1. Phylogeny  
   Serine/threonine‐protein kinase MARK1 (UniProt: Q9P0L2) belongs to the microtubule affinity‐regulating kinase (MARK) family, which comprises four paralogous isoforms: MARK1, MARK2, MARK3, and MARK4. MARK1 is the human homolog of the evolutionarily conserved Par‐1 kinases found in Caenorhabditis elegans and Drosophila melanogaster, and its orthologs have been identified throughout metazoans. This kinase is a member of the AMPK/Snf1‐related kinase subfamily within the CAMK group, representing an ancient branching in the eukaryotic kinome that underlies fundamental processes such as cell polarity and cytoskeletal regulation (drewes1997markanovel pages 1-2, matenia2009thetauof pages 1-2, naz2013microtubuleaffinityregulatingkinase pages 1-3).
2. Reaction Catalyzed  
   MARK1 catalyzes the transfer of a phosphate group from ATP to the hydroxyl group of serine or threonine residues on substrate proteins. In biochemical terms, the reaction is as follows:  
     ATP + protein – OH → ADP + protein – O‑phosphate + H⁺  
   This kinase phosphorylates specific substrates, including several microtubule‐associated proteins, thereby directly altering their binding affinity to microtubules (drewes1997markanovel pages 1-2, annadurai2017microtubuleaffinityregulatingkinases pages 2-4).
3. Cofactor Requirements  
   Like other serine/threonine kinases, MARK1 requires divalent metal ions—most notably Mg²⁺—as an essential cofactor for its catalytic activity. Mg²⁺ facilitates the binding of ATP in the catalytic cleft and is critical for the phosphoryl transfer reaction (drewes1997markanovel pages 1-2).
4. Substrate Specificity  
   MARK1 displays a high degree of substrate specificity for microtubule‐associated proteins. Its chief substrates include tau (MAPT), MAP2, MAP4, and the neuronal migration regulator doublecortin (DCX). MARK1 phosphorylates these substrates at conserved KXGS motifs within their microtubule‐binding domains; for instance, phosphorylation of tau occurs at residues such as Ser262, Ser293, Ser324, and Ser356. Such modifications decrease the affinity of these proteins for microtubules and promote microtubule disassembly, a mechanism critical for the regulation of cell polarity and neuronal process formation (annadurai2017microtubuleaffinityregulatingkinases pages 2-4, annunziata2020phosphorylationsitesin pages 19-20, matenia2009thetauof pages 2-4).
5. Structure  
   MARK1 is organized into multiple distinct domains that function cooperatively to regulate its activity. At the N-terminus, a variable header sequence is followed by a highly conserved catalytic domain that contains the typical bi-lobal arrangement of protein kinases, including the glycine-rich P-loop, catalytic loop, activation segment (T-loop), and residues that form the hydrophobic spine and C-helix. Adjacent to the catalytic domain is a ubiquitin-associated (UBA) domain that, although sharing the characteristic fold of UBA domains, does not exhibit strong ubiquitin-binding affinity but instead contributes to the regulation of kinase activity through intramolecular interactions (panneerselvam2006structureofthe pages 5-7, naz2013microtubuleaffinityregulatingkinase pages 3-4). A flexible spacer region follows the UBA domain, and at the C-terminus, MARK1 contains a kinase-associated (KA1) domain. The KA1 domain is implicated in autoinhibition; it binds to the catalytic domain, obstructing the substrate peptide-binding site in the inactive conformation. Binding to anionic phospholipid membranes releases this autoinhibition by displacing the KA1 domain, thereby enhancing kinase activation (emptage2018structuralbasisfor pages 1-3, emptage2018structuralbasisfor pages 9-11, matenia2009thetauof pages 4-6).
6. Regulation  
   MARK1 is tightly regulated by multiple mechanisms that include both phosphorylation events and allosteric modulation. Activation of MARK1 is achieved by phosphorylation of a conserved threonine residue within the activation loop—typically performed by upstream kinases such as LKB1 and MARKK—leading to a conformational rearrangement that stabilizes the active form of the kinase (drewes1997markanovel pages 2-4, annadurai2017microtubuleaffinityregulatingkinases pages 2-4, emptage2018structuralbasisfor pages 1-3). In its basal state, the KA1 domain exerts an autoinhibitory effect by binding to the catalytic domain; this interaction is disrupted when the KA1 domain engages with acidic phospholipids at membrane sites, resulting in a further increase in kinase activity (emptage2018structuralbasisfor pages 5-6, emptage2018structuralbasisfor pages 9-11, naz2013microtubuleaffinityregulatingkinase pages 7-8). In addition, although reported most prominently for MARK2 and related family members, binding of regulatory proteins—including 14-3-3 and PAK5 (which interacts with the catalytic domain to inhibit phosphorylation activity)—is a mechanism that may also apply to MARK1, thereby modulating its localization and substrate access (goransson2006regulationofthe pages 2-3, timm2006signalingfrommark pages 2-3).
7. Function  
   MARK1 plays a central role in the regulation of cell polarity and microtubule dynamics. By phosphorylating microtubule-associated proteins such as tau, MAP2, MAP4, and DCX at conserved KXGS motifs, MARK1 induces the detachment of these proteins from microtubules. This modulation of protein–microtubule interactions leads to increased microtubule dynamics that are essential for processes including neurite extension, neuronal migration, and the establishment of asymmetric cell polarity. In addition, MARK1 functions as a positive regulator of the Wnt signaling pathway, most likely through the phosphorylation of dishevelled (DVL1, DVL2, and/or DVL3) proteins, thus linking cytoskeletal regulation to signal transduction pathways that control cell fate and development (annadurai2017microtubuleaffinityregulatingkinases pages 2-4, annunziata2020phosphorylationsitesin pages 19-20, matenia2009thetauof pages 1-2). MARK1 expression is high in fetal tissues and in the brain, which underscores its roles in neuronal differentiation and cellular polarity (drewes1997markanovel pages 4-5, matenia2009thetauof pages 1-2).
8. Other Comments  
   The emerging interest in MARK1 as a druggable target stems from its critical involvement in tau phosphorylation and microtubule destabilization, processes that are central to the pathogenesis of Alzheimer’s disease and related tauopathies. Inhibitors that specifically target MARK kinases are being considered for therapeutic intervention to modulate abnormal tau phosphorylation. In addition, alterations in the activity of MARK1 may have broader implications in disorders related to cell polarity dysregulation, including certain forms of cancer. Although direct inhibitor data for MARK1 are less abundant than for some of its paralogs, the structural and regulatory insights provided by studies on MARK1 and related family members support ongoing efforts to develop selective modulators of its kinase activity (annadurai2017microtubuleaffinityregulatingkinases pages 2-4, matenia2009thetauof pages 9-10, emptage2018structuralbasisfor pages 9-11).
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Each of the above references is drawn from peer-reviewed sources and has contributed to the comprehensive nomenclature and functional profile presented herein.

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