Volume 16, Supplement Nucleic Acids Research

A compilation of large subunit RNA sequences presented in a structural format

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INTRODUCTION

The present review provides a summary of all the published large subunit rRNAs as of December 1987. Instead of the usual linear alignment the sequences are tabulated here as a series of secondary structure diagrams in which individual nucleotides are indicated. The reasons for this departure from past practice are several. The foremost is simply that in our experience this format is more useful. For example, considerable effort is now being expended to study the higher order structure of the large rRNAs. Thus it is common to be reading a paper only to find reference to position X in Sequence Y. With diagrams such as those provided here the reader will be able to readily identify such statements in the context of the known major outline of the secondary structure of Sequence Y or for that matter any other published sequence. Secondarily this collection, as is traditional, tabulates all the currently known sequences in one place. Finally we believe the collection as a whole is educational in that it will make the reader aware of the extent of secondary structure variation in the large subunit RNAs and the magnitude of work that still could be done to further refine the secondary structures by collection of appropriate additional data.

ORIGIN OF THE STRUCTURE

All of the structure diagrams are drawn in a format that coincides with that used for Escherichia coli. The E. coli structure itself is based on a secondary structure model first published in 1981 (1). The present version contains important unpublished modifications made by Gutell, Noller and Woese (2) and further unpublished refinements (Gutell, Noller and Woese, unpublished results; Jurka and Fox, unpublished results). All of the structures shown were established by comparative sequence analysis as discussed below. Due to data limitations some regions of some of the sequences are best regarded as of unknown structural content at this time. No attempt has been made here to compare the structures presented to the various sequence specific secondary structures that frequently accompany the publication of each sequence, though excellent agreement exists with one recently published general model (3). Likewise no putative tertiary interactions have been indicated on the figures though a few are known (Gutell, unpublished results and ref (3). In many cases there is evidence for a pseudoknot in the vicinity of E. coli position 2350 (Gutell, unpublished results and ref (3)) and when that evidence is favorable the interaction is indicated on the figures.

COMPARATIVE SEQUENCE ANALYSIS

For pragmatic reasons the primary tool used in constructing the individual structures has been comparative (or phylogenetic) analysis. This approach had its origin in the discovery of the cloverleaf structure for tRNA (4). It first began to reach its modern form with the analysis of 5S rRNA (5) and has emerged as a well documented procedure (2,6-8) The underlying assumption is that functionally equivalent regions of the large rRNAs from phylogentically diverse sources will have biologically equivalent structures. The procedure begins by aligning the primary sequences using conserved sequence segments as a guide. Next the various columns of bases are individually intercompared to detect compensating base changes that maintain Watson-Crick complementarity between the potential pairing regions. If an individual helical element is independently tested several times it is considered phylogenetically proven.

The comparative method has certain limitations that the reader should appreciate in perusing the figures presented here. First and foremost is the need for sequences that exhibit the structure being studied. For highly conserved features this may be the entire data base. In other cases features may be extremely variable so that particular versions are only found in individual phylogenetic groups, mammamalian mitochondria for example. Secondly the feature must exhibit sequence variation within the subset of sequences that contain the feature. Without such variation a region can not be structured. Thirdly it should be recognized that the approach necessarily produces minimal structures. It is the nature of the method to allow the identification of additional features as the data base grows. Thus, for example, the continuing refinement of the E. coli structure discussed above. Finally it should be appreciated that it is very difficult to assess the significance of base pairs that that can extend a particular helix in some organisms but not all. Such base pairs are strongly supported by thermodynamic arguements but conflict with the comparative concept. The proper resolution in such circumstances may have to wait until such time that more high resolution structure data is available.

CURRENT DATA BASE

As of late in 1987 there were 40 distinct complete large subunit RNA sequences published and at least five extensive partial sequences in which at least 500 bases of the large subunit RNA have been sequenced (We have not exhaustively searched for these). In addition in some instances sequence information is available from more than one large subunit RNA gene from the same organism. Multiple rRNA genes frequently exhibit heterogeneity in sequence and this phenomenona may be of more than academic interest. The present collection does not address this matter however and in those few instances where information from more than one large subunit rRNA gene is available we have arbitrarily picked one sequence for inclusion here. The 40 known sequences provide a diverse sample covering the three *major urkingdoms; eubacteria, archaebacteria and* eukaryotes as well as the organelles. Table 1 lists the sequences, the common name of the RNAs involved, the total length of the large subunit RNA inclusive of fragments such as 5.8S and 4.5S rRNAs, at least one relevant GENBANK/EMBL accession numbers if the sequence is in the data bases, a highly abbreviated reference and a key to the complete references that accompany this text.

HOW TO READ THE DIAGRAMS

The structure diagrams were drawn to a single scale so that they may be readily superimposed or intercompared. This was accomplished by a computer program described elsewhere (6). Each diagram encompasses two pages with a crossover point to the next page indicated. In most bacterial cases a possible helical structure exists between the 5'and 3' termini of the molecule. It is uncertain whether this helix is present in the functional RNA or is simply a remnant of processing. In any event the reader needs to be aware that when it is possibly present it appears on both halves of the figure. Extensive base numbering occurs on the E. coli diagram. On the other sequence diagrams only occasional numbers are included. These occasional numbers refer to the specific sequence on which they appear. In those cases in which more than one molecule is include (eg 5.8S and 28S RNAs) each is numbered separately.

When a region contains no known structure it is drawn by the computer program as a circular loop. In order to maintain the scale and layout of the drawings it is not always possible to draw large uncharacterized regions as unstructured loops. When this occurs the region of unknown structure is included as a detached linear array listed from 5' to 3'. The Homo sapiens and other eukaryotic cytoplasmic sequences contain many examples of this, though the same phenomenon will also be seen on mitochondrial and chloroplast diagrams. These linear arrays are labeled with a bold letter and the positions included in the array indicated. A second bold letter specifies where in the sequence the linear array belongs. These bold letters are used in a consistent fashion so that a large unstructured area at the same location in several diagrams always receives the same bold letter. In a few instances the uncharacterized array is small enough to be shown as a loop in some but not all the diagrams. In those instances a bold letter is used to label the loops so that it is obvious that an equivalent unstructured region is present.

The reader should not conclude that the regions assigned bold letters are the only unstructured regions. Whenever room exists the computer program draws the unstructured regions as a large loop. A letter has only been assigned if the computer has used the linear array display in at least one case. Many of the unlabeled unstructured regions are rather large. Obvious examples can be seen by examining any of the mammalian mitochondria structures. Thus in many of the sequences presented here local regions which are often substantial in size are shown as unstructured. These regions clearly have a different

Table 1. Listing of Large Subunit RNA Sequences that have been completely or extensively sequenced.

ORGANISM	RNA TYPE	LENGTH	SHORT REFERENCE	ACCESSION #	FIGURE #	REFERENCE #
A: EUBACTERIA						
1. Escherichia coli	23S	2904	PNAS 77: 201 1980	J01695	1	17
2. Pseudomonas aeruginosa	23S	2893	NAR 15:7182 1987	Y00432	2	18
3. Bacillus subtilis	23S	2927	GENE 37: 261 1985	K00637, M10606	3	19
4. Bacillus stearothermophilus	23S	2928	DNA 3: 347 1984	——	4	20
5. Anacystis nidulans	23S	2876	GENE 24: 219 1983	X00512	5	21
			NAR 12: 3373 1984	X00343		13
Chloroplasts						
6. Zea mays	23S & 4.5S	2981	NAR 9: 2853 1981	X01365	6	22
7. Nicotiana tabacum	23S & 4.5S	2907	EJB 124: 13 1982	J01446, J01447	7	23
8. Marchantia polymorpha	23S & 4.5S	2914	Nature 322:572 1986	X04465, X01647	8	24
9. Chlorella ellipsoidea	23S	3207	Cur.Gen. 11:347 1987	——	9	14
Mitochondria						
10. Zea mays	26S	3549	PLASMID 11: 1984	K01868	11	25
11. Oenothera berteriana	26S	3265	Cur.Gen. 9: 1985	——	12	26
12. Aspergillus nidulans	——	2768	NAR 10: 4795 1982	——	13	27
13. Saccharomyces cerevisiae	21S	3273	NAR 11: 339 1983	J01527	14	28
14. Schizo. pombe	——	2705	EJB 169: 527 1987	——	—	29
15. Paramecium primaurelia	7S & 20S	2634	NAR 9: 6391 1981	K00634	15	30
16. Paramecium tetraurelia	7S & 20S	2631	JBC 259: 5173 1984	K01749	--	31
17. Homo sapiens	16S	1559	Nature 290: 457 1981	J01415	17	32
18. Mouse	16S	1582	Cell 22:157 1980	J01420	18	33
19. Rat	16S	1559	NAR 9:4139 1981	J01438	19	34
20. Bovine	16S	1571	JMB 156: 683 1982	J01394	20	35
21. Xenopus laevis	16S	1640	JBC 260: 9759 1985	M10217,X00136	21	36
22. Drosophila yakuba	——	1326	NAR 13: 4029 1985	——	22	37
23. Aedes albopictus (mosquito)	——	1335	NAR 12: 7771 1984	X01078	23	38
24. Crithidia fasciculata	12S	1141	NAR 13: 4171 1985	X02548	25	39
25. Trypanosoma brucei	12S	1152	NAR 13: 4171 1985	X02547	26	39
26. Leishmania tarentolae	12S	1157	NAR 13: 2337 1985	——	27	40
B: ARCHAEBACTERIA						
27. Halococcus morrhuae	23S	2927	JMB 195: 43 1987	——	29	3
28. Halobacterium halobium	23S	2905	MGG 202: 152 1986	X03047,X00872	30	41
29. Methanococcus vanniellii	23S	2958	MGG 200: 305 1985	——	31	42
30. Methanobacterium thermoautotrophicum	23S	3019	JMB 195: 43 1987	——	32	3
31. Desulfurococcus mobilis	23S	3077	JMB 195: 43 1987	——	33	3
32. Thermoproteus tenax	23S	3031	NAR 15: 4821 1987	Y00346	—	43
C: EUKARYOTIC CYTOPLASMIC						
33. Saccharomyces cerevisiae	5.8S & 25S	3549	NAR 9: 6953 1981	J01355	35	44
			JBC 248: 3860 1973			45
34. S. carlsbergensis	5.8S & 26S	3550	NAR 9: 6935 1981	V01285	—	46
35. Homo sapiens	5.8S & 28S	5184	PNAS 82: 7666 1985	K03433,K03434	36	47
			NAR 4: 2495 1977			48
36. Mouse	5.8S & 28S	4869	NAR 12: 3563 1984	X00525	37	49
			NAR 10: 5273 1982			50
37. Rat	5.8S & 28S	4943	NAR 11: 7819 1983	X01069,K01591	38	51
			NAR 12: 3677 1984	X00521		52
			RIBOSOMES 86: 391			16
38. Xenopus laevis	5.8S & 28S	4270	NAR 11: 7795 1983	X00136	39	53
			JBC 260: 9759 1985			54
39. Oriza sativa	5.8S & 25S	3541	GENE 37: 255 1985	M11585	40	55
40. Caenohabditis elegans	5.8S & 26S	3662	NAR 14: 2345 1986	X03680	41	56
41. Physarum polycephalum	5.8S & 26S	3943	PNAS 80:3163 1983	V01159	42	57
			NAR 10: 2379 1982			58
42. Crithidia fasciculata	5.8S & frag.	4085	EMBO J. 6: 1063 1987		43	12
Major Partial Sequences*						
43. Mycoplasma PG50	23S	869	NAR 15: 1327 1987	——	--	59
44. Apis mellifera mito.	——	1267	NAR 15: 2388 1987	——	--	60
45. Dictylostellium discoidium	5.8S & 28S	3471	NAR 12: 4171 1984	X00601	--	61
46. Lytechinus variegatus	5.8S & 28S	664	NAR 12: 1737 1984	X00350	--	62
47. Chimpanzee	28S	1429	PNAS 82: 766 1985	K03433	--	47

* Lengths indicated represent the portion of the molecule for which sequence has been published.

structure than is seen in E. coli or some of the other molecules but we do not as yet know what it is.

This should not be seen as bothersome but rather as defining an opportunity to obtain data from additional organisms in order to allow resolution of the problem area. In many cases the difficulty stems from the fact that too few sequences are available or too little sequence variation has been displayed in the known sequences to deduce a structure. In a few cases time did not permit a though analysis and a recognizeable structural feature may have been overlooked. Also the reader should realize that the comparative approach is a convergent one. The current model should at best be perceived as a minimal one awaiting the discovery of additional interactions. Thus small two and three base helices may ultimately be found even in regions in which considerable structure has already been identified as more data accumulates.

5.8S RNA, 4.5S RNA AND OTHER LARGE SUBUNIT FRAGMENTS

It is one of the pecularities of the large subunit RNA that it is sometimes genetically fragmented. The most well known example is the 5.8S rRNA and its equivalents that are found in most eukaryotic organisms. This RNA has been shown (9,10) to be homologous to approximately the first 150 positions of the E. coli 23S rRNA. Although genetically distinct it interacts with the large subunit RNA through base pairing. In effect then the two together form a single RNA with a backbone nick in one of its loops. The same phenomenon is also seen at the 3' end of several chloroplast large subunit RNAs where the last 100 or so bases are separately encoded as a 4.5S RNA (11). In this case the homology to the E. coli 3' terminus is obvious but the the mechanism by which the 4.5S rRNA and the main large subunit RNA component are held together is not. The most extreme case of this fragmentation phenomenon that is known is in Crithidia fasciculata where the large subunit RNA is actually assembled from six fragments plus a 5.8S rRNA (12). These various fragmentation phenomenon are indicated on the diagram by labels that indicate where the respective 5' and 3' ends are located. The Crithidia fragments are labeled with the same lower case letters that were used in the original publication (12) and numbered as if they were a single large RNA.

OVERLAY DIAGRAMS AND COLLECTION ARRANGEMENT

It is very useful in comparing structures to produce overlay diagrams that display one structure relative to another. Several such diagrams are included here. In each case the underlying structure is that of E. coli. Where the E. coli is unique it can be seen as a light gray. The bold structure is that of the other organism indicated in the legend. Base numbers on these diagrams always refer to E. coli. These overlay figures show immediately where the sites of structural variation between the two RNAs are located. The overlay figures are used to introduce the various sections of the collection. In each case a particularly representative overlay is chosen so that the major variations in the group relative to E. coli can be seen.

The collection begins with the five eubacterial sequences.

These are virtually identical structurally and therefore no overlay figure is included. They are followed by the four chloroplast figures which again follow the virtually identical structural pattern. The Anacystis sequence used was arbitrarily that of Douglas and Doolittle (13). The plant chloroplasts all have a detached 4.5S at the 3' terminus but the alga, Chlorella ellipsoidea does not. The C. ellipsoidea sequence also is unusal in that it is claimed to contain an intron (14). We believe that this assertion is not convincingly established and thus the putative intron is shown on Figure 9a as an insertion region of class D. Several large subunit sequences have an insertion at this location. If the C. ellipsoidea insertion is in fact an intron this would be very atypical as none of the known large subunit introns correspond with common insertion regions. It is possibile that experimental difficulties may have arisen due to the propensity of large subunit RNAs such as E. coli 23S rRNA (15) to readily fragment. The location of this fragmentation site has been localized in E. coli (1) to the region of the RNA that corresponds to that which contains the putative intron in C. ellipsoidea.

The largest portion of the collection contains the mitochondrial sequences. These are assembled into three groups each prefaced by a separate overlay figure. The first and most internally variable group are those with large mitochondrial RNAs as typified by the overlay of Zea mays, Fig. 10. These mitochondrial RNAs resemble the eubacterial ones in size and structure more than any of the other mitochondria do. Nevertheless they are marked by considerable varibility even within the group. One unifying feature is the presence of an unstructured region H in the vicinity of E. coli position 1400 in all cases. Structures are provided for all of these RNAs except Paramecium tetraaurelia which is virtually identical to P. primaurelia, Fig. 15. and Schizosaccharomyces pombe which was published after the structures were completed. The second major mitochondrial group are the rather small 16S RNAs that are found in most higher organisms. Although much smaller, as the human overlay shows, Fig. 16, considerable structural similarity with the eubacterial RNAs continues to exist. Finally the three kinetoplast mitochondrial 12S rRNAs follow. Here as is indicated by the overlay, Fig. 24, virtually none of the structure in the 5' half of the molecule is preserved, though considerable structural conservation does exist in the 3' half of the molecule.

The remaining figures are devoted to the archaebacteria and eucaryotic cytoplasm. As indicated by the Halococcus morrhuae structural overlay, Fig. 28, the archaebacteria exhibit significant variation that exceeds anything that is seen among the eubacteria alone. Close examination of the archaebacterial figures also reveals that unlike the eubacteria, the archaebacteria, do exhibit some variation within the group as a whole. A figure is not included for Thermoproteus tenax because this sequence was inadvertantly overlooked. The main theme from the eucaryotic cytoplasmic sequences sems to be growth in size. Although not all the RNAs exhibit the effect to the same extent it is clear that several regions seem to be favored for macroscopic insertions of new material. As indicated by the Saccharomyces cerevisiae overlay, Fig. 34, the main theme of secondary structure is again repeated in the eukaryotic cytoplasmic RNAs. Excluding the large insertions, the eukaryotic RNA structure is remarkably like that of the eubacteria ,and archaebacteria. The sequence of S. carlsbergenesis 26S rRNA is very similar to that of S. cerevisiae and thus is not shown as a separate figure. In the case of rat, the corrected sequence (16) has been chosen for the figure presented here.

AVAILABILITY AND ACCURACY OF THE DATA

The sequences presented here are maintained in aligned data bases according to phylogenetic type. Due to the numerous macroscopic insertions and deletions no attempt is made to maintain a single aligned data base of all the sequences. We therefore cannot provide such an alignment on electronic medium. We can however provide individual sequences. Alternatively the interested reader may get sequences directly from the electronic databases. When base ambiguity existed the IUPAC nomenclature recommendations were followed. Post-transcriptional modifications have not been indicated since these have not been determined in most cases. The reader should be aware however that the large rRNAs do have a number of such modified nucleotides. In the case of the 5.8S rRNAs which mostly have been sequenced at the RNA level the post-transcriptional modifications are frequently known, though not indicated here. The sequences presented here and the position number labels have been extensively checked but nevertheless may contain an occasional error. The structures themselves are the best we currently have available. Although occasionally a helix indicated may be in error it is far more likely that one will have been overlooked. Readers are invited to inform us about errors and ommissions of published sequences.

ACKNOWLEDGEMENTS

Dr. Robin Gutell's efforts in this undertaking were supported by NIH grant #GM-17129 to Dr. Harry F. Noller of the University of Santa Cruz and NASA grant NSG-7044 to Dr. Carl R. Woese at the University of Illinois. Dr. George E. Fox's efforts were supported by NASA grant NSG-7440 and NIH grant GM-37655.

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Secondary Structure of eubacterial 23S Ribosomal RNA: *Escherichia coli*

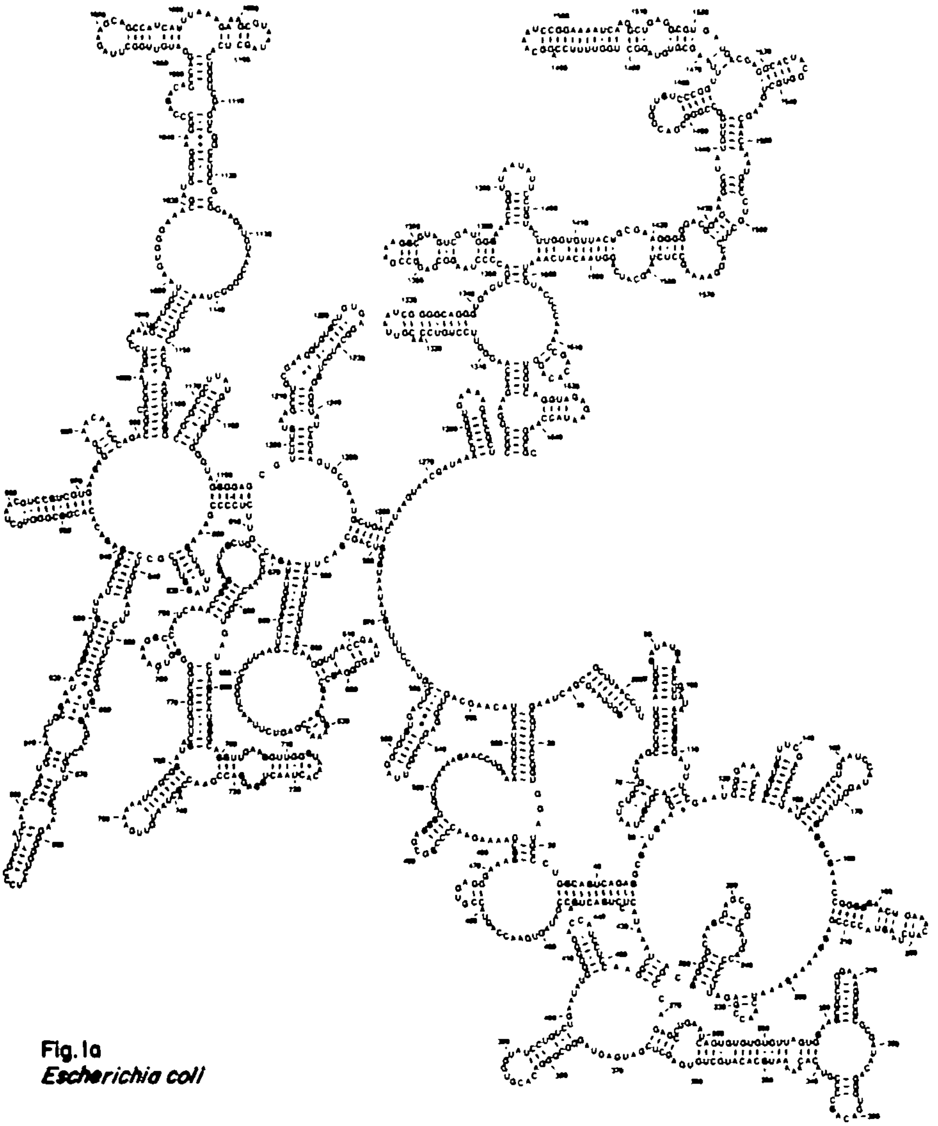


Fig. 1a
Escherichia coli

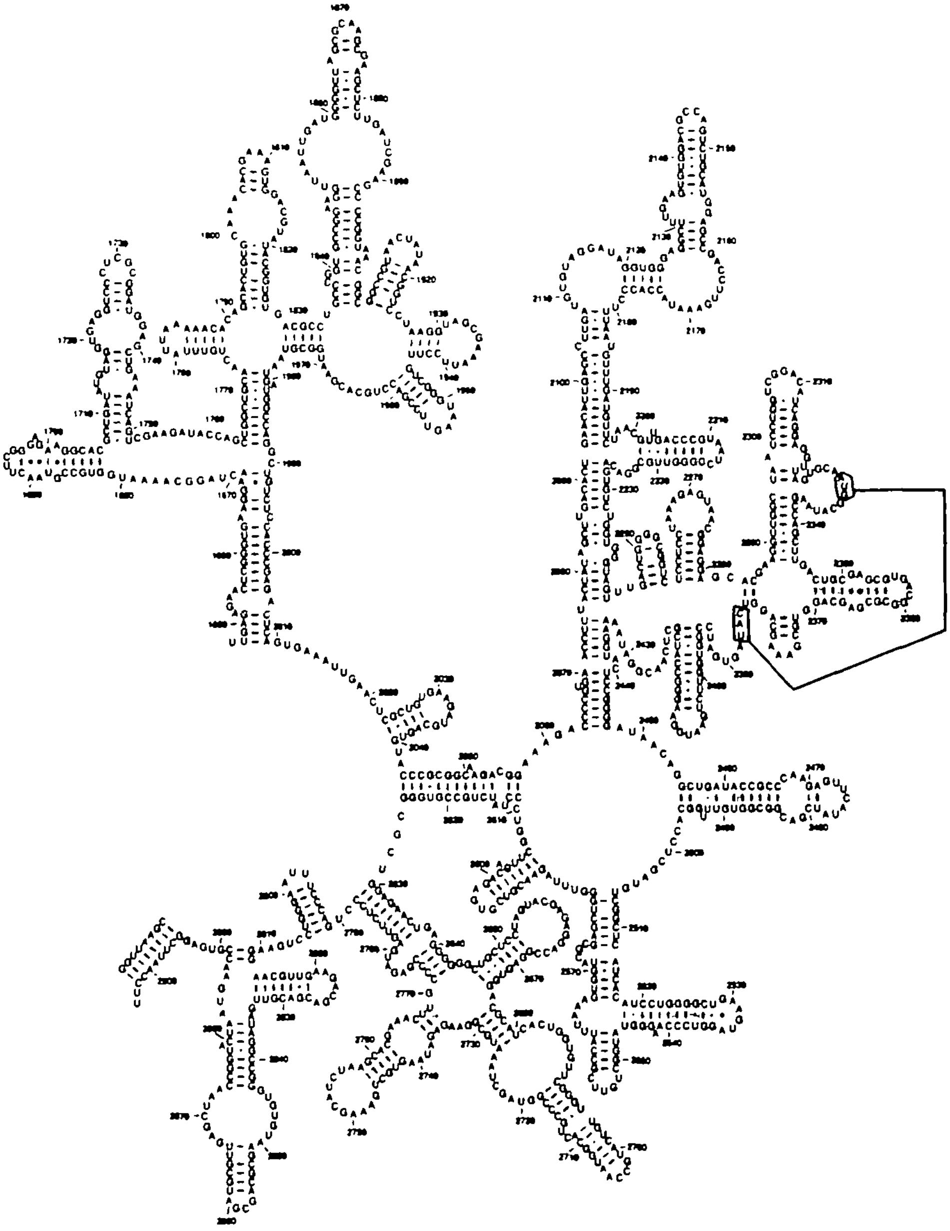


Fig. Ib
Escherichia coli

Secondary Structure of eubacterial 23S Ribosomal RNA: 5'half

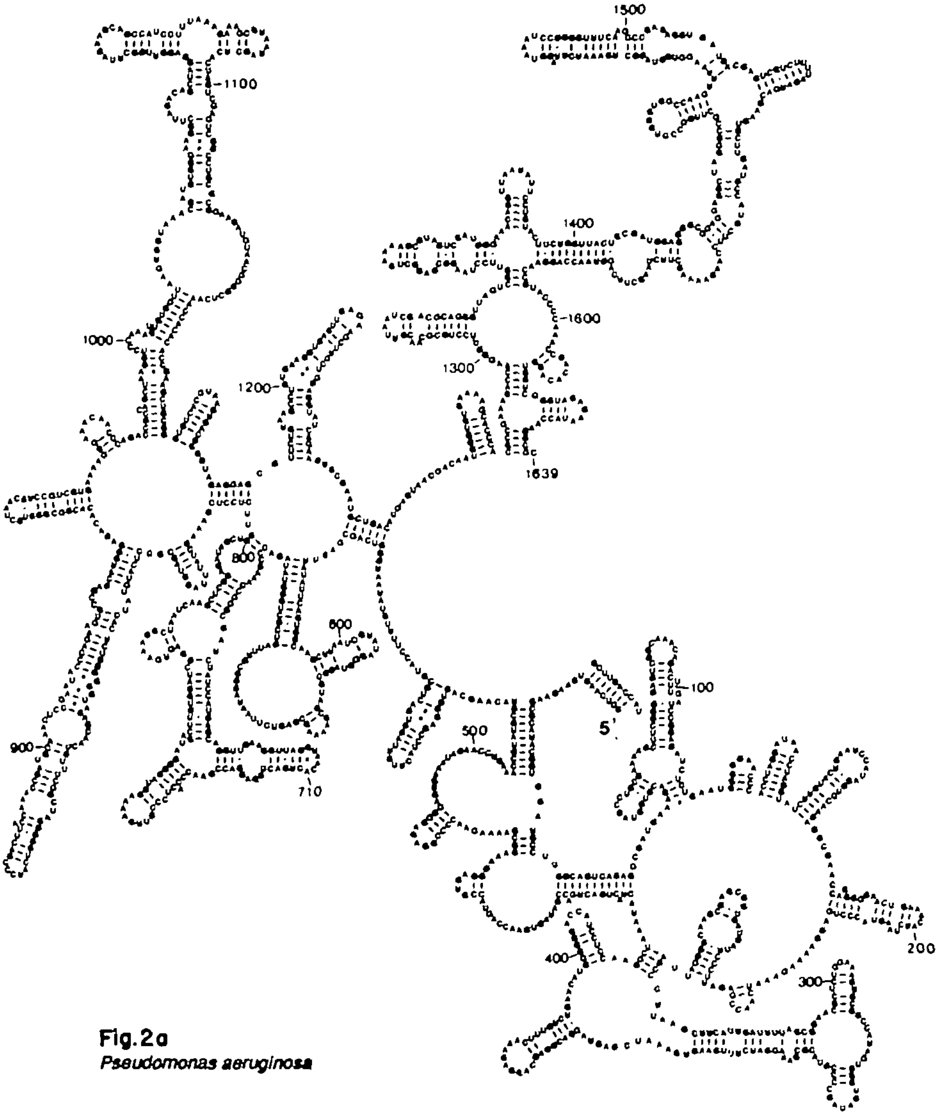


Fig.2a
Pseudomonas aeruginosa

Secondary Structure of eubacterial 23S Ribosomal RNA: 3'half

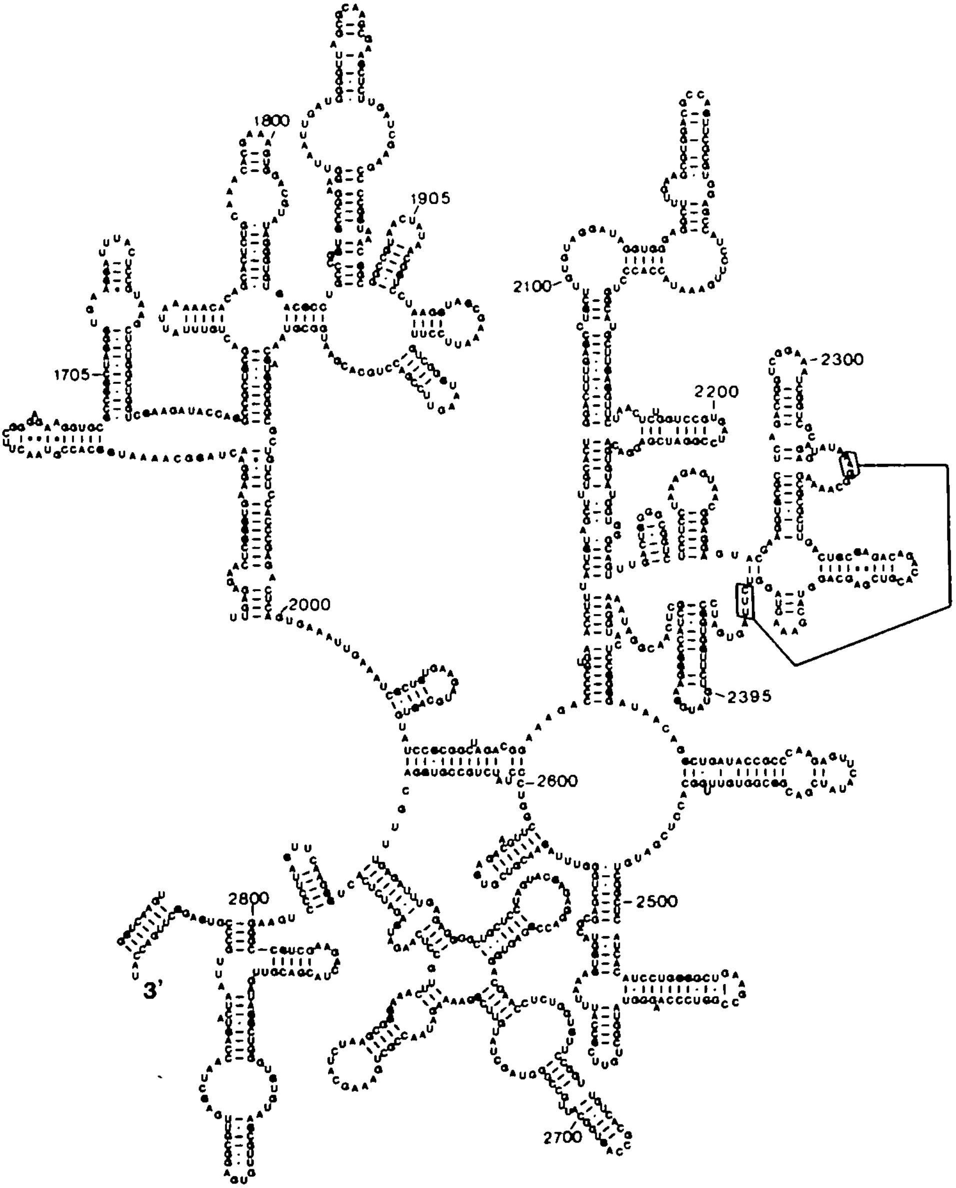


Fig.2b
Pseudomonas aeruginosa

Secondary Structure of eubacterial 23S Ribosomal RNA: 5'half

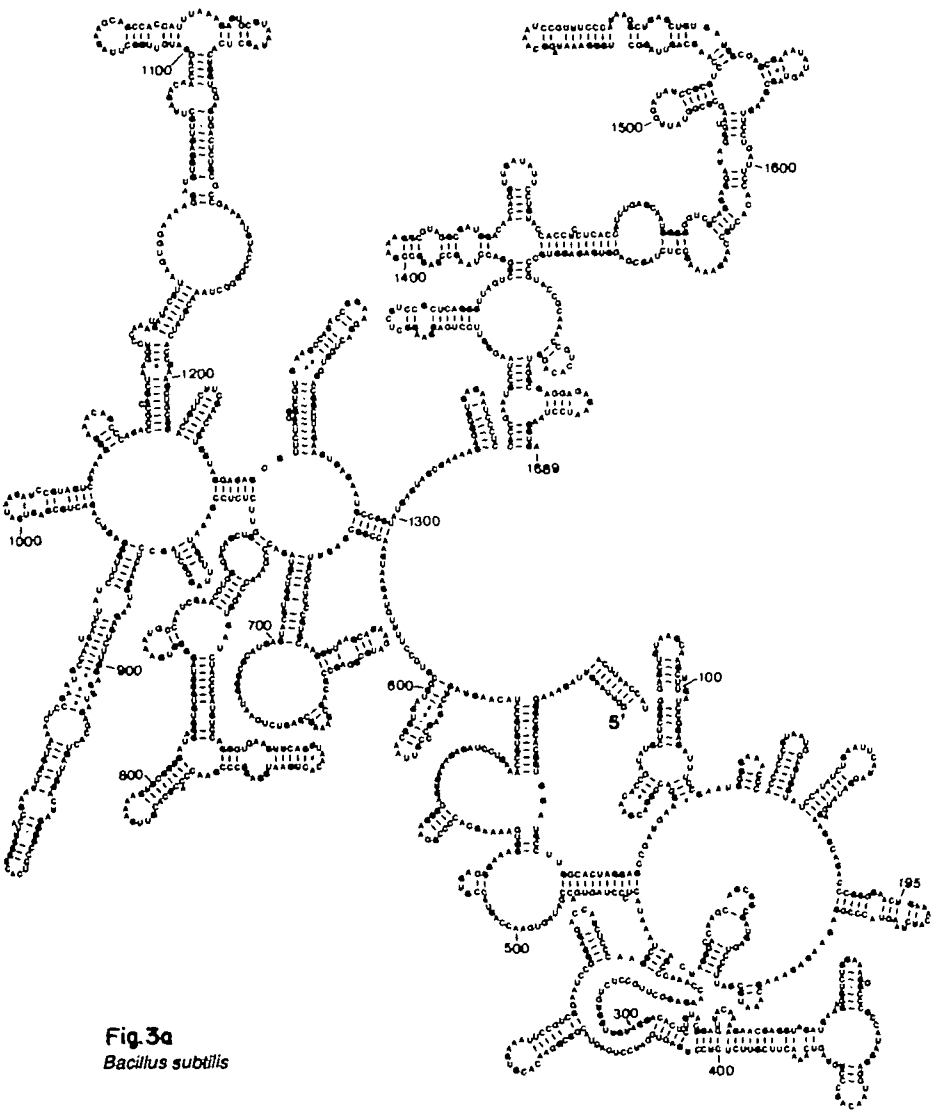


Fig.3a
Bacillus subtilis

Secondary Structure of eubacterial 23S Ribosomal RNA: 3'half

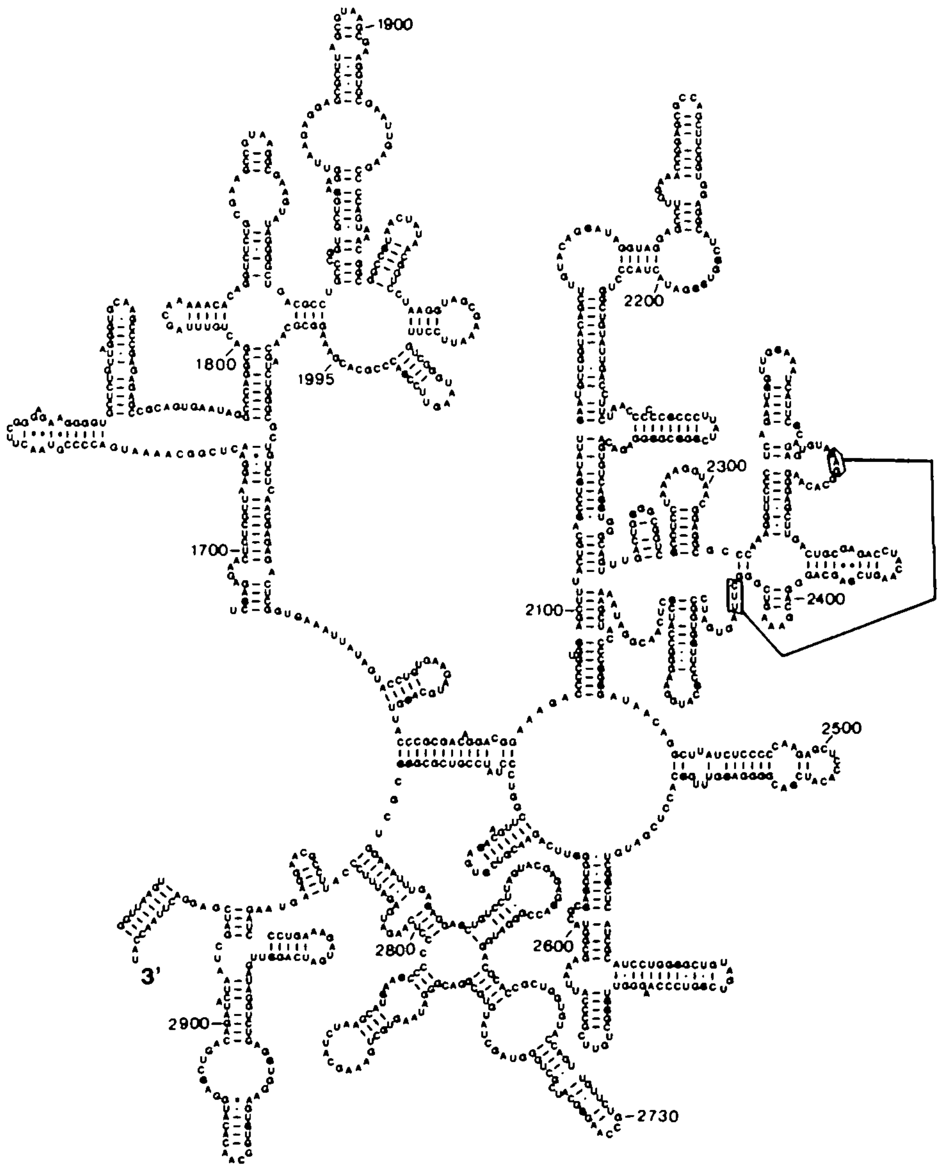


Fig.3b
Bacillus subtilis

Secondary Structure of eubacterial 23S Ribosomal RNA: 5'half

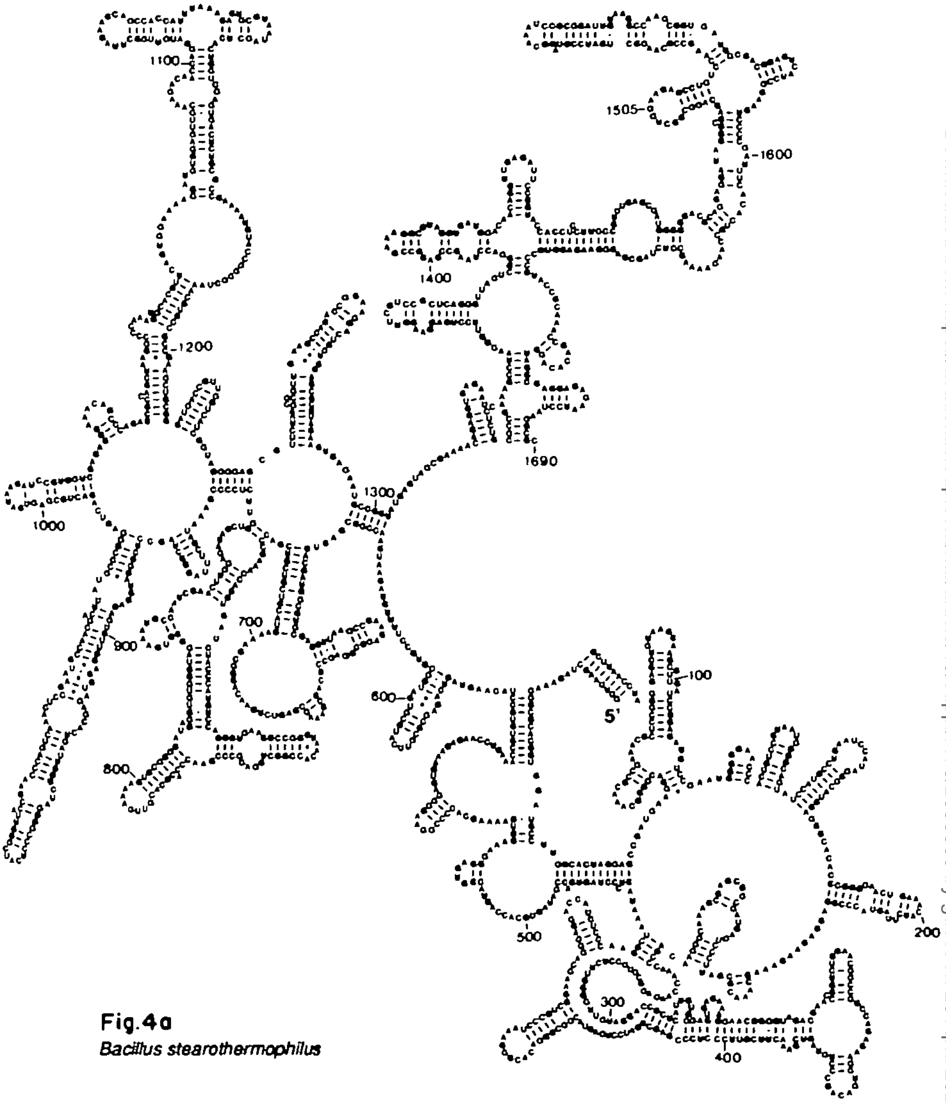


Fig.4a
Bacillus stearothermophilus

Secondary Structure of eubacterial 23S Ribosomal RNA: 3'half

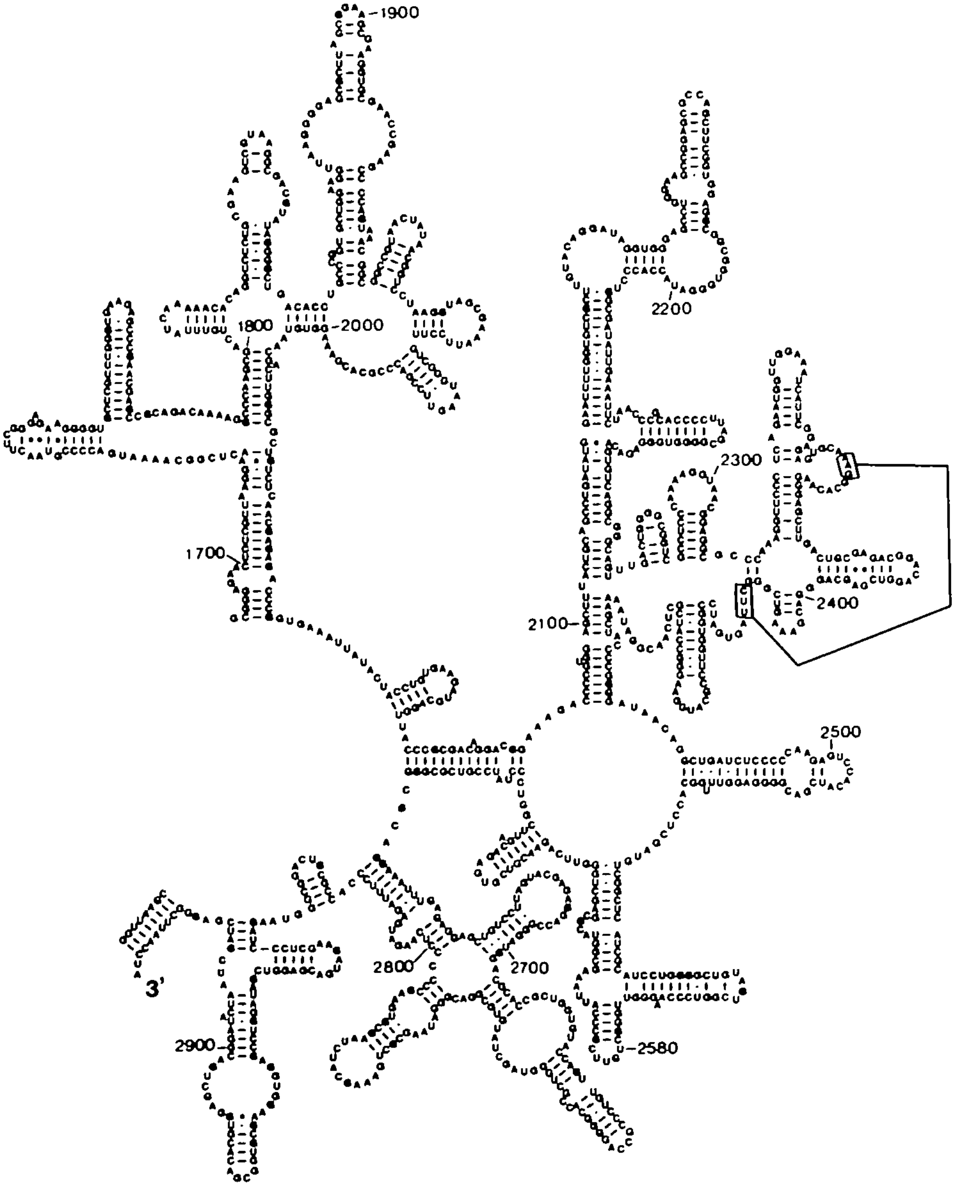


Fig.4b
Bacillus stearothermophilus

Secondary Structure of eubacterial 23S Ribosomal RNA: 5'half

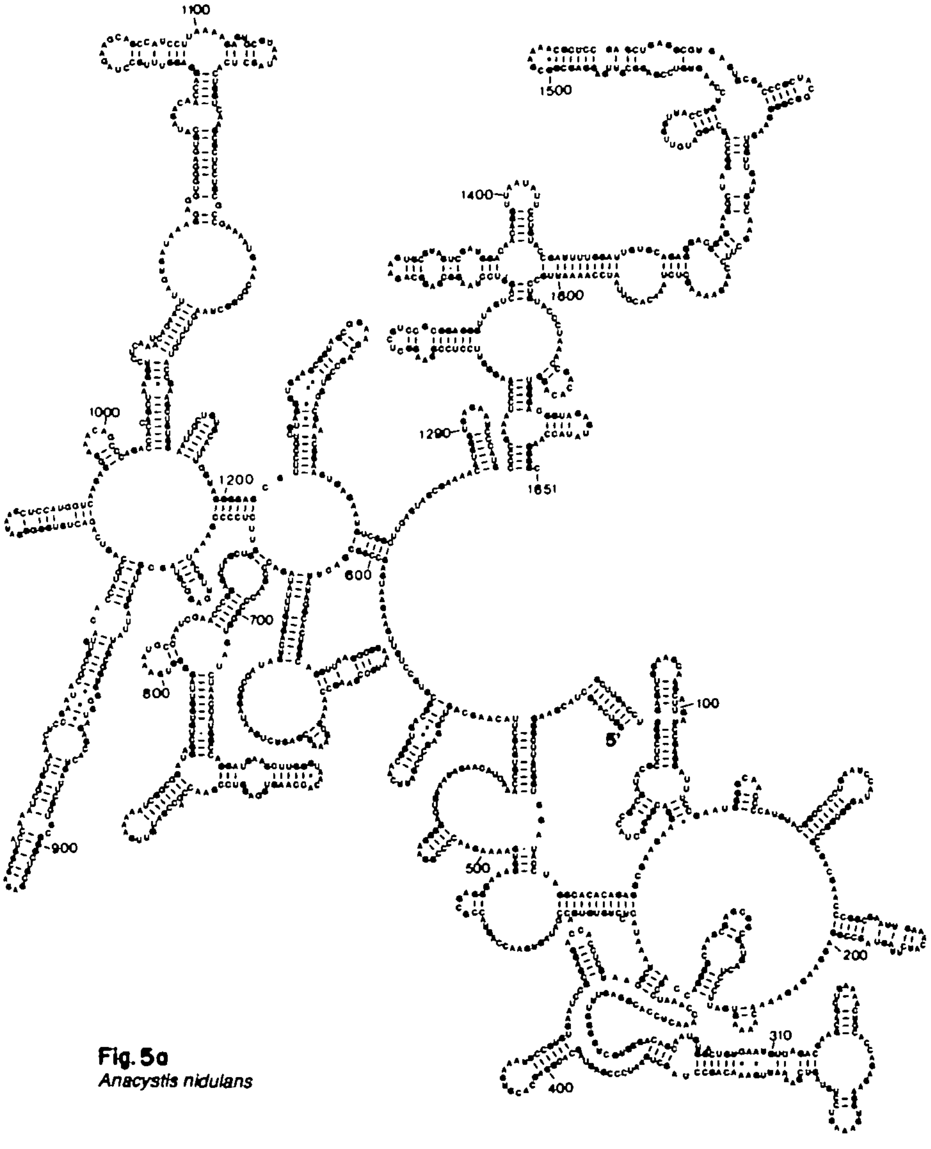


Fig. 5a
Anacystis nidulans

Secondary Structure of eubacterial 23S Ribosomal RNA: 3'half

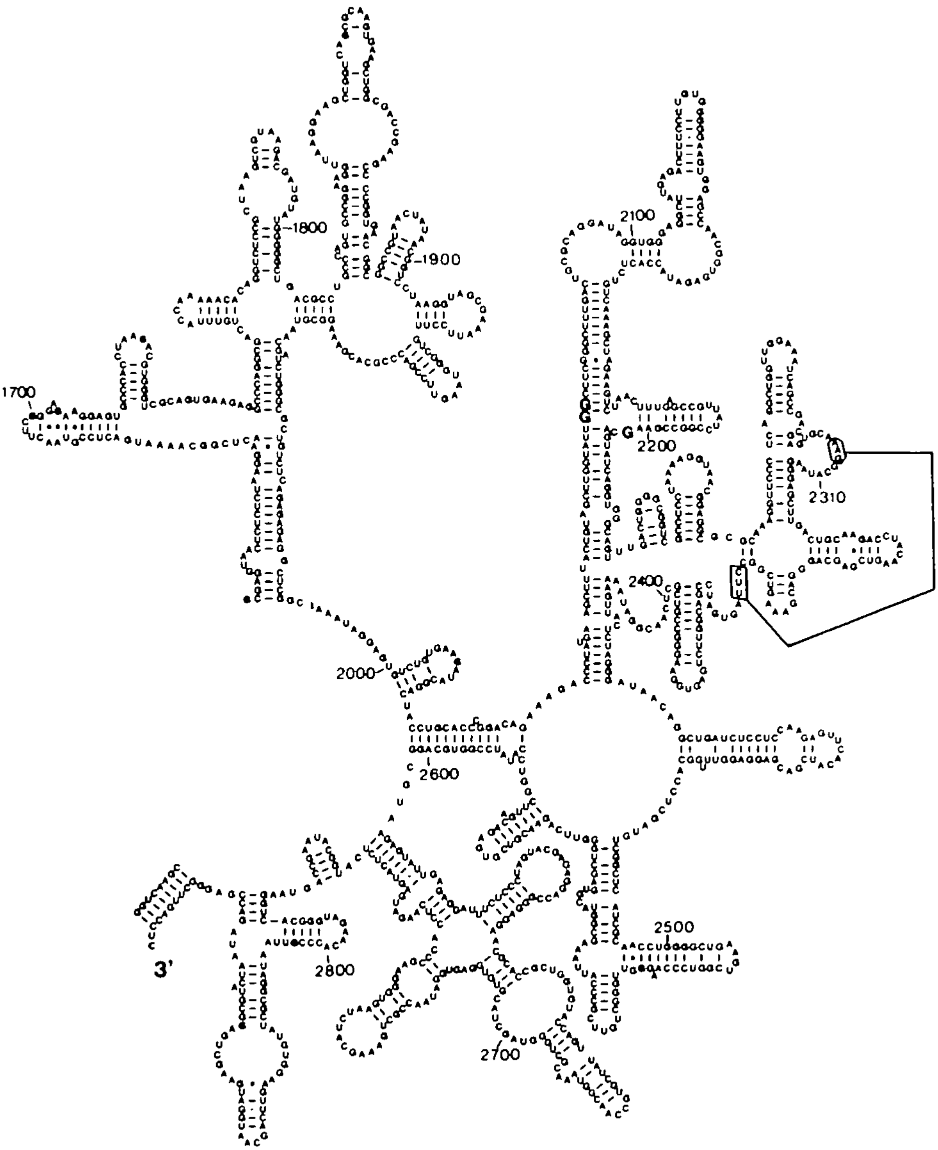


Fig.5b
Anacystis nidulans

Secondary Structure of chloroplast 23S Ribosomal RNA: 5'half

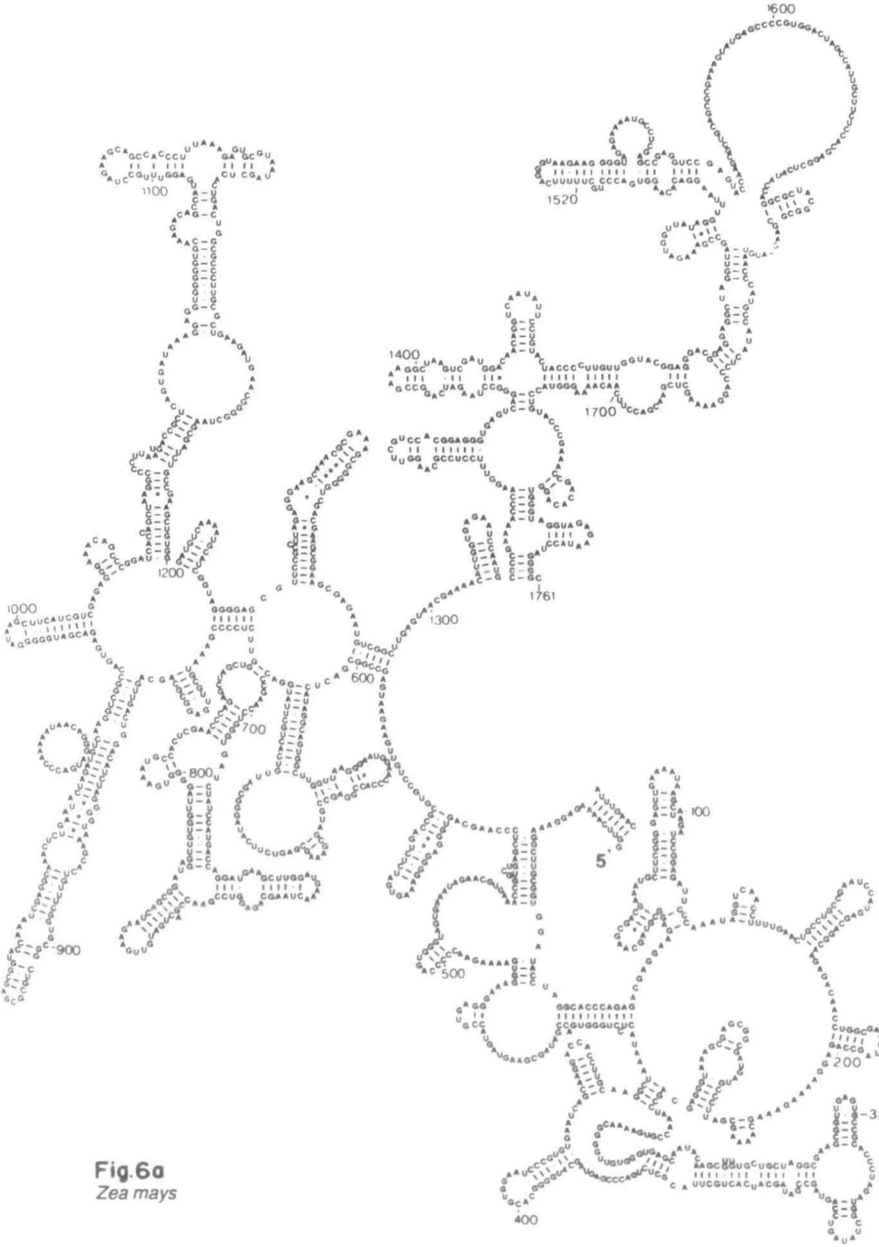


Fig.6a
Zea mays

Secondary Structure of chloroplast 23S Ribosomal RNA: 3'half

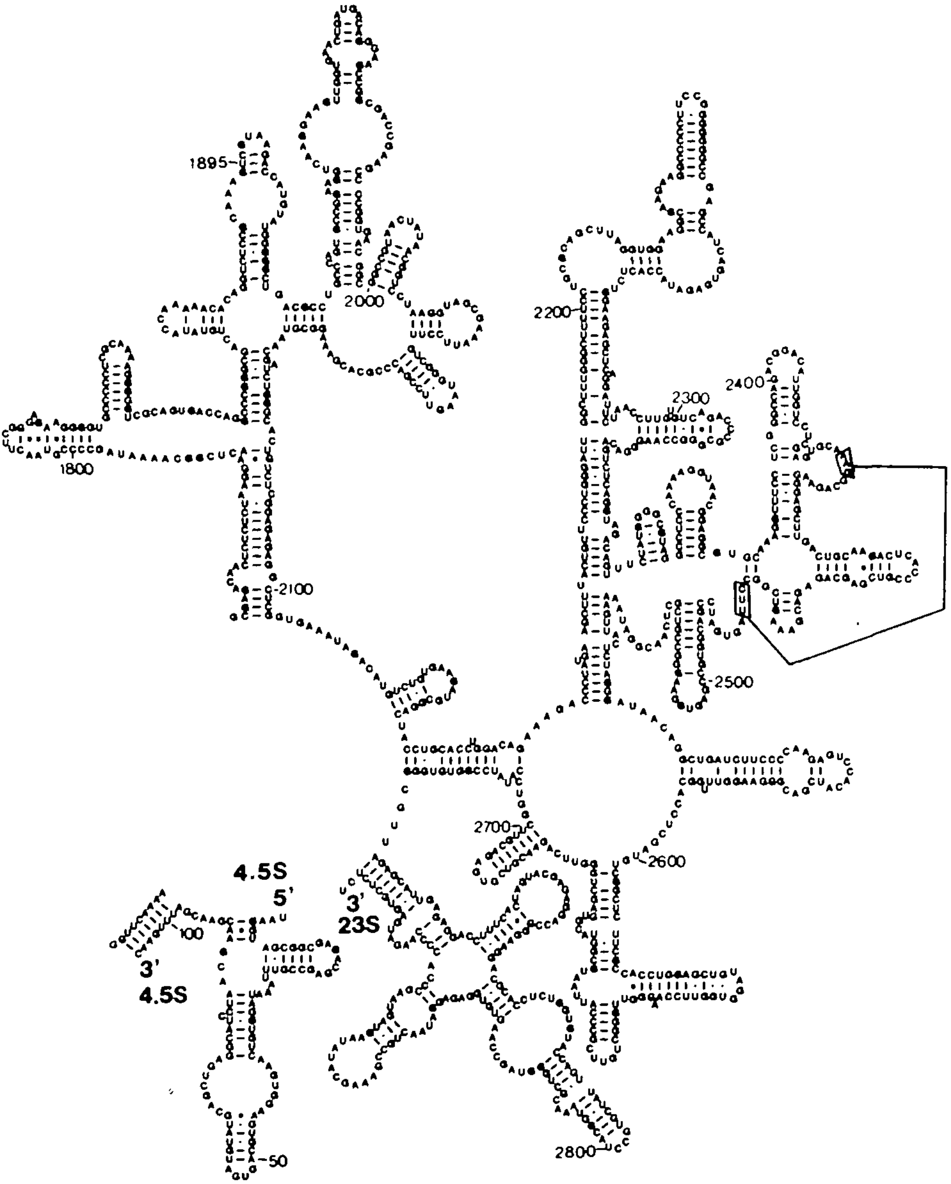


Fig.6b
Zea mays

Secondary Structure of chloroplast 23S Ribosomal RNA: 5'half

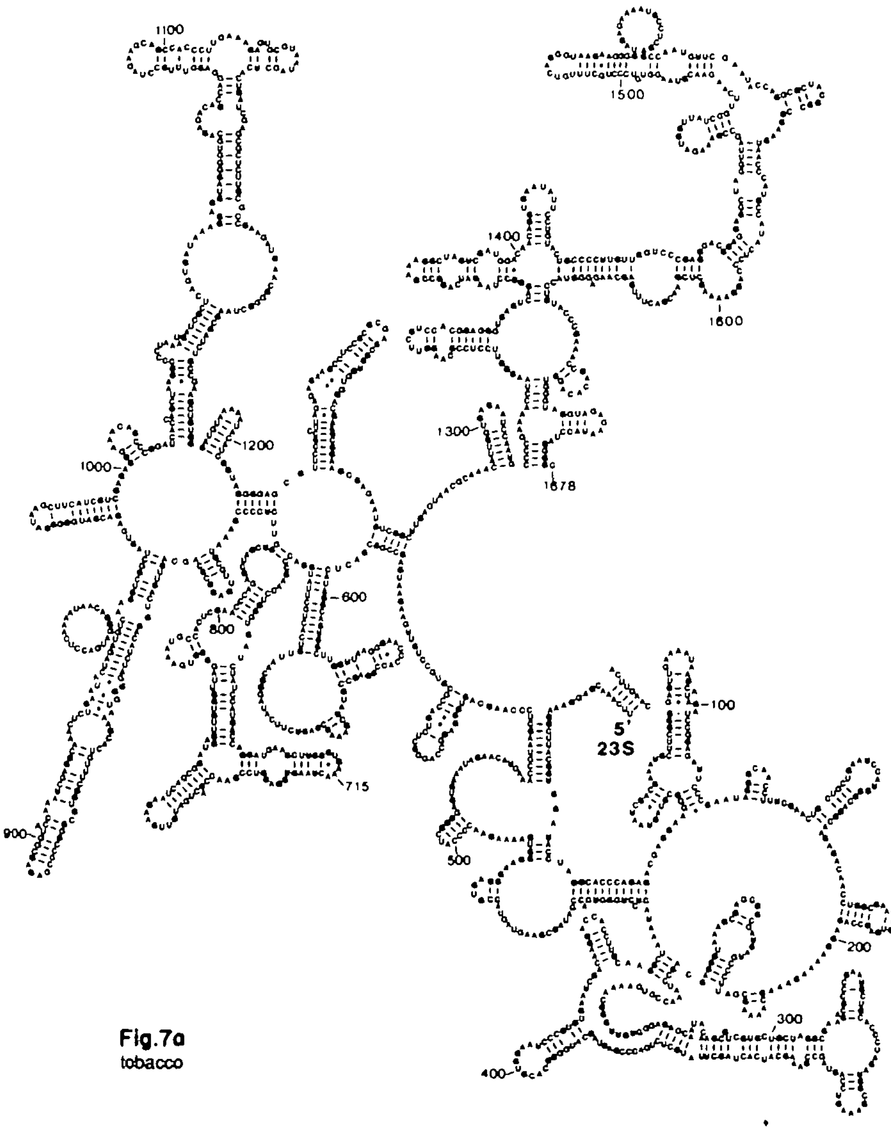


Fig.7a
tobacco

Secondary Structure of chloroplast 23S Ribosomal RNA: 3'half

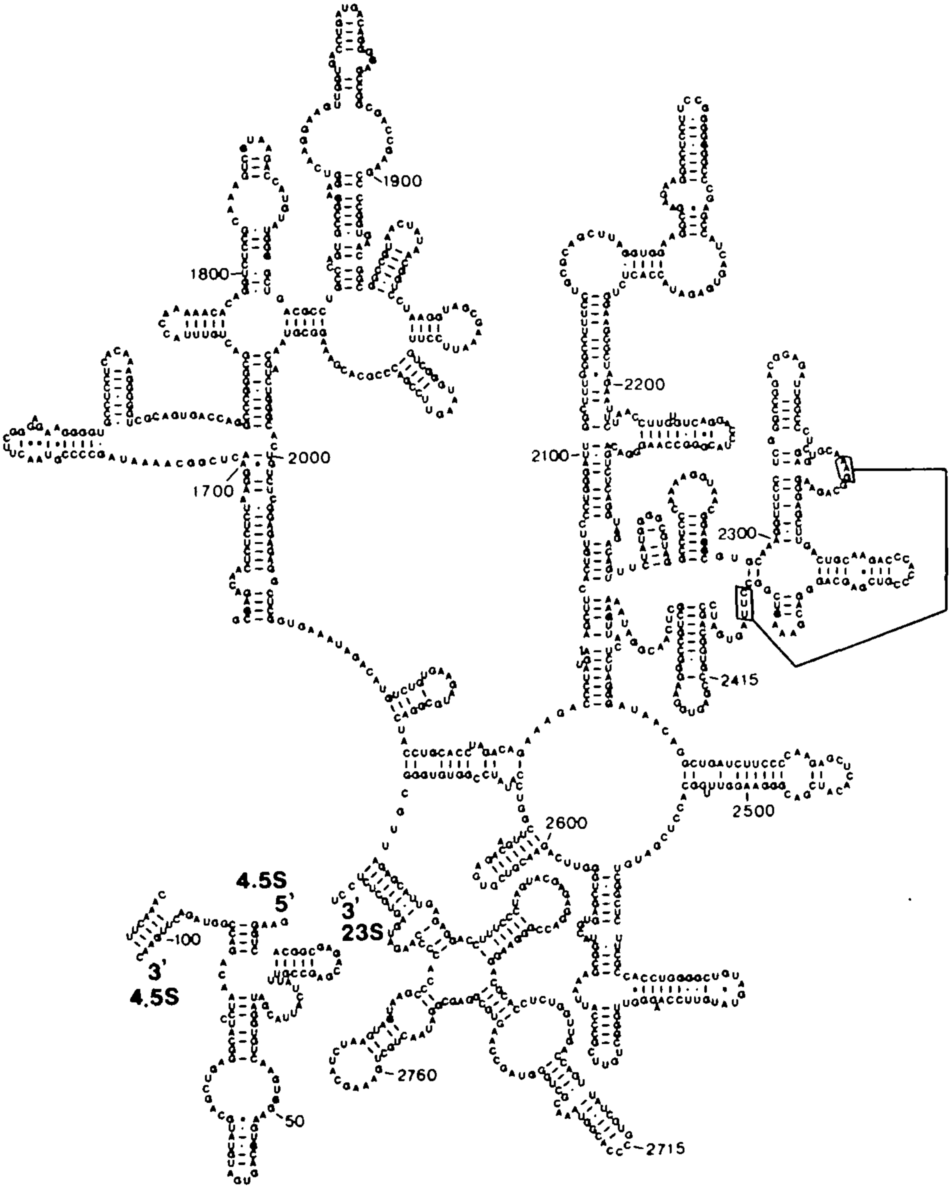


Fig. 7b
tobacco

Secondary Structure of chloroplast 23S Ribosomal RNA: 5'half

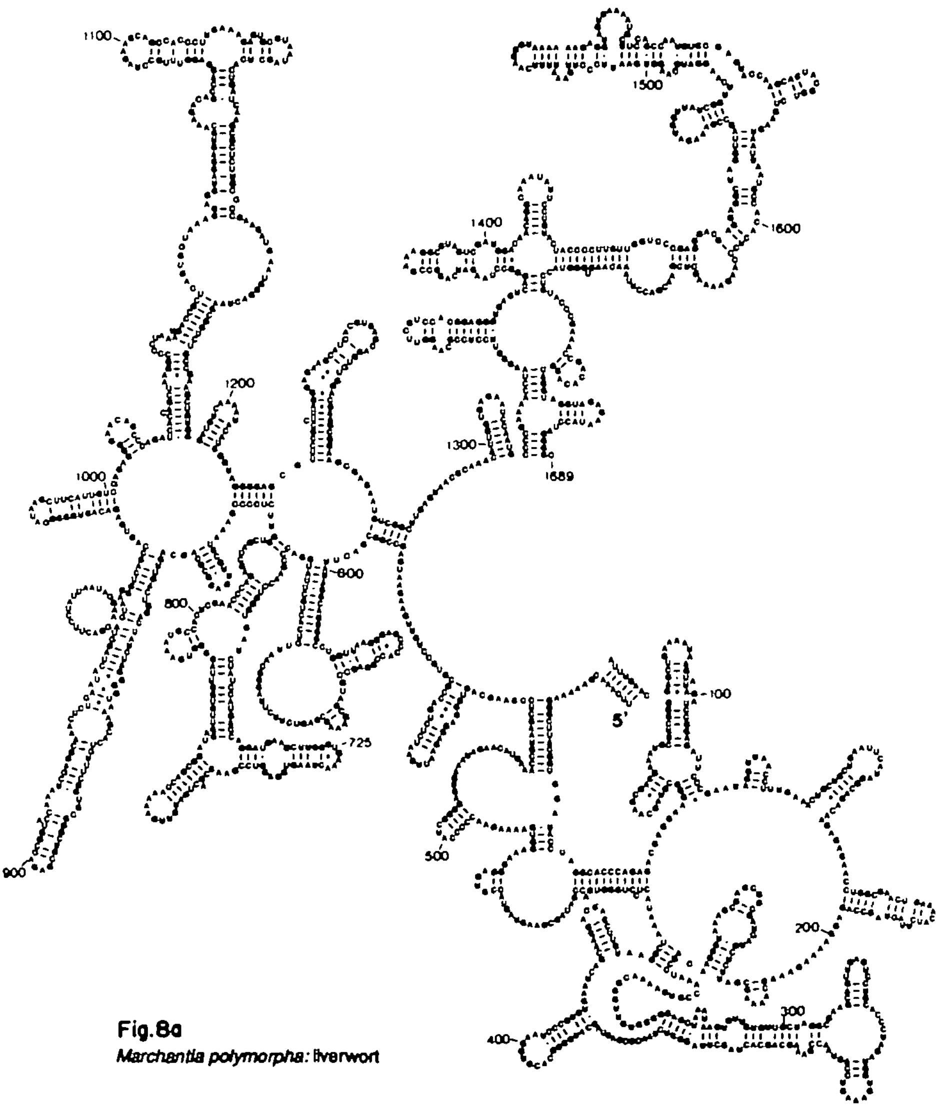


Fig.8a
Marchantia polymorpha: liverwort

Secondary Structure of chloroplast 23S Ribosomal RNA: 3'half

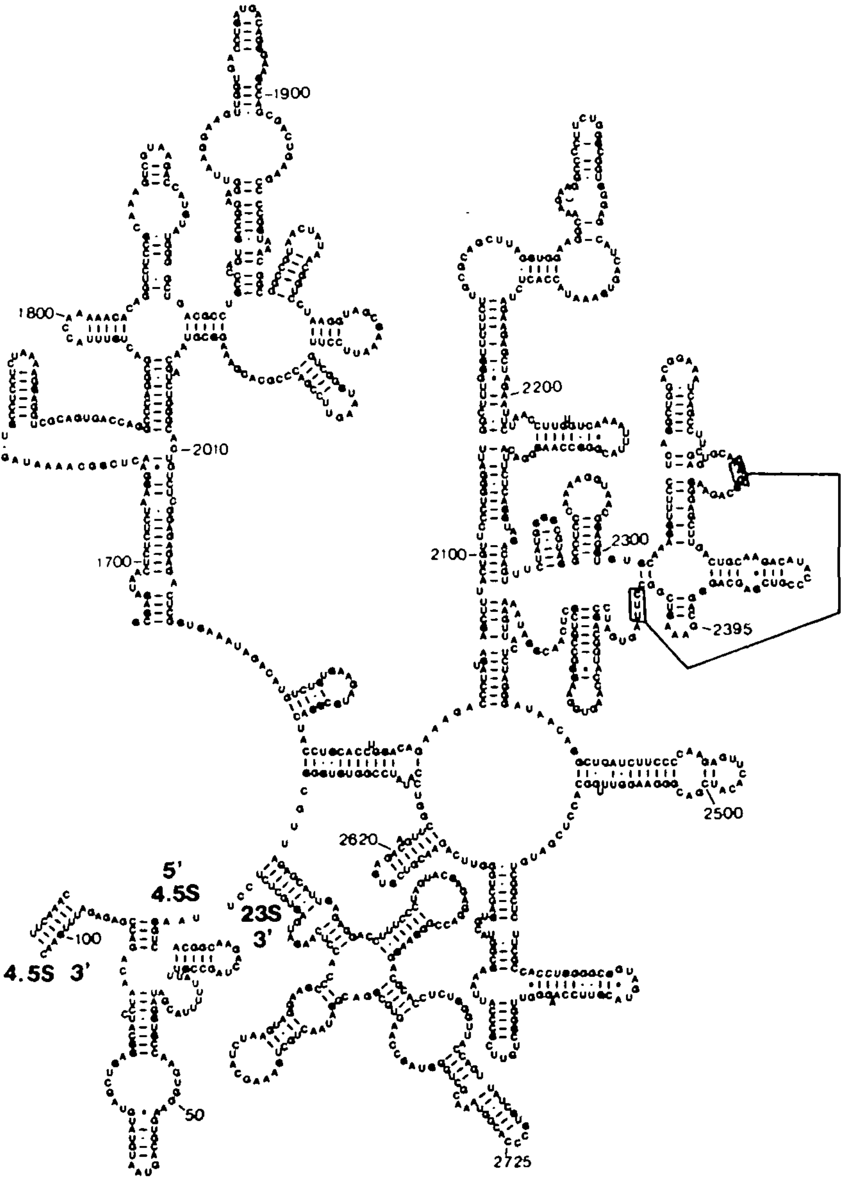


Fig. 8b
Marchantia polymorpha: liverwort

Secondary Structure of chloroplast 23S Ribosomal RNA: 5'half

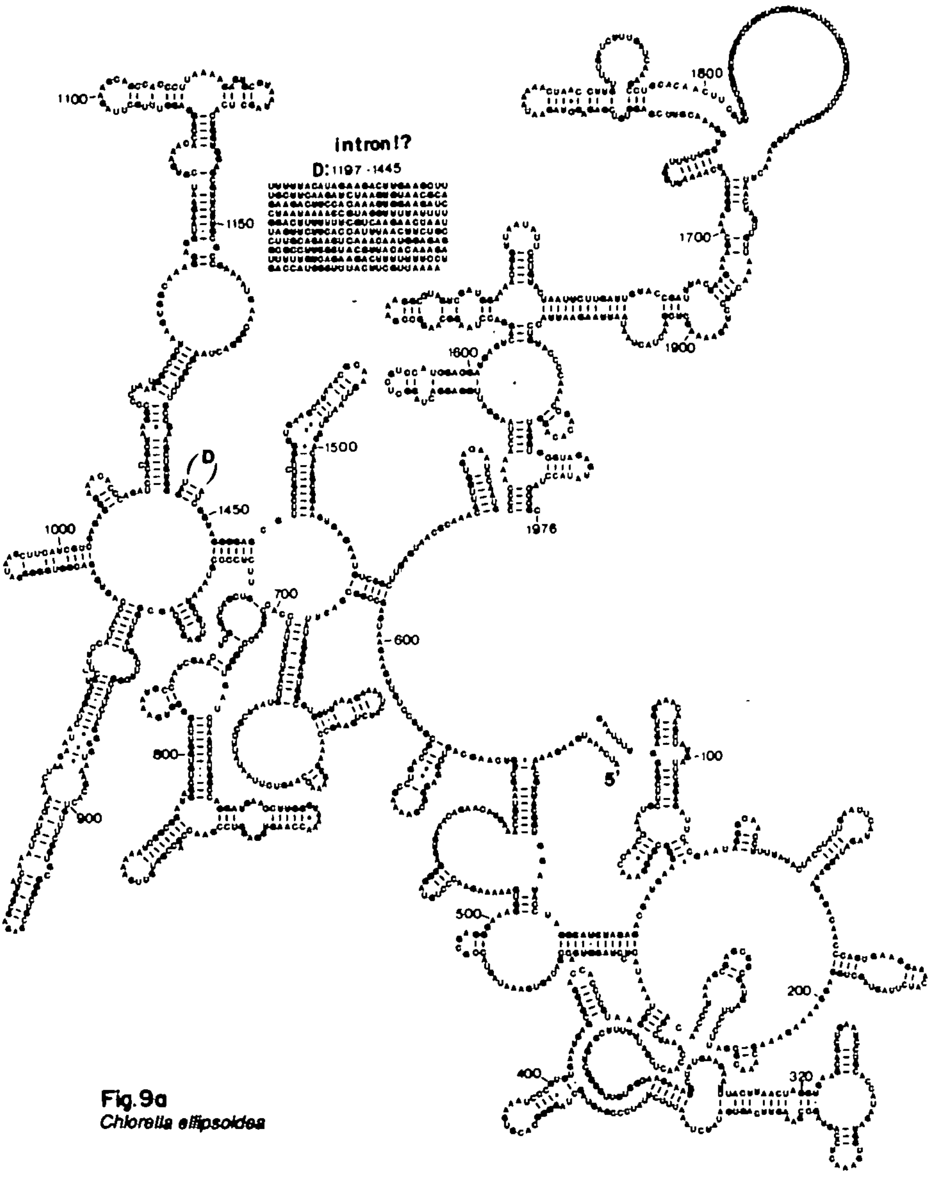


Fig. 9a
Chlorella ellipsoidea

Secondary Structure of chloroplast 23S Ribosomal RNA: 3'half

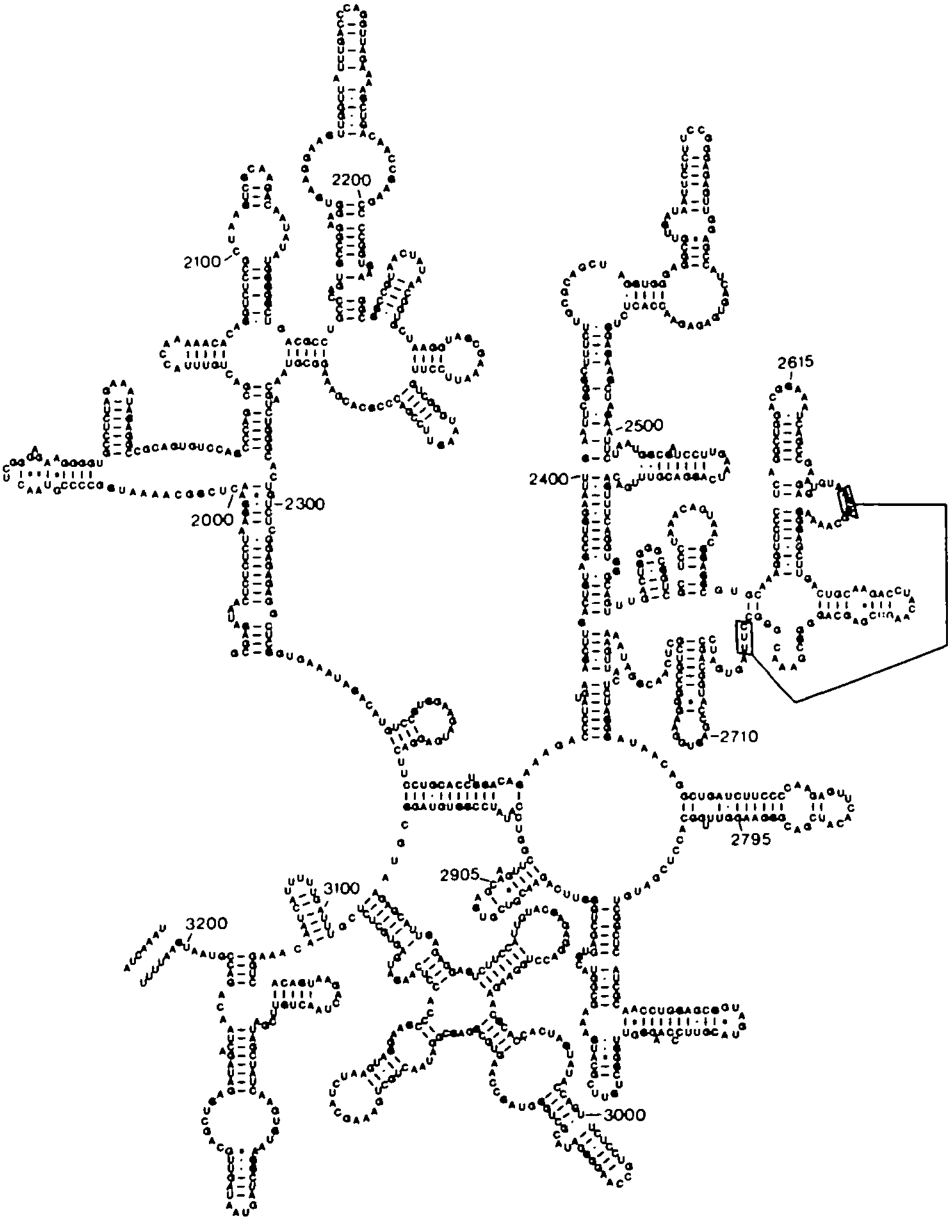


Fig. 9b
Chlorella ellipsoidea

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

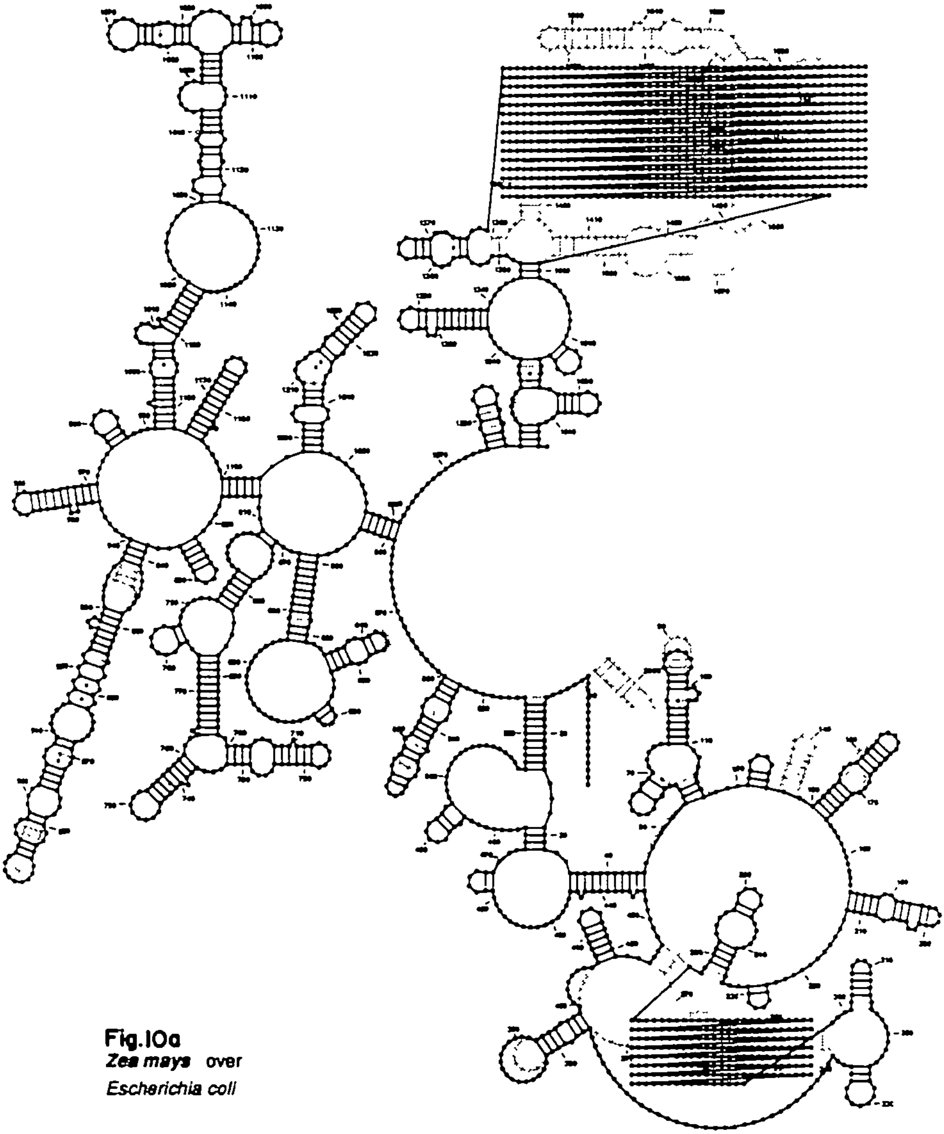


Fig.10a
Zea mays over
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

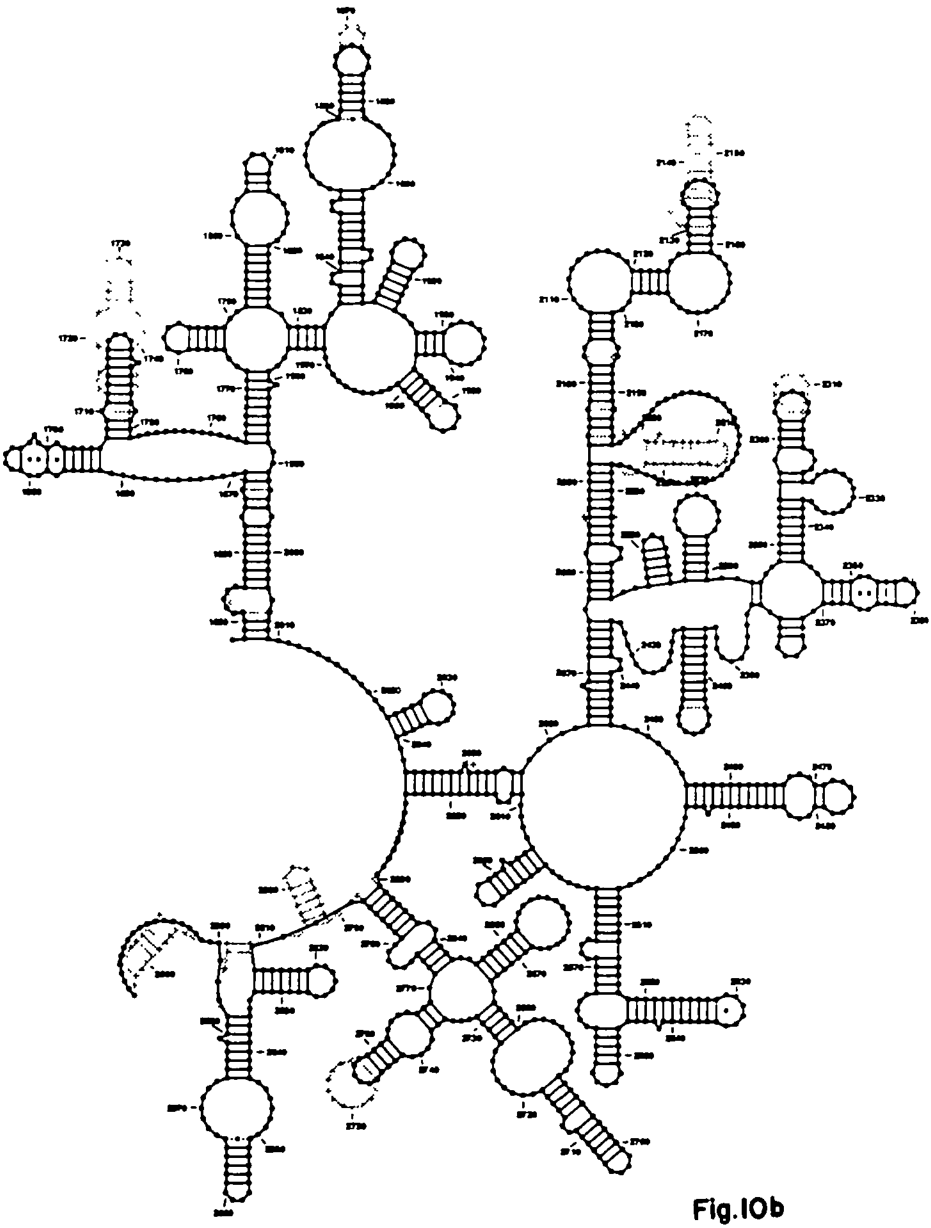


Fig.10b
Zea mays over
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

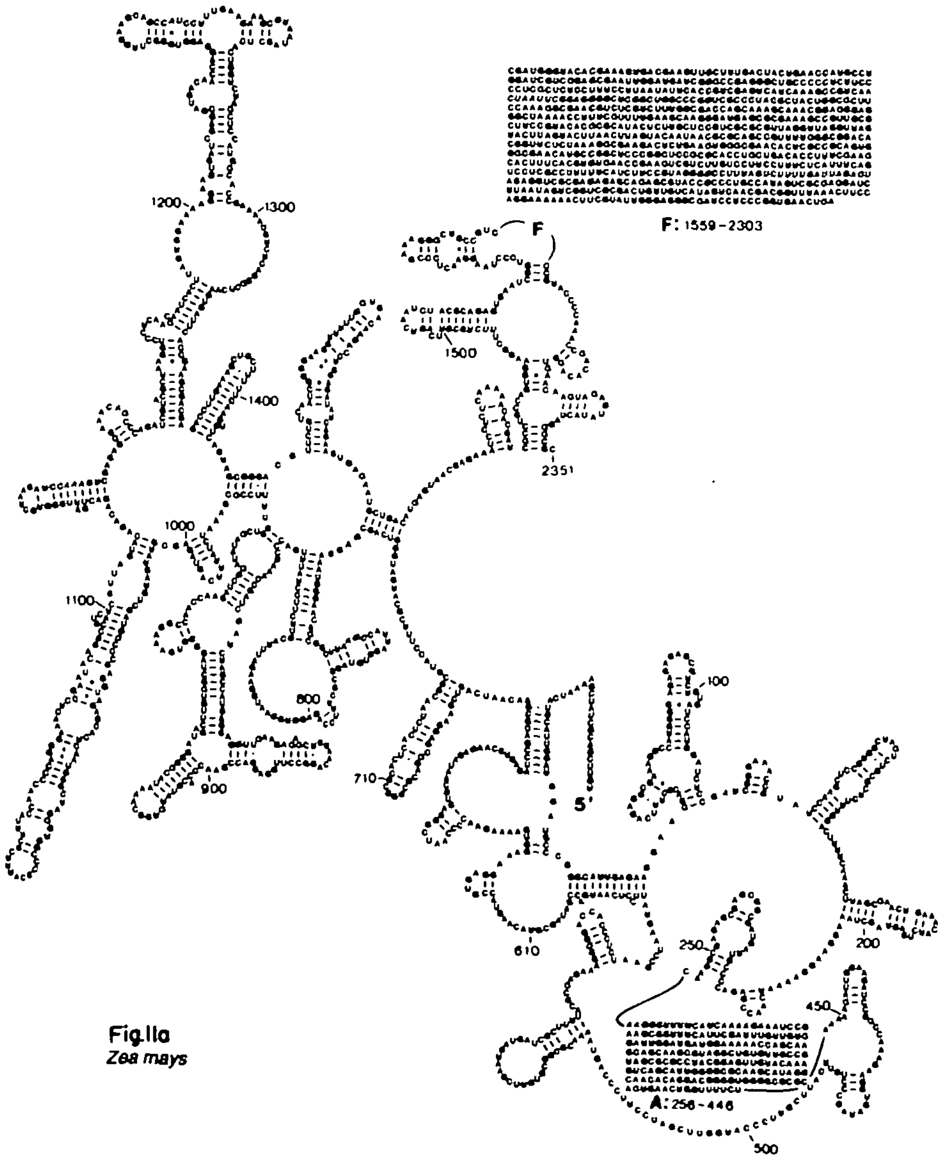


Fig.IIa
Zea mays

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

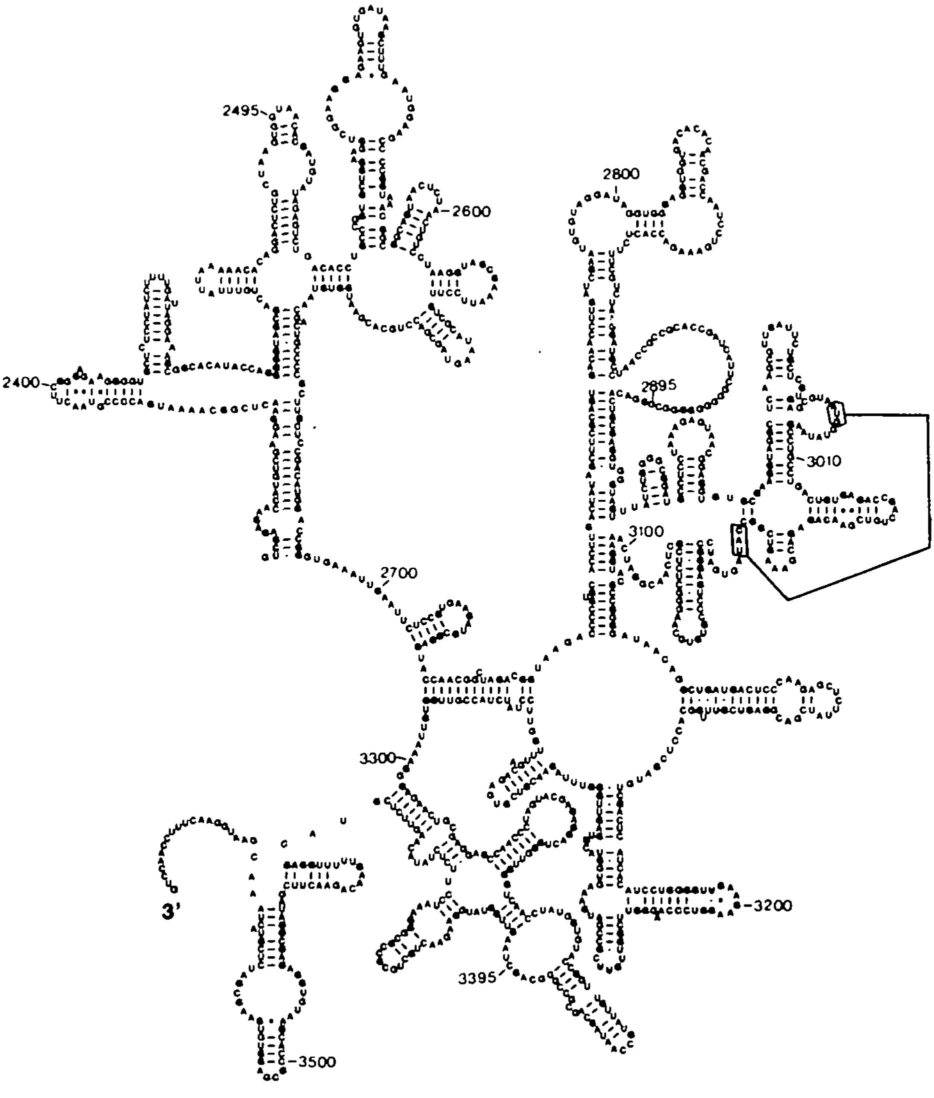


Fig.IIb
Zea mays

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

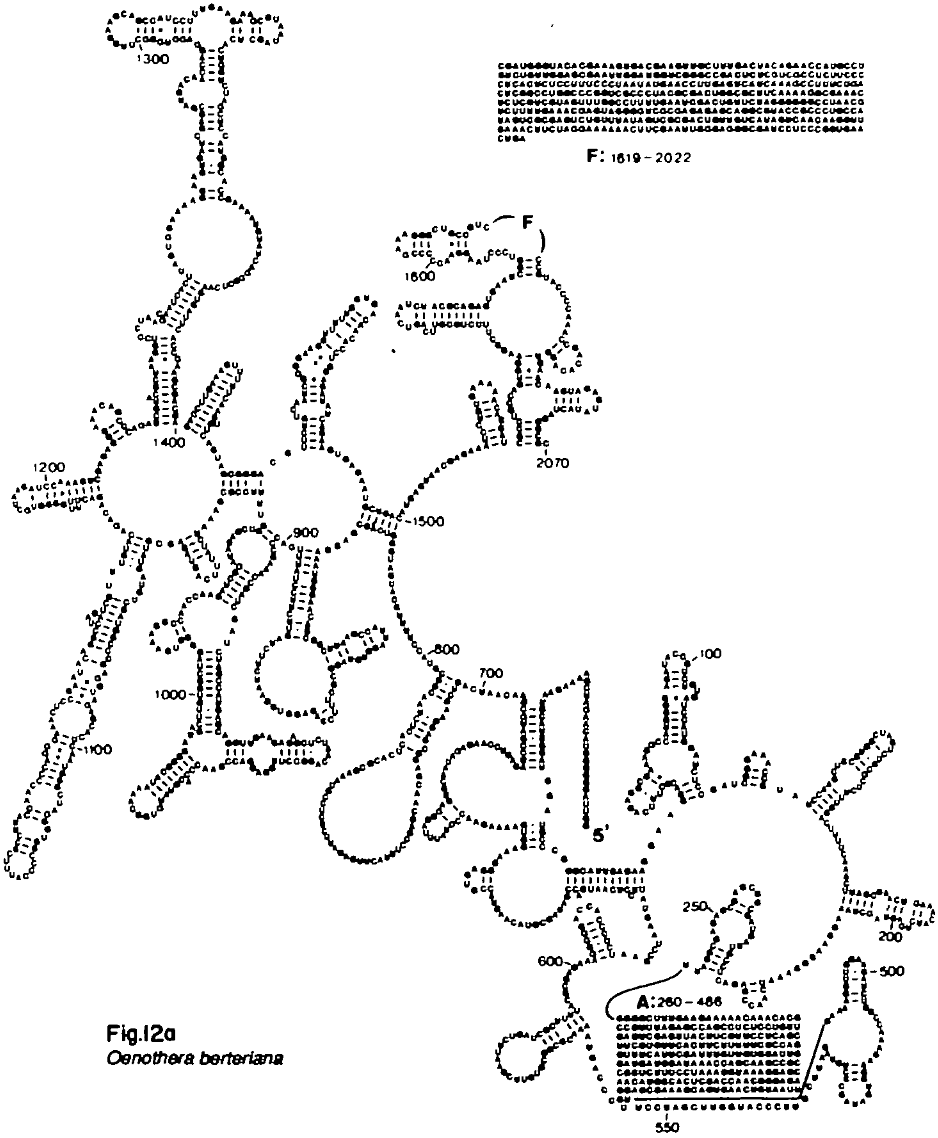


Fig.12a
Oenothera berteriana

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

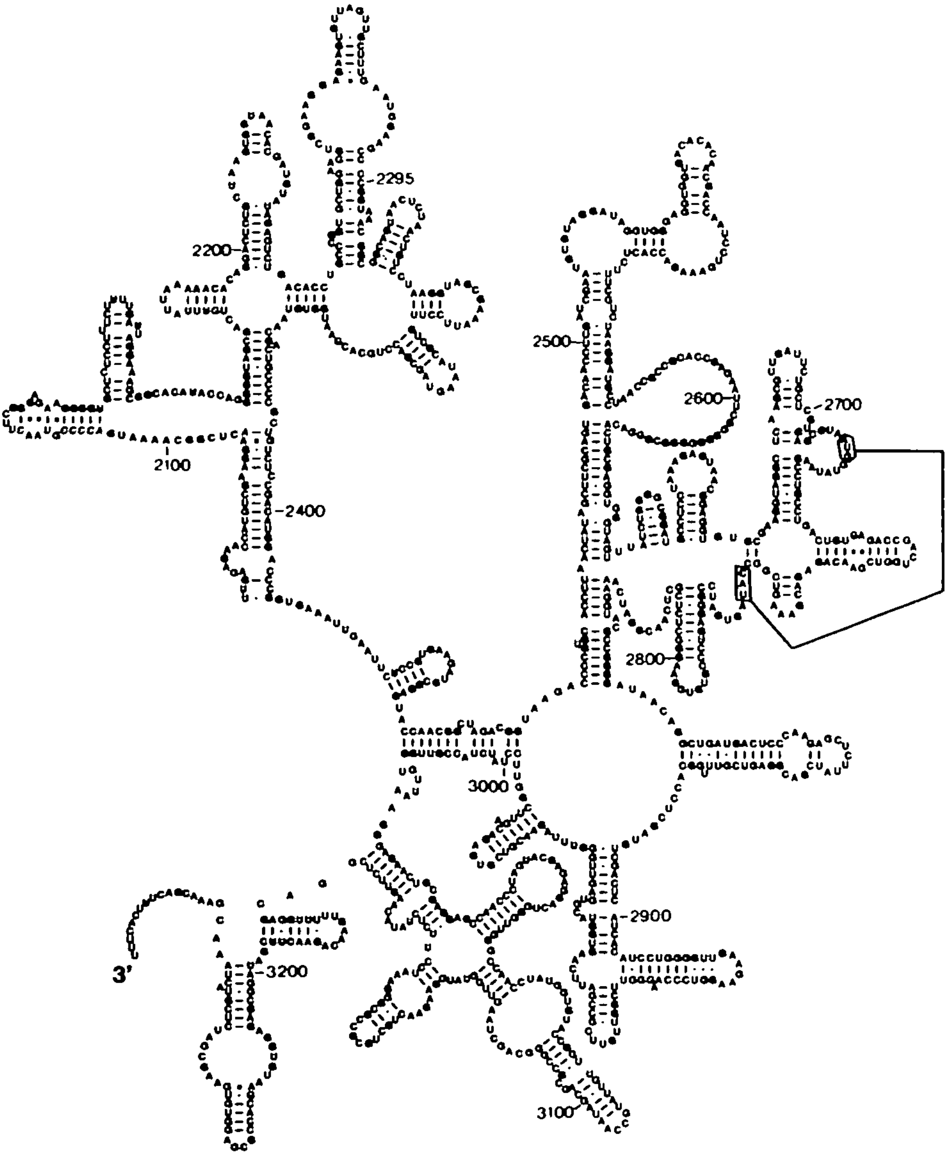


Fig.12b
Oenothera berteriana

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

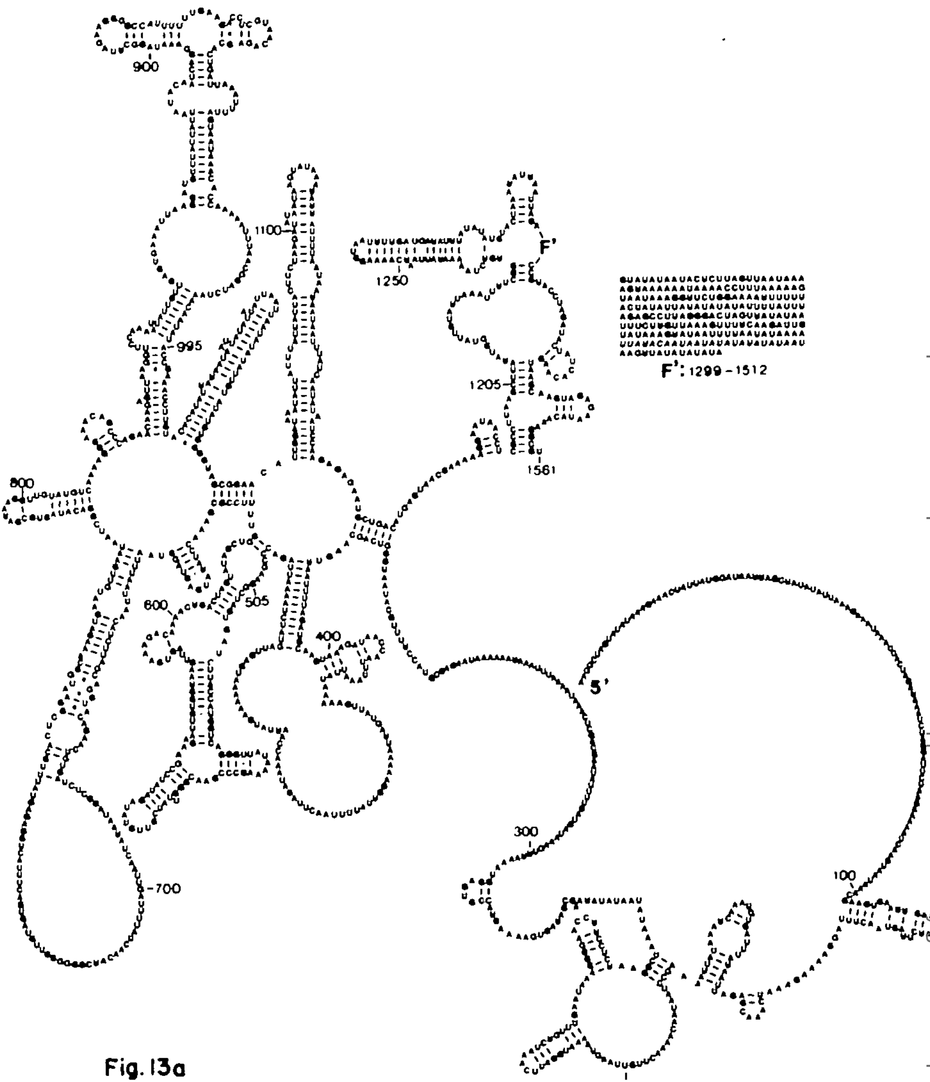
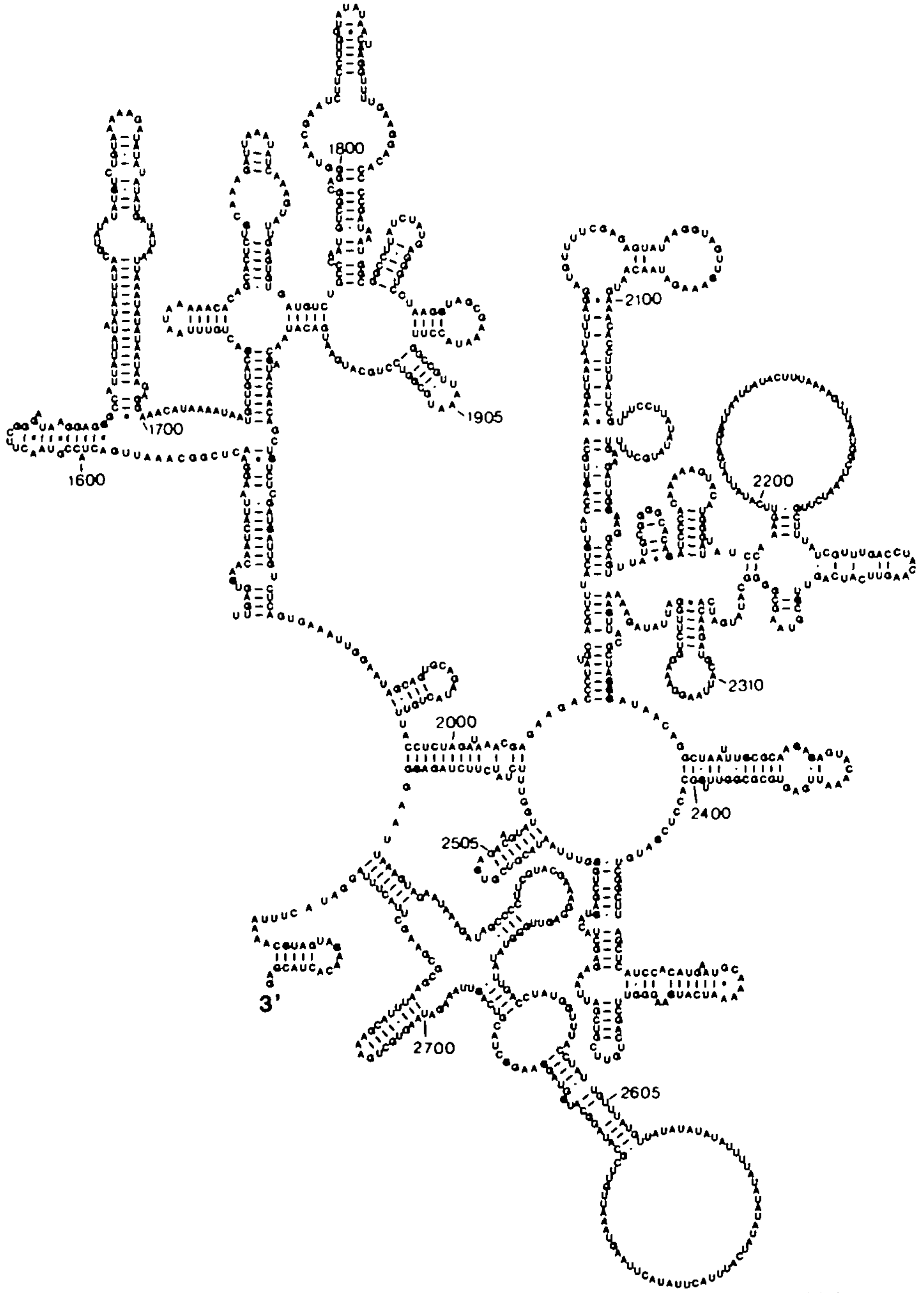


Fig. 13a
Aspergillus nidulans

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half



Aspergillus nidulans

Fig. 13b

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

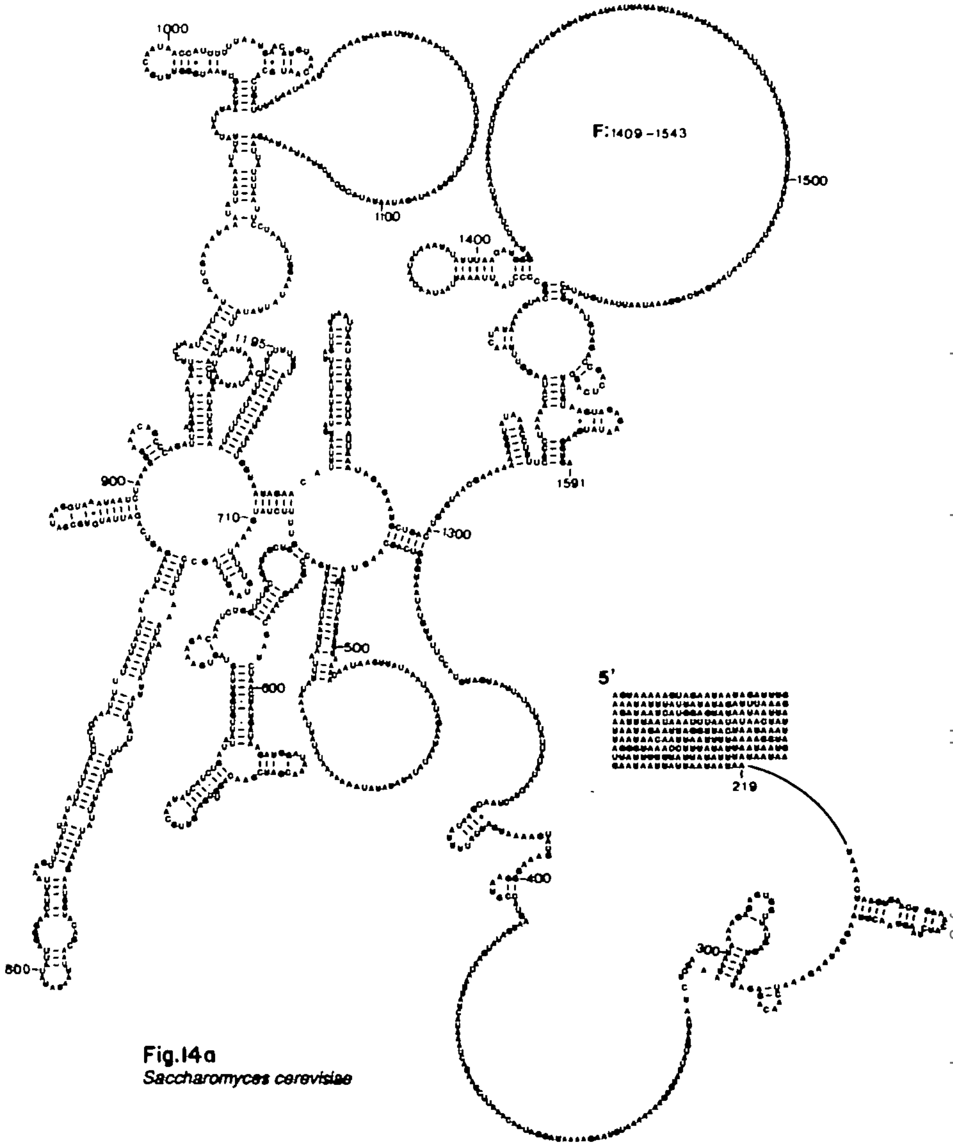


Fig.14a
Saccharomyces cerevisiae

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

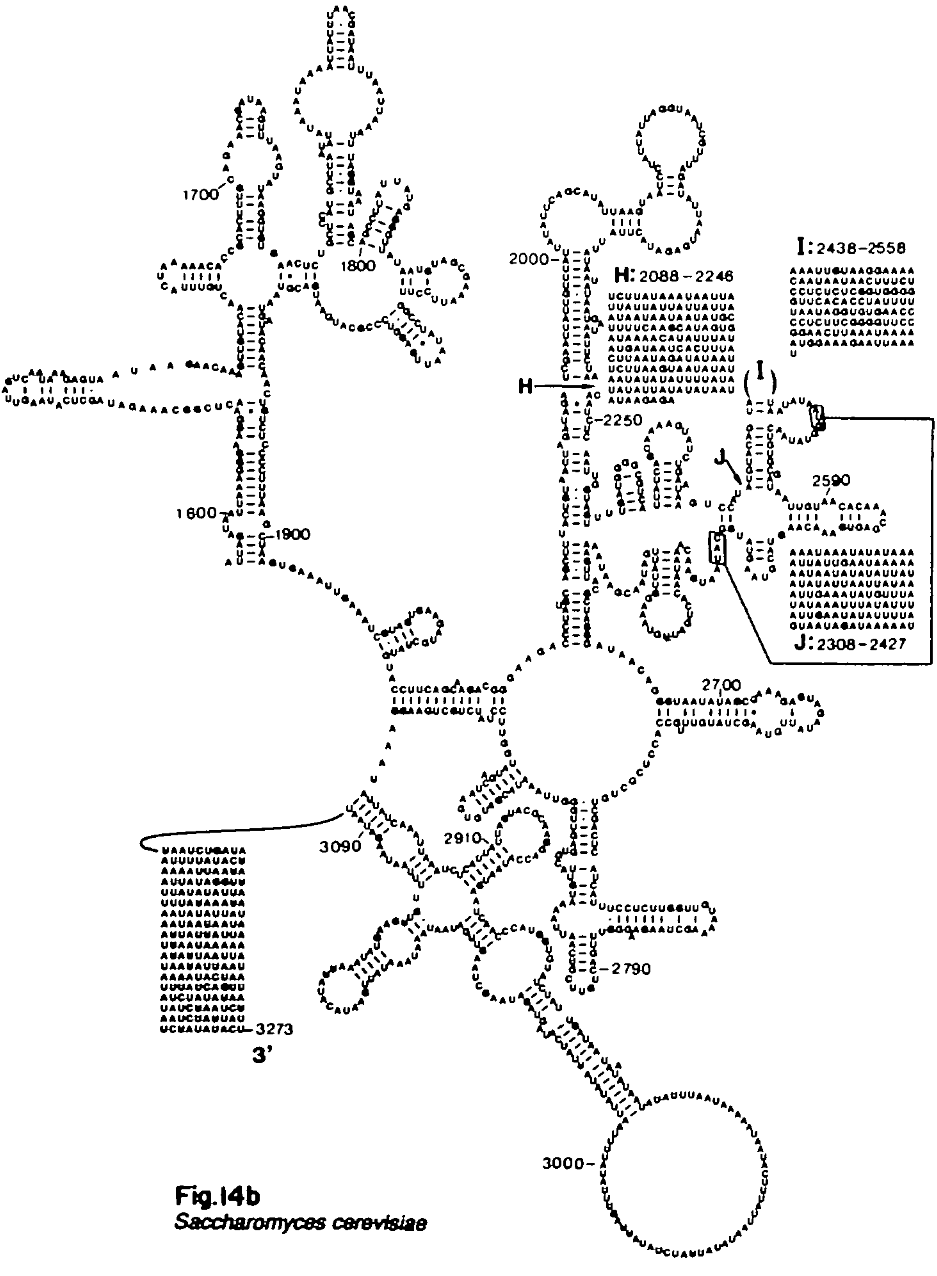


Fig.14b
Saccharomyces cerevisiae

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

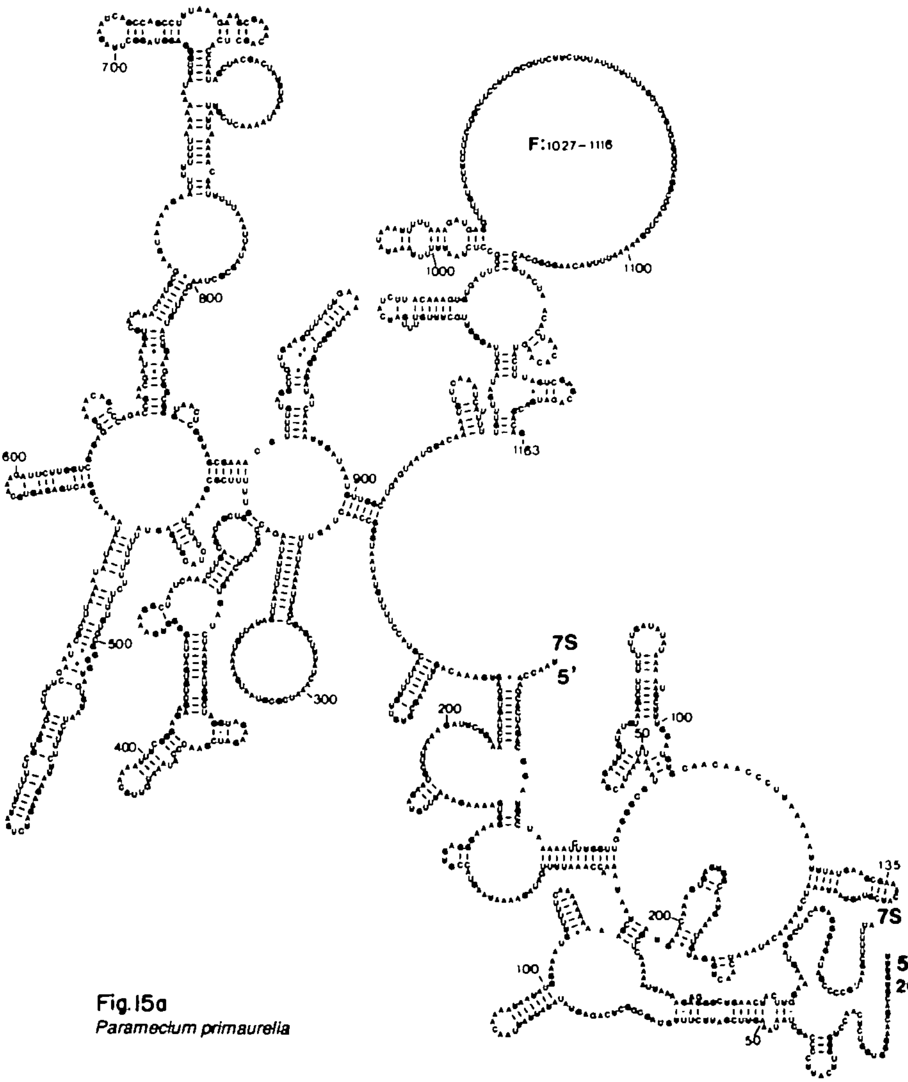


Fig. 15a
Paramecium primaurelia

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

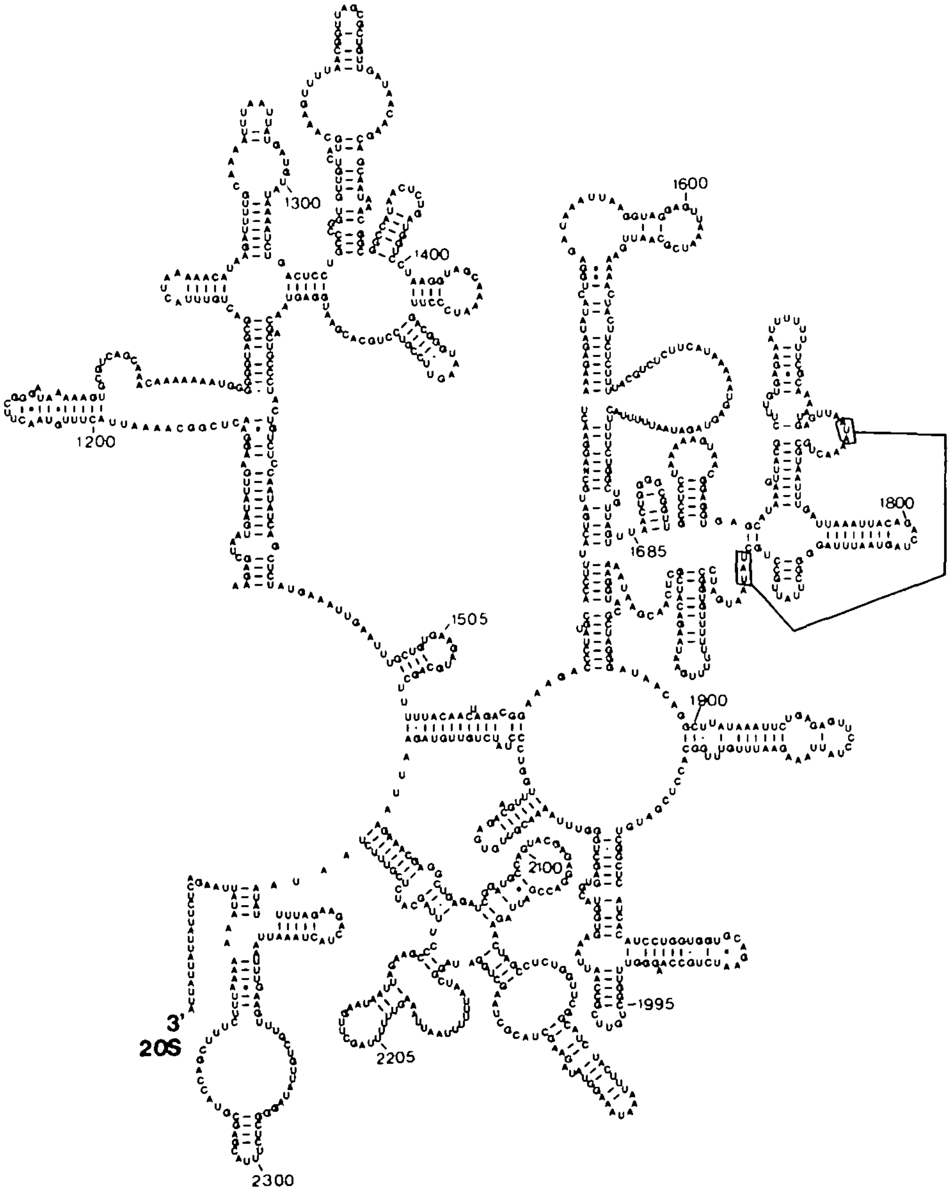


Fig.15b

Paramecium primaurelia

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

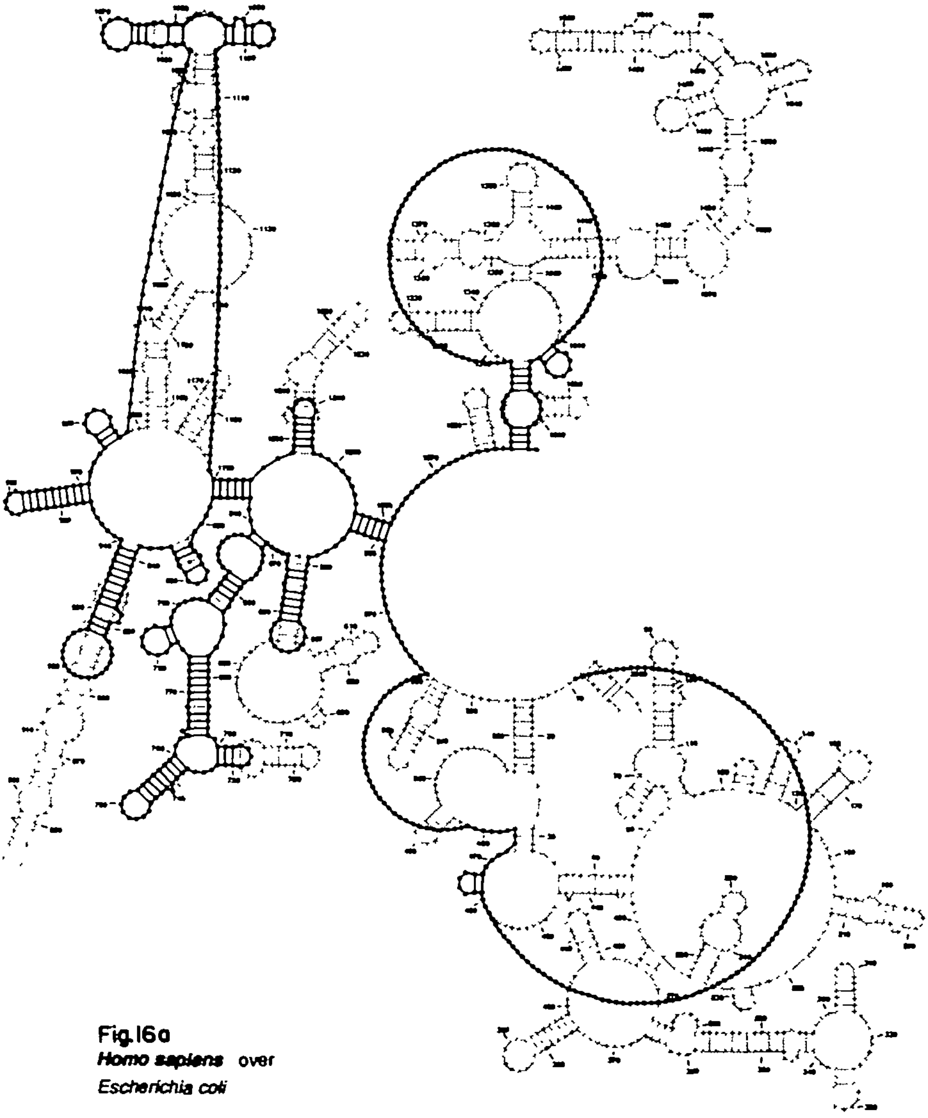


Fig.16a
Homo sapiens over
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

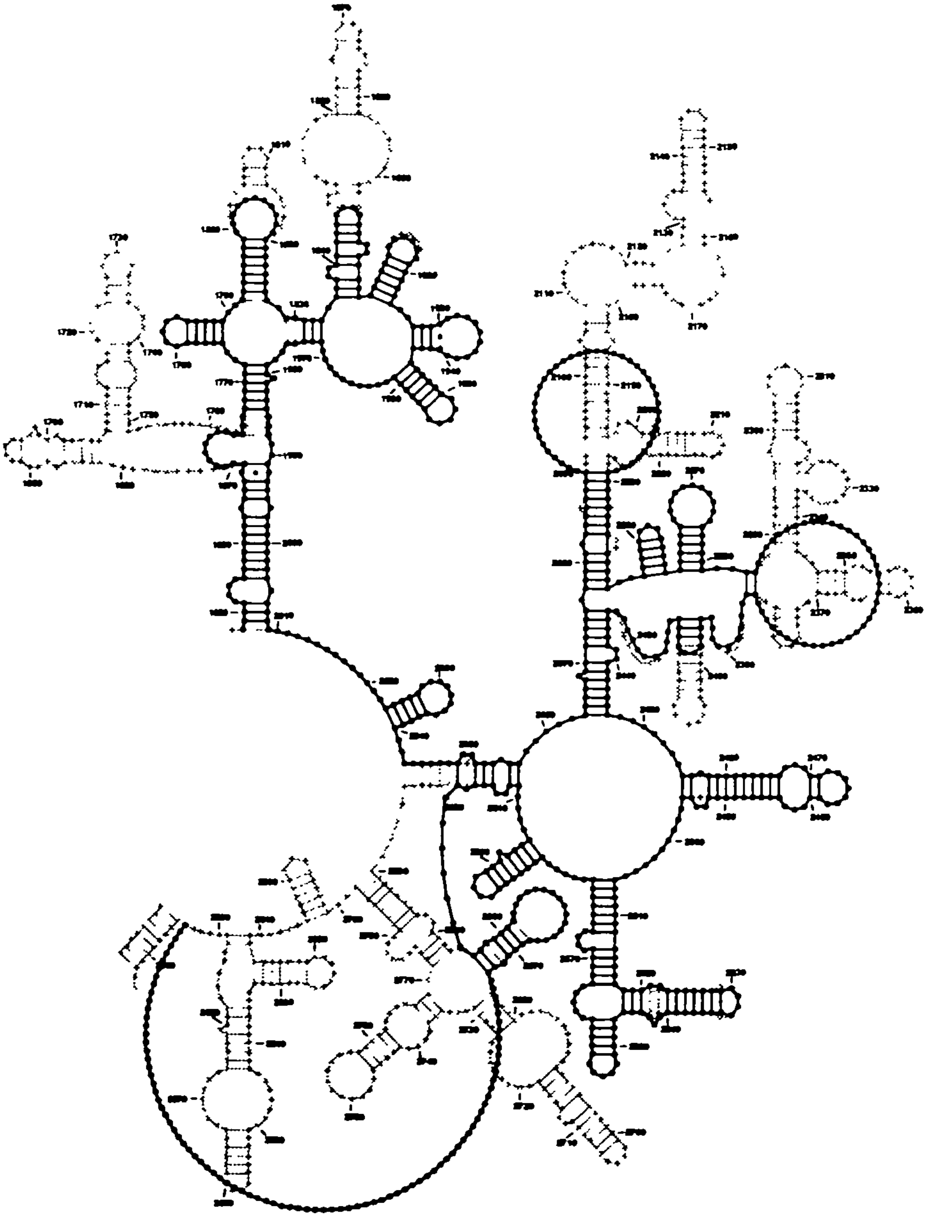


Fig.16b
***Homo sapiens* over**
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

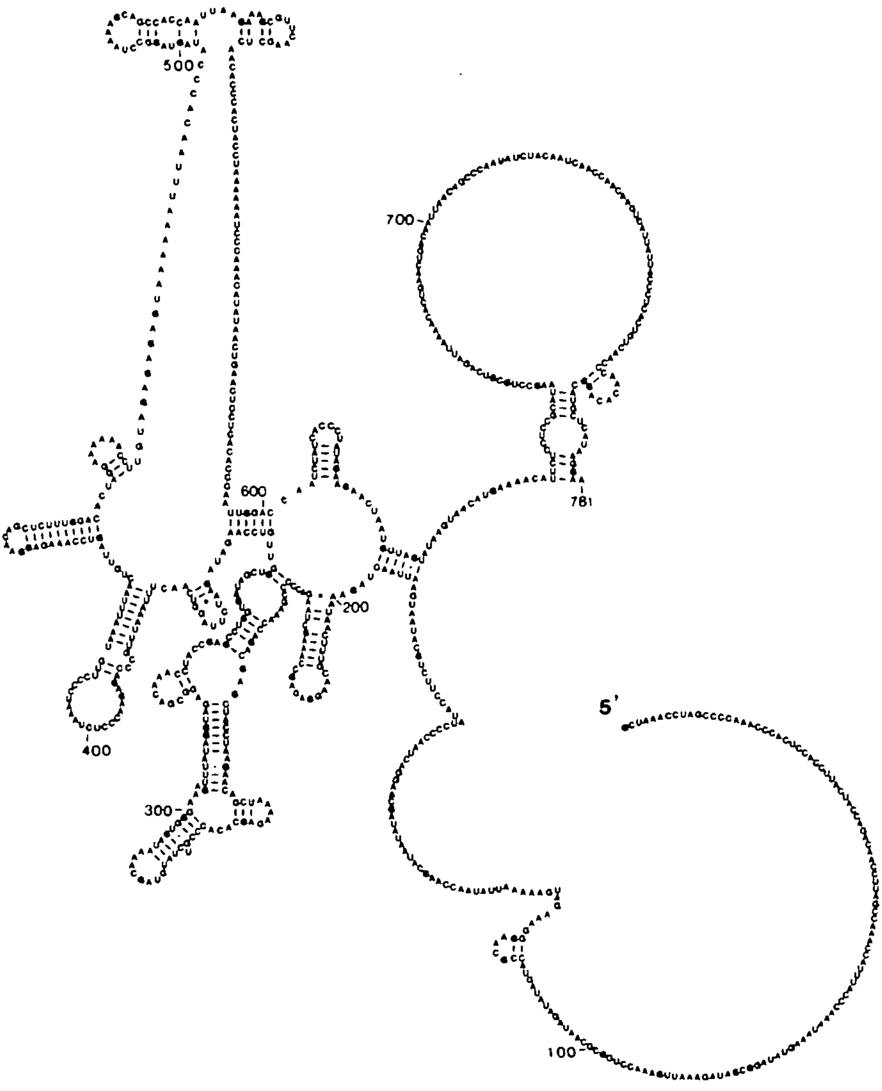


Fig.17a
Homo sapiens

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

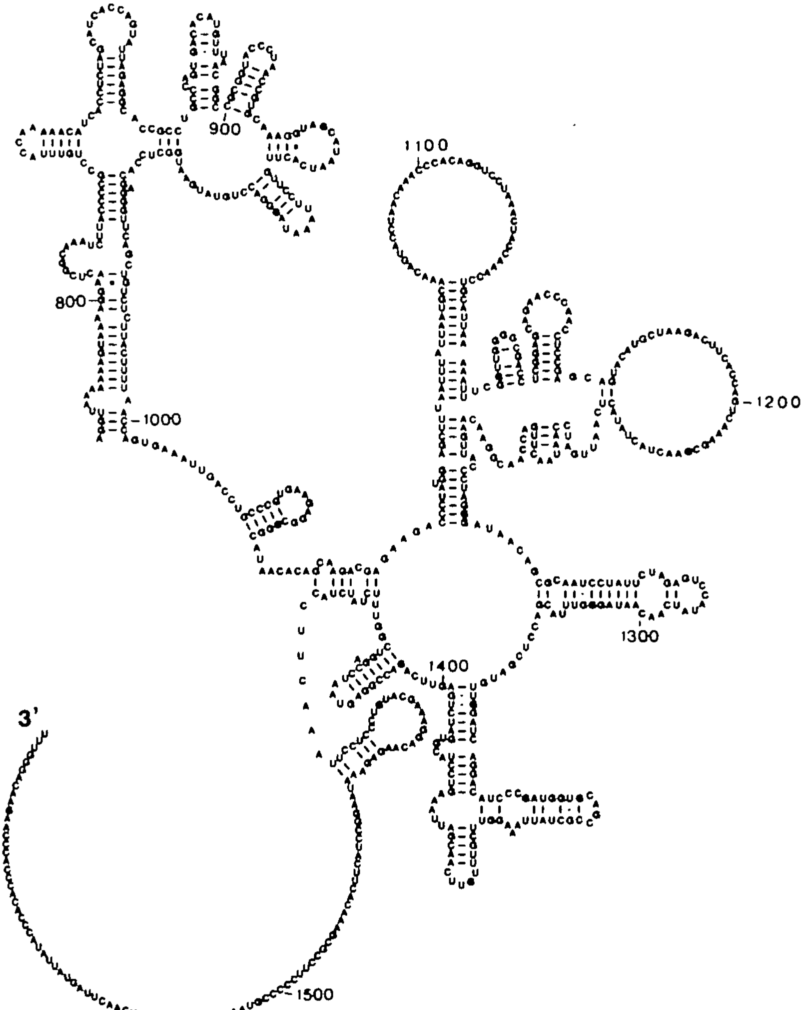


Fig.17b
Homo sapiens

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

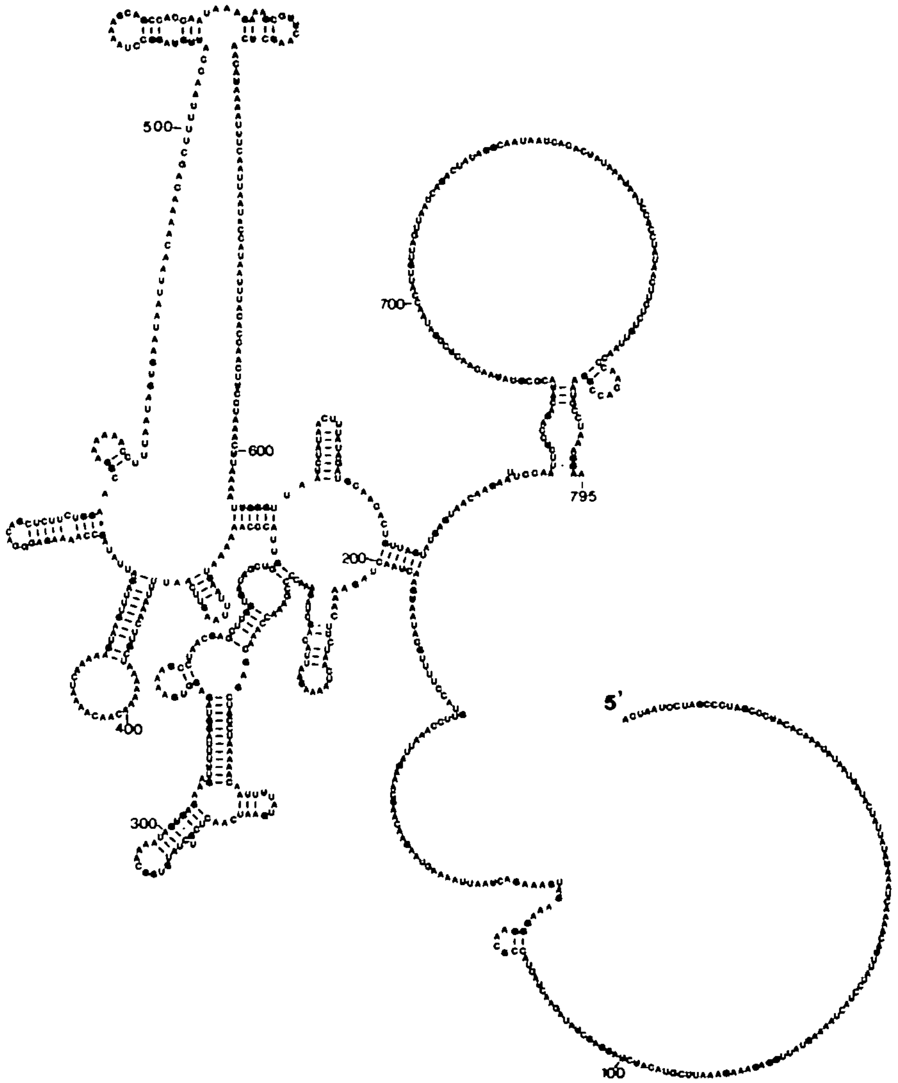


Fig.18a
Mouse

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

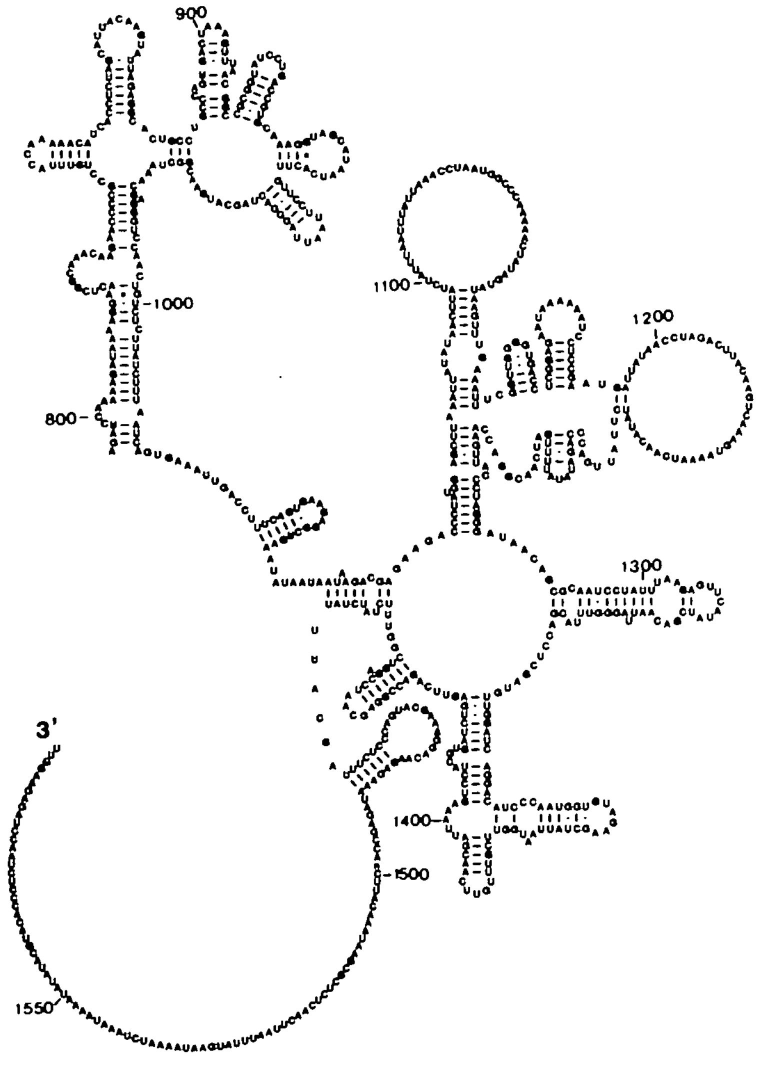


Fig.18b
Mouse

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

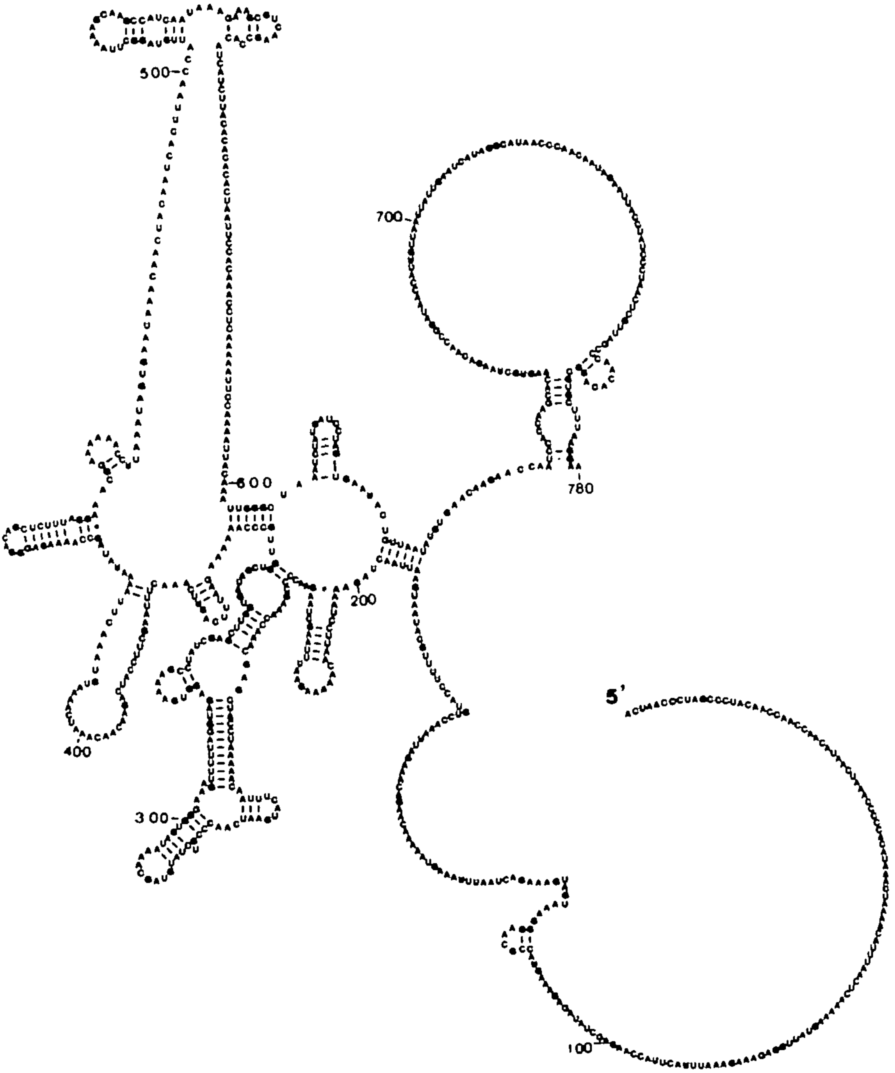


Fig.19a
Rat

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

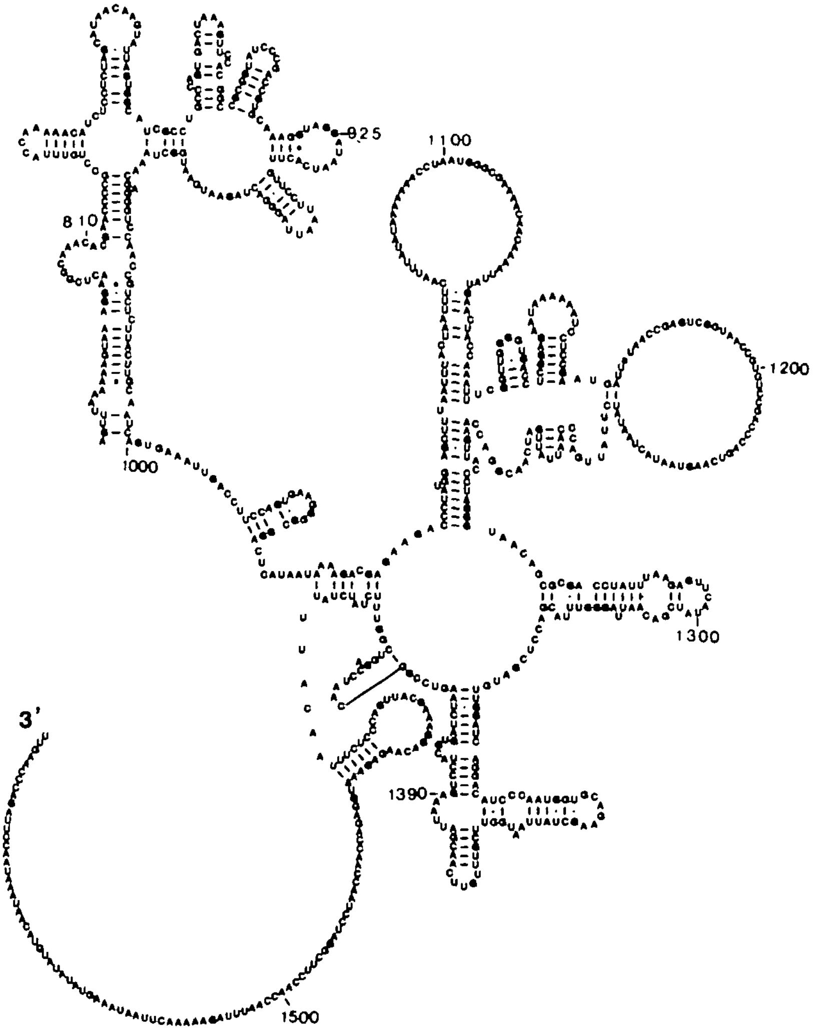


Fig.19b
Rat

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

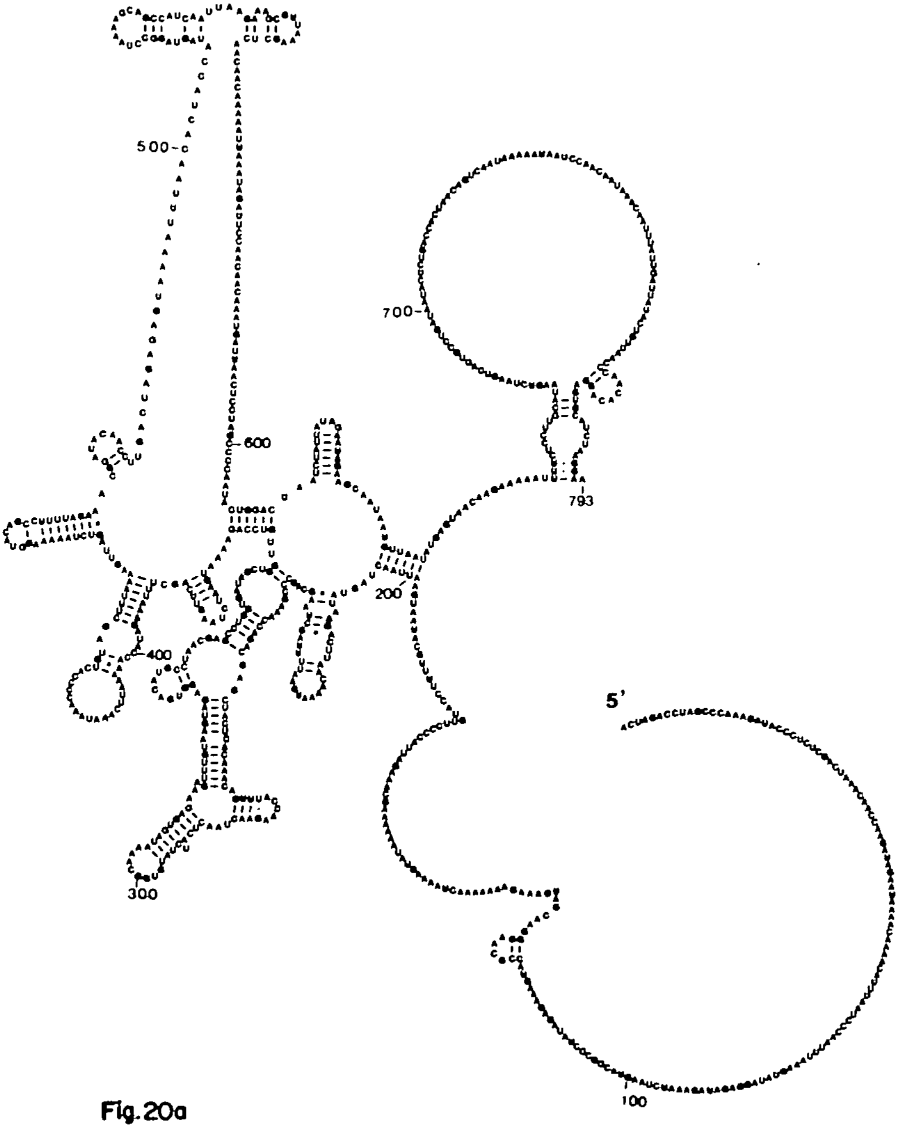


Fig.20a
Bovine

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

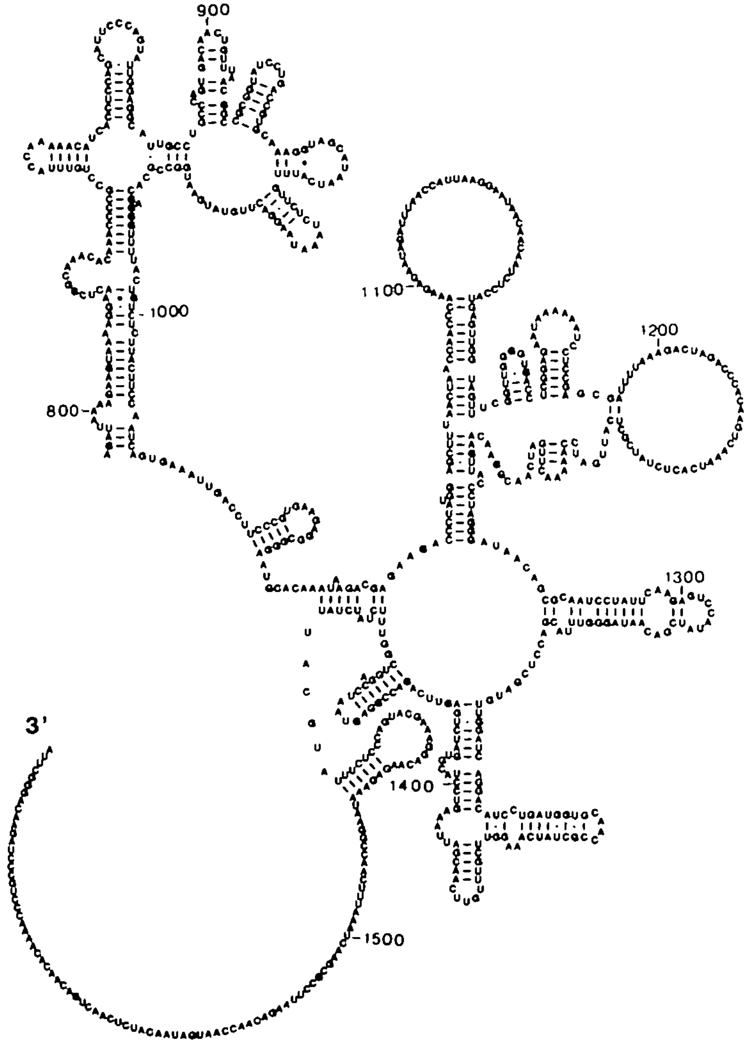


Fig. 20b
Bovine

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

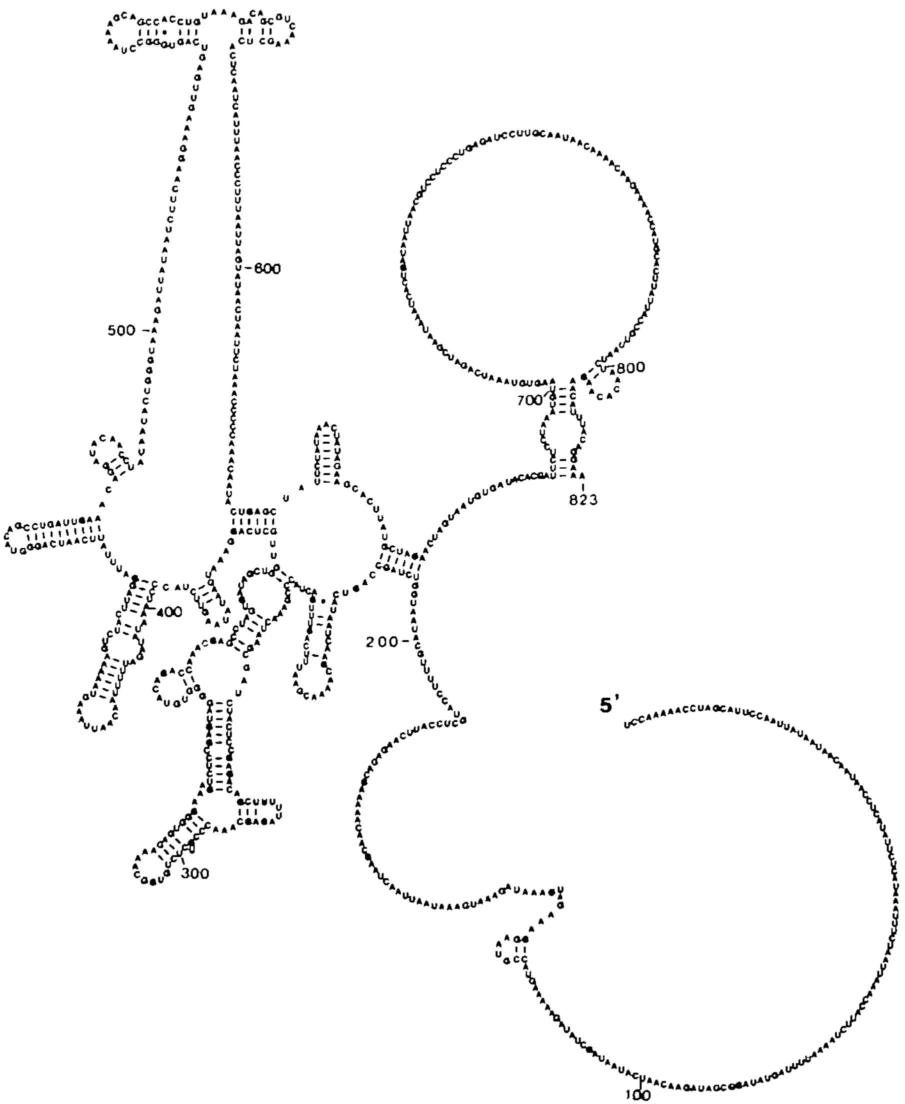


Fig.2Ia
Xenopus laevis

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

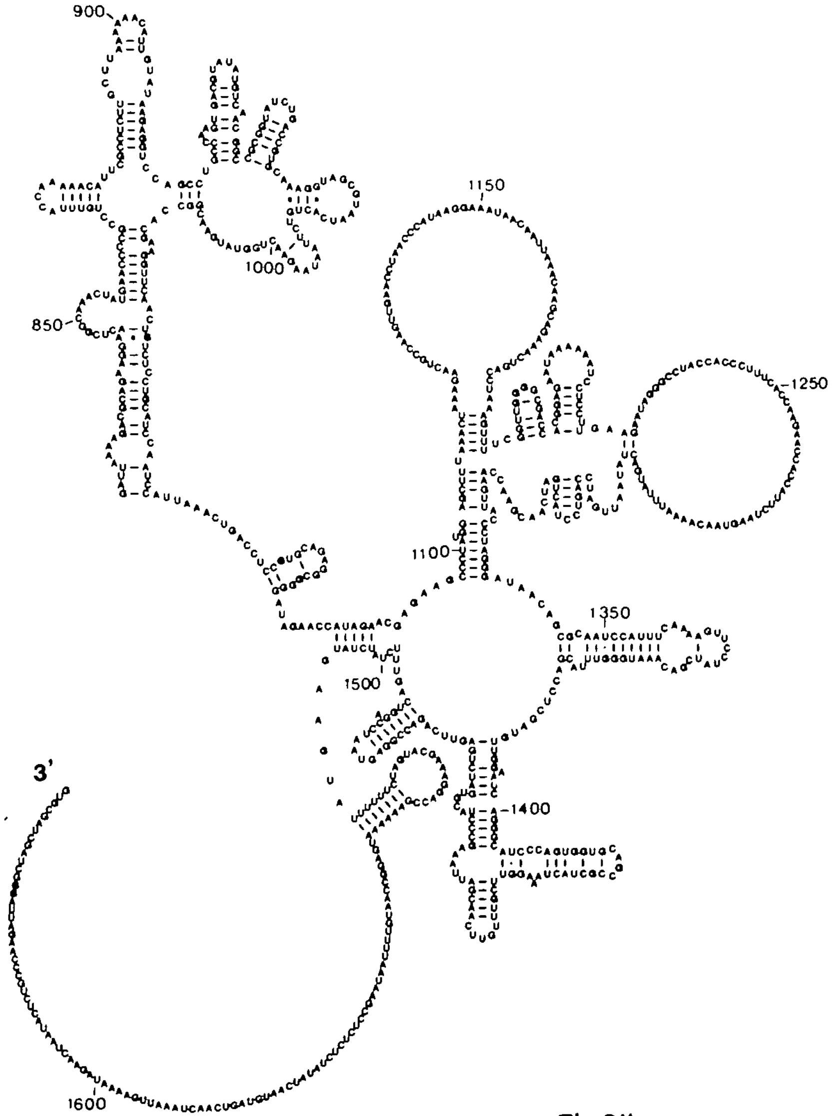


Fig.2Ib
Xenopus laevis

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

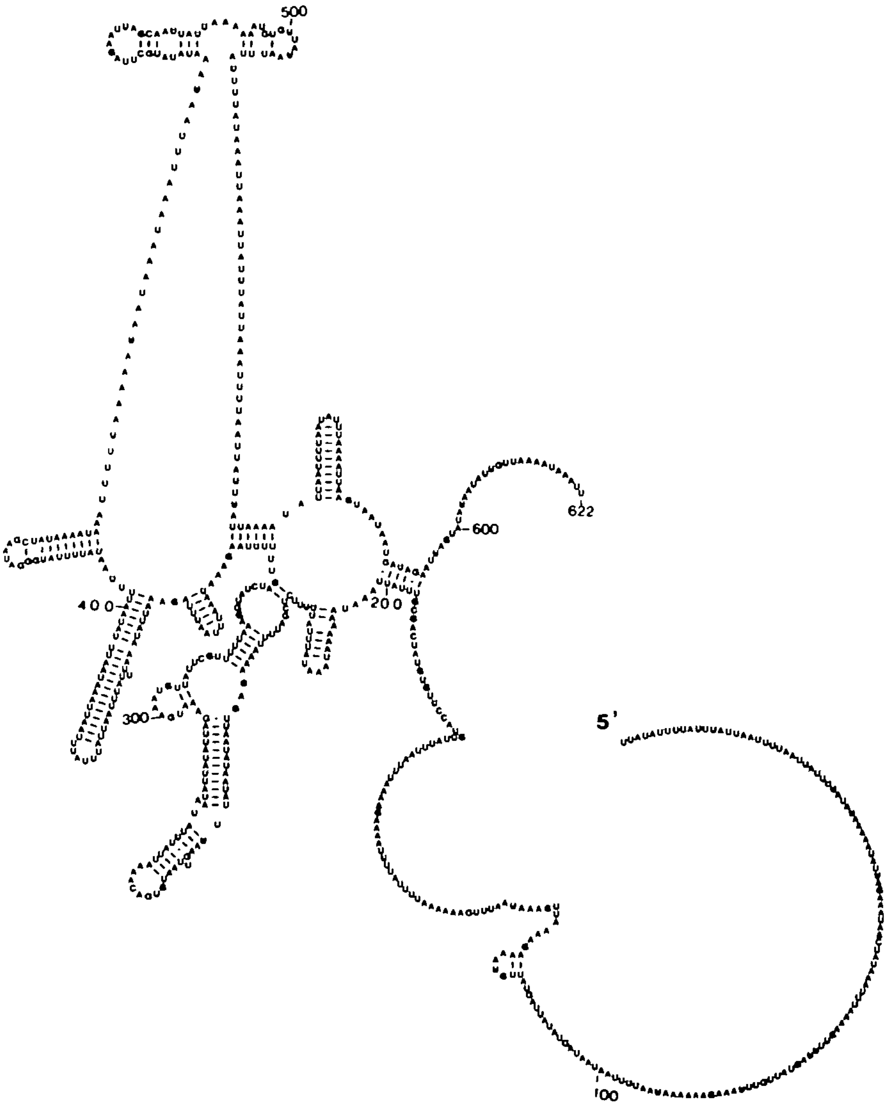


Fig.22a
Drosophila yakuba

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

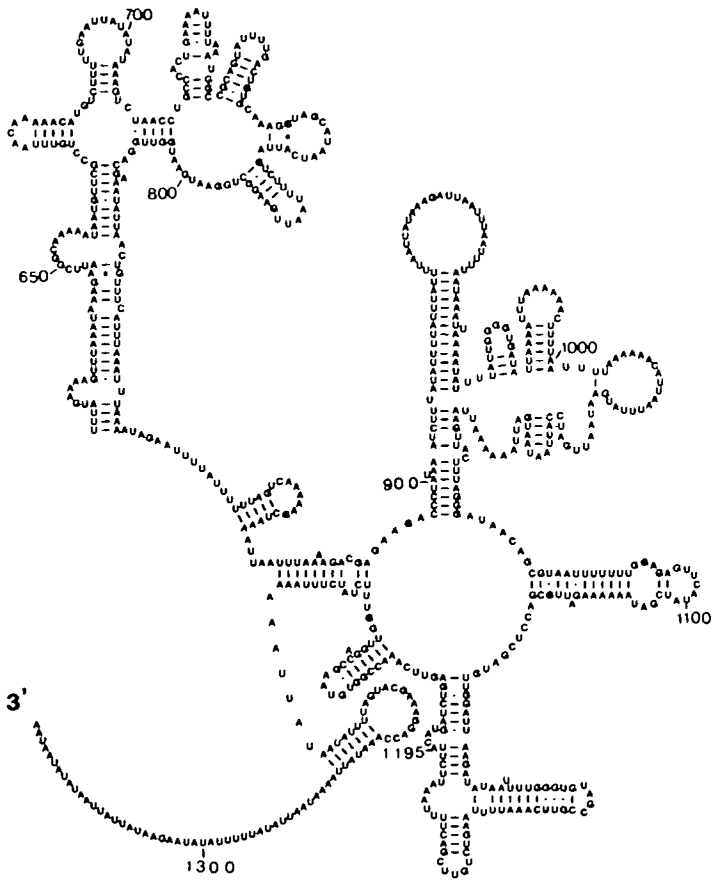


Fig.22b
Drosophila yakuba

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

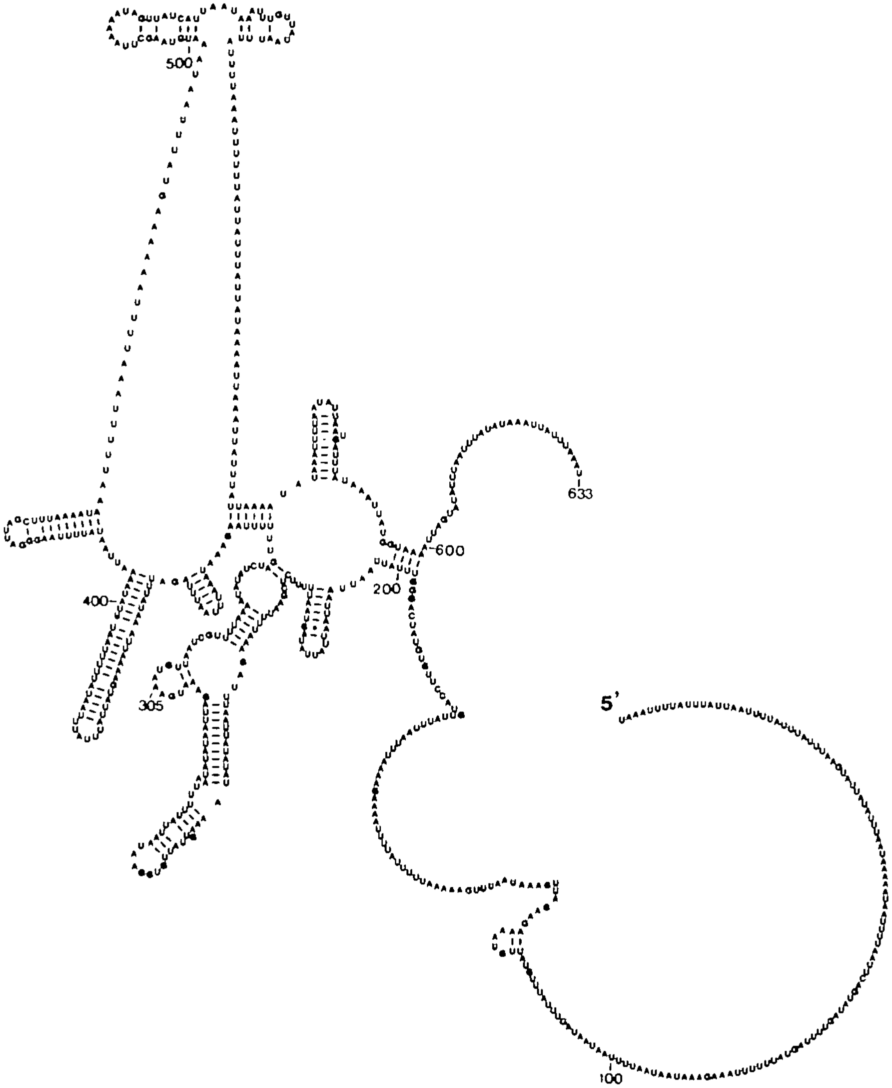


Fig.23a
Aedes albopictus: mosquito

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

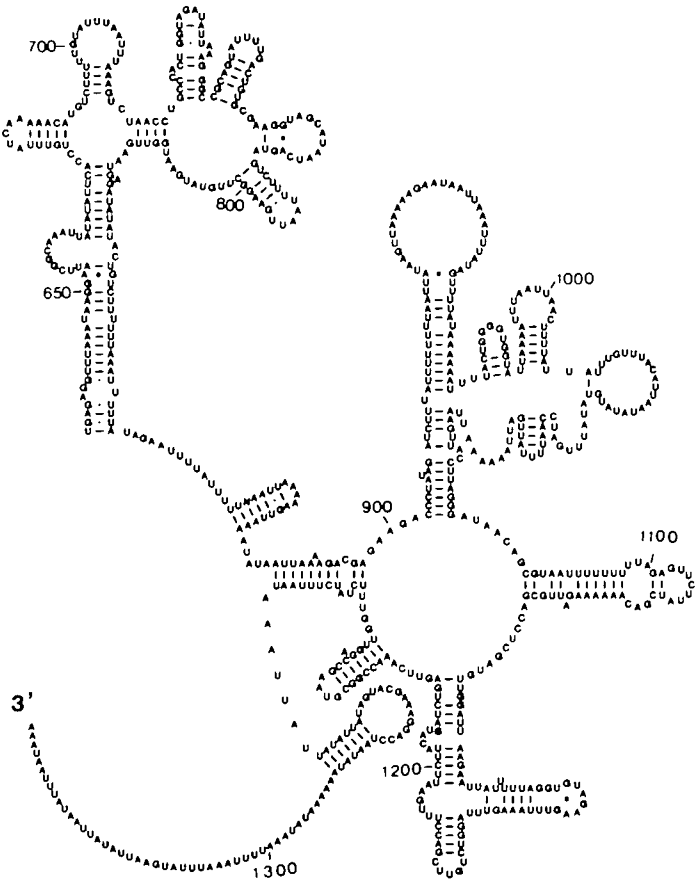


Fig.23b

Aedes albopictus: mosquito

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

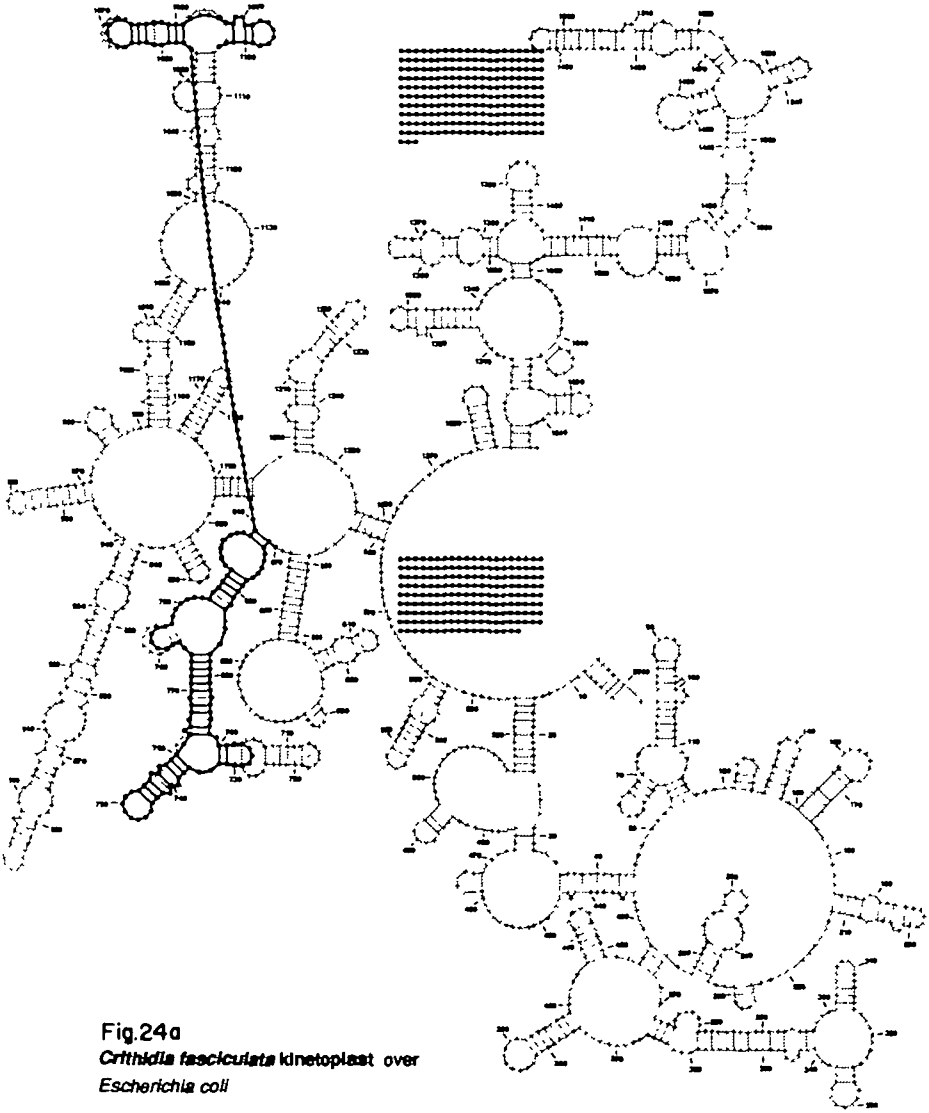


Fig.24a
Crithidia fasciculata **kinetoplast** over
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

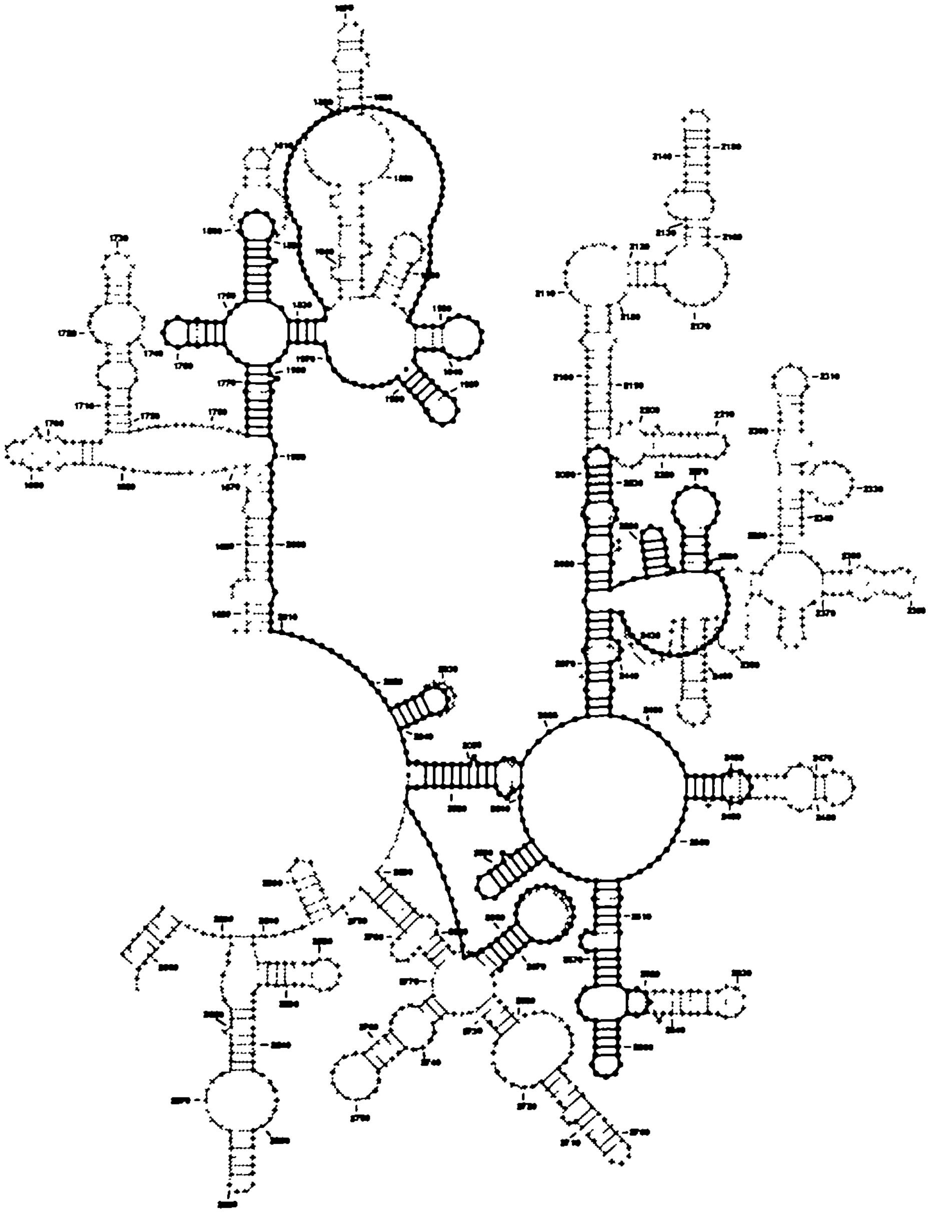


Fig. 24b

Crithidia fasciculata **kinetoplast over**
Escherichia coli

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

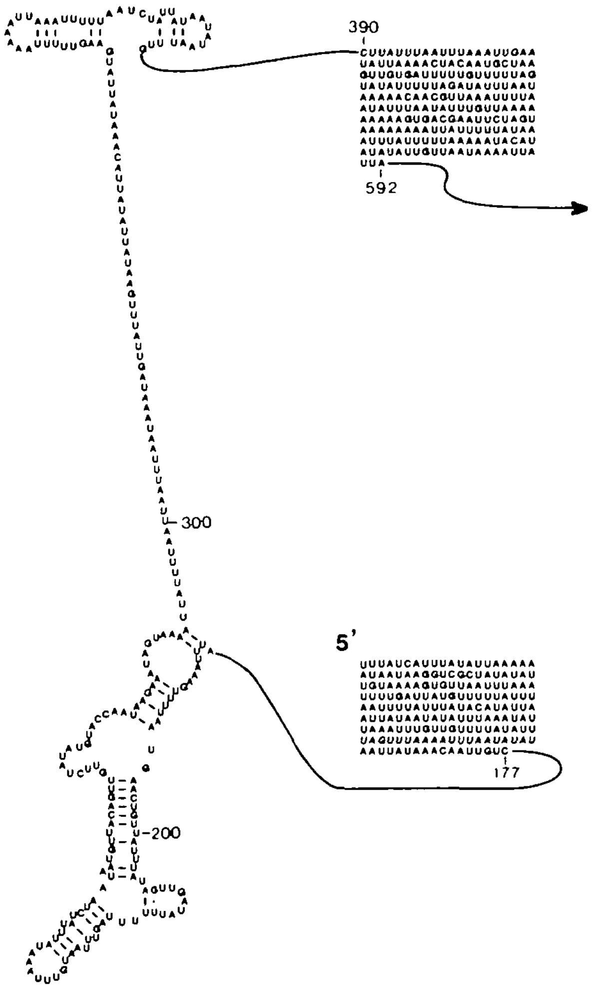


Fig.25a
Crithidia fasciculata

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

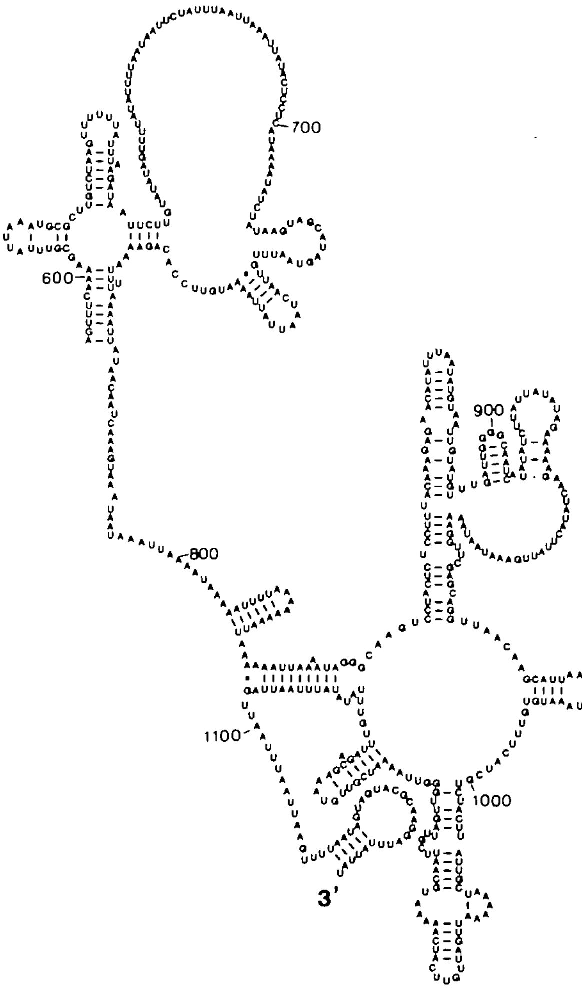


Fig.25b
Crithidia fasciculata

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

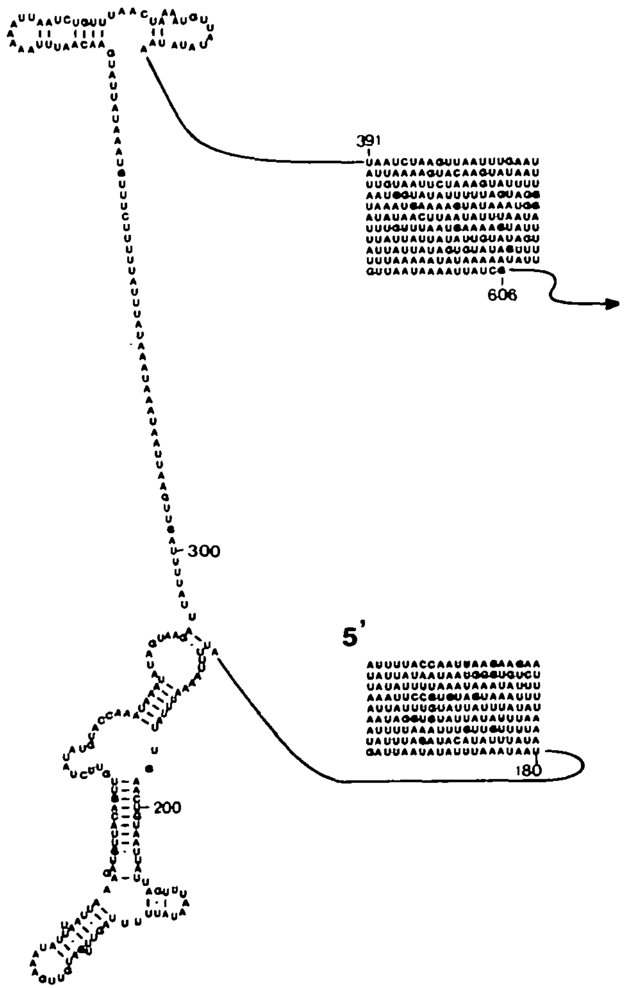


Fig.26a
Trypanosome brucei

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

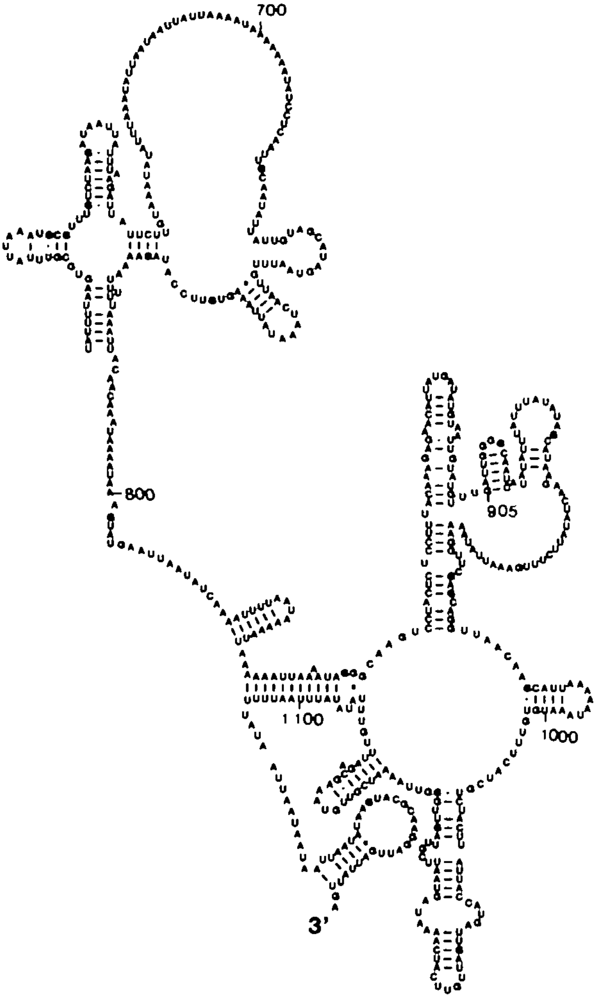


Fig.26b
Trypanosome brucei

Secondary Structure of mitochondrial 23S Ribosomal RNA: 5'half

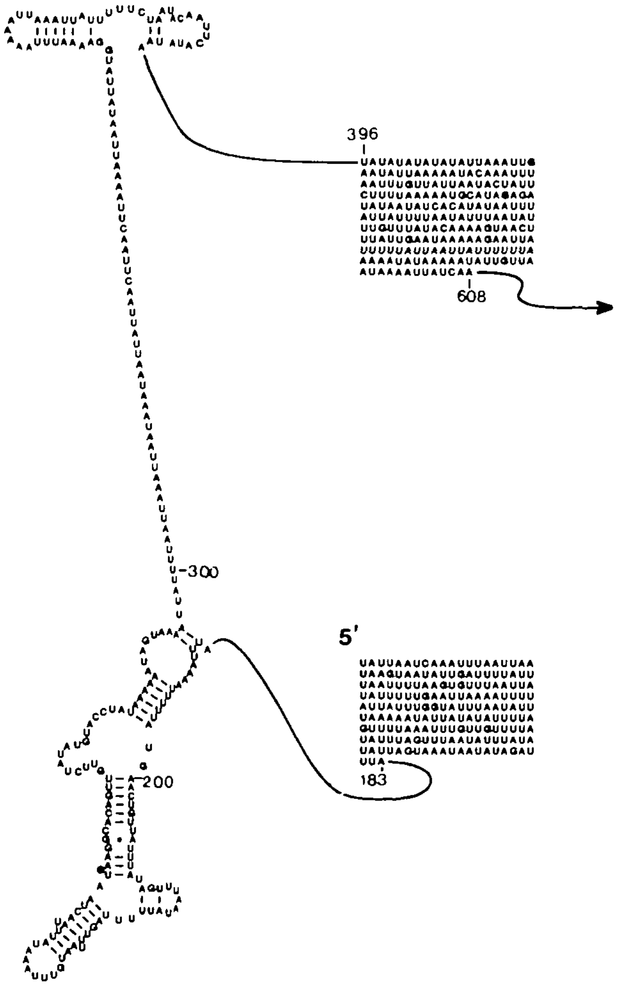


Fig.27a
Leishmania tarentolae

Secondary Structure of mitochondrial 23S Ribosomal RNA: 3'half

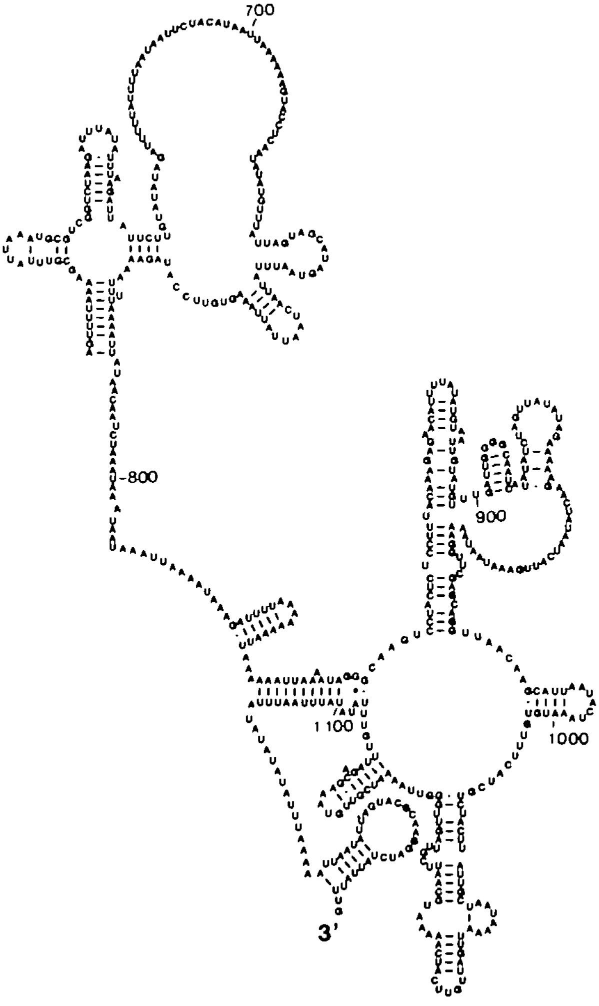


Fig.27b
Leishmania tarentolae

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

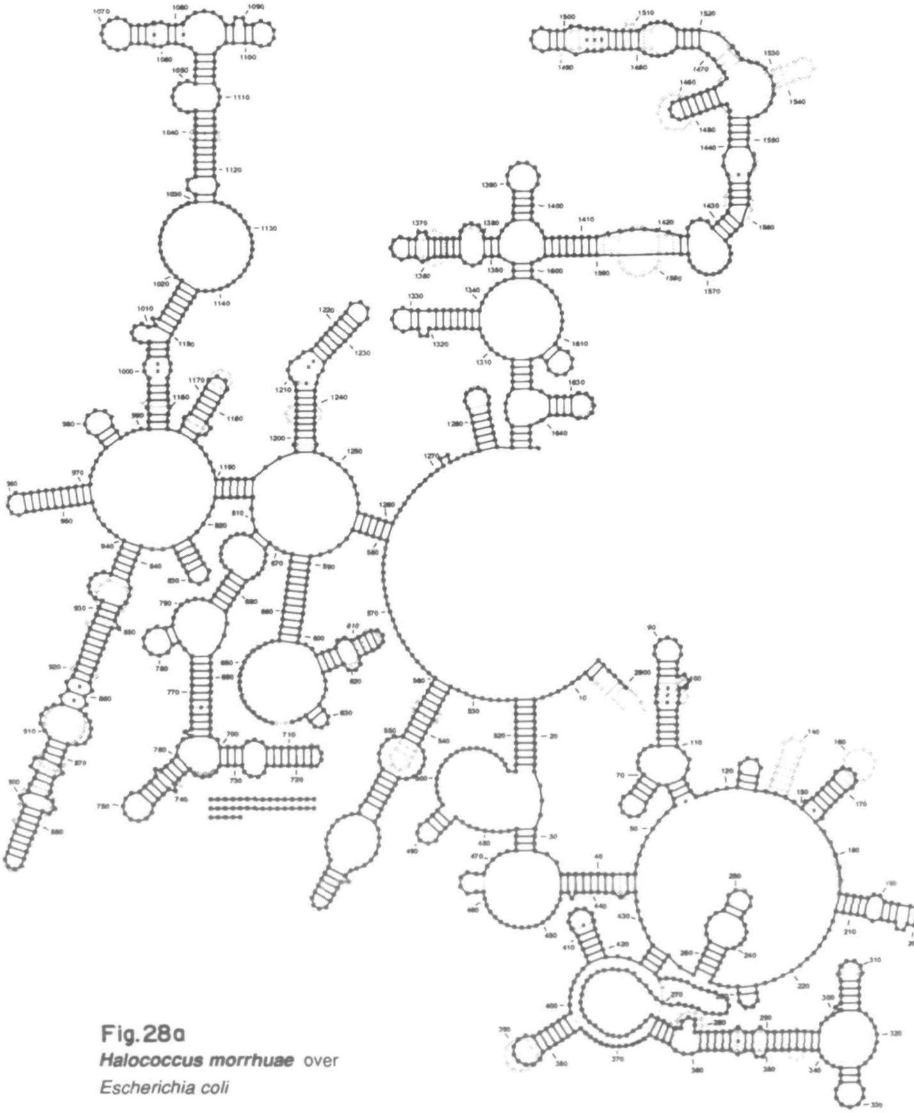


Fig.28a
Halococcus morrhuae over
Escherichia coli

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

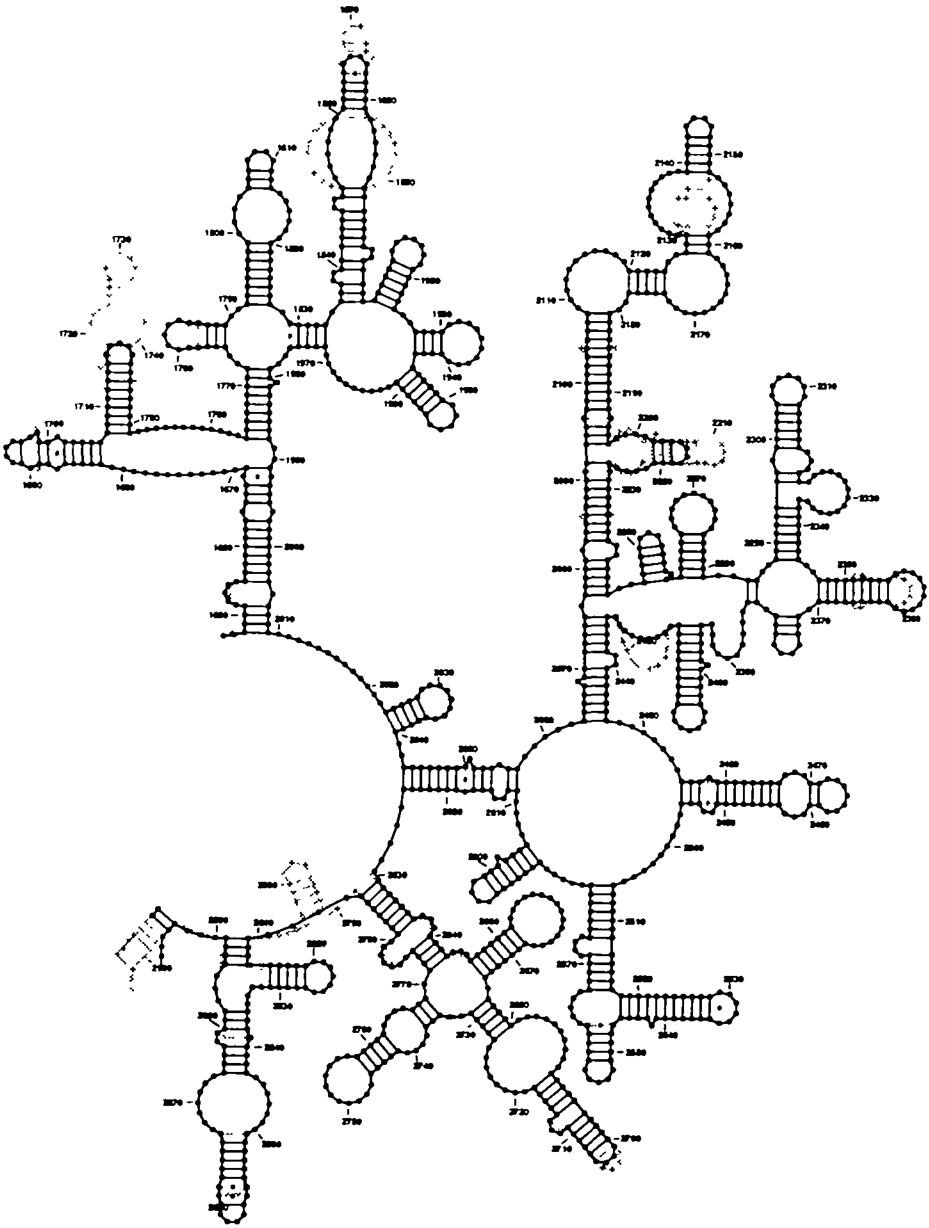


Fig. 28b

Halococcus morrhuae over

Escherichia coli

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

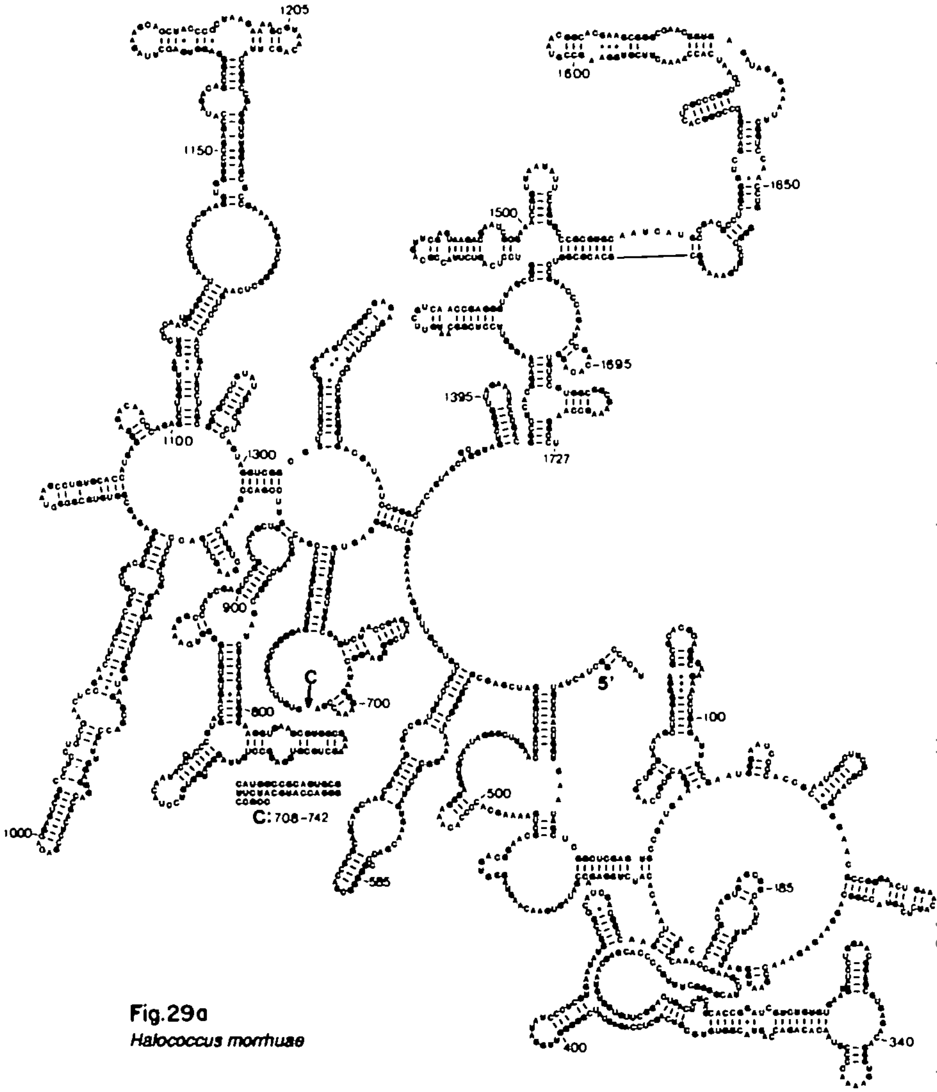


Fig.29a
Halococcus morrhuae

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

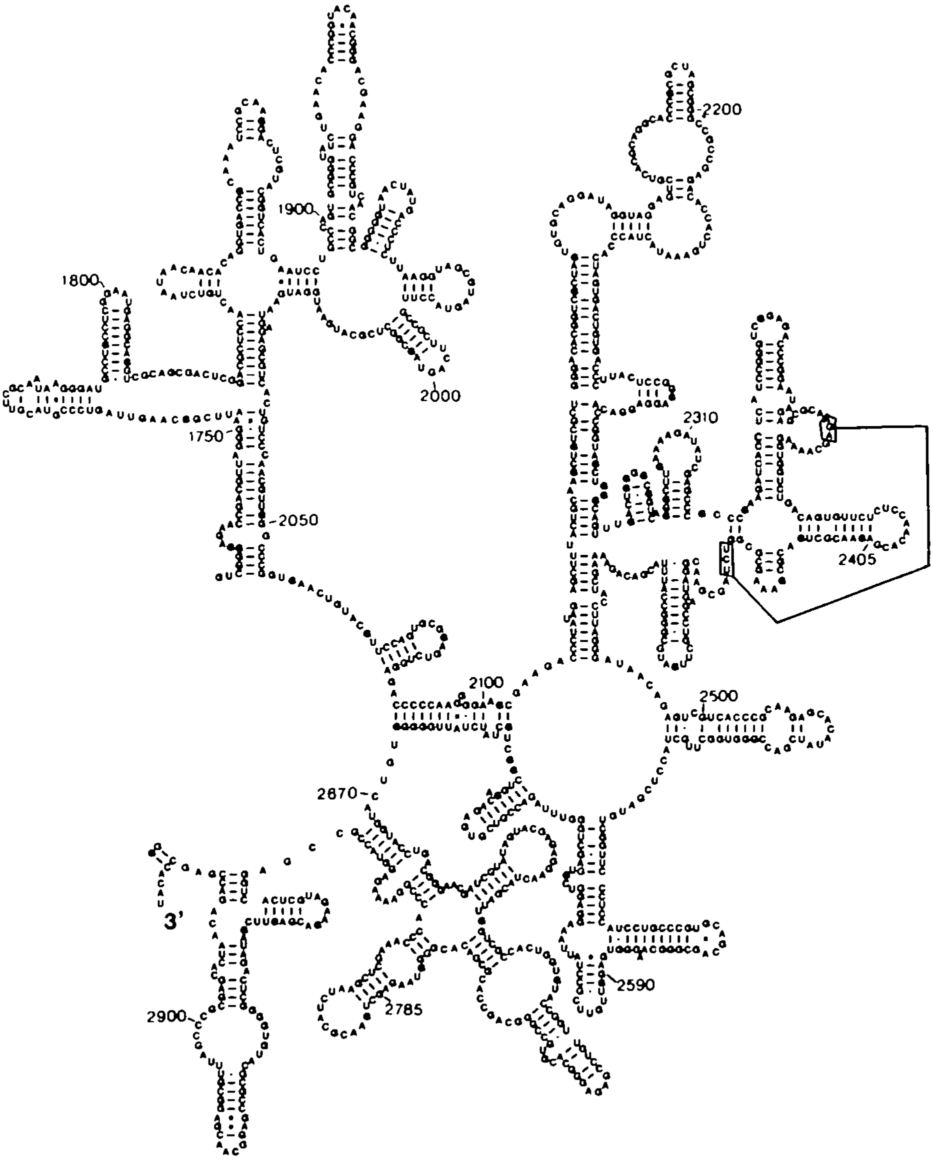


Fig.29b

Halococcus morrhuae

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

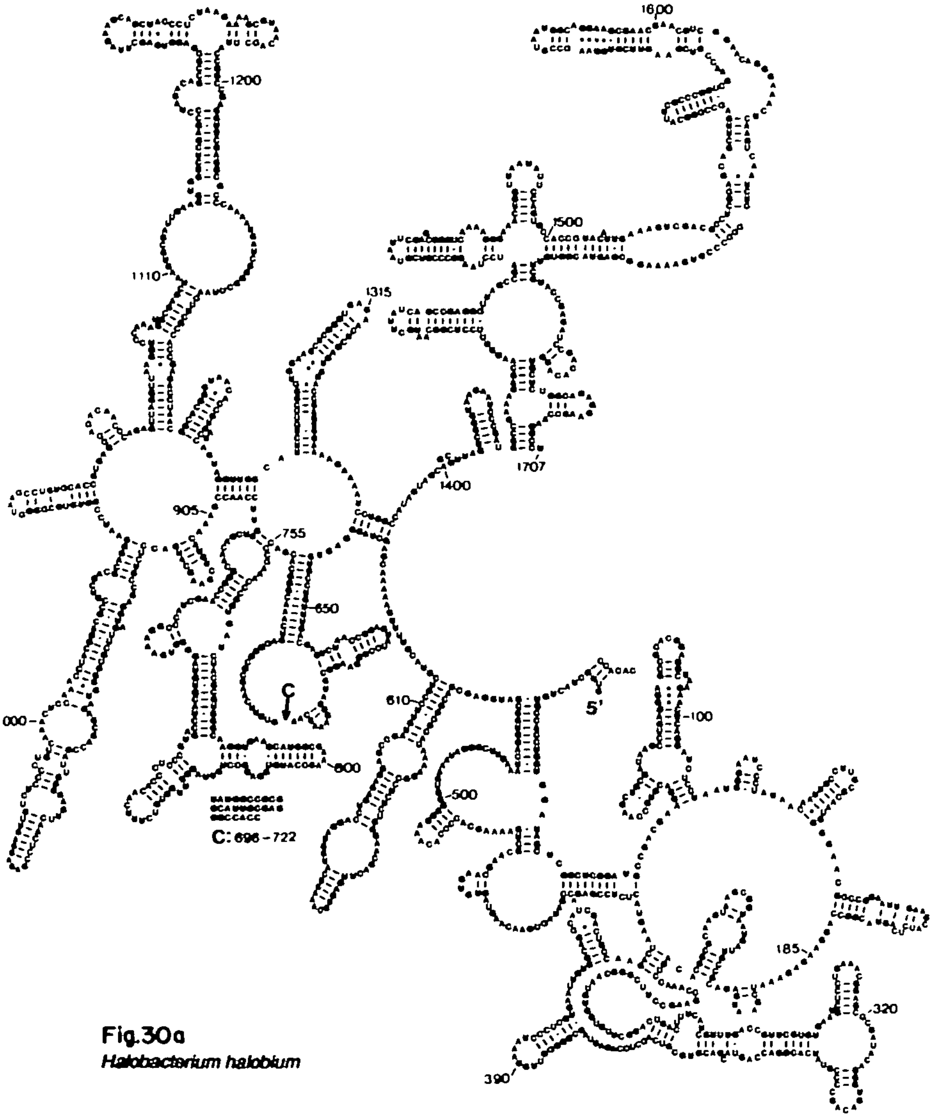


Fig.30a
Halobacterium halobium

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

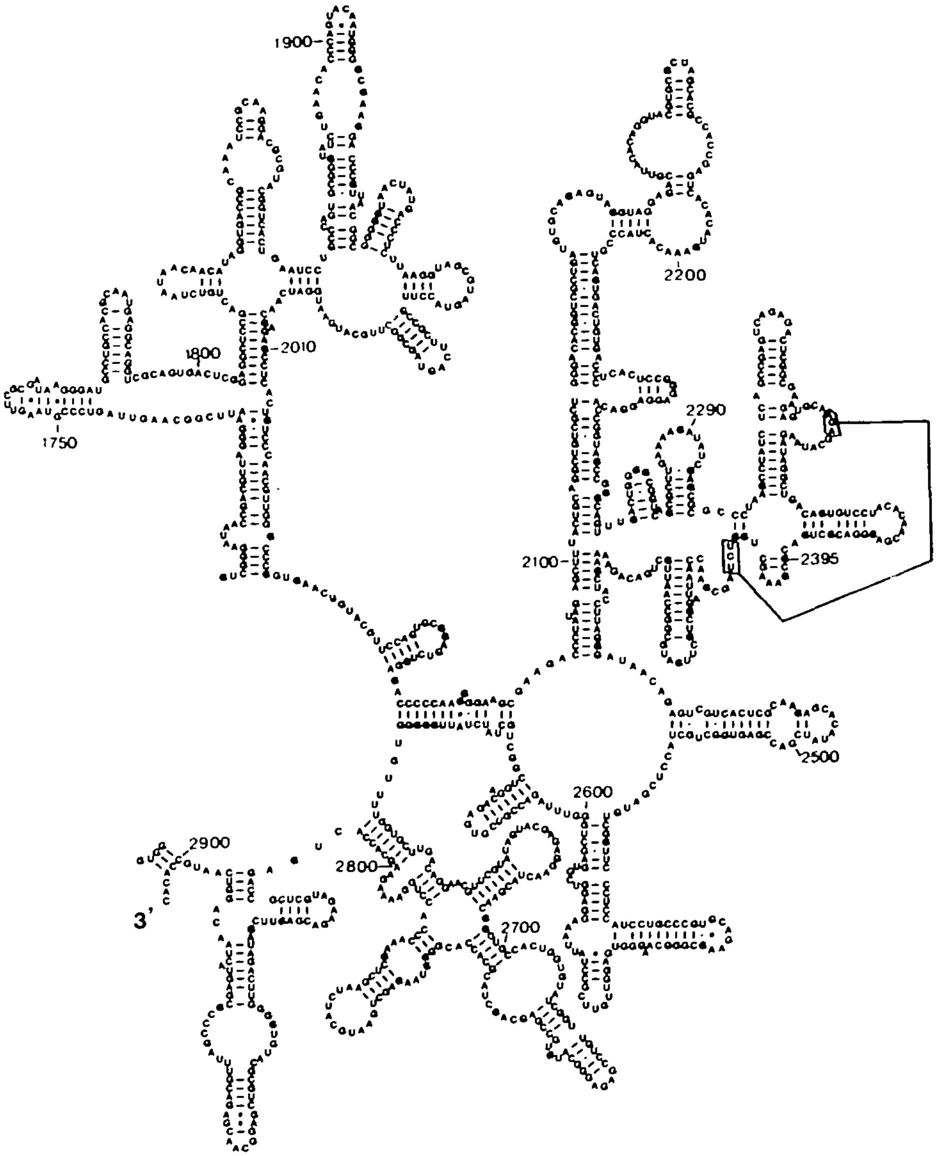


Fig.30b
Halobacterium halobium

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

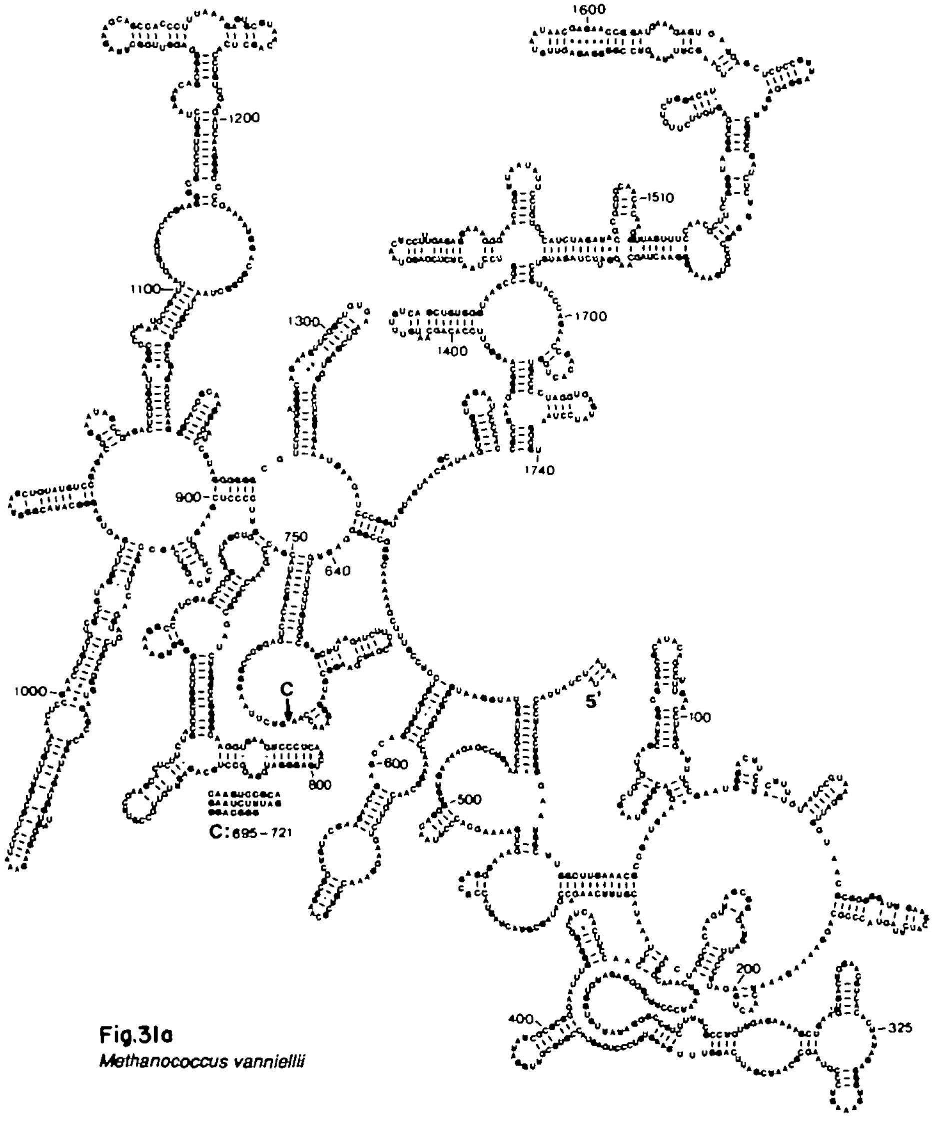


Fig.3Ia
Methanococcus vannielii

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

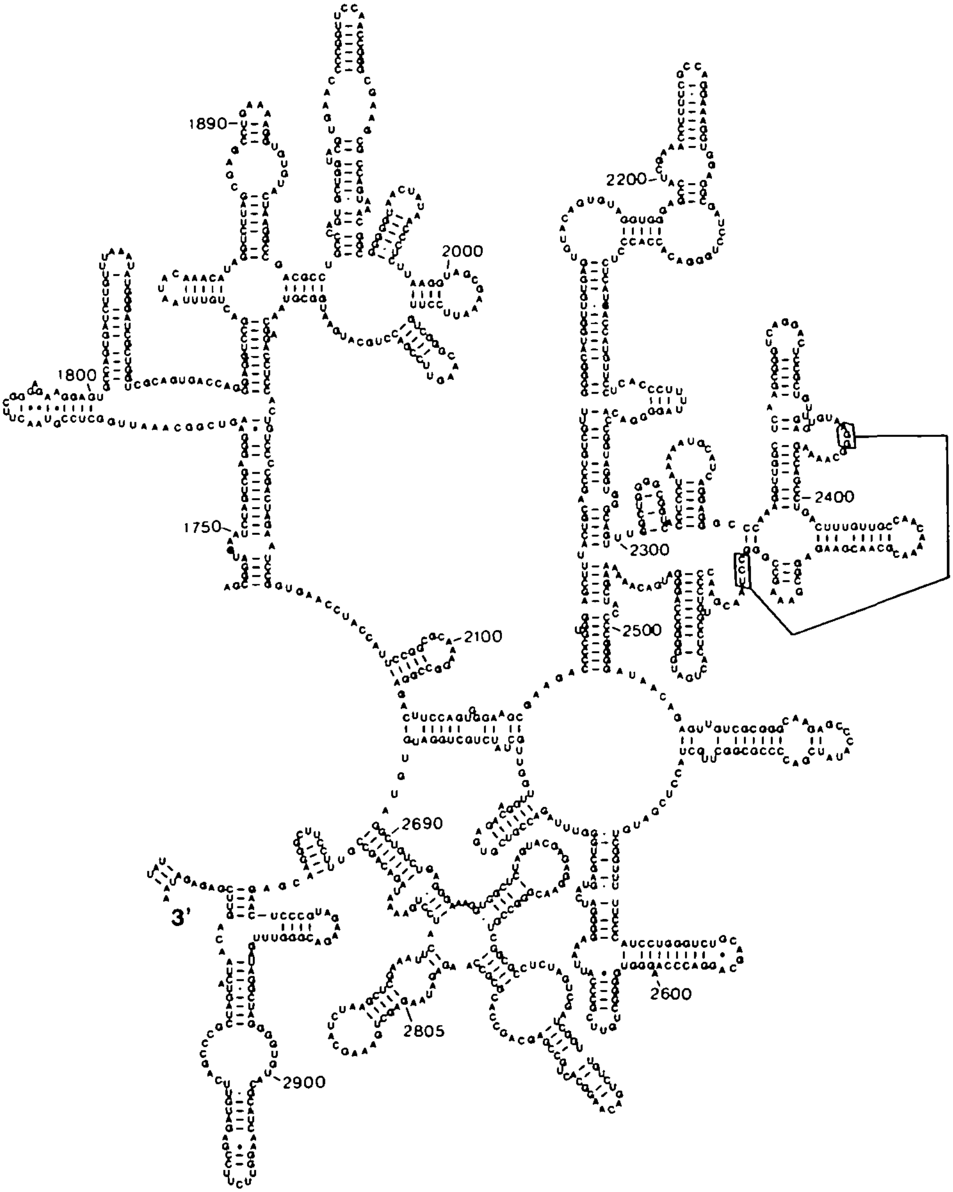


Fig.3Ib
Methanococcus vannielii

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

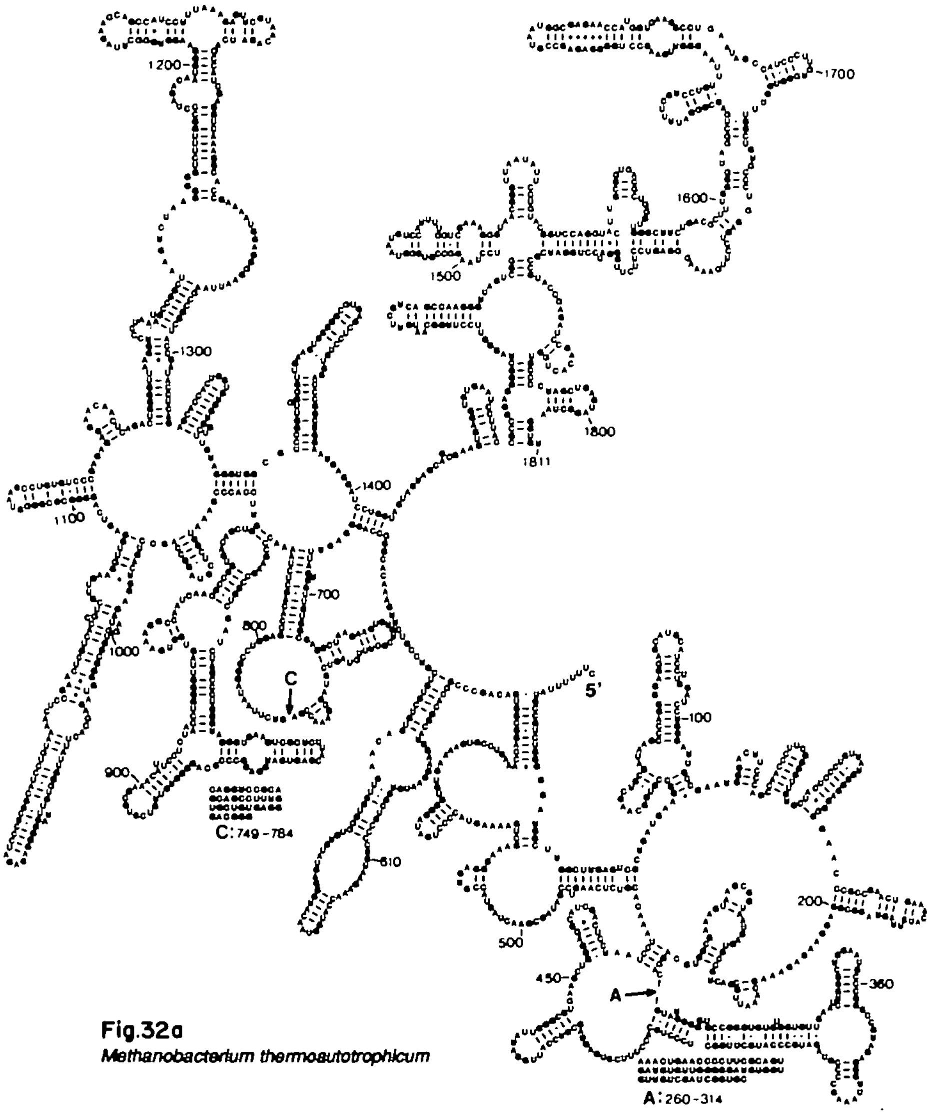


Fig.32a
Methanobacterium thermoautotrophicum

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

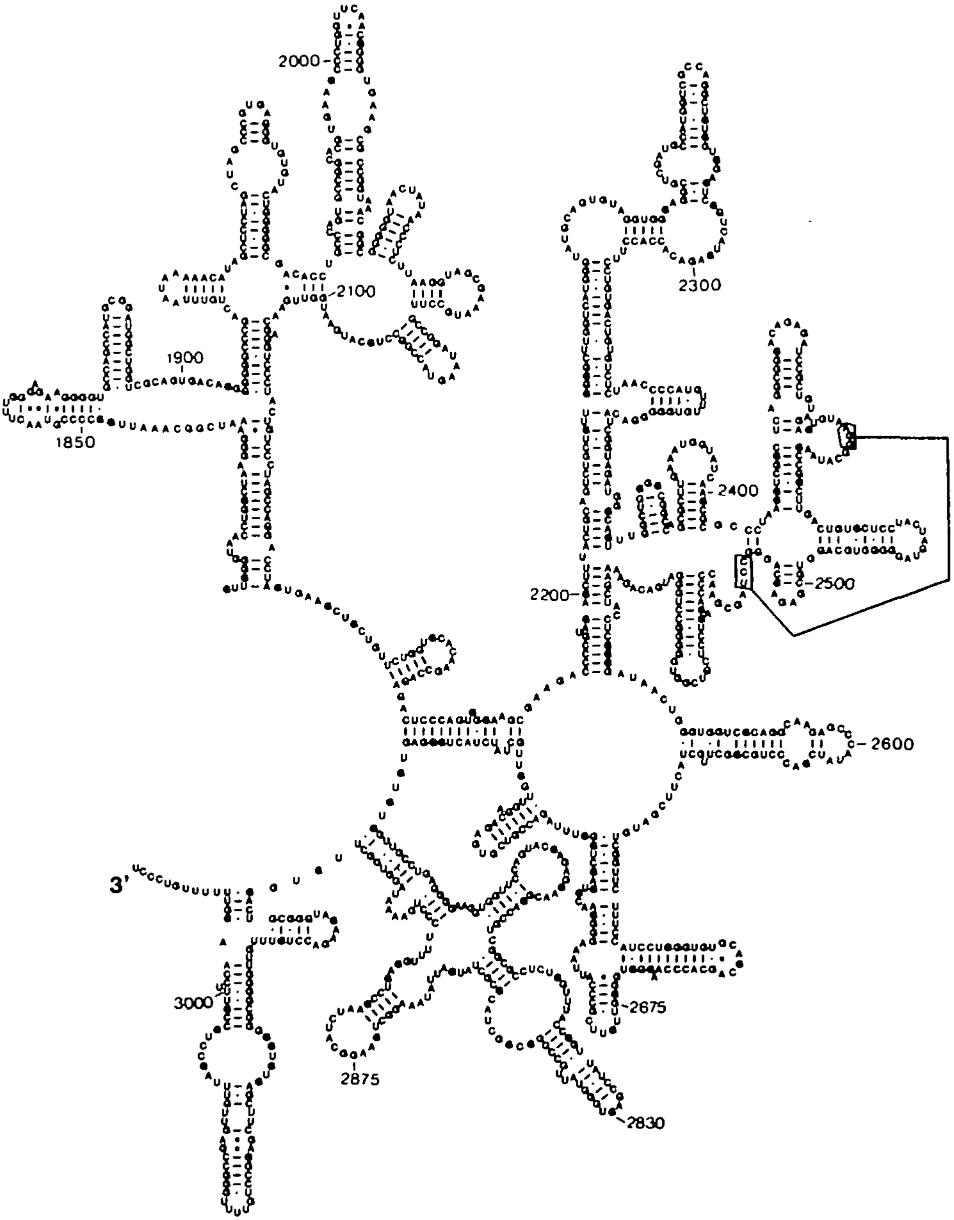


Fig.32b

Methanobacterium thermoautotrophicum

Secondary Structure of archaebacterial 23S Ribosomal RNA: 5'half

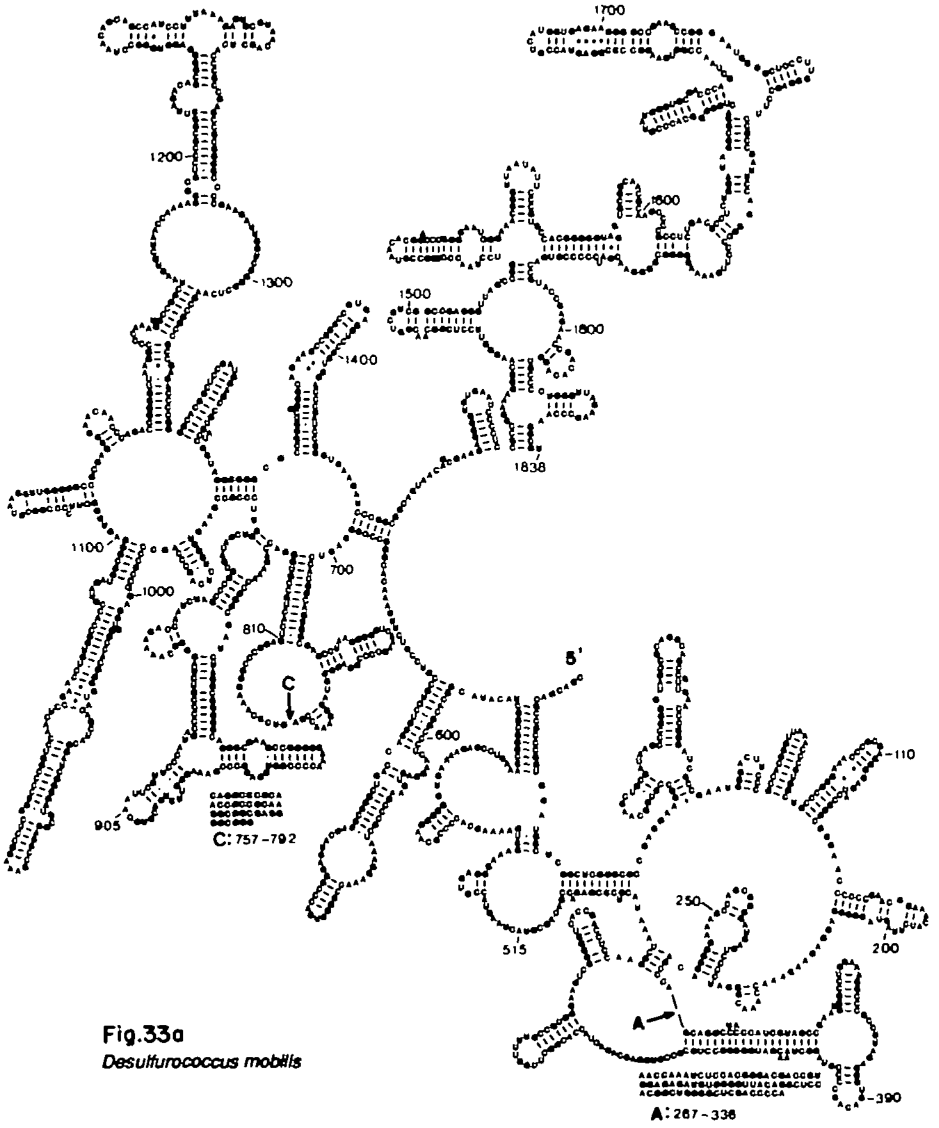


Fig.33a
Desulfurococcus mobilis

Secondary Structure of archaebacterial 23S Ribosomal RNA: 3'half

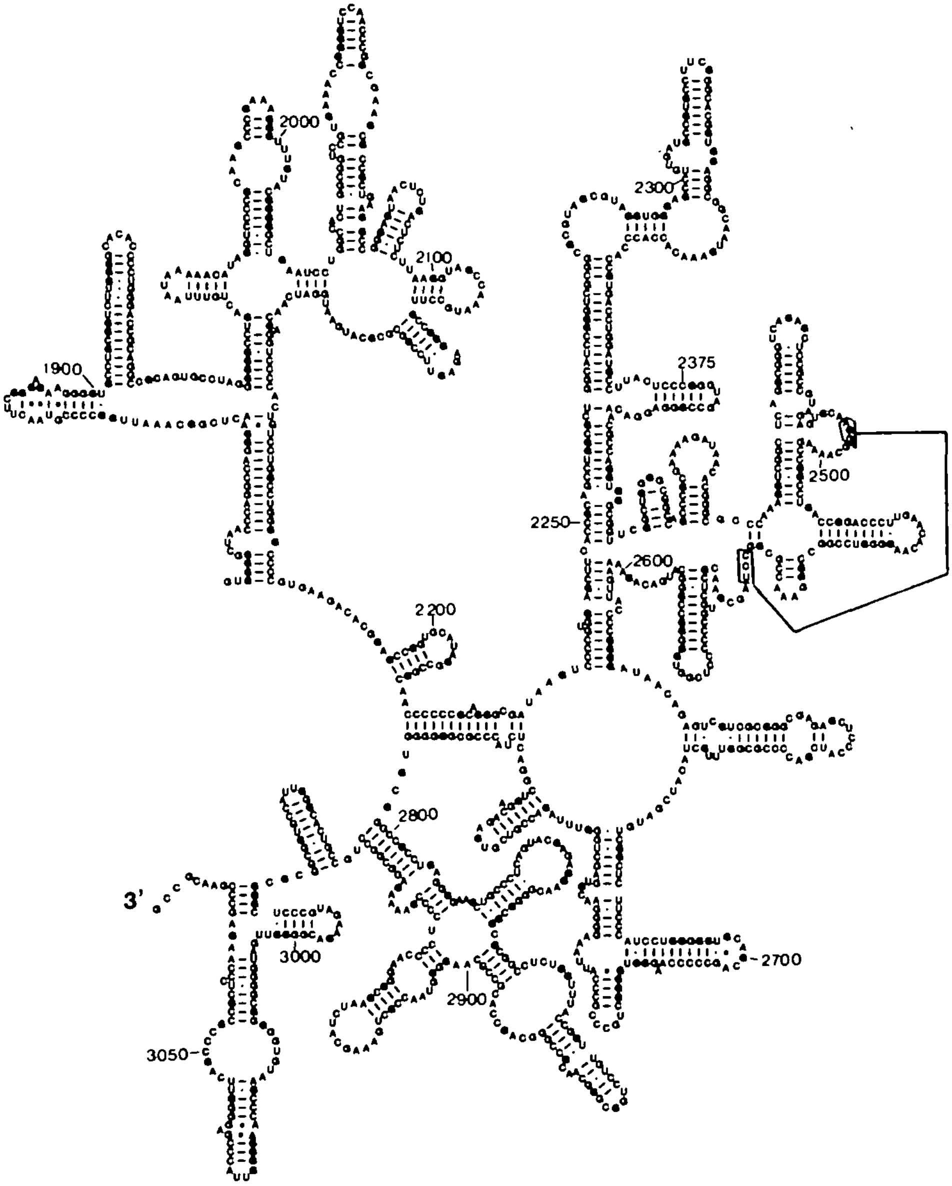


Fig.33b
Desulfurococcus mobilis

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

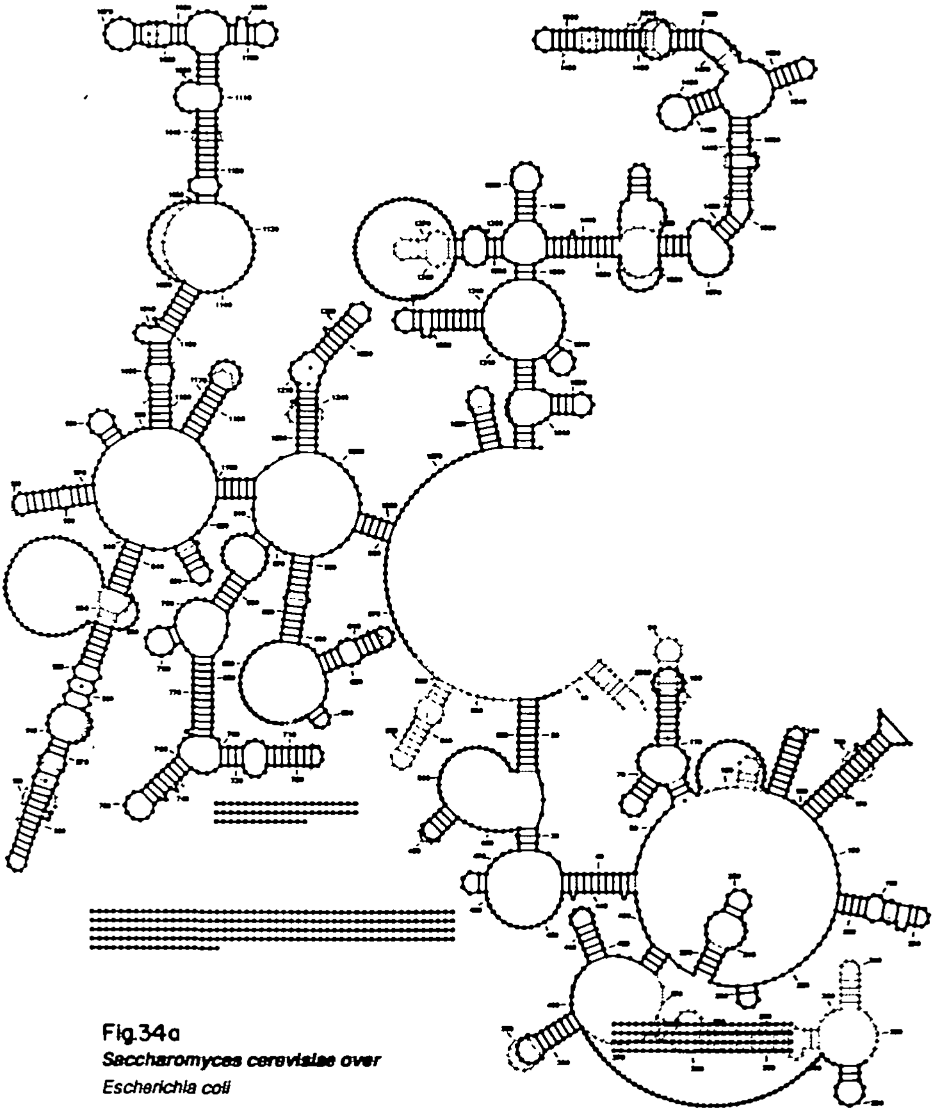


Fig.34a

***Saccharomyces cerevisiae* over**

Escherichia coli

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

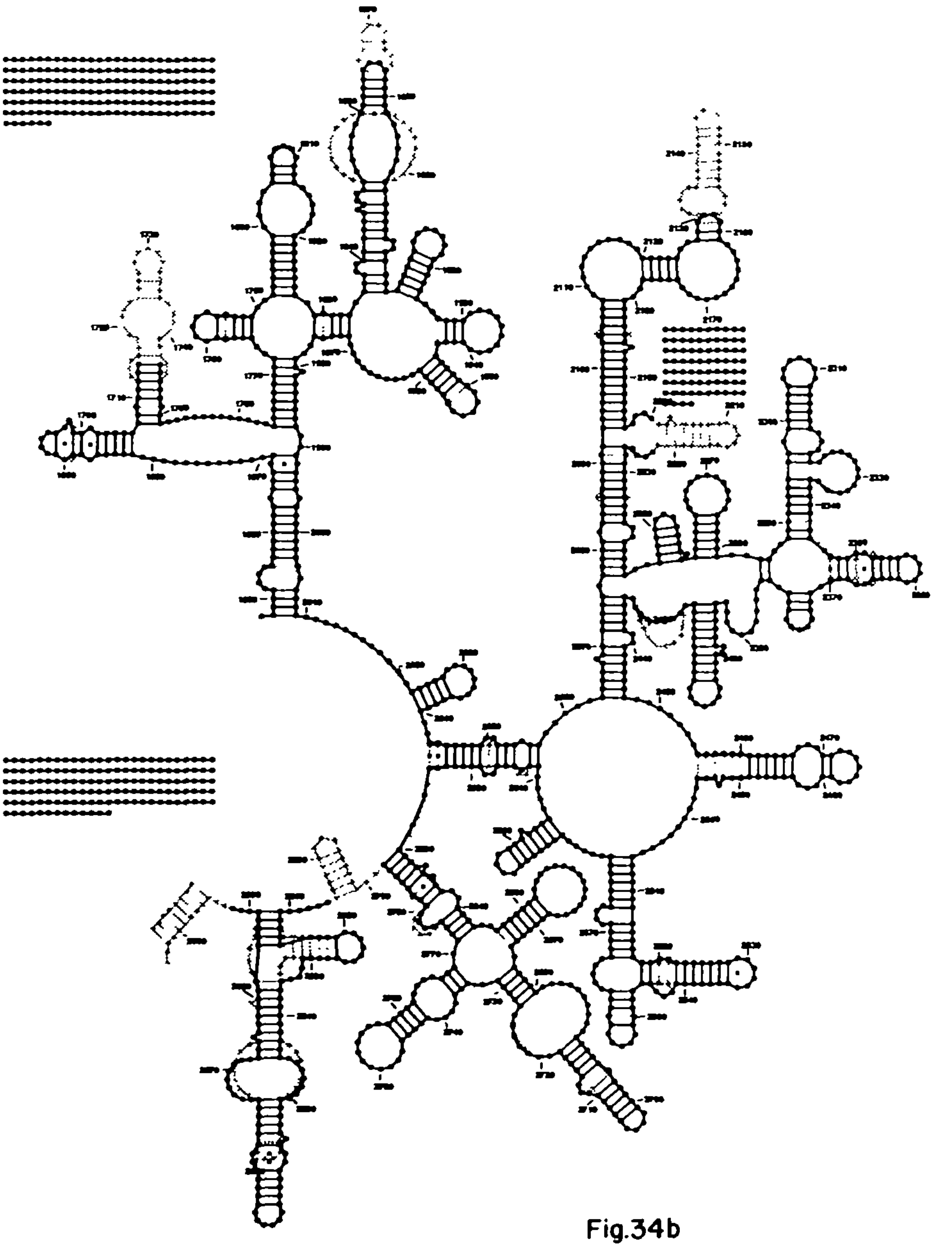


Fig.34b

Saccharomyces cerevisiae over

Escherichia coli

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

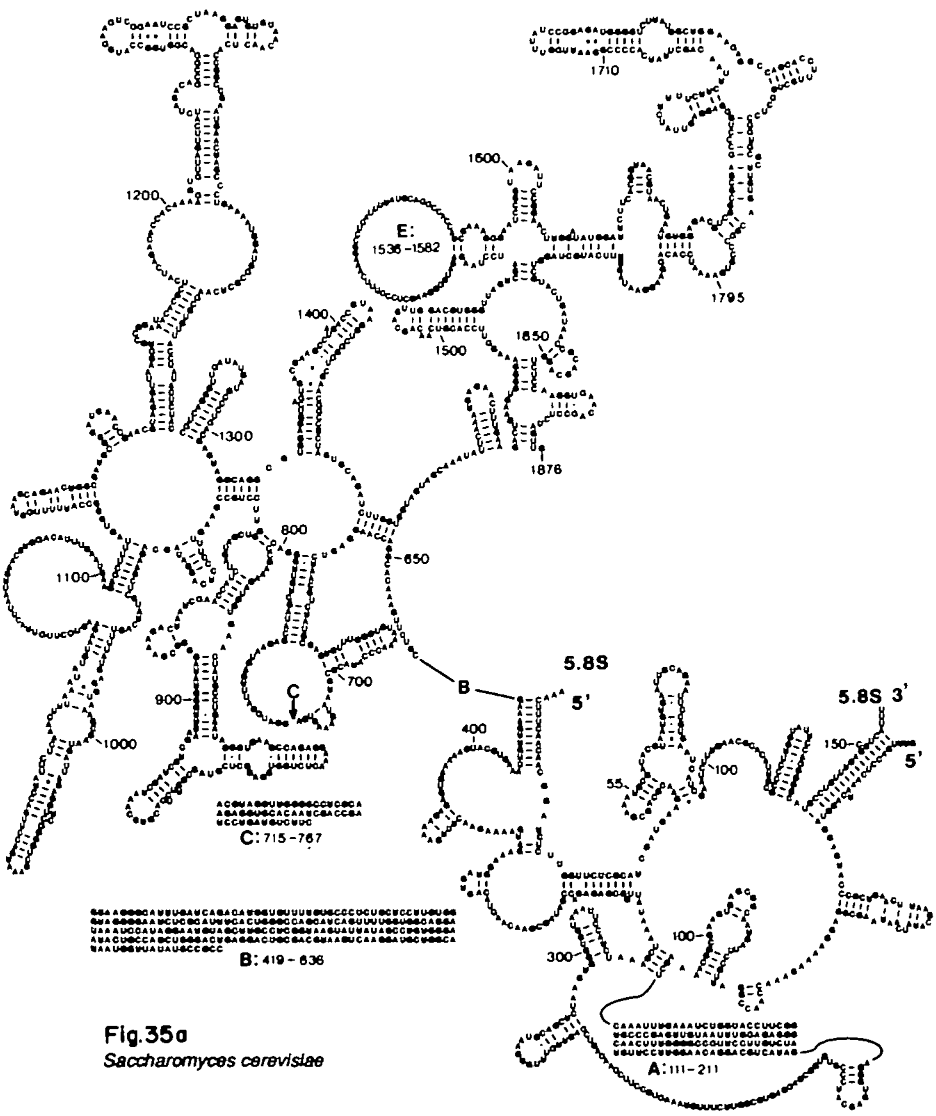


Fig.35a
Saccharomyces cerevisiae

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

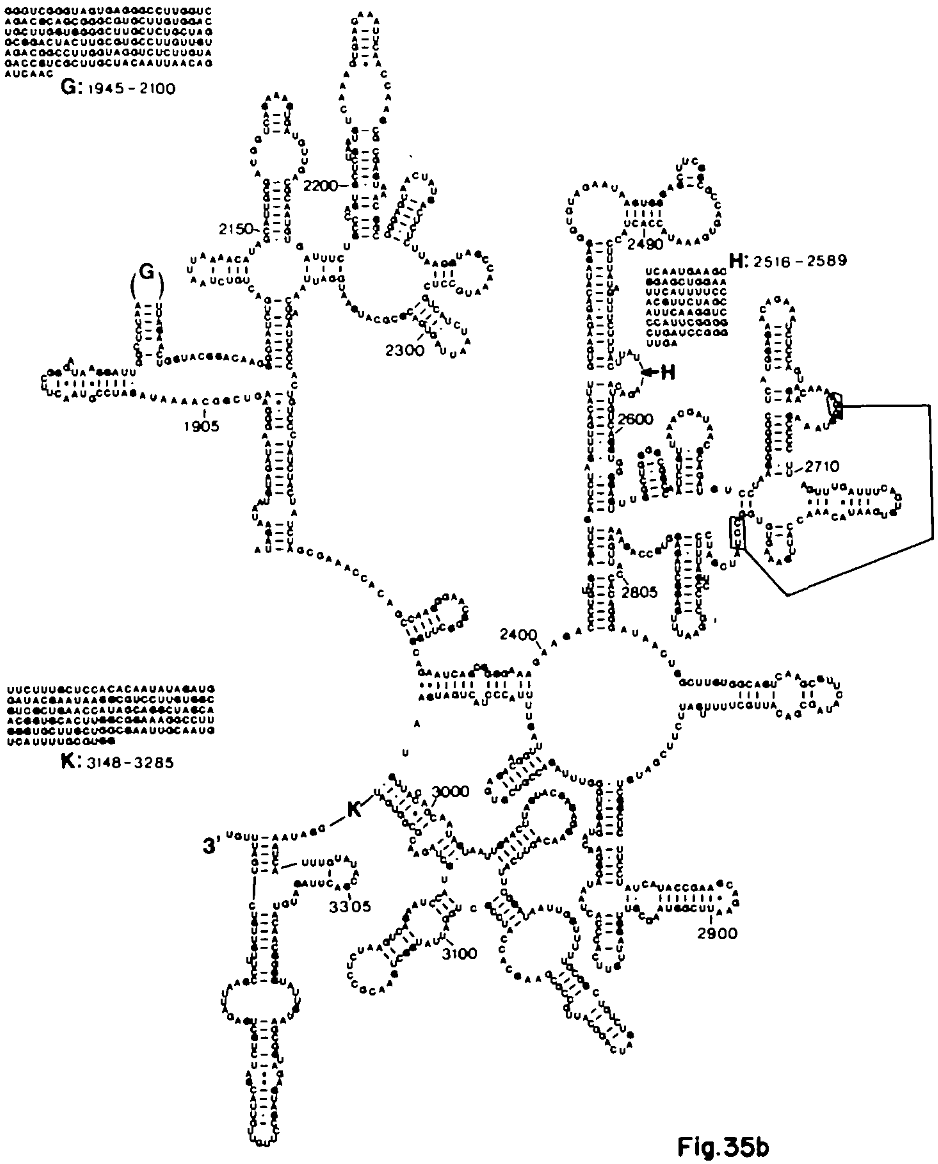
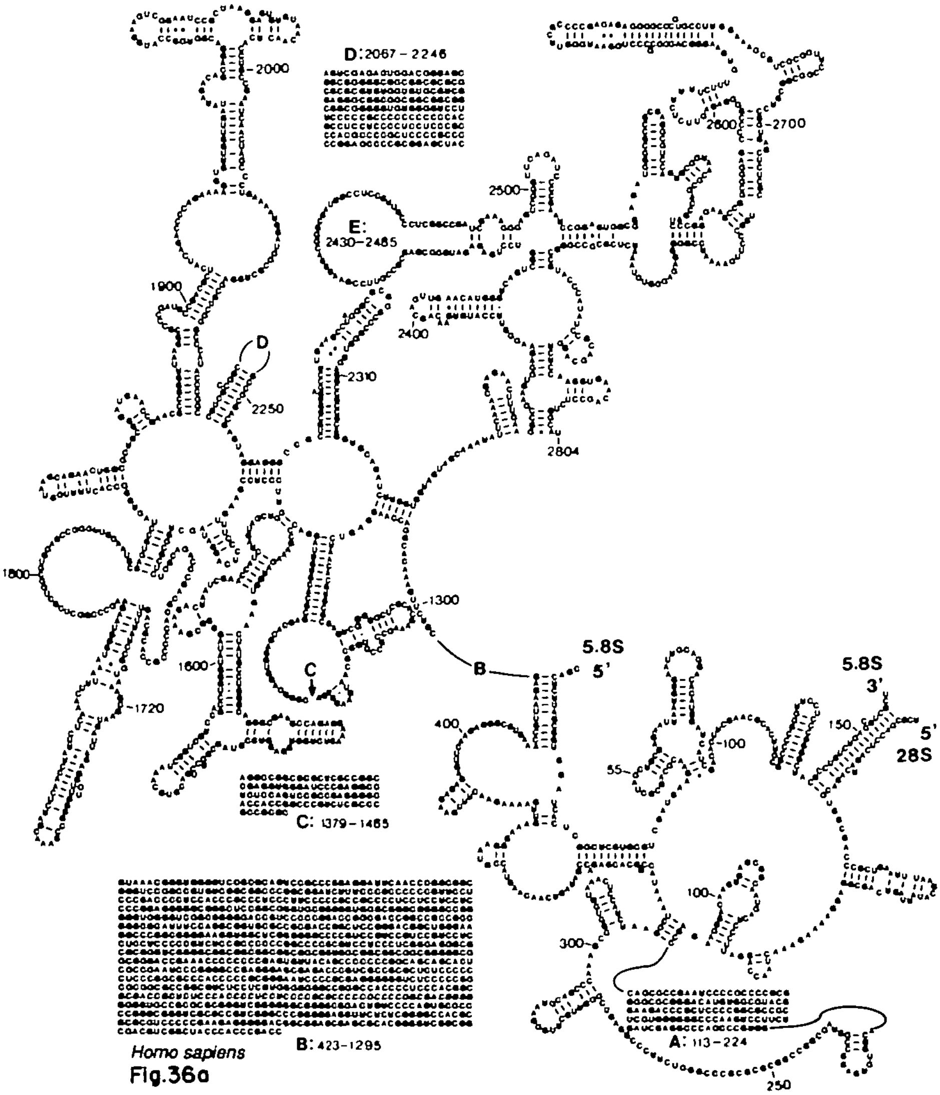


Fig.35b
Saccharomyces cerevisiae

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half



Homo sapiens

Fig.36a

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

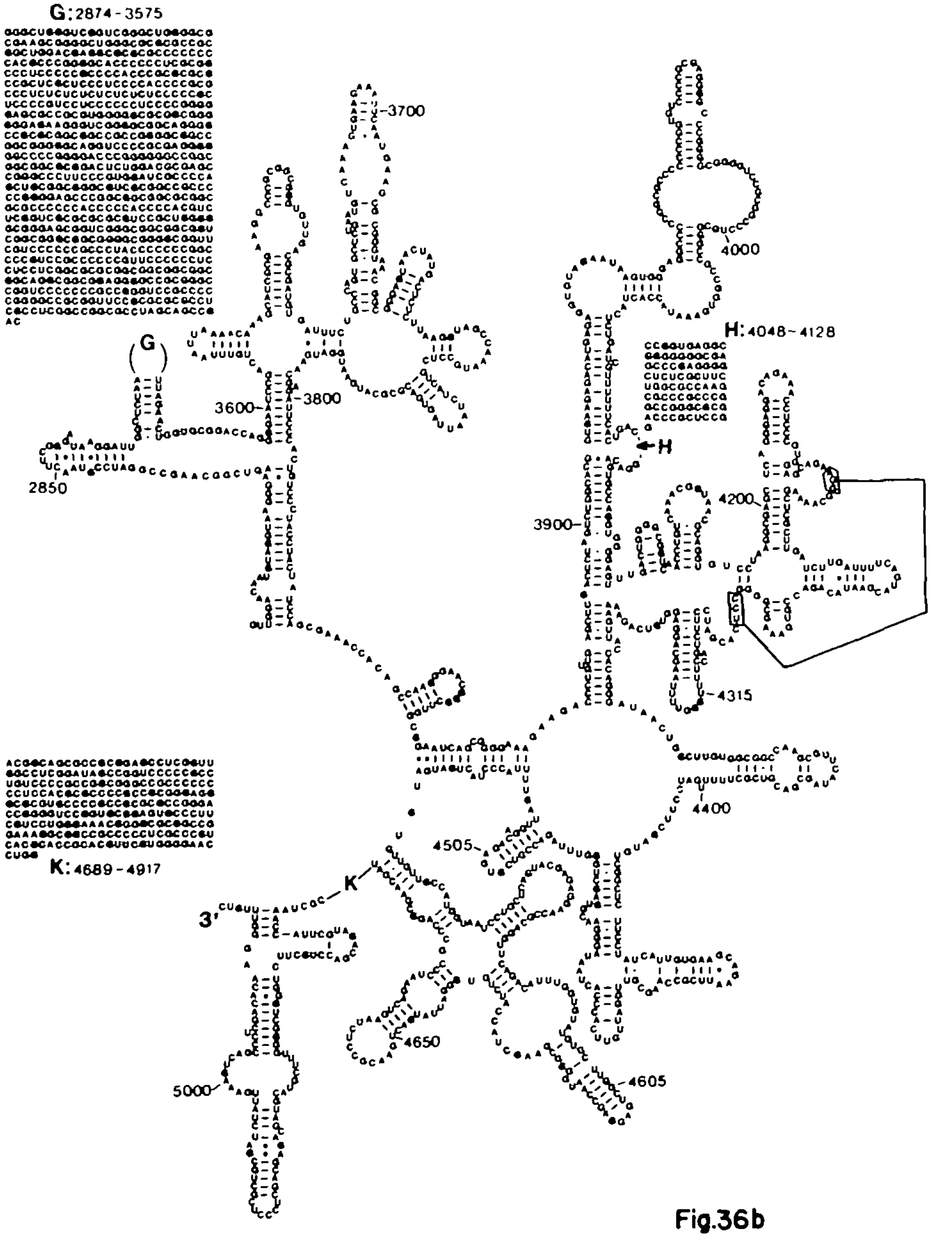
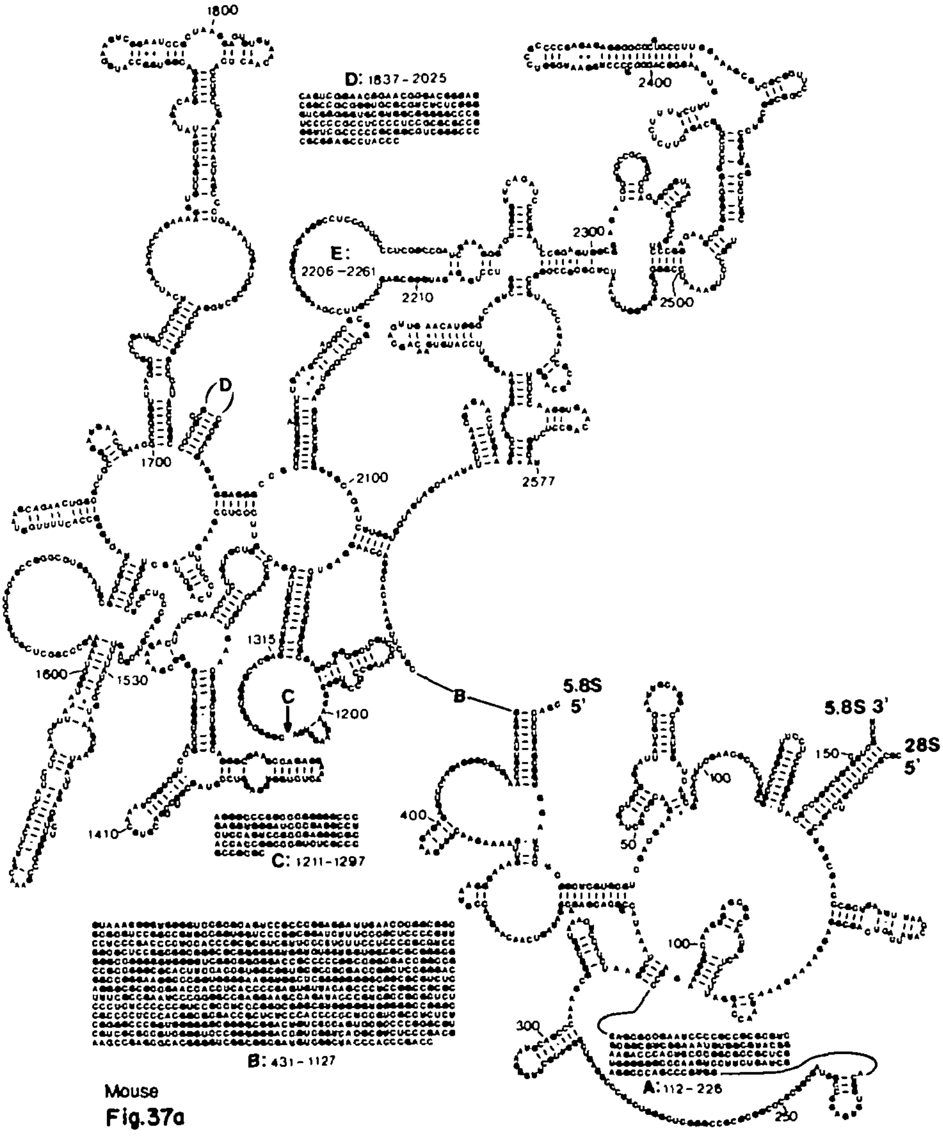


Fig.36b
Homo sapiens

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half



Mouse
Fig.37a

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

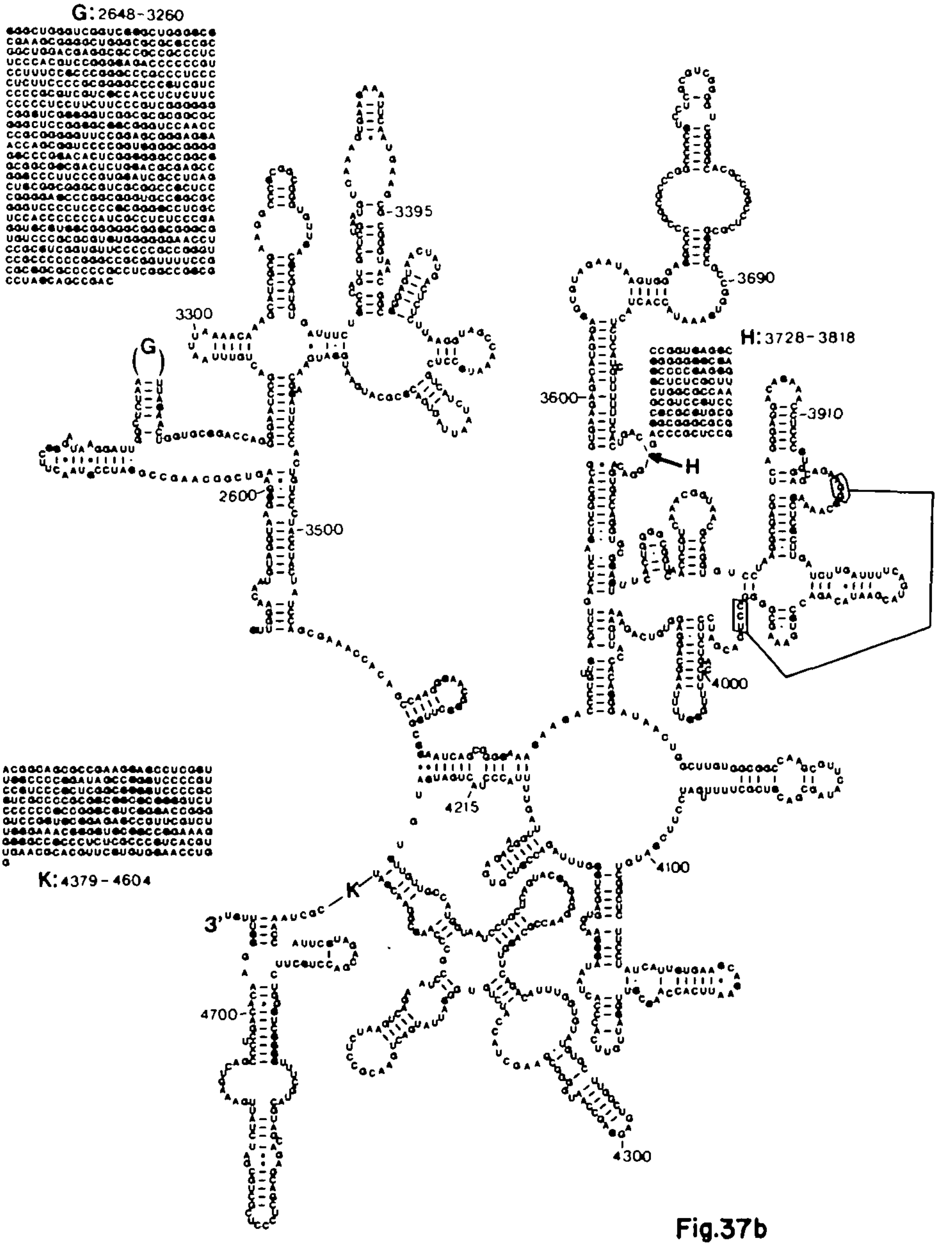
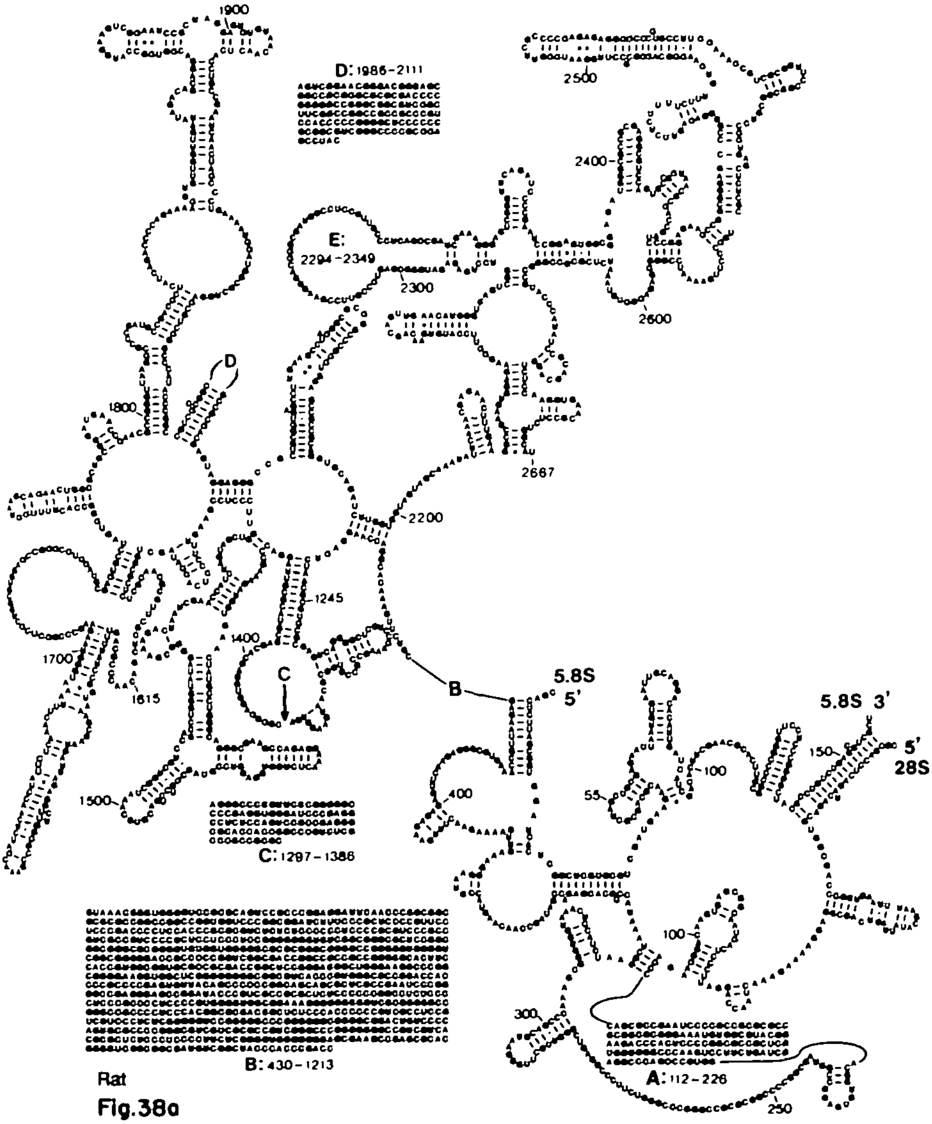


Fig.37b
Mouse

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half



Rat

Fig.38a

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

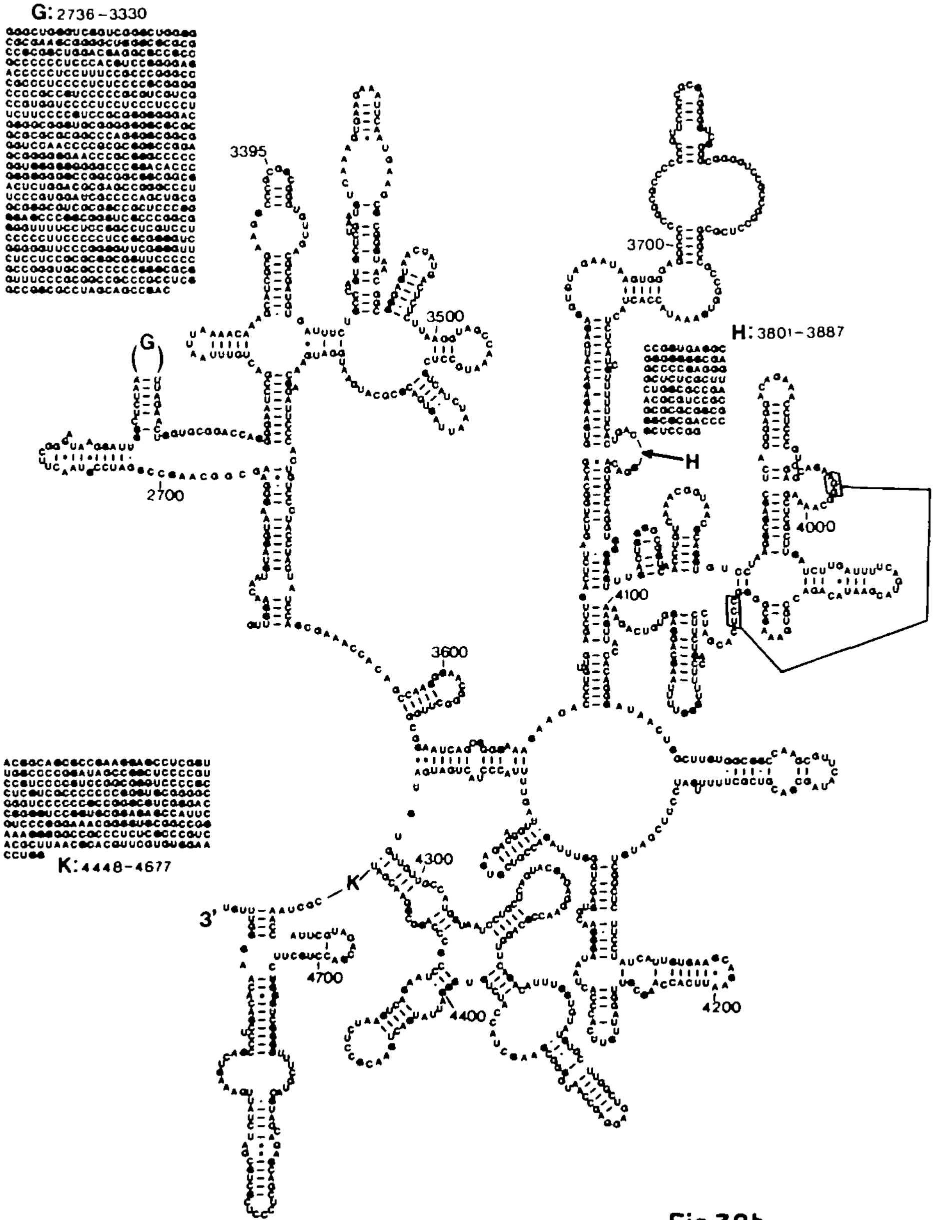
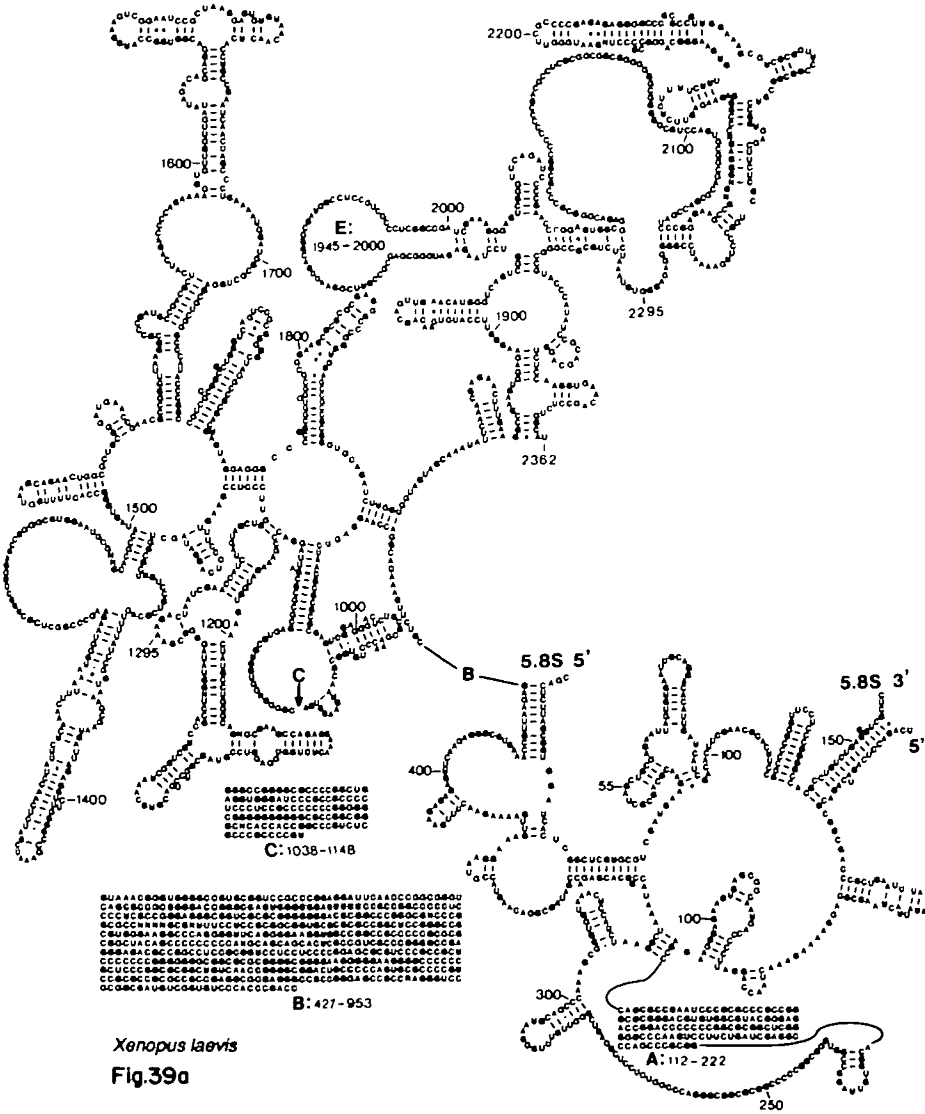


Fig.38b
Rat

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half



Xenopus laevis

Fig.39a

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

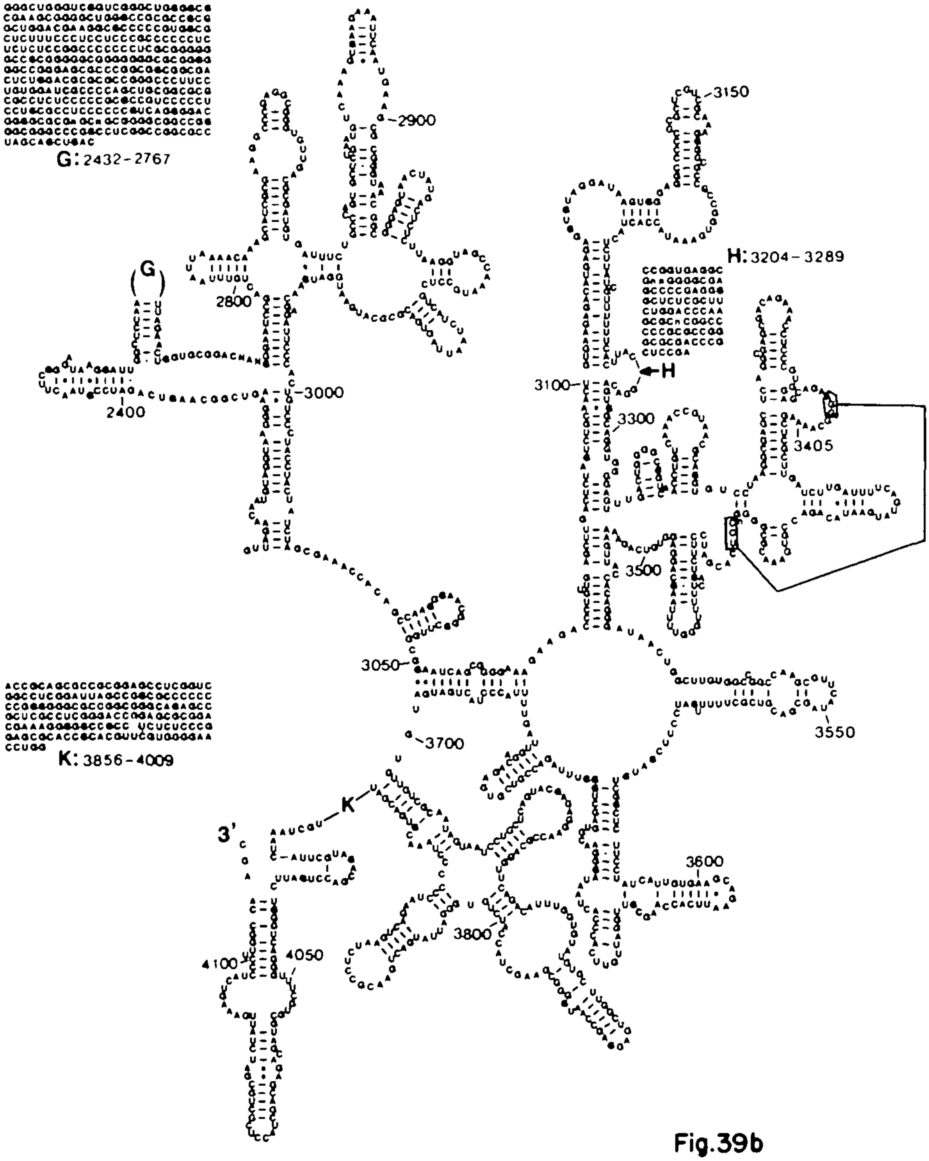


Fig.39b
Xenopus laevis

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

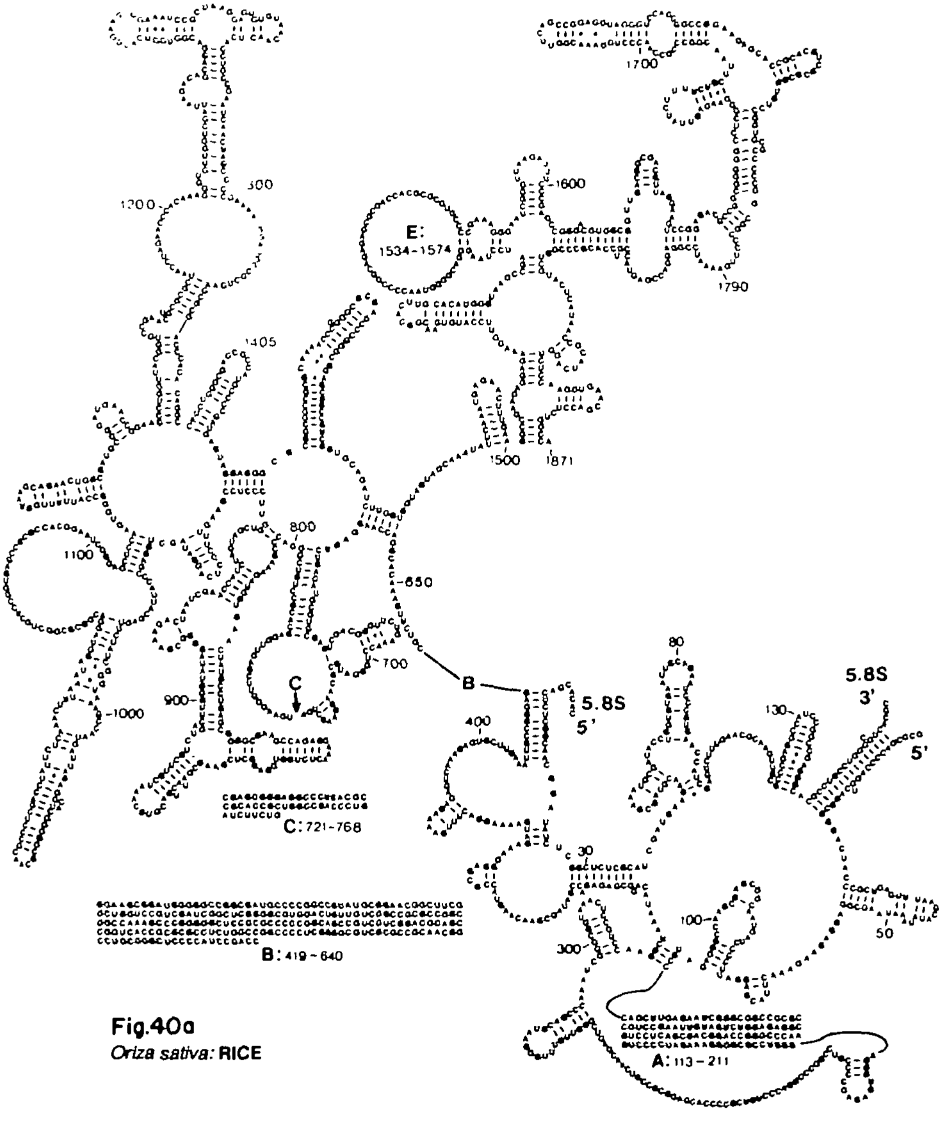


Fig.40a
Oriza sativa: **RICE**

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

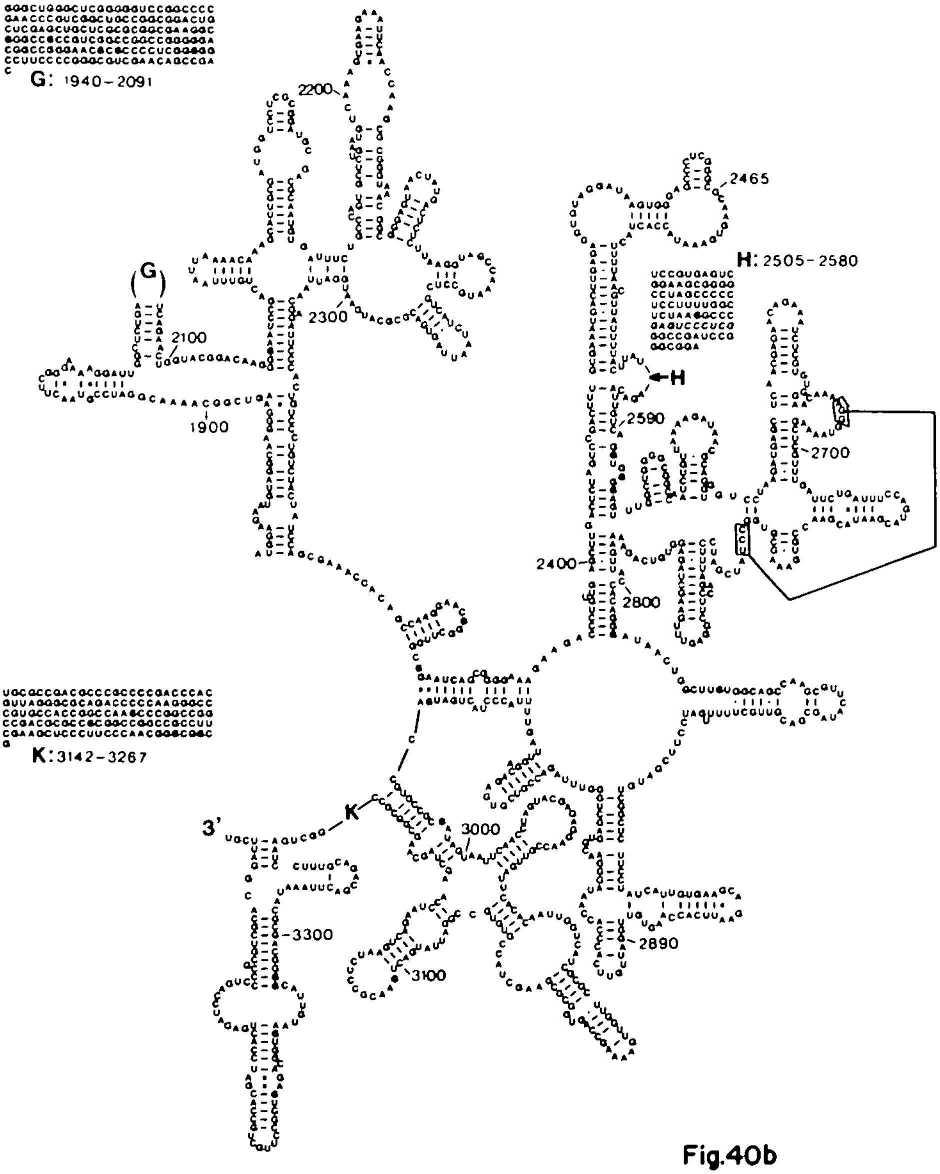


Fig.40b
Oriza sativa: **RICE**

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

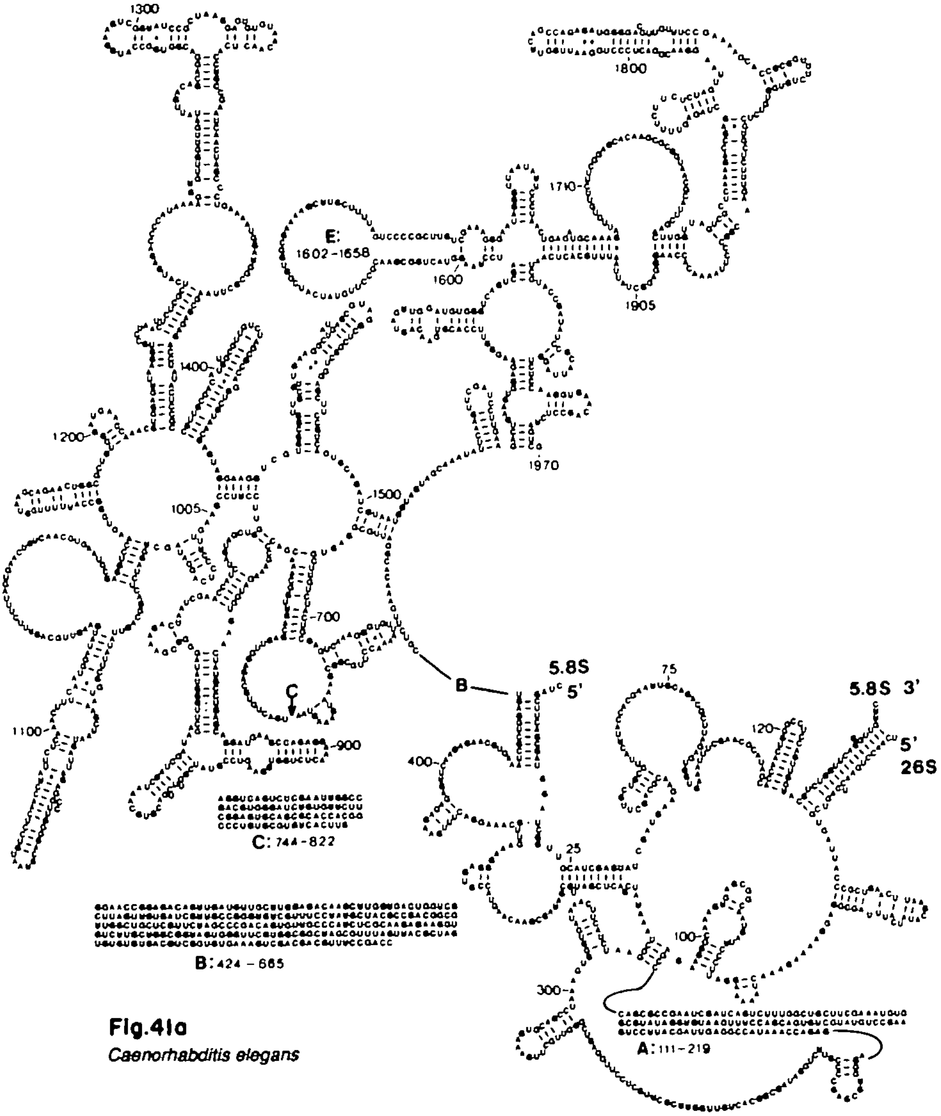


Fig.4a
Caenorhabditis elegans

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

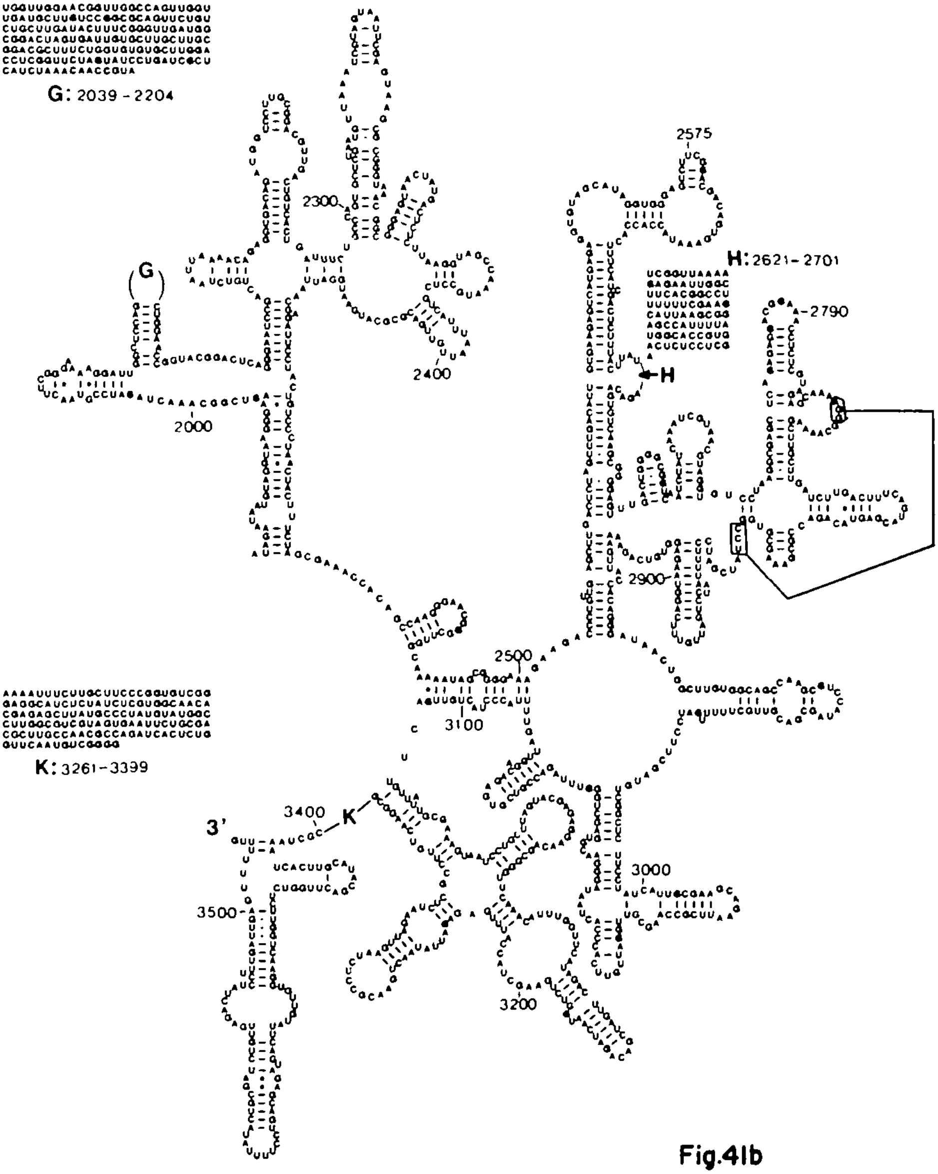


Fig.4Ib
Caenorhabditis elegans

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

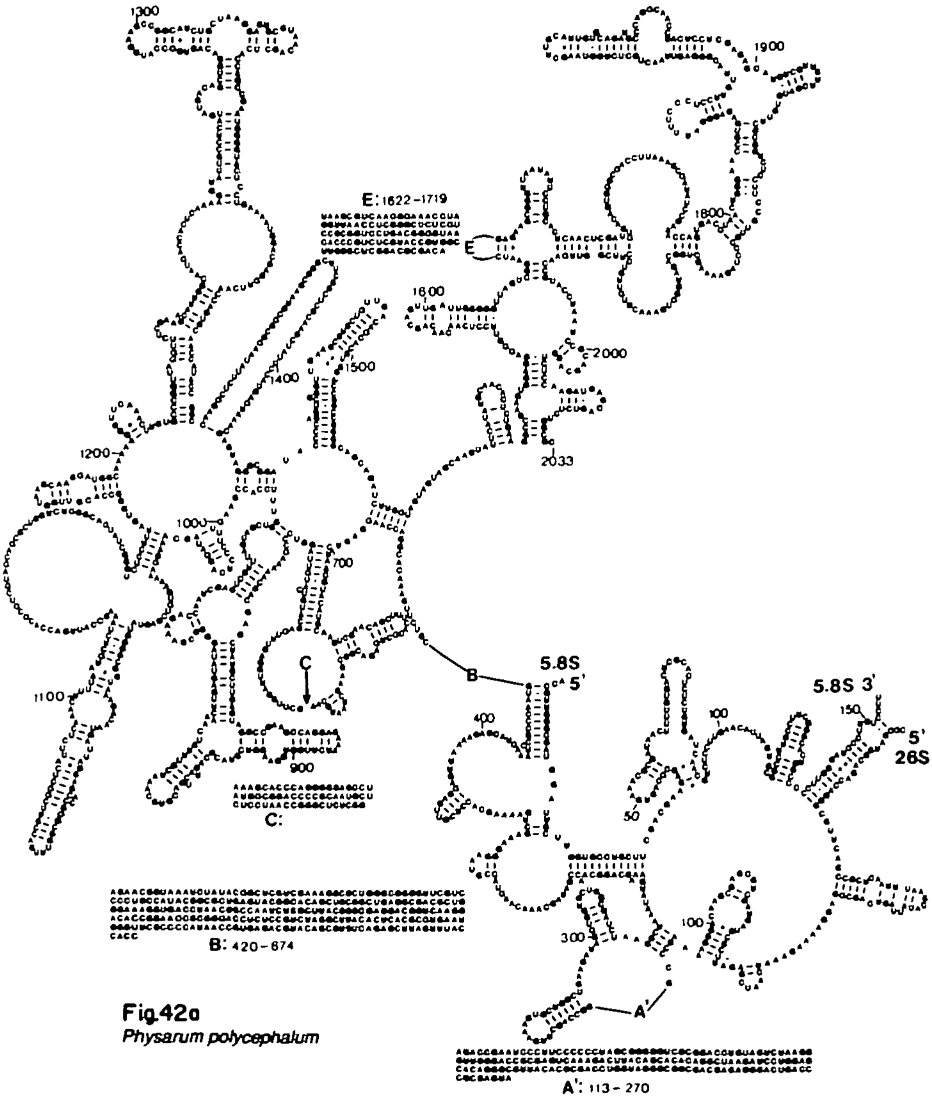


Fig.42a
Physarum polycephalum

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

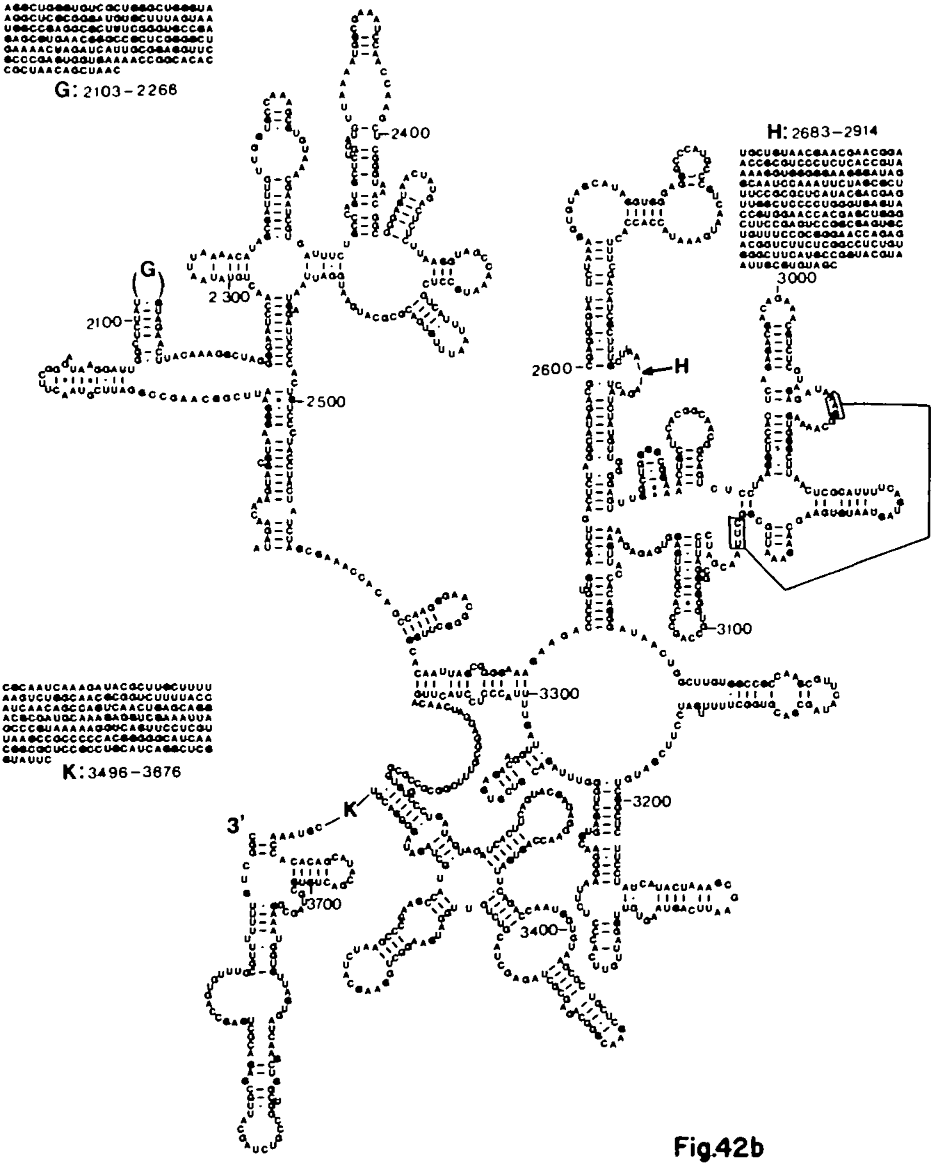


Fig.42b
Physarum polycephalum

Secondary Structure of eucaryotic 23S Ribosomal RNA: 5'half

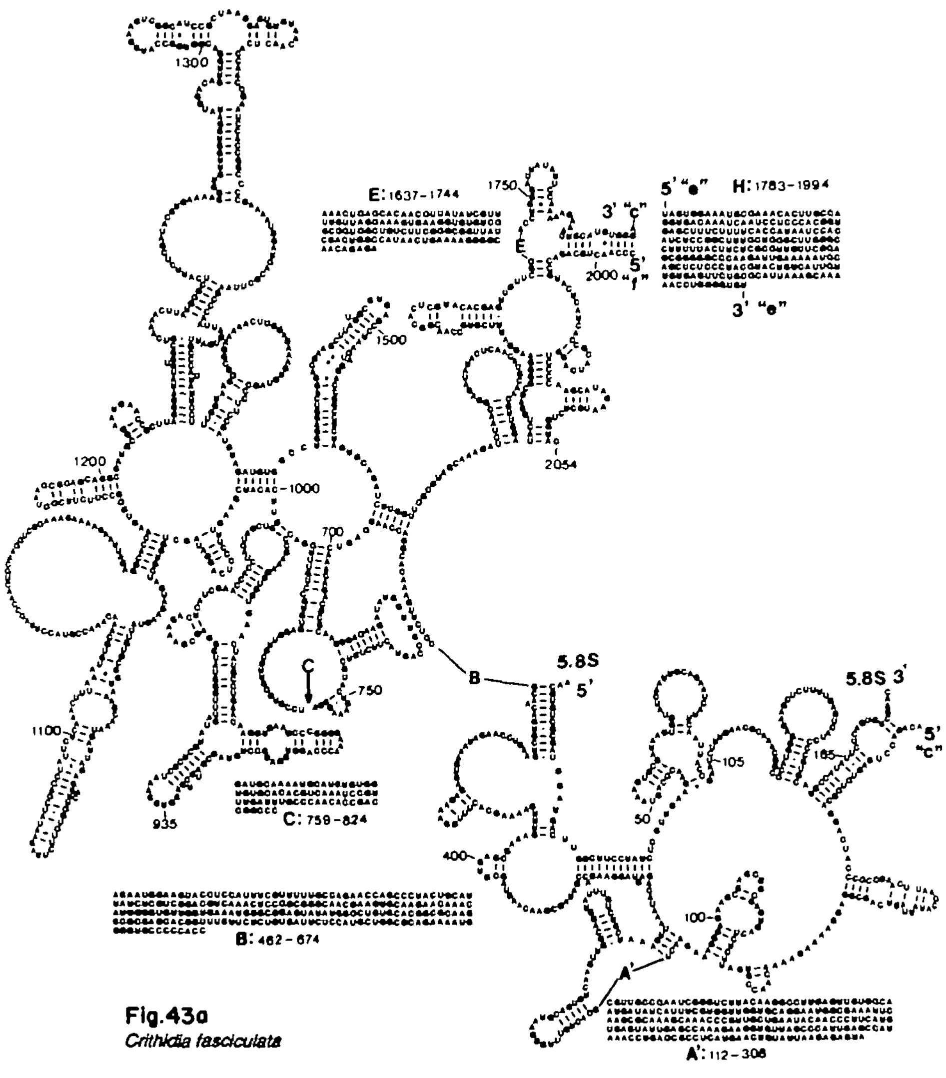


Fig.43a
Crithidia fasciculata

Secondary Structure of eucaryotic 23S Ribosomal RNA: 3'half

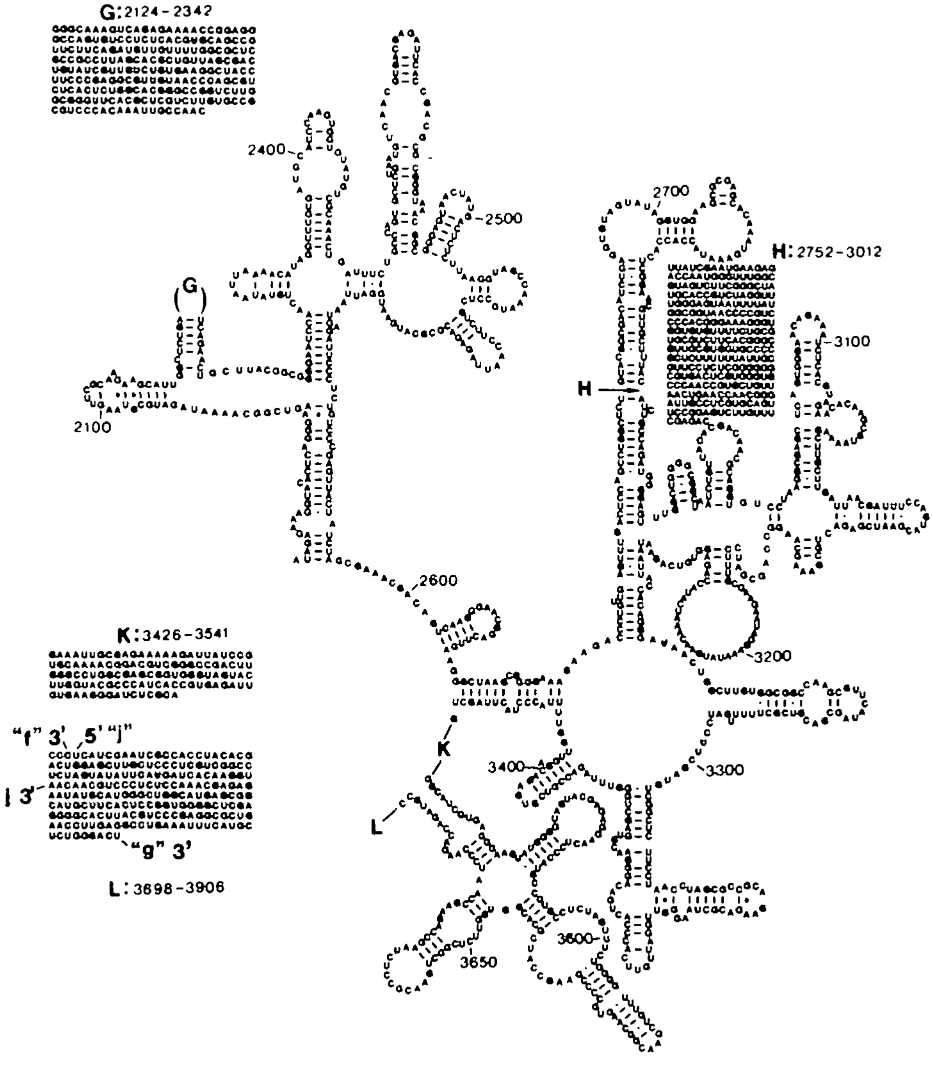


Fig.43b

Crithidia fasciculata