Light- and Guanosine 5′-3-O-(Thio)triphosphate-sensitive Localization of a G Protein and Its Effector on Detergent-resistant Membrane Rafts in Rod Photoreceptor Outer Segments*

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Keiji Seno†, Mika Kishimoto‡, Masayoshi Abe‡, Yusuke Higuchi‡, Masanori Mieda‡, Yuko Owada‡, Wataru Yoshiyama§, Han Liu‡, and Fumio Hayashi¶

From the ‡Graduate School of Science and Technology and §Department of Biology, Faculty of Science, Kobe University, Nada, Kobe 657, Japan

Detergent-resistant membrane microdomains in the plasma membrane, known as lipid rafts, have been implicated in various cellular processes. We report here that a low-density Triton X-100-insoluble membrane (detergent-resistant membrane; DRM) fraction is present in bovine rod photoreceptor outer segments (ROS). In dark-adapted ROS, transducin and most of cGMP-phosphodiesterase (PDE) were detergent-soluble. When ROS membranes were exposed to light, however, a large portion of transducin localized in the DRM fraction. Furthermore, on addition of guanosine 5′-3-O-(thio)triphosphate (GTPγS) to light-bleached ROS, transducin became detergent-soluble again. PDE was not recruited to the DRM fraction after light stimulus alone, but simultaneous stimulation by light and GTPγS induced a massive translocation of all PDE subunits to the DRM. A cholesterol-removing reagent, methyl-β-cyclodextrin, selectively but partially solubilized PDE from the DRM, suggesting that cholesterol contributes, at least in part, to the association of PDE with the DRM. By contrast, transducin was not extracted by the depletion of cholesterol. These data suggest that transducin and PDE are likely to perform their functions in phototransduction by changing their localization between two distinct lipid phases, rafts and surrounding fluid membrane, on disc membranes in an activation-dependent manner.

The phototransduction system in the photoreceptor rod outer segments (ROS)1 of vertebrates is a typical G protein-mediated signaling system. In the prevailing model of phototransduction (1), light-excited rhodopsin interacts with the GDP form of the heterotrimeric G protein transducin and stimulates GDP-GTP exchange on its α-subunit (Tα). GTP-Tα separates from its counterpart, the βγ subunit of transducin (Tβγ), and binds the inhibitory subunit (Pbg) of cGMP-phosphodiesterase (PDE), thus releasing the constraint of Pbg on the catalytic subunits (Pα and Pβ) of PDE. The resulting decrease in cytoplasmic cGMP leads to the closure of cGMP-gated channels and the hyperpolarization of photoreceptor plasma membranes. Although the signaling cascade of ROS has been intensively studied during the past two decades, the whole mechanism has not yet been elucidated (for review see Ref. 2).

Most of the signaling proteins in ROS are membrane proteins, and they are often modified with lipids. Rhodopsin is modified by tandem palmitic acids at the carboxyl end of the fourth cytoplasmic loop (3). Tα is modified by a fatty acyl chain, and Tβγ is both modified by a farnesyl group and carboxymethylated (4–6). By contrast, Pα and Pβ are modified by farnesyl and geranylgeranyl, respectively (7), and Pbg subunits are carboxymethylated (8).

The lipid modification of signaling proteins has recently been discussed in connection with its ability to lead proteins to cholesterol- and sphingolipids-enriched membrane microdomains called lipid rafts (9). It has been proposed that lipid rafts exist in a separate phase from the rest of the bilayer, in a state similar to the liquid-ordered phase described in model membranes. Surrounding fluid membrane is in a state similar to the liquid-disordered (lα) phase. Biochemically, the components of lipid rafts are characterized by their insolubility in the detergent Triton X-100 (10). Increasing evidence suggests that cholesterol and sphingolipid-rich lipid microdomains or rafts exist in eukaryotic cell membranes where they have important functions (11). Trimeric G proteins have also been implicated in signal transduction in the raft (12).

Here, we have characterized the detergent-insoluble fraction of bovine photoreceptor ROS using sucrose density gradient ultracentrifugation. We demonstrate that important signaling proteins such as transducin and PDE exert massive translocation between detergent-resistant membrane (DRM) and detergent-soluble membrane domains, depending on their activation steps. The importance of raft-like membrane domains on disc membranes in phototransduction will be discussed.

EXPERIMENTAL PROCEDURES

Preparation of Triton X-100-insoluble Membrane Fraction from Bovine ROS—Dark-adapted bovine frozen retinas were from Lawson Co., Ltd., Nebraska. ROS were prepared in the dark by using an image converter (Noctovision™, Nippon Electric Company) as described previously (13). ROS were suspended (12 mg protein/ml) in Buffer A (10 mM MOPS (pH 7.2), 60 mM KCl, 30 mM NaCl, 5 mM MgCl2, 1 mM dithiothreitol, 1 mM BAPTA, 1 mM phenylmethylsulfonyl fluoride, 5 μM aprotinin, 1 μM leupeptin, 1 μM pepstatin A, 1 μM E64), and stored in the dark at –95 °C. 100 μl of Buffer A or Buffer B containing 2 mM GTPγS was added to 400 μl of ROS suspension. The suspensions were incubated at 0 °C for 30 min in the dark or under normal room lighting. The following procedures were all carried out at 4 °C, and for dark-adapted ROS all procedures were done in complete darkness. After incubation, each suspension was mixed with a 1/2 volume of Buffer A containing 3% (w/v) Triton X-100 to a final

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detergent concentration of 1% (w/v) and then homogenized by passing through a 21-gauge needle three times. The homogenate was mixed with 2.4 m sucrose in Buffer A to a final sucrose concentration of 0.9 m and placed in the bottom of centrifuge tubes (SW55-T; Beckman). Samples were overlaid with 0.8, 0.7, 0.6, and 0.5 m sucrose solutions in Buffer A (900 ml each) and subjected to ultracentrifugation (46,000 rpm for 20 h at 4 °C). 500-microliter fractions were collected from the top of the centrifuge tube downwar ds and stored at 0 °C.

To exclude the possibility that our results were artifact from freezing and thawing of ROS membranes, we performed DRM preparation using ROS prepared from fresh bovine retinas purchased from a local slaughterhouse. Exactly the same results were obtained by using such native ROS membranes.

**Immunoblotting Detection of Various Subunits of PDE and Transducin in Fractions from Sucrose Gradient Centrifugation—**To analyze the distribution of PDE and transducin subunits, aliquots of each fraction were subjected to SDS-polyacrylamide gel electrophoresis (PAGE), followed by immunoblotting with antibodies or antisera as described previously (14).

**Antibodies—**Rabbit polyclonal antibodies were raised against peptides corresponding to various bovine antigens as follows: Asn24-Ala40 of Pγ; Gly24-Cys40 of Pβ; and Val16-Pro28 of Pα. Antibodies against Pγ and Pβ showed high selectivity to each antigen. An antibody against Tα (Gly10-Leu47) was obtained from Calbiochem; antibodies against Tβi (Gly16; C-16), Tγ (Gly1; P-19), and heat-shock protein 90 (Hsp90) were from Santa Cruz Biotechnology, Inc.

**Cholesterol Extraction with Methyl-β-Cyclodextrin (MCD)—**MCD was used to remove cholesterol from membrane fractions. After dilution with Buffer A, the DRM (32 μg protein) was sedimented by centrifugation and resuspended in 100 μl of Buffer A containing various amounts of MCD. After incubation on ice for 1 h, fractions were centrifuged at 100,000 × g for 30 min at 4 °C. The supernatants and pellets were separated and processed for SDS-PAGE. Cholesterol was assayed spectrophotometrically using a diagnostic kit (Cholesterol CII-Test; Wako).

**Other—**Proteins were analyzed by SDS-PAGE using the following types of gradient gels: 1) 8–18% T, 0.4% C gels for general purpose; 2) 8–18% T, 0.08% C gels for visualizing the characteristic double bands of Pγ and Pβ with CBB staining (15). PDE activity was assayed by a phosphate release assay as described previously (16). Protein assay was performed routinely by the Bradford assay (17). The content of PDE in each fraction was assayed by densitometric scanning of immunoblotting data on x-ray film using NIH image software. Purified PDE was used as a standard, and protein content was measured in the linear region of standard curves.

**RESULTS**

**Effect of Light and GTPγS on Appearance and Protein Composition of the DRM—**First, we examined whether the DRM could be isolated from bovine ROS. Suspensions of ROS were incubated in the dark or under room light with or without GTPγS and then homogenized in a buffer containing 1% Triton X-100. In each case, DRMs were observed as a diffuse yellow-white band in a low-density region (1.1 ± 0.05 g/ml at 4 °C) (Fig. 1, upper panels). Light-bleached and GTPγS-stimulated ROS gave a slightly denser band in a slightly higher-density region (Fig. 1B, upper panel).

Protein compositions in fractions from sucrose density gradients were analyzed by SDS-PAGE with CBB staining (Fig. 1, lower panels). Several characteristic proteins were observed in the buoyant fractions derived from all ROS (fractions 4–5). Among these proteins, three components with molecular masses of 90,000, 88,000, and 40,000 Da seemed to vary their distribution in a stimulus-dependent manner. In the absence of GTPγS, light exposure of ROS elicited massive translocation of the 40,000 Da protein from the detergent-soluble (see Fig. 1C; fractions 9–10) to the DRM fractions (see Fig. 1A; fraction 5). This light-dependent accumulation of the 40,000 Da protein in the DRM fraction was prevented by the addition of GTPγS to light-bleached ROS (compare Fig. 1, A and B). In contrast, no effect of GTPγS on the distribution of the 40,000 Da protein was observed in the dark-adapted ROS (Fig. 1, C and D). On the basis of its molecular mass and its quantity relative to rhodopsin, we thought that the 40,000 Da protein was highly likely to be the transducin α subunit.

The 90,000- and 88,000-Da proteins accumulated in the DRM fraction after simultaneous stimulation of ROS by light and GTPγS, whereas protein bands of these molecular masses diminished in the detergent-soluble protein fractions (compare Fig. 1, A and B). Even in dark-adapted ROS, GTPγS induced indistinct but detectable translocation of 90,000- and 88,000-Da components to the DRM (compare fraction 5 of Fig. 1, C and D). We thought that these bands were likely to be the β and δ subunits of PDE. In addition, it is noteworthy that the 88,000-Da protein, which has the same apparent molecular mass as Pβ, is in the soluble fraction (fraction 10). We identified this protein as Hsp90 in terms of immunoblotting (data not shown).

We assayed the molecular activity of PDE in fractions derived from light-bleached and GTPγS-stimulated ROS. Without exposure to GTPγS, the molecular activity of PDE was negligible in all fractions. In contrast, PDE in either the DRM or detergent-soluble fractions from ROS stimulated by both light and GTPγS showed considerably higher molecular activities. The activities in the DRM- (Fig. 1B, fraction 5) and Triton X-100-soluble fractions (Fig. 1B, fraction 10) were 125 ± 10 (n = 3), and 467 ± 27 (n = 3) cGMP molecule/sec/PDE molecule, respectively.

Next, we examined the localization of transducin and PDE subunits in the fractions using specific antibodies (Fig. 2). Tβi showed exactly the same behavior as the 40,000-Da protein shown in Fig. 1. In dark-adapted ROS, all subunits of transducin were detergent-soluble (Fig. 2B). In light-bleached ROS, 30–50% of all transducin subunits were detergent-insoluble.
and located in the DRM (Fig. 2A). On addition of GTP\(\gamma\)S to light-bleached ROS, these subunits became detergent-soluble again. P\(_{b}\) and P\(_{g}\) were detected at the same positions as the CBB-stained 90,000- and 88,000-Da bands. In light-bleached ROS, GTP\(\gamma\)S elicited a massive translocation of all PDE subunits from the detergent-soluble to the DRM fractions (Fig. 2C). More than 80\% of all PDE subunits were in the DRM under our experimental conditions. Even in dark-adapted ROS, transducin, rhodopsin showed no significant translocation in any case.

**Solubilization of PDE with MCD Extraction**—It is known that the cholesterol-removing regent, methyl-\(\beta\)-cyclodextrin, can solubilize a certain protein component of the Triton X-100-resistant membrane of rat brain (18). Thus, we examined the effect of MCD on the protein composition of DRM derived from light- and GTP\(\gamma\)S-exposed ROS. Addition of MCD to the DRM fraction resulted in a dose-dependent and selective solubilization as described in Fig. 1. Proteins in 0.2-\(\mu\)l aliquots of each fraction were separated by SDS-PAGE and blotted onto nitrocellulose membranes. Immunoblotting was done by using specific antibodies against the subunits of PDE (P\(_{a}\), P\(_{b}\), and P\(_{g}\)) or transducin (T\(_{a}\), T\(_{b}\), and T\(_{g}\)). A and B, subunits of transducin; C and D, subunits of PDE; A and C, light; B and D, dark.

**DISCUSSION**

Although the lateral organization of membrane lipids on the disc membrane of ROS has been expected, there has been no concrete evidence to support the presence of raft-like phases in ROS. However, we have found that a low-density buoyant fraction, *i.e.*, a DRM, can be prepared from bovine photoreceptor disc membranes, suggesting that there are raft-like lipid domains in ROS. Here we have explored the effect of light and the unhydrolyzable GTP analog GTP\(\gamma\)S on the distribution of photosignaling proteins in this raft-like fraction of ROS.

First, we found that all transducins in the dark-adapted ROS, seemingly GDP-T\(_{a}\) were detergent-soluble, whereas light exposure elicited the recruitment of a considerable amount of transducins to DRM. Insolubility in detergents like Triton X-100 is observed in lipid bilayers that exist in physical fluid membrane domains of disc membranes. On the contrary, at least a portion of transducin seems to be recruited to a raft-like tightly packed lipid phase on disc membranes. The addition of GTP\(\gamma\)S to light-bleached ROS prior to solubilization inhibited this recruitment. Because light-bleached rhodopsin (Rh\(^{abg}\)) has high affinity to GDP-T\(_{a}\), and GTP\(\gamma\)S inhibited the recruitment of transducin to DRM in light-bleached ROS, the transducin-binding site in DRM is highly likely rhodopsin. In addition, it should be emphasized that, although the distribution pattern of rhodopsin along the sucrose density gradient was apparently constant in all conditions, that of transducin was drastically changed by light exposure of ROS. Light-dependent recruitment of transducin to DRM might be explained in two ways: 1) Rh\(^{abg}\) binds with GDP-T\(_{a}\), in the detergent-soluble regions of ROS membranes, and then the complex was recruited to the DRM; 2) some rhodopsins are originally localized on DRM, and when bleached, they recruit GDP-T\(_{a}\) from

![Figure 2](http://www.jbc.org/content/738/6/20815/F2.large.jpg)  
**Fig. 2.** Effect of light and GTP\(\gamma\)S on the partitioning of transducin and PDE subunits in the DRM. Dark-adapted or light-bleached ROS was incubated in the presence or absence of GTP\(\gamma\)S (400 \(\mu\)M), solubilized, and then subjected to sucrose density gradient centrifugation as described in Fig. 1. Proteins in 0.2-\(\mu\)l aliquots of each fraction were separated by SDS-PAGE and blotted onto nitrocellulose membranes. Immunoblotting was done by using specific antibodies against the subunits of PDE (P\(_{a}\), P\(_{b}\), and P\(_{g}\)) or transducin (T\(_{a}\), T\(_{b}\), and T\(_{g}\)). A and B, subunits of transducin; C and D, subunits of PDE; A and C, light; B and D, dark.

![Figure 3](http://www.jbc.org/content/738/6/20815/F3.large.jpg)  
**Fig. 3.** Specific solubilization of PDE in the DRM with MCD. A, protein solubilized with MCD from light- and GTP\(\gamma\)S-induced DRM. After incubating DRM (32 \(\mu\)g of protein) with the indicated concentrations of MCD in 100 \(\mu\)l of Buffer A for 60 min on ice, the samples were centrifuged at 100,000 \(\times\) g for 30 min. Supernatants were recovered. Pellets were resuspended in the original volume, and the same sample volume (10-\(\mu\)l) was analyzed on a CBB-stained SDS-PAGE gel (8-16\%T, 0.4\%C). B, identification of extracted protein as PDE. Proteins separated by SDS-PAGE were immunoblotted with (IB) with P\(_{b}\) and P\(_{g}\)-specific antibodies. C, extraction of cholesterol by MCD from DRM derived from light- and GTP\(\gamma\)S-stimulated ROS. DRM containing 1.2 pmol of PDE was treated with varying concentration of MCD. Cholesterol contents of extracts and residual membranes were determined. Data are plotted as a percentage of the total cholesterol content (0.67 nmol) in DRM. D, MCD treatment of DRM prepared from light-bleached ROS without GTP\(\gamma\)S. DRM was treated with 10 \(\mu\)M MCD, and sp and pt were analyzed on a CBB-stained SDS-PAGE gel.
detergent-soluble membrane. In the former case, light-dependent increase in rhodopsin should be observed with the assembly of transducin to the DRM, though no increase in the amount of rhodopsin in DRM was detected. Thus, this hypothesis seems to be unlikely. However, to exclude this hypothesis, more accurate measurement of rhodopsin, which is bound by transducin, in DRM should be done. On the other hand, the latter explanation seems to fit well with our data, though it may require heterogeneity of rhodopsin in the disc membrane as a basal assumption. Our data suggest that there are two rhodopsin pools in ROS, one in DRM and one in the detergent-soluble membranes. Rh* on DRM seems to have a priority to make contact with GDP-T
t, in comparison to Rh* in the detergent-soluble membranes. So far, it is difficult to estimate the real size of the pool of rhodopsin on the raft-like phase in native ROS. The experiment shown in Fig. 1 may lead us to underestimate the amount of Rh*-GDP-T
, complex on the raft-like phase in native system if it exists, because we used a detergent to prepare the raft-like membranes from ROS. A detergent-independent preparation method of rafts (20) may be useful to assess the real size of such a rhodopsin pool. So far, our data indicate that at least ~10% of rhodopsin in ROS localizes in the raft-like phase, and a certain group of transducins selectively interacts with them. The functional significance of the rhodopsin in DRM and that of the transducin having affinity to such Rh* are obscure by this time. Exploration on the localization of the raft-like phase on disc membranes may clarify their roles in phototransduction.

By contrast, PDE showed light- and GTPγS-dependent translocation from the detergent-soluble to the DRM fractions. As isoprenyl moieties on peripheral membrane proteins are considered to be a negative targeting signal to lipid rafts (21), the two isoprenyl residues on P
 may cause its exclusion from the raft-like domains on the disc membrane. Proteins in l
 phase membranes are soluble in Triton X-100 (10), which is in agreement with the high detergent-solubility of unexcited PDE. Further, we speculate that the activation of PDE may bring about a conformational change of PDE, which might reduce its targeting signal to the l
 phase presumably by rearranging the two isoprenyl moieties to an unexposed location.

In addition to such a reduction in the negative targeting signal, however, a component, either protein or lipid, or a physical condition of the DRM is probably required to recruit activated PDE to the DRM. As cholesterol depletion by MCD selectively but partially releases PDE from the DRM, cholesterol seems to contribute, at least in part, to the recruitment of PDE to DRM. The incomplete solubilization of PDE by MCD suggests, however, that there is an additional component(s) or a physical condition that holds PDE in the DRM.

A stimulus-dependent assembly of proteins, including PDE, at the rim region of the disc membrane has been proposed (22). The contribution of GARBP2 (63,000 Da) has been implicated both in this PDE assembly and in the inhibition of PDE. So far, however, we have not observed a 63,000-Da protein that co-translocates with PDE to DRM, though the existence of GARBP2 in DRM has not been excluded.

It should be noted that the molecular activity of PDE in the DRM prepared from light- and GTPγS-stimulated ROS seemed not to be suppressed. Apparent molecular activity of PDE in the DRM was suppressed only partially, although almost the same proportions of P
 and P
 were co-localized as discussed above. We have observed uni- or multilamellar vesicles (100–200 nm in diameter) in the DRM fraction by electron microscopy. Therefore, the apparent suppression of the activity is highly likely because of the inaccessibility of cGMP to enzymes facing the inner surface of the vesicles. If this is true, GARBP2 would not be a good candidate as an anchor for PDE on DRM, because it strongly inhibits PDE (22).

On the other hand, there may be another possible mechanism with which active PDE is anchored to the DRM. We observed major fractions of retina-specific regulator of G protein signaling (RGS9; 55,000 Da) and a novel Gβ subunit (Gβ01; 44,000 Da) in DRM.4 Because they have a high-affinity to the AlF
-GDP-DT
 complex (23), it is highly likely that they form multiprotein complex with GTPγST
,T
 on the raft-like membrane domains on the disc membrane. Although T
 remaining in the DRM was scarcely detected by immunoblotting (Fig. 2A), such a little portion of T
 may be sufficient for the activation of all PDE in DRM. In any case, to elucidate the mechanism that keeps PDE in its active form despite the co-localization of P
 in DRM, more accurate measurement of the amounts of PDE and T
 and knowledge about the composition of the multiprotein complex containing the activated PDE in DRM are essentially needed.

Conclusively, our data strongly suggested that the raft-like phase in bovine ROS disc membranes are highly likely the place where the signaling proteins involved in phototransduction make contact with each other in their own activation step-dependent manners. By exploring the structure, temporal behavior, and function of this raft-like phase on the disc membranes, deeper insights into phototransduction system of vertebrate photoreceptors and its adaptation mechanism would be obtained.

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REFERENCES

1. Koutalos, Y., and Yau, K.-W. (1996) Trends Neurosci. 19, 73–81
2. Pugh, E. N., Jr., Nikonov, S., and Lamb, T. D. (1999) Curr. Opin. Neurobiol. 9, 410–418
3. Ovcinnikov, Y. A., Abdulrae, N. G., and Bogachuk, A. S. (1988) FEBS Lett. 230, 1–5
4. Kokame, K., Fujikawa, Y., Yoshizawa, T., Takao, T., and Shimoni, Y. (1992) Nature 359, 749–752
5. Fukuda, Y., Takao, T., Ohguro, H., Yoshizawa, T., Akino, T., and Shimoni, Y. (1990) Nature 346, 658–660
6. Fukuda, Y., Matsuosa, T., Kokame, K., Takao, T., Shimoni, Y., Akino, T., and Yoshizawa, T. (1994) J. Biol. Chem. 269, 5163–5170
7. Anant, J. S., Ong, O. C., Xie, H. Y., Clarke, S., O'Brien, P. J., and Fung, B. K. (1992) Proc. Natl. Acad. Sci. U. S. A. 89, 8928–8924
8. Brown, D. A., and London, E. (2000) J. Biol. Chem. 275, 17221–17224
9. London, E., and Brown, D. A. (2000) Biochim. Biophys. Acta 1508, 182–195
10. Simons, K., and Ikonen, E. (1997) Nature 387, 569–572
11. Rehm, A., and Pleogh, H. L. (1997) J. Cell Biol. 137, 305–317
12. Hayashi, F., and Yamasaki, A. (1991) Proc. Natl. Acad. Sci. U. S. A. 88, 4764–4770
13. Hayashi, F., Matsuura, I., Kachi, S., Maeda, T., Yamamoto, M., Fujii, Y., Liu, H., Yamazaki, M., Usukura, J., and Yamasaki, A. (2000) J. Biol. Chem. 275, 32958–32965
14. Catty, P., and Forster, P. (1991) Eur. J. Biochem. 199, 263–269
15. Liu, W., Clark, W. A., Sharma, P., and Northup, J. K. (1998) J. Biol. Chem. 273, 34284–34292
16. Bradford, M. M. (1970) Anal. Biochem. 27, 248–254
17. Maekawa, S., Sato, C., Kitajima, K., Funatsu, N., Kumanogoh, H., and Sokaya, Y. (1990) J. Biol. Chem. 274, 21369–21374
18. Funig, B. K. (1983) J. Biol. Chem. 258, 10495–10502
19. Song, K. S., Li, S., Okamoto, T., Quilillas, L. A., Sargiacomo, M., and Lisanti, M. P. (1990) J. Biol. Chem. 271, 9690–9697
20. Meleson, K. A., Ostermeyer, A. G., Chen, J. Z., Roth, M. G., and Brown, D. A. (1999) J. Biol. Chem. 274, 3910–3917
21. Krogsgaard, M. G., Beyer, M., Mueller, G., Heck, M., Vantillier, M., Koch, K.-W., Roliner, R., Wolfrum, U., Bode, C., Hofmann, K. P., and Kaupp, U. B. (1999) Nature 400, 761–766
22. Skiba, N. P., Hopp, J. A., and Arshavsky, V. Y. (2000) J. Biol. Chem. 275, 32716–32720

2 M. Mieda, M. Kishimoto, H. Liu, K. Seno, T. Suzuki, and F. Hayashi, unpublished observation.

3 K. Seno, M. Abe, Y. Higuchi, M. Mieda, Y. Owada, H. Liu, and F. Hayashi, unpublished observation.
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