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Fully Complementary Interactions of LmiRNA with mRNA of Human Genes

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Abstract

Londin et al. previously identified a large group of novel microRNAs, here referred to as LmiRNAs; however, their biological functions remain poorly understood. In this study, we investigated fully complementary interactions between LmiRNAs and the mRNAs of human genes using the MirTarget program. Analysis of 3,707 LmiRNAs revealed numerous target genes containing fully complementary LmiRNA binding sites characterized by high interaction free energy values. Binding sites for 75 LmiRNAs were identified in the 5′ untranslated regions (5′UTRs) of target gene mRNAs, whereas 81 target genes contained binding sites within coding sequences (CDSs). Only seven LmiRNAs formed fully complementary interactions within 3′ untranslated regions (3′UTRs). Notably, mRNAs of several genes, including *KIFC3*, *PHF15*, *RPL15*, and *SNX11*, were identified as capable of binding to LmiRNA-5p and LmiRNA-3p. Most target gene mRNAs interacted with only a single LmiRNA. In addition, the *BMP8B*, *FGFRL1*, and *SDC3* genes contained binding sites for the LmiRNA pair ID00121.5p and ID02992.5p. These findings expand current understanding of the interaction properties of LmiRNAs and suggest their potential utility as diagnostic and therapeutic biomarkers for human diseases.

Keywords: miRNA; LmiRNA; mRNA; gene regulation; diagnostics; biomarkers

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1. Introduction

MicroRNAs (miRNAs) are small non-coding RNAs that regulate gene expression at the post-transcriptional level through interactions with messenger RNAs (mRNAs). For more than three decades, miRNAs deposited in public databases have been extensively investigated because of their important roles in cellular regulation, development, and disease progression. However, many computational approaches used for miRNA target prediction generate a large number of false-positive results, complicating the interpretation of miRNA–mRNA interactions and limiting the reliability of predicted target genes.

Londin et al. identified 3,707 previously uncharacterized miRNAs, which are referred to in this study as LmiRNAs [1]. Despite the large number of identified molecules, the biological properties and functional significance of these LmiRNAs remain poorly studied. Investigation of their interactions with human genes may provide new insights into regulatory mechanisms involved in gene expression.

Fully complementary interactions between small RNAs and mRNAs are of particular interest because they may result in efficient suppression of gene expression. Previous studies demonstrated that fully complementary RNA interactions can strongly influence translation and mRNA stability [2]. Therefore, identification of fully complementary LmiRNA binding sites may provide valuable information regarding potential regulatory pathways and disease-associated genes.

In the present study, we analyzed fully complementary interactions between 3,707 LmiRNAs and the mRNAs of 17,508 human genes using the MirTarget program. The aim of this work was to

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identify target genes containing fully complementary LmiRNA binding sites and to characterize the localization and energetic properties of these interactions within the 5′UTR, CDS, and 3′UTR regions of mRNAs. These findings expand current knowledge regarding the potential biological role of LmiRNAs in the regulation of human gene expression.

2. Materials and Methods

The nucleotide sequences of 17,508 human genes were obtained from the National Center for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih.gov) database. The nucleotide sequences of 3,707 LmiRNAs were obtained from the study by Londin et al. [1].

Prediction of LmiRNA binding sites (BSs) within mRNAs was performed using the MirTarget program [3]. This program determines several characteristics of miRNA–mRNA interactions, including: (i) initiation of miRNA binding from the first nucleotide of the miRNA sequence; (ii) localization of binding sites within the 5′ untranslated region (5′UTR), coding sequence (CDS), or 3′ untranslated region (3′UTR) of mRNAs; (iii) nucleotide interaction patterns between miRNAs and mRNAs; and (iv) the free energy of interaction (ΔG, kJ/mol) between miRNAs and mRNAs.

The ratio ΔG/ΔGm (%) was calculated for each predicted binding site, where ΔGm corresponds to the free energy of interaction between a miRNA and its fully complementary nucleotide sequence. Only fully complementary interactions involving canonical nucleotide pairs (G–C and A–U) were selected for further analysis.

The MirTarget program identifies hydrogen bonds formed between miRNAs and mRNAs according to the physicochemical properties of nucleotide interactions [3–6]. Unlike many commonly used prediction tools, MirTarget analyzes interactions across the entire miRNA sequence and calculates the free energy of miRNA–mRNA binding, thereby enabling quantitative assessment of interaction stability.

Because the canonical nucleotides G, A, C, and U possess identical physicochemical interaction properties in microorganisms, plants, and animals, the principles underlying nucleotide pairing are universal and do not require additional validation under standard biological conditions [3–6].

The biological significance of fully complementary RNA interactions was previously demonstrated by Andrew Fire et al., who showed that fully complementary double-stranded RNAs can effectively suppress gene expression [2]. Their discovery established RNA interference as a fundamental mechanism of gene regulation and was recognized with the 2006 Nobel Prize in Physiology or Medicine.

3. Results

Interaction of LmiRNAs with mRNAs in the 5′UTR. Analysis of interactions between 3,707 LmiRNAs and the mRNAs of 17,508 human genes revealed that 145 LmiRNAs formed fully complementary interactions with 149 target genes through canonical G–C and A–U nucleotide pairing. The predicted interactions were characterized by high free energy values, indicating strong binding affinity between LmiRNAs and their target mRNAs. Selected results of these analyses are presented in Table 1.

Table 1. Characteristics of fully complementary LmiRNA interactions within the 5′UTRs of human gene mRNAs.

mRNA of gene	LmiRNA	BS, nt	ΔG, kJ/mole	mRNA of gene	LmiRNA	BS, nt	ΔG, kJ/mole
ADRBK2	ID02187.5p	111	-138	*KIAA2018*	ID02368.3p	242	-140
ALK	ID01810.3p	52	-129	*KLHL15*	ID03422.3p	110	-123
ANKRD9	ID00943.3p	86	-127	*LANCL2*	ID02988.5p	425	-117
ARSI	ID02715.3p	511	-127	*LMX1A*	ID00230.5p	182	-129
ASTN2	ID03318.3p	334	-119	*LOXL4*	ID00411.5p	77	-144
C10orf25	ID00351.3p	70	-140	*MAP2K2*	ID01574.5p	221	-142
C11orf87	ID00616.5p	73	-134	*MAP3K1*	ID02634.3p	101	-129

CAMK1D	ID00323.3p	105	-123	*MSL1*	ID01311.3p	155	-149
CBLL1	ID03040.3p	184	-117	*N4BP1*	ID01157.5p	190	-125
CD164	ID02875.5p	68	-123	*NIPBL*	ID02626.5p	176	-123
CDYL	ID02781.3p	39	-125	*NLRX1*	ID00628.5p	167	-123
CERK	ID02992.5p	2	-115	*OGFOD3*	ID03179.5p	97	-138
CLDND2	D01758.3p	594	-138	*OXR1*	ID02217.5p	31	-134
CLIC4	ID00087.3p	34	-125	*PLA2G6*	ID02357.3p	242	-125
CMTM6	ID02300.3p	77	-144	*PROS1*	ID02292.5p	74	-134
DENND6A	ID02350.5p	11	-125	*RFTN1*	ID01075.3p	102	-140
DUSP15	ID02046.3p	315	-136	*RHBDL1*	ID01856.3p	243	-132
E2F1	ID02052.5p	85	-149	*RNF103*	ID03367.5p	37	-125
ERCC6L2	ID03301.3p	131	-123	*RXRA*	ID02911.5p	244	-138
FAM131C	ID00064.3p	1	-123	*SCAF8*	ID02686.5p	77	-121
FAM178A	ID00414.3p	209	-117	*SEPT8*	ID01903.3p	313	-115
FAM81A	ID01009.5p	14	-125	*SFT2D3*	ID00185.5p	58	-144
GATAD2A	ID01675.5p	109	-132	*SLC22A15*	ID01492.3p	16	-129
GBA2	ID03260.3p	38	-115	*SMAD2*	ID01020.5p	193	-123
GSTZ1	ID00910.3p	34	-123	*SMAD3*	ID02853.3p	54	-125
HDAC4	ID02002.5p	236	-115	*SMAP1*	ID00053.5p	265	-115
HTRA3	D02487.5p	37	-117	*UBIAD1*	ID00921.3p	61	-121
ISL1	ID02632.5p	106	-117	*UBR7*	ID03019.5p	345	-125
KIAA1217	ID00330.5p	145	-140				

A notable feature of the identified LmiRNAs was that the binding sites of 75 LmiRNAs were localized within the 5′UTRs of target gene mRNAs. The free energy of LmiRNA–mRNA interactions depended on both the GC content of the interacting sequences and the length of the LmiRNAs. For 15 LmiRNAs, the interaction free energy exceeded −140 kJ/mol, indicating highly stable binding to target mRNAs. Localization of LmiRNA binding sites within the 5′UTR may contribute to efficient inhibition of translation initiation, potentially reducing cellular energy expenditure associated with inefficient protein synthesis. Several target genes, including *ANKRD9*, *CERK*, and *HYI*, contained two binding sites for ID00121.5p within the 5′UTR region (Table 2).

Table 2. Characteristics of interactions of ID00121.5p and ID02992.5p with target gene mRNAs within the 5′UTR region.

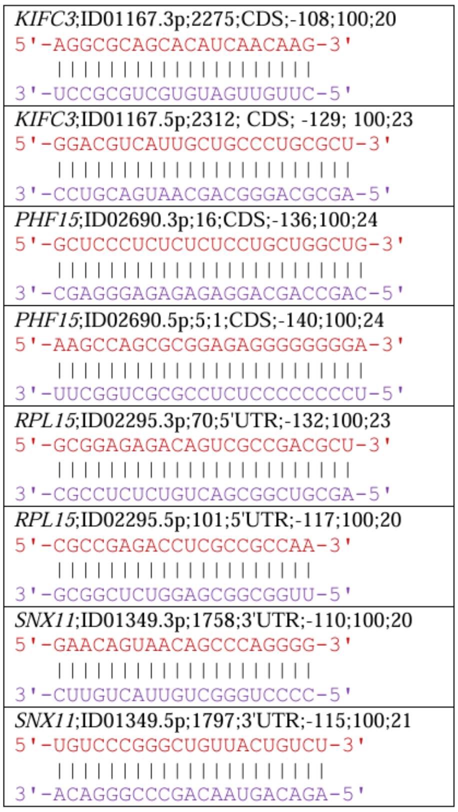
mRNA of gene	LmiRNA	BS, nt	ΔG, kJ/mole
ANKRD9	ID00121.5p	43	-115
ANKRD9	ID00121.5p	50	-115
CERK	ID00121.5p	1	-115
CERK	ID00121.5p	8	-115
HYI	ID00121.5p	126	-115
HYI	ID00121.5p	133	-115
HYI	ID02992.5p	127	-115
HYI	ID02992.5p	134	-115

Interaction of LmiRNAs with mRNAs in the CDS and 3′UTR. A total of 81 target genes were identified with fully complementary LmiRNA binding sites located within coding sequences (CDSs) (Table 3). For 12 target genes, the free energy of LmiRNA–mRNA interaction exceeded −140 kJ/mol, indicating highly stable interactions between LmiRNAs and their target mRNAs. In addition, seven target genes contained fully complementary LmiRNA binding sites within the 3′UTR region (Table 3). The free energy values of interactions within the 3′UTRs ranged from −110 to −132 kJ/mol, which were generally lower than those observed for interactions localized within the 5′UTRs and CDS regions.

Table 3. Characteristics of fully complementary LmiRNA interactions within the CDS and 3′UTRs of target gene mRNAs.

mRNA of gene	LmiRNA	BS, nt	ΔG, kJ/mole	mRNA of gene	LmiRNA	BS, nt	ΔG, kJ/mole
AATK	ID01431.3p	2178	-142	*LHX4*	ID00245.3p	558	-123
ADAMTS8	ID00648.5p	821	-136	*LONRF2*	ID01873.3p	654	-132
ADRA1B	ID02729.5p	1320	-121	*LRRC26*	ID03389.3p	706	-121
ANGPTL4	ID01593.5p	259	-134	*MAP3K6*	ID00093.5p	542	-134
APC2	ID01540.3p	3174	-129	*METRNL*	ID01458.5p	187	-146
APRT	ID01212.5p	205	-110	*MIB2*	ID00017.3p	1432	-127
ARHGEF17	ID00592.3p	5054	-134	*MMP17*	ID00794.3p	223	-123
ARID1B	ID02914.3p	589	-125	*MMP24*	ID01804.3p	35	-146
BPTF	ID01377.3p	295	-127	*MORC4*	ID03448.3p	287	-136
C10orf95	ID00424.5p	845	-115	*MROH8*	ID02061.3p	188	-129
C19orf21	ID01521.3p	1055	-125	*MSH3*	ID02653.3p	464	-132
C2CD4D	ID00202.5p	1225	-146	*MXRA8*	ID00014.3p	210	-121
C9orf66	ID03226.3p	742	-123	*MYBBP1A*	ID01242.3p	2597	-138
CACNA1B	ID03398.5p	2997	-123	*MYO3A*	ID00333.3p	5184	-121
CAMSAP1	ID03370.5p	63	-121	*NEURL1B*	ID02740.3p	240	-119
CCDC6	ID00364.5p	246	-121	*PHLDA1*	ID00722.5p	282	-121
CDHR5	ID00474.3p	2204	-121	*PIK3IP1*	ID02201.3p	428	-119
CEBPB	ID02084.3p	687	-151	*PIK3R2*	ID01662.3p	1273	-142
CELSR1	ID02250.3p	546	-142	*PLXNC1*	ID00731.5p	582	-121
CELSR2	ID00178.5p	8114	-129	*PLXND1*	ID02398.3p	1058	-123
CHADL	ID02231.3p	1228	-115	*POU3F1*	ID00117.5p	1220	-125
CTF1	ID01150.3p	610	-144	*PROB1*	ID02701.5p	808	-138
DCAF13	ID03178.5p	317	-134	*REPIN1*	ID03072.5p	1168	-115
DUSP28	ID02005.5p	669	-138	*RHBDD3*	ID02191.5p	943	-121
E2F1	ID02051.3p	291	-153	*RNF169*	ID00594.3p	281	-134
EPM2A	ID02899.3p	481	-149	*SETD9*	ID02635.5p	398	-117
F2	ID00524.3p	532	-119	*SHISA8*	ID02233.3p	952	-132
FAM160B2	ID03113.3p	2279	-125	*SLC44A2*	ID01602.5p	93	-121
FAM8A1	ID02789.5p	399	-132	*TONSL*	ID03220.3p	2763	-127
FBRSL1	ID00799.3p	2503	-129	*TPM1*	ID01010.5p	333	-123
FCRLB	ID00226.5p	772	-136	*TRIO*	ID02611.3p	6927	-138
FGFRL1	ID02002.5p	209	-115	*TTC39B*	ID03248.3p	57	-123
FGFRL1	ID02457.3p	206	-138	*USP22*	ID01275.5p	207	-123
GATA5	ID02103.5p	311	-129	*ZFP36L2*	ID01824.3p	1287	-115
GNAS	ID02093.5p	1626	-127	*FPM1*	ID01206.3p	2213	-142
GP1BB	ID02171.5p	384	-129	*ZNF488*	ID00356.3p	499	-123
GYS1	ID01747.5p	2354	-110	*ZNF628*	ID01775.3p	3586	-125
HCN2	D01804.3p	112	-146	*ZNF750*	ID01456.3p	2085	-125
HIC1	ID01236.5p	846	-125	*C9orf62*	ID03369.3p	1261*	-110
IGFBP3	ID02982.3p	435	-123	*MAPKAPK3*	ID02335.5p	2746*	-127
JUND	D01663.3p	298	-125	*MLL4*	ID01699.5p	8280*	-117
KCNC3	ID01755.3p	377	-127	*MLLT1*	ID01582.3p	4023*	-123
KDM1A	ID00081.3p	342	-136	*SFT2D3*	ID01905.5p	1157*	-132
KDM3B	ID02695.3p	242	-138	*SOX11*	ID01787.3p	3226*	-129
				ZNF804B	ID01451.3p	1957*	-132

Features of Selected Target Genes. Four genes containing regions encoding both LmiRNA-5p and LmiRNA-3p molecules capable of binding to their own mRNAs were identified (Figure 1). In addition, the *RTL1* gene was found to encode four miRNA-5p and miRNA-3p molecules interacting with the mRNA of the same gene [8]. The biological significance of this phenomenon remains unclear and requires further investigation, particularly regarding the potential role of self-regulatory LmiRNA-mediated gene expression control. Analysis of LmiRNA-mediated regulation demonstrated that a single LmiRNA may interact with multiple target genes. An example of this regulatory pattern is presented in Figure 1. Furthermore, gene expression may be influenced either by an individual LmiRNA or through the combined action of multiple LmiRNAs (Figure 2). The present study primarily focused on the identification and characterization of fully complementary LmiRNA binding sites. Functional analysis of the identified target genes was beyond the scope of this work, as comprehensive evaluation of their biological roles would require extensive analysis of published experimental and clinical studies. In many cases, currently available studies describe only correlations between gene expression and disease development without establishing direct causal relationships. The *HYI* gene contained two binding sites for ID02992.5p within its mRNA sequence. In addition, ID00121.5p and ID02992.5p were identified as interacting with the mRNAs of three genes at neighboring sites differing by only one nucleotide in the translational region (Figure 2). These findings suggest that multiple LmiRNAs may cooperatively regulate the same target genes, which should be considered when evaluating the potential diagnostic or therapeutic significance of individual LmiRNAs.



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KIFC3;ID01167.3p;2275;CDS;-108;100;20
5'-AGGCGCAGCACAUCAACAAG-3'
   ||||||||||||||||||||
3'-UCCGCGUCGUGUAGUUGUUC-5'

KIFC3;ID01167.5p;2312; CDS; -129; 100;23
5'-GGACGUCAUUGCUGCCCUGCGCU-3'
   |||||||||||||||||||||||
3'-CCUGCAGUAACGACGGGACGCGA-5'

PHF15;ID02690.3p;16;CDS;-136;100;24
5'-GCUCCCUCUCUCUCCUGCUGGCUG-3'
   ||||||||||||||||||||||||
3'-CGAGGGAGAGAGAGGACGACCGAC-5'

PHF15;ID02690.5p;5;1;CDS;-140;100;24
5'-AAGCCAGCGCGGAGAGGGGGGGGA-3'
   ||||||||||||||||||||||||
3'-UUCGGUCGCGCCUCUCCCCCCCCU-5'

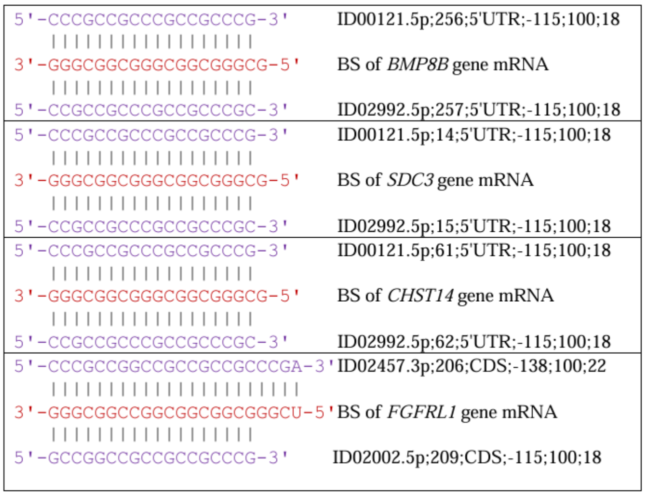
RPL15;ID02295.3p;70;5'UTR;-132;100;23
5'-GCGGAGAGACAGUCGCCGACGCU-3'
   |||||||||||||||||||||||
3'-CGCCUCUCUGUCAGCGGCUGCGA-5'

RPL15;ID02295.5p;101;5'UTR;-117;100;20
5'-CGCCGAGACCUCGCCGCCAA-3'
   ||||||||||||||||||||
3'-GCGGCUCUGGAGCGGCGGUU-5'

SNX11;ID01349.3p;1758;3'UTR;-110;100;20
5'-GAACAGUAACAGCCCAGGGG-3'
   ||||||||||||||||||||
3'-CUUGUCAUUGUCGGGUCCCC-5'

SNX11;ID01349.5p;1797;3'UTR;-115;100;21
5'-UGUCCCGGGCUGUUACUGUCU-3'
   |||||||||||||||||||||
3'-ACAGGGCCCGACAAUGACAGA-5'
```

Figure 1. Schematic representation of interactions between the mRNAs of the *KIFC3*, *PHF15*, *RPL15*, and *SNX11* genes and the LmiRNAs encoded by these genes.



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5'-CCCGCCGCCCGCCGCCCG-3'       ID00121.5p;256;5'UTR;-115;100;18
   ||||||||||||||||||
3'-GGGCGGCGGGCGGCGGGCG-5'      BS of BMP8B gene mRNA
   ||||||||||||||||||
5'-CCGCCGCCCGCCGCCCGC-3'       ID02992.5p;257;5'UTR;-115;100;18

5'-CCCGCCGCCCGCCGCCCG-3'       ID00121.5p;14;5'UTR;-115;100;18
   ||||||||||||||||||
3'-GGGCGGCGGGCGGCGGGCG-5'      BS of SDC3 gene mRNA
   ||||||||||||||||||
5'-CCGCCGCCCGCCGCCCGC-3'       ID02992.5p;15;5'UTR;-115;100;18

5'-CCCGCCGCCCGCCGCCCG-3'       ID00121.5p;61;5'UTR;-115;100;18
   ||||||||||||||||||
3'-GGGCGGCGGGCGGCGGGCG-5'      BS of CHST14 gene mRNA
   ||||||||||||||||||
5'-CCGCCGCCCGCCGCCCGC-3'       ID02992.5p;62;5'UTR;-115;100;18

5'-CCCGCCGGCCGCCGCCGCCCGA-3'ID02457.3p;206;CDS;-138;100;22
   ||||||||||||||||||||||
3'-GGGCGGCCGGCGGCGGCGGGCU-5'BS of FGFRL1 gene mRNA
   ||||||||||||||||||
5'-GCCGGCCGCCGCCGCCCG-3'      ID02002.5p;209;CDS;-115;100;18
```

Figure 2. Schematic representation of interactions between two LmiRNAs and a single target mRNA.

4. Discussion

The present study provides a comprehensive characterization of fully complementary interactions between LmiRNAs and human target genes. However, the biological significance of these interactions and the functional roles of the identified target genes require extensive experimental validation. Determining the involvement of specific genes in disease development is essential before considering modulation of their expression through LmiRNA-mediated regulation. Regulation of LmiRNA activity may potentially be achieved using miRNA-binding sponges and related inhibitory approaches [9].

A total of 149 target genes interacting with LmiRNAs were identified, providing a basis for further investigation of their potential roles in human diseases. Several identified target genes belong to the zinc finger protein (ZNF) family of transcription factors (Table 3). Previous studies demonstrated that increased expression of *ZNF488* promotes pancreatic cancer cell proliferation and tumor progression [10]. Therefore, LmiRNA ID00356.3p may represent a potential regulator of *ZNF488* expression. Similarly, *ZNF628* has been proposed as a potential marker of follicular atresia, and its expression may be influenced by ID01775.3p [11]. In addition, *ZNF750* has been reported as a prognostic biomarker for metastatic prostate cancer and may represent a potential target for novel therapeutic strategies [12]. Overexpression of *ZNF804B* on chromosome 7 has been also associated with tumor development and may serve as a molecular tumor marker [13]. Taken together, these findings highlight the potential biological and clinical relevance of LmiRNA-mediated regulation of transcription factor genes. These findings expand current knowledge regarding fully complementary LmiRNA–mRNA interactions and provide a foundation for future experimental studies investigating the diagnostic and therapeutic potential of LmiRNAs in human diseases.

Author Contributions: Conceptualization, A.I.; methodology, A.I. and A.P.; software, A.I. and A.P.; validation, S.O. and R.N.; formal analysis, S.O. and R.N.; investigation, A.I. and A.P.; resources, S.O. and R.N.; data curation, R.N.; writing—original draft preparation, A.I.; writing—review and editing, A.I. and A.P.; visualization, S.O. and R.N.; supervision, A.I. and A.P.; project administration, A.I. All authors have read and agreed to the published version of the manuscript.

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