

The Forces that Drive Low Complexity Region Evolution

Submitted by:

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Abstract

Low complexity regions (LCR) are areas within genomes that are of unknown evolutionary history despite being present in all species. Among different species, they are known to be variable in length and conservation, but their variability within species (e.g., among strains) is unknown. Much research has been done on LCRs in Eukaryotes, but prokaryotes have been mostly overlooked despite the fact that they constitute the basis of every ecosystem on Earth and also include many human pathogens. Therefore, understanding the way their genomes evolve is a fundamental step to predict future adaptations, whether in response to environmental changes or to new drugs to combat diseases. This study aims to investigate the evolutionary processes of LCRs in bacteria strains by analyzing changes in their length, composition, and frequency within their genomes. We focus on strains rather than species because this level provides information on the evolution of these poorly known regions at short timescales, thus filling a gap in current knowledge that previously has only focused on longer (species-level) evolutionary timescales. Using a fully computational approach, we analyzed hundreds of proteomes across multiple Bacteria classes and determined the relative frequency, amino acid composition, and length of LCRs. Our data show that the overall composition of LCRs compared to the proteome favors higher levels of Leucine, Lysine, Alanine, and Glycine. This could suggest a potential role of selection in the evolution of these regions. In terms of LCR length, we observe that there is a relatively small variation among strains but there are numerous outliers present and further research is needed to determine why they do not follow the pattern of their species. It is expected that the variations have to do with habitats and pathogenicity.

Introduction

LCRs are areas within genomes that are of unknown evolutionary history despite being present in all species. Among different species, they are known to be variable in length and conservation, but their variability within species (e.g., among strains) has not been investigated. Our research focuses on the evolutionary processes of LCRs in bacteria strains by analyzing changes in their length, composition, and frequency within their genomes. With this new information, we will be able to decipher the evolution of these poorly known regions at short timescales, thus filling a gap in current knowledge that previously has only focused on longer (species-level) evolutionary timescales. The results from the research will give a better insight into the roles LCRs play in a genomic sequence, which can include adaptations to new conditions or neutral evolution due to random changes.

The scientific community has previously dismissed these regions as junk DNA, but this may not be an accurate definition for at least some of these regions (Gemayel, Cho, Boeynaems, & Verstrepen, 2012). LCR expansion is due to replication slippage and unequal crossover recombination (Depristo, Zilversmit, & Hartl, 2006), which produces genetic variability in the genomes that is most likely to be negative or neutral for the fitness of the strain, but can also be beneficial based on the function of the gene that hosts the LCRs (e.g., antigenic variability in viruses) (Velasco et al., 2013). LCRs vary substantially among species and are more common in Eukaryotes. While they may be more common in Eukaryotes, they are still present in prokaryotes, and this research aims to achieve a better understanding of their importance in the evolution of species. Research done with the yeast *Saccharomyces cerevisiae* has shown that LCRs may be involved in flexible binding associations with specific functions and may be important in determining biological roles (Coletta, et al., 2010). Coletta et al. also proposes that

LCRs are a common source of genetic variation to help generate different surface antigens to adapt to fast evolving environments. However, all these inferences are based on eukaryotic model organisms. The goal of our research is to bridge the gap in knowledge of the role they play in a prokaryotic genomic sequence based on techniques developed in eukaryotes to evaluate their evolutionary history (Troyanskaya, Arbell, Koren, Landau, & Bolshoy, 2002).

Specifically, this thesis project will test if prokaryotic LCRs follow the same patterns as Eukaryotic LCRs and, more deeply, if they evolve by different patterns across and within species. The research will provide an insight into regions for which little knowledge exists (Yadav, et al., 2015). This information will provide a better understanding on how species evolve over time and how LCRs help to bring about change. It could also show that LCRs do not play any specific functional roles in genomic sequences, but rather exist as a neutral emergent property of genomes. To achieve this we will be looking at several different components of LCRs such as their frequency, composition, and length to obtain a better understanding of their existence.

Methods

This project is fully computational using proteomes obtained from NCBI for 1266 strains of Bacteria. These proteomes were ran through SEG with parameters: 12 length, threshold complexity $K_1=1.9$, threshold complexity $K_2=2.2$. (Wootton and Federer 1993), which reads genetic sequences and, based on a set of specified parameters, identified the number and composition of LCRs in the genomic sequences. Using in-house scripts we then obtained information on the types of amino acids composing each LCR and their lengths relative to the total length of the protein they are embedded in. We analyzed the collected data through basic

statistical metrics (averages and standard deviations, box plots) and comparisons of trends across and within species. After identifying outliers, we then analyzed these by comparing their lifestyle (e.g., pathogenic vs. free-living strains) and phylogenetic history to that of the other lineages.

Results

Our first analysis focused on the length of LCRs to determine if there is a difference among strains and among genera. We found that LCRs are fairly consistent in length being 16 amino acids long with a standard deviation of 1.9. See table. This result shows that the length of the LCR is unrelated to the length of the proteins that the LCRs are embedded in, suggesting that these regions might be under purifying selection to prevent them from growing.

Our second analysis was running the proteome files through a script in Perl to calculate what the percentage of each amino acid in the proteome is. Next, we found all of the low complexity regions in the proteome and compared the amino acid make-up of the whole proteome vs. that of the LCRs. We found was that, in general, the LCR composition is fairly consistent with the composition of the whole proteome with a few exceptions. Alanine, Glycine, Leucine, Isoleucine are the common amino acids that do not follow the general trend. In fact, they tend to be significantly favored in the LCRs vs. the whole proteome (Fig. 1). This is interesting because they all deal with the biosynthesis of proteins and are α - amino acids, suggesting a compositional preference that might be driven by selection.

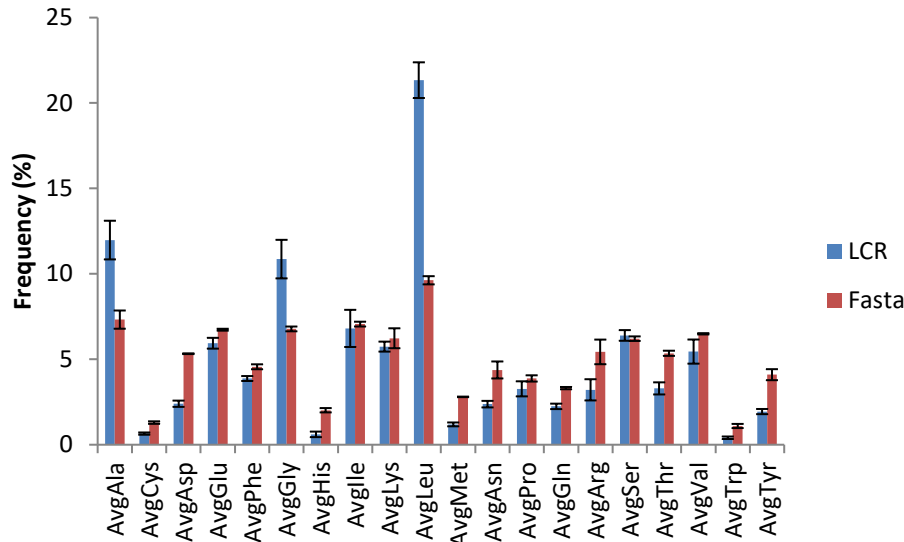


Figure 1 Average amino acid composition of LCRs and proteomes in the order Bacteroidales. Blue shows the frequency of each of the 20 amino acids in the low complexity regions. Red shows the frequency of the 20 amino acids in the whole proteome. The error bars represent the standard deviation. Similar figures for all other species analyzed are not shown.

When we ran our test for frequency we found that the frequency varied amongst the different genera, but were consistent between the strains of each individual species with a few outliers. The total average frequency of LCRs amongst all the strains is 18% with a standard deviation of 8%. (Table. 1) In comparing standard deviations of strains of the same species with the total number of proteins we found several strains that cause their standard deviations to be much higher. (Figure. 2) The outlier strains are: *Candidatus Portiera aleyrodidarum* BTBHRs, *Carsonella ruddii* CE isolate Thao, *Wigglesworthia glossinidia* endosymb *Glossina morsitans morsitans* Yale, *Buchnera aphidicola* BCc and *Desulfovibrio vulgaris*.

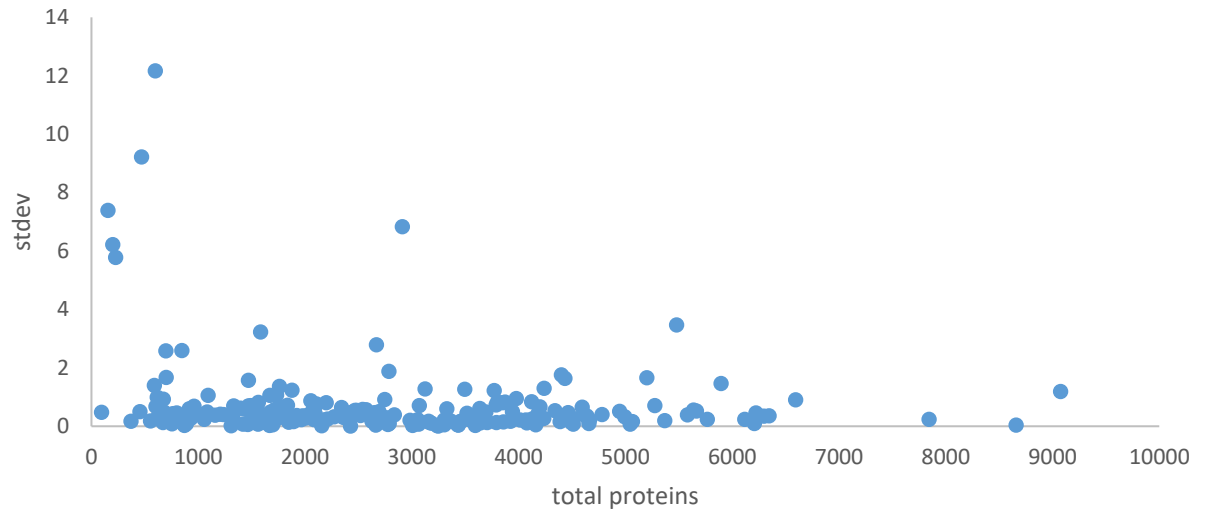


Figure 2 Correlation of the variation among LCR frequencies per species with total number of proteins. The variation of LCR frequencies is shown by its standard deviation (stdev).

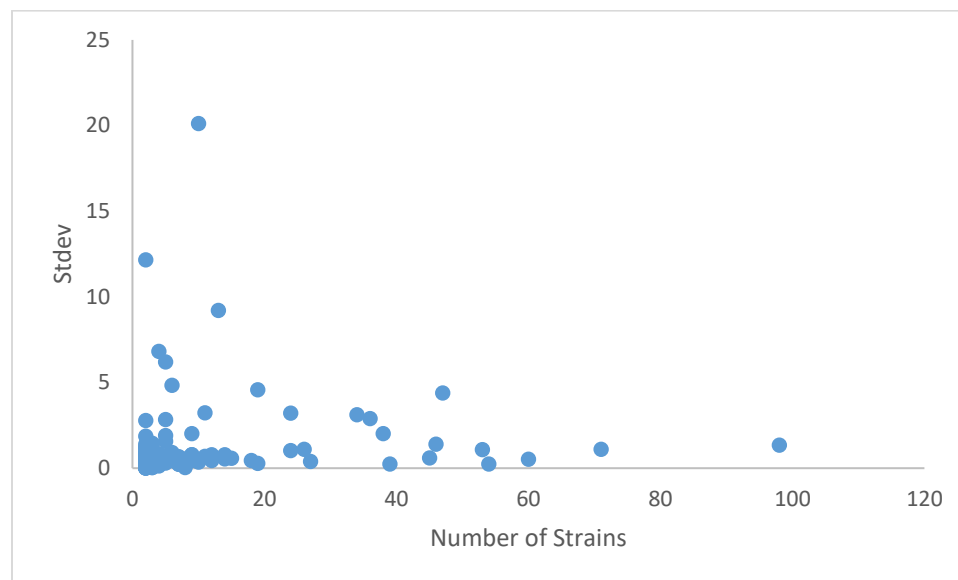


Figure 3 Correlation of the variation among LCR frequencies per Genus with total number of strains in each Genus. The variation of the LCR frequencies is shown by its standard deviation. (stdev)

Discussion

Not much is understood about low complexity regions and the role they play within genomes. For example, one of the biggest debates is about their role as neutral or selected regions in genome evolution and how these two viewpoints can be supported by evidence regarding the composition, length, and frequency of these regions. To investigate this question, we worked with hundreds of bacterial lineages to determine general evolutionary patterns of LCRs.

We found multiple lines of evidence that support a role of selection in the evolution of LCRs. First, our results from testing frequencies of LCRs show that, at the species level, frequencies remain generally constant but vary at the levels of genus and order (Fig 2 and 3). An exception to this trend is the genus *Salmonella*. The species analyzed are all very closely related and the LCRs are more conserved as compared to other species. This could be an example of sampling bias where most of the species of *Salmonella* are examined in the US and, therefore, expected share high genetic similarity. Another species that needs to be more closely observed is a *Candidatus* genus in the group Bacteroidetes. Taxonomically, it is still unsure exactly where this species fits in and its LCR pattern is vastly different from the other species taxonomically close to it. This suggests that this species might have been classified incorrectly. These results are significant because they show that unique patterns in genome complexity could be used as additional evidence for taxonomic classification and geographic distribution analyses.

We also had unique findings when viewing the composition of the LCRs. When observing the amino acids that compose the LCRs we found that there were no aromatic rings involved. All of the favored amino acids in the prokaryotes analyzed are nonpolar and are not electrically charged (Fig. 1). This is different from the amino acids favored in Eukaryotes which

tend to favor polar amino acids such as Asparagine and Glutamine. It is also interesting that the amino acids that make up most of the LCRs in prokaryotes are not species dependent as they are in Eukaryotes, meaning that the composition of LCRs in eukaryotes is highly dependent on the species analyzed. (Zilversmit et al., 2010) The different chemical structure of the LCR amino acids in prokaryotes and eukaryotes allow us to hypothesize a possible difference in their cellular location and function. Polar amino acids, such as those in Eukaryotes, are often used in transmembrane proteins to allow communication between the inside and the outside of the cell or organelle. On the other hand, the non-polar amino acids preferred by prokaryotes are more likely used by cytoplasm proteins, suggesting that these regions might be preferentially involved in intra-cellular signaling and functions.

Finally, in regards to length, we found that on average the LCR length in prokaryotes is twice as long as that in eukaryotes, being approximately 16 amino acids (Battistuzzi et al., 2016; Huntley & Clark, 2007). Although this trend is shared by most genera, there are several species that do not follow their genus trends but instead have average LCR lengths either much higher or lower than the other species in their genus. Although further research is needed to explain this pattern, a few hypotheses can be formulated. For example, small genomes have extreme outliers, with LCRs that are much longer than the average. This is also consistent in what was observed with the LCR frequency (higher frequency in small genomes) and could be explained by the fact that variations among small genomes will be more impactful in a relative sense than they would be in larger genomes. Another hypothesis is that unique trends in both length and frequency of LCRs could be driven by geographic separation of species within the same genus, suggesting that prokaryotes genome evolution is influenced by their ecology more than previously thought.

Conclusion

Through a comprehensive analysis of LCR data we are able to conclude some broad trends within prokaryotes with further research being needed into specific outliers. The formation of LCRs does not seem to be random, but rather preferentially driven by selective pressures. One example of this is when we look at *Desulfovibrio vulgaris Hildenborough* vs. *Desulfovibrio vulgaris Miyazaki*. The frequency of the LCRs varies substantially between the two strains and one possible explanation could be the different selective pressures present in different geographic regions. Hildenborough is located in England while Miyazaki is located in Japan, which are two drastically different areas and can explain why there is such a difference in frequency of the LCRs in these two closely related strains. Another observation that we made in regards to frequency is that at the strain level frequencies are similar from one strain to another but start to have a wider variation as you move up the taxonomic scale to the levels of genus and order. This means that LCRs are not changing as much at the strain level but have a more gradual shift over evolutionary times. In regards to the five outlier strains for LCR frequencies we suspect that the first four strains are outliers due to their small proteome sizes of < 600 proteins. With small proteome sizes slight variations in the number of LCRs has a significant impact on the overall frequency. *Desulfovibrio Vulgaris* however, has a longer proteome of 2,910 proteins and may signal that a bigger factor is taking effect on its frequency of LCRs. *Desulfovibrio Vulgaris* is a sulfate reducer which could be providing selective pressures in increasing the frequency. The other outlier species are all gram-negative bacteria with most being endosymbionts of insects.

Since some amino acids are more favored in LCRs than in the whole proteome, it is also possible to hypothesize a role of selection in their evolution. Indeed, if they were evolving

neutrally, they would be expected to follow the composition of the proteome. Since they are different, it means that preferentially they use only some of the available amino acids which means a selective pressure must be acting to choose the amino acids necessary.

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Appendix**Table 1** Strain-specific frequencies of LCRs

Name	Freq(%)
Acidithiobacillus.ferrooxidans.ATCC.23270_243159	20.39
Acidithiobacillus.ferrooxidans.ATCC.53993_380394	21.16
Aeromonas.hydrophila.ML09119_1288394	22.37
Aeromonas.hydrophila.subsp..hydrophila.ATCC.7966_380703	23.06
Alteromonas.macleodii.AltDE1_1004786	11.04
Alteromonas.macleodii.ATCC.27126_529120	11.66
Alteromonas.macleodii.str..Aegean.Sea.MED64_1300254	11.65
Alteromonas.macleodii.str..Balearic.Sea.AD45_1004787	11.91
Alteromonas.macleodii.str..Black.Sea.11_1004785	11.63
Alteromonas.macleodii.str..Deep.ecotype_314275	10.85
Alteromonas.macleodii.str..English.Channel.615_1300253	10.56
Alteromonas.macleodii.str..English.Channel.673_1004788	11.85
Alteromonas.macleodii.str..Ionian.Sea.U7_1300256	11.15
Alteromonas.macleodii.str..Ionian.Sea.U8_1300257	10.88
Alteromonas.macleodii.str..Ionian.Sea.UM4b_1300259	11.10
Alteromonas.macleodii.str..Ionian.Sea.UM7_1300258	11.00
Idiomarina.loihiensis.GSL.199_1321370	13.07
Idiomarina.loihiensis.L2TR_283942	13.08
Marinobacter.aquaeolei.VT8_351348	16.20
Marinobacter.hydrocarbonoclasticus.ATCC.49840_1163748	17.06
Shewanella.baltica.BA175_693974	14.52
Shewanella.baltica.OS117_693970	14.07
Shewanella.baltica.OS155_325240	14.16
Shewanella.baltica.OS185_402882	14.29
Shewanella.baltica.OS195_399599	13.85
Shewanella.baltica.OS223_407976	14.26
Shewanella.baltica.OS678_693973	14.10
Shewanella.putrefaciens.200_399804	12.76
Shewanella.putrefaciens.CN32_319224	13.07
Buchnera.aphidicola.BCc_372461	50.62
Buchnera.aphidicola.Cinara.tujafilina_261317	25.46
Buchnera.aphidicola.str..5A.Acyrtosiphon.pisum_563178	18.32
Buchnera.aphidicola.str..Ak.Acyrtosiphon.kondoi_1005090	20.27

Buchnera.aphidicola.str..APS.Acyrtosiphon.pisum_107806	18.30
Buchnera.aphidicola.str..Bp.Baizongia.pistaciae_224915	16.84
Buchnera.aphidicola.str..JF98.Acyrtosiphon.pisum_713600	15.80
Buchnera.aphidicola.str..JF99.Acyrtosiphon.pisum_713601	18.00
Buchnera.aphidicola.str..LL01.Acyrtosiphon.pisum_713603	16.97
Buchnera.aphidicola.str..Sg.Schizaphis.graminum_198804	24.65
Buchnera.aphidicola.str..TLW03.Acyrtosiphon.pisum_713602	16.56
Buchnera.aphidicola.str..Tuc7.Acyrtosiphon.pisum_561501	18.00
Buchnera.aphidicola.str..Ua.Uroleucon.ambrosiae_1005057	22.95
Candidatus.Moranella.endobia.PCIT_903503	12.43
Candidatus.Moranella.endobia.PCVAL_1234603	12.67
Cronobacter.sakazakii.ATCC.BAA894_290339	17.07
Cronobacter.sakazakii.ES15_1138308	17.41
Cronobacter.sakazakii.SP291_956149	16.44
Dickeya.dadantii.3937_198628	17.90
Dickeya.dadantii.Ech586_590409	16.43
Dickeya.dadantii.Ech703_579405	17.16
Edwardsiella.tarda.C07087_1288122	23.48
Edwardsiella.tarda.EIB202_498217	23.69
Edwardsiella.tarda.FL660_718251	23.89
Enterobacter.aerogenes.EA1509E_935296	16.28
Enterobacter.aerogenes.KCTC.2190_1028307	15.91
Enterobacter.cloacae.EcWSU1_1045856	14.60
Enterobacter.cloacae.subsp..cloacae.ATCC.13047_716541	13.99
Enterobacter.cloacae.subsp..cloacae.ENHKU01_1211025	14.50
Enterobacter.cloacae.subsp..dissolvens.SDM_1104326	14.42
Erwinia.amylovora.ATCC.49946_716540	18.08
Erwinia.amylovora.CFBP1430_665029	18.05
Escherichia.coli.042_216592	13.56
Escherichia.coli.536_362663	13.28
Escherichia.coli.55989_585055	13.60
Escherichia.coli.ABU.83972_655817	13.57
Escherichia.coli.APEC.O1_405955	13.04
Escherichia.coli.APEC.O78_1274814	13.65
Escherichia.coli.ATCC.8739_481805	14.03
Escherichia.coli.B.str..REL606_413997	13.88
Escherichia.coli.BL21DE3_469008	13.92
Escherichia.coli.BL21GoldDE3pLysS.AG_866768	13.89

Escherichia.coli.BW2952_595496	14.01
Escherichia.coli.CFT073_199310	13.44
Escherichia.coli.DH1_536056	13.74
Escherichia.coli.E24377A_331111	13.45
Escherichia.coli.ETEC.H10407_316401	13.31
Escherichia.coli.HS_331112	13.80
Escherichia.coli.IA1_585034	13.71
Escherichia.coli.IA139_585057	12.88
Escherichia.coli.IHE3034_714962	13.63
Escherichia.coli.KO11FL_595495	13.74
Escherichia.coli.LF82_591946	13.65
Escherichia.coli.LY180_1335916	13.85
Escherichia.coli.NA114_1033813	13.81
Escherichia.coli.O103H2.str..12009_585395	13.28
Escherichia.coli.O104H4.str..2009EL2050_1134782	13.52
Escherichia.coli.O104H4.str..2009EL2071_1133853	13.64
Escherichia.coli.O104H4.str..2011C3493_1133852	13.70
Escherichia.coli.O111H.str..11128_585396	13.32
Escherichia.coli.O127H6.str..E234869_574521	13.59
Escherichia.coli.O157H7.str..EC4115_444450	13.59
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Escherichia.coli.SE15_431946	13.55
Escherichia.coli.SMS35_439855	13.77
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Escherichia.coli.str..clone.D.i2_885276	13.82
Escherichia.coli.str..K12.substr..DH10B_316385	13.97
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Salmonella.enterica.subsp..enterica.serovar.Heidelberg.str..CFSAN002069_1271864	15.18
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Salmonella.enterica.subsp..enterica.serovar.Javiana.str..CFSAN001992_1267753	14.45
Salmonella.enterica.subsp..enterica.serovar.Newport.str..SL254_423368	14.91
Salmonella.enterica.subsp..enterica.serovar.Newport.str..USMARCS3124.1_877468	14.65
Salmonella.enterica.subsp..enterica.serovar.Paratyphi.A.str..AKU.12601_554290	14.82
Salmonella.enterica.subsp..enterica.serovar.Paratyphi.A.str..ATCC.9150_295319	14.79
Salmonella.enterica.subsp..enterica.serovar.Paratyphi.B.str..SPB7_1016998	14.54
Salmonella.enterica.subsp..enterica.serovar.Paratyphi.C.strain.RKS4594_476213	14.36
Salmonella.enterica.subsp..enterica.serovar.Pullorum.str..S06004_1298917	14.71
Salmonella.enterica.subsp..enterica.serovar.Schwarzengrund.str..CVM19633_439843	14.58
Salmonella.enterica.subsp..enterica.serovar.Typhi.str..CT18_220341	14.16
Salmonella.enterica.subsp..enterica.serovar.Typhi.str..Pstx12_1132507	14.27
Salmonella.enterica.subsp..enterica.serovar.Typhi.str..Ty21a_527001	14.46
Salmonella.enterica.subsp..enterica.serovar.Typhi.str..Ty2_209261	14.57
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..14028S_588858	14.42
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..798_1008297	14.41
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..D23580_568708	14.34
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..LT2_99287	14.62
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..SL1344_216597	14.21
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..ST474_909946	14.40
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..T000240_718274	14.44
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..U288_1171376	14.64
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.str..UK1_990282	14.66
Salmonella.enterica.subsp..enterica.serovar.Typhimurium.var..5.str..CFSAN001921_1271862	14.62
Serratia.marcescens.FGI94_1249634	19.88
Serratia.marcescens.WW4_435998	20.83
Serratia.plymuthica.4Rx13_682634	17.57
Serratia.plymuthica.AS9_768492	17.82
Serratia.plymuthica.S13_1348660	17.36
Shigella.boydii.CDC.308394_344609	13.57
Shigella.boydii.Sb227_300268	13.65
Shigella.flexneri.2002017_591020	12.43
Shigella.flexneri.2a.str..2457T_198215	12.89
Shigella.flexneri.2a.str..301_198214	12.35
Shigella.flexneri.5.str..8401_373384	12.69

Shigella.sonnei.53G_216599	13.61
Shigella.sonnei.Ss046_300269	13.43
Wigglesworthia.glossinidia.endosymb.Glossina.morsitans.morsitans.Yale_114251 1	16.02
Wigglesworthia.glossinidia.endosymbiont.of.Glossina.brevipalpis_36870	33.22
Yersinia.enterocolitica.subsp..enterocolitica.8081_393305	14.90
Yersinia.enterocolitica.subsp..paleartica.105.5Rr_994476	15.33
Yersinia.enterocolitica.subsp..paleartica.Y11_930944	14.96
Yersinia.pestis.A1122_1035377	15.53
Yersinia.pestis.Angola_349746	15.21
Yersinia.pestis.Antiqua_360102	15.42
Yersinia.pestis.biovar.Medievalis.str..Harbin.35_547048	15.00
Yersinia.pestis.biovar.Microtus.str..91001_229193	15.77
Yersinia.pestis.CO92_214092	15.71
Yersinia.pestis.D106004_637382	15.18
Yersinia.pestis.D182038_637385	15.15
Yersinia.pestis.KIM10_187410	15.55
Yersinia.pestis.Nepal516_377628	15.64
Yersinia.pestis.Pestoides.F_386656	15.59
Yersinia.pestis.Z176003_637386	15.54
Yersinia.pseudotuberculosis.IP.31758_349747	15.67
Yersinia.pseudotuberculosis.IP.32953_273123	15.79
Yersinia.pseudotuberculosis.PB1_502801	15.63
Yersinia.pseudotuberculosis.YPIII_502800	15.50
Coxiella.burnetii.CbuG.Q212_434923	13.48
Coxiella.burnetii.CbuK.Q154_434924	13.07
Coxiella.burnetii.Dugway.5J108111_434922	14.22
Coxiella.burnetii.RSA.331_360115	13.89
Coxiella.burnetii.RSA.493_227377	14.20
Legionella.pneumophila.230099.Alcoy_423212	10.26
Legionella.pneumophila.str..Corby_400673	10.08
Legionella.pneumophila.str..Lens_297245	10.48
Legionella.pneumophila.str..Paris_297246	10.40
Legionella.pneumophila.subsp..pneumophila.ATCC.43290_933093	9.65
Legionella.pneumophila.subsp..pneumophila.str..Philadelphia.1_272624	10.03
Legionella.pneumophila.subsp..pneumophila.str..Thunder.Bay_1199191	9.87
Legionella.pneumophila.subsp..pneumophila_91891	10.44
Candidatus.Carsonella.ruddii.CE.isolate.Thao2000_1202536	71.43

Candidatus.Carsonella.ruddii.CS.isolate.Thao2000_1202537	70.32
Candidatus.Carsonella.ruddii.DC_667013	54.82
Candidatus.Carsonella.ruddii.HC.isolate.Thao2000_1202538	74.84
Candidatus.Carsonella.ruddii.HT.isolate.Thao2000_1202539	68.49
Candidatus.Carsonella.ruddii.PC.isolate.NHV_1202540	59.73
Candidatus.Carsonella.ruddii.PV_387662	60.40
Candidatus.Portiera.aleyrodidarum.BTBHRs_1206109	22.83
Candidatus.Portiera.aleyrodidarum.BTQVLC_1239881	23.29
Candidatus.Portiera.aleyrodidarum.TV_1297582	33.06
Actinobacillus.pleuropneumoniae.serovar.3.str..JL03_434271	12.13
Actinobacillus.pleuropneumoniae.serovar.5b.str..L20_416269	11.87
Actinobacillus.pleuropneumoniae.serovar.7.str..AP76_537457	11.84
Aggregatibacter.actinomycetemcomitans.ANH9381_754507	10.98
Aggregatibacter.actinomycetemcomitans.D11S1_668336	11.01
Aggregatibacter.actinomycetemcomitans.D7S1_694569	11.94
Haemophilus.influenzae.10810_862964	10.49
Haemophilus.influenzae.86028NP_281310	10.59
Haemophilus.influenzae.F3031_866630	10.05
Haemophilus.influenzae.F3047_935897	10.14
Haemophilus.influenzae.KR494_1334187	11.10
Haemophilus.influenzae.PittEE_374930	10.31
Haemophilus.influenzae.PittGG_374931	9.36
Haemophilus.influenzae.R2846_262727	10.70
Haemophilus.influenzae.R2866_262728	10.86
Haemophilus.influenzae.Rd.KW20_71421	9.92
Haemophilus.parasuis.SH0165_557723	10.25
Haemophilus.parasuis.ZJ0906_1322346	10.95
Haemophilus.somnus.129PT_205914	11.87
Haemophilus.somnus.2336_228400	11.94
Mannheimia.haemolytica.D153_1261126	11.34
Mannheimia.haemolytica.D171_1311759	11.63
Mannheimia.haemolytica.D174_1311760	11.53
Mannheimia.haemolytica.M42548_1316932	11.29
Mannheimia.haemolytica.USDAARSUSMARC183_1249531	10.91
Mannheimia.haemolytica.USDAARSUSMARC185_1249526	11.07
Mannheimia.haemolytica.USMARC.2286_1366053	11.21
Pasteurella.multocida.36950_1075089	12.76
Pasteurella.multocida.subsp..multocida.str..3480_584721	12.79

Pasteurella.multocida.subsp..multocida.str..HN06_1132496	12.72
Pasteurella.multocida.subsp..multocida.str..Pm70_272843	13.21
Acinetobacter.baumannii.16562_696749	12.46
Acinetobacter.baumannii.AB0057_480119	11.79
Acinetobacter.baumannii.AB3070294_557600	12.10
Acinetobacter.baumannii.ACICU_405416	12.03
Acinetobacter.baumannii.ATCC.17978_400667	10.04
Acinetobacter.baumannii.AYE_509173	11.99
Acinetobacter.baumannii.BJAB07104_1096995	12.18
Acinetobacter.baumannii.BJAB0715_1096996	12.12
Acinetobacter.baumannii.BJAB0868_1096997	12.15
Acinetobacter.baumannii.D1279779_945556	12.49
Acinetobacter.baumannii.MDRTJ_889738	12.34
Acinetobacter.baumannii.MDRZJ06_497978	12.07
Acinetobacter.baumannii.TCDCAB0715_980514	11.95
Acinetobacter.baumannii.TYTH1_1100841	12.29
Azotobacter.vinelandii.CA6_1283331	26.97
Azotobacter.vinelandii.CA_1283330	27.05
Azotobacter.vinelandii.DJ_322710	27.06
Pseudomonas.aeruginosa.B13633_1280938	27.86
Pseudomonas.aeruginosa.DK2_1093787	27.83
Pseudomonas.aeruginosa.LESB58_557722	27.53
Pseudomonas.aeruginosa.M18_941193	27.80
Pseudomonas.aeruginosa.NCGM2.S1_1089456	27.52
Pseudomonas.aeruginosa.PA7_381754	28.04
Pseudomonas.aeruginosa.PAO1_208964	28.00
Pseudomonas.aeruginosa.RP73_1340851	27.86
Pseudomonas.aeruginosa.UCBPPPA14_208963	28.01
Pseudomonas.fluorescens.A506_1037911	18.52
Pseudomonas.fluorescens.F113_1114970	19.68
Pseudomonas.fluorescens.Pf01_205922	18.01
Pseudomonas.fluorescens.SBW25_216595	18.94
Pseudomonas.mendocina.NK01_1001585	23.39
Pseudomonas.mendocina.ymp_399739	25.88
Pseudomonas.protegens.CHA0_1124983	22.97
Pseudomonas.protegens.Pf5_220664	22.23
Pseudomonas.putida.BIRD1_931281	21.30
Pseudomonas.putida.DOTT1E_1196325	21.31

Pseudomonas.putida.F1_351746	21.58
Pseudomonas.putida.GB1_76869	22.40
Pseudomonas.putida.H8234_1331671	20.77
Pseudomonas.putida.HB3267_1215088	21.31
Pseudomonas.putida.KT2440_160488	21.91
Pseudomonas.putida.NBRC.14164_1211579	22.15
Pseudomonas.putida.ND6_231023	20.76
Pseudomonas.putida.S16_1042876	21.53
Pseudomonas.putida.W619_390235	21.54
Pseudomonas.stutzeri.A1501_379731	24.48
Pseudomonas.stutzeri.ATCC.17588..LMG.11199_96563	24.39
Pseudomonas.stutzeri.CCUG.29243_1196835	22.58
Pseudomonas.stutzeri.DSM.10701_1123519	21.70
Pseudomonas.stutzeri.DSM.4166_996285	24.56
Pseudomonas.stutzeri.RCH2_644801	22.79
Francisella.cf..novicida.3523_676032	13.32
Francisella.cf..novicida.Fx1_984129	13.23
Francisella.novicida.U112_401614	13.47
Francisella.tularensis.subsp..holarctica.F92_1232394	11.95
Francisella.tularensis.subsp..holarctica.FSC200_351581	12.74
Francisella.tularensis.subsp..holarctica.FTNF00200_458234	12.20
Francisella.tularensis.subsp..holarctica.LVS_376619	11.75
Francisella.tularensis.subsp..holarctica.OSU18_393011	12.61
Francisella.tularensis.subsp..mediasiatica.FSC147_441952	13.75
Francisella.tularensis.subsp..tularensis.FSC198_393115	13.36
Francisella.tularensis.subsp..tularensis.NE061598_510831	12.74
Francisella.tularensis.subsp..tularensis.SCHU.S4_177416	13.37
Francisella.tularensis.subsp..tularensis.TI0902_1001534	13.25
Francisella.tularensis.subsp..tularensis.TIGB03_1001542	13.24
Francisella.tularensis.subsp..tularensis.WY963418_418136	12.82
Listonella.anguillarum.M3_882944	11.83
Vibrio.anguillarum.775_882102	11.69
Vibrio.cholerae.IEC224_1134456	13.38
Vibrio.cholerae.LMA39844_935297	13.22
Vibrio.cholerae.M662_579112	13.68
Vibrio.cholerae.MJ1236_593588	13.67
Vibrio.cholerae.O1.biovar.El.Tor.str..N16961_243277	13.51
Vibrio.cholerae.O1.str..2010EL1786_914149	13.54

Vibrio.cholerae.O395_345073	13.36
Vibrio.parahaemolyticus.BB220P_1211705	11.85
Vibrio.parahaemolyticus.O1K33.str..CDC.K4557_1338032	11.46
Vibrio.parahaemolyticus.O1Kuk.str..FDA.R31_1338034	11.87
Vibrio.parahaemolyticus.RIMD.2210633_223926	11.74
Vibrio.vulnificus.CMCP6_216895	12.97
Vibrio.vulnificus.MO624O_914127	12.80
Vibrio.vulnificus.YJ016_196600	12.55
Stenotrophomonas.maltophilia.D457_1163399	35.15
Stenotrophomonas.maltophilia.JV3_868597	34.69
Stenotrophomonas.maltophilia.K279a_522373	33.25
Stenotrophomonas.maltophilia.R5513_391008	34.45
Xanthomonas.campestris.pv..campestris.str..8004_314565	32.68
Xanthomonas.campestris.pv..campestris.str..ATCC.33913_190485	33.02
Xanthomonas.campestris.pv..raphani.756C_990315	34.26
Xanthomonas.axonopodis.pv..citri.str..306_190486	31.49
Xanthomonas.citri.subsp..citri.Aw12879_1137651	31.66
Xanthomonas.oryzae.pv..oryzae.KACC.10331_291331	29.04
Xanthomonas.oryzae.pv..oryzae.MAFF.311018_342109	28.71
Xanthomonas.oryzae.pv..oryzae.PXO99A_360094	29.25
Xanthomonas.oryzae.pv..oryzicola.BLS256_383407	29.56
Xylella.fastidiosa.9a5c_160492	19.61
Xylella.fastidiosa.M12_405440	20.01
Xylella.fastidiosa.M23_405441	21.33
Xylella.fastidiosa.subsp..fastidiosa.GB514_788929	21.04
Xylella.fastidiosa.Temecula1_183190	20.75
Candidatus.Kinetoplastibacterium.blastocrithidii.ex.Strigomonas.culicis_1208923	9.08
Polynucleobacter.necessarius.subsp..asymbioticus.QLWP1DMWA1_312153	13.15
Polynucleobacter.necessarius.subsp..necessarius.STIR1_452638	12.68
Candidatus.Kinetoplastibacterium.crithidii.ex.Angomonas.deanei.ATCC.30255_1267577	8.76
Candidatus.Kinetoplastibacterium.crithidii.TCC036E_1208918	9.44
Candidatus.Kinetoplastibacterium.blastocrithidii.TCC012E_1208922	9.25
Desulfovibrio.desulfuricans.subsp..desulfuricans.str..ATCC.27774_525146	24.79
Desulfovibrio.desulfuricans.ND132_641491	20.85
Anaeromyxobacter.dehalogenans.2CP1_455488	56.14
Anaeromyxobacter.dehalogenans.2CPC_290397	57.32
Campylobacter.jejuni.subsp..jejuni.NCTC.11168..ATCC.700819_192222	14.89

Campylobacter.jejuni.subsp..jejuni.NCTC.11168BN148_1211776	14.97
Candidatus.Liberibacter.asiaticus.str..gxpsy_1174529	9.55
Candidatus.Liberibacter.asiaticus.str..psy62_537021	9.15
Wolbachia.endosymbiont.of.Drosophila.simulans.wHa_1236909	12.55
Wolbachia.endosymbiont.of.Drosophila.simulans.wNo_1236908	12.16
Amycolatopsis.mediterranei.RB_1221524	36.19
Amycolatopsis.mediterranei.S699_713604	36.25
Amycolatopsis.mediterranei.U32_749927	36.28
Clavibacter.michiganensis.subsp..michiganensis.NCPPB.382_443906	43.42
Clavibacter.michiganensis.subsp..nebraskensis.NCPPB.2581_1097677	43.35
Clavibacter.michiganensis.subsp..sepedonicus_31964	43.00
Corynebacterium.diphtheriae.241_698966	21.50
Corynebacterium.diphtheriae.31A_698962	22.00
Corynebacterium.diphtheriae.BH8_698973	21.77
Corynebacterium.diphtheriae.C7.beta_698963	22.23
Corynebacterium.diphtheriae.CDCE.8392_698965	22.22
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Corynebacterium.diphtheriae.HC02_698968	21.65
Corynebacterium.diphtheriae.HC03_698969	21.51
Corynebacterium.diphtheriae.HC04_698970	21.90
Corynebacterium.diphtheriae.INCA.402_698972	22.66
Corynebacterium.diphtheriae.PW8_698964	21.97
Corynebacterium.diphtheriae.VA01_698971	21.77
Corynebacterium.glutamicum.ATCC.13032_196627	21.40
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Corynebacterium.glutamicum.MB001_1310161	21.81
Corynebacterium.glutamicum.R_340322	21.60
Corynebacterium.glutamicum.SCgG1_1232381	21.01
Corynebacterium.glutamicum.SCgG2_1232383	20.97
Corynebacterium.pseudotuberculosis.1002_679896	22.80
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Corynebacterium.pseudotuberculosis.258_1168865	22.44
Corynebacterium.pseudotuberculosis.267_1089446	22.33
Corynebacterium.pseudotuberculosis.316_1074485	22.35
Corynebacterium.pseudotuberculosis.31_1087451	21.63
Corynebacterium.pseudotuberculosis.3995_1087452	22.34
Corynebacterium.pseudotuberculosis.4202A_1087453	22.57
Corynebacterium.pseudotuberculosis.C231_681645	22.51

Corynebacterium.pseudotuberculosis.CIP.52.97_935697	22.57
Corynebacterium.pseudotuberculosis.Cp162_1161911	21.89
Corynebacterium.pseudotuberculosis.FRC41_765874	22.28
Corynebacterium.pseudotuberculosis.I19_889513	22.53
Corynebacterium.pseudotuberculosis.P54B96_1117942	22.36
Corynebacterium.pseudotuberculosis.PAT10_935298	22.42
Corynebacterium.ulcerans.0102_996634	21.50
Corynebacterium.ulcerans.809_945711	21.58
Corynebacterium.ulcerans.BRAD22_945712	22.28
Corynebacterium.urealyticum.DSM.7109_504474	30.52
Corynebacterium.urealyticum.DSM.7111_1267754	30.86
Leifsonia.xyli.subsp..cynodontis.DSM.46306_1389489	35.57
Leifsonia.xyli.subsp..xyli.str..CTCB07_281090	35.06
Mycobacterium.abscessus.subsp..bolletii.50594_1303024	27.36
Mycobacterium.abscessus_36809	26.93
Mycobacterium.massiliense.str..GO.06_1198627	25.55
Mycobacterium.avium.104_243243	32.33
Mycobacterium.avium.subsp..paratuberculosis.K10_262316	34.81
Mycobacterium.avium.subsp..paratuberculosis.MAP4_1199187	34.22
Mycobacterium.bovis.BCG.str..Korea.1168P_1206780	34.69
Mycobacterium.bovis.BCG.str..Mexico_717522	34.66
Mycobacterium.bovis.BCG.str..Pasteur.1173P2_410289	34.63
Mycobacterium.bovis.BCG.str..Tokyo.172_561275	34.67
Mycobacterium.gilvum.PYRGCK_350054	31.68
Mycobacterium.gilvum.Spyr1_278137	31.58
Mycobacterium.intracellulare.ATCC.13950_487521	29.32
Mycobacterium.intracellulare.MOTT02_1138382	29.24
Mycobacterium.intracellulare.MOTT64_1138383	28.92
Mycobacterium.smegmatis.JS623_710686	28.71
Mycobacterium.smegmatis.str..MC2.155_246196	28.84
Mycobacterium.tuberculosis.719999_1138877	34.54
Mycobacterium.tuberculosis.CASNITR204_1310114	32.28
Mycobacterium.tuberculosis.CCDC5079_443149	34.59
Mycobacterium.tuberculosis.CCDC5180_443150	34.26
Mycobacterium.tuberculosis.CDC1551_83331	34.69
Mycobacterium.tuberculosis.CTRI2_707235	34.58
Mycobacterium.tuberculosis.EAI5_1306414	34.20
Mycobacterium.tuberculosis.EAI5NITR206_1310115	34.24

Mycobacterium.tuberculosis.F11_336982	34.97
Mycobacterium.tuberculosis.H37Ra_419947	34.60
Mycobacterium.tuberculosis.H37Rv_83332	34.68
Mycobacterium.tuberculosis.KZN.1435_478434	34.63
Mycobacterium.tuberculosis.KZN.605_478435	34.85
Mycobacterium.tuberculosis.RGTB327_1091500	33.15
Mycobacterium.tuberculosis.RGTB423_1091501	33.38
Mycobacterium.tuberculosis.str..BeijingNITR203_1306400	34.20
Mycobacterium.tuberculosis.str..Erdman..ATCC.35801_652616	34.25
Mycobacterium.tuberculosis.str..Haarlem_395095	34.49
Mycobacterium.tuberculosis.str..HaarlemNITR202_1304279	38.97
Propionibacterium.acnes.266_909952	22.97
Propionibacterium.acnes.6609_1031709	22.06
Propionibacterium.acnes.ATCC.11828_1091045	22.49
Propionibacterium.acnes.C1_1234380	22.89
Propionibacterium.acnes.HL096PA1_1134454	22.89
Propionibacterium.acnes.KPA171202_267747	22.57
Propionibacterium.acnes.SK137_553199	22.77
Propionibacterium.acnes.TypeIA2.P.acn17_1114967	22.04
Propionibacterium.acnes.TypeIA2.P.acn31_1114969	22.14
Propionibacterium.acnes.TypeIA2.P.acn33_1114966	22.27
Streptomyces.hygroscopicus.subsp..jinggangensis.5008_1133850	38.83
Streptomyces.hygroscopicus.subsp..jinggangensis.TL01_1203460	39.16
Bifidobacterium.animalis.subsp..animalis.ATCC.25527_703613	19.69
Bifidobacterium.animalis.subsp..lactis.AD011_442563	19.07
Bifidobacterium.animalis.subsp..lactis.B420_1168290	18.71
Bifidobacterium.animalis.subsp..lactis.BB12_552531	20.38
Bifidobacterium.animalis.subsp..lactis.Bi07_742729	18.72
Bifidobacterium.animalis.subsp..lactis.BI04_580050	18.92
Bifidobacterium.animalis.subsp..lactis.BI12_1281781	19.24
Bifidobacterium.animalis.subsp..lactis.BLC1_1075106	19.15
Bifidobacterium.animalis.subsp..lactis.CNCM.I2494_1042403	20.36
Bifidobacterium.animalis.subsp..lactis.DSM.10140_555970	18.93
Bifidobacterium.animalis.subsp..lactis.V9_573236	18.96
Bifidobacterium.bifidum.BGN4_484020	26.74
Bifidobacterium.bifidum.PRL2010_702459	26.65
Bifidobacterium.bifidum.S17_883062	26.59
Bifidobacterium.breve.ACS071VSch8b_866777	23.18

Bifidobacterium.breve.UCC2003_326426	23.29
Bifidobacterium.longum.DJO10A_205913	25.21
Bifidobacterium.longum.NCC2705_206672	25.34
Bifidobacterium.longum.subsp..infantis.157F_565040	24.81
Bifidobacterium.longum.subsp..infantis.ATCC.15697..JCM.1222_391904	21.96
Bifidobacterium.longum.subsp..longum.BBMN68_890402	25.67
Bifidobacterium.longum.subsp..longum.JCM.1217_565042	26.49
Bifidobacterium.longum.subsp..longum.JDM301_759350	25.83
Bifidobacterium.longum.subsp..longum.KACC.91563_1035817	25.57
Gardnerella.vaginalis.40905_553190	22.47
Gardnerella.vaginalis.ATCC.14019_525284	22.01
Gardnerella.vaginalis.HMP9231_1009464	21.72
Bacteroides.fragilis.638R_862962	12.08
Bacteroides.fragilis.NCTC.9343_272559	12.09
Bacteroides.fragilis.YCH46_295405	11.57
Porphyromonas.gingivalis.ATCC.33277_431947	13.81
Porphyromonas.gingivalis.TDC60_1030843	13.22
Porphyromonas.gingivalis.W83_242619	13.86
Candidatus.Sulcia.muelleri.CARI_706194	51.13
Candidatus.Sulcia.muelleri.DMIN_641892	43.15
Candidatus.Sulcia.muelleri.GWSS_444179	40.40
Candidatus.Sulcia.muelleri.SMDSEM_595499	48.42
Candidatus.Sulcia.muelleri.str..SulciaALF_1343076	35.58
Riemerella.anatipestifer.ATCC.11845..DSM.15868_693978	11.32
Riemerella.anatipestifer.RACH1_1228997	11.30
Riemerella.anatipestifer.RACH2_1271752	11.14
Riemerella.anatipestifer.RAGD_992406	11.04
_Rhodothermus.marinus.DSM.4252_518766	29.47
Rhodothermus.marinus.SG0.5JP17172_762570	28.87
Salinibacter.ruber.DSM.13855_309807	30.54
Salinibacter.ruber.M8_761659	30.62
Chlamydia.pecorum.P787_1234369	18.65
Chlamydia.pecorum.PV30563_1234367	18.60
Chlamydia.pecorum.W73_1234368	18.88
Chlamydophila.pecorum.E58_331635	18.21
Chlamydophila.pneumoniae.AR39_115711	15.21
Chlamydophila.pneumoniae.CWL029_115713	14.84
Chlamydophila.pneumoniae.J138_138677	14.91

Chlamydomophila.pneumoniae.LPCoLN_406984	16.28
Chlamydomophila.pneumoniae.TW183_182082	14.49
Chlamydia.psittaci.01DC11_1112252	15.70
Chlamydia.psittaci.02DC15_1112254	15.65
Chlamydia.psittaci.08DC60_1112267	15.49
Chlamydia.psittaci.6BC_331636	15.42
Chlamydia.psittaci.8455_1218176	14.50
Chlamydia.psittaci.C1998_1112250	15.43
Chlamydia.psittaci.CP3_1050219	13.89
Chlamydia.psittaci.GR9_1218353	14.62
Chlamydia.psittaci.M56_1218357	14.19
Chlamydia.psittaci.Mat116_500464	14.77
Chlamydia.psittaci.MN_1218354	14.44
Chlamydia.psittaci.NJ1_1050221	14.87
Chlamydia.psittaci.VS225_1218355	14.19
Chlamydia.psittaci.WC_1218358	15.23
Chlamydia.psittaci.WSRTE30_1218356	14.30
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Chlamydia.trachomatis.A7249_1071755	16.51
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Chlamydia.trachomatis.DEC_759363	16.73
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Chlamydia.trachomatis.E150_707184	16.36
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Chlamydia.trachomatis.FSW5_1071763	16.89
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Chlamydia.trachomatis.G9768_707185	17.35
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Chlamydia.trachomatis.laSotonla3_1071767	17.08
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Chlamydia.trachomatis.L1440LN_1071769	17.07
Chlamydia.trachomatis.L225667R_1071772	16.97
Chlamydia.trachomatis.L2434Buf_1262673	16.91
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Chlamydia.trachomatis.L2b795_1071777	16.81
Chlamydia.trachomatis.L2b820007_1071773	16.81
Chlamydia.trachomatis.L2bUCH1proctitis_471473	16.81
Chlamydia.trachomatis.L2bUCH2_1071774	16.81
Chlamydia.trachomatis.L2c_887712	16.63
Chlamydia.trachomatis.L3404LN_1071783	16.91
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Chlamydia.trachomatis.RCFs852_907265	17.00
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Chlamydia.trachomatis.RCJ953_907267	17.22
Chlamydia.trachomatis.RCJ966_907271	16.85
Chlamydia.trachomatis.RCJ971_1007871	17.48
Chlamydia.trachomatis.RCJs122_907270	16.59
Chlamydia.trachomatis.RCL255_1007870	16.97
Chlamydia.trachomatis.RCL2s3_907268	17.06
Chlamydia.trachomatis.RCL2s46_907264	16.97
Chlamydia.trachomatis.Sweden2_634464	16.65
Chlorobium.phaeobacteroides.BS1_331678	11.10
Chlorobium.phaeobacteroides.DSM.266_290317	12.24
Dehalococcoides.ethenogenes.195_243164	12.47
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Dehalococcoides.mccartyi.DCMB5_1193807	11.72
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Dehalococcoides.sp..CBDB1_255470	11.54
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Dehalococcoides.sp..VS_311424	11.39
Synechococcus.elongatus.PCC.6301_269084	24.38
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Prochlorococcus.marinus.str..AS9601_146891	14.77

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Prochlorococcus.marinus.str..MIT.9301_167546	14.09
Prochlorococcus.marinus.str..MIT.9303_59922	21.75
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Prochlorococcus.marinus.str..MIT.9313_74547	22.12
Prochlorococcus.marinus.str..MIT.9515_167542	14.75
Prochlorococcus.marinus.str..NATL1A_167555	12.80
Prochlorococcus.marinus.str..NATL2A_59920	13.53
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Prochlorococcus.marinus.subsp..pastoris.str..CCMP1986_59919	16.13
Thermus.thermophilus.HB27_262724	39.31
Thermus.thermophilus.HB8_300852	38.10
Thermus.thermophilus.JL18_798128	38.80
Thermus.thermophilus.SG0.5JP1716_762633	38.36
Alicyclobacillus.acidocaldarius.subsp..acidocaldarius.DSM.446_521098	19.30
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Bacillus.amyloliquefaciens.subsp..plantarum.UCMB5036_1150475	13.37
Bacillus.amyloliquefaciens.subsp..plantarum.UCMB5113_1150476	13.54
Bacillus.amyloliquefaciens.subsp..plantarum.YAU.B9601Y2_1155777	13.68
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Bacillus.anthraxis.str..Ames_198094	11.89
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Bacillus.thuringiensis.MC28_1195464	12.23
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Bacillus.thuringiensis.str..Al.Hakam_412694	12.51

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Listeria.monocytogenes.J1816_930781	12.07
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Listeria.monocytogenes.N531_1234142	11.58
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Listeria.monocytogenes.SLCC2479_882020	12.98
Listeria.monocytogenes.SLCC2540_879089	13.05
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Listeria.monocytogenes.SLCC5850_882096	13.19
Listeria.monocytogenes.SLCC7179_879090	13.15
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Paenibacillus.polymyxa.E681_349520	13.36
Paenibacillus.polymyxa.M1_1052684	13.41
Paenibacillus.polymyxa.SC2_886882	13.23
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Enterococcus.faecalis.D32_1206105	14.24
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Enterococcus.faecalis.V583_226185	14.59
Enterococcus.faecium.Aus0004_1155766	13.05
Enterococcus.faecium.Aus0085_1305849	12.86
Enterococcus.faecium.DO_333849	12.93
Enterococcus.faecium.NRRL.B2354_1104325	14.02
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Lactobacillus.brevis.ATCC.367_387344	17.97
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Lactobacillus.casei.ATCC.334_321967	15.74
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Lactobacillus.casei.LC2W_999378	14.92
Lactobacillus.casei.LOCK919_1318635	15.67
Lactobacillus.casei.str..Zhang_498216	15.72
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Lactobacillus.rhamnosus.Lc.705_568704	15.85
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Streptococcus.anginosus.C238_862971	14.29
Streptococcus.constellatus.subsp..pharyngis.C1050_862969	14.14
Streptococcus.constellatus.subsp..pharyngis.C232_696216	14.43
Streptococcus.constellatus.subsp..pharyngis.C818_862968	14.45
Streptococcus.dysgalactiae.subsp..equisimilis.AC2713_759913	13.38
Streptococcus.dysgalactiae.subsp..equisimilis.ATCC.12394_663954	13.07
Streptococcus.dysgalactiae.subsp..equisimilis.GGS.124_486410	12.70
Streptococcus.dysgalactiae.subsp..equisimilis.RE378_617121	13.42
Streptococcus.equi.subsp..equi.4047_553482	15.35
Streptococcus.equi.subsp..zooepidemicus.ATCC.35246_1051072	15.34
Streptococcus.equi.subsp..zooepidemicus.MGCS10565_552526	15.72
Streptococcus.equi.subsp..zooepidemicus_40041	15.42
Streptococcus.gallolyticus.subsp..gallolyticus.ATCC.43143_981539	16.13
Streptococcus.gallolyticus.subsp..gallolyticus.ATCC.BAA2069_990317	15.57
Streptococcus.gallolyticus.UCN34_637909	16.00
Streptococcus.intermedius.B196_862967	14.03
Streptococcus.intermedius.C270_862966	13.74
Streptococcus.intermedius.JTH08_591365	13.54
Streptococcus.mutans.GS5_1198676	14.98
Streptococcus.mutans.LJ23_1155071	14.23
Streptococcus.mutans.NN2025_511691	14.80
Streptococcus.mutans.UA159_210007	15.28
Streptococcus.parasanguinis.ATCC.15912_760570	16.29
Streptococcus.parasanguinis.FW213_1114965	17.02
Streptococcus.pneumoniae.6706B_189423	12.73
Streptococcus.pneumoniae.70585_488221	13.20
Streptococcus.pneumoniae.AP200_574093	12.88
Streptococcus.pneumoniae.ATCC.700669_561276	12.94
Streptococcus.pneumoniae.CGSP14_516950	12.84
Streptococcus.pneumoniae.D39_373153	13.13
Streptococcus.pneumoniae.G54_512566	13.39
Streptococcus.pneumoniae.gamPNI0373_697283	12.99
Streptococcus.pneumoniae.Hungary19A6_487214	13.06
Streptococcus.pneumoniae.INV104_869269	13.81
Streptococcus.pneumoniae.INV200_869216	13.74

Streptococcus.pneumoniae.JJA_488222	12.72
Streptococcus.pneumoniae.OXC141_869215	13.41
Streptococcus.pneumoniae.P1031_488223	13.56
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Streptococcus.pneumoniae.SPN994038_869306	13.34
Streptococcus.pneumoniae.SPN994039_869307	13.33
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Streptococcus.pneumoniae.Taiwan19F14_487213	13.54
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Streptococcus.pyogenes.MGAS10270_370552	12.81
Streptococcus.pyogenes.MGAS10394_286636	12.43
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Streptococcus.pyogenes.MGAS15252_798300	12.84
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Streptococcus.pyogenes.MGAS2096_370553	12.31
Streptococcus.pyogenes.MGAS315_198466	12.33
Streptococcus.pyogenes.MGAS5005_293653	11.85
Streptococcus.pyogenes.MGAS6180_319701	12.86
Streptococcus.pyogenes.MGAS8232_186103	12.48
Streptococcus.pyogenes.MGAS9429_370551	12.43
Streptococcus.pyogenes.NZ131_471876	12.66
Streptococcus.pyogenes.SSI1_193567	12.12
Streptococcus.pyogenes.str..Manfredo_160491	12.79
Streptococcus.salivarius.57.I_1046629	15.95
Streptococcus.salivarius.CCHSS3_1048332	16.89
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Streptococcus.suis.05ZYH33_391295	14.59
Streptococcus.suis.98HAH33_391296	14.05
Streptococcus.suis.A7_993512	15.47
Streptococcus.suis.BM407_568814	14.52
Streptococcus.suis.D12_1004952	15.18

Streptococcus.suis.D9_1005042	14.18
Streptococcus.suis.GZ1_423211	14.66
Streptococcus.suis.JS14_945704	15.32
Streptococcus.suis.P17_218494	15.41
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Streptococcus.suis.SC84_568813	15.32
Streptococcus.suis.SS12_1005041	14.87
Streptococcus.suis.ST1_1004951	14.70
Streptococcus.suis.ST3_1007064	14.34
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Streptococcus.thermophilus.ND03_767463	12.86
Candidatus.Arthromitus.sp..SFBmouseJapan_1029718	16.55
Candidatus.Arthromitus.sp..SFBmouseYit_1041809	16.08
Clostridium.acetobutylicum.ATCC.824_272562	13.64
Clostridium.acetobutylicum.DSM.1731_991791	13.71
Clostridium.acetobutylicum.EA.2018_863638	13.68
Clostridium.botulinum.A.str..ATCC.19397_441770	16.18
Clostridium.botulinum.A.str..ATCC.3502_413999	16.42
Clostridium.botulinum.A.str..Hall_441771	16.24
Clostridium.botulinum.A2.str..Kyoto_536232	16.43
Clostridium.botulinum.A3.str..Loch.Maree_498214	16.04
Clostridium.botulinum.B.str..Eklund.17B_508765	14.21
Clostridium.botulinum.B1.str..Okra_498213	15.71
Clostridium.botulinum.Ba4.str..657_515621	17.08
Clostridium.botulinum.BKT015925_929506	15.62
Clostridium.botulinum.E3.str..Alaska.E43_508767	15.43
Clostridium.botulinum.F.str..230613_758678	15.17
Clostridium.botulinum.F.str..Langeland_441772	15.90
Clostridium.botulinum.H04402.065_941968	16.23
Clostridium.difficile.630_272563	14.42
Clostridium.difficile.B11_699034	14.18
Clostridium.difficile.CD196_645462	14.52

Clostridium.kluyveri.DSM.555_431943	13.77
Clostridium.kluyveri.NBRC.12016_583346	13.77
Clostridium.perfringens.ATCC.13124_195103	16.40
Clostridium.perfringens.SM101_289380	15.46
Clostridium.perfringens.str..13_195102	15.75
Clostridium.thermocellum.ATCC.27405_203119	13.67
Clostridium.thermocellum.DSM.1313_637887	14.38
Desulfitobacterium.hafniense.DCB2_272564	14.14
Desulfitobacterium.hafniense.Y51_138119	14.04
Sulfobacillus.acidophilus.DSM.10332_679936	15.95
Sulfobacillus.acidophilus.TPY_1051632	15.63
Thermoanaerobacterium.thermosaccharolyticum.DSM.571_580327	11.98
Thermoanaerobacterium.thermosaccharolyticum.M0795_698948	12.90
Fusobacterium.nucleatum.subsp..animalis.4.8_469607	17.77
Fusobacterium.nucleatum.subsp..nucleatum.ATCC.25586_190304	16.15
Fusobacterium.nucleatum.subsp..vincentii.3.1.36A2_469604	18.57
Caulobacter.crescentus.CB15_190650	32.63
Caulobacter.crescentus.NA1000_565050	32.40
Micavibrio.aeruginosavorus.ARL13_856793	17.39
Micavibrio.aeruginosavorus.EPB_349215	18.02
Bartonella.quintana.RM11_1225179	10.64
Bartonella.quintana.str..Toulouse_283165	10.30
Brucella.abortus.A13334_1104320	19.12
Brucella.abortus.bv..1.str..9941_262698	18.82
Brucella.abortus.S19_430066	19.05
Brucella.melitensis.biovar.Abortus.2308_359391	18.77
BacteriBrucella.canis.ATCC.23365_483179	18.81
Brucella.canis.HSK.A52141_1104321	19.21
Brucella.melitensis.ATCC.23457_546272	18.73
Brucella.melitensis.bv..1.str..16M_224914	17.11
Brucella.melitensis.M28_941967	19.33
Brucella.melitensis.M590_703352	19.19
Brucella.melitensis.NI_1029825	19.15
Brucella.suis.1330_204722	18.89
Brucella.suis.ATCC.23445_470137	19.06
Brucella.suis.VBI22_1112912	18.91
Hyphomicrobium.denitrificans.1NES1_670307	22.19
Hyphomicrobium.denitrificans.ATCC.51888_582899	24.00

Methylobacterium.extorquens.AM1_272630	35.28
Methylobacterium.extorquens.CM4_440085	34.31
Methylobacterium.extorquens.DM4_661410	34.64
Methylobacterium.extorquens.PA1_419610	34.65
Oligotropha.carboxidovorans.OM4_1031710	23.40
Oligotropha.carboxidovorans.OM5_504832	23.36
Rhizobium.etli.bv..mimosae.str..Mim1_1328306	19.16
Rhizobium.etli.CFN.42_347834	19.39
Rhizobium.etli.CIAT.652_491916	20.22
Rhizobium.leguminosarum.bv..trifolii.WSM1325_395491	19.23
Rhizobium.leguminosarum.bv..trifolii.WSM2304_395492	20.04
Rhizobium.leguminosarum.bv..viciae.3841_216596	19.29
Rhodopseudomonas.palustris.BisA53_316055	27.65
Rhodopseudomonas.palustris.BisB18_316056	27.95
Rhodopseudomonas.palustris.BisB5_316057	27.47
Rhodopseudomonas.palustris.DX1_652103	28.51
Rhodopseudomonas.palustris.HaA2_316058	28.74
Rhodopseudomonas.palustris.TIE1_395960	27.54
Sinorhizobium.meliloti.1021_266834	21.09
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Sinorhizobium.meliloti.AK83_693982	21.02
Sinorhizobium.meliloti.BL225C_698936	21.13
Sinorhizobium.meliloti.GR4_1235461	20.92
Sinorhizobium.meliloti.Rm41_1230587	20.86
Sinorhizobium.meliloti.SM11_707241	20.42
Ketogulonicigenium.vulgare.WSH001_759362	24.35
Ketogulonicigenium.vulgare.Y25_880591	24.48
Rhodobacter.sphaeroides.ATCC.17025_349102	32.64
Rhodobacter.sphaeroides.ATCC.17029_349101	34.24
Rhodobacter.sphaeroides.KD131_557760	33.77
Acetobacter.pasteurianus.IFO.32830142C_634458	20.56
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Acetobacter.pasteurianus.IFO.328303_634453	20.45
Acetobacter.pasteurianus.IFO.328307_634454	20.46
Acetobacter.pasteurianus.IFO.328312_634459	20.44
Acetobacter.pasteurianus.IFO.328322_634455	20.44
Acetobacter.pasteurianus.IFO.328326_634456	20.44
Acetobacter.pasteurianus.IFO.328332_634457	20.45

Azospirillum.lipoferum.4B_862719	34.38
Azospirillum.sp..B510_137722	34.92
Gluconobacter.oxydans.621H_290633	20.24
Gluconobacter.oxydans.H24_1224746	17.58
Rhodospirillum.rubrum.ATCC.11170_269796	32.35
Rhodospirillum.rubrum.F11_1036743	32.08
Anaplasma.marginale.str..Florida_320483	16.76
Anaplasma.marginale.str..St..Maries_234826	16.72
Anaplasma.phagocytophilum.str..HZ2_1184253	12.93
Anaplasma.phagocytophilum.str..HZ_212042	13.69
Anaplasma.phagocytophilum.str..JM_1173064	13.28
Ehrlichia.ruminantium.str..Gardel_302409	16.17
Ehrlichia.ruminantium.str..Welgevonden_254945	16.00
Orientia.tsutsugamushi.str..Boryong_357244	15.12
Orientia.tsutsugamushi.str..Ikeda_334380	13.62
Rickettsia.bellii.OSU.85389_391896	11.60
Rickettsia.bellii.RML369C_336407	12.19
Rickettsia.canadensis.str..CA410_1105107	14.06
Rickettsia.canadensis.str..McKiel_293613	13.53
Rickettsia.prowazekii.str..Breinl_1290428	12.44
Rickettsia.prowazekii.str..BuV67CWPP_1105096	12.91
Rickettsia.prowazekii.str..Chernikova_1105094	13.02
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Rickettsia.prowazekii.str..Katsinyan_1105095	12.91
Rickettsia.prowazekii.str..NMRC.Madrid.E_1290427	12.03
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Rickettsia.rickettsii.str..Iowa_452659	10.85
Rickettsia.rickettsii.str..Sheila.Smith_392021	11.04
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Rickettsia.slovaca.str..DCWPP_1105109	11.31
Rickettsia.typhi.str..B9991CWPP_1003202	12.62
Rickettsia.typhi.str..TH1527_1003201	12.73

Rickettsia.typhi.str..Wilmington_257363	12.58
Zymomonas.mobilis.subsp..mobilis.ATCC.10988_555217	16.04
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Zymomonas.mobilis.subsp..mobilis.ZM4..ATCC.31821_264203	16.03
Zymomonas.mobilis.subsp..pomaceae.ATCC.29192_579138	15.36
Alicyclophilus.denitrificans.BC_596153	33.91
Alicyclophilus.denitrificans.K601_596154	33.53
Bordetella.bronchiseptica.253_568707	34.28
Bordetella.bronchiseptica.MO149_1208658	34.93
Bordetella.pertussis.18323_568706	33.36
Bordetella.pertussis.CS_1017264	33.18
Burkholderia.ambifaria.AMMD_339670	30.86
Burkholderia.ambifaria.MC406_398577	30.53
Burkholderia.cenocepacia.AU.1054_331271	32.09
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Burkholderia.cenocepacia.J2315_216591	31.91
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Burkholderia.mallei.ATCC.23344_243160	39.99
Burkholderia.mallei.NCTC.10229_412022	40.52
Burkholderia.mallei.NCTC.10247_320389	39.57
Burkholderia.mallei.SAVP1_320388	40.41
Burkholderia.pseudomallei.1026b_884204	37.97
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Burkholderia.pseudomallei.668_320373	40.69
Burkholderia.pseudomallei.BPC006_1229785	40.15
Burkholderia.pseudomallei.K96243_272560	37.68
Burkholderia.pseudomallei.MSHR305_1335307	37.31
Burkholderia.thailandensis.E264_271848	38.59
Burkholderia.thailandensis.MSMB121_1249661	36.24
Cupriavidus.necator.N1_1042878	29.35
Ralstonia.eutropha.H16_381666	30.62
Ralstonia.pickettii.12D_428406	25.96
Ralstonia.pickettii.12J_402626	26.89
Ralstonia.solanacearum.GMI1000_267608	31.40
Ralstonia.solanacearum.Po82_1031711	32.62
Ralstonia.solanacearum.PSI07_859657	29.37

Taylorella.equigenitalis.ATCC.35865_743973	11.97
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Variovorax.paradoxus.B4_1246301	30.99
Variovorax.paradoxus.EPS_595537	30.16
Variovorax.paradoxus.S110_543728	33.01
Candidatus.Tremblaya.princeps.PCIT_891398	15.63
Candidatus.Tremblaya.princeps.PCVAL_1053648	16.30
Neisseria.gonorrhoeae.FA.1090_242231	16.60
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Neisseria.meningitidis.8013_604162	16.36
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Neisseria.meningitidis.alpha710_630588	16.77
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Neisseria.meningitidis.Z2491_122587	16.97
Desulfovibrio.vulgaris.DP4_391774	23.21
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Desulfovibrio.vulgaris.str..Hildenborough_882	23.96
Desulfovibrio.vulgaris.str..Miyazaki.F_883	37.43
Lawsonia.intracellularis.N343_1234378	14.36
Lawsonia.intracellularis.PHEMN100_363253	14.38
Geobacter.sulfurreducens.KN400_663917	21.43
Geobacter.sulfurreducens.PCA_243231	21.32
Sorangium.cellulosum.So.ce56_448385	50.16
Sorangium.cellulosum.So01572_1254432	48.47
Arcobacter.butzleri.7h1h_1036172	15.29
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Arcobacter.butzleri.RM4018_367737	15.02

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Campylobacter.jejuni.subsp..jejuni.81176_354242	14.72
Campylobacter.jejuni.subsp..jejuni.IA3902_567106	14.87
Campylobacter.jejuni.subsp..jejuni.ICDCCJ07001_757425	13.38
Campylobacter.jejuni.subsp..jejuni.M1_645464	14.84
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Helicobacter.cetorum.MIT.007128_182217	15.38
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Helicobacter.pylori.F16_866344	14.78
Helicobacter.pylori.F30_866345	14.19
Helicobacter.pylori.F32_102608	14.23
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Helicobacter.pylori.G27_563041	13.82
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Helicobacter.pylori.UM037_1321939	15.14
Helicobacter.pylori.UM066_1321940	15.18
Helicobacter.pylori.UM298_1321941	14.75
Helicobacter.pylori.UM299_1321938	14.80
Helicobacter.pylori.v225d_637913	15.15
Helicobacter.pylori.XZ274_1127122	14.09
Borrelia.afzelii.HLJ01_1239934	19.87
Borrelia.afzelii.PKo_390236	20.48
.burgdorferi.B31_224326	19.55
Borrelia.burgdorferi.CA382_1328311	19.95
Borrelia.burgdorferi.JD1_521008	20.75
Borrelia.burgdorferi.N40_521007	20.19
Borrelia.burgdorferi.ZS7_445985	19.62
Borrelia.garinii.BgVir_1081646	20.17
.garinii.NMJW1_1234596	20.81
Brachyspira.pilosicoli.951000_759914	22.84
Brachyspira.pilosicoli.B2904_1133568	22.49
Brachyspira.pilosicoli.P43678_1042417	22.46

Leptospira.biflexa.serovar.Patoc.strain.Patoc.1.Ames_355278	13.09
Leptospira.biflexa.serovar.Patoc.strain.Patoc.1.Paris_456481	13.00
Leptospira.borgpetersenii.serovar.Hardjobovis.str..JB197_355277	11.32
Leptospira.borgpetersenii.serovar.Hardjobovis.str..L550_355276	11.65
Leptospira.interrogans.serovar.Copenhageni.str..Fiocruz.L1130_267671	12.67
Leptospira.interrogans.serovar.Lai.str..56601_189518	12.64
Leptospira.interrogans.serovar.Lai.str..IPAV_573825	12.58
Spirochaeta.thermophila.DSM.6192_665571	24.46
Spirochaeta.thermophila.DSM.6578_869211	23.39
Candidatus.Phytoplasma.australiense_59748	20.08
Candidatus.Phytoplasma.australiense_Strawberry.lethal.yellows.phytoplasma.CP A.str..NZSb11_980422	22.05
Mycoplasma.agalactiae.PG2_347257	16.21
Mycoplasma.agalactiae_2110	19.86
Mycoplasma.bovis.HB0801_767465	15.18
Mycoplasma.bovis.Hubei1_956483	14.75
Mycoplasma.bovis.PG45_289397	14.77
Mycoplasma.fermentans.JER_637387	14.53
Mycoplasma.fermentans.M64_943945	15.11
Mycoplasma.gallisepticum.CA06.2006.05252P_1159203	23.89
Mycoplasma.gallisepticum.NC06.2006.08052P_1159202	23.71
Mycoplasma.gallisepticum.NC08.2008.03143P_1159204	22.82
Mycoplasma.gallisepticum.NC95.1329522P_1159198	22.81
Mycoplasma.gallisepticum.NC96.159642P_1159199	24.04
Mycoplasma.gallisepticum.NY01.2001.04751P_1159200	23.47
Mycoplasma.gallisepticum.str..F_708616	21.48
Mycoplasma.gallisepticum.str..Rhigh_710128	24.39
Mycoplasma.gallisepticum.str..Rlow_710127	24.43
Mycoplasma.gallisepticum.VA94.799417P_1159197	22.89
Mycoplasma.gallisepticum.WI01.2001.043132P_1159201	22.27
Mycoplasma.genitalium.G37_243273	17.04
Mycoplasma.genitalium.M2288_662947	16.45
Mycoplasma.genitalium.M2321_663918	16.19
Mycoplasma.genitalium.M6282_662946	15.68
Mycoplasma.genitalium.M6320_662945	16.16
Mycoplasma.haemofelis.Ohio2_859194	34.18
Mycoplasma.haemofelis.str..Langford.1_941640	34.96
Mycoplasma.hyopneumoniae.168_907287	22.42

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