Research in Veterinary Science 97 (2014) S5–S19

Contents lists available at ScienceDirect

Research in Veterinary Science

journal homepage: www.elsevier.com/locate/rvsc

Overview and phylogeny of *Mycobacterium tuberculosis* complex organisms: Implications for diagnostics and legislation of bovine tuberculosis

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ARTICLE INFO

Article history:
Available online

Keywords:
Mycobacterium tuberculosis complex
Mycobacterium bovis
Mycobacterium caprae
Bovine tuberculosis
Phylogeny
Legislation

ABSTRACT

Members of the *Mycobacterium tuberculosis* complex (MTBC) cause a serious disease with similar pathology, tuberculosis; in this review, bovine tuberculosis will be considered as disease caused by any member of the MTBC in bovids. Bovine tuberculosis is responsible for significant economic loss due to costly eradication programs and trade limitations and poses a threat to both endangered and protected species as well as to public health. We here give an overview on all members of the MTBC, focusing on their isolation from different animal hosts. We also review the recent advances made in elucidating the evolutionary and phylogenetic relationships of members of the MTBC. Because the nomenclature of the MTBC is controversial, its members have been considered species, subspecies or ecotypes, this review discusses the possible implications for diagnostics and the legal consequences of naming of new species.
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1. Introduction

Mycobacterial species causing tuberculosis in humans and animals are merged in the *Mycobacterium tuberculosis* complex (MTBC). To date, the following organisms are considered members of the MTBC: *M. tuberculosis* (Koch, 1882), *Mycobacterium bovis* (Karlson and Lessel, 1970), *M. bovis* Bacillus Calmette and Guérin (BCG) (Guérin and Rosenthal, 1957), *Mycobacterium africanum* (Castets et al., 1968; Castets and Sarrat, 1969), *Mycobacterium microti* (Wells and Oxon, 1937; Reed, 1957), *Mycobacterium canettii* (van Soolingen et al., 1997), *Mycobacterium pinnipedii* (Cousins et al., 2003), and *Mycobacterium caprae* (Aranaz et al., 2003); moreover, the MTBC includes the oryx bacillus (Lomme et al., 1976) that has recently been proposed to be elevated to *Mycobacterium orygis* (van Ingen et al., 2012) and the dassie bacillus (Wagner et al., 1958). A pathogen of mongooses similar to the dassie bacillus has been suggested to be named *Mycobacterium mungi* (Alexander et al., 2010).

The division into different species is based on host preference, supported by molecular phylogenetics (Brosch et al., 2002). However, it has been suggested that the MTBC may instead represent a series of host-adapted clades consistent with the ecotype concept of Cohan (Cohan, 2002; Smith et al., 2006a). Nevertheless, these species, or ecotypes, can be distinguished by their distinct cultural and biochemical characteristics (Collins and de Lisle, 1985; Grange et al., 1996).

We review the members of the MTBC and their range of hosts, the phylogenetic markers that have been used to-date in order to identify lineages or clonal complexes relevant for tuberculosis in animals and describe the phylogeny and spread of these pathogens. Finally, we discuss the implications that naming new species within the MTBC may have on legislation of animal tuberculosis.

2. The *M. tuberculosis* complex

The MTBC is characterised by 99.9% similarity at the nucleotide level and virtually identical 16S rRNA sequences (Böddinghaus et al., 1990; Sreevatsan et al., 1997; Huard et al., 2006). Strains of the MTBC have a highly clonal population structure with little or no evidence for recombination (exchange of chromosomal DNA) between strains (Supply et al., 2003; Smith et al., 2006b; Hershberg et al., 2008). An analysis of 24 whole genome sequences of *M. tuberculosis* using four different methods concluded that there was evidence for recombination of very short segments in *M. tuberculosis* (Namouchi et al., 2012). However, more recently Pepperell and colleagues (2013) did not find any evidence for lateral gene transfer in an analysis of 64 genomes of *M. tuberculosis*, an observation which is consistent with the many empirical observations of clonality in this group of organisms (Supply et al., 2003; Smith

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http://dx.doi.org/10.1016/j.rvsc.2014.02.009
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et al., 2006b; Hershberg et al., 2008). Despite their high similarity at nucleotide level, the members of the MTBC can be distinguished by several molecular markers (a selection is shown in Table 1).

2.1. M. tuberculosis *(sensu stricto)*

M. tuberculosis is the cause of human tuberculosis and is the most important bacterial pathogen of humans, with an estimated 12 million cases in 2011 (WHO, 2012). Nevertheless, it can also affect animals as shown in many reports concerning cattle (*Bos taurus*) (Lesslie, 1960; Ocepek et al., 2005; Prasad et al., 2005; Srivastava et al., 2008; Ameni et al., 2011; Fetene et al., 2011; Romero et al., 2011), goats (*Capra aegagrus hircus*) (Cadmus et al., 2009; Hiko and Agga, 2011), domestic pigs (*Sus scrofa domestica*) (Mohamed et al., 2009; Jenkins et al., 2011), cats (*Felis silvestris catus*) and dogs (*Canis lupus familiaris*) (Clercx et al., 1992; Aranaz et al., 1996b; Erwin et al., 2004; Parsons et al., 2008b), birds (Hoop et al., 1996; Schmidt et al., 2008) and also wildlife species including zoo animals (Montali et al., 2001; Alexander et al., 2002; Une and Mori, 2007; van Helden et al., 2009; Angkawanish et al., 2010).

2.2. M. canettii

M. canettii is the most divergent organism within the MTBC, exhibiting a smooth and glossy colony morphology and rapid growth *in vitro*. It was first mentioned by the French microbiologist Georges Canetti in 1969 and preserved and studied extensively at the Pasteur Institute (Daffé et al., 1987, 1991). Van Soolingen and colleagues (1997) described *M. canettii* isolated from a Somali child as a novel pathogenic taxon of the MTBC. An isolate of *M. canettii* was subsequently isolated from a 56-year-old Swiss man with abdominal lymphatic tuberculosis who lived in Kenya (Pfyffer et al., 1998) and from two soldiers of the French Foreign Legion in Djibouti (Miltgen et al., 2002). Tuberculosis caused by *M. canettii* appears to be an emerging disease in the Horn of Africa. Koeck and colleagues (2011) suggested an environmental reservoir; however, the natural reservoir and host range of this pathogen are still unknown. *M. canettii* is nowadays considered an outgroup of the MTBC due to its divergence from all other members of the complex and the evidence for recombination (Gutierrez et al., 2005); however, the status of *M. canettii* as an outgroup to the MTBC complex has been challenged (Smith et al., 2009b). Recently, Supply and colleagues (2013) showed by whole genome analysis of five representative strains of *M. canettii* that the smooth tubercle bacilli are highly recombinogenic and evolutionarily early branching, with larger genome sizes and higher rates of genetic variation. Despite the highly conserved core genome of all tuberculosis-causing mycobacteria, Supply and colleagues (2013) found *M. canettii* to be less virulent than *M. tuberculosis* in mouse infection experiments and, hence, proposed that *M. tuberculosis* has evolved its pathogenic lifestyle starting from a pool of ancestral smooth tubercle bacilli with lower virulence.

2.3. M. africanum

This species was first described as tuberculosis bacilli of the African type in Dakar, Senegal, in 1968 (Castets et al., 1968). The strains were described as intermediate between *M. tuberculosis* and *M. bovis*. This pathogen causes half of the human tuberculosis cases in West Africa (Källenius et al., 1999; de Jong et al., 2009) and it has been suggested that there is specific adaptation between the pathogen and its host (Gagneux et al., 2006; Intemann et al., 2009). *M. africanum* was first divided into two types, I and II, based on cultural, biochemical and molecular characteristics, but in 2004 *M. africanum* type II was reclassified into *M. tuberculosis sensu stricto* (Mostowy et al., 2004b), while *M. africanum* type I was subdivided into West African I, prevalent around the Gulf of Guinea, and West

Table 1
Overview of selected molecular characteristics for members of the *Mycobacterium tuberculosis* complex based on the following publications: Parra et al. (1991), Liébana et al. (1996), Espinosa de Los Monteros et al. (1998), Kasai et al. (2000), Niemann et al. (2000b), Cousins et al. (2003), Aranaz et al. (2003), Chimara et al. (2004), Viana-Niero et al. (2004), Goh et al. (2006), Huard et al. (2006), Alexander et al. (2010), van Ingen et al. (2012). V, variable results; ND, no data available. The superscript indicates the position of the mutation at either the nucleotide (n) or the codon (c) of the respective genes.

Organism and variety	$oxyR^{n285}$ mutation (G to A)[a]	$pncA^{c57}$ mutation (CAC to GAC)	*katG* mutation at codon:		$mmpL6^{n551}$ mutation (C to G)	$gyrA^{c95}$ mutation (AGC to ACC)	*gyrB* mutation at nucleotide:				$Rv2042c^{c38}$ (GTC to GGC)
			203(ACC to ACT)	463(CTG to CGG)			675 (C to T)	756 (G to A)	1311 (T to G)	1410 (C to T)	1450 (G to T)	
M. tuberculosis	G	CAC	ACC	V	C	V	C	G	T	C	G	T
M. africanum	G	CAC	ND	CTG	C	ACC	C	G	T	C	T	T
Dassie bacillus	G	CAC	ACT	CTG	C	AGC	C	G	T	C	T	T
M. mungi	ND	ND	ND	ND	ND	ND	C	G	T	C	T	T
M. orygis	G	CAC	ACT	CTG	G	AGC	C	G	T	C	T	G
M. pinnipedii	G	CAC	ACT	CTG	G	ACC	C	G	T	C	T	T
M. microti	G	CAC	ACT	CTG	G	ACC	T	G	T	C	T	T
M. caprae	A	CAC	ACT	CTG	G	ACC	C	A	G	C	T	T
M. bovis	A	GAC	ACT	CTG	G	ACC	C	A	T	T	T	T
M. bovis BCG	A	GAC	ACT	CTG	G	ACC	C	A	T	T	T	T

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