We characterize CrRLK1, a novel type of receptor-like kinase (RLK), from the plant Catharanthus roseus (Madagascar periwinkle). The protein (90.2 kDa) deduced from the complete genomic and cDNA sequences is a RLK by predicting a N-terminal signal peptide, a large extracytoplasmic domain, a membrane-spanning hydrophobic region followed by a transfer-stop signal, and a C-terminal cytoplasmic protein kinase with all 11 conserved subdomains. It is a novel RLK type because the predicted extracytoplasmic region shares no similarity with other RLKs. The autophosphorylation was investigated with affinity-purified proteins expressed in Escherichia coli. The activity was higher with Mn$^{2+}$ than with Mg$^{2+}$ and achieved half-maximal rates at 2–2.5 μM ATP. The phosphorylation was predominantly on Thr, less on Ser, and not on Tyr. In contrast to other plant RLKs, the kinase used an intra- rather than an intermolecular phosphorylation mechanism. After protein cleavage with formic acid, most of the radioactivity was in a 14.1-kDa peptide located at the end of the kinase domain. Mutagenesis of the four Thr residues in this peptide identified Thr-720 in the subdomain XI as important for autophosphorylation and for phosphorylation of β-casein. This Thr is conserved in other related kinases, suggesting a subfamily sharing common autophosphorylation mechanisms.

Animal receptor protein kinases (RPK) located in the membranes play an important role in the perception and transmittance of external signals. All RPK contain an extracellular domain connected by a membrane-spanning amino acid (AA) stretch to the intracellular kinase domain. The proteins can be subdivided into two groups that autophosphorylate on Ser/Thr rather than an intermolecular phosphorylation mechanism. After protein cleavage with formic acid, most of the radioactivity was in a 14.1-kDa peptide located at the end of the kinase domain. Mutagenesis of the four Thr residues in this peptide identified Thr-720 in the subdomain XI as important for autophosphorylation and for phosphorylation of β-casein. This Thr is conserved in other related kinases, suggesting a subfamily sharing common autophosphorylation mechanisms.

Several plant cDNAs and genes for RPK homologs sharing the same basic domain structure have been described. They were called receptor-like kinases (RLK), because the ligands are unknown and their function as receptors has not yet been demonstrated. Several groups are presently distinguished, and the classification is usually based on the sequences in the extracellular domain (reviewed in Ref. 2): (a) the S-domain type, with similarities to the S-locus glycoproteins in Brassica; these proteins also contain ten or more cysteines in conserved positions; (b) the leucine-rich repeat type, with 9–26 Leu-rich repeats; and (c) the epidermal growth factor (EGF)-like type that contains several EGF-like repeats. Very recent data suggest two additional types, with the extracellular region related either to plant defense proteins (3) or to lectins (4), but the investigations have not been extended much beyond the sequences.

The physiological functions of plant RLKs are unknown, except for the S-domain type RLKs from Brassica that appear to be involved in the self-incompatibility phenotype (5–7). There is considerable interest also in the other RLK because they are thought to be involved in extracellular signal perception, in particular in plant development, plant/microbe interactions, and disease resistance phenomena (reviewed in Ref. 8).

Biochemical studies after heterologous protein expression in Escherichia coli showed that autophosphorylation of the plant RLK is on Ser and/or Thr, with the possible exception of a Petunia RLK that uses Ser and Tyr residues (9). Autophosphorylation appears to occur predominantly by intermolecular phosphorylation (trans), and it has been suggested that oligomerization may be involved in the regulation of the kinase activity (10). The sites of autophosphorylation have not yet been identified in any RLK.

CrRLK1, the protein kinase from Catharanthus roseus described in this work, is interesting for several reasons. It represents a novel RLK type, and in contrast to other plant RLK it autophosphorylates predominantly with an intra- rather than with an intermolecular mechanism. We also report the first identification of a Thr residue in a RLK that is important for both autophosphorylation and the activity of the kinase to phosphorylate other proteins. The Thr is conserved in some other related plant kinases, suggesting that these may follow the same activation mechanism.

**EXPERIMENTAL PROCEDURES**

**Plant Material**—The cell suspension culture of Madagascar periwinkle (C. roseus L. G. Don, line CP3a), its maintenance on MX medium, and the nutritional downshift by incubating the cells in an 8% sucrose solution have been described (11, 12).

**cDNA, cDNA Library, and cRACE for the 5′ End of the mRNA**—Poly(A)$\beta$-enriched RNA was isolated (13) from C. roseus cell cultures treated for 7.5 h with a change from MX medium to 8% sucrose (14). The Northern blots were performed according to published procedures (15). The cDNA library was constructed using 5 μg of poly(A)$\beta$-
enriched RNA and cDNA synthesis kits from Amersham Corp. (cDNA Synthesis Kit No. 1304-02) and Pharmacia LKB Biotechnology Inc. (You-Prime cDNA Synthesis Kit No. 27-9273-01). After addition of EcoRI linkers and digestion with EcoRI, the cDNAs were ligated to EcoRI-digested phage ANM1149 (13) and packaged with a kit from Amersham Corp. (Lambda In Vitro Packaging Kit No. N334L). The screening procedures have been described (13–15).

The 5’ end of the mRNA was obtained with the cRACE technique that uses the circularization of single-stranded cDNA and polymerase chain reaction amplifications with two sets of primers (16). The positions of the primers in the first cDNA were 396–375 (first strand cDNA synthesis), 215–198 and 254–272 (first amplification of circularized cDNA), and 103–81 and 327–348 (nested primers for second amplification). The DNA fragments were cloned blunt-end into the Smal site of vector pTZ19R.

**Genomic Southern Blot and Genomic Clones**—The Southern blots were performed with published procedures (15). They identified a 3.3-kbp EcoRI and a 2.5-kbp Asp718 fragment (see “Results”), and both were analyzed. For the EcoRI fragment, the fragments in the range from 7–10 kbp were eluted from the gel and cloned into the EcoRI site of ANM1149 (13). The fragment was recloned into vector pTZ19R after its isolation by screening with the cDNA. With the Asp718 frag- ment, the 5’ end of the gene was obtained by inverse PCR (17) with the circularized 2.5-kbp genomic Asp718 fragment, using oligonucleotides corresponding to the positions 348–327 and 969–990 of the cDNA. The blunt-end-fragment was cloned into vector pTZ19R.

**DNA Sequence and Computer Analysis**—The cDNA and the gene were sequenced by the DNA sequenc- ing technique using vectors and phages as described in Ref. 18. The pTZ18R and pTZ19R system, helper phage M13K07, E. coli strain JM109 (Pharmacia LKB Biotechnology Inc.), and the reverse sequence and the universal primers (Boehringer Mannheim) or custom-synthesized oligonucleotides were used with subclone cDNA fragments. DNA polymerization reactions were performed with [32P]dATP (37 TBg/mmol, Amersham Corp.) and modified T7 DNA polymerase (Se- quenase, Biochemical Corp.). The protein motifs were identified according to Refs. 19 and 20. TBLASTN (21) was employed for similarity searches in the data bases.

**Expression of Kinase Fusions in Escherichia coli and Protein Purifi- cation**—We used translational fusions of the 42.7-kDa maltose-binding protein (MBP, expressed from vector pMAL-c2; New England Biolabs) (22) with polypeptides encoded in the first cDNA. The expression was carried out with the complete coding region in the cDNA (MCPK0, fusion = 126 kDa), with the N-terminal 55.3-kDa (MCPK2, fusion = 98 kDa), and with the 43.2-kDa catalytic domain (MCPK1, fusion = 86 kDa) (see Fig. 1C for overview). To express MCPK0, the cDNA was excised with SmaI, and with the 43.2-kDa catalytic domain, the single-strand ends were filled in, and the EcoRI-digested phage packaging Kit No. NM1149 (13) and packaged with the MBP part in the fusion proteins alloweda one-step affinity purification for overview). To express MCPK0, the cDNA was

**Identification of Phosphorylated AA—**The incubations followed the standard assays except for the following modifications. The amount of MBP-protein kinase fusion was raised to 10 μg, the γ-32P[ATP] was increased to 10 μCi, and the incubations were carried out at 37 °C for 40 min. The radioactive proteins from 10 assays were analyzed by gel electrophoresis, blotted to a nitrocellulose membrane, and stained with Ponceau S red (0.5% solution in 10% acetic acid). The 126-kDa bands were excised and treated with 6 ml of 70% formic acid for 48 h with vigorous shaking at 37 °C to cleave the protein between Asp-Pro resi- dues (24) and to solubilize the polypeptides (25). The nitrocellulose membrane was removed, and the extract was dried by vacuum centrifugation. The residue was dissolved in 70 μl of sample buffer and subjected to Tricine-sodium dodecyl sulfate-polyacylamide gel electrophoresis (26). Labeled polypeptides were detected by autoradiography.

**Antiserum and Immunoblotts**—A fragment containing the complete 2667-bp cDNA, but with the Lys in the phosphotransfer site mutated to Arg, was inserted into the NcoI site of the expression vector pQE-6 (29), thus providing a start codon and the signals necessary for regulated protein expression. The plasmid was maintained in *E. coli* strain M15[pREP4] (29). The cultures were grown in Luria-Bertani medium (1% Bacto-tryptone, 0.5% Bacto-yeast extract, 0.5% NaCl, 0.2% glycerol, 0.02% MgSO4 (pH 7.5)), and protein expression was induced with 2 mM isopropyl-1-thio-β-D-galactopyranoside for 3 h at 37 °C. The protein (PKO) was isolated with the techniques detailed in Strebel et al. (30) and then used to raise antibodies in a hen. The immunoblots (14) were performed with the IgY fraction (BioTools, Denzlingen, Germany) and a secondary antibody (rabbit anti-chicken) coupled with alkaline phos- phatase (Sigma).

**RESULTS**

**Molecular Analysis of CrRLK1, a Novel Type of Plant RLK**—The first cDNA was identified fortuitously during a screen of a library from cell cultures transferred from the standard growth medium to an aqueous 8% sucrose solution. This nutritional downshift was originally used for the induction of alkaloid biosynthesis (11, 12) and more recently for the cloning of induced cytochrome P450 (14). The cDNA contained 2667 bp and an open reading frame of 750 AA that started in the EcoRI site and terminated at position 2251 (see scheme in Fig. 1A). Similarity searches in the data bases indicated that the C-terminal 300 AA represented the catalytic domain of a protein kinase that was separated from the large N-terminal region by a putative membrane-spanning stretch. This suggested that the cDNA encoded a RLK.

The expected N-terminal hydrophobic signal sequence was absent in the cDNA, and the size of the mRNA (3 kb, Fig. 2B) suggested that the cDNA lacked the 5’ end of the mRNA. The RNA blots also showed that the mRNA was of very low abun-dance and that it was in fact not induced by the nutritional...
downshift of the cultures. The 5' end was obtained with the cRACE technique, and several independent clones indicated that the mRNA started at least 336 bp upstream of the EcoRI site. The first AUG was 159 bases upstream of the restriction site, and this increased the size of the protein by 53 AA.

The genomic blot revealed a simple pattern of strongly hybridizing fragments (Fig. 2A), suggesting a single copy gene. The 8.3-kbp EcoRI fragment was cloned and analyzed. The kinase sequence was located at the end of the fragment, terminating in an EcoRI site that corresponded to that at the 5' end of the cDNA. No introns were detected in the protein coding region, but the cDNA and genomic sequences diverged in the last 109 bp of the 3' noncoding region in the cDNA. A repeated database search showed that the sequences in the cDNA were from E. coli (x in Fig. 1A). The genomic DNA contained at the point of divergence an almost perfect direct repeat of 43 bp (rr in Fig. 1B). The junction with the E. coli sequences was predicted to be responsible for the recombination. The 5' end of the gene was obtained by inverted PCR with the 2.5-kbp Asp718 fragment indicated by the genomic blot (Fig. 2A). It also contained no introns.

The deduced protein CrRLK1 (Fig. 3) contained 803 AA (calculated size 90.2 kDa). Its predicted domain structure followed the definition of the RLK type kinases: a hydrophobic N-terminal putative signal peptide, a large N-terminal region that is thought to be extracytoplasmic, a putative hydrophobic membrane-spanning stretch of 24 AA followed by a membrane transfer-stop signal, and a C-terminal kinase catalytic domain with all 11 subdomains described for protein kinases. The highest similarity scores for the kinase domain (58% and 54% identity, respectively) were obtained with the Lycopersicon pimpinellifolium kinases Pto (32) and Fen (33); interestingly, these do not belong to the RLK class because they consist of little more than the catalytic kinase domain (Fig. 3).
reach with 0.5–0.75 mM MnCl₂ (Fig. 4). This distribution is characteristic for RLK, and there is no obvious difference between the two proteins. MCPK₁* was a mutant in which the essential Lys (Lys-499 in the complete protein) in the phosphotransfer site of MCPK₁ had been mutagenized to Arg, and the protein was inactive (lane 3). This protein was then co-incubated with MCPK₀ to test whether the active kinase phosphorylated the inactive mutant. The result showed no significant phosphorylation of MCPK₁* (lane 5, the weak band at 80 kDa is a degradation product from MCPK₀, see lanes 1 and 6). The same result was observed in the combination of MCPK₁ (active) with MCPK₀* (inactive mutant) (not shown). The kinase also did not trans-phosphorylate MCPK₂ (98 kDa) that contained the N-terminal part of the kinase plus a small part of the catalytic domain (lane 8), indicating that they did not hinder each other in activity. In summary, these results showed that the *C. roseus* kinase predominantly performed an intramolecular autophosphorylation, and an intermolecular phosphorylation of other kinase molecules was only detectable after very long exposures.

The results after total hydrolysis of both MCPK₀ and MCPK₁ and subsequent analysis of the radioactive AA showed that the autophosphorylation was mostly on Thr (80%) and much less in Ser residues (20%), and radioactive Tyr was not detectable.
Identification of a Thr Residue Important for Auto- and Substrate Phosphorylation—MCPK0 was used to identify the region of the protein that was autophosphorylated. The radioactive protein was treated with formic acid to cleave between Asp and Pro residues, and the fragments were separated by electrophoresis. Fig. 6A shows that most of the radioactivity was in a 14.1-kDa polypeptide. Counting from the N-terminal, the MCPK0 protein sequence indicated that polypeptides of 34.6 (MBP-part), 26.1 (partly MBP), 6.5, 41.2, 3.7, and 14.1 kDa were to be expected from the formic acid cleavage. Due to the large size differences, the labeled 14.1-kDa peptide could be unambiguously located to the C-terminal of the kinase, more precisely to the region containing the subdomains X and XI of the kinase catalytic domain and the C-terminal end of the protein (see Fig. 3, the cleavage site is marked with DP). Most of the other radioactive polypeptides could be explained as partial digests containing the 14.1-kDa peptide. The exception was a 32.6-kDa protein (Fig. 6A) that could represent the sum of the 26.1- and the 6.5-kDa peptides, and this suggested a low level of phosphorylation at the N-terminal. The 14.1-kDa peptide was isolated, and the analysis after total hydrolysis demonstrated about 90% of the radioactivity in Thr, the rest in Ser, and none in Tyr (Fig. 6B).

The 14.1-kDa peptide contained four Thr residues (positions 720, 734, 767, and 795 in CrRLK1; marked by T in Fig. 3). All four were mutated in MCPK0 individually to Ala to investigate their role in the autophosphorylation. Assays with the affinity-purified proteins showed that the Thr-720 mutant was nearly inactive (Fig. 7B), although the protein was present in the same amount as the unmodified protein (Fig. 7A). Only long exposures of the film revealed a clear radioactive band, but it was too weak to attempt an identification of the phosphorylated AA. It may represent the Ser autophosphorylation that was too weak to attempt an identification of the phosphorylating Thr, Tyr, and Ser in the chromatogram.

The experiments with the MBP-fusion indicated that MBP or the glutathione S-transferase, and therefore it seems very unlikely that a different approach was responsible for the difference to CrRLK1. The two RLK5 fusion proteins had very similar apparent $K_m$ values for ATP (17.8 and 15.2 $\mu$M), suggesting that the MBP or the glutathione S-transferase parts of the proteins had no differential effect on the enzyme activity. The experiments with the C. roseus MBP-fusion indicated half-maximal rates at 2–2.5 $\mu$M ATP, and the higher affinity is likely to reflect one of the differences between intra- and intermolecular phosphorylation. This property is interesting because it suggests that CrRLK1 activation does not require oligomerization.

A higher autophosphorylation activity with Mn$^{2+}$ than with Mg$^{2+}$ has also been described for other RLK (10, 34), but the significance in vivo is not clear. The preferential phosphorylation of Thr residues was also reported for a Leu-rich (37) and a S-domain type RLK (41), but a generalization is not possible because a preference for Ser was described for other RLK of the S-domain type (42).

The results with the Thr-720 → Ala mutant suggest that this Thr is not autophosphorylated residue. It should be noted, however, that it is not possible at this point to rigorously exclude the possibility that Thr-720 is necessary for these activities, but is not phosphorylated itself. The exchanges of the other Thr residues had no such drastic effects on autophospho-
The high abundance of Ser residues in the protein. The combination of Thr residues in the C-terminal 14.1 kDa of CrRLK1 and alignment with related sequences. The numbers refer to the AA position in the complete kinase. Dots, identical AA; underlined, sequence similarity. The peptides OSR07581A (from rice, Oryza sativa) and ATT84134 and H36409 (both from Arabidopsis thaliana) were translated from the partial cDNA sequences in the EST data base; ?, unknown residue (undefined base in sequence).

The Thr-734 (end of subdomain XI) in CrRLK1 in a region that is otherwise highly conserved (Fig. 8). A possible functional significance of this Thr residue is its conservation among RLKs and the presence of a Thr residue in a similar position (Fig. 7C). The Ser autophosphorylation remains to be investigated, but this will be difficult because it is very low and because of the high abundance of Ser residues in the protein. The complete loss of β-casein phosphorylation with the Thr-720 mutant suggests that Ser autophosphorylation plays a minor role, if any, in the phosphorylation of other proteins.

The Thr Important for Auto- and Substrate Phosphorylation Is Conserved in Other Plant Protein Kinases—This is the first identification of a residue in a plant kinase that is important for auto- and substrate phosphorylation. The other plant RLK do not contain a Thr in the position corresponding to Thr-720 in CrRLK1, but the most closely related kinases (Pto and Fen from tomato) do have a Thr (Fig. 8). These do not belong to the RLK group because they contain not much more than the catalytic kinase domain, but they may be membrane-anchored via a myristyl residue (43). Interestingly, these proteins also predominantly autophosphorylated on Thr residues (44), but a further characterization is not available. The EST (expressed sequence tag) data base contained three partial putative plant kinase sequences with about 50% identity to the C-terminal of Pto, Fen, and CrRLK1, and these also had a Thr at the same position (Fig. 8). It would be interesting to see whether the proteins belong to one of the known RLK types. Remarkably, all of the related proteins contain a Ser at the position of Thr-734 (end of subdomain XI) in CrRLK1 in a region that is otherwise highly conserved (Fig. 8). A possible functional significance of these similarities remains to be elucidated.

Acknowledgment—We are grateful to G. Lurz for competent assistance.

REFERENCES

1. Ulrich, A., and Schlessinger, J. (1990) Cell 61, 203–212
2. Braun, D. M., and Walker, J. C. (1996) Trends Biochem. Sci. 21, 70–73
3. Wang, X., Zafian, P., Choudhary, M., and Lawton, M. A. (1996) Proc. Natl. Acad. Sci. U. S. A. 93, 2598–2602
4. Swarup, R., Dumais, C., and Cook, J. M. (1996) Plant Physiol., Plant Gene Regist Register PGR 96–022
5. Stein, J. C., Howlett, B., Boyes, D. C., Nasrallah, M. E., and Nasrallah, J. B. (1991) Proc. Natl. Acad. Sci. U. S. A. 88, 8816–8820
6. Goringer, D. R., Graflin, T., Schaefer, U., and Rothstein, S. J. (1993) Plant Cell 5, 531–539
7. Nasrallah, J. B., Rundle, S. J., and Nasrallah, M. E. (1994) Plant Cell 5, 373–384
8. Hammond-Kosack, K. E., Jones, D. A., and Jones, J. D. G. (1996) New Phytol. 133, 11–24
9. Mu, J. H., Lee, H.-S., and Kao, T.-H. (1994) Plant Cell 6, 709–721
10. Horn, M. A., and Walker, J. C. (1994) Biochim. Biophys. Acta 1208, 65–74
11. Knobloch, K.-H., and Berlin, J. (1980) Z. Naturforsch. 35c, 551–556
12. Schiel, O., Witte, L., and Berlin, J. (1987) Z. Naturforsch. 42c, 1075–1081
13. Schroder, G., Brown, J. W. S., and Schroer, J. (1988) Eur. J. Biochem., 170, 161–169
14. Veiter, H.-P., Mangel, U., Schroder, G., Marner, F.-J., Werck-Reichhart, D., and Schroder, J. K. (1992) Plant Physiol. 100, 998–1007
15. Sambrook, J., Fritsch, E. F., and Maniatis, T. (1989) Molecular Cloning: A Laboratory Manual, Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY
16. Maruyama, I. N., Rakow, T. L., and Maruyama, H. I. (1995) Nucleic Acids Res. 23, 3796–3797
17. Hengen, P. N. (1995) Trends Biochem. Sci. 20, 372–373
18. Von Lintig, J., Zanker, H., and Schroer, J. (1991) Mol. Plant-Microbe Interact. 4, 370–378
19. Baireach, A. (1992) Nucleic Acids Res. 20, 2013–2018
20. Hanke, S. K., and Hunter, T. (1995) FASEB J. 9, 576–596
21. Altschul, S. F., Gish, W., Miller, W., Myers, E. W., and Lipman, D. J. (1990) J. Mol. Biol. 215, 403–410
22. Mains, C. V., Riggs, P. D., Grandea, A. G. I., Slatko, B. E., Moran, L. S., Taglamont, J. A., McReynolds, L. A., and Guan, C. (1988) Gene (Amst.) 74, 365–373
23. Kunke, T. A. (1985) Proc. Natl. Acad. Sci. U. S. A. 82, 488–492
24. Landos, M. (1977) Methods Enzymol. 47, 145–149
25. Anderson, P. J. (1985) Anal. Biochem. 146, 105–110
26. Schagger, H., and Von Jagow, G. (1987) Anal. Biochem. 166, 368–379
27. Kamps, M. P. (1991) Methods Enzymol. 201, 21–27
28. Neufeld, E., Goren, H. J., and Balond, D. (1989) Anal. Biochem. 177, 138–143
29. Crowe, J., and Hanco, K. (1992) The QIAexpressionist, QIagen Inc., Chatsworth, CA
30. Strebel, K., Beck, E., Strohmaier, K., and Schaller, H. (1986) J. Virol. 57, 983–981
31. Blobel, G. (1980) Proc. Natl. Acad. Sci. U. S. A. 77, 1496–1500
32. Martin, G. B., Brommonschenkel, S. H., Chunwongse, J., Frary, A., Ganal, M. W., Spaye, R., Wu, T., Earle, E. D., and Tanksley, S. D. (1993) Science 262, 1432–1436
33. Martin, G. B., Frary, A., Wu, T., Chunwongse, J., Brommonschenkel, S. H., Earle, E. D., and Tanksley, S. D. (1994) Plant Cell 6, 1543–1552
34. Schaller, G. E., and Bleecker, A. B. (1993) Methods Enzymol. 221, 368–379
35. Zhang, R., and Walker, J. C. (1993) Plant Mol. Biol. 21, 1171–1174
36. Song, W.-Y., Wang, G.-L., Chen, L.-L., Kim, H.-S., Pi, L.-Y., Holsten, T., Gardner, J., Wang, B., Zhai, W.-X., Zhu, L.-H., Faquett, C., and Ronald, P. (1995) Science 270, 1804–1808
37. Chang, C. S., Schaller, G. E., Patterson, S. E., Kwon, S. F., Meyerowitz, E. M., and Bleecker, A. B. (1992) Plant Cell 4, 1263–1271
38. Tobias, C. M., Howlett, B., and Nasrallah, J. B. (1992) Plant Physiol. 99, 284–290
39. Dwyer, K. G., Kandasamy, M. K., Mahosky, D. I., Acciaj, K., Kudish, B. I., Miller, J. E., Nasrallah, M. E., and Nasrallah, J. B. (1994) Plant Cell 6, 1829–1843
40. Torii, K. U., Mitsukawa, N., Osumi, T., Matsuura, Y., Yokoyama, R., Whittier, R. F., and Komeda, Y. (1996) Plant Cell 7, 249–257
41. Loh, Y.-T., and Martin, G. B. (1995) Plant Physiol. 108, 1735–1739
Novel Type of Receptor-like Protein Kinase from a Higher Plant (Catharanthus roseus): cDNA, GENE, INTRAMOLECULAR AUTOPHOSPHORYLATION, AND IDENTIFICATION OF A THREONINE IMPORTANT FOR AUTO- AND SUBSTRATE PHOSPHORYLATION

Paul Schulze-Muth, Stefan Imler, Gudrun Schröder and Joachim Schröder

J. Biol. Chem. 1996, 271:26684-26689.
doi: 10.1074/jbc.271.43.26684

Access the most updated version of this article at http://www.jbc.org/content/271/43/26684

Alerts:
- When this article is cited
- When a correction for this article is posted

Click here to choose from all of JBC's e-mail alerts

This article cites 41 references, 19 of which can be accessed free at http://www.jbc.org/content/271/43/26684.full.html#ref-list-1