The Isolation and Characterization of cDNA Encoding the Mouse Bifunctional ATP Sulfurylase-Adenosine 5'-Phosphosulfate Kinase*

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Biosynthesis of the activated sulfate donor, adenosine 3'-phosphate 5'-phosphosulfate, involves the sequential action of two enzyme activities: ATP sulfurylase, which catalyzes the formation of adenosine 5'-phosphosulfate (APS) from ATP and free sulfate, and APS kinase, which subsequently phosphorylates APS to produce adenosine 3'-phosphate 5'-phosphosulfate. Oligonucleotide primers were derived from a human infant brain-expressed sequence tag putatively encoding a portion of APS kinase. Using these primers, reverse transcriptase-polymerase chain reaction was performed on mRNA from neonatal mouse brain, yielding a 2.2-kb clone. Primers were designed from the 5'-end of the 2.2-kb clone, and 5'-rapid amplification of cDNA ends was used to obtain the translation start site. Sequence from the overlapping clones was assembled into a 2475-bp composite sequence, which contains a single open reading frame that translates into a 624-deduced amino acid sequence. Northern blots of total RNA from neonatal mice yielded a single message species at approximately 3.3 kb. Southern blots of genomic DNA digested with several restriction enzymes suggested the gene is present as a single copy. Comparison against sequence data bases suggested the composite sequence was a fused sulfurylase-kinase product, since the deduced amino acid sequence showed extensive homology to known separate sequences of both ATP sulfurylase and APS kinase from several sources. The first 199 amino acids corresponded to APS kinase sequence, followed by 37 distinct amino acids, which did not match any known sequence, followed by 388 amino acids that are highly homologous to known ATP sulfurylase sequences. Finally, recombinant enzyme expressed in COS-1 cells exhibited both ATP sulfurylase and APS kinase activity.

Sulfate activation involves the transfer of a sulfate group to ATP by ATP sulfurylase (ATP sulfamate adenyltransferase, EC 2.7.7.4) to yield adenosine 5'-phosphosulfate (APS) and pyrophosphate. Subsequently, APS kinase (ATP adenosine-5'-phosphosulfate 3'-phosphotransferase, EC 2.7.1.25) transfers a phosphate group from ATP to APS to yield ADP and adenosine 3'-phosphate 5'-phosphosulfate (PAPS). Since the equilibrium for the ATP sulfurylase reaction is rather unfavorable (K_{eq} = 10^{-9}) in the physiologic direction, APS kinase plays an important role by continually removing APS, thus driving the overall sulfate activation pathway in the forward direction. Moreover, APS itself is structurally unstable and is subject to spontaneous degradation under physiologic conditions. PAPS is the sole source of sulfate for sulfate esters in mammals, and APS appears to be only an intermediate in the sulfate-activating pathway.

The purification of ATP sulfurylase and APS kinase from a single species has been reported for the fungus Penicillium chrysogenum (1, 2) and Escherichia coli (3, 4). ATP-sulfurylase has been purified from a number of lower organisms (5-8), usually varies between 42 and 67 kDa, and may form oligomers. In addition to fungi and bacteria, APS-kinase has been isolated from Chlamydomonas reinhardii (9); most kinases of these lower organisms are small (21-44 kDa) and often form dimers. Although ATP sulfurylase has been previously cloned in Saccharomyces cerevisiae (10), E. coli (11), Arabidopsis thaliana (12), Rhizobium meliloti (13), P. chrysogenum (14), and Riftia pachyptila (15), and although APS kinase has been cloned in E. coli (16) and R. meliloti (17), neither enzyme has been cloned from a mammalian source.

We have had a long-standing interest in the sulfate-activating pathway since characterizing the unique defect in the brachymorphic mouse, which affects both ATP sulfurylase and APS kinase (18, 19). Attempts to purify these two enzyme activities from rat chondrosarcoma showed that they copurified over 2000-fold, suggesting that the activities are inseparable (20). Recent studies have demonstrated that rat chondrosarcoma ATP sulfurylase and APS kinase reside on a single bifunctional enzyme (21), which uses a channeling mechanism to efficiently synthesize PAPS (22). Most recently, we demonstrated that the defect in the brachymorphic mouse results from a mutation that primarily alters the function of the novel coupling mechanism between the two active sites (23). Therefore, we have directed our efforts toward cloning and sequencing this unique enzyme to further understand the channeling function and eventually elucidate the brachymorphic defect. Here, we report the isolation of a 2475-bp cDNA from Mus musculus, which yields a 624-deduced amino acid sequence encoding both ATP sulfurylase and APS kinase activities.

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1The abbreviations used are: APS, adenosine 5'-phosphosulfate; bp, base pair; kb, kilobase; RT, reverse transcription; PCR, polymerase chain reaction.
EXPERIMENTAL PROCEDURES

Materials—Common reagents were high grade commercial products. Restriction endonucleases, with the exception of SaeI, were purchased from New England Biochemicals. SaeI, T4 DNA ligase, and Taq polymerase were obtained from Promega. The T7 DNA polymerase sequencing kit was purchased from U.S. Biochemical Corp. Primer-it II random hexamer labeling kit and phosphoecitride were synthesized on an Applied Biosystems 380B DNA synthesizer. Radionucleotides were purchased from DuPont NEN. Oligonucleotides were synthesized on an Applied Biosystems 380B DNA synthesizer. An 18-day-old mouse brain cDNA library was from ATCC, RNA or DNA was routinely obtained from neonatal (day 0–2) C57Bl mouse brain.

DNA Isolation and Analysis—The techniques used for screening cDNA libraries, isolation of plasmid DNA, manipulation of DNA fragments, and transformation of E. coli were as described by Sambrook et al. (24). Mouse genomic DNA was isolated and analyzed by typical DNA blot analysis (24). Approximately 20 μg of genomic DNA from neonatal mice was digested overnight with BamHI, EcoRI, HindIII, KpnI, PstI, SacI, and XhoI. DNA fragments were resolved on an agarose gel and blotted onto a nylon membrane via capillary action. The blot was prehybridized in 5 × SSPE, 5 × Denhardt’s reagent, 50% formamide, and 200 μg/ml salmon sperm DNA at 42°C for 2 h and hybridized with the 32P-labeled 127-bp or the 2.2-kb clone for 12–16 h at 42°C followed by three 1-h washes in 0.1% SDS and 0.5 × SSC at 52°C. DNA sequencing was performed by the dideoxynucleotide chain termination method (24, 25).

5′ Rapid Amplification of cDNA Ends—5′-rapid amplification of cDNA ends was performed according to the protocol provided by Life Technologies, Inc. Briefly, two antisense primers were designed that were the anchor sequence of clone SK9-1 and were synthesized. The primers were SK2 (5′-TTCGAGGACGGCGGAGGTTGAC-3′) and SK3 (5′-TGATCTGTCCTTGCGGAGTTGTT-3′). First strand cDNA was synthesized from 1 μg of neonatal mouse brain total RNA, using the SK2 primer, and RNA was removed with RNase H and cDNA purified by GlassMAX Spin cartridge. The first cDNA strand was subsequently excised using KpnI and sequenced. Primers and conditions for reverse transcription of 2 μg of mRNA from neonatal C57Bl mice, and the isolated 127-base pair fragment was subcloned into phoecitride KS+ and sequenced. When compared to sequence data bases by BLAST searches, the 127-base pair sequence was seen to be 85% identical to the human cDNA sequence from which the RT-PCR primers were derived and to predict a peptide sequence having 58–76% identity to various APS kinase peptide sequences. The insert was subsequently excised using KpnI and SacI, run on a 1% low melting agarose gel, purified, and radiolabeled with 32P via the random hexamer labeling technique.

This probe was then used to screen approximately 500,000 recombinants of an 18-day-old mouse brain cDNA library (31) as was used as a source sequence for two primers US and DS, which included KpnI and SacI sites, respectively. These primers were used for reverse transcription of 2 μg of mRNA from neonatal C57Bl mice, and the isolated 127-base pair fragment was subcloned into phoecitride KS+ and sequenced. When compared to sequence data bases by BLAST searches, the 127-base pair sequence was seen to be 85% identical to the human cDNA sequence from which the RT-PCR primers were derived and to predict a peptide sequence having 58–76% identity to various APS kinase peptide sequences. The insert was subsequently excised using KpnI and SacI, run on a 1% low melting agarose gel, purified, and radiolabeled with 32P via the random hexamer labeling technique.

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Sequence Comparison among Species—When compared against the non-redundant combined set of SWISS-PROT, PDB, PIR, and GenPept data bases, the deduced amino acid sequence shows extensive homology to known separate sequences of both ATP sulfurylases and APS kinases from several sources. Pairwise GAP alignments of the kinase (residues 1–220) or sulfurylase (220–624) portions of the mouse amino acid sequence to individual APS kinase or ATP sulfurylase sequences from other species revealed homologies to both enzyme types. The APS kinases (listed in descending order of their similarity to mouse) include the putative human APS kinase (partial sequence, 97% identity and similarity), *S. cerevisiae* MET14 (55% identity, 71% similarity), *E. coli* CysC (51%, 68%), *A. thaliana* APS kinase (47%, 67%), *R. meliloti* NodQ (44%, 64%), and *Azospirillum brasilense* NodQ (45%, 62%). Overall, the kinase peptide sequences appear well conserved from bacteria to the mouse. The ATP sulfurylases exhibited a wider range of relatedness to the mouse sequence, i.e. from strong similarities in the plant proteins from *A. thaliana* (57% identity, 75% similarity) and *Solanum tuberosum* (58%/74%), through the fungal/yeast enzymes *P. chrysogenum* Aps (26%, 51%) and *S. cerevisiae* MET3 (24%, 46%), to the low correspondence observed against the bacterial peptide sequences of *E. coli* CysD (20%, 46%), *E. coli* CysN (16%, 44%), *R. meliloti* NodP (16%, 45%), and *A. brasilense* NodP (19%, 44%).

The Wisconsin Package program COMPARE was used for pairwise comparisons between the putative sulfurylase-kinase sequence and each of the known individual sulfurylase and kinase sequences from several sources, both to localize the kinase and sulfurylase domains and to check for the presence of repeating elements or internal rearrangements. The results were displayed with the program DOTPLOT, and outcomes of pairwise comparisons with *Arabidopsis* and *Saccharomyces* sequences are shown in Fig. 2. Each plotted point represents a register of alignment and window location at which 15 of 30 residues in the window matched; identical or very similar colinear sequences result in a single diagonal line with a slope of 1. Repeats occurring in both sequences produce pairs of shorter diagonals paralleling the main register line, and a gap in one sequence of a pair is seen as a break or displacement of the main line. The APS-kinase comparisons (Fig. 2, A and C) reveal the greatest amount of colinear similarity across species, as represented by the dominant diagonal line. The ATP sulfurylase comparisons show more variability among species, with greater similarity to *Arabidopsis* than to *Saccharomyces* (Fig. 2, B and D).

A multiple alignment of the mouse sequence and representative APS kinases and ATP sulfurylases was done to examine the detail of the molecules' similarities (Fig. 3). Based on those alignments, we postulate that the first 199 amino acids (nucleotides 34–630) correspond to APS kinase activity. This region became aware of a recent entry in GenBank, UUNPASY (accession no. L39001), an as yet unpublished combined ATP-sulfurylase-APS-kinase coding sequence from the worm *Urechis caupo*. Comparison via GAP reveals high overall relatedness (70% identity, 83% similarity) to the mouse amino acid sequence.

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3 *A. brasilense* NodP and NodQ sequences were translations from the GenBank entry AZSNODPQ (accession no. M94886), *R. meliloti* NodP was from RHMNODPQA (M68858), and *E. coli* CysD and CysN were from ECOCCYSNDC (M74586). The remaining amino acid sequences were obtained as described in the legend for Fig. 2.

4 While performing the sequence analyses for this manuscript, we became aware of a recent entry in GenBank, UUNPASY (accession no. L39001), an as yet unpublished combined ATP-sulfurylase-APS-kinase coding sequence from the worm *Urechis caupo*. Comparison via GAP reveals high overall relatedness (70% identity, 83% similarity) to the mouse amino acid sequence.
is followed by a 37-amino acid stretch (nucleotides 631–742), which is not similar to either ATP sulfurylase or APS kinase. Subsequent amino acids from 237 to 624 (nucleotides 743-1905) are highly homologous to sequences with known ATP sulfurylase activity. As mentioned, the region that correlates closely to an ATP-GTP binding motif (P-loop) and the FISP sequence are identified only in the putative APS-kinase sequence and are also flanked by several highly conserved cysteine residues, as previously reported in

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**Northern Blotting**—The cDNA insert from the jagI clones was labeled with ³²P and used as a probe in Northern blotting (Fig. 4). Both the 127-bp fragment (data not shown) and the 2.2-kb clone recognize a single message species of approximately 3.3 kb in neonatal mouse brain (Fig. 4, lane 1). The size of the transcript indicates that the composite cDNA clone lacks approximately 0.8 kb of 5' or 3' untranslated region. The presence of intact RNA was confirmed by hybridization with a ³²P-labeled glyceraldehyde-3-phosphate dehydrogenase probe (Fig. 4, lane 2).

**Southern Blotting**—To assess the sulfurylase-kinase gene copy number, Southern blot analysis was performed. Genomic DNA digested with several restriction enzymes and probed with the 127-bp fragment reveals a simple pattern having only a single band in each of several restriction digests (Fig. 5). These results suggest there is a single functional gene for this sulfurylase-kinase and therefore provides no evidence for multiple genes or pseudo genes.

**Heterologous Expression of Sulfurylase-Kinase**—A DNA construct in the pSVL vector (see “Experimental Procedures”) that contains a version of sulfurylase-kinase sequence was expressed in COS-1 cells. This construct lacks the first 21 amino acids of the mouse sequence and was used to transfect COS-1 cells as described in the figure. The expression of the fusion protein was analyzed by Western blotting using an antibody raised against the S. cerevisiae APS-kinase (Fig. 6). The fusion protein was detected at the predicted size of 58 kDa, confirming the identity of the expressed protein.

**Fig. 2. Comparison of A. thaliana, S. cerevisiae, and M. musculus ATP sulfurylase and APS kinase deduced amino acid sequences.** Dot-matrix comparison of the deduced amino acid sequence of mouse ATP sulfurylase-APS kinase against A. thaliana APS kinase (A), A. thaliana ATP sulfurylase (B), S. cerevisiae APS-kinase (C), and S. cerevisiae ATP sulfurylase (D) sequences obtained using the Wisconsin package programs COMPARE (window = 30, stringency = 15) and DOTPLOT. The A. thaliana APS kinase, A. thaliana ATP sulfurylase, S. cerevisiae APS kinase, and S. cerevisiae ATP sulfurylase sequences are translations of the GenBank DNA sequences with accession numbers U05238, U05218, S55315, and X60157, respectively.
acid of the predicted protein, initiating the coding sequence at the second methionine. Cell lysates expressing this construct were found to contain both ATP sulfurylase and ATP kinase activities (Fig. 6), when assayed for individualsulfurylase (28), kinase (29), or the overall reaction (22). Extracts from COS-1 cells that were not transfected, transfected with expressing vector only, or transfected with vector containing the construct in the opposite orientation exhibited base-line activity (Fig. 6). In contrast, cells transfected with the construct in the correct orientation contained high levels of both ATP sulfurylase and ATP kinase activities (Fig. 6).

**Fig. 3. Alignment of various ATP sulfurylase and APS kinase sequences from several species.** A, schematic diagram of APS-kinase and ATP-sulfurylase domains identified by protein analysis. P-loop motif (*), PAPS-dependent enzyme motif (**), and PP-motif (***). B, the peptide sequences aligned to the mouse sulfurylase-kinase sequence were obtained by translation of the following GenBank entries with data base accession numbers of the sequences in parentheses: Rmel-nodQ (M68858), Eco-cysC (M74586), Sac-kin (555315), Athal-kin (U05238), HumEST-kin (T09181), Sub-sulf (U05218), Pchry-sulf (U07353), and Scer-sulf (X60157). Kinase and sulfurylase sequences were separately aligned to the mouse sulfurylase-kinase (shaded) sequence using the program PILEUP. The two groups of sequences were then merged with the program LINEUP using the PRETTY output option. Invariant residues are boxed; proposed functional domains are designated (*) and defined in the text.

**Fig. 4. Northern blot analysis of ATP sulfurylase APS kinase RNA.** 30 μg of total RNA from neonatal mouse brain was loaded on a 1% agarose gel. The blot was hybridized with a 32P-labeled 2.2-kb probe to yield a single message species at approximately 3.3 kb (lane 1). A control, the same blot was stripped and hybridized with a mouse glyceraldehyde-3-phosphate dehydrogenase cDNA probe (lane 2). The location of RNA size markers (in kb) is shown on the left. Autoradiograph was exposed for 5 days; prolonged exposure did not reveal any additional message species.

**Fig. 5. Southern blot of mouse genomic DNA.** Two different isolations of mouse genomic DNAs were digested with the indicated restriction endonucleases. 15 μg of DNA were loaded in each lane and electrophoresed on 1% agarose gel. The probe was the 127-bp fragment used to screen the cDNA library. Size markers are indicated on the right.
We have now isolated overlapping cDNA fragments whose composite sequence is postulated to encode a fused sulfurylase-kinase product based on the following criteria. The encoded protein derives from a single reading frame and exhibits a molecular weight commensurate with that previously obtained for the native bifunctional enzyme (21); when compared to protein sequence data bases, the deduced amino acid sequence shows extensive homology to separate sequences of both ATP sulfurylases and APS kinases from several sources; the expressed recombinant protein catalyzed the synthesis of both APS (ATP sulfurylase activity) and PAPS (APS kinase activity) as well as overall activity (i.e. synthesizing PAPS from ATP and SO$_4^{2-}$). Furthermore, the mouse sulfurylase-kinase sequence contains highly conserved residues, which are found in all ATP sulfurylases that have been sequenced, and are postulated to be involved in MgATP and SO$_4^{2-}$ binding (14). There are also invariant Lys and Arg residues, often a part of a homologous sequence, across all six APS kinases that have been sequenced, including now the mouse sulfurylase-kinase. In addition, the kinase domain exhibits a region that correlates closely to a ATP-GTP binding motif (P-loop), as might be expected for a phosphate binding protein (33). The sequence (GXXGXXGT(TT)) is identical to the pattern in thymidine kinase (39) and to the octapeptide signature (GESGAGKT) in myosin heavy chain (40). A PAPS-dependent enzyme motif (KAXAGXXXFTG) (34, 35) is also present in the N-terminal APS-kinase portion. A sequence resembling a portion of the recently proposed ATP pyrophosphatase PP motif (36), found in several ATP sulfurylases as well as PAPS reductase, was also found in the mouse brain sulfurylase-kinase sequence.

Although all these data strongly suggest that the fused mammalian sulfurylase-kinase is related to similar activities previously isolated and cloned from lower organisms, the gene organization found in E. coli and P. chrysogenum differs significantly from the organization of the product we have isolated. Our sequence shows strong homology in the N-terminal domain to known APS kinases and strong homology in the C-terminal domain to known ATP sulfurylases. This is the opposite orientation from the fungal ATP sulfurylase, which has 75% of APS kinase at its C-terminal sequence. In addition to resulting in interspecies structural differences, this reverse orientation (as well as the fact that most of the sulfurylases and kinases are clearly separate gene products) may contribute to significant mechanistic differences. Rat chondrosarcoma sulfurylase-kinase releases PP$_i$ followed by APS, with concomitant binding of the APS to the APS kinase active site, while P. chrysogenum sulfurylase releases APS first followed by PP$_i$. The former specific order of product release and substrate addition may result in a more efficient pathway via substrate channeling of the APS intermediate, as we have demonstrated occurs in the rat chondrosarcoma enzyme system (22). In contrast, APS bound to the ATP sulfurylase does not serve as a substrate for the APS kinase of P. chrysogenum (39), suggesting a different mechanism pertains for the fungal ATP sulfurylase fused with a partial APS kinase sequence.

The combined ATP sulfurylase-APS kinase described in this paper may represent an evolutionary trend toward a more efficient sulfate activation pathway in higher organisms. Although procaryotes can achieve coordinate expression of consecutive reactions through linkage of different polypeptides in a single operon, eucaryotic coordinate expression is more often realized by linking multiple functions in a single polypeptide. Bazan et al. (41) have proposed that certain bifunctional enzymes such as 6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase represent the gene fusion of catalytic units. The newly cloned mouse brain bifunctional sulfurylase-kinase may have
followed such a combinatorial process to maintain stoichiometry of the two activities and to achieve the maximal functional efficiency necessary for optimal PAPS production.

The cloning of sulfurylase-kinase will allow its role in the PAPS activation pathway to be studied further in higher organisms. Homology of the single open reading frame-generated PAPS activation pathway to be studied further in higher organisms. Homology of the single open reading frame-generated PAPS activation pathway to be studied further in higher organisms.

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