



Genes involved in translation of *Mycoplasma hyopneumoniae* and *Mycoplasma synoviae*

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Abstract

This is a report on the analysis of genes involved in translation of the complete genomes of *Mycoplasma hyopneumoniae* strain J and 7448 and *Mycoplasma synoviae*. In both genomes 31 ORFs encoding large ribosomal subunit proteins and 19 ORFs encoding small ribosomal subunit proteins were found. Ten ribosomal protein gene clusters encoding 42 ribosomal proteins were found in *M. synoviae*, while 8 clusters encoding 39 ribosomal proteins were found in both *M. hyopneumoniae* strains. The L33 gene of the *M. hyopneumoniae* strain 7448 presented two copies in different locations. The genes encoding initiation factors (IF-1, IF-2 and IF-3), elongation factors (EF-G, EF-Tu, EF-Ts and EF-P), and the genes encoding the ribosome recycling factor (*rrf*) and one polypeptide release factor (*prfA*) were present in the genomes of *M. hyopneumoniae* and *M. synoviae*. Nineteen aminoacyl-tRNA synthetases had been previously identified in both mycoplasmas. In the two strains of *M. hyopneumoniae*, J and 7448, only one set of 5S, 16S and 23S rRNAs had been identified. Two sets of 16S and 23S rRNA genes and three sets of 5S rRNA genes had been identified in the *M. synoviae* genome.

Key words: mycoplasmas, *Mycoplasma synoviae*, *Mycoplasma hyopneumoniae*, translation, genome.

Received: April 12, 2006; Accepted: October 5, 2006.

Introduction

Mycoplasmas comprise a very large group of prokaryotes widely distributed in nature as parasites and pathogens of humans, animals, plants and insects (Razin, 1992). Because mycoplasmas have an extremely small genome (0.58-2.20 Mb compared to the 4.64 Mb of *Escherichia coli*), these organisms have limited metabolic options for replication and survival (Maniloff, 1996).

Mycoplasma-induced arthritis of poultry is almost entirely caused by *Mycoplasma synoviae* infection, which is present on poultry farms all over the world, either sporadically or endemically (Jordan, 1981; Bencina *et al.*, 1999). Infection most frequently occurs as a subclinical respiratory tract infection, which can progress to respiratory disease or to infectious synovitis, in which the synovial membranes of joint and tendon sheaths are affected. Under so far unknown conditions, the *M. synoviae* disease can become systemic, causing systemic vasculitis and pathological changes in numerous organs. Porcine enzootic pneumonia, with *M. hyopneumoniae* as the primary agent,

is a chronic respiratory disease present in the vast majority of swine farms worldwide, that causes respiratory distress resulting from pneumonia in growing pigs (Kobisch and Friis, 1996; Kobisch, 2000).

Translation is a key step in gene expression, converting the genetic information encoded in messenger RNAs (mRNAs) into contiguous chains of amino acids with structural and/or catalytic properties (Lafontaine and Tollervey, 2001). In this work, we analyzed several aspects of the translation machineries by searching the genes involved in translation of *M. hyopneumoniae* strain J, *M. hyopneumoniae* strain 7448, and *M. synoviae* in the Mycoplasma database and by comparing the results to *Mycoplasma* and other genomes.

Methods

Genes involved in translation of *M. hyopneumoniae* strains J and 7448 and *M. synoviae* were retrieved in the Mycoplasma database. Annotation data were used to compare the gene organization among the three mycoplasmas and to the *E. coli* and *Corynebacterium glutamicum* models (Martín *et al.*, 2003). The translated amino acid sequences of L33 ribosomal and gat (A, B and C) proteins were retrieved from the database and used to search for related sequences by using BLAST tools (Altschul *et al.*, 1997).

Seventeen and twenty-two amino acid sequences of L33 and gat proteins, respectively, were used to construct phylogenetic trees by multiple sequence alignments, using the Clustal X program, version 1.8 (Thompson *et al.*, 1997) and the neighbor-joining method (Saitou and Nei, 1987). Robustness of branches was estimated using 100-bootstrap replicates. The amino acid sequences were visualized using the TreeView software.

Results and Discussion

Genes encoding ribosomal proteins

The amino acid sequences of the ribosomal proteins of *M. synoviae*, *M. hyopneumoniae* strain J, and *M. hyopneumoniae* strain 7448 have been deduced from the genome sequence (Vasconcelos *et al.*, 2005). Thirty-one ORFs (Open Reading Frames) encoding large ribosomal subunit proteins, and 19 ORFs encoding small ribosomal subunit proteins were found in the genomes of *M. synoviae*,

M. hyopneumoniae J and *M. hyopneumoniae* 7448, as shown in Table 1.

Those ribosomal protein families including L1-L6, L9-L24, L27-L29 and L31-36, as well as S2 to S20, correspond to the stable pool of 50 ribosomal proteins described in bacteria. S1, S21, L25 and L30 are the only four well-established bacterial ribosomal proteins which exhibit a disparate distribution (Lecompte *et al.*, 2002). Those four genes were not found in the three mycoplasma genomes sequenced. Among the mycoplasmas, the S1 protein was also absent in the genomes of *M. genitalium* and *M. pneumoniae*, but has been identified in *M. pulmonis* (GenBank accession number: Q98R80). The S21 gene has been identified in the genomes of *M. gallisepticum*, *M. genitalium*, *M. penetrans*, *M. pneumoniae* and *Ureaplasma urealyticum* (Lecompte *et al.*, 2002).

Many of the ribosomal proteins have been shown to be crucial for ribosome assembly, such as the early assembling proteins S4p, S7p, S8p, S15p, S17p, L2p, L3p, L4p, L5p, L15p, L18p (Held *et al.*, 1974; Rohl and Nierhaus,

Table 1 - Genes encoding ribosomal proteins identified in the genomes of *M. synoviae*, *M. hyopneumoniae* J, and *M. hyopneumoniae* 7448.

Product	ORF <i>M. synoviae</i>	ORF <i>M. hyopneumoniae</i> J	ORF <i>M. hyopneumoniae</i> 7448	Product	ORF <i>M. synoviae</i>	ORF <i>M. hyopneumoniae</i> J	ORF <i>M. hyopneumoniae</i> 7448
Ribosomal large subunit				Ribosomal small subunit			
L1	MS00507	MH10385	MP01569	L31	MS06767	MH14988	MP07171
L2	MS00378	MH02612	MP04292	L32	MS06893	MH10338	MP07170
L3	MS00334	MH02630	MP04310	L33	MS06951	MH10377	MP12668/MP12594
L4	MS00343	MH15027	MP04305	L34	MS06957	MH04919	MP07097
L5	MS00437	MH02516	MP12664	L35	MS06887	MH10352	MP07167
L6	MS00450	MH02493	MP04205	L36	MS06935	MH10380	MP07166
L7/L12	MS02743	MH01479	MH01479	S2	MS02838	MH04101	MP12674
L9	MS02675	MH10381	MP03703	S3	MS00405	MH10344	MP04271
L10	MS02747	MH01488	MP12655	S4	MS02216	MH04390	MP12704
L11	MS12947	MH19654	MP18913	S5	MS06783	MH02490	MP04182
L13	MS05775	MH05352	MP03756	S6	MS01398	MH01222	MP07141
L14	MS06954	MH02527	MP04228	S7	MS06010	MH03876	MP05936
L15	MS00485	MH02489	MP04181	S8	MS06885	MH10396	MP07133
L16	MS00409	MH02573	MP12667	S9	MS06897	MH05346	MP03749
L17	MS06953	MH10382	MP00474	S10	MS06955	MH10370	MP12640
L18	MS06886	MH15043	MP07134	S11	MS06958	MH10341	MP00487
L19	MS06900	MH10337	MP07138	S12	MS05989	MH10388	MP05913
L20	MS00655	MH10351	MP07168	S13	MS00910	MH02418	MP00493
L21	MS06883	MH09954	MP02359	S14	MS06952	MH10364	MP07130
L22	MS06928	MH02596	MP12665	S15	MS06949	MH10387	MP07135
L23	MS00356	MH02615	MP04295	S16	MS13161	MH10336	MP07137
L24	MS06929	MH02520	MP04222	S17	MS00414	MH02540	MP12523
L27	MS01224	MH09955	MP10612	S18	MS01383	MH10335	MP12686
L28	MS06941	MH10386	MP07143	S19	MS00392	MH15042	MP07132
L29	MS00411	MH10365	MP07165	S20	MS06926	MH15044	MP07163

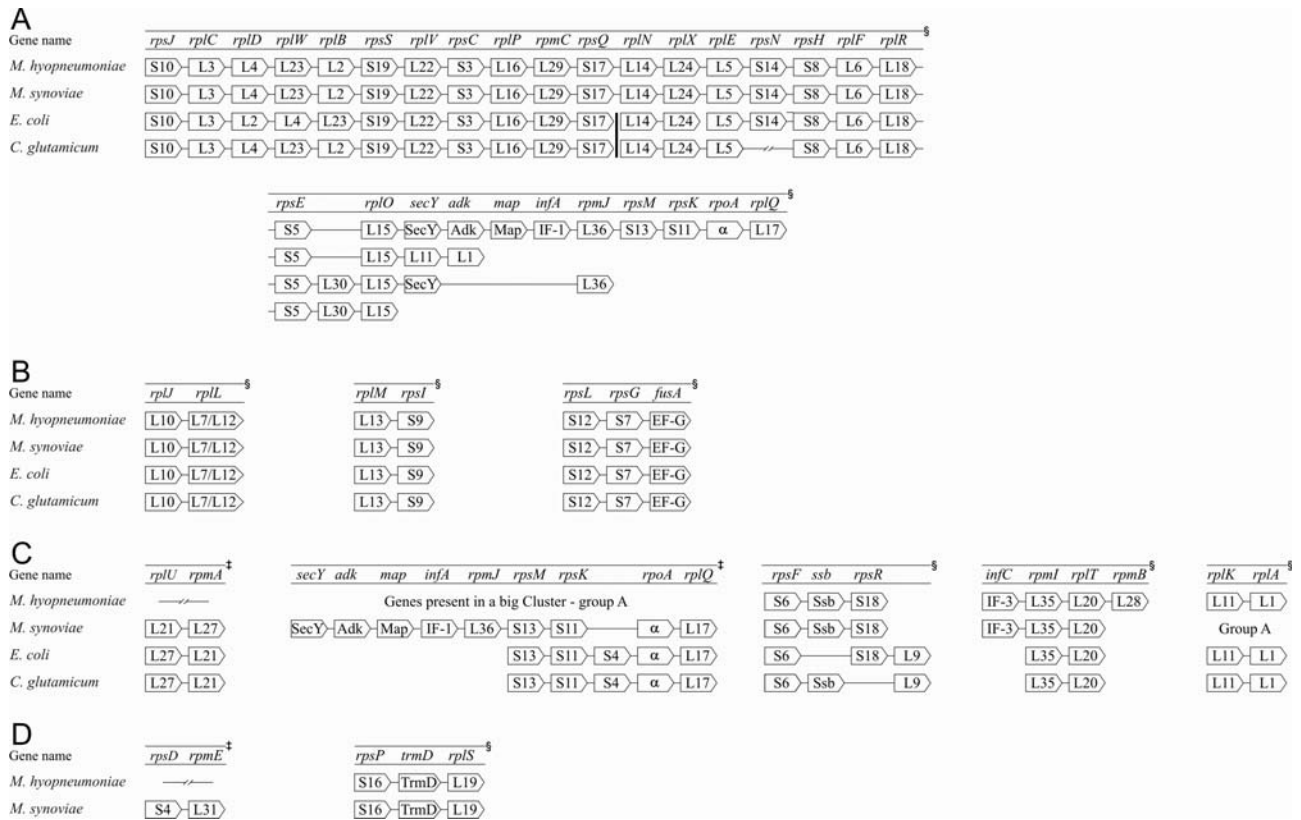


Figure 1 - Gene clusters of ribosomal proteins in *Mycoplasma synoviae*, *Mycoplasma hyopneumoniae*, *Escherichia coli* and *Corynebacterium glutamicum*. Arrows represent genes with their relative orientation in the genomes. Contiguous arrows represent adjacent genes, while interrupted lines indicate loss of proximity. The solid bar indicates the limit of the S10 and *spc* operons in *E. coli* and *C. glutamicum*. The names of the genes were obtained from *M. hyopneumoniae* (§) or from *M. synoviae* (§) (when the name was not defined for *M. hyopneumoniae*). (A) A big cluster showing differences between the four organisms; (B) Clusters with identical organization in the four organisms; (C) Another cluster showing differences between the organisms; (D) Clusters presenting particularities in *M. synoviae* and *M. hyopneumoniae*. Abbreviations used for gene names: SecY (preprotein translocase secY subunit), Adk (adenylate kinase), Map (methionyl aminopeptidase), IF-1 (translation initiation factor IF-1), α (DNA-directed RNA polymerase subunit alpha), EF-G (elongation factor EF-G), Ssb (single-stranded DNA-binding protein), IF-3 (translation initiation factor IF-3), TrmD (tRNA (guanine-N1)-methyltransferase). Data for *E. coli* and *C. glutamicum* were retrieved from NCBI's complete genome section and from Martín *et al.* (2003).

1982), and some have been implicated in the formation of bridges between the two subunits (S13p, S15p, S19p, L2p, L5p, L14p) (Yusupov *et al.*, 2001). Binding of ribosomes to mRNA involves the ribosomal proteins S1, S3, S4, S5, S9, S12 and S18, in addition to the 16S rRNA (Stern *et al.*, 1988). Proteins L2, L11, L15, L16, L18, L23 and L27, together with the 23S rRNA, are involved in the peptidyl transferase function of ribosomes (Voet and Voet, 1992). The four proteins L7/L12 form a protruding domain of the large subunit that participates in the GTPase activity of ribosomes (Uchiumi *et al.*, 2002). Other proteins, such as S7p, S9p, S12p, S13p, L1p and L5p, are in contact with the tRNA or surround the polypeptide exit channel (L22p, L24p and L29p) (Yusupov *et al.*, 2001).

Organization of gene clusters encoding ribosomal proteins

Most genes encoding ribosomal proteins are clustered forming operons. In the three sequenced genomes, we found 10 ribosomal protein gene clusters encoding 42 ribo-

somal proteins in *M. synoviae*, and 8 clusters encoding 39 ribosomal proteins in both *M. hyopneumoniae* strains, as shown in Figure 1. In the *E. coli* and *C. glutamicum* models (Martín *et al.*, 2003), there are 11 gene clusters encoding 41 and 42 ribosomal proteins, respectively. In *E. coli*, the S10 operon encodes 11 ribosomal proteins in the following order: S10, L3, L2, L4, L23, S19, L22, S3, L16, L29 and S17, and is located close to the *spc* operon that includes 12 genes which encode the proteins L14, L24, L5, S14, S8, L6, L18, S5, L30, L15, Sec Y and L36 (Cerretti *et al.*, 1983). These two operons correspond in organization to the big cluster in *M. hyopneumoniae* and *M. synoviae* with minor differences, as shown in Figure 1A. In *M. hyopneumoniae*, the large block of approximately 15 kb contains 29 genes, 24 of which encode ribosomal proteins. This block of genes also contains those encoding the SecY subunit of the preprotein translocase (*secY*), adenylate kinase (*adk*), methionine aminopeptidase (*map*), translation initiation factor IF-1 (*infA*), and the RNA polymerase subunit alpha (*rpoA*). In *M. synoviae*, there is a cluster of 22 genes encoding ribo-

somal proteins in a region of about 10 kb. The block of genes *secY-adk-map-infA-L36-S13-S11-rpoA-L17* is located in another region of the genome when compared to *M. hyopneumoniae* (Figure 1C). In addition, the L11 and L1 genes are not grouped in a separate cluster as in *M. hyopneumoniae*, *E. coli* and *C. glutamicum* (Figure 1C). The clusters “L10-L7/L2”, “L13-S9” and “S12-S7-EF-G” of *M. hyopneumoniae* and *M. synoviae* are organized as in *E. coli* and *C. glutamicum* (Figure 1B). Figures 1C and 1D show particularities of the analyzed mycoplasma ribosomal protein clusters compared to *E. coli* and *C. glutamicum*. For example, the “L21-L27” gene cluster is absent in *M. hyopneumoniae* and present in *E. coli* and *C. glutamicum* in inverted position, as compared to *M. synoviae* (Figure 1C). Cluster “S16-TrmD-L19” is identical in the three mycoplasmas, while cluster “S4-L31” is specific to *M. synoviae* (Figure 1D). Neither cluster “S16-TrmD-L19” nor cluster “S4-L31” are present in *E. coli* or *C. glutamicum*.

Organization and phylogenetic relationships among L33 ribosomal proteins

Comparing the two *M. hyopneumoniae* strains, the organization of the ribosomal genes was identical, except for the L33 gene, of which strain 7448 presented two ORFs (MHP0638 and MHP0658) in different locations, while strain J presented only one (MHJ0658) (Table 1). The extra ORF in strain 7448 encodes a predicted protein of 46 amino acid residues, while the conserved ORF encodes a protein with 50 amino acid residues.

The phylogenetic relationships of the L33 ribosomal proteins were visualized by grouping into two big clades, A and B (Figure 2). Some mycoplasmas (*M. pulmonis*, *M. pneumoniae* M129, *M. genitalium* G37 and MP12668) presented two L33 genes. When present in duplicates, the orthologues were clustered in different clades, suggesting interphylum horizontal transfer and a possible specialized function to those proteins.

Ribosomal RNAs

In the *M. synoviae* genome, the 16S rDNA is separated from the 23S rDNA by 259 bp, while in the *M. hyopneumoniae* strains the distance is about 490 bp (data not shown). Downstream of the 23S rDNA, there is another spacer region followed by the 5S rDNA gene. This region is located at a greater distance (about 100 kb) than usual from the 16S-23S cluster. In *M. pulmonis*, for example, the 5S gene is located 350 bp distant from the genes encoding 16S and 23S rRNAs (Chambaud *et al.*, 2001). Those data confirm the previous observation that these sets of genes are localized in different regions of the *M. hyopneumoniae* genome (Taschke *et al.*, 1986; Stemke *et al.*, 1994). All mycoplasmas presented intervening tRNA genes, which seems to be common to all Mollicutes, except the phytoplasmas (Chambaud *et al.*, 2001). In both *M. hyopneumoniae* strains only one set of 5S, 16S and 23S

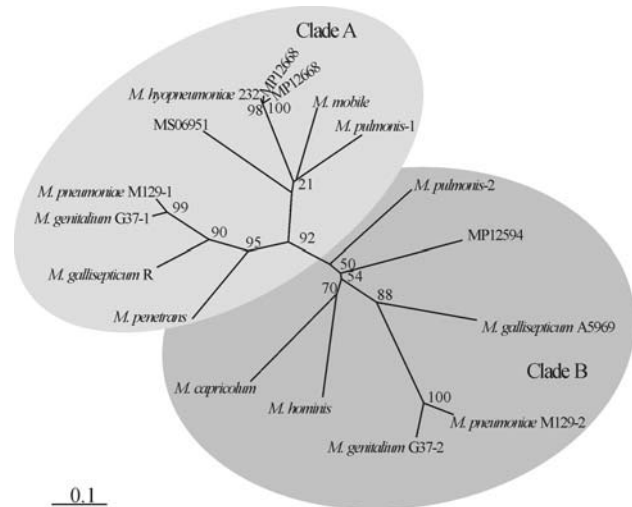


Figure 2 - Phylogenetic tree illustrating the relationships of L33 proteins. Sequences were aligned and subjected to phylogenetic analysis by using the minimum evolution (neighbor-joining) method. Numbers on branches indicate bootstrap values obtained for 100 replications. ORF identifications of *M. synoviae*, *M. hyopneumoniae* J, and *M. hyopneumoniae* 7448 are referred in Table 1, and the amino acid sequences are available at Mycoplasma databases. Other L33 protein sequences obtained were: *M. capricolum* (GenBank: Z33076 REGION: 279..440); *M. gallisepticum* A5969 (GenBank: L35043_REGION: 269..415); *M. gallisepticum* R (GenBank: AE016969_REGION: 9206..9367); *M. genitalium* G37-1 (GenBank: U39713.1:9938..10099); *M. genitalium* G37-2 (GenBank: U39684 L43967_REGION: 14657..14803); *M. hominis* (GenBank: AF443617_REGION: 2827..2976); *M. hyopneumoniae* 232 (GenBank: AE017332_REGION:856080..856232); *M. mobile* (GenBank: AE017308_REGION: 684469..684621); *M. penetrans* (GenBank: BA000026_REGION: 511349..511537); *M. pneumoniae* M129-1 (GenBank: AE000035 U00089_REGION: 3699..3860); *M. pneumoniae* M129-2 (GenBank: AE000010 U00089_REGION: 3699..3860); *M. pulmonis*-1 (GenBank: AL445563 REGION: 188281..188421); *M. pulmonis*-2 (GenBank: AL445564 REGION: 268039..268191).

rRNAs was identified. Two sets of 16S and 23S rRNA genes and three sets of 5S rRNA genes were identified in the *M. synoviae* genome.

Translation initiation, elongation and termination

The genes encoding initiation factors (IF-1, IF-2 and IF-3) are present in the genomes of *M. synoviae* and *M. hyopneumoniae* J and 7448. IF-1 is part of a cluster containing the genes which encode L36, S13, S11, *rpoA* and L17, among others (Figures 1A and 1C). In the two *M. hyopneumoniae* genomes, the gene encoding IF-2 is located between the genes coding for the ribosome-binding factor A (*rbfA*) and the N utilization substance protein A (*nusA*). In *M. synoviae*, the gene is located between the genes encoding adenine phosphoribosyltransferase (*apt*) and *nusA* (data not shown). The gene encoding IF-3 is part of a block of genes which encode the ribosomal proteins L35, L-20 and L28 in the genomes of both *M. hyopneumoniae* strains (Figure 1C). In *M. synoviae*, this gene is part of a block containing the genes which encode L35 and L20 (Figure 1C).

The elongation factors EF-Ts, EF-Tu, EF-G and EF-P are present in the genomes of *M. synoviae*, *M. hyopneumoniae* J, and *M. hyopneumoniae* 7448. As mentioned before, the gene encoding EF-G is part of the operon S12-S7-EF-G (Figure 1B). The gene encoding EF-Ts is located close to the gene encoding S2 in the genomes of both *M. hyopneumoniae* strains and of *M. synoviae* (data not shown).

The gene encoding the ribosome recycling factor (*frr*), which is responsible for the dissociation of the ribosomes from the mRNA after termination of translation, and is essential for bacterial growth (Janosi *et al.*, 1996), is also present in the genomes of *M. synoviae*, *M. hyopneumoniae* J, and *M. hyopneumoniae* 7448. Only one polypeptide release factor (*prfA*) was identified in both *M. hyopneumoniae* strains and in *M. synoviae*. This finding is consistent with the use of UAA and UAG as stop codons (Fraser *et al.*, 1995; Himmelreich *et al.*, 1996; Inagaki *et al.*, 1996). Similar to the situation in other mycoplasma genomes, the UGA codon encodes tryptophan instead of stop codon. As a consequence, the peptide-chain release factor 2 (RF2), which recognizes the stop codons UGA and UAA, has become obsolete and was deleted, as proved experimentally in *M. capricolum* (Inagaki *et al.*, 1993).

Phylogenetic relationships among aminoacyl-tRNA synthetases

Aminoacyl-tRNA synthetases catalyze the ligation of specific amino acids to their cognate tRNAs, which is the initial step in protein synthesis (Kim *et al.*, 1993; Park *et al.*, 2005). In the three sequenced genomes, *M. hyopneumoniae* strains J and 7448 and *M. synoviae*, nineteen aminoacyl-tRNA synthetases were identified. Of the 20 standard tRNA-synthetases, glutamyl-tRNA synthetase is the only one not detected in *M. genitalium* (Fraser *et al.*, 1995) and *M. pneumoniae* (Himmelreich *et al.*, 1996). In *Bacillus subtilis*, this problem is solved by charging the tRNA^{Gln} first with glutamate, which is subsequently converted to glutamine by an amidotransferase (Strauch *et al.*, 1988). It has been shown that Glu-tRNA^{Gln} amidotransferase is a heterotrimeric enzyme encoded by the genes *gatA*, *gatB*, and *gatC*, which are part of an operon in *B. subtilis* (Curnow *et al.*, 1997). In *M. hyopneumoniae* strain J, the genes *gatC* (MH12539), *gatA* (MH15039), and *gatB* (MH21623) are organized in a cluster. The same kind of organization is observed in *M. hyopneumoniae* strain 7448 (*gatC* - MP09881, *gatA* - MP18574, *gatB* - MP12574). The organization of those genes in *M. synoviae* follows the order *gatA* - MS05589, *gatB* - MS05595, *gatC* - MS10482.

In order to analyze the grouping of the *gat* protein subunits, a phylogenetic tree was constructed and visualized, as shown in Figure 3. The deduced amino acid sequences of the ORFs encoding *gatA*, *gatB* and *gatC* proteins of *M. synoviae*, *M. hyopneumoniae* J, *M. hyopneumoniae* 7448 and complete sequences of other

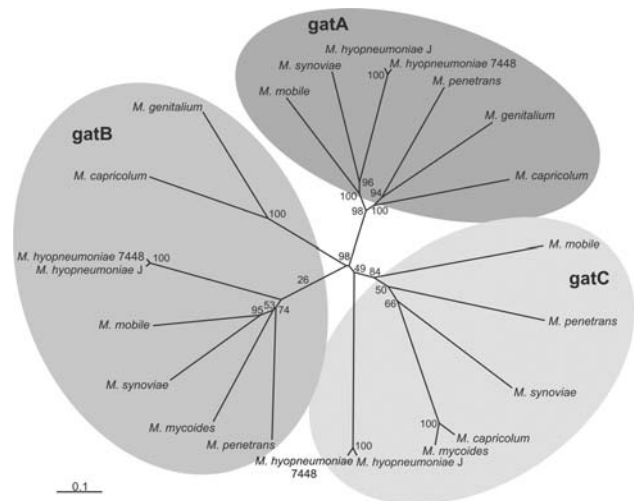


Figure 3 - Phylogenetic tree illustrating the relationships of *gatA*, *B* and *C* and related sequences. Phylogenetic analysis was based on the complete amino acid sequences of *gat* proteins. The tree was calculated by the neighbor-joining method implement in the program Clustal X, and drawn by using the TreeView program. The amino acid sequences are available at Mycoplasma databases. *Gat* protein sequences obtained from Mycoplasma databases were: *M. capricolum* (GenBank: YP_424670; YP_424122; YP_424671); *M. genitalium* (GenBank: AAC71317; AAC72482); *M. hyopneumoniae* J (GenBank: AAZ44118; AAZ44119; AAZ44117); *M. hyopneumoniae* 7448 (GenBank: AAZ53405; AAZ53406; AAZ53404); *M. mobile* (GenBank: AAT27863; AAT27862; AAT27864); *M. mycoides* (GenBank: CAE77379; CAE77381); *M. penetrans* (GenBank: BAC44001; BAC44002; BAC44000); *M. synoviae* (GenBank: AAZ43513.1; AAZ43512.1; AAZ43514).

mycoplasma proteins from databases were aligned. The bootstrap values (98%) among *gatA*, *gatB* and *gatC* indicate the high identity among the *gat* groups of the mycoplasmas. In Figure 3, separated clades comprising *gatA*, *gatB* and *gatC* can be observed. Only one *gat* protein subunit has been described for each mycoplasma. A higher identity was found between *gatA* (97%), *gatB* (94%), and *gatC* (96%) of *M. hyopneumoniae* 7448 and *M. hyopneumoniae* J (data not shown) when compared to other mycoplasmas and formed single groups inside the clades. This observation suggests a common ancestral.

Acknowledgments

This work was performed by the Brazilian National Genome Program (Southern Network for Genome Analysis and Brazilian National Genome Project Consortium) with funding provided by MCT/CNPq and SCT/FAPERGS (RS).

References

- Altschul SF, Madden TL, Schaffer AA, Zhang J, Zhang Z, Miller W and Lipman DJ (1997) Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. *Nucleic Acids Res* 25:3389-3402.
- Bencina D, Narat M, Dovc P, Drobnic-Valic M, Habe F and Kleven SH (1999) The characterization of *Mycoplasma*

- synoviae* EF-Tu protein and proteins involved in hemadherence and their N-terminal amino acid sequences. *FEMS Microbiol Lett* 173:85-94.
- Cerretti DP, Dean D, Davis GR, Bedwell DM and Nomura M (1983) The *spc* ribosomal protein operon of *Escherichia coli*: Sequence and cotranscription of the ribosomal protein genes and a protein export gene. *Nucleic Acids Res* 11:2599-2616.
- Chambaud I, Heilig R, Ferris S, Barbe V, Samson D, Galisson F, Moszer I, Dybvig K, Wroblewski H, Viari A, *et al.* (2001) The complete genome sequence of the murine respiratory pathogen *Mycoplasma pulmonis*. *Nucleic Acids Res* 29:2145-2153.
- Curnow AW, Hong K, Yuan R, Kim S, Martins O, Winkler W, Henkin TM and Soll D (1997) Glu-tRNAGln amidotransferase: A novel heterotrimeric enzyme required for correct decoding of glutamine codons during translation. *Proc Natl Acad Sci USA* 94:11819-11826.
- Fraser CM, Gocayne JD, White O, Adams MD, Clayton RA, Fleischmann RD, Bult CJ, Kerlavage AR, Sutton G, Kelley JM, *et al.* (1995) The minimal gene complement of *Mycoplasma genitalium*. *Science* 270:397-403.
- Held WA, Ballou B, Mizushima S and Nomura M (1974) Assembly mapping of 30 S ribosomal proteins from *Escherichia coli*. Further studies. *J Biol Chem* 249:3103-3111.
- Himmelreich R, Hilbert H, Plagens H, Pirkel E, Li BC and Herrmann R (1996) Complete sequence analysis of the genome of the bacterium *Mycoplasma pneumoniae*. *Nucleic Acids Res* 24:4420-4449.
- Inagaki Y, Bessho Y and Osawa S (1993) Lack of peptide-release activity responding to codon UGA in *Mycoplasma capricolum*. *Nucleic Acids Res* 21:1335-1338.
- Inagaki Y, Bessho Y, Hori H and Osawa S (1996) Cloning of the *Mycoplasma capricolum* gene encoding peptide-chain release factor. *Gene* 169:101-103.
- Janosi L, Hara H, Zhang S and Kaji A (1996) Ribosome recycling by ribosome recycling factor (RRF) - an important but overlooked step of protein biosynthesis. *Adv Biophys* 32:121-201.
- Jordan FT (1981) *Mycoplasma*-induced arthritis in poultry. *Isr J Med Sci* 17:622-625.
- Kim S, Landro JA, Gale AJ and Schimmel P (1993) C-terminal peptide appendix in a class I tRNA synthetase needed for acceptor-helix contacts and microhelix aminoacylation. *Biochemistry* 32:13026-13031.
- Kobisch M (2000) *Mycoplasma* diseases in pigs - Old diseases still causing trouble. In: *Proceedings 16th International Pig Veterinary Society Congress*: 434-438, Melbourne, Australia.
- Kobisch M and Friis NF (1996) Swine mycoplasmoses. *Révue Scientifique et Technique de l'Office International de Epizooties* 15:1569-1605.
- Lafontaine DL and Tollervy D (2001) The function and synthesis of ribosomes. *Nat Rev Mol Cell Biol* 2:514-520.
- Lecompte O, Ripp R, Thierry JC, Moras D and Poch O (2002) Comparative analysis of ribosomal proteins in complete genomes: An example of reductive evolution at the domain scale. *Nucleic Acids Res* 30:5382-5390.
- Maniloff J (1996) The minimal gene genome: "On being the right size". *Proc Natl Acad Sci USA* 93:10004-10006.
- Martín JF, Barreiro C, Gonzalez-Lavado E and Barriuso M (2003) Ribosomal RNA and ribosomal proteins in corynebacteria. *J Biotechnol* 104:41-53.
- Park SG, Ewalt KL and Kim S (2005) Functional expansion of aminoacyl-tRNA synthetases and their interacting factors: New perspectives on housekeepers. *Trends Biochem Sci* 30:569-574.
- Razin S (1992) *Mycoplasma* taxonomy and ecology. In: Maniloff J, McElhane RN, Finch LR and Baseman JB (eds) *Mycoplasmas: Molecular Biology and Pathogenesis*. Am Soc Microbiol, Washington, DC, pp 3-22.
- Rohl R and Nierhaus KH (1982) Assembly map of the large subunit (50S) of *Escherichia coli* ribosomes. *Proc Natl Acad Sci USA* 79:729-733.
- Saitou N and Nei M (1987) The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406-425.
- Stemke GW, Huang Y, Laigret F and Bove JM (1994) Cloning the ribosomal RNA operons of *Mycoplasma flocculare* and comparison with those of *Mycoplasma hyopneumoniae*. *Microbiology* 140:857-860.
- Stern S, Powers T, Changchien LM and Noller HF (1988) Interaction of ribosomal proteins S5, S6, S11, S12, S18 and S21 with 16 S rRNA. *J Mol Biol* 201:683-695.
- Strauch MA, Zalkin H and Aronson AI (1988) Characterization of the glutamyl-tRNA(Gln)-to-glutaminy-tRNA(Gln) amidotransferase reaction of *Bacillus subtilis*. *J Bacteriol* 170:916-920.
- Taschke C, Klinkert MQ, Wolters J and Herrmann R (1986) Organization of the ribosomal RNA genes in *Mycoplasma hyopneumoniae*: The 5S rRNA gene is separated from the 16S and 23S rRNA genes. *Mol Gen Genet* 205:428-433.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F and Higgins DG (1997) The CLUSTAL X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* 25:4876-4882.
- Uchiumi T, Honma S, Nomura T, Dabbs ER and Hachimori A (2002) Translation elongation by a hybrid ribosome in which proteins at the GTPase center of the *Escherichia coli* ribosome are replaced with rat counterparts. *J Biol Chem* 277:3857-3862.
- Vasconcelos AT, Ferreira HB, Bizarro CV, Bonatto SL, Carvalho MO, Pinto PM, Almeida DF, Almeida LG, Almeida R, Alves-Filho L, *et al.* (2005) Swine and poultry pathogens: The complete genome sequences of two strains of *Mycoplasma hyopneumoniae* and a strain of *Mycoplasma synoviae*. *J Bacteriol* 187:5568-5577.
- Voet D and Voet JG (1992) Ribosomas. In: *Bioquímica*. Ediciones Omega S.A., Barcelona, pp 979-982.
- Yusupov MM, Yusupova GZ, Baucom A, Lieberman K, Earnest TN, Cate JH and Noller HF (2001) Crystal structure of the ribosome at 5.5 Å resolution. *Science* 292:883-896.

Internet Resources

- M. synoviae* complete genome database, <http://www.brgene.lncc.br/finalMS/>.
- M. hyopneumoniae* strain J and *M. hyopneumoniae* strain 7448 complete genome databases, <http://www.genesul.lncc.br>.
- BLAST tools, <http://www.ncbi.nlm.nih.gov/BLAST/>.

Associate Editor: Arnaldo Zaha