Evolution of gene expression between closely related taxa of *Mus*

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Christian Voolstra

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Berichterstatter:	Prof. Dr. Diethard Tautz
	Prof. Dr. Thomas Wiehe

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“Everything is a result of comparison.”
J-F. Champollion (translator of the Rosetta Stone), Grenoble, April 1818, letter to his brother

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Zusammenfassung

Regulatorische Änderungen in der Expression von Genen scheinen für evolutionäre Divergenz von großer Bedeutung zu sein. Es wird angenommen, dass ein großer Teil der Änderungen, die relevant für differentielle Adaption und Artentstehung sind, auf Änderungen in der Regulation von Genen beruht. Unterschiede in der Expression von Genen sind vererbbar und können somit selektiert werden.

Um genomweite evolutionäre Muster in der Divergenz zwischen Spezies bzw. Subspezies zu untersuchen, wurde die evolutionäre Veränderung der Genexpression von *Mus musculus* mit ihrem nächsten Verwandten *Mus spretus* verglichen sowie innerhalb der Subspezies von *Mus musculus* (*Mus musculus domesticus*, *Mus musculus musculus*, *Mus musculus castaneus* und *Mus musculus ssp.*). Zu diesem Zweck wurde RNA aus Individuen verschiedener Wildpopulationen und wild gefangener Laborpopulationen isoliert und Expressionsunterschiede im Gehirn, in Leber und Niere und im Testis mit Hilfe von Microarrays untersucht. Es wurden je sechs männliche Individuen von *M. m. domesticus*, *M. m. musculus* und *M. m. ssp.*, sowie drei männliche Individuen von *M. m. castaneus* und *M. spretus* verglichen. Ein „common reference“ Design wurde benutzt, d.h. alle Samples wurden gegen cDNA eines Pools von Labormäusen (C57BL/6) hybridisiert. Durch die Verwendung mehrerer Tiere jeder Population war es möglich, intra- und inter-spezifische Varianzen getrennt zu betrachten, um dadurch Erkenntnisse über individuenspezifische bzw. populationsweite Divergenzmuster zu erhalten. Genexpression fungierte hierbei als gemeinsamer Nenner, um die evolutionäre Divergenz zwischen den verschiedenen Organen zu vergleichen.

Eine statistische Analyse der signifikant differentiell exprimierten Gene zeigt, dass die Anzahl der Gene, deren Expression zwischen den Taxa verschieden, ist sowohl von der Divergenzzeit als auch vom Gewebe abhängig ist. Zwischen Subspezies findet man die meisten Unterschiede in der Leber und Niere und nahezu keine Unterschiede im Testis. Im Gegensatz dazu findet man im Speziesvergleich die meisten differentiell exprimierten Gene im Testis. Hybridisierungen genomischer DNA von *Mus spretus* auf den Microarrays zeigten, dass Unterschiede in der Hybridisierungseffizienz als Ursache für das beobachtete Muster ausgeschlossen werden können. Um die phylogenetischen Verhältnisse zu untersuchen, wurden die mitochondrialen D-loop Sequenzen miteinander verglichen. Die Analyse zeigt, dass *Mus spretus* klar von den *Mus musculus* Subspezies separiert ist, und dass *Mus musculus* *ssp.* keine phylogenetische Einheit bildet. Die funktionelle Annotation der differentiell exprimierten Gene zeigt, dass eine Vielzahl verschiedener Gene betroffen ist, und dass Transkriptionsfaktoren eine große Gruppe der differentiell exprimierten Gene in allen drei untersuchten Geweben bilden. Es ist möglich, anhand der Klassifizierung funktioneller Annotationen die Identität der Gewebe zu bestimmen. Mittels quantitativer Realtime PCR wurde die Expression ausgesuchter Gene verifiziert.

Neben der Untersuchung differentiell exprimierter Gene wurde eine genomweite Analyse evolutionärer Divergenzmuster durchgeführt. Eine Analyse der genomweiten Expressionsdivergenz („scaled divergence“) zeigt dasselbe Muster wie die Studie der differentiell exprimierten Gene: Divergenz zwischen Subspezies ist in der Leber und Niere am höchsten und zwischen Spezies im Testis. Weiterhin wurde eine mögliche Korrelation von Sequenz- und Expressionsevolution untersucht. Die Analyse zeigt, dass eine negative Korrelation zwischen Expressionsevolution und Sequenzevolution („dN/dS ratio“) der differentiell exprimierten Gene zwischen den Subspezies besteht. Im Speziesvergleich ist diese Korrelation positiv.

Die Beobachtung, dass insbesondere in Leber und Niere Expressionsunterschiede zwischen Subspezies zu finden sind deutet darauf hin, dass ökologische und physiologische Anpassungen eine große Rolle in frühen Divergenzstadien spielen. Spätere Divergenzstadien hingegen scheinen mehr von nichtökologischen Faktoren beeinflusst zu werden. Die Korrelationsanalyse von Expressions- und Sequenzevolution deutet auf positive Selektion der Gene hin, die sich zwischen Subspezies unterscheiden. Ob die Divergenz der Genexpression in späteren Stadien Ursache oder Wirkung von Speziation ist und ob sexuelle Selektion oder genetische Drift diese Divergenz bewirkt, bleibt zum jetzigen Zeitpunkt offen. Weitere Experimente sind notwendig, um diese Fragen zu beantworten.

Abstract

Regulatory changes in gene expression are thought to play an important role in evolutionary divergence. It has been suggested that a large proportion of the changes relevant to the process of differential adaptation and species formation can be attributed to changes in gene regulation. Moreover, differences in gene expression are heritable and thus provide a target for selection.

To infer genome-wide evolutionary patterns of species divergence, I studied the evolution of gene expression in a comparison of *Mus musculus* with its closest relative *Mus spretus*, and among subspecies of *Mus musculus* (*Mus musculus domesticus*, *Mus musculus musculus*, *Mus musculus castaneus*, *Mus musculus ssp.*). RNA of individuals from different wild populations and wild-derived populations at and below the species level were screened for expression differences in three tissues (brain, pooled liver/kidney, testis) with a microarray approach. Six male individuals from *M. m. domesticus*, *M. m. musculus* and *M. m. ssp.* and three male individuals from *M. m. castaneus* and *M. spretus* were compared. A common reference design was employed, and all samples were hybridized against labeled cDNA from laboratory mice (C57BL/6). Using multiple animals from each population allowed to differentiate between the fraction of variation stemming from within- and that stemming from between-terms of population differences. Gene expression measures served as a common currency to compare evolutionary divergence across different tissues.

A statistical analysis based on the identification of differentially expressed genes shows that the number of genes that changed expression between taxa depends on divergence time and the tissue under study. Across subspecies most expression changes are identified in the liver/kidney and almost none in the testis, whereas across species the highest number of differentially expressed genes is identified in the testis. Comparative Genomic Hybridizations (CGHs) ruled out hybridization differences as a cause for the observed pattern. Mitochondrial D-loop sequencing shows that *Mus spretus* is separated from the *Mus musculus* subspecies and that *Mus musculus ssp.* is not resolved as a phylogenetic entity. Functional annotation analysis of the differentially expressed genes shows that a wide variety of genes change expression, that transcription factors are a major group in all three tissues, and that functional classification categorization is able to reflect the tissues identity. Quantitative real-time PCR was used to confirm chosen target loci.

In another approach, genome-wide patterns of evolution of gene expression were investigated. A study of the overall rates of divergence of gene expression shows the same tendency as the study based on gene counts: across subspecies, divergence is highest in the liver/kidney and across species, it is highest in the testis. In addition, it was tested whether a correlation between sequence divergence and gene expression divergence exists. Across subspecies there is a negative correlation between variation in gene expression and dN/dS ratios for genes that changed expression, whereas across species this correlation is positive.

The observation of divergent gene expression in metabolic organs among incipient subspecies of the house mouse suggests a pervasive role of ecological and physiological adaptations in the early stage of divergence while late divergence seems to be primarily driven by non-ecological factors. The dN/dS analysis points to a role of positive selection for the genes that changed expression between subspecies. Whether or not gene expression divergence in later stages of divergence is a cause or a consequence of speciation and whether sexual selection or genetic drift is the major driving force behind this divergence remains open. Additional experiments are necessary to answer these questions.

1 Introduction

1.1 Microarrays as a tool to study evolution of gene expression

The study of molecular evolution began in the 1950s when it first became possible to compare the amino acid sequences of proteins among related species. With advances in DNA sequencing technologies, homologous genes and their regulatory regions could be analyzed between and within different taxa, respectively populations. The advent of microarray technology over the past few years makes it nowadays possible to study the evolution of genome-wide patterns of gene *expression*. Recent studies have used microarrays to compare patterns of expression between closely related species (Enard et al. 2002; Caceres et al. 2003; Karaman et al. 2003; Meiklejohn et al. 2003; Ranz et al. 2003; Fortna et al. 2004; Khaitovich et al. 2004; Nuzhdin et al. 2004; Saetre et al. 2004). Those studies revealed a large diversity in the level, timing, and location of gene expression, interpreted partly as lineage-specific adaptations, although the precise nature of the evolutionary forces causing intra-specific and inter-specific transcriptome divergence are not yet fully understood. The current belief is that genome-wide expression studies will eventually help to understand the evolution of gene expression and to identify genes that are responsible for differential adaptation. The underlying opinion is that changes in time, level and location of gene expression are directly responsible for evolutionary changes and adaptational processes. This view has a long history and is based on the finding that rates of morphological evolution are poorly correlated with rates of protein evolution (Wilson et al. 1974). For this reason, it is assumed that most of the differences we see between taxa are of regulatory nature. All the more, it is remarkable how little we know concerning patterns, rates and mechanisms of change at the regulatory level, despite accumulating evidence that regulatory changes can have exceptional evolutionary consequences (Carroll 2001; Wilkins 2002). The perspective is that with the help of high-throughput technologies, such as microarrays, one can study the evolution of gene expression within and among species on a genome-wide scale. This should enable one to extend the view from a few genes and single pathways to a more generalized global understanding of the evolution and dynamics of gene expression.

Then again, a neutral model of transcriptome evolution is assumed (Khaitovich et al. 2004; Khaitovich et al. 2005) predicting that the majority of expression differences are neutral and of no or little adaptive value. This model is based on the finding that expression differences between species accumulate approximately linearly with time. Lemos *et al.* (Lemos et al. 2005) used the implications from a neutral model as a yardstick against which they measured patterns of gene expression polymorphism and divergence in several datasets. Their results indicate that stabilizing selection is a major force regarding the evolution of gene expression and that stabilizing selection on transcription levels has prevented greater evolutionary changes in mRNA levels.

Overall, high levels of variation in gene expression patterns have been found on an intra- and inter-specific level and their interpretation is different depending on the specific model system used. Nevertheless, it seems clear that a substantial fraction of transcriptional variation is genetically hard-wired, either in *cis* or *trans*.

1.2 Intra-specific transcriptome variation

The study of gene expression variation in natural populations shows that there is significant intra-specific variation for a large number of genes assayed so far. In *Drosophila*, at least 10% of the genes surveyed show significant variation among genotypes (Jin et al. 2001; Gibson et al. 2004; Nuzhdin et al. 2004; Wayne et al. 2004). In the most extreme case in vertebrates as much as 94% of the genes showed significant differences among individuals of the same population of killifish *Fundulus heterolitus* when comparing gene expression in heart tissue (Oleksiak et al. 2005). This lead to the conclusion that intra-specific variation in gene expression is in general higher than the level of polymorphism observed for DNA or protein sequences. This is mainly due to two reasons. First, while sequence data are direct, accurate and complete, expression data are indirect and covers only a subset of all possible expression states of a cell, making comparative analysis challenging. Secondly, due to the pleiotropic nature of genes, change of expression of a gene involved in more than one pathway can affect the expression of many different downstream genes that comprise altogether a large fraction of the genome, as has been shown in artificial selection experiments in *D. melanogaster* (Anholt et al. 2003; Mackay et al. 2005). Hence, there is no consensus or rule of how big the variation of gene expression in natural populations is. Even for laboratory mice variation in gene expression between inbred strains is considerable (Wade et al. 2002). A study by Pritchard *et al.* (Pritchard et al. 2001) looked for expression differences in C57BL/6 mice in different tissues in a highly replicated experiment. They found significant variances in gene expression ranging from 0.8% to 3.3% of the genes assayed, depending on the tissue tested. All in all, regarding the amount of intra-specific transcriptome variation there is certainly a dependency on the taxa one looks at, environmental inputs, and the tissue under investigation.

1.3 Inter-specific transcriptome variation - tempo and mode of transcriptome evolution

Extending the comparison between individuals of one species to a comparison across species makes it possible to distinguish patterns of polymorphism from patterns of divergence and to assess the temporal dynamics of change of the transcriptome; and finally, allows conclusions about the interdependence between transcriptome evolution and the formation of new species. The main limitation that comes with comparative studies between different taxa is that microarray platforms exist only for model organisms. Using microarrays that were designed for one species in a closely related (non-focal) species could bias the results of a study, i.e. sequence divergence is the primary factor of hybridization differences and not differences in gene expression (Gilad et al. 2005). Different measures to account for this type of bias have been proposed as reviewed in Ranz *et al.* (Ranz and Machado 2006).

Of general interest is the question whether transcriptome divergence increases linearly with time, that is, if change of expression can be explained neutrally. Analyses of gene expression divergence among *Drosophila* species and between strains of *Drosophila melanogaster* during early metamorphosis showed that the magnitude of change was in accordance with what was expected from the phylogenetic relationships (Rifkin et al. 2003). Further studies were conducted in which the this trend was also found. A comparison of the expression profile of the prefrontal cortex of human, *Pan troglodytes*, *Pongo pygmaeus* and *Macaca mulatta* (Khaitovich et al. 2004) showed an increase in the amount of change of gene expression with time.

If the majority of changes is selectively neutral, one might ask what is the amount of transcriptome divergence that is caused by natural selection. This question has been adressed using different approaches leading to inconsistent results across different taxa. The basic idea behind all these approaches is similar to the McDonald-Kreitman-test for coding sequences. The amount of polymorphism (expression variation) within a species is compared to the amount of divergence (expression divergence) between species. According to the model, genes whose expression is under directional selection should show little intra-specific variation but large inter-specific divergence, whereas genes under purifying selection are expected to show low levels of polymorphism *and* divergence. Genes under balancing selection show large intra-specific variation but low inter-specific divergence. One metric that was introduced is the scaled divergence metric (Lemos et al. 2005) that compares measures of within-species to between-species variances. Datasets that were analyzed with this model among studies of genes that changed during development in the *D. melanogaster* subgroup (Rifkin et al. 2003), on expression profiles in the brain among primates (Hsieh et al. 2003) and in *C. elegans* (Denver et al. 2005) all point to an omnipresent role of stabilizing selection on gene expression levels, and that only a minor fraction is positively selected, respectively changed adaptively. Other studies indicate that the transcriptome is evolving approximately neutral, i.e. differences accumulate linearly with time (Khaitovich et al. 2004). There is no common consensus yet. The percentages of genes evolving under selective forces strongly depend on the method used and the system analyzed.

Nevertheless, there is an emerging signal that shows up in studies using *Drosophila*. Most transcriptome changes (83%) detected between *D. melanogaster* and *D. simulans* are found in genes with sex-biased expression (Ranz et al. 2003). Moreover, Meiklejohn *et al.* (Meiklejohn et al. 2003) showed that male-biased genes are also over-represented among those genes that exhibit intra-specific changes in the level of expression by comparing eight strains of *D. melanogaster*. Together with the notion that coding sequences and morphological characters related to sex and reproduction evolve faster in comparison to other genetic characters, these findings support sexual selection theories as well as models of sexual conflict, driving traits in arbitrary directions (Arnqvist and Rowe 2005). Such signals of rapid evolution of the male reproductive system are also found among abalone (Swanson and Vacquier 1995), *Drosophila* (Civetta and Singh 1998), rodents (Good and Nachman 2005) and primates (Wyckoff et al. 2000). This would indicate, at least for genes with sex-biased expression, that positive selection drives divergence.

1.4 Transcriptome divergence and speciation

Understanding the genetic basis of speciation is of central interest in evolutionary biology. Under the biological species concept, species are “groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1963). Reproductive isolation therefore refers to the independence of gene pools, among which new mutations and allele frequency changes are not shared. Differences that limit gene flow between the diverging populations therefore play an important role in speciation (Wu 2001).

Up to now only very few genes contributing to reproductive isolation have been isolated (so-called „speciation genes“) (Orr et al. 2004; Wu and Ting 2004). Microarrays offer an alternative to genetic screens in their potential to isolate genes that contribute to species differences. They assay a large amount of genes in the genome for differences in expression levels, and these differences can then be related to reproductive isolation. Three of the five known speciation genes are associated with transcriptional regulation, supporting the hypothesis that gene regulatory incompatibilities might be the cause of lower fitness in species hybrids, respectively that species differences are of regulatory nature (Barbash et al. 2003), as shown by two recent microarray studies in *Drosophila* (Michalak and Noor 2003; Ranz et al. 2004). The first study, a study of expression dysfunction in sterile hybrid males of *D. simulans*/*D. mauritiana* identified loci related to spermatogenesis (Michalak and Noor 2003). The results provide support to the faster-male theory that is regarded as a cause of Haldane‘s rule (Coyne and Orr 2004). The rapid evolution of hybrid male sterility is caused by the faster divergence of male-specific fertility genes, either driven by sexual selection or by the inherent sensitivity of spermatogenesis to the genetic perturbations experienced by hybrids (Wu and Davis 1993). They then fail to correctly interact in a hybrid genome. Those loci are prime candidates for causing post-zygotic reproductive isolation. Concerning hybrid females, the second study in a more distant comparison between *D. melanogaster* and *D. simulans* showed that 69% of the assayed genes were either under- or over-expressed in the hybrid females (Ranz et al. 2004).

Taken together, although distorted patterns of gene expression in hybrids do not necessarily have to be associated with fitness reduction, respectively reproductive isolation, microarrays have shown to be instrumental in identifying acquired regulatory, respectively expression differences between species that are of biological significance.

1.5 The genetic basis of gene expression differences

Although one can use microarrays to find genes that are differentially expressed within or between populations/species, information about the actual genetic background is missing. Studies on the relative contributions of *cis* versus *trans* regulatory variation are contradictory. Studies in yeast (Yvert et al. 2003), humans (Morley et al. 2004), flies (Wayne et al. 2004) and worms (Denver et al. 2005) found an excess of *trans*-acting effects in gene expression across the genome. In other studies the opposite was found, i.e. a pre-dominant role of *cis*-acting factors, even when the same model organism was under study (Cowles et al. 2002; Yan et al. 2002; Schadt et al. 2003; Wittkopp et al. 2004). At least partly this was attributed to the different statistical methods and cutoffs that were used. This shows that one has to take care when drawing conclusions from such data, and that studies as these are particularly susceptible to biased results. Nevertheless, the studies agree that differences in expression are heritable, have a genetic background and can therefore be selected.

1.6 Model/study system – the *Mus* species complex

When looking at evolutionary patterns of gene expression, the house mouse provides an ideal study system for a number of reasons. The complete genome sequence of a laboratory strain of the house mouse is available (Waterston et al. 2002). Divergence can be compared across recently separated species as well as across subspecies, so that a fine-scale resolution is on hand when looking at evolutionary dynamics of expression divergence. The emergence of the genus *Mus* started about 5 million years ago (Guenet and Bonhomme 2003). The house mouse *Mus musculus* is separated from its closest relative *Mus spretus* by 1.1 to 1.5 million years (Boursot et al. 1993), whereas the different *Mus musculus* subspecies diverged from each other 0.5 to 0.8 million years ago (Guenet and Bonhomme 2003) (Figure 1).

Mus spretus, known as the Algerian mouse, is found in regions spanning the western Mediterranean Sea. Although sympatric with some *Mus musculus* subspecies, hybrids have been rarely observed. *Mus musculus* has its evolutionary origin in Asia and has now spread across the world. At least 3 different house mouse subspecies exist that occupy different geographical areas, with a western (*Mus musculus domesticus*), a central (*Mus musculus musculus*) and an eastern house mouse (*Mus musculus castaneus*). The western house mouse *M. m. domesticus* is common in Western Europe and was brought by humans to Africa, America and Australia. The habitat of the central house mouse *M. m. musculus* spans from Eastern Europe to Japan, across Russia and northern China. The eastern house mouse *M. m. castaneus* is found from Sri Lanka to South East Asia. None of these subspecies is completely genetically isolated. They are only partially reproductively isolated from each other as indicated by the presence of hybrid zones that form in areas of secondary contact between them as well as by the presence of sterile hybrid males in experimental crosses between them

(Forejt 1996; Storchova et al. 2004). The fourth, less well-characterized subspecies (*Mus musculus ssp.*) occurs in the centre of the assumed origin of the house mouse (throughout North-West India, Iran and Pakistan).

The close relationship among house mice is beneficial because the identified genetic changes are less likely a consequence rather than a cause of divergence, i.e. the various *Mus musculus* taxa are actively adapting to different environments. *M. m. musculus* and *M. m. domesticus* are the best-studied subspecies and can be distinguished morphologically. They differ in relative tail length (longer in *M. m. domesticus*) as well as craniofacial shape (longer and narrower in *M. m. domesticus* (Macholan 1996)).

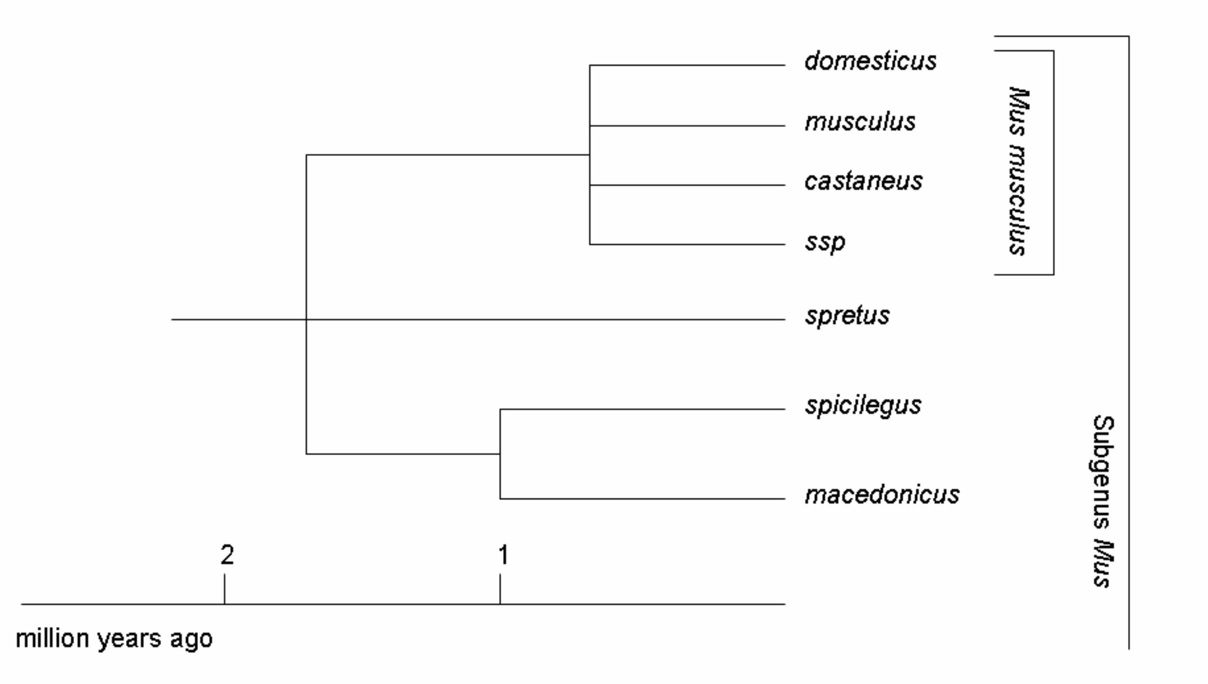


Figure 1: Section of the evolutionary tree of the genus *Mus*. The last node represents the *Mus musculus* subspecies complex (adapted from (Guenet and Bonhomme 2003)).

1.7 Project description

To investigate divergence among recently separated species I studied the evolution of gene expression in a comparison of *Mus musculus* with its closest relative *Mus spretus*, and among the subspecies of *Mus musculus* (*Mus musculus domesticus*, *Mus musculus musculus*, *Mus musculus castaneus*, *Mus musculus ssp.*). RNA from individuals from different wild populations and wild-derived populations at and below the species level were screened for expression differences in different tissues (brain, pooled liver/kidney, testis) with a microarray approach. Six male individuals from *M. m. domesticus*, *M. m. musculus* and *M. m. ssp.* and three individuals from *M. m. castaneus* and *M. spretus* were used. A common reference design was employed, and all samples were hybridized against labeled cDNA from laboratory mice (C57BL/6).

Gene expression measures served as a common currency to compare evolutionary divergence across different tissues. Differences in reproductive organs such as testis are thought to reflect processes relating to sexual selection, whereas differences in liver/kidney may reflect ecological and physiological adaptations. Expression differences in the brain may imply information regarding evolution of behavirol traits, respectively cognitive perception. A study of gene expression should be particularly germane because it is thought that changes in gene expression play a critical role in divergence. Using multiple animals from each population allows to differentiate between the fraction of variation stemming from within- and that stemming from between-terms of population differences.

The main interest was to find out how many genes contribute to species, respectively subspecies differences in expression profiles, if there is a difference in the number of genes differentially expressed when analyzing different tissues/phylogenetic distances, and the identity of the differentially expressed genes and which biological processes are affected, respectively targeted. The other point of interest was in finding genome-wide patterns of evolution of gene expression. For this purpose, overall rates of divergence of gene expression across subspecies and across species for the tissues under study were compared. Furthermore, it was analyzed whether evolution of proteins and gene expression levels is coupled, respectively whether they behave differently when comparing subspecies and species.

2 Material & Methods

2.1 Animals

Unrelated male mice were collected from the wild in the Czech Republic (*M. m. musculus*) and Germany (*M. m. domesticus*). Mice are known to live in small family groups with home ranges rarely exceeding a radius of 2 km. For strictly indoor living mice, home ranges can even be restricted to a few square meters (Berry and Bronson 1992; Pocock et al. 2005). In order to have a representative sample of mouse populations within a given area and to avoid the influence of specific family effects, individuals unrelated to each other from different demes were sampled. Mouse populations were sampled according to the following scheme: trapped mice were assigned to different locations only if the trapping sites were at least 0.5 km apart from each other. Mouse traps were set up in private houses, barns or stables, or in fields in the case of *Mus spretus*. Animals were captured in live traps and transferred to the lab, where they were kept individually under common laboratory conditions for 3 to 5 days. Six males of similar age (judged based on their body weight and size) of both subspecies were selected for further experiments. Six male individuals of the central subspecies *M. m. ssp.* and three male individuals of the subspecies *M. m. castaneus*, with similar age and body weight as individuals collected in the wild, were selected. *M. m. ssp*. and *M. m. castaneus* had been kept between 2 and 10 generations in the Laboratoire Génome Populations Interactions Adaptation in Montpellier under standard conditions.

Three male mice of the species *Mus spretus* were also included in the analysis. These were F1 offspring derived from three pairs of wild-caught, unrelated mice collected in Spain near Madrid in August 2004.

The reference strain C57BL/6 was obtained from the Charles River Laboratories, Germany. All animals were sacrificed using CO_2. Tissues were excised and immediately snap frozen in liquid nitrogen. Frozen tissues were stored at –80°C for not longer than one week. Exact geographic origins of the animals used are given in Table 1.

Table 1: Sample locations and number of generations mouse strains were kept in the lab.

subspecies	generation	geographic origin	strain name
M. m. musculus	collected in the wild	Czech Republic, Studenec	M2
M. m. musculus	collected in the wild	Czech Republic, Tresov	M3
M. m. musculus	collected in the wild	Czech Republic, Rousek	M4
M. m. musculus	collected in the wild	Czech Republic, Pozdatin	M5
M. m. musculus	collected in the wild	Czech Republic, Rejtar	M7
M. m. musculus	collected in the wild	Czech Republic, Pozdatin	M8
M. m. domesticus	collected in the wild	Germany, Niederbachem	D1
M. m. domesticus	collected in the wild	Germany, Züllighofen	D3
M. m. domesticus	collected in the wild	Germany, Arzdorf	D5
M. m. domesticus	collected in the wild	Germany, Kürrighofen	D6
M. m. domesticus	collected in the wild	Germany, Swisttal	D10
M. m. domesticus	collected in the wild	Germany, Heimerzheim	D13
M. m. ssp.	8	Iran, Teheran	THE
M. m. ssp.	5	Iran, Birdjand	BID
M. m. ssp.	5	Iran, Machad	MAC
M. m. ssp.	5	Iran, Khak	KAK
M. m. ssp.	10	India, Delhi	DHA
M. m. ssp.	9	Pakistan, Rawalpindi	MPK
M. m. castaneus	8	India, Masinagudi	CIM
M. m. castaneus	2	Thailand, Pathumthani	CTP
M. m. castaneus	8	Taiwan, He-mei	CTA
M. spretus	1	near Madrid	SP1
M. spretus	1	near Madrid	SP2
M. spretus	1	near Madrid	SP3

2.2 Microarrays

The mouse oligolibrary by Sigma-Genosys/Compugen (Haverhill, UK) was duplicate-spotted on Schott/Nexterion Slides H using a Biorobotics MicroGrid II Spotter (Genomic Solutions, Cambridgeshire, UK). The library consists of 21,997 5′-C6 amino modified 65mers with 21,766 unique transcripts and 231 controls. The oligos represent all of the mouse genes associated with public mRNA sequences found in GenBank release 126 (October 2001). Each array consists of 46,128 spots, representing the oligolibrary in duplicate, plus external controls and reference spots.

2.3 Sample preparation

Tissue samples were homogenized in TRIzol (Invitrogen, Carlsbad, CA) using an electric homogenizer. RNA was extracted following the manufacturer's protocol. After resuspension of the RNA in DEPC-H_2O, the RNA was precipitated in 4 M LiCl for storage at -80°C.

20 µg of each total RNA was reverse transcribed using the FairPlay Microarray Labeling Kit (Stratagene, La Jolla CA) and labeled by incorporation of Alexa Fluor 555 and Alexa Fluor 647 (Molecular Probes, Eugene, OR), respectively, according to the manufacturer's protocols. Half of the labeled cDNA was used for hybridization.

2.4 Hybridization

The two labeled cDNA samples to be compared were combined in 65 µl of 5x SSC and competitively hybridized on a microarray under a coverslip (Implen LifterSlip 24x60l) for 16 hours at 42°C in an Advalytix SlideBooster. Slides were washed in graded SSC/SDS and spun dry.

2.5 Data Acquistion

Arrays were scanned with a GeneTAC LS IV (Genomic Solutions, Cambridgeshire, UK) confocal laser scanner. Scanner settings were adjusted individually for every channel and microarray. Images were analyzed using the software Spotfinder from the TIGR institute (Saeed et al. 2003), and the extracted intensities were stored as tab-delimited .mev files. The arrays were normalized using block-wise LOWESS and SD regularization (Yang et al. 2002) as described in (Saeed et al. 2003).

2.6 Experimental design

Microarray analysis was performed on three different tissue samples. For each individual, labeled cDNA from total RNA of the whole brain and testis tissues was individually hybridized to the chip, whereas RNA from liver and kidney was pooled in equivalent amounts and hybridized jointly. A common reference design was employed with experimental samples labeled with Alexa Fluor 647 and the reference sample labeled with Alexa Fluor 555. To obtain enough reference RNA for each of the tissues, RNA was extracted from nine animals of the reference inbreed strain C57BL/6 and pooled tissuewise. Thus, for each tissue the exact same reference RNA was used for all hybridizations. The experimental samples were hybridized together with the reference sample. Since I used a common reference design and all experimental samples are labeled with the same dye, differences in the amount of label per amount of cDNA (i.e. “dye bias”) do not affect the results.

Altogether 72 hybridizations were performed, i.e. six individuals times three tissue samples (brain, liver/kidney, testis) for each of the subspecies *M. m. musculus*, *M. m. domesticus* and *M. m. ssp.* and three tissue samples for each of the *M. m. castaneus* individuals *CTP* and *CIM* and *CTA*. For *M. spretus*, nine hybridizations were performed: three tissue samples (brain, testis and liver/kidney) for each of the three individuals.

2.7 Genomic DNA hybridizations

To correct for possible differences in hybridization efficiencies of individual oligos because of sequence divergence between *Mus musculus* and *Mus spretus* I performed Comparative Genomic Hybridizations (CGHs) for all 3 *Mus spretus* samples using DNA from C57BL/6 as the reference. For each *Mus spretus* animal, 1.5 µg of genomic DNA was labeled using the BioPrime Plus Array CGH Indirect Genomic Labeling Systems (Invitrogen) according to the manufacturer’s instructions. The C57BL/6 reference was labeled three times independently each time using 1.5 µg of genomic DNA. Labeled genomic DNA of both species were combined in equal amounts and hybridized competitively to a microarray under a coverslip (Implen LifterSlip 24x60l) for 16 hours at 52°C in an Advalytix SlideBooster. As before, slides were washed in graded SSC/SDS and spun dry. The arrays were normalized using block-wise LOWESS and SD regularization (Yang et al. 2002) as described in (Saeed et al. 2003). All oligos are located within the 3’UTR of the respective genes so that they are expected to bind equally well to genomic DNA and cDNA.

2.8 Data processing and statistical analyses

For the cDNA hybridizations I calculated the log2-transformed ratio of the normalized signal intensity of the “sample” channel relative to the “reference” channel for each gene. Log2-ratios for the duplicate spots were averaged. These values were submitted to the Gene Expression Omnibus (GSE2597) and were used for all subsequent analyses.

2.9 Identification of differentially expressed genes with SAM (*S*ignificance *A*nalysis of *M*icroarrays)

I used the SAM (*S*ignificance *A*nalysis of *M*icroarrays) software (Tusher et al. 2001) in a 2-class unpaired comparison to identify genes differentially expressed between *Mus spretus* and all *Mus musculus* subspecies. This analysis was performed for each tissue independently. In

SAM, the relative difference (*d(i)*) in gene expression is compared to the distribution of *d(i)* following random permutation of the sample categories (*here:* 200 permutations). For each *d(i)*, a certain proportion of all genes in the permutation set (control set) will be found to be "significant" by chance and this parameter is then used to calculate a False Discovery Rate (FDR). Only genes with a False Discovery Rate < 5% were selected as differentially expressed in this "between species" comparison. The FDR emphasizes the proportion of errors among the identified differentially expressed genes, i.e. the percentage of genes falsely assigned significant.

To identify the genes that are differentially expressed among subspecies I used the multiclass analysis in SAM with 200 permutations and a False Discovery Rate < 5%. Genes identified by the multiclass analysis are those where all house mouse subspecies differ significantly from each other as well as genes where combinations of two subspecies differ from each other as well as genes that are differentially expressed only in one subspecies lineage relative to all other lineages (so called "lineage-specific" genes).

2.10 Identification of lineage-specific genes of subspecies of *Mus musculus*

To isolate genes that are subspecies-specifically expressed, i.e. genes that are different in one subspecies in comparison to all other subspecies, a series of 2-class unpaired comparisons in SAM (200 permutations, FDR < 5%) was performed using all possible pairwise comparisons of the four subspecies (*M. m. domesticus* vs. *M. m. musculus*, *M. m. domesticus* vs. *M. m. castaneus*, *M. m. domesticus* vs. *M. m. ssp.*, *M. m. musculus* vs. *M. m. castaneus*, *M. m. musculus* vs. *M. m. ssp.* and *M. m. castaneus* vs. *M. m. ssp.* for all three tissues). Among the genes that were identified in the 2-class comparisons, only those genes were selected, where one subspecies differed significantly from all others but these did not differ significantly from each other. This procedure was done for all subspecies.

2.11 Mitochondrial D-loop sequencing

For each individual used in the study, the mitochondrial D-loop region was sequenced. A 30 µl PCR was set up using primers F: 5'-CATTATTCTGGTCTTGTAAACC-3' and R: 5'-GCCAGGACCAAACCTTTGTGT-3' (Prager et al. 1993). PCR products were purified using

96 well plates (Millipore, Hertfordshire, UK) according to the supplier's protocol. All PCR products were sequenced in both directions using the BigDye sequencing chemistry on an ABI3700 automated sequencer. Sequencing reactions were purified using Sephadex columns (Millipore, Hertfordshire, UK). Sequences have been submitted to GenBank with the accession numbers DQ266049-DQ266072.

2.12 Confirmation of differentially expressed genes from the SAM analyses with quantitative real-time PCR (qRT-PCR)

The qRT-PCRs were performed with RNA from the same individuals that were used in the microarray study. Genes that were identified as signficantly differentially expressed in the SAM analyses were chosen for confirmation (see 6.1, 6.2). Prior to qRT-PCR, RNA was reverse transcribed using random hexamers (Fermentas) and the ThermoScript Reverse Transcriptase Kit (Invitrogen, Carlsbad, CA) according to the manufacturer's protocol. All genes were verified using the TaqMan Gene Expression Assays from Applied Biosystems (Foster City, CA) and reactions were performed using 2 ul of a 1:10 diluted cDNA in a reaction volume of 8 ul. Briefly, 4 ul of TaqMan Universal PCR Master Mix, 0.4 ul of TaqMan Gene Expression Assay, 1.6 ul H_2O and 2 ul diluted cDNA were used per reaction. For each individual, a single cDNA synthesis per tissue was performed which was used in all qRT-PCR reactions. The reactions were done in triplicate per gene and individual. Averaged C_T values of each qRT-PCR reaction from the target gene were standardized in relation to the averaged C_T of a house-keeping gene that ran in the same reaction plate. Two different house-keeping genes were used. Tbp, TATA box binding protein, Assay ID Mm00446973_m1 was used to normalize expression levels in the brain and liver/kidney. Gapdh, glyceraldehyd-3-phosphate dehydrogenase, Assay ID Mm99999915_g1 was used to normalize expression levels for the genes that were found to be differentially expressed in the testis. These house-keeping genes showed a similar expression height in all species/subspecies and had the lowest standard deviation across individuals for the corresponding tissues (data not shown).

Genes that were picked for confirmation had the following GenBank accession numbers and assay IDs: AK003742: Mm01217369_m1, AK015921: Mm01282622_m1, AK014677: Mm01217598_g1, Z48496: Mm02017439_g1, BC007147: Mm00453021_m1, NM_008917: Mm01192227_m1, NM_009529: Mm00784689_s1, NM_011560:

Mm00843984_s1, AK004920: Mm01168596_m1, NM_009638: Mm00731639_m1, AF351196: Mm01174266_m1, U94828: Mm00450997_m1, NM_009138: Mm00436443_m1 and NM_008701: Mm00435145_m1.

For each qRT-PCR reaction the (averaged) C_T value of the house-keeping gene was subtracted from the (averaged) C_T value of the target gene, yielding the ΔC_T value. In the case of confirmation of differentially expressed genes between *Mus spretus* and *Mus musculus*, these ΔC_T values were then used in a Mann-Whitney-U test analogous to the 2-class unpaired test in the SAM analysis to confirm results from the microarray study, thereby contrasting all *Mus musculus* subspecies to *Mus spretus*. The following formula was used to calculate the fold-change between *Mus spretus* in relation to *Mus musculus* from the ΔCT values:

$$\text{fold-change} = 2^{-(\overline{\Delta C_T\_Mus\_spretus} - \overline{\Delta C_T\_Mus\_musculus})},$$

where $\overline{\Delta C_T\_Mus\_spretus}$ is the average ΔC_T value across the *Mus spretus* individuals and $\overline{\Delta C_T\_Mus\_musculus}$ is the average ΔC_T value across all *Mus musculus* subspecies (averaged first across individuals within subspecies and then across subspecies).

In the case of confirmation for differentially expressed genes across subspecies, ΔC_T values were used in a Kruskal-Wallis-test that differentiated between all four subspecies analogous to the multiclass analysis in SAM. Since no lineage-specific genes were tested, I abstained from calculating all possible combinations of fold-changes and concentrated on the confirmation of differential expression between subspecies.

2.13 Identification of functional categories within lists of differentially expressed genes with DAVID (*D*atabase for *A*nnotation, *V*isualization and *I*ntegrated *D*iscovery)

The DAVID Functional Classification tool (Dennis et al. 2003), available at http://david.abcc.ncifcrf.gov/, was used to annotate the genes that were called signficantly differentially expressed from the SAM analyses. The functional classification tool helps to sort large lists of genes into functionally related groups of genes to explore the biological content captured by high throughput technologies. This tool generates a gene-to-gene similarity matrix based on shared functional annotations using over 75,000 terms from 14 functional annotation sources. It is a program to identify co-occurrences of functional annotations. In that aspect it is different from tools that use a single classification system, such as GO ontologies. A clustering algorithm classifies highly related genes into functionally related groups. During the course of the analysis, I concentrated on the listing of the "consensus terms" shared by the genes in the corresponding cluster. This tool was used to get an overview over putatively underlying biological processes that are contained in the candidate gene lists from the SAM analyses. All settings were used as the default given, except for the liver/kidney analyses. Here, the classification stringency "highest" was chosen.

2.14 Identification of biological processes within lists of differentially expressed genes with PANTHER (***P**rotein **AN**alysis **TH**rough **E**volutionary **R**elationships*)

The gene lists for the between species and the between subspecies analysis obtained from SAM were submitted to PANTHER (http://www.pantherdb.org). PANTHER identifies over-represented functional categories among the significant genes (Mi et al. 2005). Significance is based upon comparing the gene list with a reference list (*here:* the full gene content that was represented on the microarray) by means of a binomial test (Cho and Campbell 2000). For the analysis, the "Biological Process PANTHER ontology" was chosen and only those genes with a p-value of less than 0.05 in the category of significantly over-represented genes were analyzed.

2.15 Scaled divergence analysis

The scaled divergence metric is basically a measure of the rate of gene expression divergence in that it compares the between species to the within species components of the variance, as determined from the meansquares (MS) from an ANOVA (Lemos et al. 2005). The scaled divergence is defined as

$$\Delta t = {}^{v_b}\!\big/_{v_w},$$

where t is the total number of generations separating the 2 lineages, v_b is the between-species component of variance and v_w is the within-species component of variance. Note that:

$$v_b = \frac{MS_b - MS_w}{n_0},$$

where MS_b and MS_w are the between-population and within-population meansquares from an ANOVA, and n_0 is the average sample size. Therefore, the between-population component of variance is already corrected for the within-population component, since MS_w is subtracted from MS_b.

Two different group assignments were used that reflect the two different levels of divergence. The first grouping assorted all individuals from all *musculus* subspecies into one group and all *spretus* individuals into a second group, yielding an ANOVA model with only two levels. The second grouping comprised only the subspecies of house mouse in a 4 level One-Way ANOVA. Statistical analyses were performed using the statistical language R and scripts written in *Perl*.

2.16 dN/dS analysis

To obtain dN/dS ratios from mouse-rat alignments for all the genes on the array, the BioMart data mining tool was used at http://www.ensembl.org/ (Hubbard et al. 2005). The BioMart tool was used to query assembly NCBI m34 of May 2005, *Ensembl* Genebuild of March 2005, database version 36.34d. For this reason, the GenBank accession numbers were converted to UniGene identifiers. For the analysis, 7724 genes could be mapped to a UniGene identifier with a corresponding dN/dS ratio from the mouse-rat alignment (see 6.4). Variation in gene expression was calculated as standard deviations from log2-ratios. Standard deviations for the across subspecies divergence were first calculated subspecies-wise and after that averaged over subspecies.

3 Results

3.1 Differentially expressed genes between species and subspecies of *Mus*

High-density two-color oligonucleotide (65mers) microarrays designed from *Mus musculus* were used to study gene expression differences in animals caught from wild populations and from wild-derived animals that were kept under outbreeding conditions for several generations. Using multiple animals from each population allowed to differentiate between within-population and between-population variation. The whole genome expression profile between different subspecies of *Mus musculus* as well as between all *Mus musculus* subspecies and *Mus spretus* was compared. Hence, two levels of analysis were chosen, i.e. the differentiation across subspecies, and the differentiation across species.

3.1.1 Genomic DNA hybridizations (CGHs)

A potential problem with using microarrays that were designed for one species in another closely related (non-focal) species is that divergence in the sequences, that are represented as oligos on the array, could confound the measurements of gene expression in the non-focal species (Gilad et al. 2005). This phenomenon is likely to be more severe, the more distantly related the non-focal species is, relative to the species for which the microarray has been designed. Moreover, genes expressed in the testis may evolve more rapidly than genes expressed in other tissues (Swanson and Vacquier 2002; Good and Nachman 2005). This means that a higher than average rate of divergence at identified genes could result in lower hybridization efficiencies for *Mus spretus*. However, *Mus musculus* and *Mus spretus* are very closely related and show only 1-2% sequence divergence (She et al. 1990; Galtier et al. 2004). Since the microarrays consist of relatively long oligos (65mers), one would expect only marginal effects of sequence divergence on hybridization efficiency in *Mus spretus*. Nevertheless, to rule out any difference in hybridization intensity I performed hybridizations of genomic DNA from *Mus spretus* against the genomic DNA of a *Mus musculus* reference. Different hybridization characteristics at some oligos between both species would be manifested as being outliers in an RI plot (Ratio-to-Intensity), respectively in a low correlation of signal intensities from *Mus musculus* and *Mus spretus*. As shown in Figure 2, for the three individuals of *Mus spretus*, hybridized against a common *Mus musculus* reference, there is no systematic pattern of higher intensities in one of the species. A few outliers are present in both species but these are unlikely to affect the genome-wide trend. For all three *Mus spretus* individuals used in the study, correlation coefficients with *Mus musculus* range from 0.97 – 0.98 (Figure 3).

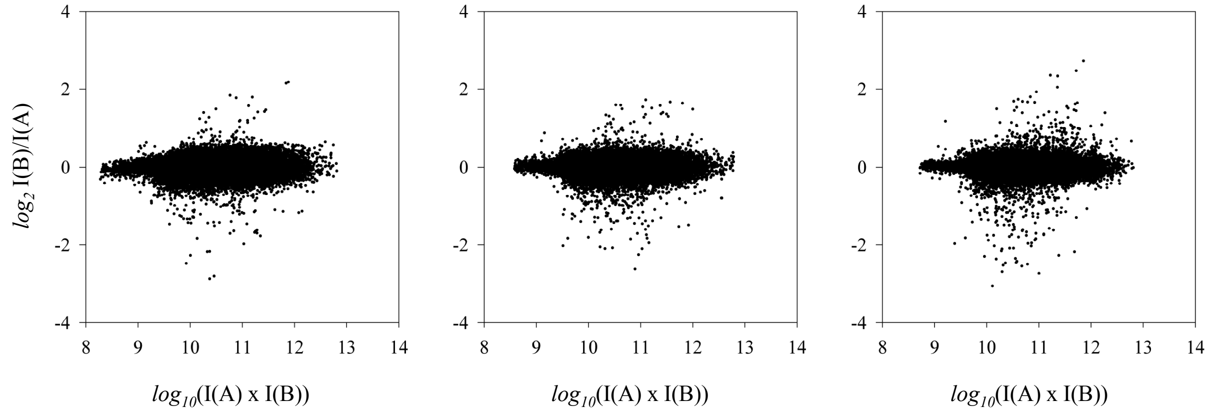


Figure 2: RI (Ratio-to-Intensity) plot from hybridizations of genomic DNA from *Mus musculus* and *Mus spretus* on the same slide. Each panel shows one of the three *Mus spretus* individuals used in the study (*SP1*, *SP2*, *SP3* from left to right).

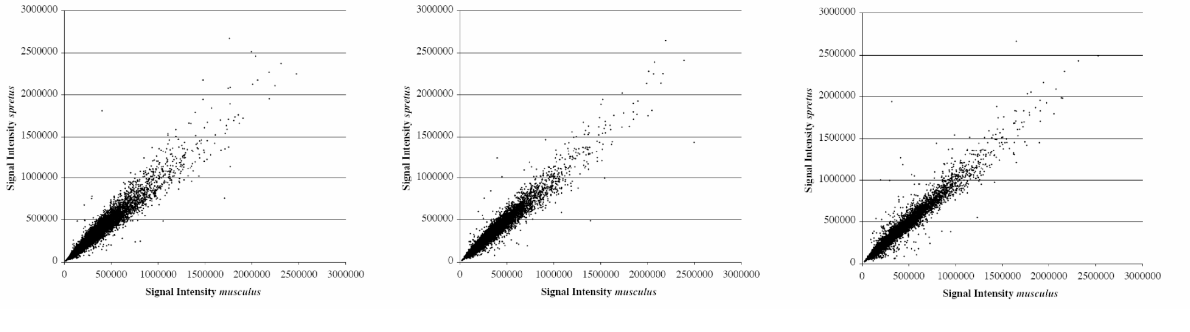


Figure 3: Scatter plot of signal intensities obtained from genomic DNA hybridizations in the *Mus musculus* sample (x-axis) and the *Mus spretus* sample (y-axis) on the same slide. Each panel shows one of the three *Mus spretus* individuals used in the study (*SP1*, *SP2*, *SP3* from left to right).

3.1.2 SAM (*S*ignificance *A*nalysis of *M*icroarrays) analysis – number of differentially expressed genes between species/subspecies for the different tissues

Having ruled out major biases stemming from differences in hybridization efficiencies between taxa of *Mus*, the program "*S*ignificance *A*nalysis of *M*icroarrays" (SAM, (Tusher et al. 2001)) was used to identify and count the number of differentially expressed genes in each tissue for both levels of divergence, between subspecies of *Mus musculus* and between all subspecies and *Mus spretus*. The SAM algorithm is a non-parametric t-test variant that does not have strong parametric assumptions, and does not involve any complex estimation procedures. For all analyses, 200 permutations and a False Discovery Rate (FDR) of < 5% were chosen. The FDR controls the expected proportion of false positives among a set of predictions. A FDR threshold is determined from the observed p-value distribution, and hence is adaptive to the amount of signal in the data. Between 3 to 6 unrelated individuals from each of the species/subspecies represented the individual replicates in the SAM analyses (see 2.1).

3.1.2.1 Gene expression differences between *Mus musculus* and *Mus spretus*

To estimate the number of differentially expressed genes between all *Mus musculus* subspecies and *Mus spretus*, a 2-class unpaired comparison was performed. All individuals from all *Mus musculus* subspecies were compared to all *Mus spretus* individuals for all three tissues (brain, pooled liver/kidney, testis). SAM identified 222 genes differentially expressed in the brain, 1373 that are differentially expressed in the liver/kidney comparison, and 1688 genes were identified that show significant differences in expression in the testis. Thus, the highest number of differentially expressed genes between species is found in the testis, followed by liver/kidney and the least number of genes significantly differentially expressed is found in the brain (Table 2). Overall, 3283 genes were found to be differentially expressed between *Mus musculus* and *Mus spretus*. A list of all differentially expressed genes is given in Appendix 6.1.

Table 2: Differentiation across species/subspecies. Given are the number of genes differentially expressed as determined from the SAM analyses (200 permutations, FDR < 5%).

	brain	liver/kidney	testis
across species	222	1373	1688
across subspecies	281	1244	23

3.1.2.2 Gene expression differences between subspecies of *Mus musculus*

To test for differentially expressed genes within subspecies of *Mus musculus*, all subspecies were compared in a SAM multiclass analysis. Genes identified in a multiclass analysis are those where all subspecies differ significantly from each other as well as combinations of two subspecies or a single subspecies against all remaining subspecies (“lineage-specific” genes). When comparing across *Mus musculus* subspecies, 281 genes are identified as being differentially expressed across subspecies in the brain, 1244 genes are found for the liver/kidney comparison and the least number of genes is found in the testis. Only 23 genes are captured for a given FDR < 5% in the SAM analysis (Table 2). In total, the SAM multiclass analysis identified 1548 genes that are differentially expressed across subspecies. A list of all genes identified as differentially expressed is given in Appendix 6.2.

3.1.2.3 Comparison of gene expression differences between species and subspecies of *Mus*

Looking at the number of differentially expressed genes in the brain and liver/kidney analyses, the amount of genes across species and subspecies is quite similar. In contrary, the difference in the number of genes for the testis is striking (Table 2).

The low number of genes identified in the brain in both analyses, in comparison to liver/kidney, points to a high intra-specific variation that prevents genes from getting significant in the brain SAM analysis. Enard *et al.* (Enard et al. 2002) found, in a comparison of expression profiles between chimpanzee and human, that a human brain sample could differ more from other human brain samples than from chimpanzee samples. Based on the same dataset, Hsieh *et al.* (Hsieh et al. 2003) showed that more differences at high significance levels were observed for liver than for brain between species. Furthermore, it has been shown that expression of genes in the brain is associated with life history (Aubin-Horth et al. 2005) and that expression of certain genes is associated with learning and memory (Atkins et al. 1998; de Ortiz et al. 2003; Mons et al. 2003). All these results point to a high level of intra-specific variation in gene expression in the brain. A more detailed analysis regarding expression variance is given in the scaled divergence analysis (3.5.1), when genome-wide patterns of divergence are examined.

The comparatively high number of genes found to be significantly differentially expressed in liver/kidney in both analyses could be explained by the function these tissues have. They are the interface between ecology and physiology. The function of these organs (among others) is food utilization, metabolism and detoxification. Since all species are exposed to different environments we may expect gene expression levels that are adjusted towards the different conditions these taxa are exposed to.

Regarding the genes found to be differentially expressed in the testis, it is a general finding that genes related to the male reproductive system evolve fast when comparing species (Swanson and Vacquier 1995; Civetta and Singh 1998; Wyckoff et al. 2000; Good and Nachman 2005). This is true regarding the evolution of coding sequence as well as the evolution of gene expression. Hence, one would expect to identify a high number of genes to be differentially expressed in testis tissues between species. In contrary, the same is not true when comparing subspecies, i.e. taxa at lower stages of divergence.

Apart from the fact that the numbers of genes found to be differentially expressed in brain and liver/kidney are quite similar in both analyses, comparing the portion of these genes to all genes that are differentially expressed gives a different picture. About 15% of all genes represented on the microarray were differentially expressed between *Mus spretus* and *Mus musculus* (a total of 3283 genes). Among these 3283 genes approximately half were identified in the testis (~51%, 1688 genes), 42% (1373 genes) in the liver/kidney and 7% (222 genes) in the brain (Figure 4). In contrast, for the subspecies comparison about 7% of all genes (1548 genes) were identified as differentially expressed, which is about half of the genes identified in the across species comparison. Of these genes, 1.5% (23 genes) are found in the testis, 80% (1244 genes) are from genes found to be differentially expressed in the liver/kidney and 18.5% (281 genes) differ in expression in the brain (Figure 5). Hence, in the comparison of all tissues in the across species analysis the testis is dominating, whereas in the across subspecies analysis genes differentially expressed in liver/kidney are preponderant.

Taken together, a highly significant difference in the distribution of the number of genes across tissues is found when comparing the species and subspecies level ($\chi_2^2 = 1160.03$, $P < 0.00001$). The within-species (between subspecies) pattern of gene expression divergence is different from the between-species pattern. Most of the differentially expressed genes in the subspecies comparison were identified in liver/kidney and almost none in the testis. By contrast, in the species comparison about half of the genes are found in the testis tissue. The number of genes found to be differentially expressed in the testis for the across subspecies comparison is negligible. This shows that the expression divergence across subspecies follows a different pattern than that found in the across species comparison. The differences in the across species and across subspecies analysis indicate that in early stages of gene expression divergence between taxa (subspecies-level) different mechanisms, respectively selective forces are operating than in late stages of divergence (species-level).

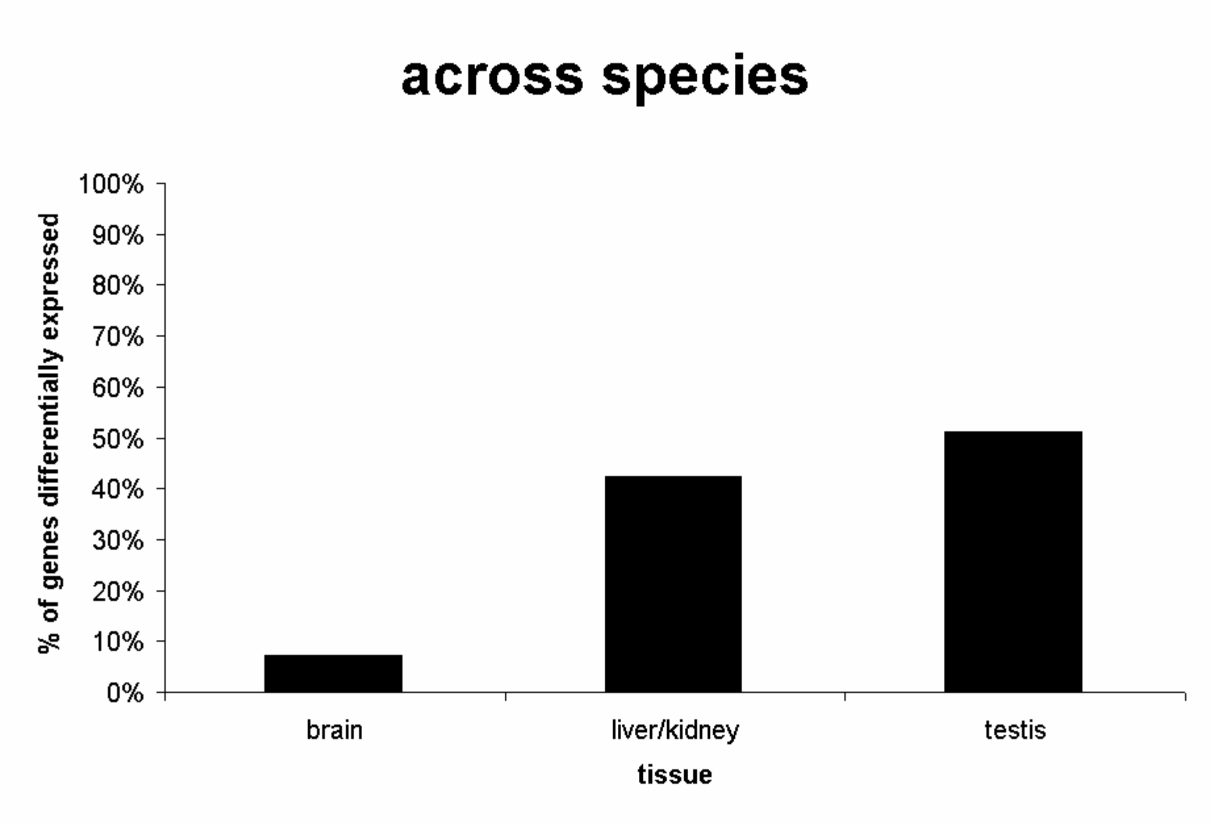


Figure 4: Percentages of genes differentially expressed across species (SAM, 200 permutations, FDR < 5%).

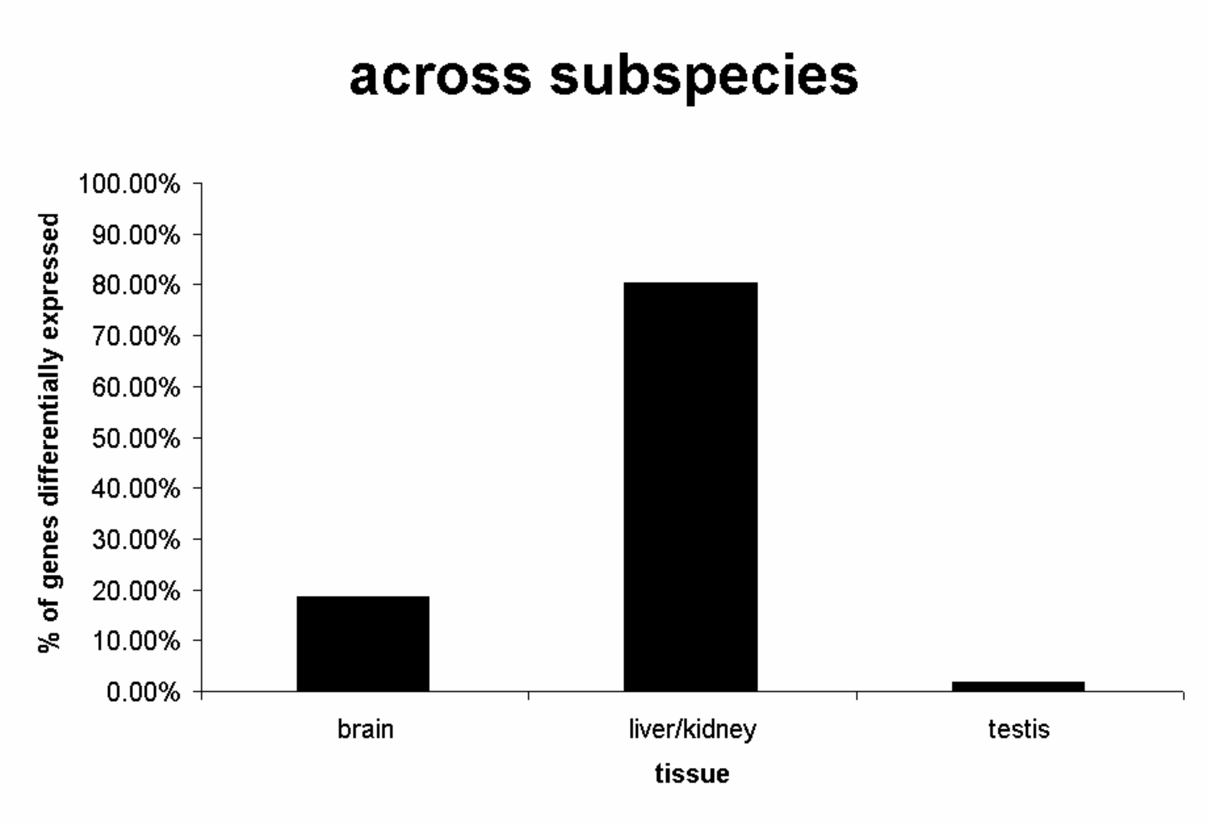


Figure 5: Percentages of genes differentially expressed across subspecies (SAM, 200 permutations, FDR < 5%).

3.1.2.4 Distribution of fold-changes (FC) among significantly differentially expressed genes

A comparison of the magnitude of gene expression change for the significantly differentially expressed genes between the house mouse subspecies and *Mus spretus* is shown in Figure 6. These magnitudes are best described in absolute fold-changes (absFC). Absolute fold-changes are converted log2 intensity ratios, e.g. a log2-ratio of 1 corresponds to a fold-change of 2. By taking the absolute fold-change (absFC), the direction of change is not considered just the quantity of change. For the subspecies, all significant genes from the multiclass analysis were taken and the absFCs were calculated as the change of expression relative to the average of all other subspecies. For the species comparison, all significantly differentially expressed genes from the across species analysis were taken and absFCs were computed as the change of expression of *Mus spretus* relative to the average of all *Mus musculus* subspecies.

In general, the median fold-change (FC) over all genes differentially expressed is higher in *Mus spretus* compared to the *Mus musculus* subspecies (Figure 6). This is even more evident, when comparing the mean of change for all differentially expressed genes (Table 3). The mean of change for the across species comparison is 1.72 for the brain, 1.52 for the liver/kidney and 1.44 for the testis. This finding is similar to what Hsieh *et al.* (Hsieh et al. 2003) observed. In a reanalysis of the study of Enard *et al.* (Enard et al. 2002), they discovered that mean fold-changes between human and chimp are about 1.2- to 1.3-fold. Since the mean fold-changes are small, it might also be true that the magnitude of change is not necessarily a good predictor of biological significance, as shown in recent studies on natural populations of fish (Oleksiak et al. 2005). In the across subspecies comparison all tissues show a similar mean of change of expression. For genes expressed in the brain the calculated mean absFC is 1.23, for the liver/kidney it is 1.20 and for the testis analysis it is 1.23 (Table 3). Furthermore, standard deviations of mean fold-changes are smaller across subspecies than across species. In general, changes in gene expression across subspecies tend to be smaller and less diverse.

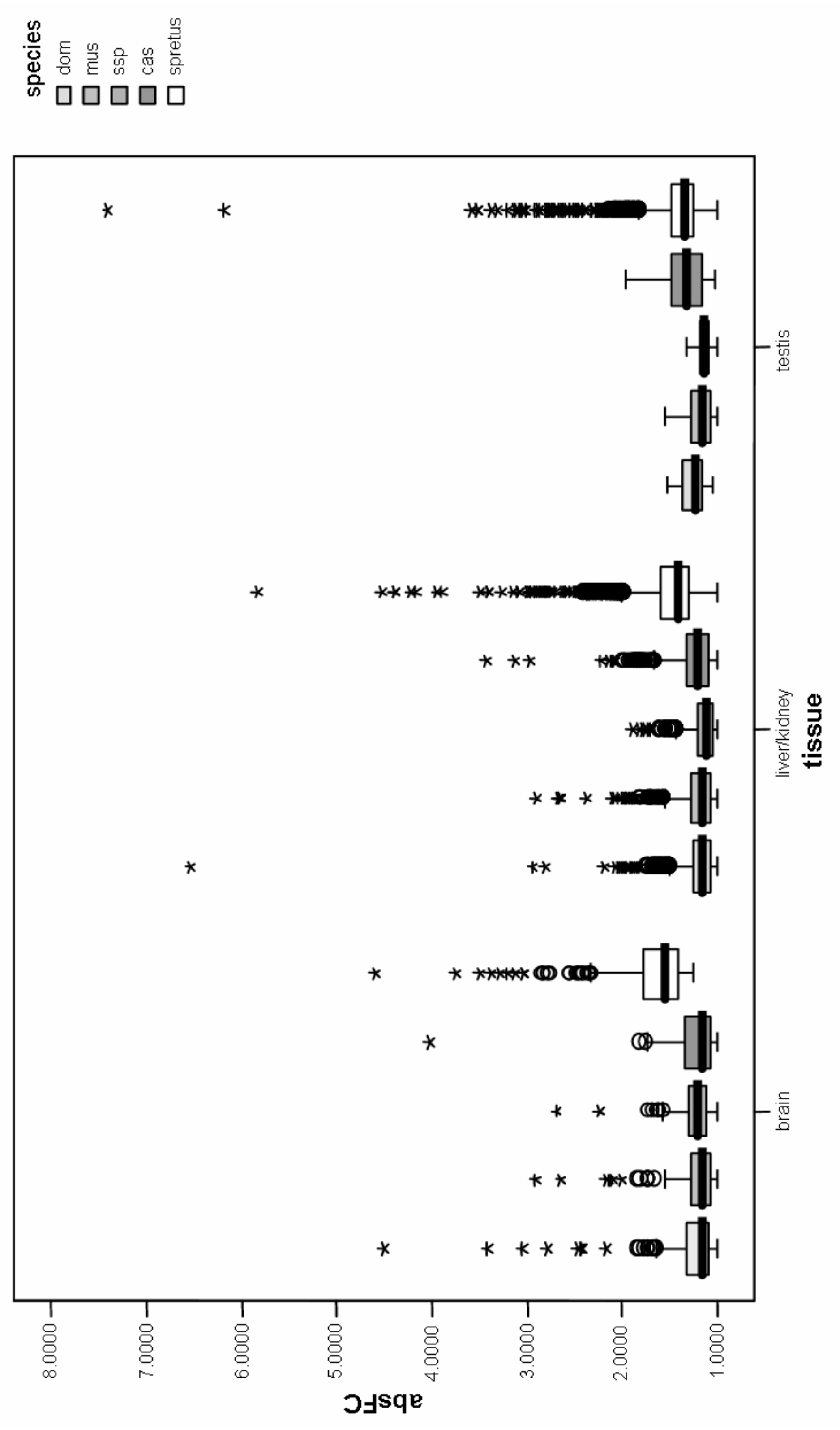


Figure 6: Boxplot describing the distribution of absolute fold-changes for significantly differentially expressed genes across species/subspecies. For each gene the fold-change is calculated for one (sub-)species relative to the average of all others. The median for each dataset is indicated by the black center line, and the first and third quartiles are the edges of the box, known as inter-quartile range (IQR). Points at a greater distance from the median than 1.5 times the IQR are plotted individually as asteriks or circles. absFC = absolute fold-change, dom = *M. m. domesticus*, mus = *M. m. musculus*, ssp = *M. m. ssp.*, cas = *M. m. castaneus*, spretus = *M. spretus*

Table 3: Comparison of change of expression across species and subspecies as determined from significantly differentially expressed genes from the SAM analyses (200 permutations, FDR < 5%). Numbers given are the mean absolute fold-changes and the standard deviations.

tissue	across species	across subspecies
brain	1.72 ± 0.48	1.23 ± 0.25
liver/kidney	1.52 ± 0.40	1.20 ± 0.19
testis	1.44 ± 0.36	1.23 ± 0.15

Interestingly, regarding single fold-changes it is not necessarily true that they are highest in the species comparison. In the across species comparison, the highest FCs ranged up to 4.61 for the genes differentially expressed in brain, up to 5.84 for the genes identified in the liver/kidney comparison and up to 7.41 in the testis analysis. For the across subspecies comparison, FCs ranged up to 4.52 for the brain comparison, up to 6.54 in the liver/kidney analysis and only up to 1.95 in the testis analysis. Thus, whereas for the brain highest FCs are similar in both analyses (4.61 in species comparison vs. 4.52 in subspecies comparison), for the liver/kidney analysis single FCs are greater among subspecies (5.84 in species comparison vs. 6.54 in subspecies comparison), whereas for the testis dataset single FCs are clearly higher in the among species comparison (7.41 in species comparison vs. 1.95 in subspecies comparison) (Table 4). This is another indication that evolutionary forces, that shape the pattern of species and subspecies divergence, are different.

Table 4: Single highest fold-changes across species and subspecies as determined from significantly differentially expressed genes from the SAM analyses (200 permuations, FDR < 5%).

tissue	across species	across subspecies
brain	4.61	4.52
liver/kidney	5.84	6.54
testis	7.41	1.95

3.1.2.5 Lineage-specific genes in *Mus musculus*

To test whether the pattern of differential gene expression among subspecies of house mice can be attributed to a specific subspecies lineage, pairwise comparisons among subspecies were computed in SAM and only those genes were selected where one of the four subspecies differed in expression compared to *all* remaining subspecies, but the individuals of the remaining subspecies did not differ significantly among themselves (see 2.10). Pooled over all subspecies, I identified 74 such subspecies lineage-specifically expressed genes. As shown in Table 5, among the lineage-specific genes most were found to be differentially expressed in the liver/kidney sample for the subspecies *M. m. domesticus* and *M. m. musculus* and, to a lesser extent, in *M. m. castaneus*. *Mus musculus ssp.* did not show any differentially expressed gene confined to this particular lineage. The fact that one can find subspecies-specific genes over-proportionally in the liver/kidney sample three times independently in the different subspecies of house mice rules out the possibility of a statistical artifact, in which case different organs should be affected in the subspecies (Exact Binomial probability $p = 0.012$). Regarding the finding that no lineage-specific genes for *Mus musculus ssp.* were identified, it should be noted that this subspecies is poorly characterized and may *de facto* be a mixture of the other subspecies (Din et al. 1996; Prager et al. 1998).

Table 5: Lineage-specific genes in subspecies of *Mus musculus*. Given are the number of genes lineage-specifically expressed among subspecies of the house mouse in different tissues.

	brain	**liver/kidney**	**testis**
M. m. domesticus	3	39	0
M. m. musculus	0	27	0
M. m. castaneus	0	5	0
M. m. ssp.	0	0	0

The mitochondrial D-loop was sequenced for all animals used in this study. As shown in Figure 7, all subspecies but *Mus musculus ssp.* are monophyletic. Within *Mus musculus ssp.*, however, two animals cluster with *Mus musculus musculus* and four animals cluster with the subspecies *Mus musculus castaneus*. Thus, consistent with the unresolved and ancestral status of *Mus musculus ssp.*, this group most likely does not represent a unique subspecies but is comprised of a mixture of different subspecies, which would explain the absence of *Mus musculus ssp.* lineage-specific genes. The pairwise comparisons were repeated among the subspecies, omitting *Mus musculus ssp.* from the analysis. It can be seen that the number of lineage-specific genes increases noticeably in all subspecies, with all subspecies showing a strong over-representation of liver/kidney genes to be lineage-specifically expressed (Table 6). This result suggests that high gene expression divergence in the liver/kidney among subspecies of house mice is not a characteristic of only a single house mouse subspecies. Instead, it appears that change of expression in the liver/kidney could be a general characteristic of early species divergence.

Table 6: Lineage-specific genes in subspecies of *Mus musculus*. Given are the number of genes lineage-specifically expressed among subspecies of the house mouse in different tissues (excluding *Mus musculus ssp.* in defining lineage-specificity).

	brain	**liver/kidney**	**testis**
M. m. domesticus	7	69	0
M. m. musculus	0	66	0
M. m. castaneus	0	217	13

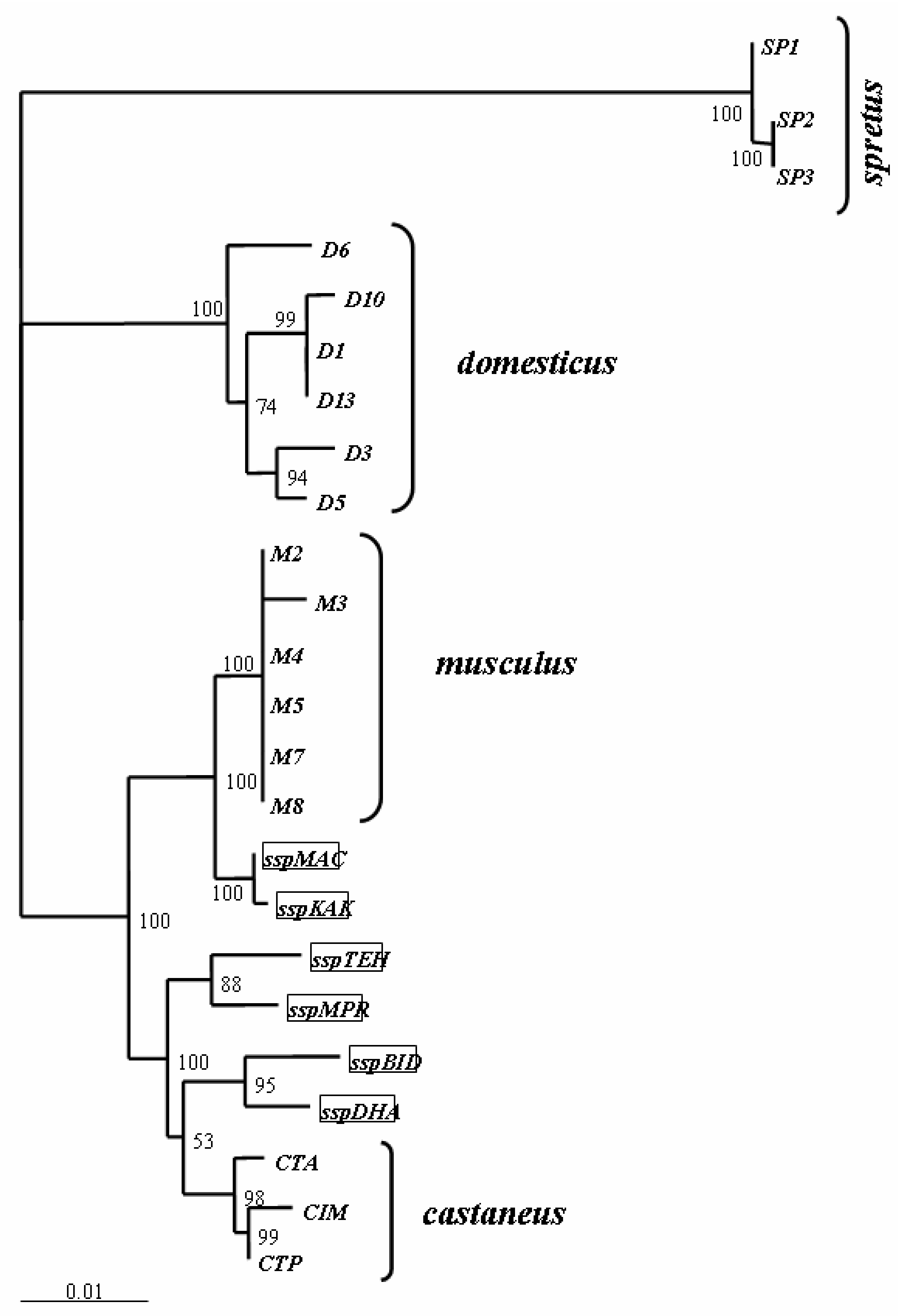


Figure 7: Maximum likelihood tree of mitochondrial D-loop sequences obtained from *Mus musculus* and *Mus spretus* animals.

3.2 Confirmation of SAM candidate genes with quantitative real-time PCR (qRT-PCR)

3.2.1 Genes differentially expressed between *Mus spretus* and *Mus musculus*

To confirm some of the genes found to be differentially expressed in the SAM analyses, qRT-PCR was carried out as described in Material & Methods (2.12). From the genes that showed up as differentially expressed in the brain between species, two genes were chosen for confirmation: AK003742 (RIKEN cDNA 1110017D15) and AK015921 (Synaptic vesicle glycoprotein 2c). AK003742 is also known as spermatid specific manchette related protein 1 (smrp1) although it is expressed in other tissues as well, e.g. the whole brain is a common cDNA source as confirmed by the UniGene database at http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=UniGene. In the SAM analyses, AK003742 appeared on position 1 in the list of upregulated genes (see 6.1.1) with a circa 3-fold over-expression in *Mus spretus* in comparison to all *Mus musculus* subspecies. In the qRT-PCR the gene turned out to be non-significantly differentially expressed with a fold-change of 1.4. The other gene, AK015921 or synaptic vesicle glycoprotein 2c is involved in synaptic transmission and a component of the synaptic vesicle, according to GeneOntology by MGI (http://www.informatics.jax.org/). This gene is significantly differentially expressed on the microarray and in the qRT-PCR. The gene is predicted to be about 2-fold (2.15) over-expressed in *Mus spretus* as calculated from microarray log2-ratios. The fold-change in the qRT-PCR is significant and 1.91-fold. This gene showed a similar behavior on the microarray and in the qRT-PCR.

From the SAM list of liver/kidney genes, the following were chosen for confirmation: AK014677, Z48496, BC007147 and NM_008917. AK014677 or RIKEN cDNA 4833411C07 is a not further characterized transcript that appeared on position 1 of the SAM list for genes differentially expressed between species in liver/kidney with a 2.59-fold upregulation in *Mus spretus* in comparison to *Mus musculus* (see 6.1.3). In the qRT-PCR it is 1.49-fold upregulated in *Mus spretus*, but not significantly so. Z48496 known as Tmsb10 or Thymosin beta 10 is known to function in actin cytoskeleton organization and biogenesis where its function is to bind actin as a monomer. From the microarray data a fold-change of 5.84 was calculated, whereas in the qRT-PCR the gene barely missed significance with a 1.75-fold upregulation in *Mus spretus* (Mann-Whitney-U test, p = 0.08). BC007147 or Rab4b is a member of the RAS oncogene family. Its function is GTP binding and it is involved in processes related to intracellular protein transport via GTPase mediated signal transduction. The gene is significantly differentially expressed in the microarray data and the qRT-PCR (Mann-Whitney-U test, p = 0.007). It is about 4-fold over-expressed in the array data, whereas in the qRT-PCR it shows a 2.31-fold upregulation. The last gene chosen for confirmation with qRT-PCR was NM_008917, a palmitoyl-protein thioesterase 1 (Ppt1) that is found in lysosomes and is involved in protein modification. According to KEGG (http://www.genome.jp/kegg/) it plays a role in the process of fatty acid elongation in mitochondria. It shows up highly significant in the qRT-PCR reaction (Mann-Whitney-U test, p = 0.001) with a calculated fold-change of 1.63. From the microarray data a 1.72-fold over-expression in *Mus spretus* was determined.

Four genes were chosen for confirmation of differential expression between species in the testis. NM_009529 or Xlr-related, meiosis regulated (Xmr) is abundantly expressed in primary spermatocytes associated with nonrecombining segments of sex chromosomes (Escalier et al. 2002). It appears to be sex-specifically expressed. Xlr is the female counterpart of the gene. It is expressed in mouse fetal oocytes. Both genes are found on regions of the X-chromosome. According to the database HomoloGene (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?DB=homologene) it is exclusively found in *Mus musculus*, whereas UniGene finds a protein similarity to a *Rattus norvegicus* gene (synaptonemal complex protein 3, A55925) with only 26.04% identity over 186 amino acids. Thus, it is either unique to *Mus musculus* or rapidly evolving. From the microarray data a 2.23-fold down-regulation is seen in *Mus spretus* compared to *Mus musculus*. Indeed, a highly significant 6.03-fold down-regulation (Mann-Whitney-U test, p = 0.002) is found with qRT-PCR. The next gene, NM_011560 or t-complex-associated testis expressed 3 gene (Tcte3, LC2, Tctex2, Tctex4, Tctex-2, Tctex-4, D17Leh117c) has homology to dynein light chains and is conserved across amniota (HomoloGene database). Bai *et al.* (Bai et al. 2004) showed that it interacts specifically with casein kinase 2 beta, one of the subunits of casein kinase 2 (CK2), in an *in vitro* interaction assay. CK2 plays an essential role in regulatory pathways in cell transformation and proliferation. The microarray data suggests that this gene is 1.62-fold upregulated in the *Mus musculus* species. The qRT-PCR could significantly confirm the over-expression in *Mus musculus* (Mann-Whitney-U test, p = 0.004), but the upregulation is almost 3-fold (2.97). The third gene AK004920 or Tmem24 is known as transmembrane protein 24.

According to the HomoloGene database it is conserved across amniota. Microarray data suggests a small up-regulation in the *Mus musculus* species (1.26-fold). Again, results from the qRT-PCR significantly confirm the direction of change (Mann-Whitney-U test, p = 0.001), although the fold-change is much higher (14.32-fold). The last gene that was chosen for confirmation is NM_009638 or Cysteine-rich secretory protein 1 (Crisp1), respectively acidic epididymal glycoprotein 1. The name already implies that it is expressed in the testis, more exactly in the epididymi. It is a sperm surface protein involved in the fusion of the sperm and egg plasma membranes (Hayashi et al. 1996), and as such a prime candidate for causing reproductive isolation. The microarray data shows only a slight upregulation of 1.33-fold in *Mus musculus*. The direction of change was confirmed with qRT-PCR, but with a much higher fold-change. It is nearly 134-fold over-expressed in the *Mus musculus* species in comparison to *Mus spretus* (Mann-Whitney-U test, p = 0.016). This gene is unique in another aspect. It shows differentiation between species as well as between subspecies. It is almost 40-fold upregulated in *Mus musculus domesticus* in comparison to all other subspecies. In a Kruskal-Wallis test among the subspecies the difference is not significant which is most probably caused by the high intra-specific variation in *Mus musculus castaneus* and *Mus musculus ssp.*. At least in the case of *Mus musculus castaneus* (n = 3), it can be attributed to sample size . Nevertheless, in a pairwise comparison between *Mus musculus domesticus* and *Mus musculus musculus* the gene is significantly differentially expressed (Mann-Whitney-U test, p = 0.041). This gene did not turn up in the SAM subspecies analysis, most probably because of high intra-specific variation it seems to be associated with. Given the high differential expression between species and also the pattern of divergence among subspecies, this gene is an interesting candidate for further evolutionary studies.

All in all, 7 out of 10 genes were significantly confirmed (Table 7). In all other cases the direction of change of expression was the same. The fold-changes of the microarray and qRT-PCR analysis differ. Whereas fold-changes seem deflated in the case of genes confirmed from the brain and liver/kidney SAM analyses, in the qRT-PCR the reverse is true regarding change of expression in the testis. There is a scientific debate that the ratios are inflated for low intensity spots in arrays. Conversly, ratios in the high intensity range are compressed in arrays. Nevertheless, the exact cause of the compression/decompression is not clear and the nature and degree of this effect is not predictable. For the genes analyzed here, signal intensities are higher than average for the genes chosen for confirmation from brain and liver/kidney and lower than average for the genes from testis. This would argue for a deflation of ratios for high intensity spots and an inflation of ratios for low intensity spots in qRT-PCR (Table 7).

Another point to consider is that microarray analysis is not absolutely quantitative upuntil now, so a perfect match between qRT-PCR and microarray data is not expected. In general, qRT-PCR results in this study reflect the microarray data. The data are well suited for the analysis of global patterns of expression divergence. When working on single genes, confirmation of expression change is advised.

Table 7: Overview of genes confirmed with qRT-PCR that are differentially expressed between *Mus spretus* and *Mus musculus* (FC = fold-change).

	Gene ID	FC microarray	FC qRT-PCR	p-value	significant	signal intensity array
brain	AK003742	3.22	1.43	0.309	no	higher than average
	AK015921	2.15	1.91	0.035	yes	higher than average
liver/kidney	AK014677	2.59	1.49	0.452	no	higher than average
	Z48496	5.84	1.75	0.082	no	higher than average
	BC007147	4.39	2.31	0.007	yes	higher than average
	NM_008917	1.72	1.63	0.001	yes	higher than average
testis	NM_009529	2.23	6.03	0.002	yes	lower than average
	NM_011560	1.62	2.97	0.004	yes	lower than average
	AK004920	1.26	14.32	0.001	yes	lower than average
	NM_009638	1.33	133.94	0.016	yes	lower than average

3.2.2 Genes differentially expressed between subspecies of *Mus musculus*

Confirmation of differentially expressed genes across subspecies was done by using ΔC_T values in a Kruskal-Wallis-test (see 2.12) that differentiates between all four subspecies, since all possible combinations of differential expression across subspecies of *Mus musculus* were detected in the SAM multiclass analysis. From the genes that showed up as differentially expressed in the SAM analysis in the brain between subspecies, AF351196 or Down syndrome cell adhesion molecule-like 1 (Dscaml1), was chosen. It is involved in calcium-independent cell-cell adhesion and it is a component of the plasma membrane. Since it was not identified as a lineage-specific gene, it is no gene that is specifically differentially expressed in one species in comparison to all others. A Kruskal-Wallis-test on the qRT-PCR data confirmed the gene to be differentially expressed between subspecies ($p = 0.048$).

From the liver/kidney SAM analysis the genes U94828 and NM_009238 were chosen for confirmation with qRT-PCR. U94828 or regulator of G-protein signaling 16 (Rgs16), is involved in G-protein coupled receptor protein signaling pathways and has GTPase activator activity. The gene was significantly differentially expressed between subspecies in a Kruskal-Wallis-test ($p = 0.014$). The other gene, NM_009138 or chemokine (C-C motif) ligand 25 (Ccl25), is involved in a number of processes such as immune response and inflammatory response. The differential expression was confirmed in qRT-PCR (Kruskal-Wallis-test, $p = 0.020$).

For testis, the gene NM_008701 or NK2 transcription factor related, locus 9 (*Drosophila*) (Nkx2-9), was chosen for confirmation via qRT-PCR. The gene failed to amplify in the qRT-PCR reaction in 10 out of 21 animals (4 *M. m. domesticus*, 4 *M. m. musculus*, 1 *M. m. ssp.* and 1 *M. m. castaneus* animal). Rather high C_T values (> 34) were found, which shows that the gene is expressed at very low levels. As gene measurements are expressed in ratios, absolute expression is not captured in microarray data, which tends to sometimes diversify microarray and qRT-PCR data.

Overall, 3 out of 4 genes were verified to be significantly differentially expressed across subspecies of *Mus musculus*. This is about the same range as the genes that were verified for differential expression between species. As the analysis of Nkx2-9 shows, it is not possible to infer expression height from log2-ratios. Therefore, one has to take into account that many of the lowly expressed genes might fail to get confirmed in a downstream qRT-PCR.

3.3 Identification of functional categories within lists of differentially expressed genes with DAVID (***D***atabase for ***A***nnotation, ***V***isualization and ***I***ntegrated ***D***iscovery)

The genes that are differentially expressed between species, respectively subspecies in the different tissues were analyzed with the DAVID functional classification tool (Dennis et al. 2003) in order to get an overview of the biological function and the biological processes the genes are involved in. This tool is unique in that it looks for annotation co-occurrences regarding given gene lists. By that, the program finds higher structured annotations that are shared by genes in a given list. Currently, the program is limited to the analysis of 3000 gene identifiers, so it was not possible to get information about a "neutral" expectation from the functional classification of all the genes on the array. Nevertheless, since the program clusters genes based on concordance from multiple annotations it should be quite specific. Table 8 displays some basic statistics associated with the functional classification. Between 93% and 96% of the genes are annotated. This does not mean that all genes are equally well annotated, just that they were identified in at least one of the databases DAVID uses. The whole analysis is based on the clustering of genes into functional categories. If one takes a look at the percentages of genes clustered into functional categories, the distribution in all analyses is similar. Between 14% and 20% of the differentially expressed genes can be clustered into functional groups in the analyses, except for the across subspecies comparison of the testis (Table 8). Taking into account that only 23 genes were identified to be differentially expressed in this comparison, the lack of functional group assignments is most probably due to the low number of genes that were identified in the analysis. Regarding the number of functional categories found for the different analyses, there is a dependency on the number of genes that were identified in the corresponding analyses, i.e. the more genes are identified in a SAM analysis, the more functional categories are assigned.

Table 8: DAVID analysis of differentially expressed genes from SAM analyses (200 permutations, FDR < 5%).

	across species brain 222 genes	**across subspecies** brain 281 genes	**across species** liver/kidney 1373 genes	**across subspecies** liver/kidney 1244 genes	**across species** testis 1688 genes	**across subspecies** testis 23 genes
% of genes annotated	93%	94%	95%	95%	94%	96%
% of genes clustered in functional categories	14%	20%	19%	16%	17%	0%
no. of functional categories	5	7	28	25	34	0

3.3.1 Categories of functional classification within the list of differentially expressed genes identified in the brain

Table 9 shows the results of the functional classification based on the genes that were identified as differentially expressed in the brain in the SAM analyses. The majority of functional classes is found in both comparisons. The term “ion channel activity” is unique to the across species comparison, whereas cell signalling themes (“protein kinase activity”, “G-protein-coupled receptors”) are unique to the across subpecies comparison. Given that cognitive abilities, learning and memory are associated with specific proteins and their synthesis and catabolism, it makes sense to identify “protein catabolism” and “protein biosynthesis” in both analyses. Regarding identification of the term “cytoskeleton”, it has been shown that axon growth is associated with proteins of the cytoskeleton (Hasaka et al. 2004). Interestingly, “regulation of transcription” is also a term that is identified in both analyses. About 10% of the genes that show up as differentially expressed are transcription factors (17 genes = 8% of the genes differentially expressed between species, 24 genes = 9% of the genes differentially expressed between subspecies; see 6.3.1 and 6.3.2). Since transcription factors control a number of downstream target genes, their change in expression could have a profound influence on the transcriptomic state of a cell, respectively tissue. To name just a few genes: in the across species analysis Sox2 (NM_011441) belongs to the functional classification "regulation of transcription". This gene has a crucial role in the maintenance of neurons (Ferri et al. 2004). In the across subspecies comparison Lhx2/apterous (NM_010710) is found in the category "regulation of transcription". This gene is required for correct axon guidance and fasciculation of interneurons (Herzig et al. 2001). These examples illustrate that the categories of functional classification identified by DAVID make sense in regard to the categories as well as the genes that constitute the categories in relation to tissue identity. A complete list of genes assorted to the different categories is found in Appendix 6.3.1 and 6.3.2.

Table 9: DAVID functional classification based on the genes that were identified as differentially expressed in the brain in the SAM analyses (200 permutations, FDR < 5%). Not all identified categories are shown; for a complete list refer to 6.3.1 and 6.3.2.

across species brain, 222 genes			**across subspecies** brain, 281 genes		
functional categories	**no. of genes**	**% of all genes differentially expressed (rounded)**	**functional categories**	**no. of genes**	**% of all genes differentially expressed (rounded)**
protein catabolism	6	2.7%	protein catabolism	5	1.8%
protein biosynthesis	6	2.7%	protein biosynthesis	9	3.2%
cytoskeleton	9	4.1%	cytoskeleton	4	1.4%
regulation of transcription	17	7.7%	regulation of transcription	24	8.5%
ion channel activity	4	1.8%			
			protein kinase activity	6	2.1%
			G-protein-coupled receptors (GPCRs)	8	2.8%

3.3.2 Categories of functional classification within the list of differentially expressed genes identified in the liver/kidney

Table 10 shows the results for the functional classification based on the genes that were identified as differentially expressed in the liver/kidney in the SAM analyses. As for the brain analyses, common as well as unique categories are identified in the across species comparison in comparison to the across subspecies comparison. The categories found are combined according to their higher-level affiliation. A lot of categories identified are associated with all kinds of biosynthesis, metabolism and catabolism. Given that the liver is the most important organ of metabolism these processes most probably refer to liver function. In the category "regulation of transcription" many transcription factors can be found that are associated with liver and kidney function and play a role in the regulation of metabolism. Again, about 10% of all differentially expressed genes are assorted to the category "regulation of transcription" (108 genes = 8% in the across species analysis, 108 genes = 9% in the across subspecies analysis; see 6.3.3 and 6.3.4). In the across species analysis Foxa2 (NM_010446) from the category "regulation of transcription", also known as hepatocyte nuclear factor 3beta, is identified, causing diminished hepatocyte glycogen levels and reduced expression of glucose homeostasis genes (Rausa et al. 2003). Tcf1/HNF1 (NM_009327), found in the same category, has a major role in up-regulating alternative transcription of the AE2 gene in the liver, and therefore it may contribute to the biliary secretion of bicarbonate in response to certain stimuli (Malumbres et al. 2003). Similarly, for the across subspecies comparison a number of transcription factors were identified that play a role in liver/kidney related processes, e.g. Lhx1/HNF1B partially rescues Pax8/lim1-induced kidney malformations (Wu et al. 2004). Interestingly, apoptosis is also identified as a functional category. A database search for co-occurrences with "liver" and "kidney" and the corresponding list of apoptosis-related genes gave no result. Nevertheless, T cells, when disappearing from lymph nodes and spleen, accumulate in the liver where they undergo apoptosis. This is likely a general clearance pathway for T cells (Kobayashi et al. 2003).

As for the brain analyses, doing this type of examination for all genes is discouraging, since the genes and categories are numerous. But again the categories found and the associated genes characterize the tissue under study very well. A complete list of genes belonging to the different categories is given in 6.3.3 and 6.3.4.

Table 10: DAVID functional classification based on the genes that were identified as differentially expressed in the liver/kidney in the SAM analyses (200 permutations, FDR < 5%). Not all identified categories are shown; for a complete list refer to 6.3.3 and 6.3.4.

across species liver/kidney, 1373 genes			**across subspecies** liver/kidney, 1244 genes		
functional categories	**no. of genes**	**% of all genes differentially expressed (rounded)**	**functional categories**	**no. of genes**	**% of all genes differentially expressed (rounded)**
ribosome biogenesis	6	0.4%	ribosome biogenesis	9	0.7%
protein biosynthesis	10	0.7%	protein biosynthesis	6	0.5%
protein metabolism	15	1.1%	protein metabolism	14	1.1%
protein catabolism	30	2.2%	protein catabolism	25	2.0%
glycoprotein metabolism	20	1.5%	glycoprotein metabolism	6	0.5%
lipoprotein metabolism	7	0.5%	lipoprotein	5	0.4%
protein folding	6	0.4%			
protein modification	6	0.4%	protein modification	5	0.4%
protein localization and transport	6	0.4%	protein localization and transport	5	0.4%
carbohydrate metabolism	9	0.7%			
			lipid biosynthesis	6	0.5%
cell organization and biosynthesis	11	0.8%	cell organization and biosynthesis	12	1.0%
regulation of metabolism	13	0.9%	regulation of metabolism	41	3.3%
regulation of transcription	108	7.9%	regulation of transcription	108	8.7%
protein phosphatase activity	5	0.4%	protein phosphatase activity	5	0.4%
protein kinase activity	47	3.4%	protein kinase activity	34	2.7%
G-protein coupled receptor activity	41	3.0%	G-protein coupled receptor activity	57	4.6%
ion channel activity	6	0.4%	ion channel activity	8	0.6%
apoptosis	35	2.5%	apoptosis	5	0.4%
hormone activity	6	0.4%			
mRNA processing	13	0.9%			

3.3.3 Categories of functional classification within the list of differentially expressed genes identified in the testis

As already mentioned, for the across subspecies analysis there were no functional categories associated with the testis gene list, most probably due to the low number of genes found to be differentially expressed between subspecies in the testis. The identified functional categories for the across species comparison are given in Table 11. One can find terms related to energy comsumption (“glycolysis”, “mitochondrion”), all kinds of cell signalling, respectively signal transduction (“growth factor activity”, “protein kinase activity”, “protein phosphatase activity”, “G-protein-coupled receptor activity”) and cell division including chromosome organization/biogenesis. All these processes play a role in sperm production. Again “regulation of transcription” is identified as a functional categroy. And again about 10% of all the genes that are differentially expressed are assorted to this category (132 genes = 8% in the across species analysis). The category “protein kinase activity” contains proteins that are specifically expressed either in the testis or in germ cells, e.g. Gsg2 (germ cell-specific gene 2), which is specifically expressed in mouse testicular germ cells and is suggested to play a role in cell cycle arrest in haploid spermatids as shown from studies in humans (Tanaka et al. 2001). Tssk3 (NM_021479) belongs to the family of testis-specific serine-threonine kinases (TSSKs) that consists of four members whose expression is confined almost exclusively to testis. The physiological role is unknown, but *in vitro* studies with Tssk3 showed that the kinase is able to autophosphorylate and to phosphorylate test substrates such as histones, myelin basic protein and casein (Bucko-Justyna et al. 2005). Mapkapk2 (AK020200) belongs to the family of MAP kinase-activated protein kinases. Recently, it has been shown that a member of this family (Map2k7) has changed expression in the house mouse *Mus musculus domesticus* in comparison to other *Mus musculus* subspecies, and that this change is associated with a selective sweep (in press (Harr et al. 2006)). Again the genes identified in the different categories are too numerous to be individually analyzed, but make sense given the tissue under study and its functional role. A complete list of all identified categories and genes is given in 6.3.5.

Table 11: DAVID functional classification based on the genes that were identified as differentially expressed in testis in the SAM analyses (200 permutations, FDR < 5%). Not all identified categories are shown; for a complete list refer to 6.3.5. For the genes differentially expressed in the testis between subspecies no functional classifications were identified.

across species testis, 1688 genes			**across subspecies** liver/kidney, 23 genes		
functional categories	**no. of genes**	**% of all genes differentially expressed (rounded)**	**functional categories**	**no. of genes**	**% of all genes differentially expressed (rounded)**
glycolysis	10	0.6%			
protein catabolism	34	2%			
protein metabolism	24	1.4%			
ion channel activity	8	0.5%			
growth factor activity	6	0.4%			
protein kinase activity	41	2.4%			
protein phosphatase activity	7	0.4%			
G-protein-coupled receptor activity	43	2.5%			
mitochondrion	35	2.1%			
chromosome organization and biogenesis	21	1.2%			
DNA packaging	6	0.4%			
helicase, ATPase activity	10	0.6%			
cell cycle, cell division	41	2.4%			
spindle organization and biosynthesis	6	0.4%			
regulation of transcription	132	7.8%			

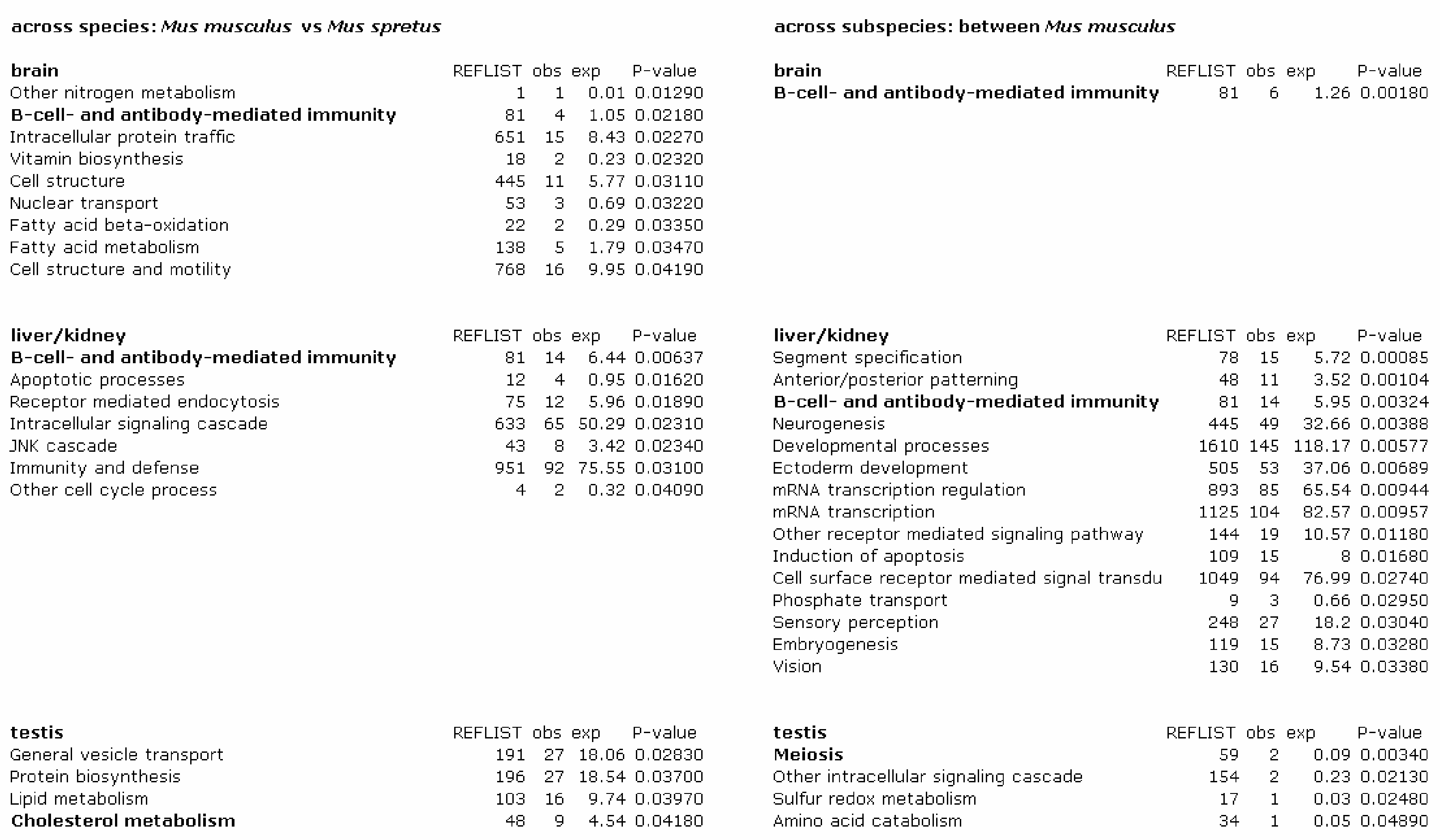
3.4 Identification of biological processes within lists of differentially expressed genes with PANTHER (***P***rotein ***AN***alysis ***TH***rough ***E***volutionary ***R***elationships)

The candidate genes that were identified by the SAM analyses to be differentially expressed across species and subspecies of *Mus* were additionally functionally annotated with PANTHER (http://www.pantherdb.org). The PANTHER classification system is a resource that classifies genes by their functions, using published scientific experimental evidence and evolutionary relationships. I looked for significantly over-represented gene categories among the differentially expressed genes. In this study, significance is based upon comparing the differentially expressed genes to the list of all genes on the array by means of a binomial test. In Table 12 all over-represented biological processes are shown that contain more significant genes than expected by chance ($p < 0.05$) for the different tissues and levels of divergence. Besides the processes that were already identified in the DAVID analysis, one common theme is apparent: there is a large representation of immune system related genes among the differentially expressed genes for both divergence levels. Being involved in host-pathogen interactions, such genes have been shown to be common targets of directional selection (Tanaka and Nei 1989; Schlenke and Begun 2003).

From the differentially expressed genes identified in the testis, cholesterol metabolism was identified as an over-represented biological process in the across species comparison. The role of cholesterol differs in the two compartments of the testis. In the interstitial tissue, cholesterol is necessary for the synthesis of testosterone, whereas in the seminiferous tubules, the membrane cholesterol content in developing germ cells influence the gametes' fertility. In the across subspecies comparison, meiosis was identified as a term that is significantly over-represented. Meiosis is a major biological process that takes place in testis during spermatogenesis.

One also finds processes that are not connected to the function of an organ, e.g. segment specification and anterior/posterior patterning in the liver/kidney in the across subspecies comparison. Since many genes play a role in mulitple processes, and by far not all of the processes are known for all genes, it could well be that biological themes come up that are not directly related to the analyzed tissue. Since this study is based on biological process annotation of single genes and not on cross-referenced co-occurrences of annotations for genes, the outcome is different in regard to the DAVID analysis. The PANTHER analysis is more sensitive to processes that are caught by only few genes.

Table 12: PANTHER biological process annotation. Shown are significantly over-represented biological processes ($p < 0.05$) within the lists of genes that were identified as differentially expressed in the SAM analyses (200 permutations, FDR < 5%) across species and across subspecies. REFLIST = no. of genes found for the corresponding annotation on the microarray, obs = no. of genes found for the corresponding annotation within the list of differentially expressed genes, exp = no. of genes expected to be found within the list of differentially expressed genes, p-value = corresponding p-value from binomial test.



across species: *Mus musculus* vs *Mus spretus*

brain	REFLIST	obs	exp	P-value
Other nitrogen metabolism	1	1	0.01	0.01290
B-cell- and antibody-mediated immunity	81	4	1.05	0.02180
Intracellular protein traffic	651	15	8.43	0.02270
Vitamin biosynthesis	18	2	0.23	0.02320
Cell structure	445	11	5.77	0.03110
Nuclear transport	53	3	0.69	0.03220
Fatty acid beta-oxidation	22	2	0.29	0.03350
Fatty acid metabolism	138	5	1.79	0.03470
Cell structure and motility	768	16	9.95	0.04190

liver/kidney	REFLIST	obs	exp	P-value
B-cell- and antibody-mediated immunity	81	14	6.44	0.00637
Apoptotic processes	12	4	0.95	0.01620
Receptor mediated endocytosis	75	12	5.96	0.01890
Intracellular signaling cascade	633	65	50.29	0.02310
JNK cascade	43	8	3.42	0.02340
Immunity and defense	951	92	75.55	0.03100
Other cell cycle process	4	2	0.32	0.04090

testis	REFLIST	obs	exp	P-value
General vesicle transport	191	27	18.06	0.02830
Protein biosynthesis	196	27	18.54	0.03700
Lipid metabolism	103	16	9.74	0.03970
Cholesterol metabolism	48	9	4.54	0.04180

across subspecies: between *Mus musculus*

brain	REFLIST	obs	exp	P-value
B-cell- and antibody-mediated immunity	81	6	1.26	0.00180

liver/kidney	REFLIST	obs	exp	P-value
Segment specification	78	15	5.72	0.00085
Anterior/posterior patterning	48	11	3.52	0.00104
B-cell- and antibody-mediated immunity	81	14	5.95	0.00324
Neurogenesis	445	49	32.66	0.00388
Developmental processes	1610	145	118.17	0.00577
Ectoderm development	505	53	37.06	0.00689
mRNA transcription regulation	893	85	65.54	0.00944
mRNA transcription	1125	104	82.57	0.00957
Other receptor mediated signaling pathway	144	19	10.57	0.01180
Induction of apoptosis	109	15	8	0.01680
Cell surface receptor mediated signal transdu	1049	94	76.99	0.02740
Phosphate transport	9	3	0.66	0.02950
Sensory perception	248	27	18.2	0.03040
Embryogenesis	119	15	8.73	0.03280
Vision	130	16	9.54	0.03380

testis	REFLIST	obs	exp	P-value
Meiosis	59	2	0.09	0.00340
Other intracellular signaling cascade	154	2	0.23	0.02130
Sulfur redox metabolism	17	1	0.03	0.02480
Amino acid catabolism	34	1	0.05	0.04890

3.5 Genome-wide patterns of expression divergence

3.5.1 Scaled divergence analysis

Differences in expression among tissues can be measured on a genomic scale using the metric of scaled divergence, originally designed as a test for neutrality (Lemos et al. 2005). The scaled divergence metric can be seen as a measure of the rate of gene expression divergence in that it compares the ratio of the between group (v_b) to the within group (v_w) components of the variance (as determined from the meansquares from an ANOVA). Hence, gene expression polymorphism within taxa is compared to gene expression divergence between taxa. If v_w is small and v_b is large, the scaled divergence becomes large, similarly if v_w is large and v_b is small, the scaled divergence becomes small. This measure takes into account (1) the magnitude of change, (2) the magnitude of variability within each population in comparison to the variability between populations and (3) the divergence time. All genes were included in this analysis. As for the SAM analyses, two levels of divergence were chosen: the gene expression divergence across species and the gene expression divergence across subspecies. In the across species analysis, all individuals of all *Mus musculus* subspecies were contrasted to all *Mus spretus* individuals. This is analogues to the 2-class unpaired comparison done with SAM. As shown in Figure 8, the scaled divergence is highest in the testis for the between species analysis. In the among subspecies comparison, the scaled divergence is highest in the liver/kidney tissue. This analysis, which is based on measures of genome-wide expression divergence, as well as the SAM analysis, in which differentially expressed genes were identified and counted across the different tissues and levels of divergence, give the same result. Even the order concerning the absolute numbers of differentially expressed genes found for the different tissues in SAM is recaptured in this analysis. For the across species comparison, the highest number of genes was identified in the testis, followed by liver/kidney, followed by brain. Looking at the divergence of tissues for the across species analysis it is the same sequence. The scaled divergence is highest for testis, followed by liver/kidney, followed by brain. The same is true for the across subspecies analyses. The SAM analysis identified most genes to be differentially expressed in the liver/kidney tissue, followed by the brain tissue, followed by the testis tissue. The scaled divergence reflect this order in that in the between subspecies analysis the divergence is highest in the liver/kidney, followed by brain, followed by testis.

As expected, the scaled divergence is generally higher across species than across subspecies (Figure 8, y-axis). Across species it is between 0.07 and 0.15, across subspecies it is between 0.01 and 0.06. Hence, the maximum values are about half as high across subspecies than across species.

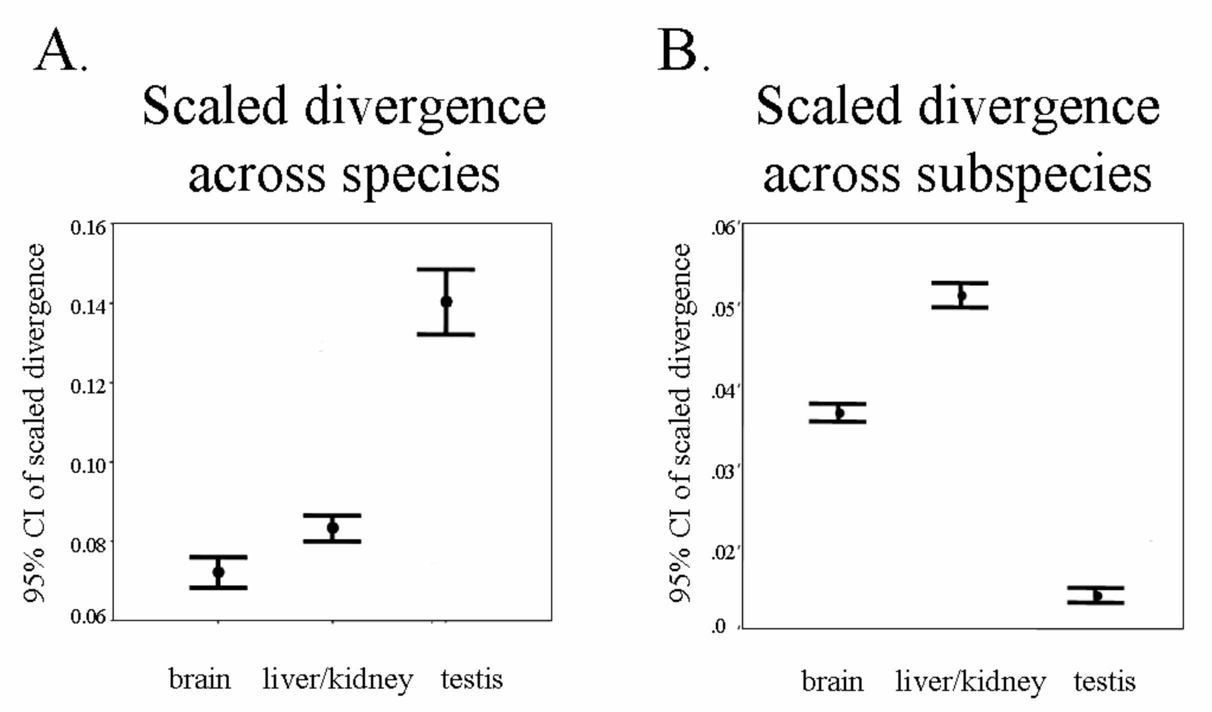


Figure 8: Mean and 95% confidence intervals (CI) of scaled divergences between *Mus musculus* and *Mus spretus* (A.) and between subspecies of *Mus musculus* (B.).

To further explore the genome-wide pattern of evolution of gene expression, respectively divergence, the means of the variance components (v_b and v_w) were plotted for the across species comparison (Figure 9) and for the across subspecies comparison (Figure 10). In the across species comparison, a high variance is found in the brain within species, whereas the variance is quite low between species. This sums up to a scaled divergence that is quite low in the across species comparison, which indicates that no accelerated rate of expression divergence is seen in the brain. For the liver/kidney the variance is large within species as well as between species which totals into a medium to small scaled divergence. In the testis, the genes show little to no intra-specific variation and a larger inter-specific variation. This pattern is expected when genes of a given tissue show signs of directional, respectively positive selection (see 1.3).

In the across subspecies analysis the situation is different (Figure 10). For the brain, there is a high intra-specific variance (v_b) as well as a medium to high inter-specific variance (v_w). This adds up to a medium to high scaled divergence. For the liver/kidney, the situation is similar as for the testis in the across species comparison. There is low intra-specific variation matched by high inter-specific variation. Hence, when comparing across subspecies, it is gene expression divergence in the liver/kidney that bears traces of positive selection. For the testis, there is a low intra-specific variation as well as a low inter-specific variation. This could mean that the genes are under negative selection, where one would expect low levels of both, intra- and inter-specific variation (see 1.3). Given that only 23 genes were identified in the SAM analyses, one has to assume that there is some mechanism that retains genes expressed in the testis from changing expression status.

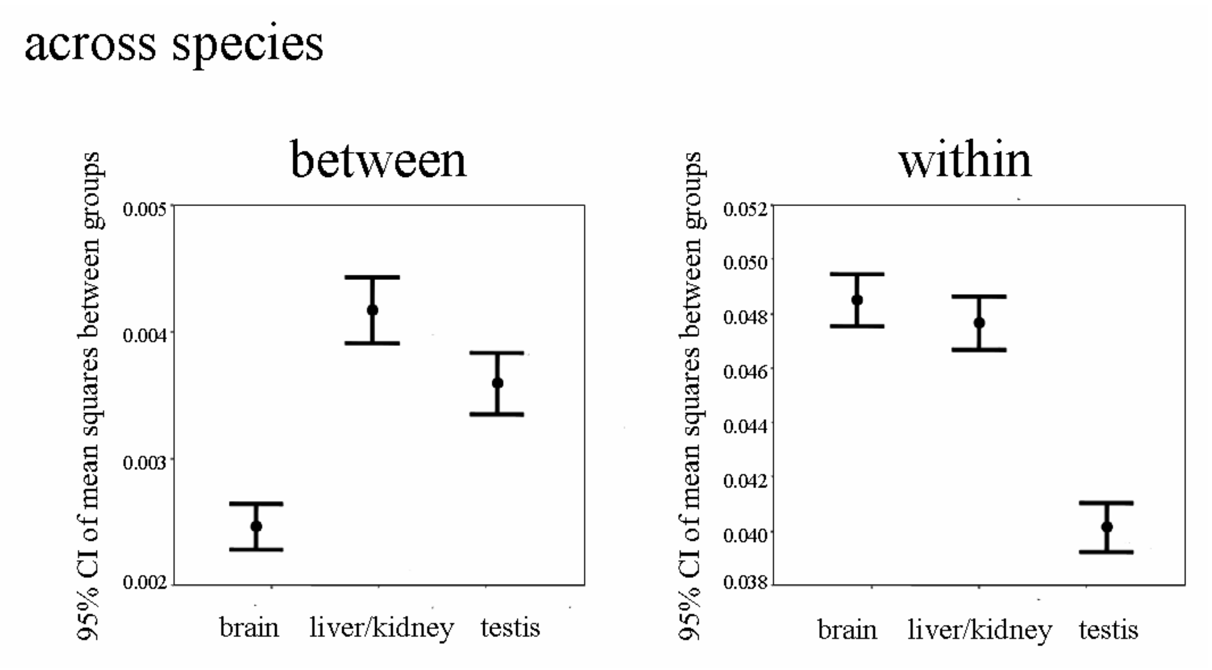


Figure 9: Mean and 95% confidence intervals (CI) for the variance components v_b (between species variance) and v_w (within species variance) used to calculate the scaled divergence metric.

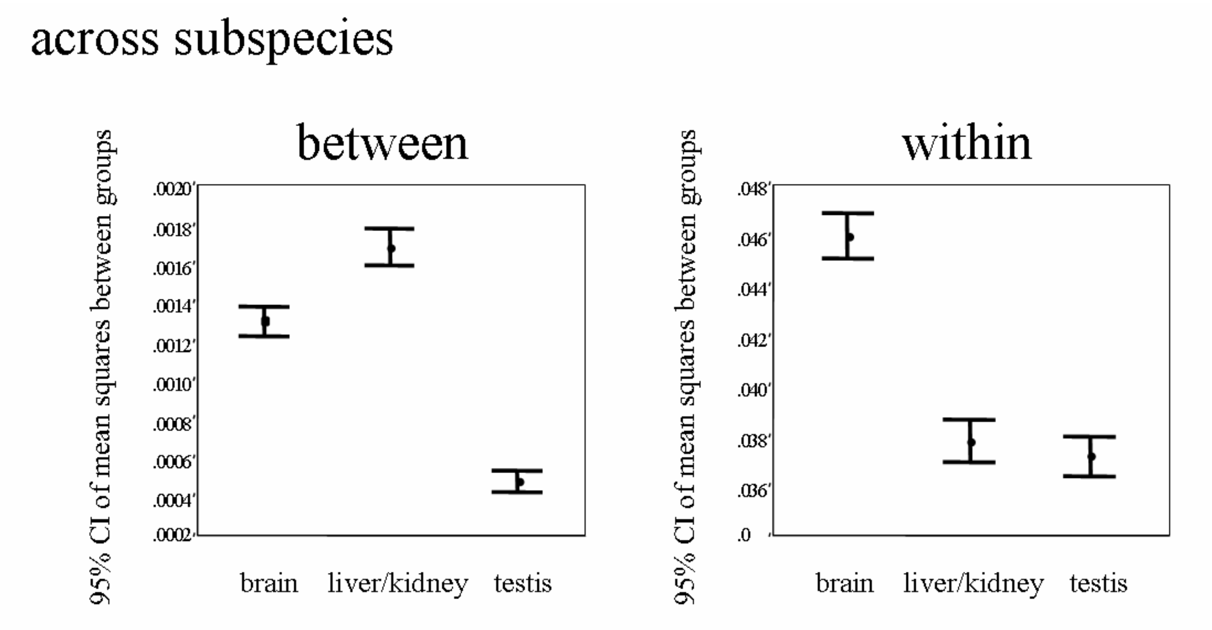


Figure 10: Mean and 95% confidence intervals (CI) for the variance components v_b (between subspecies variance) and v_w (within subspecies variance) used to calculate the scaled divergence metric.

One explanation for the low number of testis related differences across subspecies of *Mus musculus* might be that these only arise at a late stage in the divergence between populations or after speciation is complete. The subspecies of house mouse do show partial reproductive isolation but interbreed in hybrid zones (Boursot et al. 1993). It is possible that sexually selected genes are favorable across populations, respectively subspecies. For this reason, they get exchanged in regions where *Mus musculus* subspecies meet, i.e. in hybrid zones. It is possible that those genes move across hybrid zones, homogenizing the species, as has been shown for one Y-linked haplotype (Boissinot and Boursot 1997). If some sort of "infectious sex genes" exist that are beneficial across populations and therefore spread across subspecies, one would expect that genes that are differentially expressed in the testis between *Mus musculus* and *Mus spretus*, are homogeneously expressed in the testis across subspecies. The differentially expressed genes in the testis between species are sexually selected genes that are not able to get exchanged across species boundaries since *Mus spretus* does not hybridize with *Mus musculus* (Guenet and Bonhomme 2003). However, these genes will readily sweep through subspecies and therefore be homogenously expressed. Figure 11 shows the mean of the standard deviation for genes that are differentially expressed between *Mus musculus* and *Mus spretus*. As predicted, these genes show a significant lower expression variation within subspecies of *Mus musculus* than within *Mus spretus*. This hints to sweep-like mechanisms that homogenize expression traits of sexually selected genes between subspecies and could account for the low number of differentially expressed genes detected in the testis.

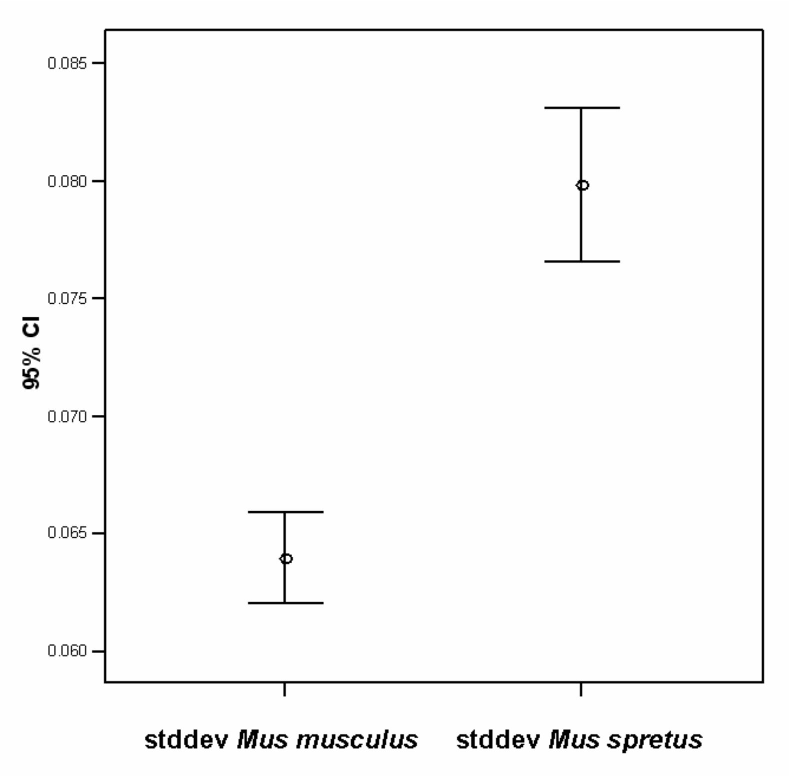


Figure 11: Plot of mean and confidence intervals (CI) of the expression standard deviation (stddev) in the different species of the genes that are differentially expressed in the testis between *Mus musculus* and *Mus spretus*.

3.5.2 dN/dS analysis

The dN/dS ratio is the ratio of the number of nonsynonymous substitutions per nonsynonymous site (dN) to the number of synonymous substitutions per synonymous site (dS). A dN/dS ratio that is smaller than 1 is indicative of negative/purifying selection because typically the synonymous changes outweigh the nonsynonymous changes (most of the nonsynonymous changes are believed to be deleterious). A dN/dS ratio that is higher than 1 is indicative of positive/adaptive selection. There is agreement that these cutoffs are quite conservative because most of the time it is not the whole sequence that is under positive selection. Instead, a segment of a sequence that codes for a defined protein domain is adapting, e.g. the binding region of an immune-related receptor. For this reason dN/dS ratios that are higher than 1 are quite rare (Nei and Kumar 2000), because nearly all proteins are under negative selection regarding overall function and amino acid sequence. Thus, amino acid replacements tend to be conservative (synonymous) in most of the cases.

To combine the analysis of sequence evolution with genome-wide evolution of gene expression, the dN/dS values for the mouse-rat alignments for all the genes on the array were determined (see 2.16 and 6.4) and associated with patterns of gene expression divergence. For a given gene, the dN/dS value between mouse and rat is too far apart to infer recent patterns of evolutionary history but can serve as a good proxy of how fast the sequence evolves or how constrained it is, due to purifying selection. This information can be opposed to features of evolution of gene expression. By that one can test whether there is a correlation between evolution of gene expression and sequence evolution.

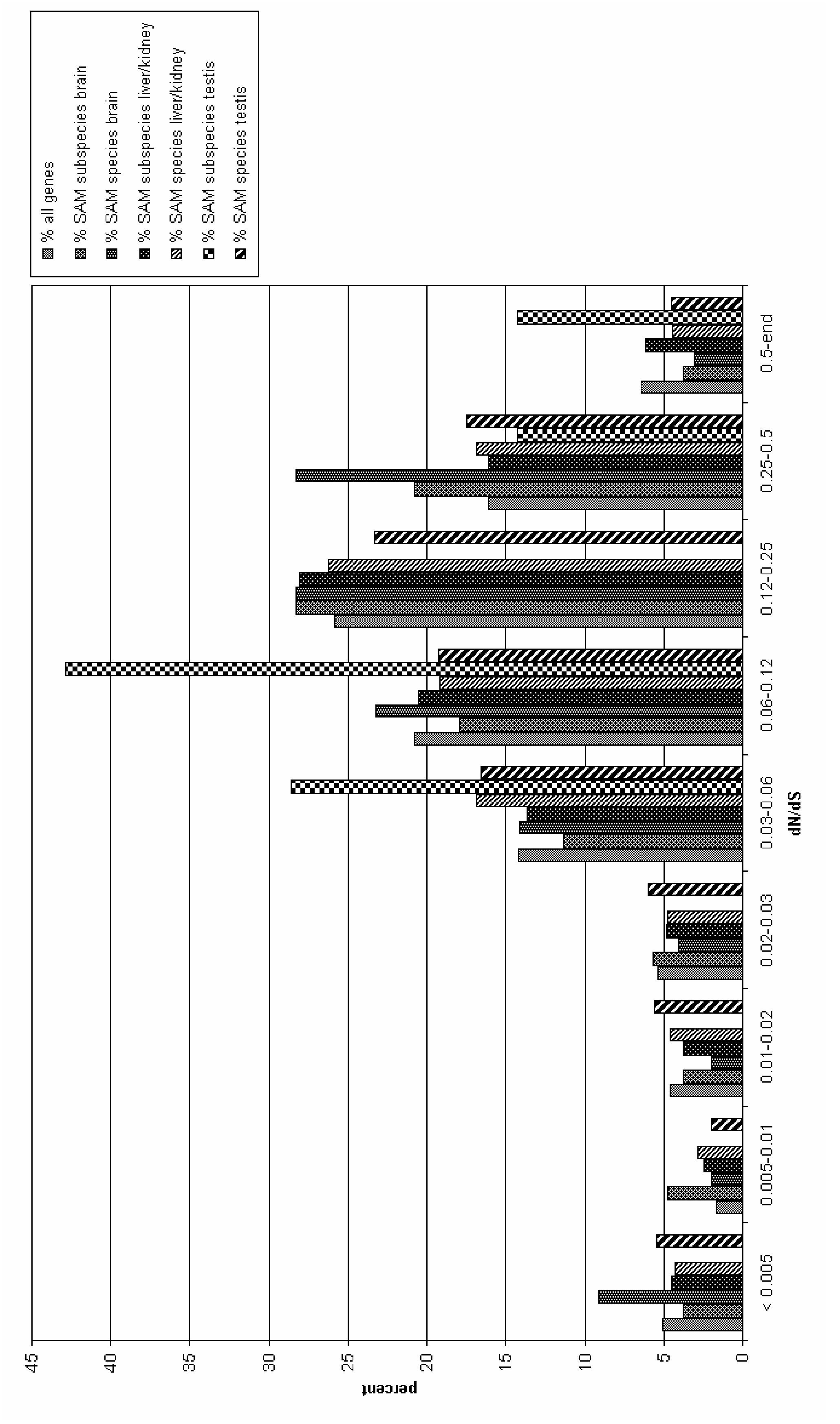


Figure 12: Discrete distribution of dN/dS ratios for all genes on the array and the subclasses of genes that are identified as differentially expressed by the SAM analyses between species, respectively subspecies for the different tissues. Note the logarithmic scale for representing the dN/dS ratio classes.

3.5.2.1 Distribution of dN/dS ratios

The distribution of dN/dS ratios for all the genes on the array and for the genes that were identified as differentially expressed by the SAM analyses is shown in Figure 12. A logarithmic scale was chosen for sorting the dN/dS ratios into discrete bins as suggested by Domazet-Loso and Tautz (Domazet-Loso and Tautz 2003). A chi-square test found no significant distributions when the distribution of all genes on the array was tested against the subclasses of genes that were identified as differentially expressed in the SAM analyses, except for the genes identified in the across subspecies comparison in the testis. For those, a highly significant distribution is found ($\chi_2^2 = 58.14$, $p < 0.001$). No genes are found in the lower dN/dS ratio bins (< 0.005 – 0.03) and more genes are found in the higher dN/dS ratio bins (0.03 – 0.06, 0.06 – 0.12, 0.5 – end). More than 14% of the genes that are differentially expressed in testis across subspecies have a dN/dS ratio higher or equal to 0.5. Most probably, there is a bias that stems from the low number of genes that were idientified in this SAM analysis (23 genes).

3.5.2.2 Patterns of correlation of evolution of gene expression and sequence evolution

To answer whether there is a correlation between sequence evolution and evolution of gene expression, i.e. whether DNA divergence and expression divergence is coupled between species, respectively subspecies, the expression variance was plotted against the dN/dS ratios for all genes and for all subsets of genes from the SAM analyses. The standard deviations of the log2-ratios across subspecies and across species were plotted against the dN/dS ratios from the mouse-rat alignments for the corresponding genes. For all genes on the array either weak positive or weak negative correlations (R^2 in the order of 10^{-7} to 10^{-4}) were found between dN/dS ratios and the variance in expression. This is true for the level of species and subspecies (data not shown). In contrast, considering just the genes that were identified as differentially expressed in the SAM analyses across species, respectively across subspecies, an intriguing pattern emerges. When the standard deviations of expression for the genes that were identified as differentially expressed between species is plotted against their dN/dS ratios, the correlation is positive for all tissues (Figure 13). When the standard deviations of expression for the genes that were identified as differentially expressed between subspecies is plotted against their dN/dS ratios, the correlation is negative for all tissues (Figure 14). The correlations are not too strong but consistent in that they have the same direction and magnitude (10^{-3}) across all tissues. The correlations for the differentially expressed genes are at least an order of magnitude higher than the correlations found for all genes (10^{-3} vs. 10^{-7} to 10^{-4}). This means that on the species level there is a positive correlation between sequence divergence and expression divergence, whereas the reverse correlation is found between subspecies. The results from the across species analysis are in line with assuming a "synchronized" molecular clock for evolution of gene expression *and* sequence evolution. The more time has passed between two populations/taxa/species, the more mutations have accumulated and hence, the more divergent the expression status, respectively the sequence is. For the differentially expressed genes between subspecies I find the reverse correlation. The higher the dN/dS ratio is, the lower is the variance in gene expression. If a higher dN/dS ratio is indicative of a history of positive selection, then the finding that those genes show less variance in gene expression point to a recent selective sweep that homogenized the expression status of these genes. The relaxed selective constraints (high dN/dS ratio) of these genes makes them amenable to be picked by positive selection since the gene can more readily evolve to take over new functions either by evolution of coding sequence or expression status. The outcome would be the same: if the adaptation is favorable, the given allele will sweep through the population, coding sequence and promoter coupled, and the variance in expression would drop.

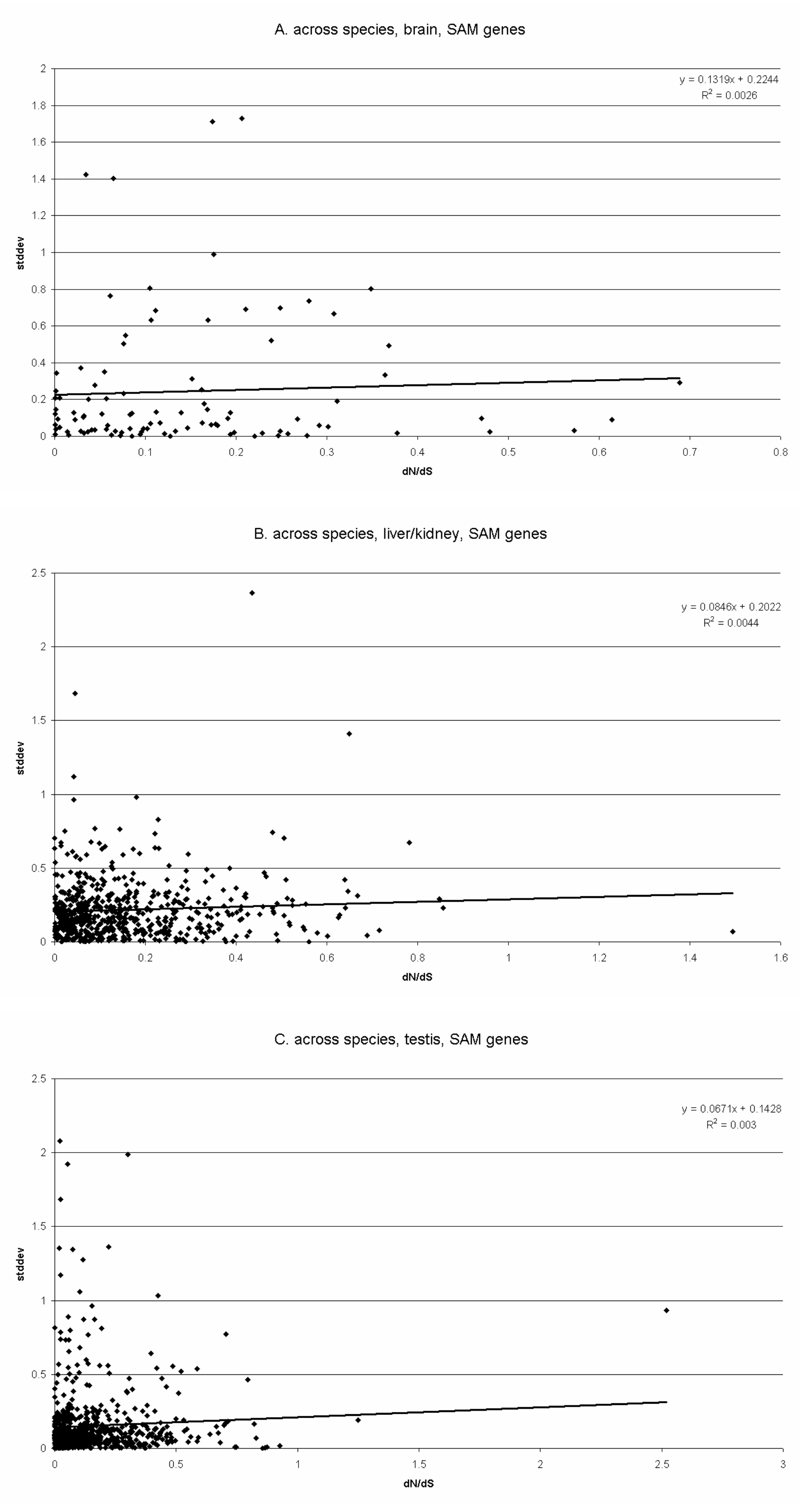


Figure 13: Correlation of variation in gene expression (stddev = standard deviation) for the differentially expressed genes between *Mus musculus* and *Mus spretus* and sequence divergence (dN/dS) for A. brain, B. liver/kidney and C. testis.

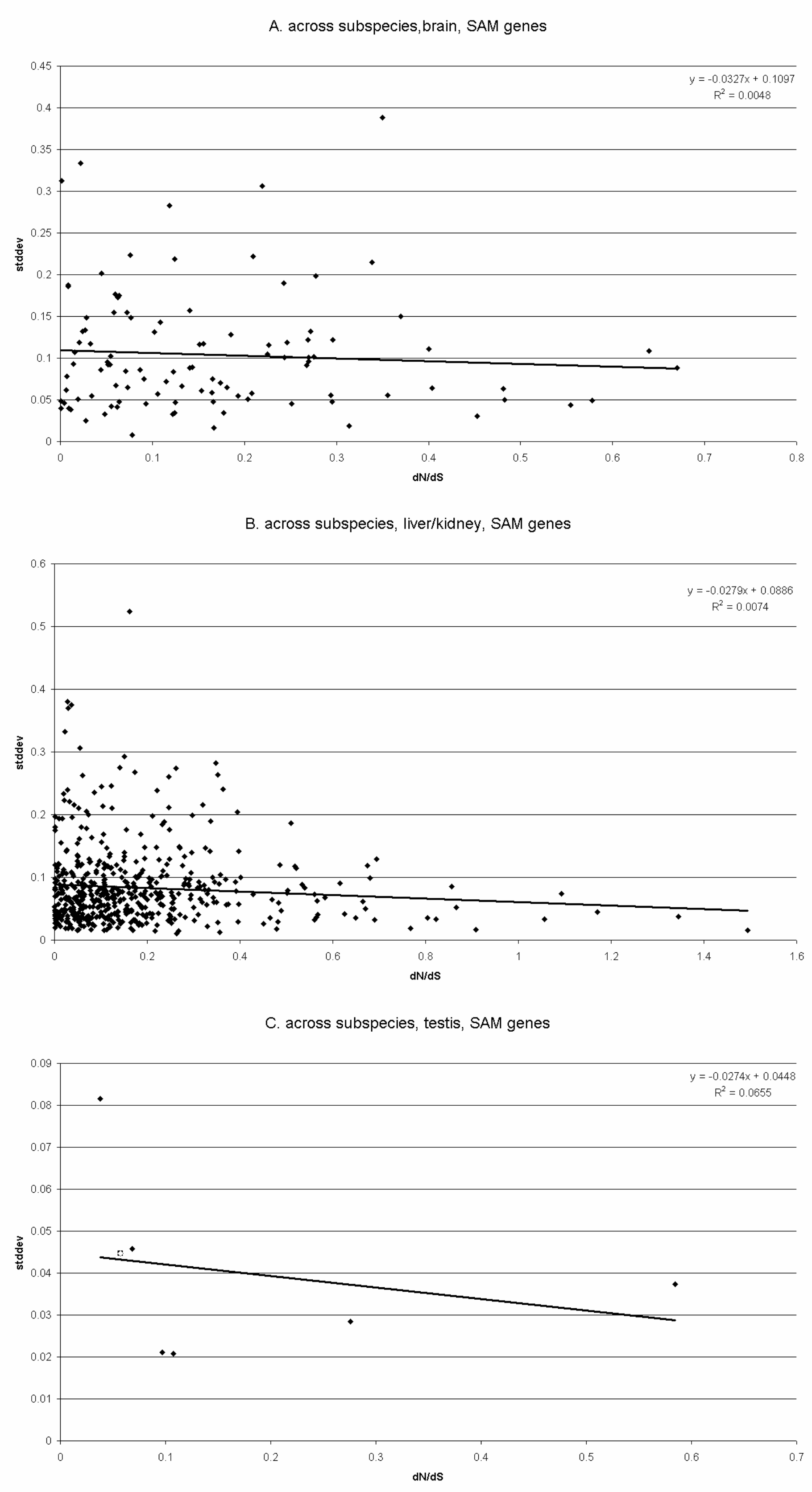


Figure 14: Correlation of variation in gene expression (stddev = standard deviation) for the differentially expressed genes between subspecies of *Mus musculus* and sequence divergence (dN/dS) for A. brain, B. liver/kidney and C. testis.

Taken together, the results suggest that in early stages of divergence (subspecies-level) there is a negative correlation between dN/dS and the variance in gene expression which would be explained by selective sweeps due to positive selection that homogenize the expression status of a gene within a population. In later stages of divergence (species-level), more time for neutral changes to take place was available and the pattern of sequence divergence and expression divergence is linked through the evolutionary rate that is determined by the molecular clock, i.e. the mutation rate. Moreover, this means that in the analysis between species more genes tend to be different because of neutral evolution. A gene that is differentially expressed between species is less likely a consequence of adaptive evolution than a gene that is differentially expressed between subspecies.

If the mean dN/dS over the genes identified by SAM is compared (Figure 15), it is consistently lower for the genes that are differentially expressed between species in comparison to the genes that are differentially expressed between subspecies. Therefore, the genes that change expression between subspecies tend to have a higher dN/dS ratio indicative of “faster” evolution or less selective constraints. This is another cue that early stages of divergence obey different patterns of evolution of gene expression than late stages. The correlations as well as the mean dN/dS are not biased by a different samplesize, since the numbers of identified genes between species and subspecies of *Mus* is nearly identical for the brain and liver/kidney. For the testis where there is a striking difference in the number of genes identified, the patterns seen in brain and liver/kidney still hold true, which just underlines the generality of the found correlation.

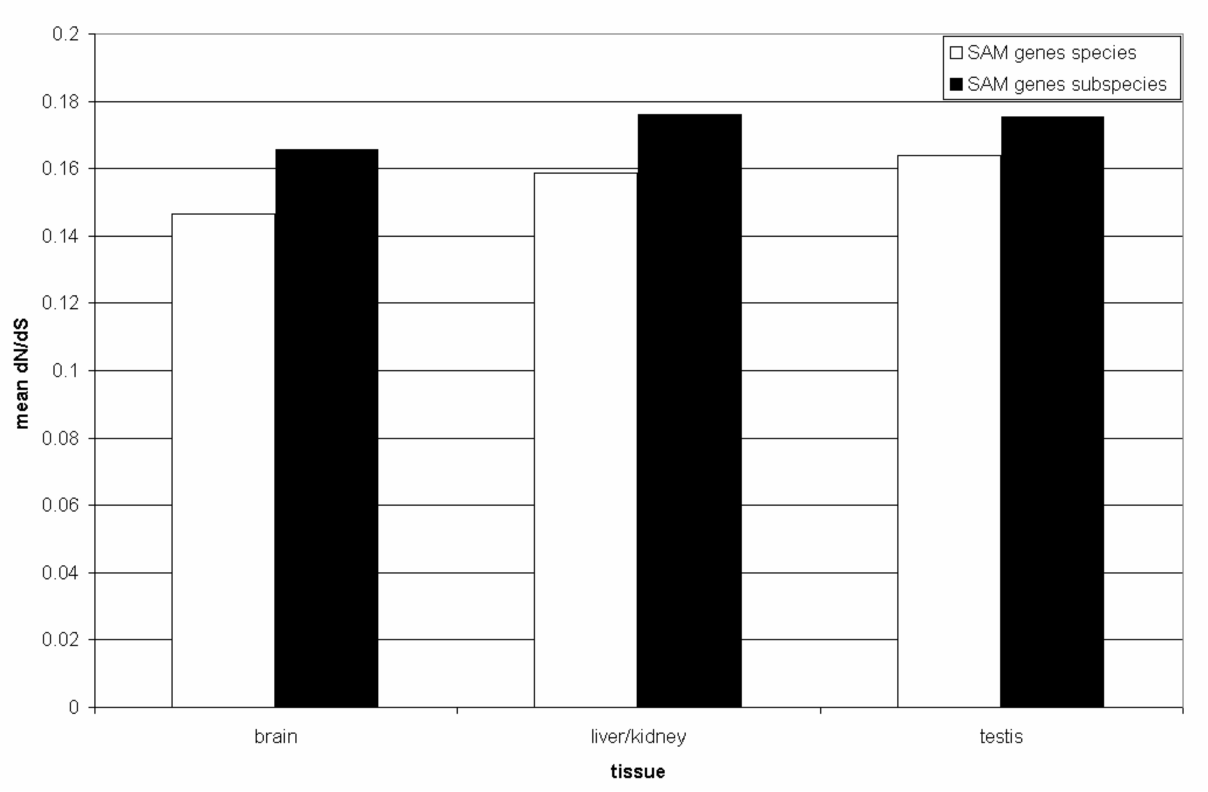


Figure 15: Mean dN/dS of the genes identified by SAM as differentially expressed between *Mus spretus* and *Mus musculus* (white bars), respectively between subpecies of *Mus musculus* (black bars) for the different tissues.

4 DISCUSSION

4.1 Gene expression differences between species and subspecies of *Mus*

The commonly employed SAM method was used to contrast the evolution of gene expression between different tissues and on different taxonomic levels in the genus *Mus*. SAM estimates the null distribution from the data itself. With microarray data, testing thousands of hypotheses simultaneously, the control of false positives among the genes called “significant” becomes the critical issue. Throughout this study a FDR (False Discovery Rate) of < 5% was chosen. This means that within the list of genes called significant, one expect 5% of them to be falsely assigned significantly differentially expressed. Several FDR-controlling methods exist that all perform differently regarding microarray data. In a recent study (Qian and Huang 2005), it has been shown that among five of those FDR-controlling methods, the q-value method that is also used by SAM performs best given the structure of microarray data. It is possible that the result is biased if there is a large proportion of differentially expressed genes in the dataset (Efron et al. 2000; Pan et al. 2001). Since the number of genes differentially expressed is larger in a comparison between species than in a comparison between subspecies, because of longer evolutionary time to accumulate differences, this problem might be more severe for the comparison between species.

As shown by the CGH experiments, differences in hybridization efficiencies between taxa of *Mus* can be ruled out as a possible explanation for the high proportion of gene expression changes in the testis in the full species comparison. Hence, one may exclude a higher rate of coding sequence evolution at these genes, a finding that is also supported by the distribution of dN/dS classes. There is no significant difference in the distribution of dN/dS ratios for the genes that are differentially expressed in the testis between species in comparison to the distribution for all genes on the array (Figure 12).

The SAM and scaled divergence analyses show similar outcomes when species/subspecies are being compared. This is true for the SAM analyses that is based on gene numbers as well as for the scaled divergence analysis that incorporates measures of genome-wide expression divergence. Since the scaled divergence metric was originally designed as a test for neutrality one would expect that all organs/tissue behave similarly over all genes. If there is a difference in how different organs/tissues evolve, then they are not evolving neutrally. Instead, different selective constraints may apply to the different tissues. In fact, I find clear differences when comparing the subspecies and species level for the different tissues. Between the two species of *Mus*, testis expression differences are accumulated. In contrast, testis expression does not diverge between subspecies. Liver/kidney does diverge fast between subspecies but between species this effect is seen to a lesser extent. The effects in the brain are less clear. Roughly the same number of genes seem to diverge between species and subspecies and there is no particular pattern that can be attributed to the different levels of divergence concerning change in gene expression in the brain. For this reason, I have focused the study on a comparison of testis versus liver and kidney, taking brain as a baseline with which to compare divergence in the other tissues.

The relative importance of gene expression change in the different tissues and divergence levels is also reflected in the fold-changes. Whereas across species single highest fold-changes can clearly be found in the testis, in the across subspecies analyses, single highest fold-changes were identified in the liver/kidney. They exceeded even those for the between species liver/kidney comparison (FC = 5.84 across species vs. FC = 6.54 across subspecies). The mean of change of expression is fairly constant across subspecies (about 1.2-fold), and differs between species regarding the different tissues analyzed. Interestingly, the highest mean fold-change is found in the brain in the between species comparison. Thus, whereas the general divergence in the brain is small (lowest number of differentially expressed genes between species), the quantitative change is high (highest mean fold-change).

4.2 Taxonomic status of *Mus musculus ssp.*

The taxonomic status of *Mus musculus ssp.* is not clear. As the study of lineage-specific genes (see 3.1.2.5) shows, *Mus musculus ssp.* does not show any differentially expressed gene in all tissues examined that is confined to this particular lineage. The mitochondrial D-loop analysis reveals that the *Mus musculus ssp.* individuals in this study are not of monophyletic origin. Two animals cluster with *Mus musculus musculus* and four animals cluster with *Mus musculus castaneus*. In a study by Boursot *et al.* (Boursot et al. 1996) that is based on restriction site polymorphism of mitochondrial DNA from a multidude of *Mus musculus* samples, three major lineages were defined and named *d*, *m* and *o*. Lineages *d* and *m* correspond to the *domesticus* and *musculus* lineages. The *o* lineage is a diversified group that contains the *Mus musculus bactrianus*, *Mus musculus castaneus* and *Mus musculus ssp.* samples for which they coined the term “oriental group of haplotypes”. The D-loop phylogeny presented here does not support the groupings proposed, since two of the *Mus musculus ssp.* samples cluster with *Mus musculus musculus* and would therefore be accounted to the *musculus* lineage. Furthermore, the *Mus musculus ssp.* samples do not cluster according to geographical origin. *Mus musculus ssp.* BID (“western oriental”) and *Mus musculus ssp.* DHA (“eastern oriental”) cluster together as well as *Mus musculus ssp.* TEH (“eastern oriental”) and *Mus musculus ssp.* MPR (“western oriental”) (see Table 1 and Figure 7).

In general, three groupings of *Mus musculus ssp.* animals are evident: one pair that clusters with *M. m. musculus* (*M. m. ssp.* MAC and *M. m. ssp.* KAK), one pair that clusters with *M. m. castaneus* (*M. m. ssp.* BID and *M. m. ssp.* DHA) and the third pair that forms a group separated from *M. m. castaneus* (*M. m. ssp.* BID and *M. m. ssp.* DHA). The bootstrap support for all splits between the different *Mus musculus ssp.* groups is 100. In consequence, the taxonomic statues of *Mus musculus ssp.* is not clear and further studies that clarify the taxonomic status have to be conducted.

4.3 Confirmation of differentially expressed genes with qRT-PCR

The use of qRT-PCR for confirmation of microarray results is not uncontroversial. The validation of results from one mRNA-measurement procedure using a different mRNA-measurement procedure assuming that this is more accurate is debatable (Allison et al. 2006). Even more so when non-focal species are used. In a parallel study, it was found that TaqMan assays are prone to amplification differences when related species are used for which the assays were not specifically designed (personal communication Fabian Staubach, unpublished data), due to SNPs and differentially spliced transcripts. One would have to sequence all amplicons in all species/subspecies under study to make sure that the assays capture only differences in mRNA levels. Nevertheless, most of the differentially expressed genes were significantly confirmed in direction of change, albeit the fold-changes were different. As already laid out in 3.2, it is often seen that microarray fold-changes tend to be inflated, respectively deflated depending on the absolute expression level, i.e. signal intensity, which is not captured in log2-ratios from microarrays.

It would be of particular interest whether the pattern found in the crisp1 gene can be confirmed after sequencing of the corresponding amplicon region in all animals. It would provide a prime candidate for the postmating prezygotic form of reproductive isolation, since it is about 130-fold differentially expressed between *Mus spretus* and *Mus musculus* and it is involved in the fusion of sperm and egg, a function that is critical in mediating species specificity (Swanson et al. 2003), and therefore in maintaining species borders by preventing interbreeding. Interestingly, it also shows a non-uniform expression across the subspecies of *Mus musculus*. So it could have adapted between species as well as between subspecies. Moreover, it has a dN/dS ratio of 0.68, which suggests at least relaxed selective constraints, if not positive selection. It is proposed that positive selection drives the rapid evolution of reproductive isolation (Orr et al. 2004). To find out if change in expression of this gene is due to an adaptive event, one could measure if there is a reduced nucleotide diversity in the surrounding region indicative of a selective sweep, as done in a recent study (in press (Harr et al. 2006)). By this, proof that the change in expression is associated with positive selection, respectively is adaptive would be supported. Likewise, it could be that the adaptation is within the coding sequence and the corresponding promoter allele has become fixed because it has been hitchhiked. Furthermore, sequencing of the coding region in all animals would determine if the dN/dS ratio is higher in *Mus musculus* than in *Mus spretus*, respectively in *Mus musculus domesticus* than in the remaining *Mus musculus* subspecies.

4.4 Functional annotation of candidate genes

High-density technologies such as microarrays enable us to study biological processes on a genome-wide level. The net result is commonly one or more lists of differentially expressed genes like in this study. Taking into account that these lists can contain thousands of genes, it is not possible to annotate them one at-a-time using databases or literature searches. In order to make sense of lists of genes, one has to identify the salient biological themes that are contained within them. DAVID and PANTHER are two software tools that facilitate the biological interpretation of lists of genes in that they look for co-occurrences of biological themes within a list of genes, respectively capture over-represented biological processes. In a study of divergence of gene expression, it is hard to estimate what biological themes are expected to be identified. Since I was looking at divergence in natural populations there exists 1. variation, 2. functional divergence, 3. genetic drift. So a list of differentially expressed genes contains by definition all kinds of categories, processes, annotations. Nevertheless, the analyses with DAVID show that it is possible to catch biological themes that reveal the tissues' identity, i.e. one can identify the tissue under study on the basis of the functional categories identified within the list of differentially expressed genes. Interestingly, whereas many of the categories overlap when comparing the across species and across subspecies analyses for a given tissue, the genes that constitute the categories do not overlap. This could either mean that gene expression in general evolves neutrally, so that one would expect to find a homogenous distribution of genes and categories when comparing different levels of divergence, or that genes belonging to predominant functional categories are selected on a recurrent basis to adapt to environmental change. A remarkable outcome is that in all DAVID analyses regulation of transcription was found as a functional category. One might expect that transcription factors evolve under strong selective constraints since they most often control sets of target genes and are assumed to have a high pleiotropic load. Nevertheless, they readily show up in all analyses as a functional category within the genes that changed expression (see 6.3) and constitute about 10% of the genes that changed expression. In a recent study, Gilad *et al.* (Gilad et al. 2006) looked at differences in expression in liver among humans, chimpanzees, orangutans and rhesus macaques. They found that there is an excess of transcription factors with increased expression specifically in the human lineage. In general, between 14% and 20% of the genes from a given SAM analysis could be asorted to functional categories with the DAVID software.

As laid out, I was looking at patterns of expression divergence in natural populations, which is by definition "noisy" in terms of genetic drift or neutral evolution concerning evolution of expression levels of genes. PANTHER is a tool that is more error-prone in such studies. The biological process finding of this tool is based on a gene-by-gene basis so that it is easy to catch the biological content in e.g. wildtype vs. mutant studies, where one expects discrete biological processes to be affected. In a study of gene expression divergence in wild populations of mice, where a lot of variation and stochastic processes play a role in divergence of gene expression levels, a tool such as DAVID is performing more robust since it is based on co-similarities between genes from multiple databases. In general, DAVID is more granular and less specific. Nonetheless, PANTHER readily identified immune-related processes to be present in the list of genes that diverge.

4.5 Correlations of expression divergence and nucleotide sequence divergence

Lemos *et al.* (Lemos et al. 2005) found in a study using *Drosophila melanogaster* and sister species that nucleotide sequence divergence is positively coupled with divergence of gene expression within and between species. In the present study, a positive correlation between gene expression divergence and nucleotide divergence is also observed, but only for genes that are differentially expressed between species (*Mus spretus* and *Mus musculus*). When comparing genes that are differentially expressed between subspecies of *Mus musculus*, there is a negative correlation between evolution of gene expression and coding sequence evolution. When taking data from all genes that were assayed into account, no consistent pattern of correlation is seen.

As the SAM and scaled divergence analyses, this analysis underlines the differences in patterns when looking at different divergence time frames. The species level shows a different pattern than the subspecies level in all tissues examined. Depending on the time frame chosen, the correlation between sequence divergence and expression divergence is either positive or negative. In the between species comparison a positive correlation between gene expression and sequence divergence is seen, consistent with a neutral model of evolution, transcriptome- and genome-wise. Variation in mutation rate and strength of selection among genes is expected to result in similar pressures on variation in coding sequences and gene expression, which thus leads to a correlation between structural and regulatory evolution (Lemos et al. 2005). Looking at a shorter divergence time frame, the correlations above get reversed. Genes whose sequences evolve faster are less variant in expression. It is intriguing to find the pattern in the particular order. This is consistent with assuming that, in early stages of divergence, genes that are under relaxed selective constraints (higher dN/dS ratio) are swept expression-wise, and that these genes constitute the repository from which evolution “draws” to adapt to new circumstances. Gilad *et al.* (Gilad et al. 2006) show that there seems to be a correspondence between genes with altered expression and genes that have a high dN/dS ratio, a finding which they explain with positive selection on the protein-coding regions of those genes. It is suggested that speciation results from positive darwinian selection within species (Orr et al. 2004), a notion that is supported in this study.

In general, the correlations found are small but one has to keep in mind that multiple factors influence the rate of protein divergence (Duret and Mouchiroud 2000; Williams and Hurst 2000; Subramanian and Kumar 2004; Zhang et al. 2004), as well as the extent of gene expression divergence (Meiklejohn et al. 2003; Ranz et al. 2003; Rifkin et al. 2003; Lemos et al. 2005). It would be interesting to see if the correlations found in this study are useful for a test of adaptive evolution: take genes that are differentially expressed, have a low intra-specific variance and a higher than average dN/dS ratio and test those for signs of adaptive evolution.

The dN/dS ratios for this analysis are from *Mus*-*Rattus* alignments and can serve as a general proxy of how constraint the coding sequence evolves but, one has to keep in mind that a higher dN/dS ratio does not necessarily point to a faster coding sequence evolution in the *Mus* lineage. A high dN/dS ratio, implying faster rates of evolution, can just as well be caused by a higher rate of sequence evolution in the rat lineage. The relationship between variation in gene expression and coding sequence evolution is still under debate and subject of ongoing research (Wagner 2000; Gu et al. 2002; Makova and Li 2003; Jordan et al. 2004; Nuzhdin et al. 2004).

4.6 Towards evolutionary patterns of species divergence/speciation regarding gene expression divergence

It has been suggested that a large proportion of the changes relevant to the process of differential adaptation and species formation can be attributed to changes in gene regulation (King and Wilson 1975; Davidson 2001; Wray et al. 2003). Moreover, differences in gene expression are heritable and thus provide a target for selection (Schadt et al. 2003; Morley et al. 2004). I compared the whole-genome expression profile between *Mus spretus* and *Mus musculus* and between different subspecies of *Mus musculus* to infer patterns of evolutionary divergence at different stages of species divergence. Of course, gene expression divergence in itself does not prove a functional consequence or any adaptive value. Nevertheless, by comparing gene expression changes between 1. different organs and 2. different stages of divergence, one can deduce evolutionary patterns of species divergence, respectively speciation.

The process by which new species are formed is of central interest in evolutionary biology. The generation of reproductive isolation is an essential part of this process, since it prevents species, from merging back into one through hybridization. Recent interest focuses on the identification of mechanisms that drive the evolution of reproductive isolation. These mechanisms have been broadly classified as ecological or non-ecological (Gulick 1890; Schluter 2000). In the ecological model, divergence in naturally and sexually selected traits is driven by natural selection (adaptation to different environments). In the non-ecological model, reproductive isolation is driven by sexual selection, i.e. divergence in mating traits as a response to sexual conflict/sexual "arms race" (Arnqvist and Rowe 2005). The reason for assuming sexual selection is important to speciation is that so many closely related species differ in sexual characters (often more than in other traits). Comparisons in secondary sexual traits (Panhuis et al. 2001), in reproductive proteins (Swanson and Vacquier 2002) and in sperm precedence (Price 1997) among species have shown that genes involved in reproduction are prime targets for divergence during speciation. These findings lead to increasing acceptance that non-ecological mechanisms may be very important in speciation. After all, natural selection *and* sexual selection are probably involved in most cases of speciation, but it has been difficult to separate them, since those processes can rarely be directly observed but have to be inferred from patterns among populations and species. Comparisons of gene expression changes across different tissues could serve as a common currency to compare evolutionary divergence. Differences in reproductive organs such as testis are likely to reflect processes relating to sexual selection (Meiklejohn et al. 2003; Ranz et al. 2003), whereas differences in liver/kidney reflect ecological and physiological adaptations. Divergence in the brain could reflect evolved behavioral differences among the mouse species and subspecies. The study of gene expression should be particularly germane because it is thought that changes in gene expression play a critical role in speciation (Ting et al. 1998; Kazianis et al. 1999; Barbash et al. 2003).

Rapid evolution of the male reproductive system is a common finding in comparisons at the *species* level such as among abalone (Swanson and Vacquier 1995), *Drosophila* (Civetta and Singh 1998) and primates (Wyckoff et al. 2000). In rodents it has also been demonstrated, but only in comparisons between mouse and rat (Good and Nachman 2005), two species that split 10 million years ago (Guenet and Bonhomme 2003). In this study, divergence among more recently separated species is examined. *Mus spretus* and its closest relative *Mus musculus* are separated from each other by 1.1 - 1.5 million years (Boursot et al. 1993). Among the tissues tested, testis expression divergence exceeded divergence in liver/kidney, which exceeded divergence in the brain. Hence, the finding that the male reproductive system is rapidly evolving is confirmed, but only at the species level. When subspecies of *Mus musculus* are compared that diverged from each other 500,000 to 800,000 years ago (Guenet and Bonhomme 2003), far more liver/kidney expressed genes diverge than testis expressed genes. This over-representation of liver/kidney genes was observed in multiple independent subspecies, albeit two of the subspecies in the experiment (*M. m. domesticus* and *M. m. musculus*) were held in a common environment for only 3 to 5 days after collection in the wild, prior to performing the experiment. In contrast, individuals of *Mus musculus ssp.* and *Mus musculus castaneus* were derived from strains that have been maintained in the lab for several generations but show the same pattern. Thus, although the animals were kept under laboratory conditions for different time intervals, they all show a similar over-representation of divergence in genes expressed in the liver/kidney, implying that the differences can be attributed to genetic divergence, rather than phenotypic plasticity. I conclude that the over-representation of differentially expressed genes in the liver/kidney among subspecies most likely is a result of selection rather than a chance effect. The strong over-representation of liver/kidney differences among subspecies may be a consequence of ecological and physiological adaptations (e.g. adaptations to different food sources or detoxification potential). In a study between primate species, liver divergence exceeded brain divergence as it does in *Mus* (Hsieh et al. 2003; Lemos et al. 2005). A finding that is explained as a consequence of changes in diet (Lemos et al. 2005).

The results from this study suggest the following model of species divergence/speciation: adaptation to different environments by natural selection (Schluter 2000; Dieckmann 2004) is the primary source of divergence (as seen in the divergence pattern between subspecies), while sexual selection seems to be the major driving force in later stages of divergence (as seen in the divergence pattern between species). In other words: continued accumulation of ecological differences among subspecies may set up the conditions to eventually reduce gene flow to zero, and only once this is achieved can differentiation at other loci, such as those involved in sexual selection, accumulate. Thus, the contribution of sexual selection to the initial process of speciation may have been over-emphasized.

Since comparative genomics started with comparisons of distantly related genomes, the association of evolutionary change and differences in ecology, respectively physiology between taxa was not previously seen. The genus *Mus* is especially suitable for evolutionary genomics in vertebrates because it allows comparative studies at all levels of divergence (population, subspecies and species). A feature that should facilitate the identification of evolutionary patterns that emerge when species/subspecies diverge. This study shows that species divergence/speciation is a multi-level, multi-facet *dynamic* process instead of a linear accumulation of differences that eventually leads to reproductive isolation. One has to carefully look which divergence level is chosen when inferring conclusions about the underlying processes. My observation of divergent gene expression in metabolic organs among incipient subspecies of house mouse suggests a pervasive role of ecological adaptations in the early stages of divergence, while late divergence seems to be primarily non-ecologic. Whether or not gene expression divergence in later stages of divergence is a cause or a consequence of speciation, and whether sexual selection or genetic drift is the major driving force behind this divergence, remains to be seen.

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6 Appendix

Data format and access: in this appendix, data is formatted as simple .csv text documents. ”Commas” were replaced with “comma and space”, “line breaks” were replaced with “semicolon and space”. In order to make use of the data, simply copy and paste the according data in a text editor and replace “comma and space” with “comma”, and “semicolon and space” with “line break”. After that you can import the file in Excel and easily work with it.

6.1 Differentially expressed genes between *Mus spretus* and *Mus musculus* (SAM 2-class unpaired analysis, 200 permutations, FDR < 5%)

For a definition of Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value (%) please refer to the SAM users guide and technical document at http://www-stat.stanford.edu/~tibs/SAM/.

6.1.1 brain – over-expressed genes in *Mus spretus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); AK003742, 10.77848197, 1.683850319, 0.156223327, 3.243094996, 0; M12194, 9.847624592, 1.524918751, 0.15485143, 2.881817358, 0; BC002294, 8.505228577, 2.202908498, 0.259006384, 4.72888114, 0; AK012264, 7.612734489, 1.74108354, 0.228706721, 3.545400193, 0; AK014379, 6.335986368, 1.789613447, 0.282452225, 3.891862079, 0; AK019581, 5.569584465, 1.714672067, 0.307863554, 3.836286862, 0; AK011611, 5.498457106, 1.204708678, 0.219099405, 2.360710635, 0; NM_009324, 5.441372949, 0.939415679, 0.172643134, 1.926032783, 0; AK004439, 5.349029425, 1.200322925, 0.224400135, 2.27632382, 0; AK007391, 5.056838468, 1.096172652, 0.216770351, 2.246908796, 0; NM_011544, 5.021569108, 0.913090443, 0.181833691, 1.903070609, 0; AF240782, 4.774250682, 1.150402581, 0.240959819, 2.210959555, 0; AK010827, 4.710905078, 1.846984085, 0.392065655, 3.411232938, 0; NM_008845, 4.61059375, 0.836618892, 0.181455782, 1.795264162, 0; BC015275, 4.559545786, 0.83370559, 0.182848387, 1.785666052, 0; NM_011664, 4.516385928, 1.111431131, 0.246088609, 2.152199658, 0; AK009918, 4.35500584, 1.048773795, 0.240820296, 2.053548483, 0; U01314, 4.300038301, 1.014176062, 0.235852797, 1.994617293, 0; AK015921, 4.125420446, 1.106540765, 0.268224967, 2.507175486, 0; Z12551, 4.101301405, 0.919791533, 0.224268212, 1.957746121, 0; NM_013554, 4.046795468, 0.916101382, 0.226376991, 1.869206098, 0; NM_029703, 4.034643818, 0.823339016, 0.204067336, 1.771684751, 0; NM_011431, 3.99958461, 1.015862828, 0.253992083, 2.121979596, 0; BC006699, 3.950651668, 0.794188942, 0.201027326, 1.808808583, 0; NM_019815, 3.947141152, 0.688810751, 0.174508771, 1.659857956, 0; NM_007992, 3.914710571, 0.862904078, 0.220426022, 1.802898209, 0; M57960, 3.907670492, 0.747869606, 0.191385023, 1.73371378, 0; AK017384, 3.90097432, 0.614071982, 0.157415028, 1.531368813, 0; NM_009427, 3.862402086, 0.860121116, 0.222690724, 1.801362628, 0; AK010322, 3.846725287, 0.671895526, 0.174666886, 1.600825716, 0; NM_009086, 3.756586348, 1.487457648, 0.395959925, 4.124161354, 0; AK019586, 3.738661706, 0.936193394, 0.250408694, 2.079820839, 0; AK006819, 3.690220247, 1.125422888, 0.30497445, 2.145728007, 0; AK020866, 3.683572929, 1.266504547, 0.343825023, 2.524963362, 0; AK018205, 3.670000333, 1.226056997, 0.334075446, 2.242118754, 0; U58337, 3.621625538, 0.759039921, 0.209585423, 1.672490224, 0; AK012640, 3.593174173, 0.980872632, 0.272982211, 1.939798372, 0; AK006372, 3.578123448, 0.708479606, 0.19800312, 1.688674653, 0; AF357403, 3.548944002, 0.473113997, 0.133311204, 1.395954998, 0; BC007147, 3.478023799, 0.832704183, 0.239418771, 1.812537389, 0; AJ231262, 3.459142245, 0.637969104, 0.184429855, 1.569929776, 0; AK006525, 3.443645258, 0.530338726, 0.15400504, 1.44103698, 0; NM_011671, 3.379306019, 0.989697617, 0.292870078, 1.947550036, 0; BC009151, 3.376221815, 0.550035029, 0.162914364, 1.49266698, 0; M35662, 3.366884393, 0.762125666, 0.226359321, 1.673450334, 0; Z83810, 3.359383186, 0.499115841, 0.148573656, 1.410106043, 0; BC004020, 3.358077826, 0.538353628, 0.160316007, 1.450953237, 0; NM_010671, 3.295864924, 0.55664852, 0.168893002, 1.471574721, 0; AK006696, 3.283159398, 0.540517503, 0.164633342, 1.451632772, 0; AK015713, 3.27784497, 0.763059419, 0.232793017, 1.814248178, 0; NM_019934, 3.239218212, 0.752974963, 0.23245577, 1.664915059, 0; NM_008027, 3.23514204, 0.771413551, 0.238448124, 1.724572191, 0; AK010546, 3.220484255, 0.559237986, 0.173650278, 1.492867577, 0; Z48496, 3.206080711, 0.749489452, 0.233771236, 1.718194743, 0; AF346413, 3.179971366, 1.013949174, 0.318854812, 2.311838907, 0.904357723; AK017700, 3.150115984, 0.530563208, 0.168426563, 1.45929726, 0.904357723; Y08382, 3.126413268, 0.501292742, 0.160341164, 1.409834182, 0.904357723; AK004235, 3.117585135, 1.530134042, 0.49080746, 5.927725513, 0.904357723; AK015113, 3.061658156, 1.120645417, 0.36602565, 2.855224886, 0.904357723; AJ279951, 3.061314458, 0.865996311, 0.282883814, 1.993379826, 0.904357723; AF154337, 3.048065748, 0.64146782, 0.210450782, 1.547772407, 0.904357723; BC002238, 3.047975724, 0.649144107, 0.212975484, 1.585088812, 0.904357723; AK004884, 3.044914574, 0.515679567, 0.169357647, 1.426881418, 0.904357723; AF068116, 3.000225239, 0.578947506, 0.192968014, 1.504146298, 0.904357723; X81632, 2.994215303, 0.748599361, 0.250015208, 1.837770313, 0.904357723; AK005733, 2.978580312, 0.40880544, 0.13724842, 1.326369085, 0.904357723; X84014, 2.971773074, 0.661105735, 0.222461715, 1.606033455, 0.904357723; AK003969, 2.960790493, 0.681807368, 0.230278829, 1.586454181, 0.904357723; NM_009498, 2.954386161, 0.729018513, 0.246758031, 1.809989622, 0.904357723; AK015173, 2.946088466, 0.491660563, 0.166885879, 1.408277335, 0.904357723; NM_008577, 2.932462514, 0.83759545, 0.285628698, 1.96855924, 0.904357723; AK019180, 2.898800347, 0.591550416, 0.204067319, 1.524313568, 0.904357723; AK021043, 2.893492757, 0.570608744, 0.197204138, 1.492647919, 0.904357723; AK018644, 2.887780837, 1.680143578, 0.581811319, 9.055179687, 0.904357723; AF384162, 2.86835598, 0.424762258, 0.148085614, 1.348602725, 2.007674144; AK017324, 2.866146728, 1.611990484, 0.562424271, 8.293938902, 2.007674144; BC004749, 2.86151886, 0.582475635, 0.203554708, 1.484643654, 2.007674144; NM_010100, 2.854039912, 0.45741551, 0.160269486, 1.368654243, 2.007674144; M13446, 2.852025698, 0.53259361, 0.18674222, 1.446317961, 2.007674144; AK018780, 2.850118835, 0.568867216, 0.199594209, 1.523669037, 2.007674144; NM_025592, 2.841883949, 0.574193777, 0.202046877, 1.506727323, 2.007674144; AJ409493, 2.840902843, 0.772577343, 0.271947823, 1.680697826, 2.007674144; NM_007556, 2.839866236, 0.714361655, 0.251547642, 1.623699255, 2.007674144; AY030406, 2.838088593, 0.397454025, 0.140042854, 1.316800612, 2.007674144; NM_015776, 2.837477653, 0.634493514, 0.22361181, 1.64751464, 2.007674144; NM_021331, 2.833961944, 0.641875609, 0.226494082, 1.654311857, 2.007674144; NM_019791, 2.83205243, 0.737258011, 0.260326399, 1.879243069, 2.007674144; AK015307, 2.82686195, 0.603796639, 0.213592545, 1.607811506, 2.007674144; NM_010301, 2.813224105, 0.927658736, 0.32974932, 2.406708732, 2.007674144; NM_019790, 2.800303698, 0.834985166, 0.298176647, 2.002761798, 2.007674144; AK005951, 2.776109564, 0.49271825, 0.17748516, 1.398371457, 2.007674144; AJ279843, 2.776051431, 0.79726863, 0.287195194, 2.129410097, 2.007674144; X94418, 2.773497263, 0.521210328, 0.187925308, 1.432194325, 2.007674144; AK015582, 2.77297387, 0.533652066, 0.192447564, 1.463972713, 2.007674144; AK020562, 2.761286238, 0.446022319, 0.161527013, 1.356442549, 2.007674144; NM_026202, 2.748113142, 0.476151623, 0.173264927, 1.39198255, 2.007674144; AF093560, 2.742518926, 0.578035256, 0.21076801, 1.565263434, 2.007674144; NM_008146, 2.738168575, 0.547880917, 0.20009028, 1.517174543, 2.007674144; NM_013920, 2.736642581, 0.595476025, 0.217593642, 1.559307999, 2.007674144; AK020861, 2.732292833, 0.698803605, 0.255757215, 1.598328812, 2.007674144; AJ308964, 2.723379296, 0.893836216, 0.328208494, 2.211017876, 3.13699085; AJ409474, 2.713671073, 0.679983204, 0.25057687, 1.670755269, 3.13699085; NM_013722, 2.711348203, 0.78399212, 0.289152134, 1.683528026, 3.13699085; AK016056, 2.709711139, 0.603778082, 0.222820091, 1.58270049, 3.13699085; AF226324, 2.701133848, 0.7746752, 0.286796303, 2.086176976, 3.13699085; AF084548, 2.693668853, 0.577459428, 0.214376547, 1.475184932, 3.13699085; NM_010327, 2.686098471, 0.947994971, 0.352926366, 2.321268547, 3.13699085; AF172276, 2.675620247, 0.750413372, 0.280463333, 1.974308525, 3.13699085; NM_008281, 2.671181426, 0.591283299, 0.221356473, 1.600035182, 3.13699085; AF374476, 2.67111824, 0.451089158, 0.168876522, 1.372479988, 3.13699085; NM_016666, 2.665177418, 1.25120339, 0.469463452, 4.771518328, 3.13699085; AK006761, 2.663119198, 0.438189463, 0.164539936, 1.348975858, 3.13699085; NM_008997, 2.660500244, 0.578975956, 0.217619208, 1.510251493, 3.13699085; NM_021477, 2.659032202, 0.688614552, 0.258971874, 1.583211104, 3.13699085; AF216290, 2.648734123, 0.767897952, 0.2899113, 2.0596581, 3.13699085; AK015344, 2.639777822, 0.465842864, 0.176470482, 1.415507244, 3.13699085; NM_021355, 2.637776556, 0.461913466, 0.175114706, 1.372062808, 3.13699085; AI326558, 2.636529038, 0.489450156, 0.185641861, 1.414928912, 3.13699085; BC012521, 2.635267846, 0.667019846, 0.253112733, 1.753022418, 3.13699085; AK020855, 2.632257707, 0.571547152, 0.217131913, 1.592253935, 3.13699085; AK008985, 2.629708171, 0.960877948, 0.365393377, 1.853302277, 3.13699085; NM_019771, 2.628632538, 0.391893892, 0.149086601, 1.309438312, 3.13699085; D28530, 2.619989058, 0.468161914, 0.1786885, 1.375978271, 3.13699085; AK019987, 2.615530951, 1.107360976, 0.423379037, 3.741100924, 3.13699085; NM_008143, 2.615415095, 0.454554548, 0.173798243, 1.384817111, 3.13699085; AK021082, 2.611727973, 0.466103148, 0.178465427, 1.42886712, 3.13699085; BC006920, 2.610424291, 0.520475244, 0.19938339, 1.424191505, 3.13699085; AK016136, 2.607040424, 0.508737092, 0.195139702, 1.439365798, 3.13699085; AK015780, 2.606978934, 0.745520936, 0.285971216, 2.0026363, 3.13699085; AK016928, 2.605085008, 0.778048416, 0.298665269, 2.158413183, 3.13699085; BC002178, 2.595026917, 1.219739952, 0.470029788, 4.713648022, 3.13699085; NM_010027, 2.585385013, 0.465688699, 0.180123539, 1.398174741, 3.13699085; AK017317, 2.581632073, 0.427308954, 0.16551892, 1.36175375, 3.13699085; AF131169, 2.577250703, 0.422281734, 0.163849692, 1.338249339, 3.13699085; AK003290, 2.575192198, 1.363493847, 0.529472654, 6.156351657, 3.13699085; AK020969, 2.567022487, 1.172084296, 0.456592921, 4.233172528, 3.13699085; NM_011703, 2.561619866, 0.504758109, 0.197046453, 1.406216706, 4.220336039; AK013476, 2.553812382, 0.606079558, 0.237323447, 1.690314887, 4.220336039; AK008077, 2.55192214, 0.706853312, 0.276988589, 1.887221839, 4.220336039; AF235035, 2.540893391, 0.967008457, 0.380578131, 2.628170963, 4.220336039; X53636, 2.539811322, 0.652762299, 0.257012123, 1.781852245, 4.220336039; NM_019576, 2.535138059, 0.799624346, 0.315416489, 2.054849714, 4.220336039; AK014677, 2.533132865, 0.577188974, 0.227855784, 1.471400605, 4.220336039; X02930, 2.531532235, 1.192244269, 0.47095757, 4.625332141, 4.220336039; U38940, 2.530355453, 0.977730877, 0.386400605, 2.562206626, 4.220336039; AK013819, 2.522741104, 0.498467503, 0.197589639, 1.401479368, 4.220336039; 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AF388573, 2.487335708, 0.474580259, 0.190798635, 1.387844775, 4.220336039; NM_011295, 2.483413285, 0.505776602, 0.203661874, 1.441166752, 4.220336039; AK006310, 2.476643382, 0.347311321, 0.140234692, 1.283700267, 4.220336039; NM_016738, 2.476246556, 0.709237245, 0.286416247, 1.603464193, 4.220336039; NM_007388, 2.474755504, 0.479306629, 0.193678377, 1.384149319, 4.220336039; AK020207, 2.471551401, 0.722277008, 0.292236288, 1.902428826, 4.220336039; AB050554, 2.468091699, 0.45812097, 0.185617483, 1.411185152, 4.220336039

6.1.2 brain – over-expressed genes in *Mus musculus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); NM_008004, -4.103558824, -0.646812681, 0.157622373, 0.637402044, 1.01397684; NM_011441, -4.101146794, -0.758056092, 0.184840029, 0.589191195, 1.01397684; NM_011602, -4.009006365, -0.472131574, 0.117767729, 0.721527158, 1.01397684; NM_007441, -3.857307847, -0.675832705, 0.175208392, 0.625687979, 1.01397684; NM_009302, -3.63647104, -0.557891085, 0.153415517, 0.678259769, 2.007674144; AK009844, -3.611486829, -0.577496402, 0.159905443, 0.668941188, 2.007674144; AK016455, -3.596948458, -0.50498035, 0.140391322, 0.703646273, 2.007674144; NM_011387, -3.591391714, -0.636635736, 0.17726714, 0.639576371, 2.007674144; X14096, -3.577528749, -0.686816652, 0.19198075, 0.619235144, 2.007674144; Z12264, -3.536087796, -0.502103135, 0.141993967, 0.70478083, 2.007674144; AK017539, -3.478994522, -0.50177075, 0.144228669, 0.711821634, 3.13699085; U26231, -3.473687092, -0.596964993, 0.171853416, 0.661145455, 3.13699085; U55612, -3.445562078, -1.375554175, 0.3992249, 0.360650821, 3.13699085; NM_008084, -3.429374772, -0.495153658, 0.144385986, 0.710173002, 3.13699085; X76018, -3.350800921, -0.664673765, 0.198362654, 0.625033016, 3.13699085; D30730, -3.316121489, -1.580911329, 0.476735045, 0.310412239, 3.13699085; AK011215, -3.264058729, -0.560052356, 0.171581581, 0.676111536, 3.13699085; AK004353, -3.234715845, -0.652598896, 0.201748446, 0.630712785, 3.13699085; NM_016767, -3.232559758, -0.568291, 0.175802164, 0.678735401, 3.13699085; BC006581, -3.230226765, -0.498431743, 0.1543024, 0.70730596, 3.13699085; AB010343, -3.229426006, -0.658585053, 0.203932542, 0.63012557, 3.13699085; BC005669, -3.208965064, -0.444763114, 0.138600173, 0.733934289, 3.13699085; M14833, -3.207574408, -0.50439248, 0.157250438, 0.704390161, 3.13699085; NM_009943, -3.161205126, -0.581007016, 0.183792887, 0.664008835, 4.220336039; AB000121, -3.153752413, -0.47983618, 0.152147701, 0.714733691, 4.220336039; NM_007693, -3.124933326, -0.469330646, 0.150189011, 0.720203565, 4.220336039; AK005772, -3.121215275, -0.861023854, 0.275861733, 0.537883386, 4.220336039; NM_030251, -3.112810573, -0.573433343, 0.18421723, 0.67072391, 4.220336039; AK004093, -3.09798727, -0.51504616, 0.166251865, 0.697729434, 4.220336039; NM_007981, -3.095438064, -0.438369346, 0.14161787, 0.736295584, 4.220336039; AK013061, -3.094895023, -0.747792848, 0.241621393, 0.593849655, 4.220336039; M30693, -3.090903331, -0.564423109, 0.182607817, 0.671795852, 4.220336039; NM_011366, -3.061370319, -0.443714914, 0.144939967, 0.73324302, 4.220336039; BC006820, -3.058366999, -0.634393656, 0.207428885, 0.643297228, 4.220336039; S85736, -3.040308184, -0.50631903, 0.16653543, 0.70270583, 4.220336039; NM_016861, -3.037377966, -1.265162125, 0.416531014, 0.384385999, 4.220336039; BF531396, -3.032641841, -0.547748064, 0.180617459, 0.680319977, 4.220336039; U73200, -3.027664613, -0.546269096, 0.180425894, 0.680150006, 4.220336039; NM_019512, -3.024226839, -0.711549655, 0.235283163, 0.601114562, 4.220336039; Z12256, -3.006064389, -0.462741923, 0.153936132, 0.722993669, 4.220336039; AK008924, -2.992421485, -1.45492969, 0.4862048, 0.330115035, 4.220336039; NM_008550, -2.989994514, -0.444946452, 0.148811796, 0.736111384, 4.220336039; NM_008084, -2.980766884, -0.500882476, 0.168038124, 0.706575992, 4.220336039; NM_008672, -2.976354448, -0.4853245, 0.163060048, 0.711936819, 4.220336039; NM_025855, -2.971869057, -0.473603756, 0.159362255, 0.71789481, 4.220336039; NM_011239, -2.96215761, -0.706149003, 0.238390085, 0.605355045, 4.220336039; NM_026419, -2.956811195, -0.45463772, 0.153759469, 0.728309482, 4.220336039; NM_009542, -2.954373409, -0.52363659, 0.177241167, 0.692862241, 4.220336039; NM_008517, -2.946671746, -0.837498036, 0.284218301, 0.546445882, 4.220336039; Z12436, -2.935075264, -0.508952354, 0.17340351, 0.699415, 4.220336039; AK017992, -2.928404732, -0.434358264, 0.148325899, 0.738605884, 4.220336039; NM_020487, -2.924415819, -0.571962881, 0.195581927, 0.669926176, 4.220336039; U39200, -2.919752728, -0.494394256, 0.169327441, 0.706599821, 4.220336039; AJ275988, -2.919720627, -0.461185157, 0.157955235, 0.72408684, 4.220336039; AK018419, -2.919573775, -0.502636223, 0.172160823, 0.704358209, 4.220336039

6.1.3 liver/kidney – over-expressed genes in *Mus spretus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); AK014677, 9.544213835, 1.384895101, 0.145103109, 2.651004308, 0; AK006372, 8.994725643, 1.047673717, 0.116476451, 2.096193673, 0; AJ231262, 8.948534742, 1.541840693, 0.172300912, 3.012156725, 0; AK019879, 8.819065942, 2.13757829, 0.242381484, 4.802294127, 0; AK016983, 8.076646504, 1.498556828, 0.185541961, 2.789078423, 0; NM_007813, 8.066912859, 1.058218472, 0.131180105, 2.081869907, 0; AK019877, 7.824983233, 2.197033824, 0.280771697, 4.427296382, 0; NM_013554, 7.413558042, 1.838720372, 0.248021309, 3.481088248, 0; AK014278, 7.282955431, 0.922751537, 0.126700149, 1.944972455, 0; NM_010164, 7.249142819, 1.513199306, 0.208741826, 2.871282052, 0; AK019946, 7.197647803, 1.323350296, 0.183858718, 2.599388684, 0; Z48496, 6.837339875, 2.576823044, 0.376875085, 9.713438514, 0; NM_011671, 6.786139414, 1.544726395, 0.227629629, 2.908789209, 0; BC004801, 6.473571122, 1.054807155, 0.162940537, 2.196760095, 0; NM_026526, 6.272960998, 0.69852472, 0.111354864, 1.619313899, 0; BC002238, 6.20507331, 1.208364518, 0.194738153, 2.393542556, 0; AK013819, 6.187361907, 0.870149717, 0.140633396, 1.838477325, 0; M35662, 6.171719331, 1.007423811, 0.163232279, 2.038506758, 0; NM_008845, 6.146220461, 1.076675874, 0.175176904, 2.157122932, 0; M33863, 6.027566308, 1.231345851, 0.204285741, 2.350319195, 0; BC007147, 5.989619236, 2.149001146, 0.358787606, 7.283454568, 0; NM_025629, 5.933213652, 1.587904201, 0.267629702, 3.749167659, 0; AK003777, 5.874312016, 1.287637425, 0.219197997, 2.526325008, 0; AK015267, 5.865211099, 0.480303649, 0.081890258, 1.396890505, 0; NM_019779, 5.858869058, 0.746530133, 0.127418812, 1.678999082, 0; AK010515, 5.846294227, 1.377994209, 0.235703876, 2.808307356, 0; X65506, 5.787422342, 1.207021525, 0.208559433, 2.542992908, 0; AK014027, 5.728796845, 0.457927915, 0.079934396, 1.372344077, 0; NM_012044, 5.714134599, 1.307726167, 0.228858131, 2.774243527, 0; AK016874, 5.667946436, 0.645912716, 0.11395886, 1.566374421, 0; AK004439, 5.531469533, 0.946456732, 0.17110403, 1.909735853, 0; BC004841, 5.494183457, 1.007322387, 0.18334342, 2.149145398, 0; NM_010100, 5.48126819, 1.273143943, 0.232271784, 2.871098877, 0; AK015173, 5.472643005, 0.755419735, 0.138035632, 1.704412614, 0; NM_011498, 5.43272317, 1.024517035, 0.188582595, 2.023162757, 0; NM_021507, 5.414373633, 0.9805145, 0.181094724, 2.068627563, 0; NM_011723, 5.338560987, 0.832354221, 0.155913592, 1.775507497, 0; BE569926, 5.31297241, 1.151645182, 0.216760994, 2.279146118, 0; AK008985, 5.146547446, 0.87234467, 0.169500948, 1.900008842, 0; AK007545, 5.144161614, 1.200821501, 0.23343386, 2.36439076, 0; D31768, 5.121263234, 1.12876793, 0.220408106, 2.165588944, 0; AK015307, 5.115511629, 0.824234736, 0.161124594, 1.860327687, 0; AF208026, 5.11443315, 0.554526885, 0.108423919, 1.487970654, 0; Z12551, 5.112683198, 0.83803324, 0.163912609, 1.812401729, 0; AK018097, 5.100055778, 0.745059289, 0.146088459, 1.69426511, 0; BC012632, 5.074173468, 1.132621695, 0.223213042, 2.317428546, 0; AF108215, 4.997993007, 1.554540597, 0.311032968, 4.092044741, 0; AK012078, 4.991697871, 0.833331803, 0.166943558, 1.782604624, 0; AK004289, 4.986420254, 0.485060185, 0.097276234, 1.398595176, 0; AK007391, 4.922384496, 1.040352031, 0.211351233, 2.284253845, 0; BC010790, 4.897006071, 0.658067266, 0.13438155, 1.571358566, 0; NM_029121, 4.861260862, 0.543762129, 0.111856192, 1.45695622, 0; AK015484, 4.854996651, 1.458405841, 0.300392759, 3.71954601, 0; AK015288, 4.845085804, 0.950536218, 0.196185631, 2.09219817, 0; AF313913, 4.721931226, 0.802295607, 0.169908363, 1.813016882, 0; NM_008422, 4.688075131, 0.852339827, 0.181810189, 1.821134962, 0; X84014, 4.683038493, 0.69860164, 0.149177001, 1.653585831, 0; NM_008917, 4.677112456, 0.794134981, 0.169791723, 1.715850463, 0; AK019023, 4.673619858, 0.797848699, 0.170713221, 1.7447159, 0; NM_007950, 4.64914136, 0.449824766, 0.096754375, 1.36604943, 0; AK006696, 4.61870826, 0.680291736, 0.147290476, 1.618262628, 0; NM_009627, 4.605626877, 0.639187395, 0.138784016, 1.60681208, 0; NM_019934, 4.600983016, 0.860083973, 0.186934829, 1.897415964, 0; AK003895, 4.597225754, 0.663002065, 0.144217861, 1.621296688, 0; AK017133, 4.58697451, 1.507627801, 0.328675862, 3.57836809, 0; NM_013498, 4.584898189, 1.010896078, 0.220483866, 2.151150974, 0; NM_025295, 4.564771432, 0.735002549, 0.161016288, 1.706327717, 0; AJ310366, 4.552266938, 0.567563933, 0.124677208, 1.476111174, 0; AK002481, 4.547177373, 0.735182585, 0.161678889, 1.709866448, 0; AK011240, 4.546639872, 0.707431547, 0.155594366, 1.670842382, 0; AK006294, 4.527500542, 0.661518525, 0.146111197, 1.584403217, 0; NM_023160, 4.515899146, 1.223791448, 0.270996187, 2.925554357, 0; NM_009707, 4.513512819, 0.579279274, 0.128343332, 1.488524158, 0; S66385, 4.501365594, 0.722418319, 0.160488701, 1.649485148, 0; NM_026630, 4.492527617, 0.590406368, 0.131419641, 1.522288969, 0; AK015069, 4.434555686, 0.708537337, 0.159776399, 1.646880179, 0; NM_010361, 4.423319014, 0.439410631, 0.099339575, 1.353463467, 0; AK019180, 4.406090629, 1.001019148, 0.227189868, 2.276052041, 0; NM_013918, 4.402883804, 0.6058783, 0.137609423, 1.548633795, 0; AK012765, 4.398850511, 0.582274921, 0.132369791, 1.543871629, 0; AK015395, 4.380987393, 0.605632121, 0.13824101, 1.576177499, 0; NM_007881, 4.377125519, 0.910451924, 0.208002243, 2.036942616, 0; BC004015, 4.36070427, 0.918050745, 0.210528091, 1.860303822, 0; AK020958, 4.354853886, 0.627511507, 0.144094733, 1.608485945, 0; NM_026292, 4.354629824, 0.648344495, 0.148886248, 1.619333108, 0; AF357397, 4.354594948, 0.717315668, 0.164726152, 1.742879765, 0; AK015520, 4.338906658, 0.61834506, 0.142511722, 1.551166888, 0; Z18958, 4.300274883, 0.551429046, 0.128231116, 1.47360804, 0; AK010499, 4.299373154, 0.615738841, 0.143215957, 1.544836179, 0; NM_026535, 4.29442577, 1.35132845, 0.314670348, 2.503654309, 0; NM_026596, 4.282640465, 0.866976639, 0.202439744, 1.861396362, 0; Z86026, 4.276016472, 0.435342963, 0.101810404, 1.349203813, 0; AK013334, 4.27190162, 0.896217576, 0.20979359, 1.876361354, 0; AF154337, 4.263896924, 0.789307536, 0.185114122, 1.836422296, 0; NM_013646, 4.261533943, 1.109201561, 0.260282231, 2.178066714, 0; NM_009357, 4.248805765, 1.824873039, 0.42950258, 3.453660085, 0; NM_007692, 4.211703691, 0.800125512, 0.189976687, 1.733153478, 0; AK015195, 4.211397679, 0.904949801, 0.214881108, 2.009915089, 0; NM_008906, 4.207023347, 0.811591822, 0.192913553, 1.915652116, 0; NM_009324, 4.184335218, 0.6250243, 0.149372425, 1.571227765, 0; AK021041, 4.179154835, 1.475835932, 0.3531422, 4.459409174, 0; NM_007905, 4.17740177, 0.686804064, 0.164409387, 1.596476944, 0; AB046714, 4.155518228, 0.698742599, 0.168148125, 1.655156681, 0; AK012790, 4.128891505, 0.479125931, 0.116042267, 1.393070247, 0; AL358753, 4.112035884, 1.191382873, 0.28973066, 2.725993504, 0; NM_013581, 4.110631428, 0.723989757, 0.176126167, 1.68693908, 0; NM_026639, 4.102818434, 0.540668604, 0.131779803, 1.449234929, 0; AK021000, 4.102543296, 0.437156846, 0.106557522, 1.372664313, 0; AF052218, 4.101051879, 0.847287584, 0.206602503, 1.912639061, 0; AK021335, 4.097345261, 0.433635693, 0.10583333, 1.358456581, 0; AK008891, 4.082825108, 0.891074464, 0.218249482, 1.886042387, 0; NM_026096, 4.07681073, 0.962311744, 0.236045234, 2.019845167, 0; NM_013908, 4.064495174, 0.985236981, 0.242400824, 2.12769936, 0; AK017487, 4.062738203, 0.824141612, 0.202853733, 1.880408925, 0; AF037256, 4.045324081, 0.522402232, 0.129137301, 1.445481238, 0; NM_009362, 4.04124048, 0.495944494, 0.122720857, 1.428883548, 0; AK012977, 4.022932366, 0.470736965, 0.117013393, 1.400930388, 0; AK020337, 4.018524189, 0.475698834, 0.118376501, 1.400312751, 0; AK017384, 4.011659003, 0.570892944, 0.142308442, 1.543610177, 0; AF288525, 4.004781112, 1.37057715, 0.342235221, 3.877186973, 0; S74567, 4.002132826, 0.526574163, 0.131573385, 1.447515229, 0; M29395, 3.999788079, 1.066437984, 0.266623622, 2.087569415, 0; U55178, 3.998694768, 0.570813243, 0.142749891, 1.553878603, 0; AK007234, 3.995949335, 0.909808606, 0.227682718, 1.83711378, 0; NM_017395, 3.982939003, 1.03445285, 0.259720987, 1.976048092, 0; NM_019422, 3.973822179, 0.799445516, 0.201177979, 1.768884321, 0; NM_009569, 3.966448918, 0.765570959, 0.193011677, 1.677761189, 0; 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6.1.4 liver/kidney – over-expressed genes in *Mus musculus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); AK020589, -6.749294668, -0.626225083, 0.092783782, 0.649188938, 0; Z83811, -5.82881524, -1.227993462, 0.21067634, 0.442368574, 0; M14872, -5.606062291, -0.653454715, 0.116562157, 0.640927297, 0; NM_026925, -5.325402475, -0.896702363, 0.168382083, 0.538836623, 0; AK004353, -5.290327926, -1.089497478, 0.205941388, 0.475099725, 0; U96693, -5.127216549, -0.6381456, 0.124462385, 0.641183932, 0.391171002; AK008926, -4.986468039, -0.938286249, 0.188166502, 0.513129738, 0.391171002; AK006211, -4.826701539, -0.622104807, 0.128888186, 0.665325206, 0.391171002; NM_008190, -4.795368123, -1.189527571, 0.248057613, 0.466493043, 0.391171002; AK005379, -4.785084796, -0.703438205, 0.147006424, 0.614038236, 0.391171002; U15218, -4.768426215, -0.437233474, 0.091693455, 0.738011257, 0.391171002; Z71173, -4.69375483, -0.708890159, 0.151028374, 0.637776945, 0.391171002; Z47773, -4.690390297, -0.812763604, 0.173282723, 0.583929456, 0.391171002; 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6.1.5 testis – over-expressed genes in *Mus spretus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); NM_021519, 12.03999077, 2.890909381, 0.240108937, 8.187387967, 0; AK016105, 11.73000905, 1.677600866, 0.143017866, 3.210848582, 0; NM_026064, 11.6351813, 2.622618566, 0.225404186, 6.146448388, 0; AK012336, 10.34202258, 1.645632842, 0.159120987, 3.15561486, 0; NM_024251, 9.760911736, 1.813026124, 0.185743522, 3.621725514, 0; AK021406, 9.359235396, 1.767548949, 0.188856127, 3.513360574, 0; AK019066, 9.203559121, 1.428736488, 0.155237389, 2.702531678, 0; NM_013560, 8.924846835, 1.309489917, 0.146724077, 2.485402136, 0; NM_011134, 8.780725102, 1.527031327, 0.173907201, 2.884509085, 0; AB048527, 8.638126448, 1.30912591, 0.151552066, 2.475174035, 0; AK016242, 8.402369045, 1.474300625, 0.175462494, 2.806749541, 0; NM_008753, 8.296157641, 1.133690132, 0.136652434, 2.193682659, 0; AJ288061, 8.280421955, 1.17606852, 0.142030023, 2.265481175, 0; Z12278, 8.263501985, 1.47694505, 0.17873113, 2.883663171, 0; NM_007603, 8.100179831, 1.033619159, 0.127604471, 2.044732405, 0; 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6.1.6 testis – over-expressed genes in *Mus musculus*

Gene Name, Score(d), Numerator(r), Denominator(s+s0), Fold Change, q-value(%); AK006746, -6.153092545, -1.230703499, 0.200013813, 0.426292755, 0; AK009987, -5.095253813, -0.80914661, 0.158803985, 0.575210492, 0; AK013028, -4.871674498, -0.736714419, 0.151224065, 0.605960286, 0; AK005637, -4.780064288, -0.873191368, 0.182673562, 0.549116302, 0; X83919, -4.652951609, -0.778410554, 0.167293929, 0.583702349, 0; AK003459, -4.648636445, -0.582196107, 0.125240189, 0.668460881, 0; AK020854, -4.628733658, -0.819197139, 0.176980833, 0.570471421, 0; NM_008813, -4.593451585, -0.808187945, 0.175943499, 0.569621509, 0; AK013199, -4.53849942, -0.946963372, 0.208651205, 0.512863751, 0; AF305427, -4.467023598, -1.021275006, 0.228625389, 0.488127234, 0; NM_025675, -4.411433294, -0.646003397, 0.146438437, 0.645152363, 0; AK011396, -4.274738862, -0.802865728, 0.187816321, 0.576633828, 0; AF060873, -4.217899352, -0.91785364, 0.217609185, 0.53227231, 0; AK016161, -4.174577927, -0.619950836, 0.148506232, 0.657823446, 0; 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6.2 Differentially expressed genes across subspecies of *Mus musculus* (SAM multiclass analysis, 200 permutations, FDR < 5%)

6.2.1 differentially expressed genes across subspecies of *Mus musculus* in the brain

Gene Name, Score(d), Numerator(r), Denominator(s+s0), contrast-1, contrast-2, contrast-3, contrast-4, q-value(%); AK018205, 1.010956201, 0.302859881, 0.299577648, -0.400573309, 2.690316915, -1.309743383, -1.960000446, 0; AK020118, 0.904670064, 0.680833344, 0.752576404, -1.688442675, 0.090190569, 1.617690072, -0.038875932, 0; AF351196, 0.903566751, 0.476828252, 0.527717793, 2.099670089, -0.781346711, -0.917628476, -0.801389804, 0; AK009887, 0.875589455, 0.232295246, 0.265301558, -1.303845177, 2.491083099, -1.192625819, 0.010775793, 0; U16277, 0.867255251, 0.228756193, 0.263770318, 2.061530978, -2.158450167, 0.377426554, -0.561014729, 0; M94300, 0.841878038, 0.301710867, 0.358378355, -1.717724413, -0.492613788, 1.723884844, 0.972906714, 0; AK015229, 0.836596004, 0.233320037, 0.278892125, -0.035645924, 0.855898356, 0.970135079, -3.580775022, 0; AK019653, 0.820495955, 0.206433131, 0.25159555, -1.925269504, 2.20154218, -0.012069115, -0.528407123, 0; NM_007668, 0.814786617, 0.185879181, 0.228132344, -2.268132097, 0.429166205, 2.06687761, -0.455823435, 0; 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U96701, 0.56696774, 0.22493003, 0.396724565, -1.100229418, 1.226726393, -0.258650881, 0.264307811, 4.899120614; AK014697, 0.566672967, 0.144437679, 0.254887188, -1.25330455, 0.860839744, 1.007786614, -1.230643616, 4.899120614; NM_026243, 0.566619855, 0.142099226, 0.250784058, 0.030270087, 0.690243789, 0.574503901, -2.590035554, 4.899120614; NM_025991, 0.566532259, 0.164968133, 0.291189301, 1.06754881, -1.511138608, 0.323302525, 0.240574545, 4.899120614; NM_007805, 0.566276804, 0.152015148, 0.268446715, 1.13978148, -1.478756433, 0.537125131, -0.396300358, 4.899120614; AJ279835, 0.566023131, 0.203289122, 0.359153382, 1.028655037, -1.28456804, 0.455974123, -0.400122241, 4.899120614; AK014729, 0.565880844, 0.124895883, 0.220710569, 0.097194572, -0.689789951, -0.786070071, 2.7573309, 4.899120614; NM_011305, 0.565825348, 0.153312044, 0.270952944, 0.579863082, -0.449482062, 0.955475624, -2.171713289, 4.899120614; AK007639, 0.565329171, 0.208896151, 0.36951242, 1.358595445, -0.511236582, -0.225550604, -1.243616518, 4.899120614; AK014547, 0.565220916, 0.191905867, 0.339523648, 1.112642052, -1.354570223, 0.162308691, 0.159238961, 4.899120614; S69333, 0.565135533, 0.152416741, 0.269699448, 0.023751261, -0.087974158, 1.169390432, -2.21033507, 4.899120614; AK006733, 0.565000244, 0.123571475, 0.218710481, -1.208218355, 1.003834691, -0.769204353, 1.947176032, 4.899120614; AK014629, 0.56399634, 0.124197068, 0.220208996, 0.444879972, 0.363287944, 0.633514694, -2.88336522, 4.899120614; U25100, 0.563995557, 0.131695906, 0.233505219, -1.062809021, -0.682903817, 1.705055933, 0.08131381, 4.899120614; NM_025722, 0.563919196, 0.151598014, 0.26882932, -0.219168688, 1.556669657, -1.116193198, -0.442615542, 4.899120614; NM_021893, 0.563487179, 0.161519117, 0.286642045, -0.294208736, 0.103889414, 1.199237267, -2.01783589, 4.899120614; AK003705, 0.563479301, 0.12747975, 0.226236794, 0.972463834, 0.441027397, -1.803132641, 0.77928282, 4.899120614; AY042211, 0.56337568, 0.126409258, 0.224378266, 0.667480402, -0.29709321, 0.925352327, -2.591479037, 4.899120614; BC014869, 0.563293101, 0.172818845, 0.306800927, -0.787971618, 1.481376114, -0.19235581, -1.002097372, 4.899120614; NM_023557, 0.563198362, 0.227986566, 0.404806871, -1.197832865, 0.04095698, 1.144319239, 0.025113293, 4.899120614; NM_008084, 0.563030972, 0.219288509, 0.389478591, 0.663503281, 0.433671282, -0.053410294, -2.087528538, 4.899120614; NM_025556, 0.562930574, 0.123276076, 0.21898984, 0.926795467, -1.837749995, 0.807240088, 0.20742888, 4.899120614; AK015743, 0.562704537, 0.176053001, 0.312869347, 0.874208611, -0.971734006, 0.790045061, -1.385039332, 4.899120614; D32210, 0.562606594, 0.160405259, 0.285110875, -0.525159545, -0.216928533, 1.475983344, -1.46779053, 4.899120614; AA543920, 0.562353043, 0.179029596, 0.318358011, 1.296655252, -1.109346531, 0.19402157, -0.762660584, 4.899120614; NM_025456, 0.562312988, 0.135462124, 0.240901646, -1.720329391, 0.378626458, 0.907168818, 0.869068231, 4.899120614; AK008047, 0.56154194, 0.161702208, 0.287961053, -0.748349278, -0.861918885, 1.481619986, 0.257296353, 4.899120614

6.2.2 differentially expressed genes across subspecies of *Mus musculus* in the liver/kidney

Gene Name, Score(d), Numerator(r), Denominator(s+s0), contrast-1, contrast-2, contrast-3, contrast-4, q-value(%); AK018205, 2.592868316, 0.538142783, 0.207547286, -3.071685133, 6.219159166, -2.103214848, -2.088518371, 0; AK012039, 1.735038109, 0.477789923, 0.275377192, -2.960070994, 3.270662517, -1.05105033, 1.480917614, 0; NM_007959, 1.608558352, 0.361237802, 0.224572395, -1.235539956, 3.671626845, -2.281101401, -0.309970975, 0; U94828, 1.586134766, 0.393953586, 0.248373338, 1.008323122, -3.597025896, 1.351191117, 2.475023315, 0; AK020118, 1.568346046, 1.05163093, 0.670535009, -3.156388849, 1.757873427, 1.080826895, 0.635377054, 0; NM_011547, 1.535848526, 0.382501831, 0.24904919, -2.3396311, 3.379485467, -0.589117283, -0.901474169, 0; NM_010151, 1.533284197, 0.312341053, 0.203707214, -2.184229966, -1.354759582, 1.152969231, 4.772040635, 0; NM_010441, 1.480569683, 0.371638004, 0.25101014, 3.367387893, -1.1130968, -1.859594115, -0.789393954, 0; BC005734, 1.464843914, 0.338244823, 0.23090844, 3.134666051, -0.210655753, -1.367214413, -3.113591769, 0; NM_031163, 1.444176227, 0.325314598, 0.225259627, -1.663159188, 3.346017101, -0.731766267, -1.902183291, 0; AK021399, 1.435936398, 0.636169342, 0.443034484, -2.182212748, 2.818549138, -0.398991323, -0.474690134, 0; NM_018737, 1.405860762, 0.372546131, 0.264995042, -3.067329738, 2.078209934, 0.785128484, 0.407982641, 0; AK015330, 1.400236678, 0.246724003, 0.176201643, -2.75401465, 3.137962661, -0.26442511, -0.239045803, 0; NM_008035, 1.389299099, 0.2452266, 0.176511019, -3.220215469, 0.17855158, 1.555768079, 2.97179162, 0; NM_011671, 1.386030806, 0.23156388, 0.167069793, 3.498083872, -1.500701604, -0.869104148, -2.256556238, 0; BF138866, 1.380978325, 0.334494676, 0.242215732, -3.008053666, 2.11890544, 0.944274491, -0.110252529, 0; AK008666, 1.375600125, 0.238674803, 0.173505948, -2.002739712, 3.424444466, -0.972839743, -0.897730021, 0; NM_008099, 1.355733387, 0.297344548, 0.219323763, 2.763923045, -0.037724589, -2.625333428, -0.201730055, 0; AK003605, 1.319309601, 0.413950286, 0.313762808, 1.248361454, -2.638213518, 1.778164933, -0.776625739, 0; AK014461, 1.315758967, 0.303644418, 0.230775108, -2.700167423, -0.212399412, 1.579018043, 2.667097585, 0; NM_010735, 1.3130416, 0.259726869, 0.197805514, -1.132407037, -2.296327546, 2.315767636, 2.225933892, 0; NM_023268, 1.305157843, 0.279827884, 0.214401565, -2.707747096, 0.272680787, 0.751799994, 3.366532631, 0; U20780, 1.301800926, 0.30931118, 0.23760252, -1.291491636, -1.988819818, 1.97249764, 2.615627629, 0; AK017021, 1.292697641, 0.336663301, 0.260434684, -1.443085881, 2.927497916, -1.219422216, -0.529979639, 0; AK017339, 1.291041157, 0.270329494, 0.20938875, 3.062189548, -1.166986473, -1.615177555, -0.560051039, 0; AK021134, 1.285682856, 0.253354709, 0.197058479, -0.606984146, -2.583031134, 2.171817237, 2.036396087, 0; AK017352, 1.275283296, 0.249774011, 0.195857667, -2.871035273, 0.065038926, 2.100027145, 1.411938405, 0; U49507, 1.254924729, 0.240418113, 0.191579708, -2.549808052, 2.474535367, 0.552968249, -0.95539113, 0; NM_013925, 1.246799453, 0.21478762, 0.172271185, -2.530614349, -0.386150994, 1.153311849, 3.526906988, 0; 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AB016586, 0.611171939, 0.067369476, 0.110229989, -0.437606521, 1.793159954, -1.297898089, -0.115310688, 4.83695212; AF218416, 0.611089032, 0.107424468, 0.175791845, 1.294041754, 0.23542608, -0.885181168, -1.288573332, 4.83695212; AK009349, 0.610936154, 0.117252233, 0.191922237, -0.447081154, -1.123549722, 0.902503946, 1.336253861, 4.83695212; NM_025718, 0.610686901, 0.191688417, 0.313889845, -1.132546595, 1.108329857, 0.15217101, -0.255908544, 4.83695212; AK008250, 0.610666166, 0.156008, 0.255471825, -1.325754493, 0.381703859, 0.925942167, 0.036216932, 4.83695212; X53484, 0.610639831, 0.212858313, 0.348582424, -1.111069545, -0.229889107, 0.920742426, 0.840432451, 4.83695212; M13051, 0.610212662, 0.237912232, 0.389884128, 0.721549359, -1.168109976, -0.065187591, 1.023496415, 4.83695212; AK020434, 0.609932096, 0.10730555, 0.175930323, -1.422777592, 0.023949762, 0.928352796, 0.940950067, 4.83695212; AY029253, 0.609458547, 0.151634922, 0.248802684, 0.890066406, 0.295119228, -0.223144053, -1.924083163, 4.83695212; AK009199, 0.609275641, 0.260337934, 0.427290894, -0.894344114, 0.98201069, 0.383373126, -0.942079403, 4.83695212; BC004760, 0.609224465, 0.122822883, 0.201605303, 0.442347788, 0.761938623, -0.138484973, -2.131602877, 4.83695212; AK020559, 0.6091498, 0.150121076, 0.24644361, -0.947919151, 0.930161456, -0.572508552, 1.180532492, 4.83695212; Y17856, 0.60902103, 0.165942853, 0.27247475, -0.084969884, 0.483532489, 0.616012803, -2.029150817, 4.83695212; NM_026811, 0.609005437, 0.093315132, 0.153225449, 0.839610916, 0.43637879, -0.1031714, -2.345636614, 4.83695212; AK014755, 0.609005277, 0.144091586, 0.236601539, -0.36320883, -0.107349672, -0.607345946, 2.155808895, 4.83695212; AK006641, 0.608897078, 0.078344847, 0.128666813, 0.036794924, -1.568990506, 1.29825118, 0.467888803, 4.83695212; NM_023707, 0.608806807, 0.09984318, 0.163998134, -0.823564966, 0.712867646, 0.945982637, -1.670570633, 4.83695212; AK019904, 0.608576576, 0.087857154, 0.144364995, -0.925326375, 0.881060625, -0.826215875, 1.740963249, 4.83695212; NM_019392, 0.608472986, 0.077660475, 0.127631755, 1.325651693, -0.979405626, 0.473882123, -1.640256381, 4.83695212; NM_033321, 0.608438143, 0.100774752, 0.16562859, 1.529871115, -0.478549645, -0.483082418, -1.136478104, 4.83695212; NM_008832, 0.608414226, 0.092864118, 0.152633048, -0.556929215, -1.117175887, 1.395460915, 0.557288374, 4.83695212; AK002612, 0.608225865, 0.139467868, 0.229302758, 1.300696277, 0.008594867, -0.979356601, -0.659869086, 4.83695212; NM_018797, 0.608004173, 0.117144999, 0.192671374, -1.089589475, 0.335750456, -0.193493531, 1.894665101, 4.83695212; NM_019389, 0.607929464, 0.122858034, 0.20209258, 1.110611812, -0.092061972, -0.068913519, -1.899272642, 4.83695212; NM_024283, 0.607657068, 0.16828716, 0.276944298, -0.516472198, -0.581375258, 0.088181707, 2.019331498, 4.83695212; NM_013715, 0.607629967, 0.109506069, 0.180218348, -0.456025135, -0.685149358, 0.005993554, 2.270361878, 4.83695212; NM_009570, 0.607222771, 0.135463651, 0.223087239, -0.017318082, -1.094557921, 0.201678678, 1.820394652, 4.83695212; U64446, 0.607188097, 0.089986612, 0.1482022, -0.905551868, 1.527810225, -0.088475105, -1.067566504, 4.83695212; AK017634, 0.6067839, 0.168105885, 0.277044076, 0.670242854, 0.23306919, 0.1271474, -2.060918888, 4.83695212

6.2.3 differentially expressed genes across subspecies of *Mus musculus* in the testis

Gene Name, Score(d), Numerator(r), Denominator(s+s0), contrast-1, contrast-2, contrast-3, contrast-4, q-value(%); NM_008579, 1.298407818, 0.342981975, 0.264155815, -1.192318718, -1.58083185, 0.982351964, 3.581597209, 0; NM_019425, 1.260685826, 0.147705487, 0.117162805, 1.323102706, 1.932827793, -1.137994138, -4.235872721, 0; NM_018786, 1.24413238, 0.234125609, 0.18818384, -1.636872879, -1.459350193, 1.667984295, 2.856477556, 0; L10901, 1.072174444, 0.170239048, 0.158779244, -2.371114709, 0.01494058, 1.425952156, 1.860443946, 0; AK015913, 1.023977108, 0.248393586, 0.242577284, -2.115009704, 0.14760793, 1.521985557, 0.890832433, 0; NM_027356, 0.99937393, 0.24230448, 0.242456275, -1.657803659, -0.084923805, 0.327777649, 2.829899629, 0; AK014388, 0.967310556, 0.126191432, 0.130455965, 1.665843336, 0.780658775, -0.996704047, -2.899596127, 0; D29987, 0.956841872, 0.128675811, 0.134479703, 0.846995473, 1.679120534, -1.301149658, -2.449932698, 0; AK011893, 0.942120116, 0.218873827, 0.232320511, -0.830259078, -1.323231117, 0.968413664, 2.370153063, 0; NM_010659, 0.937206249, 0.086785543, 0.092600261, -2.344780195, -0.301608196, 2.197008756, 0.898759269, 0; AK004276, 0.932567722, 0.09784811, 0.104923329, -0.50576198, 2.223556868, -2.018878542, 0.602167309, 0; NM_011660, 0.927769686, 0.107674075, 0.116056902, 1.260134437, -2.130240704, 1.389258083, -1.038303633, 4.063788649; AK002997, 0.921617064, 0.251024543, 0.272374018, 1.143736247, 0.923988157, -0.919333876, -2.296781057, 4.063788649; AK006132, 0.919742293, 0.288253368, 0.313406669, -1.110446853, -0.969026676, 1.03475584, 2.089435378, 4.063788649; NM_025393, 0.911013203, 0.169270366, 0.185804515, -

0.991656192, -1.248742475, 1.127199888, 2.226397556, 4.063788649; NM_009529, 0.908210484, 0.21811286, 0.24015673, -1.953905256, 0.33613489, 1.144127407, 0.947285919, 4.063788649; AK019195, 0.907497936, 0.177896038, 0.196029137, 0.903314987, 1.179339487, -0.808872433, -2.547564082, 4.063788649; NM_021437, 0.90145624, 0.16901334, 0.187489234, 1.452635258, -0.400689373, 0.319872626, -2.743637023, 4.063788649; AK014502, 0.889744695, 0.16216854, 0.182264127, 1.312217105, 0.897915425, -1.175088815, -2.070087429, 4.063788649; AF052218, 0.889038483, 0.207210685, 0.233072796, 0.923237639, -0.696800406, 1.022563294, -2.498001054, 4.063788649; BC011413, 0.886691255, 0.1139545, 0.128516549, -1.061367645, -1.338138492, 2.019543016, 0.759926241, 4.063788649; AB037665, 0.87388068, 0.277358796, 0.31738749, -0.824227349, -1.177740102, 1.114460599, 1.775013705, 4.063788649; NM_008701, 0.867926817, 0.08153245, 0.093939315, 2.516518557, -0.993057381, -0.715810795, -1.615300761, 4.063788649

6.3 Functional categories within the lists of differentially expressed genes (SAM, 200 permutations, FDR < 5%) identified by the DAVID software

6.3.1 Categories of functional classification for genes differentially expressed in the brain between species

Functional Group 1 ,protein catabolism,; 1,NM_026419,"elastase 3B, pancreatic"; 2,NM_020487,"protease, serine, 32"; 3,NM_008281,hepsin; 4,NM_008517,leukotriene A4 hydrolase; 5,Z12264 ,RIKEN cDNA 1810049H19 gene; 6,AK010546 ,ubiquitin specific protease 46; ; Functional Group 2 ,protein biosynthesis,; 1,U58337 ,ligatin; 2,AF068116 ,eukaryotic translation initiation factor 4E member 2; 3,NM_011295 ,ribosomal protein S12; 4,NM_016738 ,ribosomal protein L13; 5,NM_025592 ,ribosomal protein L35; 6,NM_011664 ,ribosomal protein S27a; ; Functional Group 3,cytoskeleton,; 1,M13446 ,"tubulin, alpha 1"; 2,AK004235 ,"dynein, cytoplasmic, light intermediate chain 1"; 3,M13446 ,Alpha-tubulin 1; 4,M13446 ,"tubulin, alpha, ubiquitous"; 5,M13446 ,Alpha-tubulin 1; 6,M13446 ,Alpha-tubulin 1; 7,M13446 ,"tubulin, alpha 2"; 8,NM_010301 ,"guanine nucleotide binding protein, alpha 11"; 9,BC006581 ,"tubulin, gamma 1"; ; Functional Group 4,"regulation of transcription, transcription factors",; 1,NM_008275,homeo box D13; 2,NM_016767,"basic leucine zipper transcription factor, ATF-like"; 3,NM_011441,SRY-box containing gene 17; 4,AJ275988,trans-acting transcription factor 6; 5,AK012264,"nuclear receptor subfamily 1, group I, member 3"; 6,NM_009324,T-box 2; 7,NM_007441,aristaless 3; 8,NM_019512,transcription elongation regulator 1 (CA150); 9,NM_011544,transcription factor 12; 10,NM_016861,PDZ and LIM domain 1 (elfin); 11,NM_008275,homeo box D13; 12,AK017992,Wolf-Hirschhorn syndrome candidate 1 (human); 13,NM_013554,homeo box D10; 14,AB010343,Mszf85; 15,NM_013920,"hepatocyte nuclear factor 4, gamma"; 16,NM_030251,ankyrin repeat and BTB (POZ) domain containing 1; 17,NM_009542,zinc finger protein 101; ; Functional Group 5,ion channel activity,; 1,AK003969 ,"transient receptor potential cation channel, subfamily M, member 4"; 2,AK004093 ,"sodium channel, voltage-gated, type VI, alpha polypeptide"; 3,AK017384 ,potassium channel tetramerisation domain containing 6; 4,NM_011387 ,"solute carrier family 10 (sodium/bile acid cotransporter family), member 1"

6.3.2 Categories of functional classification for genes differentially expressed in the brain between subspecies

protein catabolism,; NM_029636 ,cathepsin Q; AK012039 ,a disintegrin-like and metalloprotease (reprolysin type) wit ...; BC006869 ,RIKEN cDNA 2400006A19 gene; NM_011855 ,odd Oz/ten-m homolog 1 (Drosophila); NM_010060 ,"dynein, axonemal, heavy chain 11"; ; protein biosynthesis,; NM_009095 ,ribosomal protein S5; BC005709 ,PET112-like (yeast); AJ279835 ,laminin receptor 1 (ribosomal protein SA); NM_011692 ,von Hippel-Lindau binding protein 1; BC006938 ,"phosphatidylinositol glycan, classC"; AK012351 ,glutaminyl-tRNA synthase (glutamine-hydrolyzing)-like 1; NM_025437 ,"eukaryotic translation initiation factor 1A, Y-linked"; AK006554 ,RIKEN cDNA 1700030K01 gene; NM_013647 ,ribosomal protein S16; ; protein kinase activity,; NM_007668 ,cyclin-dependent kinase 5; AK019023 ,RIKEN cDNA 1810024B03 gene; AK008047 ,"protein kinase, lysine deficient 4"; AK009506 ,calcium/calmodulin-dependent protein kinase IV; NM_007668 ,cyclin-dependent kinase 5; NM_011062 ,3-phosphoinositide dependent protein kinase-1; ; "regulation of transcription, transcription factors",; NM_010635,Kruppel-like factor 1 (erythroid); NM_011762,zinc finger protein 59; NM_016861,PDZ and LIM domain 1 (elfin); NM_011305,retinoid X receptor alpha; NM_008273,homeo box D11; X66902,zinc finger protein 462; AK016708,"zinc finger, X-linked, duplicated A"; AK017487,bobby sox homolog (Drosophila); NM_008759,OG9 homeobox gene; BF580261,cAMP responsive element binding protein 3-like 1; AK004386,cDNA sequence BC031407; AK016252,goosecoid-like; AK016252,RIKEN cDNA 4930568H22 gene; BF577415,RIKEN cDNA C330002I19 gene; NM_023816,RIKEN cDNA 1700012M14 gene; NM_011762,zinc finger protein 60; NM_010134,engrailed 2; AF370121,odd-skipped related 2 (Drosophila); NM_007792,cysteine and glycine-rich protein 2; AK009322,"TAF9 RNA polymerase II, TATA box binding protein (TBP)-associated factor"; NM_010441,high mobility group AT-hook 2; AK019761,GLIS family zinc finger 1; NM_010812,forkhead box K1; NM_010710,LIM homeobox protein 2; ; G-protein-coupled receptors (GPCRs),; NM_008041 ,"formyl peptide receptor, related sequence 4"; AY042211 ,"MAS-related GPR, member F"; AF394596 ,hypocretin (orexin) receptor 1; AK018844 ,leucine-rich repeat-containing G protein-coupled receptor 8; NM_007762 ,corticotropin releasing hormone receptor 1; NM_029565 ,open reading frame 18; NM_019485 ,olfactory receptor 70; NM_008058 ,frizzled homolog 8 (Drosophila); ; cytoskeleton,2%; NM_019767,"actin related protein 2/3 complex, subunit 1A"; NM_009798,"capping protein (actin filament) muscle Z-line, beta"; NM_019813,drebrin 1; NM_021278,"thymosin, beta 4, X chromosome"; ; defense response,3%; AK017898 ,"T-cell receptor beta, joining region"; U03067 ,defensin related cryptdin 14; U03067 ,defensin related cryptdin 2; U21409 ,"T-cell receptor alpha, joining region"; AF012191 ,T-cell receptor alpha chain; NM_030006 ,RIKEN cDNA A030005L19 gene; U03067 ,defensin related cryptdin 2

6.3.3 Categories of functional classification for genes differentially expressed in the liver/kidney between species

"mRNA processing, RNA binding, metabolism",, ; NM_008956,polypyrimidine tract binding protein 1,; NM_018813,cleavage and polyadenylation specificity factor 3, ; NM_026175,"splicing factor 3a, subunit 1", ; NM_019402,"poly(A) binding protein, nuclear 1", ; BC006805,heterogeneous nuclear ribonucleoprotein L-like , ; ; "mRNA processing, splicing, metabolism", ,; NM_008956,polypyrimidine tract binding protein 1,; NM_018813,cleavage and polyadenylation specificity factor 3, ; NM_025520,"LSM5 homolog, U6 small nuclear RNA associated (S. cerevisiae)", ; NM_026175,"splicing factor 3a, subunit 1", ; X65704,small nuclear ribonucleoprotein E, ; BF168044,"mago-nashi homolog, proliferation-associated (Drosophila)", ; X65704,small nuclear ribonucleoprotein polypeptide E, ; X65704,SmE protein,; ; "ribosome biogenesis, rRNA metabolism", ,; AK013334,"DNA segment, Chr 1, Wayne State University 40, expressed",; AK011648,RIKEN cDNA 2610033H07 gene, ; AK021029,EBNA1 binding protein 2, ; AK006281,exosome component 3, ; NM_026031,RIKEN cDNA 2700082D03 gene, ; BC012277,exosome component 4, ; ; "Glycoprotein, monosaccharide binding", ,; BE285667,basigin,; NM_007425,advanced glycosylation end product-specific receptor, ; BF581574,glycoprotein A33 (transmembrane), ; BE285667,basigin, ; NM_008728,natriuretic peptide receptor 3, ; NM_031254,triggering receptor expressed on myeloid cells 2, ; ; "G-protein coupled receptor activity, Lipoprotein, Glycoprotein", ,; AY042192,"MAS-related GPR, member A2",; NM_009102,retinal pigment epithelium derived rhodopsin homolog, ; AK020548, RIKEN cDNA 0610010I15 gene, ; NM_019475,olfactory receptor 157, ; NM_009218,somatostatin receptor 3, ; X89680,olfactory receptor 30, ; AF200349,G protein-coupled receptor 35, ; NM_008286,histamine receptor H 2, ; NM_008728,natriuretic peptide receptor 3, ; AK013598,G protein-coupled receptor 85, ; AF133093,arginine vasopressin receptor 2, ; AF331658,cysteinyl leukotriene receptor 2, ; AL133159,Novel 7 transmembrane receptor (Rhodopsin family) (Olfactory ..., ; NM_007419,"adrenergic receptor, beta 1", ; U05671,adenosine A1 receptor, ; NM_008154,G-protein coupled receptor 3, ; NM_007699,"cholinergic receptor, muscarinic 4", ; AF102528,olfactory receptor 52, ; AL133159,olfactory receptor 108, ; AF321235,olfactory receptor 708, ; AK021124,dopamine receptor D1A, ; NM_008330,olfactory receptor 56, ; AL133159,Novel 7 transmembrane receptor (Rhodopsin family),

; AL133159,olfactory receptor 102, ; AF321235,B6 olfactory receptor, ; AF321235,B4 olfactory receptor, ; NM_007901,endothelial differentiation sphingolipid G-protein-coupled receptor 1, ; D26157,prostaglandin I receptor (IP), ; AF102539,olfactory receptor 60, ; AL133159,olfactory receptor 107, ; AK020337,G protein-coupled receptor 45, ; NM_008311,5-hydroxytryptamine (serotonin) receptor 2B, ; AL133159,Novel 7 transmembrane receptor (Rhodopsin family) (Olfactory ..., ; NM_007416,"adrenergic receptor, alpha 1b", ; AL133159,olfactory receptor 101, ; NM_007699,"cholinergic receptor, muscarinic 4", ; NM_008285,histamine receptor H 1, ; AL133159,olfactory receptor 103, ; AF282282,olfactory receptor 876, ; AF282294,olfactory receptor 948, ; NM_007416,"adrenergic receptor, alpha 1b", ; ; "regulation of transcription, regulation of metabolism", ,; S74567,Transcription factor Maf,; U67885,transformation related protein 53 binding protein 1, ; S74567,avian musculoaponeurotic fibrosarcoma (v-maf) AS42 oncogene homolog, ; AK005588,RIKEN cDNA 1700001F22 gene, ; NM_017395,"regulatory factor X, 5 (influences HLA class II expression)", ; NM_016707,B-cell CLL/lymphoma 11A (zinc finger protein), ; L08074,"NK6 transcription factor related, locus 2 (Drosophila)", ; X51959,"POU domain, class 4, transcription factor 1", ; AJ276456,Doublesex-related protein Dmrt2, ; NM_013646,RAR-related orphan receptor alpha, ; X51959,"POU domain, class 4, transcription factor 1", ; AF312858,myeloid/lymphoid or mixed lineage-leukemia translocation to 1 homolog (Drosophila), ; D87966,TEA domain family member 4, ; NM_010402,heart and neural crest derivatives expressed transcript 2, ; NM_009769,Kruppel-like factor 5, ; NM_009234,SRY-box containing gene 11, ; NM_018812,protein inhibitor of activated STAT 3, ; NM_007498,activating transcription factor 3, ; NM_013646,RAR-related orphan receptor alpha, ; AK014657,CBFA2T1 identified gene homolog (human), ; NM_021501,"protein inhibitor of activated STAT, 4", ; NM_016974,D site albumin promoter binding protein, ; M36516,zinc finger protein 28, ; NM_013554,homeo box D10, ; NM_013498,cAMP responsive element modulator, ; AK006780,basic transcription factor 3, ; X61753,heat shock factor 1, ; X56570,"retinoic acid receptor, alpha", ; AK014800,RIKEN cDNA 4921501E09 gene, ; BC005647,"bromodomain and PHD finger containing, 1", ; S74567,avian musculoaponeurotic fibrosarcoma (v-maf) AS42 oncogene homolog, ; U34361,lymphoid nuclear protein related to AF4, ; AK020111,lymphoid enhancer binding factor 1, ; NM_008453,Kruppel-like factor 3 (basic), ; NM_009542,zinc finger protein 101, ; NM_010446,forkhead box A2, ; AJ278340,zinc finger protein 296, ; NM_008686,"nuclear factor, erythroid derived 2,-like 1", ; BC004062,"cofactor required for Sp1 transcriptional activation, subunit 6", ; NM_013646,RAR-related orphan receptor alpha, ; NM_008636,metal response element binding transcription factor 1, ; NM_013646,RAR-related orphan receptor alpha, ; AJ278435,zinc finger protein 143, ; AK017963,high mobility group 20A, ; NM_018823,nuclear factor of activated T-cells 5, ; AK015019,homeo box D8, ; NM_008759,OG9 homeobox gene, ; X56570,"retinoic acid receptor, alpha", ; AK018115,BTB (POZ) domain containing 11, ; AJ276456,Doublesex-related protein Dmrt2, ; NM_007804,cut-like 2 (Drosophila), ; L28116,peroxisome proliferator activator receptor delta, ; NM_009990,cytoplasmic linker 2, ; AK009120,RIKEN cDNA 2610016F04 gene, ; NM_009333,"transcription factor 7-like 2, T-cell specific, HMG-box", ; NM_011078,PHD finger protein 2, ; AK013605,"zinc finger protein 422, related sequence 1", ; NM_008818,placentae and embryos oncofetal gene, ; NM_016746,cyclin C, ; AF265229,DNA methyltransferase 1-associated protein 1, ; S79041,genomic screened homeo box 2, ; AF277992,forkhead box P3, ; NM_020000,"mediator of RNA polymerase II transcription, subunit 8 homolog (yeast)", ; NM_010757,"v-maf musculoaponeurotic fibrosarcoma oncogene family, protein K (avian)", ; AK016628,ELL associated factor 1, ; NM_011146,peroxisome proliferator activated receptor gamma, ; NM_011768,zinc finger protein X-linked, ; AK016708,"zinc finger, X-linked, duplicated A", ; NM_010909,nuclear factor of kappa light polypeptide gene enhancer in B-cells inhibitor-like 1, ; AK019851,RIKEN cDNA 4931408L03 gene, ; D83146,sine oculis-related homeobox 5 homolog (Drosophila), ; NM_031184,GLIS family zinc finger 2, ; AK019909,"zinc finger, FYVE domain containing 20", ; AK020455,RIKEN cDNA 9430034D17 gene, ; NM_009569,"zinc finger protein, multitype 1", ; AK007727,"protein phosphatase 1, regulatory (inhibitor) subunit 12B", ; AK006780,basic transcription factor 3, ; AJ276456,Doublesex-related protein Dmrt2, ; BC011226,PHD finger protein 3, ; AB046714,"brain abundant, membrane attached signal protein 1", ; Z18958,SRY-box containing gene 9, ; NM_009327,transcription factor 1, ; BC003430,single-stranded DNA binding protein 3, ; L36435,"v-maf musculoaponeurotic fibrosarcoma oncogene family, protein B (avian)", ; AK017487,bobby sox homolog (Drosophila), ; NM_007441,aristaless 3, ; U13878,RE1-silencing transcription factor, ; BC006021,"CCR4-NOT transcription complex, subunit 7", ; NM_011498,"basic helix-loop-helix domain containing, class B2", ; AK012264,"nuclear receptor subfamily 1, group I, member 3", ; NM_011680,upstream transcription factor 2, ; NM_011919,"inhibitor of growth family, member 1", ; BF579673,"nuclear receptor subfamily 1, group H, member 2", ; NM_013498,cAMP responsive element modulator, ; NM_011757,zinc finger proliferation 1, ; NM_024467,zinc finger protein 319, ; NM_008578,myocyte enhancer factor 2B, ; NM_009324,T-box 2, ; AK018550,RIKEN cDNA 9030612M13 gene, ; L13171,myocyte enhancer factor 2C, ; U12142,"nuclear receptor subfamily 1, group D, member 2", ; NM_013729,Mix1 homeobox-like 1 (Xenopus laevis), ; NM_019935,OVO homolog-like 1 (Drosophila), ; U41465,B-cell leukemia/lymphoma 6, ; AY037807,cut-like 1 (Drosophila), ; AJ276456,Doublesex-related protein Dmrt2, ; BC003430,single stranded DNA binding protein 3, ; AK010794,Smad nuclear interacting protein 1, ; ; "Clathrin binding, calcium binding, lipoprotein", ,; BC011162,neurocalcin delta,; BC011162,Neurocalcin delta, ; NM_012038,visinin-like 1, ; BC011162,neurocalcin delta, ; BC011162,neurocalcin delta, ; ; "protein localization, protein transport", ,; NM_021392,"adaptor-related protein complex AP-4, mu 1",; NM_007454,"adaptor protein complex AP-1, beta 1 subunit", ; AK009844,"clathrin, light polypeptide (Lcb)", ; AK014958,RIKEN cDNA 4921524J06 gene, ; NM_009679,"adaptor protein complex AP-2, mu1", ; NM_016760,"clathrin, light polypeptide (Lca)", ; ; "chemokine receptor binding, polysaccharide binding, inflammation", ,; L04694,chemokine (C-C motif) ligand 7,; NM_009139,chemokine (C-C motif) ligand 6, ; L04694,chemokine (C-C motif) ligand 7, ; NM_011335,chemokine (C-C motif) ligand 21c (leucine), ; NM_021443,chemokine (C-C motif) ligand 8, ; NM_021274,chemokine (C-X-C motif) ligand 10, ; ; defense response, ,; X61761,"T-cell receptor beta, variable 13",; M71214,"T-cell receptor gamma, variable 7", ; AE008685,"T-cell receptor alpha, variable 2.5", ; Z12256,"T-cell receptor beta, variable 8.3", ; M71214,"T-cell receptor gamma, variable 5", ; AE008685,"T-cell receptor alpha, variable 2.2", ; ; "ion channel activity, transport, glycoprotein", ,; AF064874,"hyperpolarization-activated, cyclic nucleotide-gated K+ 4",; AK017384,potassium channel tetramerisation domain containing 6, ; NM_008422,"potassium voltage gated channel, Shaw-related subfamily, member 3", ; NM_008227,"hyperpolarization-activated, cyclic nucleotide-gated K+ 3", ; AK013641,"potassium channel, subfamily K, member 2", ; NM_008422,"otassium voltage gated channel, Shaw-related subfamily, member 3", ; ; hormone activity, ,; NM_007745,cortistatin,; M35662,chorionic somatomammotropin hormone 1, ; NM_011168,prolactin-like protein F, ; NM_031191,proliferin, ; NM_008190,guanylate cyclase activator 2a (guanylin), ; NM_011954,"mitogen regulated protein, proliferin 3", ; ; "lipoprotein, GTP-binding, protein transport", ,; X80473,"RAB19, member RAS oncogene family",; X80332,"RAB20, member RAS oncogene family", ; NM_028238,"Rab38, member of RAS oncogene family", ; BC007147,"RAB4B, member RAS oncogene family", ; AB041575,"RAB6, member RAS oncogene family", ; NM_011229,"RAB5B, member RAS oncogene family", ; BC007147,"RAB4B, member RAS oncogene family", ; ; "actin, cytoskeleton, calmodulin, cell organization and biogenesis", ,; U04443,"myosin, light polypeptide 6, alkali, smooth muscle and non-muscle",; NM_016754,"myosin light chain, phosphorylatable, fast skeletal muscle", ; U04443,"myosin, light peptide 6, alkali, smooth muscle and non-muscle", ; U04443,"myosin, light polypeptide 6, alkali, smooth muscle and non-muscle", ; AK003182,"myosin, light polypeptide 1", ; U04443,LC17, ; ; "Glutathione Transferase, Glutathione metabolism", ,; NM_010361,"glutathione S-transferase, theta 2",; J03953,"glutathione S-transferase, mu 3", ; NM_013541,"glutathione S-transferase, pi 1", ; NM_008181,"glutathione S-transferase, alpha 1 (Ya)", ; NM_008182,"glutathione S-transferase, alpha 2 (Yc2)", ; ; "microtubule cytoskeleton, cell organization and biogenesis", ,; AB054025,kinesin family member 18B,; AB053955,kinesin family member 26B, ; BC006841,kinesin family member 2C, ; AB001435,kinesin family member 7, ; AB054031,kinesin family member 26A, ; ; "Glycosyltransferase, Glycoprotein", ,; NM_010265,"glucosaminyl (N-acetyl) transferase 1, core 2",; AK019308,exostoses (multiple)-like 3, ; NM_010163,exostoses (multiple) 2, ; AJ133523,UDP-N-acetyl-alpha-D-galactosamine:polypeptide N-acetylgalactosaminyltransferase 6, ; NM_008595,manic fringe homolog (Drosophila), ; ; "Tyrosine-protein kinase, ATP binding, protein metabolism", ,; NM_008809,"platelet derived growth factor receptor, beta polypeptide",; NM_007584,"discoidin domain receptor family, member 1", ; AK021278,"neurotrophic tyrosine kinase, receptor, type 2", ; AK020397,interleukin-1 receptor-associated kinase 4, ; NM_015755,hormonally upregulated Neu-associated kinase, ; AK021278,"neurotrophic tyrosine kinase, receptor, type 2", ; NM_009184,PTK6 protein tyrosine kinase 6, ; AK017630,Eph receptor B2, ; AF240782,MAP/microtubule affinity-regulating kinase 3, ; NM_009539,zeta-chain (TCR) associated protein kinase, ; NM_010208,Gardner-Rasheed feline sarcoma viral (Fgr) oncogene homolog, ; AK009054,Eph receptor A7, ; ; "protein kinase activity, cell cycle, apoptosis", ,; AK019023,RIKEN cDNA 1810024B03 gene,; AK009788,dual-specificity tyrosine-(Y)-phosphorylation regulated kinase 1a, ; X86367,Nsk1 protein, ; NM_019924,"ribosomal protein S6 kinase, polypeptide 4", ; NM_009436,testis-specific serine kinase 2, ; AK018636,RIKEN cDNA 9130019I15 gene, ; NM_010433,homeodomain interacting protein kinase 2, ; NM_007700,conserved helix-loop-helix ubiquitous kinase, ; AJ278435,wee 1 homolog (S. pombe), ; AF312007,serum/glucocorticoid regulated kinase 3, ; AB041802,serine/threonine kinase 35, ; NM_022012,mitogen activated protein kinase kinase kinase 11, ; AK004809,RIKEN cDNA 1200016D23 gene, ; NM_009539,zeta-chain (TCR) associated protein kinase, ; AK012223,mitogen-activated protein kinase kinase kinase kinase 6, ; NM_009469,Unc-51 like kinase 1 (C. elegans), ; NM_010208,Gardner-Rasheed feline sarcoma viral (Fgr) oncogene homolog, ; BC006037,mitogen-activated protein kinase kinase kinase kinase 3, ; NM_011361,serum/glucocorticoid regulated kinase, ; NM_016693,mitogen-activated protein kinase kinase kinase 6, ; X76850,MAP kinase-activated protein kinase 2, ; NM_007584,"discoidin domain receptor family, member 1", ; AK020397,interleukin-1 receptor-associated kinase 4, ; AK021230,glycogen synthase kinase 3 beta, ; AK011451,RIKEN cDNA 2610019A05 gene, ; AK004737,RIKEN cDNA 1200013B22 gene, ; AF240782,MAP/microtubule affinity-regulating kinase 3, ; AF033565,CDC-like kinase 3, ; AF314149,"myosin, light polypeptide kinase", ; AK020521,tousled-like kinase 1, ; NM_011103,"protein kinase C, delta", ; AF133093,serine/threonine kinase 23, ; NM_015755,hormonally upregulated Neu-associated kinase, ; AK014278,aarF domain containing kinase 1, ; NM_009184,PTK6 protein tyrosine kinase 6, ; ; "protein catabolism, catabolism, protein metabolism", ,; NM_007602,calpain 5,; NM_008572,mast cell protease 8, ; NM_008454,kallikrein 16, ; J00390,kallikrein 1, ; AY034574,cathepsin 3, ; NM_026419,"elastase 3B, pancreatic", ; BC015296,secernin 3, ; NM_008944,"proteasome (prosome, macropain) subunit, alpha type 2", ; NM_010779,mast cell protease 4, ; AK018595,ubiquitin specific protease 39, ; NM_008906,protective protein for beta-galactosidase, ; Z12245, RIKEN cDNA 1810049H19 gene,; AK018326,RIKEN cDNA 6530406M24 gene, ; NM_010371,granzyme C, ; NM_011186,"proteasome (prosome, macropain) subunit, beta type 5", ; BC002296,O-sialoglycoprotein endopeptidase, ; NM_009350,testis nuclear RNA binding protein, ; AJ278170,nuclear receptor interacting protein 2, ; NM_026545,"proteasome (prosome, macropain) 26S subunit, non-ATPase, 8", ; NM_013918,ubiquitin specific protease 25, ; AK012765,secernin 1, ; NM_053243,trypsin 4, ; AK005069,trypsin domain containing 1, ; AK011064,RIKEN cDNA 2510040D07 gene, ; NM_008792,proprotein convertase subtilisin/kexin type 2, ; AK008397,RIKEN cDNA 2010111I01 gene, ; AK015256,carboxypeptidase A5, ; NM_008939,"protease, serine, 12 neurotrypsin (motopsin)", ; NM_009985,cathepsin W, ; AK013995,peptidase (mitochondrial processing) beta, ; ; "Glycoprotein metabolism, protein biosynthesis, carbohydrate metabolism", ,; NM_010265,"glucosaminyl (N-acetyl) transferase 1, core 2",; AY043479,"UDP-GlcNAc:betaGal beta-1,3-N-acetylglucosaminyltransferase 1", ; NM_008548,"mannosidase 1, alpha", ; NM_012028,"sialyltransferase 7 ((alpha-N-acetylneuraminyl 2,3-betagalac ...", ; NM_009182,"sialyltransferase 8 (alpha-2, 8-sialyltransferase) C", ; AY050569,"UDP-Gal:betaGal beta 1,3-galactosyltransferase, polypeptide 6", ; AK018439,O-linked N-acetylglucosamine (GlcNAc) transferase (UDP-N-ace ..., ; NM_019934,secretory blood group 1, ; NM_008595,manic fringe homolog (Drosophila), ; ; "Zinc finger, DNA-dependent transcription, regulation of metabolism", ,; NM_009769,Kruppel-like factor 5,; AK016708,"zinc finger, X-linked, duplicated A", ; X94291,matrin 3, ; AK019851,RIKEN cDNA 4931408L03 gene, ; AK013605,"zinc finger protein 422, related sequence 1", ; AK018550,RIKEN cDNA 9030612M13 gene, ; AK020461,LIM domain containing preferred translocation partner in lipoma, ; AK019909,"zinc finger, FYVE domain containing 20", ; NM_009542,zinc finger protein 101, ; BC005719,RNA binding motif protein 5, ; AJ278340,zinc finger protein 296, ; AF277992,forkhead box P3, ; AK013752,zinc finger protein 50, ; ; "protein folding, chaperone, macromolecule metabolism", ,; NM_007637,chaperonin subunit 5 (epsilon),; AK011873,chaperonin subunit 4 (delta), ; NM_025362,Williams-Beuren syndrome chromosome region 18 homolog (human), ; AJ278735,"chaperone, ABC1 activity of bc1 complex like (S. pombe)", ; NM_009840,chaperonin subunit 8 (theta), ; NM_026508,TNF receptor-associated protein 1, ; ; "phosphatase activity, protein modification, protein metabolism", ,; AK012831,"DnaJ (Hsp40) homolog, subfamily C, member 6",; NM_013643,"protein tyrosine phosphatase, non-receptor type 5", ; BC012436,RIKEN cDNA 1110061O04 gene, ; NM_013643,"protein tyrosine phosphatase, non-receptor type 5", ; AF237619,dual specificity phosphatase 22, ; ; "protein biosynthesis, protein metabolism, ribosome, regulation of biosynthesis", ,; AK005192,translation factor sui1 homolog,; AK016918,RIKEN cDNA 4933425L03 gene, ; BE569926,"eukaryotic translation initiation factor 1A, Y-linked", ; AK003937,ribosomal protein L24, ; NM_025586,ribosomal protein L15, ; AK005192,translation factor sui1-like protein, ; AK005192,RIKEN cDNA 1500010M16 gene, ; NM_025796,mitochondrial ribosomal protein L33, ; NM_012011,"eukaryotic translation initiation factor 2, subunit 3, structural gene Y-linked", ; AK006554,RIKEN cDNA 1700030K01 gene, ; ; "Ribosome, protein metabolism, ribosome biogenesis, mitochondrial ribosome", ,; AB049657,mitochondrial ribosomal protein L43,; BC009166,mitochondrial ribosomal protein L36, ; BC005734,RIKEN cDNA 2610012O22 gene, ; AK003937,ribosomal protein L24, ; NM_007990,Finkel-Biskis-Reilly murine sarcoma virus (FBR-MuSV) ubiquitously expressed (fox derived), ; NM_025586,ribosomal protein L15, ; NM_026147,ribosomal protein S20, ; NM_025796,mitochondrial ribosomal protein L33, ; NM_018860,ribosomal protein L41, ; AK006554,RIKEN cDNA 1700030K01 gene, ; NM_026055,ribosomal protein L39, ; AK016918,RIKEN cDNA 4933425L03 gene, ; NM_025974,ribosomal protein L14, ;

AK003500,mitochondrial ribosomal protein L14, ; NM_009081,ribosomal protein L28, ; ; "protein modification, protein ubiquitination", ,; AK014075,axotrophin,; AK009364,ring finger protein 153, ; AK007391,RIKEN cDNA 1810009A16 gene, ; BC004781,RIKEN cDNA 4732452J19 gene, ; AK019706,zinc finger protein 294, ; AK005859,RIKEN cDNA 2610034H20 gene, ; ; "protein modification, protein ubiquitination, posttranslational modification", ,; U55178,TCDD-inducible poly(ADP-ribose) polymerase,; AK014075,axotrophin, ; NM_011632,Tnf receptor-associated factor 3, ; AF321921,BRCA1 associated protein, ; AK006757,RIKEN cDNA 1700051E09 gene, ; BC004781,RIKEN cDNA 4732452J19 gene, ; BC011287,mindbomb homolog 1 (Drosophila), ; AK019706,zinc finger protein 294, ; AK009364,ring finger protein 153, ; AF230385,tripartite motif protein 32, ; NM_011634,TRAF-interacting protein, ; AF360997,RIKEN cDNA C330018L13 gene, ; AK016874,retinoblastoma binding protein 6

6.3.4 Categories of functional classification for genes differentially expressed in the liver/kidney between subspecies

"Zinc ion binding, regulation of transcription, metabolism", ,; NM_009574,Zic finger protein of the cerebellum 2,; D10627,cDNA sequence D10627,; NM_009575,zinc finger protein of the cerebellum 3,; NM_009567,zinc finger protein 93, ; AF370121,odd-skipped related 2 (Drosophila),; NM_021390,sal-like 1 (Drosophila), ; NM_010278,growth factor independent 1, ; AK004693,forkhead box P4, ; AK020525,zinc finger protein 462, ; NM_019935,OVO homolog-like 1 (Drosophila),; AF277992,forkhead box P3,; AK016708,"zinc finger, X-linked, duplicated A",; NM_008453,Kruppel-like factor 3 (basic), ; BC003258,RIKEN cDNA 4930488P06 gene, ; AF117382,hypermethylated in cancer 2, ; AB010345,Mszf52, ; BC002310,RIKEN cDNA 9530033F24 gene, ; ,, ; "Zn-finger, regulation of metabolism, regulation of transcription", ,; NM_009574,Zic finger protein of the cerebellum 2,; AB010342,cDNA sequence BC029127,; NM_028842,RIKEN cDNA 1700045I19 gene,; AK016103,ring finger protein 125, ; D10627,cDNA sequence D10627, ; X12592,zinc finger protein 26, ; NM_009575,zinc finger protein of the cerebellum 3, ; AK013356,RIKEN cDNA 2810455K09 gene, ; NM_020287,insulinoma-associated 2,; AB010338,zinc finger protein 472,; AF370121,odd-skipped related 2 (Drosophila),; AF191309,serologically defined colon cancer antigen 33, ; AK018550,RIKEN cDNA 9030612M13 gene, ; AK004693,forkhead box P4, ; AK020525,zinc finger protein 462, ; AF277992,forkhead box P3, ; AK016708,"zinc finger, X-linked, duplicated A",; NM_011769,"zinc finger, imprinted 1",; AB010363,Regulator of sex-limitation candidate 18,; NM_009568,zinc finger protein 94, ; BC003258,RIKEN cDNA 4930488P06 gene, ; BC002310,RIKEN cDNA 9530033F24 gene, ; AB010345,Mszf52, ; NM_016793,zinc finger protein 98, ; ,, ; "regulation of transcription, regulation of metabolism, protein ubiquitination", , ; NM_028842,RIKEN cDNA 1700045I19 gene, ; AK005948,RIKEN cDNA 1700013G10 gene, ; X12592,zinc finger protein 26, ; NM_010635,Kruppel-like factor 1 (erythroid), ; NM_009575,zinc finger protein of the cerebellum 3, ; BC006925,elongation factor RNA polymerase II 2, ; NM_009570,"zinc finger protein 1, Y linked", ; BC002090,Dr1 associated protein 1 (negative cofactor 2 alpha), ; NM_010812,forkhead box K1, ; AK018550,RIKEN cDNA 9030612M13 gene, ; NM_010827,musculin, ; AF277992,forkhead box P3, ; NM_020614,"TATA box binding protein (Tbp)-associated factor, RNA polymerase I, B", ; NM_008578,myocyte enhancer factor 2B, ; AF362750,"D4, zinc and double PHD fingers, family 3", ; NM_017395,"regulatory factor X, 5 (influences HLA class II expression)", ; NM_011769,"zinc finger, imprinted 1", ; AF277399,"cat eye syndrome chromosome region, candidate 6 homolog (human)", ; U49507,liver-specific bHLH-Zip transcription factor, ; NM_008627,myeloid ecotropic viral integration site-related gene 2, ; AK020911,ankyrin repeat domain 15, ; NM_009709,aryl hydrocarbon receptor nuclear translocator, ; BC003430,single-stranded DNA binding protein 3, ; NM_011498,"basic helix-loop-helix domain containing, class B2", ; NM_009986,cut-like 1 (Drosophila), ; AF015275,"hepatic nuclear factor 4, alpha", ; AJ292189,"TAF3 RNA polymerase II, TATA box binding protein (TBP)-associated factor", ; BC003430,single stranded DNA binding protein 3, ; D85612,"nuclear factor of activated T-cells, cytoplasmic, calcineurin-dependent 3", ; NM_010151,"nuclear receptor subfamily 2, group F, member 1", ; AB010363,Regulator of sex-limitation candidate 18, ; NM_009233,SRY-box containing gene 1, ; NM_008498,LIM homeobox protein 1, ; AK004572,poly(A)-specific ribonuclease (deadenylation nuclease),; NM_007959,ets related protein 71,; NM_010441,high mobility group AT-hook 2,; NM_008259,forkhead box A1, ; AB010338,zinc finger protein 472, ; NM_008782,paired box gene 5, ; NM_008498,LIM homeobox protein 1, ; Y17859,RIKEN cDNA 1810043J12 gene, ; NM_021390,sal-like 1 (Drosophila), ; U62906,zinc finger protein 99, ; AK004108,nuclear factor of activated T-cells 5, ; NM_011547,"transcription factor AP-2, alpha", ; NM_010725,LIM homeobox transcription factor 1 beta, ; L35549,Y-box binding protein, ; AK012587,homeo box B7, ; AK019761,GLIS family zinc finger 1, ; AK008111,RIKEN cDNA 2010005A06 gene, ; AK005195,RIKEN cDNA C330018L13 gene, ; AF067774,B-cell leukemia/lymphoma 3, ; NM_009553,zinc finger protein 29, ; NM_016707,B-cell CLL/lymphoma 11A (zinc finger protein), ; NM_008273,homeo box D11, ; U57328,T-box 3, ; NM_016746,cyclin C, ; AK014075,axotrophin, ; AK005588,RIKEN cDNA 1700001F22 gene, ; NM_013715,"COP9 (constitutive photomorphogenic) homolog, subunit 5 (Arabidopsis thaliana)", ; AF117382,hypermethylated in cancer 2, ; U20366,"homeo box A11, opposite strand transcript", ; X66177,homeo box B3, ; NM_020287,insulinoma-associated 2, ; NM_007442,aristaless 4, ; AF191309,serologically defined colon cancer antigen 33, ; NM_010225,forkhead box F2, ; BC008103,RIKEN cDNA 5830417I10 gene, ; AF015275,"hepatocyte nuclear factor 4, alpha", ; AK004386,cDNA sequence BC031407, ; NM_013779,"melanoma antigen, family L, 2", ; NM_008242,forkhead box D1, ; NM_013874,neuronal d4 domain family member, ; NM_008849,pituitary specific transcription factor 1, ; NM_026584,"general transcription factor II E, polypeptide 2 (beta subunit)", ; AK017346,checkpoint supressor 1, ; NM_019663,protein inhibitor of activated STAT 1, ; NM_013905,hairy/enhancer-of-split related with YRPW motif-like, ; AF002670,TEA domain family member 3, ; NM_010134,engrailed 2, ; NM_008500,LIM homeobox protein 6, ; NM_030555,pre-B-cell leukemia transcription factor 4, ; NM_018809,"pancreas specific transcription factor, 1a", ; AK011250,myeloid ecotropic viral integration site 1, ; AK021120,transcription factor 4, ; NM_013554,homeo box D10, ; NM_011766,"zinc finger protein, multitype 2", ; NM_020496,T-box 20, ; NM_013736,"transcription elongation factor B (SIII), polypeptide 3", ; AB030906,sex comb on midleg homolog 1, ; NM_009233,SRY-box containing gene 11, ; AK016252,RIKEN cDNA 4930568H22 gene, ; NM_019935,OVO homolog-like 1 (Drosophila), ; NM_026570,YEATS domain containing 4, ; NM_008453,Kruppel-like factor 3 (basic), ; BC003258,RIKEN cDNA 4930488P06 gene, ; NM_016793,zinc finger protein 98, ; AK016707,BCL2-associated transcription factor 1, ; NM_008090,GATA binding protein 2, ; NM_009545,ring finger protein 110, ; NM_009567,zinc finger protein 93, ; AK020455,RIKEN cDNA 9430034D17 gene, ; NM_026305,"transcription elongation factor B (SIII), polypeptide 2", ; NM_010278,growth factor independent 1, ; AK004693,forkhead box P4, ; NM_011544,transcription factor 12, ; NM_009568,zinc finger protein 94, ; AK021120,transcription factor 4, ; ,, ; "protein modification, protein metabolism", , ; NM_028842,RIKEN cDNA 1700045I19 gene, ; BC014812,RIKEN cDNA 1700022N24 gene, ; NM_024231,zinc finger like protein 1, ; AK005195,RIKEN cDNA C330018L13 gene, ; NM_013874,neuronal d4 domain family member, ; NM_009545,ring finger protein 110, ; AK014075,axotrophin, ; AK009344,RIKEN cDNA 2310014L17 gene, ; AF362750,"D4, zinc and double PHD fingers, family 3", ; AK015130,retinoblastoma binding protein 6, ; NM_019705,expressed sequence AL033326, ; AF151110,expressed sequence C80879, ; AF361000,ubiquitin conjugating enzyme 7 interacting protein 1, ; NM_011787,autocrine motility factor receptor, ; ,, ; "protein modification, protein metabolism, Ubiquitin", , ; AK005859,RIKEN cDNA 2610034H20 gene, ; U20780,RIKEN cDNA B230113M03 gene, ; NM_019949,ubiquitin-conjugating enzyme E2L 6, ; AK016520,cullin 2, ; NM_025785,F-box only protein 25, ; ,, ; "ribosome, protein biosynthesis, ribosome biogenesis, metabolism, mitochondrion", , ; AF279255,mitochondrial ribosomal protein L32, ; NM_011290,ribosomal protein L6, ; NM_011287,ribosomal protein L10A, ; NM_026490,mitochondrial ribosomal protein L19, ; NM_009081,ribosomal protein L28, ; AB049953,mitochondrial ribosomal protein S18A, ; AK003500,mitochondrial ribosomal protein L14, ; BC005734,RIKEN cDNA 2610012O22 gene, ; NM_013647,ribosomal protein S16, ; ,, ; "protein catabolism, peptidase activity, protein metabolism, protease", ,; Z12196,RIKEN cDNA 1810049H19 gene,; NM_011645,"protease, serine, 3",; AE000663,RIKEN cDNA 1810009J06 gene, ; AE000663,Trypsinogen 5, ; NM_026545,"proteasome (prosome, macropain) 26S subunit, non-ATPase, 8", ; NM_008946,"proteasome (prosome, macropain) subunit, beta type 6", ; AK014228,RIKEN cDNA 3110056O03 gene,; NM_027344,RIKEN cDNA 2310051M13 gene,; NM_053243,trypsin 4,; NM_015830,small optic lobes homolog (Drosophila), ; AJ307017,"ubiquitin specific protease 9, Y chromosome", ; AK011112,prolylcarboxypeptidase (angiotensinase C), ; AE000663,hypothetical protein 1700020H15, ; AF229643,"ubiquitin specific protease 27, X chromosome", ; AB049453,RIKEN cDNA 4931440B09 gene,; AK003823,carboxypeptidase A4,; NM_027288,"mannosidase, beta A, lysosomal",; NM_010089,deubiquitinating enzyme 2, ; AF285235,dipeptidylpeptidase 7, ; BC008156,ubiquitin specific protease 43, ; NM_011855,odd Oz/ten-m homolog 1 (Drosophila), ; AE000663,RIKEN cDNA 2210010C04 gene, ; U22058,a disintegrin and metalloprotease domain 4,; NM_030127,serine protease HTRA3,; AK018595,ubiquitin specific protease 39,; ,, ; "protein phosphastase activity, metabolism, tyrosine protein phophatase", , ; NM_008979,"protein tyrosine phosphatase, non-receptor type 8", ; AK002934,RIKEN cDNA 0710001B24 gene, ; NM_013643,"protein tyrosine phosphatase, non-receptor type 5", ; NM_013643,"protein tyrosine phosphatase, non-receptor type 5",; AF262986,myotubularin related protein 4,; ; "protein kinase activity, phosphate metabolism, protein metabolism", , ; NM_019392,TYRO3 protein tyrosine kinase 3, ; AK013153,death associated protein kinase 1, ; AK019402,"DNA segment, Chr 8, ERATO Doi 82, expressed", ; NM_007668,cyclin-dependent kinase 5, ; NM_007779,colony stimulating factor 1 receptor,; AF335470,"myosin, light polypeptide kinase",; NM_009288,serine/threonine kinase 10,; NM_009863,cell division cycle 7 (S. cerevisiae), ; NM_019945,microtubule associated serine/threonine kinase 1, ; AK003718,homeodomain interacting protein kinase 2, ; AK019023,RIKEN cDNA 1810024B03 gene, ; M68513,Eph receptor A3, ; NM_011946,mitogen activated protein kinase kinase kinase 2,; AB041802,serine/threonine kinase 35,; NM_008547,male germ cell-associated kinase,; NM_013482,Bruton agammaglobulinemia tyrosine kinase, ; NM_011973,renal tumor antigen, ; AK020957,RIKEN cDNA B230104P22 gene, ; AK004180,fucokinase, ; NM_019777,inhibitor of kappaB kinase epsilon, ; NM_007779,colony stimulating factor 1 receptor, ; NM_010768,megakaryocyte-associated tyrosine kinase,; J02995,v-abl Abelson murine leukemia oncogene 1,; U49952,dual-specificity tyrosine-(Y)-phosphorylation regulated kinase 1c,; AK008047,"protein kinase, lysine deficient 4", ; NM_009436,testis-specific serine kinase 2, ; NM_021479,testis-specific serine kinase 3, ; NM_007938,Eph receptor A6, ; AK013132,oxidative-stress responsive 1, ; NM_007668,cyclin-dependent kinase 5,; AK020509,Eph receptor A7,; NM_013731,serum/glucocorticoid regulated kinase 2,; BC012437,cDNA sequence BC011468, ; AK019468,mitogen-activated protein kinase kinase kinase kinase 5, ; ,, ; translational elongation, , ; M17878,Elongation factor 1-alpha 1,; M76131,eukaryotic translation elongation factor 2,; M17878,eukaryotic translation elongation factor 1 alpha 1,; M17878,eukaryotic translation elongation factor 1 alpha 1, ; M17878,Elongation factor 1-alpha 1, ; M17878,Elongation factor 1-alpha 1, ; ,, ; "microtubule cytoskeleton, cell organization and biogenesis", ,; NM_010630,kinesin family member C2,; AB001435,kinesin family member 7,; AK014461,kinesin-like 7, ; AB054025,kinesin family member 18B, ; AB001423,kinesin family member 16B, ; ,, ; "intermediate filament protein, cytoskeleton, cell organization and biogenesis", ,; NM_010665,"keratin complex 1, acidic, gene 2",; NM_027563,"keratin complex 1, acidic, gene 4",; NM_008691,"neurofilament 3, medium", ; NM_008470,"keratin complex 1, acidic, gene 16", ; L22550,desmin, ; S78809,glial fibrillary acidic protein, ; NM_008471,"keratin complex 1, acidic, gene 19", ; ,, ; "apoptosis, regulation of apoptosis", , ; AK018648,modulator of apoptosis 1, ; NM_009742,B-cell leukemia/lymphoma 2 related protein A1a, ; NM_009761,BCL2/adenovirus E1B 19kDa-interacting protein 3-like, ; AY029253,Bcl2 modifying factor, ; NM_007545,"BH3 interacting (with BCL2 family) domain, apoptosis agonist",; ; "cytochrome P450, cellular metabolism", ,; NM_029562,"cytochrome P450, family 2, subfamily d, polypeptide 26", ; NM_007822,"cytochrome P450, family 4, subfamily a, polypeptide 14", ; AF204959,"cytochrome P450, family 3, subfamily a, polypeptide 25", ; BC016256,"cytochrome P450, family 2, subfamily d, polypeptide 22", ; NM_007812,"cytochrome P450, family 2, subfamily a, polypeptide 5", ; ,, ; defense response, , ; AE008685,"T-cell receptor alpha, variable 2.5", ; AE008685,"T-cell receptor alpha, variable 2.2", ; U07662,T-cell receptor alpha chain, ; AE008684,"T-cell receptor alpha, variable 2.4", ; AE008684,"T-cell receptor alpha, variable 8", ; ,, ; cell adhesion, , ; U86016,desmoglein 3, ; AY013770,protocadherin beta 1, ; AK006648,cadherin-like 24, ; AK008111,RIKEN cDNA 2010005A06 gene, ; AK020530,cadherin 11, ; X06340,cadherin 3, ; AY013776,protocadherin beta 15, ; ,, ;

"glycoprotein metabolism, protein biosynthesis, biosynthesis, lipid biosynthesis", , ; AK005721,"sialyltransferase 8 (alpha-2, 8-sialyltransferase) F", ; AK004442,"UDP-Gal:betaGlcNAc beta 1,3-galactosyltransferase, polypeptide 5", ; AF153680,"beta galactoside alpha 2,6 sialyltransferase 1", ; NM_013814,UDP-N-acetyl-alpha-D-galactosamine:polypeptide N-acetylgalactosaminyltransferase 1, ; BC011201,RIKEN cDNA 4930467B06 gene, ; AY029203,"UDP-GlcNAc:betaGal beta-1,3-N-acetylglucosaminyltransferase 5", ; ,, ; ion channel activity, , ; NM_008424,"potassium voltage-gated channel, Isk-related subfamily, member 1", ; NM_019697,"potassium voltage-gated channel, Shal-related family, member 2", ; NM_008422,"potassium voltage gated channel, Shaw-related subfamily, member 3", ; NM_008417,"potassium voltage-gated channel, shaker-related subfamily, member 2",; NM_008422,"potassium voltage gated channel, Shaw-related subfamily, member 3",; AF295095,"potassium large conductance calcium-activated channel, subfamily M, alpha member 1",; NM_010595,"potassium voltage-gated channel, shaker-related subfamily, member 1", ; AK015001,"potassium voltage-gated channel, subfamily G, member 4", ; ,, ; "protein localization, protein transport", , ; AF295402,secretory carrier membrane protein 2, ; NM_016797,syntaxin 7, ; NM_019829,syntaxin 5A, ; NM_020270,secretory carrier membrane protein 5, ; NM_019650,golgi SNAP receptor complex member 2, ; ,, ; "lipoprotein, glycoprotein", ,; AK020118,glypican 6, ; NM_007910,ephrin A4, ; NM_010109,ephrin A5, ; NM_009016,"retinoic acid early transcript 1, alpha", ; NM_009016,retinoic acid early transcript 1E, ; ,, ; G-protein coupled receptor activity, , ; NM_008152,G-protein coupled receptor 65, ; U05671,adenosine A1 receptor, ; AF282302,olfactory receptor 934, ; NM_007412,adrenomedullin receptor, ; AF271038,olfactory receptor 394, ; NM_007412,adrenomedullin receptor, ; NM_019486,olfactory receptor 71, ; X89686,olfactory receptor 18, ; X89687,"olfactory receptor 22, pseudogene 1", ; AF394596,hypocretin (orexin) receptor 1, ; AF102525,olfactory receptor 51, ; AF042360,Putative olfactory receptor,; NM_010983,olfactory receptor 2,; NM_020291,olfactory receptor 480,; NM_008038,"formyl peptide receptor, related sequence 1", ; NM_010983,olfactory receptor 2, ; AY042201,"MAS-related GPR, member B3", ; NM_008552,MAS1 oncogene, ; NM_009835,chemokine (C-C motif) receptor 6, ; AF042360,olfactory receptor 1355, ; AK009450,membrane progestin receptor alpha, ; NM_008038,"formyl peptide receptor, related sequence 2", ; BC006923,olfactory receptor 73,; AF022254,"G protein-coupled receptor, family C, group 2, member A, related sequence 5",; AJ300198,G protein-coupled receptor 109B,; AF331658,cysteinyl leukotriene receptor 2, ; ,, ; "G-protein coupled receptor activity, lipoprotein", , ; NM_008152,G-protein coupled receptor 65, ; U05671,adenosine A1 receptor, ; NM_008359,interleukin 17 receptor, ; NM_013461,"adrenergic receptor, alpha 1a", ; NM_008101,glucagon receptor, ; NM_007412,adrenomedullin receptor, ; NM_011013,"opioid receptor, mu 1", ; X89687,"olfactory receptor 22, pseudogene 1", ; AF394596,hypocretin (orexin) receptor 1, ; AF042360,Putative olfactory receptor,; NM_008101,glucagon receptor,; NM_010170,coagulation factor II (thrombin) receptor-like 2,; NM_008038,"formyl peptide receptor, related sequence 1", ; NM_020291,olfactory receptor 480, ; NM_008154,G-protein coupled receptor 3, ; AY042201,"MAS-related GPR, member B3", ; NM_008561,melanocortin 3 receptor, ; NM_008151,G-protein coupled receptor 12,; NM_007877,dopamine receptor 3,; NM_013461,"adrenergic receptor, alpha 1a",; NM_008552,MAS1 oncogene, ; NM_009835,chemokine (C-C motif) receptor 6, ; AK009450,membrane progestin receptor alpha, ; NM_008311,5-hydroxytryptamine (serotonin) receptor 2B, ; NM_008038,"formyl peptide receptor, related sequence 2",; NM_011703,vasoactive intestinal peptide receptor 1,; AF022254,"G protein-coupled receptor, family C, group 2, member A, related sequence 5",; NM_007877,dopamine receptor 3, ; AF331658,cysteinyl leukotriene receptor 2, ; BC008228,"G protein-coupled receptor, family C, group 5, member C", ; AJ300198,G protein-coupled receptor 109B, ; ,, ; glycoprotein, , ; NM_021487,"potassium voltage-gated channel, Isk-related family, member 1-like", ; BF178619,open reading frame 18, ; AK014255,chondrolectin, ; S65735,glycoprotein m6a,; S65735,glycoprotein m6a,; AK013584,pecanex homolog (Drosophila),; ,, ; "glycoprotein, signal", , ; NM_008101,glucagon receptor, ; NM_008359,interleukin 17 receptor, ; AK014255,chondrolectin, ; BF178619,open reading frame 18, ; NM_010161,ecotropic viral integration site 2a, ; AK020555,anthrax toxin receptor 1, ; ,, ; "glycoprotein, signal peptide, transmembrane", , ; NM_021487,"potassium voltage-gated channel, Isk-related family, member 1-like", ; NM_028007,"DNA segment, Chr 8, Wayne State University 49, expressed", ; NM_008359,interleukin 17 receptor, ; BF178619,open reading frame 18, ; AK014255,chondrolectin,; NM_010161,ecotropic viral integration site 2a,; AK013584,pecanex homolog (Drosophila)

6.3.5 Categories of functional classification for genes differentially expressed in the testis between species

G-protein coupled receptor activity, ,; AF282303,olfactory receptor 959,; NM_011013,"opioid receptor, mu 1",; AK002481,RIKEN cDNA 0610010I15 gene,; U28784,olfactory receptor 150,; NM_011798,chemokine (C motif) receptor 1, ; AY042199,"MAS-related GPR, member B1", ; NM_008731,neuropeptide Y receptor Y2, ; NM_009747,"bradykinin receptor, beta 2", ; X15643,"adrenergic receptor, beta 2", ; NM_031872,"taste receptor, type 1, member 3", ; AB042408,G-protein coupled receptor 88, ; AF071080,olfactory receptor 631, ; NM_010935,neuropeptide Y receptor Y6, ; NM_008772,"purinergic receptor P2Y, G-protein coupled 1", ; AF071080,olfactory receptor 632, ; NM_021382,tachykinin receptor 3, ; NM_010934,neuropeptide Y receptor Y1, ; NM_030733,G protein-coupled receptor 63, ; NM_008552,MAS1 oncogene, ; ,, ; "G-protein coupled receptor activity, Glycoprotein", , ; AK013576,brain-specific angiogenesis inhibitor 3, ; AK002481,RIKEN cDNA 0610010I15 gene, ; NM_008057,frizzled homolog 7 (Drosophila),; NM_030733,G protein-coupled receptor 63,; NM_008552,MAS1 oncogene, ; ,, ; Glycoprotein, , ; NM_016715,"thymic stromal-derived lymphopoietin, receptor", ; NM_031254,triggering receptor expressed on myeloid cells 2, ; NM_013584,leukemia inhibitory factor receptor,; NM_010954,neural cell adhesion molecule 2,; NM_013584,leukemia inhibitory factor receptor, ; ,, ; "Glycoprotein, Erythropoietin", , ; NM_016715,"thymic stromal-derived lymphopoietin, receptor", ; NM_010149,erythropoietin receptor, ; NM_010149,erythropoietin receptor,; NM_013584,leukemia inhibitory factor receptor,; NM_013584,leukemia inhibitory factor receptor, ; ,, ; "G-protein coupled receptor activity, Glycoprotein", , ; AF282303,olfactory receptor 959, ; AK002481,RIKEN cDNA 0610010I15 gene, ; U28784,olfactory receptor 150,; AF071080,olfactory receptor 65,; AY042199,"MAS-related GPR, member B1", ; NM_011798,chemokine (C motif) receptor 1, ; NM_008731,neuropeptide Y receptor Y2, ; AF102524,olfactory receptor 50, ; NM_008330,olfactory receptor 56, ; AF071080,olfactory receptor 631, ; AB042408,G-protein coupled receptor 88, ; NM_010935,neuropeptide Y receptor Y6, ; NM_008772,"purinergic receptor P2Y, G-protein coupled 1", ; AF071080,olfactory receptor 632, ; AF358859,histamine H4 receptor, ; NM_030733,G protein-coupled receptor 63, ; AF071080,olfactory receptor 64, ; AF071080,olfactory receptor 66, ; NM_008552,MAS1 oncogene, ; ,, ; "Fibronectin, cell motility, cell adhesion", , ; NM_011248,roundabout homolog 3 (Drosophila), ; NM_008478,L1 cell adhesion molecule, ; NM_013584,leukemia inhibitory factor receptor,; NM_013584,leukemia inhibitory factor receptor,; NM_010954,neural cell adhesion molecule 2, ; ,, ; "Glycoprotein, transmembrane", , ; NM_023596,"solute carrier family 29 (nucleoside transporters), member 3", ; BC003482,transmembrane 4 superfamily member 7, ; AF204174,blood vessel epicardial substance,; NM_008536,transmembrane 4 superfamily member 1,; BF178619,open reading frame 18, ; ,, ; catabolism, , ; NM_030709,"transmembrane protease, serine 5 (spinesin)", ; AK017175,a disintegrin and metalloproteinase domain 12 (meltrin alpha), ; AF314187,thimet oligopeptidase 1,; AK012039,a disintegrin-like and metalloprotease (reprolysin type) wit ...,; NM_008486,alanyl (membrane) aminopeptidase, ; NM_019724,matrix metalloproteinase 16, ; M55333,angiotensin converting enzyme, ; ,, ; ion channel activity, , ; NM_008435,"K+ voltage-gated channel, subfamily S, 1", ; AK017384,potassium channel tetramerisation domain containing 6, ; BF159781,"potassium intermediate/small conductance calcium-activated channel, subfamily N, member 4",; AB016197,"potassium inwardly-rectifying channel, subfamily J, member 16",; NM_032397,"potassium intermediate/small conductance calcium-activated channel, subfamily N, member 1", ; AJ002199,"potassium voltage-gated channel, subfamily Q, member 1", ; AF112185,"sodium channel, nonvoltage-gated, type I, alpha polypeptide", ; NM_008227,"hyperpolarization-activated, cyclic nucleotide-gated K+ 3", ; ,, ; "prenylation, lipoprotein", , ; U38498,"guanine nucleotide binding protein (G protein), gamma 5 subunit", ; U38498,"guanine nucleotide binding protein (G protein), gamma 5", ; U38498,"guanine nucleotide binding protein (G protein), gamma 5 subunit",; U38498,"guanine nucleotide binding protein (G protein), gamma 5",; U38499,"guanine nucleotide binding protein (G protein), gamma 7 subunit", ; U38498,Guanine nucleotide-binding protein G(I)/G(S)/G(O) gamma-5 subunit, ; ,, ; lectin, , ; NM_008459,"killer cell lectin-like receptor subfamily A, member 10", ; AF288377,"killer cell lectin-like receptor, subfamily A, member 18", ; AF074459,"killer cell lectin-like receptor subfamily A, member 23",; U10094,"killer cell lectin-like receptor, subfamily A, member 7",; AF074459,"killer cell lectin-like receptor subfamily A, member 13", ; ,, ; growth factor activity, , ; AF020738,fibroblast growth factor 12, ; AF020738,fibroblast growth factor 12, ; AK020501,fibroblast growth factor 13,; NM_010198,fibroblast growth factor 11,; AF020738,FGF-12, ; AF020738,fibroblast growth factor 12, ; ,, ; defense response, , ; AK003665,"DNA segment, Chr 12, ERATO Doi 647, expressed", ; AE008684,"T-cell receptor alpha, variable 8", ; AE008685,"T-cell receptor alpha, variable 2.5",; AE008684,"T-cell receptor alpha, variable 2.4",; Z12138,"T-cell receptor beta, variable 13", ; AE008685,"T-cell receptor alpha, variable 2.2", ; AF034162,"T-cell receptor beta, variable 8.2", ; AF358859,histamine H4 receptor, ; ,, ; "myogenesis, cytoskeleton", , ; U04443,LC17, ; U04443,LC17, ; U04443,"myosin, light peptide 6, alkali, smooth muscle and non-muscle",; U04443,"myosin, light polypeptide 6, alkali, smooth muscle and non-muscle",; U04443,"myosin, light polypeptide 6, alkali, smooth muscle and non-muscle", ; ,, ; "protein catabolism, peptidase activity", , ; AK009212,SUMO/sentrin specific protease 2, ; NM_013918,ubiquitin specific protease 25, ; NM_030709,"transmembrane protease, serine 5 (spinesin)",; AE000663,hypothetical protein 1700020H15,; NM_011269,Rhesus blood group-associated A glycoprotein, ; NM_007603,calpain 6, ; AK013327,ubiquitin specific protease 43, ; AK021408,trophinin associated protein, ; NM_008454,kallikrein 16, ; AE000663,RIKEN cDNA 2210010C04 gene, ; AE000663,Trypsinogen 5, ; NM_008243,macrophage stimulating 1 (hepatocyte growth factor-like), ; NM_027344,RIKEN cDNA 2310051M13 gene, ; BC002100,kallikrein 10, ; NM_009462,ubiquitin specific protease 10, ; AE000665,Trypsinogen 15, ; NM_025985,"ubiquitin-conjugating enzyme E2G 1 (UBC7 homolog, C. elegans)", ; BC010784,secernin 2, ; AE000665,similar to trypsinogen 12, ; NM_008873,"plasminogen activator, urokinase", ; NM_020487,"protease, serine, 32", ; AE000663,RIKEN cDNA 1810009J06 gene, ; NM_015779,elastase 2, ; NM_007602,calpain 5, ; Z12280,RIKEN cDNA 1810049H19 gene, ; NM_013921,"transmembrane protease, serine 8 (intestinal)", ; AK014891,ubiquitin specific protease 15, ; NM_025827,RIKEN cDNA 1300002A08 gene, ; AF356627,coagulation factor XI, ; NM_021522,ubiquitin specific protease 14, ; AK006746,RIKEN cDNA 1700049K14 gene, ; NM_025583,chymotrypsinogen B1, ; AF314187,thimet oligopeptidase 1, ; NM_011969,"proteasome (prosome, macropain) subunit, alpha type 7", ; ,, ; "glucose catabolism, hexose catabolism, glycolysis ", , ; NM_013580,"lactate dehydrogenase 3, C chain, sperm specific", ; NM_013631,pyruvate kinase liver and red blood cell, ; NM_013631,pyruvate kinase liver and red blood cell,; AK006506,"enolase 3, beta muscle",; NM_013509,"enolase 2, gamma neuronal", ; NM_008084,glyceraldehyde-3-phosphate dehydrogenase, ; NM_013580,"lactate dehydrogenase 3, C chain, sperm specific", ; NM_013509,"enolase 2, gamma neuronal", ; BF584997,pyruvate dehydrogenase E1 alpha 1, ; NM_008155,glucose phosphate isomerase 1, ; ,, ; "Helicase, ATPase activity", , ; AF217319,RIKEN cDNA 0610007P08 gene, ; NM_026500,RIKEN cDNA 1210002B07 gene, ; BC009147,DEAH (Asp-Glu-Ala-His) box polypeptide 16,; AK004665,DEAH (Asp-Glu-Ala-His) box polypeptide 35,; BC011321,DEAD (Asp-Glu-Ala-Asp) box polypeptide 27, ; AK012782,DEAD (Asp-Glu-Ala-Asp) box polypeptide 55, ; AK007156,"ATP-binding cassette, sub-family A (ABC1), member 14", ; AK019495,DEAD (Asp-Glu-Ala-Asp) box polypeptide 10, ; AK010015,DEAD (Asp-Glu-Ala-Asp) box polypeptide 51, ; NM_021891,fidgetin-like 1, ; ,, ; pyrophosphatase activity, , ; AK019833,vacuolar protein sorting 4a (yeast), ; AK004676,nuclear VCP-like, ; NM_009190,vacuolar protein sorting 4b (yeast),; AK007156,"ATP-binding cassette, sub-family A (ABC1), member 14",; NM_011835,katanin p60 (ATPase-containing) subunit A1, ; NM_021891,fidgetin-like 1, ; ,, ; "GTP-binding, Ras GTPase, protein localization, protein transport", , ; NM_016858,"RAB33B, member of RAS oncogene family", ; NM_008999,"RAB23, member RAS oncogene family", ; AK010874,RIKEN cDNA 1810048P08 gene,; NM_025404,ADP-ribosylation factor 4-like,; NM_007487,ADP-ribosylation factor-like 4, ; ,, ; "protein kinase activity, cell cycle, cell division", , ; NM_011161,mitogen-activated protein kinase 11, ; NM_021479,testis-specific serine kinase 3, ; AK014760,RIKEN cDNA 4833424K13 gene,; NM_008641,microtubule associated serine/threonine kinase 2,; AF314149,"myosin, light polypeptide kinase", ; BC010539,aarF domain containing kinase 1, ; NM_007939,Eph receptor A8, ; AK018639,"casein kinase

1, gamma 1", ; AK015170,RIKEN cDNA 4930420O11 gene, ; NM_013690,endothelial-specific receptor tyrosine kinase, ; NM_010206,fibroblast growth factor receptor 1, ; AF302138,nuclear receptor binding protein, ; NM_010568,insulin receptor, ; NM_013690,endothelial-specific receptor tyrosine kinase, ; NM_010353,germ cell-specific gene 2, ; NM_020572,aurora kinase C, ; NM_011163,"protein kinase, interferon-inducible double stranded RNA dependent", ; AK017713,p21 (CDKN1A)-activated kinase 4, ; NM_008745,"neurotrophic tyrosine kinase, receptor, type 2", ; NM_009465,AXL receptor tyrosine kinase, ; L21707,receptor-like tyrosine kinase, ; NM_008745,"neurotrophic tyrosine kinase, receptor, type 2", ; NM_007938,Eph receptor A6, ; AK009373,cell division cycle 2-like 5 (cholinesterase-related cell division controller), ; AK004069,TAO kinase 2TAO kinase 2, ; AK004211,RIKEN cDNA C230081A13 gene, ; NM_011163,"protein kinase, interferon-inducible double stranded RNA dependent", ; L21707,receptor-like tyrosine kinase, ; AF059177,v-erb-a erythroblastic leukemia viral oncogene homolog 4 (avian), ; U11822,cyclin-dependent kinase 7 (homolog of Xenopus MO15 cdk-activating kinase), ; NM_008854,"protein kinase, cAMP dependent, catalytic, alpha", ; AK013366,"thrombospondin, type I, domain 2", ; NM_007463,aortic preferentially expressed gene 1, ; AK020200,MAP kinase-activated protein kinase 2, ; NM_011973,renal tumor antigen, ; AK004199,RIKEN cDNA 1110048D14 gene, ; NM_011951,mitogen activated protein kinase 14, ; NM_007668,cyclin-dependent kinase 5, ; NM_007668,cyclin-dependent kinase 5, ; U40827,"v-abl Abelson murine leukemia viral oncogene 2 (arg, Abelson-related gene)", ; NM_009759,BMX non-receptor tyrosine kinase, ; ,, ; "protein ubiquitination, protein modification, protein metabolism", , ; AK006367,"zinc finger, SWIM domain containing 2", ; AK011391,RIKEN cDNA 2610014F08 gene, ; NM_025863,tripartite motif-containing 59,; AF151110,expressed sequence C80879,; U20780,RIKEN cDNA B230113M03 gene, ; AK020657,PDZ domain containing RING finger 3, ; AK011926,"DNA segment, Chr 6, ERATO Doi 365, expressed", ; AK007391,RIKEN cDNA 1810009A16 gene, ; AK021070,RIKEN cDNA 4931406I20 gene, ; AK005386,"zinc finger, FYVE domain containing 19", ; AB015425,deltex 3 homolog (Drosophila), ; AK002414,RIKEN cDNA 0610009J22 gene, ; AF033664,cDNA sequence BC065123, ; NM_009174,seven in absentia 2, ; AK002387,RIKEN cDNA 0610009F02 gene, ; NM_019719,STIP1 homology and U-Box containing protein 1, ; AK009324,ubiquitin-conjugating enzyme E2Q (putative), ; AK010429,ring finger protein 135, ; BC003945,ring finger protein 123, ; AF220135,tripartite motif protein 17, ; AK004344,RIKEN cDNA 1110061N23 gene, ; AF361000,ubiquitin conjugating enzyme 7 interacting protein 1, ; AK005929,RIKEN cDNA C330018L13 gene, ; AF230385,tripartite motif protein 32, ; ,, ; "clathrin vesicle coat, protein transport", , ; NM_007454,"adaptor protein complex AP-1, beta 1 subunit", ; NM_019877,"coatomer protein complex, subunit zeta 2", ; NM_007458,"adaptor protein complex AP-2, alpha 1 subunit",; L39116,"golgi associated, gamma adaptin ear containing, ARF binding protein 2",; NM_007459,"adaptor protein complex AP-2, alpha 2 subunit", ; ,, ; "microtubule, cytoskeleton", , ; AK013867,RIKEN cDNA 3000004C01 gene, ; AB054031,kinesin family member 26A, ; M61952,kinesin family member C5A,; BC006841,kinesin family member 2C,; AB001431,kinesin family member 14, ; AK017434,kinesin family member 5B, ; AB001456,kinesin family member 1C, ; AK015814,kinesin family member 27, ; ,, ; protein phosphatase activity, , ; AK008492,dual specificity phosphatase 11 (RNA/RNP complex 1-interacting), ; BC006582,"protein tyrosine phosphatase, non-receptor type 23", ; NM_011200,protein tyrosine phosphatase 4a1,; AF073881,myotubularin related protein 9,; NM_008748,dual specificity phosphatase 8, ; AK010841,dual specificity phosphatase 12, ; NM_010146,"epilepsy, progressive myoclonic epilepsy, type 2 gene alpha", ; ,, ; glycoprotein metabolism, , ; NM_033149,"UDP-Gal:betaGlcNAc beta 1,3-galactosyltransferase, polypeptide 5", ; AK003089,UDP-glucose ceramide glucosyltransferase-like 1, ; BC002175,ribophorin I,; NM_020283,"UDP-Gal:betaGlcNAc beta 1,3-galactosyltransferase, polypeptide 1",; AK019824,"sialyltransferase 4C (beta-galactoside alpha-2,3-sialytransferase)", ; AK014029,fucosyltransferase 11, ; ,, ; "nuclear import, protein import, spindle organization and biosynthesis", , ; AF159256,"RAN, member RAS oncogene family", ; AF159256,"RAN, member RAS oncogene family", ; AF159256,"RAN, member RAS oncogene family",; AF159256,RAN protein,; AF159256,GTPase Ran, ; AF159256,"RAN, member RAS oncogene family", ; ,, ; "mitochondrion, ligatin, ribosome", , ; AK012937,RIKEN cDNA 2410005K20 gene, ; U58337,ligatin, ; NM_025380,eukaryotic translation elongation factor 1 epsilon 1,; BF299809,ribosomal protein S26,; AK003500,mitochondrial ribosomal protein L14, ; U54563,"eukaryotic translation initiation factor 3, subunit 6", ; AB049641,mitochondrial ribosomal protein L13, ; BC003426,"eukaryotic translation initiation factor 2B, subunit 1 (alpha)", ; NM_007990,Finkel-Biskis-Reilly murine sarcoma virus (FBR-MuSV) ubiquitously expressed (fox derived), ; BC005709,PET112-like (yeast), ; NM_026007,eukaryotic translation elongation factor 1 gamma, ; U11248,40S ribosomal protein S28, ; NM_011297,ribosomal protein S24, ; NM_025553,mitochondrial ribosomal protein L11, ; AB049657,mitochondrial ribosomal protein L43, ; U11248,ribosomal protein S28, ; U54563,"eukaryotic translation initiation factor 3, subunit 6 48kDa", ; NM_021338,ribosomal protein L35a, ; NM_009081,ribosomal protein L28, ; NM_025302,mitochondrial ribosomal protein L2, ; U11248,40S ribosomal protein S28, ; AJ279835,laminin receptor 1 (ribosomal protein SA), ; NM_026055,ribosomal protein L39, ; NM_025586,ribosomal protein L15, ; U11248,ribosomal protein S28, ; NM_025425,ribosomal protein L3-like, ; AK010610,ribosomal protein S21, ; U54563,"eukaryotic translation initiation factor 3, subunit 6", ; U11248,40S ribosomal protein S28, ; NM_019883,ubiquitin A-52 residue ribosomal protein fusion product 1, ; NM_020600,ribosomal protein S14, ; NM_017404,mitochondrial ribosomal protein L39, ; NM_025829,eukaryotic translation initiation factor 4E member 3, ; NM_026423,RIKEN cDNA 2410018C20 gene, ; U11248,ribosomal protein S28, ; ,, ; RNA polymerase activity, , ; NM_025298,polymerase (RNA) III (DNA directed) polypeptide E, ; BC004810,polymerase (RNA) II (DNA directed) polypeptide D, ; NM_011293,polymerase (RNA) II (DNA directed) polypeptide J,; BC004810,polymerase (RNA) II (DNA directed) polypeptide D,; NM_025901,polymerase (RNA) III (DNA directed) polypeptide K, ; ,, ; "RNA processing, splicing", , ; AK003520,transcription factor INI, ; NM_009159,"splicing factor, arginine/serine-rich 5 (SRp40, HRS)", ; AK003520,PHD finger protein 5A,; AK003520,PHD finger protein 5A,; AF060873,P-Frk, ; AF060873,forkhead box L2, ; AF060873,forkhead box L2, ; AK003520,PHD finger protein 5A, ; NM_010095,early B-cell factor 2, ; ,, ; chromosome organization and biogenesis, , ; U62673,"histone 2, H2bb", ; AK009512,"heterochromatin protein 1, binding protein 3", ; X16496,Histone H3.1 protein,; NM_013926,chromobox homolog 8 (Drosophila Pc class),; X16496,"histone 1, H3f", ; AF033664,bromodomain adjacent to zinc finger domain 1A, ; U62673,"histone 2, H2ac", ; X16496,"histone 1, H3a", ; U62673,Histone H2a(B)-613, ; U62673,"histone 2, H2ac", ; NM_009881,"chromodomain protein, Y chromosome-like", ; X16496,"histone 1, H3a", ; AK020244,chromodomain helicase DNA binding protein 9, ; X16496,Histone H3.1 protein, ; NM_008229,histone deacetylase 2, ; ,, ; "Ankyrin repeat, DNA-dependet transcription", , ; NM_024204,ankyrin repeat domain 22, ; BC012275,ankyrin repeat and MYND domain containing 2, ; AK011987,fem-1 homolog c (C.elegans),; AK019475,ankyrin repeat domain 24,; AK014667,"DNA segment, Chr 1, ERATO Doi 161, expressed", ; AK017844,RIKEN cDNA 5730557B15 gene, ; ,, ; regulation of transcription, , ; AK018267,thyroid hormone receptor associated protein 2, ; AF277399,"cat eye syndrome chromosome region, candidate 6 homolog (human)", ; NM_009504,vitamin D receptor,; AF060873,forkhead box L2,; NM_009575,zinc finger protein of the cerebellum 3, ; NM_019483,MAD homolog 9 (Drosophila), ; NM_009555,zinc finger protein 40, ; NM_011939,heat shock transcription factor 4, ; NM_010150,"nuclear receptor subfamily 2, group F, member 6", ; BC011070,myocyte enhancer factor 2D, ; AK020639,runt related transcription factor 2, ; AK016816,SRY-box containing gene 5, ; NM_024204,ankyrin repeat domain 22, ; NM_010813,max binding protein, ; NM_013468,ankyrin repeat domain 1 (cardiac muscle), ; AK021059,RIKEN cDNA 5830403E09 gene, ; NM_009327,transcription factor 1, ; AF169968,AT rich interactive domain 5B (Mrf1 like), ; NM_013646,RAR-related orphan receptor alpha, ; M32073,"retinoic acid receptor, gamma", ; U12142,"nuclear receptor subfamily 1, group D, member 2", ; NM_009346,TEA domain family member 1, ; AB010368,zinc finger protein 458, ; NM_025821,calcium regulated heat stable protein 1, ; U29510,KRAB-zinc finger protein 76, ; AJ238332,death inducer-obliterator 1, ; NM_010791,mesenchyme homeobox 1, ; NM_013554,homeo box D10, ; AK009218,SKI interacting protein, ; NM_007526,BarH-like homeobox 1, ; AF033664,cDNA sequence BC065123, ; AK007768,RIKEN cDNA 4933432P15 gene, ; AK003347,trans-acting transcription factor 1, ; NM_010638,basic transcription element binding protein 1, ; BC008233,basic transcription factor 3, ; NM_010637,Kruppel-like factor 4 (gut), ; NM_013844,zinc finger protein 68, ; NM_010751,Max dimerization protein, ; NM_025901,polymerase (RNA) III (DNA directed) polypeptide K, ; NM_009335,"transcription factor AP-2, gamma", ; NM_013646,RAR-related orphan receptor alpha, ; NM_020625,zinc finger protein 297, ; BC012278,cDNA sequence BC012278, ; AK020523,RIKEN cDNA C630016O21 gene, ; AK011776,RIKEN cDNA 2610044O15 gene, ; AK007201,"nuclear receptor subfamily 6, group A, member 1", ; NM_008719,neuronal PAS domain protein 2, ; AK017987,transcription factor 12, ; AK003919,trans-acting transcription factor 6, ; AK004823,PHD finger protein 15, ; AB020974,"nuclear factor of kappa light polypeptide gene enhancer in B-cells inhibitor, zeta", ; AK018654,forkhead box P1, ; AF165984,Iroquois related homeobox 1 (Drosophila), ; NM_010836,"homeo box, msh-like 3", ; L13204,forkhead box J1, ; NM_009537,YY1 transcription factor, ; NM_009547,zinc finger protein 161, ; U57329,T-box 4, ; AK010742,protein kinase C binding protein 1, ; AK004745,ring finger protein (C3H2C3 type) 6, ; AK007587,RIKEN cDNA 1810022O10 gene, ; AB010345,Mszf52, ; NM_009559,zinc finger protein 57, ; NM_010157,estrogen receptor 2 (beta), ; NM_016861,PDZ and LIM domain 1 (elfin), ; Z18958,SRY-box containing gene 9, ; NM_008829,progesterone receptor, ; BC011070,myocyte enhancer factor 2D, ; AK019930,trichorhinophalangeal syndrome I (human), ; AK003347,trans-acting transcription factor 1, ; AK009725,zinc finger protein 180, ; AK007318,COMM domain containing 3, ; AF060873,P-Frk, ; BC005508,"cofactor required for Sp1 transcriptional activation, subunit 3", ; AK017346,checkpoint supressor 1, ; NM_008616,zinc finger protein 239, ; NM_026570,YEATS domain containing 4, ; NM_007524,bagpipe homeobox gene 1 homolog (Drosophila), ; BC008233,basic transcription factor 3, ; NM_016767,"basic leucine zipper transcription factor, ATF-like", ; NM_009343,PHD finger protein 1, ; AB010309,zinc finger protein 566, ; BF577415,RIKEN cDNA C330002I19 gene, ; NM_023239,necdin-like 2, ; AB010372,Mszf87, ; Y17859,RIKEN cDNA 1810043J12 gene, ; NM_019797,thyroid hormone receptor interactor 4, ; D83147,sine oculis-related homeobox 2 homolog (Drosophila), ; BF579673,"nuclear receptor subfamily 1, group H, member 2", ; NM_010095,early B-cell factor 2, ; AK021354,"jumonji, AT rich interactive domain 1A (Rbp2 like)", ; NM_019969,pleiomorphic adenoma gene 1, ; NM_019563,"Cbp/p300-interacting transactivator, with Glu/Asp-rich carboxy-terminal domain, 4", ; U29510,zinc finger protein 52, ; AK011987,fem-1 homolog c (C.elegans), ; AJ278340,zinc finger protein 296, ; NM_016710,nucleosome binding protein 1, ; AK017574,PHD finger protein 8, ; AK005818,zinc finger protein 297B, ; NM_007520,BTB and CNC homology 1, ; AK013488,hepatic leukemia factor, ; BC005782,RIKEN cDNA 4732460K03 gene, ; AK013393,PR domain containing 4, ; AK017176,"general transcription factor IIH, polypeptide 3", ; AK012336,RIKEN cDNA 2700038I16 gene, ; NM_020493,serum response factor, ; AY046077,Notch-regulated ankyrin repeat protein, ; NM_010347,amino-terminal enhancer of split, ; NM_009542,zinc finger protein 101, ; AF033664,bromodomain adjacent to zinc finger domain 1A, ; U29511,zinc finger protein 78, ; NM_011441,SRY-box containing gene 17, ; BC003941,zinc finger protein 639, ; AK012264,"nuclear receptor subfamily 1, group I, member 3", ; AB047007,ring finger protein 134, ; AF060873,forkhead box L2, ; AB010331,Mszf17, ; NM_013646,RAR-related orphan receptor alpha, ; BC011226,PHD finger protein 3, ; NM_009346,TEA domain family member 1, ; NM_023162,"zinc ribbon domain containing, 1", ; NM_009557,zinc finger protein 46, ; AK011845,general transcription factor III A, ; U29507,"zinc finger protein 71, related sequence 1", ; AK012874,zinc finger protein 248, ; AK014667,"DNA segment, Chr 1, ERATO Doi 161, expressed", ; NM_008394,interferon dependent positive acting transcription factor 3 gamma, ; AK014523,ankyrin repeat and IBR domain containing 1, ; AF357389,RIKEN cDNA D030022P06 gene, ; AK004085,HCF-binding transcription factor Zhangfei, ; NM_013646,RAR-related orphan receptor alpha, ; NM_010757,"v-maf musculoaponeurotic fibrosarcoma oncogene family, protein K (avian)", ; ,, ; "chromosome organization and biogenesis, DNA packaging", , ; AK013316,"sirtuin 6 (silent mating type information regulation 2, homolog) 6 (S. cerevisiae)", ; NM_009881,"chromodomain protein, Y chromosome-like", ; NM_013926,chromobox homolog 8 (Drosophila Pc class),; AF033664,bromodomain adjacent to zinc finger domain 1A,; NM_008229,histone deacetylase 2, ; AK008751,RIKEN cDNA 2210018M11 gene, ; ,, ; "regulation of transcription, chromosome organization and biogenesis", , ; AK017176,"general transcription factor IIH, polypeptide 3", ; AF169968,AT rich interactive domain 5B (Mrf1 like), ; NM_013926,chromobox homolog 8 (Drosophila Pc class),; NM_008229,histone deacetylase 2,; AF033664,bromodomain adjacent to zinc finger domain 1A, ; AK008751,RIKEN cDNA 2210018M11 gene

6.4 List of genes with available UniGene ID and *Mus-Rattus* dN/dS ratio

Unigene ID, GenBankAcc, dN/dS_mouse_rat; Mm.102183, AK017757, 0; Mm.122366, AK017138, 0; Mm.182746, NM_008098, 0; Mm.259079, AK011126, 0; Mm.277533, AK010201, 0; Mm.299737, NM_009920, 0; Mm.340315, NM_025985, 0; Mm.358579, NM_007545, 0; Mm.379140, BC002177, 0; Mm.41484, AK005257, 0; Mm.43358, NM_008783, 0; Mm.42051, NM_011021, 0.000668; Mm.274308, X61455, 0.0006725; Mm.214950, X03766, 0.0006734; Mm.10091, NM_011106, 0.0006739; Mm.260943, NM_019570, 0.0006739; Mm.28540, AK007763, 0.0006739; Mm.246605, AL358753, 0.0006798; Mm.21697, AK017926, 0.0006835; Mm.259506, AK013433, 0.0006882; Mm.1155, AI840604, 0.0006887; Mm.73608, NM_025318, 0.0006911; Mm.12814, NM_008004, 0.0006944; Mm.20294, BF101088, 0.0006944; Mm.7106, NM_007561, 0.0006969; Mm.338713, NM_010250, 0.0006974; Mm.343095, AY037837, 0.0006983; Mm.10699, NM_016796, 0.0007027; Mm.21198, NM_008124, 0.0007042; Mm.41558, BC012515, 0.0007107; Mm.5127, NM_008426, 0.0007112; Mm.41603, AK007352, 0.0007138; Mm.87277, AK010717, 0.0007138; Mm.340658, NM_011289, 0.0007143; Mm.289248, BC009104, 0.0007148; Mm.28265, BC008547, 0.0007236; Mm.29952, AK019452, 0.0007257; Mm.68933, NM_016961, 0.0007278; Mm.68933, NM_016961, 0.0007278; Mm.45616, NM_028502, 0.000731; Mm.291708, NM_021383, 0.0007358; Mm.271178, NM_026011, 0.0007369; Mm.288765, NM_017374, 0.0007479; Mm.338723, NM_008070, 0.0007491; Mm.41678, AK012063, 0.000761; Mm.274846, NM_010562, 0.0007794; Mm.314338, NM_007396, 0.0007812; Mm.27064, AK005032, 0.0007831; Mm.294138, NM_016891, 0.0007918; Mm.22780, NM_025294, 0.0007949; Mm.200770, NM_019827, 0.0007968; Mm.372086, NM_024214, 0.0008052; Mm.226435, NM_020283, 0.0008107; Mm.250441, AK006171, 0.0008117; Mm.200859, NM_008775, 0.000813; Mm.353006, NM_021428, 0.0008137; Mm.234261, Z29629, 0.0008187; Mm.234261, Z29629, 0.0008187; Mm.3955, NM_018749, 0.0008254; Mm.30214, BC010790, 0.0008292; Mm.269188, NM_026532, 0.0008326; Mm.215971, NM_007897, 0.0008382; Mm.313244, AK010454, 0.0008432; Mm.290810, AK011979, 0.000846; Mm.313236, BF140573, 0.0008485; Mm.37274, NM_025921, 0.000854; 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Mm.34145, AF214653, 0.0009145; Mm.379015, NM_009223, 0.0009145; Mm.24564, BC013800, 0.0009204; Mm.245394, X68882, 0.0009208; Mm.1536, NM_008631, 0.0009217; Mm.379044, NM_011740, 0.0009217; Mm.1478, NM_007909, 0.0009228; Mm.154581, Z78147, 0.0009238; Mm.287544, NM_009524, 0.0009264; Mm.5039, D83147, 0.0009307; Mm.260271, NM_011513, 0.000932; Mm.260271, NM_011513, 0.000932; Mm.290027, NM_026554, 0.0009341; Mm.376184, NM_010225, 0.0009341; Mm.246240, AK010974, 0.0009355; Mm.29965, BC010601, 0.0009363; Mm.29965, BC010601, 0.0009363; Mm.282706, AK018153, 0.0009372; Mm.23960, AK014009, 0.0009416; Mm.24838, AB035322, 0.0009425; Mm.307455, AK005902, 0.0009479; Mm.56946, NM_008901, 0.0009497; Mm.241121, NM_019430, 0.0009515; Mm.23690, NM_026594, 0.0009542; Mm.277408, NM_008569, 0.000956; Mm.29582, AA512422, 0.0009569; Mm.1972, NM_009008, 0.0009574; Mm.241931, M27073, 0.0009615; Mm.25652, NM_008128, 0.0009615; Mm.25652, NM_008128, 0.0009615; Mm.379001, NM_019647, 0.0009625; Mm.274610, AK004167, 0.0009634; 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Christian Voolstra

Köln, den 20.03.2006

Lebenslauf

Name: Christian Voolstra

Anschrift: Falkenburgstraße 26
50935 Köln

Geburtstag, Geburtsort: 23.08.1975 in Offenbach/Main

Staatsangehörigkeit: deutsch

Schulbildung:

1982 – 1986: Brüder-Grimm-Schule, Lämmerspiel
1986 – 1995: Franziskaner Gymnasium Kreuzburg, Groß-Krotzenburg

Wehrersatzdienst:

1995 – 1996: Frühförderung in Stadt und Kreis Offenbach/Main

Studium:

1996 – 1998: Universität Köln – Vordiplom Biologie
1998 – 2000: Universität Köln – Hauptstudium mit den Schwerpunkten Genetik, Biochemie, Organische Chemie
2000 – 2001: Diplomarbeit bei Professor Dr. Diethard Tautz am Institut für Genetik der Universität Köln – Titel: „Evolution von Gen- und Promotor-Strukturen durch vergleichende Analyse eines Gens und seines Promotors in den Schwesterspezies *Drosophila melanogaster* und *Drosophila yakuba*“
seit Januar 2002: Beginn der Promotion bei Professor Dr. Diethard Tautz am Institut für Genetik der Universität Köln – Titel: „Evolution of gene expression between closely related taxa of *Mus*“
Juni 2006: voraussichtlicher Abschluss der Promotion

Christian Voolstra

Köln, den 20.03.2006