DOI: 10.29326/2304-196X-2021-10-4-266-270

Centenary of the discovery
of African swine fever by R. Montgomery

Nature of viruses and the radical change in viral taxonomy

V. V. Makarov[1], **L. P. Buchatsky**[2]
[1] People's Friendship University of Russia (RUDN University), Moscow, Russia
[2] Institute of Fisheries of the National Academy of Agrarian Sciences (NAAS), Kyiv, Ukraine
[1] *https://orcid.org/0000-0002-8464-6380, e-mail: vvm-39@mail.ru*
[2] *e-mail: iridolpb@gmail.com*

SUMMARY

A short report is devoted to the radical changes in the taxonomy of viruses. The metagenomic sequencing has revealed the presence of a vast variety of viruses in diverse environmental samples without any connections with banal parasitism, infectivity, or pathogenicity. The understanding of viruses has expanded beyond the original parasitic–pathogen model, and now virologists recognize the role of viruses in host regulation and the maintenance of natural ecosystems. Co-evolution of the viral and cellular genomes includes mutual horizontal gene transfer and joint development of new biological functions, such as the mechanism of phylogenesis and phylodynamics of coactants. The concepts of the origin of viruses and their relation to the Universal Tree of Life are formulated. In this regard, the International Committee on the Taxonomy of Viruses (ICTV) changed the previous Code of their classification hierarchy from five ranks to a fifteen-rank one, that emulates a Linnaean framework and accommodates the entire spectrum of genetic divergence in the virosphere. Changes in the rank hierarchy are based on the evolution of the recognition of virus taxa over time, from a traditional phenotype-based characterization process to a multistage process that includes comparative sequence analyses of conserved genes and proteins, including gene phylogeny, gene synteny and shared gene content. The ICTV, that oversees the official classification of viruses and nomenclature of taxa, accepts possible non-hierarchical classifications of viruses beyond taxonomic attribution. The above provisions are illustrated with schemes of chimeric polyphyletic origin of viruses and a new rank structure; the table gives examples of the modern classification of viruses that cause some socially significant infections.

Keywords: review, viruses, taxonomy

For citation: Makarov V. V., Buchatsky L. P. Nature of viruses and the radical change in viral taxonomy. *Veterinary Science Today*. 2021; 10 (4): 266–270. DOI: 10.29326/2304-196X-2021-10-4-266-270.

Conflict of interest: The authors declare no conflict of interest.

For correspondence: Vladimir V. Makarov, Doctor of Science (Biology), Professor, RUDN University, 117198, Russia, Moscow, ul. Miklukho-Maklaya, 6, *e-mail: vvm-39@mail.ru*.

УДК 619:578:57.06

О природе вирусов и радикальном изменении их таксономии

В. В. Макаров[1], **Л. П. Бучацкий**[2]
[1] ФГАОУ ВО «Российский университет дружбы народов» (РУДН), Москва, Россия
[2] Институт рыбного хозяйства НААН, Киев, Украина
[1] *https://orcid.org/0000-0002-8464-6380, e-mail: vvm-39@mail.ru*
[2] *e-mail: iridolpb@gmail.com*

РЕЗЮМЕ

Краткое сообщение посвящено радикальным изменениям в таксономии вирусов. С помощью метагеномного анализа установлено существование огромного количества разнообразных вирусов в окружающей среде во всех сферах жизни без каких-либо связей с тривиальными паразитизмом, инфекционностью, патогенностью. Представление о вирусах вышло за рамки первоначальной модели паразитических патогенов с признанием их роли в биологии хозяина и поддержании естественных экосистем. Коэволюция вирусного и клеточного геномов включает взаимный горизонтальный перенос генов и совместное создание новых биологических функций как механизм филогенеза и филодинамики соактантов. Сформулированы представления о происхождении вирусов и их отношении ко Всеобщему Древу Жизни. В связи с этим Международный комитет по таксономии вирусов изменил прежний код их классификационной иерархии из пяти рангов на пятнадцатиранговый, тесно согласующийся с современной линнеевской таксономией и вмещающий в систему органического мира весь спектр генетического многообразия виросферы. Изменения в ранговой иерархии таксонов базируются на прогрессе от традиционной сегрегации вирусов на основе фенотипа до многоступенчатого процесса, включающего сравнительные характеристики последовательностей консервативных генов и белков, филогению генов, их синтез, общее содержание. Международный комитет по таксономии вирусов, осуществляющий надзор за официальной классификацией вирусов и номенклатурой таксонов, допускает возможные неиерархические классификации вирусов вне таксономической компетенции. Приведенные положения иллюстрированы схемами химерного полифилетического происхождения вирусов и новой ранговой структуры, в таблице даны примеры современной классификации вирусов – возбудителей некоторых социально значимых инфекций.

Ключевые слова: обзор, вирусы, таксономия

Для цитирования: Макаров В. В., Бучацкий Л. П. О природе вирусов и радикальном изменении их таксономии. *Ветеринария сегодня*. 2021; 10 (4): 266–270. DOI: 10.29326/2304-196X-2021-10-4-266-270.

Конфликт интересов: Авторы заявляют об отсутствии конфликта интересов.

Для корреспонденции: Макаров Владимир Владимирович, доктор биологических наук, профессор, ФГАОУ ВО «Российский университет дружбы народов», 117198, Россия, г. Москва, ул. Миклухо-Маклая, 6, *e-mail: vvm-39@mail.ru*.

Viruses in the biosphere are ubiquitous and as obligate intracellular parasites infect organisms of all biological species, including giant viruses. Therefore, they are probably the most abundant organism on the planet, forming a specific community of living matter of an independent type, defined as the virosphere. Based on this, the original principle of dividing biological entities into two groups of organisms is defined: ribosomal organisms, which include eukaryotes, archaea, and bacteria, and capsid organisms, which include viruses. For other self-replicating structures, the term 'orphan replicons' has been proposed (plasmids and viroids) [1, 2].

Up to some moment, science and practice were focused mainly on the negative effects of viral existence, based on the definition given by Andre Lwoff (1957) when formulating the concept of viruses as «strictly intracellular and potentially pathogenic entities, with an infectious phase, and possessing only one type of nucleic acid, multiplying in the form of their genetic material, unable to grow and to undergo binary fission and devoid of a "Lipmann system" (i.e. a system of enzymes for the production of energy)» [3]. In the modern view, virus is a capsid-encoding organism that is composed of proteins and nucleic acids, self-assembles in a nucleocapsid and uses a ribosome-encoding organism for the completion of its life cycle [4, 5].

Recent virological studies of the biosphere, their fundamental and applied results have become a new impetus for the development of virology as a science of a peculiar form of life, living matter at one of the initial stages of its origin and evolution, previously united into a separate kingdom of *Vira*. Hundreds of thousands of predominantly unknown giant deoxyriboviruses forming the marine viral metagenome (or virome), mainly of *Prochlorococcus* bacteria – the main element of photosynthesis on Earth, suggested a different role of viruses in the biosphere, in the planetary cycle of genes, matter, energy, in the economy of nature in general. They are responsible for the extraordinary abundance of living creatures in an important, if not the most important part of the planet – the World Ocean, the primary source of living matter. Under these conditions, detritus, the products of viral-induced lysis of plankton single-celled organisms, provides more than a third of organic resources in aquatic ecosystems; a bypass, simplifying and accelerating vital processes viral shunt is formed, giving a total annual yield of about 0.5 gigatons of carbon [6]. Herewith, the density of the viral population in the surface layers of the ocean is apparently estimated in hundreds of millions of viral particles per liter of water [7].

The data obtained during the study of new elements of virology allowed us to suggest a hypothesis regarding the role of virogenesis in the development of cellular life forms. The structure and biochemistry of the newly discovered largest mimiviruses have much in common with the eukaryote nucleus and suggest possible viral eukaryogenesis by analogy with the vector of endosymbiotic origin of other important cellular organelles, in particular marine free-living alphaproteobacteria → mitochondria, cyanobacteria → chloroplasts of fungi and plants [4, 8].

However, conceptually, the attribution of viruses to the living world is still questioned by many, and living cells, *de facto* hosts in viral parasitic systems, are considered to be a kind of reaction medium for the metabolic realization of alien genetic information. In particular, one of the founders of Russian virology, Academician V. M. Zhdanov (1914–1987), denied the existence of viruses on the population level, giving the preference exclusively to biosynthetic aspects in research. The strict separation between living and non-living beings puts viruses far from the Universal Tree of Life and, in fact, excludes them from the modern system of the organic world, although objectively they play an important role in evolution – the force that drives the development of all life on Earth.

Advances in genomic sequencing and comparative genomics over the past decade have made it possible to elucidate many elements of the evolutionary relationships between organisms at the subcellular and cellular levels. The metagenomic sequencing has revealed the presence of a vast variety of viruses in diverse environmental from apparently healthy environment samples without any connections with banal parasitism, infectivity, and pathogenicity.

The understanding of viruses has expanded beyond the original parasitic-pathogen model, and now virologists recognize the role of viruses in host regulation and

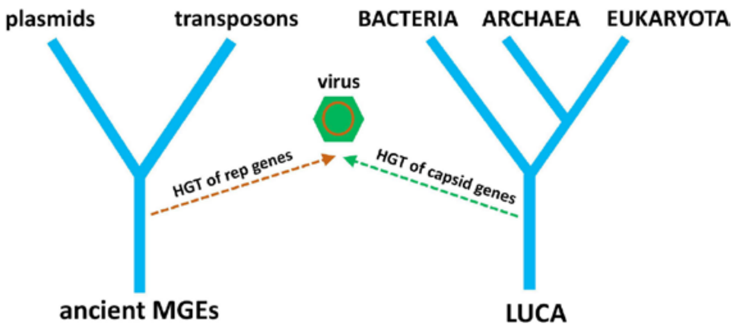

Fig. 1. A simple tree diagram showing the chimeric origin of viruses from pre-LUCA replication genes and post-LUCA structural genes. Ancient MGE ancestors replace ancient cells, reflecting the origin of virus replication genes from MGEs. The evolution of modern plasmids and transposons from ancient MGEs is also depicted [10]

the maintenance of natural ecosystems [9]. In particular, co-evolution of the viral and cellular genomes includes mutual horizontal gene transfer and joint development of new biological functions, such as existent and widely "used" mechanism of phylogenesis and phylodynamics of coactants. From the tiny circoviruses, 12–27 nm in size, harboring only two genes replicated and transcribed by cellular enzymes having one structural protein to novel giant deoxyriboviruses 400–800 nm in size, containing 1,200 b.p. genome, which encodes more than 900 polypeptides; viruses and their host cells are ecologically and evolutionarily intertwined [10].

The following diagram defining the origin of viruses and their relation to the Universal Tree of Life can serve as a kind of summarizing evidence (Fig. 1).

Virus taxonomy emerged as a discipline in the middle of the twentieth century. Traditionally, classification by virus taxonomists has been focused on the grouping of evidently closely related viruses. The earliest version, the nomenclature of viruses often connected to their 'micro-evolution' and recognizing only genera and families, has developed over time into a five-rank hierarchy of species, genus, subfamily, family and order based on Linnaean system of classification, which remained in place until 2017. However, today taxonomy as a branch science in biology, studying the principles, methods and rules of organism classification, is one of the developing areas, deploying more and more novel methods of mathematical statistics and computational biology, computer analysis, DNA and RNA comparative analysis, analysis of cell ultrastructure and many other possibilities [11].

In this regard during the past few years, the International Committee on Taxonomy of Viruses (ICTV) has recognized that the taxonomy it develops can be usefully extended to include the basal evolutionary relationships among distantly related viruses. Consequently, the ICTV has changed its 5-rank code to allow a 15-rank classification hierarchy that closely aligns with the Linnaean taxonomic system and may accommodate the entire spectrum of genetic divergence in the virosphere (Fig. 2) [12].

The novel structure includes eight principal (or primary) ranks and seven derivative (or secondary) ranks. The eight principal ranks include four that were already in use (*species*, *genus*, *family*, and *order*), and four that are new (*class*, *phylum*, *kingdom*, *realm*). Six new ranks are derivatives of most of the remaining principal ranks. This nomenclature of principal and derivative ranks includes defined suffixes for taxa, follow those used in the Linnaean system.

Changes in the rank hierarchy are based on the evolution of the recognition of virus taxa over time, from a traditional phenotype-based characterization process to a multistage process that includes comparative sequence analyses of conserved genes and proteins, including gene phylogeny, gene synteny, shared gene content and other molecular features [12]. To illustrate the adopted changes, the table shows the hierarchical position of some current viruses.

As follows from the above examples, the divergence of viruses progressively increases within the hierarchical cluster from the basal (realm) to the apical (species) rank (compare representatives of the *Riboviria* realm). Not all derivative ranks are fully populated by the

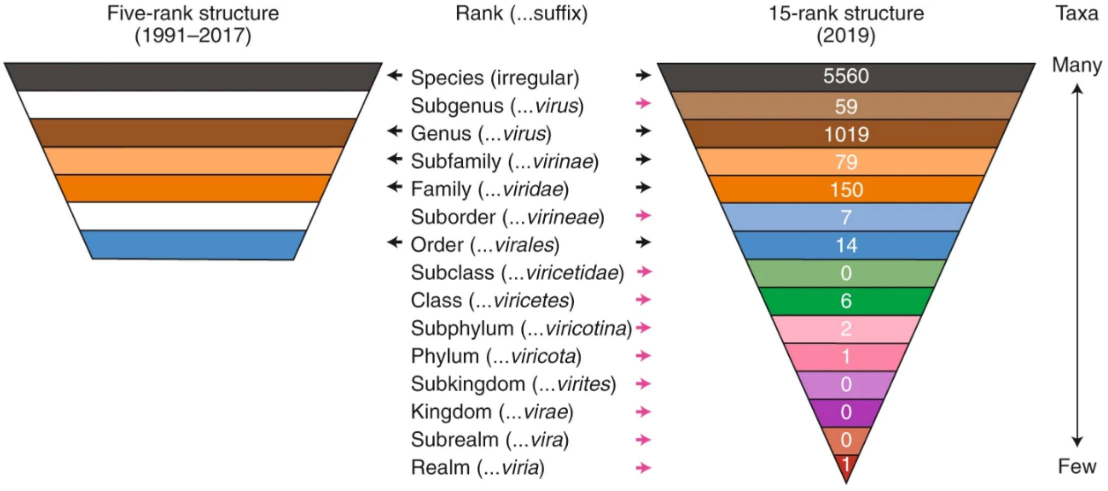

Fig. 2. The previous and the new taxonomic ranks and the number of taxa (shown in white font on the 15-rank structure). Black arrows mean ranks common to both structures; pink arrows denote ranks introduced in the 15-rank structure [12]

viruses (compare African swine fever, avian influenza and SARS-CoV-2 viruses). There are many unresolved issues due to the insufficient characteristics of macroevolutionary ranking of individual viruses, so their taxonomy, as well as in the whole organic world, is a dynamic and continuous process.

In particular, the family *Asfarviridae* is assigned to the order *Asfuvirales* of the *Pokkesviricetes* class and ranks higher (see Table). However, in addition to the official nomenclature the inclusion of the family of the unique African swine fever virus in the assumed order *Megavirales*, composed of members of a monophyletic, but heterogeneous lineage of large nuclear-cytoplasmic deoxyriboviruses, formerly called giruses, which also included the poxviruses, iridoviruses, phycodnaviruses, mimiviruses and other members of similar families, is still discussed [1]. With the constant discovery of new giant viruses (pandoroviruses, faustoviruses, molliviruses, etc.), this group is likely to increase in the near future and the taxonomy of its members remains debatable [13].

The International Committee on the Taxonomy of Viruses is a committee of the Virology Division of the International Union of Microbiological Societies (IUMS), which supervises the official classification of viruses and the nomenclature of taxa. Since ICTV is a voluntary, largely self-regulating and non-profit global organization, it allows, in addition to the official taxonomy, possible classifications of viruses outside the taxonomic competence of the ICTV.

For example, a non-hierarchical classification of viruses by D. Baltimore groups viruses into just seven classes according to their genome type, and the way their genetic information is realized, is generally recognized and widely used. The classification takes into consideration whether the DNA viruses contain double-stranded or single-stranded genome or replicate through single-stranded RNA; and RNA viruses containing positive or negative double or single-stranded genome or whether they replicate by reverse transcription [14]. For practical epidemiology, the real phylodynamic systematics of viruses based on parasite systems and other biological system approaches with distribution into such ecological categories as reservoirs, amplifiers, sources of infection, transmission is certainly important. Among other existing and possible non-hierarchical classifications, systematization techniques based on models of viral morphogenesis and morphology would be extremely interesting and useful, where the nature and mechanisms of formation of icosahedral capsid structures have practical significance from the point of view of virus resistance outside the body.

Table
Current classification of the viruses causing some infections of social importance in the 15-rank taxonomic hierarchy [12]

Ranks	Viruses					
	African swine fever	Bovine leukemia	Avian influenza	Rabies	FMD	SARS-CoV-2
Species	*African swine fever virus*	*Bovine leukemia virus*[*]	*Influenza A virus*[**]	*Rabies lyssavirus*[***]	*Foot-and-mouth-disease virus*	*Severe acute respiratory syndrome-related coronavirus*[****]
Subgenus	–	–	–	–	–	*Sarbecovirus*
Genus	*Asfivirus*	*Deltaretrovirus*	*Alphainfluenzavirus*	*Lyssavirus*	*Aphthovirus*	*Betacoronavirus*
Subfamily	–	–	–	–	–	*Orthocoronavirinae*
Family	*Asfarviridae*	*Retroviridae*	*Orthomyxoviridae*	*Rhabdoviridae*	*Picornaviridae*	*Coronaviridae*
Suborder	–	–	–	–	–	*Cornidovirineae*
Order	*Asfuvirales*	*Ortervirales*	*Articulavirales*	*Mononegavirales*	*Picornavirales*	*Nidovirales*
Subclass	–	–	–	–	–	–
Class	*Pokkesviricetes*	*Revtraviricetes*	*Insthoviricetes*	*Monjiviricetes*	*Pisoniviricetes*	*Pisoniviricetes*
Subphylum	–	–	*Polyploviricotina*	*Haploviricotina*	–	–
Phylum	*Nucleocytoviricota*	*Artverviricota*	*Negarnaviricota*	*Negarnaviricota*	*Pisuviricota*	*Pisuviricota*
Subkingdom	–	–	–	–	–	–
Kingdom	*Bamfordvirae*	*Pararnavirae*	*Orthornavirae*	*Orthornavirae*	*Orthornavirae*	*Orthornavirae*
Subrealm	–	–	–	–	–	–
Realm	*Varidnaviria*	*Riboviria*	*Riboviria*	*Riboviria*	*Riboviria*	*Riboviria*

[*] synonyms *Bovine leucosis virus*, *Bovine type C oncovirus*;

[**] serotype *Influenza A virus subtype H5N1*;

[***] members *Rabies virus*, *Arctic rabies virus*;

[****] no rank *SARS-CoV-2*.

REFERENCES

1. Makarov V. V., Bondarenko V. M. Giruses. *Byulleten' Orenburgskogo nauchnogo tsentra UrO* RAN (*elektronnyi zhurnal)*. 2012; 2: 1–12. Available at: http://elmag.uran.ru:9673/magazine/Numbers/2012-2/Articles/Makarov-Bondarenko-2012-2.pdf. (in Russ.)

2. Suzan-Monti M., La Scola B., Raoult D. Genomic and evolutionary aspects of *Mimivirus*. *Virus Res*. 2006; 117 (1): 145–155. DOI: 10.1016/j.virusres.2005.07.011.

3. Luria S. E., Darnell J. E., Jr. General Virology. 2nd ed. New York: Wiley; 1967. 528 p.

4. Claverie J.-M. Viruses take center stage in cellular evolution. *Genome Biol*. 2006; 7 (6):110. DOI: 10.1186/gb-2006-7-6-110.

5. Claverie J.-M., Abergel C., Ogata H. Mimivirus. *Curr. Top. Microbiol. Immunol*. 2009; 328: 89–121. DOI: 10.1007/978-3-540-68618-7_3.

6. Danovaro R., Dell'Anno A., Corinaldesi C., Magagnini M., Noble R., Tamburini C., Weinbauer M. Major viral impact on the functioning of benthic deep-sea ecosystems. *Nature*. 2008; 454 (7208): 1084–1087. DOI: 10.1038/nature07268.

7. Angly F. E., Felts B., Breitbart M., Salamon P., Edwards R., Carlson C., et al. The marine viromes of four oceanic regions. *PLoS Biol*. 2006; 4 (11):e368. DOI: 10.1371/journal.pbio.0040368.

8. Bell P. J. The viral eukaryogenesis hypothesis: a key role for viruses in the emergence of eukaryotes from a prokaryotic world environment. *Ann. NY Acad. Sci*. 2009; 1178: 91–105. DOI: 10.1111/j.1749-6632.2009.04994.x.

9. Moelling K. Viruses: More Friends than Foes. Singapore: World Scientific Publishing Co. Pte. Ltd.; 2017. 416 p.

10. Harris H. M. B., Hill C. A place for viruses on the tree of life. *Front. Microbiol*. 2021; 11:604048. DOI: 10.3389/fmicb.2020.604048.

11. Koonin E. V. The Logic of Chance. The Nature and Origin of Biological Evolution. Upper Saddle River, N.J.: Pearson Education Pearson Education, Inc.; 2012. Available at: http://evolocus.com/Textbooks/Koonin2011.pdf.

12. International Committee on Taxonomy of Viruses Executive Committee. The new scope of virus taxonomy: partitioning the virosphere into 15 hierarchical ranks. *Nat. Microbiol*. 2020; 5 (5): 668–674. DOI: 10.1038/s41564-020-0709-x.

13. Blome S., Franzke K., Beer M. African swine fever – A review of current knowledge. *Virus Res*. 2020; 287:198099. DOI: 10.1016/j.virusres.2020.198099.

14. Baltimore D. Expression of animal virus genomes. *Bacteriol. Rev*. 1971; 35 (3): 235–241. DOI: 10.1128/br.35.3.235-241.1971.

Received 05.08.2021
Revised 27.08.2021
Accepted 10.09.2021

INFORMATION ABOUT THE AUTHORS / ИНФОРМАЦИЯ ОБ АВТОРАХ

Vladimir V. Makarov, Doctor of Science (Biology), Professor, RUDN University, Moscow, Russia.

Leonid P. Buchatsky, Doctor of Science (Biology), Professor, Institute of Fisheries NAAS, Kyiv, Ukraine.

Макаров Владимир Владимирович, доктор биологических наук, профессор, ФГАОУ ВО «Российский университет дружбы народов», г. Москва, Россия.

Бучацкий Леонид Петрович, доктор биологических наук, профессор, Институт рыбного хозяйства НААН, г. Киев, Украина.