## Phylogeny

ALPK1 is a member of the atypical alpha-kinase (α-kinase) family, which is classified within the ‘Atypical’ kinase group of the human kinome (manning2002theproteinkinase pages 1-2, ko2022systematicreviewof pages 1-2). The alpha-kinase family, which includes six members in humans, possesses a catalytic domain with structural homology to myosin heavy chain kinases (MHCKs) from *Dictyostelium discoideum* but shares little sequence similarity with conventional protein kinases (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitrokinase pages 1-2). The family is found only in eukaryotes and is considered to be of recent evolutionary origin (garciaweber2023invitroalpk1kinase pages 1-5, middelbeek2010thealphakinasefamily pages 1-2).

ALPK1 orthologs are conserved across many species (williams2019alpk1missensepathogenic pages 2-3, manning2002theproteinkinase pages 2-3). The residue Thr237, for example, is conserved in numerous mammalian orthologs, including those from *Pongo abelii* (orangutan), *Pan troglodytes* (chimpanzee), *Macaca mulatta* (rhesus macaque), *Equus caballus* (horse), *Canis familiaris* (dog), *Bos taurus* (cow), *Mus musculus* (mouse), and *Rattus norvegicus* (rat) (williams2019alpk1missensepathogenic pages 2-3).

## Reaction Catalyzed

ATP + a protein → ADP + a phosphoprotein (garciaweber2023invitroalpk1kinase pages 1-5, snelling2024discoveryandfunctional pages 5-6).

## Cofactor Requirements

Catalytic activity requires the Mg²⁺ cofactor (garciaweber2023invitrokinase pages 11-12, garciaweber2023invitrokinase pages 12-13).

## Substrate Specificity

A consensus substrate specificity motif for ALPK1 was not reported in the atlas of the human serine/threonine kinome by Johnson et al., 2023 (johnson2023anatlasof pages 2-3, johnson2023anatlasof pages 9-10, johnson2023anatlasof pages 12-18).

ALPK1 is a serine/threonine kinase that phosphorylates substrates on threonine residues (garciaweber2023invitroalpk1kinase pages 1-5). It specifically phosphorylates the adaptor protein TIFA primarily at threonine 9 (T9) and to a lesser extent at T2, T12, and T19 (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitrokinase pages 1-2). It exhibits substrate selectivity, as demonstrated by its inability to phosphorylate the generic kinase substrate myelin basic protein (MBP) (garciaweber2023invitroalpk1kinase pages 10-13, garciaweber2023invitrokinase pages 4-4). The alpha-kinase family often recognizes and phosphorylates substrates within alpha-helical regions (ko2022systematicreviewof pages 1-2, middelbeek2010thealphakinasefamily pages 2-3).

## Structure

ALPK1 is a 139 kDa protein composed of an N-terminal alpha-helical domain (NTD), an unstructured linker, and a C-terminal alpha-kinase catalytic domain (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitrokinase pages 1-2). The NTD (residues 1-473) serves as the allosteric binding site for ADP-heptose (ADPH) (snelling2023alpk1mutantscausing pages 6-6).

The crystal structure of the human ALPK1 NTD (PDB: 5z2c) shows it contains 18 alpha-helices organized into seven antiparallel pairs that form a right-hand solenoid, creating a concave pocket for ADPH binding (garciaweber2023invitroalpk1kinase pages 1-5, snelling2024discoveryandfunctional pages 6-7). Key residues for ADPH binding in the NTD include Arg150, which forms electrostatic interactions with the phosphate groups, and Thr237, which forms a hydrogen bond with the sugar moiety (snelling2024discoveryandfunctional pages 5-6, snelling2023alpk1mutantscausing pages 6-6). The kinase domain contains Lys1067, a residue critical for ATP binding and catalytic function (snelling2024discoveryandfunctional pages 5-6).

By homology to other alpha-kinases like ChaK1 and TRPM7, the kinase domain of ALPK1 is inferred to have several unique structural features (drennan2004alphakinasesanalysisof pages 10-13, middelbeek2010thealphakinasefamily pages 7-8). The **C-helix** is elongated compared to that of conventional kinases, contributing to active site organization and structural stability (drennan2004alphakinasesanalysisof pages 10-13). The **activation loop**, corresponding to the catalytic loop, is significantly shortened and described as a kink rather than a loop, though it preserves the orientation of key catalytic residues (drennan2004alphakinasesanalysisof pages 13-16). The **hydrophobic spine** is composed of conserved hydrophobic residues with some substitutions that differ from conventional kinase motifs, forming a pocket for adenine binding (drennan2004alphakinasesanalysisof pages 13-16).

## Regulation

ALPK1 activity is regulated allosterically by the binding of pathogen-associated metabolites to its NTD (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitroalpk1kinase pages 10-13). The primary activator is ADP-L-glycero-β-D-manno-heptose (ADPH), which upon binding induces a conformational change that exposes the previously occluded catalytic cleft (garciaweber2023invitroalpk1kinase pages 1-5). Other human and mammalian nucleotide sugars, including UDP-α-d-mannose, can also serve as activating ligands (snelling2024discoveryandfunctional pages 5-6, snelling2023alpk1mutantscausing pages 6-6).

ALPK1 undergoes autophosphorylation as a post-translational modification upon ADPH recognition, which is required for full catalytic activation (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitroalpk1kinase pages 13-17). This autophosphorylation event is dependent on its own kinase activity and occurs independently of the presence of its substrate, TIFA (garciaweber2023invitroalpk1kinase pages 10-13, garciaweber2023invitrokinase pages 4-4).

## Function

ALPK1 is expressed in multiple human tissues, including the macula retina, retinal pigment epithelium (RPE)/choroid, optic nerve, and spleen (williams2019alpk1missensepathogenic pages 3-4). It is also expressed in primary fibroblasts, ARPE19 retinal epithelial cells, human monocytes, and kidney cells (williams2019alpk1missensepathogenic pages 3-4, ko2022systematicreviewof pages 5-7). Cellularly, ALPK1 protein localizes to centrosomes, spindle poles, and primary cilia, including the basal body of photoreceptor cilia (williams2019alpk1missensepathogenic pages 7-7). Its expression is downregulated in lung and colorectal cancers compared to adjacent normal tissues (liao2016downregulatedandcommonly pages 1-2).

As an intracellular pathogen recognition receptor (PRR), ALPK1 detects ADP-heptose from Gram-negative bacteria such as *Shigella flexneri* and *Helicobacter pylori* (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitrokinase pages 1-2). Activated ALPK1 phosphorylates the adaptor protein TIFA, which is its primary downstream substrate (garciaweber2023invitroalpk1kinase pages 1-5). Phosphorylated TIFA oligomerizes into a complex called the TIFAsome, which recruits TRAF6 and activates the NF-κB and AP-1 signaling pathways, leading to the expression of pro-inflammatory genes (garciaweber2023invitroalpk1kinase pages 1-5, snelling2024discoveryandfunctional pages 4-5). ALPK1 also phosphorylates non-muscle myosin IIA, which modulates the trafficking of TNF-α during monosodium urate (MSU)-induced inflammation in gout (garciaweber2023invitroalpk1kinase pages 1-5, lee2016alpk1phosphorylatesmyosin pages 4-5).

## Other Comments

Mutations in the *ALPK1* gene are associated with inflammatory diseases and cancers (garciaweber2023invitroalpk1kinase pages 1-5). These conditions include ROSAH syndrome (Retinal dystrophy, Optic nerve atrophy, Splenomegaly, Anhrosis, and Hellux valgus), spiradenoma, spiradenocarcinoma, gout, recurrent periodic fevers like PFAPA syndrome, and chronic kidney disease (garciaweber2023invitroalpk1kinase pages 1-5, garciaweber2023invitrokinase pages 2-4, williams2019alpk1missensepathogenic pages 2-3, sangiorgi2019raremissensevariants pages 8-8).

Specific disease-associated mutations and their functional effects include: - **T237M**: Associated with ROSAH syndrome, this mutation within the ADPH-binding site results in increased basal kinase activity and constitutive TIFAsome formation (garciaweber2023invitroalpk1kinase pages 1-5, snelling2023alpk1mutantscausing pages 6-6). - **V1092A**: Linked to spiradenoma and spiradenocarcinoma, this mutation resides in the kinase domain and leads to enhanced kinase activity upon ADPH stimulation (garciaweber2023invitroalpk1kinase pages 1-5). - **S277F**: Identified in ROSAH syndrome, this variant causes constitutive activation of NF-κB/AP-1-dependent transcription, independent of the ADPH ligand (snelling2024discoveryandfunctional pages 4-5).

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