The same authors affirm that ontogenetic heterodonty is present only in males by a low tooth cusp, which grows to large size in maturing specimens.

Sexual heterodonty, dignathic heterodonty (differences in tooth morphology between upper and lower jaw), and monognathic heterodonty (variation in the morphology of teeth from different positions on the same jaw) are well represented in cartilaginous fish (Elasmobranchii) (HERMAN et al., 1994; 1995; 1996). In batoids, gynandric heterodonty is mentioned in Rajidae, *Hypanus sabinus* (Lesueur 1824), *Fontitrygon colarensis* (Santos, Gomes & Charvet-Almeida 2004), Dasyatidae, *Dasyatis hypostigma* Santos & Carvalho 2004, Rhinobatidae, *Zapteryx brevirostris* (Müller & Henle 1841), Urotrygonidae, *Urotrygon microphthalmum* Delsman 1941 (FEDUCCIA; SLAUGHTER, 1974; KAJIURA; TRICAS, 1996; SANTOS; CHARVET-ALMEIDA, 2007; RANGEL et al., 2014; 2016); gynandric, monognathic and ontogenetic heterodonty in Rhinobatidae, *Aptychotrema rostrata* (Shaw 1794) (GUTTERIDGE; BENNETT, 2014). In the Arhynchobatidae, monognathic, sexual, and ontogenetic heterodonty occurs in juvenile males of *Pavoraja asperula* (= *Brochiraja asperula* (Garrick & Paul 1974)) (HERMAN et al., 1994); monognathic heterodonty in *Pavoraja laxipella* (= *Insentiraja laxipella* (Yearsley & Last 1992)) and *Notoraja tobitukai* (Hiyama 1940) (HERMAN et al., 1996). Sexual heterodonty is seen in *Psammobatis bergi*, *P. extenta*, and *Atlantoraja castelnaui* (Miranda Ribeiro 1907), *A. cyclophora* (Regan 1903), *A. platana* (Günther 1880) (BARBINI; LUCIFORA, 2012; RANGEL et al., 2014).

In this study, three species of the genus *Psammobatis* (*P. extenta*, *P. lentiginosa* and *P. rutrum*) were investigated to determine if they show sexual heterodonty and ontogenetic variation.

Material and Methods

Specimens examined belong to the following institutions: Instituto de Ciências Biológicas da Universidade Federal de Rio Grande (FURG), caught between August 2013 and August 2014, by commercial fishing off the coast of Rio Grande do Sul State, between latitudes 34°28'S and 31°29'S, at depths from 40 to 142

m; and Universidade do Estado do Rio de Janeiro, Rio de Janeiro (UERJ), captured off the coast of Cabo Frio, Rio de Janeiro State, between latitudes 22°40'S and 22°41'S at depths of 50 to 55 m. Species identification and the measurements follow Paragó (2001) and Gomes et al. (2010). In the text and tables, the measurements are in cm. The specimens from FURG were received with their ontogenetic stage determined by examining gonads and clasper (MARTINS; ODDONE, 2017). All immature specimens were from UERJ. Twenty-eight sets of jaws (both upper and lower) were prepared and examined by scanning electron microscopy (SEM).

For SEM, the dental plates were cleaned with soft toothbrushes with fine bristles and toothpaste. The samples were subsequently dehydrated in an alcohol series (24 h in 70%, 30 min in 80%, and 30 min in 90%), dried in a 50°C oven, coated with gold ions, and photographed with a Philipps XL 30 SEM of the Central de Microscopia e Microanálise (LabCEMM – PUCRS). This technique, when applied to teeth of *P. lentiginosa* (males), caused the teeth to crack at the depression on the labial crown face (sulcus). Because of this, the term “sulcus” is maintained in the text even though the images reveal the cracks.

For comparisons and analyses, both upper and lower dental plates were examined for each set of jaws, and three regions from each were highlighted: left lateral, right lateral and symphysis, totaling six regions in each specimen. Each region was compared between males and females of the same species, as well available specimens of each ontogenetic stage (adult/immature) and between species. The description of the teeth, including size, arrangement, morphology and

number, follows Moss (1977) and Rangel et al. (2015), and the shape of the cusp (elliptical or circular) was inferred from the external shape of the tooth. The ratio between the length and width of the symphyseal teeth (an average of fourteen teeth measured in each dental plate) as a function of total length was plotted in graphs to show the relation between tooth development and sexual maturity (see Table 1).

Tooth measurements (Figure 1) follow Gutteridge and Bennett (2014). The dental formula follows Belleggia et al. (2014) and corresponds to the number of rows of teeth in each jaw (minimum and maximum numbers in upper jaw/minimum and maximum numbers in lower jaw).

Results

The size range of specimens examined is shown in Table 1. In all species, there was the occurrence of monognathic and gynandric heterodonty and absence of dignathic heterodonty.

Immature specimens

Immature individuals smaller than 20.0 TL (Figure 2A and 2B), both males and females, had monocuspid teeth of the crushing type, with a small cusp (symphyseal teeth) or lacking a cusp (lateral teeth), and a smooth lozenge-shaped crown with rounded margins. Lateral teeth had a greater distance in between (Figure 2C), whereas for symphyseal teeth this space was almost nonexistent.

TABLE 1: Morphometric data of examined specimens of *Psammobatis*. N = number of set of jaws – upper and lower –, TL = total length, DW = disc width.

Species	Immatures			Adult females			Adult males		
	N	Range TL	Range DW	N	Range TL	Range DW	N	Range TL	Range DW
<i>P. extenta</i>	3	15.0-18.0	7.8-9.5	3	24.8-29.5	14.7-16.0	4	26.0-31.7	14.0-18.5
<i>P. lentiginosa</i>	0	0	0	2	43.0-46.6	24.0-26.7	6	42.8-48.4	25.0-28.0
<i>P. rutrum</i>	0	0	0	2	27.5-27.5	16.5-17.0	8	22.5-28.5	13.6-16.5

FIGURE 1: *Psammobatis extenta* FURG (not numbered), 24.8 cm TL, adult female, Rio Grande do Sul State, Brazil, upper jaw, symphyseal region. Horizontal axis (blue arrow) = tooth width, vertical axis (yellow arrow) = tooth length.

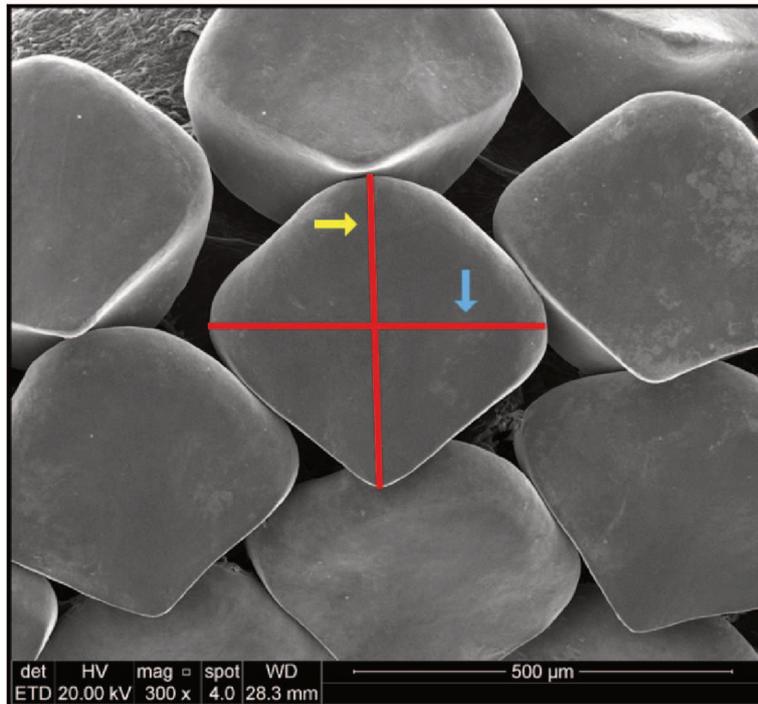
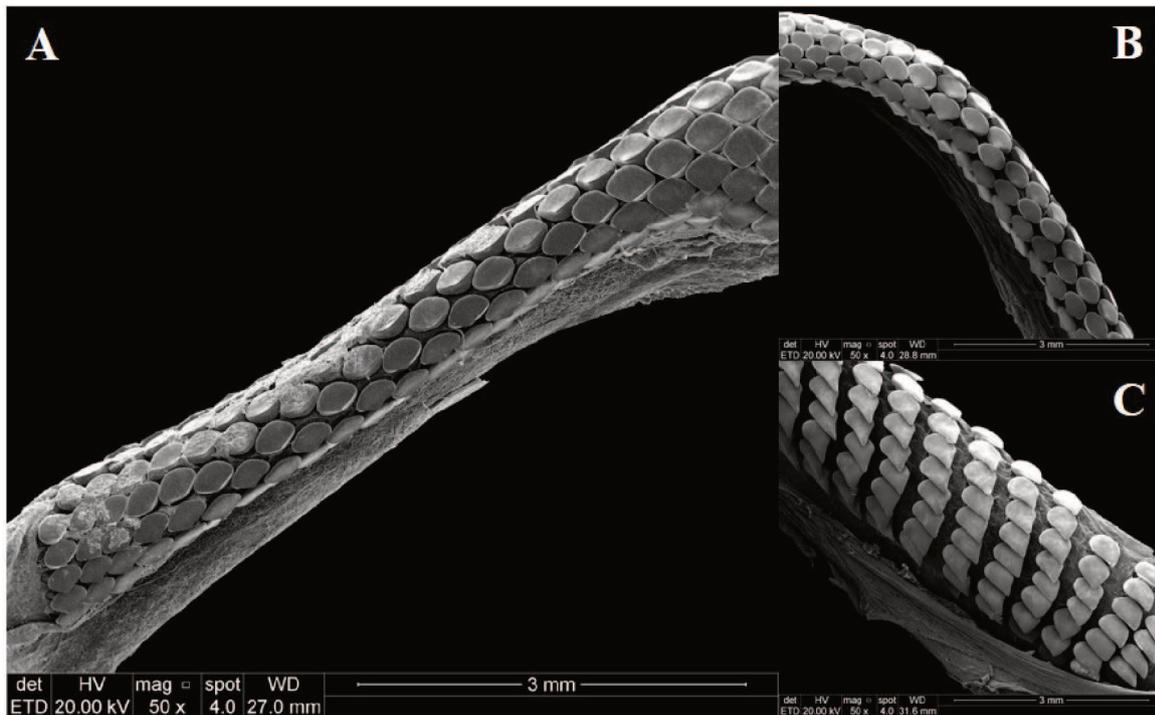


FIGURE 2: (A) *Psammobatis extenta* UERJ (not numbered), 15.0 cm TL, immature female, Rio de Janeiro State, Brazil. Occlusal view, upper dental plate, right region. (B) *P. extenta* UERJ (not numbered), 18.0 cm TL, immature male, Rio de Janeiro State, Brazil. (C) *P. extenta* UERJ (not numbered), 17.5 cm TL immature female, Rio de Janeiro State, Brazil. Occlusal view, upper dental plate, left lateral region.



The length/width ratio of the symphyseal teeth varied from 0.9 to 1.1 in immature specimens, as seen in Figure 3A. This figure shows that the symphyseal cusps of immature and female specimens are smaller than those of adult males. Dental formula was: *P. extenta*, immature specimens, 16-20/17-20 (n = 3).

Adult females

Adult females of all species between 24.0 and 44.0 TL (Figure 4) had monocuspid teeth of the crushing type, with a small cusp (symphyseal teeth) or lacking a cusp (lateral teeth), and a smooth lozenge-shaped crown with rounded margins. The length/width ratio of the symphyseal teeth varied in adult females of *P. extenta* (Figure 3A); from 0.7 and 0.8 in *P. lentiginosa*

(Figure 3B), and from 0.9 and 1.0 in *P. rutrum* (Figure 3C). Figure 3 shows that the symphyseal cusps of female specimens are smaller than the adult males in all three species. Dental formula was: *P. extenta*, 19-23/20-23 (n = 3); *P. lentiginosa*, 22-24/23-24 (n = 2); and *P. rutrum*, 27-28/27-28 (n = 8).

Adult males

Psammobatis extenta

Monocuspid teeth of the clutching type, with pointed and well-pronounced cusps, especially those of the symphyseal region, which had a perpendicular orientation and were smooth and rounded (Figure 5A). Crown was smooth and lozenge-shaped, and

FIGURE 3: (A) The length/width ratio of symphyseal teeth (STL/STW) as a function of total length of *Psammobatis extenta*. (B) The length/width ratio of symphyseal teeth (STL/STW) as a function of total length of *Psammobatis lentiginosa*. (C) Ratio of the length/width symphyseal teeth (STL/STW) as a function of total length of *Psammobatis rutrum*. Females – red squares; males – blue triangles; immatures – green circles (if shown).

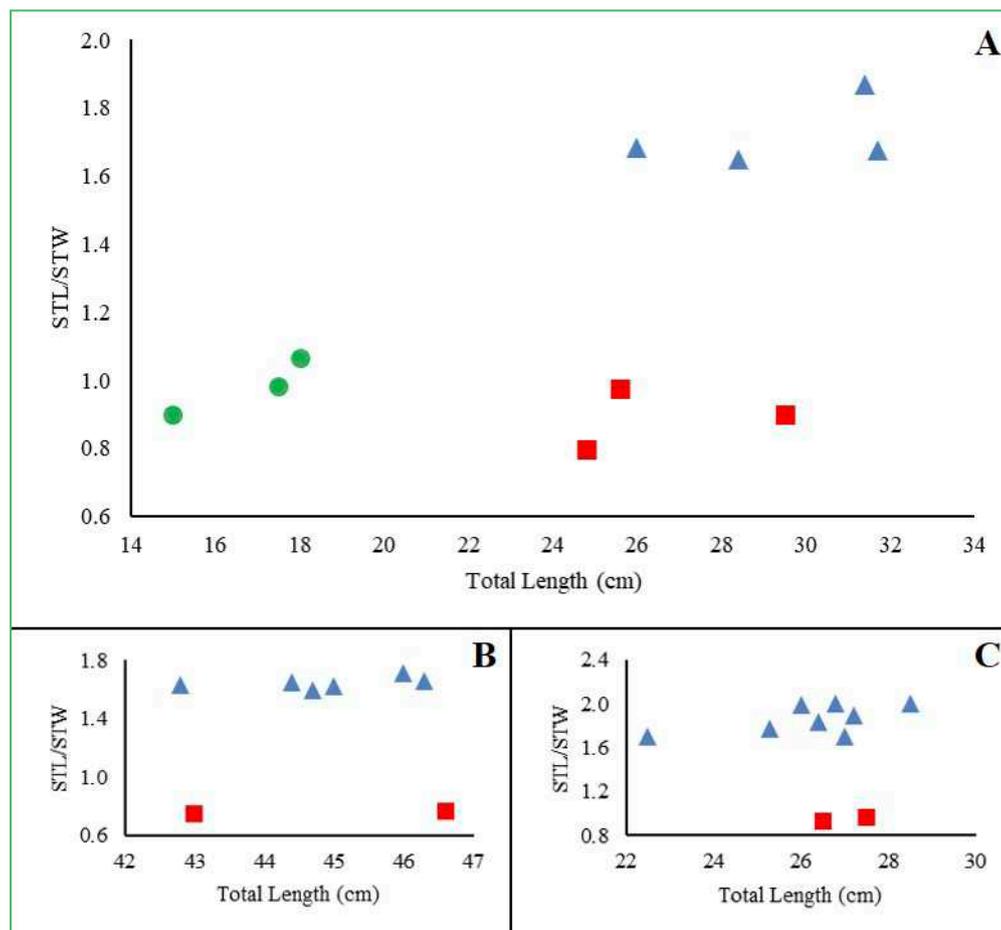
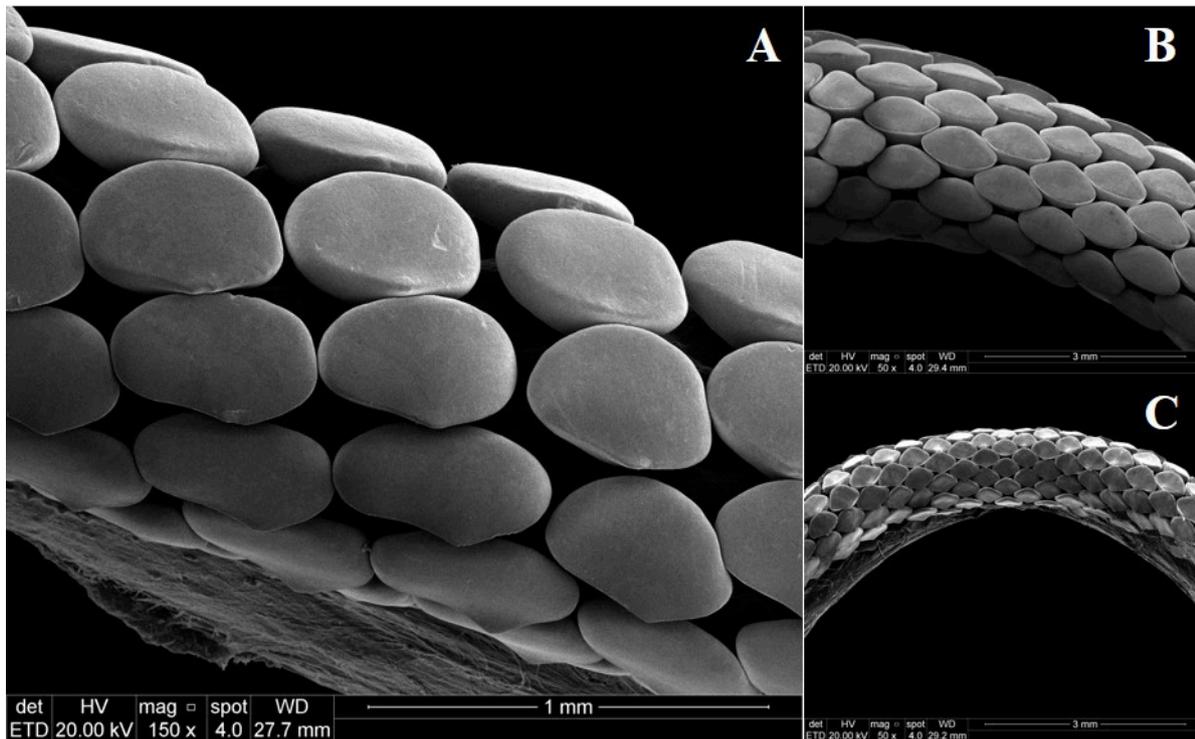


FIGURE 4: (A) *Psammobatis extenta* FURG (not numbered), 29.5 cm TL, adult female, Rio Grande do Sul State, Brazil. Occlusal view, upper dental plate, left lateral region. (B) *P. lentiginosa* FURG (not numbered), 44.0 cm TL, adult female, Rio Grande do Sul State, Brazil. Occlusal view, upper dental plate, left lateral region. (C) *P. rutrum* FURG (not numbered), 27.5 cm TL, adult female, Rio Grande do Sul State, Brazil. Occlusal view, upper dental plate, symphyseal region.



with rounded margins. Monognathic heterodonty was observed in all adult male specimens. In males larger than 30 TL, the lateral teeth had cusps that varied from short to well-developed, even though most teeth were morphologically similar. Specimens smaller than 28 TL had fewer teeth with developed cusps in comparison with larger males, as their lateral regions had only poorly developed cusps (Figure 5B). The length/width ratio of symphyseal teeth varied from 1.7 to 1.9 (Figure 3A). Dental formula was 19-23/20-23 (n = 3).

Psammobatis lentiginosa

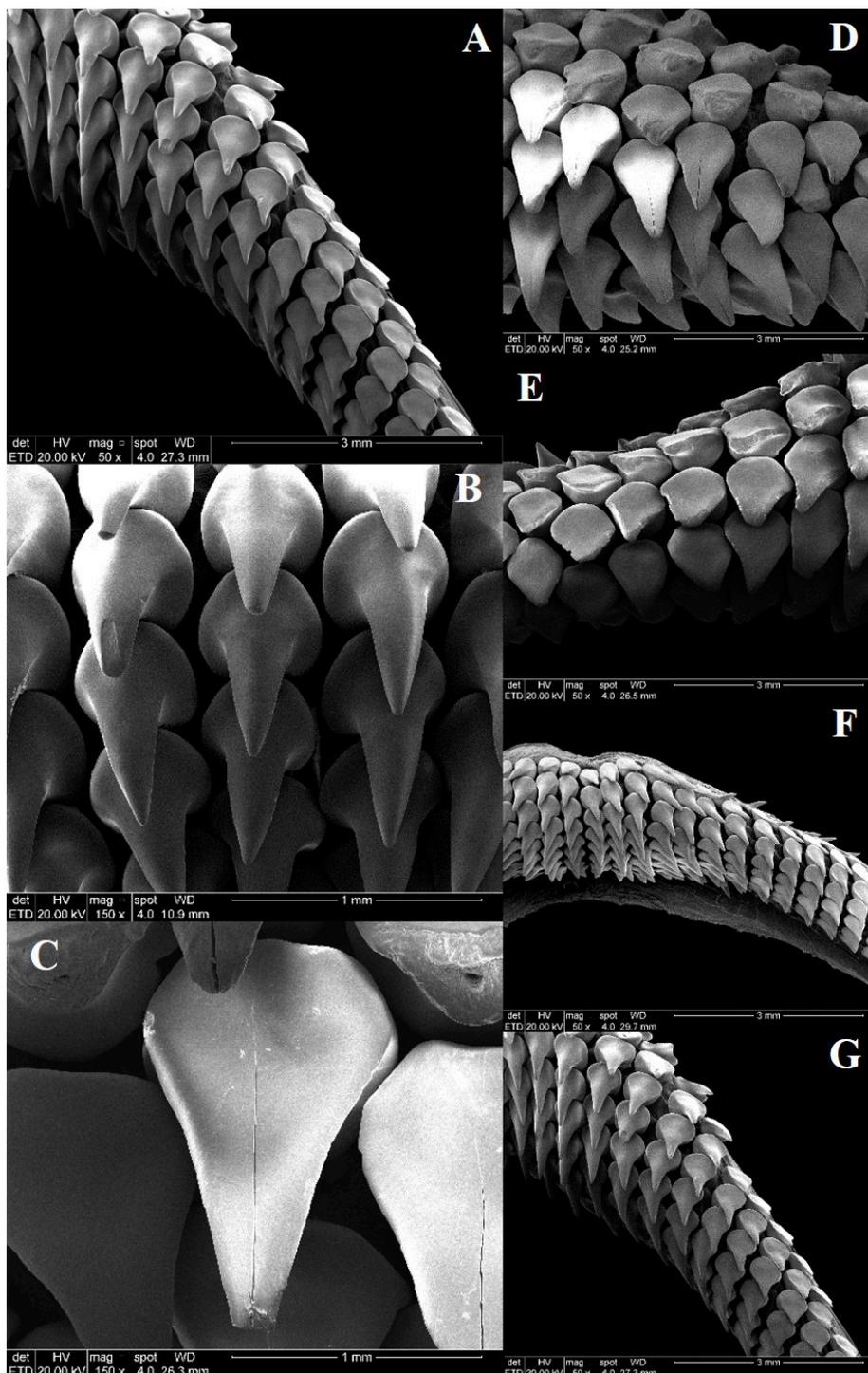
Monocuspoid teeth were of the clutching type, with pointed and well-pronounced cusps, especially on symphysis, with a perpendicular orientation, a longitudinal sulcus on the apical face, and elliptical shape (Figure 5C). Crown was smooth, lozenge-shaped, and had rounded margins (Figure 5D). Monognathic heterodonty was observed in all adult males. In specimens greater than 48 TL, the jaws had morphologically similar

teeth, with lateral teeth having short to developed cusps. Specimens smaller than 47 TL have fewer teeth with developed cusps in comparison with larger males, as their lateral regions had only poorly developed cusps (Figure 5E). The length/width ratio of symphyseal teeth ranged from 1.6 to 1.7 (Figure 3B). Dental formula was 21-22/21-23 (n = 6).

Psammobatis rutrum

Monocuspoid teeth were of the clutching type, with pointed and well pronounced cusps, especially on symphysis, with a perpendicular orientation, smooth and elliptical (Figure 5F). Crown was smooth, lozenge-shaped and had rounded margins. Monognathic heterodonty was observed in all adult males. Specimens smaller than 28 TL had fewer teeth with developed cusps in comparison with larger males, since their lateral regions had only poorly developed cusps (Figure 5G). In specimens greater than 30 TL, all teeth had developed cusps; the largest cusps always occurred

FIGURE 5: (A) *Psammobatis extenta* FURG (not numbered), 26.0 cm TL, adult male, Rio Grande do Sul State, Brazil. Occlusal view, upper dental plate, symphyseal region. (B) *P. extenta* FURG (not numbered), 17.2 cm TL, adult male, Rio Grande do Sul State, Brazil. Occlusal view, lower dental plate, right region. (C) *Psammobatis lentiginosa* FURG (not numbered), 48.4 cm TL, adult male, Rio Grande do Sul, State, Brazil. Occlusal view, upper dental plate, symphyseal region. (D) *P. lentiginosa* FURG (not numbered), 46.3 cm TL, adult male, Rio Grande do Sul, State. Occlusal view, upper dental plate, symphyseal region and (E) occlusal view, upper dental plate, right lateral region. (F) *Psammobatis rutrum* FURG (not numbered), 25.5 cm TL, adult male, Rio Grande do Sul, State, Brazil. Occlusal view, lower dental plate, symphyseal region. (G) *P. rutrum* FURG (not numbered), 26.0 cm TL, adult male, Rio Grande do Sul State, Brazil. Occlusal view, lower dental plate, right lateral region.



in the symphyseal region. The length/width ratio of symphyseal teeth ranged from 1.7 and 2.0 (Figure 3C). Dental formula was 25-27/25-27 (n = 8).

Discussion

Adults of the species examined showed monognathic heterodonty, mainly in the anterior teeth (symphyseal) when compared to the lateral ones. Females of the three species were differentiated from adult males by having a crushing type of dentition as opposed to a clutching type of dentition in males, thus indicating also a gynandric heterodonty. Specimens of *P. extenta* also showed ontogenetic heterodonty with the immature males showing monocuspid teeth of the crushing type, with a negligible or lacking cusp; while adult males had monocuspid teeth of the clutching type, with pointed and well-pronounced cusps, especially those of the symphyseal region.

This ontogenetic heterodonty is related to different feeding habits regarding *P. extenta*. It is in line with Barbini and Lucifora (2012) who mentioned that “small individuals consume amphipods and small crabs, and that large individuals consume cumaceans [small crustaceans] and isopods”. Muto et al. (2001) and Braccini and Perez (2005) also analyzed diets and found no differences between adult males and adult females. However, the ontogenetic and seasonal patterns seem in feeding habits correlated with the skate’s body size and prey availability, respectively; and these features seem to be of more importance to the species’ ecological role.

The development of the cusp of males’ teeth of all three species coincides with sexual maturity: between 25 and 26 TL for *P. extenta* and *P. rutrum* and between 40 and 42 TL for *P. lentiginosa* (GOMES et al., 2010; PERIER et al., 2011; MARTINS; ODDONE, 2017). The analysis of the length/width ratio of symphyseal teeth in the adults of the three species examined here (Figure 3) demonstrated that teeth in males can be almost twice as long as wide. This does not occur in adult females of the three species or in the immature specimens of *P. extenta*, in which the ratio is close to 1. The variations in tooth shape in males, related to length/width ratio and

the respective size range and sex, support the hypothesis that the observed gynandric heterodonty is related to the mating strategies. This same pattern was found for *P. bergi* and *P. extenta* (BARBINI; LUCIFORA, 2012). The relationship between sexual maturation and development of teeth in males is also reported for *Amblyraja doellojuradoi* (Pozzi 1935) (Rajidae) (DELPIANI et al., 2012), *Aptychotrema rostrata* (Shaw 1794) (Trygonorrhinidae) (GUTTERIDGE; BENNETT, 2014), *Atlantoraja cyclophora* (Regan 1903) (Arhynchobatidae) (OLIVEIRA; ODDONE, 2012; RANGEL et al., 2015), and *Hypanus sabinus* (Leuseur 1824) (Dasyatidae) (KAJIURA; TRICAS, 1996; KAJIURA et al., 2000); in all these cases, males exhibit a copulatory behavior of “hugging” females with their jaws. *A. doellojuradoi* and *H. sabinus* show differences in diets between males and females, but *A. rostrata* and *A. cyclophora* seem to have a narrower niche, as males and females have a significant overlap in their feeding habitats (KAJIURA; TRICAS, 1996; KYNE; BENNETT, 2002; DELPIANI et al., 2013; VIANA; VIANNA, 2014).

Regarding their taxonomy, *P. extenta* is differentiated from *P. rutrum* by their dental formula (33-46 tooth rows on upper jaw vs 50-54 and 42-45, respectively) and from *P. lentiginosa* by the shape of the cusp (circular, rounded shaped vs elliptical). McEachran (1983) reported 36-50 upper tooth rows and used this range to distinguish *P. glansdissimilis* McEachran (= *P. extenta*) from *P. rutrum*, which possesses 43-66. Braccini and Chiaramonte (2002) recorded for *P. extenta* 34-46 rows of teeth in the upper jaw in both sexes. *P. lentiginosa* is distinguished from *P. rutrum* and *P. extenta* by the presence of a sulcus on the apical face, which is absent in the latter species. These new data may help in the discrimination of these species, since they are morphologically very similar. Comparing the dental formulas of immature and adults of *P. extenta*, the number of tooth rows appears to increase proportionally to specimen size, as suggested for this species by Braccini and Chiaramonte (2002) and for *Mustelus henlei* (Gill 1863) by Bellenggia et al. (2014). Unfortunately, immature individuals of *P. lentiginosa* and *P. rutrum* were not available for this study, but comparing small adults (approx. 44 TL and

25 TL for *P. lentiginosa* and *P. rutrum*, respectively) with large adults (approx. 47 TL and 28 TL for *P. lentiginosa* and *P. rutrum*, respectively) the pattern seems to be the same as in *P. extenta*.

The sulcus on the apical face of the teeth of *P. lentiginosa* not seen in other *Psammobatis* or related species so far, is present in a similar condition in *Dasyatis hypostigma* (RANGEL et al., 2014). Morphological (MCEACHRAN; DUNN, 1998) and molecular (NAYLOR et al., 2016) analyses have shown that Dasyatidae is not closely related to Arhynchobatidae, which leads us to assume that the presence of a sulcus is most parsimoniously interpreted as having occurred independently in *D. hypostigma* and *P. lentiginosa*.

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