1. Phylogeny  
   Integrin‐linked kinase (ILK), encoded by the ILK gene (also referred to as ILK1 and ILK2; UniProt ID Q13418), is an evolutionarily conserved protein that has been identified from early metazoans to mammals. ILK orthologs have been reported in invertebrate models such as Drosophila melanogaster and Caenorhabditis elegans as well as in vertebrates including Xenopus laevis and mammals, indicating that this protein belongs to an ancient kinase–related family present in the common ancestor of eukaryotes (gorska2022integrinlinkedkinase(ilk) pages 2-5, savari2005roleofxenopus pages 13-17, morgner2014roleofintegrinlinked pages 1-7). Although initially classified based on its sequence similarity to serine/threonine kinases, subsequent comparative genomic analyses have revealed that ILK exhibits several key deviations in conserved catalytic residues, suggesting that its role is primarily as a scaffold rather than a conventional enzyme. ILK occupies a unique position within the integrin‐associated kinome. It is grouped with proteins that link extracellular matrix signals to intracellular cytoskeletal and signaling networks, and its phylogeny has been explored within the context of the broader eukaryotic kinase superfamily, which includes other pivotal regulatory enzymes such as PDK1, Akt (PKB), and members of the AGC kinase family (gorska2022integrinlinkedkinase(ilk) pages 2-5, savari2005roleofxenopus pages 13-17).
2. Reaction Catalyzed  
   Canonical serine/threonine kinases catalyze the transfer of a phosphate group from ATP to the hydroxyl group of serine or threonine residues within their substrate proteins, following the chemical reaction:  
     ATP + [protein]-(L-serine/threonine) → ADP + [protein]-(L-serine/threonine)-phosphate + H⁺.  
   ILK was originally reported to phosphorylate substrates such as glycogen synthase kinase-3β (GSK-3β) and protein kinase B (Akt), indicating a potential reaction of this type; however, extensive studies have challenged the intrinsic catalytic activity of ILK, and current evidence favors its role as a pseudokinase, wherein the kinase-like domain is employed predominantly for stabilization and scaffolding functions rather than for catalysis (cabodi2010integrinsignallingadaptors pages 29-31, gorska2022integrinlinkedkinase(ilk) pages 8-10).
3. Cofactor Requirements  
   The reports that initially ascribed kinase activity to ILK indicated a dependency on divalent metal ions in its catalytic assays. In particular, ILK activity in some in vitro studies has been noted as Mn²⁺-dependent, with the presence of manganese ions enhancing phosphorylation events on certain substrates. Although other serine/threonine kinases classically require Mg²⁺ as a cofactor, the data available for ILK specifically point to a requirement for Mn²⁺ ions in the reported catalytic conditions (cabodi2010integrinsignallingadaptors pages 29-31).
4. Substrate Specificity  
   Early studies on ILK demonstrated that it could phosphorylate a range of substrates integral to integrin-mediated signaling, most notably GSK-3β and Akt, which are central to cell proliferation and survival pathways. The phosphorylation of GSK-3β at serine-9, for example, has been linked to attenuation of its kinase activity and subsequent stabilization of downstream effectors such as β-catenin. Similarly, phosphorylation of Akt has been proposed to occur at residue serine-473. Despite these observations, ILK’s substrate specificity remains difficult to define by means of a consensus phosphorylation motif because the kinase domain lacks several residues that are typically essential for catalysis in active kinases. In essence, while ILK has been associated with the phosphorylation of these substrates in early reports, later investigations have established that its role in substrate modification may be indirect and facilitated by its function as a scaffold, thereby bringing together substrates and other active kinases in focal adhesion complexes (cabodi2010integrinsignallingadaptors pages 29-31, marotta2002dysregulationofintegrinlinked pages 75-81).
5. Structure  
   ILK is a 452–amino acid protein that exhibits a modular organization with distinct domains supporting its multifaceted functions. The N-terminal region comprises an ankyrin repeat domain (ARD) that typically contains five ankyrin repeats; these repeats fold into a super-helical structure essential for mediating protein–protein interactions. One of the primary binding partners for this domain is the LIM domain–containing protein PINCH, which is instrumental in the assembly of the ILK–PINCH–Parvin (IPP) complex. Connecting the ARD to the C-terminal region is a pleckstrin homology (PH)-like domain. Although initially believed to bind phosphoinositides, structural studies later excluded such a lipid-binding role for the PH-like domain in ILK, instead suggesting that it acts as a structural linker between the anchoring and catalytic regions (gorska2022integrinlinkedkinase(ilk) pages 7-8, gorska2022integrinlinkedkinase(ilk) pages 8-10).  
   The C-terminal domain of ILK resembles a serine/threonine kinase fold but notably lacks certain conserved catalytic residues—such as the invariant aspartate required for phosphotransfer—that are essential for catalytic activity in classical kinases. This deficiency categorizes ILK as a pseudokinase, a status that is counterbalanced by its ability to engage in critical protein–protein interactions. The kinase-like domain of ILK is responsible for binding to α-parvin, a partner that further contributes to the recruitment of the IPP complex to focal adhesions and to the coupling of integrins with the actin cytoskeleton (gorska2022integrinlinkedkinase(ilk) pages 7-8, lange2010geneticanalysisof pages 7-11).  
   Structural analyses—using approaches ranging from crystallography to computational predictions via AlphaFold—have underscored the importance of the ARD for enforcing correct spatial orientation of ILK within adhesion sites, while the pseudokinase domain provides a rigid platform for docking its binding partners. Furthermore, the interdomain linker region, although not catalytically active, is critical for the overall stability and conformational flexibility of the protein, enabling ILK to function as an integrative adaptor between the extracellular matrix and intracellular signaling networks (gorska2022integrinlinkedkinase(ilk) pages 8-10, gorska2022integrinlinkedkinase(ilk) pages 25-26).
6. Regulation  
   ILK regulation is multifactorial and mediated through several layers of control, which include transcriptional, post-transcriptional, and post-translational mechanisms. At the transcriptional level, ILK expression is modulated by transcription factors such as Sp1, AP-2α, Ets-1, and hypoxia-inducible factors; in addition, several microRNAs (for example, miR-542-3p, miR-625, and miR-145/miR-143) interact with the 3′ untranslated region of ILK mRNA, suppressing its translation (gorska2022integrinlinkedkinase(ilk) pages 5-7, gorska2022integrinlinkedkinase(ilk) pages 2-5).  
   Post-translational modifications of ILK further refine its activity and cellular localization. Several phosphorylation events have been described on key residues such as serine 343, threonine 173, threonine 181, and serine 246; these modifications have been implicated in regulating downstream signaling pathways, including the activation of Akt and the modulation of nuclear-cytoplasmic shuttling (gorska2022integrinlinkedkinase(ilk) pages 13-15, marotta2002dysregulationofintegrinlinked pages 81-87).  
   Another critical regulatory mechanism of ILK is its participation in the formation and stability of the IPP complex. The binding of ILK to PINCH via the ARD is essential for its recruitment to focal adhesions, where it can interact with integrin β cytoplasmic tails and α-parvin. This complex not only stabilizes ILK but also protects it from proteasomal degradation mediated by ubiquitination; chaperones such as Hsp90, along with ubiquitin ligases like CHIP, have been shown to influence ILK stability (radovanac2012regulationofintegrinlinked pages 9-15, gorska2022integrinlinkedkinase(ilk) pages 21-22). Additionally, interaction with ILK-associated phosphatases (e.g., ILKAP) provides a negative feedback loop to modulate its downstream signaling (gorska2022integrinlinkedkinase(ilk) pages 21-22).  
   Collectively, these regulatory mechanisms ensure that ILK’s scaffolding functions—and any residual catalytic activities—are tightly controlled, permitting a dynamic yet exact spatial and temporal regulation of integrin-mediated signaling at focal adhesions (gorska2022integrinlinkedkinase(ilk) pages 16-18, marotta2002dysregulationofintegrinlinked pages 81-87).
7. Function  
   ILK functions primarily as a scaffold protein that mediates protein–protein interactions essential for the assembly and maintenance of focal adhesions, the specialized structures that link integrin receptors to the actin cytoskeleton. By recruiting and stabilizing key interacting partners such as PINCH and α-parvin, ILK forms the heterotrimeric ILK–PINCH–Parvin (IPP) complex, which is critical for the bundling of F-actin filaments and the generation of forces required for cell spreading, adhesion, and migration (gorska2022integrinlinkedkinase(ilk) pages 7-8, gorska2022integrinlinkedkinase(ilk) pages 2-5).  
   In addition to its structural role, ILK participates in the regulation of integrin-mediated signal transduction. It has been linked to the activation of downstream survival pathways, notably through modulation of protein kinase B (Akt) phosphorylation. Although its intrinsic kinase activity remains controversial, early studies suggested that ILK can phosphorylate Akt on serine-473 and inhibit GSK-3β by phosphorylating it on serine-9, thereby influencing processes such as cell proliferation and survival (cabodi2010integrinsignallingadaptors pages 29-31, marotta2002dysregulationofintegrinlinked pages 75-81).  
   ILK is ubiquitously expressed but its levels are often upregulated in pathological conditions such as cancer, where overexpression has been correlated with tumor progression, epithelial–mesenchymal transition (EMT), and metastasis. In these contexts, ILK contributes to the remodeling of the extracellular matrix and the regulation of intracellular signaling cascades that promote invasive phenotypes (tan2006theroleof pages 184-187, zhang…2019significanceofintegrinlinked pages 1-2).  
   Beyond its role in cancer, ILK has been implicated in various physiological processes including cardiomyogenesis, renal development, and neuronal differentiation. Its ability to orchestrate the assembly of adhesive complexes and regulate cytoskeletal dynamics marks it as a critical mediator of cellular architecture and mechanotransduction. Furthermore, ILK influences inside-out integrin activation, which is necessary for the modulation of integrin affinity and the dynamic regulation of cell–matrix adhesion (gorska2022integrinlinkedkinase(ilk) pages 21-22, gorska2022integrinlinkedkinase(ilk) pages 19-20).
8. Other Comments  
   Ongoing research into ILK has led to the exploration of small molecule inhibitors that target its functions. For instance, compounds such as QLT267 have been evaluated as potential inhibitors of ILK activity, with a focus on disrupting its interaction with binding partners rather than inhibiting a catalytic activity that is classified as “pseudo” in nature (gorska2022integrinlinkedkinase(ilk) pages 18-19).  
   ILK is also notable for its disease associations; dysregulation and overexpression of ILK have been observed in a variety of cancers—including colorectal, pancreatic, breast, and melanoma—where such alterations are often linked to poor prognosis. In addition, aberrant ILK function has been implicated in cardiac pathologies, kidney fibrosis, and musculoskeletal disorders, underscoring its broad physiological relevance (tan2006theroleof pages 184-187, gorska2022integrinlinkedkinase(ilk) pages 25-26).  
   Notably, despite extensive study over more than two decades, ILK remains a challenging target from a pharmacological perspective because its kinase domain lacks conventional catalytic residues, and its primary function appears to be as a scaffolding adaptor protein. As such, therapeutic strategies under investigation are increasingly aimed at disrupting critical protein–protein interactions—such as the ILK–α-parvin or ILK–PINCH contacts—rather than inhibiting catalytic activity per se (morgner2014roleofintegrinlinked pages 22-27, radovanac2012regulationofintegrinlinked pages 33-36).
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Each reference has contributed to establishing the nomenclature and functional profile of ILK as a scaffold protein with putative kinase‐like features regulating focal adhesion assembly, integrin signalling, and wide-ranging cellular processes.

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