*Excellence in Separations*

# OptiPrep™ Mini-Review MS10

## Purification of caveolae in gradients prepared from OptiPrep™

◆ 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 analyse caveolae from vertebrate and non-vertebrate cells/tissues (see Section 2). Section 1 contains a brief survey of the technique; it has its own short reference list distinct from the comprehensive reference list in Section 2.

### 1. Background

Early methods for the purification of lipid-rich plasma membrane domains largely relied on their insolubility in Triton X-110 (or some other non-ionic detergent) relative to that of the bulk plasma membrane or that of all the other subcellular membranes. Sometimes detergent was added to the whole homogenate or more frequently a partially-purified plasma membrane fraction was first isolated before treating with detergent. Smart et al [1] however pointed out that, while use of a non-ionic detergent did permit the isolation of a lipid-rich membrane domain, that some characteristic caveolar proteins can be lost in the procedure. These workers therefore developed a method that avoids the use of Triton X-100. After isolation of a plasma membrane fraction from either human skin fibroblasts or MA104 cells, the caveolae are released by sonication in a standard cell homogenization medium. The first part of the isolation procedure is a flotation through a continuous iodixanol gradient (0-20%); this gradient is essentially a resolving gradient in which the caveolin-rich vesicles are concentrated in the top third of the gradient, while the predominantly caveolin-poor vesicles band in denser regions. A second discontinuous gradient is essentially a concentration gradient to band the caveolin-rich vesicles sharply at an interface.

Smart et al [1] used a Percoll™-based method for the initial purification of the plasma membrane, but there is no obvious requirement that such a method must be used. Kumanogoh et al [2] for example used a sucrose gradient to purify a synaptic plasma membrane before using the method devised by Smart et al [1]. There are many examples in the literature of iodixanol gradients being used to purify plasma membrane from a homogenate. The McDonald and Pike [3] method for the isolation of lipid rafts incorporates elements of both the detergent and the sonicated plasma membrane approaches. It involves performing two rounds of homogenization of CHO cells using multiple passages through a syringe needle. A post-nuclear supernatant is then adjusted to 25% (w/v) iodixanol and loaded under a 0-20% iodixanol gradient for floating the lipid-rich plasma membrane fragments. In effect it resembles a Smart et al [3] method without a plasma membrane purification step. It also omits the final iodixanol caveolae concentration gradient. Occasionally the Percoll™ gradient is omitted, see for example ref 4.

1. Smart, E.J., Mineo, C. and Anderson, R.G.W. (1996) *Clustered folate receptors deliver 5-methyltetra-hydrofolate to cytoplasm of MA104 cells* J. Cell Biol., **134**, 1169-1177
2. Kumanogoh, H., Miyata, S., Sokawa, Y. and Maekawa, S. (2001) *Biochemical and morphological analysis on the localization of Rac1 in neurons* Neurosci. Res., **39**, 189-196
3. Macdonald, J.L. and Pike, L.J. (2005) *A simplified method for the preparation of detergent-free lipid rafts* J. Lipid Res., **46**, 1061-1067
4. Tome, M.E., Schaefer, C.P., Jacobs, L.M., Zhang, Y., Hemdon, J.M., Matty, F.O. and Davis, T.P. (2015) *Identification of P- glycoprotein co-fractionating proteins and specific binding partners in rat brain microvessels* J. Neurochem., **134**, 200-210

Detailed descriptions of the OptiPrep™-based techniques for isolation of caveolae and lipid rafts can be found in the following OptiPrep™ Application Sheets:

- **OptiPrep™ Application Sheet S34: Isolation of caveolae**
- **OptiPrep™ Application Sheet S32: Isolation of lipid rafts (detergent strategy)**
- **OptiPrep™ Application Sheet S33: Isolation of lipid rafts (detergent-free strategy)**

These can be found on the OptiPrep™ Applications flash-drive or on the following website: www.axis-shield-density-gradient-media.com (click on “Methodology”, then “Organelles and Subcellular Membranes”). Scroll down the Index to “Plasma membrane domains”. There is also a large literature on the fractionation of plasma membrane, endoplasmic reticulum, Golgi and endosomes and several Application Sheets, based on this literature, may be accessed from the Index entry for “Endoplasmic reticulum”.

## 2. Comprehensive bibliographies

Papers have been divided into **cell or tissue type**; and additionally, when required, into **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 cell headings.

All publications reporting **brain-derived caveolae** are listed under **"22. Neural tissue and cells"**. Papers reporting on **heart-derived caveolae** are listed under **"3. Cardiac muscle"** but see also **"27. Smooth muscle and smooth muscle cells"** for related cells. Cultured cell and tissue-derived caveolae will generally have been prepared from a partially purified plasma membrane fraction. An exception to this is a paper on "signalosomes", cytoplasmic organelles, that resemble caveolae and which have been purified from cardiac muscle (see **Quinlan et al in Section 3**). Review articles are listed in **Section 30**. Note also the following:

**OptiPrep™ Mini-Review MS08**: Lipid rich detergent-resistant membranes from mammalian cells, tissues and organelles
**OptiPrep™ Mini-Review MS09**: Detergent-free strategy for lipid raft isolation from mammalian cells and tissues

### 1. Caco-2 cells

**Delmas, O.**, Breton, M., Sapin, C., Le Bivic, A., Colard, O. and Trugnan, G. (2007) *Heterogeneity of raft-type membrane micrdomains associated with VP4, the rotavirus spike protein, in Caco-2 and MA 104 cells* J. Virol., **81**, 1610-1618

### 2. Carcinoma cells

**Cai, C.**, Zhu, H. and Chen, J. (2004) *Overexpression of caveolin-1 increases plasma membrane fluidity and reduces P-glycoprotein function in Hs578T/Dox* Biochem. Biophys Res. Commun., **320**, 868-874
**Chaterjee, S.**, Cao, S., Peterson, T.E., Simari, et al (2003) *Inhibition of GTP-dependent vesicle trafficking impairs internalization of plasmalemmal eNOS and cellular nitric oxide production* J. Cell Sci., **116**, 3645-3655
**Grądzka I.**, Sochanowicz, B., Brzóska, K., Wójciuk, G., et al (2013) *Cis-9,trans-11-conjugated linoleic acid affects lipid raft composition and sensitizes human colorectal adenocarcinoma HT-29 cells to X-radiation* Biochim. Biophys. Acta, **1830**, 2233–2242
**Huhtakangas, J.A.**, Olivera, C.J., Bishop, J.E., Zanello, L.P. et al (2004) *The vitamin D receptor is present in caveolae-enriched plasma membranes and binds $1\alpha,25(OH)_2$-vitamin $D_3$ in vivo and in vitro* Mol. Endocrinol., **18**, 2660-2671
**McDonald, J.F.**, Zheleznyak, A. and Frazier, W.A. (2004) *Cholesterol-independent interactions with CD47 enhance $\alpha_v\beta_3$ activity* J. Biol. Chem., **279**, 17301-17311
**Nion, S.**, Briand, O., Lestavel, S., Torpier, G., et al (1997) *High-density-lipoprotein subfraction 3 interaction with glycosylphosphatidyl-inositol-anchored proteins* Biochem. J., **328**, 415-423
**Piazza, T.M.**, Lu, J-C., Carver, K.C. and Schuler, L.A. (2009) *Src family kinases accelerate prolactin receptor internalization, modulating trafficking and signaling in breast cancer cells* Mol. Endocrinol., **23**, 202-212
**Pitto, M.**, Parenti, M., Guzzi, F., Magni, F., et al (2002) *Palmitic is the main fatty acid carried by lipids of detergent-resistant membrane fractions from neural and non-neural cells* Neurochem. Res., **27**, 729-734
**Sitaraman, S.V.**, Wang, L., Wong, M., Bruewer, M., et al (2002) *The adenosine 2b receptor is required to the plasma membrane and associates with E3KARP and ezrin upon agonist stimulation* J. Biol. Chem., **277**, 33188-33195
**Sun, J.**, Nanjundan, M., Pike, L.J., Wiedmer, T., et al (2002) *Plasma membrane phospholipid scramblase 1 is enriched in lipid rafts and interacts with the epidermal growth factor receptor* Biochemistry, **41**, 6338-6345
**Thiel, K.W.** and Carpenter, G. (2006) *ErbB-4 and TNF-α converting enzyme localization to membrane microdomains* Biochem. Biophys. Res. Commun., **350**, 629-633
**Turk, H.F.**, Barhoumi, R. and Chapkin, R.S. (2012) *Alteration of EGFR spatiotemporal dynamics suppresses signal transduction* PLoS One, **7**: e39682
**Waugh, M.G.**, Lawson, D., Tan, S.K. and Hsuan, J.J. (1998) *Phosphatidylinositol 4-phosphate synthesis in immunoisolated caveolae-like vesicles and low buoyant non-caveolar membranes* J. Biol. Chem., **273**, 17115-17121

### 3. Cardiac muscle (see also "Smooth muscle")

**Huhtakangas, J.A.**, Olivera, C.J., Bishop, J.E., Zanello, L.P., et al (2004) *The vitamin D receptor is present in caveolae-enriched plasma membranes and binds $1\alpha,25(OH)_2$-vitamin $D_3$ in vivo and in vitro* Mol. Endocrinol., **18**, 2660-2671

**Quinlan, C.L.**, Costa, A.D.T., Costa, C.L., Pierre, S.V., et al *Conditioning the heart induces formation of signalosomes that interact with mitochondria to open* $mitoK_{ATP}$ *channels* Am. J. Physiol. Heart Circ. Physiol., **295**, H953-H961

## 4. CHO cells

**Babitt, J.**, Trigatti, B., Rigotti, A., Smart, E.J., et al (1997) *Murine SR-BI, a high density lipoprotein receptor that mediates selective lipid uptake, is N-glycosylated and fatty acylated and colocalizes with plasma membrane caveolae* J. Biol. Chem., **272**, 13242-13249

**Graf, G.G.**, Connell, P.M., van der Westhuyzen, D.R. and Smart, E.J. (1999) *The class B, type I scavenger receptor promotes the selective uptake of high density lipoprotein cholesterol ethers into caveolae* J. Biol. Chem., **274**, 12043-12048

**Guo, L.**, Chen, M., Song, Z., Daugherty, A., et al (2011) *C323 of SR-BI is required for SR-BI-mediated HDL binding and cholesteryl ester uptake* J. Lipid Res., **52**, 2272–2278

**Uittenbogaard, A.**, Everson, W.V., Matveev, S.V. and Smart, E.J. (2002) *Cholesteryl ester is transported from caveolae to internal membranes as part of a caveolin-annexin II lipid-protein* J. Biol. Chem., **277**, 4925-4931

**Webb, N.R.**, Connell, P.M., Graf, G.A., Smart, E.J., et al (1998) *SR-BII, an isoform of the scavenger receptor BI containing an alternate cytoplasmic tail, mediates lipid transfer between high density lipoprotein and cells* J. Biol. Chem., **273**, 15241-15248

**Zhang, J.**, Chu, W. and Crandall, I. (2008) *Lipoprotein binding preference of CD36 is altered by filipin treatment* Lipids Health Dis., **7,** 23

## 5. Chondrocytes

**Elbaradie, K.B.Y.**, Wang, Y., Boyan, B.D. and Schwartz, Z. (2013) *Sex-specific response of rat costochondral cartilage growth plate chondrocytes to 17β-estradiol involves differential regulation of plasma membrane associated estrogen receptors* Biochim. Biophys. Acta, **1833**, 1165–1172

## 6. COS cells

**Grossmann, S.**, Higashiyama, S., Oksche, A., Schaefer, M., et al (2009) *Localisation of endothelin B receptor variants to plasma membrane microdomains and its effects on downstream signaling* Mol. Memb. Biol., **26**, 279-292

**Heberden, C.**, Reine, F., Grosse, B., Henry, C., et al (2006) *Detection of a raft-located estrogen receptor-like protein distinct from ERα* Int. J. Biochem. Cell Biol., **38**, 376-391

**Hinkovska-Galcheva, V.**, Boxer, L.A., Kindzelski, A., Hiraoka, M., Abe, A., Goparju, S., Spiegel, S., Petty, H.R. and Shayman, J.A. (2005) *Ceramide 1-phosphate, a mediator of phagocytosis* J. Biol. Chem., **280**, 26612-26621

**Hinkovska-Galcheva, V.**, Clark, A., VanWay, S., Huang, J-B., et al (2008) *Ceramide kinase promotes Ca21 signaling near IgG-opsonized targets and enhances phagolysosomal fusion in COS-1 cells* J. Lipid Res., **49,** 531-542

**Ikezu, T.**, Trapp, B.D., Song, K.S., Schlegel, A., et al (1998) *Caveolae, plasma membrane microdomains for α-secretase-mediated processing of the amyloid precursor protein* J. Biol. Chem., **273**, 10485-10495

**Mansfield, P.J.**, Hinkovska-Galcheva, V., Borofsky, M.S., Shayman, J.A. et al (2005) *Phagocytic signaling molecules in lipid rafts of COS-1 cells transfected with FcγRIIA* Biochem. Biophys. Res. Commun., **331**, 132-138

**Nishiyama, K.**, Trapp, B.D., Ikezu, T., Ransohoff, et al (1999) *Caveolin-3 upregulation activates β-secretase-mediated cleavage of the amyloid precursor protein in Alzheimer's disease* J. Neurosci., **19**, 6538-6548

**Oh, P.** and Schnitzer, J.E. (1999) *Immunoisolation of caveolae with high affinity antibody binding to the oligomeric caveolin cage* J. Biol. Chem, **274**, 23144-23154

## 7. Embryonic stem cells

**Hernandez, V.J.**, Weng, J., Ly, P., Pompey, S., et al (2013) *Cavin-3 dictates the balance between ERK and Akt signaling* eLife, **2:** e00905

## 8. Endothelial (vascular) cells

### Alzheimer's disease

**David, M.A.**, Jones, D.R. and Tayebi, M. (2014) *Potential candidate camelid antibodies for the treatment of protein-misfolding diseases* J. Neuroimmunol., **272**, 76–85

### ATP synthase

**Yamamoto, K.**, Shimizu, N., Obi, S., Kumagaya, S., Taketani, Y., Kamiya, A. and Ando, J. (2007) *Involvement of cell surface ATP synthase in flow-induced ATP release by vascular endothelial cells* Am. J. Physiol. Heart Circ. Physiol., **293**, H1646-H1653

### Caspase-3

**Oxhorn, B.C.** and Buxton, I.L.O. (2003) *Caveolar compartmentation of caspase-3 in cardiac endothelial cells* Cell. Signal., **15**, 489-496

### Caveolin-2

**Boyd, N.L.,** Park, H., Sun, W-P., Coleman, S.E., et al (2004) *Bovine caveolin-2 cloning and effects of shear stress on its localization in bovine aortic endothelial cells* Endothelium, **11**, 189-198

### FC5

**Abulrop, A.**, Sprong, H., Van Bergen en Henegouwen P. and Stanimirovic, D. (2005) *The blood-brain barrier transmigrating single domain antibody: mechanism of transport and antigenic epitopes in human brain endothelial cells.* J. Neurochem., **95**, 1201-1214

### Glycolipids

**Czarny, M.**, Liu, J., Oh, P. and Schnitzer, J.E. (2003) *Transient mechanoactivation of neutral sphingomyelinase in caveolae to generate ceramide* J. Biol. Chem., **278**, 4424-4430

**Shu, L.** and Shayman, J.A. (2007) *Caveolin-associated accumulation of globotriaosylceramide in the vascular endothelium of α-glactosidase A null mice* J. Biol. Chem., **282**, 20960-20967

### HDL uptake

**Balazs, Z.**, Panzenboeck, U., Hammer, A., Sovic, A., et al. (2004) *Uptake and transsport of high-density lipoprotein (HDL) and HDL-associated α-tocopherol by an in vitro blood-brain barrier model* J. Neurochem., **89**, 939-950

### Ion transport

**Wang, X-L.**, Ye, D., Peterson, T.E., Cao, S., et al (2005) *Caveolae targeting and regulation of large conductance $Ca^{2+}$ -activated $K^{+}$ channels in vascular endothelial cells* J. Biol. Chem., **280**, 11656-11664

### Lung

**Jiang, Y.**, Sverdlov, M.S., Toth, P.T., Huang, L.S., Du, G., Liu, Y., Natarajan, V. Minshall, R,D, (2016) *Phosphatidic acid produced by RalA-activated PLD2 stimulates caveolae-mediated endocytosis and trafficking in endothelial cells* J. Biol. Chem., **291**, 20729–20738

### Nitric oxide synthase

**Blair, A.**, Shaul, P.W., Yuhanna, I.S., Conrad, P.A., et al (1999) *Oxidized low density lipoprotein displaces endothelial nitric-oxide synthase (eNOS) from plasmalemmal caveolae and impairs eNOS activation* J. Biol Chem., **274**, 32512-32519 (1999)

**Joshi, M.S.**, Mineo, C., Shaul, P.W. and Bauer, J.A. (2007) *Biochemical consequences of the NOS3 Glu298Asp variation in human endothelium: altered caveolar localization and impaired response to shear* FASEB J., **21**, 2655-2663

**Kincer, J.F.**, Uittenbogaard, A., Dressman, J., Guerin, T. M., et al (2002) *Hypercholesterolemia promotes a CD36-dependent and endothelial nitric oxide synthase mediated vascular dysfunction* J. Biol. Chem., **277**, 23525-23533

**Peterson, T.E.**, Poppa, V., Ueba, H., Wu, A., et al (1999) *Opposing effects of reactive oxygen species and cholesterol on endothelial nitric oxide synthase and endothelial cell* caveolae. Circ. Res., **85**, 29-37

**Peterson, T.E.**, d'Uscio, L.V., Cao, S., Wang, X-L., et al (2009) *Guanosine triphosphate cyclohydrolase I expression and enzymatic activity are present in caveolae of endothelial cells* Hypertension, **53**, 189-195

**Shaul, P.W.**, Smart, E.J., Robinson, L.J., German, Z., et al (1996) *Acylation targets endothelial nitric-oxide synthase to plasmalemmal caveolae* J. Biol. Chem., **271**, 6518-6522 (1996)

**Uittenbogaard, A.**, Shaul, P.W., Yuhanna, I.S., Blair, A. et al (2000) *High density lipoprotein prevents oxidized low density lipoprotein-induced inhibition of endothelial nitric-oxide synthase localization and activation in caveolae* J. Biol. Chem., **275**, 11278-11283

### Vascular barrier/integrity

**Birukova, A.A.**, Singleton, P.A., Gawlak, G., Tian, X., et al (2014) *GRP78 is a novel receptor initiating a vascular barrier protective response to oxidized phospholipids* Mol. Biol. Cell, **25**, 2006-2016

**David, M.A.**, Jones, D.R. and Tayebi, M. (2014) *Potential candidate camelid antibodies for the treatment of protein-misfolding diseases* J. Neuroimmunol., **272**, 76–85

**Heemskerk, N.,** Asimuddin, M., Oort, C., van Rijssel, J. and van Buul, J.D. (2016) *Annexin A2lLimits neutrophil transendothelial migration by organizing the spatial distribution of ICAM-1* J. Immunol., **196**, 2767–2778

### VEGF Receptors

**Galvagni, F.**, Anselmi, F., Salameh, A., Orlandini, M., et al (2007) *Vascular endothelial growth factor receptor-3 activity is modulated by its association with caveolin-1 on endothelial membrane* Biochemistry**, 46**, 3998-4005

**Ikeda, S.**, Ushio-Fukai, M., Zuo, L., Tojo, T., et al (2005) *Novel role of ARF6 in vascular endothelial growth factor-induced signaling and angiogenesis* Circ. Res., **96**, 467-475

**Labrecque, L.**, Royal, I., Surprenant, D.S., Patterson, C., et al (2003) *Regulation of vascular endothelial growth factor receptor-2 activity by caveolin-1 and plasma membrane cholesterol* Mol. Biol. Cell, **14**, 334-347

## 9. Endothelial progenitor cells

**Chilla, A.**, Magherini, F., Margheri, F., Laurenzana, A., et al (2013) *Proteomic identification of VEGF-dependent protein enrichment to membrane caveolar-raft microdomains in endothelial progenitor cells*. Mol. Cell. Proteom., **12**, 1926-1938

**Margheri, F.**, Chilla, A., Laurenzana, A., Serratì, S., et al (2011) *Endothelial progenitor cell–dependent angiogenesis requires localization of the full-length form of uPAR in caveolae* Blood, **118**, 3743-3755

## 10. Epithelial cells

**Bolander Jr., F.F.** (2005) *The compartmentalization of prolactin signaling in the mouse mammary gland* Mol. Cell. Endocrinol., **245**, 105-110

**Bradbury, N.A.**, Clark, J.A., Watkins, S.C., Widnell, C.C., et al (1999) *Characterization of the internalization pathways for the cystic fibrosis transmembrane conductance regulator* Am. J. Physiol. Lung Cell. Mol. Physiol., **276**, L659-L668

**Briand, O.**, Lestavel, S., Pilon, A., Torpier, G., et al (2003) *SR-BI does not require raft/caveola localization for cholesteryl ester selective uptake in the human adrenal cell line NCI-H295R* Biochim. Biophys. Acta, **163**, 42-50

**Chen, J.**, Chen, J-K. and Harris, R.C. (2012) *Angiotensin II induces epithelial-to-mesenchymal transition in renal epithelial cells through reactive oxygen species/Src/caveolin-mediated activation of an epidermal growth factor receptor–extracellular signal-regulated kinase signaling pathway* Mol. Cell. Biol., **32**, 981–991

**Delmas, O.**, Breton, M., Sapin, C., Le Bivic, A., et al (2007) *Heterogeneity of raft-type membrane micrdomains associated with VP4, the rotavirus spike protein, in Caco-2 and MA 104 cells* J. Virol., **81**, 1610-1618

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**Kifor, O.**, Diaz, R., Butters, R., Kifor, I., et al (1998) *The calcium-sensing receptor is localized in caveolin-rich plasma membrane domains of bovine parathyroid cells* J. Biol. Chem., **273**, 1708-21713

**Lalor, D.**, Liu, P. and Hayashi, J. (2004) *Fas ligand is enriched in the caveolae membrane domains of thymic epithelial cells* Cell. Immunol., **230**, 10-16

**McMahon, K-A.**, Zhu, M., Kwon, S.W., Liu, P., et al (2006) *Detergent-free caveolae proteome suggests an interaction with ER and mitochondria* Proteomics, **6**, 143-152

**Norman, A.W.**, Olivera, C.J., Silva, F.R.M.B. and Bishop, J.E. (2002) *A specific binding protein/receptor for $1\alpha$,25-dihydroxyvitamin $D_3$ is present in an intestinal caveolae membrane fraction* Biochem. Biophys. Res. Commun., **298**, 414-419

**Pike, L.J.**, Han, X., Chung, K-N and Gross, R.W. (2002) *Lipid rafts are enriched in arachidonic acid and plasmenylethanolamine and their composition is independent of caveolin-1 expression: a quantitative electrospray ionization/mass spectrometric analysis* Biochemistry, **41**, 2075-2088

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**Subramanian, P.S.** and Johnson, H.M. (2002) *Lipid microdomains are required sites for the selective endocytosis and nuclear translocation of IFN-$\gamma$, its receptor chain IFN-$\gamma$ receptor-1, and phosphorylation and nuclear translocation of STAT1$\alpha$* J. Immunol, **169**, 1959-1969

## 11. Fibroblasts

### Cholesterol

**Dufour, D.**, Zhao, W-Q., Ravindranath, L. and Alkon, D.L. (2003) *Abnormal cholesterol processing in Alzheimer's disease patient's fibroblasts* Neurobiol. Lipids., **1**, 34-44

**Furuchi, T.** and Anderson, R.G.W. (1998) *Cholesterol depletion of caveolae causes hyperactivation of extracellular signal-related kinase (ERK)* J. Biol. Chem., **273**, 21009-21104

**Gallegos, A.M.**, McIntosh, A.L., Atshaves, B.P. and Schroeder, F. (2004) *Structure and cholesterol domain dynamics of an enriched caveolae/raft isolate* Biochem. J., **382**, 451-461

**Laitinen, S.**, Lehto, M., Lehtonen, S., Hyvarinen, K., et al (2002) *ORP2, a homolog of oxysterol binding protein, regulates cellular cholesterol metabolism* J. Lipid Res., **43**, 245-255

**Landry, Y.D.**, Denis, M., Nandi, S., Bell, S., et al (2006) *ATP-binding cassette transporter A1 expression disrupts raft membrane microdomains through its ATPase-related functions* J. Biol. Chem., **281**, 36091-36101

**Lu, X.**, Kambe, F., Cao, X., Yoshida, T., et al (2006) *DHCR24-Knockout embryonic fibroblasts are susceptible to serum withdrawal-induced apoptosis because of dysfunction of caveolae and insulin-Akt-Bad signaling* Endocrinology, **147**, 3123-3132

**Matthews, L.C.**, Taggart, M.J. and Westwood, M. (2005) *Effect of cholesterol depletion on mitogenesis and survival: the role of caveolar and noncaveolar domains in insulin-like growth factor-mediated cellular function* Endocrinology, **146**, 5463-5473

**Smart, E.J.**, Ying, Ys., Donzell, W.C. and Anderson, R.G.W. (1996) *A role for caveolin in transport of cholesterol from endoplasmic reticulum to plasma membrane* J. Biol. Chem., **271**, 29427-29435

**Uittenbogaard, A.**, Ying, Y.S. and Smart, E.J. (1998) *Characterization of a cytosolic heat-shock protein-caveolin chaperone complex* J. Biol. Chem., **273**, 6525-6532

**Yin, Y.**, Liu, P., Anderson, R.G.W. and Sampson, N.S. (2002) *Construction of a catalytically inactive cholesterol oxidase mutant: inverstigation of the interplay between active site-residues glutamate 361 and histidine 447* Arch. Biochem. Biophys., **402**, 235-242

### Composition and structure

**Landry, Y.D.**, Denis, M., Nandi, S., Bell, S., et al (2006) *ATP-binding cassette transporter A1 expression disrupts raft membrane microdomains through its ATPase-related functions* J. Biol. Chem., **281**, 36091-36101

**Marks, D.L.**, Bittman, R. and Pagano, R.E. (2008) *Use of Bodipy-labeled sphingolipid and cholesterol analogs to examine membrane microdomains in cells* Histochem. Cell. Biol., **130**, 819-832

**McMahon, K-A.**, Zhu, M., Kwon, S.W., Liu, P., et al (2006) *Detergent-free caveolae proteome suggests an interaction with ER and mitochondria* Proteomics, **6**, 143-152

**Smart, E.J.**, Ying, Y-S, Mineo, C. and Anderson, R.G.W. (1995) *A detergent-free method for purifying caveolae membrane from tissue culture cells* Proc. Natl. Acad. Sci. USA, **92**, 10104-10108

**Westermann, M.**, Leutbecher, H. and Meyer, H.W. (1999) *Membrane structure of caveolae and isolated caveolin-rich vesicles* Histochem. Cell Biol., **111**, 71-81

### Glycosphingolipids

**Kim, S-Y**., Wang, T-k., Singh, R.D., Wheatley, C.L., Marks, D.L. and Pagano, R.E. (2009) *Proteomic identification of proteins translocated to membrane microdomains upon treatment of fibroblasts with the glycosphingolipid, C8-β-D-lactosylceramide* Proteomics, **9**, 4321-4328

### Growth factor receptors (see also "Protein targeting and activation" and "Signal transdiction")

**Boucher, P.**, P., Liu, P., Gotthardt, M., Hiesberger, T., et al (2002) *Platelet-derived growth factor mediates tyrosine phosphorylation of the cytoplasmic domain of the low density lipoprotein receptor-related protein in caveolae* J. Biol. Chem., **277**, 15507-15513

**Liu, P.**, Ying, Y., Ko, Y.G and Anderson, R.G.W. (1996) *Localization of platelet-derived growth factor-stimulated phosphorylation cascade to caveolae* J. Biol. Chem., **271**, 10299-10303

**Liu, P.**, Ying, Y-S., and Anderson. R.G.W. (1997) *Platelet-derived growth factor activates mitogen-activated protein kinase in isolated caveolae* Proc. Natl. Acad. Sci., USA, **94**, 13666-13670

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