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ZOVER: the database of zoonotic and vector-borne viruses

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ABSTRACT

Emerging infectious diseases significantly threaten global public health and socioeconomic security. The majority of emerging infectious disease outbreaks are caused by zoonotic/vector-borne viruses. Bats and rodents are the two most important reservoir hosts of many zoonotic viruses that can cross species barriers to infect humans, whereas mosquitos and ticks are well-established major vectors of many arboviral diseases. Moreover, some emerging zoonotic diseases require a vector to spread or are intrinsically vector-borne and zoonotically transmitted. In this study, we present a newly upgraded database of zoonotic and vector-borne viruses designated ZOVER (http://www.mgc.ac.cn/ZOVER). It incorporates two previously released databases, DBatVir and DRodVir, for bat- and rodent-associated viruses, respectively, and further collects up-to-date knowledge on mosquito- and tick-associated viruses to establish a comprehensive online resource for zoonotic and vector-borne viruses. Additionally, it integrates a set of online visualization tools for convenient comparative analyses to facilitate the discovery of potential patterns of virome diversity and ecological characteristics between/within different viral hosts/vectors. The ZOVER database will be a valuable resource for virologists, zoologists and epidemiologists to better understand the diversity and dynamics of zoonotic and vector-borne viruses and conduct effective surveillance to monitor potential interspecies spillover for efficient prevention and control of future emerging zoonotic diseases.

INTRODUCTION

The past decade has witnessed significant threats and profound impacts to global public health and the socioeconomic security from emerging infectious diseases, including the previous Ebola and Zika endemics, as well as the ongoing COVID-19 pandemic (1–3). A retrospective analysis revealed that during the past ∼70 years, >80% of emerging infectious disease outbreaks are caused by zoonotic or vector-borne pathogens, of which the majority are viruses (4,5). In addition, evidence suggests that the increased global travel, urbanization and climate changes in recent years have dynamically affected the outbreak pattern of emerging infectious diseases (6,7). Therefore, recent studies have intensely focused on surveys of a massive number of different viruses (collectively termed the virome) carried by key animals that are recognized as the most relevant natural reservoirs or vectors for the causative agents of zoonotic and vector-borne diseases.

Bats and rodents are the two most important reservoir hosts of many zoonotic viruses that can cross species barriers to infect humans, including lyssaviruses, ebolaviruses, hantaviruses and coronaviruses. In particular, bats have been suggested to be potential reservoirs of SARS-CoV-2, the causative agent of COVID-19, which is still posing a challenge to global public health (8). Mosquitos and ticks are well-established major vectors for the spread of many arboviral diseases, including dengue, chikungunya, West Nile encephalitis, yellow fever and Zika (6,9). These arthropod vectors can harbor a heterogeneous group of arboviruses and spread them among vertebrate hosts with a unique transmission mode (10). Moreover, some emerging zoonotic diseases require an ectoparasitic arthropod vector to be effectively transmitted, whereas mammals can serve as potentially competent amplifying hosts for several arboviruses (11). For example, rodents play essential roles in the natural circulation of vector-borne viruses, such as the Crimean-Congo hemorrhagic fever virus from the family *Nairoviridae* and the tick-borne encephalitis virus and Omsk hemorrhagic fever virus from the family *Flaviviridae*

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(12). In addition, molecular and serological evidence from the field have documented that the mosquito-bat-mosquito transmission cycle of Japanese encephalitis viruses and Chikungunya viruses was established in the laboratory (10). Therefore, it is critical to establish a comprehensive and integrative resource of zoonotic and vector-borne viruses worldwide for efficient identification of novel pathogens to detect potential interspecies spillover. Furthermore, a better understanding of the biodiversity, geographical distribution, and host/vector specificity of zoonotic and vector-borne viruses is intrinsically important to estimate risks and design strategies for the prevention and control of future emerging infectious diseases (13).

Herein, we present a newly integrated and upgraded database of zoonotic and vector-borne viruses, designated ZOVER (http://www.mgc.ac.cn/ZOVER). It has successfully incorporated two previously released databases, DBatVir (14) and DRodVir (15), of bat- and rodent-associated viruses, respectively. Additionally, it collects up-to-date knowledge on mosquito- and tick-associated viruses to construct a comprehensive online resource for zoonotic and vector-borne viruses. Furthermore, we have designed a set of online visualization tools for various comparative analyses to facilitate the discovery of potential patterns of virome diversity and ecological characteristics between/within different viral hosts/vectors that could be valuable for the surveillance and prescience of future emerging infectious diseases.

DATA PREPARATION AND DATABASE IMPLEMENTATION

Data preparation

The current version of the ZOVER database collects information on viruses from bats, rodents, mosquitos and ticks (Table 1). The datasets of the bat- and rodent-associated viruses were directly integrated from the up-to-date versions of previously released DBatVir and DRodVir databases, respectively. Nevertheless, due to years of consistent updates, the ZOVER database now covers 12 986 bat-associated viruses and 10 743 rodent-associated viruses, which represents approximately triple and double the original releases of the two databases, respectively, in terms of data size, implying a continuous hotspot of zoonotic viruses in recent years.

Then, to retrieve all known sequences and related publications of mosquito- and tick-associated viruses available from the public domain, we conducted an exhaustive search within the nucleotide and literature databases of National Center for Biotechnology Information (16) using the keyword '(mosquitos OR mosquitoes OR mosquito OR ticks OR tick) AND (virus OR viruses)'. To ensure the integrity of data collection, extra searches were performed with additional keywords of taxonomic family names of mosquitos and ticks as complements. Since the ZOVER database focuses on natural mammalian viruses that are most relevant to zoonotic infectious diseases, all records that matched the aforementioned keyword(s) were then precollected into the database by considering the following three criteria: (i) excluding all records of phages, as well as insect, fungal and plant viruses; (ii) removing all viruses derived from animals other than mosquitos and ticks and (iii) filtering out laboratory-cultured viruses in the model of mosquitos or ticks. All remaining records were then downloaded to the local system and converted by in-house BioPerl (17) scripts into relational tables of meta-information, including virus name, sampling time and location, associated vector, detection methods, cell culture method (if available), accession, sequence submitter(s) and affiliation, and related publication (if exists). To ensure the accuracy of the meta-data, we further performed an intensive double-check for published records by proofreading any inconsistencies and incompleteness based on the information described in related literature. Thus far, a total of 10 761 mosquito-associated viruses and 4849 tick-associated viruses have been included in the current ZOVER database (Table 1).

Finally, additional information on the viral families (e.g. associated diseases, genome organization and average size, and virion illustrations) and the vectors (e.g. common names and known geographic distribution) were further collected from the ViralZone database (18) and the International Union for Conservation of Nature Red List (www.iucnredlist.org), respectively.

Database implementation

All information mentioned above was organized to fit into our predesigned generic data schema as previously used in the DBatVir and DRodVir databases and stored in a local MySQL system to form the background datasets of ZOVER. The front end of the database consists of a set of Perl CGI scripts running on an Apache webserver. To make the interface of the ZOVER database more user-friendly and interactive than traditional HTML pages, additional web programming was introduced by using the cascading style sheet (CSS), asynchronous JavaScript and XML (AJAX), the cross-platform and feature-rich JavaScript library JQuery (http://jquery.com), and the open-source web development framework Semantic-UI (https://semantic-ui.com). Moreover, for the implementation of online data analysis and visualization tools, we further employed the modern SVG-based multi-platform charting library HighCharts (https://highcharts.com), a JavaScript library for providing an interactive tree known as jsTree (https://www.jstree.com), and a plugin-rich JavaScript library for manipulating grid data known as DataTables (https://www.datatables.net/). The standalone BLAST program (19) was integrated into the website to allow users to search the database by any query sequence for homology within the full/partial dataset of ZOVER. An internal pipeline incorporating the MUSCLE (20) and FastTree (21) programs was developed to provide online analyses of multiple sequence alignment and phylogenetic tree construction, respectively.

DATABASE CONTENT AND FEATURES

The ZOVER database is publicly accessible through a highly intuitive and responsive web interface (http://www.mgc.ac.cn/ZOVER). Just as in the previous DBatVir and DRodVir databases, the ZOVER platform offers basic

Table 1. Statistics of the related information of viruses collected in the ZOVER database (as of August 2021)

Host/vector	Number of viruses	Number of sequences	Number of viral families	Number of related host/vector species	Number of sampling countries
Bat	12 986	14 893	30	340	95
Rodent	10 743	14 373	31	266	107
Mosquito	10 761	13 507	18	250	115
Tick	4849	6567	18	101	90

utilities for users to browse the data for any individual host/vector and search the entire contents of the database with any keywords or query sequences. To supplement the scientific community with an overall landscape on the spatial and temporal diversity and dynamics of zoonotic and vector-borne viruses, we further developed a general comparison module of all four hosts/vectors currently involved. Moreover, a highly configurable online analysis panel is also available for advanced users who hope to perform customized comparisons between different subsets of viral hosts/vectors housed by the ZOVER database.

Basic database browse and search

Since the ZOVER database is an upgraded version of the previous DBatVir and DRodVir databases, some returned users may have a particular interest in the virome diversity of bats/rodents only. Therefore, we retained the basic utility of browsing the full information of any individual host- or vector-associated viruses by introducing a recently designed interface on the ZOVER platform. The new web interface can efficiently present the full contents of the previous DBatVir and DRodVir databases with much better user experiences than before, as it is built on a set of lightweight JavaScript libraries that can effectively organize a large amount of tabular data in a uniform grid. Each line of the grid describes an identified virus with full meta-information along with a clickable linear map for complete viral sequences. Additional features, such as collapsible menus, expandable trees, sortable and filterable grids, and live statistical pie charts, are also available from the refreshed interface for easy online data analysis and visualization as previously described. In contrast, some web utilities of the original DBatVir and DRodVir interface now malfunction due to intrinsic deficiency within the obsolete version of the JavaScript library. Thus, although the original interfaces of DBatVir and DRodVir will remain publicly accessible for consistency, no further upgrade of the web interface will be available hereafter. Instead, we highly recommend returning users of the DBatVir and DRodVir databases switch to the new web interface of the ZOVER platform in the future.

The ZOVER website provides a powerful search engine for users to easily retrieve related information in the background database by any keywords. Following the style of previous DBatVir and DRodVir databases, users have two optional choices for searching in the ZOVER platform: quick search by a simple query text and advanced search with a highly configurable form. Nevertheless, a major enhancement in the current search utility is that all results are automatically grouped into four categories by associated hosts/vectors, which are present in individual tabs within a single webpage. The organization of the output page is instantly familiar to all users, as it behaves similarly to an Excel workbook with multiple sheets. Additionally, the online BLAST service is supplied for users who want to perform sequence similarity searches among complete or partial datasets of the ZOVER database. Furthermore, an integrated pipeline to conduct multiple sequence alignment and phylogenetic tree construction is available to facilitate the follow-up genetic diversity analyses.

The general comparison portals

The current ZOVER database provides integrated information on zoonotic viruses from two major mammalian hosts (i.e. bats and rodents) and vector-borne viruses from two main arthropod vectors (i.e. mosquitos and ticks). Therefore, it is dedicated to providing users with a comprehensive overview of the diversity of zoonotic and vector-borne viruses from a comparative perspective. For convenience, all viral families related to zoonotic and vector-borne viruses have been organized into a three-dimensional dynamic tree with each taxonomic node represented as a colored ball (Figure 1A). The size of each ball is proportional to the total number of associated viruses currently collected in the ZOVER database. Additionally, the ball of each viral family can be highlighted when the mouse hovers over it and provides a direct link to the detailed comparison page for the corresponding viruses. By default, the general comparison page of each viral family provides a comparative visualization landscape for the associated viruses detected from bats, rodents, mosquitos and ticks in terms of spatial/temporal distribution and host/vector diversity. For instance, a zoomable global map with gradient coloring scaled to the number of associated viruses detected in each country/region is provided for each host/vector (Figure 1B). The four maps of bat-, rodent-, mosquito- and tick-associated viruses are tiled within a single webpage simultaneously for intuitive comparison. It is particularly helpful for investigating potential linkage(s) among the existing viral population of different hosts/vectors. Moreover, the general comparison page also includes additional tabs for details of associated viruses identified from bats, rodents, mosquitos and ticks. Each tab is clearly labeled with the total number of viruses reported thus far from the corresponding host/vector and directly linked to the uniform grid of detailed information as aforementioned.

Previous studies have shown that the emergence of some zoonotic diseases is spatially correlated with host diversity and environmental changes in a certain period (13). Therefore, comparative analysis of virome diversity within a specific geographic region or time frame could be helpful to unveil potential patterns or trends in virome

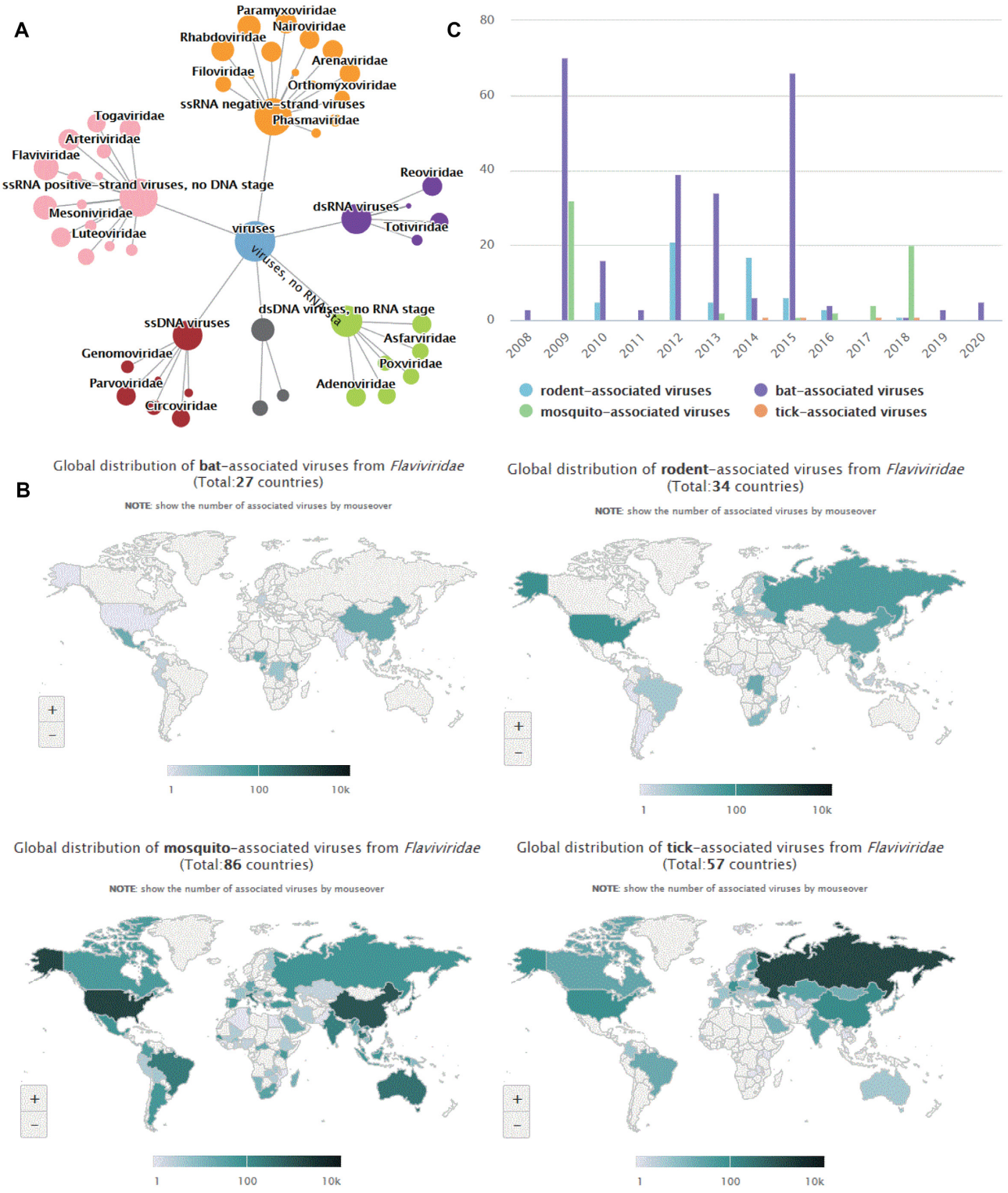

Figure 1. Some comparative utilities of ZOVER database. (**A**) A visualization landscape for the associated viral families in a dynamic tree. The size of each node ball is proportional to the total number of associated viruses currently collected in the database, and provides direct link to the detailed comparison page of the corresponding viruses. (**B**) An example of the comparative distribution maps for the viruses of family *Flaviviridae* identified from bats, rodents, mosquitos, and ticks. Each country/region is gradient colored by the number of associated viruses detected (to scale). (**C**) An example of the clustered column chart for the comparative analysis of sampling time of viruses of family *Flaviviridae* from different hosts/vectors.

dynamics. The ZOVER platform provides two parallel panels for users to easily conduct comparative analyses on any spatial/temporal subset of zoonotic and vector-borne viruses. The left panel for regional data analysis consists of a gradient-colored global map with each country/region being clickable to show the corresponding comparison page, whereas the right panel allows users to select a decade/year to perform comparative analysis within the specified period of time. The detailed comparison pages usually present side-by-side the summary results of bat-, rodent-, mosquito- and tick-associated viruses individually for comparison. The spatial and temporal distributions are visualized as zoomable global maps and clustered column charts, respectively (Figure 1B and C), whereas diversities of virome and host/vector species are both represented by pie charts. All aforementioned maps and charts are interactive, with popup detailed messages available when the mouse hovers over each individual part. Moreover, both column and pie charts are animated and configurable by a single click for easy online analyses.

Advanced online analysis utility

The availability of an integrated and comprehensive dataset of various zoonotic and vector-borne viruses from major reservoir hosts and arthropod vectors enables plentiful comparative analyses to discover virome diversity. The predefined general comparison modules are very convenient for users to initiate study but lack the necessary flexibility for further in-depth deciphering. We therefore introduced an additional utility to the ZOVER platform to guide advanced users in performing a highly customized comparative analysis based on the background integrative datasets. The current database collects information on zoonotic and vector-borne viruses from bats, rodents, mosquitos and ticks. All of these hosts/vectors themselves are known to be highly diversified in terms of taxonomy. Rodents and bats are the two most diverse orders of known mammals that together comprise >60% of existing mammalian species (22,23), while mosquitos and ticks are comprised of ∼3500 and ∼900 species, respectively (9,24). Hence, unlike the aforementioned general comparison that focuses on inter-host/vector virome diversity only, the customized analysis utility allows users to conduct both inter- and intra-host/vector comparisons. Customized analyses can be performed at different taxonomic levels, such as family, genus and species, to fulfill various demands from database users. Moreover, the submission form is fully configurable to focus the comparison on any specified geographic region and/or any customized period of time to disclose possible spatial or temporal patterns of virome diversity and dynamics.

To facilitate online analyses of the comparison results, the output page further integrates a set of visualization tools to help users better decipher the data from the two specified taxonomic groups. First, a comparative bubble chart with two different colored and shaped bubbles is presented to depict an overview of the virome diversity between the two groups in terms of viral family, host/vector species and geographic distribution (Figure 2A). The horizontal positions of bubbles represent the associated viral families identified from either of the two groups, whereas the vertical position of each bubble denotes the number of host/vector species reported to be associated with the corresponding viral family. Furthermore, the size of each bubble is proportional to the number of sampling countries. Then, a statistical Venn diagram is used to summarize the relationship between viral families detected from the two predefined host/vector groups (Figure 2B). The size of the overlapping region (if it exists) by the two circles is positively correlated with the number of viral families shared by the two groups. The details of the related viral families for both groups are also available as individual pie charts at the bottom of the result page for further investigation (Figure 2C). Finally, a zoomable global map is provided for users to better understand the geographic distribution of identified viruses associated with the two specified groups. The map is gradient-colored by the total number of viruses reported within each country/region as aforementioned. All visualization charts displayed in the comparison page are animated and responsive with popup detailed messages available when the mouse hovers over any components. In addition, all charts can be easily downloaded as various types of images or PDF documents for further offline analyses.

DISCUSSION AND FUTURE DIRECTIONS

The ZOVER database is dedicated to providing integrated and comprehensive virological, ecological, and epidemiological data to enhance our knowledge of zoonotic and vector-borne viruses. As of August 2021, ZOVER had collected a total of 39 339 viruses from 34 viral families identified from 957 species of bats/rodents/mosquitos/ticks distributed in 151 countries/regions worldwide (Table 1). All the incorporated information and devoted tools for online analysis and visualization facilitate ZOVER as a valuable resource for virologists, zoologists and epidemiologists to better understand the diversity and dynamics of zoonotic and vector-borne viruses to conduct effective surveillance to monitor and trace the current and future emerging zoonotic diseases.

Nevertheless, we would like to point out some potential limitations of the current ZOVER database. First, it was constructed as a sequence-centric database since molecular methods are now commonly used in the diagnosis and functional studies of viruses. However, there are indeed some reports of viral identification based on alternative approaches without sequencing (e.g. immunological methods). Therefore, these results will be intrinsically excluded from the ZOVER database. In addition, although we conducted exhaustive searches with different combinations of keywords to retrieve related records (sequences and literature) available from the public domain, it still cannot guarantee the inclusion of all records. Therefore, we highly appreciate and encourage users to contact us for any missed sequences/literature from the ZOVER database. Second, >35% of the sequences collected in the database are currently unpublished (without related literature). Thus, the meta-information associated with these sequences is only available from the related GenBank records deposited by the submitters. Unfortunately, some of the GenBank records do not provide sufficient meta-information as expected. For instance, >10% of the aforementioned

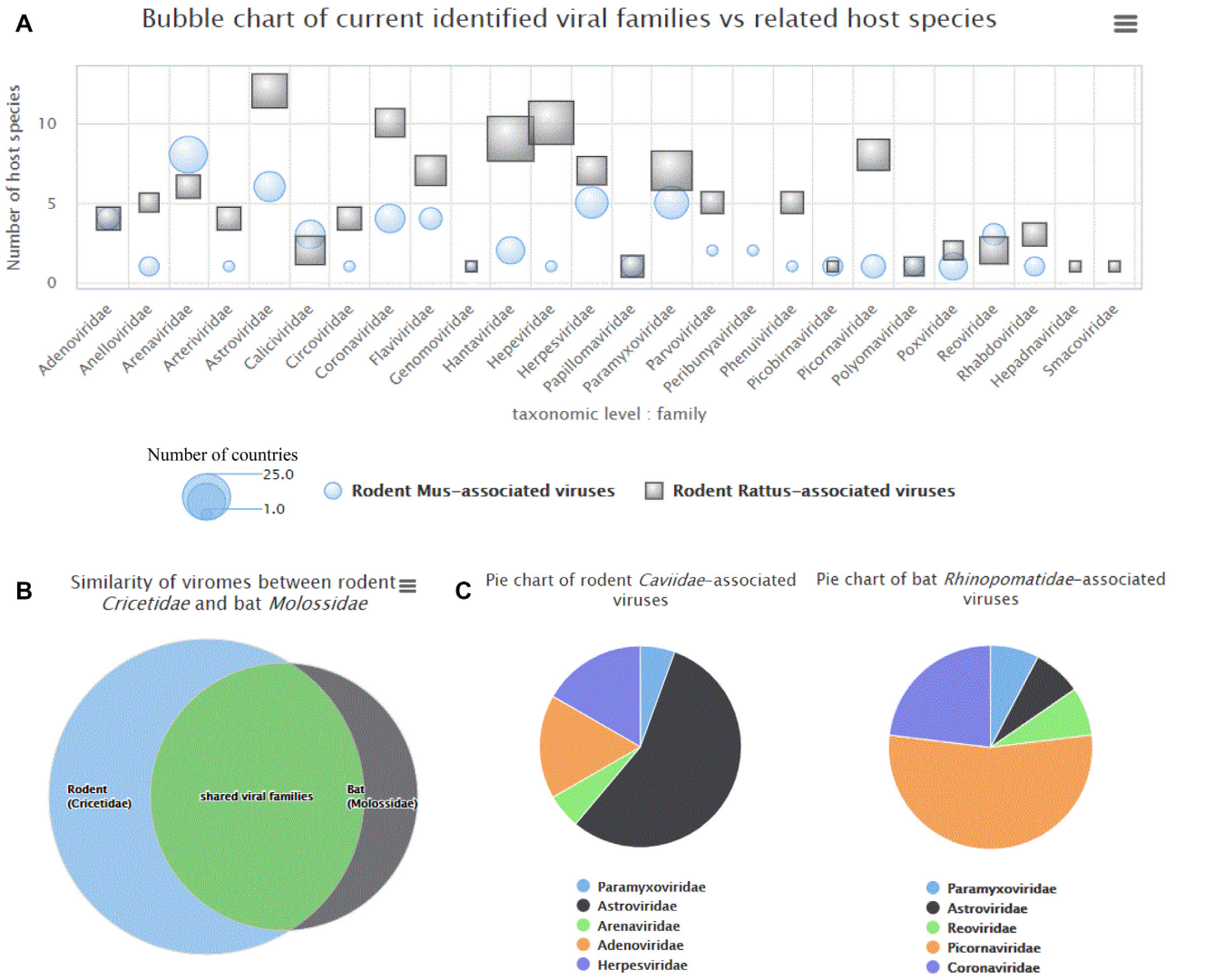

Figure 2. Illustrations of customized comparative analysis outputs from the ZOVER platform. (**A**) A comparative bubble chart of currently identified Mus- and Rattus-associated viral families vs. related host species. The size of each bubble indicates the number of sampling countries (to scale). (**B**) A Venn chart summarizing the number of shared/specific viral families detected from rodent family *Caviidae* and bat family *Rhinopomatidae*. The size of the each pie and overlapping region is positively correlated with the number of viral families. (**C**) Two comparative pie charts for dichipering the details of the related viral families identified from families *Caviidae* and *Rhinopomatidae*, respectively.

unpublished sequences in the current database do not have sampling time/country available. The absence of necessary meta-information will undoubtedly hamper further data mining. We therefore propose all data submitters to provide enough meta-information along with the sequences before release to the public or alternatively to send supplementary information to the ZOVER database to make the sequencing data indeed reusable and valuable to the community. Third, the numbers of zoonotic and vector-borne viruses detected from different regions/periods collected in the ZOVER database are not exactly correlated with the corresponding surveillance efforts that have been completed. The current database includes only viruses with sequences available and therefore virtually overlooks the possible large number of negative samples tested in those studies. Indeed, the principal prevalence of each virus is unavailable from the current database since it is generally absent from most original literature. Many current studies focus on the identification of new viruses or variants rather than the prevalence of known viruses. For example, metagenomic-based methods with pooled samples have been increasingly applied in the high-throughput surveillance of zoonotic and vector-borne viruses in recent years. Thus, it is technically impossible to directly deduce or estimate the positive rate of the detected viral sequences among individual samples. Therefore, although the overall spatial/temporal features of zoonotic and vector-borne viruses observed from the large amount of data in the ZOVER database are generally reasonable and acceptable, we prefer to recommend users to interpret the customized comparison results with caution, particularly in the case of conclusions based on a limited number of data.

The database will continue to have regular updates of the existing datasets bimonthly in the future to keep

providing users up-to-date information. Moreover, we will try to recruit more zoonotic and vector-borne viruses detected from other established reservoir hosts or arthropod vectors associated with emerging infectious diseases to further extend the coverage of the ZOVER database. Thus, the scientific community can comprehensively catalog zoonotic and vector-borne viruses, develop a reference library for rapid identification and risk assessments, and further test vaccines and therapies against related emerging infectious diseases. In addition, we will continue to develop and integrate more interactive visualization tools in the ZOVER platform for convenient online genomic, evolutionary and network analyses of zoonotic and vector-borne viruses.

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