1. Phylogeny  
   Serine/threonine‐protein kinase DCLK2, also known by the gene symbols DCLK2, DCAMKL2, DCDC3B, and DCK2, is a member of the doublecortin (DCX) superfamily. This family is characterized by the presence of tandem doublecortin (DCX) domains, which mediate microtubule binding, and a C‐terminal serine/threonine kinase domain that is linked to the calcium/calmodulin‐dependent kinase (CaMK) clade. Within the human kinome, DCLK2 is grouped with its paralogs DCLK1 and DCLK3; the phylogenetic analysis indicates that the divergence between DCLK1 and DCLK2 occurred during vertebrate evolution, with both forming distinct monophyletic clades that are absent in invertebrates, whereas DCLK3 represents a more divergent and ancestral paralog within the DCX‐containing kinases (hu2024kinomewidesirnascreen pages 3-5, venkat2023mechanisticandevolutionary pages 4-5, reiner2006theevolvingdoublecortin pages 1-2). Further, seminal studies on the protein kinase complement of the human genome have placed DCLK2 within the calcium/calmodulin‐dependent kinase group, which itself traces its origins to the last common ancestor of eukaryotes; this evolutionary framework establishes DCLK2 as part of an ancient and conserved signaling module that has undergone gene duplication and subsequent specialization in vertebrates (venkat2023mechanisticandevolutionary pages 1-2, reiner2006theevolvingdoublecortin pages 2-4, Manning2002Science, Manning2002Trends).
2. Reaction Catalyzed  
   DCLK2 catalyzes the transfer of a phosphate group from ATP to the –OH group of serine or threonine residues on substrate proteins. The overall catalyzed reaction can be represented as:  
     ATP + [protein]-(L-serine or L-threonine) → ADP + [protein]-(L-serine/threonine)-phosphate + H⁺  
   This reaction is a hallmark of serine/threonine kinases and underpins the role of DCLK2 in modulating the phosphorylation state of its substrates (template information).
3. Cofactor Requirements  
   The kinase activity of DCLK2 requires the presence of divalent cations, with Mg²⁺ serving as the key cofactor. Mg²⁺ ions are essential for optimal binding of ATP within the nucleotide-binding pocket and thereby facilitate the transfer of the phosphate group to substrate proteins (template information).
4. Substrate Specificity  
   DCLK2, as a member of the serine/threonine kinases within the CaMK-related subgroup, phosphorylates substrates on serine/threonine residues. Although detailed substrate motifs for DCLK2 have not been exclusively delineated in the provided context, the atlas of substrate specificities for the human serine/threonine kinome indicates that kinases in similar families often display preferences for motifs enriched in basic residues preceding the phosphorylatable serine or threonine. In the context of clear cell renal cell carcinoma (ccRCC), DCLK2 phosphorylates TANK-binding kinase 1 (TBK1) at Ser172, a modification that is critical for TBK1 activation and subsequent tumorigenic processes (hu2024kinomewidesirnascreen pages 3-5, hu2024kinomewidesirnascreen pages 10-11, johnson2023anatlasof pages 4-4, johnson2023anatlasof pages 4-5). Thus, in addition to its general serine/threonine kinase activity, DCLK2 exhibits substrate selectivity that underlies its role in specific signaling cascades and cellular contexts.
5. Structure  
   DCLK2 possesses a modular architecture that is typical of proteins within the doublecortin family. The N-terminal region comprises two DCX domains that are critical for binding to microtubules, thereby contributing to the regulation of microtubule dynamics and neuronal migration. Each DCX domain is approximately 90 amino acids in length and contains conserved motifs critical for interaction with polymerized tubulin (reiner2006theevolvingdoublecortin pages 1-2, reiner2006theevolvingdoublecortin pages 11-12). Following the DCX domains, DCLK2 contains a C-terminal serine/threonine kinase domain that adopts a conventional bilobal fold. This catalytic domain contains the characteristic glycine-rich loop, the catalytic HRD motif within the activation loop (T-loop), and the DFG motif that coordinates the binding of Mg²⁺ and ATP (venkat2023mechanisticandevolutionary pages 23-24, patel2016biochemicalandstructural pages 3-4). In certain isoforms identified in cancer cells, variations in the C-terminal tail have been observed; for instance, the DCLK2203 isoform, which lacks an autoinhibitory threonine (T693) that is present in the DCLK2201 isoform, displays higher intrinsic kinase activity (hu2024kinomewidesirnascreen pages 10-11). Although high-resolution structural data on full-length DCLK2 are not provided in the context, available information from related DCLK family members and AlphaFold modeling predict that the kinase domain of DCLK2 is flanked by flexible regulatory regions that could contribute to allosteric control and interaction with other proteins. The conserved key residues within the kinase domain, including those that form the hydrophobic spine and the C-helix, are essential for its catalytic function and are maintained within DCLK2 (venkat2023mechanisticandevolutionary pages 23-24, reiner2006theevolvingdoublecortin pages 12-14).
6. Regulation  
   The activity of DCLK2 is regulated at multiple levels. Post-translational modifications, particularly phosphorylation, play a pivotal role in modulating its kinase activity. For example, the phosphorylation of its substrates, such as TBK1 on Ser172, is a critical regulatory event that enhances downstream signaling in oncogenic contexts like clear cell renal cell carcinoma (hu2024kinomewidesirnascreen pages 3-5, hu2024kinomewidesirnascreen pages 10-11). In addition, isoform-specific regulatory mechanisms have been described in related DCLK family kinases; differences in the length and composition of the C-terminal regulatory segments can lead to autoinhibition or “supercharging” of the catalytic activity, as seen in comparisons between DCLK1 isoforms (venkat2023mechanisticandevolutionary pages 15-17, venkat2023mechanisticandevolutionary pages 14-15). Although such detailed dissection has been performed primarily for DCLK1, the conservation of key regulatory motifs—such as residues that mimic ATP binding and modulate the hydrophobic spine—suggests that similar mechanisms operate in DCLK2. In addition, regulation by mRNA decay pathways appears to be significant; for instance, in ccRCC, decreased activity of the nonsense-mediated decay (NMD) pathway results in elevated levels of the active DCLK2 isoform (hu2024kinomewidesirnascreen pages 10-11). This transcriptional and post-transcriptional regulation, combined with the potential for phosphorylation-dependent conformational changes, constitutes the multifaceted regulation of DCLK2.
7. Function  
   DCLK2 is implicated in a range of cellular processes through its dual functionality as both a microtubule-associated protein and a serine/threonine kinase. The doublecortin domains facilitate binding to microtubules, thereby influencing neuronal migration, axon growth, and microtubule polymerization—a function that is critically important during brain development (reiner2006theevolvingdoublecortin pages 4-7, ramkumar2018remappingthemicrotubule pages 17-19, ayanlaja2017distinctfeaturesof pages 8-9). In addition, DCLK2’s kinase activity plays a key role in signaling pathways relevant to both neurodevelopment and oncogenesis. In clear cell renal cell carcinoma, for example, DCLK2 phosphorylates TBK1 at Ser172, an event that is essential for TBK1 activation and supports tumor cell proliferation, tumor growth, and metastasis (hu2024kinomewidesirnascreen pages 3-5, hu2024kinomewidesirnascreen pages 10-11). Beyond cancer, by similarity to its paralog DCLK1, DCLK2 is predicted to contribute to the down-regulation of cyclic AMP response element (CRE)-dependent gene activation, likely via phosphorylation of the CREB coactivator CRTC2/TORC2, resulting in the retention of TORC2 in the cytoplasm (Information section; carli2022thefunctionof pages 42-45). DCLK2’s expression pattern is observed in neural tissues given its shared domain architecture with other DCX family proteins; this suggests a role in neuronal migration and neural network formation, as well as in the maintenance of microtubule stability in mature neurons (reiner2006theevolvingdoublecortin pages 2-4, chard2022investigatingproteinsproximal pages 205-208). The involvement of DCLK2 in both developmental and oncogenic signaling pathways underscores its function as a critical regulatory node in cellular homeostasis and disease.
8. Other Comments  
   Selective inhibition of the DCLK family has become an area of active investigation due to the oncogenic potential of these kinases. Notably, DCLK1-IN-1, a potent and selective inhibitor originally developed for DCLK1, has been shown to effectively target both DCLK1 and DCLK2 kinase activities with high specificity, as demonstrated by chemoproteomic profiling and kinome-wide screening assays (ferguson2020discoveryofa pages 1-2, ferguson2020discoveryofa pages 7-8). This selectivity is particularly important given the challenges associated with inhibiting kinases with conserved ATP-binding sites. Furthermore, the dysregulation of DCLK2—evidenced by its increased expression via modulation of the nonsense-mediated decay pathway in ccRCC—provides a rationale for its consideration as a therapeutic target in cancer (hu2024kinomewidesirnascreen pages 10-11). Despite the overlap in function and structure with DCLK1, differences in the C-terminal tail and autoinhibitory mechanisms between DCLK1 and DCLK2 may yield isoform-specific sensitivity to inhibitors. In addition, while the role of DCLK2 in neuronal development is inferred from its structural conservation with other DCX family members, its direct implication in neurodevelopmental disorders remains to be further elucidated. The availability of selective chemical probes and advanced structural models, such as those derived from AlphaFold predictions, will facilitate a more detailed understanding of the biochemical regulation and potential disease mutations affecting DCLK2.
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