## Phylogeny

STK38L/NDR2 is a member of the NDR (nuclear Dbf2-related) kinase family, which is a subgroup of the AGC (protein kinase A/G/C-like) family of serine/threonine kinases (bichsel2004mechanismofactivation pages 101-105, cornils2010functionalcharacterizationof pages 151-153, hergovich2008mammalianndrprotein pages 1-2). The human NDR kinase family includes four members: NDR1 (STK38), NDR2 (STK38L), LATS1, and LATS2 (cornils2010functionalcharacterizationof pages 9-14, cornils2010functionalcharacterizationof pages 151-153). This kinase family is highly conserved from yeast to humans (bichsel2004mechanismofactivation pages 19-24, cornils2010functionalcharacterizationof pages 9-14). Orthologs include *Saccharomyces cerevisiae* Dbf2p, Dbf20p, and Cbk1p; *Schizosaccharomyces pombe* Sid2p and Orb6p; *Caenorhabditis elegans* SAX-1 and LATS; and *Drosophila melanogaster* Tricornered (Trc) and Warts/Lats (bichsel2004mechanismofactivation pages 19-24, cornils2010functionalcharacterizationof pages 9-14, cornils2010functionalcharacterizationof pages 151-153, martin2021thestk38–xpo1axis pages 2-4). Phylogenetically, NDR kinases are linked to the Ste20-like kinases, such as MST3, MST1, and MST2, which function as upstream regulators (stegert2005regulationofndr pages 1-2).

## Reaction Catalyzed

The kinase catalyzes the ATP-dependent transfer of the γ-phosphate group to the hydroxyl group of a serine or threonine residue on a protein substrate (cornils2010functionalcharacterizationof pages 9-14, hergovich2008mammalianndrprotein pages 1-2, hergovich2016therolesof pages 1-3). ATP + [a protein] → ADP + [a phosphoprotein] (hergovich2008mammalianndrprotein pages 1-2, cornils2010functionalcharacterizationof pages 9-14).

## Cofactor Requirements

The catalytic activity of the kinase requires Mg²⁺ as a cofactor to facilitate ATP binding and the phosphoryl transfer reaction (bichsel2004mechanismofactivation pages 101-105, hergovich2008mammalianndrprotein pages 1-2, stegert2005regulationofndr pages 2-3). In vitro kinase assays use 10 mM MgCl₂ (stegert2005functionalcharacterisationof pages 78-83, stegert2005regulationofndr pages 2-3).

## Substrate Specificity

The comprehensive atlas of substrate specificities by Johnson et al. (2023) provides experimentally determined consensus motifs for human serine/threonine kinases, including STK38L (UniProt Q9Y2H1) (johnson2023anatlasof pages 1-2). The provided context contains contradictory definitions of the optimal motif from this source. One excerpt reports the motif as H-X-R-R-X-S/T, indicating a preference for histidine (H) at position -5 and arginines (R) at positions -3 and -2 (johnson2023anatlasof pages 6-7). A second excerpt reports the motif as H-R-x-x-S/T, with histidine at -5 and arginine at -4 (johnson2023anatlasof pages 12-18). A third excerpt summarizes the motif as [R/K]-X-[pS/pT]-[L/V], reflecting a preference for a basic residue at -2 and a hydrophobic residue at +2 (johnson2023anatlasof pages 3-4). Generally, STK38L prefers basophilic motifs with basic residues N-terminal to the phosphorylation site (johnson2023anatlasof pages 2-3, johnson2023anatlasof pages 12-18). Separately, a consensus sequence of HXRXXpS/T has also been proposed for NDR1/2 kinases (hergovich2016therolesof pages 3-5). In vitro assays use the synthetic peptide KKRNRRLSVA as a substrate, which is consistent with a preference for arginine-rich sequences (stegert2005functionalcharacterisationof pages 78-83, kohler2012functionalcharacterizationof pages 74-78).

## Structure

STK38L/NDR2 has a conserved primary structure composed of three main domains (martin2020thehippokinase pages 7-9): - An N-terminal regulatory (NTR) domain contains basic and hydrophobic residues that mediate binding to regulatory proteins, including MOB family proteins and S100B (cornils2010functionalcharacterizationof pages 14-18, cornils2010functionalcharacterizationof pages 9-14). - A central catalytic kinase domain is organized into 12 subdomains with conserved residues essential for ATP binding, metal binding, and catalysis (cornils2010functionalcharacterizationof pages 9-14). - A C-terminal hydrophobic motif (HM) contains a key regulatory phosphorylation site, Thr442 (cornils2010functionalcharacterizationof pages 14-18, martin2020thehippokinase pages 7-9).

A unique structural feature is a 30-60 amino acid insertion between kinase subdomains VII and VIII, located just before the activation loop (bichsel2004mechanismofactivation pages 19-24, cornils2010functionalcharacterizationof pages 9-14). This insert contains an auto-inhibitory sequence (AIS), which is rich in basic amino acids and negatively regulates kinase activity (cornils2010functionalcharacterizationof pages 14-18, hergovich2008mammalianndrprotein pages 1-2). AlphaFold models depict these conserved domain arrangements (cornils2010functionalcharacterizationof pages 14-18, martin2020thehippokinase pages 7-9). X-ray crystallography of the related human STK38 kinase reveals an elongated activation segment that blocks substrate binding in the inactive conformation and an αC helix that functions as an auto-inhibitory element (martin2021thestk38–xpo1axis pages 2-4).

## Regulation

STK38L/NDR2 activation is a multi-step process involving phosphorylation and protein-protein interactions (stegert2005regulationofndr pages 1-2).

**Phosphorylation** Full activation requires phosphorylation at conserved residues: - **Ser282**: Located in the activation loop, this site is phosphorylated primarily via autophosphorylation and is essential for kinase activity (cornils2010functionalcharacterizationof pages 14-18, cornils2010functionalcharacterizationof pages 151-153, hergovich2008mammalianndrprotein pages 1-2). - **Thr442**: Located in the C-terminal hydrophobic motif, this site is phosphorylated by upstream kinases of the Ste20-like MST family (MST1, MST2, MST3) (cornils2010functionalcharacterizationof pages 14-18, stegert2005regulationofndr pages 1-2). Phosphorylation by MST3 increases NDR2 kinase activity approximately 10-fold (stegert2005functionalcharacterisationof pages 67-73, stegert2005functionalcharacterisationof pages 93-98). - **Thr74/Thr75**: Located in the NTR domain, phosphorylation at this site is required for full kinase activity and may modulate protein interactions (martin2020thehippokinase pages 7-9, martin2021thestk38–xpo1axis pages 2-4, stegert2005functionalcharacterisationof pages 63-67).

**Dephosphorylation** The protein phosphatase PP2A dephosphorylates and inactivates STK38/STK38L (martin2020thehippokinase pages 7-9, martin2021thestk38–xpo1axis pages 2-4).

**Regulatory Proteins** - **MOB Proteins**: MOB family proteins act as co-activators. MOB1A/B bind to the NTR domain, which relieves AIS-mediated auto-inhibition and facilitates autophosphorylation at Ser282 (cornils2010functionalcharacterizationof pages 151-153, hergovich2008mammalianndrprotein pages 1-2, martin2020thehippokinase pages 7-9). In contrast, MOB2 binds to unphosphorylated NDR1/2 and acts as a negative regulator (kohler2012functionalcharacterizationof pages 7-12, martin2021thestk38–xpo1axis pages 4-6). - **S100B**: The calcium-binding protein S100B binds to the NTR domain and can activate NDR kinases in vitro; its in vivo role may involve maintaining the proper kinase conformation (bichsel2004mechanismofactivation pages 101-105).

**Other Modifications** NDR1/2 kinases can be regulated by ISGylation, ubiquitination, and acetylation, though the functional consequences of these modifications are not fully characterized (hergovich2016therolesof pages 1-3).

## Function

STK38L/NDR2 is involved in the regulation of cell cycle progression, cell morphology, cell spreading, neurite outgrowth, centrosome duplication, and mitotic chromosome alignment (bichsel2004mechanismofactivation pages 101-105, stegert2005functionalcharacterisationof pages 67-73, hergovich2013regulationandfunctions pages 12-12). It is predominantly localized to cytoplasmic structures (stegert2005functionalcharacterisationof pages 63-67). Expression is high in proliferative tissues with rapid turnover, such as the stomach and intestines (stegert2005functionalcharacterisationof pages 63-67).

**Signaling** - **Upstream regulators**: The kinase is activated by upstream kinases from the Ste20-like MST family (MST1, MST2, MST3, MST4, MST5) and the MAP4K family (cornils2010functionalcharacterizationof pages 14-18, martin2020thehippokinase pages 7-9, stegert2005regulationofndr pages 1-2). - **Downstream substrates**: Known substrates include the transcriptional co-activator YAP (phosphorylated at Ser127, leading to its cytoplasmic retention), TAZ, Rabin8, HP1α, and the nuclear export receptor XPO1 (hergovich2016therolesof pages 5-7, martin2021thestk38–xpo1axis pages 1-2). - **Signaling pathways**: STK38L/NDR2 is a component of the Hippo signaling pathway, where it acts downstream of MST kinases and MOB1 to inhibit the activity of the oncoproteins YAP and TAZ (bichsel2004mechanismofactivation pages 101-105, hergovich2016therolesof pages 5-7).

## Inhibitors

No direct small-molecule inhibitors of STK38L/NDR2 are described in the provided context (bichsel2004mechanismofactivation pages 101-105, hergovich2016therolesof pages 5-7, stegert2005functionalcharacterisationof pages 63-67). However, selective inhibitors of nuclear export (SINEs), such as Selinexor, target the STK38L substrate XPO1 (martin2020thehippokinase pages 7-9).

## Other Comments

Dysregulation of STK38L/NDR2 is associated with several diseases. The STK38L gene is located at 12p11, a chromosomal region corresponding to known cancer amplicons (bichsel2004mechanismofactivation pages 101-105). Upregulation of NDR2 mRNA has been observed in aggressive forms of breast cancer, certain melanoma cell lines, and metastatic non-small cell lung cancer cell lines (bichsel2004mechanismofactivation pages 101-105, stegert2005functionalcharacterisationof pages 63-67). In mouse models, loss of intestinal Ndr1/2 results in tissue hyperplasia and increased tumor incidence following carcinogen exposure (hergovich2016therolesof pages 5-7). An exonic SINE insertion in the STK38L gene causes canine early retinal degeneration (hergovich2013regulationandfunctions pages 12-12).

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