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Regulatory sequences in the transcription of Neurospora crassa genes: CAAT box, TATA box, Introns, Poly(A) tail formation sequences

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Abstract

Minireview. Regulatory sequences in the transcription of Neurospora crassa genes: CAAT box, TATA box, Introns, Poly(A) tail formation sequences.

MINIREVIEW

Regulatory sequences in the transcription of *Neurospora crassa* genes: CAAT box, TATA box, Introns, Poly(A) tail formation sequences

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We have analyzed the sequences of 77 nuclear genes of *N. crassa* thought to be transcribed by RNA polymerase II (references 1-72 of the accompanying paper). In Table I we present the data on regulatory sequences in the 5' region, in Table II the data on the regulatory sequences located at the 3' end of the genes, in Table III the regulatory sequences involved in intron splicing of *N. crassa* genes, and, in Table IV, a study of the distribution of these introns.

While in mammalian systems the binding proteins for at least two regulatory sequences, the CAAT and TATA boxes (Montague, 1987, Gene Structure in Eukaryotic Microbes, Kinghorn, Ed., IRL Press p. 263), are known, in *N. crassa* no binding proteins for any such sequences have yet been identified. The validity of the boxes presented here is therefore based entirely upon statistical analysis. Note, though, that Selker et al. (1986) Mol. Gen. Genet. **205**:189-192) have shown through deletion analysis that a (A/T)TATA(A/G) box, highly conserved in both sequence and position, appears to play a role in the regulation of transcription of the 5S rRNA genes of *N. crassa*. This is unusual as such a sequence is not usually associated with other Pol III transcribed genes.

When is a box statistically significant?

N. crassa has a G+C content of 54% (Villa and Storck, 1968, J. Bacteriol. **96**:184-190); we assume 50% here for simplicity in our calculations. Whether a box is statistically significant or not depends both on the length of the sequence, on its stringency to a defined consensus and the window (expressed in bp) in which it is to be found. A box of 4 given bases, no matter whether contiguous or not, has a probability of 1 in 256 to be found in a region of DNA just large enough to house the particular sequence, a window of 1 bp. We define a window as the number of possible positions that each base in the box is permitted to occupy on the DNA sequence. It will be found with a probability of 256/256 = 100% in a window of 256 bp. Given below are the probabilities to find boxes of given length and stringency in a 1 bp window:

4/4 = 1/256	5/5 = 1/1024	6/6 = 1/4096	7/7 = 1/16384
	4/5 = 1/68	5/6 = 1/227	6/7 = 1/781
		5/7 = 1/86	

Regulatory sequences in the 5' region

The CAAT box

Fifty genes had determined 5' mRNA ends (+1) and were screened for possible CAAT type boxes around the -80 bp position, the usual location for mammalian CAAT boxes. When several 5' ends were given, +1 was taken to be the most distal from the ATG except when the authors indicated the major site themselves. Six genes were found to harbor a CAAAT sequence (underlined in Table I) in a range of -75 to -88, a window of 13 bp. The cumulative window of 13 bp in 50 genes is 650 bp. The probability of finding a 5/5 box in a 1 bp window is 1/1024, therefore in a window of 650 bp, the box should occur 650/1024 = 0.6 times. In other words, on a statistical basis we should find the CAAAT sequence in this position only 0.6 times

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out of all 50 genes. The fact that we find 6 indicates that the CAAAT box is of statistical significance, 10 times above statistical background. For comparison the mammalian CAAT box has a consensus of GG(C/T)CAATCT at around -80 bp. (Montague, 1987, Gene Structure in Eucaryotic Microbes, J. Kinghorn Ed., IRL Press, P. 263)

The TATA box

The genes with a defined +1 were also screened for the presence of a possible TATA box around 30 bp upstream of the +1. This revealed a statistically highly significant TATATAA box which is present in 5 of the genes (double underlined in Table I) at a distance from the first +1 of 34-44 bp (window 10 bp). The probability that 1 gene out of 50 has such a sequence is (10 x 50)/16384=0.03. We have found 5 such genes giving a factor of 150 above statistical background. If there is indeed a factor that can bind to this sequence even with one wrong base then there are 6 more genes with a degenerate TATATAA (single underlined in Table I). For comparison, the mammalian and yeast TATA box is: TAT(A/T)A(A/T) at around -30 bp (Montague, 1987, Gene Structure in Eucaryotic Microbes, J. Kinghorn Ed., IRL Press, P. 263)

+1 Sequence Consensus

The most striking consensus sequence around the +1 is TCATCANC (double underlined in Table I) which has a probability of 1/16384 of being found in a 1 bp window as a 7/7 sequence. There are 6 genes in which 16 transcription starts lie either within the TCATCANC sequence itself or up to two bases away so that we can consider the window to be 12 bp. The probability that out of 50 genes, there is one gene with at least one +1 (there are 107 +1's highlighted in Table I) lying within a 12 bp window of such a sequence is (107 x 12)/16384=0.08. Having found 6 genes with 16 transcription starts, that gives us a factor of 200 over background. Similar results are obtained if we consider only the first transcription start point. We have scored 5 other genes with this sequence at single base degeneration (single underlined in Table I).

Regulatory Sequences in the 3' Region

Polyadenylation signal sequences

Among the 77 genes in consideration there are 29 which have a 3' end of their mRNA determined by the poly(A) of their cDNA. Some have several 3' ends, so in total there are 34 3' ends given. The polyadenylation sequence in mammals is AATAAA, and in yeast is AATAA, both located 10 to 30 bp upstream of the poly(A) tail (Montague, 1987, Gene Structure in Eucaryotic Microbes, J. Kinghorn Ed., IRL Press, P. 263). We looked within the same region and found two genes, *nit-4* and *spe-1*, with the AATAAA sequence 20 and 17 bases respectively upstream from their 3' ends (double underlined in Table II). Statistically we expect (34 x 20)/4096=0.16 such sequences in a window of 20 bases. Therefore 2 is 12 times more than expected. There are then 14 more 3' ends showing the same sequence 3 to 23 bp upstream, window 20 bp, but with a stringency of 5/6 (single underlined in Table II). Statistically we expect (34 x 20)/227=4 so there is a factor of 3 over statistical background.

Intron Regulatory Sequences

Table III presents the introns from the 77 genes analyzed. There are in total 149 introns with a distribution similar to the Poisson distribution (Table IV). The number of introns seems to be quite independent of the length of the gene, for example, the three genes with 7 introns,

atp-2, crp-1, and *nur-40* have coding regions of 2200 bp, 950 bp, and 1600 bp, respectively, including the introns. Among the genes without introns there are some very large, e.g. *frq* 2360 bp, *nuc-1* 2565 bp, *qa-1F* 2400 bp, and some very short or middle length, e.g. *cys-3* 710 bp, *met-7* 1630 bp, *qa-4* 1100 bp. Of the 14 genes without introns there are 5 in the *qa* cluster of 7 genes. This indicates that the location of the gene might be important in determining whether or not it contains introns.

The 5' signal is:

$$G_{51}\text{-}G_{99}T_{99}(A_{77}/G_{17})(A_{50}/C_{23})G_{94}(T_{76}/C_{15})$$

The Lariat or internal sequence is:

$$(G_{45}/A_{37})C_{94}T_{94}(A_{48}/G_{40})A_{93}C_{82}$$

with a distance of 6 to 29 bases from the 3' splice site.

The 3' signal is:

$$\not{G}_4(A_{56}/T_{20})(T_{62}/C_{33})A_{100}G_{100}\text{-}G_{40}$$

where the subscript number indicates the % occurrence of the particular nucleotide, $\not{G}$ indicates a conserved absence of that particular nucleotide, and - shows the splicing site.

We have determined the majority of the internal lariat sequences presented here. These *N. crassa* intron signals are very similar to the mammalian signals which are:

5':	AG-GT(A)AGT
Lariat:	CT(A/C)A(T/C)?
3':	$(T/C)_{11}$NCAG-G

(Montague 1987 Gene Structure in Eucaryotic Microbes, J. Kinghorn Ed., IRL Press, P. 263) For *N. crassa*, intron lengths lie between 46 and 856 with a tendency toward 60 bp.

Table I Regulatory sequences in the 5' region of *Neurospora crassa* genes

Gene	CAAT box	Dist C[a]	TATA box	Dist T[b]	TCATCANC at +1
am	-	-	TCTTGTATAAAGT	38	
arg-2	AATCAAATGTC	85	-	-	CCGTCATCAACTCT
atp-1	-	-	-	-	CCTCCATCAACCTCCCGCTACATCT
atp-2	GAGCAAATCAC	78	-	-	-
bli-7	-	-	GTGTATATAAGAC	42	TCATCATCAGCATC
chs-1	-	-	-	-	CTAGCATCATCTAG
cmt	-	-	GGGTATATAAAGC	44	TTGTCATCAACCGA
con-10	-	-	GTGTATATAAGCA	42	-
con-13	-	-	ATGCATATAAGAA	30	-
cys-3	-	-	TTGTATATCAGAT	37	-
for	-	-	-	-	CCTTCATCATCCTC
grg-1	-	-	GCCTATATAAGAC	42	CCATCATCAGCCAA
his-3	TACCAAATCAC	88	CTGTACATAAGCG	46	-
hsp30	-	-	TCAAATATAAATC	46	-
laccase	-	-	ACGTGTATAAAGT	45	TCTTCATCATCATA
lox	-	-	GTCTATATAAGAG	34	-
pho-4	-	-	-	-	TTCTCTTCAGCACC
qa-4	GGTCAAATCAAATCTT	88	-	-	ATTTCCTCACCATT
qa-x	CAGCAAATGCT	75	-	-	-
spe-1	TCACAAATTTC	81	-	-	-
T	-	-	-	-	ACTACATCAGCAGT

Key: Double Underlining indicates a box showing perfect stringency.
Single Underlining indicates a box showing a single nucleotide degeneracy.
a is the distance from the end of the CAAT box to the first major +1
b is the distance from the end of the TATA box to the first major +1
Nucleotides shown in *italics* are major +1 transcription initiation sites.

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Table II Regulatory sequences located at the 3' end of *Neurospora crassa* genes among the 29 genes with 3' determined by poly(A) tail in their cDNA:

Gene	Dist. 3[a]	AATAAA	Dist. A[b]	3' terminal sequence
acp	218	TGTAATACAAGA	19	GCTGTTTCCCCATGTGTATTC
al-1	128	GGGTATAAACGA	14	TTCGTAGATAAAGTCTTGGGA
	160	GGGAATATATAG	15	GTTTTGTTTTTATGTCGAAGA
atp-1	27	TTGAATTAATTC	7	CTATTCCCGTGGTTCTTGAGA
atp-2	73	TAGAGTAAAGAA	15	GGTTTTTCGGGACGTTCCTCC
	194	GTTAATGAATAC	17	TGAATGAACTCAGCCTATGTG
cys-3	540	TGAAAGAAAAAGA	23	ACGAGTCATGGAAAAAAGAAG
grg-1	223	GCCAATTAATAC	3	TTAATACCTTCACATCTGTTT
hsp30	374	ATAACTAAAGTT	22	GAACACAACTACGCCAGTTCG
ilv-2	327	GTCAATGAACTT	21	TTTTCTCTGTTCAATGGCTTG
nit-3	50	AGCAATGAATTG	17	CCTTCAGATGACCTTTTGTGT
nit-4	129	CACAATAAATGC	20	GTCGTTCTATACACAAATTCC
nur22	266	TCCAATAACATT	15	TCTCCTTCTTTGAATCATCAT
nur40	135	AGCAATCAAGAG	9	AGAGATTTGCGCAACGTTTGA
spe-1	201	ACGAATAAAATT	17	TTGGACCCTATAAGATATTTG
T	430	ACAAAAAAAGAC	18	TTTTTCATCGCCGTAACCACC

Key: Double Underlining indicates a AATAAA box showing perfect stringency.
Single Underlining indicates a AATAAA box showing a single nucleotide degeneracy or poly(A) tail addition sites. .
a is the distance between last codon and first poly(A) site.
b is the distance between AATAAA consensus and first poly(A) tail site.
al-1 and *atp-2* each have two poly(A) tail addition sites.

Table III Regulatory sequences involved in intron splicing in *Neurospora crassa* genes.

5' Consensus: G_{51}-$G_{99}T_{99}(A_{77}/G_{17})(A_{50}/C_{23})G_{94}(T_{76}/C_{15})$
Lariat Consensus: $(G_{45}/A_{37})C_{94}T_{94}(A_{48}/G_{40})A_{93}C_{82}$
3' Consensus: $G_4(A_{56}/T_{20})(T_{62}/C_{33})A_{100}G_{100}/G_{40}$

Ref.	Gene	Id[a]		5' signal	Lariat signal	Dist[b]	3'signal	L[c]
				G GTRNGY	RCTRAC	6-29	N YAG G	
1	*acp*	D	1)	CCGOGTATGT	ACATGCTAACATCGC	18	CTACAG CCC	380
			2)	CAGOGTACGT	GTGTGCTGACGACCC	10	CCCTAG GAT	192
2	*acu-3*	D	1)	GCTOGTTAGT	ACAATCTCACTGACA	21	CGACAG AAG	70
					or ACAATCTCACTCGGC	10		
			2)	TACOGTGAGT	AGCCCCTCCCATACT	18 x	ATCTAG ACC	66
					or CCATACTGATATTCG	12 x		
3	*acu-5*	S	1)	ACT1GTAAGT	AGATACTAACAGCTG	12	AAATAG CTC	58
4	*acu-8*	D	1)	CAA1GTAAGT	AGTTGCTAACCCATG	13	CTACAG GAA	73
			2)	TACOGTAAGT	GTTTGCTAACCCCTA	20	CAACAG GGC	67
5	*acu-9*	S	1)	CAGOGTATGT	TCATACTAACAACCA	11	CAACAG GAG	46
6	*al-1*	D	1)	TTG1GTATGT	GCTAACTTCTTCCCC	15 x	CAACAG GCG	77
			2)	TTCOGTAAGT	TCCAACTAACTTCAC	21	GAACAG TAC	108
7	*al-3*		NO INTRONS					
8	*alc*	D	1)	TCG1GTCCGT	TTCAACTAACGGAAG	21	ATACAG ATC	72
9	*amd*	C	1)	AGG1GTACGT	CAGAGCTGACTTGAT	17	CCACAG AGT	67
			2)	GCC1GTAAGT	ATTTGCTGACTCGGC	13	CTCTAG TGA	61

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Ref.	Gene	Id[a]		5′ signal	Lariat signal	Dist[b]		3′signal	L[c]
10	*arg-2*	D	1)	AGGOGTGCGT	TAAACCTAACATTTT	14		GCTCAG GAT	56
11	*atp-1*	D	1)	GCGOGTAGGT	TAGGGCTAACTCGAC	8		CAGCAG CGA	202
			2)	CGG1GTACGT	GGATGCTGACGTGTC	16		GTATAG TGA	309
			3)	CGA2GTATGT	CAAATCTGACCCTTT	13		CCCCAG GTT	63
			4)	GGTOGTAAGT	ACTGGCTAACCAGAA	18		ACACAG GCG	323
			5)	CGTOGTAAGT	CAGAGCTGACGAGTC	14		CTACAG TTG	61
11	*atp-2*	D	1)	GAG2GTGAGT	TTGGCCTTCCTCTTG	16	x	ATATAG CGG	111
			2)	TTG1GTAAGC	CCTTGCTAACCGCGC	21		CCACAG GTG	157
			3)	ATG1GTCAGT	TTATACTGACCCCGC	18		CAACAG TCA	101
			4)	TCGOGTACGT	ATGCGCTAACCAGCC	11		CCGCAG CAA	88
			5)	ACA1GTAAGC	ATTCGCTGACATGAT	17		TTATAG CTG	69
			6)	CCC2GTGGGT	TTTTACTGACGCAAA	12		GTGTAG TGT	83
			7)	ATG1GTATGT	CGTTGCTAACGCAGT	11		CTGTAG TGT	61
12	*bli-7*	D	1)	AACOGTAAGT	CCTTGCTAACCTTCG	26		AAAAAG ACC	95
13	*Bml*	D	1)	ATTOGTAAGT	CGACGCTGACACGAT	21		CTATAG GTT	240
			2)	TGCOGTAAGT	CAGGACTAACACAAC	17		GATCAG GGT	74
			3)	CTG2GTACGT	CGACGCTGACAGAAT	11		AAACAG GCA	68
			4)	TGT2GTACGT	GAAAGCTCACCGCCC	12		CTACAG GTA	66
			5)	GAGOGTGAGC	GCTCGCTAACTAGCT	18		TGACAG GCT	73
			6)	CTT2GTAAGT	TAATACTGACGAATC	11		AAACAG CCG	57
14	*chs-1*	D	1)	CAG1GTAAGT	TAACACGAACGTCGT	12	x	ATCCAG GGG	73
			2)	GGG2GTAAGC	AACCACTTACTAATA	16		TGATAG CAA	59
15	*cmt*	D	1)	GCT1GTAAGT	TGGTACTAACTTTGA	15		TTCTAG GCT	94
16	*con-8*	D	1)	CGGOGTATGT	ATGTGCTAACAGCTC	23		ACATAG CCA	169
			2)	TAA2GTACGT	TTAAGCTAACTCGTT	17		TAATAG TTG	69
17	*con-10*	D	1)	CCG2GTATGT	CTTTGCTAACATAAT	17	x	CTCCAG CCC	70
			2)	CAGOGTATGT	GTTGACCAACACATG	17		AAACAG CGC	74
18	*con-13*	D	1)	GATOGTAGGT	CTGTGCTTACCTTAA	16		CAATAG TGC	57
			2)	GGA2GTAAGT	CTGTGCTGACCGGAA	14		AAACAG CAC	62
19	*cot-1*	C	1)	CCA2GTATGC	TCATTCTAACATTGA	14		TACTAG CAA	78
			2)	CAG2GTAAGC	AGATACTGACACGGT	16		ATGCAG AGA	59
			3)	AAG2GTATGC	ACGCGCTCACCATAT	18		TCATAG CCT	58
20	*cpc-1*	D	1)	CAG1GTAATT	ATGCGCTTACAATCT	12		GCACAG AAC	57
21	*cpi*	S	1)	CCG?GTACGT	ATTGGCTGACCCCTC	18		TTTTAG TGA	856
			2)	GGT?GTAAGT	ACCGACTGACCTGCA	13		CTTTAG TTT	94
			3)	AGG?GTAAGT	GATGTCTAACTCCCA	11		ATGCAG CTC	271
			4)	AAC?GTAAGT	AAGACCTAACCTCTC	12		GAACAG GGG	66
22	*crp-1*	D	1)	ATGOGTATGG	AAACGCTGATTCAGT	15	x	ATGTAG CCT	47
			2)	CATOGTAAGC	GATGACTGACTGTAG	16		TTATAG GTT	50
			3)	GGG1GTATGT	GAGTATTGACAGCAT	13	x	TTCCAG CCG	62
			4)	AGG2GTACGT	TGATGCTAACAATGG	11		GAACAG TGG	62
			5)	CAGOGTATGC	CGATACTAACCCGAC	11		GATAAG CAC	63
			6)	AGT1GTACGC	AAACGCTGACGATGA	12		GGATAG ACC	126
			7)	AGG1GTAAGA	CTCGTCTAACAACAC	12		TTCTAG GCC	61
23	*crp-2*	C	1)	GCG1GTAAGT	GGAGGCTGACAATCA	11		ATTTAG TTG	73
			2)	CAG2GTTCGT	TGAGGCTAACATCCT	17		TTCCAG TGG	215
			3)	GTG1GTATGT	TGATCCTAACATTTT	10		TCATAG TCA	54
24	*crp-3*	D	1)	AAGOGTGCGT	GGGATCTAACATGTT	17		CAATAG ATT	93
			2)	GGCOGTAAGT	TTTGTCTAACTTACC	14		GAACAG TTC	98
				or	TCTAACTTACCTTCG	10			
25	*cya-4*	D	1)	CTG1GTAAGT	AAAGACTGACATGTA	21		ACGCAG CCT	398
			2)	AAGOGTGCGT	ATCAACTAACACATA	21		AAACAG GCC	68
26	*cys-3*	NO INTRONS							

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Ref.	Gene	Id[a]		5′ signal	Lariat signal	Dist[b]		3′signal	L[c]
27	*cys-14*	D	1)	TCC2GTTTGT	AGATACTGACAAGAT	18		TAACAG CAA	162
			2)	AAT2GTATGG	TATTGCTAACATAAT	15		CCACAG GTC	59
			3)	GTG1GTAAGT	CGTAACTTACGAACC	17		CAACAG GCT	72
			4)	GGTOGTACGT	CAGAACTGACAGAAG	17		CAACAG GAC	87
28	*cyt-2*	C	1)	CCTOGTATGT	CTGATCTAACCTCTT	21		ATGTAG CCT	92
		D	2)	TGC2GTAAGT	TTTTGCTAACGATGT	24			
				or	CTTTACTCACTATCT	7		ATCTAG CAC	95
29	*cyt-18*	S	1)	TGG2GTAAGT	CATGACTAACACGAT	16		TACCAG CAC	64
30	*cyt-20*	C	1)	ACG1GTTCGT	ACCAACTTACACCTG	22		TTGTAG ACA	62
31	*cyt-21*	D	1)	CAG2GTACGC	ACCAGCTAACTCTCT	19		TATTAG AAC	73
				or	ACTCTCTGACTCCCA	11			
			2)	CTTOGTACGT	ATTGACTGACATTGC	25		AAACAG GTC	100
32	*for*	D	1)	GCCOGTACGT	GTTGACTCATAATCC	16	x	ATACAG ATG	80
			2)	CAA2GTGAGT	CCAAACTAACCCACC	17		CTCCAG GAT	63
33	*frq*	NO INTRONS							
34	*grg-1*	D	1)	AGG1GTAGGT	AGACACTGACATCTC	16		TCACAG GCG	88
			2)	TCG2GTAAGC	AGACACTAACATTCA	18		TCTCAG TCT	65
35	*H3*	C	1)	CTCOGTAAGT	CGTTGCTAACGCGTC	14		ACCCAG GTC	67
35	*H4*	C	1)	GAC1GTAAGT	GTGTTGTAACATCAT	29		CATCAG GCG	69
				or	CATGACTGACTCGTA	17			
			2)	CCA1GTACGT	GTCAACTAACATGTC	17		CAACAG TGA	67
36	*his-3*	C	1)	TGC1GTAAGT	TTTAACTCAAGACAC	9	x	ACATAG CTA	59
37	*hsp30*	NO INTRONS							
38	*ilv-2*	D	1)	ACG1GTGAGT	GTTTACTGACGAGCT	19		ACACAG AGC	90
			2)	CTTOGTGAGT	CCATGCTGACCCTTT	18		CTTCAG GAC	236
			3)	AAGOGTGAGT	GCGAGCTAACAAACA	15		CAACAG ACC	77
			4)	CGCOGTTCGG	CCTGACTAACATTTG	18		TCCTAG TCC	69
39	*laccase*	P	1)	CGGOGTAAGT	AATGACTGACACACA	10		ACCTAG TAC	56
40	*leu-5*	S	1)	TGCOGTGCGT	CCATGCTAACCCAGC	9		GCCCAG GAA	60
41	*leu-6*	D	1)	CAGOGTACGC	CGGTACTAACTCGTC	11		TTCCAG GCC	63
42	*lox*	NO INTRONS							
43	*met-7*	NO INTRONS							
44	*mrp-3*	D	1)	AACOGTAAGT	CCATGCTGACCATGC	23		CTCTAG CCC	307
45	*mta-1*	C	1)	CAA2GTAAGT	TTGTACTGACCATTT	12		CACTAG GAA	53
			2)	TTT2GTAAGT	TGAGACTAACCTCAC	9		ACTTAG CGG	57
46	*mtA-1*	D	1)	GAT1GTGAGT	CATGGCTGATTGCTC	15	x	TTTCAG CGT	59
47	*nac*	S	1)	GAG2GTGAGT	TCAAACTAACGGGTG	29		CTACAG CAG	234
			2)	GACOGTACGT	CGTAACTGACCATTG	17		ACACAG GAC	691
			3)	GAGOGTATGT	AGAGACTAAAGTTCC	14	x	TTACAG ACA	64
48	*ncypt1*	D	1)	TGA2GTAGTA	CCCTGCTGACGATGC	11		AACCAG ATA	258
			2)	TTTOGTACGT	ACATGCTGACCGTTT	11		GGCTAG AAA	70
			3)	ATCOGTAAGC	ATTCGCTGACCCAGT	16		ATTCAG TGG	68
			4)	AAGOGTACAC	ACATACTTACACATC	14		CAACAG GAG	58
49	*nit-2*	D	1)	CCG2GTATGT	GCAAGCTAATTATAA	27	x	AAAAAG GAC	99
			2)	CGCOGTGAGT	CTGGTCTGATATATT	16	x	GTCTAG AAC	78
50	*nit-3*	D	1)	TTC1GTAAGT	TCCATCTAACTGACT	13		TCACAG ACA	61

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Ref.	Gene	Id[a]		5′ signal	Lariat signal	Dist[b]		3′signal	L[c]
51	*nit-4*	D	1)	GCA2GTAGGT	AGTTACTCACCTTTT	8		TCACAG CAT	59
52	*nuc-1*		NO INTRONS						
53	*nur22*	D	1)	TTA1GTACGA	CTTGACTGACTTGTT	16		CAAAAG CTC	84
			2)	GAT1GTACGT	AACAACTAATATTTT	17	x	TCACAG CCC	197
			3)	GGG1GTAGGT	ACTTGCTAACCGAGC	19		ACAAAG GTA	81
54	*nur40*	D	1)	GCC1GTAATT	GATTGCTAACACGTC	19		CCACAG GCT	66
			2)	TAG1GTACGA	CATGGCTTATATCAA	17	x	TTGCAG CGA	71
			3)	ATTOGTGAGC	AGCTACTAAGCATAA	17	x	CTCCAG GAG	93
			4)	CAA2GTGAGT	TTGACCTGGGTCCCA	6	x	TCCCAG GAA	63
			5)	CAA2GTACGA	GGTTTCTGATTGGAT	11	x	CTGTAG GGC	65
			6)	CACOGTCTTC	AGCATCTGACAGCCG	11		TTTTAG GTG	59
			7)	CTT2GTAAAG	GATGACTGATTCCCA	10	x	ATGCAG GCA	57
55	*nur49*	D	1)	ATGOGTGAGT	TCAATCTAATATGTG	16	x	CCTTAG GAA	158
			2)	TTG1GTAAGT	GGTAGCTAACCCTTT	20		TTCCAG GTG	84
56	*pho-4*	S	1)	TTG1GTATGT	ATTCACTGACAACCA	21		CAACAG GAG	80
		D	2)	TGA1GTAAGT	GCTTGCTAACGACGA	16		TTACAG AGC	83
57+58	*pma-1*	D	1)	GCTOGTAAGT	GCATACTAACCCATT	11		GAATAG GAG	58
			2)	GAGOGTACGT	CGATGCTGACTAGTT	14		CTACAG GGT	124
			3)	GAA2GTAGGT	ACGCGCTAACCCGTT	15		TTTCAG GAC	64
			4)	TTG1GTAAGT	AATAGCTAACAATAC	16		TCACAG TTG	67
59	*preg*	D	1)	CCG2GTAGGC	AGCTGCTGACATGAA	14		TCATAG AAC	83
60	*pyr-4*		NO INTRONS						
61	*qa-1F*		NO INTRONS						
61+62	*qa-1S*	S	1)	TAG1GCACGT	TCGTACTAACAGTCA	15		CACCAG GCT	66
61	*qa-2*		NO INTRONS						
61	*qa-3*		NO INTRONS						
61+63	*qa-4*		NO INTRONS						
61	*qa-x*	S	1)	AAG2GTAAGT	AAGTCCTGACACTGA	10		AAACAG CGC	69
			2)	ATG2GTGCGT	GTTGACTAACAAGAA	19		GCTTAG GGA	74
61	*qa-y*		NO INTRONS						
64	*sod-1*	P	1)	CTG1GTAAGC	TACGGCTAACCTCTT	19		GTCCAG TCG	286
			2)	ACT1GTAAGT	CTAGACTGACCAATG	24		CCGCAG TCA	100
			3)	GGCOGTATGT	TCTTGCTAACTTTTA	11		CAACAG CGC	58
65	*spe-1*	D	1)	ATG1GTGAGT	GTTTGCTGACTTGGA	18		CATCAG CCG	70
66	*T*	D	1)	ATG1GTGACC	TTGTACTAACACAAA	12		ACCCAG GAG	52
			2)	TGT2GTATGT	CGTCGCTGACAAGAA	20		CTGAAG TAA	99
67	*trp-1*		NO INTRONS						
68	*trp-3*	C	1)	AGGOGTGCGT	GCATGCTAACATCAC	18		CAACAG GCC	77
			2)	ACTOGTAAGA	TCTTTCTGACACTTC	19		CTATAG ATT	72
69	*Ubi*	D	1)	CTT1GTAAGT	CGATGCTAACTATCT	13		TCGCAG TGA	68
70	*ucr*	D	1)	AGG1GTGAGT	GACAGCTGACGAGGC	20		ATACAG AGT	323
			2)	AACOCTAAGG	GAATGCTGACCCCGG	14		TTACAG GTC	122
			3)	TTG1GTACGC	GGAGACTGACATTTG	22		AAACAG GCG	101

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Ref.	Gene	Id[a]		5′ signal	Lariat signal	Dist[b]		3′signal	L[c]
71	*vma-1*	D	1)	CCCOGTAAGC	GCCTGCTGACATGGC	15		GAATAG CAA	131
			2)	CCG1GTAAGT	TTATGCTAATAGCTC	9	x	TCGCAG GCA	74
			3)	CGG2GTGCGT	GCTCGCTAACCCATA	14		CCAAAG CCC	65
			4)	TTGOGTATGG	CTGAGCTGAGACTGG	11	x	AATTAG GTT	60
			5)	CGG1GTAAGG	GATGGCTAACCAATC	14		CGATAG CTG	63
			6)	AAGOGTATGT	TAAGGCTAACCATTT	18		CTATAG TAC	80
72	*vma-2*	D	1)	AATOGTTGGT	CATGTCTAACAACGG	11		CCGCAG GTC	56
			2)	GAG1GTGTGT	AACAGCTGACAGCCA	18		CTACAG GAA	71
			3)	CAGOGTAGAT	ATGCGCTGATATCAT	11	x	GAACAG GTC	59
			4)	AAGOGTGAGG	AGAAACTGACCAGGA	12		CAACAG ACC	55
			5)	AGAOGTAAGT	TTGTGCTGACAAGAC	9		ACATAG GAA	58

Key: Ref. - Reference number for publication describing gene sequence, see list in accompanying paper.

a - Introns Identified by, C - computer analysis
D - cDNA sequencing
P - protein synthesis
S - Sl mapping

b - Distance between lariat consensus sequence and splice site of 3' consensus (bp).

c - Length of intron (bp).

x - Introns without a perfect CTNAC sequence within the Lariat consensus

The subscript number in the consensus sequences at the top of the table indicates the % occurrence of the particular nucleotide.

The number present within the 5' signal indicates the splicing position within the codon:

0 - does not cut codon
1 - cuts after 1st nucleotide within codon
2 - cuts after 2nd nucleotide within codon

Table IV Actual number of genes with a given number of introns compared with a Poisson Distribution

Number of introns n present in gene	0	1	2	3	4	5	6	7	8
Genes with n introns									
Expected Poisson Distribution	10	21	21	14	7	2.8	0.9	0.3	0.08
Observed Distribution	14	22	23	5	5	2	2	3	0

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