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TITLE:

A Complete Pipeline for Isolating and Sequencing MicroRNAs, and Analyzing Them Using Open Source Tools

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SUMMARY:

Here, we describe a step-by-step strategy for isolating small RNAs, enriching for microRNAs, and preparing samples for high-throughput sequencing. We then describe how to process sequence reads and align them to microRNAs, using open source tools.

ABSTRACT:

Half of all human transcripts are thought to be regulated by microRNAs. Therefore, quantifying microRNA expression can reveal underlying mechanisms in disease states and provide therapeutic targets and biomarkers. Here, we detail how to accurately quantify microRNAs. Briefly, this method describes isolating microRNAs, ligating them to adaptors suitable for high-throughput sequencing, amplifying the final products, and preparing a sample library. Then, we explain how to align the obtained sequencing reads to microRNA hairpins, and quantify, normalize, and calculate their differential expression. Versatile and robust, this combined experimental workflow and bioinformatic analysis enables users to begin with tissue extraction and finish with microRNA quantification.

INTRODUCTION:

First discovered in 1993¹, it is now estimated that nearly 2000 microRNAs are present in the human genome². MicroRNAs are small non-coding RNAs that are typically 21-24 nucleotides long. They are post-transcriptional regulators of gene expression, often binding to complementary sites in the 3'-untranslated region (3'-UTR) of target genes to repress protein expression and degrade mRNA. Quantifying microRNAs can give valuable insight into gene expression and several protocols have been developed for this purpose³.

We have developed a defined, reproducible, and long-standing protocol for small RNA

sequencing, and for analyzing normalized reads using open source bioinformatics tools. Importantly, our protocol enables the simultaneous identification of both endogenous microRNAs and exogenously delivered constructs that produce microRNA-like species, while minimizing reads that map to other small RNA species, including ribosomal RNAs (rRNAs), transfer RNA-derived small RNAs (tsRNAs), repeat-derived small RNAs, and mRNA degradation products. Fortunately, microRNAs are 5'-phosphorylated and 2'-3' hydroxylated⁴, a feature that can be leveraged to separate them from these other small RNAs and mRNA degradation products. Several commercial options exist for microRNA cloning and sequencing that are often quicker and easier to multiplex; however, the proprietary nature of kit reagents and their frequent modifications makes comparing sample runs challenging. Our strategy optimizes collecting only the correct size of microRNAs through acrylamide and agarose gel purification steps. In this protocol, we also describe a procedure for aligning sequence reads to microRNAs using open source tools. This set of instructions will be especially useful for novice informatics users, regardless of whether our library preparation method or a commercial method is used.

This protocol has been used in several published studies. For example, it was used to identify the mechanism by which the Dicer enzyme cleaves small hairpin RNAs at a distance of two nucleotides from the internal loop of the stem-loop structure – the so-called “loop-counting rule”⁵. We also followed these methods to identify the relative abundance of delivered small hairpin RNAs (shRNA) expressed from recombinant adeno-associated viral vectors (rAAVs), to identify the threshold of shRNA expression that can be tolerated prior to liver toxicity associated with excess shRNA expression⁶. Using this protocol, we also identified microRNAs in the liver that respond to the absence of microRNA-122 – a highly expressed hepatic microRNA – while also characterizing the degradation pattern of this microRNA⁷. Because we have used our protocol consistently in numerous experiments, we have been able to observe sample preparations longitudinally, and see that there are no discernible batch effects.

In sharing this protocol, our goal is to enable users to generate high quality, reproducible quantification of microRNAs in virtually any tissue or cell line, using affordable equipment and reagents, and free bioinformatics tools.

PROTOCOL:

Animal experiments were authorized by the Institutional Animal Care and Use Committee of the University of Washington.

Small RNA library preparation

1. RNA isolation

1.1. Isolate RNA from a biological source using a standard RNA isolation reagent, or a kit that enriches for microRNAs. For tissues, it is best to start with samples snap-frozen in liquid nitrogen and ground to a powder using a pre-chilled mortar and pestle.

1.2. Measure each sample's RNA integrity on an instrument that can quantify RNA and provide

an RNA integrity number (RIN). RINs should be >7.

2. 3' adaptor ligation

2.1. Prepare a ligation reaction in PCR strip tubes, by combining: 11 μ L of RNA (1-3 μ g, using the same amount for each sample), 1.5 μ L of 10x T4 RNA ligase reaction buffer, ATP-free, 1 μ L of poly-ethylene glycol (PEG), and 0.5 μ L of 3'-linker (100 μ M Universal miRNA cloning linker).

NOTE: The absence of ATP helps enrich for miRNAs and minimizes cloning of mRNA degradation products. PEG acts as a molecular crowding agent, enhancing successful ligation. The Universal miRNA cloning linker has a 3' blocking group (amine) to prevent self-ligation, circularization, and ligation to RNA at the 5' end.

2.2. Heat the samples at 95 °C on a thermocycler for 30-40 s. Cool on ice for 1 min. Add 1 μ L of T4 RNA ligase 2 and incubate at room temperature for 2 h. Prepare the gel (step 2.3) while the samples are incubating.

NOTE: Incubation at room temperature helps prevent linker-linker ligation. We have also successfully used T4 RNA ligase 1.

2.3. Prepare 30 mL of a 15% polyacrylamide gel with 8 M urea (for a 20x20 cm gel): 14.4 g of urea, 3 mL of 10x Tris-buffered ethylenediaminetetraacetic acid (TBE), 11.2 mL of 40% 19:1 acrylamide, and H₂O to 30 mL. Solution is best dissolved at 42 °C. Immediately before casting, add 150 μ L of 10% ammonium persulfate (APS) and 30 μ L of tetramethylethylenediamine (TEMED) for polymerization.

2.4. Pour between 0.8 mm separated glass plates in a plastic cast and insert comb. Once the gel is solidified (about 20 min), add 0.5x TBE to tank and wash wells of residual urea by pipetting vigorously.

2.5. Pre-run the gel at a constant 375 V for 25 min without samples so urea can enter the gel, then wash the wells again.

NOTE: The amount of voltage may need to be reduced depending on the type of power supply and electrophoresis system that is used.

2.6. Once the samples are done ligating, add 15 μ L of acrylamide loading dye to the samples (for a 1:1 ratio), then denature for 5 min at 95 °C on a thermocycler.

2.7. Prepare 25 ng/ μ L of 37 and 44 bp size markers, diluted with one part acrylamide loading dye. Sequences are listed in **Table 1**.

2.8. Load the samples on the polyacrylamide gel, leaving at least one lane in between each

sample. Load 20 μL of at least two sets of markers, in an asymmetrical pattern to keep track of gel orientation.

2.9. Run the gel at a constant 375 V for the first 15 min and then increase to a constant 425 V for the remaining run. Run until bromophenol blue is about 1-4 cm from the bottom, which takes approximately 2 h.

NOTE: If necessary, the gel may be run at a lower constant voltage for a longer period of time until the bromophenol blue is about 1-4 cm from the bottom.

2.10. Remove the gel from the glass plates using a plate separator, and place the gel on a plastic page protector. Dilute 5 μL of ethidium bromide in 500 μL of distilled water, and pipette onto marker lanes just above the top light blue marker (see **Figure 1A**).

CAUTION: Use gloves for ethidium bromide and dispose of waste in accordance with local regulations. Let sit for 5 min.

2.11. Under ultraviolet (UV) light, cut the gels from upper to lower marker in each lane using clean razor blade (see **Figure 1A**). Transfer to a 4 x 4 cm square of laboratory sealing film, then cut the gel with about 4 cuts horizontally and 3 vertically to produce 12 small squares (see **Figure 1B**).

2.12. Pipette 400 μL of 0.3 M NaCl on to the sealing film square, and funnel gel pieces into 1.5 mL siliconized tubes (see **Figure 1C**). Agitate the samples on a nutator at 4 $^{\circ}\text{C}$ overnight.

NOTE: Other low-retention 1.5 mL tubes can be substituted for siliconized tubes.

2.13. After at least 12 h of agitation at 4 $^{\circ}\text{C}$, retrieve the samples and put them on ice, along with a conical tube of 100% ethanol.

2.14. Transfer 400 μL of supernatant to a new tube, and then add 1 mL of 100% ethanol and 1 μL of 15 mg/mL glycogen coprecipitant. Ensure to collect as much supernatant as possible, spinning down at 4 $^{\circ}\text{C}$ and pipetting more as necessary. Place at -80 $^{\circ}\text{C}$ for 1 h, or -20 $^{\circ}\text{C}$ for 2 h or longer. Glycogen coprecipitant improves pellet visibility and recovery.

2.15. Spin at 4 $^{\circ}\text{C}$ at 17,000 x g for 20-30 min. Remove all traces of ethanol and let pellet air dry for 5 min.

3. 5' linker ligation

3.1. Re-suspend the pellet by pipetting in 6.5 μL of nuclease-free water. Letting the pellet sit in water for a few minutes first will help with re-suspension.

3.2. After spinning down the pellet and resuspending in water, add 0.5 μL of 100 μM 5'-linker (with barcodes; see **Table 1**), 1 μL of T4 RNA ligase buffer, 1 μL of 10 mM ATP, and 1 μL of PEG. Heat at 90 $^{\circ}\text{C}$ for 30 s, then place on ice. Add 1 μL of T4 RNA ligase 1 and let incubate at room temperature for 2 h.

3.3. Add 400 μL of 0.3 M NaCl, followed by 400 μL of acid phenol/chloroform. Vortex 30 s - 1 min (solution will look cloudy), and then spin at 4 $^{\circ}\text{C}$ for 10-15 min at max speed in a microcentrifuge ($\sim 17,000 \times g$). Draw off the top layer and place in new 1.5 mL tube.

NOTE: Avoid pipetting any of the bottom layer.

3.4. Add 350 μL of chloroform, vortex briefly, and then spin at 4 $^{\circ}\text{C}$ for 10 min at max speed ($\sim 17,000 \times g$). Draw off the top layer and place in new 1.5 mL tube. Add 1.5 μL of glycogen coprecipitant and 1 mL of 100% ethanol.

NOTE: Again, avoid pipetting any of the bottom layer.

3.5. Vortex briefly, then place at -80 $^{\circ}\text{C}$ for at least 1 h, or -20 $^{\circ}\text{C}$ overnight.

4. Reverse transcription (RT)

4.1. Turn on the 42 $^{\circ}\text{C}$ heat block. Spin the samples at 4 $^{\circ}\text{C}$ and $\sim 17,000 \times g$ for 20-30 min. Remove all supernatant and let the pellet air dry for 5 min.

4.2. Re-suspend pelleted sample in 8.25 μL of nuclease-free water, then add: 0.5 μL of 100 μM RT primer (**Table 1**), and 5 μL of 2x RT Reaction Mix from a cDNA synthesis kit. Incubate at 42 $^{\circ}\text{C}$ for 3 min.

4.3. Add 1.5 μL of 10x RT enzyme to each sample and incubate at 42 $^{\circ}\text{C}$ for 30 min in a thermocycler. Place at -20 $^{\circ}\text{C}$ or continue with hydrolysis and neutralization.

NOTE: Several RT kits can be utilized for steps 4.2 and 4.3.

4.4. Perform alkaline hydrolysis and neutralization: Make 1 mL of 150 mM potassium hydroxide (KOH) solution (150 μL of 1 M KOH, 20 μL of 1 M Tris Base pH 7.5, and 830 μL of H_2O) and 1 mL of 150 mM hydrochloric acid (HCl) (150 μL of 1 M HCl and 850 μL of H_2O).

4.5. Before adding to the samples, determine the amount of HCl needed to neutralize the KOH solution. Generally, around 20-24 μL of HCl will neutralize the 25 μL of KOH. Check the combination on a pH strip to ensure it is in the right range (pH 7.0 to 9.5).

4.6. Hydrolyze the samples by adding 25 μL of 150 mM KOH solution and incubate for 10 min at 95 $^{\circ}\text{C}$.

4.7. Neutralize the samples by adding the amount of 150 mM HCl determined in step 4.4, to obtain a final sample pH between 7.0 and 9.5.

5. PCR amplification

5.1. After neutralization, prepare a PCR reaction with: 29.5 μ L of water, 5 μ L of 10x Taq buffer, 1 μ L of dNTP, 2 μ L of 25 μ M forward primer (**Table 1**), 2 μ L of 25 μ M reverse primer (**Table 1**), 0.5 μ L of Taq, and 10 μ L of the reverse transcribed cDNA from step 4.6.

5.2. Run the following PCR reaction: 94 °C for 2 min, then 20 cycles of 94 °C for 45 s, 50 °C for 75 s and 72 °C for 60 s.

5.3. Run a second PCR reaction of about 2-4 more cycles using 5 μ L of product from step 5.2. Mix: 34.8 μ L of water, 5 μ L of 10x Taq buffer, 1 μ L of dNTP, 1 μ L of 25 μ M forward primer (**Table 1**), 1 μ L of 25 μ M reverse primer (**Table 1**), and 0.2 μ L of Taq polymerase. Follow the same thermocycler parameters outlined in step 5.2.

NOTE: The purpose of doing two PCR reactions – with the first for 20 cycles and the second for just 2-4 more – is to ensure that the amount of cDNA amplified is in a dynamic range (i.e., not a saturated amount).

6. Agarose gel purification

6.1. Prepare a 4% agarose gel with low-melting agarose. Load 40 μ L or more of the PCR product on the gel, along with loading dye. Load 100 bp and 25 bp size markers.

NOTE: The 25 bp ladder helps to distinguish amplified product from linker-linker ligation products. Low-melting agarose gels must be cast with greater care than traditional agarose gels, so closely follow the instructions from the manufacturer.

6.2. For gel extraction, select the cycle number that is visible on the gel but is not saturated (usually 22–24 cycles). Choose similar intensity bands when running multiple samples.

6.3. Cut the band that is above the 125 bp band (the darker band on 25 bp ladder; see **Figure 1D**). Using a gel extraction kit, follow the manufacturer's instructions for adding buffer based on a 4% gel, then shake to dissolve agarose in buffer at room temperature.

NOTE: Dissolving at 55 °C increases the potential for linker-linker ligation.

6.4. Follow the manufacturer's gel extraction instructions and elute in 30 μ L of elution buffer or water. If the product looked weak on the gel, then reduce elution to 20 μ L.

6.5. Measure cDNA concentration using a sensitive technique, and prepare sample library for sequencing. Preparation will depend on the type of sequencing used.

NOTE: Minimum requirements for a sequencing library are typically a 10 µL volume of 10 µM product. If concentrations are too low, pool and ethanol precipitate samples to bring library to the desired concentration.

6.6. Sequence the samples using available equipment. A common example would be to run samples using a kit for 50 bp single reads, to obtain approximately 15-25 million reads in a FASTQ output format.

Small RNA sequence alignment and bioinformatics

7. Data upload

7.1. Download FASTQ files generated from each sequencing run. Download a list of microRNA hairpin sequences from miRbase.org⁸⁻¹⁰.

7.2. Generate a Galaxy account at www.usegalaxy.org and upload a FASTQ file of sequence reads to this account.

7.3. Upload a text file of barcode sequences to the Galaxy account, such as barcodes.txt, which is available as a text file (**Supplementary Table 1**).

7.4. Upload a FASTA file of microRNA hairpins to the Galaxy account from a database like miRBase.org. Examples of mouse (mousehairpins.fa) or human (humanhairpins.fa) microRNA precursors are provided in **Supplementary Table 2** and **Supplementary Table 3**.

8. Adaptor removal, barcode sort, and trim

8.1. In the left-hand tab, navigate to **Genomic file manipulation > FASTA/FASTQ > Clip adapter sequences**.

8.2. In **Input file in FASTA or FASTQ format**, enter FASTQ file from the drop-down list. Change **Minimum sequence length** to 18. Change **Source** to **Enter custom sequence**. Enter **CTGTAGGC**. Keep all other default parameters. Click **Execute**.

NOTE: Sequence reads that are shorter than 18 nucleotides are difficult to map uniquely to microRNAs and contain many degradation products.

8.3. In the left-hand tab, navigate to **Genomic file manipulation > FASTA/FASTQ > Barcode Splitter**.

NOTE: Galaxy functions and headers are updated periodically, so the search function may be

necessary to find an equivalent tool or its location. Commercial kits using indexed primers are often already sorted by barcode. Therefore, this step and the barcode trim step are not necessary if starting from a commercial kit.

8.4. For **Barcodes to use**, point to **barcodes.txt**. For **Library to split**, use **Clip on data** file produced in the previous step. In **Number of allowed mismatches**, enter **1**. Click **Execute**.

8.5. Trim the first 4 nucleotides: navigate to **Text Manipulations > Trim leading or trailing characters**. For **Input dataset**, click on the folder icon, which is a dataset collection. Select the batch file of samples, which includes the label **Barcode splitter on data**. In **Trim from the beginning up to this position**, enter **5**. In **Is input dataset in FASTQ format?** enter **Yes**. Click **Execute**. Execution may take several minutes.

9. Alignment of reads to microRNAs

9.1. In Galaxy, navigate to **Genomics Analysis > RNA-Seq > Sailfish transcript quantification**¹¹.

9.2. For the question **Select a reference transcriptome from your history or use a built-in index?** select **Use one from the history**. Enter the uploaded file **mousehairpins.fa** from the drop-down list. In **FASTA/Q file**, click the folder icon to use a dataset collection and select the file that includes **Trim on collection**. Click **Execute**. Execution may take several minutes.

9.3. In the history tab on the right, click on **Sailfish on collection...** which is a list with 19 items. Click on each individual file and click the disk icon to save to local computer. Individually downloaded files first need to be uncompressed. They also may need to be re-saved with a **.txt** extension for the purpose of importing into a spreadsheet.

9.4. Open each spreadsheet file in and re-name the **NumReads** column to the treatment condition. Merge the columns together to generate a matrix of microRNAs in the first column and read counts per condition in subsequent columns.

9.5. To calculate differentially expressed microRNAs for each treatment condition, use the file with raw microRNA read counts as input for programs such as DESeq2¹². DESeq2 is present in Galaxy in the **Genomics Analysis > RNA-seq > DESeq2** tab.

9.6. Convert raw reads to normalized microRNA read counts. Counts are normalized to the library sequence depth of the library through the following calculation: $[(\text{raw reads}/\text{total microRNA reads}) * (1,000,000 - \text{number of microRNAs counted}) + 1]$.

NOTE: This calculation provides a normalized reads per million (RPM) mapped microRNAs that can be compared across datasets and biological conditions. The output is a tab delimited file. Sailfish provides a **tpm** output column, though this value is normalized by microRNA hairpin length, which is not necessary in this context.

9.7. If relevant, repeat alignment with custom input sequences (e.g., a vector) to identify reads that map to delivered constructs, like shRNAs.

REPRESENTATIVE RESULTS:

Schematic of steps involved in library preparation

An overall schematic of small RNA extraction, sequencing, and alignment is outlined in **Figure 2**. Liver samples from one male and one female mouse were collected and snap frozen in liquid nitrogen. Total RNA was extracted and evaluated for quality and concentration.

Small RNA sequencing yields sufficient RNA for sequencing

3 µg of RNA from two independent RNA extractions were used as starting material for small RNA sequencing. Samples were run on an acrylamide gel and cut out between size markers corresponding to 17-28 nt of RNA (**Figure 1A**). Samples were chopped into fragments for RNA isolation (**Figure 1B**) and transferred to a low-retention 1.5 mL centrifuge tube (**Figure 1C**). Barcodes bc7 and bc17 (**Table 1**) were ligated to the 5' end of the small RNA. Small RNA libraries were PCR amplified using 22 cycles of PCR to yield 8.0 and 11.2 ng/µL product, respectively. Samples were pooled and a 10 nM pooled sample was submitted for high-throughput sequencing using a 50 bp read length.

MiR-122 is the most abundant microRNA in the mouse liver

After barcode sorting, 851,931 reads contained barcodes from liver sample 1 and 650,154 from liver sample 2. Of the reads, 83.5% and 90.0% mapped to microRNAs respectively, with the remaining reads mapping to rRNAs (1.8% and 0.6% respectively), tRNAs and mRNA degradation fragments. After alignment to human microRNA hairpins, we observed strong concordance between microRNA read counts in each replicate ($R^2 = 0.998$; **Figure 3**). A total of 306 microRNA species were detected, with the greatest number of reads mapping to miR-122 (**Supplementary Table 4**). MicroRNA abundance was similar between male and female liver samples.

FIGURE AND TABLE LEGENDS:

Figure 1. Extraction of small RNAs from an acrylamide gel. (A) Acrylamide gel and region that is cut corresponding to the size of microRNAs. (B) Gel pieces before and after cutting into smaller fragments. (C) Process for transferring gel fragments into siliconized tubes. (D) PCR reaction on low-melt agarose gel demonstrating correct cloned product compared with linker-linker product and unsaturated (22 cycles) versus saturated (24 cycles) samples.

Figure 2. Schematic of protocol. A timeline showing the major steps involved in the procedure.

Figure 3. Reproducibility of results from two independent RNA extractions. Scatterplot of microRNA read counts from a male mouse liver (x-axis) compared with a female mouse liver (y-axis) using a log₁₀-based scale. Each point represents the reads per million (RPM) mapped microRNA count for each individual microRNA.

Table 1. List of primers.

Supplemental Table 1. List of barcode sequences.

Supplemental Table 2. Curated list of mouse microRNA precursor sequences.

Supplemental Table 3. Curated list of human microRNA precursor sequences.

Supplemental Table 4. Raw and normalized microRNA read counts.

DISCUSSION:

Despite the identification of microRNAs over 20 years ago¹³, the process of microRNA sequencing remains laborious and requires specialized equipment, hindering laboratories from routinely adopting in-house protocols¹⁴. Other techniques can simultaneously evaluate microRNAs, like microRNA microarrays and multiplexed expression panels; however, these approaches are limited in that they only quantify the microRNAs present in their probe set. Because of this, they miss important features of small RNA sequencing, like the identification of novel microRNAs, and of microRNA isoforms – nucleoside changes that can have important biological function^{6,7,15}.

When starting a new experiment, using a commercial vendor is often easiest because they offer technical support and ease of use. Several commercial options are available for microRNA sequencing, which can be multiplexed to reduce the workload when processing large numbers (>100) of samples. These commercial kits are continually being improved, which is both an advantage and disadvantage. On the one hand, the companies who make these kits have developed novel microRNA capture methods, for example, through circularization of their 5' and 3' ends prior to sequencing or using degenerate linkers with random sequences at each end to reduce ligation bias. They have also developed methods to remove adaptor-dimers, for example, through ligation of double-stranded adaptors or hybridization of complementary oligonucleotides. On the other hand, commercial kits recommend against modification or alteration of any step. Therefore, if any updates are made to a kit, it is difficult or impossible to compare data derived from old and new versions of kits, as well as data derived from kits from different commercial vendors. Here, we have described a protocol that has staying power in the face of commercial alternatives. Our focus on gel purification steps – while they add time to the protocol – enables consistent microRNA capture and reproducibility over the many years we have used it. Several evaluations of the reproducibility between commercial kits and in-house protocols have been made, and we refer the reader to a few of these studies¹⁶⁻¹⁹. Importantly, the steps we outline for bioinformatics analysis of microRNAs can be employed regardless of the choice of kit or in-house protocol.

MicroRNA sequencing is often troubled by the choice of barcodes: in some instances, the ligation efficiency of the various barcodes may not be equivalent, leading to biased distributions of sequences in the samples²⁰. It is now recommended to use degenerate bases at the 5' and 3' end to minimize ligation biases of specific microRNAs^{21,22}. In this protocol, we have not observed these ligation issues and have observed consistent readouts for technical and biological replicates evaluated with different barcodes^{5-7,23}, but it is important to be aware of them. Methods to avoid ligation bias include the incorporation of index primers in the PCR primers, or to add one or more

random RNA nucleosides at the 3' end of the 5' adaptor sequence (**Table 1**). Introducing one or more synthetic spike-in RNA, such as the *C. elegans* miR-39 microRNA²⁴, is also an option for normalization purposes, which is critical for low-yield situations, like quantifying microRNAs from exosomes. Likewise, for RNA ligation, we have successfully used T4 RNA ligase 1, but ligation with less bias has been demonstrated for a truncated form of T4 RNA ligase 2²⁵. Finally, Superscripts III and IV are alternative reverse transcription enzymes that we have used without issue.

The choice of microRNA database can also influence the final normalized results. A challenge with curating microRNA databases is that several novel small RNAs listed as microRNAs are actually fragments of repeat elements and not *bona fide* microRNAs². Efforts have been made to retire microRNAs that do not conform to standard criteria, so that the next version of a microRNA database is more refined; however, the next iteration also contains new candidates that need confirmation. When repeat-derived microRNAs are included in alignments, they can skew the results and overwhelm data from existing microRNAs. Therefore, the use of well-curated datasets of microRNAs from different species is essential^{26,27}. We have experienced greatest reproducibility when aligning small RNA sequencing reads to curated lists of conserved microRNAs and have included these hairpins in **Supplementary Table 2** and **Supplementary Table 3**. These lists match estimates of about 500 high confidence microRNAs in the human genome^{2,26}.

As with any technique, results should be confirmed with an orthogonal approach. We have successfully reproduced small RNA sequencing results with small RNA northern blots that incorporate radiolabeled probes to confirm the size and relative abundance of candidate microRNAs^{6,7,23}. Quantitative PCR of microRNAs using split-read sequencing, and confirmation of target mRNA changes using qPCR and western blotting are other options for validation.

In summary, we have provided a method to isolate and sequence microRNAs and perform alignments against existing microRNA databases. The affordability of the reagents and equipment and the use of open source tools for analysis should make this protocol accessible to anyone. Finally, this protocol can be used in any tissue or cell line to yield highly reproducible, high-quality reads.

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DISCLOSURES:

The authors have nothing to disclose.

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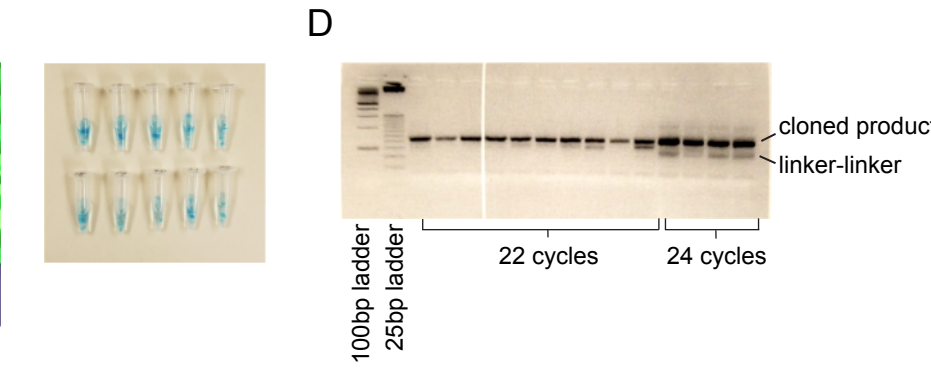
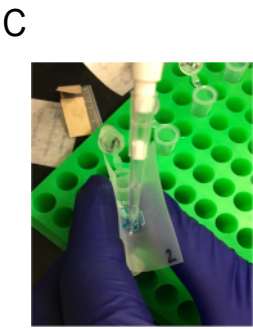
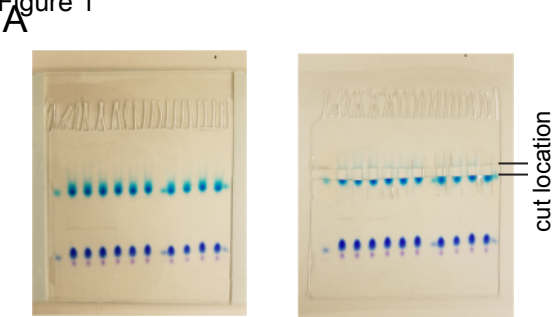
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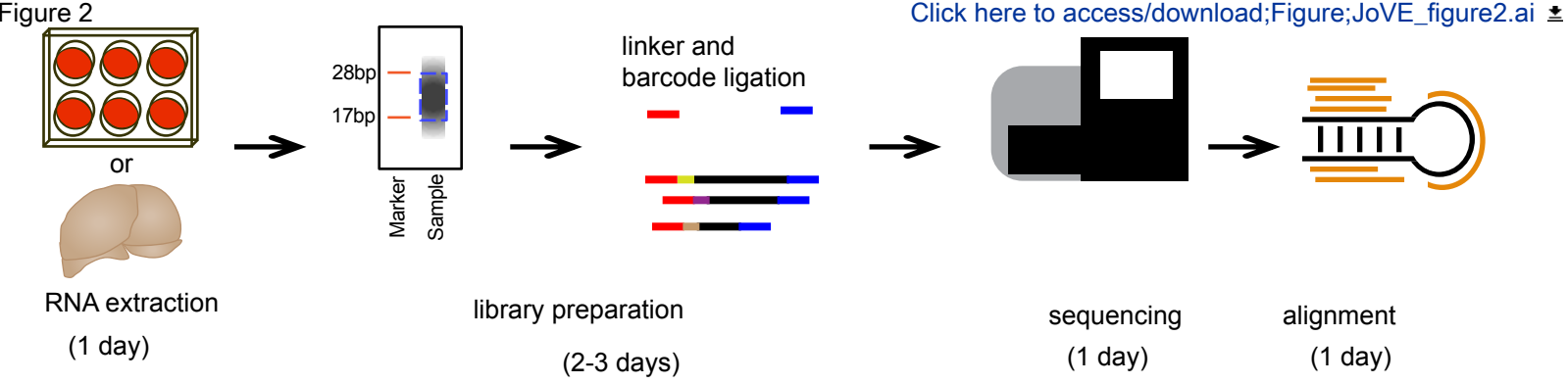
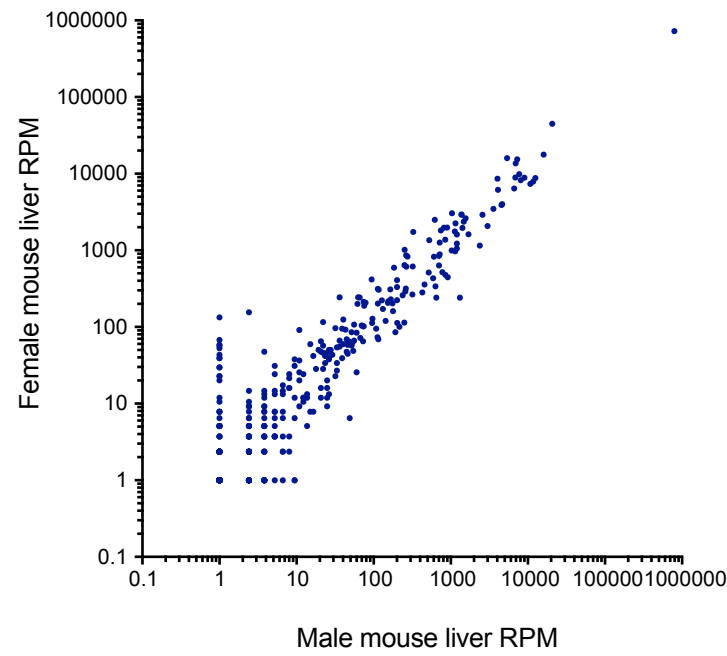


Figure 3



Primer	Sequence
3' linker 1	rAppCTGTAGGCACCATCAAT–NH ₂
lower size marker	rArUrCrGrCrArUrGrCrUrGrArCrGrUrArCrUrArGGTAACCGCATCATGCGTC
upper size marker	rArArUrCrArGrCrGrGrArUrUrGrCrArUrGrArArCrGrUrArCrArUrArGGTAA(
barcode1	/5AmMC6/ACGCTCTTCCGATCTrArGrCrG
barcode2	/5AmMC6/ACGCTCTTCCGATCTrCrGrUrC
barcode3	/5AmMC6/ACGCTCTTCCGATCTrCrUrGrG
barcode4	/5AmMC6/ACGCTCTTCCGATCTrArCrUrU
barcode5	/5AmMC6/ACGCTCTTCCGATCTrGrGrGrU
barcode6	/5AmMC6/ACGCTCTTCCGATCTrGrUrUrA
barcode7	/5AmMC6/ACGCTCTTCCGATCTrUrArUrG
barcode8	/5AmMC6/ACGCTCTTCCGATCTrUrCrGrC
barcode9	/5AmMC6/ACGCTCTTCCGATCTrGrCrArG
barcode10	/5AmMC6/ACGCTCTTCCGATCTrArUrArC
barcode11	/5AmMC6/ACGCTCTTCCGATCTrUrUrCrU
barcode12	/5AmMC6/ACGCTCTTCCGATCTrCrArArU
barcode13	/5AmMC6/ACGCTCTTCCGATCTrArArGrA
barcode14	/5AmMC6/ACGCTCTTCCGATCTrUrGrArA
barcode15	/5AmMC6/ACGCTCTTCCGATCTrUrGrGrG
barcode16	/5AmMC6/ACGCTCTTCCGATCTrArUrUrG
barcode17	/5AmMC6/ACGCTCTTCCGATCTrUrCrArU
barcode18	/5AmMC6/ACGCTCTTCCGATCTrGrUrArU
RT primer	ATTGATGGTGCCTACAG
PCR primer F	AATGATACGGCGACCAACCGAGATCTACACTCTTCCCTACACGACGCTCTTCC
PCR primer R	CAAGCAGAAGACGGCATAACGAGCTCTTCCGATCTATTGATGGTGCCTACAG

CCGCATCATGCGTC

GATCT

Name of Material/ Equipment	Company	Catalog Number
100 bp DNA ladder	NEB	N3231
19:1 bis-acrylamide	Millipore Sigma	A9926
25 bp DNA step ladder	Promega	G4511
Acid phenol/chloroform	ThermoFisher	AM9720
Acrylamide RNA loading dye	ThermoFisher	R0641
Ammonium persulfate (APS)	Biorad	161-0700
Bioanalyzer instrument	Agilent	G2991AA
Chloroform	Fisher Scientific	C298-500
Ethanol (100%)	Sigma	E7023
Gel Loading Buffer II	ThermoFisher	AM8547
GlycoBlue	ThermoFisher	AM9516
HCl	Sigma	320331
KOH	Sigma	P5958
Maxi Vertical Gel Box 20 x 20cm	Genesee	45-109
miRVana microRNA isolation kit	ThermoFisher	AM1560
miSeq system	Illumina	SY-410-1003
NaCl	Fisher Scientific	S271-500
Nusieve low-melting agarose	Lonza	50081
Parafilm (laboratory sealing film)	Millipore Sigma	P7793
Poly-ethylene glycol 8000	NEB	included with M0204
ProtoScript II First strand cDNA Synthesis Kit	NEB	E6560S
QIAquick Gel Extraction kit	Qiagen	28704
Qubit Fluorometer	ThermoFisher	Q33226
Qubit RNA HS Assay kit	ThermoFisher	Q32855
Razor Blades	Fisher Scientific	12640
Siliconized Low-Retention 1.5 ml tubes	Fisher Scientific	02-681-331
T4 RNA ligase 1	NEB	M0204
T4 RNA Ligase 2, truncated	NEB	M0242S
TapeStation	Agilent	G2939BA
Taq DNA Polymerase	NEB	M0273X

TEMED	Biorad	161-0800
Tris Base pH 7.5	Sigma	10708976001
Tris-buffered EDTA	Sigma	T9285
Trizol	ThermoFisher	15596026
UltraPure Ethidium bromide (10 mg/ml)	Invitrogen	15585-011
Universal miRNA cloning linker	NEB	S1315S
Urea	Sigma	U5378

Comments

For assessing RNA quality and concentration

Blue color helps in visualizing pellet

For generating small RNA sequencing data

For quantifying DNA concentration

For assessing RNA quality and concentration



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Reviewers' comments:

Reviewer #1:

Major Concerns:

The most important thing for any measurement method is to demonstrate the consistency and accuracy of the results. The method presented in the manuscript is interesting; however, it failed to provide any comparative analysis or accuracy assessment. The authors should include a comparative study with commercial kit(s) to demonstrate the advantage of the protocol (for example less ligation associated bias). In addition, the authors should include synthetic miRNA with known concentration as input so that the accuracy of the miRNA profiling results can be assessed.

- We agree that comparative studies are helpful for readers to make decisions about which protocol to use, and we now point the reader to manuscripts that compare several protocols simultaneously. Our primary goal here is to provide detailed steps involved in generating small RNA sequencing libraries. In the introduction, we focus on the strength of using a defined and long-standing protocol. Several commercial options are available, which have minimized biases all while trying to ensure ease of use and multiplexing capacity. As these options often include proprietary components, any changes to the protocol makes it difficult to compare data from old and new versions. We expand the discussion to describe alternatives that commercial kits use. We have also added our observation that we have used many different barcodes for the same technical and biological replicates, and yield similar results, indicating that we do not observe barcode bias.

- We have also made a note that synthetic spike-in RNAs are an option for normalization purposes, which are critical for low-yield situations, like quantifying microRNAs from exosomes. We typically focus on normalized microRNA reads and so did not include spike-ins in our protocol, but recognize their importance in certain contexts.

Reviewer #2:

1) A problem with this protocol is the fact that it uses a 5' adapter with a barcode sequence. As the authors indicate themselves, (even small) changes in adapter sequences can alter miRNA expression profiles in NGS libraries (e.g. Jayaprakash et al Nucleic Acids Res 39, e141, doi:gkr693 [pii];10.1093/nar/gkr693 [doi] (2011) and Van Nieuwerburgh et al. PLoS One 6, e26969, doi:10.1371/journal.pone.0026969 (2011). It is therefore of major importance to use exactly the same adapter sequences for all libraries in a series to be compared. The authors state that they have not observed such biases themselves but they do not explain how they have tested this. I would therefore strongly advice to remove the barcode from the 5' adapter and add a barcode by PCR as in the Illumina TruSeq system. This implies only a minor modification of the protocol.

- We appreciate the efforts by researchers to minimize bias in 5' adaptors. We have made a point to mention the optimized approaches in the discussion as well as referencing the aforementioned articles and provide the barcode choice as an option in the procedure. Since our representative results are based on the protocol we have designed, we were hesitant to remove our strategy completely and instead encourage the readers to consider the internal barcode option. We have included the references to the manuscripts that are listed.

1) The authors state that their protocol is better than commercial protocols, but the arguments are not very clear. First, commercial protocols would be less reproducible because they do not use acrylamide-based enrichment of small RNAs. While I agree that it is probable better to enrich for small RNAs, I do not really see how not doing so would reduce reproducibility. In addition, commercial protocols are generally perfectly compatible with small RNA enrichment prior to library preparation. The second argument is that other methods would suffer more of adapter dimer issues. Is this based on the fact that other methods do not gel-purify 3' adapter-miRNA ligation products as do the authors? Please explain better, knowing that kits now exist that eliminate unligated 3' adapter through beads purification, modified adapters or by hybridizing complementary oligos.

- The reviewer makes some excellent points and suggestions. In general, we have toned down the rhetoric that our approach is better, to make the point that we have a protocol that has stood the test of time and yielded consistent results between labs and for experiments performed years apart. We clarify that commercial kits often change, making comparison of data produced using different versions of kits difficult; in contrast, our protocol can remain exactly the same, which is one source of reproducibility. In the discussion, we describe commercial improvements for removing adaptor-dimers.

2) Reference 2 is at the wrong position, it should be after the year "1993"

- Thank you, we have made this change.

3) Lines 45-46 : "and their similarity to... [snoRNAs]" : I don't understand, why do the authors state the miRNAs are similar to tRNAs, rRNAs etc?

- We appreciate the comment and have provided more detail to clarify that tRNA-derived small RNAs, small RNAs that come from repetitive elements, or ribosomal RNA fragments are around the same size as the mature microRNAs, and so microRNAs need to be enriched. We use an input file of tRNA and rRNA (and snoRNA) precursors for the alignment but agree that we should really focus on the small RNAs that are produced. In cases where library quality is poor, we see a relative enrichment of these other classes of small RNAs.

4) Step 2.2: it would be more logical to use RNL2 by default rather than RNL1

- We agree and have modified the protocol and updated the list of reagents.

5) Line 416 "our method obviates...barcode bias": it introduces barcode bias rather than obviating it.... see major point 1.

- We have removed this portion of the sentence.

Reviewer #3:

Major Concerns:

This is a technically sound protocol in used for more than 15 years now. The time and number of steps that it takes may be a deterrent for some users. While the others indicate that some commercial kits may have so limitations, it seems that others may provide acceptable solutions with a much shorter and simple protocol such as <https://www.takarabio.com/products/next-generation-sequencing/epigenetics-and-small-rna-sequencing/microrna-seq-kit>

A more extensive comparison and discussion with commercially available products could be

useful for users to discern under what circumstances this protocol may be more advantageous or appropriate for specific research needs.

- We concur that several commercial protocols have now optimized their strategies to minimize bias in small RNA sequencing and are especially useful for handling large sample numbers. We have expanded the discussion to reflect the many options that are available and the strengths and limitations to the different approaches. For users that do not need to invest in the infrastructure for many experiments, a kit is a great option. One of the challenges of commercial kits is that if the components are modified from one version to the next, it is harder to ensure reproducibility between experiments. Therefore, one strength of our protocol is the long-term stability of the procedure and ability to adjust components. We also highlight the point that our bioinformatics strategy is helpful even if users start with a commercial kit, and provide greater detail on how to analyze data using these starting points.

We have also added a note in the introduction about the length of protocol: "Several commercial options exist for microRNA cloning and sequencing that are often quicker and easier to multiplex." Also, as mentioned in the response to other reviewers, we have expanded the discussion to list the advantages of commercial kits, including the use of multiplexed barcodes and methods to enrich for microRNAs. We also provide more reference to the article by Giraldez *et al. Nature Biotech*, 2018, and others, which systematically assess several commercial kits.

Minor Concerns:

The voltage for pre-running at 375V and run at 425V for 2 hrs seems rather high. the authors may want to provide more info on amperage and whether this is a constant voltage run.\

- We agree that the voltage is high and that not all users will have a power apparatus that reaches these levels. We updated the protocol to specify constant voltage (which avoids overheating) and that the gel can be run at a lower voltage for a longer period of time. What matters is that the gel is run until the bromophenol blue is about 1-4 cm from the bottom.

bc1	AGCG
bc2	CGTC
bc3	CTGG
bc4	ACTT
bc5	GGGT
bc6	GTTA
bc7	TATG
bc8	TCGC
bc9	GCAG
bc10	ATAC
bc11	TTCT
bc12	CAAT
bc13	AAGA
bc14	TGAA
bc15	TGGG
bc16	ATTG
bc17	TCAT
bc18	GTAT

```
>mmu-let-7b
GCAGGGTGAGGTAGTAGGTTGTGTGGTTTCAGGGCAGTGATGTTGCCCCCTCCGAAGATAA
CTATACAACCTACTGCCTTCCCTGA
>mmu-let-7c-2
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ACTATACAATCTACTGTCTTTCCTGAAGTGCCGC
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TATACGGCCTCCTAGCTTTCCTCAGGCTGCGCC
>mmu-let-7f-2
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TACAGTCTACTGTCTTTCCTCAG
>mmu-let-7i
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mouse miRNA	liver_M_bc7	liver_M_bc7	liver_F_bc13	liver_F_bc13_normalized
mmu-let-7a-2	11400	16073.7	7740	13288.5
mmu-let-7b	8890	12534.9	4077	7000.1
mmu-let-7c-1	7658	10797.9	4390	7537.5
mmu-let-7c-2	8338	11756.6	4797	8236.2
mmu-let-7d	4713	6645.8	2672	4588.1
mmu-let-7e	420	593.2	383	658.5
mmu-let-7f-1	4932	6954.6	5737	9849.9
mmu-let-7f-2	5172	7292.9	6086	10449.0
mmu-let-7g	3816	5381.1	4862	8347.8
mmu-let-7i	2544	3587.8	2152	3695.4
mmu-mir-1-1	32	46.1	1	2.7
mmu-mir-1-2	25	36.2	1	2.7
mmu-mir-1-2-as	17	25.0	1	2.7
mmu-mir-100	124	175.8	69	119.5
mmu-mir-101a	178	252.0	425	730.6
mmu-mir-101b	2874	4053.0	6369	10934.9
mmu-mir-103-1	430	607.3	231	397.6
mmu-mir-103-2	500	705.9	223	383.8
mmu-mir-105	0	1.0	0	1.0
mmu-mir-106a	1	2.4	0	1.0
mmu-mir-106b	15	22.1	25	43.9
mmu-mir-107	1205	1699.9	347	596.7
mmu-mir-10a	811	1144.4	1084	1861.9
mmu-mir-10b	1	2.4	2	4.4
mmu-mir-1186	6	9.5	1	2.7
mmu-mir-1187	2	3.8	2	4.4
mmu-mir-1188	0	1.0	0	1.0
mmu-mir-1190	1	2.4	0	1.0
mmu-mir-1191	2	3.8	2	4.4
mmu-mir-1192	1	2.4	0	1.0
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mmu-mir-1196	2	3.8	1	2.7
mmu-mir-1197	0	1.0	0	1.0
mmu-mir-1198	5	8.0	5	9.6
mmu-mir-1199	0	1.0	0	1.0
mmu-mir-122	565715	797595.2	445357	764559.7
mmu-mir-1224	0	1.0	0	1.0
mmu-mir-124-1	0	1.0	0	1.0
mmu-mir-124-2	0	1.0	1	2.7
mmu-mir-124-3	0	1.0	0	1.0
mmu-mir-125a	53	75.7	90	155.5

mmu-mir-125b-1	187	264.6	253	435.3
mmu-mir-125b-2	195	275.9	250	430.2
mmu-mir-126	4886	6889.7	9064	15561.5
mmu-mir-127	15	22.1	27	47.4
mmu-mir-128-1	3	5.2	5	9.6
mmu-mir-128-2	5	8.0	3	6.2
mmu-mir-129-1	3	5.2	2	4.4
mmu-mir-129-2	1	2.4	2	4.4
mmu-mir-1306	0	1.0	0	1.0
mmu-mir-130a	820	1157.1	1137	1952.9
mmu-mir-130b	17	25.0	6	11.3
mmu-mir-132	1	2.4	4	7.9
mmu-mir-133a-1	2	3.8	0	1.0
mmu-mir-133a-2	1	2.4	0	1.0
mmu-mir-133b	0	1.0	0	1.0
mmu-mir-134	0	1.0	0	1.0
mmu-mir-135a-1	2	3.8	0	1.0
mmu-mir-135a-2	0	1.0	1	2.7
mmu-mir-135b	0	1.0	0	1.0
mmu-mir-136	6	9.5	3	6.2
mmu-mir-137	143	202.6	56	97.1
mmu-mir-138-1	0	1.0	0	1.0
mmu-mir-138-2	0	1.0	0	1.0
mmu-mir-139	37	53.2	58	100.6
mmu-mir-140	142	201.2	144	248.2
mmu-mir-141	3	5.2	3	6.2
mmu-mir-142	499	704.5	578	993.3
mmu-mir-143	374	528.3	1689	2900.6
mmu-mir-144	553	780.7	102	176.1
mmu-mir-145	80	113.8	93	160.7
mmu-mir-146a	185	261.8	187	322.0
mmu-mir-146b	17	25.0	5	9.6
mmu-mir-147	0	1.0	0	1.0
mmu-mir-148a	25	36.2	75	129.8
mmu-mir-148b	7	10.9	22	38.8
mmu-mir-149	2	3.8	6	11.3
mmu-mir-150	16	23.6	30	52.5
mmu-mir-151	851	1200.8	885	1520.3
mmu-mir-152	27	39.1	33	57.7
mmu-mir-153	0	1.0	0	1.0
mmu-mir-154	13	19.3	6	11.3
mmu-mir-155	2	3.8	11	19.9
mmu-mir-15a	737	1040.1	441	758.1

mmu-mir-15b	1006	1419.3	608	1044.8
mmu-mir-16-1	978	1379.9	632	1086.0
mmu-mir-16-2	981	1384.1	646	1110.0
mmu-mir-17	142	201.2	204	351.2
mmu-mir-181a-1	76	108.2	83	143.5
mmu-mir-181a-2	67	95.5	82	141.8
mmu-mir-181b-1	14	20.7	8	14.7
mmu-mir-181b-2	23	33.4	21	37.1
mmu-mir-181c	18	26.4	38	66.2
mmu-mir-181d	10	15.1	10	18.2
mmu-mir-182	7	10.9	37	64.5
mmu-mir-183	2	3.8	7	13.0
mmu-mir-1839	39	56.0	30	52.5
mmu-mir-184	1	2.4	0	1.0
mmu-mir-185	648	914.6	377	648.2
mmu-mir-186	25	36.2	30	52.5
mmu-mir-187	1	2.4	3	6.2
mmu-mir-188	9	13.7	21	37.1
mmu-mir-18a	6	9.5	12	21.6
mmu-mir-18b	0	1.0	0	1.0
mmu-mir-190	5	8.0	13	23.3
mmu-mir-190b	0	1.0	1	2.7
mmu-mir-191	1690	2383.7	903	1551.2
mmu-mir-192	5736	8088.1	9089	15604.4
mmu-mir-193	130	184.3	210	361.5
mmu-mir-193b	1	2.4	5	9.6
mmu-mir-194-1	179	253.4	252	433.6
mmu-mir-194-2	441	622.8	587	1008.7
mmu-mir-195	80	113.8	103	177.8
mmu-mir-196a-1	2	3.8	0	1.0
mmu-mir-196a-2	1	2.4	0	1.0
mmu-mir-196b	0	1.0	0	1.0
mmu-mir-197	0	1.0	4	7.9
mmu-mir-199a-1	11	16.5	28	49.1
mmu-mir-199a-2	15	22.1	26	45.6
mmu-mir-199b	9	13.7	19	33.6
mmu-mir-19a	20	29.2	23	40.5
mmu-mir-19b-1	51	72.9	24	42.2
mmu-mir-19b-2	49	70.1	44	76.5
mmu-mir-200a	42	60.2	33	57.7
mmu-mir-200b	36	51.8	121	208.7
mmu-mir-200c	18	26.4	16	28.5
mmu-mir-201	2	3.8	4	7.9

mmu-mir-202	0	1.0	0	1.0
mmu-mir-203	43	61.6	90	155.5
mmu-mir-204	0	1.0	0	1.0
mmu-mir-205	0	1.0	1	2.7
mmu-mir-206	4	6.6	0	1.0
mmu-mir-207	0	1.0	0	1.0
mmu-mir-208a	0	1.0	0	1.0
mmu-mir-208b	0	1.0	0	1.0
mmu-mir-20a	66	94.1	88	152.1
mmu-mir-20b	2	3.8	3	6.2
mmu-mir-21	14699	20724.9	11146	19135.7
mmu-mir-210	27	39.1	13	23.3
mmu-mir-211	0	1.0	0	1.0
mmu-mir-212	2	3.8	0	1.0
mmu-mir-214	16	23.6	10	18.2
mmu-mir-215	0	1.0	7	13.0
mmu-mir-216a	0	1.0	0	1.0
mmu-mir-216b	0	1.0	0	1.0
mmu-mir-217	0	1.0	0	1.0
mmu-mir-218-1	1	2.4	3	6.2
mmu-mir-218-2	1	2.4	2	4.4
mmu-mir-219-1	3	5.2	2	4.4
mmu-mir-219-2	1	2.4	0	1.0
mmu-mir-22	231	326.7	232	399.3
mmu-mir-220	0	1.0	0	1.0
mmu-mir-221	118	167.4	179	308.3
mmu-mir-222	19	27.8	16	28.5
mmu-mir-223	81	115.2	62	107.4
mmu-mir-224	0	1.0	0	1.0
mmu-mir-23a	801	1130.3	915	1571.8
mmu-mir-23b	852	1202.2	740	1271.4
mmu-mir-24-1	55	78.5	107	184.7
mmu-mir-24-2	52	74.3	108	186.4
mmu-mir-25	168	237.9	104	179.5
mmu-mir-26a-1	3229	4553.5	2832	4862.8
mmu-mir-26a-2	3295	4646.6	2813	4830.2
mmu-mir-26b	2916	4112.2	2565	4404.4
mmu-mir-27a	44	63.0	80	138.3
mmu-mir-27b	511	721.5	438	752.9
mmu-mir-28	225	318.2	196	337.5
mmu-mir-290	0	1.0	0	1.0
mmu-mir-291a	0	1.0	1	2.7
mmu-mir-291b	0	1.0	0	1.0

mmu-mir-292	1	2.4	0	1.0
mmu-mir-293	0	1.0	0	1.0
mmu-mir-294	3	5.2	3	6.2
mmu-mir-295	0	1.0	0	1.0
mmu-mir-296	2	3.8	3	6.2
mmu-mir-297a-1	2	3.8	0	1.0
mmu-mir-297a-2	0	1.0	0	1.0
mmu-mir-297a-3	1	2.4	0	1.0
mmu-mir-297a-4	1	2.4	0	1.0
mmu-mir-297a-5	0	1.0	0	1.0
mmu-mir-297a-6	0	1.0	0	1.0
mmu-mir-297b	0	1.0	0	1.0
mmu-mir-297c	0	1.0	0	1.0
mmu-mir-298	0	1.0	1	2.7
mmu-mir-299	5	8.0	3	6.2
mmu-mir-29a	6425	9059.5	9793	16813.0
mmu-mir-29b-1	511	721.5	596	1024.2
mmu-mir-29b-2	602	849.8	768	1319.5
mmu-mir-29c	5484	7732.8	8672	14888.5
mmu-mir-300	4	6.6	2	4.4
mmu-mir-301a	8	12.3	10	18.2
mmu-mir-301b	0	1.0	1	2.7
mmu-mir-302a	0	1.0	0	1.0
mmu-mir-302b	0	1.0	0	1.0
mmu-mir-302c	0	1.0	0	1.0
mmu-mir-302d	0	1.0	0	1.0
mmu-mir-30a	1834	2586.7	1512	2596.7
mmu-mir-30b	528	745.4	609	1046.5
mmu-mir-30c-1	637	899.1	702	1206.1
mmu-mir-30c-2	578	815.9	756	1298.8
mmu-mir-30d	729	1028.8	626	1075.7
mmu-mir-30e	852	1202.2	674	1158.1
mmu-mir-31	142	201.2	217	373.5
mmu-mir-32	68	96.9	60	104.0
mmu-mir-320	450	635.4	163	280.8
mmu-mir-322	101	143.4	91	157.2
mmu-mir-323	0	1.0	0	1.0
mmu-mir-324	51	72.9	69	119.5
mmu-mir-325	0	1.0	0	1.0
mmu-mir-326	4	6.6	17	30.2
mmu-mir-327	0	1.0	0	1.0
mmu-mir-328	47	67.3	35	61.1
mmu-mir-329	1	2.4	0	1.0

mmu-mir-33	5	8.0	22	38.8
mmu-mir-330	2	3.8	4	7.9
mmu-mir-331	9	13.7	3	6.2
mmu-mir-335	606	855.4	434	746.1
mmu-mir-337	0	1.0	0	1.0
mmu-mir-338	5	8.0	5	9.6
mmu-mir-339	22	32.0	35	61.1
mmu-mir-340	108	153.3	99	171.0
mmu-mir-341	0	1.0	1	2.7
mmu-mir-342	42	60.2	17	30.2
mmu-mir-343	0	1.0	0	1.0
mmu-mir-344-1	0	1.0	0	1.0
mmu-mir-344-2	0	1.0	0	1.0
mmu-mir-345	39	56.0	85	146.9
mmu-mir-346	0	1.0	1	2.7
mmu-mir-34a	38	54.6	110	189.8
mmu-mir-34b	3	5.2	0	1.0
mmu-mir-34c	1	2.4	0	1.0
mmu-mir-350	17	25.0	21	37.1
mmu-mir-351	153	216.7	72	124.6
mmu-mir-361	93	132.1	97	167.5
mmu-mir-362	28	40.5	30	52.5
mmu-mir-363	1	2.4	0	1.0
mmu-mir-365-1	116	164.5	109	188.1
mmu-mir-365-2	82	116.6	97	167.5
mmu-mir-367	0	1.0	0	1.0
mmu-mir-369	4	6.6	4	7.9
mmu-mir-370	0	1.0	0	1.0
mmu-mir-374	23	33.4	17	30.2
mmu-mir-375	2	3.8	0	1.0
mmu-mir-376a	31	44.7	14	25.0
mmu-mir-376b	15	22.1	4	7.9
mmu-mir-376c	7	10.9	4	7.9
mmu-mir-377	3	5.2	0	1.0
mmu-mir-378	1108	1563.2	2227	3824.2
mmu-mir-379	3	5.2	5	9.6
mmu-mir-380	1	2.4	0	1.0
mmu-mir-381	0	1.0	0	1.0
mmu-mir-382	6	9.5	0	1.0
mmu-mir-383	1	2.4	0	1.0
mmu-mir-384	0	1.0	0	1.0
mmu-mir-409	0	1.0	1	2.7
mmu-mir-410	1	2.4	0	1.0

mmu-mir-411	12	17.9	5	9.6
mmu-mir-412	0	1.0	0	1.0
mmu-mir-421	8	12.3	5	9.6
mmu-mir-423	182	257.6	112	193.3
mmu-mir-425	79	112.4	59	102.3
mmu-mir-429	8	12.3	7	13.0
mmu-mir-431	0	1.0	0	1.0
mmu-mir-432	0	1.0	0	1.0
mmu-mir-433	0	1.0	0	1.0
mmu-mir-434	0	1.0	0	1.0
mmu-mir-448	0	1.0	0	1.0
mmu-mir-449a	0	1.0	0	1.0
mmu-mir-449b	0	1.0	0	1.0
mmu-mir-449c	0	1.0	0	1.0
mmu-mir-450a-1	14	20.7	16	28.5
mmu-mir-450a-2	10	15.1	9	16.5
mmu-mir-450b	3	5.2	5	9.6
mmu-mir-451	2132	3006.9	729	1252.5
mmu-mir-452	0	1.0	0	1.0
mmu-mir-453	0	1.0	0	1.0
mmu-mir-455	46	65.9	50	86.8
mmu-mir-463	0	1.0	0	1.0
mmu-mir-464	0	1.0	0	1.0
mmu-mir-465a	0	1.0	0	1.0
mmu-mir-465b-1	0	1.0	0	1.0
mmu-mir-465b-2	0	1.0	0	1.0
mmu-mir-465c-1	0	1.0	0	1.0
mmu-mir-465c-2	2	3.8	0	1.0
mmu-mir-466a	1	2.4	1	2.7
mmu-mir-466b-1	2	3.8	0	1.0
mmu-mir-466b-2	3	5.2	0	1.0
mmu-mir-466b-3	1	2.4	0	1.0
mmu-mir-466c	2	3.8	0	1.0
mmu-mir-466d	2	3.8	2	4.4
mmu-mir-466e	1	2.4	0	1.0
mmu-mir-466f-1	4	6.6	0	1.0
mmu-mir-466f-2	0	1.0	0	1.0
mmu-mir-466f-3	1	2.4	0	1.0
mmu-mir-466f-4	0	1.0	0	1.0
mmu-mir-466g	0	1.0	0	1.0
mmu-mir-466h	0	1.0	0	1.0
mmu-mir-466i	1	2.4	0	1.0
mmu-mir-466j	1	2.4	0	1.0

mmu-mir-466k	1	2.4	0	1.0
mmu-mir-466l	0	1.0	0	1.0
mmu-mir-467a	2	3.8	1	2.7
mmu-mir-467b	0	1.0	0	1.0
mmu-mir-467c	2	3.8	1	2.7
mmu-mir-467d	1	2.4	1	2.7
mmu-mir-467e	6	9.5	11	19.9
mmu-mir-467f	0	1.0	0	1.0
mmu-mir-467g	2	3.8	0	1.0
mmu-mir-467h	0	1.0	1	2.7
mmu-mir-468	0	1.0	0	1.0
mmu-mir-469	0	1.0	0	1.0
mmu-mir-470	0	1.0	0	1.0
mmu-mir-471	0	1.0	0	1.0
mmu-mir-483	0	1.0	0	1.0
mmu-mir-484	126	178.6	78	134.9
mmu-mir-485	2	3.8	0	1.0
mmu-mir-486	933	1316.4	145	249.9
mmu-mir-487b	0	1.0	0	1.0
mmu-mir-488	0	1.0	0	1.0
mmu-mir-489	0	1.0	0	1.0
mmu-mir-490	0	1.0	1	2.7
mmu-mir-491	1	2.4	1	2.7
mmu-mir-493	0	1.0	0	1.0
mmu-mir-494	6	9.5	0	1.0
mmu-mir-495	0	1.0	0	1.0
mmu-mir-496	1	2.4	0	1.0
mmu-mir-497	7	10.9	48	83.4
mmu-mir-499	1	2.4	0	1.0
mmu-mir-500	18	26.4	23	40.5
mmu-mir-501	8	12.3	6	11.3
mmu-mir-503	22	32.0	25	43.9
mmu-mir-504	0	1.0	4	7.9
mmu-mir-505	34	48.9	16	28.5
mmu-mir-509	0	1.0	0	1.0
mmu-mir-511	52	74.3	60	104.0
mmu-mir-532	31	44.7	37	64.5
mmu-mir-539	0	1.0	0	1.0
mmu-mir-540	0	1.0	0	1.0
mmu-mir-541	32	46.1	3	6.2
mmu-mir-542	7	10.9	9	16.5
mmu-mir-543	0	1.0	0	1.0
mmu-mir-544	0	1.0	0	1.0

mmu-mir-546	1	2.4	0	1.0
mmu-mir-547	1	2.4	3	6.2
mmu-mir-551b	2	3.8	3	6.2
mmu-mir-568	0	1.0	0	1.0
mmu-mir-574	177	250.5	48	83.4
mmu-mir-582	0	1.0	1	2.7
mmu-mir-590	0	1.0	0	1.0
mmu-mir-592	3	5.2	0	1.0
mmu-mir-598	1	2.4	2	4.4
mmu-mir-599	0	1.0	0	1.0
mmu-mir-615	0	1.0	0	1.0
mmu-mir-652	28	40.5	45	78.3
mmu-mir-653	0	1.0	0	1.0
mmu-mir-654	0	1.0	0	1.0
mmu-mir-664	23	33.4	17	30.2
mmu-mir-665	3	5.2	2	4.4
mmu-mir-666	0	1.0	0	1.0
mmu-mir-667	1	2.4	0	1.0
mmu-mir-668	0	1.0	0	1.0
mmu-mir-669a-1	0	1.0	1	2.7
mmu-mir-669a-2	0	1.0	2	4.4
mmu-mir-669a-3	0	1.0	0	1.0
mmu-mir-669b	1	2.4	0	1.0
mmu-mir-669c	1	2.4	1	2.7
mmu-mir-669d	0	1.0	2	4.4
mmu-mir-669e	1	2.4	1	2.7
mmu-mir-669f	0	1.0	0	1.0
mmu-mir-669g	0	1.0	0	1.0
mmu-mir-669h	0	1.0	1	2.7
mmu-mir-669i	2	3.8	0	1.0
mmu-mir-669j	0	1.0	0	1.0
mmu-mir-669k	0	1.0	0	1.0
mmu-mir-669l	1	2.4	0	1.0
mmu-mir-669m-1	0	1.0	1	2.7
mmu-mir-669m-2	0	1.0	0	1.0
mmu-mir-669n	0	1.0	0	1.0
mmu-mir-669o	2	3.8	1	2.7
mmu-mir-670	0	1.0	0	1.0
mmu-mir-671	30	43.3	30	52.5
mmu-mir-672	0	1.0	0	1.0
mmu-mir-673	0	1.0	0	1.0
mmu-mir-674	460	649.5	349	600.1
mmu-mir-675	0	1.0	0	1.0

mmu-mir-676	36	51.8	33	57.7
mmu-mir-677	4	6.6	1	2.7
mmu-mir-678	0	1.0	0	1.0
mmu-mir-679	0	1.0	0	1.0
mmu-mir-680-1	0	1.0	0	1.0
mmu-mir-680-2	0	1.0	0	1.0
mmu-mir-680-3	0	1.0	0	1.0
mmu-mir-681	0	1.0	0	1.0
mmu-mir-682	0	1.0	0	1.0
mmu-mir-683-1	0	1.0	0	1.0
mmu-mir-683-2	0	1.0	0	1.0
mmu-mir-684-1	0	1.0	0	1.0
mmu-mir-684-2	0	1.0	0	1.0
mmu-mir-685	0	1.0	0	1.0
mmu-mir-686	0	1.0	0	1.0
mmu-mir-687	0	1.0	0	1.0
mmu-mir-688	0	1.0	0	1.0
mmu-mir-690	17	25.0	4	7.9
mmu-mir-691	0	1.0	0	1.0
mmu-mir-692-1	0	1.0	0	1.0
mmu-mir-692-2	11	16.5	0	1.0
mmu-mir-693	0	1.0	0	1.0
mmu-mir-694	0	1.0	0	1.0
mmu-mir-695	0	1.0	0	1.0
mmu-mir-696	0	1.0	0	1.0
mmu-mir-697	0	1.0	0	1.0
mmu-mir-698	0	1.0	0	1.0
mmu-mir-700	2	3.8	2	4.4
mmu-mir-701	0	1.0	0	1.0
mmu-mir-702	0	1.0	0	1.0
mmu-mir-703	4	6.6	2	4.4
mmu-mir-704	0	1.0	0	1.0
mmu-mir-705	0	1.0	0	1.0
mmu-mir-706	33	47.5	6	11.3
mmu-mir-707	0	1.0	0	1.0
mmu-mir-708	0	1.0	1	2.7
mmu-mir-709	1	2.4	0	1.0
mmu-mir-710	0	1.0	0	1.0
mmu-mir-711	0	1.0	0	1.0
mmu-mir-712	0	1.0	0	1.0
mmu-mir-713	0	1.0	0	1.0
mmu-mir-714	0	1.0	0	1.0
mmu-mir-715	0	1.0	0	1.0

mmu-mir-717	0	1.0	0	1.0
mmu-mir-718	0	1.0	0	1.0
mmu-mir-719	0	1.0	0	1.0
mmu-mir-720	4	6.6	5	9.6
mmu-mir-721	0	1.0	0	1.0
mmu-mir-741	1	2.4	0	1.0
mmu-mir-742	0	1.0	0	1.0
mmu-mir-743a	0	1.0	0	1.0
mmu-mir-743b	0	1.0	0	1.0
mmu-mir-744	110	156.1	87	150.4
mmu-mir-758	0	1.0	0	1.0
mmu-mir-759	0	1.0	0	1.0
mmu-mir-760	0	1.0	1	2.7
mmu-mir-761	0	1.0	0	1.0
mmu-mir-762	0	1.0	0	1.0
mmu-mir-763	0	1.0	0	1.0
mmu-mir-764	0	1.0	0	1.0
mmu-mir-767	0	1.0	0	1.0
mmu-mir-770	0	1.0	0	1.0
mmu-mir-7a-1	324	457.8	329	565.8
mmu-mir-7a-2	304	429.6	261	449.1
mmu-mir-7b	2	3.8	3	6.2
mmu-mir-802	135	191.3	91	157.2
mmu-mir-804	0	1.0	0	1.0
mmu-mir-805	228	322.5	107	184.7
mmu-mir-871	0	1.0	0	1.0
mmu-mir-872	3	5.2	9	16.5
mmu-mir-873	0	1.0	0	1.0
mmu-mir-874	14	20.7	9	16.5
mmu-mir-875	0	1.0	0	1.0
mmu-mir-876	0	1.0	0	1.0
mmu-mir-877	4	6.6	7	13.0
mmu-mir-878	0	1.0	0	1.0
mmu-mir-879	0	1.0	0	1.0
mmu-mir-880	1	2.4	0	1.0
mmu-mir-881	0	1.0	0	1.0
mmu-mir-882	0	1.0	0	1.0
mmu-mir-883a	0	1.0	0	1.0
mmu-mir-883b	0	1.0	0	1.0
mmu-mir-9-1	0	1.0	0	1.0
mmu-mir-9-2	0	1.0	0	1.0
mmu-mir-9-3	0	1.0	0	1.0
mmu-mir-92a-1	188	266.1	246	423.3

mmu-mir-92a-2	14	20.7	10	18.2
mmu-mir-92b	0	1.0	0	1.0
mmu-mir-93	90	127.9	100	172.7
mmu-mir-96	2	3.8	8	14.7
mmu-mir-98	368	519.8	251	431.9
mmu-mir-99a	1050	1481.4	316	543.5
mmu-mir-99b	18	26.4	31	54.2