miRTarBase 2025: updates to the collection of experimentally validated microRNA–target interactions

Shidong Cui[1,2,†], Sicong Yu[1,2,†], Hsi-Yuan Huang [1,2], Yang-Chi-Dung Lin[1,2], Yixian Huang[1,2], Bojian Zhang[1,2], Jihan Xiao [1,2], Huali Zuo[1,2], Jiayi Wang[3], Zhuoran Li[1,2], Guanghao Li[2], Jiajun Ma[1,2], Baiming Chen[1,2], Haoxuan Zhang[1,2], Jiehui Fu[1,2], Liang Wang[3,*] and Hsien-Da Huang [1,2,4,5,*]

[1]School of Medicine, The Chinese University of Hong Kong, Shenzhen, Guangdong 518172, P.R. China
[2]Warshel Institute for Computational Biology, School of Medicine, The Chinese University of Hong Kong, Shenzhen, Guangdong 518172, P.R. China
[3]Stem Cell Clinical Research Center, The First Affiliated Hospital of Dalian Medical University, Dalian, Liaoning 116011, P.R. China
[4]Guangdong Provincial Key Laboratory of Digital Biology and Drug Development, The Chinese University of Hong Kong, Shenzhen, Guangdong, 518172, P.R. China
[5]Department of Endocrinology, Key Laboratory of Endocrinology of National Ministry of Health, Peking Union Medical College Hospital, Chinese Academy of Medical Science & Peking Union Medical College, Beijing, 100730, China

*To whom correspondence should be addressed. Tel: +86 755 2351 9601; Email: huanghsienda@cuhk.edu.cn
Correspondence may also be addressed to Liang Wang. Tel: +86 411 3970 2222; Email: wangliang@dmu.edu.cn
†These authors contributed equally to this work as first authors.
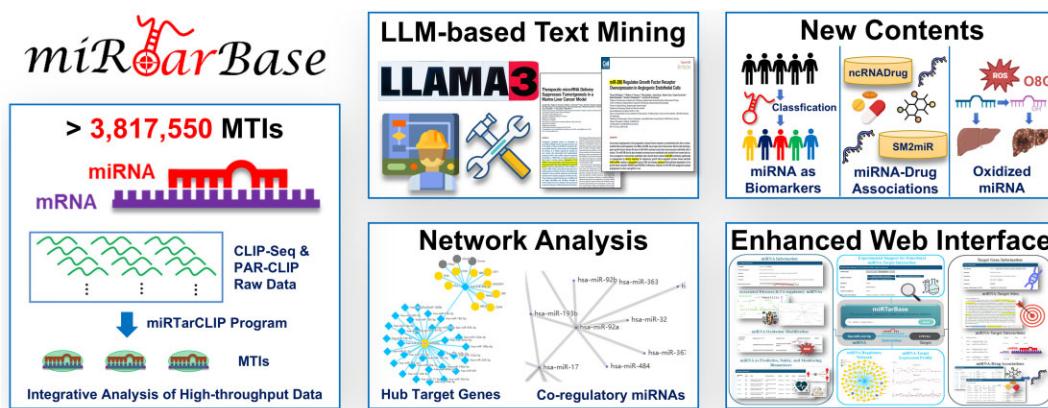
Abstract

MicroRNAs (miRNAs) are small non-coding RNAs (18–26 nucleotides) that regulate gene expression by interacting with target mRNAs, affecting various physiological and pathological processes. miRTarBase, a database of experimentally validated miRNA–target interactions (MTIs), now features over 3 817 550 validated MTIs from 13 690 articles, significantly expanding its previous version. The updated database includes miRNA interactions with therapeutic agents, revealing roles in drug resistance and therapeutic strategies. It also highlights miRNAs as predictive, safety and monitoring biomarkers for toxicity assessment, clinical treatment guidance and therapeutic optimization. The expansion of miRNA–mRNA and miRNA–miRNA networks allows the identification of key regulatory genes and co-regulatory miRNAs, providing deeper insights into miRNA functions and critical target genes. Information on oxidized miRNA sequences has been added, shedding light on how oxidative modifications influence miRNA targeting and regulation. The integration of the LLAMA3 model into the NLP pipeline, alongside prompt engineering, enables the efficient identification of MTIs and miRNA–disease associations without large training datasets. An updated data integration and a redesigned user interface enhance accessibility, reinforcing miRTarBase as an essential resource for molecular oncology, drug development and related fields. The updated miRTarBase is available at https://mirtarbase.cuhk.edu.cn/~miRTarBase/miRTarBase_2025.

Graphical abstract

Introduction

MicroRNAs (miRNAs) are short, non-coding RNAs, approximately 22 nucleotides in length, that play a crucial role in regulating biological processes in animals, plants and fungi (1). The regulatory mechanism involves miRNAs binding to their target mRNAs with perfect or partial complementarity, leading to mRNA cleavage or translational repression and ultimately altering the expression of protein-coding genes (2). This microRNA-target interaction (MTI) typically occurs between the 5′ seed region of the miRNA (3) and the 3′ untranslated region (3′UTR) of the target mRNA, potentially inducing decapping or alkylation of the target mRNA (4,5). Experimentally, miRNAs have been shown to regulate various biological processes, including the cell cycle (6), cell development, apoptosis (7,8) and pathological processes such as cancer progression (9). Therefore, identifying MTIs is of paramount importance for understanding these biological processes and for developing strategies to address pathological conditions.

The growing need to identify and analyze MTIs has recently driven the development of numerous online resources, including databases and functional tools. TarBase curates experimentally validated MTIs via manual curation and incorporates virally encoded miRNAs in its newest version (10). HMDD is a continually updated database of experimentally supported miRNA–disease associations, curated from biomedical literature, and includes 53 530 associations between 1871 miRNAs and 2360 diseases (11). miRNATissueAtlas2 is another database that curates a miRNA atlas from 188 tissue samples across 21 organ types obtained from six humans. TheMarker is a recent comprehensive database storing various types of therapeutic and monitoring biomarkers, including microRNAs (12). ncRNADrug is also a recent database that focuses on non-coding RNAs, miRNA in particular, that are associated with cancer drug resistance and potentially therapeutic targets (13). Furthermore, a large collection of single-nucleotide polymorphisms (SNPs) and disease-associated variants (DRVs) related to miRNA can be found in resources like dbSNP (14), the GWAS Catalog (15), ClinVar (16) and COSMIC (17).

MiRNA-mRNA networks are complex regulatory systems that fine-tune gene expression across various biological processes. These networks are particularly crucial in cancer biology, where they regulate tumor suppressors and oncogenes. For example, specific miRNA–mRNA networks identified in non-small cell lung cancer play central roles in disease progression and offer potential therapeutic targets (18). MiRNAs often target multiple mRNAs simultaneously, and conversely, a single mRNA can be regulated by multiple miRNAs, forming intricate networks that ensure robust gene expression control (19). In cancer, these networks undergo reprogramming, with shifts in hub miRNA contributing to disease pathogenesis (20). Beyond miRNA–mRNA interactions, miRNA–miRNA networks, where miRNAs regulate each other either directly or through shared mRNA targets, add further layers of complexity. Therefore, constructing these networks would add a valuable layer of information to miRNA research, particularly in the context of disease.

Large language models (LLMs) can generate human-like text responses to prompts without requiring task-specific training (21). This capability allows LLMs to be directly applied in microRNA text mining to extract relevant sentences about MTI or miRNA–disease associations, as well as microRNA and target/disease entities, without the need for large training data—a key advantage over traditional natural language processing (NLP) models like BERT. ChatGPT is the most well-known LLM but is computationally expensive and not open-source. In contrast, META's LLAMA is an open-source LLM with significantly fewer parameters, offering comparable performance to ChatGPT (22). This makes LLAMA more accessible for researchers, enabling them to localize the model within their computing environments and process biomedical documents at scale.

Recent studies have highlighted the significant impact of oxidative stress on miRNA function. Reactive oxygen species (ROS) can induce oxidative modifications in miRNA sequences, leading to altered base pairing and changes in their target recognition (23,24). Such modifications can cause miRNAs to bind to different mRNA targets than they would in their unmodified state, potentially altering downstream gene expression and regulatory pathways. These changes may result in different biological outcomes, particularly under conditions of oxidative stress, where the regulation of key genes can be significantly affected. Understanding these oxidative modifications is crucial for comprehending the full spectrum of miRNA-mediated gene regulation, especially in disease contexts where oxidative stress is prevalent.

miRTarBase is a manually curated database of experimentally validated MTIs and has been updated ten times since its launch in 2011 (25–30). This time, miRTarBase expands its scope by constructing miRNA regulatory networks linked to diseases and incorporating data on miRNA biomarkers, drug resistance, small molecule effects on miRNA expression and miRNA oxidation, thus offering a richer, multidimensional resource than counterparts like TarBase (10). In this latest update, miRTarBase integrates over 3 817 550 validated MTIs from 13 690 research articles, reflecting a significant expansion of data and improved curation processes. To aid in the manual curation of MTIs, this release incorporates the LLAMA3 model (22) into its NLP pipeline, which enables the identification of MTIs and miRNA–disease associations from extensive biomedical documents without the need for large training datasets. New data on miRNA interactions with therapeutic agents (31), including their roles in drug resistance (13), have been added, providing critical insights into therapeutic strategies. Additionally, this update highlights the potential of miRNAs as predictive, safety and monitoring biomarkers (12) for evaluating toxicity, guiding clinical treatments and optimizing therapeutic outcomes. Moreover, this update features miRNA–mRNA and miRNA–miRNA regulatory networks, enabling the identification of key regulatory nodes and co-regulatory miRNAs, which provides deeper insights into miRNA functions and highlights critical target genes, opening new avenues for therapeutic target discovery and biomarker identification. Notably, this update also includes the collection of oxidized miRNA sequences, further expanding our understanding of how oxidative modifications can alter miRNA targeting and regulation. The newly redesigned user interface and architecture have also enhanced usability and data accessibility, making miRTarBase an invaluable tool for researchers studying miRNA-related processes in fields like molecular oncology, toxicology and drug development.
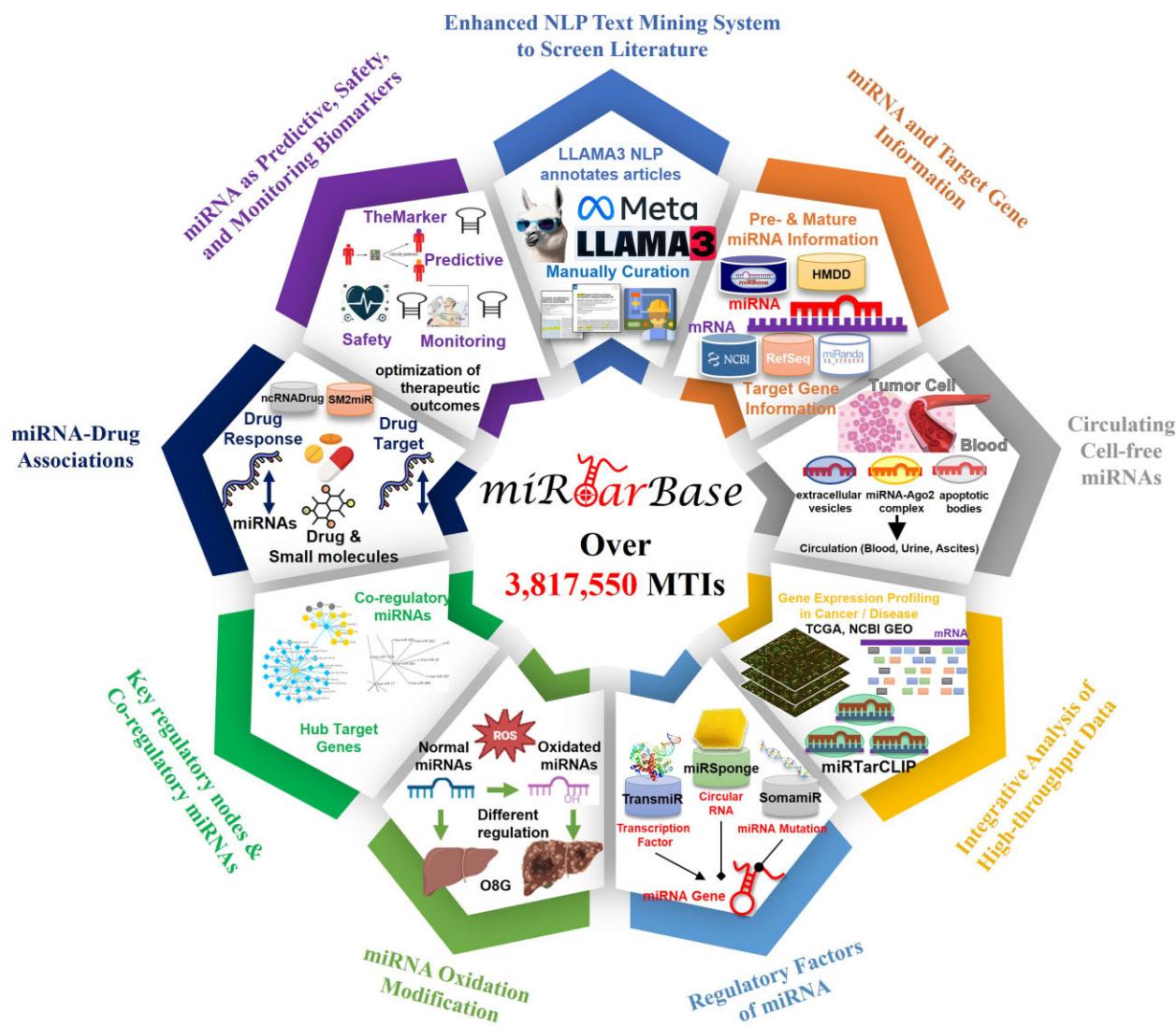
Figure 1. Highlighted improvements of miRTarBase. As the most comprehensive resource on MTIs, this update accumulates >3 817 550 manually confirmed MTIs supported with experimental evidence.

System overview and database content

Since its launch in 2011, miRTarBase has been a leading resource in microRNA research which is continuously updated to maintain its relevance and accuracy. miRTarBase has consistently been improved in each update, refining its data collection methods and offering a more user-friendly interface. This ensures that researchers in the miRNA field have access to a comprehensive, efficient and high-quality platform.

In this latest update, we have harnessed the power of LLM for the first time, integrating META's LLAMA3 LLM model (22) into our NLP pipeline. This has significantly facilitated the manual curation of MTIs and miRNA–disease associations without requiring a large amount of training data compared to previous versions. miRTarBase now also includes data on miRNA interactions with therapeutic agents, highlighting their role in drug resistance and therapeutic strategies. Furthermore, the update emphasizes the importance of miRNAs as predictive biomarkers for toxicity assessment, clinical treatment guidance and optimization of therapeutic outcomes. Additionally, this update has incorporated data on oxidized miRNA sequences, providing insights into how oxida-

tive modifications can alter miRNA targeting and regulatory functions. A substantial expansion of MTIs validated through high-throughput methods, including CLIP-seq (32) and PAR-CLIP (33), has also been incorporated. Additionally, the entire database architecture and user interface have been redesigned to improve visualization, accessibility and data retrieval. Figure 1 illustrates the current structure and major advancements in miRTarBase.

Several key databases have been integrated to further enrich miRTarBase, including TransmiR (34) for miRNA regulation, miRSponge (35) for miRNA sponging, HMDD (11) for disease associations, miRBase (36) for miRNA sequences and NCBI Gene (37) and RefSeq (38) for target gene information. Data on SNPs and DRVs have been drawn from dbSNP (14), GWAS Catalog (15), ClinVar (16) and COSMIC (17), while gene and miRNA expression profiles have been incorporated from GEO (39), TCGA (40,41), CMEP (42), TissueAtlas (43) and EVmiRNA (44). miRNA editing events have been integrated from MiREDiBase (45). Associations between miRNAs and small molecules have been obtained from SM2miR (31) and ncRNADrug (13), while data on miRNAs as biomarkers

Table 1. List of the databases that are integrated by miRTarBase

Type	Database name
Gene and miRNA-specific databases	miRBase (36), NCBI Gene (37), NCBI RefSeq (38)
SNPs and disease-related variants	dbSNP (14), GWAS Catalog (15), ClinVar (16), COSMIC (17)
microRNA-disease association database	HMDD (11)
The regulation of microRNAs	TransMir (34), miRSponge (35)
miRNAs expression	TissueAtlas (43), EVmiRNA (44), Gene Expression Omnibus (GEO) (39), The Cancer Genome Atlas (TCGA) (40,41), CMEP (42)
Editing events in miRNAs	MiREDiBase (45)
microRNA-small molecule association databases	SM2miR (31), ncRNADrug (13)
miRNA as biomarkers	TheMarker (12)

have been sourced from TheMarker (12). A detailed list of integrated databases is provided in Table 1.

Updated database content and statistics

The updated miRTarBase introduces significant advancements and expanded database content, as detailed in Table 2. This version integrates over 3 817 550 curated MTIs from 13 690 articles, marking a substantial increase in both the quantity and quality of data since the previous release. Notably, miRTarBase now employs the LLAMA3 model (22) within its NLP pipeline, significantly enhancing data curation. This update also introduces new data on miRNA interactions with therapeutic agents, emphasizing the role of miRNAs in drug resistance (13) and clinical applications (31). Additionally, miRTarBase 2025 has expanded its collection of high-throughput experimental data, incorporating 497 CLIP-seq and PAR-CLIP datasets from various studies, further enriching the validated MTIs.

This version also features an expanded range of species, increasing from 37 to 39, and has integrated updates to the gene and miRNA reference entries, ensuring alignment with the latest databases. Furthermore, miRTarBase supports the analysis of miRNA biomarkers for toxicity and therapeutic outcomes (12), offering valuable insights into miRNAs' roles in disease diagnostics and treatment optimization. The update also includes data on oxidized miRNA sequences, shedding light on how oxidative modifications can influence miRNA targeting and regulation. The newly redesigned architecture and user interface enhance accessibility and facilitate more efficient data retrieval. These improvements make miRTarBase an even more indispensable resource for researchers focusing on MTIs, particularly in molecular oncology and drug development.

miRNAs associated with drug resistance

The latest update of miRTarBase includes comprehensive data on miRNAs that play a pivotal role in drug resistance mechanisms. Based on emerging evidence, specific miRNAs have been found to regulate key processes in cancer drug resistance, such as miR-149–3p, which promotes cisplatin resistance in ovarian cancer by targeting CDKN1A and TIMP2 (46). Additionally, miRNAs such as miR-491 have been implicated

Table 2. Improvements and the number of MTIs with different validation methods provided by miRTarBase

Features	miRTarBase 9.0	miRTarBase 10.0
Release date	15 September 2021	30 September 2024
Known miRNA entry	miRbase v22	miRbase v22.1
Known gene entry	Entrez 2021	Entrez 2024
Species	37	39
Curated articles	13 389	13 690
miRNAs	4630	4854
Target genes	27 172	31 439
CLIP-seq and PAR-CLIP datasets	440	497
Curated MTIs	2 200 449	3 817 550
Text mining technique to prescreen literature	Enhanced NLP + Scoring system	LLM-based model + Enhanced NLP + Scoring system
Download by validated miRNA-target sites	Yes	Yes
Browse by miRNA, gene, and disease	Yes	Yes
Regulation of microRNAs	Yes	Yes
Cell-free miRNA expression	Yes	Yes
miRNAs in extracellular vesicles	Yes	Yes
Human miRNA tissue atlas	Yes	Yes
Editing events in miRNAs	Yes	Yes
SNPs and disease-related variants	Yes	Yes
miRNA associated with drug resistance	No	Yes
Small molecules' effects on miRNA expression	No	Yes
miRNA as biomarkers	No	Yes
miRNA oxidation modification	No	Yes
MTIs Supported by strong experimental evidence		
Number of MTIs validated by 'Reporter assay'	16 257	24 530
Number of MTIs validated by 'Western blot'	14 665	18 292
Number of MTIs validated by 'qPCR'	16 483	19 308
Number of MTIs validated by 'Reporter assay and Western blot'	12 171	15 227
Number of MTIs validated by 'Reporter assay or Western blot'	18 751	27 595

in overcoming resistance to therapeutic agents like doxorubicin, highlighting their potential as therapeutic targets (47). In collaboration with datasets from the ncRNADrug database (13), miRTarBase now incorporates miRNA interactions with 266 drugs, facilitating the identification of drug–miRNA relationships that impact drug sensitivity and resistance. This expanded dataset significantly enhances the understanding of miRNAs' roles in drug resistance, offering researchers a powerful tool to explore miRNAs not only as biomarkers but also as key regulators in the development of new therapeutic strategies aimed at reversing drug resistance. These insights have the potential to shape the future of cancer treatment by guiding the design of more effective combination therapies and personalized medicine approaches.

Small molecules' effects on miRNA expression

In recent years, research has revealed that bioactive small molecules can regulate the expression of miRNAs (48), influencing key biological pathways and offering potential therapeutic strategies. The latest update of miRTarBase includes curated data from the SM2miR database (31), which contains 2925 experimentally validated relationships between 151 small molecules and 747 miRNAs across 17 species. These small molecules, including chemotherapeutic agents like 5-fluorouracil and histone deacetylase inhibitors like trichostatin A, have been shown to either upregulate or downregulate specific miRNAs, altering cancer cell behavior and therapy response (49,50). By providing a detailed repository of small molecule–miRNA interactions, this update enables researchers to explore how small molecules can modulate miRNA expression, potentially reversing disease-related dysregulation of miRNAs. This expanded dataset will be instrumental in advancing miRNA-based therapies, guiding drug development, and facilitating the discovery of novel treatments for cancer and other diseases.

miRNA as predictive, safety and monitoring biomarkers

MicroRNAs have emerged as key players in the realm of predictive, safety, and monitoring biomarkers, offering significant potential for personalized medicine and enhancing the precision of therapeutic interventions (51). In this latest update, miRTarBase integrates a wealth of data from TheMarker database (12), which provides comprehensive insights into the role of miRNAs across various stages of drug development and clinical practice. miRNAs, such as miR-21 and miR-146a, have been identified as crucial predictive and safety biomarkers, helping to determine which patients are most likely to respond positively to treatments such as immunotherapies (52,53). Meanwhile, miR-122 has gained prominence as a reliable safety biomarker for monitoring liver toxicity, particularly in response to hepatotoxic drugs (54). Furthermore, miRNAs serve as monitoring biomarkers, enabling the continuous assessment of patient status throughout treatment, facilitating early detection of adverse reactions, and adjusting therapeutic approaches in real time (55). This expanded dataset, backed by TheMarker, strengthens the ability of researchers and clinicians to utilize miRNAs as non-invasive, dynamic biomarkers, significantly improving the safety, efficacy and personalization of clinical treatments.

Accumulated CLIP-seq and PAR-CLIP data

The accumulation of CLIP-seq and PAR-CLIP data has significantly contributed to identifying biologically relevant microRNA-target interactions (56). As of the latest update, miRTarBase has incorporated 413 CLIP-seq and 60 PAR-CLIP datasets for human samples and 65 CLIP-seq and 17 PAR-CLIP datasets for mouse samples, covering the period from 1 September 2021 to 15 June 2024 (Table 3 and Supplementary Table S1). These datasets were systematically analyzed using miRTarCLIP (57), a tool developed by our lab and validated for robustness on both CLIP-seq and PAR-CLIP datasets, enabling the discovery of a substantial number of MTIs. The integration of these high-throughput sequencing datasets into miRTarBase not only expands the database's content but also enhances its utility for researchers, allowing the identification of MTIs that might not have been discov-

Table 3. CLIP-seq and PAR-CLIP datasets from GEO that are incorporated into miRTarBase v10.0

Species	Type of high-throughput sequencing	Number of experiments	Number of MTIs	Publication date
Human	CLIP-Seq	413	1 433 920	1 September 2021 to 15 June 2024
	PAR-CLIP	60		
Mouse	CLIP-Seq	65	181 606	
	PAR-CLIP	17		

ered through traditional methods. However, high-throughput data from CLIP sequencings provide weaker experimental evidence compared to more robust methods such as Luciferase Reporter Assay and Western Blotting. Users could select the MTI data of interest according to different confidence levels and their specific needs.

Analysis of miRNA-mediated regulatory networks

miRNA-mediated post-transcriptional regulation plays a pivotal role in controlling gene expression, with miRNAs extensively implicated in various cancers and other diseases (58,59). Given their broad regulatory capacity, miRNAs hold great promise for both diagnostic and therapeutic applications (60). Typically, miRNAs exert their effects by targeting mRNAs, leading to mRNA degradation or translation inhibition. However, deciphering the most critical MTIs is challenging due to the polygenic nature of miRNA interactions, where a single miRNA can regulate multiple target genes. We utilized protein–protein interaction (PPI) networks to address this to prioritize relevant target genes. We selected miRNA target genes with strong experimental evidence (e.g. reporter assays, Western blot, qPCR) and applied STRING (61) to construct PPI networks, setting a minimum interaction score of 0.150 for comprehensive inclusion. Integrating PPI network analysis is essential for identifying key target genes regulated by miRNAs and gaining deeper insights into biological regulatory mechanisms. PPI networks reveal the roles of miRNA target genes in disease-related signaling pathways, especially when these target genes serve as 'hub' nodes within the network (62). Significant interactions were then analyzed using Cytoscape (63,64) to compute Degree Centrality, Closeness Centrality and Betweenness Centrality, helping refine the network by identifying key regulatory nodes. In PPI networks, Degree Centrality identifies important hub genes with many connections, Closeness Centrality highlights genes that efficiently propagate signals and Betweenness Centrality pinpoints genes that bridge different network parts. These measures help prioritize genes critical for maintaining network functionality and biological impact. This combined approach of using PPI data, experimental evidence, and computational analysis enables more accurate identification of key regulatory nodes, offering a deeper understanding of miRNA-mediated regulatory mechanisms.

Additionally, miRNA–miRNA interactions, especially those involving miRNAs with common target genes, are crucial for understanding their cooperative regulatory roles in disease contexts (65,66). To explore this, we constructed a network of all miRNAs associated with a specific disease, treating miRNAs as nodes with edges representing the num-

ber of shared target genes between pairs. Using Cytoscape (63,64) again, we calculated centrality metrics to evaluate each miRNA's significance within the broader network. This miRNA interaction network provides a platform for investigating miRNA–disease associations, allowing researchers to visualize cooperative or competitive miRNA interactions. By mapping shared targets and interconnections among miRNAs, this approach enhances our understanding of miRNA regulatory networks and opens new avenues for identifying therapeutic targets and biomarkers for clinical applications.

miRNA oxidation data integration

Oxidative modifications of miRNAs have gained increasing attention due to their significant impact on miRNA function and gene regulation. Oxidation can alter miRNA sequences, leading to changes in their target recognition and regulatory outcomes, which can influence various biological processes, including disease progression and response to therapies (23,24). Recognizing the importance of this phenomenon, the latest update of miRTarBase has integrated data on oxidized miRNA sequences from existing literature, providing researchers with access to detailed information on miRNA oxidation events. This addition allows for a deeper understanding of how oxidative modifications affect miRNA targeting and their broader roles in cellular regulation. By offering these data, miRTarBase enables researchers to explore new avenues in the study of oxidative stress and its implications in disease, thereby enhancing the utility of the database in advanced miRNA research.

Enhanced text mining system

The increasing volume of biomedical literature on MTI has made manual curation impractical without computational tools. To support manual data curation, we implemented a text-mining pipeline that consists of a scoring system and a LLM. The scoring system initially scans titles and abstracts, assigning relevance scores based on heuristic searches for terms like miRNA and experimental methodologies. Articles with high scores are prioritized and then processed by the LLM-based system. In this update, we replaced the BioBERT and Long Short-Term Memory model with the LLAMA3 LLM from META (65), selecting the 8-billion-parameter version for computational efficiency. LLAMA3's ability to perform both text classification (TC) and named entity recognition (NER) without additional NER-specific training data provided a key advantage over the previous models. This enabled direct annotation of miRNA, target, and disease entities from relevant sentences. We used LLAMA3 to annotate articles by highlighting texts containing MTIs or miRNA–disease associations, aiding our focus on relevant content. While prioritizing these highlighted texts, we also reviewed unhighlighted text to ensure no important details were missed.

To tailor LLAMA3 for miRNA-specific tasks, we fine-tuned it using QLoRA (66) with only 1000 manually crafted question-answer pairs, employing 4-bit quantization, a 2e-4 learning rate, and training over 10 epochs. The pipeline splits, filters, and tokenizes sentences before LLAMA3 processes them in batches using custom prompts. The model performs TC to highlight sentences related to MTI or miRNA–disease associations and NER to highlight miRNA, target,

and disease entities. Experimental validation methods and cell lines were highlighted using dictionary-based entity matching, and all data were manually verified before database entry. Figure 2 presents a schematic overview of our text mining pipeline.

To evaluate LLAMA3's reliability in pre-screening, we randomly selected 12 615 previously curated sentences related to MTIs for a QA task, where LLAMA3 8B correctly identified 11 496 (91%) sentences containing MTI information. In comparison to competing LLMs of similar parameter sizes, Gemma2 9B (67) identified 11 816 (94%) sentences and Mistral 7B (68) identified 10 107 (80%) sentences. In terms of scalability, on 4 A100 (40GB) GPUs, LLAMA3 8B completed the task in 7 713 seconds, while Gemma2 9B and Mistral 7B required 60 464 and 10 457 seconds, respectively. LLAMA3 thus outperformed both models in terms of performance and scalability combined. Moreover, LLAMA3 and similar LLMs are ready for broader scientific applications, being easily prompt-engineered for diverse tasks, unlike traditional models that rely on high-quality datasets for specific use cases. However, human verification remains necessary due to potential errors, and limitations in handling complex logic and high computational costs may restrict the use of LLMs in certain tasks.

Enhanced web interface

Previous versions of miRTarBase provided researchers across various fields with a user-friendly interface for exploring MTIs. In this release, the web interface has undergone a complete redesign, offering a more modern, efficient, and visually appealing platform that enhances user experience. The new interface is optimized for faster navigation and improved accessibility, making it easier for users to interact with the database (Figure 3). Several new functional sections have been introduced to accommodate the display of newly added data, including (1) miRNA–Drug Associations, (2) miRNA–Drug Resistance Associations, and (3) Biomarker Information. Furthermore, we recognized that the previous method of network visualization had become outdated. As a result, we have incorporated the advanced ECharts library (69) to offer a more dynamic and interactive experience for visualizing complex networks. The newly recalculated centrality and importance of nodes within the MTI network are also integrated into this updated visualization, providing users with deeper insights into the structural hierarchy and functional relevance of the miRNA networks. These enhancements make the web interface a highly accessible and invaluable resource, solidifying miRTarBase as a go-to platform for miRNA research in the modern scientific community.

Summary and perspectives

miRTarBase has evolved into a leading resource for experimentally validated MTIs since its launch in 2011. The latest release, miRTarBase 10.0, now includes over 3 817 550 curated MTIs from 13 690 articles, showcasing significant growth in both data volume and quality. The integration of the LLAMA3 model into the NLP pipeline has significantly facilitated the curation of miRNA–target and miRNA–disease association, and improved overall data integrity. The platform is more user-friendly and accessible with a complete web interface redesign and including new features such as
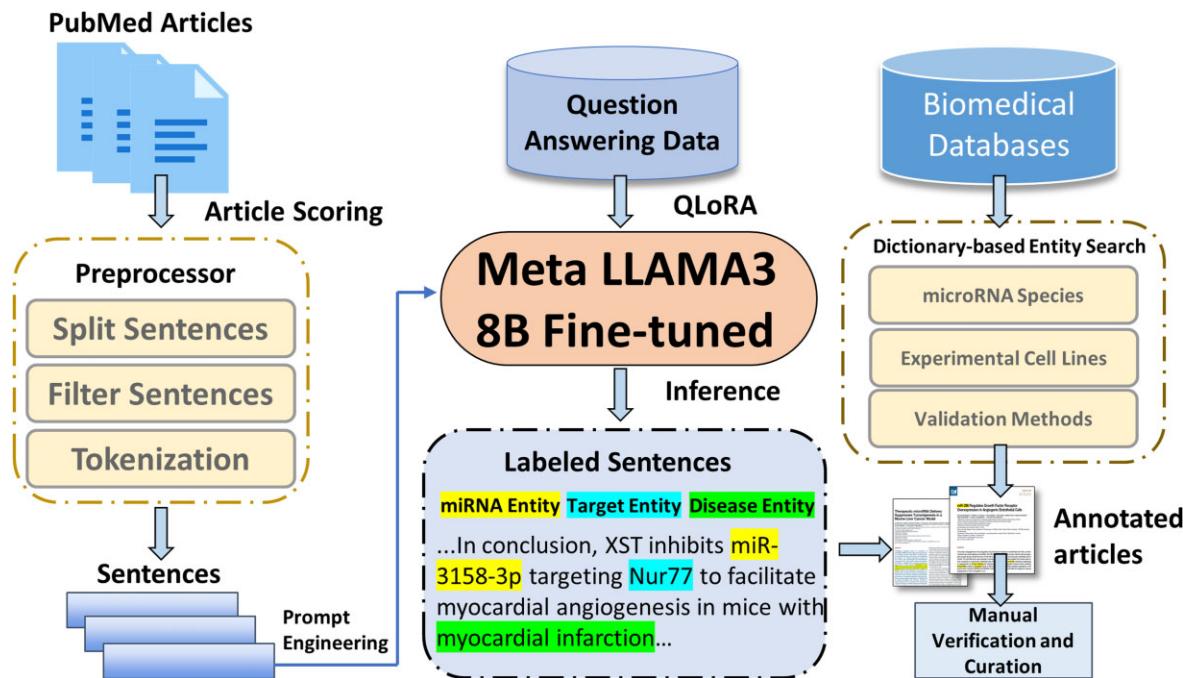
Figure 2. The complete workflow of the NLP pipeline using LLAMA3 LLM for annotating miRNA articles and aiding in manual curation.
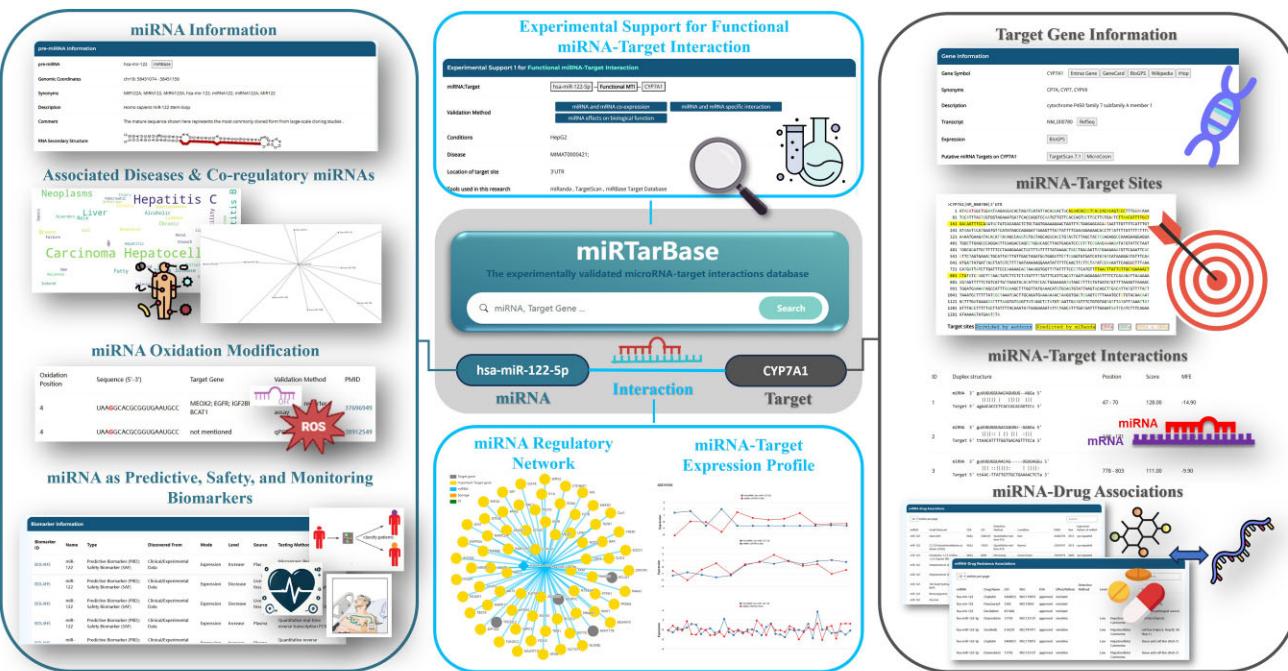

Figure 3. The enhanced web interface of miRTarBase. More comprehensive information related to miRNA–Drug associations, drug resistance, biomarker, and oxidation modification data is now accessible with improved visualization and network analysis features.

miRNA-Drug associations and biomarker information. Additionally, the expansion of high-throughput validated MTIs, including CLIP-seq and PAR-CLIP datasets, enriches the database's utility for studying miRNA regulation in disease and therapeutic contexts. Moving forward, miRTarBase will continue to expand and integrate advanced technologies, ensuring it remains a vital resource for researchers investigating miRNA-related processes in disease diagnostics, therapeutic development and beyond.

The scientific contribution of miRTarBase

The scientific contribution of miRTarBase is evident in its significant impact on miRNA research, as demonstrated by its citation in several highly influential databases and web server articles. For instance, the DIANA-miRPath v4.0 web-server uses miRTarBase data to enable target-based miRNA functional analysis, incorporating both experimentally supported interactions and predictions for enriched miRNA-target insights ([70]). Similarly, the g:Profiler service integrates

miRTarBase into its extensive suite of functional enrichment analysis tools, assisting researchers in identifying and mapping gene functions associated with miRNA regulation (71).

Moreover, several high-impact studies focus on critical biological questions and use miRTarBase for solid research. One study investigates the regulatory role of microRNAs in cardiovascular disease, demonstrating the therapeutic potential of targeting specific miRNA interactions to reduce atherosclerosis (72). Another study explores the role of miRNAs in DNA double-strand break gene repair, using miRTarBase to validate gene targets (73). Additionally, research on miRNA-based transcriptional regulation employs miRTarBase to support the identification and analysis of MTIs at the genome scale (74). Together, these examples showcase miRTarBase as an invaluable resource, significantly advancing research in molecular biology and disease treatment development.

In the field of miRNA research, particularly regarding tools for studying MTIs, several databases have provided valuable functionalities, including miRTargetLink (75), StarBase (76), miRPathDB (77), IMOTA (78) and miEAA (79), among others, each contributing unique insights. miRTargetLink offers dynamic visualization of miRNA-target gene and pathway networks; StarBase integrates large-scale CLIP-Seq data to explore miRNA–ceRNA and miRNA–ncRNA interactions, focusing on competitive endogenous RNA regulatory networks; miRPathDB supports functional pathway analysis of miRNAs and target genes in human and mouse models; IMOTA provides a multi-omics tissue atlas for identifying highly expressed miRNAs and target genes in specific tissues; miEAA facilitates multi-species miRNA enrichment analysis and can be integrated into complex workflows. Collectively, these databases enhance our understanding of miRNA interactions and regulatory networks.

The latest update of miRTarBase has significantly expanded its dataset and incorporated new data types, adding substantial value to existing resources. As a manually curated, experimentally validated MTI database, miRTarBase continues to provide researchers with the latest data to uncover critical biological insights. This update includes additional data types, offering deeper insights into miRNA's role on MTIs. By integrating these new dimensions, miRTarBase becomes a more comprehensive resource that complements existing tools and further enhances their capabilities, promoting a more systematic evaluation of miRNA interactions. This update ensures better synergy with other databases and strengthens the overall miRNA research infrastructure.

Data availability

The miRTarBase 10.0 database will be continuously maintained and updated. The database is now publicly accessible at https://mirtarbase.cuhk.edu.cn/~miRTarBase/miRTarBase_2025.

Supplementary data

Supplementary Data are available at NAR Online.

Acknowledgements

Funding

Conflict of interest statement

The authors declare that they have no competing interests.

References

1. Bartel,D.P. (2004) MicroRNAs: genomics, biogenesis, mechanism, and function. *Cell*, **116**, 281–297.
2. Engels,B.M. and Hutvagner,G. (2006) Principles and effects of microRNA-mediated post-transcriptional gene regulation. *Oncogene*, **25**, 6163–6169.
3. Stroynowska-Czerwinska,A., Fiszer,A. and Krzyzosiak,W.J. (2014) The panorama of miRNA-mediated mechanisms in mammalian cells. *Cell. Mol. Life Sci.*, **71**, 2253–2270.
4. Bartel,D.P. (2009) MicroRNAs: target recognition and regulatory functions. *Cell*, **136**, 215–233.
5. Shukla,G.C., Singh,J. and Barik,S. (2011) MicroRNAs: processing, maturation, target recognition and regulatory functions. *Mol. Cell Pharmacol.*, **3**, 83–92.
6. Carleton,M., Cleary,M.A. and Linsley,P.S. (2007) MicroRNAs and cell cycle regulation. *Cell Cycle*, **6**, 2127–2132.
7. Harfe,B.D. (2005) MicroRNAs in vertebrate development. *Curr. Opin. Genet. Dev.*, **15**, 410–415.
8. Lynam-Lennon,N., Maher,S.G. and Reynolds,J.V. (2009) The roles of microRNA in cancer and apoptosis. *Biol. Rev. Camb. Philos. Soc.*, **84**, 55–71.
9. Jiao,X., Qian,X., Wu,L., Li,B., Wang,Y., Kong,X. and Xiong,L. (2019) microRNA: the impact on cancer stemness and therapeutic resistance. *Cells*, **9**, 8.
10. Skoufos,G., Kakoulidis,P., Tastsoglou,S., Zacharopoulou,E., Kotsira,V., Miliotis,M., Mavromati,G., Grigoriadis,D., Zioga,M., Velli,A., *et al.* (2024) TarBase-v9.0 extends experimentally supported miRNA-gene interactions to cell-types and virally encoded miRNAs. *Nucleic Acids Res.*, **52**, D304–D310.
11. Cui,C., Zhong,B., Fan,R. and Cui,Q. (2024) HMDD v4.0: a database for experimentally supported human microRNA-disease associations. *Nucleic Acids Res.*, **52**, D1327–D1332.
12. Zhang,Y., Zhou,Y., Zhou,Y., Yu,X., Shen,X., Hong,Y., Zhang,Y., Wang,S., Mou,M., Zhang,J., *et al.* (2024) TheMarker: a

comprehensive database of therapeutic biomarkers. *Nucleic Acids Res.*, **52**, D1450–D1464.

13. Cao,X., Zhou,X., Hou,F., Huang,Y.E., Yuan,M., Long,M., Chen,S., Lei,W., Zhu,J., Chen,J., *et al.* (2024) ncRNADrug: a database for validated and predicted ncRNAs associated with drug resistance and targeted by drugs. *Nucleic Acids Res.*, **52**, D1393–D1399.

14. Sherry,S.T., Ward,M.H., Kholodov,M., Baker,J., Phan,L., Smigielski,E.M. and Sirotkin,K. (2001) dbSNP: the NCBI database of genetic variation. *Nucleic Acids Res.*, **29**, 308–311.

15. Buniello,A., MacArthur,J.A.L., Cerezo,M., Harris,L.W., Hayhurst,J., Malangone,C., McMahon,A., Morales,J., Mountjoy,E., Sollis,E., *et al.* (2019) The NHGRI-EBI GWAS Catalog of published genome-wide association studies, targeted arrays and summary statistics 2019. *Nucleic Acids Res.*, **47**, D1005–D1012.

16. Landrum,M.J., Chitipiralla,S., Brown,G.R., Chen,C., Gu,B., Hart,J., Hoffman,D., Jang,W., Kaur,K., Liu,C., *et al.* (2020) ClinVar: improvements to accessing data. *Nucleic Acids Res.*, **48**, D835–D844.

17. Tate,J.G., Bamford,S., Jubb,H.C., Sondka,Z., Beare,D.M., Bindal,N., Boutselakis,H., Cole,C.G., Creatore,C., Dawson,E., *et al.* (2019) COSMIC: the catalogue of somatic mutations In cancer. *Nucleic Acids Res.*, **47**, D941–D947.

18. Ma,R., Wang,C., Wang,J., Wang,D. and Xu,J. (2016) miRNA-mRNA interaction network in non-small cell lung cancer. *Interdiscip. Sci.*, **8**, 209–219.

19. Peter,M.E. (2010) Targeting of mRNAs by multiple miRNAs: the next step. *Oncogene*, **29**, 2161–2164.

20. Volinia,S., Galasso,M., Costinean,S., Tagliavini,L., Gamberoni,G., Drusco,A., Marchesini,J., Mascellani,N., Sana,M.E., Abu Jarour,R., *et al.* (2010) Reprogramming of miRNA networks in cancer and leukemia. *Genome Res.*, **20**, 589–599.

21. Thirunavukarasu,A.J., Ting,D.S.J., Elangovan,K., Gutierrez,L., Tan,T.F. and Ting,D.S.W. (2023) Large language models in medicine. *Nat. Med.*, **29**, 1930–1940.

22. Dubey,A., Jauhri,A., Pandey,A., Kadian,A., Al-Dahle,A., Letman,A., Mathur,A., Schelten,A., Yang,A. and Fan,A. (2024) The llama 3 herd of models. arXiv doi: https://arxiv.org/abs/2407.21783, 31 July 2024, preprint: not peer reviewed.

23. Wang,J.X., Gao,J., Ding,S.L., Wang,K., Jiao,J.Q., Wang,Y., Sun,T., Zhou,L.Y., Long,B., Zhang,X.J., *et al.* (2015) Oxidative modification of miR-184 enables it to target bcl-xL and bcl-w. *Mol. Cell*, **59**, 50–61.

24. Eom,S., Peak,J., Park,J., Ahn,S.H., Cho,Y.K., Jeong,Y., Lee,H.S., Lee,J., Ignatova,E., Lee,S.E., *et al.* (2023) Widespread 8-oxoguanine modifications of miRNA seeds differentially regulate redox-dependent cancer development. *Nat. Cell Biol.*, **25**, 1369–1383.

25. Hsu,S.D., Lin,F.M., Wu,W.Y., Liang,C., Huang,W.C., Chan,W.L., Tsai,W.T., Chen,G.Z., Lee,C.J., Chiu,C.M., *et al.* (2011) miRTarBase: a database curates experimentally validated microRNA-target interactions. *Nucleic Acids Res.*, **39**, D163–D169.

26. Hsu,S.D., Tseng,Y.T., Shrestha,S., Lin,Y.L., Khaleel,A., Chou,C.H., Chu,C.F., Huang,H.Y., Lin,C.M., Ho,S.Y., *et al.* (2014) miRTarBase update 2014: an information resource for experimentally validated miRNA-target interactions. *Nucleic Acids Res.*, **42**, D78–D85.

27. Chou,C.H., Chang,N.W., Shrestha,S., Hsu,S.D., Lin,Y.L., Lee,W.H., Yang,C.D., Hong,H.C., Wei,T.Y., Tu,S.J., *et al.* (2016) miRTarBase 2016: updates to the experimentally validated miRNA-target interactions database. *Nucleic Acids Res.*, **44**, D239–D247.

28. Chou,C.H., Shrestha,S., Yang,C.D., Chang,N.W., Lin,Y.L., Liao,K.W., Huang,W.C., Sun,T.H., Tu,S.J., Lee,W.H., *et al.* (2018) miRTarBase update 2018: a resource for experimentally validated microRNA-target interactions. *Nucleic Acids Res.*, **46**, D296–D302.

29. Huang,H.Y., Lin,Y.C., Li,J., Huang,K.Y., Shrestha,S., Hong,H.C., Tang,Y., Chen,Y.G., Jin,C.N., Yu,Y., *et al.* (2020) miRTarBase 2020: updates to the experimentally validated microRNA-target interaction database. *Nucleic Acids Res.*, **48**, D148–D154.

30. Huang,H.Y., Lin,Y.C., Cui,S., Huang,Y., Tang,Y., Xu,J., Bao,J., Li,Y., Wen,J., Zuo,H., *et al.* (2022) miRTarBase update 2022: an informative resource for experimentally validated miRNA-target interactions. *Nucleic Acids Res.*, **50**, D222–D230.

31. Liu,X., Wang,S., Meng,F., Wang,J., Zhang,Y., Dai,E., Yu,X., Li,X. and Jiang,W. (2013) SM2miR: a database of the experimentally validated small molecules' effects on microRNA expression. *Bioinformatics*, **29**, 409–411.

32. Ule,J., Jensen,K., Mele,A. and Darnell,R.B. (2005) CLIP: a method for identifying protein-RNA interaction sites in living cells. *Methods*, **37**, 376–386.

33. Hafner,M., Landthaler,M., Burger,L., Khorshid,M., Hausser,J., Berninger,P., Rothballer,A., Ascano,M., Jungkamp,A.C., Munschauer,M, *et al.*2010) Transcriptome-wide identification of RNA-binding protein and microRNA target sites by PAR-CLIP. *Cell*, **141**, 129–141.

34. Tong,Z., Cui,Q., Wang,J. and Zhou,Y. (2019) TransmiR v2.0: an updated transcription factor-microRNA regulation database. *Nucleic Acids Res.*, **47**, D253–D258.

35. Wang,P., Zhi,H., Zhang,Y., Liu,Y., Zhang,J., Gao,Y., Guo,M., Ning,S. and Li,X. (2015) miRSponge: a manually curated database for experimentally supported miRNA sponges and ceRNAs. *Database (Oxford)*, **2015**, bav098.

36. Kozomara,A., Birgaoanu,M. and Griffiths-Jones,S. (2019) miRBase: from microRNA sequences to function. *Nucleic Acids Res.*, **47**, D155–D162.

37. Brown,G.R., Hem,V., Katz,K.S., Ovetsky,M., Wallin,C., Ermolaeva,O., Tolstoy,I., Tatusova,T., Pruitt,K.D., Maglott,D.R., *et al.* (2015) Gene: a gene-centered information resource at NCBI. *Nucleic Acids Res.*, **43**, D36–D42.

38. O'Leary,N.A., Wright,M.W., Brister,J.R., Ciufo,S., Haddad,D., McVeigh,R., Rajput,B., Robbertse,B., Smith-White,B., Ako-Adjei,D., *et al.* (2016) Reference sequence (RefSeq) database at NCBI: current status, taxonomic expansion, and functional annotation. *Nucleic Acids Res.*, **44**, D733–D745.

39. Clough,E., Barrett,T., Wilhite,S.E., Ledoux,P., Evangelista,C., Kim,I.F., Tomashevsky,M., Marshall,K.A., Phillippy,K.H., Sherman,P.M., *et al.* (2024) NCBI GEO: archive for gene expression and epigenomics data sets: 23-year update. *Nucleic Acids Res.*, **52**, D138–D144.

40. Tomczak,K., Czerwinska,P. and Wiznerowicz,M. (2015) The Cancer Genome Atlas (TCGA): an immeasurable source of knowledge. *Contemp. Oncol. (Pozn)*, **19**, A68–A77.

41. Deng,M., Bragelmann,J., Schultze,J.L. and Perner,S. (2016) Web-TCGA: an online platform for integrated analysis of molecular cancer data sets. *BMC Bioinf.*, **17**, 72.

42. Li,J.R., Tong,C.Y., Sung,T.J., Kang,T.Y., Zhou,X.J. and Liu,C.C. (2019) CMEP: a database for circulating microRNA expression profiling. *Bioinformatics*, **35**, 3127–3132.

43. Keller,A., Groger,L., Tschernig,T., Solomon,J., Laham,O., Schaum,N., Wagner,V., Kern,F., Schmartz,G.P., Li,Y., *et al.* (2022) miRNATissueAtlas2: an update to the human miRNA tissue atlas. *Nucleic Acids Res.*, **50**, D211–D221.

44. Liu,T., Zhang,Q., Zhang,J., Li,C., Miao,Y.R., Lei,Q., Li,Q. and Guo,A.Y. (2019) EVmiRNA: a database of miRNA profiling in extracellular vesicles. *Nucleic Acids Res.*, **47**, D89–D93.

45. Marceca,G.P., Distefano,R., Tomasello,L., Lagana,A., Russo,F., Calore,F., Romano,G., Bagnoli,M., Gasparini,P., Ferro,A., *et al.* (2021) MiREDiBase, a manually curated database of validated and putative editing events in microRNAs. *Sci. Data*, **8**, 199.

46. Wang,J. and Liu,L. (2021) MiR-149-3p promotes the cisplatin resistance and EMT in ovarian cancer through downregulating TIMP2 and CDKN1A. *J. Ovarian Res.*, **14**, 165.

47. Xie,Z.Y., Liu,M.S., Zhang,C., Cai,P.C., Xiao,Z.H. and Wang,F.F. (2018) Aspirin enhances the sensitivity of hepatocellular carcinoma side population cells to doxorubicin via miR-491/ABCG2. *Biosci. Rep.*, **38**, BSR20180854.

48. Chen,X., Guan,N.N., Sun,Y.Z., Li,J.Q. and Qu,J. (2020) MicroRNA-small molecule association identification: from experimental results to computational models. *Brief. Bioinform.*, **21**, 47–61.

49. Rossi,L., Bonmassar,E. and Faraoni,I. (2007) Modification of miR gene expression pattern in human colon cancer cells following exposure to 5-fluorouracil in vitro. *Pharmacol. Res.*, **56**, 248–253.

50. Rhodes,L.V., Nitschke,A.M., Segar,H.C., Martin,E.C., Driver,J.L., Elliott,S., Nam,S.Y., Li,M., Nephew,K.P., Burow,M.E., *et al.* (2012) The histone deacetylase inhibitor trichostatin A alters microRNA expression profiles in apoptosis-resistant breast cancer cells. *Oncol. Rep.*, **27**, 10–16.

51. Detassis,S., Grasso,M., Del Vescovo,V. and Denti,M.A. (2017) microRNAs make the call in cancer personalized medicine. *Front. Cell Dev. Biol.*, **5**, 86.

52. Motawi,T.M., Rizk,S.M., Shaker,O.G. and Mokhtar,O.Z. (2015) MicroRNAs as predictor markers for response to interferon treatment of chronic hepatitis C genotype-4 in Egyptian patients. *PLoS One*, **10**, e0121524.

53. Marschner,D., Falk,M., Javorniczky,N.R., Hanke-Muller,K., Rawluk,J., Schmitt-Graeff,A., Simonetta,F., Haring,E., Dicks,S., Ku,M., *et al.* (2020) MicroRNA-146a regulates immune-related adverse events caused by immune checkpoint inhibitors. *JCI Insight*, **5**, 6.

54. Harrill,A.H., Eaddy,J.S., Rose,K., Cullen,J.M., Ramanathan,L., Wanaski,S., Collins,S., Ho,Y., Watkins,P.B. and Lecluyse,E.L. (2014) Liver biomarker and in vitro assessment confirm the hepatic origin of aminotransferase elevations lacking histopathological correlate in beagle dogs treated with GABAA receptor antagonist NP260. *Toxicol. Appl. Pharmacol.*, **277**, 131–137.

55. De Guire,V., Robitaille,R., Tetreault,N., Guerin,R., Menard,C., Bambace,N. and Sapieha,P. (2013) Circulating miRNAs as sensitive and specific biomarkers for the diagnosis and monitoring of human diseases: promises and challenges. *Clin. Biochem.*, **46**, 846–860.

56. Diener,C., Keller,A. and Meese,E. (2024) The miRNA–target interactions: an underestimated intricacy. *Nucleic Acids Res.*, **52**, 1544–1557.

57. Chou,C.H., Lin,F.M., Chou,M.T., Hsu,S.D., Chang,T.H., Weng,S.L., Shrestha,S., Hsiao,C.C., Hung,J.H. and Huang,H.D. (2013) A computational approach for identifying microRNA-target interactions using high-throughput CLIP and PAR-CLIP sequencing. *BMC Genomics [Electronic Resource]*, **14**, S2.

58. Pu,M., Chen,J., Tao,Z., Miao,L., Qi,X., Wang,Y. and Ren,J. (2019) Regulatory network of miRNA on its target: coordination between transcriptional and post-transcriptional regulation of gene expression. *Cell. Mol. Life Sci.*, **76**, 441–451.

59. Ali Syeda,Z., Langden,S. S. S., Munkhzul,C., Lee,M. and Song,S. J. (2020) Regulatory mechanism of MicroRNA expression in cancer. *Int. J. Mol. Sci.*, **21**, 1723.

60. Sempere,L.F., Azmi,A.S. and Moore,A. (2021) microRNA-based diagnostic and therapeutic applications in cancer medicine. *Wiley Interdiscip. Rev. RNA*, **12**, e1662.

61. Szklarczyk,D., Kirsch,R., Koutrouli,M., Nastou,K., Mehryary,F., Hachilif,R., Gable,A.L., Fang,T., Doncheva,N.T., Pyysalo,S., *et al.* (2023) The STRING database in 2023: protein-protein association networks and functional enrichment analyses for any sequenced genome of interest. *Nucleic Acids Res.*, **51**, D638–D646.

62. Zhang,J., Nie,R., Liu,M. and Zhang,X. (2022) A novel strategy for identifying NSCLC MicroRNA biomarkers and their mechanism analysis based on a brand-new CeRNA-hub-FFL network. *Int. J. Mol. Sci.*, **23**, 11303.

63. Shannon,P., Markiel,A., Ozier,O., Baliga,N.S., Wang,J.T., Ramage,D., Amin,N., Schwikowski,B. and Ideker,T. (2003) Cytoscape: a software environment for integrated models of biomolecular interaction networks. *Genome Res.*, **13**, 2498–2504.

64. Otasek,D., Morris,J.H., Boucas,J., Pico,A.R. and Demchak,B. (2019) Cytoscape Automation: empowering workflow-based network analysis. *Genome Biol.*, **20**, 185.

65. Xu,J., Shao,T., Ding,N., Li,Y. and Li,X. (2017) miRNA-miRNA crosstalk: from genomics to phenomics. *Brief Bioinform*, **18**, 1002–1011.

66. Hill,M. and Tran,N. (2021) miRNA interplay: mechanisms and consequences in cancer. *Dis Model Mech*, **14**, dmm047662.

67. Riviere,G.T.M., Pathak,S., Sessa,P.G., Hardin,C., Bhupatiraju,S., Hussenot,L.e., Mesnard,T., Shahriari,B., Ram'e,A., Ferret,J., *et al.* (2024) Gemma 2: improving open language models at a practical size. arXiv doi: https://arxiv.org/abs/2408.00118, 31 July 2024, preprint: not peer reviewed.

68. Jiang,A.Q., Sablayrolles,A., Mensch,A., Bamford,C., Chaplot,D.S., Casas,D.d.L., Bressand,F., Lengyel,G., Lample,G., Saulnier,L., *et al.* (2023) Mistral 7B. arXiv doi: https://arxiv.org/abs/2310.06825, 10 October 2023, preprint: not peer reviewed.

69. Li,D., Mei,H., Shen,Y., Su,S., Zhang,W., Wang,J., Zu,M. and Chen,W. (2018) ECharts: a declarative framework for rapid construction of web-based visualization. *Visual Inform.*, **2**, 136–146.

70. Tastsoglou,S., Skoufos,G., Miliotis,M., Karagkouni,D., Koutsoukos,I., Karavangeli,A., Kardaras,F.S. and Hatzigeorgiou,A.G. (2023) DIANA-miRPath v4.0: expanding target-based miRNA functional analysis in cell-type and tissue contexts. *Nucleic Acids Res.*, **51**, W154–W159.

71. Kolberg,L., Raudvere,U., Kuzmin,I., Adler,P., Vilo,J. and Peterson,H. (2023) g:profiler-interoperable web service for functional enrichment analysis and gene identifier mapping (2023 update). *Nucleic Acids Res.*, **51**, W207–W212.

72. Cimen,I., Natarelli,L., Abedi Kichi,Z., Henderson,J.M., Farina,F.M., Briem,E., Aslani,M., Megens,R.T.A., Jansen,Y., Mann-Fallenbuchel,E., *et al.* (2023) Targeting a cell-specific microRNA repressor of CXCR4 ameliorates atherosclerosis in mice. *Sci. Transl. Med.*, **15**, eadf3357.

73. McDonald,J.T., Kim,J., Farmerie,L., Johnson,M.L., Trovao,N.S., Arif,S., Siew,K., Tsoy,S., Bram,Y., Park,J., *et al.* (2024) Space radiation damage rescued by inhibition of key spaceflight associated miRNAs. *Nat. Commun.*, **15**, 4825.

74. Santinha,A.J., Klingler,E., Kuhn,M., Farouni,R., Lagler,S., Kalamakis,G., Lischetti,U., Jabaudon,D. and Platt,R.J. (2023) Transcriptional linkage analysis with in vivo AAV-perturb-seq. *Nature*, **622**, 367–375.

75. Kern,F., Aparicio-Puerta,E., Li,Y., Fehlmann,T., Kehl,T., Wagner,V., Ray,K., Ludwig,N., Lenhof,H.P., Meese,E., *et al.* (2021) miRTargetLink 2.0-interactive miRNA target gene and target pathway networks. *Nucleic Acids Res.*, **49**, W409–W416.

76. Li,J.H., Liu,S., Zhou,H., Qu,L.H. and Yang,J.H. (2014) starBase v2.0: decoding miRNA-ceRNA, miRNA-ncRNA and protein-RNA interaction networks from large-scale CLIP-Seq data. *Nucleic Acids Res.*, **42**, D92–D97.

77. Kehl,T., Kern,F., Backes,C., Fehlmann,T., Stockel,D., Meese,E., Lenhof,H.P. and Keller,A. (2020) miRPathDB 2.0: a novel release of the miRNA Pathway Dictionary Database. *Nucleic Acids Res.*, **48**, D142–D147.

78. Palmieri,V., Backes,C., Ludwig,N., Fehlmann,T., Kern,F., Meese,E. and Keller,A. (2018) IMOTA: an interactive multi-omics tissue atlas for the analysis of human miRNA-target interactions. *Nucleic Acids Res.*, **46**, D770–D775.

79. Kern,F., Fehlmann,T., Solomon,J., Schwed,L., Grammes,N., Backes,C., Van Keuren-Jensen,K., Craig,D.W., Meese,E. and Keller,A. (2020) miEAA 2.0: integrating multi-species microRNA enrichment analysis and workflow management systems. *Nucleic Acids Res.*, **48**, W521–W528.