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The problem of norovirus infection in animals (literature review)

Vladimir A. Mischenko[1], Alexey A. Mischenko[2], Tatiana B. Nikeshina[1], Olga N. Petrova[1], Yuliya V. Brovko[3], Alfiya I. Kushlubaeva[4]

[1] Federal Centre for Animal Health, Yur'evets, Vladimir 600901, Russia

[2] Federal Scientific Centre VIEV, 24/1 Ryazansky Prospekt, Moscow 109428, Russia

[3] Tula Branch of Federal Centre for Animal Health, 1a Nekrasova str., Tula 300045, Russia

[4] Tatarian Branch of Federal Centre for Animal Health, 25a/3 Rodiny str., Kazan 420087, Republic of Tatarstan, Russia

ABSTRACT

Livestock industry efficiency strongly depends on the livability of young animals, mainly during the early postnatal period. Infectious gastroenteritis of newborns manifested as diarrhea occupies the leading place among the diseases of young animals and brings the production and economic losses. The cause of numerous gastrointestinal disorders are physiological, hygienic, infectious and other factors. This pathology is reported in 50–80% of newborn calves, while 15–55% of diseased animals die. The investigations of the etiology of numerous diarrhea cases revealed rota-, corona-, parvo-, enteroviruses and bovine viral diarrhea virus in fecal samples from calves. Inactivated vaccines have been developed in the Russian Federation to prevent viral diarrhea in cattle. Despite their high antigenicity and field effectiveness, numerous cases of diarrhea in newborn calves have been reported in a number of large livestock farms. In fecal samples collected from diseased individuals, noroviruses along with the above-mentioned viruses were detected by electron microscopy. The noroviruses were detected in fecal samples from humans, cattle, pigs, sheep, dogs, cats, mice, as well as in pork and milk samples. The norovirus genome is prone to mutations, resulting in antigenic shifts and recombination, as well as the emergence and rapid spread of new epidemic and epizootic variants. Epidemiological features of norovirus infection include: prolonged shedding of the virus by the diseased animals and carriers, various transmission routes (fecal-oral, contact) and high contagiousness. In late 20th and early 21st century a large number of dairy and meat cattle were imported to the Russian Federation from various countries, including norovirus-infected countries. All this suggests the need to take noroviruses and other viruses (neboviruses, toroviruses, astroviruses, kobuviruses) into account when investigating the etiology of numerous diarrhea cases in newborn calves and necessitates the development of norovirus diagnostic tools and methods, as well as control measures.

Keywords: review, noroviruses, *Caliciviridae,* diarrhea, calves, pigs, genotypes, genogroups, zoonosis, fecal-oral transmission

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For correspondence: Vladimir A. Mischenko, Dr. Sci. (Veterinary Medicine), Professor, Chief Researcher, Laboratory of Biotechnology and Design of Viral Drugs, Federal Centre for Animal Health, Yur'evets, Vladimir 600901, Russia, *e-mail: mishenko@arriah.ru*

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Проблема норовирусной инфекции животных (обзор литературы)

В. А. Мищенко[1], А. В. Мищенко[2], Т. Б. Никешина[1], О. Н. Петрова[1], Ю. В. Бровко[3], А. И. Кушлубаева[4]

[1] ФГБУ «Федеральный центр охраны здоровья животных» (ФГБУ «ВНИИЗЖ»), мкр. Юрьевец, г. Владимир, 600901, Россия

[2] ФГБНУ «Федеральный научный центр – Всероссийский научно-исследовательский институт экспериментальной ветеринарии имени К. И. Скрябина и Я. Р. Коваленко Российской академии наук» (ФГБНУ ФНЦ ВИЭВ РАН), Рязанский проспект, 24/1, г. Москва, 109428, Россия

[3] Тульский филиал ФГБУ «Федеральный центр охраны здоровья животных» (Тульский филиал ФГБУ «ВНИИЗЖ»), ул. Некрасова, 1а, г. Тула, 300045, Россия

[4] Татарский филиал ФГБУ «Федеральный центр охраны здоровья животных» (Татарский филиал ФГБУ «ВНИИЗЖ»), ул. Родины, 25а/3, г. Казань, 420087, Республика Татарстан, Россия

РЕЗЮМЕ

Основой повышения эффективности животноводства является сохранность молодняка, главным образом в ранний постнатальный период. Ведущее место среди болезней молодняка занимают инфекционные гастроэнтериты новорожденных животных, которые проявляются диареей и приводят к производственным и экономическим потерям. Причиной массовых нарушений функции органов пищеварения являются физиологические, санитарно-гигиенические, инфекционные и другие факторы. Данная патология регистрируется у 50–80% новорожденных телят, во многих случаях отмечается гибель от 15 до 55% больных животных. При установлении этиологии массовых диарей в пробах фекалий телят выявляли рота-, корона-, парво-, энтеровирусы и возбудители вирусной диареи – болезни слизистых. Для профилактики вирусных диарей крупного рогатого скота в Российской Федерации были разработаны инактивированные вакцины. Несмотря на их высокую антигенную активность и полевую эффективность, в ряде крупных животноводческих

хозяйств были зарегистрированы случаи массовых диарей новорожденных телят. В пробах фекалий, отобранных от отдельных больных животных, наряду с возбудителями указанных инфекций методом электронной микроскопии выявлялись норовирусы. Возбудитель норовирусной инфекции был обнаружен в пробах фекалий человека, крупного рогатого скота, свиней, овец, собак, кошек, мышей, а также в свинине и молоке. Геном норовируса подвержен мутациям, что приводит к антигенному сдвигу и рекомбинациям, а также возникновению и быстрому распространению новых эпидемических и эпизоотических вариантов возбудителя. Эпизоотологическими особенностями норовирусной инфекции являются: длительное выделение возбудителя из организма больных животных и животных-вирусоносителей, реализация различных путей передачи (фекально-орального, контактного) и высокая контагиозность. В конце XX и в начале XXI века в Российскую Федерацию из разных стран, в том числе и из неблагополучных по норовирусной инфекции, было завезено большое количество крупного рогатого скота молочных и мясных пород. Все это свидетельствует о необходимости учета норовирусов и других патогенов (небовирусов, торовирусов, астровирусов, кобувирусов) при выяснении этиологии массовых случаев диарей новорожденных телят, а также разработки средств и методов диагностики и мер борьбы с норовирусной инфекцией животных.

Ключевые слова: обзор, норовирусы, *Caliciviridae*, диарея, телята, свиньи, генотипы, геногруппы, зооноз, фекально-оральный путь заражения

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Для корреспонденции: Мищенко Владимир Александрович, д-р вет. наук, профессор, главный научный сотрудник лаборатории биотехнологий и конструирования вирусных препаратов ФГБУ «ВНИИЗЖ», мкр. Юрьевец, г. Владимир, 600901, Россия, *e-mail: mishenko@arriah.ru*

Historically, new pathogens of viral gastrointestinal infections in cattle were described based on electron microscopy results of faecal samples from newborn diarrheic calves. Subsequently, other methods, including molecular biology, began to be used for this purpose. Rotaviruses, coronaviruses, caliciviruses, toroviruses, astroviruses, kobuviruses, neboviruses and pestiviruses (causing bovine mucosal complex) were found in fecal samples from diarrheic calves using electron microscopy, molecular biology and fecal immunochemical test) [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13]. A study of 269 fecal samples from sheep, goats, cattle, pigs and rabbits taken from livestock farms in Hungary revealed a new picornavirus, which was classified as *Bopivirus* genus [14].

Caliciviruses infecting a wide range of vertebrates, as well as humans, were separated from the *Picornaviridae* family in 1979 [12]. The *Caliciviridae* family unites a group of RNA viruses with similar morphology and different antigenic properties [15]. Caliciviruses are stable and highly resistant to physical and chemical exposures (factors) of the environment; remain infectious at pH 2.7 for 3 hours at room temperature. Viruses are resistant to ether, chloroform, guanidine, sodium deoxycholate, as well as to pH 4–5, and are active for 30 minutes when heated to 60 °C [3, 15, 16, 17]. Calicivirus virions are small non-enveloped particles 27–40 nm in diameter with icosahedral symmetry (T = 3). A characteristic feature of calicivirus capsid architecture is 32 cup-shaped depressions at each of the icosahedral five-fold and three-fold axes (*calyx* is derived from the Latin which means cup). The molecular weight of the virion is 15 MDa, the sedimentation constant is 170–183 S, the buoyant density in CsCl gradient is 1.36–1.41 g/cm^3. The capsid is comprised of 180 copies of the major capsid protein VP1 and 1–2 copies of the minor structural protein VP2, around the VPg-linked genome. VP1 dimers form 90 arch-shaped capsomers that form visible 40 Å deep and 90 Å wide depressions (cups). The genome of caliciviruses is positive-sense, single-stranded RNA with a molecular weight of 2.6–2.8 MDa and 7,500–7,700 bp in size. The infectivity of calicivirus RNA is caused by the VPg peptide covalently linked to genomic RNA [2, 3, 16, 17, 18, 19, 20]. The classification of caliciviruses was approved by the decision of the International Committee on Taxonomy of Viruses in 2002. This classification was based on the results of nucleotide sequence phylogenetic analysis [20, 21, 22]. Currently, the *Caliciviridae* family comprises pathogens belonging to eleven genera, among them noroviruses, neboviruses, sapoviruses, vesiviruses, lagoviruses, etc.[1]

In 1972, a new virus was discovered by immune electron microscopy in an infectious stool filtrate derived from an outbreak of human gastroenteritis in Norwalk, Ohio. The virus was named *Norwalk virus* [16, 17, 23], and the disease was named a norovirus infection. The results of numerous studies conducted in many countries indicate that all identified noroviruses have closely related genome structures, but are genetically and antigenically highly diverse and infect a wide range of mammalian host species including humans. This virus was detected in biological samples from cattle [24, 25, 26], pigs [12, 27, 28], sheep [29], cats [30, 31], dogs [32, 33], and mice [34].

Based on the phylogenetic analysis of the genome nucleotide sequences, noroviruses were classified into 7 genogroups [16, 18, 35]. Subsequently, separate clusters (genotypes) and genetic variants were recognized in each genogroup [11, 16, 18, 20, 35, 36, 37, 38, 39, 40, 41, 42, 43]. Noroviruses are characterized by rapid genetic variability [18]. The results of the VP1 phylogenetic analysis suggest that new norovirus strains emerge every 2–3 years and there is a risk of highly virulent strain occurrence. About 5% of *Norwalk virus* population evolve into new genetic variants every year [16, 44]. Recombinations of caliciviruses are frequently reported, being the reason of antigenically altered viral strain emergence [16, 39, 45, 46]. The *Norwalk virus* genome is prone to mutations, resulting in antigenic shifts and recombinations, as well as the

[1] Current ICTV Taxonomy Release. https://ictv.global/taxonomy

emergence and rapid spread of new epidemic and epizootic variants [17, 18, 24, 41, 45]. The mutation processes involve the genome regions responsible for the virus binding to host receptors on the intestinal mucosal epithelium [16, 41].

Epidemiological features of norovirus infection include: prolonged shedding of the virus by the diseased animals and carriers, various transmission routes (fecal-oral, contact) and high contagiousness [16, 18]. Norovirus-contaminated feed and water can serve as transmission factors. The virus reservoir and source are infected (diseased and convalescent) animals. Bovine norovirus or human norovirus are responsible for the infection in cattle [24, 28]. One gram of feces from a diseased animal contains 10^8 viral particles or norovirus RNA copies [2, 8, 16, 17, 18, 38]. It has been proven that the ingestion of 10 norovirus virions is sufficient for the development of clinical manifestations [8, 16, 17, 18]. The norovirus infection incubation period in newborn calves infected with the virus isolated from cattle is 14–48 hours, the duration of the disease is from 2 to 30 days. Following the recovery, the virus is still shed for 5–50 days in the amount of 10^4 copies of viral RNA per 1 g of feces. Calves infected with human norovirus start demonstrating clinical signs 2–6 days post infection [47].

Virions replicate and assemble in the cytoplasm, and viral particles are released when the cell is destroyed. The replication cycles of the caliciviruses are similar as far as they have been explored: viruses interact with a multitude of cell surface attachment factors (glycans) and co-receptors (proteins) for adsorption and penetration, use cellular membranes for the formation of replication complexes [48].

Noroviruses propagate in the epithelium cells of small intestinal villi, as well as the immune system cells (macrophages, dendritic cells, T and B-lymphocytes) [18, 38, 49, 50, 51]. At the same time, a broadening and blunting of the intestinal villi, epithelial cell peeling, crypt epithelial hyperplasia, cytoplasmic vacuolization, infiltration of the affected cells into the *lamina propria* are observed. The lesions are more severe in the small intestine (duodenum, jejunum and ileum), where mucosal inflammation involving atrophy of intestinal villi and hypertrophy of intestinal glands are detected. Decreased cell enzymatic activity and development of secondary disaccharide deficiency are observed. In the setting of this infection gastric motility disorder frequently occurs. Increased intestinal epithelial apoptosis, epithelial barrier malfunction, and development of diarrhea due to loss of ions and water from subepithelial capillaries into the lumen are observed [16, 18]. Moreover, villous necrosis and villous atrophy are reported [38, 45, 50, 51]. Norovirus was detected in the epithelial cells of the duodenum, jejunum and ileum, Peyer's patches and large intestinal mesenteric lymph nodes [38].

Table
Genetic characteristics of noroviruses isolated from fecal samples

Hosts	Genogroups
Human	GI, GII, GIV, GVI, GVII
Ruminants (cattle, sheep)	GIII, GV
Pigs	GII
Mice	GV
Dogs	GIV, GVII
Cats	GIV

Macroscopic lesions and clinical signs caused by norovirus infection are similar to those caused by rotavirus and coronavirus infections, which complicates clinical and post-mortem diagnosis [1, 3, 4, 8, 19, 52]. Noroviruses are detected in fecal samples from cattle of different ages. The greatest economic losses are caused by norovirus infection in calves, who manifest diarrhea, depression, fever, and digestive disorders. Diarrhea is observed on days 3–7 post infection and can persist for a month. Diarrhoea is more severe in 3-week old calves than in neonatal animals [24]. In addition to norovirus, rota-, corona-, neboviruses, bovine diarrhea virus [53], and other microorganisms [10, 11] were frequently isolated from fecal samples collected from diarrheic calves. When investigating the reasons of gastrointestinal disorders in newborn calves in England, Belgium, Hungary, Germany, Italy, the Netherlands, France, Slovenia, Norway, Sweden, China, South Korea, India, Iran, Turkey, Egypt, Tunisia, the USA, Australia and New Zealand, noroviruses were detected in faecal samples. The results of numerous tests suggested that norovirus infection is a highly contagious zoonotic disease with the fecal-oral route of transmission [11, 20, 28, 29, 36, 38, 39, 40, 41, 44, 49, 53, 54, 55, 56].

The table provides data on the detection of different norovirus genogroups in different hosts. Each norovirus genogroup comprises several genetic clusters (genotypes) depending on the similarity of genetic characteristics [45, 57].

The results of the VP1 phylogenetic analyses suggest a high frequency of norovirus recombination. Noroviruses of genogroup II (GII) isolated from fecal samples of diseased humans and pigs are characterized by a high level of variability [16, 12, 28, 58]. The study of genogroup GII norovirus RNA isolated from pig faecal samples in Japan, the USA and several European countries, revealed that porcine/human recombinants can emerge in subclinically infected adult animals, and pigs may be reservoirs of new human noroviruses [42, 52, 59].

Noroviruses have been shown to undergo extensive genetic recombination. Co-infection of calves with bovine and human strains of norovirus can produce a recombinant virus with altered virulence properties [46, 60]. Noroviruses of genogroup GIII (bovine) and genotype GII.4 (human) were simultaneously identified in fecal samples from diarrheic calves in Canada [12].

There is a high probability that recombinant norovirus strains can emerge which potentially can transmit to human population.

The results of the experimental infection of gnotobiotic calves and piglets with human norovirus confirmed virus replication and seroconversion in infected animals [45, 47]. Spontaneous infections of piglets with norovirus have been reported. In this case, diarrhea occurred 2–6 days after the experimental infection. The data from these studies led to the assumption that cattle and pigs may serve as a reservoir of human norovirus, due to viral mutations in the animal organism and emergence of strains with new properties. Long-term contacts between humans and viruses, which previously infected only animals, can lead to mutations and replication in the intestinal epithelium of the human [9, 11, 12, 38, 42, 46, 47, 52, 58, 59, 61]. It is

believed that humans can be infected with bovine and porcine noroviruses through contaminated animal meat and milk [46]. The detection of human noroviruses in animals, as well as the simultaneous presence of human and animal noroviruses in bivalves, suggests a risk of the human norovirus transmission [62].

The results of serological tests showed antibodies to human norovirus in porcine sera in 36–71% of cases [27]. In the Netherlands, antibodies (IgG) to bovine norovirus were detected in 28 and 20% of serum samples, collected from 210 veterinarians and 630 animal owners, respectively [49]. In Sweden, 26.7% of blood donors were antibody-positive for bovine norovirus (GIII.2) [61]. It has been established that human norovirus has a clear tropism to the canine intestinal epithelial cells [18].

These data are based on the assumption that zoonotic transmission is typical for norovirus [20, 45, 46, 59, 61, 63].

CONCLUSION

These data suggest a high prevalence of highly contagious norovirus infection in the world, which is of social and economic importance. Noroviruses are the most common cause of epidemic gastroenteritis, responsible for at least 50% of all gastroenteritis outbreaks in humans worldwide, and a major cause of foodborne illness. Norovirus infection outbreaks among children have also been reported in the Russian Federation. Norovirus is extremely contagious, with an estimated infectious dose as low as 10–1,000 viral particles. Many researchers have revealed that transmission might occur directly through the fecal-oral route and there is a potential for zoonotic transmission. Noroviruses have been found in fecal samples from humans, cattle, pigs, sheep, dogs, cats, as well as in pork and milk. Epidemiological features of the norovirus infection include long-term viral shedding with feces in high concentrations. Transmission of noroviruses occurs in three general routes typical of acute gastrointestinal infections: waterborne, foodborne, and contacts. At the beginning of the 21st century, a large number of cattle were imported to Russia from norovirus-infected countries. This suggests the need for monitoring tests, the development of diagnostic agents and methods, and measures to control norovirus and other emergent infections.

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INFORMATION ABOUT THE AUTHORS / ИНФОРМАЦИЯ ОБ АВТОРАХ

Vladimir A. Mischenko, Dr. Sci. (Veterinary Medicine), Professor, Chief Researcher, Laboratory of Biotechnologies and Viral Product Construction, Federal Centre for Animal Health, Vladimir, Russia; *https://orcid.org/0000-0003-3751-2168, e-mail: mishenko@arriah.ru*

Alexey V. Mischenko, Dr. Sci. (Veterinary Medicine), Chief Researcher, Federal Scientific Centre VIEV, Moscow, Russia; *https://orcid.org/0000-0002-9752-6337, e-mail: viev@admin.ru*

Tatiana B. Nikeshina, Cand. Sci. (Biology), Head of Sector, Education and Scientific Support Department, Federal Centre for Animal Health, Vladimir, Russia; *https://orcid.org/0000-0002-0959-5915, e-mail: nikeshina@arriah.ru*

Olga N. Petrova, Cand. Sci. (Biology), Deputy Head of the Sector, Information and Analysis Centre, Federal Centre for Animal Health, Vladimir, Russia; *https://orcid.org/0000-0003-3939-1929, e-mail: petrova@arriah.ru*

Yuliya V. Brovko, Postgraduate Student, Veterinarian, Tula Testing Laboratory, Federal Centre for Animal Health, Tula, Russia; *https://orcid.org/0009-0004-5314-3918, e-mail: brovko@arriah.ru*

Alfiya I. Kushlubaeva, Postgraduate Student, Head of Tatarian Testing Laboratory, Federal Centre for Animal Health, Kazan, Republic of Tatarstan, Russia; *https://orcid.org/0009-0002-2021-7656, e-mail: kulushbaeva@arriah.ru*

Мищенко Владимир Александрович, д-р вет. наук, профессор, главный научный сотрудник лаборатории биотехнологий и конструирования вирусных препаратов ФГБУ «ВНИИЗЖ», г. Владимир, Россия; *https://orcid.org/0000-0003-3751-2168, e-mail: mishenko@arriah.ru*

Мищенко Алексей Владимирович, д-р вет. наук, главный научный сотрудник ФГБНУ ФНЦ ВИЭВ РАН, г. Москва, Россия; *https://orcid.org/0000-0002-9752-6337, e-mail: viev@admin.ru*

Никешина Татьяна Борисовна, канд. биол. наук, заведующий сектором отдела образования и научной информации ФГБУ «ВНИИЗЖ», г. Владимир, Россия; *https://orcid.org/0000-0002-0959-5915, e-mail: nikeshina@arriah.ru*

Петрова Ольга Николаевна, канд. биол. наук, заместитель заведующего сектором информационно-аналитического центра ФГБУ «ВНИИЗЖ», г. Владимир, Россия; *https://orcid.org/0000-0003-3939-1929, e-mail: petrova@arriah.ru*

Бровко Юлия Владимировна, аспирант, ветеринарный врач Тульской испытательной лаборатории ФГБУ «ВНИИЗЖ», г. Тула, Россия; *https://orcid.org/0009-0004-5314-3918, e-mail: brovko@arriah.ru*

Кушлубаева Альфия Исрафиловна, аспирант, руководитель Татарской испытательной лаборатории ФГБУ «ВНИИЗЖ», г. Казань, Республика Татарстан, Россия; *https://orcid.org/0009-0002-2021-7656, e-mail: kulushbaeva@arriah.ru*

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