

Contents

General preface	v
Contents of previous volumes	vii
Contents of forthcoming volumes	ix
Preface	xi
List of Contributors	xiii

1 *Membrane fusion events during invertebrate fertilization, by D. Epel and V. D. Vacquier*

1. Overview of fertilization	2
1.1. Experimental material	3
1.2. General strategy of fertilization	3
2. The acrosome reaction	8
2.1. Triggers of the acrosome reaction	9
2.2. Mechanism of induction of the acrosome reaction	10
3. Sperm-egg binding	12
3.1. Characteristics of sperm-egg binding	13
3.2. The vitelline layer	17
3.3. Egg-binding proteins on the sperm surface	19
3.4. Passage of sperm through the vitelline layer	27
3.5. The role of sperm binding in fertilization	27
3.6. Other roles of the vitelline layer	29
3.7. Role of sperm motility in binding	29
4. Sperm-egg fusion	29
4.1. Specific sites for fusion	30
4.2. Sperm and egg as fusible cells	31
4.3. The block to polyspermy—a natural regulator of fusion	32
4.4. Experimental means of promoting fusion	37
4.5. Fertilization inhibitors	38
4.6. Ionic requirements for fertilization	38
4.7. Enzymes involved in fusion	39
5. Incorporation of the fused sperm into the egg	39
5.1. Cell cortex and sperm entry	39
5.2. Acrosomal process and sperm entry	42

6. Exocytosis of cortical granules	43
6.1. Introduction	43
6.2. Initiation of the cortical granule reaction	46
6.3. Membrane fusion and cell surface rearrangement—morphology	52
6.4. Membrane fusion and cell surface rearrangement—molecular changes	54
6.5. Isolated cortical granules as a model for studying exocytosis	55

2 *Membrane fusion events in the fertilization of vertebrate eggs,* *by J. M. Bedford and G. W. Cooper*

1. Introduction	66
2. The plasmalemma of the mammalian spermatozoon	67
2.1. General considerations	67
2.2. Biochemical character	68
2.3. Regional differentiation	71
3. The membrane of the acrosome	79
4. Maturation of sperm membranes	79
4.1. Changes in the male tract	79
4.2. Changes in the female tract	83
5. Sperm membrane behavior during penetration	86
5.1. Interaction with egg vestments	86
5.2. The acrosome reaction	87
6. The oolemma	98
6.1. General characteristics	98
6.2. Acquisition of penetrability	100
6.3. Exocytosis of cortical granules	102
7. Sperm-egg fusion in mammals	106
7.1. General features	106
7.2. Role of microvilli	108
8. Post-penetration events	109
9. Interaction of spermatozoa with somatic cells	110
10. Concluding remarks	111

3 *Myoblast fusion, by R. Bischoff*

1. Introduction	128
2. Specificity of fusion	130
3. Prefusion activities	131
3.1. Myoblast-myotube adhesion	131
3.2. Role of the glycocalyx in mediating adhesion	134
3.3. Cell coupling and junctions	139
4. Morphology of fusion	141
4.1. Behavioral aspects	141
4.2. Ultrastructure	141
5. Fusion inhibitors	147
5.1. Calcium withdrawal	147

5.2. Cytoskeletal	150
5.3. Lectins	152
5.4. Metabolic	155
5.5. Enzymes	156
5.6. Lipids	157
5.7. Other inhibitors	159
6. Environmental factors	159
7. Surface coats of myogenic cells	161
7.1. Ultrastructure and staining of surface coats	162
7.2. Is the basal lamina a block to fusion?	166
8. Membrane composition and alterations during myogenesis	167
8.1. Lipids	167
8.2. Carbohydrates	169
8.3. Proteins	170
9. Summary and conclusions	171

4 *Macrophage fusion in vivo and in vitro: a review, by J. M. Papadimitriou*

1. Historical perspectives	182
2. Macrophage fusion in vivo	183
2.1. Introduction	183
2.2. Direct observations of macrophage fusion	184
2.3. Indirect evidence of macrophage fusion	189
2.4. The role of the "resident" macrophage	189
2.5. The efficiency of fusion in macrophage populations	190
2.6. Macrophage fusion in relation to the cell cycle	191
2.7. Agents influencing macrophage fusion	191
2.8. Miscellaneous factors influencing macrophage fusion	194
3. Properties of macrophage polykaryocytes induced in vivo	195
3.1. Structural characteristics	195
3.2. Cytochemical and biochemical properties	196
3.3. Chromosomal studies	201
3.4. The lifespan of multinucleate giant cells	202
3.5. The motility of multinucleate giant cells	202
3.6. Endocytotic processes	203
4. Macrophage fusion in vitro	206
4.1. Introduction	206
4.2. Macrophage homokaryocytes and heterokaryocytes	208
5. A comparison of in vivo- and in vitro-induced macrophage polykaryocytes	210
6. The role of multinucleate giant cells in inflammatory reactions	212
7. Summary	213

5 *Cell fusion in myxomycetes and fungi, by M. J. Carlile and G. W. Gooday*

1. Introduction	220
2. Myxomycetes	220

2.1. Structure and life cycle	220
2.2. Sexual fusion and plasmodium initiation	222
2.3. Somatic fusion between plasmodia	227
3. Fungi	234
3.1. Life cycles	235
3.2. Somatic fusion	235
3.3. Sexual fusion	244
4. Acrasiales	256
5. Discussion	256

6 *Mechanisms of chemically induced cell fusion, by J. A. Lucy*

1. Introduction	268
2. Cell fusion and membrane lipids	268
2.1. Membrane cholesterol	268
2.2. Membrane phospholipids	271
3. Cell fusion and membrane permeability	287
3.1. Cell swelling	287
3.2. Calcium ions	288
4. Cell fusion and membrane proteins	293
5. Conclusions	297

7 *Virus-induced cell fusion, by G. Poste and C. A. Pasternak*

1. Introduction	306
2. Two kinds of virus-induced cell fusion	307
3. Optimum conditions for virus-induced cell fusion	309
4. Identification of the viral components associated with the induction of membrane fusion	312
5. Virus-cell interactions in virus-induced cell fusion	323
6. Mechanisms	331
6.1. Virus-to-cell and cell-to-cell fusion	331
6.2. Calcium-induced lateral phase separation of membrane phospholipids as a possible mechanism for fusion	349

8 *Fusion of plant protoplasts, by J. B. Power, P. K. Evans and E. C. Cocking*

1. Introduction	370
2. Initial studies on protoplast fusion	370
3. Recent studies on protoplast fusion	372
4. Mechanisms of fusion	375
5. Somatic hybrids	378
6. Applications of somatic hybridization	381

9 *Endocytosis: regulation of membrane interactions, by P. J. Edelson and Z. A. Cohn*

1. The modern concept of endocytosis	388
2. What determines the intrinsic pinocytic rate?	391
3. Do plasma membrane binding sites function as endocytic receptors?	392
4. How is the membrane organized for endocytosis?	397
5. What determines the fate of endocytic membrane?	399
6. What regulates phago-lysosome formation?	400
7. Conclusions	402

10 *Mechanisms of mediator release by inflammatory cells, by P. M. Henson, M. H. Ginsberg and D. C. Morrison*

1. Introduction	411
1.1. "Inflammatory" cells and host-defense	411
1.2. Secretion of mediators	413
2. Mast cells and basophils	417
2.1. Morphologic features of mast cell and basophil secretion	417
2.2. Mast cell activities and mediators	419
2.3. Stimuli for mast cell and basophil secretion	422
2.4. Biochemical mechanisms of mast cell and basophil secretion	428
2.5. Stimulus-receptor triggering at the cell membrane	431
2.6. Cytoskeletal elements and secretion	434
2.7. Membrane fusion	436
2.8. Summary	437
3. Platelets	438
3.1. Platelet activities and mediators	438
3.2. Morphologic aspects of secretion	440
3.3. Stimuli for platelet activation: stimulus-membrane interactions	441
3.4. Biochemical mechanisms of platelet activation with particular reference to secretion	450
4. Neutrophils	457
4.1. Introduction	457
4.2. Neutrophil activities and mediators	458
4.3. Morphologic aspects of secretion	462
4.4. Stimuli for neutrophil activation	464
4.5. Biochemical mechanisms of neutrophil stimulation with particular reference to secretion	470
4.6. Summary and speculations	479
5. Concluding remarks	481

11 *Cytoplasmic membranes and the secretory process, by J. Meldolesi, N. Borgese, P. De Camilli and B. Ceccarelli*

1. Introduction	510
2. Intracellular transport of secretion products	511

2.1. The orthodox view	513
2.2. An evaluation of alternative views	526
3. Composition and organization of the cellular membranes involved in transport and release of secretion products	531
3.1. ER membranes	533
3.2. Membranes of the Golgi complex	534
3.3. Membranes of secretory granules and vesicles	538
3.4. Plasma membrane	540
3.5. Composition and structure of membranes: comparative evaluation	543
4. Biogenetic relations between membranes involved in secretion	545
4.1. Kinetic studies on membrane biogenesis	546
4.2. Products synthesized by free and membrane-bound ribosomes	550
4.3. Other experimental evidence on membrane biogenesis	552
4.4. Conclusions	555
5. Discharge of secretion products	555
5.1. Topology of exocytosis at the cell surface	556
5.2. Membrane fusion-fission in exocytosis	569
5.3. Regulation of secretion and stimulus-secretion coupling	575
6. Surface remodeling after exocytosis: removal and fate of discharged granule and vesicle membranes	583
6.1. Membrane retrieval after exocytosis: where, when, and how	584
6.2. The fate of discharged secretory granule membranes	593
6.3. Final considerations on granule membrane retrieval	598

12 *Ultrastructural aspects of exocytotic membrane fusion, by L. Orci and A. Perrelet*

1. Introduction	630
2. Technical approaches to the study of membrane fusion	630
2.1. Thin sectioning	630
2.2. Freeze-fracture	632
3. Protozoan membrane fusion	633
4. Membrane fusion in mammalian secretory cells	633
4.1. Mast cells	634
4.2. Polymorphonuclear leukocytes	635
4.3. Spermatozoa	636
4.4. Acinar cell of the exocrine pancreas	639
4.5. Secretory cells of the neurohypophysis	640
4.6. B cell of the islet of Langerhans	643
5. Membrane events related to endocytosis	648
6. Summary and conclusions	651

13 *Membranes of ciliates: ultrastructure, biochemistry and fusion, by R. D. Allen*

1. Introduction	658
2. Membrane morphology of ciliates	659
2.1. Membrane systems in sectioned cells	659

2.2. Membrane systems in freeze-fractured cells	661
3. Membrane biochemistry of ciliates	669
3.1. Lipids	669
3.2. Proteins	673
3.3. Surface and excreted chemicals	678
4. Changes in membrane constituents of ciliates	682
4.1. Lipid and protein exchange between membranes	682
4.2. Changes correlated with the cell cycle	685
4.3. Changes induced by physical and chemical alterations of the environment	685
5. Membrane fusions in the ciliates	693
5.1. Secretory organelles	693
5.2. Digestive vacuole membranes and lysosomes	700
5.3. Pulsating vacuole system	708
5.4. Endomembrane system	710
5.5. Division of cells and organelles	712
5.6. Other fusions at the plasma membrane	714
6. General discussion and conclusions	716

14 *Calcium-induced phase changes and fusion in natural
and model membranes, by D. Papahadjopoulos*

1. Introduction	766
2. Molecular exchange and fusion between pure phospholipid membranes	767
3. The role of lysolecithin, fatty acids, and DMSO in fusion of phospholipid membranes	769
4. The role of proteins and polypeptides in fusion of phospholipid membranes	772
5. The role of divalent metals (calcium and magnesium) in fusion of vesicle membranes	773
6. The role of lipid phase changes in fusion of phospholipid membranes	776
7. The possible role of calcium-induced phase changes in triggering fusion of natural membranes	780

15 *Problems in the physical interpretation of membrane interaction and fusion,
by D. Gingell and L. Ginsberg*

1. Introduction	792
2. Theoretical and experimental aspects of vesicle fusion	793
2.1. Experimental evidence for bilayer lipid vesicle fusion	793
2.2. Energetic considerations in liposome interaction	794
3. The triggering event in membrane fusion	800
3.1. Changes in small ion concentrations	802
3.2. Changes in membrane field	805
3.3. Membrane interaction and transition temperature	806
4. Structural changes in lipid bilayers during fusion	807
5. Fusion of natural membranes	811
5.1. Behavior of membrane macromolecules in fusion	811
5.2. Possible mechanisms for particle displacement	812
6. Summary	817

Appendix A.	Electrostatic energy of sphere-sphere interaction: linear approximation	817
Appendix B.	Model for phosphatidylserine ionization	821
B.1.	Membrane surface potential in the absence of calcium	821
B.2.	Presence of calcium	825
Appendix C.	Effect of vesicle interaction and contact on the transition temperature of membrane phospholipids	828
<i>Subject Index</i>		835