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Morphological analysis of the oviduct, oviducal gland and isthmus of the blue shark *Prionace glauca* (Linnaeus, 1758) (Elasmobranchii: Carcharhiniformes)

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Oviducal gland present in elasmobranchs is correlated to the organism's reproductive strategy, and its functions are to produce mucus, to form the egg's tertiary envelope and to store sperm. The gland contains four zones: club, papillary, baffle and terminal. The structures of the oviduct, oviducal gland and isthmus of blue shark *Prionace glauca* were described using macroscopic, light microscopy and scanning electron microscopy techniques. The epithelium of the oviduct and isthmus is folded and is a simple, columnar, ciliated lining epithelium with glandular cells. In the oviducal gland, the lining tissues in the four zones are similar to the oviduct and isthmus lining. The terminal zone shows the presence of sperm in the lumen of the secretory tubules, which remains stored even in the absence of recent copulation. Here, these organs were studied and their connections in an attempt to elucidate the mechanisms of reproduction in the blue shark, showing the three-dimensional aspects, thus adding morphological information important for the understanding of the structure and functioning of these organs of fundamental importance in the life of the majority of elasmobranchs.

A glândula oviducal presente nos elasmobrânquios está correlacionada com a estratégia reprodutiva, cuja função é de produzir o muco, formar o envelope terciário do ovo e armazenar espermatozóides. A glândula contém quatro zonas: club, papilar, baffle e terminal. Foi descrita a estrutura do oviduto, glândula oviducal e istmo do tubarão-azul, *Prionace glauca*, pelas técnicas macroscópica, microscópica de luz e eletrônica de varredura. Foi observado que no oviduto e istmo o epitélio é pregueado de revestimento simples, colunar, ciliado com células glandulares. Na glândula oviducal o tecido de revestimento é semelhante ao oviduto e istmo nas quatro zonas. Na zona terminal observou-se a presença de espermatozoides no lúmen dos túbulos secretores que permanecem estocados mesmo na ausência de copula recente. Aqui, estudaram-se esses órgãos e suas conexões na tentativa de elucidar os mecanismos da reprodução no tubarão azul, apresentando os aspectos tridimensionais, desta forma agregando informações morfológicas importantes para o entendimento da estrutura e funcionamento desses órgãos de fundamental importância na vida da maioria dos elasmobrânquios.

Keywords: Cartilaginous fish, Electron microscopy, Nidamental gland, Reproduction, Shell gland.

Introduction

Elasmobranchs share very particular reproductive characteristics, such as external sexual dimorphism, internal fertilization, paired reproductive organs, late sexual maturation, diverse strategies of embryonic development and the absence of parental care (Dodd, 1983; Wourms & Demski, 1993). The ovaries are paired structures or only, and generally, the two ovaries are functional in more primitive forms (Carrier *et al*., 2004; Lutton *et al*., 2005), the female of the blue shark *Prionace glauca* (Linnaeus, 1758) just the right ovary is functional and the left ovary is vestigial or absent (Pratt, 1979). The female reproductive system of the blue shark consists of one ovary, one ostium, two oviducts, two oviducal glands, two isthmuses, two uterus and one common urogenital sinus (Pratt, 1979). The oviducal gland, also known as the nidamental or shell gland, is a specialized structure found right below the oviduct and above the uterus in almost all elasmobranchs, and its development and structural complexity correlate

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with the mode of reproduction (Hamlett *et al*., 1998; Hamlett & Koob, 1999; Hamlett *et al*., 2005). The oviducal gland produces mucus that surrounds the fertilized egg in the early stages of embryogenesis, forms the egg's tertiary envelope and stores have also been implicated in sperm storage (Metten, 1939; Prasad, 1945; Pratt, 1979; 1993; Hamlett *et al*., 1998; Hamlett & Koob, 1999; Hamlett *et al*., 2002, 2005).

Hamlett *et al*. (1998) observed that despite the variations between species regarding the different reproductive strategies, the same basic functional design is present in the species studied by them. Four zones are distinguished in most of the studied species: an anterior club zone, followed by a papillary zone that produces mucus that surrounds the fertilized ovum in the early stages of embryogenesis, a baffle zone that forms the tertiary envelope of the egg, and a terminal zone where the sperm is stored (Hamlett *et al*., 1998; Hamlett & Koob, 1999; Hamlett *et al*., 2005; Storrie *et al*., 2008).

Prionace glauca belongs to the Carcharhinidae family. It is an oceanic species that is distributed globally, present in tropical, subtropical and temperate waters, and can be found from the water surface to a depth of 150 m (Compagno, 1984). On the Brazilian coast, *P. glauca* occurs from northeast to south, and the distribution and abundance of females is associated to a migratory pattern related to their reproductive cycle (Amorim, 1992; Hazin *et al*., 1994). This species is captured in pelagic longline fisheries worldwide, intentionally or as by-catch (Amorim *et al*., 1998). Because this species is in the category of "near threatened" according to the Red List of Threatened Species (IUCN) and has large economic and commercial importance, a better understanding of the morphological characteristics involved in its reproduction and of its particularities in southern Brazil is of fundamental importance (Stevens, 2009).

The work of Pratt (1979) and Hazin (1991) about the oviductal gland of blue shark address fundamental issues about the function of the gland in this species, adding detailed information about the reproductive cycle, and on the storage of sperm. However, these studies have used the technique of light microscopy to the study of such features, making necessary the use of other techniques, such as scanning electron microscopy, complementing those jobs and bringing our observations on this very important organ in the reproduction of most sharks and rays.

Material and Methods

Animals. The oviduct, oviducal gland and isthmus of 10 samples from five *Prionace glauca* (Linnaeus, 1758) (Elasmobranchii: Carcharhiniformes), individuals were adult and pregnant females. Specimens captured by Austria longliner based in Santos City, São Paulo State in southern Brazil, from March to May 2013 were analyzed, corresponding to the period of early embryonic development (Amorim, 1992). The samples were donated by the Austria captain to the Instituto de Pesca, from Santos-SP and transferred to the Department of Anatomy of the School of Veterinary Medicine and Animal Science of the University of São Paulo. This study were approved by the Commission for Ethics on Animal Use (CEUA) nº 8278141113, of the School of Veterinary Medicine and Animal Science of the University of São Paulo (FMVZ-USP).

Light microscopy (LM). After taking the innards of the animal, the fishermen immediately placed the entire organs, including the oviduct, oviducal gland and isthmus in the 4% paraformaldehyde solution, where they remained for more than 20 days. With the taking of samples in the landing, the organs were fragmented; samples were cut as regions of interest, washed under running water and dehydrated in a series of increasing ethanol concentrations (70 to 100%), with each pass of 30 minutes to 60 minutes, being diaphanized in xylol with subsequent inclusion in Paraplast. Slices of 5 µm thickness were made in the Paraplast blocks using a Leika-German microtome, and the slices were stained with hematoxylin-eosin (HE). A Nikon Eclipse E-800 (FMVZ/USP) light microscope was used to perform the photo-documentation.

Scanning electron microscopy (SEM). The samples also forms collected in 4% paraformaldehyde, where three samples of oviduct, oviducal gland and isthmus were subjected to a tissue-corrosion procedure by immersion in an aqueous solution of sodium hydroxide (NaOH) for 4 days and kept at room temperature to remove the epithelium. In the next step, all samples were post-fixed in an aqueous solution of 1% osmium tetroxide and dehydrated in series of increasing ethanol concentration (70% to 100%). After dehydration, the samples were dried in a Balzers CPD 020 critical-point device, mounted onto metal stubs with carbon adhesive and sputtered with gold in a Emitech K550 sputter apparatus. Finally, the samples were photographed in a LEO 435VP (FMVZ-USP) scanning electron microscope. The results of the morphology of cells and areas were analyzed and differentiated using concepts and definitions used by Hamlett *et al*. (1998) and Hamlett & Koob (1999).

Results. In *Prionace glauca*, the oviduct (Fig. 1A-B) is a narrow tubular organ anterior to the oviducal gland (OG). Externally, the OG is a symmetrical organ, with two protrusions on the anterior lateral surfaces (Fig. 1A). The OG connection to the uterus is tubular and made through the isthmus (Is) (Fig. 1A). The divisions of the club (C), papillary (P), baffle (B) and terminal zones (T) can be observed in coronal (Fig. 1A) and sagittal (Fig. 1B) sections of the OG. The lumen (L) of the OG can be found in the center, and it extends from the oviduct to the isthmus. The transition between the oviduct and the OG can be observed in the anterior region, and the transition between the OG and the isthmus can be observed in the posterior region.

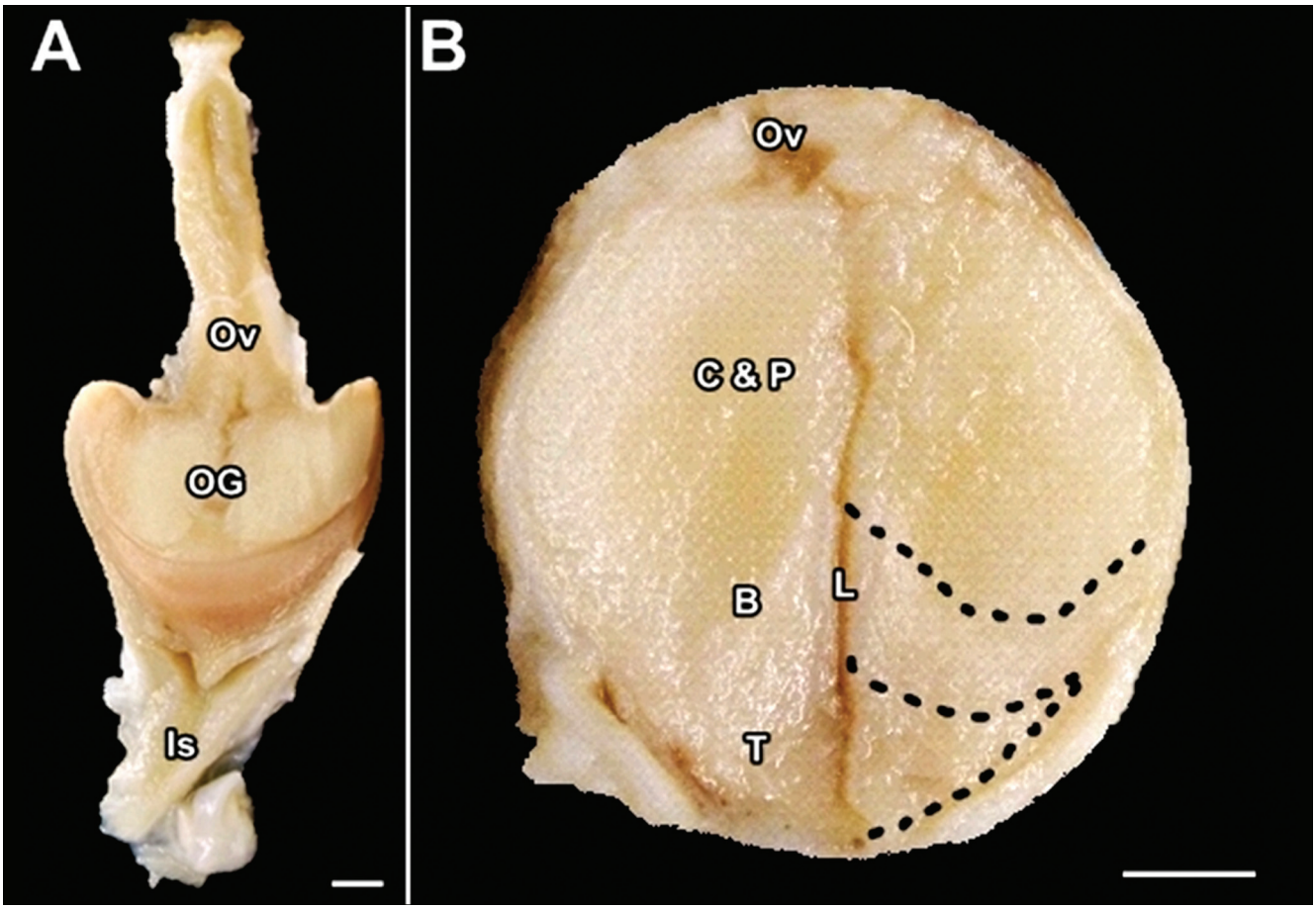

Fig. 1. Macrographs of the oviduct, oviducal gland and isthmus of *Prionace glauca*. **(A):** coronal section. Oviduct (Ov), oviducal gland (OG) and Isthmus (Is). **(B):** sagittal section of OG identifying the division of zones: Club (C), Papillary (P), Baffle (B) and Terminal (T); central lumen (L). Scale bars: 10 mm.

Microscopic description. Oviduct. A tube with crypts and longitudinal folds can be observed in a cross-section of the oviduct close to the OG using SEM (Fig. 2A-B) and LM (Fig. 2C). Fig. 2B shows the three-dimensional structure of the crypts and folds. The transition between these crypts and the anterior region of the OG in the club zone can be observed with the HE staining (Fig. 2C). The simple columnar, ciliated lining epithelium with secretory cells can be observed in a higher magnification of the connective tissue of the crypts (Fig. 2D, F-G). The cilia on the surface of the lining epithelium can be observed using SEM at higher magnifications (Fig. 2E).

Oviducal gland. The medial section of the oviducal gland of *Prionace glauca* is divided into the four zones described below:

Club zone. The club zone (Fig. 3) is a segment located in the cranial region of the OG, near the oviduct. Fig. 3A and 3B show an SEM image of the region closest to the central lumen, into which the round-shaped secretory tubules open. The transition from the oviduct to the club zone can be observed in Fig. 3A. The elongated secretory tubules, the connective tissue and the simple columnar ciliated lining epithelium with glandular secretory cells can be observed under LM, as shown in Fig. 3C and 3D.

Papillary zone. The papillary zone (Fig. 4) is found below the club zone. The opening of the secretory tubules in the central lumen between the projections can be observed under SEM (Fig. 4A-B). Fig. 4C shows the opening of the secretory tubules in grooves, forming epithelial projections in the central lumen of the OG, under LM, with the simple columnar ciliated lining epithelium of the tubule, similar to the club-zone epithelium (Figs. 4C-D).

Baffle zone. The baffle zone (Fig. 5) has well-differentiated projections in the central lumen region. The round secretory tubules and the lamellae-like projections with short epithelial folds are observed by SEM (Fig. 5A-B). The epithelial projections surrounded by short epithelial folds are evidenced in LM (Fig. 5C). The secretory tubules (Fig. 5C-D) are surrounded by connective tissue and are also composed of simple columnar ciliated epithelium with glandular cells.

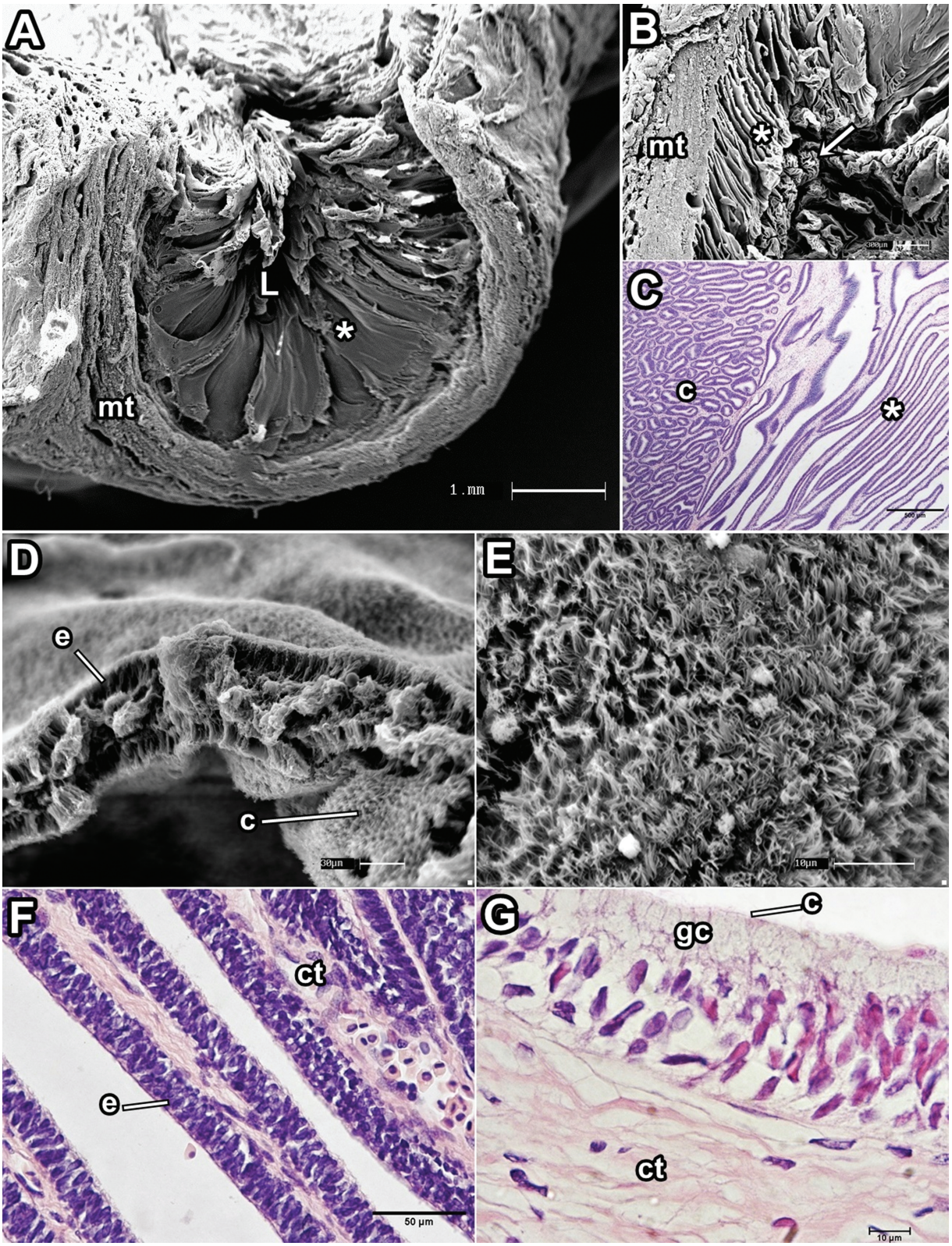

Fig. 2. Micrographs of the oviduct of *Prionace glauca*. (**A):** cross-section, tube with crypts (*), muscle tissue (mt) and a central lumen (L). SEM. **(B):** three-dimensional aspect of the structure of the crypts (*) and folds (arrows). **(C)**: transition of the Oviduct (Ov) with the club zone (C). HE. **(D):** the crypt epithelium (e) distributed, where you can see the layer of cells that form each crypt and the ciliated epithelium (c). SEM. **(E):** ciliated epithelium. SEM. **(F-G):** crypt epithelium (e) in biggest increase, composed of connective tissue (ct), simple ciliated columnar lining epithelium (c) with glandular cells (gc). HE. Scale bars: 1 mm (A); 500 µm (C); 300 µm (B); 50 µm (F); 30 µm (D); 10 µm (E and G).

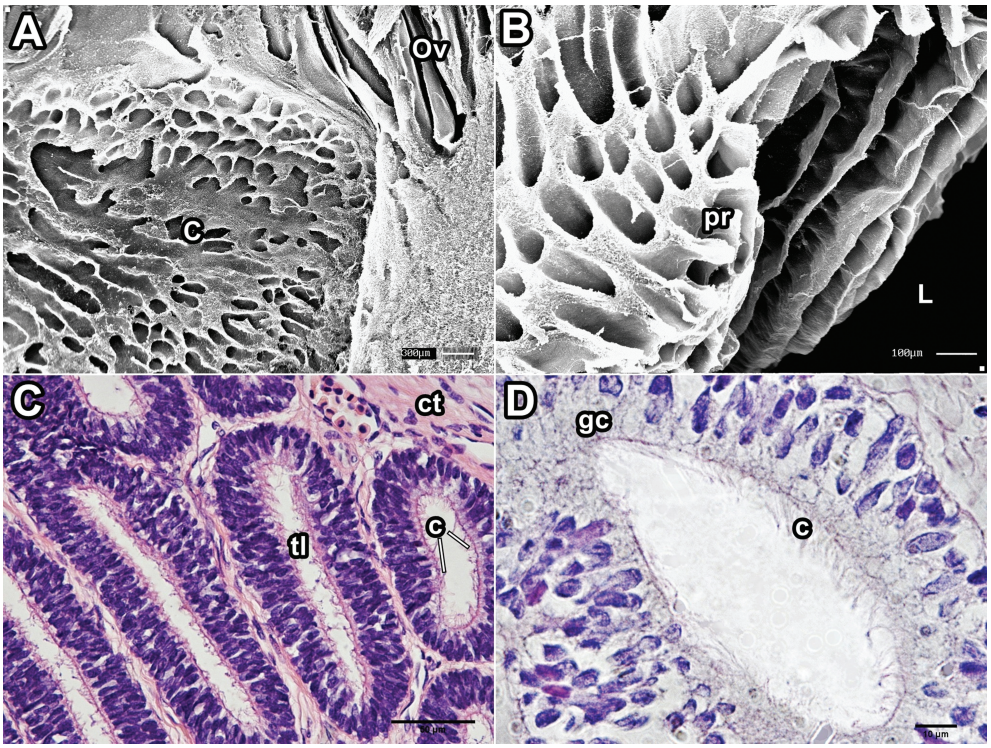

Fig. 3. Micrographs of the Club zone of *Prionace glauca*. **(A):** transition from Club zone (C) with the oviduct (Ov). SEM. **(B):** three-dimensional aspects of the tubules secretory and the opening of these in the central lumen (L) between the projections (pr). SEM. **(C):** disposition of the tubules secretory; simple ciliated columnar lining epithelium (c); tubule lumen (tl) and connective tissue (ct). HE. **(D)**: secretory tubule in biggest increase; presence of simple ciliated columnar lining epithelium (c) with glandular cells (gc). HE. Scale bars: 300 µm (A); 100 µm (B); 50 µm (C); 10 µm (D).

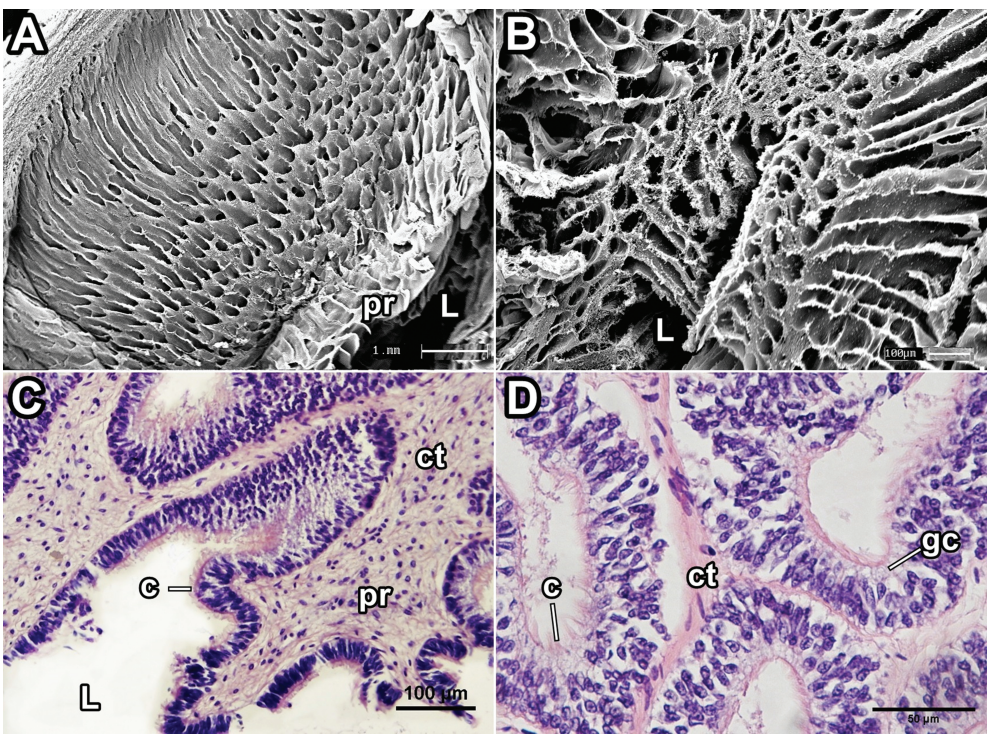

Fig. 4. Micrographs of the Papilar zone of *Prionace glauca*. **(A):** three-dimensional aspects of the tubules secretory and the opening of these in the central lumen (L) between the projections (pr). SEM. **(B):** tubules in biggest increase; central lumen (L). SEM. **(C):** tubules and epithelial projections (pr), central lumen (L). HE. **(D):** secretory tubule in biggest increase; lining epithelium is simple columnar ciliated (c) with glandular cells (gc); connective tissue (ct). Scale bars: 1 mm (A); 100 µm (B and C); 50 µm (D).

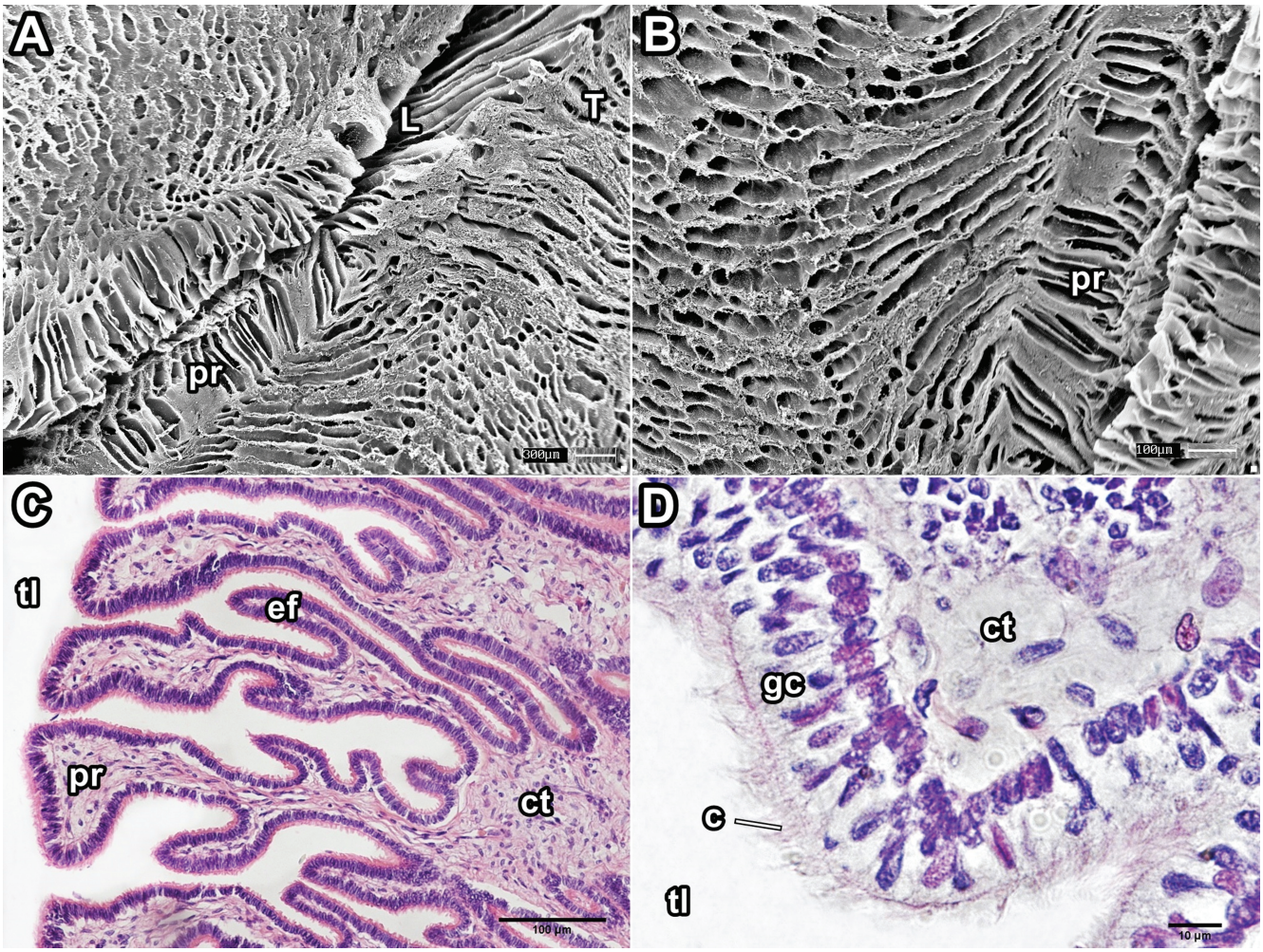

Fig. 5. Micrographs of the Baffle zone of *Prionace glauca*. **(A):** tubules that open between epithelial projections (pr) in the central lumen (L) of the GO; Terminal zone (T). SEM. **(B):** projections (pr) in greater increase, similar to the lamellae. SEM. **(C):** each epithelial projection (pr) is surrounded by short epithelial folds (ef). HE. **(D):** tubules are formed by cells ciliated columnar (c) and glandular (gc); connective tissue (ct); tubule lumen (tl). HE. Scale bars: 300 µm (A); 100 µm (B and C); 10 µm (D).

Terminal zone. The terminal zone (Fig. 6) is found in the posterior region of the OG, near the isthmus. SEM (Fig. 6A-B) shows the presence of elongated tubules on the section surface, which do not form epithelial projections in the area of contact with the central lumen, unlike in other zones. The tubules deepen and open into the central lumen of the OG, being parallel and inclined (Fig. 6A-B). Invaginations of the epithelial lining are observed in the region facing the transition zone between the OG and isthmus in the terminal zone (Fig. 6A-B); epithelial projections and folds can also be found in the lining wall of OG in this area.

The tubules are elongated and rounded when observed using LM. The lining epithelium does not form projections as it does in other areas, but some invaginations resulting from the opening of the secretory tubules are observed in the region in contact with the central lumen (Fig. 6C-D).

The tubules are formed by simple columnar ciliated epithelium with glandular cells, and few sperm cells were found lodged in the lumen of the tubules (Fig. 6E-F). The sperm found in this study were observed farther from the central lumen of the gland, in low density and not aligned.

Isthmus. A tube surrounded by muscle tissue in the region inside the longitudinal crypts can be observed in the longitudinal section of the isthmus (Fig. 7A) based on SEM. The ciliated surface of the crypts can be observed at higher magnification (Fig. 7B). The epithelial projections and folds can be observed in the sagittal section near the OG (Fig. 7C-E). The folds with simple columnar ciliated lining epithelium with glandular cells and connective tissue can be observed under LM (Fig. 7D-F). This organ interconnects the OG to the uterus, where the sperm while driving to the OG, and where the fertilized egg to the uterus.

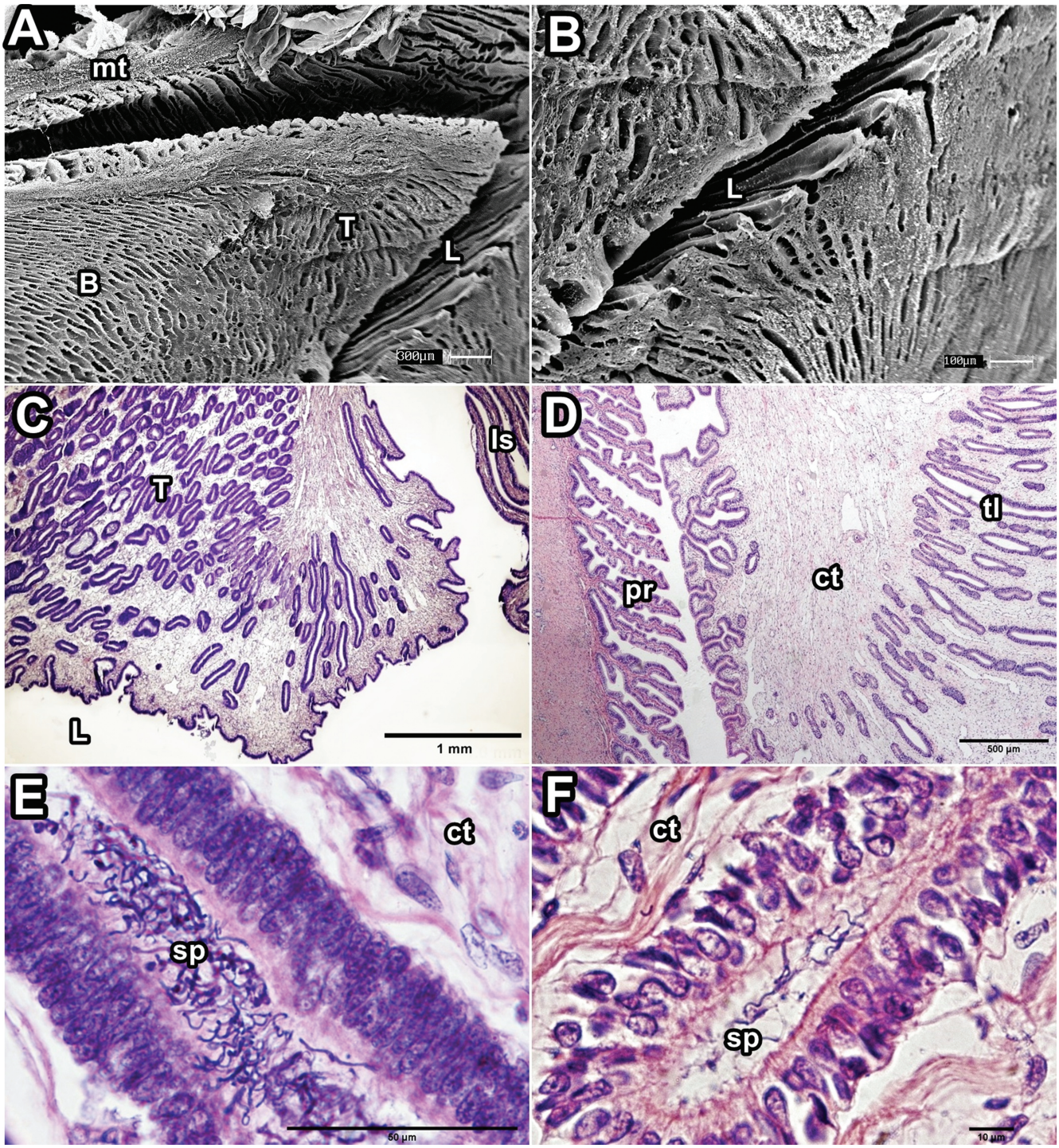

Fig. 6. Micrographs of the Terminal zone of *Prionace glauca*. **(A):** Terminal zone (T) transiting the zone Baffle (B) and the isthmus (Is); central lumen (L) and muscle tissue (mt) of GO. SEM. **(B):** region of the central lumen (L) of the GO, the deeper, opening parallel and slanted. SEM. **(C):** region contact the central lumen (L), coating epithelium does not form projections; tubules are elongated and rounded; Isthmus (Is). HE. **(D):** region facing the transition zone of GO, invaginations in the coating epithelium and connective tissue (ct) and projections (pr) in the lining of the GO; tubule lumen (tl). HE. **(E e F):** tubules are simple ciliated columnar epithelium consisting of (c) with glandular cells, the presence of a few sperm (sp) found in the lumen of the tubule. HE. **(G):** central lumen (L); tubule lumen (tl); connective tissue (ct). PS. **(H):** central lumen (L); tubule lumen (tl); connective tissue (ct). Type I collagen fibers. PS polarized. Scale bars: 1 mm (C); 500 µm (D); 300 µm (A); 100 µm (B); 50 µm (E); 10 µm (F).

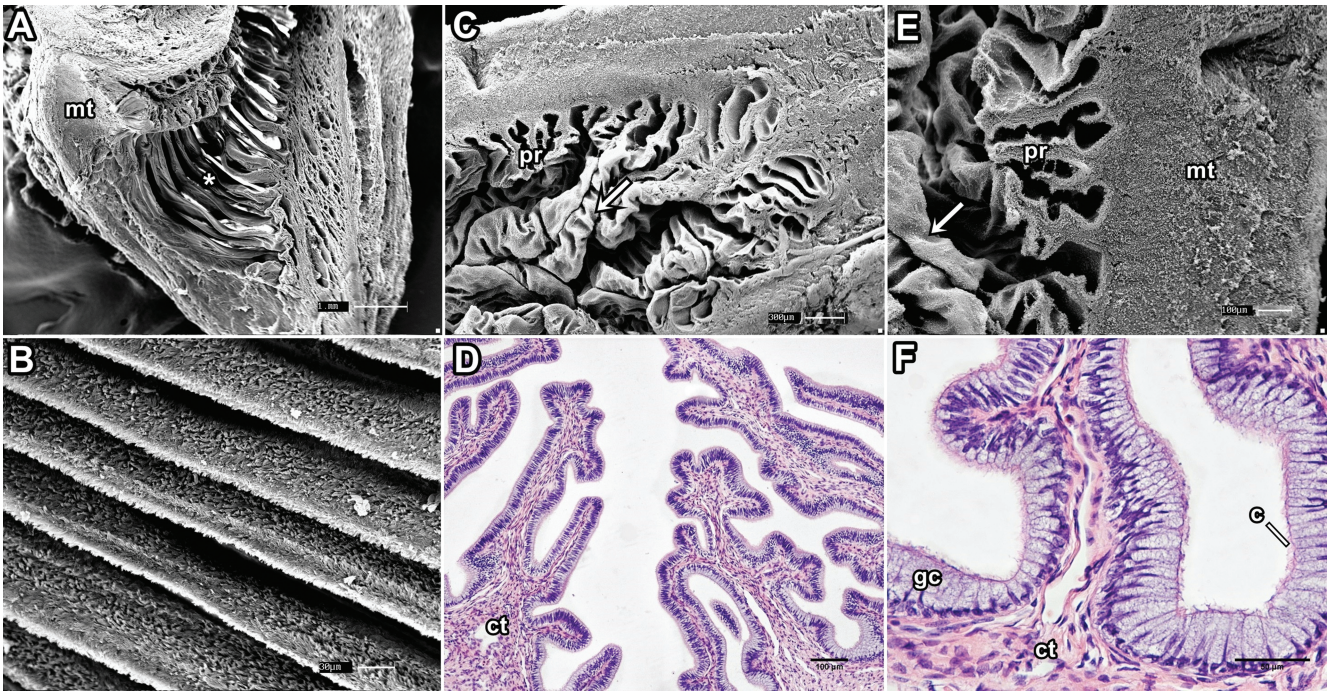

Fig. 7. Micrographs of the isthmus of *Prionace glauca*. **(A):** longitudinal section; tube with crypts (*); muscle tissue (mt). SEM. **(B):** surface release of the crypts, ciliated epithelium. SEM. **(C):** sagittal section, projections (pr) and folds (arrows). SEM. **(D):** folds; connective tissue (ct). HE. **(E):** epithelial projections (pr) in greater increase. SEM. **(F):** folds in biggest increase; simple ciliated columnar lining epithelium (c) with glandular cells (gc) and connective tissue (ct). HE. Scale bars: 1 mm (A); 300 µm (B); 100 µm (C and D); 50 µm (F); 30 µm (D).

Discussion

Regarding its reproductive strategy, *Prionace glauca* is placental viviparous, forming a placental structure that establishes a direct contact between the female and the embryo (Bigelow & Schroeder, 1948; Compagno, 1984). The gestational period is estimated to be between 9 and 12 months (Suda, 1953; Pratt, 1979). According to Pratt (1979), males reach sexual maturity between 182 and 281 cm, and females reach maturity when they gain over 221 cm of furcal length.

According to Amorim (1992), the reproductive cycle of *P. glauca* off southern Brazil, where they mate, usually from November to March (Spring/Summer), fertilizing the oocytes, initiating the embryonic development. The samples used in this study are derived from pregnant females, caught between March and May in southern Brazil. During copulation, sperm are injected by clasper on the female cloaca, where through the uterus and the Isthmus to bid on oviducal gland, where they are stored until the female is ready for fertilization (Pratt, 1979; Amorim, 1992). According to Wourms (1977), the oocytes released from the ovary into the body cavity are transported to the ostium and oviduct by ciliary action. *P. glauca*, similarly to other species of the family Carcharhinidae, has a high fertility rate, giving birth to up to 135 pups (Compagno, 1984).

The oviduct and isthmus observed macro and microscopically were very similar to those present in *Mustelus antarcticus* (Storrie *et al*., 2008) and *Iago omanensis* (Fishelson & Baranes, 1998; Hamlett *et al*., 2002), both placental viviparous species, like *P. glauca*. According to Pratt (1979), the oviduct in *P. glauca* expands to form the oviducal gland and then returns to its original diameter of approximately 10 mm; this area is called the isthmus. The encapsulation of the egg is clearly a fundamental process that elasmobranchs maintained during the evolutionary divergence in modes of reproduction, except some rays (Hamlett & Koob, 1999).

The oviducal gland of *P. glauca* has the same morphological characteristics observed in other elasmobranchs (Hamlett *et al*., 1998, 2002; Storrie *et al*., 2008; Moura *et al*., 2011). However, Mattews (1950) studied the reproductive system of *Cetorhinus maximus*, a shark species of the family Laminidae with aplacental viviparous reproduction of type Oophagia, and described the oviducal gland as a structure different from that of other elasmobranchs: apparently uniform, without clear divisions and without any sign of secretion of shell material.

As observed by Pratt (1979), in *P. glauca*, the secretory tubules are formed around the circumference of the oviducal gland, extending inward, parallel to one another, until the region of the central lumen.

The club and papillary zones have the same morphology as observed in other species, especially in *Mustelus antarcticus* (Storrie *et al*., 2008), with only some differences in the shape and number of glandular tubules. Earlier descriptions generally refer to the club zone as the albumen zone and the papillary zone as the mucous zone (Hamlett *et al*., 1998; Hamlett & Koob, 1999).

Pratt (1979) describes the mucous zone (papillary zone) as reduced or absent in *P. glauca*. In the present study, it was observed that these zones vary, suggesting that they change due to the reproductive cycle because this zone was visualized in glands collected from females that were in early stages of pregnancy. It was not possible to observe this zone in the oviducal glands of females in more advanced gestation periods.

These zones are responsible for the production of the mucus that initially surrounds the egg (Hamlett *et al*., 2005). The material secreted in the two zones is identified as neutral mucopolysaccharides, but there is a great diversity in the chemical nature of the mucus, which varies according to the reproductive mode of the species (Rusaouën, 1976 *apud* Hamlett *et al.,* 2005; Moura *et al*., 2011). The glandular cells found in these zones were not very evident under LM, and a large number of nuclei in glandular tubules were observed.

The projections and epithelial folds of the baffle zone in the central lumen region are very similar to those observed in other elasmobranchs. According to the nomenclature used by other authors, the baffle zone is composed of secretory tubules that open into a secretory duct between folds called baffle plates, located between a transverse groove and two *plateau* projections. The function of those projections and folds is the manipulation of the material secreted for the formation of the egg's tertiary envelope (Hamlett *et al*., 1998; Hamlett & Koob, 1999; Hamlett *et al*., 2005). Despite the similar morphology of the examined species that produce the tertiary envelope of the egg, there is diversity in composition and function (Hamlett *et al*., 1998; Hamlett & Koob, 1999). *Urobatis jamaicensis* is an example of a species that does not have such projections and has highly modified non-secretory cells; therefore, members of this species do not form the egg's envelope (Hamlett *et al*., 2005).

According to Hamlett & Koob (1999), the oviducal gland function is altered in sharks with placental viviparous development; in this case, the membrane that surrounds the embryo is thin and almost transparent in relation to the eggshell generated by oviparous species.

The storage of sperm in the oviducal gland is an evolutionary mechanism conserved in elasmobranchs, which most likely ensured the successful insemination of species with nomadic habits or of those with relatively low population density (Pratt, 1993). The presence of few sperm cells lodged in the lumen of the tubules most likely occurred due to the time of collection and the reproductive cycle in the southern Brazil, where oocytes had already been fertilized.

The organization, distribution and morphology of the tubules were very similar to that found in other elasmobranchs in the studies cited above. Pratt (1979) reports that sperm was found in 79 of 160 *P. glauca* females analyzed in the western North Atlantic over a period of three years. Hazin (1991) analyzed the oviducal gland of 44 *P. glauca* females in the western Equatorial Atlantic, reporting the presence of sperm in 38 of them, in other words, 86%. Twenty of these 38 females were classified as in pre-ovulation, three were in post-ovulation, two were sub-adult, and 13 were pregnant. Storrie *et al*. (2008) also reported the presence of sperm in *M. antarcticus* both in pregnant, mature non-pregnant, postpartum and immature females throughout the year.

The sperm found in this study were observed farther from the central lumen of the gland, in low density and not aligned. The same pattern was observed in the same species by Pratt (1979, 1993), who described those same characteristics for *Carcharhinus obscurus* and *Sphyrna lewini* (Pratt, 1993), classifying this system as long-term sperm storage. The same characteristic was suggested for *M. antarcticus* (Storrie *et al*., 2008) and *Centroscymnus coelolepis* (Moura *et al*., 2011).

It is concluded that the presence of sperm in the terminal zone and the number of gland cells in the club and papillary zones vary with the reproductive cycle of the species. Seasonal studies are needed to confirm this hypothesis.

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