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Original Article

Polarized Epithelium-Sperm Co-Culture System Reveals Stimulatory Factors for the Secretion of Mouse Epididymal Quiescin Sulfhydryl Oxidase 1

Running head: Sperm-epididymal epithelium interactions

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Abstract

Spermatozoa acquire fertilization ability through post-translational modifications. These membrane surface alterations occur in various segments of the epididymis. Quiescin sulfhydryl oxidases, which catalyze thiol-oxidation reactions, are involved in disulfide bond formation, which is essential for sperm maturation, upon transition and migration in the epididymis. Using castration and azoospermia transgenic mouse models, in the present study, we showed that quiescin sulfhydryl oxidase 1 (QSOX1) protein expression and secretion are positively correlated with the presence of testosterone and sperm cells. A two-dimensional *in vitro* epithelium-sperm co-culture system provided further evidence in support of the notion that both testosterone and its dominant metabolite, 5 α -dihydrotestosterone, promote epididymal QSOX1 secretion. We also demonstrated that immature caput spermatozoa, but not mature cauda sperm cells, exhibited great potential to stimulate QSOX1 secretion *in vitro*, suggesting that sperm maturation is a key regulatory factor for mouse epididymal QSOX1 secretion. Proteomic analysis identified 582 secretory proteins from the co-culture supernatant, of which 258 were sperm-specific and 154 were of epididymal epithelium-origin. Gene Ontology analysis indicated that these secreted proteins exhibit functions known to facilitate sperm membrane organization, cellular activity, and sperm-egg recognition. Taken together, our data demonstrated that testosterone and sperm maturation status are key regulators of mouse epididymal QSOX1 protein expression and secretion.

Introduction

Epididymal maturation and transition are prerequisite steps for the functional competence of testicular sperms. Since spermatozoa are considered transcriptionally and translationally inactive, acquisition of additional components from the epididymal epithelium allows for

post-testicular surface rearrangements and/or attachments of fertility-essential proteins, lipids, and small RNAs prior to ejaculation [1, 2]. Accumulating evidence supports that the epididymis exhibits a segmental-specific cellular signature, with distinct gene expression patterns, which enables the creation and maintenance of a stage-wise and maturation-requiring microenvironment [3-5]. For example, it is known that testicular sperm cells are immotile; however, upon epididymal migration from the caput toward the cauda, activation or inhibition of specific signaling pathways and protein post-translational modifications trigger sperm motility [6]. Therefore, a better understanding of sperm-epididymal epithelial interactions would contribute to fertilization success.

The epididymis is a continuous and convoluted duct, with a single layer of epithelial cells surrounding the lumen. Upon sperm transition in the epididymis, spermatozoa progressively change their surface compositions and maturation status along with alternations in the epididymal microenvironment [4, 5]. All these changes in the sperm membrane surface are thought to be driven primarily by interactions between spermatozoa and the complex components bathed within the epididymal lumen [7]. Disulfide bonds are formed between sulfur atoms of pairs of cysteine residues (thiol groups) within or across proteins. An earlier study showed that among post-spermiogenesis modifications, the formation of disulfide bonds is essential for the stabilization of sperm structure [8]. In addition, the oxidation of thiol groups is also critical for stabilizing various sperm structures, such as the chromatin, sperm midpiece, and tail [8]. Evidence from previous publications have demonstrated that an increased amount of disulfide bonds detected on the sperm membrane, from the caput toward the cauda epididymis, coincide with the advances in sperm maturation status, demonstrating that disulfide bond formation is part of the maturation process during sperm epididymal transition [9]. Among the different maturation processes, the increased potential for forward motility is the most obvious alteration.

Scientists have demonstrated that sulfhydryl oxidation is important for the stabilization of sperm tail structure and maintenance of motility wave patterns [10]. For example, outer dense fiber protein 1 (ODF1), a flagellar protein, is oxidized to form disulfides during the epididymal transition and is associated with the bending torque of the tail. Hetherington et al. also demonstrated that sperm cells from ODF1-knockout mice exhibit thinner filament fibers and fail to fertilize oocytes, owing to defective sperm movement [11].

Quiescin sulfhydryl oxidase (QSOX) catalyzes the thiol-oxidation reaction of $2R-SH + O_2 \rightarrow R-SS-R + H_2O_2$. The hypothetical functions of QSOX include generation of disulfide bonds within seminal plasma proteins or maturing spermatozoa, preservation of sperm membrane integrity, antimicrobial activity (through the release of H_2O_2), and protection of spermatozoa against the harmful effects of thiols after ejaculation [12, 13].

Two splice variants (QSOX1a, b) of human *QSOX1* gene have been reported. QSOX1a contains a complete transmembrane domain and is translated by the whole sequence of 3314 nucleotide bases that encodes 747 amino acids; QSOX1b, on the other hand, encodes a peptide of 604 amino acids, is a spliced variant of QSOX1a, and is known to be a secretory form of QSOX1 protein in the absence of the transmembrane domain [14, 15]. Similar to that in humans, the mouse QSOX1 family contains four splice variants, QSOX1a to d; mouse QSOX1a consists of a transmembrane domain (748 amino acids), whereas all other isoforms (QSOX1b to d) are truncated forms without a transmembrane domain, due to alternative splicing variants (661, 568, and 154 amino acids for mouse QSOX1b, c, and d, respectively) [16, 17].

We have previously described that the secretory form of the mouse QSOX1 protein, QSOX1c, is detected mainly in the epididymal lumen and exhibits a region-specific distribution in the epididymis. Luminal detection of QSOX1c suggested that this protein is secreted into the lumen by the epididymal epithelium and likely plays a role at different

maturation stages of spermatozoa [18]. In an earlier study, we showed that the expression and secretion of mouse epididymal QSOX2 is regulated by a fine coordinated mechanism between testosterone and glutamate [19]. Although we also demonstrated that mouse QSOX1c could aggregate defective human and mouse sperm *in vitro* and *in vivo* [20], the regulatory mechanism directing QSOX1c secretion remains unknown. Thus, in this study, we aimed to apply different mouse models with a two-dimensional polarized co-culture system, to investigate potential regulatory factors responsible for epididymal QSOX1 protein secretion.

Materials and Methods

Chemicals, reagents, and antibodies

Chemicals and reagents were obtained from Sigma-Aldrich (St. Louis, MO, USA) unless stated otherwise. Rabbit polyclonal anti-QSOX1, which detects all splicing variants, was purchased from Abcam (catalog no. Ab82713, Cambridge, UK). To specifically investigate QSOX1 variant c (secretory QSOX1), anti-QSOX1c anti-serum was generated and kindly provided by Dr. S.H. Li from the Mackay Memorial Hospital (Taiwan), as previously described [20, 21]. For use as the western blot loading control, rabbit polyclonal anti-eukaryotic elongation factor 2 antibody (catalog no. Ab40812) was purchased from Abcam. For indirect immunofluorescence, rabbit polyclonal anti-calreticulin antibody (catalog no. Ab92516, Abcam), which is an endoplasmic reticulum (ER) marker, was obtained from Abcam. The mouse monoclonal anti-enhanced green fluorescent protein (eGFP) antibody was purchased from Invitrogen (catalog no. MA5-15256; Waltham, MA, USA). All secondary antibodies were obtained from Jackson ImmunoResearch (West Grove, PA, USA).

Animals and hormone manipulations

Ten-week-old male Institute of Cancer Research (ICR) mice were obtained from the National Laboratory Animal Center, Taiwan, and acclimatized (3 mice/cage) for 1 week prior to the experiments. To examine the effect of sperm cells on QSOX1 protein expression, the *Cre/loxP* system was used to generate sperm-null knockout mice. As described earlier, *Vasa* was used as a germ-line specific promoter and *Elp1* (also known as inhibitor of kappa light polypeptide gene enhancer in B-cells, kinase complex-associated protein [*IKBKAP*] in mice), a critical gene in the meiosis process, was flanked by two *loxP* sites [22]. After recombination, spermatogenesis was disrupted in *Vasa-Cre:Elp^{-/-}* animals and characterized in terms of the absence of sperm cells in the epididymis, as described earlier [22]. The animal housing room was maintained at a constant temperature (22°C–24°C) with a 12 h/12 h alternating light/dark cycle. The animals were provided water and standard mouse lab chow (Oriental yeast, Tokyo, Japan) *ad libitum*. Animal experiments were carried out with the regulation and permission of the Institutional Animal Care and Use Committee protocol at National Taiwan University (NTU-107-EL-00102, Taiwan). To evaluate QSOX1 expression at different postnatal developmental stages, epididymal tissues were harvested from 20-, 30-, 40-, 50-, 60-, and 80-postpartum day mice. To investigate the effects of sex hormones on QSOX1 protein expression and secretion, loss- and restoration-of-function animal models were established. Briefly, 10 adult ICR mice were randomly allocated into the sham operation (n=3) and castration (n=7) groups. Castration was performed by means of bilateral removal of the testes, following which the remaining epididymis was placed back into the abdominal cavity. Animals in the sham operation group underwent the same surgical procedures, except for the removal of testes. Fourteen days post-surgery, four castrated animals received only 100 µl corn oil (catalog no. C8267, Sigma-Aldrich) as vehicle controls (castration+corn oil), while three other castrated

mice were subcutaneously administered testosterone propionate (catalog no. T1875, Sigma-Aldrich, 5 mg/kg body weight, dissolved in 100 μ l corn oil) for 10 consecutive days (castration+testosterone).

Collection of epididymal sperm cells and epididymal fluid

After the mice were euthanized, the epididymes were carefully dissected from their fat and connective tissue, and mouse epididymes were punched using an 18 G syringe needle in 50 μ l PBS, on a temperature-controlled dissection stage (Tokai Hit, Fujinomiya, Japan). To release sperm cells from either the caput or cauda epididymal lumen, a further 5 min incubation at 37°C was allowed. Epididymal fluid and sperm cells were separated by means of centrifugation at 600 $\times$ g for 10 min, following which the epididymal sperm cells were washed twice with pre-warmed PBS before further experiments. To obtain a sufficient amount of epididymal fluid, the epididymal fluid from three male mice at the same postnatal time point was pooled. The sperm cells and epididymal fluid were used without further storage.

Immuno-blotting

For protein sample preparation, freshly obtained epididymes were homogenized on ice with tissue homogenization buffer (250 mM sucrose, 1 mM ethylenediaminetetraacetic acid [EDTA], 20 mM Tris/HEPES, 1% Triton™ X-100, pH 7.4) supplemented with protease inhibitor cocktail tablet (EDTA-free, Roche, Mannheim, Germany). Protein concentrations were determined using the bicinchoninic acid (BCA) protein assay kit (Pierce Biotechnology, Rockford, IL, USA), according to the manufacturer's instructions. Equivalent amounts of total protein were resuspended in lithium dodecyl sulfate loading buffer (NuPAGE™, catalog no. NP0007, Thermo Fisher Scientific, Waltham, MA, USA)

in the presence of a reducing agent (50 mM dithiothreitol, catalog no. NP0009, Thermo Fisher Scientific). The samples were heated at 95°C for 10 min and cooled on ice before loading on the gels. The Bio-Rad Mini-PROTEIN[®] electrophoresis system was used (Bio-Rad Laboratories, Hertfordshire, DX, USA) according to the manufacturer's protocol, as previously described [18, 23]. Briefly, proteins were separated using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (gradient T-Pro EZ Gel Solution, catalog no. JB02-B010M, T-Pro Biotechnology, NTC, Taiwan) and wet-blotted onto polyvinylidene difluoride membranes (Immobilon-P, Millipore, Billerica, MA, USA). After blocking for 1 h with blocking buffer (Tris-buffered saline/Triton[™] X-100 [TBST; 5 mM Tris, 250 mM sucrose, pH 7.4, 0.05% v/v Tween-20] supplemented with 5% milk powder) at room temperature (RT), the blots were incubated with primary antibody (1:1000 dilution for QSOX1 and 1:5000 dilution for QSOX1c), overnight at 4°C. After washing in TBST, anti-mouse or anti-rabbit secondary antibodies were added to the blots at a 1:10000 dilution and incubated at RT for an additional 1 h. Protein signals were visualized using chemiluminescence (Merck, Kenilworth, NJ, USA) and detected using the ChemiDoc[™] XRS+ system (Bio-Rad Laboratories, Hercules, CA, USA). The relative intensity of each band was semi-quantified using the ImageJ (NIH) software. When necessary, the blots were stripped with stripping buffer (Restore[™] Western Blot Stripping Buffer, catalog no. 21059, Thermo Fisher Scientific) and re-probed for other proteins of interest.

Cell culture

Mouse caput epididymal epithelial cells (meCap18), which lack an endogenous androgen receptor [24], were kindly provided by Dr. Petra Sipilä (University of Turku, Finland) and used as a control cell line for steroid-induced QSOX1 secretion experiments. The cells were cultured in Dulbecco's modified Eagle medium (DMEM, Gibco, Waltham, MA, USA)

supplemented with 10% fetal bovine serum (FBS) and 1% antibiotic-antimycotic (Gibco), at 37.5°C, in a humidified atmosphere with 5% CO₂. Immortalized mouse distal caput epididymal epithelial cells (DC2) obtained from Applied Biological Materials (catalog no. T0599 Richmond, BC, Canada) were cultured in Iscove's modified Dulbecco's medium (Gibco) supplemented with 10% FBS and 1% antibiotic-antimycotic medium (Gibco), at 33°C, in a humidified atmosphere with 5% CO₂. For whole cell lysates, after the designed treatments, the cells were rinsed three times with ice-cold Dulbecco's phosphate-buffered saline (DPBS, Gibco) and subsequently scraped into radioimmunoprecipitation assay buffer lysis buffer (catalog no. BP115, Boston BioProducts, Boston, MA, USA) supplemented with EDTA-free protease inhibitors (Roche). The cells were lysed on ice for 15 min and sonicated for 1 min in an ice-cold water bath. Lysates were centrifuged at 10,000 × g for 10 min at 4°C, to remove the cellular debris. Protein quantification was performed using a BCA protein assay kit (Pierce Biotechnology), and cell lysates were stored at -20°C until use.

Mouse QSOX1-eGFP plasmid construction and transient transfection

The plasmid mRNA containing mouse QSOX1 (mQSOX1, variant 1, clone ID no. OMu01097, accession no. nm_001024945. 1) nucleotide sequence was purchased from GenScript (Piscataway, NJ, USA). The 2263 bp QSOX1 sequence was cloned into the pcDNA3.1(+)-eGFP vector using *Bam*HI/*Not*I restriction enzymes from the original pcDNA3.1-C-(k)DYK vector. To amplify the plasmid, the mQSOX1-eGFP plasmid was transformed into One Shot™ TOP10 competent E. coli (catalog no. C404010, Invitrogen), and the bacteria were spread onto ampicillin-containing lysogeny broth (LB) agar plates and incubated at 37°C for 12–16 h. Isolated single colonies were selected and amplified in LB broth containing ampicillin, at 37°C for 12–16 h, on a constant rotating shaker (225

rpm). The plasmid was extracted using the QIAprep[®] Spin Miniprep Kit (catalog no. 27106X4, Qiagen, Hilden, Germany), according to the manufacturer's protocol. The concentration and quality of the plasmid were determined using a Picodrop Microliter UV/Vis spectrophotometer (Pico p100, Hinxton, UK). To validate the plasmid structure, it was cleaved using *Bam*HI/*Not*I restriction enzymes. The cleaved vector and DNA fragments were separated using 1% agarose gel electrophoresis and visualized using ultraviolet illumination, after ethidium bromide staining.

Mouse QSOX1-eGFP plasmid was chemically transfected into meCap18 and DC2 cells using Lipofectamine[™] 3000 Transfection Reagent (catalog no. L3000001, Invitrogen). In brief, 2×10^6 cells were cultured in 24-well plates for 24 h, until 90% confluence. Thirty minutes before transfection, the medium was refreshed and the standard transfection protocol was followed, according to the manufacturer's instructions. Twenty-four hours after transfection, the transfection efficiency was evaluated using an IX83 epifluorescent microscope (Olympus, Tokyo, Japan). To further validate the expression and secretion of mQSOX1-eGFP in transfected cells, western blot analysis and indirect immunofluorescence staining were performed using antibodies against QSOX1, secretory QSOX1c, and eGFP.

Establishment of an in vitro two-dimensional sperm-epididymal epithelium co-culture system

To establish an *in vitro* polarized co-culture system, mQSOX1-eGFP-transfected cells were cultured in Transwell[®] (catalog no. 3470, Corning, New York, USA) with a 0.4 μ m pore size membrane. The cells were washed twice with DPBS before incubation with Phenol Red and FBS-free FluoroBrite[™] DMEM medium (Gibco). The cell culture medium was collected at different time-points (12, 24, 36, 48, and 60 h post-transfection) and

centrifuged at $3000 \times g$, 4°C for 10 min, to remove the cellular debris. The cultured supernatant was further concentrated using a VivaspinTM protein concentrator spin column (GE Healthcare, Chicago, IL, USA) with a molecular weight cut-off of 3 kDa (VivaspinTM 2 MWCO 3000, catalog no. 28932240). The fluorescence intensity, which correlated with the concentration of mQSOX1-eGFP, was measured using a SpectraMax[®] M5 Multi-Mode Microplate Reader (Molecular Devices, San Jose, CA, USA).

To standardize the measurement with minimal spontaneous secretion, all stimulation experiments were performed after spontaneous QSOX1-eGFP protein secretion reached a plateau, in the absence of exogenous stimulation. To examine the effects of sex steroids on QSOX1 secretion, 5–40 nM testosterone or 5α -dihydrotestosterone (DHT, Sigma-Aldrich) was added to transfected epididymal epithelial cells, following which the accumulated fluorescence intensity was measured, at intervals of 12 h, until 60 h post-transfection. To investigate the effects of sperm cells on QSOX1 secretion, sperm cells from caput or cauda epididymis were retrieved as described above and incubated further in pre-warmed Whitten's HEPES medium (WH medium, 100 mM NaCl, 4.7 mM KCl, 1.2 mM KH_2PO_4 , 1.2 mM MgSO_4 , 5.5 mM glucose, 1 mM pyruvic acid, 4.8 mM calcium L-lactate hydrate, 20 mM HEPES, pH 7.4). The sperm suspension was collected and further filtered through a $40\text{ }\mu\text{m}$ pore size FalconTM Cell Strainer (Fisher Scientific, Hampton, NH, USA). Direct and indirect interaction assays were performed using Transwell[®] (Corning) with a $0.4\text{ }\mu\text{m}$ pore size membrane.

Proteomic analysis using liquid chromatography-tandem mass spectrometry (LC-MS/MS)

To identify candidate proteins responsible for sperm-epithelium communication, media from the lower chamber of the above-mentioned indirect co-culture system were collected and analyzed. Media in the presence and absence of 2×10^6 caput sperm cells were used as

the stimulation and control groups, respectively. To achieve a sufficient protein concentration, the collected medium was centrifuged at $3300 \times g$, 4°C until a 15- to 30-fold concentrated volume was achieved. Soluble protein samples were denatured in reduction buffer (2 mM dithioerythritol/8 M urea) for 1 h at 37°C . Lys-C (1 h, 37°C) and trypsin (16 h, 37°C) were subsequently used as the digestion enzymes, and the digested peptides were suspended in 0.1% formic acid and desalted using Ziptips. Liquid chromatography-tandem mass spectrometry was performed using an Orbitrap Fusion™ Tribrid™ Mass Spectrometer (Thermo Scientific). The mass spectra data files were analyzed using Mascot Daemon (version 2.6.0, Matrix Science, London, UK) searched against the SwissProt *Mus musculus* protein database (dated: 5/17/2019). Only two missed cleavages were allowed, and a MASCOT score ≥ 35 was used to identify proteins of interest (score: E-value <0.05). These protein IDs were converted into UniProt gene IDs for future categorization and molecular function annotation studies. Protein IDs that reached the above-mentioned requirements were first categorized into three major subgroups, (1) sperm-origin, (2) epithelium/luminal fluid-origin, and (3) uncategorized, based on published literature [2, 4, 7, 25-28]

Gene Ontology (GO) analysis and network analysis

Protein network analysis was conducted using Cytoscape (version 3.7.1), with the addition of the ClueGo plugin (version 2.5.4) [29]. GO Biological Process Annotation (downloaded 27.02.2019) for caput sperm protein, epididymal lumen protein, and uncharacterized protein were compared for gene enrichment (right-sided hypergeometric test) using Benjamini–Hochberg multiple test correction. Network parameters were set as follows: GO tree levels (min=3, max=8), GO term restriction (minimum number of genes=5, minimum %=4), and GO term connection restriction (kappa score threshold=0.4). Only

terms with $p \leq 0.05$ are shown. Following GO analysis, PANTHER (protein analysis through evolutionary relationships; version 14.1) was used to classify proteins based on their biological process and molecular function.

Statistical analyses

Results are expressed as mean $\pm$ standard deviation. Comparative studies of means were performed using one-way analysis of variance, followed by Kruskal–Wallis test. Statistical significance was set at $p < 0.05$.

Results

Postnatal epididymal QSOX1 protein expression coincided with the presence of spermatozoa and testosterone surge

To investigate potential stimuli for postnatal mouse epididymal QSOX1 protein expression and secretion, whole epididymal tissue and epididymal fluid from 20-, 30-, 40-, 50-, 60-, and 80-day-old ICR mice were collected and subjected to western blot analysis. The QSOX1 antibody, which detected both membrane and secretory forms of QSOX1 at 75 kDa and 63 kDa, respectively, was used for whole tissue analysis. As shown in Fig. 1A, while a weak signal was detected in the postnatal tissue on day 20, at the molecular size of 75 kDa, which corresponds to the membrane form of QSOX1, an apparent increase in total QSOX1 was detected after day 30 in postnatal samples, which coincided with the first appearance of sperm cells and testosterone surge in the epididymis. In agreement with our earlier finding [18], the dominant form of epididymal QSOX1 at the later postnatal stages was the secretory form, QSOX1c, present at ~65 kDa (Fig. 1A). The secretory activity of QSOX1c was evidenced as we also detected a significant increase (2.4-fold increase) of QSOX1c protein in postnatal epididymal fluid using anti-QSOX1c antibody, after day 30

(Fig. 1B), while the luminal QSOX1c signal became relatively stable 30 days after birth (Fig. 1B).

In most cases, epididymal protein expression and secretion are regulated by luminal factors [19], and to demonstrate whether sperm cells or other stimuli (*e.g.*, steroid hormones) affect QSOX1 protein expression and secretion, we applied the castration model, as described earlier [19]. As shown in Fig. 1C, removal of the testes significantly decreased epididymal QSOX1 protein expression (62.5% decrease when compared to the sham operation group), and supplementation with exogenous testosterone rescued QSOX1 protein expression (238.9% increase when compared to the castration group, Fig. 1C). When we further dissected QSOX1 signal into membrane or secretory form, we observed no significant changes in the percentage of either membrane or secretory QSOX1 in castrated animals; however, upon testosterone supplementation, an increase in secretory QSOX1 was apparent (74.7% and 89.5% in the castration and testosterone addition groups, respectively), suggesting that testosterone affected not only total QSOX1 protein expression but also altered QSOX1 secretion activity (Fig. 1C). Interestingly, when we examined the effect of sperm cells on secretory QSOX1 protein expression in azoospermic mice (*Vasa-Cre:Elp1^{-/-}*), despite no apparent changes in the size or the morphology of the epididymis, a sharp decline (59%) in QSOX1c was detected at 65 kDa (Fig. 1D).

Validation of the two-dimensional polarized culture system

To elucidate the potential stimulatory factors for QSOX1 secretion, we established an *in vitro* two-dimensional polarized culture system and an analysis platform. As shown in Figure 2A, the mQSOX1-eGFP plasmid was transiently transfected into the epididymal epithelium after a polarized monolayer was observed. Culture supernatants were collected, centrifuged, measured, and analyzed at intervals of 12 h. To standardize the measurement,

the transfection rate was calculated based on the % of cells expressing eGFP and used for signal intensity correction in each measurement. As shown in Fig. 2B, when the anti-eGFP antibody was used, the QSOX1-eGFP fusion protein was detected in the perinuclear region, similar to the known cellular localization of endogenous QSOX1 (Fig. 2B), and the signal of the QSOX1-eGFP fusion protein largely overlapped with the ER marker calreticulin, in both meCap18 and DC2 cells, suggesting that QSOX1-eGFP fusion proteins might be secreted *via* the ER-mediated secretory pathway (Fig. 2B). Overexpression of the QSOX1-eGFP fusion protein was validated using western blot. A single protein band corresponding to the molecular weight of the QSOX1-eGFP fusion protein, at ~97 kDa, was detected in the cell lysates of both meCap18 and DC2 (Fig. 2C). Moreover, to demonstrate the secretory activity of these transfected cells, culture supernatants from transfected meCap18 and DC2 cells were collected for ELISA detection. Based on the data provided in Fig. 2D, no significant changes in the eGFP signal were detected in the meCap18 culture supernatant; in contrast, positive secretory activities were measured in the DC2 culture supernatant (Fig. 2D). To minimize the detection of spontaneous secretion, time-course eGFP detection from the collected culture supernatant was performed. We measured a gradual increase in eGFP signal, from 12 h to 36 h post-transfection, in DC2 cells; however, the accumulated eGFP signal became relatively stable between 36 h and 60 h post-transfection, indicating that without exogenous stimuli, spontaneous secretion of the QSOX1-eGFP fusion protein reached a plateau at 36 h. Thereafter, we applied 36 h post-transfection as the time-point to start our stimulatory experiments (Fig. 2D).

Testosterone and DHT stimulated epididymal QSOX1 secretion

To examine whether the most important male sex steroids, testosterone and DHT, stimulated QSOX1 secretion, two mouse epididymal epithelial cell lines, meCap18 and

DC2, were used. When meCap18 was used, no significant elevation of the QSOX1 signal was detected in the culture medium, after addition of either testosterone or DHT (Fig. 3A). In contrast, when DC2 was used, a dose-dependent increase in QSOX1 signals was observed in both testosterone- and DHT-addition groups. Interestingly, as compared to the testosterone effect, a persistent stimulatory effect was observed from 36 h to 52 h, upon addition of DHT (Fig. 3B). Although many reasons could lead to the observed lack of changes in QSOX1 signal in meCap18 cells, such as low ligand-receptor binding efficiency, dull secretory activity, or responses to stimuli, one of the many possibilities may be meCap18's natural lack of endogenous androgen receptors, that results in no or minimal response to either testosterone or DHT stimulation [26].

Caput, but not cauda spermatozoa, stimulated epididymal QSOX1 secretion

As we showed a significant decrease in QSOX1 protein expression in azoospermic mice (Fig. 1D), we further evaluated whether sperm cells of different maturation statuses resulted in different levels of stimulatory outcomes. Caput or cauda spermatozoa, representing immature or fully mature sperm cells, respectively, were used as exogenous stimuli. As sperm effects on epididymal proteins may be due to their direct physical contact or *via* intercellular communications by means of secretory or releasing factors, we established direct and indirect sperm-epididymal epithelium co-culture systems, as illustrated in Fig. 4. Because meCap18 did not respond to our earlier steroid stimulations and showed relatively low transfection and overexpression outcomes, to ensure successful detection of the signal, only DC2 cells were used in the following sets of experiments. To correct for the effects of residual luminal components on QSOX1 secretion, which may bias our measurements, we first established the baseline signal intensity using epididymal fluid as the stimulus. As shown in Fig. 4A, epididymal fluid significantly stimulated QSOX1 secretion, as compared

to that in the control group (WH medium). This was likely due to the presence of luminal testosterone or DHT, which supports our earlier findings (Fig. 3). However, when caput sperm cells were used as a stimulus, a sharp increase (3.26-fold) was detected in the QSOX1 signal, indicating that sperm could serve as a stimulatory factor for the secretion of mouse epididymal QSOX1 (Fig. 4A). In both direct and indirect assays, caput sperm, but not cauda sperm, efficiently stimulated QSOX1 secretion, and a dose-dependent stimulation effect was observed when caput spermatozoa were used (Fig. 4B–C). Interestingly, we observed a better stimulatory effect when the indirect assay was applied (1.2- to 2.6-fold *vs.* 2- to 6-fold increase for direct and indirect stimulations, respectively), indicating that non-physical communication between spermatozoa and epididymal epithelium *via* secretory and/or sperm releasing factors may exist and stimulate mouse epididymal QSOX1 secretion (Fig. 4B–C).

Proteomic identifications on sperm- and epididymal-derived secretomes

To identify potential secretory components that are responsible for inter-cellular communications, we collected supernatants from the lower chamber of an indirect co-culture system for proteomic identification, at 52 h of co-incubation of cauda sperm with DC2 (Fig. 5A). This time-point was chosen based on the detection of a significant increase in QSOX1-eGFP signals at this time-point in Fig. 4C. Among the 1871 proteins identified in the co-culture supernatant, 773 proteins were exclusively present in the sperm-containing group (stimulated), and 582 proteins were considered significant and reliable protein IDs, based on the criteria described in the Materials and Methods section (Fig. 5B, circle in purple). A literature search was performed to categorize the origins of these proteins. Among the 582 protein IDs, 258 were sperm-specific or sperm-origin proteins (Fig. 5C, Supplementary Table 1), 154 were epithelial-origin proteins (Fig. 5D, Supplementary Table

2), and 170 protein IDs could not be specified. Further analyses showed that the majority of the proteins released from sperm cells had known functions related to cellular catalytic activity (144 proteins, such as oxidoreductase and phospholipase) and cellular binding activity (70 proteins, such as hemoglobin and synaptotagmin) (Fig. 5C). Similar to sperm-origin proteins, a large proportion of epithelial-origin proteins were responsible for cellular catalytic activity (76 proteins) and cellular binding activity (50 proteins). It is worth noting that we also identified many proteins that are known to facilitate structural rearrangement or regulate molecular functions, and can be important to facilitate sperm maturation. Because we were interested in the sperm-derived secretome, which might be responsible for stimulating QSOX1 secretion, GO analysis of these 258 proteins was performed. As shown in Fig. 6, most of the identified sperm-origin proteins belonged to the following categories: metabolic process, oxidoreductase activity, antibiotic catabolic process, regulation of RNA process, and Golgi vesicle transportation. These proteins secreted or released from sperm cells may promote or activate various cellular activities, to promote the secretion or transportation of cytosolic proteins, such as QSOX1 (Fig. 6).

Discussion

Spermatozoa are not functionally mature after being released from testes. They acquire the capacity for progressive motility and fertilization ability through PTMs that occur in different segments of the epididymis [1, 4, 27, 28]. Among these PTMs, disulfide bond formation is essential for sperm proteins and structural stabilization. Quiescin sulfhydryl oxidases, which catalyze thiol oxidation and disulfide bond formation, have been identified in the epididymis [12, 18, 23]. In this study, we showed that mouse QSOX1 protein expression was upregulated from postnatal day 30, which coincided with the presence of sperm cells and the 1st surge in epididymal testosterone, suggesting the involvement of

testosterone and sperm cells in the regulation and stimulation of QSOX1 protein expression/secretion. Moreover, we observed that secretory QSOX1 (QSOX1c) became more dominant at the later maturation stages in mice, which is consistent with our earlier finding that QSOX1 was mostly detected in the secretory form within the epididymal lumen in adult mice [18], which may also explain its function in eliminating defective sperm cells in adult animals [20]. To mimic the *in vivo* situation, we established a 2D-polarized sperm-epididymal epithelium co-culture system to investigate the effects of potential stimuli and measure the level of QSOX1 secretion *in vitro*. Our data showed that QSOX1 secretion can be stimulated *via* the addition of sex steroid hormones (testosterone and DHT) and sperm cells, and that the stimulatory effects were more apparent in the presence of caput sperm cells, suggesting that besides male sex steroids (such as testosterone and DHT), sperm cells *per se* and sperm maturation status are also the key regulators for mouse epididymal QSOX1 protein expression and secretion. LC-MS/MS and proteome analysis identified 582 secretory proteins that were exclusively present in the sperm-stimulated group. Further analysis showed that 258 sperm-origin proteins might be responsible for stimulating QSOX1 secretion in the epididymis.

Interactions between epididymal epithelium and spermatozoa in the facilitation of sperm maturation have been studied intensively in the past decades [2, 30-33]. Since sperm cells are considered inactive in gene and *de novo* protein synthesis, essential surface modifications for competent sperm-egg interactions rely mostly on constant epididymal epithelium-sperm interactions. It is known that the region-specific composition of epididymal epithelial cells creates a suitable microenvironment for stage-wise sperm maturation. For example, luminal acidification established by cell-cell cross-talk between epididymal clear cells and principal cells maintains epididymal sperm in a quiescent state [30, 33-35]. The complexity of the transcriptome network and endocrine, lumicrine, and

paracrine factors tightly regulate epididymal protein expression, synthesis, and secretion [2-4, 26, 27]. Consistent with this, we observed that epididymal QSOX1 protein expression coincided with the postnatal testosterone surge, with peaks detected at days 30 and 60. Moreover, our *in vitro* data provided solid evidence that an essential male sex steroid, testosterone, and its catalytic metabolite, DHT, efficiently promoted QSOX1 secretion. Interestingly, although testosterone and DHT could both induce QSOX1 secretion at similar levels in DC2 cells, at 36 h, DHT showed a more persistent stimulatory effect until 52 h. One of the possibilities behind this observation could be that testosterone has to be converted into a more biologically active metabolite DHT by 5-alpha reductase; however, compared to testosterone, DHT is a primary and more dominant form of androgen in the male reproductive organ. Therefore, despite the fact that DC2 utilizes testosterone and converts testosterone into the active metabolite DHT, under our *in vitro* setup, DHT likely binds to the AR with higher affinity, so DC2 may utilize DHT more efficiently and directly, without additional conversion processes. Future cell uptake experiments with fluorescently labeled testosterone and DHT may confirm this hypothesis.

In addition to hormones, the maturation status of migrating sperm cells has been considered a critical factor that regulates epididymal activities. In agreement with this, we observed that compared to cauda sperm, caput sperm cells, which are considered “immature sperm cells”, were more effective in stimulating QSOX1 secretion *in vitro*. Upon post-testicular modification, disulfide bond formation is essential for the stabilization of sperm structure and sperm membrane proteins. The amount of disulfide bonds on the sperm membrane exhibits a progressive increase from the caput toward the cauda epididymis, and coincides with advances in sperm maturation status. This essential thiol-to-disulfide bond conversion supports the need for the QSOX protein in the maturation of spermatozoa [9]. In agreement with this concept, we also detected the presence of QSOX2 in the co-culture

512 supernatant, and based on the known epididymal distribution of QSOX2 [18], it was
513 detected in the co-culture supernatant, suggesting epithelium-initiated proactive secretion
514 activity or a stimulated secretory mechanism initiated by immature sperm.
515 Sperm-epididymal epithelium interactions have long been thought to be unidirectional,
516 from the epithelium toward sperm cells, and it is known that during sperm transit in the
517 epididymis, sperm receives additional proteins, mRNA, sugars, and lipids from the
518 epithelium, *via* specific tethering and cargo transfer mechanisms [2, 36-38]. However, a
519 proactive signaling mechanism from the sperm towards the epididymal epithelium should
520 also be considered. Most of the current studies have focused on unidirectional
521 epithelium-to-sperm interactions [2, 4, 7, 28, 39-41], and there is little information
522 available regarding sperm proactive participation in the stimulation of epididymal protein
523 secretion. Using the azoospermia mouse model, we observed a sharp decrease in
524 epididymal QSOX1c levels. In combination with an *in vitro* assay, we demonstrated that
525 epididymal QSOX1 secretion was highly correlated with sperm maturation status, which
526 was evidenced by the fact that caput spermatozoa elicited significantly 3–6-fold more
527 QSOX1 protein secretion into the culture medium than epididymal fluid or cauda sperm
528 cells alone. Since one of the intriguing observations was that indirect assay showed a better
529 stimulatory effect on QSOX1 secretion from caput sperm, we hypothesize that sperm
530 transit within the epididymal does not necessary require physical contact with the
531 epithelium as it does in the oviduct. Interestingly, there is evidence from literature or our
532 observation that the binding of sperm to epididymal epithelium is hardly observed.
533 However, we do not believe that contact of immature sperm with epithelial cells inhibits
534 QSOX1 expression, as both direct and indirect assays showed pronounced stimulatory
535 effects on QSOX1 secretion. Thus, one of the reasons could be that when immature sperm
536 cells migrate through the epididymal lumen, the secretion or release of “communication

molecules” serves better as stimulation signals to the epithelium for QSOX1 secretion, which could also be a combined effect of various molecules (those we identified from the proteomics data of the indirect assay) that were being secreted or released by sperm during epididymal transition. Taken together, our data demonstrated that not only epididymal luminal factors but also immature sperm cells actively stimulate the epididymal epithelium to secrete maturation-essential proteins (such as QSOX1), thus facilitating sperm membrane stabilization.

Based on proteomics identification, the majority (55.8%) of sperm-releasing factors belong to catalytic activity; these sperm-origin proteins are likely to serve as signals or promote cellular activity of the epithelium to release or secrete molecules that facilitate sperm maturation and surface modifications, which was also evidenced by the fact that many identified epithelium releasing factors are known to have the functions related to cellular adhesion or binding (Supplementary Table 2). Of particular interest is that we identified dynamin-2 (DNM2), a large GTPase with a region-specific epididymal distribution present in our co-culture supernatant. DNM2 is highly expressed in both caput epididymal principal cells and in the sperm acrosome region [7, 28, 42], DNM2 is known to regulate bi-directional membrane trafficking events [43], which supports our idea of bi-directional sperm-epithelium communication that is essential for sperm maturation. The epididymis exhibits distinct gene and protein expression patterns, ensuring segmental-specific functions essential for different steps of sperm maturation [4, 5, 44, 45]. In line with this, we also identified the presence of beta-defensin 20, 47 and lipocalin 5, 8 (Lcn) in the co-culture supernatant, and these proteins have been shown to be located at the proximal region of the epididymis and have been postulated to facilitate sperm maturation and motility acquisition upon sperm epididymal transition [44, 46, 47].

In conclusion, we showed that epididymal QSOX1 secretion can be stimulated by both steroids (testosterone and DHT) and immature sperm cells. Epididymal sperm with different maturation statuses exhibited different stimulatory effects on QSOX1 secretion. Moreover, using a combination of a co-culture system and proteomics analysis, we demonstrated that sperm cells could actively participate in signaling the epididymal epithelium to secrete proteins that are essential for sperm membrane surface modification.

Conflict of interests

The authors declare no conflicts of interest that could prejudice the impartiality of the research reported.

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Figure 1 Effects of testosterone and spermatozoa on QSOX1 protein expression and secretion in the mouse epididymis. (A) Epididymal tissue from 20- to 80-postnatal day mice were analyzed using western blot, and a representative blot has been presented. Postnatal epididymal QSOX1 expression coincided with the presence of spermatozoa and 1st testosterone surge at day 30. (B) Epididymal fluid collected from 20 to 80-postnatal day mice was subjected to western blot analysis for the detection of secretory QSOX1 (QSOX1c). A significant 2.4-fold increase in QSOX1c was detected at postnatal day 30, following which the signal became steady. For each postnatal time-point, epididymal fluid from 3 individual animals was collected, for quantitative analysis. (C) Epididymal tissues from loss- and gain-of-function mouse castration models were homogenized to examine the effect of testosterone on QSOX1 protein expression. Ten ICR mice were randomly allocated into sham operation (n=3), castration+corn oil (n=4, IP 100 µl corn oil), and castration+testosterone (n=3, IP 5 mg/kg body weight in 100 µl dissolved in corn oil) groups. Significant decreases in both membrane and secretory forms of epididymal QSOX1 were detected after castration; addition of exogenous testosterone rescued epididymal QSOX1 protein expression. (D) Azoospermia mouse model supported a positive association between the presence of sperm and epididymal QSOX1 protein expression, as a pronounced decline (-59%) in QSOX1c was detected in the absence of sperm cells. Four animals for each phenotype (wild-type or *Vasa-Cre:Elp*^{-/-}) were used for western blot quantification analysis, and a representative blot has been presented. Statistical analysis was performed as described in the Materials and Methods section. Bars represent mean +/- standard deviation. Statistical significance was considered at p<0.05 (*). N.S indicates a non-significant difference.

Figure 2 Validation of mouse QSOX1-eGFP transfection and secretion in epididymal epithelial cell lines. (A) Mouse caput epididymal epithelium were transiently transfected with mouse QSOX1-eGFP plasmid. After the designed experimental procedures, the culture supernatant was collected for ELISA detection of the eGFP signal. (B) Indirect immunofluorescent staining against eGFP was used to validate the presence of transfected mQSOX1-eGFP fusion protein. The perinuclear eGFP staining was similar to the known cellular localization of endogenous QSOX1. The eGFP signal largely overlapped with calreticulin, an ER marker, indicating that eGFP-QSOX1 is involved in the ER-mediated secretory pathway. Representative images from DC2 cells have been presented. (C) Western blot analysis for QSOX1c confirmed the presence and overexpression of transfected mQSOX1-eGFP, at the size of ~97 kDa, both in meCap18 and DC2 cells. Representative western blot images have been presented. (D) Culture supernatants from transfected meCap18 and DC2 cells were collected at intervals of 12 h, following which the accumulated eGFP signals were measured. No apparent changes were detected from the meCap18 culture supernatants. An elevated signal was detected in the DC2 culture supernatants at 24 h and 36 h post-transfection; the fact that the signal became steady after 36 h indicated a minimal spontaneous secretion activity after this time-point. Statistical analysis was performed, as described in the Materials and Methods section. Bars represent mean +/- standard deviation. Statistical significance was considered at $p < 0.05$ (*). N.S. indicates a non-significant difference.

Figure 3 Testosterone and 5 α -dihydrotestosterone (DHT) stimulate QSOX1 secretion *in vitro*. (A) Upon transfection of meCap18 with mQSOX1-eGFP, neither testosterone nor DHT stimulated QSOX1 secretion, as no significant changes were detected in the eGFP signal, at all time-points measured. (B) When DC2 was used, testosterone exerted a dose-dependent stimulatory effect at 36 h. In comparison to testosterone, DHT showed persistent stimulatory effects on QSOX1 secretion, until 52 h. Statistical analysis was performed as described in the Materials and Methods section. Six experimental repeats were performed for each concentration tested, at each time-point. Bars represent mean +/- standard deviation. Statistical significance was considered at $p < 0.05$ (*).

Figure 4 *In vitro* evaluation of sperm as a factor for QSOX1 secretion. (A) Transfected DC2 was used to examine the effects of exogenous stimuli on the secretion of QSOX1. Epididymal fluid exerted significant stimulatory effect (1.42-fold) on QSOX1 secretion. A 3.26-fold increase in eGFP signal was detected when 2×10^6 caput sperm cells were co-cultured with DC2, which indicated that the caput sperm was more effective in stimulating epididymal QSOX1 secretion than luminal factors. (B) In the direct stimulation assay, we observed dose-dependent stimulatory effects on QSOX1 secretion from the caput sperm, but not the cauda sperm, at 52 h. (C) In the indirect stimulation assay, we observed dose-dependent effects from the caput sperm, but not the cauda sperm, on promoting QSOX1 secretion, at 52 h. Moreover, the level of stimulation was more apparent (2- to 6-fold), as compared to that upon direct stimulation (1.2- to 2.6-fold). For each concentration tested at each time-point, 6 experimental repeats were performed. Bars represent mean $\pm$ standard deviation. Statistical significance was considered at $p < 0.05$. Asterisks indicate levels of significance, *= $p < 0.05$; **= $p < 0.01$.

A **B** **C** **D**

Figure 5 Proteomic identification of sperm-epithelium interactomes responsible for QSOX1 secretion. (A) To identify sperm-releasing factors that might be responsible for stimulating QSOX1 secretion, supernatant from the lower chamber of the indirect co-culture (sperm-DC2) system was collected at 52 h, for proteomics analysis. (B) After subtracting protein IDs from the control group (without the presence of sperm cells), 773 proteins were found to be exclusively present in the stimulated group (in grey). Based on MASCOT proteomic criteria described in the Materials and Methods section, 582 proteins were considered reliable IDs (in purple circle). (C) Further analyses showed that among the 582 identified IDs, 258 were sperm-origin proteins. The majority of sperm-origin proteins (55.8%) had known function for catalytic activity, while around 27% were responsible for the cellular binding process. (D) Analysis of 154 epididymal epithelium proteins indicated that two major functions for epithelium secretomes were related to catalytic activity (49.4%) and cellular binding process (32.5%).

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775 **Figure 6 Panther Gene Ontology (GO) analyses of proteomics data based on biological processes and molecular functions.** Reliable protein IDs
776 (n=582) were processed for Panther GO analysis. Subcategories were created and are shown using different colors. Associated molecular functions
777 have also been indicated accordingly. The majority of the identified proteins exhibited a known function related to metabolic process, oxidoreductase
778 activity, and antibiotic catabolic process. Other proteins identified were also highly related to sperm maturation processes, such as sperm oocyte
779 recognition, sperm-oocyte binding, chromatin assembly, plasma membrane organization, and lipid modification. Another group of proteins were found
780 to have function in regulating Golgi vesicle transport, which might be responsible for the ER-mediated cellular secretory pathway of epididymal
781 QSOX1.

Supplementary Table 1. List of sperm-origin proteins identified from proteomic analysis

Accession	uniprot id	Score	Mass	Num. of significant matches	Num. of significant sequences	emPAI	Description
ABCD3_MOUSE	Abcd3	36	75426	1	1	0.06	ATP-binding cassette sub-family D member 3 OS=Mus musculus OX=10090 GN=Abcd3 PE=1 SV=2
ABHDA_MOUSE	Abhd10	97	33019	3	3	0.47	Mycophenolic acid acyl-glucuronide esterase, mitochondrial OS=Mus musculus OX=10090 GN=Abhd10 PE=1 SV=1
ABD12_MOUSE	Abhd12	80	45241	1	1	0.1	Monoacylglycerol lipase ABHD12 OS=Mus musculus OX=10090 GN=Abhd12 PE=1 SV=2
THIKA_MOUSE	Acaa1a	39	43926	2	2	0.21	3-ketoacyl-CoA thiolase A, peroxisomal OS=Mus musculus OX=10090 GN=Acaa1a PE=1 SV=1
THIM_MOUSE	Acaa2	356	41803	15	14	3.14	3-ketoacyl-CoA thiolase, mitochondrial OS=Mus musculus OX=10090 GN=Acaa2 PE=1 SV=3
ACADL_MOUSE	Acadl	38	47877	2	2	0.19	Long-chain specific acyl-CoA dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Acadl PE=1 SV=2
THIL_MOUSE	Acat1	159	44787	7	7	0.95	Acetyl-CoA acetyltransferase, mitochondrial OS=Mus musculus OX=10090 GN=Acat1 PE=1 SV=1
GCP60_MOUSE	Acbd3	93	60144	3	2	0.15	RecName: Full=Golgi resident protein GCP60; AltName: Full=Acyl-CoA-binding domain-containing protein 3; AltName: Full=Golgi complex-associated protein 1; Short=GOCAP1; AltName: Full=Golgi phosphoprotein 1; Short=GOLPH1; AltName: Full=PBR- and PKA-as
ACE_MOUSE	Ace	299	150822	19	16	0.58	Angiotensin-converting enzyme OS=Mus musculus OX=10090 GN=Ace PE=1 SV=3
ACOT2_MOUSE	Acot2	128	49626	5	4	0.41	Acyl-coenzyme A thioesterase 2, mitochondrial OS=Mus musculus OX=10090 GN=Acot2 PE=1 SV=2
ACRO_MOUSE	Acr	204	48898	6	6	0.68	Acrosin OS=Mus musculus OX=10090 GN=Acr PE=1 SV=1
ACSL1_MOUSE	Acsl1	74	77901	2	2	0.12	Long-chain-fatty-acid--CoA ligase 1 OS=Mus musculus OX=10090 GN=Acsl1 PE=1 SV=2
ACTB_MOUSE	Actb	1886	39161	85	20	22.18	put. beta-actin (aa 27-375), partial [Mus musculus]
ADA28_MOUSE	Adam28	51	88612	2	2	0.1	Disintegrin and metalloproteinase domain-containing protein 28 OS=Mus musculus OX=10090 GN=Adam28 PE=1 SV=3
ADAM7_MOUSE	Adam7	301	89129	16	14	0.96	Disintegrin and metalloproteinase domain-containing protein 7 OS=Mus musculus OX=10090 GN=Adam7 PE=2 SV=2
KAD3_MOUSE	Ak3	146	25410	6	6	1.71	GTP:AMP phosphotransferase AK3, mitochondrial OS=Mus musculus OX=10090 GN=Ak3 PE=1 SV=3
ALBU_MOUSE	Alb	623	68648	24	19	2.26	Serum albumin OS=Mus musculus OX=10090 GN=Alb PE=1 SV=3
CD166_MOUSE	Alcam	169	65051	7	7	0.58	CD166 antigen OS=Mus musculus OX=10090 GN=Alcam PE=1 SV=3
AL1A1_MOUSE	Aldh1a1	762	54433	32	22	5.06	Retinal dehydrogenase 1 OS=Mus musculus OX=10090 GN=Aldh1a1 PE=1 SV=5
ALDH2_MOUSE	Aldh2	815	56502	36	21	4.26	Aldehyde dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Aldh2 PE=1 SV=1
SSDH_MOUSE	Aldh5a1	84	55933	3	3	0.26	Succinate-semialdehyde dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Aldh5a1 PE=1 SV=1
MMSA_MOUSE	Aldh6a1	418	57878	18	15	2.02	Methylmalonate-semialdehyde dehydrogenase [acylating], mitochondrial OS=Mus musculus OX=10090 GN=Aldh6a1 PE=1 SV=1
PPBT_MOUSE	Alpl	52	57478	2	2	0.16	Alkaline phosphatase, tissue-nonspecific isozyme OS=Mus musculus OX=10090 GN=Alpl PE=1 SV=2
APOA1_MOUSE	Apoa1	66	30597	3	3	0.51	Apolipoprotein A-I OS=Mus musculus OX=10090 GN=Apoa1 PE=1 SV=2
MIC27_MOUSE	Apool	86	29242	3	3	0.54	MICOS complex subunit Mic27 OS=Mus musculus OX=10090 GN=Apool PE=1 SV=1
ARF5_MOUSE	Arf5	178	20517	7	5	1.78	ADP-ribosylation factor 5 OS=Mus musculus OX=10090 GN=Arf5 PE=1 SV=2
ARGI2_MOUSE	Arg2	65	38854	3	3	0.39	Arginase-2, mitochondrial OS=Mus musculus OX=10090 GN=Arg2 PE=1 SV=1
ASGL1_MOUSE	Asrgl1	133	33928	5	5	0.87	Isoaspartyl peptidase/L-asparaginase OS=Mus musculus OX=10090 GN=Asrgl1 PE=1 SV=1
AT1A1_MOUSE	Atp1a1	149	112910	5	5	0.21	Sodium/potassium-transporting ATPase subunit alpha-1 OS=Mus musculus OX=10090 GN=Atp1a1 PE=1 SV=1
AT2A2_MOUSE	Atp2a2	346	114784	15	11	0.56	Sarcoplasmic/endoplasmic reticulum calcium ATPase 2 OS=Mus musculus OX=10090 GN=Atp2a2 PE=1 SV=2
AT2B1_MOUSE	Atp2b1	107	134662	4	4	0.14	Plasma membrane calcium-transporting ATPase 1 OS=Mus musculus OX=10090 GN=Atp2b1 PE=1 SV=1

AT2B4_MOUSE	Atp2b4	122	132984	4	4	0.14	Plasma membrane calcium-transporting ATPase 4 OS=Mus musculus OX=10090 GN=Atp2b4 PE=1 SV=1
BAP31_MOUSE	Bcap31	51	27939	1	1	0.16	B-cell receptor-associated protein 31 OS=Mus musculus OX=10090 GN=Bcap31 PE=1 SV=4
BCAT2_MOUSE	Bcat2	58	44099	1	1	0.1	Branched-chain-amino-acid aminotransferase, mitochondrial OS=Mus musculus OX=10090 GN=Bcat2 PE=1 SV=2
BPHL_MOUSE	Bphl	97	32830	4	4	0.68	Valacyclovir hydrolase OS=Mus musculus OX=10090 GN=Bphl PE=1 SV=1
BPNT1_MOUSE	Bpnt1	81	33222	6	5	0.89	Bisphosphate 3'-nucleotidase 1 [Mus musculus]
BASI_MOUSE	Bsg	50	42418	2	1	0.11	Basigin OS=Mus musculus OX=10090 GN=Bsg PE=1 SV=2
CABYR_MOUSE	Cabyr	63	48303	3	3	0.3	Calcium-binding tyrosine phosphorylation-regulated protein OS=Mus musculus OX=10090 GN=Cabyr PE=1 SV=1
PYR1_MOUSE	Cad	473	243084	17	13	0.26	CAD protein OS=Mus musculus OX=10090 GN=Cad PE=1 SV=1
CALX_MOUSE	Canx	268	64971	15	10	0.93	calnexin, partial [Mus musculus domesticus]
CAPZB_MOUSE	Capzb	243	31326	4	4	0.72	F-actin-capping protein subunit beta OS=Mus musculus OX=10090 GN=Capzb PE=1 SV=3
CBR1_MOUSE	Cbr1	100	30622	5	5	1	Carbonyl reductase [NADPH] 1 OS=Mus musculus OX=10090 GN=Cbr1 PE=1 SV=3
CC136_MOUSE	Ccdc136	57	35870	1	1	0.13	RecName: Full=BTB/POZ domain-containing protein KCTD12; AltName: Full=Pfetin; AltName: Full=Predominantly fetal expressed T1 domain
EST5A_MOUSE	Ces5a	74	64126	2	2	0.14	Carboxylesterase 5A OS=Mus musculus OX=10090 GN=Ces5a PE=2 SV=1
MIC19_MOUSE	Chchd3	158	26318	3	3	0.62	MICOS complex subunit Mic19 OS=Mus musculus OX=10090 GN=Chchd3 PE=1 SV=1
CLPP_MOUSE	Clpp	136	29781	5	3	0.53	ATP-dependent Clp protease proteolytic subunit, mitochondrial OS=Mus musculus OX=10090 GN=Clpp PE=1 SV=1
CLPT1_MOUSE	Clptm1	71	75243	2	2	0.12	Cleft lip and palate transmembrane protein 1 homolog OS=Mus musculus OX=10090 GN=Clptm1 PE=1
CLUS_MOUSE	Clu	241	51623	13	8	0.93	Clusterin OS=Mus musculus OX=10090 GN=Clu PE=1 SV=1
COPG2_MOUSE	Copg2	101	97617	4	4	0.19	Coatomer subunit gamma-2 OS=Mus musculus OX=10090 GN=Copg2 PE=1 SV=1
COQ9_MOUSE	Coq9	52	35061	1	1	0.13	Ubiquinone biosynthesis protein COQ9, mitochondrial OS=Mus musculus OX=10090 GN=Coq9 PE=1 SV=1
CACP_MOUSE	Crat	181	70794	8	8	0.62	Carnitine O-acetyltransferase OS=Mus musculus OX=10090 GN=Crat PE=1 SV=3
CISY_MOUSE	Cs	160	51703	6	5	0.51	Citrate synthase, mitochondrial OS=Mus musculus OX=10090 GN=Cs PE=1 SV=1
CTNA1_MOUSE	Ctnna1	331	100044	13	11	0.6	Catenin alpha-1 OS=Mus musculus OX=10090 GN=Ctnna1 PE=1 SV=1
CTNB1_MOUSE	Ctnnb1	404	85416	17	16	1.23	Catenin beta-1 OS=Mus musculus OX=10090 GN=Ctnnb1 PE=1 SV=1
CATC_MOUSE	Ctsc	86	52343	3	3	0.28	Dipeptidyl peptidase 1 OS=Mus musculus OX=10090 GN=Ctsc PE=1 SV=1
CUZD1_MOUSE	Cuzd1	102	68038	5	5	0.37	CUB and zona pellucida-like domain-containing protein 1 OS=Mus musculus OX=10090 GN=Cuzd1 PE=1 SV=2
CYB5B_MOUSE	Cyb5b	88	16308	2	2	0.67	Cytochrome b5 type B OS=Mus musculus OX=10090 GN=Cyb5b PE=1 SV=1
NB5R3_MOUSE	Cyb5r3	48	34106	2	2	0.28	NADH-cytochrome b5 reductase 3 OS=Mus musculus OX=10090 GN=Cyb5r3 PE=1 SV=3
DBIL5_MOUSE	Dbil5	44	9858	3	2	1.3	Diazepam-binding inhibitor-like 5 OS=Mus musculus OX=10090 GN=Dbil5 PE=1 SV=1
OST48_MOUSE	Ddost	44	48997	1	1	0.09	Dolichyl-diphosphooligosaccharide--protein glycosyltransferase 48 kDa subunit OS=Mus musculus OX=10090 GN=Ddost PE=1 SV=2
DFB20_MOUSE	Defb20	65	11032	3	3	2.09	Beta-defensin 20 OS=Mus musculus OX=10090 GN=Defb20 PE=3 SV=1
Q30KN1_MOUSE	Defb47	92	8834	2	2	1.51	beta-defensin 130-like precursor [Mus musculus]
DGUOK_MOUSE	Dguok	63	32202	1	1	0.14	deoxyguanosine kinase 1 [Mus musculus]
DHRS1_MOUSE	Dhrs1	39	33983	2	2	0.28	Dehydrogenase/reductase SDR family member 1 OS=Mus musculus OX=10090 GN=Dhrs1 PE=1 SV=1
DHRS4_MOUSE	Dhrs4	53	29866	1	1	0.15	Dehydrogenase/reductase SDR family member 4 OS=Mus musculus OX=10090 GN=Dhrs4 PE=1 SV=3
DBLOH_MOUSE	Diablo	91	26804	3	3	0.61	Diablo homolog, mitochondrial OS=Mus musculus OX=10090 GN=Diablo PE=1 SV=2
ODP2_MOUSE	Dlat	134	67899	4	4	0.29	Dihydrolipoylysine-residue acetyltransferase component of pyruvate dehydrogenase complex, mitochondrial OS=Mus musculus OX=10090 GN=Dlat PE=1 SV=2
DJB11_MOUSE	Dnajb11	46	40530	3	2	0.23	DnaJ homolog subfamily B member 11 OS=Mus musculus OX=10090 GN=Dnajb11 PE=1 SV=1
DJC10_MOUSE	Dnajc10	296	90525	12	12	0.76	DnaJ homolog subfamily C member 10 OS=Mus musculus OX=10090 GN=Dnajc10 PE=1 SV=2

DNJ3_MOUSE	Dnajc3	64	57428	1	1	0.08	DnaJ homolog subfamily C member 3 OS=Mus musculus OX=10090 GN=Dnajc3 PE=1 SV=1
DPEP3_MOUSE	Dpep3	155	54213	8	7	0.73	Dipeptidase 3 OS=Mus musculus OX=10090 GN=Dpep3 PE=1 SV=1
DYSF_MOUSE	Dysf	48	237759	1	1	0.02	Dysferlin OS=Mus musculus OX=10090 GN=Dysf PE=1 SV=3
ECH1_MOUSE	Ech1	216	36095	6	6	1.03	Delta(3,5)-Delta(2,4)-dienoyl-CoA isomerase, mitochondrial OS=Mus musculus OX=10090 GN=Ech1 PE=1 SV=1
ECHM_MOUSE	Echs1	131	31454	5	3	0.5	Enoyl-CoA hydratase, mitochondrial OS=Mus musculus OX=10090 GN=Echs1 PE=1 SV=1
ENPP1_MOUSE	Enpp1	57	103109	3	3	0.13	Ectonucleotide pyrophosphatase/phosphodiesterase family member 1 OS=Mus musculus OX=10090 GN=Enpp1 PE=1 SV=4
ENPP5_MOUSE	Enpp5	322	54352	14	11	1.56	Ectonucleotide pyrophosphatase/phosphodiesterase family member 5 OS=Mus musculus OX=10090 GN=Enpp5 PE=1 SV=3
EPCAM_MOUSE	Epcam	243	34996	8	6	1.07	Epithelial cell adhesion molecule OS=Mus musculus OX=10090 GN=Epcam PE=1 SV=1
EPIPL_MOUSE	Eppk1	261	724195	11	11	0.07	Epiplakin OS=Mus musculus OX=10090 GN=Eppk1 PE=1 SV=2
ERAP1_MOUSE	Erap1	73	106531	2	2	0.08	Endoplasmic reticulum aminopeptidase 1 OS=Mus musculus OX=10090 GN=Erap1 PE=1 SV=2
ERP44_MOUSE	Erp44	203	46823	12	9	1.26	Endoplasmic reticulum resident protein 44 OS=Mus musculus OX=10090 GN=Erp44 PE=1 SV=1
ESYT1_MOUSE	Esyt1	55	121478	2	2	0.07	Extended synaptotagmin-1 OS=Mus musculus OX=10090 GN=Esyt1 PE=1 SV=2
ETFB_MOUSE	Etfb	109	27606	4	4	0.84	Electron transfer flavoprotein subunit beta OS=Mus musculus OX=10090 GN=Etfb PE=1 SV=3
FABP9_MOUSE	Fabp9	247	15008	7	6	4.31	Fatty acid-binding protein 9 OS=Mus musculus OX=10090 GN=Fabp9 PE=1 SV=2
FAF2_MOUSE	Faf2	54	52438	1	1	0.08	FAS-associated factor 2 OS=Mus musculus OX=10090 GN=Faf2 PE=1 SV=2
FAHD1_MOUSE	Fahd1	130	25156	3	3	0.65	Acylpyruvase FAHD1, mitochondrial OS=Mus musculus OX=10090 GN=Fahd1 PE=1 SV=2
FA71B_MOUSE	Fam71b	100	68842	3	3	0.2	Protein FAM71B OS=Mus musculus OX=10090 GN=Fam71b PE=3 SV=3
FIS1_MOUSE	Fis1	48	16998	3	3	1.09	Mitochondrial fission 1 protein OS=Mus musculus OX=10090 GN=Fis1 PE=1 SV=1
FSCB_MOUSE	Fscb	103	114909	4	4	0.16	Fibrous sheath CABYR-binding protein OS=Mus musculus OX=10090 GN=Fscb PE=1 SV=1
FSIP2_MOUSE	Fsip2	38	784366	1	1	0.01	RecName: Full=Fibrous sheath-interacting protein 2
GALNS_MOUSE	Galns	69	57637	4	4	0.34	N-acetylgalactosamine-6-sulfatase OS=Mus musculus OX=10090 GN=Galns PE=1 SV=2
GALT2_MOUSE	Galnt2	57	64473	2	2	0.14	Polypeptide N-acetylgalactosaminyltransferase 2 OS=Mus musculus OX=10090 GN=Galnt2 PE=1 SV=1
KBL_MOUSE	Gcat	75	44902	2	2	0.21	2-amino-3-ketobutyrate coenzyme A ligase, mitochondrial OS=Mus musculus OX=10090 GN=Gcat PE=1 SV=2
GCC2_MOUSE	Gcc2	56	194325	1	1	0.02	GRIP and coiled-coil domain-containing protein 2 OS=Mus musculus OX=10090 GN=Gcc2 PE=1 SV=2
GCSH_MOUSE	Gcsh	144	18577	4	3	0.97	Gcsh protein [Mus musculus]
GLPK2_MOUSE	Gk2	53	60590	2	2	0.15	Glycerol kinase 2 OS=Mus musculus OX=10090 GN=Gk2 PE=1 SV=1
BGAL_MOUSE	Glb1	146	73074	4	4	0.26	Beta-galactosidase OS=Mus musculus OX=10090 GN=Glb1 PE=1 SV=1
GPRL1_MOUSE	Glpr1l1	114	27057	3	3	0.6	GLIPR1-like protein 1 OS=Mus musculus OX=10090 GN=Glpr1l1 PE=1 SV=1
GLNA_MOUSE	Glul	1000	42092	48	17	9.21	Glutamine synthetase OS=Mus musculus OX=10090 GN=Glul PE=1 SV=6
B2RWH8_MOUSE	Gm4846	146	61604	4	2	0.15	flavin-containing monooxygenase 13 [Mus musculus]
GBB1_MOUSE	Gnb1	157	37353	6	5	0.76	Guanine nucleotide-binding protein G(I)/G(S)/G(T) subunit beta-1 OS=Mus musculus OX=10090 GN=Gnb1 PE=1 SV=3
GOGA5_MOUSE	Golga5	211	82318	8	8	0.51	Golgin subfamily A member 5 OS=Mus musculus OX=10090 GN=Golga5 PE=1 SV=2
AATM_MOUSE	Got2	1504	47382	72	29	18.35	aspartate aminotransferase precursor [Mus musculus]
GPDA_MOUSE	Gpd1	62	37548	3	3	0.4	Glycerol-3-phosphate dehydrogenase [NAD(+)], cytoplasmic OS=Mus musculus OX=10090 GN=Gpd1 PE=1 SV=3
GPD1L_MOUSE	Gpd1l	41	38201	1	1	0.12	Glycerol-3-phosphate dehydrogenase 1-like protein OS=Mus musculus OX=10090 GN=Gpd1l PE=1 SV=2
Q6PAC1_MOUSE	Gsn	387	80712	15	13	0.99	gelsolin isoform 2 [Mus musculus]
GSTK1_MOUSE	Gstk1	103	25687	3	3	0.64	Glutathione S-transferase kappa 1 OS=Mus musculus OX=10090 GN=Gstk1 PE=1 SV=3
GSTM1_MOUSE	Gstm1	260	25953	10	6	2.12	Glutathione S-transferase Mu 1 OS=Mus musculus OX=10090 GN=Gstm1 PE=1 SV=2
GSTM5_MOUSE	Gstm5	246	26617	15	13	8.21	Glutathione S-transferase Mu 5 OS=Mus musculus OX=10090 GN=Gstm5 PE=1 SV=1

GSTM7_MOUSE	Gstm7	422	25693	18	12	6.21	Glutathione S-transferase Mu 7 OS=Mus musculus OX=10090 GN=Gstm7 PE=1 SV=1
Q0VDQ2_MOUSE	Gykl1	89	59864	2	2	0.15	Glycerol kinase-like 1 [Mus musculus]
H1O_MOUSE	H1f0	123	20848	3	2	0.5	Histone H1.0 OS=Mus musculus OX=10090 GN=H1f0 PE=2 SV=4
H2AY_MOUSE	H2afy	395	39710	16	12	2.61	Core histone macro-H2A.1 OS=Mus musculus OX=10090 GN=H2afy PE=1 SV=3
G6PE_MOUSE	H6pd	122	88872	3	3	0.16	GDH/6PGL endoplasmic bifunctional protein OS=Mus musculus OX=10090 GN=H6pd PE=1 SV=2
ECHA_MOUSE	Hadha	96	82617	3	3	0.17	Trifunctional enzyme subunit alpha, mitochondrial OS=Mus musculus OX=10090 GN=Hadha PE=1 SV=1
ECHB_MOUSE	Hadhb	41	51353	1	1	0.09	Trifunctional enzyme subunit beta, mitochondrial OS=Mus musculus OX=10090 GN=Hadhb PE=1 SV=1
HBB2_MOUSE	Hbb-b2	153	15868	6	5	2.73	Hemoglobin subunit beta-2 OS=Mus musculus OX=10090 GN=Hbb-b2 PE=1 SV=2
HDHD3_MOUSE	Hdhd3	94	28009	5	4	0.83	Haloacid dehalogenase-like hydrolase domain-containing protein 3 OS=Mus musculus OX=10090 GN=Hdhd3 PE=1 SV=1
HEXA_MOUSE	Hexa	63	60574	2	2	0.15	Beta-hexosaminidase subunit alpha OS=Mus musculus OX=10090 GN=Hexa PE=1 SV=2
HEXB_MOUSE	Hexb	171	61077	10	10	1.01	Beta-hexosaminidase subunit beta OS=Mus musculus OX=10090 GN=Hexb PE=1 SV=2
3HIDH_MOUSE	Hibadh	131	35417	6	4	0.61	3-hydroxyisobutyrate dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Hibadh PE=1 SV=1
HIBCH_MOUSE	Hibch	137	43010	6	6	0.81	3-hydroxyisobutyryl-CoA hydrolase, mitochondrial OS=Mus musculus OX=10090 GN=Hibch PE=1 SV=1
HINT2_MOUSE	Hint2	41	17309	1	1	0.27	Histidine triad nucleotide-binding protein 2, mitochondrial OS=Mus musculus OX=10090 GN=Hint2 PE=1 SV=1
HNRPK_MOUSE	Hnrnpk	625	50944	29	17	3.14	Heterogeneous nuclear ribonucleoprotein K OS=Mus musculus OX=10090 GN=Hnrnpk PE=1 SV=1
HPCL1_MOUSE	Hpcal1	43	22324	1	1	0.21	Hippocalcin-like protein 1 OS=Mus musculus OX=10090 GN=Hpcal1 PE=1 SV=2
HPDL_MOUSE	Hpdl	104	39884	4	4	0.53	4-hydroxyphenylpyruvate dioxygenase-like protein OS=Mus musculus OX=10090 GN=Hpdl PE=2 SV=1
HS71L_MOUSE	Hspa1l	611	70593	25	14	1.33	Heat shock 70 kDa protein 1-like OS=Mus musculus OX=10090 GN=Hspa1l PE=1 SV=4
HSP72_MOUSE	Hspa2	813	69599	35	21	2.63	Heat shock-related 70 kDa protein 2 OS=Mus musculus OX=10090 GN=Hspa2 PE=1 SV=2
HYOU1_MOUSE	Hyou1	647	111112	28	19	1.24	Hypoxia up-regulated protein 1 OS=Mus musculus OX=10090 GN=Hyou1 PE=1 SV=1
IAH1_MOUSE	Iah1	67	27956	3	3	0.57	Isoamyl acetate-hydrolyzing esterase 1 homolog OS=Mus musculus OX=10090 GN=Iah1 PE=1 SV=1
MIC60_MOUSE	Immt	252	83848	11	9	0.58	MICOS complex subunit Mic60 OS=Mus musculus OX=10090 GN=Immt PE=1 SV=1
Q80UW7_MOUSE	Iqgap1	569	188652	25	23	0.69	IQ motif containing GTPase activating protein 1 [Mus musculus]
IQGA2_MOUSE	Iqgap2	42	180416	1	1	0.02	Ras GTPase-activating-like protein IQGAP2 OS=Mus musculus OX=10090 GN=Iqgap2 PE=1 SV=2
ISC2A_MOUSE	Isoc2a	113	22403	4	4	1.12	Isochorismatase domain-containing protein 2A OS=Mus musculus OX=10090 GN=Isoc2a PE=1 SV=1
ITM2B_MOUSE	Itm2b	65	30240	3	2	0.32	Integral membrane protein 2B OS=Mus musculus OX=10090 GN=Itm2b PE=1 SV=1
IVD_MOUSE	Ivd	46	46296	1	1	0.1	Isovaleryl-CoA dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Ivd PE=1 SV=1
K1C18_MOUSE	Krt18	1186	47509	40	25	9.27	Keratin, type I cytoskeletal 18 OS=Mus musculus OX=10090 GN=Krt18 PE=1 SV=5
K1C19_MOUSE	Krt19	555	44515	24	18	5.14	Keratin, type I cytoskeletal 19 OS=Mus musculus OX=10090 GN=Krt19 PE=1 SV=1
K2C7_MOUSE	Krt7	396	50678	17	15	2.52	Keratin, type II cytoskeletal 7 OS=Mus musculus OX=10090 GN=Krt7 PE=1 SV=1
K2C71_MOUSE	Krt71	90	57347	3	3	0.25	Keratin, type II cytoskeletal 71 OS=Mus musculus OX=10090 GN=Krt71 PE=1 SV=1
K2C8_MOUSE	Krt8	744	54531	39	26	7.93	Keratin, type II cytoskeletal 8 OS=Mus musculus OX=10090 GN=Krt8 PE=1 SV=4
LCN5_MOUSE	Lcn5	272	21000	7	6	2.33	Epididymal-specific lipocalin-5 OS=Mus musculus OX=10090 GN=Lcn5 PE=1 SV=1
LCN8_MOUSE	Lcn8	49	19853	2	2	0.53	Epididymal-specific lipocalin-8 OS=Mus musculus OX=10090 GN=Lcn8 PE=2 SV=1
PLSL_MOUSE	Lcp1	351	70105	18	18	1.99	Plastin-2 OS=Mus musculus OX=10090 GN=Lcp1 PE=1 SV=4
Q8BVP2_MOUSE	Ldhal6b	272	42022	7	5	0.66	L-lactate dehydrogenase A-like 6B [Mus musculus]
LDHC_MOUSE	Ldhc	1757	35889	71	22	23.41	L-lactate dehydrogenase C chain OS=Mus musculus OX=10090 GN=Ldhc PE=1 SV=2
LDHD_MOUSE	Ldhd	417	51815	16	13	1.91	Probable D-lactate dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Ldhd PE=1 SV=1
LETM1_MOUSE	Letm1	119	82937	5	4	0.23	Mitochondrial proton/calcium exchanger protein OS=Mus musculus OX=10090 GN=Letm1 PE=1 SV=1
LMAN1_MOUSE	Lman1	157	57753	5	4	0.34	Protein ERGIC-53 OS=Mus musculus OX=10090 GN=Lman1 PE=1 SV=1
LMAN2_MOUSE	Lman2	195	40404	6	6	0.88	Vesicular integral-membrane protein VIP36 OS=Mus musculus OX=10090 GN=Lman2 PE=1 SV=2
LMNB1_MOUSE	Lmnbl	873	66719	44	36	10.37	lamin B [Mus musculus]
AMRP_MOUSE	Lrpap1	71	42189	3	3	0.35	Alpha-2-macroglobulin receptor-associated protein OS=Mus musculus OX=10090 GN=Lrpap1 PE=1 SV=1

LY65B_MOUSE	Ly6g5b	38	21601	1	1	0.21	Lymphocyte antigen 6 complex locus protein G5b OS=Mus musculus OX=10090 GN=Ly6g5b PE=1 SV=1
LYPD4_MOUSE	Lypd4	131	26979	3	3	0.6	Ly6/PLAUR domain-containing protein 4 OS=Mus musculus OX=10090 GN=Lypd4 PE=1 SV=1
MACD1_MOUSE	Macrod1	73	35272	2	2	0.27	ADP-ribose glycohydrolase MACROD1 OS=Mus musculus OX=10090 GN=Macrod1 PE=1 SV=2
MA2B2_MOUSE	Man2b2	222	115537	10	9	0.4	Epididymis-specific alpha-mannosidase OS=Mus musculus OX=10090 GN=Man2b2 PE=1 SV=2
MCCB_MOUSE	Mccc2	55	61340	2	2	0.15	Methylcrotonoyl-CoA carboxylase beta chain, mitochondrial OS=Mus musculus OX=10090 GN=Mccc2 PE=1 SV=1
MSPD2_MOUSE	Mospd2	37	59817	2	2	0.15	Motile sperm domain-containing protein 2 OS=Mus musculus OX=10090 GN=Mospd2 PE=1 SV=2
LYRIC_MOUSE	Mtdh	41	63808	2	2	0.14	Protein LYRIC OS=Mus musculus OX=10090 GN=Mtdh PE=1 SV=1
MVP_MOUSE	Mvp	83	95865	4	4	0.2	Major vault protein OS=Mus musculus OX=10090 GN=Mvp PE=1 SV=4
MYH10_MOUSE	Myh10	151	228855	3	3	0.06	Myosin-10 OS=Mus musculus OX=10090 GN=Myh10 PE=1 SV=2
MYO5B_MOUSE	Myo5b	39	210438	2	2	0.04	Unconventional myosin-Vb OS=Mus musculus OX=10090 GN=Myo5b PE=1 SV=2
NAGAB_MOUSE	Naga	40	47204	1	1	0.09	Alpha-N-acetylgalactosaminidase OS=Mus musculus OX=10090 GN=Naga PE=1 SV=2
O88325_MOUSE	Naglu	404	82544	14	13	0.96	alpha-N-acetylglucosaminidase precursor [Mus musculus]
NDUA2_MOUSE	Ndufa2	56	10909	1	1	0.46	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit 2 OS=Mus musculus OX=10090 GN=Ndufa2 PE=1 SV=3
NDUA7_MOUSE	Ndufa7	40	12568	1	1	0.39	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit 7 OS=Mus musculus OX=10090 GN=Ndufa7 PE=1 SV=3
NDUA8_MOUSE	Ndufa8	79	19979	3	3	0.88	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit 8 OS=Mus musculus OX=10090 GN=Ndufa8 PE=1 SV=3
NDUB4_MOUSE	Ndufb4	45	15072	1	1	0.32	NADH dehydrogenase [ubiquinone] 1 beta subcomplex subunit 4 OS=Mus musculus OX=10090 GN=Ndufb4 PE=1 SV=3
NDUS1_MOUSE	Ndufs1	37	79726	3	3	0.17	NADH-ubiquinone oxidoreductase 75 kDa subunit, mitochondrial OS=Mus musculus OX=10090 GN=Ndufs1 PE=1 SV=2
NDUS4_MOUSE	Ndufs4	57	19772	2	1	0.24	NADH dehydrogenase [ubiquinone] iron-sulfur protein 4, mitochondrial OS=Mus musculus OX=10090 GN=Ndufs4 PE=1 SV=3
NDUS5_MOUSE	Ndufs5	69	12639	2	2	0.93	NADH dehydrogenase [ubiquinone] iron-sulfur protein 5 OS=Mus musculus OX=10090 GN=Ndufs5 PE=1 SV=3
NDUS8_MOUSE	Ndufs8	45	24023	1	1	0.19	NADH dehydrogenase [ubiquinone] iron-sulfur protein 8, mitochondrial OS=Mus musculus OX=10090 GN=Ndufs8 PE=1 SV=1
NDUV2_MOUSE	Ndufv2	94	27268	5	4	0.86	NADH dehydrogenase [ubiquinone] flavoprotein 2, mitochondrial OS=Mus musculus OX=10090 GN=Ndufv2 PE=1 SV=2
Q91WP8_MOUSE	Ndufv3	60	50494	1	1	0.09	NADH dehydrogenase (ubiquinone) flavoprotein 3 [Mus musculus]
NHLC3_MOUSE	Nhlrc3	108	38171	3	3	0.4	NHL repeat-containing protein 3 OS=Mus musculus OX=10090 GN=Nhlrc3 PE=1 SV=1
NSDHL_MOUSE	Nsdhl	73	40660	3	3	0.37	Sterol-4-alpha-carboxylate 3-dehydrogenase, decarboxylating OS=Mus musculus OX=10090 GN=Nsdhl PE=1 SV=1
NSF_MOUSE	Nsf	117	82561	7	7	0.44	Vesicle-fusing ATPase OS=Mus musculus OX=10090 GN=Nsf PE=1 SV=2
5NT1B_MOUSE	Nt5c1b	44	64962	1	1	0.07	Cytosolic 5'-nucleotidase 1B OS=Mus musculus OX=10090 GN=Nt5c1b PE=2 SV=2
NUCB2_MOUSE	Nucb2	357	50273	21	18	4	Nucleobindin-2 OS=Mus musculus OX=10090 GN=Nucb2 PE=1 SV=2
Q80VE6_MOUSE	Nup205	50	48521	1	1	0.09	Nup205 protein, partial [Mus musculus]
OCAD1_MOUSE	Ociad1	66	27593	1	1	0.17	OCIA domain-containing protein 1 OS=Mus musculus OX=10090 GN=Ociad1 PE=1 SV=1
ODO1_MOUSE	Ogdh	458	116375	21	18	0.94	2-oxoglutarate dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Ogdh PE=1 SV=3
TIM16_MOUSE	Pam16	73	13776	1	1	0.35	Mitochondrial import inner membrane translocase subunit TIM16 OS=Mus musculus OX=10090 GN=Pam16 PE=1 SV=1
PCCA_MOUSE	Pcca	61	79871	1	1	0.05	Propionyl-CoA carboxylase alpha chain, mitochondrial OS=Mus musculus OX=10090 GN=Pcca PE=1 SV=2
PCCB_MOUSE	Pccb	60	58372	2	2	0.16	Propionyl-CoA carboxylase beta chain, mitochondrial OS=Mus musculus OX=10090 GN=Pccb PE=1 SV=2

PCKGM_MOUSE	Pck2	39	70482	1	1	0.06	Phosphoenolpyruvate carboxykinase [GTP], mitochondrial OS=Mus musculus OX=10090 GN=Pck2 PE=1 SV=1
ODPAT_MOUSE	Pdha2	77	43385	2	2	0.22	Pyruvate dehydrogenase E1 component subunit alpha, testis-specific form, mitochondrial OS=Mus musculus OX=10090 GN=Pdha2 PE=1 SV=1
ODPB_MOUSE	Pdhb	190	38912	8	6	0.92	Pyruvate dehydrogenase E1 component subunit beta, mitochondrial OS=Mus musculus OX=10090 GN=Pdhb PE=1 SV=1
PGRC1_MOUSE	Pgrmc1	271	21681	9	6	2.21	Membrane-associated progesterone receptor component 1 OS=Mus musculus OX=10090 GN=Pgrmc1 PE=1 SV=4
PREP_MOUSE	Pitrm1	64	117297	3	3	0.12	Presequence protease, mitochondrial OS=Mus musculus OX=10090 GN=Pitrm1 PE=1 SV=1
PLBL2_MOUSE	Plbd2	62	66247	4	4	0.29	Putative phospholipase B-like 2 OS=Mus musculus OX=10090 GN=Plbd2 PE=1 SV=2
MPPA_MOUSE	Pmpca	42	58242	1	1	0.08	Mitochondrial-processing peptidase subunit alpha OS=Mus musculus OX=10090 GN=Pmpca PE=1 SV=1
IPYR2_MOUSE	Ppa2	169	38090	6	5	0.75	Inorganic pyrophosphatase 2, mitochondrial OS=Mus musculus OX=10090 GN=Ppa2 PE=1 SV=1
PPIF_MOUSE	Ppif	69	21723	1	1	0.21	Peptidyl-prolyl cis-trans isomerase F, mitochondrial OS=Mus musculus OX=10090 GN=Ppif PE=1 SV=1
PP1G_MOUSE	Ppp1cc	318	36960	14	11	2.54	Serine/threonine-protein phosphatase PP1-gamma catalytic subunit OS=Mus musculus OX=10090 GN=Ppp1cc PE=1 SV=1
PPT1_MOUSE	Ppt1	191	34467	11	7	1.36	Palmitoyl-protein thioesterase 1 OS=Mus musculus OX=10090 GN=Ppt1 PE=1 SV=2
PREB_MOUSE	Preb	71	45409	1	1	0.1	Prolactin regulatory element-binding protein OS=Mus musculus OX=10090 GN=Preb PE=1 SV=1
Q8K1M3_MOUSE	Prkar2a	200	45561	9	7	0.92	cAMP-dependent protein kinase type II-alpha regulatory subunit [Mus musculus]
P5CR2_MOUSE	Pycr2	44	33638	2	2	0.29	Pyrroline-5-carboxylate reductase 2 OS=Mus musculus OX=10090 GN=Pycr2 PE=1 SV=1
QSOX2_MOUSE	Qsox2	70	77726	3	3	0.18	Sulfhydryl oxidase 2 OS=Mus musculus OX=10090 GN=Qsox2 PE=1 SV=1
RAB10_MOUSE	Rab10	36	22527	1	1	0.21	Ras-related protein Rab-10 OS=Mus musculus OX=10090 GN=Rab10 PE=1 SV=1
RAB18_MOUSE	Rab18	45	23021	2	2	0.44	Ras-related protein Rab-18 OS=Mus musculus OX=10090 GN=Rab18 PE=1 SV=2
RAB1B_MOUSE	Rab1b	142	22173	5	4	1.14	Ras-related protein Rab-1B OS=Mus musculus OX=10090 GN=Rab1b PE=1 SV=1
RAB5B_MOUSE	Rab5b	88	23692	3	3	0.71	Ras-related protein Rab-5B OS=Mus musculus OX=10090 GN=Rab5b PE=1 SV=1
RCN1_MOUSE	Rcn1	158	38090	8	8	1.44	Reticulocalbin-1 OS=Mus musculus OX=10090 GN=Rcn1 PE=1 SV=1
ROP1_MOUSE	Ropn1	155	23987	7	5	1.87	Ropporin-1 OS=Mus musculus OX=10090 GN=Ropn1 PE=1 SV=1
RL13_MOUSE	Rpl13	133	24290	5	5	1.38	60S ribosomal protein L13 OS=Mus musculus OX=10090 GN=Rpl13 PE=1 SV=3
RL18A_MOUSE	Rpl18a	90	20719	3	3	0.84	60S ribosomal protein L18a OS=Mus musculus OX=10090 GN=Rpl18a PE=1 SV=1
RL3_MOUSE	Rpl3	254	46081	11	7	1.52	60S ribosomal protein L3 OS=Mus musculus OX=10090 GN=Rpl3 PE=1 SV=3
RL32_MOUSE	Rpl32	88	15850	4	3	1.2	60S ribosomal protein L32 OS=Mus musculus OX=10090 GN=Rpl32 PE=1 SV=2
RL8_MOUSE	Rpl8	67	28007	2	2	0.35	60S ribosomal protein L8 OS=Mus musculus OX=10090 GN=Rpl8 PE=1 SV=2
RPN1_MOUSE	Rpn1	228	68486	10	6	0.45	Dolichyl-diphosphooligosaccharide--protein glycosyltransferase subunit 1 OS=Mus musculus OX=10090 GN=Rpn1 PE=1 SV=1
RPN2_MOUSE	Rpn2	258	69020	9	8	0.64	Dolichyl-diphosphooligosaccharide--protein glycosyltransferase subunit 2 OS=Mus musculus OX=10090 GN=Rpn2 PE=1 SV=1
RS2_MOUSE	Rps2	284	31212	19	12	5.69	40S ribosomal protein S2 OS=Mus musculus OX=10090 GN=Rps2 PE=1 SV=3
RS8_MOUSE	Rps8	327	24190	17	12	7.1	40S ribosomal protein S8 OS=Mus musculus OX=10090 GN=Rps8 PE=1 SV=2
SCAM1_MOUSE	Scamp1	35	38004	1	1	0.12	Secretory carrier-associated membrane protein 1 OS=Mus musculus OX=10090 GN=Scamp1 PE=1 SV=1
SCAM2_MOUSE	Scamp2	49	41154	1	1	0.11	PREDICTED: secretory carrier-associated membrane protein 2 isoform X1 [Mus musculus]
NLTP_MOUSE	Scp2	242	59088	11	8	0.78	Non-specific lipid-transfer protein OS=Mus musculus OX=10090 GN=Scp2 PE=1 SV=3
SDF2L_MOUSE	Sdf2l1	52	23634	2	2	0.43	Stromal cell-derived factor 2-like protein 1 OS=Mus musculus OX=10090 GN=Sdf2l1 PE=1 SV=2
SDHA_MOUSE	Sdha	307	72539	10	8	0.6	Succinate dehydrogenase [ubiquinone] flavoprotein subunit, mitochondrial OS=Mus musculus OX=10090 GN=Sdha PE=1 SV=1
SDHB_MOUSE	Sdhb	97	31793	3	3	0.49	Succinate dehydrogenase [ubiquinone] iron-sulfur subunit, mitochondrial OS=Mus musculus OX=10090 GN=Sdhb PE=1 SV=1

SC23A_MOUSE	Sec23a	156	86106	7	6	0.35	Protein transport protein Sec23A OS=Mus musculus OX=10090 GN=Sec23a PE=1 SV=2
A1AT1_MOUSE	Serpina1a	126	45974	3	3	0.32	Alpha-1-antitrypsin 1-1 OS=Mus musculus OX=10090 GN=Serpina1a PE=1 SV=4
ADT4_MOUSE	Slc25a31	49	35235	1	1	0.13	ADP/ATP translocase 4 OS=Mus musculus OX=10090 GN=Slc25a31 PE=1 SV=1
GTR3_MOUSE	Slc2a3	97	53444	2	1	0.17	Solute carrier family 2, facilitated glucose transporter member 3 OS=Mus musculus OX=10090 GN=Slc2a3 PE=1 SV=1
S38AA_MOUSE	Slc38a10	39	117120	1	1	0.04	Putative sodium-coupled neutral amino acid transporter 10 OS=Mus musculus OX=10090 GN=Slc38a10 PE=1 SV=2
LAT1_MOUSE	Slc7a5	59	55836	2	1	0.08	Large neutral amino acids transporter small subunit 1 OS=Mus musculus OX=10090 GN=Slc7a5 PE=1 SV=2
SODM_MOUSE	Sod2	236	24619	10	5	1.35	manganese superoxide dismutase [Mus musculus]
SACA1_MOUSE	Spaca1	375	33321	12	6	1.77	Sperm acrosome membrane-associated protein 1 OS=Mus musculus OX=10090 GN=Spaca1 PE=1 SV=1
MIEAP_MOUSE	Spata18	324	60360	11	7	0.89	Mitochondria-eating protein OS=Mus musculus OX=10090 GN=Spata18 PE=1 SV=2
SPESP_MOUSE	Spesp1	191	44674	10	10	1.59	Sperm equatorial segment protein 1 OS=Mus musculus OX=10090 GN=Spesp1 PE=1 SV=2
SRPRB_MOUSE	Srprb	99	29561	4	4	0.77	Signal recognition particle receptor subunit beta OS=Mus musculus OX=10090 GN=Srprb PE=1 SV=1
SIAT1_MOUSE	St6gal1	72	46556	3	3	0.32	Beta-galactoside alpha-2,6-sialyltransferase 1 OS=Mus musculus OX=10090 GN=St6gal1 PE=1 SV=2
SUCB1_MOUSE	Sucla2	104	50082	5	5	0.53	Succinate--CoA ligase [ADP-forming] subunit beta, mitochondrial OS=Mus musculus OX=10090 GN=Sucla2 PE=1 SV=2
SUCA_MOUSE	Suclg1	35	36132	1	1	0.12	Succinate--CoA ligase [ADP/GDP-forming] subunit alpha, mitochondrial OS=Mus musculus OX=10090 GN=Suclg1 PE=1 SV=4
SUOX_MOUSE	Suox	424	60718	19	15	1.87	Sulfite oxidase, mitochondrial OS=Mus musculus OX=10090 GN=Suox PE=1 SV=2
SYTL4_MOUSE	Sytl4	122	75974	4	4	0.25	Synaptotagmin-like protein 4 OS=Mus musculus OX=10090 GN=Sytl4 PE=1 SV=1
TX101_MOUSE	Tex101	97	26980	3	3	0.6	Testis-expressed protein 101 OS=Mus musculus OX=10090 GN=Tex101 PE=1 SV=1
THEM4_MOUSE	Them4	72	26015	2	2	0.38	Acyl-coenzyme A thioesterase THEM4 OS=Mus musculus OX=10090 GN=Them4 PE=1 SV=1
TIM50_MOUSE	Timm50	75	39752	2	2	0.24	Mitochondrial import inner membrane translocase subunit TIM50 OS=Mus musculus OX=10090 GN=Timm50 PE=1 SV=1
TLN1_MOUSE	Tln1	1120	269653	37	33	0.69	Talin-1 OS=Mus musculus OX=10090 GN=Tln1 PE=1 SV=2
TM9S2_MOUSE	Tm9sf2	107	75280	6	5	0.33	Transmembrane 9 superfamily member 2 OS=Mus musculus OX=10090 GN=Tm9sf2 PE=1 SV=1
TM9S4_MOUSE	Tm9sf4	35	74644	2	2	0.12	Transmembrane 9 superfamily member 4 OS=Mus musculus OX=10090 GN=Tm9sf4 PE=1 SV=1
TMED3_MOUSE	Tmed3	101	25449	2	2	0.39	Transmembrane emp24 domain-containing protein 3 OS=Mus musculus OX=10090 GN=Tmed3 PE=1 SV=1
TMED4_MOUSE	Tmed4	40	26005	2	2	0.38	Transmembrane emp24 domain-containing protein 4 OS=Mus musculus OX=10090 GN=Tmed4 PE=1 SV=1
TMF1_MOUSE	Tmf1	150	121729	5	3	0.11	TATA element modulatory factor OS=Mus musculus OX=10090 GN=Tmf1 PE=1 SV=2
TMX1_MOUSE	Tmx1	92	31376	3	2	0.31	Thioredoxin-related transmembrane protein 1 OS=Mus musculus OX=10090 GN=Tmx1 PE=1 SV=1
TMX3_MOUSE	Tmx3	54	51815	1	1	0.09	Protein disulfide-isomerase TMX3 OS=Mus musculus OX=10090 GN=Tmx3 PE=1 SV=2
TOM22_MOUSE	Tomm22	150	15527	3	3	1.24	Mitochondrial import receptor subunit TOM22 homolog OS=Mus musculus OX=10090 GN=Tomm22 PE=1 SV=3
TPP1_MOUSE	Tpp1	55	61304	3	3	0.23	Tripeptidyl-peptidase 1 OS=Mus musculus OX=10090 GN=Tpp1 PE=1 SV=2
Q7M739_MOUSE	Tpr	790	266764	29	28	0.57	TPA_exp: nuclear pore complex-associated intranuclear coiled-coil protein TPR [Mus musculus]
TBA3_MOUSE	Tuba3a	622	49928	24	14	2.59	Tubulin alpha-3 chain OS=Mus musculus OX=10090 GN=Tuba3a PE=1 SV=1
TXD12_MOUSE	Txndc12	87	19036	4	4	1.42	Thioredoxin domain-containing protein 12 OS=Mus musculus OX=10090 GN=Txndc12 PE=1 SV=1
VAMP3_MOUSE	Vamp3	84	11473	1	1	0.44	Vesicle-associated membrane protein 3 OS=Mus musculus OX=10090 GN=Vamp3 PE=1 SV=1
VAPB_MOUSE	Vapb	84	26929	3	2	0.37	Vesicle-associated membrane protein-associated protein B OS=Mus musculus OX=10090 GN=Vapb PE=1 SV=3
Q9Z2P7_MOUSE	Vti1b	63	26465	2	2	0.38	GES30 [Mus musculus]
E9PWQ7_MOUSE	Zan	124	584262	9	9	0.07	zonadhesin precursor [Mus musculus]
ZFPL1_MOUSE	Zfp11	41	34133	1	1	0.13	Zinc finger protein-like 1 OS=Mus musculus OX=10090 GN=Zfp11 PE=1 SV=1
ZBP1_MOUSE	Zbbp	511	39206	21	11	2.29	Zona pellucida-binding protein 1 OS=Mus musculus OX=10090 GN=Zbbp PE=1 SV=2

Supplementary Table 2. List of epididymal epithelium-origin proteins identified from proteomic analysis

Accession	uniprot id	Score	Mass	Num. of significant matches	Num. of significant sequences	emPAI	Description
THIM_MOUSE	Acaa2	356	41803	15	14	3.14	3-ketoacyl-CoA thiolase, mitochondrial OS=Mus musculus OX=10090 GN=Acaa2 PE=1 SV=3
ACADL_MOUSE	Acadl	38	47877	2	2	0.19	Long-chain specific acyl-CoA dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Acadl PE=1 SV=2
GCP60_MOUSE	Acbd3	93	60144	3	2	0.15	RecName: Full=Golgi resident protein GCP60; AltName: Full=Acyl-CoA-binding domain-containing protein 3; AltName: Full=Golgi complex-associated protein 1; Short=GOCAP1; AltName: Full=Golgi phosphoprotein 1; Short=GOLPH1; AltName: Full=PBR- and PKA-as
ACE_MOUSE	Ace	299	150822	19	16	0.58	Angiotensin-converting enzyme OS=Mus musculus OX=10090 GN=Ace PE=1 SV=3
ACRBP_MOUSE	Acrbp	299	61101	14	11	1.16	Acrosin-binding protein OS=Mus musculus OX=10090 GN=Acrbp PE=1 SV=1
ACTB_MOUSE	Actb	1886	39161	85	20	22.18	put. beta-actin (aa 27-375), partial [Mus musculus]
ACTN1_MOUSE	Actn1	1706	103004	71	42	5.21	Alpha-actinin-1 OS=Mus musculus OX=10090 GN=Actn1 PE=1 SV=1
ADA28_MOUSE	Adam28	51	88612	2	2	0.1	Disintegrin and metalloproteinase domain-containing protein 28 OS=Mus musculus OX=10090 GN=Adam28 PE=1 SV=3
ADAM7_MOUSE	Adam7	301	89129	16	14	0.96	Disintegrin and metalloproteinase domain-containing protein 7 OS=Mus musculus OX=10090 GN=Adam7 PE=2 SV=2
FETUA_MOUSE	Ahsg	36	37302	1	1	0.12	Alpha-2-HS-glycoprotein OS=Mus musculus OX=10090 GN=Ahsg PE=1 SV=1
ARK72_MOUSE	Akr7a2	107	40586	5	4	0.52	Aflatoxin B1 aldehyde reductase member 2 OS=Mus musculus OX=10090 GN=Akr7a2 PE=1 SV=3
ALBU_MOUSE	Alb	623	68648	24	19	2.26	Serum albumin OS=Mus musculus OX=10090 GN=Alb PE=1 SV=3
AL1A1_MOUSE	Aldh1a1	762	54433	32	22	5.06	Retinal dehydrogenase 1 OS=Mus musculus OX=10090 GN=Aldh1a1 PE=1 SV=5
AL1A7_MOUSE	Aldh1a7	422	54553	20	13	1.99	Aldehyde dehydrogenase, cytosolic 1 OS=Mus musculus OX=10090 GN=Aldh1a7 PE=1 SV=1
ALDH2_MOUSE	Aldh2	815	56502	36	21	4.26	Aldehyde dehydrogenase, mitochondrial OS=Mus musculus OX=10090 GN=Aldh2 PE=1 SV=1
MMSA_MOUSE	Aldh6a1	418	57878	18	15	2.02	Methylmalonate-semialdehyde dehydrogenase [acylating], mitochondrial OS=Mus musculus OX=10090 GN=Aldh6a1 PE=1 SV=1
PPBT_MOUSE	Alpl	52	57478	2	2	0.16	Alkaline phosphatase, tissue-nonspecific isozyme OS=Mus musculus OX=10090 GN=Alpl PE=1 SV=2
NAGA_MOUSE	Amdhd2	38	43473	1	1	0.1	N-acetylglucosamine-6-phosphate deacetylase OS=Mus musculus OX=10090 GN=Amdhd2 PE=1 SV=1
AP1M2_MOUSE	Ap1m2	118	48106	3	3	0.3	AP-1 complex subunit mu-2 OS=Mus musculus OX=10090 GN=Ap1m2 PE=1 SV=3
APOA1_MOUSE	Apoa1	66	30597	3	3	0.51	Apolipoprotein A-I OS=Mus musculus OX=10090 GN=Apoa1 PE=1 SV=2
APOA4_MOUSE	Apoa4	69	45001	2	2	0.21	Apolipoprotein A-IV OS=Mus musculus OX=10090 GN=Apoa4 PE=1 SV=3
ASGL1_MOUSE	Asrgl1	133	33928	5	5	0.87	Isoaspartyl peptidase/L-asparaginase OS=Mus musculus OX=10090 GN=Asrgl1 PE=1 SV=1
ATG3_MOUSE	Atg3	54	35773	1	1	0.13	Ubiquitin-like-conjugating enzyme ATG3 OS=Mus musculus OX=10090 GN=Atg3 PE=1 SV=1
BPNT1_MOUSE	Bpnt1	81	33222	6	5	0.89	Bisphosphate 3'-nucleotidase 1 [Mus musculus]
CO3_MOUSE	C3	35	186366	2	2	0.05	Complement C3 OS=Mus musculus OX=10090 GN=C3 PE=1 SV=3
PYR1_MOUSE	Cad	473	243084	17	13	0.26	CAD protein OS=Mus musculus OX=10090 GN=Cad PE=1 SV=1
CAPZB_MOUSE	Capzb	243	31326	4	4	0.72	F-actin-capping protein subunit beta OS=Mus musculus OX=10090 GN=Capzb PE=1 SV=3
CBR1_MOUSE	Cbr1	100	30622	5	5	1	Carbonyl reductase [NADPH] 1 OS=Mus musculus OX=10090 GN=Cbr1 PE=1 SV=3
CD2AP_MOUSE	Cd2ap	88	70407	6	6	0.44	CD2-associated protein OS=Mus musculus OX=10090 GN=Cd2ap PE=1 SV=3
EST5A_MOUSE	Ces5a	74	64126	2	2	0.14	Carboxylesterase 5A OS=Mus musculus OX=10090 GN=Ces5a PE=2 SV=1
CING_MOUSE	Cgn	49	136365	3	3	0.1	Cingulin OS=Mus musculus OX=10090 GN=Cgn PE=1 SV=1
CLUS_MOUSE	Clu	241	51623	13	8	0.93	Clusterin OS=Mus musculus OX=10090 GN=Clu PE=1 SV=1
COPG2_MOUSE	Copg2	101	97617	4	4	0.19	Coatomer subunit gamma-2 OS=Mus musculus OX=10090 GN=Copg2 PE=1 SV=1
CREG1_MOUSE	Creg1	68	24436	2	2	0.41	Protein CREG1 OS=Mus musculus OX=10090 GN=Creg1 PE=1 SV=1
CRIS1_MOUSE	Crisp1	78	27661	4	4	0.84	Cysteine-rich secretory protein 1 OS=Mus musculus OX=10090 GN=Crisp1 PE=2 SV=1
CTNA1_MOUSE	Ctnna1	331	100044	13	11	0.6	Catenin alpha-1 OS=Mus musculus OX=10090 GN=Ctnna1 PE=1 SV=1
CNBP1_MOUSE	Ctnnbip1	46	9169	1	1	0.56	Beta-catenin-interacting protein 1 OS=Mus musculus OX=10090 GN=Ctnnbip1 PE=1 SV=1
CATH_MOUSE	Ctsh	282	37146	7	5	0.77	Pro-cathepsin H OS=Mus musculus OX=10090 GN=Ctsh PE=1 SV=2
CUL4B_MOUSE	Cul4b	51	110630	1	1	0.04	Cullin-4B OS=Mus musculus OX=10090 GN=Cul4b PE=1 SV=1
CUZD1_MOUSE	Cuzd1	102	68038	5	5	0.37	CUB and zona pellucida-like domain-containing protein 1 OS=Mus musculus OX=10090 GN=Cuzd1 PE=1 SV=2
CYC2_MOUSE	Cyct	348	11706	11	5	10.99	Cytochrome c, testis-specific OS=Mus musculus OX=10090 GN=Cyct PE=1 SV=3

DBIL5_MOUSE	Dbil5	44	9858	3	2	1.3	Diazepam-binding inhibitor-like 5 OS=Mus musculus OX=10090 GN=Dbil5 PE=1 SV=1
DCTN3_MOUSE	Dctn3	57	20965	1	1	0.22	Dynactin subunit 3 OS=Mus musculus OX=10090 GN=Dctn3 PE=1 SV=2
DDX46_MOUSE	Ddx46	66	117376	3	3	0.12	Probable ATP-dependent RNA helicase DDX46 OS=Mus musculus OX=10090 GN=Ddx46 PE=1 SV=2
ODP2_MOUSE	Dlat	134	67899	4	4	0.29	Dihydrolipoyllysine-residue acetyltransferase component of pyruvate dehydrogenase complex, mitochondrial OS=Mus musculus OX=10090 GN=Dlat PE=1 SV=2
DJC10_MOUSE	Dnajc10	296	90525	12	12	0.76	DnaJ homolog subfamily C member 10 OS=Mus musculus OX=10090 GN=Dnajc10 PE=1 SV=2
DYN2_MOUSE	Dnm2	67	98084	3	3	0.14	Dynamin-2 OS=Mus musculus OX=10090 GN=Dnm2 PE=1 SV=2
DPEP3_MOUSE	Dpep3	155	54213	8	7	0.73	Dipeptidase 3 OS=Mus musculus OX=10090 GN=Dpep3 PE=1 SV=1
ENOPH_MOUSE	Enoph1	53	28582	1	1	0.16	Enolase-phosphatase E1 OS=Mus musculus OX=10090 GN=Enoph1 PE=1 SV=1
ENPP1_MOUSE	Enpp1	57	103109	3	3	0.13	Ectonucleotide pyrophosphatase/phosphodiesterase family member 1 OS=Mus musculus OX=10090 GN=Enpp1 PE=1 SV=4
ENPP5_MOUSE	Enpp5	322	54352	14	11	1.56	Ectonucleotide pyrophosphatase/phosphodiesterase family member 5 OS=Mus musculus OX=10090 GN=Enpp5 PE=1 SV=3
EPIPL_MOUSE	Eppk1	261	724195	11	11	0.07	Epiplakin OS=Mus musculus OX=10090 GN=Eppk1 PE=1 SV=2
ERP44_MOUSE	Erp44	203	46823	12	9	1.26	Endoplasmic reticulum resident protein 44 OS=Mus musculus OX=10090 GN=Erp44 PE=1 SV=1
ESYT1_MOUSE	Esyt1	55	121478	2	2	0.07	Extended synaptotagmin-1 OS=Mus musculus OX=10090 GN=Esyt1 PE=1 SV=2
ETFB_MOUSE	Etfb	109	27606	4	4	0.84	Electron transfer flavoprotein subunit beta OS=Mus musculus OX=10090 GN=Etfb PE=1 SV=3
F169A_MOUSE	Fam169a	60	73195	2	2	0.12	Soluble lamin-associated protein of 75 kDa OS=Mus musculus OX=10090 GN=Fam169a PE=1 SV=3
F16P1_MOUSE	Fbp1	200	36889	8	7	1.24	Fructose-1,6-bisphosphatase 1 OS=Mus musculus OX=10090 GN=Fbp1 PE=1 SV=3
FHL1_MOUSE	Fhl1	38	31867	2	2	0.3	Four and a half LIM domains protein 1 OS=Mus musculus OX=10090 GN=Fhl1 PE=1 SV=3
FNTA_MOUSE	Fnta	42	43986	2	2	0.21	Protein farnesyltransferase/geranylgeranyltransferase type-1 subunit alpha OS=Mus musculus OX=10090 GN=Fnta PE=1 SV=1
GALNS_MOUSE	Galns	69	57637	4	4	0.34	N-acetylgalactosamine-6-sulfatase OS=Mus musculus OX=10090 GN=Galns PE=1 SV=2
GAMT_MOUSE	Gamt	61	26319	2	2	0.38	Guanidinoacetate N-methyltransferase OS=Mus musculus OX=10090 GN=Gamt PE=1 SV=1
GET4_MOUSE	Get4	44	36502	1	1	0.12	Golgi to ER traffic protein 4 homolog OS=Mus musculus OX=10090 GN=Get4 PE=1 SV=2
GGCT_MOUSE	Ggct	50	21099	2	2	0.49	Gamma-glutamyl cyclotransferase [Mus musculus]
GIPC1_MOUSE	Gipc1	65	36107	2	2	0.27	PDZ domain-containing protein GIPC1 OS=Mus musculus OX=10090 GN=Gipc1 PE=1 SV=1
GLPK_MOUSE	Gk	78	61188	3	3	0.23	Glycerol kinase OS=Mus musculus OX=10090 GN=Gk PE=1 SV=2
GBAL_MOUSE	Glb1	146	73074	4	4	0.26	Beta-galactosidase OS=Mus musculus OX=10090 GN=Glb1 PE=1 SV=1
GLB1L_MOUSE	Glb1l	43	73232	2	2	0.12	Beta-galactosidase-1-like protein OS=Mus musculus OX=10090 GN=Glb1l PE=1 SV=1
GLNA_MOUSE	Glul	1000	42092	48	17	9.21	Glutamine synthetase OS=Mus musculus OX=10090 GN=Glul PE=1 SV=6
GOPC_MOUSE	Gopc	58	50631	1	1	0.09	Golgi-associated PDZ and coiled-coil motif-containing protein OS=Mus musculus OX=10090 GN=Gopc PE=1 SV=1
GPDA_MOUSE	Gpd1	62	37548	3	3	0.4	Glycerol-3-phosphate dehydrogenase [NAD(+)], cytoplasmic OS=Mus musculus OX=10090 GN=Gpd1 PE=1 SV=3
GPD1L_MOUSE	Gpd1l	41	38201	1	1	0.12	Glycerol-3-phosphate dehydrogenase 1-like protein OS=Mus musculus OX=10090 GN=Gpd1l PE=1 SV=2
GSK3A_MOUSE	Gsk3a	55	51628	1	1	0.09	Glycogen synthase kinase-3 alpha OS=Mus musculus OX=10090 GN=Gsk3a PE=1 SV=2
Q6PAC1_MOUSE	Gsn	387	80712	15	13	0.99	gelsolin isoform 2 [Mus musculus]
GSTM5_MOUSE	Gstm5	246	26617	15	13	8.21	Glutathione S-transferase Mu 5 OS=Mus musculus OX=10090 GN=Gstm5 PE=1 SV=1
GSTM7_MOUSE	Gstm7	422	25693	18	12	6.21	Glutathione S-transferase Mu 7 OS=Mus musculus OX=10090 GN=Gstm7 PE=1 SV=1
HBB1_MOUSE	Hbb-b1	504	15830	16	9	17.09	Hemoglobin subunit beta-1 OS=Mus musculus OX=10090 GN=Hbb-b1 PE=1 SV=2
A8DUK2_MOUSE	Hbbt1	509	16223	18	10	21.09	beta-globin [Mus musculus]
HEXA_MOUSE	Hexa	63	60574	2	2	0.15	Beta-hexosaminidase subunit alpha OS=Mus musculus OX=10090 GN=Hexa PE=1 SV=2
HIP1R_MOUSE	Hip1r	89	119353	5	5	0.2	Huntingtin-interacting protein 1-related protein OS=Mus musculus OX=10090 GN=Hip1r PE=1 SV=2
HMGB1_MOUSE	Hmgb1	388	24878	25	12	8.08	High mobility group protein B1 OS=Mus musculus OX=10090 GN=Hmgb1 PE=1 SV=2
HNRPD_MOUSE	Hnrnpd	163	38330	10	8	1.71	Heterogeneous nuclear ribonucleoprotein D0 OS=Mus musculus OX=10090 GN=Hnrnpd PE=1 SV=2
HNRPK_MOUSE	Hnrnpk	625	50944	29	17	3.14	Heterogeneous nuclear ribonucleoprotein K OS=Mus musculus OX=10090 GN=Hnrnpk PE=1 SV=1
HPCL1_MOUSE	Hpcal1	43	22324	1	1	0.21	Hippocalcin-like protein 1 OS=Mus musculus OX=10090 GN=Hpcal1 PE=1 SV=2
HRG_MOUSE	Hrg	66	59126	3	3	0.24	Histidine-rich glycoprotein OS=Mus musculus OX=10090 GN=Hrg PE=1 SV=2
HSP72_MOUSE	Hspa2	813	69599	35	21	2.63	Heat shock-related 70 kDa protein 2 OS=Mus musculus OX=10090 GN=Hspa2 PE=1 SV=2
Q3U2G2_MOUSE	Hspa4	904	94149	42	34	3.68	heat shock 70 kDa protein 4 [Mus musculus]
HTSF1_MOUSE	Htatsf1	152	86188	3	3	0.16	HIV Tat-specific factor 1 homolog OS=Mus musculus OX=10090 GN=Htatsf1 PE=1 SV=1
HYOU1_MOUSE	Hyou1	647	111112	28	19	1.24	Hypoxia up-regulated protein 1 OS=Mus musculus OX=10090 GN=Hyou1 PE=1 SV=1
I23O1_MOUSE	Ido1	76	45612	2	2	0.21	Indoleamine 2,3-dioxygenase 1 OS=Mus musculus OX=10090 GN=Ido1 PE=1 SV=1

OXLA_MOUSE	Il4i1	125	70147	4	4	0.28	L-amino-acid oxidase OS=Mus musculus OX=10090 GN=Il4i1 PE=1 SV=1
Q80UW7_MOUSE	Iqgap1	569	188652	25	23	0.69	IQ motif containing GTPase activating protein 1 [Mus musculus]
ITM2B_MOUSE	Itm2b	65	30240	3	2	0.32	Integral membrane protein 2B OS=Mus musculus OX=10090 GN=Itm2b PE=1 SV=1
K1C18_MOUSE	Krt18	1186	47509	40	25	9.27	Keratin, type I cytoskeletal 18 OS=Mus musculus OX=10090 GN=Krt18 PE=1 SV=5
K1C19_MOUSE	Krt19	555	44515	24	18	5.14	Keratin, type I cytoskeletal 19 OS=Mus musculus OX=10090 GN=Krt19 PE=1 SV=1
K2C8_MOUSE	Krt8	744	54531	39	26	7.93	Keratin, type II cytoskeletal 8 OS=Mus musculus OX=10090 GN=Krt8 PE=1 SV=4
LTOR1_MOUSE	Lamtor1	120	17738	4	3	1.03	Regulator complex protein LAMTOR1 OS=Mus musculus OX=10090 GN=Lamtor1 PE=1 SV=1
LCN5_MOUSE	Lcn5	272	21000	7	6	2.33	Epididymal-specific lipocalin-5 OS=Mus musculus OX=10090 GN=Lcn5 PE=1 SV=1
LCN8_MOUSE	Lcn8	49	19853	2	2	0.53	Epididymal-specific lipocalin-8 OS=Mus musculus OX=10090 GN=Lcn8 PE=2 SV=1
PLSL_MOUSE	Lcp1	351	70105	18	18	1.99	Plastin-2 OS=Mus musculus OX=10090 GN=Lcp1 PE=1 SV=4
LDHC_MOUSE	Ldhc	1757	35889	71	22	23.41	L-lactate dehydrogenase C chain OS=Mus musculus OX=10090 GN=Ldhc PE=1 SV=2
LSM2_MOUSE	Lsm2	142	10828	5	5	5.66	U6 snRNA-associated Sm-like protein LSm2 OS=Mus musculus OX=10090 GN=Lsm2 PE=1 SV=1
LY65B_MOUSE	Ly6g5b	38	21601	1	1	0.21	Lymphocyte antigen 6 complex locus protein G5b OS=Mus musculus OX=10090 GN=Ly6g5b PE=1 SV=1
LZTL1_MOUSE	Lztf1l	41	34752	1	1	0.13	Leucine zipper transcription factor-like protein 1 OS=Mus musculus OX=10090 GN=Lztf1l PE=1 SV=1
MA2B1_MOUSE	Man2b	45	114576	2	2	0.08	Lysosomal alpha-mannosidase OS=Mus musculus OX=10090 GN=Man2b1 PE=1 SV=4
MA2B2_MOUSE	Man2b2	222	115537	10	9	0.4	Epididymis-specific alpha-mannosidase OS=Mus musculus OX=10090 GN=Man2b2 PE=1 SV=2
MAP1B_MOUSE	Map1b	73	270089	3	3	0.05	Microtubule-associated protein 1B OS=Mus musculus OX=10090 GN=Map1b PE=1 SV=2
MP2K1_MOUSE	Map2k1	44	43446	1	1	0.1	Dual specificity mitogen-activated protein kinase kinase 1 OS=Mus musculus OX=10090 GN=Map2k1 PE=1 SV=2
MP2K2_MOUSE	Map2k2	66	44374	1	1	0.1	Dual specificity mitogen-activated protein kinase kinase 2 OS=Mus musculus OX=10090 GN=Map2k2 PE=1 SV=2
MK03_MOUSE	Mapk3	43	43039	3	3	0.34	Mitogen-activated protein kinase 3 OS=Mus musculus OX=10090 GN=Mapk3 PE=1 SV=5
METK2_MOUSE	Mat2a	87	43661	3	3	0.34	S-adenosylmethionine synthase isoform type-2 OS=Mus musculus OX=10090 GN=Mat2a PE=1 SV=2
MVP_MOUSE	Mvp	83	95865	4	4	0.2	Major vault protein OS=Mus musculus OX=10090 GN=Mvp PE=1 SV=4
NAGAB_MOUSE	Naga	40	47204	1	1	0.09	Alpha-N-acetylgalactosaminidase OS=Mus musculus OX=10090 GN=Naga PE=1 SV=2
NENF_MOUSE	Nenf	78	18893	2	2	0.56	Neudessin OS=Mus musculus OX=10090 GN=Nenf PE=1 SV=1
NSF_MOUSE	Nsf	117	82561	7	7	0.44	Vesicle-fusing ATPase OS=Mus musculus OX=10090 GN=Nsf PE=1 SV=2
NUCB2_MOUSE	Nucb2	357	50273	21	18	4	Nucleobindin-2 OS=Mus musculus OX=10090 GN=Nucb2 PE=1 SV=2
PARP1_MOUSE	Parp1	56	113028	3	3	0.12	Poly [ADP-ribose] polymerase 1 OS=Mus musculus OX=10090 GN=Parp1 PE=1 SV=3
NHRF3_MOUSE	Pdzk1	123	56464	7	6	0.57	Na(+)/H(+) exchange regulatory cofactor NHE-RF3 OS=Mus musculus OX=10090 GN=Pdzk1 PE=1 SV=1
PEX19_MOUSE	Pex19	58	32477	1	1	0.14	RecName: Full=Peroxisomal biogenesis factor 19; AltName: Full=Peroxin-19; AltName: Full=Peroxisomal farnesylated protein; Flags: Precursor
PGAM2_MOUSE	Pgam2	280	28809	17	14	8.01	Phosphoglycerate mutase 2 OS=Mus musculus OX=10090 GN=Pgam2 PE=1 SV=3
PGK2_MOUSE	Pgk2	566	44824	25	18	4.51	Phosphoglycerate kinase 2 OS=Mus musculus OX=10090 GN=Pgk2 PE=1 SV=4
PLBL1_MOUSE	Plbd1	152	62958	5	5	0.4	Phospholipase B-like 1 OS=Mus musculus OX=10090 GN=Plbd1 PE=1 SV=1
IPYR2_MOUSE	Ppa2	169	38090	6	5	0.75	Inorganic pyrophosphatase 2, mitochondrial OS=Mus musculus OX=10090 GN=Ppa2 PE=1 SV=1
PPM1B_MOUSE	Ppm1b	46	42768	1	1	0.1	Protein phosphatase 1B OS=Mus musculus OX=10090 GN=Ppm1b PE=1 SV=1
PPT1_MOUSE	Ppt1	191	34467	11	7	1.36	Palmitoyl-protein thioesterase 1 OS=Mus musculus OX=10090 GN=Ppt1 PE=1 SV=2
PRDX6_MOUSE	Prdx6 Aop2 Ltw4 Prd	572	24811	24	14	11.75	peroxiredoxin-6 isoform 1 [Mus musculus]
KPRB_MOUSE	Prpsap2	82	40854	4	4	0.52	Phosphoribosyl pyrophosphate synthase-associated protein 2 OS=Mus musculus OX=10090 GN=Prpsap2 PE=1 SV=1
PTGDS_MOUSE	Ptgds	90	21053	1	1	0.22	Prostaglandin-H2 D-isomerase OS=Mus musculus OX=10090 GN=Ptgds PE=1 SV=1
PUF60_MOUSE	Puf60	303	60211	12	10	1.03	Poly(U)-binding-splicing factor PUF60 OS=Mus musculus OX=10090 GN=Puf60 PE=1 SV=2
RAB18_MOUSE	Rab18	45	23021	2	2	0.44	Ras-related protein Rab-18 OS=Mus musculus OX=10090 GN=Rab18 PE=1 SV=2
RABL6_MOUSE	Rabl6	38	79782	1	1	0.05	Rab-like protein 6 OS=Mus musculus OX=10090 GN=Rabl6 PE=1 SV=2
RBM47_MOUSE	Rbm47	54	64021	2	2	0.14	RNA-binding protein 47 OS=Mus musculus OX=10090 GN=Rbm47 PE=1 SV=1
RET1_MOUSE	Rbp1	47	15836	1	1	0.3	Retinol-binding protein 1 OS=Mus musculus OX=10090 GN=Rbp1 PE=1 SV=2
RCN1_MOUSE	Rcn1	158	38090	8	8	1.44	Reticulocalbin-1 OS=Mus musculus OX=10090 GN=Rcn1 PE=1 SV=1
RIPL1_MOUSE	Rilpl1	38	47294	1	1	0.09	RILP-like protein 1 OS=Mus musculus OX=10090 GN=Rilpl1 PE=1 SV=1
RL10_MOUSE	Rpl10	133	24588	6	6	1.79	60S ribosomal protein L10 OS=Mus musculus OX=10090 GN=Rpl10 PE=1 SV=3
RL13_MOUSE	Rpl13	133	24290	5	5	1.38	60S ribosomal protein L13 OS=Mus musculus OX=10090 GN=Rpl13 PE=1 SV=3
RL13A_MOUSE	Rpl13a	108	23449	3	3	0.72	60S ribosomal protein L13a OS=Mus musculus OX=10090 GN=Rpl13a PE=1 SV=4

RL24_MOUSE	Rpl24	93	17768	3	3	1.03	60S ribosomal protein L24 OS=Mus musculus OX=10090 GN=Rpl24 PE=1 SV=2
RL8_MOUSE	Rpl8	67	28007	2	2	0.35	60S ribosomal protein L8 OS=Mus musculus OX=10090 GN=Rpl8 PE=1 SV=2
RS8_MOUSE	Rps8	327	24190	17	12	7.1	40S ribosomal protein S8 OS=Mus musculus OX=10090 GN=Rps8 PE=1 SV=2
S10A1_MOUSE	S100a1	46	10498	1	1	0.48	Protein S100-A1 OS=Mus musculus OX=10090 GN=S100a1 PE=1 SV=2
RISC_MOUSE	Scpep1	38	50932	1	1	0.09	Retinoid-inducible serine carboxypeptidase OS=Mus musculus OX=10090 GN=Scpep1 PE=1 SV=2
SC23A_MOUSE	Sec23a	156	86106	7	6	0.35	Protein transport protein Sec23A OS=Mus musculus OX=10090 GN=Sec23a PE=1 SV=2
A0AUN0_MOUSE	Sec23ip	85	95057	3	2	0.09	Sec23ip protein, partial [Mus musculus]
SPA3K_MOUSE	Serpina3k	176	46850	5	5	0.57	Serine protease inhibitor A3K OS=Mus musculus OX=10090 GN=Serpina3k PE=1 SV=2
GTR3_MOUSE	Slc2a3	97	53444	2	1	0.17	Solute carrier family 2, facilitated glucose transporter member 3 OS=Mus musculus OX=10090 GN=Slc2a3 PE=1 SV=1
SMRC2_MOUSE	Smarcc2	210	132522	5	4	0.14	SWI/SNF complex subunit SMARCC2 OS=Mus musculus OX=10090 GN=Smarcc2 PE=1 SV=2
DHSO_MOUSE	Sord	311	38225	16	12	2.8	Sorbitol dehydrogenase OS=Mus musculus OX=10090 GN=Sord PE=1 SV=3
SP17_MOUSE	Spa17	66	17285	2	1	0.27	Sperm surface protein Sp17 OS=Mus musculus OX=10090 GN=Spa17 PE=1 SV=1
ISK2_MOUSE	Spink2	223	9716	10	4	7.19	Serine protease inhibitor Kazal-type 2 OS=Mus musculus OX=10090 GN=Spink2 PE=1 SV=1
B9EKJ1_MOUSE	Sptan1	1329	285004	58	54	1.29	Spna2 protein [Mus musculus]
SUCB1_MOUSE	Sucla2	104	50082	5	5	0.53	Succinate--CoA ligase [ADP-forming] subunit beta, mitochondrial OS=Mus musculus OX=10090 GN=Sucla2 PE=1 SV=2
TB22A_MOUSE	Tbc1d22a	37	59325	1	1	0.07	TBC1 domain family member 22A OS=Mus musculus OX=10090 GN=Tbc1d22a PE=1 SV=3
TX101_MOUSE	Tex101	97	26980	3	3	0.6	Testis-expressed protein 101 OS=Mus musculus OX=10090 GN=Tex101 PE=1 SV=1
TRFE_MOUSE	Tf	99	76674	4	4	0.25	Serotransferrin OS=Mus musculus OX=10090 GN=Tf PE=1 SV=1
TKFC_MOUSE	Tkfc	103	59653	5	5	0.43	Triokinase/FMN cyclase OS=Mus musculus OX=10090 GN=Tkfc PE=1 SV=1
TLN1_MOUSE	Tln1	1120	269653	37	33	0.69	Talin-1 OS=Mus musculus OX=10090 GN=Tln1 PE=1 SV=2
TM9S2_MOUSE	Tm9sf2	107	75280	6	5	0.33	Transmembrane 9 superfamily member 2 OS=Mus musculus OX=10090 GN=Tm9sf2 PE=1 SV=1
TPD53_MOUSE	Tpd52i1	48	22501	1	1	0.21	Tumor protein D53 OS=Mus musculus OX=10090 GN=Tpd52i1 PE=1 SV=1
TPM1_MOUSE	Tpm1	224	32661	21	15	6.98	Tropomyosin alpha-1 chain OS=Mus musculus OX=10090 GN=Tpm1 PE=1 SV=1
TPM2_MOUSE	Tpm2	193	32817	16	12	3.7	Tropomyosin beta chain OS=Mus musculus OX=10090 GN=Tpm2 PE=1 SV=1
Q8C7C3_MOUSE	Tpm3	239	28879	20	16	11.08	tropomyosin alpha-3 chain isoform Tpm3.5cy [Mus musculus]
UCHL1_MOUSE	Uchl1	46	24822	1	1	0.18	Ubiquitin carboxyl-terminal hydrolase isozyme L1 OS=Mus musculus OX=10090 GN=Uchl1 PE=1 SV=1
UFM1_MOUSE	Ufm1	56	9112	1	1	0.57	Ubiquitin-fold modifier 1 OS=Mus musculus OX=10090 GN=Ufm1 PE=1 SV=1
WASF2_MOUSE	Wasf2	52	54040	2	2	0.17	Wiskott-Aldrich syndrome protein family member 2 OS=Mus musculus OX=10090 GN=Wasf2 PE=1 SV=1
Q60950_MOUSE	Ybx1	274	35986	8	6	1.03	mYB-1a [Mus musculus]
ZP3R_MOUSE	Zp3r	162	64908	9	8	0.69	Zona pellucida sperm-binding protein 3 receptor OS=Mus musculus OX=10090 GN=Zp3r PE=1 SV=1
ZYX_MOUSE	Zyx	166	60507	9	9	0.89	Zyxin OS=Mus musculus OX=10090 GN=Zyx PE=1 SV=2