OptiPrep™ Reference List RS05

Analysis of membrane trafficking in mammalian tissues and cells: fractionation of ER, Golgi, TGN, PM and endosomes

- **This Reference List provides in Sections 1-5 a brief summary of some of the OptiPrep™ methodology and in Section 6 a comprehensive list of references**

1. Continuous buoyant density gradients

One of the first published papers to report the use of iodixanol gradients for the analysis of endoplasmic reticulum (ER), Golgi and plasma membrane (PM) from COS-7 cells was by Yang et al [1] in 1997. A post-nuclear supernatant, loaded on to a 0-26% (w/v) iodixanol gradient was centrifuged at 200,000 *g* for approx. 2 h. Analysis of the gradient established that the density of the three major membrane compartments increased in the order PM<Golgi<ER (see Fig. 1) and that banding sequence has been widely observed for the membranes from many other, but not all, mammalian cultured cells. This gradient and centrifugation format (spanning an approximate density range of 1.04-1.075 g/ml) has since been widely used at broadly similar (*g* x time) factors e.g. 280,000 *g* for 2 h and 100-200,000 *g* for 3 h in a swinging-bucket rotor of approx. tube volume 13 ml (e.g. Beckman SW41Ti). Shorter times at a lower radial centrifugal force (RCF) (e.g. 150,000 *g* for 1.5 h) may be required for smaller volume rotors (e.g. 5 ml tubes) with a shorter sediment-ation path length.

- **This methodology is described in Application Sheet S21**

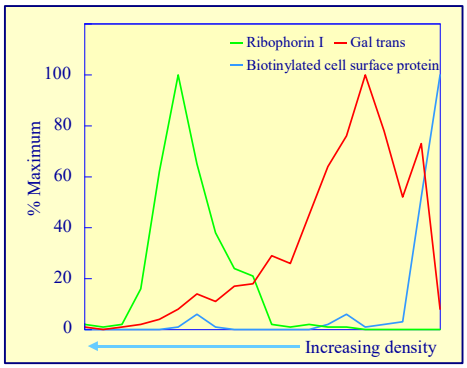

Figure 1: Distribution of Golgi, ER and PM markers from COS-7 cells in a 0-26% iodixanol gradient (115 min at 200,000g_{av}). Gal trans = galactosyl transferase. Figure adapted from ref 1 with kind permission of the authors and the American Society for Biochemistry and Molecular Biology

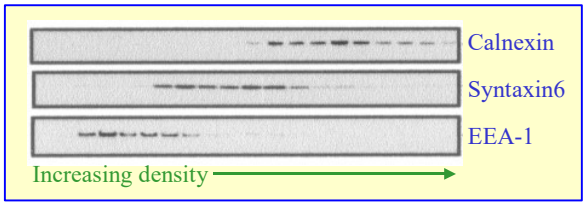

Figure 2 Fractionation of a PNS from CHO cells fractionated on a continuous iodixanol gradient: distribution of ER (calnexin), Golgi (syntaxin6) and early endosome (EEA-1) markers. Reproduced from ref 2 with kind permission of the authors and Macmillan Magazines Ltd.

Some workers maintain that the highest resolution of membrane vesicles is only obtained if the centrifugation is carried out at relatives low RCFs for extended time periods; for example 50,000-100,000 *g* for 18 h. An example is given in Figure 2; an 8-34% (w/v) iodixanol gradient was used to study the processing of the amyloid β peptide From CHO cells stably transfected with PS1 [2]. The gradient gave excellent resolution of early endosomes Golgi and ER. The method has also been able to resolve perinuclear ER from the bulk ER of mouse 3T3 fibroblasts [3]. This long-spin strategy however is not the only one that provides the ability to fractionate sub-domains of the same membrane compartment (see Section 2)

- **This methodology is described in Application Sheet S22**

2. Discontinuous gradients

Discontinuous iodixanol gradients in which the sample is bottom loaded in the densest solution are rather more variable in their detail; most run from 3 or 5% to 25% (w/v) iodixanol in 3.5% or 5% steps (e.g. refs 4 and 5), others are much simpler running from 20%-32% in three steps [6]. The centrifugation times are also variable: 88,000 *g* for 18 h [5] to 90,000 *g* for 2.5 h [6]. The banding position of the membranes is also rather variable, but some of this variability may arise from the variety of cell types. The 5-25% iodixanol gradient [5] resolved ER, Golgi and early endosomes from cortical neurons.

- **This methodology is described in Application Sheet S23**

There are many more examples in which the discontinuous gradients have been top-loaded. In many cases the gradients span the usual range from of 2.5-30% (w/v) iodixanol, but often neither the increment between each step nor the volume of each step are constant. During the centrifugation, which is never more than 3h, diffusion of iodixanol will occur and a non-linear continuous gradient will form. Non-linear gradients can provide an important feature that may potentially improve the resolution of certain membrane compartments. Figure 3 shows that this gradient effectively resolves ER, TGN and *cis*-Golgi from neuroglioma cells [7]. At the longer centrifugation time separations are certainly based on buoyant density but some of the shorter ones (1 h) are probably sedimentation velocity (see Section 3).

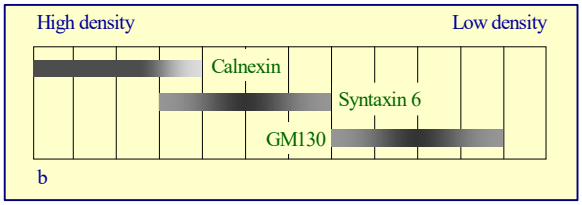

Figure 3 Fractionation of H4 neuroglioma cells, approximate disposition of ER, syntaxin 6 (TGN) and GM130 (*cis*-Golgi). Data adapted from ref 7.

- **This methodology is described in Application Sheet S24**
- It is important to note that 5-25% (w/v) iodixanol discontinuous gradients (3h at 90,000 *g*) were able to resolve mitochondrial associated ER from the bulk of the ER [8-10] and that unlike Percoll™, OptiPrep™ was able to achieve this separation effectively and reliably [11].

3. Sedimentation velocity gradients

This strategy using either a multi-step discontinuous gradient (2.5%, 5%, 7.5%, 10%, 12.5%, 15%, 17.5%, 20%, and 30% (w/v) iodixanol) or a continuous gradient over the same density range were introduced by Majoul et al [12] and Schroder et al [13] respectively. The former was widely used by the St. George-Hyslop group at the Centre for Research in Neurodegenerative Diseases in Toronto [14] for studying the processing of the β-amyloid precursor protein in neuroblastoma cells. The RCFs vary from 54,000-126,000 *g* and the centrifugation times from 25 to 90 min. An example of the fractionating power of this rapid centrifugation is shown in Figure 4.

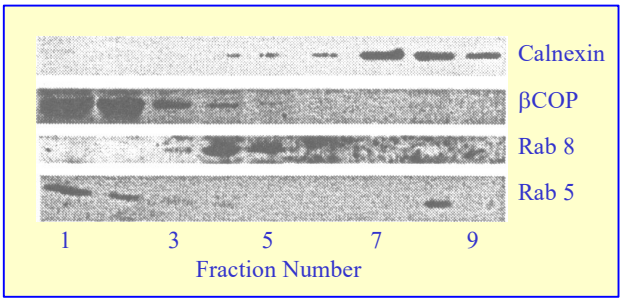

Figure 4 Subcellular fractionation of neuroblastoma (N2a) cells on a 2.5-30% discontinuous iodixanol gradient: immunoblotting of SDS-PAGE on gradient fractions (high density on right). See text for more details. Reproduced from ref 10 with kind permission of the authors and Blackwell Publishing

- **This methodology is described in Application Sheet S25**
- **There are also papers reporting the use of a self-generated iodixanol gradient, normally used for the separation of Golgi and smooth and rough ER – see Application Sheets S18 and S20**

4. Pre-gradient strategies

A point worth noting is the widely adopted strategy of using a post-nuclear supernatant (PNS) as a gradient input. It has much to recommend it: notably time-saving, minimal sample manipulations and avoidance of any losses of membrane vesicle material. It should be borne in mind however that, with the exception of nuclei, every other major organelle and membrane vesicle derived from every membrane compartment, are going to band somewhere in the gradient. The use of a more substantial differential centrifugation scheme prior to the gradient was much more commonly used twenty or thirty years ago than is now the case. Removal of major organelle fractions prior to gradient fractionation may improve the purity of membrane vesicle fractions. A classic differential centrifugation scheme of 1000 *g* for 5-10 min, 3000 *g* for 10 min and 15,000 *g* for 15 min however is time-consuming and will lead to progressive loss of vesicles unless each pellet is carefully washed.

Other Application Sheets that are relevant to the fractionation of subcellular membranes are:

- Application Sheet S01 – Preparation of gradient solutions
- Application Sheet S03 – Preparation of continuous and discontinuous gradients
- Application Sheet S04 – Preparation of self-generated gradients
- Application Sheet S05 – Homogenization of mammalian tissues
- Application Sheet S06 – Homogenization of mammalian cells
- Application Sheet S07 – Differential centrifugation of homogenates
- Application Sheet S08 – Gradient harvesting
- Application Sheet S09 – Gradient analysis

5. References (for Sections 1-3)

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6. Comprehensive bibliography

Papers have been divided into **mammalian cells** (**pp 3-25**) or **tissue** (**pp 25-38**) Within each group, papers are listed alphabetically according to **first author.** Multiple first author papers are sorted chronologically. Key words in the titles have been highlighted in light blue to facilitate visual searches for a particular research topic. If the fractionation of more than one cell type is reported in a paper, the reference will appear in each relevant cell section.

IMPORTANT NOTE

Although many of the publications described below may include the analysis of endosomes OptiPrep Reference List RS12 deals more specifically with endocytosis

Mammalian cells

1. Adipocytes

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2. Astrocytoma

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