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Bluetongue virus in South America, Central America and the Caribbean

Danilo M. Legisa, Fernanda N. Gonzalez, Maria José Dus Santos*

Instituto de Virología, CICVyA, INTA, Las Cabañas y de los Reseros S/N, Hurlingham, 1686 Buenos Aires, Argentina

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ABSTRACT

Bluetongue virus (BTV) has been detected in many parts of the world but the data available from each continent are substantially different. Some regions are not covered by proper surveillance programs and thus, the real situation concerning the incidence of BTV in those regions is unknown. This is the case of Central America, South America and the Caribbean, where few outdated data about the presence and spread of BTV have been reported. In the present review, we update the BTV situation in those regions by compiling the serologic data available and analyzing the genetic information reported by the different research groups which are studying the disease in the region.

1. Introduction

Information about bluetongue virus (BTV) in the American continent, especially Central America, the Caribbean and South America is limited. Many of the BTV surveillance programs have not been done systematically and the resultant publications have reported few data which do not allow a full understanding of the presence and circulation of the virus in the region. However, the serologic data reported by some groups allow updating the information about the virus.

In this review, the recent published serologic and genetic information is reviewed to better understand the epidemiology of BTV in the Caribbean and South and Central America.

The traditional idea claims that BTV spread is limited to latitudes 35°S and 40°N or 50°N (Coetzee et al., 2012), i.e. almost all the American continent. Latitude 35°S reaches the middle of Argentina and nearly all the Pampas region, where the main cattle production is carried out, whereas latitude 50°N reaches the south of Canada. Nowadays, it is empirically known that BTV is widely spread between those limits, an idea supported mainly by serologic evidence (Legisa et al., 2013). In North America, BTV was first described in 1948 (Coetzee et al., 2012). Since then, several reports have shown widespread BTV circulation and putative incursions from the Caribbean Basin and Central America, especially to the south east of the USA (MacLachlan et al., 2013). Wilson (Mertens et al., 2009) and Lager (Lager, 2004) have previously reviewed the virus presence in the continent but due to the global epidemiology features of the virus, an update is needed. In this review, we summarize some of the data previously compiled and enlarge the information both with new bibliography and with own genetic analysis of BTV in the Caribbean and Central and South America.

2. BTV in Central America and the Caribbean

In Central America and the Caribbean, and even in the Lesser Antilles, BTV is widespread (Greiner et al., 1993; Martinez et al., 2011; MacLachlan et al., 2007). This region seems to be a source of BTV for the rest of the continent with neither ecologic nor geographic barriers described to geographically isolate central America from North or South America (Mertens et al., 2009). In fact, it has been reported that not even the sea can prevent the virus from spreading from the Caribbean islands to the American mainland (Thompson et al., 1992).

Most of the information available for this region is due to the efforts of the Regional Bluetongue team which started to work in the early 1980s (Greiner et al., 1992, 1993; Thompson et al., 1992) studying the disease over eleven countries in the region. The Bluetongue Regional team and the Interamerican Bluetongue team (Gibbs et al., 1992; Mo et al., 1994) performed a large surveillance over eleven countries in the region. Their findings included serologic detections and virus isolations (Walton and Osburn, 1992). From the early 1980s to the early 1990s, BTV was detected in Guatemala, El Salvador, Honduras, Costa Rica, Nicaragua, Panamá, Trinidad and Tobago, Barbados, Puerto Rico, Jamaica, French Martinique Island, French Guadeloupe Island and Dominican Republic (MacLachlan et al., 2007; Mo et al., 1994; Walton and Osburn, 1992). In this region, serotypes 1, 3, 4, 6, 8, 11, 12, 14 and 17 were detected by serotype specific antibodies and serotypes 1, 3, 4, 6,

* Corresponding author. Tel.: +54 11 46211676.
E-mail addresses: dlegisa@cnia.inta.gov.ar (D.M. Legisa), fgonzalez@cnia.inta.gov.ar (F.N. Gonzalez), mdussantos@cnia.inta.gov.ar (M.J. Dus Santos).

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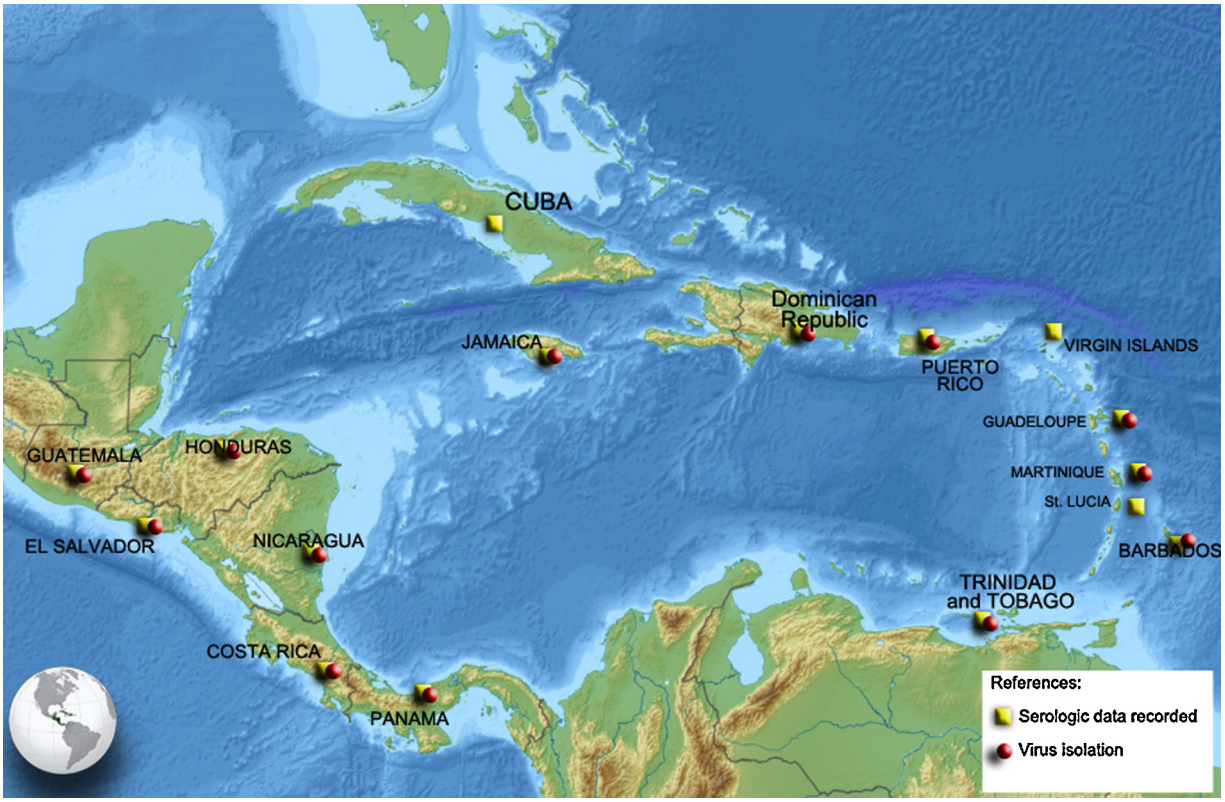

Fig. 1. Map of Central America and the Caribbean Basin showing locations for bluetongue virus (BTV) surveillances and areas where the virus was isolated. Yellow squares indicate serologic data recorded and red dots indicate area where the virus was isolated.

8, 12 and 17 by virus isolation (Mo et al., 1994; Gibbs et al., 1992, 1983; Greiner et al., 1989, 1993; Gumm et al., 1984; Homan et al., 1990). In 1981, Metcalf et al. (1981) detected almost 80% of prevalence in Puerto Rico and Virgin Islands. In the 1980s, Gibbs et al. (1983) described an overall seroprevalence of 70% in cattle, 67% in sheep and 76% in goats, detected by Agar Gel Immuno-Diffusion (AGID). These authors also described high prevalence percentages in Jamaica (77%), Antigua (76%), St Lucia (82%), Barbados (61%), Grenada (88%) and Trinidad and Tobago (79%). In 1992, Mo et al. (1994) evaluated and detected BTV in the region, and stated that some of the serotypes previously detected were still circulating. In Cuba, a country never sampled by the Regional teams, the only report about the situation of BTV was made by Martinez et al. (2011), who found a seropositivity of 99.7% in 1100 animals sampled (Fig. 1 and Table 1).

Regarding the vector species suspected to be responsible for BTV transmission among ruminants, Walton and Osburn (1992), Greiner et al. (1990) and Mo et al. (1994) isolated BTV from *Culicoides insignis*, *C. filerifer* and *C. pusillus*. Additionally, they suggested that these three species, mainly *C. insignis*, were the primary

Table 1
Serotypes determined by isolation or serologic techniques in South America, Central America and the Caribbean.

Country	Virus isolation	Serotype determination	References
Central America and the Caribbean			
Guatemala	1, 3, 6, 17	1, 3, 6, 11, 14	Thompson et al. (1992)
El Salvador	1, 3, 6	1, 6	Thompson et al. (1992)
Honduras	1, 3, 6, 17	1, 3, 6, 17	Thompson et al. (1992)
Nicaragua	1, 3, 6	1, 3, 6	Thompson et al. (1992)
Costa Rica	3, 6,12, 14, 17	1, 3, 6	Homan et al. (1985a), Thompson et al. (1992)
Panama	3, 6	3, 6	Thompson et al. (1992)
Trinidad and Tobago	3	1, 3, 4, 6, 8, 12, 17	Thompson et al. (1992)
Barbados	1, 3	1, 3, 4, 8, 12, 17	Thompson et al. (1992)
Puerto Rico	4, 17	3, 4, 6, 8, 17	Thompson et al. (1992)
Dominican Republic	4, 6, 8	3, 4, 6, 8, 17	Thompson et al. (1992)
Jamaica	3, 12	3, 12	Thompson et al. (1992)
Martinique	2, 10, 11, 13, 17, 18, 22, 24		MacLachlan et al. (2007)
Guadeloupe	5,17		GenBank
Southamerica			
Colombia		12, 14, 17	Homan et al. (1985a)
Guyana	1, 2, 6, 10, 12, 13, 17, 24		GenBank
Brazil*	4, 12	4, 12	Clavijo et al. (2012), Groocock and Campbell (1982) and Martins et al. (2011)
Argentina	4	4	Legisa et al. (2013)

*Groocock and Campbell (1980) isolated BTV4 from zebu cattle from Brazil that had been admitted into quarantine in Florida.

species involved in the virus transmission in the region. *C. insignis* is one of the most frequent species found in Southeastern USA, the Caribbean Basin, and Central and South America (MacLachlan et al., 2007) and is, of course, directly associated with BTV transmission between natural ruminant and non-ruminant hosts. Other *Culicoides* species which could act as vectors in that region are *C. pusillus*, *C. furens*, *C. filarifer* and *C. trilineatus*.

It is important to note that in the study conducted by the Regional and the InterAmerican Bluetongue teams from the early 1980s to the early 1990s, researchers were able to evaluate the dynamics of the virus in the region. Thompson et al. (Thompson et al., 1992) reported the change of frequencies in detection of several serotypes in the region and described an infection pathway for BTV3. BTV3 was first detected in Trinidad and Tobago (September 1987), then spread rapidly to Jamaica and Central America mainland (December 1987), and further disseminated in Panama (1989). It was also later isolated in Honduras, El Salvador and Guatemala. Regarding BTV4, it was first detected in Trinidad and Tobago in August 1989, and then isolated from samples taken in Puerto Rico and Dominican Republic in 1990. Also in 1990, antibodies were detected in Trinidad and Tobago, Barbados, Puerto Rico and Dominican Republic. No data about BTV 4 had been recorded in the region before 1986. Additionally, and in contrast with that found in the North American region, Mo et al. demonstrated that the serotypes detected in the Caribbean Basin had marked differences from those detected in North America (Mo et al., 1994).

2.1. Molecular epidemiology in Central America and the Caribbean

The Bluetongue Regional Team recorded many genetic data in the 1980s. Also, in the last years, new isolates were obtained in some islands from the Lesser Antilles such as French Martinique Island and Guadeloupe Island.

The surveillance performed in the 1980s resulted in several BTV sequences from Jamaica, Dominican Republic, Honduras, Puerto Rico, Guatemala, Panama, Costa Rica, Trinidad and Tobago, El Salvador and Barbados (BTV 1, 3, 4, 6, 8, 12, 17), which were analyzed in three foundational papers released by Wilson et al. (2000), MacLachlan et al. (2007) and Balasuriya et al. (2008). These authors described a polyphyletic feature for the isolates from the Caribbean and Central America based on the analysis of Segment 7 (Seg-7) and Segment 10 (Seg-10). They showed large heterogeneity all along the region and found that some isolates have a South African ancestor as well as a South African origin, suggesting a direct introduction from the West African continent into the New World (MacLachlan et al., 2007). Also, they found that some isolates from the Caribbean and Central America presented high identity with those from the USA, suggesting that North America could be another way of virus introduction to the Caribbean Basin and Central America. Even more, from that sequence analysis, Balasuriya et al. (2008) suggested that there is a history of genetic continuity between the isolates from North America, Central America and the Caribbean.

As previously mentioned, in the last years, a few new field strains have been isolated from the Caribbean region. These strains were obtained in French Martinique Island (BTV 2, 10, 11, 13, 17, 18, 22, and 24) and Guadeloupe Island (BTV5 and 17) (Fig. 1 and Table 1). In the same way, analysis based on Seg-2, 3, 6, 7, 8, 9 and 10 conducted by Legisa et al. (2013) including these new sequences supported the two putative origins for the isolates from the Caribbean and Central America previously proposed by Balasuriya et al. (2008). Moreover, the genetic continuity mentioned could be extended to South America, based on the analysis of whole American sequences. This idea is later discussed in the section "BTV in South America".

3. BTV in South America

According to bibliography data, in South America, only Argentina and Brazil have been able to isolate the virus from field samples (Clavijo et al., 2012; Lager, 2004; Legisa et al., 2013). However, sequences from Guyana have recently appeared on databases, thus indicating that new South American isolates have been obtained.

In the north and north-west of South America (Ecuador, Colombia, Venezuela, Trinidad and Tobago, Guyana, Suriname and French Guyana), the weather conditions are, in general terms, suitable for the development of the vector species and thus for BTV spreading through invertebrate hosts (Homan et al., 1985a; Lopez et al., 1985). In addition, Culicoides density is higher than in arid areas such as Chile, Peru, Bolivia and northwest of Argentina. The few serologic tests performed in the early 1980s showed that the virus was present all over this north region of South America. Costa Rica, which in fact belongs to Central America, could be the closest terrestrial source of infected cattle or vectors. Homan et al. (1985a,b,c, 1990, 1992) detected a seroprevalence of 48.1% in cattle in Costa Rica and a seroprevalence of 51.8% in Córdoba and Antioquia, two departments in the north of Colombia. These authors also detected and reported the presence of serotypes 1, 6, 12, 14 and 17 in Antioquia (Homan et al., 1985c) (Fig. 2 and Table 1).

In Ecuador, Lopez et al. described the serologic presence of BTV in 9 out of 87 bovines (10.3% seroprevalence) in El Oro province, in the south of the country (Lopez et al., 1985). In Manabi, in the west of Ecuador, Mantilla et al. showed the presence of antibodies against BTV in caprines with a seroprevalence of 7.4% (Mantilla, 1998). In addition, in 2011, Merino Mena reported a seroprevalence of 8% in sheep in several areas of the north east of Ecuador such as Beaterio and Tandapi, showing that the virus was still circulating (Merino Mena, 2011).

In Venezuela, BTV data were first described by Siger et al. (1990), who reported a seroprevalence of 56.4% in 1973–1983 and a seroprevalence of 43.3% in 1988–1990. Perez Barrientos et al. (1995) detected a seroprevalence of 62.39% in Zulia State (in the west of the country) after testing sera from 1543 cattle without clinical signs. These authors hypothesized that the virus may have been introduced in the 1980s due to uncontrolled cattle importation. On the other hand, in Aragua State, in the center of Venezuela, Gonzalez and Perez (2001) reported positive serology data showing a seroprevalence in cattle of 74.8% by AGID and of 94.7% by competitive enzyme-linked immunosorbent assay (cELISA) in 1996. In the same year, these authors showed seroconversion by natural infection in Aragua State by using 47 sentinel cattle, and detected 89.4% seropositive animals by AGID and 100% by cELISA (Fig. 2 and Table 1).

Gibbs et al. (1983, 1992) conducted an exhaustive analysis including several countries of that region in 1983 and found seroprevalence values for Trinidad and Tobago, Guyana and Surinam of 79, 52 and 84%, respectively.

Besides the fact that Costa Rica and Panama could be the main terrestrial ways of BTV introduction to South America, it is well described that infected Culicoides could travel over long distances to colonize new regions (Rao et al., 2012; Sellers et al., 1979; Thompson et al., 1992). Based on this, the Caribbean Basin could also act as a source of BTV to South America.

In the center-west region of South America, a region including west Bolivia, South Peru and North of Chile, clinical cases have been suspected since 1968 (Tamayo et al., 1985). However, recent BTV records are missing except for data already reviewed by Lager (Lager, 2004). In that review, Lager reported a seroprevalence of 19.6 and 0.001% in cattle and sheep from Chile, respectively. In addition, during 1993–1996, a surveillance program was conducted in Chile by the European Union in which 1139 bovines, 1224

Fig. 2. Map of South America showing locations for BTV surveillances and areas where the virus was isolated. Yellow squares indicate positive serologic data recorded, purple squares indicate negative serologic data recorded and red dots indicate area where the virus was isolated.

ovines and 4153 camelids were tested for BTV, with negative results (ECH&CP, 2000).

In Peru, only one surveillance program was carried out with ram serum samples, which showed a seroprevalence of 55.9% along the country, clearly indicating that the virus was present at least at the moment of animal sampling (Rivera et al., 1987; Rosadio et al., 1984) (Fig. 2 and Table 1).

In Bolivia, no positive cases have been described. Moreover, a survey of free ranging Gray Brocket Deers reported the absence of positive serologic results for BTV in the Gran Chaco, a south eastern region of Bolivia characterized by weather conditions suitable for vector life cycle (Deem et al., 2004).

Brazil is the largest country in South America, with an area of 8,514,877 km^2 which represents almost 50% of the total area of South America (www.faostat.fao.org). Also, Brazil borders most of the countries of South America. Its weather is mostly tropical, although temperate in the southern region (www.cia.gov). In Brazil, BTV was first described by Silva (1978) in São Paulo in 1978. After that, several reports have shown that the virus is widespread all over Brazil (Antoniassi, 2010; Costa et al., 2006). Serologic data can be found in the whole country, although the virus was isolated only in two opportunities (Clavijo et al., 2012; Groocock and Campbell, 1982): in 1980, BTV4 was isolated in Florida (USA) from Brazilian zebu cattle which had been quarantined; and in 2001, BTV12 was isolated from sheep showing clinical signs of bluetongue (Clavijo et al.). BTV reports from the 1980s and 1990s were reviewed and summarized by Lager et al. (Lager, 2004; Mertens et al., 2009), who detailed several serologic cases. Besides the serologic studies, the only serotypes identified were 4 (Groocock and Campbell, 1982) and 12 (Clavijo et al., 2012). Since 2000, several new reports have studied BTV in different regions of Brazil, providing insights about BTV status.

In the north and northeast regions of Brazil, seroprevalence values from 8 to 54.39% were calculated in sheep (Azevedo Ramos

et al., 2010; Dias et al., 2007; Alves et al., 2009; Mota et al., 2011; Souza et al., 2010). BTV specific antibodies were also detected in buffaloes and goats (Martins et al., 2011; Silva, 2002; Silva et al., 2011). In cattle, only one report is available in that region, evaluating 12 herds and showing a seroprevalence between 3.94 and 4.82% (Melo et al., 2000).

In the center-west region, in Mato Grosso do Sul state, Pantanal region is one of the most important areas for cattle production (Embrapa, 2006). BTV antibodies were detected in cattle and sheep since 1991 (Pellegrin et al., 1997). Also in Pantanal region, Tomich et al. (2009) tested pampas deer (*Ozotoceros bezoarticus celer*) without detecting BTV antibodies.

In the limit between the center-west region and southeast region, Gerber et al. (2012) sampled Collared peccaries (*Tayassu tajacu*) along the course of the Paraná river in 2000–2001 and found a seroprevalence of 39% (19/49), demonstrating that the animals had been exposed to the virus. However, the finding was not indicative of the potential role of that species as a reservoir of BTV in the region. In Minas Gerais state, several surveillances were conducted. High seroprevalence values were reported in goats, sheep and cattle (Oliveira Laender, 2002; Gouveia et al., 2003; Konrad, 2003) The last confirmation of the disease in this region was reported by the Ministry of Agriculture in May 2010 (MAPA-DSA, 2011) (Fig. 2 and Table 1).

In São Paulo State, in Aracatuba region, Hellmeister de Campos Nogueira et al. (Hellmeister de Campos Nogueira, 2008; Hellmeister de Campos Nogueira et al., 2009) tested sheep and detected a seroprevalence of 74.3 and 65.1% (using ELISA CFS and AGID respectively). The authors pointed out that the temperature and humidity conditions for that special region were more than favorable for vector life cycle, making the disease to be putatively endemic. In 2012, Lima et al. (2012) detected antibodies against BTV in buffaloes using ELISA CFS (99.52%), virus neutralization (93%) and AGID (75%) (Fig. 2 and Table 1).

The south region of Brazil limits with Uruguay, Argentina and Paraguay. In that region the weather conditions for virus spread are the most suitable. Rezende Costa (2000b) detected a seroprevalence of 0.63% and 0.15% in cattle and sheep respectively in the southwest of the southern region, however, in Paraná state, Scolari et al. (2010) detected a seroprevalence of 54 and 46% in cattle and sheep respectively. The seroprevalences reported in southern Brazil, the isolation achieved by Clavijo et al. and the favorable weather conditions for the vector life cycle suggest that BTV could spread to areas and countries surrounding that region, including Paraguay, Uruguay and Argentina, where BTV has in fact been detected and isolated (Legisa et al., 2013) (Fig. 2 and Tables 1 and 2).

Very recently, in June 2013, a BTV4 outbreak was reported by the Coordinator of Animal Protection of the State Department of Agriculture and Livestock and the Ministry of Agriculture, Livestock and Supply (MAPA) in Vassouras, in Rio de Janeiro State in a herd of 99 dairy sheep (ewes and rams) of the Lacaune breed. Four pregnant sheep died and six were seriously ill. In addition 37 non-pregnant females were affected, 16 male lambs were sick and 2 died (Balaro, 2013; MAPA-DSA, 2013).

Argentina is the second largest country in South America, with an area of 2,780,400 km^2 (www.faostat.fao.org). As it is well known, BTV infection was recognized as an enzootic disease between latitude 53°N and 40°S. This southern boundary reaches the central region of Argentina. However, recent climate change around the world makes necessary a new configuration of those boundaries. BTV presence has not been well documented in Argentina but, since 1996, this country has been considered serologically positive according to OIE parameters (Gorchs and Lager, 2001). The virus was first detected by Lager et al. (2004), who conducted two surveillances in 1995–1996 and 1998. These authors detected seroconversion and isolated the virus from sentinel cattle in Corrientes Province, in the northeast of Argentina. In their studies, they detected seroprevalence values of up to 40.7% in cattle and of 95% in sheep, both in Misiones province. In Corrientes province, they found a seroprevalence of 0.7–2.7% in cattle and 3.13% in sheep. They did not find positive serology for BTV in Chaco, Formosa, Entre Ríos and Santa Fe provinces in the north east of Argentina. Since then, no formal surveillances have been conducted. In 2009 and 2010, the virus was isolated from two bovines which had been detected as seropositive at the National Agricultural Technology Institute (INTA) service. Those two cases were a source for two new viral isolates (see the section "Molecular epidemiology") (Fig. 2 and Table 1).

Given the above-mentioned boundaries, animal movement or vector spread, animals out of subtropical areas have been tested as part of other virus research surveillances. In 1993, Puntel et al. (1998) tested 390 camelids (*Lama glama*) in three Argentine provinces: Buenos Aires, Córdoba (center region) and Jujuy (north western region). In 1995 and 1998, Uhart and Marull (Marull et al., 2012; Uhart et al., 2003) tested 14 free ranging pampas deer from the Campos del Tuyu wildlife reserve in Buenos Aires. In 2002, Marcoppido et al. (2010) tested 11 wild born male guanacos (*Lama guanicoe*) and 128 wild vicuñas (*Vicugna vicugna*) in Jujuy Province. Between 2001 and 2010, Marull et al. (2012) tested 395 wild guanacos from Neuquén and Río Negro provinces in the Patagonia region. None of the animals tested in all these studies showed positive serology against BTV (Fig. 2 and Table 1).

In the north-east of Argentina, the dominant *Culicoides* species are *C. insignis*, *C. paraensis* and *C. venezuelensis* (Ronderos et al., 2003). In the north-west of Argentina, Veggiani Aybar et al. (2013) described *C. paraensis* Goeldi and *C. lahillei* Iches as the most frequent *Culicoides* species. Other reports also point *C. insignis* and *C. pusillus* as the main representatives of the genus *Culicoides* in all South America (Felippe-Bauer et al., 2008; Gibbs et al., 1983; Gouveia et al., 2003; Greiner et al., 1992; Homan et al., 1990; Legisa et al., 2013). BTV has been isolated from *C. insignis* and *C. pusillus* both in Central America and the Caribbean but not in South America. This allows us to think about the importance of this abundant species in the region but also to think that other species may be involved in BTV transmission.

3.1. Molecular epidemiology in South America

As previously described, until 2012, the virus had been isolated only in two countries of South America: Argentina and Brazil. Clavijo et al. isolated BTV12 from an outbreak reported in Paraná state in Brazil (Clavijo et al., 2012) and Lager et al. (2004) isolated BTV4 from sentinel cattle which seroconverted in 1999–2001 from Argentina's northeast region. Legisa et al. (2013) further detected and isolated BTV4 in two more opportunities in 2007 and 2009 from cattle in Corrientes province. All Argentine isolates were characterized as BTV4 with a high genetic stability over the 10 years of distance. The isolates were also characterized through the analysis of seven out of ten genomic segments (Seg-2, 3, 6, 7, 8, 9 and 10) as belonging to the known western topotype but with a strong independent lineage evolution, even when they were compared with other American isolates, representing a well-defined South American cluster in each segment analysis. These results could indicate that the virus has been circulating in Argentina for at least the last ten years maintaining a strong genetic stability. Genetic data for Brazilian BTV12 (Clavijo et al., 2012) are limited to only a Seg-7 sequence, which was characterized as a western strain, with a high similarity with strains from Central America and the Caribbean (Legisa et al., 2013; Maan et al., 2010). This sequence showed a stronger similarity with Argentine strains with high identity values and, even more, sharing several punctual mutations with one of the Argentine viral strains, thus suggesting that they share a close

Table 2
Table summarizing serologic data recorded from Brazil.

State/Region	Species	*N*	Seroprevalence	Year	References
Pará/North	Sheep	456	54.39% AGID	nd	Azevedo Ramos et al. (2010)
Pará/North	Buffaloes	147	6.8% (SN BTV-4) 25.9% (AGID)	nd	Martins et al. (2011)
Ceará/Northeast	Goats	1865	30.6%	nd	Silva (2002)
Ceará/Northeast	Sheep	271	27.31%	October 2005–December 2006	Dias et al. (2007)
Paraíba/Northeast	Cattle	137 serum samples – 12 herds	3.94–4.82%	1997	Melo et al. (2000)
Paraíba/Northeast	Sheep	506	8.4%	nd	Alves et al. (2009)
Paraíba/Northeast	Dairy goats	1088	12.1%	nd	Silva et al. (2011)
Sertão de Pernambuco/Northeast	Goats	410	3.9%	nd	Mota et al. (2011)
	Sheep	400	4.3%		
Bahia/Northeast	Sheep	469	0.43%	nd	Souza et al. (2010)
Mato Grosso do Sul/Central West	Cattle	13	20.6%	1991	Pellegrin et al. (1997)
		117	37%	1992	
		79	19.5%	1993	
Pantanal	Cattle	219	42%	2009	Tomich et al. (2009)
	Sheep	55	19.2%		
	Pampas deer	49	0%		
Corumbá	Cattle	353	51.3%	nd	Tomich (2007)
Central West-South east limit	Collared peccaries	49	39%	2000–2001	Gerber et al. (2012)
Minas Gerais/Southeast	Goat	1295	41.2%	2002	Oliveira Laender (2002)
	Cattle	577	58.36%		
Minas Gerais/Southeast	Sheep	nd	53.8%	nd	Gouveia et al. (2003)
	Goats		44.5%		
Minas Gerais/Southeast	Cattle	1304	59.51%	2001–2002	Konrad (2003)
São Paulo	Sheep	1002	74.3% (ELISA CFS) 65.1% (AGID)	2006	Hellmeister de Campos Nogueira (2008) and Hellmeister de Campos Nogueira et al. (2009)
São Paulo	Buffaloes	212	99.52% (ELISA CFS)	nd	Lima et al. (2012)
		212	93% (SN)		
		212	75% (AGID)		
South west	Cattle	1272	0.63% (AGID)	nd	Rezende Costa (2000a)
	Sheep	1341	0.15% (AGID)		
Parana	Cattle	37	54%	nd	Scolari et al. (2010)
	Sheep	66	46%		

nd: not determined.

common origin. These data also indicate that the introduction pathway for the Argentine isolates could have involved a Central American-Brazilian route or a Caribbean-Brazilian route (Legisa et al., 2013), which has been postulated and supported by the genetic continuity shown by the analysis of some segments. In 2012, the sequences of new isolates from Guyana belonging to serotypes BTV1, 2, 6, 10, 12, 13, 17 and 24 appeared in databases. As expected, Seg-2 analysis showed strong correlation with the serotype and gave genealogic information which linked isolates from Guyana with a putative African or North American origin. That information was concordant with Caribbean and Central American analysis and strongly supported the proposed genetic continuity between the Caribbean, and North and Central America. Legisa et al. (unpublished results) analyzed isolates from the whole American continent, using Seg-2, 3, 6, 7, 8, 9 and 10 and showed that the continuity observed could be extended to the whole continent and not only to North America and the Caribbean Basin. This is a special American feature when the situation is compared with the European scenario, where lineages have been mixed and reassortants have been changing the known viral evolution in which a strain could be followed to trackback its origin. The known genetic landscape in the American continent is still useful to understand the history and circulation of BTV, although the lack of data is predominant.

4. Natural barriers

Certain geographical features should be considered when analyzing the distribution of BTV in South America. One of them is the geographical isolation of Chile from the rest of South American countries given by the high Andes Mountains and dry and desert areas like Atacama Desert. This desert/arid region in the north of Chile reaches the northern provinces of Argentina as well as the south of Bolivia; these regions have been suggested as barriers for the disease because the climate conditions are not suitable for the Culicoides life cycle (Legisa et al., 2013; Marcoppido et al., 2010, 2011; Puntel et al., 1998). This could explain the lack of detection in the area formed by the north of Argentina and Chile and the southwest of Bolivia. Also in geographical terms, altitude has been associated with the absence of BTV detection in certain areas of Brazil, Colombia and Venezuela (Gonzalez et al., 2000; Homan et al., 1985b,c; Tomich, 2007), probably because of the biology behind the vector's life cycle and its negative correlation with altitude. In the same way, there was a lack of serologic detection in Patagonia, even when this area is in contact with the pampas and central region of Argentina. This is an important fact because this area is one of the principal sheep breeding areas in Argentina (www.faostat.fao.org), but given the characteristics learned from north European outbreaks, the Patagonia region as well as the pampas and the north eastern region of Argentina need to be under surveillance programs.

5. Perspectives

In the last years, several unexpected outbreaks recorded in new areas have led us to think in new boundaries or even more, in no boundaries for BTV presence in the world (Zientara and Sanchez-Vizcaino, 2013). Animal and vector movement have been responsible for the expansion of the disease beyond the traditional

limits or boundaries (Maan et al., 2012; Rao et al., 2012). The virus is able to overcome natural barriers like large water extensions (Thompson et al., 1992) or to start an outbreak in remote lands flying along with particles in wind streams (Sellers et al., 1979). World climate change driven by global warming could also contribute to the spread of BTV over those boundaries, mainly by creation of more suitable conditions for vector spread and reproduction (Wittmann and Baylis, 2000). Also the genetic evolution due to reassortants or fixed mutations by founder effect could result in the emergence of new field strains with possible new ecological features (Balasuriya et al., 2008). In the same way, as the new serotypes 25 and 26 were discovered (Hofmann et al., 2008; Maan et al., 2011), the American continent could be a source of new virus types with new biological features.

Surveillance programs and control networks are thus needed in Central America, South America and the Caribbean Basin to understand the real situation beyond the eventual findings. In the same way, diagnosis techniques should be optimized and molecular diagnosis should be developed. AGID and ELISA are useful for a routine diagnosis but not for accurate viral detection. Thus, there is a need for a permanent surveillance program in the American continent, given the genetic flow detected all along the continent and the serological evidence, which confirms the virus circulation over the last decades. These efforts would be necessary to detect any change in BTV disease status and to face any putative problem in the area which could lead to large economic losses to farmers, a situation that was evident in the last Brazilian outbreak in June 2013 (Balaro, 2013; MAPA-DSA, 2013). An uncontrolled outbreak could lead to spread of the virus to areas previously declared as free of BTV.

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