

Contents

Preface	v
1. Discovery and Rediscovery	1
1.1. The Discovery of the Golgi Apparatus	1
1.2. The Controversy	4
1.3. Modern Rediscovery	6
1.4. Summary	7
2. Structure	9
2.1. Cisternae	10
2.2. The Cisternal Stack or Dictyosome	17
2.3. Golgi Apparatus (Denotes either Singular or Plural)	28
2.4. Golgi Apparatus Functioning as Part of an Integrated Endomembrane System	29
2.5. Associations with Other Organelles and Cell Components	31
2.6. Vesicles of the Golgi Apparatus	32
2.6.1. COP (COPII)-Coated Transition Vesicles	32
2.6.2. Clathrin-Coated Vesicles	32
2.6.3. Secretory Vesicles	32
2.6.4. Secretion Granules and Condensing Vacuoles	33
2.6.5. Fusiform Vesicles and Cisternal Remnants	35
2.6.6. Trans Golgi Apparatus Network	36
2.6.7. Cis Golgi Apparatus Network (Intermediate Compartment)	37
2.7. Summary	37
3. Isolation and Subfractionation	39
3.1. Golgi Apparatus Isolation	39
3.1.1. Procedure for Rodent Liver	40
3.1.2. Preparation of Reference Fractions from Rodent Liver	44
3.1.3. Isolation of Golgi Apparatus Fractions from Plant Cells	49
3.1.4. Isolation of Golgi Apparatus from Mammalian Cells Grown in Culture	52
3.2. Subfractionations of Golgi Apparatus based on Density	53
3.3. Golgi Apparatus Subfractionation by Free-Flow Electrophoresis	57
3.4. Summary	61

4. Tubules	63
4.1. Function of Golgi Apparatus Peripheral Tubules in Delivery of Cargo from Endoplasmic Reticulum to the Golgi Apparatus	66
4.1.1. Liver Parenchyma and Intestinal Absorptive Cells	66
4.1.2. Peripheral Tubule Function in Acinar Cells of Pancreas and Parotid Gland and Chromaffin Cells of the Adrenal Medulla	71
4.2. Golgi Apparatus Buds – Vesicles or Coated Ends of Tubules?	71
4.2.1. Isolation of Tubule-Enriched Fractions	74
4.3. Summary	76
5. Endomembrane Biogenesis	77
5.1. Role of Endoplasmic Reticulum in Membrane Biogenesis	78
5.2. Biosynthetic Capabilities of Golgi Apparatus Relevant to Membrane Biogenesis	79
5.3. Biosynthesis of Membrane Lipids	80
5.4. Biosynthesis of Membrane Sterols	83
5.5. Biosynthesis of Membrane Proteins	84
5.5.1. The Origins of Golgi Apparatus Proteins	85
5.6. Glycosylation of Membrane Glycoproteins	88
5.7. Glycosylation of Membrane Glycolipids	88
5.8. Formation of Sugar Nucleotides and Other Active Intermediates of Glycosylation Reactions	88
5.9. Sulfation Reactions	90
5.10. Distribution of Glycosyltransferases Across the Polarity Axis of the Golgi Apparatus	90
5.11. Summary	91
6. Function in the Flow-Differentiation of Membranes	93
6.1. Morphological Evidence for Membrane Differentiation within the Golgi Apparatus	94
6.1.1. Measurements of Membrane Thickness	94
6.1.2. Organization of Membrane Constituents	96
6.1.3. Evidence from Cytochemistry	99
6.2. Biochemical Evidence for Membrane Differentiation within the Golgi Apparatus	101
6.2.1. Survey of Biochemical Constituents Common to All Endomembranes	102
6.2.2. Changes in Constituents Concentrated in a Particular Membrane Compartment	104
6.3. Immunological Manifestations of Endomembrane Differentiation	110
6.3.1. Evidence from Induced Systems	112
6.4. Mechanisms of Membrane Differentiation	118
6.4.1. Biosynthetic Contributions to Membrane Differentiation	118
6.4.2. Selectivity of Membrane Differentiation Mechanisms	119
6.4.3. Golgi Apparatus Polyribosomes – A Means to Achieve Selective Addition of Proteins?	119

6.4.4. Examples of Selective Enzyme Deletion	120
6.4.5. Summary of Flow-Differentiation Mechanisms	122
6.5. Functional Significance of Flow-Differentiation of Membranes	124
6.5.1. Cell, Tissue and Organ Differentiation	125
6.6. Dynamic Aspects of the Flow-Differentiation of Membranes – Membrane Flow	125
6.6.1. General Morphological Basis for Membrane Flow	126
6.6.2. Kinetics of Membrane Flow	130
6.6.3. Bulk Flow of Membrane Lipids	133
6.6.4. Evidence from Induced Systems	134
6.6.5. Energetics of Membrane Flow-Differentiation and Problems of Regulation	135
6.7. Summary	135
7. Biochemistry	137
7.1. Introduction	137
7.2. Enzymology of the Golgi Apparatus	138
7.3. Glycosphingolipid Synthesis	143
7.4. Nucleotide Sugar Transporters	146
7.5. Golgi Apparatus Markers for Medial Cisternae	147
7.6. Lipid Composition	147
7.7. Phospholipid Biosynthesis	148
7.8. Protein Composition of the Golgi Apparatus	149
7.9. Summary	152
8. Function in Secretion	155
8.1. Role of the Golgi Apparatus in Secretion	155
8.2. A General Model for Golgi Apparatus Functioning in Secretion	156
8.3. Specific Examples of Golgi Apparatus Secretion	158
8.3.1. Enzyme and Proenzyme Secretion by Acinar Cells of Pancreas and Parotid Gland	158
8.3.2. Secretion of Lipoprotein Particles by Liver Parenchymal Cells and Adsorptive Cells of the Small Intestine	161
8.3.3. Mucin Secretion	162
8.3.4. Cell Walls and Cell Wall Units	166
8.3.5. Hormones	173
8.3.6. Fat-Soluble Vitamins and Essential Oils	173
8.3.7. Protein Secretion	175
8.3.8. Simple Sugars, Ions and Other Small Molecules	175
8.4. Processing of Large Molecules: An Integral Aspect of Golgi Apparatus Function in Secretion	175
8.4.1. Glycosylation of Glycoproteins	176
8.5. Signal Hypothesis	178
8.6. Control of Secretion	179
8.7. Segregation of Lysosomal Enzymes	181
8.8. NSF, SNAPS, and SNARES in Membrane Fusion and the Regulation of Membrane Traffic	183
8.9. Summary	185

9. Replication	187
9.1. A Mechanism of Golgi Apparatus Multiplication	187
9.1.1. Extension of Forming Face Regions	187
9.1.2. Appearance of Cisternae with Twice Normal Diameters at the Forming Face	189
9.1.3. Replicating Forms having Two Stacks of Cisternae with Normal Dimensions on Top of a Single Stack of Cisternae with Twice Normal Dimensions	189
9.1.4. Separation into Two Stacks having Normal Dimensions	191
9.1.5. Control of Multiplication of Golgi Apparatus Stacks	191
9.2. Precisternal Stages of Golgi Apparatus Ontogeny	191
9.3. Golgi Apparatus Fragmentation and Reformation during Mitosis	194
9.4. Experimental Golgi Apparatus Fragmentation and Reformation	194
9.5. Summary	196
10. Cell-Free Analysis	197
10.1. Cell-Free Systems Development	197
10.2. Cell-Free Transfer Assay Development	198
10.3. Reconstitution of Transitional Endoplasmic Reticulum to Golgi Apparatus Transfer	198
10.3.1. Fidelity and Efficiency of Cell-Free Transfer in Rat Liver: Comparison to Studies with Liver Slices and Tissues	203
10.3.2. Donor and Acceptor Specificity	203
10.3.3. Temperature Dependence and 16° C Temperature Block	203
10.3.4. Lipid and Protein Cotransfer	204
10.3.5. Processing of Transferred Constituents: Evidence for Functional Fusion of Donor and Acceptor Compartments	205
10.3.6. Lipid Processing	205
10.3.7. Glycoconjugate Processing	207
10.4. Nucleoside Triphosphate Dependence of Endoplasmic Reticulum to Golgi Apparatus Membrane Transfer	208
10.5. Reconstitution of Golgi Apparatus to Plasma Membrane Transfer	211
10.5.1. Cell-Free Transfer in Cultured Cells	211
10.5.2. Cell-Free Transfer in Yeast	213
10.5.3. ATP-Independent Vesicle Budding	214
10.6. Cell-Free Membrane Transfer in Plants	214
10.7. Model for ATP-Dependent Vesicle Budding based on the Rat Liver System	215
10.7.1. Retinol Stimulation of Vesicle Budding in Rat Liver	218
10.8. Summary	219
11. Growth and Cell Enlargement	221
11.1. Golgi Apparatus and Growth	222
11.1.1. Inhibitor Studies	222
11.2. Evidence from Tip-Growing Cells for a Role of Golgi Apparatus Activity in Cell Enlargement	228

Contents	xiii
11.3. Physical Membrane Displacement	228
11.3.1. Membrane Budding	229
11.4. Energy Requirements for Physical Membrane Displacement	233
11.5. Summary	237
12. Cancer	239
12.1. The Ultrastructural Cancer Phenotype of the Endomembrane System	239
12.1.1. Rough (with attached ribosomes) Endoplasmic Reticulum	239
12.1.2. Smooth Endoplasmic Reticulum	241
12.1.3. Golgi Apparatus	241
12.1.4. Plasma Membrane	245
12.2. Role of Endomembranes in Signal Transduction and Oncogene Expression in Cancer	248
12.3. Summary	251
Epilogue	253
Appendix Tables	257
References	271
Index	301