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Review

From Africa to Europe: the rise of epizootic haemorrhagic disease virus serotype 8

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Abstract

Since late 2022, epizootic haemorrhagic disease virus serotype 8 (EHDV-8) has emerged as a major threat to ruminant health in Europe, most likely introduced from North Africa through windborne *Culicoides* midges. The virus has caused extensive outbreaks in cattle and red deer across Italy, Spain, France, and Portugal, exposing vulnerabilities in current outbreak prevention and control measures. This review provides an updated overview of EHDV-8, focusing on its clinical presentation in domestic and wild ruminants, its recent geographic spread in Europe, and the rapid development of targeted vaccines. The European experience highlights the virus's capacity to induce substantial morbidity not only in cattle but also in wild and farmed cervid populations, particularly red deer. However, several aspects of EHDV-8 biology remain poorly understood, including host susceptibility and the mechanisms underlying viral overwintering. Furthermore, the limited availability of genomic data from Africa hampers efforts to trace the evolution and dissemination of EHDV. Strengthening collaboration with North African and Sub-Saharan countries will be crucial to enhance and harmonize surveillance systems across regions. Closing these knowledge gaps is essential for improving preparedness and response strategies, including the development of vaccines tailored to the serotypes currently circulating in endemic areas.

Keywords

Epizootic haemorrhagic disease virus, Europe, EHDV-8, vector-borne diseases, Climate Change

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Introduction

The Mediterranean macroregion, which includes Southern Europe, North Africa and parts of the Middle East, is particularly vulnerable to climate change, with rising temperatures recognized as a major driver of the emergence and spread of arthropod-borne diseases.

Moreover, the shared ecological and climatic characteristic of the region allow for the co-circulation of the same arthropod-borne viruses (Negev et al., 2015; Paz, 2024).

A recent example is the emergence of a novel pathogen, the epizootic haemorrhagic disease virus (EHDV) likely introduced via infected insects from the Maghreb region of Northern Africa.

In particular, EHDV serotype 8 was first reported in Italy and Spain in November 2022, raising concerns due to its potential to cause clinical outbreaks in previously unexposed livestock and wild ruminant populations.

In this review, we examine the emergence and spread of EHDV-8 in Europe, highlight the initial diagnostic challenges,

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and explore the potential role of sheep in maintaining viral circulation. Finally, we assess the current state of vaccine development and future prospects for control.

Etiology, transmission and clinical relevance

Epizootic haemorrhagic disease (EHD) is a non-contagious, vector-borne viral infection affecting domestic and wild ruminants. It has been a notifiable disease to the World Organisation for Animal Health (WOAH) since 2008 and is also listed under the EU Animal Health Law.The aetiological agent, EHD virus (EHDV), belongs to the family *Sedoreoviridae*, genus *Orbivirus*, and is officially classified as *Orbivirus ruminatium* according to the latest ICTV Master Species List (March 3rd, 2025 - https://ictv.global/taxonomy).

Analogous to other orbiviruses, EHDV has a segmented dsRNA genome consisting of ten segments (S1 to S10), which encode 7 structural (VP1 to VP7) and at least 4 non-structural proteins (NS1, NS2, NS3/3a and NS4) (Huismans et al., 1979; Mecham and Dean, 1988; Mertens et al., 2004; Belhouchet et al., 2011; Ratinier et al., 2011; Stewart, et al., 2015). Globally, at least seven serotypes (1, 2, and 4 to 8) have been identified based on cross-neutralisation assays and phylogenetic analysis of VP2, the outermost capsid protein and the major target of neutralising antibodies (Anthony et al., 2009; Yang et al., 2020).

Although rare cases of vertical transmission have been documented – for instance, with the Ibaraki strain of EHDV-2 in Japan (Ohashi et al., 1999) and EHDV-6 (Golender et al., 2017) in Israeli cattle - and oral and faecal shedding of EHDV-1 has been reported in experimentally-infected white-tailed deer (*Odocoileus virginianus*) (Gaydos et al., 2002), EHDV is almost exclusively transmitted by certain species of haematophagous *Culicoides* midges (Family *Ceratopogonidae*). As a result, the virus’s distribution is restricted to regions where competent vectors are present.

In temperate regions, outbreaks typically occur in late summer and autumn, when vector activity peaks. Conversely, transmission in tropical and subtropical regions can persist throughout the year due to the continuous presence of active vectors (Maclachlan et al., 2019; Jiménez-Cabello et al., 2023).

Once infected, susceptible ruminants develop a transient viremia of variable duration, supporting the ingestion of the virus by naïve *Culicoides* midges during blood feeding, thereby perpetuating the transmission cycle (Mills et al., 2017; Mendiola et al., 2019).

EHD primarily affects North American white-tailed deer and cattle; however, several other wild and domestic ruminant species within the *Bovidae* and *Cervidae* families have also been shown to be susceptible to natural infection (Dubay et al., 2004; Savini et al., 2011; VanCampen et al., 2013; Stevens et al., 2015; McGregor et al., 2023; Torii et al., 2024).

In white-tailed deer, the disease typically manifests as peracute or acute and is frequently lethal. Clinical signs encompass high fever, weakness, erythema, erosions and ulcerations of the oral mucosa, ptyalism, nasal discharge, severe oedema of the head and neck, dyspnoea, widespread haemorrhages, and swelling and cyanosis of the tongue, with a very high case-fatality rate reported (Noon et al., 2002; Rivera et al., 2021; Ruder and Howerth, 2024). In contrast, cattle infections have historically been associated with subclinical or mild disease. Nonetheless, several EHDV serotypes and strains exhibiting increased virulence has been reported in recent years. Notably, the Ibaraki strain of EHDV-2 in Japan caused severe clinical outbreaks in cattle (Hirashima et al., 2015). Likewise, EHDV serotypes 6 and 7 have been associated with more severe disease in bovine populations across North Africa, the Middle East and Réunion Island (Bréard et al., 2004; Yadin et al., 2008; Temizel et al., 2009; Golender et al., 2017; Mejri et al., 2018). More recently, EHDV-8, first identified in Tunisia in 2021, has raised further concern due to its association with overt clinical signs in infected cattle, including pyrexia, oral and nasal lesions, oedema and cyanosis (Sghaier et al., 2022).

EHDV emerges in Europe

EHDV is endemic in many regions worldwide, including North America, Australia and several countries in the Middle East, Asia, and Africa (Noronha et al., 2021). However, over the past two decades, likely due to climate change and global warming, EHDV infections have been reported in previously unaffected regions, such as Réunion Island, Ecuador, Mayotte, French Guiana, and Trinidad (Cêtre-Sossah et al., 2014; Viarouge et al., 2014; Verdezoto et al., 2018; Dommergues et al., 2019; Rajko-Nenow et al., 2019). A significant increase in outbreaks has also been observed in North African countries bordering the Mediterranean Sea, particularly involving EHDV serotype 6 (Yadin et al., 2008; Temizel et al., 2009; Golender et al., 2017).

In parallel, the distribution of EHDV has expanded northward in North America, reaching east-central Canada, with increasing frequency and severity of outbreaks reported in previously less affected regions (Stallknecht et al., 2015; Allen et al., 2019).

Until November 2022, Europe had remained free of EHDV. That month, EHDV-8 was detected for the first time in both domestic and wild ruminant species in Italy and Spain. The virus was likely introduced via windborne *Culicoides* midges originating from North Africa. Supporting this hypothesis, Tunisia reported over 200 confirmed cases of EHDV-8 in bovine populations during the 2021-2022 vector season, as well as in local wildlife (Sghaier et al., 2022; Thabet et al., 2023; Ben Hassine et al., 2024). Although *Culicoides* midges typically travel short distances (around 2 km), wind-assisted dispersal over long distances - especially over open water - is well documented. This mechanism has previously been implicated in the introduction of other orbiviruses, such as bluetongue virus, into Europe from North Africa (Aguilar-Vega et al., 2019; Bibard et al., 2025; Cappai et al., 2019; Lorusso et al., 2017).

The spread of EHDV-8, along with that of other arthropod-borne viruses in the past, from North Africa to Southern Europe highlights the importance of viewing the Mediterranean as a single epidemiological macroregion.

In Italy, the first clinical suspicion of EHD was raised in October 2022, on a farm in the province of Trapani, Sicily, where three cattle exhibited signs of respiratory distress, erosions of the oral and muzzle mucosa and ptyalism. A few days later, on a farm in Arbus, Sardinia, cattle presented with loss of appetite, cyanosis and swelling of the tongue, conjunctivitis, and pyrexia; some animals died. Infection was later confirmed by the Istituto Zooprofilattico Sperimentale dell'Abruzzo e del Molise (IZSAM, ROR ID 04es49j42), which identified EHDV-8 as the aetiological agent.

Molecular characterisation of the strain showed >99.9% genetic identity with the strain circulating in Tunisia since 2021 (Lorusso et al., 2023), strongly supporting its North African origin and wind-borne introduction via infected *Culicoides*.

Fortunately, despite the presence of competent vectors in the areas of initial emergence, (Federici et al., 2016; Quaglia et al., 2023), the virus did not spread beyond the islands and was never detected in mainland Italy. The last reported outbreak in domestic animals in Sardinia occurred in September 2023, on a farm with 55 cattle, where one animal tested positive by real time RT-PCR (RRT-PCR).

Coinciding with the Italian cases, two cattle farms in Southern Spain, specifically in the provinces of Seville and Cádiz, also reported cases in November 2022 (WAHIS – report ID 157991 of 23/11/2022). Around the same time, outbreaks in farmed and wild red deer (*Cervus elaphus*) were also reported in the same area (Ruiz-Fons et al., 2024). Affected animals exhibited clinical signs such as depression, anorexia, weakness, ataxia, and severe respiratory distress. EHDV-8 infection was confirmed by the Central Veterinary Laboratory (LCV) of Algete. The virus successfully overwintered in Spain, with new cases emerging as early as June 2023. It subsequently experienced a significant expansion across the country, affecting both cattle and red deer populations and resulting in numerous outbreaks and mortalities. By October 2023, EHDV-8 had spread across the entire Spanish national territory and reached neighbouring countries, Portugal and France (MAPA, 2025).

As of the end of 2024, Spain had reported 464 outbreaks across 43 provinces in 15 regions.

Portugal reported its index EHDV-8 case in July 2023 in Alentejo region, which borders the Spanish regions of Andalusia and Extremadura. The virus then spread nationwide, with a progressive increase in the number of confirmed cases. By the end of 2023, Portugal had reported 73 outbreaks, mainly in the eastern part of the country. In July 2024, the first EHDV-8 detection of the year was confirmed (Plateforme ESA, 2025).

In France, the first outbreaks were confirmed in September 2023 on three cattle farms in departments along the southwestern border with Spain. The virus spread rapidly during the following vector season (DEFRA, 2024). By the end of 2023, over 4,000 outbreaks had been reported across 20 departments, mostly in the south but also along the western coast extending to Brittany. From June 2024 to April 2025, a further 3,873 outbreaks were notified across 34 departments (MASA, 2025).

In conclusion, the emergence and rapid dissemination of EHDV-8 across Northern Africa and Southern and Western Europe since late 2022 signify a substantial shift in the epidemiology of the disease. It underscores the importance of windborne *Culicoides* in facilitating transcontinental transmission. This phenomenon is likely facilitated by climate and landscape changes, as suggested by surveys in Southern Ontario, Canada, where previously unrecorded *Culicoides* species have recently been identified (Allen et al., 2022).

A similar pattern has been modelled for North America and Europe, indicating northward shifts in *Culicoides* distribution (Guichard et al., 2015). These changes, driven by environmental factors and global warming, raise concerns for disease surveillance and vector control in newly affected areas. Indeed, predictive models of *Culicoides* abundance have accurately depicted the spread of EHDV-8 in Spain and Portugal (Aguilar-Vega et al., 2020; Mestre et al, 2024).

Clinical features of EHD in European domestic and wild ruminant populations

In Europe, EHD has been detected in both wild and domestic ruminants. However, the vast majority of cases and outbreaks have involved cattle, with additional reports in red deer and other ruminant species.

Among domestic ruminants, some infected cattle exhibited overt clinical signs such as pyrexia, oral and nasal lesions, oedema and cyanosis and even sudden death was reported (Lorusso et al., 2023). In Spain, questionnaires and in-field outbreak investigations identified the most frequent symptoms as anorexia, fever, prostration and apathy, sialorrhoea, erythema and ulcers on the muzzle and on udder, respiratory distress, haemorrhagic diarrhoea, reduced milk production and reproductive disorders including abortions and stillbirths (Risalde et al., 2024).

Sheep are also susceptible to EHDV infection, as demonstrated by the detection of viral RNA in blood or tissue, or antibodies in serum. However, they very rarely show clinical signs. Despite this, the role of sheep in the maintenance and transmission of EHDV has been historically considered negligible or null (Gibbs and Lawman, 1977; Thompson et al., 1988; Kedmi et al., 2011; Eschbaumer et al., 2012; Mahmoud et al., 2021; Duan et al., 2022).

Regarding EHDV-8 circulation in Europe, only a few field studies have investigated its presence in domestic ruminants other than cattle. No clinical suspicions have been reported in goats, and the few suspected cases in sheep in France were not confirmed by RRT-qPCR (Gondard et al., 2024).

In contrast, during the early phases of the EHDV-8 outbreak in Italy, 73 sheep out of 85 tested positive by RRT-PCR in November 2022 on a farm in Fluminimaggiore, Sardinia, which had epidemiological connections to the cattle outbreaks (Spedicato et al., 2025). Furthermore, in Spain, EHDV-8 antibodies and RNA were detected in sheep from several geographical regions, persisting for up to eleven and four months respectively (Valero-Lorenzo et al., 2024).

The unusually high positivity rate for a vector-borne disease reported in sheep in Sardinia prompted further investigation into the dynamics of this newly emerged strain of EHDV-8 in the species.

To this end, Spedicato et al. (2023) conducted an experimental infection study in cattle, sheep and goats. While cattle exhibited clinical signs such as fever and ulcerative lesions of the muzzle, and goats showed no detectable RNA-emia, one sheep developed fever and two out of five had persistent RNA-emia lasting up to 78 days post infection, when the study was terminated. Notably, infectious virus was detected in one sheep on day 7 post-infection.

Similarly, Valero-Lorenzo et al. (2024) also conducted an experimental infection study in sheep yielding comparable findings. Neither clinical signs nor fever were observed in the infected animals, while although low-level viremia was detected and virus isolation was successful from one sheep on days 3 and 5 post-infection.

According to the authors, these findings, combined with field observations, suggest that sheep are much less susceptible to the EHDV-8 infection than cattle. Despite this, under certain conditions they may contribute to viral maintenance and onward transmission. Further research is warranted before definitive conclusions can be drawn.

Among wild species, red deer appear to be the most susceptible to EHDV-8, with the disease typically manifesting in a peracute or acute form and frequently resulting in death. In Spain, a broad range of clinical signs, including loss of fight response, incoordination, ataxia, fever, prostration and apathy, sialorrhea, absence of ocular reflex, erythema and ulcers on the muzzle, respiratory distress, haemorrhagic diarrhoea and haematuria, lameness and hoof abnormalities, alopecia and reproductive disorders such as abortions and perinatal mortality, have been described (Muñoz-Fernández et al., 2024a,b; Ruiz-Fons et al., 2024;).

In addition, between 2022 and 2024 in Spain, high EHDV-8 seropositivity was also reported in fallow deer (*Dama dama*) and mouflon (*Ovis aries musimon*), and to a lesser extent in Iberian ibex (*Capra pyrenaica*) and roe deer (*Capreolus capreolus*). Fatal cases of EHD have also been reported. Outbreaks and serological evidence have also been described in zoos and conservation centres, affecting red deer and other wild ruminant species from the *Bovidae*, *Cervidae* and *Camelidae* families (Muñoz-Fernández et al., 2024a,b).

In Italy, only limited reports exist of EHDV-8 positivity, with two red deer and two fallow deer testing virologically or serologically positive (WAHIS - https://wahis.woah.org/#/event-management; last accessed July 7th, 2025).

In 2023 in France, spleen samples collected from dead Pyrenean chamois (*Rupicapra pyrenaica*), roe deer and red deer were found positive for EHDV-8, with high viral loads indicative of recent infection (Gondard et al., 2024).

Beyond these cases, data on the susceptibility of wild European ruminants to EHDV-8 and its spread within wildlife remain limited.

EHDV-8, a new diagnostic challenge

When the first cases of EHDV were suspected in Tunisia between September and November 2021, serum and blood samples were initially tested to investigate the geographic extent of the disease, using competitive ELISA (cELISA), serum neutralisation test (SNT) and RRT-PCR.

When cELISA-positive serum samples were subsequently tested by SNT to identify the serotype involved in the outbreaks, over half of the sera tested positive for both EHDV-6 and EHDV-8, or for EHDV-6 alone (Sghaier et al., 2022).

Unexpectedly, the genotype-specific RRT-PCR targeting segment 2, which was available at that time, failed to identify the serotype of PCR-positive samples.

Consequently, based solely on serological data, EHDV-6 was initially suspected as the causative serotype, consistent with its previous circulation in Tunisia in 2006 (Mejri et al., 2018).

Subsequently, isolates that tested positive for EHDV by RRT-PCR were further analysed using virus neutralisation test (VNT) (Sailleau et al., 2019; Sghaier et al., 2022) in the presence of reference antisera. In these tests, EHDV-8 specific antisera showed a much higher neutralisation of the isolate cytopathic effect compared to anti-EHDV-6-specific antisera.

To further characterize the strain, six samples were selected for whole genome sequencing. Analysis of segment 2 revealed only approximately 77% identity with an EHDV-8 strain previously isolated in Australia in 1982. This finding confirmed that the Tunisian strain was genetically distinct and represented only the second reported isolate of EHDV-8 in nearly four decades (Sghaier et al., 2022).

The low sequence identity between the Australian and Tunisian isolates, and the known serological cross-reactivity between EHDV-6 and EHDV-8 (Sailleau et al., 2019), contributed to the initial misidentification.

In fact, the molecular typing tools available at the time were based on the segment 2 sequence of the sole Australian reference strain, which proved genetically distant from both the Tunisian and European strains.

To address this diagnostic gap, the Istituto Zooprofilattico Sperimentale dell'Abruzzo e del Molise (IZSAM) developed and validated a one-step RRT-PCR assay capable of detecting the RNA of the European EHDV-8 strain (Portanti et al., 2023). This advancement was critical for the accurate detection and characterisation of the newly emerged strain.

Prevention measures against EHDV-8 in Europe

In accordance with European and national regulations, control measures for EHD are primarily based on restrictions on the movement of animals from affected regions to virus-free areas.

Although these measures may help to some extent in slowing the spread of the virus, based on past experiences with the closely related bluetongue virus (BTV) in Europe, vaccination of susceptible hosts, particularly cattle and red deer, coupled with robust epidemiological surveillance in both domestic and wild animals, as well as in vector population, is likely the most effective strategy to limit the spread of EHDV-8.

In Japan, two commercial vaccines are available: a dual inactivated vaccine against bovine ephemeral fever and Ibaraki disease (caused by EHDV-2), and a live monovalent vaccine against Ibaraki disease, both manufactured by Kyoto Biken Laboratories, Inc.

In North America, autogenous inactivated vaccines are occasionally produced using EHDV isolates—typically EHDV-1 and EHDV-2—obtained from affected white-tailed deer. These vaccines are administered within the same herd from which the virus was isolated and are subject to approval by the United States Department of Agriculture.

Although widely used in cervid farming, these products lack standardized efficacy data. To date, no peer-reviewed studies have been published on the duration of immunity or the field efficacy of these autogenous vaccines.

In contrast, when EHDV-8 first emerged in Europe, no vaccines were commercially available. The absence of effective vaccines hindered the containment of the outbreaks in subsequent vector seasons, allowing the virus to spread rapidly across Spain, France and Portugal. Nevertheless, the emergence of EHDV-8 in 2022 triggered research and development efforts in vaccines research.

A significant initial effort was the production and testing of an inactivated EHDV-8 vaccine (vEHDV8-IZSAM) by the IZSAM. Experimental studies in cattle demonstrated that this vaccine is safe, immunogenic and effective in protecting against clinical signs and preventing viremia (Spedicato et al., 2024). However, the vaccine has not yet reached the market.

In parallel, pharmaceutical companies developed vaccines that were subsequently authorized for emergency use in different European countries, in accordance with Article 110 (2) of Regulation (EU) 2019/6.

The Zendal Group, through its animal health division Vetia Animal Health, developed an inactivated adjuvanted vaccine named Hepizovac, containing the EHDV-8 strain SPA 2022/LCV_03. In controlled trials, calves vaccinated with two doses administered 21 days apart exhibited significantly reduced viraemia following challenge, compared to unvaccinated controls. The Spanish Agency for Medicines and Health Products (AEMPS) granted emergency authorisation for use in cattle in July 2024. The development of this vaccine reflects the increasing demand for effective immunisation strategies in Spain, where the virus has become widespread.

On 13 March 2025, the Committee for Veterinary Medicinal Products (CVMP) of the European Medicines Agency (EMA) issued a positive opinion recommending of its marketing authorisation. The application, submitted by CZ Vaccines S.A.U., is currently under review by the European Commission for EU-wide approval.

In addition, the pharmaceutical company Syva has developed a recombinant subunit vaccine, Syvac® EH Marker, with DIVA (Differentiating Infected from Vaccinated Animals) capability. This vaccine allows serological differentiation between infected and vaccinated animals, a critical asset for disease surveillance and control. The vaccine has been authorized for emergency use in both cattle and red deer by the AEMPS and the Belgian Federal Agency for Medicines and Health Products. The Belgian approval was issued considering the high risk of EHDV-8 introduction from neighbouring France, highlighting the urgent need of early immunisation in the absence of fully licensed alternatives.

Collectively, these efforts represent a significant advancement in the availability of EHDV vaccines, particularly in response to the emergence and spread of EHDV-8 in Europe. The development and deployment of vaccines based on diverse technologies provide essential tools for the prevention and control of this vector-borne disease in farmed domestic ruminants.

Conclusions and research gaps

The recent emergence and rapid spread of EHDV-8 in Europe represent a significant and evolving threat to animal health, with serious implications for domestic livestock and, consequently, for international animal trade.

The European experience has highlighted the virus's potential to cause substantial morbidity in cattle, as well as in both wild and farmed cervid populations, such as red deer. Despite this, key aspects of EHDV-8 remain poorly understood.

Indeed, there are clues suggesting other domestic and wild ruminant species may serve as potential reservoirs, but definitive data are missing. This aspect warrants targeted investigation.

Similarly to other arboviruses, the mechanisms by which EHDV-8 overwinters are still unknown. It also remains unclear which factors enabled the virus to persist and spread extensively in Spain and France, but not in Italy. The movements of infected animals, the density of susceptible hosts and environmental factors related to the vector insect may all be contributing causes.

Diagnostic capacity represents another critical area for improvement. While some commercial kits are available to assess serological responses, the development of antigen-detecting assays and pen-side tests would significantly improve early diagnosis and outbreak management. Furthermore, serotype-specific ELISAs are currently unavailable, and certain existing RT-PCR assays may fail to detect emerging EHDV strains due to genetic divergence.

Substantial research gaps persist in our understanding of the fundamental aspects of EHDV-8 transmission dynamics. Key areas requiring further investigation include the duration of RNA-emia and viraemia, the kinetics of antibodies responses following infection and vaccination, as well as the duration of colostral immunity. The environmental conditions that enable field transmission and the susceptibility profiles of diverse animal species would also be a field to explore.

Further research is also recommended to elucidate the vector competence and capacity of various *Culicoides* species.

Finally, to prevent the introduction of novel EHDV serotypes into Europe, it is essential to strengthen collaboration with North African countries. Robust and integrated epidemiological surveillance systems will be crucial to ensure early detection and timely control.

At the same time, enhanced and coordinated surveillance efforts are urgently needed in sub-Saharan Africa, where EHDV likely circulates undetected. Indeed, the genome segments of EHDV-8 strain detected in Tunisia and Europe clearly point to an African origin, underscoring the need to better understand the virus's evolutionary history (Sghaier et al., 2022).

A major obstacle in this context is the extremely limited number of complete EHDV genome sequences available from the African continent. This significantly hampers our ability to trace viral emergence, track reassortment events and monitor viral evolution.

Closing these knowledge gaps will be critical for designing effective preparedness and response strategies, including vaccine development tailored to the serotypes circulating in endemic regions.

Ethical approval

No ethical approval was required for this study, as it did not involve the collection of data from experimental animals or human subjects.

Conflict of interest

The Authors declare no conflict of interest

Author Contributions

Conceptualization: Alessio Lorusso; Writing - original draft preparation: Massimo Spedicato, Remigio Martínez; Writing - review and editing: María de los Ángeles Risalde, David Cano-Terriza, Alessio Lorusso; Supervision: Alessio Lorusso

All authors have read and agreed to the published version of the manuscript.

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