

Influenza D virus is a relatively recent discovery, first identified in 2011 in pigs in the United States, although evidence suggests that it has been circulating in cattle populations since at least 2003 (Kwasnik et al., 2023). The virus is currently distributed across Europe, North America, South America, Africa, Asia, and, more recently, Australia (Figure 1) (Chiapponi et al., 2016; Jiang et al., 2014; Salem et al., 2017).

Although IDV was originally discovered in pigs, cattle are considered the main reservoir. A growing number of studies suggest that IDV may be associated with BRDC. The virus has been isolated from cattle and pigs, and antibodies against IDV have been detected in various animal species (Hause et al., 2013; Jiang et al., 2014). Histochemical studies confirm the ability of IDV to bind to receptors in the respiratory tract of numerous domestic and wild animals. Seroprevalence of IDV has also been reported in humans, particularly those with occupational exposure to cattle. Studies in poultry have not demonstrated susceptibility to IDV infection; however, IDV RNA has been detected in aerosol samples from poultry farms in Malaysia (Kwasnik et al., 2023).

Etiological agent

Influenza D virus (IDV) is spherical, 80–120 nm in diameter, and enveloped by a lipid membrane. Its genome consists of seven single-stranded RNA segments encoding nine proteins. Genetically, IDV is most closely related to influenza C virus, sharing approximately 50% amino acid identity and a similar gene structure. Both influenza D and C viruses possess a hemagglutinin-esterase fusion (HEF) protein that combines the functions of hemagglutinin and neuraminidase found in influenza A and B viruses. HEF mediates viral attachment and entry into host cells.

Five genetic lineages of IDV based on HEF have been identified: D/OK, D/660, D/Yama2016, D/Yama2019, and D/CA2019 (Kwasnik et al., 2023). The HEF glycoprotein, together with the M1 and M2 proteins, plays a crucial role in viral infectivity and host specificity. HEF is responsible for receptor binding, membrane fusion, and viral entry, and it is the main determinant of the high thermal and acid stability of IDV.

Sialic acid residues on host cell surface glycoproteins serve as receptors for influenza viruses. IAV and IBV recognize α 2,3- or α 2,6-linked sialic acids. IDV binds both Neu5,9Ac2- and Neu5Gc9Ac-containing glycans, irrespective of whether they are linked to galactose via α 2,3 or α 2,6 bonds. In contrast, ICV preferentially binds Neu5,9Ac2. Despite differences in the expression of these receptors among hosts, IDV appears capable of efficient binding and transmission.

Yu et al. demonstrated that exposure of IDV to low pH has little effect on infectivity, whereas it completely inactivates IAV. IDV remains infectious at temperatures above 53°C for up to 120 minutes and loses only about 20% of infectivity after exposure to pH 3.0 for 30 minutes, in contrast to IAV, IBV, and ICV, which are fully inactivated under these conditions (Yu et al., 2017). These findings indicate that IDV is the most environmentally stable of the four influenza virus types (Kwasnik et al., 2023).

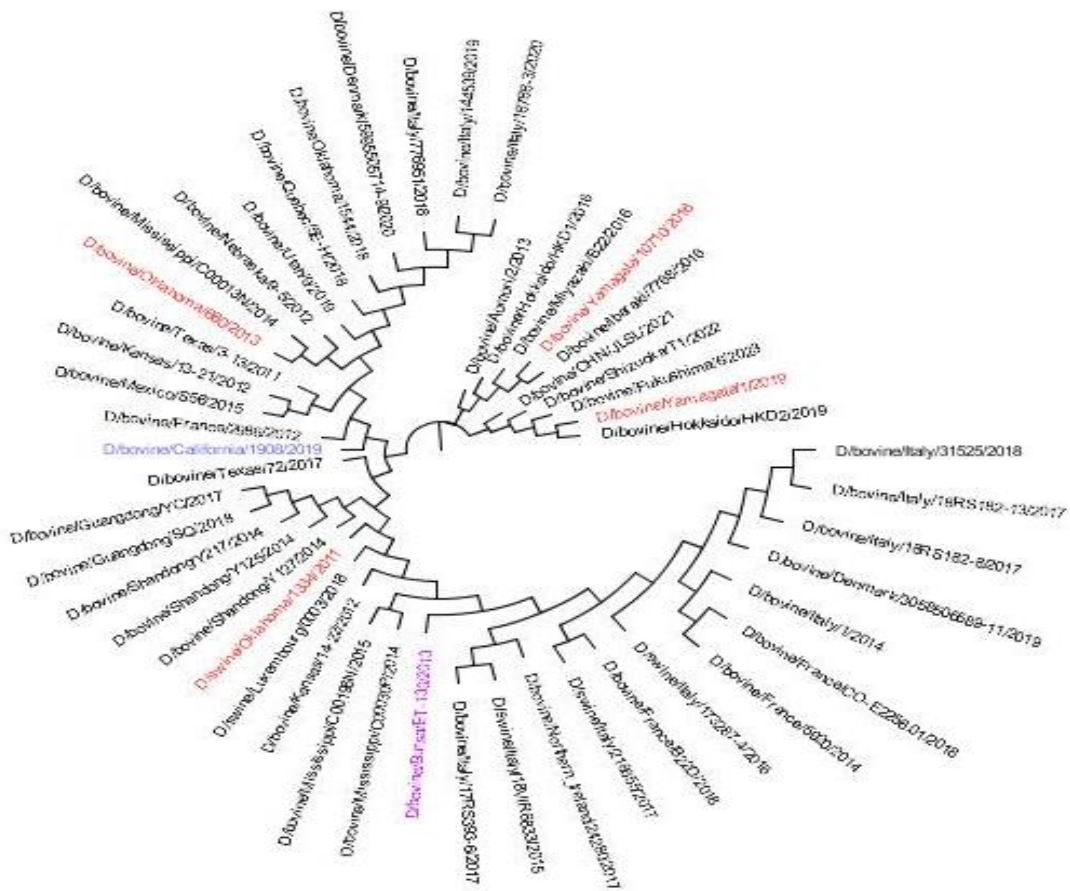
Despite extensive research, many aspects of IDV biology remain unclear, particularly regarding virus–host interactions and innate immune responses. It is still unknown how the increased stability conferred by the HEF protein affects viral persistence and transmission, or how IDV NS1 protein interactions modulate host immunity (Skelton and Huber, 2022).

Phylogenetics

Phylogenetic analyses indicate the circulation of four main IDV lineages:

- D/swine/Oklahoma/1334/2011 (D/OK), detected in Europe, the United States, Mexico, China, and Namibia;
- D/bovine/Oklahoma/660/2013 (D/660), identified in Italy, the United States, and Mexico;
- D/bovine/Yamagata/10710/2016 (D/Yama/2016), detected in Japan; and
- D/bovine/Yamagata/1/2019 (D/Yama/2019), detected in Japan and China.

Additionally, strains belonging to potentially novel lineages have been identified in California (D/CA/2019), Brazil, and Turkey. Phylogenetic relations are shown in Figure 2.



2.0

Figure 2. Phylogenetic tree based on nucleotide sequences of the IDV HEF segment (D/OK, D/660, D/Yama/2016, D/Yama/2019, D/CA/2019, D/Bursa/2013). Sequences were retrieved from the NCBI database, and the tree was constructed using MEGA11.

Strains from the D/OK and D/660 lineages frequently reassort and show antibody cross-reactivity. In contrast, Japanese strains appear to have distinct evolutionary origins (Trombetta et al., 2019). Genetic analyses of European IDV strains from 2009–2022 indicate increasing diversity driven by mutations in the HEF glycoprotein. The nucleotide substitution rate of IDV HEF is higher than that of ICV HEF and comparable to that of HA in seasonal human influenza viruses (Gaudino et al., 2022).

Pathogenesis

Cattle are the main reservoir of IDV. Following infection, the virus has been detected in several predilection tissues, including the nasal cavity, trachea, lung tissue, and bronchioles, particularly around day 8 post-inoculation. Viral RNA has also been identified in the tracheobronchial and mediastinal lymph nodes.

The highest viral loads are typically observed in the nasal cavity, especially in the ethmoidal sinuses. High levels of viral RNA have additionally been detected in the olfactory bulb and tonsils of animals infected via aerosol exposure. However, viral tropism for these tissues has not been confirmed by immunohistochemistry or virus isolation, and further studies are required. Overall, IDV shows a clear tropism for the upper respiratory tract, where it preferentially replicates in epithelial cells, but it can also replicate in the lower respiratory tract, causing mild to moderate interstitial pneumonia. The precise target cells in the lung, as well as the temporal dynamics and mechanisms of virus-induced respiratory damage, remain poorly understood (Ruiz et al., 2022).

IDV exhibits optimal replication at both 33 °C and 37 °C in cell culture, indicating that elevated temperatures do not limit viral replication in the lower respiratory tract (Ruiz et al., 2022). Seroconversion to IDV-specific IgG has been demonstrated by ELISA in all experimentally inoculated animals within 10 days' post-infection. In addition to the humoral immune response, IDV also induces a cellular immune response. The mean duration of viral shedding was estimated at 8.1 ± 1.9 days (Ruiz et al., 2022).

Detection of IDV RNA in serum samples from infected cattle suggests the occurrence of transient viremia and possible dissemination to other organs. Viral RNA has also been detected by RT-PCR in feces on day 5 post-infection and in the jejunum on day 6 post-infection, coinciding with peak viral replication in the respiratory tract. Although intestinal tropism requires confirmation by immunohistochemistry or virus isolation, these findings suggest a potential additional route of viral excretion via the digestive tract, alongside the established oronasal route. The high acid stability of IDV may facilitate such intestinal involvement, similar to that observed for IAV and IBV (Yu et al., 2022).

Experimental studies demonstrate that both single and co-infections with IDV elicit a humoral immune response in cattle. Antibodies against IDV were detected using hemagglutination assays, with calves seroconverting approximately seven days' post-infection. IDV-specific IgA and IgG were detected at seven and ten days' post-infection, respectively, indicating a rapid local (IgA) and systemic (IgG) immune response (Ruiz et al., 2022).

Clinical signs, diagnosis, and vaccines

Influenza D virus is transmitted primarily through direct contact and short-range aerosols and mainly affects cattle, although asymptomatic infections have been reported in several species. Experimental infection in calves results in mild to moderate respiratory signs, including coughing, nasal and ocular discharge, depression, and dyspnea, associated with inflammation of both the upper and lower respiratory tract. Disease severity may increase in the presence of co-infections (Kwasnik et al., 2023). In pigs, IDV replicates in the respiratory tract but generally does not cause overt clinical disease (Gorin et al., 2019).

Diagnosis is based on detection of viral RNA by real-time RT-PCR in respiratory samples or on serological assays such as hemagglutination inhibition and virus neutralization tests. ELISA-based methods for antibody detection and differentiation from influenza C virus have been developed but are not yet widely implemented.

Currently, no licensed vaccines against IDV are available. Several experimental vaccines have shown promising results in animal studies; however, none have been approved for field use.

Hosts

Since its first isolation from pigs in 2011, IDV has been detected in a wide range of hosts, including cattle, pigs, wild boars, camels, small ruminants, horses, and wildlife (Gaudino et al., 2022). Cattle are considered the principal reservoir (Luo et al., 2017), and IDV is suspected to contribute to BRDC alongside other viral and bacterial respiratory pathogens (Ruiz et al., 2022).

Calves. Most IDV research has focused on calves, revealing widespread exposure worldwide. High seroprevalence, often exceeding 70–90%, has been reported in cattle populations in North America, Europe, and Asia, whereas molecular detection rates in respiratory samples are generally low ($\leq 10\%$). In Sweden, 32% and 40% of milk samples in storage tanks collected in 2019 and 2020 were found to be positive for IDV antibodies, respectively (Alvarez et al., 2023). IDV circulation has been confirmed throughout Europe, with particularly high seroprevalence in Ireland, Italy, and Luxembourg, and lower but consistent detection in France and other countries (Snoeck et al., 2018;

Kwasnik et al., 2023). In Asia, IDV has circulated in cattle since at least 2010, with high seroprevalence reported in China, Japan, and the Republic of Korea (Jiang et al., 2014; Hayakawa et al., 2020; Lim et al., 2023).

Experimental infections show that IDV causes mild respiratory disease in cattle and is efficiently transmitted by direct contact, supporting the role of cattle as a natural reservoir and suggesting a facilitating role in mixed respiratory infections (Ferguson et al., 2016). IDV has also been detected in Africa, South America, and Australia, with variable seroprevalence and genetically distinct lineages, underscoring its broad geographic distribution and ongoing evolution (Da Silva et al., 2022; Brito et al., 2023; Yu et al., 2024).

Pigs. Circulation of IDV in pigs has been reported in Europe, North America, Asia, and Africa, but at much lower levels than in cattle (Kwasnik et al., 2023). Seroprevalence is typically below 10%, and molecular detection is rare or absent in large-scale surveys. Although higher detection rates have been reported in Italy and China, overall evidence suggests limited adaptation of IDV to pigs and an unclear role of swine in virus maintenance (Foni et al., 2017; Zhai et al., 2017).

Camels. Extremely high IDV seroprevalence, often exceeding 95%, has been reported in camels across Africa, Asia, and Australia (Salem et al., 2017; Kwasnik et al., 2023). Despite limited sample sizes and potential cross-reactivity with influenza C virus, these findings suggest that camels may play a significant role in IDV circulation, potentially acting as reservoirs alongside cattle.

Small ruminants. Sheep and goats are susceptible to IDV infection, but seroprevalence is generally low compared with cattle and camels. Most studies report seroprevalence below 5% in Europe, North America, and Africa, with occasional higher values in China and southern Italy (Mazzetto et al., 2020; Lanave et al., 2024). These species are therefore considered incidental hosts.

Horses. Serological evidence of IDV exposure has been reported in horses, with seroprevalence of approximately 11–12% in the U.S. Midwest, while very low seropositivity and no viral RNA detection have been reported in the United Kingdom (Kwasnik et al., 2023). Experimental infections indicate that IDV can replicate in the equine respiratory tract and induce seroconversion without causing clinical disease, suggesting possible interspecies transmission (Sreenivasan et al., 2022).

Wild animals. Wild boars may contribute to IDV ecology by acting as a bridge between domestic and wild species. Studies in the United States report viral replication without clinical disease and seroprevalence up to 19–43% (Ferguson et al., 2018). In Europe, exposure levels in wild boars and deer are generally lower, although antibodies have been detected in several cervid species. Viral RNA has also been identified in wildlife in Africa, including giraffes and wildebeest (Gorin et al., 2019; Guan et al., 2022; Molini et al., 2022).

Experimental models and cell lines IDV infects **mice, guinea pigs, and ferrets** without causing overt disease but induces inflammatory lung changes, supporting their use as experimental models. The virus also replicates efficiently in multiple mammalian cell lines, demonstrating broad cellular tropism (Hause et al., 2013; Oliva et al., 2020).

Zoonotic potential. Serological surveys indicate human exposure to IDV. A 2011 study in the United States and Canada reported a seroprevalence of 1.3%, while a study in Italy found seroprevalence increasing from 5.1% in 2005 to 46% in 2014 (Hause et al., 2013). Leibler et al. (2023) detected IDV in nasal washes of 67% of dairy farm workers, none of whom reported respiratory symptoms. Although no confirmed cases of clinical IDV infection in humans have been reported, receptor studies, replication in human respiratory epithelium models, and detection of viral RNA in bioaerosols and nasal swabs suggest that humans may be susceptible.

Risk assessment

Influenza D virus is a relatively new virus, first detected in pigs in the USA in 2011, although evidence suggests that it has been circulating in cattle populations since at least 2003.

Bulgaria has not been screened for this disease, but its spread is monitored globally. The presence of IDV in Turkey is a signal of a possible risk of the virus entering the country, if it is not already present.

As of November 1, 2022, the number of cattle in Bulgaria was 559.5 thousand, which is 5.1% less than in 2021. Dairy cows were 7.9% fewer (198 thousand). An increase of 15.2% compared to 2021

was observed in male animals aged 1 to 2 years and in breeding heifers (by 12%). The number of heifers for fattening aged 2 years and older increased by more than 64.8%.

The number of sheep was 1,096.4 thousand (−8.6%). The average size of sheep herds in the country was 69.4 animals and increased by 11.7% compared to the previous year. The number of ewes decreased by 8.3%. As of November 1, 2022, dairy ewes numbered 758.8 thousand (−11.8%), and meat ewes numbered 170 thousand (+11.4%).

The total number of goats decreased by 14.4% (to 184 thousand), and the number of ewes decreased by 13.1%. Compared to the previous year, 2021, the number of pigs decreased to 601.7 thousand (−13.4%). The number of inseminated sows was 8.2% higher than in 2021, and the number of young unseminated pigs over 50 kg was 30.8% higher than in 2021 (Agrostatistics, MAF, 2022).

According to the EFSA supporting publication by Álvarez et al. (2024), the main risk factors for the occurrence of IDV include farm size, live animal trade, age of cattle, and the presence of respiratory signs. However, further studies are needed to determine the true prevalence of respiratory clinical signs in cows, as well as to assess human exposure to IDV, especially on cattle farms. Viral diversity is still being studied: new virus introductions and new reassortants have been identified, and their clinical impact and levels of cross-protection remain poorly understood. In this context of increasing viral diversity, a standardized nomenclature system for IDV genotypes is needed.

The circulation of the virus in different animal populations naturally raises continuous concern regarding the possible zoonotic potential of IDV, particularly the risk of human-to-human transmission.

The first three risk factors for the introduction of the virus into cattle or pig herds are:
weaned young animals introduced to the farm;
unweaned young animals introduced to the farm;
return of animals from the farm that have participated in competitions or gatherings.

For pigs, an additional risk factor is proximity to other ruminant species (mixed farms or farms within a radius of 500 m).

Given that there is currently no specific commercial vaccine against IDV and that testing strategies are limited, greater efforts should be made to improve biosecurity measures to protect farms. Biosecurity assessments should cover infrastructure, ventilation, visitors, vehicles, and procedures, and should ideally be generated automatically and in real time. Close cooperation between veterinarians and farmers is essential. Farmers should be informed about the disease and its clinical signs in order to report suspected cases in a timely manner.

Considering all factors and the lack of data on this disease, the risk level for the occurrence of IDV cases in Bulgaria is assessed as **low (L) to medium (M)**, with a tendency to increase if the disease is introduced from Turkey.

Conclusions and implications

- Influenza D virus differs from other influenza viruses in terms of virion properties, host range, and reservoir. As with influenza A, the wide host range of IDV provides increased opportunities for reassortment and mutation. IDV exhibits high thermal and acid stability, indicating a high potential for environmental resistance.
- In most European countries where seroprevalence studies in cattle have been conducted, a high proportion of positive animals has been observed; similar findings have been reported in parts of Asia and the USA. Cattle may play a key role in the global spread of IDV, including as a source of infection for other farm animals, wildlife, and humans.
- Sequencing and phylogenetic analysis of the hemagglutinin-esterase fusion (HEF) gene showed that the Turkish strain is 95% identical to European and American strains, suggesting intercontinental spread. These findings highlight the need to initiate similar studies in Bulgaria.
- High seroprevalence has also been observed in camels, which may represent an important reservoir of IDV in tropical regions.
- Seroprevalence of IDV is much lower in pigs, small ruminants, and horses compared to cattle.
- Among wild animals, the most extensive studies have been conducted in wild boars in the USA and in various deer species in both the USA and Europe. These studies confirm the presence of antibodies

against IDV. Given the abundance of wild boars in the USA and deer in Europe, these species may be important for the ecology of the virus.

- Molecular and serological tests confirm IDV infection not only in domestic animals but also in various wild species, including giraffes, kangaroos, wildebeests, wallabies, llamas, and hedgehogs. Influenza D may pose a zoonotic threat, as seroprevalence has been demonstrated in humans with occupational exposure to cattle. Monitoring IDV emergence in both domestic and wild animals that may act as natural reservoirs is therefore important.
- The infectivity and ability of IDV to transmit between species make it an increasing epidemiological threat that requires continued surveillance and further research.
- Positive surveillance findings highlight the need to include this emerging virus in national animal health surveillance programs to control its emergence and spread and to protect public health.
- The circulation of IDV in diverse animal populations, together with its genetic proximity to human influenza C virus, naturally raises ongoing concern regarding its zoonotic potential, particularly the risk of human-to-human transmission.

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