# The Human Mitochondrial Ribosomal Protein Genes: Mapping of 54 Genes to the Chromosomes and Implications for Human Disorders

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Mitochondria possess their own translational machinery, which is composed of components distinct from their cytoplasmic counterparts. To investigate the possible involvement of mitochondrial ribosomal defects in human disease, we mapped nuclear genes that encode mitochondrial ribosomal proteins (MRPs). We generated sequence-tagged sites (STSs) of individual MRP genes that were able to be detected by PCR. They were placed on an STS content map of the human genome by typing of radiation hybrid panels. We located 54 MRP genes on the STS-content map and assigned these genes to cytogenetic bands of the human chromosomes. Although mitochondria are thought to have originated from bacteria, in which the genes encoding ribosomal proteins are clustered into operons, the mapped MRP genes are widely dispersed throughout the genome, suggesting that transfer of each MRP gene to the nuclear genome occurred individually. We compared the assigned positions with candidate regions for mendelian disorders and found certain genes that might be involved in particular diseases. This map provides a basis for studying possible roles of MRP defects in mitochondrial disorders.

Key words: mitochondria, ribosomal protein, MRP gene, gene mapping, STS, human disease

## **INTRODUCTION**

Mitochondria are thought to be descendants of ancient bacteria that became incorporated into the pre-eukaryotic cell by endosymbiosis during evolution [1,2]. They have their own translation system for production of 13 proteins essential for oxidative phosphorylation in mammals [3]. The mitochondrial ribosome, a central player in this translation system, is also distinct from its cytoplasmic counterpart, consisting of two RNA species (rRNAs) and over 70 different proteins (MRPs) [4,5]. Although the RNA molecules are transcribed from the mitochondrial DNA, the proteins involved in the mitochondrial translation system are encoded by the nuclear genome. They are synthesized in the cytoplasm and imported into the mitochondria where they are assembled into the ribosome. In the case of mammals, only limited information has been available regarding the identities of these proteins and their relationship to bacterial ribosomal proteins. Recently, however, we and other investigators have characterized 31 proteins of the large subunit and 24 proteins of the small subunit through peptide sequencing of purified proteins and extensive screening of the EST databases for corresponding cDNA sequences [6-12]. Interestingly, 38 of these proteins were found to have bacterial homologues

and the other 17 proteins were found to fall into new classes of ribosomal proteins.

Mutations in mitochondrial DNA are known to be associated with a wide spectrum of human diseases with different clinical features, including neuromuscular disorders, diabetes, aplastic anemia, and deafness [reviewed in 13]. Because point mutations in mitochondrial tRNA and rRNA genes have been found in patients with neuromuscular disorders and deafness, respectively [14–17], we are intrigued by the possibility that mutations in MRP genes may result in mitochondrial dysfunction and thereby cause similar pathological conditions. *MRPS12*, the most extensively studied human MRP gene [18–20], has been proposed as a candidate gene for autosomal dominant sensorineural hearing loss, DFNA4 [21].

To systematically explore this possibility, we must first establish the chromosomal map position of each of the human MRP genes. Although a physical map of the human genome based on the genome sequence has been published [22,23], only six MRP genes appeared on the map. Here we localize 54 MRP genes within the human chromosomes using sequence-tagged sites (STSs) identified in individual MRP genes. The assigned positions were further compared with candidate regions for mendelian disorders to investigate the possible roles of MRPs in human disease.

**TABLE 1:** Identification and localization of STSs for human mitochondrial ribosomal protein genes

RRPLI   4q2.1.1   GTGGTACGTGCTTCCTCCC   TTCCCATTGCTTGTAACCA   161   WI-9200   5   SHGC-24579   14   AB09474   AB0						GeneBridge 4		Stanford G3		
MRPL2         6-\$21.3         CETTECATECADAGAGGGG         AGAGGGATRICAGCETTEGGG         181         WI-8282         8         SHCC-3056         4         AB051637           MRPL3         32-1-q23         CCCAAGGCCCTGACTACAC         GACCACTGCTTAATGAATGGG         20         WI-6248         13         SHCC-1562         9         AB049635           MRPL7/LI2         1913.2         GCTGGACAATGCAAGGCCACG         GAGGGCCTCTCCCAGG         201         wI-557         11         SHCC-1983         6         AB051337           MRPL7         121         CGTGGACATTCAGAGACCAC         CTGGACACTCAGAGCCACG         TTGGAGAGCCACGCCACT         18         D178806         7         SHGC-3979         33         AB049636           MRPL11         1133         TAGGATGGACACCCACT         GACACAGACGCAGCGACT         18         D178916         7         SHGC-33767         7         AB05138           MRPL14         6921.3         GCCCACCTGACAGGCAC         CAGCCCCATTCCCACACCT         13         W1-5071         6         SHGC-33767         7         AB05138           MRPL14         1912-913         GATTAGCACCACCCCCACACCTAGA         CAGCTCCACACTAGCCACT         13         W1-5098         2         SHGC-33767         7         AB05138           MRPL14         1912-913	Gene	Location	Forward primer	Reverse primer						
MRP14         9p13.2         CCCAGGCCTACTACAC         GAGCCATCCTTAATGAATGGG         209         WI-6248         13         SHCC-136112         0         AB03136           MRP14         19p13.2         CCCTAGATGGCACCAGCATG         GAGGGGCTTCACATCACAGCT         210         WI-7575         1         SHCC-1362         9         AB04635           MRP13         1q21         GCGGGACAAAGGCACACC         CTGCACCATCTCCCAC         27         NIB288         2         SHCC-3793         33         AB049636           MRP13         1q21.3         CAGGACACAGACCACCAC         TAGGACAGACACCACCAT         148         D175806         7         SHCC-6893         5         AB051338           MRP13         4p21.3         CTCCACCTGAGAGTATATCGC         GACCACAGAGGACACGAGA         20         D115913         0         SHCC-63767         7         AB05138           MRP14         6p12.3         CTCCACACTGCACTCT         GACCACAGAGGACACGAGA         20         D115913         0         SHCC-63284         0         AB051618           MRP14         1p15-5p154         CTCCAGAGCACACCACACA         GACCACAGAGGACCCCAAAT         175         D115945         15         SHCC-1363         A         AB05162           MRP120         1p15-5p154         CTCCAGAGCACACACACACACACACACACACACA	MRPL1	4q21.1	GTGGTACGTGCTTTCCTTCG	TTCTCCATTGCTTCTTAAACCA	161	WI-9200	5	SHGC-24579	14	AB049474
MRP14         19p13.2         GCCTAARTGGCACACATG         GAGGTGCTTCACATCAACAGT         21         WT.7557         1         SHCC-12652         9         AB094935           MRPLIVIL         17q21         CGTGGGACAAGTTGAGACCC         CTTGCACATTTCTCCCCCA         21         n o link         SHCC-12652         9         AB091935           MRPLII         11q13         CAGGTACACACAGACACACC         TTGGGACATTCTCTCCCCA         157         NIB288         2         SHCC-68693         5         AB051618           MRPLII         11q133         TAGATTGGACACCCCATG         CAGGACACACACGACGAGC         148         D175806         7         SHCC-68693         5         AB051618           MRPLI4         6p11.2-q13         CTCCACCTGAGAGTATTCTGCCC         CAGCACACACACGAGGGCA         13         WL5098         2         SHCC-69272         29         AB094640           MRPLI4         6p11.2-q13         CATCACACCACCCCACACGAGAC         CAGCACACACCACACACACACACACACACACACACACAC	MRPL2	6p21.3	CGTTGATCATAACAAACGGG	ACAGGGATATCAGCTTTGGG	181	WI-4822	8	SHGC-30556	47	AB051617
MRPL71121         UPQ25         CGTGGGACAGTGGAGGCAGGC         CTTGGACACTTCGCGGG         157         NIB288         2         SHGC-31983         6         A8051328           MRPL91         17q21.3         CCCAGTACATTCGAGGAGCAGC         CTTGGGAGCACCAGCCAGT         157         NIB288         2         SHGC-6893         3         A8090668           MRPL11         17q21.3         CACAGTACATGGAGGACCACC         CACAGACAGCACGAGGGGTA         17         NIB286         2         SHGC-68972         2         A8091388           MRPL13         6221-q22.3         CTCCAGCTCAGAGATTACGGC         CAGGTCTGAGACTCAGGCCC         176         NIF-5098         2         SHGC-6922         2         A8094694           MRPL14         621.3         CTCCTGACTTCTGGTCGC         GAGGTCTGAGCACTTTCC         176         AFMAGMAWHT         2         SHGC-3928         0         A8091494           MRPL14         1915-59154         ACTCCTAAACCACCTCCTCC         CACATGGAGGCAACACGAA         CATAGGAGGCGACACGAA         CACATGAGAGGCGAACCACGAA         154         CHLCAGTASAG         4         SHGC-11981         AB051621           MRPL20         1936-3-p36.2         CACTTAGGAGGGCACACCAAGA         CACATTCCTCATCTCCAA         188         NIB364         9         SHGC-3198         0         A8051622	MRPL3	3q21-q23	CCCAAGGCCCTGACTACAC	GACCAACTGCTTAATGAATGGG	209	WI-6248	13	SHGC-35112	0	AB051336
MRPLI0         1q21         GEOGGAACTTTGGGAAGCC         CTGGCACATTCTCCCAC         15         NIB288         2         SHGC-5793         33         AB04963           MRPLI0         17q21.3         CCAGTACATCAGAGGAGCACC         TTGAGGAGGACCACCACT         148         D175806         7         SHGC-33767         7         AB051388           MRPLI3         4q221-q223         CTCCACCTGAGATTATCGGC         CAGAACAGACGACGGGGTA         270         D115913         10         SHGC-33767         7         AB051388           MRPLI3         8q12-q13         CTCGGAGGGATCCAGGCGA         CAGCAGTGTACTCGCCCCACTC         176         AFMA084WHI         2         SHGC-5796         0         AB051399           MRPLI5         8q112-q13         GAGAGGGACCCAGCCCCACTC         GACCTCTAACCACCTCCTCC         AGCCTGAGGGATTCCACCC         AGCCTGAGGGACACCACCACC         AGCCTGAGGGACACCACCACCACC         AGCCTGAGGGAGACACCACCACCACCACCACCACCACCACCACCA	MRPL4	19p13.2	GCCTAAATGTGCACAGCATG	GAGGTGCTTCACATCAACAGTG	210	WI-7557	1	SHGC-12652	9	AB049635
MRPLID         17q21.3         CCAGTACATCAGAGAGCACACCATG         TAGGAGAGCACAGCCATT         148         D17S806         7         SHGC-68693         5         A8051618           MRPLII         11q13.3         TAAGATTGGCACACCCCCTG         CACACAGAGACGACAGGGATA         270         D115913         10         SHGC-33767         7         A805138           MRPL14         6 p21.3         GTCCGCCTGACATTTCTGTTGCTGC         CAGGTGCTGCACTTTCTGTTTGCTGC         GCAGGTGATTCTGGTGCG         307         W1-5971         6         5HGC-32834         10         A805139           MRPL15         8112-q13.1         GAATAGCACACTCCCAACATG         AGCTGAGAGGAGATACAAAGCC         16         D115925         5         SHCC-13951         0         A8051619           MRPL16         11q12-q13.1         GAATAGCACTGCCCAACATG         AGCTGAGAGGGAATAGAAATG         175         D115965         5         SHCC-13951         0         A8051619           MRPL12         11p15-5p15.4         ACTCCTAAACCAGCTGCCTC         CAGAGAGGACAAAGGC         166         D115922         14         SHCC-13951         0         A8051621           MRPL20         1p36.3-p36.2         CAGTAGAGAGGCACAAGAG         CCTCATATTTCCGATAGCTC         18         NB1364         9         SHCC-57364         7         A8049642      <	MRPL7/L12	17q25	CGTGGACAAAGTGAAGCTGA	CTGAACACAAGTCCTCCGAG	291	no link		SHGC-31983	6	AB051337
MRPLII         11q13.3         TAAGATTGGACAGCCCACTG         GACAACAGACAGACGGGTA         270         D11S913         10         SHGC-33767         7         AB051338           MRPLI3         6q22-1-q22         CTCCACCTGAACATTATGGGC         CAGGAGGATCCAACGCGC         GACGAGGATCCAACGCGC         33         W1-5098         2         SHGC-69272         29         AB049640           MRPLI5         6q21.3         GTCGGACTTCTCTCTCTGTGCGC         367         W1-5971         6         SHGC-3376         0         AB05139           MRPLI5         11q12-q13.1         CAAGAAGGATCCAACACTG         GGCCGATATGCAACTG         175         D11S996         5         SHGC-13951         0         AB051620           MRPL17         11p155-p15.4         ACTCCTAAACCAGCTCCTCACACTG         GGACCAATGTTCTCTCCAACGC         16         CHILC GATA85A0         48         SHGC-5766         18         AB051621           MRPL20         1913-3-p36.2         CAGTAGGAGCACAGAGA         CCTCATTTCTTCTCCAA         14         CHLC GATA85A0         48         SHGC-5766         7         AB049642           MRPL23         1913-92         593         GTCAACTTCCAGCAGGAC         CCTCATTTCTTCTTCCAA         18         NIB1364         -9         SHGC-57364         7         AB049622           MRPL23 <td>MRPL9</td> <td>1q21</td> <td>GTCGTGAACTTTGAGAAGCC</td> <td>CTTGCACATTTCTGCTCCAC</td> <td>157</td> <td>NIB288</td> <td>2</td> <td>SHGC-57939</td> <td>33</td> <td>AB049636</td>	MRPL9	1q21	GTCGTGAACTTTGAGAAGCC	CTTGCACATTTCTGCTCCAC	157	NIB288	2	SHGC-57939	33	AB049636
MRPL13         8q21-q223         CTCCACCTGAGGATTATCGGC         CAGGTGCTGACTTTCGTTGTCGC         CAGGTGCTGACTTTCTGTTCGCCC         37         W1-5991         6         SHCC-32834         10         AB051339           MRPL14         6p21.3         GTCCTGACTTTCTGTTGTCGCCCCCATTTCC         176         AFMA08WHII         2         SHCC-32841         10         AB051339           MRPL16         11q12-q13.1         GAATAGCACCTGCCAACATG         AGGTGAGGGGGAATAGAAATG         175         D1151965         5         SHCC-13951         0         AB049642           MRPL17         17p15-5-p15.4         CACTCCAAGCACCGCCCAACAGC         GAGCAATAGAAATG         176         D1151965         5         SHCC-13951         0         AB049642           MRPL12         17p13-5-p15.4         CACTCCAAGACCC         CAGGCGCACCAAGACCCCAAGACCCCAAGACCCCAAGACCCCCAAGACCCCCC	MRPL10	17q21.3	CCAGTACATCAGAGAGCAACG	TTGAGGAGAGCACAGCCAAT	148	D17S806	7	SHGC-68693	5	AB051618
MRPL14         6p21.3 of correctact tension of correctact tension of the square tension of the squar	MRPL11	11q13.3	TAAGATTGGACAGCCCACTG	GACAACAGACGACAGGGGTA	270	D11S913	10	SHGC-33767	7	AB051338
MRPL15         8q11.2-q13         CTAGGAAGGATCCAAGGCAG         GATCCTTCAGCCCCTATTCC         176         AFMA084WHI         2         SHGC-5796         0         AB051619           MRPL16         11q12-q13.1         GAATAGCCACTGCCAACATG         AGCTCAGAGGAATAGAARTG         175         D1151965         5         SHGC-13951         0         AB049642           MRPL17         11p15.5-p15.4         ACTCCTAAACCAGCTGCTGC         GTAAAGTCTCCAAAGGC         6         D115922         14         SHGC-1986         8         AB051621           MRPL10         1p36.3-p36.2         CAGTAGGAGGCACACGAAG         GACTAGTGTGATAGCC         GACCTGTGTTTATTGGGTTG         188         NIB1364         -9         SHGC-57364         7         AB049644           MRPL23         1p15.5-p15.4         CTTACAGTTGGAGGGC         ACACTGTGGAGTCTCATCCT         189         PB25D10         2         SHGC-57364         7         AB051621           MRPL23         1p15.5-p15.4         CTTACAGTTGCAGGAGGC         ACCTTGAGTCTGATCCCT         161         D115922         7         SHGC-57627         15         AB051340           MRPL23         1p15.5-p15.4         CTTACAGTTGATCACCAG         AGCATTCCTTCAGCTTCAGC         205         WI-8330         3         SHGC-3627         15         AB051349	MRPL13	8q22.1-q22.3	CTCCACCTGAAGATTATCGGC	CAGGTGCTGAACTGTAGCAG	133	WI-5098	2	SHGC-69272	29	AB049640
MRPL16 $1\bar{q}12-q\bar{1}3.1$ GARTAGCCACTGCCAACATG         AGGCTGAGGGGATAGAAATG         175         D11S1965         5         SHGC-13951         0         AB049642           MRPL17         11p15-5p15.4         ACTCCTAAACCACCTGCTGC         GTAAAATTGCTCCAAAGCGC         166         D11S922         14         SHGC-13951         0         AB051621           MRPL19         1p36.3-p36.2         CACTAGGAGGCGACCGAAG         CCTCATGTCTGTTATTGGGTTG         188         NIB1364         -9         SHGC-57864         7         AB049644           MRPL23         5q33         GTGAAGTGGATGCACGAGG         ACCTCTGTGAGGTCTCCAAGTCTCC         19         FB25D10         2         SHGC-57864         7         AB049644           MRPL24         1q21-q22         CTTAACACTCAGGCAGGGC         ACCTCTGTGAGGCTCTCACCTCTCAG         20         WI-8330         3         SHGC-34121         13         AB051342           MRPL24         1q21-q22         GCTGTGGATCTGATCACCA         ACCTTGACTCTAAG         20         WI-8330         3         SHGC-31935         15         AB049647           MRPL30         1q21         CCTCACTTGACCCAAGACCAC         ACCTTGAGTTCACC         183         D17S797         5         SHGC-31935         15         AB049647           MRPL30         2p1 <td>MRPL14</td> <td>6p21.3</td> <td>GTCCTGACTTTCTGTTGCTGC</td> <td>GGCCAGTAGTATCTGGTCGC</td> <td>307</td> <td>WI-5971</td> <td>6</td> <td>SHGC-32834</td> <td>10</td> <td>AB051339</td>	MRPL14	6p21.3	GTCCTGACTTTCTGTTGCTGC	GGCCAGTAGTATCTGGTCGC	307	WI-5971	6	SHGC-32834	10	AB051339
MRPL17 $1115.5$ - $15.5$ Actoctaraccagctected         GTAAAAGTGCTCCAAAGGCC         166         D118922         14         SHGC-1124         5         AB051621           MRPL19         2p11.2-q11.2         cectagaactagaatcagce         GAGCCAATGTTCTCTCCAA         154         CHLC.GATA85A06         48         SHGC-56989         18         AB051621           MRPL20         136.3-p36.2         cactagacgaccacacagaa         cactagactectaratagger         188         NIB1364         -9         SHGC-57644         7         AB049644           MRPL23         5q33         crtacattectagaacgac         Accattectagactectect         261         D115922         7         SHGC-57627         15         AB051340           MRPL24         1q21-q22         cttaacattectacacacaca         GACATGCCTCAGCCTCAAC         205         WI-8330         3         SHGC-57627         15         AB051340           MRPL30         2q11.2         CCTAGCATACCCCTCAACTCAC         GACATTCCACTCAGCTCTCAACACC         183         D175797         5         SHGC-3167         0         AB051342           MRPL30         2p11.2         CCTCATGTAGACCTCTCATCACACAC         GCACTTAGCACAACACACATCGGAACC         19         WI-4861         3         SHGC-15167         0         AB051342           MRPL30	MRPL15	8q11.2-q13	CTAGGAAGGATCCAAGGCAG	GATCCTTCAGCCCCTATTCC	176	AFMA084WH1	2	SHGC-5796	0	AB051619
MRPL19 $2p11.2-q11.2$ GCTCAGAGAGGGGACACGAGA         GAGCCAATGTATCTTCTGCAA         154         CHLCGATA85A06         48         SHGC-57364         AB051621           MRPL20         1p36.3-p36.2         CAGTAGGGGGGACACGAGAG         CCTCATGTTATTGGGTTG         188         NIB1364         -9         SHGC-57364         7         AB049644           MRPL23         1p15.5-p15.4         CTTACATTCCAGGCAGGAC         AGCATGTGGAGTCTCAATCCC         139         FB25D10         2         SHGC-57627         15         AB051340           MRPL24         1q21-q22         CTTAACAGATGGCCCCAAAG         GAGTGCCTCAGCCTTCAAG         205         WI-8330         3         SHGC-36121         13         AB051341           MRPL37         1q21.3-q22         GCGCACTCACCCACAG         ACCCTTCACTCTCAGGTATCCC         18         D175797         5         SHGC-31935         15         AB049647           MRPL30         2p11         CACCATACCCCTCAAGTTCA         GCATTTCCCATGCACATCAGAC         619         WI-4861         3         SHGC-31935         15         AB049647           MRPL33         2p21         CAAAGAGTCCTCTTCCTGGAC         AGCATTACCCACAAAAGGACCATCAAAC         182         D75668         13         SHGC-3368         7         AB051622           MRPL34         1p32.1 <td>MRPL16</td> <td>11q12-q13.1</td> <td>GAATAGCCACTGCCAACATG</td> <td>AGGCTGAGGGGAATAGAAATG</td> <td>175</td> <td>D11S1965</td> <td>5</td> <td>SHGC-13951</td> <td>0</td> <td>AB049642</td>	MRPL16	11q12-q13.1	GAATAGCCACTGCCAACATG	AGGCTGAGGGGAATAGAAATG	175	D11S1965	5	SHGC-13951	0	AB049642
MRPL20         1p36.3-p36.2         CAGTAGGAGGCGACACGAAG         CCTCATGTCTGTTATTGGGTTG         188         NIB1364         -9         SHGC-57364         7         AB049644           MRPL22         5q33         GTGAAGTTGGGAAGGC         ACACTGTGGAGTCTGAAGTCTC         139         FB25D10         2         SHGC-13988         0         AB051622           MRPL23         11p15.5-p15.4         CTTACATCCAGGCAGGGA         AGCATGCTGTGAGGTCTC         139         FB25D10         2         SHGC-13988         0         AB051622           MRPL24         12p15.5-p15.4         CTTACATCCAGGCAGGGAC         AGCATGCTCTAGAGCTCTCAGGCTTCAGG         205         WI-8330         3         SHGC-31935         15         AB01341           MRPL30         2q11.2         GCACATACCCCTCAAGTTCA         GCATTTTCCAATCGGAAGC         619         WI-4861         3         SHGC-31935         15         AB049647           MRPL30         2q11.2         GCACATACCACACCACCAACAGAACACCACACACACACAC	MRPL17	11p15.5-p15.4	ACTCCTAAACCAGCTGCTGC	GTAAAAGTGCTCCAAAGGCC	166	D11S922	14	SHGC-1124	5	AB051620
MRPL22 $5q33$ GTGAAGTTGGTGGAAGGGC         ACACTGTGGAGTCTGAATCTCC         139         FB25D10         2         SHGC-13988         0         AB051622 $MRPL23$ 11p15-p154         CTTACATTCCAGGCAGGGA         AGCATGCTTAGAGGTCGTC         261         D115922         7         SHGC-37627         15         AB051340 $MRPL24$ 1q21-q22         CTTAACAGATGGCCCAAG         GAAGTGCTCTAGGCTTCAAG         25         WI-8330         3         SHGC-34121         13         AB051341 $MRPL30$ 2q11.2         GCACATACCCCTCAAGTTCA         ACCTTTGAGTTCACCAG         183         D175797         5         SHGC-31935         15         AB049647 $MRPL30$ 2q11.2         GCACATACCCCTCAAGTTCA         GCAGTTGGGAGCACAAGGAGC         182         D75668         13         SHGC-15167         0         AB051342 $MRP132$ 7p14         CCTCATGTAGCCTGAACATC         GCAGTGGGCACAAAGGACATG         182         D75668         13         SHGC-3536         10         AB051342 $MRP133$ 1p31.1         CAGCCGACACAACATCAAC         CCAGCTCCCTGCAAAAATCACAGT         163         WI-4341         12         SHGC-31086         7         AB049652 $MRP137$ 1p32.1 <td>MRPL19</td> <td>2p11.2-q11.2</td> <td>GCTCAGAAGTGGAATCAGCC</td> <td>GAGCCAATGTATCTTCTGCAA</td> <td>154</td> <td>CHLC.GATA85A06</td> <td>48</td> <td>SHGC-56989</td> <td>18</td> <td>AB051621</td>	MRPL19	2p11.2-q11.2	GCTCAGAAGTGGAATCAGCC	GAGCCAATGTATCTTCTGCAA	154	CHLC.GATA85A06	48	SHGC-56989	18	AB051621
MRPL22 $5q33$ GTGAAGTTGGTGGAAGGGC         ACACTGTGGAGTCTGAATCTCC $139$ FB25D10         2         SHGC-13988         0         AB051622 $MRPL23$ $11p15.5-p154$ CTTACATTCCAGGCAGGGA         AGCATGCTTAGAGGTCGTC         261         D115922         7         SHGC-57627 $15$ AB051340 $MRPL24$ $1q21-q22$ CTTAACAGATGGCCCAAAG         AGCATGCTTCAGGCTTCAAC $20$ WI-8330 $3$ SHGC-34121 $13$ AB051341 $MRPL30$ $2q11.2$ GCACATACCCCTCAAGTCA         ACCTTGAGTTCACCA         ACCTTGAGTCACACA         ACCTTGAGTCACACA         ACCTTGAGTCACACA         ACCTTGAGTCACACACACACACACACACACACACACACAC	MRPL20	1p36.3-p36.2	CAGTAGGAGGCGACACGAAG	CCTCATGTCTGTTATTGGGTTG	188	NIB1364	-9	SHGC-57364	7	AB049644
MRPL24         1q21-q22         CTTAACAGATGGCCCCAAAG         GAAGTGCCTCAGCCTTCAAG         205         WI-8330         3         SHGC-34121         13         AB051341           MRPL27         17q21.3-q22         GCTGTGGATCTGATCACCAG         ACCCTTGACTTCTGGTATCACC         183         D17S797         5         SHGC-31935         15         AB049647           MRPL30         2q11.2         GCACATACCCCTCAGTTCA         GCATTTTCCAATCGGAACC         619         WI-4861         3         SHGC-31935         15         AB049647           MRPL32         7p14         CCTCATGTAGCCTGAACATCC         GCAGTAGGCACAAAGGACA         182         D7S668         13         SHGC-4556         10         AB051342           MRPL33         2p21         CAAAGAGTCCTCTTCGTGA         AGGAGGCAGTGATTCCATG         163         WI-4431         2         SHGC-3568         7         AB051623           MRPL33         1p13.1         CAGCCGAGCAACATCAAAC         CCAGCTCCCCAGTCACTGA         163         WI-4431         12         SHGC-31082         7         AB049652           MRPL36         5p15.3         GGAAAATGGAACCCTCTG         CATTCTCCCAGTGAGCAGC         20         D1S417         2         SHGC-1082         7         AB049652           MRPL37         1p32.1         CAGGATCCTAAT	MRPL22		GTGAAGTTGGTGGAAGGGC	ACACTGTGGAGTCTGAATCTCC	139	FB25D10	2	SHGC-13988	0	AB051622
MRPL27         17q21.3-q22         GCTGTGGATCTGATCACCAG         ACCCTTGACTTCTGGTATCACC         183         D17S797         5         SHGC-31935         15         AB049647           MRPL30         2q11.2         GCACATACCCCTCAAGTTCA         GCATTTCCAATCGGAAGC         619         WI-4861         3         SHGC-15167         0         AB051342           MRPL32         7p14         CCTCATGTAGCCTGGAACATCC         GCAGTAGGCACAAAAGGACAT         182         D7S668         13         SHGC-6356         10         AB051343           MRPL33         2p21         CAAAGAGTCCTCTGTGGA         AGGAGGCAGTATTCCATG         163         WI-4431         2         SHGC-33508         7         AB051623           MRPL34         19p13.1         CAGCCGAGCACATCAAAC         CCAGCTCCCTGCAAAATAG         205         WI-6344         12         SHGC-21082         7         AB049652           MRPL36         5p15.3         GGAAAATGCTGGAACCCTCT         CATTCTCCCAAGTCACCG         348         WI-9907         8         SHGC-10589         15         AB049652           MRPL37         1p32.1         CAGGATCCTAATGACCGTGGTCTCTCCAG         20         D15417         2         SHGC-35180         5         AB049654           MRPL38         17q23-q25         GGTGAGGATGACCTGATGC	MRPL23	11p15.5-p15.4	CTTACATTCCAGGCAGGGAC	AGCATGCTGTAGAGGTCGTC	261	D11S922	7	SHGC-57627	15	AB051340
MRPL30         2q11.2           GCACATACCCCTCAAGTTCA         GCATTTTCCAATCGGAAGC         619         WI-4861         3         SHGC-15167         0         AB051342           MRPL32         7p14         CCTCATGTAGCCTGAACATCC         GCAGTAGGCACAAAGGACATG         182         D7S668         13         SHGC-6356         10         AB051343           MRPL33         2p21         CAAAGAGTCCTCTTCGTGGA         AGGAGGCAGTGATTCCATG         163         WI-4431         2         SHGC-33508         7         AB051623           MRPL34         19p13.1         CAGCCGAGCAACATCAAC         CCAGCTCCCTGCAAAAATAG         205         WI-6344         12         SHGC-31082         7         AB049652           MRPL36         5p15.3         GGAAAATGGTGAACCCTCT         CATTCTCCCAGTGAGCAGG         348         WI-9907         8         SHGC-10589         15         AB049654           MRPL37         1p32.1         CAGGATCCTAATGAACCGTG         TATTGTCAGCGAGAGCAGG         20         D15417         2         SHGC-35810         5         AB051344           MRPL37         1p32.1         CAGGAGGAGCCTCGATGCG         TATTGTCAGCGAGAGCACCA         190         no link         5HGC-37061         5         AB051344           MRPL39         21q11.2         CCTCCAGGCTAGAGCAGC         <	MRPL24	1q21-q22	CTTAACAGATGGCCCCAAAG	GAAGTGCCTCAGCCTTCAAG	205	WI-8330	3	SHGC-34121	13	AB051341
MRPL32         7p14         CCTCATGTAGCCTGAACATCC         GCAGTAGGCACAAAGGACATC         182         D7S668         13         SHGC-6356         10         AB051343           MRPL33         2p21         CAAAGAGTCCTCTTCGTGGA         AGGAGGCAGTGATTCCATG         163         WI-4431         2         SHGC-33508         7         AB051623           MRPL34         19p13.1         CAGCCGAGCAACATCAAAC         CCAGCTCCCTGCAAAAATAG         205         WI-6344         12         SHGC-21082         7         AB049652           MRPL36         5p15.3         GGAAAATGGTCAACCGTG         CATTCTCCCAAGTGATCGC         348         WI-9907         8         SHGC-10589         15         AB049664           MRPL37         1p32.1         CAGGGATCCTAATGAACCGTG         TATTGTCAGCGAGAGCAGC         220         D15417         2         SHGC-58180         5         AB051345           MRPL38         17q23-q25         GGTGAGATGACCTGATGC         GTCATGACAGGAGGCACC         190         no link         SHGC-58180         5         AB051345           MRPL40         22q11.2         CCTCCCAGTCCAGGAATATC         CCTCGATACCGAGCTACTC         370         WI-326         4         SHGC-3725         6         AB051625           MRPL41         19q34.3         GCAGCATCTGGCATAAT <th< td=""><td>MRPL27</td><td>17q21.3-q22</td><td>GCTGTGGATCTGATCACCAG</td><td>ACCCTTGACTTCTGGTATCACC</td><td>183</td><td>D17S797</td><td>5</td><td>SHGC-31935</td><td>15</td><td>AB049647</td></th<>	MRPL27	17q21.3-q22	GCTGTGGATCTGATCACCAG	ACCCTTGACTTCTGGTATCACC	183	D17S797	5	SHGC-31935	15	AB049647
MRPL33         2p21         CAAAGAGTCCTCTTCGTGGA         AGGAGGCAGTGATTCCATG         163         WI-4431         2         SHGC-33508         7         AB051623           MRPL34         19p13.1         CAGCCGAGCAACATCAAAC         CCAGCTCCCTGCAAAAATAG         205         WI-6344         12         SHGC-21082         7         AB049652           MRPL36         5p15.3         GGAAAATGGTGAACCCTCTG         CATTCTCCCAAGTGATGCG         348         WI-9907         8         SHGC-10589         15         AB049654           MRPL37         1p32.1         CAGGATCCTAATGAACCGTG         TTATTGTCAGCGAGAGCACC         220         D15417         2         SHGC-58180         5         AB051344           MRPL38         17q23-q25         GGTGAGGATGACCTGATGC         GTCATGGCGAGCACCA         190         no link         SHGC-37061         5         AB051344           MRPL39         21q11.2-q21         ATACAGCTCTGCCAGCAGCACC         CGTCATAACAGAAGCCACA         192         WI-7427         6         SHGC-37061         5         AB051344           MRPL40         22q11.2         CCTCCCAGTCCACGAATATC         CCTGTAATCCGAGCTACTCC         370         WI-326         4         SHGC-37250         6         AB051624           MRPL41         9q34.3         GCAGCTCTGATAATAT	MRPL30	2q11.2	GCACATACCCCTCAAGTTCA	GCATTTTCCAATCGGAAGC	619	WI-4861	3	SHGC-15167	0	AB051342
MRPL34         19p13.1         CAGCCGAGCAACATCAAAC         CCAGCTCCCTGCAAAAAATAG         205         WI-6344         12         SHGC-21082         7         AB049652           MRPL36         5p15.3         GGAAAATGGTGAACCCTCTG         CATTCTCCCAAGTGATGCG         348         WI-9907         8         SHGC-10589         15         AB049654           MRPL37         1p32.1         CAGGATCCTAATGAACCGTG         TTATTGTCAGCGAGAGCAGC         220         D15417         2         SHGC-37061         5         AB051344           MRPL38         17q23-q25         GGTGAGGATGACCTGATGC         GTCATGACGGAGCACCA         190         no link         SHGC-37061         5         AB051345           MRPL39         21q11.2-q21         ATAGAGCTCTGCACAGAATATC         CCTGTAATCCGAGCTCACCG         192         WI-7427         6         SHGC-37061         5         AB051346           MRPL40         22q11.2         CCTCCCAGCTCTACAGGAAGC         CGTGAATCCTGGGGTAGAGC         140         D9S158         5         SHGC-37831         56         AB051625           MRPL41         19q22         GGCCAGATCCTGGCATAAT         CCGTCCATGAGGAACCAC         155         D12S351         4         SHGC-37119         10         AB051626           MRPL43         10q24         CCCAGGCTTTGCATAGTAC </td <td>MRPL32</td> <td>_</td> <td>CCTCATGTAGCCTGAACATCC</td> <td>GCAGTAGGCACAAAGGACATG</td> <td>182</td> <td>D7S668</td> <td>13</td> <td>SHGC-6356</td> <td>10</td> <td>AB051343</td>	MRPL32	_	CCTCATGTAGCCTGAACATCC	GCAGTAGGCACAAAGGACATG	182	D7S668	13	SHGC-6356	10	AB051343
MRPL365p15.3GGAAAATGGTGAACCCTCTGCATTCTCCCAAGTGATGCG348WI-99078SHGC-1058915AB049654MRPL371p32.1CAGGATCCTAATGAACCGTGTTATTGTCAGCGAGAGCAGC220D1S4172SHGC-581805AB051344MRPL3817q23-q25GGTGAGGATGACCTGATGCGTCATGGTGTCGTCTTCCAG190no linkSHGC-370615AB051345MRPL3921q11.2-q21ATAGAGCTCTGGCAAGCAGCCGTCATAACAGAAGGCACCA192WI-74276SHGC-652310AB051346MRPL4022q11.2CCTCCCAGTCCACGAATATCCCTGTAATCCGAGCTACTCG370WI-3264SHGC-783156AB051624MRPL419q34.3GCAGCTCTTCAGCGAAGCGGAAGTTCCTGGGGTAGAGC140D9S1585SHGC-372506AB051625MRPL4212q22GGCCAGATCCTGTGCATAATCCGTCCATGAGGGTACCAAC155D12S3514SHGC-3111910AB051626MRPL4310q24CCCAGGCCTTTGGACTGTTACGATGCCACTTGCATAAAAATG195AFM183XB123SHGC-34187AB049656MRPS29q34GCTTCCCAGCCCATAGTGGTGGCTGTCTGTTCCAGGTC199WI-14054SHGC-6347238AB051627MRPS415q24GGAGGCACTTGTCACTTGGGGCACCCTCATAGAATCTCCAG171CHLC.GATA85D027SHGC-1342140AB051628MRPS52p11.2-q11.2GGATCCAGAGCCAGAAGATGGGCTGAGTCTCTCCTAGGTGC174CHLC.GATA85A0673SHGC-5704224AB049940MRPS621q21.3-q2	MRPL33	2p21	CAAAGAGTCCTCTTCGTGGA	AGGAGGCAGTGATTCCATG	163	WI-4431	2	SHGC-33508	7	AB051623
MRPL37         1p32.1         CAGGATCCTAATGAACCGTG         TTATTGTCAGCGAGAGCAGC         220         D1S417         2         SHGC-58180         5         AB051344           MRPL38         17q23-q25         GGTGAGGATGACCTGATGC         GTCATGGTGTCGTCTTCCAG         190         no link         SHGC-37061         5         AB051345           MRPL39         21q11.2-q21         ATAGAGCTCTGGCAAGCAGC         CGTCATAACAGAAGGCACCA         192         WI-7427         6         SHGC-37061         5         AB051345           MRPL40         22q11.2         CCTCCCAGTCCACGAATATC         CCTGGTAATCCGAGCTCTCG         370         WI-326         4         SHGC-37250         6         AB051624           MRPL41         9q34.3         GCAGCTCTTCAGCGAAGC         GGAAGTTCCTGGGGTAGACC         140         D9S158         5         SHGC-37250         6         AB051625           MRPL42         12q22         GGCCAGATCCTGTGCATAAT         CCGTCCATGAGGATACCAAC         155         D12S351         4         SHGC-31119         10         AB051626           MRPL43         10q24         CCCAGGCTTTGGACTGTTAC         GATGCCACTTGAGTAATAT         195         AFM183XB12         3         SHGC-24148         7         AB049656           MRPS4         15q24         GGAGGACTTGACTTGCCTGAGATCT	MRPL34	19p13.1	CAGCCGAGCAACATCAAAC	CCAGCTCCCTGCAAAAATAG	205	WI-6344	12	SHGC-21082	7	AB049652
MRPL38         17q23-q25         GGTGAGGATGACCTGATGC         GTCATGGTGTCTCTCCAG         190         no link         SHGC-37061         5         AB051345           MRPL39         21q11.2-q21         ATAGAGCTCTGGCAAGCAGC         CGTCATAACAGAAGGCACCA         192         WI-7427         6         SHGC-37061         5         AB051346           MRPL40         22q11.2         CCTCCCAGTCCACGAATATC         CCTGTAATCCGAGCTACTCG         370         WI-326         4         SHGC-37831         56         AB051624           MRPL41         9q34.3         GCAGCTCTTCAGCGAAGC         GGAAGTTCCTGGGGTAGAGC         140         D9S158         5         SHGC-37250         6         AB051625           MRPL42         12q22         GGCCAGATCCTGTGCATAAT         CCGTCCATGAGGATACCAAC         155         D12S351         4         SHGC-37119         10         AB051626           MRPL43         10q24         CCCCAGGCTTTGGACTGTTAC         GATGCCACTTGCATAAAAAATG         195         AFM183XB12         3         SHGC-34148         7         AB049656           MRPS2         9q34         GCTTCCCAGCCCATAGTG         GTGGCTGTTCTCTCAGGTC         199         WI-1405         4         SHGC-3472         38         AB051628           MRPS4         15q24         GGAGGACTTTGCACTTGGG	MRPL36	5p15.3	GGAAAATGGTGAACCCTCTG	CATTCTCCCAAGTGATGCG	348	WI-9907	8	SHGC-10589	15	AB049654
MRPL39         21q11.2-q21         ATAGAGCTCTGGCAAGCAGC         CGTCATAACAGAAGGCACCA         192         WI-7427         6         SHGC-6523         10         AB051346           MRPL40         22q11.2         CCTCCCAGTCCACGAATATC         CCTGTAATCCGAGCTACTCG         370         WI-326         4         SHGC-7831         56         AB051624           MRPL41         9q34.3         GCAGCTCTTCAGCGAAGC         GGAAGTTCCTGGGGTAGAGC         140         D9S158         5         SHGC-37250         6         AB051625           MRPL42         12q22         GGCCAGATCCTGTGCATAAT         CCGTCCATGAGGATACCAAC         155         D12S351         4         SHGC-37119         10         AB051626           MRPL43         10q24         CCCAGGCTTTGGACTGTTAC         GATGCCACTTGCATAAAAATG         195         AFM183XB12         3         SHGC-24148         7         AB049656           MRPS2         9q34         GCTTCCCAGCCCATAGTG         GTGGCTGTCTGTTCCAGGTC         199         WI-1405         4         SHGC-63472         38         AB051628           MRPS4         15q24         GGAGGACTTTGCACTTGGG         GCACCCTCATAGAATCTCCAG         171         CHLC.GATA85A06         73         SHGC-13421         40         AB049940           MRPS6         21q21.3-q22.1	MRPL37	1p32.1	CAGGATCCTAATGAACCGTG	TTATTGTCAGCGAGAGCAGC	220	D1S417	2	SHGC-58180	5	AB051344
MRPL40 $22q11.2$ CCTCCCAGTCCACGAATATCCCTGTAATCCGAGCTACTCG $370$ WI-326 $4$ SHGC-7831 $56$ $AB051624$ $MRPL41$ $9q34.3$ GCAGCTCTTCAGCGAAGCGGAAGTTCCTGGGGTAGAGC $140$ D9S158 $5$ SHGC-37250 $6$ $AB051625$ $MRPL42$ $12q22$ GGCCAGATCCTGTGCATAATCCGTCCATGAGGATACCAAC $155$ D12S351 $4$ SHGC-31119 $10$ $AB051626$ $MRPL43$ $10q24$ CCCAGGCTTTGGACTGTTACGATGCCACTTGCATAAAAATG $195$ $AFM183XB12$ $3$ $SHGC-24148$ $7$ $AB049656$ $MRPS2$ $9q34$ GCTTCCCAGCCCATAGTGGTGGCTGTTTCCAGGTC $199$ WI-1405 $4$ $SHGC-63472$ $38$ $AB051627$ $MRPS4$ $15q24$ GGAGGACTTTGTCACTTGGGGCACCCTCATAGAATCTCCAG $171$ $CHLC.GATA85D02$ $7$ $SHGC-13421$ $40$ $AB051628$ $MRPS5$ $2p11.2-q11.2$ GGATCCAGAGCCAGAAGATGGGCTGAGTCTCTCCTAGGTGC $174$ $CHLC.GATA85A06$ $73$ $SHGC-57042$ $24$ $AB049940$ $MRPS6$ $21q21.3-q22.1$ GCCCTGATGGACAGAGGGGATCATAGTCCACGAAGGGC $296$ $WI-4888$ $10$ $SHGC-21163$ $31$ $AB051348$ $MRPS7$ $17q23-q25$ GGTGAGGGAAGCTCGAAGA $CCGGCACTCAGTGATCATC$ $228$ $no link$ $SHGC-329$ $3$ $AB051348$	MRPL38	17q23-q25	GGTGAGGATGACCTGATGC	GTCATGGTGTCGTCTTCCAG	190	no link		SHGC-37061	5	AB051345
MRPL40 $22q11.2$ CCTCCCAGTCCACGAATATCCCTGTAATCCGAGCTACTCG $370$ WI-326 $4$ SHGC-7831 $56$ AB051624 $MRPL41$ $9q34.3$ GCAGCTCTTCAGCGAAGCGGAAGTTCCTGGGGTAGAGC $140$ D9S158 $5$ SHGC-37250 $6$ AB051625 $MRPL42$ $12q22$ GGCCAGATCCTGTGCATAATCCGTCCATGAGGATACCAAC $155$ D12S351 $4$ SHGC-31119 $10$ AB051626 $MRPL43$ $10q24$ CCCAGGCTTTGGACTGTTACGATGCCACTTGCATAAAAATG $195$ AFM183XB12 $3$ SHGC-24148 $7$ AB049656 $MRPS2$ $9q34$ GCTTCCCAGCCCATAGTGGTGGCTGTTTCCAGGTC $199$ WI-1405 $4$ SHGC-63472 $38$ AB051627 $MRPS4$ $15q24$ GGAGGACTTTGTCACTTGGGGCACCCTCATAGAATCTCCAG $171$ CHLC.GATA85D02 $7$ SHGC-13421 $40$ AB051628 $MRPS5$ $2p11.2-q11.2$ GGATCCAGAGCCAGAAGATGGGCTGAGTCTCTCCTAGGTGC $174$ CHLC.GATA85A06 $73$ SHGC-57042 $24$ AB049940 $MRPS6$ $21q21.3-q22.1$ GCCCTGATGGACAGAGGGGATCATAGTCCACGAAGGGC $296$ WI-4888 $10$ SHGC-21163 $31$ AB051347 $MRPS7$ $17q23-q25$ GGTGAGGGAAGCTCGAAGACCGGCACTCAGTGATCATC $228$ no linkSHGC-329 $3$ AB051348	MRPL39	21q11.2-q21	ATAGAGCTCTGGCAAGCAGC	CGTCATAACAGAAGGCACCA	192	WI-7427	6	SHGC-6523	10	AB051346
MRPL42         12q22         GGCCAGATCCTGTGCATAAT         CCGTCCATGAGGATACCAAC         155         D12S351         4         SHGC-31119         10         AB051626           MRPL43         10q24         CCCAGGCTTTGGACTGTTAC         GATGCCACTTGCATAAAAATG         195         AFM183XB12         3         SHGC-24148         7         AB049656           MRPS2         9q34         GCTTCCCAGCCCATAGTG         GTGGCTGTCTGTTCCAGGTC         199         WI-1405         4         SHGC-63472         38         AB051627           MRPS4         15q24         GGAGGACTTTGTCACTTGGG         GCACCCTCATAGAATCTCCAG         171         CHLC.GATA85D02         7         SHGC-13421         40         AB051628           MRPS5         2p11.2-q11.2         GGATCCAGAGCCAGAAGATG         GGCTGAGTCTCTCCTAGGTGC         174         CHLC.GATA85A06         73         SHGC-57042         24         AB049940           MRPS6         21q21.3-q22.1         GCCCTGATGGACAGAGGG         GATCATAGTCCACGAAGGGC         296         WI-4888         10         SHGC-21163         31         AB051348           MRPS7         17q23-q25         GGTGAGGGAAGCTCGAAGA         CCGGCACTCAGTGATCATC         228         no link         SHGC-329         3         AB051348	MRPL40		CCTCCCAGTCCACGAATATC	CCTGTAATCCGAGCTACTCG	370	WI-326	4	SHGC-7831	56	AB051624
MRPL43         10q24         CCCAGGCTTTGGACTGTTAC         GATGCCACTTGCATAAAAATG         195         AFM183XB12         3         SHGC-24148         7         AB049656           MRPS2         9q34         GCTTCCCAGCCCATAGTG         GTGGCTGTTCTGTTCCAGGTC         199         WI-1405         4         SHGC-63472         38         AB051627           MRPS4         15q24         GGAGGACTTTGTCACTTGGG         GCACCCCTCATAGAATCTCCAG         171         CHLC.GATA85D02         7         SHGC-13421         40         AB051628           MRPS5         2p11.2-q11.2         GGATCCAGAGCCAGAAGATG         GGCTGAGTCTCTCCTAGGTGC         174         CHLC.GATA85A06         73         SHGC-57042         24         AB049940           MRPS6         21q21.3-q22.1         GCCCTGATGGACGAGGG         GATCATAGTCCACGAAGGGC         296         WI-4888         10         SHGC-21163         31         AB051347           MRPS7         17q23-q25         GGTGAGGGAAGCTCGAAGA         CCGGCACTCAGTGATCATC         228         no link         SHGC-329         3         AB051348	MRPL41	9q34.3	GCAGCTCTTCAGCGAAGC	GGAAGTTCCTGGGGTAGAGC	140	D9S158	5	SHGC-37250	6	AB051625
MRPL43 $10q24$ CCCAGGCTTTGGACTGTTACGATGCCACTTGCATAAAAATG $195$ $AFM183XB12$ $3$ $SHGC-24148$ $7$ $AB049656$ $MRPS2$ $9q34$ GCTTCCCAGCCCATAGTGGTGGCTGTCTGTTCCAGGTC $199$ $WI-1405$ $4$ $SHGC-63472$ $38$ $AB051627$ $MRPS4$ $15q24$ GGAGGACTTTGTCACTTGGGGCACCCTCATAGAATCTCCAG $171$ $CHLC.GATA85D02$ $7$ $SHGC-13421$ $40$ $AB051628$ $MRPS5$ $2p11.2-q11.2$ GGATCCAGAGCCAGAAGATGGGCTGAGTCTCTCCTAGGTGC $174$ $CHLC.GATA85A06$ $73$ $SHGC-57042$ $24$ $AB049940$ $MRPS6$ $21q21.3-q22.1$ GCCCTGATGGACAGAGGGATCATAGTCCACGAAGGGC $296$ $WI-4888$ $10$ $SHGC-21163$ $31$ $AB051347$ $MRPS7$ $17q23-q25$ GGTGAGGGAAGCTCGAAGACCGGCACTCAGTGATCATC $228$ $no$ link $SHGC-329$ $3$ $AB051348$	MRPL42	12q22	GGCCAGATCCTGTGCATAAT	CCGTCCATGAGGATACCAAC	155	D12S351	4	SHGC-31119	10	AB051626
MRPS2         9q34         GCTTCCCAGCCCATAGTG         GTGGCTGTCTGTTCCAGGTC         199         WI-1405         4         SHGC-63472         38         AB051627           MRPS4         15q24         GGAGGACTTTGTCACTTGGG         GCACCCTCATAGAATCTCCAG         171         CHLC.GATA85D02         7         SHGC-13421         40         AB051628           MRPS5         2p11.2-q11.2         GGATCCAGAGCCAGAAGATG         GGCTGAGTCTCTCCTAGGTGC         174         CHLC.GATA85A06         73         SHGC-57042         24         AB049940           MRPS6         21q21.3-q22.1         GCCCTGATGGACAGAGGG         GATCATAGTCCACGAAGGGC         296         WI-4888         10         SHGC-21163         31         AB051347           MRPS7         17q23-q25         GGTGAGGGAAGCTCGAAGA         CCGGCACTCAGTGATCATC         228         no link         SHGC-329         3         AB051348	MRPL43	_	CCCAGGCTTTGGACTGTTAC	GATGCCACTTGCATAAAAATG	195	AFM183XB12	3	SHGC-24148	7	AB049656
MRPS415q24GGAGGACTTTGTCACTTGGGGCACCCTCATAGAATCTCCAG171CHLC.GATA85D027SHGC-1342140AB051628MRPS52p11.2-q11.2GGATCCAGAGCCAGAAGATGGGCTGAGTCTCTCCTAGGTGC174CHLC.GATA85A0673SHGC-5704224AB049940MRPS621q21.3-q22.1GCCCTGATGGACAGAGGGGATCATAGTCCACGAAGGC296WI-488810SHGC-2116331AB051347MRPS717q23-q25GGTGAGGGAAGCTCGAAGACCGGCACTCAGTGATCATC228no linkSHGC-3293AB051348	MRPS2	_	GCTTCCCAGCCCATAGTG	GTGGCTGTCTGTTCCAGGTC	199	WI-1405	4	SHGC-63472	38	AB051627
MRPS5 2p11.2-q11.2 GGATCCAGAGCCAGAAGATG GGCTGAGTCTCTCCTAGGTGC 174 CHLC.GATA85A06 73 SHGC-57042 24 AB049940 MRPS6 21q21.3-q22.1 GCCCTGATGGACAGAGGAG GATCATAGTCCACGAAGGGC 296 WI-4888 10 SHGC-21163 31 AB051347 MRPS7 17q23-q25 GGTGAGGGAAGCTCGAAGA CCGGCACTCAGTGATCATC 228 no link SHGC-329 3 AB051348	MRPS4	-	GGAGGACTTTGTCACTTGGG	GCACCCTCATAGAATCTCCAG	171	CHLC.GATA85D02	7	SHGC-13421	40	AB051628
MRPS6 21q21.3-q22.1 GCCCTGATGGACAGAGGA GATCATAGTCCACGAAGGGC 296 WI-4888 10 SHGC-21163 31 AB051347 MRPS7 17q23-q25 GGTGAGGGAAGGACTCGAAGA CCGGCACTCAGTGATCATC 228 no link SHGC-329 3 AB051348	MRPS5	1	GGATCCAGAGCCAGAAGATG	GGCTGAGTCTCTCCTAGGTGC	174	CHLC.GATA85A06	73	SHGC-57042	24	AB049940
MRPS7 17q23-q25 GGTGAGGGAAGCTCGAAGA CCGGCACTCAGTGATCATC 228 no link SHGC-329 3 AB051348	MRPS6		GCCCTGATGGACAGAGGAG	GATCATAGTCCACGAAGGGC	296	WI-4888	10	SHGC-21163	31	AB051347
	MRPS7		GGTGAGGGAAGCTCGAAGA	CCGGCACTCAGTGATCATC	228	no link		SHGC-329	3	AB051348
	MRPS11		GCAGAAAGTTGAACAGAACGC	CTCTGTACCACGGCTCATCTG	253	D15S151	3	SHGC-57656	14	AB051349

			TABLE 1: continued	nued					
					GeneBridge 4		Stanford G3	63	
Gene	Location	Forward primer	Reverse primer	Size (bp)	Linked D marker (c	Dist. (cR) <sup>a</sup>	Linked marker	Dist. (cR) <sup>a</sup>	Accession no. <sup>b</sup>
MRPS12	19q13.1-q13.2	CTGGGGTCCTCCAAATCTAC	CAAGTTAGGGACGTGTTGAGG	331	D19S425	8	SHGC-11892	11	AF058761
MRPS14	1q23-q25	GTAGACTGGAGAATGTGGCG	GCTGGCATAATGAAACAGTTG	333	WI-5780	e ;	SHGC-19939	ro (	AB051350
MRPS15 MRPS16	1p35-p34.1 10a22 1	GCTGAAGAAGCGAAGAAGAGC	GAACAGAATTTAATTGGCTGTCT	327	WI-611 WI-2997	111	SHGC-57691 SHGC-17474	10	AB049946 AB051351
MRPS17	7p11-q11.21	CCTGGCTTGTTTTCCATACG	CCCAACTGTGCACTGCTG	158	WI-4253	. го	SHGC-11581	_	AB051352
MRPS18A	6p21.3	GTCACCCCTTCTGAGGGAC	GGAGTATAGTTGTGGCCAAGG	148	WI-6092	3	SHGC-421	20	AB049952
MRPS21	1921	GGACACCCAGTGCGAAAC	GTCCACTGCTGACTAATGGG	154	WI-497	^	SHGC-32206	16	AB051353
MRPS22	3q23	GCCTCCAGATTTCTCTCTAACC GAATGGCGACTGAGTGCTTC	GAATGGCGACTGAGTGCTTC	401	D3S1576	5	SHGC-12501	0	AB061314
MRPS23	17q22-q23	GTGTATGGGTCTGGTCAAAGAG	TTCCAAGCAGTCACATTTTAGG	189	WI-6277	4	SHGC-2434	25	AB061206
MRPS24	7p14	GAGAAGAGGCTGGGGGTG	GCGCTTTAAAACCAGCTGG	237	D7S668	12	SHGC-13468	0	AB061207
MRPS25	3p25	GCACCCTGCAATATCTGAGC	GTAAAATGGGGGTAACAGCG	246	WI-7376	0	SHGC-64041	7	AB061208
MRPS26	20p13	CTCAGTGGGGTGAGAGGC	GTGATGGCCCAGTTGTAGTTC	180	WI-3904	7	SHGC-14786	16	AB051354
MRPS28	8q21.1-q21.2	GTTCCAATGCCAAGGAGC	CGCAACTCCGGAAAACTG	229	CHLC.GATA85E10	10	SHGC-10609	38	AB061209
MRPS29	1q21-q22	AGCCTCCAACCTTTTCAAGG	GTTCCTCACCCGTGTTATGC	271	D1S305	3	SHGC-84872	20	AB061210
MRPS30	5p12-q11	TCAAACGGCAGTATGAAAACC	CATGCATGGCACAAATAGGA	392	no link		SHGC-56603	19	AB061211
MRP63	13p11.1-q11	AGTGGATCGGGAAGCACC	GTGACATTGAGATGGTCGAGC	247	WI-8572	-20	SHGC-6104	35	AB049957
MRP64	12p13.3-p13.1	CCAAAGTGGTTGATCGTTG	CACCAGCTAAGCTTTCAACC	412	CHLC.GATA7F09.414	5	SHGC-12737	16	AB051355
<sup>a</sup> Distance from	the linked marker in o	rentiBays, for example, MRPL1 was placed	Pistance from the linked marker in centifiavs, for example, MRPL1 was placed at 5 cR from WL-9200 or at 14 cR from SHCC-24579	3C-24579.					

# Distance from the linked marker in centiRays, for example, MRPL1 was placed at 5 cR from WI-9200 or at 14 cR from SHGC-2457 STS sequence or sequence from which the STS was generated.

# **R**ESULTS

### **Identification of STSs in Human MRP Genes**

We have purified mitochondrial ribosomes from bovine liver and identified more than 70 bovine MRPs by two-dimensional gel electrophoresis [12]. The partial amino acid sequences of these proteins enabled us to obtain the cDNA sequences of the human MRP genes. We developed 54 STSs using these cDNA sequences (Table 1). Among them, 24 STSs contain only exon sequences, thus were chosen from a single exon of the gene, whereas the other 30 STSs contain a part of an intron sequence, as determined by resequencing of the draft sequence of the human genome. We confirmed the specificity of these STSs to the individual human MRP genes by PCR followed by sequencing of the products. The primer sequences along with the product size and the accession number for the cDNA sequence or the partial genomic sequence are listed in Table 1.

# Mapping of 54 MRP Genes

The STSs were then subjected to typing on the basis of two different radiation hybrid mapping panels: GeneBridge 4 and Stanford G3 [24,25]. They were placed on the STS-content map of the human genome (Fig. 1). The results obtained from the two panels were in agreement, except in four cases (MRPL7/12, MRPL38, MRPS7, and MRPS30) in which the data vector obtained with the GeneBridge 4 panel indicated no linkage (Table 1). The 54 genes mapped are widely dispersed throughout the genome. Clustering of RP genes into operons, characteristic of bacteria [26], is not apparent in the case of the MRP genes, even though mitochondria are thought to have been generated originally by bacterial endosymbiosis.

# Assignment to the Cytogenetic Map

To facilitate investigation of the possible involvement of MRP genes in human disease, it would be helpful to know the cytogenetic positions of these genes. We referred to a cytogenetic BAC-STS map of the human genome, constructed by **FISH** analysis of 957 human BACs(http://www.csmc.edu/genetics/korenberg/int-bac-sts.html) [27], and assigned the MRP genes to the cytogenetic bands of individual chromosomes (Fig. 1). Almost all of the genes were placed in a region corresponding to one or two cytogenetic bands. Furthermore, we compared the positions of these genes with candidate

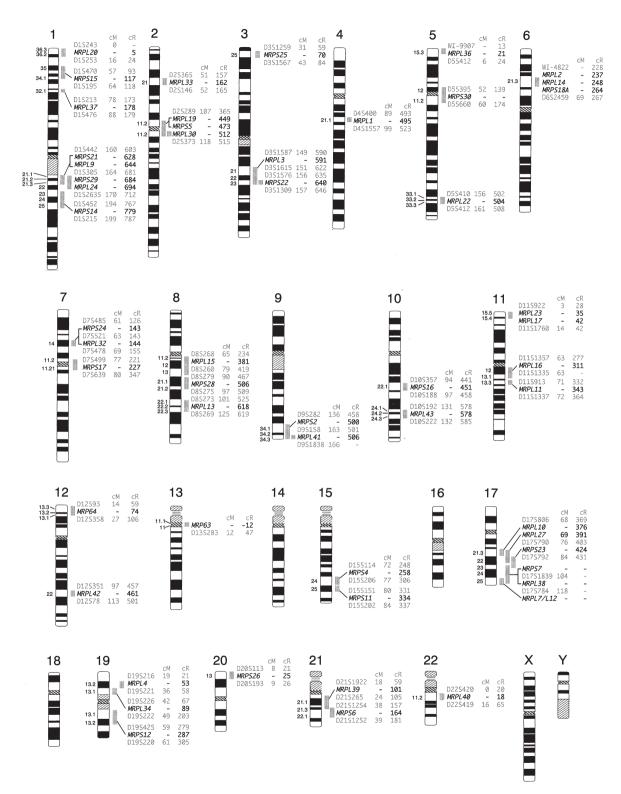


FIG. 1. A map of 54 human mitochondrial ribosomal protein (MRP) genes. To the right of each chromosome are shown the MRP genes, nearby markers, and the approximate distances (in cM and/or cR) from the most distal short-arm marker on the STS-content map constructed at the Whitehead Institute/MIT Center for Genome Research (http://www-genome.wi.mit.edu/cgi-bin/contig/phys-map) [24]. Bold vertical lines indicate the cytogenetic locations according to the cytogenetic BAC-STS map of the human genome (http://www.csmc.edu/genetics/korenberg/int-bac-sts.html) [27].

TABLE 2: Intervals for human mitochondrial RP genes and linked disorders

		Region		Region	MIM
Gene	Location	(cM)	Disorder	(cM)	No.
MRPL3	3q21-q23	149-151	Moebius syndrome 2	144-156	601471
MRPL4	19p13.2	19-36	DFNB15 <sup>a</sup>	11-36	601869
MRPL9	1q21	160-164	Retinitis pigmentosa 18	160-164	601414
MRPL39	21q11.2-q21	18-24	USH1E <sup>b</sup>	19-29	602097
MRPS12	19q13.1-q13.2	59-61	DFNA4 <sup>c</sup>	59-70	600652
MRPS14	1q23-q25	194-199	DFNA7 <sup>d</sup>	183-194	601412
MRPS23	17q22-q23	76-84	Retinitis pigmentosa 17	76-84	600852
MRPS26	20p13	8-9	Hallervorden-Spatz syndrome	8-11	234200

<sup>&</sup>lt;sup>a</sup>Deafness, autosomal recessive 15

regions for mendelian disorders and found certain MRP genes that reside within the small intervals for particular disorders (Table 2).

### **DISCUSSION**

Only six human MRP genes, MRPS12, MRPL3, MRPL7/L12, MRPL19, MRPL23, and MRPL37, have been mapped previously [21,23,28,29]. Here we have mapped an additional 48 genes to the chromosomes. Recent identification of mammalian MRPs [6–12] allowed us to accomplish this mapping. So far, 57 mammalian MRPs have been identified: 31 and 24 in the large and small subunits, respectively, and 2 proteins for which the subunit localization remains to be determined. To simplify the nomenclature, we have named the human MRPs after their bacterial homologues; that is, the MRP genes given the designations MRPL1 to MRPL36 correspond to the bacterial RPs L1 to L36, MRPS1 to MRPS21 correspond to the bacterial RPs S1 to S21, and those given other designations are specific to the human mitochondrion, for example, MRPL37 and MRPS22. Although the exact number of MRPs is still unclear, we estimate that it is between 70 and 80 in total, based on the results of two-dimensional gel electrophoresis of these proteins (data not shown). Identification of the rest of the proteins and mapping of the genes are under way.

In contrast, localization of the cytoplasmic RP genes has been completed [30–32]. Though scattered about the genome like the MRP genes, each cytoplasmic RP gene has a large number of processed pseudogenes at sites dispersed throughout the genome. It is unlikely that the MRP genes also have such pseudogenes because no variation was detected in the sequences of the PCR products amplified using the genomic DNA as a template and all genes were mapped unambiguously even if the STS was chosen from a single exon sequence. If there were processed pseudogenes, such STSs would not have worked properly on the RH mapping panels

because of possible crossamplification of the pseudogene. The only exception is MRPL10. We found a possible pseudogene having a sequence slightly different from the original sequence. It was mapped to chromosome 5, whereas the original sequence was mapped to chromosome 17. To avoid cross-amplification of pseudogene, we chose a primer from the intron sequence in many cases. We have compared the positions of 134 mitochondrial and cytoplasmic RP genes and have found no cross-linkage between any of these genes (data not shown). Clustering of

RP genes into operons, characteristic of bacteria, is not evident in the case of the human mitochondrial or cytoplasmic RP genes, which are randomly scattered about the genome. Though encoded at dispersed genomic sites, these proteins are assembled into the ribosome with stoichiometric precision. It is of great interest to investigate the control mechanism for coordinate expression of these genes. Systematic analysis of the promoter regions is viewed as a key approach to understand such regulation at the transcriptional level.

We have compared the assigned positions of the MRP genes with candidate regions for human disorders. Because defects in the translation apparatus in mitochondria result in abnormal phenotypes such as MELAS (mitochondrial myopathy, encephalopathy, lactic acidosis, and stroke-like episodes), MERRF (myoclonus epilepsy associated with ragged-red fibers), and deafness [reviewed in 13], it is also possible that defects in MRPs result in mitochondrial dysfunction and associated pathological conditions. Particularly intriguing is the possible involvement of MRPs in deafness. In fact, we have placed several MRP genes in regions critical for hereditary hearing loss (Table 2). Among these genes, MRPS12 has been extensively characterized as a candidate gene for autosomal dominant sensorineural hearing loss, DFNA4 [21]. In Drosophila melanogaster, the MRPS12 gene was cloned on the basis of its ability to confer a phenotype known as technical knock-out, tho [33]. This allele was originally identified through the isolation of a viable mutant with a phenotype of temporary paralysis induced by mechanical vibration, caused by a mechanoreceptor cell defect, and thus it was considered to be a useful model of human deafness. Therefore, MRPS12 and other MRP genes could be attractive candidates for genes involved in hereditary hearing loss. Our findings suggest that systematic screening to detect mutations in the MRP genes should be carried out. Besides deafness, we have found that certain MRP genes are present in candidate regions for retinitis pigmentosa and for disorders involving neural dysfunction such as Moebius syndrome and Hallervorden-Spatz syndrome (Table 2).

<sup>&</sup>lt;sup>b</sup>Usher syndrome, type 1E.

c,dDeafness, autosomal dominant nonsyndromic sensorineural 4 and 7, respectively.

Because patients with a mitochondrial disease frequently show features such as retinopathy, myopathy, and neuropathy, it is worthwhile pursuing the possibility that defects or mutations in the MRP genes may result in such pathological conditions.

# MATERIALS AND METHODS

Development of STSs. STSs were developed from either cDNA sequences or partial genomic sequences of the human MRP genes. The cDNA sequences were assembled in silico from retrieved human EST sequences by BLASTN search, using peptide sequences of bovine MRPs. The bovine MRPs were purified from liver [34,35], then separated by radical-free high-reducing (RFHR) two-dimensional PAGE [36,37]. The peptide sequences were determined by mass spectrometric analysis of the proteins using an LC/MS/MS spectrometry system [12]. The partial genomic sequences were retrieved from the public sequence database of the human genome by BLAST search using the assembled cDNA sequences as the query. Identified STSs were verified by PCR followed by sequencing of the products, using the human genomic DNA as template. The STS sequences and the sequences from which the STSs were generated will appear in the DDBJ/EMBL/GenBank DNA databases under the accession numbers listed in Table 1.

Radiation hybrid (RH) mapping. We used two different RH mapping panels, the GeneBridge 4 and G3 panels (Research Genetics, Huntsville, AL), for localizing MRP genes to the human chromosomes. We tested the panels by PCR using the above-mentioned STSs (Table 1). The data vectors were submitted to the RH servers at the Whitehead Institute/MIT Center for Genome Research (GeneBridge 4; http://www-genome.wi.mit.edu/cgi-bin/contig/rhmapper.pl) or the Stanford Human Genome Center (G3; http://shgc-www.stanford.edu).

Cytogenetic localization. A cytogenetic bacterial artificial chromosome (BAC)-STS map [27] was used for cytogenetic mapping of the MRP genes. The map was constructed by FISH analysis of 975 human BACs. BACs corresponding to the individual MRP genes were identified using the nearby markers obtained from RH mapping of the genes. Each MRP gene was assigned to a cytogenetic band according to the results of FISH analysis of these BACs. Detailed map information about these BACs is available (http://www.csmc.edu/genetics/korenberg/int-bac-sts.html).

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Sequence data from this article have been deposited with the DDBJ/EMBL/GenBank Data Libraries under accession numbers AB051336 to AB051355, AB051617 to AB051628, AB061206 to AB061211, and AB061314.