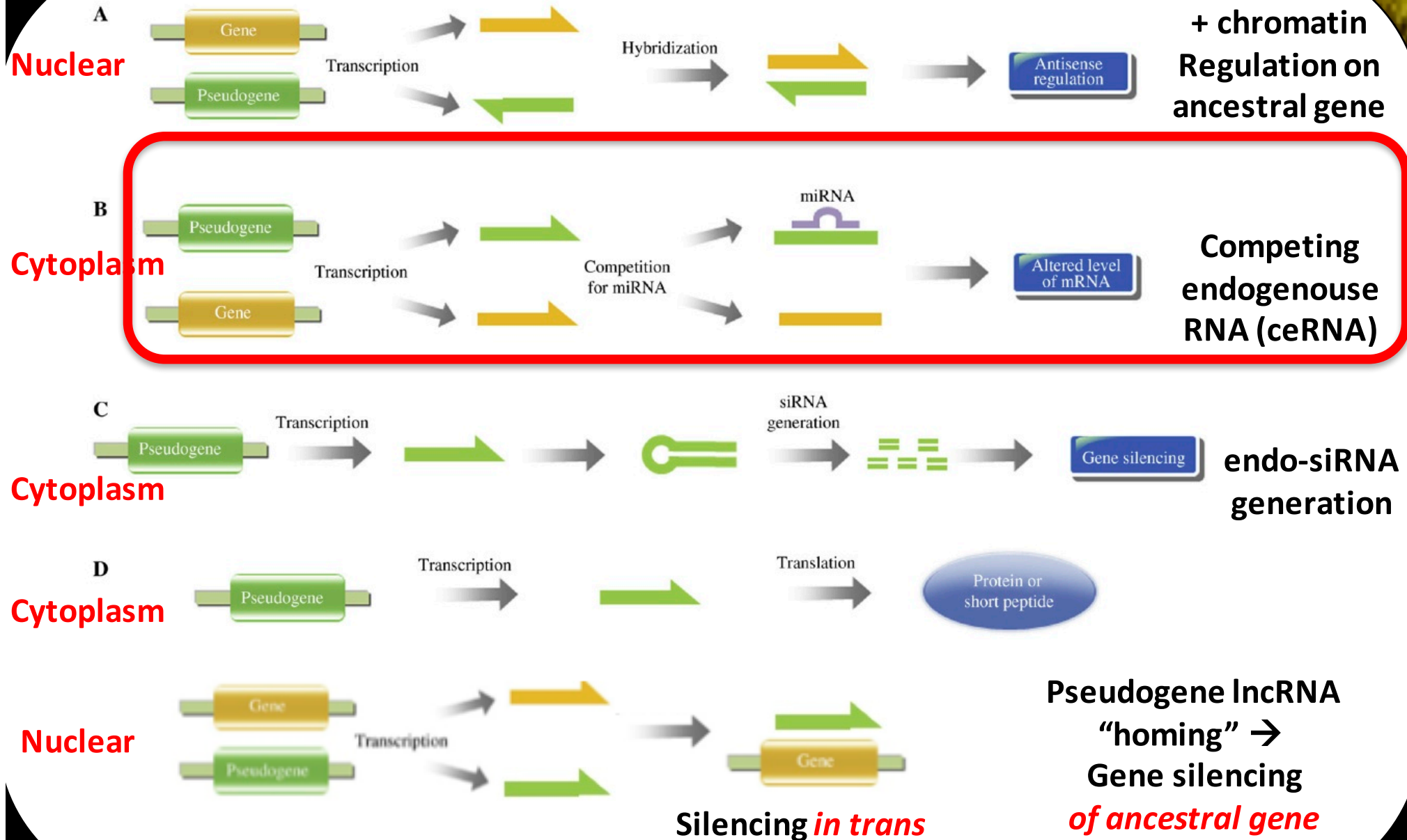*PSEUDOGENE lncRNAs*

COMPETING ENDOGENOUS RNAs (ceRNAs)

ceRNAs derived from pseudogenes
PTENP1

seudogenes are powerful regulators of gene expression

A Nuclear — Gene / Pseudogene → Transcription → Hybridization → Antisense regulation → **+ chromatin Regulation on ancestral gene**

B Cytoplasm — Pseudogene / Gene → Transcription → Competition for miRNA → miRNA → Altered level of mRNA → **Competing endogenouse RNA (ceRNA)**

C Cytoplasm — Pseudogene → Transcription → siRNA generation → Gene silencing → **endo-siRNA generation**

D Cytoplasm — Pseudogene → Transcription → Translation → Protein or short peptide

Nuclear — Gene / Pseudogene → Transcription → Gene — **Silencing *in trans*** → **Pseudogene lncRNA "homing" → Gene silencing *of ancestral gene***

# Small ncRNA and gene/chromatin regulation

micro-RNAs = miRNAs

short interfering RNAs = siRNAs

**miRNAs and siRNAs are generated
by the same machinery**

1. Long precursor dsRNA or stem loop RNA **(pri-miRNA)**
    note: pre-miRNA: loop RNA cleaved off by Drosha
    in nucleus

2. Processing into small RNAs by Dicer (still double-stranded)

    - **production of siRNAs**
    - **pre-miRNA processed to mature miRNAs (21-23 nt)**

3. Processing by RISC complex
    (RNA induced silencing complex)

4. guide RNA → regulatory RNA
    passenger RNA → will be eliminated

5. RISC complex+guide RNA → regulatory function

A. **RNA degradation = siRNA effect (cutting = "slicing"**
B. **inhibition of mRNA translation =mRNA effect**
C. **transfer to nucleus and chromatin
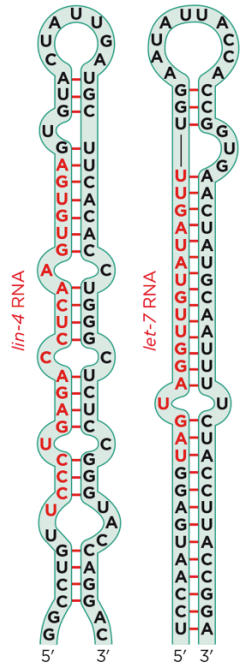   regulation = siRNA mediated silencing**

miRNAs: always "trans"-acting on mRNAs
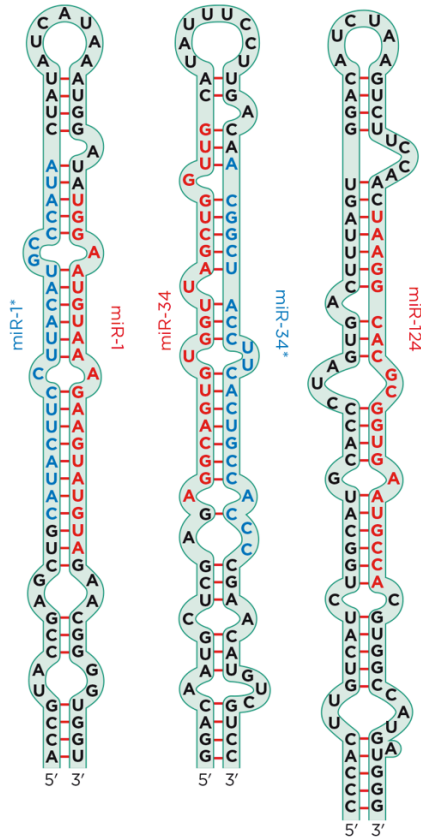**siRNAs: mostly "cis" acting on chromatin (S-pombe)**
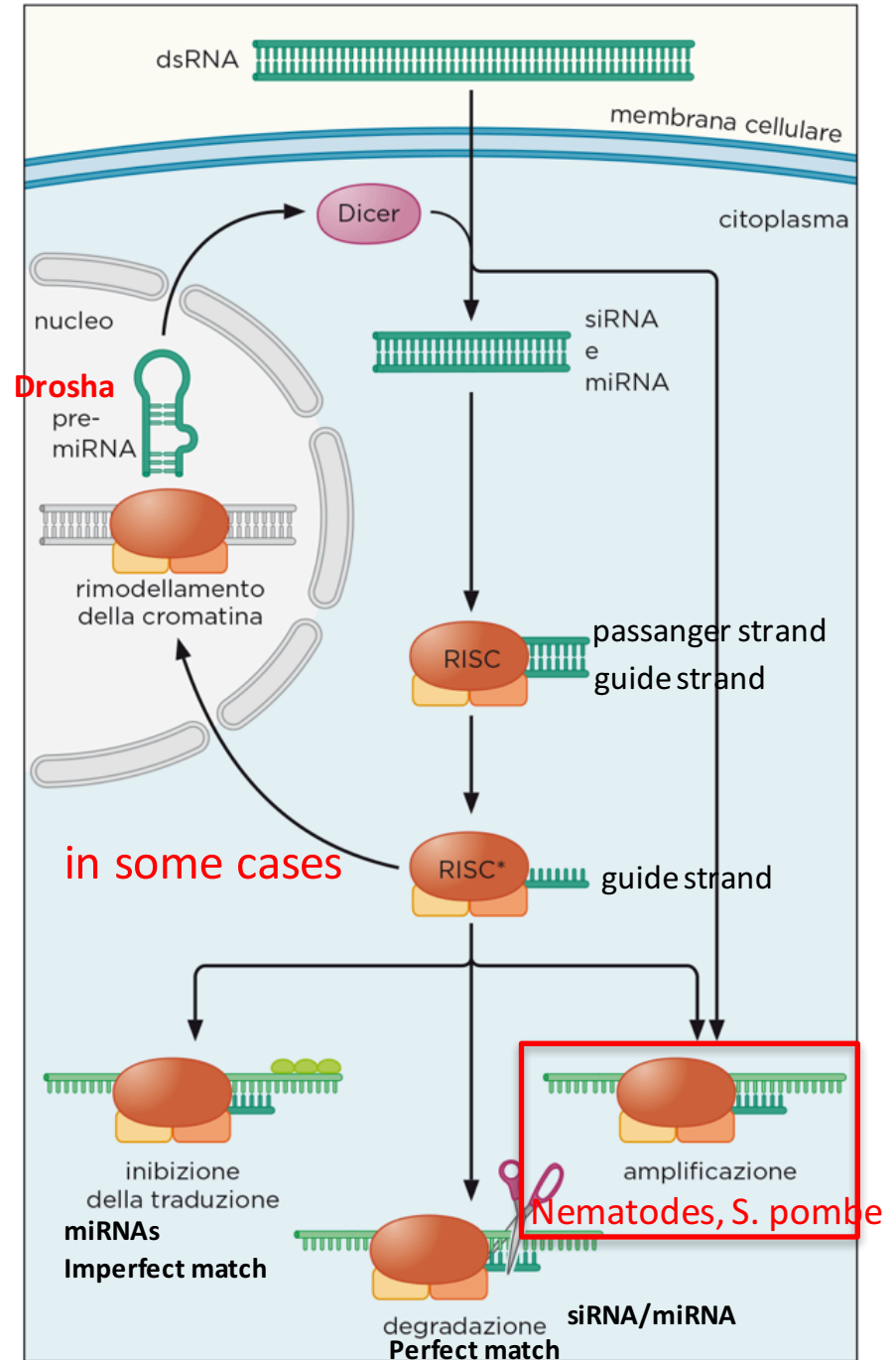
miRNA dependent regulation of gene expression

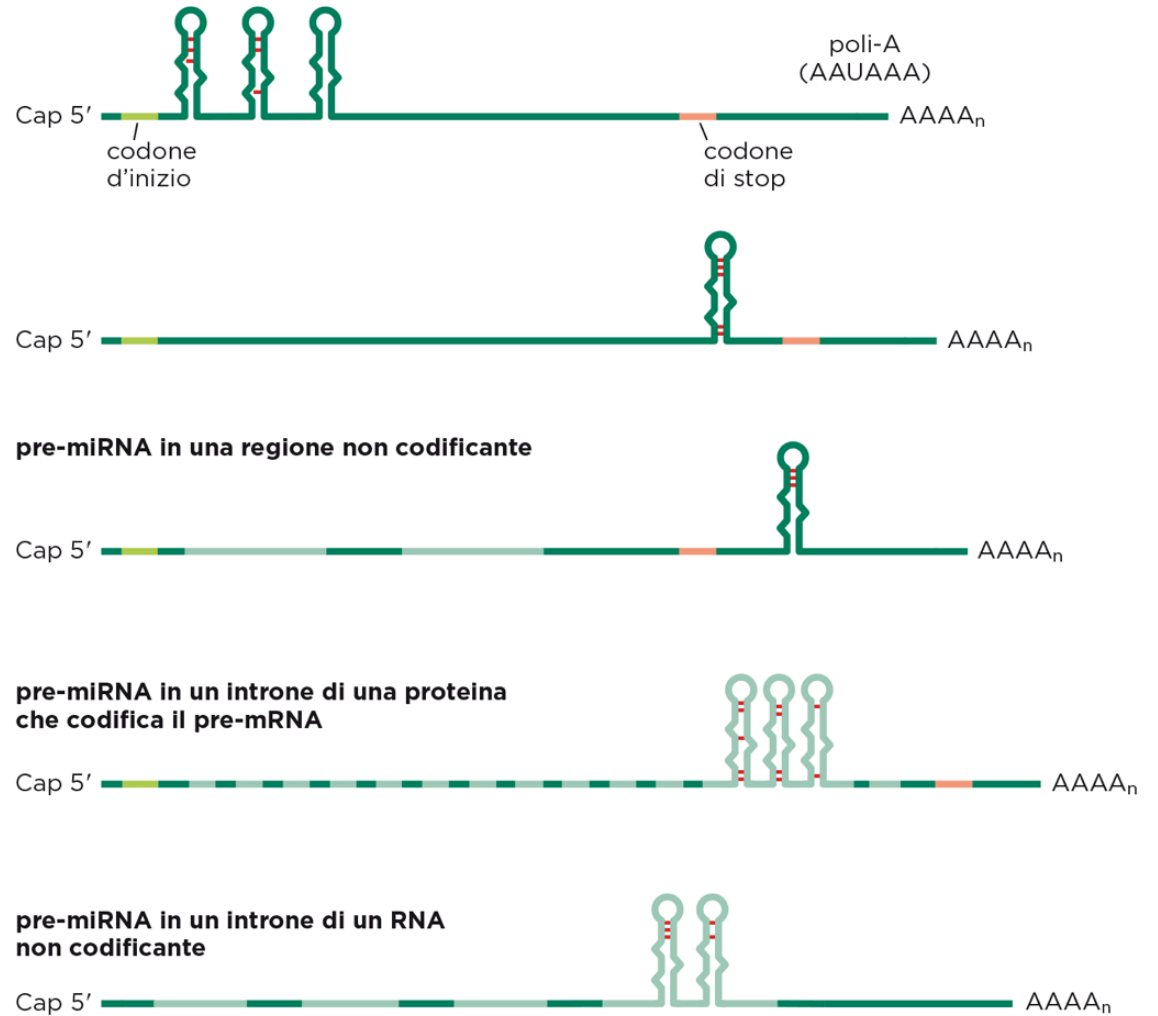**One strand generates miRNA**

both strand Generate miRNA

lin-4 RNA   *let-7 RNA*   miR-1*   miR-1   miR-34   miR-34*   miR-124

pri-miRNA (primary miRNA

↓ **Drosha**

pre-miRNA (precursor miRNA)

↓ **Dicer**

miRNA (mature miRNA)

pre-mIRNA nella regione codificante

poli-A (AAUAAA)

Cap 5' —— AAAA$_n$

codone d'inizio   codone di stop

Cap 5' —— AAAA$_n$

pre-miRNA in una regione non codificante

Cap 5' —— AAAA$_n$

pre-miRNA in un introne di una proteina che codifica il pre-mRNA

Cap 5' —— AAAA$_n$

pre-miRNA in un introne di un RNA non codificante

Cap 5' —— AAAA$_n$

Pre-miRNA encoded by:
- **mRNA genes: INRTONS and few exons**
- **separate small genes**
- **Introns and exons of lncRNAs**

a
pri-miRNA

~11 bp ~22 bp

passaggio di riconoscimento del substrato

DGCR8 — Drosha

b
passaggio della reazione catalitica

centro di processamento

~11 bp

prodotti

F1   F2 (pre-miRNA)
F3
~11 bp   ~22 bp

taglio da parte di Drosha

taglio da parte di Dicer

5' NNNNN ... +1

miRNA maturo

3' NNNNN ... −2

segmenti di base | stelo inferiore (~11 bp) | stelo superiore (~22 bp) | ansa terminale
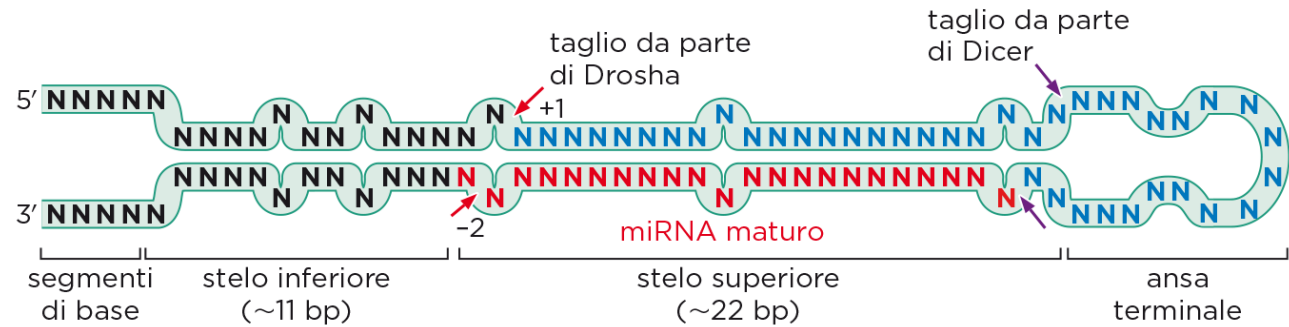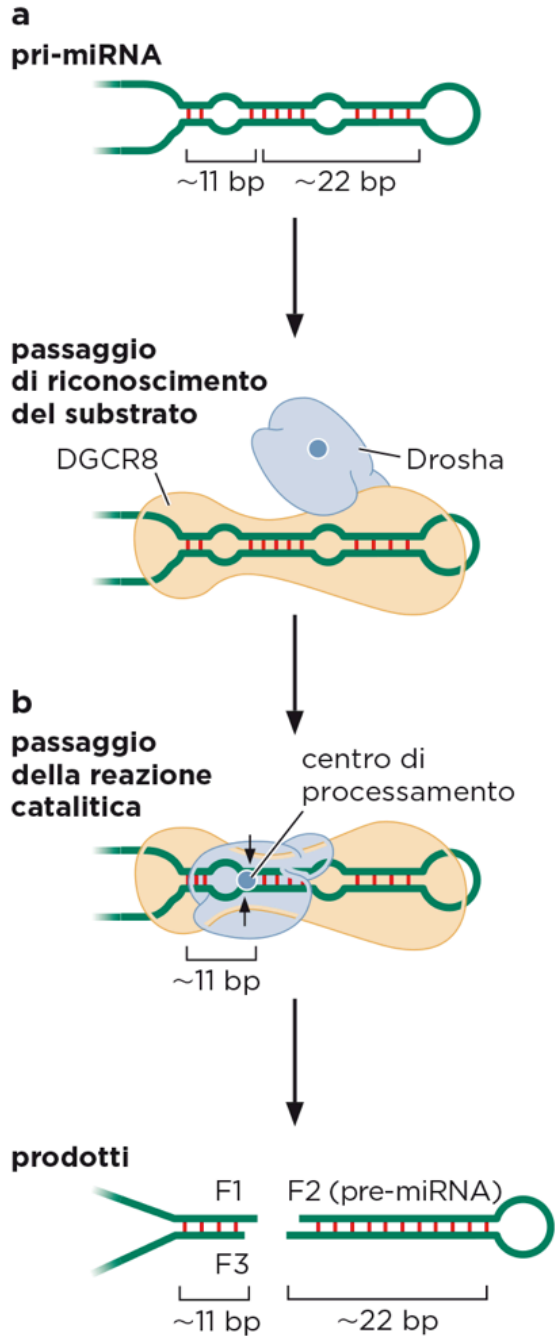
Drosha, Dicer: **Type III RNases**: cut 2 RNA strands in RNA duplex, leave overhang!!

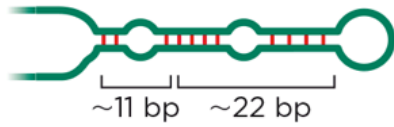**1. Microprocessor (Drosha and DGCR8) generates a 65-70 nt RNA stem loop:**

Drosha cuts app. 11 nt after start of dsRNA region
5 components: stelo inferiore (11 bp); stelo superiore (22 nt)
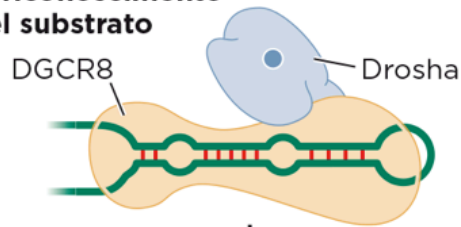ansa terminale; segmenti di base

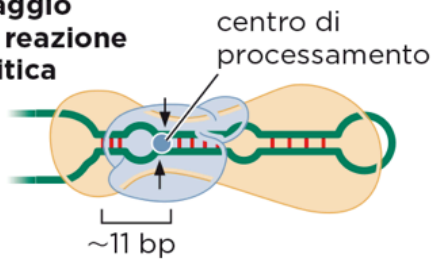**2. Transfer to cytoplasma**

miRNA generation - DICER

a
pri-miRNA

~11 bp ~22 bp

passaggio di riconoscimento del substrato

DGCR8 Drosha

b
passaggio della reazione catalitica

centro di processamento

~11 bp

Dicer

prodotti

F1 F2 (pre-miRNA)

F3

~11 bp ~22 bp

taglio da parte di Drosha

taglio da parte di Dicer

5′ NNNNN ... +1
3′ NNNNN ... -2

miRNA maturo

segmenti di base | stelo inferiore (~11 bp) | stelo superiore (~22 bp) | ansa terminale
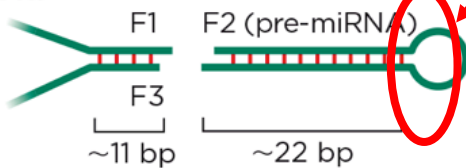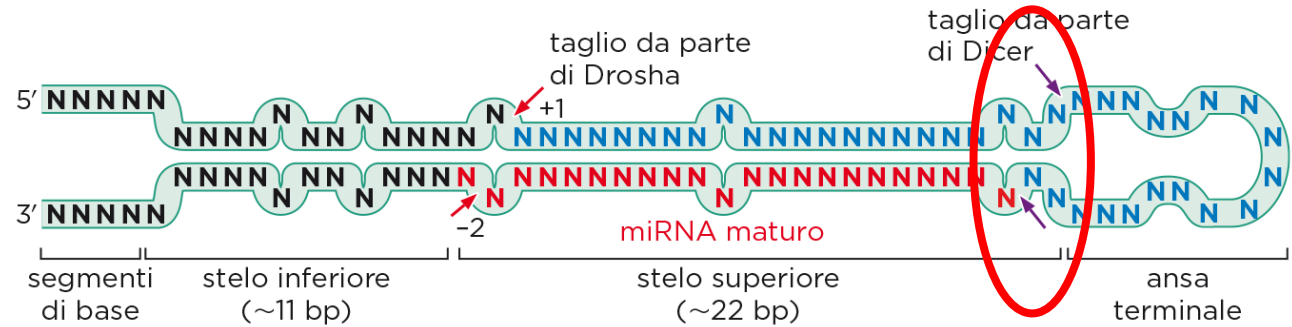
Dicer

DICER processes all dsRNAs (NOT SEQUENCE SPECIFIC)

a modello di Dicer (*Giardia intestinalis*)

lama

manico

dominio PAZ all'estremità 3′ dell'RNA

3′
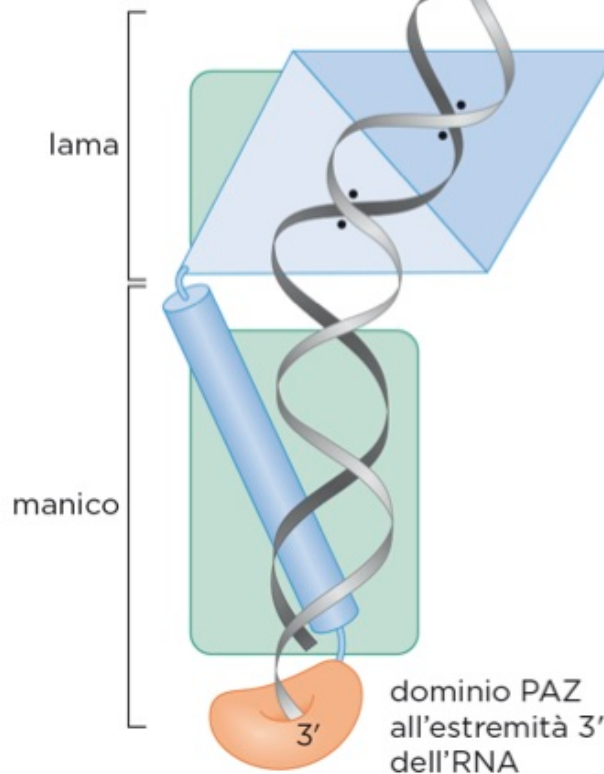
2 RNase domains: act on ALL dsRNAs

manico interacts with dsRNA

PAZ interacts with dsRNA

STUDENT's SEMINAR PROGRAM

	Group 1	Group 2			Group 3
Topic Number	5	2			11
Title	Genomic Imprinting regulated by lncRNAs	Dosage Compensation in vertebrates (Xist-Tsix)	No lecture	No lecture	lncRNAs and resistance of tumors to chemotherapy
Student 1	Alessio Conci	Annamaria Regina			Daniele Ammeti
Student 2	Eleonora Lucantonio	Claudio Antonio Coppola			Gabriele Di Giustino
Student 3	Ermelinda Sabarese	Giulia Maria Clemenza			Lorenzo Graziani
Presentation of draft to Prof.	31.10.2019	07.11.2019			15.11.2019
Date of presentation	14.11.2019	15.11.2019	21.11.2019	22.11.2019	28.11.2019

	Group 4	Group 5	Group 6	Group 7	Group 8
Topic Number	6	9	12	13	8
Title	lncRNAs and Hyperconserved elements	R-loops and regulation of gene expression	lncRNAs and resistance of tumors to immunotherpay	cancer formation and progression	R-loops and genomic instability
	Lucia D'Amico	Violina Potlog			
Student 1	Maria Pia Viscomi	Margot Ladislas	Debora Maffeo	Enrico Bagnariol	Annalisa Scapolatiello
Student 2	Agata Valentino	Isabella Concina	Carmela Tangredi	Jessica Fiorino	Marta Stancampiano
Student 3			Ilaria Ziccardi	Angelica Vanini	Michela Porcari
Presentation of draft to Prof.	15.11.2019	28.11.2019	29.12.2019	05.12.2019	06.12.2019
Date of presentation	29.11.2019	05.12.2019	06.12.2019	12.12.2019	13.12.2019

	Group 9	Group 10	Group 11	Group 12	
Topic Number	10	3	4	1	
Title	R-loops and genomic instability	Telomerase RNA maturation and Cajal Bodies	RNA:Protein bodies: Paraspeckles (NEAT-1)	Dosage Compensation in D.melanogaster (rox RNAs)	
Student 1	Ciro Danubio	Emeline Callac-Rouxel	Simone Bellini	Séverine Nozownik	
Student 2	Carmen Tucci	Clarissa Orrico	Luigi Ferrara	Roberta Palmitessa	
Student 3	Michele Tonetti		Teresa Bannino		
Presentation of draft to Prof.	12.12.2019	13.12.2019	19.12.2019	20.12.2019	
Date of presentation	19.12.2019	20.12.2019	08.01.2020	09.01.2020	

miRNA gene

pri-miRNA

Cap

Drosha

DGCR8/Pasha

pre-miRNA

Exportin-5

Nucleus

Cytoplasm

pre-miRNA

5'
3'

Dicer

TRBP/Loquacious
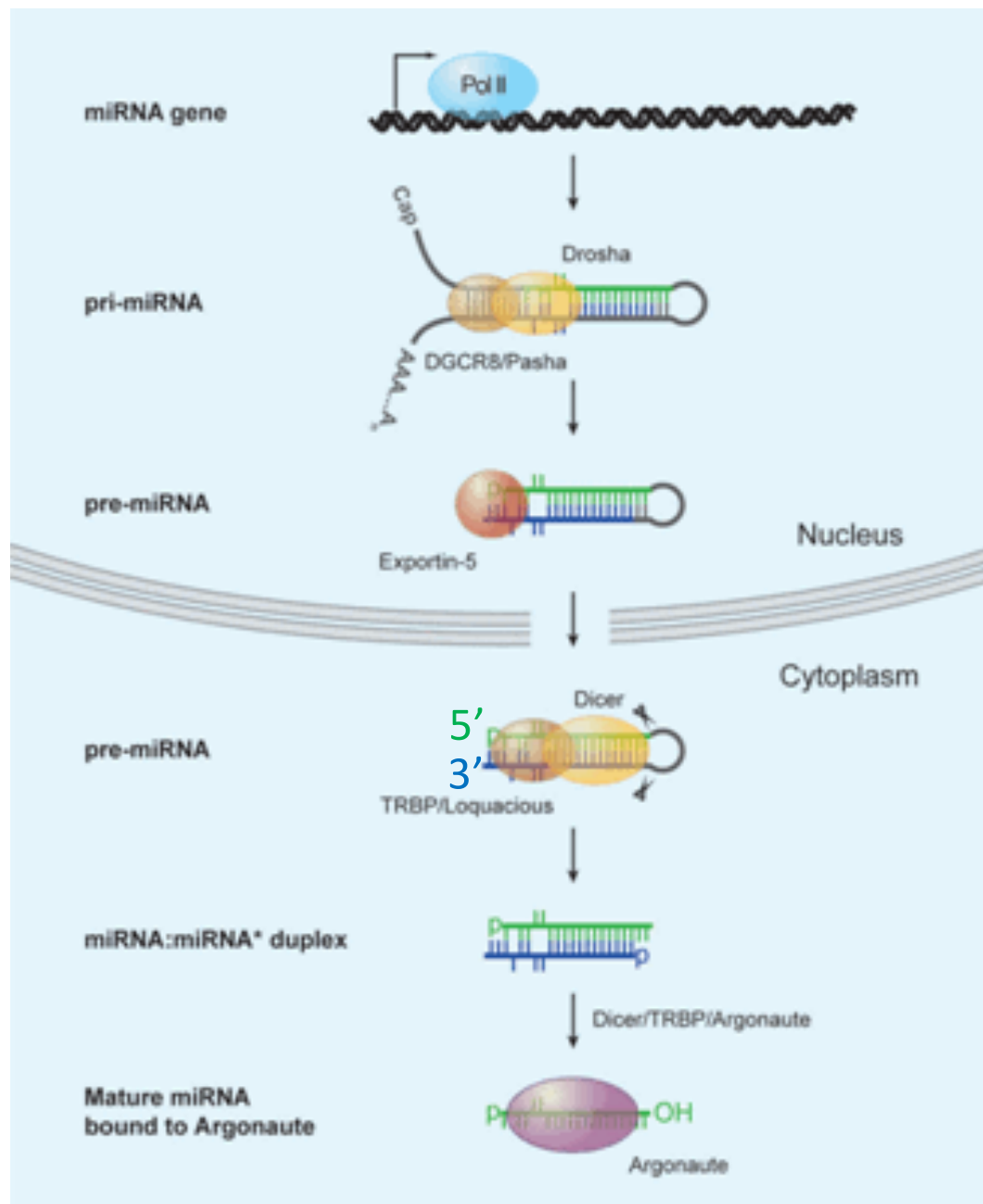
-5p or -3p miRNA
i.e. miR-296-5p
miR-296-3p

miRNA:miRNA* duplex

Dicer/TRBP/Argonaute

Mature miRNA
bound to Argonaute

Argonaute

'hD Cou...applications   PICA - Indice   CARGO File Delivery Facility   intranet.pre...ReturnUrl=%2F   Test PreCanMed   Coupling of H...olecular Cell   Alternative le...nline Library   ic-Rom - +++... Marino +++   >>

en microRNAs with star and...   minra maturation - Cerca con Google   miRNA Entry for MI0000747

miRBase

Home **Search** **Browse** **Help** **Download** **Blog** **Submit** **hsa-mir-296**   **Search**

Stem-loop sequence hsa-mir-296

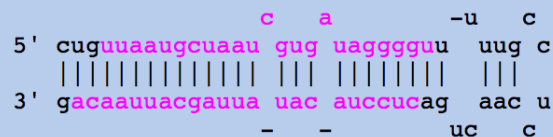|	
Accession	MI0000747
Symbol	HGNC:MIR296
Description	Homo sapiens miR-296 stem-loop
Gene family	MIPF0000159; mir-296

This text is a summary paragraph taken from the Wikipedia entry entitled miR-296. miRBase and Rfam are facilitating community annotation of microRNA families and entries in Wikipedia. Read more ...

Community annotation

miR-296 is a family of microRNA precursors found in mammals, including humans. The ~22 nucleotide mature miRNA sequence is excised from the precursor hairpin by the enzyme Dicer. This sequence then associates with RISC which effects RNA interference. miR-296 has been named an "angiomiR" due to being characterised as a microRNA which regulates angiogenesis, the process of growth and creation of new blood vessels. miR-296 is thought to have a specific role in cancer in promoting tumour angiogenesis. It achieves this by targeting HGS mRNA, reducing its expression in endothelial cells which then results in greater number of VEGF receptors. miR-296 has predicted target sites in the transcription factor NANOG and may also contribute to carcinogenesis by dysregulating p53.

Show Wikipedia entry   View @ Wikipedia   Edit Wikipedia entry

Stem-loop

```
         ga     ca       c  c        g   ugc
5' ag  cccuuc  gagggcc cc cucaauccu uug        c
   ||  ||||||  ||||||| || ||||||||| |||        u
3' uc  gggaag  cucucgg gg ggguuggga gac        a
         uc     uc       a  u        -   uua
```

Get sequence

Deep sequencing

1633 reads, 355 reads per million, 59 experiments

AGGACCCUUCCAGAGGGCCCCCCCUCAAUCCUGUUGUGCCUAAUUCAGAGGGUUGGGUGGAGGCUCUCCUGAAGGGCUCU

Stem-loop sequence hsa-mir-155

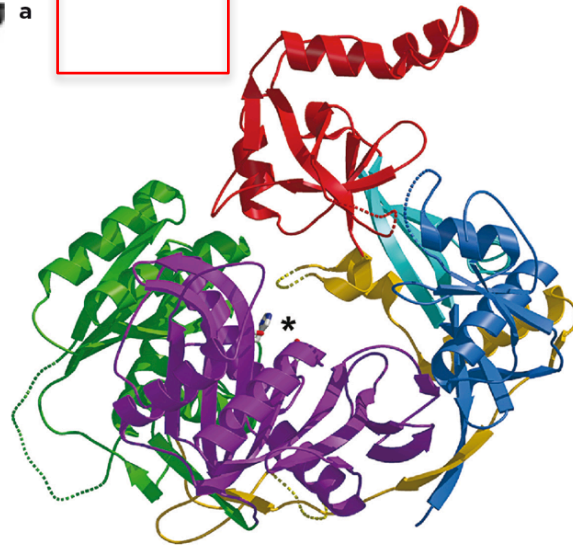|	
Accession	MI0000681
Symbol	HGNC:MIR155
Description	Homo sapiens miR-155 stem-loop
Gene family	MIPF0000157; mir-155
Community annotation	This text is a summary paragraph taken from the Wikipedia entry entitled Mir-155. miRBase and Rfam are facilitating community annotation of microRNA families and entries in Wikipedia. Read more ... MiR-155 is a microRNA that in humans is encoded by the MIR155 host gene or MIR155HG. MiR-155 plays an important role in various physiological and pathological processes. Exogenous molecular control in vivo of miR-155 expression may inhibit malignant growth, viral infections, and attenuate the progression of cardiovascular diseases. Show Wikipedia entry View @ Wikipedia Edit Wikipedia entry
Stem-loop	``` c a -u c 5' cuguuaaugcuaau gug uagggguu uug c ||||||||||||| ||| |||||||| ||| 3' gacaauuacgauua uac auccucag aac u - - uc c ``` Get sequence
Deep sequencing	55243 reads, 2.94e+03 reads per million, 62 experiments CUGUUAAUGCUAAUCGUGAUAGGGGUUUUUGCCUCCAACUGACUCCUACAUAUUAGCAUUAACAG

Regulation of gene expression by miRNAs

```
hsa-miR155        3'-UGGGGAUAGUG-----CUAAUCGUAAUU-5'
                     |    || |:::     |||||||
Human         5'GUAAUUUAAAACUUUUGU-----UUAAAGCAUUAC--------AGUAU-----------3'
Chimpanzee    5'GUAAUUUAAAACUUUUGU-----UUAAAGCAUUAC-------AGUAU-----------3'
Cow           5'------CAAAA-UUCUGU-----UUAAAGCAUUAC-------AACAU-----------3'
Rabbit        5'--------AAAUUUUGGU-----UUAAAGCAUUAU-------UU--------------3'

Mouse         5'AUGAUAAAGCAUUAUGGUGGUGGUGGGGCAGUGAGGAGGGGGAAGAGAAAGAGAGUUU-3'
Rat           5'AAGAUGAAGCAUUAUUGU----GU a                              b
```
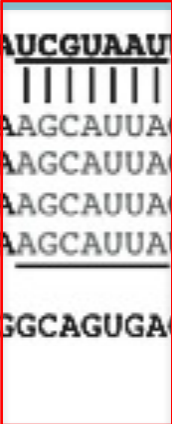
Seed sequence: pos 2-8 in miRNA
(5' → 3')

il dominio PAZ
riconosce
l'estremità 3'
dell'RNA

PAZ

Mid

N

dominio
RNasico

sito attivo dell'RNasi posizionato
per tagliare nel centro della regione
appaiata tra il piccolo RNA e l'mRNA
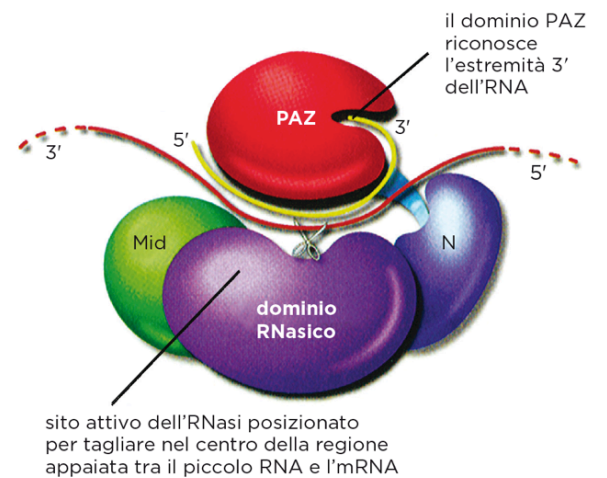
One strand of pre-miRNA is incorporated into the RISC complex (RNA induced
Silencing complex) = guide strand
Passenger strand degraded by RISC complex

Base pairing miRNA/siRNA – target RNA
(seed sequence in miRNA is most important for target identification

RNAse domain cleaves target transcript   OR   translational repression

Regulation of gene expression by miRNAs

Gene regulation

RISC uses the bound guide strand to target complementary 3'-untranslated regions (3'UTR) of mRNA transcripts via Watson-Crick base pairing. RISC can now regulate gene expression of the mRNA transcript in a number of ways.

mRNA degradation

The most understood function of RISC is degrading target mRNA which reduces the levels of transcript available to be translated by ribosomes. There are two main requirements for mRNA degradation to take place:

a near-perfect complementary match between the guide strand and target mRNA sequence, and,
a catalytically active Argonaute protein, called a **'slicer'**, to cleave the target mRNA.
mRNA degradation is localised in cytoplasmic bodies called **P-bodies**.

Translational repression

RISC can modulate the loading of ribosome and accessory factors in translation to repress expression of the bound mRNA transcript. Translational repression only requires a partial sequence match between the guide strand and target mRNA.

Translation can be regulated at the **initiation** step by:
- preventing the binding of the eukaryotic translation initiation factor (eIF) to the 5' cap. It has been noted RISC can de-adenylate the 3' poly(A) tail which might contribute to repression via the 5' cap.
- preventing the binding of the 60S ribosomal subunit binding to the mRNA can repress translation.

Translation can be regulated at **post-initiation steps** by:
-promoting premature termination of translation ribosomes, or,
-slowing elongation.
There is still speculation on whether translational repression via initiation and post-initiation is mutually exclusive.

…note: some imprefect matching miRNAs can also lead to reduced target target mRNA levels
(debated topic…. what could be the reason

MicroRNA Nomenclature

Different miRNA genes that have different location in the genome, but each of them produces a miRNA with identical seqeunce (i.e. hsa-miR-7

Alleles: all express same mature microRNA

hsa-mir-7-1
hsa-mir-7-2
hsa-mir-7-3

Mature miR-7 microRNA expressed

miRBase

http://www.mirbase.org

Dual precursors: express two mature microRNAs equally

Stem-loop sequence MI0003129

Accession	MI0003129
ID	hsa-mir-146b
Symbol	HGNC:MIR146B
Description	Homo sapiens miR-146b stem-loop

miR-146b-5p

miR-146b-3p

```
           u        g       au        cu  ca  u
         cc ggcacu agaacuga uccauagg  cu  gc c
Stem-loop || ||||||| |||||||| ||||||||| ||  || 
         gg ccgugg ucuugacu  aggugucc  ua  cg u
           u        -       -c        cg  -a a
```

SBI System Biosciences
Accelerating Discoveries in Functional Genomics

Current nomenclature

Star forms: express two mature microRNAs unequally

Mature sequence MIMAT0000076

Accession	MIMAT0000076
ID	hsa-miR-21
Sequence	8 - uagcuuaucagacugauguuga - 29

Minor miR* sequence MIMAT0004494

Accession	MIMAT0004494
ID	hsa-miR-21*
Sequence	46 - caacaccagucgaugggcugu - 66

Old nomenclature:
* miRNA referes to the strand present at lower levels → thought to be non-functional

ARTICLES

A coding-independent function of gene and pseudogene mRNAs regulates tumour biology

Laura Poliseno[1]*†, Leonardo Salmena[1]*, Jiangwen Zhang[2], Brett Carver[3], William J. Haveman[1] & Pier Paolo Pandolfi[1]

BACKGRUND ON PTEN

PTEN: heterozygous mutations: CANCER FORMATION (=haploinsuffcient tumorsuppressor gene)

TARGETING OF PTEN BY **miRNAs****: reduction of PTEN expression → promotion of tumor formation!!!!**

CELLS ARE EXTREMLY SENSITIVE TO SLIGHT CHANGES IN GENE EXPRESSION LEVELS

*PTEN has generated one processed pseudogene: PTENP1
highly conserved to PTEN*

*QUESTION: DOES PTENP1 IMPACT ON PTEN EXPRESSION
VIA SPONGING miRNAs???*

PTEN Wikipedia: Phosphatase and tensin homolog (PTEN) is a protein that, in humans, is encoded by the PTEN gene. Mutations of this gene are a step in the development of many cancers. PTEN orthologs have been identified in most mammals for which complete genome data are available.

This gene was identified as a tumor suppressor that is mutated in a large number of cancers at high frequency. The protein encoded by this gene is a phosphatidylinositol-3,4,5-trisphosphate 3-phosphatase. It contains a tensin-like domain as well as a catalytic domain similar to that of the dual specificity protein tyrosine phosphatases. Unlike most of the protein tyrosine phosphatases, this protein preferentially dephosphorylates phosphoinositide substrates. It negatively regulates intracellular levels of phosphatidylinositol-3,4,5-trisphosphate in cells and functions as a tumor suppressor by negatively regulating Akt/PKB signaling pathway.

THE PTEN PSEUDOGENE PTENP1

a

PTENP1 mRNA

PTENP1 has shorter 3'UTR then ancestral gene (- 1kb)

PTEN mRNA

b

3' UTR

ORF

ORF

1 kb

Some target sites of PTEN specific miRNAs are also present in PTENP1

Seed region

```
5' GGAUUAAUAAAGAUGGCACUUU   3' PTEN
   ||||  ||  |  | |||||||||
3' GAUGGACGUGAUAUUCGUGAAAU   5' miR-20a
   ||||  ||  |  | |||||||||
5' GGAUUAAUAAAGAUGGCACUUU   3' PTENP1
```

```
5' UUCACAUCCUACCCCUUUGCAC   3' PTEN
   ||| |         ||||||||
3' AGUCAAAACGUACCUAAACGUGU   5' miR-19b
   ||| |         ||||||||
5' UUCACAUCAUACCCCUUUGCAC   3' PTENP1
```

```
5' ACUUGUGGCAACAGAUAAGUU   3' PTEN
   |        |  |||||||||
3' AGUUGUAGUCAGACUAUUCGAU   5' miR-21
   |        |  |||||||||
5' ACUUGUGGCAACAGAUAAGUU   3' PTENP1
```

```
5' ACACCAUGAAAAUAAACUUGAA   3' PTEN
   |   | ||       ||||||||
3' UCGGAUAGGACCUAAUGAACUU   5' miR-26a
   |   |||        ||||||||
5' ACACCAUGAAAACAAACUUGAA   3' PTENP1
```

```
5' UUUCAAUCAUAAUACCUGCUG   3' PTEN
   ||| |    |  |  |||||||||
3' UGACGGACAGACACGGACGACA   5' miR-214
   ||| |    |  |  |||||||||
5' UUUCAAUCAUA-UACCUGCUG   3' PTENP1
```

miRNAs target both RNAs: PTEN and PTENP1

Transefection of cells
with miRNAs specific
for PTEN and PTENP1

Check expression levels
of PTEN and PTENP1
By RT-PCR
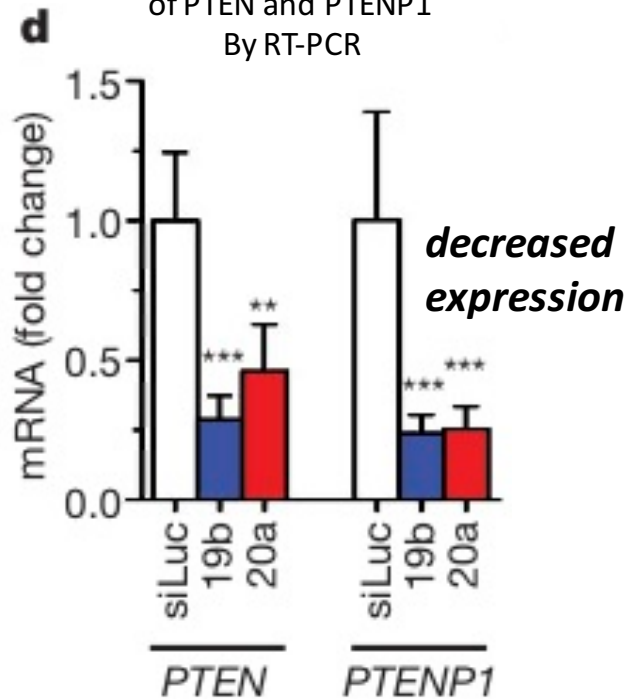
Transefection of cells
with siRNAs that target
miRNAs that are specific
for PTEN and PTENP1

Check expression levels
of PTEN and PTENP1
By RT-PCR

decreased expression

increased expression
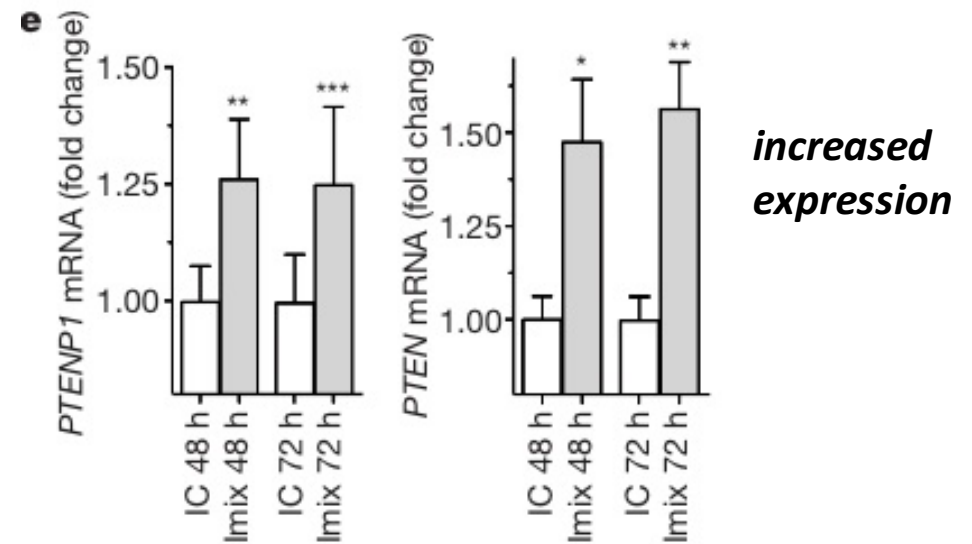
miR-19c and miR-20c target both RNAs

DEMONSTRATION OF miRNA – PTENP1_3'UTR INTERACTION USING A LUCIFERASE REPORTER ASSAY

Point mutations that destroy miRNA target sites
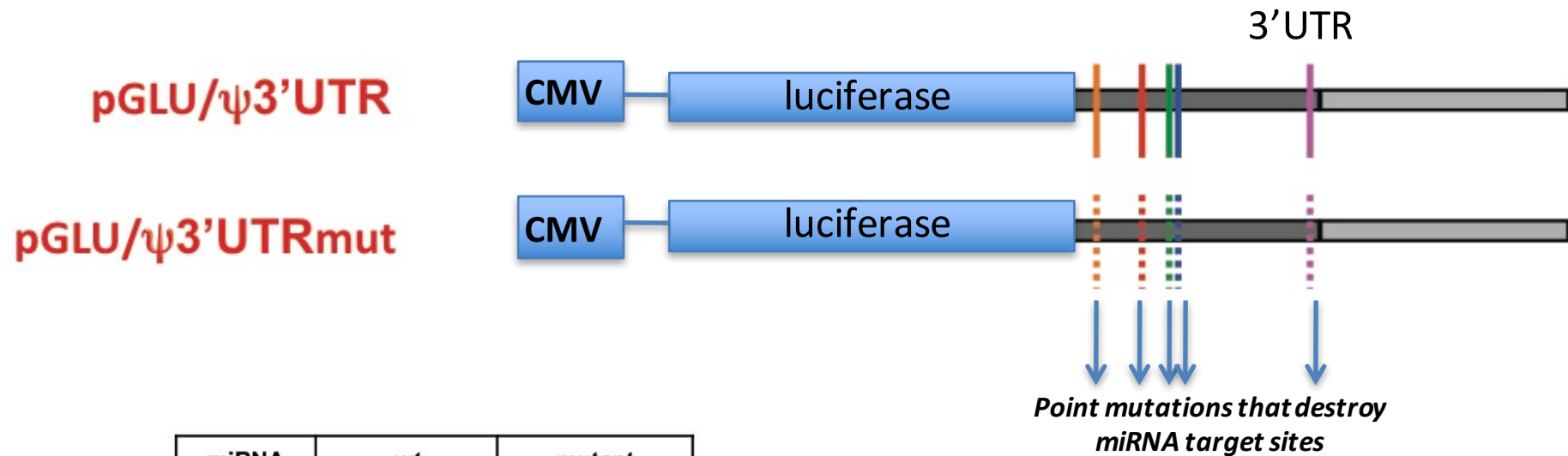
miRNA family	wt seed match	mutant seed match
17	GGCACTTT	GcCtCaTa
19	TTTGCAC	aTaGgAg
21	GATAAGTT	GtTtAcTt
26	ACTTGAA	tCaTcAt
214	CCTGCTG	gCaGgTc
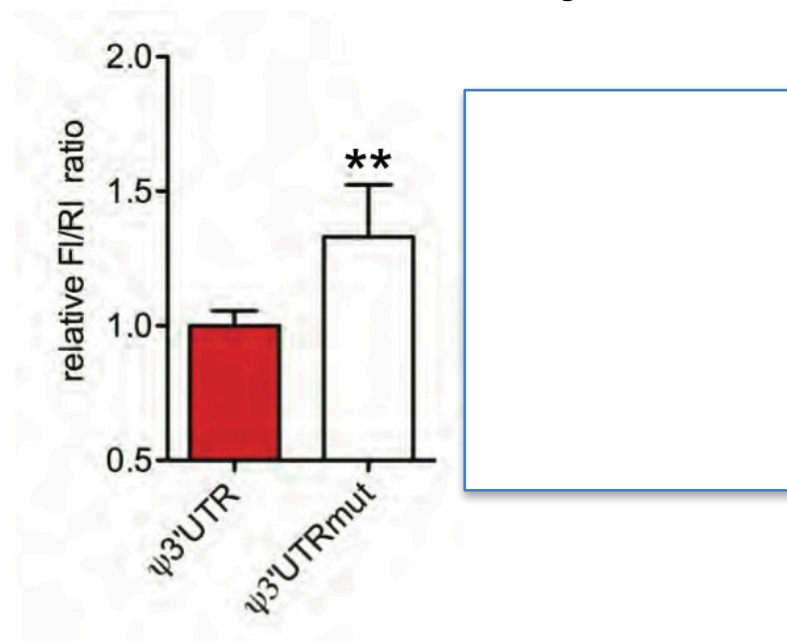
The 3'UTR of PTENP1 sequesters miRNAs

PTENP1 CONTROLS THE EXPRESSION OF PTEN

a

PTEN mRNA (fold change)

**

PIG   ψ3' UTR

PTEN

HSP90

h

siLuc   si-PTEN/PTENP1   si-PTEN   si-PTENP1

PTEN

1.0   0.1   0.5   0.6

HSP90

ion
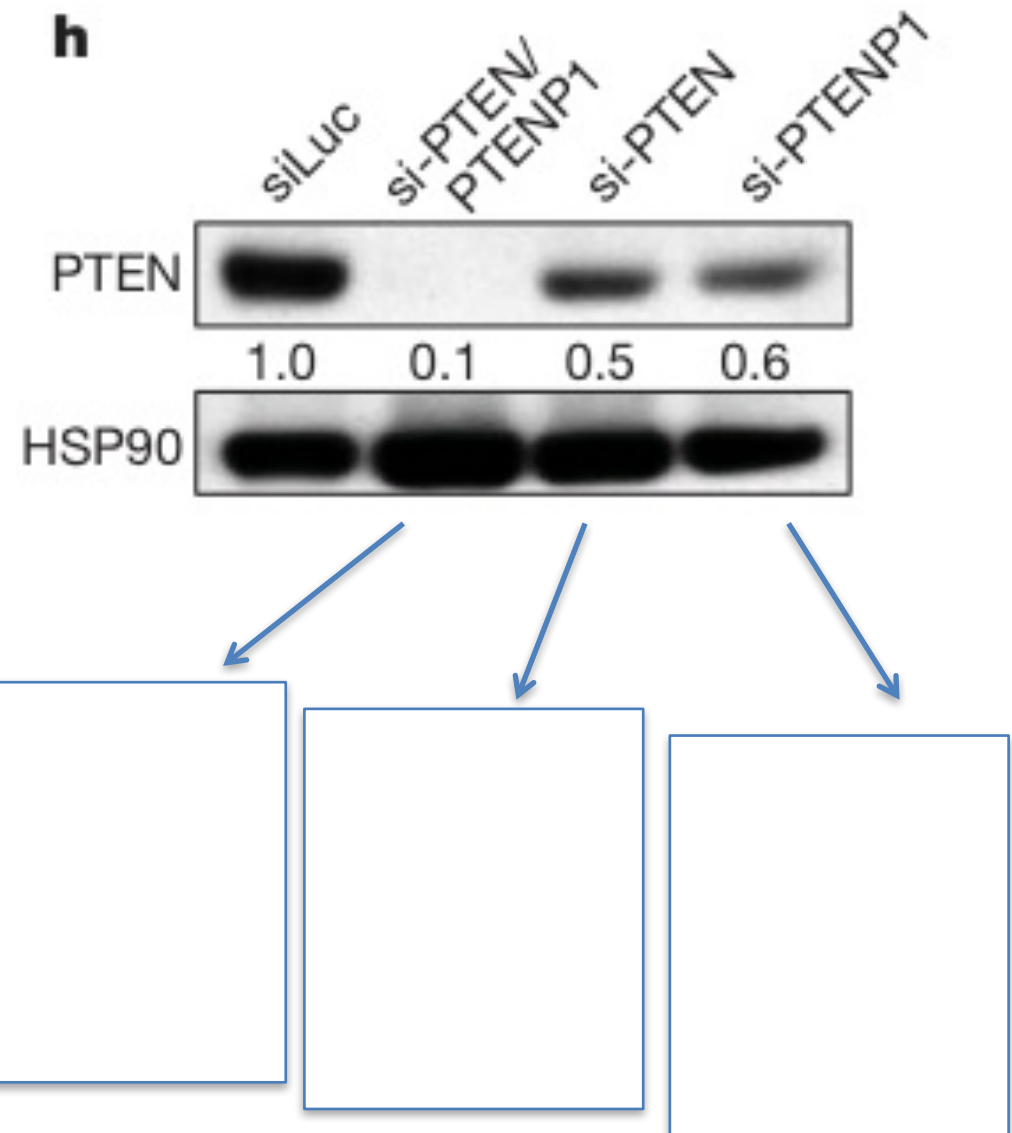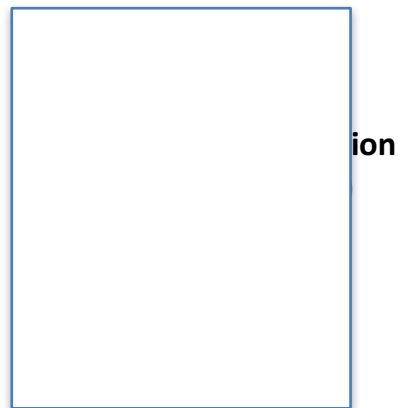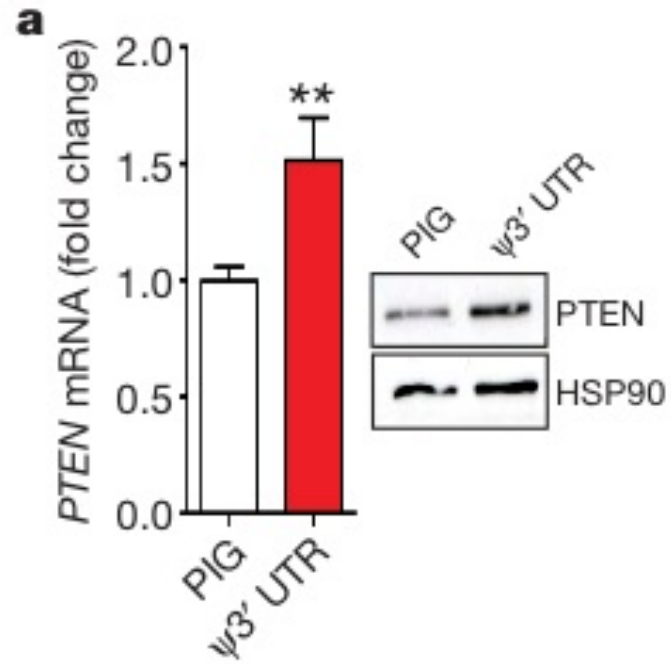
PTENP1 suppresses tumor cell proliferation
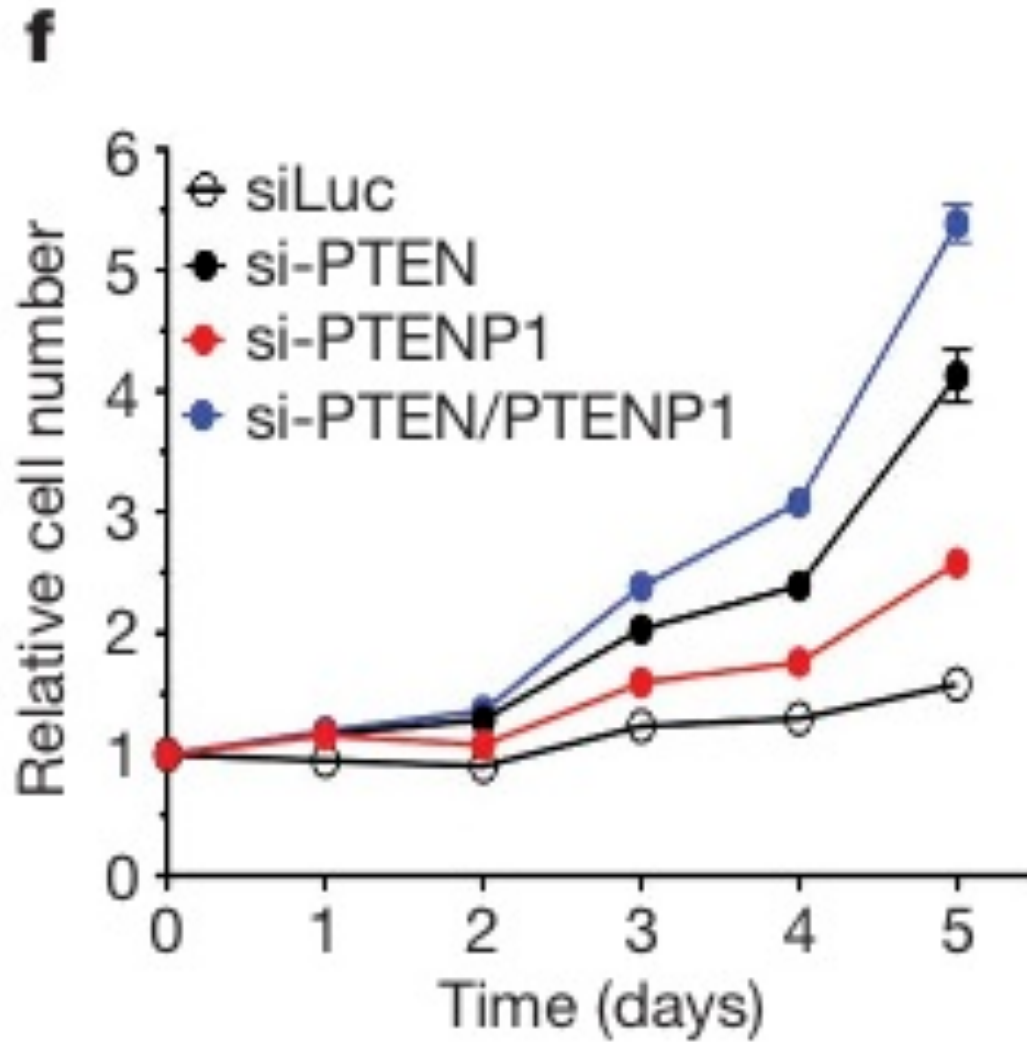
Cumulative cell numbers:
Cancer cells proliferate quickly;
cells with tumorsuppression
proliferate at low rates

Anchorage independent cell proliferation – colony formation assay
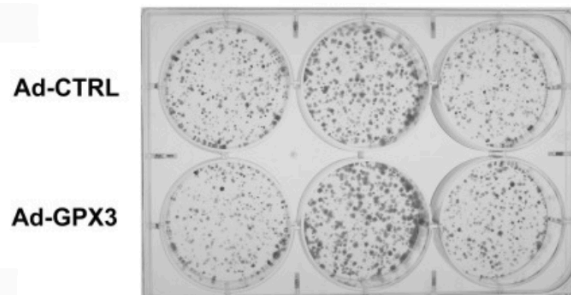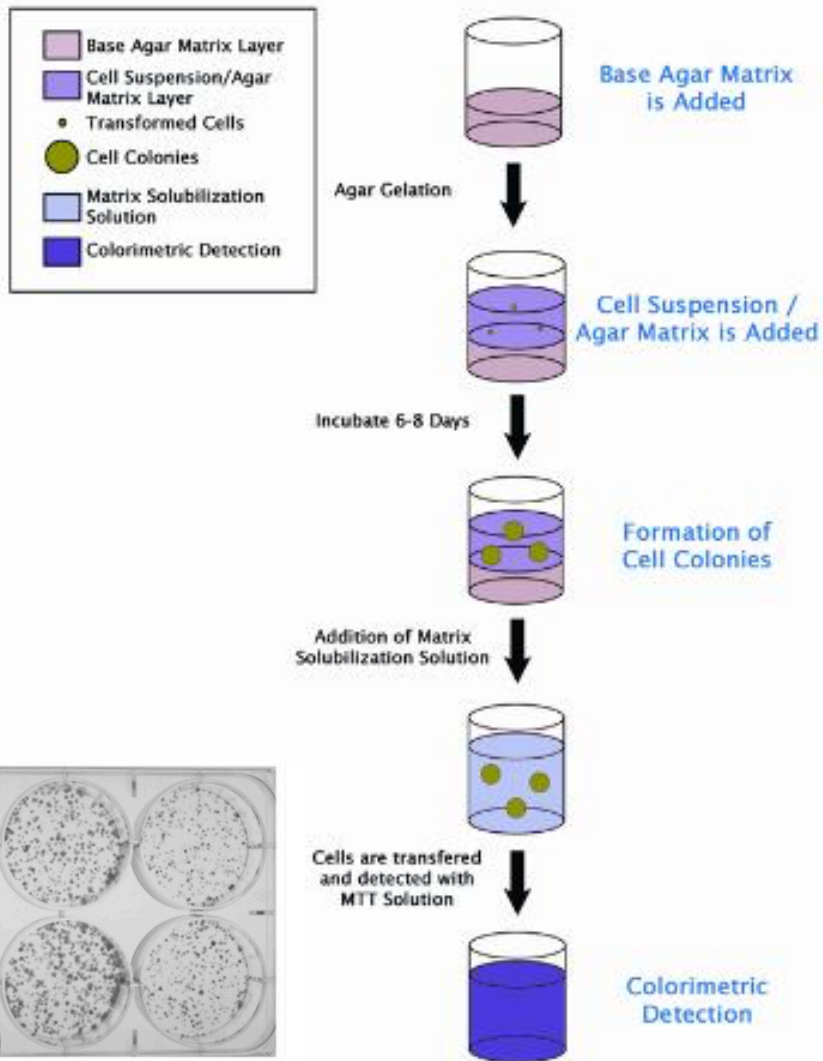
An example
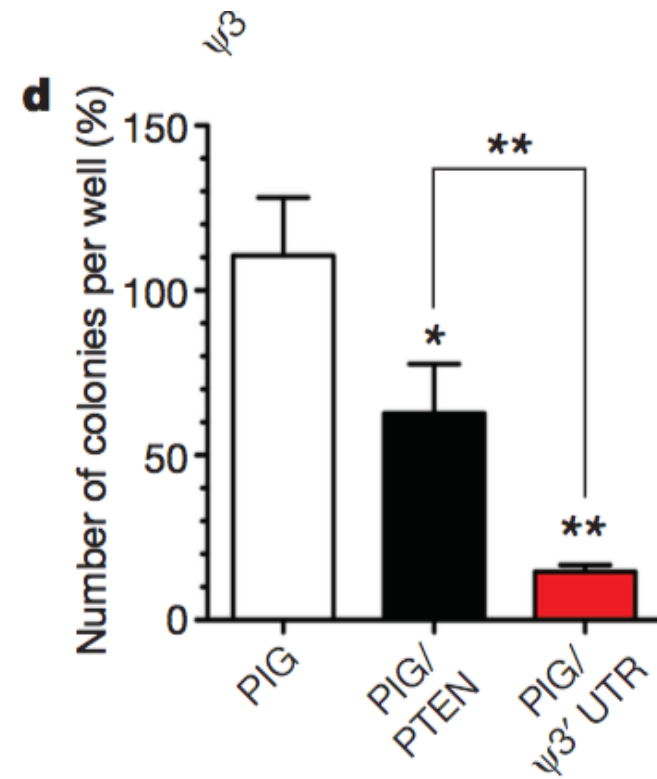
Ectopic expression of PTEP-P1 3'UTR sequence reduces cancer cell proliferation
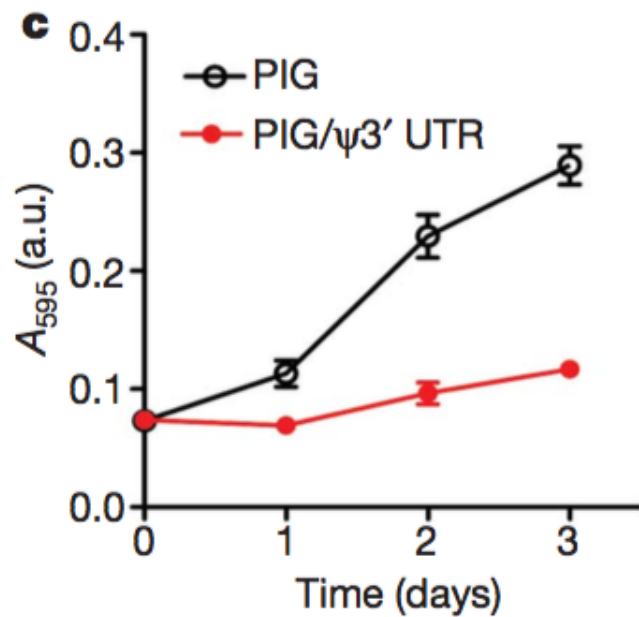
Cell proliferation (normal)
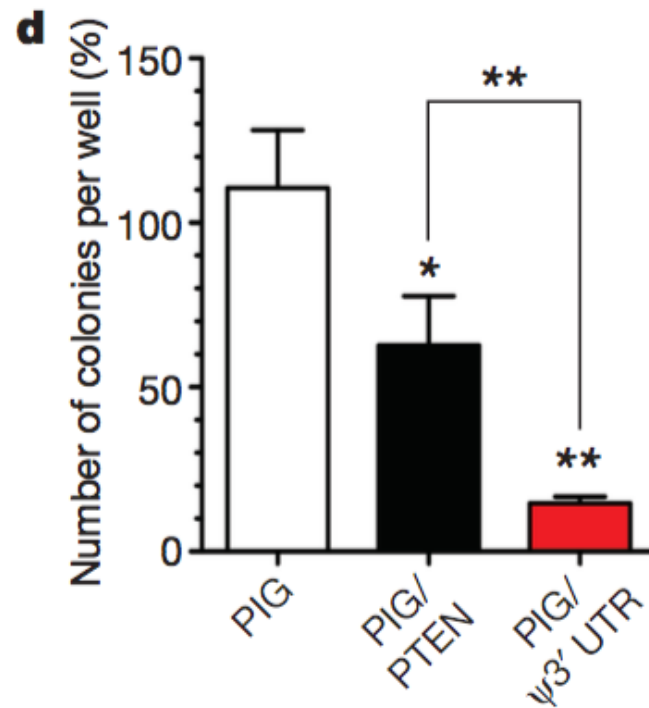
Colony formation in semi-solid medium

RELEVANCE IN VIVO (HEALTHY AND CANCER)?

PTEN mRNA expression
Positively correlates with
PTENP1 expression:

Presence of PTENP1 sponges miRNAs
→ increased levels of PTEN

RELEVANCE IN HUMAN CANCER????

ACUTE LYMPHOBLASTIC LEUKEMIA

CDKN2A   PTENP1
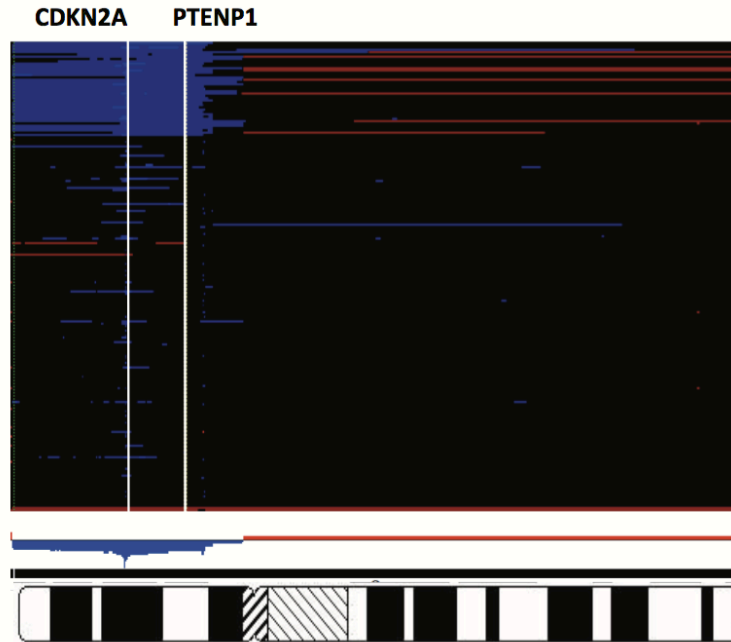
colon cancer. a. Non clustered heat map downloaded from the Cancer Workbench website (https://cgwb.nci.nih.gov/cgi-bin/heatmap) displaying the TARGET Acute Lymphoblastic Leukemia (ALL) project CGH database from St. Jude/NCI. Data points have been sorted for loss copy number at the *PTENP1* locus. Red represents copy number gains. Blue represents copy number losses.

Copy number gains (red)
Copy number losses (blue)

BREAST CANCER

CDKN2A   PTENP1

9p
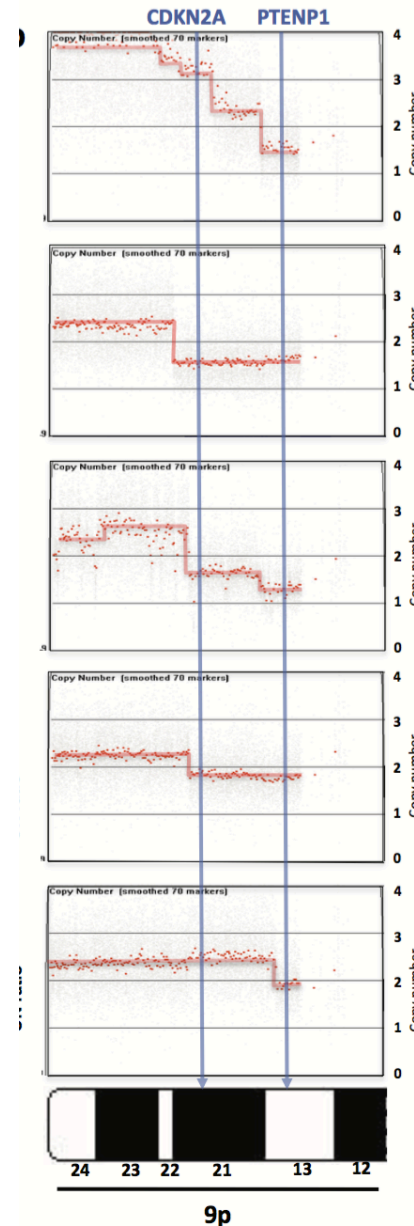
Red line: interesting genes with Copy number alteration

b. Examples of five specific breast cancer patient samples demonstrating losses at the *PTENP1* locus. The graphs were generated using Partek Genomics Suite. X-axis represents chromosome 9p position and Y-axis represents copy number. The red lines highlight regions of gene loss. **c.**

CDKN2A, also known as **cyclin-dependent kinase Inhibitor 2A**, is a gene which in humans is located at chromosome 9, band p21.3.[5] It is ubiquitously expressed in many tissues and cell types.[6] The gene codes for two proteins, including the INK4 family member p16 (or p16INK4a) and p14arf.[7] Both act as tumor suppressors by regulating the cell cycle. p16 inhibits cyclin dependent kinases 4 and 6 (CDK4 and CDK6) and thereby activates the retinoblastoma (Rb) family of proteins, which block traversal from G1 to S-phase. p14ARF (known as p19ARF in the mouse) activates the p53 tumor suppressor. Somatic mutations of CDKN2A are common in the majority of human cancers, with estimates that CDKN2A is the second most commonly inactivated gene in cancer after p53. Germline mutations of CDKN2A are associated with familial melanoma, glioblastoma and pancreatic cancer.[8] The *CDKN2A* gene also contains one of 27 SNPs associated with increased risk of coronary artery disease.[9]
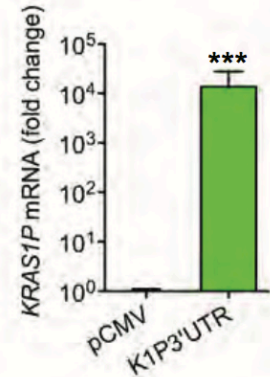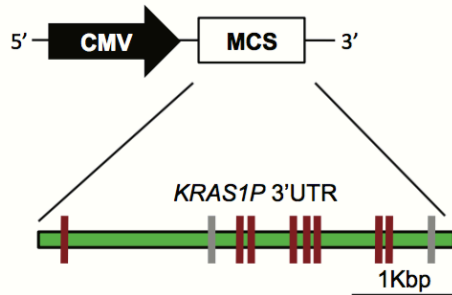
SAME HOLDS TRUE FOR OTHER CANCER RELEVANT GENE: KRAS, KRAS-P1 and miRNAs
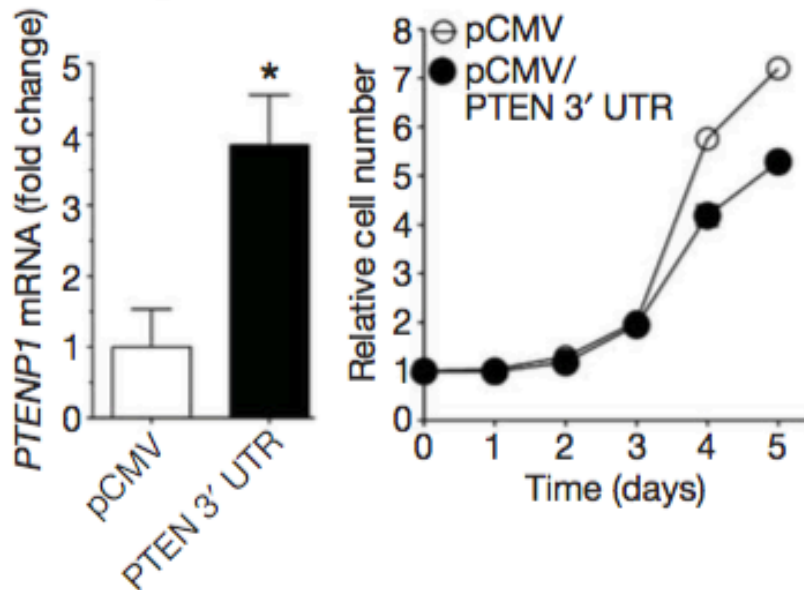

a *miR-143* binding sites
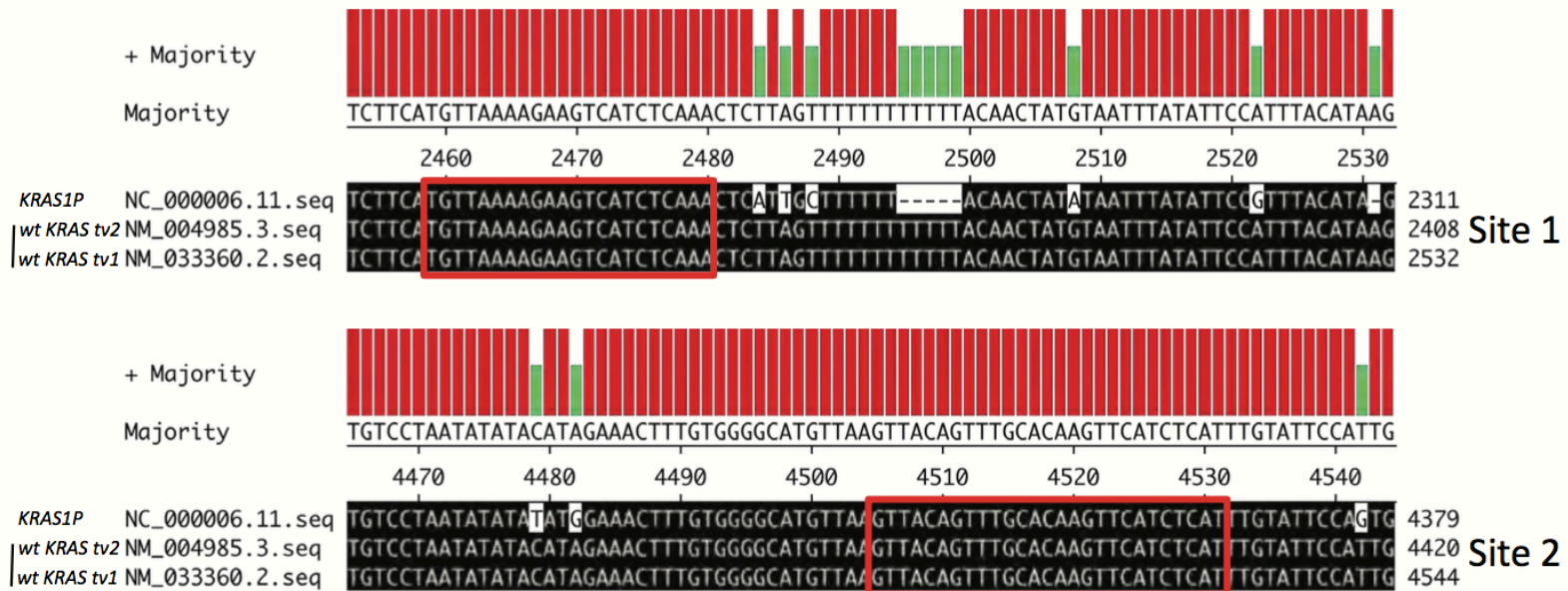
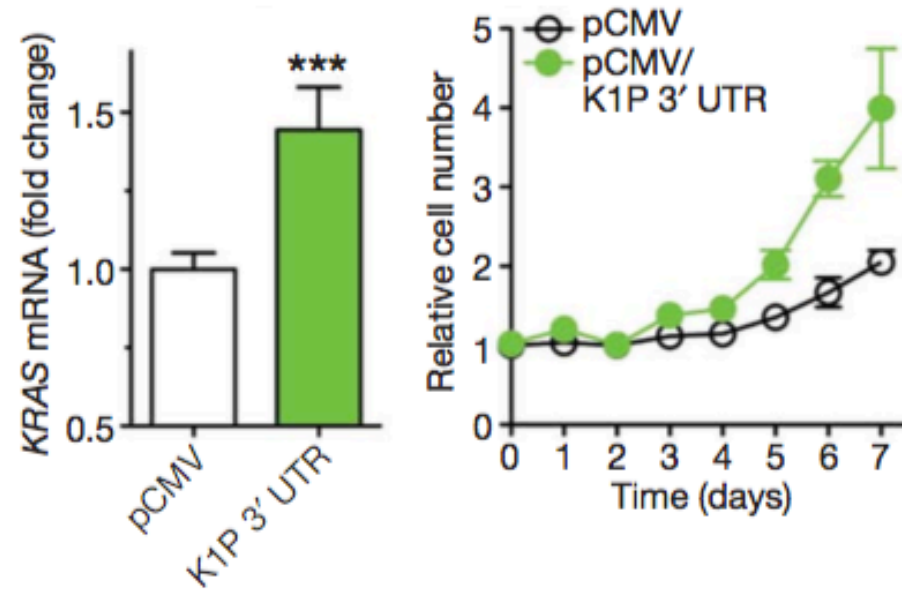# SAME HOLD TRUE FOR OTHER CANCER RELEVANT GENE: KRAS

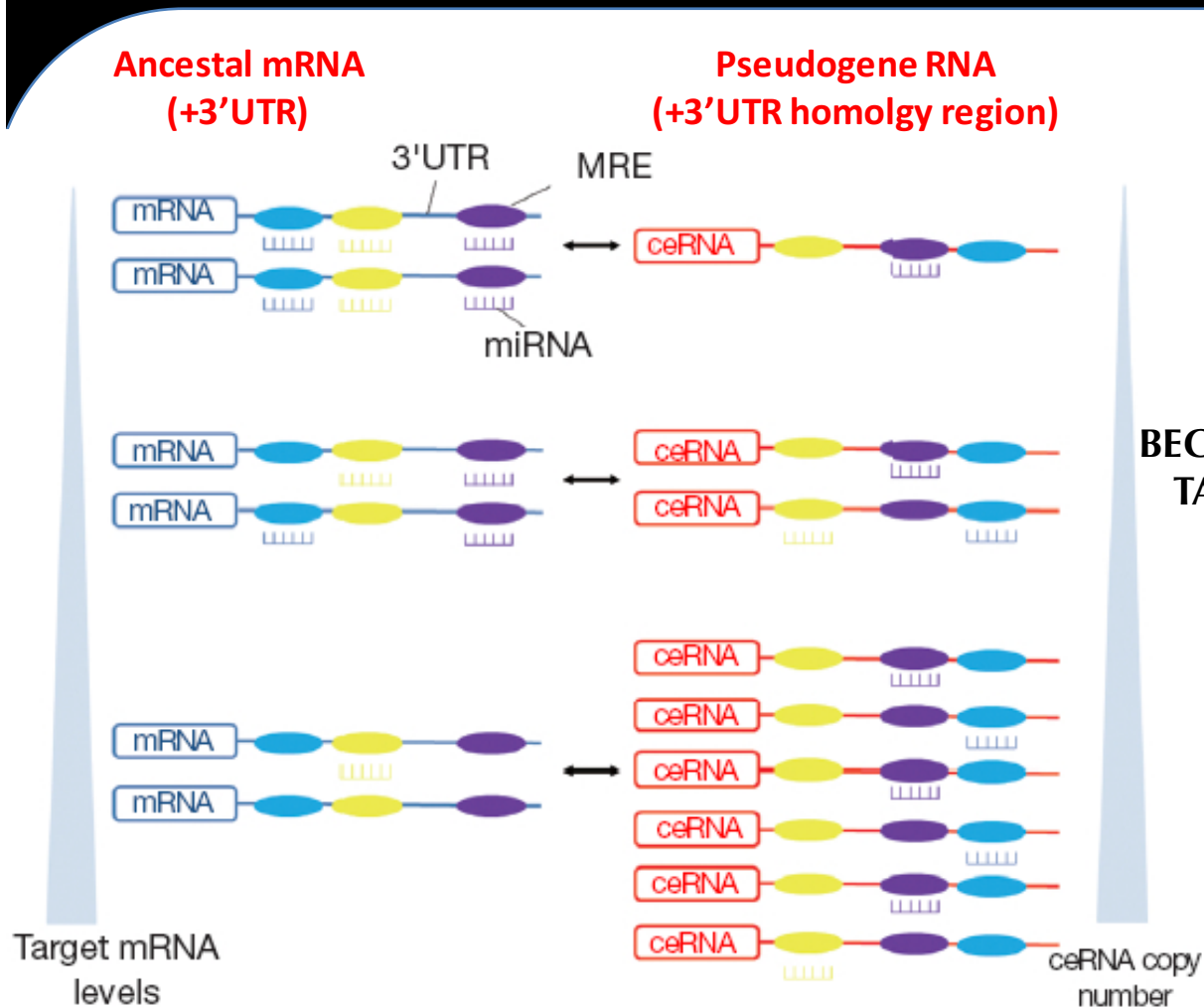Overexpression of KRAS1P 3'UTR increases KRAS mRNA expression

Pseudogene sponge miRNAs that target the ancestral gene

Ancestal mRNA
(+3'UTR)

Pseudogene RNA
(+3'UTR homolgy region)

3'UTR   MRE

miRNA

Target mRNA levels

ceRNA copy number

The model holds
true for all RNAs
that share a miRNA binding site
=ceRNAs

PSEUDOGENES ARE POTENT
BECAUSE THEY SHARE MORE THEN 1 miRNA
TARGET SITE WITH A CORRESPONDING
mRNA FROM AN ANCESTRAL GENE

Evolution of
ncRNAs
to fine-tune the
expression
of ancestral genes

PubMed   ceRNA

Create RSS   Create alert   Advanced

Article types
Clinical Trial
Review
Customize ...

Text availability
Abstract
Free full text
Full text

Publication dates
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