UDC 575
DOI: 10.2298/GENSR1501357S
Review *paper*

70 YEARS OF RESEARCH ON THE AMERICAN MINK (*Neovison vison* SCHREB., 1777) GENETICS – WHERE ARE WE NOW?

Jakub Jan SKORUPSKI

Department of Genetics and Animal Breeding, West Pomeranian University of Technology in Szczecin, Poland

Skorupski J. J. (2015): *70 years of research on the American mink (Neovison vison schreb., 1777) genetics – where are we now?*- Genetika, Vol 47, No. 1, 357-373.

The purpose of this review is to present the current state of knowledge about the genetics of the American mink (*Neovison vison* Schreb., 1777) – a species that achieved in the twentieth century an unprecedented ecological success associated with the dynamic development of its economic use. However, despite the large popularity and economic importance of the American mink as a fur animal, and the scale of the problems associated with its introduction beyond the range of natural occurrence, genetic research, particularly molecular genetics and genomics of this species, show relatively little progress. The article contains a comprehensive description of the studies undertaken on the genetics of the species, both in terms of cytogenetics, molecular genetics, genomics, population genetics and phylogenetics. The progress of the genome sequencing project of the American mink is also described as well as its transcriptome annotation. The article also deals with still unexplained and not completed, despite 70 years of genetic research, issues such as the standard karyotype, the precise molecular basis of coat color inheritance and systematic position of the species.

Key words: American mink, genetics, cytogenetics, genomics, molecular genetics, phylogenetics, genome sequencing, transcriptomics

INTRODUCTION

The American mink (*Neovison vison* Schreb., 1777) is a species that experienced unprecedented ecological success in the 20th century (GENOVESI *et al.*, 2010). This can be seen in both the dynamic increase in zoogeographical range of the species, and in its effective adaptation to ecological niches in new areas (GENOVESI *et al.*, 2010; SINITSYN, 1992; HALLIWELL and

Corresponding author: Jakub Jan Skorupski, Department of Genetics and Animal Breeding, West Pomeranian University of Technology in Szczecin, Piastów 45 Ave., 70-311 Szczecin, Poland; phone: +48 512 014 658; e-mail: jakub@gajanet.pl

MACDONALD, 1996). Nevertheless, despite the increasing economic importance of the American mink and its wide geographical spread, the genome of this species remains one of the least studied among livestock species (ANISTOROAEI *et al.*, 2009; BENKEL *et al.*, 2012).

First organized and systematic investigation of the genetics of the American mink (*Neovison vison* Schreb., 1777) was conducted by CASTLE and MOORE (1946), as well as by SHACKELFORD and WIPF in the 40s of the last century (SHACKELFORD and WIPF, 1947; SHACKELFORD, 1948). Their pioneering research focused on the genetic inheritance of coat color of animals kept on farms and cytogenetics of the species, and was related to the development of farming and breeding of the American mink. The first textbook on the genetics of the American mink was developed by KING (1951), whose *Genetics of mink* was the first comprehensive description of the state of research on the genetics of the American mink, describing the then state of the art in this field.

Genetic studies of the American mink conducted over the last 70 years are primarily associated with three areas – breeding and fur application, genetics of wild American mink in North America, and the American mink genetics as invasive alien species beyond its natural range.

Genetic studies related to the economic use of the American mink focus on the inheritance of coat color (SHACKELFORD, 1948; TRAPEZOV, 1997; ANISTOROAEI *et al.*, 2008; BENKEL *et al.*, 2009), chromosome banding (MANDAHL and FREDGA, 1975), location of genes by comparative cytogenetics and somatic hybridization methods (PACK *et al.*, 1992; HAMEISTER *et al.*, 1997; GRAPHODATSKY *et al.*, 2000; KUZNETSOV *et al.*, 2003), identification of microsatellite markers (ANISTOROAEI *et al.*, 2006; ANSARI *et al.*, 2007), construction of genetic maps (linkage maps) and physical maps (ANISTOROAEI *et al.*, 2007; ANISTOROAEI *et al.*, 2009; BENKEL *et al.*, 2012), mapping of single nucleotide polymorphisms (SNPs) (BENKEL *et al.*, 2008; SKORUPSKI, 2009; SKORUPSKI and KMIEĆ 2011; KMIEĆ *et al.*, 2013a, KMIEĆ *et al.*, 2013b) and identification of quantitative trait loci (QTLs) (THIRSTRUP *et al.*, 2012).

Research on the genetics of wild American mink relates primarily to intra-species differentiation using microsatellite sequences (SHIMATANI *et al.*, 2010), non-invasive methods to determine species affinity (RIDDLE *et al.*, 2003), phylogenetic relationships of the species (NIE *et al.*, 2002), and the impact of farm-escaped animals on wild populations of the American mink (BOWMAN *et al.*, 2007).

Research on the American mink accidentally or intentionally introduced outside North America is focused on the determination of genetic diversity and population genetic structure of these animals (MICHALSKA-PARDA *et al.*, 2009; ZALEWSKI *et al.*, 2011; PERTOLDI *et al.*, 2013) and the genetic differences between them and farm minks (HAMMERSHØJ *et al.*, 2005; MICHALSKA-PARDA *et al.*, 2009; SKORUPSKI, 2012; SKORUPSKI and KMIEĆ, 2013b).

CYTOGENETICS – PIONEERING STUDIES AND STILL UNSOLVED PROBLEMS

Diploid number of chromosomes of the American mink is 30, which is low in comparison with other members of the family *Mustelidae* – in over 60% of the species of the group 2n=38 (LANDE, 1957; HUMPHREY and SPENCER, 1959; GRAPHODATSKY *et al.* 2000; FRANCO-DE-SÁ *et al.*, 2007). This difference is particularly evident when compared with the genus *Mustela*, in which the diploid number of chromosomes ranges from 38 to 44 (EWER, 1973; KUROSE *et al.*, 2008).

Pioneering research on the American mink karyotype was conducted by SHACKELFORD and WIPF (1947). Subsequent studies resulted in the development of two systems of mink chromosome nomenclature (ANISTOROAEI *et al.*, 2007). The first was introduced in 1975 by

MANDAHL and FREDGA and currently it is rather of historical significance. The second, now widely used, has been proposed by CHRISTENSEN *et al.* in 1996. The works on the development of standard karyotype of this species are still ongoing (HAMEISTER *et al.*, 1997; FRANCO-DE-SÁ *et al.*, 2007).

Table 1. Nomenclature systems of the American mink chromosomes and their morphological characteristics

CHROMOSOME TYPE	CHROMOSOME NUMBER		MORPHOLOGY											
			relative length						centromere position (%)					
	Ch1	M	N	M	Ch1	Ch2	S	$\overline{x}$	N	M	Ch1	Ch2	S	$\bar{x}$
AUTOSOMES	1	1	117	117	119	120	111	117	52	51	52	52	52	52
	2	2	94	95	94	94	105	96	54	54	54	54	54	54
	3	4	83	84	86	87	87	85	52	51	52	55	50	52
	4	3	87	87	84	85	87	86	52	50	54	56	50	52
	5	8*	72	71	70	71	70	71	52	50	47	53	46	50
	6	5	82	81	83	83	79	82	64	66	67	65	56	64
	7	7	76	76	78	79	82	78	60	57	63	64	57	60
	8	11	54	54	53	53	49	53	60	60	66	66	55	61
	9	12	38	38	39	40	38	39	62	64	62	62	50	60
	10	13	32	32	30	31	35	32	58	58	66	66	58	61
	11	6	80	79	81	81	76	79	72	75	76	76	65	73
	12	9	60	57	59	60	52	58	68	76	73	74	57	70
	13	10	55	54	55	55	49	54	69	75	77	77	60	72
	14	14	24	19	17	18	20	20	100	100	100	100	100	100
HETEROSOMES	X	X	48	49	44	45	52	48	56	55	61	62	66	60
	Y	Y	–**	–	12	–	9	11	–	–	–	–	–	–

developed based on NES (1962) – N, MANDAHL and FREDGA (1975) – M, SEROV *et al.* (1987) – S, CHRISTENSEN *et al.* (1996) – Ch1, CHRISTENSEN and ANISTOROAEI (2008) – Ch2; * inverted by 180°; ** '–' indicates no data.

The American mink chromosomes consists of 13 pairs of biarmed autosomes (4 meta-, 5 submeta- and 4 subtelocentric chromosomes) and a pair of uniarmed autosomes, submetacentric X chromosome and a metacentric Y chromosome (FREDGA 1961; ŚWITOŃSKI *et al.*, 2006). A slightly different formula of metaphase chromosomes' morphology is provided by MANDAHL and FREDGA (1975) and NIE *et al.* (1998). According to these authors, the karyotype of *N. vison* consists of 5 pairs of metacentric autosomes, 8 pairs of submetacentric autosomes, 1 pair of acrocentric autosomes, metacentric X chromosome and a biarmed Y chromosome. CHRISTENSEN *et al.* (1996) have identified 5 pairs of metacentric autosomes, 5 submetacentric pairs, 3 acrocentric pairs, 1 telocentric pair and 1 pair of sex chromosomes. The fundamental autosomal number (FNa) is 54 (ZIMA and KRÁL 1984). Details of the morphology of mink chromosomes are summarized in Table 1.

FREDGA (1961) distinguished three groups of *N. vison* chromosomes in terms of size: 7 large, 5 medium (including X chromosome), 4 small (including the smallest of all chromosomes – Y chromosome). ITOH (1968) distinguished seven morphological groups of mink autosomes – 4 pairs of large meta- and submetacentric chromosomes, 3 pairs of large submeta- and subtelocentric chromosomes, 1 pair of medium-sized submetacentric chromosomes, 2 pairs of medium subtelocentric chromosomes, 1 pair of small submetacentric chromosomes, 2 pairs of small submetacentric chromosomes and 1 pair of small telocentric chromosomes (Table 1). The Y chromosome, according to this author, is submetacentric.

The exact characteristics of Q, G and C bands of the American mink chromosomes is provided by MANDAHL and FREDGA (1975). Also R band patterns, DAPI banding and N bands, located on chromosomes 2 and 5, and obtained by silver staining of nucleolar organiser regions (AgNOR), have been described for the species (GRAPHODATSKY and RADJABLI, 1988; CHRISTENSEN *et al.*, 1996; HAMEISTER *et al.*, 1997).

CHARACTERIZATION OF THE AMERICAN MINK GENOME

The size of the genome of *N. vison* is estimated at 1327 cM (BORODIN *et al.*, 2009). At the same time, it is believed that its size should be similar to the size of relatively closely related ferret (*Mustela putorius furo* L., 1758), which genome comprises approx. 2700 Mb (ANISTOROAEI *et al.*, 2011). Genomic linkage maps, developed based on 114 marker sequences deposited in the BAC (bacterial artificial chromosome) library of this species, allowed to determine the size of the genome of individuals of both sexes; in females this value is approx. 1379 cM, while in male approx. 1015 cM (ANISTOROAEI *et al.*, 2012d).

Preliminary analysis of the sequenced genome fragments, representing approximately one-thousandth part of it, indicates the contents of GC bases at 41-43%, which approximately corresponds to their content in the human genome (LANDER *et al.*, 2001; ANISTOROAEI *et al.*, 2011; BENKEL *et al.*, 2012). The content of interspersed mobile genetic elements have been also determined, which in the American mink constitute approx. 31% of the genome fragments sequenced thus far (BENKEL *et al.*, 2012). A total of 2416 elements was found, of which over 45% were SINE (Short Interspersed Nuclear Elements), nearly 36% were LINE (Long Interspersed Nuclear Elements), 12% represented LTR (Long Terminal Repeats), while DNA transposons – 7% (BENKEL *et al.*, 2012).

In the past, a project was carried out on establishing a cosmid library for the American mink, primarily to identify repetitive sequences (BRUSGAARD *et al.*, 1998).

GENETIC MARKERS

Studies on genetic markers in *N. vison* include both class I markers (genes encoding the qualitative traits of the body) as well as class II markers (non-coding DNA sequences). Among class I genetic markers in mink, polymorphism of plasma esterase has been described – seven allelic forms, (SIMONSEN *et al.*, 1992; KUŹNIEWICZ and FILISTOWICZ, 1999), B and D peptidases (EC 3.4) – two allelic forms each (MULLAKANDOV *et al.*, 1986), α-2 lipoprotein/HDL (high density lipoprotein) – eight allelic forms (BARANOV *et al.*, 1987), LDL (low density lipoprotein) – two allelic forms (BARANOV and SAVINA, 1981), an inhibitor of α-1 protease – two allelic forms (BORODIN *et al.*, 1995) and immunoglobulin G (IgG) – twelve allelic forms (FOMICHEVA, 1991). Polymorphisms of plasma fraction, erythrocytic antigens and MHC class I protein of the American mink were also investigated (BIEGUSZEWSKI, 1966; RAPACZ and SHACKELFORD, 1966; RAPACZ *et al.*, 1970; WEINBERG and AASTED, 1991; ŚLASKA *et al.*, 2003).

Best-studied class II genetic markers in the American mink are microsatellite sequences (or STR – Short Tandem Repeats, SSR – Simple Sequence Repeats) which are several nucleotide long tandemly repeated sequential DNA motifs (O'BRIEN *et al.*, 1993; KWIATKOWSKA and SŁOMSKI, 1996). They are widely used in the construction of genomic marker maps, phylogenetic studies and analysis of interindividual and interpopulational genetic variability of the American mink (O'CONNELL *et al.*, 1996; BELLIVEAU *et al.*, 1999; PROST *et al.*, 2003; VINCENT *et al.*, 2003; KIDD *et al.*, 2009).

Names of the microsatellite markers of this species are composed of a unique number preceded by the acronym Mvi, e.g., Mvi232. Thus far, approx. 350 SSR-type sequences have been identified in the American mink, of a length typically from 20 to 52 nucleotides (ANISTOROAEI *et al.*, 2009; ANISTOROAEI *et al.*, 2011). The most common type of microsatellite markers are sequences of di- (approx. 34-37%), tetra- (approx. 27-31%) and mononucleotide (approx. 18-25%) motifs, while the least frequent are sexanucleotide repeats (ANISTOROAEI *et al.*, 2011; BENKEL *et al.*, 2012). Microsatellite *loci* occur in the genome of mink on average once every 8.4 kb (BENKEL *et al.*, 2012).

Microsatellite markers of American mink were successfully amplified in other species of the class *Mammalia*, including ferret (ANISTOROAEI and CHRISTENSEN, 2006), the black-footed ferret (*Mustela nigripes* Audubon & Bachman, 1851), the steppe polecat (*Mustela eversmanii* Les., 1827), the European polecat (*Mustela putorius* L., 1758) (WISELY *et al.*, 2002), the weasel (*Mustela nivalis* L., 1766), the stoat (*Mustela erminea* L., 1758), the wolverine (*Gulo gulo* L., 1758), the American marten (*Martes americana* Turton, 1806), the North American river otter (*Lontra canadensis* Schreb., 1777) and the sea otter (*Enhydra lutris* L., 1758) (FLEMING *et al.*, 1999). This proves the applicability of *N. vison* STR markers in the genome studies of other members of the family *Mustelidae* (FLEMING *et al.*, 1999).

In turn, DAVIS and STROBECK (1998) and PROST *et al.* (2003) positively evaluated the possibility of using primer sequences designed to amplify microsatellite sequences in the domestic dog genome (*C. lupus familiaris* L., 1758), the American marten, wolverine and the American badger (*Taxidea taxus* Schreb., 1777) to construct genetic maps and population genetics studies of the American mink.

Among the class II genetic markers RFLP (Restriction Fragment Length Polymorphism) polymorphisms have been also investigated in *N. vison*, including mitochondrial DNA (HANSEN and JACOBSEN, 1999; RIDDLE *et al.*, 2003; GÓMEZ-MOLINER *et al.*, 2004).

GENOME MAPPING

The chromosomal location of at least 127 genes of the American mink has been established (KUZNETSOV *et al*., 2003; BENSON *et al.*, 2012). Gene mapping is based here on the use of somatic cellular hybrids of the American mink-Chinese hamster (*Cricetulus griseus* Milne-Edwards, 1867) and the American mink-house mouse (*Mus musculus* L., 1758) (RUBSTOV *et al.*, 1981; PACK *et al.*, 1992; KUZNETSOV *et al.*, 2003), methods of comparative cytogenetics – FISH (Fluorescence *in situ* Hybridization), Zoo-FISH (Cross-Species Fluorescent *in situ* Hybridization), comparative gene mapping and breeding tests (SEROV, 1998; SEROV and RUBSTOV, 1998). It is worth noting that the somatic cell hybrids of the American mink-domestic pig type (*Sus scrofa* f. *domestica* L., 1758) are successfully used for cytogenetic studies in the latter species (ZHDANOVA *et al.*, 1996; KOROLEVA *et al.*, 1998).

The first genetic map of *N. vison* chromosomes was created by ANISTOROAEI *et al.* in 2007 based on the linkage analysis of 85 microsatellite *loci*, located in 12 autosomes. Microsatellite markers were categorized in 17 linkage groups, and the total size of the map was 690 cM (ANISTOROAEI *et al.*, 2007). Two years later, linkage maps were published for all 14 autosomes, developed on the basis of 157 microsatellite markers. Sixteen linkage groups were established, and the joint size of the maps cover a total of 1340 cM (ANISTOROAEI *et al.*, 2009).

Comparative mapping is used to construct physical maps of the American mink based on the analysis of sequenced genomes of closely related species, e.g., domestic dog (KUKEKOVA *et al*., 2009). The most important tool in comparative genomics, in this case, is Zoo-FISH technique, allowing interspecies searches of genomic BAC library of the dog using probes containing gene and microsatellite sequences (BENKEL *et al.*, 2012). Due to limitations in the use of the dog BAC library in chromosomal mapping of the American mink genome, resulting from the phylogenetic distance separating the two species, great expectations are currently held for the possibility of using the ferret BAC library for this purpose, as its genome is almost completely sequenced (GenBank: AEYP00000000.1 and AGTQ00000000.1) (KUKEKOVA *et al.*, 2009; BENSON *et al.*, 2012).

A project has been initiated of mapping single nucleotide polymorphisms (SNPs) in the whole genome of the American mink, based on the comparative genomic analysis with phylogenetically close species, with sequenced genomes and STS (Sequence Tagged Sites) technique (BENKEL *et al.*, 2008). It is postulated to utilize SNP maps in breeding and identify genes responsible for resistance to infections with the Aleutian disease virus (ADV) (BENKEL *et al.*, 2008).

GENOME SEQUENCING PROJECT OF THE AMERICAN MINK

Genome sequencing project of the American mink has been initiated (ANISTOROAEI *et al.*, 2012a). For this purpose, genomic BAC library was created in 2009 – *CHORI-231: American mink (Neovison vison) BAC Library*, which contains 165888 clones with an average insert size of 170 kb. This gives a total of more than 28220 Mb, i.e., theoretical ten-fold coverage of the *N. vison* genome (ANISTOROAEI *et al.*, 2011; ANISTOROAEI, 2012d). Sequencing of the inserts' ends of the isolated BAC clones yielded nearly 3800 of BES sequences (BAC-end sequences), including approx. 1800 with paired ends, of an average length of 730 bp (BENKEL *et al.*, 2012). BES sequences have been deposited in the GenBank database under accession numbers HN339419 – HN341884, HN604664 – HN604702, ET186968 – ET189568 and ET901803-FI903053 (ANISTOROAEI *et al.*, 2011; BENKEL *et al.*, 2012; BENSON *et al.*, 2012).

Currently, sequencing of the American mink genome is performed using combined methods based on the shotgun technique and NGS (Next Generation Sequencing) as well as physical maps constructed on the basis of BAC libraries (ANISTOROAEI *et al.*, 2012d). *N. vison* is the first mammal, in which such an approach has been applied, and is referred to as BAC-NGS. It is estimated that approx. 15% of the mink genome has been decoded using the method described (ANISTOROAEI *et al.*, 2012a).

Complete mitochondrial genome sequence of the American mink is known. It consist of nearly 16.6 kbp and contains 13 protein-coding genes, 22 tRNA genes and 2 rRNA genes. GC nucleotide content is 38.6%. Both the quantity, location, and size of particular segments of the mitochondrial genome of the American mink are typical of the subphylum vertebrates (SUN *et al.*, 2014).

The nucleotide sequence of approx. 160 *N. vison* genes has been deciphered (BENSON *et al.*, 2012). This includes primarily the coding sequences of the genes, while complete nucleotide sequences containing introns, untranslated sequences and flanking regions are known to a lesser extent. Similarly, exon-intron structure has been described only for a part of the sequenced mink genes, e.g. for prolactin and growth hormone genes (SKORUPSKI and KMIEĆ, 2012; SKORUPSKI and KMIEĆ, 2013c).

In parallel with sequencing of the American mink genome, the research on the transcriptome of the species is carried out, including the analysis of long non-coding RNA (lncRNA) and miRNA (microRNA) (ANISTOROAEI *et al.*, 2012b). CHRISTENSEN and ANISTOROAEI (2014) described the transcriptome of the species comprising transcripts of more than 16 thousand genes.

'PHYLOGENETIC REVOLUTION' AND THE AMERICAN MINK SYSTEMATICS

Many authors point to a very significant karyotypic, morphological and biochemical differences between American mink and species of the genus *Mustela*, as a justification for the separation of the species into a separate genus *Neovison* on the basis of the observed differences (PETROV, 1958; ABROMOV, 2000; KUROSE *et al.*, 2000; KUROSE *et al.*, 2008). The ongoing discussion on the systematic ambiguity of the species has been extensively described by HARDING and SMITH (2009), and refers to the opinion of revising the taxonomy of the species, while this revision is supposed to concern issues such as leaving the American mink in the genus *Mustela*, while assigning it to the subgenus *Neovison* or *Vision*, depending on the proposed composition of such a taxon. It was also suggested, in view of the high phylogenetic similarity between the American mink and the long-tailed weasel (*Mustela frenata* Lich., 1831), the Amazon weasel (*M. africana* Desmarest, 1818) and the Colombian weasel (*M. felipei* Izhora River and de la Torre, 1978), to include all of these species in a separate genus *Vison* (HARDING and SMITH 2009).

Studies on phylogenetic relationships of *N. vison* are focused on a comparative analysis of the nucleotide sequences of mitochondrial genes – *12S rRNA* gene (HOSODA *et al.*, 2000; KUROSE *et al.*, 2000) and the *cytb* gene (KOEPFLI and WAYNE, 1998; KUROSE *et al.*, 2008) as well as nuclear genes (usually with the use of STS markers) – gene encoding interreceptor retinoid binding protein (*irbp*) (SATO *et al.*, 2003; SATO *et al.*, 2004), recombinase activating gene (*rag1*), apolipoprotein B gene (*apob*), transthyretin gene (*ttr*), polypeptide 1 nicotinic cholinergic receptor alpha gene (*chrna1*), proto-oncogene of feline sarcoma (*c-fes*), growth hormone receptor gene (*ghr*) and the rhodopsin gene (*rho*) (YONEZAWA *et al.*, 2007).

Phylogenetic analysis based on a comparison of the sequences of those genes demonstrated a high degree of divergence between American mink and species of the genus *Mustela* (SATO *et al.*, 2003; FULTON and STROBECK, 2006; KOEPFLI *et al.*, 2008; KUROSE *et al.*, 2008; HARDING and SMITH, 2009). It is worth emphasizing that the estimated genetic distance between *N. vison* and representatives of the genus *Mustela* is comparable to the genetic distance separating the species of the genus *Mustela*, and species of the genus *Martes* and *Meles* (KUROSE *et al.*, 2000; KUROSE *et al.*, 2008).

Based on molecular phylogeny, divergence time of evolutionary lines of genera *Neovison* and *Mustela* is dated at approx. 6.0 (KOEPFLI *et al.*, 2008), approx. 9.5-6.6 (MARMI *et al.*, 2004), approx. 9.9-8.5 (SATO *et al.*, 2003), approx. 11.0-8.0 (KUROSE *et al.*, 2000), or approx. 14.0-11.0 (HOSODA *et al.*, 2000) million years ago. The long-tailed weasel shows the highest phylogenetic relationship with the American mink (FULTON and STROBECK, 2006; KOEPFLI *et al.*, 2008), and the first fossil record, indicating the occurrence of *N. vison*, comes from the United States and dates back to the early Pleistocene (KURTÉN and ANDERSON, 1980).

Phylogenetic analysis of the American mink genome is utilized in research on the evolution of mammalian genomes (MURPHY *et al.*, 2001; GRAPHODATSKY *et al.*, 2000; NIE *et al.*, 2012). On the basis of structural homology analysis of *N. vison* chromosomes and dozens of other mammalian species, consisting mainly of G band patterns comparison, fluorescence *in situ* hybridization, interspecies fluorescence *in situ* hybridization and comparative mapping of genes, the presence of 32-33 conserved segments has been demonstrated in mink chromosomes (HAMEISTER *et al.*, 1997; CHOWDHARY *et al.*, 1998), and a high degree of synteny and collinearity of gene arrangements on the chromosomes, indicating a high evolutionary conservation of the mammalian carnivore genomes (GRADOV *et al.*, 1983; PERELMAN *et al.*, 2005; FERGUSON-SMITH and TRIFONOV, 2007). KHLEBODAROVA *et al.* (1995) have identified characteristic of American mink syntenic region on chromosome 14, encompassing gene *loci* for glutamic-pyruvate transaminase (GPT, EC 2.6.1.2), phosphoglycolate phosphatase (PGP, EC 3.1.3.18) and phosphoserine phosphatase (PSP, EC 3.1.3.3). It is assumed that this region, which was also found in mammals of other families, evolved in *Mustelidae de novo* (SEROV, 1998; SEROV and RUBSTOV, 1998). The presence of syntenic groups was also demonstrated in the mink chromosome 8, comprising nucleolus organizer region (LARKIN *et al.*, 2006; ZHDANOVA 2007). BENKEL *et al.* (2012), in turn, indicated the presence of 95 syntenic segments in the genome of the American mink, domestic dog and human.

It is believed that the evolution of the genome of the American mink from a hypothetical 2n=42 ancestral *Carnivora* karyotype (ACK), proposed by MURPHY *et al.* (2001), included 8 centric fusions (Robertsonian translocations), 2 centric divisions and 1 chromosomal inversion (NIE *et al.*, 2002). The rate of disturbance in the *N. vison* lineage synteny is estimated at 0.3/million years, as in the case of baboons (*Papio* sp. Erxl., 1777), chimpanzees (*Pan* sp. Oken, 1816), and domestic cattle (*Bos taurus* L., 1758) – EHRLICH *et al.* (1997).

POPULATION GENETICS

The application of genetic analysis to determine the genetic diversity and population genetic structure of the American mink is associated with the identification of its origin (the differentiation of wild and feral animals, gene flow analysis, etc.) and studying directions and trends of invasions, in the case of species introduction beyond its natural range (BELLIVEAU *et al.*, 1999; ZALEWSKI *et al.*, 2011, SKORUPSKI, 2012; SKORUPSKI and KMIEĆ, 2013b). Non-invasive

identification of the American mink is important in this case, and it is performed on the basis of RFLP restriction analysis of mitochondrial DNA (fragments of the *cytb* gene) isolated from feces samples or hair follicles. The former method, described in detail by HANSEN and JACOBSEN (1999), applies the *Taq*I and *Nla*IV restriction enzymes, while the latter – *Hinf*I and *Mbo*I restriction enzymes (RIDDLE *et al.*, 2003). Identification by sequencing the amplification products of *cytb* gene fragment is also used (HARRINGTON *et al.*, 2010).

STATHAM *et al.* (2007) and SHIMATANI *et al.* (2010) proposed an efficient and effective method of determining gender of the American mink based on the presence or absence of the *SRY* gene fragment amplicons, and restriction analysis (*Bsm*1-RFLP) of allosomal *zfx* and *zfy* genes (zinc-finger X-protein, zinc-finger Y-protein). Genes located on sex chromosomes in the American mink were also studied by YAMADA and MASUDA (2010).

In view of a major environmental problem, i.e. spreading, introduction and naturalization of the species outside its natural geographic range, number of research projects are being undertaken. The most important here is the differentiation of animals kept on farms from free-living animals and hybrids of both of these forms, based on the molecular genetics analysis. Such identification was successfully carried out in the case of the American mink in Canada (BELLIVEAU *et al.*, 1999; HAMMERSHØJ *et al.*, 2005; KIDD *et al.*, 2009). The basis for genetic identification was profiling based on microsatellite or mitochondrial DNA. In the available literature, there are no reports on the identification of hybrids based on single nucleotide polymorphisms.

GENETICS OF THE AMERICAN MINK FUNCTIONAL TRAITS

Studies are under way aimed at identifying quantitative trait loci (QTL) of the American mink, such as guard hairs length, their thickness and density of the fur (THIRSTRUP *et al.*, 2011; THIRSTRUP *et al.*, 2012). Thus far it has been established that QTLs conditioning the length of guard hairs are located on three chromosomes, thickness of guard hairs on five, and the thickness of fur on two chromosomes (THIRSTRUP *et al.*, 2014).

Based on the BAC library developed for the species, ANISTOROAEI *et al.* (2011, 2012c), selected at least 21 candidate genes for functional traits important from an economic point of view (such as coat color, hair length, genes coding for receptors associated with viral infections).

CIRERA *et al.* (2013) analyzed the gene encoding melanophilin (MLPH), controlling coat color phenotypes in American mink, while MARKAKIS *et al.* (2014) investigated the association between the *MITF* gene and the Hedlund phenotype in mink. In behavioral genetics, most important for the farm breeding, are studies on the heritability of aggressive behavior (ALEMU *et al.*, 2014). The effect of diet on the extent of DNA damage and telomere length was also studied in farmed mink (BOUDREAU *et al.,* 2014).

AMERICAN MINK AS A MODEL ORGANISM IN GENETIC RESEARCH

American mink is sometimes used as a model organism in the studies of genetic diseases, such as Type II tyrosinemia (LEIB *et al.*, 2005). Genetic background of the albinism has been also described (nonsense mutation in the tyrosinase gene, EC 1.14.18.1), and diploid-triploid chimerism (30, XX/45, XXY) associated with true hermaphroditism in mink (NES, 1966; ANISTOROAEI *et al.*, 2008). Triploidy in mink shows tissue specificity and has been found in lung and corneal epithelium cells (NES, 1966).

CONCLUSIONS

Currently, the most important appears to be the completion of the American mink genome sequencing project as well as the continuation of research projects initiated earlier, on the basis of genomic analyzes. This is particularly relevant in the context of unclear systematic status of the species that can be precisely explained based on the complex analyses in the field of comparative genomics. No less important is the search for a reliable and efficient system of genetic identification of wild, farm and feral animals. Development of a simple and cost-effective test with a high degree of reliability based on a genome-wide representative set of microsatellite markers and SNPs, would solve the problem of unambiguous identification of animals escaped from farms, which is important in the monitoring and control programs of wild populations as well as reducing escapes from farms themselves. The use of molecular genetics knowledge and complementing ecological research results is necessary for the proper conduct of specified activities (DARLING and BLUM, 2007).

Received December 12th, 2014
Accepted March 03rd, 2015

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70 GODINA ISTRAŽIVANJA GENETIKE AMERIČKE VIDRICE (*Neovison vison* SCHREB., 1777) – U KOJOJ SMO SADA FAZI?

Jakub Jan SKORUPSKI

Fakultet za Genetiku i Opšti uzgoj životinja, Zapadno Pomorski Tehnološki Univerzitet u Szczecinu, Poljska

Izvod

Cilj ovog članka je prikazivanje stanja našeg savremenog znanja na temu genetike američke vidrice (*Neovison vison* Schreb., 1777) – vrste koja je u 20. veku doživela ekološki uspeh bez presedana, vezano za dinamički razvoj njene upotrebe u industrijske svrhe. Ipak bez obzira na veliki uspeh i porast privrednog značaja američke vidrice zbog njenog krzna i skalu problema vezanih za nastanjivanje na područjima izvan njene prirodne sredine, istraživanja ove vrste u oblasti genetike, a naročito molekularne genetike i genomike, su relativno malo unapređena. Ovaj članak sadrži sintetički opis istraživanja koja se provode po pitanju genetike ove vrste, a koja se odnose kako na citogenetiku, molekularnu genetiku, genomiku, populacionu genetiku, tako i filogeniju. Prikazuje napredak projekta vezanog za sekvencioniranje genoma američke vidrice i analizu njenog transkriptoma. Sem toga članak govori i o pitanjima koja još uvek, nakon 70 godina genetičkih istraživanja, ostaju ne pojašnjena i ne istražena do kraja, kao što su: određivanje kariotipa, tačna molekularna struktura nasleđivanja boje dlake i pozicija vrste u sistematici.

Primljeno 12. XII 2014.
Odobreno 03. III. 2015.