Dentition of the apron ray *Discopyge tschudii* (Elasmobranchii: Narcinidae)

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The present study provides quantitative and qualitative analyses of the dentition of *Discopyge tschudii*. Overall, 193 individuals (99 males and 94 females) of *D. tschudii* were collected on scientific trawl surveys conducted by the National Institute for Fisheries Research and Development (INIDEP) and commercial vessels in Argentina. *Discopyge tschudii* has rhombic-shaped teeth, arranged in a semipavement-like dentition; each tooth has an erect cusp slightly inclined posteriorly and holaulachorized root. Mature males have greater tooth lengths than females and immature specimens. *Discopyge tschudii* exhibits dignathic homodonty and gradient monognathic heterodonty where teeth of the commissural row are shorter than those of the symphyseal and internal rows.

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Key words: *Discopyge tschudii*; Elasmobranchii; jaws; morphology; Narcinidae; teeth.

INTRODUCTION

Elasmobranchs have polyphyodont dentitions (Moss, 1972), meaning that their teeth are continuously replaced (Motta, 2004). Teeth are moved rostrally to be replaced by new generations of teeth (Dean *et al.*, 2008), maintaining full dentition at all growth stages (Moss, 1972). The dentition can be homodont or heterodont, but is typically homodont or uniform in tooth shape which is considered less effective at prey processing in comparison to heterodonty (Liem *et al.*, 2001). The variety of tooth shapes and sizes in heterodont elasmobranchs can be related to different roles of teeth during capture and handling of prey (Applegate, 1965). Therefore, these variations can be correlated with feeding habits (McEachran *et al.*, 1976; Motta & Huber, 2012), but also to sexual dimorphism (Leible, 1988; Herman *et al.*, 1996) and ontogeny (*i.e.* variation in tooth morphology at different stages in the animal's life) (Compagno, 2003). Differentiation of teeth may occur in the same jaw (monognathic heterodonty) or between opposing teeth in the upper and lower jaws (dignathic heterodonty; Compagno, 2003).

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Although qualitative descriptions of the teeth of some species are available (Herman *et al.*, 2002; Sáez & Lamilla, 2012), the dentition of Torpediniformes in general has been poorly studied. Herman *et al.* (2002) and Sáez & Lamilla (2012) divided the order into two different groups; those with teeth that have low and broad roots and those with high and narrow roots. The genus *Discopyge* Heckel 1846 is in this last group. All species of Torpediniformes as described as having a holaulacorhizous root type (*i.e.* vascularization through many small foramina concentrated in a median groove running from outer to inner face, Herman *et al.*, 2002) with osteodentine and the absence of inner foramina (pores in the root through which blood vessels penetrate the vascular channels of the pulp cavity, Herman *et al.*, 2002). The teeth of *Discopyge tschudii* Heckel 1846 have a crown with erect cusps without an apron or any ornamentation and an oval, high and narrow root, with a well-developed median groove containing the central foramen (Herman *et al.*, 2002; Sáez & Lamilla, 2012).

Differences in elasmobranch dentition are important for species determination, establishing phylogenetic relationships of living and extinct taxa and for describing ontogenetic and morphological changes (Long, 1994; Sáez & Lamilla, 2004; Purdy & Francis, 2007; Adnet & Cappetta, 2008; Straube *et al.*, 2008; Maisey, 2012). The aim of the present paper is to provide qualitative and quantitative analyses of the dentition of *D. tschudii* according to sex and stages of maturity.

MATERIALS AND METHODS

SAMPLING AND SAMPLE PROCESSING

Overall, 193 *D. tschudii* individuals (99 males and 94 females) were collected in the south-west Atlantic Ocean between 36–52° S and 53–66° W. Specimens were measured (total length, L_T, mm) and sexed. The maturity stage (mature or immature) was determined according to the degree of clasper calcification, development of testes and reproductive ducts in males and on the condition of uteri and ovarian follicles in females, according to Colonello (2009). The jaws were excised and frozen for subsequent analyses. Once in the laboratory, the entire series of functional and developing teeth were removed from the jaw cartilage and attached to onion skin paper for dehydration treatment, maintaining their original jaw position. Four groups were determined by sex and stage of sexual maturity in order to analyse variation in teeth: mature males, immature males, mature females and immature females.

QUALITATIVE ANALYSES

The external morphology of the teeth was described from isolated teeth that were removed from the onionskin paper and cleaned in 5% aqueous KOH to macerate the soft tissues. A sagittal section of a tooth was made with a scalpel to describe the internal morphology. Subsequently, teeth were photographed using a Nikon Coolpix P500 digital camera (www.nikon.com) and a Leica MZ8 binocular microscope (www.leica.com). Detailed observations of the teeth were made, using a JSM-6460LV scanning electron microscope (SEM; JEOL; www.jeoluk.com). Samples were mounted on 5 cm aluminium stubs and coated with gold using a sputter-coating Denton Vacuum Desk II (www.dentonvacuum.com). Teeth were photographed from the image generated by the SEM JSM6460LV at an accelerating voltage of 15 kV.

QUANTITATIVE ANALYSES

According to definitions by Compagno (2003) and Motta (2004), a row is a single line of teeth transverse to the jaw axis that includes both functional teeth and their replacements. A tooth series is a line of teeth along the jaws parallel to the jaw axis that includes teeth from all rows.
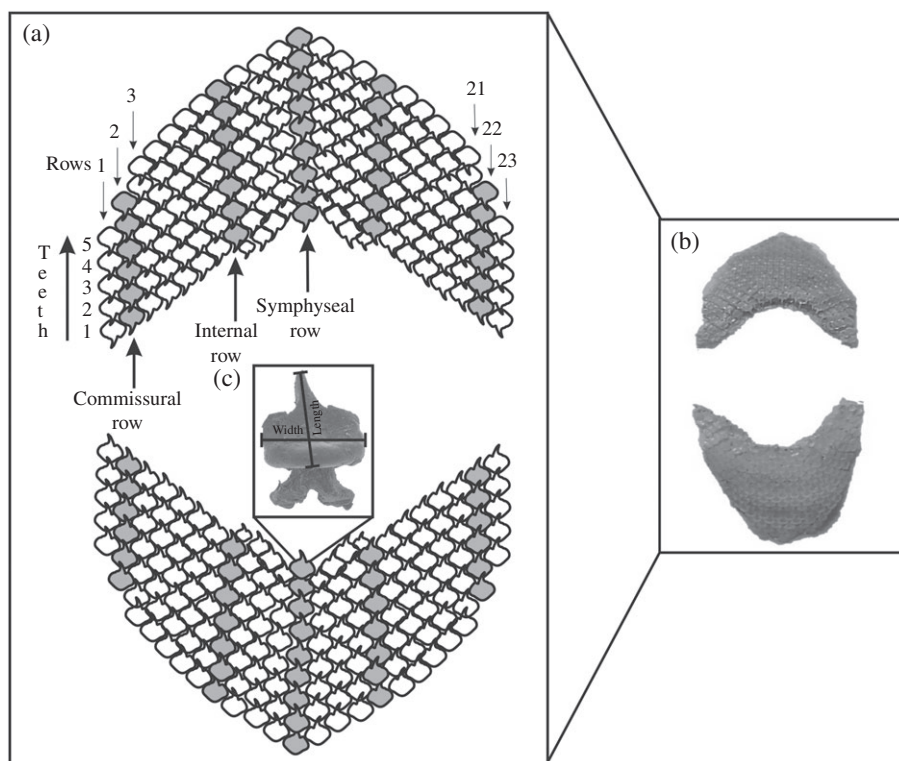
FIG. 1. (a) Diagram illustrating upper and lower jaws of *Discopyge tschudii* and the method for row counts alongside (b) photograph of corresponding *in situ* tooth arrangement. (c) Measurements of width and length made for each tooth located on the symphyseal, internal and commissural rows.

The total number of tooth rows in each jaw was recorded (Fig. 1) and posteriorly analysed with a Mann–Whitney *U*-test to ascertain significant differences between upper and lower jaws. The relationship between rows and L_T of *D. tschudii* by sex was evaluated by fitting a quantile regression model (Koenker & Bassett, 1978; Cade & Noon, 2003) at 50% (simple linear regression model), 90 and 10% levels (most extreme values in the dataset) with the quantreg package in R 3.2.1″ (www.r-project.org; Koenker, 2007). The tooth measurements were carried out on three representative rows in each jaw, over the entire series of functional and developing teeth (Fig. 1), so all mandible regions were represented: (1) symphyseal row (row located at the symphysis, in the middle of the jaw), (2) internal row (row located six rows from the commissural row) and (3) commissural row (second row located from the commissure, where jaws are joined) (Fig. 1). The tooth located closest to the inner side of the mouth was numbered tooth 1 and teeth were numbered (*e.g.* 2, 3) up to the oldest outer tooth (Fig. 1). The width and length of each tooth were measured in representative rows in both lower and upper jaws according to Sáez & Lamilla (1997) (Fig. 1). The tooth measurements were carried out using a magnifying glass binocular eyepiece graticule with 0·001 mm precision.

Average length and width of each tooth of the upper and lower jaw for all groups of the three selected rows was calculated and these values were compared between the teeth of the same row using a Kruskal–Wallis test. When there were differences between the mean values of these teeth, a Dunn's test was used to determine differences. According to these results, the tooth number of the functional series was determined and used to compare among groups (mature males, mature females, immature males and immature females). The functional tooth was considered as the first tooth having approximately the same length and width of the preceding teeth in the same row; *i.e.* the oldest tooth with no wear within the selected row (Belleggia
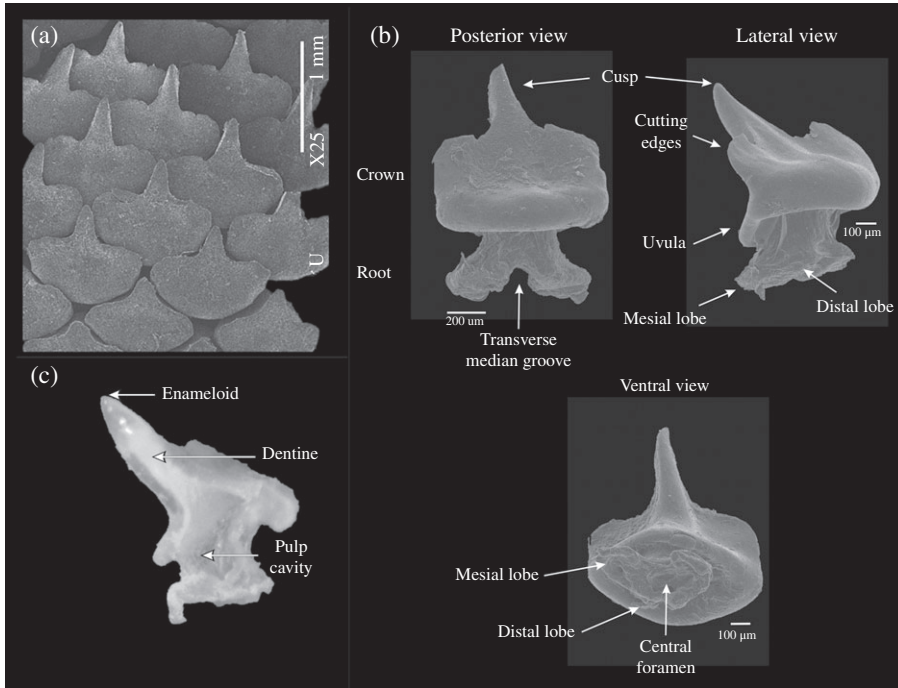
FIG. 2. Scanning electron microscope images of (a) portion of mandible and (b) isolated teeth in posterior, lateral and basal view from *Discopyge tschudii*. (c) Sagittal section showing internal structures of the tooth.

et al., 2014; Delpiani, 2014). Generalized linear models (GLM; Venables & Ripley, 2002) were used to determine the subset of measures that best explained variability among groups. This was done for both upper and lower jaws, with length being the response variable. No differences in width of teeth between rows and jaws were found, so this variable was not considered in the analysis. Thus, tooth length was considered to be the response variable and a model was built for each group (mature male, mature female, immature males and immature female) comparing the functional tooth length with sex, maturity stage and tooth row as the independent variables. Four models were also constructed with the combination of the independent variables (sex + maturity stage; sex + tooth row; maturity stage + tooth row; and sex + maturity stage + tooth row). Finally, to test the hypothesis that none of the variables have an effect on the response variable, tooth length, a null model without any independent variables was built (Lucifora *et al.*, 2009). This model has error-type γ-distribution due to the nature of the continuous dependent variable, with positive values and log-link function (link = log; Zuur *et al.*, 2009). The model of multiple hypotheses approach was used to identify which model fit best (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). For each model, the Akaike Information Criterion (AIC) and the model with the lowest AIC were selected (Crawley, 2005).

RESULTS

QUALITATIVE ANALYSES

Discopyge tschudii tooth arrangement shows a semi-mosaic type distribution [Fig. 2(a)]. Each rhombic-shaped tooth is surrounded by six others: two of the same row and the remaining four of the right and left adjacent rows. The crown, used in

the feeding process, has a sharp and erect cusp, angled posteriorly (Fig. 1). At the base of the crown, each tooth has a cutting edge, which becomes worn as the tooth moves toward the outer face of the jaw. The inner and basal face of the tooth lacks an apron and uvula; the teeth are devoid of any ornamentation [Fig. 2(b)]. The root, which fastens the tooth to the jaw, has an ovoid cross-sectional shape. The tall, narrow holaulachorizous root is bilobed. The root base has a well-developed transverse groove that divides the basal surface of the root into two lateral lobes. The medial region of the tooth root has a central foramen, through which blood vessels penetrate the vascular channels of the pulp cavity [Fig. 2(b)]. Internal and external foramina are absent. The sagittal section of the tooth shows the outer surface of the tooth is covered with an outer enameloid layer and below this there is a dentine layer and a well-developed, internal pulp cavity in which vascular channels connect the pulp region to the crown and root [Fig. 2(c)].

QUANTITATIVE ANALYSES

The upper and lower jaws of *D. tschudii* have the same number of rows within each of the four groups studied (Mann–Whitney: mature males $U = 2432$, $P > 0.05$; mature females $U = 424$, $P > 0.05$; immature males $U = 450.5$, $P > 0.05$; immature females $U = 802.5$, $P > 0.05$; Table I). The total number of rows increases with growth for the minimum, medium and maximum number of rows, in the upper jaw (10% quantile regression slope 0·0322, $P < 0.001$; 50% quantile regression slope 0·0352, $P < 0.001$; 90% quantile regression slope 0·0394, $P < 0.001$) and lower jaw (10% quantile regression slope 0·0316, $P < 0.001$; 50% quantile regression slope 0·0343, $P < 0.001$; 90% quantile regression slope 0·0377, $P < 0.001$) (Fig. 3).

The average tooth width within a row did not show significant differences among the four groups (mature males, mature females, immature males and immature females; $P < 0.001$). Average tooth length within each row significantly differed among the four groups for the upper (mature males, mature females, immature males and immature females; $P > 0.05$) and lower (mature males, mature females, immature males and immature females; $P > 0.05$) jaws. According to differences found between the tooth lengths of each row, the third tooth of each row was chosen for comparison among

TABLE I. Total number of specimens sampled (n), total length range (L_T) and row counts in both upper and lower jaws in *Discopyge tschudii* by sex and maturity stage

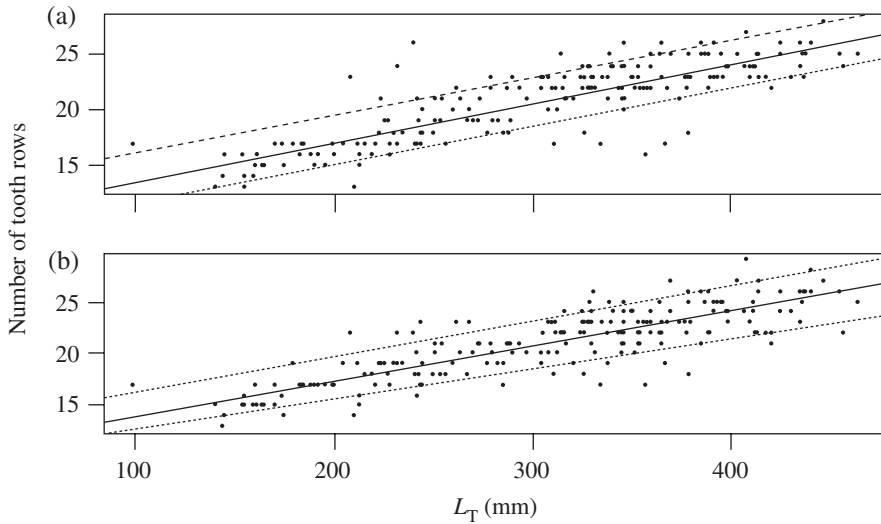| | | | Number of rows of teeth | | | | | |
| | | | Upper jaw | | | Lower jaw | | |
Group	n	L_T range(mm)	Range	Mean	S.D.	Range	Mean	S.D.
Male								
Mature	49	341–487	18–31	23·97	1·736	19–31	23·62	2·325
Immature	50	174–367	16–26	22·53	4·083	15–28	22·33	3·708
Female								
Mature	44	224–391	18–25	21·85	1·671	18–24	21·57	1·751
Immature	50	99–280	14–25	20·69	3·088	14–26	20·46	3·210

FIG. 3. Quantile regression of tooth-row counts and total length (L_T) of all specimens of *Discopyge tschudii* in (a) upper jaw and (b) lower jaw. ——, 50% quantile regression; ...., 90 and 10% quantile regression, respectively.

the four groups and among the selected rows. These teeth are involved in grasping prey.

GLM results suggest several patterns relating to functional tooth length, including sex, maturity stage and rows of the jaw (Table II). In the upper jaw, males have longer tooth lengths than females, being much longer in mature individuals than in immature specimens [Fig. 4(a)]. The tooth lengths of the internal row are slightly longer than those of the symphyseal row, being shorter than the teeth from the commissural row [Fig. 4(a)]. In the lower jaw, males also have longer teeth than females, being much longer in mature individuals [Fig. 4(b)]. There is a gradual decrease in tooth length starting from the symphyseal row to the commissural row [Fig. 4(b)].

DISCUSSION

Discopyge tschudii exhibits homodont dentition. The species bears a large number of small teeth (Underwood *et al.*, 2015) arranged in a semi-pavement-like dentition. The teeth are similar in shape and the peg of each tooth extends under the basal edge of the next tooth in succession in the same row. The internal tooth composition of *D. tschudii* is similar to that observed in other elasmobranchs (Kemp, 1999): the crown is formed by an outer enameloid layer above a layer of dentine surrounding the pulp cavity. The presence of a holaulacorhizous root type has been found in other studies of Torpediniformes teeth (Herman *et al.*, 2002; Sáez & Lamilla, 2012) and also in other batoids (Herman *et al.*, 1995, 1996, 2002; Sáez & Lamilla, 2004). The transverse groove of the root divides the attachment surface into mesial and distal lobes, common characteristic in the majority of batoids (Herman *et al.*, 1994, 1995, 1996; Sáez & Lamilla, 1997, 2004) and sharks (Belleggia *et al.*, 2014); elasmobranchs rarely have multiple root

lobes (*e.g.* Myliobatidae; Underwood *et al.*, 2015). According to Moyer *et al.* (2015) root morphology of newly formed teeth is very similar to functional teeth. This is also the case in *Discopyge* spp., suggesting that tooth root morphology is established very early in tooth morphogenesis.

Discopyge tschudii is a small, gape-limited batoid and its dentition is characteristic of a species that feeds on soft-bodied prey (such as polychaetes and other small invertebrates; García, 1984; Arrighetti *et al.*, 2005; Spath *et al.*, 2013, 2015). *Discopyge tschudii*, like other narcinids such as *Narcine brasiliensis* (Olfers 1831), use extreme jaw protrusion to capture and process prey (Dean & Motta, 2004). Posteriorly oriented tooth cusps could facilitate retention of soft-bodied prey, preventing the prey-sliding off the jaws as has been suggested for *N. brasiliensis* (Dean *et al.*, 2008) and *Potamotrygon motoro* (Müller & Henle 1841) (Kolmann *et al.*, 2016).

The number of tooth rows in *D. tschudii* does not differ between the upper and lower jaws within each group (mature males, mature females, immature males and immature females). The number of tooth rows has been used to characterize elasmobranch species. Since the number of tooth rows can vary with increasing specimen size, however, this character has to be considered with caution (Bass, 1973). This is the case of *D. tschudii*, in which the number of rows reveals that mature males have more rows than do females, both in mature and immature individuals. This difference may be directly related to the increase in body size [male *D. tschudii* reach larger sizes than females (García, 1984; Estalles *et al.*, 2011), being a unique characteristic among Torpediniformes] and therefore also mouth size. In *Narcine insolita* (de Carvalho *et al.*, 2002) the number of tooth rows varies from 11 to 24 according to maturity stage. The series of teeth are added one after another, with series bearing a symphyseal tooth alternating with those lacking this tooth, but having a pair of parasymphyseal teeth (Underwood *et al.*, 2015). Each successive tooth row has an additional pair of proximal teeth present, so that the number of tooth series along the jaw (added proximally) increases rapidly. Sexually dimorphic dentitions are known within a large proportion of batoids (Castillo Geniz *et al.*, 2007). In *D. tschudii*, the teeth of adult males are more cuspate than those of adult females for the same body size, indicating independence between tooth length and body size.

TABLE II. The intercept (s.e.) and the coefficients (s.e.) of the variables from general linear models explaining variation in the length of the upper and lower jaw functional-tooth length of *Discopyge tschudii*

Dependent variable	Intercept	Coefficients	AIC	*w*
Upper jaw length	1·72 (0·02)	0·27(0·02)male + 0·39(0·02) mature + 0·64(0·03)hinternal 0·27(0·02) male + 0·39(0·02) mature + 0·43(0·02)hsymphyseal	861·62	0·96
Lower jaw length	0·63 (0·04)	0·28(0·04)male + 0·32(0·04) mature + 0·07(0·05)hinternal0·28 (0·04)male + 0·32(0·04) mamatureture + 0·11(0·04)hsymphyseal	411·92	0·99

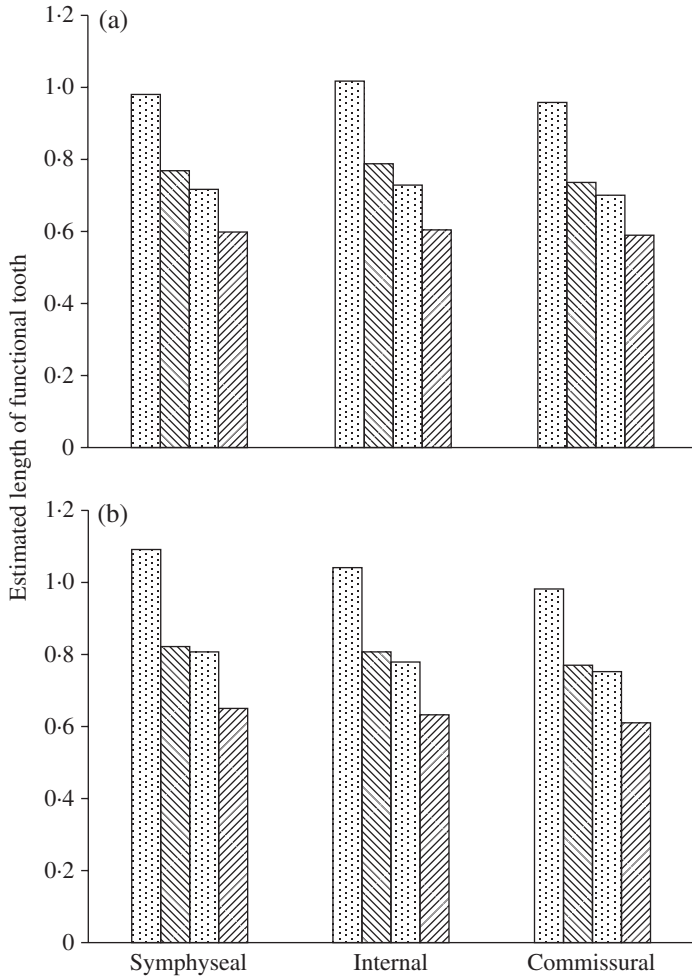Hinternal, internal tooth row; Hsymphyseal, symphyseal tooth row.

FIG. 4. Differences in tooth-length with sex and maturity stage of *Discopyge tschudii* estimated by general linear models for (a) upper jaw and (b) lower jaw. The models have a log-link and γ-error distribution. ▨, mature males; ◩, mature females; ▣, immature males; ▨, immature females.

Similar sized teeth were noted for the upper and lower jaws of *D. tschudii*, consistent with them having homodont dentition (uniform tooth morphology; Herman *et al.*, 2002). Tooth lengths of the commissural row, however, were shorter than those of both the internal and symphyseal rows for the same jaw. This is a common phenomenon in the dentition of elasmobranchs (Compagno, 2003; Cappetta, 2012) and has been called gradient monognathic heterodonty (Herman *et al.*, 2002), in which teeth exhibit a gradual variation in size between the symphysis and the distal portion of the jaw. In *D. tschudii,* the teeth become shorter toward the commissure as in *N. brasiliensis* (Herman *et al.*, 2002). According to Sáez & Lamilla (1997, 2004) the decrease in tooth size toward the commissure facilitates jaw closure during apprehension of prey. Moreover, commissural teeth play a less important role in grasping prey than do the symphyseal teeth (Delpiani, 2014). The decrease in tooth length within each row from the inner to

the outer side of the jaw can be considered as a consequence of wear. Worn teeth continue to move past their functional position to the outer side of the jaw (postfunctional stage) where the tooth is no longer involved in food grasping (Underwood *et al.*, 2015). In *N. brasiliensis* tooth function varies as a result of the tooth shape and replacement process: occlusal (erect) teeth may pierce and grasp prey, preventing it from slipping out of the jaws and external (depressed) flattened teeth may provide a renewable surface that may protect the rostral surfaces of the jaws (Dean *et al.*, 2008). Hence, the retention of the teeth well beyond the functional row creates a new functional niche for older teeth, where the labial surfaces are used as a battering surface and to protect the symphysis during excavation (Dean *et al.*, 2008). Owing to similarity in the structure of the mandible with *N. brasiliensis*, it could be thought that retention of the teeth in *D. tschudii* presents a protective surface for the functional teeth.

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