

# OptiPrep™ Mini-Review MS06

## Lipid rich detergent-resistant membranes from mammalian cells and tissues

- ◆ The principal aim of this OptiPrep™ Mini-Review is to present a bibliography of all of the current papers reporting the use of an iodixanol gradient to purify and analyze lipid rafts from vertebrate cells/tissues as detergent-resistant domains (see Section 2). Section 1 contains a brief survey of the technique; it has its own short reference list (Section 1f) distinct from the comprehensive reference list in Section 2.

### 1. Methodological survey

#### 1a. Introduction

Lipid-rich plasma membrane domains have commonly been isolated from tissues and cultured cells as detergent-resistant membranes (DRMs), principally by flotation from a dense solution through a discontinuous or continuous density gradient containing a non-ionic detergent, usually Triton X-100 (TX100), but sometimes CHAPS. The resolution of DRMs is based on their low buoyant density and a flotation strategy is regarded as the best method for resolving any minor low-density fraction from predominantly denser material. Sucrose gradients were originally used in the separations but the much lower viscosity of Nycodenz® solutions, compared to those of sucrose, allowed the centrifugation time at 200,000  $g_{av}$  to be reduced from 18 h to 4 h [1]. Although iodixanol gradients are slightly more viscous than the corresponding Nycodenz® ones, the ease of preparation of gradient solutions from a commercial 60% (w/v) solution (OptiPrep™) has made use of this medium very popular.

#### 1b. Cell lysis and iodixanol discontinuous gradients

Figure 1 summarizes the most commonly used basic strategy and includes the three types of pre-gradient procedure. Using the blue pathway sometimes the membranes may be concentrated by a 100,000  $g$  centrifugation prior to addition of detergent. The lysis buffer composition varies; an isotonic medium containing 150 mM NaCl is probably the most commonly used, buffered with 15-50 mM Tris, HEPES or MES (pH 7.0-7.6), usually containing 1-5 mM EDTA and sometimes including 1-5 mM DTT. The osmotic balancer sometimes is 0.25 M sucrose with or without 50 mM NaCl.

Other lysis media are hypotonic, for example 25 mM MES, 2 mM EDTA, 5 mM DTT. The detergent is usually TX100 at concentrations from 0.1-1.0% (w/v); occasionally CHAPS is used at approx 20 mM.

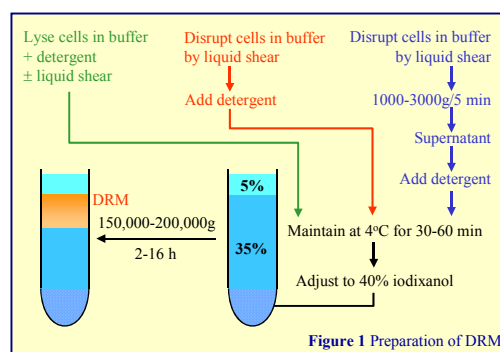


Figure 1 Preparation of DRMs

The gradient is routinely comprises three layers: the bottom sample layer, which may be 35-45% (w/v) iodixanol, the middle layer of 25-25% iodixanol and the top layer of 5-10% iodixanol or the lysis buffer. The volume of the middle layer is always larger than that of the sample layer (2-8x) to maximize the linear separation of the DRM and detergent soluble fractions. The volume of the top layer is usually no more than about 10% of the total volume. Sometimes an additional layer is inserted into the gradient, e.g. 50% (sample layer), 30%, 25% and 3% iodixanol or 35% (sample layer), 30%, 20% iodixanol and buffer. There are also some examples of six-layer gradients, e.g. 40% (sample layer), 35%, 30%, 25%, 20% iodixanol and buffer. The simple three-layer gradients are the most widely used for the separation of DRM and detergent-soluble fractions but they do not generally allow much scope for possible resolution of raft sub-domains. The more the number of layers the greater the opportunity for the identification of DRMs of different density.

#### 1c. Centrifugation

Centrifugation is normally in the range 200,000-300,000  $g$ , usually for 2-6 h, but may be for as long as 16 h. Small volume gradients are commonly carried out in the Beckman TLS55, large volume gradients in the Beckman SW41Ti (or similar). During extended centrifugations significant diffusion of the iodixanol will occur and the gradient will become continuous (but not necessarily linear) and this too may permit some finer resolution of subdomains of lipid-rich complexes.

#### 1d. Double gradient strategies

There are a few published examples of the use of a primary discontinuous gradient not containing detergent to obtain a low-density membrane fraction, which is then further fractionated in a detergent-containing gradient.

The first gradient will eliminate all of the major organelles such as mitochondria, lysosomes and peroxisomes and also most of the endoplasmic reticulum, Golgi and denser endosomes. Since the plasma membrane is one of the lightest of the cellular membranes in iodixanol, it is highly likely that the DRMs obtained in the second gradient are indeed derived from (or at least preferentially enriched in) this membrane rather than from internal membranes. This strategy was first reported for adult mouse brain [2]; the tissue was homogenized in 0.25 M sucrose, 50 mM NaCl, 1 mM DTT, 20 mM Tris-HCl, pH 7.4 and a post-nuclear supernatant adjusted to 35% (w/v) iodixanol, upon which were layered 30%, 20% and 5% iodixanol (total vol. approx. 13 ml). After centrifugation at approx. 200,000  $g_{av}$  for 3 h the low-density membrane from the 20%/5% iodixanol interface was harvested; adjusted to 35% iodixanol and 0.25% TX100 and overlaid with 30% iodixanol and buffer (containing 0.1% TX100). The gradient (total vol. 2.2 ml) was centrifuged at approx 170,000  $g_{av}$  for 1 h. In other examples there are small variations in the precise make-up of the two gradients; the method has been used for cultured cortical neurons [3], rat brain [4,5] and cultured chicken ciliary ganglion neurons [6]

### 1e. Other gradient strategies

Before OptiPrep™ became the medium of choice Naslavsky et al [7] described the use of a very effective Nycodenz® gradient in the analysis of prion proteins in neuroblastoma cells. The lysate was adjusted to 35% (w/v) Nycodenz® (total volume 0.8 ml) and overlaid by 0.2 ml each of 25, 22.5, 20, 18, 15, 12 and 8% Nycodenz®. The small volume of the gradient and the small difference in density between each layer probably allows the gradient to become more or less continuous by the end of the centrifugation (200,000 g for 4 h). This gradient was used widely in studies on neuroblastoma cells [e.g. refs 8-10]. The gradients cover predominantly a range of lower densities than the iodixanol ones and maybe enhance the potential for DRM subfractionation. The importance of using lower density gradients was confirmed by Hering et al [11] who, in their studies on rat brain, were able to show a clear density separation of two DRM markers (Thy-1 and caveolin) in 30%, 25%, 15% and 5% Nycodenz® gradients; this was less definitive in 30%, 25% and 5% gradients.

Rouvinski et al [12] used the same 8-25% Nycodenz® flotation gradient (in 2.2 ml tubes) as in ref 7 but introduced a novel two-gradient concept in which the first gradient was centrifuged for only 45 min (separation by rate of flotation), after which the low density fractions were collected; adjusted to a 35% Nycodenz® and analyzed in a second identical gradient centrifuged for 150 min (density separation). In this manner it was possible to identify large, intermediate and small DRMs [12] from neuroblastoma cells.

- ◆ It is likely that these higher resolution strategies can be directly transcribed to the use of OptiPrep™

A detailed description of the OptiPrep™ methodology (see Application Sheet S32) can be found on the OptiPrep™ Applications flash-drive or on the following website: [www.axis-shield-density-gradient-media.com](http://www.axis-shield-density-gradient-media.com) (click on “Methodology”, then “Organelles and Subcellular Membranes”) and scroll down the Index.

### 1f. References to Section 1

1. Naslavsky, N., Stein, R., Yanai, A., Friedlander, G. and Taraboulos, A. (1997) *Characterization of detergent-insoluble complexes containing the cellular prion protein and its scrapie isoform* J. Biol. Chem., **272**, 6324-6331
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5. Yu, W., Guo, W. and Feng, L. (2004) *Segregation of Nogo66 receptors into lipid rafts in rat brain and inhibition of Nogo66 signaling by cholesterol depletion* FEBS Lett., **577**, 87-92
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9. Ben-Zaken, O., Tzaban, S., Tal, Y., Horonchik, L., Esko, J.D., Vlodavsky, I. and Taraboulos, A. (2003) *Cellular heparan sulfate participates in the metabolism of prions* J. Biol. Chem., **278**, 40041-40049
10. Gilch, S., Kehler, C. and Schätzl, H.M. (2006) *The prion protein requires cholesterol for cell surface localization* Mol. Cell. Neurosci., **31**, 346-353

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12. Rouvinski, A., Gahali-Sass, I., Stav, I, m Metzer, E., Atlan, H. and Taraboulos, A. (2003) *Both raft- and non-raft proteins associate with CHAPS-insoluble complexes: some APP in large complexes* Biochem. Biophys. Res. Comm., **308**, 750-758

## 2. Comprehensive bibliography of OptiPrep™ papers

Papers have been divided (alphabetically) into:

- (1) **Mammalian cells and tissues**
- (2) **Mammalian subcellular organelles**
- (3) **Review articles**

When required, papers have been listed according to **research topic**. Within each group, papers are listed alphabetically according to **first author**. To facilitate identification of references of interest **key words in titles are highlighted in light blue**. When a paper reports the study of more than one cell type, reference to that paper will appear under all relevant headings.

### 1. Mammalian cells and tissues

#### 1-1. Adipocytes

**Jacobs, C.**, Onnockx, S., Vandenbroere, I. and Pirson, I. (2004) *Endogenous SHIP2 does not localize in lipid rafts in 3T3-L1 adipocytes* FEBS Lett., **565**, 70-74

**Jansen, M.**, Pietiäinen, V.M., Pölonen, H., Rasilainen, L. et al (2008) *Cholesterol substitution increases the structural heterogeneity of caveolae* J. Biol. Chem., **283**, 14610-14618

**Mansbach, C.M.** and Siddiqi, S. (2016) *Control of chylomicron export from the intestine* Am. J. Physiol. Gastrointest. Liver Physiol., **310**, G659–G668

**Nakamichi, Y.**, Wada, E., Aoki, K., Ohara-Imaizumi, M. et al (2004) *Functions of pancreatic  $\beta$  cells and adipocytes in bombesin receptor subtype-3-deficient mice* Biochem. Biophys. Res. Commun., **318**, 698-703

**Pohl, J.**, Ring, A., Korkmaz, U., Eehalt, R. et al (2005) *FAT/CD36-mediated long-chain fatty acid uptake in adipocytes requires plasma membrane rafts* Mol. Biol. Cell, **16**, 24-31

#### 1-2. BHK cells

**Abrami, L.**, Leppla, S.H. and Gisou van der Gaat, F. (2006) *Receptor palmitoylation and ubiquitination regulate anthrax toxin endocytosis* J. Cell Biol., **171**, 309-320

**Bhattacharya, B.** and Roy, P. (2008) *Bluetongue virus outer capsid protein VP5 interacts with membrane lipid rafts via a SNARE domain* J. Virol., **82**, 10600-10612

**Fivaz, M.**, Vilbois, F., Thurnheer, S., Pasquali, C., Abrami, L., et al (2002) *Differential sorting and fate of endocytosed GPI-anchored proteins* EMBO J., **21**, 3989-4000

**Glende, J.**, Schwegmann-Wessels, C., Al-Falah, M., Pferfferle, S., et al (2008) *Importance of cholesterol-rich membrane microdomains in the interaction of the S protein of SARS-coronavirus with the cellular receptor angiotensin-converting enzyme 2* Virology, **381**, 215-221

**Harder, T.**, Scheiffle, P., Verkade, P. and Simons K (1998) *Lipid domain structure of the plasma membrane revealed by patching of membrane components* J. Cell Biol., **141**, 929-942

**Heino, S.**, Lusa, S., Somerharju, P., Ehnholm, C., Olkkonen, V.M., et al (2000) *Dissecting the role of the Golgi complex and lipid rafts in biosynthetic transport of cholesterol to the cell surface* Proc. Natl. Acad. Sci., USA, **97**, 8375-8380

**Simons, M.**, Kramer, E-M., Macchi, P., Rathke-Hartlieb, S., et al (2002) *Overexpression of the myelin proteolipid protein leads to accumulation of cholesterol and proteolipid protein in endosomes/lysosomes: implications for Pelizaeus-Merzbacher disease* J. Cell Biol., **157**, 327-336

**Zhao, Y.**, Ishigami, M., Nagao, K., Hanada, K., Kono, N., Arai, H., Matsuo, M., Kioka, N. and Ueda, K. (2015) *ABCB4 exports phosphatidylcholine in a sphingomyelin-dependent manner* J. Lipid Res., **56**, 644–652

#### Brain (see “1-31. Neural tissue, neural cells and related cells” )

#### 1-3. Caco-2 cells

**Broquet, A.H.**, Thomas, G., Masliah, J., Trugnan, G., et al (2003) *Expression of the molecular chaperone Hsp70 in detergent-resistant microdomains correlates with its membrane delivery and release* J. Biol. Chem., **278**, 21601-21606

**Cuadras, M.A.** and Greenberg, H.B. (2003) *Rotavirus infectious particles use lipid rafts during replication for transport to the cell surface in vitro and in vivo* Virology, **313**, 308-321

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- Treede, I.**, Braun, A., Jeliaskova, P., Giese, T., et al (2009) *TNF- $\alpha$ -induced up-regulation of pro-inflammatory cytokines is reduced by phosphatidylcholine in intestinal epithelial cells* BMC Gastroenterol., **9**:53
- Tyska, M.J.** and Mooseker, M.S. (2004) *A role for myosin-1A in the localization of a brush border disaccharidase* J. Cell Biol., **165**, 395-405

#### 1-4. Carcinoma cells

##### Angiogenesis/carcinogenesis (see also “Cannabinoid receptor”)

- Bourguignon, L.Y.W.**, Singleton, P.A., Diedrich, F., Stern, R. et al (2004) *CD44 interaction with  $Na^+-H^+$  exchanger (NHE1) creates acidic microenvironment leading to hyaluronidase-2 and cathepsin B activation and breast tumor cell invasion* J. Biol. Chem., **279**, 26691-27007
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- Mazzone, M.**, Baldassarre, M., Beznoussenko, G., Giacchetti, G., et al (2004) *Intracellular processing and activation of membrane type 1 matrix metalloprotease depends on its partitioning into lipid domains* J. Cell Sci., **117**, 6275-6287
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- Remacle-Bonnet, M.**, Garrouste, F., Baillat, G., Andre, F., et al (2005) *Membrane rafts segregate pro- from anti-apoptotic insulin-like growth factor-1 receptor signaling in colon carcinoma cells stimulated by members of the tumor necrosis factor superfamily* Am. J. Pathol., **167**, 761-773
- Yang, J.**, Qian, J., Wezeman, M., Wang, S., et al (2006) *Targeting  $\beta$ 2-microglobulin for induction of tumor apoptosis in human hematological malignancies* Cancer Cell, **10**, 295-307

##### Apoptosis

- Elyassaki, W.** and Wu, S. (2006) *Lipid rafts mediate ultraviolet light-induced Fas aggregation in M624 melanoma cells* Photochem. Photobiol., **82**, 787-792
- Katsogiannou, M.**, El Boustany, C., Gackiere, F., Delcourt, P., et al (2009) *Caveolae contribute to the apoptosis resistance induced by the  $\alpha$ 1A-adrenoceptor in androgen-independent prostate cancer cells* Plos One, **4**: e7068
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- Xu, L.**, Hu, X., Qu, X., Hou, K., et al (2013) *Cetuximab enhances TRAIL-induced gastric cancer cell apoptosis by promoting DISC formation in lipid rafts* Biochem. Biophys. Res. Comm., **439**, 285–290
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##### Bacterial toxins

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- Hutton, M.L.**, Kaparakis-Liaskos, M., Turner, L., Cardona, A., et al (2010) **Helicobacter pylori* exploits cholesterol-rich microdomains for induction of *NF-κB*-dependent responses and peptidoglycan delivery in epithelial cells* Infect. Immun., **78**, 4523–4531
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- Smith, D.C.**, Spooner, R.A., Watson, P., Murray, J.L., Hodge, T.W. (2006) *Internalized *Pseudomonas* exotoxin A can exploit multiple pathways to reach the endoplasmic reticulum* Traffic, **7**, 379-393
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### Ca<sup>2+</sup>-signalling

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### Cannabinoid receptor

- DeMorrow, S.**, Glaser, S., Francis, H., Venter, J., et al (2007) *Opposing actions of endocannabinoids on *cholangiocarcinoma* growth* J. Biol. Chem., **282**, 13098-13113
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### Chemotaxis

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- Van Rheenen, J.**, Song, X., van Roosmalen, W., Cammer, M., et al (2007) **EGF*-induced *PIP<sub>2</sub>* hydrolysis releases and activates *cofilin* locally in carcinoma cells* J. Cell Biol., **179**, 1247-1259

### Endothelial cell adhesion

- Chanvorachote, P.** and Chunhacha, P. (2013) **Caveolin-1* regulates endothelial adhesion of lung cancer cells via reactive oxygen species-dependent mechanism* PLoS One, **8**: e57466

### **Glycolipids (see also “Lipid composition”)**

**Bonardi, D.**, Papini, N., Pasini, M., Dileo, L., et al (2014) *Sialidase NEU3 dynamically associates to different membrane domains specifically modifying their ganglioside pattern and triggering Akt phosphorylation* PLoS One, **9**, e99405

**Marques, L.**, Auriac, A., Willemetz, A., Banha, J., et al (2012) *Immune cells and hepatocytes express glycosylphosphatidylinositol-anchored ceruloplasmin at their cell surface* Blood Cells Mol. Dis., **48**, 110–120

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### **Green tea phenolics**

**Sánchez-Tena, S.**, Vizán, P., Dudeja, P.K., Centelles, J.J. et al, (2013) *Green tea phenolics inhibit butyrate-induced differentiation of colon cancer cells by interacting with monocarboxylate transporter* Biochim. Biophys. Acta, **1832**, 2264–2270

### **Growth factor receptors**

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### **Ion transport**

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### **Kinases/signaling**

**Baillat, G.**, Siret, C., Delamarre, E. and Luis, J. (2008) *Early adhesion induces interaction of FAK and Fyn in lipid domains and activates raft-dependent Akt signaling in SW480 colon cancer cells* Biochim. Biophys. Acta, **1783**, 2323–2331

**Cinar, B.**, Mukhopadhyay, N.K., Meng, G. and Freeman, M.R. (2007) *Phosphoinositide 3-kinase-independent non-genomic signals transit from androgen receptor to Akt1 in membrane raft microdomains* J. Biol. Chem., **282**, 29584–29593

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**Glycolipids, see “Lipids, lipoproteins and lipid precursors”**

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