1. Phylogeny  
   FAM20C belongs to the FAM20 family of secreted protein kinases and is evolutionarily conserved across metazoans. Orthologs of FAM20C have been identified from Caenorhabditis elegans up to mammals, and its homologs include paralogs FAM20A and FAM20B, which are expressed in vertebrates and even in some invertebrate species involved in biomineralization or extracellular matrix regulation (chen2021proteolyticprocessingof pages 1-2, zhang2018structureandevolution pages 1-2). FAM20C is classified as a Golgi-resident kinase historically referred to as Golgi casein kinase or DMP4. Phylogenetic studies demonstrate that FAM20C and other family members diverge early from the canonical eukaryotic protein kinase superfamily, representing a distinct group whose evolutionary origins trace back at least to the common ancestor of animals and perhaps before (gersongurwitz2018ancestralrolesof pages 40-42, palmalara2021fam20coverviewclassic pages 1-2).
2. Reaction Catalyzed  
   FAM20C catalyzes the transfer of a phosphate group from ATP to serine residues on substrate proteins, leading to the formation of ADP and a phosphorylated protein product. In chemical terms, the reaction is as follows:  
     ATP + [protein]-L-serine (or L-threonine) → ADP + [protein]-O-phosphoserine (or phosphothreonine) + H⁺  
   This reaction is performed within the secretory pathway and is central to the generation of the extracellular phosphoproteome (tagliabracci2012secretedkinasephosphorylates pages 1-2).
3. Cofactor Requirements  
   FAM20C requires divalent cations for catalytic activity, with a strong preference for manganese ions (Mn²⁺) over magnesium ions (Mg²⁺) under in vitro conditions. The kinase activity has been optimized using elevated concentrations of MnCl₂ in biochemical assays, suggesting that Mn²⁺ acts as a critical cofactor in coordinating the phosphate transfer from ATP to the substrate (cozza2015“genuine”caseinkinase pages 9-12, cui2015asecretorykinase pages 4-6).
4. Substrate Specificity  
   FAM20C displays a strong substrate preference for secretory pathway phosphoproteins. It phosphorylates serine residues within a defined consensus motif, most commonly the Ser-x-Glu (S-x-E) sequence or with a phosphorylated serine at the +2 position (Ser-x-pSer). Although its substrate scope has been shown to be broad, the primary known motif is S-x-E/pS, which accounts for the majority of the phosphorylated sites present in secreted proteins. This specificity underlies its role as the main kinase generating the extracellular phosphoproteome and includes substrates such as casein as well as several proteins involved in biomineralization (chen2021proteolyticprocessingof pages 1-2, cozza2015anewrole pages 1-2, sreelatha2015thesecretorypathway pages 6-7).
5. Structure  
   FAM20C is a type II transmembrane serine/threonine kinase predominantly localized in the Golgi apparatus. Its structure comprises an N-terminal signal peptide and a short transmembrane domain (approximately 20 amino acids) that mediate its retention within the Golgi membranes (chen2021proteolyticprocessingof pages 1-2, palmalara2021fam20coverviewclassic pages 2-4). The catalytic kinase domain is positioned in the lumen and exhibits an atypical protein kinase fold. Notably, crystal structures from its Caenorhabditis elegans ortholog reveal a two-lobe arrangement consisting of an N-lobe with 18 α-helices and a C-lobe with nine β-strands. Unlike canonical kinases, FAM20C lacks a readily identifiable activation loop and possesses a unique insertion domain that forms a cap-like structure over the active site. Key catalytic features include conserved residues for ATP binding and metal ion coordination, such as a catalytic aspartate and residues contributing to the hydrophobic spine and the position of the regulatory αC helix. These features support a constitutively active architecture optimized for efficient catalysis in the secretory environment (xiao2013crystalstructureof pages 1-1, xiao2013crystalstructureof pages 5-6, palmalara2021fam20coverviewclassic pages 32-33).
6. Regulation  
   FAM20C is regulated via post-translational modifications and interactions that influence its localization and activity. Proteolytic processing plays a critical role in its regulation; the kinase undergoes cleavage of an N-terminal propeptide by the Golgi-resident site-1 protease (S1P), a reaction that enhances its secretion and enzymatic activity (chen2021proteolyticprocessingof pages 8-10). In addition, FAM20C forms homo- and heterodimers, with the latter involving the binding of the pseudokinase FAM20A. Although FAM20A lacks catalytic activity, it acts as an allosteric activator that increases FAM20C’s activity and promotes its extracellular secretion (ohyama2016fam20abindsto pages 1-2, cui2015asecretorykinase pages 11-13). Other layers of regulation are mediated by cellular stresses and possibly by lipid-derived molecules such as sphingosine that have been shown to stimulate kinase activity, although detailed molecular mechanisms remain under investigation (cozza2017fam20cisunder pages 15-17).
7. Function  
   FAM20C is critical for the phosphorylation of secreted proteins and thereby plays a key role in biomineralization processes. It phosphorylates enamel matrix proteins (such as amelogenin, ameloblastin, enamelin, and amelotin) and dentin matrix proteins (including dentin matrix protein 1) that are essential for proper tooth development and bone mineralization. In addition, FAM20C phosphorylates extracellular proteins such as osteopontin, which function to regulate hydroxyapatite formation and mineral deposition in skeletal tissues (liu2018fam20cregulatesosteoblast pages 1-3, ishikawa2012therainesyndrome pages 1-2). Beyond its role in biomineralization, FAM20C regulates endoplasmic reticulum proteostasis by phosphorylating ERO1A and P4HB, thereby modulating oxidative protein folding and ER stress responses. Expression patterns indicate that FAM20C is present in tissues with high secretory activity, including bone, teeth, lactating mammary glands, and various other secretory epithelia. This central role in extracellular protein phosphorylation makes FAM20C integral to pathways governing osteoblast differentiation, mineral metabolism, cell migration, adhesion, and lipid homeostasis (chen2021proteolyticprocessingof pages 1-2, ishikawa2012therainesyndrome pages 2-3, palmalara2021fam20coverviewclassic pages 2-4).
8. Other Comments  
   FAM20C mutations are causally linked with Raine syndrome, a rare osteosclerotic bone dysplasia characterized by abnormal bone mineralization, craniofacial dysmorphisms, dental defects, and in many cases neonatal lethality. In addition, altered FAM20C activity has been associated with hypophosphatemic rickets and defective enamel formation. No highly selective direct inhibitors of FAM20C have been described; however, its responsiveness to agents such as sphingosine and related compounds indicates potential avenues for pharmacological modulation aimed at enhancing kinase activity in disease contexts. Moreover, FAM20C phosphorylates a broad spectrum of secreted substrates that include not only classical biomineralization proteins but also factors involved in lipid homeostasis, cell migration, and wound healing, thereby expanding its functional profile beyond traditional roles in bone and tooth development (cozza2015anewrole pages 7-8, ishikawa2012therainesyndrome pages 1-2, venerando2022editorialcaseinkinases pages 4-5).
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