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Original Research Paper

SOME MORPHOLOGICAL ASPECTS OF THE CREMASTER MUSCLE IN BROWN HARE AND DOMESTIC RABBIT

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Summary: The cremaster muscle is formed by muscle fibres that are descended from the caudal border of *m. obliquus internus abdominis* in males. The extent and functioning of the cremaster muscle differs among mammals. In rodents and lagomorphs testes migrate between scrotum and abdominal cavity and therefore the cremaster is extensive and highly active. There were hypotheses that the functioning of cremaster muscle is correlated with the seasonal testicular regression in brown hare. We previously established that position of the testes in hares is strongly correlated to the ambient temperature and not to the reproductive activity. Our present aim was to establish fibre type profile of the cremaster muscle in comparison with its origin, the internal oblique abdominal muscle, in both brown hare and laboratory rabbits. Muscle samples from 6 hares (3 in quiescent and 3 in reproductively active period) and 6 rabbits were collected and subjected to enzyme histochemistry (fibre typing according to mATPase, SDH and α-GPDH activity and glycogen content) and immunohistochemistry directed to different myosin heavy chain isoforms. The cremaster muscle completely surrounded the testicle and epididymis in both species. While enzyme- and immunohistology revealed *m. obliquus internus abdominis* as a predominantly fast muscle, central bundles of cremaster muscle contained mainly slow fibre types. However, the peripheral parts of cremaster were predominantly composed of fast IIA fibre type indicating functionally important intra-muscular variability. In rabbits, which were housed in constant ambient temperature, the central "slow" bundle was substantially smaller. Furthermore *m. cremaster* had high glycogen content and high glycolitic capacity, including the presence of uncommon SOG fibres. No prominent differences in fibre types between breeding and non-breeding seasons were found.

Key words: *m. cremaster*; brown hare; rabbit; skeletal muscle fibres; mATPase; myosin

Introduction

In rodents and lagomorphs testes can freely migrate between scrotum and abdominal cavity because of open inguinal canal. Abdominal displacement is important in regulating intratesticular temperature (in favourable nutritional conditions most rodents breed also in the coldest months), protecting testes in fights and also slightly helping the ejaculation (1). *M. cremaster* is extensive and likely active muscle. Some rodents (i.e. chinchillas, degus) are referred to as nonscrotal rodents, where testes remain inside abdomen and only tail of epididymis lays inside scrotal sac (2). Lagomorpha seem to lie further apart, being phylogenetically more close to primates than rodents, however, they still share many physiological and anatomical features with rodents (3). Scrotal sac is doubled and clearly evident in descended testis. In laboratory rodents, the cremaster muscle consists of fairly thin fleshy bundle arranged in a manner to form a sac that encloses the testicle. The muscle is usually referred as an extension of *m. obliquus abdominis internus* but in rat and human also contribution of *m. transversus abdominis* is reported (4, 5, 6). Despite *m. cremaster* being used in physiological experiments and experimental surgery for decades (7), exact morphological aspects or the fibre type profile of the cremaster muscle is not widely known among mammals. In rat and hamster the reported predominant fibre type (60-80% of the muscle area) was IIB according to Brooke and Keiser classification at the time – today's methods would probably demonstrate the majority of IIX fibres. Besides, the number of those

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fibres decreased with age in favour to IIA fibres (8). In contrast, in carnivore ferret the type I fibres predominated with 66.2% (9). In guinea pigs both slow and fast fibres were reported but no details on ratio was given (10). In a comparative study of domestic and laboratory mammals the highest proportion of proprioreceptors (muscle spindles) in cremaster were found in rabbits, followed by sheep and rodents (11) indicating an active muscle in species we decided to research.

In previous research on brown hare reproductive activity we found a strong correlation between the testis location and ambiental temperature. In coldest months, the testes were displaced abdominally halfway or totally, regardless of the current reproductive activity – full or arrested spermatogenesis (12). Therefore we assumed that *m. cremaster* must be specifically adapted to special functioning and the fibre type profile would differ from it's origin – *m. obliquus abdominis* internus. Differences in fibre types between breeding and non-breeding season (or warm and cold months) were expected in brown hare, but not in domestic rabbit, bred in constant laboratory conditions. The aim of this study was therefore to evaluate the position and extent of *m. cremaster* and to establish basic fibre type profile in brown hare and domestic rabbit.

Material and methods

Muscle samples

The muscles were sampled from 6 brown hares (*Lepus europaeus*) bred in outdoor pens. 3 were sacrificed in reproductively active period (July) and 3 in quiescent period (November). About 1 cm ring of *m. cremaster* was cut on three locations: proximal part (at the point of attachment to tunica vaginalis), middle part (at the head of epididymis) and lower part (at the tail of epididymis). 1 cm^2 of m. obliquus internus abdominis was also taken from most caudal border of the muscle, where the distinction between abdominal wall and scrotal sac becomes evident.

For comparison purposes cremaster and internal oblique abdominal muscles from 6 conventional laboratory rabbits (New Zealand white rabbit) were also taken. They share very similar anatomy with brown hare, including the location of reproductive organs and muscles. The animals were housed at constant ambient temperature of 18°C.

Muscle samples were frozen with submersion in liquid nitrogen and stored at -80°C. Transverse serial cryosections (10 μm) were cut on Leica CM 1800 cryostat at -17°C, mounted on 3-aminopropyl triethoxysilane (APES) covered slides and air-dried.

mATPase histochemistry

To determine fibre types the sections were processed for mATPase reaction following the procedure by Brooke and Keiser (13). The sections were incubated in 0.1 M Na-acetate at pH 4.35 and in 0.2 M Na-acetate at pH 4.4 and 4.6 for 5 minutes at room temperature. For the alkaline preincubation, the solutions of 0.1 M $CaCl_2$, 0.07 M Na-acetate and 0.075 M Na-barbital adjusted to pH 9.8 and 10.2 were used (15 minutes, room temperature). After preincubation sections were washed and incubated in solution of 0.1 M CaCl2, 0.07 M Na-acetate and 0.075 M Na-barbital, pH 9.45 with addition of 1.5 mg/ml of ATP for 60 minutes (following the acid preincubation) or 30 minutes (following the alkaline preincubation) at 37°C. For fibre type designation the described results by Hämäläinen and Pette (14) were observed.

Immunohistochemistry

To demonstrate the myosin heavy chain (MHC) isoform expression, different primary monoclonal antibodies specific to MHC isoforms of different mammals were used. MHC-I was revealed with antibody MHC-slow (diluted 1:40 in PBS) supplied by Novocastra Laboratories. To demonstrate the expression of fast MHC isoforms MHC-fast (diluted 1:40 in PBS; Novocastra Laboratories), A4.74 (diluted 1:40 in PBS, Alexis Biochemicals) specific to MHC-IIa in man and rodents but also reacting with MHC-IIx in dog (15), BF-F3 directed against MHC-IIb and BF-35, an antibody specific to all MHC isoforms except MHC-IIx (16) were used. Serial cryosections were air-dried, washed with phosphate buffer saline (PBS) and then incubated with primary antibody in humidified box overnight at 4°C. Novostain Super ABC Kit (Novocastra Laboratories) was used to reveal immunohistochemical reaction according to the manufacturer's instructions. The stained sections were then dehydrated and mounted with Syntetic Moutant (Shandon, USA).

Metabolic profile of muscle fibres

To estimate the fibres' basic metabolic profile the activity of the oxidative enzyme succinate dehydrogenase (SDH) and the glycolytic one, i.e. mitochondrial menadion-linked α-glycerophosphate dehydrogenase (α-GPDH) was demonstrated as previously described by Nachlas et al. (17) and Dubowitz and

Brooke (18), respectively. Glycogen content in the fibres was demonstrated with PAS staining (Periodic acid-Schiff reaction).

Serial cryosections were analyzed with Nikon Microphot FXA microscope (Nikon instruments Europe B.V., Badhoevedorp, The Netherlands) and Lucia-G image analysing system (Laboratory Imaging, Prague, Czech Republic).

Results

The position and extent of m. cremaster

In scrotally located testes, that is in all rabbits and hares from summer, the cremaster muscle was thin, practically translucent layer, completely encircling processus vaginalis (Fig 1a). On dorsal aspect, especially in the pampiniform plexus region, the muscle was darker to naked eye - seemingly thicker (Fig 1b). This part originated on and parallel to *lig. inguinale* (Fig 1c). In retracted testis (hares from November) the cremaster was a reddish creased sac, about 1 centimetre long still encircling the *cauda epididymis* (Fig. 2).

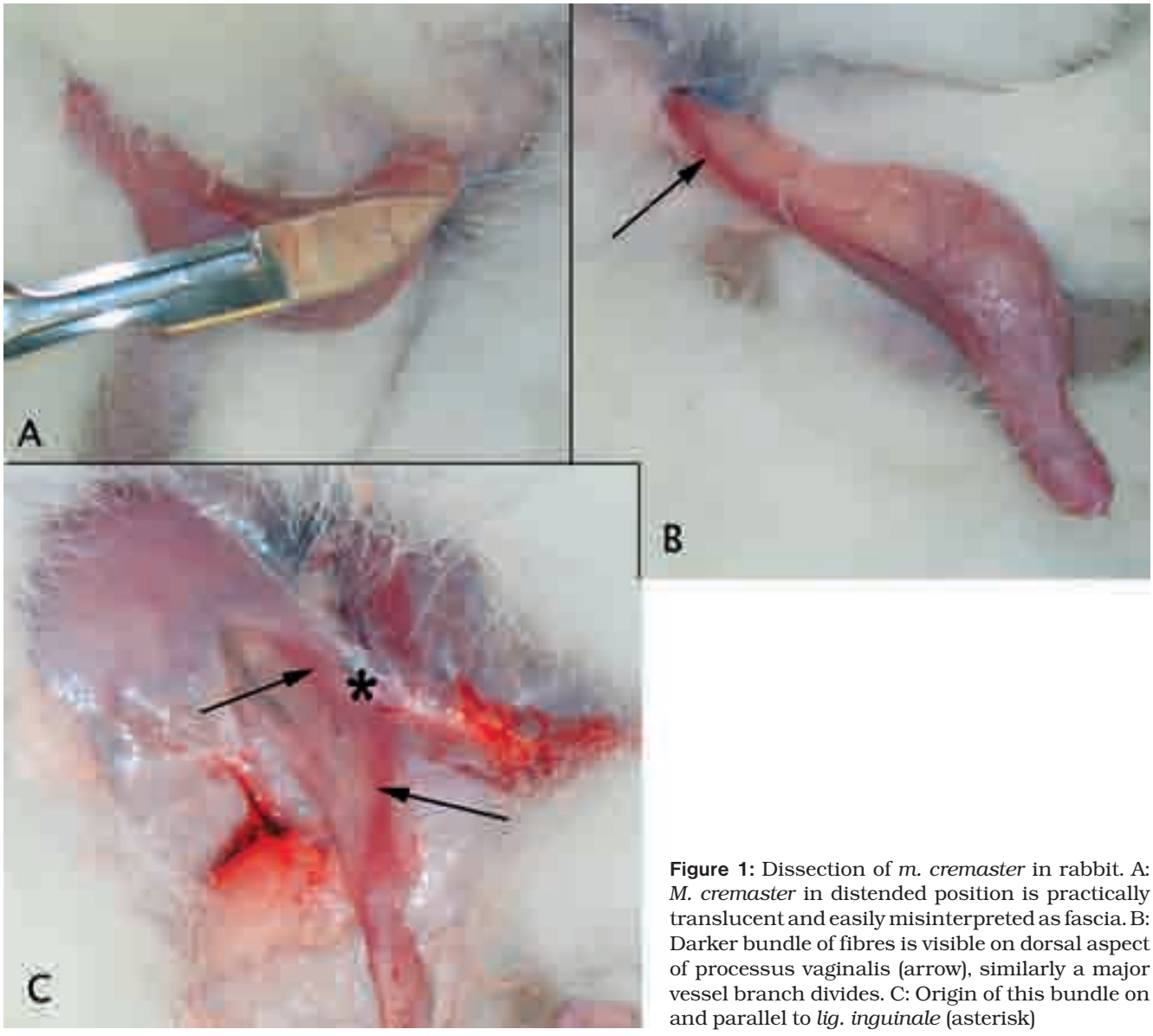

Figure 1: Dissection of *m. cremaster* in rabbit. A: *M. cremaster* in distended position is practically translucent and easily misinterpreted as fascia. B: Darker bundle of fibres is visible on dorsal aspect of processus vaginalis (arrow), similarly a major vessel branch divides. C: Origin of this bundle on and parallel to *lig. inguinale* (asterisk)

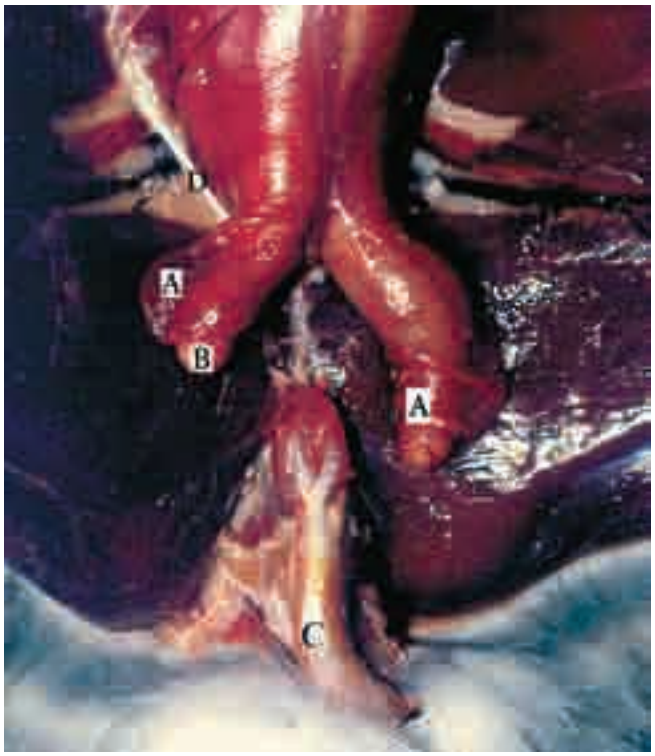

Figure 2: Inguinal and abdominal displacement of testes during cold months in brown hare. Skin removed. *M. cremaster* (A) is visibly thick and creased over the *cauda epididimis* (B). Penis (C), *lig. inguinale* (D)

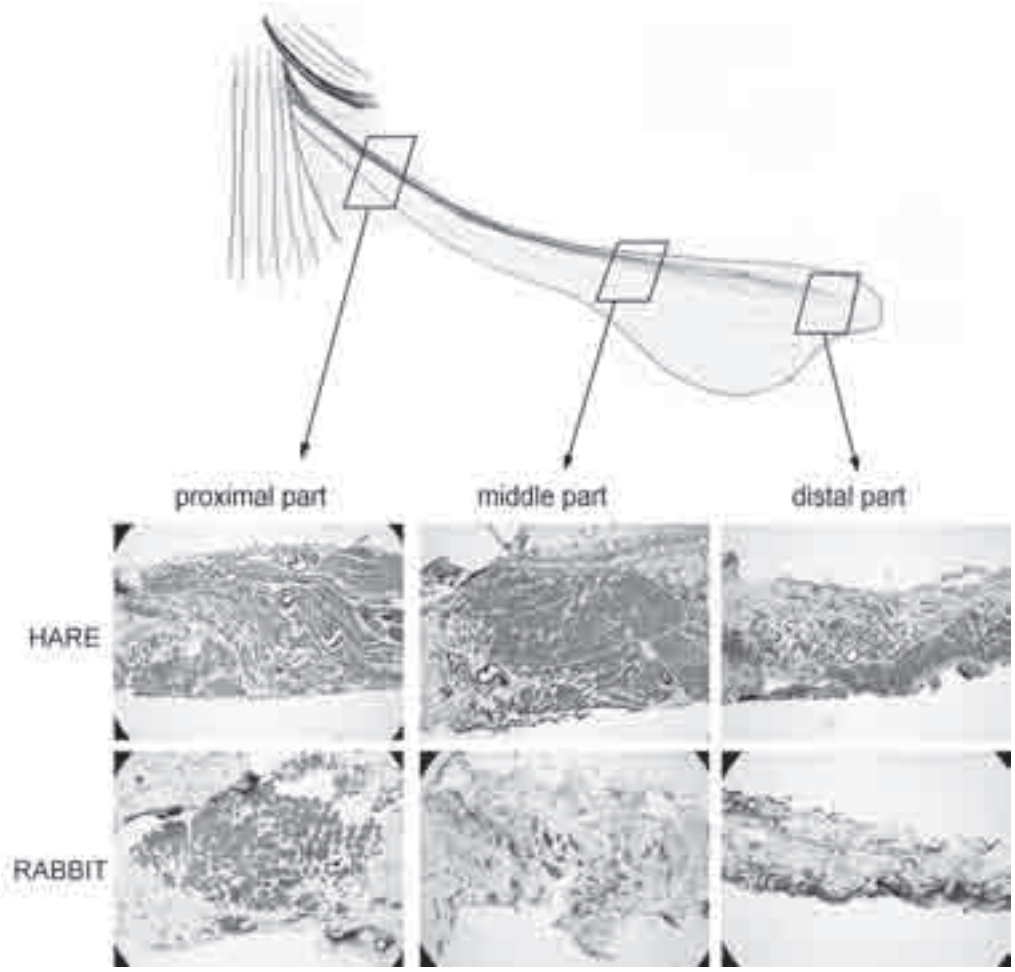

Figure 3: Cross sections of cremaster muscle on three different locations, as graphically represented above, at small magnification shoving the region of dorsal muscle aspect. Muscle fibres in this region stained predominantly dark (slow fibres) in mATPase reaction with acid preincubation in hare. In rabbit such bundle was evident only in proximal region of muscle and became superficially located in distal parts

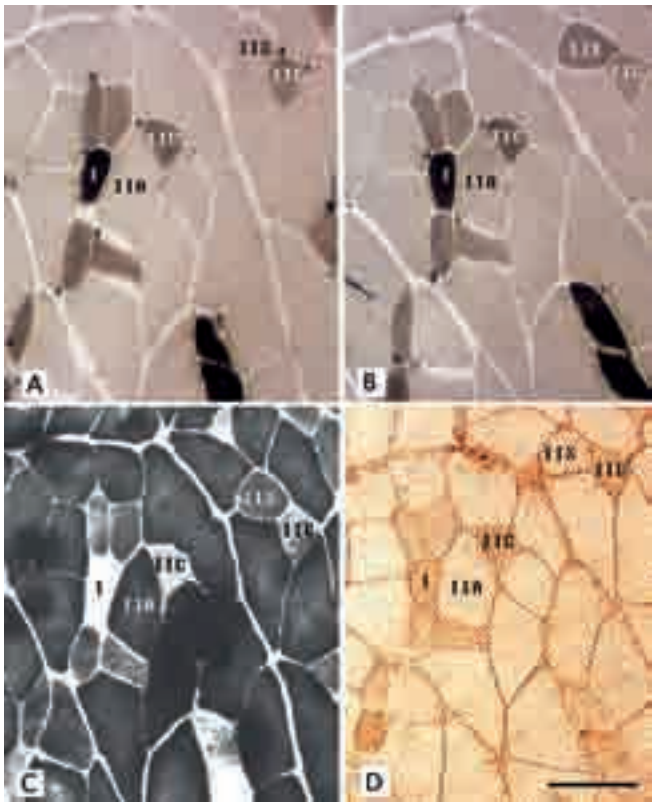

Figure 4: Serial cross-sections of *m. obliquus internus* abdominis in rabbit. Fibre types I, IIC, IIA and IIX were distinguished. A: staining for mATPase after preincubation at pH 4.3, B: 4.5, C: 10.2, D: immunohistochemistry with MHC-slow antibodies. Scale bar = 100 μm

Fibre types in m. cremaster and m. obliquus abdominis internus

Based on mATPase typing and immunohistochemistry demonstration of slow and fast isoforms fibres I, IIC, IIA, IIX and IIAX were demonstrated. Antibody A4.74 gave the same results as MHC-fast antibody (positive in IIA, IIAX and IIX and weakly positive in IIC) and this agreed with mATPase typing and MHC-slow reactions. No clear positive reactions in staining with BF-F3 were found therefore no IIB fibres were demonstrated. Also no clear negative reaction with BF-35 antibodies was encountered (results not shown) therefore this antibody is not very specific to distinguish between IIA, IIAX and IIX fibres in rabbit or hare.

The *m. cremaster* was not homogenous. It was clear that the central portion, as graphically represented in Figure 3, predominantly contained different fibre types than peripheral parts. This central congregation of predominantly slow fibres corresponded to dorsal aspect of vaginal process and was extensive in hare, but in rabbit pronounced only in the proximal part, while distally the slow fibres remained congregated superficially in the dorsal aspect (lower right in Fig. 3). Peripheral parts had high counts of fast IIA fibres, comparable to *m. obliquus abdominis* internus (Fig. 4) and even higher – there were no slow fibres at all in some distal and peripheral fascicles. Bundle of slow fibres normally didn't have distinct boundaries – the transitional area had mixed count of fibres (Fig. 5). Fibre diameter differed between the two muscles – in *m. obliquus abdominis* internus the average diameter was close to 50 μm, in *m. cremaster* 25 μm.

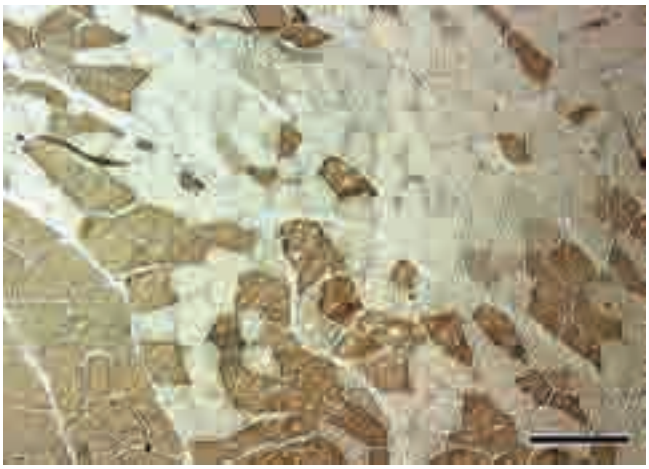

Figure 5: Section of transitional area between bundles of exclusively type I fibres (dark staining – lower left) and other parts of the muscle that contain predominately type IIA fibres (weak staining - upper right) in *m. cremaster* of brown hare. mATPase histochemistry, pH 4.5. Scale bar = 100 μm

Further distinction between rabbit and hare was evident in the number of hybrid fibres, which were scarce in cremaster of rabbit (data not shown) but averaged 15% in cremaster of hare, especially type IIC (Figure 6); a few IIAX fibres were also noted. Interestingly, in both animals all muscle fibres had a pronounced glycolitic capacity (α-GPDH); the enzyme-histochemistry staining intensity varied moderately in rabbit but only slightly in hare. A classification of SOG (slow oxidative-glycolitic), FOG (fast oxidative-glycolitic) fibre types could be applied (Figure 7). Compared to *m. obliquus internus abdominis* the cremaster muscle also had substantively higher glycogen content in the muscle fibres as established with PAS staining (Fig. 8). No significant variations in fibre type proportions between breeding and non-breeding season were found in hare.

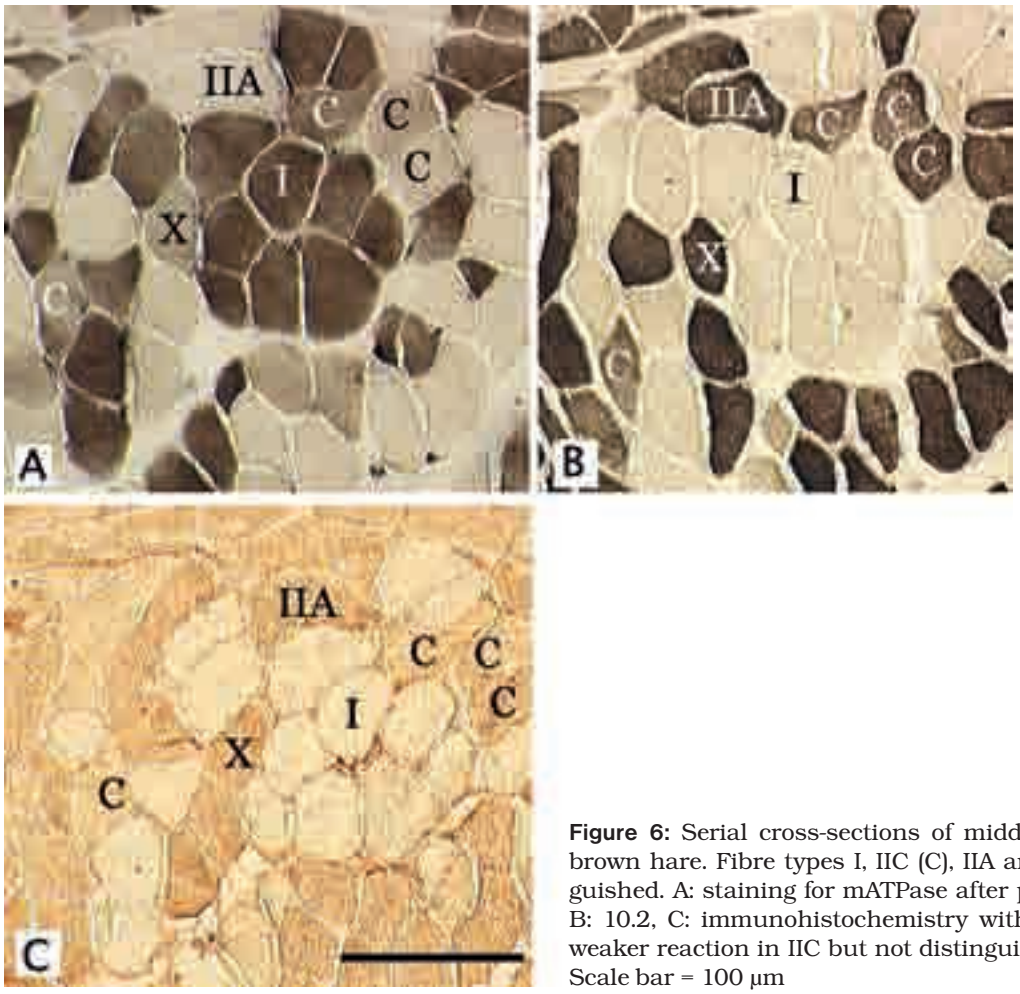

Figure 6: Serial cross-sections of middle part of *m. cremaster* in brown hare. Fibre types I, IIC (C), IIA and IIX (X) fibres are distinguished. A: staining for mATPase after preincubation at pH A: 4.5, B: 10.2, C: immunohistochemistry with A4.74 antibody (showing weaker reaction in IIC but not distinguishing between IIA and IIX). Scale bar = 100 μm

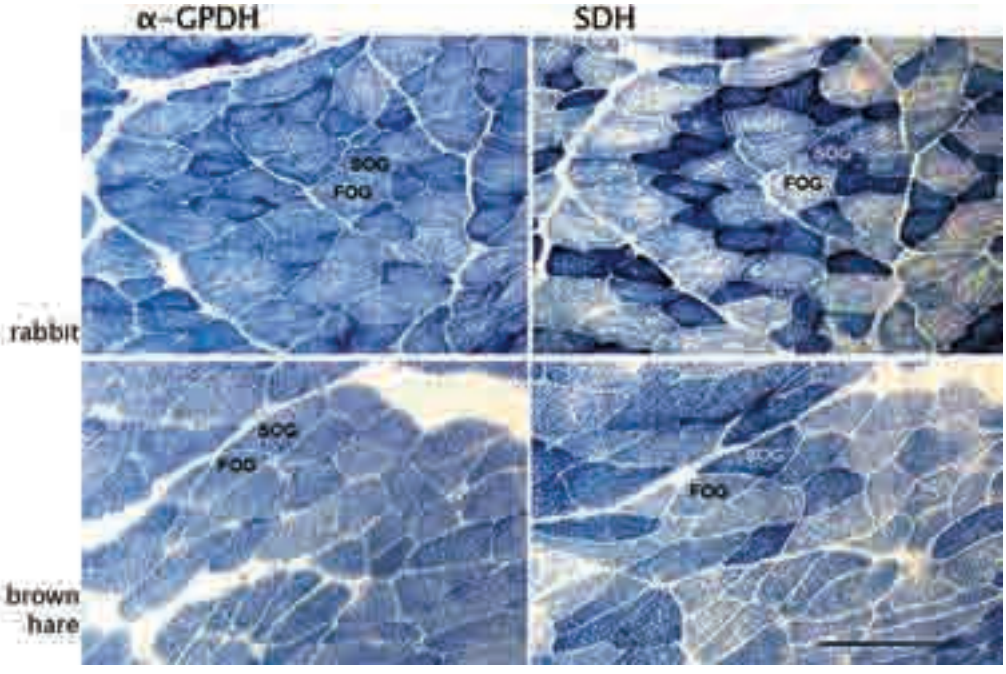

Figure 7: Enzyme histochemistry for α-GPDH and SDH in *m. cremaster* of rabbit and hare in mixed fibres area. Glycolitic capacity is high in all fibres, although variation is more evident in rabbit. Comparing with mATPase or immunohistochemistry one can determine mainly SOG and FOG fibres. Scale bar = 100 μm

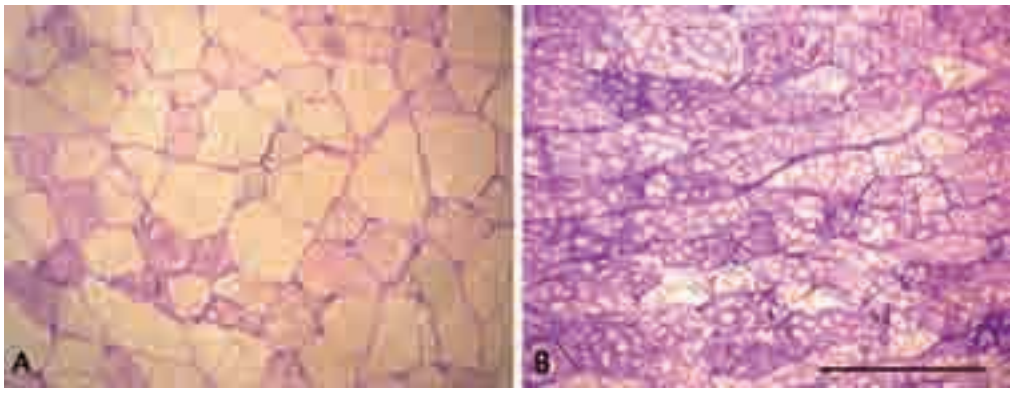

Figure 8: PAS reaction in *m. obliquus internus abdominis* (A) and *m. cremaster* (B) in the same brown hare. Scale bar = 100 μm

Discussion

The results of our study clearly indicate that *m. cremaster* is adapted to special functioning, since it differs from its origin, the caudal border of *m. obliquus abdominis* internus. It has different fibre type profile – the central bundle of *m. cremaster* consists almost exclusively of type I fibres, all fibres have pronounced glycolitic capacity and fibres throughout the muscle have a smaller diameter than those in abdominal muscle. We also noted the cremaster muscle is quite well developed. In widely used anatomical atlases by Popesko (19), the sketch of *m. cremaster* in rabbit is rather misleading. It depicts cremaster as a thin muscle bundle, limited to the dorsal aspect of tunica vaginalis and extending until head region of the testis. As expected, in all dissected animals the cremaster muscle composed a complete pouch. The name of cremaster in Slovene language literarily means the "lifter of the testis" but in lagomorphs (and rodents) when contracting, the effect would not be pulling the tunica vaginalis with testis towards abdominal cavity but rather squeezing out the scrotal sac, like contents of a tube.

Occasionally the textbooks and manuals refer to the cremaster muscle as *m. cremaster externus* as opposed to *m. cremaster* – smooth muscle fibres associated with connective and vascular components of spermatic cord, which are not present in all mammal species neither in all individuals. Due to the structure of the latter (smooth muscle) such terminology is also misleading and should be abandoned.

Although the rabbit muscles regularly express 3 fast MHC: IIa, IIx and IIb (20), in cremaster muscle the used antibodies did not demonstrate MHC-IIb or MHC-IIx fibres, at least not in a pure form. The IIB fibres were also not demonstrated with mATPase reaction considering the classification described for rabbit (14), but the antibody unspecifity must be taken into consideration at least for demonstrating IIx isoforms. Antibody A4.74, although according to manufacturer directed against MHC-IIa in rat, mouse, humans and rabbit, obviously cross reacts with IIx isoform in many species, as was noted before (15, 21). Small amounts of faster MHC may be present , but even if detected with other methods, it is clear that their functional importance is not significant.

Considering the fibre type composition we found that hares had a higher percentage of slow fibres along the length of cremaster muscle than rabbits. This speaks of greater adaptation of muscle to specific function in hare. But both species exhibited intramuscular variations – different central and peripheral parts of the muscle. The peripheral parts, consisting of predominantly IIA fibres, were more extensive in rabbit. Because these two parts were not clearly demarked (a transitional area with mixed fibres existed) we did not perform quantitative analysis of fibre types. While one can determine much higher content of oxidative enzyme in slow muscle fibres compared to fast, there is unusually high reaction to glycolitic enzyme content, almost not distinguishable between fibre types in brown hare. We determined SOG fibres (type I fibres with high SDH and α-GPDH) which are rarely mentioned in the literature as it is expected that slow fibres do not have active glycolitic enzymes. The prominent activity of α-GPDH in our case might be a peculiarity of *m. cremaster*.

We have two hypotheses how the central part of *m. cremaster* on dorsal aspect of vaginal process, which was thicker and had a distinctive fibre composition, is formed. It can represent fibres, which are descended from different muscle as the rest of *m. cremaster* i.e. *m. transversus abdominis* like in rats or man (4, 5, 6). But no clear appositions (transverse against circular) were found in rabbit or hare in selected transverse sections nor thicker perymisium separating the bundles. A detailed micro-dissection

should be performed to confirm or reject uniform distribution of muscle fibres in these species.

On the other hand, different innervations can be the cause of different immuno- and enzyme-histochemical characteristics. In rat a small nucleus in ventral columns of lumbar segments L1 and L2 was demonstrated to innervate cremaster muscle (22). In fact, the femoral branch of genitofemoral nerve innervates first caudal portions of transversus and oblique internus abdominis and initial part of cremaster, and then disperses into dorsal, ventral and most notably lateral face of cremaster muscle. Genital branch of genitofemoral nerve innervates abdominal-inguinal skin as well dorsal, ventral and medial parts of cremaster. For innervation of transitional muscle region that may represent kind of cremasteric sphincter, also ventrolateral nucleus is responsible (5). Therefore we can suppose that nerve fibres contribution from the two different motoneuron regions might be the case in lagomorphs.

In either case, the consequence is the physiology. The central part of *m. cremaster*, located on the dorsal aspect of processus vaginalis, seems responsible for a sustainable pull of testes during the cold months since it contains predominantly slow fibres. The imminent cremasteric reflex (in stress, fights) would be achieved by the rest of the muscle (fast, but fatigue resistant IIA fibres). This supposition can be supported by the fact that in rabbit the central slow fibre part of the cremaster was narrower and shorter, as those animals were not subjected to cold ambient temperatures. More numerous hybrid fibre types in hare also indicate muscle plasticity – animals living in wild had higher capacity to adapt to environmental conditions as laboratory animals.

Surprisingly however, no significant differences between muscle fibre type profile was found in hares between warm and cold months and it seems *m. cremaster* is highly responsive throughout the year regardless of reproductive state.

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NEKAJ MORFOLOŠKIH ZNAČILNOSTI MIŠICE VZDIGOVALKE MOD (*M. CREMASTER*) PRI POLJSKEM ZAJCU IN DOMAČEM KUNCU

M. Štrbenc, G. Fazarinc, A. Pogačnik

Povzetek: Mišica vzdigovalka mod (*m. cremaster*) pri samcih izvira iz mišičnih snopov kavdalne meje notranje poševne trebušne mišice (*m. obliquus internus abdominis*). Med sesalci so opazne razlike v velikosti in delovanju vzdigovalke mod. Pri glodavcih in lagomorfih se moda prosto premikajo med mošnjo in trebušno votlino, zato je vzdigovalka mod obsežna in dejavna mišica. V preteklosti so domnevali, da je njeno delovanje pri teh vrstah živali povezano s sezonskim nazadovanjem mod, vendar smo v prejšnji raziskavi ugotovili, da je položaj mod odvisen od temperature okolja in ne od paritvene sezone. Namen te študije pa je bil ugotoviti profil mišičnih vlaken v vzdigovalki mod v primerjavi z izvorno, notranjo poševno trebušno mišico pri poljskem zajcu in domačem kuncu. Mišične vzorce smo vzeli šestim zajcem (3 iz paritvene sezone in 3 izven nje) in šestim kuncem. Histološke rezine mišic smo obarvali po postopku encimske histokemije (klasifikacija mišičnih vlaken po metodi mATPaze, aktivnosti encimov SDH in α-GPDH ter vsebnosti glikogena) in imunohistokemično za različne izoforme težkih verig miozina. Ugotovili smo, da vzdigovalka mod popolnoma obkroža modo in nadmodek pri obeh vrstah živali. Na histoloških rezinah smo ugotovili, da zadnji del notranje poševne trebušne mišice po profilu vlaken predstavlja hitro mišico. Nasprotno pa je vsaj osrednji del vzdigovalke mod vseboval predvsem počasna vlakna, ki v perifernih delih mišice nadomestijo vlakna IIA. Vzdigovalka mod torej ni homogena mišica. Pri kuncih, ki so bili nameščeni v okolju z nespremenljivo temperaturo, je bil osrednji »počasni« snop vlaken bistveno manjši oz. krajši kot pri zajcu. V vzdigovalki mod smo ugotovili še visok nivo glikogena in visoko glikolitično kapaciteto vključno s t. i. vlakni SOG (počasi krčljiva oksidativno-glikolitična). Med vzorci mišic iz paritvene sezone in izven nje ni bilo razlik.

Ključne besede: *m. cremaster*; poljski zajec; kunec; skeletna mišična vlakna; mATPaza; miozin