A compilation of large subunit (23S-like) ribosomal RNA sequences presented in a secondary structure format

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INTRODUCTION

The compendium presented here is the immediate successor of the collection of large subunit (LSU; 23S-like) rRNA secondary structures compiled by Gutell and Fox [1] in 1988. As in [1], we present each LSU rRNA sequence in the form of a secondary structure, as it is this structure that is a fundamental aspect of the biological activity of the LSU rRNA molecule. As such, the secondary structure provides valuable information on phylogenetically conserved and variable regions, as well as data relating form to function. Often, especially when dealing with homologous LSU rRNAs that are very divergent in structure (e.g., mitochondrial LSU rRNAs), it is considerably easier to extract required information from comparisons of secondary structures than from comparisons of the corresponding primary sequences.

As much as possible, we have attempted to configure all of these LSU rRNA secondary structures according to the E. coli 23S rRNA model, which may be regarded as the standard or prototype structure upon which the others are based. This format facilitates comparison of homologous structural features among the different LSU rRNAs. The current E. coli 23S rRNA secondary structure has been slightly revised from that in the previous compendium (see [2]).

The database of LSU rRNA sequences has expanded rapidly over the last two years. The listing presented here includes 7 archaebacterial, 13 eubacterial, 16 eukaryotic cytoplasmic (nuclear-encoded), 8 plastid, and 27 mitochondrial LSU rRNA sequences. Newly modeled secondary structures not included in the previous compilation are indicated in the table.

The basic premise of the comparative method is that all LSU rRNA sequences fold into a similar secondary structure. Thus, the process of configuring each newly determined sequence according to the existing secondary structure model tests the validity of the latter model, and extends it when novel compensatory base changes are found. At this time, we are confident of the basic secondary structure that is common to all 23S (and 23S-like) rRNA sequences. However, there remain regions of some LSU rRNAs that have yet to be structured into helical arrays, or that have been structured by others on the basis of minimal comparative information. It is these structures that will be subject to further refinement as additional primary structures from select phylogenetic groupings are determined. We anticipate that the majority of such changes will occur in the existing eukaryotic cytoplasmic and mitochondrial LSU rRNA secondary structures, in regions of the rRNA that are common only to those phylogenetic groups, or to certain divisions therein.

The decision by the editors to change to electronic media presentation provides us with an opportunity to improve upon the previous LSU rRNA compilation. Starting with the current collection, the actual 23S rRNA secondary structures will not be published here. Instead, readers will find (i) a table of complete LSU rRNA sequences, grouped according to phylogenetic division and including GenBank/EMBL Accession Numbers, and (ii) a publication reference list for these sequences. The comprehensive set of LSU rRNA secondary structures may be obtained in one of two ways. Hardcopy printouts of this set will be available directly from us (inquiries should be directed to M.W.G. at the address listed at the end of this compendium). Individuals with access to the Internet telecommunications network and a laser printer capable of processing PostScriptTM files may elect to obtain such files of LSU rRNA secondary structures. These files will be available on the GenBank computer in the near future. Information concerning this on-line service should be directed to R.R.G. (E-mail and postal addresses as noted below).

As time and facilities permit, the rRNA information available from the on-line service will be increased. Initially we will include the complete set of LSU rRNA secondary structures (in PostScriptTM format), the table of LSU rRNA sequences, and the associated publication reference list. Refinements to existing secondary structures as well as newly modeled secondary structures will be available on-line as soon as we have completed our own analysis. At that time we will also update the associated table and reference list. Currently we include only those LSU rRNA sequences that are complete (or nearly so). However, we are in the process of incorporating partial sequences (that contain a significant proportion of the rRNA primary sequence) into our tabulation.

ACCURACY OF THE DATA

Where sequence ambiguity exists in a published sequence, we have specified such positions according to the nomenclature recommended by IUPAC (e.g., Y = pyrimidine; R = purine; etc.). As noted in the table, independently determined versions of the same primary sequence exist for several LSU rRNAs. Usually, these alternative versions differ from each other at a number of positions, and at least some of these differences are likely to be the result of sequencing errors. Often, the secondary

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structure is very useful for deducing which version of the sequence is likely to be correct at a particular position. On the other hand, it is probable that some of the variation actually reflects genuine inter- or intrastrain sequence heterogeneity, particularly if the differences occur within variable regions [3]. We have also noted that a few published primary sequences differ at one or more positions from their GenBank/EMBL listings, without an indication that the database entry represents a subsequently revised version of the original published sequence. Again, secondary structure modeling may or may not indicate which version is likely to be correct. In the hard copy and electronic versions of the secondary structure figures, we will provide brief annotation to indicate which version of the primary sequence has been used at discrepant positions.

We have included here a complete listing (including titles) of pertinent references to the LSU rRNA sequences listed in the table. In subsequent editions, only references to newly determined sequences or published revisions to existing sequences will be cited in this way. In compiling this list, we have proofed each of these citations against the original published paper. We note that the GenBank/EMBL database listing is occasionally inaccurate in this regard.

Finally, we invite further corrections from readers, and welcome suggested revisions/alternative interpretations to the proposed secondary structures, as well as suggestions for improvement of the content and/or form of the database. We hope that it will be possible, in due course, to expand the current database to include small subunit (SSU; 16S-like) rRNA secondary structures, as well as other types of rRNA structural information. In this regard, we would particularly like to solicit newly determined LSU and SSU rRNA sequences in advance of publication. As a result of the change to electronic format, new secondary structures will be able to be incorporated into the compilation as soon as they are published or we have permission to release them.

[1] Gutell, R.R. and Fox, G.E. (1988) Nucleic Acids Res. 16, Supplement, r175-r269.

[2] Gutell,R.R. and Woese,C.R. (1990) Proc. Natl. Acad. Sci. U.S.A. 87, 663-667.

[3] Gonzalez, I.L., Gorski, J.L., Campen, T.J., Dorney, D.J., Erickson, J.M., Sylvester, J.E. and Schmickel, R.D. (1985) Proc. Natl. Acad. Sci. U.S.A. 82, 7666-7670.

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REQUESTS

Requests for hard copies of LSU rRNA secondary structures (either the complete compilation, or selected portions therefore) should be directed to:

Dr. M.W. Gray, Department of Biochemistry, Sir Charles Tupper Medical Building, Dalhousie University, Halifax, Nova Scotia B3H 4H7, Canada. FAX: (902)494-1355 E-mail: mgray@ac.dal.ca (via Bitnet)

Requests for information regarding on-line availability of LSU rRNA secondary structure files and other information contained in this compendium should be directed to:

Dr. R. R. Gutell, Cangene Corporation, 3403 American Drive, Mississauga, Ontario L4V 1T4, Canada. E-mail: rrna@gpu.utcs.utoronto.ca (via Bitnet)

TABLE OF COMPLETE LSU rRNA SEQUENCES

Organism name ¹	New ²	Accession no.
ARCHAEBACTERIA		
Extreme halophiles		
Halobacterium halobium		X03407
Halobacterium marismortui	*	X13738
Halococcus morrhuae		X05481
Methanobacter		
Methanobacterium thermoautotrophicum		X15364
Methanococcus		
Methanococcus vannielii		X02729
Extreme thermophiles		
Desulfurococcus mobilis		X05480
Thermoproteus tenax	*	X06157
EUBACTERIA		
Gram positive bacteria		
High G+C subdivision		
Micrococcus luteus	*	X06484
Streptomyces ambofaciens	*	M27245
Low G+C subdivision		
Bacillus stearothermophilus		K02663
Bacillus subtilis	•	K00637,M10600 X00007
Dumle abote mathetic besteric and relatives		A00007
Purple photosynthetic bacteria and relatives		
Alpha subdivision	*	VOCARE
Rhodobacter capsulatus	+	X06485
Beta subdivision	*	¥16260
Pseudomonas cepacia	*	X16368
Gamma subdivision		101/05
Escherichia coli	·	J01695
Pseudomonas aeruginosa	•	Y00432
Ruminobacter amylophilus	*	X06765
Cyanobacteria		NO0610 N000 4
Anacystis nidulans	•	X00512,X00343
Spirochetes and relatives	.	W14040
Leptospira interrogans	*	X14249
Planctomyces and relatives		1000
Pirellula marina	*	X07408
Radioresistant micrococci and relatives		
Thermus thermophilus	*	X12612

Protocticta³

Protoctista ³		
Euglenophyta (euglenoid flagellates)		
Astasia longa	*	X14386
Euglena gracilis	*	X13310
Chlorophyta (unicellular green algae)		
Chlamydomonas reinhardtii	*	X16686,X15727
Chlorella ellipsoidea	•	?
Plantae		
Bryophyta		
Marchantia polymorpha (liverwort)	•	X04465

Angiospermaphyta (flowering plants)		
Nicotiana tabacum (tobacco)	·	J01446,Z00044
Oryza sativa (rice)	*	X15901
Zea mays (maize)	•	X01365
MITOCHONDRIA		
Protoctista ³		
Zoomastigina (zooflagellates)		
Crithidia fasciculata		X02548
Leishmania tarentolae		X02354
Leptomonas sp.	*	J03814
Trypanosoma brucei	•	X02547
Chlorophyta (unicellular green algae)	_	
Chlamydomonas reinhardtii	*	M22649,M25123
		25130.
Ciliophora (ciliates)		201001
Paramecium primaurelia		K00634
Paramecium tetraurelia	*	K01749
Fungi		
Ascomycota		?
Aspergillus nidulans Saccharomyces cerevisiae	•	ہ J01527
Schizosaccharomyces pombe	•	X06597
Podospora anserina	*	?
F		
Plantae		
Angiospermaphyta (flowering plants)		
Oenothera berteriana (primrose)	•	X02559
Triticum aestivum (wheat)	*	?
Zea mays (maize)	•	K01868
Animalia		
Arthropoda		
Aedes albopictus (mosquito)		X01078
Apis mellifera (honeybee)	*	X05011
Artemia salina (brine shrimp)	*	X12965,M21833
Drosophila yakuba (fruit fly)		X03240
Locusta migratoria (locust)	*	X05287
Echinodermata (sea urchins)		
Paracentrotus lividus	*	J04815
Strongylocentrotus purpuratus Chordata	-	X12631
Bos taurus (bovine)		J01394
Homo sapiens (human)	•	J01415,M12548,
nomo suprens (numun)	•	V00710
Mus muscuslus (mouse)		J01420
Rana catesbeiana (frog)	*	X12841
Rattus norvegicus (rat)	•	J01438
Xenopus laevis (toad)	•	M10217,X00136
EUCARYOTES (NUCLEAR)		
Protoctista ³		
Dinoflagellata (dinoflagellates)	*	X1/100 X15072
Prorocentrum micans	*	X16108,X15973
Zoomastigina (zooflagellates) Crithidia fasciculata		Y00055
Acrasiomycota (cellular slime molds)	·	100055
Dictyostelium discoideum	*	X00601
Myxomycota (plasmodial slime molds)		
Physarum polycephalum		V01159
Euro-		
Fungi		
Zygomycota Mucor racemosus	*	M26190
Ascomycota		
Saccharomyces carlsbergensis	*	V01285
Saccharomyces cerevisiae	•	J01355
Plantae		
Angiospermaphyta (flowering plants)	*	X05910
Citrus limon (lemon)		A03710

Lycopersicon esculentum (tomato) Oryza sativa (rice)	*	X13557 M11585
Oryza sauva (nce)	•	M11383
Animalia		
Nematoda		
Caenorhabditis elegans		X03680
Arthropoda		
Drosophila melanogaster	*	M21017
Chordata		
Homo sapiens (human)		M11167
Mus musculus (mouse)		X00525
Rattus norvegicus (rat)		X01069,K01591.
6 ,		X00521
Xenopus laevis (toad)	•	X00136

¹Eukaryotic organisms are classified according to the scheme of Margulis, L. and Schwartz, K.V. (1988) Five Kingdoms. An Illustrated Guide to the Phyla of Life on Earth (2nd edition). W.H. Freeman and Co., New York. ²Newly modeled secondary structures which did not appear in the previous compilation are denoted by '*' ³The term 'Protoctista', as defined and used by Margulis and Schwartz, includes but is not limited to the 'Protoctista' (unicallular substructures or protiot)

but is not limited to the 'Protista' (unicellular eukaryotes, or protists).

LIST OF REFERENCES TO LSU rRNA SEQUENCES

ARCHAEBACTERIA

Desulfurococcus mobilis Halococcus morrhuae Methanobacterium thermoautotrophicum

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Evolutionary relationships amongst archaebacteria. A comparative study of 23 S ribosomal RNAs of a sulpur-dependent extreme thermophile, an extreme halophile and a thermophilic methanogen.

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Halobacterium marismortui

Brombach, M., Specht, T., Erdmann, V.A. and Ulbrich, N. (1989) Nucleic Acids Res. 17, 3293. Complete nucleotide sequence of a 23S ribosomal RNA gene from *Halobacterium* marismortui.

Methanococcus vannielii

Jarsch, M. and Böck, A. (1985) Mol. Gen. Genet. 200, 305-312. Sequence of the 23S rRNA gene from the archaebacterium *Methanococcus* vannielii: evolutionary and functional implications.

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EUBACTERIA

Anacystis nidulans

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Kop,J., Wheaton,V., Gupta,R., Woese,C.R. and Noller,H.F. (1984) DNA 3, 347-357. Complete nucleotide sequence of a 23S ribosomal RNA gene from Bacillus stearothermophilus.

Bacillus subtilis

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Leptospira interrogans

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Micrococcus luteus

Regensburger, A., Ludwig, W., Frank, R., Blöcker, H. and Schleifer, K.H. (1988) Nucleic Acids Res. 16, 2344. Complete nucleotide sequence of a 23S ribosomal RNA gene from *Micrococcus luteus*.

Pirellula marina

Liesack, W., Höpfl, P. and Stackebrandt, E. (1988) Nucleic Acids Res. 16, 5194. Complete nucleotide sequence of a 23S ribosomal RNA gene from *Pirellula* marina.

Pseudomonas aeruginosa

Toschka,H.Y., Höpfl,P., Ludwig,W., Schleifer,K.H., Ulbrich,N. and Erdmann,V.A. (1987) Nucleic Acids Res. 15, 7182. Complete nucleotide sequence of a 23S ribosomal RNA gene from *Pseudomonas* aeruginosa.

Pseudomonas cepacia

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Rhodobacter capsulatus

Höpfl,P., Ludwig,W. and Schleifer,K.H. (1988) Nucleic Acids Res. 16, 2343. Complete nucleotide sequence of a 23S ribosomal RNA gene from Rhodobacter capsulatus.

Ruminobacter amylophilus

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Complete nucleotide sequence of a 23S ribosomal RNA gene from Ruminobacter amylophilus.

Streptomyces ambofaciens

Pernodet, J.-L., Boccard, F., Alegre, M.-T., Gagnat, J. and Guérineau, M. (1989) Gene 79, 33-46.

Organization and nucleotide sequence analysis of a ribosomal RNA gene cluster from *Streptomyces ambofaciens*.

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PLASTIDS

Astasia longa

Siemeister, G. and Hachtel, W., unpublished.

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Lemieux, C., Boulanger, J., Otis, C, and Turmel, M. (1989) Nucleic Acids Res. 17, 7997.

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MITOCHONDRIA

Aedes albopictus

HsuChen, C.-C., Kotin, R.M. and Dubin, D.T. (1984) Nucleic Acids Res. 12, 7771-7785.

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Paracentrotus lividus

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The complete nucleotide sequence, gene organization, and genetic code of the mitochondrial genome of *Paracentrotus lividus*.

Paramecium primaurelia

Paramecium tetraurelia

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