



DOI: 10.29326/2304-196X-2023-12-4-278-283



Bovine nebovirus infection (review)

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ABSTRACT

Animal husbandry is one of the main agricultural industries in most countries over the world as well as in the Russian Federation, and its profitability is determined by three main factors: the animal genetic potential, complete diet and freedom from infectious, invasive and mass non-infectious diseases. One of the most significant and difficult tasks is to generate and rear healthy young cattle. Digestive disorders clinically manifested by diarrhea resulting in apparent dehydration, toxemia, enophthalmos, membrane pathology, immunodeficiency and metabolic disorders are prevalent among neonatal calf diseases in early postnatal period. Massive diarrhea in neonatal calves is characterized by significant polymorphism, involving a wide range of various factors including genetic, physiological, sanitary and hygienic as well as infectious factors. Infectious agents are the main causes of massive gastroenteritis in neonatal calves. In most cases viruses serve as triggers for gastrointestinal pathology development and bacteria play the secondary role. For a long time, rotaviruses, coronaviruses and pestiviruses have been believed to play the main role in etiology of massive neonatal calf diarrhea. In recent years, a number of new and understudied viruses, including kobuvirus, nebovirus, norovirus, torovirus and astrovirus, have been detected in fecal samples from diarrheic calves and their role in diarrhea development has not been definitively determined. Their role as primary pathogens, coinfection agents or commensals remains unclear. Recently these animal pathogens have widely spread in different countries of the world. At the end of the XX century – beginning of the XXI century, large numbers of cattle were imported to the Russian Federation, including cattle from the nebovirus-infected countries. Data on nebovirus infection (occurrence, pathogen characteristics, disease clinical signs and epizootological features) are given in the paper.

Keywords: review, dairy and meat cattle, neonatal calves, yaks, diarrhea, neboviruses, genetic heterogeneity, recombinations

For citation: Mischenko V. A., Mischenko A. V., Nikeshina T. B., Brovko Yu. V., Kushlubaeva A. I. Bovine nebovirus infection (review). *Veterinary Science Today*. 2023; 12 (4): 278–283. DOI: 10.29326/2304-196X-2023-12-4-278-283.

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

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УДК 619:616.98:578:616.3-053.2(048)

Небовирусная инфекция крупного рогатого скота (обзор литературы)

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РЕЗЮМЕ

Животноводство является одной из основных отраслей сельского хозяйства в большинстве стран мира, в том числе и в Российской Федерации, рентабельность которой обуславливают три основных фактора: генетический потенциал животных, полноценное кормление и благополучие по инфекционным, инвазионным и массовым незаразным болезням. Получение и выращивание здорового молодняка крупного рогатого скота является одной из наиболее важных и трудных задач. В структуре заболеваний новорожденных телят в ранний постнатальный период превалирующее место занимают нарушения функции пищеварительной системы, клинически проявляющиеся диареей, обуславливающей развитие выраженной дегидратации, токсемии, энотальмией, мембранопатологией, иммунодефицитами и нарушениями обмена веществ. Массовые диареи новорожденных телят отличаются значительным полиморфизмом, включающим широкий спектр различных факторов, в том числе генетических, физиологических, санитарно-гигиенических и инфекционных. Ведущей причиной массовых гастроэнтеритов новорожденных телят являются инфекционные агенты. В большинстве случаев вирусы служат пусковым механизмом в развитии патологии желудочно-кишечного тракта, а бактерии играют вторичную роль. Долгое время считалось, что первостепенное значение в этиологии массовых диарей новорожденных телят имеют ротавирусы, коронавирусы и пестивирусы (возбудители вирусной диареи –

болезни слизистых). В последние годы в пробах фекалий больных диареей телят был обнаружен ряд новых и малоизученных вирусов, в том числе кобувирус, небовирус, норовирус, торовирус и астровирус, роль которых в развитии диареи окончательно не определена. Остается невыясненной их роль в качестве первичных патогенов, агентов коинфекции или комменсалов. В последнее время произошло широкое распространение данных возбудителей болезней животных в различных странах мира. В конце XX – начале XXI века в Российскую Федерацию было импортировано большое количество крупного рогатого скота, в том числе из стран, неблагополучных по небовирусной инфекции. В статье приведены сведения о небовирусной инфекции крупного рогатого скота (распространение, характеристика возбудителя, клинические признаки заболевания, эпизоотологические особенности болезни).

Ключевые слова: обзор, крупный рогатый скот молочных и мясных пород, новорожденные телята, яки, диарея, небовирусы, генетическая гетерогенность, рекомбинации

Для цитирования: Мищенко В. А., Мищенко А. В., Никешина Т. Б., Бровко Ю. В., Кушлубаева А. И. Небовирусная инфекция крупного рогатого скота (обзор литературы). *Ветеринария сегодня*. 2023; 12 (4): 278–283. DOI: 10.29326/2304-196X-2023-12-4-278-283.

Конфликт интересов: Авторы заявляют об отсутствии конфликта интересов.

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For a long time, rotaviruses, coronaviruses, parvoviruses, enteroviruses and pestiviruses, one of which is bovine viral diarrhea – mucosal disease agent have been believed to play the main role in etiology of massive diarrhea in neonatal calves [1, 2, 3, 4, 5, 6, 7, 8, 9, 10]. Inactivated vaccines were developed in the Russian Federation for prevention of rotavirus, coronavirus infections and bovine viral diarrhea-mucosal disease caused by genotype I virus [1, 2, 3, 4]. To date, bovine viral diarrhea-mucosal disease agents belonging to more than 15 subgenotypes of all 3 genotypes have been reported to circulate in the country [3]. Recently, some new and understudied viruses including kobuviruses, toroviruses, neboviruses, noroviruses and astroviruses were detected in fecal samples from diarrheic calves [5, 6, 11, 12, 13, 14, 15] which role in the disease development has not been yet clearly defined. Such agent diversity makes difficult identification of etiological factors responsible for gastrointestinal pathologies in neonatal calves and leads to the choice of insufficiently effective specific preventive tools and great economic losses. This aspect is very important for the holdings involved in high-yielding animal breeding.

In 1976, RNA virus was detected in fecal samples collected from diarrheic neonatal calves kept in the settlement located near Newbury in the South England and was named *Newbury agent 1*. Electronic microscopy showed that the said virus virions were small (36.6 nm in diameter) non-enveloped icosahedral (E = 3) particles consisting of 90 dimers of main structural protein VP1 (58–62 kDa). There were calicivirus-characteristic 32 cup-shaped depressions on the external capsid surface. Isolated agent was classified to *Caliciviridae* family. The virion molecular mass was 15 MDa, sedimentation coefficient was 170–187 S, buoyant density in CsCl is 1.34 g/cm³. As all other caliciviruses, the isolated agent was stable in the environment, resistant to acid, heating and to chloroform agent. Calves were found to be infected with nebovirus by fecal-oral route or by contact. However, the isolated virus differed from *Caliciviridae* family representatives known at that time [6, 16, 17, 18, 19].

New system for calicivirus classification based on results of molecular biological tests of the viruses was proposed in the beginning of XXI century [20]. *Caliciviridae* family com-

prised four genera: vesiviruses, sapoviruses, noroviruses, and lagoviruses. *Newbury 1* virus was classified to *Norovirus* genus. Therewith, molecular biological test results showed that *Newbury 1/76UK* virus as some viruses identical to it isolated from feces of diarrheic neonatal calves differed from all known noroviruses. In 1980, the calicivirus related to *Newbury 1/76UK* virus was isolated from fecal samples collected from diarrheic calves in the holding located in Nebraska (Ohio, USA). However phylogenetic analysis of the nucleotide sequences showed that this agent named after the place of sampling (*Nebraska/80/US*), differed from all known viruses and, as a result, the isolated virus was classified to a new genus – *Nebovirus* genus [18, 21].

Nebovirus is a non-enveloped virus with icosahedral geometries, and T = 3, T = 1 symmetry and is 35 nm in diameter. Cattle is the main host of the virus. This pathogen can cause necrotic hepatitis resulting in fatal hemorrhages. Nebovirus replicates in intestinal epithelial cell cytoplasm. Neboviruses, as all other caliciviruses, are stable, highly resistant to physical and chemical environmental factors and retain infectivity at pH 2.7 for 3 hours at room temperature. The viruses are resistant to ether, chloroform, guanidine, sodium deoxycholate, bile acids. The agent remains infectious at 60 °C for 30 minutes [6, 19, 22, 23].

In 2010, *Newbury 1/76/UK* and *Nebraska/80/US* viruses were classified to new *Nebovirus* genus of *Caliciviridae* family. Then, isolated nebovirus strains were classified based on the results of VP1 nucleotide sequence phylogenetic analysis [14, 21, 23]. Nebovirus genome is a single-stranded RNA with molecular weight of 2.6–2.8 MDa, 7.4 kbp in length and is organized into two major ORFs encoding nonstructural polypeptide with the major structural capsid protein (VP1) gene in the frame with non-structural polypeptide.

All isolated neboviruses have closely related genome structures but genetically and antigenically diverse. Nebovirus genome is liable to mutations that resulting in antigenic drift and recombinations as well as emergence of new antigenically altered agent variants [14, 24, 25, 26, 27, 28]. Mutations occur in the genome segments responsible for calicivirus binding to receptors of intestinal mucosal epithelial cells [1]. The neboviruses are believed to evolve through recombination [23, 24, 27, 29, 30]. Nebovirus replication and assembly take place in cytoplasm and

the viral particles are released from the cell by lysis. All known caliciviruses have similar replication cycles: they interact with many cell attachment factors (glycans) and with co-receptors (proteins) for adsorption and penetration, use cell membranes for formation of replication complexes [1, 16, 17, 29]. Attempted cultivation of nebovirus in MDBK and PB cells was unsuccessful [6, 21].

Pathomorphological changes and clinical signs caused by nebovirus infection are similar to that ones caused by rotavirus, coronavirus and kobuvirus infections, as well as by bovine viral diarrhea – mucous disease virus that makes difficult clinical and postmortem diagnosis [11, 31].

Neboviruses replicate in intestinal villi epithelium as well as in the immune system cells. The virus replication is characterized with intestinal villus expanding and blunting, epithelial cell detachment, crypt epithelial hyperplasia, cytoplasm vacuolization, infiltration of affected cells. The most pronounced changes are recorded in the mucous membrane of the proximal intestine (duodenum, jejunum and ileum), where inflammatory processes accompanied by intestinal villus atrophy and intestinal gland hypertrophy are found [9, 29, 31, 32]. Necrosis of small intestine villi epithelium was reported. Decreased enzymatic activity in cells and secondary disaccharide deficiency development resulting in diarrhea were reported [9, 32].

Nebovirus infection has the following epizootological characteristics: long-term agent shedding by diseased animals and virus carrier animals, high contagiousness and virus persistence in the environment. Infected (diseased and convalescent) animals are the nebovirus reservoir and source. The virus-contaminated feed and water can be nebovirus transmission factors.

Incubation period in the nebovirus-infected neonatal calves is considered to be 12–48 hours, and the disease lasts for 2–30 days. Duodenum and jejunum mucosal lesions were detected in gnotobiotic calves 12 hours after experimental infection with *Newbury 1/76UK*. Nebovirus was detected in enterocytes located on villi sides [18]. Anorexia, diarrhea, enophthalmos, dehydration and metabolism disorders were reported in neonatal calves with the disease caused by nebovirus infection kept in animal holdings. Duodenum and jejunum mucosal inflammation was observed in necropsied dead animals. No difference in clinical signs was observed in colostrum-deprived calves experimentally infected with nebovirus *Newbury 1/76UK* and *Nebraska 80/US* strains. No difference in postmortem lesions was also observed in necropsied dead calves [9, 16, 18, 21, 26, 33, 34].

Chinese researchers investigated the causes of diarrhea outbreaks in newborn yak calves kept on the Qinghai-Tibetan Plateau. For this purpose, 354 fecal samples were taken from newborn animals on 55 farms. Nebovirus RNA was detected with polymerase chain reaction in 22% of the samples. Phylogenetic analysis of 78 virus isolates showed that 69 of them were closely related to *Nebraska*-like strains, and 9 isolates circulating on 6 farms in 2 administrative districts were representatives of a new nebovirus genotype [13].

In 2012, mass gastrointestinal disorder was reported in neonatal calves on the farm located in the town of Kirklareli (East Thrace, Turkey) where 250 cows and 200 calves were kept. About 60% of calves became diseased and 30% of them died. Lesions characteristic for rotavirus and coronavirus infections were detected in necropsied dead animals. Rotavirus, coronavirus and *Cryptosporidium* were detected

in fecal samples collected from diseased calves. Calicivirus demonstrating 65% homology to *Nebraska* nebovirus was detected in 3 fecal samples when the samples were tested with molecular methods. Isolated pathogen was named as *Kirklareli virus* after the sampling place. It was classified to *Nebovirus* genus based on phylogenetic analysis data. Detailed analysis of the obtained data has suggested that *Kirklareli virus* may be the ancestor of *Nebovirus* genus [21].

Guo Z. et al. detected norovirus and nebovirus in fecal samples collected from gastroenteritis-affected neonatal calves on one Chinese dairy farm that was indicative of co-circulation of these pathogens causing mixed infections [14].

Rotavirus was detected in 73.2% of fecal samples, coronavirus was detected in 36.6% of fecal samples, bovine viral diarrhea virus was detected in 31.7% of fecal samples and nebovirus was detected in 41.8% of fecal samples during tests of the fecal samples collected from neonatal calves kept on 13 commercial dairy farms located in 5 Chinese provinces for etiology of mass gastrointestinal diseases. Two-three pathogens were detected in many samples and all 4 viruses were detected in some samples. Phylogenetic analysis data showed that all tested nebovirus isolates belonged to *Nebraska* group (*Nebraska-like strains*), 14 out of them belonged to lineage 1 and 4 out of them belonged to lineage 3. Also recombinations in nebovirus VP1 were detected [32]. The data obtained by Chinese researchers indicate that nebovirus is widespread in meat and dairy cattle herds as well as yak herds in the country [13, 14, 26, 27, 32].

According to numerous publications, nebovirus was isolated from fecal samples taken from diarrheic neonatal calves in England [16, 18, 19, 23], Brazil [12], Hungary [15], Germany [34], France [30], Italy [24], Sweden [35], Iran [36], China [13, 14, 26, 27, 32], USA [33, 37], Tunisia [28], Turkey [21, 38, 39], South Korea [40] and other countries. Some researchers detected the virus in fecal samples collected from both diseased and clinically healthy calves kept on the same farms. It is suggested that the biological materials have been collected at different periods of the pathological process (incubation period or convalescence stage). This could also explain the different level (4.8–41.8%) of the detected nebovirus prevalence.

Characteristics of neboviruses detected in the fecal samples from neonatal calves and circulating in various countries are given in the table below.

CONCLUSION

Nebovirus infection of neonatal calves is registered in many countries of the world having close economic ties with the Russian Federation. A large number of dairy and meat cattle were imported into Russia from Germany, the USA, France, Hungary and some other countries where nebovirus infection was diagnosed. All this is indicative of high probability of importation of animals infected with various infectious disease pathogens that is confirmed by the presence of pestiviruses (bovine viral diarrhea – mucosal disease agents) in biological material samples taken from aborted fetuses and dead neonatal calves born from imported heifers. Evidence of recombinant nebovirus strain circulation was found. In some cases, other pathogens including norovirus and astrovirus, were detected together with nebovirus in pathological material samples taken from the same animals.

Table
Characteristics of the neboviruses circulating in the countries

Countries	Nebovirus genotype	Publication number
England	<i>Newbury 1/76/UK; Nebraska80/US</i>	16, 18, 19, 23
USA	<i>Nebraska80/US</i>	33, 37
Germany	<i>Newbury 1/76/UK</i>	34
France	<i>Nebraska80/US; Dijon A216/06/FR</i>	30
China	<i>Newbury 1-like strains; Nebraska-like strains; Dijon A216-like strains</i>	13, 14, 26, 27, 32
Brazil	<i>Newbury 1/76/UK</i>	12
Turkey	<i>Newbury 1-like strains; Nebraska-like strains; Kirklareli virus</i>	21, 38, 39
Italy	<i>Newbury 1/76/UK; Nebraska80/US</i>	24
Hungary	<i>Newbury 1/76/UK</i>	15
Iran	<i>Newbury 1/76/UK; Nebraska80/US</i>	36
Tunisia	<i>Nebraska80/US; Dijon A216-like strains</i>	28
South Korea	<i>Newbury 1/76/UK; Nebraska-like strains</i>	40
Sweden	<i>Newbury 1-like strains; Nebraska-like strains</i>	35

Pathomorphological changes caused by nebovirus infection are similar to that ones caused by rotavirus, coronavirus, norovirus, torovirus infections, as well as of bovine viral diarrhea – mucous disease. Diarrhea in neonatal calves is generally caused by mixed infections. All this makes much more difficult clinical and postmortem diagnosis of detected gastrointestinal disorders as well as specific prevention of viral diarrheas.

Presented data on bovine nebovirus infection and its wide spread in many countries of the world show that further studies, particularly on breeding farms, monitoring tests of pathological material samples from neonatal calves with clinical signs of gastrointestinal diseases, development of tools and methods for this infection control and prevention are required.

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Received 07.07.2023

Revised 31.07.2023

Accepted 14.08.2023

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