**Elovl1 and p55Cdc Genes Are Localized in a Tail-to-Tail Array and Are Co-expressed in Proliferating Cells***

Abolfazl Asadi, Johanna Jörgensen, and Anders Jacobsson

From the Wenner-Gren Institute, The Arhenius Laboratories F3, Stockholm University, SE-106 91 Stockholm, Sweden

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*Elovl1* is a ubiquitously expressed gene, the product of which belongs to a highly conserved family of microsomal enzymes, which are involved in the formation of very long chain fatty acids and sphingolipids in yeast to man. To elucidate the structure and regulation of the *Elovl1* gene we have isolated a lambda phage genomic DNA clone containing the entire mouse gene and found that *Elovl1* consists of eight exons that are dispersed over 5.4 kb of genomic sequence. Interestingly, sequencing of the lambda clone to completion revealed that the insert contained a segment of the cell cycle gene *p55Cdc* directed in the opposite orientation. The genes are very tightly linked so that the 3′-end of the long mRNA species are complementary over a short stretch of nucleotides. Although both *Elovl1* and *p55Cdc* are highly conserved genes, a BLAST search implies that the tail-to-tail arrangement has evolved in vertebrates. Despite the non-similar expression pattern in different tissues, mRNA analysis of the two genes disclosed simultaneous transcription during a proliferation-differentiation transition state, which suggests that the two genes may be regulated through a common bi-directional transcription mechanism under specific conditions.

Very long chain fatty acids (VLCPs) have been recognized as structural components in a variety of fat molecules such as glycerophospholipids, sphingolipids, and wax- and sterol esters. Depending on their chain length and degree of unsaturation, they contribute to the fluidity and other physical and chemical properties of the membrane. VLCPs are found in virtually all cells and are major constituents of the brain, skin and testes. For example, the brain contains high amounts of VLCPAs consisting of 24 or more carbons, which are required for normal brain myelination (1). VLCPs are also needed in the synthesis of ceramides, which are necessary for the formation of other components of the perimembrane layer of the skin. The ceramides, together with free VLCPAs, comprise more than 50% of the fatty acids found in the epidermis, the outermost layer of the skin, which is the highest amount present in any mammalian tissue (2).

Synthesis of VLCPs is performed in the endoplasmic reticulum and in mitochondria by membrane-bound enzymes; the former is more prominent (3). *Elovl1* (4) is a highly conserved gene that shows extensive sequence identity to the earlier identified gene *Elovl3* (5, 6). Both are members of a recently identified mammalian gene family whose products have been shown to be involved in the formation of VLCPAs and sphingolipids (4, 7–13).

*Elovl1* is expressed in all tissues tested and the enzyme is believed to elongate very long fatty acids up to C₉₀ (4). Especially high levels of expression are found in stomach, lung, kidney, skin, and intestine (4), which suggests that *ELOVL1* may be important for developing a proper barrier in epithelial cells and skin. In addition, *ELOVL1* has also been suggested to be a crucial enzyme involved in the formation of myelin in the central nervous system in mouse (4).

Although the *Elovl1* mRNA sequence has been identified, very little is known about the genetic nature of mammalian fatty acid chain elongation enzymes. To scrutinize the genomic background and regulation of *Elovl1* in greater detail we have isolated a lambda phage genomic DNA clone containing the entire mouse *Elovl1* gene. Surprisingly, we found that the *Elovl1* gene is linked to the gene coding for the cell cycle protein *p55Cdc* (14) in a bi-directional manner. Despite the fact that both genes are very tightly linked and expressed in all cell types at some point, our findings indicate a complex co-regulation during the cell cycle. Even more surprising is that a similar tail-to-tail arrangement was also found for the *Elovl3* gene and the homeobox gene *Pitx3* (6). It is therefore intriguing that two closely related genes from the same gene family are both juxtaposed with two completely unrelated genes in a tail-to-tail arrangement.

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**MATERIALS AND METHODS**

**Mouse Elovl1 Genomic Cloning—**Genomic clones of *Elovl1* were isolated by plaque hybridization of a commercial mouse 129 strain liver genomic DNA library in the Lambda FIX II vector (Stratagene, cat. no. 946308) with a 32P-labeled probe corresponding to 0.92 kb from the 5′-end of the *Elovl1* cDNA (GenBank™ accession no. AF170907). Hybridization was carried out overnight at 45 °C in 50% formamide, 5× SSC, 5× Denhardt’s solution, 50 mM sodium phosphate, pH 6.5, 0.5% SDS, and 100 μg/ml degraded herring sperm DNA. The membranes were first washed twice for 15 min at room temperature in 2× SSC, 0.1% SDS, and a high stringency wash was then performed at 55 °C in 0.1× SSC, 0.1% SDS for 15–30 min. Screening of ~1.5 × 10⁶ plaques yielded one positive recombinant, which was isolated by two additional rounds of plaque purification. Phage DNA was prepared on a large scale by the polyethylene glycol precipitation method according to Ref. 15. Restriction fragments generated by various combinations of restriction enzymes were analyzed by Southern blotting.

**Mouse p55Cdc cDNA Cloning—**For sequencing of a full-length mouse *p55Cdc* cDNA, we combined the sequences from three EST clones (accession nos. AI327152, AA497914, and AA537091) obtained from the

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† To whom correspondence should be addressed: The Wenner-Gren Institute, The Arhenius Laboratories F3, Stockholm University, SE-106 91 Stockholm, Sweden. Tel.: 46-8-164127; Fax: 46-8-156756; E-mail: anders.jacobsson@wgi.su.se.

‡ The abbreviations used are: VLCPAs, very long chain fatty acids; EST, expressed sequence tag; RT, reverse transcription; ORF, open reading frame; PAM, pre-adipocyte medium; nt, nucleotides.
FIG. 1. Schematic representation of the Elovl1 and p55Cdc loci. A, exon/intron structure and orientation of Elovl1 and p55Cdc. Exons are numbered and indicated by boxes on the transcribed DNA strand. Protein-coding regions within the mouse genomic sequence are solid, 5’ and 3’ untranslated regions are hatched and correspond to the Elovl1 and p55Cdc mRNA sequence (previously published by us (4) and in this paper, respectively) (GenBank™ accession nos. AF170907 and AF312208). Polyadenylation signal consensus sequences (pA) are marked by small vertical arrows. Numbers above the sketch refer to nucleotide positions in GenBank™ accession no. AF322919 of the mouse genomic sequence. One EST cDNA fragment (GenBank™ accession no. AA718173/BM445297) corresponding to the 3’-end of mouse Elovl1 mRNA is positioned according to its homology with the genomic sequence. The hatched intron sequence and the solid white exons within the p55Cdc gene correspond to data obtained from the rat gene (14) (GenBank™ accession no. AF652689). B, PCR analysis of 3’ Elovl1/p55Cdc genomic mouse DNA. Genomic DNA (gDNA; 1.5 μg) was amplified with mouse sequence-specific primers as described under “Materials and Methods” and shown in A. M, 1-kb Plus DNA Ladder molecular weight marker (Invitrogen).
of an extra 5′-exon. Furthermore, we have not been able to retrieve any EST sequence containing the extra 41 bp. This difference is presumably due to a cloning artifact of the mouse cDNA because the human gene (GenBankTM accession no. AL139289) also lacks the corresponding sequence. The translation initiation codon (ATG) is located in the second exon, and the protein coding sequence stretches into the eighth exon. The proximal promoter sequence does not contain a TATA-box consensus site. Instead, there are several short interspersed GC-rich elements in the close vicinity of the transcription start site. The polyadenylation signal earlier described by Tvrdik et al. (4) is located within the eighth exon at 5064–5070 bp.

**Elovl1 Is a Single Copy Gene**—To verify if Elovl1 is a single copy gene we performed a Southern blot analysis of mouse DNA. As shown in Fig. 2, following digestion with *Bgl* I, *Sac* I, and *Xba* I, the mouse Elovl1 ORF probe only strongly hybridized to genomic fragments that were of the predicted size, suggesting that Elovl1 is a single copy gene in the mouse genome.

**Elovl1 Is Tightly Linked to p55Cdc**—Sequencing of the untranscribed flanking regions of the Elovl1 gene revealed that the cloned insert contained part of yet another gene closely linked to the 3′-end of the Elovl1 gene. A BLAST search identified the sequence as corresponding to the cell cycle gene p55Cdc (Fig. 1A) (14). p55Cdc is a mammalian homolog of a family of cell cycle proteins from widely divergent species that has been implicated in cell cycle-regulated ubiquitin–mediated proteolysis (22–25). The p55Cdc gene consists of 10 exons and has been analyzed in detail in rat (GenBank™ accession no. AF-052695) (14) (Fig. 1A) but not in mouse or man. Our lambda genomic clone covers the last 688 nucleotides of the p55Cdc gene including the last exon and intron and part of exon number 9. The sequence identity between the published genomic rat p55Cdc and the sequence we have determined from our genomic clone is 86% over a total region of 1189 nucleotides.

To confirm the Elovl1/p55Cdc organization in mouse we ran a PCR with mouse genomic DNA as a template. An expected fragment of ~2200 bp was obtained with primers complementary to a sequence within exon 8 of Elovl1 and within the mouse p55Cdc mRNA corresponding to a sequence within exon 8 ~1900 bp into the p55Cdc gene (see below and under “Materials and Methods”) (Fig. 1, A and B). Sequence analysis of the DNA fragment confirmed the nucleotide identity as mouse Elovl1/p55Cdc.

Although both Elovl1 and p55Cdc are highly conserved genes, a BLAST search suggests that the tail-to-tail arrangement has evolved in vertebrates (Table II). Linkage data from the WICGR Mouse RH Gene Map Release Data suggests that this region of human chromosome 1 has its equivalence on mouse chromosome 4.

### Identification of Full-length Mouse p55Cdc cDNA Sequence

The mRNA for p55Cdc has been sequenced for rat and human (23) but not for mouse. To confirm the p55Cdc sequence, we compared the genomic p55Cdc sequence from mouse to the EST data base and found several highly similar nucleotide sequences. Three clones (accession nos. AL27152, AA497914, and AA537091) were acquired from the I.M.A.G.E. Consortium. The full-length cDNA sequence was obtained by

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**Table I**

Exon/intron boundary sequences of the mouse Elovl1 gene

| Exon | Exon size (bp) | Location in cDNA | Splice donor | Intron size (bp) | Splice acceptor |
|------|----------------|------------------|--------------|-----------------|----------------|
| 1    | 75             | 1-75             | TTCCACTG/gttagt | 2285            | tcctag/AGTCTCTTAG |
| 2    | 60             | 76-135           | GCATGCGGG/gttaagc HA D(16) | 159 | tcacag/ATCCCCCAGG |
| 3    | 191            | 136-326          | TCTATGAG/gttagc Y E(29) | 156 | tcctag/TTTCTGTAG |
| 4    | 81             | 327-407          | CACTTCCGG/gttag L R(50) | 123 | ctcacag/AGGGTCGA |
| 5    | 57             | 408-464          | TGGACACA/gttag D T(125) | 83 | ccccgag/GTGATATT |
| 6    | 106            | 465-570          | TGCTCCAG/gttag A P G(161) | 77 | atctagag/GAGGAATG |
| 7    | 137            | 571-707          | TTCAGCTG/gttagg Q L(260) | 162 | atccag/ATCCAGTT |

**FIG. 2. Detection of the Elovl1 gene in mouse genomic DNA.** Southern blot analysis was performed with 10 µg/lane of mouse genomic DNA digested with the indicated restriction enzymes: B, BglI; S, SacI; X, XbaI. The blot was hybridized to the Elovl1 ORF probe and washed as described under “Materials and Methods.”
The chromosomal arrangement of the Elovl1 and p55Cdc genes is indicated as tail-to-tail or as separate based on genomic sequences obtained by us (this paper) or through BLAST search. The genomic sequences are indicated as accession numbers.

| Organism       | Arrangement     | Chromosome | Accession number       |
|----------------|-----------------|------------|------------------------|
| H. sapiens     | tail-to-tail     | I          | AL139299               |
| M. musculus    | tail-to-tail     | Not mapped | AF329219 (this paper)  |
| R. norvegicus  | tail-to-tail     | Not mapped | AF052695               |
| D. melanogaster| separate         | 3R/2L      | AE0037729/AAA83150     |
| C. elegans     | separate         | III/II     | Z47358/CAA87433        |
| S. cerevisiae  | separate         | XII/VII    | CAA55129/CAA96703      |

sequencing the overlap of these three clones and a 735-bp RT-PCR product covering the 3'-end of p55Cdc mRNA. The nucleotide sequence is shown in Fig. 3.

Sequence identity between the cDNA sequence and the sequence we determined from our genomic clone was 100% over a total region of 243 nucleotides. The sequence identity between the published rat cDNA p55Cdc and the mouse cDNA was 91%.

Overlapping 3'-Ends of a Long Elovl1 and p55Cdc mRNA Species—Elovl1 and p55Cdc are oriented in a tail-to-tail manner in a remarkably tight linkage. In fact, there exists a submitted EST sequence from the WashU-HHMI Mouse EST Project with accession number AA718173 corresponding to an Elovl1 mRNA from mammary gland that appears to overlap the transcribed p55Cdc mRNA with 16 nucleotides. We acquired the clone and verified the complete nucleotide sequence versus our genomic clone over a total region of 560 nucleotides. From our sequence data, we were able to identify 37 additional nucleotides, which were complementary to exon 10 of the p55Cdc gene, as well as a 50-bp-long pol(y)A tail (GenBank™ accession no. BM445297). These results show that there is a total overlap of 53 nucleotides in the two transcripts (Figs. 1A and 4C). Because we have not detected more than one mRNA species on our Northern blots (see Fig. 6), this is probably not a major cleavage site of Elovl1 transcription.

To confirm the presence of overlapping mRNA species in different tissues, we performed RT-PCR on total RNA from brown adipose tissue, kidney, heart, and lung with primers corresponding to the 3'-untranslated region of the long Elovl1 mRNA from mammary gland (GenBank™ accession no. AA718173). As shown in Fig. 5A, we amplified the anticipated 307 bp product (primers from nt 5075 to 5094 and nt 5363 to 5382 in the genomic clone) in brown adipose tissue, kidney, heart, and lung, confirming that such Elovl1 transcripts exist that overlap p55Cdc by 53 bp (Fig. 4C). In contrast, we were unable to amplify a specific fragment within the same tissues with primers specific for p55Cdc (primers from nt 516 to 535 and nt 1234 to 1253 in the cDNA clone) (Fig. 5B).

Contrasting Expression of Elovl1 and p55Cdc in Different Mouse Tissues—The ELOVL1 protein is involved in the formation of membrane lipids and earlier results revealed that Elovl1 was ubiquitousity expressed (4). The p55Cdc is highly expressed in proliferating but not in differentiated or growth-arrested cells (24).

To verify the Elovl1 and p55Cdc expression, we first compared the mRNA levels within different tissues. As seen in Fig. 6, the expression pattern in different tissues was dissimilar for the two genes. In agreement with our earlier results, the Elovl1 expression was diversified in different mouse tissues, with the highest steady-state mRNA levels in stomach, lung, kidney, skin, intestine, and some specific brain tissues, whereas white fat, liver, spleen, brown fat, heart, and muscle showed moderate Elovl1 expression. Only a very weak Elovl1 mRNA signal was found in the testis.

In contrast, the highest level of p55Cdc mRNA was found in testis, whereas spleen and intestine showed moderate expression. Low or undetectable amounts of p55Cdc mRNA were obtained from fat tissue, liver, brain, lung, stomach, muscle tissue, and skin.

Elovl1 and p55Cdc Expression Is Affected in a Similar Way During Differentiation of HIB-1B Cells—To see if the pattern of mRNA levels for the two genes was synchronously affected during cell growth, we analyzed the expression pattern in a brown fat cell line, HIB-1B, during a proliferative stage and when cells were induced to differentiate. These cells, which are derived from a brown fat hibernoma, are known to differentiate in culture when they reach confluence and are subsequently exposed to a differentiation medium (18). During the preconfluent stage, the cells showed the highest level of expression of both genes (Fig. 7). After confluence, the cells showed decreased levels of both Elovl1 and p55Cdc mRNA with time, even if the culture medium was not changed to differentiation medium. This indicates that, although the genes were shown to be independently regulated in a tissue-specific manner, during a specific phase of development, certain cells may have a synchronized expression of Elovl1 and p55Cdc mRNA.

**DISCUSSION**

Elovl1 is a highly conserved gene and a member of a recently recognized mammalian gene family whose products have been indicated as being involved in the formation of very long chain fatty acids and sphingolipids (4).

We have isolated here a lambda phage genomic DNA clone containing the entire mouse Elovl1 gene. Although the length of the gene, as well as the transcript, is relatively similar to the closely related gene Elovl3, the exon-intron structure is markedly different (8 exons versus 4 exons) (6). Because the encoded polypeptides are very similar both in size and sequence, there is no obvious explanation for these structural differences.

Surprisingly, sequencing of the lambda clone revealed that the insert contained the 3' part of the newly identified cell cycle gene p55Cdc (14) in the opposite orientation. The genes are very tightly linked, so the 3'-ends of their long mRNA species are complementary over a short stretch of nucleotides.

Despite the fact that overlapping genes are rare events in eukaryotes (26–28), a similar tail-to-tail arrangement was also found for the Elovl1 gene and the homeobox gene Pitz3 (6). Except for homologous genes that may have arisen by gene duplication, adjacent genes are normally separated by tens to hundreds of kilobases within the mammalian genome. It is therefore intriguing that two closely related genes from the same gene family are both juxtaposed with two completely unrelated genes within an 8–9-kb stretch in a tail-to-tail arrangement.

The ELOVL1 protein has been identified as a fatty acid elongase, which elongs VLCFAs up to 26 carbon atoms (4). Under normal circumstances, a substantial amount of VLCFA is linked to a long chain sphingoid base sphinganine, forming a ceramic, which constitutes the lipid backbone of sphingomyelin and other sphingolipids. Sphingolipids are essential for cell proliferation. Impaired sphingolipid synthesis leads to cessation of cell growth both in yeast (29) and mammalian cells (30). Concomitantly, p55Cdc is the mammalian homolog to the cell cycle protein CDC20p in yeast (22, 23) and the Fizzy protein in Drosophila (31) and is required for the metaphase-anaphase transition (32). EST sequences corresponding to both mRNAs can be found as early as in the fertilized egg during mouse development. It is therefore probable that the two genes are
expressed during the proliferative phase in any cell type. Obviously, overlapping genes in opposite orientation generate transcripts that could form RNA duplexes if present in the same cell. In particular, several recent reports show that short stretches of double-stranded RNA molecules may serve as a template for specific RNA nuclease activity leading to gene

**FIG. 3.** Nucleotide sequences of p55Cdc cDNA. Indirect amino acid sequences of the corresponding p55Cdc polypeptide were shown below the open reading frame. Polyadenylation signal consensus sequence is underlined. Sequence data have been deposited under the GenBank™ accession no. AF312208.
silencing (33–35). Because both Elovl1 and p55Cdc genes exhibit a rather ubiquitous tissue expression pattern at some point, we can therefore not exclude this possibility that a short tail-to-tail sense-antisense structure may serve as a template for specific RNA nuclease activity leading to gene silencing.

Interestingly, there is an identical 9-bp element, CTCAAAAGA, within the 3′-untranslated region of each gene, 124 and 126 bp, respectively, downstream from the sites where the poly(A) tails are added onto each of the genes. We searched the data base for factors that could recognize this element but no such finding occurred.

The promoter of the p55Cdc gene has been analyzed in rat and contains several cell cycle regulatory motifs, which are known to repress constitutive transcription during G0 and early G1 phases of the cell cycle (14). In our study, we show that Elovl1 and p55Cdc have a distinct tissue-specific expression. However, in synchronized brown fat cells, we found that the expression of both genes was high during the proliferative phase and decreased upon differentiation of the cells. This is in agreement with p55Cdc being strictly expressed during mitosis. Notably, although Elovl1 is ubiquitously expressed, its expression is also decreased during differentiation of the cells. This may indicate that both genes are under a common regulator(s) during the cell cycle. One could speculate that there are common constitutive factors that keep the Elovl1-p55Cdc locus in a transcriptionally open position but only during a prolifer-

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**Figure 4.** Nucleotide sequence alignment of one Elovl1 EST clone obtained from mammary gland with genomic DNA (GenBank™ accession no. AF322919) and 3′-end of p55Cdc cDNA. A, 3′-end cDNA sequences corresponding to primary mRNA species cleaved immediately downstream of the polyadenylation signal (AAUAAA) in Elovl1 (AF170907). B, cDNA sequences corresponding to overlapping transcripts and predicted polyadenylation signal for the long Elovl1 transcript obtained from mammary gland (GenBank™ accession no. BM445297). AF312208, p55Cdc cDNA GenBank™ accession no.

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**Figure 5.** PCR analysis of 3′ Elovl1 mRNA (A) and p55Cdc mRNA (B) expression in mouse tissues. DNase-treated total RNA (1.5 µg) was reverse-transcribed and amplified. Lane 1, brown fat; lane 2, kidney; lane 3, heart; lane 4, liver; lane 5, p55Cdc cDNA. M, 1-kb Plus DNA Ladder molecular weight marker (Invitrogen).

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**Figure 6.** Elovl1 and p55Cdc mRNA levels in mouse tissues. Northern blot analyses were performed with 10 µg of total RNA isolated from the tissues indicated. BAT, 4 °C refers to RNA isolated from the brown adipose tissue of a mouse exposed to 4 °C for 3 days. All other RNA samples were isolated from animals kept at thermoneutral temperature (28 °C). WAT, white adipose tissue; SK MUSCLE, skeletal muscle. The membranes were probed with 32P-labeled cDNA fragments corresponding to open reading frames of Elovl1 and p55Cdc, respectively and subsequently exposed to DuPont Cronex x-ray films for up to 1 week. The position of the ribosomal 18 S RNA is indicated on the right.

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**Figure 7.** Elovl1 and p55Cdc mRNA levels in cultured HIB-1B cells. Northern blot analyses were performed with 10 µg of total RNA isolated from cells cultured in pre-adipocyte medium (PAM) until confluence (PAM, 0), after confluence for 2 days in pre-adipocyte medium (PAM, 2), or for 2 or 3 days in adipocyte medium (AM, 2 and 3).

The promoter of the p55Cdc gene has been analyzed in rat and contains several cell cycle regulatory motifs, which are known to repress constitutive transcription during G0 and early G1 phases of the cell cycle (14). In our study, we show that Elovl1 and p55Cdc have a distinct tissue-specific expression. However, in synchronized brown fat cells, we found that the expression of both genes was high during the proliferative phase and decreased upon differentiation of the cells. This is in agreement with p55Cdc being strictly expressed during mitosis. Notably, although Elovl1 is ubiquitously expressed, its expression is also decreased during differentiation of the cells. This may indicate that both genes are under a common regulator(s) during the cell cycle. One could speculate that there are common constitutive factors that keep the Elovl1-p55Cdc locus in a transcriptionally open position but only during a prolifer-
ative phase, and in addition to this there are specific cell cycle factors that apply a specific restriction on the p55Cdc gene. However, an understanding of the mechanism of action of this interesting gene interaction must await further knowledge about interacting factors within the Elovl1 gene.

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Abolfazl Asadi, Johanna Jörgensen and Anders Jacobsson

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