1. Phylogeny:  
   CDK1 is a member of the cyclin‐dependent kinase family, a highly conserved group of serine/threonine protein kinases present in eukaryotes from yeast to humans. Orthologs of CDK1 include CDC28 in Saccharomyces cerevisiae and CDC2 in Schizosaccharomyces pombe, which indicate that the fundamental mechanism of cyclin-dependent control of cell division was established early in evolution (liu2000evolutionofcyclindependent pages 1-1, łukasik2021cyclindependentkinases(cdk) pages 1-2). Within the human kinome, CDK1 belongs to the core set of cell-cycle kinases and is evolutionarily related to other CDKs such as CDK2, CDK4, and CDK6, which together coordinate distinct phases of the cell cycle (malumbres2014cyclindependentkinases pages 1-2, malumbres2014cyclindependentkinases pages 2-3). Phylogenetic analysis based on conserved catalytic domains has placed CDK1 in the CMGC branch of kinases, which includes cyclin-dependent kinases, MAP kinases, GSKs, and CDK-like kinases, highlighting its central role in controlling mitotic entry and progression (łukasik2021cyclindependentkinases(cdk) pages 29-30). Moreover, evolutionary analyses based on the work of Manning and colleagues show that kinases like CDK1 emerged from an ancestral gene present in the Last Eukaryotic Common Ancestor, with subsequent diversification of cyclin partners to fulfill specialized functions in complex multicellular organisms (liu2000evolutionofcyclindependent pages 1-1).
2. Reaction Catalyzed:  
   CDK1 catalyzes the phosphorylation of substrate proteins using ATP, transferring the gamma-phosphate from ATP to the hydroxyl group of serine or threonine residues in target proteins; the overall catalytic reaction can be summarized as: ATP + [protein]-(L-serine/threonine) → ADP + [protein]-(L-serine/threonine)-phosphate + H⁺ (malumbres2014cyclindependentkinases pages 3-5).
3. Cofactor Requirements:  
   The catalytic activity of CDK1 requires the presence of divalent metal ions, predominantly Mg²⁺, which facilitate ATP binding and proper positioning within the kinase active site (shafiq2011molecularmodellingand pages 16-21).
4. Substrate Specificity:  
   CDK1 is a serine/threonine kinase that phosphorylates substrates typically within a context that often includes a proline residue immediately following the phosphorylated serine/threonine, reflecting a proline-directed consensus motif; experimental atlases of substrate specificities for the human serine/threonine kinome indicate that this kinase exhibits selectivity toward motifs found on key cell cycle regulatory proteins (malumbres2014cyclindependentkinases pages 3-5, pellarin2025cyclindependentproteinkinases pages 9-10, johnson2023substrate*). For additional information regarding the intrinsic substrate preferences of human serine/threonine kinases, see the recent atlas describing kinetic motif interactions (johnson2023substrate*); similarly, in contrast, tyrosine kinases follow distinct substrate recognition rules, as characterized in studies of the human tyrosine kinome (yaron-barir2024substrate\*).
5. Structure:  
   CDK1 contains a conserved catalytic kinase domain that is organized into two lobes: an N-terminal lobe primarily composed of β-sheets and a larger C-terminal lobe rich in α-helices; the ATP binding cleft is situated in the inter-lobal region and includes critical residues that form hydrogen bonds with ATP (wood2018structuralinsightsinto pages 1-2, malumbres2014cyclindependentkinases pages 5-6). Central to the structure is the PSTAIRE helix, a conserved motif that is essential for cyclin binding and activation, as its orientation regulates the positioning of the activation loop – a segment that undergoes phosphorylation (typically at threonine residue T161 in human CDK1) to convert the enzyme to an active conformation (gomes2007analysisofcyclin pages 32-36, malumbres2014cyclindependentkinases pages 6-7). Additional structural features include a glycine-rich loop that participates in nucleotide binding and a hydrophobic spine that stabilizes the active conformation, with the C-helix playing a key role in aligning catalytic residues during substrate engagement (wood2018structuralinsightsinto pages 2-3, meschini2011purinebaseddualinhibitors pages 51-57). Overall, the three-dimensional organization of CDK1 is characterized by a modular kinase fold that supports both catalytic activity and regulation via conformational changes induced by cyclin binding (malumbres2014cyclindependentkinases pages 8-9).
6. Regulation:  
   CDK1 regulation occurs primarily through a series of phosphorylation and dephosphorylation events as well as through cyclin binding; association with cyclins A and B induces a conformational rearrangement that is a prerequisite for catalytic activity (gomes2007analysisofcyclin pages 32-36, pellarin2025cyclindependentproteinkinases pages 2-4). Its full activation depends on phosphorylation at the T-loop (for instance, T161 in human CDK1), a modification catalyzed by the CDK-activating kinase (CAK), which in mammals is formed by the CDK7/Cyclin H/MAT1 complex (meschini2011purinebaseddualinhibitors pages 35-41, pellarin2025cyclindependentproteinkinases pages 8-9). In contrast, inhibitory phosphorylation at residues T14 and Y15 by kinases such as Wee1 and Myt1 prevents premature activation; removal of these inhibitory phosphates by a CDC25 family phosphatase triggers mitotic entry (inze2007cellcyclecontrol pages 130-133, pellarin2025cyclindependentproteinkinases pages 7-8). Additional regulation is provided by cell-cycle inhibitors such as the Cip/Kip family members, which can bind to and inhibit CDK1-cyclin complexes under conditions of stress or DNA damage (pellarin2025cyclindependentproteinkinases pages 54-55, łukasik2021cyclindependentkinases(cdk) pages 11-12). This multi-layered regulatory mechanism ensures that CDK1 activity is tightly coupled to proper cell cycle progression and genomic integrity (wang2023targetingcdk1in pages 1-2, shafiq2011molecularmodellingand pages 16-21).
7. Function:  
   CDK1 is essential for the progression of the eukaryotic cell cycle, particularly for the transition from the G2 phase to mitosis; by phosphorylating a myriad of substrates such as components of the centrosome, nuclear lamina, and various regulatory proteins, it orchestrates key events including centrosome separation, nuclear envelope breakdown, chromatin condensation, spindle assembly, and ultimately cytokinesis (gomes2007analysisofcyclin pages 32-36, pellarin2025cyclindependentproteinkinases pages 9-10). CDK1 also phosphorylates proteins involved in the regulation of DNA repair, apoptosis, and transcription, thereby integrating cellular responses to stress and damage; for instance, phosphorylation of FOXO1 in neural cells contributes to the regulation of apoptotic pathways, while modification of lamins facilitates nuclear envelope disassembly during mitosis (pellarin2025cyclindependentproteinkinases pages 9-10, pellarin2025cyclindependentproteinkinases pages 19-20). Its interaction with various cyclins not only modulates its substrate specificity but also ensures temporally controlled activation during distinct cell cycle phases. The critical nature of CDK1 is further underscored by its essentiality for early embryonic development and its role in controlling pronuclear union in fertilized eggs, with aberrant CDK1 activity closely linked to oncogenic transformations (gomes2007analysisofcyclin pages 32-36, łukasik2021cyclindependentkinases(cdk) pages 11-12).
8. Other Comments:  
   Several small molecule inhibitors have been developed that target CDK1, with some acting as ATP-competitive inhibitors that occupy the conserved nucleotide-binding pocket; these inhibitors are under investigation for their potential therapeutic use in cancer, where dysregulated CDK1 activity contributes to unchecked cell proliferation and genomic instability (meschini2011purinebaseddualinhibitors pages 73-80, wang2023targetingcdk1in pages 5-5). CDK1 is also known as CDC2 or p34CDC2, and its alternative nomenclature reflects historical naming conventions that arose from early studies in yeast and mammalian systems (gomes2007analysisofcyclin pages 32-36, pellarin2025cyclindependentproteinkinases pages 9-10). In addition, mutations or alterations in regulatory mechanisms affecting CDK1 and its cyclin partners are implicated in various cancers and may serve as biomarkers or targets in precision oncology strategies (wang2023targetingcdk1in pages 8-8, meschini2011purinebaseddualinhibitors pages 64-69). Further research continues to elucidate the complete repertoire of CDK1 substrates and interacting proteins, which include key cell cycle regulators, transcription factors, and proteins involved in DNA repair pathways, enhancing our understanding of its pivotal role in maintaining cellular homeostasis (pellarin2025cyclindependentproteinkinases pages 52-53, rout2018deepinsightsinto pages 15-18).
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   gomes2007analysisofcyclin pages 32-36; liu2000evolutionofcyclindependent pages 1-1; malumbres2014cyclindependentkinases pages 1-2; malumbres2014cyclindependentkinases pages 2-3; meschini2011purinebaseddualinhibitors pages 280-282; meschini2011purinebaseddualinhibitors pages 284-286; meschini2011purinebaseddualinhibitors pages 35-41; pellarin2025cyclindependentproteinkinases pages 19-20; pellarin2025cyclindependentproteinkinases pages 2-4; pellarin2025cyclindependentproteinkinases pages 7-8; pellarin2025cyclindependentproteinkinases pages 8-9; pellarin2025cyclindependentproteinkinases pages 9-10; shafiq2011molecularmodellingand pages 21-26; wang2023targetingcdk1in pages 1-2; wang2023targetingcdk1in pages 5-5; wang2023targetingcdk1in pages 5-8; wang2023targetingcdk1in pages 8-8; wood2018structuralinsightsinto pages 20-20; zheng2022cyclindependentkinasesand pages 8-9; łukasik2021cyclindependentkinases(cdk) pages 1-2; łukasik2021cyclindependentkinases(cdk) pages 11-12; ferrer2006structuralbasisfor pages 10-10; geyer2005targetingmalariawith pages 3-4; inze2007cellcyclecontrol pages 130-133; inze2007cellcyclecontrol pages 146-149; inze2007cellcyclecontrol pages 15-20; karimbayli2024insightsintothe pages 17-17; li2016recentprogressof pages 1-2; li2016recentprogressof pages 4-5; malumbres2014cyclindependentkinases pages 3-5; malumbres2014cyclindependentkinases pages 5-6; malumbres2014cyclindependentkinases pages 6-7; malumbres2014cyclindependentkinases pages 8-9; meschini2011purinebaseddualinhibitors pages 41-45; meschini2011purinebaseddualinhibitors pages 64-69; meschini2011purinebaseddualinhibitors pages 73-80; pellarin2025cyclindependentproteinkinases pages 18-19; pellarin2025cyclindependentproteinkinases pages 50-51; pellarin2025cyclindependentproteinkinases pages 54-55; pepino2021overviewofpctk3cdk18 pages 16-16; rout2018deepinsightsinto pages 15-18; wood2018structuralinsightsinto pages 1-2; wood2018structuralinsightsinto pages 2-3; wood2018structuralinsightsinto pages 20-21; łukasik2021cyclindependentkinases(cdk) pages 29-30; meschini2011purinebaseddualinhibitors pages 277-280; meschini2011purinebaseddualinhibitors pages 51-57; pellarin2025cyclindependentproteinkinases pages 52-53; shafiq2011molecularmodellingand pages 103-108; shafiq2011molecularmodellingand pages 16-21

\*Note: The citations labeled johnson2023substrate and yaron-barir2024substrate are included in the substrate specificity section as required by the task instructions, even though their specific page numbers were not provided in the context.

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