
A survey on intron and exon lengths

John D.Hawkins

Department of Biochemistry, Medical College of St Bartholomew's Hospital, Charterhouse Square,
London, EC1M 6BQ, UK

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ABSTRACT

The lengths of introns and exons in various parts of genes of vertebrates, insects, plants and fungi are tabulated. Differences between the various groups of organisms are apparent. The results are discussed and support the idea that, generally speaking, introns were present in primitive genomes, though in some cases they may have been inserted into pre-existing genes.

INTRODUCTION

Since their discovery, late in the 1970s (reviewed and discussed by Witkowski (1)) the idea that eukaryotic and some viral protein encoding genes are generally interrupted by non-coding introns has been an intriguing one, and has given rise to speculation and discussion about their origin and existence (e.g. 2-5). Naora & Deacon (6), Blake (4) and Traut (7) collected some information about the lengths of introns and exons, and Senapathy (8) has shown that coding sequences of longer than 600 nt are extremely unlikely to be found among random sequences of nucleotides because of the intervention of stop codons.

I have culled data from the literature on the exon/intron structure of a large number of eukaryotic genes. In making this collection, it has become apparent that there are significant differences in the exon/intron organisation between different phyla, so it seems worthwhile to document them.

METHODS

For this survey, the structure of genes was noted and various elements defined as follows:

- separate 5'-non-coding exons, separated by an intron from the exon containing the codon for the site of initiation of translation (5'-ncex):

- introns wholly within the 5'-non-coding region (5'-in):

- the 5'-untranslated part of the first coding exon, further subdivided according to whether or not there is a preceding untranslated exon (5'-ncexwin) or (5'-ncexnin):

- the coding portion of the first exon (5'-cex):

- internal exons and introns:

- the 3'-coding portion of the last exon (3'-cex):

- the 3'-non-coding part of the last exon, with and without following non-coding exons (3'-win and 3'-nin):

- introns within the 3'-untranslated part of the gene (3'-in):

- separate 3'-exons with no coding information (3'-ncex).

Not all these elements, particularly the first and last and their associated introns, are always present. In many cases the extents of the 5'- and 3'-non-coding elements of the

first and last coding exons have not been accurately established.

Since there seem to be differences in the size and frequency of occurrence of some of these elements in different groups of organisms, they have been separated into four groups – vertebrates, insects (mostly *Drosophila* species), higher plants and fungi. Genes for only a few other invertebrates and protista have been sequenced but they do not form large enough groups to show whether they fall into consistently different patterns from the groups analysed.

Some selection of which genes to include has had to be made to avoid bias. Genes specifying the same protein in different species frequently have the same numbers and sizes of exons (e.g. the α - and β -globin genes). In such cases only one example has been included, but where the sizes of the introns in such genes differ appreciably they have all been included. In the case of gene families, such as the cytochrome-P450 family, I have excluded several members whose gene structures are almost identical, though I have included some where the structure is at least partially different. Such selection is inevitably arbitrary but necessary if a useful picture is to be obtained. Collagen genes possess many exons of the same size – presumably as a result of multiplication of a basic unit – and only one exon of any one size has been included.

A number of genes show considerable heterogeneity in the point at which transcription is commenced. In these cases I have tried to choose the length of the most abundant transcript or, where this is not clear-cut, I have arbitrarily taken the longest transcript.

RESULTS AND DISCUSSION

A summary of the lengths of introns and different kinds of exons is presented in Tables I and II.

Introns (Figs. 1 & 2)

There are marked differences in the distribution of intron size among the various groups of organisms.

Fungi have the shortest introns. In this group I have not included introns in ribosomal

Table I. Average length (nt) and number of introns

	5'-introns	internal introns	3'-introns
Vertebrates	1811 (91)	1127 (1941)	681 (25)
Insecta	5507 (19)	622 (210)	
Fungi		86 (126)	
Plants		249 (200)	

The number of introns examined in each category is shown in brackets.

Table II. Average lengths (nt) and number of exons

	5'-ncex	5'-ncexwin	5'-ncexnin	5'-cex	intex	3'-cex	3'-nin	3'-win	3'-ncex
Vertebrates	94(111)	26(89)	77(193)	134(302)	137(1305)	198(291)	434(291)	39(23)	409(24)
Insecta	312 (18)	68(14)	138 (49)	223 (66)	392 (149)	505 (71)	317 (61)		
Fungi			71 (27)	133 (54)	260 (77)	418 (52)	175 (19)		
Plants			60 (45)	209 (45)	183 (149)	302 (46)	90 (33)		

For abbreviations, see Methods.

The number of exons examined in each category is shown in brackets.

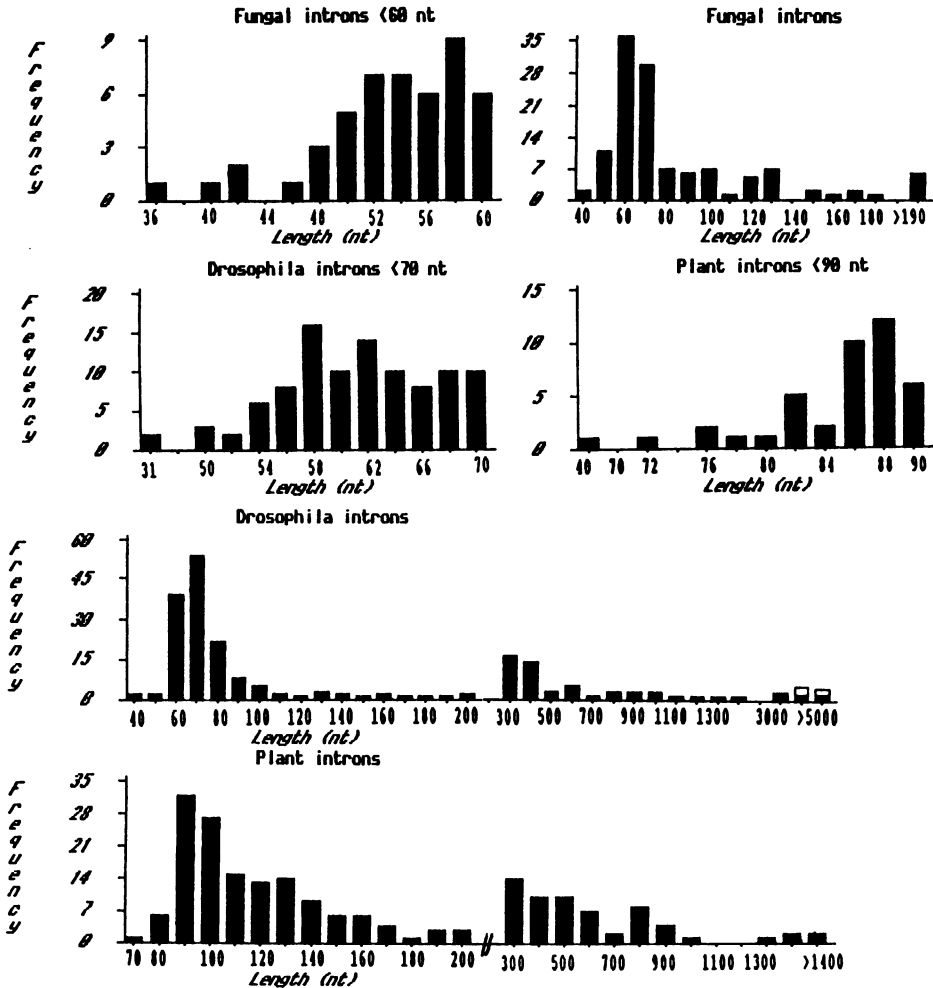


Fig. 1. Lengths of internal introns. The figures on the abscissae are the upper lengths of the bins.

protein genes, since they seem to show a fairly constant pattern which is different from the other fungal genes. Apart from these, the mean length of fungal introns is 85 nt with well over half containing less than 100 nt and none more than 520 nt.

The ribosomal protein genes of *Saccharomyces cerevisiae* that have so far been sequenced display interesting features (Table III). They nearly all have an intron, which is unusual for genes in this species, and these are all relatively long (230–513 nt). There are also two other ribosomal protein genes (in *Candida* and *Dictyostelium*) that have single introns of 356 and 389 nt. In all these genes the intron is near the 5'-end of the coding sequence. Several of the other *Saccharomyces* genes that do possess introns have relatively long ones (actin–309 nt; ubiquitins–367 & 434 nt; CRY-1–305 nt; tubulin–298 nt), but this is not a universal feature of this species.

Insects also have many short introns—again over half are shorter than 100 nt: in fact 80% are between 50 and 75 nt long. There are also a few longer ones of at least 2000 nt.

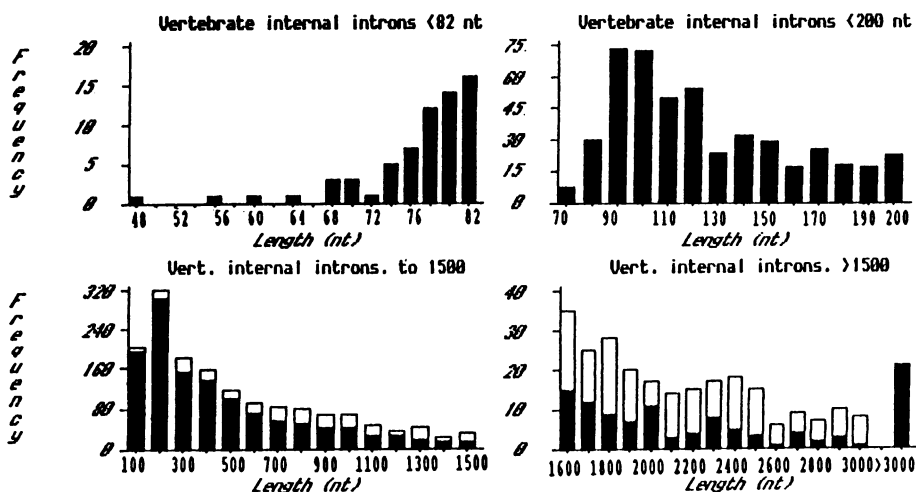


Fig. 2. Lengths of internal introns of vertebrates. The filled bars are of introns whose length is accurately known. The open bars are of introns whose length is only known approximately. The figures on the abscissae are the upper lengths of the bins. There are also 119 introns over 3000 nt long whose length is only known approximately.

As in the case of vertebrates (see below), a number of the longer ones have not been sequenced so their lengths are only known approximately. Including these, the average length is 622 nt.

Higher plants have fewer very short introns, with only a third of 100 nt or less, and none longer than 2000 nt have so far been described. Their mean length is 249 nt.

In contrast, vertebrates have introns with a wide range of lengths, although shorter ones predominate. The largest single size range is 80–99 nt—in this respect like higher plants. The precise lengths of many of the larger vertebrate introns have not been determined accurately, but are only known from measurements of either electron microscope images of mRNA-DNA duplexes or restriction endonuclease fragments separated by electrophoresis. In spite of the uncertainties arising, these estimated lengths must be included since they comprise a very considerable proportion of the longer introns. Taking them into account, 19% (out of 1941) are longer than 1600 nt, and the mean length is 1127 nt.

The shortest recorded intron is 31 nt long (found in the *Drosophila* genes *white* and for the Na^+ channel), so this may be near the minimum length required to include suitable sequences to mark the 5'- and 3'- ends, a site for lariat formation in the splicing reaction, and enough flexibility to take up a suitable conformation for this process. *Drosophila* and fungal genes contain a majority of introns between 50 and 75 nt long, suggesting that they have got down to very near the minimum length required for proper splicing. Bingham *et al.* (9) have recently proposed that, in some cases, longer introns in *Drosophila* may contain sequences that can control their own splicing so as to determine whether or not a particular protein is produced under any given physiological condition. Introns may also contain other elements, such as enhancers (10) which require them to be longer than the minimum length needed for correct splicing.

Introns outside the coding region (Fig. 3)

The vertebrate introns separating exons preceding the coding ones show a tendency to be fairly long. Only 12 out of 91 are less than 200 nt long, and their average length is 1811 nt. Similarly the 5'-introns in insects are longer than the internal ones, though

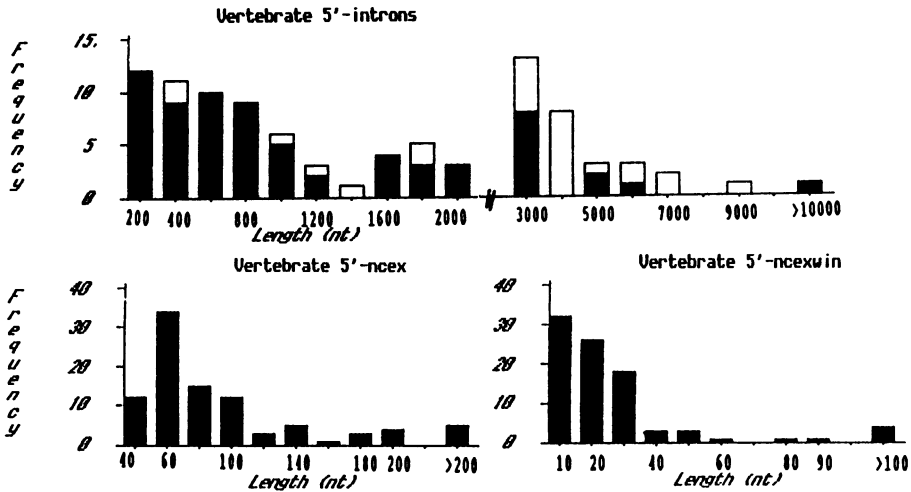


Fig. 3. Lengths of vertebrate introns and exons preceding the coding exons. The filled bars are of introns whose length is accurately known. The open bars are of introns whose length is only known approximately. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last bins are: Introns — 14 257; 5'-ncex — 273, 292, 706, 1121, 1317; 5'-ncexwin — 115, 149, 280, 314. For abbreviations, see Methods.

not to such a great extent, except in the case of the *antennapedia* gene where there are three enormous introns of approximately 25 000, 30 000 and 35 000 nt.

The small number of introns in the 3'-non-coding region of vertebrate genes are of fairly typical length.

Internal exons (Figs. 4 & 5)

The sizes of internal exons vary between the different groups. For vertebrates there is a fairly broad peak in the size distribution between 100 and 170 nt, with a mean length of 137 nt. Only 7 out of 1305 are over 550 nt long—the possible length of a primordial gene, according to Naora *et al.* (5). Quail troponin I contains the shortest exon so far recorded with only 7 nt. The rat troponin T gene is unusual in containing 7 exons shorter than 20 nt out of a total of 15 exons.

Exons of higher plants show a similar size distribution though the peak is less sharp. The mean length is 183 nt, perhaps because there is a slightly higher proportion of longer exons: 2.7% are over 550 nt long. Only 4 are shorter than 50 nt, and three of these (37, 39, 48 nt) are in the Alfalfa gene for glutamine synthetase.

In the fungi the most abundant exons contain less than 100 nt, but there is a large spread and the mean length is 260 nt. 7.8% are more than 550 nt long. This figure does not include the many *Saccharomyces* genes that contain no introns. Short exons are found in some tubulin genes—in *Aspergillus* the β -tubulin genes have exons of 24, 25, 26 and 27 nt, while a *Candida* tubulin gene has one of 36 nt. The *Neurospora* ribosomal protein L-29 gene has a structure completely different from the genes listed in Table III, containing exons of 39, 17, 30, 25, 28 nt.

The length of majority of exons in the insects is in the range of 100–180 nt, but there is an appreciable number of longer ones, with 15% being more than 550 nt long. The mean length in this group is 392 nt. Small exons are rather rare, but *Drosophila* has exons of 28, 32 and 34 nt in the myosin L-chain, protein kinase C and Rh. opsin genes respectively.

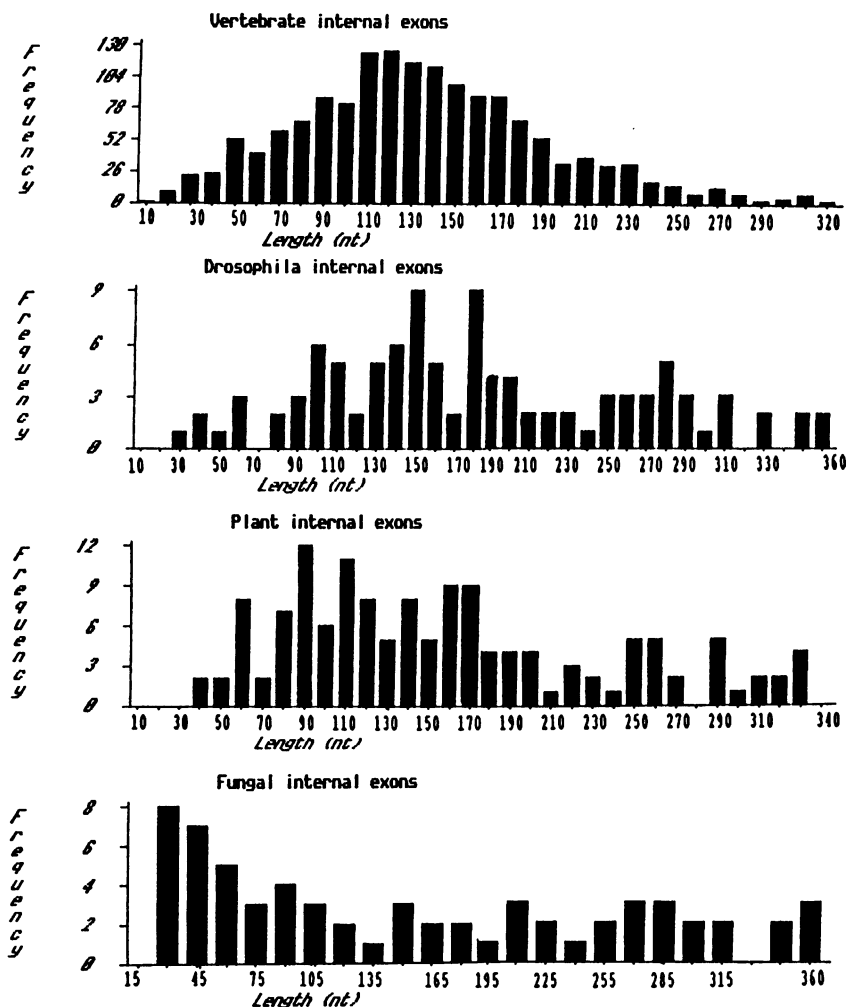


Fig. 4. Lengths of internal exons. The figures on the abscissae are the upper lengths of the bins. Only the shortest exons are shown.

Naora & Deacon (6) have suggested that exons may be grouped into 3 major and 2 minor discrete groups according to length. The analysis of this larger data base (using bins of 10 as against 25 used by Naora & Deacon) suggests that in vertebrates the major peak in the distribution is at 100–120 nt, but there may be shoulders at around 50, 170 and 200–230 nt. In insects there appear to be peaks at 90–110, 140–150 and around 280 nt. In higher plants there are peaks at 80–110, 150–170 and possibly between 240–290 nt. The lengths of fungal exons have a completely different distribution with the greatest number being short—between 17 and 45 nt. However the numbers in these last three groups are rather small so it is premature to draw any definite conclusions.

Intronless genes

It is well known that the majority of genes of *Saccharomyces* have no introns, even though

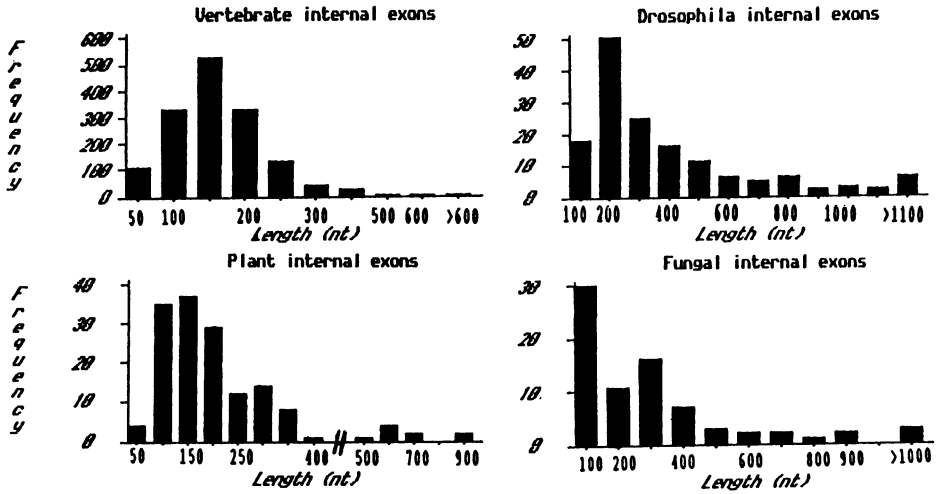


Fig. 5. Lengths of internal exons. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last vertebrate bin are: 690, 961, 1101, 1375, 7572. The long exons in the other graphs are listed in Table IV.

Table III. Fungal ribosomal protein genes

Ribosomal protein	Exons	Introns
S10	5' + 6/705 + 3'	352, 394*
S16A	5' + 20/415 + 3'	390, 551*
L3	5' + 1164 + 3'	none
L16	35 + 525 + 90	none
L25	24 + 13/401 + 80	415
L29	35 + 48/402 + 87	510
L32	58 + 3/315 + 100	230
L34	5' + 57/285 + 3'	349, 421*
L46	5' + 6/450 + 3'	383
rp28	5' + 112/449 + 3'	429, 427*
rp29	38,7 + 468 + 131	458 (5') †
46	35 + 525 + 90	none
rp51	5' + 3/408 + 3'	325, 398*
59	5' + 7/407 + 3'	307
L25	25 + 13/416 + 3'	389
1024	15 + 12/546 + 35	350

*There are two copies of these genes in the genome.

† This intron interrupts the 5'-non-coding portion of the gene. The figures in the exons column are (in order): 5'-non-coding nt; 5'-coding nt; 3'-coding nt; 3'-non-coding nt.

All are genes of *Saccharomyces cerevisiae*, except the last two which are *Candida* and *Dictyostelium* respectively.

their length frequently exceeds 1000 nt. There are some cases of intronless genes in other fungi. In the series presented here 18% of recorded fungal genes have no introns and their coding lengths vary between 312 and 6351 nt. These include the exceptionally long gene of *Dictyostelium* mysoin H chain which has 6351 nt, as well as a miscellaneous collection of other genes.

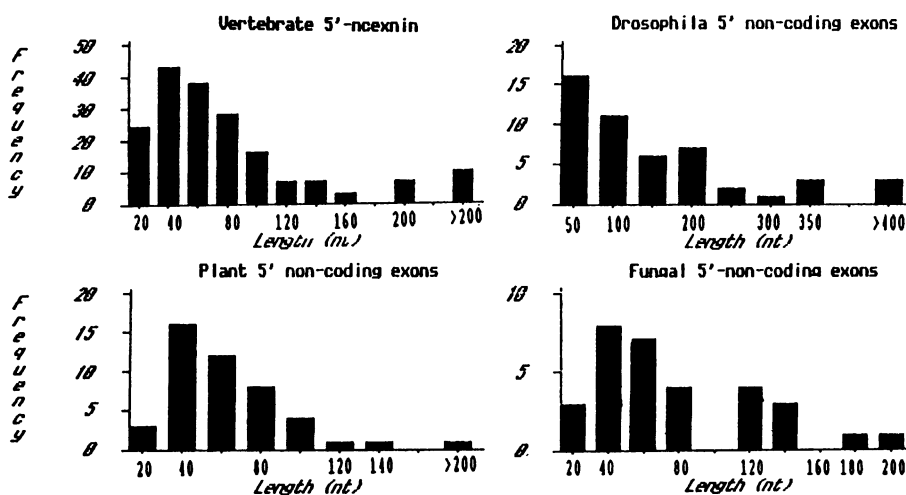


Fig. 6. Lengths of 5'-untranslated parts of 5'-exons. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last bins are: Vertebrates — 212, 220, 238, 333, 337, 526, 684, 843, 1022; *Drosophila* — 460, 489, 798; Plants — 422 nt.

Intronless genes occur with a similar frequency in higher plants (17%) and in insects (19%). Prominent among these are 3 globin genes of *Chiromonas* and 5 heat shock protein genes of *Drosophila*.

Such genes seem to be much rarer in vertebrates where only 13 out of 328 genes display this trait. One is a chicken heat shock protein (which may be homologous to a similar protein in *Drosophila*), and four, with appreciable homology to each other are the genes for the α_2 -, β_1 -, and β_2 -adrenergic receptors and the M1-muscarinic receptor. The coding portions of these genes are all approximately 1300 nt long.

Among the few protistan genes that have been sequenced two thirds (14 out of 21) contain no introns (data not shown).

Histone genes with very rare exceptions have no introns. They encode short proteins and the genes are of such a length that it is unlikely that randomly generated polynucleotides of these lengths would contain termination codons. They are present in multiple copies in the genome, but for the purposes of this survey, I have counted the gene for each type of histone only once.

5'-non-coding exons (Fig. 6)

111 separate 5'-non-coding exons occur in 328 vertebrate genes. Very occasionally there is more than one in a single gene. They tend to be rather smaller than the internal exons. This is interesting because there are no constraints imposed by the necessity not to have in frame termination codons.

They are also found in 18 out of 80 insect genes, and again are shorter than the internal exons.

In both plants and fungi there is so far only a single recorded example of this phenomenon.

5'-untranslated parts of 5'-exons (Figs. 3 & 6)

In all groups the non-coding parts of these exons are on average shorter than the mean lengths of the internal exons, particularly where there is a preceding wholly non-coding

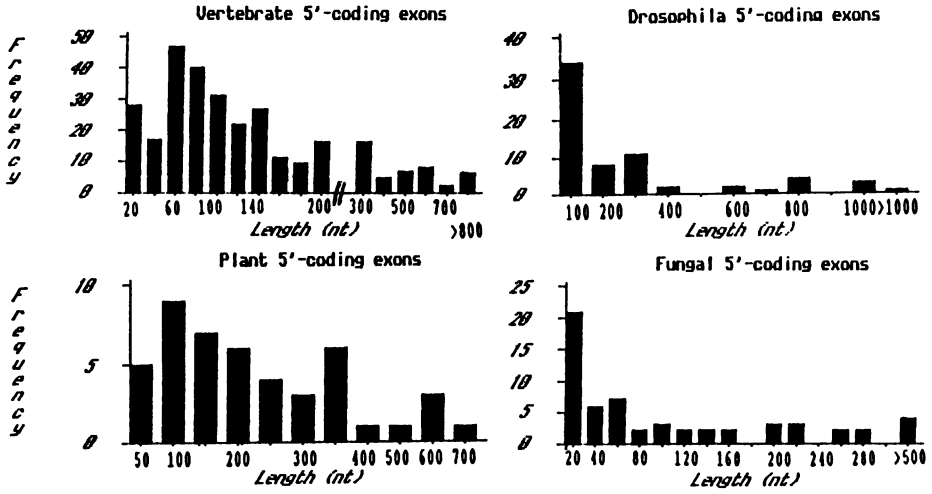


Fig. 7. Lengths of 5'-coding exons. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last bins are: Vertebrates — 828, 829, 831, 837, 1047, 1080; Drosophila — 1312; Fungi — 578, 651, 770, 1224 nt.

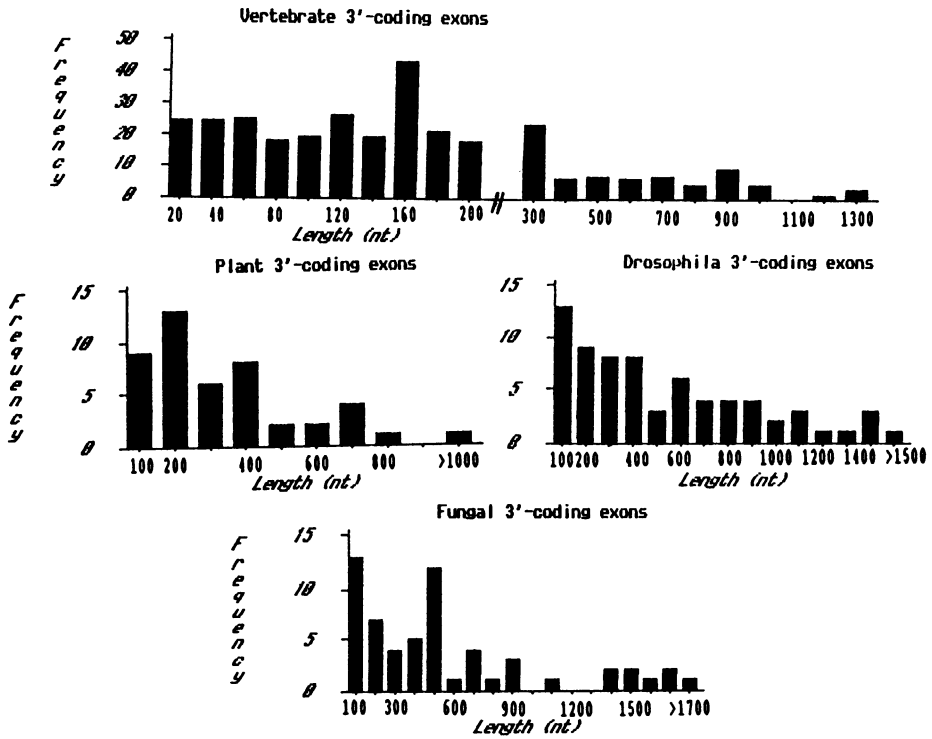


Fig. 8. Lengths of 3'-coding exons. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last bins are: Vertebrates — 1259, 1546, 1802; Drosophila — 2523; Fungi — 2331; Plants — 1732 nt.

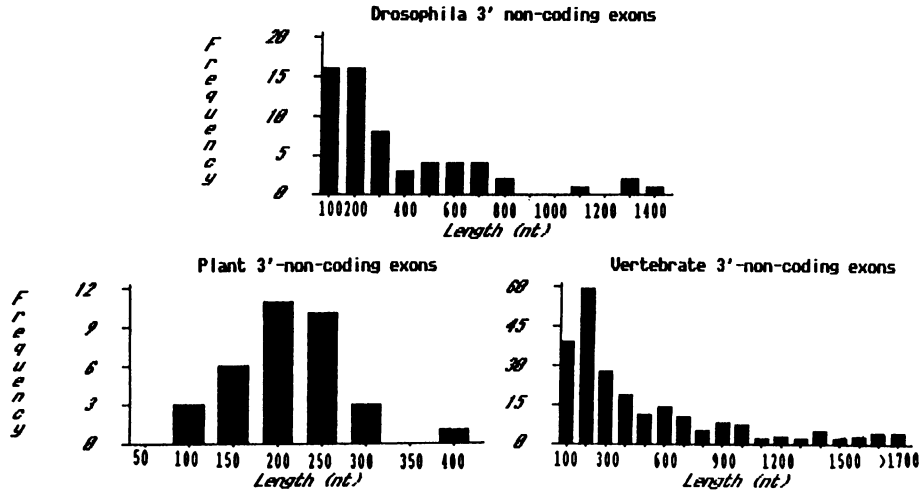


Fig. 9. Lengths of 3'-untranslated parts of 3'-exons. The figures on the abscissae are the upper lengths of the bins. The lengths of the exons in the last bins are: Vertebrates — 1815, 1970, 2413, 2499 nt.

Table IV. Genes with long exons

	5'	internal	3'
VERTEBRATES			
<i>Rat</i>			
angiotensinogen	829		
apo-AIV			1000
cytochrome P-450d	828		
α-fibrinogen			1140
acyl-CoA dehydrogenase			1259
<i>Human</i>			
cytochrome P-450-4	837		
clotting factor VII			1802
clotting factor VIII		3106	
apo-B		7572	
pre-EGF			1062
mid-size neurofilament pr.	1080		1546
elastin	950		
preproenkephalin B			975
<i>Mouse</i>			
Cytochrome-P1-450	837		
68 kD neurofibrillar pr.	1047		
<i>Chicken</i>			
β-tubulin			1061
AcCh receptor		1375, 961	
PLANTS			
<i>Zea hsp 70</i>			
			1733
<i>Hordeum amylase</i>			
		814	
<i>Pisum amylase</i>			
		891	

FUNGI

<i>Neurospora</i> ATPase			2192
ATP/ADP carrier			810
Glu dehydrogenase			1043
<i>Saccharomyces</i> actin			1436
nin 28			896
CDC 17			1615
TUB 1			1319
tubulin		886	
<i>Aspergillus</i> acetamidase			821
aldehyde dehydr.		1202	
<i>Candida</i> β -tubulin			1422
<i>Dictyostelium</i> DG17	1224		
<i>Mucor</i> TEF2		1090	
<i>Drosophila</i>			
yellow			1388
dopa decarboxylase			1350
per	949	824	
yolk protein 1			1100
yolk protein 2			1094
notch		6147	
zest			818
actin	920		
tubulins			1337
			814
eve			990
Rh2 opsin		915	
chorion protein			813
Kruppel			1364
srg			984
I(2)g1		1191	
glued		1304	
tny		1314, 2649	
Na channel		1031	
engrailed	1312		
chaoptin		911	
Gart		1051	1289
abl		1635	
nina c		864, 938	
Draf-1	906		
metallothionein			1011
glucose-6-P dehydrogenase			1075

exon. Again, there are no constraints on the nucleotide sequence except for the requirement for a preferred sequence immediately preceding the initiation codon (11). Perhaps there is a preference for only a short sequence of nucleotides immediately before the initiation codon to ease scanning mechanisms for the correct positioning of the mRNA on the ribosome prior to translation.

5'-coding exons (Fig. 7)

The 5'-coding parts of the first exons in vertebrates and plants are, on average, about the same size as the internal exons. However, their length is rather more variable, with a few as short as only 3 nt, coding just for the initiating methionine residue. There are

a few long ones, some of which clearly belong to protein gene families, such as cytochrome P-450, neurofilament proteins and keratins, so they may be somewhat over-represented in the sample chosen. In insects and fungi the 5'-coding part of the first exon is, on average, shorter than the length of the internal exons, but this may be a consequence of the greater length of the internal exons in these groups.

3'-coding exons (Fig. 8)

On average, these are longer than the internal exons in each group, though there is no obvious explanation for this.

3'-non-coding exons (Fig. 9)

In vertebrates, on average, these are more than twice as long as the 3'-coding exons. There is no obvious reason for this, though perhaps the chance of generating the poly-A addition signal AAATAA from a random sequence is low and therefore not likely to occur within a short distance of the termination codon.

In other groups, the 3'-non-coding exons tend to be shorter than the 3'-coding ones. In the fungi only a small number have been reported.

Separate 3'-non-coding exons

These are rare – only 23 examples have been reported in vertebrates, one in a plant and 3 in insects. The non-coding end of the 3'-coding exon is less than 45 nt in 21 out of these 23 cases and the lengths of the separate 3'-non-coding exons are generally longer than most other vertebrate exons. 9 are longer than 300 nt. A plausible mechanism for their origin is the insertion of a non-coding intron into an already existent long exon.

Long exons (Table IV)

Naora *et al.* (5) have calculated that there is only a very low chance of a random sequence of nucleotides exceeding 550 nt without encountering an in frame termination codon, while Senapathy (8) puts 600 nt as a likely upper limit for the length of exons for the same reason. It may be objected that protein-coding exons are not random sequences of nucleotides, but they must surely have originated from random processes. A small but significant number of exons are over 800 nt in length and some of these may obviously have arisen by chance but this will have been a rare occurrence. A more probable explanation of their origin is their incorporation into the genome following the action of a reverse transcriptase on an mRNA transcribed from a gene that already contained introns.

In vertebrates these long exons occur in only 6% of recorded genes and are commonest in the first and last coding exons. Several of the long exons which form the first coding exon are found in families of genes such as the cytochrome P-450 family and genes coding for structural proteins. In these cases they have probably arisen as a single event and spread through the families concerned during their evolution.

The genes for Factor VIII and lipoprotein apo-B have exceptionally long exons of 3106 and 7572 nt respectively.

In plants there are only 3 exons more than 800 nt long. In insects long exons are more common as 31% of sequenced genes contain them, most frequently in the 3'-coding position or internally. Fungal genes also contain an appreciable proportion of longer exons. They are found in 21% of the sequenced genes, most frequently in the 3'-coding position. These facts, combined with the comparatively large proportion of small introns in these groups (see above), suggest that there may be selective pressure to reduce the sizes of their genomes by removing introns and making those that are left as small as possible.

CONCLUSIONS

This survey confirms the idea that exons are rarely over 800 nt long, except in some organisms—particularly *Saccharomyces*, some other fungi and *Drosophila*. A plausible explanation is that introns were probably present in primitive organisms. New proteins could have arisen by splicing out useless coding information between blocks of coding sequences thereby creating proteins containing more than one domain, each of which might have had distinctive binding or other functions. There is some evidence that certain exons do code for domains with specific functions, but this is by no means a universal rule (4). In some species there may have been pressures to contract the size of the genome so that introns would have been lost. This has been carried to extremes in *Saccharomyces*. *Drosophila* may represent a part way house in this direction. Prokaryotes have gone even further down this road with the virtually complete exclusion of introns from their genomes.

However, there may be some situations in which introns have been inserted into genes. This is the most satisfactory explanation for the presence of introns in the 5'- and 3'-non-coding parts of genes, though it is also possible that exonic sequences around them could have mutated to give sequences which no longer have coding functions.

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APPENDIX

INSECTS

Drosophila melanogaster
 Myosin H chain (part)
 Myosin H chain (part)
 Myosin L chain
 ftz
 Alcohol dehydrogenase
 Alcohol dehydrogenase related
 antennapedia
 yellow
 Dopa decarboxylase
 engrailed
 per
 Tropomyosin
 Amylase
 Yolk protein 1
 Yolk protein 2
 Yolk protein 3
 dunce
 dunce
 Protein kinase C
 Opsin (rtna E)
 Rh2 opsin
 Opsin
 notch
 Ribosomal protein 49
 Ribosomal protein A1
 zeste
 cad
 Actin
 Heat shock proteins (4)
 Heat shock protein
 Heat shock protein
 heat shock protein
 α -tubulins (3)
 β -tubulins (2)
 eve
 Dfd
 Cuticle proteins (3)
 Cuticle protein

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 Kreitman N. 83, 304, 414
 Schaefer G. 87, 117, 61
 Schneuwly EMBO 86, 5, 734
 Geyer EMBO 86, 5, 2657
 Eveleth EMBO 86, 5, 2665
 Kassiss EMBO 86, 5, 3583
 Jackson N. 86, 320, 187
 Basi JBC 86, 261, 829
 Boer NAR 86, 14, 8399
 Hung NAR 81, 9, 6410
 Hung JMB 83, 164, 481
 Yan NAR 87, 15, 67
 Chen P. 86, 83, 9313
 Chen N. 87, 329, 7211
 Rosenthal EMBO 87, 6, 433
 O'Tousa Cell 85, 40, 839
 Cowman Cell 86, 44, 705
 Fryxell EMBO 87, 6, 443
 Kidd MCB 86, 6, 3094
 O'Connell NAR 84, 12, 5495
 Qian NAR 87, 15, 987
 Pirrotta EMBO 87, 6, 791
 Mlodzik Cell 87, 48, 465
 Sanchez JMB 83, 163, 533
 Southgate JMB 83, 165, 35
 Hackett NAR 83, 11, 7016
 Delaney JMB 86, 189, 1
 Paull JMB 88, 200, 47
 Theurkauf P. 86, 83, 8477
 Rudolph MCB 87, 7, 2231
 Frasch EMBO 87, 6, 749
 Reguibti EMBO 87, 6, 767
 Snyder Cell 82, 29, 1047
 Henikoff Cell 86, 44, 33
- Gart, Cuticle protein
 Contractile protein
 P element
 H and L
 dash
 Chorion genes (2)
 kruppel
 white
 srg (3)
 rudimentary
 epi 28/29
 sgs 3,7,8
 sgs 5
 hunchback
 Calmodulin
 I(2)g1
 Dmt-1
 tra
 shaker
 glued
 Metallothioneine
 rosy
 Na⁺ channel
 sup-white apricot
 Cu-Zn O dismutase
 spalt
 chaupin
 mst(3)gl-9
 AcCh receptor
 Ac Ch receptor related
 c-abl
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 Draf-1
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G-CSF	Nagata	EMBO 86, 5, 575	c-H-ras	Ruta	MCB 86, 6, 1706
Interleukin-1 α	Furutani	NAR 86, 14, 3167	Calmodulin	Nojima	JMB 87, 193, 439
Interleukin-1 β	Clark	NAR 86, 14, 7897	Androgen sensitive protein	Delacy	NAR 87, 15, 1631
Interleukin-6	Yasukawa	EMBO 87, 6, 2939	hsc 73	Songer	EMBO 87, 6, 993
Interleukin-5	Campbell	P. 87, 84, 6629	MBP A	Drickamer	JBC 87, 262, 2582
Heat shock protein	Hickey	NAR 86, 14, 4127	Fibrinogen- α	Crabtree	JMB 85, 185, 1
Aldolase B	Tolan	MBM 86, 3, 245	Fibrinogen- γ	Morgan	NAR 87, 15, 2774
Catalase	Quan	NAR 86, 14, 5327	GSH S-transferase	Okuda	JBC 87, 262, 3858
Preproglucagon	White	NAR 86, 14, 4719	Tropomyosin- α	Opazo	JBC 87, 262, 4755
T3	Tunnacliffe	EMBO 86, 5, 1245	Mast cell protease II	Benfey	JBC 87, 262, 5377
Glucose-6-P dehydrogenase	Marim	EMBO 86, 5, 1849	Enoyl-CoA hydratase	Falany	JBC 87, 262, 5924
Osteocalcin	Ceise	EMBO 86, 5, 1885	Neuropeptide Y	Larhammar	P. 87, 84, 2068
Furin	Roebrock	EMBO 86, 5, 2199	Heme oxygenase	Muller	JBC 87, 262, 6795
Factor VIII	Gitschier	N. 84, 312, 328 1	Tropoin T	Breitbar	JMB 86, 188, 313
Factor IX	Yoshitake	BC 85, 24, 3736	Ferritin L-chain	Leibold	JBC 87, 262, 7335
Factor X	Leytus	BC 86, 25, 5098	Acyl-CoA oxidase	Osumi	JBC 87, 262, 8138
Factor XI	Asakai	BC 87, 26, 7221	Parvalbumin	Reichold	JBC 87, 262, 8696
Factor VII	O'Hara	P. 87, 84, 5158	Pyruvate kinase	Cognet	JMB 87, 196, 11
Factor XII	Cool	JBC 87, 262, 13662	MAP-1	Fung	JBC 87, 262, 9298
Prothrombin	Frizner Degen	BC 87, 26, 6165 1	Glycine N-methyl transferase	Okawa	EJB 87, 168, 141
Neuropeptide Y	Mintih	JBC 86, 261, 11974	Ornithine transcarbamylase	Takiguchi	P. 87, 84, 6136
γ -crystallin	Den Dunnen	Gene 85, 38, 197	p9Ka	Barraclough	JMB 87, 198, 13
β -crystallin	Hogg	JBC 86, 261, 14230	Calcium binding protein	Salkin	JBC 87, 262, 1033
Epidermal growth factor	Bell	NAR 86, 14, 3949	Arginase	Perret	EJB 88, 172, 43
Phenylalanine hydroxylase	DiLella	BC 86, 25, 743	Pancreatic polypeptide	Ohtake	JBC 88, 263, 2245
SLP1	Stierl	NAR 86, 14, 7883	GdX	Yonekura	JBC 88, 263, 2990
CANP	Miyake	NAR 86, 14, 8809	Creatine kinase B	Toniolo	P. 88, 85, 851
LCAT	McLean	NAR 86, 14, 9397	Neurotensin	Benfield	Gene 88, 63, 227
Adenosine deaminase	Wiginton	BC 86, 25, 8234	Mouse	Klauskausk	JBC 88, 263, 4963
Myelin proteolipid	Diehl	P. 86, 83, 9807	Hypoxanthine-P-ribosyl-transferase	Holm	EMBO 84, 3, 557
Metallothionein-1F	Varshney	MCB 86, 6, 26	Immunoglobulin-C γ 3	Melton	P. 84, 81, 2147
Ribosomal protein S-14	Rhoads	MCB 86, 6, 2774	Immunoglobulin A-5	Weis	EMBO 84, 3, 2041
Lactalbumin	Hill	JBC 87, 262, 798	Tumour antigen p53	Kudo	EMBO 87, 6, 103
α -fetoprotein	Gibbs	BC 87, 26, 1332	Duodov	Bienz	EMBO 84, 3, 2179
pS2	Jeltsch	NAR 87, 15, 1401	Ribosomal protein L-32	Robov	Cell 84, 37, 457
PNP	Williams	JBC 87, 262, 2332	Myosin L-chain	Madant	Cell 84, 39, 129
Tumour growth factor	Derynck	NAR 87, 15, 3188	Interleukin 3	Miyatake	P. 85, 82, 316
β -hexosaminidase	Proia	JBC 87, 262, 5677	Interleukin 4	Onsaku	NAR 87, 15, 333
β -tubulin	Lewis	JMB 85, 182, 11	H-2D	Sher	P. 85, 82, 1176
Mitosis neurofilament subunit	Myers	EMBO 87, 6, 1617	H-2-T1	Obata	P. 85, 82, 5475
β -adrenergic receptor	Kobikla	JBC 87, 262, 7321	Cytochrome P1-450	Gonzalez	JBC 85, 260, 5040
β -adrenergic receptor	Frielle	P. 87, 84, 7920	Chaplin	P. 86, 83, 9601	
α -adrenergic receptor	Kobikla	S. 87, 238, 650 1	Balcarac	NAR 85, 13, 5527	
M1 ACh receptor	Allard	NAR 87, 15, 10604	Dush	P. 85, 82, 2731	
hsc-71	Dzwonczak	NAR 87, 15, 5181	Fukusawa	G. 87, 116, 99	
Calycin	Ferrari	JBC 87, 262, 8325	Urinary protein	EMBO 85, 4, 3159	
Sialyls amyase	Nishida	Gene 86, 41, 299	Nerve growth factor	EMBO 85, 4, 133	
Thyroglobulin	Parma	JMB 87, 196, 769	H-2 A β -chain	JBC 85, 260, 14111	
Thymidine kinase	Flemington	Gene 87, 52, 267	Ann	JBC 85, 260, 15863	
Phospholipase A2	Seilhamer	DNA 86, 5, 519	Stearman	NAR 86, 14, 797	
Elastin	Indig	P. 87, 84, 5680	Lowell	JBC 86, 261, 8442 1	
Anitrypsin S	Long	BC 84, 23, 4828	Immunoglobulin I chain	Matsuuchi	P. 86, 83, 456 1
Fc receptor	Suter	NAR 87, 15, 7295	Renal kallikrein	JBC 86, 261, 5532	
IF-10	Luster	MCB 87, 7, 3723	Thy-1	Ingraham	J1 86, 136, 1482
ISG-15	Reich	P. 87, 84, 6394	int-2	Moore	EMBO 86, 5, 919
Thrombomodulin	Jackman	P. 87, 84, 6425	Adipocyte P2	Hunt	P. 86, 83, 3786
Tyrosine hydroxylase	O'Malley	BC 87, 26, 6910	pim-1	Selten	Cell 86, 46, 603
Pepsinogen	Sogawa	JBC 83, 258, 5306	C5aH peroxidase	Chambers	EMBO 86, 5, 1221
hst	Hayano	JBC 88, 263, 1382	3-glycero-P dehydrogenase	Phillips	JBC 86, 261, 10821
Complement factor B	Yoshida	P. 87, 84, 7305	3T3 serine protease	idem	JBC 86, 261, 16000
Preproenkephalin B	Campbell	P. 83, 80, 4464	Thymidylate synthetase	McDonald	MCB 86, 6, 842
ERC-1	Molishita	JBC 87, 262, 12508	Erythropoietin	Jaynes	MCB 86, 6, 2855
Medullasin	Horikawa	N. 83, 306, 611	Creatine kinase	Hu	MCB 86, 6, 15
Alkaline phosphatase	Van Duin	NAR 87, 15, 9195	α -actin	Lewis	EMBO 87, 6, 651
Leucocyte common antigen	Millan	NAR 87, 15, 10599	3/10	Gewert	EJB 87, 165, 7
Fatty acid binding protein	Streltin	JEM 87, 166, 1548	G-CSF	Tsuchiya	P. 87, 84, 1609
CD1a	Sweetser	JBC 87, 262, 16060	T49	Koyama	EMBO 87, 6, 1678
Elastase III	Martin	P. 87, 84, 9189	Band 3 protein (erythrocyte)	Koch	NAR 87, 15, 4337
Creatine kinase B	Tani	JBC 88, 263, 1231	Protamine I	Kepito	JBC 87, 262, 8035
Rar	Daouk	JBC 88, 263, 2442	L-myc	Pos	P. 87, 84, 5316
Lactalbumin	Qasba	N. 84, 308, 377	Glutamate-oxaloacetate TA	Legoux	EMBO 87, 6, 3359
Somatostatin	Moniminy	P. 84, 81, 3337	Urinary plasminogen activator	Tsuzuki	JMB 87, 198, 21
Angiotensinogen	Tanaka	JBC 84, 259, 8063	Nucleolin	Frizner Degen	BC 87, 26, 8270
Myosin L-chain	Nadel	NAR 84, 12, 7175	Multifinger mK α 2	Bourbon	JMB 88, 200, 627
Myosin H-chain	Periasamy	JBC 84, 259, 13595	Chicken	Chowdhury	EMBO 88, 7, 1345
Embryonic myosin H-chain	Periasamy	JBC 85, 260, 15856	Ovalbumin	Woo	BC 81, 20, 6437
Trypsin	Craik	JBC 84, 259, 14255	Cycloheximide c	Limbach	NAR 83, 11, 8931
Chymotrypsin	Bell	JBC 84, 259, 14265	Myosin L-chain	Nabeshima	N. 84, 308, 333
Elastase	Swift	JBC 84, 259, 14271	Myosin H-chain	Molina	JBC 87, 262, 6478
Luteinising hormone β -chain	Jameson	JBC 84, 259, 15474	Thymidylate kinase	Kwak	NAR 84, 12, 3963
Growth hormone releasing factor	Mayo	N. 85, 314, 464	Ac Ch receptor- γ - δ	Nef	P. 84, 81, 7975
Atrial natriuretic factor	Argentin	JBC 85, 260, 4568	α -actin	Nef	EMBO 88, 7, 595
Myosin L-chain	Sagawa	JBC 85, 260, 5026	Glyceraldehyde-P dehydrogenase	So	P. 85, 82, 1628
Cytochrome P-450d	Suwa	JBC 85, 260, 7980	α -crystallin I	Ohn	NAR 85, 13, 1593
Cytochrome P-450b	Ueno	JBC 88, 263, 4956	α -crystallin	Thompson	Gene 87, 56, 173
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Cholestyramin	Reinke	JBC 85, 260, 4397	α -aminolvalinate synthetase	Maguire	NAR 86, 14, 1376
α 1 acidic glycoprotein	Jones	JBC 85, 260, 7042	α -actin (cardiac)	Eldridge	Gene 85, 36, 55
β -casein	Beale	JBC 85, 260, 10748	β -actin (smooth muscle)	Carroll	JBC 86, 261, 8965
PEP carboxylase	Laurent	JBC 85, 260, 11476	β 5-tubulin	Sullivan	MCB 86, 6, 4409
Retinol binding protein	Demmer	JBC 87, 262, 2453	β 3-tubulin	Sullivan	JBC 86, 261, 13317
Retinol binding protein	Leung	JBC 85, 260, 12523	α -tubulin	Pratt	EMBO 88, 7, 931
Asialoglycoprotein receptor	Sweetser	JBC 86, 261, 5553	Carbonic anhydrase II	Yoshihara	NAR 87, 15, 753
Fatty acid binding protein	den Dunnen	P. 86, 83, 2857	N-CAM	Owens	P. 87, 84, 294
β -crystallin	Cohen	NAR 86, 14, 3641	Ferritin H-chain	Wilkins	MCB 87, 7, 1751
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Vitellogenin	Gerber Huber	NAR 87, 15, 4737
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α -globin (larval)	Knochel	NAR 88, 16, 1625
Flounder Anti-freeze protein	Davies	JBC 84, 259, 9241
Guinea pig Insulin	Chan	P, 84, 81, 5046
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Only the first-named author is given.

Abbreviations for journals: P. Proc. Natl. Acad. Sci.; NAR Nucleic Acids Res.

EJB Europ. J. Biochem.; JBC J. Biol. Chem.; S. Science; N. Nature;

MGG Mol. Gen. Genetics; CG Curr. Genetics; MCB Mol. Cell Biol.

BC Biochemistry; PP Plant Physiol.; G. Genetics; BJ Biochem J.

JB J. Bact.; MBM. Mol. Biol. & Med.; IG Immunogenetics; RPHR Recent Progr.

Hormone Res.

Since no sequences were published before the twentieth century, the dates of all references omit the first two figures.