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Distribution and morphology of macrophages in the epithelium and stroma of each region of the mouse epididymis

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Running Title: Macrophages in the mouse epididymis

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Abstract

Purpose: This study aimed to clarify the regional distribution and morphology of macrophages in the epididymal epithelium and stroma and to examine the morphological relationship between epithelial macrophages and basal cells.

Materials and Methods: Three 13-week-old male C57BL/6 mice (*Mus musculus* Linnaeus, 1758) were used. The epididymis was analyzed by immunohistochemical staining to compare the morphology of macrophages and basal cells and to assess their distribution in the epithelium and stroma.

Results: In the initial segment, both epithelial macrophages and basal cells exhibited projections extending into the epididymal duct lumen. In the caput, basal cells were present along the basal layer without extending into the lumen, whereas a small number of epithelial macrophages extended into the lumen. In both the corpus and cauda, epithelial macrophages and basal cells exhibited a flattened morphology along the basal layer, with no projections extending into the lumen. Stromal macrophages were rounded in all regions, and no morphological differences among the regions. Regarding macrophage distribution, the proportion of epithelial macrophages was highest in the initial segment, while the proportion of stromal macrophages increased toward the cauda.

Conclusions: In mouse epididymides, epithelial macrophages possessed region-specific morphologies and shared similarities with basal cells. In contrast, stromal morphology showed no regional differences. The

proportion of epithelial macrophages was highest in the initial segment and decreased toward the cauda. These findings suggest that macrophage distribution is associated with the region-specific function of the epididymis.

Keywords: epididymis; epithelial cells; immunohistochemistry; macrophages; mice, inbred c57bl

Mini-abstract: Epithelial macrophages in the mouse epididymis display region-specific morphologies resembling basal cells, and their proportion decreases from the initial segment toward the cauda.

1. Introduction

The epididymis consists of a single elongated tube (the epididymal duct) that is markedly coiled and folded, along with stromal tissue. It is divided into four segments based on the morphological differences in the epithelial cells lining the lumen: the initial segment (IS), caput, corpus, and cauda.

The primary functions of the epididymis are sperm maturation, storage, and transportation. The IS of the epididymis receives immature sperm from the testis and induces initial changes that confer motility and fertilization capacity by actively absorbing secretions from the testis. The caput and corpus of the epididymis secrete substances involved in sperm maturation, whereas the cauda absorbs and processes excess secretions and stores sperm (Hermo and Robaire 2002; Robaire et al. 2006).

Furthermore, the epididymis plays a key role in sperm maturation and supports sperm development without triggering harmful immune responses, even though sperm emerge long after the establishment of self-tolerance and immune system maturation (Fijak and Meinhardt 2006). The epididymis is thought to form a subset of immune cells optimized to address the unique immunological challenges arising in the male reproductive tract (Battistone et al. 2020). Immune cells in the epididymis have attracted increasing research interest in recent years, particularly macrophages (MPs). MPs are specialized phagocytic cells found in all organs that maintain tissue integrity, remove debris, and initiate innate immunity following infection or tissue injury (Gordon and Taylor 2005).

The morphology and functions of epididymal MPs vary by region. The IS has a higher proportion of CX3CR1+ MPs, which capture and process antigens, than other regions (Battistone et al. 2020). In the IS, caput, and corpus regions, both interstitial and epithelial MPs internalize and process circulating antigens, whereas in the cauda, this function is restricted to interstitial MPs (Battistone et al. 2020). $CD64^{+}$ MPs and $CD64^{+}MHCII^{+}$ MPs are also abundant in the IS, with their number decreasing toward the cauda. Conversely, $CD64^{+}MHCII^{+}$ MPs, $CD64^{-}MHCII^{+}$ MPs, and $CD64^{-}CD103^{+}$ MPs are reported to be scarce in the IS, with their number increasing toward the cauda (Mendelsohn et al. 2020).

Distinct morphological features are observed across epididymal regions: in the IS, cells protrude from the basal side toward the lumen, whereas in the cauda, they appear flattened and closely opposed to the basement membrane (Silva et al. 2011). The basal cells of the epididymis also exhibit similar morphological features (Shum et al. 2008); however, it has been reported that MPs and basal cells are not the same cell type (Shum et al. 2014). These mononuclear phagocytes are termed epididymal mononuclear phagocytes (eMPs) (Shum et al. 2014).

MPs appear to play crucial roles in maintaining epididymal homeostasis as well as sperm maturation, storage, and transport. Previous studies suggested that eMPs and stromal MPs (sMPs) differ across distinct regions of the epididymis, implying that they may perform distinct functions. However, to the best of our

knowledge, no studies have investigated the distribution or morphological differences between eMPs and sMPs.

In this study, we used ionized calcium-binding adapter molecule 1 (Iba1), a pan-macrophage marker that identifies all macrophage subpopulations in mice except alveolar macrophages (Köhler 2007), to examine the regional distribution and morphological characteristics of MPs in the epithelium and stroma and to evaluate the morphological relationship between eMPs and basal cells.

2. Materials and Methods

2.1 Animals

Three 12-week-old male mice (C57BL/6J; *Mus musculus* Linnaeus, 1758) were obtained from JAPAN SLC, Inc. (Hamamatsu, Japan). The mice were housed under sterile conditions with free access to food and water. One week later, the animals were euthanized under deep anesthesia via sevoflurane inhalation. The testes, epididymides, and vasa deferentia were dissected using a fine steel blade and forceps under a dissecting microscope after perfusion with 4% paraformaldehyde (PFA). The tissues were processed for histological and immunohistochemical analyses. Animal experiments were approved by the Institutional Animal Care Committee of Kurume University, Fukuoka, Japan (approval no. 2024-066). This study was performed in accordance with the ARRIVE guidelines and conducted in compliance with Guidance on the

operation of the Animals (Scientific Procedures) Act 1986 and associated guidelines, EU Directive 2010/63 for the protection of animals used for scientific purposes or the NIH (National Research Council) Guide for the Care and Use of Laboratory Animals (PDF).

2.1.1 Antibodies

Primary antibodies included a rabbit polyclonal anti-cytokeratin 5 antibody (CK5; ab53121), purchased from Abcam (Cambridge, UK), and a goat polyclonal anti-Iba1 antibody (NB100-1028), purchased from Novus Biologicals, Ltd. (Centennial, CO, USA). As secondary antibodies, a donkey anti-rabbit secondary antibody conjugated with both peroxidase and Alexa Fluor 488 (Invitrogen, Carlsbad, CA, USA) was used for CK5, and a donkey anti-goat antibody conjugated with both peroxidase and Alexa Fluor 568 (Invitrogen) was used for Iba1. The antibodies used in this study are summarized in Table 1.

2.1.2 Fixation and embedding of the tissues

The tissues were further fixed for 3 h in 4% PFA and washed thrice with phosphate-buffered saline (PBS, pH 7.4) for 5 min each, followed by overnight immersion in a buffer solution containing 30% sucrose. For histology and immunohistochemistry, specimens were frozen in an optimal cutting temperature compound (Sakura Finetek, Torrance, CA, USA). An embedding protocol was devised to observe the epididymis in the long-axis direction when preparing frozen sections. The tissue blocks were stored at −80 °C until use.

2.1.3 Preparation of the epididymal sections

For each animal, tissues from one side were randomly selected for analysis. The unselected tissue from the contralateral side was not used in this experiment. Frozen blocks of mouse epididymis were sliced into 4-mm sections, fixed onto charged slides, and air-dried for approximately 20 min. Sections were taken from the entire epididymis, including all regions. Two sections were fixed onto each slide.

2.1.4 Histology

The selected slides were stained with hematoxylin and eosin (H&E) to identify epididymal structures across all regions.

2.1.5 Immunohistochemistry

Frozen sections were cut at 3–5 μm in thickness, adhered to charged slides, and air-dried for approximately 10 min. The slides were then washed with PBS for 5 min. Subsequently, the cells were incubated with 3% normal donkey serum and 0.05% Triton-X100 in PBS for 30 min at room temperature. The sections were then incubated overnight at 4 °C with CK5 and Iba1 antibodies, followed by 1.5 h of incubation with the secondary antibodies. The dilution values of the primary and secondary antibodies are summarized in Table 1. The sections were counterstained with 4',6-diamidino-2-phenylindole (DAPI; Wako, Kumamoto, Japan) at a 1:2,000 dilution to define the nuclei, and Permafluor (Thermo Fisher Scientific, Fremont, CA, USA)-mounted sections were observed on a confocal laser scanning microscope (Fluo View® FV1000-D;Olympus, Tokyo, Japan).

2.1.6 Quantification of Iba1-positive cells in the epithelium and stroma

Six immunostained slides were selected, with two slides from each of the three mice. Using a confocal laser microscope, one random location was selected in each of the IS, caput, corpus, and cauda regions and imaged at 10× magnification using the objective lens. Images were examined to count Iba1-positive cells within the epithelium that overlapped with CK5 and those in the stroma that were clearly separated from CK5. The number of Iba1-positive cells present within the epithelium and stroma were recorded, and the ratio of epithelial to stromal cells was calculated.

3. Results

3.1 Histological analysis

Histological analysis of the tissues was performed using H&E staining. All regions of the epididymis (IS, caput, corpus, and cauda) were included in this section (Fig. 1).

3.2 Immunohistochemical analysis

In the IS, Iba1-positive cells had cell bodies located on the basal side, exhibited a flattened morphology, and extended processes toward the lumen. Basal cells exhibited a morphology similar to that of Iba1-positive cells, displaying a characteristic shape with projections extending into the lumen. Basal cells and Iba1-positive cells were not co-immunostained; cells of each type were intermingled (Fig. 2).

In the caput region, Iba1-positive cells were observed extending projections toward the lumen, similar to the IS, but their number was significantly reduced compared with that in the IS. The basal cells exhibited a flattened morphology along the basal side, and no projections toward the lumen were observed. Iba1-positive cells and basal cells were intertwined toward the basal side; however, unlike those in the IS, the basal cells did not possess projections (Fig. 3).

In the corpus, Iba1-positive cells were long, flat, and tightly adhered to the basal side, lacking projections. Although their morphology was clearly longer than that of the Iba1-positive cells in the IS or caput regions, their numbers were markedly reduced. The basal cells were also markedly elongated compared with those in the IS or caput regions, adhering tightly to the basal side and exhibiting a morphology without projections. The basal and Iba1-positive cells were in close proximity. In the basal regions lacking basal cells, some areas were devoid of both basal cells and Iba1-positive cells (Fig. 4).

In the cauda region, similar to the corpus region, Iba1-positive cells exhibited a long, flattened morphology that adhered closely to the basal side. No cells with projections were observed. Basal cells, like Iba1-positive cells, exhibited elongated shapes along the basal side, and no cells with projections were observed. The basal cells in this area were elongated and covered the basal layer, resulting in a very narrow layer lacking basal cells (Fig. 5).

Unlike the epithelial side, stromal Iba1-positive cells exhibited a similar rounded and elongated morphology throughout all regions. In the caudal region, the density of Iba1-positive stromal cells was higher (Fig. 2–5).

3.2 Number and ratio of Iba1-positive cells in the epithelium and stroma

In the IS region, the number of Iba1-positive cells present in the epithelium was 625, whereas that in the stroma was 140. The proportion of cells in the epithelium was 81.7%, and that in the stroma was 18.3%. In the caput region, the number of Iba1-positive cells present in the epithelium was 944, whereas that in the stroma was 344. The proportion of cells in the epithelium was 73.3%, whereas that in the stroma was 26.7%. In the corpus, the number of Iba1-positive cells present in the epithelium was 316, whereas that in the stroma was 349. The proportion of cells present in the epithelium was 47.5%, and that in the stroma was 52.5%. In the caudal region, the number of Iba1-positive cells present in the epithelium was 243, whereas that in the stroma was 687. The proportion of cells in the epithelium was 26.1%, and that in the stroma was 73.9%. As the region transitioned from the IS to the cauda, the proportion of Iba1-positive cells present in the stroma increased, whereas the proportion of cells present in the epithelium decreased (Fig. 6).

4. Discussion

Sperm released from the testes are not yet completely mature; they acquire motility and fertilization capacity during transport and storage in the epididymis (Yanagimachi 1994; Cornwall 2009). Sperm passing through the epididymis are considered non-self or antigens to post-pubertal organisms because of their reduced chromosome number. The epididymis, a long, coiled tubular organ, can initiate highly efficient immune responses against pathogenic microorganisms while preventing the development of autoimmune reactions against antigenic sperm. Various immune cells perform their functions in this environment. Disruption of homeostasis between the epididymal mucosa and sperm may be involved in many cases of male infertility (Silva and Barton 2016; Fijak et al. 2018; Voisin et al. 2018).

The epididymis is divided into the IS, caput, corpus, and cauda regions, and characteristic immune cells have been reported to be distributed throughout these regions (Battistone et al. 2020; Mendelsohn et al. 2020). According to reports from mouse experiments (Mendelsohn et al. 2020), the IS region contains the highest abundance of CD11c+ MP cells expressing the MP phenotype (CD64+ and F4/80+). Immune cells expressing CD64- major histocompatibility complex class II (MHCII), which is characteristic of dendritic cells, were abundant in the caudal region. Furthermore, the report indicated that CD11+ MP cells within the IS actively phagocytosed antigens, and that this cell population was located in the stroma near the epithelium. In the cauda, cells that phagocytose antigens were reported to be CD11c- cells residing in the

stroma, away from the epithelium. This suggests that the epididymis is populated by distinct immune cells in each region, and each region performs unique functions.

In the present study, the morphology of Iba1-positive cells was observed in distinct regions of the epididymis, revealing the characteristic morphological features of each region. In the IS, MPs are characterized by projections extending toward the epithelial lumen, and morphologically distinct cells are occasionally observed in the caput region. However, their numbers decreased significantly in the caput region. Furthermore, in the IS, the morphology of basal cells resembled that of MPs, and they existed in an intertwined form. In the caput region, no basal cells extended projections toward the lumen. Therefore, it was inferred that MPs in the IS and caput regions likely interact with the epithelial lumen. They may serve various roles, such as consumption, surveillance, and sensing; however, their specific function remains unclear. Furthermore, the morphological similarity between MPs and basal cells is highly intriguing, yet it remains largely unknown. Typically, basal cells and MPs differ significantly in origin and function, rendering morphological similarities unlikely. MPs reside in nearly all organs including the liver (Kupffer cells), lungs (alveolar macrophages), and skin (Langerhans cells). Their morphology varies according to their location and function, in contrast to the regular single-layer cell arrangement of basal cells. In the epididymis, however, basal cells and eMPs exhibit characteristic and similar morphological features across different regions. As these morphological features have not been reported in organs, interactions between

epididymal basal cells and eMPs may contribute to region-specific immune functions. Elucidating these interactions remains an important challenge for future research.

The constitutive presence of eMPs within the epididymal epithelium is particularly noteworthy. To our knowledge, no studies have reported the presence of MPs in the epithelium of organs other than the epididymis. In the small intestine, MPs residing in the lamina propria extend their dendrites to phagocytose antigens within the epithelial lumen (Niess et al. 2005); however, the cell bodies themselves are located in the extraluminal stroma. Epididymial eMPs are thought to play a unique role and function. Investigating eMPs may provide new insights into epididymal biology and help elucidate the mechanisms underlying sperm maturation.

Furthermore, to our knowledge, no previous studies have clarified the distribution of eMPs and sMPs; therefore, this study is the first to report on this subject. In the present study, the proportion of eMPs was higher than that of sMPs in the IS, and the proportion of sMPs increased progressively toward the cauda of the epididymis. Consequently, in the IS, sperm within the epididymal lumen have more opportunities to come into contact with MPs, whereas in the cauda, MPs have fewer opportunities to come into contact with sperm. This finding likely supports the theory that, in the IS, MPs monitor and filter sperm and other substances transported from the testes, whereas the caudal region serves to store sperm and prevent infection from bacteria, viruses, and other pathogens.

Iba1 is considered a pan-macrophage marker because, in mice, all macrophage subpopulations except alveolar macrophages express Iba1/AIF1 (Köhler 2007). Therefore, a limitation of this study is that the types of MPs represented by eMPs and sMPs remain unidentified, warranting further investigation.

In the mouse epididymis, MPs are found in both the epithelium and the stroma. In all regions of the epididymis, eMPs and basal cells showed high morphological similarity. The eMP-to-sMP ratio was highest in the IS and decreased toward the cauda, whereas the proportion of sMPs increased in the same direction, suggesting that the distribution of MPs is associated with the region-specific function of the epididymis.

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Declarations:

Ethics approval:

All animal experiments were approved by the Institutional Animal Care Committee of Kurume University (Approval No. 2024-066) and were conducted in accordance with the relevant guidelines.

Conflict of Interest

The authors declare that they have no conflict of interest.

Declaration of Generative AI and AI-assisted Technologies in the Manuscript Preparation Process

We have not used AI tools in the preparation of this manuscript.

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Author Contributions

K Uemura and KO: conceptualization. K Uemura, TH, K Ueda, AT, HS and HK: data curation. K Uemura and MN: formal analysis. K Uemura, TH, K Ueda, HS and HK: methodology. AT: visualization. KO and K Nishihara: project administration. K Nishihara, TI, K Nakamura: supervision. K Uemura: writing - original draft. MN, TI, and K Nakamura: writing - review & editing. All authors have reviewed the final version of the manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request

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Figure Legends

Fig. 1 Histopathological findings of hematoxylin and eosin-stained sections of the testis and epididymis. All four regions of the epididymis are present within the section. a: Initial segment. b: Caput. c: Corpus. d: Cauda.

Fig. 2 Immunohistochemical findings for Iba1, cytokeratin 5 and 4; 6-diamidino-2-phenylindole in the initial segment.

Fig. 3 Immunohistochemical findings for Iba1, cytokeratin 5 and 4; 6-diamidino-2-phenylindole in the caput region.

Fig. 4 Immunohistochemical findings for Iba1, cytokeratin 5 and 4; 6-diamidino-2-phenylindole in the corpus region.

Fig. 5 Immunohistochemical findings for Iba1, cytokeratin 5 and 4; 6-diamidino-2-phenylindole in the cauda region.

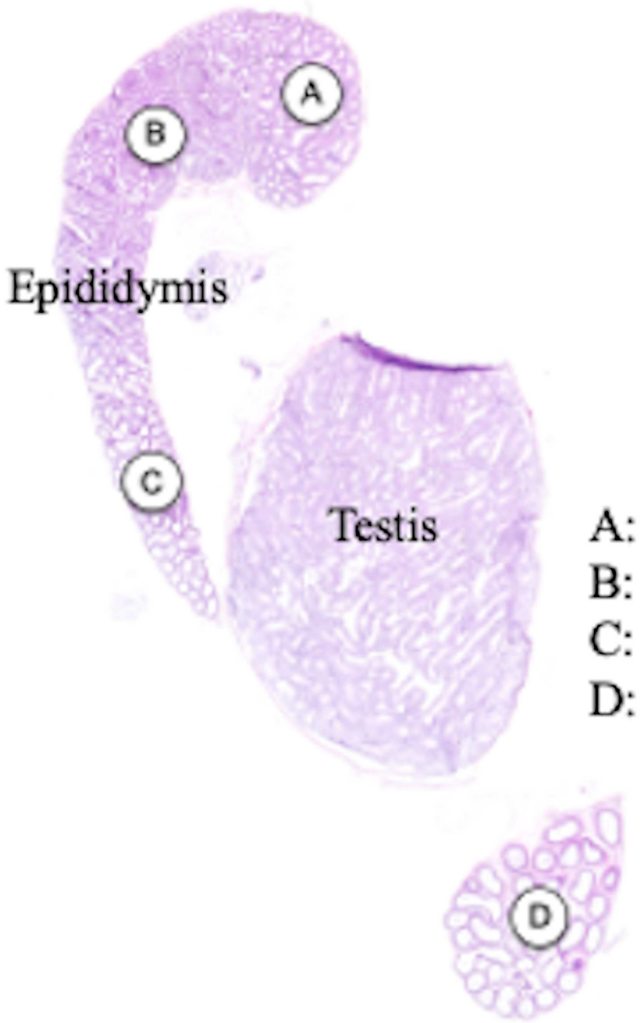
Fig. 6 The proportion of macrophages present in the epithelium and stroma for each region of the epididymis.

Tables

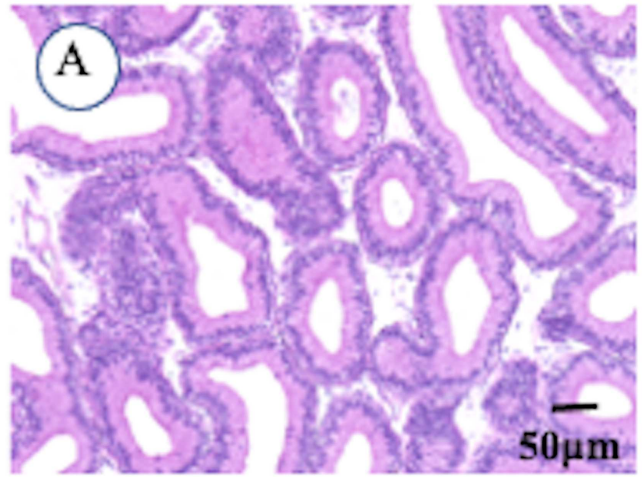
Table 1. Primary and secondary antibodies used for immunohistochemistry.

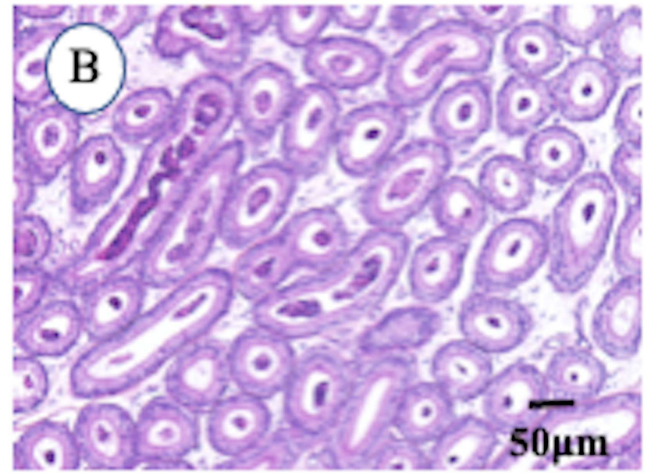
Antigen	Primary antibody	Secondary antibody	Dilution
CK5	Anti-CK5, rabbit, polyclonal (Abcam, Cambridge, UK)	Anti-rabbit IgG, donkey 1/500 (Invitrogen, Carlsbad, CA, USA)	1/200
Iba1	Anti-Iba1, goat, polyclonal (Novus Biologicals, Centennial, CO, USA)	Anti-goat IgG, donkey 1/500 (Invitrogen, Carlsbad, CA, USA)	1/1000

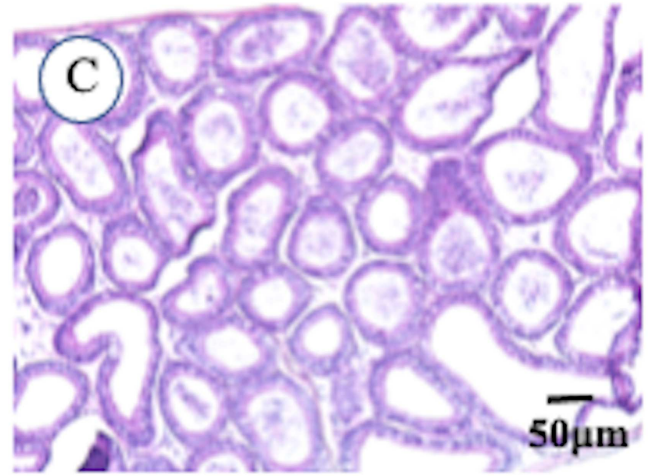
Figure 2 Histological analysis (HE staining)



A: Initial State (IS)
B: Caput Epididymis
C: Cortex Epididymis
D: Cauda Epididymis







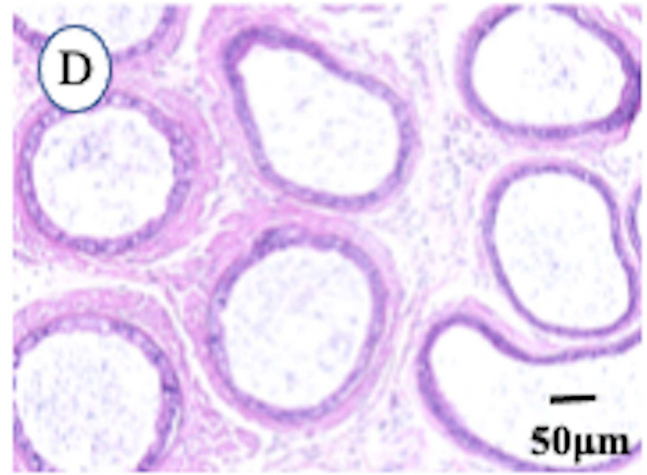


Figure 3 Initial Segment

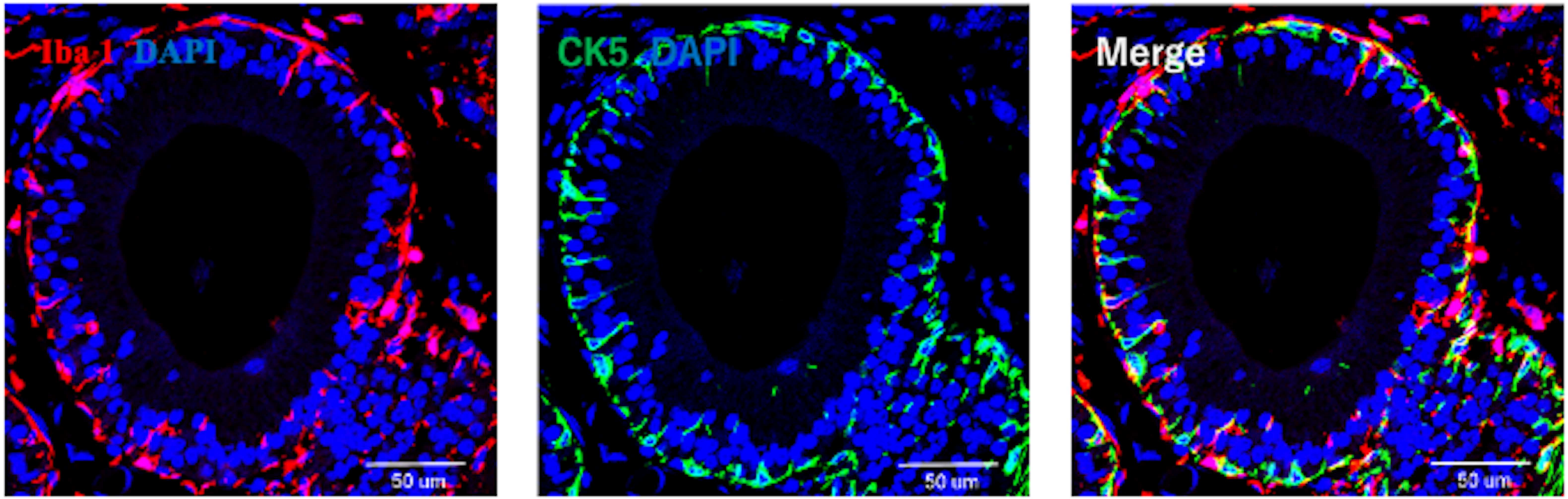


Figure 4 Caput Epididymis

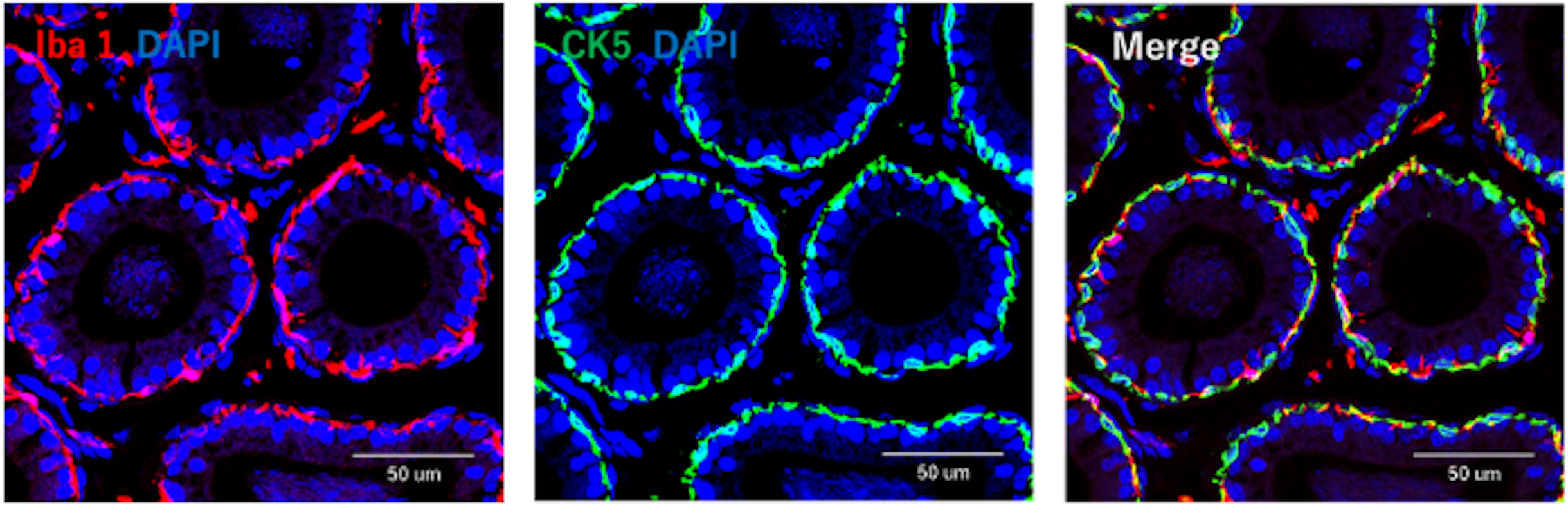
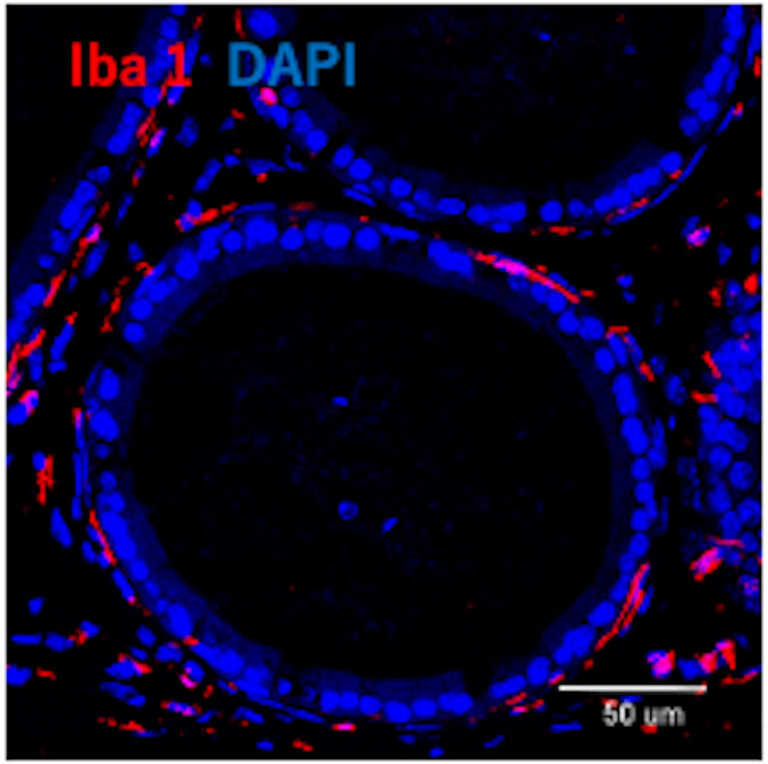
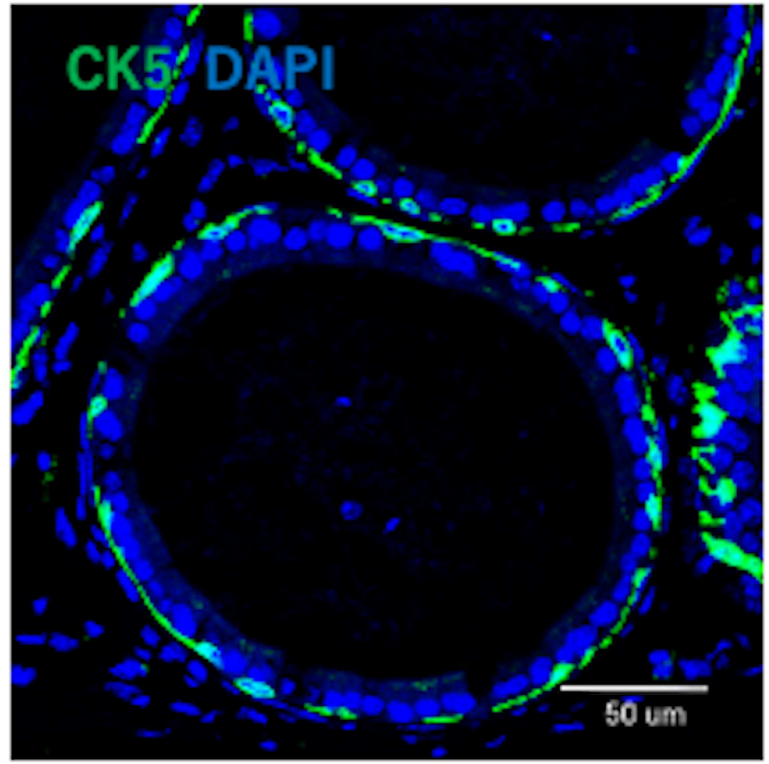


Figure 5 Corpus Epididymis





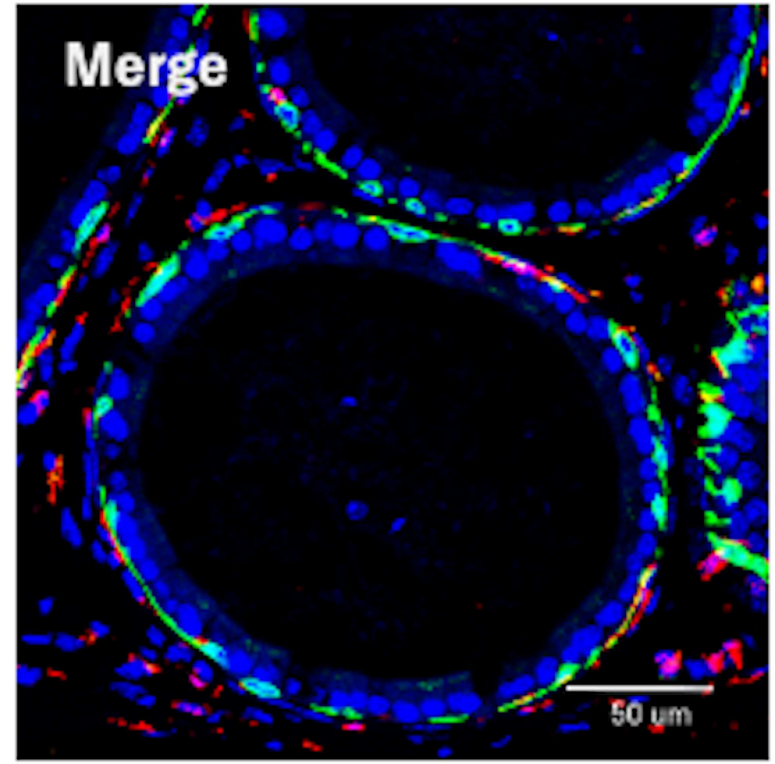


Figure 6 Cauda Epididymis

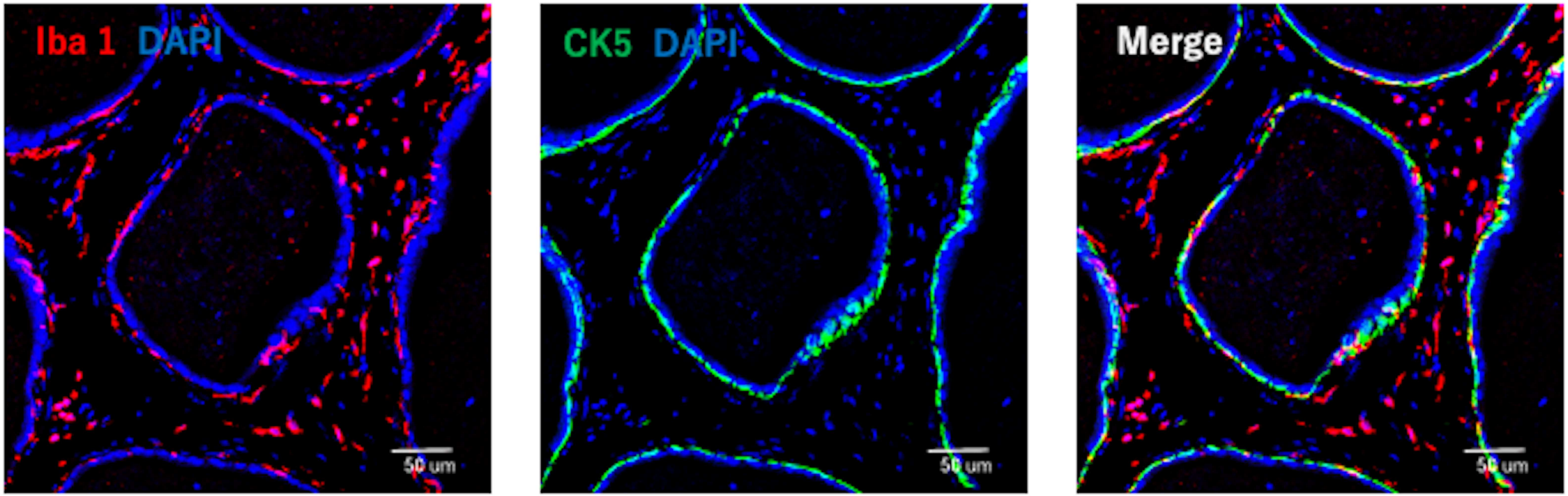
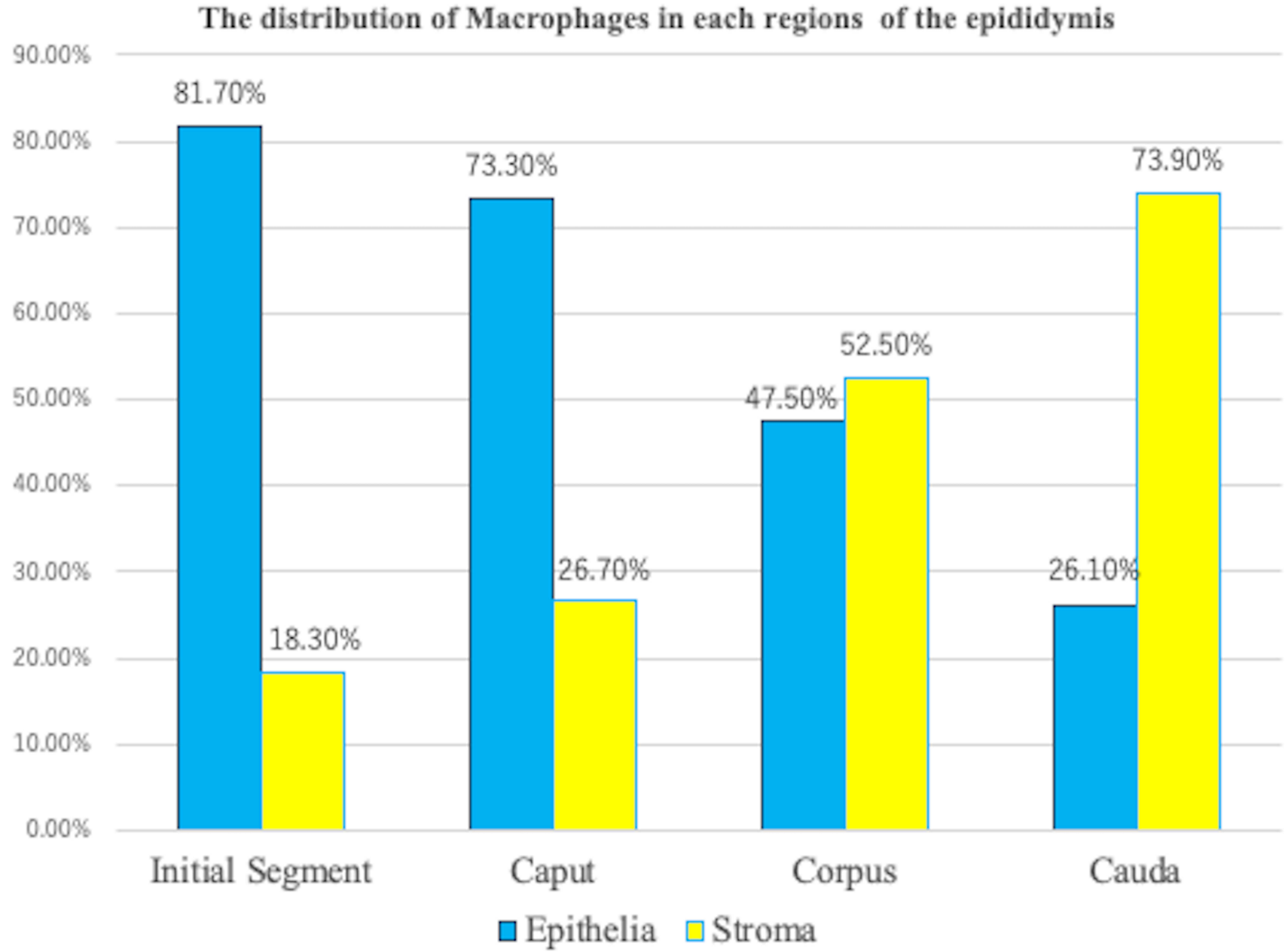


Figure 7 The distribution of Macrophages in epididymis



Supplementary Files

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- SupplFigure1.tiff