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Research article

Biometrical, anatomical, and histological characterization of the Thai female dugong (*Dugong dugon*) reproductive system: Estimating sexual maturity and conservation applications

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Abstract

Dugongs (*Dugong dugon*) are vulnerable marine mammals with poorly understood reproductive biology in Southeast Asia. This study aimed to establish comprehensive reproductive parameters for Thai female dugongs and develop reliable maturity assessment criteria for conservation applications. Five female dugong carcasses were examined using biometric, gross anatomical, and histological analyses. Specimens were categorized as prepubertal (n = 2; body lengths 1.85 and 2.28 m) and pubertal (n = 3; body lengths 2.24, 2.59, and 2.80 m), based on ovarian size, ovarian morphology, and the presence of corpora lutea, or corpora hemorrhagica. Morphometric and histological examinations were conducted on all reproductive organs, and statistical comparisons were made between maturity groups. Body length was not a reliable indicator of sexual maturity due to overlapping ranges, whereas ovarian luteal structures (corpora lutea, hemorrhagica, and albicans) consistently distinguished mature from immature individuals. Vaginal and vestibular widths were significantly greater in pubertal specimens ($P<0.05$). Placental scars confirmed reproductive history, while multiple corpora lutea suggested polyovular cycles. Thai dugongs showed broader maturity size ranges compared to Australian populations. This study establishes the first regional reproductive baseline for Thai dugongs, providing morphological and histological criteria essential for field assessments and evidence-based conservation planning in Southeast Asian populations.

Keywords: Anatomy, Dugong, Histology, Marine mammal, Reproductive tract

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INTRODUCTION

Marine mammals are typically long-lived species with slow life histories, characterized by delayed sexual maturity, low reproductive rates, and high parental investment. These traits make populations particularly vulnerable to anthropogenic threats such as exploitation, fisheries bycatch, vessel strikes, and pollution (Clapham et al., 1999; Schipper et al., 2008), as well as non-anthropogenic threats (Keawchana, 2026; Kaewnoi, 2026).Population recovery relies on reproductive potential, determined by key life history traits including growth, age at maturity, and reproductive cycles. In fully aquatic taxa, such as cetaceans and sirenians, these parameters are challenging to quantify due to cryptic behavior, wide-ranging movements, and limited access for direct study (Costa, 1993). Consequently, reproductive scientists often employ indirect approaches, among which biometrical, anatomical, and histological characterization of reproductive organs provides critical insights into sexual maturity and reproductive capacity. Establishing such reproductive benchmarks is essential for assessing population resilience, guiding conservation strategies, and mitigating anthropogenic pressures, particularly for vulnerable populations such as the dugong (Dugong dugon) (Lanyon and Burgess, 2014).

Dugongs are large, fully aquatic mammals of the order Sirenia, closely related to manatees. They inhabit shallow coastal waters, estuaries, lagoons, and seagrass beds across 37 countries in the Indo-Pacific region (Lawler et al., 2002). As obligate herbivores, dugongs play an important role in maintaining the structure, diversity, and productivity of seagrass ecosystems, which in turn support numerous other marine species (Adulyanukosol, 2010; Said et al., 2024). In Thailand, the dugong (Dugong dugon) is legally classified as a Reserved Wild Animal under the Wild Animal Reservation and Protection Act B.E. 2562 (Department of National Parks, Wildlife and Plant Conservation, 2019). It is regarded as a flagship species for marine conservation due to its ecological dependence on seagrass ecosystems and its role as an indicator of coastal ecosystem health (Adulyanukosol, 2007). Their populations are primarily distributed along the Andaman Sea and the Gulf of Thailand, with the largest group occurring in Trang Province (Cherdsukjai et al., 2014). Recent observations indicate seasonal migration to Krabi and Phuket (Department of Marine and Coastal Resources (DMCR), unpublished data). Genetic analyses reveal considerable variation within this population, which is structured into five distinct groups, corresponding to mitochondrial clades A, B, C, D1, and D2, with significant gene flow occurring in the middle and lower Andaman. Its high genetic diversity and unique haplotypes, evolved separately from other global populations, underscore its conservation value and establish it as a priority for targeted management strategies (Poommouang et al., 2021). However, the Thai dugong population continues to face significant threats from habitat degradation, particularly the loss of seagrass meadows due to coastal development and pollution, as well as incidental capture in fishing gear and boat strikes (Adulyanukosol, 2010; Cherdsukjai et al., 2014). Natural causes also contribute substantially to mortality, with a study conducted from 2018 to 2023 reporting that non-anthropogenic factors account for the majority of dugong deaths (Daochai et al., 2024). These pressures have led to its Vulnerable status on the IUCN Red List (Marsh, 2019), emphasizing the need for targeted conservation and improved understanding of reproductive biology, particularly female reproductive processes, which have a direct impact on population dynamics (Wells et al., 2025).

Given the critical importance of female reproduction for population recovery, understanding dugong reproductive biology becomes essential. However, female reproductive parameters remain poorly defined in Thailand (Infantes et al., 2020). Limited data on reproductive biology restricts assessments of sexual maturity, reproductive cycles, and overall population resilience. Research on dugong reproduction has employed macroscopic and histological examinations, hormone

analysis, and behavioral observations (Marsh et al., 1984a; Adulyanukosol et al., 2007; Matsuo et al., 2014). For instance, dugongs exhibit polyovular and polyoestrus cycles with multiple Graafian follicles. Additionally, corpora lutea persist throughout pregnancy, reflecting the species' complex reproductive physiology (Marsh et al., 1984a). Dugongs also exhibit an extended reproductive cycle, with gestation lasting about one year, lactation extending for at least 1.5 years, and calving intervals of three to seven years, contributing to low fecundity (Marsh et al., 1984a). Despite these insights, reproductive endocrinology, including hormone profiles and estrous cyclicity, remains under-studied (Brammer-Robbins et al., 2024). Non-invasive methods, such as fecal progesterone measurement, have shown potential for monitoring reproductive status without disturbing animals (Matsuo et al., 2014). While hormone analysis and behavioral monitoring provide useful insights, biometrical, anatomical, and histological examinations remain the most reliable means of assessing sexual maturity and breeding capacity in marine mammal (Palmer et al., 2022). These approaches enable the establishment of reproductive benchmarks, which are particularly valuable for species such as dugongs, where direct behavioral observations are limited.

While these general principles apply globally, regional variations in reproductive parameters necessitate location-specific studies. Most existing knowledge of dugong reproductive biology originates from studies conducted in Australia, where detailed descriptions of ovarian and uterine morphology, reproductive seasonality, and age at maturity have been reported (Marsh et al., 1984a; Marsh et al., 1984b; Burgess, 2012). Histological examinations, for example, have clarified criteria for identifying ovarian activity and distinguishing between immature, pubertal, and mature females (Marsh et al., 1984a). Comparable information from other parts of the species' range, including Southeast Asia, remains scarce and fragmented. In Thailand, research has primarily focused on dugong distribution, mortality, and genetic diversity, with limited attention to female reproductive anatomy and histology (Cherdsukjai et al., 2014; Poommouang, 2021; Daochai et al., 2024). This lack of region-specific data restricts the accurate determination of sexual maturity and reproductive capacity, thereby constraining conservation planning. To address this gap, the present study (1) characterize the biometrical, anatomical, and histological features of the female reproductive system in Thai dugongs, (2) establish morphological criteria to distinguish prepubertal from pubertal individuals, and (3) provide baseline reproductive parameters for assessing sexual maturity in field applications and conservation planning for dugong populations in Thailand.

MATERIALS AND METHODS

Animal and Sample Collection

Reproductive organs were obtained from female dugong (*Dugong dugon*) carcasses provided by the Department of Marine and Coastal Resources and the Marine and Coastal Resources Research Center, Lower Andaman Sea, during the period from April, May, September, and October within the October 2023–September 2024 sampling year. A total of five female carcasses were examined by licensed veterinarians. Specifically, the following identification codes have been included: FPP001 and FPP002 (FPP: Female Prepubertal), and FPB001, FPB002, and FPB003 (FPB: Female pubertal). The abdominal cavity was accessed using the kidneys as anatomical landmarks, with reproductive organs located caudal to the kidneys. Dissections were extended to the vulva, and the organs were carefully isolated, placed in Styrofoam containers with ice packs (4–8 °C), and transported to the Faculty of Veterinary Science, Prince of Songkla University. Post-mortem intervals ranged from 6 to 36 hours. Tissue quality was assessed macroscopically (absence of severe bloating, sloughing, or discoloration) and confirmed histologically (preservation of cellular architecture). Only carcasses with minimal

autolysis were included in the study. While the sample size was limited (n = 5), reflecting the inherent challenges of studying endangered species, this cohort nonetheless represented 45.45% of all documented female dugong mortalities in Thai waters during 2024 based on annual monitoring records from the Department of Marine and Coastal Resources (DMCR, unpublished data). All carcasses suitable for reproductive analysis and accessible to researchers were included.)

Ethical Approval

This study was conducted under the Institutional Animal Care and Use Committee (IACUC) protocol number A1066/2023. Authorization to utilize dugong carcasses was obtained from the Department of Marine and Coastal Resources and the Department of Fisheries of Thailand.

Classification of Maturity Groups

This study hypothesized that sexual maturity in female dugongs could be classified based on ovarian size, ovarian morphology, and the presence of corpora lutea or corpora hemorrhagica. Individuals were categorized into prepubertal and pubertal groups according to these parameters. The prepubertal group was characterized primarily by the absence of any corpus luteum or corpus hemorrhagicum and by distinctly shorter ovarian length, whereas the pubertal group was characterized by the presence of at least one corpus luteum or corpus hemorrhagicum and by greater ovarian length, consistent with the observed trend. Notably, variation in ovarian length relative to body length, particularly between FPP001 and FPB003, did not yield a clear separation between groups; therefore, ovarian morphology was ultimately applied as the defining criterion (Figure 1).

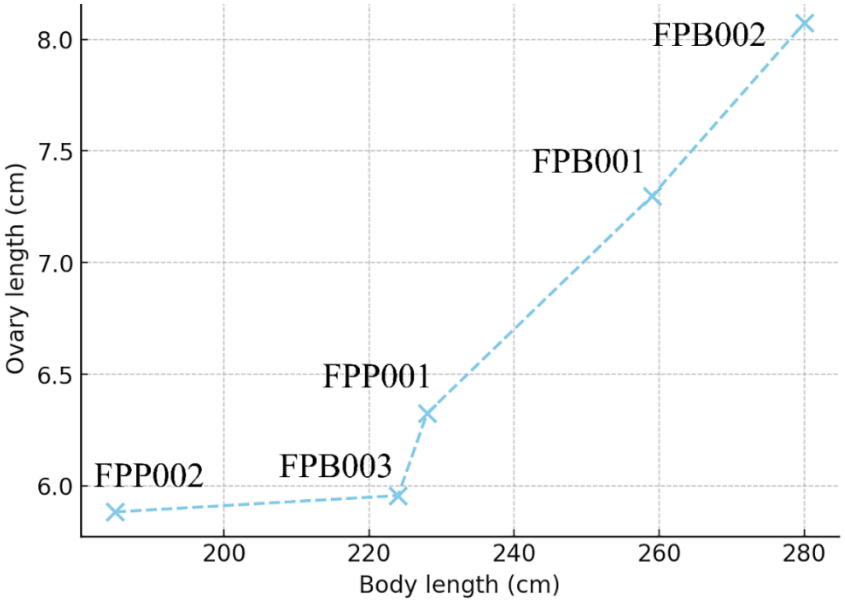


Figure 1 Relationship between body length and ovary length in female dugongs. Observed data points are connected to illustrate individual variation across sizes.

Gross Examination and Morphometric Measurements

Gross examination of the female reproductive organs was performed to document their morphology, location, and distinct characteristics. Organs examined included the ovary, oviduct, uterine horns, uterine body, cervix, vagina, vestibule, vulva, and clitoris. Each organ was photographed to record its gross

appearance. All measurements were averaged across both the left and right sides of organs. Morphometric measurements were carried out by three veterinarians, who were well trained for assessing the reproductive organs, and the mean values from repeated measurements were used for analysis. Inter-observer reliability was assessed using intraclass correlation coefficients (ICC), and all measurements showed good reliability (ICC > 0.8). Measurements were performed using a vernier caliper and a steel ruler. The following parameters were recorded: width (W), measured at the widest point of the organ; length (L), measured at the longest point; depth (D), measured at the deepest point; circumference (C), measured at the largest external circumference; lumen circumference (LC), measured at the largest internal circumference of the organ's lumen; and wall thickness (WT), measured at the thickest region of the organ wall. Specifically, the ovary and clitoris were measured in width, length, and depth at perpendicular axes, the oviduct was measured in width and length, and the uterine horns, uterine body, cervix, vagina, and vestibule were measured in width, length, wall thickness, and circumference.

Histological Examination

Histological analyses were conducted on female reproductive organs, including the ovary, oviduct, uterine horns, uterine body, cervix, vagina, vestibule, vulva, and clitoris. Each organ was sectioned into approximately 1 cm^3 pieces, fixed in 10% (w/v) neutral buffered formalin for at least 24 hours, rinsed in 70% ethanol, embedded in paraffin using standard protocols, and sectioned at a thickness of 4.5 µm using a rotary microtome. Sections were mounted on glass slides, stained with hematoxylin and eosin (H&E), and examined under a light microscope at ×40, ×100, and ×400 magnifications (Eiamcharoen et al., 2025). In the ovaries, oocytes were identified at different stages of follicular development by 10 serial sections. Histological features of the uterus and associated reproductive tissues were described and recorded following established morphological criteria. All histological sections were reviewed independently by three veterinarians, with discrepancies resolved through consensus review.

Statistical Analysis

Data obtained from the gross and histological examinations of female reproductive organs were presented in descriptive form. Morphometric measurements of reproductive organs were expressed as means ± standard error of the mean (SEM). Differences between sexual maturity groups (prepubertal and pubertal) were evaluated using independent t-tests. All statistical analyses were performed using GraphPad Prism® version 9.5.0 (GraphPad Software, San Diego, CA, USA).

RESULTS

This study examined reproductive organs from five female dugong specimens, categorized into two developmental groups: prepubertal (FPP, n = 2; body lengths 1.85 and 2.28 m), and pubertal (FPB, n = 3; body lengths 2.24, 2.59, and 2.80 m). Figure 2-A and 2-B illustrate representative prepubertal and pubertal specimens, respectively.

All specimens were recovered in decomposition stages 1-3 according to Rowles et al. (2001) criteria and exhibited traumatic injuriesi consistent with vessel strike or fishing gear entanglement as the probable cause of mortality (Table 1).

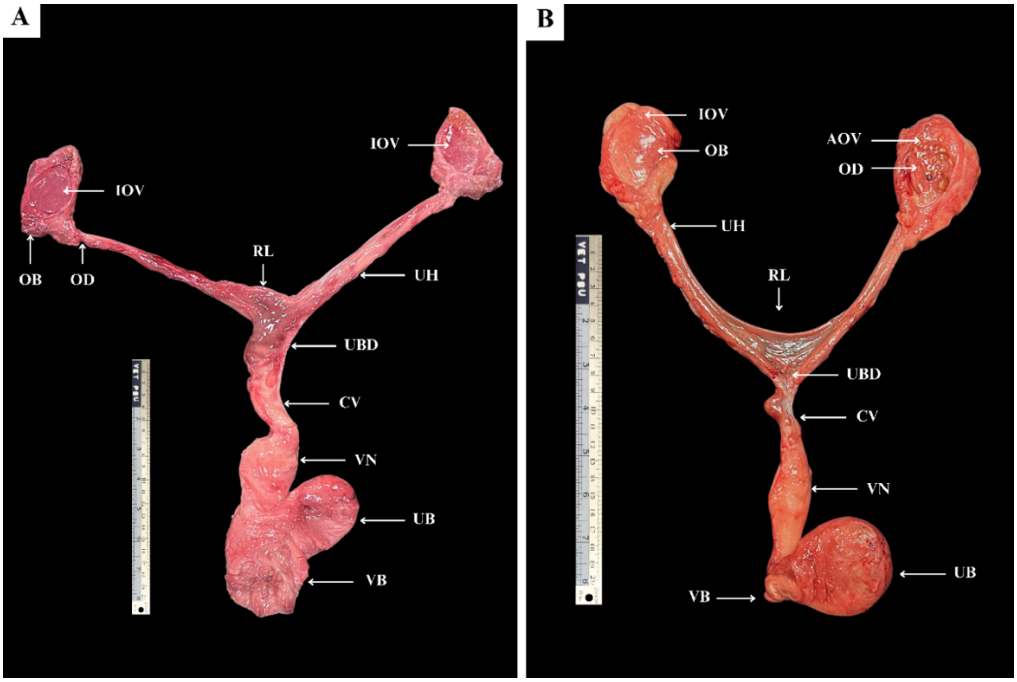


Figure 2 Comparative female reproductive tract dissection between A) prepubertal group (FPP001) and B) pubertal group (FPB003). Ventral view. Scale bar = 1 cm. Caption: ovarian bursa (OB), activated ovary (AOV), inactivated ovary (IOV), oviduct (OD), uterine horn (UH), round ligament (RL), uterine body (UBD), cervix (CV), vagina (VN), urinary bladder (UB), and vestibule (VB).

Table 1 Female dugong carcasses fundamental and identification data were ordered by body length from smallest to largest.

Group	Study ID	Body length (m)	Stage of carcass	Cause of death
Prepuberty	FPP002	1.85	Moderate	TI
Puberty	FPB003	2.24	Mild	TI
Prepuberty	FPP001	2.28	Mild	TI
Puberty	FPB001	2.59	Mild	TI
Puberty	FPB002	2.80	Mild	N/A

TI- Traumatic injury, N/A indicates not applicable

Gross Anatomical Characteristics

The ovaries, located at the terminal end of the reproductive tract and connected to the fimbriae of the oviducts, were oval in shape, positioned posterolateral to the kidneys, and fully enclosed within the ovarian bursa. Each ovary comprised a darker cortex and a lighter medulla separated by a transitional line. Developmental differences were evident between age groups: prepubertal ovaries displayed smooth cortical surfaces (Figure 3), whereas pubertal ovaries showed irregular surfaces with follicular development and corpora lutea indicative of cyclic ovarian function (Figure 4).

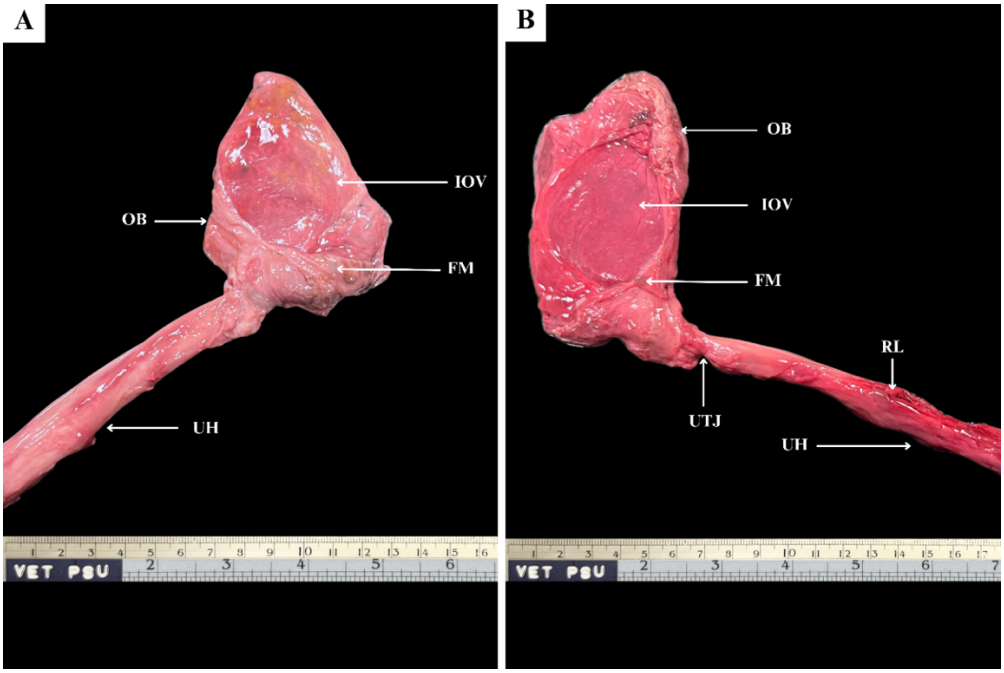
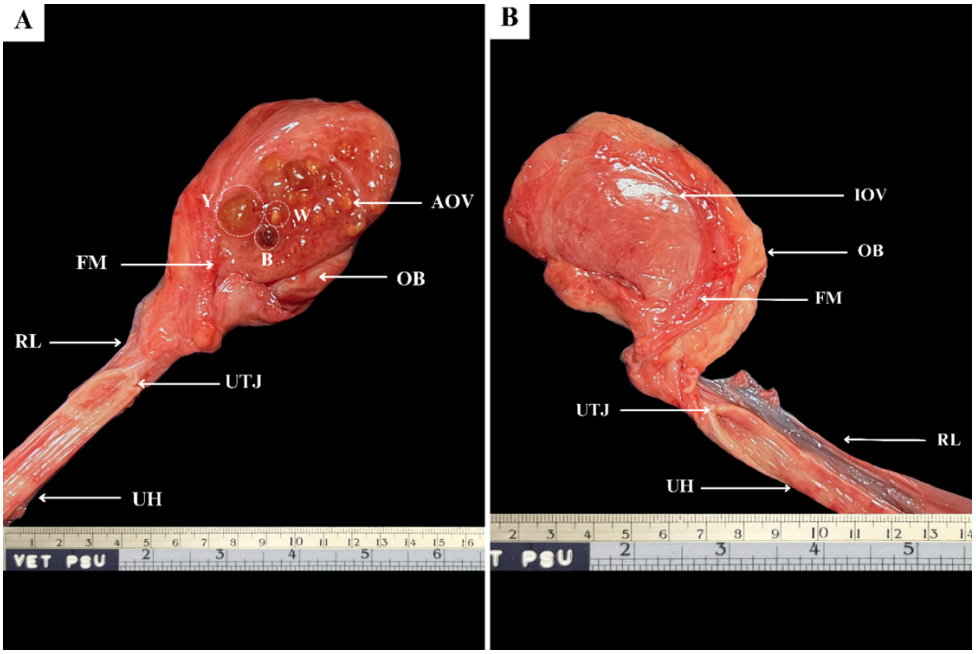


Figure 3 Close-up dissection of ovaries and oviducts of prepubertal group (FPP001). Left side (A) and right side (B). Ventral view. Prepubertal ovaries had smooth external surfaces with no additional structures on or within the cortex. The utero-tubal junction, marking the transition from the uterine horn to the isthmus. Scale bar = 1 cm. Caption: ovarian bursa (OB), inactivated ovary (IOV), fimbriae (FM), utero-tubal junction (UTJ), uterine horn (UH), round ligament (RL).



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Morphometric analysis demonstrated that ovarian dimensions did not differ significantly between prepubertal and pubertal groups, with detailed values presented in Table 2. The oviducts were short, slender, and slightly coiled tubular structures extending from the ovaries to the uterine horns. Each oviduct comprised anatomically distinct segments, including the utero-tubal junction, isthmus, ampulla, and the funnel-shaped infundibulum with fimbriae partially surrounding the ovarian pole. Despite their small size, the anatomical regions were clearly distinguishable during gross examination. Morphometric comparisons revealed no significant differences in oviduct dimensions between prepubertal and pubertal groups, as detailed in Table 2.

Table 2 Mean parameters of ovaries and oviduct. All morphometric data were presented as mean ± SEM. The P-values represented the comparison of parameter between each group.

Parameters (cm)	FPP	FPB
Ovaries		
Width	4.05 ± 0.31	4.59 ± 0.37
Length	5.92 ± 0.04	7.23 ± 0.51
Depth	0.57 ± 0.10	0.59 ± 0.10
Oviducts		
Width	0.77 ± 0.15	1.25 ± 0.61
Length	3.80 ± 2.39	4.40 ± 1.37

No superscript within the same row indicates no significantly different values ($P \geq 0.05$).

The uterus was bicornuate, with paired horns extending from the utero-tubal junctions and converging toward the uterine body in a characteristic V-shape (Rodrigues et al., 2008; Bezerra et al., 2018). Both horns exhibited comparable dimensions bilaterally and contained prominent longitudinal endometrial folds along the luminal surface. In pubertal specimens, distinct darkened areas consistent with placental scars were observed within the endometrium, providing clear evidence of prior implantation. These were unilateral in FPB002 and bilateral in FPB003, reflecting individual variation in reproductive history (Figure 5-A). Additionally, mucus accumulation within the luminal folds was present in pubertal samples, suggestive of functional uterine activity. The uterine body, positioned caudal to the horn bifurcation, was marked by the velum uteri, which projected ventrally to partially partition the horns. Its mucosal architecture mirrored that of the horns, with continuation of the longitudinal folds into the uterine lumen, creating a continuous pattern throughout the uterine segments (Figure 5-A). The cervix was distinguished by its thick-walled structure and firm consistency, positioned between the uterine body and the vagina. Internally, the endocervical lumen was narrow and lined with longitudinal mucosal folds, typically numbering six, though one pubertal specimen (FPB002) presented eight. The lumen was bounded by the internal and external os, both showing characteristic angular bends (Figure 5-B). Morphometric evaluation revealed that both the uterine horns and body, as well as the cervix, tended to be larger in pubertal individuals compared to prepubertal counterparts, particularly in overall length and lumen dimensions. Despite these apparent developmental trends, statistical analysis showed no significant differences between groups, with detailed measurements presented in Tables 3.

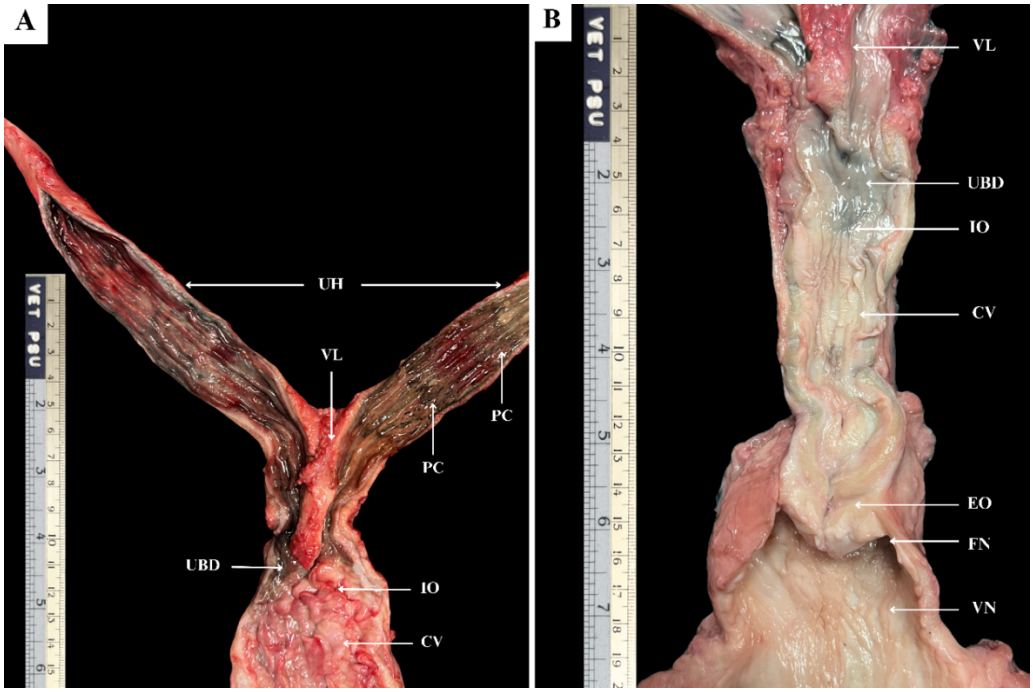

Figure 5 Close-up dissection of uterus (A, FPB002) and cervix (B, FPB001). The round ligament runs parallel to both uterine horns and converges at the velum. Placental scars were observed in FPB002 on one side. The endocervical lumen of the cervix was narrow, containing longitudinal mucosal folds, typically six, though eight folds. The lumen of the cervix has two openings: the internal os, adjacent to the uterine body, and the external os, adjacent to the vagina. Scale bar = 1 cm. Caption: uterine horn (UH), velum (VL), placental scar (PC), uterine body (UBD), internal os (IO), cervix (CV), external os (EO), fornix (FN), and vagina (VN).

Table 3 Mean parameters of ovaries and oviduct. All morphometric data were presented as mean ± SEM. The P-values represented the comparison of parameter between each group.

Parameters (cm)	FPP	FPB
Uterine horns		
Width	1.26 ± 0.06	2.20 ± 0.31
Length	14.70 ± 2.22	18.00 ± 1.50
Wall thickness	0.29 ± 0.10	0.35 ± 0.02
Lumen circumference	1.56 ± 0.13	2.30 ± 0.55
Uterine body		
Width	1.49 ± 0.15	2.91 ± 0.75
Length	3.95 ± 0.15	5.88 ± 1.26
Wall thickness	0.58 ± 0.22	0.29 ± 0.15
Lumen circumference	2.47 ± 0.95	3.37 ± 1.14
Cervix		
Width	2.47 ± 0.21	3.64 ± 0.47
Length	6.25 ± 0.34	10.08 ± 1.56
Wall thickness	1.64 ± 0.02	1.58 ± 0.01
Lumen circumference	3.96 ± 0.02	4.95 ± 0.62

The vagina extended from the cervix to the vestibule and displayed a progressive decrease in luminal diameter from cranial to caudal regions. Longitudinal mucosal folds were consistently observed, and the fornix, formed by cervical protrusion into the cranial vagina, was presented in all specimens. In pubertal individuals, mucus was frequently detected within the fornix and along the folds, indicating active secretory function (Figure 5-A). The vestibule, positioned

caudal to the clitoris and serving as a shared passage for the urinary and reproductive tracts, was clearly demarcated from the vulvar epithelium by a transitional line. Internally, it contained longitudinal folds and a prominent cingulum housing the urethral tubercle and external urethral orifice. The mucosa of the cingulum formed an annular thickening that narrowed the lumen before its junction with the vagina (Figure 6-A). The clitoris was proportionally large relative to the vaginal opening and positioned dorsally between the labia majora. It exhibited an irregular oval form with a distinct glans clitoridis at its free extremity. The vulva was externally defined by slightly raised labia majora and visible labial commissures, whereas labia minora were absent in all specimens (Figure 6). Morphometric assessment demonstrated significant increases in the widths of both the vagina and vestibule in pubertal specimens compared to prepubertal animals ($P < 0.05$), indicating that vaginal and vestibular widths serve as additional morphometric markers for maturity assessment. In contrast, other parameters of vaginal and vestibular measurements showed no group differences, and no hymenal structures were identified in any specimen. Clitoral dimensions did not differ significantly between developmental groups. Detailed values are presented in Table 4

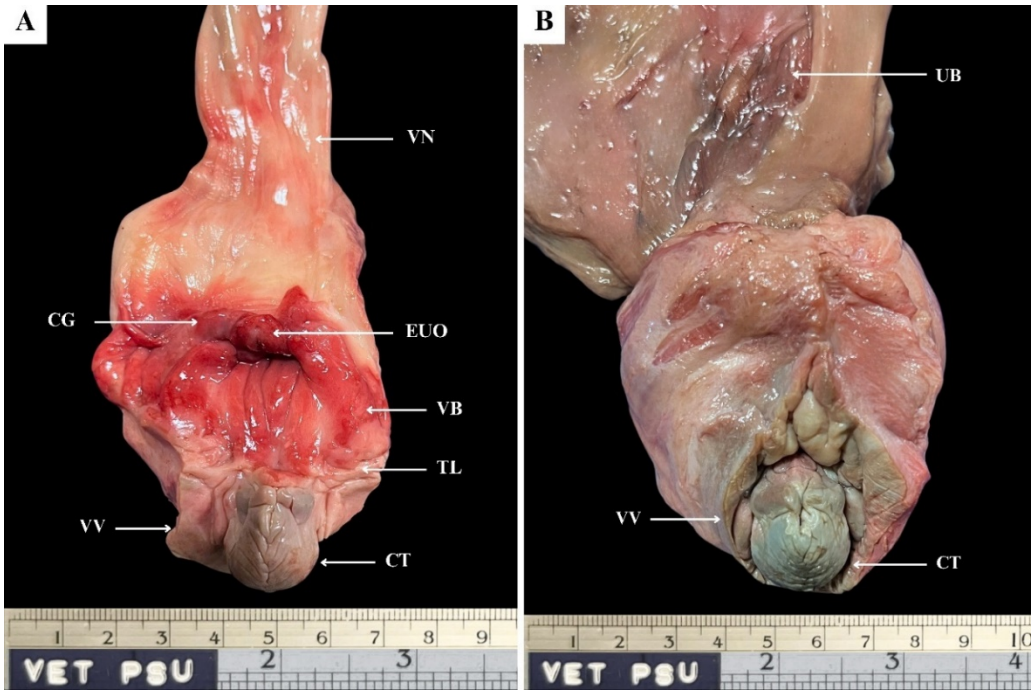

Figure 6 Close-up dissection of vagina and vestibule (A, FPB002) and external genitalia (B, FPP001). The labia were removed. Internal diameter of the vagina increased from the caudal portion to the cranial portion. The vestibule had a transitional line marks the boundary between the vulvar skin and the mucosa of the vestibule. A Cingulum contains the urethral tubercle and the opening of the external urethral orifice. The clitoris was relatively large compared to the vaginal opening. The clitoris has an irregular shape, typically tending toward an oval form, with a skin-like surface that varies in color from light to dark gray. The caudal part of the clitoris featured a small protuberance referred to as the glans clitoridis. Scale bar = 1 cm. Caption: vagina (VN), urinary bladder (UB), cingulum (CG), external urethral orifice (EUO), vestibule (VB), transitional line (TL), vulva (VV), and clitoris (CT).

Table 4 Mean parameters of vagina, vestibule and clitoris. All morphometric data were presented as mean ± SEM. The P-values represented the comparison of parameter between each group.

Parameters (cm)	FPP	FPB
Vagina		
Width	2.46 ± 0.80 [a]	7.58 ± 1.12 [b]
Length	6.67 ± 2.11	6.64 ± 1.21
Wall thickness	0.93 ± 0.27	1.06 ± 0.00
Lumen circumference	5.47 ± 1.06	9.32 ± 3.18
Vestibule		
Width	3.75 ± 0.07[a]	11.83 ± 1.15[b]
Length	4.21 ± 0.62	7.40 ± 1.19
Wall thickness	1.00 ± 0.04	1.76 ± 0.00
Lumen circumference	5.14 ± 0.33	14.25 ± 3.35
Clitoris		
Width	1.71 ± 0.00	1.67 ± 0.00
Length	2.69 ± 0.00	2.76 ± 0.00
Depth	1.47 ± 0.00	1.40 ± 0.00

Different superscripts within the same row indicate significantly different values ($P < 0.05$). No superscript within the same row indicates no significantly different values ($P \geq 0.05$).

Histological Characteristics

The ovary exhibited a typical mammalian organization with a dense tunica albuginea, a follicle-rich cortex, and a vascularized medulla. Follicles at different developmental stages were identified, progressing from primordial to tertiary stages (Figure 7). Clear developmental differences were evident between groups (Figure 8). Prepubertal ovaries (FPP) contained primordial, primary, and secondary follicles, with a single tertiary follicle identified in one specimen. Pubertal ovaries (FPB) lacked tertiary follicles but consistently exhibited luteal structures; corpus luteum was observed bilaterally in all specimens, while corpus hemorrhagicum and corpus albicans were present in one case. These findings, corresponding to grossly visible nodules, indicate active ovulation and luteal transformation in pubertal females, in contrast to the predominance of pre-antral follicles in prepubertal animals (Table 5). These ovarian features provide primary morphological criteria supporting the distinction between prepubertal and pubertal individuals. The oviduct exhibited a consistent layered organization in both maturity groups, characterized by a ciliated epithelium supported by connective tissue, smooth muscle, and a vascularized serosa. The overall architecture was conserved, and no maturity-related differences were observed (Figure 9).

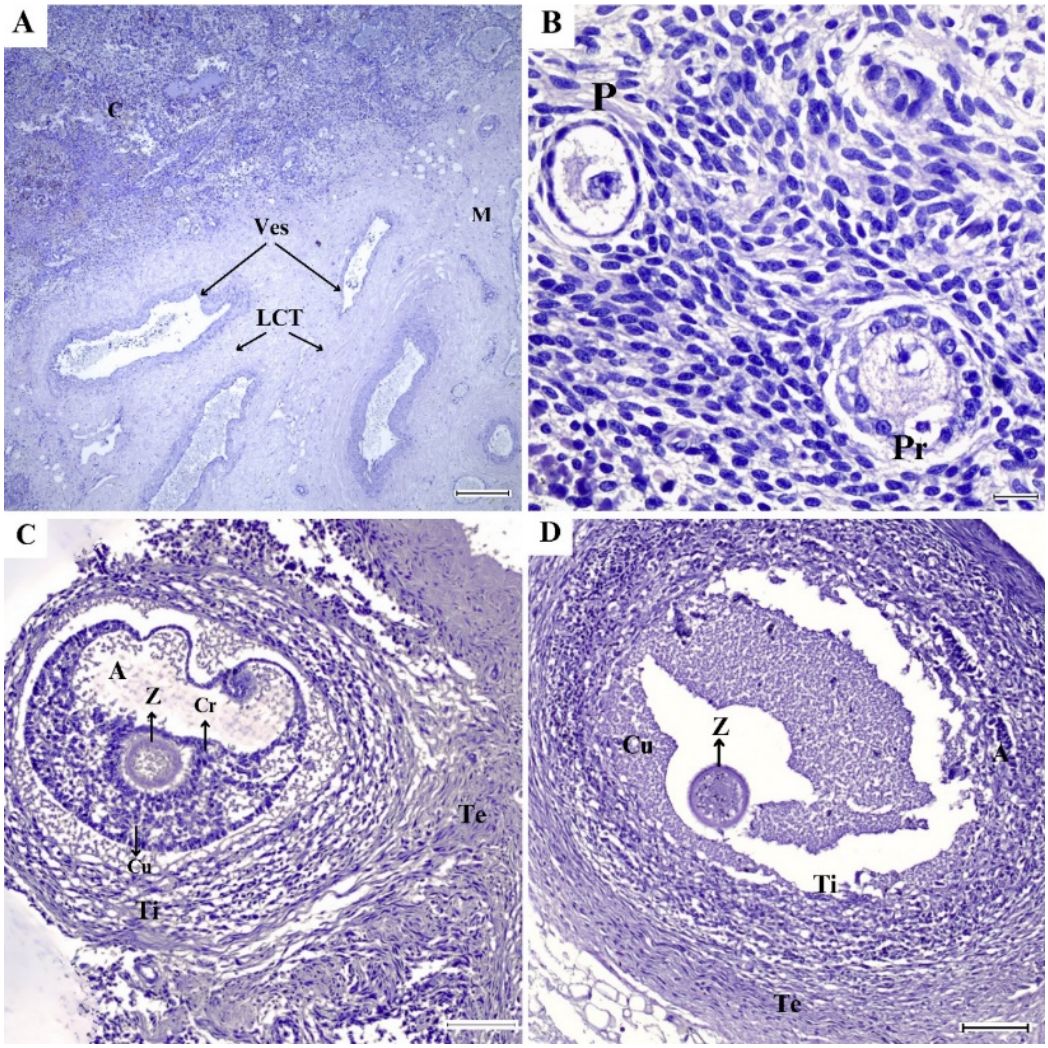

Figure 7 A histological study of the ovary was performed by H&E staining. A) Ovary (FPB002), 40x, divided into two parts: ovarian cortex composed of various stages of follicle, and ovarian medulla, composed of loose connective and the vessels. Scale bar = 240 µm. B) Primordial and primary follicles (FPP002), 400x. The primordial follicle was composed of an oocyte, surrounded by by a single squamous epithelium of follicular cells. The primary follicle has a distinct single layer of cuboidal-shaped follicular cells. Scale bar = 20 µm C) Secondary follicle (FPB002), 100x, presented the small size of antrum and oocyte covered by zona pellucida. The follicle was surrounded by cumulus cells (corona radiata and cumulus oophorus), theca interna, and theca externa. Scale bar = 90 µm. D) Tertiary follicle (FPP002), 100x, was surrounded by theca externa and theca interna and presented the same character as the secondary follicle but represented a large amount of the antrum, more than half the area of the follicle. Scale bar = 90 µm. Caption: antrum (A), ovarian cortex (C), corona radiata (Cr), cumulus oophorus (Cu), loose connective tissue (LCT), ovarian medulla (M), Primordial follicle (P), primary follicle (Pr), theca externa (Te), theca interna (Ti), vessels (Ves) and zona pellucida (Z).

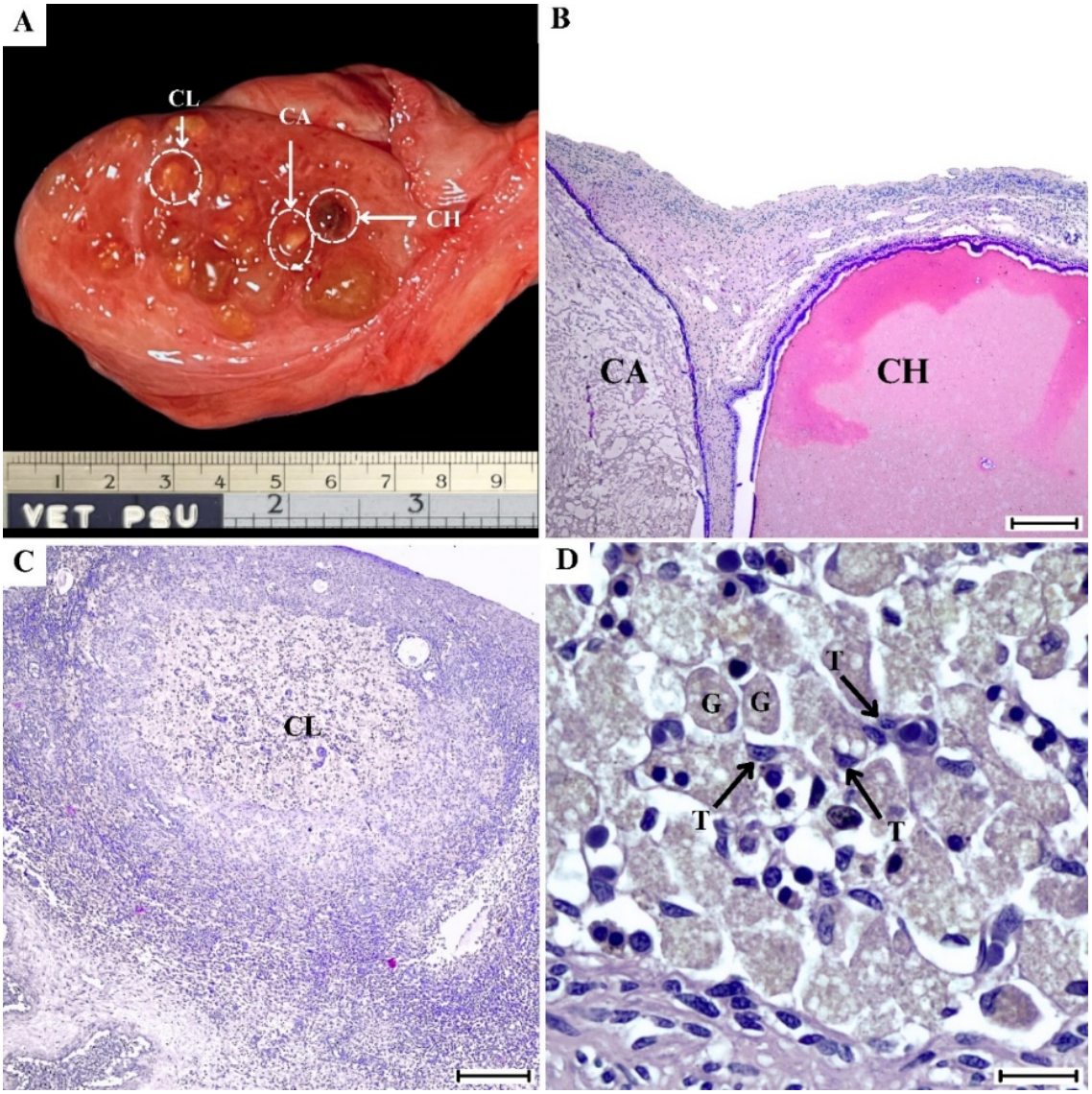

Figure 8 A) Left sided of ovary in the pubertal group (FPB003). A histological study of the ovary was performed by H&E staining. B) Corpus hemorrhagicum and corpus albicans (FPB003), 100x. The corpus hemorrhagicum presented large blood filled in the antrum. The corpus albicans was connective tissue scar. Scale bar = 90 µm. C) Corpus luteum (FPB002), 100x, was composed of central granulosa lutein cells and theca lutein cells. Scale bar = 90 µm. D) Close-up corpus luteum (FPB002), 400x. The larger central polygonal cells, granulosa lutein cells, were surrounded by smaller cells with condensed and darker-stained nuclei, theca lutein cells. Scale bar = 20 µm. Caption: corpus luteum (CL), corpus albicans (CA), corpus hemorrhagicum (CH), granulosa lutein cells (G), and theca lutein cells (T).

Table 5 The occurrence of various structures on the ovary found in female dugongs were ordered by body length from smallest to largest

Group	Study ID	Body length (m)	P		Pr		Sf		Tf		CH		CL		CA	
			L	R	L	R	L	R	L	R	L	R	L	R	L	R
Prepuberty	FPP002	1.85	F	F	F	F	NF	F	F	NF	NF	NF	NF	NF	NF	NF
Puberty	FPB003	2.24	F	F	F	F	F	F	NF	NF	F	NF	F	NF	F	NF
Prepuberty	FPP001	2.28	F	F	F	F	F	NF	NF	NF	NF	NF	NF	NF	NF	NF
Puberty	FPB001	2.59	F	F	F	F	F	F	NF	NF	NF	NF	F	NF	NF	NF
Puberty	FPB002	2.80	F	F	F	F	F	F	NF	NF	NF	NF	F	NF	NF	NF

L: Left side of the ovary, R: Right side of the ovary, F: Found, NF: Not found, P: Primordial follicle, Pr: Primary follicle, Sf: Secondary follicle, Tf: Tertiary follicle, CH: Corpus hemorrhagicum, CL: Corpus luteum, and CA: Corpus albicans.

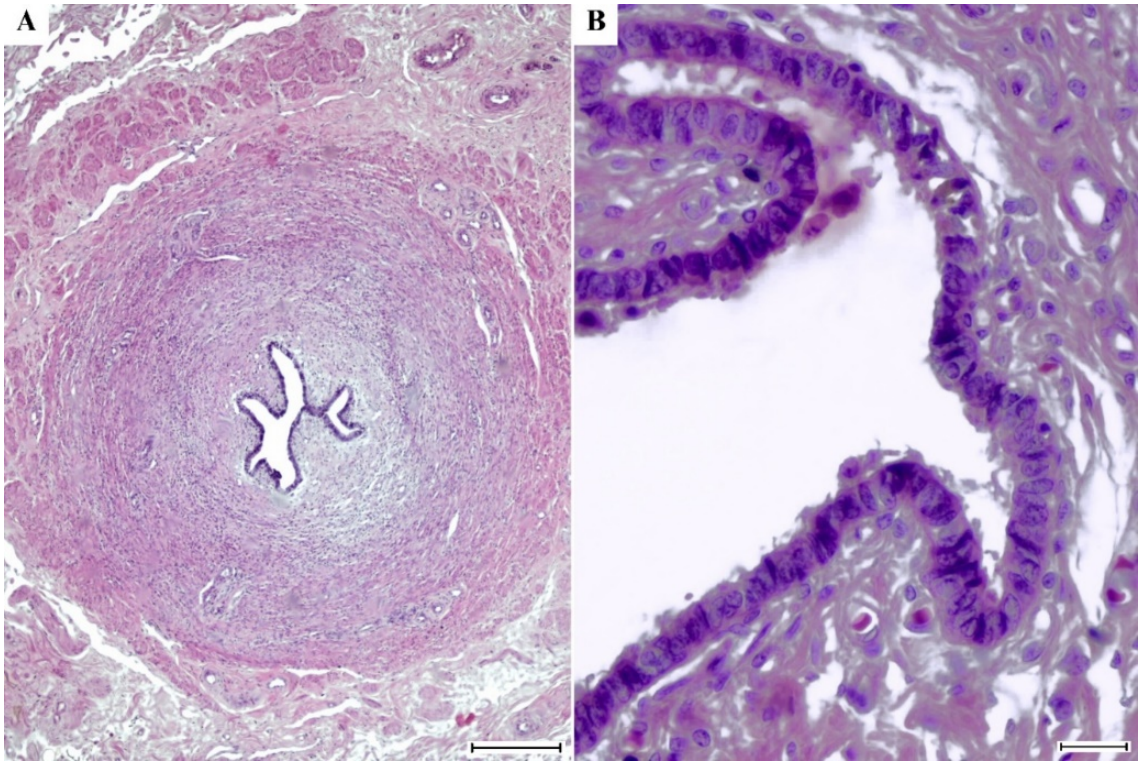

Figure 9 A histological study of the oviduct (isthmus) was performed by H&E staining (FPB001). A) Oviduct, 40x, was lined by a ciliated simple low columnar epithelium. The lamina propria consisted of dense connective tissue. The tunica muscularis consisted of an inner circular layer and an outer longitudinal layer of smooth muscle. The serosa was composed of loose connective tissue. Scale bar = 240 µm. B) Close-up the layers of ciliated simple low columnar epithelium, 400x. Scale bar = 20 µm.

The uterine horns, body, and cervix exhibited comparable histological features across both maturity groups. The uterine horns displayed a layered organization, with numerous tubular glands distributed throughout the submucosa, supported by dense connective tissue, smooth muscle layers, and an outer vascularized serosa, with no maturity-related differences observed (Figure 10). The uterine body shared the same general organization but showed denser stromal composition, a higher abundance of glands, and a markedly thickened velum

region that provided greater stromal support, again without group-related variation (Figure 11). The cervix showed the most complex morphology within the uterine tract. It was characterized by extensive mucosal folding and abundant glandular secretory elements. The highly vascularized stroma was supported by a robust tunica muscularis, particularly in the outer longitudinal layer. (Figure 12).

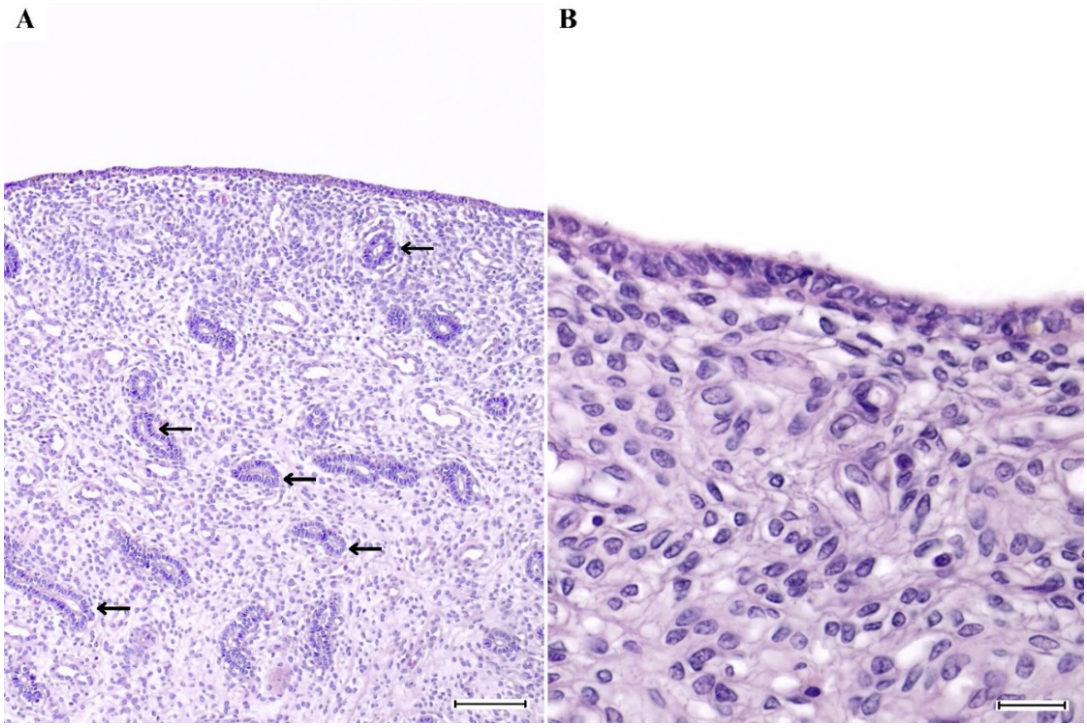

Figure 10 A histological study of the uterine horn was performed by H&E staining (FPB001). A) Uterine horn, 100x, was lined by a non-ciliated simple low columnar epithelium. The propria submucosa contained uterine glands, and dense connective tissue. The uterine glands were lined with ciliated columnar epithelium distributed throughout the submucosa, supported by dense connective tissue, smooth muscle layers, and an outer vascularized serosa. Scale bar = 90 µm. B) Close-up the layers of non-ciliated simple low columnar epithelium, 400x. Scale bar = 20 µm. Caption: uterine gland (black arrow).

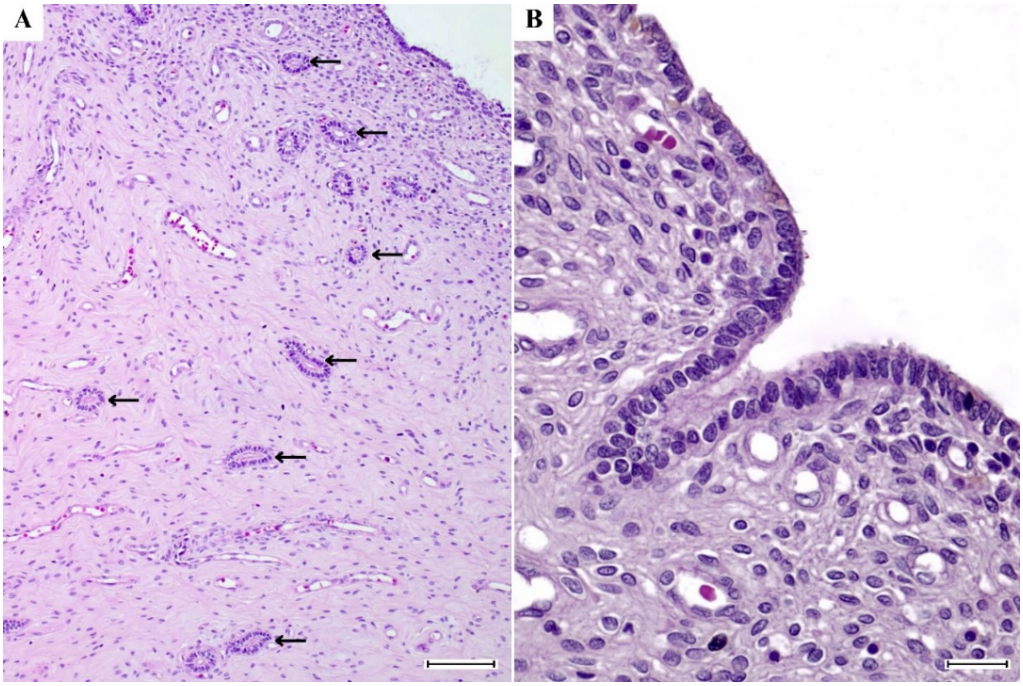

Figure 11 A histological study of the uterine body was performed by H&E staining (FPB001). A) Uterine body, 40x, was lined by non-ciliated low simple columnar epithelium. The propria-submucosa was composed of dense connective tissue, vessels and numerous uterine glands. Scale bar = 240 µm. B) Close-up the layers of non-ciliated low simple columnar epithelium, 400x. Scale bar = 20 µm. Caption: uterine gland (black arrow).

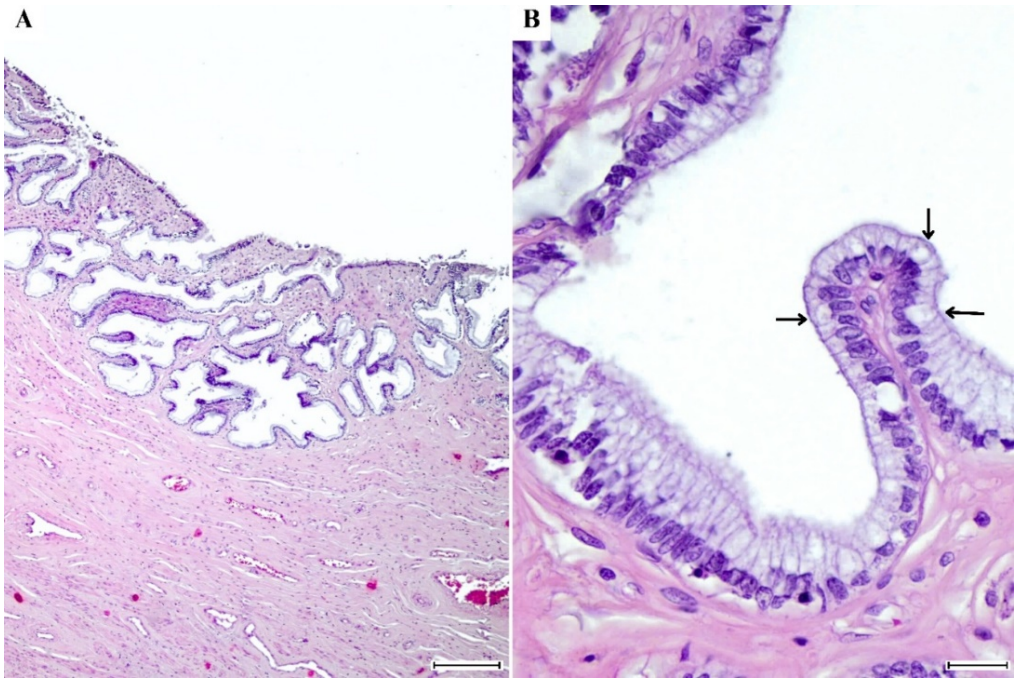

Figure 12 A histological study of the cervix was performed by H&E staining (FPB001). A) Cervix 40x, was lined by ciliated simple columnar epithelium with goblet cells. The mucosa appeared many primary folds, some of which become subdivided into secondary and tertiary folds. The lamina propria was composed of dense connective tissues and highly vascularized. Scale bar = 240 µm. B) Close-up the layers of ciliated simple columnar epithelium with goblet cells, 400x. Scale bar = 20 µm. Caption: goblet cells (black arrow).

The vagina exhibited a columnar epithelial lining supported by vascular connective tissue and mucosal folds, sharing structural similarities with the cervix (Figure 13). The vestibule featured a multilayered epithelium overlying dense irregular connective tissue and a distinct three-layered muscular wall (Figure 14). In contrast, the vulva was lined by a keratinized stratified squamous epithelium, akin to skin, supported by dense connective tissue, though it lacked major or minor vestibular glands (Figure 15). The clitoris comprised erectile tissue within the corpora cavernosa, encased by a fibrous tunica albuginea and covered by keratinized squamous epithelium with a prominent stratum corneum (Figure 16). Meissner corpuscles were noted near the epithelial surface, while sebaceous and sweat glands were absent. No maturity-related differences were observed in any of these structures. Histological characteristics further reinforce the anatomical criteria defining reproductive maturity.

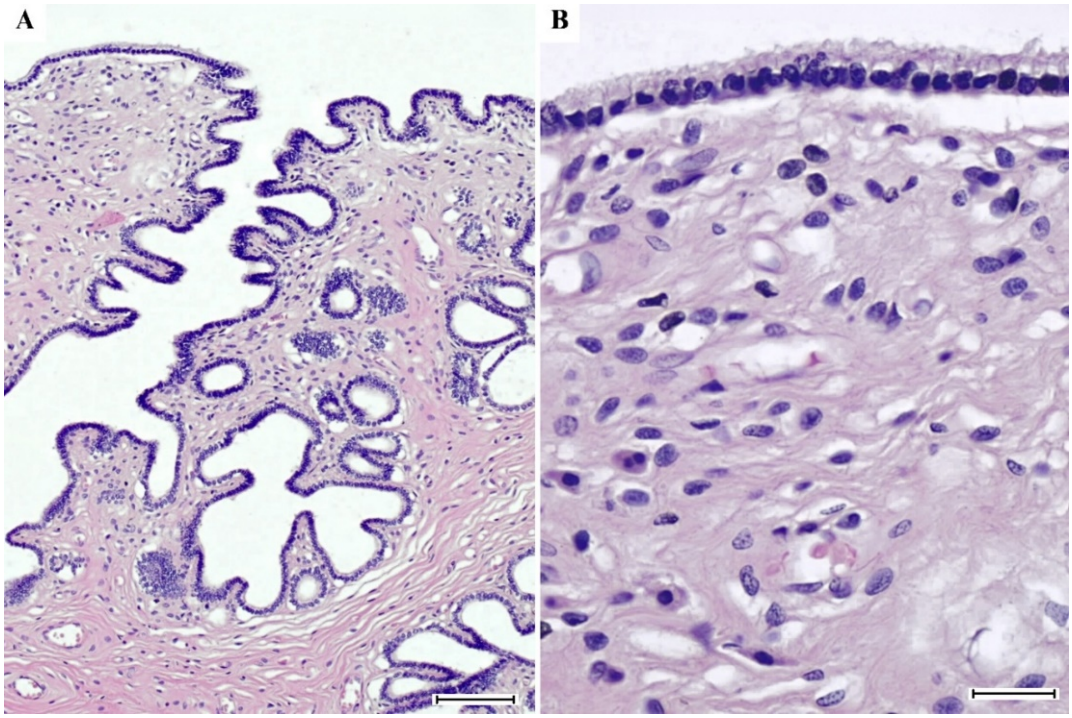

Figure 13 A histological study of the vagina was performed by H&E staining (FPB002). A) Vagina 40x, was lined by ciliated simple columnar epithelium. The propria-submucosa elevated into primary, secondary and tertiary folds. Scale bar = 240 µm. B) Close up the layers ciliated simple columnar epithelium, 400x. Scale bar = 20 µm.

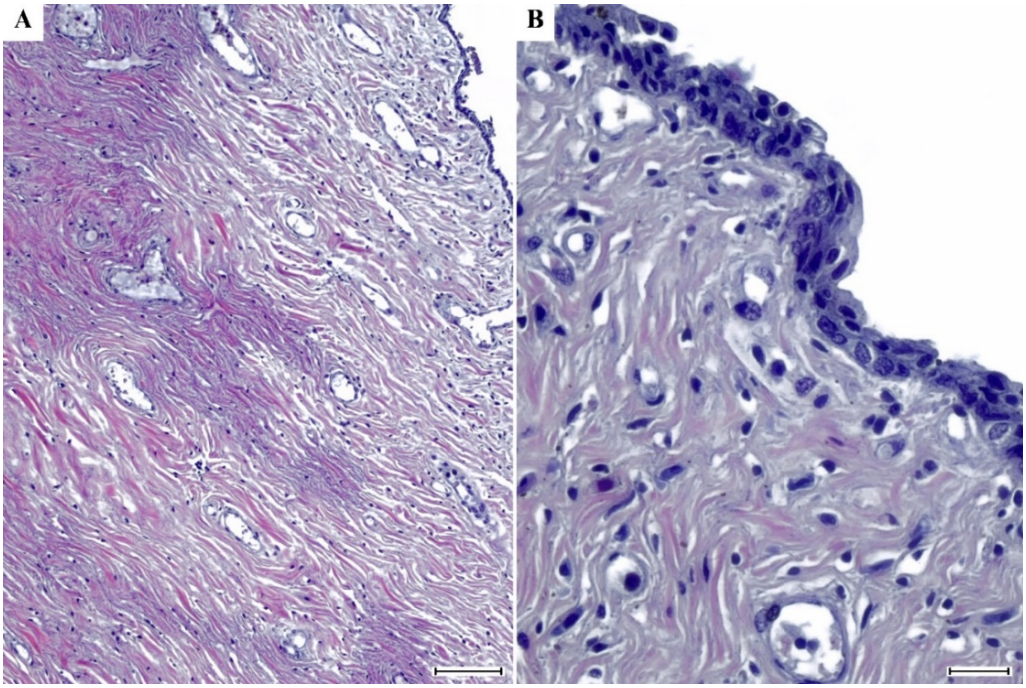

Figure 14 A histological study of vestibule was performed by H&E staining (FPP001). A) Vestibule 40x, was lined by the few layers of polyhedral cells. The propria-submucosa was composed of dense irregular connective tissue. Scale bar = 240 µm. B) Close up the layers of polyhedral cells, 100x. Scale bar = 90 µm.

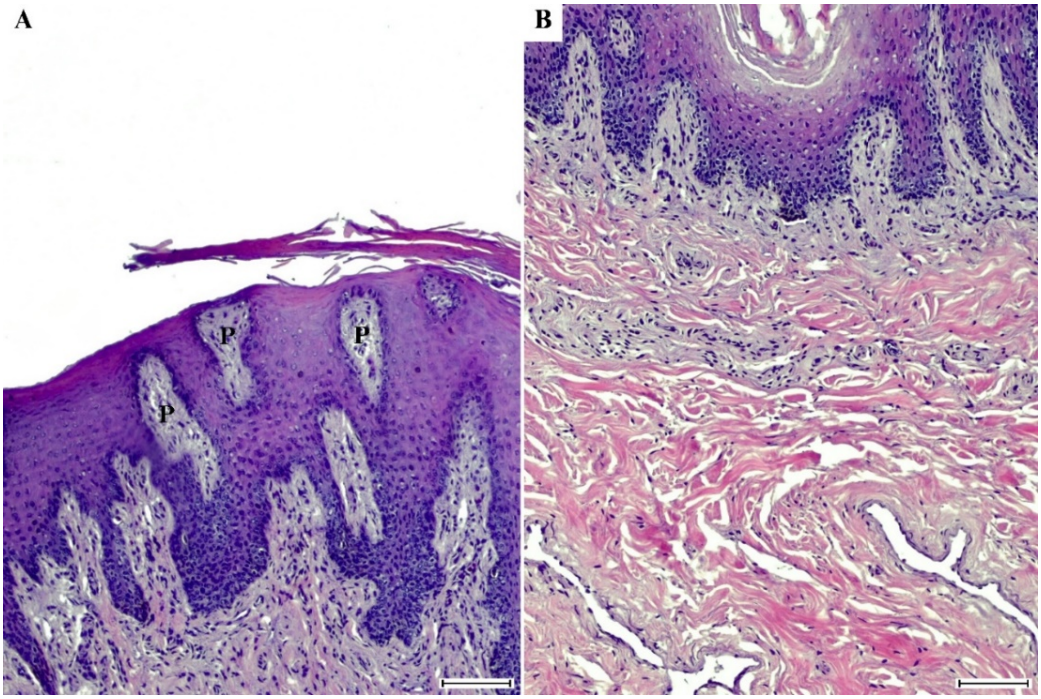

Figure 15 A histological study of the vulva was performed by H&E staining (FPB003). A) Vulva, 100x, was lined by skin-like epithelium, keratinized stratified squamous epithelium. The propria-submucosa protruded to the epithelial layer and formed dermal papillae. B) The propria-submucosa, 100x, was composed of dense irregular connective tissue. Scale bar = 90 µm. Caption: dermal papillae (P).

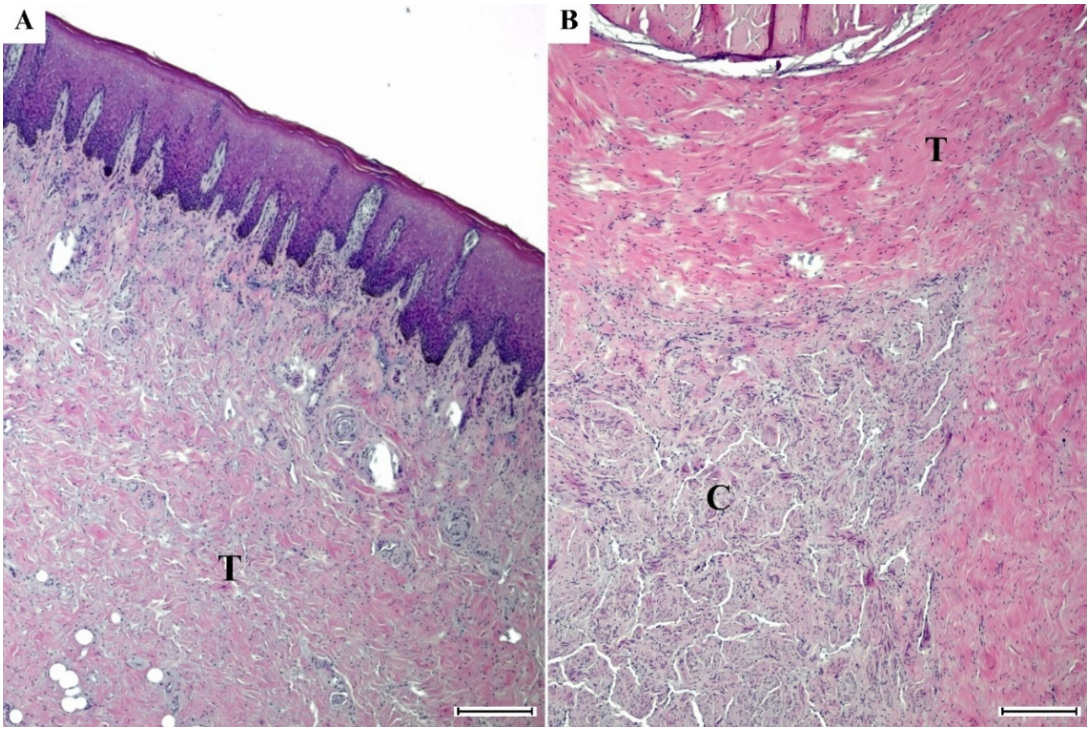

Figure 16 A histological study of the clitoris was performed by H&E staining (FPP001). A) Tunica albuginea, 40x, was lined with keratinized stratified squamous epithelium. B) Corpora cavernosa clitoridis, 40x, composed of abundant strands of smooth muscle embedded in connective tissue. The corpus cavernosum was surrounded by the tunica albuginea. Scale bar = 240 μm. Caption: tunica albuginea (T), corpora cavernosa clitoridis (C).

DISCUSSION

This study presents the first comprehensive characterization of female reproductive biology in Thai dugongs, directly addressing the research aims of: (1) characterizing biometric, anatomical, and histological features, (2) establishing criteria to distinguish prepubertal from pubertal individuals, and (3) providing practical assessment tools for conservation. By distinguishing prepubertal from pubertal groups, the findings establish baseline parameters essential for assessing sexual maturity and reproductive capacity. Clear morphological and histological differences between groups offer practical tools for evaluating reproductive status in wild populations while advancing knowledge of dugong reproductive biology in Southeast Asian waters. Anatomical differences, particularly in ovarian structures and vaginal-vestibular morphometry, emerged as robust indicators of reproductive maturity. Although based on a limited sample, the examined specimens represented nearly half of all documented female dugong mortalities in Thai waters during the study period, emphasizing the rarity of such opportunities and the urgent need for systematic reproductive monitoring to support conservation of this Vulnerable species.

Body length alone could not reliably determine female maturity due to overlapping size ranges between maturity groups. Ovarian structures provided more consistent maturity indicators. Specifically, corpora hemorrhagica, corpora lutea, and corpora albicans served as reliable markers. These findings align with previous studies on dugongs and other marine mammals (Palmer et al., 2022). This emphasizes the importance of incorporating anatomical and histological criteria into maturity assessments. The present findings indicate that individuals measuring 2.24–2.28 m exhibited ovarian features that were difficult to categorize as either

prepubertal or pubertal, suggesting a transitional phase of puberty influenced by factors such as genetic background, nutritional condition, and environmental variability (Shine, 1988; Bronson, 2001; Gergely and Tökölyi, 2023). In contrast, the individual at 2.59 m showed unequivocal evidence of prior ovulation, supporting this size as a reliable threshold for maturity. In line with observations in other mammalian species, the initiation of puberty is not solely dependent on linear growth but rather on attaining adequate body size and sufficient energetic reserves. Furthermore, the ability to visualize these structures using ultrasonography, as demonstrated in cetaceans (Brook, 2001), may offer a valuable non-invasive approach for evaluating reproductive status in free-ranging dugong populations. Importantly, the significant increase in vaginal and vestibular widths in mature specimens represents a novel morphometric indicator. Unlike ovarian assessment requiring necropsy, external genital measurements could be obtained from live-stranded individuals. This provides a practical, non-invasive tool for assessing reproductive status in the field. Compared with North Queensland dugongs, where females are considered mature at body lengths of more than 2.5 m. and immature at less than 2.2 m. (Marsh et al., 1984b), Thai dugongs appear to attain maturity across a broader size range, with pubertal individuals observed from 2.24 meters and prepubertal individuals as small as 1.85 m. These differences may reflect genetic divergence among populations. Genetic analyses have shown that Thai dugongs form distinct clades from Australian populations, with unique haplotypes in the Andaman Sea (Poommouang et al., 2021). Supporting this, morphometric studies revealed larger cranial dimensions in Thai dugongs compared with those from the Gulf of Thailand (Nganvongpanit et al., 2017), suggesting localized adaptations that may contribute to reproductive variation across populations.

The presence of multiple corpora lutea (CL) and corpora hemorrhagica (CH) was observed, consistent with earlier reports in dugongs and manatees, despite their predominantly uniparous reproductive strategy (Marsh et al., 1984a; Rodrigues et al., 2008). Similar patterns occur in elephants, where non-ovulatory follicles undergo luteinization to form accessory CLs during each estrous cycle (Hermes et al., 2000; Hildebrandt et al., 2000). These structures play a paracrine or autocrine role in supporting subsequent ovulation rather than directly influencing systemic progesterone concentrations (Hildebrandt et al., 2011). However, there are documented instances of tertiary follicle development occurring during the mini-puberty event in various mammalian species. This event is a transitional phase characterized by significant shifts in gonadotropin hormone levels, which transiently allow for increased follicular maturation (Chester et al., 2022; Devillers et al., 2022). This differs from the mature, cycling ovary of a reproductively competent individual, where a secondary follicle would typically not progress to a tertiary follicle unless it is destined to become a preovulatory follicle. This is in sharp contrast to the pubertal group in our study, where we were able to observe structures indicative of complete ovulation. Some individuals showed corpora lutea restricted to one ovary while the contralateral ovary remained inactive. Similar unilateral ovarian activity has been documented in elephants (Hildebrandt et al., 2011) and may represent asynchronous ovarian cycling in large mammals. Combined with the absence of seasonal breeding evidence, these findings indicate that Thai dugongs may not follow the seasonal reproductive patterns documented in Australian populations. These possibly reflect the minimal variation in daylight hours in tropical latitudes (Marsh et al., 1984; Boyd et al., 1999). Moreover, the concurrent occurrence of pregnant females nursing calves further supports the likelihood of post-partum ovulation in this population, highlighting a flexible reproductive strategy that may enhance reproductive output under favourable conditions. The oviduct in dugongs exhibited similar characteristics to previous findings in other sirenians (Marsh, 1984a; Hill, 1945, Rodrigues et al., 2008). Distinguishing the three sections of the oviduct, infundibulum, ampulla, and isthmus based on gross anatomical features were challenging due to their external similarities. Histological examination of the oviduct in dugongs revealed a similar

structure to the other domestic animals (Aughey and Frye, 2001; Eurell and Frappier, 2013). The three parts of the oviduct did not be distinguished in our study. The study in sirenias still lacked.

The uterus was observed to have features consistent with previous studies on sirenians, including a short lumen of the uterine body and longitudinal folds (Hill, 1945; Marsh et al., 1984a; Marmontel et al., 1992; Rodrigues et al., 2008). The longitudinal folds play a crucial role in increasing the uterine diameter, thereby facilitating fetal development and growth during pregnancy (Rodrigues et al., 2008). The placental scars observed in our study share similarities with findings in previous research on dugongs. These scars are characterized by massive deposits of hemosiderin, and most are believed to persist for life. The width of a placental scar depends on both its age and the individual's reproductive activity level (Marsh et al., 1984a). Placental scars provided the first histological evidence of reproductive history in Thai dugongs. We identified unilateral scars in specimen FPB002 and bilateral scars in FPB003. These findings confirm successful breeding activity and indicate individual variation in reproductive experience. Bilateral scarring suggests either multiple pregnancies or long-term scar retention. The presence of such reproductive markers supports evidence of population viability (Poommouang et al., 2021) and demonstrates that reproductively active females maintain cyclic ovarian function despite persistent threats. Histological examination of the uterus in dugongs revealed a thin layer of endometrium and branch tubular uterine gland to the previous study in dugongs and manatees (Marsh et al., 1984a; Bezerra et al., 2018). Uterine glands were poorly developed in prepubertal dugongs with inactive ovaries but proliferated in pubertal dugongs with tertiary follicles in the ovaries (Marsh et al., 1984a). This event indicated by sufficient estrogen secretion from the developing follicle, plays an important role in uterine gland proliferation, or uterine adenogenesis, similar to the physiology of other mammals (Kelleher et al., 2019). The cervix, based on its various features, closely resembles findings from previous studies on dugongs and the Amazonian manatee (Hill, 1945; Marsh et al., 1984a). The longitudinal endocervical folds of the lumen are similar to those observed in horses. In sirenians, these folds provide mechanical protection, shielding the uterus from external pressures and potentially harmful substances, which could otherwise cause infection or damage (Hill, 1945; Marmontel et al., 1992).

A transitional line was observed separating the vulva from the vestibule, and a distinct cingulum separating the vestibule from the vagina that have not previously been described in dugong studies. These structures suggest that the vestibule functions not only as a passageway but also as a barrier that helps maintain the appropriate separation and direction of reproductive and urinary fluids, thereby reducing the risk of contamination during copulation (Marsh et al., 1984a; Marmontel et al., 1992). Although these characteristics have not been reported in dugongs before, similar structures have been described in the Amazonian manatee (Rodrigues et al., 2008), indicating potential shared anatomical adaptations within Sirenia. From the measurements, both vaginal and vestibular widths were greater in pubertal than in prepubertal individuals, reflecting overall developmental maturation. In some pubertal females, particularly those in the parous stage, recent parturition or ongoing birth may further contribute to the enlargement of vaginal dimensions. Conversely, if pregnancy occurred, fetal pressure on the reproductive tract could potentially reduce vestibular length relative to its normal size (Rodrigues et al., 2008).

These findings emphasize the need for region-specific reproductive benchmarks to improve maturity classification, fecundity estimates, and demographic modeling in dugongs. Histological and morphological criteria established here provide reliable diagnostic tools for necropsy assessments and form a foundation for developing non-invasive monitoring approaches. The identification of unique anatomical traits and evidence of non-seasonal reproduction further highlight the value of integrating hormonal, genetic, and ecological perspectives to clarify reproductive strategies across the species' range.

The reproductive markers identified in this study have direct applications for dugong management in Thailand. The ability to distinguish maturity stages using ovarian luteal structures, placental scars, and external genital morphometrics enables practical assessments during necropsy, stranding evaluations, and rehabilitation decisions. These maturity indicators enhance demographic assessments and support identification of priority habitats for reproductively active females, thereby strengthening region-specific conservation planning. Despite these insights, the study was limited by the small number of suitable female carcasses available, as female stranding events are relatively uncommon in Thailand and many specimens are in poor condition for reproductive examination. Nonetheless, this work provides one of the first detailed anatomical and histological characterizations of female dugongs in the region, establishing essential baseline data. Continued multi-year monitoring and expanded sampling efforts will be necessary to validate these preliminary benchmarks and refine reproductive maturity assessments for conservation. Future research should incorporate endocrine profiling and apply imaging techniques to validate reproductive markers in live animals. Comparative studies across populations are also warranted to determine whether observed differences reflect genetic divergence, environmental influences, or both, thereby informing management strategies for dugongs in Thailand and the wider Indo-Pacific.

CONCLUSIONS

This study provides the first comprehensive reproductive baseline for Thai female dugongs, highlighting population-specific variation in sexual maturity. Ovarian luteal structures and external genital morphometry emerged as reliable maturity indicators, whereas body length alone was insufficient. Compared with Australian populations, Thai dugongs exhibited a broader maturity size range, suggesting possible genetic divergence and the need for region-specific conservation strategies. Among the examined parameters, ovarian features proved the most robust criterion, while a body length of approximately 2.6 m may serve as a practical benchmark for reproductive maturity, with smaller sizes cautiously interpreted as transitional states. Evidence of repeated ovulation and non-seasonal breeding further indicates population viability despite ongoing threats. Collectively, these morphological and histological benchmarks provide valuable tools for field assessments and demographic modeling, strengthening evidence-based conservation planning for this vulnerable Indo-Pacific species.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Chayanis Daochai: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Writing – review & editing (equal); Supervision (equal); Investigation (supporting); Methodology (supporting).
Piyarat Khumraksa: Resources (lead); Writing – original draft (supporting); Investigation (equal).
Pontakorn Sririrak: Data curation (equal); Writing – original draft (equal); Investigation (equal); Methodology (equal).
Chanoknan Suwannarit: Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal).
Norrapat Sopipan: Visualization; Formal analysis (equal); Writing – original draft (equal); Investigation (equal); Methodology (equal).
Tatsawan Suttiboon: Resources (equal); Investigation (supporting).
Santi Ninwat: Resources (supporting); Investigation (supporting).
Pokchon Khirilak: Investigation (supporting); Methodology (supporting).
Narong Tiptanavattana: Conceptualization (lead); Writing – review & editing (equal); Data curation (lead); Project administration (equal); Supervision (equal)

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