## Phylogeny

Hematopoietic cell kinase (HCK) is classified within the Tyrosine Kinase (TK) group of the eukaryotic protein kinase (ePK) superfamily (manning2002evolutionofprotein pages 1-2, sicheri1997structuresofsrcfamily pages 5-6). Within the TK group, HCK is a member of the Src family of non-receptor tyrosine kinases (alvarado2010crystalstructureof pages 7-8, penedumitrescu2008aninhibitorresistantmutant pages 7-8). The Src kinase family in humans consists of nine members which are subdivided into ubiquitously expressed kinases (SRC, YES, FYN) and those with expression restricted to hematopoietic or specific lineages, which includes HCK, LCK, FGR, BLK, LYN, and YRK (poh2015hematopoieticcellkinase pages 1-3, roversi2017hematopoieticcellkinase pages 1-6). The TK and TKL families represent metazoan-specific expansions within the kinome (manning2002evolutionofprotein pages 1-2). Phylogenetic classification based on kinase domain sequence similarity places HCK within the Src family, which is part of the larger TK group (yaronbarir2024theintrinsicsubstrate pages 16-16, manning2002theproteinkinase pages 2-3).

## Reaction Catalyzed

HCK catalyzes the transfer of a γ-phosphate group from ATP to the hydroxyl group of a tyrosine residue on a protein substrate (alvarado2010crystalstructureof pages 7-8, guiet2008hematopoieticcellkinase pages 16-16, tintori2013identificationofhck pages 1-3). This reaction is characterized as ATP-dependent tyrosine phosphorylation (alvarado2010crystalstructureof pages 1-2, banavali2007anatomyofa pages 1-2).

## Cofactor Requirements

The kinase activity of HCK requires ATP as the phosphoryl donor cofactor (alvarado2010crystalstructureof pages 7-8, poh2015hematopoieticcellkinase pages 1-3, penedumitrescu2008aninhibitorresistantmutant pages 7-8). The catalytic reaction also requires a divalent metal ion; ATP bound to magnesium ions (ATP-2Mg²⁺) is an essential cofactor (banavali2007anatomyofa pages 1-2, alvarado2010crystalstructureof pages 1-2). In vitro, HCK has been reported to prefer Mn²⁺ ions over Mg²⁺ as cofactors (unknownauthors2008investigationofthe pages 71-75).

## Substrate Specificity

HCK’s optimal substrate specificity motif is defined by preferred amino acids at positions relative to the phosphorylated tyrosine (position 0) (yaronbarir2024theintrinsicsubstrate pages 16-16). At position P-3, HCK prefers either histidine (H) or arginine (R) (yaronbarir2024theintrinsicsubstrate pages 16-16). At position P-1, the preferred amino acid is lysine (K) (yaronbarir2024theintrinsicsubstrate pages 16-16). At position P+1, HCK shows a preference for glutamine (Q), and at position P+3, the preferred amino acid is asparagine (N) (yaronbarir2024theintrinsicsubstrate pages 16-16).

## Structure

HCK possesses the conserved domain architecture of Src family kinases (SFKs), comprising an N-terminal domain, followed by Src Homology 3 (SH3), SH2, and SH1 (catalytic kinase) domains, and a C-terminal regulatory tail (poh2015hematopoieticcellkinase pages 1-3, sicheri1997structuresofsrcfamily pages 1-2). The SH3 domain binds to proline-rich sequences, while the SH2 domain recognizes phosphotyrosine-containing motifs (unknownauthors2008investigationofthe pages 71-75, poh2015hematopoieticcellkinase pages 1-3). The catalytic domain is bilobal, with a smaller N-terminal lobe containing a dynamic αC-helix and a larger C-terminal lobe; the active site is located between them (selzer2024cocrystallizationofthe pages 1-2, sicheri1997structuresofsrcfamily pages 2-3). Experimentally determined 3D structures for human HCK are available in the Protein Data Bank, including NMR structures of the SH3 domain (PDB IDs 4hck, 5hck), and crystal structures of various constructs: the SH3-SH2 linker region (3NHN), near full-length kinase (1QCF), inhibitor-bound conformations (4LUE), and the isolated kinase domain (5ZJ6) (horita1998solutionstructureof pages 9-10, alvarado2010crystalstructureof pages 1-2, alvarado2010crystalstructureof pages 3-4, selzer2024cocrystallizationofthe pages 2-3). A predicted structure for human HCK (UniProt P08631) is also available from the AlphaFold Protein Structure Database (horita1998solutionstructureof pages 9-10). Key catalytic features include the activation loop with autophosphorylation site Tyr416 (Src numbering) and a conserved DFG motif, and the αC-helix (selzer2024cocrystallizationofthe pages 1-2). A critical ion pair between Lys295 and Glu310 in the αC-helix is essential for ATP positioning and catalysis (sicheri1997structuresofsrcfamily pages 5-6).

## Regulation

The activity of HCK is principally regulated by phosphorylation and intramolecular interactions (poh2015hematopoieticcellkinase pages 1-3). In its inactive state, HCK is maintained in an autoinhibited conformation through the phosphorylation of a C-terminal tyrosine residue (Tyr522, homologous to Tyr527 in c-Src) by kinases such as C-terminal Src kinase (CSK) or CHK (penedumitrescu2008aninhibitorresistantmutant pages 2-4, poh2015hematopoieticcellkinase pages 1-3, selzer2024cocrystallizationofthe pages 8-8). This phosphotyrosine binds intramolecularly to the HCK SH2 domain, while the SH3 domain binds to the SH2-kinase linker, stabilizing the closed, repressed state (sicheri1997structuresofsrcfamily pages 2-3, dorman2019discoveryofnonpeptide pages 1-2). Activation is triggered by the dephosphorylation of this inhibitory C-terminal tyrosine by phosphatases such as CD45, PTPα, TCPTP, or receptor tyrosine phosphatase T (poh2015hematopoieticcellkinase pages 1-3, poh2015hematopoieticcellkinase pages 4-5, carvalho2024comprehensiveanalysisof pages 9-10). This releases the intramolecular constraints and allows for the subsequent trans-autophosphorylation of a tyrosine residue in the activation loop (Tyr410 in human p61HCK, also referred to as Tyr411 or Tyr416), which is required for maximal kinase activity (roversi2017hematopoieticcellkinase pages 1-6, selzer2024cocrystallizationofthe pages 8-8). The engagement of the SH3 and SH2 domains with extracellular signals also contributes to kinase activation, with structural evidence supporting an SH3-dominant activation mechanism (alvarado2010crystalstructureof pages 7-8).

## Function

HCK is a proto-oncogene predominantly expressed in hematopoietic cells of the myeloid (e.g., macrophages, neutrophils) and B-lymphocyte lineages (poh2015hematopoieticcellkinase pages 1-3, carvalho2024comprehensiveanalysisof pages 1-2). It exists as two isoforms, p59HCK and p61HCK, generated by alternative translation initiation (poh2015hematopoieticcellkinase pages 1-3). HCK acts as a signal transducer downstream of various cell surface receptors, including cytokine receptors (IL-2, IL-6, GM-CSF, EpoR), immunoreceptors (TLR4, FCGRs), and integrins (poh2015hematopoieticcellkinase pages 1-3, roversi2017hematopoieticcellkinase pages 1-6). Upstream activators also include mutated MYD88 (yang2016hckisa pages 16-17). Key downstream signaling pathways activated by HCK include PI3K/AKT, MAPK/ERK, and STAT3/STAT5 (roversi2017hematopoieticcellkinase pages 1-6, poh2015hematopoieticcellkinase pages 4-5, carvalho2024comprehensiveanalysisof pages 9-10). HCK interacts with and is activated by oncogenic fusion proteins like BCR/ABL and TEL/ABL (poh2015hematopoieticcellkinase pages 5-7). Other interacting partners include STAT3, RasGAP, paxillin, FLT3, CAMK2G, and HIV-1 Nef (unknownauthors2008investigationofthe pages 71-75, poh2015hematopoieticcellkinase pages 10-11). HCK plays critical roles in innate immunity, regulating macrophage and neutrophil functions such as phagocytosis, degranulation, and migration (carvalho2024comprehensiveanalysisof pages 6-8, poh2015hematopoieticcellkinase pages 5-7). It is also involved in hematopoiesis, particularly the regulation of erythropoiesis and myeloid cell differentiation (roversi2017hematopoieticcellkinase pages 1-6, carvalho2024comprehensiveanalysisof pages 6-8).

## Inhibitors

Multiple small molecule inhibitors target HCK. Broad-spectrum Src family kinase inhibitors that also inhibit HCK include dasatinib, bosutinib, saracatinib, imatinib, SU6656, A-419259, PP1, and PP2 (penedumitrescu2008aninhibitorresistantmutant pages 2-4, poh2015hematopoieticcellkinase pages 10-11, poh2015hematopoieticcellkinase pages 5-7). Ibrutinib, a Bruton tyrosine kinase (BTK) inhibitor, is also a direct HCK inhibitor (yang2016hckisa pages 16-17). More selective or novel pharmacological inhibitors studied in preclinical models include iHCK-37, RK-20449, and KIN-8194, a dual HCK/BTK inhibitor (roversi2017hematopoieticcellkinase pages 1-6, carvalho2024comprehensiveanalysisof pages 6-8).

## Other Comments

Aberrant HCK activation or overexpression is associated with several hematological malignancies, including acute myeloid leukemia (AML), chronic myeloid leukemia (CML), multiple myeloma (MM), and Waldenström’s macroglobulinemia (roversi2017hematopoieticcellkinase pages 1-6, poh2015hematopoieticcellkinase pages 5-7, yang2016hckisa pages 16-17). In AML, elevated HCK expression correlates with unfavorable prognosis (carvalho2024comprehensiveanalysisof pages 6-8). In CML, HCK is implicated in signaling downstream of Bcr-Abl and contributes to imatinib resistance (penedumitrescu2008aninhibitorresistantmutant pages 2-4). HCK is also implicated in solid tumors such as breast, colon, and gastric cancer, often through its role in tumor-associated immune cells (poh2015hematopoieticcellkinase pages 1-3, poh2015hematopoieticcellkinase pages 10-11). Specific disease-linked mutations in HCK are not commonly reported (carvalho2024comprehensiveanalysisof pages 6-8, poh2015hematopoieticcellkinase pages 4-5). However, engineered mutations have revealed key functional sites: the T338M ‘gatekeeper’ mutation confers resistance to the inhibitor A-419259 via steric hindrance, and the Y527F mutation in the C-terminal tail is constitutively activating and oncogenic (penedumitrescu2008aninhibitorresistantmutant pages 2-4).

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