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Review

Global distributions and strain diversity of avian infectious bronchitis virus: a review

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Abstract

The poultry industry faces challenge amidst global food security crisis. Infectious bronchitis is one of the most important viral infections that cause huge economic loss to the poultry industry worldwide. The causative agent, infectious bronchitis virus (IBV) is an RNA virus with great ability for mutation and recombination; thus, capable of generating new virus strains that are difficult to control. There are many IBV strains found worldwide, including the Massachusetts, 4/91, D274, and QX-like strains that can be grouped under the classic or variant serotypes. Currently, information on the epidemiology, strain diversity, and global distribution of IBV has not been comprehensively reported. This review is an update of current knowledge on the distribution, genetic relationship, and diversity of the IBV strains found worldwide.

Keywords: avian infectious bronchitis virus, global distribution, and strain diversity.

1. Introduction

Infectious bronchitis (IB) is a severe and acute disease of poultry caused by the infectious bronchitis virus (IBV). The virus is distributed worldwide and primarily infects the respiratory tract, kidneys, and the reproductive system causing respiratory distress, kidney damage, and decrease in egg production (Cavanagh, 2007). IB was first reported in 1931 and since then it has become a disease that affects the poultry industries in virtually all parts of the world and posing serious challenges to the industry by threatening sustainable poultry farming and the global protein supply. The disease is known to also affect non-domestic galliforms, including exotic and ornamental birds (Liu *et al.*, 2005; Chen *et al.*, 2013).

The emergence of multiple IBV serotypes invariably has hampered control and preventions of the disease. IBV is associated with rapid mutation rates, viral recombination, and host selection pressure. Vaccination has been the most important method for controlling the disease. Live attenuated vaccines are most often used in the vaccination program; however it is plagued with limitations including poor thermostability, reversion to virulence, and recombination between vaccine and field viruses (Tarpey *et al.*, 2006; McKinley *et al.*, 2008; Lee *et al.*, 2010, 2012; Bande *et al.*, 2015). These factors may have contributed to the increased emergence of genetically diverse IBV strains that undermines efforts in the control of the disease.

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2. Etiology and general characteristics

IB is an economically important poultry disease (Cavanagh, 2005). According to genome characteristics, the causative agent, IBV is classified under the gammacoronavirus of family *Coronaviridae*, order *Nidovirales*. The viral genome is made up of structural and non-structural protein coding gene segments. The structural protein includes the spike S1 and S2, envelop (E), matrix (M), and nucleocapsid (N) proteins (King and Cavanagh, 1991; Lai and Cavanagh, 1997). The spike S1 is a glycoprotein that plays a major role in viral attachment, diversity, and antibody neutralization. Variations in the S1 glycoprotein are used in the determination of new viral genotypes and also possibly antiviral response (Valastro *et al.*, 2016).

Most IBV strains are inactivated at 45 °C after 90 min of exposure. The virus can survive at pH 6 to 7.3 (Cowen and Hitchner, 1975).

3. Host range and susceptibility

IBV has a wide host range among avian species, but susceptibility of birds to the virus strains is influenced by factors including age, genetics, and/or environmental stress (Liu *et al.*, 2009). The domestic fowls of the *Gallus gallus* family and pheasants (*Phasianus* spp.) are natural hosts for IBV (Cavanagh *et al.*, 1988). Several strains have been reported and identified in other avian species to include peafowl, turkeys, teal, geese, pigeons, quill, ducks, and parrots. IBV isolates have also been reported in quail, penguins, and Guinea fowl (Ignjatović and Sapats, 2000; Gough *et al.*, 2006; Circella *et al.*, 2007; Liais *et al.*, 2014). There seems to be antigenic similarities between Turkey coronavirus (TCoV) and avian IBV (Breslin *et al.*, 1999; Ismail *et al.*, 2003). However, experimental infection of TCoV and pheasant coronavirus (PhCoV) in chicken only resulted in virus replication without causing clinical disease (Gough *et al.*, 1996; Ismail *et al.*, 2003).

4. Viral evolution and genotype diversity

There are several widely distributed classic and variant IBV genotypes (de Wit *et al.*, 2011a). Wildtype IBV isolates differ phenotypically from the parental vaccine strain (McKinley *et al.*, 2008; van Santen & Toro 2008; Gallardo *et al.*, 2010). IBV serotypes show variations in approximately 20–25% in their S1 glycoprotein sequences; however the variation can sometimes be as high as 50%, which affects the cross-protection toward virus strains (Cavanagh *et al.*, 1992). As with most of the RNA viruses, changes in IBV often involve the viral genome, leading to generation of several viral genotypes, altered tissue tropism, and infection outcomes (Jia *et al.*, 1995; Lim *et al.*, 2011; Jackwood *et al.*, 2012). Although it is not clearly known how coronaviruses, particularly IBV, evolve, it is postulated that this involves one or more of the following: (i) mutation from nucleotide insertions, deletions, or point mutations as a result of polymerase proof-reading activity; (ii) genomic recombination between vaccines and field strains, leading to multiple template switches as typically observed in the more virulent CK/CH/2010/JT-1 IBV isolate that originated from recombination of QX-like, CK/CH/LSC/99I-, tl/CH/LDT3/03-, and 4/91-type IBV (Kusters *et al.*, 1990; Rowe *et al.*, 1998; Nix *et al.*, 2000; Zhou *et al.*, 2017). IBV genome analysis showed that regions encoding non-structural proteins 2, 3, and 16, and the S1 glycoprotein have the highest degree of diversity (Thor *et al.*, 2011); and (iii) viral selection pressure that may result from vaccination and presence of partially immune birds.

Changes in tissue tropism has also been reported to cause alterations in the coding sequences of several coronaviruses (Kuo and Masters, 2002; Read *et al.*, 2015). The alteration in the S1 amino acid sequence could occur during adaptation of IBV in Vero cells or following several passaging in chicken embryo (Fang *et al.*, 2005; Ammayappan *et al.*, 2009). Ultimately, viruses that are not 'fit' are eliminated, leaving only 'fit' ones to strive, spread, and cause devastating disease (Zhao *et al.*, 2017).

5. Pathogenesis and clinical manifestation

Based on tissue tropism, there are two major IBV pathotypes, the respiratory and nephropathogenic pathotypes. Most classic IBV, such as the Massachusetts (Mass) serotype, infects the respiratory tract. However, the nephropathogenic strains, which occurr mostly in Asia and Middle Eastern countries, infect and damage the kidneys. The Moroccan IBV-G reportedly shows tropism for the gastrointestinal tract (GIT). The QX IBV, first isolated in China from the proventriculus (Yudong *et al.*, 1998), are now present in other parts of Asia, Europe, Middle East, and Africa; they show altered tissue tropism, infecting both the kidneys and reproductive tract, causing 'false layers syndrome' and high mortality (Beato *et al.*, 2005; Irvine *et al.*, 2010; de Wit *et al.*, 2011b; Amin *et al.*, 2012; Ganapathy *et al.*, 2012; Naguib *et al.*, 2016).

The upper respiratory tract is the primary replication site for IBV replication and initial infection starts at the epithelium of the Harderian gland, trachea, lungs, and air sacs, then the kidneys, urogenitals, and gastrointestinal tract causing lesions and diseases (Toro *et al.*, 1996; Bande *et al.*, 2016). The replication of IBV pathotypes in the respiratory tract stimulates goblet cell mucus secretion at the mucosal epithelium without causing obvious clinical signs to the birds. However, infected birds may show conditions to include gasping, sneezing tracheal rales, listlessness, and nasal discharges (Britton and Cavanagh, 2008). The QX-like IBV strains infect the kidneys, respiratory, and reproductive tracts, causing severe clinical disease within 48 h of exposure with signs such as frothy-conjunctivitis, profuse lachrymation, edema, and cellulitis of the periorbital tissues. Infected birds become lethargic, reluctant to move, and in some cases, dyspnoeic. The QX strain infects the kidneys and causes wet droppings, excessive water intake, and depression (Terregino *et al.*, 2008; de Wit *et al.*, 2011b). In the reproductive tract, the QX strain may cause generalized lesions in the oviducts, decrease in egg quality, with misshapen rough soft-shelled

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eggs, and watery egg yolk. The egg production in affected birds declines, but may return to normal following interventions (Winterfield and Hitchner, 1962; Chousalkar *et al.*, 2009; Bande *et al.*, 2016).

6. Epidemiology and geographical distribution

Some IBV genotypes and serotypes are closely related to the vaccines strains while others are variants that are unique to their geographical regions. In fact, the diversity of IBV in each region should be characterized to determine prevalent strains or genotypes, to improve the efficacy of existing vaccines while developing new ones for control and prevention of the disease.

Recently, a S1-gene-based phylogenetic classification of IBV identified six different viral genotypes, 32 distinct lineages, and several unassigned recombinants with inter-lineage origin. Interestingly, the distribution and diversity of these IBV genotypes differs with geographical location (de Wit *et al.,* 2011a; Valastro *et al.*, 2016). The global distributions of major IBV serotypes such as Mass-type, 4/91 (793B or CR88)-like, D274-like (D207, D212 or D1466, D3896), and D3128, QX-like, and Italy02 are shown in Fig. 1. Some serotypes, for example the QX-like IBV, Mass strain from the USA), 4/91 (CR88) from the UK, and the H120 strains from Netherland are variants causing local and regional impacts but with potentials to spread far and wide to other countries (de Wit *et al.,* 2011a; Jackwood, 2012). For that reason, the QX-based and anti-IBV variants vaccines are being developed to prevent and control the treats of these viruses (Jones *et al.*, 2005; Sasipreeyajan *et al.*, 2012; Kim *et al.*, 2013).

6.1 United States of America

In the USA, the first case of IB was reported in early 1930s (Schalk and Hawn, 1931). Since then numerous IBV strains have been identified, of which the Massachusetts or 'Mass' serotype is the most used vaccine serotype. Other IBV strains reported in the USA include the Arkansas, Connecticut, SE17 and Delaware strains (Jackwood *et al.*, 2005). From the IBV field isolates collected in the 1960s, seven isolates belonged to Mass, five were SE17, and one was of the Connecticut (Conn) genotype. This shows that these viruses have long been in existence in this country (Jia *et al.*, 2002; Mondal *et al.*, 2013). The Delaware IBV variant, designated DE072 (Gelb *et al.*, 1997), was first reported in 1992 and found to be distributed across the Northeastern USA. Based on S1 sequence, this variant resembles the Dutch D1466 variant (Lee and Jackwood, 2001). It is not known how the D1466 variant entered the country. The variant was later found to be prevalent in Georgia. The DE072-specific vaccine was then used to control the infection with little or no success. However, use of the DE072 vaccine probably led to the emergence of Georgia 98 (GA98) and GA08 variants (Lee and Jackwood, 2001).

Respiratory disease-causing serotypes have been present mostly in broiler-chicken-producing central California since the 1980s. These serotypes have a unique matrix protein polymorphism, which is different for the Mass, Conn, and Ark-99 serotypes (Case *et al.*, 1997). In 1999, a nephropathogenic IBV strain, designated as CAL99, was identified. Later, three more variants, CA557/03, CA706/03, and CA1737/04, were identified (Jackwood *et al.*, 2007). The S1 amino acid sequence analysis showed that the California variants, CV-56b, CV-9437, and CV-1686 were 97.6–99.3% similar and showed only 76.6–76.8% identity with the Arkansas strains. When 19 IBV isolates were compared, the amino acid variations were significant at positions 55–96, 115–149, 255–309, and 378–395. These variations may be responsible for the lack of virus cross-protection and vaccine failures to control infections (Moore *et al.*, 1997, 1998).

6.2 Canada

Characterization of Canadian IBV isolates derived from outbreaks revealed S1 gene sequence with close similarity to the Mass vaccine strains, which include the M41 and Connecticut strains. Two important IBV variants were reported in Ontario, Canada. Of these, the IBV-ON1 variant affects the respiratory system while the IBV-ON4 variant was associated with nephritis. Interestingly, vaccination of chickens with the Mass serotype vaccine protected chickens against challenge with the Ontario IBV strains (Grgić *et al.*, 2008, 2009). Later, 9 IBV genotypes were identified and classified into four groups namely; Canadian variant (strain Qu_mv), classic (vaccine-like viruses, Conn and Mass), US variant-like virus strains (California 1734/04, California 99, CU_82792, Pennsylvania 1220/98 and Pennsylvania Wolg/98), and non-Canadian, non-US virus or European strains (4/91 strain) (Martin *et al.*, 2014). The 4/91 strain affected poultry production and there has been a call for the introduction of 4/91-specific vaccine to control the infection (Grgić *et al.*, 2008; Martin *et al.*, 2014).

6.3 Latin America

6.3.1 Brazil

The first incidence of IB reported in Brazil was the isolation of Mass IBV serotype (Hipólito, 1957). About 10 years later, the Ark variant emerged, causing devastations to Brazilian poultry (Branden & Da Silva, 1986). Subsequently, 12 new Brazilian isolates were identified based on S1-gene-specific reverse transcriptase polymerase chain reaction (RT-PCR) and restriction fragment length polymorphism (RLFP). Five of these isolates were the vaccine genotypes of Mass origin, while seven were classified under four Brazilian IBV groups, namely, isolates A ($n = 2$), B ($n = 2$), C ($n = 2$), and D ($n = 1$). Interestingly, the IBVPR07 isolate, belonging to the Mass serotype, was found to have high tropism for the gonads and trachea (Montassier *et al.,* 2008). Between 2007 and 2008, analysis of positive IB cases among chickens revealed 20 strains, 15 of which were

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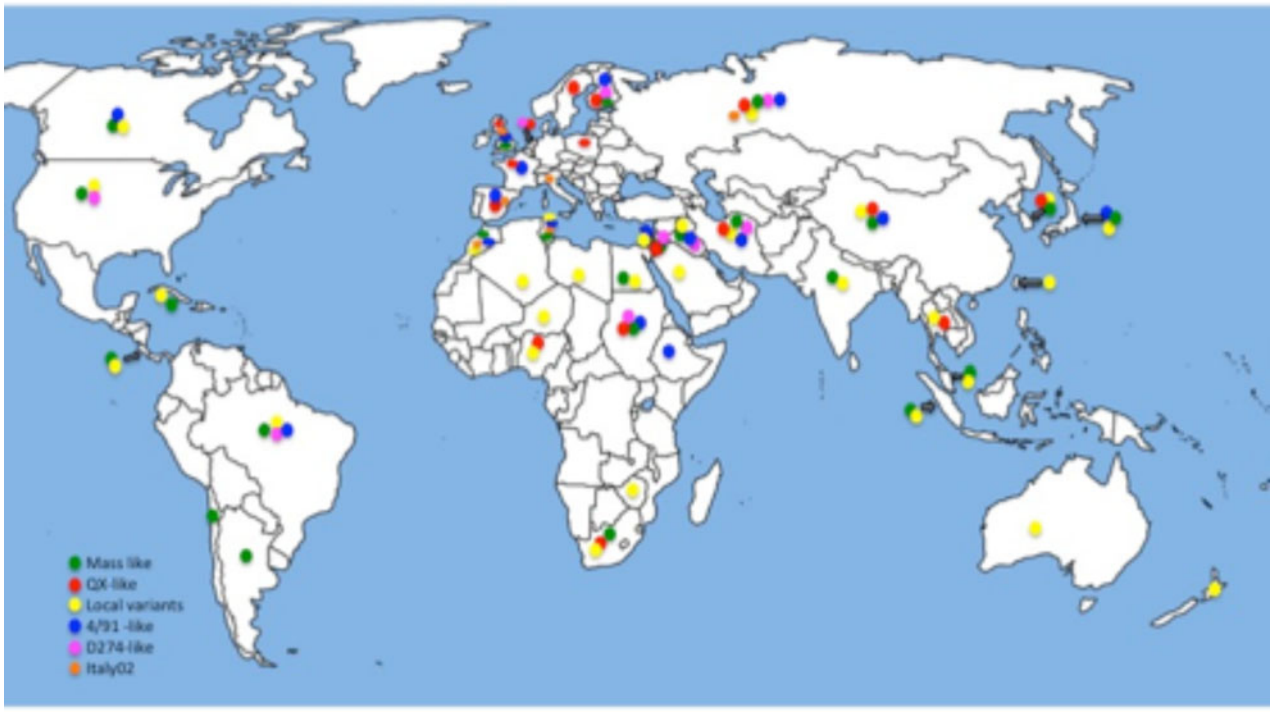

Fig. 1. Distribution of major IBV serotypes including the Massachusetts (first reported in USA), 4/91 and D274 (Europe origin); QX-like (originating from China) and several local variants.

assigned to a major cluster that was sub-classed into the Brazil 01, 02, and 03 isolates. Three isolates were genetically grouped with Mass genotypes while two with the European 4/91 or 793B strain (Villarreal *et al.*, 2007, 2010). In a recent analysis of samples from 63 poultry farms from several regions of Brazil, 11 out of 49 isolates sequenced (22.4%) were of the Mass vaccine strains, 34 (69.4%) are similar to the previously identified and frequently isolated BR-I genotype, and four isolates (8.2%) belong to new IBV variant genotype, Brazil-II or BR-II, which are clearly different from the BR-I genotype. All Brazilian variants from BR-I and BR-II genotypes were characterized by nucleotide sequence insertion coding for five amino acid residues within their S1 glycoprotein. These variants show unique intra-geographic diversity with BR-1 commonly isolated from the South and Southeast regions of Brazil, with the majority of BR-II isolated from the Midwest, and the D207 predominantly in Northeastern parts of Brazil (Fraga *et al.*, 2013). The Brazilian IBV variants, when compared with vaccine genotypes, were found to be >25% divergent, which probably accounts for the low immunogenicity of commercial IBV vaccines (Wei *et al.*, 2008; Chacon *et al.*, 2011).

6.3.2 Argentina

In Argentina, where IB is endemic, vaccination was done with the Mass H120, Ma5 and M41 serotypes. However, sporadic outbreaks still occurred in commercial chicken farms. The likely reason for the vaccine failure was not known until recently, when 20 local IBV isolates from commercial broiler and layer farms were analyzed during the 2001 and 2008 outbreaks. The sequencing and phylogenetic characterization based on the Hyper Variable Regions (HVR) 1 and HVR 1/2 showed that five isolates are of the Mass vaccine genotype, whereas 15 isolates showed unique clustering patterns different from any known vaccine isolates (Rimondi *et al.*, 2009). Amino acid sequence analysis revealed only an average identity of 73.6% between the local variants A, B, and C and the Mass vaccine viruses, which may be the main reason for vaccine failures in this country.

6.3.3 Republic of Chile

Chile had reported cases of IBV infection since 1969 (Garcia and Norambuena, 1969). However, the IBV isolates identified during early outbreaks were serologically classified under the Mass serotype (Hidalgo *et al.*, 1976). Ten years later, a non-Mass IBV serotype was identified to be associated with the frequent vaccination failures (Hidalgo *et al.*, 1986).

6.3.4 Costa Rica

During a 10-week survey in Costa Rica, two new IBV isolates were identified as variant strains. One strain, designated IBV-CR-53, was found to be unique to the country while the other strain was similar to Mass vaccine serotype. Serological evidences of the presence of IBV were obtained from *Zenaida asiatica* and *Columba fasciata* pigeons, suggesting that they play a role in the transmission and persistence of IBV in Costa Rica (Lindahl, 2004).

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6.3.5 Cuba

Although IBV has seen in the Caribbean region since the mid-80s (Guilarte, 1985), only recently have novel variants been reported in Cuba (Acevedo *et al.*, 2012). These strains differed genetically from the H120 vaccine serotype that has been approved for use in Cuba. Bioinformatic analysis of the new Cuban isolates, designated Cuba/La Habana/CB6/2009, showed 91.3% nucleotide and 78.3% amino acid sequence identity with the USA/DMV/5642/06 strain that was reported to cause 2006 outbreaks in broilers in Delmarva (Wood *et al.*, 2009). The other Cuban variant, Cuba/La Habana/CB19/2009, presented the highest nucleotide (87.8%), and amino acid (77.4%) sequence identity with B1648, a highly lethal nephropathogenic IBV strain that was first reported in Belgium (Meulemans *et al.*, 2001). On the other hand, the Cuba/La Habana/CB6/2009 and Cuba/La Habana/CB19/2009 strains had only 51 and 45% amino acid sequence similarity, respectively, to the Mass genotype. Thus, it was reasonable to predict that vaccination with Mass serotype would not protect chickens from infection with the new Cuban genotype (Acevedo *et al.*, 2012).

6.3.6 Mexico

Mexico has been an important poultry-producing country, which has been plagued with IBV outbreaks. For example, Ark variant, which originated from the USA, was isolated and reported in in the early 1990s (Quiroz *et al.*, 1993). Later, Escorcia *et al.* (2000) reported four new variants specific to Mexico, as evidenced by RT–PCR and RFLP. Similarly, in 2001 new variants were identified. Of these, Max/1765/99 variant was isolated from 64% of chickens showing respiratory problems; three new isolates were found to be similar with BL-56 earlier reported in 1996, whereas two other indigenous isolates were antigenically similar to Conn genotypes (Gelb *et al.*, 2001).

6.4 Africa

In many African countries, the Mass IBV serotypes cause sporadic IB outbreaks in the commercial poultry industry. A number of local variants are reported in Africa in addition to the widely known vaccine serotypes such as Mass and 4/91 strains (de Wit *et al.,* 2011a). In the late 1980s, the IBV-G serotype was identified as a unique African variant with tropism to gastrointestinal system. However, recent studies identified several other local non-vaccine types, including the QX-like strains and Italy 02, originally localized in China and Europe, respectively.

6.4.1 Morocco

The IBV has been present in Morocco since 1989. Five different isolates were identified and designated as D, E, F, H, and M, and classified as the Mass serotypes. However, one isolate, IB-G, was found to be antigenically different from the five isolates and is unique to Morocco. It was later shown that this isolate has tropism for gastrointestinal tissues instead of the respiratory tract. Vaccine efficacy studies showed that immunization of chickens with a Mass-serotype vaccine, such as H120, only protected against challenge with IBV-E and -F and not -G (El-Houadfi *et al.*, 1986; Ambali, 1992). Following an outbreak of IB, where affected birds showed signs typical to that caused by the nephropathogenic strains, Al arabi (2004) conducted RT-PCR and RFLP analyses on several samples from different outbreaks and reported three IBV groups designated I, II and III. Members of group I were classified as the Mass serotype, whereas groups II and III were unique to Morocco. Within the group III types, isolate 12/97 showed high resemblance to previously known enteropathogenic IB-G isolates. This isolate, when experimentally inoculated into chickens, resulted in more severe kidney lesions and higher mortality than the local 7/97 isolate of the same group.

In 2005, five genotypes, three of which differed from the known vaccine strains, and the above viruses were reported to cause serious kidney damage chickens (El Bouqdaoui *et al.,* 2005). More recently, in January 2010 and December 2013, other IBV variants, including the IBV/Morocco/01 IBV/Morocco/30, and IBV/Morocco/38, were isolated in southern and central regions of Morocco. There were nucleotide sequence identities of 89.5–90.9% between these strains; however, amino acid sequence identities were 29.7% between IBV/Morocco/38 and Egypt SCU-14/2013-1 and 78.2% between IBV/Morocco/01 and Spanish Spain/05/866 isolates. Italy 02, a strain that is common in Europe, is the second most common genotype in this country while the 4/91 vaccine strain is diminishing (Dolz *et al.*, 2006, 2012; Fellahi *et al.*, 2015a, b).

6.4.2 Libya

Information on the prevalence of IBV in Libya is scarce. However, recent studies conducted in Eastern Libya showed the presence of 12 IBV strains that are phylogenetically classified in two distinctive clusters. Isolates from four farms formed a cluster with 94–99% relatedness to the Egyptian IBV strains, CK/Eg/BSU-2/2011, CK/Eg/BSU-3/2011, and Eg/1212B. Isolates from three other farms were of another cluster that had 100% relatedness to Egyptian Eg/CLEVB-2/IBV/012 and Israeli IS/1494/06 strains (Awad *et al.*, 2014). While the Eg/CLEVB-2/IBV/012 strain was reported to cause respiratory and renal pathology (Abdel-Moneim *et al.*, 2012), the IS/1494/06 strain can cause severe acute renal disorder with morbidity and mortality rates ranging from 15 to 25% (Meir *et al.*, 2004).

6.4.3 Tunisia

Tunisia reported new IBV variants, notably, N20/00, TN200/01, and TN335/01. These isolates were phylogenetically classified under the same cluster as the CR88 (IB 4/91) and D274 isolates. Co-circulation of N20/00, TN200/01, and TN335/01 variants was suggested to be associated with severe

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clinical disease and losses to the Tunisian poultry industry (Bourogâa *et al.*, 2009). Between 2007 and 2010, four new variants, designated TN295/07, TN296/07, TN556/07, and TN557/07, were identified. These isolates were closely related to TN200/01, TN335/01, and Italy 02 variants, but distantly related to the H120 vaccine strains commonly used for poultry immunization in Tunisia (Bourogâa *et al.*, 2012).

6.4.4 Algeria

New IBV genotypes, Algeria28/b1, Algeria28/b2, and Algeria28/b3, were identified in chickens in Algeria. These strains were determined as variants based on the S1 partial sequences. The pathogenic characteristics or immunogenicity of these genotypes have not yet been reported (Sid *et al.*, 2015).

6.4.5 Egypt

Serological evidence of IB was first documented in Egypt in the 1950s (Ahmed, 1954). In spite of efforts to control the infection using Mass vaccines, the disease continues to be a major problem in Egyptian poultry flocks. Attempts to identify the strains involved in the IB outbreaks lead to the discovery of a local variant in 2002, designated Egypt/Beni-Suef/01 (Abdel-Moneim *et al.*, 2002). This isolate was found to be unique to Egypt but closely related to nephropathogenic strains, IS/1494/06 and IS/720/99 isolated in Israel (Meir *et al.*, 2004). Inoculation of the Egypt/Beni-Suef/01 IBV in chickens resulted in severe respiratory and renal diseases (Abdel-Moneim *et al.*, 2005). In 2006, another nephropathogenic variant, Egypt/F/03 closely related to the Dutch (D3128), Mass, and Israel IBV variants, were also identified (Abdel-Moneim *et al.*, 2006). In 2011, five other variants were identified, Ck/Eg/BSU-1/2011, Ck/Eg/BSU-4/2011, Ck/Eg/BSU-5/2011 (which clustered with Egypt/Beni-Suef/01 and Israeli IS/1494/06) Ck/Eg/BSU-2/2011, and Ck/Eg/BSU-3/2011. The variants were distinct from any known Egyptian variants or vaccine serotypes (Abdel-Moneim *et al.*, 2012). Molecular characterization suggested the presence of two distinct genotypes that were classified as the vaccine strain GI-1 genotype and the GI-23 genotype, a variant field strain. The variant genotype was subdivided Egy/var I and Egy/var II, which resembled Israeli variants IS/1494 and IS885 respectively. The two variant subgroups exhibited deletion mutation at amino acid position 63 as well as a substitution at residue 169 of the S1 glycoprotein. These changes are likely associated with the unique tissue tropism of these viruses. Amino acid sequence analysis suggested that the variant subgroups differ in genetic features from the classical vaccine group, the H120 lineage. The differences in genetic features include the additional N-glycosylation sites. The IBV-EG/1586CV-2015 emerged following recombination of two viruses from the variant groups, Egy/var I and Egy/var II, which also suggests the intra-genomic diversity of IBV, particularly in the GI-23 genotypes (Zanaty *et al.*, 2016b). Subsequent studies of pathogenicity, by comparison with the classical genotypes, showed that the Egyptian IBV variant has multiple heterogeneous origins and diverse pathogenicity (Zanaty *et al.*, 2016a).

6.4.6 Sudan

In Sudan, out of four isolates, M114/2000, K179/2000, and K158/2000 belonged to the European 4/91 subgroup, while K110/200 was closely related to the Mass vaccine serotype (Ballal *et al.*, 2005). In a recent study, the novel IBV variants, designated Ck/Sudan/AR251-15/2014 and Ck/Sudan/AR252-15/2014, were isolated from outbreaks of severe respiratory disease among broiler chickens. Next generation whole-genome sequencing and bioinformatics analyses of HVR 1 and HVR 2 revealed nucleotide identity of 97% between these isolates and the SLO/305/08 from Slovenia and Kr/D42/05 isolate from Korea. Based on amino acid sequence, 95% similarity was observed between these isolates and the Kr/354/03 from Korea and RF/28/2011 from Russia. Analysis of the HVR 3 amino acid sequence showed 98% highest identity with two Italian strains, the ITA/90254/2005 and AZ-40/05. The overall phylogenetic relationship using the HVR 1-2 and HVR 3 nucleotide sequencing of the S1 gene of IBV Ck/Sudan/AR251-14/2014 and Ck/Sudan/AR252-14/2014 showed clustering pattern with QX and QX-like, thus highlighting the importance of these variants genotypes in IB outbreaks in Sudan. The prevalence of these QX and QX-like variants calls for change in the intervention and control approaches from the normally used vaccines of the Mass and 4/91 serotypes. It should be noted that the presence of recombination points especially at amino acid position 1–6468 and 9988–12498 in the ORF1a and ORF1b, and within 18369–23219 region of the ORF1b and S gene, indicate there are recombinant genotypes that could have likewise risen from H120, 4/91 and Italy/90254/2005 isolates (Naguib *et al.*, 2016).

6.4.7 Ethiopia

Little is known of the epidemiology of IB in East Africa, particularly within the regions of the 'Horn of Africa'. IB was only recently reported to be present in Ethiopia (Hutton *et al.*, 2016) in a study using serology and sequencing approaches to detect IBV isolates from a non-vaccinated institutional farm in Debre Zeit, Ethiopia. The virus was found to be of European 793B genotype, with 92–95% sequence identity with the French isolate, FR-94047-94, and the virulent 4/91 (Cavanagh *et al.*, 2005). Because neither the Mass nor 4/91 IBV vaccine is commonly used in African farms, the virus is assumed to be a field isolate.

6.4.8 Nigeria

Although serological evidence for the prevalence of IBV in Eastern Nigeria was shown early in the 1990s (Komolafe

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et al., 1990) and from South West Nigeria in the late 2000s (Owoade et al., 2006), only recently was a QX-like IBV reported from the backyard poultry in northern and southern parts of the country. The QX-like IBV variant, designated IBADAN strain (NGA/A116E7/2006), has a nucleotide diversity of 9.7–16.4% with previously known IBV genotypes. The NGA/A116E7/2006 isolate failed to cross-react with IT02 strain from Italy or with vaccine strains such as M41, D274, Conn or 793/B serotypes. The NGA/A116E/2006 variant showed minimal reaction with a QX-like strain, ITA/90254/2005, suggesting that it is a distinct variant unique to Nigeria. There is little information on the pathogenicity or immunogenicity of Nigerian IBV variants, but it is likely that the widely used H120 and M41 vaccines may not protect chickens against these local variants (Ducatez et al., 2009; Valastro et al., 2016).

6.4.9 South Africa

One IBV variant was described in South Africa in 1984; however, this variant has not been fully characterized (Morley and Thomson, 1984). Recently, it was discovered that the Mass IBV serotype is predominant while some QX-like and 793/B genotypes, the CK/ZA/2034/99 and CK/ZA/2281/01, were present in country (Knoetze et al., 2014). The MJT1 and MJT2 variants were reported in non-vaccinated indigenous chickens in the Beitbridge region, bordering Zimbabwe. These chickens presented clinical signs that included dropping of wings, leg paralysis, greenish-watery diarrhea, and respiratory distress. Remarkably, the MJT1 and MJT2 isolates showed 98.6% nucleotide sequence similarity with a QX-like IBV strain, QX L-1148, suggesting that QX-like variants are involved in IB outbreaks South Africa (Toffan et al., 2011, 2013).

6.5 The Middle East

The prevalence of IBV strains and the disease in the Middle East varied from country to country. A Chinese-like recombinant virus (DY12-2-like) was reported for the first time in the Middle East (Seger et al., 2016).

6.5.1 Iran

Initial reports from Iran showed that the Mass-like IBVs are the most commonly isolated serotypes (12 isolates), followed by the European D274 and 4/91 (793/B)-like strains (3/2001 and 14/2001) (Mayahi and Charkhkar 2002). Subsequently, it was shown that the 4/91-like is the more prevalent in broiler chickens than the Mass type serotypes. Between 1999 and 2004, 150 flocks were tested for the IBV variants and 57 (52.7%) were positive for 793/B serotype, 18 (16.6%) positive for Mass type IBV, while 33 (30.5%) had dual infection with the two genotypes. It was then suggested that the currently used Mass and 4/91 serotypes vaccines do not adequately protect chickens against IBV infection; in fact, these vaccines may even complicate the viral epidemiology (Shoushtari et al., 2008). The Iranian IRFIBV32 variant, 793/B or CR88-like serotype, has wide tissue distribution, causing marked lesions in the respiratory, urogenital, and digestive systems (Boroomand et al., 2012). These virus strains were also shown to exhibit tropism for the bursa of Fabricius, as observed following inoculation with Iranian IR/773/2001. This suggests that the IRFIBV32 variants have immunosuppressive potential (Mahdavi et al., 2007). The Iranian IBV isolates were also characterized by S1 gene sequencing, and these isolates were then grouped into six-distinct phylogenetic clusters; namely, IS/1494/06 (Var2)-like, 4/91-like, QX-like, IS/720-like, Mass-like, and IR-1 (3%), with isolation rates of 32, 21, 10, 8, 4, and 3%, respectively (Najafi et al., 2016).

6.5.2 Iraq

The 4/91 IBV serotype is prevalent in Sulaimani, Iraq. There are vaccines available for this and the Ma5 and H120 serotypes. A novel IBV variant, the Sul/01/09, is also prevalent in Iraqi broiler farms, and this variant is distinct from the vaccine and other serotypes reported in Iraq and neighboring countries (Mahmood et al., 2011). More recently, between 2014 and 2015, four major groups were reported in Iraq; namely, group I: variant 2 [IS/1494-like], group II: 793/B-like, group III: QX-like, and group IV: DY12-2-like genotypes. There were 96.42–100, 99.68–100, and 99.36–100% nucleotide sequence identity within groups I, II, and III, respectively. Group I (variant 2) was the most commonly isolated IBV in Iraq.

6.5.3 Jordan

The IBV strains identified in Jordan include Ark, DE-072, and Mass (Gharaibeh, 2007). Other IBV variants later detected were 4/91 and D274; however, two other variants could not be amplified using existing IBV primers (Roussan et al., 2008). Using serotype-specific antisera, antibodies to M41, 4/91 and D274 were detected in clinically healthy flocks (Roussan et al., 2009). Recently, five QX-like IBVs, designated JOA2, JOA4, Saudi Arabia-like [Saudi-1, Saudi-2], and Iraq-like strains were also identified. Phylogenetic analysis showed that the five IBV isolates were 96.6–99.1% related to a Chinese QX-like strain, CK/CH/LDL/97I, and with <80% nucleotide similarity to the M41 and H120 vaccine serotypes. The CK/CH/LDL/97 strain was thought to be associated with sporadic IB outbreaks in the Middle East. It was postulated that the appearance of new IBV strains in Middle Eastern countries is the result of recombination between live attenuated vaccine viruses and field strains (Ababneh et al., 2012).

6.5.4 Israel

In Israel, similar to the earlier reports, 13 new IBV variants were identified (Abdel-Moneim et al., 2006). Of these, 11 are closely

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related to the previously reported Israel variant strains, IS/885 and IS/1494/06, and two isolates are clustered with the European CR/88121 and/or 4/91strains (Selim *et al.*, 2013).

6.6 India, Pakistan, and Bangladesh

There is serological evidence of IBV in Bangladesh (Das *et al.*, 2009), India (Sarma *et al.*, 1984), and Pakistan (Ahmed *et al.*, 2007). In Pakistan, based on antibody titers, the prevalent IBV variants were M41, D-274, D-1466, and 4–91. Recently, a novel nephropathogenic IBV variant, PDRC/Pune/Ind/1/00, in Western India was molecularly characterized. This variant was isolated from commercial broiler chickens that manifested clinical signs such as visceral gout and severe nephrosis (Bayry *et al.*, 2005). Although IB vaccines are used in these countries, their effectiveness toward the local strains has not been evaluated (de Wit *et al.,* 2011a).

6.7 Australia and New Zealand

Most of the Australian IBV strains are nephropathogenic, and only a few cause respiratory diseases. The nephropathogenic strains were of particular interest as these isolates cause clinical nephritis and mortality in chickens (Ignjatovic *et al.*, 2002). There are two established and distinct IBV groups in Australia. Group 1 comprises Vic S, V5/90, N1/62, N3/62, N9/74, and N2/75, which share 80.7–98.3% amino acid sequence similarities among them. Of these, only Vic S, N1/62, N9/74, and N2/75 cause both respiratory and kidney-related disorders. Experimental infections with N1/62, N9/74, and N2/75 cause 32–96% mortality. Group 2 isolates include N1/88, Q3/88, and V18/91, which caused respiratory symptoms but not mortality (Sapats *et al.*, 1996). Recently, a third group was added to the list of prevalent IBV. A representative of the third group, Chicken/Australia/N2/04, had only a slight homology to the strains from groups 1 and 2. This variant is closely related to the D1466 and DE072 strains from Netherlands and the USA, respectively. Nephropathogenic IBV strains are known as 'T' strains, e.g strains T (N1/62), common to Australia, causes kidney lesions and 5–90% mortality in infected birds (Ignjatovic *et al.*, 2002, 2006).

Four serologically unique IBV serotypes, A, B, C, and D, were first reported in New Zealand in 1967 (Pohl, 1967; JE. 1988). A vaccine developed against the serotype A was shown to provide protection against all four serotypes, thus has been used to control IB in the country. Recently, T6, K43, and K87 isolates, similar to the strains C and D, and isolate K32, similar to B strain, were identified (McFarlane and Verma, 2008).

6.8 Russia and neighboring countries

The Russian IBV isolates are predominantly of the Mass serotypes, although some isolates are related to D274, 4/91, B1648, 624/I, and It-02 genotypes of European origin. Two novel QX-like isolates were reported in regions bordering Russia, the Far East and Europe. Among these isolates, 27 are unique Russian variants, distinct from known IBV strains (Bochkov *et al.*, 2006). An extensive epidemiological study on IB in this region that included Russia, Ukraine and Kazakhstan, between 2007 and 2010, showed the dynamics of IBV has changed with the Mass, 793/B, D274 and QX-like IBV, now becoming the most prevalent genotypes, followed by the B1648, Italy-02, and Arkansas variants. Eleven 4/91-related IBV isolates were reported, which included recombinants of the field and vaccine strains and the local strains designated UKR/02/2009 (or 4/91), RF/03/2010, and RF/01/2010 (Ovchinnikova *et al.*, 2011).

6.9 Europe

Variant IBV isolates were first reported in Europe in early 1970s (Dawson and Gough, 1971). Later, the Doorn Institute of The Netherlands isolated four serotypes designated as D207 (also known as D274), D212 (also known as D1466), D3896, and D3128, from Mass isolate-vaccinated flocks (Davelaar *et al.*, 1984). In the UK, 793/B (also known as 4/91 and/or CR88) was identified as the predominant serotype (Cavanagh *et al.*, 1999). Other European serotypes of Mass IBV genotype were also identified in the UK (Gough *et al.*, 1992), France (Auvigne *et al.*, 2013), Belgium (Meulemans *et al.*, 2001), Italy (Capua *et al.*, 1994; Zanella *et al.*, 2003), Poland (Domańska-Blicharz *et al.*, 2007), and Spain (Dolz *et al.*, 2006, 2008). Nevertheless, of the European serotypes, 793/B, also known as 4/91 and CR88, and D274 remained of international concern because of their propensity to spread within and outside Europe (Gough *et al.*, 1992; Abro *et al.*, 2012).

A study that determined IBV variants in Western Europe showed that 793B serotype was predominant, followed by Mass type, H120, M41, IBM, Italy02, and a variant closely related to the Chinese QX isolate (Worthington *et al.*, 2008). It is important to note that QX-like IBV, which was first isolated in Europe in 2004, has recently emerged as the most challenging IBV in Europe. Although, in China, this isolate was initially known to cause mild proventriculitis (Yudong *et al.*, 1998), in Europe its tropism had changed to the kidneys and oviduct (Monne *et al.*, 2008). QX-like IBV serotypes have been reported in Scotland (Worthington *et al.*, 2008), Italy (Beato *et al.*, 2005), The Netherlands, Poland (Domańska-Blicharz *et al.*, 2007), Slovenia (Krapez *et al.*, 2011), Spain, UK (Valastro *et al.*, 2010; Ganapathy *et al.,* 2012), and Sweden (Abro *et al.*, 2012). Similarly, QX, D274-like and 4/91-like IBV serotypes have recently been reported in Finland where the use of live IBV vaccines is not practiced (Pohjola *et al.*, 2014).

6.10 Asia

It has been speculated that the IBV strains have long been in existence in Asia. This speculation is based on the phylogenetic diversity of various isolates found the region (Yu *et al.*, 2001).

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Among these countries, China has experienced the emergence of several distinct IBV variants. The QX strain, in particular, has spread to other parts of the world to include Europe, the Middle East and Africa. This strain is the result of remarkable change in the genetics of IBV, and currently there is no effective vaccine available to control the infection by this virus variant (W Yudong *et al.*, 1998; Worthington *et al.*, 2008).

6.10.1 Malaysia and Singapore

Malaysia first documented cases of IBV infection in 1967. Most IBV isolated before the 1990s were antigenically similar to the vaccine strain viruses of the Mass serotype (Arshad, 1993). Subsequent studies identified two unique IBV variants, the nephropathogenic variant, MH5365/95, and the respiratory pathogenic strain, V9/04, isolated in 1995 and 2004, respectively. These variants were later shown to have remarkable similarity with several Chinese isolates (Zulperi *et al.*, 2009).

Singapore also suffered from IB infections. Most serotypes identified, based on their antigenic relatedness, were classified under Mass-like serotype (Yu *et al.*, 2001).

6.10.2 Thailand

Outbreaks of IBV infection began to occur in Thailand in the early 1960s (Chindavanig, 1962). Sequence analysis of 13 samples isolated in 2008 in Thailand revealed two IBV groups. Group 1 isolates, THA20151, THA40151, THA50151, and THA60151, were unique to Thailand, and group 2 isolates, THA30151, THA 70151, THA 80151, THA100151, THA110351, THA120351, THA130551, and THA140551, had 97–98% and 96–98% nucleotide and amino acid sequence identities, respectively, with the QX A2, SH and QXIBV serotypes that are endemic in China. An attenuated vaccine was developed from the Thailand QX-like THA80151IBV isolate, which was shown to prevent clinical disease despite evidence of viral replication and pathologic lesions in the trachea and kidneys (Sasipreeyajan *et al.*, 2012).

6.10.3 Indonesia

In Indonesia, IBV was first described in the 1970s (Ronohardjo, 1977). Based on antigenic characteristics, an Indonesian isolate, I-37, cross-reacted with the Conn 46 strain of US origin; three isolates, I-269, I-624, and PTS-II, cross-reacted with the Mass 41 vaccine strain, while two isolates, I-625 and PTS-III, were related to Australian N2/62 strain (Darminto, 1995; Indriani, 2000). Further analysis of the I-37 isolate showed differences of approximately 6.9 and 15.6% in nucleotide and amino acid sequences, respectively, with the Conn-46 isolate. Thus, I-37 was suggested to be a variant of Conn 46 serotype, probably arising from vaccine-virus recombination events. Whether there are any functional and/or genomic differences between the two isolates is yet to be determined (Dharmayanti *et al.*, 2005).

6.10.4 South Korea

Most IBV variants in South Korea are of nephropathogenic pathotypes, classified either as KM91-like, QX-like, or recombination strain (Song *et al.*, 1998; Jang *et al.*, 2007; Lim *et al.*, 2011). A recent analysis of 27 IBV variants isolated from 1990 to 2011 classified the Korean IBV isolates into five genotypes: (i) Mass vaccine serotype, (ii) Korean-I (K-I), (iii) Chinese QX-strain-related, (iv) KM91-like isolates, and (v) isolates that do not fit into any known group of Korean strains. Two genotypes, 11036 and 11052, appeared to be generated from recombination events between the new Korean genotype in cluster 1 and Chinese QX-like strain and between K-I and H120-vaccine serotype, respectively (Mo *et al.*, 2013).

6.10.5 Japan

In Japan, variant IBV co-exists with Grey and Mass isolates (Mase *et al.*, 2004). Local variants have shown a different clustering pattern from existing isolates but are closely related to isolates from China and Taiwan. Local isolates such as JP/Wakayama/2003, JP/Iwate/2005, and JP/Saitama/2006 from non-vaccinated flocks share identity with 4/91 variant, possibly of French or Spanish origin. On the other hand, one Japanese variant, JP/Wakayama-2/2004, isolated from 4/91-vaccinated flocks is related to the vaccine strain (Mase *et al.*, 2008; Shimazaki *et al.*, 2009).

6.10.6 China

In China, IBV was first reported in the mid-1980s. To control IBV infection in chickens in this country, the live attenuated and killed-oil adjuvant vaccines, derived from Mass (H120 and Ma5) and Conn serotypes, were used. However, these vaccines only served to reduce, not eradicate, the problem, because the disease continued to remain a major treat to the poultry industry (Han *et al.*, 2011). IBV in China showed great diversity, although several Mass and 4/91-like isolates were reported in the country (Liu and Kong, 2004; Xie *et al.*, 2011; Ma *et al.*, 2012). The QX and LX-like IBV strains were also isolated, which are distinct from known vaccine serotypes (Yudong *et al.*, 1998; Zhao *et al.*, 2017) and these strains are broadly classified as A2-like and QX-IBV strains (Xu *et al.*, 2007; Zou *et al.*, 2010; Li *et al.*, 2013).

6.10.7 Taiwan

In Taiwan, IBVs were first described in the early 1960s with isolates of the Mass vaccine serotypes. Most local IBV variants are grouped together with the Chinese strains (Huang and Wang, 2006). A Taiwanese IBV strain, designated Taiwan II, is closely related to TW2296/95 serotype, which was also isolated in mainland China (Ma *et al.*, 2012).

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8. Conclusion

It is evident that IBV has become endemic worldwide. It is of great concern to the poultry industry that new IBV variants are persistently emerging. These new virus variants do not respond to existing vaccines currently in use. Although some genotypes are restricted to certain geographic regions, others such as Mass, IBV 4/91 (CR88 or 7/91B) and the recently emerging QX-like IBV are more global in distribution. As such, these global genotypes can be considered for the development of novel multivalent universal vaccines. However, a regional vaccination strategy based on specific local strains can be adapted in addition to the general vaccines based on the ubiquitous genotypes.

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