1. Phylogeny  
   Extracellular serine/threonine protein kinase FAM20C belongs to the FAM20 family of secretory kinases, which also includes Fam20A and Fam20B. FAM20C orthologs have been identified across a range of species, including Caenorhabditis elegans (ceFam20), Danio rerio (drFam20C), and Hydra magnipapillata, reflecting a high degree of evolutionary conservation in the kinase domain and overall fold (zhang2018structureandevolution pages 1-2, cui2017structureoffam20a pages 1-2). Phylogenetic analyses indicate that the Fam20 kinases form a distinct clade within the human kinome that diverges from canonical protein kinases and is primarily associated with the secretory pathway. This family is evolutionarily related to ancient kinases, having undergone diversification that culminated in functionally distinct members: Fam20B, a glycosylation-related xylosylkinase, and Fam20C, which functions as a bona fide protein kinase (filatova2015theroleof pages 17-20, zhang2018structureandevolution pages 2-3). The evolutionary studies based on sequence alignments and structural modelling further suggest that the emergence of Fam20C coincided with the advent of vertebrate-specific biomineralization processes, consistent with its key role in bone and tooth formation (palmalara2023potentialroleof pages 1-2).
2. Reaction Catalyzed  
   FAM20C catalyzes the phosphorylation of serine/threonine residues in secreted substrates. The chemical reaction can be described as follows:  
   ATP + [protein]–(L-serine or L-threonine) → ADP + [protein]–(L-serine/threonine)-phosphate + H⁺.  
   This reaction occurs predominantly on secretory proteins, thereby generating the majority of the extracellular phosphoproteome (xu2021fam20cinhuman pages 1-2, da2019invitrophosphorylation pages 1-2).
3. Cofactor Requirements  
   The kinase activity of FAM20C depends on divalent cations for optimal ATP binding and catalysis. Although many kinases utilize magnesium ions (Mg²⁺), FAM20C exhibits a preference for manganese ions (Mn²⁺), which enhance its catalytic efficiency in the Golgi environment (zhang2018secretorykinasefam20c pages 1-2, xiao2013crystalstructureof pages 1-1).
4. Substrate Specificity  
   FAM20C phosphorylates secretory pathway proteins with a high degree of substrate specificity. Its primary consensus phosphorylation motif is Ser-x-Glu/pSer, where ‘x’ represents any amino acid. In addition to this canonical motif, FAM20C demonstrates a broader substrate specificity and is capable of phosphorylating residues within similar variants such as Ser-x-Sp motifs, as observed in secreted salivary proteins (messana2023theposttranslationalmodifications pages 12-13, cui2015asecretorykinase pages 1-2). The specificity for these motifs underlies the enzyme’s role in modulating phosphorylation patterns on proteins involved in biomineralization, extracellular matrix remodeling, and additional extracellular processes (palmalara2023potentialroleof pages 9-10).
5. Structure  
   FAM20C is synthesized with an N-terminal signal peptide that directs the polypeptide into the secretory pathway, where the mature enzyme is predominantly localized to the Golgi apparatus. The mature protein contains a central kinase domain that adopts a two-lobed structure characteristic of the protein kinase-like (PKL) fold. Within this domain, key structural features include a glycine-rich loop that covers the ATP-binding pocket, a catalytic loop with a conserved aspartate residue, and an αC helix that contributes to the proper positioning of residues involved in catalysis (filatova2015theroleof pages 20-24, xiao2013crystalstructureof pages 1-3).  
   Crystal structures of Fam20 family orthologs, such as ceFam20 from Caenorhabditis elegans, reveal that the catalytic core is flanked by an N-terminal segment and an insertion domain. The N-terminal segment wraps around the lower half of the molecule and forms the base of the C-lobe, whereas the insertion domain forms a cap-like structure over the N-lobe. Unique features of FAM20C’s structural organization include the absence of a canonical activation loop, which contributes to its constitutive catalytic activity, and specific residue substitutions (e.g., within the glycine-rich loop) that determine the enzyme’s binding orientation for ATP and substrate peptides (xiao2013crystalstructureof pages 4-5, xiao2013crystalstructureof pages 5-6).  
   AlphaFold-predicted models further reinforce these observations by illustrating that FAM20C retains the overall kinase fold with a well-defined ATP-binding site and conserved catalytic residues, while also accommodating secretory pathway-specific modifications such as potential glycosylation and disulfide bonds that are essential for its stability and function in the Golgi (xu2021fam20cinhuman pages 1-2, cui2017structureoffam20a pages 2-5).
6. Regulation  
   The regulation of FAM20C activity is mediated by several mechanisms that ensure precise control over extracellular protein phosphorylation. A key regulatory mechanism involves the formation of homo- or heterodimeric complexes. Fam20A, a closely related pseudokinase that lacks key catalytic residues, acts as an allosteric activator of FAM20C by forming a complex that enhances its kinase activity (cui2015asecretorykinase pages 11-13, cui2017structureoffam20a pages 15-16). This dimerization not only potentiates enzymatic activity but also contributes to the stabilization of FAM20C, including mutant forms that are associated with disease phenotypes.  
   In addition to its regulation by Fam20A, FAM20C exhibits autophosphorylation events that may play a role in modulating its activity within the Golgi, as suggested by studies on its kinase parameters (ishikawa2012therainesyndrome pages 1-2). Under conditions of endoplasmic reticulum stress, FAM20C also phosphorylates specific ER-resident proteins such as P4HB/PDIA1; this post-translational modification induces a functional switch in P4HB from an oxidoreductase to a molecular chaperone and contributes to the overall maintenance of ER proteostasis (liu2023fam20cregulatesthe pages 19-20, cui2015asecretorykinase pages 1-2).  
   The regulatory network further extends to the modulation of redox homeostasis via the phosphorylation of ERO1A, which enhances its oxidase activity and is required for oxidative protein folding. This phosphorylation event is crucial for maintaining the ER redox state under various stress conditions (fulcher2020functionsandregulation pages 14-15, xu2021fam20cinhuman pages 1-2).
7. Function  
   FAM20C plays a central role in the phosphorylation of secretory proteins, thereby contributing to a wide array of physiological processes. Its most well‐characterized role is in biomineralization, where it phosphorylates proteins such as casein, amelogenin (AMELX), ameloblastin (AMTN), enamelin (ENAM), and osteopontin (SPP1/OPN) to regulate the formation and mineralization of bone and dental tissues (filatova2015theroleof pages 20-24, xiao2013crystalstructureof pages 5-6).  
   In addition to its functions in bone and tooth formation, FAM20C is critical in maintaining endoplasmic reticulum homeostasis. By phosphorylating ERO1A, FAM20C enhances oxidative protein folding, which is essential for proper ER function. Under stress conditions, phosphorylation of P4HB/PDIA1 alters its functional role, thereby reducing ER stress and preventing cell death (liu2023fam20cregulatesthe pages 19-20, xu2021fam20cinhuman pages 1-2).  
   FAM20C is also involved in lipid homeostasis, wound healing, and the regulation of cell migration and adhesion through phosphorylation of a broad spectrum of extracellular proteins; this activity establishes FAM20C as the principal kinase responsible for generating the secreted phosphoproteome (palmalara2023potentialroleof pages 1-2, brutsch2022thesecretedkinase pages 37-41). A consequence of its central role is that mutations or loss-of-function events in FAM20C are linked to severe developmental disorders, most notably Raine syndrome, which is characterized by osteosclerotic dysplasia, hypophosphatemia, and defects in bone mineralization (ishikawa2012therainesyndrome pages 1-2, palmalara2023potentialroleof pages 10-13).
8. Other Comments  
   FAM20C is known by several alternative names including Dentin Matrix Protein 4 (DMP4), Golgi casein kinase, and Golgi-enriched fraction casein kinase. Although inhibitors specifically targeting FAM20C are not extensively characterized, experimental data indicate that the enzyme is insensitive to broad-spectrum kinase inhibitors such as staurosporine, suggesting a unique inhibitor profile (zhang2018secretorykinasefam20c pages 1-2).  
   Clinically, mutations in FAM20C are associated with Raine syndrome, a rare skeletal dysplasia that can present in both lethal and non-lethal forms. These mutations typically disrupt key residues within the kinase domain, leading to impaired substrate phosphorylation and subsequent defects in biomineralization processes. In addition, FAM20C dysfunction has been implicated in dental anomalies due to its role in enamel formation (filatova2015theroleof pages 17-20, palmalara2023potentialroleof pages 13-14).  
   The enzyme’s broad substrate repertoire also extends into pathways involved in cell adhesion and migration, highlighting its potential as a therapeutic target in diseases related to extracellular matrix dysregulation (du2023regulationofsecretory pages 4-5). Further research into the development of specific inhibitors may provide new avenues for modulating FAM20C activity in pathological contexts.
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