



Horticultural Reviews

VOLUME 48

Edited by
IAN WARRINGTON

WILEY

HORTICULTURAL REVIEWS
Volume 48

Horticultural Reviews is sponsored by:

American Society for Horticultural Science

International Society for Horticultural Science

Editorial Board, Volume 48

A. Ross Ferguson

Robert E. Paull

HORTICULTURAL REVIEWS

Volume 48

Edited by
Ian Warrington

Massey University
New Zealand

WILEY

This edition first published 2021
© 2021 John Wiley & Sons, Inc.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by law. Advice on how to obtain permission to reuse material from this title is available at <http://www.wiley.com/go/permissions>.

The right of Ian Warrington to be identified as the author of this editorial material has been asserted in accordance with law.

Registered Offices

John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA
John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Office

The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

For details of our global editorial offices, customer services, and more information about Wiley products visit us at www.wiley.com.

Wiley also publishes its books in a variety of electronic formats and by print-on-demand. Some content that appears in standard print versions of this book may not be available in other formats.

Limit of Liability/Disclaimer of Warranty

While the publisher and authors have used their best efforts in preparing this work, they make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives, written sales materials or promotional statements for this work. The fact that an organization, website, or product is referred to in this work as a citation and/or potential source of further information does not mean that the publisher and authors endorse the information or services the organization, website, or product may provide or recommendations it may make. This work is sold with the understanding that the publisher is not engaged in rendering professional services. The advice and strategies contained herein may not be suitable for your situation. You should consult with a specialist where appropriate. Further, readers should be aware that websites listed in this work may have changed or disappeared between when this work was written and when it is read. Neither the publisher nor authors shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

Library of Congress Cataloging-in-Publication Data

Names: Warrington, I. J. (Ian J.) editor.

Title: Horticultural reviews. Volume 48 / Ian Warrington.

Description: First edition. | Hoboken, NJ, USA : Wiley, 2021. | Includes bibliographical references and index.

Identifiers: LCCN 2020037759 (print) | LCCN 2020037760 (ebook) | ISBN 9781119750772 (cloth) | ISBN 9781119750789 (adobe pdf) | ISBN 9781119750796 (epub)

Subjects: LCSH: Horticulture—Bibliography. | Horticulture—Research.

Classification: LCC SB318.3 .H678 2021 (print) | LCC SB318.3 (ebook) | DDC 635—dc23

LC record available at <https://lccn.loc.gov/2020037759>

LC ebook record available at <https://lccn.loc.gov/2020037760>

Cover Design: Wiley

Cover Image: Courtesy of Jules Janick

Set in 10/12pts Melior LT Std by SPi Global, Chennai, India

Contents

Contributors	ix
Dedication: Gregory L. Reighard	xiii
<i>Juan Carlos Melgar, Ksenija Gasic and Ian Warrington</i>	
1. Pollination-Induced Changes in the Morphology and Physiology of <i>Dendrobium</i> Orchid Flowers Prior to Fertilization: The Roles of Ethylene and Auxin	1
<i>Wouter G. van Doorn and Saichol Ketsa</i>	
I. Introduction	2
II. Orchid Flower Structure	3
III. Post-Pollination Effects in Orchids other than <i>Dendrobium</i>	5
IV. Role of Hormones in Orchids other than <i>Dendrobium</i>	6
V. Pollination in <i>Dendrobium</i>	8
VI. Visible Post-Pollination Effects in <i>Dendrobium</i>	13
VII. Role of Hormones in the Visible Post-Pollination Phenomena in <i>Dendrobium</i>	21
VIII. Conclusions	31
Acknowledgment	31
Literature Cited	32
2. <i>Actinidia arguta</i> (Kiwiberry): Botany, Production, Genetics, Nutritional Value, and Postharvest Handling	37
<i>Piotr Latocha, Filip Debersaques and Iago Hale</i>	
I. Introduction	39
II. Botany	41
III. Cultivation and Management	54
IV. Genetics and Breeding	84
V. Chemical Composition, Nutritional Value, and Health Benefits	105

VI. Harvesting and Postharvest Handling	119
VII. Utilization	128
VIII. Conclusions	131
Literature Cited	133
3. Advances in Cassava-Based Multiple-Cropping Systems	153
<i>V. Ravi, G. Suja, R. Saravanan and Sanket J. More</i>	
I. Introduction	156
II. Intercropping Cassava	170
III. Crop Rotation Involving Cassava	206
IV. Cassava-Based Sequential/Intercropping Systems Involving Pulses and/or Rice	208
V. Cassava + Plantation Crops	209
VI. Pests and Diseases in Cassava-Based Intercropping	212
VII. Conclusions and Future Prospects	214
Literature Cited	219
4. Arrowroot (<i>Maranta arundinacea</i> L.): Botany, Horticulture, and Uses	233
<i>Vitor Brito, Renata Nascimento, Jeniffer Narcisa-Oliveira, Nathalia Joffer, André Fattori, Marney Cereda, Carina Oliveira, Reginaldo Costa, Lorene Tiburtino-Silva and Josemar Maciel</i>	
I. Introduction	234
II. Occurrence and Distribution	236
III. Botany: Taxonomy, Morphology, and Genetics	238
IV. Horticultural Aspects	248
V. Processing	252
VI. Uses and Applications	253
VII. Conclusions	264
Acknowledgment	264
Literature Cited	265
5. Jamun (<i>Syzygium cumini</i> L. Skeels): A Promising Fruit for the Future	275
<i>Babak Madani, Amin Mirshekari, Elhadi M. Yahia, John B. Golding, Shokrollah Hajivand and Abdolmajid Mirzaalian Dastjerdy</i>	
I. Introduction	276
II. Economic Significance	277

III. Botany, Taxonomy, and Genetics	278
IV. Cultivation Practices	281
V. Nutritional Value	286
VI. Health-Promoting Effects	289
VII. Postharvest Practices	290
VIII. Processing	297
IX. Conclusions	299
Literature Cited	300
6. Coconut Micropropagation and Cryopreservation	307
<i>Ana S. Lédo and Wagner A. Vendrame</i>	
I. Introduction	309
II. <i>In Vitro</i> Propagation Technology	311
III. Bioreactor Technology	320
IV. Cryopreservation	322
V. Summary and Conclusions	330
Literature Cited	330
7. The Puzzling Phenomenon of Seedling Yellows Recovery and Natural Spread of Asymptomatic Infections of Citrus Tristeza Virus: Two Sides of the Same Coin	339
<i>Moshe Bar-Joseph, Antonino F. Catara and Grazia Licciardello</i>	
I. Introduction	341
II. The CTV Genome and Biology	341
III. A Short Account of the Israeli CTV Suppression Program (1970–1986)	343
IV. Comparisons of Severe and Mild CTV-VT Isolates From Sicily	347
V. Discussion	352
Acknowledgments	356
Literature Cited	357
8. Yield Alternation: Horticulture, Physiology, Molecular Biology, and Evolution	363
<i>Eliezer E. Goldschmidt and Avi Sadka</i>	
I. Introduction	365
II. Molecular Mechanisms of Flowering Control in Model Plants and Fruit Trees	366
III. Effect of Fruit Load on Changes in Gene Expression, Protein, and Metabolite Levels in Leaves and Buds	377

IV. The Effect of Fruit Load on Hormone Homeostasis	381
V. Mitigation of Alternate Bearing	385
VI. Discussion	393
Acknowledgment	402
Literature Cited	402
Subject Index	419
Cumulative Subject Index	421
Cumulative Contributor Index	455

Contributors

Moshe Bar-Joseph, The S. Tolkowsky Laboratory, Department of Plant Pathology, Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel

Vitor Brito, Departamento de Produção e Gestão Agroindustrial, Universidade para o Desenvolvimento do Estado e Região do Pantanal (UNIDERP), Campo Grande, Brazil

Antonino F. Catara, Science and Technology Park of Sicily, Catania, Italy (Present address: Agrobiotech Soc. Coop., Catania, Italy)

Marney Cereda, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil

Reginaldo Costa, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil

Abdolmajid Mirzaalian Dastjerdy, Department of Horticultural Science, Faculty of Agriculture and Natural Resources, University of Hormozgan, Bandar Abbas, Iran

Filip Debersaques, Department of Plants and Crops, Faculty of Bioscience Engineering, Ghent University, Valentin Vaerwyckweg 1, B-9000 Ghent, Belgium

André Fattori, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil

Ksenija Gasic, Department of Plant and Environmental Sciences, Clemson University, Clemson, SC 29634, USA

John B. Golding, NSW Department of Primary Industries, Gosford, NSW, Australia

Eliezer E. Goldschmidt, Institute of Plant Sciences and Genetics in Agriculture, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot, 761000 Israel

- Shokrollah Hajivand**, Horticultural Research Institute, AREEO, Karaj, Iran
- Iago Hale**, Department of Agriculture, Nutrition, and Food Systems, University of New Hampshire, Durham, NH 03824, USA
- Nathalia Joffer**, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil
- Saichol Ketsa**, Department of Horticulture, Kasetsart University, Chatuchak, Bangkok 10900, Thailand *and* Academy of Science, The Royal Society of Thailand, Dusit, Bangkok 10300, Thailand
- Piotr Latocha**, Department of Environmental Protection and Dendrology, Faculty of Horticulture and Biotechnology, Warsaw University of Life Sciences – SGGW, Nowoursynowska str 166, 02-787 Warsaw, Poland
- Ana S. Lédo**, Embrapa Tabuleiros Costeiros, Aracaju, SE, Brazil
- Grazia Licciardello**, Agrobiotech Soc. Coop., Catania, Italy (Present address: Council for Agricultural Research and Economics, Research Centre for Olive, Citrus and Fruit Trees (CREA-OFA), Rende (Cosenza), Italy)
- Josemar Maciel**, Departamento de Desenvolvimento Local, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil
- Babak Madani**, Horticultural Crops Research Department, Natural Resources Research and Education Center of Hormozgan, AREEO, Bandar Abbas, Iran
- Juan Carlos Melgar**, Department of Plant and Environmental Sciences, Clemson University, Clemson, SC 29634, USA
- Amin Mirshekari**, Department of Agronomy and Plant Breeding, Faculty of Agriculture, University of Yasouj, Yasouj, Iran
- Sanket J. More**, ICAR – Central Tuber Crops Research Institute, Sreekarriyam, Thiruvananthapuram, India
- Jeniffer Narcisa-Oliveira**, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil
- Renata Nascimento**, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil
- Carina Oliveira**, Departamento de Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil
- V. Ravi**, ICAR – Central Tuber Crops Research Institute, Sreekarriyam, Thiruvananthapuram, India

Avi Sadka, Department of Fruit Tree Sciences, The Institute of Plant Sciences, Agricultural Research Organization, The Volcani Center, Rishon LeZion, 7528809 Israel

R. Saravanan, ICAR – Central Tuber Crops Research Institute, Sreekaraiyam, Thiruvananthapuram, India

G. Suja, ICAR – Central Tuber Crops Research Institute, Sreekaraiyam, Thiruvananthapuram, India

Lorene Tiburtino-Silva, Departamento de Desenvolvimento Local, Universidade Católica Dom Bosco (UCDB), Campo Grande, Brazil

Wouter G. van Doorn,[†] Mann Laboratory, Department of Plant Sciences, University of California, Davis, CA 95616, USA

Wagner A. Vendrame, Environmental Horticulture Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, USA

Ian J. Warrington, Massey University, Palmerston North, New Zealand

Elhadi M. Yahia, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, Mexico

[†]Deceased.



Dedication: Gregory L. Reighard

This volume of *Horticultural Reviews* is dedicated to Dr Gregory L. Reighard, Professor Emeritus at Clemson University, for his contributions to horticulture and horticultural research, especially in areas relating to fruit production.

Dr Reighard was born in Johnstown, Pennsylvania, in the midst of a rural coal-mining area. He lived next to his grandparents who had a small mountain farm near South Fork, Pennsylvania, where he helped with farm chores and developed an interest in growing fruits and vegetables. He also spent a lot of time in the mountain forests hunting and foraging, so he developed a love for trees. He was the first in his wider family to go to college and attended Pennsylvania State University, attaining his B.S. in Forestry in 1977. He completed his M.S. in Biology at the University of Michigan in 1978, and a Ph.D. in Forestry at Michigan State University in 1984. After working in forest management in Montana and Florida, he decided that he did not want to “harvest” trees as his legacy, but instead nurture and improve them for what fruits or nuts they could provide. After graduation and working at the University of Florida as a research associate, he applied and interviewed for a tree fruit (pomology) position in the Department of Horticulture at Clemson, where he subsequently spent his entire professional career as a faculty member in the College of Agriculture, Forestry and Life Sciences, with research, extension, and teaching appointments. In 2017, he served as Interim Chair of the Department of Plant and Environmental Sciences. At this institution, he has demonstrated excellence in scholarship, and dedication to the discipline of pomology and to the commercial tree fruit industry.

Dr Vance Baird, Chair of the Department of Horticulture at Michigan State University, has observed that “you know someone has been well-educated and possesses adaptable insight when he can take two degrees in Forestry and one in Biology and translate that into one of the most successful careers in tree fruit physiology and germplasm improvement – and developed a career that has evolved with the state-of-the-science and with commercial production needs.”

Dr Reighard's accomplishments in pomology are impressive, especially as they span the range from applied, field-based work to the fundamentals of molecular biology. His research interests include the study of physiological phenomena of genetically compound fruit trees in terms of effects of rootstocks, interstems, and cultural practices on vegetative growth, fruiting, frost protection, nutrition, disease resistance, and cold injury. Additional research has involved developing new rootstocks that are resistant to nematodes, determining how interstems and growth hormones affect root growth and scion phenology, developing flower bud thinning techniques, and finding molecular markers for traits such as nematode resistance and dormancy control for use in applied breeding programs.

One of his greatest accomplishments came about through his commitment to the performance evaluation and genetic analysis of rootstocks that could provide tolerance to the peach tree short life (PTSL) disease complex. His insight and perseverance, and his collaboration with colleagues at the USDA, resulted in the identification, selection, development, and commercialization of the Guardian® peach rootstock, which provided the industry with a rootstock choice that protected trees from PTSL. This was an outstanding contribution at a critical time when the industry was losing traditional chemical control options. It allowed the peach industry in the southeastern United States to thrive by improving the long-term sustainability and profitability of many farms. Today, at least 90% of all commercial peaches newly planted in the southeastern United States are planted on Guardian® rootstock. Furthermore, Guardian® rootstock is having a similarly positive impact on peach production in other major stone fruit-producing areas around the world, including California, South Africa, and Australia.

Chalmers R. Carr III, President and CEO of Titan Farms, a 2000 ha peach operation, states, "The southern peach industry, most especially the South Carolina peach industry, second only to California in peach production, was truly headed toward extinction due to PTSL disease. Research by Dr Reighard and colleagues that was dedicated to developing and releasing the Guardian® rootstock not only stopped the dwindling spiral of peach production in the southeast but has allowed the industry to thrive and flourish."

Other than the development of Guardian®, Dr Reighard's program has also been very successful in achieving an improved understanding of crop load management, harvest modeling, tree habit, bud dormancy, and structural and comparative genomics, not just in peach but also in other important fruit crops such as apple, apricot, pear, and plum. His enthusiasm to collect and evaluate various germplasm for its potential to serve as *Prunus* rootstocks was very fortunate, as the stone fruit

industry in the United States is facing yet another extinction-threatening soil pathogen, *Armillaria* spp. Germplasm he collected and maintained at Clemson University is showing tolerance, and it is already being evaluated for its rootstock potential (www.nc140.org) and used in breeding efforts to combat this replant disease.

His research program quickly incorporated the newly emerging prospects made available from molecular plant genetics, an emerging science in the 1980s. Working closely with Dr Bert Abbott, his graduate students and postdoctoral colleagues were some of the first to find genes for nematode resistance in *Prunus* and the *evg* mutant that was important in identifying the MAD Box genes that control shoot growth and bud dormancy in peach. In addition, the first sequenced peach genome was from a double haploid tree that he had planted at the university research farm.

His extension emphasis is fueled by his passion for growers' success and is based on disseminating current information on orchard management systems for peaches and apples, communicating the relevance of his research findings to commercial growers, and establishing cultivar trials to promote alternative fruit crops for fruit grower diversification. His trials are extensive, often located on commercial properties to achieve the scale necessary for grower acceptance and for their adoption of the findings from that research.

Although teaching and advising have been a small part of his appointment, he has advised 17 M.S. and Ph.D. students to completion. Furthermore, more than 120 undergraduate students have been involved in the projects within his research program. Dr Reighard has also hosted 13 visiting postdoctoral scholars and scientists on sabbatical leave from the United States, China, Turkey, Spain, France, Ukraine, South Africa, and Brazil.

Dr Reighard has an extensive list of over 170 peer-reviewed research publications, and nearly 200 additional outputs in the form of conference proceedings and book chapters, including two chapters in the major text *The Peach: Botany, Production and Uses*, one in *Almonds: Botany, Production and Uses*, and one in a Fruit Breeding series. He has given more than 500 presentations, including 170 invited presentations.

Greg has been highly active within the International Society for Horticultural Science for many years. He has published over 90 papers in *Acta Horticulturae*, served as an editor or on the editorial board for six symposia, served on the scientific committee for seven symposia, and was the convenor for one other symposium.

Dr Reighard has served on many committees in regional, national, and international symposia. He serves as the Peach Rootstock Coordinator for the SAES-422 Multistate Project NC-140, "Improving Economic and Environmental Sustainability in Tree-Fruit Production through

Changes in Rootstock Use”; is an honorary member of the Romanian Faculty Academic Council; and has been a reviewer for more than 20 different scientific journals.

Dr Reighard has been recognized numerous times throughout his career with professional awards, including the Wilder Medal by the American Pomological Society for his work in peach tree genetics and culture (2018), his election as a Fellow of the American Society for Horticultural Science (2014), the International Fruit Tree Association Fruit Researcher Award (2012), the American Pomological Society Shepard Award for the best scientific paper published in the Society’s journal (in 2017, 2010, and 2004), the American Society for Horticultural Science – Southern Region Julian C. Miller Sr. Distinguished Research Award (2008), and the Godley-Snell Award for Excellence in Agricultural Research (2008).

In regard to his extension appointment, he has prepared and published numerous extension and outreach publications, including handbooks, trade journals, magazines, newsletters, and popular press articles. Other than this, he has also organized and hosted many field days and demonstration tours for fruit tree growers.

His industry-related achievements have been recognized with a number of awards, including the South Carolina Peach Council’s “Mr. Peach” Award (2017), the Experiment Station Section Excellence in Multistate Research Award (2015), the Clemson University CAFLS Superior Service Award (2014), the National Peach Council Career Achievement Award (2013), the National Peach Council Carroll R. Miller Award (2002), and the Clemson University Board of Trustees Award for Faculty Excellence (in 2001, 2005, 2007, 2008, and 2011).

Greg is married to Angie (1980), and they have two children: Chelsea Reighard, M.D. (Ophthalmology), and Shane Reighard, M.D. (Cardiology).

In summary, Dr Greg Reighard’s professional career is one of exemplary and sustained dedication to tree fruit improvement, which has resulted in high-quality scholarship for the discipline of horticulture, and relevant and impactful deliverables for the industry – domestically and abroad.

JUAN CARLOS MELGAR
Assistant Professor
Clemson University
Clemson, SC
United States

KSENIJA GASIC
Associate Professor
Clemson University
Clemson, SC
United States

IAN WARRINGTON
Emeritus Professor
Massey University
Palmerston North
New Zealand

Pollination-Induced Changes in the Morphology and Physiology of *Dendrobium* Orchid Flowers Prior to Fertilization: The Roles of Ethylene and Auxin

Wouter G. van Doorn[†]

Mann Laboratory, Department of Plant Sciences, University of California, Davis, CA, USA

Saichol Ketsa

Department of Horticulture, Kasetsart University, Chatuchak, Bangkok, Thailand and Academy of Science, The Royal Society of Thailand, Dusit, Bangkok, Thailand

ABSTRACT

Pollination in *Dendrobium*, as in several other orchids, induces rapid growth in the width of both the ovary and the column (the organ containing the pollinia and the stigma). The visible effects of that growth do not occur when non-pollinated flowers are exposed to ethylene or after application of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) to the stigma of non-pollinated flowers. However, growth of the ovary and column of pollinated flowers is inhibited by the ethylene antagonist 1-methylcyclopropene (1-MCP) and the ethylene synthesis inhibitor aminooxyacetic acid (AOA). The effects on growth, including column and ovary growth, were similar following the

[†]Deceased

Horticultural Reviews, Volume 48, First Edition. Edited by Ian Warrington.
© 2021 John Wiley & Sons, Inc. Published 2021 by John Wiley & Sons, Inc.

application of an auxin such as 1-naphthylacetic acid (NAA) to the stigma, while studies with ethylene inhibitors showed that NAA acted through ethylene. The known presence in the pollinia of ACC and an auxin-like compound apparently explains the initial growth of the column and ovary in response to pollination.

KEYWORDS: 1-MCP, ACC, auxin, antiauxin, ethylene, ethylene antagonist, ovary growth, column growth, pollen tube, pollinia

- I. INTRODUCTION
- II. ORCHID FLOWER STRUCTURE
- III. POST-POLLINATION EFFECTS IN ORCHIDS OTHER THAN *DENDROBIUM*
- IV. ROLE OF HORMONES IN ORCHIDS OTHER THAN *DENDROBIUM*
- V. POLLINATION IN *DENDROBIUM*
- VI. VISIBLE POST-POLLINATION EFFECTS IN *DENDROBIUM*
 - A. Color Changes
 - B. Growth Reactions
 - C. Abscission
- VII. ROLE OF HORMONES IN THE VISIBLE POST-POLLINATION PHENOMENA IN *DENDROBIUM*
 - A. Hormones and Their Precursors in *Dendrobium* Pollinia
 - B. Ethylene Production after Pollination
 - C. ACC, ACC Synthase, and ACC Oxidase
 - D. Treatment with Ethylene or ACC
 - E. Endogenous Auxin and Treatment with Auxin
 - F. Antagonists of Ethylene
 - G. Antagonists of Auxin
- VIII. CONCLUSIONS
- LITERATURE CITED

I. INTRODUCTION

Pollination can induce rapid changes in flower form and color, as well as early flower senescence. Most of these changes also occur, although later, in unpollinated flowers. These early effects of pollination have been reported in many plant families, but are quite common in the Orchidaceae, where they usually occur before fertilization. With many orchids, therefore, it is possible to distinguish between the effects of fertilization and those of pollination. Hildebrand (1863a,b,c) and Fitting (1909) noted that the post-pollination effects in orchids depended on the species.

In the first detailed study on *Dendrobium*, Hildebrand (1863a) observed that fertilization in *D. nobile* took place several months after pollination, while early post-pollination effects were visible within 2–3 weeks of pollination. The same has been found in commercial *Dendrobium*

cultivars, which are crosses of *Dendrobium* species (Luangsuwalai et al. 2008). The visible post-pollination phenomena in *Dendrobium* are, therefore, not due to fertilization but to pollination per se.

The purpose of this review is to present the data that are now available on post-pollination phenomena in *Dendrobium* orchids, more than 150 years after the publications of Hildebrand. After a short introduction to orchid flower morphology, the early post-pollination phenomena in some orchids are discussed to show the range of effects. Some examples of early work on hormones will also be reviewed in orchids other than *Dendrobium*. This is followed by an analysis of *Dendrobium* where three groups of early visible pollination effects can be distinguished: a) color changes, b) growth reactions, and c) senescence. The purpose of this review is to summarize the role of hormones, mainly ethylene and auxin, in the initial growth of the ovary and column of *Dendrobium* orchids after pollination.

II. ORCHID FLOWER STRUCTURE

The Asteraceae are likely the largest family of flowering plants, while the Orchidaceae appear to be second largest. Although new discoveries in the field are relatively rare, new orchid species currently are described at a rate of about 500 per year, mainly based on taxonomic work. New genera have been described recently at a rate of about 10–13 per year (Chase et al. 2015).

Orchids generally have a bilaterally symmetric flower made up of three sepals and three petals, forming two whorls of colored leaf-like appendages (Figure 1.1). These orchid flower appendages are also called tepals, but here we will use the terms “petal” and “sepal.” The median petal is normally bigger, more colored, and dotted and/or ornamented. This floral leaf is known as a lip or labellum and serves as a landing platform for insects. The ovary is inferior. The androecium (male parts; consisting of 1–3 fertile anthers) and gynoecium (female parts) are usually fused into a single structure called a column, whereby the male parts (pollen) are situated above the stigma and style (Singer et al. 2004). It has been suggested that orchids derive from species with six anthers, and that during evolution three, four, and five functional anthers were lost, producing the extant orchid subfamilies Apostasioideae, Cypripedioideae, and the monandrous orchids, respectively (Johnson and Edwards 2000).

In many species the pollen grains are packaged into large conglomerates (pollinia) that are removed as a single unit from the flower. The

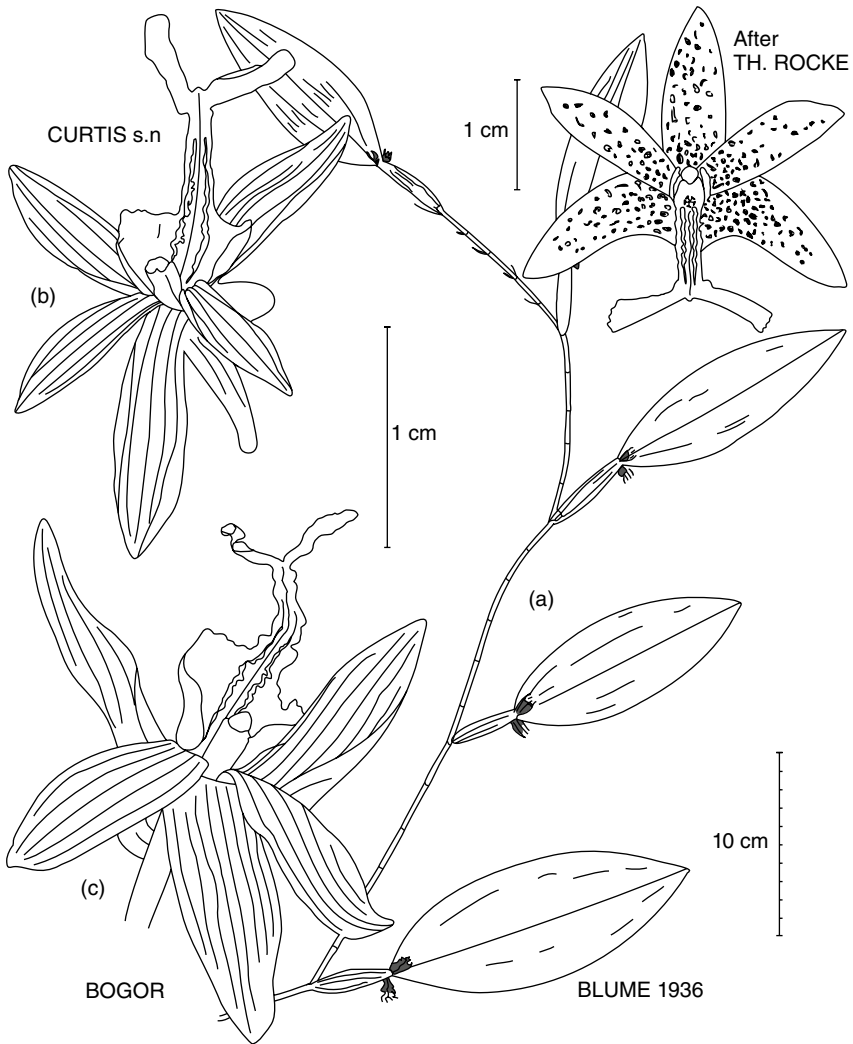


Figure 1.1 *Dendrobium appendiculatum* [syn. *Flickingeria appendiculata* (Blume)] flowers. (Source: © Seidenfaden (1980); reproduced with permission.)

pollinia, in most species four per flower, can have stalks as well as secretions that stick the pollinia to the pollinator's body. If pollinia have such accessory structures for attachment to the pollinator, they are called pollinaria. Pollinaria can consist of more than one pollinium (Pacini and Hesse 2002; Singer et al. 2004). In many orchid species

each pollinium often contains several thousands to tens of thousands of pollen grains. In one species a pollinium reportedly contained about four million pollen grains (Darwin 1877; Schill et al. 1992). In orchid flowers with pollinia/pollinaria the stigmatic surface is a cavity that fits one or a few pollinia/pollinaria.

III. POST-POLLINATION EFFECTS IN ORCHIDS OTHER THAN *DENDROBIUM*

Hildebrand (1863a,b,c) studied about 30 orchid species. The degree of ovary development, by the time of pollination, depended on the species: some (for example, *Listera ovata*, now called *Neottia ovata*, and *Neottia nidus-avis*) had ovules that showed relatively advanced development, although an embryo-sac was not yet present. After pollination, the ovary enlarged and the ovules started to grow and develop further, before the pollen tubes reached the ovary. In the absence of pollination, the ovary withered. The sepals and petals in most species soon senesced after pollination but did not show early abscission. Sepals and petals were usually found in a dry state at the top of ripe fruit. In some species these dry sepals/petals eventually fell off. In *Neottia ovata*, by contrast, little effect of pollination was found on sepals and petals. They remained attached to the dehiscent fruit while still fresh and succulent (Hildebrand 1863a).

Similar observations were reported by Fitting (1909). Pollination induced early flower senescence in species of the genera *Aerides*, *Bletia*, *Calanthe*, *Coelogyne*, *Dendrobium*, *Oncidium*, *Orchis*, *Phalaenopsis*, *Platanthera*, *Rhynchostylis*, *Stanhopea*, *Trichoglottis*, and *Vanda*. Fitting also showed this in *Rhenanthera* × *maingayi*, now *Arachnis* × *maingayi* (the updated name from Yam et al. 2009). Exceptions were the absence of early senescence in *Liparis latifolia* (now *Stichorkis latifolia*) and in *Cymbidium sanguinolentum* (now *C. chloranthum*) (updated names from Yam et al. 2009).

Phalaenopsis violacea petals and sepals are white, sometimes greenish white, with some violet. Within 2–3 days of pollination, the white parts became yellowish and the violet parts turned red. The flower closed almost fully and started to wilt. The petals and sepals became turgid again 2–3 days later and then started to become green. They subsequently stayed fresh for several months (Fitting 1909). In *Phalaenopsis lueddemanniana* the petals and sepals did not wilt after pollination, but within one week of pollination they became fleshy, turned green, and lost nonchlorophyllous pigments (red spots and stripes). Similar results were

obtained with *P. amboinensis*, *P. fasciata*, *P. hieroglyphica*, and *P. pallens*. Such regreening has also been reported in *P. mannii* and *P. mariae*, in the orchid *Menadenium labiosum*, and in *Miltonia* species (Tran et al. 1995).

In many species, Fitting (1909) observed pollination-induced swelling of the column (the organ containing the male and female parts) as well as of the subtending ovary. Additionally, pollination resulted in stigmatic closure in species from the genera *Coelogyne*, *Cymbidium*, *Stanhopea*, and *Phalaenopsis*.

Later work generally confirmed these early observations on post-pollination effects. Experiments included genera such as *Angraecum* and *Cattleya* (Strauss and Arditti 1982), *Calypso* (Proctor and Harder 1995), *Lemnoglossum* and *Odontoglossum* (Clifford and Owens 1988), *Cleistis* (Gregg 1991), *Mystacidium* (Luit and Johnson 2001), *Cochniella* (Abdala-Roberts et al. 2007), *Acampe* and *Bletilla* (Huda and Wilcock 2012), and *Epidendrum* (Vega and Marques 2014). Mathur and Mohan Ram (1978) reported an increase in anthocyanin in flowers of *Lantana camara* L. during thrips-pollinated senescence. In *Ophrys fusca*, analysis of the labellum transcriptome showed downregulation of transcripts involved in the synthesis of scents and pigments (associated with color fading of the lip), and upregulation of transcripts indicating senescence (Monteiro et al. 2012).

IV. ROLE OF HORMONES IN ORCHIDS OTHER THAN *DENDROBIUM*

Results of Burg and Dijkman (1967) suggested that at least ethylene and auxin had roles in the pollination-induced early senescence of *Vanda* orchids. This was confirmed by Arditti et al. (1970) in *Cymbidium*. Application of abscisic acid (ABA) to the stigma of *Cymbidium* increased the anthocyanin levels, which also takes place after pollination. However, ABA treatment did not induce the typical column swelling, loss of column curvature, or stigmatic closure (Arditti et al. 1970). Application of the auxin 1-naphthylacetic acid (NAA) to the stigma, by contrast, produced all the symptoms brought about by pollination, including increased anthocyanin production, early petal and sepal wilting, stigmatic closure, and the swelling and loss of curvature of the column. Application of gibberellic acid (GA₃) also induced these pollination effects, although only at high concentrations. Kinetin, a cytokinin, had almost no effect (Arditti et al. 1971). Ethylene treatment induced an increase in anthocyanin levels and petal and sepal wilting, but did not result in straightening of the column or in stigmatic closure (Arditti et al. 1973).

Application of labeled IAA (indoleacetic acid) to the stigmas of *Angraecum* and *Cattleya* orchids resulted in virtual immobilization at the point of application. Some of the auxin was conjugated into IAA-aspartate, but this also did not move. As the pollination signal spreads quickly to all floral segments, it was suggested that additional substances, either from the pollinia or produced by pollinated flowers, participated in the production of the early pollination phenomena (Strauss and Arditti 1982).

Working with *Cymbidium*, Woltering (1990) and Woltering et al. (1995) showed that 1-aminocyclopropane-1-carboxylic acid (ACC) is not mobile. Therefore, ACC is not the signal responsible for inter-organ communication during senescence. The data suggested that pollination-induced ethylene, which is the cause of the increase in ACC concentration in various flower parts, rather than ACC is transported from the column to the sepals where it induces early senescence.

O'Neill et al. (1993) found that substances from pollinia do not need to be transported out of the stigma, as pollination in *Phalaenopsis* rapidly induced transcription of genes required for ethylene production, first in the stigma and then in other parts of the flowers. The data suggested that an autocatalytic rise in ethylene production was induced first in the stigma, then in other parts of the flower. Porat et al. (1998) found that an aqueous extract of pollinia contained two high-performance liquid chromatography (HPLC) peaks, one of ACC, the direct precursor of ethylene, and the other having auxin activity while not being free auxin. This is consistent with a role of both ethylene and auxin-type compounds, but does not rule out the possibility that there are other active substances in the pollinia that help mediate the various post-pollination effects. Porat et al. (1995) concluded that an increase in ethylene sensitivity following pollination was the initial event that triggered the increase in ethylene production in *Phalaenopsis*. This increase in sensitivity has not yet been explained.

Novak et al. (2014) pointed out that the required role of auxin in the maturation of the ovaries, and of the ovules, seems unique to orchids. They concluded that the data from *Phalaenopsis* species (Zhang and O'Neill 1993; Tsai et al. 2008) indicate that an auxin-like compound from pollinia is involved in a) the initiation of elongation of ovary epidermal cells, thereby forming trichomes; b) the increase in ovary diameter; and c) depending on the species, the initiation of ovule development or the maturation of partially developed ovules. They also concluded that treatment with ethylene did not induce these effects. Nonetheless, auxin will stimulate ethylene production, and a combination of auxin and ethylene is required for optimal ovary/ovule

development. Novak et al. (2014) also concluded that auxin was a cause of stigmatic closure in *Phalaenopsis*. Closure was also partially due to auxin-induced ethylene production, but treatment with ethylene alone had no effect. They additionally suggested that flower senescence was induced by an auxin-like compound in the pollinia, whereby auxin at least in part would act by increasing ethylene production. It is indeed possible that an auxin-like compound in pollinia has this effect, but a role of ACC in pollinia, which can also lead to a rise in ethylene production through increased gene expression, should not be ignored. Furthermore, in *Dendrobium*, ethylene is adequate to explain the effect of pollination on epinasty, downward movement of the petals and sepals, venation, and senescence (see Sections VI and VII).

The idea that the effects of auxin and ethylene during pollination-induced early senescence in *Phalaenopsis* are coordinated also follows from gene expression data. Auxin upregulated the ethylene biosynthetic genes in *Phalaenopsis*, *Phal-ACS2* and *Phal-ACS3*, and auxin-induced ethylene production was secondarily enhanced through ethylene-stimulated *Phal-ACS1* expression (Bui and O'Neill 1998). Independent of ethylene, auxin lowered transcript levels of *Phalaenopsis* MADS6, which counteracts petal and sepal senescence and inhibits the completion of ovary and ovule maturation after pollination. Nonetheless, this gene has both auxin and ethylene response elements in the promoter region, which suggests that ethylene can also affect its expression (Tsai et al. 2008).

V. POLLINATION IN *DENDROBIUM*

The genus *Dendrobium* has been classified to the tribe Dendrobieae (together with *Bulbophyllum*), in the large subfamily Epidendroideae of the Orchidaceae (Pridgeon et al. 2014). The genus contains about 1200 species, found in South, East, and Southeast Asia, including India, China, Japan, and Australia. Plants are usually epiphytic (as the genus name indicates), sometimes growing on rocks, and rarely are terrestrial. Species are found in climates as diverse as alpine and desert-like, but many are from forests. Flower morphology differs widely. Examples of rather outstanding flower shapes are shown in Figure 1.2a–c (for the more common flower shape, see Figures 1.5 and 1.6).

The genus seems to contain the shortest-lived flower – flowers of *D. appendiculatum* open for five minutes only (van der Cingel 2001). The genus apparently also contains a species that produces one of the longest-lasting flowers. *D. cuthbertsonii* (Figure 1.3) plants grow on rocks and in trees at high altitudes (700 to 3500 m) and bloom in the

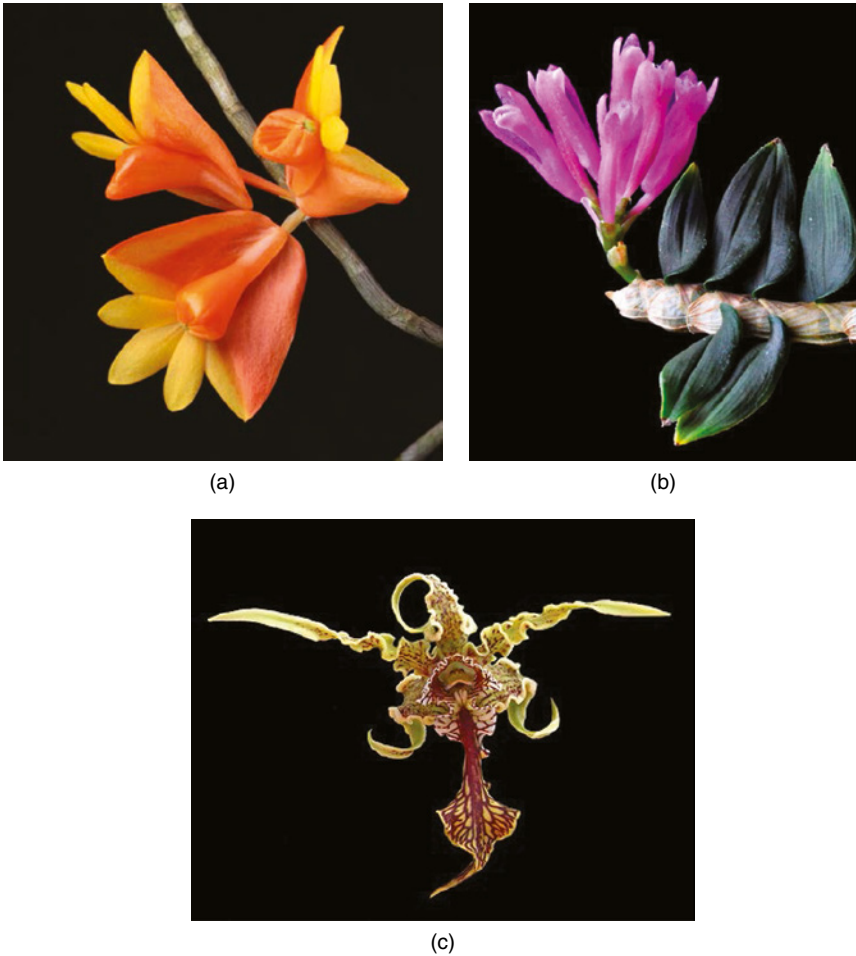


Figure 1.2 Atypical flower morphology in the genus *Dendrobium*. *Dendrobium chrysopterum* (a), *D. limpidum* (b), and *D. spectabile* (c). *D. chrysopterum* and *D. limpidum* from Papua New Guinea described by Schuiteman and de Vogel (2001 and 2003, respectively). For the common flower form of *Dendrobium*, see Figures 1.5 and 1.6. (Sources: (a) Photo credit: *Dendrobium chrysopterum* Schuit. & de Vogel. © Andre Schuiteman. (b) Photo credit: WWF/Bob Bowser/B2 Photography, Creative Commons. (c) Photo credit: © Don Dennis with permission.)

cold season. When grown in a mild climate (about 25°C), flowers are said to last up to nine months (Schordje 2013).

Many *Dendrobium* species have fragrant but nectarless flowers, which seem to be predominantly pollinated by bees, but pollination



Figure 1.3 *Dendrobium cuthbertsonii*, showing its variability in flower color and shape. (Source: Photo credit: © Simon Pugh-Jones. <https://wsbeorchids.org/2017/365-days-of-orchids-day-221-dendrobium-cuthbertsonii/>.)

by flies, wasps, bumblebees, and birds has also been recorded. Bird-pollinated flowers are usually brightly colored and are found generally only at higher altitudes. *D. antennatum* is an exceptional case as it seems to be pollinated by the struggle between a spider that resides in the flower and a visiting insect (van der Cingel 2001).

Most *Dendrobium* species seem to bear pollinia (almost always four) without attachments and with no viscous material. Two pollinia are often connected, which is usually called a pollinarium (Telepova-Texier 2005). Different species have been shown to have different shapes of pollinaria ranging from fusiform to slightly curved or comma shaped, with the inside surface slightly flattened, having two almost same-sized parts of each pair clinging together either fully along the entire length or only partially (Figure 1.4) (Chaudhary et al. 2012). Each pollinium of *Dendrobium* ‘Kenny’ contained about 38,000 pollen grains, while pollinia of ‘Pompadour’ contained about 49,000 (Luangsuwalai et al. 2008).

Upon pollination in *D. speciosum*, the pollinia become submerged into the viscous liquid of the stigmatic cup. This liquid contains detached stigmatic cells and mucilage. The mucilage is considered essential for the hydration and germination of the pollen. The stigmatic fluid and stigmatic cells apparently have a considerable osmotic potential, but water still flows into the dehydrated pollen grains (Slater 1991).

The pollen grains are hydrated progressively from the outside of the pollinium to the inside. After four days the pollen tetrads in the

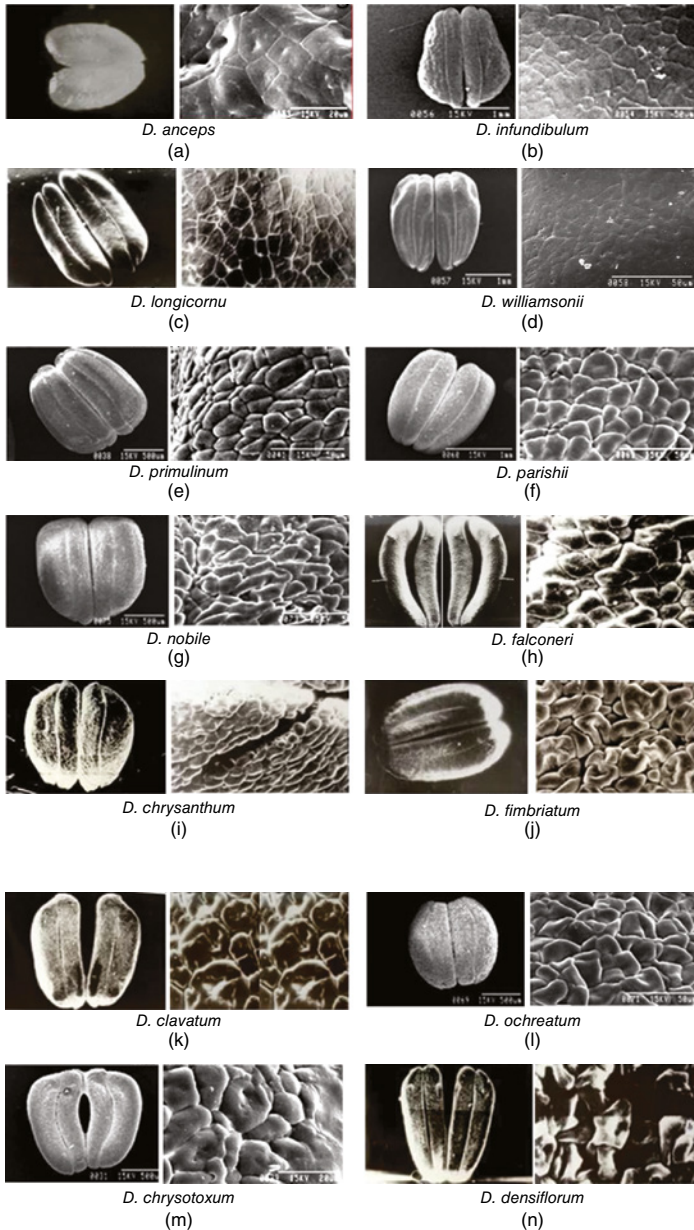


Figure 1.4 Morphology of pollinia (left) and magnified surface of pollen showing distinct types of exine morphology (right) in (a) *D. anceps*, (b) *D. infundibulum*, (c) *D. longicornu*, (d) *D. williamsonii*, (e) *D. primulinum*, (f) *D. parishii*, (g) *D. nobile*, (h) *D. falconeri*, (i) *D. chrysanthum*, (j) *D. fimbriatum*, (k) *D. ochreatum*, (l) *D. acreatum*, (m) *D. chrysotoxum*, and (n) *D. densiflorum*. (Source: Modified from Chaudhary et al. 2012).

center of the pollinium were clumped together, with individual grains non-hydrated, while the tetrads on the periphery had broken apart, the grains had hydrated, and pollen tubes were initiated. This continued until the grains in the center of the pollinium had hydrated, germinated, and produced pollen tubes, by day 7 after pollination. An area of the pollinium that was not in contact with the mucilage did not show pollen hydration and germination (Slater 1991).

Non-hydrated pollen grains had a dense cytoplasm, and were compacted together. The grains swelled as they hydrated and the cytoplasm became vacuolate. After germination the cytoplasm transferred to the growing pollen tube tip. The pollen tubes grew through the maze of mucilage, detached stigmatic cells, and pollen tubes, towards the wall of the stigmatic cup. Upon contacting this wall, they veered towards the stylar canal and then proceeded towards the ovary. The detached cells of the stigma, insofar as located near the entrance to the stylar canal, had lost starch from the amyloplasts by the time the pollen tubes had passed. It was suggested that this might nourish the growing pollen tubes, as the detached stigma cells located in the remainder of the stigmatic fluid did not lose starch (Slater 1991).

Slater and Calder (1988, 1990) showed that the stigma of *D. speciosum* provided the material that adhered the pollinia to the pollinator. Many orchids from other genera have a modified median stigmatic lobe (called a rostellum) which helps adherence of the pollinia to the pollinator. Such a structure is not present in *D. speciosa* (and in most, if not all, other *Dendrobium* species). Instead the pollinia are naked, compact, and not sticky. Pollinators get a smear of stigmatic fluid when they pass the stigma, either depositing a pollinium or not. When they advance further, pollinia will adhere to the stigmatic fluid on their body. The viscous material in the stigma of *D. speciosum* thus also functions as "glue" for the transfer of pollinia. The stigma of *D. speciosum* is rather unique as it has glandular cells that are detached and separated from each other by their highly viscous secretion (Slater 1991).

In *D. nobile*, Hildebrand (1863a) found that the pollen tubes formed a cord when passing through a channel of the column. On reaching the ovary cavity this cord divided into three parts, with each of these parts subsequently dividing into two. By day 11 of pollination, the ovary had become more developed but no ovules were yet observed. Two months after pollination ovules had formed, showing different degrees of development. At that time the cords of the pollen tubes had apparently not changed. Three months after pollination all ovules had fully developed. Their embryo-sacs were distinct, but no pollen tube had yet reached them. Four months after pollination the first two or three cells of the embryo had