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The potential roles of vesicle-enclosed miRNAs in communication between macrophages and cancer cells in tumor microenvironment

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Functional microRNA (miRNA) molecules are transported in extracellular vesicles among tumor cells and cells of the immune system. Macrophages as integral components of tumor microenvironment are known as potential contributors to tumor growth and progression. We searched for studies which could provide a direct link between the particular miRNAs transported between cancer cells and macrophages and experimental evidence of subsequent alterations in biological functions of target cells. The validated targets of such microRNAs were found using miRWalk database. These targets were further subjected to analysis by DAVID (Database for Annotation, Visualization and Integrated Discovery) to find the most prominent cellular events that could be potentially regulated in macrophages by miRNAs originated from cancer cells and vice versa. We found that the 5 miRNAs (let-7b, miR-21, miR-29a, miR-222-3p, miR-451) derived from cancer cells may together regulate 2304 target genes in macrophages. The genes involved in regulation of apoptosis, regulation of gene expression and protein transport were significantly overrepresented in this set. Four of the five sets of target genes for these individual miRNAs overlap in *MYC* oncogene. *MYC* dependent transcriptional program is responsible for cell cycle entry and regulates the inflammatory response in macrophages.

Both miRNAs for which the functional transports from macrophages to cancer cells were experimental proven (miR-223, miR-142-3p) target total 684 genes including some well-known tumor suppressors like *TP53* or *APC*. Suppression of tumor suppressor genes by miRNAs derived from macrophages may eventually contribute to cancer cell proliferation.

Due to the complexity of tumor microenvironment, the altered expression profiles of its components affected by miRNA uptake from extracellular vesicles could contribute to the outcome of carcinogenesis therefore the vesicular transport of miRNAs should be studied more extensively in this context.

Key words: microRNA, extracellular vesicles, cancer microenvironment, macrophage, cancer cell

In the last years, enormous amount of work had been done to understand the biological functions of microRNA (miRNA). MicroRNAs were recognized as powerful post-transcriptional regulators, it has been estimated that one third of human genome may be regulated by them [1, 2]. The mature miRNAs act in the post-transcriptional regulation of gene expression. The miRNA molecule is perfectly or partially complementary to its target mRNA. The degree of complementarity is crucial for the fate of the target mRNA. The perfect or nearly perfect complementarity, which is very rare in mammals, leads to a site-specific cleavage of the target mRNA and it is generally called RNA interference. Two more possibilities can happen to more mismatched mRNA – either the enhanced degradation of the target mRNA or inhibition of its translation – both representing a non-cleavage repression [3].

In this article, we focused on summarization and bioinformatic evaluation of existing experimental evidence for vesicular transport of particular functional microRNA molecules among tumor cells and macrophages in the context of carcinogenesis. Macrophages were selected not only with regards to their availability for experiments and to their frequent involvement in experimental studies, but mainly as very important components of tumor microenvironment and having the potential to utilize some mechanisms included in the process of wound healing for tumor growth and progression [4]. With regards to macrophage phenotype, the most widely accepted classification describes two basic types: classical (M1) versus alternative (M2). The response of M1 macrophages is pro-inflammatory characterized by the production of cytotoxic factors, increased rates of phagocytosis, and enhanced antigen presentation on the cell surface. M2 macrophages develop as part of the wound healing program. They antagonize inflammation, secrete angiogenesis promoting factors and produce enzymes remodeling the surrounding extracellular matrix. It is well known that chronic inflammation enhances the risk of cancer development. Tissue-resident macrophages are important for maintaining a balanced state referred to as inflammatory homeostasis [4]. Phenotypes of tumor associated macrophages (TAM) may include the combination of markers of both M1 and M2 types depending on the stage of carcinogenesis [4]. We searched for such studies which provide the direct experimental evidence that the uptake of a miRNA accepted by macrophages in the form of extracellular vesicles derived from cancer cells is able to alter biological functions of this target cells. We tried also to follow the opposite direction of vesicular miRNA transport – from macrophages to cancer cells.

We focused only on studies [5-15] documenting the altered cellular functions of recipient cells due to the uptake of specific miRNA molecules included in extracellular vesicles. The results of the studies fulfilling this criterion are summarized in Figure 1 and described in the next paragraphs. Using exosomes isolated from lung carcinoma cell line, the data were obtained that indicated that miR-29a and miR-21 secreted in exosomes could bind to endosomal TLR8 in macrophages at the tumor interface and induce TLR8-mediated activation of NF-κB and NF-κB–mediated secretion of pro-inflammatory cytokines TNF-α and IL-6 [5].

The study by Li et al. [6] demonstrated that macrophages acquired tumor-derived microRNA let-7b which was contained in vesicles and which attenuated tumor-associated inflammation by down regulation of cytokine IL-6 production [6].

Salama et al. [7] studied the effect of pancreatic beta-cell specific miRNAs transfection on macrophages and dendritic cells in mice. The *in vitro* research revealed the transport of miR-29 in exosomes from pancreatic beta-cells into macrophages and the dose dependent increase of TNF-α secretion by these recipient cells. This study demonstrated that the exosomal miRNA transfer targeted to cells of innate immunity is not limited to cancer cells as miRNA donors.

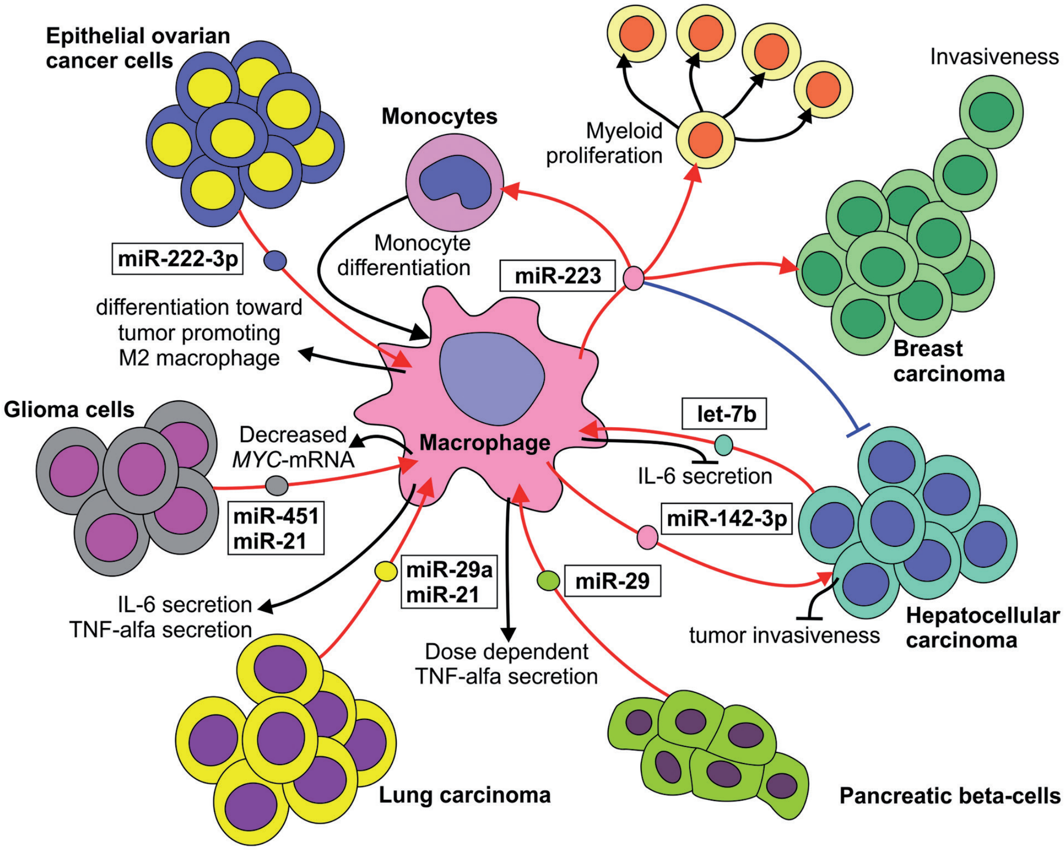

Figure 1. MicroRNAs transported via extracellular vesicles among macrophages and tumor cells. Details are discussed in the text together with references.

A miRNA molecule produced by IL-4 activated macrophages – miR-223 – was transported inside exosomes into breast cancer cells in co-cultivation experiments. The increased invasiveness of co-cultivated cancer cells was observed. The application of mR-223 antisense oligonucleotide diminished this effect [8]. Human glioblastoma–derived extracellular vesicles transported high content of miR-451/miR-21 to microglia and monocytes/macrophages from tumor-bearing brains. The reduced levels of *MYC* mRNA were observed in these target cells [9]. Epithelial ovarian cancer-derived exosomes having high content of miR-222-3p activated macrophages to a tumor-associated macrophage (TAM)- which could facilitate the progression of cancer. Overexpression of miR-222-3p in macrophages induced their polarization to the M2 phenotype [10]. The miR-223 had been found in macrophage-derived microvesicles as having the highest expression among 186 other miRNAs contained in these vesicles. The miR-223 transferred in such microvesicles was functional in the recipient cells – monocytes. MiR-223 was associated with the induction of monocyte to macrophage differentiation [11]. The miR-223 was also recognized as the most abundant miRNA in peripheral blood microvesicles. It probably plays a variety of important regulatory roles as a systemic homeostatic factor [12]. It had been demonstrated that miR-223 obtained in the form of vesicles from macrophages can stimulate the myeloid proliferation [13].

The role of exosomal miR-223 in cancer suppression has been studied by Aucher et al. [14]. The exosomes containing miR-223 and miR-142 were released by monocyte-derived macrophages and transported to co-cultivated hepato-carcinoma cells in a manner that required intercellular contact and involved gap junctions. Such a transfer inhibited proliferation of cancerous cells [14].

The tumor suppressing functions of miR-142-3p delivered in microvesicles from tumor associated macrophages to hepatocellular tumor cells was demonstrated in mice model. Animals having tumors were treated with propofol which is known for its anti-tumor effects. Down-regulation of the expression miR-142-3p using its inhibitor was able to reverse the effect of propofol on hepatocarcinoma cells [15].

Although the microenvironment in various types of tumors differs remarkably, macrophages are present here regularly. Bert Vogelstein [16] determined 12 cellular pathways which are affected in the process of carcinogenesis independently on tumor type. Due to this general aspect of carcinogenesis and due to the wide spectrum of targets of each miRNA, we could evaluate the pooled targets of miRNAs fulfilling our above described selection criteria.

Using MirWalk database [17], we searched for validated targets of miRNAs for which the functional vesicular transport between cancer cells and macrophages was experimentally proven. The validated target genes were further analyzed using the Database for Annotation, Visualization and Integrated Discovery (DAVID) [18, 19]. Overlapping gene sets playing potential roles in tuning of immune system performance were found: In the sets of target genes in macrophages, we found *MYC* as the prominent target of four out of the five analyzed miRNAs. The role of MYC expression for the determination of macrophage phenotype had been reported [20]. The sets of target genes in cancer cells contain numerous tumor suppressor genes. This fact highlights the potential tumor-promoting roles of macrophages targeted by tumor-derived vesicles containing the analyzed miRNAs.

We provide the first preview of potential pathways and regulatory events which may be affected in consequence of vesicular miRNA exchange between macrophages and cancer cells.

Material and methods

We analyzed the results of studies published till the June 2016 to find experimental evidence of functional transport of particular miRNA molecules in extracellular vesicles between cancer cells and macrophages. We included only such studies which assign the altered biological functions of target cells to the uptake of particular miRNA due to the employment of an existing method for this miRNA inhibition in their experimental workflows.

After selection of studies (cited in Introduction) fulfilling this criterion we searched using miRWalk database for the validated targets of selected miRNAs. These target genes were further analyzed using the Database for Annotation, Visualization and Integrated Discovery (DAVID) [18, 19] by the functional annotation clustering with the medium classification stringency and with calculations of Benjamini corrections and false discovery rates (FDR) to find regulatory pathways which may be significantly affected due to the uptake of miRNAs from extracellular vesicles. The Venn diagrams were constructed using the web based tool (http://bioinformatics.psb.ugent.be/webtools/Venn).

Results

Using MirWalk database [17], we searched for validated targets of miRNAs for which the functional vesicular transports from cancer cells to macrophages were proven. The numbers of detected validated targets for let-7b, miR-21, miR-29a, miR-222-3p and miR-451 and the extent of overlaps among these individual gene sets are documented in Figure 2. All target genes for each individual miRNA are listed in Supplementary Table 1. All target genes were further analyzed using DAVID [18, 19] as described in Methods. Table 1 demonstrates the results of this analysis. Overrepresented gene sets playing roles in crucial cellular pathways like regulation of apoptosis, regulation of transcription and protein transport were found.

Four out of the five sets of validated target genes for individual miRNAs overlap in the oncogene *MYC* (myelocytomatosis viral oncogene) (Figure 2). The lists of genes targeted by three out of five selected miRNAs are included also in Figure 2.

miRNAs transported from cancer cells to macrophages	No. of validated targets	miRNAs transported from macrophages to cancer cells	No. of validated targets
let -7b	1255	miR-223	335
miR-21	634	miR-142-3p	374
miR-29a	301	Both miRNAs	684
miR-222-3p	375		
miR-451	23		
All 5 miRNAs	2304		

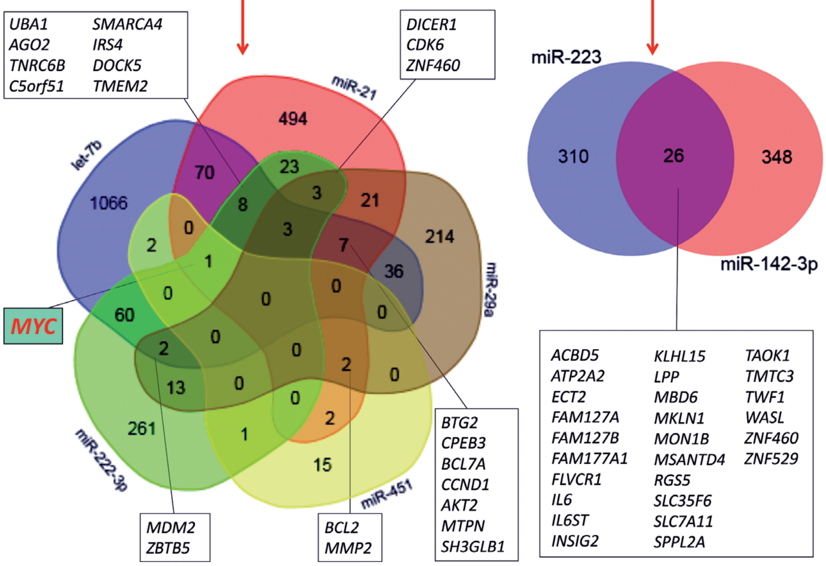

Figure 2. Numbers of validated targets for each analyzed miRNA and extent of overlaps among individual gene sets.

We searched also for validated targets of miRNAs for which the functional vesicular transport from macrophages to cancer cells was proven. We found 335 validated targets for miR-223a and 374 validated targets for miR-142-3p. The sets of target genes for each of these miRNA are listed in Supplementary Table 2. The results of DAVID analysis of all these targets are summarized in Table 2. The target genes grouped under the term "Pathways in cancer" and their functions in cancer related regulatory pathways are schematically represented in Figure 3. The validated targets of miR-223a and miR-142-3p overlap in 26 genes (Figure 2). The DAVID analysis of these 26 target genes did not revealed any overrepresented cluster of functionally associated genes.

Discussion

It is necessary to keep in mind that our analysis of validated miRNA target genes and their functional clustering provides

Table 1. Top terms identified by DAVID for all targets of miRNAs transported in vesicles from cancer cells into macrophages. p-values were subjected to Benjamini corrections, FDR – false discovery rate

Term	No. of genes	p-value	FDR
Membrane -enclosed lumen	399	5.2×10^{-35}	1.1×10^{-34}
Non-membrane bound organelle	449	2.5×10^{-18}	3.8×10^{-17}
Nucleus	750	1.1×10^{-41}	6.9×10^{-41}
Regulation of transcription	435	3.4×10^{-7}	4.3×10^{-6}
Nucleotide binding	313	3.0×10^{-18}	3.3×10^{-17}
Cell cycle	177	1.2×10^{-10}	5.3×10^{-11}
Negative regulation of gene expression	125	7.5×10^{-10}	1.3×10^{-9}
Protein transport	103	1.2×10^{-8}	4.6×10^{-7}
Regulation of cell death	167	2.6×10^{-7}	2.7×10^{-6}
Regulation of apoptosis	164	3.1×10^{-7}	3.6×10^{-6}
Pathways in cancer	92	4.4×10^{-10}	3.0×10^{-9}

Table 2. Top terms identified by DAVID for all targets of miRNAs transported in vesicles from macrophages into cancer cells. p-values were subjected to Benjamini corrections, FDR – false discovery rate

Term	No. of genes	p-value	FDR
Regulation of transcription	143	7.7×10^{-4}	2.5×10^{-3}
Nucleus	205	1.1×10^{-4}	1.3×10^{-3}
Pathways in cancer	34 (Details in Figure 3)	6.5×10^{-4}	5.2×10^{-3}

only the first preview of potential pathways and regulatory events which may be affected in macrophages and cancer cells as a consequence of uptake of miRNA molecules from vesicles exchanged between these cells.

We highlighted the role of the gene *MYC* as a prominent target of miRNAs targeted from cancer cells to macrophages (Figure 2). Recently, the central role of this gene in macrophage phenotype determination has been gradually emerging. Liu et al. [20] found that *MYC* expression plays a major role in regulating proliferation-associated metabolic programs in macrophages. Pro-inflammatory stimuli suppress *MYC* and cell proliferation and start a hypoxia-inducible factor alpha (HIF1α)-dependent transcriptional program which is responsible for heightened glycolysis. This switch may regulate the robust bioenergetic support for inflammatory response [20].

We also found the gene *DICER1* as a target gene of three out of five tumor-derived miRNAs transported to macrophages (Figure 2). The gene codes for a cytoplasmic endonuclease (RNase III enzyme Dicer) which is crucial for the process of miRNA processing itself [21, 22].

Using DAVID analysis, we found the overrepresented group of 34 genes involved in "Pathways in cancer" in the set of genes targeted in cancer cells by macrophage-derived miRNAs. This group of genes (Figure 3) deserves especial attention because it contains both oncogenes and tumor suppressor genes and therefore it may well illustrate the potential dual role of tumor associated macrophages which is highly dependent on actual state of complex tumor microenvironment.

The results documenting the communication among cancer cells and immune cells via vesicles represent the theoretical platform for the development of therapeutic approaches based on the delivery of specific miRNA molecules inside artificial exosomes to carefully selected subset of target cells to activate the immune response against tumors or to avoid tumor angiogenesis. The first attempts streaming to application of this concept had been already made [23, 24].

Despite the first promising results, an enormous effort must be made to overcome all the difficulties associated with the complexity of regulatory events operating on tumor-immune system interface with the goal to develop a safe personalized type of anti-tumor therapy based on vesicular delivery of miRNAs to target cells.

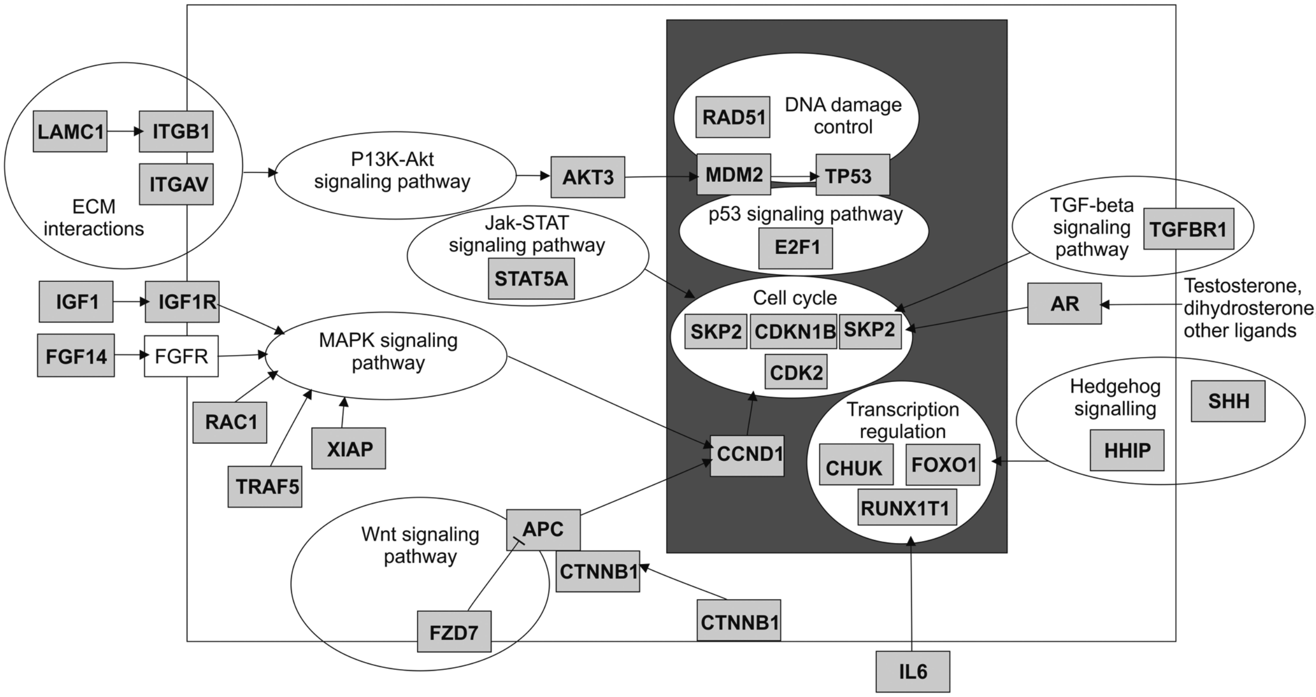

Figure 3. Target genes of miR-233 and/or miR-142-3p included in "Pathways in cancer" are depicted according to http://www.genome.jp/kegg-bin/show_pathway?hsa05200 with exception of genes *CCDC6, HSP90B1,PIK3CG* and *TFG*.

Supplementary information is available in the online version of the paper.

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Supplementary Table 1

Official Gene Symbol		Official Gene Symbol		Official Gene Symbol
AARSD1	**Validated targets of hsa-miR-21:**	ABCD3	**Validated targets of hsa-miR-29a:**	AAK1
AASDHPPT		ACAT1		ABCE1
AATF		ACBD5		ABL1
ABCB10		ACTR2		ADAMTS9
ABCB8		ADNP		AGO1
ABCC1		AFTPH		AHSA2
ABCC4		AGAP1		AIM1
ABCF1		AGBL3		AKT2
ABHD17C		AGGF1		AMER1
ABL1		AGO2		AMFR
ABT1		AGO4		AMMECR1L
ACACA		AHSA2		ASXL2
ACER2		AIM1		BACE1
ACOT9		AKAP9		BBC3
ACP1		AKT2		BCAP31
ACPP		ALMS1		BCL2
ACSL1		AMMECR1L		BCL7A
ACTA1		ANKRD28		BMPR1A
ACTB		ANKRD46		BTG2
ACTG1		ANP32A		C18orf32
ACTN4		AP1AR		C1QTNF6
ACVR1		AP3M1		C21orf91
ACVR2B		APAF1		CALCR
ADCK2		APC		CALM3
ADCY1		APOLD1		CAND1
ADH1B		APPL1		CASP8
ADH5		ARHGAP21		CBX2
ADIPOR2		ARHGEF12		CBX6
ADNP		ARID4A		CCDC117
ADRM1		ARMCX3		CCDC14

AFAP1
AFF4
AGFG2
AGL
AGO1
AGO2
AGO3
AHCTF1
AHCYL1
AHCYL2
AHR
AIDA
AK4
AKAP8
AKR1A1
AKT2
ALDH1A3
ALDH7A1
ALG10B
ALG3
AMD1
AMPH
ANAPC1
ANAPC16
ANKRD17
ANKRD46
ANKRD52
ANKZF1
ANP32E
ANTXR1
ANXA8
ANXA8L1
ANXA8L2
ARNTL
ARRDC2
ASRGL1
ATAD2B
ATF2
ATF7IP
ATMIN
ATP11B
ATP2B4
ATRX
ATXN10
AUTS2
B3GALNT1
B3GNT5
BASP1
BAZ1B
BCAT1
BCL2
BCL6
BCL7A
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BOC
BRCA1
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CDK4
CDK6
CEACAM6
CFHR3
CLSPN
CMBL
CNBP
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COL3A1
COL4A1
COL4A2
COL5A2
COLEC10
COMMD2
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CPEB4
CRKL
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CTNNBIP1

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APPL1
APRT
AR
ARAP2
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CEP97
CERS6
CKAP5
CLASP1
CLCN5
CLIP4
CLOCK
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CYR61
DAG1
DCTN6
DDX6
DHX33
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BFSP1
BGLAP
BIRC5
BIRC6
BMP7
BNIP3L
BRD2
COBLL1
COL4A1
COL5A2
CORO2A
COX20
CPEB3
CPM
CSNK1A1
CXCL10
CYBRD1
CYCS
CYP4V2
DAAM1
DAXX
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DMD
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DNAJC16
DOCK10
DOCK4
DOCK5
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FGF19
FGG
FJX1
FOS
FOXN2
FOXN3
FOXO3
FRK
FSCN1
GANAB
GAREM
GAREML
GAS2L3
GATAD2B
GEM
GLDN
GLUL
GOLGA7
GPR180
GPR82
GPR85
GRHL1
GTPBP10
H6PD
HBP1
HDGF
HECW1
HINFP
HLF
HNRNPM
HOXA10
HRH1

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BRPF3
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BTG1
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BZW2
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C11orf52
C11orf57
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CREBZF
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TRIM72
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	NDRG1

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SLC16A14
SLC16A9
SLC19A3
SLC1A4
SLC20A1
SLC25A1

SLC25A12
SLC25A13
SLC25A19
SLC25A24
SLC25A32
SLC25A4
SLC27A2
SLC30A1
SLC30A7
SLC35A5
SLC35F1
SLC35F6
SLC38A1
SLC38A2
SLC38A5
SLC38A7
SLC5A6
SLC9A3R1
SMARCA1
SMARCA4
SMARCAD1
SMARCB1
SMARCC1
SMARCC2
SMARCD1
SMC1A
SMCR8
SMG1
SMG7
SNAP23
SNRPA
SNRPE
SNX12

SNX17
SOCS1
SOD2
SON
SOX13
SOX9
SP1
SP100
SPAG9
SPATA12
SPCS3
SPN
SPR
SPRYD4
SPRYD7
SPTBN2
SRCAP
SRI
SSR1
ST13
STAT2
STEAP3
STIM1
STIP1
STK38
STK4
STRN
SUMO1
SUMO2
SUOX
SUPT16H
SUPT20H
SURF4

SYF2
SYNE1
SYNE2
SYNGR2
SYNJ2BP
SYT4
SZRD1
TAB2
TAF9B
TBC1D13
TBC1D15
TBC1D19
TBC1D20
TBRG4
TCOF1
TENM3
TERF2IP
TES
TGFBR1
TGFBR3
TGOLN2
THBS1
THEM6
THOC5
THYN1
TIAM1
TIMM23
TIMM50
TIMM8A
TIMM9
TJP1
TLN1
TLR4

TM4SF1
TMED5
TMEM115
TMEM167A
TMEM2
TMEM201
TMEM33
TMEM55B
TMEM63B
TMEM65
TMTC3
TNFRSF10B
TNFSF12
TNFSF9
TNPO1
TNRC6B
TOE1
TOR1AIP2
TOR4A
TOX3
TP53INP1
TPBG
TPD52L2
TPM4
TPP2
TPT1
TRABD
TRAPPC1
TRIM24
TRIM28
TRIM71
TRIP12
TRMT1

TRNT1
TROVE2
TRUB2
TSC22D2
TSEN15
TSPAN3
TST
TTC33
TTC9C
TTLL12
TUBA1B
TUBA1C
TUBB
TUBB2A
TUBGCP2
TUBGCP3
TUT1
TXLNA
TXLNG
TXNL4A
TYMS
UBA1
UBA3
UBAP2L
UBE2A
UBE2D2
UBE2D3
UBE2I
UBE2M
UBE2Q1
UBXN2B
UBXN8
UCK1

UCK2
UGT8
UHRF1
UNC13B
UNC13D
USO1
USP10
USP14
USP15
USP22
USP38
USP54
UTP15
UTP6
UTRN
VAMP3
VCL
VEZF1
VPS28
VPS39
VPS41
VPS51
VWA8
VWA9
WARS2
WASF1
WASL
WBP11
WBSCR16
WDR25
WDR26
WDR3
WDR33

WDR4
WDR55
WDR74
WDR75
WEE1
WLS
WNK1
XPO5
XPO7
XRN1
XYLT2
YAE1D1
YAP1
YEATS2
YIPF3
YLPM1
YOD1
YTHDC1
YWHAE
YWHAZ
ZADH2
ZBTB37
ZBTB5
ZBTB8OS
ZC3H11A
ZC3HAV1
ZC3HAV1L
ZCCHC11
ZCCHC3
ZCCHC9
ZER1
ZFAND4
ZFHX4

ZMYM2
ZNF106
ZNF136
ZNF148
ZNF181
ZNF200
ZNF207
ZNF256
ZNF264
ZNF28
ZNF3
ZNF317
ZNF417
ZNF426
ZNF443
ZNF460
ZNF507
ZNF546
ZNF556
ZNF566
ZNF578
ZNF581
ZNF584
ZNF585A
ZNF587
ZNF606
ZNF611
ZNF629
ZNF644
ZNF652
ZNF687
ZNF774
ZNF799

ZNF8
ZNF800
ZNF805
ZNF841

Supplementary Table 2

	ENTREZ ID	GENE NAME	
Validated targets for hsa-miR-142-3p:	10038	poly (ADP-ribose) polymerase 2	**Validated targets for hsa-miR-223:**
	10049	DnaJ (Hsp40) homolog, subfamily B, member 6	
	10060	ATP-binding cassette, sub-family C (CFTR/MRP), member 9	
	10165	solute carrier family 25, member 13 (citrin)	
	10228	syntaxin 6	
	10241	calcium binding and coiled-coil domain 2	
	1027	cyclin-dependent kinase inhibitor 1B (p27, Kip1)	
	10342	TRK-fused gene	
	10521	DEAD (Asp-Glu-Ala-Asp) box polypeptide 17	
	10787	NCK-associated protein 1	
	10794	zinc finger protein 460	
	10807	serologically defined colon cancer antigen 3; similar to Serologically defined colon cancer antigen 3	
	10818	fibroblast growth factor receptor substrate 2	
	10892	mucosa associated lymphoid tissue lymphoma translocation gene 1	
	10905	mannosidase, alpha, class 1A, member 2	
	10933	mortality factor 4; mortality factor 4 like 1	
	11044	polymerase (DNA directed) sigma	
	11080	DnaJ (Hsp40) homolog, subfamily B, member 4	
	11136	solute carrier family 7 (cationic amino acid transporter, y+ system), member 9	
	11143	MYST histone acetyltransferase 2; similar to MYST histone acetyltransferase 2	
	11153	FIC domain containing	
	11201	polymerase (DNA directed) iota	
	11238	inactivation escape 2 (non-protein coding); carbonic anhydrase VB, mitochondrial	

11343	monoglyceride lipase
113622	ADP-ribosylhydrolase like 1
114785	methyl-CpG binding domain protein 6
115207	potassium channel tetramerisation domain containing 12
118672	phosphoseryl-tRNA kinase
119710	chromosome 11 open reading frame 74
120534	chromosome 11 open reading frame 46
1211	clathrin, light chain (Lca)
121665	signal peptide peptidase 3
123720	WAS protein homolog associated with actin, golgi membranes and microtubules
1266	calponin 3, acidic
1314	coatomer protein complex, subunit alpha
132203	sentan, cilia apical structure protein
132864	cytoplasmic polyadenylation element binding protein 2
134553	chromosome 5 open reading frame 24
136647	chromosome 7 open reading frame 11
136895	chromosome 7 open reading frame 31
1373	carbamoyl-phosphate synthetase 1, mitochondrial
1392	corticotropin releasing hormone
1456	casein kinase 1, gamma 3
145873	mesoderm posterior 2 homolog (mouse)
1466	cysteine and glycine-rich protein 2
147339	chromosome 18 open reading frame 25
1499	catenin (cadherin-associated protein), beta 1, 88kDa
150094	salt-inducible kinase 1

151188	ADP-ribosylation-like factor 6 interacting protein 6
152006	ring finger protein 38
159119	heat shock transcription factor, Y-linked 1; heat shock transcription factor, Y linked 2
160418	transmembrane and tetratricopeptide repeat containing 3
1605	dystroglycan 1 (dystrophin-associated glycoprotein 1)
161882	zinc finger protein, multitype 1
163223	zinc finger protein 676
163590	torsin A interacting protein 2
186	angiotensin II receptor, type 2
1894	epithelial cell transforming sequence 2 oncogene
1959	early growth response 2
1983	eukaryotic translation initiation factor 5
200232	chromosome 20 open reading frame 106
200424	tet oncogene family member 3
203228	chromosome 9 open reading frame 72
205	adenylate kinase 3-like 2; adenylate kinase 3-like 1
2054	syntaxin 2
2063	nuclear receptor subfamily 2, group F, member 6
2099	estrogen receptor 1
210	aminolevulinate, delta-, dehydratase
2124	ecotropic viral integration site 2B
2180	acyl-CoA synthetase long-chain family member 1
2182	acyl-CoA synthetase long-chain family member 4
219902	transmembrane protein 136
221079	ADP-ribosylation factor-like 5B

222068	transmembrane emp24 protein transport domain containing 4
2239	glypican 4
22809	activating transcription factor 5
22820	coatomer protein complex, subunit gamma
22862	fibronectin type III domain containing 3A
22876	inositol polyphosphate-5-phosphatase F
22879	MON1 homolog B (yeast)
22936	elongation factor, RNA polymerase II, 2
23049	SMG1 homolog, phosphatidylinositol 3-kinase-related kinase (C. elegans)
23059	clusterin associated protein 1
23118	mitogen-activated protein kinase kinase kinase 7 interacting protein 2
23171	glycerol-3-phosphate dehydrogenase 1-like
23174	zinc finger, CCHC domain containing 14
23181	DIP2 disco-interacting protein 2 homolog A (Drosophila)
23198	proteasome (prosome, macropain) activator subunit 4
23235	salt-inducible kinase 2
23350	U2-associated SR140 protein
23531	monocyte to macrophage differentiation-associated
23613	zinc finger, MYND-type containing 8
23657	solute carrier family 7, (cationic amino acid transporter, y+ system) member 11
23731	chromosome 9 open reading frame 5
23787	mitochondrial carrier homolog 1 (C. elegans)
253260	RPTOR independent companion of MTOR, complex 2
253430	inositol polyphosphate multikinase
254552	nudix (nucleoside diphosphate linked moiety X)-type motif 8

256471	major facilitator superfamily domain containing 8
25776	chibby homolog 1 (Drosophila)
25823	tryptase gamma 1
25831	HECT domain containing 1
25853	WD repeat domain 40A
25888	zinc finger protein 473
25896	integrator complex subunit 7
259230	sphingomyelin synthase 1
259249	MAS-related GPR, member X1
25930	protein tyrosine phosphatase, non-receptor type 23
25932	chloride intracellular channel 4
25940	family with sequence similarity 98, member A
25948	kelch repeat and BTB (POZ) domain containing 2
25976	TCDD-inducible poly(ADP-ribose) polymerase
26035	glucuronic acid epimerase
26071	family with sequence similarity 127, member B
26145	interferon regulatory factor 2 binding protein 1
2615	leucine rich repeat containing 32
26207	phosphatidylinositol transfer protein, cytoplasmic 1
26273	F-box protein 3
26503	solute carrier family 17 (anion/sugar transporter), member 5
2672	growth factor independent 1 transcription repressor
27125	AF4/FMR2 family, member 4
27314	RAB30, member RAS oncogene family
27436	echinoderm microtubule associated protein like 4

2776	guanine nucleotide binding protein (G protein), q polypeptide
2778	GNAS complex locus
2783	guanine nucleotide binding protein (G protein), beta polypeptide 2
2800	golgi autoantigen, golgin subfamily a, 1
283635	family with sequence similarity 177, member A1
285598	ADP-ribosylation factor-like 10
286148	dpy-19-like 4 (C. elegans)
28982	feline leukemia virus subgroup C cellular receptor 1
29097	cornichon homolog 4 (Drosophila)
29904	eukaryotic elongation factor-2 kinase
29966	striatin, calmodulin binding protein 3
31	acetyl-Coenzyme A carboxylase alpha
3146	high-mobility group box 1; high-mobility group box 1-like 10
3159	hypothetical LOC100130009; high mobility group AT-hook 1
3204	homeobox A7
3205	homeobox A9
3206	homeobox A10
3209	homeobox A13
324	adenomatous polyposis coli
3281	heat shock factor binding protein 1
3295	hydroxysteroid (17-beta) dehydrogenase 4
3304	heat shock 70kDa protein 1A; heat shock 70kDa protein 1B
331	X-linked inhibitor of apoptosis
338339	C-type lectin domain family 4, member D
339500	zinc finger protein 678

340547	V-set and immunoglobulin domain containing 1
3455	interferon (alpha, beta and omega) receptor 2
3491	cysteine-rich, angiogenic inducer, 61
353500	bone morphogenetic protein 8a
3552	interleukin 1, alpha
3569	interleukin 6 (interferon, beta 2)
3572	interleukin 6 signal transducer (gp130, oncostatin M receptor)
3619	inner centromere protein antigens 135/155kDa
3632	inositol polyphosphate-5-phosphatase, 40kDa
3654	interleukin-1 receptor-associated kinase 1
3659	interferon regulatory factor 1
3685	integrin, alpha V (vitronectin receptor, alpha polypeptide, antigen CD51)
374977	chromosome 1 open reading frame 175
3752	potassium voltage-gated channel, Shal-related subfamily, member 3
378	ADP-ribosylation factor 4
3798	kinesin family member 5A
3799	kinesin family member 5B
3842	transportin 1
3915	laminin, gamma 1 (formerly LAMB2)
4015	lysyl oxidase
402055	SRR1 domain containing
4026	LIM domain containing preferred translocation partner in lipoma
406	aryl hydrocarbon receptor nuclear translocator-like
4068	SH2 domain protein 1A
4082	myristoylated alanine-rich protein kinase C substrate

4209	myocyte enhancer factor 2D
4287	ataxin 3
4289	muskelin 1, intracellular mediator containing kelch motifs
4297	myeloid/lymphoid or mixed-lineage leukemia (trithorax homolog, Drosophila)
4299	AF4/FMR2 family, member 1
440093	histone H3-like
4591	tripartite motif-containing 37
4674	nucleosome assembly protein 1-like 2
4744	neurofilament, heavy polypeptide
488	ATPase, Ca++ transporting, cardiac muscle, slow twitch 2
490	ATPase, Ca++ transporting, plasma membrane 1
5007	oxysterol binding protein
50484	ribonucleotide reductase M2 B (TP53 inducible)
50837	taste receptor, type 2, member 7
51014	transmembrane emp24 protein transport domain containing 7; toll-like receptor adaptor molecule 2
51026	golgi transport 1 homolog B (S. cerevisiae)
51141	insulin induced gene 2
51144	hydroxysteroid (17-beta) dehydrogenase 12
51164	dynactin 4 (p62)
51430	chromosome 1 open reading frame 9
51659	GINS complex subunit 2 (Psf2 homolog)
5267	serpin peptidase inhibitor, clade A (alpha-1 antiproteinase, antitrypsin), member 4
5294	phosphoinositide-3-kinase, catalytic, gamma polypeptide
54439	RNA binding motif protein 27
54619	cyclin J

54622	ADP-ribosylation factor-like 15
54662	TBC1 domain family, member 13
54726	OTU domain containing 4
54734	RAB39, member RAS oncogene family
54906	chromosome 10 open reading frame 18
54978	chromosome 2 open reading frame 18
55038	cell division cycle associated 4
5504	protein phosphatase 1, regulatory (inhibitor) subunit 2
55054	ATG16 autophagy related 16-like 1 (S. cerevisiae)
55119	PRP38 pre-mRNA processing factor 38 (yeast) domain containing B
55122	akirin 2
55125	centrosomal protein 192kDa
5522	protein phosphatase 2 (formerly 2A), regulatory subunit B, gamma isoform
55224	ethanolamine kinase 2
55251	protein-L-isoaspartate (D-aspartate) O-methyltransferase domain containing 2
55284	ubiquitin-conjugating enzyme E2W (putative)
55334	solute carrier family 39 (zinc transporter), member 9
55342	spermatid perinuclear RNA binding protein
55379	leucine rich repeat containing 59
55432	YOD1 OTU deubiquinating enzyme 1 homolog (S. cerevisiae)
55521	tripartite motif-containing 36
55619	dedicator of cytokinesis 10
55635	DEP domain containing 1
55670	peroxisomal biogenesis factor 26
55676	solute carrier family 30 (zinc transporter), member 6

55727	BTB (POZ) domain containing 7
55731	chromosome 17 open reading frame 63
55740	enabled homolog (Drosophila)
55762	zinc finger protein 701
55968	NSFL1 (p97) cofactor (p47)
56106	protocadherin gamma subfamily A, 10
56113	protocadherin gamma subfamily A, 2
56122	protocadherin beta 14
56254	ring finger protein 20
56673	chromosome 11 open reading frame 16
56902	partner of NOB1 homolog (S. cerevisiae)
5693	proteasome (prosome, macropain) subunit, beta type, 5
57016	aldo-keto reductase family 1, member B10 (aldose reductase); aldo-keto reductase family 1, member B10-like
57045	twisted gastrulation homolog 1 (Drosophila)
571	BTB and CNC homology 1, basic leucine zipper transcription factor 1
57107	prenyl (decaprenyl) diphosphate synthase, subunit 2
57128	LYR motif containing 4
5717	proteasome (prosome, macropain) 26S subunit, non-ATPase, 11
57179	KIAA1191
5718	proteasome (prosome, macropain) 26S subunit, non-ATPase, 12
57507	zinc finger protein 608
57509	mitochondrial tumor suppressor 1
57551	TAO kinase 1
5756	twinfilin, actin-binding protein, homolog 1 (Drosophila)
57649	PHD finger protein 12

57695	ubiquitin specific peptidase 37
57711	zinc finger protein 529
578	BCL2-antagonist/killer 1; BCL2-like 7 pseudogene 1
5795	protein tyrosine phosphatase, receptor type, J
58525	widely interspaced zinc finger motifs
5862	RAB2A, member RAS oncogene family
5863	ral guanine nucleotide dissociation stimulator-like 2
5879	ras-related C3 botulinum toxin substrate 1 (rho family, small GTP binding protein Rac1)
5888	RAD51 homolog (RecA homolog, E. coli) (S. cerevisiae)
6120	rcRPE; ribulose-5-phosphate-3-epimerase
6223	ribosomal protein S19 pseudogene 3; ribosomal protein S19
6282	S100 calcium binding protein A11; S100 calcium binding protein A11 pseudogene
6293	vacuolar protein sorting 52 homolog (S. cerevisiae)
6319	stearoyl-CoA desaturase (delta-9-desaturase)
63905	mannosidase, beta A, lysosomal-like; similar to mannosidase, beta A, lysosomal-like
64746	acyl-Coenzyme A binding domain containing 3
64764	cAMP responsive element binding protein 3-like 2
6502	S-phase kinase-associated protein 2 (p45)
66036	myotubularin related protein 9
6738	TROVE domain family, member 2
6760	synovial sarcoma translocation, chromosome 18
678	zinc finger protein 36, C3H type-like 2
6856	synaptophysin-like 1
6860	synaptotagmin IV
7046	transforming growth factor, beta receptor 1

7105	tetraspanin 6
717	complement component 2
7181	nuclear receptor subfamily 2, group C, member 1
725	complement component 4 binding protein, beta
7259	TSPY-like 1
7367	UDP glucuronosyltransferase 2 family, polypeptide B17
7371	uridine-cytidine kinase 2
7468	Wolf-Hirschhorn syndrome candidate 1
7525	v-yes-1 Yamaguchi sarcoma viral oncogene homolog 1
7531	similar to 14-3-3 protein epsilon (14-3-3E) (Mitochondrial import stimulation factor L subunit) (MSF L); tyrosine 3-monooxygenase/tryptophan 5-monooxygenase activation protein, epsilon polypeptide
7533	tyrosine 3-monooxygenase/tryptophan 5-monooxygenase activation protein, eta polypeptide
7543	zinc finger protein, X-linked
7572	zinc finger protein 24
7764	zinc finger protein 217
7776	zinc finger protein 236
7832	BTG family, member 2
79042	tRNA splicing endonuclease 34 homolog (S. cerevisiae)
79048	SECIS binding protein 2
79065	ATG9 autophagy related 9 homolog A (S. cerevisiae)
79443	FYVE and coiled-coil domain containing 1
79567	family with sequence similarity 65, member A
79646	pantothenate kinase 3
79841	ATP/GTP binding protein-like 2
79861	tubulin, alpha-like 3
79931	TNFAIP3 interacting protein 3

79939	solute carrier family 35, member E1
801	calmodulin 3 (phosphorylase kinase, delta); calmodulin 2 (phosphorylase kinase, delta); calmodulin 1 (phosphorylase kinase, delta)
80255	solute carrier family 35, member F5
80262	chromosome 16 open reading frame 70
80267	ER degradation enhancer, mannosidase alpha-like 3
8027	signal transducing adaptor molecule (SH3 domain and ITAM motif) 1
8030	coiled-coil domain containing 6
80311	kelch-like 15 (Drosophila)
8065	cullin 5
8091	high mobility group AT-hook 2
81706	protein phosphatase 1, regulatory (inhibitor) subunit 14C
81790	ring finger protein 170
8324	frizzled homolog 7 (Drosophila)
8360	histone cluster 1, H4l; histone cluster 1, H4k; histone cluster 4, H4; histone cluster 1, H4h; histone cluster 1, H4j; histone cluster 1, H4i; histone cluster 1, H4d; histone cluster 1, H4c; histone cluster 1, H4f; histone cluster
84224	neuroblastoma breakpoint family, member 3
84255	solute carrier family 37 (glycerol-3-phosphate transporter), member 3
84312	breast cancer metastasis-suppressor 1-like
84335	AKT1 substrate 1 (proline-rich)
84336	transmembrane protein 101
8440	NCK adaptor protein 2
84437	KIAA1826
8444	dual-specificity tyrosine-(Y)-phosphorylation regulated kinase 3
84458	ligand dependent nuclear receptor corepressor
84629	trinucleotide repeat containing 18
84888	signal peptide peptidase-like 2A

84897	transforming growth factor beta regulator 1
8490	regulator of G-protein signaling 5
84901	nuclear factor of activated T-cells, cytoplasmic, calcineurin-dependent 2 interacting protein
84919	protein phosphatase 1, regulatory (inhibitor) subunit 15B
84928	transmembrane protein 209
8500	protein tyrosine phosphatase, receptor type, f polypeptide (PTPRF), interacting protein (liprin), alpha 1
85289	keratin associated protein 4-5
85313	peptidylprolyl isomerase (cyclophilin)-like 4
8549	leucine-rich repeat-containing G protein-coupled receptor 5
8555	CDC14 cell division cycle 14 homolog B (S. cerevisiae)
8658	tankyrase, TRF1-interacting ankyrin-related ADP-ribose polymerase
871	serpin peptidase inhibitor, clade H (heat shock protein 47), member 1, (collagen binding protein 1)
8842	prominin 1
8850	K(lysine) acetyltransferase 2B
8933	family with sequence similarity 127, member A
8973	cholinergic receptor, nicotinic, alpha 6
8976	Wiskott-Aldrich syndrome-like
89790	sialic acid binding Ig-like lectin 10
900	cyclin G1
90411	multiple coagulation factor deficiency 2
905	cyclin T2
9069	claudin 12
91120	zinc finger protein 682
91272	biorientation of chromosomes in cell division 1
91452	acyl-Coenzyme A binding domain containing 5

9146	hepatocyte growth factor-regulated tyrosine kinase substrate
9217	VAMP (vesicle-associated membrane protein)-associated protein B and C
92610	TRAF-interacting protein with forkhead-associated domain
92675	histidyl-tRNA synthetase 2, mitochondrial (putative); D-tyrosyl-tRNA deacylase 1 homolog (S. cerevisiae)
93380	membrane magnesium transporter 1
93621	Mof4 family associated protein 1
94134	Rho GTPase activating protein 12
9422	zinc finger protein 264
9429	ATP-binding cassette, sub-family G (WHITE), member 2
9475	Rho-associated, coiled-coil containing protein kinase 2
9496	T-box 4
9522	secretory carrier membrane protein 1
9528	transmembrane protein 59
953	ectonucleoside triphosphate diphosphohydrolase 1
9575	clock homolog (mouse)
9643	mortality factor 4 like 2
9650	mitochondrial fission regulator 1
9655	suppressor of cytokine signaling 5
9698	pumilio homolog 1 (Drosophila)
9712	USP6 N-terminal like
9774	similar to Bcl-2-associated transcription factor 1 (Btf); BCL2-associated transcription factor 1
9778	KIAA0232
9807	inositol hexakisphosphate kinase 1
9852	EPM2A (laforin) interacting protein 1
990	cell division cycle 6 homolog (S. cerevisiae)

9950	golgi autoantigen, golgin subfamily a, 5

ENTREZ ID	GENE NAME
10000	v-akt murine thymoma viral oncogene homolog 3 (protein kinase B, gamma)
1004	cadherin 6, type 2, K-cadherin (fetal kidney)
10100	tetraspanin 2
10135	nicotinamide phosphoribosyltransferase
10150	muscleblind-like 2 (Drosophila)
10152	abl interactor 2
1017	cyclin-dependent kinase 2
10184	lipoma HMGIC fusion partner-like 2
10206	tripartite motif-containing 13
10280	sigma non-opioid intracellular receptor 1
10336	polycomb group ring finger 3
10384	butyrophilin, subfamily 3, member A3
1040	CDP-diacylglycerol synthase (phosphatidate cytidylyltransferase) 1
10472	zinc finger protein 238
10498	coactivator-associated arginine methyltransferase 1
10614	hexamethylene bis-acetamide inducible 1
10622	polymerase (RNA) III (DNA directed) polypeptide G (32kD)
10666	CD226 molecule
1073	cofilin 2 (muscle)
10741	retinoblastoma binding protein 9
10794	zinc finger protein 460
10795	zinc finger protein 268
1080	cystic fibrosis transmembrane conductance regulator (ATP-binding cassette sub-family C, member 7)

Validated targets of both miRNAs:

ENTREZ ID
10794
114785
160418
1894
22879
23657
26071
283635
28982
3569
3572
4026
4289
488
51141
54978
57551
5756
57711
80311
84437
84888
8490

10846	phosphodiesterase 10A	8933
10885	WD repeat domain 3	8976
10949	heterogeneous nuclear ribonucleoprotein A0	91452
10951	chromobox homolog 1 (HP1 beta homolog Drosophila)	
11145	phospholipase A2, group XVI	
11149	blood vessel epicardial substance	
11196	SEC23 interacting protein	
11217	A kinase (PRKA) anchor protein 2; paralemmin 2; PALM2-AKAP2 readthrough transcript	
1147	conserved helix-loop-helix ubiquitous kinase	
114757	cytoglobin	
114785	methyl-CpG binding domain protein 6	
114883	oxysterol binding protein-like 9	
118987	PDZ domain containing 8	
119	adducin 2 (beta)	
123879	DCN1, defective in cullin neddylation 1, domain containing 3 (S. cerevisiae)	
125	alcohol dehydrogenase 1B (class I), beta polypeptide; alcohol dehydrogenase 1A (class I), alpha polypeptide; alcohol dehydrogenase 1C (class I), gamma polypeptide	
126917	intermediate filament family orphan 2	
129684	contactin associated protein-like 5	
1310	collagen, type XIX, alpha 1	
1316	Kruppel-like factor 6	
133015	PARK2 co-regulated-like	
134637	adenosine deaminase, tRNA-specific 2, TAD2 homolog (S. cerevisiae)	
139065	SLIT and NTRK-like family, member 4	
139285	family with sequence similarity 123B	
140456	ankyrin repeat and SOCS box-containing 11	

140707	BRI3 binding protein
142	poly (ADP-ribose) polymerase 1
143686	sestrin 3
144608	chromosome 12 open reading frame 60
146760	reticulon 4 receptor-like 1
149478	hypothetical protein LOC149478
150350	ENTH domain containing 1
1510	cathepsin E
151050	chromosome 2 open reading frame 67
151230	kelch-like 23 (Drosophila)
1528	cytochrome b5 type A (microsomal)
153222	chromosome 5 open reading frame 41
154091	solute carrier family 2 (facilitated glucose transporter), member 12
157570	establishment of cohesion 1 homolog 2 (S. cerevisiae)
160287	lactate dehydrogenase A-like 6A
160418	transmembrane and tetratricopeptide repeat containing 3
160851	diacylglycerol kinase, eta
1629	dihydrolipoamide branched chain transacylase E2
1657	Dmx-like 1
168537	GTPase, IMAP family member 7
169200	transmembrane protein 64
1756	dystrophin
1831	TSC22 domain family, member 3; GRAM domain containing 4
1849	dual specificity phosphatase 7
1869	E2F transcription factor 1

1894	epithelial cell transforming sequence 2 oncogene
203523	zinc finger protein 449
2041	EPH receptor A1
2044	EPH receptor A5
2057	erythropoietin receptor
205717	KIAA2018
2117	ets variant 3
2120	ets variant 6
2150	coagulation factor II (thrombin) receptor-like 1
2152	coagulation factor III (thromboplastin, tissue factor)
2173	fatty acid binding protein 7, brain
220441	ring finger protein 152
221294	5'-nucleotidase domain containing 1
221981	thrombospondin, type I, domain containing 7A
222662	lipoma HMGIC fusion partner-like 5
2259	fibroblast growth factor 14
2274	four and a half LIM domains 2
22800	related RAS viral (r-ras) oncogene homolog 2; similar to related RAS viral (r-ras) oncogene homolog 2
22874	pleckstrin homology domain containing, family A member 6
22879	MON1 homolog B (yeast)
22891	zinc finger protein 365
2296	forkhead box C1
23051	zinc fingers and homeoboxes 3
23057	nicotinamide nucleotide adenylyltransferase 2
2308	forkhead box O1

2309	forkhead box O3; forkhead box O3B pseudogene
23131	G patch domain containing 8
23136	erythrocyte membrane protein band 4.1-like 3
23236	phospholipase C, beta 1 (phosphoinositide-specific)
23295	mahogunin, ring finger 1
23321	tripartite motif-containing 2
23657	solute carrier family 7, (cationic amino acid transporter, y+ system) member 11
253017	steroid 5 alpha-reductase 2-like 2
2538	glucose-6-phosphatase, catalytic subunit
254048	ubinuclein 2
254065	bromodomain and WD repeat domain containing 3
254228	family with sequence similarity 26, member E
256764	WD repeat domain 72
25816	tumor necrosis factor, alpha-induced protein 8
2591	UDP-N-acetyl-alpha-D-galactosamine:polypeptide N-acetylgalactosaminyltransferase 3 (GalNAc-T3)
25913	POT1 protection of telomeres 1 homolog (S. pombe)
25978	chromatin modifying protein 2B
26051	protein phosphatase 1, regulatory (inhibitor) subunit 16B
26071	family with sequence similarity 127, member B
26147	PHD finger protein 19
262	adenosylmethionine decarboxylase 1
26524	LATS, large tumor suppressor, homolog 2 (Drosophila)
26973	cysteine and histidine-rich domain (CHORD)-containing 1; cysteine and histidine-rich domain (CHORD)-containing 1 pseudogene
27086	forkhead box P1
27109	ATP synthase, H+ transporting, mitochondrial F0 complex, subunit s (factor B)

27161	eukaryotic translation initiation factor 2C, 2
27246	ring finger protein 115
27249	methylmalonic aciduria (cobalamin deficiency) cblD type, with homocystinuria
27287	VENT homeobox homolog (Xenopus laevis)
2742	glycine receptor, alpha 2
283	angiogenin, ribonuclease, RNase A family, 5
283635	family with sequence similarity 177, member A1
285440	cytochrome P450, family 4, subfamily V, polypeptide 2
287015	tripartite motif-containing 42
2872	MAP kinase interacting serine/threonine kinase 2
28966	sorting nexin 24
28982	feline leukemia virus subgroup C cellular receptor 1
2904	glutamate receptor, ionotropic, N-methyl D-aspartate 2B
2920	chemokine (C-X-C motif) ligand 2
2965	general transcription factor IIH, polypeptide 1, 62kDa
29761	ubiquitin specific peptidase 25
29843	SUMO1/sentrin specific peptidase 1
3021	H3 histone, family 3B (H3.3B); H3 histone, family 3A pseudogene; H3 histone, family 3A; similar to H3 histone, family 3B; similar to histone H3.3B
30845	EH-domain containing 3
3148	high-mobility group box 2
3303	heat shock 70kDa protein 1A; heat shock 70kDa protein 1B
339230	coiled-coil domain containing 137
3400	inhibitor of DNA binding 4, dominant negative helix-loop-helix protein
340533	KIAA2022
341208	hephaestin-like 1

341640	FRAS1 related extracellular matrix protein 2
342892	zinc finger protein 850 pseudogene
344787	zinc finger protein 860
3479	insulin-like growth factor 1 (somatomedin C)
3480	insulin-like growth factor 1 receptor
3569	interleukin 6 (interferon, beta 2)
3572	interleukin 6 signal transducer (gp130, oncostatin M receptor)
3667	insulin receptor substrate 1
367	androgen receptor
3672	integrin, alpha 1
3688	integrin, beta 1 (fibronectin receptor, beta polypeptide, antigen CD29 includes MDF2, MSK12)
3760	potassium inwardly-rectifying channel, subfamily J, member 3
387032	zinc finger with KRAB and SCAN domains 4
388	ras homolog gene family, member B
389072	pleckstrin homology domain containing, family M, member 3
3925	stathmin 1
3949	low density lipoprotein receptor
3976	leukemia inhibitory factor (cholinergic differentiation factor)
3977	leukemia inhibitory factor receptor alpha
4005	LIM domain only 2 (rhombotin-like 1)
4026	LIM domain containing preferred translocation partner in lipoma
402665	IgLON family member 5
4076	cell cycle associated protein 1
408	arrestin, beta 1
4084	MAX dimerization protein 1

4093	SMAD family member 9
4193	Mdm2 p53 binding protein homolog (mouse)
4208	myocyte enhancer factor 2C
4289	muskelin 1, intracellular mediator containing kelch motifs
4300	myeloid/lymphoid or mixed-lineage leukemia (trithorax homolog, Drosophila); translocated to, 3
445815	A kinase (PRKA) anchor protein 2; paralemmin 2; PALM2-AKAP2 readthrough transcript
4600	myxovirus (influenza virus) resistance 2 (mouse)
4685	neural cell adhesion molecule 2
472	similar to Serine-protein kinase ATM (Ataxia telangiectasia mutated) (A-T, mutated); ataxia telangiectasia mutated
4735	septin 2
4753	NEL-like 2 (chicken)
4774	nuclear factor I/A
4782	nuclear factor I/C (CCAAT-binding transcription factor)
4784	nuclear factor I/X (CCAAT-binding transcription factor)
4858	neuro-oncological ventral antigen 2
488	ATPase, Ca++ transporting, cardiac muscle, slow twitch 2
4899	nuclear respiratory factor 1
5013	orthodenticle homeobox 1
5078	paired box 4
5080	paired box 6
51022	glutaredoxin 2
51141	insulin induced gene 2
51232	cysteine rich transmembrane BMP regulator 1 (chordin-like)
51393	transient receptor potential cation channel, subfamily V, member 2
51533	PHD finger protein 7

5216	profilin 1
5243	ATP-binding cassette, sub-family B (MDR/TAP), member 1
5324	pleiomorphic adenoma gene 1
53344	cysteine-rich hydrophobic domain 1
5354	proteolipid protein 1
5366	phorbol-12-myristate-13-acetate-induced protein 1
538	ATPase, Cu++ transporting, alpha polypeptide
54328	G protein-coupled receptor 173
54462	KIAA1128
54516	mitochondrial translational release factor 1-like
54558	spermatogenesis associated 6
54602	Nedd4 family interacting protein 2
54664	transmembrane protein 106B
54796	basonuclin 2
54808	dymeclin
5481	peptidylprolyl isomerase D
54811	zinc finger protein 562
54978	chromosome 2 open reading frame 18
5501	protein phosphatase 1, catalytic subunit, gamma isoform
55071	chromosome 9 open reading frame 40
55183	RAP1 interacting factor homolog (yeast)
55207	ADP-ribosylation factor-like 8B
55294	F-box and WD repeat domain containing 7
55508	solute carrier family 35, member E3
55667	DENN/MADD domain containing 4C

55696	RNA binding motif protein 22
55700	MAP7 domain containing 1
55870	ash1 (absent, small, or homeotic)-like (Drosophila)
56052	asparagine-linked glycosylation 1, beta-1,4-mannosyltransferase homolog (S. cerevisiae)
56203	leiomodin 3 (fetal)
5629	prospero homeobox 1
56479	potassium voltage-gated channel, KQT-like subfamily, member 5
56660	potassium channel, subfamily K, member 12
56999	ADAM metallopeptidase with thrombospondin type 1 motif, 9
57010	calcium binding protein 4
57038	arginyl-tRNA synthetase 2, mitochondrial
57502	neuroligin 4, X-linked
57531	HECT domain and ankyrin repeat containing, E3 ubiquitin protein ligase 1
57551	TAO kinase 1
5756	twinfilin, actin-binding protein, homolog 1 (Drosophila)
57575	protocadherin 10
57711	zinc finger protein 529
57834	cytochrome P450, family 4, subfamily F, polypeptide 11
5813	purine-rich element binding protein A
58155	polypyrimidine tract binding protein 2
58516	similar to hCG2020539; family with sequence similarity 60, member A; similar to family with sequence similarity 60, member A
5905	Ran GTPase activating protein 1
59283	calcium channel, voltage-dependent, gamma subunit 8
595	cyclin D1
5999	regulator of G-protein signaling 4

60313	GC-rich promoter binding protein 1-like 1
60401	ectodysplasin A2 receptor
6304	SATB homeobox 1
6307	sterol-C4-methyl oxidase-like
6348	chemokine (C-C motif) ligand 3
63899	NOL1/NOP2/Sun domain family, member 3
639	PR domain containing 1, with ZNF domain
64121	Ras-related GTP binding C
64168	N-terminal EF-hand calcium binding protein 1
64399	hedgehog interacting protein
6469	sonic hedgehog homolog (Drosophila)
6517	solute carrier family 2 (facilitated glucose transporter), member 4
657	bone morphogenetic protein receptor, type IA; similar to ALK-3
65977	pleckstrin homology domain containing, family A (phosphoinositide binding specific) member 3
6602	SWI/SNF related, matrix associated, actin dependent regulator of chromatin, subfamily d, member 1
6643	sorting nexin 2
6660	SRY (sex determining region Y)-box 5
6667	Sp1 transcription factor
6670	Sp3 transcription factor
6776	signal transducer and activator of transcription 5A
6886	T-cell acute lymphocytic leukemia 1
7157	tumor protein p53
7184	heat shock protein 90kDa beta (Grp94), member 1
7188	TNF receptor-associated factor 5
727936	glycosyltransferase 8 domain containing 4

7357	UDP-glucose ceramide glucosyltransferase
7363	UDP glucuronosyltransferase 2 family, polypeptide B4
7517	X-ray repair complementing defective repair in Chinese hamster cells 3
7693	zinc finger protein 134
79027	zinc finger protein 655
79184	BRCA1/BRCA2-containing complex, subunit 3
79733	E2F transcription factor 8
79782	leucine rich repeat containing 31
79834	NKF3 kinase family member
79956	endoplasmic reticulum metallopeptidase 1
79991	oligonucleotide/oligosaccharide-binding fold containing 1
80018	chromosome 12 open reading frame 30
80034	cysteine-serine-rich nuclear protein 3
80167	chromosome 4 open reading frame 29
80311	kelch-like 15 (Drosophila)
8078	ubiquitin specific peptidase 5 (isopeptidase T)
8082	sarcospan (Kras oncogene-associated gene)
80830	apolipoprotein L, 6
8140	solute carrier family 7 (cationic amino acid transporter, y+ system), member 5
81848	sprouty homolog 4 (Drosophila)
8208	chromatin assembly factor 1, subunit B (p60)
83259	protocadherin 11 Y-linked
83604	transmembrane protein 47
83935	transmembrane protein 133
84056	katanin p60 subunit A-like 1

84437	KIAA1826
84529	chromosome 15 open reading frame 41
84552	par-6 partitioning defective 6 homolog gamma (C. elegans)
84826	SFT2 domain containing 3
84888	signal peptide peptidase-like 2A
84898	plexin domain containing 2
8490	regulator of G-protein signaling 5
84945	abhydrolase domain containing 13
85379	KIAA1671 protein
85440	dedicator of cytokinesis 7
85446	zinc finger homeobox 2
862	runt-related transcription factor 1; translocated to, 1 (cyclin D-related)
8674	vesicle-associated membrane protein 4
8933	family with sequence similarity 127, member A
8976	Wiskott-Aldrich syndrome-like
90141	chromosome 14 open reading frame 143
9048	artemin
9060	3'-phosphoadenosine 5'-phosphosulfate synthase 2
90624	Lyrm7 homolog (mouse)
91147	transmembrane protein 67
91452	acyl-Coenzyme A binding domain containing 5
91807	myosin light chain kinase 3
91860	calmodulin-like 4
9255	aminoacyl tRNA synthetase complex-interacting multifunctional protein 1
93034	retinol dehydrogenase 14 (all-trans/9-cis/11-cis); 5'-nucleotidase, cytosolic IB

949	scavenger receptor class B, member 1
9532	BCL2-associated athanogene 2
957	ectonucleoside triphosphate diphosphohydrolase 5
96459	folliculin interacting protein 1
9727	RAB11 family interacting protein 3 (class II)
9728	SECIS binding protein 2-like
9731	KIAA0562
9754	StAR-related lipid transfer (START) domain containing 8
9760	thymocyte selection-associated high mobility group box
989	septin 7
9899	synaptic vesicle glycoprotein 2B; hypothetical protein LOC100128403
996	cell division cycle 27 homolog (S. cerevisiae)

GENE NAME

zinc finger protein 460

methyl-CpG binding domain protein 6

transmembrane and tetratricopeptide repeat containing 3

epithelial cell transforming sequence 2 oncogene

MON1 homolog B (yeast)

solute carrier family 7, (cationic amino acid transporter, y+ system) member 11

family with sequence similarity 127, member B

family with sequence similarity 177, member A1

feline leukemia virus subgroup C cellular receptor 1

interleukin 6 (interferon, beta 2)

interleukin 6 signal transducer (gp130, oncostatin M receptor)

LIM domain containing preferred translocation partner in lipoma

muskelin 1, intracellular mediator containing kelch motifs

ATPase, Ca++ transporting, cardiac muscle, slow twitch 2

insulin induced gene 2

chromosome 2 open reading frame 18

TAO kinase 1

twinfilin, actin-binding protein, homolog 1 (Drosophila)

zinc finger protein 529

kelch-like 15 (Drosophila)

KIAA1826

signal peptide peptidase-like 2A

regulator of G-protein signaling 5

family with sequence similarity 127, member A

Wiskott-Aldrich syndrome-like

acyl-Coenzyme A binding domain containing 5