

Embryology of Angiosperms

Edited by B. M. Johri

Embryology of Angiosperms

Edited by B. M. Johri

With 278 Figures

Springer-Verlag
Berlin Heidelberg New York Tokyo 1984

Professor BRIJ MOHAN JOHRI
Department of Botany
University of Delhi
Delhi-110007, India

ISBN 3-540-12739-9 Springer-Verlag Berlin Heidelberg New York Tokyo
ISBN 0-387-12739-9 Springer-Verlag New York Heidelberg Berlin Tokyo

Library of Congress Cataloging in Publication Data. Main entry under title: Embryology of angiosperms. Includes bibliographies. 1. Angiosperms. 2. Botany—Embryology. I. Johri, B.M. QK495.A1E43 1984 582.13'0433 83-20430.

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically those of translation, reprinting, re-use of illustrations, broadcasting, reproduction by photocopying machine or similar means, and storage in data banks. Under § 54 of the German Copyright Law where copies are made for other than private use a fee is payable to "Verwertungsgesellschaft Wort", Munich.

© by Springer-Verlag Berlin Heidelberg 1984
Printed in Germany

The use of registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Typesetting, printing, and bookbinding: Brühlsche Universitätsdruckerei, Giessen
2131/3130-543210

Foreword

Thirty-four years have elapsed since the publication of the late Professor P. Maheshwari's text, *An Introduction to the Embryology of Angiosperms*, a work which for many years served as an invaluable guide for students and a rich source book for research workers. Various texts dealing with sections of the broad spectrum of topics encompassed by Maheshwari in his book have appeared in the interim, but a compendious modern work dealing with the whole field has been lacking. This present volume splendidly meets the need, and it is altogether fitting that Professor B. M. Johri, long an associate and close colleague of Professor Maheshwari and himself a prolific contributor to the subject, should have undertaken the task of editing it.

When Maheshwari wrote, it was still feasible for one author to handle the subject, but today even someone with his fine breadth of vision and depth of understanding could not, alone, do it justice. So the effort has to be a collaborative one; and Professor Johri's achievement has been to bring together a team of authoritative collaborators, assign them their responsibilities, and put them to work to produce a text as integrated in its treatment as the diversity of the subject would allow. The product vividly illustrates the advances that have been made in the study of angiosperm reproductive systems in the last 30 years, and the book is surely destined to become the new standard for student and researcher alike.

Like many surveys of its kind, the text inevitably shows just how dependent progress during the last few decades has been on the advent of new technologies. The great observers of earlier generations reached the limits set by the resolution of the optical microscope in their investigations of the cytological and karyological phenomena associated with plant reproduction, and were restricted further by the preparation techniques they had available. Their modern successors have been blessed with new extensions of vision – on the one hand through the advent of electron microscopy, and on the other, through the further technical development of optical microscopy, marked, for example, by the introduction of phase and differential interference contrast, fluorescence techniques and image-processing systems. At the same time, specimen handling methods have improved apace, and the crumbling of hitherto stoutly maintained interdisciplinary barriers has meant that many workers today have gained a new competence to interpret what they observe through the support of physiological and biochemical experimentation. All this adequately accounts for the flood of new information. Yet, if one

message emerges from the present text as a whole – urged by author after author – it is that we are now but on the threshold of a new wave of discovery. No living group shows the diversity of reproductive method to be seen in the angiosperms; and no task in the whole field of biological research is more important for mankind than working the systems out and finding how to manipulate them for practical ends, for after all the flowering plants provide the indispensable basis of human life on earth. This volume is not only an epitome of knowledge, but an invitation and a challenge – a challenge, particularly, for the next generation of workers, some of whom may well find in its pages good reason for ignoring the facile appeal of test-tube biology in favour of making their contribution towards finding out more about how real plants go about the job of reproducing.

July 1984

J. HESLOP-HARRISON, F.R.S.

Royal Society Research Professor
University College of Wales
Welsh Plant Breeding Station
Plas Gogerddan (near Aberystwyth)
Great Britain

Preface

Since the publication of *Recent Advances in the Embryology of Angiosperms* (ed. P. Maheshwari) in 1963, there has been phenomenal progress in almost all areas of reproduction in flowering plants. This progress has resulted from investigations based on optical, electron (TEM, SEM), fluorescence, phase contrast, and interference (Nomarski effect) microscopy, cytochemistry, histochemistry, physiology and biochemistry. However, all this knowledge is scattered in a large number of periodicals and it has become a formidable task for both teachers and students to collect the necessary information. Hence this volume *Embryology of Angiosperms* – an advanced treatise comprising 16 chapters written by specialists who have devoted years of study to the subject.

The significant advances of the last 20–30 years have been discussed. The authors have raised several questions to seek new information, and have made appropriate mention of many unsolved problems. The text is adequately illustrated with line drawings and half-tones, including electron micrographs.

Every effort has been made to present a comprehensive up-to-date account. I have earnestly endeavoured to achieve uniformity in the format. Suggestions for further improvement would be most welcome.

I have no doubt that post-graduate and research students will find *Embryology of Angiosperms* a good source material. To those teaching “reproduction in flowering plants”, the volume offers a fount of ready-made material.

July 1984

B. M. JOHRI

Acknowledgements

Through Dr. G.A. Nogler, Dr. Konrad F. Springer invited me to prepare an English translation of Professor A. Rutishauser's book *Embryologie und Fortpflanzungsbiologie der Angiospermen*. My experience of teaching undergraduate and postgraduate students for over three decades at the Universities of Agra, Rajasthan and Delhi has provided a deep insight into the various aspects of plant embryology. Also, over a span of almost 50 years, I have had unique opportunities to discuss problems of angiosperm embryology with eminent embryologists during my numerous visits both in India and abroad, and at international meetings. The idea of editing a volume consisting of contributions on recent developments in the embryology of angiosperms emerged out of these interactions. Dr. Springer readily agreed to my suggestion, and I am deeply indebted to him.

Professor J. Heslop-Harrison has done me a great favour in agreeing to prepare the "Foreword" to this volume.

I am grateful to the authors who accepted my invitation to write the chapters. The manuscripts were read by my colleagues in the University of Delhi and I especially thank Professor N.S. Rangaswamy, Dr. N.N. Bhandari, Dr. M.R. Vijayaraghavan, Dr. K.R. Shivanna and Dr. S. Natesh for offering valuable suggestions. I greatly appreciate the help rendered by Dr. K. B. Ambegaokar, who redrew several diagrams, reassembled many plates of illustrations, and prepared the indices.

Professor Dr. G. Melchers (Tübingen) provided photographs of the tomato + potato somatic hybrid. Professor Dr. E. Battaglia (Rome) sent a reprint containing the original diagrams of *Fritillaria* type of embryo sac. Professor Dr. F. Pospisil (Prague) sent photographs of pollen embryo sacs. Professor Dr. O. Erdélská (Bratislava) prepared an illustrated write-up on the role of microcinematography in embryology. Dr. Scott D. Russell (Norman) sent me his unpublished manuscripts, and electron micrographs of male gametes and fertilization in *Plumbago*. Dr. R. Wunderlich (Vienna), Dr. M. Luxová (Bratislava), Dr. L. Ahlstrand (Göteborg) and Dr. B.A. Fineran (Christchurch) made available the literature needed. I am much obliged to all of them for their gracious help.

The facilities at the Department of Botany, University of Delhi, made it possible to prepare the *Embryology of Angiosperms*, and I am grateful to Professor S.C. Maheshwari, Professor H.Y. Mohan Ram, Professor R.N. Kapil and Professor R.N. Chopra (present Head of the Department) who have been continuously looking after my interest since I

retired in 1974. I have received much inducement to complete the book expeditiously from my wife Raj, my daughter-in-law Meera, and my son Lahit.

My sincere appreciation is extended to Mr. R. K. Gupta for typing several chapters, and to Mr. Krishan Lal for preparing some illustrations.

From the house of Springer, I am especially thankful to Dr. Dieter Czeschlik, Life-Science Editor, for valuable advice, to the Copy-Editor who made much improvement in the text, to Mrs. Linda Teppert for processing the publication, and to Miss Claudia Grössl who looked after the production of this book.

July 1984

B. M. JOHRI

Contributors

AMBEGAOKAR, K.B., Department of Botany, University of Delhi,
Delhi 110007, India

BHANDARI, N.N., Department of Botany, University of Delhi,
Delhi 110007, India

BOESEWINKEL, F.D., Hugo de Vries Laboratory, University of Amsterdam,
1018 DD Amsterdam, The Netherlands

BOUMAN, F., Hugo de Vries Laboratory, University of Amsterdam,
1018 DD Amsterdam, The Netherlands

D'AMATO, F., Institute of Genetics, University of Pisa, 56100 Pisa,
Italy

FAVRE-DUCHARTRE, M., Botanical Laboratory, Faculty of Science,
University of Reims, 51062 Reims Cedex, France

HERR, J.M., JR., Department of Biology, University of South Carolina,
Columbia, SC 29208, USA

JACOBSEN, JOHN V., Division of Plant Industry, Commonwealth Scientific
and Research Organization, Canberra City, A.C.T. 2601, Australia

JOHRI, B.M., Department of Botany, University of Delhi, Delhi 110007,
India

KNOX, R.B., Plant Cell Biology Research Centre, School of Botany,
University of Melbourne, Parkville, Victoria 3052, Australia

LAKSHMANAN, K.K., Department of Botany, Bharathiar University,
Coimbatore 641041, India

NATESH, S., Department of Botany, SGTB Khalsa College, University
of Delhi, Delhi 110007, India. (Present address: Department of
Science and Technology, Technology Bhavan, New Mehrauli Road,
New Delhi 110016, India)

NOGLER, G.A., Institute for General Botany, Federal University of
Technology (ETH), 8092 Zurich, Switzerland

PRABHAKAR, KUMKUM, Department of Botany, Maitreyi College,
University of Delhi, Netaji Nagar, New Delhi 110023, India

RAO, P.S., Plant Morphogenesis and Tissue Culture Section, Bio-Organic Division, Bhabha Atomic Research Centre, Trombay, Bombay 400085, India

RAU, M.A., Department of Applied Botany, University of Mysore, Manasa Gangotri, Mysore 570006, India (962 Lakshmipuram, Mysore 570004, India)

VAN WENT, J.L. Department of Plant Cytology and Morphology, Agricultural University, Botanical Laboratory, 6703 BD Wageningen, The Netherlands

VIJAYARAGHAVAN, M.R., Department of Botany, University of Delhi, Delhi 110007, India

WILLEMSE, M.T.M., Department of Plant Cytology and Morphology, Agricultural University, Botanical Laboratory, 6703 BD Wageningen, The Netherlands

Contents

1 Embryology: Then and Now

B.M. JOHRI and K.B. AMBEGAOKAR (With 22 Figures) 1

1.1	Introduction	1
1.2	Techniques to Study Embryology	2
1.3	Embryo Sacs in Anthers	5
1.3.1	<i>Leptomeria</i>	5
1.3.2	<i>Calotis</i>	6
1.3.3	<i>Hyacinthus</i>	6
1.4	Fritillaria Type of Embryo Sac	12
1.5	Unusual Embryological Features in Loranthaceae	14
1.5.1	Ovary-Ovule Complex	14
1.5.2	Embryo Sac	16
1.5.3	Endosperm	18
1.5.4	Embryo	19
1.5.5	Reproductive Calendar in <i>Struthanthus vulgaris</i>	21
1.6	Nutrition of the Ovule and Seed	22
1.6.1	Vascular Supply	23
1.6.2	Haustoria	23
1.6.3	Transfer Cells	28
1.7	Role of Persistent Pollen Tubes	30
1.8	Embryos of Doubtful Origin	32
1.8.1	Antipodal Embryos	33
1.8.2	Endospermal Embryos	33
1.9	Gymnospermous Characters in Angiosperms	37
1.9.1	<i>Tambourissa</i>	37
1.9.2	<i>Butomopsis</i>	39
1.9.3	<i>Paeonia</i>	42
1.10	Future Research	43
	References	47

2 The Microsporangium

N.N. BHANDARI (With 21 Figures) 53

2.1	Introduction	53
2.2	Morphology and Structure	53
2.3	Ontogeny	55
2.4	Wall Layers	57

2.4.1	Epidermis	57
2.4.2	Endothecium	58
2.4.3	Middle Layers	60
2.4.4	Tapetum	60
2.5	Urbisch Bodies/Orbicules	77
2.5.1	Origin	79
2.5.2	Relation to Exine Deposition: By-Product	82
2.6	Tapetal Membrane: Structure, Origin, and Significance	83
2.7	Pollenkitt and Tryphine	85
2.8	Sporogenous Tissue: Ultrastructure	88
2.8.1	Cytoplasmic Membranes and Ribosome Population	88
2.8.2	Nucleus	90
2.8.3	Nucleolar Cycle	92
2.8.4	Cytoplasmic Organelles During Meiosis	94
2.8.5	Plasmodesmata and Cytoplasmic Connections	95
2.9	Initiation and Control of Meiosis	97
2.9.1	Duration of Meiosis	99
2.9.2	Synthesis of Callose: Deposition and Significance	100
2.9.3	Cytokinesis	106
2.9.4	Cellulosic Wall of Microspore Mother Cell	107
2.10	Some Unusual Features	109
2.11	Conclusions	110
	References	111

3 The Ovule

F. BOUMAN (With 21 Figures)	123	
3.1	Historical	123
3.2	Ovular Morphology	125
3.3	Ovule Initiation	126
3.4	Nucellus	128
3.5	Megasporogenesis	131
3.6	Integuments	138
3.7	Types of Ovules	144
3.8	Vascular Supply of the Ovule	147
3.9	Special Structures	148
3.10	Ovule Reduction	151
3.11	Concluding Remarks	153
	References	153

4 The Female Gametophyte

M.T.M. WILLEMS and J.L. VAN WENT (With 16 Figures)	159	
4.1	Introduction	159
4.2	Types of Megagametophyte Development	159
4.3	Development of the Megagametophyte	164
4.3.1	The Megasporangium	164

4.3.2	The Coenocytic Megagametophyte	165
4.4	The Relation with the Nucellar Tissue	168
4.5	Organization of the Embryo Sac	170
4.5.1	The Synergids	174
4.5.2	The Egg Cell	183
4.5.3	The Central Cell	185
4.5.4	The Antipodal Cells	188
4.6	Female Gametophyte Development	190
	References	191

5 The Pollen Grain

R.B. KNOX (With 24 Figures)	197	
5.1	Introduction	197
5.2	Pollen Structure and Cytochemistry	198
5.2.1	Pollen Shape	199
5.2.2	Pollen Cytology	199
5.2.3	Pollen-wall Structure	204
5.2.4	The Pollen Tube	208
5.2.5	Structural Adaptations of Pollen for Dispersal	210
5.3	Formation of Pollen	225
5.3.1	Cytology of Development	225
5.3.2	The Primexine	232
5.3.3	Establishment of Apertures	237
5.3.4	Exine Differentiation and Maturation	238
5.3.5	Intine Synthesis and Deposition	242
5.3.6	Mechanism of Cohesion in Composite Pollen	244
5.3.7	Pollen Sterility	245
5.4	Pollen Germination and Pistil Interactions	245
5.4.1	Pollen Quality	245
5.4.2	Pollen Germination and Tube Development	247
5.4.3	Diagnostic Landmarks of Pollination	249
5.4.4	Role of Pollen in Fertilization and Seed-setting	252
5.5	Pollen-wall Proteins and Allergens	253
5.6	Conclusions and Future Developments	259
	References	261

6 Fertilization

J.L. VAN WENT and M.T.M. WILLEMS (With 13 Figures)	273	
6.1	Introduction	273
6.2	Stigma and Style	273
6.2.1	Function and Structure of the Stigma	273
6.2.2	The Nature of the Stigma Covering	275
6.2.3	Function and Structure of the Style	277
6.3	Pollen Germination	279
6.3.1	Sticking and Hydration	279

6.3.2	Pollen Tube Formation and Growth	281
6.3.3	The Sperm Cell	283
6.4	Pollen-Pistil Interaction	284
6.4.1	Pollen Recognition, Acceptance, and Rejection	284
6.4.2	Pollen Incompatibility	286
6.4.3	Entry of Pollen Tube into Stigma and Style	289
6.4.4	Pollination Effects	291
6.5	Entrance and Discharge in Embryo Sac	292
6.5.1	Course of the Pollen Tube	292
6.5.2	Entry into the Embryo Sac	294
6.5.3	Growth Through the Filiform Apparatus	297
6.5.4	Entry into the Synergid	298
6.5.5	Transfer of Tube Content	301
6.6	Fusion of Gametes	302
6.6.1	Fusion of Nuclei	305
6.7	The Progametic Phase and Fertilization	308
	References	309

7 The Endosperm

M.R. VIJAYARAGHAVAN and K. PRABHAKAR (With 30 Figures)	319	
7.1	Introduction	319
7.2	Nuclear Endosperm	319
7.2.1	Wall Formation	322
7.2.2	Cucurbitaceae	322
7.2.3	Leguminosae	323
7.2.4	Palmae	323
7.2.5	Proteaceae	324
7.2.6	Histochemistry and Ultrastructure	324
7.3	Cellular Endosperm	330
7.3.1	Acanthaceae	330
7.3.2	Cyrillaceae	330
7.3.3	Gesneriaceae	330
7.3.4	Icacinaceae	331
7.3.5	Santalaceae	331
7.3.6	Loasaceae	332
7.3.7	Loranthaceae	332
7.3.8	Scrophulariaceae	335
7.3.9	Histochemistry and Ultrastructure	337
7.4	Helobial Endosperm	338
7.4.1	Salient Features in Monocotyledons	339
7.4.2	Histochemistry and Ultrastructure	341
7.5	Ruminate Endosperm	342
7.6	Central Cell	345
7.6.1	Central Cell Cytoplasm	346
7.6.2	Central Cell Nucleus	349
7.6.3	Covering of the Central Cell	349

7.7	Wall Formation in Endosperm	350
7.8	Cytology of the Endosperm	355
7.9	Reserve Materials in Developing Endosperm	361
7.9.1	Protein Bodies	361
7.9.2	Starch	363
7.10	Embryo-Endosperm Relationship	364
7.11	Incorporation of Nucellus and Integument in Endosperm Formation	368
7.12	Conclusions and Prospects	369
	References	370

8 The Embryo

S. NATESH and M.A. RAU (With 29 Figures)	377
--	-----

8.1	Historical	377
8.2	Zygote	378
8.2.1	Structure and Composition	379
8.2.2	Size Adjustments	382
8.2.3	Polarity	383
8.3	Early Embryogenesis	384
8.3.1	Cell Patterns	384
8.3.2	Tetrad, Quadrant, and Octant Proembryos	385
8.3.3	Stages Leading to Mature Embryo	387
8.4	Classification Based on Early Development of the Embryo	388
8.4.1	Systems Suggested by Schnarf and Johansen	388
8.4.2	System Suggested by Souèges	392
8.4.3	Other Systems of Classification	393
8.5	Differentiation in Embryo	397
8.6	Dicot and Monocot Embryo	398
8.7	The Grass Embryo	400
8.8	The Embryo in Palms	403
8.9	Ultrastructural and Cytochemical Aspects	405
8.10	Suspensor: Structure and Function	414
8.11	Deviations from Usual Development	424
8.11.1	Embryogeny in <i>Paeonia</i>	424
8.11.2	Embryos Devoid of Organs	425
8.11.3	Chimeral Embryos	430
8.12	Concluding Remarks	433
	References	434

9 Polyembryony

K.K. LAKSHMANAN and K.B. AMBEGAOKAR (With 12 Figures)	445
---	-----

9.1	Introduction	445
9.2	Classification	446

9.2.1	Simple Polyembryony	447
9.2.2	Multiple Polyembryony	447
9.3	Nucellar Polyembryony	447
9.3.1	Rutaceae	448
9.3.2	Anacardiaceae	452
9.3.3	Myrtaceae	452
9.3.4	Cactaceae	454
9.3.5	Orchidaceae	454
9.4	Integumentary Polyembryony	454
9.4.1	Endothelial Polyembryony	455
9.5	Zygotic and Suspensor Polyembryony	456
9.5.1	Zygotic Polyembryony	456
9.5.2	Suspensor Polyembryony	458
9.6	Synergid Polyembryony	458
9.6.1	Twins and Triplets	461
9.7	Polyembryony in Hybrids	463
9.8	Causes of Polyembryony	465
9.9	Induction of Polyembryony	466
9.10	Utilization of Plural Embryos	470
	References	470

10 Gametophytic Apomixis

G.A.	NOGLER (With 8 Figures)	475
10.1	Introduction	475
10.1.1	Definitions	475
10.1.2	Synonyms	476
10.1.3	Remarks on Terminology	477
10.2	Embryology of Gametophytic Apomicts	477
10.2.1	Development of Unreduced Embryo Sacs	477
10.2.2	Formation of Endosperm and Embryo	487
10.2.3	Male Meiosis and the Male Gametophyte	493
10.3	Apomixis and Sexuality	494
10.3.1	Sexual Potentials in Gametophytic Apomicts	494
10.3.2	Possibilities of Influencing the Degree of Apomixis	495
10.4	Causes and Consequences of Apomixis	497
10.4.1	Heterozygosity and Variability	497
10.4.2	Causes of Gametophytic Apomixis; Components of Apomixis in Sexual Plants	498
10.4.3	Apomixis and Polyploidy	500
10.4.4	Agamic Species Complexes and Their Evolution	501
10.5	Genetics of Gametophytic Apomixis	503
10.5.1	Dominant or Recessive Inheritance?	503
10.5.2	Some Critical Remarks	504
10.5.3	Some Results, Conclusions, and Prospects	506
10.6	Apomixis and Breeding. Conclusions	508
	References	510

11 Role of Polyploidy in Reproductive Organs and Tissues

F. D'AMATO (With 16 Figures)	519
11.1 Introduction	519
11.2 Methods of Polyploidization and Ploidy Determination	519
11.2.1 Acytokinetic Mitosis (AM)	520
11.2.2 Spindle Fusion (SF)	520
11.2.3 Restitutioinal Mitosis (RM)	520
11.2.4 Endomitosis (Em)	520
11.2.5 Chromosome Endoreduplication (Er)	521
11.2.6 Ploidy Determination	522
11.3 Anther	523
11.3.1 Anther Wall and Connective	523
11.3.2 Tapetum	523
11.3.3 Pollen Grains	529
11.4 Ovule	530
11.4.1 Nucellus	530
11.4.2 Integument(s) and Endothelium	530
11.5 Embryo Sac	531
11.5.1 Egg Cell	531
11.5.2 Synergids	532
11.5.3 Proendospermic Cell	533
11.5.4 Antipodal Cells	534
11.6 Endosperm	537
11.6.1 Origin and Types of Endosperm	537
11.6.2 Polyploidy in the Endosperm	537
11.7 Embryo	543
11.7.1 Embryo Proper	543
11.7.2 Suspensor	546
11.7.3 Nonzygotic Embryos	557
11.8 Physiological Role of Polyploidy	558
11.9 Future Research	560
References	561

12 The Seed: Structure

F.D. BOESEWINKEL and F. BOUMAN (With 16 Figures)	567
12.1 Introduction	567
12.1.1 Importance of Seeds	567
12.1.2 Historical Survey	568
12.2 Structure of Seeds	569
12.2.1 General Morphology	569
12.2.2 Vascular Supply of the Seed	571
12.2.3 Seed Types	572
12.2.4 Development and Structure of Seed-coats	575
12.2.5 Differentiation	579