## Phylogeny

According to the kinome classification by Manning et al., LIMK2 is assigned to the Tyrosine Kinase-Like (TKL) group, the LISK family, and the LIMK subfamily (manning2002theproteinkinase pages 3-3, shah2023limk2amultifaceted pages 1-3, shah2023limk2amultifaceted pages 13-16). Other studies have placed LIMK2 within the STE, CaMK, or AGC kinase groups (vallee2018limk21anew pages 24-27, smolich1997cloningandbiochemical pages 5-6, shah2023limk2amultifaceted pages 10-11). The LIMK family is present in vertebrates and some insects but is absent in *C. elegans* and yeast; it contains only two members, LIMK1 and LIMK2 (shah2023limk2amultifaceted pages 1-3). LIMK1 and LIMK2 are closely related paralogs that likely resulted from a gene duplication event early in vertebrate evolution (manning2002theproteinkinase pages 3-3, scott2007limkinasesfunction pages 3-4). The ancestral form is thought to be LIMK1, as only a LIMK1-like homolog has been found in insects (scott2007limkinasesfunction pages 1-3). Orthologs of LIMK2 are found in multiple vertebrate species, including humans, mice, rats, chickens, and *Xenopus*, as well as in *Drosophila* (scott2007limkinasesfunction pages 1-3, ribba2022theroleof pages 13-15).

## Reaction Catalyzed

LIMK2 is a dual-specificity kinase that catalyzes the transfer of a phosphate group from ATP to serine, threonine, and tyrosine residues on a protein substrate (hanke2022developmentandcharacterization pages 1-3, scott2007limkinasesfunction pages 3-4, chatterjee2022structuralaspectsof pages 4-6). ATP + a protein -> ADP + a phosphoprotein

## Cofactor Requirements

Like other protein kinases, the catalytic activity of LIMK2 requires a divalent metal ion cofactor (knape2017divalentmetalions pages 1-2). In vitro kinase assays indicate that either magnesium (Mg²⁺) or manganese (Mn²⁺) can support its phosphoryl transfer activity (knape2017divalentmetalions pages 1-2, lovitt2010differentialeffectsof pages 4-5). Mg²⁺ is considered the most physiologically relevant and efficient cofactor for kinase catalytic cycles (knape2017divalentmetalions pages 1-2).

## Substrate Specificity

The specific optimal substrate motif for LIMK2 is not detailed in the provided context from Johnson et al., 2023 (johnson2023anatlasof pages 6-7). However, kinome-wide analysis places LIMK2 in the CAMK group, suggesting its substrate preferences align with this family, which typically favors certain basic or hydrophobic residues near the phosphorylation site (johnson2023anatlasof pages 4-4). As a dual-specificity kinase, LIMK2 also has a defined phosphotyrosine motif, though its specific sequence is not provided (yaronbarir2024theintrinsicsubstrate pages 2-3). Substrate recognition is also mediated by a unique ‘rock-and-poke’ mechanism, where the substrate protein docks via an anchor helix distal to the kinase active site, allowing a rocking motion to position the phosphoacceptor residue for catalysis (chatterjee2022structuralaspectsof pages 4-6). The LIMK2-1 isoform recognizes a R/K-V/I-X-F consensus sequence to interact with protein phosphatase 1 (vallee2018limk21anew pages 18-22).

## Structure

LIMK2 contains two N-terminal LIM domains, a central PDZ domain, a proline/serine-rich region, and a C-terminal kinase domain (scott2007limkinasesfunction pages 3-4, manetti2012limkinasesare pages 1-3). The LIM domains are tandem cysteine/histidine-rich zinc finger motifs that facilitate protein-protein interactions (manetti2012limkinasesare pages 1-3). The PDZ domain is involved in cytoplasmic localization via nuclear export signals (manetti2012limkinasesare pages 1-3). The kinase domain adopts a canonical two-lobed fold with a smaller N-lobe composed of an antiparallel β-sheet and a larger α-helical C-lobe, which together enclose the ATP-binding cleft (chatterjee2022structuralaspectsof pages 1-3, chatterjee2022structuralaspectsof pages 3-4).

Key structural motifs in the kinase domain include the ATP-capping glycine-rich loop, the VAIK motif that forms part of a hydrophobic pocket for the ATP adenine, the HRDXKXXN catalytic loop with the catalytic aspartate, and the DFG motif in the activation loop that regulates ATP binding via its conformation (DFG-in/active, DFG-out/inactive) (chatterjee2022structuralaspectsof pages 1-3). The active conformation is stabilized by a salt bridge between a lysine in the VAIK motif and a glutamate in the αC helix (LIMK1 numbering: K368-E384) (chatterjee2022structuralaspectsof pages 1-3, chatterjee2022structuralaspectsof pages 3-4). Unique features of LIMK2 include an atypical catalytic loop sequence (DLNSHN) and an asparagine residue at the HRD+2 position, which may affect ATP affinity (villalonga2023limkinaseslimk1 pages 2-6, shah2023limk2amultifaceted pages 3-4, chatterjee2022structuralaspectsof pages 3-4). The kinase domain shows significant conformational flexibility, particularly in the G-rich loop, αC helix, DFG motif, and activation loop (chatterjee2022structuralaspectsof pages 1-3).

## Regulation

LIMK2 activity is principally regulated by phosphorylation within its activation loop at Threonine 505 (Thr505) for the LIMK2a isoform, or the analogous Thr484 in LIMK2b and LIMK2-1 isoforms (hanke2022developmentandcharacterization pages 1-3, chatterjee2022structuralaspectsof pages 3-4, vallee2018limk21anew pages 10-14). This activating phosphorylation is catalyzed by upstream kinases including Rho-associated kinases (ROCK1/2), p21-activated kinases (PAK1/2/4), MRCKα, and Aurora kinase A (AURKA) (villalonga2023limkinaseslimk1 pages 2-6, hanke2022developmentandcharacterization pages 1-3, shah2023limk2amultifaceted pages 6-8). Phosphorylation of Thr505 induces the formation of a salt bridge with Arginine 483 (the DFG+3 residue), which stabilizes the kinase in an active DFG-in conformation, reorients the activation loop to favor substrate docking, and markedly increases kinase activity (chatterjee2022structuralaspectsof pages 3-4, shah2023limk2amultifaceted pages 6-8).

Additional regulatory mechanisms include an autoinhibitory function of the N-terminal LIM and PDZ domains (manetti2012limkinasesare pages 1-3). LIMK2 stability and activity are also modulated by homodimerization and transphosphorylation, which are facilitated by binding to the chaperone Hsp90 (scott2007limkinasesfunction pages 3-4, manetti2012limkinasesare pages 3-6). Phosphorylation by PKC at Ser283 and Thr494 can inhibit LIMK2a nuclear import (vallee2018limk21anew pages 18-22). The activity is negatively regulated by phosphatases such as Slingshot (SSH), which dephosphorylate key activating residues (manetti2012limkinasesare pages 3-6).

## Function

LIMK2 is ubiquitously expressed in human tissues, with enriched expression in the testis and brain, and localizes to both the cytoplasm and the nucleus (ribba2022theroleof pages 13-15, chatterjee2022structuralaspectsof pages 10-11, shah2023limk2amultifaceted pages 1-3). It functions as a key regulator of actin filament dynamics downstream of Rho family GTPases (RhoA, Rac, Cdc42) (hanke2022developmentandcharacterization pages 1-3). Activation of LIMK2 by upstream kinases (ROCK, PAK, MRCKα) leads to the phosphorylation of its primary downstream substrate, the actin-depolymerizing factor (ADF)/cofilin, at Serine 3 (chatterjee2022structuralaspectsof pages 1-3, villalonga2023limkinaseslimk1 pages 2-6). This phosphorylation inactivates cofilin’s actin-severing ability, resulting in the stabilization and accumulation of actin filaments (scott2007limkinasesfunction pages 3-4, villalonga2023limkinaseslimk1 pages 2-6). This regulatory role in cytoskeletal remodeling is essential for cellular processes such as cell motility, morphology, invasion, neurite outgrowth, cell cycle progression, spermatogenesis, and platelet function (scott2007limkinasesfunction pages 3-4, chatterjee2022structuralaspectsof pages 10-11, manetti2012limkinasesare pages 1-3). Known interacting partners of LIMK2 include Hsp90, Neurofibromin (NF1), and the upstream kinase ROCK1 (scott2007limkinasesfunction pages 3-4, shah2023limk2amultifaceted pages 3-4, vallee2018limk21anew pages 10-14).

## Inhibitors

Several selective, small-molecule inhibitors targeting LIMK1/2 have been developed, distinguished by their binding mode to the kinase domain (hanke2022developmentandcharacterization pages 1-3). These include the type I inhibitor LIMKi3, the type II inhibitor TH470, and the type III inhibitor TH257 (hanke2022developmentandcharacterization pages 1-3). Type III inhibitors like TH257 specifically bind to the inactive, DFG-out conformation of the kinase (hanke2022developmentandcharacterization pages 1-3, chatterjee2022structuralaspectsof pages 10-11). These compounds exhibit low nanomolar affinity and high kinase selectivity in biochemical assays (hanke2022developmentandcharacterization pages 1-3).

## Other Comments

The dysregulation of LIMK2 is implicated in several human pathologies, including cancer invasion and metastasis, cognitive disabilities like fragile X syndrome, cardiovascular disorders, and urogenital diseases such as erectile dysfunction and infertility (scott2007limkinasesfunction pages 1-3, manetti2012limkinasesare pages 3-6, hanke2022developmentandcharacterization pages 1-3, ribba2022theroleof pages 12-13).

In humans, LIMK2 exists as at least three distinct isoforms (LIMK2a, LIMK2b, LIMK2-1) produced by alternative splicing (shah2023limk2amultifaceted pages 1-3, villalonga2023limkinaseslimk1 pages 1-2). These isoforms have different lengths, subcellular localizations, and functional properties (shah2023limk2amultifaceted pages 3-4). The LIMK2-1 isoform is unique in that it possesses a C-terminal protein phosphatase 1 inhibitory (PP1i) domain and does not directly phosphorylate cofilin; instead, it regulates actin dynamics by inhibiting the dephosphorylation of cofilin by PP1 (vallee2018limk21anew pages 18-22, vallee2018limk21anew pages 18-22).

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