1. Phylogeny  
   Tyrosine‐protein kinase transmembrane receptor ROR2, encoded by the ROR2 (also known as NTRKR2) gene, is a member of the receptor tyrosine kinase‐like orphan receptor family. ROR2 is evolutionarily conserved across metazoans, with orthologs observed from nematodes to mammals. In vertebrates, high sequence similarity is noted between human ROR2 and its murine ortholog (approximately 92% identity), implying conserved structural and functional roles in development. Phylogenetically, ROR2 and other Ror‐family receptors form a distinct branch within the larger tyrosine kinase superfamily; they display a unique domain architecture that distinguishes them from classical receptor tyrosine kinases despite sharing the common catalytic core. This subgroup shares similarity with muscle‐specific kinase (MuSK) receptors regarding extracellular domain organization and is embedded within an evolutionary framework that includes numerous kinases traced back to early eukaryotes (yoda2003expressionandfunction pages 1-3, rebagay2012ror1andror2 pages 1-2).
2. Reaction Catalyzed  
   ROR2 catalyzes the transfer of the terminal phosphate from ATP to tyrosine residues on substrate proteins. In biochemical terms, the reaction can be represented as follows:  
     ATP + [substrate]-tyrosine → ADP + [substrate]-phosphotyrosine + H⁺.  
   This phosphotransfer reaction is central to its role as a signaling enzyme, although in vitro studies indicate that ROR2 exhibits minimal intrinsic kinase activity under basal conditions (Information; template).
3. Cofactor Requirements  
   The kinase activity of ROR2 depends on divalent metal ions that serve as essential cofactors. In practice, Mg²⁺ is required to facilitate the proper positioning of ATP within the active site and to stabilize the transition state during phosphoryl transfer (template).
4. Substrate Specificity  
   While a definitive consensus substrate motif for ROR2 has not been rigorously established, ROR2 is known to phosphorylate specific intracellular targets. One of the reported substrates is 14-3-3 β (YWHAB), whose phosphorylation is associated with downstream signaling events that induce osteogenesis and bone formation. Moreover, ROR2 signals primarily in the context of non‐canonical Wnt pathways activated by Wnt5a; thus, its substrate specificity is functionally linked to the modulation of signaling cascades mediated by proteins such as filamin A. However, detailed consensus sequences or comprehensive in vitro substrate specificity profiles remain to be fully characterized (Information; debebe2015ror2asa pages 1-3, liu2008wnt5ainduceshomodimerization pages 1-2).
5. Structure  
   ROR2 is a multidomain, single‐pass transmembrane receptor with a well‐defined domain organization. Its extracellular region comprises three main modules:  
    • An immunoglobulin (Ig)‐like domain, which likely contributes to receptor dimerization or interactions with cell surface partners;  
    • A cysteine‐rich domain (CRD) that resembles the Wnt‐binding region of Frizzled receptors and plays a critical role in ligand recognition, particularly for Wnt5a;  
    • A kringle domain, which is implicated in protein–protein interactions.  
   These domains establish the framework for ligand binding and extracellular signaling events (rebagay2012ror1andror2 pages 1-2, yoda2003expressionandfunction pages 5-6).

A single α‐helical transmembrane segment anchors the receptor within the plasma membrane. The intracellular part is composed of a tyrosine kinase (TK) domain flanked by serine/threonine‐rich regions and a proline‐rich (PR) domain. The TK domain is organized into the canonical bilobal structure typical of kinases, featuring an N-terminal lobe predominated by β-sheets and a regulatory C-terminal lobe that includes the αC-helix, activation loop, and other catalytic motifs. Notably, structural analyses and mutagenesis studies indicate that the kinase domain adopts an autoinhibited conformation, akin to that seen in the insulin receptor family; alterations in conserved catalytic residues contribute to the observation that ROR2 exhibits very little intrinsic tyrosine kinase activity in vitro (alfaro2015theror2tyrosine pages 30-36, debebe2015ror2asa pages 6-8). Thus, although the domain architecture supports catalytic activity, regulatory modifications and conformational constraints may restrict its phosphorylation efficiency under basal conditions.

1. Regulation  
   The activation and regulation of ROR2 occur primarily through ligand binding and post-translational modifications. Engagement of the extracellular CRD by the non-canonical Wnt ligand Wnt5a initiates receptor dimerization—a critical step for activation. Wnt5a binding induces homodimerization of ROR2, which facilitates subsequent autophosphorylation on key tyrosine residues within the intracellular domain (liu2008wnt5ainduceshomodimerization pages 1-2, riquelme2023ror2homodimerizationis pages 11-12). Autophosphorylation is further modulated by interactions with additional kinases; for instance, casein kinase Iε and glycogen synthase kinase 3 (GSK3) have been shown to phosphorylate ROR2, thereby contributing to full receptor activation and amplifying downstream signal propagation (debebe2015ror2asa pages 10-11, debebe2015ror2asa pages 11-12).

Moreover, the receptor’s intracellular regulatory domains (including serine/threonine-rich regions) may serve as platforms for further modifications that affect protein stability and interactions with downstream adaptor proteins. Ligand-induced conformational changes modulate the accessibility of the activation loop and catalytic cleft, thereby playing an essential role in determining ROR2’s functional state. These multilayered regulatory mechanisms ensure that ROR2 signaling is tightly controlled, enabling appropriate cellular responses to environmental cues such as Wnt5a stimulation.

1. Function  
   Biologically, ROR2 plays a multifaceted role in both developmental and pathological contexts. During embryogenesis, ROR2 is expressed in mesenchymal and neural crest-derived tissues and is critically involved in the early formation of chondrocytes, cartilage, and growth plates. By phosphorylating substrates such as 14-3-3 β (YWHAB), ROR2 contributes to the induction of osteogenesis and bone formation. In this role, ROR2-mediated signaling is essential for skeletal development and proper morphogenesis of the cartilage template (Information; billiard2005theorphanreceptor pages 1-2, yoda2003expressionandfunction pages 8-10, wright2009ror2adevelopmentally pages 6-8).

In addition to its developmental functions, ROR2 serves as a receptor for Wnt5a in non-canonical Wnt signaling pathways. Ligand binding to ROR2 results in inhibition of canonical Wnt3a-mediated signaling while activating intracellular cascades such as the planar cell polarity (PCP) pathway. These signaling events are known to regulate cellular processes including cell polarity, migration, and adhesion. For example, in hippocampal neurons, ROR2 plays a role in the regulation of dendritic spine morphogenesis and the modulation of synaptic transmission, thereby influencing neuronal connectivity and plasticity (alfaro2015theror2tyrosine pages 1-6, cerpa2015ror2functionsas pages 1-2).

Furthermore, aberrant expression of ROR2 has been documented in various cancers. Overexpression of ROR2 in tumor cells correlates with enhanced migratory and invasive capabilities, as well as increased extracellular matrix remodeling—processes that contribute to tumor progression and metastasis. Such oncogenic activity has been observed in malignancies including osteosarcoma, renal cell carcinoma, and melanoma, establishing ROR2 as both a prognostic biomarker and a potential therapeutic target in oncology (billiard2005theorphanreceptor pages 8-9, debebe2015ror2asa pages 1-3, wright2009ror2adevelopmentally pages 12-14).

1. Other Comments  
   In terms of clinical relevance, mutations in ROR2 have been implicated in congenital skeletal disorders. Loss-of-function mutations are causative for autosomal recessive Robinow syndrome, a condition characterized by limb shortening, craniofacial dysmorphism, and vertebral segmentation defects, whereas heterozygous mutations can result in brachydactyly type B. These disease associations underscore the critical role of ROR2 in skeletal development and highlight the importance of its precise regulatory control (yoda2003expressionandfunction pages 14-15).

In cancer, ROR2’s overexpression in select tumor types supports its candidacy as a therapeutic target. Although specific small-molecule inhibitors that target the kinase activity of ROR2 have not been definitively characterized—possibly due to its low intrinsic catalytic activity—therapeutic strategies employing monoclonal antibodies to block the extracellular domain of ROR2 are under investigation. Such approaches aim to interrupt aberrant Wnt5a-ROR2 signaling and mitigate tumor invasiveness (rebagay2012ror1andror2 pages 6-7, thorup2020ror2blockadeas pages 5-10).

Other experimental interventions include RNA interference techniques, which have been used to suppress ROR2 expression and consequently reduce migratory and invasive properties in cancer cells. These observations reinforce the role of ROR2 in modulating key aspects of cell behavior and further justify its investigation as a promising target in both developmental disorders and oncology.

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