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Mapping rRNA 2'-O-methylations and identification of C/D snoRNAs in Arabidopsis thaliana plants

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ABSTRACT

In all eukaryotic cells, the most abundant modification of ribosomal RNA (rRNA) is methylation at the ribose moiety (2'-O-methylation). Ribose methylation at specific rRNA sites is guided by small nucleolar RNAs (snoRNAs) of C/D-box type (C/D snoRNA) and achieved by the methyltransferase Fibrillarin (FIB). Here we used the Illumina-based RiboMethSeq approach for mapping rRNA 2'-O-methylation sites in *A. thaliana* Col-0 (WT) plants. This analysis detected novel C/D snoRNA-guided rRNA 2'-O-methylation positions and also some orphan sites without a matching C/D snoRNA. Furthermore, immunoprecipitation of Arabidopsis FIB2 identified and demonstrated expression of C/D snoRNAs corresponding to majority of mapped rRNA sites. On the other hand, we show that disruption of Arabidopsis Nucleolin 1 gene (NUC1), encoding a major nucleolar protein, decreases 2'-O-methylation at specific rRNA sites suggesting functional/structural interconnections of 2'-O-methylation with nucleolus organization and plant development. Finally, based on our findings and existent database sets, we introduce a new nomenclature system for C/D snoRNA in Arabidopsis plants.

Introduction

In all eukaryotic cells, ribosomal RNAs (rRNAs) precursors are substrate of two major types of nucleotide modifications: methylation of sugars (2'-O-ribose methylation) and isomerization of uridine to pseudouridine. Purine and pyrimidine rings in rRNAs can be also be methylated (m1N, m6N and m7N), aminocarboxypropilated (acp3N) and/or acetylated (ac4N) [1–4].

2'-O-methylation of rRNA might stabilize rRNA-mRNA, rRNA-tRNA or rRNA-protein interactions [5,6]. Furthermore, the significance of 2'-O-methylation of rRNAs is highlighted through studies in animal cells showing that alterations of rRNA 2'-O-methylation can be associated to diseases, mainly cancer and autoimmune syndromes. Indeed, ribosomes with altered rRNA 2'-O-methylation profile translate mRNA with lower fidelity and increase internal ribosome entry site (IRES)-dependent translation initiation of key cancer genes [4–9].

2'-O-ribose methylations are guided by small nucleolar RNAs (snoRNAs), referred as C/D-box snoRNA (C/D snoRNA). The box C (5'PuUGAUGA3') and D (5'CUGA3') of C/D snoRNAs are short consensus sequences that localize a few nucleotides away from the 5'- and 3'-ends, respectively.

In the central part, the C/D snoRNA might contain also less conserved C' and D' motifs. One or two of so-called antisense elements are located upstream of the D and/or D' box. These antisense sequences are about 10–21 nucleotides long and are complementary to the region surrounding the site of 2'-O-ribose methylation. The rRNA nucleotide to be methylated is located precisely at the fifth position upstream from the D or D' box. The C/D snoRNA associates to four nucleolar proteins called the C/D-box core proteins: Fibrillarin/Nop1p, Nop56p/NOP56, Nop58p/NOP58 and snu13/L7Ae. Fibrillarin contains a characteristic SAM-binding methyltransferase motif required for the 2'-O-ribose methylation activity Reviewed in [10–13].

In plants, 2'-O-methylation of rRNAs has been demonstrated at specific rRNA sites and/or predicted throughout *in silico* and functional characterization of C/D snoRNAs. On one hand, in *Arabidopsis thaliana* plants, over one hundred of C/D snoRNAs were first identified by computational screening of genomic sequences [14,15] and a plant snoRNA database was created [16]. Later, sequencing of plant small RNA reported the expression of 151 C/D snoRNAs [17] and sequencing of nucleolar RNA fraction identified 9 additional C/D snoRNA candidates [18]. These results expanded the number

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Supplemental data for this article can be accessed here.

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ARTICLE HISTORY

Received 13 October 2020 Revised 10 December 2020 Accepted 23 December 2020

KEYWORDS

2'-O-Methylation; C/D snoRNA; rRNA; fibrillarin; nucleolin; arabidopsis



of known C/D snoRNAs in Arabidopsis plants to over 200 (including variants). Similarly, hundreds of C/D snoRNAs predicted to guide 2'-O-methylation of rRNA, were reported in O. sativa [19,20] and also other plant species [21]. Notably, studies in Arabidopsis demonstrate that knockout of a single snoRNA (HID2) triggers strong developmental and growing defects [22], while gene disruption of the C/D-box snoRNP assembly factor NUFIP inhibits 2'-O-methylation at specific rRNA sites and leads to severe developmental phenotypes [23]. On the other hand, over 125 2'-O-methylated rRNA sites have been predicted in Arabidopsis [24]. However, only about half of these potential rRNA modification sites has been mapped and/or validated [14,15,22,23,25]. This is essentially due to the limits of current experimental approaches, like RT primer extension at low [dNTP] used to determine the methylation state of a single target site at a time.

Here, we used RiboMethSeq approach for global mapping all rRNA 2'-O-methylation sites in leaves from *Arabidopsis thaliana* Col-0 (WT) and nucleolin 1 (*nuc1*) mutant plants. RiboMethSeq is based on the resistance of RNA at 2'-O-methylated sites to alkaline fragmentation and employs Illumina sequencing of cloned RNA fragments for simultaneous mapping and quantification of hundreds ribose methylated sites in RNA [26]. Furthermore, to identify C/D snoRNAs linked to the mapped 2'-O-methylated rRNA candidate sites, we performed bioinformatics screening of the Arabidopis genome as well as experimental identification of expressed snoRNAs in a Fibrillarin immunoprecipitated fraction by small RNA-seq.

Results

rRNA 2'-O-methylation in A. thaliana leaves

To map rRNA 2'-O-methylated sites in *A. thaliana*, we extracted total RNA from Arabidopsis leaves (3 biological replicates, Figure S1) and performed RiboMethSeq analysis as previously reported [10,26].

After trimming and alignment of reads to the reference A. thaliana rRNA sequence [25-29], we found substantial differences between the reference sequences for 18S (GenBank X16077.1) and 25S rRNA (GenBank X52320.1) and the observed rRNA reads. These rRNA sequences were thus corrected to fit to the observed sequencing data (Supplementary Information and Methods). Then, in order to map all possible candidate sites, we performed the same approach as reported in [30]. We used threshold values for ScoreMEAN and Score A2, respectively 0.93 and 0.5; although in some cases, less strict ScoreMEAN limit (0.92 or lower) was applied. Combination of these parameters was found to give the best results for human rRNA having now wellestablished 2'-O-methylation profile and thus to limit the number of false-positive/false-negative hits. We also compared the obtained RiboMethSeq hits with previously known [14,25] or tentatively assigned locations and rRNA 2'-O-methylation list [24]. See Supplemental Information and Methods and Table S1 for details.

RiboMethSeq mapped 117 potential ribose methylated sites: 38 in the 18S rRNA, 2 in the 5.8S rRNA and 77 in the 25S rRNA sequences (Table 1 and S1 for details): Among the 117

RiboMethSeq mapped sites, 52 were previously mapped [14,15,22,23,25] while 25 others were only predicted from the sequences of C/D snoRNA guides [24] but not experimentally validated in the previous studies. Notably, RiboMethSeq also mapped 40 potential rRNA methylated sites not reported in [14,13,25] or predicted previously (Table S2). Nine (18S Um123, Cm1219 and 25S Cm2198, Am2257, Am2362, Gm2396, Um2494, Um2922 and Gm2923) of these 40 mapped candidates have an equivalent position in human, and for 31 of newly mapped positions we assigned the corresponding snoRNA. However, 7 candidate sites (18S Am812, Am1188 and Um1554 and 25S Um378, Cm2294, Gm2410 and Am2561) showing high RiboMethSeq signal still have no assigned snoRNA guide (Table 1).

To validate 2'-O-methylated candidates mapped by RiboMethSeq we performed additional orthogonal mapping of *A. thaliana* rRNA residues by high-throughput version of primer extension at low [dNTP]/low [Mg2+] conditions. The protocol was derived from published 2OMe-Seq [31], with minor modifications at the adapter ligation step and uses RT enzymes AMV and MMLV (Supplemental Information and methods). Using this technique we validated 97 sites over the 117 mapped by RiboMethSeq, including 5 rRNA sites without a corresponding C/D snoRNA guide (Figure S2 and Table S2).

All sites mapped by RiboMethSeq are shown in the predicted 18S and 25S/5.8S RNA secondary structures (Figure 1). All domains in the 18S, 25S and 5.8 rRNA sequences are 2'-O-methylated at different extents. Noteworthy, the 5' domain in the 18S rRNA and the domain V in the 25S rRNA contain the highest number of 2'-O-methylation sites under our plant growth conditions.

Identification and characterization of C/D snoRNAs associated to Arabidopsis FIB2

To identify C/D snoRNAs that might guide 2'-O-methylation of mapped rRNA sites, we characterized C/D snoRNAs that co-purify with Arabidopsis Fibrillarin 2 (FIB2). We performed immunoprecipitation (IP) experiments in triplicate using Arabidopsis plants expressing the 35S:FIB2-YFP (Yellow Fluorescent Protein) construct. The FIB2-YFP is a 61kDa protein and localizes in the nucleolus (Figure S3(A-B) and [32,33]).

Following IP with antibodies against GFP, we analysed by Western blot whole cell extract (WCE-input, lanes 1 and 4), unbound (lanes 2, 5, 7 and 9) and co-immunoprecipitated (CoIP, lanes 3, 6, 8 and 10) protein fractions. We observed that anti-GFP antibodies immunoprecipitate FIB2-YFP protein in all three FIB2-YFP samples (CoIP_1 to 3), but not from Col-0 (CoIP_1 mock) protein extract (Figure S3C).

Firstly, we performed LC-MS/MS and differential analysis on FIB2-YFP and Col-0 IP fractions to verify that C/D snoRNP proteins co-immunoprecipitate with FIB2-YFP. A total of 197 proteins were specifically identified in fractions FIB2-YFP compared to the Col-0 CoIP fractions (Table S3). Arabidopsis orthologues of Fibrillarin, NOP56, NOP58 and L7Ae proteins were identified and the first three were among the most enriched (top 10) proteins. The genome of Arabidopsis contains two Fibrillarin (FIB1 and FIB2), NOP56 and NOP58 and at least five L7Ae protein genes

| <i>iana</i> 5.85, 185 and 255 rRNAs. Mapped rRNA Nm sites ('Mapped site') are compared with previously known locations ('Position 3D rRNAdb' and associated ('Position in human') and yeast ('Position in yeast') profile was determined based on 2D rRNA structure and sequence [8]. Human rRNA sites located in the Vewly detected snoRNA guides corresponding to the modified positions are shown ('Assigned snoRNA'). The absence of identified snoRNA guide is shown columns 'ScoreC nuc1' with corresponding <i>p-value</i> . Asterisks ****(≤ 0.001), **(≤ 0.001), **(≤ 0.01), *(≤ 0.05) represent significance level and ns, non- | ScoreC nuc1 db snoRNA, 3D rRNA db Position in human Position in yeast reduction p-value Assigned snoRNA | snoR9 - 0.000609127 *** At1gCDbox61 At5gCDbox62 | snoR39BY Gm75 6.47E-06 **** At2gCDbox68.1 At2gCDbox68.2 | AtU2/ Am2/ Am28 0.20149285 ns At3GLDbox92.1 At3GLDbox92.2 At4GLDbox92.3 0.016003452 At43GLDbox92.3 | 0.00345432 **** AriaCDbox51.1 0.000345542 **** AriaCDbox51.1 | AtsnoP18 Amile 2.80281E-05 **** At440Dbox105.2 Amile 2.80281E-05 **** At440Dbox105.2 | 7.72863E-05 **** At1gCDbox33.1 | 0.000240838 *** At5gCDbox141.1 | AtsnoR30 Gm436 0.02012768 * At5gCDbox138.1 | AtU14 CE442 Cm414 0.2448665 ns At49CDbox1201 At49CDbox1202 At49CDbox1203 At49CDbox1204 At145 0.2449CDbox1204 | AU U/ABIONI3 ANII444 U.U3004403 II AU U/ABIONI2 ANZULUXX4.I AFECUDUXX4.I AF | AtU56 Cm517 0.409665359 ns At3gCDbox102.1 At5gCDbox102.2 | AtsnoR41Y/ Am590 Am541 0.008517727 ** At1gCDbox7.1* At1gCDbox8.1* At4gCDbox107.1 | AtsnoR43 AtsnoR43 11m.627 11m.620 0.050505142 mi At2ncDhoue2 1 At2ncDhoue2 2 | AGNONY 1 OLINOZ ONIZZO ONIZZO 14 DI AZGUDUAZZI AZGUDUAZZI AZGUDUAZZIZ ANIZZO ANIZZO AGNOZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZZ | 0.09999745 ns AttgCDbox/17.2 | 0.181336315 ns At3gCDbox78.1 At5gCDbox78.2 | AtU36 Am668 Am619 0.295248869 ns At5gCDbox127.1 | 0.068617102 ns At5gCDbox122.1 0.0001000 *** At12CDbcx0212 | AtsnoR53Y Am796 0.017023118 Attl@CDbox36.1 | ns snoRNA not | | ALU29 AITI 1031 AITI 91 AITI 9124 0.01134302.74 *** AITI 9CU200X22.1 AITI 9CU200X22.2 AtsnoR20.1 0.00012.7129 **** At3aCDbox99.1 | 0.441879451 ns snoRNA not | found | Cm12/2 Curr2/2 0.000222591 **** At1gC/D0047.1 AtsnoR14 Um1288 2.81944E-06 **** At1gC/Dbox31.1 At1gC/Dbox31.2 | 0.156858336 ns At3gCDbox95.1 At3gCDbox95.2 At5gCDbox144.1 | AtsnoR32 0.385921318 ns At3gCDbox93.1 At4gCDbox93.2 | Attu33/AtmoH34 Um or Psi/ 1326 Un1289 0.038906432 * AttigCUbbox2/.1 AttigCUbbox2/.2 | AISIOAZI DILLI-26 GIII.221 U.1102212 IN ALGUDUXXV ALGUDUXXV.2 Afron,R32 An1333 (8742)09847 ns AfracDhovo31 AfracDhovo32 | Attl61 Um1442 0.00514469 ** Att3CDbox66 0.00514469 ** | AtsnoR19 Gm1490 Gm1428 0.154113634 ns At3gCDbox97.1 At5gCDbox97.2 | AtsnoR19 0.00032463 *** At3gCDbox97.1 At5gCDbox97.2 | UJUUSI ZUU92 *** SNOKINA NOT found | 0.246143245 ns At3gCDbox95.1 At3gCDbox95.2 | At143 Cm1703 Cm1639 0.06961813 ns At19CDbox191 At19CDbox192 | AtsnoR/23/AtsnoR/0/ AtsnoR1214 AtsnoR121 | 0.00244844 ** At5gCDbx125.1 | 000024019 *** At1gCDbox18.1 At1gCDbox18.2 | 0.001361127 *** At4gCUD0x108.1 0.565722843 ns snoRNA not | found | AH118 Am340, Am6400 0.0008.4608 *** At19.CDbx33.1 AH118 Am1240 Am640 0.003601143 ** At36.CDbxx271 Af6.CDbxx272 | |
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| 10 255 Am816 y Am814 AtU51 Am1524 Am807 0.001726194 ** At19CDbox281 11 255 Am826 n Am824 AtsnoR77 Am1534 Am817 0.001726194 ** At19CDbox281 12 255 Am826 n Am824 AtsnoR72Y Am1534 Am817 0.013303555 * At39CDbox911 12 255 Am845 n Gm915 AtsnoR72Y Gm1625 Gm1635 * At39CDbox911 13 255 Gm915 n Gm915 At1480 Gm1635 * At39CDbox911 15 255 Mm1143 n Am1140 At138 Am1871 Am1133 0.003730149 ** At19CDbox1071 16 255 Am1143 n Am1140 At138 Am1871 Am1133 0.0035948 ** At19CDbox1071 16 255 Am1260 N At1038 Am1871 Am1137 0.00319149 <td>9 25S</td> <td>Gm814</td> <td>λ</td> <td>Gm812</td> <td>AtsnoR39Y</td> <td>Gm1522</td> <td>Gm805</td> <td>0.000473233</td> <td>***</td> <td>At2gCDbox68.1</td> <td></td> | 9 25S | Gm814 | λ | Gm812 | AtsnoR39Y | Gm1522 | Gm805 | 0.000473233 | *** | At2gCDbox68.1 | |
| 11 255 Am826 n Am824 AtsnoR77 Am1534 Am817 0.013332955 * At3GCbox91.1 12 255 Gm917 n Am885 AtsnoR72Y Am876 0.013932956 * At3GCbox91.1 12 255 Gm917 n Am883 AtsnoR72Y Gm1625 Gm918 * At3GCbox91.1 13 255 Am947 n Gm919 AttsnoR72Y Gm1635 Km956 A 13GCbox91.1 15 255 Am1143 n Am1143 Am1143 AttsnoR72 AttsGCbox10.1 16 255 Am1143 n Am1143 Am1143 AttsGCbox10.1 16 255 Am1143 n Atts000221 Atts000221 AttsGCbox10.1 17 255 Am1143 n Am11871 Am1133 0.000159115 AttgCDbox10.1 18 255 Um1278 M11871 Am1871 Am137 0.000159148 AttgGCDbox10.1 20 <td>10 255</td> <td>Am816</td> <td>. ></td> <td>Am814</td> <td>AtU51</td> <td>Am 1524</td> <td>Am807</td> <td>0.001726194</td> <td>**</td> <td>At1gCDbox28.1</td> <td></td> | 10 255 | Am816 | . > | Am814 | AtU51 | Am 1524 | Am807 | 0.001726194 | ** | At1gCDbox28.1 | |
| 12 255 Am885 n Am883 AtsnoR72Y Am876 0.010638536 * At3GCbox73.1 13 255 Gm917 n Gm915 AtU80 Gm1625 Gm908 0.010638536 * At3GCbox73.1 13 255 Mm945 n Gm915 AtU80 Gm1625 Gm908 0.016538536 * At3GCbox73.1 14 255 Mm1067 n A AtU80 Gm143 * At3GCbox73.1 16 255 Mm1133 n Am1133 Am1357 At14GDbox17.1 * At3GCbbox89.1 17 255 Am1133 n Am1263 At1038 Am1377 * At3GCbbox89.1 18 255 Am1377 n Am1263 At1024 Cm1437 0.001701115 ** At3GCbbox89.1 18 255 Am1479 y Um1275 At1024 Cm1437 0.001701115 ** At3GCbbox89.1 18 255 Am1479 y Um1275 At1024 Cm1437 0.001701115 ** At4 | 11 255 | Am826 | . c | Am824 | AtsnoR77 | Am 1534 | Am817 | 0.013932955 | * | At3gCDbox91.1 | |
| 13 255 Gm917 n Gm915 AtU80 Gm1625 Gm908 0.031093264 * AtgCDbox91.1 14 255 Mm945 n m 0.031093264 * AtgGCDbox91.1 15 255 Mm945 n Am140 AtU38 Am1871 0.031093264 * AtgGCDbox91.1 16 255 Mm143 n Am140 AtU38 Am1871 Am1133 0.00559152 ** AtgCDbox017.1 17 255 Am1240 Atu387 Am1871 Am1133 0.00559152 ** AtgCDbox017.1 18 255 Um1278 Y Um1275 Atu810b Atu37 0.001101115 ** AtgCDbox102.1 19 255 Am1449 Y | 12 25S | Am885 | ч | Am883 | AtsnoR72Y | | Am876 | 0.010638536 | * | At2gCDbox73.1 | |
| 14 255 Am945 n Att4GCbbox[14] *** Att4GCbbox[14] 15 255 Um1067 n Am143 n Am143 *** Att4GCbbox[14] 16 255 Am1143 n Am1140 AtU38 Am1871 Am1133 0.000579152 *** Att4GCbbox[07] 17 255 Am1263 y Um1275 AtsnoR22 AtsnoR22 0.00101115 ** Att9CDbox891 18 255 Um1278 y Um1275 AtsnoR22 0.001101115 ** Att9CDbox891 19 255 Am1447 y Um1276 AtsnoR22 0.00101115 ** Att9CDbox1011 20 255 Am1449 0.00101115 ** Att9CDbox1012 0.005109488 ** Att9CDbox1021 21 255 Am1459 y Att0246 Att4GCDbox1131 2.000599488 ** Att4GCDbox1021 21 255 Gm1460 y 2.000599488 ** < | 13 25S | Gm917 | ч | Gm915 | AtU80 | Gm1625 | Gm908 | 0.031093264 | * | At3gCDbox91.1 | |
| 15 255 Um1067 n Am1140 AtU38 Am1871 Am1133 0.045524699 * At4gCDbox1071 16 255 Am1143 n Am1143 0.00157915 *** At19GCDbox891 17 255 Am1143 n Am1260 Atu38 Am1871 Am1133 0.00057915 *** At19GCDbox891 17 255 Am1377 n Nm1250 AtsnR22 AtsnR22 Am1377 Nm320Box891 ** At19GCDbox891 19 255 Am1377 n 0.001101115 ** At39CDbox891 0.001101115 ** At39CDbox891 20 255 Am1459 y Um1278 At1024 Cm2351 Cm1437 0.00310115 ** At49CDbox1031 20 255 Am1459 y At1024 Gm2364 Gm1470 0.001101115 ** At49CDbox1031 21 255 Am1459 y Gm1479 0.00210598 ** At49CDbox1131 22 255 Gm1460 y Gm1450 0.145653216 n | 14 25S | Am945 | с | | | | | 0.000320149 | *** | At4gCDbox114.1 | |
| 16 255 Am1143 n Am1340 AtU38 Am1871 Am1133 0.000579152 *** At1GCDbox21 17 255 Am1263 y Am1260 AtsnR22 Am1871 Am1133 0.000579152 *** At1GCDbox21 17 255 Am1260 AtsnR22 AtsnR22 AtsnR22 0.00111115 ** At3GCDbox89.1 19 255 Am1377 n 0.00159488 ** At3GCDbox102.1 20 255 Cm1447 y Um1278 At1024 Cm2351 Cm1437 0.002105908 ** At3GCDbox102.1 20 255 Cm1440 y Cm1439 AtU24 Cm2351 Cm1437 0.002105908 ** At49CDbox113.1 21 255 Gm1460 y Gm1452 AtU24 Am2363 Am1449 0.002105908 ** At49CDbox113.1 21 255 Gm1460 y Gm1450 0.145653216 ns <n0r1021< td=""> noR14149 0.002105908</n0r1021<> | 15 25S | Um1067 | ч | | | | | 0.045524699 | * | At4gCDbox107.1 | |
| 17 255 Am1263 y Am1260 Atsn0822 Atsn082 8.26471E-05 **** At3gCDbox89.1 18 255 Um1278 y Um1275 Atsn0812 0.001101115 ** At3gCDbox89.1 19 255 Am1377 n 0.001301115 ** At3gCDbox89.1 20 255 Cm1447 y Cm1439 AtU24 Cm2351 0.001301948 ** At3gCDbox102.1 20 255 Gm1460 y Cm1437 0.002346846 ** At3GCDbox113.1 21 255 Gm1460 y Gm1451 AtU24 Gm2364 Gm1449 0.002105908 ** At3GCDbox113.1 21 255 Gm1460 y Gm1452 Gm2364 Gm1450 0.01563216 ns <norn 13.1<="" td=""> 22 255 Gm1460 y Gm1450 0.145653216 ns<norn 13.1<="" td=""> 23 255 Cm1479 0 0.14565316 ns<norn 13.1<="" td=""> 23 255<!--</td--><td>16 25S</td><td>Am1143</td><td>ч</td><td>Am1140</td><td>AtU38</td><td>Am 1871</td><td>Am1133</td><td>0.000579152</td><td>***</td><td>At1gCDbox2.1</td><td></td></norn></norn></norn> | 16 25S | Am1143 | ч | Am1140 | AtU38 | Am 1871 | Am1133 | 0.000579152 | *** | At1gCDbox2.1 | |
| 18 255 Um1278 y Um1275 AtsnoR22 AtsnoR22 0.001101115 ** At3gCDbox89.1 19 255 Am1377 n 0.0059488 ** At3gCDbox89.1 19 255 Cm1447 y Cm1439 AtU24 Cm1437 0.003846846 ** At4gCDbox8113.1 20 255 Cm1447 y Cm1439 AtU24 Cm2351 Cm1437 0.003846846 ** At49CDbox113.1 21 255 Am1459 y Am1451 AtU24 Am2363 Am1449 0.002105996 ** At49CDbox113.1 22 255 Gm1460 y Gm1452 AtU24 Gm2364 Gm1450 0.14563216 ns <snorn not<="" td=""> 22 255 Cm1479 n O.00130194 ** At19CDbox23.1 23 255 Cm1479 n O.00130194 *** At19CDbox23.1</snorn> | 17 25S | Am1263 | λ | Am1260 | AtsnoR22 | | | 8.26471E-05 * | **** | At3gCDbox89.1 | |
| 19 255 Am1377 n 0.0059488 ** At3gCDbox102.1 20 255 Cm1447 y Cm1439 AtU24 Cm2351 Cm1437 0.00346846 ** At4gCDbox102.1 20 255 Cm1447 y Am1459 0.002105908 ** At4gCDbox113.1 21 255 Gm1460 y Am1451 AtU24 Am2363 Am1449 0.002105908 ** At4gCDbox113.1 22 255 Gm1460 y Gm1452 AtU24 Gm2364 Gm1450 0.145653216 ns <norna found<="" not="" td=""> 23 255 Cm1479 n 0.000130194 *** At19CDbox23.1</norna> | 18 25S | Um1278 | ~ | Um1275 | AtsnoR22 | | | 0.001101115 | * | At3gCDbox89.1 | |
| 20 255 Cm1447 y Cm1439 AtU24 Cm2351 Cm1437 0.003846846 ** At4gCDbox113.1 21 255 Am1459 y Am1451 AtU24 Am2363 Am1449 0.002105908 ** At4gCDbox113.1 21 255 Gm1460 y Am1451 AtU24 Am2363 Am1449 0.002105908 ** At4gCDbox113.1 22 255 Gm1460 y Gm1452 AtU24 Gm2364 Gm1450 0.145653216 ns <norna found<="" not="" td=""> 23 255 Cm1479 n 0.000130194 *** At19CDbox23.1</norna> | 19 25S | Am1377 | Ē | | | | | 0.00599488 | ** | At3gCDbox102.1 | |
| 21 25 Am1459 y Am1451 AtU24 Am2363 Am1449 0.002105908 ** At4gCDbox113.1 22 255 Gm1460 y Gm1452 AtU24 Gm2364 Gm1450 0.145653216 ns snoRNA not 23 255 Cm1479 n 0.000130194 *** At19CDbox23.1 | 20 25S | Cm1447 | λ | Cm1439 | AtU24 | Cm2351 | Cm1437 | 0.003846846 | ** | At4gCDbox113.1 | |
| 22 25S Gm1460 y Gm1452 AtU24 Gm2364 Gm1450 0.145653216 ns snoRNA not found 23 25S Cm1479 n 0.000130194 *** At19CDbox23.1 | 21 25S | Am1459 | ~ | Am1451 | AtU24 | Am 2363 | Am1449 | 0.002105908 | ** | At4gCDbox113.1 | |
| found 23 25S Cm1479 n 0.000130194 *** At19CDbox23.1 | 22 25S | Gm1460 | ~ | Gm1452 | AtU24 | Gm2364 | Gm1450 | 0.145653216 | ns | snoRNA not | |
| 23 25S Cm1479 n 0.000130194 *** At1gCDbox23.1 | | | | | | | | | | found | |
| | 23 25S | Cm1479 | L | | | | | 0.000130194 | *** | At1gCDbox23.1 | |

| | | | | | At2gCDbox74.3 | | | | | At4qCDbox89.4 | At4aCDbox89.4 | | | | | | | | | | | | | At5gCDbox124.1 | | | | | | | | | | | | | | At5gCDbox16.4 | | At4gCDbox88.3 | | | | | | | | | | | | | |
|----------------------|----------------|----------------|---------------|---------------|---------------|---------------|----------------|----------------|----------------|------------------|---------------|----------------|----------------|----------------|---------------|-------|----------------|---------------|------------------|------------------|---------------|-----------------|---------------|----------------|---------------|----------------|-----------------|----------------|---------------|----------------|--------------|----------------|--|--|-------------|---------------|---------------|---------------|------------------|----------------|--------------------|---------------|------------------|-------|-----------------|------------------|----------------------|------------|-------|----------------|-----------------------|-----------------|-------------------------|
| snoRNA | | | | | At2gCDbox74.2 | | | | At4qCDbox2.3 | At4qCDbox89.3 | At4aCDbox89.3 | | | | | | | | | | | | | At2gCDbox59.1 | | | At5gCDbox114.3 | | | At4gCDbox3.3 | | | At5gCDb0X103.3 | AL79-LUUX 103.3 | | | | At1gCDbox16.3 | | At4gCDbox88.2 | | | | | | At4gCDbox88.3 | | | | | | | |
| Assigned | At1gCDbox31.2 | At2gCDbox68.2 | At1gCDbox28.2 | At4gCDbox91.2 | At2gCDbox74.1 | At4gCDbox91.2 | At4gCDbox114.2 | 5 | At1qCDbox2.2 | At4qCDbox89.2 | At4aCDbox89.3 | At5aCDbox102.2 | At5aCDhox113.2 | At5aCDbox113.2 | | | | | | | At1gCDbox22.2 | At2gCDbox65.1 | | At2gCDbox58.1 | | At5gCDbox112.2 | At4gCDbox114.2 | | | At1gCDbox3.2 | At1gCDbox3.2 | At5gCDbox121.1 | At5gCDB0X103.2 | | | | | At1gCDbox16.2 | | At3gCDbox88.1 | At5gcUboX142.1 | | | | At5gCDbox142.1 | At4gCUbox88.2 | 4t4n/Dhov118 1 | | | At1gCDbox25.2 | AttaChove 2 | ALDGCUUUXJ.2 | |
| | At1gCDbox31.1 | At2gCDbox68.1 | At1gCDbox28.1 | At3gCDbox91.1 | At2gCDbox73.1 | At3gCDbox91.1 | At4gCDbox114.1 | At4aCDbox107.1 | At1qCDbox2.1 | At3qCDbox89.1 | At3aCDbox89.1 | At3aCDbox102.1 | At4nCDhox113.1 | At4aCDbox113.1 | snoRNA not | found | At1gCDbox23.1 | At3gCDbox85.1 | At5gCDbox123.1 | At2gCDbox69.1 | At1gCDbox22.1 | At1gCDbox32.1 | At2gCDbox55.1 | At2gCDbox57.1 | At1gCDbox52.1 | At4gCDbox112.1 | At4gCDbox114.1 | At3gCDbox86.1 | At1gCDbox12.1 | At1gCDbox3.1 | At1gCDbox3.1 | At4gCDbox104.1 | AtsgcDbox103.1 | snoRNA not | found found | At3qCDbox83.1 | At5gCDbox16.4 | At1gCDbox16.1 | At2gCDbox63.1* | At3gCDbox84.1 | At5gLUB0X137.1 | found | snoRNA not | found | At5gCDbox137.1 | At3gCDbox88.1 | At ArCDhox 10.1 | snoRNA not | found | At1gCDbox25.1 | At/gc/box/1.1 | snoRNA not | found At5aCDbox136.1 |
| eduction p-value | .000249067 *** | .000473233 *** | .001726194 ** | .013932955 * | .010638536 * | .031093264 * | .000320149 *** | .045524699 * | .000579152 *** | 3.26471E-05 **** | .001101115 ** | 0.00599488 ** | 003846846 ** | .002105908 ** | .145653216 ns | | .000130194 *** | .001840695 ** | '.91855E-05 **** | i.71437E-06 **** | .005039323 ** | .50041E-05 **** | .365959473 ns | 0.00106097 ** | .002058348 ** | .152002072 ns | .49825E-05 **** | .000237866 *** | .949154016 ns | .000775621 *** | .012020963 * | .833140865 ns | 20 20 20 20 20 20 20 20 20 20 20 20 20 2 | <pre><!--! /1002010000 ***</pre--></pre> | 666610700. | 0.02232348 * | .012534812 * | .017495006 * | F.70613E-07 **** | .000616952 *** | | CII (/710/701 | :.17807E-06 **** | | .91313E-05 **** | .03695E-06 **** | 55473F-05 **** | ns | | .071590958 ns | /.3/65E-06 **** | .40177E-05 **** | 2.0631E-05 **** |
| Position in yeast | 0 | Gm805 0 | Am807 0 | Am817 0 | Am876 0 | Gm908 0 | 0 | 0 | Am1133 0 | 8 | 0 | | Cm1437 0 | Am1449 0 | Gm1450 0 | | 0 | 0 | 2 | | 0 | 1 | 0 | Um1888 (| 0 | 0 | - | 0 | 0 | Am2220 0 | 0 0 | 0 1000 4 | 0 1822m2 | | D | | 0 | Cm2337 0 | 4 | 0, | | > | | | - | 2 Um2421 5 | 0 - | - | | Gm2619 0 | Am 2640 | 5 00 | |
| Position in human | | Gm1522 | Am1524 | Am1534 | | Gm1625 | | | Am1871 | | | | Cm2351 | Am 2363 | Gm2364 | | | Cm2422 | | | | Cm2804 | Am2815 | Um2837 | | Gm3627 | | Cm3701 | Am3718 | Am3724 | | Am3/60 | C072m2 | | | Am3825 | Am3830 | Cm3841 | Am3867 | Cm3869 | Gm3800 | | | | | Um3925 | Cm4054 | | | Gm4196 | 700 Mm11 | Gm4228 | |
| snoRNA, 3D rRNA db | | AtsnoR39Y | AtU51 | AtsnoR77 | AtsnoR72Y | AtU80 | | | AtU38 | AtsnoR22 | AtsnoR22 | | AtU24 | AtU24 | AtU24 | | | AtU49 | | Z42 | AtU59 | AtU55/AtsnoR15 | AtsnoR33 | AtU34 | | AtsnoR60 | AtsnoR12 | | AtU37 | AtU36a | | AtU40 | AtU15 | | | AtU30 | AtsnoR44 | AtsnoR44 | | AtU53/AtsnoR37 | | | | | AtsnoR53 | Atsnok37 | | | | AtU31/AtsnoR35 | AtsnoK68Y AtsnoB10 | | |
| Position, 3D rRNA db | | Gm812 | Am814 | Am824 | Am883 | Gm915 | | | Am1140 | Am1260 | Um1275 | | Cm1439 | Am1451 | Gm1452 | | | Cm1510 | | Cm1840 | Gm1845 | Cm1850 | Am1861 | Um1882 | | Gm2114 | Am2116 | | Am2204 | Am2210 | | | 1/770W | 0/771110 | | Am2311 | Am2316 | Cm2327 | | Cm2355 | Gm 2381 | | | | Um 2400 | Um 2411 | | | | Gm2610 | Am2631 | Gm 2642 | |
| Mapped published | ч | λ | Y | Ľ | L | L | ч | c | c | ٨ | ~ > | ~ = | : > | ~ > | ~ > | | ۲ | y | L | y | y | У | λ | λ | L | У | У | ۲ | У | У | c | c : | > : | ~ - | = | > | ~ ~ | У | с | У | | = | c | | У | <u>د</u> د | = = | : = | | У | ~ > | ~ ~ | . <u>c</u> |
| Mapped RiboMethSeq | Um803 | Gm814 | Am816 | Am826 | Am885 | Gm917 | Am945 | Um 1067 | Am1143 | Am1263 | Um1278 | Am1377 | Cm1447 | Am1459 | Gm 1460 | | Cm1479 | Cm1518 | Cm1847 | Cm1850 | Gm 1855 | Cm1860 | Am1871 | Um1892 | Um2114 | Gm2125 | Am2127 | Cm2198 | Am2215 | Am2221 | Gm2237 | / 9722 | Am2282 | 7022010 | | Am2322 | Am2327 | Cm2338 | Am2362 | Cm2366 | Gm 2392 Gm 7306 | | Gm2410 | | Um2411 | Um2422 | 01112450 11m 2494 | Am2561 | | Gm2620 | Am2641 | Gm2652 | Cm2683 |
| r RNA | 8 25S | 9 25S | 10 255 | 11 25S | 12 25S | 13 25S | 14 25S | 15 25S | 16 25S | 17 25S | 18 255 | 19 255 | 20 255 | 21 255 | 22 25S | | 23 25S | 24 25S | 25 25S | 26 25S | 27 25S | 28 25S | 29 25S | 30 255 | 31 25S | 32 25S | 33 25S | 34 25S | 35 25S | 36 25S | 37 25S | 38 255 255 | 202 202 40 250 | 41 25S | | 42 25S | 43 25S | 44 25S | 45 25S | 46 25S | 4/ 255 48 755 | | 49 25S | | 50 255 | 51 255 57 755 | 22 200 257 53 | 54 25S | | 55 25S | 262 06 57 75 | 58 255 | 59 255 |

(Continued)

| | | | | | | At4gCDbox115.4 | | | | | | | | | | | | | | | |
|-----------|----------------------|---------------|---------------|----------------|----------------|----------------|---------------|---------------|----------------|---------------|-------------|-------|-------------|-------|----------------|---------------|---------------|---------------|---------------|---------------|---------------|
| | snoRNA | | | | | At4gCDbox115.3 | At4gCDbox54.3 | | | | | | | | | | | | | | |
| | Assigned | | | | At5gCDbox100.2 | At4gCDbox115.2 | At2gCDbox54.2 | | | | | | | | At4gCDbox105.2 | | | | | At1gCDbox27.2 | At5gCDbox78.2 |
| | | At2gCDbox75.1 | At3gCDbox94.1 | At3gCDbox101.1 | At3gCDbox100.1 | At4gCDbox115.1 | At2gCDbox54.1 | At3gCDbox98.1 | At5gCDbox139.1 | At1gCDbox13.1 | snoRNA not | found | snoRNA not | found | At4gCDbox105.1 | At1gCDbox38.1 | At1gCDbox39.1 | At2gCDbox56.1 | At1gCDbox20.1 | At1gCDbox27.1 | At3gCDbox78.1 |
| c1 | /alue | ** | ns | ns | **** | ** | ** | *** | ns | ns | ns | | ns | | *** | *** | ** | * | ** | ** | ns |
| ScoreC nu | reduction p-v | 0.002043458 | 0.200622753 | 0.205258169 | 4.17794E-05 | 0.005432031 | 0.009929072 | 0.000863839 | 0.614273202 | 0.178388459 | 0.305290635 | | 0.948521456 | | 0.000782662 | 0.000255634 | 0.002038487 | 0.033711211 | 0.00734276 | 0.001637291 | 0.930282471 |
| | Position in yeast | | Gm2791 | Gm2793 | Gm2815 | | | | | | | | | | | Am2946 | Cm2948 | | Cm2959 | | |
| | Position in human | | | Gm4370 | Gm4392 | | Cm4456 | | | Gm4494 | Um4498 | | Gm4499 | | | Am4523 | | | Cm4536 | | |
| | inoRNA, 3D rRNA db | | AtsnoR1 | ż | AtsnoR38Y | AtsnoR24 | AtU49/ZmU49 | AtsnoR64 | | AtsnoR34 | | | | | | AtU29 | snoR69Y | ż | AtU35 | | |
| | Position, 3D rRNA db | | Gm2781 | Gm2783 | Gm2805 | Cm2826 | Cm2869 | Um2873 | | Gm2907 | | | | | | Am2936 | Cm2938 | Um2943 | Cm2949 | | |
| | Mapped published | L | λ | ~ | Ē | λ | ~ | ~ | Ē | c | L | | L | | L | L | L | λ | . > | Ē | ۲ |
| | Mapped RiboMethSeq | Um2736 | Gm2792 | Gm2794 | Gm2816 | Cm2837 | Cm2880 | Um2884 | Am2912 | Gm2918 | Um2922 | | Gm2923 | | Am2935 | Am2947 | Cm2949 | Um2954 | Cm2960 | Gm3292 | Um3301 |
| | rRNA | 25S | 25S | 25S | 25S | 25S | 25S | 25S | 25S | 25S | 25S | | 25S | | 25S | 25S | 25S | 25S | 25S | 25S | 25S |
| | | 60 | 61 | 62 | 63 | 64 | 65 | 99 | 67 | 68 | 69 | | 70 | | 71 | 72 | 73 | 74 | 75 | 76 | 77 |

Table 1. (Continued).



Figure 1. Predicted 18S, 5.8S and 25S rRNA structures with mapped 2'-O-methylations sites (A) 18S and (B) 5.8S/25S rRNA structures were generated on the basis of 2D structural predictions [24]. 2'-O-methylated sites in yellow circles or grey circles show rRNA sites with or without matching C/D snoRNAs (respectively). Star inside the circles indicates observed dependency of rRNA 2'-O-methylation on NUC1 gene expression. In B, the 5.8S rRNA structure is coloured in green and two 25S fragments (5'-fragment and 3'-fragment, a and b, respectively) are split in the main structure for clarity. The 18S (5', central, 3'Major and 3'Minor) and 25S (I–VI) rRNA domains are designated according to [1]. P and A loop are indicated by arrows.



Figure 1. (Continued).

| S. cerevisiae | H. sapiens | A. that | iana | Peptides / Coverage |
|---------------|-------------------|-----------|-----------|---------------------|
| Nen1 | EDI /Eihrillerin | FIB1 | At5g52470 | 22 / 62% |
| морт | FBL/Fibilialili | FIB2 | At4g25630 | 25 / 67% |
| Non56/Sik1 | NORSE | NORSE | At1g56110 | 23 / 48% |
| N0p36/SIK I | NOP 56 | NOP 56 | At3g12860 | 15 / 26% |
| NonE9/E | NOR59 | NORES | At5g27120 | 19 / 42% |
| 100058/5 | NOF 36 | NOF 38 | At3g05060 | 28 / 53% |
| | | | At4g12600 | 1 / 12% |
| | | | At4g22380 | ND |
| Snu13 | 15,5K/NHP2-like 1 | L7Ae/L30e | At5g20160 | ND |
| | | | At2g47610 | 4 / 18% |
| | | | At3g62870 | N/D |

| 141 C/D snoRNA | 25S | 18S | 5.8S | Total |
|-----------------------|-----|-----|------|-------|
| Predicted target (5') | 66 | 41 | 0 | 107 |
| Predicted target (3') | 54 | 23 | 4 | 81 |
| Unique target sites | 66 | 37 | 2 | 105 |

В



Figure 2. Characterization of FIB2-YFP snoRNP **(A)** Arabidopsis C/D-box protein orthologues (left) and C/D snoRNA (right) detected in the FIB2-YFP IP fractions using LC-MS/MS and RNA-seq approaches. The number of peptides and % of protein coverage for each protein is shown and the number of predicted 25S, 18S and 5.8S rRNA targets identified in the 5' and 3' antisense sequences of 141 C/D snoRNA. **(B)** Representation of 6 novel C/D snoRNA detected in the FIB2-IP fraction. C and D boxes are boxed. These C/D snoRNA do not contain a matching rRNA target sequence.

Table 2. List of C/D box snoRNAs identified from RNA-seq data. The number of C/D snoRNA reads are provided for each Co_IP fraction. Are indicated, rRNA positions mapped as 2'-O-methylated in this study, when predicted to be guided by a snoRNA and the names of known C/D snoRNA in databases Are highlighted in red snoRNAs with predicted rRNA methylation sites but not detected by RiboMethSeq. ID with an asterisk identifies a snoRNA which is dicistronic with a tRNA. ID with two asterisks represents a snoRNA which is polycistronic with a miRNA.

| the asteristic represent | to a shoring which is polycistronic | | | | | |
|--------------------------|-------------------------------------|---------|---------|---------|------------------------|-----------------------|
| Box C/D sRNA | Known Id | CoIP_1 | CoIP_2 | CoIP_3 | Predicted target (5') | Predicted target (3') |
| At1gCDbox1.1 | AtsnoR6-1 | 29,792 | 22.096 | 21,345 | | |
| At1gCDbox3.1 | AtU36a-1 | 3110 | 3338 | 3171 | Gm2237 25S | Am2221 25S |
| At1gCDbox5.1 | AtsnoR10-1 | 176,840 | 127,190 | 126,633 | Um2651_25S | |
| At1gCDbox6.1 | AtsnoR9-1 | 6842 | 5905 | 5520 | | Am47 5.8S |
| At1gCDbox3.2 | AtU36a-2 | 2534 | 2350 | 2117 | Gm2237_25S | Am2221_25S |
| At1gCDbox1.2 | AtsnoR6-2 | 30,690 | 23,145 | 22,939 | — | — |
| At1aCDbox7.1* | SnoR43.2 | 5422 | 4728 | 4674 | Am545 18S | |
| At1gCDbox8.1* | SnoR43.1 | 197,481 | 168,698 | 168,566 | Am545_18S | |
| At1gCDbox11.1 | U3 | 945 | 857 | 999 | _ | |
| At1gCDbox12.1 | AtU37 | 8944 | 7347 | 7129 | Am2215_25S | |
| At1gCDbox13.1 | AtsnoR34 | 191,705 | 149,781 | 141,542 | Gm2918_25S | |
| At1gCDbox14.1 | AtsnoRNA_R38 | 291 | 254 | 240 | _ | |
| At1gCDbox15.1 | snoR122 | 117 | 136 | 137 | | |
| At1gCDbox16.1 | AtU79-1b ou AtsnoR44-1b | 31,030 | 26,453 | 26,368 | Cm2338_25S | Gm2327_25S |
| At1gCDbox16.2 | AtU79-1a ou AtsnoR44-1a | 53,154 | 47,539 | 46,891 | Cm2338_25S | Gm2327_25S |
| At1gCDbox17.1 | Z267 | 6378 | 5913 | 6178 | Um604_18S | |
| At1gCDbox18.1 | AtsnoR16-1 | 23,730 | 20,825 | 19,757 | Um2456_25S | Um48_25S |
| At1gCDbox19.1 | AtU43-1 | 86,681 | 72,783 | 73,809 | Cm1645_18S | |
| At1gCDbox20.1 | AtU35 | 30,832 | 23,099 | 22,599 | Cm2960_25S | |
| At1gCDbox21.1 | AtsnoR101 | 9314 | 6949 | 6911 | | |
| At1gCDbox22.1 | AtU59b | 9988 | 8160 | 8183 | Am978_18S | Gm1855_25S |
| At1gCDbox22.2 | AtU59a | 125,292 | 106,451 | 112,345 | Am978_18S | Gm1855_25S |
| At1gCDbox23.1 | AtsnoTAIRsnoRNA6 | 78,189 | 68,892 | 64,353 | | Cm1479_25S |
| At1gCDbox24.1 | AtsnoR105 | 17,441 | 14,677 | 14,231 | | |
| At1gCDbox25.1 | AtU31a/HID2 | 43,635 | 42,762 | 39,045 | Gm2620_25S | |
| At1gCDbox26.1 | AtsnoR4a | 167,211 | 140,369 | 132,738 | | |
| At1gCDbox27.1 | AtU33a | 90,503 | 71,938 | 72,290 | Gm3292_25S | Um1273_18S |
| At1gCDbox28.1 | AtU51a | 114 | 92 | 73 | | Am816_25S |
| At1gCDbox25.2 | AtU31b | 9205 | 8916 | 8560 | Gm2620_25S | |
| At1gCDbox26.2 | AtsnoR4b | 17,348 | 14,959 | 14,460 | | |
| At1gCDbox27.2 | AtU33b | 18,424 | 13,612 | 13,136 | Gm3292_25S | Um1273_18S |
| At1gCDbox28.2 | AtU51b | 84 | 57 | 56 | | Am816_25S |
| At1gCDbox29.1 | | 376 | 287 | 302 | | |
| At1gCDbox31.1 | AtsnoR14-2 | 633 | 459 | 461 | Um1235_18S | Um803_25S |
| At1gCDbox32.1 | AtsnoR15 | 11,650 | 10,327 | 10,208 | Am440_18S | Cm1860_25S |
| At1gCDbox9.2* | SnoR43.10 | 2331 | 1963 | 2095 | _ | _ |
| At1gCDbox9.3* | SnoR43.9 | 58 | 78 | 74 | | |
| At1gCDbox33.1 | AtsnoR65 | 40,967 | 35,353 | 32,666 | Um213_18S | Gm399_25S |
| At1gCDbox34.1 | snoR113 | 9635 | 8275 | 8385 | | |
| At1gCDbox35.1 | snoR114 | 7223 | 4748 | 5284 | | |
| At1gCDbox36.1 | AtsnoR53Y | 7874 | 7704 | 7403 | Am801_18S | |
| At1gCDbox37.1 | AtsnoR25 | 4936 | 4092 | 3856 | Am796_18S or Cm797_18S | |
| At1gCDbox38.1 | AtU29 | 22,365 | 21,744 | 21,262 | Am2947_25S | |
| At1gCDbox39.1 | AtsnoR69Y | 19,662 | 17,455 | 16,644 | Cm2949_25S | |
| At1gCDbox40.1* | SnoR43.7 | 58,869 | 50,112 | 49,216 | | |
| At1gCDbox41.1* | SnoR43.8 | 178,707 | 139,589 | 137,628 | | |
| At1gCDbox43.1* | SnoR43.6 | 1257 | 1332 | 1410 | | |
| At1gCDbox24.2 | Z279 ou snoR105 | 2491 | 2134 | 2056 | | |
| At1gCDbox44.1 | AtsnoR102 | 1798 | 1743 | 1714 | | |
| At1gCDbox45.1 | snoR17 | 2226 | 1733 | 1681 | | |
| At1gCDbox46.1 | AtsnoR17 | 74,719 | 57,795 | 57,805 | | Am468_18S |
| At1gCDbox16.3 | AtU79-2 ou AtsnoR44-2 | 197,875 | 174,821 | 167,417 | Cm2338_25S | Gm2327_25S |
| At1gCDbox17.2 | Z267 | 52,829 | 42,299 | 43,150 | Um604_18S | |
| At1gCDbox18.2 | AtsnoR16-2 | 12,596 | 10,424 | 10,348 | | Um48_25S |
| At1gCDbox19.2 | AtU43-2 | 91,375 | 73,859 | 73,358 | Cm1645_18S | |
| At1gCDbox47.1 | At_snoTAIRsnoRNA16 | 37,870 | 30,906 | 29,897 | Cm1219_18S | |
| At1gCDbox48.1 | | 13,102 | 10,348 | 10,696 | | |
| At1gCDbox49.1 | | 284 | 277 | 263 | | |
| At1gCDbox50.1 | | 198 | 134 | 148 | | |
| At1gCDbox51.1 | AtsnoTAIRsnoRNA16 | 193,801 | 143,224 | 141,301 | Um123_18S | |
| At1gCDbox52.1 | AtsnoTAIRsnoRNA17 | 34,154 | 24,685 | 24,197 | Um2114_25S | |
| At2gCDbox53.1 | At77Y-2 | 216,644 | 171,303 | 167,532 | Um582_18S | |
| At2gCDbox54.1 | AtU49-2 | 96,660 | 80,342 | 79,563 | Cm2880_25S | |
| At2gCDbox54.2 | AtU49-1 | 171 | 148 | 141 | Cm2880_25S | |
| At2gCDbox53.2 | At77Y-1 | 1593 | 1398 | 1616 | Um582_18S | |
| At2gCDbox56.1 | SnoRNA R4 | 729 | 598 | 636 | Um2954_25S | |
| At2gCDbox57.1 | AtU34c | 49,130 | 40,248 | 38,388 | Um1892_25S | |
| At2gCDbox58.1 | AtU34b | 3809 | 3712 | 3848 | Um1892_25S | |
| At2gCDbox59.1 | AtU34a | 98,590 | 90,168 | 83,378 | Um1892_25S | |
| At2gCDbox60.1** | AtsnoTAIRsnoRNA19 | 137,218 | 125,343 | 125,025 | | |
| At2gCDbox61.1** | AtsnoTAIRsnoRNA20 | 7490 | 6932 | 7099 | | |
| At2gCDbox62.1* | AtsnoTAIRsnoRNA21 | 6346 | 4876 | 5005 | | |
| At2gCDbox63.1* | AtsnoTAIRsnoRNA22 | 19,528 | 18,462 | 18,567 | Am2362_25S | |
| At2gCDbox62.2* | AtsnoTAIRsnoRNA23 | 221,115 | 149,030 | 154,503 | | |
| At2gCDbox64.1 | AtU16 | 62,676 | 57,905 | 55,828 | Am440_18S | |
| At2gCDbox65.1 | AtU55 | 60,488 | 54,352 | 52,021 | | Cm1860_25S |

Table 2. (Continued).

| Alg.Chous.12 Assumit-1 116.561 101.000 100.006 Um138-1.165 Um138-1.165 Alg.Chous.31 Assumit-1 101.16 0.116 <th>Box C/D sRNA</th> <th>Known Id</th> <th>CoIP_1</th> <th>CoIP_2</th> <th>CoIP_3</th> <th>Predicted target (5')</th> <th>Predicted target (3')</th> | Box C/D sRNA | Known Id | CoIP_1 | CoIP_2 | CoIP_3 | Predicted target (5') | Predicted target (3') | | |
|--|--|--------------------------|---------------|-------------------|-------------|-----------------------|-----------------------|-------------|--|
| Alag(20bas) Alubi 13.74 9768 10.16 Utilization Alag(20bas) Alabel Signal Grif 2.55 Grif 2.55 Grif 2.55 Alag(20bas) Alabel Signal Signal Grif 2.55 Arag(20bar) Arabel 2.55 Arabe | At2gCDbox31.2 | AtsnoR14-1 | 118,361 | 101,090 | 100,066 | Um1235_18S | Um803_25S | | |
| Abardback Abardback 21333 17.104 67.72 Gm127.318 Gm127.318 Gm127.318 Gm127.318 Abardbacks Abardbacks Abardbacks 208.675 175.574 165.999 Gm127.318 Gm127.318 Abardbacks Abardbacks Abardbacks Gm27.318 Gm27.318 Gm27.318 Abardbacks Abardbacks B3019 Gold S Gm127.318 Gm127.318 Abardbacks B3019 Gold S Gm127.318 Gm27.318 Ama85.255 Abardbacks B319 Gold S Gold S Gm127.318 Ama85.255 Abardbacks B319 Gold S S111 Ama85.255 Ama85.255 Abardbacks Abardbacks B319 Gold S S113 Cm073.253 Mm88.255 Abardbacks Abardbacks B319 Gold S B313 Gm272.253 Mm88.255 Abardbacks Abardbacks B310 B320 Cm073.253 Mm88.255 Abardbacks Abardbacks B3210 F77.353 B | At2gCDbox66.1 | AtU61 | 13,714 | 9708 | 10,316 | | Um1384_18S | | |
| Abg (2006) At 2007 121 1171 Contel (1, 25) Contel (1, 25) Abg (2006) Attention (21) 2005 Gm/72, 56 Gm/72, 56 Abg (2006) Attention (21) 6007 115 Gm/72, 56 Abg (2006) Attention (21) 6700 6700 Attention (21) Abg (2006) Attention (21) 6700 6700 Attention (21) Abg (2006) Attention (21) 6700 6700 Attention (21) Abg (2006) Attention (21) 6700 Attention (21) Attention (21) Abg (2006) Attention (21) 6700 Attention (21) Attention (21) Abg (2006) Attention (21) 6700 Attention (21) Attention (21) Abg (2006) Attention (21) 7743 3593 35138 Um/274, 235 Abg (2006) Attention (21) 7743 3693 35138 Um/374, 255 Abg (2006) Attention (21) 7743 36949 Attention (21) Attention (21) Abg (2006) Attention (21) | At2gCDbox67.1 | AtsnoR21b | 21,923 | 17,104 | 16,779 | Gm1275_18S | | | |
| Alg. Cuber 2011 Alg. Cuber 2015 Class 1 21.291 Class 1 Class 1 Alg. Cuber 2011 Atsoc 6647 9665 10,468 10,162 cm115,2,153 cm12,255 cm12,255 Alg. Cuber 2011 Atsoc 6647 9665 10,468 10,162 Atsoc 642,255 Alg. Cuber 2011 Atsoc 6647 6,152 Atsoc 643,255 Atsoc 843,255 Alg. Cuber 2011 Atsoc 643,177 0,237 8427 8361 Am885,255 Alg. Cuber 2013 Atsoc 74,237 10,327 8427 8361 Cm675,255 Alg. Cuber 2013 Atsoc 74,237 10,327 10,327 10,327 Atsoc 2015,185 Um2326,255 Alg. Cuber 2013 Atsoc 74,237 10,348 12,247 Atsoc 10,255 Atsoc 2015,185 Um2326,255 Alg. Cuber 2013 Atsoc 74,245 16,461 15,398 Atsoc 225 Atsoc 10,255 Alg. Cuber 2013 Atsoc 74,255 15,348 42,755 12,325 Cm1310,225 Alg. Cuber 2014 Atsoc 74,2455 16,81 12,255 | At2gCDbox68.1 | At39BYb | 2212 | 1817 | 1773 | Gm814_25S | Gm79_5.8S | | |
| Add_DDBL2_J Attool 18 JBAC 7 17.5.6 19.549 Cm1/J_180 Cm1/J | At2gCDbox69.1 | Atsno1AIRsnoRNA24 | 301,655 | 212,851 | 212,975 | Cm1850_255 | | | |
| Alg. Construct Alg. 200 Dis. 200 | At2gCDbox67.2 | AtsnoR21a | 208,675 | 1/5,5/4 | 165,999 | Gm1275_185 | C==70 5.05 | | |
| Alg. Construction Absolution Series Ansatz Ansatz Alg. Construction Ansatz Series Ansatz Series Alg. Construction Ansatz Series Series Ansatz Alg. Construction Ansatz Series Series Series Alg. Construction Ansatz Series Series Series Series Alg. Construction Ansatz Series Series Series Series Alg. Construction Ansatz Series Series Series Series < | At2gCDbox68.2 | Atage DCOV | 216,657 | 191,596 | 191,892 | Gm814_255 | Gm/9_5.85 | | |
| Angleboxi2:1 Associated and a standard and a standa | At2gCDbox70.1 | Atsnok681 | 9865 | 10,468 | 10,162 | Am 2641 255 | | | |
| AnageDexiX1 Ar727b C111 C411 C413 C413 Arr852 25S Al2QCDexX4.1 Ar727b G337 G202 S710 Arr852 25S Al2QCDexX4.2 Ar727c 10.327 8427 8361 Arr852 25S Al2QCDexX4.2 Ar727c 10.327 8427 8361 Arr852 25S Al2QCDexX4.1 Arrande 37.469 35.383 Cm675 25S Un2756 25S Al2QCDex78.1 Atron Al8moRMA25 13.464 11.579 Creation Al12 Ma320 1.25S Al2QCDex78.1 Atron Al8moRMA25 13.464 11.559 Arr322 2.25S Creation Al12 Ma320 1.25S Al2QCDex83.1 Atron Al8moRMA25 13.464 11.559 Arr322 2.25S Creation Al12 Al25D Al3QCDex83.1 Atron Al8moRMA26 40.571 34.299 34.742 Creation Al12 Al123D Creation Al12 Al12 Al123D | ALZYCDD0X/1.1 | AtsnoP26 | 83 510 | 60 54 2 | 61 592 | AIII2041_255 | | | |
| Alagebox/A1 AL72Yb 6327 6026 5710 Am885_255 Alagebox/A2 AL72Yb 11327 8427 8361 Am885_255 Alagebox/A3 AL72Yb 11327 8427 8361 Am885_255 Alagebox/A1 AL72Yb 19278 255 Am86_255 Alagebox/A1 AL88Y12 114,357 99,2583 91,080 Am61_253 Alagebox/A1 AL89Y12 127,156 66,677 Am61_253 Mind1_253 Alagebox/A1 Ateno/AlknoRNA25 66,21 5725 5723 723 724 Am220_255 Cm1318_255 Alagebox/A1 Ateno/AlknoRNA25 66,23 5725 5723 723 724 Cm1318_255 Cm1318_255 Cm1318_255 Alagebox/255 | At2gCDb0x72.1 | Δ+72V2 | 5141 | 4011 | 4638 | | Am885 255 | | |
| AddgCbback2 AM22 MA22 Bit27 | At2gCDbox73.1 At2gCDbox74.1 | At72Yh | 6337 | 6026 | 5710 | | Am885_255 | | |
| Arg20Dbar/1 Arb/271 11629 10650 9554 Arb85/255 Arb20Dbar/5.1 ArtsonRe8 37/43 36/63 35,138 Um3276,255 Arb20Dbar/5.1 ArtsonRe8 37/43 36/63 35,138 Um301,255 Arb20Dbar/5.1 ArtsonRe8 37/43 36/63 35,138 Um301,255 Arb20Dbar/5.1 ArtsonTAlknonRvA26 66/1 5775 5773 Arb20Dbar/5.1 ArtsonTAlknonRvA26 66/1 5775 5773 Arb20Dbar/5.1 ArtsonTAlknonRvA26 66/1 5775 5773 Arb20Dbar/5.1 ArtsonTAlknonRvA26 67/12.55 6/12.55 Cm1518,255 Arb20Dbar/5.1 ArtsonRe8 40/571 34/380 32,516 Cm2198,255 Um1728,255 Arb20Dbar/5.1 ArtsonRe6 40/877 34/380 32,516 Cm2198,255 Um1728,255 Arb20Dbar/5.1 ArtsonRe6 40/877 34/380 32,516 Cm2198,255 Um1728,255 Arb20Dbar/5.1 ArtsonRe5 32,592 35,541 Arban26,255 <td< td=""><td>At2gCDbox74.2</td><td>At72Yc</td><td>10.327</td><td>8427</td><td>8361</td><td></td><td>Am885_255</td></td<> | At2gCDbox74.2 | At72Yc | 10.327 | 8427 | 8361 | | Am885_255 | | |
| AL2_CDBAY3.1 AtsonoRes 37,433 26,963 33,138 Um220,225 AL3_CDBAY7.1 Attulle 2 157,637 123,863 127,897 Amob1 225 AL3_CDBAY8.1 AtsonoFAIS2 138,412 175,126 66,878 Um301 .255 AL3_CDBAY8.1 AtsonoFAIRsonoFAA25 13,844 11,156 109,300 AL3_CDBAY8.1 AtsonoFAIRsonoFAA26 66,21 5725 5723 AL3_CDBAY8.1 AtsonoFAIRsonoFAA26 66,21 5725 5723 AL3_CDBAY8.1 AtsonoFAIRsonoFAA28 104,277 76,466 79,098 Cm1218,255 Cm1218,255 AL3_CDBAY8.1 AtsonoFAIRsonoFAA28 104,277 76,466 79,098 Cm2198,255 Cm2266,255 M17278,125 AL3_CDBAY8.1 AtsonoFAIR 22,809 2564 Atson26,255 Cm2198,255 Cm2198,255 Cm2198,255 Cm2198,255 Cm2198,255 Cm2198,255 Cm2198,255 Cm1278,255 AtsonoFAIR AtsonoFAIR AtsonoFAIR AtsonoFAIR AtsonoFAIR AtsonoFAIR AtsonoFAIR AtsonoFAIR <td>At2gCDbox74.3</td> <td>At72Yd</td> <td>11,629</td> <td>10,050</td> <td>9554</td> <td></td> <td>Am885_25S</td> | At2gCDbox74.3 | At72Yd | 11,629 | 10,050 | 9554 | | Am885_25S | | |
| Adg/Ebbox/6.1 AdSV:2 104.37 99.295 91.003 Cm075.255 Adg/Ebbox/7.1 AtmoR1.32 88.121 75.126 66.762 Um65.185 Um3301_255 Adg/Ebbox/7.1 AtmoR1MaceNNA25 16.74 177.25 16.75 177.25 Adg/Ebbox/8.1 AtmoR1MaceNNA25 16.74 177.25 177.25 177.25 Adg/Ebbox/8.1 AtmoR1MaceNNA25 16.74 177.25 177.25 177.25 Adg/Ebbox/8.1 AtmoR1MaceNNA26 16.42.37 77.26 177.25 177.25 Adg/Ebbox/8.1 AtmoR1MaceNNA29 40.271 34.299 34.742 Cn1218_2.55 107.256 255 Adg/Ebbox/9.1 AtmoR623-1 2.209 259 150.03 Am22.25 M1728_2.255 Adg/Ebbox/9.1 AtmoR623-1 7.209 259 150.03 Am22.25 M1728_2.255 Adg/Ebbox/9.1 AtmoR23-1 7.209 259 95.00 Am32.185 M172.25 Adg/Ebbox/9.1 AtmoR23-1 7.209 7.923.8 67. | At2gCDbox75.1 | AtsnoR68 | 37,403 | 36,963 | 35,138 | | Um2736 25S | | |
| AtigCbox7:1 Atul8:2 17,28 12,2837 12,2837 Atm61,25 AtigCbox7:1 Atm613:2 23,488 24,764 24,198 umbis_185 umbis_185 um301_255 AtigCbox8:1 Atm61AikmeRNA22 67,825 51,838 50,940 Cm151_255 Cm151_255 AtigCbox8:1 Atm61AikmeRNA28 104,257 76,646 79,098 Cm2198_255 Cm151_255 AtigCbox8:1 Atm61AikmeRNA28 104,257 76,646 79,098 Cm229_255 Cm2366_2355 AtigCbox8:1 Atm668 40,877 34,329 34,742 Cm238_255 Lim177_255 AtigCbox8:1 Atm66871 24,265 18,831 18,841 Um2422_255 Cm2366_2355 AtigCbox9:1 Atm6871 24,265 18,831 19,003 Am262_235 Cm171_255 AtigCbox9:1 Atm72 32,92 71,541 Am262_155 Um1266_185 AtigCbox9:1 Atm72 23,92 71,541 Am157_255 Um1266_185 AtigCbox9:1 Atm61a_145,57 | At3gCDbox76.1 | At58Y-2 | 104,547 | 99,295 | 91,003 | Cm675_25S | _ | | |
| AtagCbox78.1 Atsnof13-2 88,121 75,126 66,762 Um615,185 Um3301_2S5 AtagCbox8.1 AtsnoTARsneRNA25 13,804 11,135 10,223 AtagCbox8.1 AtsnoTARsneRNA25 13,804 11,35 10,223 < | At3gCDbox77.1 | AtU18-2 | 157,637 | 123,863 | 127,897 | Am661_25S | | | |
| AtagCDbox07:1 25.488 24,764 24,198 AtagCDbox01:1 Atano71AlkinoRNA26 62.1 5725 3720 AtagCDbox03:1 Atano71AlkinoRNA26 62.1 5725 3720 AtagCDbox03:1 Atano71AlkinoRNA28 104.257 76.66 79.086 Cm1518_255 AtagCDbox03:1 Atano71AlkinoRNA28 104.257 76.66 79.086 Cm226_255 AtagCDbox03:1 AtanoRNTN 43.200 32.516 Cm32.825 Cm128_255 AtagCDbox03:1 AtanoRNT 43.200 32.516 Cm32.255 Cm128_255 AtagCDbox03:1 AtanoRNT 32.300 32.516 Cm32.255 Cm128_255 AtagCDbox02:1 AtanoRX1 23.301 3500 Am28_255 Cm178_2185 AtagCDbox02:1 AtanoRX1 23.301 3500 Am32.55 Um126_6.185 AtagCbbox03:1 AtanoRX2 23.516 Cm329_2.255 Um126_6.185 AtagCbbox03:1 AtanoRX2 23.339 4.773 23.2010 Am139_2.185 Um126_6.185 | At3gCDbox78.1 | AtsnoR13-2 | 88,121 | 75,126 | 68,762 | Um615_18S | Um3301_25S | | |
| AtsgCbox80.1 AtsnoTAREsnoRNA25 13.804 11.156 10.920 AtsgCbox82.1 AtsnoTAResnoRNA25 662.1 572.5 <td>At3gCDbox79.1</td> <td></td> <td>25,488</td> <td>24,764</td> <td>24,198</td> <td></td> <td></td> | At3gCDbox79.1 | | 25,488 | 24,764 | 24,198 | | | | |
| Aligo Doox31. Atsno I Altsno I Max 25 662.1 57.2 57.3 Aligo Doox31. Atsno Dimox31. Atsno Dimox32. Cm 2136.255. Cm 236.255. Cm 236.255. Atsno Dimox32. Atsno Dimox33. Cm 236.255. Cm 236.255. Cm 236.255. Cm 236.255. Cm 236.255. Cm 236.255. Atsno Dimox33. Atsn | At3gCDbox80.1 | AtsnoTAIRsnoRNA25 | 13,804 | 11,156 | 10,920 | | | | |
| Alsg.Dbox82.1 AlsG01ARES0RM2/2 6/.225 10.83 30.940 Alsg.Dbox85.1 AlsG07ARES0RM2/2 17.636 16.160 15.356 Ann2322_255 Alsg.Dbox85.1 AlsG07ARES0RM2/2 17.636 15.356 Cm38_185 Alsg.Dbox85.1 AlsG07ARES0RM2/2 18.357 73.450 Cm38_185 Alsg.Dbox81.1 AlsG07ARES0RM2/2 17.637 73.450 Cm38_185 Alsg.Dbox81.1 AlsG07ARES0RM2/2 25.09 25.64 Um128_2.255 Cm236_2.255 Alsg.Dbox90.1 Alu27-1 23.07 9.399 91.42 Am1758_185 Alsg.Dbox92.1 Alu27-1 23.07 9.399 91.42 Am1758_185 Alsg.Dbox92.1 Alu27-1 23.849 21.273 20.109 Am132.185 Um1264_185 Alsg.Dbox93.1 Atson81.2 23.391 Gm372_2.25 Um1264_185 Um1264_185 Alsg.Dbox93.1 Atson81.2 11.357 56.738 9.050 Am1572_185 Um1264_185 Alsg.Dbox93.1 Atson674 42.72 37.32< | At3gCDbox81.1 | AtsnoTAIRsnoRNA26 | 6621 | 5725 | 5723 | | | | |
| Algs_Dbox83.1 Attax/dbox128 I/A897 I/A897 <th a897<="" th=""> I/A897 <th a897<="" th=""> <</th></th> | I/A897 <th a897<="" th=""> <</th> | < | At3gCDbox82.1 | AtsnoTAIRsnoRNA2/ | 67,825 | 51,683 | 50,940 | Am 2222 256 | |
| Alg.Clouds.1 Abbil Tribuin Marka Mod 20 Compare Taylog Clin 13 (2, 2) Alg.Clouds.1 Abbil Tribuin Marka Mod 20 Taylog Compare | AL3GCDD0X83.1 | ALU3U | 17,030 | 10,100 | 15,590 | Am2322_255 | Cm1E19, 2E5 | | |
| Alg.Chouse:1 Alg.Double:1 Alg.Double:1 Alg.Double:1 Alg.Double:1 Alg.Chouse:1 Attondis/ 42,625 Imitize:25 Cmitize:25 Amitize:25 Alg.Chouse:1 Attondis/:1 2580 2580 2564 Amitize:25 Amitize:255 Alg.Chouse:1 Attondis/:1 12,037 9239 9142 Amitize:255 Amitize:155 Alg.Chouse:1 Attuscion:1 12,037 9239 5980 Ama26,255 Gmit17:255 Alg.Chouse:1 Attuscion:1 12,348 12,352 Cmit126:155 Amitize:155 Alg.Chouse:2 Attuscion:1 23,449 12,727 23,839 Amitize:155 Mit126:6;185 Alg.Chouse:5:1 Attuschika:1 43,330 24,173 23,591 Gmit124:185 Umit264:185 Alg.Chouse:5:1 Attuschika:1 6,732 96,738 95,050 Amitise:1 Umit26:185 Alg.Chouse:5:1 Attuschika:1 6,269 53,471 5288 Gmit279:255 Mit264:185 Alg.Chouse:5:1 Attuschika:1 12,352 72,888 Gmit134:185 Umit26:185 Umit26:185 | AL3GCDD0X85.1 | ALSOUTAIRSOURNA28 | 104,257 | 70,040 | 79,098 | Cm2109 255 | Cm1518_255 | | |
| AtsgCDbasel: Atsn683*1 24,265 18,831 18,844 Um242_255 Cm3366_255 AtsgCDbasel: Atsn682-11 2500 2564 Am1263_255 Um1728_255 AtsgCDbasel: Atsn622-22 Am178_185 Am178_185 Am178_185 AtsgCDbasel: Atu27-2 23,112 18,833 19,003 Am826_255 Gm172_255 AtsgCDbasel: Atu27-1 23,849 21,273 20,109 Am38.165 Um1266_185 AtsgCDbasel: Atsn68a 114,537 66,788 95,050 Am1759_185 Um1264_185 AtsgCDbasel: Atsn68b 114,537 66,788 95,050 Am1579_185 Um1264_185 AtsgCDbasel: Atsn68b 114,537 66,788 95,050 Am1579_185 Um1264_185 AtsgCDbasel: Atsn68b 114,537 96,788 95,050 Am1579_185 Um1264_185 AtsgCDbasel: Atsn68b 114,537 96,788 95,050 Am1579_185 Um1264_185 AtsgCDbasel: Atsn68b 114,537 96,788 95,850 Am157_2185 Um1264_185 Um1264_185 | At3gCDb0x80.1 | AtsnoR66 | 40,371 | 34,299 | 34,742 | Cm38 185 | | | |
| Aright Disorder, 1 Attendit2:-1 2500 2564 Am 1263_255 Um 1272_255 Aright Disorder, 1 1,037 9239 9142 Am 1758_185 Am 1758_185 Aright Disorder, 1 Aut07-1 213,07 9239 9142 Am 126_255 Gm 917_255 Aright Disorder, 1 Aut07-1 23,849 21,273 20,109 Am 130,185 Um 1266_185 Aright Disorder, 3 Aut07-1 23,849 21,273 20,109 Am 130,185 Um 1266_185 Aright Disorder, 2 AturoR8 114,357 95,050 Am 1579_185 Um 1264_185 Aright Disorder, 2 AtsnoR8 114,357 95,050 Am 1579_185 Um 1264_185 Aright Disorder, 1 AtsnoR1b 10,279 36 Gm 1434_185 Um 1264_185 Aright Disorder, 1 AtsnoR1b 10,272 27,980 271,088 Um 1013_185 Um 1013_185 Aright Disorder, 1 AtsnoR172 36,720 271,088 Cm 473_185 Am 227_255 Aright Disorder, 1 AtsnoR172 36,720 | At3aCDbox88 1 | AtsnoB37-1 | 24 265 | 18 831 | 18 854 | llm2422_25S | (m2366_255 | | |
| AlsgCbose01 Atson623-1 12.037 9 239 9 142 Att 1752 Att 1752 <t< td=""><td>At3gCDbox89.1</td><td>AtsnoR22-1</td><td>2580</td><td>2509</td><td>2564</td><td>Am1263 255</td><td>Um1278_25S</td></t<> | At3gCDbox89.1 | AtsnoR22-1 | 2580 | 2509 | 2564 | Am1263 255 | Um1278_25S | | |
| ArágCboseji.1 AUBO-1 7413 5920 5890 Am226_255 Gm317_255 ArágCboseji.2 AUU7-1 88,895 73,932 71,541 Am28_185 ArágCboseji.1 AtsoRbaseji.2 AUU7-1 88,895 73,932 71,541 Am28_185 ArágCboseji.1 AtsnoR8a 14,337 95,738 95,505 Am1379_185 Um1266_185 ArágCboseji.2 AtsnoR8a 14,337 95,738 95,050 Am1579_185 Um1264_185 ArágCbboséj.2 AtsnoR8b 144,337 95,738 95,050 Am1579_185 Um1264_185 ArágCbboséj.1 AtsnoR84 142,237 3732 3005 Um1014_185 ArágCbboséj.1 AtsnoR72 36 41 40 Um1014_185 ArágCbboséj.1 AtsnoR84 4272 3732 3005 Um1044_185 ArágCbboséj.1 AtsnoR84 4272 3732 3005 Um1014_185 ArágCbboséj.2 AtsnoR84 227.9 21,028 Cm2816_255 Am2227_255 <t< td=""><td>At3gCDbox90.1</td><td>AtsnoR23-1</td><td>12.037</td><td>9239</td><td>9142</td><td>/</td><td>Am1758 18S</td></t<> | At3gCDbox90.1 | AtsnoR23-1 | 12.037 | 9239 | 9142 | / | Am1758 18S | | |
| At3CDbox92: AtU27-2 23,712 18,833 19,003 Am28_18S At3CDbox92: AtU27-1 88,895 73,932 71,541 Am28_18S At3CDbox93:1 AtsnoR1a 30,339 24,173 20,109 Am130_18S Um1266_18S At3CDbox95:1 AtsnoR1a 30,337 96,738 95,050 Am1579_18S Um1264_18S At3CDbox95:2 AtsnoR8a 114,537 96,738 95,050 Am1579_18S Um1264_18S At3GDbox95:3 AtsnoR72 36 41 40 Um1284_12S Um1284_2S5 At3GDbox96:1 AtsnoR8b 114,537 96,738 95,050 Am1579_18S Um1284_2S5 At3GDbox91:1 AtsnoR80-1 100,894 227,990 221,098 Um1434_18S Um2884_2S5 At3GDbox10:1 AtsnoR80-1 100,287 72,884 66,76 Gm282_2S5 Am2282_2S5 At3GDbox10:1 AtsnoR80 874 755 712 Am228_2S5 Am162_185 At3GDbox10:1 AtsnoR818 32,750 | At3qCDbox91.1 | AtU80-1 | 7413 | 5920 | 5890 | Am826 25S | Gm917 25S | | |
| A136 (Dbox92.2 AtU27-1 88,895 73,932 71,541 Am22,185 A136 (Dbox94.1 AtsnoR32.1 23,849 21,273 20,109 Am1330,185 Um1266_185 A136 (Dbox94.1 AtsnoR8a 114,373 96,738 95,050 Am1579,185 Um1264_185 A136 (Dbox94.2 AtsnoR8b 114,373 96,738 95,050 Am1579,185 Um1264_185 A136 (Dbox96.2 AtsnoR8b 114,373 96,738 95,050 Am1579,185 Um1264_185 A136 (Dbox96.1 AtsnoR8b 114,373 96,739 95,000 Am1579,185 Um1264_185 A136 (Dbox96.1 AtsnoR64 4272 373,2 3905 Um1013_185 Um1011_185 A136 (Dbox10.1 AtsnoR64 4272 373,2 3905 Um1013_185 Am1377_255 A136 (Dbox10.1 AtsnoR74 130,52 72,888 66,762 Gm2816_255 Am162_185 A136 (Dbox10.1 AtsnoR74 37,755 71,718 54,489 52,322 Gm282,255 Am162_185 A136 (Dbox14 AtsnoR74 75,757 71,74 Am257_255 <td< td=""><td>At3gCDbox92.1</td><td>AtU27-2</td><td>23,212</td><td>18,833</td><td>19,003</td><td>Am28 185</td><td></td></td<> | At3gCDbox92.1 | AtU27-2 | 23,212 | 18,833 | 19,003 | Am28 185 | | | |
| At3gCbox93.1 AtsnoR32-1 23,849 21,273 20,109 Am130_185 Um1266_185 At3gCbox94.1 AtsnoR1a 30,39 24,173 23,505 Am1579_185 Um1264_185 At3gCbox94.2 AtsnoR1b 62,69 53,47 52,88 Gm2792_255 M10264_185 At3gCbox95.3 AtsnoR1b 62,69 53,47 52,88 Gm2792_255 Um1264_185 At3gCbox96.3 AtsnoR1b2 06,73 95,050 Am1579_185 Um1264_255 At3gCbox98.1 AtsnoR1b2 101 98 86 Gm1434_185 Um1284_255 At3gCbox98.1 AtsnoR2b-1 30,894 227,990 221,098 Um1284_255 At3gCbox10.1 AtsnoR8h4 4272 3732 Gm2206_255 Am225_255 At3gCbox10.1 AtsnoR8h3 32,59 25,91 25,280 Am225_255 Am127_255 At3gCbox10.5 AtsnoR18h 32,569 25,91 25,280 Am162_185 Am225_255 Am162_185 At3gCbox10.5 AtsnoR18b 119,756 101,487 93,44 Am235_255 Am162_185 At | At3gCDbox92.2 | AtU27-1 | 88,895 | 73,932 | 71,541 | Am28_18S | | | |
| At3gCbox94.1 AtsnoR1a 30,339 24,173 23,591 Gm2792_255 At3gCbox94.2 AtsnoR8a 114,527 67,378 55,000 Am1579_185 Um126_185 At3gCbox94.2 AtsnoR8b 114,527 67,378 55,000 Am1579_185 Um126_185 At3gCbox94.2 AtsnoR172 36 41 40 Um126_185 Um126_185 At3gCbox94.3 AtsnoR172 36 41 40 Um144_185 Um126_185 At3gCbox99.1 AtsnoR0-1 30,894 227,990 221,090 Um103_185 Um103_185 At3gCbox100.1 AtsnoR2+1 102,352 72,888 66,762 Gm2361_6,255 Am1377_255 At3gCbox10.1 AtsnoR18a 13,755 77 12 Am227_255 Am227_255 At3gCbox10.3 AtsnoR18a 13,756 101,487 93,449 Am293_255 Am162_185 At3gCbox10.5 AtsnoR18a 13,757 710 8 Ma2Gbbox13 AtsnoR18a 114,793 97,592 94,243 Am126_185 Ma162_185 At3gCbbox13 AtsnoR63 102,000 < | At3gCDbox93.1 | AtsnoR32-1 | 23,849 | 21,273 | 20,109 | Am1330_18S | Um1266_18S | | |
| AtagCbbox/51 AtsnoR8a 114,537 96,738 95,050 Am1570_185 Um1264_185 AtagCbbox/52 AtsnoR8b 114,537 96,738 95,050 Am1570_185 Um1264_185 AtagCbbox/52 AtsnoR72c 36 41 40 Um1484_185 Um1284_185 AtagCbbox/51 AtsnoR64 4272 3732 3905 Um1284_185 Um1381 AtagCbbox/91 AtsnoR64 4272 3732 3905 Um1013_185 AtagCbbox/91 AtsnoR74 101.52 71,018 54,899 52,322 Gm2816_255 Am2257_255 AtagCbbox/101 AtsnoR148 32,599 25,911 25,200 Am229_255 Am162_185 AtgCbbox/105.1 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 AtgCbbox/105.1 AtsnoR18b 12,757 56,450 56,188 Um1067_255 Am545_185 AtgCbbox/13 AtsnoR63 102,050 85,752 80,379 AtgCbbox/3 AtsnoR64 12,264 12,449 | At3gCDbox94.1 | AtsnoR1a | 30,339 | 24,173 | 23,591 | Gm2792_25S | | | |
| At3gCbox94.2 AtsnoR8b 6269 5347 5288 Gm2792_255 At3gCbbox95.2 AtsnoR8b 114,573 96,783 95,000 AtsnoR84 Um1244_185 At3gCbbox96.3 AtsnoR872 36 41 40 Um284_255 At3gCbbox97.1 AtsnoR84 4272 3732 3905 Um1484_185 At3gCbbox99.1 AtsnoR84 4272 3732 3905 Um1013_185 At3gCbbox100.1 AtsnoR82-1 30,084 227,90 221,981 Um1013_185 Am1377_255 At3gCbbox102.1 AtsnoR82-2 71,018 54,889 52,322 Gm228_255 Am1257_255 At3gCbbox105.1 AtsnoR18a 13,756 10,487 93,494 Am2935_255 Am162_185 At4gCbbox105.1 AtsnoR18a 13,756 10,487 93,494 Am2935_255 Am162_185 At4gCbbox103.1 AtsnoR18a 12,757 56,405 56,188 Um1067_255 Am545_185 At4gCbbox13.3 AtsnoR36 94,730 75,162 70,439 Um144_255 4460Cbbox34 At4gCbbbox33 AtU36a-4 | At3gCDbox95.1 | AtsnoR8a | 114,537 | 96,738 | 95,050 | Am1579_18S | Um1264_18S | | |
| AtagCbbx/s5.2 AtsnoR72c 36 41 40 AtagCbbx/S0.3 AtsnoR72c 36 41 40 AtagCbbx/S0.1 AtsnoR64 4272 3732 3905 Um1848_185 AtagCbbx/S0.1 AtsnoR64 4272 3732 3905 Um1013_185 AtagCbbx/S0.1 AtsnoR64 4272 3732 3905 Um1013_185 AtagCbbx/10.1 AtsnoR7-2 34,200 29,003 27,824 Cm286_255 Am2282_255 AtagCbbx/10.1 AtsnoR87-2 34,2569 25,911 25,820 Am2935_255 Am2282_255 AtagCbbx/10.1 AtsnoR18a 32,569 25,911 25,800 Am2935_255 Am162_185 AtagCbbx/10.1 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 AtagCbbx/10.1 AtsnoR18b 119,756 56,450 56,188 Um1067_255 Am545_185 AtagCbbx/13 AtsnoR6-3 102,050 85,752 80,379 Am2421_255 AtagCbbx/13 Atu36-3< | At3gCDbox94.2 | AtsnoR1b | 6269 | 5347 | 5288 | Gm2792_25S | | | |
| AtsgQDbox/b.3 AtsnoR1/2 30 41 40 AtsgQDbox/8.1 AtsnoR19-2 101 98 86 Gm1434_185 Um284_255 AtsgQDbox/9.1 AtsnoR20-1 300.894 227,990 221,098 Um1013_185 AtsgQDbox/10.1 AtsnoR20-1 300.894 227,990 221,098 Cm473_185 Am1377_255 AtsgQDbox/10.1 AtsnoR38Y-1 102,352 72,884 66,762 Gm2816_255 Am2257_255 AtsgQDbox/10.1 AtsnoR1Msa0 874 755 712 Am2257_255 Am2257_255 AtsgQDbox/10.2 AtsnoR18a 32,569 25,911 25,282 Am2935_255 Am162_185 AtsgQDbox/10.1 AtsnoR18a 32,569 25,911 93,449 Am2935_255 Am162_185 AtsgQDbox/10.2 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 AtsgQDbox/10.1 AtsnoR18b 119,756 56,450 56,188 Um106_7_255 Am55_185 AtsgQDbox/23 AtsnoR63 94,730 75,162 70,439 Um144_255 Am221_255 Am221_255 Am22 | At3gCDbox95.2 | AtsnoR8b | 114,537 | 96,738 | 95,050 | Am1579_18S | Um1264_185 | | |
| Arag Dbox/8.1 Attsnoft-92 101 98 80 Gm (H44, 165) Um (H48, 165) Arag Obox/8.1 Attsnoft-92 101 30.894 227,990 Um (101, 165) Arag Obox/10.1 Attsnoft-84 4272 3732 3905 Um (101, 165) Arag Obox/10.1 Attsnoft-72 34,720 29,003 27,824 Gm 228,255 Am 228,255 Arag Obox/10.1 Attsnoft-72 34,720 29,003 27,824 Gm 228,255 Am 127,255 Arag Obox/10.1 Attsnoft-72 34,720 29,003 27,824 Gm 228,255 Am 162,185 Arag Obox/10.1 Attsnoft-88 32,569 25,911 25,80 Am 235,255 Am 162,185 Arag Obox/10.1 Attsnoft-88 19,756 101,487 94,44 Am 235,255 Am 162,185 Arag Obox/10.1 Attsnoft-8 19,750 56,450 56,188 Um 1067,255 Am 54,185 Arag Obox/3.3 Att/36-3 17,733 97,552 80,379 Um 144,255 Arag Obox/3.3 Att/36-4 <td>At3gCDbox96.3</td> <td>AtsnoR/2c</td> <td>36</td> <td>41</td> <td>40</td> <td>C == 1 42 4 10C</td> <td>14.0 100</td> | At3gCDbox96.3 | AtsnoR/2c | 36 | 41 | 40 | C == 1 42 4 10C | 14.0 100 | | |
| AlsgLDbox8.1 Atsin020-1 30.084 227,990 Um1013_185 AlsgCDbox991 Atsin020-1 30.084 227,990 227,990 27,824 Gm2816_255 AlsgCDbox100.1 Atsin072-2 34,720 29,003 27,824 Gm473_185 An1377_255 AlsgCDbox102.1 Atsin072-2 71,018 54,889 52,322 Gm2289_255 Am2257_255 AlsgCDbox104.1 Atsin0714RsinoRNA30 874 755 712 Am2257_255 Am162_185 AlsgCDbox105.1 AtsinoR18b 119,756 11,487 93,449 An2935_255 Am162_185 AlsgCDbox105.1 AtsinoR18b 119,756 11,487 93,449 Am2935_255 Am162_185 AlsgCDbox108.1 AtsinoR63 94,730 75,162 70,439 Um104_255 Am545_185 AlsgCDbox13.3 AtsinoR63 102,050 85,752 80,379 Am221_255 AlsgCDbox443.3 AtsinoR32-2 1727 1580 Am1143_255 AlsgCDbox453.3 AtsinoR32-2 174 | At3gCDbox97.1 | AtsnoR19-2 | 101 | 98 2222 | 86 | Gm1434_185 | Um1448_185 | | |
| At3gCbbox/100.1 AtsnoR38Y-1 102,352 72,888 66,762 Gm2816_255 At3gCbbx/102.1 AtsnoR7-2 34,720 29,003 27,824 Gm473_185 Am1377_255 At3gCbbx/103.1 AtU15-2 71,018 54,889 52,332 Gm2289_255 Am2282_255 At3gCbbx/105.1 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 At3gCbbx/105.1 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 At4gCbbx/10.1 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am545_185 At4gCbbx/10.1 AtsnoR6-3 102,650 85,752 80,379 M144_255 At4gCbbx/3.3 AtU38-3 117,493 97,592 94,243 Am1143_255 Am221_255 At4gCbbx/3.3 AtU38-3 117,493 97,592 94,243 Am1143_255 Am221_255 At4gCbbx/3.3 AtU38-3 117,493 97,592 94,243 Am128_2 S7 At4gCbbx/3.3 AtU38-3 <td>AL3GCDD0X98.1</td> <td>ALSNOR04</td> <td>4272</td> <td>3/32</td> <td>3905</td> <td></td> <td>UM2884_255</td> | AL3GCDD0X98.1 | ALSNOR04 | 4272 | 3/32 | 3905 | | UM2884_255 | | |
| At3gCDbox102.1 Atsnob101-1 102.022 72.003 0.72 0.112.002.05 Am1377_255 At3gCDbox102.1 Attsnob172 71.018 54.889 52.322 Gm2289_255 Am2287_255 At3gCDbox104.1 Atsnob18a 32.569 25.911 25.280 Am295_255 Am162_185 At3gCDbox105.2 Atsnob18b 119.756 56.450 56.188 Um1067_255 Am545_185 At4gCDbox107.1 At41Y 75.750 56.450 56.188 Um1067_255 Am545_185 At4gCDbox108.1 AtsnoR18b 117.493 97.592 94.243 Am1143_255 Am2221_255 At4gCDbox2.3 At1336-4 12.645 12.449 12.223 Ma280_255 Am221_255 At4gCDbox3.3 At136-4 12.645 12.449 12.223 Ma2221_255 At420Dbox16.1 Am2221_255 At4gCDbox3.3 At136-4 12.645 12.449 12.223 Ma1263_255 Gm917_255 At420Dbox54.3 At14049-3 32 20 18 Am1330_185 Um1266_185 At420Dbox92.3 Atsno7AlRsnoNA322 3145 2915 | At3gCDbox99.1 | AtspoP38V-1 | 102 322 | 227,990 | 66 762 | Gm2816 255 | 0111015_185 | | |
| ArageDox/10.1 Attults-2 71,018 24,805 25.7 Gm/2-0.5 Am2257 ArageDox/10.1 Attsno71AlksnoRNA30 874 755 712 Am2257_255 ArageDox/10.1 Attsno71AlksnoRNA30 874 755 712 Am2935_255 Am162_185 ArageDox/10.1 Attsno7181b 119,756 101,487 93,449 Am2935_255 Am162_185 ArageDox/10.1 Attsno7181b 17,756 101,487 93,449 Am2935_255 Am162_185 ArageDox/10.1 Attan0816 94,730 75,162 70,439 Um1067_255 Am545_185 ArageDox/13 Attan086-3 102,050 85,752 80,379 Min144_255 ArageDox/13 Attan086-3 102,050 85,752 80,379 Am1225 ArageDox/14 15,554 16,083 44620box/3 Attu38-3 117,493 97,223 4331 Am1143_255 ArageDox/32 AttsnoR32-2 1727 1580 1531 Am1330_185 Um1266_185 AradgObox/92.3 | At3gCDbox100.1 | AtsnoB7-2 | 34 720 | 2,000 | 27 824 | Cm473 18S | Am1377 255 | | |
| At3GCDbax104.1 AtsnoTARsnoRNA30 874 755 712 Att2005 Att2257_255 At3GCDbax105.1 AtsnoR18a 32,569 25,911 25,280 Am2935_255 Am162_185 At3GCDbax105.2 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 At4GCDbax11.3 U3 16 17 14 | At3gCDbox102.1 | AtU15-2 | 71 018 | 54 889 | 52 322 | Gm2289_255 | Am2282 255 | | |
| At3gCDbxx105.1 AtsnoR18a 32,559 25,911 25,280 Am2935_255 Am162_185 At3gCDbxx105.2 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 At4gCDbx11.3 U3 16 17 14 T T 14 At4gCDbx107.1 At41Y 75,750 56,450 56,188 Um1067_255 Am545_185 At4gCDbx108.1 AtsnoR36 94,730 75,162 70,439 Um144_255 At4gCDbx33 AtU36a-4 12,645 12,449 12,223 Am2221_255 At4gCDbx33 AtU49-3 32 20 18 Cm2880_255 Gm917_255 At4gCDbx33 AtU49-3 32 20 18 Cm2880_255 Gm917_255 At4gCDbx043.2 AtsnoR82-2 1727 1580 1531 Am1330_185 Um1266_185 At4gCDbx049.2 AtsnoR12-2 189 1340 1414 Am826_255 Gm917_255 At4gCDbx049.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 At4gCDbx0110.1 AtsnoR22-2 | At3gCDbox104.1 | AtsnoTAIRsnoRNA30 | 874 | 755 | 712 | 0207_200 | Am2257 25S | | |
| At3_GCbbx(105.2 AtsnoR18b 119,756 101,487 93,449 Am2935_255 Am162_185 At4qCDbx(17.1 At41Y 75,750 56,450 56,188 Um1067_255 Am545_185 At4qCDbx(107.1 At41Y 75,750 56,450 56,188 Um1067_255 Am545_185 At4qCDbx(18.1 AtsnoR6-3 102,050 85,752 80,379 M144_255 At4qCDbx3.3 AtU38-3 117,493 97,592 94,243 Am1143_255 Am2221_255 At4qCDbx3.3 AtU49-3 32 20 18 Cm2880_255 M2221_255 At4qCDbx083.2 AtsnoR32-2 1727 1580 1531 Am130_185 Um1266_185 At4qCDbx083.2 AtsnoR32-2 1727 1580 1531 Am223_255 Gm917_255 At4qCDbx081.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 At4qCDbx081.2 AtsnoR22-3 3739 3730 3522 M1758_185 M1758_185 At4qCDbx0411.2 AtsnoR22-30 174 194 224 Am1263_255 Um1278_255 A | At3qCDbox105.1 | AtsnoR18a | 32,569 | 25,911 | 25,280 | Am2935_25S | Am162_18S | | |
| At4gCDbox11.3 U3 16 17 14 At4gCDbox107.1 At41Y 75,750 56,450 56,188 Um1067,255 Am545_185 At4gCDbox108.1 AtsnoR36 94,730 75,162 70,439 Um144_255 At4gCDbox108.1 AtsnoR6-3 102,050 85,752 80,379 Am123_255 At4gCDbox3.3 AtU36a-4 12,645 12,449 12,223 Am2221_255 At4gCDbox3.3 AtU49-3 32 20 18 Cm2880_255 Am2221_255 At4gCDbox93.2 AtsnoR32-2 1727 1580 1531 Am130_185 Um1266_185 At4gCDbox92.3 AtsnoR32-2 1892 1340 1414 Am826_255 Gm917_255 At4gCDbox91.2 Atu80-2 1892 1340 1414 Am826_255 Gm917_255 At4gCDbox91.2 AtsnoR2-2 3739 3730 3522 M178_2185 M178_2185 At4gCDbox111.1 AtsnoR2-3 19,137 17,750 17,045 Am1758_185 At4gCDbox112.1 Atu800.2 5,027 4993 34957 Gm212_255 <td< td=""><td>At3gCDbox105.2</td><td>AtsnoR18b</td><td>119,756</td><td>101,487</td><td>93,449</td><td>Am2935_25S</td><td>Am162_18S</td></td<> | At3gCDbox105.2 | AtsnoR18b | 119,756 | 101,487 | 93,449 | Am2935_25S | Am162_18S | | |
| At4gCDbox107.1 At41Y 75,750 56,450 56,188 Um1067_25S Am545_185 At4gCDbox108.1 AtsnoR6-3 102,050 85,752 80,379 Um144_25S At4gCDbox2.3 AtU38-3 117,493 97,592 80,379 Am221_25S At4gCDbox3.3 AtU38-3 117,493 97,592 94,243 Am1143_25S Am221_25S At4gCDbox9.3 AtU49-3 32 20 18 Cm2880_25S Am221_25S At4gCDbox93.2 AtsnoR32-2 1727 1580 1531 Am1330_18S Um1266_18S At4gCDbox91.2 AtsnoR32-2 1345 2915 3005 Am28_18S M1728_25S At4gCDbox91.2 AtsnoR2-2 1892 1340 1414 Am826_25S Gm917_25S At4gCDbox91.2 AtsnoR2-3 19,137 17,705 17,045 Am1758_18S At4gCDbox94.4 AtsnoR2-3 19,137 17,705 17,045 Am1758_18S At4gCDbox94.4 AtsnoR2-3a 18,14 722 770 Am1263_2SS Um1278_2SS At4gCDbox112.1 AtsnoR2-3a 174 | At4gCDbox11.3 | U3 | 16 | 17 | 14 | | | | |
| At4gCDbox108.1 AtsnoR36 94,730 75,162 70,439 Um144_255 At4gCDbox13 AtsnoR6-3 102,050 85,752 80,379 Att3255 At4gCDbox23 AtU38-3 117,493 97,592 94,243 Am1143_255 At4gCDbox54.3 AtU36-4 12,645 12,449 12,223 Am2221_255 At4gCDbox54.3 AtU49-3 32 20 18 Cm2880_255 At4gCDbox54.3 AtsnoR32-2 1727 1580 1531 Am130_185 Um1266_185 At4gCDbox92.3 AtsnoR32-2 1892 1340 1414 Am826_255 Gm917_255 At4gCDbox91.2 AtU80-2 1892 1340 1414 Am826_255 Um1278_255 At4gCDbox91.2 AtsnoR2-3 19,137 17,750 70 Am1263_255 Um1278_255 At4gCDbox111.1 AtsnoR2-3a 19,137 17,750 17,045 Am1263_255 Um1278_255 At4gCDbox112.1 Atu08.2 50,77 4993 4957 Gm2125_255 M1278_255 At4gCDbox112.1 Atu60.2 F 50,27 4993 495 | At4gCDbox107.1 | At41Y | 75,750 | 56,450 | 56,188 | Um1067_25S | Am545_18S | | |
| At4gCDbox1.3 AtsnoR6-3 102,050 85,752 80,379 At4gCDbox2.3 AtU38-3 117,493 97,592 94,243 Am1143_25S At4gCDbox3.3 AtU36a-4 12,645 12,449 12,223 Am221_25S At4gCDbox10.1 18,344 15,554 16,083 Image: Comparison of Compari | At4gCDbox108.1 | AtsnoR36 | 94,730 | 75,162 | 70,439 | | Um144_25S | | |
| At4gCDbox2.3 AtU38-3 117,493 97,592 94,243 Am1143_255 At4gCDbox3.3 AtU36a-4 12,645 12,449 12,223 Am221_255 At4gCDbox3.3 AtU49-3 32 20 18 Cm2880_255 At4gCDbox93.2 AtsnoR32-2 1727 1580 1531 Am1330_185 Um1266_185 At4gCDbox92.3 AtsnoR32-2 145 2915 3005 Am28_185 M1278_255 At4gCDbox91.2 Atu80-2 1892 1340 1414 Am826_255 Gm917_255 At4gCDbox89.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 At4gCDbox89.4 AtsnoR23-3 19,137 17,750 17,045 Am1758_185 At4gCDbox89.3 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 At4gCDbox111.1 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 At4gCDbox112.1 Att060.2 F 5027 4993 4957 Gm2125_255 Cm1447_255 At4gCDbox112.1 Att060.2 F 502758 53,486 </td <td>At4gCDbox1.3</td> <td>AtsnoR6-3</td> <td>102,050</td> <td>85,752</td> <td>80,379</td> <td></td> <td></td> | At4gCDbox1.3 | AtsnoR6-3 | 102,050 | 85,752 | 80,379 | | | | |
| At4gCbbox3.3 At036a-4 12,645 12,449 12,223 Am221_225 At4gCbbox54.3 At49Cbbox54.3 At49Cbbox54.3 At49Cbbox54.3 At19,554 16,083 At4gCbbox93.2 AtsnoR32-2 1727 1580 1531 Am1330_185 Um1266_185 At4gCbbox92.3 AtsnoR1A8noRNA32 3145 2915 3005 Am28_185 At4gCbbox92.3 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 At4gCbbox91.2 AtsnoR22-3 3739 3730 3522 Am1758_185 Am1758_185 At4gCbbox91.11.1 AtsnoR32-33 19,137 17,750 17,045 Am1263_255 Um1278_255 At4gCbbox89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 At4gCbbox112.1 AtU60.2 F 5027 4993 4957 Gm2125_255 Um1278_255 At4gCbbox113.1 AtU60.2 F 5027 4993 4957 Gm2125_255 Cm147_255 At4gCbbox114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 Cm2837_255 | At4gCDbox2.3 | AtU38-3 | 117,493 | 97,592 | 94,243 | Am1143_25S | 1 0001 075 | | |
| AtdgCDbox34.3 AtU49.3 3.2 2.0 18 Cm2880_255 AtdgCDbox93.2 AtsnoR32-2 1727 1580 1531 Am1330_185 Um1266_185 AtdgCDbox93.2 AtsnoTAIRsnoRNA32 3145 2915 3005 Am28_185 AtdgCDbox89.2 AtsnoR2-2 1892 1340 1414 Am826_255 Gm917_255 AtdgCDbox89.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 AtdgCDbox89.3 AtsnoR23-3 19,137 17,750 17,045 Am1758_185 AtdgCDbox89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 AtdgCDbox89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 AtdgCDbox112.1 AttoR2-5a 8144 725 Gm2125_255 Cm1447_255 AtdgCDbox113.1 AttO24-1 17,050 12712 12,613 Am1459_255 Cm1447_255 AtdgCDbox114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 AtdgCDbox114.2 AtsnoR24d 10,657 </td <td>At4gCDbox3.3</td> <td>AtU36a-4</td> <td>12,645</td> <td>12,449</td> <td>12,223</td> <td>6 2000 256</td> <td>Am2221_255</td> | At4gCDbox3.3 | AtU36a-4 | 12,645 | 12,449 | 12,223 | 6 2000 256 | Am2221_255 | | |
| At4gCDbox110.1 16,344 15,354 16,063 At4gCDbox93.2 AtsnoR32-2 1727 1580 1531 Am1330_18S Um1266_18S At4gCDbox91.2 Atus0-2 1892 1340 1414 Am826_25S Gm917_25S At4gCDbox91.2 Atus0-2 249 245 283 Am1263_25S Um1278_25S At4gCDbox111.1 AtsnoR23-2 3739 3730 3522 Am1758_18S At4gCDbox111.2 AtsnoR23-3 19,137 17,750 17,045 Am1758_18S At4gCDbox89.3 AtsnoR22-3b 174 194 224 Am1263_25S Um1278_25S At4gCDbox89.4 AtsnoR22-3a 814 722 770 Am1263_25S Um1278_25S At4gCDbox113.1 AtU60.2 F 5027 4993 4957 Gm2125_25S Cm147_25S At4gCDbox114.1 AtsnoR12-1b 80,996 52,758 53,486 Am2127_25S Am945_25S At4gCDbox114.2 AtsnoR12-1a 39,043 26,538 26,191 Am2127_25S Am945_25S At4gCDbox115.1 AtsnoR24d 10,657 8288 | At4gCDbox54.3 | At049-3 | 32 | 20 | 16 002 | Cm2880_255 | | | |
| AtdgCbbox92.2 AtsinoR322 172 1500 1531 Atm326_163 011200_163 AtdgCbbox92.3 AtsinoR1ARsnoRNA32 3145 2915 3005 Am38_185 AtdgCbbox89.2 AtsinoR22-2 249 245 283 Am1263_255 Um1278_255 AtdgCbbox91.1.1 AtsinoR23-2 3739 3730 3522 Am1758_185 AtdgCbbox89.3 AtsinoR22-3b 174 194 224 Am1263_255 Um1278_255 AtdgCbbox11.1 AtsinoR22-3a 814 722 770 Am1263_255 Um1278_255 AtdgCbbox112.1 AttloC0_F 5027 4993 4957 Gm2125_255 AtdgCbbox114.1 AtsinoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 AtdgCbbox114.1 AtsinoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 AtdgCbbox115.1 AtsinoR24d 10,657 8288 8309 Cm2837_255 Cm2837_255 AtdgCbbox115.2 AtsinoR24b 18,253 13,263 13,022 Cm2837_255 Cm2837_255 A | At4gCDb0x110.1 | Atono P22 2 | 10,344 | 15,554 | 10,005 | Am1220 195 | Um1266 199 | | |
| ArtgCDb032.3 AtBiol Anishon (NSD2 3143 2915 3003 Anis2103 Anis2103 ArtgCDb0x91.2 AtU80-2 1892 1340 1414 Am826_255 Gm917_255 ArtgCDb0x89.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 ArtgCDb0x89.3 AtsnoR23-3 19,137 17,750 17,045 Am1758_185 ArtgCDb0x89.3 AtsnoR22-3b 174 194 224 Am1263_255 Um1278_255 ArtgCDb0x89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 ArtgCDb0x113.1 AttU24-1 17,050 12712 12,613 Am1459_255 Cm1447_255 ArtgCDb0x114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 AtdgCDb0x114.2 AtsnoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 AtdgCDb0x115.1 AtsnoR24c 6282 4477 4456 Cm2837_255 AtdgCDb0x115.2 AtsnoR24b 18,253 13,263 13,022 Cm2837_255 AtdgCDb0x115.4 | At4gCDb0x95.2 | AtspoTAIRspoPNA32 | 31/5 | 2015 | 3005 | Ann 28 185 | 0111200_183 | | |
| ArtgCbbx89.2 AtsnoR22-2 249 245 283 Am1263_255 Um1278_255 ArtgCbbx111.1 AtsnoR23-2 3739 3730 3522 Am1758_185 ArtgCbbx89.2 AtsnoR23-3 19,137 17,750 17,045 Am1263_255 Um1278_255 ArtgCbbx89.3 AtsnoR22-3b 174 194 224 Am1263_255 Um1278_255 ArtgCbbx89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 ArtgCbbx112.1 AtU60.2 F 5027 4993 4957 Gm2125_255 Um1278_255 ArtgCbbx114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 ArtgCbbx114.1 AtsnoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 ArtgCbbx115.1 AtsnoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 ArtgCbbx115.2 AtsnoR24d 10,657 8288 8309 Cm2837_255 AttgCbbx15.3 AtsnoR24a 12,920 9877 9467 Cm2837_255 AttgCbbx115.3 AtsnoR24a <td< td=""><td>At4gCDbox92.3</td><td>Atli80-2</td><td>1892</td><td>1340</td><td>1414</td><td>Am20_105 Am826_255</td><td>Gm917 255</td></td<> | At4gCDbox92.3 | Atli80-2 | 1892 | 1340 | 1414 | Am20_105 Am826_255 | Gm917 255 | | |
| ArtgCDbox111.1 AtsnoR23-2 3739 3730 3522 Am1758_185 ArtgCDbox111.2 AtsnoR23-3 19,137 17,750 17,045 Am1758_185 ArtgCDbox89.3 AtsnoR22-3b 174 194 224 Am1263_255 Um1278_255 ArtgCDbox112.1 AttoR22-3a 814 722 770 Am1263_255 Um1278_255 ArtgCDbox112.1 AtU60.2 F 5027 4993 4957 Gm2125_255 Gm1447_255 AttgCDbox113.1 AtU24-1 17,050 12712 12,613 Am1459_255 Cm1447_255 AttgCDbox114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 AttgCDbox114.2 AtsnoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 AttgCDbox115.1 AtsnoR24d 10,657 8288 8309 Cm2837_255 AttgCDbox115.2 AtsnoR24c 6282 4477 4456 Cm2837_255 AttgCDbox115.2 AtsnoR24a 12,920 9877 9467 Cm2837_255 AttgCDbox175.4 AtsnoR102-2 420 355 379 <t< td=""><td>At4gCDbox89.2</td><td>AtsnoB22-2</td><td>249</td><td>245</td><td>283</td><td>Am1263_255</td><td>Um1278 255</td></t<> | At4gCDbox89.2 | AtsnoB22-2 | 249 | 245 | 283 | Am1263_255 | Um1278 255 | | |
| At4gCDbox111.2 AtsnoR23-3 19,137 17,750 17,045 Am1758_185 At4gCDbox89.3 AtsnoR22-3b 174 194 224 Am1263_255 Um1278_255 At4gCDbox89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 At4gCDbox112.1 AtU60.2 F 5027 4993 4957 Gm2125_255 At4gCDbox114.1 AttonR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 At4gCDbox114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_255 Am945_255 At4gCDbox115.1 AtsnoR12-1a 39,043 26,538 26,191 Am2127_255 Am945_255 At4gCDbox115.1 AtsnoR24d 10,657 8288 8309 Cm2837_255 At4gCDbox115.2 AtsnoR24c 6282 4477 4456 Cm2837_255 At4gCDbox115.3 AtsnoR24a 12,920 9877 9467 Cm2837_255 At4gCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm2837_255 At4gCDbox115.4 AtsnoR102-2 420 355 | At4gCDbox111.1 | AtsnoR23-2 | 3739 | 3730 | 3522 | / | Am1758 18S | | |
| At4gCDbox89.3 AtsnoR22-3b 174 194 224 Am1263_255 Um1278_255 At4gCDbox89.4 AtsnoR22-3a 814 722 770 Am1263_255 Um1278_255 At4gCDbox112.1 AtU60.2 F 5027 4993 4957 Gm2125_255 | At4gCDbox111.2 | AtsnoR23-3 | 19,137 | 17,750 | 17,045 | | Am1758 18S | | |
| AtagCDbox89.4AtsnoR22-3a814722770Am1263_25SUm1278_25SAt4gCDbox112.1AtU60.2 F502749934957Gm2125_2SSAt4gCDbox113.1AtU24-117,0501271212,613Am1459_2SSCm1447_2SSAt4gCDbox114.1AtsnoR12-1b80,89652,75853,486Am2127_2SSAm945_2SSAt4gCDbox114.2AtsnoR12-1a39,04326,53826,191Am2127_2SSAm945_2SSAt4gCDbox115.1AtsnoR24d10,65782888309Cm2837_2SSAt4gCDbox115.2AtsnoR24c628244774456Cm2837_2SSAt4gCDbox115.3AtsnoR24a12,92098779467Cm2837_2SSAt4gCDbox115.4AtsnoR102-2420355379At4gCDbox118.1AtsnoTAIRsnoRNA3370,72161,80460,659Um2494_2SSAt4gCDbox118.1AtsnoTAIRsnoRNA3480,58765,55065,323Um2494_2SSAt4gCDbox120.1AtU14a224618311760Cm418_18SAt4gCDbox120.2AtU14b852693758Cm418_18SAt4gCDbox120.3AtU14c236318281793Cm418_18SAt4gCDbox120.4AtU14d837565566362Cm418_18S | At4gCDbox89.3 | AtsnoR22-3b | 174 | 194 | 224 | Am1263_25S | Um1278_255 | | |
| At4gCDbox112.1AtU60.2 F502749934957Gm2125_25SAt4gCDbox113.1AtU24-117,0501271212,613Am1459_25SCm1447_25SAt4gCDbox114.1AtsnoR12-1b80,89652,75853,486Am2127_25SAm945_25SAt4gCDbox114.2AtsnoR12-1a39,04326,53826,191Am2127_25SAm945_25SAt4gCDbox115.1AtsnoR24d10,65782888309Cm2837_25SAt4gCDbox115.2AtsnoR24c628244774456Cm2837_25SAt4gCDbox115.3AtsnoR24b18,25313,26313,022Cm2837_25SAt4gCDbox115.4AtsnoR24a12,92098779467Cm2837_25SAt4gCDbox115.1AtsnoR102-2420355379Cm2837_25SAt4gCDbox117.1AtsnoTAIRsnoRNA3370,72161,80460,659Um2494_25SAt4gCDbox118.1AtsnoTAIRsnoRNA3480,58765,55065,323Um2494_25SAt4gCDbox120.1AtU14a224618311760Cm418_18SAt4gCDbox120.2AtU14b852693758Cm418_18SAt4gCDbox120.3AtU14c236318281793Cm418_18SAt4gCDbox120.4AtU14d837565566362Cm418_18S | At4gCDbox89.4 | AtsnoR22-3a | 814 | 722 | 770 | Am1263_25S | Um1278_25S | | |
| At4gCDbox113.1AtU24-117,0501271212,613Am1459_25SCm1447_25SAt4gCDbox114.1AtsnoR12-1b80,89652,75853,486Am2127_25SAm945_25SAt4gCDbox114.2AtsnoR12-1a39,04326,53826,191Am2127_25SAm945_25SAt4gCDbox115.1AtsnoR24d10,65782888309Cm2837_25SAt4gCDbox115.2AtsnoR24c628244774456Cm2837_25SAt4gCDbox115.3AtsnoR24b18,25313,26313,022Cm2837_25SAt4gCDbox115.4AtsnoR24a12,92098779467Cm2837_25SAt4gCDbox117.1AtsnoR102-2420355379At4gCDbox117.1AtsnoTAIRsnoRNA3370,72161,80460,659Um2494_25SAt4gCDbox118.1AtsnoTAIRsnoRNA3480,58765,55065,323Um2494_25SAt4gCDbox120.1AtU14a224618311760Cm418_18SAt4gCDbox120.2AtU14b852693758Cm418_18SAt4gCDbox120.3AtU14c236318281793Cm418_18SAt4gCDbox120.4AtU14d837565566362Cm418_18S | At4gCDbox112.1 | AtU60.2 F | 5027 | 4993 | 4957 | Gm2125_25S | | | |
| AttgCDbox114.1 AtsnoR12-1b 80,896 52,758 53,486 Am2127_25S Am945_25S AttgCDbox114.2 AtsnoR12-1a 39,043 26,538 26,191 Am2127_25S Am945_25S AttgCDbox115.1 AtsnoR24d 10,657 8288 8309 Cm2837_25S AttgCDbox115.2 AtsnoR24c 6282 4477 4456 Cm2837_25S AttgCDbox115.3 AtsnoR24b 18,253 13,022 Cm2837_25S AttgCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm2837_25S AttgCDbox117.1 AtsnoR102-2 420 355 379 Cm2837_25S AttgCDbox117.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um2494_25S AttgCDbox118.1 AtsnoTAIRsnoRNA34 80,587 65,550 65,323 Um2494_25S AttgCDbox120.1 AtU14a 2246 1831 1760 Cm418_18S AttgCDbox120.2 AtU14b 852 693 758 Cm418_18S AttgCDbox120.3 AtU14c 2363 1828 1793 Cm418_18S | At4gCDbox113.1 | AtU24-1 | 17,050 | 12712 | 12,613 | Am1459_25S | Cm1447_25S | | |
| AttgCUbox114.2 AtsnoR12-1a 39,043 26,538 26,191 Am2127_25S Am945_25S AttgCDbox115.1 AtsnoR24d 10,657 8288 8309 Cm2837_25S AttgCDbox115.2 AtsnoR24c 6282 4477 4456 Cm2837_25S AttgCDbox115.3 AtsnoR24b 18,253 13,263 13,022 Cm2837_25S AttgCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm2837_25S AttgCDbox117.1 AtsnoR102-2 420 355 379 AttgCDbox118.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um2494_25S AttqCDbox120.1 AttU14a 2246 1831 1760 Cm418_18S AttqCDbox120.2 AtU14b 852 693 758 Cm418_18S AttqCDbox120.3 AtU14c 2363 1828 1793 Cm418_18S AttqCDbox120.4 AtU14d 8375 6556 6362 Cm418_18S | At4gCDbox114.1 | AtsnoR12-1b | 80,896 | 52,758 | 53,486 | Am2127_255 | Am945_25S | | |
| At4gcubox115.1 AtsnoR24d 10,65/ 8288 8309 Cm2837_255 At4gCDbox115.2 AtsnoR24c 6282 4477 4456 Cm2837_255 At4gCDbox115.3 AtsnoR24b 18,253 13,263 13,022 Cm2837_255 At4gCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm2837_255 At4gCDbox115.4 AtsnoR102-2 420 355 379 Cm2837_255 At4gCDbox117.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um2494_255 At4gCDbox118.1 AtsnoTAIRsnoRNA34 80,587 65,550 65,323 Um2494_255 At4gCDbox120.1 AtU14a 2246 1831 1760 Cm418_185 At4gCDbox120.2 AtU14b 852 693 758 Cm418_185 At4gCDbox120.3 AtU14c 2363 1828 1793 Cm418_185 At4gCDbox120.4 AtU14d 8375 6556 6362 Cm418_185 | At4gCDbox114.2 | AtsnoR12-1a | 39,043 | 26,538 | 26,191 | Am2127_255 | Am945_25S | | |
| At4gc_Dbox115.2 AtsnoR24c 6282 44// 4456 Cm2837_25S At4gCDbox115.3 AtsnoR24b 18,253 13,263 13,022 Cm2837_25S At4gCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm2837_25S At4gCDbox14.2 AtsnoR102-2 420 355 379 | At4gCDbox115.1 | AtsnoR24d | 10,657 | 8288 | 8309 | | Cm2837_255 | | |
| Attragebox 115.3 Atsiton 240 18,233 13,203 13,022 Cm/2837_255 AttgCDbox115.4 AtsnoR24a 12,920 9877 9467 Cm/2837_255 AttgCDbox44.2 AtsnoR102-2 420 355 379 AttgCDbox117.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um/2494_25S AttgCDbox118.1 AtsnoTAIRsnoRNA34 80,587 65,550 65,323 Um/2494_25S AttgCDbox120.1 AtU14a 2246 1831 1760 Cm418_18S AttgCDbox120.2 AtU14b 852 693 758 Cm418_18S AttgCDbox120.3 AtU14c 2363 1828 1793 Cm418_18S AttgCDbox120.4 AtU14d 8375 6556 6362 Cm418_18S | At4gCDbox115.2 | AtsnoK24C | 6282 | 44// | 4456 | | Cm2837_255 | | |
| AttagCDb0x113.4 Atsinon24a 12,920 9877 9467 Cm2837_255 AttagCDb0x14.2 AtsnoR102-2 420 355 379 AttagCDb0x117.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um2494_25S AttagCDb0x118.1 AtsnoTAIRsnoRNA34 80,587 65,550 65,323 Um2494_25S AttagCDb0x120.1 AtU14a 2246 1831 1760 Cm418_18S AttagCDb0x120.2 AtU14b 852 693 758 Cm418_18S AttagCDb0x120.3 AtU14c 2363 1828 1793 Cm418_18S AttagCDb0x120.4 AtU14d 8375 6556 6362 Cm418_18S | AL49CDD0X115.3 | | 18,253 | 13,203 | 13,022 | | CIII283/_255 | | |
| AttgCDbox117.1 AtsnoTAIRsnoRNA33 70,721 61,804 60,659 Um2494_25S AttgCDbox118.1 AtsnoTAIRsnoRNA34 80,587 65,550 65,323 Um2494_25S AttgCDbox120.1 AtU14a 2246 1831 1760 Cm418_18S AttgCDbox120.2 AtU14b 852 693 758 Cm418_18S AttgCDbox120.3 AtU14c 2363 1828 1793 Cm418_18S AttgCDbox120.4 AtU14d 8375 6556 6362 Cm418_18S | At49CDD0X115.4 | ALSHUKZ4d AtspoP102 2 | 12,920 | 3611 | 9407 270 | | CIII2037_235 | | |
| At4gCDbox118.1 AtsnoTAIRsnoRNA34 80,527 65,550 65,323 Um2494_255 At4gCDbox120.1 AtU14a 2246 1831 1760 Cm418_185 At4gCDbox120.2 AtU14b 852 693 758 Cm418_185 At4gCDbox120.3 AtU14c 2363 1828 1793 Cm418_185 At4gCDbox120.4 AtU14d 8375 6556 6362 Cm418_185 | At4aCDbox1171 | AtsnoTAIRsnoRNA33 | 70 721 | 61 804 | 60 659 | Um2494 255 | | | |
| AttgCDbox120.1 AtU14a 2246 1831 1760 Cm418_185 AttgCDbox120.2 AtU14b 852 693 758 Cm418_185 AttgCDbox120.3 AtU14c 2363 1828 1793 Cm418_185 AttgCDbox120.4 AtU14d 8375 6556 6362 Cm418_185 | At4aCDbox1181 | AtsnoTAIRsnoRNA34 | 80,587 | 65,550 | 65,323 | Um2494_255 | | | |
| At4gCDbox120.2 AtU14b 852 693 758 Cm418_185 At4gCDbox120.3 AtU14c 2363 1828 1793 Cm418_185 At4gCDbox120.4 AtU14d 8375 6556 6362 Cm418_185 | At4aCDhox1201 | Atl114a | 2746 | 1831 | 1760 | | Cm418 185 | | |
| At4gCDbox120.3 AtU14c 2363 1828 1793 Cm418_185 At4gCDbox120.4 AtU14d 8375 6556 6362 Cm418_185 | At4qCDbox120.2 | AtU14b | 852 | 693 | 758 | | Cm418 185 | | |
| At4gCDbox120.4 AtU14d 8375 6556 6362 Cm418_18S | At4gCDbox120.3 | AtU14c | 2363 | 1828 | 1793 | | Cm418_18S | | |
| | At4gCDbox120.4 | AtU14d | 8375 | 6556 | 6362 | | Cm418_18S | | |

Table 2. (Continued).

| Box C/D sRNA | Known Id | CoIP_1 | CoIP_2 | CoIP_3 | Predicted target (5') | Predicted target (3') |
|----------------|-------------------|---------|---------|---------|-----------------------|-----------------------|
| At5gCDbox121.1 | AtU40-2 | 856 | 845 | 765 | | Am2257_25S |
| At5gCDbox122.1 | AtsnoTAIRsnoRNA35 | 40,647 | 35,080 | 36,274 | Am780 18S | — |
| At5gCDbox125.1 | AtsnoTAIRsnoRNA36 | 9618 | 9481 | 8923 | _ | Um44 25S |
| At5gCDbox126.1 | AtsnoTAIRsnoRNA37 | 106,792 | 92,982 | 92,873 | | — |
| At5gCDbox127.1 | AtU36 | 78,308 | 60,602 | 60,263 | | Am623 18S |
| At5aCDbox78.2 | AtsnoR13-1 | 12,081 | 10,646 | 9726 | Um615 18S | Um3301 25S |
| At5gCDbox77.2 | AtU18-1 | 179,675 | 139,901 | 136,562 | Am661_25S | |
| At5aCDbox128.1 | AtU54 | 31,942 | 29,406 | 27,817 | Gm599_18S | |
| At5gCDbox76.2 | At58Y-1 | 82,390 | 80,850 | 77,589 | Cm675_25S | |
| At5gCDbox130.1 | snoR106 | 63,042 | 59,937 | 59,720 | | |
| At5gCDbox131.1 | atsnoR106b | 44,824 | 40,029 | 40,207 | | |
| At5gCDbox132.1 | AtsnoR28-1 c | 5120 | 4176 | 4128 | | |
| At5gCDbox132.2 | AtsnoR28-1b | 11,497 | 10,145 | 9652 | | |
| At5gCDbox133.1 | AtsnoTAIRsnoRNA28 | 68,747 | 61,581 | 57,194 | | |
| At5gCDbox134.1 | AtsnoTAIRsnoRNA39 | 869 | 778 | 645 | | |
| At5gCDbox132.3 | SnoR28-2b | 20 | 12 | 2 | | |
| At5gCDbox24.3 | AtsnoR108 | 1692 | 1400 | 1241 | | |
| At5gCDbox136.1 | AtsnoTAIRsnoRNA40 | 463 | 397 | 355 | | Cm2683 25S |
| At5gCDbox6.2 | AtsnoR9-2 | 13,136 | 13,580 | 12,599 | | Am47 5.8S |
| At5gCDbox5.2 | AtsnoR10-2 | 58,815 | 50,880 | 49,942 | Um2651 25S | _ |
| At5gCDbox137.1 | AtsnoR29-1 | 291,496 | 222,950 | 215,519 | Um2411_25S | Gm2392 25S |
| At5gCDbox138.1 | AtsnoR30 | 156,956 | 127,555 | 122,733 | Gm392 18S | — |
| At5gCDbox139.1 | AtsnoR31 | 71,940 | 54,894 | 48,793 | Am2912 25S | |
| At5gCDbox112.2 | AtU60.1 F | 22,146 | 19,138 | 19,022 | Gm2125 25S | |
| At5gCDbox11.4 | U3 | 658 | 619 | 635 | _ | |
| At5gCDbox11.5 | U3 | 175 | 154 | 154 | | |
| At5gCDbox11.8 | U3 | 1119 | 1093 | 1152 | | |
| At5gCDbox114.3 | AtsnoR12-2 | 331 | 357 | 332 | Am2127_25S | |
| At5gCDbox100.2 | SAtsnoR38Y-2 | 7651 | 8224 | 7944 | Gm2816_25S | |
| At5gCDbox140.1 | AtsnoR20-2 | 438 | 289 | 325 | | |
| At5gCDbox97.2 | AtsnoR19-1 | 23 | 24 | 28 | Gm1434_18S | Um1448_18S |
| At5gCDbox141.1 | AtsnoTAIRsnoRNA42 | 8447 | 8529 | 8296 | Gm246_18S | _ |
| At5gCDbox16.4 | AtsnoR79-3 | 17,608 | 15,165 | 14,993 | Cm2338_25S | Am2327_25S |
| At5gCDbox142.1 | AtsnoR29-2 | 539 | 402 | 378 | Um2411_25S | Gm2392_25S |
| At5gCDbox143.1 | AtsnoTAIRsnoRNA43 | 19,162 | 15,772 | 15,927 | | |
| At5gCDbox144.1 | AtsnoR67 | 93,237 | 79,011 | 80,230 | | Um1264_18S |
| At5gCDbox103.2 | AtU15-1a | 12,819 | 11,273 | 11,365 | Gm2289_25S | Am2282_25S |
| At5gCDbox103.3 | AtU15-1b | 6327 | 6159 | 5853 | Gm2289_25S | Am2282_25S |
| At5gCDbox102.2 | AtsnoR7-1 | 5143 | 3915 | 3799 | Cm473_18S | Am1377_25S |

(Figure 2). LC-MS/MS data did not allow precise discrimination of orthologue(s) co-immuno-precipitating with FIB2-YFP, but clearly detected at least one orthologue of each protein factor. Altogether, these data indicate that FIB2-YFP interacts with C/D-box snoRNP core proteins and likely forms a functional C/D-box snoRNP complex.

Next, to identify C/D snoRNAs in the FIB2-YFP fractions (CoIP_1 to 3), we performed RNA-seq analysis. Total RNAs were extracted from FIB2-YFP CoIP fractions, converted to library and sequenced. Between $7-8.7 \times 10^6$ C/D snoRNA reads are detected in each RNA samples (Figure S3D) and count for a total of 193 C/D snoRNAs (with at least 10 reads in one of the CoIP fractions; Table 2). Among these, 187 were known C/D snoRNAs while the other 6 were novel species. Noticeable, 141 C/D snoRNAs target respectively 66, 37 and 2 sites in the 25S, 18S and 5.8S rRNA sequences while the other 52 C/D snoRNAs do not target rRNAs sites identified by RiboMethSeq (Fig. 2B and Table 2 and S4).

Up to four C/D snoRNA might target each of the 105 ribose methylated sites detected by RiboMetSeq (Tables 1 and 2). However, based on the number of mapped reads in the same replicate, some C/D snoRNAs targeting the same rRNA methylation site seem to be differentially expressed. For instance ~80 thousands and ~3 thousands reads are respectively counted for At3gCDbox92.2 and At4gCDbox92.3 targeting 18S-Am28 while ~14 thousands reads are counted for At4gCDbox113.1 and none for At5gCDbox113.2 (not detected), both targeting 25S-Am1459. In contrast, for 14 rRNA 2'-O-methylated sites (all with at least one annotated C/D snoRNA) we have not detected a corresponding C/D snoRNA in the FIB2-IP fraction, including 25S-Gm2794 and 25S-Cm1847 sites for which C/D snoRNAs were identified *in silico* (Table 1 and S4).

In conclusion, this analysis demonstrated expression for most of C/D snoRNA driving 2'-O-methylation of rRNA sites detected by RiboMethSeq and also identified novel FIB2 interacting C/D snoRNAs without rRNA target site(s).

C/D snoRNA bioinformatics search

To identify RNA guides of ribose methylated rRNA sites (Table 1) without known and/or immunoprecipitated C/D box snoRNAs, we performed a bioinformatics analysis of the Arabidopsis genome (Table 2).

A first catalogue of 217 C/D box snoRNA sequences was established by collecting data from existing resources including SNOOPY [34], ARAPORT [35] and TAIR [36]. This first catalogue was enriched by 3 novel C/D snoRNAs (At3gCDbox101.1, At5gCDbox123.1, At5gCDbox129.1) identified by searching the genome sequence for C/D snoRNA targeting orphan rRNA 2'-O-methylated sites (Fig. 3 and Table 2 and S4). FIB2-YFP CoIP sequencing gave experimental evidence for 6 novel species mentioned before (Fig. 2B) resulting in an extended catalogue of 226 C/D snoRNAs. Altogether, 193 of the 226 C/D snoRNAs show expression evidence and represent 144 families. Most of them are organized into clusters of C/D snoRNAs. Notably, as previously described, 12 C/D box snoRNAs share a dicistronic organization with tRNAs [14] and 2 snoRNA clusters share a polycistronic organization with miRNAs [37].

All C/D box snoRNA genes were (re)named as AtchrgCDboxnumber.isoform and consecutively numbered. For example, At4gCDbox94.3 is the name of the C/D box (CDbox) snoRNA which is located on chromosome 4 of the genome (At4g) and is the third isoform of a previously annotated C/D box snoRNA which is numbered 94 (94.3). This nomenclature simplifies current annotation and provide useful information concerning the genomic organization of C/D snoRNA variants.

All identified C/D box snoRNAs were searched for their ability to guide known predicted and/or mapped rRNA 2'-O-methylations (Table S4). We found 181 C/D box snoRNAs that contain predicted guide sequences upstream of their D' or D box. Among them, 111 have predicted guide sequences upstream of each box, 155 have a predicted guide sequence upstream the D' box and 136 have a predicted guide sequence upstream the D box (predicted target 5' and 3' respectively in Table S4). Several box C/D snoRNAs may have close homologs that are able to guide methylation at similar rRNA sites. Members of different families may also guide a modification at the same rRNA site. For instance, 3 different C/D snoRNAs potentially guide methylation of 18S-Am545 and 4 others guide methylation of 25S-Cm2338 (Tables 1, 2 and S4). Altogether, 4 snoRNAs are able to guide 2'-O-methylation at the 2 positions of 5.8S rRNA, 101 at the 65 mapped/predicted positions of 18S rRNA and 183 at the 100 mapped/predicted positions of 25S rRNA. Exploring the updated catalogue of Arabidopsis thaliana C/ D box snoRNAs with pairing constraints as defined in Materials and Methods, we could not find C/D box snoRNA guides for 12 of the mapped rRNA modifications (Table 1).

Differential 2'-O-Methylation in nuc1-2 mutant plants

To determine if variations of rRNA 2'-O-methylation might occur in Arabidopsis plants, we performed RiboMethSeq analysis of Nucleolin 1 (*nuc1-2*) mutants. Nucleolin is a phylogenetically conserved multifunctional protein required for transcription and processing of 45S pre-rRNA and assembly of ribosomes [38,39]. In Arabidopsis, NUC1 gene disruption affects rRNA expression and functional nucleolar structure and provokes major growth and development defects [40–42]. RiboMethSeq analysis was performed in 3 biological replicates from 21-days-old Arabidopsis *nuc1-2* mutant plants and compared with results from Col-0 (WT) control plants.

Quantitative 2'-O-methylation score was calculated for each mapped position in 18S, 5.8S and 25S rRNAs both in Col-0 and *nuc1-2* plants (Table S1) and compiled in a heat map (Fig. 4). All methylation scores were clustered with the software 'R' (hclust). This analysis revealed 65 sites that were significantly (*p-value* <0.01) hypo-methylated in the *nuc1-2* compared to WT plants (Table 1). Remarkably, the RiboMethSeq analysis has not detected any hypermethylation of mapped sites in *nuc1-2* mutant compared to Col-0 plants.

65 rRNA 2'-O-methylation sites were differentially down regulated in the *nuc1-2* plants. 61 are guided by C/D snoRNA, while the other 4 (18S Um1554 and 25S Cm2294, Gm2410, Gm2652) have no matching C/D snoRNA (Table 1 and yellow circles and grey circles with star in Fig. 2). Noteworthy, the rRNA site 25S-Gm2652, is located in the domain V and close to the P loop (Fig. 1B). We also noticed that out of 65 sites undermethylated in *nuc1-2* plants, 30 and 16 are conserved in human and yeast rRNA respectively, including the 25S-Gm2652, equivalent to the 28S-Gm4228 in human (Table 1).

Altogether, this analysis supports the idea that 2'-O-methylation of conserved and non-conserved rRNA sites could be modulated in Arabidopsis plants.

Discussion

In this work we used RiboMethSeq and mapped 117 rRNA 2'-O-methylation sites in leaves from 21-days-old *Arabidopsis thaliana* plants; among these sites, 65 are mapped for the first time. Notably, 38 of the 65 sites mapped in leaves were recently reported as well in plant stems using a nucleasebase detection protocol [43], ratifying that they are truthfully rRNA methylation targets in *Arabidopsis thaliana* rRNA (Table S2). Only 6 rRNA sites mapped by RiboMethSeq were not supported by at least two independent protocols or reported elsewhere (Table S2). Sites without such orthogonal validation were thus considered as potential false-positive hits. Thus, together with 66 previously [14,15,22,23,25] and the 20 newly mapped sites in stems reported in [41] a total of 151 ribose methylated sites have been now mapped in Arabidopsis (Fig. 5).

We noted that the majority of the mapped rRNA sites are guided by ~150 distinct C/D snoRNAs (Table 1). As expected, a number of these rRNA sites is targeted by different C/D snoRNA isoforms resulting from gene duplications of the Arabidopsis genome [14,15,25].

Interestingly, 49 rRNA 2'-O-methylation sites previously mapped or predicted were not detected by RiboMethSeq (Table S2). Among these, 4 sites were mapped in young seedlings [15,25], indicating that 2'-O-methylation of these sites might occur specifically only at early plant growth and/ or developmental stages. Then, it can be expected, that a fraction of rRNA methylated sites detected by RiboMetSeq could be specific to later stage of plant organs, including leaves.

The total number of rRNA mapped sites (117, Table 1) in our plant growth conditions is relatively similar to human with 110 positions guided by 118 C/D snoRNA [10,44] but much higher compared to yeast with 55 positions guided by 43 C/D snoRNA [45]. A subset of 63 and 36 rRNA 2'-O-methylated sites in Arabidopsis are conserved in human and/or yeast, respectively (Table 1), indicating that these rRNA sites may be important for ribosome assembly and/or function in eukaryotic cells. On the other hand, most of the Arabidopsis specific sites are located in the 25S rRNA and more precisely in the domain V (Fig. 1), responsible for peptidyl-transferase activity and tRNA binding [4,46]. This might suggest that rRNA methylation at these specific sites in domain V could be required for tuning translation in plants, and likely linked to the usage of synonymous codons and cognate tRNAs to optimize protein translation at particular conditions, including tissue-specific translation in Arabidopsis [47].

Plants are constantly subjected to different cellular and environmental stress conditions and might require additional RNA modifications to protect ribosome integrity or activity. We do not know yet if the Arabidopsis-specific rRNA sites are conserved in other plant species. However, specific rRNA methylation sites can be anticipated in other plant species, as reported in rice [19].

Among the 12 rRNA sites without predictable guiding C/D snoRNAs, 6 were also mapped in Arabidopsis stems [42] including 18S Um1554 and 25S Gm1460, Cm2294, Gm2396, Gm2652 and Gm2923 (Table S2). However, it is possible that some snoRNAs might guide methylation of the rRNA site adjacent to the targeted site. Indeed as shown for U24 in yeast [48] and hypothesized in snoRNAdb for U24 in human [49], the snoRNA At4gCDbox113.1, proposed to guide the modification of 25S-Am1459, might also guide the conserved 2'-O-methylation of 25S-Gm1460. Similarly, the snoRNA At1gCDbox5.1 proposed to guide methylation at 25S-Um2651, might also guide the conserved 2'-O-methylation of 25S-Gm2652. Interestingly, we have not found any C/D snoRNA guide able to guide modification at positions Gm2396, Um2922 and Gm2923 in 25S rRNA, as it is the case for conserved 2'-O-methylated positions in human.

While most of the eukaryotic rRNA ribose modifications are guided by snoRNA, four different modifying enzymes direct ribose methylation in E. coli: rsmH/rsmL methylates 16S-Cm1402 while rlmB, rlmM and rlmE/rrmJ methylate Gm2251, Cm2498 and Um2552 in the 23S, respectively [50]. For Arabidopsis 18S-Cm1645 and 25S-Gm2620, equivalent to E. coli 16S-Cm1402 and 23S-Gm2251, respectively, we have identified at least 2 C/D snoRNAs for each. In contrast, for 25S-Um2922, the equivalent of E. coli 23S-Um2552, we have not found either a specific and/or adjacent snoRNA that might guide methylation. This is an significant observation since methylation of E. coli 23S-U2552 influences the interaction of aminoacyl-tRNA with the ribosomal A-site and lack of methylation affect accuracy of translation [50]. An Arabidopsis protein gene phylogenetically related to yeast genes encoding close homologues of E. coli rlmE/rrmJ and able to 2'-O-methylate tRNA was reported [51]. However, potential 2'-O-metyltransferase activity of this Arabidopsis protein has not been demonstrated and requires further investigation.

For most of the rRNA methylated sites we detected, guiding C/D snoRNAs co-precipitate with FIB2 (Table 2). However, C/D snoRNAs At3gCDbox101.1 and At5gCDbox123.1 directing ribose methylation of Gm2794 and Cm1847 in the 25S, were not detected in any of the FIB2-IP fractions, suggesting that they are probably low expressed in our conditions. On the other hand, in the FIB2-IP fraction found C/D snoRNAs At1gCDbox5.1 we and At4gCDbox113.1, which, as mentioned before, might methylate adjacent rRNA sites without matching C/D snoRNA (Table 2). Interestingly, 6 novel C/D snoRNA that coprecipitated with FIB2, do not have recognized rRNA targets (Fig. 2) and then they might guide fibrillarin methylation activity to other coding and/or non-coding RNA. Indeed, in eukaryotes, ribose methylation has been found in snRNA, tRNA, snoRNA and also mRNA [16,52,53]. Alternatively, specialized C/D snoRNPs might also guide RNA base acetylation [54].



Figure 3. Mfold structure of At3gCDbox1011 and At5gDbox123.1 identified *in silico* and alignment with 25S rRNA sequences. Arrows show mapped rRNA sites Gm2794 and Cm1847 in the 25S and their counterpart in the snoRNA. Blue and red bars underline potential C and D boxes sequences.



Figure 4. Heat map representation of rRNA 2'-O-methylation in Arabidopsis. Differential methscore levels for 115 rRNA 2'-O-methylated sites observed in three Col-O and three *nuc1-2* biological replicates (R1-R3) are shown. The rRNA sites are clustered according to hclust/ward.D2 method. Arrow heads show rRNA sites without associated guiding snoRNA. The colour key, histogram and values are shown.



Figure 5. Illustration shows the number of 2'-O-methylated sites mapped by RiboMethSeq (117) and C/D snoRNA detected in the FIB2 immunoprecipitated fraction (193) and/or identified by bioinformatics search (9). From these analyses we account 65 first time mapped 2'-O-methylated sites and 9 novel C/D snoRNAs, increasing the number of 2'-O-methylated mapped sites and C/D snoRNA identified and listed in Arabidopsis databases to 151 and 226 respectively.

Further bioinformatics analysis revealed that 18 C/D snoRNAs detected in the FIB2-IP fraction target 2'-O-methylation of major U1, U2, U4, U6, and minor U12 and U6atac snRNAs (Figure S4). Among these 18 C/D snoRNA we have found that 5 are 'orphans' since do not have predicted rRNA target sites (Table S4). Furthermore, 5 other C/D box snoRNAs found in the FIB2-IP fraction and having no rRNA target are isoforms of U3 snoRNAs (Table 2). Unlike other C/D box snoRNAs, U3 is not directing 2'-O methylation of other RNAs. Rather, U3 snoRNA is required to guide site-specific cleavage of rRNA during pre-rRNA processing and contains a longer 5' region downstream the C box that pairs with pre-rRNA rRNA [55-57]. All orphan snoRNAs (Table S4) were submitted to RNA central [58] and show high conservation of all sequences and C/D box motifs in Arabidopsis lyrata.

138 C/D snoRNA in the FIB2- IP fraction were also detected among 154 C/D snoRNA recently reported in a nuclear fraction from Arabidopsis cell suspension culture [59]. However, 16 others C/D snoRNAs detected in the nuclear fraction were not found to be associated to FIB2 in our conditions (Table S2). Altogether, the data and observations indicate specific expression of snoRNA in 21 days-old plant compared to Arabidopsis cell suspension culture. Indeed differential expression of C/D snoRNA has been reported in plants [22,60,61] and in animal cells [62,63]. However, we do not rule out the possibility that some C/D snoRNA not detected in the FIB2-IP fraction are in fact expressed, but not assembled into C/D snoRNP in our plant conditions. Indeed, proper assembly of C/D snoRNA with core proteins, including Fibrillarin, is essential for activity of C/D snoRNP [64]. Finally, the comparative analysis of FIB2-IP and *in silico* search analysis demonstrated expression of nearly two hundred C/D snoRNA species and identified 9 novel ones from which at least two direct rRNA 2'-O-methylation (Fig. 3), expanding the number of known C/D snoRNA to 226 (Fig. 5).

Differentially 2'-O-ribose methylated ribosomes and their impact in cellular function have been reported in animal and yeast cells (reviewed in [4,9,10,65]). Our results revealed rRNA 2'-O-methylation alterations in the *nuc1-2* mutant plants (Fig. 4), which display strong developmental phenotypes [40–42]. Surprisingly, in the *nuc1-2* plants we have not

detected hypomethylation of 25S-Gm2620. Indeed, lack of methylation of 25S-Gm2620, by inhibiting expression of the guiding C/D snoRNA HID2, provokes developmental defects, which are reminiscent of plant mutants for specific ribosomal proteins and ribosome biogenesis factors, including Nucleolin [22]. In contrast, the Um2422 and Am2641, located structurally closed to 25S-Gm2620 are strongly hypomethylated (Fig. 1B), proposing a functional and/or structural connection between these three rRNA sites.

rRNA ribose hypomethylation of specific sites and major growth and developmental phenotypes were also observed in nufip mutant plants [23]. NUFIP (Rsa1p in yeast) is a conserved and a central protein factor directing assembly of C/D snoRNPs [66,67]. Though, a functional link between Nucleolin and C/D snoRNP biogenesis/assembly has not been demonstrated yet, the mouse Nucleolin directly interacts with the MBII-52 snoRNA that assembles into a non-canonical snoRNPs and might function as a chaperone or assist shuttling of MBII-52 RNPs between nucleoplasm and nucleoli [68]. Assembly and maturation of C/D-box snoRNP occurs in the nucleoplasm in human cells while in yeast maturation initiates in the nucleoplasm and terminates in the nucleolus [69]. To our knowledge, it is not known where precisely assembly of snoRNP occurs in plants. The nucleolus is disorganized in nucl-2 mutant plants [42] and it is tempting to speculate its direct impact on C/D snoRNP biogenesis in plants and/or more directly on 2'-O-methylation activity. If the assembly and/or maturation of pre-mature snoRNPs in functional C/D snoRNP is affected or not in nucl mutant plants remains an open question. Finally, how precisely rRNA ribose modification is impacted at different developmental stages and in response to environmental conditions, is also a next challenging question to be addressed.

Material and methods

Plant materials and growth conditions

All lines were derived from *Arabidopsis thaliana* Columbia (Col-0) ecotype. Plants mutant *nuc1-2* and plants expressing FIB2-YFP nucleolar marker constructs were previously described in [32,42,70]. Seeds were sown on soil (1/5

vermiculite and 4/5 soil) and left for 2 days at 4°C to synchronize. Plants were then grown in controlled growth chambers under a 16 h light/8 h dark cycle at 20°C. Light 100 μ E. m⁻².s⁻¹ and Relative Humidity 60% (CLF Plant Climatics GmbH, Wertingen Germany). Aerial parts from three-weekold plant seedlings were collected, shock-frozen in liquid nitrogen and grinded in fine powder and store at -80°C.

RNA isolation

For RiboMethSeq, about 800 μ L of frozen powder were supplemented with 5 mL of TRI Reagent[®] (Molecular Research Center, Inc), then 1 mL of cold chloroform was added and incubated for 3 minutes. The mix was centrifuged at 8,000xg for 15 min at 4°C. The aqueous phase was recovered and precipitated with 3 mL of cold isopropanol. After 30 min incubation, the mix was centrifuged at 8,000xg for 30 min at 4°C. Isopropanol was removed and 1.25 mL of 75% ethanol was added to the pellet and incubated over-night at -20°C. After centrifugation, the ethanol was removed and the pellet air dried. The RNA was suspended in RNAse free water and purity verified using Agilent RNA 6000 Pico Kit, analysed in an Agilent 2100 Bioanalyzer, according to the manufacturer's protocol (Figure S1).

2'-O-methylation sites cartography by RiboMethSeq

RiboMethSeq analysis was performed as previously described in [24]. Briefly, 100 ng of total RNA from WT plants was subjected to alkaline hydrolysis for 12 min at 96°C. RNA was precipitated and end-repaired before being converted to library using NEBNext©Small RNA Library kit (NEB, USA). Library quality and quantity were assessed using a High Sensitivity DNA chip on a Bioanalyzer 2100 and using Qubit 2.0 fluorometer, respectively. Libraries were multiplexed and subjected for high-throughput sequencing using an Illumina HiSeq 1000 instrument with a 50 bp single-end read mode.

Heat map

Heatmap to compare RiboMethSeq methylation score for Col-0 and *nucl-2* mutants was constructed using positionnormalized variations of MethScore relative to average value observed for a given position. In this presentation overmethylated sites are in red, while undermethylation compared to average is represented by green colour. Highly constitutive and invariable sites are in white. Clustering was performed using heatmap.2/hclust R functions using ward.D2 method.

Immunoprecipitation: Protein and RNA extraction

Leaves from 3 weeks-old Col-0 (WT) and p35S:FIB2-YFP seedlings were grinded into fine powder in liquid nitrogen. The whole cell extracts (2.4 g of p35S-FIB-YFP and 0.8 g for Col-0) were prepared in 3 volumes of buffer EB150 (50 mM Tris-HCl pH 7.5, 150 mM NaCl, 5 mM MgCl₂, 10% glycerol, and EDTA free proteases inhibitor cocktail from Roche) supplemented with 0.1% NP-40. p35S:FIB2-YFP cell extracts (input) were divided into three reactions, and

all samples were incubated with 20 μ L of GFP-Trap_ MA beads (Chromotek) for 2 h at 4°C with gentle rotation. The unbound fractions were collected and the beads were then washed three times with EB150.

RNA and proteins in IP fraction were extracted using TRI-Reagent (MRC research). RNA separated in aqueous phase were precipitated using glycogen as a carrier (SIGMA, 20 mg) following supplier instructions. Proteins were precipitated from phenolic phase by adding three volumes of cold acetone. After washing, pellets were resuspended in 4X SDS-Laemmli buffer, denatured to perform western blot analysis.

Alternatively, proteins bound to the beads were eluted and recovered in 4X SDS-Laemmli buffer (250 mM Tris-HCl pH 6.7; 8% SDS; 40% glycerol; 0.2% bromophenol bleu, 0.4 M DDT) in the experiments dedicated to Liquid Chromatography-Tandem Mass Spectrometry (LC-MS/MS) analysis.

SDS-PAGE and Western blot analysis

For SDS-PAGE and Western blot, proteins extracts were diluted in SDS-Laemmli buffer, supplemented with β-Mercaptoethanol, heated at 95°C for 10 min and subjected to 10% SDS-polyacrylamide gel electrophoresis. After electrophoresis proteins were either visualized by coomassie-blue staining or transferred to PVDF (Millipore) or nitrocellulose membranes (Bio-Rad) according to manufacturer's instructions. The membranes were then blotted with a-GFP 1:5,000 (Tebu-Bio) and goat anti-rabbit coupled HRP antibodies (Biorad). Immunoreactive proteins were detected using Immobilon western chemiluminescent substrates (Millipore) and the acquisition of images was performed using Fusion Solo S camera (Vilber Lourmat). Once immunodetections performed, the membranes used to control IP experiments intended to RNAseq analysis were stained with colloidal blue coomassie solution.

Liquid Chromatography-Tandem Mass Spectrometry (LC-MS/MS) analyses

Immuno-precipitated protein fractions were diluted to 1X SDS-Laemmli buffer and supplemented with 10 mM DTT before being loaded on an in-house poured 4% acrylamide stacking gel. Gel was stained with Coomassie Blue and the stacking bands were manually excised. Proteins were then reduced, alkylated and digested overnight at 37° C with modified trypsin in a 1:100 enzyme:protein ratio (Promega, Madison, USA). Peptides were extracted during 1 hour with 80 µL of 80% acetonitrile, 0.1% formic acid, before being dried and suspended in water acidified with 0.1% formic acid prior to nanoLC-MS/MS analysis.

LC-MS/MS analyses were performed on a NanoAcquity LCsystem (Waters, Milford, MA, USA) coupled to a Q-Exactive plus Orbitrap (Thermo Fisher Scientific, Waltham, MA, USA) mass spectrometer operated in Data-Dependent Acquisition mode as previously described [32]. Peptides/proteins were identified using the Mascot search engine (version 2.5.1, MatrixScience, London, UK) against an *Arabidopsis thaliana* protein sequences database downloaded from The Arabidopsis Information Resource TAIR site (TAIR10 version gene model) to which common contaminants and decoy sequences were added (total of 2×27 534 protein entries). Identifications were validated and label-free extracted ion chromatogrambased quantification was performed using the Proline software suite. False Discovery Rate was optimized to be below 1% at PSM level using Mascot Adjusted E-value and below 1% at Protein Level using Mascot Mudpit score. Statistical analysis was performed using the Prostar software suite (version 1.12.11). Pairwised Limma t-tests were performed. P-values calibration was corrected using adapted Benjamini-Hochsberg method, and FDR was set to <1-2%. (For more details see Supplementary Information)

RNAseq of RNA from FIB2:YFP fractions

RNA samples from CoIP_1 (150 ng), CoIP_2 (300 ng) and CoIP_3 (225 ng) samples were subjected to alkaline hydrolysis for 5 min at 96°C. RNA was precipitated and endrepaired before being converted to library using NEBNext©Small RNA Library kit (NEB, USA). Library quality and quantity were assessed using a High Sensitivity DNA chip on a Bioanalyzer 2100 and using Qubit 2.0 fluorimeter, respectively. Libraries were multiplexed and subjected for high-throughput sequencing using an Illumina HiSeq 1000 instrument with a 50 bp single-end read mode.

C/D snoRNA bioinformatic search and analysis

Data. The genomic sequence of *Arabidopsis thaliana* used in these analyses is available at ftp.ensemblgenomes.org/pub/plants/current/fasta/arabidopsis_thaliana/dna/

Arabidopsis_thaliana.TAIR10.dna.toplevel.fa.gz. Annotations are from TAIR. Fasta sequences of used ribosomal RNAs and snRNA are given in Supplemental Information.

C/D box snoRNA identification. The catalogue of Arabidopsis thaliana C/D box snoRNA genes was established using three approaches. The initial dataset of C/D box snoRNA genes was built from sequences available in the snoRNA Orthological Gene Database (snOPY) [34] and in Arabidopsis thaliana repositories such as ARAPORT portal [35] and TAIR resource [36]. SnoRNA genes from ARAPORT and TAIR were manually curated to distinguish between H/ACA box and C/D box snoRNA sequences. Only C/D box snoRNA sequences that mapped on the genomic sequence with 100% of identity were kept for further analysis. The initial dataset of C/D box snoRNA sequences was enriched by using PatScan [71] to search the genomic sequence for patterns encoding new C/D box snoRNAs. Such patterns were defined to contain motifs corresponding to the C box (RUGAUGA allowing one mismatch), the C/D box snoRNA region of the snoRNA:rRNA interaction (defined from each rRNA position orphan of a C/D box snoRNA guide at the region around a mapped methylation site and with at most three mismatches in the first eleven base pairs) and the D'/D box motifs (CUGA allowing one mismatch). This updated catalogue was enriched with

regions expressed in the sequenced FIB2-YFP coIP fractions and matching the C/D box snoRNA gene pattern not considering the snoRNA:rRNA interaction constraint. Reads from sequenced FIB2-YFP coIP fractions were trimmed for the Illumina 3' adaptor sequence using Cutadapt [72] and aligned using the bowtie2 aligner [73]. Highly expressed intronic and intergenic regions without annotation were inspected in IGV [74], assembled in transcripts and searched for the C/D box snoRNA pattern. This dataset was also used to modify boundaries of previously identified C/D box snoRNA genes. All C/D box snoRNA genes were named as AtchrgCDboxnumber.isoform and consecutively numbered with chr giving the chromosome number, number increasing for each new C/D box snoRNA seen for the first time (paralogs have the same number) and isoform giving the number+1 of times an isoform was already found in preceding chromosomes or before this C/D box snoRNA in the same chromosome.

RNA folding structure prediction of C/D snoRNAs was performed using the mfold Web server http://unafold.rna. albany.edu/?q=mfold

Acknowledgments

We thank our master student, Clarisse Mariez, who contributed to IP-LC MS/MS and Anne de Bures for technical assistance.

Disclosure and availability Statement

The authors report no conflict of interest. Raw data were generated at the Epitranscriptomics and RNA Sequencing (EpiRNA-Seq) Core Facility, Nancy, France. Derived data supporting the findings of this study are available from the corresponding author [JSV] on request.

Disclosure statement

No potential conflict of interest was reported by the authors.

Author contributions

J. A-F designed and performed protein related and IP experiments for sRNA analysis; and supervised master degree student training for IP LC-MS/MS experiments. C.M. and E.J performed RNA related experiments. Y.M., L. A. and V.M. performed RiboMethSeq analysis. M.R. and C.C performed LC-MS/MS and analyzed the data. C.G performed bioinformatics analysis. J. S-V, C.G and Y.M supervised and analyzed the data. J.S-V wrote the manuscript with the assistance of J. A-F., C.C., C.G and Y.M.

Funding

This work was supported by the CNRS, INRAE and by the ANR (Agence Nationale de la Recherche) under Grant RiboStress 17-CE12-0026-01 and MetRibo and a BQR (Bonus Qualité Recherche) from the UPVD to JSV. YM was supported by EpiARN FRCR project from Grand Est Region (France). This study is set within the framework of the "Laboratoires d'Excellence (LABEX) TULIP (ANR-10-LABX-41). Mass spectrometry experiments were supported by the French Proteomic Infrastructure (ProFI; ANR-10-INBS-08-03);ANR [17-CE12-0026-01]; ANR [MetRibo]; ANR [10-INBS-08-03]; Grand Est Region [EpiARN FRCR].

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