International Journal of Environmental Sciences
ISSN: 2229-7359
Vol. 11 No. 8, 2025
https://theaspd.com/index.php

Study Of The Seminiferous Epithelium Cycle And Identification Of MMP-2 In The Seminiferous Tubules Of Jaculus Jaculus Testes During The Reproductive Cycle

Nesrine Zeghloul [1]*, Nemcha Lebaili-Benmoussa [1] & Salim Lamine [2]
[1]Department of Biological Sciences, Higher Normal School of Kouba Bachir El Ibrahimi, Algiers 16050, Algeria. Email: hzeghloulnesrine@gmail.com | nlebaili@yahoo.fr
[2]Higher School of Saharan Agriculture Adrar, National Road N°06, Adrar 01000, Algeria. Email: salim.lamine@gmail.com

Abstract
Our study explores the histo-functional characteristics of the testicles in Jaculus jaculus, a nocturnal rodent from North Africa that reproduces seasonally, collected in the regions of Biskra and M'sila in Algeria from Autumn to early Spring. Although it is included in the list of protected non-domestic animal species in Algeria, very few studies have focused on the reproductive activity of this species. The objectives of this study are: to determine the different stages of the seminiferous epithelium cycle in adult Jaculus jaculus during the reproductive cycle, by studying the cellular association on PAS-stained histological sections, supplemented by light green and Masson's trichrome staining. Analysis of matrix metalloproteinases (MMP-2) on histological sections of testicles during the active phase using an indirect immunohistochemistry protocol with streptavidin-biotin-peroxidase amplification. The seminiferous epithelium cycle in Jaculus jaculus is characterized by 14 well-defined stages classified from I to XIV. In the testis, seminiferous epithelium cells strongly express MMP-2 during all stages of the seminiferous epithelium cycle. MMP-2 plays a fundamental role in testicular function in Jaculus jaculus, and its expression at the interstitial and germinal levels suggests involvement in spermatogenesis and speriogenesis.
Keywords: *Jaculus jaculus; Testis; seminiferous epithelium cycle; Matrix metalloproteinases; MMP-2; Immunohistochemistry*

1. INTRODUCTION

The lesser jerboa is a small rodent that is mainly nocturnal and reproduces seasonally, adapted to extreme environmental conditions. There are about 30 to 35 species of jerboas in the order Rodentia, superfamily Dipodoidae, and family Dipodidae. Jerboas belonging to the genus Jaculus (Erxleben, 1777) are widely distributed in the arid and semi-arid regions of North Africa and Central Asia (Holden & Musser, 2005). Ecologically speaking, Jaculus jaculus (Linnaeus, 1758) is a granivorous and insectivorous species, feeding mainly on seeds, plant parts, and occasionally insects. These small mammals dig burrows that serve as shelter from predators and extreme weather conditions.

The breeding season in Jaculus jaculus begins at the onset of winter (December–January) and extends until early spring (April), when food resources are available. The rapid increase in ambient temperature, combined with the decrease in precipitation, promotes the transition to sexual quiescence, which is observed in spring (May–June) (Amirat et al., 1977). Gestation lasts approximately 20 to 25 days. Each litter generally consists of 2 to 6 offspring, born hairless, blind, and entirely dependent on the mother. Like most jerboas, Jaculus jaculus adopts a reproductive strategy that allows adjustment of the number of litters in response to environmental conditions, representing an adaptation to the variability of the unstable North African desert ecosystems (Amori & Hutterer, 1995).

Jaculus represents a model species for the study of reproductive function; unfortunately, very little data exist regarding the reproductive biology of these small mammals. In the testes of these rodents, spermatogenesis is a highly coordinated cyclical process (Russell et al., 1990). The complete series of changes occurring in the seminiferous epithelium between two successive appearances of the same cellular association is defined as the seminiferous epithelium cycle (Leblond & Clermont, 1952; Leal & França, 2006; Xiao et al., 2014).

The stages of the seminiferous epithelium cycle can be classified according to changes in the shape of spermatid nuclei, the occurrence of meiotic divisions, and the arrangement of spermatids within the germinal epithelium (Berndtson, 1977). They can also be characterized on the basis of the development

of the acrosomal system and the morphology of developing spermatid nuclei (Leblond & Clermont, 1952a, 1952b; Russell et al., 1990). The length of the spermatogenic cycle is controlled by the genotype of germ cells and is not influenced by Sertoli cells or by the hormonal environment, thereby implicating MMPs in the dynamic remodeling of the extracellular matrix as well as in the maintenance of seminiferous tubule architecture during the reproductive cycle (França et al., 1998).

Matrix metalloproteinases (MMPs) are endogenous Zn-dependent proteinases that catalyze glycoproteins of the extracellular matrix (Massova et al., 1998; Rivera et al., 2010). MMPs are responsible for remodeling the extracellular matrix of various tissues under both physiological and pathological conditions (Di Nezza et al., 2002; Kessenbrock et al., 2010). MMPs are divided into soluble and membrane-bound forms. Soluble MMPs include the collagenases (MMP-1, -8, -13, and -18), gelatinases (MMP-2 and -9), matrilysins (MMP-3, -10, and -11), stromelysins (MMP-7 and -26), and other enzymes (MMP-12, -19, -20, -21, -23, -27, and -28). Membrane-bound MMPs include MMP-14, -15, -16, -17, -24, and -25 (Lohi et al., 2001; Nagase et al., 2006). MMPs play important roles in the development of many organisms; they are involved in organ morphogenesis, ovulation, apoptosis, angiogenesis, and embryogenesis (Vu and Werb, 2000; Roy et al., 2006; Jones, 2014). MMPs also participate in the regulation of activity of extracellular matrix components (Sternlicht et al., 2000) and signaling molecules (Roy et al., 2009). MMPs are inhibited by tissue inhibitors of metalloproteinases (TIMPs) (Brew et al., 2000).

MMP-2 (gelatinase A) is involved in the degradation of proteins and polysaccharides, such as collagens (IV, V, and XI) (Bode et al., 1999), laminins, and cartilage (Nagase et al., 2006). This gelatinase is indispensable for the remodeling of matrix membranes (Stetler-Stevenson, 1994). In organs undergoing perpetual cyclical or seasonal structural changes orchestrated by hormones, growth factors, cytokines, and cell–stroma interactions (Brown et al; 2007). Several studies have demonstrated the importance of MMPs in male reproductive function in mammals. MMPs have been identified in human seminal plasma (Baumgart et al; 2002) and a deficiency in MMP-2 has been associated with reduced fertility (Atabakhsh et al; 2018). During spermiation, spermatozoa detach from Sertoli cells, a process requiring a protease system to orchestrate these cellular events.

The objective of our study is to investigate the histo-functional changes occurring during the active phase of the reproductive cycle in the lesser jerboa. Furthermore, we aim to define, for the first time, the stages of the seminiferous epithelium cycle and to demonstrate the immunohistochemical presence of metalloproteinases (MMP-2) in the testes of this species throughout the active phase. The purpose of this investigation is to highlight the potential role of MMP-2 in reproductive physiology and in the tissue remodeling processes affecting these glands during seasonal reproduction.

2. MATERIALS AND METHODS

2.1. Animals

Our study was conducted on 10 adult male jerboas weighing between 59 and 75 g. The animals were captured between September 2020 and April 2021 in two semi-arid regions of the Algerian Sahara: loutaya, located 25 km northwest of the province of Biskra (35° 02′ 00″ N, 5° 36′ 00″ E), and the region of Ain Lahdjel in the province of M'sila (35° 40′ 26″ N, 3° 52′ 54″ E). To minimize stress, the animals were placed in separate cages equipped with food and maintained under the natural temperature and photoperiod conditions of the season for a maximum of 10 hours, in order to avoid the influence of the nychthemeral rhythm.

2.2. Anatomical and Structural Study of the Testes

The testes were dehydrated using a graded ethanol series, followed by clearing in cyclohexane and embedding in paraffin. Serial sections of 6 µm thickness were then prepared for staining (light green, PAS, H&E, and Masson's trichrome).

2.3. Stages of the Seminiferous Epithelium Cycle

The stages of the seminiferous epithelium cycle were identified and characterized according to the "tubular morphology system" method (Berndtson, 1977), based on changes in the shape of spermatid nuclei, the arrangement of spermatids within the germinal epithelium, and the overall composition of the seminiferous tubule epithelium (Roosen-Runge & Giesel, 1950). The stages were determined from 10 testicular sections for each adult individual at magnifications of 40× and 100×.

2.4. Immunohistochemical Study of MMP-2

This study employed an indirect immunohistochemical method using streptavidin–biotin–peroxidase

amplification, following the peroxidase immunohistochemistry protocol of the LSAB2 KIT (DAKO), as described by MacNeil (20). Sections of 6 µm were deparaffinized and rehydrated in ethanol. The primary antibody, MMP-2 mouse anti-human monoclonal antibody (Invitrogen, dilution 1/70, pH = 6), was applied to the sections for one hour. All procedures were carried out in accordance with the guidelines of the Algerian Association of Experimental Animal Sciences (AASEA) and were approved by the local ethics committee of Houari Boumediene University of Science and Technology (USTHB), Algeria (Approval No. 45/DGLPAG/DVA.SDA.14). The laboratory work was conducted at the Laboratory of Animal Ecology within the National Superior School of Kouba in Algiers.

3. RESULTS

3.1. Characterization of the Different Stages of the Seminiferous Epithelium Cycle in Adult Jaculus jaculus

The different stages of spermatogenesis in Jaculus jaculus have never been described. In this study, we present a detailed and illustrated description:

Stage I: This stage is characterized by the initiation of renewal of the germ cell lineage, entry into meiosis, and the appearance of the first spermatids. Spermatogonia A are located in close proximity to Sertoli cells. Primary spermatocytes are observed at the beginning of the pachytene phase, along with newly formed round spermatids at step 1 of spermiogenesis (Figure 1).

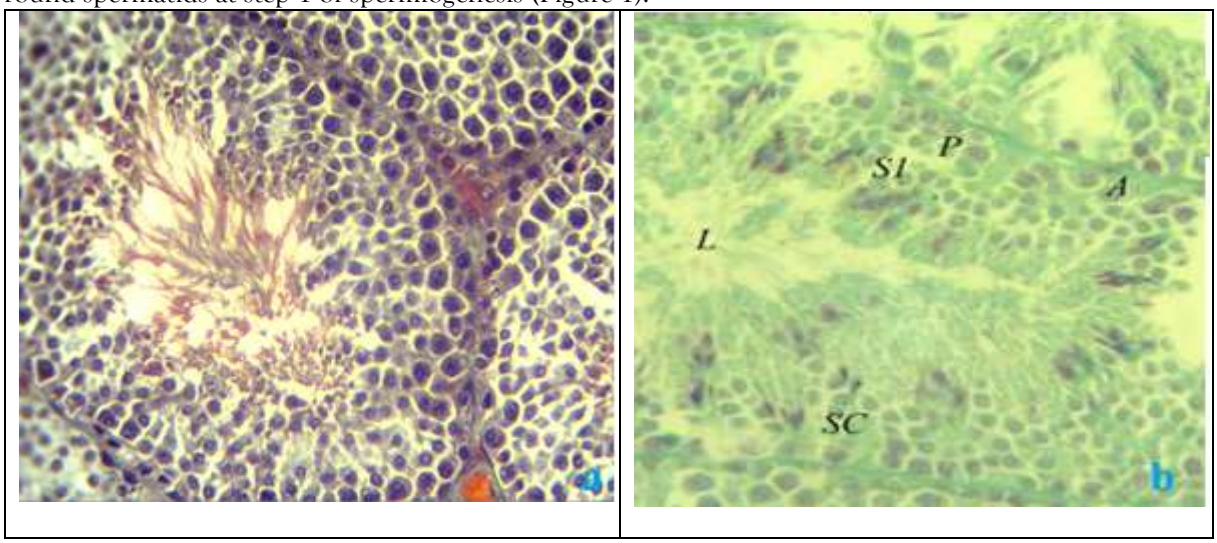


Figure 1 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's trichrome staining, magnification ×40. **b**: Light green staining, magnification ×40. P = pachyten stage; L = lumen of the tubule; A = type A spermatogonia; S1 = stage 1 of the epithelial cycle; SC = Sertoli cell.

Stage II: This stage is characterized by the appearance of intermediate spermatogonia, primary spermatocytes in the zygotene stage, immature spermatozoa at step 16 of spermiogenesis, and round spermatids (Figure 2).

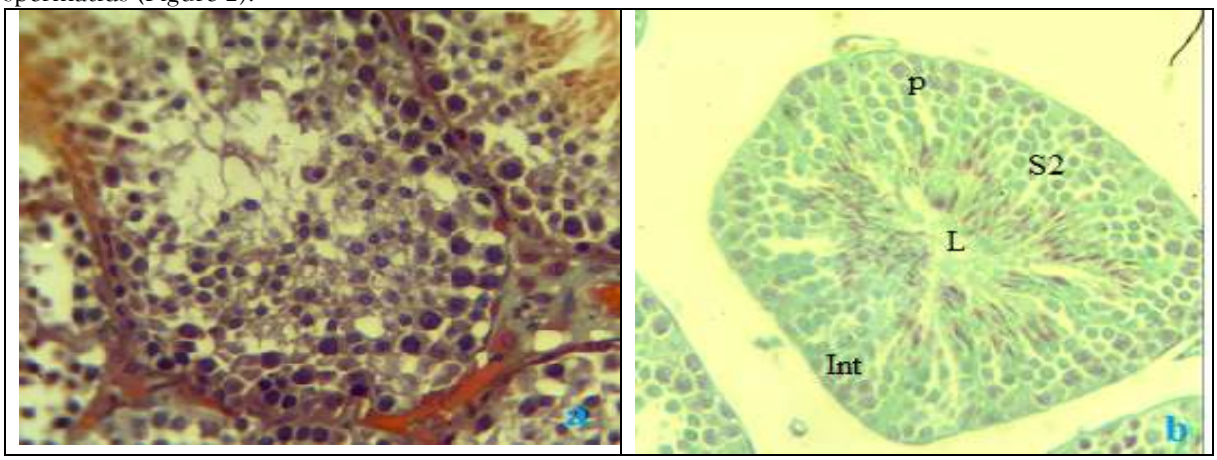


Figure 2. Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the

period of sexual activity. **a**: Masson's trichrome staining, magnification ×40. **b**: Light green staining, magnification ×40. P = pachyten stage; L = lumen of the tubule; Int = intermediate type spermatogonia; S2 = stage 2 of the epithelial cycle.

Stage III: Presence of type B spermatogonia, with round and immature spermatozoa at step 16, distributed at various levels within the luminal compartment. The spermatozoa heads are oriented toward the basal lamina of the seminiferous tubules (Figure 3).

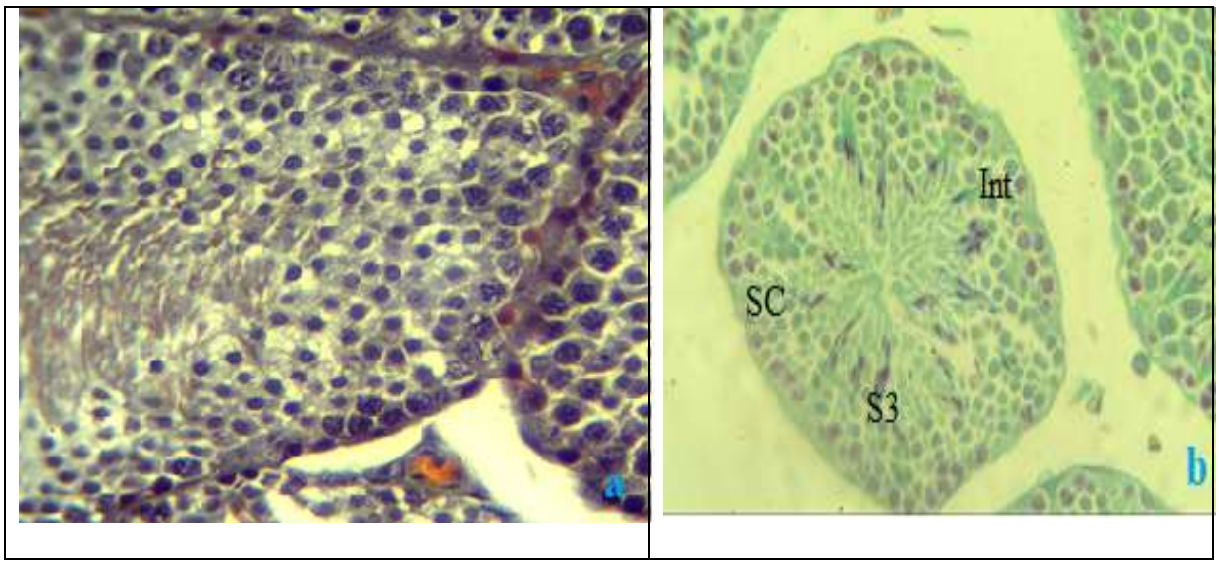


Figure 3 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. Int: intermediate spermatogonium; S3: stage 3 of the epithelial cycle; A: type A spermatogonium; SC: Sertoli cell.

Stage IV: The immature spermatozoa reach stage 17, exhibiting a tubular form. Their heads penetrate even more deeply into the epithelium toward the basal lamina of the seminiferous tubules. Secondary spermatocytes appear (Figure 4).

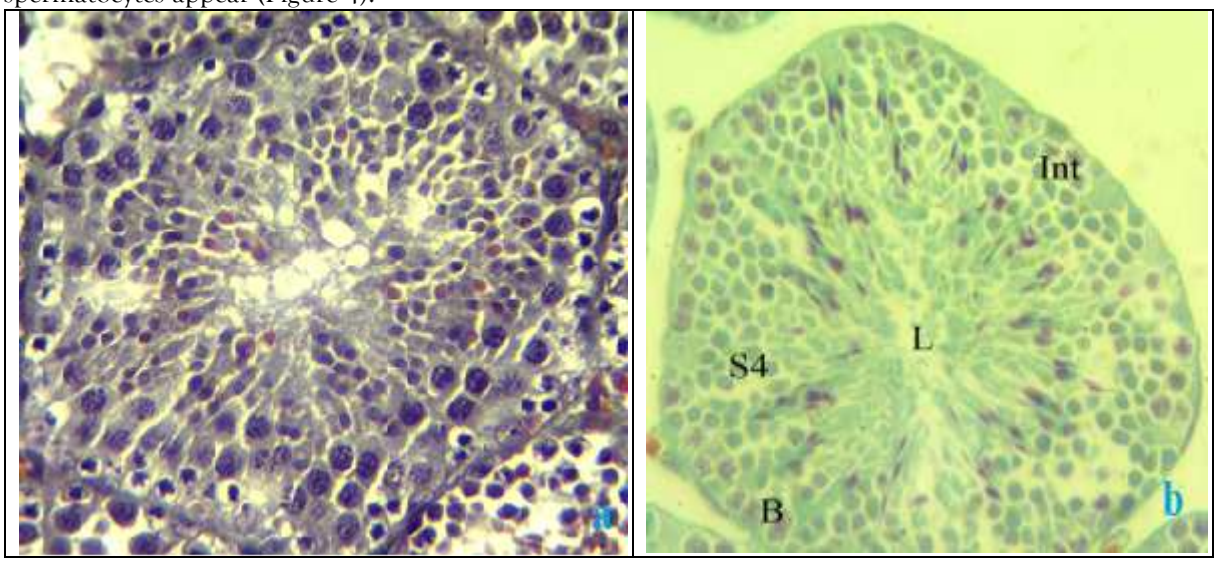


Figure 4: Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40.
Int: intermediate spermatogonium; S4: stage 4 of the epithelial cycle; B: type B spermatogonium.

Stage V: The round and immature spermatids at stage 17 integrate into the epithelium, extending as far as the nuclei of the Sertoli cells. Their tails begin to form whorls at the center of the lumen of the

seminiferous tubules (Figure 5).

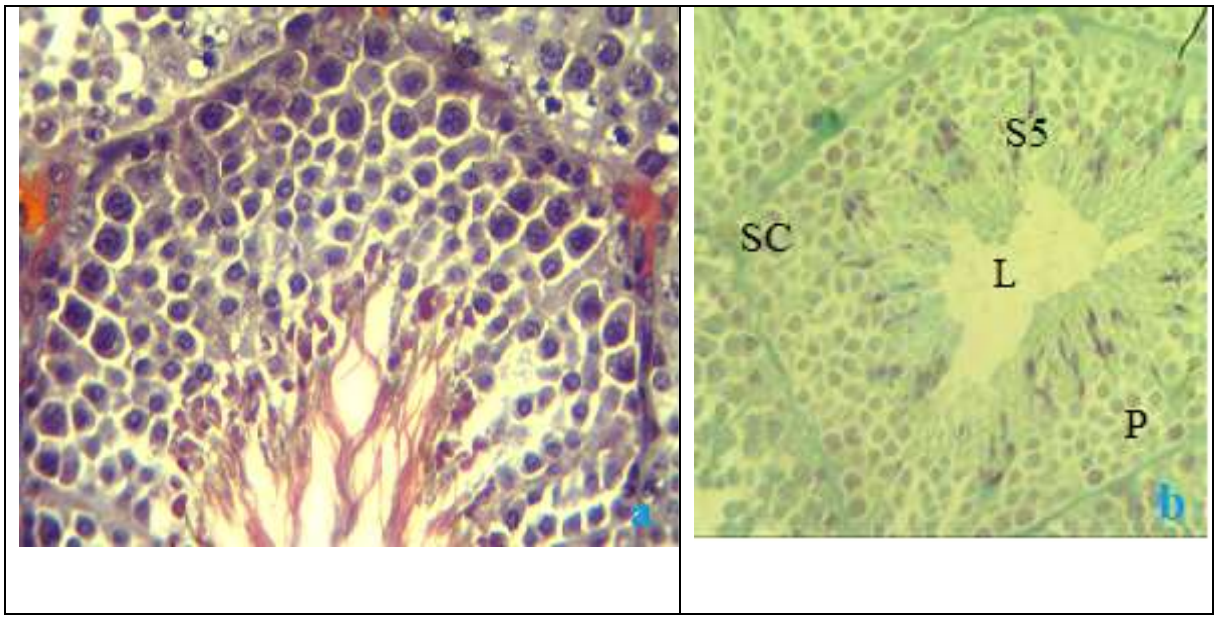


Figure 5: Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: dust-like material; L: lumen of the tubule; A: type A spermatogonium; S5: stage 5 of the epithelial cycle; SC: Sertoli cell.

Stage VI : Advanced stage of spermiogenesis: Pre-leptotene and pachytene spermatocytes are present. Bundles of elongated spermatids at stage 18 begin to migrate toward the lumen of the seminiferous tubules (Figure 6).

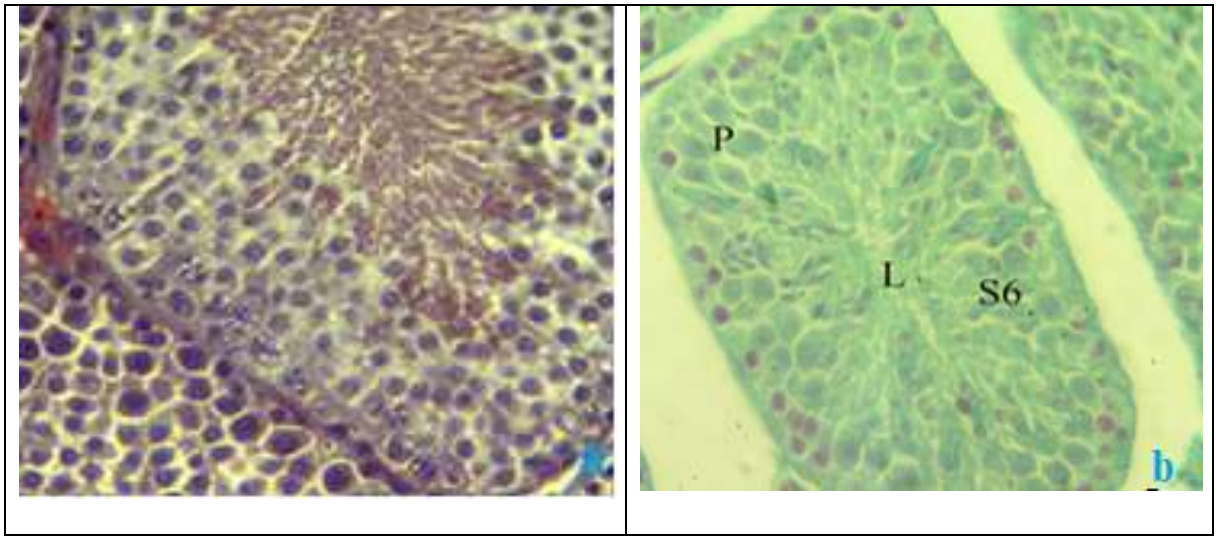


Figure 6 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: pachyten stage; L: lumen of the tubule; B: type B spermatogonium; S6: stage 6 of the epithelial cycle.

Stage VII : The heads of the immature spermatozoa surround the lumen of the seminiferous tubule (Figure 7).

International Journal of Environmental Sciences
ISSN: 2229-7359
Vol. 11 No. 8, 2025
https://theaspd.com/index.php

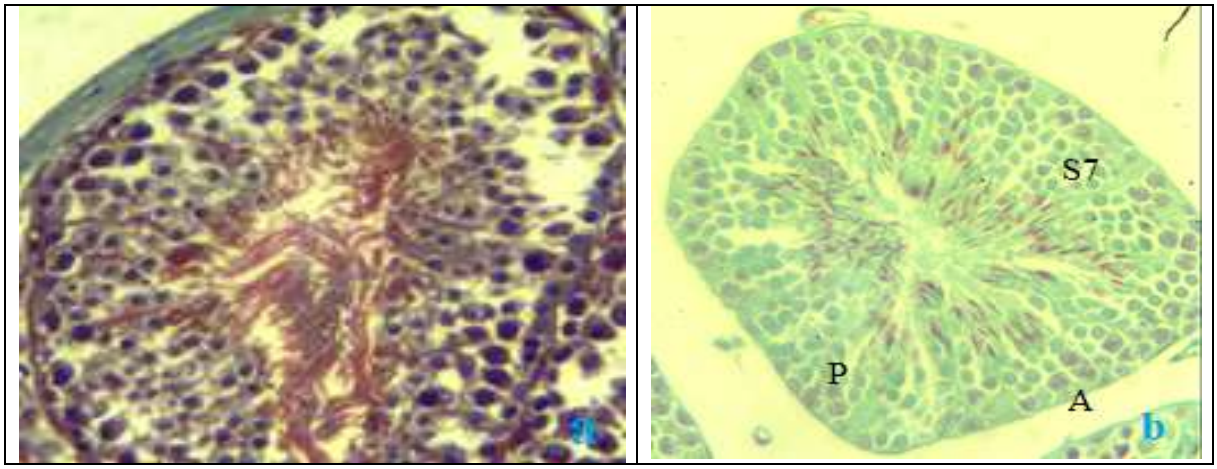


Figure 7 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40.

b: Light Green staining, G×40. P: pachyten stage; A: type A spermatogonium; S7: stage 7 of the epithelial cycle.

Stage VIII : Absence of primary and secondary spermatocytes. The elongated and immature spermatozoa are released into the lumen through a process known as spermiation (Figure 8).

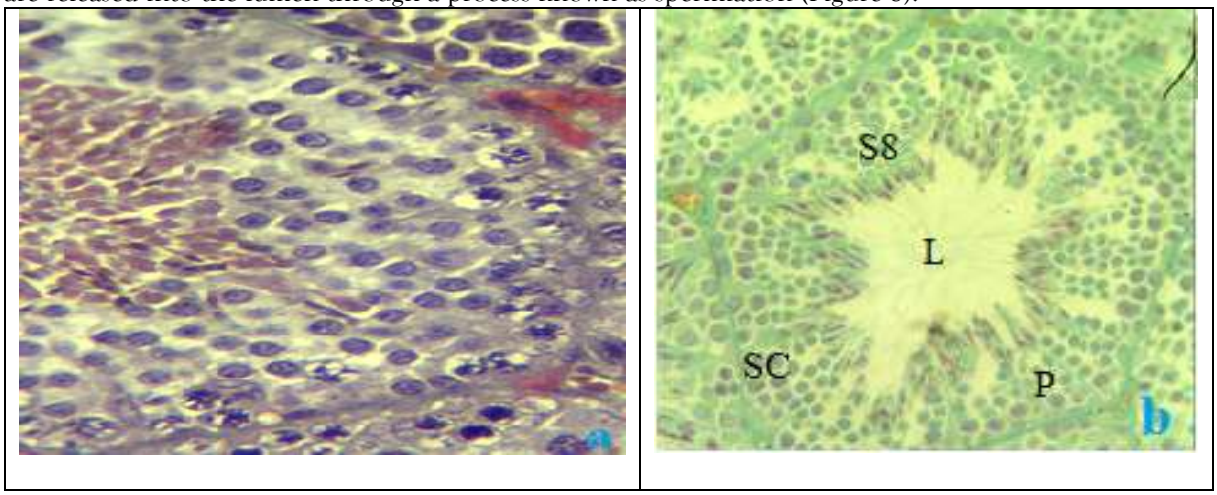


Figure 8 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: pachytén stage; L: lumen of the tubule; B: type B spermatogonium; SC: Sertoli cell; S8: stage 8 of the epithelial cycle.

Stage IX : Leptotene-phase primary spermatocytes, onset of cytoplasmic elongation of spermatids, and progressive disappearance of residual bodies of spermatozoa (Figure 9).

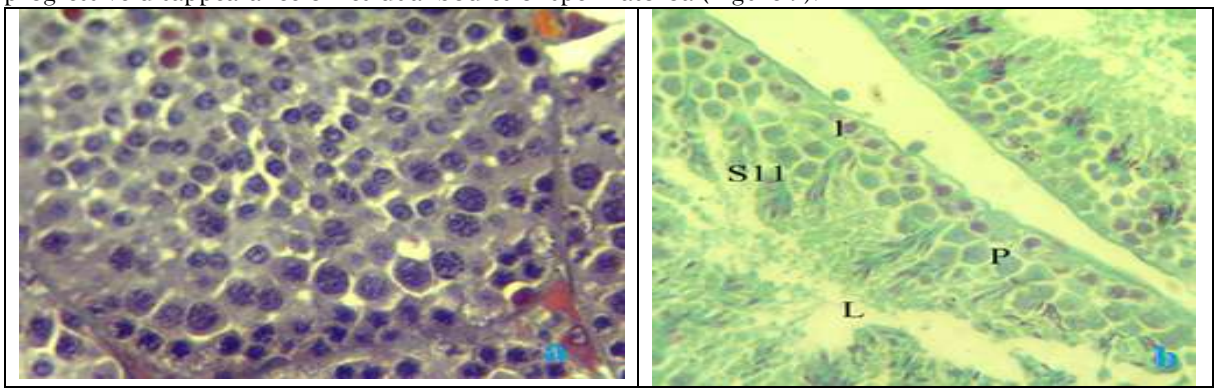


Figure 9 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40.
b: Light Green staining, G×40. P: pachyten stage; L: lumen of the tubule; l: leptotene stage; S9: stage 9 of the epithelial cycle.

Stage X : Well-differentiated spermatids with triangular nuclei, and primary spermatocytes at the zygotene stage (Figure 10).

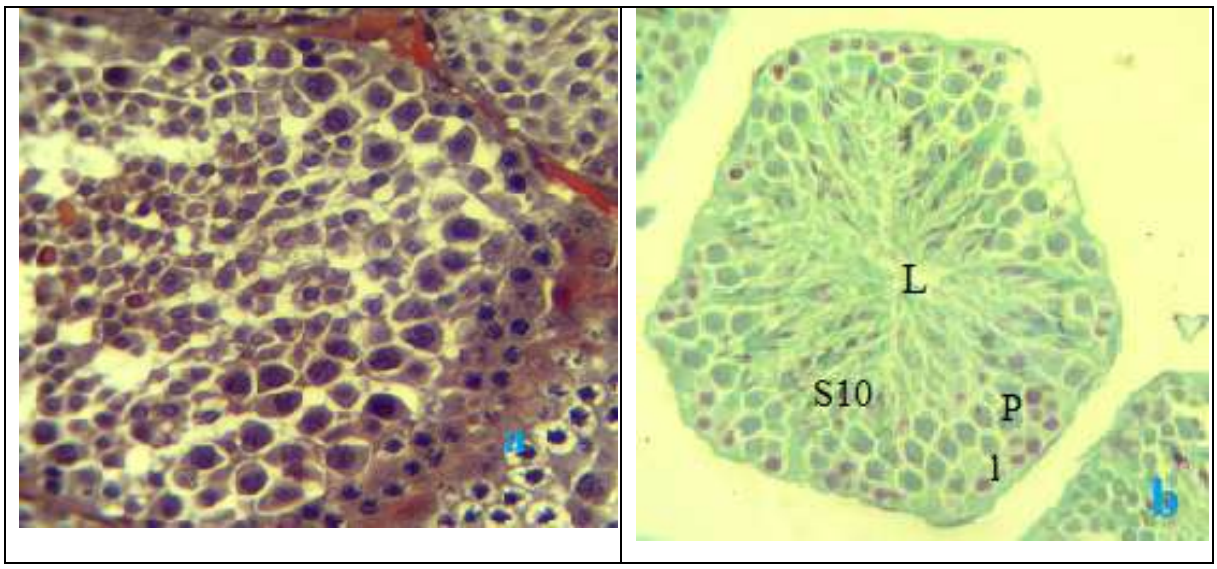


Figure 10 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: pachyten stage; L: lumen of the tubule; l: leptotene stage; S10: stage 10 of the epithelial cycle.

Stage XI : Spermatozoa with elongated nuclei form bundles oriented toward the Sertoli cells (Figure 11).

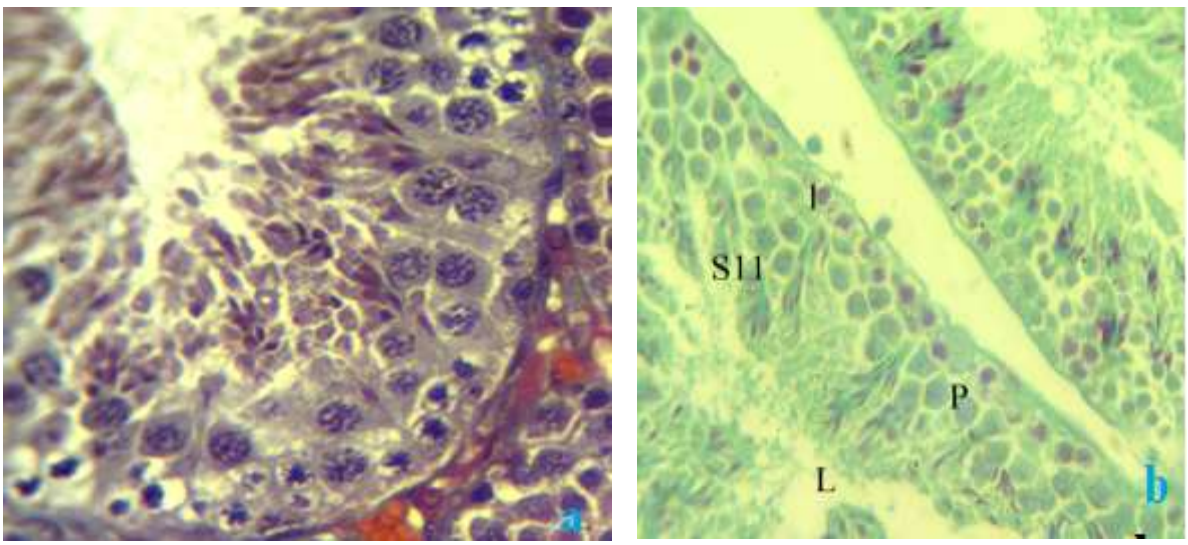


Figure 11 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: pachyten stage; L: lumen of the tubule; l: leptotene stage; S11: stage 11 of the epithelial cycle.

Stage XII: Spermatozoa with elongated and slender nuclei (Figure 12).

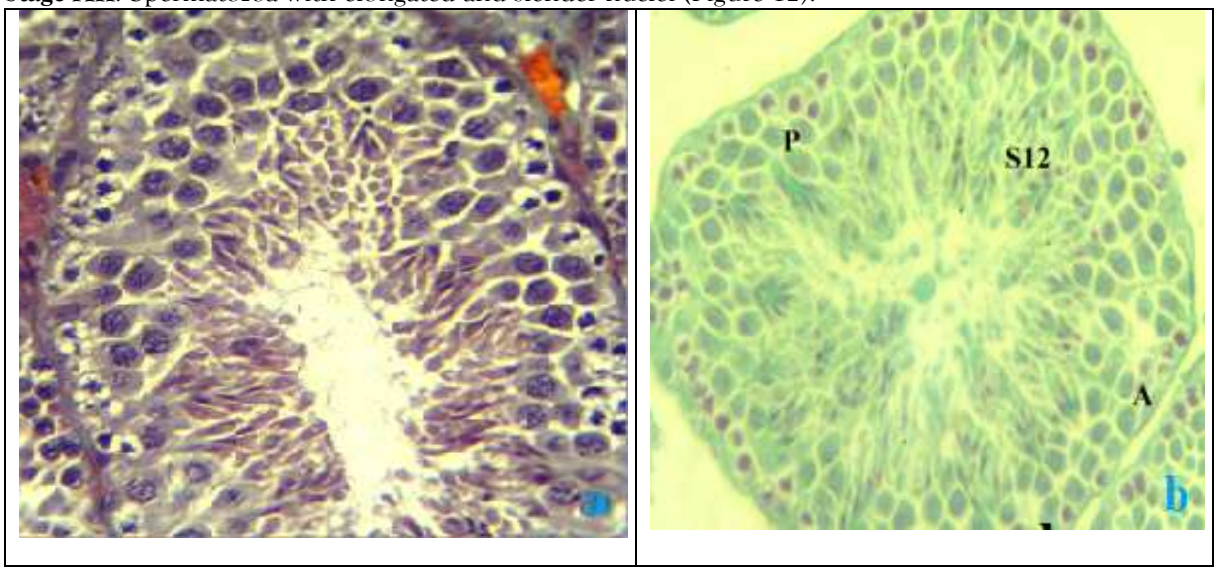


Figure 12 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. P: pachyten stage; A: type A spermatogonium; S12: stage 12 of the epithelial cycle.

Stage XIII : Primary spermatocytes at the pachytene and diplotene stages. Elongated spermatids with thin and slender nuclei (Figure 13).

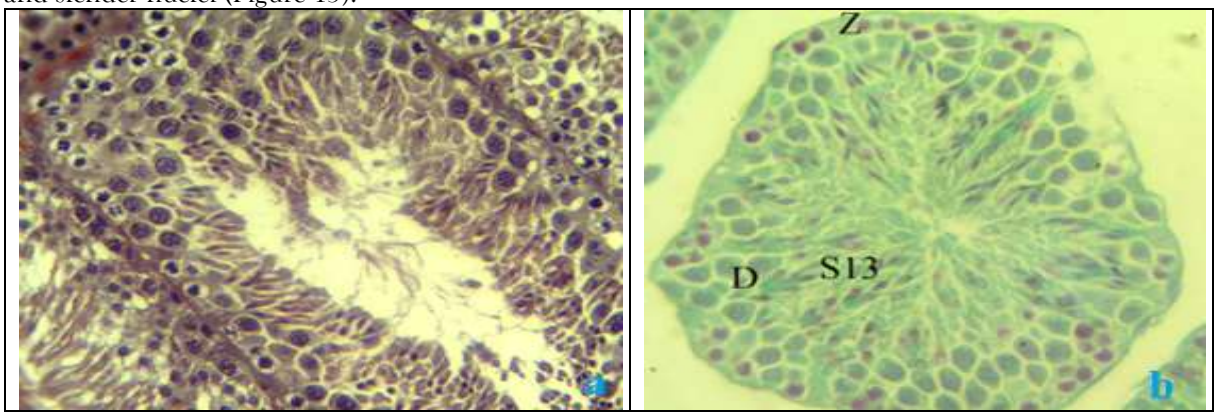


Figure 13 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. B: type B spermatogonium; S13: stage 13 of the epithelial cycle; z: zygotene stage; D: diplotene stage.

Stage XIV: Diplotene-stage primary spermatocytes generate secondary spermatocytes, which divide to produce spermatids that will appear at the next stage (Stage I) (Figure 14).

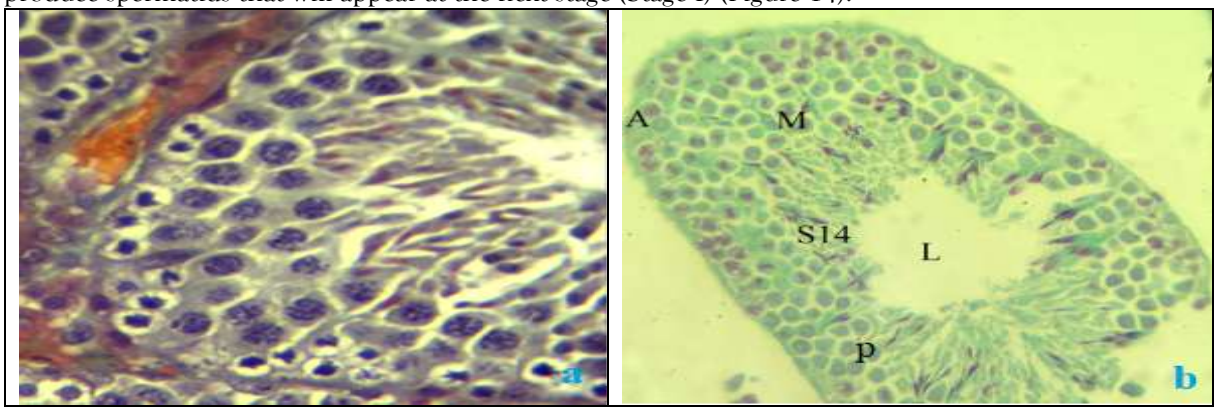
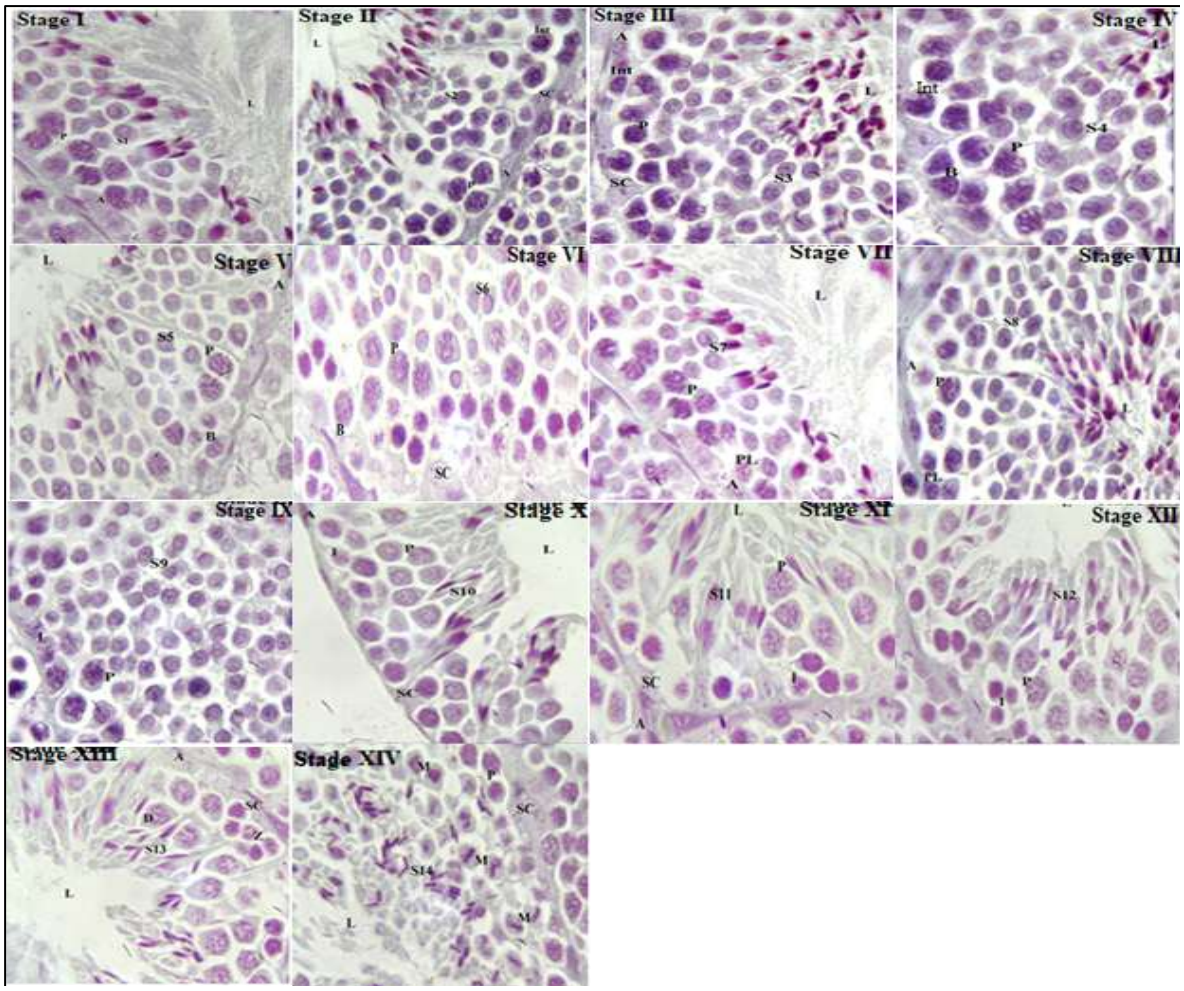


Figure 14 : Histological section of the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. **a**: Masson's Trichrome staining, G×40. **b**: Light Green staining, G×40. A:

type A spermatogonium; S14: stage 14 of the epithelial cycle; P: pachyten stage; M: mitosis.



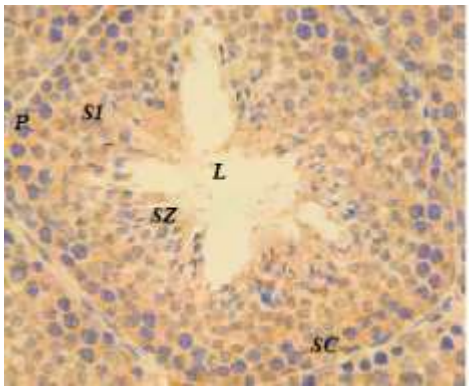
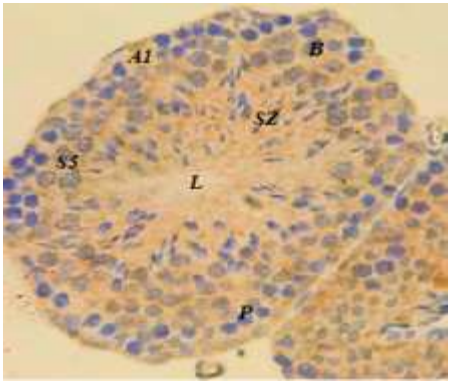
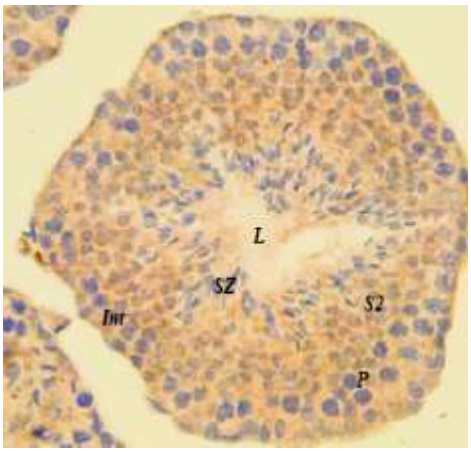
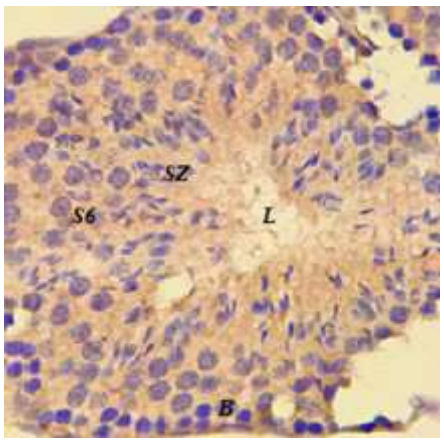
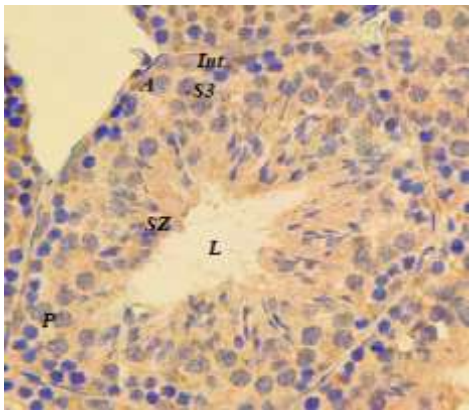
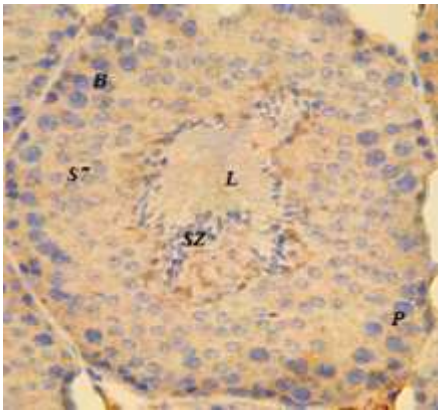
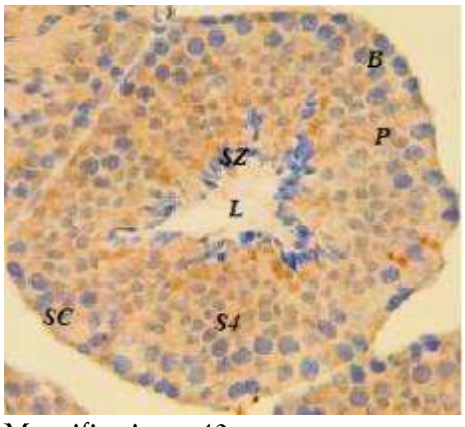
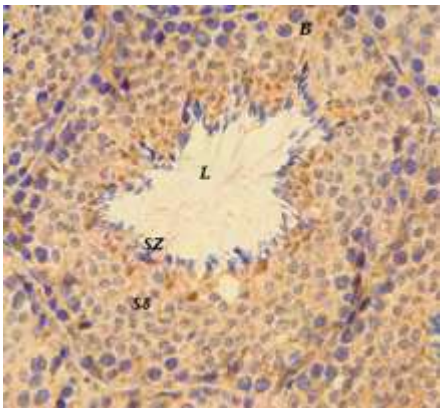
A: spermatogonium; Int: intermediate spermatogonium; S1–S14: different stages of the seminiferous epithelial cycle. PAS staining, magnification ×100.

3.2. Immunohistochemistry of MMP-2 in testicular sections during the active phase of the reproductive cycle

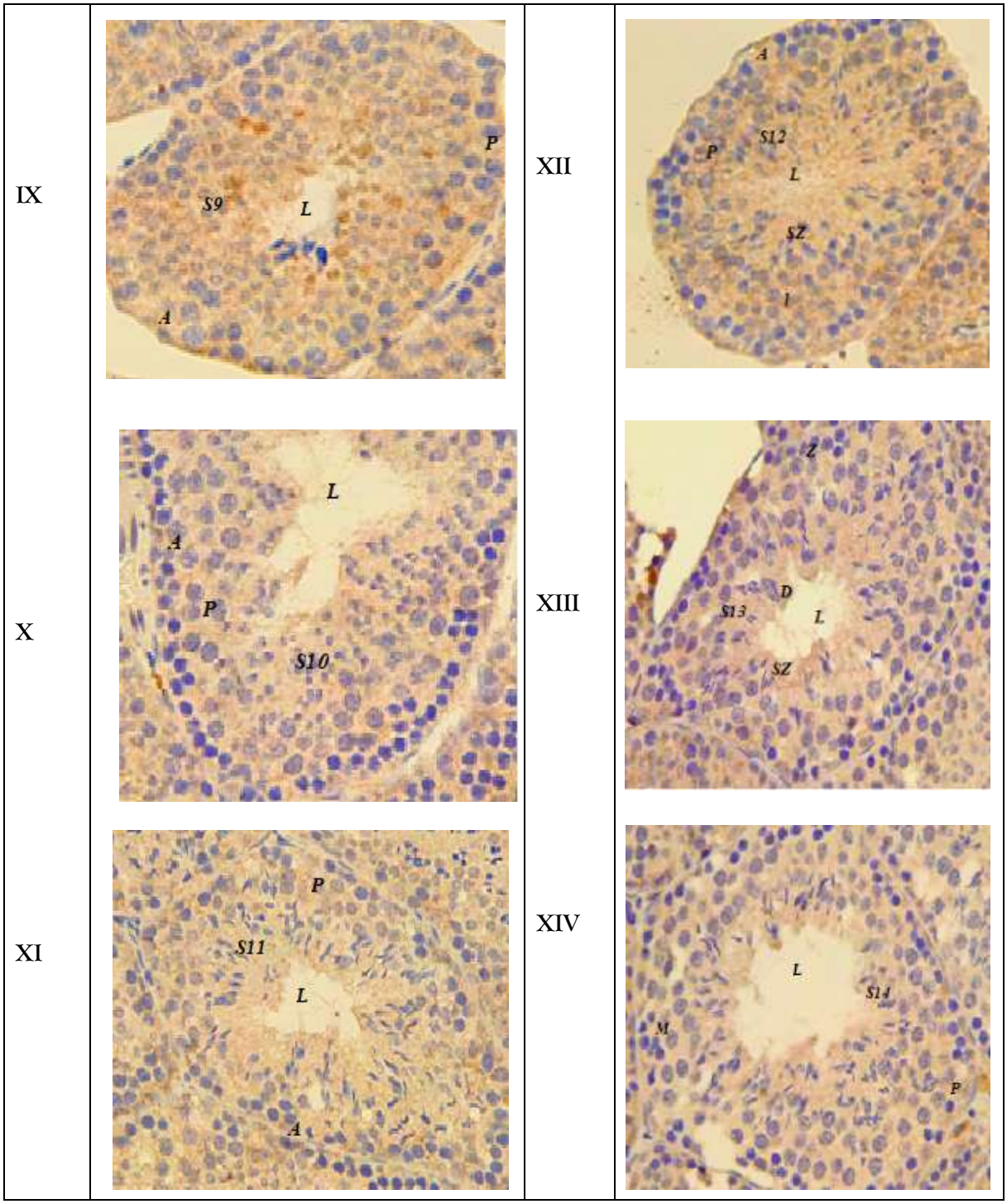
During the active period in the testes, MMP-2 exhibited high levels of expression in the intercellular space of the seminiferous epithelial layer (Table 1). In particular, the epithelial cells showed a strong immunohistochemical signal for MMP-2. However, the signal was notably weak in the lumen of the tubules. It is important to note that this gelatinase was not detected in the extracellular matrix delimiting the seminiferous tubules. In all positive controls, where the primary antibody was omitted, the immunohistochemical signal of MMP-2 remained positive. (Table 1)

Table 1 : Immunohistochemistry of MMP-2 in the seminiferous tubules of the testes in adult Jaculus jaculus during the period of sexual activity. Magnification G×40. S1–S14: stages of spermatid development; A: type A spermatogonium; B: type B spermatogonium; Int: intermediate spermatogonium; l: leptotene stage; Z: zygotene stage; P: pachytene stage; D: diplotene stage; M: mitosis ; SC: Sertoli cell; L: lumen of the tubule.

International Journal of Environmental Sciences
ISSN: 2229-7359
Vol. 11 No. 8, 2025
https://theaspd.com/index.php

Stage	Magnification x 40	Stage	Magnification x 40
I		V	
II		VI	
III		VII	
IV		VIII	
	Magnification x 40		Magnification x 40
Stage		Stage	

Magnification x 40



4. DISCUSSION

The aim of this study is to identify the cycle of the seminiferous epithelium in Jaculus jaculus in order to expand our basic knowledge of spermatogenesis in desert-dwelling species with seasonal reproduction, and to evaluate the role of MMPs, particularly MMP-2, during this process. Jaculus jaculus, a small nocturnal rodent found in both arid and semi-arid regions, employs adaptive mechanisms primarily related to reproductive function. This species demonstrates the ability to modulate its reproductive activity according to seasonal changes. In Jaculus jaculus, the testes exhibit a morphology characteristic of the genus, resembling smooth, relatively large beans compared to other desert rodents such as Gerbillus gerbillus (Aknoun et al., 2017), Meriones crassus (Smai-Hamdidouche et al., 2015), Meriones libycus (Zaim et al., 1992), and Meriones shawi (Flaitz et al., 2002).

The structural analysis of seminiferous tubules in the lesser jerboa during the period of sexual activity, using a histological approach with three topographic staining techniques (PAS staining, light green

staining and Masson's trichrome staining) has enabled us to establish for the first time the cycle of the seminiferous epithelium. In the lesser jerboa, the seminiferous tubules exhibit a segmental arrangement, with each transverse section of a tubule corresponding to a specific stage. This situation is also observed in currently studied rodent models: the rat (Rattus norvegicus) (Leblond & Clermont, 1952); the golden hamster (Mesocricetus auratus) (Clermont & Harvey, 1965); and the guinea pig (Cavia porcellus) (Clermont, 1963).

The identification of the stages of the epithelial cycle is based on the morphological characteristics of the spermatids, the abundance of certain types of germ cells, meiotic divisions, as well as the cellular appearance and composition of the seminiferous epithelium (Russell et al., 1990). The analysis of these criteria allowed us to identify the different stages of the epithelial cycle in the lesser jerboa**.** The seminiferous epithelium cycle of Jaculus jaculus is characterized by 14 stages of cellular development and maturation, designated I–XIV. These stages follow one another along the tubule in a well-defined order from I to XIV, forming a "spermatogenetic wave" (Leblond & Clermont, 1952), which ensures the continuous production of spermatozoa. Although the principle of the seminiferous epithelium cycle is common to many mammals, the number of stages and their duration vary according to species. This perfectly corroborates the results reported by Leblond and Clermont (1952), who described 14 stages of the seminiferous epithelium cycle in the rat, and 14 stages in the gerbil (Gerbillus tarabuli) (Hamidatou-khatti et al., 2018), as well as the same result in Psammomys obesus (Leblond & Clermont, 1952). In the mouse, by contrast, 12 stages have been identified, with 16 steps of spermiogenesis (Oakberg, 1956). The seminiferous epithelium cycle comprises 8 stages in the wild boar (Swierstra, 1968), in the goat (Capra hircus) (França et al., 1999), in the capybara (Hydrochoerus hydrochaeris) (Paula et al., 1999), in the domestic cat (Felis catus) (França & Godinho, 2003), in the dog (Soares et al., 2009), and in bats (Sturnira lilium) (Morais et al., 2013).

During the period of sexual activity in the lesser jerboa, the thickness of the seminiferous epithelium varies along the seminiferous epithelial cycle. Stages I–V show a progressive increase in epithelial thickness, reaching its maximum at stages VI and VII, where the diameter of the lumen is almost absent. This is due to a significant and progressive increase in the number of cells within the epithelial layer, resulting from mitotic and meiotic divisions of the progenitor cells. At stage IX, the spermatozoa, having left the tubules through spermiation, release the seminiferous lumen, which reappears once again. This observation corroborates the findings of Leblond and Clermont (1952) and Hamidatou-Khati et al (2018).

Immunohistochemical analysis revealed the presence of matrix metalloproteinases (MMP-2) in the seminiferous tubules of the testes of the desert jerboa (Jaculus jaculus) throughout the active period (autumn and winter) of the reproductive cycle. These enzymes were identified in the intercellular space of the seminiferous epithelium, as well as in the lumen of the tubules along the epithelial cycle. Previous studies have also detected MMP-2 in the same cells of other desert rodent species, such as Meriones and Psammomys (Kareskoski et al., 2021). This suggests that these enzymes play a role in intercellular processes, as well as in cell migration and differentiation, and confirms their involvement in extracellular processes and fertility (Dike et al., 2018). These observations are consistent with the results of other studies on rodents, such as Meriones libycus and Psammomys obesus (Legend et al., 1999).

MMP-2, being a proteolytic enzyme, targets both matrix and non-matrix substrates; however, maintaining an appropriate cellular concentration of this protein appears to be crucial for polarized cell migration, the development of reproductive organs, and spermatogenesis in adult rats (Metayer et al., 2002). MMP-2 produced by epithelial cells also participates in re-epithelialization, the regulation of cell migration (Ayvazova et al., 2016), and cell invasion (Shahed & Young, 2008). It is further involved in the controlled degradation of the extracellular matrix (ECM) and junctional complexes. Throughout all stages of the seminiferous epithelial cycle, MMP-2 plays a fundamental role in the tissue remodeling required for spermatogenesis (Cheng & Mruk, 2010) as well as spermiation (Vihko et al., 2003). The controlled degradation of junctional complexes between Sertoli cells and elongated spermatids is necessary for the displacement, differentiation, and maturation of germ cells during the cycle (Siemens et al., 2007; Mruk & Cheng, 2004).

5. CONCLUSION

Our results revealed, for the first time, that the seminiferous epithelium cycle in Jaculus jaculus is characterized by 14 well-defined stages, classified from I to XIV. The stages of the seminiferous epithelium

cycle were identified using the method of cellular associations. PAS staining and light green staining were preferred for the fine discrimination of stages, as they allow clear visualization of the acrosome and cell nuclei, while Masson's trichrome was used complementarily to analyze tubular architecture and cellular associations. Throughout the epithelial cycle, the cells produce matrix metalloproteinases (MMP-2). The identification of MMP-2 in the testes of Jaculus jaculus during the active phase of the reproductive cycle suggests that this enzyme plays a crucial role in various cellular activities, particularly in spermatogenesis and spermiogenesis. These findings significantly enhance our understanding of the reproductive system in semi-desert rodents with seasonal reproduction.

REFERENCES

1. Amirat, Zaina, Farida KHAMMAR, and Roger BRUDIEUX (1977). Variations saisonnières comparées de l'activité sexuelle (données pondérales) chez deux espèces de rongeurs (Psammomys obesus et Gerbillus gerbillus) du Sahara occidental algérien. Mammalia, 41(3), 341–??.
2. Amori, G., & Hutterer, R. (1995). Jaculus jaculus (Linnaeus, 1758) — Lesser Egyptian Jerboa. In: Mammalian Species (Vol. 495, pp. 1–5). American Society of Mammalogists. https://doi.org/10.2307/3504022
3. Areskoski M., Vakkamäki J., Laukkanen K., Palviainen M., Johannisson A., Katila T. (2021) Matrix metalloproteinase (MMP)-2, MMP-9, semen quality and sperm longevity in fractionated stallion semen — Theriogenology, Volume 164, pages 93-99.
4. Atabakhsh, M., Khodadadi, I., Amiri, I., Mahjub, H., & Tavilani, H. (2018). Activity of matrix metalloproteinase-2 and -9 in follicular fluid and seminal plasma and its relation to embryo quality and fertilization rate. Journal of Reproduction & Infertility, 19(3), 140–145.
5. Ayvazova, N., Rilcheva, V., Konova, E., Roussev, R., & Rashev, P. (2016). Matrix metalloproteinase MMP-2 and MMP-9 activities in seminal plasma. Journal of Biomedical and Clinical Research, 9(2), 114–120. https://doi.org/10.1515/jbcr-2016-0016
6. Baumgart, E., Lenk, S. V., Loening, S. A., & Jung, K. (2002). Quantitative differences in MMP-2, MMP-9, TIMP-1 and TIMP-2 in seminal plasma of normozoospermic and azoospermic patients. Human Reproduction, 17(11), 2919–2923. https://doi.org/10.1093/humrep/17.11.2919
7. Berndtson, W.E., 1977. Methods for quantifying mammalian spermatogenesis: a review. J. Anim. Sci. 44, 818–833.
8. Bode, W., Fernandez-Catalan, C., Tschesche, H., Grams, F., Nagase, H., & Maskos, K. (1999). Structural properties of matrix metalloproteinases. Cellular and Molecular Life Sciences CMLS, 55(4), 639-652.
9. Brew, K., Dinakarpandian, D., & Nagase, H. (2000). Tissue inhibitors of metalloproteinases: evolution, structure and function. Biochimica et Biophysica Acta (BBA)-Protein Structure and Molecular Enzymology, 1477(1-2), 267-283.
10. Brown, R. D., Jones, G. M., Laird, R. E., Hudson, P., & Long, C. S. (2007). Cytokines regulate matrix metalloproteinases and migration in cardiac fibroblasts. Biochemical and Biophysical Research Communications, 362(1), 200–205. https://doi.org/10.1016/j.bbrc.2007.08.003
11. Cheng CY, Mruk DD. A local autocrine axis in the testes that regulates spermatogenesis.2010
12. Clermont, Y. (1963). The cycle of the seminiferous epithelium in man. The American Journal of Anatomy, 112(3), 35–51. https://doi.org/10.1002/aja.1001120104
13. Clermont, Y., & Harvey, S. C. (1965). The duration of the cycle of the seminiferous epithelium in the rat. American Journal of Anatomy, 117(3), 507–523. https://doi.org/10.1002/aja.1001170306
14. Di Nezza, L. A., Misajon, A., Zhang, J., Jobling, T., Quinn, M. A., Ostör, A. G., Nie, G., Lopata, A., & Salamonsen, L. A. (2002). Presence of active gelatinases in endometrial carcinoma and correlation of matrix metalloproteinase expression with increasing tumor grade and invasion. Cancer, 94(5), 1466–1475.
15. Erxleben, J. C. P. (1777). Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium: classis I. Mammalia (Vol. 1). Weygand.
16. Franca, A., Loi, A., Davies, W. D. (1998). Selection of annual ryegrass for adaptation to semi-arid conditions. European Journal of Agronomy, 9, 71–78. https://doi.org/10.1016/S1161-0301(98)00024-0
17. França, L. R., & Godinho, C. L. (2003). Testis morphometry, seminiferous epithelium cycle length, and daily sperm production in domestic cats (Felis catus). Biology of Reproduction, 68(5), 1554-1561.
18. França, L. R., Becker-Silva, S. C., & Chiarini-Garcia, H. (1999). The length of the cycle of seminiferous epithelium in goats (Capra hircus). Tissue and Cell, 31(3), 274-280.
19. Hamidatou-Khati, W., Moudilou, E., Exbrayat, J.-M., & Hammouche, S. (2018). Immunolocalization of RFamide-Related Peptide-3 (RFRP-3) in a desert rodent Gerbillus tarabuli during the seminiferous epithelium cycle. Tissue and Cell, 56, 16–27. https://doi.org/10.1016/j.tice.2018.09.004
20. Holden, M.E. & Musser, G.G. (2005). Family Dipodidae. In: Wilson, D.E. & Reeder, D.M. (Eds.), Mammal Species of the World: A Taxonomic and Geographic Reference (3rd ed.), Vol. 2, pp. 871–893. Johns Hopkins University Press, Baltimore, Maryland, USA.
21. Kessenbrock, K., Plaks, V., & Werb, Z. (2010). Matrix metalloproteinases: regulators of the tumor microenvironment. Cell, 141(1), 52–67.
22. Kheddache, A., Moudilou, E. N. T., Zatra, Y., Aknoun-Sail, N., Amirat, Z., Exbrayat, J. M., & Khammar, F. (2017). Seasonal morphophysiological variations in the prostatic complex of the Tarabul's gerbil (Gerbillus tarabuli). Tissue and Cell, 49(2), 345-357.
23. Leal, M. C., & França, L. R. (2006). The seminiferous epithelium cycle length in the black tufted-ear marmoset (Callithrix penicillata) is similar to humans. Biology of Reproduction, 74(4), 616–624

24. Leblond, C. P., & Clermont, Y. (1952). Definition of the stages of the cycle of the seminiferous epithelium in the rat. American Journal of Anatomy, 90(1), 91–126. https://doi.org/10.1002/aja.1000900106
25. Leblond, C. P., & Clermont, Y. (1952). Definition of the stages of the cycle of the seminiferous epithelium in the rat. Annals of the New York Academy of Sciences, 55(4), 548–573. https://doi.org/10.1111/j.1749-6632.1952.tb27330.x
26. Linnaeus, C. (1758). Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 10e édition, Vol. 1, pp. 1–824. Holmiae (Stockholm), Sweden.
27. Lohi, J., Wilson, C. L., Roby, J. D. & Parks, W. C. (2001). Epilysin, a novel human matrix metalloproteinase (MMP-28) expressed in testis and keratinocytes and in response to injury. The Journal of Biological Chemistry, 276(13), 10134–10144. https://doi.org/10.1074/jbc.M001599200
28. MacNeil, T., Vathiotis, I. A., Martinez-Morilla, S., Yaghoobi, V., & Rimm, D. L. (2020). Antibody validation for protein expression on tissue slides: A protocol for immunohistochemistry. BioTechniques, 69(6), 460-468. https://doi.org/10.2144/btn-2020-0095
29. Massova, I., Kotra, L. P., Fridman, R., & Mobashery, S. (1998). Matrix metalloproteinases: structures, evolution, and diversification. FASEB Journal, 12(12), 1075–1095
30. Métayer, S., Dacheux, F., Dacheux, J.-L., & Gatti, J.-L. (2002). Comparison, characterization, and identification of proteases and protease inhibitors in epididymal fluids of domestic mammals. Matrix metalloproteinases are major fluid gelatinases. Biology of Reproduction, 66(5), 1219–1229. https://doi.org/10.1095/biolreprod66.5.1219
31. Morais, D.B., de Paula, T.A.R., Barros, M.S., Balarini, M.K., de Freitas, M.B.D., da Matta, S.L.P., 2013. Stages and duration of the seminiferous epithelium cycle in the bat Sturnira lilium. J. Anat. 222, 372–379. https://doi.org/10.1111/joa.12016.
32. Morgunova, E., Tuuttila, A., Bergmann, U., Isupov, M., Lindqvist, Y., Schneider, G., & Tryggvason, K. (1999). Structure of human pro-matrix metalloproteinase-2: activation mechanism revealed. Science, 284(5420), 1667–1670. https://doi.org/10.1126/science.284.5420.1667
33. Nagase, H., Visse, R., & Murphy, G. (2006). Structure and function of matrix metalloproteinases and TIMPs. Cardiovascular Research, 69(3), 562–573.
34. Oakberg, E. F. (1956a). A description of spermiogenesis in the mouse and its use in analysis of the cycle of the seminiferous epithelium and germ cell renewal. American Journal of Anatomy, 99, 391–413.
35. Oakberg, E. F. (1956b). Duration of spermatogenesis in the mouse and timing of stages of the cycle of the seminiferous epithelium. American Journal of Anatomy, 99, 507–516
36. Paula, T.A.R., Chiarini-Garcia, H., França, L.R., 1999. Seminiferous epithelium cycle and its duration in capybaras (Hydrochoerus hydrochaeris). Tissue Cell 31, 327–334. https://doi.org/10.1054/tice.1999.0039.
37. Ray, J. M., & Stetler-Stevenson, W. G. (1994). The role of matrix metalloproteases and their inhibitors in tumour invasion, metastasis and angiogenesis. European Respiratory Journal, 7(11), 2062-2072.
38. Rivera-Ruiz, M. E., Rodríguez-Quiñones, J. F., Akamine, P. & Rodríguez-Medina, J. R. (2010). Post-transcriptional regulation in the myo1Δ mutant of Saccharomyces cerevisiae. BMC Genomics, 11, 690. https://doi.org/10.1186/1471-2164-11-690.
39. Roosen-Runge, E. C., & Giesel, L. O. Jr. (1950). Quantitative studies on spermatogenesis in the albino rat. American Journal of Anatomy, 87(1), 1–30
40. Roy, M. J., Kraus, P. L., Cooper, J. A., Cherstniakova, S., Coll, R., Seegers, C. A., ... & Cantilena, L. (2006). Initial evaluation of N, N-diethyl-m-toluamide and permethrin absorption in human volunteers under stress conditions. Military medicine, 171(2), 122-127.
41. Roy, P. P., Paul, S., Mitra, I., & Roy, K. (2009). On two novel parameters for validation of predictive QSAR models. Molecules, 14(5), 1660–1701. https://doi.org/10.3390/molecules14051660
42. Russell LD, Ettlin RA, Sinha-Hikim AP, Clegg ED. Histological and histopathological evaluation of the testis. Clearwater (FL): Cache River Press; 1990.
43. Russell, L.D., Ettlin, R.A., Sinha-Hikin, A.P., Clegg, E.D., 1990. Histological and Histopathological Evaluation of the Testis. Cache River Press, Clearwater.
44. Salverson, T. J., McMichael, G. E., Sury, J. J., Shahed, A., & Young, K. A. (2008). Differential expression of matrix metalloproteinases during stimulated ovarian recrudescence in Siberian hamsters (Phodopus sungorus). General and Comparative Endocrinology, 155(3), 749–761. https://doi.org/10.1016/j.ygcen.2007.09.003
45. Siemens K, et al. Matrix metalloproteinases and their inhibitors in testicular function. Reproductive Biology and Endocrinology, 2007; Mruk DD, Cheng CY. Cellular junctions in the testis: a perspective.trends in endocrinology metabolism 2004
46. Smai-Hamdidouche, S., Menad, R., Belhocine, M., Gernigon-Spychalowicz, T., Khammar, F., & Exbrayat, J.-M. (2015). Histophysiologie du vagin chez le mérion de Libye Meriones libycus, rongeur gerbillidé nocturne, au cours du cycle de reproduction. Annales d'Endocrinologie, 76(4), 500.
47. Soares, J.M., Avelar, G.F., França, L.R., 2009. The seminiferous epithelium cycle and its duration in different breeds of dog (Canis familiaris). J. Anat. 215, 462–471. https:// doi.org/10.1111/j.1469-7580.2009.01122.x.
48. Sternlicht, M. D., & Werb, Z. (2001). How matrix metalloproteinases regulate cell behavior. Annual Review of Cell and Developmental Biology, 17, 463–516. https://doi.org/10.1146/annurev.cellbio.17.1.463 SCIRP
49. Swierstra, E. E. (1968). Cytology and duration of the cycle of the seminiferous epithelium of the boar; duration of spermatozoan transit through the epididymis. The Anatomical Record, 161(2), 171-185.
50. Vihko KK, et al. Regulation of extracellular matrix and cell adhesion during spermatogenesis. 2003
51. Vu, T. H., & Werb, Z. (2000). Matrix metalloproteinases: effectors of development and normal physiology. Genes & Development, 14(17), 2123–2133. https://doi.org/10.1101/gad.815400

52. Xiao, W., Sun, M., & Santosh, M. (2023). Continental reconstruction and metallogeny of the Circum-Junggar areas and termination of the southern Central Asian Orogenic Belt. Geoscience Frontiers, 6(2), 137-140.
53. Yang, W. J., Liu, F. C., Hsieh, J. S., Chen, C. H., Hsiao, S. Y., & Lin, C. S. (2015). Matrix metalloproteinase 2 level in human follicular fluid is a reliable marker of human oocyte maturation in in vitro fertilization and intracytoplasmic sperm injection cycles. Reproductive Biology and Endocrinology, 13, 1.
54. Zaime, A., Laraki, M., Gautier, J. Y., & Garnier, D. H. (1992). Seasonal variations of androgens and of several sexual parameters in male Meriones shawi in southern Morocco. General and Comparative Endocrinology, 86(2), 289–296. https://doi.org/10.1016/0016-6480(92)90113-X
55. Zaime, A., Laraki, M., Gautier, J. Y., & Garnier, D. H. (1992). Seasonal variations of androgens and of several sexual parameters in male Meriones shawi in southern Morocco. General and Comparative Endocrinology, 86(2), 289–296. https://doi.org/10.1016/0016-6480(92)90113-X